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Characterization, diversification, and evolution of the Silurian-Devonian plant group Zosterophyllopsida

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Colophon

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Caractérisation, diversification et évolution du groupe de plantes Siluro-Devonien Zosterophyllopsida

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To my mom who nurtured my passion from an early age, and trusted me when I wouldn't myself.

To my partner, who grew up alongside me and helped, accompanied and supported me without ever doubting my abilities.

Whenever a theory appears to you as the only possible one, take this as a sign that you have neither understood the theory nor the problem which it was intended to solve.

Karl Popper

Even the most original and meticulous scientists are not immune to the influence of culture, and Darwin's androcentric reading of the sexes was no doubt shaped by the prevailing chauvinism of the era.

Lucy Cooke

Foreword

There is no better way to start a scientific dissertation than with a friendly reminder of how biased the human mind is. The two abovementioned quotes both highlight this issue, the first one from an epistemological point of view, and the second, with a satirical example from the history of science.

Karl Popper has always had a special place in my relationship with science. This philosopher of science reconnects me with my literary background and my love of philosophy. Discovering his texts during my undergraduate studies was liberating, as they brought me this familiar philosophical approach to things, applied to a subject of study that had since invaded my daily life, namely the sciences of evolution. Popper's famous thesis is about the "empirical falsification" of sciences, as an approach to test the hypotheses. It is by exposing the hypotheses and observations under a bunch of experiments that we can truly apprehend their strength, and expand our understanding. This view of "thinking outside the box" is now commonly accepted in our daily practice, but understanding why we are doing sciences this way today is a first step into an ethical approach of science. This is for this reason that I chose this quote, which is an invitation to question our practice by focusing on our own understanding of phenomenons. Not only the theory itself shall be questioned, but we should not put ourselves apart from the equation, as our understanding has impacts on science.

Lucy Cooke's provocative quote is just another side of the same coin. The vision here is less academic and much more direct, but the message is the same as its philosophical counterpart: we must question the way in which our knowledge has been acquired and reaches us. This knowledge comes from people with their own cultural backgrounds and worldviews, which can greatly influence what is assigned as universal by default. In targeting Darwin like so, Cooke does not hesitate to undermine a fundamental foundation of the evolutionary sciences, a specialization from which I myself come. However, it is not a matter of destroying, but of questioning, in order to push further our knowledge, that the basis of which can be biased. Darwin, despite his unquestionable impact on science with his theory of evolution by natural selection has biases that impacted the way the next generations of scientists studied this phenomenon. This quote carries then the same information as the previous one. It is always important to question what we learn, no matter where does the information come from, the emeritus professors or students.

And it is precisely this problem of knowledge acquisition that I particularly encountered during the course of this PhD. My background is about paleontology and evolutionary sciences. I consider myself as an outsider in the field of paleobotany, that I truly discovered with this PhD. When I started this project, the goal was clear: I had to update the phylogeny of this group of plants (which I did not even know existed until then). A simple task that many before me have tried to complete, and struggled with. In fact, until now the previous analyses were all based on samplings of the studied group, due to methodological and computational limitations. I did not know it at the time, but behind this apparent simplicity lay a much more complex problem,

which is developed throughout this essay. This thesis is therefore the product of three years of reflection on the evolution of zosterophylls, but also on broader issues such as the limits of our knowledge in relation to sampling, or the question of methodological approaches based on limited data sets.

In our society, the study of ancient times can be seen as a matter of simple curiosity. However, the evolutionary history of living organisms provides us with the keys to understand the world around us, as well as ourselves as human beings. It addresses my childhood curiosity to understand the origins of things, and I have come away from these three years of work having had the chance to explore such a crucial chapter in the history of life. Because behind this specialist question of zosterophyll evolution lays the context of the terrestrialization of land by one of the most successful and fascinating organism: the plants. They were among the first organisms to invade the barren lands and this step drastically changed the Earth dynamics, and shaped the evolution of other living beings. One could easily imagine a world before and after this event, and notice the impact of this evolutionary step that led to you, today, sitting in front of this essay.

These two quotations are a reminder: it is by doubting and questioning the established order that we can rough out the features of our knowledge. Question the founders of our fields, question your work and question this PhD. This thesis is part of a larger project to understand our past world, and I hope that this modest brick can also help to push further our understanding.

I wish you a pleasant reading.

If you are curious about the quotes, here are the work where they come from:

Popper, K. R. (1979). *Objective knowledge: An evolutionary approach* (Vol. 49). Oxford: Clarendon press.

Cooke, L. (2022). *Bitch: a revolutionary guide to sex, evolution and the female animal*. Random House.

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Finally, I would like to take some time to thank the members of my jury, starting with Brigitte Meyer-Berthaud, senior researcher at the CNRS and José B. Diez, professor at Vigo University, for agreeing to become the referees. I hope you will find this research interesting. Additionally, I would like to thank the members of my jury for taking the time to follow this project, professor Catherine Crônier (Lille), Dr. Cyrille Prestianni (Liège), Dr. Anne-Laure Decombeix (Montpellier) and associate professor Celine Poux (Lille).

Last but not least, I will take some time to express my gratitude to my family and friends, who have supported me in the pursuit of my dreams. My parents have always been receptive to my aspirations and tried their best to provide me with a good education, cheering and following even my smallest successes. Thank you to my grand-parents as well, for always supporting my interests from an early age as well as for your financial help, which enabled me to study in good conditions. I would also thank my sister, Marylou Claisse for being unconditionally supportive, this PhD experience has been sweeter thanks to you. There is no words to express the amount of gratitude I have for my life-long partner, Nathan Romaszko. You have always been there to support me no matter what challenges happened in our life. From high school and my doubts in pursuing a scientific track, to our best years in Montpellier, when you helped me catching up my weaknesses in science, and now your unfailing support in this PhD. Thank you for your help with the technical issues I met (especially on R), the time you took to discuss with me about my project, and develop the ideas, and more than ever, your emotional support during the darkest moments of this PhD. I would like to thank Drs. Mireille and Christophe Romaszko for your help and financial support throughout my studies. Thank you to all my friends that provided unconditional support and love during these three years, Josselin Griffet, Hugo Fraignaud, Maxence Ducros, Marine Matringhem, Jérémie Morel, Diane Dabir and many others that I forgot to mention here (but not in my heart).

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To conclude, I would like to thank you, who is reading these lines. Thank you for your interest in this project.

Keywords: evolution, Devonian, dispersion, diversity, phylogeny, zosterophylls

Mots clés : évolution, Dévonien, diversité, dispersion, zosterophylles

Characterization, diversification, and evolution of the Silurian-Devonian plant group Zosterophyllopsida

Abstract

The Silurian-Devonian group of plants Zosterophyllopsida is the scope of the present essay. Because of their key position as the dominant group of plants at the onset of land plant diversification, the study and understanding of their evolutionary history is crucial. Moreover, numerous recent discoveries enriched our knowledge about this group, and Zosterophyllopsida appears today more complex than ever. With this complexity and diversity rises uncertainty, and previous statements about Zosterophyllopsida need to be reviewed under the light of these new discoveries. By exploring different aspects of Zosterophyllopsida's evolution (systematic, temporal, geographic), this PhD is the first review of the group at a global scale. Results support previous statements about their relationships and diversity, and showcase the impact of regionalism on the group's evolution. Some, but not all Zosterophyllopsida are closely related to the Lycopsida, and both are regrouped together into a clade named Lycophytina. The studied group is thus paraphyletic, and refers to the stem-group Lycophytina. This stem group is particularly abundant during the Pragian, went through a first phase of extinction during the Emsian, and some zosterophylls members survived until the end of the Devonian. Lastly, it has been showed that a geographical distribution structures the tree. While the origin of the group seems to be from Gondwana, a Laurussian divergent line bears derived and unique characteristics like emergences or circination.

Keywords: evolution, Devonian, dispersion, diversity, phylogeny, zosterophylls

Caractérisation, diversification et évolution du groupe de plantes Siluro-Devonien Zosterophyllopsida

Résumé

Le groupe de plantes Siluro-Devonien Zosterophyllopsida est le modèle d'étude de cette thèse. Il est en effet considéré comme le groupe dominant durant cette période, marquée par les premières diversifications des plantes terrestres. Ainsi, comprendre l'histoire évolutive d'un tel groupe est crucial pour comprendre les dynamiques mises en place durant cette période. De plus, les connaissances ont été enrichies par de nombreuses découvertes récentes, et Zosterophyllopsida revèle une complexité jusqu'alors insoupçonnée. Cette augmentation de la complexité et de la diversité va de pair avec une incertitude croissante, et les précédentes observations faites sur le groupe doivent être révisées et consolidées. Cette thèse se présente donc comme une étude globale du groupe, abordant divers aspects de leur évolution (systématique, temporel, géographique). Les résultats sont concordants avec des travaux précédents concernant leur phylogénie et leur diversité, mais mettent également en avant l'impact de leur distribution spatiale sur leur évolution. Certains Zosterophyllopsida sont ainsi proche des Lycopsida, mais tous sont regroupés ensemble au sein du clade Lycophytina. Ainsi, le groupe d'étude est paraphylétique, et référé comme groupe souche Lycophytina. C'est un groupe particulièrement abondant durant le Pragien, puis après une première chute de la diversité à l'Emsien, n'est représenté que par quelques membres jusqu'à la fin du Dévonien. Enfin, les résultats montrent une distribution géographique au sein de l'arbre. En effet, l'origine du groupe semble provenir du Gondwana, puis une lignée Laurussienne diverge rapidement, portant des caractéristiques dérivées uniques tel que les émergences et la circination.

Mots clés : évolution, Dévonien, diversité, dispersion, zosterophylles

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Résumé étendu

La présente thèse intitulée "Caractérisation, diversification et évolution du groupe de plantes Siluro-Dévonien Zosterophyllopsida" est une révision et une mise à jour des connaissances sur ces plantes fossiles. En effet, les zosterophylles sont un groupe de plantes terrestres caractérisées par une distribution temporelle restreinte entre la fin du Silurien jusqu'au Dévonien supérieur, et sont reconnaissables grâce à leurs sporanges arrangés latéralement sur leurs axes, qui s'ouvrent grâce à une ligne de déhiscence distale. Depuis leur définition en 1968, de nombreux fossiles aux morphologies variées ont rejoint cette cohorte, avec à ce jour une richesse atteignant une quarantaine de genres décrits. Entre temps, différentes études ont exploré d'un point de vue phylogénétique et de la diversité l'évolution de ce groupe. Ainsi, les zosterophylles sont considérés parmi les plantes vasculaires, comme l'un des groupes les plus abondants de son époque, avec un maximum de richesse atteint au début du Dévonien. Les fossiles de ses représentants ont été retrouvés à divers endroits du globe, soulignant sa dimension cosmopolite. Enfin, les zosterophylles se placent dans un contexte global de terrestrialisation des plantes. Leur étude et leur compréhension en font donc des organismes de choix afin de lever le voile sur l'installation de la dynamique de végétalisation sur terre. Cependant, les études de ce groupe restent parcellaires et ne sont pas encore consensuelles sur sa caractérisation. En l'absence d'un cadre systématique défini, et d'un travail inclusif, les études se basant sur ce groupe ne peuvent apporter une vision d'ensemble de leur évolution. Afin de pallier ce problème, cette thèse propose une révision de leur évolution, en prenant en compte un échantillonnage exhaustif et à jour du groupe. Ainsi, trois chapitres aborderont cette exploration, sous des aspects complémentaires de systématique, de distribution temporelle et géographique, afin d'avoir une compréhension générale de ces plantes pionnières.

D'un point de vue phylogénétique, il n'existe pas encore de consensus quant au statut des zosterophylles, ainsi que de leur lien de parenté entre eux, et avec les autres groupes de plantes. En effet, le groupe a été initialement rapproché des lycopsides de par la forme de leurs sporanges ainsi que leur xylème à maturation exarche. Cepedant, l'anatomie des lycopsides présente un degrés de complexité non atteint par les zosterophylles, et si les zosterophylles sont caractérisés par des axes nus, les lycopsides quant à eux possèdent des sporophylles et autres microphylles végétatives. Malgré tout, ces observations morphologiques ont été appuyées par les premières phylogénies, montrant les zosterophylles comme un groupe paraphylétique et partageant un ancêtre commun avec les lycopsides. Plus tard, une autre phylogénie a apporté des résultats contrastés, montrant cette fois Zosterophyllopsida, un clade à part des autres groupes de plantes terrestres. Jusqu'à présent, toutes les études de ce type se sont concentrées sur un échantillonnage réduit de zosterophylles, pour des raisons de limitation méthodologiques. De plus, avec les découvertes constantes de nouveaux spécimens, la richesse morphologique du groupe s'aggrandit, questionnant leurs relations intrinsèques et leur histoire évolutive. Le but de ce chapitre est donc de proposer une phylogénie prenant en compte le maximum de diversité

connu à ce jour afin de résoudre ces incertitudes phylogénétiques. Zosterophyllopsida est-il bel et bien un groupe monophylétique, et quelles sont ses relations de parenté avec les plantes contemporaines ?

Pour répondre à ces questions, une nouvelle matrice a été proposée. Il s'agit de la plus grande matrice phylogénétique faite à ce jour sur ce groupe, incluant notamment 38 genres de zosterophylles et 42 caractères aussi bien morphologiques qu'anatomiques. Cette matrice a été analysée par approche de maximum de parcimonie, puis par inférence bayésienne, et enfin sous différent types d'échantillonnage, afin de tester la congruence des arbres.

Les résultats obtenus sont en accord avec les premières observations et analyses faites sur ce groupe. En effet, tout les taxons définis comme zosterophylle sont issus d'un même noeud, qu'ils partagent également avec les lycopsides. Cette configuration ayant été précédemment observée dans une étude pionnière, le terme "Lycophytina" Kenrick et Crane 1997, a donc été repris pour définir ce noeud. Ainsi, selon ces résultats, Zosterophyllopsida apparaît comme paraphylétique, répartis au sein des Lycophytina. Tout les zosterophylles pris en compte dans ce travail peuvent être considérés comme le groupe souche Lycophytina, tandis que les lycopsides sont considérés comme le groupe couronne. De plus, malgré le nombre important de taxons sélectionnés et d'information manquante encodée, les arbres obtenus sont suffisamment résolus pour pouvoir observer des tendances. Les lycopsides par exemple apparaissent en position dérivée, proche d'un groupe de zosterophylles caractérisés par des émergences et de la circination. Cette famille appelé Sawdoniaceae, avait précédemment été définie sur la base de ces caractéristiques morphologiques, qui sont une fois de plus retrouvées. Les implications évolutives de ces résultats sont par la suite discutées et replacées dans leur contexte scientifique.

Le second chapitre de cette thèse se concentre sur leur évolution spatiale avec l'aide de méthodes de phylogéographie. En effet, tout au long de la période du Dévonien, des restes de zosterophylles ont été retrouvés à différents endroits du globe, comme en Europe, Amérique du Nord ou en Chine. Or d'un point de vue de la tectonique des plaques, le Dévonien est caractérisé par un morcellement des continents. Comment les zosterophylles ont-ils réussi à outrepasser de telles barrières géographiques pour venir coloniser une importante surface du globe ?

Pour répondre à cette question des analyses paléogéographiques se concentrant sur les zosterophylles ont été produites. A l'aide d'analyses multivariées, des paléoprovinces floristiques ont été définies et couplées avec des phylogénies calibrées dans le temps. Grâce à des méthodes de reconstruction ancestrale de caractères appliquées à des modèles de dispersion écologiques, il est possible de reconstruire des scénarios de dispersion du groupe. Cela permet dans un premier temps de remarquer si d'éventuels schémas géographiques existent au sein de la topologie. Ce schéma a ensuite été mis en parallèle avec les informations morphologiques du groupe.

Les résultats montrent une phylogénie divisée en deux grandes provinces : la Laurussie (Europe, Amérique du Nord) d'un côté et le Gondwana (Chine) de l'autre. On constate que les taxons Gondwaniens sont plutôt localisés à la base de l'arbre tandis que les taxons Laurussiens sont globalement plus proches des extrémités. Enfin, plusieurs caractères comme la forme et la distribution des sporanges, ou bien la présence d'émergences et de circination suivent une distribution similaire. Ainsi, les taxons Laurussiens auront plus tendance à posséder des sporanges réniformes, distribués tout le long de la plante. Ils auront de plus, plus facilement des emergences et des enroulements circinés. Ce lien entre géographie et diversification morphologique est ensuite discuté dans un contexte historique de définition du groupe.

Le troisième chapitre de thèse aborde l'évolution temporelle des zosterophylles par le biais d'analyses de diversité. En effet, les zosterophylles s'inscrivent dans un contexte "d'explosion" de la diversité des plantes sur les continents, et marquent la mise en place de nouvelles étapes dans

la formation des écosystèmes terrestres et de la dynamique de végétalisation. Cet évènement est caractérisé par le remplaçement progressif de la flore dite Eotracheophytique (dominée par les rhyniophytes), par la flore Eophytique (Cleal & Cascales–Miñana, 2021). Cette dernière est représentée au début du Dévonien par les zosterophylles et leur forte diversification. Ainsi, un contraste morphologique fort est remarqué entre la flore précédente, caractérisée par des plantes à la dichotomie simple et aux sporanges terminaux, et la nouvelle, reconnaissable par ses divisions anisotomes, ses nombreux sporanges à organisation latérale sur les axes, s'ouvrant distalement en deux valves.

Par le biais d'études de diversité, l'objectif de ce chapitre est donc de mettre à jour les informations concernant leur rythme de diversification ainsi que leur impact sur l'évolution de la végétation Eophytique. Pour cela, un jeu de données d'occurrence a été compilé et analysé aussi bien à l'échelle des genres que des espèces pour pouvoir retracer des motifs de diversité. Ces analyses, basées sur la paléobiologie analytique, prennent en compte des approches telles que des processus de réechantillonnage, de redivision temporelle, ou encore des estimations classiques de comptage de taxons au cours du temps. En plus de ce comptage de la diversité basé sur une base de données d'occurrence, un travail similaire a été effectué sur la phylogénie calibrée dans le temps.

Les résultats montrent une similitude avec les études précédentes, avec un pic de diversité atteint au Pragien, encadré par une forte diversification Siluro-Dévonienne et une chute de diversité Emsienne. En revanche, ce travail a aussi mis en exergue la subsistance de quelques rares taxons zosterophylles entre le milieu et la fin du Dévonien. Les résultats basés sur la phylogénie sont en général similaires aux précédents, renforçant la confiance dans le signal estimé. Ces courbes peuvent être mises en parallèle avec celles du climat, dessinant un lien entre des températures élevées et la diversification des zosterophylles. La morphologie semble également jouer un rôle important dans un contexte de compétition entre les différents groupes. Ainsi, les zosterophylles persistants à la fin du Dévonien semblent surtout caractérisés par des sporanges regroupés en strobiles. Les zosterophylles ayant des sporanges distribués le long des axes semblent suivre une extinction synchrone avec la diversification des lycopsides. Ainsi, en suivant ces distributions, il semblerait que les zosterophylles aient été progressivement supplantés par les lycopsides. Ce remplacement pourrait être expliqué par la présence des microphylles chez les lycopsides, pouvant protéger plus efficacement les sporanges.

Pour conclure, en s'intéressant à l'un des groupes les plus abondants présent au Dévonien Inférieur, ce travail a permis non seulement de renforcer et mettre à jour nos connaissances sur ces plantes, mais également de mieux comprendre les dynamiques de végétalisation durant cette période cruciale de diversification des plantes terrestres. La phylogénie, en particulier, répond à un besoin grandissant de contexte évolutif et systématique du groupe. En effet, de part les informations contradictoires entre les études précédentes, et l'augmentation importante du nombre de taxons décrits, il était nécessaire de redéfinir les zosterophylles, et ainsi, créer un cadre stable pour les études ultérieures. Les zosterophylles sont donc des taxons regroupés au sein du clade "Lycophytina". Il font référence au groupe-souche de ce clade, retrouvé principalement entre la fin du Silurien et au début du Dévonien. L'origine et le succès évolutif du groupe peuvent être expliqué par leur augmentation importante du nombre de sporanges portés par individu, grâce à un phénomène de latéralisation des organes. De par cette stratégie, ils surpassent ainsi le groupe précédemment établi durant le Silurien. Leur intense diversification fait miroir à l'augmentation croissante de la température annuelle, et peut également être rapprochée de ce succès reproducteur, leur permettant de coloniser une plus grande surface du globe. De leur extinction à la fin du Dévonien ne subsistera que le groupe couronne, les lycopsides, moins inféodés aux environnements chauds et développant de nouvelles stratégies évolutives comme

les microphylles ou encore la forme arborescente. Les zosterophylles marquent ainsi le registre fossile Dévonien par leur étonnante richesse morphologique, et leur importante distribution géographique. L'omniprésence de ce groupe dans les registres terrestres sont signe de leur abondance durant une période temporelle encore peu comprise, renforçant l'intérêt de l'étude de ces plantes pour comprendre la mise en place des dynamiques de végétalisation.

Contents

Foreword xi

Acknowledgments xiii

Abstract xvii

Résumé étendu xix

Contents xxiii

List of Figures xxv

List of Tables xxvii

1 Introduction 1
- 1.1 The terrestrialization phenomenon . . . 1
- 1.2 The evolutionary context of Embryophyta . . . 3
- 1.3 The importance of the Silurian-Devonian periods . . . 8
- 1.4 The case study of zosterophylls . . . 12
- 1.5 Context and aims of this thesis . . . 21

2 Phylogeny 25
- 2.1 Introduction . . . 25
- 2.2 Material and methods . . . 28
- 2.3 Results . . . 34
- 2.4 Discussion . . . 46
- 2.5 Conclusion . . . 66

3 Phylogeography 69
- 3.1 Introduction . . . 70
- 3.2 Material and methods . . . 73
- 3.3 Results . . . 82
- 3.4 Discussion . . . 96
- 3.5 Conclusion . . . 102

4 Diversity 103
- 4.1 Introduction . . . 103
- 4.2 Material and methods . . . 107
- 4.3 Results . . . 110

4.4 Discussion . . . 116
4.5 Conclusion . . . 125

5 Bias and limits on the methods used **127**
5.1 Study model . . . 127
5.2 Phylogeny . . . 130
5.3 Phylogeography and sampling bias . . . 137
5.4 Diversity analyses . . . 139
5.5 Conclusion . . . 140

6 Conclusion **141**
6.1 Study limits . . . 144
6.2 Perspectives . . . 146
6.3 Main messages . . . 149

A Supplementary information from introduction **151**

B Phylogeny **155**
B.1 Supplementary Methods . . . 155
B.2 Methods S3. . . . 168
B.3 Supplementary tables and figures . . . 171

C Phylogeography **175**
C.1 Tables and datasets . . . 175
C.2 R scripts . . . 177
C.3 Tables and figures . . . 204

D Diversity **213**
D.1 Dataset . . . 213
D.2 Figures . . . 240
D.3 R script . . . 240

E Anatomy **245**
E.1 Introduction . . . 245
E.2 Material and methods . . . 246
E.3 Results . . . 249
E.4 Discussion . . . 249
E.5 Conclusion . . . 253

F Anatomy **255**
F.1 Supplementary lists . . . 255
F.2 Supplementary table . . . 256
F.3 Scripts . . . 256

Bibliography **261**

List of Figures

1.1 Tree summarizing the relationships between land plants during the Paleozoic. . 7
1.2 Geological time scale of the studied period. Modified from the International Chronostratigraphic Chart (v.2023) . . . 9
1.3 Geographical map reconstructing the continent dispersion during the Early Devonian. Modified from Scotese (2014) . . . 11
1.4 Schematic representation of a zosterophyll. . . . 13
1.5 Characterizing main zosterophyll traits (Part 1) . . . 17
1.6 Characterizing main zosterophyll traits (Part 2) . . . 18
1.7 Characterizing main zosterophyll traits (Part 3) . . . 19

2.1 Strict consensus tree (parsimony, all taxon sampling). . . . 34
2.2 Tree from parsimony, with taxon sampling. . . . 37
2.3 Time-scaled tree. . . . 38
2.4 Taxon stability and cohorts of phylogenetic divergence. . . . 42
2.5 Ancestral state reconstruction . . . 44
2.6 Ancestral state reconstruction (continued). . . . 45
2.7 Topological comparison between previous studies and the current one. . . . 48

3.1 Distribution of zosterophylls during the late Silurian . . . 71
3.2 Distribution of zosterophylls during the Lochkovian and the Pragian . . . 72
3.3 Distribution of zosterophylls during the Emsian . . . 73
3.4 Distribution of zosterophylls during the Middle Devonian . . . 74
3.5 Distribution of zosterophylls during the Late Devonian . . . 75
3.6 Cluster and multivariate analyses applied to zosterophylls. . . . 86
3.7 Geographical reconstruction of zosterophyll distribution. . . . 88
3.8 Geographical distribution (left tree) compared to the ancestral state reconstruction of the circination (right tree). . . . 90
3.9 Geographical distribution compared to the ancestral state reconstruction of the emergences. . . . 92
3.10 Geographical distribution compared to the ancestral state reconstruction of the sporangium shape. . . . 94
3.11 Geographical distribution compared to the ancestral state reconstruction of the distribution of the sporangia. . . . 95
3.12 Geographical distribution compared to the ancestral state reconstruction of the distribution of the sporangia along the axis. . . . 96

4.1 Temporal distribution of zosterophylls. . . . 105

4.1 Temporal distribution of zosterophylls (cont.). 106
4.2 Diversity analyses of zosterophylls. 112
4.3 Evolutionary rates of zosterophylls. 114
4.4 Diversity analyses of zosterophylls using time-scaled phylogenies. 115
4.5 Rarefaction curves. 116

B.1 Majority rule consensus tree of Bayesian analysis, full taxon sampling. 174

C.1 Cluster dendrogram showing the closeness of the localities based on the zosterophyll composition. This dendrogram is based on the Raup-Crick dissimilarity matrix. Three groups are found out and represented by the coloured boxes. Color code as in fig 3.6b. Locality abbreviation in table 3.1 205
C.2 Definition of Devonian paleoprovinces of zosterophylls, excluding the singletons 211

D.1 Maximum richness estimate (spindle shaped), between Zosterophylls (in red) and Barinophytes (in blue) among the Devonian. 240
D.2 Diversity analyses through spatial distribution. 241

E.1 Plate showing the Battery Point Formation specimens. 247
E.2 Boxplots of the maximum tracheid diameter. 250
E.3 Scatterplot of the mean maximum tracheid diameter compared to xylem strand diameter. 251

List of Tables

2.1 Measures of taxon stability between parsimony and bayesian. 40
2.2 Summary of ancestral character state reconstruction analysis. SBLC = Small Basal Lycophytina Clade; LBLC = Large Basal Lycophytina Clade (see Fig. 2.1). 43
2.3 Taxonomy and relationships of zosterophylls and lycopsids in this and previous studies. 55

3.1 Locality names and assignation to a geographical province 77
3.2 Summary description of the biogeographical models used. 82
3.3 Model tests for the paleogeographical model. 85

A.1 List od zosterophylls currently described 151
A.2 List of all the *Zosterophyllum* species currently described. 153

B.1 First Appearance Datum (FAD) and Last Appearance Datum (LAD) of the taxa selected for the phylogenetic analysis. 172
B.2 Stratigraphic indexes between the six most parsimonious trees. 173

C.1 Dataset of presence-absence of genera of zosterophylls in a given locality (Capel, Cleal, et al., 2023) 176
C.2 Geographical distribution of taxa over the paleoprovinces. 206
C.3 Results from SIMPER analysis between Laurussia and Eastern Laurussia 207
C.4 Results from SIMPER analysis between Laurussia and Northeastern Gondwana 208
C.5 Results from SIMPER analysis between Eastern Laurussia and Northeastern Gondwana 209

D.1 Occurrence database of zosterophylls. 239

E.1 Previously described anatomically preserved species: species, xylem size (range or measurement), max tracheid size (range and measurement) 248

F.1 Summary of all the zosterophyll species known in the Battery Point Formation . 256

Chapter 1

Introduction

This work, entitled "Characterization, diversification, and evolution of the Silurian-Devonian plant group Zosterophyllopsida" is a revision project of an extinct group of plants, among the first known to diversify at a global scale on lands. During this Introduction section, the context behind the terrestrialization of plants will be first drawn. Then a detailed summary of the studied group and its historical context will be provided, leading to the questions asked for this dissertation. The methodologies developed to study Zosterophyllopsida and answer the different questions will be summarized.

1.1 The terrestrialization phenomenon

The Phanerozoic is an era of biological innovations, that started with the Cambrian explosion of life, 540 Ma ago and still last to this day. Numerous life forms succeeded one another and brought at their pace novelty. The shape of organisms also changed a lot through time, with groups showing some trends on specific time periods, and a morphological evolution is recorded since the Cambrian (Deline et al., 2018). In particular, the study of the earliest forms of life represents a challenge. In fact, these life forms are surprising by their strange morphology, afar from the modern ones. Moreover, as usually pointed in paleontology, the scarcity of the fossil record prevents for a whole, complete view of the history of life. This is particularly the case for the oldest deposits, that due to their longer time compared to the more recent ones, will be

more likely exposed to erosion, and thus, will tend to be less easily recovered (Gregor, 1970; Kenrick et al., 2012; Buffan et al., 2023). The fossil record is also biased in the preservation of groups, because of the difficulty to recover organisms with soft tissues (Muscente et al., 2017), and ancient deposits (Foote & Sepkoski, 1999). In addition, terrestrial deposits are less easily preserved than the marine ones (Benton, 1989). Thus, information about the early evolution of life on lands is fragmentary.

The Paleozoic, in particular, crystallizes these notions, and appears as an era worth studying in order to understand the establishment of the first ecosystems. Additionally, this era recorded numerous crucial events in the history of life, one of the most noteworthy being the earliest terrestrialization phenomenon (D. Edwards & Selden, 1992; Selden, 2001; Wellman et al., 2023). This can be defined as events when life forms transition from one environment to another, and leave the aquatic environment for the terrestrial one. This transition triggers new adaptation on the morphology and anatomy of the organisms involved, since the change is drastic and induces strong selection pressures. The main challenges organisms are facing among others are gravity, desiccation (homoiohydry, (Selden & Edwards, 1989)), UV protection, and new reproduction or locomotion strategies (Janvier, 2010). Despite these constraints, terrestrialization is a rewarding process for lineages that survived since it provides brand-new environments to develop. Groups that are able to overcome the transition of environments will then be able to strongly diversify in order to occupy as best as possible the new ecological niches. At any time, and even today there are transitions between these two environments. However, during the Paleozoic the first unequivocal fossil data provides evidence of the first events of terrestralization (Dunlop, 1996; Wilson & Anderson, 2004; Kenrick et al., 2012; Gerrienne et al., 2016). To complete this view, new methodologies are constantly pushing back the estimated origins, completing the lack of data induced by the fossil record, opening new debates and enhancing interest in finding fossils to check these hypotheses (George & Blieck, 2011; Lozano-Fernandez et al., 2016; Morris et al., 2018; Tihelka et al., 2022; Beaulieu et al., 2025).

Among the different candidates in the early terrestrialization is the land plants, whose unquestionable impacts are still studied today.

1.2 The evolutionary context of Embryophyta

Land plants are key organisms when studying terrestrialization, because of their undeniable impact on the history of life. In fact, these engineer organisms restructured the Earth system. They are known to have caused drastic changes in the soil formation (Mitchell et al., 2016), climate (Gibling & Davies, 2012), and geochemical cycles (Lenton et al., 2016), thanks to the erosive work of their roots and their photosynthetic activities. This, coupled with the fact that plants are considered as primary source of nutrients in the ecosystems, created inhabitable environments for other organisms like Metazoan - particularly the Ecdysozoa (Rota-Stabelli et al., 2013) - who could transition to a complete life cycle on land (Shear, 1991). Little is known about the reasons behind this important environmental transition. The first hypotheses invoked an abrupt change in the UV and atmospheric oxygen. However, these statements have been questioned ever since (D. Edwards & Selden, 1992; Ward et al., 2006).

The fossil record of plants is particular since different types of fossils can be found. In fact, plants are particularly known for their ability to produce numerous fragmentary fossils. This fragmentation can occur during the life of the plant, like the annual growth of leaves, flowers and seeds, but also after the death of the organism and the dislocation of branches or rooting system (Forey et al., 2004). This particularity generates a parataxonomy phenomenon in paleobotany, when the different fragments are given a specific epithet until more information can link different parts to the same plant (McNeill et al., 2012). In addition, there is also a distinction between micro, meso and macroflora (D. Edwards & Wellman, 2001). The fossils composing the microflora are spores and pollen and are regrouped in palynofloras (Strother et al., 2015). The mesoflora regroups all the phytodebris, which are among other composed of cuticle fragments. The macroflora is defined as remains providing information about the morphology and/or anatomy of the plant. In the context of this PhD, only this type of fossils will be taken into account. The morphology of plants is recovered thanks to compression fossils. The three-dimensionality of the organism is usually lost as the weight of sediments flattens the plant. In some cases, it is also possible to find anatomical information thanks to three-dimensional preservation. Cross sections of the fossil can be produced, allowing for a tissular and even cellular exploration. Permineralized fossils bear important anatomical data, that sheds light

in the development, architecture, systematic and relationship of the plants. Since the present work emphasizes mainly on the morphology, more details about the different debates on the anatomical nomenclature are given in the well detailed chapter of Bateman (1991). The plant evolutionary history can be reconstructed thanks to the combination of all these fossils.

Microfossils and palynofloras represent the earliest evidences for the presence of land plants, which currently dates back to the Middle Ordovician (Dapingian, Fig. 1.1) (Rubinstein et al., 2010). More specifically, cryptospores are found showing Embryophyta characteristics like the tetrad organization. On the other hand, the oldest morphologically preserved macrofossil known to date is from the Silurian (Sheinwoodian), and belongs to the famous rhyniophyte *Cooksonia* (Libertín et al., 2018). There is then a gap in the fossil record, between the earliest traces of land plants and the first known morphologically preserved, that hinders the understanding of their early terrestrial evolutionary processes. Hotton et al. (2001) noted that despite a temporal gap of 70 myrs, the earliest floras seem to be composed of morphologically simple structures, without any important changes during the course of this period. Different hypotheses were formulated to explain this observation, starting with the absence of herbivorous predators, a potential trigger for morphological evolution (Hotton et al., 2001), to reproductive isolation through wetlands preventing early land plants from spreading (Knoll et al., 1979). Despite this morphological stasis pacing the early land plant evolution, we can observe from the earliest macrofloral remains, a gradual increase in diversity in land plants.

The land plants, represented by the group Embryophyta Engler are a diverse lineage with unclear origins (L. A. Lewis & McCourt, 2004). The emergence of the group is from a unique event of terrestrialization (Karol et al., 2001), originated from one of the three candidates of green algaes, namely Charophyceae Rabenhorst, Coleochaetophyceae Jeffrey and Zygnematophyceae Round & Guiry. The recent reviews of Donoghue et al. (2021) and Donoghue and Clark (2024) strongly favor the results of Wickett et al. (2014) about an Embryophyta origination from the Zygnematophyceae algaes, the most recent statement among all the configurations proposed (Kenrick & Crane, 1997; Turmel et al., 2009; Timme et al., 2012).

Embryophyta is composed by various groups of land plants, some of them with unknown affinities. In the basalmost position is regrouped what are commonly called the "bryophytes"

and comprise Bryophyta Braun (the mosses), Anthocerotophyta Stotler (the hornworts), and Marchantiophyta Stotler (the liverworts). They are characterized by a gametophytic dominance of the life cycle and a vascular system composed of hydroids (Kenrick & Crane, 1997). Their phylogenetic affinities have long been debated, and almost all the configurations proposed, especially to explain the relationships of Polysporangiophyta Kenrick & Crane between the three groups of bryophytes (Bowman et al., 2017; Cox, 2018; Donoghue et al., 2021). The recent molecular analysis of Puttick et al. (2018), based on transcriptomic information, propose a monophyletic hypothesis for the "bryophytes" called in that study Bryophyta. This clade is composed at its basis by the hornworts and followed by a "Setaphyta" clade regrouping the liverworts and mosses (see Fig. 1.1 for an updated view of their relationships). Bryophyta appears then under this hypothesis, the clade sister to Polysporangiophyta.

Polysporangiophyta, on the other hand, is a diverse group with more than 300 000 described species (Lecointre et al., 2016). They are characterized by a sporophytic dominance of their life cycle with a reproductive system composed of sporangia. Recently, the publication of D. Edwards et al. (2022) defined the Eophytidae (eophytes), an extinct group of plants with a poikilohydric strategy, and sporangia bearing cryptospores. Due to these transverse characteristics between bryophytes and polysporangiophytes, the authors propose a potential position for this group as basalmost Polysporangiophyta.

The basis of the clade encompasses, furthermore, basal polysporangiophtya represented by extinct genera such as *Rhynia* Kidston & Lang or *Aglaophyton* Edwards.

All extant Polysporangiophyta are Tracheophyta Cavalier-Smith i.e. organisms with a complex vascular system composed of xylem cells. Among Tracheophyta, a first dichotomy divides Lycophytina composed of Lycopsida Bartling and Zosterophyllopsida Kenrick & Crane from Euphyllophytina Kenrick & Crane.

Even if Lycophytina is represented today by Lycopsida only, the group is ancient, rooting in the late Silurian, and is considered as one of the oldest Tracheophyta. However, the fossil record shows a more important diversity in species and morphologies, especially during the Paleozoic, contrasting with the four extant remaining genera (*Lycopodium*, *Phylloglossum*, *Selaginella*, *Isoetes*, Gensel and Berry (2001)). It is characterized by the presence of microphylls, photosynthetic outgrowths carrying a similar function as leaves.

Euphyllophytina is one of the most diverse groups of Tracheophyta, comprising the majority of the plant diversity since the Carboniferous. The majority of Euphyllophytes are characterized by leaves, considered as an analog of microphylls, and being a structure originating from a determinate lateral branching system (Tomescu, 2009; Tomescu & Whitewoods, 2024). The group includes Equisetales De Candolle ex Bercht. & Presl, different groups of ferns, and Spermatophyta Cavalier-Smith, along with extinct groups such as Cladoxylopsida Novák, Pteridospermatophyta, Trimerophyta Foster & Grifford, or Progymnospermopsida Beck. As highlighted in figure 1.1, there is a lot of uncertainties concerning their phylogenetic relationships, and more particularly, the monophyly of most of the extinct groups (Paratracheophyta, Zosterophyllopsida, Pteridospermatophyta, and Trimerophyta) is not established yet.

The plant record is thus complex and some trends are noticed in it. Depending on the time period studied, the plant beds will be composed by some dominant groups of plants, characterizing a "Flora" (Potonié, 1952). According to recent results, five "Evolutionary Floras" pace the Phanerozoic (Cleal & Cascales-Miñana, 2014), expanding and confirming previous observations on plant diversity (Niklas et al., 1983). The first flora defined is called Eotracheophytic and is composed mostly of rhyniophytes such as *Rhynia* or *Cooksonia* (Morris et al., 2011). It is then followed by the Devonian Eophytic flora - the scope of this work - dominated by Lycophytina. During the Carboniferous and until the Mesozoic, Pteridospermatophyta dominate the Paleophytic flora. During the Mesozoic, the Mesophytic flora is characterized by a dominance of gymnosperms and was supplanted by the angiosperms during the Cretaceous, into the current Cenophytic flora. This evolutionary history of land plants is of particular interest since it does not follow the well-established curve of Metazoan diversity and seems especially unaffected by the five major biological crises defined on the marine fauna (Raup & Sepkoski, 1982). This consequently provides a different insight of the evolution of life on Earth (Cascales-Miñana et al., 2018). In this context, the Paleozoic is a critical era to study since it encompasses three over the five flora described, dominated by completely different groups of plants.

More particularly, the Devonian period sees the rise and the fall of the Eophytic flora, the focus of this work. This one is of particular interest since a global greening dynamic is growing at that time, mainly triggered by the studied group. The Eophytic flora is divided into two phases, as recently highlighted by Capel et al. (2021). The early Eophytic phase encompasses the Silurian-

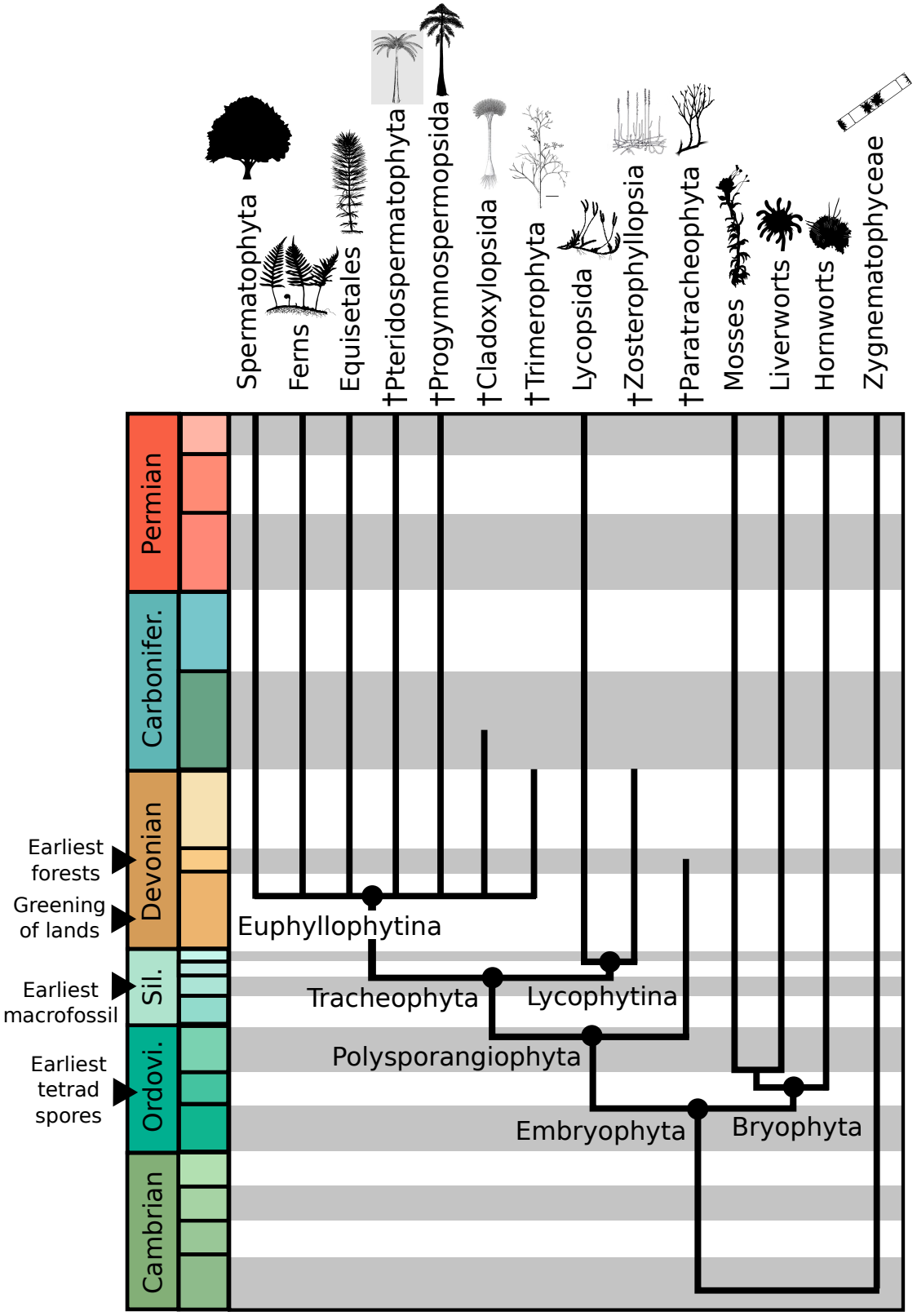


Figure 1.1: Tree summarizing the relationships between the land plants during the Paleozoic. Information modified from Gerrienne et al. (2016) completed with Wickett et al. (2014) and Puttick et al. (2018). Arrows on the left are the main plant events extracted from the fossil record. Crosses before names indicate extinct groups. Silhouettes extracted from Phylopic.

Devonian transition to the Middle Devonian, and is composed mainly of Zosterophyllopsida taxa. The late Eophytic phase, on the other hand, is bounded by the Middle and the Late Devonian, characterized by Lycopsida.

The present work will put the scope on the early Eophytic phase. The Silurian-Devonian transition is of particular interest since it gave rise to new advantageous strategies represented by the dominant group of Zosterophyllopsida. This group has indeed supplanted the previous Eotracheophytic flora, both morphologically and in term of spatial distribution. In order to better understand the establishment of this first global dynamic, a focus will be made on the main group of the late Silurian-Early Devonian time interval.

1.3 The importance of the Silurian-Devonian periods

The Silurian and the Devonian are respectively the third and the fourth periods of the Paleozoic. They are preceded by the Ordovician (485-444 Ma) and followed by the Carboniferous (359-299 Ma). The Silurian has a temporal range of 25 myr, from 444 Ma to 419 Ma and is the period in which the first macrofossil remains of terrestrial plants are found (see above) (Libertín et al., 2018). The Devonian is the next period after the Silurian, from 419 Ma to 359 Ma, for a total range of 60 myr and will be particularly studied in the next chapters (Fig. 1.2) (Cohen et al., 2024). The Devonian is divided into three main series, the Lower (Early), Middle and Upper (Late) Devonian (House, 1988). The Lower Devonian, that will be studied in more detail through this work includes three stages, the Lochkovian, which is the earliest one, the Pragian and the Emsian. The Middle Devonian is the shortest section, regrouping the Eifelian and Givetian stages. The Upper Devonian regroups two stages as well, the Frasnian and the Famennian. It is also important to note that the seven stages composing the Devonian have an uneven temporal distribution, the Pragian being the smallest stage (3.2 myr) and the Emsian the longest (14.4 myr).

This period saw the establishment of the land ecosystems, with an Early Devonian phenomenon of "terrestrial revolution", were the earliest life forms invaded the emerged lands at a global scale (Capel, Cleal, et al., 2022). Land plants recovered at that time display a simple morphology and a limited size of few centimeters tall, characteristic of a herbaceous dominance.

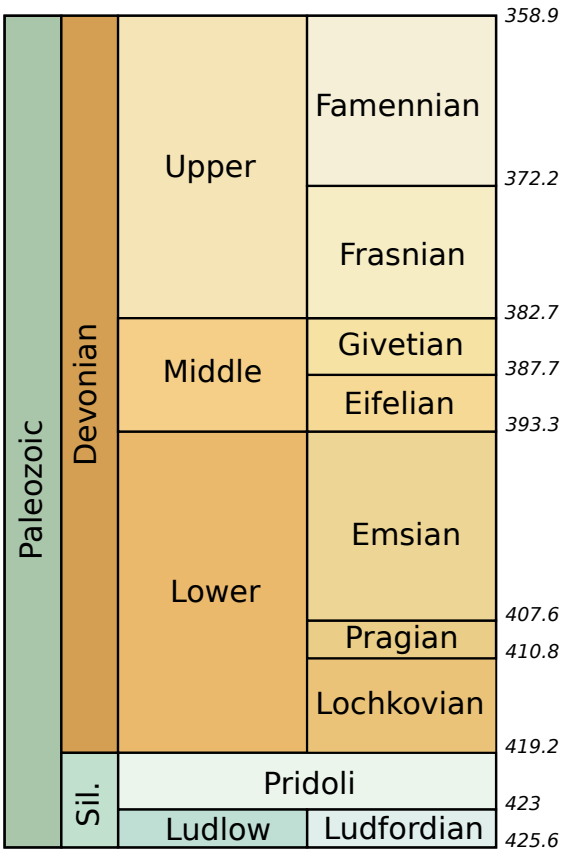


Figure 1.2: Geological time scale of the studied period. Modified from the International Chronostratigraphic Chart (v.2023)

The Middle Devonian induces a drastic change in the plant ecosystems, with a transition between these herbaceous plants to the first arboreal forms (Berry, 2019). During the Late Devonian, the characteristics skeletal innovation found in the vertebrate fossil record suggests an onset in tetrapod terrestrialization (Clack, 2002). This period is also known to host an event of crisis in the Frasnian-Famennian boundary, that had impacts, especially on marine ecosystems (Schindler, 1990). From the land plants perspective, modern structures appear on the fossil record, through preserved seeds (Prestianni & Gerrienne, 2010).

From a paleogeographical point of view, the early Paleozoic shows a fragmentation of continents. During the Silurian, and particularly the late Silurian, three terranes (Laurentia, Baltica and Avalonia) regrouped to form Laurussia (Caledonian orogeny) (Golonka et al., 2023). During

the Devonian, this geographic area has undergone intense orogenesis periods with the formation of the Appalachian and Acadian mountain ranges. Laurussia regroups present-day Moscovite plate, Northern Europe, North America, and some parts of South America. At that time, this continent straddled the equator. It extended into both the northern and southern hemispheres. The second Devonian continent is the Gondwana, composed of the southern part of South America, Africa, Australia, India, and South China. This continent seems to be present in the southern hemisphere mainly, with the South America part in the southern pole, while South China reaches the equator. Two other terranes, Siberia and Kazakhstania were in-between the continents even if their exact positions remain unclear (Torsvik & Cocks, 2017; Scotese, 2021). Figure 1.3 is a reconstruction of the Lower Devonian paleogeography, showing the position of the different continents at that time. During the Silurian and the Devonian, all these emerged land are gradually moving close together. For example, by the Late Devonian, the Gondwana and the Southern Laurussia are connecting, inducing the closure of the Rheic ocean, in between these continents. These are a milestone in Pangea formation, that started in the Neoproterozoic, and completing its formation during the Carboniferous (Blakey, Wong, et al., 2003). Because the Rheic ocean had a position between two main continents during the Devonian, it is assumed that its particular paleoceanography had impacts on organisms at that time. A reconstruction from Crasquin and Horne (2018) suggests that the Early to Middle Devonian is characterized by warm water surface in the northern part of the ocean, (southern Laurussia), while cold surface and deep currents cross the south of the Rheic ocean (northern ridge of Gondwana), in a similar fashion than the current Circum Antartic. With the progressive joint between Laurussia and Gondwana in the Late Devonian, the water circulation of the Rheic ocean becomes colder and is hypothesized to explain the Frasnian-Famennian crisis. In fact, since the Rheic ocean was positioned in the equatorial to mid latitudes, tropical reef systems could develop and thrive. But with the gradual installation of colder current systems, such tropical ecosystems could not survive anymore these new conditions. This hypothesis can also be invoked to describe potential changes on land.

From a climatic context, after a brief late Silurian cooling to 16°C, the Early Devonian is characterized by a temperature rise, with a reach of a thermal maximum during the Lochkovian (20- 22 °C). Two other thermal maxima are reached during the Middle (Givetian) and Late



Figure 1.3: Geographical map reconstructing the continent dispersion during the Early Devonian. Modified from Scotese (2014)

(Famennian) Devonian (Joachimski et al., 2009; Le Hir et al., 2011; Scotese et al., 2021). Generally, the Silurian and the Devonian are considered as globally warm periods, and the hypothesis of the impact of land plants has been put forward to explain the Carboniferous cooling (Le Hir et al., 2011; Gibling & Davies, 2012). Related by these climatic effects, important eustatic changes took place during the Devonian especially during the Givetian, that faced an important regression event (Scotese et al., 2021), linked to the formation of a southern ice cap (Crasquin & Horne, 2018).

The studied periods are thus characterized by numerous events, in terms of evolutionary changes, tectonics dynamics, and climatic patterns. Since all these events are interlinked, the purpose of this PhD will be to explore the temporal and spatial dynamics of macroflora, from their initial diversification and contribution to the greening of lands, until the establishment of the first forests (the Middle Devonian series). For that reason, Zosterophyllopsida is the ideal study group: they are diversifying during this time period and are the dominant group of the corresponding flora.

1.4 The case study of zosterophylls

Zosterophyllopsida is an extinct group of Tracheophyta with a stratigraphic distribution mainly constrained to the Devonian, more particularly between the end of the Silurian (Ludfordian) until the Late Devonian.

The most recent occurrence of this group is represented by the genus *Barinophyton* White, in the Tournaisian (Scheckler, 1984) while the oldest one is the Ludfordian taxon *Macivera* Kotyk et al. (Kotyk et al., 2002). A maximum of diversity of the group is reached during the Early Devonian (Pragian-Emsian) (Cascales-Miñana & Meyer-Berthaud, 2014, 2015; Capel et al., 2021). Remains of zosterophylls are found in various places of the world, in Europe, America, China, Russia or Australia (Senkevich, 1975; D. Edwards & Kenrick, 1986; Hao & Xue, 2013; McSweeney et al., 2020), that suggests a Devonian cosmopolitan distribution of the group. Despite this important dispersion, some places are over represented. Like many other plant fossils of this time (Kenrick et al., 2012), sampling efforts were concentrated in Europe (UK (D. Edwards, 1968), Germany (Schweitzer, 1999), Norway (Schweitzer & Heumann, 1993) and Belgium (Gerrienne, 1993) more particularly), North America (eastern and arctic Canada (Kotyk, 1998)) and China (in the Yunnan, and Sichuan provinces more particularly (Hao & Xue, 2013)). On the other hand, Africa or Southern America are poorly sampled continents that delivered a few amounts of zosterophylls' remains (Plumstead, 1977; Berry & Edwards, 1994). This bias in the fossil record has been previously pointed (Capel, Cleal, et al., 2022), and some studies suggested a preference in the group for an equatorial distribution (Capel, Cleal, et al., 2023).

In the context of early land plant radiation, zosterophylls is one the most abundant group of its time, with a high diversity comprising today around 40 genera described (see supplementary table A.1 for an exhaustive list). Figure 1.4 summarizes the different concepts used to describe these sporophytic plants. This schematic representation is coupled with plates of zosterophyll specimens, from the Université de Liège (ULg) (figs. 1.5 to 1.7).

This group possesses a few stable synapomorphies that makes them easily recognizable (well represented in fig. 1.5 A, B). But with the recent fossil discoveries, numerous autapomorphic characters were revealed, revealing a mozaïc of characters inside the group (represented by taxa

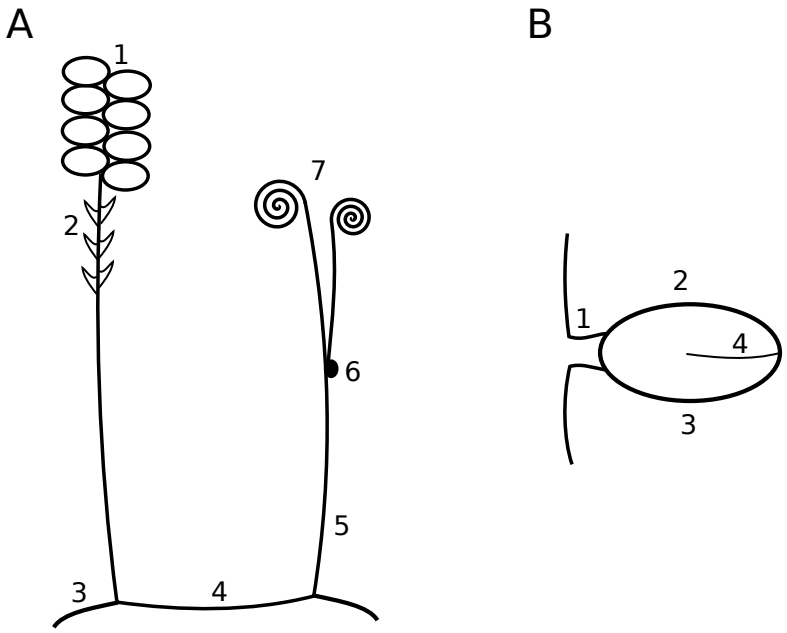


Figure 1.4: Schematic representation of the organs labeled in zosterophylls, vocabulary used in the present essay (see glossary for a definition of the words used). A Chimeric reconstruction of the whole plant: 1: strobilus, 2: emergencess, 3: K-H branching, 4: rhizome, 5: stem, 6: subaxillary branching, 7: circination. B close-up on a sporangium: 1: stalk, 2: adaxial valve, 3: abaxial valve, 4: dehiscence margin.

such as *Gosferia curvata*, fig. 1.5 C), hindering the reconstruction of the evolutionary process behind these structures. Before developing the terminology used, it is important to keep in mind that the fossils studied belong to the sporophytic phase of the plant. Little is known about the gametophytic phase in the fossil record, because they are asynchronous. In fact, even if it is possible to find gametophytes, they are not generally associated to the sporophyte, compromising thus the taxonomical identification. The gametophyte *Sciadophyton* is generally interpreted as associated to *Zosterophyllum* (Schweitzer, 1983), and one specimen of *Crenaticaulis verruculosus* has a presumed connection with a gametophyte remain (Gensel et al., 2001).

Morphologically speaking, a few organs compose this organism, namely the stems (aerial or prostrate) considered as photosynthetic (fig. 1.5 D to F), and sporangia (fig. 1.6 A to C), the reproductive parts that protect the spores. The rooting system is less easily preserved, since a majority of zosterophylls fragments are known by the axis apex. However, the recurrent discovery of strange dichotomies sometimes perpendicular to the main axis suggests an absence of true roots in this group, but a system composed of rhizomes (4A in Fig. 1.4), or creeping-axes (Gensel et al., 2001). In the literature, this particular configuration attributed to a rhizomic system is called "K or H branching" (3A in Fig. 1.4).

The branching organization of this group consists of dichotomies, and for some species of zosterophylls, bumps below them suggest a remaining of a subaxillary branching ((D. Edwards et al., 1989; Kenrick & Crane, 1997) 6A in figure 1.4). Other branching types are visible in the literature, such as the "axillary branching" (D. Edwards, 1970; Kenrick & Edwards, 1988a), or "Angular-Organe" (Hass & Remy, 1986), generally used for *Selaginella*.

Various types of branching were described within this group, like the common isotomous one, that produces equal branches at each dichotomy. This branching is opposed to the anisotomous or pseudomonopodial, were it is possible to make a distinction between a main axis and lateral smaller ones. Combinations are visible in some zosterophylls, with differentiation between a basal and axial branching (D. Edwards et al., 1989), bringing complexity in the evolution of the branching process.

Understanding the three-dimensional exploration of these plants can be a challenge given the flat nature of the preserved fossils. There is, however, evidence of both planar (Hao et al., 2003) and three-dimensional branching (D.-M. Wang & Hao, 2002) pattern among zosterophylls.

This volume exploration is not strictly correlated to the branching pattern described above (D. Edwards et al., 1989).

Some zosterophylls also present structures called emergences (fig.1.6 D to F) and defined as unvascularized spines (Gensel & Berry, 2001). This characteristic has been particularly interesting since the shape, function and distribution changes among species, bringing numerous taxonomical information. Such is the case of the shelf-like emergences observed in *Bathurstia* (Hueber, 1971a), fairly different from the spiny, putative glandular ones of *Discalis* (Hao, 1989b). Less frequently, axes coiling are recorded, similar to the circination in ferns (7A in Fig. 1.4).

At the apex of the axis, is a well studied structure represented by the sporangium (fig. 1.6 A to C). The sporangium is the organ that contains the spores, generally of equal size (isosporous) in this group. However, few zosterophylls, and some members of the barinophytes (considered as zosterophylls as well) display a strange form of heterospory. In these species, micro and megaspores are found together in the same sporangium (anisospory). The release of these spores is made thanks to an aperture called a dehiscence line (4B in Fig. 1.4). In zosterophylls, this dehiscence is made on the distal side of the sporangium, which opens in two valves. In some of them, this dehiscence line is a few layers of cells thick, around the margin. Sporangium shape is variable among zosterophylls, initially defined as reniform (kidney-shaped), but diversity is visible on the flattening, orientation, valve size and overall shape. It is thus possible to describe the sporangia as rounded (Hao & Xue, 2011), disc-shaped (Hao, 1989b), or elliptical (D. Edwards & Li, 2018b). The sporangia are located on the sides of the axis, and can be held by a stalk of variable size, or even absent, depending on the species (Hueber, 1971a; Lyon & Edwards, 1991; C.-S. Li & Edwards, 1992; Powell et al., 1999; Kotyk et al., 2002) (fig. 1.5, C). Different strategies of sporangium distribution are visible inside the group. Some zosterophylls such as *Zosterophyllum* Penhallow have sporangia regrouped into a cluster called a strobilus (Penhallow, 1892) (fig. 1.7 A to C). Strobili are located on the upper, terminal part of the axes. The strobilus generally displays a structured, rowed organization of sporangia (Banks & Davis, 1969; D. Edwards, 1970; Gensel, 1982b). Other zosterophylls such as *Discalis* did not have any clustering, but sporangia distributed along the axis instead (Hao, 1989b) (fig. 1.7 D, E). In this configuration, the distribution of these sporangia can be regular or irregular. Less frequently, some configurations fall outside the two main described above. Such is the case of *Konioria*

whose sporangia are located below the dichotomies (Zdebska, 1982).

Even if the morphology of the group is well established, little is still known concerning their anatomy. In fact, due to the vagaries of preservation, little information on anatomy has come down to us. On the 49 zosterophylls regrouped in Table A.1, only 11 are anatomically preserved. Thanks to these taxa, zosterophylls are known to present a simple, elliptical to rounded exarch xylem strand. The tracheid cells, composing the xylem, are characterized by two layers of walls. Reinforcement of the layers gives to the tracheid an "annular to helical secondary thickening" shape, (D. Edwards, 2003). Kenrick and Edwards (1988b) reconstruction of the wall of a zosterophyll tracheid shows that these typical thickenings are formed by the lignified secondary wall towards the interior of the cell, but also by the cellulosic primary wall. In the protoxylem, vertical perforations are observed through the primary wall and are interpreted as results of wall stretching during the growth of the plant. The combination of these characteristics allows to categorize this tracheid shape as a "G-type" (*Gosslingia*-type) sensu Kenrick and Edwards (1988b). Since the xylem is composed of lignified cells, they are more easily preserved and recognizable than the other type of cells. It is thus common in zosterophyll's stem to find the xylem strand "floating" or surrounded by unidentifiable cells. It is assumed that these cells represent the phloem and the inner, parenchymatous, part of the cortex. The external layer of the stem, however, is sometimes recovered, and in some cases, a sterome is visible (Kenrick & Edwards, 1988b). The sterome is a tissue composed of thickened cells, which are therefore easier to preserve.

Even if anatomical information is confined to a small number of taxa, and shows preservation limited to a few structures, a recent study emphasized the importance of anatomy in the understanding of zosterophylls' relationships and insists on using these characters to complete the group's understanding (Nibbelink & Tomescu, 2022).

Not only zosterophylls display a simple anatomy, but they were also small plants, measuring a few centimeters tall. This group is, therefore, one of the only tracheophytes not to have developed arborescent forms in the course of its history.

Zosterophylls is also a group with a complex nomenclatural history. During the XIXth century, all the zosterophyll taxa discovered at that time were assigned to a "Psilophyta" group,

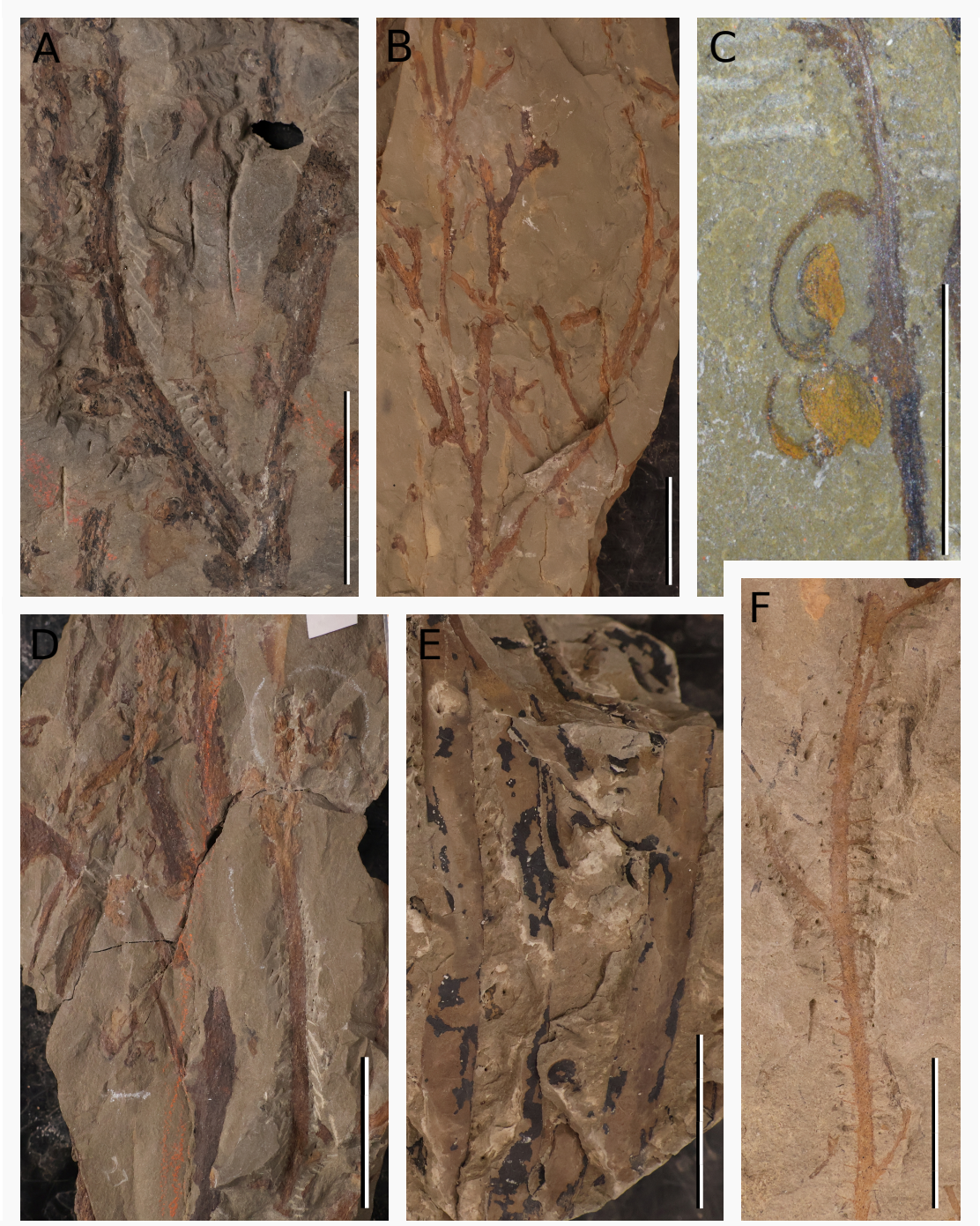


Figure 1.5: Plate I. Characterizing main zosterophyll traits (Part 1). A) *Sawdonia deblondii* (ULg 13404E), fertile axes showing a dichotomy, scale bar= 2 cm, B) *Faironella valentula* (ULg 13367), fertile axes showing dichotomies, scale bar= 2 cm, C) *Gosferia curvata* (ULg 12332), fertile axis, showing sporangia bore on long and coiled stalks, scale bar= 0.5 cm, D) *Odonax borealis* (ULg 13361), fertile axes showing a dichotomy, scale bar= 1 cm, E) *Oricilla bilinearis*, smooth axes, scale bar= 2 cm, F) *Anisophyton* cf. *gothanii* (ULg 13393), sterile axes showing dichtomies and emergences, scale bar= 2 cm. Raw images courtesy of E. Capel. Specimens housed at the paleobotanical collections of the University of Liège.

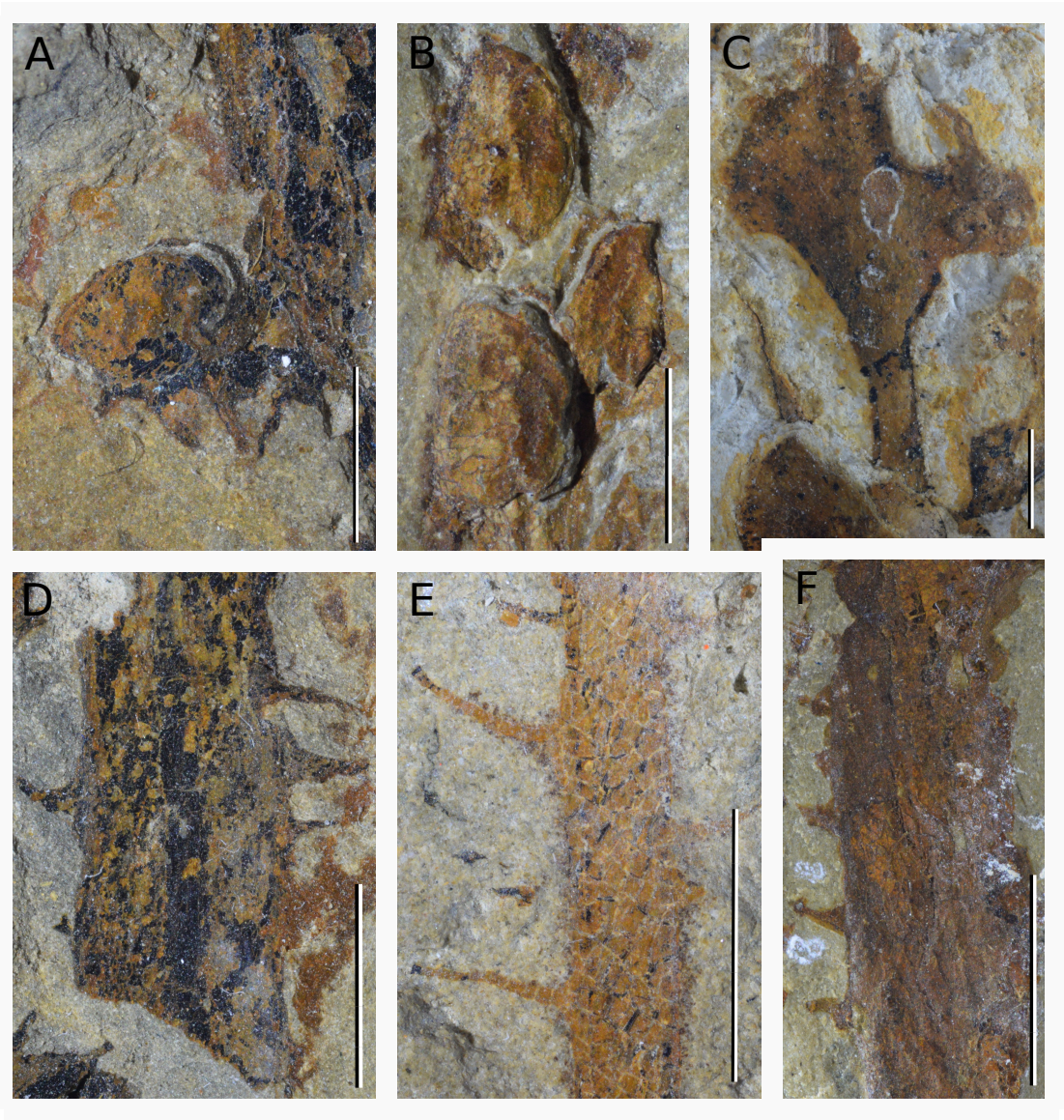


Figure 1.6: Plate II. Characterizing main zosterophyll traits (Part 2). A) *Sawdonia deblondii* (ULg 13404E), close-up on a sporangium, scale bar= 0.3 cm, B) *O. borealis* (ULg 13361), close-up on sporangia, scale bar= 0.2 cm, C) *Adoketophyton subverticillatum* (CBYn9002015), close-up on a sporangium, scale bar= 0.2 cm, D) *S. deblondii* (ULg 13477), close-up on emergences, scale bar= 0.5 cm, E) *Anisophyton* cf. *gothanii* (ULg 13393), close-up on emergences, scale bar= 0.5 cm, F) *O. borealis* (ULg 13361), close-up on emergences, scale bar= 0.4 cm. Raw images courtesy of E. Capel. Specimens housed at the paleobotanical collections of the University of Liège.

