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Systematics and evolution of cladoxylopsids: a consequential yet underappreciated tracheophyte group with a deep fossil history

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Abstract

The cladoxylopsids are the first of the major euphyllophyte groups recognized in Middle Devonian and younger floras to acquire individuality from among a plexus of simple Early Devonian euphyllophytes. The first plants to evolve arboreous growth habits were members of this group, which has also been hypothesized to lie at the origin of ferns and equisetophytes. However, despite such multifaceted importance, and despite having been first recognized more than one-and-a-half centuries ago and subsequently documented from Early Devonian to Mississippian localities worldwide, our understanding of the cladoxylopsid clade is still quite incomplete. Nevertheless, the last 30 yr have seen consequential discoveries that provided key insights on their development, architecture, and evolution. Our review of the cladoxylopsids, aimed at providing an entry point to the study of this particularly challenging group, addresses their taxonomic history and the current status and diversity of the different subgroups (iridopterids, and pseudosporochnalean and cladoxylalean cladoxylopsids); their geographic distribution across their stratigraphic range; and evolutionary trends in their stelar architecture and ultimate appendage morphology, position in the body plan and taxis, and their ontogeny and growth habits as formalized in architectural models. Reviewing all of these aspects led us to identify the main gaps in our understanding of cladoxylopsids and to formulate questions about the developmental and functional significance of their unique vascular system in relation to their morphologies, the evolutionary patterns of their reproductive organs, and the still unresolved phylogenetic relationships of the group with other major lineages of pteridophytes and lignophytes within the euphyllophytes.

Non-technical Summary

The cladoxylopsids are a group of Early Devonian to early Carboniferous plants known primarily for including the first species that grew as trees. They are also hypothesized to have given rise to the living horsetails and ferns and, thus, hold the key to understanding the deep evolutionary history and relationships of these groups. Despite these aspects of evolutionary importance and the fact that the group was recognized more than one-and-a-half centuries ago, the study of cladoxylopsids poses challenges due to their complexity and (in some cases) size, and the group has consequently remained relatively understudied. Fossil discoveries and substantial progress in our understanding of the group over the last 30 years have nevertheless increased our knowledge of these plants in areas such as the diversity and evolution of their vascular tissue organization, lateral appendages, growth patterns and architecture; their geographic distribution over time; and the pattern of evolutionary relationships within the group. This review, aimed at providing an entry point to the study of this particularly challenging group, addresses their taxonomic history and the current status and diversity of the different subgroups (iridopterids, and pseudosporochnalean and cladoxylalean cladoxylopsids); their distribution across time and space; and evolutionary trends in their anatomy, morphology, and developmental patterns. Reviewing these aspects led us to identify the main gaps in our understanding of cladoxylopsids and to formulate a series of outstanding questions.

Introduction

The cladoxylopsids, a group of seed-free plants that range from the Early Devonian (Gerrienne, 1992; Durieux et al., 2021; Chu et al., 2024) into the early Carboniferous (Mississippian) (Bertrand, 1935; Durieux et al., 2026), are likely the most underappreciated major lineage of early Paleozoic tracheophytes. The Devonian period witnessed the first major tracheophyte radiation that gave rise to all of the major groups of the clade represented today—lycophytes, sphenophytes, ferns, and seed plants. During the Devonian, multiple lineages within these groups

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underwent broad diversification (Gensel and Berry, 2001; Toledo et al., 2018, 2021; Durieux et al., 2021) and evolved key structures, e.g., leaves (Tomescu and Whitewoods, 2024), seeds (Gerrienne et al., 2004), deep rooting systems (Morris et al., 2015), and woody axes (Gerrienne et al., 2011; Hoffman and Tomescu, 2013). Among all of these lineages and evolutionary innovations, it has recently become apparent that cladoxylopsids were the first group to acquire a distinct identity, from a morphological standpoint, from among the diverse plexus of early euphyllophytes present in the Early Devonian floras. Something that has not been emphasized enough is that subsequent to their early rise, in a geologically short span of time (~20 Myr), the cladoxylopsids reached impressive taxonomic diversity and a level of morphological disparity paralleled only much later in a few other lineages (Durieux et al., 2021; Chu et al, 2024). They are also the first euphyllophyte group to have evolved tall statures (arboreousness), by the Middle Devonian (Goldring, 1927; Berry and Fairon-Demaret, 2002; Stein et al., 2007; Meyer-Berthaud et al., 2010; Giesen and Berry, 2013; Davies et al., 2024). Additionally, specific groups among the cladoxylopsids are thought to have represented the ancestral stocks from which ferns and equisetophytes evolved (Skog and Banks, 1973; Stein et al., 1984; Kenrick and Crane, 1997; Rothwell, 1999). Yet, for all their multifaceted importance, cladoxylopsids have been typically sidelined, if not downright ignored, in discussions of euphyllophyte evolution —'neontological' studies rarely mention, let alone thoroughly consider, their presumably crucial connections to living lineages. In addition, on the paleobotanical realm, no targeted phylogenetic studies have to date addressed deliberately and thoroughly their position among the diverse living and extinct euphyllophyte lineages. This is at least in part due to their autapomorphies—they are unlike any of the other groups that succeeded them in plant history —and to the complexity of the organization of these plants. Together, these features make the cladoxylopsids a daunting group to study, especially given the fragmentary state of plant fossils that offer only partial glimpses into the structure of any given species, greatly hindering holistic understanding of these complex plants. Our review of the diversity, structure, systematics, and evolution of cladoxylopsids aims to provide a baseline and framework for addressing the key evolutionary questions raised by this old and important group.