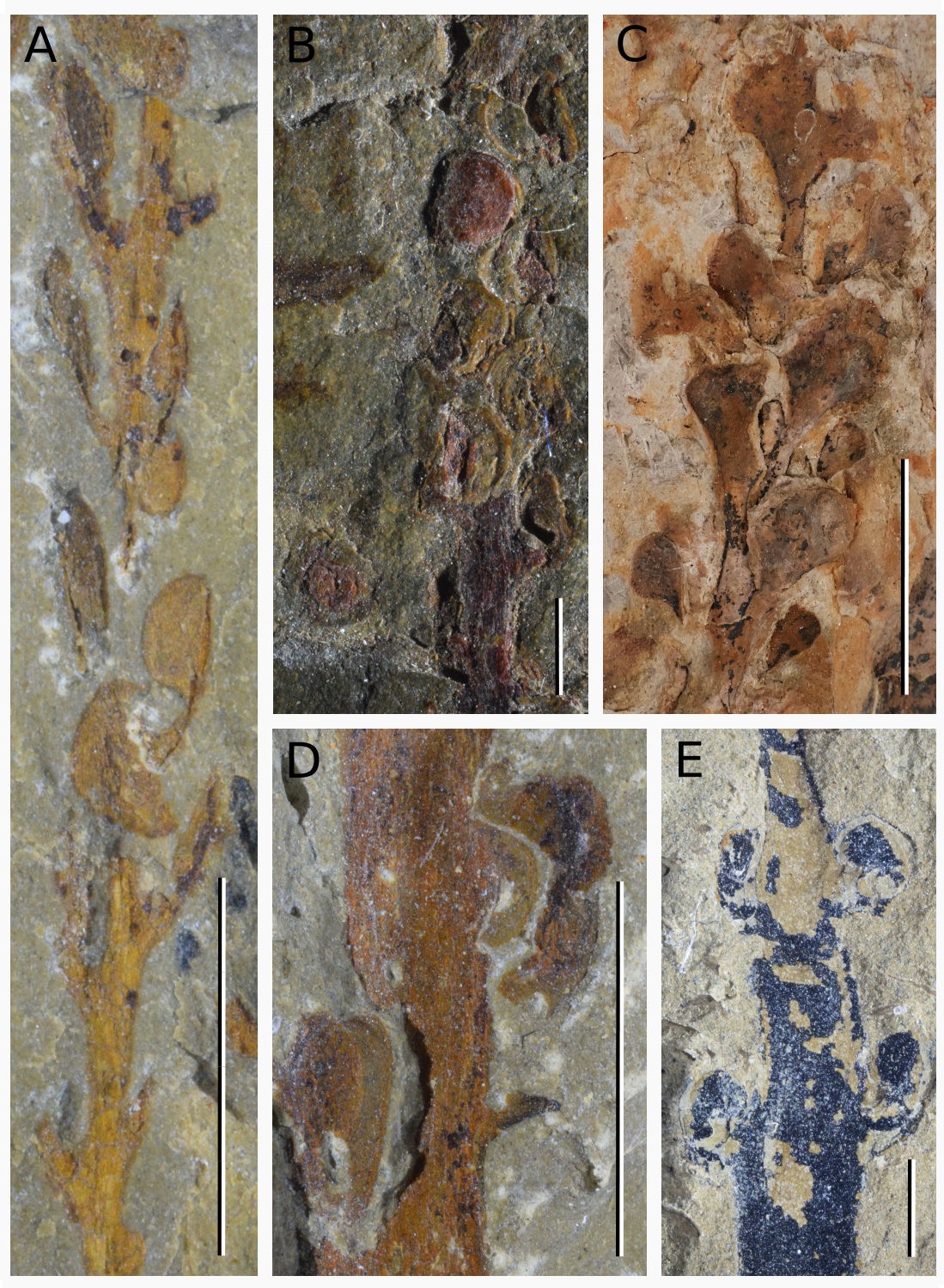


Figure 1.7: Plate III. Characterizing main zosterophyll traits (Part 3). A) *Zosterophyllum deciduum* (ULg 13155), fertile axis showing sporangia, scale bar= 0.4 cm, B) *Zosterophyllum fertile* (ULg 1485), fertile axis (strobilus), scale bar= 0.2 cm, C) *Adoketophyton subverticillatum* (CBYn9002015), fertile axis (stobilus), scale bar= 1 cm, D) *Faironella valentula* (ULg 13367), close-up on sporangia and emergences, scale bar= 0.5 cm, E) *Odonax bilinearis* close-up on sporangia, scale bar= 0.2 cm. Raw images courtesy of E. Capel. Specimens housed at the paleobotanical collections of the University of Liège.

among the other Silurian-Devonian plant fossils presenting a morphology too simple to be assessed with certainty in one of the Tracheophyta groups. It is only in the middle of the XXth century that publications attempting to precise this Psilophyta classification started to come out. The subdivision "Zosterophyllophytina" was established by Banks (1968), based on the most representative genus *Zosterophyllum*. This group contains the small amount of zosterophylls known at that time, namely *Gosslingia*, *Sawdonia*, *Distichophytum* and *Zosterophyllum*. They are characterized as Zosterophyllophytina on the basis of naked axes, a lateral distribution of sporangia with a reniform shape and a distal dehiscence. In his publication, Banks was able to distinguish two families among Zosterophyllophytina, despite the poor diversity known at that time. The Zosterophyllaceae encompassing *Distichophytum* and *Zosterophyllum*, is characterized by naked axes and sporangia aggregated into strobili. The Gosslingiacaea composed of *Sawdonia* and *Gosslingia*, shows naked or spiny stems, and sporangia scattered along the axis. Later on, Gosslingiaceae was removed from the Zosterophyllophytina by Banks (1975). This pioneer work led the foundations to what is currently used in taxonomy (D. Edwards et al., 2016; D. Edwards & Li, 2018a, 2018b).

However, with the discovery of new fossils and the development of new technologies to observe this material, morphological gaps were progressively filled, with a link between Zosterophyllopsida and Lycopsida more and more highlighted (Banks, 1968; Gensel & Berry, 2001). In fact, despite the presence of microphylls, a characteristic of Lycopsida only, some of them like *Baragwanathia*, *Leclercqia* or *Drepanophycus* (the so-called pre-lycopsids) have an in-between morphology between Zosterophyllopsida and Lycopsida. In fact, these taxa display an exarch xylem strand and reniform sporangia with a distal dehiscence. Phylogenies complete these morphological observations with parsimony-based studies showing a close relationship between Zosterophyllopsida and Lycopsida (Gensel, 1992; Kenrick & Crane, 1997). The publication of 1997 is still commonly used today, and shows a proximity between zosterophylls and lycopsids, into a "Lycophytina" clade. Inside, only a few taxa were regrouped into the class "Zosterophyllopsida" (*Anisophyton*, *Konioria*, *Crenaticaulis*, *Serrulacaulis*, *Deheubarthia*, *Sawdonia*, *Thrinkophyton*, *Hsua*, *Gosslingia*, *Oricilla*, *Tarella* and *Zosterophyllum divaricatum*). In addition, an enigmatic group of early land plants, known for their particular heterospory as well as their sporangiferous appendages are nested into Zosterophyllopsida. This group, taxonomically defined as

Incertae sedis (Arnold, 1939) is called barinophytes, and are presented here as a family, the Barinophytacaea, comprising *Barinophyton* and *Protobarinophyton*. In total, one order and three families were defined into Zosterophyllopsida. The order is called Sawdoniales and excludes *Z. divaricatum*. Kenrick and Crane (1997) defined in their chapter 5 Sawdoniales as plants with a pseudomonopodial branching, a planated branching system and sporangia distributed along several orders of branches. Alongside the family Barinophytaceae are regrouped the Sawdoniaceae, comprising *Sawdonia*, *Deheubarthia*, *Serrulacaulis*, *Crenaticaulis*, *Konioria*, *Anisophyton*, and a paraphyletic Gosslingiaceae with *Gosslingia*, *Oricilla*, *Tarella*. The other zosterophylls fall outside this grouping (*Distichophytum*, *Discalis*, *Nothia*, *Adoketophyton*, *Gumuia*, *Huia*, *Hicklingia* and some species of *Zosterophyllum*), which suggests a paraphyly for the group. The following phylogenies - except the contrasted results of Hao and Xue (2013), presenting a monophyletic Zosterophyllopsida - support this configuration.

Thus, zosterophylls have a complex nomenclatural background, with the use of different names to define Early Devonian taxa with a simple morphology composed of lateral sporangia and an exarch xylem. With the aim of consistency, the term "zosterophylls" will be used in the present essay, to encompass all the taxa defined as zosterophylls as well as barinophytes, but not including Lycopsida. Despite being an initially small group, the zosterophylls showed over the years an increasing diversity, with discoveries still ongoing today. Since the bases of this group have been established in a drastically different context, the present work is an attempt to update our understanding by taking into account the maximum knowledge gathered.

1.5 Context and aims of this thesis

By focusing on the late Silurian-Early Devonian time interval, this PhD takes place in a context of intense radiation in the fossil record of early land plants. This event is regularly compared to the Cambrian explosion of life, in term of unique morphological and spatial exploration of Embryophyta (Le Hir et al., 2011). The studied group is emphasized on zosterophylls which are a good representation of this morphological exploration and are particularly abundant during this time period. Moreover, despite its impact on the Lower Devonian ecosystems, this group remains poorly understood (see above). Because of their morphological simplicity compared to

Lycopsida or Euphyllophytina, and their stratigraphic distribution constrained to the Devonian, zosterophylls are regularly assimilated to Lycopsida (Liu et al., 2024). Additionally, early land plants are generally addressed all together, in a context of paleoecological or paleoenvironmental studies (Raymond, 1987; D. Edwards, 1990; Raymond et al., 2006; Capel, Cleal, et al., 2023). This approach is generally preferred since taking into account the total known diversity prevents issues linked to taxonomy or group uncertainty.

As developed in the section above, there is today no consensus regarding the definition of zosterophylls, considered either as paraphyletic and closely related to the Lycopsida (Kenrick & Crane, 1997; Liu et al., 2024) or as a clade on its own (Hao & Xue, 2013; Cascales-Miñana & Meyer-Berthaud, 2014). In addition, the sustained rate of discoveries of fossils with zosterophyll affinities adds more complexity in the interpretation of the group's evolutionary history. Improving the group phylogenetic uncertainties thanks to a wide sampling is a solution to bring a stable framework of study. Thus, this PhD is positioned as a review of the evolutionary history of zosterophylls. Different aspects of this question and subsequent methodologies will be developed among the chapters. To that aim, a review of i) their phylogenetic position and relationships ii) combined with their spatial evolution using phylogeography and iii) their evolution through time using diversity analyses will be proposed. Three chapters compose this dissertation, each of them represents one of the three main aspects studied for the group.

The first chapter addresses the burning question of their phylogenetic relationships. Establishing a stable framework concerning their position in the tree of life, as well as their intrinsic positions is the first step to understand the group. Thus, in chapter 2, a revision of the phylogeny of zosterophylls based on an extensive sampling will be proposed and the results discussed.

The second chapter is an exploration into paleogeographical analyses. Here the choice fell on the use of phylogeography, to detect any geographical pattern that can explain the topology obtained in the first work. This information, coupled with the morphological signal, provides an original insight on zosterophylls' evolution.

The third chapter addresses the question of the group's temporal evolution. Diversity analyses are the methodologies chosen for this question, and for the first time, applied to an occurrence database, the most complete to date for the group. The topologies produced in chapter 2 will

also be used in order to compare the congruence of the diversity signals.

By reviewing the phylogeny of the group, an updated, extended morphological matrix has been created. This information, one of the most complete for zosterophylls to date has then been cross-analysed with their distribution over time and over space in order to measure the impact of morphology on their evolutionary, temporal and geographical history. Thus, by using morphological information, evolutionary history of zosterophylls will be explored in the next chapters.

Chapter 2

Phylogeny

This chapter unfolds the yet unresolved question of phylogenetic affinities of Zosterophyllopsida s.l. In fact, with the important number of taxa newly described over the years, an unsuspected diversity composes the group. It is then necessary to test if this group is still a constant taxonomic unit. Additionally, morphological evidences point for a close relationship with the extant Lycopsida. By creating a complete matrix of the group, the goal is then twofold: testing the relationships within the group, and toward the Lycopsida

2.1 Introduction

The zosterophylls are an emblematic group of early land plants with worldwide distribution, and the main component of the Devonian Eophytic flora (Capel et al., 2021; Cleal & Cascales–Miñana, 2021). Compared to other major groups of early land plants, zosterophylls were particularly abundant during the Early Devonian, from Europe (D. Edwards, 2006) to Asia (Hao & Xue, 2013), Australia (McSweeney et al., 2020) and North America (Hueber, 1971a). The group was designated initially as Subdivision Zosterophyllophytina of Division Tracheophyta by Banks (1968), in a seminal paper aimed at clarifying the poorly understood relationships among early vascular plants, of which few were known at the time. Morphologically, they were initially defined by leafless axes with laterally attached sporangia and exarch xylem (Banks, 1968, 1975).

Since the publication of Banks' oft-cited classification, more than 40 additional genera have

been assigned to the group, expanding considerably its morphological breadth, with implications for how the group is defined. That is because alongside "typical" forms (i.e., conforming to Banks' definition of the group), a number of taxa present more unusual morphologies, such as *Konioria* (Zdebska, 1982) with individual sporangia located at points of axis dichotomy or *Xitunia* (Xue, 2009), a plant with big spike-like extensions on the sporangia. As a result of this dramatic expansion of known zosterophyll diversity, the group has become difficult to define in a taxonomic context.

New fossil discoveries of the past decade, many of them from South China (Xu et al., 2011; X. Zhu et al., 2011; Hao & Xue, 2013; D. Edwards et al., 2016; D. Edwards & Li, 2018b; Y. Wang et al., 2018; Y. Wang et al., 2020), prompted studies that assessed the patterns of diversity in the group (Cascales-Miñana & Meyer-Berthaud, 2015; D. Edwards & Li, 2018a). However, despite the large amount of recent data, an updated zosterophyll phylogeny including all or most of the new taxa is still lacking. In fact, the first study including zosterophylls in a phylogenetic context is the one of Gensel (1992). The author tried to solve the relationships between zosterophylls and lycopsids, and included a limited number of zosterophyll taxa (n= 7) and characters (n= 12). In her study, Gensel found out a clade comprising *Zosterophyllum* at its basis, and followed by a dichotomy. The first group is called the "*Sawdonia*" clade consisting of *Sawdonia* (Hueber, 1971b), *Crenaticaulis* (Banks & Davis, 1969), *Gosslingia* (D. Edwards, 1970), *Tarella* (D. Edwards & Kenrick, 1986), *Konioria* and *Thrinkophyton* (Kenrick & Edwards, 1988a), while the second group, called "*Asteroxylon*" clade regroups pre-lycopsids such as *Asteroxylon* (Kidston & Lang, 1920b), *Drepanophycus* (Göppert, 1852), *Baragwanathia* (Lang & Cookson, 1935), and lycopsids like *Leclercqia* (Banks et al., 1972), and *Lycopodium* and *Lepidophloios* (Macfarlane, 1883).

Subsequently, in an extensive study that remains a key reference almost 30 years later, Kenrick and Crane (1997) laid the foundations of the currently accepted understanding of early tracheophyte phylogeny. Kenrick and Crane's results supported a basal stem-group composed, among others of *Cooksonia* species, and a monophyletic Subdivision Euphyllophytina sister to a clade (subdivision Lycophytina) that included Class Zosterophyllopsida and Class Lycopsida. They defined Zosterophyllopsida based on axes with circinate (spirally coiled) apices and laterally attached sporangia arranged in two rows. Kenrick and Crane (1997) further noted groups with distinguishing features within Zosterophyllopsida, including the enigmatic Barinophytaceae,

recognized for their heterospory, an absence of dehiscence line, and "sporangiferous appendages" (Brauer, 1980), and the Sawdoniaceae, characterized by the presence of emergences on the axes. However, despite providing a much-needed benchmark, Kenrick and Crane's results also revealed issues in phylogenetic resolution. For instance, some zosterophylls such as *Hicklingia* (Kidston & Lang, 1924), *Discalis* (Hao, 1989b), *Gumuia* (Hao, 1989a) and some species of *Zosterophyllum* (Penhallow, 1892) were recovered in a polytomic relationship with Lycopsida and Zosterophyllopsida, raising questions about the monophyly of zosterophylls. Even if the study of Kenrick and Crane (1997) includes an extensive sampling for that time (around 20 species of zosterophylls and 6 putative ones), the majority of the sampling came from Europe and North America, raising additional questions about sampling bias in the group.

This work was followed by other phylogenetic analyses (Hao & Xue, 2013; Nibbelink & Tomescu, 2022), but none of those included all (or even the majority) of the zosterophyll diversity known at the respective time. For example, the analysis by Hao and Xue (2013) focused mainly on the taxa discovered in the Posongchong Formation of China. These authors found support for a pattern of relationships different from those of previous studies, with Zosterophyllopsida a monophyletic group distinct from Lycopsida. Based on Hao and Xue's results, Zosterophyllopsida is defined by an elliptical or strap-shaped primary xylem strand with exarch maturation, an absence of perforations in the thickening bars of the tracheids and a rowed arrangement of lateral sporangia. In Hao and Xue (2013) analyses, the two clades, Zosterophyllopsida and Lycopsida, are part of a grade paraphyletic to Euphyllophytina. The latest analysis of zosterophylls (Nibbelink & Tomescu, 2022) explored the influence of anatomical characters on the resolution of phylogenetic relationships. As a result of their approach, taxon sampling in that study was constrained by the availability of anatomical data. Nibbelink and Tomescu's analysis found consistent support for two clades that included the relatively small number of zosterophylls sampled, with Lycopsida nested in a clade that also included *Ventarura* (Powell et al., 1999).

Taken together, previous analyses of zosterophyll relationships sampled different subsets of taxa and support conflicting patterns of relationships. This inconvenient situation creates much confusion on the taxonomy of the group, with the result that zosterophyll studies have to define the group for their own purposes in the absence of a phylogenetic framework. One such example

is the study of plant diversity over time by Cascales-Miñana and Meyer-Berthaud (2014), in which the authors used their own definitions of Zosterophyllopsida sensu stricto, which included only zosterophylls and closely allied taxa, and Zosterophyllopsida sensu lato, which also included the Barinophytaceae. Thus, availability of a solid phylogenetic framework is important for further studies of the group. Furthermore, numerous zosterophylls have autapomorphic characteristics that confuse the understanding of their relationships. This, coupled with the significant slice of zosterophyll diversity uncovered by the more recent discoveries, has created a need for redefining the group, and reassessing relationships both within the group and with other groups of tracheophytes. Here, the aim is to (i) test whether zosterophylls are monophyletic, (ii) elucidate the evolutionary relationships of lycophytes and zosterophylls, and (iii) shed light on the tempo and mode of lycophyte and zosterophyll evolution.

2.2 Material and methods

2.2.1 Taxon sampling

A matrix of morphological and anatomical characters was prepared, including 44 Silurian and Devonian genera, all extracted from literature (see Supplementary Methods, list of taxa p. 155). To polarize the analysis, outgroups comprise coeval non-zosterophyll taxa: the protracheophyte *Aglaophyton* (D. S. Edwards, 1986) and the paratracheophyte *Rhynia* (Kidston & Lang, 1920a); trees were rooted in *Aglaophyton* in all the analyses. Two lycopsids, *Asteroxylon* and *Drepanophycus*, and two euphyllophytes, *Psilophyton* (Dawson, 1859) and *Polythecophyton* (Hao et al., 2001), are also included for testing relationships between zosterophylls and other groups.

Zosterophylls and related taxa were sampled extensively. For instance, this dataset includes 15 taxa that were not previously integrated in any phylogenetic analysis: *Baoyinia* (D. Edwards & Li, 2018b), *Bathurstia* (Hueber, 1971a), *Craswallia* (Morris & Edwards, 2014), *Demersatheca* (C.-S. Li & Edwards, 1996), *Euthursophyton* (Mustafa, 1978), *Forania* (Jensen & Gensel, 2013), *Gosferia* (Gerrienne, 1999), *Guangnania* (D.-M. Wang & Hao, 2002), *Gutzeitia* (Snigirevsky et al., 2007), *Macivera* (Kotyk et al., 2002), *Odonax* (Gerrienne, 1996b), *Omniastrobus* (Bonacorsi et al., 2021), *Ornicephalum* (D. Edwards & Li, 2018a), *Sichuania* (D. Edwards & Li, 2018b), and

Xitunia (Xue, 2009) (see Supplementary Methods for further information on taxa). These taxa are included alongside the 22 other genera of zosterophylls, representing the most extensive sampling of the group for a single analysis, to date. I did not include in the analysis genera viewed as putative zosterophylls but considered *incertae sedis*: *Bracteophyton* (D.-M. Wang & Hao, 2004), *Danziella* (D. Edwards, 2006), *Dibracophyton* (Hao et al., 2012), *Faironella* (Gerrienne, 1996a), *Jugumella* (Senkevich, 1975), *Huia* (Geng, 1985b), *Hsua* (C.-S. Li, 1982), *Krithodeophyton* (D. Edwards, 1968), *Nothia* (El-Saadawy & Lacey, 1979), and *Renalia* (Gensel, 1976). I also excluded genera known from single, poorly preserved specimens, such as *Parazosterophyllum* and *Gippslandites* (McSweeney et al., 2020); see Supplementary Methods for further information on taxa not included in the analysis. While the majority of the genera included in this study are monotypic, *Guangnania* has two species (D.-M. Wang & Hao, 2002; D. Edwards et al., 2016) and *Sawdonia* has at least four (Hueber, 1971b; Gerrienne, 1996a; Gensel & Berry, 2016; Berry & Gensel, 2019); in their cases, character scoring took into account all the species. In contrast, *Zosterophyllum* and *Psilophyton* each include multiple species. However, because these genera may be paraphyletic or polyphyletic (Kenrick & Crane, 1997; Hao & Xue, 2013; Nibbelink & Tomescu, 2022) and resolving relationships among their diverse species falls beyond the scope of this study, which focuses on genus-level relationships, I only included for each of the two genera one of the most completely characterized species: *Zosterophyllum myretonianum* (Penhallow, 1892) and *Psilophyton crenulatum* (Doran, 1980).

2.2.2 Character construction and scoring

In constructing the characters used in my analyses I strived to define them in such a way as to account as much as possible for all the discrete features of their morphology and anatomy. In doing this, I took special care to avoid (1) implicit hypotheses of homology, and (2) constructs of the "tail color problem" type (Hawkins et al., 1997). Most characters are based on those previously defined by Kenrick and Crane (1997), Hao and Xue (2013), and Nibbelink and Tomescu (2022), with some modifications, but the matrix also includes 10 new characters. They are based on observations made while reviewing old and more recently published zosterophyll taxa, that display a mosaic of characters to explore. This implies that some characters were

discarded because of their poor visibility through the data set. Such is the case of characters scoring for stomata, or the number of walls inside sporangia that despite providing crucial information about the organisms, these information are too rare among the taxa studied to be taken into account. Of the 42 characters, thus constructed (see Supplementary Methods, Characters used in the phylogenenetic analyses, p. 161 for a detailed description), 13 describe the vegetative aspect of the plants (branching, rooting system, architecture...), 23 score for the reproductive parts, and 6 for the anatomy. Thus, the majority of the characters are defined for fertile parts and anatomy is under-represented.

Whenever possible, characters were defined as binary. Multi-state characters were used when multiple states could be assessed as homologous with certainty (such as the sporangium shape). As much as possible, one trait was assigned to one character, in order to avoid multiplying information that could artificially group together taxa devoid of the studied structure. One notable exception are the characters defined for emergences. Because of the variety of shape, function and distribution of zosterophyll emergences, it was impossible to summarize all that information into a single character. The characters were treated as unordered, without weighting, in order to limit further subjective bias in the analysis.

The characters were scored for each taxon using publicly available information from the primary literature. Character scorings are based as much as possible on information contained in the published descriptions, but also on my own direct observations based on published figures (pictures, line drawings). The resulting matrix of 44 taxa and 42 characters (see supplementary methods for the matrix) has 20% missing data. The matrix was managed in Mesquite which allows for extraction of the data into various file formats, depending of the software used for the tree search method.

2.2.3 Tree search methods

All previous studies of zosterophyll relationships have employed parsimony-constrained cladistic analyses (Gensel, 1992; Kenrick & Crane, 1997; Hao & Xue, 2013; Nibbelink & Tomescu, 2022). Recently, model-based approaches to phylogenetic questions have started gaining traction in paleontology (A. M. Wright, 2019). Here, both parsimony-constrained cladistics and a Bayesian

approach are used to address zosterophyll relationships.

Parsimony analyses were conducted in TNT (Goloboff & Catalano, 2016) using a traditional search (command mult). Bayesian analyses were conducted using MrBayes (Huelsenbeck & Ronquist, 2001). The analyses were run under a Mkv model (P. O. Lewis, 2001), with 1,000,000 generations burn in, two parallel runs and 3 chains, in order to ensure broad exploration of the tree space. Since the consensus trees obtained in the Bayesian analyses had very low phylogenetic resolution (see Supplementary Fig B.1), I computed the all compatible group tree (allcompat) for the Bayesian analysis conducted under GGE taxon sampling (see below).

2.2.4 Taxon exclusion experiments

High taxon to character ratios are more likely to increase the lack of phylogenetic resolution (Scotland et al., 2003). Additionally, some of the zosterophyll taxa are known only from fragmentary material and have high proportions of missing data, another factor known to lower phylogenetic resolution (Wiens, 2003). For these reasons and in order to improve the level of resolution obtained by the parsimony analysis with full taxon sampling (FTS hereafter), I conducted several parsimony-constrained analyses with different subsets of taxa excluded. The choice of taxa for the exclusion experiments was driven by the amount of missing data - taxa excluded in those analyses were those with the highest proportions of missing data: *Euthursophyton* (64.3% missing data), *Craswallia* (40.5%), *Xitunia* (40.5%), *Gutzeitia* (38.1%), *Trichopherophyton* (Lyon & Edwards, 1991) (38.1%), *Gosferia* (35.7%) and *Baoyinia* (35.7%). While taxon exclusion in most of these analyses improved phylogenetic resolution compared to the FTS analysis, the only reduced taxon sampling analysis that produced a single, fully resolved most parsimonious tree was the one with *Gutzeitia* and *Gosferia* excluded (GGE hereafter).

2.2.5 Phylogenetic congruence, taxon stability and cohorts of phylogenetic divergence

Phylogenetic congruence, taxon stability and the cohorts of phylogenetic divergence were assessed by considering the phylogenetic relationships supported by the parsimony-constrained and the Bayesian analyses performed in the GGE taxon sampling regime, as reflected in (i) the

single most parsimonious tree obtained in the parsimony-constrained analysis and (ii) the all compatible group (allcompat) tree obtained in the corresponding Bayesian analysis. Phylogenetic congruence was assessed based on the proportion of nodes that are supported in both trees out of the total nodes on each of the two fully resolved trees.

Because the two trees are not fully congruent, I further characterized the stability of each taxon by comparing its position in the two trees. The position of a taxon in the tree was given by the rank of the node from which it diverged (R). Node ranks were numbered starting with the basal node of Lycophytina (the sister clade to the euphyllophytes), which was assigned rank 1; from there, node ranks were numbered up the tree, with the nodes immediately succeeding node of rank n in a clade being assigned the rank $n+1$ on each of the two lineages that diverge from node n, so the higher a node is in a tree, the higher its rank. To facilitate direct comparisons between the positions of a taxon on the two trees, the number of node ranks was normalized ($R+$) in the tree with a higher number of ranks ($h = 15$ node ranks in the maximum parsimony tree) to match the number of node ranks ($R-$) in the tree with fewer node ranks ($f = 13$ ranks, in the Bayesian Allcompat tree):

$$normR+ = (R + *f)/h.$$

A measure of overall *taxon stability* (TS), a new concept introduced here, was calculated as the positive value of the difference between the rank of the nodes at which that taxon diverges in the two trees:

$$TS = R- - normR+.$$

Thus, the most stable taxa diverge from nodes of the same or closely similar ranks in both trees (TS equal or close to 0) and the higher the TS value of a taxon, the least stable its phylogenetic position. Pairs of sister taxa that are supported in both analyses are each treated as a single lineage in the analyses of taxon stability and of the cohorts of phylogenetic divergence.

The ranks of the nodes at which each taxon diverges were also used to identify cohorts of phylogenetic divergence, another new concept introduced here. The cohorts of phylogenetic divergence group the taxa based on the node ranks at which they diverge from the phylogenetic trees. Thus, the cohorts are a reflection of how phylogenetically derived a taxon is: the higher the cohort, the more derived the taxa included in that cohort. This concept can be useful in

providing a rough image of evolutionary patterns, especially in cases where the phylogenetic relationships supported by different methods of inference (for the same taxon sampling) involve some degree of incongruence. Cohorts were separated visually along the most obvious breaks in the taxon divergence rank graph, placing highest emphasis on the most stable taxa (TS < 1.5) and downweighing the most unstable taxa with TS > 2.

2.2.6 Stratigraphic fit and ancestral character state reconstruction

Ancestral character state reconstruction was performed in Mesquite (Maddison & Maddison, 2022) on the strict consensus tree from the FTS analysis. I employed a maximum likelihood probability model to infer the ancestral character state at a node, which was the character state with >50% probability. Ancestral state reconstruction was performed for four characters selected because of their relevance to discussions on the taxonomic circumscription and the evolution of zosterophylls and lycophytes (Kenrick & Crane, 1997; Gerrienne et al., 2016). The characters are circinate axis tips (character 6), sporangium shape (character 20), relative sporangium valve size (character 25) and sporangium arrangement along axes (character 33).

The stratigraphic fit analysis was conducted using the R package strap (Bell & Lloyd, 2015). The workflow involved time-scaling each of the most parsimonious trees produced by the FTS parsimony analysis and computation of multiple stratigraphic fit indices, which allowed for selection of the most parsimonious tree with the Best Stratigraphic Fit (BSF). This fully resolved FTS tree was used to discuss patterns of evolutionary diversification, infer ghost lineages and estimate the timing of evolutionary events. This tree was also considered in comparisons with the results of previous phylogenetic analyses and is recommended for consideration in comparisons with the results of future analyses that require fully resolved trees and broadest taxon sampling.

Figures were built using Inkscape (Inkscape Project, 2023) and Photoshop (Adobe, San Jose, California, USA).

2.3 Results

2.3.1 Parsimony analyses

The FTS analysis recovered six most parsimonious (MP) trees (L = 149; CI = 0.313; RI = 0.534). The strict consensus tree of the six MP trees (Fig. 2.1) supports the same pattern of relationships supported in the 50% majority rule consensus tree. The tree separates the euphyllophytes (trimerophytes: *Psilophyton* and *Polythecophyton*) from a Lycophytina clade that groups all the zosterophylls and the lycopsids. The clade consisting of the two sister lineages, the euphyllophytes and Lycophytina, is sister to *Rhynia*. The synapomorphies that support the Lycophytina clade are laterally attached sporangia (character 14) that dehisce along their distal margin (character 23) and have bilateral symmetry (character 21); the latter character presents reversals to radial symmetry in *Margophyton* and *Craswallia*, and cannot be scored with certainty (missing data) in the barinophytes and *Euthursophyton*.

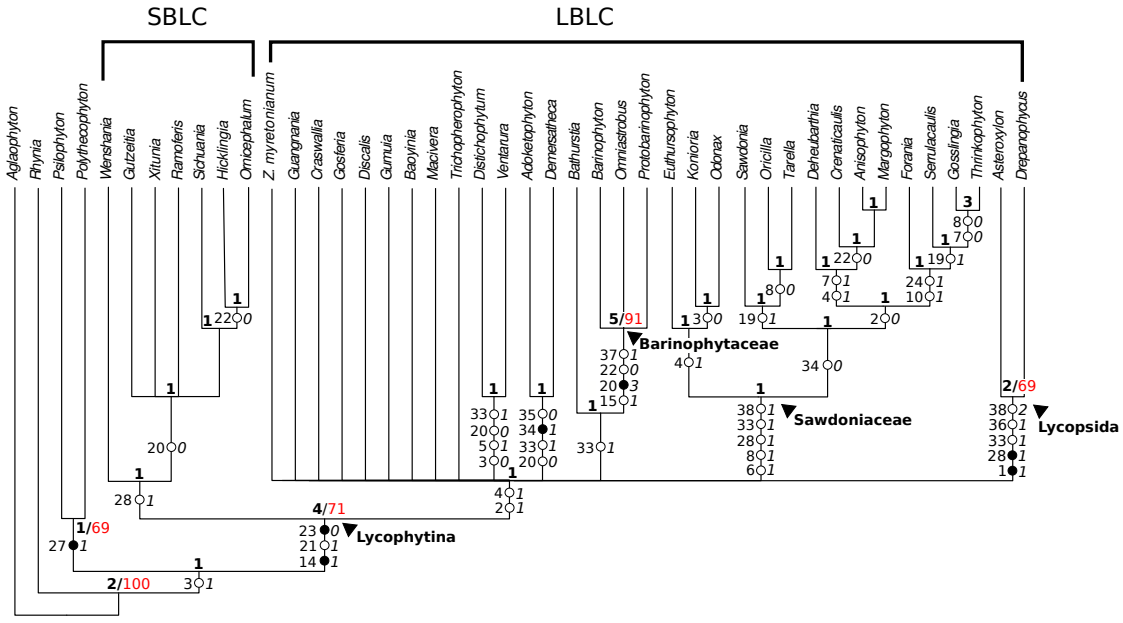


Figure 2.1: Strict consensus of six most parsimonious trees (L = 149; CI = 0.313; RI = 0.534) obtained in the full taxon sampling (FTS) analysis. Numbers above nodes are Bremer (in bold) and bootstrap (in red) support values. Note that the bootstrap values with more than 50% support are represented. Black dots are hard synapomorphies; white dots are putative synapomorphies; numbers at left of dots are character numbers, numbers at right, in italics, are character states. SBLC = Small Basal Lycophytina Clade; LBLC = Large Basal Lycophytina Clade.

The Lycophytina has a basal dichotomy that separates two clades. The smaller of these two clades – hereafter termed the small basal Lycophytina clade (SBLC) – includes a ((*Hicklingia*, *Ornicephalum*) *Sichuania*) clade that forms a polytomy with *Ramoferis*, *Xitunia* and *Gutzeitia*.; this polytomic node is sister to *Wenshania* (Fig. 2.1). All the other members of Lycophytina are recovered in the second, larger basal clade – hereafter termed the large basal Lycophytina clade (LBLC). This clade has a large basal polytomy in which a few clades are supported: *Distichophytum*+*Ventarura*, *Adoketophyton*+*Demersatheca*, the Barinophytaceae+*Bathurstia*, the lycopsids (*Asteroxylon* and *Drepanophycus*), and a larger clade referred to here as the Sawdoniaceae, due to its membership, which is similar to that of the Sawdoniaceae defined by Kenrick and Crane (1997).

The Barinophytaceae clade – *Barinophyton*, *Protobarinophyton* and *Omniastrobus* – is supported by the lenticular, vertically flattened shape of sporangia.

The Sawdoniaceae clade is supported by a number of synapomorphies, each of which either shows reversals within the clade or cannot be scored unequivocally in all the clade members: (i) circinate axis tips (character 6) and (ii) emergences (character 8), (iii) sporangia distributed on the highest and lower orders of branching (character 28), and (iv) xylem strand with elliptical cross-sectional shape (character 38). Circinate axis tips show a reversal in *Margophyton* and the presence of emergences sees reversals in *Gosslingia*, *Thrinkophyton*, *Oricilla* and *Tarella*. The elliptical cross-sectional shape of the xylem cannot be scored (due to lack of anatomical data) in *Anisophyton*, *Odonax*, *Serrulacaulis*, *Oricilla*, *Forania* and *Tarella*, and is therefore only predicted for these taxa based on support of the character state as synapomorphic in the clade; the same is true about the distribution of sporangia (along highest and lower order branches) in *Euthursophyton* and *Serrulacaulis*. A fifth putative synapomorphy, the regular arrangement of sporangia (character 33) sees a reversal in *Forania* and cannot be scored in *Euthursophyton*; more importantly, this character is inapplicable in *Anisophyton*, *Konioria* and *Margophyton*, which indicates that its synapomorphic status in the Sawdoniaceae, supported by these analyses, is an artifact of the tree-search algorithm, which takes into account each possible state of a given character in taxa where the respective character is scored inapplicable.

Within the Sawdoniaceae, one can note a clade that includes (*Konioria*+*Odonax*) *Euthursophyton*) sister to another clade in which an (*Oricilla*+*Tarella*) *Sawdonia*) clade is sister to a clade that

consists of two sister groups: one including *Gosslingia*, *Thrinkophyton*, *Serrulacaulis* and *Forania*, and the other including *Anisophyton*, *Margophyton*, *Crenaticaulis* and *Deheubarthia*.

In the single, fully resolved most parsimonious tree recovered in the GGE analysis (L = 145; CI = 0.386; RI = 0.663; Fig. 2.2 left) the same clades supported within Lycophytina in the FTS consensus tree (Fig. 2.1) are also supported. The SBLC – including (((((*Hicklingia*, *Ornicephalum*) *Sichuania*) *Ramoferis*) *Xitunia*) *Wenshania*) – is sister to a clade that includes all the remaining lycophytes (LBLC). In the latter, a basal split separates a clade including ((((*Discalis*, *Gumuia*) *Craswallia*) *Guangnania*) *Zosterophyllum*) from a larger clade. In this larger clade, a paraphyletic grade that consists (starting at the base) of *Baoyinia*, *Macivera*, *Distichophytum*+*Ventarura*, *Adoketophyton*+*Demersatheca*, and *Trichopherophyton* leads to a clade that includes the Barinophytaceae+*Bathurstia*, the lycopsids (*Asteroxylon* and *Drepanophycus*) and the Sawdoniaceae clade, each with the same membership as in the full taxon sampling analysis. Notably, the lycopsids are sister to the Sawdoniaceae and the clade they form together is sister to the Barinophytaceae+*Bathurstia* (Fig. 2.2 left).

The same clades and relationships supported by the GGE analysis are supported in the most parsimonious tree of the FTS analysis that is characterized by the best stratigraphic fit (see below) from among the six most parsimonious trees recovered in the FTS analysis (BSF tree hereafter; Fig. 2.3). The only differences between the GGE and BSF trees concern the placement of *Gutzeitia* and *Gosferia*, which are not included in the GGE tree. Thus, *Gutzeitia* is placed in the SBLC. In that clade, addition of *Gutzeitia* brings *Xitunia* and *Ramoferis* into a clade (*Xitunia* sister to *Gutzeitia*+*Ramoferis*) that is sister to the (*Sichuania* (*Hicklingia*, *Ornicephalum*)) clade (Fig. 2.3). *Gosferia* is placed as sister to *Discalis*.

In the BSF tree, the SBLC is supported by a potential synapomorphy – sporangia distributed on both highest and lower order branches (character 28) – that shows a reversal to sporangia borne only on highest order branches in *Gutzeitia* and cannot be scored unequivocally in *Xitunia*, *Sichuania* and *Ornicephalum*. The clade that includes *Zosterophyllum* is supported by a branching pattern in which branches curve apically close to their base to run more-or-less parallel with the subtending axis (character 5). However, this is only a putative synapomorphy, as missing data preclude its unequivocal scoring in *Craswallia*, *Gumuia*, *Discalis* and *Gosferia*. The large clade sister to *Macivera* has two potential synapormorphies (both of which present character state

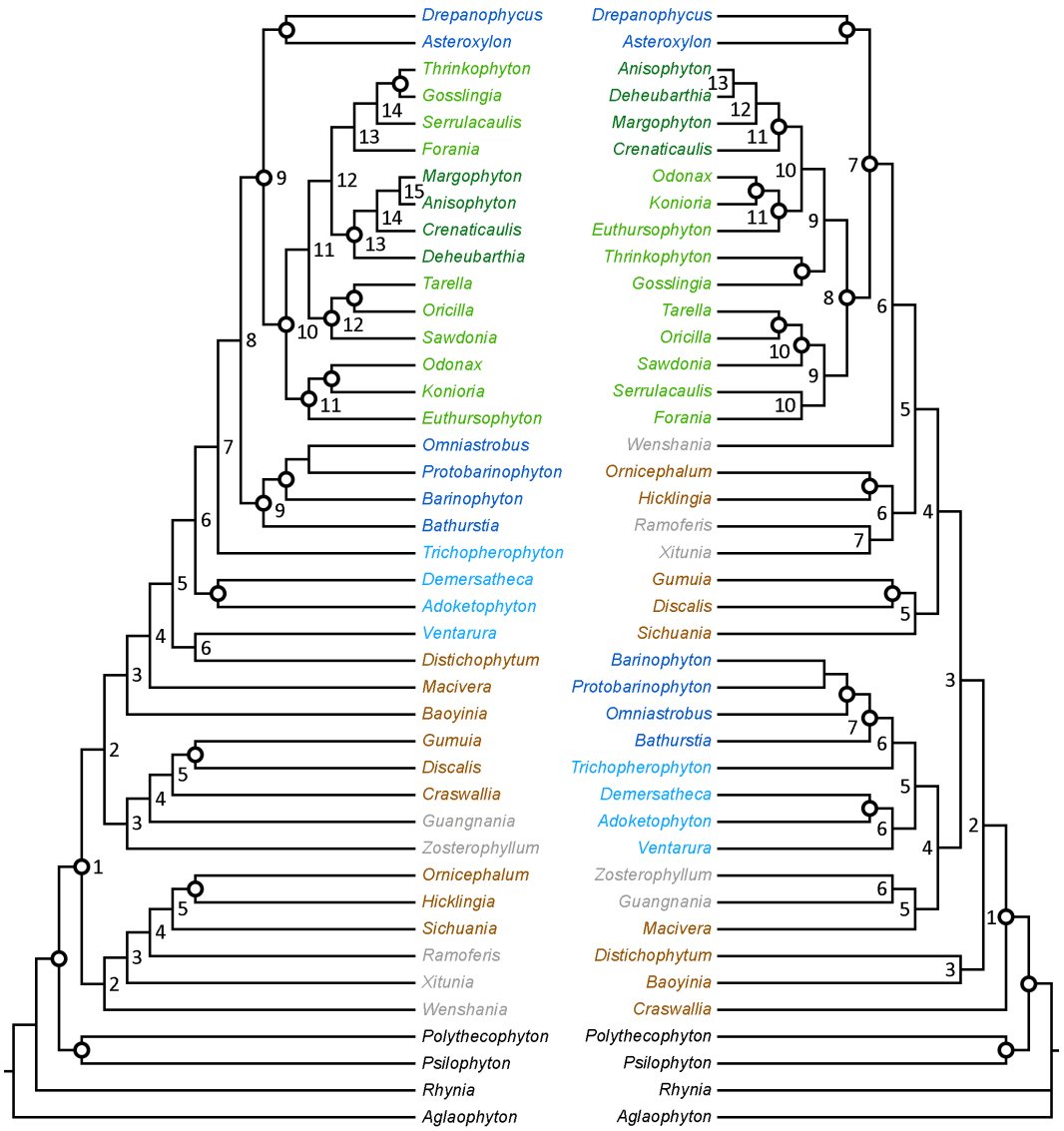


Figure 2.2: Results of the reduced taxon sampling (*Gosferia* and *Gutzeitia* excluded; GGE) analyses; at left – single most parsimonious tree (L = 145; CI = 0.386; RI = 0.663) obtained in the parsimony analysis; at right – all compatible group tree (allcompat) from the Bayesian analysis. Numbers at nodes show the node ranks used in the taxon stability analysis. Circles mark nodes supported in both trees that give a measure of congruence between the results of the two methods. Colors correspond to cohorts of phylogenetic divergence (see also Fig. 2.4): green – highest diverging taxa (higher diverging subgroup in dark green, lower subgroup in light green); blue – middle cohort (higher diverging subgroup in dark blue, lower subgroup in light blue); brown – lowest diverging cohort; gray – lycophytes not assignable to a cohort due to high instability; black – non-lycophyte taxa.

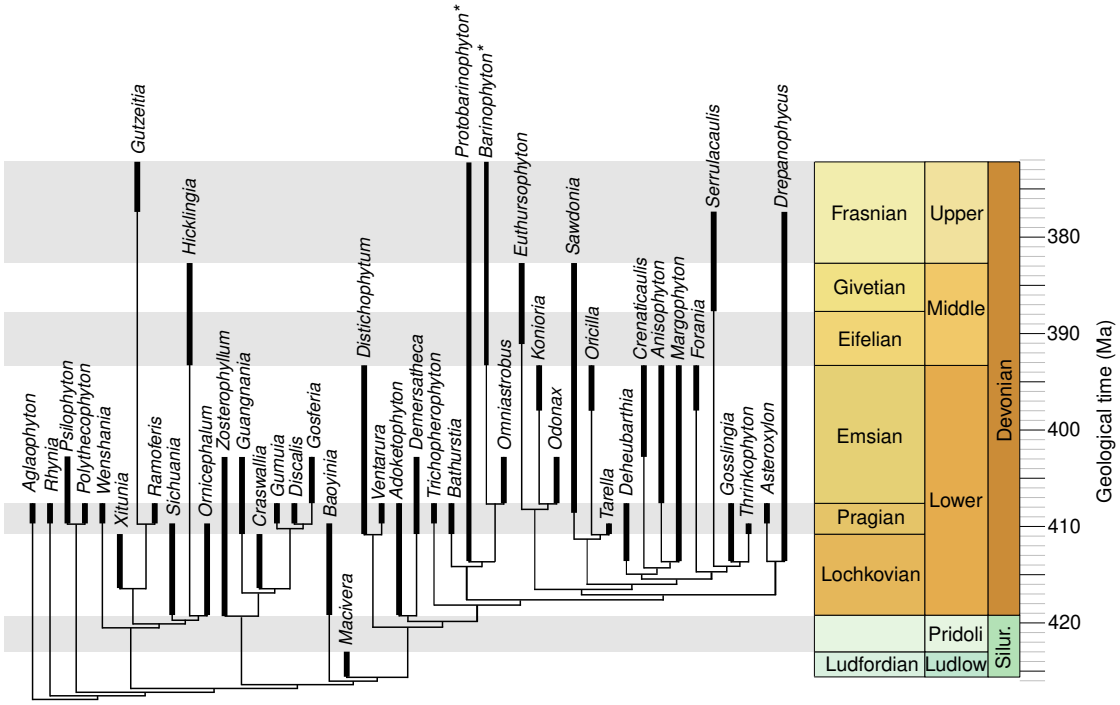


Figure 2.3: Time-scaled tree number 6 from the full taxon sampling (FTS) parsimony analysis, which has the best fit to stratigraphy (see Supplementary Table B.2 for stratigraphic fit indices and tests). The stratigraphic ranges of taxa (thicker lines) are those shown in Supplementary Methods); asterisks mark taxa whose ranges extend beyond the Frasnian. Chronostratigraphy based on Cohen et al. (2013).

reversals or missing data in some members of the clade): roughly spherical sporangia (character 20) and sporangia irregularly arranged along axes (character 33).

2.3.2 Bayesian analyses

Analyses of the dataset in a Bayesian framework obtain low resolution. The 50% majority rule consensus tree of the FTS analysis (Supplementary Fig. B.1, p.174) separates the euphyllophytes from the broad Lycophytina clade and within the latter, which is highly polytomic, a few of the clades are supported that are also recovered in the parsimony-constrained trees: the lycopsids, the Barinophytaceae+*Bathurstia*, *Oricilla*+*Tarella* and *Adoketophyton*+*Demersatheca*. Bayesian analyses of the matrix with taxon exclusion obtain the same majority rule consensus tree as the FTS analysis.

The all compatible group (allcompat) tree computed based on the results of the GGE Bayesian

analysis also separates the euphyllophytes from the Lycophytina (Fig. 2.2 right). This tree supports the same Sawdoniaceae clade as the parsimony-constrained GGE analysis sister to the lycopsids (Fig. 2.2 left), but the remaining members of the Lycophytina are recovered in relationships incongruent with those supported by the parsimony-constrained GGE analysis (Fig. 2.2).

2.3.3 Phylogenetic congruence, taxon stability and cohorts of phylogenetic divergence

The relationships supported by the GGE parsimony analysis and those supported by the corresponding Bayesian analysis (as reflected in the Bayesian allcompat tree) have a moderate-to-low level of mutual congruence: only 43.6% (17 out of 39) of the nodes counted starting with (and including) the divergence of euphyllophytes from Lycophytina are supported in both trees (Fig. 2.2). The most notable points of congruence are the unequivocal separation of euphyllophytes and Lycophytina (also supported in the strict consensus trees of all Bayesian analyses) and the relationships between lycopsids and Sawdoniaceae.

Taxon stability (TS), as reflected by the ranks of the nodes at which a taxon diverges in the parsimony-constrained vs Bayesian analysis (Table 2.1), varies from very stable taxa – TS < 1 (*Anisophyton*, *Trichopherophyton*, *Baoyinia*, *Sawdonia*, *Oricilla+Tarella*, *Sichuania*, *Discalis+Gumuia*, *Ventarura*, *Adoketophyton+Demersatheca*, *Bathurstia*, Barinophytaceae and lycopsids) – to the most unstable taxa – TS ≥ 2.5 (*Guangnania*, *Gosslingia+Thrinkophyton*, *Craswallia*, *Zosterophyllum*, *Ramoferis*, *Wenshania* and *Xitunia*) (Table 2.1). Other stable taxa (1 ≤ TS < 1.5) include *Margophyton*, *Crenaticaulis*, *Forania*, *Konioria+Odonax* and *Euthursophyton*, whereas less stable taxa (1.5 ≤ TS < 2.5) include *Macivera*, *Hicklingia+Ornicephalum*, *Deheubarthia*, *Serrulacaulis* and *Distichophytum*. The most stable taxa are *Anisophyton* (TS = 0) and *Trichopherophyton* (TS = 0.07) and the most unstable taxa (TS > 4) are *Xitunia* and *Wenshania*.

Three cohorts of phylogenetic divergence were easily separated using the taxon divergence rank graph (Fig. 2.4). The highest cohort, comprising the most derived taxa includes *Anisophyton*, *Margophyton*, *Crenaticaulis* and *Deheubarthia* as the top diverging taxa, as well as *Serrulacaulis*, *Forania*, *Oricilla+Tarella*, *Sawdonia*, *Euthursophyton* and *Konioria+Odonax*; *Gosslin-*

Table 2.1: Rank of node of divergence and stability of taxa included in the GGE analyses, based on the single most parsimonious tree (MP) and the maximum clade credibility tree resulting from the Bayesian analysis (allcompat); see Fig. 2.2 for the numbering of node ranks. The third column (MP norm/13) represents ranks of the nodes of divergence in the MP tree normalized to the same total number of nodes as the Bayesian tree (see text). Taxon stability is the positive value of the difference between MP norm/13 and allcompat.

Taxon	MP	MP norm/13	allcompat	Taxon stability
Adoketophyton-Demersatheca	6	5.20	6	0.80
Anisophyton	15	13.00	13	0.00
Baoyinia	3	2.60	3	0.40
Barinophytes	9	7.80	7	0.80
Bathurstia	9	7.80	7	0.80
Craswallia	5	4.33	1	3.33
Crenaticaulis	14	12.13	11	1.13
Deheubarthia	13	11.27	13	1.73
Discalis Gumuia	5	4.33	5	0.67
Distichophytum	6	5.20	3	2.20
Euthursophyton	11	9.53	11	1.47
Forania	13	11.27	10	1.27
Gosslingia-Thrinkophyton	14	12.13	9	3.13
Guangnania	4	3.47	6	2.53
Hicklingia-Ornicephalum	5	4.33	6	1.67
Konioria-Odonax	11	9.53	11	1.47
Lycopsids	9	7.80	7	0.80
Macivera	4	3.47	5	1.53
Margophyton	15	13.00	12	1.00
Oricilla-Tarella	12	10.40	10	0.40
Ramoferis	4	3.47	7	3.53
Sawdonia	12	10.40	10	0.40
Serrulacaulis	14	12.13	10	2.13
Sichuania	5	4.33	5	0.67
Trichopherophyton	7	6.07	6	0.07
Ventarura	6	5.20	6	0.80
Wenshania	2	1.73	6	4.27
Xitunia	3	2.60	7	4.40
Zosterophyllum myretonianum	3	2.60	6	3.40

gia+Thrinkophyton, despite their significant phylogenetic instability, are also undeniably part of the most derived cohort (Fig. 2.4). At the opposite end of the sequence of phylogenetic divergence, the lowest cohort includes many of the most phylogenetically unstable taxa; *Discalis+Gumuia*, *Sichuania*, *Macivera*, *Distichophytum* and *Baoyinia*; *Craswallia* is also undeniably part of the lowest cohort, despite its significant phylogenetic instability. Other unstable taxa have ranges that cross into that of the median cohort of divergence but span mostly in that of the lowest cohort - *Wenshania*, *Zosterophyllum* and *Guangnania*. On the other hand, the ranges of *Xitunia* and *Ramoferis* span almost equally into the lowest and median cohorts, so they cannot be assigned to either cohort unequivocally. *Hicklingia+Ornicephalum*, a stable clade, also spans into both the lowest and median cohorts (Fig. 2.4) and is associated with the former only because of its lower position of divergence in the parsimony-constrained analysis. Finally, the median cohort comprises a lower diverging subgroup (*Ventarura*, *Adoketophyton+Demersatheca* and *Trichopherophyton*) and a higher diverging subgroup (*Bathurstia*, Barinophytaceae and lycopsids) (Fig. 2.4).

Both the highest and lowest cohort include taxa of widely variable stability (from very stable to very unstable; Fig. 2.2, 2.4), suggesting there is no strong correlation between the phylogenetic stability of a taxon and its cohort of phylogenetic divergence. Nevertheless, all the taxa of the middle cohort have very high stability (TS < 1) and most of the taxa in the highest cohort are stable to very stable phylogenetically (TS < 1.5). Conversely, the lowest cohort includes the highest proportion of unstable taxa. Correspondingly, the taxa of the highest cohort maintain the same phylogenetic relationships in the parsimony and Bayesian analyses (Fig. 2.2) and so do lycopsids, which are among the higher-diverging group of the median cohort, whereas the less phylogenetically stable taxa of the lowest cohort are recovered in different relationships in the parsimony vs Bayesian analyses (Fig. 2.2).

2.3.4 Ancestral character state reconstruction

Apical circination of axes is reconstructed as present in the Sawdoniaceae ancestor and absent ancestrally in Lycophytina and all its other major clades; its ancestral state is equivocal in the Barinophytaceae and in the clade that the latter form with *Bathurstia* (Table 2.2, Fig. 2.5 left).

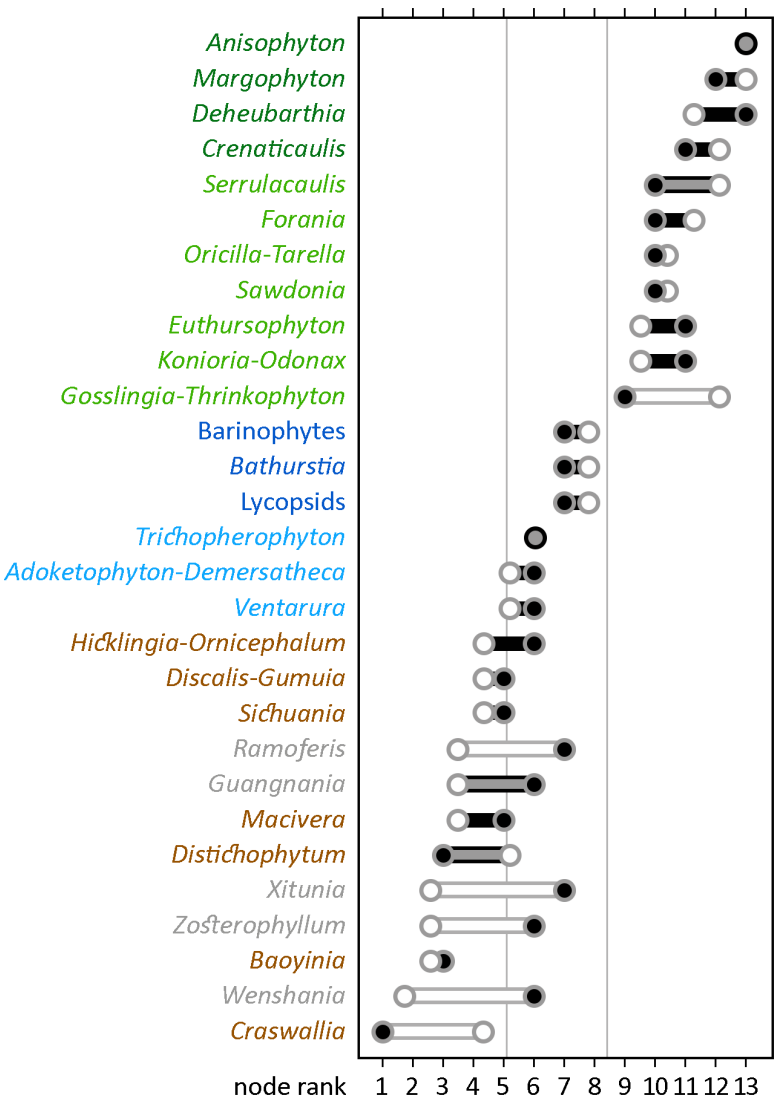


Figure 2.4: Taxon stability and cohorts of phylogenetic divergence. Taxa are organized in increasing order of the ranges of their nodes of divergence in the maximum parsimony and Bayesian GGE analyses (see Fig. 2.2 for node rank numbering); node ranks on the x-axis. Ranges of the nodes of divergence are defined by the node of divergence in the parsimony analysis (white circles) and the node of divergence in the Bayesian allcompat tree (black circles) (see Table 2.1); gray circles indicate same node rank in both parsimony and Bayesian tree. Black range bars (and gray circles) indicate taxa with high phylogenetic stability; gray bars denote less stable taxa; white bars indicate unstable taxa. The two vertical lines separate the three cohorts of phylogenetic divergence also indicated by the color of the taxon names (see also Fig. 2.2): green – highest diverging taxa (higher diverging subgroup in dark green, lower subgroup in light green); blue – middle cohort (higher diverging subgroup in dark blue, lower subgroup in light blue); brown – lowest diverging cohort; gray – lycophytes not assignable to a cohort due to high instability.

Table 2.2: Summary of ancestral character state reconstruction analysis. SBLC = Small Basal Lycophytina Clade; LBLC = Large Basal Lycophytina Clade (see Fig. 2.1).

Clade	**Apical circination of axes** (ch. 6)	**Sporangium arrangement along axes** (ch. 33 and 34)	**Sporangium shape** (ch. 20)	**Sporangium valve size** (ch. 25)
Lycophytina	Absent	Not in rows (irregular or helical)	Reniform	Isovalvate
SBLC	Absent	Not in rows (irregular or helical)	Reniform	Isovalvate
LBLC	Absent	Always two-rowed	Reniform	Isovalvate
Barinophytaceae	Unknown	Always two-rowed	Lenticular, vertically flattened	Unknown
Sawdoniaceae	Present	Always two-rowed	Reniform	Isovalvate
Lycopsida	Absent	Not in rows (irregular or helical)	Reniform	Isovalvate

Sporangium arrangement along the axes is reconstructed as ancestrally irregular (i.e., not in rows) in Lycophytina and in the SBLC, and is also not ancestrally rowed in the lycopsids (Table 2.2, Fig. 2.5 right). The arrangement is ancestrally two-rowed in the LBLC, although it is either irregular or not necessarily two-rowed in most members of this clade. Within this clade, the Barinophytaceae and Barinophytaceae+*Bathurstia*, as well as the Sawdoniaceae are reconstructed as ancestrally possessing two-rowed sporangia, although the ancestral state is reversed in most members of the latter. Sporangium shape is reconstructed as ancestrally reniform in Lycophytina and all its major clades, except for the Barinophytaceae, in which the ancestor is reconstructed with vertically flattened lenticular sporangia like those of the three representatives of the group (Table 2.2, Fig. 2.6 left). Finally, sporangia are reconstructed as ancestrally isovalvate all across Lycophytina (Table 2.2, Fig. 2.6 right). The one exception is Barinophytaceae+*Bathurstia*, in which the ancestral state is equivocal, although this is probably an artifact of the particular shape of barinophyte sporangia, for which relative valve size could not be scored.

2.3.5 Stratigraphic fit

Of the six most parsimonious trees recovered in the FTS analysis, the tree with best stratigraphic fit based on multiple measures is tree 6 (Supplementary Table B.2). Since different groups are supported within Lycophytina, I integrated the stratigraphic information of the taxa (Supple-

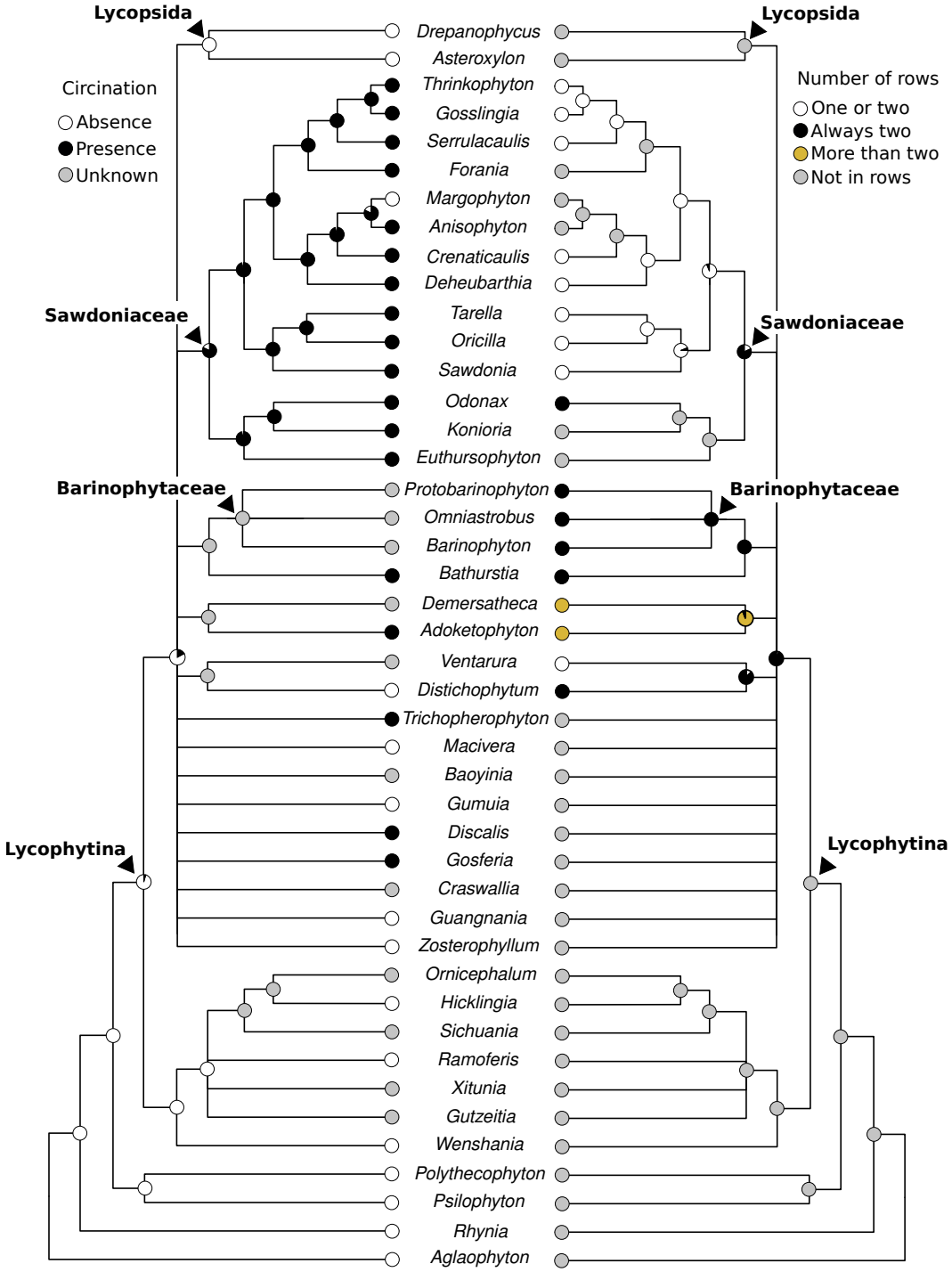


Figure 2.5: Ancestral character state reconstruction for characters 6 (presence/absence of apical circination) and 34 (sporangium arrangement in rows) based on the strict consensus topology of the full taxon sampling (FTS) analysis.

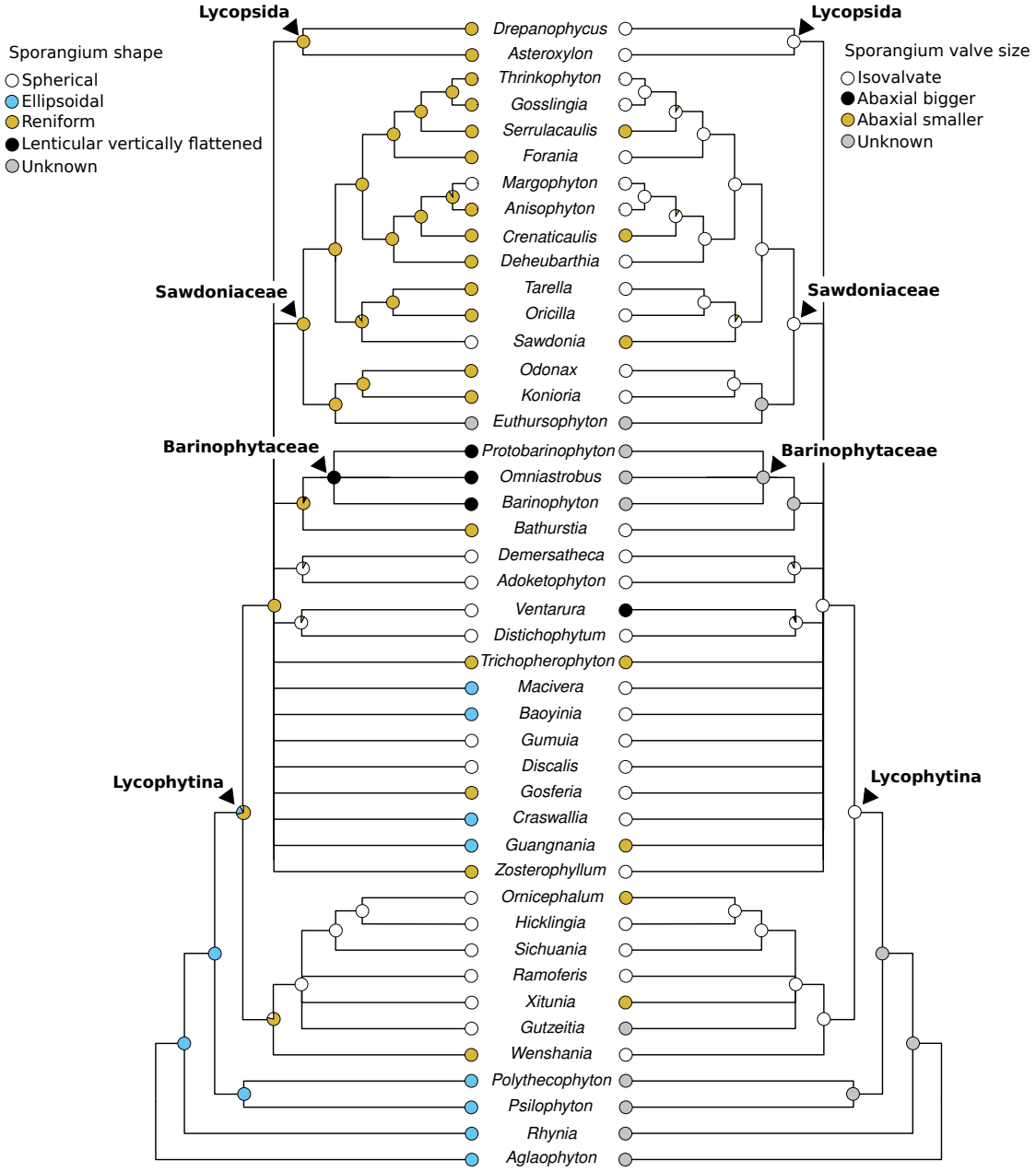


Figure 2.6: Ancestral character state reconstruction for characters 20 (sporangium shape) and 25 (sporangium valve size) based on the strict consensus topology of the full taxon sampling (FTS) analysis.

mentary Methods) with the topology of this tree to obtain a better image of their evolutionary relationships and history over time (Fig. 2.3).

2.4 Discussion

2.4.1 The pattern of relationships among lycophytes: past and present

Phylogenetic resolution and relationships supported by the analyses.

The low resolution of the consensus trees produced by the full taxon sampling analyses (both parsimony-constrained and Bayesian; Fig. 2.1, Supplementary Fig. B.1) has as causes the same conditions – discussed by numerous authors – that affect the datasets of most phylogenetic analyses that include significant proportions of fossils. One of these conditions is usually incomplete preservation of fossils that allow, as a result, the scoring of only subsets of the total set of characters constructed for the analysis: some fossils preserve only morphology, others preserve anatomy but little of the gross morphology can be reconstructed. Another major impediment is the uneven temporal sampling allowed by the uneven stratigraphic distribution of fossil localities. As a result, this sampling covers better the Pragian and Emsian ages (Fig. 2.3), but there is a dearth of sedimentary deposits from terrestrial environments representing the preceding intervals, especially the Silurian, which causes a lack of data (Capel, Monnet, et al., 2023). The missing data of these less derived taxa hinders the understanding of the group evolution, since we are forced to extrapolate the basal morphology based on the known information. Last, but not least is the adverse effect of the dearth of morphological characters, which is amplified in the case of plants with simple morphology, like the early tracheophytes with simple sporophytes consisting of undifferentiated photosynthetic axes.

Given the above factors, which produced a matrix (i) in which the number of taxa surpasses that of the characters; (ii) that has a moderate amount of missing data (20%); and (iii) that samples unevenly the stratigraphic interval of the groups of interest, the amount of resolution recovered in the strict consensus of the parsimony-constrained analysis is notable. In a parsimony-constrained context this set of characters separates unequivocally the euphyllophytes from the lycophytes (Lycophytina), it separates the latter into two major clades, and within one of the two clades it

separates the lycopsids, Barinophytaceae+*Bathurstia*, and the Sawdoniaceae (Fig. 2.1).

Also notable is the fact that the consensus tree of the Bayesian analysis (Supplementary Fig. B.1) also separates the euphyllophytes from the lycophytes and, within the latter, it supports as clades the lycopsids and Barinophytaceae+*Bathurstia*. Moreover, while the Bayesian consensus topology does not recover a well-supported Sawdoniaceae, the Bayesian maximum clade credibility tree (Fig. 2.2 right) supports a Sawdoniaceae clade with the same membership as that supported by the parsimony-constrained analyses. However, Bayesian majority rule consensus trees tend to present low resolution with morphology-only datasets (O'Reilly & Donoghue, 2018), like those addressing exclusively fossils (Toledo et al., 2021). For this reason and because all the previous studies addressing zosterophyll phylogeny employed parsimony-constrained tree searches, I will limit the discussion and comparisons of phylogenetic relationships below to those supported by the phylogeny-constrained analyses.

More remarkable is the fact that exclusion of only two terminals (*Gosferia* and *Gutzeitia*), which results in a "square" matrix, leads to a fully resolved topology (Fig. 2.2 left). In fact, analysis of the alternative placements of the two "wildcard" terminals (see below) shows that only one of them – *Gosferia* – is responsible for the lower level of resolution. Thus, the present dataset supports an unexpected level of phylogenetic resolution for the densest sampling of zosterophylls and allied taxa to date, which is especially notable given the structure of the dataset.

Comparison with previous studies

Placement of the lycopsids nested within a broader clade (termed here the Lycophytina, following Kenrick and Crane (1997)) that includes all the zosterophylls, supported by the results, is in accord with previous results or predictions made by several authors, e.g., (Gensel, 1992; Kenrick & Crane, 1997; Crepet & Niklas, 2019). The placement of the Barinophytaceae nested within Lycophytina (specifically, within a sub-clade of the latter) is also congruent with the results of Kenrick and Crane (1997) (Fig. 2.7). In contrast to this pattern of relationships, Hao and Xue (2013) have found support for a monophyletic clade of zosterophylls (Zosterophyllopsida) that excludes the lycopsids and the barinophytes, whether represented by *Barinophyton* or *Adoketophyton*. In their results, lycopsids and *Barinophyton* are recovered in a clade that is sister to the

clade that includes the zosterophylls. *Adoketophyton*, recovered as sister to Zosterophyllopsida by Hao and Xue (2013), is nested deeply among zosterophylls (sister to *Demersatheca*) in this analysis, a placement not entirely incongruent with its position in Kenrick and Crane's analysis.

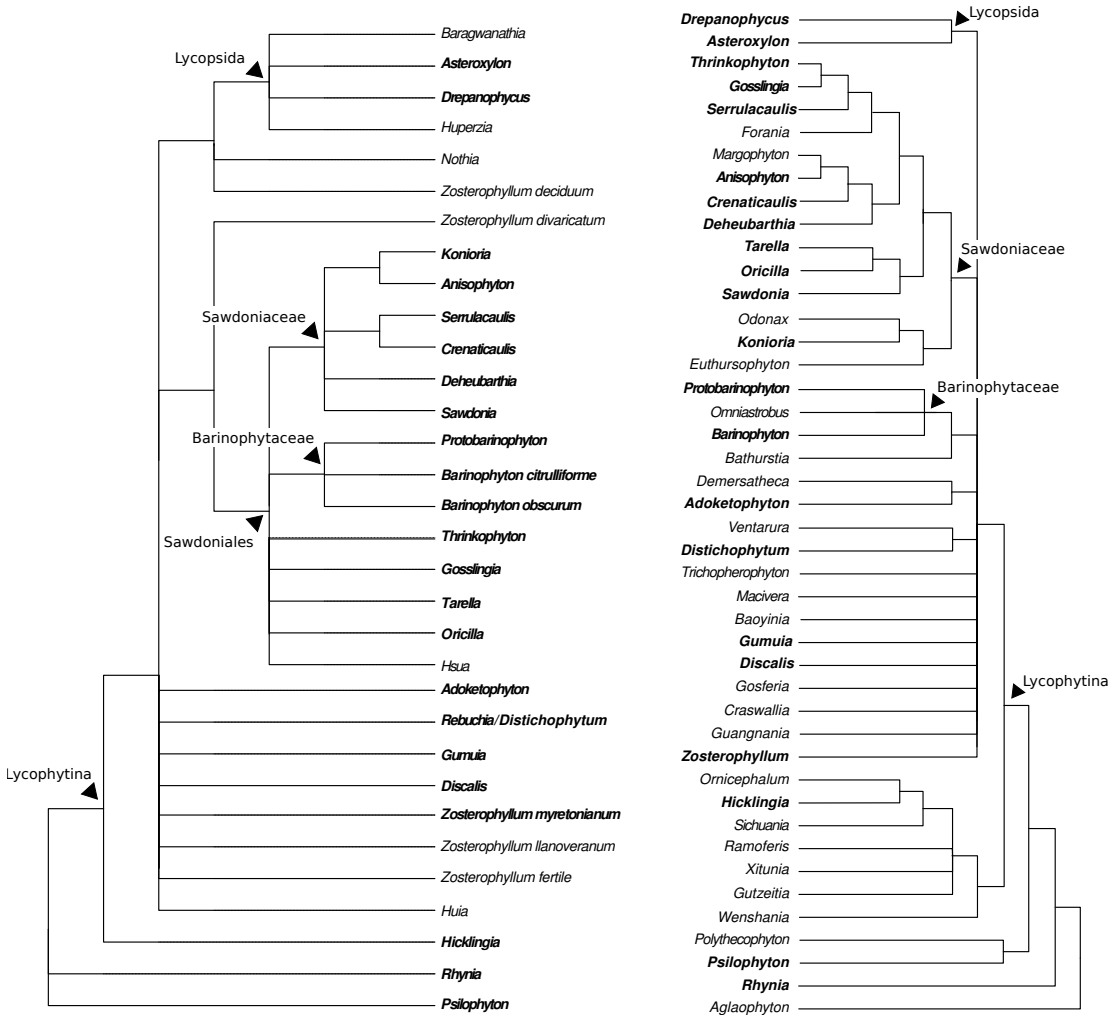


Figure 2.7: Comparison of topology between strict consensus topologies supported by full taxon sampling (FTS) analysis (right) and analysis 5.1 by Kenrick and Crane (1997); fig. 5.25) (left; clade names same as in the original figure). Taxa in boldface are those common to the two analyses.

The Sawdoniaceae clade supported in these analyses includes all the taxa included in the Sawdoniaceae of Kenrick and Crane (1997) (Fig. 2.7), as well as in polytomic crown clade consistently recovered under different tree rooting and taxon sampling schemes by Nibbelink and Tomescu (2022). Beyond the overall similarity with Kenrick and Crane's results, we note differences in the

relationships of different taxa. *Anisophyton* is recovered sister to *Margophyton* and not to *Konioria*, which is included in a different sub-clade. While *Crenaticaulis* and *Serrulacaulis* are recovered in sister clades within Sawdoniaceae, echoing their sister group relationship in Kenrick and Crane's results, the former is more closely related to *Anisophyton* and *Margophyton* in these analyses. *Oricilla* and *Tarella*, included by Kenrick and Crane in an unresolved "Gosslingiaceae" group that is not directly related to the Sawdoniaceae, are nested in this analysis well within a clade that includes other members of Kenrick and Crane's Sawdoniaceae, wherein they form a clade sister to *Sawdonia*.

The differences between the present results and those of Kenrick and Crane (1997) may derive from (i) differences in the characters used; (ii) differences in the scoring of some characters due to different interpretation of fossil features or additional data generated on some of the taxa in post-1997 studies; or (iii) the inclusion of additional taxa that may alter the polarization of characters. Irrespective of what causes the differences, it is important to note that in this case, Sawdoniaceae include all the zosterophyll taxa recovered by Kenrick and Crane in their Sawdoniales clade (Fig. 2.7). While Kenrick and Crane's Sawdoniales also include the Barinophytaceae clade, the latter are part of the basal polytomy of the clade in the strict consensus tree. This pattern of relationships indicates that in some of the 18,500 most parsimonious trees found by Kenrick and Crane the Sawdoniales clades has a basal split between the Barinophytaceae and a clade whose members are all included in our Sawdoniaceae. Thus, the similarity between the present results and those of Kenrick and Crane (1997) is deeper than suggested by differences between the placement of individual taxa. The main difference between the two analyses is that whereas Kenrick and Crane's allows for sister-group relationship between Barinophytaceae and the remaining Sawdoniales (all of which are included in our Sawdoniaceae), with the lycopsids only distantly related to either of the two clades, the present analyses provide strongest support for lycopsids sister to the Sawdoniaceae and forming a clade that is sister to the Barinophytaceae.

Another noteworthy result in the context of previous zosterophyll phylogenies is the placement of *Hicklingia* in the SBLC (Fig. 2.7). *Hicklingia* was recovered as sister to all the other lycophytes by Kenrick and Crane (1997), in apparent contrast to its placement in the analysis. However, when considering that all the other five species included in the SBLC with *Hicklingia* were discovered or revised taxonomically post-1996, the congruence between the two placements

becomes obvious.

Zosterophyllum the eponym genus of the group studied here and its first representatives to be discovered (Penhallow, 1892), covers significant stratigraphic and geographic ranges among its ca. 31 species. Although this study does not directly address the relationships among all these species, the results are consistent with the polyphyletic status of genus *Zosterophyllum* demonstrated by the analyses of Kenrick and Crane (1997). Specifically, *Demersatheca*, *Gutzeitia* and *Ornicephalum*, three genera based on species segregated from, or placed at some point in, *Zosterophyllum* (C.-S. Li & Edwards, 1996; Snigirevsky et al., 2007; D. Edwards & Li, 2018a), are scattered across the trees (Fig. 2.1, 2.2 left) instead of being grouped together. Phylogenetic studies that address directly the relationships between different species of *Zosterophyllum* and closely allied taxa are needed to clarify the taxonomy of this iconic taxon and its evolutionary relationships.

Unstable taxa

Taxon exclusion experiments demonstrated that *Gutzeitia* (Snigirevsky et al., 2007) and *Gosferia* (Gerrienne, 1991a, 1999) are the two terminals that lower the phylogenetic resolution obtainable from the dataset. Although both these genera have relatively high amounts of missing data, neither of them has the highest amount. This suggests that their impact on resolution is more likely due to their specific combinations of characters.

Among the six most parsimonious tree recovered in the FTS analysis, *Gutzeitia* oscillates between only two placements, both of them located in the small basal clade of Lycophytina (SBLC). Thus, rather than impacting heavily phylogenetic resolution across broad areas of the phylogeny, *Gutzeitia* only affects resolution of the SBLC. There, *Gutzeitia* is either sister to *Xitunia* or to *Ramoferis*, the latter being the placement supported in the tree with the best stratigraphic fit (Fig. 2.3).

Gosferia has a much more dramatic impact on overall tree resolution, despite the fact that it has a smaller amount of missing data than *Gutzeitia* and that it, too, only oscillates between only two alternative placements. The main point of difference between the effect of the two genera and the cause of the higher impact of *Gosferia* is that its two alternative placements are distant phylogenetically, in two different major clades of Lycophytina, but neither is supported by

multiple synapomorphies. One of the placements is as sister to the lycopsid clade, a relationship supported only by the proportions of sporangial stalks (longer than they are wide). The other placement is as sister to *Discalis*, a relationship supported by the absolute length of sporangial stalks and by circination, which is only putatively present in the axes of *Gosferia* (but the long sporangial stalks are coiled). The highly unstable position of this genus is consistent with both its highly fragmentary state (it is known from very few, small axis fragments that exhibit no branching and the largest of which holds only two sporangia) and its unusual characters (the sporangia are borne on long, filiform, coiled stalks). Nevertheless, it is worth noting that while phylogenetically remote, *Discalis* and the lycopsid clade are not quite as far apart in terms of how phylogenetically derived they are (Fig. 2.4) and this may be related in some way to the specific placements between which *Gosferia* oscillates. In the end, placement of *Gosferia* as sister to *Discalis* has better support, as the tree with the best stratigraphic fit (Fig. 2.3) features this placement, which is also consistent with Gerrienne's hypothesis on its taxonomic affinities discussed in the original description (Gerrienne, 1991a).

An updated perspective on relationships among lycophytes

The main result regarding phylogenetic relationships among lycophytes is that the dataset developed here produced, under parsimony constraints, a fully resolved tree that includes the broadest sampling of currently recognized zosterophylls to date (Fig. 2.2 left). This tree reiterates the main aspects of the overall pattern of relationships supported in the consensus of the full taxon sampling analysis: lycophyte monophyly with basal dichotomy into two major clades, the larger of which (LBLC) includes a Sawdoniaceae clade, a Barinophytaceae+*Bathurstia* clade and a lycopsid clade. The fully resolved tree adds another layer of detail beyond this general pattern of relationships, supporting a sister group relationship between Sawdoniaceae and lycopsids, with the clade formed by the two sister to Barinophytaceae+*Bathurstia* and the remaining zosterophylls forming a grade paraphyletic to the Barinophytaceae+*Bathurstia* and Sawdoniaceae+lycopsids clade.

Another notable result is that the overall pattern of relationships supported by the parsimony-constrained analyses is overall more similar to, and supports some of the implications of Kenrick and Crane (1997) results, despite a different taxon sampling and a different (although partially

overlapping) set of characters that were scored anew based on published descriptions and illustrations, independent of previous studies.

In a more conservative interpretation of the results, we can look at the topologies supported by the Bayesian analyses, drawing parallels with those supported by the parsimony-constrained analyses. I acknowledge the moderate-to-low level of congruence in topologies. Even under this more conservative perspective, recovery of the same Sawdoniaceae clade (same membership) and its sister group relationship to the lycopsids provides the strongest support to date for this pattern of relationships, despite differences in other respects between the results of the two tree-search methods.

In a most conservative perspective, inspired by the parsimony vs Bayesian comparison, the results can be assessed independently of the specific topologies supported by the two tree-search methods. In this perspective, a relative order (cohorts) of phylogenetic divergence is still identifiable that provides a rough idea of how derived a taxon is. While not all the taxa can be assessed from this perspective (due to their differing degrees of stability), we identify among the most derived taxa the members of the Sawdoniaceae, the lycopsids, the Barinophytaceae and *Bathurstia*, and among the least derived taxa *Craswallia*, *Baoyinia*, *Distichophytum*, *Macivera*, *Sichuania*, *Discalis* and *Gumuia*.

2.4.2 Zosterophylls and lycophytes: taxonomy in the light of phylogenetic relationships

Previous taxonomic schemes

Since Banks (1968) initial classification, zosterophylls, lycopsids and lycophytes have been included in multiple classification schemes. In Banks' classification, of early vascular plants, zosterophylls are placed in Subdivision Zosterophyllophytina of Division Tracheophyta (Table 2.3). Banks separated the zosterophylls from the lycopsids, which he placed in their own subdivision, Lycophytina. Subsequently, based on the six genera included in the group at the time, Banks (1975) listed as defining characters of Zosterophyllophytina: leafless axes with isotomous to pseudomonopodial branching, laterally borne sporangia with distal line of dehiscence and central primary xylem strand with exarch maturation, consisting of tracheids with scalariform

thickenings. Banks' classification was maintained as the number of species and genera discovered increased; Gensel (1992), for instance, mentioned 18 zosterophyll genera, of which she included seven in a phylogenetic analysis. Nevertheless, addition of new genera broaden the range of morphologies included in the group and showed that the wall thickenings of tracheids formed a very specific pattern, documented initially in *Gosslingia* (Kenrick & Edwards, 1988b) and termed G-type thickenings (Kenrick & Crane, 1997).

Studies	Zosterophylls	Zosterophyll membership included	Lycopsids	Zosterophyll-lycopsid relationships
Banks (1968, 1975)	Subdivision Zosterophyllophytina	6 genera	Subdivision Lycophytina	lycopsids hypothesized as evolved from zosterophyll ancestor (zosterophylls form grade paraphyletic to lycopsid clade)
Gensel (1992)	equated with Subdivision Zosterophyllophytina Banks	18 genera (7 included in phylogeny)	lycopsids	zosterophylls form grade paraphyletic to lycopsid clade
Kenrick and Crane (1997)	Plesion Zosterophyllopsida (=Zosterophyllaceae) clade + Plesion -*Z. myretonianum* + other taxa; relationships poorly resolved	23 species included in phylogeny (12 in Zosterophyllopsida, along with Barinophytaceae)	Class Lycopsida (=Lycophyceae)	zosterophylls polyphyletic, part of grade paraphyletic to lycopsid clade; together included in Subdivision Lycophytina (clade)
Hao and Xue (2013)	Zosterophyllopsida clade	8 species (6 genera) included in phylogeny	Lycopsida clade	zosterophylls form with *Adoketophyton* a clade that is sister to clade that includes lycopsid clade and euphyllophyte clade
Gerrienne et al. (2016)	Zosterophyllopsida lineage (i.e., implied clade)	not listed	Lycopsida lineage (i.e., implied clade)	not explicitly discussed; zosterophylls and lycopsids are considered separate lineages within a clade Lycophytina sensu Kenrick and Crane (1997)

Studies	Zosterophylls	Zosterophyll membership included	Lycopsids	Zosterophyll-lycopsid relationships
Nibbelink and Tomescu (2022)	zosterophylls	19 species (18 genera) included in phylogeny	lycopsids	zosterophylls form grade paraphyletic to lycopsids
This study	zosterophylls	33 genera included in phylogeny	lycopsids (= Class Lycopsida)	zosterophylls form grade paraphyletic to lycopsids; together included in Subdivision Lycophytina (clade)

Table 2.3: Taxonomy and relationships of zosterophylls and lycopsids in this and previous studies.

Using a phylogenetic framework in their influential study that included at that time 23 species of unequivocal or putative zosterophyll affinity, Kenrick and Crane (1997) concluded that these did not form a coherent group. Thus, in their classification scheme, some of the taxa recognizable as zosterophylls using Banks' criteria are included in a clade (termed Plesion Zosterophyllopsida or Zosterophyllaceae), while others, excluded from that clade, are members of the more inclusive clade – Subdivision Lycophytina of Division Tracheophyta – but with poorly resolved relationships to each other and to the Zosterophyllopsida. Overall, Kenrick and Crane's analysis supports a polyphyletic status of zosterophylls as a whole (Table 2.3).

For Zosterophyllopsida, Kenrick and Crane list as synapomorphies circinate apical development, two-rowed arrangement of the laterally attached sporangia and, putatively, elliptical cross-sectional shape of the xylem. Additionally, zosterophyllopsids share with all other members of Lycophytina the following synapomorphies: exarch xylem maturation, reniform, dorsiventral isovalvate sporangia borne laterally along axes on short stalks, with distal dehiscence line featuring conspicuous cellular thickening.

Gerrienne et al. (2016), in their phylogenetically framed taxonomic compilation, followed broadly Kenrick and Crane (1997) classification scheme. However, in their view, the Lycophytina, circumscribed by the same synapomorphies, is split strictly into two lineages (Table 2.3), Lycopsida and Zosterophyllopsida, the latter characterized by circinate growth and two-rowed arrangement of sporangia. Although not explicitly stated, this classification scheme implies that, contrary to Kenrick and Crane's findings, all non-lycopsid lycophytes form a clade (Zosterophyllopsida) sister to the Lycopsida.

In a phylogenetic treatment of the diverse Pragian Posongchong flora of China, Hao and Xue (2013) recovered the eight zosterophyll species (representing six genera) included in the analysis as a clade called Zosterophyllopsida sister to *Adoketophyton* (Table 2.3), with which they share circinate apical development and tracheids with wall microperforations between scalariform thickenings (like those of G-type tracheids). The synapomorphies of Zosterophyllopsida include a rowed arrangement of sporangia along axes and elliptical or strap-shaped cross section of xylem that has exarch maturation and consists of tracheids with G-type wall thickenings. Hao and Xue's results do not support a Lycophytina clade.

In summarizing the relationships between zosterophylls, lycopsids and lycophytes, the dif-

ferent taxonomic schemes explicitly or implicitly involve two major patterns. In one of these patterns of relationships, zosterophylls form, or are part of, a grade paraphyletic to the lycopsids. The first pattern of relationships is implied in Banks (1968) evolutionary hypothesis, wherein lycopsids (termed Lycophytina) arise from among a zosterophyll (Zosterophyllophytina) plexus, and is supported by the results of Gensel (1992) and Nibbelink and Tomescu (2022) (Table 2.3). Similar but not equivalent to this pattern of relationships, Kenrick and Crane (1997) Lycophytina clade consists of a grade paraphyletic to the lycopsids (Lycopsida); within this grade, zosterophylls are polyphyletic and only a subset of them form a clade (Zosterophyllopsida) (Table 2.3). In the other major pattern of relationships, zosterophylls form a clade. This pattern is supported by the analyses of Hao and Xue (2013), wherein the clade formed by zosterophylls (Zosterophyllopsida) is sister to a clade that includes the lycopsid clade (Lycopsida) and the euphyllophyte clade (Table 2.3); this pattern of relationships does not support a grouping of zosterophylls and lycopsids such as Kenrick and Crane (1997) Lycophytina clade. A zosterophyll clade is also implied by Gerrienne et al. (2016) sister-group relationship between the Zosterophyllopsida and Lycopsida lineages within a more inclusive Lycophytina clade.

Updated perspective

Zosterophylls are polyphyletic and part of a grade (that also includes the barinophytes+*Bathurstia* clade) paraphyletic to the lycopsid clade, within a more inclusive Lycophytina clade (Table 2.3), consistent with the results of Kenrick and Crane (1997) and Nibbelink and Tomescu (2022). This cements the position of lycopsids as crown-group Lycophytina, with zosterophylls defining the stem of the clade. The synapomorphies supporting Lycophytina – laterally attached sporangia with bilateral symmetry and dehiscence along their distal margin – are also listed as synapomorphies for the clade by Kenrick and Crane (1997) (with bilateral symmetry reflected in their sporangium dorsiventrality). Other synapomorphies listed by Kenrick and Crane – exarch xylem maturation, short-stalked sporangia and conspicuous cellular thickening of the sporangium dehiscence line – are not supported as synapomorphic by these results. Nevertheless, two of those – the reniform isovalvate morphology of sporangia – are predicted as present in the Lycophytina ancestor by ancestral character stare reconstruction (Table 2.2, Fig. 2.6).

Lycopsids, defined by the possession of leaves and a lobed protostele (actinostele), are

consistently found nested among zosterophylls and their position as sister to Sawdoniaceae is well supported. This phylogenetic position can inform hypotheses on the evolution of their defining features.

The Sawdoniaceae, themselves a well supported clade, regroup almost all the zosterophylls traditionally used and grouped together in previous analyses. They share with Kenrick and Crane (1997) Sawdoniaceae the spinescent emergences as a synapomorphy. However, in contrast to their Sawdoniaceae, ours are defined by three other synapomorphies and zosterophyll membership of the clade is broader than that of Kenrick and Crane's Sawdoniaceae, overlapping much more closely with their Sawdoniales (Fig. 2.7). Despite this similarity in membership, Kenrick and Crane's Sawdoniales clade also includes the barinophytes, alongside zosterophylls, and is supported by three synapomorphic characters that are not synapomorphies for any of the clades recovered in our analyses. In this context it is notable that two other synapomorphies of our Sawdoniaceae – circinate axis tips and xylem with elliptical cross-sectional shape – are considered synapomorphic by Kenrick and Crane (1997) for the Zosterophyllopsida, a clade almost synonymous to their Sawdoniales, as it only includes one species of *Zosterophyllum* alongside the latter (Fig. 2.7). Additionally, another synapomorphy of Kenrick and Crane's Zosterophyllopsida – two-rowed arrangement of sporangia – although not a synapomorphy of our Sawdoniaceae, is predicted as ancestral for that clade (as well as for the more inclusive LBLC; Table 2.2, Fig. 2.5 right).

In a nomenclatural perspective, our use of Sawdoniaceae is justified by three observations. First, the clade designated by us as Sawdoniaceae is more similar in its zosterophyll membership to Kenrick and Crane (1997) Sawdoniales instead of their Sawdoniaceae. Second, our Sawdoniaceae is also more similar in synapomorphies to their even more inclusive Zosterophyllopsida. However, despite the previous two observations, our Sawdoniaceae differs from Kenrick and Crane's Sawdoniales and Zosterophyllopsida in excluding the barinophytes. On the other hand, because in our phylogeny any clade that includes Sawdoniaceae and barinophytes also includes the lycopsids, which are excluded from Kenrick and Crane's Sawdoniales and Zosterophyllopsida, the latter two taxa have no equivalent in our phylogeny. Thus, because of their paraphyletic status, the only way to refer collectively to non-sawdoniacean zosterophylls is as stem-group Lycophytina (stem-group lycophytes).

2.4.3 Evolutionary implications

Tempo of evolution

In a phylogenetic context, the lower limit of the stratigraphic range of a terminal provides a minimum age for the cladogenetic event that gave rise to the least inclusive clade of which that terminal is a member. This line of reasoning, overlaid on the parsimony-constrained pattern of relationships with best stratigraphic fit (Fig. 2.3), provides the best supported reconstruction of evolutionary tempo in the lycophyte clade allowed by the dataset.

This lycophyte clade is closely related to the Euphyllophytes, diverging during the Devonian (Ludfordian). Euphyllophytes are characterized in this study by the presence of paired sporangia, while Lycophytina have as synapomorphies the presence of numerous lateral sporangia, generally bilateral and opening in two valves. Thus, the difference between these two sister groups is based on the reproductive organs. The common ancestor of these groups may therefore display a similar vegetative morphology, with small dichotomous and leafless axes. Given that anisotomy is prevalent in both groups, this may be an ancestral character as well, and the isotomous configuration visible in some zosterophyll taxa may be reversals. Moreover, the sporangial distribution being two independent acquisitions among the descendants (Fig 2.1), the ancestor is interpreted as having single sporangia, at the top of the axis. It is more likely to assume that these sporangia may be radially symmetrical, with a dehiscence along a lateral line. This configuration is similar to the morphologies of plants found during that time period such as *Cooksonia* (Libertín et al., 2018), and is consistent with the close relationship found between the node regrouping Euphyllophytes and Lycophytina, with the one including *Rhynia* (Fig. 2.3).

The age and position of *Macivera* suggest that an initial Silurian radiation gave rise to all the major lycophyte clades during the early Ludlow (Gorstian) or possibly earlier. However, stem lineages in each of those clades may have remained in relative stasis until close to the end of the Silurian, throughout the late Ludlow (Ludfordian) and the Pridoli, as indicated by the Lochkovian age of high-divergent terminals in the small basal clade of Lycophytina (SBLC), in the clade sister to *Macivera*, and also to some extent in the clade that includes *Zosterophyllum* (Fig. 2.3). The later-Silurian (Pridoli) gap in the zosterophyll fossil record means that we don't know what the ancestors of these major clades looked like, other than what we can infer about

them from the terminals engendered by their basal cladogenetic events and from reconstructed ancestral character states (see below).

The stratigraphic distribution of terminals also supports a major evolutionary radiation that gave rise to much of the known genus-level diversity in all the lycophyte clades before the Devonian, in the 6 million-year interval between the end of the Gorstian and the Lochkovian, most likely in the Pridoli. As a part of this major radiation, the ancestor of the lycopsid clade diverged from its zosterophyll sister group, most likely the ancestor of Sawdoniaceae, and the *Bathurstia*+Barinophytaceae clade diverged from the Sawdoniaceae+lycopsids clade (Fig. 2.3). The major end-Silurian diversification episode is succeeded by progressive reduction of diversification rates among zosterophylls. The first 8 million-years of the Devonian (Lochkovian) saw modest diversification within the lycophyte sub-clades (probably including the early barinophyte radiation), with the Pragian witnessing diversification only in a few minor clades across the lycophyte phylogeny, and virtually no diversification after the Pragian, 408 million-years ago.

Cross-validating the best stratigraphic fit topology and cohorts of phylogenetic divergence.

Taxa placed in the lowest diverging cohort (Fig. 2.2, 2.4), which should have arisen in the earliest pulses of diversification, are, indeed, products of early, pre-Devonian (Silurian) radiations. A good example of such congruence between stratigraphic position and membership in the lowest diverging cohort are the taxa of the SBLC (Fig. 2.2, 2.3). However, there are also exceptions: *Craswallia*, *Discalis*, *Gumuia* and *Distichophytum*, which may have arisen from smaller diversification bursts in the Lochkovian or earliest Pragian.

Conversely, most taxa of the highest diverging cohort and the highest-diverging group of the median cohort are products of post-Silurian (Lochkovian and Pragian) diversification pulses. Here, the exceptions are the lycopsid clade and the *Deheubarthia-Crenaticaulis-Anisophyton-Margophyton* clade. This is intriguing, at first glance, because this clade is one of the most highly derived clades of the Sawdoniaceae and, as such, it is also the highest-diverging group among the high-diverging cohort. However, it is important to recognize that this incongruence between phylogenetic topology and cohorts of divergence is generated exclusively by the long and deeply reaching stratigraphic range of *Margophyton*, which is along with *Anisophyton* the most derived terminal in the clade sister to *Deheubarthia* (Fig. 2.3).

The case of *Margophyton* merits further discussion because it is emblematic for the influence of single taxa and, more generally, of the accuracy of taxonomic and stratigraphic data, on the congruence between phylogenetic topology and cohorts of divergence. *Margophyton* is a monotypic genus established in 1981 based on specimens from multiple localities in Russia (Zakharova, 1981). The stratigraphic constraints on the fossil bearing layers were relatively imprecise at the time – Pragian-Emsian for all but one of the localities, which was even less stringently dated as Lower Devonian. The stratigraphic imprecision on the Russian material is compounded by the fact that *Margophyton* was defined by Zakharova as a new genus for transferring fertile specimens that would have otherwise corresponded to the species *Psilophyton goldschmidtii*. The latter was a form-species previously based on vegetative material of morphologically simple early tracheophytes. As such, *P. goldschmidtii* probably represents more than one natural species and possibly multiple higher-order taxa. Moreover. *P. goldschmidtii* has been reported from multiple localities around the world that span the entire Lower Devonian (Zakharova, 1981). Despite these caveats, Zakharova advocated inclusion of all *P. goldschmidtii* material in *Margophyton*, without critical assessment of material previously assigned to the former species. As a result, the taxonomic imprecision introduced by treating all *P. goldschmidtii* specimens as *Margophyton* inflates the stratigraphic range of the latter. Thus, the stratigraphic range of *Margophyton* used in this analysis may well be considerably broader than the real age of the taxon, for instance not reaching as deeply as the basal Devonian. If *Margophyton* was limited to the Russian material described by Zakharova and its age was more tightly constrained, even just as Pragian-Emsian (i.e., like the majority of Zakharova's material), this would still make the minimum age of the *Deheubarthia* node no older than the late Lochkovian, consistent with placement of clade in the highest-diverging cohort (Fig. 2.3). With it, the minimum age of the whole Sawdoniaceae clade, lycopsids, *Bathurstia*+Barinophytaceae and the *Trichopherophyton* node would also be late Lochkovian and consistent with their placement in the respective cohorts of phylogenetic divergence.

Several factors affect the prediction power of the best stratigraphic fit tree, the separation of taxa into cohorts of phylogenetic divergence, or both those analyses and, consequently, the congruence between their results. Such factors include (1) the incompleteness of the fossil record (e.g., the Pridoli gap) and, related to it, the fact that it only provides minimum ages of

cladogenetic events; (2) inconsistencies in the stringency of constraints on stratigraphic position (and thus age range) of some fossils, sometimes associated with (3) taxonomic imprecision due to old or unrevised treatments of taxa (e.g., *Margophyton*); (4) the level of congruence between the topologies supported by the parsimony-constrained vs the Bayesian analysis for the same dataset; and (5) the relatively arbitrary way in which taxa were separated into three cohorts of phylogenetic divergence. Given all these factors potentially biasing either or both the analyses, the level of congruence between the evolutionary tempo supported by the parsimony-constrained topology and the membership of the cohorts of phylogenetic divergence is remarkable.

Results suggest that approaches – like the analysis of cohorts of phylogenetic divergence – that quantify relative sequences of phylogenetic divergence based on comparing more-or-less congruent topologies supported by different methods of phylogenetic inference – e.g., maximum parsimony and Bayesian – but independently of the specific topologies, may hold value. This may be true especially in cases of high incongruence between the results of different methods of inference, where such analyses could at least identify common denominators, such as the cohorts separated in this analysis. So, I encourage further exploration of, and experimentation with, such approaches, both in terms of the metrics used to order the sequences and of the criteria used to separate cohorts, at the same time without abandoning the continued updating and refining of the ages and taxonomy of fossil taxa.

Mode of evolution

The distribution of character on phylogenetic trees states allows for reconstructing aspects of evolutionary mode: in which group certain character states evolved and how or whether they changed subsequently in some regions of that clade. Such inferences are informed by the distribution of character states among terminals, combined with clade synapomorphies and reconstruction of ancestral character states. In this study a conservative approach was favored, choosing to examine these aspects that inform morphological evolution – primarily in terms of evolutionary pattern, but not process – based on the strict consensus tree of the parsimony-constrained analysis with full taxon sampling (Fig. 2.1, 2.5, 2.6).

Results support a reconstruction of the common ancestor of Lycophytina as a late Silurian (pre-Ludfordian) plant with simple axes devoid of apical circination that bore laterally attached

sporangia with irregular arrangement (i.e., not in rows). The lycophyte ancestor had reniform sporangia that were bilaterally symmetrical, bivalvate, with equal valves (isovalvate) that dehisced along their distal margin. The isovalvate morphology of sporangia is broadly conserved within the clade; exceptions are the evolution of sporangia with larger abaxial valves in *Ventarura* and independent evolution of sporangia with smaller abaxial valves in a few members of the small clade of the basal lycophytina dichotomy (SBLC), of the Sawdoniaceae and some other members of the small clade of the basal lycophytina dichotomy (LBLC).

Pre-Ludfordian speciation within the ancestral lycophyte lineage generated the ancestors of two clades. One of these clades (SBLC) conserved the irregular arrangement of sporangia, typically distributed on highest as well as lower orders of branching; however, the ancestrally reniform sporangia, conserved in *Wenshania*, evolved to a more spherical morphology in the rest of the clade. The other clade (LBLC), typically characterized by the presence of K-/H-branching and three-dimensional branch arrangement, evolved two-rowed sporangia that conserved their ancestrally reniform morphology. However, within the clade, both the reniform sporangial morphology and two-rowed arrangement saw evolution to different states – reversals to irregular sporangiotaxis or changes to a taxis not strictly two-rowed, as well as many changes in sporangial morphology outside the Sawdoniaceae and lycopsid clades.

Within the LBLC, the *Bathurstia*+Barinophytaceae ancestor, arising sometime between the latest Silurian and the late Lochkovian, conserved the regular, two-rowed arrangement of sporangia, which diverged from the ancestrally reniform morphology present in *Bathurstia* to evolve the barinophyte-specific lenticular, vertically flattened sporangia held on specialized appendages.

The Sawdoniaceae ancestor, which originated from the same ancestral lineage as the *Bathurstia*+Barinophytaceae ancestor sometime between the latest Silurian and the late Lochkovian, evolved apical circination of axes and emergences on the surface of axes (which were subsequently lost in some members of the clade). This plant probably had xylem with elliptical shape in cross sections and sporangia distributed on highest as well as lower orders of branching. The sporangia were borne in two rows, but this feature was not conserved in the clade, with most members either reversing to irregular sporangiotaxis or to different configurations of rowed sporangia, so that the presence of two-rowed sporangia in *Odonax*, a relatively highly

derived member of the Sawdoniaceae probably represents independent evolution of the ancestral condition.

The evolution of some zosterophyll features – such as apical circination, surface emergences on the axes, and specific branching morphologies – merits consideration in light of these results. Apical circination, typical of many zosterophylls, probably evolved independently in several lineages of the LBLC: the *Discalis+Gosferia* group, in *Adoketophyton*, *Trichopherophyton* and *Bathurstia*, and in the Sawdoniaceae, where they are a synapomorphy of the clade (with the sole reversal in *Margophyton*) (Fig. 2.3, 2.5).

Branching morphologies present among lycophytes and not encountered in other early tracheophyte groups include the feature termed here "branches parallel to subtending axis" (character 5; Supplementary Methods), subaxillary branching (character 7) and the K-/H-branching (character 2). The former is a branching morphology wherein branches curve apically close to their base to run more-or-less parallel with the subtending axis (e.g., in *Oricilla*; Gensel (1982b)). This morphology is a putative synapomorphy for the least inclusive clade that contains *Zosterophyllum* (Fig. 2.2 left, 2.3), although missing data preclude its unequivocal scoring throughout the clade (*Craswallia*, *Gumuia*, *Discalis* and *Gosferia*). This branching morphology is also present in other members of the LBLC that are distantly related to each other – the *Distichophytum+Ventarura* clade and members of the Sawdoniaceae (*Odonax*, *Sawdonia*, *Oricilla* and *Forania*) – so it probably evolved independently several times.

Subaxillary branching, defined by Kenrick and Crane (1997) and D. Edwards et al. (1989) refers to an additional branch, generally found below the dichotomy in zosterophylls. In Lycopsida such as *Selaginella*, this additional branching takes the form of a rhizophore. Only a few zosterophylls are known with this characteristic namely *Anisophyton*, *Crenaticaulis*, *Deheubarthia*, *Gosslingia*, *Margophyton*, *Odonax*, *Thrinkophyton*, all regrouped in the LBLC. More particularly, they are all members of the Sawdoniaceae clade. However, since all these taxa are also closely related to others without subaxillary branching detected, it is assumed that this character may have appear multiple times through the Sawdoniaceae, or saw multiple reversals from the Sawdoniaceae common ancestor.

K-/H-branching is a morphology (reviewed by Matsunaga and Tomescu (2017)) present in rhizomatous portions of the plants. It involves a lateral branch that dichotomizes apically close to

its base forming two branches with different orientations: one grows in the same direction as the main axis, whereas the other grows in the opposite direction; the latter usually takes on a rooting function. K-/H-branching has been documented in zosterophylls and lycopsids scattered all across the LBLC that are not directly related (*Zosterophyllum*, *Adoketophyton*, *Bathurstia*, *Odonax*, *Sawdonia*, *Tarella*, *Drepanophycus* and possibly *Asteroxylon*; see Hetherington et al. (2021) for the latter), which would indicate that it, too, evolved independently several times in this clade. However, it is important to keep in mind that presence or absence of K-/H-branching can be documented unequivocally in a given taxon only under particular circumstances: (1) when many specimens that represent well the entire body plan of a taxon are available for analysis; or (2) if fortuitously exceptional specimens preserve it. Additionally, (3) K-/H-branching is present mainly in rhizomatous portions of the plants, which are the least likely parts of a plant's body to be preserved in allochthonous fossil assemblages (i.e., consisting of fossils that have been removed from their growth environment and transported to a depositional setting); and (4) most lycophyte fossils are known exclusively from such allochthonous assemblages. As a result of all these factors, presence or absence of K-/H-branching cannot be documented unequivocally in many of the taxa included in this analysis. This leaves open the possibility of this branching morphology evolved in the common ancestor of a clade that includes lycopsids and (at least some) zosterophylls, the more so as echoes of it may well be present in derived, living lycopsids (Matsunaga & Tomescu, 2017; Fujinami et al., 2021).

Multicellular emergences on the surface of axes, typically more-or-less conical and sometimes referred to as enations are supported as a synapomorphy of the Sawdoniaceae. Absence of such emergences on some members of the clade indicates character state reversal. In this context, we note that two such members that for a clade within the Sawdoniaceae – *Gosslingia* and *Thrinkophyton* – possess fine trichomes on their axes (D. Edwards, 1970; Kenrick & Edwards, 1988b). This character was not included in the present analysis due to its overall low likelihood of preservation (easily destroyed during transport of the plant material prior to burial) or of observation (easily missed in observations of fossil preserved as coalified compressions). The phylogenetic placement of *Gosslingia* and *Thrinkophyton* among the most highly derived members of Sawdoniaceae allows us to speculate that their trichomes may have evolved by reduction of enations.

The patterns and processes of leaf evolution in the lycophyte clade (reviewed recently by Tomescu and Whitewoods (2024)) explained by several competing hypotheses (Stewart, 1964; Zimmermann, 1965; Kenrick & Crane, 1997) remain shrouded in mystery. The sister-group relationship between enation-bearing Sawdoniaceae and leaf-bearing lycopsids could be construed, at first glance, as supporting one of the three hypotheses – evolution of leaves by vascularization of enations. One could even point to reports of consistent cellular strands present in the enations two sawdoniacean genera – *Konioria* (Zdebska, 1982) and *Sawdonia* (Rayner, 1983). However, careful reading of the descriptions of these two taxa reveals that evidence for a conducting nature of those strands could not be substantiated. Because of that and considering that this study was not designed to address these questions –in terms of neither taxon sampling nor character construction – I cannot provide any meaningful for the vascularization hypothesis.

Nevertheless, considered in a broader perspective, results suggest a complex pattern of evolution of specialized sporangium-bearing appendages among lycophytes. On one hand, the phylogenetic placement of *Adoketophyton* far from taxa with sporangium-bearing appendages suggest that the fan-shaped appendages associated with the sporangia of this genus evolved independently. On the other hand, the sister-group relationship between the *Bathurstia*+Barinophytace and the Sawdoniaceae+lycopsids clades, wherein *Bathurstia* and Sawdoniaceae bear enations, and Barinophytaceae and lycopsids possess sporangium-bearing appendages, allows for some evolutionary speculation. Thus, the common ancestor of the *Bathurstia*+Barinophytace - Sawdoniaceae+lycopsids clade may have possessed enations that were 'primed' in some way to evolve into sporangium-bearing appendages, a process that occurred independently in the Barinophytace lycopsids. However, tempering such speculations is the observation that while in the derived lycopsids sporangia are borne adaxially on leaves, the plesiomorphic condition present in the drepanophycalean members of the lineage involves sporangia that are not necessarily borne on leaves (Schweitzer, 1980; Turner et al., 2023).

2.5 Conclusion

Zosterophylls, the dominant tracheophyte group during the first part of the Early Devonian are thought to have given rise to the lycopsid lineage. However, phylogenetic relationships among

lycophytes – i.e., among and between zosterophylls and lycopsids – have remained incompletely resolved and the subject of competing hypotheses. Analyses of the most densely sampled zosterophyll dataset to date in a parsimony-constrained approach allowed us to obtain a higher level of resolution than previously reported and to address, based on this, different aspects of evolution within the lycophyte clade. I found support for zosterophylls forming a grade paraphyletic to the lycopsids, congruent with results of some previous analyses; thus, zosterophylls can be regarded as a diverse, extinct stem-group of the lycophyte clade. Within the zosterophyll grade, a few main clades have moderate support, whereas a larger Sawdoniaceae clade is consistently recovered. Barinophytes, forming a clade, are nested within the zosterophyll grade. I also find moderate support for Sawdoniaceae sister to the lycopsids, with the Sawdoniaceae-lycopsids clade sister to a clade consisting mainly of barinophytes. I also introduce new methods of: (1) quantifying taxon stability when dealing with incongruent topologies generated by different inference methods using the same dataset; (2) making broad inferences on phylogenetic succession, i.e., organizing taxa based on their position of phylogenetic divergence with respect to the stem vs crown of a phylogenetic tree; and I demonstrate the applicability of these methods.

In the context of the system of phylogenetic relationships supported by these analyses, the stratigraphic distribution of different taxa and groups, combined with analysis of apomorphic characters and ancestral character state reconstruction, shed light on some aspects of the tempo and mode of their zosterophyll and lycophyte evolution. Results support a single major diversification phase of zosterophylls (which also gave rise to the ancestral lycophyte) during the late Silurian. This phase was followed by progressive reduction of diversification rates among zosterophylls during the Lochkovian and Pragian, and virtually no diversification afterwards. According to the current results, lycophytes (Lycophytina) are ancestrally defined by sporangia attached laterally on axes, possessing bilateral symmetry, bivalvate and opening along their distal margin. Lycophytina comprises two clades – one characterized by irregular distribution of sporangia along axes and the other (including the majority of zosterophylls along with lycopsids and barinophytes) hosting members with reniform sporangia arranged in rows and possessing three dimensional branching architectures and K-/H-branching in the rhizomatous portions.

A previous study by Capel, Cleal, et al. (2023), suggested preferential distribution of zosterophylls in equatorial areas. While integrating the evolutionary information contained in

phylogenies with the geographic distribution of taxa falls outside the scope of this study, future studies addressing this aspect based on an expanded dataset will add another layer to the understanding of evolutionary tempo and mode among zosterophylls and lycophytes. This is especially relevant since zosterophylls are found all around the world and the Devonian is thought to have witnessed significant plate tectonics movement (Scotese, 2016).

Chapter 3

Phylogeography

The relationships of zosterophylls have been reviewed. Results shed light on their fast and complex evolutionary history. Their relationships towards Lycopsida have been clarified as their closest relatives, representing therefore the Early Devonian stem-group Lycophytina. Since the group is paraphyletic, the term "zosterophylls" will be referring to the stem-group Lycophytina. When including the Lycopsida, the group will therefore be mentioned as Lycophytina. In the present chapter, a spatial approach of the stem-group's evolution will be explored. In fact, as mentioned in Chapter 1, remains of zosterophylls are known from various places in the world (Senkevich, 1975; Kenrick & Crane, 1997; Hao & Xue, 2013; McSweeney et al., 2020). During the Devonian, landmasses are separated into different blocks, namely a Laurussian, Siberian, Kazakhstanian and Gondwanan blocks, not forgetting the various archipelagos whose position remain uncertain (Scotese, 2016). With the notable exception of the southern Gondwanan block, zosterophylls' fossils have been discovered in all the terranes, indicating a widespread distribution of the group during a remote time. Since their diversification is very fast, during a time period punctuated by geographical barriers hindering their dispersion, mystery remains about their efficient colonization strategies. The present chapter is an attempt to shed light on this part of their history, using paleogeographical methods, applied to phylogeny.

3.1 Introduction

Zosterophylls are extinct Devonian land plants, among the earliest to globally diversify on Earth, during the greening of lands. Despite their undeniable impacts on Earth, the majority of the studies on these fossils are based on taxonomy (Gerrienne, 1983; Kotyk, 1998; D. Edwards & Li, 2018a), diversity (Cascales-Miñana & Meyer-Berthaud, 2014, 2015; Capel et al., 2021) and phylogeny (Kenrick & Crane, 1997; Hao & Xue, 2013; Nibbelink & Tomescu, 2022). Zosterophylls are therefore well morphologically constrained, identifiable thanks to their herbaceous strategy of leafless axes, bearing lateral sporangia opening in two valves. They are particularly present during the Lower Devonian (Lochkovian to Emsian), even if fossil remains are also found between the late Silurian to the Late Devonian. This group is paraphyletic, representing the Devonian stem-group Lycophytina.

However, a few studies focused on the paleogeography of zosterophylls. While some studies took into account Devonian paleogeography, they tend to focus on the entire flora known at that time (Raymond, 1987; D. Edwards, 1990; Raymond et al., 2006; Capel, Cleal, et al., 2023). In contrast, the pioneering study of Cascales-Miñana and Meyer-Berthaud (2015) is a first approach to combine diversity signal and geographical dispersion among the zosterophylls. If the pattern of diversification is similar among the different regions studied, they all appear highly endemic, confirming previous phytogeographic units, and preventing massive floral exchanges. This study paves the way for others, in order to further understand the link between these areas.

As represented in maps 3.1 to 3.5, indicating the position of all the currently known zosterophyll-bearing localities over the Devonian, zosterophylls are mainly constrained between the equatorial belt to the Northern paleocontinents. This preferential distribution has been previously highlighted (Capel, Cleal, et al., 2023) and geographical sampling biases have been pointed out.

The Silurian and the Devonian epochs are also characterized by a fragmentation of continents. This continental dispersion implies the presence of geographic barriers that can hinder the progression of a given group of organisms. Despite this limitation, zosterophylls seem to thrive, since their remains are found in various places of the world, and relatively early in their history

(maps 3.1, 3.2).

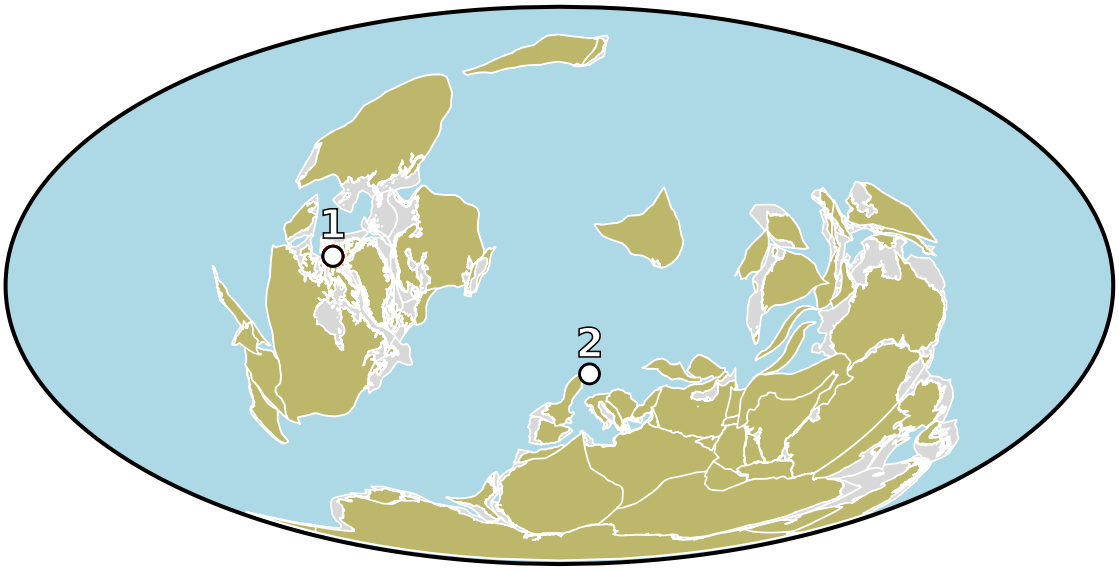


Figure 3.1: Paleogeographical distribution of zosterophyll bearing localities over the Silurian (Ludfordian). 1 - Polar Bear Pass (Canada), 2 - Dniestr Valley (Ukraine). Maps extracted from the Golonka model (N. Wright et al., 2013).

All the above-mentioned studies used taxon-based approaches to define their biomes. However, morphology can also be a precious tool to understand the spatial evolution of a given group. Such is the case of the study of Hao and Gensel (1998) that pointed a morphological proximity between the Australian and Chinese zosterophylls. On the other hand, the study of Hao et al. (2007) suggested that the distribution of sporangia is representative of particular provinces. Thus, rowed-arranged strobili are more likely to be found in Europe or North America, while helically-distributed sporangia are characteristic of China.

Therefore, questions about their diversification strategies and geographical dispersion arise.

Since this group had a fast and global diversification process, the present chapter will try to figure out if there is any geographical pattern that influenced their evolutionary history, especially on their morphology. To do so, phylogeography analyses will be applied for the first time on the group. Therefore, any geographical signals behind Lycophytina's topology will be unfolded by this approach. To complete this view, a comparison with the morphological

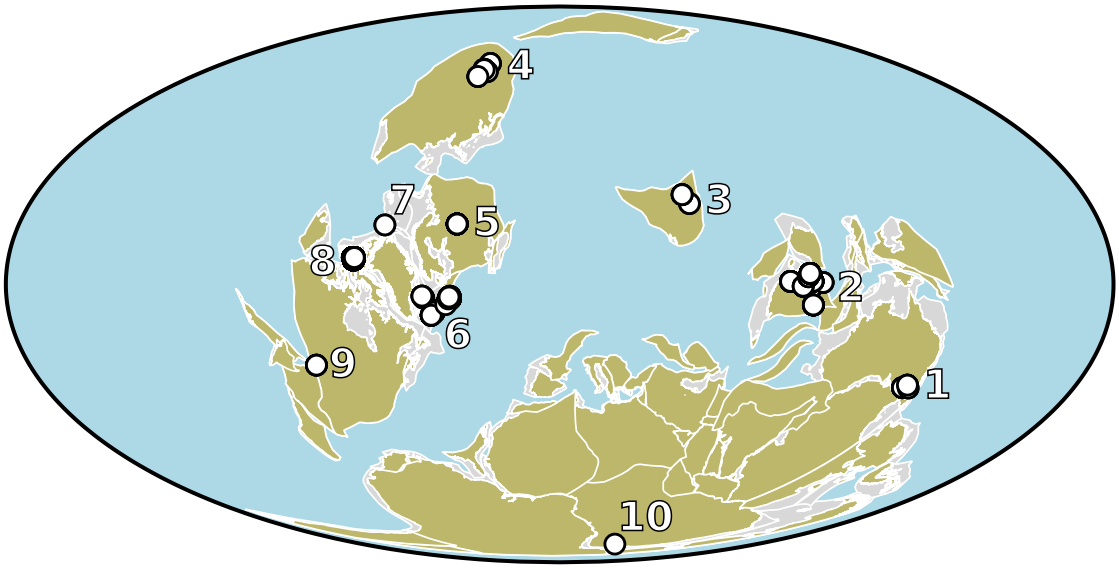


Figure 3.2: Paleogeographical distribution of zosterophyll bearing localities over the Lower Devonian (Lochkovian-Pragian). 1 – Australia: Lochkovian – Pragian: Boola Quarry, Pragian: Ghin-Ghin road, Mt. Pleasant road, North road quarry. 2 – China: Lochkovian – Pragian: Yanmenba, Lochkovian: Xiaxishan reservoir, Huaguoshan, Baoyang, Pragian: Caoziping, Dahe, Lizhai, Longhuashan, Shiqiao, Xujiachong, Changputang, Daliatang, Gegu-Daigu, Gumu Town, Zhichang. 3 – Kazakhstan: Lochkovian: PriBalkhash, Pragian: Aigyrzhal mountain. 4 – Russia: Pragian: Karasug, Minusink basin, Rybinsk. 5 - Russia: Lochkovian – Pragian: Shira. 6 - Europe. Belgium: Lochkovian – Pragian: Gileppe, Lochkovian: Nonceveux, Pragian: Ensival, Racheneur Quarry. Germany: Lochkovian: Venn Sadle, Pragian: Abandoned quarry below Katzenlei near Walporzheim, Abandonned quarry at Vinxtbach Valley, Brohl quarry, Bürdenbach/Westerwald outcrop, Oberlahr/Westerwald outcrop, Outcrop below 'Hohe Schleif', Road outcrop 'Ettringer Heuweg', Rurtal, Sieg Valley, Vineyard above the Ahr Valley, Vinxtbach Valley, Excavation at Breidt near Lohmar, Jabach Valley, Pionerweg, Rosenburg, Wahnbach Valley. Scotland: Lochkovian: Aberlemno Quarry, Balgavies Quarry, Clocksbriggs Quarry, Kelly Den, Pragian: Rhynie. Wales: Lochkovian: Brynglas Tunnel, Cwm Mill, Milford Haven, Allt Du, Mascle Bridge Quarry, Pragian: Brecon Beacon Quarry, Burton Cliff, Craig Ddu, Llanover Quarry, Mill Bay. England: Lochkovian: Newton Dingle. 7 – Norway: Lochkovian: Svalbard. 8 – Canada: Lochkovian – Pragian: Polar Bear Pass, Pragian: Cheyne River Region, Young Inlet. 9 – USA: Lochkovian – Pragian: Cottonwood Canyon. 10 - South Africa: Lochkovian - Pragian: Warmwaterberg. Maps extracted from the Golonka model (N. Wright et al., 2013)

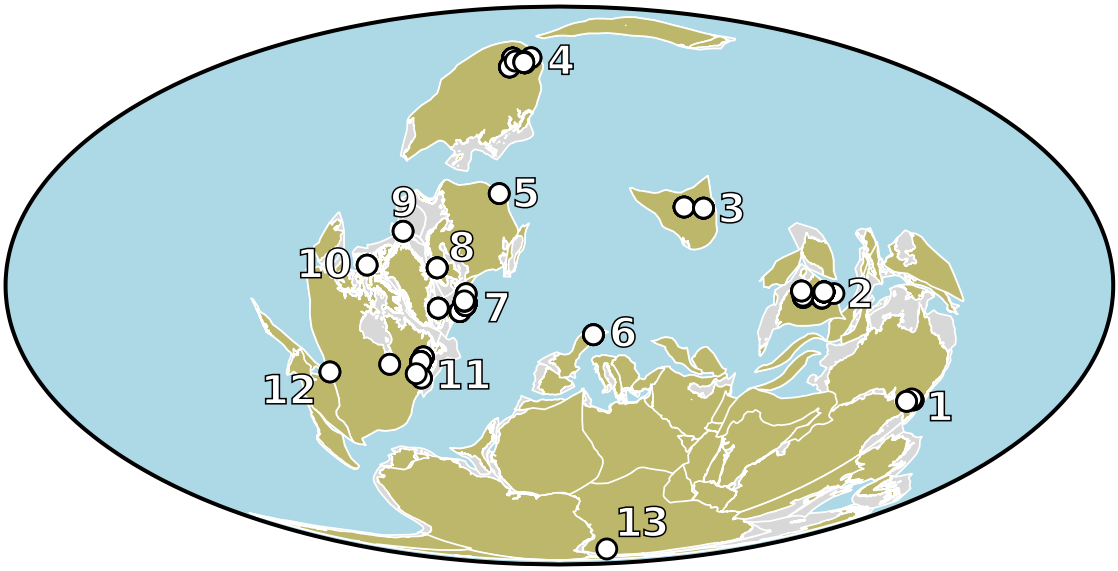


Figure 3.3: Paleogeographical distribution of zosterophyll bearing localities over the Lower Devonian (Emsian). 1- Australia: Ghin-Ghin road, Mt. Pleasant road, North road quarry, Frenchman Spur. 2 – China: Caoziping, Lizhai, Longhuashan, Shiqiao, Xujiachong, Huangguan Section, Yuankou Section. 3 – Kazakhstan: PriBalkhash, Karaganda Synclinorium. 4 – Russia: Shira, Karasug, Minusink basin, Gorny Altai, Khondelen Graben, Kyrlyk River, Nyrna River, Sarazonka. 5 - Russia : Kok-Sair region. 6 – Poland: Andrychow. 7 – Europe: Belgium: Quarry du Bois Collet, Quarry les Forges. France: Rebreuve. Germany: Ahr Valley, Alken Quarry Herfterath, Hoffeld, Konder Valley, Külbach, Müsch, Ufersmühle Quarry, Waxweiler, Feckelsberg, Heetdberg quarry, Kahleberg sandstone, Neugrunen, Abandoned Quarry Westerberg, Outcrop in the Kupfersiefer Valley near Rösrath. Scotland: Auchensail quarry. 8 - Norway: Andrée Land. 9 – Norway: Roragen. 10 - Canada : Young Inlet. 11 – North America: Canada D'Aiguillon to Seal Rock, Dalhousie Junction, Peuplier Point, St. Francis Group, Abitibi River. USA: Trout Brook. 12 – USA: Beartooth Butte. 13 - South Africa: Warmwaterberg. Maps extracted from the Golonka model (N. Wright et al., 2013).

evolution over the topology will be proposed, in order to link the geographical history with the overall Lycophytina evolutionary process.

3.2 Material and methods

In order to link the geographical distribution of Lycophytina to its morphological evolutionary history, the present work will be divided into two main sections. The first one is the estimation of zosterophylls provinces, using the classic multivariate analyses approach (Raymond, 1987; Vörös & Escarguel, 2020). Once the paleoprovinces are estimated, their geographical evolution

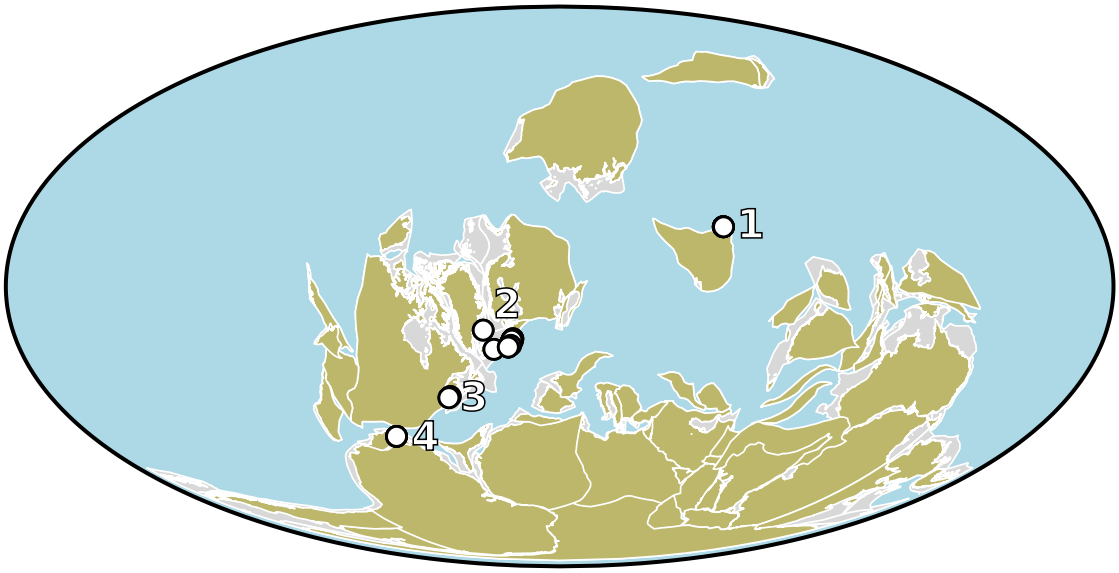


Figure 3.4: Paleogeographical distribution of zosterophyll bearing localities over the Middle Devonian (Eifelian - Givetian). 1 – China: Givetian: Hoxtolgay Town. 2 – Europe: Germany: Eifelian – Givetian: Korzert, Eifelian: Hagen-Ambrock, Koster quarry, Lasbeck quarry, Givetian: Lindlar Bergisches land, Lückhofen quarry. Scotland: Eifelian – Givetian: Hill of Forss. Norway: Eifelian – Givetian: Gjegnalund Glacier. Belgium: Givetian: Niaster, Plan incliné de Ronquières, Railroad cut near Feluy. 3 – USA: Eifelian; Trout Brook, Givetian: Winslow Farm. 4 – Venezuela: Givetian: Sierra de Perijá. Maps extracted from the Golonka model (N. Wright et al., 2013).

will be reconstructed using ecological dispersion models (Ronquist, 1997; Ree & Smith, 2008; Landis et al., 2013) applied to phylogenies, and compared with ancestral state reconstruction.

3.2.1 Data acquisition

Previous studies defining Devonian provinces are based at the biome level, taking into account the maximum plant diversity known (Raymond, 1987; Raymond et al., 2006; Capel, Cleal, et al., 2023). Given that the current study will emphasize on the geographical distribution of only one group, it is not relevant to use this biome nomenclature previously described. In contrast the focus here will be the definition of provinces characterizing the known distribution for zosterophylls. Even if this group is dominant during the Lower Devonian, their impact on the biome definition will be limited. In fact, as pointed by Capel, Cleal, et al. (2023), this group is preferentially distributed in the tropical areas. In addition, fossils of this group are also absent in some regions of the world (i.e. the Gondwana). Consequently, if some zosterophylls provinces

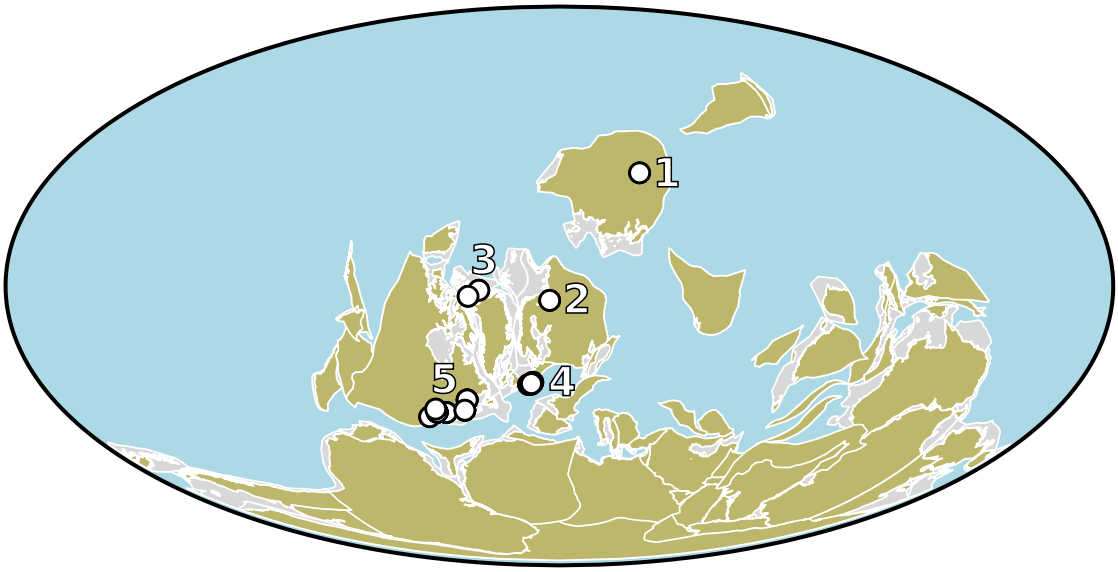


Figure 3.5: Paleogeographical distribution of zosterophyll bearing localities over the Late Devonian (Frasnian - Famennian). 1 - Russia : Famennian: Esaulovka river. 2 – Russia: Frasnian: Nenets Autonomous Okrug. 3 – Belgium: Frasnian: Vieux-Leuze, Famennian: Beaupère quarry, Herbestal-Bleiberg, Quarry l'Ecluse d'Evieux-Esneux, Rorive quarry, Strud-Haltinne. 4 – Canada: Frasnian: Bird Fiord, Okse Bay Group. 5 – North America: Canada: Frasnian: Scaumenac Bay and Miguasha. USA: Frasnian – Famennian: St Andrews Basin, Frasnian: Livingstonville, Steenberg Quarry, Famennian: Burtville, Elkins Randolph County, Red Hill, Rock city. Maps extracted from the Golonka model (N. Wright et al., 2013).

will overlap the previous biomes definition, not all the same biomes will be recovered, because of the particular, restricted zosterophyll distribution.

Because of zosterophylls' wide distribution, the first step is to see if there is any preferential grouping of taxa that could subset their distribution into "paleoprovinces". Here, a paleoprovince is defined as areas regrouped together based on their similar zosterophyll composition. The definition of these provinces is a prerequisite for the morphological comparison. Therefore, a presence-absence dataset of zosterophylls among areas has been created. The areas used in this study are similar to the ones defined in Capel, Cleal, et al. (2023), and the localities retained contain at least one zosterophyll species, for a total of 21 areas. Such a list is summarized in table 3.1. The choice of taxa is based on the 38 genera of zosterophylls taken into account in Chapter 2. Taxa with an open nomenclature (*cf.*, *aff.*, sp.) were not considered for the present work in order to reduce the distribution uncertainty.

Additionally, those with an ambiguity in regard of their classification (i.e. *Bracteophyton* (D.-M. Wang & Hao, 2004), *Danziella* (D. Edwards, 2006), *Dibracophyton* (Hao et al., 2012), *Faironella* (Gerrienne, 1996a), *Gippslandites* (McSweeney et al., 2020) *Hsua* (C.-S. Li & Edwards, 1992), *Huia* (Geng, 1985b), *Jugumella* (Senkevich, 1975), *Kaulangiophyton* (Gensel et al., 1969), *Krithodeophyton* (D. Edwards, 1968), *Parazosterophyllum* (McSweeney et al., 2020) and *Nothia* (El-Saadawy & Lacey, 1979) (Gensel, 1976)) were not included. The genus *Zosterophyllum* being paraphyletic and broadly distributed, localities were accounted for the type species *Z. myretonianum* (Penhallow, 1892) only. This species selection has been applied only for *Zosterophyllum*. Other zosterophylls are based at the genus level since most of them are monotypic, known by a few number of species or known by a single occurrence only.

This database regroups the presence or absence of a given taxon along the different countries sampled for all the Devonian. The choice was made to keep a broad temporal resolution, at the Devonian level due to the vagaries of the fossil record. In fact, the maximum diversity of zosterophylls is sampled in the Pragian and the Emsian, but poorly sampled in the other time series. Consequently, a finer temporal binning would have been misleading at such a global scale.

Once the paleoprovinces estimated, the phylogeny based on a matrix of 44 taxa of early land plants, including 38 genera of zosterophylls. and 42 morphological and anatomical characters was used as a backbone for phylogeography (Chapter 2). For consistency between analyses, all the genera of zosterophylls included in the phylogeny are the same as the ones selected for the provinces estimations (see above).

In addition, the geographical model needs a fully dichotomous tree. Thus, one among the six most parsimonious tree has been retained. For consistency with the fossil record, the most parsimonious tree with the best fit to stratigraphy (tree number 6, Fig. 2.3) was chosen. The tree obtained was time scaled on R, using the package "strap" (Bell & Lloyd, 2015). An equal length method has been applied to the tree in order to have branch length higher than zero, which is a requirement for the paleoreconstruction analyses (Bauer, 2021).

Table 3.1: Locality names and assignation to a geographical province. The abbreviation are from Capel, Cleal, et al. (2023)

Abbreviation	Complete name	Palegeographical province
ARC-CAN	Arctic Canada	Laurussia
BEL	Belgium	
E-CAN	Eastern Canada	
EN-WLS	England-Wales	
E-USA	Eastern USA	
GER	Germany	
N-FRA	Northern France	
NOR	Norway	
SBR	Siberia	
VNZ	Venezuela	
W-USA	Western USA	
XNJ	Xinjiang	
MOS	Moscovite plate	Eastern Laurussia
SCT	Scotland	
SVL	Svalbard	
UKR	Ukraine	
POL	Poland	Poland
GGX	Guangxi	Northeastern Gondwana
GZH	Guizhou	
SCH	Sichuan	
YUN	Yunnan	

Ancestral state reconstruction and comparison with morphology

The matrix, built for the phylogeny in Chapter 2 was used again (see Supplementary Material B, Methods S.3 p. 168), for an estimation of the ancestral states of the characters. This reconstruction was performed on the Mesquite software (vers. 3.70) (Maddison & Maddison, 2022). As for Chapter 2, ancestral state reconstruction is based on a likelihood model, and a state is considered as present in the ancestor (the node) when it reaches more than 50% of the probability.

3.2.2 Definition of Devonian geographical areas

Devonian paleogeography

The geography of the Devonian is reconstructed as having two main continents, Laurussia and Gondwana which are gradually coming together. By the end of the Devonian, they are starting to form the future Pangea (Scotese, 2016). Additionally, some terranes such as Siberia or Kazakhstania are found out, in between the main continents. The maps in figure 3.1 to 3.5 are a reconstruction of the continents over the Devonian. The Gondwana continent has a southern configuration, with a latitudinal expansion all along the southern hemisphere, and reaching the south pole. It regroups present-day Australia, India, some regions of China, as well as the African and Southern American continents. Laurussia, whose southern part gradually comes close to Gondwana is rather located on the equatorial and tropical latitudes. This continent encompasses present-day northern America, Greenland, northeastern Europe and western Russia. Siberia is on the map located north of Laurussia, composed by the Siberian plate, while Kazakhstania is the block on the eastern part of Laurussia, composed of some regions of China and Middle East.

As pictured in maps 3.1 to 3.5, zosterophylls' geographical distribution is uneven, centered in the equatorial latitudes and mainly absent from Gondwana. As mentioned in introduction, the group is principally sampled on the southern ridges of Laurussia and northeastern Gondwana (south China), which can introduce a sampling bias in the analyses. For all these reasons, new provinces based on zosterophylls' distribution will be defined, using the following methodology.

Methodology for paleoprovinces estimations

A dissimilarity matrix has been extracted from the presence-absence database (see above for the database composition). The dataset being based on fossil remains of terrestrial organisms, the information is assumed to be broadly incomplete. It is then important to emphasize on the common presence of taxa between the sites rather than a common absence. For this reason, the Bray-Curtis index has been favored for this study. For a comparative purpose, the Raup and Crick dissimilarity index was run as well (Raup & Crick, 1979). This index was established for paleontological data and is based on the probability of sites to share the same species. In order to illustrate the groups produced, results of the dissimilarity indexes were plotted into classification dendrograms.

The cluster dendrograms (Neighbor joining, NJ) and ordination methods (Non Metric Multidimensional Scaling, NMDS Legendre and Legendre (2012)), were produced following Vörös and Escarguel (2020) approach. The results provide groupings based on the similarities of the floral composition. In order to see which species contributed the most in the establishment of the different paleoprovinces, SIMPER analyses was run (Clarke, 1993).

Number of paleoprovinces

An *a priori* division of the distribution of paleoprovinces has been originally set on three groups ($k = 3$). Then, in order to explore the different grouping possible, the abovementioned methodology was applied for different numbers of groups ($k = 4, 5, 6$). Group significance was tested using ANOSIM (Clarke, 1993).

Impact of singletons

Since zosterophylls are particularly known for their monospecific taxa, as well as their single occurrences (Barrett, 2016), a similar process as mentioned above has been applied without singletons. A singleton is defined here as a species of zosterophyll recorded in only one locality. The idea is to measure the impact of single-known locality species on the dataset and see what information these taxa bring to the complete dataset.

The multivariate analyses and statistical tests were performed on Rstudio (R Core Team, 2023), using the packages vegan (Oksanen et al., 2013) and ape (Paradis et al., 2019) (see Supplementary Material C for the scripts).

Based on these results, paleoprovinces occupied by zosterophylls have been extracted and used for the paleogeographical analyses.

3.2.3 Phylogeography analyses

Methodological overview

Biogeography using phylogenies are popular methods based on the ancestral state reconstruction at nodes and are widely used for extant taxa (Teeling et al., 2005; Hedtke et al., 2013; Williams et al., 2017). Different methods were developed in the bibliography (Ronquist, 1997; Ree, 2005), but recently, the work of Matzke (2012) drastically improved the process, thanks to the development of the package "BiogeoBEARS" (Berger et al., 2016; Funk & Burns, 2018; Toussaint et al., 2021). By using a fully dichotomic time-scaled topology, geographical information of the taxa at the tip and dispersion models, the package allows for a reconstruction of the geographical distribution at each node. Recently and for the first time, promising analyses of this kind was performed on a dataset composed only by fossil data (Bauer, 2021). A similar methodology will be applied here in the context of early land plant radiation.

Tree selection and area assignation

The paleogeographical provinces previously estimated have been assigned at the tips of a fully dichotomous phylogeny, following the known distribution of each taxon. Some species of Lycophytina are known from more than one paleoprovince, while others are restricted to one paleoprovince only. Consequently, the range of paleoprovinces that can be assigned at each tip vary between one and the maximum number of paleoprovinces estimated.

The tree selected for the present work is one of the six most parsimonious trees obtained in Chapter 2. More particularly, the tree having the best fit to stratigraphy has been retained for the present study (tree number 6, Fig. 2.3). The best fit for stratigraphy has been favored in this

study in order to best match the evolutionary information with the fossil record.

Thanks to the geographical information provided by the cluster analyses and the temporal and topographical information brought by the phylogeny, it is then possible to apply biogeographical models in order to predict the spatial distribution of the group at each node.

Model summary

Different biogeographical models can be computed with the package BiogeoBEARS and are summarized in table 3.2. BiogeoBEARS currently handles three families of models, that can be run with additional parameters.

The first family of models is called the Dispersal-Extinction Cladogenesis (DEC) and was developed by Ree and Smith (2008). This likelihood-based model uses the cladogenesis events as opportunities for the daughter lineage to explore other areas (dispersal parameter), while maintaining (or not - extinction parameter) their ancestral range. The second family of models is Dispersal-Vicariance Analysis (DIVA), which is parsimony-based (Ronquist, 1997). In this model, parsimony is the optimality criterion to estimate the area inheritance of daughter lineages, with some colonization strategies costly, and therefore discarded. The last model implemented into the package is the BayArea developed by Landis et al. (2013). The area inheritance is this time computed using the MCMC algorithm, improving the calculations especially for a great number of areas (>20).

In addition, founder events speciation i.e. a few representatives of the daughter lineages arriving in a new area previously not ancestrally explored have been implemented, with the parameter $+J$ (Matzke, 2012). All the models have been run, and the best one selected thanks to the Akaike Information Criterion (AIC) (Burnham & Anderson, 2004). This estimator allows for a comparison between the different parameters (k) composing a model, and its maximum Likelihood function (ML). The criterion is defined as the following:

$$AIC = 2k - 2ln(ML)$$

AIC detects the model representing best the data without over-fitting (i.e. selecting a higher number of parameters than needing for said model). The lower an AIC value, the better the

Table 3.2: List and summary description of the biogeographical models used. See text for further description of these models. In bold is the one selected for this study.

Model name	Founder event	Dispersion at cladogenesis
DEC	No	One area inheritance
DEC + J	**Yes**	**One area inheritance**
DIVALIKE	No	Vicariance
DIVALIKE + J	Yes	Vicariance
BayArea	No	Ancestral range to daughter
Bayarea + J	Yes	Ancestral range to daughter

model.

3.2.4 Character state reconstruction

In order to see if the morphology of Lycophytina is influenced by their geographical dispersion, ancestral state reconstruction has been performed on the Mesquite software (Maddison & Maddison, 2022), using the matrix built for phylogeny analysis (Chapter 2). Only the characters having an evolutionary history close to the biogeographical signal have been retained. The following characters are "Circinate axis tip" (character 6), "Emergences" (character 8), "Sporangium shape" (character 20), "Sporangium distribution by order of branches" (character 28) and "Sporangium, distribution along axis" (character 33). For more information about these characters, see Supplementary Material B.

3.3 Results

3.3.1 Estimation of geographical provinces

Definition and interpretation

Cluster analyses based on the dissimilarity matrix obtained from the localities showed some preferential configurations, according to the zosterophyll floral composition (Fig. 3.6a). The group divisions are better explained when $k = 3$. In fact, no better precision in the grouping was found out with a number of groups higher than three, so for the following analyses, the three paleoprovinces will be defined as the following (Table 3.1, ANOSIM p.value= 0.001):

- **Laurussia** is the largest province that includes 12 areas from this continent (Table 3.1). SIMPER analyses show that Laurussia is characterized by the common presence of the genus *Sawdonia* (see Supplementary Tables C.3 p. 207 and C.4 p. 208 for more information). However, among the localities composing this group is included Xinjang (XNJ), whose paleoreconstruction is usually located in Kazakhstania (Capel, Cleal, et al., 2023). In fact, a look at figure 3.6b indicates that Xinjang is far left on the two dimensional reconstruction, closely associated to Venezuela (VNZ). This odd association can be explained by the common presence of *Serrulacaulis*, not to mention the fact that no other zosterophyll included in this study has been recovered in other Kazakhstanian places. Thus, this grouping is more likely due to a sampling artifact rather than a real biogeographical signal, and caution is needed when interpreting this area in an evolutionary context. Surprisingly, Siberia (SBR) is included into this province, and not considered as a province on its own, as defined by Capel, Cleal, et al. (2023). In fact, some *Sawdonia* are mentioned in Siberia, even if their nomenclature remain open (Fedoseev, 2008).

- **Eastern Laurussia** is defined as a place regrouping the Moscovite plate (MOS), Scotland (SCT), Svalbard (SVL) and Ukraine (UKR), which are all located in the Eastern side of the continent. These areas are regrouped together thanks to the common presence of *Z. myretonianum*, and *Protobarinophyton* (see Supplementary Tables C.3 and C.5). Norway (NOR) is geographically close to Svalbard and also contain *Z. myretonianum* remains, but it is nonetheless outside this group. In fact, unlike the other localities, Norway contains remains of *Sawdonia*, a characteristic defined above as of the Laurussian province. Furthermore Siberia, which is also associated to Laurussia thanks to the presence of *Sawdonia* is geographically farther from the continent than the localities composing the Eastern Laurussia province. Thus, the fact that *Sawdonia* is not recovered in Moscovia, Scotland and Svalbard may be due to a sampling effect rather than a real absence and should be further tested. However, the fact that this area is distinguishable from Laurussia suggests a transitional flora between Laurussia and the east (Kazakhstania and Gondwana).

- On the Gondwanan continent, only the northeastern part is relevant (**Northeastern Gondwana**), with a common paleoprovince composed of Guangxi (GGX), Guizhou (GZH),

Sichuan (SCH) and Yunnan (YUN). These areas regroup unique zosterophyll flora, composed of *Adoketophyton* and *Demersatheca*, taxa found only in these places. Other Northeastern Gondwanan taxa encompass *Ornicephalum*, *Sichuania*, *Xitunia*, *Baoyinia*, *Guangnania*, *Ramoferis*, *Gumuia*, *Discalis* and *Wenshania*. If these taxa are not systematically found in the areas composing this paleoprovince, they are nonetheless completely absent from the two other paleoprovinces, defining thus a rich flora composed of numerous endemic taxa.

Figure 3.6b shows the sites configuration under an NMDS analysis. Three main groups are easily distinguished. The first one (in red), is the biggest one, regrouping the localities preferentially on the left side of the graph. These localities mainly come from the Laurussian paleocontinent, with the notable exception of Xinjang which is usually attributed to the Kazakhstanian block and Siberia, to the Siberian block. The second group (in green), at the top of the graph is composed of Svalbard, Ukraine, Moscovia and Scotland and represents the Eastern Laurussia province. These localities are geographically present on the Laurussian continent, but appear in this result separated from the first group because of their absence of *Sawdonia*. The last group (in blue) located at the right of the figure regroups Yunnan, Sichuan, Guangxi and Ghuizou, into a Northeastern Gondwanan flora. We can notice that this group encompasses Yunnan which is the locality with the most central position.

Other analyses and exploration

This group configuration is consistent when other dissimilarity indexes are used, such as the Raup-Crick (Supplementary Fig. C.1, p. 205), bringing more confidence in the paleoprovinces estimations. Since the results provided are similar, only the analyses ran with the Bray-Curtis dissimilarity index was represented in this chapter.

Additionally, a similar conclusion can be drawn from the singleton analysis. In fact, because the important number of singletons composing the dataset (62.2%) can strongly influence the group estimation, measuring their impact by removing them is a good approach to test the confidence of the above mentioned signal. Surprisingly, the group estimation remains the same with and without singletons (Supplementary Fig. C.2, p. 211). They seem then to have a homogeneous distribution between the areas. Thus, despite the important number of singletons,

Table 3.3: Model tests for the paleogeographical analyses. In bold is represented the model selected for the analysis.

Model name	LnL	Nb parameters	AIC
DEC	-72.22	2	148.4
DEC + J	**-64.77**	**3**	**135.5**
DIVALIKE	-74.71	2	153.4
DIVALIKE + J	-64.82	3	135.6
BayArea	-78.61	2	161.2
BayAea + J	-65.6	3	137.2

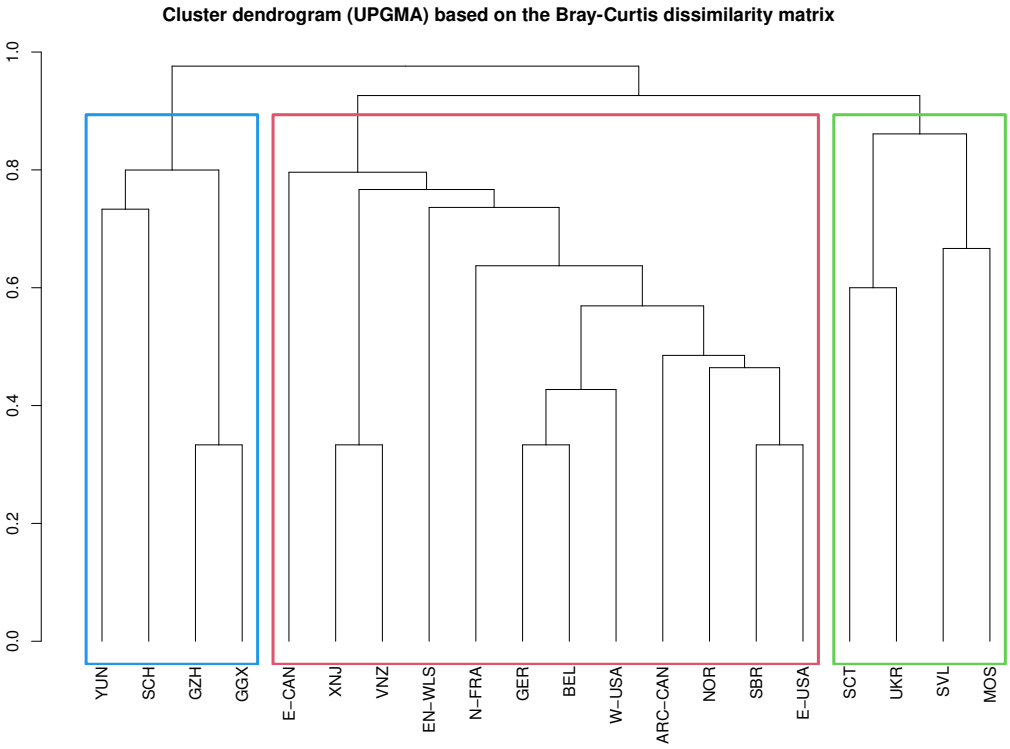
their distribution remains consistent with the analysis presented in this chapter (refereed as the main analysis), and shows that the signal is in majority driven by the taxa that are present in multiple areas.

The special case of Poland

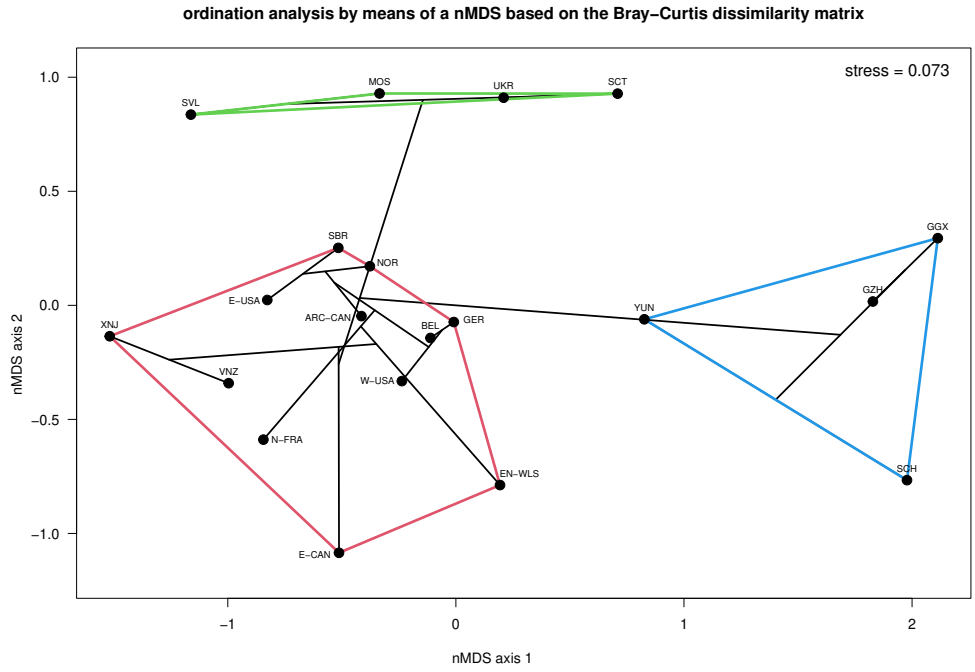
In addition to these three defined groups, a fourth one will be included in the phylogeography analysis, comprising the outlier Poland and its endemic taxon *Konioria*. Poland is not the sole area bearing only one zosterophyll species. Svalbard, Xinjang, Northern France, Ukraine and Guangxi are also known with only one zosterophyll discovered (see Supplementary table). However, these areas differ from Poland by bearing a non-endemic zosterophyll species (*Protobarinophyton*, *Serrulacaulis*, *Sawdonia*, *Zosterophyllum* and *Demersatheca* respectively). This combination of an area containing only one endemic species is so different from the other areas that no resolution is visible on the NMDS analysis when it is included, grouping all the other areas together, apart from Poland. Since *Konioria* is included in the phylogeny, the area is thus considered as a paleoprovince of its own for this study. However, it is important to keep in mind that almost no locality bearing zosterophyll remains are known from Poland, and *Konioria* is known from two boreholes (Zdebska, 1982). So caution is the watchword concerning this geographical province, and future discoveries in the area can help redefine this division.

3.3.2 Phylogeography

The best model selected for the dataset is the DEC+J model, with an AIC value of 135.5 (Table 3.3). The following results are thus based on the best fit to stratigraphy tree following this model.



(a) Cluster dendrogram (NJ) showing the closeness of the localities based on the zosterophyll composition. Three groups are found out and represented by the colored boxes. Color code as in Fig. 3.6b. Locality abbreviation in table 3.1



(b) Non metric MultiDimensional Scaling (nMDS) analysis showing the group composition of the different localities. Color code as in Fig. 3.6a. Locality abbreviation in table 3.1

Figure 3.6: Cluster and multivariate analyses applied to zosterophylls.

Lycophytina paleophylogeography

Figure 3.7 shows the geographical reconstruction of Lycophytina. According to the figure, two trends are visible among the four paleoprovinces estimated. The tree highlights then a preferential distribution of Lycophytina in two main groups, a basal Northeastern Gondwana one, and a Laurussian one. More particularly, the Lycophytina node is estimated to have more likely a Northeastern Gondwanan origin. Among the Northeastern Gondwanan group, some taxa are from Laurussia only (*Gutzeitia*, *Hicklingia*, *Craswallia*, *Gosferia*, *Macivera* and *Ventarura*) or cosmopolitan (*Zosterophyllum*, *Distichophytum*). This information suggests multiple and individual events of dispersion outside Gondwana. The oldest migration event is dated in the Ludfordian, with the Canadian taxon *Macivera*, while the latest is represented by the Russian *Gutzeitia*, estimated in the Pragian.

The Laurussian cladogenesis starts after the Ludfordian and encompasses the Lycophytina sharing a common ancestor at the *Trichopherophyton* node. That includes among other Barinophytaceae, Sawdoniaceae as well as the Lycopsida. Inside this clade, a few taxa seem to have migrated, making it less likely to change provinces compared to the ones in Gondwana. For example, only one taxon, *Oricilla*, shows a reversal migration to Northeastern Gondwana during the Pragian.

Inside Lycopsida, *Drepanophycus* is the sole member in this sample with a cosmopolitan distribution. It is closely related to *Asteroxylon*, discovered only in the Rhynie chert (UK) (Kidston & Lang, 1920b). However, since the sample of this class is comprising only two taxa, caution is called for the geographical interpretation of Lycopsida, because of its clear bias towards a Laurussian origination.

Eastern Laurussian taxa are not found grouped together, but spread out on the tree instead. This configuration confirms the limits pointed in the previous section about this specific subdivision being more likely the result of a sampling bias. Additionally, this result surprises since it was assumed that the eastern part of the continent being in between the two main Devonian blocks, could play the role of transitional area. This lack of resolution may be due mainly to the bias of the fossil sampling, strongly favoring the two main blocks. In addition, six out of the nine taxa assigned to this province are cosmopolitan, hence reducing the confidence about this

province's definition.

Konioria appears on the tree closely related to *Odonax* and *Euthursophyton*, two Laurussian taxa. During the Devonian, Poland was located on the Laurussian paleocontinent, close to Germany and Belgium, the two areas bearing the sister taxa. Thus, a continuity between this province and Laurussia can be easily drawn, according to the relationships.

Now that the geographical distribution of the group has been estimated, a comparison with the morphology will be performed in order to detect any geographical pattern influencing the evolutionary history of Lycophytina.

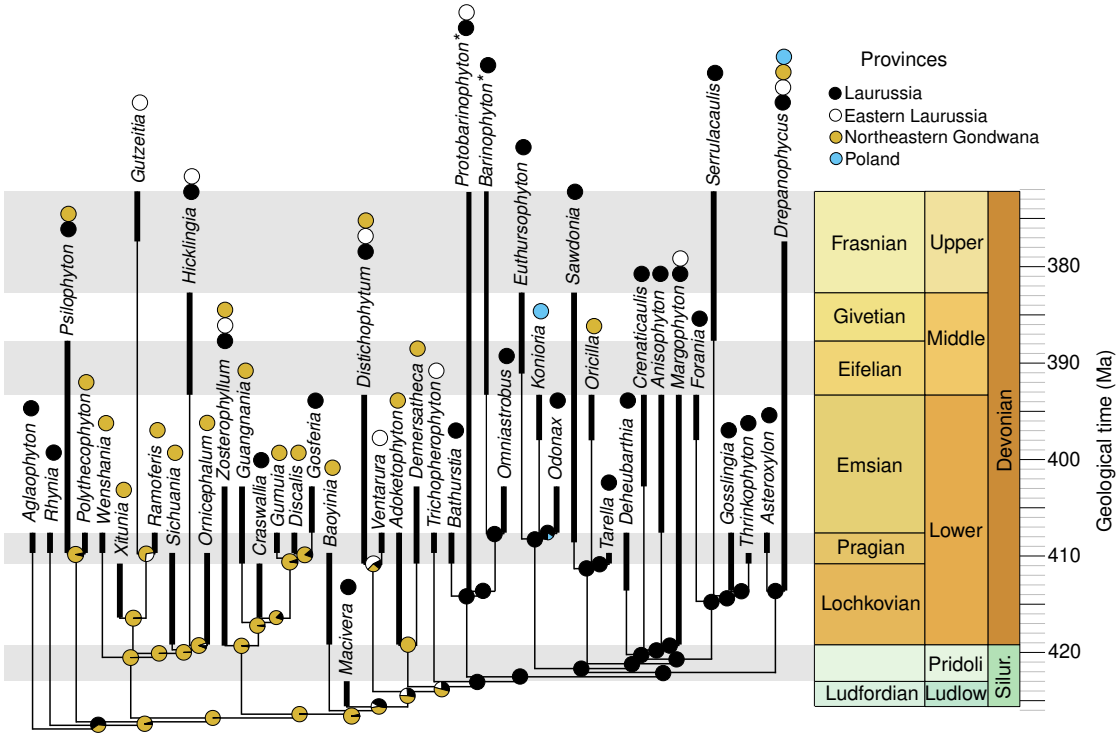


Figure 3.7: Geographical reconstruction of zosterophylls distribution. Time scaled most parsimonious tree of 148 steps over the Devonian (number 6). "*" indicates taxa going farther in the time scale. The circles on top of tips represent the known geographical distribution for each taxa, while the circles at the nodes are the geographical prediction estimated with the DEC+J model.

Comparison with morphology

This information, coupled with morphology brings some insights on Lycophytina evolutionary history. The following figures show for each of the morphological characters retained for the analysis, its evolutionary changes on the tree. The morphological tree (on the right side of the figures) is then associated with the geographical reconstruction, as shown in figure 3.7. The phylogeography tree, on the left side of the figures, aims to compare the closeness of the geographic signal with the morphological one.

Circination

The first character presented is the circination or coiling of axes (Fig. 3.8). This character is somewhat difficult to attribute to all the Lycophytina because of the fragmentation of the fossils. However, the majority of the studied taxa do not show circinate tips. This is a character found in the clade regrouping the Sawdoniacaeae, with some other zosterophylls such as *Adoketophyton*, *Trichopherophyton*, *Bathurstia* or *Discalis-Gosferia*. It is however unknown among Barinophytaceae and numerous other taxa (*Demersatheca*, *Ventarura*, *Baoyinia*, *Craswallia*, *Ornicephalum*, *Sichuania*, *Gutzeitia*, *Xitunia*). This tree clearly shows a trend between the presence of circination and Laurussian taxa. Some exceptions like *Adoketophyton* or *Discalis* are characterized with circination despite being Gondwanan taxa. Lycopsida, on the other hand, are not characterized by this structure. The fact that this character is not found among Lycopsida suggests that this characteristic may be of stem-group Lycophytina only. Among the Laurussian taxa, *Margophyton*, *Distichophytum*, *Macivera*, *Zosterophyllum*, *Hicklingia* are exceptions, without circination. Thus, despite a pattern of presence of circination in the Laurussian stem-Lycophytina, this character shows a great variability with some cases of homoplasy among the tree. Is the circination in Gondwanan taxa of the same condition and origin than the one detected in Laurussian taxa, or is it a common response to a particular developmental function?

Emergences

Another emblematic character representative of zosterophylls is the presence of emergences. Even if emergences are not consistently found within fossils taxonomically assigned as zostero-

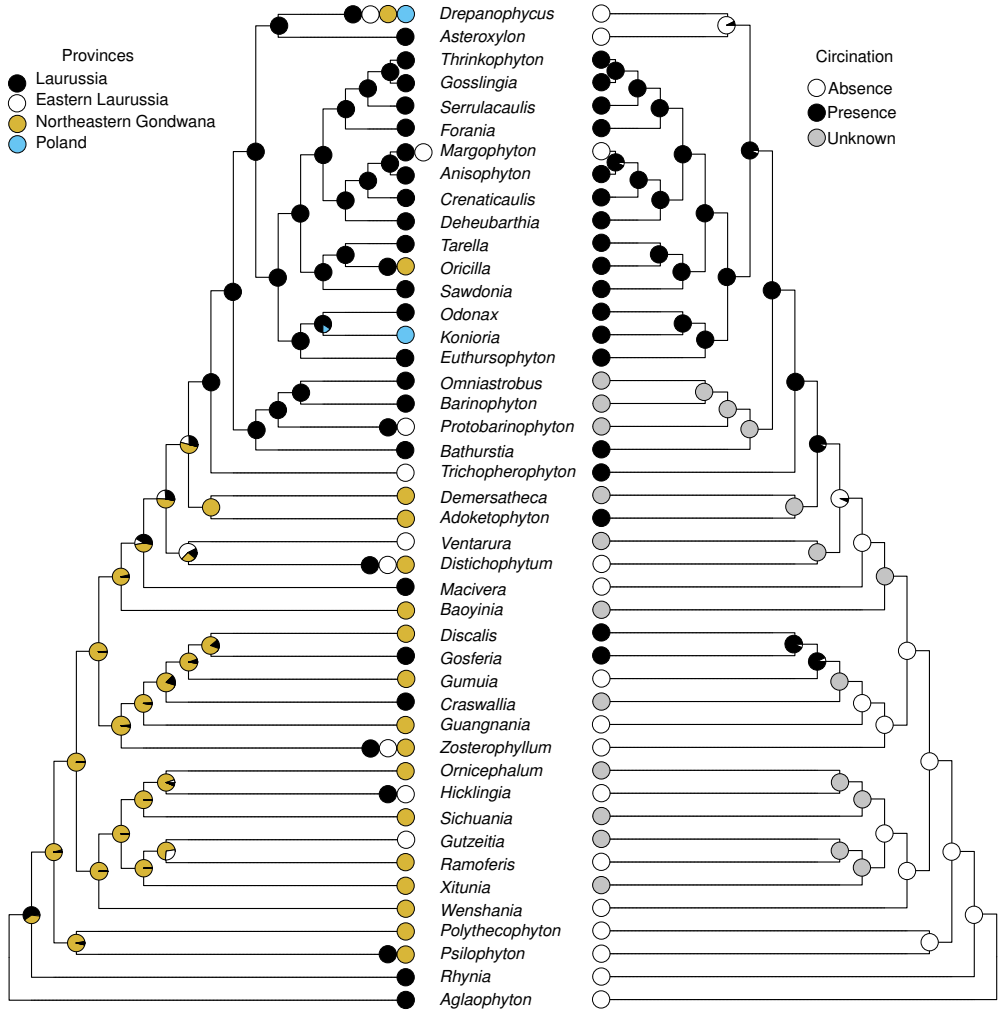


Figure 3.8: Geographical distribution (left tree) compared to the ancestral state reconstruction of the circination (right tree).

phylls, numerous discussions concerning their homology with Lycopsida microphylls make them an important characteristic to study (Bower, 1935). This character follows a configuration similar to that of the circination (Fig. 3.9). However, this structure is more likely to be preserved and found on the fossil record. Thus, a better signal of its evolutionary history is recorded. According to figure 3.9, this structure is mainly absent among Lycophytina. The Sawdoniaceae is the group with the most representatives bearing emergences, with two secondary losses recorded for the clade regrouping *Oricilla* and *Tarella* and the one regrouping *Gosslingia* and *Thrinkophyton*. According to these results, emergences first appear during the Pridoli. The secondary loss from

Oricilla/Tarella and from *Gosslingia/Thrinkophyton* are both synchronous, occurring during the late Lochkovian. The Sawdoniaceae being a group restricted to Laurussia, it is possible to assume that this character reflects a geographical signal.

Barinophytaceae have as sister taxon *Bathurstia*, characterized by "shelf-like" emergences, a unique morphology not found in other zosterophylls (Kotyk & Basinger, 2000). These emergences are arranged in two rows, which is again uncommon. Due to its close relationship with taxa characterized by a sporangiferous appendage, and the particular shape and organization of its emergences, questions arise regarding the homology of this structure towards the Barinophytaceae sporangiferous appendages.

Gondwanan taxa like *Discalis* or *Xitunia* also have "emergences", that may not be homologuous with the ones of the Sawdoniaceae. *Discalis*, for example, is characterized by emergences with a darken tip and interpreted as glandular by Hao (1989b). *Xitunia* on the other hand bears structures called emergences on the sporangia (Xue, 2009). However, these long spines are unique among zosterophylls, and according to their phylogenetic position, this structure may have its own evolutionary pathways. In addition, *Xitunia* is known from terminal strobili only. Finding complete specimens could be interesting to check the presence of similar structures particularly in the stem of the plant.

These Gondwanan taxa have an origin estimated in the middle Lochkovian for *Xitunia* and the middle Pragian for *Discalis*. On the other hand, the Sawdoniaceae have an origination estimated to the Pridoli. Thus, the acquisition of emergences in Gondwanan taxa is asynchronous with the Sawdoniaceae, emphasizing the converging history of this structure.

Sporangium shape

The shape of the sporangium has long been used to determine taxa. However, with the continuous fossil discoveries, diversity of morphologies has been highlighted (Hao, 1989b; Hao & Xue, 2011; D. Edwards & Li, 2018b). The clade Lycophytina is in this study, interpreted as ancestrally bearing ellipsoidal sporangia (Fig. 3.10). One of the earliest groups to emerge is a Northeastern Gondwanan one, mainly characterized by a spherical shape, with the notable exception of *Wenshania* and its reniform shape (W.-Q. Zhu & Kenrick, 1999). A spherical shape will appear again later with *Discalis* (Hao & Xue, 2011) and *Gumuia* (Hao, 1989b), in the clades

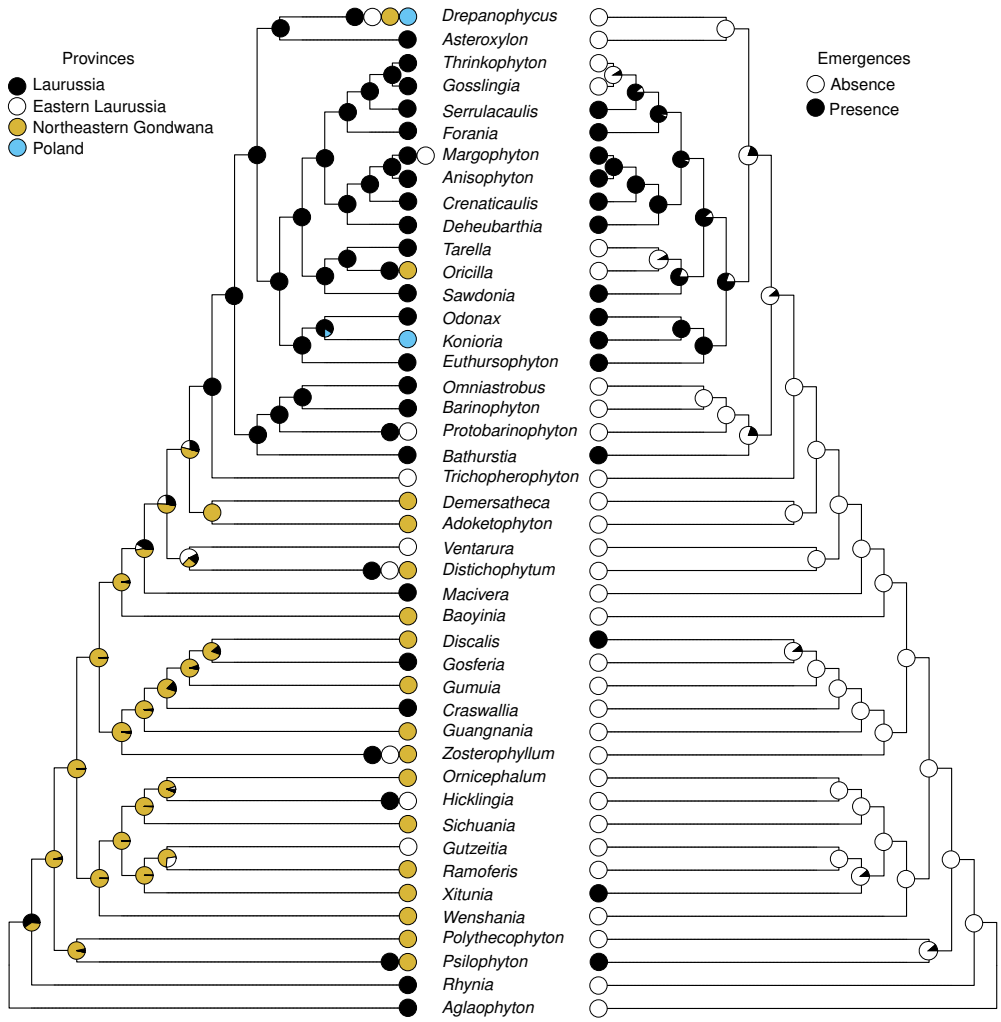


Figure 3.9: Geographical distribution compared to the ancestral state reconstruction of the emergences.

comprising *Adoketophyton-Demersatheca* and *Distichophytum-Ventarura*. This shape is also visible in *Margophyton* and *Sawdonia*. The basal part of the tree is thus divided between a spherical and ellipsoidal shape, two forms relatively close to each other, and that can be easily interchanged in the literature.

With the notable exception of *Wenshania* which is purely a Northeastern Gondwanan fossil, two other basal taxa display a reniform shape, *Zosterophyllum* and *Gosferia*. Nontheless, these two other taxa are known from Laurussia, despite their close phylogenetic proximity with Northeastern Gondwanan ones.

The main trend change among the tree is visible at the *Trichopherophyton* node, where the zosterophylls sharing this common ancestor are characterized by a reniform sporangium. Here again, the geography and the morphology seem to be connected to each other. Reniform sporangia are thus known in derived zosterophyll taxa like the Sawdoniaceae, or *Bathurstia* as well as Lycopsida.

The Barinophytaceae, on the other hand, are characterized by a particular sporangium shape found only in this group and was defined in Chapter 2 as a synapomorphy. According to the ancestral state reconstruction, this configuration seems to be derived from an ancestral reniform shape.

Sporangium, distribution by order of branches

Even if the distribution of sporangia along the plant shows a geographical pattern, as highlighted in figure 3.11, caution is called for since this character needs a good preservation of the fossil, showing at least two orders of branches to be scored. Thus, this information is lacking for numerous taxa (n= 12).

In general, the clade Lycophytina is characterized by sporangia located only in the highest orders of branching i.e. on the latest dichotomous branches, near the apex extremity. However, the Sawdoniaceae and its sister group Lycopsida are characterized by a different strategy, with sporangia distributed also below the dichotomies. These clades are mainly from Laurussia. *Hicklingia*, a genus close to the Gondwanan taxa shows a similar characteristic, and is also present in Laurussia.

Among the Gondwanan taxa, *Ramoferis* and *Wenshania* are the unique zosterophylls sharing this particularity with the Laurussian ones. Thus, the distribution by order of branches seems to appear multiple times in the Lycophytina lineage.

Sporangium, distribution along axis

Among the characters that were previously linked to a geographical pattern is the sporangium distribution. According to Hao et al. (2007), zosterophylls bearing "radially arranged sporangia" are more likely to be found in Gondwana while those having one or two rows will be found preferentially in Laurussia. The present results support this hypothesis, highlighted in

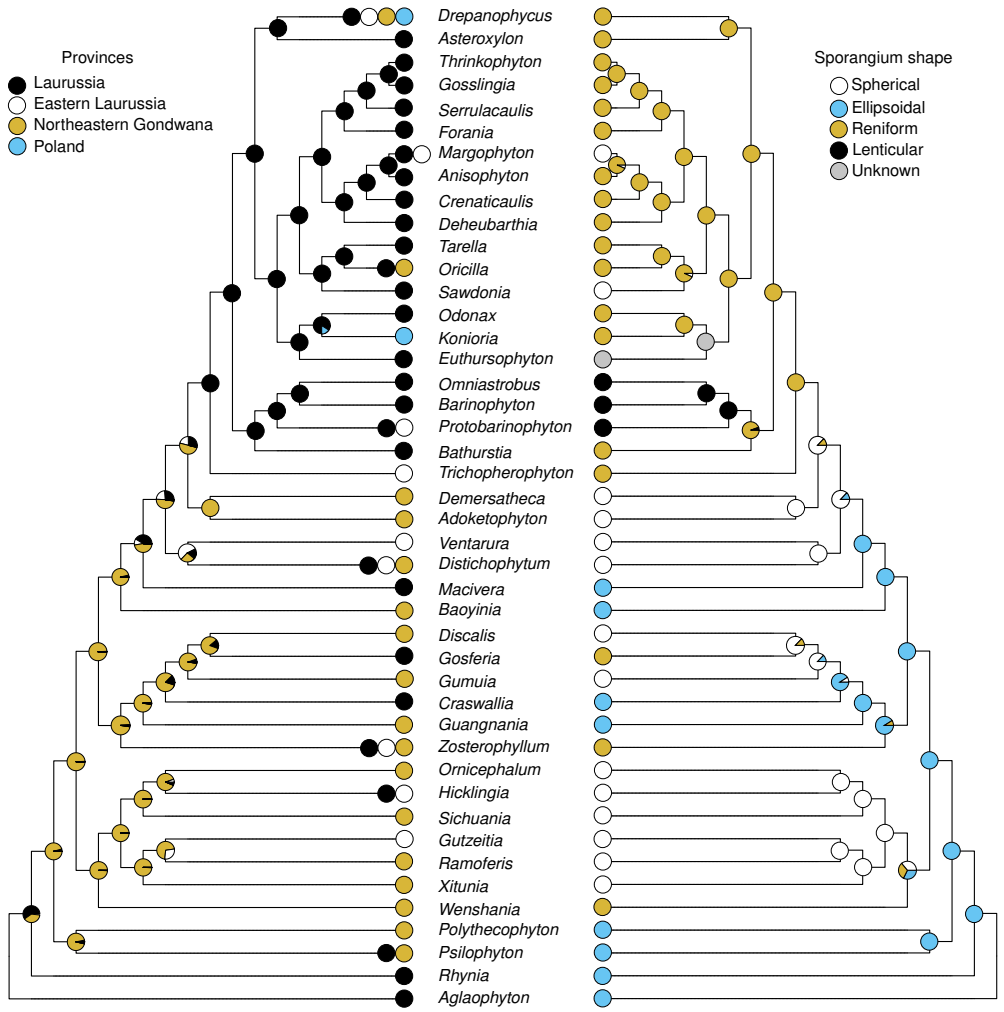


Figure 3.10: Geographical distribution compared to the ancestral state reconstruction of the sporangium shape.

figure 3.12.

In fact, the basal part of the tree is characterized by radially arranged sporangia (in white) for all the zosterophylls. The acquisition of some form of regularity in the sporangium distribution appeared once, in the common ancestor encompassing *Distichophytum* to the Lycopsida (represented in black in fig. 3.12). One exception inside this clade is *Forania*, that is defined as "sparsely scattered" (Jensen & Gensel, 2013), and thus, interpreted here as radially distributed. On the other hand, not all Gondwanan taxa have a radial arrangement of sporangia. *Adoketophyton* and *Demersatheca* two taxa discovered in China display a longitudinal arrangement of sporangia,

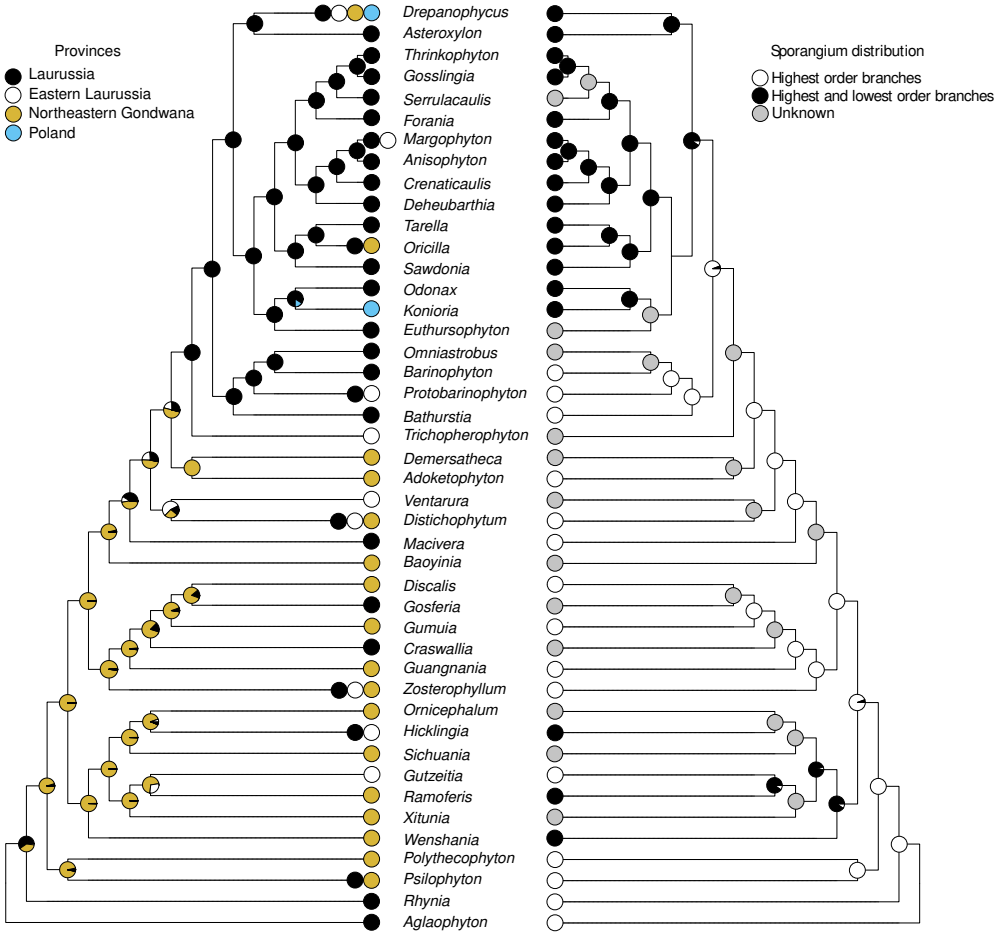


Figure 3.11: Geographical distribution compared to the ancestral state reconstruction of the distribution of the sporangia.

in four rows. This row number is additionally unique among Lycophytina. Consequently, this configuration can explain their derived position inside the tree, being the last Gondwanan representative before the change for a Laurussian distribution.

Thus, the assessment hypothesized by previous authors is strongly visible in the tree, with figure 3.12 showing one of the best resolved character change of this analysis.

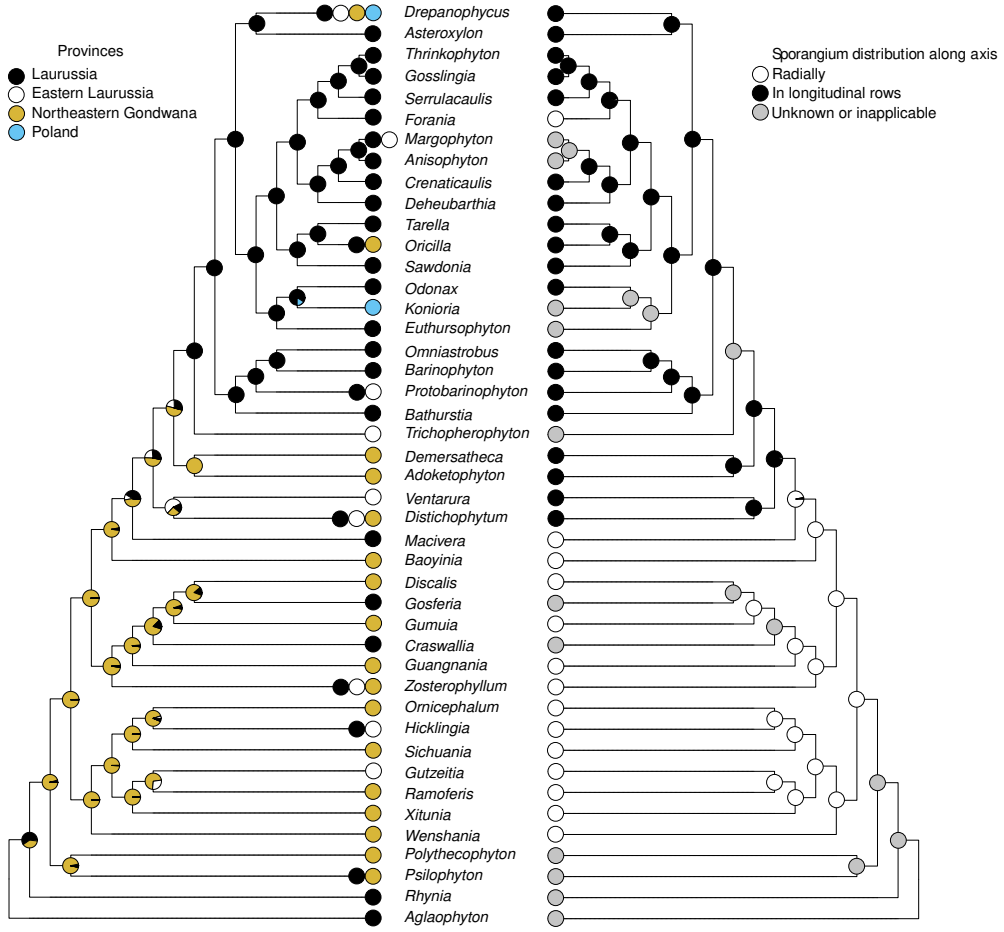


Figure 3.12: Geographical distribution compared to the ancestral state reconstruction of the distribution of the sporangia along the axis.

3.4 Discussion

3.4.1 Phylogeography and sampling bias

The current phylogeny of Lycophytina reflects then a geographical signal. The tree is divided into two parts, with a Ludfordian origin of the group in the Gondwana, and a Laurussian migration during the Pridoli. Thus, according to these results, the process of colonization of lands by these plants is fast, occurring in less than 5 myrs.

This result of Gondwanan origin of early land plants has previously been mentioned in the literature (Steemans et al., 2009), enhancing the confidence in this statement. Lycophytina seems

to be among one of the first groups of early land plants emerging from the Gondwana and progressively reaching other continents.

However, on the four paleoprovinces defined in this study, only two drive the geographical signal on the topology. This is due to the fact that the majority of zosterophylls come from either Laurussia or Northeastern Gondwana. Consequently, this sampling bias is also reflected in the analyses. We reiterate here the precautions called in previous studies and invite for a careful interpretation of their evolutionary history since it is for the moment greatly incomplete. More research on the poorly sampled continents can bring crucial information for the understanding of the group. In fact, since two provinces bring two different morphologies, we can hypothesize that future discoveries in undersampled areas can provide zosterophyll fossils with unique morphologies and enrich our understanding of the group.

Interestingly, we can notice that the basalmost taxa are not the oldest ones. It is particularly well represented in fig. 3.7, with *Macivera*, a Laurussian taxon, present during the Ludfordian, and located on the middle part of the tree, in a more derived position than *Baoynia*. This is the oldest zosterophyll known so far, discovered in Canada (Kotyk et al., 2002), and this unexpected position raises questions about the impact of the fossil gap in our understanding of zosterophylls. For example, a gap in the fossil record is visible in fig. 3.7, during the Pridoli. The first notable observations of zosterophylls in the fossil deposits are starting in the Lochkovian and regroups Gondwanan taxa such as *Baoynia*, *Adoketophyton*, *Ornicephalum* and *Sichuania*. It appears then important to remain critical and cautious concerning the interpretation of these results, in regard of the incompleteness of the information.

The particular case of Lycopsida is also worth mentioning in this section. The group seems in fact to emerge later, during the late Lochkovian, on the Laurussian continent. According to these results, one could easily infer an origination of the group in this continent. However, only two representatives of Lycopsida have been selected for the phylogeny, including one cosmopolitan genus. This taxon selection is based on an emphasis of zosterophylls taxa, and a trade-off between the number of characters used for the phylogeny and the taxa selected have been done in order to keep some resolution on the tree. In this case, Lycopsida were selected only to test their position towards zosterophylls, and no particular emphasis has been done on

this crown group. This observation is thus the result of their phylogenetic position nested into a Laurussian clade, that favors this hypothesis. *Asteroxylon* and *Drepanophycus* are considered as pre-lycopsids (Gensel, 1992) alongside with *Baragwanathia* not sampled in this study. This later genus is mainly composing the Silurian plant assemblages of Australia (Garratt, 1978; D. Edwards, 1990), even if some remains were also described in Laurussia (Hueber, 1983; Kraft & Kvaček, 2017). Because of the Silurian age of *Baragwanathia* and its worldwide distribution, caution is called for when interpreting the geographical history of the Lycopsida, which was not the scope of the present study and is consequently broadly incomplete. For this reason, little interpretation has been applied to Lycopsida in this chapter.

Both paleoprovinces have their own evolutionary history, which is reflected by the morphology. Laurussian taxa for example are more likely to show circination, emergences, and reniform sporangia distributed regularly in more than one order of branching. But despite these differences in their morphologies and strategies, taxa from Gondwana and Laurussia both got extinct during the Emsian. This trend is visible in figure 3.7, where the majority of the branches stop during this stage. In both cases, this trend shows that the extinction of the stem-group Lycophytina is i) global ii) synchronous iii) not linked to any specific geographical or morphological configuration.

3.4.2 Redefinition of the group's evolutionary history

Gondwana as the origin of Lycophytina

The present study finds out Northeastern Gondwana as the place were Lycophytina originated. This observation is further supported by the different characters represented generally at a plesiomorphic state for this paleoprovince. This phylogenetic statement is also supported by the NMDS analysis (Fig. 3.6b) that recovered Yunnan almost centered in the figure, suggesting a reference flora represented by this area. Thus, fossils from South China are precious for the interpretation of the evolutionary history of the group, since the plesiomorphic forms will be more likely recovered in this place, and can be interpreted as the reference flora. Northeastern Gondwana zosterophylls are thus more likely to be found with radially arranged sporangia,

spherical to elliptical in shape. Emergences and circination will be less likely found in this area. This observation can already be applied on the non selected zosterophyll taxa. In fact, as mentioned in Chapter 2, some plant fossils eligible for this kind of analyses were discarded, either because of their uncertain affinity towards zosterophylls and barinophytes, or because of their poor preservation state (see Supplementary material B, list of discarded taxa p. 158). Among these plants, *Hsua* (C.-S. Li & Edwards, 1992) and *Huia* (Geng, 1985a) from China and *Gippslandites* and *Parazosterophyllum* (McSweeney et al., 2020) from Australia are all characterized by radially distributed sporangia (*Hsua* does not have any strobilus), spherical to elliptical sporangia, and no emergences or circination.

Wenshania is, however, an exception among Gondwanan zosterophyll. This taxon shows a surprisingly complex morphology like the reniform sporangia, distributed into multiple orders of branching, which are generally found among Laurussian taxa. This observation is all the more astonishing when it is coupled with its phylogenetic position. Despite bearing some derived characteristics, *Wenshania* is positioned as one of the basalmost Lycophytina taxon. A possible justification lays behind one of this derived characters: the distribution of sporangia by order of branching. In fact, among Gondwanan taxa, *Wenshania* is not the sole taxon displaying this particularity. Such is the case of its closest relatives *Ramoferis* and *Hicklingia*. Since *Xitunia*, *Sichuania* and *Ornicephalum* are scored with a "?" and *Gutzeitia* is the only one with a score of "0", then we can assume that the phylogeny software favored a reconstruction of the "?" as a presence ("1"), making consequently an apomorphy for the group. Once the group is based on an apomorphy, inner relationships are clarified. In the case of the sporangium shape, *Wenshania* is the only one displaying a reniform shape and thus is considered as a separate taxon, in a basal position. This odd observation of *Wenshania* can be then explained by the methodological approach of the software and its paleogeographical implications shall be interpreted with caution. Unfortunately, no further observation can be made on the position of *Wenshania* when the character scoring for the distribution of sporangia is removed, since the consensus tree appears completely unresolved at the Lycophytina node.

The clade *Adoketophyton-Demersatheca* seems to be well supported by a geographic signal. In fact, the phylogenetic analyses consistently recovered these two taxa closely related to each other.

Additionally, they are the taxa used to define the Northeastern Gondwana paleoprovince, according to the SIMPER analysis (Supplementary Tables C.4 p. 208, C.5 p. 209). Thus, the proximity of these two taxa is supported both by the phylogeny and the geography. Additionally, these Gondwanan taxa are more closely related to the Laurussian clade rather than the Gondwanan basal group. They are in fact in the most derived position, located at the node right before the Laurussian cladogenesis. This phylogenetic proximity can be explained by their arrangement of sporangia into longitudinal rows. In fact, as mentioned by Hao et al. (2007), the difference between taxa discovered in Gondwana and the Laurussian ones lies in the arrangement of the sporangia. Gondwanan taxa are more likely to have a radial sporangial arrangement. The clade *Adoketophyton-Demersatheca* and *Distichophytum* are notable exceptions. This character seems to appear in the most derived forms of Lycophytina including some Gondwanan taxa and appears thus before the Laurussian radiation. In addition, Gondwanan clades show a particularity in sporangia distribution, that are arranged in four rows, and not two, as it is observed in Laurussian taxa. This difference coupled with this particular configuration suggests that this sporangial arrangement is more likely homoplasic with the Laurussian taxa.

The historical case of Laurussian taxa

Additionally, by emphasizing on the provincial morphological differences of Lycophytina, this analysis highlights and takes a fresh look at the evolution of the group. In fact, zosterophylls were historically defined as plants with a lateral arrangement of sporangia, generally reniform in shape. The presence or absence of emergences and circination already played an important role in the classification of the group in different orders (Banks, 1968; Gensel, 1992; Kenrick & Crane, 1997). These preliminary studies, that led to our current knowledge of zosterophylls were mainly emphasizing on Laurussian taxa, mostly known at that time. With the later discovery of the rich Gondwanan flora, the studies of the group tried to fit the previous morphological assumptions on the expanded zosterophylls, and this geographical distribution still went unnoticed. Thus, structures defined as part of zosterophyll's identity end up with this analysis to be provincial particularities, enriching the understanding of the group's evolutionary history. This is best represented by the presence of emergences summarized in figure 3.9. The great variability of these structures, in term of shape and distribution makes it difficult to study this character,

despite its notable importance in the eyes of specialists. As mentioned in Chapter 2, some taxa like *Gosslingia* and *Thrinkophyton* are described as bearing "unicellular hairs", or trichomes (D. Edwards, 1970; Kenrick & Edwards, 1988b). Since emergences were defined here as pluricellular, spine-like structures, these taxa were scored as "0". But according to their evolutionary history, the unicellular structures can be interpreted as a secondary loss of an ancestral emergences, showing a fast evolutionary history of this character. Here, the emergences seem to be the prerogative of the family Sawdoniaceae, even if some isolated taxa display similar structures (*Bathurstia*, *Discalis*, *Xitunia*). Thus, Laurussian fossils bearing emergences can be put among Sawdoniaceae with confidence, while spiny structures found in Gondwanan taxa are more likely homoplasic.

Barinophytaceae is more likely to be a clade of Laurussian origin. In fact, the present results found out *Barinophyton*, *Protobarinophyton* and *Omniastrobus* together, in the Laurussian paleoprovince. *Adoketophyton* on the other hand, was defined as a barinophyte due to the fan-shape structure below the sporangium that was interpreted as homologous to a sporangiferous appendage. However, the results showed no phylogenetic proximity between *Adoketophyton* and the other Barinophytaceae. Additionally, *Adoketophyton* is the sole Northeastern Gondwana "barinophyte" sampled for the study. Since this taxon is not associated to the Barinophytaceae, it is more likely to assume that the family is restricted to Laurussia, and the fan-like structure of *Adoketophyton* may be homoplasic to the sporangiferous appendages. Inclusion of other Laurussian barinophytes such as *Kaulangiophyton* (Gensel et al., 1969), *Krithodeophyton* (D. Edwards, 1968) or *Faironella* (Gerrienne, 1996a) could enhance the understanding of this family, depending of their inclusion or exclusion from the group. *Faironella*, in particular, may question this phylogenetic position because of its emergences, and close morphological proximity with *Sawdonia* (see discussion in Chapter 2 for further information). Additionally, Gondwanan barinophytes such as *Bracteophyton* (D.-M. Wang & Hao, 2004) can either confirm or deny this geographical distinction for Barinophytaceae, depending of its phylogenetic position.

From the taxon selection (Supplementary material B, list of discarded taxa p. 158), two plants in particular may impact this view. In fact, *Danziella* (D. Edwards, 2006) and *Nothia* (Saadawy & Lacey, 1979) are both known in Europe, with a radial arrangement of sporangia. Despite

this difference, they both have a reniform sporangium, and *Nothia* even displays a particular emergence shape (Saadawy & Lacey, 1979). Thus, if these taxa were to be included inside this work, they may end up at the basal position of the Laurussian clade for *Danziella*, and among the Sawdoniaceae for *Nothia*.

Thus, zosterophylls display a richer diversity than previously established.

3.5 Conclusion

The geographical distribution of Lycophytina was herein explored through phylogeography, in order to detect any pattern inside the topology that could help further understanding their evolution on lands. Unsurprisingly, two terranes are more prevalent, namely Laurussia and Northeastern Gondwana, due to the richness sampled in these two paleoregions. Results suggest that Gondwanan taxa are preferentially regrouped together at the basis of the tree. Laurussian taxa, on the other hand, appear regrouped together in a distal most position, suggesting a main event of dispersion from Gondwana to Laurussia. In addition, these Laurussian taxa display more likely derived characteristics compared to the Gondwanan ones, suggesting a different evolutionary pathway. Therefore, the origination of the group seems to be from Gondwana, supporting previous hypothesis on the emergence of land plants. These observations could be further tested thanks to sampling effort on the poorly studied regions, in order to detect at a thinner scale the different geographical pathways taken by this group.

Chapter 4

Diversity

Throughout this PhD, the relationships of zosterophylls have been revised, and their geographical dispersion explored. In the present chapter, their evolution over time will be updated, thanks to the use of diversity analyses. With the inclusion of this method, a broad vision of their evolutionary history will be presented.

4.1 Introduction

The evolution of life on land is a series of events that began in the Paleozoic. Among the first organisms to transition from water to barren land are the plants, in a process that started during the Ordovician (Rubinstein et al., 2010). First unequivocal macrofossil remains of land plants date back in the Silurian (Libertín et al., 2018). Starting from this point, a gradual increase of diversity and complexity has been discovered in the fossil record, starting with the Silurian - Devonian "terrestrial revolution" (Hetherington et al., 2021)

Among the observations made on the plant fossil record, some time periods are dominated by specific group of plants (Niklas et al., 1980; Niklas et al., 1983; Niklas & Tiffney, 1994). From this observation different "Evolutionary Floras" (Cleal & Cascales-Miñana, 2014; Capel et al., 2021) have been named, referring to these specific plant communities. The first unequivocal flora is called Eotrachophytic (Cascales-Miñana, 2016), designating the Silurian rhyniophytes plants, particularly abundant in the earliest terrestrialization phase. They are characterized by a

small size, and simple isotomous branching, with axes bearing terminal, elliptical sporangia. But this first flora has been quickly supplanted by the one addressed in this work, named the Eophytic flora.

This latter one is characterized by a dominance of Lycophytina, during the Devonian period. Lycophytina is a group of Tracheophyta characterized by numerous lateral sporangia, opening thanks to a distal dehiscence line. This morphology contrasts with the one found in the Eotracheophytic flora. Thus, the change of group dominance is marked by a more complex morphology, enhancing better colonization strategies, particularly thanks to a higher number of reproductive organs. This phenomenon has been recently brought to light, thanks to numerous studies (Capel et al., 2021; Capel, Cleal, et al., 2022; Capel, Cleal, et al., 2023; Capel, Monnet, et al., 2023). Authors put their scope on the Silurian-Devonian transition, considered as a "terrestrial revolution" of critical interest. Thanks to their global studies of the plants known at that time, we now have a better understanding of the Silurian-Devonian evolution of land plants. Thus, according to Capel et al. (2021), the Lochkovian sees the last remains of the Eotracheophytic flora, while the Eophytic flora expands during the Early Devonian. Lastly, the Famennian sees the rise of the Palaeophytic flora, typical of the Carboniferous period. Accordingly, the early land plant radiation is a process taking place over the Devonian period (-420 Ma to -359 Ma) and needs to be studied in detail to grasp its nuances.

The Eophytic flora, in particular, is divided into two phases, composed of different groups within Lycophytina. The early Eophytic flora is bounded by the end of the Silurian to the Eifelian and is dominated mainly by the extinct zosterophylls (Fig. 4.1). They are of particular interest for the present study, because it is one of the first group of plants that dominated the first continental environments worldwide (see Chapter 3), and have largely supplanted the previous flora, both in abundance and colonization strategy. Because of their preponderance in the fossil deposits during a period of low plant diversity, zosterophylls are the ones shaping the early Eophytic phase from Capel et al. (2021). The trend shows a fast diversification process before they reach a peak during the Pragian, quickly followed by a decrease of diversity during the Emsian, for the benefit of the Lycopsida, the main component of the Late Eophytic flora.

The Eophytic curve has been initially established in a study focusing on zosterophylls genera (Cascales-Miñana & Meyer-Berthaud, 2014). Later on, the authors have specified the results

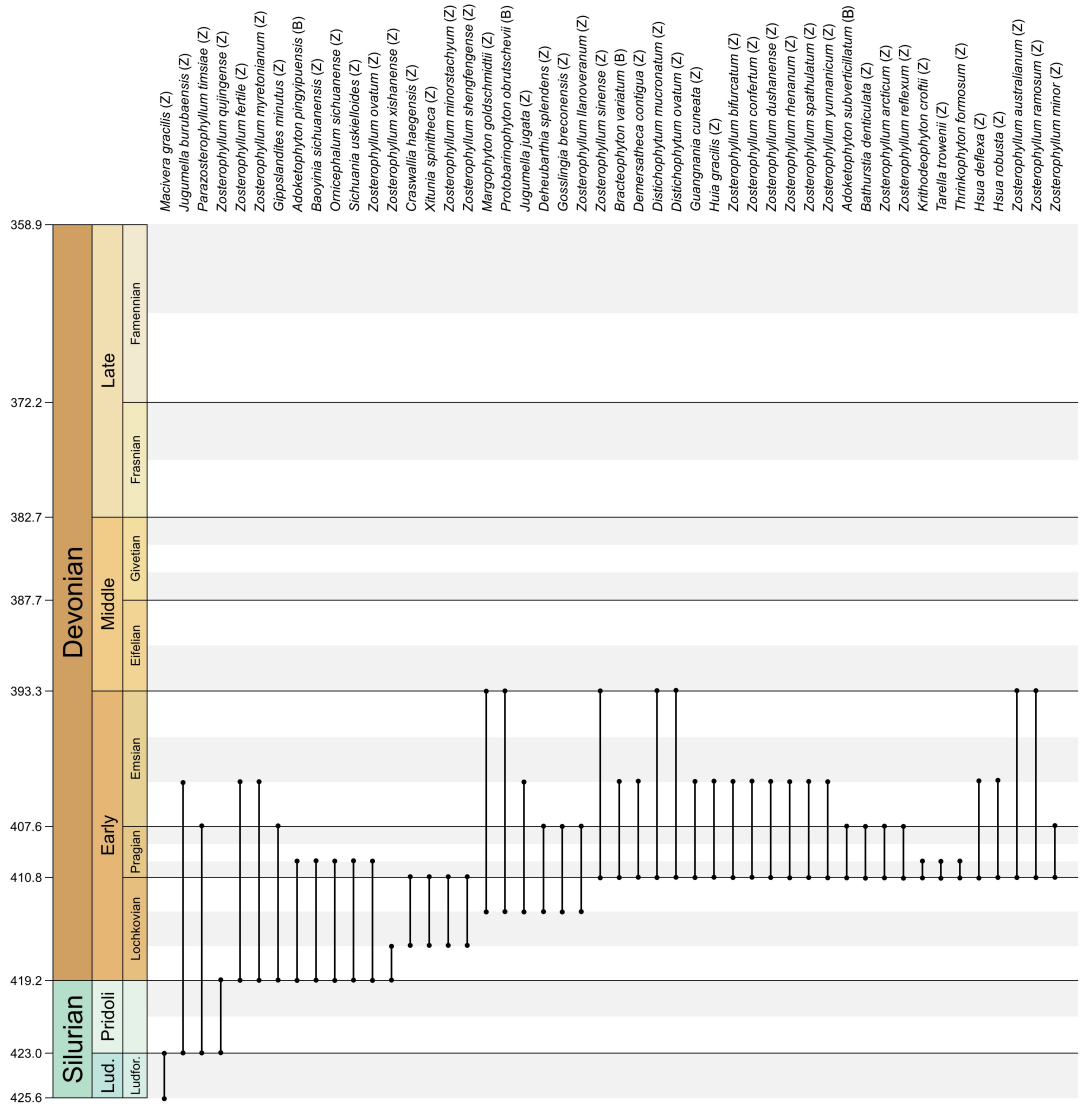


Figure 4.1: Temporal distribution of zosterophylls. Each vertical bar represents the current known temporal distribution of a given taxon. The points at each extremity picture the earliest and latest occurrence known. The left part of the figure is the chronostratigraphic chart from the late Silurian and covering the Devonian. Each taxon is chronologically ordered from their First Occurence Datum. Species name are located at the top of the figure. The letter "Z" after the species name refers to "Zosterophyll", while the letter "B" stands for "Barinophytes".

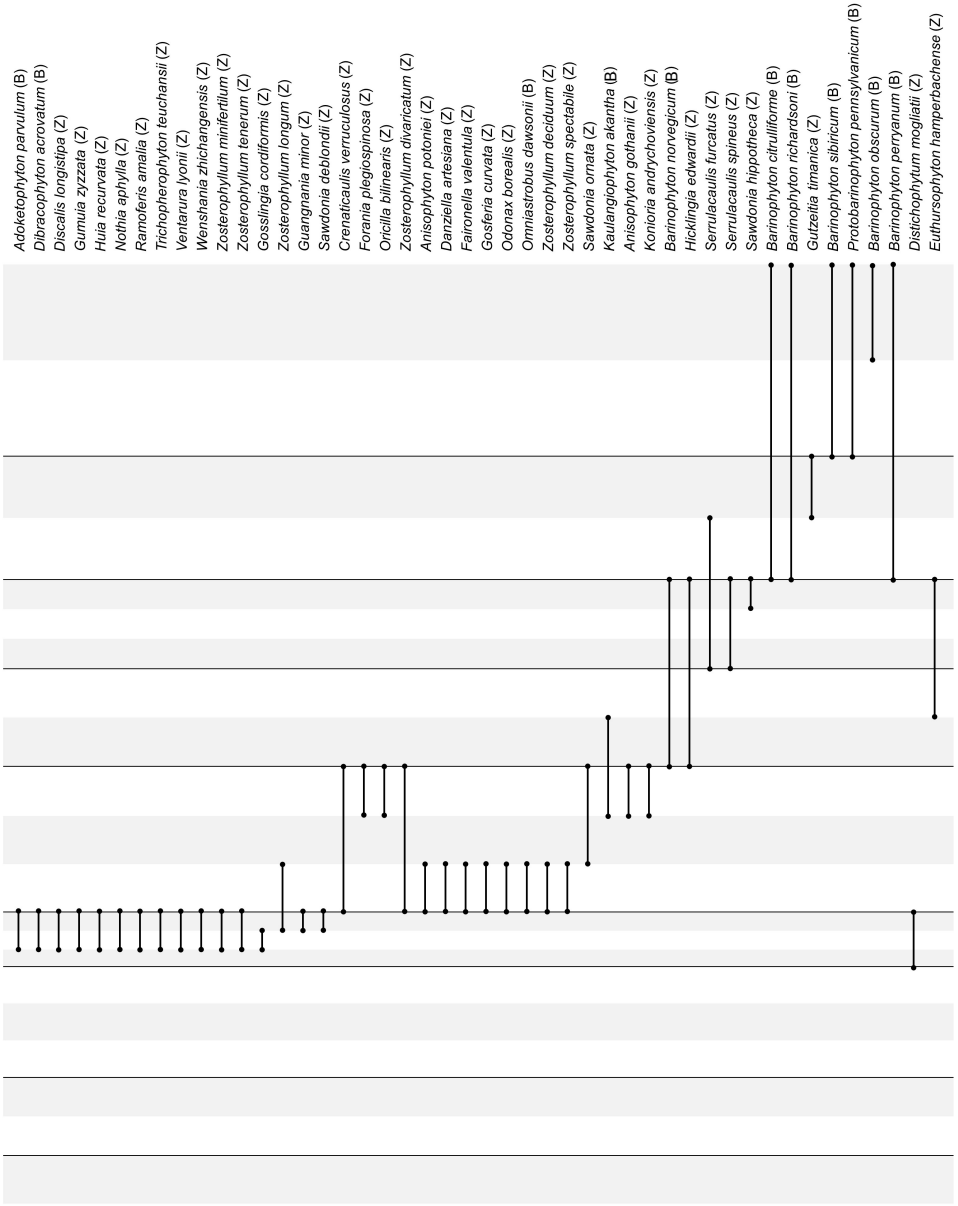


Figure 4.1: Temporal distribution of zosterophylls (cont.).

with a focus at the species level, and with a spatial cut-out (Cascales-Miñana & Meyer-Berthaud, 2015). Despite this improved precision, the results remained consistent with the original one, suggesting that global triggers are behind the zosterophyll's trend. The latest study taking into account this group is the one of Capel, Cleal, et al. (2022), and again, a similar trend has been found. These previous studies were all based on range-through databases, using the temporal distributions of their taxonomical units. Despite being a common way of measuring diversity, no studies tried so far to measure the temporal distribution of this key group using more precise methodologies based on occurrences datasets (Alroy, 2010; Chao & Jost, 2012). They allow for a better resolution in the curve, as well as bias correction and uncertainty estimation thanks to resampling strategies and the elaboration of new diversity indexes (Alroy, 2020). Additionally, numerous recent fossil discoveries of zosterophyll affinities increased both their abundances and their morphological inconsistency. More than ever, studying this group into a phylogenetic context is important to catch the Early Devonian dynamics of land plants. For this reason, a diversity count taking into account the phylogenetic lineages will be performed in this study. It provides precise results based on relationships between the taxa and an extended sampling inference through ghost lineages. Using for the first time these methodologies on zosterophylls, the idea is to provide the most complete dataset for the group to i) create a resolved diversity curve ii) measure the impact of bias corrections on the curve iii) link this information with any morphological or environmental signal. According to the previous recent results found in literature, the current study will not differ strongly from the previous publications. But thanks to this improvement in the resolution and methodological exploration, we aim to gain a better understanding of the evolution of this group during these remote times.

4.2 Material and methods

4.2.1 Data

An occurrence dataset (Supplementary Table D.1, p. 239) regrouping all known taxa of zosterophylls has been compiled, thanks to data extracted from literature. For this study, each occurrence has been considered, at the species level. Taxa with a doubtful identification (refereed

as "?" in the publication) were not added, in order to prevent from taxonomical errors. Taxonomical ambiguity on the other hand (i.e: *cf.* or *aff.*, representing 4% of the dataset) were considered in this study. In fact, recent taxonomical reinvestigation generally replaced ambiguous taxa inside the zosterophylls (D. Edwards & Li, 2018a, 2018b). Thus, the taxonomical qualifiers seem to be at least from zosterophyll affinity, and are therefore relevant to include. Within zosterophylls, barinophytes are included as well, considered as a group on its own (Fig. 4.1). Additionally, the sample includes taxa defined as *incertae sedis* but commonly viewed as zosterophylls such as *Bracteophyton* (D.-M. Wang & Hao, 2004), *Danziella* (D. Edwards, 2006), *Dibracophyton* (Hao et al., 2012), *Faironella* (Gerrienne, 1996a), *Huia* (Geng, 1985a), *Hsua* (C.-S. Li, 1982), *Jugumella* (Senkevich, 1975), *Kaulangiophyton* (Gensel et al., 1969) *Krithodeophyton* (D. Edwards, 1968), *Nothia* (El-Saadawy & Lacey, 1979). Lycopsida are not included in this analysis, despite their close affinity (see Chapter 2). In fact, since they are defined as the dominant group of the Late Eophytic flora (Capel et al., 2021) and the present analysis focuses on the Early phase of this flora, the emphasis has been made on the stem-group Lycophytina only. Caution is then advised when interpreting the curves, since it does not include all the descendants of the studied group. The dataset is available in Supplementary Material and is composed of 387 entries, with a temporal range of 81 myr, from the Ludlow to the Tournaisian, for a total of 50 genera and 95 species. Data concerning the taxonomy, the locality, formation, age, and the province have been filled. Age, in particular, has been entered at the substage level thanks to information extracted from literature. For consistency, if only a larger stratigraphic information is available (e.g. "Early Devonian", or "Emsian"), the time span is converted at the substage level (e.g. "early Lochkovian to late Emsian", or "early to late Emsian"). Some stages have been divided into three substages (early, middle, late) due to some age description in the literature, specifying a middle substage (Stockmans, 1968; Schweitzer, 1979; Hueber, 1983; Wellman et al., 2000; Hao & Xue, 2013; Morris & Edwards, 2014). In addition, a spatial cut-out has been added in order to detect for any regional pattern. The regions selected are the ones defined in Chapter 3. This comprehensive dataset is the most complete for zosterophylls to date.

4.2.2 Methods

Diversity estimates

Occurrence-based datasets provide a more precise information about the temporal distribution of taxa and the abundance of specimens within a given species, that help to correct for some biases. In fact, a precise information of the stratigraphic distribution, and refined information about the abundance of the species studied allow for resampling strategies. Here, the richness of a given zosterophyll is provided thanks to the number of localities recording this species. These strategies help correcting the sampling bias of the fossil record and correct for the uneven stratigraphic divisions. Multiple diversity curves were built in order to see the different trends and compare for the bias corrections. Among these analyses, results from Shareolders Quorum Sampling (SQS) (Alroy, 2010), correct for the species occurrence, while a uniform time bin (UTB) of 1.7 myr each has been applied, correcting for the unevenness of time division. Since the aim of this study is to compare the results with the previous ones, range-through and boundary crossers (BC) estimates (Foote, 2000) have been done, for comparison. These analyses were performed at both genus and species levels for comparison and were conducted on R (R Core Team, 2023).

Evolutionary rates

To complete the view of their temporal distribution, evolutionary rates have been estimated. These indexes have been measured for taxa present only in the studied time interval (per taxa rates), as well as taxa crossing the time boundaries (per capita) in order to estimate the difference in the sampling. The rates have additionally been estimated with a UTB of 1.7 myr in order to further notice the impact of the unevenness of the stratigraphic ranges.

Rarefaction

Since the dataset is based on occurrences, information about the richness of the zosterophylls sampled over time can be estimated, through rarefaction analyses. Rarefaction analyses are based on the estimation of species richness inside a community. This approach evaluates the efficiency of the sampling and can detect potential biases such as the unequal sample size (Hurlbert, 1971).

Thus, Classical Rarefaction were performed with its 95% confidence interval, for each time bin (here at the substage level).

Diversity count on phylogenies

This compilation of raw data has been then compared with diversity analyses that take into account the phylogenetic relationships. To do so, the phylogeny from Chapter 2 has been included. Thus, a data matrix containing 38 genera of zosterophylls and two lycopsids has been created and ran under parsimony analyses (Goloboff & Catalano, 2016). The most parsimonious trees were time calibrated and the resulting diversity estimated thanks to the package strap (Bell & Lloyd, 2015) on the R software. This calibration takes into account the divergence time between lineages and reconstructs an ancestral origination, sometimes outside the range sampled. This phenomenon, called "ghost lineages" allows for an estimate non-constrained by the fossil record and can extrapolate the origination time of the fossils.

4.3 Results

4.3.1 Genus and species diversity

Figure 4.2 shows the taxonomic diversity of zosterophylls over time, at the species (A) and genus (B) levels. The curves for the range-through (in blue), boundary-crossers (in red), SQS (in green), and uniform time bin (in purple) are superimposed to compare their trends. The overall dynamic for species and genera is similar, with an important diversification phase between the end of the Silurian until the Pragian. An inflection point changes the steepness of the curve for a more drastic diversification during the late Lochkovian or early Pragian, depending of the index used. The maximum diversity of the group is reached by the late Pragian, forming a peak in the zosterophyll distribution over time. It is immediately followed by an important decrease between the early Emsian until the early Eifelian. This drop reaches its lowest point by the middle Emsian, while a progressive increase takes place by the late Emsian. This trend forms a second peak in the diversity curve, lower than the Pragian one. Hereafter, a second important drop of diversity is occurring between the late Emsian and early Eifelian. Starting from this time

period, a final stochastic plateau of low diversity spans until the Famennian.

This similarity in the pattern is also recovered between the different methods used, with the notable exception of SQS (in green). In fact, this curve infers generally a lower diversity for a similar time period considered. This estimated diversity is generally twice as low as when traditional metrics are used, and even the highest estimations provided by the error bars hardly reach the other metrics values. The trend in this curve is additionally different when estimated at the species level compared to the genus one. For example, the species estimation presents a gap between the middle and late Lochkovian, and an additional one between the late Emsian and the middle Eifelian. The maximum of diversity estimated with the SQS index is visible on the early Emsian at the species level. This peak is immediately followed by a drop of diversity by the middle Emsian, before raising up again during the late Emsian, but in a lower estimate than the previous peak. After the late Emsian, the SQS distribution follows a stochastic plateau similar to the ones of the other metrics. At the genus level on the other hand, only one gap is visible, earlier than in the species estimate, between the early Pridoli to the early Lochkovian. This gap is preceded by a decrease of diversity between the Ludfordian and the early Pridoli, contrasting with the trends given by the other metrics. The highest point of diversity is also contrasting, because occurring earlier than the Pragian. In fact, a first peak is visible by the late Lochkovian and is rapidly decreasing to a relative stable value of less than ten taxa sampled. A slight decrease takes place during the Pragian. By the middle Emsian, this trend reaches its lowest point before rising up again during the late Emsian. From this time period, a drop in diversity is observed, and the curve reaches a stochastic dynamic from the Eifelian until the extinction in the Famennian. Here again, a notable difference is visible with the other metrics as well as the species estimation. This plateau is in fact low, with a number of genera sampled close to one, reinforcing its distinction from other metrics.

Apart from the SQS analysis and its contrasting dynamic, the three other metrics are globally similar. The range-through index (in blue) is the one with the highest diversity estimations, while boundary crossers (in red) is the one of the trio with the lowest estimate values. The uniform time binning (in purple) displays more precision in the shape of the diversity curve, compared to the two others.

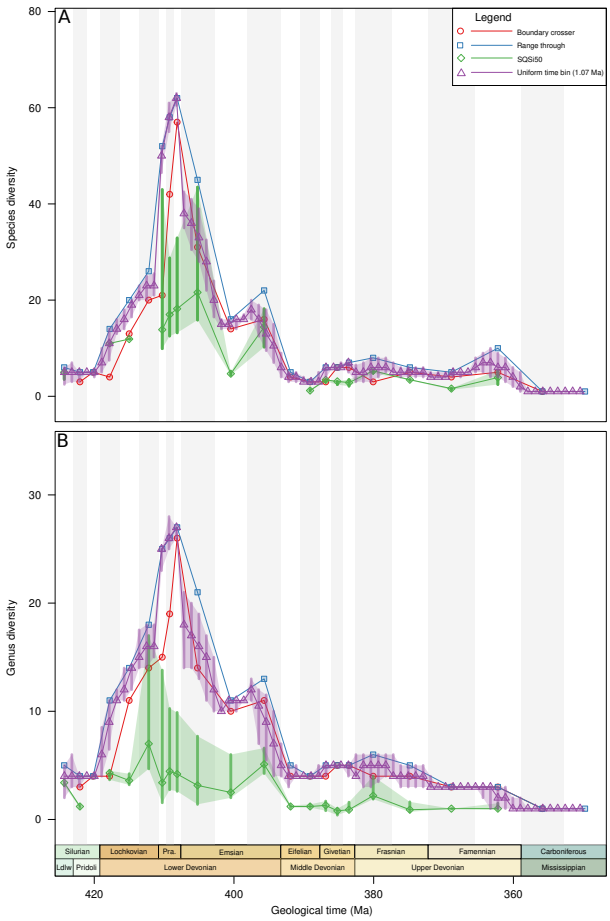


Figure 4.2: Diversity analyses measuring the richness of zosterophyll taxa across the late Silurian and the Devonian, with a temporal resolution at the substage level. Measures done at the A) species and B) genus level. Four diversity metrics are represented. Range through and boundary crossers (in blue and red respectively) are the conventional index used, while uniform time bin and SQS (in purple and green) are based on resampling processes.

4.3.2 Origination and extinction rates

Origination and extinction rates have been estimated and summarized in figure 4.3. In both cases, trends are different when measured at the species (Fig. 4.3 A and C) and genus (Fig. 4.3 B and D) level.

At the species level, origination and extinction are occurring regularly along the zosterophylls' time span, providing curves with a sawtooth distribution. The late Silurian and Early Devonian are characterized by important origination events, with the Pragian being one of

the most important peak measured (Fig. 4.3A). Origination peaks are recorded during the late Ludfordian, early Lochkovian, early Pragian, late Emsian, middle Givetian, early Frasnian and early Famennian. On the other hand, origination rates are at their lowest during the late Pridoli, late Lochkovian, middle Emsian, late Eifelian, late Givetian, late Frasnian and late Famennian. This distribution can be paralleled with the extinction rates. In contrast to the origination rate, the highest extinction peaks occur during the early Famennian and early Emsian, and are thus more visible by the Middle and Late Devonian (Fig. 4.3C). Because of this particular sawtooth distribution, different stages are recorded with high extinction rate such as late Ludfordian, late Pragian, late Emsian, late Givetian, and late Famennian. The extinction rate is at its lowest during the middle Lochkovian, middle Emsian, late Eifelian to early Givetian, early Famennian.

On the other hand, at the genus level, both origination and extinction rates are restricted to a particular time period for the highest record. For example, origination peaks are high during the Ludfordian, early Lochkovian and early Pragian (Fig. 4.3B). Then, some individual peaks, with a relative low rate compared to the previous ones are visible in the early Emsian, early Eifelian and early Givetian. Outside of these stages, origination rate is close to 0. The extinction rates, on the other hand, are particularly visible during the Pragian, late Emsian, and surprisingly, Ludfordian (Fig. 4.3D). Smaller peaks are punctually visible by the late Givetian and late Famennian. Otherwise, the other time bins do not show any extinction rates.

Evolutionary rates were performed using different metrics. Counts were based either on taxa strictly confined to the interval (per taxa rates), or by including boundary crossers (per capita rates). In addition to these estimations, a second count was done by standardizing the time span into equal time bins, both for the per taxa and per capita rates. Despite the use of these four metrics, the trends in figure 4.3 display a similar pattern. Globally, the "per capita" estimate is a bit higher than the "per taxa", except for fig. 4.3 A, were the trend is reversed.

4.3.3 Phylogeny estimate

Figure 4.4 shows the diversity analyses using phylogenies. In figure 4.4A, the best fit to stratigraphy (tree number 6) among the most parsimonious trees (n= 6) is shown, with known stratigraphic distribution represented in the branches in bold while the ghost lineages are recon-

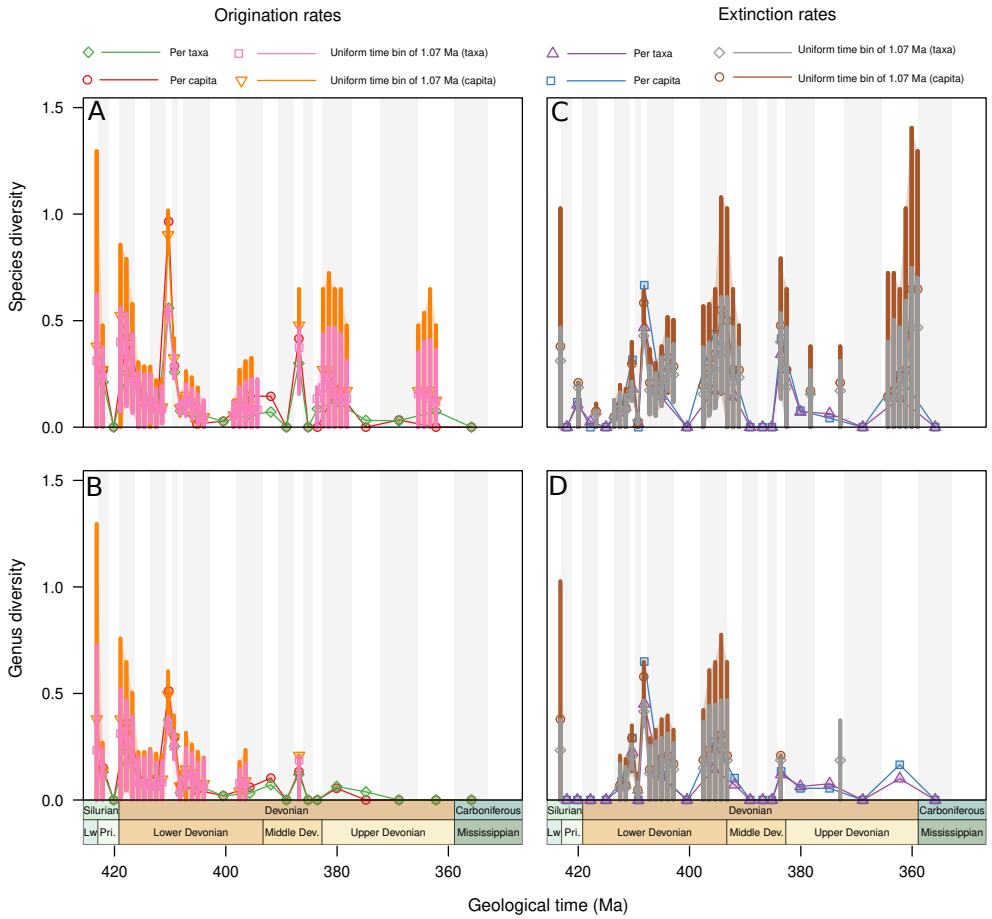


Figure 4.3: Estimation of the evolutionary rates of zosterophylls across the late Silurian to the Devonian. Time resolution at the substage level. A and B) regroup the origination rates while C and D) the extinction rates. Measures done at the species A and C) and genus B and D) levels. Four metrics are used for each of these configurations. Raw estimation per taxa and per capita, with an additional standardization of the time bins, per taxa and per capita.

structed in thin lines. Figure 4.4B is the diversity count along the most parsimonious trees. Uncertainty is represented by the grey area around the curve, due to the differences in tree topologies. The diversification of the group takes place between the Homerian to the Lochkovian, while a gradual decrease starts from the Pragian until the end of the Devonian. No plateau is visible whatsoever.

The combination between the curve and the topology can give detailed information about the temporal dynamics among zosterophylls. For example, the Pragian drop is congruent with the majority of the branches that stop at the same time (n= 19). The tail of the curve is represented

by a few taxa, which in the topology, were present before the Pragian. Therefore, these remaining taxa show a surprisingly important branch length. *Drepanophycus*, *Serrulacaulis*, *Sawdonia*, *Euthursophyton*, *Barinophyton*, *Protobarinophyton*, *Hicklingia*, *Psilophyton* and *Gutzeitia* are the taxa involved in the distribution of the tail of the curve.

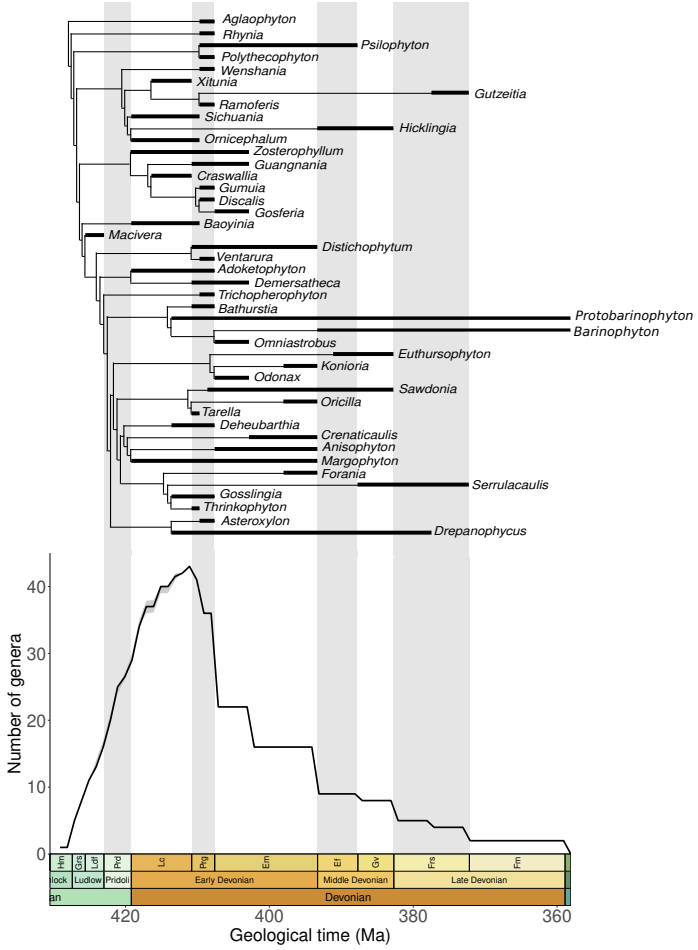


Figure 4.4: Diversity analyses of zosterophylls using time-scaled phylogenies. A) Topology with the best fit to stratigraphy (tree n°6 from chapter 2). B) Diversity curve of the group based on the most parsimonious trees. The grey area around the curve shows the differences in estimate between the topologies.

4.3.4 Rarefaction

Rarefaction curves are produced for each substage between the late Silurian to the Late Devonian and are represented in fig. 4.5. No plateau is reached for each of these time bins, even if among

the 23 substages, only four (early Emsian and Pragian) appear sufficiently sampled, with a threshold of 65 taxa reached. This indicates a weak sampling of zosterophylls in 19 Devonian substages.

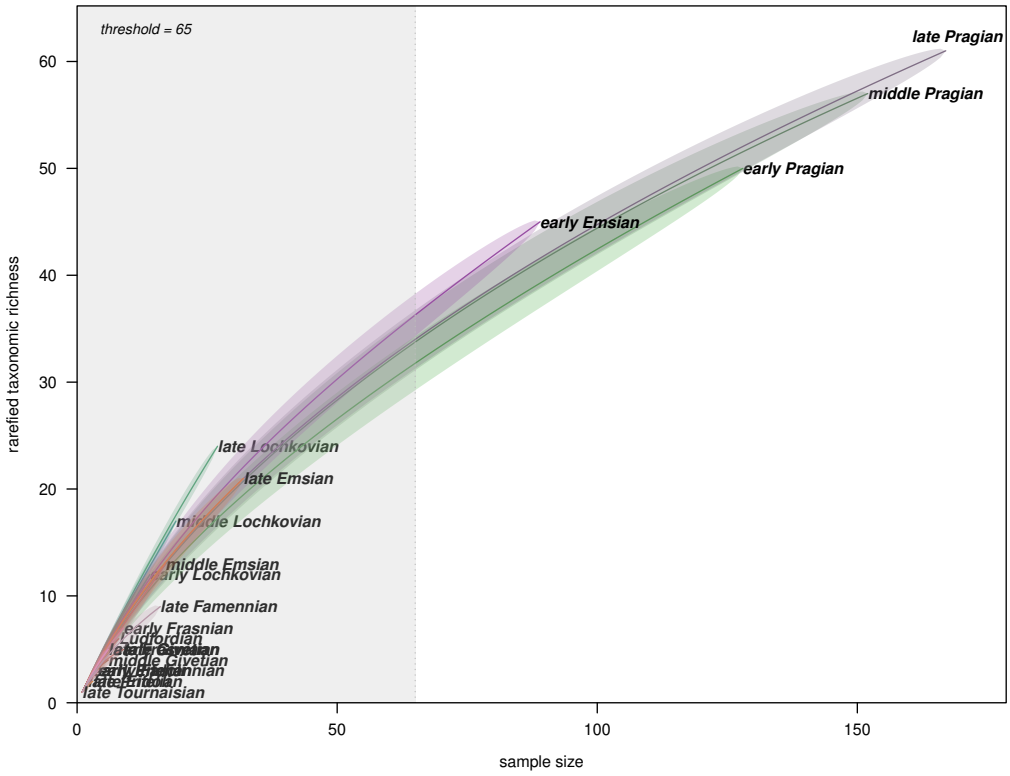


Figure 4.5: Rarefaction curves of the species sampled for each of the Devonian substages. The threshold indicates the minimum number of zosterophylls sampled for the trend interpretation.

4.4 Discussion

4.4.1 General discussion

Zosterophyll diversity curve

Despite the differences between the curves in figure 4.2, similar trends are noteworthy: the first diversification at the end of the Silurian, until a Pragian peak and an important decrease starting at the Emsian up to the reach of a final stochastic plateau during the Middle Devonian. Both the diversity increase and decrease of the zosterophylls are two-phases events. The diversification of

the group starts during the Ludlow, with a change of steepness in the Pridoli and the Lochkovian. For the diversity drop on the other hand, the first event to change the curve dynamic takes place in the Emsian, right after the diversity peak, and the beginning of the Eifelian marks the transition with the final stochastic pattern. In between these two events, the middle Emsian depletion followed by a late Emsian peak let suggest a quick recovery phase. However, this change in the trend can be more likely associated to a sampling effect. In fact, 45 taxa are recorded by the early Emsian, followed by 16 during the middle Emsian, and 22 at the end of this stage, so the late Emsian looks slightly more sampled than the preceded time bin. This sampling effect can be explained by the lack of precision in the dating of the fossil record. In fact, numerous taxa are dated either in the beginning (Scott et al., 1976; X.-X. Li & Cai, 1977; Schweitzer, 1979; Remy, Hass, & Schultka, 1986; Schweitzer, 1987; Kotyk et al., 2002; D.-M. Wang & Hao, 2004; Korzhnev, 2014; Capel, Prestianni, et al., 2022; Y. Wang et al., 2022) or the end of the stage (Schweitzer, 1979; Gensel, 1982b; Zdebska, 1982; Remy, Schultka, et al., 1986; Jensen & Gensel, 2013; Korzhnev, 2014; Gensel & Berry, 2016), or even spanning from the whole Emsian (Hueber, 1971a; Gensel et al., 1975; Zakharova, 1981; Gensel, 1982a; Schweitzer & Heumann, 1993; McSweeney et al., 2020; McSweeney et al., 2022) but less likely in the middle of it (Banks & Davis, 1969; Hueber, 1983; Tanner, 1983; Korzhnev, 2014). Taxa are more likely assigned to the upper or lower boundary than identified in the middle of a given time period, without some degree of certainty. For this reason, no biological interpretation will be provided for this curve change.

The diversity record of zosterophylls is thus surprising since different trends are visible during a relative short time period. These drastic changes suggest an instability in the establishment of zosterophylls' groups. These observations are globally similar either at the species and the genus level, suggesting little taxonomic effect visible on the curve.

Diversity measures and substage sampling

In order to grasp this diversity signal, it is important to consider the zosterophyll richness during the different time periods. The rarefaction distributions in fig. 4.5 highlight the fact that despite zosterophylls being diverse, the different substages are individually poorly sampled. This is largely due to the fact that Early Devonian terrestrial deposits are scarce (Capel, Monnet, et al.,

2023), limiting thus the fossil availability for this time period. The Pragian and Emsian are the two best sampled stages, due to the fact that important outcrops have been discovered for these ages. The Pragian fossils mainly come from the Posongchong formation in China (Hao & Xue, 2013), and Bathurst Island, Canada (Kotyk, 1998). Emsian deposits, on the other hand, are much diverse, with an important number of deposits (n= 43). This contrast can be explained by the time span. The Pragian is in fact the shortest stage of the Devonian, of 3.2 myr, while the Emsian is the longest, of 14.4 myr. Two phenomenon can be invoked to explain this richness, a Pragian Lagerstätte effect in one hand, and an Emsian richness in the sampling due to a longer time span on the other hand.

SQS metric is based on the dataset's inherent richness, because the algorithm relies on subsamplings of the total diversity for each given time period. The curve appears in the results as the most contrasting one, compared to the others. In particular, some gaps are recovered, in the late Lochkovian and during the Emsian-Eifelian transition at the species level, and during the Pridoli at the genus level. These gaps, associated with an overall lower diversity estimation are due to the composition of the dataset. In fact, as demonstrated by figure 4.5, only four substages (composing the Pragian and Emsian stages) have a sufficient sampling, with a richness higher than the threshold estimated at 65 taxa per time bin (Fig. 4.5). All the other substages appear then poorly sampled, and can not reach the conditions for a proper SQS analysis. Additionally, these few taxa recorded per substages are generally rare, restricted to one or a few occurrences and thus not representative of the zosterophyll's distribution. Because the conditions are not met for a proper SQS approach, the curve produced in figure 4.2 can be interpreted only for the Pragian-Emsian interval. In such intervals, we can observe that the distribution follows the same pattern as the other curves i.e. a Pragian peak followed by an Emsian decrease. Here, the quorum set for the resampling process represents 50% of the total diversity. The more we increase the quorum, the closer this Pragian-Emsian distribution gets to the other curves. Thus, even if the SQS signal is not well pictured due to a limiting zosterophyll sampling, the well-resolved parts are congruent with the other metrics.

Impact of different biases on the diversity estimate

These curves are also highly dependent on the quality of the fossil record. These can summarized as i) the availability of the rock volume, ii) the sampling effort, and iii) the relevance of taxonomical identification.

Some precautions need to be pointed concerning the geological impact on the biological measures. In fact, as previously discussed by Knoll et al. (1979) and Wall et al. (2011), the availability of the rock volume will impact the known diversity of a group in a specific time period. The recent study of Capel, Monnet, et al. (2023) highlighted such a phenomenon for the pre Emsian terrestrial rock record. Considering the fact that zosterophylls are diversifying during this time period, this rock sampling issue has little effect on this diversity estimation. The Eifelian epoch, on the other hand, is known for its little rock deposit available (Capel, Monnet, et al., 2023). According to the distribution visible in figure 4.2, we can assume that the low diversity recorded is enhanced by this geological bias.

As developed in the previous chapter, the sampling effort of the group is mainly concentrated in two paleogeographical areas, which are Laurussia (comprising North America, Europe, Western Russia) and Northeastern Gondwana (represented by Australia and Southern China mainly). This signal can also be detected with the diversity analyses (Supp. Fig. D.2, p. 241). When the diversity curve is divided by geographical area, we can notice the predominance of Laurussia and Northeastern Gondwana. Northeastern Gondwanan fossils are restricted to the Lower Devonian and are particularly abundant during the Pragian. This is due to the fact that a few deposits from this time period unveiled an important richness, as mentioned above (Xue, 2009; Hao & Xue, 2013; D. Edwards & Li, 2018a). Future discoveries of post-Pragian deposits will be crucial to understand Northeastern Gondwanan's dynamic, and settle if this temporal restriction is due to a sampling effect or a real local extinction.

On the other hand, taxa from Laurussia are consistently found during the Devonian, showcasing a good sampling effort and confidence in the diversity interpretation of this paleoprovince. The Pragian-Emsian dynamic is once again recovered, suggesting that this observation is trig-

gered mainly by taxa from this province. The diversity peak seems thus to be a real phenomenon rather than a sampling bias.

On a more occasional basis, some zosterophyll fossils are found out in Kazakhstania or Northwestern Gondwana. They appear preferentially found in the Middle Devonian (Supp. Fig. D.2). Since this time bin is poorly sampled in Laurussia and Northeastern Gondwana, fossils from these paleogeographical areas stand out more easily such as *Serrulacaulis* from Kazakhstania (Xu et al., 2011), and Venezuela (Berry & Edwards, 1994) and *Sawdonia* from Venezuela (Berry, 2019). Siberian taxa are more likely found in the Pragian and Emsian stages.

The last bias that impacts the quality of the fossil record is the one related to the identification of taxa. In fact, zosterophylls being ancient land plants, their morphology remain simple, and fossils can easily be discovered fragmented and poorly preserved. Therefore, fossil identification can be misleading, and zosterophyll taxa can be misinterpreted as an other group of tracheophyte, such as *Sawdonia*, initially assigned to *Psilophyton* (D. Edwards et al., 1989), or some other tracheophytes identified as zosterophylls like *Yanmenia longa*, previously identified as *Zosterophyllum longa* (D. Edwards et al., 2016). Thus, the diversity curves estimates is highly dependent on the identification of fossil taxa. In that context, some caution are highlighted regarding taxa from Siberia and Kazakhstania. These are included in the present study, but some doubts remain concerning the certainty of their taxonomical identification. In fact, the majority of the studies of these specimens date back in the 70s, when the group was defined on a limited number of taxa (Ananiev, 1960; Petrosyan, 1967; Yurina, 1969; Senkevich, 1975; Zakharova, 1981; Nikitin & Bandaletov, 1986). These publications, not easily accessible, were not consistently integrated into zosterophyll's studies, and thus, may lack some community validation. Recent publications allow for a better accessibility of this fossil material, but no taxonomical review has been yet provided (Fedoseev, 2008; Korzhnev, 2014; Naugolnykh, 2021). A revision of this fossil material can bring more certainty in the zosterophyll distribution.

Zosterophyll distribution in association to evolutionary rates

Zosterophyll dynamic can be explained in parallel with the evolutionary rates (Fig. 4.3).

The late Silurian - Early Devonian diversification of the group is associated with a high

origination rate during this time period, with the notable exception of the late Pridoli, whose origination is at zero (no new occurrence is recorded for this substage). This absence of origination highlights a gap in the fossil record of the group. In fact, *Macivera* and some *Zosterophyllum* remains are dated from the Ludfordian, and the Lochckovian is a stage with important zosterophylls discoveries. Therefore, some zosterophyll taxa may have cross the Pridoli stage, but are yet to be discovered. During the Pragian, the extinction rate arises at the same level as the origination rate. Since both of the rates are high, the turnover is at its balance, explaining the presence of the late Pragian diversity peak. However, while the origination rate starts to decrease after this time period, the extinction rate remains at a higher level. Consequently, the first diversity decrease of zosterophylls can be explained by an unbalance in favor of the extinction rate. At the genus level (Fig. 4.3 B and D), the highest extinction rate takes place during the late Emsian, while the origination remains low, suggesting an extinction phase during this time period. A second important extinction peak is visible during the Famennian, at the species level only (Fig. 4.3 C). This can be explained by the fact that the Late Devonian is characterized by only a few remaining genera (*Protobarinophyton*, *Barinophyton*), with an overall higher number of species (n= 12). This signal can be linked with the extinction of the group, since no other zosterophylls are found after the Famennian, except for the dubious presence of *Protobarinophyton* in the Tournaisian (Scheckler, 1984).

Surprisingly, a high extinction rate is also recorded during the Ludfordian. This signal is more likely an artifact. During this time period, six species are recorded (aff *Zosterophyllum* sp. A and B, *Macivera gracilis*, *cf. Bathurstia sp. Distichophytum sp.* and *Zosterophyllum sp.* from Bathurst Island, Canada (Kotyk, 1998; Kotyk et al., 2002)). Among these taxa, three of them are not found anymore after the Ludfordian (aff. *Zosterophyllum sp.* A and B and *Macivera gracilis* respectively). Thus, half of the diversity of this time period got extinct, but considering that only a few occurrences are recorded this extinction is more likely the consequence of a sampling artifact rather than a real signal.

In addition, a majority of this sampling presents open nomenclature, that tends to overestimate its diversity since these uncertain taxa are considered as their own species. Review and assignation to a defined taxonomic framework may impact this earliest diversity dynamic.

4.4.2 Evolutionary implications

Zosterophylls are plants characterized by a leafless stem and a lateral arrangement of bivalvate sporangia. However, among this diversity, some fossils are contrasting by the presence of a structure that helps holding the sporangium, called the sporangiferous appendage, and particular lenticular sporangia bearing spores of different size. Thus, fossils with a morphology close to zosterophylls but displaying these particular structures are usually identified as "Barinophytes". In the present diversity analysis, a distinction has been made between zosterophylls and barinophytes, in order to compare their respective distributions (Supp. Fig. D.1). Zosterophylls are encompassing the majority of the diversity studied, but are observed especially constrained during the Lower Devonian. Their diversity decreases by the Middle Devonian, until extinction during the Late Devonian. Barinophytes on the other hand, despite being less diversified, survived by the Middle, Late Devonian, and are the main representatives of the stochastic plateau. Since Barinophytaceae is a family among zosterophylls, their diversity will consequently be lower than the one estimated for zosterophylls. This is supported by the phylogeny results of Chapter 2, showing a small Barinophytaceae clade, among a stem-group composed of zosterophyll taxa. As noticed in supplementary figure D.1, one occurrence extends the barinophyte distribution until the Lower Carboniferous. This signal was created by an occurrence of *Protobarinophyton sp.* in the Tournaisian of Pennsylvania (Scheckler, 1984). However, due to its open nomenclature and the surprisingly long temporal distribution of the genus (from late Lochkovian to late Mississippian), this identification is dubious. Further examination of this fossil material can help settle this uncertainty.

There is then a taxonomic turnover within zosterophyll diversity, with a Late Devonian survival of the Barinophytes. This change in dynamic can be explained in regard of overall land plant diversity. In fact, the Middle Devonian is characterized by the rise of the first arboreal forms (Berry, 2019). There may be a link between the two events, the stratification of the ecosystems being linked to morphological innovations in plants which strengthened the competition between land plants. This gradual shift impacted the already declining zosterophylls. In parallel, the lycopsids are at that time particularly abundant, dominating the Middle-Late Devonian terrestrial ecosystems (Capel et al., 2021). This clade, despite being closely affiliated to zostero-

phylls (see Chapter 2), is morphologically characterized by an abundance of sporangia along the stem, helically distributed and protected by microphylls. With this particular sporangium configuration, they may have outcompeted zosterophylls and their naked, unprotected sporangia. Barinophytes on the other hand, have a different strategy, with sporangia regrouped into clusters on the apical part of the plant, and more or less protected by a sporangiferous appendage (*Barinophyton*, *Protobarinophyton*), or a bract-like structure (*Adoketophyton*, *Bracteophyton*). This difference in strategy can explain the Middle to Late Devonian survival of the group, occupying a different ecological niche than the lycopsids. However, by reaching critically low diversity values by the Middle Devonian, it appeared difficult for the group to recover from the Emsian loss of diversity. This is observed by the stochastic plateau that remains at low values until a complete extinction by the end of the Devonian.

The diversity change among zosterophylls can also be paralleled with the climate dynamic during the Devonian. A recent study of Capel, Cleal, et al. (2023) pointed out a tropical distribution for zosterophylls, and thus, a preference in this group for warm temperatures. Studies of paleotemperatures reconstruction during the Devonian showed a gradual increase during the beginning of the Devonian, until the reach of a mean annual temperature of 20°C (Joachimski et al., 2009; Le Hir et al., 2011). This rise seems then congruent with the diversity expansion observed in the results. However, these measures are based on marine taxa, and caution is advised when extrapolating this information into terrestrial realms.

Thus, multiple factors can be invoked to explain the zosterophyll's diversity dynamics, from environmental ones to morphological.

4.4.3 Phylogeny estimates

Phylogenetic diversity estimation brings similar trends than in figure 4.2. However, a time shift is visible between the two figures, with the main events of diversification, peak richness and drop of diversity occurring earlier in the phylogenetic estimation. This result can be explained by the ghost lineages that infer the presence of the taxon earlier than the sole information provided by the fossil record. Additionally, the gaps in the fossil record are highlighted during the end of the Silurian, according to the uncertainty during the diversification phase (grey area around the

curve).

4.4.4 Comparison with previous studies

Diversity analyses on Early Devonian land plants

These results are in line with the previous studies made on the group (Cascales-Miñana & Meyer-Berthaud, 2014, 2015; Capel, Cleal, et al., 2022), despite the differences in methodology. In fact, the current study is based on occurrences and phylogenetic databases, measured at the genus and species levels, while the previous studies were based on ranged databases, and generally sampled at the genus level. Since the change of methodology and the measure of biases do not affect the shape of the curves, more confidence can be assessed on the evolutionary history of zosterophylls. As mentioned by Capel, Monnet, et al. (2023), it is important to keep in mind that these fossils are under a strong sampling bias. Thus, despite the present study being the most complete for zosterophylls to date, there is still missing information, and future discoveries can improve the distribution of this now well-established curve. This observation is congruent with the weak rarefaction estimate (Fig. 4.5) indicating that the total diversity of the group is yet to be reached. Additionally, according to the results in figure 4.4B, more fossils are to be discovered during the diversification phase, between the Homerian and the Lochkovian. However, the rock record available for these time periods is limited, preventing for a full understanding of the first terrestrial ecosystems.

Zosterophyll distribution and diversity estimates

The zosterophyll curve does not display a traditional diversity dependent distribution predicted by Sepkoski (1978). A main difference between the results and the estimated trend is represented by the final plateau that changes the dynamic of the curve. In a diversity-dependent model, the plateau is reached when the diversity is at its highest, displaying a form of balance between the originations and extinctions. Here, a final stochastic plateau is showcased when diversity is at its lowest, during the Middle to Late Devonian. It is important to first take into account the context of early land plant radiation in this trend. During the Devonian, terrestrial environments are not stabilized, with a Lower Devonian dominance of herbaceous forms, followed by a Middle

Devonian appearance of the first trees, and an Upper Devonian emergence of modern structures into Tracheophyta. Therefore, the environment was not stable enough to allow zosterophylls to maintain themselves. This statement is supported by the discussion above, highlighting the impact of both the climate change during this time period and the strong competition with other groups of land plants. Additionally Lycopsida play a key-role in this unusual dynamic. In fact, this group is considered as closely related to zosterophylls, and was not included in this analysis. The previous analysis of Capel, Cleal, et al. (2022) emphasized on a two-steps dynamic into the Eophytic flora, with a Middle and Late Devonian dominance of lycopsids, supplanting the early Eophytic trend triggered by zosterophylls. Even if the stem-group has initiated a decreasing phase during the Emsian, the crown-group for its part is on a diversification dynamic.

Even if the curve does not follow a diversity-dependent distribution, the part constrained to the Lower Devonian has a similar distribution than the one hypothesized by Alroy (2010), fig. 1C. According to the author, this type of curve follows an exponential growth law, with inflection points triggered by external factors, supporting once again the abovementioned statements.

4.5 Conclusion

Diversity analyses based on an occurrence database of zosterophylls showed no substantial difference with previous similar studies made on them, bringing more support and confidence in this signal. Results highlighted an important diversification phase in the late Silurian and Lower Devonian interval, until the reach of the maximum diversity during the Pragian, and immediately followed by a decrease in diversity during the Emsian. Thus, the majority of zosterophylls' evolution can be encompassed during the Lower Devonian. However, a stochastic plateau at low diversity persists during the Middle and Late Devonian. This trend is dominated by one particular group among zosterophylls, regrouped under the name "barinophytes", and is composed of a few genera, the two most noteworthy being *Barinophyton* and *Protobarinophyton*. This pattern of diversification can be paralleled with the concordant evolution of Lycopsida, dominating the Middle and Late Devonian epochs, as well as the emergence of most complex ecosystems and new terrestrial plant strategies. The environment seems to play a role in the diversification and decrease of zosterophylls' richness, with a strong dependence of the group

on warm temperatures. Thus, despite having a constrained stratigraphic range in the Lower Devonian, zosterophylls are characteristic of this fast turnover observed in Devonian terrestrial ecosystems, by representing the early herbaceous forms, quickly supplanted by more complex strategies.

Chapter 5

Bias and limits on the methods used

This PhD emphasized on the study of one specific group of plants, applying various methods on them in order to better understand their definition and evolutionary history. Before concluding this essay, it is important to come back to this material and methods developed in order to discuss the limits behind each of them.

5.1 Study model

Zosterophylls are ancient vascular plants, among the earliest to globally diversify on land. Despite their undeniable impact on Earth, they all went extinct by the Middle Devonian, without any extant representative to compare this group with. The group is therefore difficult to study; our knowledge depending on i) the preservation state of the available material, and ii) the interpretations made on these fossils. Furthermore, zosterophylls are small plants, with a limited number of organs and tend to fragment upon death, leading to only a few complete fossil specimens. Therefore, it is difficult to obtain a whole understanding for each species studied (Forey et al., 2004). In addition, plant taphonomy is generally biased, due to both the ability of the plants to do fragmentation of their parts during their life (Greenwood & Donovan, 1991), and their weak preservation potential compared to animals (Locatelli, 2014). In zosterophylls' studies, the fertile parts are generally better studied than the sterile parts, due to the amount of additional information available. But fertile parts represent only one aspect of the plant's

life cycle and function, and we today still lack crucial data on other parts such as the rhizomic structures, or other steps of their life cycle such as the gametophyte form. The understanding of the plant is therefore incomplete, generally based on the sexually mature sporophyte.

In addition to these inherent limitations on the morphology of the group, zosterophylls, as any fossils are subject to preservation biases. In fact, as mentioned in Chapter 3, there is a disparity in the fossil distribution, with a majority studied either in Europe, North America or China, that strongly influences the evolutionary history of the group. In fact, a few fossils were discovered in Africa or South America, leading to a partial understanding of the group distribution. For example, only one species of *Zosterophyllum* has been described in South Africa (Plumstead, 1977). If this discovery sounds promising for their geographical distribution, no recent study reviewed this fossil or further explored South African localities to complete the view. On the other hand, *Serrulacaulis* and *Sawdonia* are the sole zosterophylls described from Venezuela (Berry & Edwards, 1994; Berry & Gensel, 2019). If the presence of these taxa in South America suggests a hidden diversity, their scarcity prevents for a full understanding of the richness in such areas. Consequently, the total distribution of zosterophylls, particularly in the Southern continents depends on three factors, i) the real distribution of zosterophylls, ii) the sampling efforts provided by researchers and iii) the availability of terrestrial Devonian fossiliferous strata in these areas. These potential discoveries may shape a new understanding of the group's evolutionary history, so it is important to keep in mind that the information currently collected are provisional and subject to change.

Similarly, the different stages between the Silurian and the Devonian are unevenly sampled. As demonstrated in Chapter 4, some stages such as the Pragian or the Emsian are better sampled than others (Ludfordian, Lochkovian). Some did not provide any fossil, despite the inferred presence of the group at that time (Pridoli). The oldest deposits are usually the less easily preserved (Raup, 1972), and thus, crucial information about the basal morphologies of the studied taxa and the pace of evolutionary acquisitions are missing (Holland, 2016).

Last but not least, taxonomy plays a role in the study of fossils. In zosterophylls, numerous

fossils are identified with an open nomenclature (cf., aff., ?, see Supplementary Material D, p. 213). There are then uncertainties concerning the presence of some species in specific areas or time interval that hinders the broad distribution of the taxa. Since the study of zosterophylls ultimately showed an important diversity of the group, there is a gap between the earliest descriptions of the fossils and the current ones. If the majority of these earliest species are among the best zosterophylls described and systematically integrated into various studies (i.e *Sawdonia*, *Gosslingia*), others are still little considered (i.e *Jugumella*) and redescription of these specimens, in particular, are welcomed.

In parallel, *Zosterophyllum* is the genus bearing the name of the group, and is known today for being paraphyletic. Around 30 species compose this genus, but the phylogenies integrating multiple *Zosterophyllum* species systematically found them scattered inside the tree (Kenrick & Crane, 1997; Nibbelink & Tomescu, 2022). For this reason, the present work considered the type species *Z. myretonianum* only. Further work reattributing these species among zosterophylls will greatly help in the understanding of the group as well as *Zosterophyllum*'s definition.

More specifically, this work is based mainly on information obtained from literature. In fact, because zosterophyll fossils are present in a wide range of collections, the detailed observation of each zosterophyll integrated in the studies fell out the scope of this PhD. If during this PhD some observations has been made on the Belgium specimens (Liège collection), a direct observation of the whole fossil dataset is lacking. Thus, the interpretation of zosterophylls relies on i) the published description of the specimens and ii) the reinterpretation of the figures (pictures, line drawing).

As demonstrated here zosterophylls are, like many Paleozoic fossils, subject to numerous biases, both in terms of external factors, and of the group's understanding and interpretation. The vision of this group, therefore, remains fragmentary, and the results and conclusions drawn from these studies should be treated with caution.

5.2 Phylogeny

5.2.1 Study model and way of scoring

One of the main issues with the use of phylogenies applied to deep time studies is linked to the study model. Zosterophylls provide limited morphological information, both because of their morphological simplicity, and their preservation states. This limit is particularly visible inside the matrix (Supplementary material B.2, p. 168), which is made up of a large amount of missing information (?). Parsimony softwares can process only numeric information (i.e. the character states) and thus, generally consider this missing information as to be reconstructed, based on the states provided by the closest taxa (Strong & Lipscomb, 1999). Therefore, the more information is missing from the dataset, the less reliable the software will be in reconstructing this information. However, despite this issue, some authors advise for the inclusion of characters containing missing information nonetheless, that provide better information than if they are simply removed (Wiens, 1998).

This is particularly challenging when combined with the non-applicable state (-). A non-applicable state generally refers to a state not observed for a specific character, because the organism lacks the organ observed. In this work, this is the case of the characters linked to the emergences for example. Their shape or distribution across the plant can not be scored in specimens not presenting emergences in first hand. Therefore, missing information and non applicable states are two ways of representing "ignorance about the relationships of a character state" (Wilkinson, 1995). Consequently, non-applicable states are treated the same way as missing information.

In the present matrix, the combination of these two particular states brings a lot of uncertainties that may hinder the final resolution of the tree or provide a misleading tree (Wiens, 1998).

Another limit worth mentioning in phylogeny is the availability of taxa and characters in morphological studies. In fact, even if zosterophylls display a simple morphology, this group is nonetheless highly diversified, and presenting a mosaic of characters. This taxonomic richness

is the result of unique characteristics called autapomorphies. If autapomorphies are useful in taxonomy to identify taxa, they provide no evolutionary information for the softwares to process, since it is applicable to only one taxon, and not visible among the common ancestors (Bryant, 1995). Consequently, this morphological richness based on unique morphological characteristics is difficult to see in the results, and its interpretation depends heavily on our own understanding of the group.

Among zosterophylls, autapomorphies allowed for the identification of an important number of taxa, but only a few usable characters. Thus, a trade-off between the number of taxa and characters is necessary, in order to gain some resolution on the final tree. In general, it is recommended in phylogeny to have at least twice the number of characters than taxa (Graybeal, 1998; Wiens, 2004), which could not be applied here. Additionally, the main goal was to provide a complete phylogenetic view of zosterophyll evolution, by selecting the maximum diversity of the group, in order to prevent misleading results from taxon-selection analyses (Wiens, 2006). Therefore, some choices to improve resolution have been made. For example, the study focused at the genus level, rather than the species one. The question of the choice of terminal taxa in paleontological studies has been greatly debated (Hendricks et al., 2014), even if authors seem to agree on studies based at the genus level (Forey et al., 2004). Thus, if this taxonomical consideration has been previously discussed by some authors, a genus level analysis helps to maintain some resolution inside the tree, while limiting the number of taxa selected. More particularly, Hendricks et al. (2014) demonstrated a "hollow-shaped distribution" of the number of species per genus, with a majority of monotypic genera and a few genera containing a high number of species. Zosterophylls are no exception to this distribution, since the majority of taxa are monospecific, so studies at the genus level have a limited impact on the results. In this study, a few zosterophyll genera are composed of numerous species. The information scored comes then from the combination of all the species composing the genus. If this gives the advantage of completing as best as possible the character scoring, it creates in the end a chimeric plant, composed of all the structures seen in different species. This applies for six out of the 42 genera studied, each including two species (supplementary material B.1.1, p. 155). Some exceptions like *Zosterophyllum* or *Psilophyton*, because of their important species diversity and dubious

monophyly were selected on the basis of one species only, in order to reduce the taxonomical bias. However, as mentioned above, future studies solving their phylogenetic relationships and redescriptions are necessary. In addition, some taxa were discarded, due to their dubious taxonomic attribution, in order to lower the irresolution that they might have brought.

On the other side, because this work is the widest applied on zosterophylls so far, it was necessary to think about the way of defining and scoring characters. The majority of the characters used in this work comes from previous publications (Kenrick & Crane, 1997; Hao & Xue, 2013; Nibbelink & Tomescu, 2022), as they proved to be stable and reliable. Additionally, the inclusion of new taxa allowed for a development or a redefinition of characters (see Supplementary material B.1.3, p. 161). In particular, when building a matrix based on morphology, the definition of characters, the number of characters used, the number of character state, as well as the weighting or the ordination for each is subjective and depends on the matrix's creator (Hawkins et al., 1997; Wiens, 2001). Previous studies already pointed out how the character scoring may drastically change the results (Pleijel, 1995; Strong & Lipscomb, 1999). Since subjectivity plays a role in the development of such methodologies, it is important to proceed with caution, and in the case of character definition, some guidelines are generally advised (Brazeau, 2011).

For example, it is recommended to reduce as much as possible the number of characters applied to one specific structure, as the multiplicity may artificially regroup together taxa without this structure (Maddison, 1993). Equally, multiplying character states means running the risk of grouping structures with potentially different origins under the same character (Brazeau, 2011).

It is therefore recommended to define, when possible, binary characters. Multi-state characters can be used if the states refer to homologous structures with certainty. Weighting or ordering the characters is another solution available, but is also based on some personal *ad hoc* hypotheses. Debates on the literature are still ongoing about this topic, with today, no clear answer about the use of this strategy (Neff, 1986; Vogt, 2002; Congreve & Lamsdell, 2016).

With these constraints in mind, the present matrix is an attempt to reach some stability between the number of taxa and the number of characters. When possible, binary characters were used, referring to specific structures on the plant such as the branching or the anatomy.

Some others, such as the emergences needed multiple characters to better catch the whole information about this complex structure. Multi-states characters are based on homologous structures such as the sporangium shape for example. However, as mentioned earlier in this chapter, zosterophylls are well known through their reproductive structures. There is thus a disparity in the character distribution, with a majority scoring information on the sporangia (n= 23), while the other characters are based on vegetative axes, rhizomic structures, emergences or anatomy. A strong bias favors then the matrix for the information carried by sporangia. No weighting or ordination was performed, in order to limit the subjectivity of the matrix.

It is also important to recall that the present data matrix is based on qualitative characters only. Morphology-based phylogenies have also developed methodologies to encompass quantitative information, such as the length or number of a structure (Wiens, 2001; Goloboff et al., 2006), or through geometric morphometry (Rohlf, 2002; Goloboff & Catalano, 2011). Quantitative information has been discarded in the present study due to the preservation and accessibility of the fossil material. In fact, the compression nature of the majority of the zosterophylls remains may hinder the true three-dimensionality of the studied structures. Consequently, fossil observation is highly dependent on orientation: if a same structure is visible in two different fossils that are not oriented the same, then a quantitative approach would be burdened by the bias. Furthermore, the discrepancy of preservation between zosterophylls prevent for a full-organism comparison. A part of the dataset is composed of fossils identifiable but too fragmentary to convey appropriate quantitative analyses. In order to perform this kind of measures, it is advised to observe directly the fossils. The quantitative observations of zosterophylls should be done directly on the material, such as the size of emergences or the shape of the sporangium.

Character ordination is a process applied to multistate characters, when the different states are linked by a hypothesis of evolution (also called a "transformation series") (Hennig, 1999). As mentioned above, it was not used in the present study because of its important evolutionary assumption that may bias the results. However, according to the results obtained during this PhD, some confidence can be put in the ordination of some characters. This is particularly the case of the shape of the sporangium. In fact, it is currently scored as either spherical, ellipsoidal,

lenticular vertically flattened, or reniform. According to the present result, it seems that the two latter states may have emerged from a spherical or elliptical shape, showing a progressive flattening and complexification of the organ. Future analyses taking this information into account will be welcomed, in order to further test the stability of the tree.

In addition, some characters could be weighted, in order to enhance or potentially detect some detailed information. This could be the case of the characters scoring for the emergences. In fact, taxa such as *Xitunia* or *Bathurstia*, despite having such structures, are interpreted as being homoplasic. Weighting a character such as the shape of the emergences could help better test these relationships.

5.2.2 Methodological limits

Phylogenetic analyses are methods systematically producing a result, no matter the input (Sanderson, 1989). It is thus important to proceed with caution when reading the tree, as it may not represent the reality of the evolutionary process of the organisms. In the case of the present study, it is important to keep in mind that the tree produced comes from a squared, highly unresolved matrix. Despite this information that would bring uncertainty inside the tree, the result is surprisingly well resolved. Resolution is not synonymous with validity, and the confidence brought in the tree is rather based on node estimates such as the bootstrap or the Bremer support. These estimates applied on the topology brought confidence in a limited number of nodes, such as the one defining Lycophytina, Lycopsida and Barinophytaceae. This is particularly visible when combined with the bayesian approach. In fact, the use of this methodology provided a tree with similarity in the most stable nodes (Lycophytina, Lycopsida and Barinophytaceae are represented alongside small clades also present in parsimony such as *Oricilla-Tarella* or *Adoketophyton-Demersatheca*). However, the other relationships in the bayesian tree not only are poorly supported, but are also different from the ones observed in parsimony. Even if the broad evolutionary history of Lycophytina is consistent, their inner relationships are poorly supported and shall be treated with caution.

Despite the limited number of characters available, it was nevertheless possible to detect

inside the tree a signal, interpreted as evolutionary. However, when one of these characters is removed - such as the distribution of sporangia by orders of branching tested in Chapter 3 - the signal is completely lost, and the Lycophytina node is polytomic. This suggests that the resolution of the tree is not supported by all the characters individually, but rather by their combination within the matrix. This instability might be due to the strong homoplasy within the evolutionary history of the group.

The choice of the software is also particularly impactful in the tree production. There is currently two main softwares available for parsimony analyses: Paup* (Swofford, 2002) and Tnt (Goloboff & Catalano, 2016). While the first one is the oldest developed so far, and the one used in the first analyses of zosterophyll evolution (Gensel, 1992; Kenrick & Crane, 1997), the latter one recently gained in popularity, thanks to regular updates and the cooperation of a community of users. Even if the study of Kenrick and Crane (1997) was developed under Paup*, this present study used the Tnt software. In fact, prior to the new analyses performed, the matrix of Kenrick and Crane was run again, both in Paup* and Tnt in order to test the congruence of the softwares with the published results. Surprisingly, Paup* failed to find 1997 results and produced a polytomic consensus tree. This can be explained by an improvement in computation over the years, that allows Paup* for a complete tree search exploration nowadays, while the analyses were stopped in 1997, because it was too time consuming. On the other hand, Tnt was able to provide a similar consensus tree. Additionally, the studies of Hao and Xue (2013) and the recent one of Nibbelink and Tomescu (2022) both used Tnt, cementing the use of this software as a reference for zosterophylls' phylogeny.

Another worth mentioning observation lies in the randomization behind parsimony approach. In fact, in order to test the different topologies possible, parsimony softwares create first a starting tree (Wagner tree) which is built randomly, by selecting progressively the taxa of the data matrix (Farris, 1970). Starting from this Wagner tree, the software then applies branch swaps in order to test the different parsimony topologies. Here the software uses a computer-specific "seed" to generate pseudorandom processes such as the Wagner tree. That means that tree exploration is not completely random, as for a given computer, the same seed will be used and will produce the

same Wagner tree. It is interesting to keep this strictly computational issue in mind, because that can explain the differences encountered by two different users, working with the same database, software and scripts.

Time-scaled phylogenies

In the course of this work, a time-scaled phylogeny of Lycophytina has been created in order to observe the evolution of the group through time and develop further methodologies using these topologies, such as phylogeography. Time scaled phylogenies can be produced through different methodologies (Bapst, 2013). By testing the efficiency of these approaches, the study of Bapst (2014) found out that if its "cal3" method outperformed the others, he nonetheless called for precaution, because of the numerous biases inherent to these methodologies. This approach is therefore highly dependent on i) the known temporal distribution of each taxonomical unit as well as ii) the chosen tree. Extinct taxa are particularly impactful, since they present an incomplete sampling of the fossil record that can bias the temporal inferences made from the tree. In addition, taxon selection plays a role in the time scaling, since the inclusion or exclusion of taxa may change the time distribution of a given group (Hendricks et al., 2014). Such example is visible in *Zosterophyllum*, which is represented here by the type species only. Resolving the group's monophyly will therefore have an impact on the age distribution, affecting not only the genus, but also the whole Lycophytina interpretation.

In this study, following Bell and Lloyd (2015) notes advising against the use of consensus trees for such methodologies, the whole tree set has been analyzed. All the most parsimonious trees have been time scaled in order to observe the phylogenetic uncertainty across stratigraphy. If a single tree has been preferentially retained based on its stratigraphic indexes (tree number 6, Supplementary Material B.2, p.173), it is important to mention that this tree has a stratigraphic fit relatively close to the others, and no important contrast can be drawn between this tree and the rest of the set. Consequently, the tree selected to observe the temporal diversification of taxa and trait evolution is not based on consensus or summary trees, but rather on a hypothetical topology that may be subject to change.

5.2.3 Future studies

Zosterophylls' study has ultimately proven that Lycopsida are part of the group and should be included in order to get the full vision of the group Lycophytina. However, in the present study, only two lycopsids have been selected, which is not a good representation of the richness of the group. Future studies taking into account a better sampling of lycopsid diversity (temporal, spatial and morphological), could help better understand their history, and in particular, explore evolutionary questions such as the origin of the microphyll.

As developed in this section, deep time phylogeny analyses are prone to biases at various scales. We observed that the dataset highly depends on the availability of information and is based on the subjectivity in characters' definition. We also invited for caution in the tree interpretation, since the support is quite low despite its good resolution. Ultimately, we pointed some details extracted from the methodology itself, that can impact the results. Since the tree is later used in the other analyses of this essay, it was important to develop the different biases that lay behind the main result.

5.3 Phylogeography and sampling bias

5.3.1 Geographical bias

For the first time, a methodology combining phylogeny and geography has been applied on the Devonian group Lycophytina. If the results are promising, it is important to keep in mind that they are dependent on i) the chosen topology and ii) the known geographical dispersal of the studied taxa. In fact, the methodology relies on a fully resolved tree. In this case, one of the most parsimonious trees has been chosen based on its congruence with the stratigraphic distribution. However, as mentioned in the section above, a fully resolved tree does not mean real tree. In particular, the strict consensus obtained had low support in the majority of the nodes composing Lycophytina. Consequently, this fully resolved tree selected is a strong hypothesis regarding Lycophytina inner relationships, and thus, shall be treated with caution. The results from which this tree is based off are thus likely to change. This is particularly the case for the taxa composing

the polytomy in the LBLC.

Furthermore, the tree used in the present study is a sub sampling in zosterophylls diversity. The total geographical distribution is therefore not reconstructed since it follows the same taxon sampling as in phylogeny. This implies that some taxa are discarded in the phylogeny but could bring detailed geographical signal (*Parazosterophyllum* or *Gippslandites* in Australia, *Jugumella* in Russia, or *Zosterophyllum de vriesii* in South Africa). Consequently, the current Lycophytina distribution built in this chapter is incomplete and could benefit from the inclusion of such taxa in further studies.

In addition, as mentioned in the first section of this chapter, there is a known bias in the whole Lycophytina distribution. Since this work uses the known geographical distribution in order to detect similar provinces, absence of information such as the Southern Gondwana gap blinds a part of their potential geographical dispersion. In particular, the majority of the zosterophylls sampled come from restricted localities. There is then a lagerstatte effect in the province distribution, that could explain why the results are divided only by two main terranes. It is not possible yet to have a better resolution inside these two terranes.

5.3.2 The case of Lycopsida

Here again the constrained sampling of Lycopsida can impact the understanding of their geographical distribution. In fact, since the two lycopsids selected have as a common area Laurussia, and their closest relationships are with Laurussian taxa, they are interpreted as originating from this part of the world. However, this reflects a sampling bias, since some lycopsids are known from the Silurian of Gondwana, such as *Baragwanathia* (Garratt, 1978). Inclusion of such species of lycopsids may drastically change the geographical distribution of Lycophytina. In fact, if Lycopsida are closely related to Sawdoniaceae, then multiple events of colonization, from Northeastern Gondwana to Laurussia may have occurred, during the end of the Silurian.

5.4 Diversity analyses

Diversity analyses depend on the knowledge of the group studied. The present work is based on an exhaustive sampling extracted from literature. However, as mentioned in the first section of this chapter, a redescription of some zosterophyll fossils is welcomed. This is particularly the case of the Siberian taxa. In fact, they were poorly illustrated and seldom inclusion of these taxa into analyses are recorded. Since the description of these plants date back to the second half of the XXth century, (Ananiev, 1960; Petrosyan, 1967; Yurina, 1969; Senkevich, 1975; Zakharova, 1981; Nikitin & Bandaletov, 1986), it may be interesting to update the view of these fossils. With the present knowledge of zosterophyll's diversity, such a revision may help include or exclude the Siberian taxa into Lycophytina. It may as well revise these fossils under new interpretations, that can enrich the descriptions. The inclusion or exclusion of these taxa will have consequences on the evolutionary history of Lycophytina, because of their geographical as well as stratigraphical distributions.

Similarly, resolving the parataxonomy may impact the way of counting diversity. In fact, taxa in open nomenclature (*cf.*, *aff.*) are considered in such analyses as their own species, artificially inflating the richness among some genera. A redescription of these fossils can help either reallocate them into one of the currently known species, or creating a new species. In both cases, such a work would be beneficial for diversity estimates, by providing a clear picture of the evolution of taxa over time. *Protobarinophyton sp.* is a good example of the impact of open nomenclature in the estimates. This pseudotaxon is recorded in various time intervals, from the late Pragian, to the Mississippian and is recorded in this sampling as the taxon with the longest time span. Due to this oddly long stratigraphic distribution, it is more likely to assume that different species of *Protobarinophyton* paced this time interval, and thus, a part of the richness of the genus is lacking.

In addition, zosterophylls being plants overly sampled in two stages, resampling methodologies applicable to occurrence data base analyses can not be developed. This is particularly visible on the SQS curve, that follows a different distribution than the other indexes. The richness estimated is way lower because of the restricted information gathered in the other time bins,

preventing for an efficient sampling process.

5.5 Conclusion

This research question explored through different analyses the evolutionary history of zosterophylls and found interesting results. Thus, zosterophylls and lycopsids are regrouped together inside a clade called Lycophytina, confirming previous assessments of relationships of these groups (Gensel & Berry, 2001). The difference lies in the definition of zosterophylls, which appears in light of these results as a Devonian stem-group (paraphyletic), from which the crown lycopsids emerge. Lycophytina seems to originally diversify in Northeastern Gondwana, and an important event of dispersion in Laurussia created morphological innovations within the group, such as the emergences or circination. However, there are few limitations inherent with the study of the group as well as these analyses, that the present chapter pointed out.

Some points are for example particularly known among the specialists, such as the geographical and temporal sampling bias of zosterophylls, previously mentioned in past studies (Capel, Monnet, et al., 2023).

Others, are highly dependent on the preservation states and the interpretation of the structures. This limit, linked to the morphology of the fossils is the one particularly impactful in phylogeny analyses. Especially for long time extinct taxa, the application of a method depending highly on subjectivity is tedious.

The production of a phylogenetic tree gives precious information that can be further extracted with the combination of the topology with other methodologies. However, the current phylogeny is poorly supported, and consequently, the results found on the following chapters may be subject to change. It is thus important to stay cautious with both the topology itself, as well as the other results based on this tree.

Chapter 6

Conclusion

The Silurian-Devonian time interval is important when studying the evolution of land plants. This period begins with the introduction of the first known terrestrial ecosystems based on macrofossils, whose dynamics and morphology contrast with the modern ones (Bateman et al., 1998). During the Lower Devonian in particular, the macrofloras undergo their first diversification phase at a global scale (Cascales-Miñana et al., 2010). Thus, the small dichotomous herbaceous forms found during this time period gradually gave way to larger and more complex plants, reaching arboreal forms by the Middle Devonian (Algeo et al., 1995; Stein et al., 2007; Berry, 2019). By the Late Devonian, seeds and complex laminate leaves are found in the fossil record, suggesting another step in the complexity of land plant systems (Prestianni & Gerrienne, 2010; D.-M. Wang et al., 2015; Tomescu & Whitewoods, 2024). Thus, the Devonian encompasses major steps in the evolutionary radiation of early land plants, making it a period worth studying (Gensel et al., 2020).

When emphasizing on the Lower Devonian, one of the key protagonists of the greening of lands is represented by zosterophyll taxa. This diverse, abundant and rich group was however poorly understood regarding their phylogenetic affinities (Gensel, 1992; Kenrick & Crane, 1997; Hao & Xue, 2013; Nibbelink & Tomescu, 2022). On a morphological basis, they were regrouped together into subdivision Zosterophyllophytina due to their lateral sporangia opening thanks to a distal dehiscence (Banks, 1968). They were regularly brought close to the Lycopsida that shares

the same characteristics, but the latter appears more derived due to the presence of microphylls and a lobed protostele. The previous phylogenetic analyses have attempted to lift the veil on this uncertainty, but inherent limitations of taxon sampling left these questions unanswered. This, coupled with the gradual discovery of numerous fossil taxa of unique morphology only confused the nomenclature of the group even more. The vision of the subdivision Zosterophyllophytina gradually gave way to another nomenclatural terminology, namely Class Zosterophyllopsida. Initially referring to a clade containing only a part of the diversity of zosterophylls (Kenrick & Crane, 1997), this class has been progressively associated to a clade containing all the zosterophyll taxa only, barinophytes or lycopsids excluded (Hao & Xue, 2013; Cascales-Miñana & Meyer-Berthaud, 2014, 2015). Until now, this group has been assimilated as a clade sister to Lycopsida, without any phylogenetic support. As recently called by Y. Wang et al. (2024), it appears necessary to bridge this zosterophyll gap in order to strengthen our understanding of the Lower Devonian evolution of land plants. By focusing on zosterophylls and applying different tools, this PhD is an attempt to clarify their evolutionary history. A first chapter reviewed the systematic position of the group, then, their geographic distribution explored in a phylogenetic context, and finally, their diversity over time specified.

Phylogenetic analyses based on an extensive sampling of zosterophyll taxa was performed in order to solve this question. For the first time, an important number of genera were scored and analyzed in a common study. This extensive sampling encompasses all the unequivocal zosterophyll genera described, alongside barinophytes, lycopsids, euphyllophytes and basal embryophytes, producing the biggest data matrix created for the group so far. This matrix was analyzed under parsimony, bayesian and resampling processes in order to compare the topologies. Results consistently found a monophyletic Lycophytina, regrouping a Lycopsida clade with a stem-group composed of zosterophylls and barinophytes. Lycophytina is characterized by lateral sporangia opening thanks to a distal margin and appears sister to euphyllophytes. These results are consistent with the first established phylogenies of the group, suggesting a paraphyletic zosterophyll grouping (Gensel, 1992; Kenrick & Crane, 1997; Nibbelink & Tomescu, 2022). More particularly, the Lycopsida are found in a derived position inside the tree, closely associated to a clade regrouping zosterophylls characterized by emergences, circination and

sporangia distributed all along the stem (family Sawdoniaceae). The barinophytes, also closely associated to these two clades appear as a monophyletic group among Lycophytina, named here the Barinophytaceae family. However, they do not regroup all the barinophytes selected in the analysis, revealing a more complex evolutionary history of this particular morphology. At the basis of the tree, the taxa display morphologies close to the plesiomorphic state.

After exploring the evolution of the group through phylogeny, a spatial exploration completed this view in chapter 3. In fact, the group is surprising by its global distribution concentrated in a relative short time period, and questions about their processes, pathways and impacts arose.

For the first time, paleogeographical reconstructions has been emphasized on this Lower Devonian group. The goal of this chapter was to detect any geographic patterns among Lycophytina, that can have an influence on the topology previously obtained. The idea was also to detect any link between geography and morphology. Previous work drew hypothesis of their origin and pathways thanks to their knowledge of the fossil record (D. Edwards, 1990; Hao & Gensel, 1998; Y. Wang et al., 2024). Here, by defining paleoprovinces and apply their known geographical distribution on a time scaled tree, it is possible to detect some geographical patterns for the group.

Since fossils were mainly sampled in Laurussia and Northeastern Gondwana, a clear cutout is detected inside the tree. It is then divided by Gondwanan taxa at its basis and Laurussian ones in a more derived position. There is thus a consistent geographic signal, showing the impact of the paleoprovince on the evolutionary history of the group. In addition, some characters follow a similar pattern, showing that they are not a characteristic of Lycophytina as a whole, but geographical estimators instead. Either than defining the group, these characters are milestones in their evolutionary history. So in the light of these results, it is clear that sampling will have a strong influence on the final topology.

In addition to their widespread distribution, zosterophylls were also one of the most abundant plants on Earth during the Silurian-Devonian transition. Their stratigraphic distribution is clearly bounded between the Ludfordian for the earliest occurrence (Kotyk et al., 2002), to the Tournaisian for the latest one (Scheckler, 1984). In the context of updating the stem-group

history, their temporal distribution has been reviewed in chapter 4.

The diversity study presented here is based on occurrences data that brings a more detailed view of their distribution over time. This database, analyzed at the genus and species level used resampling methodologies to further test the trend of the curves. In addition, a diversity count based on the topologies has been provided to offer a comparison between curves.

Results show consistency between the different methods and the previous studies (Cascales-Miñana & Meyer-Berthaud, 2014, 2015; Capel, Cleal, et al., 2022). The typical distribution composed of an intense diversification phase during the late Silurian and Lower Devonian, a Pragian maximum of diversity, followed by a decrease process during the Emsian was found out again. This trend is visible both at the genus and species level. This typical distribution can be paralleled with multiple factors. The first one is a correlation between their diversity and warm temperatures (Scotese et al., 2021), as previously pointed in Capel, Cleal, et al. (2023) study. The second one is related to the land plant evolution, with the emergence of the first forests during the the Middle Devonian (Givetian (Stein et al., 2007; Stein et al., 2020) potentially Eifelian (Giesen & Berry, 2013)), that could explain their diversity drop. The beginning of the Eifelian showcases a different pattern, with a stochastic plateau composed of a few zosterophyll taxa having a long stratigraphic range, that lasts during the Middle and Late Devonian. This plateau is mainly composed of a few genera, of barinophyte affinity. These taxa display a different morphology compared to the dominant Lycopsida of this time, explaining their presence, even at a low degree of diversity. Thus, ten years after the first publication of diversity analyses on zosterophylls, results show consistency, despite the use of different methods and the compilation of a more precise database, and brings thus more confidence in the establishment of this signal.

6.1 Study limits

This research question raised a major challenge as the study of zosterophylls is marked by numerous limitations hindering the exploration and interpretations. The morphology of the studied taxa, as pointed in chapter 2 is a limiting factor, both by the restricted number of organs and characters available, but also because of the numerous autapomorphic characteristics

that are inapplicable in a phylogenetic context. The present extensive review of zosterophyll's morphology is thus limited by the fragmentary information provided by the fossil record and counterbalanced by the large number of taxa described. This issue was the main challenge of the present work, since the important morphological diversity applied on a few numbers of organs leads to characters with contradictory signals, preventing for a resolution inside the topology.

Here, even with the aim of getting the best extensive sampling possible, taxon choice was necessary in order to prevent this resolution issue. Thus, the question of the phylogeny of this group can be further solved with the inclusion of taxa defined as *incertae sedis* but considered as zosterophylls. *Gutzeitia* and *Gosferia* are the only two taxa *a posteriori* sampled since their inclusion brings uncertainty in the topology. It is still unclear why these two taxa in particular bring important changes in the topology, pointing remaining limits in our understanding of the group.

Additionally, even if the topology shows a relatively good level of resolution, the nodes are not strongly supported, suggesting other configurations possible in future studies. This lack of support is mainly found inside the Lycophytina group. Thus, the general interpretation of Lycophytina is less likely to change. The group contains Lycopsida, that is nested into a stem-group Lycophytina, and two other families are described, namely the Barinophytaceae and the Sawdoniaceae. However, the inner relationships between the members of the stem-group Lycophytina are not clear yet and may change in the future.

Since this work focused on zosterophylls mainly, a group that ultimately proved to be paraphyletic, the current results are broadly incomplete. The clade Lycophytina includes an extensive number of stem-members, but only two taxa represent the crown-group. These results could be improved by taking a broader range of Lycopsida into account. A better sampling of lycopsid fossils can help understanding the evolution of the morphology. In fact as previously mentioned by Gensel and Berry (2001), some lycophytes show a "transitional" form, between the zosterophylls and the unequivocal lycopsids. These genera encompass *Asteroxylon*, *Baragwanathia* and *Drepanophycus*. Two of these genera have been sampled in the present work, and thus, Lycopsida is currently represented by transitional forms only. Including true lycopsid genera can provide more information on the morphological evolution of the group.

Another important limit with the study of zosterophylls is the sampling bias composing the dataset. As regularly mentioned through this work, zosterophylls are mainly found in Europe, Russia, northern America and southern China. This extensive sampling may bias our understanding of the group, especially now that a geographical pattern has been recovered. This pattern highlighted a historical bias with Laurussian taxa. Laurussian fossils were among the first unequivocal zosterophyll taxa discovered and studied (Penhallow, 1892; Smith & White, 1905). Their morphology was thus used to define this group. Later on, new fossils discovered in South China have made the group's evolutionary vision more complex. With the present results, Laurussian taxa are presented as more derived in the morphology than the Northeastern Gondwana ones. Thus, future discoveries in under-sampled areas can bring new insights on the group morphology and pathways, as it was the case when the Chinese taxa were discovered.

6.2 Perspectives

This PhD focused particularly on the phylogenetic position of the different taxa composing the "zosterophyll" group. If the results highlighted a paraphyly of the group, all the taxa included share a common ancestor, confirming the previous observation and work on this subject. Thus, the stem-group Lycophytina is composed of the all taxonomically defined zosterophylls. Even if this study emphasized on a broad sampling of zosterophylls, some taxa with an uncertain identification were not included (see supplementary list B.1.2, p.158). What are their phylogenetic position, especially towards the Lycophytina clade? Further studies could acknowledge these taxa, considering the morphological limitations mentioned through this work. In fact, now that a general trend has been retrieved in Lycophytina topology, one could run similar analyses using a taxon sampling approach in order to include the above-mentioned taxa and keep some representatives composing the Lycophytina clade, in order to test the new taxa's position.

As mentioned all along this work, the study of the morphology of zosterophylls is limited. A potential solution that can be explored is to quantitatively measure the morphology of the group. Geometric morphometry is a popular approach in paleontology, of measuring the shape of structures and comparing these measures between taxa (Mitteroecker & Gunz, 2009). The methods lead to multivariate analyses as an approach to observe the patterns among taxa. This

information can also be used to complete the present analyses, especially in the building of a phylogenetic tree based on quantitative information (Rohlf, 2002). Since geometric morphometry works for determinate organs, an application of these methods could be developed on the sporangia of the plant.

In a more specific aspect, the genus *Zosterophyllum* can be the scope of future targeted phylogenetic studies. In fact, *Zosterophyllum* is the name-bearing genus of the group, and currently the only one among zosterophylls to have such a broad stratigraphic distribution (see Kotyk (1998) for the oldest and Schweitzer (1987), Korzhnev (2014), Y. Wang et al. (2018), and McSweeney et al. (2022) for the youngest) and spatial exploration. This genus is also the richest among zosterophylls with currently 31 species described (Supp. Table A.2). In this dissertation, only the type species *Z. myretonianum* was taken into account. This choice was based on a taxon selection context, focusing on one representative of the genus, in order to keep balance with the number of characters used. In addition, previous studies pointed a paraphyly (Nibbelink & Tomescu, 2022) or a polyphyly (Kenrick & Crane, 1997; Hao & Xue, 2013) among this genus. Numerous authors, in light of these results, asked for a revision of the genus (Nibbelink & Tomescu, 2022), and some publication already revised some (C.-S. Li & Edwards, 1996; D. Edwards, 2006; Snigirevsky et al., 2007; D. Edwards & Li, 2018a; McSweeney et al., 2020). Even a *Zosterophyllum* species has been attributed to a non zosterophyll plant (D. Edwards et al., 2016). All of this work is based on the discovery of new fossils, a morphological comparative work, and taxonomical revisions, which are crucial but time consuming. A phylogenetic analysis emphasizing on all the species of *Zosterophyllum* currently known can be a broad systematic solution to help revise the group, especially now that the framework has been established. What are the phylogenetic position of all the species of *Zosterophyllum* and are we able to find a geographical pattern similar to the one obtained in chapter 3? In other words, are *Zosterophyllum* species from Laurussia taxonomically different from the ones of Northeastern Gondwana?

The position of *Adoketophyton* closely related to *Demersatheca* and not associated to the Barinophytaceae raises questions about the definition of this family, and at a larger scale, on the evolution of protective structures for the sporangia. In the present study, only three taxa associated to barinophytes have been used (four when including *Adoketophyton*). Other taxa such as *Bracteophyton*, *Krithodeophyton* and *Faironnella* seem to have a barinophyte affinity. Future

studies can be conducted specifically on this group in order to better understand their affiliation inside Lycophytina and each other. In addition, *Faironella*, a Belgium barinophyte displays a very unique sporangiferous appendage, which is, following Gerrienne (1996a) encapsulating individual sporangia. However, when observing the specimen, it appears morphologically similar to a *Sawdonia* species. Further reviews on this enigmatic species would thus be welcomed.

To stay in a phylogenetic context, this kind of study can be expanded to the other groups of land plants such as the Lycopsida. In fact, i) as phylogenetically resolved as the closest relatives of the stem-group Lycophytina, ii) as one of the oldest extant group of Tracheophyta, with a temporal span covering the Lower Devonian until today (Gensel & Berry, 2001) and iii) with a parallel evolutionary line towards the euphyllophytes, Lycopsida is an ideal study group. Their rich evolutionary history and the fact that they still have extant representatives allow for the use of refined Phylogenetic Comparative Methods (PCM) as well as the inclusion of genetic information to infer their evolutionary rates.

A broad perspective that is worth mentioning is the invitation to excavate fossils in poorly sampled areas such as Africa, Australia, Russia or South America. In fact, the results in chapters 3 and 4 showed that evolutionary trends distinguish Gondwanan taxa from Laurussian ones. However, the sampling effect on zosterophylls is still strong and related to these places. Laurussia and Gondwana being two massive continents, it could be interesting to define the geographical pathways the zosterophylls may have taken to reach them. By concentrating the sampling effort in these under studied places, we may refine our geographical view of the group and gain a better understanding of their geographical and hopefully, morphological histories. Russian taxa in particular, need some revision, in order to assess with certainty their past flora.

Last but not least, this work can be expanded into an integrative perspective. In fact, the present PhD focused particularly on zosterophylls. But as pointed by Bateman (1991), the study of plants can be integrative and includes different aspects of paleontology. The impacts of zosterophylls are beyond their own evolutionary history and interact with their environments and the organisms they are living with. Fungi, in particular, are the ideal candidates when studying plants because of all the beneficial interactions they provide. And even the fossil record

revealed interactions with fungi, showing the old age of this association (Taylor et al., 1999). However, these associations are somewhat difficult to observe. A few zosterophylls have been described with an association with fungi (Gensel, 1982a; D. Edwards et al., 1986; Jensen & Gensel, 2013; Lalica & Tomescu, 2021). Thanks to the rise of the new technologies, we have now more and more access to quality material to check on such interactions on these taxa.

6.3 Main messages

The present work brings clear answers about zosterophylls' evolutionary history. The group is i) paraphyletic and closely affiliated to Lycopsida, ii) characterized by a Lower Devonian outburst, leading to the emergence of numerous different groups that will not survive the Middle Devonian, iii) strongly influenced by a geographical signal.

Zosterophylls are then members of the stem-group Lycophytina, a clade sister to the euphyllophytes, that comprises Lycopsida as the crown group. The stem-group dominated the Lower Devonian period, while the crown-group diversified strongly during the Middle to Upper Devonian.

Among Lycophytina, Gondwanan taxa are more likely to be found at the basis of the tree, displaying pleisiomorphic characters, while Laurussian taxa are generally regrouped together in a more derived position due to the presence of numerous provincial apomorphies.

In the end, the influence of zosterophylls extends beyond the Lower Devonian, as their rise and fall is the product of a switch of dominance with their sister relative Lycopsida. This latter group subsequently met a great evolutionary success during the Phanerozoic period, opening a new era in land plant evolution.

Appendix A

Supplementary information from introduction

Table A.1: List of zosterophylls currently described. NA refers to no information about their taxonomy in the literature but are commonly described as zosterophylls. "No zostero" taxa are all the taxa described as Tracheophyta *Incertae sedis* but commonly viewed as zosterophylls

Genus	Family	Anatomy	References
Adoketophyton	Incertae sedis	No	C.-S. Li and Edwards (1992)
Anisophyton	NA	No	Remy, Schultka, et al. (1986)
Baoyinia	Zosterophyllaceae	No	D. Edwards and Li (2018b)
Barinophyton	Barinophytaceae	No	Smith and White (1905)
Bathurstia	Zosterophyllaceae	No	Hueber (1971a)
Bracteophyton	Probable barinophyte	No	D.-M. Wang and Hao (2004)
Craswallia	Zosterophyllaceae	No	Morris and Edwards (2014)
Crenaticaulis	NA	Yes	Banks and Davis (1969)
Danziella	No zostero	No	D. Edwards (2006)
Deheubarthia	Zosterophyllaceae	Yes	D. Edwards et al. (1989)
Demersatheca	Incertae sedis	No	C.-S. Li and Edwards (1992)
Dibracophyton	Incertae sedis	No	Hao et al. (2012)
Discalis	Zosterophyllacaea	No	Hao (1989b)
Distichophytum	Zosterophyllaceae	No	Kotyk (1998)
Euthursophyton	NA	Yes	Mustafa (1978)
Faironella	No zostero	No	Gerrienne (1996a)
Forania	Sawdoniaceae	No	Jensen and Gensel (2013)
Gippslandites	Zosterophyllaceae	No	McSweeney et al. (2020)
Gosferia	Incertae sedis	No	Gerrienne (1991a)
Gosslingia	Gosslingiaceae	Yes	Heard (1927)
Guangnania	NA	No	D.-M. Wang and Hao (2002)
Gumuia	NA	No	Hao (1989a)
Gutzeitia	Zosterophyllaceae	No	Snigirevsky et al. (2007)
Hicklingia	NA	No	Kidston and Lang (1924)
Hsua	No zostero	No	C.-S. Li (1992)

Genus	Family	Anatomy	References
Huia	No zostero	No	Geng (1985b)
Jugumella	Probable zosterophyll	No	Senkevich (1975)
Kaulangiophyton	No zostero	No	Gensel et al. (1969)
Konioria	NA	Yes	Zdebska (1982)
Krithodeophyton	Barinophytaceae	No	D. Edwards (1968)
Macivera	NA	No	Kotyk et al. (2002)
Margophyton	NA	Yes	Zakharova (1981)
Nothia	No zostero	No	El-Saadawy and Lacey (1979)
Odonax	Zosterophyllaceae	No	Gerrienne (1996b)
Omniastrobus	Incertae sedis	No	Bonacorsi et al. (2021)
Oricilla	NA	No	Gensel (1982b)
Ornicephalum	Zosterophyllaceae	No	D. Edwards and Li (2018a)
Parazosterophyllum	Zosterophyllaceae	No	McSweeney et al. (2020)
Protobarinophyton	NA	No	Brauer (1981)
Ramoferis	Incertae sedis	No	Hao and Xue (2011)
Renalia	NA	No	Gensel (1976)
Sawdonia	Zosterophyllaceae	Yes	Hueber (1971b)
Serrulacaulis	NA	No	Hueber and Banks (1979)
Sichuania	Zosterophyllaceae	No	D. Edwards and Li (2018b)
Tarella	Zosterophyllaceae	No	D. Edwards and Kenrick (1986)
Thrinkophyton	Zosterophyllaceae	Yes	Kenrick and Edwards (1988a)
Trichopherophyton	Zosterophyllaceae	Yes	Lyon and Edwards (1991)
Ventarura	Zosterophyllaceae	Yes	Powell et al. (1999)
Wenshania	No zostero	No	W.-Q. Zhu and Kenrick (1999)
Xitunia	Zosterophyllaceae	No	Xue (2009)
Zosterophyllum	NA	Yes	Penhallow (1892)

Table A.2: List of all the *Zosterophyllum* species currently described.

Taxon name	Reference
Z. australianum	Lang and Cookson (1931)
Z. bifurcatum	X.-X. Li and Cai (1977)
Z. bohemicum	Obhrel (1961)
Z. bokkeveldense	Plumstead (1977)
Z. confertum	Gossmann et al. (2022)
Z. deciduum	Gerrienne (1988)
Z. devriesii	Plumstead (1977)
Z. dispersum	Zakharova (1983)
Z. divaricatum	Gensel (1982a)
Z. dushanense	X.-X. Li and Cai (1977)
Z. fertile	Leclercq (1942)
Z. llanoveranum	Croft and Lang (1942)
Z. longhuashanense	X.-X. Li and Cai (1977)
Z. longum	Hoeg (1942)
Z. minifertillum	Hao and Xue (2013)
Z. minor	Ananiev (1960)
Z. minorstachyum	Xue (2009)
Z. myretonianum	Penhallow (1892)
Z. ovatum	D. Edwards and Li (2018a)
Z. qujingense	Hao et al. (2007)
Z. ramosum	Hao and Wang (2000)
Z. rhenanum	Kräusel and Weyland (1935)
Z. shengfengense	Hao et al. (2010)
Z. sinense	X.-X. Li and Cai (1977)
Z. spathulatum	X.-X. Li and Cai (1977)
Z. spectabile	Schweitzer (1979)
Z. tenerum	Hao and Xue (2013)
Z. xishanense	Hao et al. (2007)
Z. yunnanicum	Hsü (1966)

Appendix B

Phylogeny

B.1 Supplementary Methods

Taxa and characters used in the phylogenetic analyses. The list includes both taxa included in the analyses (with references consulted for scoring the characters, the age of each taxon and the rock unit of provenance) and taxa considered for inclusion but ultimately excluded (with justification for their exclusion). The characters are accompanied by comments (where necessary) detailing their definitions and scoring approach.

B.1.1 1. List of taxa (in alphabetical order) included in analyses.

- *Adoketophyton* (C.-S. Li & Edwards, 1992; Hao et al., 2003; X. Zhu et al., 2011; Hao & Xue, 2013); based on *A. subverticillatum* and *A. parvulum*.
  - Range: early Lochkovian–late Pragian (419.2–407.6 Myr)
- *Aglaophyton* (Kidston & Lang, 1920a; D. S. Edwards, 1986; Remy & Hass, 1996); based on *A. major*.
  - – Range: middle–late Pragian (409.7–407.6 Myr)
- *Anisophyton* (Remy, Hass, & Schultka, 1986; Remy, Schultka, et al., 1986; Gerrienne, 1991b); based on *A. gothani* and *A. potonei*.
  - Range: early–late Emsian (407.6–393.3 Myr)
- *Asteroxylon* (Kidston & Lang, 1920b; Kerp et al., 2013; Hetherington et al., 2021); ; based on *A. mackiei*.
  - Range: middle–late Pragian (409.7–407.6 Myr)
- *Baoyinia* (D. Edwards & Li, 2018b); based on *B. sichuanensis*.
  - Range: early Lochkovian–early Pragian (419.2–409.7 Myr)
- *Barinophyton* (Arnold, 1939; Brauer, 1980, 1981); based on *B. citrulliforme* and *B. obscurum*.
  - Range: early Eifelian–late Famennian (393.3–358.9 Myr)

- *Bathurstia* (Hueber, 1971a; Kotyk & Basinger, 2000); based on *B. denticulata*.
  - Range: early–late Pragian (410.8–407.6 Myr)
- *Craswallia* (Morris & Edwards, 2014); based on *C. haegensis*.
  - Range: middle–late Lochkovian (416.4–410.8 Myr)
- *Crenaticaulis* (Banks & Davis, 1969); based on *C. verruculosus*.
  - Range: middle–late Emsian (402.8–393.3 Myr)
- *Deheubarthia* (D. Edwards et al., 1989); based on *D. splendens*.
  - Range: late Lochkovian–late Pragian (413.6–407.6 Myr)
- *Demersatheca* (C.-S. Li & Edwards, 1996; Y. Wang et al., 2022); based on *D. contigua*.
  - Range: early Pragian–early Emsian (410.8–402.8 Myr)
- *Discalis* (Hao, 1989b); based on *D. longistipa*.
  - Range: middle–late Pragian (409.7–407.6 Myr)
- *Distichophytum* (Hueber, 1972; Schweitzer, 1979, 1987; Kotyk, 1998); based on *D. ovatum* and *D. mucronatum*.
  - Range: early Pragian–late Emsian (410.8–393.3 Myr)
- *Drepanophycus* (Göppert, 1852; C.-S. Li & Edwards, 1995); based on *D. spinaeformis*.
  - Range: late Lochkovian–early Frasnian (413.6–377.4 Myr)
- *Euthursophyton* (Mustafa, 1978); based on *E. hamperbachense*.
  - Range: late Eifelian–late Givetian (390.5–382.7 Myr)
- *Forania* (Jensen & Gensel, 2013); based on *F. plegiospinosa*.
  - Range: late Emsian (398.0–393.3 Myr)
- *Gosferia* (Gerrienne, 1991a, 1999); based on *G. curvata*.
  - Range: early Emsian (407.6–402.8 Myr)
- *Gosslingia* (D. Edwards, 1970); based on *G. breconensis*.
  - Range: late Lochkovian–late Pragian (413.6–407.6 Myr)
- *Guangnania* (D.-M. Wang & Hao, 2002; D. Edwards et al., 2016); based on *G. cuneata* and *G. minor*.
  - Range: early Pragian–early Emsian (410.8–402.8 Myr)
- *Gumuia* (Hao, 1989a); based on *G. zyzzata*.
  - Range: middle–late Pragian (409.7–407.6 Myr)
- *Gutzeitia* (Snigirevsky et al., 2007); based on *G. timanica*.

  - Range: late Frasnian (377.4–372.2 Myr)

- *Hicklingia* (Kidston & Lang, 1924; D. Edwards, 1976); based on *H. edwardii*.
  - Range: early Eifelian–late Givetian (393.3–382.7 Myr)
- *Konioria* (Zdebska, 1982; D. Edwards et al., 1989); based on *K. andrychoviensis*.
  - Range: late Emsian (398–393.3 Myr)
- *Macivera* (Kotyk et al., 2002); based on *M. gracilis*.
  - Range: Ludfordian (425.6–423 Myr)
- *Margophyton* (Zakharova, 1981); based on *M. goldschmidtii*.
  - Range: late Lochkovian–late Emsian (413.6–393.3 Myr)
- *Odonax* (Gerrienne, 1996b); based on *O. borealis*.
  - Range: early Emsian (407.6–402.8 Myr)
- *Omniastrobus* (Bonacorsi et al., 2021); based on *O. dawsonii*.
  - Range: early Emsian (407.6–402.8 Myr)
- *Oricilla* (Gensel, 1982b); based on *O. bilinearis*.
  - Range: late Emsian (398–393.3 Myr)
- *Ornicephalum* (D. Edwards & Li, 2018a); based on *O. sichuanense*.
  - Range: early Lochkovian–early Pragian (419.2–409.7 Myr)
- *Polythecophyton* (Hao et al., 2001); based on *P. demissum*.
  - Range: middle–late Pragian (409.7–407.6 Myr)
- *Protobarinophyton* (Brauer, 1981); based on *P. pennsylvanicum*.
  - Range: late Lochkovian–late Famennian (413.6–358.9 Myr)
- *Psilophyton* (Doran, 1980); based on *P. crenulatum*.
  - Range: late Pragian–early Emsian (408.6–402.8 Myr)
- *Ramoferis* (Hao & Xue, 2011); based on *R. amalia*.
  - Range: middle–late Pragian (409.7–407.6 Myr)
- *Rhynia* (Kidston & Lang, 1920a; Lemoigne, 1970); based on *R. gwynne-vaughanii*.
  - Range: middle–late Pragian (409.7–407.6 Myr)
- *Sawdonia* (Hueber, 1971b; Gensel et al., 1975; Rayner, 1983; Gensel & Berry, 2016); based on *S. ornata* and *S. acanthotheca*.
  - Range: late Pragian–late Givetian (408.6–382.7 Myr)

- *Serrulacaulis* (Hueber & Banks, 1979; Berry & Edwards, 1994; Xu et al., 2011); based on *S. furcatus*.
  - Range: early Givetian–early Frasnian (387.7–377.4 Myr)
- *Sichuania* (D. Edwards & Li, 2018b); based on *S. uskielloides*.
  - Range: early Lochkovian–early Pragian (419.2–409.7 Myr)
- *Tarella* (D. Edwards & Kenrick, 1986) based on *T. trowenii*.
  - Range: early Pragian (410.8–409.7 Myr)
- *Thrinkophyton* (Kenrick & Edwards, 1988a); based on *T. formosum*.
  - Range: early Pragian (410.8–409.7 Myr)
- *Trichopherophyton* (Lyon & Edwards, 1991); based on *T. teuchansii*.
  - Range: middle–late Pragian (409.7–407.6 Myr)
- *Ventarura* (Powell et al., 1999); based on *V. lyonii*.
  - Range: middle–late Pragian (409.7–407.6 Myr)
- *Wenshania* (W.-Q. Zhu & Kenrick, 1999; Hao & Xue, 2013), based on *W. zhichangensis*
  - Range: middle–late Pragian (409.7–407.6 Myr)
- *Xitunia* (Xue, 2009); based on *X. spinitheca*.
  - Range: middle–late Lochkovian (416.4–410.8 Myr)
- *Zosterophyllum* (D. Edwards, 1975); based on *Z. myretonianum*.
  - Range: early Lochkovian–early Emsian (419.2–402.8 Myr)

B.1.2 2. List of taxa (in alphabetical order) not included in the analyses.

Many of these taxa were initially described by the different authors as "incertae sedis", although commonly viewed as zosterophylls. These taxa could be included in future analyses to test their taxonomic placement and phylogenetic relationships.

- *Bracteophyton variatum* (D.-M. Wang & Hao, 2004)
  - Age: 407.6 to 402.8 Myrs
  - Rock unit: Xuijaching Formation (China)
  - This taxon is more likely to be a Barinophytaceae. But the original description assigned it as Tracheophyta incertae sedis because of its lack of anatomical information.
- *Danziella artesiana* (D. Edwards, 2006)
  - Age: 407.6 to 410.8 Myrs
  - Rock unit: Grès de Rebreuve Formation (France), Karakudyur Formation (Russia)

  - After a revision of this specimen, the author decided to put Danziella as a Plantae incertae sedis. In fact, the plant shows some similarities with zosterophylls but also rhyniophytes, and the author advise for more specimen to study in order to assess the determination.

- *Dibracophyton acrovatum* (Hao et al., 2012)
  - Age: 409.7 to 407.6 Myrs
  - Rock unit: Posongchong Formation (China)
  - This taxon is more likely to be a Barinophytaceae. But the original description assigned it as Tracheophyta incertae sedis because of its lack of anatomical information.

- *Faironella valentula* (Gerrienne, 1996a)
  - Age: 407.6 to 402.8 Myrs
  - Rock unit: Wépion Formation (Belgium)
  - The author originally described the taxon as *incertae sedis* because of the particular fertile units. After an observation of the specimen in the collection, we noticed a close morphological proximity with *Sawdonia*, and call for an other study of the plant and its fertile entities.

- *Gippslandites minutus* (McSweeney et al., 2020)
  - Age: 419.2 to 407.6 Myrs
  - Rock unit: Boola Formation (Australia)
  - Even if the authors assigned the fossil specimen among zosterophylls, the observations are based on a single, poorly preserved specimen. In particular, we failed to determine with certainty characters linked to the dehiscence and attachement of the sporangia and thus, decided to not include this taxon in the analysis.

- *Hsua robusta* (C.-S. Li, 1992)
  - Age: 409.7 to 408.6 Myrs
  - Rock unit: Xuijachong Formation (China)
  - The original description favors a position of this taxon among the Rhyniales. Even if the specimen shows characteristics usually associated with zosterophylls (i.e. reniform sporangia), the fossil bears terminal single sporangia on the axis. For this reason, this taxon was not included in the study.

- *Huia recurvata* (Geng, 1985b)
  - Age: 410.8 to 402.8 Myrs
  - Rock unit: Xuijachong and Posongchong Formations (China)
  - The author assigned this taxon among Rhyniales, and thus, is not included in the present study.

- *Jugumella burubaensis* (Senkevich, 1975)
  - Age: 423 to 402.8 Myrs
  - Rock unit: Tokrau, Sardzhal, Balkhash and PriBalkhash Formations (Kazakhstan),

  - Even if further studies assigned this genus as a probable zosterophyll, its original uncertain placement was the reason behind the exclusion of this taxon for the present work.

- *Kaulangiophyton akanta* (Gensel et al., 1969)
  - Age: 398 to 391.1 Myrs
  - Rock unit: Trout Valley Formation (USA)
  - In the original publication, Kaulangiophyton was more likely associated with some lycopsids, close to some zosterophyll. Even if nowadays this taxon is commonly associated with this group, no clear statement has been made on the literature and thus, was discarded for this analysis.

- *Krithodeophyton croftii* (D. Edwards, 1968)
  - Age: 410.8 to 402.8 Myrs
  - Rock unit: Senni Bed Formation (UK), Wépion Formation (Belgium)
  - This taxon has been assigned to the Barinophytaceae. However, the presence of bracts being a unique characteristic not shared by the zosterophylls will induce the definition and scoring of specific characters that would bring more missing information in the matrix. Thus, in order to keep some resolution and emphasize on zosterophyll's evolutionary history, particular Barinophytaceae such as *Krithodeophyton* were not included.

- *Nothia aphylla* (El-Saadawy & Lacey, 1979)
  - Age: 409.7 to 407.6 Myrs
  - Rock unit: Rhynie Chert Formation (UK)
  - The systematic position of *Nothia* has been contested: originally attributed to the subdivision zosterophyllophytina (Banks, 1968), *Nothia* has later on been removed (Banks & Davis, 1969), because of its mozaic of characters, in between ryhniophytes and zosterophylls. In order to prevent confusion with rhyniophytes characteristics, the taxon has thus been excluded from the present analysis.

- *Parazosterophyllum timsiae* (McSweeney et al., 2020)
  - Age: 425.6 to 423 Myrs
  - Rock unit: Humevale Formation (Australia)
  - The description of this genus is based on a single, poorly preserved specimen. Since the observation of the structures lead to strong interpretations of the pictures, we decided to not include this genus.

- *Renalia hueberi* (Gensel, 1976)
  - Age: 410.8 to 393.3 Myrs
  - Rock unit: Gaspé Bay (Canada)
  - This plant is characterized by terminal sporangia and is identified as *Incertae sedis*. For this reason, it is not included in the analysis.

B.1.3 3. Characters used in the phylogenetic analyses.

The characters are inspired from Kenrick and Crane (1997), Hao and Xue (2013), and Nibbelink and Tomescu (2022). However, due to the inclusion of numerous new taxa, a revision of characters definitions and character states was needed. Where applicable, numbers in brackets after the character name correspond to the character from previous publications that it is derived from: numbers in boldface - Kenrick and Crane (1997); italicized numbers - Hao and Xue (2013); numbers in boldface and italicized - Nibbelink and Tomescu (2022).

1. Rooting system: positively geotropic axes [New]

   (0) Absence

   (1) Presence

   Many zosterophylls have been described with rhizomatous axes, which potentially bore rhizoids; these are scored "0" for this character. Lycopsids, on the other hand, have deeper rooting systems that include positively geotropic axes. Taxa in which the basal parts are not known were coded "?".

2. K-branching or H-branching ***[24]***

   (0) Absence

   (1) Presence

   K- or H-branching refers to the particular branching pattern found in some zosterophylls and lycopsids, where two closely spaced branching points result in a morphology comparable to the letters K or H (Matsunaga & Tomescu, 2017). In many cases, one of the two resulting branches has a rooting function.

3. Branching type of erected axes **[5.1]** *[4]*

   (0) Isotomous

   (1) Pseudomonopodial

   (2) Unbranched

   The branching type refers to the relative size of axes produced at a branching point. In isotomous branching the two branches are produced by an equal division of the apical meristem and have similar size (e.g., *Rynia* and *Aglaophyton*). The opposite of isotomous branching is pseudomonopodial branching. This type of branching is obtained when the division of the axis leads to an unequal branch size. Here in particular, the division leads to the formation of one main branch, and a second lateral one. Lastly, some plants, such as *Discalis* (Hao (1989b); fig. 6), have erect unbranched axes, although the rhizomatous portions of the plant are branched. Additionally, some descriptions document "isotomous and pseudomonopodial dichotomies" (e.g., D. Edwards et al. (1989)). In such cases, the taxon was scored "1", as pseudomonopodial branching, when present, can lead to additonal architectural complexity, beyond that generated exclusively by isotomous branching. (Nibbelink & Tomescu, 2022) chose to split this character in two, looking for the proximal and the distal branching (their char. 21 & 22), taking into consideration the architecture of plants such as *Deheubarthia*, *Euthursophyton*, *Margophyton* or *Thrinkophyton*. However, here we decided to use a single character, since in many of the taxa considered the fragmentary material precludes identification of proximal vs distal portions of the plant. Thus, this choice of character construction reduces the amount of missing data in our dataset.

4. Branching pattern **[5.6]** *[5]*

   (0) Planar

   (1) Three-dimensional

   (2) Branching absent

5. Branching angle [New]

   (0) Narrow to wide

   (1) Branches parallel to subtending axis

   Because observed branching angles can reflect taphonomic results, branching angle was separate into only two types: one consisting of branches that maintain more-or-less the same angle (narrow to wide) with respect to the main axes irrespective of distance from the branching point; and one in which the branch forms a narrow angle with the subtending axis at the base, but then curves apically close to its base and becomes more-or-less parallel to the axis, as seen in several taxa, e.g., *Distichophytum* (Hueber (1972) plate I 1-3), *Forania* (Jensen and Gensel (2013); fig.2E), *Guangnania* (D. Edwards et al. (2016); fig. 4B), *Odonax* (Gerrienne (1996b); fig. 5), *Oricilla* (Gensel (1982b); plate II 2-3), *Sawdonia* (Gensel and Berry (2016); fig.9A-C and Rayner (1983); fig. 1a, 1d, 7), or *Zosterophyllum* (D. Edwards (1975); fig. 15).

6. Circinate axis tip **[5.4]** *[6]* ***[26]***

   (0) Absence

   (1) Presence

   Taxa in which axes tips are not known (not preserved) are scored "?".

7. Subaxillary branching **[5.3]**

   (0) Absence

   (1) Presence

   The axes derived from subaxillary tubercles/buds are typically oriented in a "direction perpendicular to the plane defined by the forking of the subtending axis" (Matsunaga et al., 2017). The function of these axes is still up to debate, generally interpreted as roots, with a similar function to that of the rhizophores of *Selaginella*. However, just like those rhizophores, they may be able to differentiate as colineary axes (D. Edwards et al., 1989). The subaxillary tubercles (and corresponding branches, when developed) are sometimes erroneously referred to as axillary tubercles, despite their position below the branch axil. Taxa known only from fertile axes are scored "?" for this character.

8. Emergences. Modified from **[5.5]** ***[16]***

   (0) Absence

   (1) Presence

   Emergences are defined as unvascularized protrusions on the axes, sporangia or sporangial stalks. A number of characters listed below describe different features of the emergences. Those characters are scored “-“ (inapplicable) in taxa that lack emergences.

9. Emergences: localization (scored "-" in taxa that lack emergences) [New]

   (0) On vegetative parts only

   (1) On vegetative and fertile parts

   (2) On fertile parts only (sporangium or sporangium stalk)

10. Emergences: biseriate arrangement (scored "-" in taxa that lack emergences) [New]

    (0) Absence

    (1) Presence

    Some taxa show an organisation of the distribution of emergences, while other have scattered emergences, without any defined pattern. Taxa with biseriate emergences include *Bathurstia* (in Kotyk and Basinger (2000), fig.10, fig. 18), *Crenaticaulis* (in Banks and Davis (1969), fig. 12), *Forania* (in Jensen and Gensel (2013), fig. 2 C, fig. 7) and *Serrulacaulis* (in Berry and Edwards (1994), fig. 1, Hueber and Banks (1979), plate I 2-4, fig. 1, Xu et al. (2011), fig. 1 A).

11. Glandular structure on emergences (scored "-" in taxa that lack emergences) [New]

    (0) Absence

    (1) Presence

    Some taxa have emergences with a rounded or darkened tip, which are interpreted as glandular structures. These taxa include *Anisophyton* (in Remy, Hass, and Schultka (1986), fig.4), *Discalis* (in Hao (1989b), plate III 1, fig.7), *Forania* (in Jensen and Gensel (2013), fig.3 G-I) and *Sawdonia* (in Rayner (1983), fig.2 b).

12. Sporangium emergences, position (scored "-" in taxa that lack emergences) [New]

    (0) On abaxial valve

    (1) On both valves

    Among the taxa having sporangial emergences, the character distinguishes further between those bearing emergences on the abaxial valve only like *Odonax* (Gerrienne (1996b); fig. 2), *Sawdonia* (Gensel and Berry (2016); fig. 7) or *Xitunia*, and those bearing emergences on both valves like *Discalis* or *Konioria*. No taxa are known that have emergences on the adaxial valve only.

13. Emergences: shape (scored "-" in taxa that lack emergences) [New]

    (0) Conical

    (1) Shelf-like

    "Shelf-like" refers to ridge-like emergences that girdle the axes partially such as those seen in *Bathurstia* (Kotyk and Basinger (2000); fig. 3, 4, 10A-B, 18).

14. Sporangium: position on sporophyte axis **[5.18]** *[26]*

    (0) Terminal

    (1) Lateral

This character separates the basal polysporangiophytes/tracheophytes such as *Rhynia* or *Aglaophyton*, as well as trimerophytes, from the zosterophylls, which have laterally distributed sporangia.

15. Lateral sporangium: attachment: cauline (scored "-" in taxa with terminal sporangia) *[23]*

    (0) On axis

    (1) On specialized appendage

    Sporangia attached directly on axes by their stalks are not associated with any specialized structures. Sporangia attached to specialized appendages include those of the barinophytes and of *Adoketophyton* (Brauer, 1980; D. Edwards & Li, 2018a).

16. Sporangium stalk size: relative to sporangium size, modified from **[5.18]**

    (0) Sessile

    (1) Short

    (2) Long

    Sessile sporangia have no well-differentiated stalk. Taxa were scored as having long sporangial stalks (“2”) if the stalks were about the same size as (or larger than) the sporangia.

17. Sporangium stalk stoutness (based on stalk length/stalk width) (scored "-" in taxa with sessile sporangia) ***[34]***

    (0) Length/width < 1

    (1) Length/width > 1

18. Vascular bundle supplying sporangium (scored "-" in taxa with sessile sporangia) [New]

    (0) Absence

    (1) Presence

19. Sporangial stalk orientation (scored "-" in taxa with terminal sporangia or sessile sporangia) [New]

    (0) Stalk oriented at acute angle to subtending axis

    (1) Stalk oriented at right angle to subtending axis

20. Sporangium: shape modified from **[5.13]** *[17]*

    (0) more or less spherical

    (1) more or less ellipsoidal

    (2) more or less reniform

    (3) lenticular vertically flattened

    Although lycophytes, including zosterophylls, are traditionally recognized as bearing reniform sporangia, when all zosterophylls and allied taxa are considered, sporangium shape encompasses morphological diversity broader than just a reniform shape. The "lenticular vertically flattened" condition was defined for the barinophyte sporangia, which have a particular almond shape.

21. Sporangium symmetry *[18]*

    (0) Sporangia approximately radially symmetrical

    (1) Sporangia bilaterally symmetrical

    Taxa scored as having radially symmetrical sporangia include the trimerophytes, which have roughly fusiform sporangia attached at one end, the rhyniopsids, and those taxa that have spherical sporangia (*Craswallia* and *Margophyton*).

22. Sporangium: dorsiventral flattening (scored "-" in taxa with terminal sporangia) modified from ***[36]***

    (0) Absence

    (1) Presence

23. Sporangium: dehiscence: type **[5.16]**, *[20]*, ***[38]***

    (0) Along distal margin

    (1) Along a lateral line

    Zosterophylls and allied taxa have sporangia that dehisce along their distal margin, whereas those of trimerophytes dehiscence along a lateral line.

24. Sporangium: dehiscence: thickening line **[5.17]** *[21]* ***[39]***

    (0) Absence

    (1) Presence

    Presence or absence of a thickening of the sporangial wall adjacent to the dehiscence line may signal different dehiscence mechanisms (e.g., McSweeney et al. (2020)). The character was scored "0" in taxa where such a thickening is neither described, nor illustrated.

25. Sporangium: valve: size (scored "-" in taxa with sporangia dehiscing along distal margin – char. 23) **[5.15]**, modified from ***[37]***

    (0) Isovalvate

    (1) Abaxial valve bigger than adaxial valve

    (2) Abaxial valve smaller than adaxial valve

26. Sporangium: attitude **[5.19]**

    (0) Lateral (pointing outwards)

    (1) Pointing more or less apically

    (2) Curved toward the axis

27. Sporangium: paired modified from ***[27]***

    (0) Absence

    (1) Presence

    This character aims to distinguish euphyllophytes like *Psilophyton*, which have sporangia paired on one stalk, from the other groups.

28. Sporangium: distribution by order of branching **[5.12]**

    (0) Only in the highest order branches

    (1) In the highest and the lower order branches

    Lower order branches are here recognized as any axis segment between two successive dichotomies. Sporangia located only on the highest orders of branching, i.e., on terminal axis segments, suggest determinate growth of the fertile axis tips (probably produced annually), whereas sporangia on lower orders of branching are consistent with indeterminate growth of fertile axes. Taxa known only by their apical fertile portions are scored "?".

29. Sporangium: grouping modified from ***[27]***

    (0) Absence

    (1) Presence

    Absence refers to cases where sporangia are scattered distributed relatively randomly along the axes, or isolated (like in *Konioria*). Presence of grouping of sporangia refers to taxa where sporangia are distributed consistently in groups where the distance between successive sporangia is relatively constant. *Discalis* is scored "0" because although the sporangia are known only on terminal segments, it is unclear whether those segments would subsequently branch and, if so, whether the branches thus produced would also bear sporangia; additionally, the distance between successive sporangia varies relatively widely in *Discalis*. This character is not applicable for taxa with terminal sporangia (e.g., *Rhynia*, *Psilophyton*).

30. Sporangium: grouping: distribution (scored "-" in taxa that lack consistent sporangial grouping – char. 29) ***[29]***

    (0) Terminal, forming a strobilus

    (1) Intercalary

    Taxa with intercalary sporangial grouping are those with grouped sporangia on lower order branches (i.e., between successive axis branching points), such as *Crenaticaulis* (Banks and Davis (1969); fig. 1).

31. Sporangium: density in groups (scored "-" in taxa that lack consistent sporangial grouping – char. 29) ***[30]***

    (0) Lax

    (1) Compact

    Compact grouping of sporangia was scored for taxa in which neighboring sporangia are partially overlapping, in contact with each other, or at the very least spaced out at a distance smaller than their size.

32. Strobilus: position (scored "-" in taxa that lack sporangial grouping – char 29 – and in taxa with intercalary sporangial grouping – char. 30) [New]

    (0) In the main axis

    (1) In lateral axes

Scored "?" in some taxa that are known from material that is too fragmentary (e.g., only from terminal fertile regions); scored "1" for taxa with isotomous branching that lack a main axis.

33. Sporangium: distribution along axis **[5.10]** *[27]*

    (0) Radially

    (1) In longitudinal rows

    This character aims to distinguish taxa with no apparent organization of sporangia along axes. Multiple diagnoses fail to clearly set apart the helical organization with the irregular distribution of sporangia (D. Edwards & Li, 2018a, 2018b) and for this reason, a helical description is scored as "0". The notable exception is for the lycopsids, that have a regularly distributed helical sporangia, and are thus scored as "1". Other taxa scored as "1" display a rowed organization of sporangia.

34. Sporangia distributed in rows: number of rows (scored "-" in taxa with helically or irregularly distributed sporangia – char. 33); modified from **[5.10]**

    (0) One or two

    (1) More than two

    (2) Always two

35. Sporangia distributed in rows: sporangiotaxis (scored "-" in taxa with helically or irregularly distributed sporangia – char. 33); modified from ***[31]***

    (0) Opposite

    (1) Alternate

36. Leaves; modified from *[7]*

    (0) Absence

    (1) Presence

    This character distinguishes lycopsids, which bear true leaves (vascularized emergences with regular taxis, from zosterophylls.

37. Spore size **[5.20]**

    (0) Homosporous

    (1) Heterosporous (anisosporous)

    The spore size condition present in this taxon sampling does not conform to typical heterospory, as the microspores are located in the same sporangium as the macrospores, a condition that is recognized as anisospory.

38. Protostele: shape modified from **[4.14]** *[11]* ***[7]***

    (0) Terete

    (1) Elliptical

    (2) Lobed

The lobed morphology of the protostele characterizes lycopsids.

39. Pattern of primary xylem maturation **[4.15]** *[12]* ***[2]***

    (0) xylem absent
    (1) Centrarch
    (2) Exarch
    (3) No conspicuous pattern of maturation
    (4) Mesarch

40. Metaxylem: secondary wall thickening pattern; modified from *[13]* and ***[4]***

    (0) Absent
    (1) Scalariform
    (2) Pitted

41. Metaxylem: pitting *[14]* ***[6]***

    (0) S-type
    (1) C-type
    (2) G-type
    (3) P-type

    The pitting types correspond to those defined by D. Edwards (2003).

42. Sterome [New]

    (0) Absence
    (1) Presence

    A sterome is recognized as an outer layer of cells with thickened walls.

B.2 Methods S3.

B.2.1 Scored matrix

```
Rhynia 00010000-----0---1-10-???-00-------0003200
Aglaophyton 00010000-----0---1-10-10--00-------00000-0
Adoketophyton 01110100-----1100?00110001001010110 0?01221
Barinophyton ??100?00-----110-?13?0???00010111210112222
Omniastrobus ????????0-----110-?13?0???00?1011121012????
Protobarinophyton ??100?00-----110-?13?0???000101[0 1]12101?????
Anisophyton 10110111001-01010?02100?0?010------0??????
Baoyinia ????????0-----10101011000010?[0 1]01?0--0??????
Bathurstia 11000101010-1100-?-2110000001011121 00?????
Craswallia ??????00-----1011?010001010-0--????0??????
Crenaticaulis 101?0111110-01011?0210001101110-10[0 1]0?12221
Deheubarthia 10110111000-01010?021100010 11?0-10[0 1]0?12220
```

```
Demersatheca ????????0-----100-?-01100010?101?1100??????
Discalis 0122-10110110102l?00110101000---0--00????2?
Distichophytum ??0?1000-----1010?00100001001011121 00?????
Euthursophyton ??110101?00?0?????????????????????????0?12221
Forania 0?10[0 1]101011-0101??02110101010---0--0???22?
Gosferia ??????1?0-----1021?02110001 0?0---?--0??????
Gosslingia ?0110110-----1011?1211010001110-10[0 1]0012221
Guangnania 11101000-----1011?0111011100101[0 1]0--0??????
Gumuia 0122-000-----10[0 1]0?10110100000---0--00?????
Gutzeitia ??0?0?00-----101???011????0010110--01?????
Hicklingia ?01?0000-----10[1 2][0 1]?00100001011?0?0--0??????
Konioria ??0?0101100101010?02110001010------0?12221
Macivera ??100000-----100-?-111000100101[0 1]0--00?????
Margophyton ??110011000-010???100?0?0?010------0?1222?
Odonax ?10111111000010 10?02110001011[0 1]1112[0 1]0??????
Oricilla ???01100-----1010?1211010001110-10000?????
Ornicephalum ????????0-----1021?0010001 20?100?0--0??????
Ramoferis ??010000-----1011?00110001011[0 1]110--00?????
Sawdonia 1110110110100101[0 1]?10110?1101110-10[0 1]0012220
Serrulacaulis 0?000101010-11010?12110111 0?110-10100????2?
Sichuania ????????0-----10211001101010?100?0--0??????
Tarella ?1???100-----1010?1211000001110-10100????0
Thrinkophyton ??100110-----1011?1211010101110-1010?12220
Trichopherophyton ??????1?0-----100-?-21?00110????????0002220
Ventarura 0?0?1?00-----100-1-011012[0 1]0?101?1010002220
Xitunia ????????12?0001011?00110011 0?101?0--0??????
Zosterophyllum 01101000-----101[0 1]1021100010010[0 1][0 1]0--00?222?
Asteroxylon 11110000-----101110211000101111-1--10241-0
Drepanophycus 11100000-----1011?021?000101110-1--1??2220
Psilophyton 00110001000-00-----10-10--10-------0001231
Polythecophyton ??110000-----0-----10-10--10-------00?????
Wenshania ??110000-----1011?0[1 2]11010101???-0--0??????
```

B.2.2 Tnt script

```
# Load files
cdir <directory>
mxram 6000;
log analysis.out;
proc <matrix_name>;
outgroup Aglaophyton;
hold 99999;
# Run the analysis
mult= repl 100000 tbr ras;
bbreak=tbr;
nelsen*;
majority=50*;
taxname=;
export=<filename>
```

```
# For Bremer support:
proc Bremer.run;
# Apomorphies:
ttags=;
apo <tree_nb>;
ttag <filename>;
# CI/RI indexes:
proc Stats.run;
```

B.2.3 Bayesian script

```
begin mrbayes;
log start filename = "analysis.txt";
set autoclose = yes nowarn = yes;
outgroup Aglaophyton;
lset applyto = ( all ) coding = variable rates = gamma;
prset applyto = ( all ) ratepr = variable;
mcmcp ngen = 1000000 relburnin = yes burninfrac = 0.5
printfreq = 1000 samplefreq = 100 temp = 0.015 nruns = 2 nchains = 4
nswaps = 3 savebrlens = yes;
mcmc;
sump;
sumt contype = allcompat Outputname = zosterobarino_AllCompCon_CR.t;
sumt contype = halfcompat Outputname = zosterobarino_MRC_CR.t;
log stop;
END;
```

B.2.4 Measure of uncertainty among the data matrix

```
library(plyr)
library(ape)

data <- read.table("Data_matrix.txt", header=TRUE) # faut insérer ta matrice en
format txt

# % d'incertitude (?) dans les caractères

size<-ncol(data)
results <- matrix(0,1,size)
for (i in 1:size){
results[,i] <- sum(as.vector(data[,i])=="?")/(nrow(data))*100
}

colnames(results) <- colnames(data)

reject <- results[,subset(results > 15)] # Mettre ici le pourcentage de rejet désiré
(paramétré à 15%)
reject
```

```
# % d'incertitude dans les taxons

size2<-nrow(data)
results2 <- matrix(0,1,size2)
for (i in 1:size2){
results2[,i] <- sum(as.vector(data[i,])=="?")/(ncol(data))*100
}

colnames(results2) <- rownames(data)

reject2 <- results2[,subset(results2 > 15)] # Mettre ici le pourcentage de rejet
désiré (paramétré à 15%)
reject2
```

B.3 Supplementary tables and figures

Table B.1: First Appearance Datum (FAD) and Last Appearance Datum (LAD) of the taxa selected for the phylogenetic analysis.

Taxon name	FAD	LAD
Rhynia	409.7	407.6
Aglaophyton	409.7	407.6
Adoketophyton	419.2	407.6
Barinophyton	393.3	358.9
Omniastrobus	407.6	402.8
Protobarinophyton	413.6	358.9
Anisophyton	407.6	393.3
Baoyinia	419.2	409.7
Bathurstia	410.8	407.6
Craswallia	416.4	410.8
Crenaticaulis	402.8	393.3
Deheubarthia	413.6	407.6
Demersatheca	410.8	402.8
Discalis	409.7	407.6
Distichophytum	410.8	393.3
Euthursophyton	390.5	382.7
Forania	398	393.3
Gosferia	407.6	402.8
Gosslingia	413.6	407.6
Guangnania	410.8	402.8
Gumuia	409.7	407.6
Gutzeitia	377.4	372.2
Hicklingia	393.3	382.7
Konioria	398	393.3
Macivera	425.6	423.2
Margophyton	413.6	393.3
Odonax	407.6	402.8
Oricilla	398	393.3
Ornicephalum	419.2	409.7
Ramoferis	409.7	407.6
Sawdonia	408.6	382.7
Serrulacaulis	387.7	377.4
Sichuania	419.2	409.7
Tarella	410.8	409.7
Thrinkophyton	410.8	409.7
Trichopherophyton	409.7	407.6
Ventarura	409.7	407.6
Xitunia	416.4	410.8
Zosterophyllum	419.2	402.8
Asteroxylon	409.7	407.6
Drepanophycus	413.6	377.4
Psilophyton	408.6	402.8
Polythecophyton	409.7	407.6
Wenshania	409.7	407.6

Table B.2: Indices and tests of stratigraphic fit for the six most parsimonious trees recovered in the FTS analysis. Abbreviations: SRL = Simple Range Length; MIG = Minimum Implied Gap, with GMax and GMin respectively the maximum and minimum gaps within the tree; SCI = Stratigraphic Congruence Index; RCI = Relative Completeness Index; GER = Gap Excess Ratio; Est.p.[INDEX] and p.Wills are the significance tests; all tests and indices are detailed in Bell and Lloyd (2015). Tree 6 (in boldface) has the overall best stratigraphic fit (BSF) and was used for the time-scaled phylogeny (Fig. 2.3).

Tree nb	SRL	MIG	GMax	GMin	SCI	RCI	GER	MSM*	est.p.SCI	est.p.RCI	est.p.GER	est.p.MSM*	GER*	GERt	p.Wills
tree 1	433.1	388.5	748.31	48.2	0.67	10.298	0.514	0.124	0.236	0.957	0.957	0.956	0.142	0	1
tree 2	433.1	384.6	748.31	48.2	0.67	11.198	0.519	0.125	0.235	0.697	0.697	0.699	0.494	0.368	0.675
tree 3	433.1	384.6	748.31	48.2	0.67	11.198	0.519	0.125	0.235	0.697	0.697	0.699	0.325	0.367	0.858
tree 4	433.1	381.8	748.31	48.2	0.643	11.845	0.523	0.126	0.917	0.366	0.366	0.368	0.672	0.632	0.506
tree 5	433.1	380.7	748.31	48.2	0.67	12.099	0.525	0.126	0.235	0.248	0.248	0.249	0.836	0.736	0.328
tree 6	**433.1**	**377.9**	**748.31**	**48.2**	**0.643**	**12.745**	**0.529**	**0.127**	**0.917**	**0.061**	**0.061**	**0.060**	**1**	**1**	**0.164**

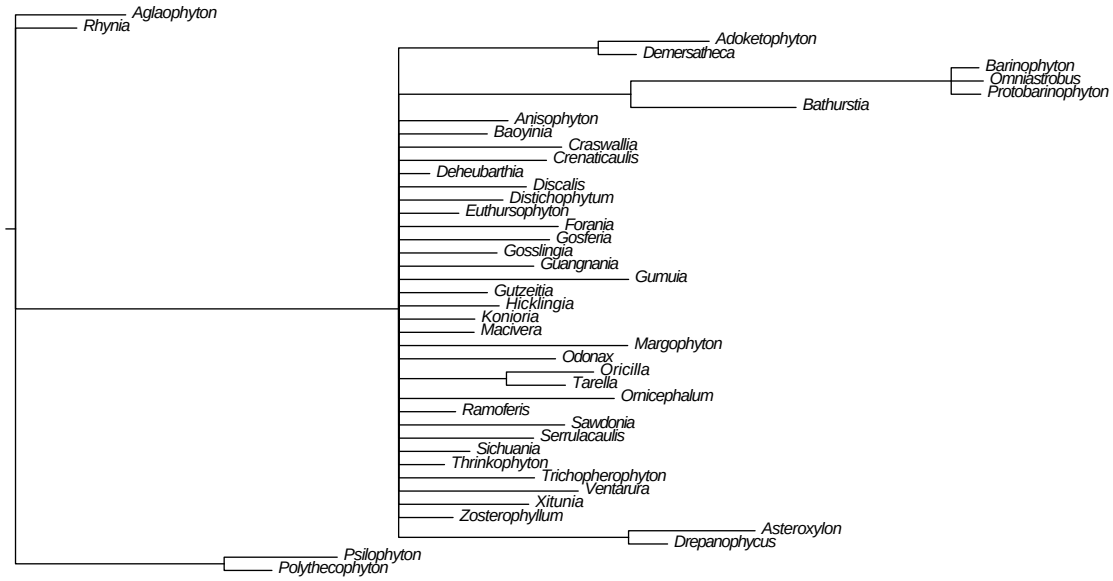


Figure B.1: Majority rule consensus tree of Bayesian analysis with full taxon sampling. The Bayesian analysis with *Gosferia* and *Gutzeitia* excluded (GGE) generated a similar majority rule consensus topology.

Appendix C

Phylogeography

C.1 Tables and datasets

Table C.1: Dataset of presence-absence of genera of zosterophylls in a given locality (Capel, Cleal, et al., 2023)

Taxon	GER	BEL	EN-WLS	SVL	SCT	ARC-CAN	SBR	XNJ	YUN	SCH	W-USA	E-CAN	N-FRA	UKR	GZH	GGX	E-USA	NOR	VNZ	MOS
Hicklingia	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ornicephalum	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Zosterophyllum	0	0	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1
Gosslingia	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Macivera	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sichuania	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Xitunia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Adoketophyton	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0
Baoyinia	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Craswallia	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Distichophytum	1	1	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	1
Guangnania	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
Margophyton	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Ramoferis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Oricilla	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0
Odonax	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tricho.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Thrinkophyton	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ventarura	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tarella	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gumuia	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Gosferia	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Forania	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Discalis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Deheubarthia	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Crenaticaulis	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Bathurstia	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Protob.	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1
Sawdonia	1	1	1	0	0	1	1	0	0	0	1	1	1	0	0	0	1	1	1	0
Demersatheca	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0
Anisophyton	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Barinophyton	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0
Serrulacaulis	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0
Euthursophyton	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gutzeitia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Omniastrobus	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Wenshania	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

C.2 R scripts

C.2.1 Group estimation

```
# This script has been elaborated by Monet C. on 06-25-2024
# Initialization
library(vegan)
library(ape)
# Data
ocmf <- read.table("all_span", header=T) #raw datamatrix
ocmf <- ocmf[rownames(ocmf) != "POL",] # Poland is an outlier
k <- (colSums(ocmf) == 0)
if(any(k)) ocmf <- ocmf[,!k]
ngp <- 3 # Group assignation

# Dissimilarity analyses
dbray <- vegdist(ocmf, method = "bray") # Bray-Curtis dissimilarity matrix
hcabray <- hclust(dbray, method = "average")
plot(hcabray)
rect.hclust(hcabray, ngp, border = 2)

den <- as.dendrogram(hcabray)
oden <- reorder(den, 1:12)
plot(oden)
rect.hclust(hcabray, 3, border = 2)

draup <- vegdist(ocmf, method = "raup") # Raup-Crick dissimilarity matrix
hcaraup <- hclust(draup, method = "average")
plot(hcaraup)
rect.hclust(hcaraup, ngp, border = 2)

# Ordination analyses
gfac <- as.factor(cutree(hcabray, ngp))
nmds <- metaMDS(dbray, trace = FALSE)
plot(nmds, disp = "sites", type = "n", las = 1,
xlab = paste0("nMDS axis 1 (R^2 = ?)"), ylab = paste0("nMDS axis 2 (R^2 = ?)"))
#ordiellipse(nmds, gfac, col = (1:nlevels(gfac))+1, draw = "polygon")
ordicluster(nmds, hcabray, lwd = 2)  #, col = cutree(hcabray, ngp))
ordihull(nmds, gfac, col = (1:nlevels(gfac))+1, lwd = 3)
points(nmds, disp = "sites", pch = 21, col = "black", bg = "yellow", cex = 1.5)
orditorp(nmds, "sites", pos = 3)
title("ordination analysis by means of a nMDS based on the Bray-Curtis dissimilarity
matrix")

# Tests
permutest(betadisper(dbray, gfac), pairwise = TRUE) # Testing the normality of data
aos <- anosim(dbray, gfac) # Significance of the groups
print(summary(aos))
```

```
sim <- simper(ocmf, gfac) # Taxa contribution to the groups
tblsim <- summary(sim)
print(tblsim)

# Test the impact of singletons
multitons <- colnames(ocmf)[colSums(ocmf) > 1]
ocmt <- ocmf[,multitons]
round((1 - ncol(ocmt) / ncol(ocmf)) * 100, 1)
dbc <- vegdist(ocmt, method = "bray")
hca2 <- hclust(dbc, method = "average")
plot(hca2)
rect.hclust(hca2, ngp, border = 2)

tree <- nj(dbc)
plot(tree)

gfac <- as.factor(cutree(hca2, ngp))

nmds2 <- metaMDS(dbc, trace = FALSE)
print(nmds2)

plot(nmds2, disp = "sites", type = "n", las = 1, xlim = extendrange(nmds2$points[,1]),
xlab = paste0("nMDS axis 1 (R^2 = ?)"), ylab = paste0("nMDS axis 2 (R^2 = ?)"))
########ordiplot(nmds2, disp = "sites", type = "t")
ordihull(nmds2, gfac, col = (1:nlevels(gfac))+1, lwd = 3)
ordiellipse(nmds2, gfac, col = (1:nlevels(gfac))+1, draw = "polygon")
ordispider(nmds2, gfac, col = (1:nlevels(gfac))+1, label = TRUE)
points(nmds2, disp = "sites", pch = 21, col = "black", bg = "yellow", cex = 1.5)
text(nmds2$points, labels = rownames(ocmt), pos = 4, cex = 1)

aos2 <- anosim(dbc, gfac)
print(summary(aos2))

sim2 <- simper(ocmt, gfac)
tblsim2 <- summary(sim2)
print(sim2)
print(tblsim2)
```

C.2.2 Paleogeographical reconstructions

```
##########Code for Biogeography
   ##################################################
#      Original Code Nick Matzke's, modified for the present
   dataset            #
#      Most of the comments are Nick's some are Adriane Lam's
    some are Brauer's  #
#      See http://phylo.wikidot.com/biogeobears for updated
   files by Nick       #
```

```
##########Code for Biogeography
    ##################################################

install.packages("GenSA")
library(GenSA)    # GenSA is better than optimx (although
    somewhat slower)
install.packages("FD")
library(FD)       # for FD::maxent() (make sure this is up-to
    -date)
install.packages("snow")
library(snow)     # (if you want to use multicore
    functionality; some systems/R versions prefer library(
    parallel), try either)
library(parallel)

install.packages("rexpokit")
install.packages("cladoRcpp")
install.packages("devtools")

library(rexpokit)
devtools::install_github(repo="nmatzke/BioGeoBEARS",
    dependencies=FALSE) # for when BioGeoBEARS fails, install
    dependencies separately

library(cladoRcpp)
library(BioGeoBEARS)

#Check out the directory to see what files are there
# move geography and newick files here
extdata_dir = np(system.file("extdata", package="BioGeoBEARS
    "))
extdata_dir
list.files(extdata_dir)

#Read in and look at your raw tree file
trfn = np(paste(addslash(extdata_dir), "06_11_timecal", sep
    =""))
moref(trfn)

#Look at phylogeny as a pdf
pdffn = "tree.pdf"
pdf(file=pdffn, width=9, height=12)

tr = read.tree(trfn)
tr
plot(tr)
title("Zosterophyllopsida")
axisPhylo() # plots branch lengths
```

```
dev.off()
cmdstr = paste0("open ", pdffn)
system(cmdstr)

#Read in the geography file
geogfn = np(paste(addslash(extdata_dir), "zostero_geo", sep
    =""))
moref(geogfn)

#Look at geographic range data
tipranges = getranges_from_LagrangePHYLIP(lgdata_fn=geogfn)
tipranges

#Maximum range size observed
max(rowSums(dfnums_to_numeric(tipranges@df)))

#IMPORTANT: set the number of areas any species can occupy;
    CANNOT be larger than the total
#number of areas, but can be smaller
#In Lam et al. 2018, I set the max number to the largest
    amount of areas any one species occupied
max_range_size = 4

####################################################
# KEY HINT: The number of states (= number of different
    possible geographic ranges)
# depends on (a) the number of areas and (b) max_range_size.
# If you have more than about 500-600 states, the
    calculations will get REALLY slow,
# since the program has to exponentiate a matrix of e.g. 600
    x600.  Often the computer
# will just sit there and crunch, and never get through the
    calculation of the first
# likelihood.
#
# (this is also what is usually happening when LAGRANGE hangs
    : you have too many states!)
#
# To check the number of states for a given number of ranges,
     try:
numstates_from_numareas(numareas=7, maxareas=7,
    include_null_range=TRUE)
numstates_from_numareas(numareas=4, maxareas=4,
    include_null_range=FALSE)
numstates_from_numareas(numareas=6, maxareas=5,
    include_null_range=TRUE)
numstates_from_numareas(numareas=4, maxareas=2,
    include_null_range=TRUE)
```

```
#If you limit the range size above using max_range_size, you
    should be OK

######################################################
######################################################
# DEC AND DEC+J ANALYSIS
######################################################
######################################################

# Intitialize a default model (DEC model)
BioGeoBEARS_run_object = define_BioGeoBEARS_run()

# Give BioGeoBEARS the location of the phylogeny Newick file
BioGeoBEARS_run_object$trfn = trfn

# Give BioGeoBEARS the location of the geography text file
BioGeoBEARS_run_object$geogfn = geogfn

# Input the maximum range size
BioGeoBEARS_run_object$max_range_size = max_range_size

BioGeoBEARS_run_object$min_branchlength = 0.000001    # Min
    to treat tip as a direct ancestor (no speciation event)
BioGeoBEARS_run_object$include_null_range = TRUE    # set to
    FALSE for e.g. DEC* model, DEC*+J, etc.

# Speed options and multicore processing if desired
BioGeoBEARS_run_object$on_NaN_error = -1e50    # returns very
     low lnL if parameters produce NaN error (underflow check)
BioGeoBEARS_run_object$speedup = TRUE          # shorcuts to
    speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$use_optimx = "GenSA"    # if FALSE,
    use optim() instead of optimx()
BioGeoBEARS_run_object$num_cores_to_use = 7

BioGeoBEARS_run_object$force_sparse = FALSE    # force_sparse
    =TRUE causes pathology & isn't much faster at this scale

# This function loads the dispersal multiplier matrix etc.
    from the text files into the model object. Required for
    these to work!
# (It also runs some checks on these inputs for certain
    errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(
    BioGeoBEARS_run_object)

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table
```

```
    = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE    # get
    ancestral states from optim run

# Set up DEC model
# (nothing to do; defaults)

# Look at the BioGeoBEARS_run_object; it's just a list of
    settings etc.
BioGeoBEARS_run_object

# This contains the model object
BioGeoBEARS_run_object$BioGeoBEARS_model_object

# This table contains the parameters of the model
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table

# Run this to check inputs. Read the error messages if you
    get them!
check_BioGeoBEARS_run(BioGeoBEARS_run_object)

#Make sure you change the file name below to match your own
    data!!!
runslow = TRUE
resfn = "zostero_DEC_M0_unconstrained_v1.Rdata"
if (runslow)
{
        res = bears_optim_run(BioGeoBEARS_run_object)
        res

        save(res, file=resfn)
        resDEC = res
} else {
        # Loads to "res"
        load(resfn)
        resDEC = res
}



######################################################
# Run DEC+J
######################################################
BioGeoBEARS_run_object = define_BioGeoBEARS_run()
BioGeoBEARS_run_object$trfn = trfn
BioGeoBEARS_run_object$geogfn = geogfn
BioGeoBEARS_run_object$max_range_size = max_range_size
BioGeoBEARS_run_object$min_branchlength = 0.000001    # Min
    to treat tip as a direct ancestor (no speciation event)
```

```
BioGeoBEARS_run_object$include_null_range = TRUE    # set to
    FALSE for e.g. DEC* model, DEC*+J, etc.

# Speed options and multicore processing if desired
BioGeoBEARS_run_object$on_NaN_error = -1e50    # returns very
     low lnL if parameters produce NaN error (underflow check)
BioGeoBEARS_run_object$speedup = TRUE          # shorcuts to
    speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$use_optimx = "GenSA"    # if FALSE,
    use optim() instead of optimx()
BioGeoBEARS_run_object$num_cores_to_use = 7
BioGeoBEARS_run_object$force_sparse = FALSE    # force_sparse
    =TRUE causes pathology & isn't much faster at this scale

# This function loads the dispersal multiplier matrix etc.
    from the text files into the model object. Required for
    these to work!
# (It also runs some checks on these inputs for certain
    errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(
    BioGeoBEARS_run_object)

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table
    = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE    # get
    ancestral states from optim run

# Set up DEC+J model
# Get the ML parameter values from the 2-parameter nested
    model
# (this will ensure that the 3-parameter model always does at
     least as good)
dstart = resDEC$outputs@params_table["d","est"]
estart = resDEC$outputs@params_table["e","est"]
jstart = 0.0001

# Input starting values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["d","init"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["d","est"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["e","init"] = estart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["e","est"] = estart

# Add j as a free parameter
```

```
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","type"] = "free"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","init"] = jstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","est"] = jstart

check_BioGeoBEARS_run(BioGeoBEARS_run_object)

#Make sure to change the file name to match your data!
resfn = "zostero_DEC+J_M0_unconstrained_v1.Rdata"
runslow = TRUE
if (runslow)
{
        #sourceall("/Dropbox/_njm/__packages/
            BioGeoBEARS_setup/")

        res = bears_optim_run(BioGeoBEARS_run_object)
        res

        save(res, file=resfn)

        resDECj = res
} else {
        # Loads to "res"
        load(resfn)
        resDECj = res
}

######################################################
# PDF plots
#MAKE SURE TO CHANGE FILE NAMES TO MATCH YOUR OWN!!!
######################################################
pdffn = "zostero_DEC_vs_DEC+J_M0_unconstrained.pdf"
pdf(pdffn, width=8.5, height=11)

######################################################
# Plot ancestral states - DEC
#I modified this code to NOT plot pie charts at the corners
    of the
#phylogeny, ONLY at the nodes. If you want to change this, I
    still
#have old emails from Nick on how to turn these on and off -
    ARL
######################################################
analysis_titletxt ="BioGeoBEARS DEC on zosterophylls
    M0_unconstrained"

# Setup
```

```
results_object = resDEC
scriptdir = np(system.file("extdata/a_scripts", package="
    BioGeoBEARS"))

# States
res2 = plot_BioGeoBEARS_results(results_object,
    analysis_titletxt, addl_params=list("j"), plotwhat="text",
     label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex
    =0.6, titlecex=0.8, plotsplits=FALSE, cornercoords_loc=
    scriptdir, include_null_range=TRUE, tr=tr, tipranges=
    tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt,
    addl_params=list("j"), plotwhat="pie", label.offset=0.45,
    tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8,
    plotsplits=FALSE, cornercoords_loc=scriptdir,
    include_null_range=TRUE, tr=tr, tipranges=tipranges)

######################################################
# Plot ancestral states - DECJ
#I modified this code to NOT plot pie charts at the corners
    of the
#phylogeny, ONLY at the nodes. If you want to change this, I
    still
#have old emails from Nick on how to turn these on and off -
    ARL
######################################################
analysis_titletxt ="BioGeoBEARS DEC+J on zosterophylls
    M0_unconstrained"

# Setup
results_object = resDECj
scriptdir = np(system.file("extdata/a_scripts", package="
    BioGeoBEARS"))

# States
res1 = plot_BioGeoBEARS_results(results_object,
    analysis_titletxt, addl_params=list("j"), plotwhat="text",
     label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex
    =0.6, titlecex=0.8, plotsplits=FALSE, cornercoords_loc=
    scriptdir, include_null_range=TRUE, tr=tr, tipranges=
    tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt,
    addl_params=list("j"), plotwhat="pie", label.offset=0.45,
    tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8,
    plotsplits=FALSE, cornercoords_loc=scriptdir,
```

```
    include_null_range=TRUE, tr=tr, tipranges=tipranges)

dev.off()  # Turn off PDF
cmdstr = paste("open ", pdffn, sep="")
system(cmdstr) # Plot it



######################################################
# DIVALIKE AND DIVALIKE+J ANALYSIS
######################################################

# NOTE: The BioGeoBEARS "DIVA" model is not identical with
# Ronquist (1997)'s parsimony DIVA. It is a likelihood
# interpretation of DIVA, constructed by modelling DIVA's
# processes the way DEC does, but only allowing the
# processes DIVA allows (widespread vicariance: yes; subset
# sympatry: no; see Ronquist & Sanmartin 2011, Figure 4).
#
# I thus now call the model "DIVALIKE", and you should also.
    ;-)
#

######################################################
# Run DIVALIKE
######################################################
BioGeoBEARS_run_object = define_BioGeoBEARS_run()
BioGeoBEARS_run_object$trfn = trfn
BioGeoBEARS_run_object$geogfn = geogfn
BioGeoBEARS_run_object$max_range_size = max_range_size

# Set up the stratified part
#BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
#BioGeoBEARS_run_object$dispersal_multipliers_fn = "
    manual_dispersal_multipliers.txt"
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed.txt
    "
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki's BioGeoBEARS
     updates page.

BioGeoBEARS_run_object$use_optimx = TRUE
BioGeoBEARS_run_object$num_cores_to_use= 7

BioGeoBEARS_run_object$force_sparse=FALSE    # sparse=FALSE
    causes pathology & isn't much faster at this scale
BioGeoBEARS_run_object$speedup=TRUE          # shorcuts to
    speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$calc_ancprobs=TRUE    # get ancestral
```

```
    states from optim run

# This function loads the dispersal multiplier matrix etc.
    from the text files into the model object. Required for
    these to work!
# (It also runs some checks on these inputs for certain
    errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(
    BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this
    for stratified analysis)
#BioGeoBEARS_run_object = section_the_tree(inputs=
    BioGeoBEARS_run_object, make_master_table=TRUE,
    plot_pieces=FALSE)
# The stratified tree is described in this table:
#BioGeoBEARS_run_object$master_table

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table
    = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE

# Set up DIVALIKE model
# Remove subset-sympatry
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","est"] = 0.0

BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["ysv","type"] = "2-j"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["ys","type"] = "ysv*1/2"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["y","type"] = "ysv*1/2"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["v","type"] = "ysv*1/2"

# Allow classic, widespread vicariance; all events
    equiprobable
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["mx01v","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["mx01v","init"] = 0.5
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
```

```
    ["mx01v","est"] = 0.5

# No jump dispersal/founder-event speciation
#
    BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","type"] = "free"
#
    BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","init"] = 0.01
#
    BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","est"] = 0.01

check_BioGeoBEARS_run(BioGeoBEARS_run_object)

#CHANGE FILE NAMES TO MATCH YOUR OWN DATA
runslow = TRUE
resfn = "zostero_DIVALIKE_M0_unconstrained.Rdata"
if (runslow)
{
        res = bears_optim_run(BioGeoBEARS_run_object)
        res

        save(res, file=resfn)
        resDIVALIKE = res
} else {
        # Loads to "res"
        load(resfn)
        resDIVALIKE = res
}
#If you get a warning message like: In (function(npt=min(n +
    2L, 2L * n), rhobeg=NA, rhoend=NA;
#       unused control arguments ignored
#Just ignore it. IDK what it means and Nick seemed fine with
    it -ARL

######################################################
# Run DIVALIKE+J
######################################################
BioGeoBEARS_run_object = define_BioGeoBEARS_run()
BioGeoBEARS_run_object$trfn = trfn
BioGeoBEARS_run_object$geogfn = geogfn
BioGeoBEARS_run_object$max_range_size = max_range_size

# Set up the stratified part
#BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
#BioGeoBEARS_run_object$dispersal_multipliers_fn = "
    manual_dispersal_multipliers.txt"
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed.txt
```

```
    "
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki's BioGeoBEARS
    updates page.

BioGeoBEARS_run_object$use_optimx = TRUE
BioGeoBEARS_run_object$num_cores_to_use= 7

BioGeoBEARS_run_object$force_sparse=FALSE    # sparse=FALSE
    causes pathology & isn't much faster at this scale
BioGeoBEARS_run_object$speedup=TRUE          # shorcuts to
    speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$calc_ancprobs=TRUE    # get ancestral
    states from optim run

# This function loads the dispersal multiplier matrix etc.
    from the text files into the model object. Required for
    these to work!
# (It also runs some checks on these inputs for certain
    errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(
    BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this
    for stratified analysis)
#BioGeoBEARS_run_object = section_the_tree(inputs=
    BioGeoBEARS_run_object, make_master_table=TRUE,
    plot_pieces=FALSE)
# The stratified tree is described in this table:
#BioGeoBEARS_run_object$master_table

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table
    = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE

# Set up DIVALIKE+J model
# Get the ML parameter values from the 2-parameter nested
    model
# (this will ensure that the 3-parameter model always does at
    least as good)
dstart = resDIVALIKE$outputs@params_table["d","est"]
estart = resDIVALIKE$outputs@params_table["e","est"]
jstart = 0.0001

# Input starting values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["d","init"] = dstart
```

```
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["d","est"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["e","init"] = estart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["e","est"] = estart

# Remove subset-sympatry
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","est"] = 0.0

BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["ysv","type"] = "2-j"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["ys","type"] = "ysv*1/2"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["y","type"] = "ysv*1/2"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["v","type"] = "ysv*1/2"

# Allow classic, widespread vicariance; all events
    equiprobable
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["mx01v","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["mx01v","init"] = 0.5
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["mx01v","est"] = 0.5

# Add jump dispersal/founder-event speciation
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","type"] = "free"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","init"] = jstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","est"] = jstart

# Under DIVALIKE+J, the max of "j" should be 2, not 3 (as is
    default in DEC+J)
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","min"] = 0.00001
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","max"] = 1.99999

check_BioGeoBEARS_run(BioGeoBEARS_run_object)
```

```
#CHANGE FILE NAMES TO MATCH YOUR DATA
resfn = "zostero_DIVALIKE+J_M0_unconstrained.Rdata"
runslow = TRUE
if (runslow)
{
        #sourceall("/Dropbox/_njm/__packages/
            BioGeoBEARS_setup/")

        res = bears_optim_run(BioGeoBEARS_run_object)
        res

        save(res, file=resfn)

        resDIVALIKEj = res
} else {
        # Loads to "res"
        load(resfn)
        resDIVALIKEj = res
}

######################################################
# Plot ancestral states - DIVALIKE
#Same here- I turned off pie charts and area reconstructions
    at corners -ARL
######################################################
pdffn = "zostero_DIVALIKE_vs_DIVALIKE+J_M0_unconstrained.pdf"
pdf(pdffn, width=8.5, height=11)

analysis_titletxt ="BioGeoBEARS DIVALIKE on zosterophylls
    M0_unconstrained"

# Setup
results_object = resDIVALIKE
scriptdir = np(system.file("extdata/a_scripts", package="
    BioGeoBEARS"))

# States
res2 = plot_BioGeoBEARS_results(results_object,
    analysis_titletxt, addl_params=list("j"), plotwhat="text",
     label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex
    =0.6, titlecex=0.8, plotsplits=FALSE, cornercoords_loc=
    scriptdir, include_null_range=TRUE, tr=tr, tipranges=
    tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt,
    addl_params=list("j"), plotwhat="pie", label.offset=0.45,
    tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8,
```

```
    plotsplits=FALSE, cornercoords_loc=scriptdir,
    include_null_range=TRUE, tr=tr, tipranges=tipranges)

########################################################
# Plot ancestral states - DIVALIKE+J
########################################################
analysis_titletxt ="BioGeoBEARS DIVALIKE+J on
    M0_unconstrained"

# Setup
results_object = resDIVALIKEj
scriptdir = np(system.file("extdata/a_scripts", package="
    BioGeoBEARS"))

# States
res1 = plot_BioGeoBEARS_results(results_object,
    analysis_titletxt, addl_params=list("j"), plotwhat="text",
     label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex
    =0.6, titlecex=0.8, plotsplits=FALSE, cornercoords_loc=
    scriptdir, include_null_range=TRUE, tr=tr, tipranges=
    tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt,
    addl_params=list("j"), plotwhat="pie", label.offset=0.45,
    tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8,
    plotsplits=FALSE, cornercoords_loc=scriptdir,
    include_null_range=TRUE, tr=tr, tipranges=tipranges)

dev.off()
cmdstr = paste("open ", pdffn, sep="")
system(cmdstr)


########################################################
# BAYAREALIKE AND BAYAREALIKE+J ANALYSIS
########################################################

# NOTE: As with DIVA, the BioGeoBEARS BayArea-like model is
# not identical with the full Bayesian model implemented
# in the "BayArea" program of Landis et al. (2013).
#
# Instead, this is a simplified likelihood interpretation
# of the model.  Basically, in BayArea and BioGeoBEARS-
    BAYAREALIKE,
# "d" and "e" work like they do in the DEC model of Lagrange
# (and BioGeoBEARS), and then BayArea's cladogenesis
    assumption
# (which is that nothing in particular happens at
```

```
    cladogenesis) is
# replicated by BioGeoBEARS.
#
# This leaves out 3 important things that are in BayArea:
# 1. Distance dependence (you can add this with a distances
#    matrix + the "x" parameter in BioGeoBEARS, however)
# 2. A correction for disallowing "e" events that drive
#    a species extinct (a null geographic range)
# 3. The neat Bayesian sampling of histories, which allows
#    analyses on large numbers of areas.
#
# The main purpose of having a "BAYAREALIKE" model is
# to test the importance of the cladogenesis model on
# particular datasets. Does it help or hurt the data
# likelihood if there is no special cladogenesis process?
#
# I thus now call the model "BAYAREALIKE", and you should
    also. ;-)
#

######################################################
# Run BAYAREALIKE
######################################################
BioGeoBEARS_run_object = define_BioGeoBEARS_run()
BioGeoBEARS_run_object$trfn = trfn
BioGeoBEARS_run_object$geogfn = geogfn
BioGeoBEARS_run_object$max_range_size = max_range_size

# Set up the stratified part
#BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
#BioGeoBEARS_run_object$dispersal_multipliers_fn = "
    manual_dispersal_multipliers.txt"
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed.txt
    "
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki's BioGeoBEARS
    updates page.

BioGeoBEARS_run_object$use_optimx = TRUE
BioGeoBEARS_run_object$num_cores_to_use= 7

BioGeoBEARS_run_object$force_sparse=FALSE    # sparse=FALSE
    causes pathology & isn't much faster at this scale
BioGeoBEARS_run_object$speedup=TRUE          # shorcuts to
    speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$calc_ancprobs=TRUE    # get ancestral
    states from optim run

# This function loads the dispersal multiplier matrix etc.
```

```
    from the text files into the model object. Required for
    these to work!
# (It also runs some checks on these inputs for certain
    errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(
    BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this
    for stratified analysis)
#BioGeoBEARS_run_object = section_the_tree(inputs=
    BioGeoBEARS_run_object, make_master_table=TRUE,
    plot_pieces=FALSE)
# The stratified tree is described in this table:
#BioGeoBEARS_run_object$master_table

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table
    = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE

# Set up BAYAREALIKE model
# No subset sympatry
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","est"] = 0.0

# No vicariance
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["v","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["v","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["v","est"] = 0.0

# No jump dispersal/founder-event speciation
#
    BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","type"] = "free"
#
    BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","init"] = 0.01
#
    BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","est"] = 0.01
```

```
# Adjust linkage between parameters
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["ysv","type"] = "1-j"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["ys","type"] = "ysv*1/1"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["y","type"] = "1-j"

# Only sympatric/range-copying (y) events allowed, and with
# exact copying (both descendants always the same size as the
     ancestor)
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["mx01y","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["mx01y","init"] = 0.9999
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["mx01y","est"] = 0.9999

# Check the inputs
check_BioGeoBEARS_run(BioGeoBEARS_run_object)

#CHANGE FILE NAMES TO MATCH YOUR OWN
runslow = TRUE
resfn = "zostero_BAYAREALIKE_M0_unconstrained.Rdata"
if (runslow)
{
        res = bears_optim_run(BioGeoBEARS_run_object)
        res

        save(res, file=resfn)
        resBAYAREALIKE = res
} else {
        # Loads to "res"
        load(resfn)
        resBAYAREALIKE = res
}

######################################################
# Run BAYAREALIKE+J
######################################################
BioGeoBEARS_run_object = define_BioGeoBEARS_run()
BioGeoBEARS_run_object$trfn = trfn
BioGeoBEARS_run_object$geogfn = geogfn
BioGeoBEARS_run_object$max_range_size = max_range_size

# Set up the stratified part
#BioGeoBEARS_run_object$timesfn = "timeperiods.txt"
#BioGeoBEARS_run_object$dispersal_multipliers_fn = "
    manual_dispersal_multipliers.txt"
```

```
#BioGeoBEARS_run_object$areas_allowed_fn = "areas_allowed.txt
    "
#BioGeoBEARS_run_object$distsfn = "distances_matrix.txt"
# See notes on the distances model on PhyloWiki's BioGeoBEARS
    updates page.

BioGeoBEARS_run_object$use_optimx = TRUE
BioGeoBEARS_run_object$num_cores_to_use= 7

BioGeoBEARS_run_object$force_sparse=FALSE    # sparse=FALSE
    causes pathology & isn't much faster at this scale
BioGeoBEARS_run_object$speedup=TRUE          # shorcuts to
    speed ML search; use FALSE if worried (e.g. >3 params)
BioGeoBEARS_run_object$calc_ancprobs=TRUE    # get ancestral
    states from optim run

# This function loads the dispersal multiplier matrix etc.
    from the text files into the model object. Required for
    these to work!
# (It also runs some checks on these inputs for certain
    errors.)
BioGeoBEARS_run_object = readfiles_BioGeoBEARS_run(
    BioGeoBEARS_run_object)

# Divide the tree up by timeperiods/strata (uncomment this
    for stratified analysis)
#BioGeoBEARS_run_object = section_the_tree(inputs=
    BioGeoBEARS_run_object, make_master_table=TRUE,
    plot_pieces=FALSE)
# The stratified tree is described in this table:
#BioGeoBEARS_run_object$master_table

# Good default settings to get ancestral states
BioGeoBEARS_run_object$return_condlikes_table = TRUE
BioGeoBEARS_run_object$calc_TTL_loglike_from_condlikes_table
    = TRUE
BioGeoBEARS_run_object$calc_ancprobs = TRUE

# Set up BAYAREALIKE+J model
# Get the ML parameter values from the 2-parameter nested
    model
# (this will ensure that the 3-parameter model always does at
     least as good)
dstart = resBAYAREALIKE$outputs@params_table["d","est"]
estart = resBAYAREALIKE$outputs@params_table["e","est"]
jstart = 0.0001

# Input starting values for d, e
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
```

```
    ["d","init"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["d","est"] = dstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["e","init"] = estart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["e","est"] = estart

# No subset sympatry
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["s","est"] = 0.0

# No vicariance
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["v","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["v","init"] = 0.0
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["v","est"] = 0.0

# *DO* allow jump dispersal/founder-event speciation (set the
    starting value close to 0)
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","type"] = "free"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","init"] = jstart
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","est"] = jstart

# Under BAYAREALIKE+J, the max of "j" should be 1, not 3 (as
    is default in DEC+J) or 2 (as in DIVALIKE+J)
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","max"] = 0.99999

# Adjust linkage between parameters
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["ysv","type"] = "1-j"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["ys","type"] = "ysv*1/1"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["y","type"] = "1-j"

# Only sympatric/range-copying (y) events allowed, and with
# exact copying (both descendants always the same size as the
    ancestor)
```

```
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["mx01y","type"] = "fixed"
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["mx01y","init"] = 0.9999
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["mx01y","est"] = 0.9999

# NOTE (NJM, 2014-04): BAYAREALIKE+J seems to crash on some
    computers, usually Windows
# machines. I can't replicate this on my Mac machines, but it
     is almost certainly
# just some precision under-run issue, when optim/optimx
    tries some parameter value
# just below zero.  The "min" and "max" options on each
    parameter are supposed to
# prevent this, but apparently optim/optimx sometimes go
    slightly beyond
# these limits.  Anyway, if you get a crash, try raising "min
    " and lowering "max"
# slightly for each parameter:
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["d","min"] = 0.0000001
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["d","max"] = 4.9999999

BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["e","min"] = 0.0000001
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["e","max"] = 4.9999999

BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","min"] = 0.00001
BioGeoBEARS_run_object$BioGeoBEARS_model_object@params_table
    ["j","max"] = 0.99999

check_BioGeoBEARS_run(BioGeoBEARS_run_object)

#CHANGE FILE NAMES TO MATCH YOUR OWN
resfn = "zostero_BAYAREALIKE+J_M0_unconstrained.Rdata"
runslow = TRUE
if (runslow)
{
        res = bears_optim_run(BioGeoBEARS_run_object)
        res

        save(res, file=resfn)

        resBAYAREALIKEj = res
} else {
```

```
        # Loads to "res"
        load(resfn)
        resBAYAREALIKEj = res
}

pdffn = "zostero_BAYAREALIKE_vs_BAYAREALIKE+
    J_M0_unconstrained.pdf"
pdf(pdffn, width=8.5, height=11)

######################################################
# Plot ancestral states - BAYAREALIKE
######################################################
analysis_titletxt ="BioGeoBEARS BAYAREALIKE on zosterophylls
    M0_unconstrained"

# Setup
results_object = resBAYAREALIKE
scriptdir = np(system.file("extdata/a_scripts", package="
    BioGeoBEARS"))

# States
res2 = plot_BioGeoBEARS_results(results_object,
    analysis_titletxt, addl_params=list("j"), plotwhat="text",
     label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex
    =0.6, titlecex=0.8, plotsplits=FALSE, cornercoords_loc=
    scriptdir, include_null_range=TRUE, tr=tr, tipranges=
    tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt,
    addl_params=list("j"), plotwhat="pie", label.offset=0.45,
    tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8,
    plotsplits=FALSE, cornercoords_loc=scriptdir,
    include_null_range=TRUE, tr=tr, tipranges=tipranges)

######################################################
# Plot ancestral states - BAYAREALIKE+J
######################################################
analysis_titletxt ="BioGeoBEARS BAYAREALIKE+J on
    zosterophylls M0_unconstrained"

# Setup
results_object = resBAYAREALIKEj
scriptdir = np(system.file("extdata/a_scripts", package="
    BioGeoBEARS"))

# States
res1 = plot_BioGeoBEARS_results(results_object,
    analysis_titletxt, addl_params=list("j"), plotwhat="text",
```

```
     label.offset=0.45, tipcex=0.7, statecex=0.7, splitcex
    =0.6, titlecex=0.8, plotsplits=FALSE, cornercoords_loc=
    scriptdir, include_null_range=TRUE, tr=tr, tipranges=
    tipranges)

# Pie chart
plot_BioGeoBEARS_results(results_object, analysis_titletxt,
    addl_params=list("j"), plotwhat="pie", label.offset=0.45,
    tipcex=0.7, statecex=0.7, splitcex=0.6, titlecex=0.8,
    plotsplits=FALSE, cornercoords_loc=scriptdir,
    include_null_range=TRUE, tr=tr, tipranges=tipranges)

dev.off()
cmdstr = paste("open ", pdffn, sep="")
system(cmdstr)

#
# CALCULATE SUMMARY STATISTICS TO COMPARE
# DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, BAYAREALIKE+
    J

# REQUIRED READING:
#
# Practical advice / notes / basic principles on statistical
    model
#     comparison in general, and in BioGeoBEARS:
# http://phylo.wikidot.com/advice-on-statistical-model-
    comparison-in-biogeobears
######################################################


# Set up empty tables to hold the statistical results
restable = NULL
teststable = NULL

######################################################
# Statistics -- DEC vs. DEC+J
######################################################
# We have to extract the log-likelihood differently,
    depending on the
# version of optim/optimx
LnL_2 = get_LnL_from_BioGeoBEARS_results_object(resDEC)
LnL_1 = get_LnL_from_BioGeoBEARS_results_object(resDECj)

numparams1 = 3
numparams2 = 2
stats = AICstats_2models(LnL_1, LnL_2, numparams1, numparams2
    )
stats
```

```
# DEC, null model for Likelihood Ratio Test (LRT)
res2 = extract_params_from_BioGeoBEARS_results_object(
    results_object=resDEC, returnwhat="table", addl_params=c("
    j"), paramsstr_digits=4)
# DEC+J, alternative model for Likelihood Ratio Test (LRT)
res1 = extract_params_from_BioGeoBEARS_results_object(
    results_object=resDECj, returnwhat="table", addl_params=c
    ("j"), paramsstr_digits=4)

# The null hypothesis for a Likelihood Ratio Test (LRT) is
    that two models
# confer the same likelihood on the data. See: Brian O'Meara'
    s webpage:
# http://www.brianomeara.info/tutorials/aic
# ...for an intro to LRT, AIC, and AICc

rbind(res2, res1)
tmp_tests = conditional_format_table(stats)

restable = rbind(restable, res2, res1)
teststable = rbind(teststable, tmp_tests)

########################################################
# Statistics -- DIVALIKE vs. DIVALIKE+J
########################################################
# We have to extract the log-likelihood differently,
    depending on the
# version of optim/optimx
LnL_2 = get_LnL_from_BioGeoBEARS_results_object(resDIVALIKE)
LnL_1 = get_LnL_from_BioGeoBEARS_results_object(resDIVALIKEj)

numparams1 = 3
numparams2 = 2
stats = AICstats_2models(LnL_1, LnL_2, numparams1, numparams2
    )
stats

# DIVALIKE, null model for Likelihood Ratio Test (LRT)
res2 = extract_params_from_BioGeoBEARS_results_object(
    results_object=resDIVALIKE, returnwhat="table",
    addl_params=c("j"), paramsstr_digits=4)
# DIVALIKE+J, alternative model for Likelihood Ratio Test (
    LRT)
res1 = extract_params_from_BioGeoBEARS_results_object(
    results_object=resDIVALIKEj, returnwhat="table",
    addl_params=c("j"), paramsstr_digits=4)

rbind(res2, res1)
```

```
conditional_format_table(stats)

tmp_tests = conditional_format_table(stats)

restable = rbind(restable, res2, res1)
teststable = rbind(teststable, tmp_tests)

########################################################
# Statistics -- BAYAREALIKE vs. BAYAREALIKE+J
########################################################
# We have to extract the log-likelihood differently,
    depending on the
# version of optim/optimx
LnL_2 = get_LnL_from_BioGeoBEARS_results_object(
    resBAYAREALIKE)
LnL_1 = get_LnL_from_BioGeoBEARS_results_object(
    resBAYAREALIKEj)

numparams1 = 3
numparams2 = 2
stats = AICstats_2models(LnL_1, LnL_2, numparams1, numparams2
    )
stats

# BAYAREALIKE, null model for Likelihood Ratio Test (LRT)
res2 = extract_params_from_BioGeoBEARS_results_object(
    results_object=resBAYAREALIKE, returnwhat="table",
    addl_params=c("j"), paramsstr_digits=4)
# BAYAREALIKE+J, alternative model for Likelihood Ratio Test
    (LRT)
res1 = extract_params_from_BioGeoBEARS_results_object(
    results_object=resBAYAREALIKEj, returnwhat="table",
    addl_params=c("j"), paramsstr_digits=4)

rbind(res2, res1)
conditional_format_table(stats)

tmp_tests = conditional_format_table(stats)

restable = rbind(restable, res2, res1)
teststable = rbind(teststable, tmp_tests)

########################################################
# RESULTS: DEC, DEC+J, DIVALIKE, DIVALIKE+J, BAYAREALIKE,
    BAYAREALIKE+J
########################################################
teststable$alt = c("DEC+J", "DIVALIKE+J", "BAYAREALIKE+J")
teststable$null = c("DEC", "DIVALIKE", "BAYAREALIKE")
row.names(restable) = c("DEC", "DEC+J", "DIVALIKE", "DIVALIKE
```

```
    +J", "BAYAREALIKE", "BAYAREALIKE+J")

# Look at the results!!
restable
teststable

#######################################################
# Save the results tables for later -- check for e.g.
# convergence issues
#######################################################

# Loads to "restable"
save(restable, file="restable2_v1.Rdata")
load(file="restable2_v1.Rdata")

# Loads to "teststable"
save(teststable, file="teststable2_v1.Rdata")
load(file="teststable2_v1.Rdata")

# Also save to text files
write.table(restable, file="restable2.txt", quote=FALSE, sep
    ="\t")
write.table(unlist_df(teststable), file="teststable2.txt",
    quote=FALSE, sep="\t")

#######################################################
# Model weights of all six models
#######################################################
restable2 = restable

# With AICs:
AICtable = calc_AIC_column(LnL_vals=restable$LnL, nparam_vals
    =restable$numparams)
restable = cbind(restable, AICtable)
restable_AIC_rellike = AkaikeWeights_on_summary_table(
    restable=restable, colname_to_use="AIC")
restable_AIC_rellike

# With AICcs -- factors in sample size
samplesize = length(tr$tip.label)
AICtable = calc_AICc_column(LnL_vals=restable$LnL,
    nparam_vals=restable$numparams, samplesize=samplesize)
restable2 = cbind(restable2, AICtable)
restable_AICc_rellike = AkaikeWeights_on_summary_table(
    restable=restable2, colname_to_use="AIC")
restable_AICc_rellike
free_params = row.names(resDECj$output@params_table[
    resDECj$output@params_table$type=="free",])
names(restable_AICc_rellike) = c("LnL", "numparams",
```

```
    free_params, "AICc", "AICc_wt")

# Also save to text files
write.table(restable_AIC_rellike, file="restable2_AIC_rellike
    .txt", quote=FALSE, sep="\t")
write.table(restable_AICc_rellike, file="
    restable2_AICc_rellike.txt", quote=FALSE, sep="\t")

# Save with nice conditional formatting
write.table(conditional_format_table(restable_AIC_rellike),
    file="restable2_AIC_rellike_formatted.txt", quote=FALSE,
    sep="\t")
write.table(conditional_format_table(restable_AICc_rellike),
    file="restable2_AICc_rellike_formatted.txt", quote=FALSE,
    sep="\t")
```

C.3 Tables and figures



Figure C.1: Cluster dendrogram showing the closeness of the localities based on the zosterophyll composition. This dendrogram is based on the Raup-Crick dissimilarity matrix. Three groups are found out and represented by the coloured boxes. Color code as in fig 3.6b. Locality abbreviation in table 3.1

Table C.2: Geographical distribution of taxa following the paleoprovinces. A=Laurussia, B= Eastern Laurussia, C= Northeastern Gondwana, D= Poland, 1= presence, 0= absence.

Taxon name	A	B	C	D
Rhynia	1	0	0	0
Aglaophyton	1	0	0	0
Adoketophyton	0	0	1	0
Barinophyton	1	0	0	0
Omniastrobus	1	0	0	0
Protobarinophyton	1	1	0	0
Anisophyton	1	0	0	0
Baoyinia	0	0	1	0
Bathurstia	1	0	0	0
Craswallia	1	0	0	0
Crenaticaulis	1	0	0	0
Deheubarthia	1	0	0	0
Demersatheca	0	0	1	0
Discalis	0	0	1	0
Distichophytum	1	1	1	0
Euthursophyton	1	0	0	0
Forania	1	0	0	0
Gosferia	1	0	0	0
Gosslingia	1	0	0	0
Guangnania	0	0	1	0
Gumuia	0	0	1	0
Gutzeitia	0	1	0	0
Hicklingia	1	1	0	0
Konioria	0	0	0	1
Macivera	1	0	0	0
Margophyton	1	1	0	0
Odonax	1	0	0	0
Oricilla	1	0	1	0
Ornicephalum	0	0	1	0
Ramoferis	0	0	1	0
Sawdonia	1	0	0	0
Serrulacaulis	1	0	0	0
Sichuania	0	0	1	0
Tarella	1	0	0	0
Thrinkophyton	1	0	0	0
Trichopherophyton	0	1	0	0
Ventarura	0	1	0	0
Xitunia	0	0	1	0
Zosterophyllum	1	1	1	0
Asteroxylon	1	0	0	0
Drepanophycus	1	1	1	1
Psilophyton	1	0	1	0
Polythecophyton	0	0	1	0
Wenshania	0	0	1	0

Table C.3: Results from SIMPER analysis between Laurussia and Eastern Laurussia

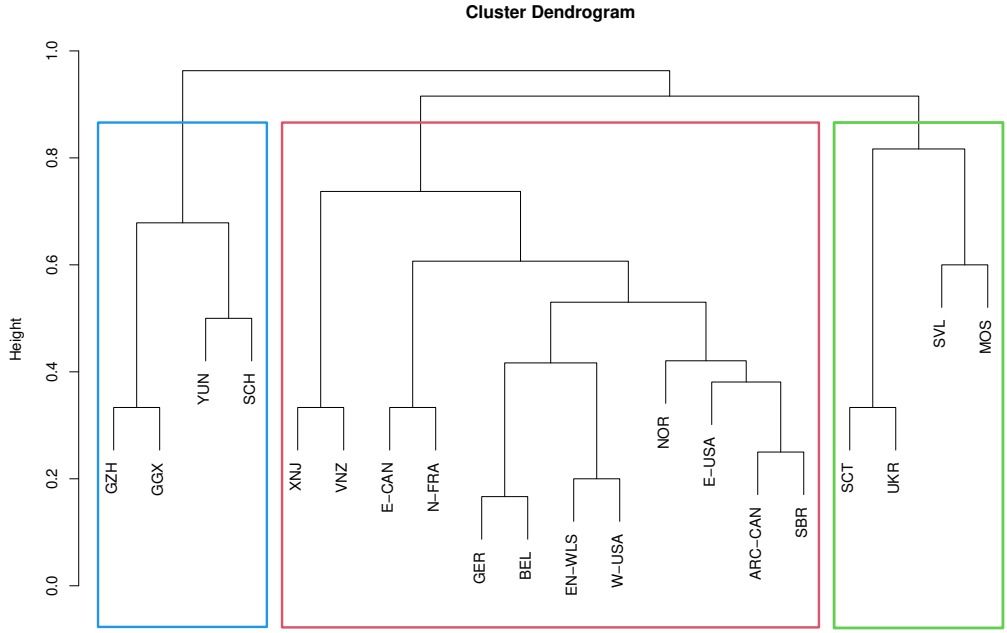
Taxon	average	sd	ratio	ava	avb	cumsum	p
Sawdonia	0.15482	0.10257	1.50940	0.91670	0.00000	0.167	0.002 **
Zosterophyllum	0.11704	0.11406	1.02610	0.08330	0.75000	0.294	0.012 *
Protobarinophyton	0.09012	0.12154	0.74150	0.16670	0.50000	0.391	0.062 .
Serrulacaulis	0.07003	0.12618	0.55500	0.33330	0.00000	0.466	0.230
Barinophyton	0.06874	0.07746	0.88740	0.50000	0.00000	0.541	0.173
Distichophytum	0.06420	0.07673	0.83660	0.41670	0.25000	0.610	0.258
Gosslingia	0.04273	0.06787	0.62970	0.33330	0.00000	0.656	0.366
Hicklingia	0.03807	0.06305	0.60380	0.08330	0.25000	0.697	0.093 .
Margophyton	0.03610	0.05943	0.60740	0.08330	0.25000	0.736	0.118
Trichopherophyton	0.03302	0.06087	0.54250	0.00000	0.25000	0.772	0.150
Ventarura	0.03302	0.06087	0.54250	0.00000	0.25000	0.807	0.150
Gutzeitia	0.02893	0.05270	0.54890	0.00000	0.25000	0.839	0.151
Anisophyton	0.01681	0.03872	0.43410	0.16670	0.00000	0.857	0.416
Macivera	0.01134	0.03907	0.29040	0.08330	0.00000	0.869	0.286
Oricilla	0.01134	0.03907	0.29040	0.08330	0.00000	0.881	0.754
Forania	0.01134	0.03907	0.29040	0.08330	0.00000	0.894	0.317
Crenaticaulis	0.01134	0.03907	0.29040	0.08330	0.00000	0.906	0.317
Bathurstia	0.01134	0.03907	0.29040	0.08330	0.00000	0.918	0.286
Omniastrobus	0.01134	0.03907	0.29040	0.08330	0.00000	0.930	0.317
Craswallia	0.00993	0.03401	0.29200	0.08330	0.00000	0.941	0.288
Thrinkophyton	0.00993	0.03401	0.29200	0.08330	0.00000	0.952	0.288
Tarella	0.00993	0.03401	0.29200	0.08330	0.00000	0.963	0.288
Deheubarthia	0.00993	0.03401	0.29200	0.08330	0.00000	0.973	0.288
Euthursophyton	0.00884	0.03014	0.29320	0.08330	0.00000	0.983	0.283
Odonax	0.00797	0.02710	0.29410	0.08330	0.00000	0.991	0.284
Gosferia	0.00797	0.02710	0.29410	0.08330	0.00000	1.000	0.284
Ornicephalum	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Sichuania	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Xitunia	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Adoketophyton	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Baoyinia	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Guangnania	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Ramoferis	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Gumuia	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Discalis	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Demersatheca	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Wenshania	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA

Table C.4: Results from SIMPER analysis between Laurussia and Northeastern Gondwana

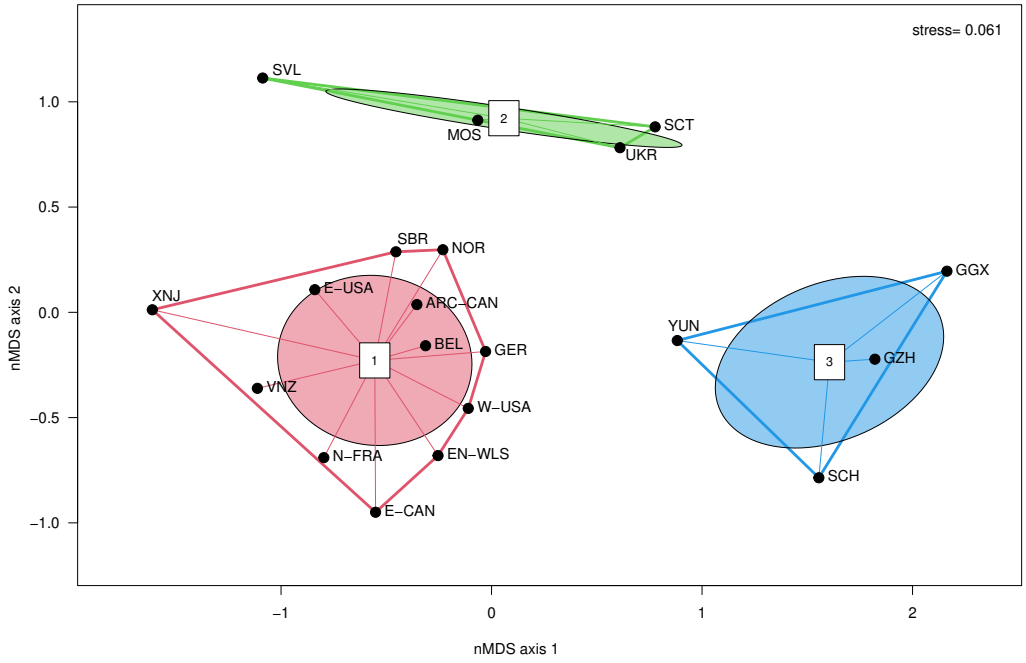
Taxon	average	sd	ratio	ava	avb	cumsum	p
Sawdonia	0.13069	0.09340	1.39920	0.91670	0.00000	0.133	0.017 *
Demersatheca	0.12433	0.12317	1.00950	0.00000	0.75000	0.260	0.007 **
Adoketophyton	0.09259	0.08074	1.14670	0.00000	0.75000	0.354	0.004 **
Barinophyton	0.05939	0.07022	0.84580	0.50000	0.00000	0.415	0.394
Serrulacaulis	0.05774	0.10831	0.53310	0.33330	0.00000	0.473	0.478
Distichophytum	0.05218	0.06584	0.79250	0.41670	0.25000	0.526	0.771
Guangnania	0.04575	0.05172	0.88470	0.00000	0.50000	0.573	0.024 *
Gosslingia	0.03708	0.06085	0.60930	0.33330	0.00000	0.611	0.540
Ornicephalum	0.02893	0.05270	0.54890	0.00000	0.25000	0.640	0.168
Sichuania	0.02893	0.05270	0.54890	0.00000	0.25000	0.670	0.168
Baoyinia	0.02893	0.05270	0.54890	0.00000	0.25000	0.699	0.168
Zosterophyllum	0.02732	0.05313	0.51410	0.08330	0.25000	0.727	0.978
Oricilla	0.02406	0.04177	0.57590	0.08330	0.25000	0.752	0.254
Protobarinophyton	0.02118	0.05160	0.41040	0.16670	0.00000	0.773	0.977
Xitunia	0.01683	0.02986	0.56350	0.00000	0.25000	0.790	0.164
Ramoferis	0.01683	0.02986	0.56350	0.00000	0.25000	0.807	0.164
Gumuia	0.01683	0.02986	0.56350	0.00000	0.25000	0.825	0.164
Discalis	0.01683	0.02986	0.56350	0.00000	0.25000	0.842	0.164
Wenshania	0.01683	0.02986	0.56350	0.00000	0.25000	0.859	0.164
Anisophyton	0.01491	0.03524	0.42310	0.16670	0.00000	0.874	0.614
Macivera	0.00983	0.03496	0.28130	0.08330	0.00000	0.884	0.584
Margophyton	0.00983	0.03496	0.28130	0.08330	0.00000	0.894	0.880
Forania	0.00983	0.03496	0.28130	0.08330	0.00000	0.904	0.568
Crenaticaulis	0.00983	0.03496	0.28130	0.08330	0.00000	0.914	0.568
Bathurstia	0.00983	0.03496	0.28130	0.08330	0.00000	0.924	0.584
Omniastrobus	0.00983	0.03496	0.28130	0.08330	0.00000	0.934	0.568
Craswallia	0.00870	0.03064	0.28390	0.08330	0.00000	0.943	0.574
Thrinkophyton	0.00870	0.03064	0.28390	0.08330	0.00000	0.952	0.574
Tarella	0.00870	0.03064	0.28390	0.08330	0.00000	0.961	0.574
Deheubarthia	0.00870	0.03064	0.28390	0.08330	0.00000	0.970	0.574
Hicklingia	0.00781	0.02732	0.28600	0.08330	0.00000	0.978	0.922
Euthursophyton	0.00781	0.02732	0.28600	0.08330	0.00000	0.986	0.583
Odonax	0.00710	0.02467	0.28760	0.08330	0.00000	0.993	0.612
Gosferia	0.00710	0.02467	0.28760	0.08330	0.00000	1.000	0.612
Trichopherophyton	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Ventarura	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Gutzeitia	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA

Table C.5: Results from SIMPER analysis between Eastern Laurussia and Northeastern Gondwana

Taxon	average	sd	ratio	ava	avb	cumsum	p
Demersatheca	0.16492	0.16838	0.97950	0.00000	0.75000	0.171	0.001 ***
Zosterophyllum	0.12316	0.13939	0.88360	0.75000	0.25000	0.298	0.034 *
Adoketophyton	0.11353	0.10467	1.08470	0.00000	0.75000	0.416	0.003 **
Protobarinophyton	0.09721	0.14300	0.67980	0.50000	0.00000	0.517	0.119
Guangnania	0.05252	0.06111	0.85940	0.00000	0.50000	0.571	0.011 *
Distichophytum	0.04018	0.05813	0.69120	0.25000	0.25000	0.613	0.887
Hicklingia	0.03403	0.06635	0.51280	0.25000	0.00000	0.648	0.330
Ornicephalum	0.03403	0.06292	0.54090	0.00000	0.25000	0.683	0.058 .
Sichuania	0.03403	0.06292	0.54090	0.00000	0.25000	0.718	0.058 .
Baoyinia	0.03403	0.06292	0.54090	0.00000	0.25000	0.753	0.058 .
Trichopherophyton	0.03403	0.06635	0.51280	0.25000	0.00000	0.789	0.244
Ventarura	0.03403	0.06635	0.51280	0.25000	0.00000	0.824	0.244
Margophyton	0.02950	0.05667	0.52060	0.25000	0.00000	0.855	0.476
Gutzeitia	0.02950	0.05667	0.52060	0.25000	0.00000	0.885	0.262
Xitunia	0.01849	0.03344	0.55300	0.00000	0.25000	0.904	0.073 .
Ramoferis	0.01849	0.03344	0.55300	0.00000	0.25000	0.923	0.073 .
Oricilla	0.01849	0.03344	0.55300	0.00000	0.25000	0.943	0.426
Gumuia	0.01849	0.03344	0.55300	0.00000	0.25000	0.962	0.073 .
Discalis	0.01849	0.03344	0.55300	0.00000	0.25000	0.981	0.073 .
Wenshania	0.01849	0.03344	0.55300	0.00000	0.25000	1.000	0.073 .
Gosslingia	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Macivera	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Craswallia	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Odonax	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Thrinkophyton	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Tarella	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Gosferia	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Forania	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Deheubarthia	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Crenaticaulis	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Bathurstia	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Sawdonia	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Anisophyton	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Barinophyton	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Serrulacaulis	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Euthursophyton	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA
Omniastrobus	0.00000	0.00000	NaN	0.00000	0.00000	1.000	NA



(a) Cluster dendrogram showing the closeness of the localities based on the zosterophyll composition, without singletons. Three groups are found out and represented by the coloured boxes. Color code as in fig **??**. Locality abbreviation in table 3.1



(b) nMDS analysis showing the group composition of the different localities, excluding the singletons. Color code as in fig **??**. Locality abbreviation in table 3.1

Figure C.2: Definition of Devonian paleoprovinces of zosterophylls, excluding the singletons

Appendix D

Diversity

D.1 Dataset

Species	Locality	Early interval	Late interval	Reference
Adoketophyton parvulum	Posongchong Fm. (bed 38 section 9) Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	X. Zhu et al. (2011)
Adoketophyton pingyipuensis	Pingyipu Gp., Horizon 1, Yanmenba Section, Jiangyou City, Sichuan, China	early Lochkovian	early Pragian	D. Edwards and Li (2018a)
Adoketophyton sp	Posongchong Fm. (bed 15 section 4), Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	D. Edwards and Li (2018a)
Adoketophyton subverticillatum	Mangshan Gp. (bed 2), Baoyang section, Duyun City, Guizhou, China	early Pragian	late Pragian	Huang et al. (2022)
Adoketophyton subverticillatum	Posongchong Fm. (bed 7), Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao et al. (2003)
Adoketophyton subverticillatum	Posongchong Fm., Daliantang Section, Guangnan county, Yunnan China	middle Pragian	late Pragian	Hao et al. (2003)
Adoketophyton subverticillatum	Posongchong Fm., Gegu-Daigu Section, Mengzi District, Yunnan, China	middle Pragian	late Pragian	Hao and Gensel (1998)
aff *Huia sp*	Xitun Fm., Huaguoshan Section, Shengfeng District, Yunnan, China	middle Lochkovian	late Lochkovian	Xue (2012)
aff *Zosterophyllum sp* A	Bathurst Island Fm., Loc US688, Polar Bear Pass, Bathurst Island, Canada	Ludfordian	Ludfordian	Kotyk et al. (2002)
aff *Zosterophyllum sp* B	Bathurst Island Fm., Loc US383, Polar Bear Pass, Bathurst Island, Canada	Ludfordian	Ludfordian	Kotyk et al. (2002)
Anisophyton cf *gothanii*	Wépion Fm., Quarry du Bois Collet, Fooz-Weépion, Belgium	early Emsian	early Emsian	Gerrienne (1991b)
Anisophyton gothanii	Rheinisches Schiefergebirge Fm., Feckelsberg, Germany	late Emsian	late Emsian	Remy, Schultka, et al. (1986)
Anisophyton gothanii	Rheinisches Schiefergebirge Fm., Heetdberg quarry, Germany	late Emsian	late Emsian	Remy, Schultka, et al. (1986)
Anisophyton gothanii	Rheinisches Schiefergebirge Fm., Neugrunen, Germany	late Emsian	late Emsian	Remy, Schultka, et al. (1986)
Anisophyton potonei	Külbach Beds, Ufersmühle Quarry, Wiehltalsperre, Germany	early Emsian	early Emsian	Remy, Hass, and Schultka (1986)
Anisophyton potonei	Nellenkopfchen Schichten Fm., Alken quarry, Germany	early Emsian	early Emsian	Schweitzer (1987)

Species	Locality	Early interval	Late interval	Reference
Anisophyton potonei	Nellenkopfchen Schichten Fm., Konder valley, Winningen, Germany	early Emsian	early Emsian	Schweitzer (1987)
Baoyinia sichuanensis	Pingyipu Gp., Horizon 2, Yanmenba Section, Jiangyou City, Sichuan, China	early Lochkovian	early Pragian	D. Edwards and Li (2018b)
Barinophyton cf *obscurum*	Catskill Fm., Burtville, Potter County, Pennsylvania, USA	late Famennian	late Famennian	Brauer (1981)
Barinophyton citrulliforme	Beaupère quarry, Annevoie, Belgium	late Famennian	late Famennian	Stockmans (1948)
Barinophyton citrulliforme	Catskill Fm., Burtville, Potter County, Pennsylvania, USA	late Famennian	late Famennian	Brauer (1980)
Barinophyton citrulliforme	Cattaraugus Fm., Loc. 3, Rock City, New York, USA	late Famennian	late Famennian	Arnold (1939)
Barinophyton citrulliforme	Evieux Fm., Quarry l'Ecluse d'Evieux-Esneux, Namur, Belgium	late Famennian	late Famennian	Stockmans (1948)
Barinophyton citrulliforme	Evieux Fm., Rorive quarry, Villers-le-Temple, Namur, Belgium	late Famennian	late Famennian	Stockmans (1948)
Barinophyton citrulliforme	Evieux Fm., Strud-Haltinne, Namur, Belgium	late Famennian	late Famennian	Stockmans (1948)
Barinophyton citrulliforme	Hell gate Fm., Okse Bay Group, Ellesmere island, Canada	early Frasnian	late Frasnian	Scheckler et al. (1990)
Barinophyton citrulliforme	Nordstrand Point Fm., Bird Fiord, Ellesmere island, Canada	early Frasnian	late Frasnian	Scheckler et al. (1990)
Barinophyton norvegicum	Brandenberg strata, Korzert Wuppertal, Germany	late Eifelian	early Givetian	Schweitzer and Giesen (2008)
Barinophyton norvegicum	Gjegnalund Glacier, Vestland, Norway	early Eifelian	late Givetian	Schweitzer and Giesen (2008)
Barinophyton obscurum	Catskill Fm., Red Hill, Clinton County, Pennsylvania, USA	late Famennian	late Famennian	Cressler (2006)
Barinophyton perrianum	Perry Fm., St Andrews Basin, Perry, Maine, USA	early Frasnian	late Famennian	Smith and White (1905)
Barinophyton richardsoni	Perry Fm., St Andrews Basin, Perry, Maine, USA	early Frasnian	late Famennian	Smith and White (1905)
Barinophyton sibericum	Esaulovka river, Rybinsk Basin, Krasnoyarskiy Kray, Russia	early Famennian	late Famennian	Petrosyan (1967)

Species	Locality	Early interval	Late interval	Reference
Barinophyton sibericum	Hampshire Fm., Elkins Randolph County, West Virginia, USA	early Famennian	late Famennian	Scheckler (1986)
Barinophyton sp	Catskill Fm., Burtville, Potter County, Pennsylvania, USA	late Famennian	late Famennian	Stein (2002) (PBDB 28291, 20814)
Barinophyton sp	Montfort Fm., Herbestal-Bleiberg, Belgium	late Famennian	late Famennian	Stockmans (1948)
Bathurstia cf *denticulata*	Bathurst Island Fm., Loc US685, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc 8370, Young Inlet, Bathurst Island, Canada	early Pragian	late Pragian	Hueber (1971a)
Bathurstia denticulata	Bathurst Island Fm., Loc US493, Young Inlet, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk and Basinger (2000)
Bathurstia denticulata	Bathurst Island Fm., Loc US604, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US607, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US609, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US617, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US620, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US633, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US636, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US637, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US640, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US641, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US642, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)

Species	Locality	Early interval	Late interval	Reference
Bathurstia denticulata	Bathurst Island Fm., Loc US644, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US645, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US664, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US680, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia denticulata	Bathurst Island Fm., Loc US704, Cheyne River Region, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Bathurstia sp	Bathurst Island Fm., Loc 8370, Young Inlet, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Hueber (1971a)
Bracteophyton variatum	Xujiachong Fm., lithological unit 4, Xujiachong, Quijing, Yunnan, China	early Pragian	early Emsian	D.-M. Wang and Hao (2004)
cf *Barinophyton sibericum*	Catskill Fm., Red Hill, Clinton County, Pennsylvania, USA	late Famennian	late Famennian	Cressler (2006)
cf *Barinophyton sp*	Escuminac Fm., Lower Horizon, Scaumenac Bay and Miguasha, Quebec, Canada	early Frasnian	early Frasnian	Gensel and Barnett-Lawrence 1996
cf *Bathurstia denticulata*	Bathurst Island Fm., Loc US625, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
cf *Bathurstia sp*	Bathurst Island Fm., Loc 8370, Young Inlet, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Hueber (1971a)
cf *Bathurstia sp*	Bathurst Island Fm., Loc US383, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Ludfordian	Ludfordian	Kotyk (1998)
cf *Bathurstia sp*	Bathurst Island Fm., Loc US384, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Ludfordian	Ludfordian	Kotyk et al. (2002)

Species	Locality	Early interval	Late interval	Reference
cf *Bathurstia sp*	Bathurst Island Fm., Loc US389, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Lochkovian	late Lochkovian	Kotyk (1998)
cf *Distichophytum ovatum*	Bathurst Island Fm., Loc US617, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
cf *Distichophytum sp*	Bathurst Island Fm., Loc US619, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
cf *Distichophytum sp*	Bathurst Island Fm., Loc US620, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
cf *Distichophytum sp*	Bathurst Island Fm., Loc US690, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Lochkovian	late Lochkovian	Kotyk (1998)
cf *Gosslingia sp*	Beartooth Butte Fm., South wall of Cottonwood Canyon, Big Horn County, Wyoming, USA	late Lochkovian	early Pragian	Noetinger et al. (2021) Tomescu pers commun 2021
cf *Gosslingia sp*	Fraenkelryggen FM., Red bay group, Raudfjorden, Svalbard, Norway	late Lochkovian	late Lochkovian	Schweitzer (1999)
cf *Hicklingia sp*	Posongchong Fm., Bed 31, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
cf *Protobarinophyton sp*	Escuminac Fm., Lower Horizon, Scaumenac Bay and Miguasha, Quebec, Canada	early Frasnian	early Frasnian	Gensel and Barnett-Lawrence 1996
Ramoferis cf *amalia*	Posongchong Fm., Fossile site 1, Changputang Section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
cf *Sawdonia sp*	Wépion Fm., Quarry les Forges, Marchin, Belgium	early Emsian	early Emsian	Gerrienne (1996a)
Serrulacaulis furcatus	Niaster, Aywaille, Belgium	early Givetian	late Givetian	Lessuise and Fairon-Demaret (1980)
cf *Zosterophyllum fertile*	Whilson Creek Shale Fm., Frenchmen spur track, Matlock, Australia	middle Pragian	early Emsian	McSweeney et al. (2022)

Species	Locality	Early interval	Late interval	Reference
cf *Zosterophyllum fertile*	Senni Fm., Allt Du, Powys, Wales, UK	late Lochkovian	late Lochkovian	D. Edwards and Richardson (2004)
cf *Zosterophyllum fertile*	Mill Bay Fm., Burton Cliff, Pembrokeshire, Wales, UK	early Pragian	late Pragian	D. Edwards and Richardson (2004)
cf *Zosterophyllum sp*	Beartooth Butte Fm., South wall of Cottonwood Canyon, Big Horn County, Wyoming, USA	late Lochkovian	early Pragian	Noetinger et al. (2021)
cf *Zosterophyllum sp*	Mill Bay Fm., Burton Cliff, Pembrokeshire, Wales, UK	early Pragian	late Pragian	D. Edwards and Richardson (2004)
cf *Zosterophyllum sp* A	Wilson Creek Shale Fm., Frenchman Spur, Victoria, Australia	middle Pragian	late Emsian	McSweeney et al. (2022)
cf *Zosterophyllum sp* B	Humevale Fm., P4, Ghin Ghin Road, Yea, Victoria, Australia	early Pragian	late Emsian	McSweeney et al. (2022)
Craswallia haegensis	Freshwater West Fm., Milford Haven Subgroup, Craswall, Herefordshire, Wales, UK	middle Lochkovian	late Lochkovian	Morris and Edwards (2014)
Crenaticaulis verruculosus	Battery Point Fm., D'Aiguillon to Seal Rock, North Gaspé Bay, Québec, Canada	early Emsian	late Emsian	Banks and Davis (1969) and Hotton et al. (2001)
Danziella artesiana	Grès de Rebreuve Fm., Rebreuve, Artois, France	early Emsian	early Emsian	Capel, Prestianni, et al. (2022)
Deheubarthia splendens	Brecon Beacon Quarry lower Old Red Sandstone South Wales UK	early Pragian	early Pragian	D. Edwards et al. (1989)
Deheubarthia splendens	Llandstadwell Fm., Mascle Bridge Quarry, Pembrokeshire, Wales, UK	late Lochkovian	late Lochkovian	D. Edwards et al. (1989)
Deheubarthia splendens	Mill Bay Fm., Burton Cliff, Pembrokeshire, Wales, UK	early Pragian	late Pragian	D. Edwards and Richardson (2004)
Deheubarthia splendens	Senni Bed Fm., Llanover Quarry, South Wales, UK	early Pragian	late Pragian	D. Edwards et al. (1989)
Deheubarthia splendens	Senni Fm., Allt Du, Powys, Wales, UK	late Lochkovian	late Lochkovian	D. Edwards and Richardson (2004)
Demersatheca contigua	Danlin Fm., Caoziping section, Caoziping village, Hezhang, Guizhou, China	early Pragian	early Emsian	Y. Wang et al. (2022)

Species	Locality	Early interval	Late interval	Reference
Demersatheca contigua	Lower–mid- Cangwu Gp., Shiqiao Section, Cangwu County, Guangxi, China	early Pragian	early Emsian	Y. Wang et al. (2020)
Demersatheca contigua	Posongchong Fm., Lower Bed 37, Zhichang section, Wenshan city, Yunnan, China	late Pragian	late Pragian	Hao and Xue (2013)
Demersatheca contigua	Posongchong Fm., Bed 20, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Demersatheca contigua	Posongchong Fm., Bed 7, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Demersatheca contigua	Posongchong Fm., Gumu Town, Wenshan district, Yunnan, China	middle Pragian	late Pragian	Y. Wang et al. (2020)
Demersatheca contigua	Posongchong Fm., Upper Bed 37, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Demersatheca contigua	Posongchong Fm., Upper Bed 38, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Dibracophyton acrovatum	Posongchong Fm., 8th lithological unit, Changputang Section, Wenshan, Yunnan, China	middle Pragian	late Pragian	Hao et al. (2012)
Dibracophyton acrovatum	Posongchong Fm., Bed 14, Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	Hao et al. (2012)
Discalis longistipa	Posongchong Fm., Bed 31, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao (1989b)
Distichophytum mogilatii	Torgashino, Rybinsk Basin, Krasnoyarsk Krai, Russia	early Pragian	late Pragian	Naugolnykh (2021)
Distichophytum mucronatum	Bargasino Fm., Gorny Altai, Russia	early Emsian	early Emsian	Korzhnev (2014)
Distichophytum mucronatum	Kahleberg sandstone, Harz mountains Germany	late Emsian	late Emsian	Schweitzer (1979)
Distichophytum mucronatum	Külbach Bergisches Land Germany	early Emsian	early Emsian	Schweitzer (1979)
Distichophytum mucronatum	Nellenkopfchen Schichten Fm., Alken quarry Germany	early Emsian	early Emsian	Schweitzer (1987)

Species	Locality	Early interval	Late interval	Reference
Distichophytum mucronatum	Nellenkopfchen Schichten Fm., Konder valley, Winningen, Germany	early Emsian	early Emsian	Schweitzer (1987)
Distichophytum mucronatum	Shunet Fm., Shira, Minusinsk Basin, Khakassia, Russia	early Pragian	late Pragian	Fedoseev (2008)
Distichophytum mucronatum	Stadtfeld Fm., Hoffeld, Eifel Region, Rhineland, Germany	early Emsian	early Emsian	Schweitzer (1987)
Distichophytum mucronatum	Stadtfeld Fm., Müsch, Ahr Valley, Eifel Region, Rhineland, Germany	early Emsian	early Emsian	Schweitzer (1987)
Distichophytum ovatum	Bargasino Fm., Gorny Altai, Russia	early Emsian	early Emsian	Korzhnev (2014)
Distichophytum ovatum	Bathurst Island Fm., Loc US486, Young Inlet, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US491, Young Inlet, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US499, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US605, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US607, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US608, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US609, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US617, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US618, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US619, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US622, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US636, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)

Species	Locality	Early interval	Late interval	Reference
Distichophytum ovatum	Bathurst Island Fm., Loc US642, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US664, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US665, Cheyne River Region, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Bathurst Island Fm., Loc US685, Polar Bear Pass, Bathurst Island, Canada	early Pragian	late Pragian	Kotyk (1998)
Distichophytum ovatum	Beartooth Butte Fm., Beartooth Butte, Park County, Wyoming, USA	middle Emsian	late Emsian	Tanner (1983) and Noetinger et al. (2021)
Distichophytum sp	Bathurst Island Fm., Loc US383, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Ludfordian	Ludfordian	Kotyk (1998)
Distichophytum sp	Posongchong Fm., Bed 13, Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Euthursophyton hamperbachense	Brandbenberg-Schichten Fm., Hagen-Ambrock, Germany	late Eifelian	late Eifelian	Mustafa (1978)
Euthursophyton hamperbachense	Brandbenberg-Schichten Fm., Köster quarry, Warstein, Germany	late Eifelian	late Eifelian	Mustafa (1978)
Euthursophyton hamperbachense	Brandbenberg-Schichten Fm., Lasbeck quarry, Germany	late Eifelian	late Eifelian	Mustafa (1978)
Euthursophyton hamperbachense	Honseler-Schichten Fm., Lückhofen quarry, Germany	early Givetian	late Givetian	Mustafa (1978)
Euthursophyton hamperbachense	Muhlenberg-Schichten Fm., Lindlar Bergisches land, Rhineland, Germany	early Givetian	late Givetian	Mustafa (1978)
Faironella valentula	Wépion Fm., Quarry les Forges, Marchin, Belgium	early Emsian	early Emsian	Gerrienne (1996a)
Forania plegiospinosa	Campbellton Fm., Loc A, Dalhousie Junction, New Brunswick, Canada	late Emsian	late Emsian	Jensen and Gensel (2013)
Forania plegiospinosa	Campbellton Fm., Loc G, Dalhousie Junction, New Brunswick, Canada	late Emsian	late Emsian	Jensen and Gensel (2013)
Forania plegiospinosa	Campbellton Fm., Loc H, Dalhousie Junction, New Brunswick, Canada	late Emsian	late Emsian	Jensen and Gensel (2013)

Species	Locality	Early interval	Late interval	Reference
Forania sp	Campbellton Fm., Loc 1 or 3, Dalhousie Junction, New Brunswick, Canada	early Emsian	early Emsian	Bonacorsi et al. (2021)
Gippslandites minutus	Boola Fm., BQ1, Boola Quarry, Tyers, Victoria, Australia	early Lochkovian	late Pragian	McSweeney et al. (2020)
Gosferia curvata	Wépion Fm., Quarry les Forges, Marchin, Belgium	early Emsian	early Emsian	Gerrienne (1991a)
Gosslingia breconensis	Affleurement A Gileppe; Belgium	late Lochkovian	early Pragian	Steemans and Gerrienne (1984)
Gosslingia breconensis	Grès de Wihéries Fm., Racheneur Quarry Belgium	late Pragian	late Pragian	Gerrienne (1990)
Gosslingia breconensis	Senni Bed Fm., Brecon Beacon Quarry, lower Old Red Sandstone, South Wales, UK	early Pragian	early Pragian	Croft and Lang (1942)
Gosslingia breconensis	Senni Bed Fm., Llanover Quarry, South Wales, UK	early Pragian	late Pragian	Croft and Lang (1942)
Gosslingia breconensis	Senni Fm., Allt Du, Powys, Wales, UK	late Lochkovian	late Lochkovian	D. Edwards and Richardson (2004)
Gosslingia breconensis	Cosheston Fm., Burton Cliff, Pembrokeshire, Wales, UK	early Pragian	late Pragian	D. Edwards and Richardson (2004)
Gosslingia breconensis	Cosheston Fm., Mill Bay, Pembrokeshire, Wales, UK	early Pragian	late Pragian	D. Edwards and Richardson (2004)
Gosslingia cf *breconensis*	Mangshan Gp., Dahe section, Duyun city, Guizhou, China	early Pragian	late Pragian	Y. Wang et al. (2024)
Gosslingia cordiformis	mid- Siegen Gp., Burgbrohl, Rhineland, Germany	middle Pragian	middle Pragian	Schweitzer (1979)
Guangnania cuneata	Posongchong Fm., Bed 37, Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Guangnania cuneata	Posongchong Fm., Daliantang Section, Guangnan county, Yunnan China	middle Pragian	late Pragian	D.-M. Wang and Hao (2002)
Guangnania cuneata	Xujiachong Fm., bed 4, Xujiachong, Qujing, Yunnan, China	early Pragian	early Emsian	D.-M. Wang and Hao (2002)
Guangnania minor	Pingyipu Gp., Horizon 3, Yanmenba Section, Jiangyou City, Sichuan, China	late Pragian	late Pragian	D. Edwards et al. (2016)

Species	Locality	Early interval	Late interval	Reference
Gumuia zyzzata	Posongchong Fm., Bed 11, Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Gumuia zyzzata	Posongchong Fm., Bed 16, Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Gumuia zyzzata	Posongchong Fm., Bed 18, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Gumuia zyzzata	Posongchong Fm., Bed 22, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Gumuia zyzzata	Posongchong Fm., Bed 25, Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Gumuia zyzzata	Posongchong Fm., Fossil site 3, Changputang Section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao (1989a)
Gutzeitia timanica	Ustje Bezmoshitsa Fm., North Timan, Nenets Autonomous Okrug, Russia	late Frasnian	late Frasnian	Snigirevsky et al. (2007)
Hicklingia edwardii	Dundee Fm., Hill of Forss, Scotland	early Eifelian	late Givetian	Kidston and Lang (1924), (PBDB 26780)
Hicklingia sp	Wahnbach Fm., Wahnbach Valley, Eifel, Germany	late Pragian	late Pragian	Schweitzer (1987)
Hsua deflexa	Xujiachong Fm., bed 7, Xujiachong, Qujing, Yunnan, china	early Pragian	early Emsian	D.-M. Wang et al. (2003)
Hsua deflexa	Xujiachong Fm., bed 8, Xujiachong, Qujing, Yunnan, China	early Pragian	early Emsian	D.-M. Wang et al. (2003)
Hsua robusta	Xujiachong Fm., Loc 1, Xujiachong, Qujing, Yunnan, china	early Pragian	early Emsian	C.-S. Li and Edwards (1992)
Hsua robusta	Xujiachong Fm., Loc 2, Xujiachong, Qujing, Yunnan, china	early Pragian	early Emsian	C.-S. Li and Edwards (1992)
Huia gracilis	Xujiachong Fm., bed 6, Xujiachong, Qujing, Yunnan, China	early Pragian	early Emsian	D.-M. Wang and Hao (2001)
Huia recurvata	Posongchong Fm., Bed 28, Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Huia recurvata	Posongchong Fm., Bed 7, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)

Species	Locality	Early interval	Late interval	Reference
Huia recurvata	Posongchong Fm., Gegu-Daigu Section, Mengzi District, Yunnan, China	middle Pragian	late Pragian	Hao and Gensel (1998)
Jugumella burubaensis	Balkhash Land Fms., PriBalkhash, Kazakhstan	early Emsian	early Emsian	Senkevich, 1992
Jugumella burubaensis	Sardzhal Fm., Karaganda Synclinorium, Central Kazakhstan	late Pragian	early Emsian	Senkevich, 1992
Jugumella burubaensis	Tokrau Fm., bed 11, Kiikbai Mt, North of Lake Balkash, Kazakhstan	early Pridoli	late Pridoli	Nikitin and Bandaletov (1986) (PBDB 53656)
Jugumella burubaensis	Tokrau Fm., bed 23, North of Lake Balkash, Kazakhstan	early Pridoli	late Pridoli	Nikitin and Bandaletov (1986) (PBDB 53609)
Jugumella burubaensis	Tokrau Horizon, Kokbaital Mountains, Balkhash, Kazakhstan	early Pridoli	late Pridoli	Senkevich (1975) (PBDB 53659)
Jugumella jugata	Balkhash Land Fms., PriBalkhash, Kazakhstan	early Emsian	early Emsian	Senkevich (1975, 1988)
Jugumella jugata	PriBalkhash horizon, PriBalkhash, Kazakhstan	late Lochkovian	late Lochkovian	Senkevich (1975, 1988)
Jugumella jugata	Sardzhal Fm., Karaganda Synclinorium, Central Kazakhstan	late Pragian	early Emsian	Senkevich (1975, 1988)
Kaulangiophyton akantha	Trout Valley Fm., Loc 1, Facies 6, Trout Brook, Maine, USA	late Emsian	early Eifelian	Allen and Gastaldo (2006)
Kaulangiophyton sp	Trout Valley Fm., Facies 6, Trout Brook, Maine, USA	late Emsian	early Eifelian	Allen and Gastaldo (2006)
Konioria andrychoviensis	Andrychow 2, Bielsko-Wadowice, Poland	late Emsian	late Emsian	Zdebska (1982)
Konioria andrychoviensis	Andrychow 4, Bielsko-Wadowice, Poland	late Emsian	late Emsian	Zdebska (1982)
Krithodeophyton croftii	Senni Bed Fm., Brecon Beacon Quarry, lower Old Red Sandstone, South Wales, UK	early Pragian	early Pragian	D. Edwards (1968)
Krithodeophyton sp	Wépion Fm., Quarry les Forges, Marchin, Belgium	early Emsian	early Emsian	Gerrienne (1993)
Macivera gracilis	Bathurst Island Fm., Loc US385, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Ludfordian	Ludfordian	Kotyk et al. (2002)

Species	Locality	Early interval	Late interval	Reference
Margophyton goldschmidtii	Aramchak Fm., Shira, Minusinsk Basin, Khakassia, Russia	late Pragian	early Emsian	Fedoseev (2008)
Margophyton goldschmidtii	Karasug loc, Tuva, Russia	early Pragian	late Emsian	Zakharova (1981)
Margophyton goldschmidtii	Kholzun Fm., Kyrlyk River, Russia	early Emsian	early Emsian	Korzhnev (2014)
Margophyton goldschmidtii	Kuboy Fm., Choya, Sarazonka, Russia	late Emsian	late Emsian	Korzhnev (2014)
Margophyton goldschmidtii	Minusink basin, Kazarmen, Russia	early Pragian	early Emsian	Zakharova (1981)
Margophyton goldschmidtii	Nyrna Fm., Nyrna River, Altai Republic, Russia	early Emsian	early Emsian	Korzhnev (2014)
Margophyton goldschmidtii	Sagla Fm., Khondelen Graben, Tuva Trough, Russia	early Emsian	early Emsian	Korzhnev (2014)
Margophyton goldschmidtii	Shunet Fm., Shira, Minusinsk Basin, Khakassia, Russia	early Pragian	late Pragian	Zakharova (1981)
Margophyton goldschmidtii	Taldydyurgun Fm., Kok-Sair region, Russia	early Emsian	early Emsian	Korzhnev (2014)
Nothia aphylla	Rhynie and Windyfield cherts, Rhynie, Aberdeenshire, Scotland, UK	middle Pragian	late Pragian	El-Saadawy and Lacey (1979)
Odonax borealis	Wépion Fm., Quarry les Forges, Marchin, Belgium	early Emsian	early Emsian	Gerrienne (1996b)
Omniastrobus dawsonii	Campbellton Fm., Loc 1 or 3, Dalhousie Junction, New Brunswick, Canada	early Emsian	early Emsian	Bonacorsi et al. (2021)
Oricilla bilinearis	Campbellton Fm., Loc E, Dalhousie Junction, New Brunswick, Canada	late Emsian	late Emsian	Gensel (1982b)
Oricilla sp	Posongchong Fm., Bed 13, Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Oricilla sp	Posongchong Fm., Bed 28, Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Ornicephalum sichuanense	Pingyipu Gp., Horizon 1, Yanmenba Section, Jiangyou City, Sichuan, China	early Lochkovian	early Pragian	Geng (1992) and D. Edwards and Li (2018a)
Parazosterophyllum timsiae	Humevale Fm., P4, Ghin Ghin Road, Yea, Victoria, Australia	early Pridoli	late Pragian	McSweeney et al. (2020)
Protobarinophyton obrutschevii	Bargasino Fm., Gorny Altai, Russia	early Emsian	early Emsian	Korzhnev (2014)

Species	Locality	Early interval	Late interval	Reference
Protobarinophyton obrutschevii	Matarak Fm., Shira, Minusinsk Basin, Khakassia, Russia	late Lochkovian	early Pragian	Fedoseev (2008)
Protobarinophyton obrutschevii	Nyrna Fm., Nyrna River, Altai Republic, Russia	early Emsian	late Emsian	Korzhnev (2014)
Protobarinophyton obrutschevii	Sagla Fm., Khondelen Graben, Tuva Trough, Russia	early Emsian	early Emsian	Korzhnev (2014)
Protobarinophyton obrutschevii	Shunet Fm., Shira, Minusinsk Basin, Khakassia, Russia	early Pragian	late Pragian	Fedoseev (2008)
Protobarinophyton pennsylvanicum	Catskill Fm., Burtville, Potter County, Pennsylvania, USA	early Famennian	late Famennian	Brauer (1981)
Protobarinophyton pennsylvanicum	Catskill Fm., Burtville, Clinton County, Pennsylvania, USA	late Famennian	late Famennian	Cressler et al. (2010)
Protobarinophyton sp	Price Fm., loc. 7, Alta, Greenbriar County, West Virginia, USA	late Tournaisian	late Tournaisian	Scheckler (1984)
Protobarinophyton sp	Wood Bay Fm., Andrée Land, Svalbard, Norway	late Pragian	early Emsian	Schweitzer (1999)
Ramoferis amalia	Posongchong Fm., Bed 18, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Ramoferis amalia	Posongchong Fm., Bed 37, Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Ramoferis sp	Posongchong Fm., Fossile site 1, Changputang Section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
cf *Sawdonia sp*	Campbellton Fm., Loc M, Peuplier Point, New Brunswick, Canada	early Emsian	late Emsian	Gensel et al. (1975)
Sawdonia deblondii	Acoz Fm., Ensival, Vesdre Massif, Belgium	late Pragian	late Pragian	Gerrienne (1996a)
Sawdonia hippotheca	Campo Chico Fm., Loc. 3, Sierra de Perijá, Zulia, Venezuela	late Givetian	late Givetian	Berry (2019)
cf *Sawdonia sp*	Aramchak Fm., Shira, Minusinsk Basin, Khakassia, Russia	late Pragian	early Emsian	Fedoseev (2008)
cf *Sawdonia sp*	Bathurst Island Fm., Loc 8370, Young Inlet, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Hueber (1971a)

Species	Locality	Early interval	Late interval	Reference
Sawdonia ornata	Battery Point Fm., Loc S, D'Aiguillon to Seal Rock, North Gaspé Bay, Québec, Canada	late Emsian	late Emsian	Hotton et al. (2001) and Gensel and Berry (2016)
cf *Sawdonia sp*	Brandenberg strata, Koster quarry, Hagen-Ambrock, Germany	late Eifelian	late Eifelian	Mustafa (1978)
cf *Sawdonia sp*	Campbellton Fm., Loc F Dalhousie Junction New Brunswick Canada	early Emsian	late Emsian	Gensel and Albright 2006
cf *Sawdonia sp*	Compton Fm., St Francis Group, Loc 14292, Quebec, Canada	early Emsian	late Emsian	Hueber et al. (1990)
cf *Sawdonia sp*	Klerf Fm., Steinbruch Koppen bei Waxweiler Eifel Germany	early Emsian	early Emsian	Schweitzer (2000)
cf *Sawdonia sp*	Lerbekk Fm., Røragen, Røros, Trøndelag, Norway	early Emsian	late Emsian	Schweitzer and Heumann (1993)
cf *Sawdonia sp*	Mapleton Fm., Winslow Farm, Presque Isle, Maine, USA	early Givetian	early Givetian	Schopf (1964)
cf *Sawdonia sp*	Oneonta Fm., Steenberg Quarry, NW slope of South mountain, Schoharie County, New York, USA	early Frasnian	early Frasnian	Hueber and Grierson (1961) (Schopf (1964), PBDB 20813)
Sawdonia ornata	Sextant Fm., Loc 6437, Abitibi River, Ontario, Canada	middle Emsian	late Emsian	Hueber (1983)
cf *Sawdonia sp*	Strathmore Fm., Facies A, Auchensail quarry, Cardross, UK	early Emsian	early Emsian	Scott et al. (1976)
cf *Sawdonia sp*	Stuart Bay Fm., Loc 8376, Young Inlet, Nunavut, Canada	early Emsian	late Emsian	Hueber (1971a)
cf *Sawdonia sp*	Wahnbach Fm., Wahnbach Valley, Eifel, Germany	late Pragian	late Pragian	Schweitzer (1987)
Sawdonia sp	Grès de Rebreuve Fm., Rebreuve, Artois, France	early Emsian	early Emsian	Capel, Prestianni, et al. (2022)
Serrulacaulis cf *furcatus*	Campo Chico Fm., Loc. 3, Sierra de Perijá, Zulia, Venezuela	late Givetian	late Givetian	Berry and Edwards (1994)
Serrulacaulis cf *furcatus*	Hujiersite Fm., 251 Hill, Hoxtolgay Town, Hoboksar, Xinjiang, China	early Givetian	late Givetian	Xu et al. (2011)

Species	Locality	Early interval	Late interval	Reference
Serrulacaulis furcatus	Oneonta Fm., Livingstonville, Schoharie County, New York, USA	early Frasnian	early Frasnian	Hueber and Banks (1979)
Serrulacaulis furcatus	Plan incliné de Ronquières, Belgium	middle Givetian	late Givetian	Stockmans (1968)
Serrulacaulis furcatus	Railroad cut near Feluy Belgium	late Givetian	late Givetian	Stockmans (1968)
Serrulacaulis furcatus	Vieux-Leuze, Leuze, Belgium	early Frasnian	early Frasnian	Stockmans (1968) and Licour et al. (2020)
Serrulacaulis spineus	Hujiersite Fm., 251 Hill, Hoxtolgay Town, Hoboksar, Xinjiang, China	early Givetian	late Givetian	Xu et al. (2011)
Serrulacaulis spineus	Hujiersite Fm., Hoxtolgay Town, Hoboksar, Xinjiang, China	early Givetian	late Givetian	Xu et al. (2011)
Sichuania uskielloides	Pingyipu Gp., Horizon 1, Yanmenba Section, Jiangyou City, Sichuan, China	early Lochkovian	early Pragian	D. Edwards and Li (2018a)
Tarella trowenii	Senni Bed Fm., Brecon Beacon Quarry, lower Old Red Sandstone, South Wales, UK	early Pragian	early Pragian	D. Edwards and Kenrick (1986)
Thrinkophyton formosum	Senni Bed Fm., Craig Ddu, Carmarthenshire, Dyfed, Wales, UK	early Pragian	early Pragian	Kenrick and Edwards (1988a)
Trichopherophyton teuchansii	Rhynie and Windyfield cherts, Rhynie, Aberdeenshire, Scotland, UK	middle Pragian	late Pragian	Lyon and Edwards (1991)
Ventarura lyonii	Rhynie and Windyfield cherts, Rhynie, Aberdeenshire, Scotland, UK	middle Pragian	late Pragian	Powell et al. (1999)
Wenshania zhichangensis	Posongchong Fm., Bed 18, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Xitunia spinitheca	Xitun Fm., Huaguoshan Section, Shengfeng District, Yunnan, China	middle Lochkovian	late Lochkovian	Xue (2009)
Zosterophyllum articum	Bathurst Island Fm., Loc US608, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum articum	Bathurst Island Fm., Loc US617, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)

Species	Locality	Early interval	Late interval	Reference
Zosterophyllum articum	Bathurst Island Fm., Loc US618, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum articum	Bathurst Island Fm., Loc US628, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum articum	Bathurst Island Fm., Loc US633, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum articum	Bathurst Island Fm., Loc US636, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum articum	Bathurst Island Fm., Loc US664, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum australianum	Mangshan Gp. Fm., Bed 16, Baoyang, Duyun, Guizhou, China	early Pragian	late Pragian	Huang et al. (2022)
Zosterophyllum australianum	Minusink basin, Kazarmen, Russia	early Pragian	early Emsian	Zakharova and Ananiev (1990)
Zosterophyllum australianum	Norton Gully Sandstone Fm., North Road Quarry, Walhalla, Victoria, Australia	early Pragian	late Emsian	McSweeney et al. (2022)
Zosterophyllum australianum	Posongchong Fm., 4th layer, Gegu-Daigu Section, Mengzi District, Yunnan, China	middle Pragian	late Pragian	Hao and Gensel (1998)
Zosterophyllum australianum	Posongchong Fm., Bed 40, Zhichang, Wenshan, Yunnan, China	middle Pragian	late Pragian	Hao and Gensel (1998)
Zosterophyllum australianum	Posongchong Fm., Daliantang Section, Guangnan county, Yunnan China	middle Pragian	late Pragian	Xiong et al. (2013)
Zosterophyllum australianum	Posongchong Fm., Fossil site 3, Changputang Section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Gensel (1998)
Zosterophyllum australianum	Sardzhal Fm., Karaganda Synclinorium, Central Kazakhstan	late Pragian	early Emsian	Senkevich (1975)
Zosterophyllum australianum	Xujiachong Fm., bed 2, Xujiachong, Qujing, Yunnan, china	early Pragian	early Emsian	D.-M. Wang and Hao (2002)

Species	Locality	Early interval	Late interval	Reference
Zosterophyllum australianum	Xujiachong Fm., bed 3, Xujiachong, Qujing, Yunnan, china	early Pragian	early Emsian	Wellman et al. (2012)
Zosterophyllum bifurcatum	Xujiachong Fm., Longhuashan Section, Yunnan, China	early Pragian	early Emsian	X.-X. Li and Cai (1977)
Zosterophyllum cf *australianum*	Aramchak Fm., Shira, Minusinsk Basin, Khakassia, Russia	late Pragian	early Emsian	Zakharova and Ananiev (1990) and Fedoseev (2008)
Zosterophyllum cf *fertile*	Freshwater West Fm., Cwm Mill, Gwent, Monmouthshire, Wales, UK	middle Lochkovian	middle Lochkovian	Wellman et al. (2000)
Zosterophyllum cf *fertile*	Freshwater West Fm., Milford Haven Subgroup, Craswall, Herefordshire, Wales, UK	middle Lochkovian	late Lochkovian	Morris and Edwards (2014)
Zosterophyllum cf *fertile*	Senni Bed Fm., Brecon Beacon Quarry, lower Old Red Sandstone, South Wales, UK	early Pragian	early Pragian	D. Edwards (1969)
Zosterophyllum cf *fertile*	Senni Bed Fm., Llanover Quarry, South Wales, UK	early Pragian	late Pragian	D. Edwards (1969)
Zosterophyllum cf *fertile*	Ditton Fm., Brynglas tunnel, Newport, Wales, UK	middle Lochkovian	middle Lochkovian	Wellman et al. (2000)
Zosterophyllum cf *fertile*	Wépion Fm., Quarry les Forges, Marchin, Belgium	early Emsian	early Emsian	Gerrienne (1996a)
Zosterophyllum cf *myretonianum*	Bargasino Fm., Gorny Altai, Russia	early Emsian	early Emsian	Korzhnev (2014)
Zosterophyllum cf *reflexum*	Bathurst Island Fm., Loc US636, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum cf *reflexum*	Bathurst Island Fm., Loc US637, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum cf *reflexum*	Bathurst Island Fm., Loc US664, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum cf *rhenanum*	Sardzhal Fm., Karaganda Synclinorium, Central Kazakhstan	late Pragian	early Emsian	Senkevich (1975, 1988)

Species	Locality	Early interval	Late interval	Reference
Zosterophyllum cf *yunnanicum*	Cangwu Fm., Shiqiao Section, Cangwu County, Guangxi, China	early Pragian	late Emsian	Cai and Li (1982)
Zosterophyllum cf *yunnanicum*	Shiqiao Fm., Huangguan Section, Guanyang County, Guangxi, China	early Emsian	early Emsian	Cai and Li (1982)
Zosterophyllum cf *yunnanicum*	Yuankou Fm., Yuankou Section, Jiangyong County, Hunan, China	early Emsian	early Emsian	Cai and Li (1982)
Zosterophyllum confertum	Lower Effelsberg Fm., Outcrop in the Limbach Valley upper Ahr region Eifel Germany	late Pragian	early Emsian	Gossmann et al. (2022)
Zosterophyllum confertum	Odenspiel Fm., Abandoned Quarry, Westerberg, Wenden, Sauerland, Germany	late Pragian	early Emsian	Gossmann et al. (2022)
Zosterophyllum confertum	Odenspiel Fm., Outcrop in the Kupfersiefer Valley near Rösrath Bergisches Land Germany	late Pragian	early Emsian	Gossmann et al. (2022)
Zosterophyllum confertum	slate facies Fm., Abandoned quarry below Katzenlei near Walporzheim Ahr Valley/Eifel Germany	early Pragian	middle Pragian	Gossmann et al. (2022)
Zosterophyllum confertum	slate facies Fm., Bürdenbach/Westerwald outcrop at forest road in the Lahrbach Valley north of the bus stop near the mouth of the Güllesheimer Bach Germany	early Pragian	middle Pragian	Gossmann et al. (2022)
Zosterophyllum confertum	slate facies Fm., Oberlahr/Westerwald abandoned quarry above and left of the Lahrbach Germany	early Pragian	middle Pragian	Gossmann et al. (2022)
Zosterophyllum confertum	slate facies Fm., Oberlahr/Westerwald outcrop 'Lammerichskaul' in the Lahrbach Valley south of the mouth of the Güllesheimer Bach and left of the Lahrbach Germany	early Pragian	middle Pragian	Gossmann et al. (2022)
Zosterophyllum confertum	slate facies Fm., Outcrop below 'Hohe Schleif' south of Brohl above the Brohl Valley Eifel Germany	early Pragian	early Pragian	Gossmann et al. (2022)

Species	Locality	Early interval	Late interval	Reference
Zosterophyllum confertum	Slate facies, Abandonned Quarry, Vinxtbach Valley, Rheineck, Eifel, Germany	early Pragian	early Pragian	Gossmann et al. (2022)
Zosterophyllum confertum	Untere Dunkle Schichten Fm., Road outcrop 'Ettringer Heuweg' (road K 20) Eifel Germany	early Pragian	early Pragian	Gossmann et al. (2022)
Zosterophyllum confertum	Wahnbach Fm., Abandoned quarry in the Jabach Valley, Bergisches Land, Germany	late Pragian	late Pragian	Gossmann et al. (2022)
Zosterophyllum confertum	Wahnbach Fm., Excavation at Breidt near Lohmar Bergisches Land Germany	late Pragian	late Pragian	Gossmann et al. (2022)
Zosterophyllum confertum	Wahnbach Fm., House constructing site Rosenburg Bonn-Kessenich Germany	late Pragian	late Pragian	Gossmann et al. (2022)
Zosterophyllum confertum	Wahnbach Fm., Outcrop at Pionierweg Bonn-Bad Godesberg Germany	late Pragian	late Pragian	Gossmann et al. (2022)
Zosterophyllum confertum	Wahnbach Fm., Road bulding site Jabach Valley Bergisches Land Germany	late Pragian	late Pragian	Gossmann et al. (2022)
Zosterophyllum confertum	Wahnbach Fm., Vineyard above the Ahr Valley near Marienthal/Eifel Germany	early Pragian	middle Pragian	Gossmann et al. (2022)
Zosterophyllum deciduum	Wépion Fm., Quarry les Forges, Marchin, Belgium	early Emsian	early Emsian	Gerrienne (1996b)
Zosterophyllum divaricatum	Campbellton Fm., Loc M, Peuplier Point, New Brunswick, Canada	early Emsian	late Emsian	Gensel (1982a)
Zosterophyllum dushanense	Danlin Fm., Lizhai Section, Dushan County, Guizhou, China	early Pragian	early Emsian	X.-X. Li and Cai (1977)
Zosterophyllum fertile	Dundee Fm., Kelly Den, Arbilot, Scotland, UK	early Lochkovian	middle Lochkovian	D. Edwards (1972) and D. Edwards and Wellman (2001)
Zosterophyllum fertile	St Hubert Fm., Nonceveux, Ardennes, Belgium	late Lochkovian	late Lochkovian	Leclercq (1942)
Zosterophyllum fertile	Stadtfeld Fm., Hoffeld, Eifel Region, Rhineland, Germany	early Emsian	early Emsian	Schweitzer (1987)
Zosterophyllum fertile	Stadtfeld Fm., Müsch, Ahr Valley, Eifel Region, Rhineland, Germany	early Emsian	early Emsian	Schweitzer (1987)

Species	Locality	Early interval	Late interval	Reference
Zosterophyllum llanoveranum	Minusink basin, Kazarmen, Russia	early Pragian	early Emsian	Zakharova and Ananiev (1990)
Zosterophyllum llanoveranum	Senni Bed Fm., Brecon Beacon Quarry, lower Old Red Sandstone, South Wales, UK	early Pragian	early Pragian	Croft and Lang (1942)
Zosterophyllum llanoveranum	Senni Bed Fm., Llanover Quarry, South Wales, UK	early Pragian	late Pragian	Croft and Lang (1942)
Zosterophyllum llanoveranum	Llandstadwell Fm., Mascle Bridge Quarry, Pembrokeshire, Wales, UK	late Lochkovian	late Lochkovian	D. Edwards and Richardson (2004)
Zosterophyllum llanoveranum	Shunet Fm., Shira, Minusinsk Basin, Khakassia, Russia	early Pragian	late Pragian	Naugolnykh (2021)
Zosterophyllum longum	Wood Bay Fm., Andrée Land, Svalbard, Norway	late Pragian	early Emsian	Schweitzer (1999)
Zosterophyllum minifertillum	Posongchong Fm., Bed 7, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Zosterophyllum minifertillum	Posongchong Fm., Fossile site 1, Changputang Section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Zosterophyllum minor	Sunnet Fm., Batensk Ridge, Shira northern Minusink basin, Russia	early Pragian	late Pragian	Ananiev (1960) and Zakharova and Ananiev (1990)
Zosterophyllum minorstachyum	Xitun Fm., Huaguoshan Section, Shengfeng District, Yunnan, China	middle Lochkovian	late Lochkovian	Xue (2009)
Zosterophyllum myretonianum	Dundee Fm., Aberlemno Quarry, Forfar, Scotland, UK	early Lochkovian	early Lochkovian	D. Edwards (1975)
Zosterophyllum myretonianum	Dundee Fm., Balgavies quarry Scotland UK	early Lochkovian	early Lochkovian	D. Edwards (1975)
Zosterophyllum myretonianum	Dundee Fm., Clocksbriggs quarry Scotland UK	early Lochkovian	early Lochkovian	D. Edwards (1975)
Zosterophyllum myretonianum	Lerbekk Fm., Røragen, Røros, Trøndelag, Norway	early Emsian	early Emsian	Schweitzer and Heumann (1993)
Zosterophyllum myretonianum	Shunet Fm., Shira, Minusinsk Basin, Khakassia, Russia	early Pragian	late Pragian	Fedoseev (2008)

Species	Locality	Early interval	Late interval	Reference
Zosterophyllum ovatum	Pingyipu Gp., Horizon 1, Yanmenba Section, Jiangyou City, Sichuan, China	early Lochkovian	early Pragian	D. Edwards and Li (2018b)
Zosterophyllum qujingense	Yulongsi Fm., Bed 2, Xiaxishan Reservoir, Qujing City, Yunnan, China	early Pridoli	late Pridoli	Hao et al. (2007)
Zosterophyllum ramosum	Norton Gully Sandstone Fm., Mt. Pleasant road, Alexandra, Victoria, Australia	early Pragian	late Emsian	McSweeney et al. (2020)
Zosterophyllum ramosum	Posongchong Fm., Bed 18, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Wang (2000)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US604, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US605, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US606, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US607, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US609, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US610, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US615, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US616, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)

Species	Locality	Early interval	Late interval	Reference
Zosterophyllum reflexum	Bathurst Island Fm., Loc US617, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US628, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US631, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US632, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US636, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US637, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US643, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum reflexum	Bathurst Island Fm., Loc US645, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum rhenanum	Ahr Fm., Ahr Valley, Eifel, Germany	early Emsian	early Emsian	Schweitzer (1987)
Zosterophyllum rhenanum	Brohl Fm., Brohl valley, Eifel, Germany	early Pragian	early Pragian	Schweitzer (1979)
Zosterophyllum rhenanum	Klerf Fm., Steinbruch Koppen bei Waxweiler Eifel Germany	early Emsian	early Emsian	Schweitzer (2000)
Zosterophyllum rhenanum	Klerf Fm., Waxweiler, Eifel, Germany	early Emsian	early Emsian	Schweitzer (1987)
Zosterophyllum rhenanum	Lower Siegen Gp., Rheineck, Vinxtbach Valley, Rhineland, Germany	early Pragian	early Pragian	Schweitzer (1987)
Zosterophyllum rhenanum	Maubacher Bleiberg, Rurtal, Eifel, Germany	early Pragian	late Pragian	Schweitzer (1987)

Species	Locality	Early interval	Late interval	Reference
Zosterophyllum rhenanum	Nellenkopfchen Schichten Fm., Alken quarry Germany	early Emsian	early Emsian	Schweitzer (1979)
Zosterophyllum rhenanum	Nellenkopfchen Schichten Fm., Konder valley, Winningen, Germany	early Emsian	early Emsian	Schweitzer (1987)
Zosterophyllum rhenanum	Sagla Fm., Khondelen Graben, Tuva Trough, Russia	early Emsian	early Emsian	Korzhnev (2014)
Zosterophyllum rhenanum	Shunet Fm., Shira, Minusinsk Basin, Khakassia, Russia	early Pragian	late Pragian	Fedoseev (2008)
Zosterophyllum rhenanum	Sieg valley, Betzdorf, Siegerland, Germany	early Pragian	late Pragian	Schweitzer (1987)
Zosterophyllum rhenanum	Stadtfeld Fm., Hoffeld, Eifel Region, Rhineland, Germany	early Emsian	early Emsian	Schweitzer (1999)
Zosterophyllum rhenanum	Stadtfeld Fm., Müsch, Ahr Valley, Eifel Region, Rhineland, Germany	early Emsian	early Emsian	Schweitzer (1999)
Zosterophyllum rhenanum	Wahnbach Fm., Wahnbach Valley, Eifel, Germany	late Pragian	late Pragian	Schweitzer (1987)
Zosterophyllum shengfengense	Xitun Fm., Huaguoshan Section, Shengfeng District, Yunnan, China	middle Lochkovian	late Lochkovian	Hao et al. (2010)
Zosterophyllum sinense	Cangwu Fm., Shiqiao Section, Cangwu County, Guangxi, China	early Pragian	late Emsian	Y. Wang et al. (2018)
Zosterophyllum sp	Aigyrzhak'skaya Suite Fm., Aigyrzhal mountain, Kazakhstan	early Pragian	late Pragian	Yurina (1969)
Zosterophyllum sp	Bathurst Island Fm., Loc US384, Polar Bear Pass, Bathurst Island, Nunavut, Canada	Ludfordian	Ludfordian	Kotyk (1998)
Zosterophyllum sp	Bathurst Island Fm., Loc US603, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum sp	Bathurst Island Fm., Loc US605, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum sp	Bathurst Island Fm., Loc US606, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)

Species	Locality	Early interval	Late interval	Reference
Zosterophyllum sp	Bathurst Island Fm., Loc US607, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum sp	Bathurst Island Fm., Loc US609, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum sp	Bathurst Island Fm., Loc US616, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum sp	Bathurst Island Fm., Loc US617, Polar Bear Pass, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum sp	Bathurst Island Fm., Loc US642, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum sp	Bathurst Island Fm., Loc US643, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum sp	Bathurst Island Fm., Loc US644, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum sp	Bathurst Island Fm., Loc US649, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum sp	Bathurst Island Fm., Loc US664, Cheyne River Region, Bathurst Island, Nunavut, Canada	early Pragian	late Pragian	Kotyk (1998)
Zosterophyllum sp	Freshwater West Fm., Newton Dingle Assemblage, Shropshire, UK	late Lochkovian	late Lochkovian	D. Edwards and Richardson (1974) and Morris and Edwards (2014)
Zosterophyllum sp	Posongchong Fm., Bed 24, Zhichang section, Wenshan city, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)

Species	Locality	Early interval	Late interval	Reference
Zosterophyllum sp	Rashkov Beds, stratum 6, Dniestr Valley Podolia Ukraine	Ludfordian	early Pridoli	Nikiforova 1977
Zosterophyllum sp	Schiefergebirge Fm., Venn Sadle, Germany	late Lochkovian	late Lochkovian	Schweitzer (1987)
Zosterophyllum sp	Strathmore Fm., Facies A, Auchensail quarry, Cardross, UK	early Emsian	early Emsian	Scott et al. (1976)
Zosterophyllum sp	Wahnbach Fm., Wahnbach Valley, Eifel, Germany	late Pragian	late Pragian	Schweitzer (1987)
Zosterophyllum spathulatum	Xujiachong Fm., Xujiachong section, Qujing , Yunnan, China	early Pragian	early Emsian	X.-X. Li and Cai (1977)
Zosterophyllum spectabile	Bensberg Fm., Herfterath, Much, Rhineland, Germany	early Emsian	early Emsian	Schweitzer (1979)
Zosterophyllum tenerum	Posongchong Fm., Bed 23, Zhichang Section, Wenshan City, Yunnan, China	middle Pragian	late Pragian	Hao and Xue (2013)
Zosterophyllum xishanense	Xiaxishancun Fm., Bed 5, Xiaxishan Reservoir, Quijing City, Yunnan, China	early Lochkovian	early Lochkovian	Hao et al. (2007)
Zosterophyllum yunnanicum	Danlin Fm., Lizhai Section, Dushan County, Guizhou, China	early Pragian	early Emsian	X.-X. Li and Cai (1977)
Zosterophyllum yunnanicum	Xujiachong Fm., bed 4, Xujiachong, Qujing, Yunnan, China	early Pragian	early Emsian	Wellman et al. (2012)
Zosterophyllum yunnanicum	Xujiachong Fm., bed 5, Xujiachong, Qujing, Yunnan, China	early Pragian	early Emsian	Wellman et al. (2012)
Zosterophyllum yunnanicum	Xujiachong Fm., bed 8, Xujiachong, Qujing, Yunnan, China	early Pragian	early Emsian	D.-M. Wang (2007)

Table D.1: Occurrence database of zosterophylls including zosterophylls and barinophytes. This database regroups the species name, the detailed locality of the fossil discovered, the earliest and latest age estimation, and the associated reference. For some references, the paleobiology database code is provided, since the information is not to be found in the primary literature.

D.2 Figures

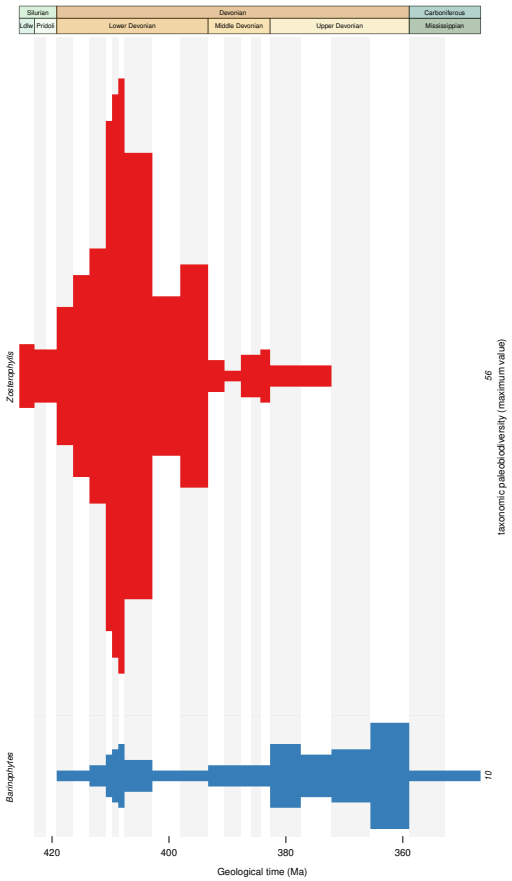


Figure D.1: Maximum richness estimate (spindle shaped), between Zosterophylls (in red) and Barinophytes (in blue) among the Devonian.

D.3 R script

See below the R script developed both for time scaling the trees, perform a diversity count based on these trees and visual representation.

```
library(paleotree)
library(ggplot2)
library(deeptime)
library(strap)
library(TreeTools)

zostage <- read.table("07_18_age.txt")
zostree <- ReadTntTree("matrix_zostero_07_09_R.tre")
```

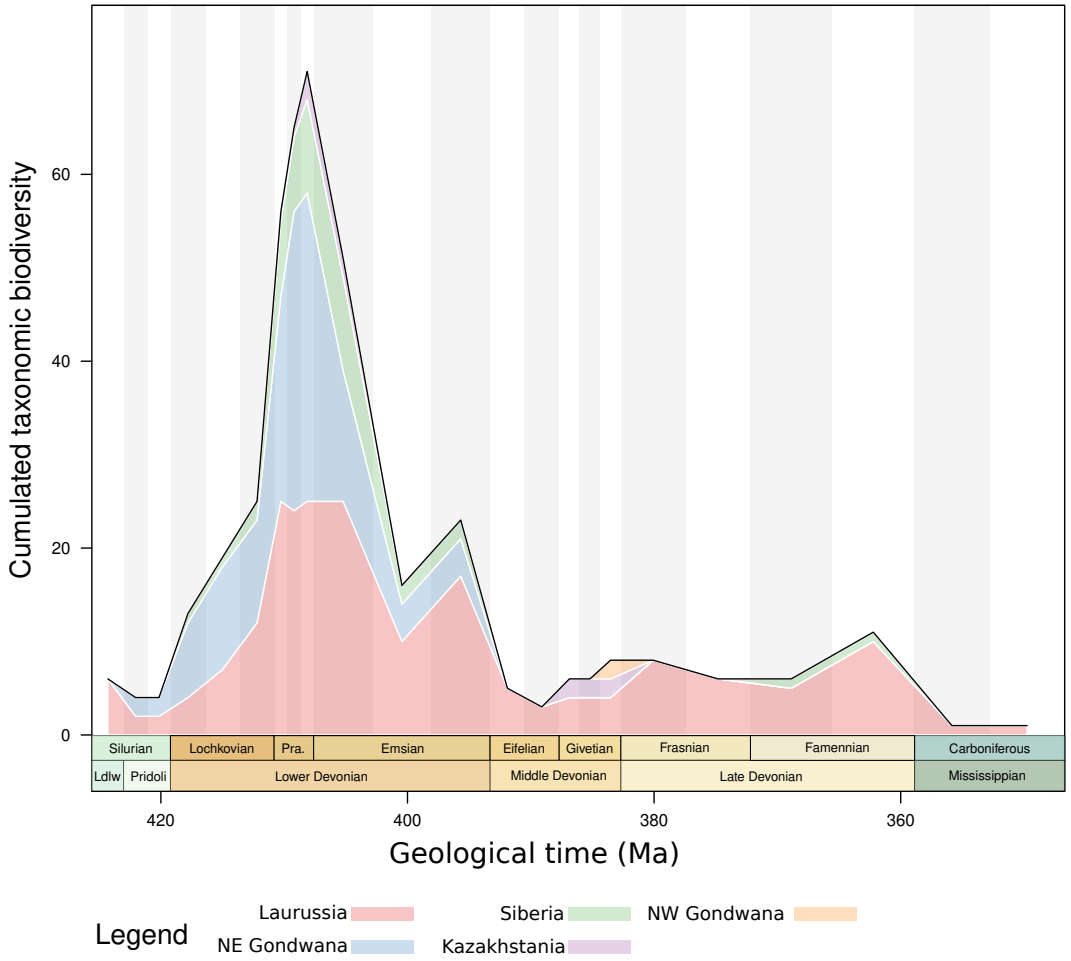


Figure D.2: Range through diversity of zosterophylls, with spatial cutting, over the Devonian. Each color refers to a given paleogeographical area (see legend). The different areas are accumulated curves of zosterophyll richness at each time bin.

```
TST <- NULL # Time Scaled Tree (TST) vector, empty at the
    start of the loop
for (i in 1:6){
        TST[[i]] <- DatePhylo(zostree[[i]], zostage, rlen=1,
            method="equal", add.terminal=TRUE)
        # The DatePhylo function from strap allows a plot for
            a tree only. The dataset is a multiphylo
        # class object, so a loop was needed

        div <- multiDiv(TST)

        ## Graphic representation
        ##########################
        taxDivTre <- div$div.counts
```

```
taxDivMed <- apply(taxDivTre,1,median) # For plotting
    the median curve
taxDivq1 <- apply(taxDivTre, 1, quantile, probs =
    0.025)
taxDivq2 <- apply(taxDivTre, 1, quantile, probs =
    0.975)

# Build the data frame for ggplot
df <-data.frame(Med=taxDivMed, q1=taxDivq1, q2=
    taxDivq2, time=div[[1]][,1])

pdf(file = "08_10_diversity_analyses.pdf", width =
    10)
graphx <- ggplot(df, aes(x=time, y=Med)) +
geom_rect(aes(xmin = 427.4, ymin = 0.2, xmax= 430.5,
    ymax = 45), fill= "#efefef") +
geom_rect(aes(xmin = 425.6, ymin = 0.2, xmax= 423,
    ymax = 45), fill= "#efefef") +
geom_rect(aes(xmin = 421.1, ymin = 0.2, xmax= 419.2,
    ymax = 45), fill= "#efefef") +
geom_rect(aes(xmin = 416.4, ymin = 0.2, xmax= 413.6,
    ymax = 45), fill= "#efefef") +
geom_rect(aes(xmin = 410.8, ymin = 0.2, xmax= 409.7,
    ymax = 45), fill= "#efefef") +
geom_rect(aes(xmin = 408.6, ymin = 0.2, xmax= 407.6,
    ymax = 45), fill= "#efefef") +
geom_rect(aes(xmin = 402.8, ymin = 0.2, xmax= 398,
    ymax = 45), fill= "#efefef") +
geom_rect(aes(xmin = 393.3, ymin = 0.2, xmax= 391.1,
    ymax = 45), fill= "#efefef") +
geom_rect(aes(xmin = 387.7, ymin = 0.2, xmax= 386,
    ymax = 45), fill= "#efefef") +
geom_rect(aes(xmin = 384.3, ymin = 0.2, xmax= 382.7,
    ymax = 45), fill= "#efefef") +
geom_rect(aes(xmin = 377.4, ymin = 0.2, xmax= 372.2,
    ymax = 45), fill= "#efefef") +
geom_rect(aes(xmin = 365.2, ymin = 0.2, xmax= 358.9,
    ymax = 45), fill= "#efefef") +
geom_ribbon(aes(ymin=q2, ymax=q1),fill="grey", alpha
    =0.75) +
geom_line(color="black", size=1) +
#  ggtitle("Diversity curve") +
theme_classic() +
theme(plot.title = element_text(hjust = 0.5),
panel.background = element_rect(colour = "black",
    size=1),
axis.text=element_text(size=22),
axis.title=element_text(size=22)) +
ylab("Number of genera") +
```

```
scale_y_continuous(expand = c(0, 0)) +
scale_x_reverse("Geological time (Ma)", expand = c
    (0,0))

p <- gggeo_scale(graphx, height = unit(1.5, "lines"),
     abbrv = FALSE)
p <- gggeo_scale(p, dat = "epochs", height = unit
    (1.5, "lines"), size = 4, abbrv = FALSE)
gggeo_scale(p, dat = "stages", height = unit(1.5, "
    lines"), rot=90, size = 4, abbrv = TRUE)
dev.off()
```

Appendix E

Anatomy

The present essay revisited zosterophyll's evolutionary history through different angles: systematic, temporal and spatial. Along these chapters, the common word was the particular morphology found in the group. Morphology is the main gate to study these remote fossils, and as demonstrated through these different analyses, this information is broadly incomplete. All of these results are the fruit of a partial information, sensible to any new discoveries. Studying the plants through their morphology is also limiting. In fact, these organisms are composed of a few number of organs, that can have different shapes. Thus, the differences observed may be due to ecological constraints or individual life history rather than common evolutionary pattern, and shall then be studied with caution. Another approach in understanding the plants' evolution can be through their anatomy. The present chapter is positioned as a suggestion for anatomical studies, especially for such an early group as zosterophylls.

E.1 Introduction

Among the different Devonian deposits that recovered zosterophyll remains is the Battery Point Formation, Gaspé Bay, Canada. This Northern American deposit, among the richest known, was located during the Paleozoic in the southern shore of Laurussia, and is interpreted as an ancient bay with a marine influence, according to the acritarchs record (Hotton et al., 2001). During the time of deposit (Emsian to Eifelian according to McGregor (1977)), the climate was estimated to be tropical (Witzke, 1990). This formation is a complex geological system composed of floodplains, channels and rivers, with some sea influence (Hotton et al., 2001). In fact, the section is characterized by an alternance of sandstones and mudstones. Mudstone in particular was deposited in a context of floodplains, during episodes of water ingression. The Gaspé Bay Formation is thus a complex fossiliferous site at the interface between different deposit contexts. The formation revealed an important number of plant fossils, interpreted both as autochtonous and allochtonous, and showing a diversity in preservation. In fact, the fossils preserved in compression are generally *in situ* specimens, discovered in the musdstone layers (Hotton et al., 2001) (see Appendix F for a list of described plant taxa). But in addition to this compressed flora, some other fossils are found in cobbles, generally anatomically preserved (Association 3, Cap-aux-Os member, Griffing et al. (2000)). The list provided in appendix F includes all the currently described anatomically-preserved taxa from this formation.

Compression zosterophyll remains have previously been described in the Battery Point

Formation (Hotton et al., 2001; Gensel & Berry, 2016). However, only *Crenaticaulis verruculosus* is known from this deposit by its anatomy (Banks & Davis, 1969) (see Supp. Table F.1 for a detailed list of zosterophylls from this locality).

Anatomically speaking, zosterophylls are characterized by small axes with an elliptical to terete exarch xylem strand, composed of G-type tracheids. However, these characteristics prevent for a detailed identification at a higher taxonomic level if based on the anatomy only. In the present work, some anatomical material attributed to zosterophylls will be studied. Using metric proxies, the present chapter is a description of these new specimens, and an attempt to identify them at a finer taxonomical level. The measurements made on the collected specimens will be compared to the data from previous studies. Therefore, by comparing the proxies, the goal is to detect any trends that can provide a more detailed taxonomical identification for the anatomical specimens. This approach is an attempt to solve the thorny question of zosterophyll identification based on a limited amount of information, such as the anatomy.

E.2 Material and methods

E.2.1 Data acquisition

24 specimens associated to zosterophylls were identified by Megan Nibbelink, from cobbles of the Cap-aux-Os member (Gaspé, Canada). These cobbles were collected by Dr Francis M. Hueber (Smithsonian Institution - NMNH) in 1965, in a locality between Douglastown and Tar Point. The environment is reconstructed as allochtonous, coastal to fluvial, of mid-to-late Emsian in age (McGregor, 1977). These cobbles previously delivered a rich fossil flora (Pfeiler & Tomescu, 2018; Bickner & Tomescu, 2019; Lalica & Tomescu, 2021; Pfeiler & Tomescu, 2021; Lalica & Tomescu, 2022, 2023), and are stored in the U.S. National Museum of Natural History – Smithsonian Institution (Washington, D.C.). Among the cobbles collected during this field trip, only four yielded the 24 specimens of zosterophylls (USNM 557820, USNM 557840, USNM 557790 and USNM 558725 respectively). Peel-sections have been prepared from these specimens using the cellulose acetate peeling technique (Joy et al., 1956). Some of these peels were mounted in slides for microscope observations thanks to the Eukitt mounting kit. Pictures were taken using a Nikon Coolpix 8800VR digital camera mounted on a Nikon E400 compound microscope for observation and measurements.

Figure E.1 is a sample of the anatomical zosterophylls found in the Battery Point Formation. As pictured in the figure, the majority of the specimens display a terete to elliptical xylem strand, with an exarch organization. These two criteria allow for a zosterophyll identification. However, the specimens generally have no further information about the axes or the other tissues composing it. This anatomical description is thus generally restricted to the xylem strand, and this limited information is the source of the metrics used.

E.2.2 Measures

After a careful review of the extant data on zosterophyll anatomy, only two characters (maximum tracheid diameter and xylem strand width) were consistently found (Table E.1). On the eleven zosterophylls known by their anatomy, ten show information about their xylem size while all of them display a maxiumum tracheid diameter value. To complete this information, the measures were done again from the publication, in order to compare the given value with the current hand measure. No particular differences were observed from our own measures and the ones given by the original authors.

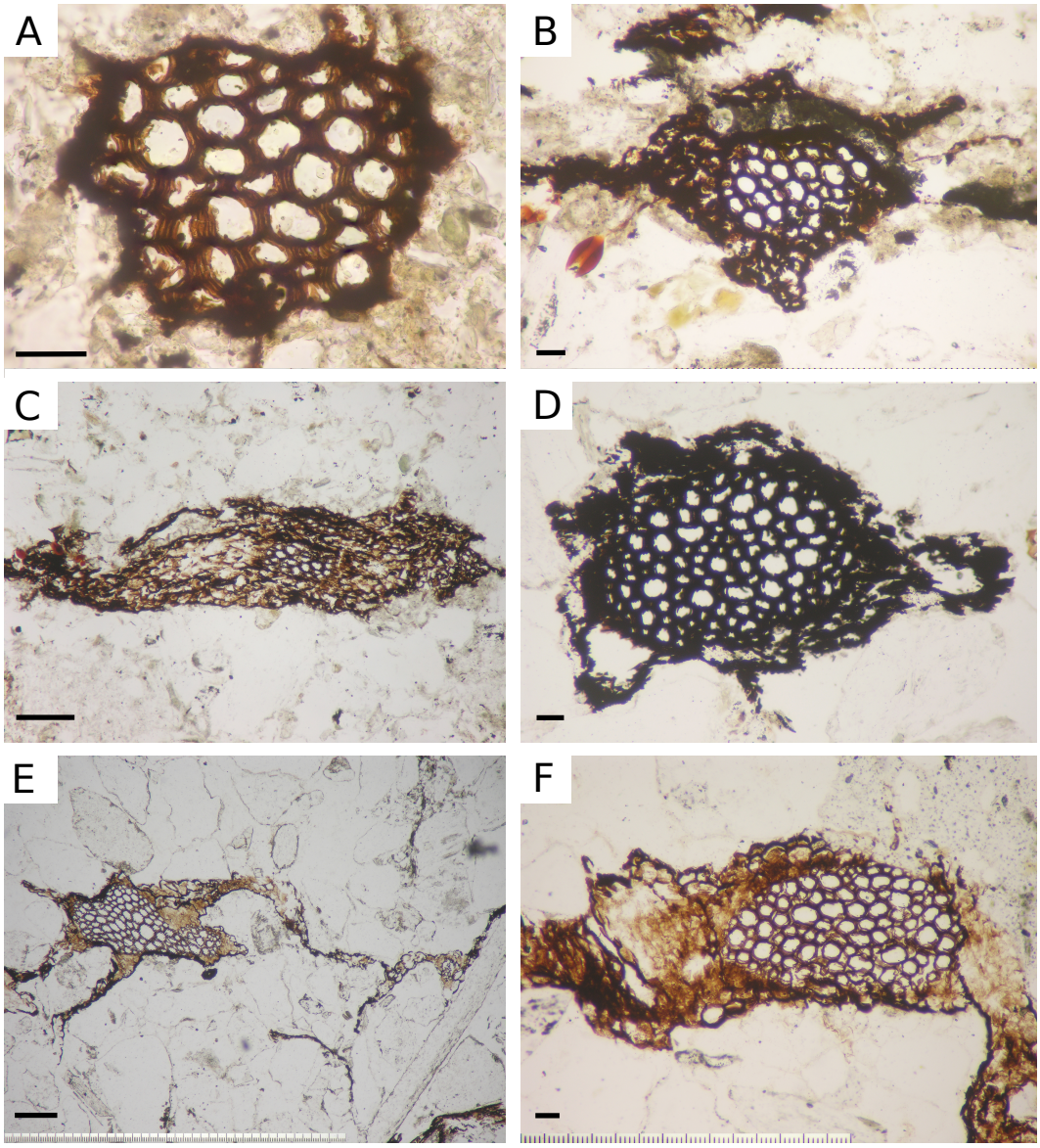


Figure E.1: Some anatomically preserved specimens from the Battery Point Formation in transverse section, displaying mainly the xylem strand. Pictures taken by M. Nibbelink A) Specimen B21 Btop 75, zostero 2, scale bar= 0.1 mm, B) Specimen B21 Btop 65 zostero 3, scale bar= 0.1 mm, C) Specimen B21 Btop 49 zostero 1, scale bar= 0.5 mm D) Specimen 557820-4 D 11b, scale bar= 0.1mm, E) 557820-48 A1 top 48b, scale bar= 0.5 mm, F) 557820-4 A1 top 145b, scale bar= 0.1 mm.

Table E.1: Previously described anatomically preserved species: species, xylem size (range or measurement), max tracheid size (range and measurement)

Species	Xylem size	Maximum tracheid size	References
Crenaticaulis verruculosus	**350-800 µm**	33-37 µm	Banks and Davis (1969)
Deheubarthia splendens	**560 µm**	avg 42, up to 65 µm	D. Edwards et al. (1989)
Euthursophyton hamperbachense	**625 µm**	25-140, mostly 60-80 µm	Mustafa (1978)
Gosslingia breconensis	**260-575 µm**	30-50 µm	Kenrick and Edwards (1988a)
Konioria andrychoviensis	**500 µm**	**99 µm**	Zdebska (1982)
Margophyton goldschmidti	-	15-77 µm	Zakharova (1981)
Sawdonia deblondii	**370 µm**	34-60 µm	Gerrienne (1996a)
Sawdonia ornata	**300-2380 µm**	20-100 µm	Rayner (1983)
Stolbergia spiralis	620/590 µm	100-149 µm	Fairon (1967)
Thrinkophyton formosum	**375 µm**	14-40 µm	Kenrick and Edwards (1988a)
Trichopherophyton teuchansii	**216 µm**	40-50 µm	Lyon and Edwards (1991)
Ventarura lyonii	640-1860 µm	11-42 µm	Powell et al. (1999)
Zosterophyllum fertile	**110 µm**	20-25 µm	D. Edwards (1969)
Zosterophyllum llanoveranum	120-250 µm	**23 µm**	D. Edwards (1969)

The 24 specimens studied were peeled to various extents, from a few millimeters to more than one cm. Therefore, there is a variability among the number of peels, comprised between 2 for the lowest number (specimen 557790-2 Dtop), to 415 for the highest number (specimen 558725 (B21) Btop a series). All the specimens were partially dissected, and no complete axes have been extracted in peels, preventing for detailed measures and architectural information of preserved axes. Therefore, for consistency among the studied specimens, a number of 5 peels per specimen was selected. To better understand the anatomy of each zosterophyll, peels were selected preferentially at the base, middle and end of the axis. The values were then averaged for each specimen. Additionally, a correction of 1.05 was applied on these measures in order to consider for the size loss caused by the shrinkage (Long et al., 2022).

The first proxy measured is the maximum tracheid diameter (MTD). For each peel selected, the five widest tracheids of the xylem strand were measured by hand. Given that the majority of the tracheid of this sample have a round shape in section, they have been preferentially selected. In the case where no round tracheid were the widest, elliptical ones were selected, and the short radius measured.

The second proxy measured is the xylem strand width (XSW). Zosterophylls xylem strands are known to display a variability of shapes, from terete to elliptical (Kenrick & Edwards, 1988a; Lyon & Edwards, 1991). In this case, it is not possible to apply the same geometrical inference as for the MTD. Consequently, xylem size measures was performed on the same peels as the ones selected for the MTD (n= 5), in order to catch its variability. The measures were done on the longest side of the xylem, inferred as the maximum size possible for the specimen.

These measures done on the 24 specimens were coupled with the ones from the previously published zosterophylls, extracted from primary literature (see above), in order to compare the ranges of values. Such information are regrouped in table E.1.

In addition to these measurements, each specimen will have its own anatomical description and illustration, that will be further developed in an upcoming publication.

E.2.3 Analyses

MTD were plotted for each Gaspé specimen in boxplots in order to see the distribution of these measures in our dataset. They were additionally ordered from the smallest to the biggest in order to detect any trend. This distribution of values is paralleled with the known values of

described zosterophylls in order to compare them.

Then, the mean MTD of each zosterophyll was plotted against the mean XSW. This combined information is more precise since it allows observations on the proportion of tracheids contained in the xylem, and detect any zosterophyll characterized by a contrast between xylem and tracheid sizes.

The analyses were performed on R studio (R Core Team, 2023), using the packages ggplot2 (Wickham et al., 2016) and dplyr (Wickham et al., 2023). Figures were made on Inkscape (Inkscape Project, 2023).

E.3 Results

E.3.1 Comparison

Figure E.2 shows the distribution of the MTD for each specimen measured. Values encompassed by the specimens are between 10 µm and 60 µm, and are representative of an important disparity among them. The anatomically described zosterophylls from the literature are represented by the crossing line on the plot, for their own tracheid size mean. We can see that the majority of Gaspé fossils are in between values close to *Z. llanoveranum* and *C. verruculosus* (n=12). The maximum size value of the dataset reaches the ones of *G. breconensis* and *Trichopherophyton teuchansii* (n=8), with two specimens ("557820-4 A/A1 top b series" and "557840 Gbot b series Zost 1") reaching a maximal size closer to *Sawdonia deblondii*. The minimal size value, despite being more closely associated to *Z. llanoveranum* than the other zosterophylls taxa appears as an outlier in this figure, with a MTD between 10 and 20 µm.

Once the MTD observed and compared, a similar approach has been performed including this time the information about the XSW, and is visible in figure E.3. On this figure, the mean MTD is plotted against the mean XSW in order to detect any pattern between these two information. Figure E.3A shows a preferential grouping into a mean MTD between 25 and 50 µm, and a mean XSW between 100 and 600 µm (the majority being concentrated to 200 µm). Some zosterophylls like *Stolbergia*, *Euthursophyton* or *Sawdonia ornata* and *Konioria* shows an important mean MTD still concentrated into a regular mean XSW. On the other hand, *Ventarura lyonii* is the sole zosterophyll known with the biggest XSW, and regular mean MTD. Figure E.3B shows a close-up on the Gaspé specimens. On this figure, the sampled specimens seem to follow an asymptotic distribution, with a maximum tracheid size between 55 to 60 µm, and a gradually bigger xylem size up to 600 µm, forming then a plateau. The majority of the specimens fall into values in between *Zosterophyllum*, *Crenaticaulis* and *Thrinkophyton*, and *Trichopherophyton* and *Gosslingia*. This distribution favors the Gaspé identification to one of this above-mentioned species, except for two specimens. One is characterized by the lowest MTD known but a regular XSW, while the other, displays a regular MTD but a bigger XSW, around 600 µm.

E.4 Discussion

E.4.1 Identification and comparison of the Gaspé specimens

According to figures E.2 and E.3, the specimens occupy a restricted subsection of the anatomical space, while maintaining a variety of sizes. Moreover, the Gaspé specimens follow a crescent-shape distribution. This particular distribution can be the consequence of i) interspecific, ii) intraspecific and iii) interindividual variation. In fact, multiple species may have coexisted in this site, with similar anatomy. It is also possible that this variation is the result of intraspecific

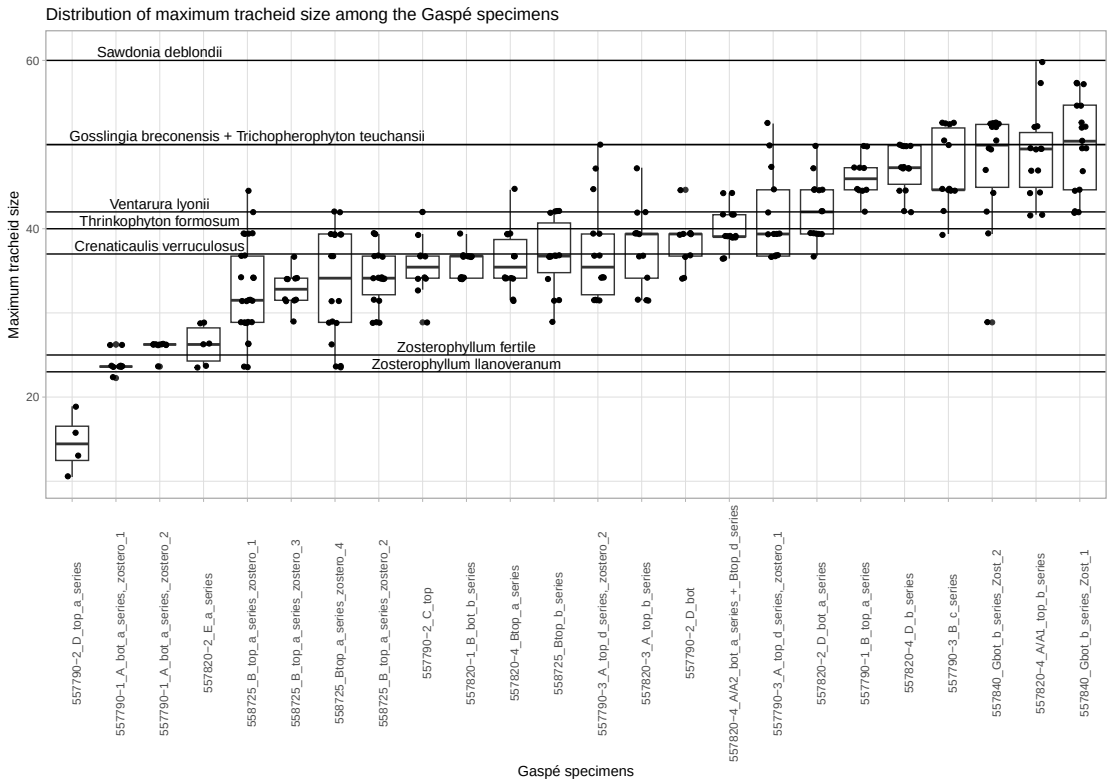


Figure E.2: Boxplots of the maximum tracheid size of the Gaspé zosterophylls. Parallel lines represent the mean maximal value of described zosterophylls. Units on the y-axis is in µm.

differences, such as ontogeny, with younger axes having smaller cells. Interindividual variation can be the result of differences in environments of growth. In fact, the cobbles collected are interpreted as allochtonous and the paleoenvironement of the formation is reconstructed as being coasts, floodplains or rivers. The fossils thus can stem from one of these environments that each have different water availability, impacting the hydric performance.

The outlier, specimen "557790-2 D top a series" is so different from the sampling and the known taxa that it is currently not possible to draw a parallel between this specimen to any known zosterophylls, without further information. No attempt of identification will be provided for this specimen in this work.

According to figure E.2, the Gaspé specimens with the lowest tracheid size values can be put close to the *Zosterophyllum* species (20 µm < specimens < 30 µm). The genus is already present in Gaspé, but identified in an open nomenclature as *Z. sp.* (Hotton et al., 2001). According to these results, *Zosterophyllum* may more likely be identified as a *Z. fertile* or *Z. llanoveranum*, two species found out in Europe (Leclercq, 1942; D. Edwards, 1972; Schweitzer, 1987), or Russia (Zakharova & Ananiev, 1990; Korzhnev, 2014; Naugolnykh, 2021), but currently unknown in Northern America. Since no other anatomically known *Zosterophyllum* is described, caution is advised for the identification of the Gaspé specimens. Additionally, *Zosterophyllum* is known to be a paraphyletic genus (Kenrick & Crane, 1997). Therefore, it is not possible to draw any taxonomical link between these two species, without further revisions on *Zosterophyllum*.

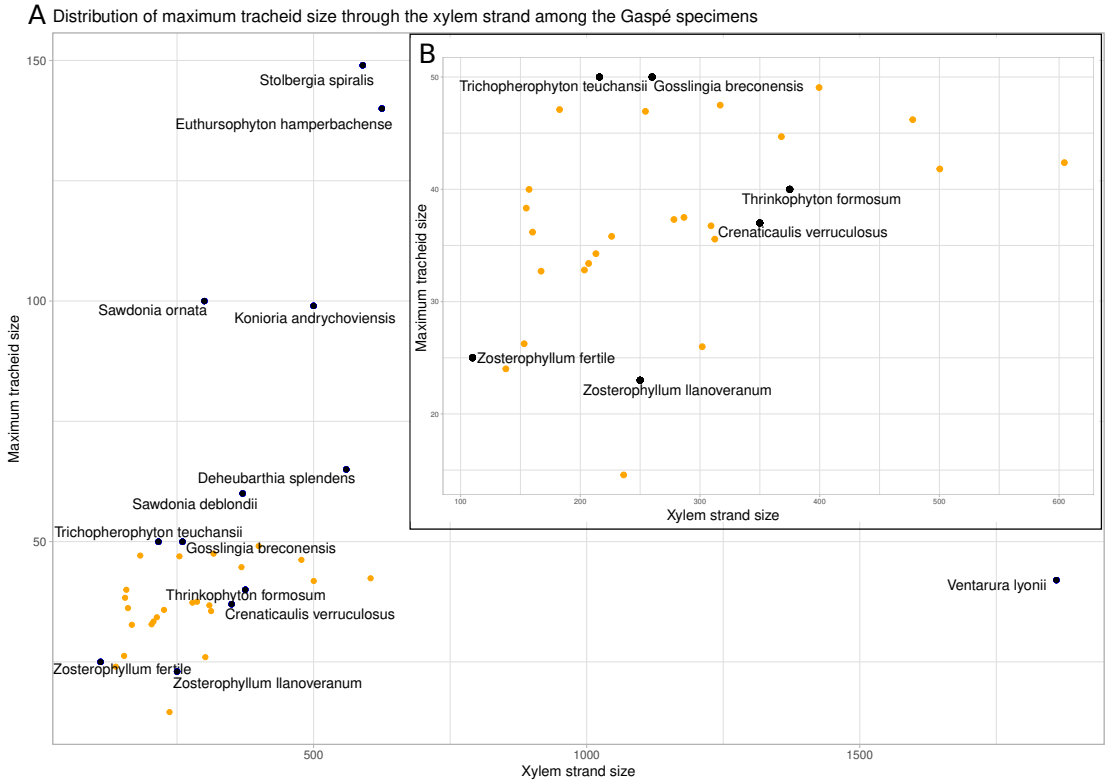


Figure E.3: Scatterplot of the mean maximum tracheid size compared to the xylem strand size. Gaspé specimens are represented by yellow dots and previously published species with dark dots. Units on the x-y-axes are in µm. A) General view among zosterophylls. B) Close-up on the distribution of the Gaspé zosterophylls.

Some specimens are close to *Crenaticaulis verruculosus* values, especially on their maximum tracheid diameters (Fig. E.2). Four in particular are closely related to the values of this species according to figure E.3 ("558725 B top a series zostero 3", "558725 B top a series zostero 2", "557790-2 C top", "557820-1 B bot b series"). Since *Crenaticaulis verruculosus* is already morphologically and anatomically known from this deposit (Banks & Davis, 1969), some confidence can be put in the interpretation of these specimens, especially in the absence of further diagnostic criteria.

According to figure E.2, some specimens reach maximum tracheid diameter values close to *Thrinkophyton* or *Ventarura*. However, cross-validation with figure E.3, prevents for a parallel to these species with certainty. Additionally these two zosterophyll species are restricted to the UK (Lyon & Edwards, 1991; Powell et al., 1999), which make their identification in the Northern America unlikely. *Ventarura* by having the biggest xylem strand known among zosterophylls can be put aside despite its similar mean tracheid diameter. This observation favors for a more integrative approach, by taking into account the maximum anatomical information possible.

The widest tracheid diameters measured in this dataset are close to the values of *Gosslingia breconensis* and *Thrinkophyton formosum*. These two species, despite being morphologically divergent, have a similar anatomy. This observation is thus an invitation for precaution, since the limited anatomical characteristics found in zosterophylls can lead to a great proximity between

fairly divergent species. In addition, these two species are restricted to the European continent (Croft & Lang, 1942; Kenrick & Edwards, 1988a; Gerrienne, 1990; D. Edwards & Richardson, 2004). Therefore, if the specimens with the widest tracheid diameter values are different species from the other Gaspé zosterophylls, they may more likely be close to *Gosslingia*, *Thrinkophyton*, or a different species.

The other anatomically described zosterophylls (*Sawdonia*, *Deheubarthia*, *Konioria*, *Euthursophyton*, *Stolbergia*) because of their bigger mean tracheid size value will not be considered for the Gaspé comparison.

The two specimens with the biggest tracheid diameter measured reach values close to the ones of *Sawdonia deblondii* (Fig. E.2). Even if this species appears in figure E.3 appart from the Gaspé specimens, we can also observe a difference in size compared to its sister species, *S. ornata*. In fact, the mean tracheid diameter of *S. deblondii* is almost twice smaller than the ones of *S. ornata*. These differences invite for precaution, since a taxonomical signal is not detected with the current used metrics.

E.4.2 Limits and perspectives

This study is a preliminary approach in the use of quantitative proxies for the identification of zosterophylls. By extracting only two metrics based on the size of the conductive system, a functional question arises about the interpretation of the values. In fact, since the xylem is a tissue specialized in water conductivity, and these Gaspé fossils live in an environment interpreted as fluvial or coastal, the size and shape of the structure can be linked to water flow efficiency, rather than being the sign of a taxonomic signal.

Consequently, in order to make the distinction between the functional and taxonomical signals, a first study based on complete and well understood zosterophylls is advised. This study, based on specimens having a maximum tissular preservation could help detect the anatomical contribution of the taxonomy and the functionality. Once the taxonomical contribution targeted, studies based on partially preserved zosterophylls such as the present one can be developed.

Additionally, since only a fragment of the axes have been extracted, questions arise concerning their position inside the plant. In fact, tracheid size can be affected by its position either on the main axis, or in the different orders of ramification inside the plant. No information about the type of the axis is currently available, and further sections of the specimens are welcomed, in order to have a better interpretation of the architecture of the plant.

For each of the 24 zosterophylls sampled for the analysis, metrics were applied only on five peels at least, no matter if the specimen is known by 10 peels or 100. This measure may not be enough to catch the whole variability of the specimens, and results can thus be improved by increasing the number of peels to measure.

In addition, measures were all done by hand, which can be limiting, especially from a reproductibility perspective (Blackwell et al., 2006). In particular, in the present study, out of the 2550 peels available, only 120 was studied. This subset could have been expanded by the use of software tools. Integration of these tools that could automatize the process not only would help to accelerate the data acquisition, but also expand the measures to all the tracheid cells. With the rise of inclusion of such computational methods in science, research is ongoing on this subject, with new softwares developing strategies for outlining cells (Lloyd et al., 2024), or detecting the lumen size with the picture's color balance (Von Arx & Carrer, 2014). Testing them on such an early group of land plant may enhance an interest in anatomical studies on limited characters.

E.5 Conclusion

The Emsian flora of the Battery Point Formation has gained richness in zosterophyll diversity thanks to the discovery and identification of an additional 24 new specimens. These specimens are only anatomically preserved. No information about their morphology or deeper degree of anatomical structure are available for a taxonomical identification. Based on the xylem only, the present work is a first attempt to identify these zosterophylls using metric proxies. The maximum tracheid size and the xylem strand size has been used in order to compare the distribution of the Gaspé specimens with the anatomically described zosterophylls. If results demonstrated that it is not possible to identify these specimens with certainty to a given zosterophyll species, some patterns were however highlighted. However, uncertainty remain concerning the taxonomical impact of these patterns, and in-depth study on anatomically known zosterophylls as well as further peeling of the Gaspé specimens are encouraged. This study has therefore focused on the need of the development of anatomical proxies for early land plants remains, in order to gain more information from these remote times.

Appendix F

Anatomy

F.1 Supplementary lists

F.1.1 List of embryophyes megafossils found in the Battery Point Formation

- Gametophytes
  - *Sciadophyton sp.*, Remy et al. (1992)
- Zosterophylls
  - *Renalia hueberi*, Gensel (1976)
  - *Sawdonia ornata*, Hueber (1971b)
  - *Crenaticaulis verruculosus*, Banks and Davis (1969)
  - *"Bathurstia" sp.*, Hotton et al. (2001)
  - *Zosterophyllum sp.*, Hotton et al. (2001)
- Lycopsids
  - *Drepanophycus spinaeformis*, Dawson (1871)
  - *D. gaspianus*, Krausel and Weyland (1948)
- Rhyniopsids
  - *Huvenia sp.*, Hotton et al. (2001)
  - *Taeniocrada dubia*, Hueber (1982)
  - *Eogaspesia gracilis* Daber (1960)
- Trimerophytes
  - *Psilophyton dawsonii*, Banks (1975)
  - *P. princeps*, Dawson (1859)
  - *P. forbesii*, Gensel (1979)
  - *Pertica varia*, Granoff et al. (1976)
  - *Pertica sp.*, Doran et al. (1978)
  - *Trimerophyton robustius*, Hopping (1956)

F.1.2 List of permineralized taxa discovered in the Battery Point Formation

- *Eddianna gaspiana*, rhyniopsida (Pfeiler & Tomescu, 2018)
- *Crenaticaulis verruculosus*, zosterophyll (Banks & Davis, 1969)
- *Franhueberia gerriennei*, euphyllophyte (Hoffman & Tomescu, 2013)
- *Leptocentroxyla tetrarcha*, euphyllophyte (Bickner & Tomescu, 2019)
- *Stenoloboxyla ambigua*, euphyllophyte (Bickner & Tomescu, 2019)
- *Jowingera triloba*, euphyllophyte (Bickner & Tomescu, 2019)
- *Tainioxyla quebecana*, euphyllophyte (Bickner & Tomescu, 2019)
- *Perplexa praestigians* (Pfeiler & Tomescu, 2023)
- *Kenrickia bivena*, euphyllophyte (Toledo et al., 2021)
- *Wilhovia phocarum*, euphyllophyte (Gensel, 2022)
- *Psilophyton dawsonii*, ephyllophyte (Banks, 1975)
- *Gmujij teraxylopteroides*, euphyllophyte (Pfeiler & Tomescu, 2021)
- *Nebuloxyla mikmaquiana*, euphyllophyte (Lalica & Tomescu, 2023)
- *Adelocladoxis praecox*, cladoxylopsid (Durieux et al., 2021)

F.2 Supplementary table

Table F.1: Summary of all the zosterophyll species known in the Battery Point Formation

Species name	Preservation type	Reference
Bathurstia sp.	Compression	(Hotton et al., 2001)
Creanticaulis verruculosus	Compression and anatomy	(Banks & Davis, 1969)
Sawdonia ornata	Compression	(Gensel & Berry, 2016)
??*Sawdonia acanthotheca*	Compression	(Gensel et al., 1975)
Zosterophyllum sp.	Compression	(Hotton et al., 2001)

F.3 Scripts

```
library(ggplot2)
library("dplyr")

TS <- read.table("Tracheid_size", header=T)
TS <- (arrange(TS, TS$Tracheid_size))
anat <- read.table("anat_zostero_BFP.txt", header=T)
```

```
# Maximum tracheid size distribution of the sampling

MTS <- c(46.872,)

boxplot <- ggplot(TS, aes(x= reorder(TS$Specimen_nb, TS$Tracheid_size
    ), y= TS$Tracheid_size)) + geom_boxplot() +
theme_light() +
theme(axis.text.x = element_text(angle = 90)) +
geom_hline(yintercept=37, color="gray87", linewidth = 1) +
annotate("text", x = 3, y = 38, label = "Crenaticaulis verruculosus")
     +
#  geom_hline(yintercept=65) +
#  geom_hline(yintercept=140) +
geom_hline(yintercept=50, color="gray87", linewidth = 1) +
annotate("text", x = 3, y = 51, label = "Gosslingia +
    Trichopherophyton") +
#  geom_hline(yintercept=99) +
#  geom_hline(yintercept=77) +
geom_hline(yintercept=60, color="gray87", linewidth = 1) +
annotate("text", x = 3, y = 61, label = "Sawdonia deblondii") +
#  geom_hline(yintercept=100) +
# geom_hline(yintercept=149) +
geom_hline(yintercept=40, color="gray87", linewidth = 1) +
annotate("text", x = 3, y = 41, label = "Thrinkophyton formosum") +
geom_hline(yintercept=50, color="gray87", linewidth = 1) +
geom_hline(yintercept=42, color="gray87", linewidth = 1) +
annotate("text", x = 3, y = 43, label = "Ventarura lyonii") +
geom_hline(yintercept=25, color="gray87", linewidth = 1) +
annotate("text", x = 10, y = 26, label = "Zosterophyllum fertile") +
geom_hline(yintercept=23, color="gray87", linewidth = 1) +
annotate("text", x = 10, y = 24, label = "Zosterophyllum llanoveranum
    ") +
xlab("Gaspe specimens") +
ylab("Maximum tracheid size") +
labs(title = "Distribution of maximum tracheid size among the Gaspe
    specimens")

boxplot +  geom_point(data = anat, aes(x=anat$Zosterophyll,y=
    anat$Max_trach_size), color="red") +
geom_jitter(width = 0.15)

# Maximum tracheid size compared to xylem size

anat <- read.table("anat_zostero_BFP.txt", header=T)

ggplot(anat, aes(x = anat$Xylem_strand_size, y=
    anat$Corrected_tracheid_size)) +
geom_point(color= "orange", size = 3) +
geom_point(aes(x=350, y= 37), size = 3) +
```

```
annotate("text", x = 410, y = 36, label = "Crenaticaulis verruculosus
    ") +
geom_point(aes(x=560, y= 65), size = 3) +
annotate("text", x = 561, y = 63, label = "Deheubarthia splendens") +
geom_point(aes(x=625, y= 140), size = 3) +
annotate("text", x = 626, y = 138, label = "Euthursophyton
    hamperbachense") +
geom_point(aes(x=260, y= 50), size = 3) +
annotate("text", x = 350, y = 51, label = "Gosslingia breconensis") +
geom_point(aes(x=500, y= 99), size = 3) +
annotate("text", x = 501, y = 97, label = "Konioria andrychoviensis")
     +
geom_point(aes(x=370, y= 60), size = 3) +
annotate("text", x = 371, y = 58, label = "Sawdonia deblondii") +
geom_point(aes(x=300, y= 100), size = 3) +
annotate("text", x = 251, y = 98, label = "Sawdonia ornata") +
geom_point(aes(x=590, y= 149), size = 3) +
annotate("text", x = 591, y = 147, label = "Stolbergia spiralis") +
geom_point(aes(x=375, y= 40), size = 3) +
annotate("text", x = 376, y = 39, label = "Thrinkophyton formosum") +
geom_point(aes(x=216, y= 50), size = 3) +
annotate("text", x = 150, y = 52, label = "Trichopherophyton
    teuchansii") +
geom_point(aes(x=1860, y= 42), size = 3) +
annotate("text", x = 1751, y = 41, label = "Ventarura lyonii") +
geom_point(aes(x=110, y= 25), size = 3) +
annotate("text", x = 150, y = 24, label = "Zosterophyllum fertile") +
geom_point(aes(x=250, y= 23), size = 3) +
annotate("text", x = 251, y = 22, label = "Zosterophyllum
    llanoveranum") +
theme_light() +
xlab("Xylem strand size") +
ylab("Maximum tracheid size") +
labs(title = "Distribution of maximum tracheid size through the xylem
     strand among the Gaspe specimens")

#close up on the species that have the same range as the sampling

ggplot(anat, aes(x = anat$Xylem_strand_size, y=
    anat$Corrected_tracheid_size)) +
geom_point(color= "orange", size = 3) +
geom_point(aes(x=350, y= 37), size = 3) +
annotate("text", x = 351, y = 36, label = "Crenaticaulis verruculosus
    ") +
geom_point(aes(x=260, y= 50), size = 3) +
annotate("text", x = 300, y = 49, label = "Gosslingia breconensis") +
geom_point(aes(x=375, y= 40), size = 3) +
annotate("text", x = 376, y = 39, label = "Thrinkophyton formosum") +
geom_point(aes(x=216, y= 50), size = 3) +
```

```
annotate("text", x = 200, y = 49, label = "Trichopherophyton
    teuchansii") +
geom_point(aes(x=110, y= 25), size = 3) +
annotate("text", x = 130, y = 24, label = "Zosterophyllum fertile") +
geom_point(aes(x=250, y= 23), size = 3) +
annotate("text", x = 251, y = 22, label = "Zosterophyllum
    llanoveranum") +
theme_light() +
xlab("Xylem strand size") +
ylab("Maximum tracheid size") +
labs(title = "Distribution of maximum tracheid size through the xylem
     strand among the Gaspe specimens")
```

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Characterization, diversification, and evolution of the Silurian-Devonian plant group Zosterophyllopsida

Abstract

The Silurian-Devonian group of plants Zosterophyllopsida is the scope of the present essay. Because of their key position as the dominant group of plants at the onset of land plant diversification, the study and understanding of their evolutionary history is crucial. Moreover, numerous recent discoveries enriched our knowledge about this group, and Zosterophyllopsida appears today more complex than ever. With this complexity and diversity rises uncertainty, and previous statements about Zosterophyllopsida need to be reviewed under the light of these new discoveries. By exploring different aspects of Zosterophyllopsida's evolution (systematic, temporal, geographic), this PhD is the first review of the group at a global scale. Results support previous statements about their relationships and diversity, and showcase the impact of regionalism on the group's evolution. Some, but not all Zosterophyllopsida are closely related to the Lycopsida, and both are regrouped together into a clade named Lycophytina. The studied group is thus paraphyletic, and refers to the stem-group Lycophytina. This stem group is particularly abundant during the Pragian, went through a first phase of extinction during the Emsian, and some zosterophylls members survived until the end of the Devonian. Lastly, it has been showed that a geographical distribution structures the tree. While the origin of the group seems to be from Gondwana, a Laurussian divergent line bears derived and unique characteristics like emergences or circination.

Keywords: evolution, Devonian, dispersion, diversity, phylogeny, zosterophylls

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Caractérisation, diversification et évolution du groupe de plantes Siluro-Devonien Zosterophyllopsida

Résumé

Le groupe de plantes Siluro-Devonien Zosterophyllopsida est le modèle d'étude de cette thèse. Il est en effet considéré comme le groupe dominant durant cette période, marquée par les premières diversifications des plantes terrestres. Ainsi, comprendre l'histoire évolutive d'un tel groupe est crucial pour comprendre les dynamiques mises en place durant cette période. De plus, les connaissances ont été enrichies par de nombreuses découvertes récentes, et Zosterophyllopsida revèle une complexité jusqu'alors insoupçonnée. Cette augmentation de la complexité et de la diversité va de pair avec une incertitude croissante, et les précédentes observations faites sur le groupe doivent être révisées et consolidées. Cette thèse se présente donc comme une étude globale du groupe, abordant divers aspects de leur évolution (systématique, temporel, géographique). Les résultats sont concordants avec des travaux précédents concernant leur phylogénie et leur diversité, mais mettent également en avant l'impact de leur distribution spatiale sur leur évolution. Certains Zosterophyllopsida sont ainsi proche des Lycopsida, mais tous sont regroupés ensemble au sein du clade Lycophytina. Ainsi, le groupe d'étude est paraphylétique, et référé comme groupe souche Lycophytina. C'est un groupe particulièrement abondant durant le Pragien, puis après une première chute de la diversité à l'Emsien, n'est représenté que par quelques membres jusqu'à la fin du Dévonien. Enfin, les résultats montrent une distribution géographique au sein de l'arbre. En effet, l'origine du groupe semble provenir du Gondwana, puis une lignée Laurussienne diverge rapidement, portant des caractéristiques dérivées uniques tel que les émergences et la circination.

Mots clés : évolution, Dévonien, diversité, dispersion, zosterophylles

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