Describing and classifying cladoxylopsid diversity

Early work. The first report of a cladoxylopsid was published by Unger in 1854, and based on it, Unger created the order Cladoxyleae. The diagnosis of the group, which Unger provided later in his 1856 study (p. 178), stated that the plants would be mostly trees and, more importantly for the subsequent studies, that the plants possessed multiple vascular bundles that can fuse or divide along their course through the axes and can be aligned radially around a parenchymatous central zone. In these pioneering studies, Unger (1854, 1856) also defined the first cladoxylopsid genus, *Cladoxylon* Unger, 1856, with three species (*Cladoxylon mirabile* Unger, 1856; *Cladoxylon dubium* Unger, 1856; and *Cladoxylon centrale* Unger, 1856), and provided the first reports of two other species that were later included in the genus as *Cladoxylon radiatum* Bertrand, 1935 and *Cladoxylon taeniatum* Solms-Laubach, 1896 (see Bertrand, 1935).

The decades that followed Unger's publications saw work on the taxonomy of the group, which led to the Cladoxyleae being renamed as order Cladoxylales (Hirmer, 1927) and finally as class Cladoxylopsida (Pichi-Sermolli, 1959). This class (i.e., Cladoxylopsida sensu lato; Berry and Stein, 2000) today includes the orders Iridopteridales and Pseudosporochnales, as well as several taxa referred to as nonpseudosporochnalean cladoxylopsids (Y. Wang and Berry, 2006; Meyer-Berthaud et al., 2007). The main strokes of this system of classification have recently received support from phylogenetic studies (Durieux et al., 2021; Chu et al., 2024), which have refined it by identifying grades and clades within the cladoxylopsids s.l.

The Cladoxylopsida and its subdivisions have been defined since their establishment primarily on anatomical criteria. However, Skog and Banks (1973) first proposed morphological criteria for distinguishing the Iridopteridales. Much earlier, Potonié and Bernard (1904) provided the first comprehensive description of the morphology of a representative of Pseudosporochnales, *Pseudosporochnus krejcii* Potonié and Bernard, 1904. In that study, they described the genus based on their own specimens and material described earlier by Stur (1882), who had interpreted them as algae. However, the first association of morphological criteria to species with cladoxylopsid anatomy only occurred in the 1960s, by Leclercq and Banks (1962) for *Pseudosporochnus* Potonié and Bernard, 1904 and Leclercq and Schweitzer (1965) for *Calamophyton* Kräusel and Weyland, 1926.

Current diversity and classification. The three groups currently included in the cladoxylopsids s.l.—the Iridopteridales, the Pseudosporochnales (pseudosporochnalean cladoxylopsids), and the cladoxylalean (nonpseudosporochnalean) cladoxylopsids—can be defined based on anatomical and morphological criteria. Their relationships have been revised in the latest phylogenetic studies (Durieux et al., 2021; Chu et al., 2024), which were conducted under the as yet untested assumption that the cladoxylopsids s.l. are monophyletic.

Iridopteridales. Erected by Stein (1982), the group includes the former Ibykales (Skog and Banks, 1973) and Iridopteridineae (Arnold, 1940). Historically, the group has been characterized by the following anatomical criteria (which, however, have not been documented in all the species included; see Table 1): (1) a deeply ribbed (lobed) actinostele with protoxylem strands exclusively at the rib tips; (2) nodes bearing (potentially) two types of lateral appendages, both of which are (3) supplied by single vascular traces diverging from a single lobe; (4) whorled organotaxis; and (5) metaxylem tracheid size decreasing toward the periphery of the xylem (Stein, 1982; Berry and Stein, 2000; Cordi and Stein, 2005; Meyer-Berthaud et al., 2007; Berry et al., 2022). In terms of morphology, iridopterids are characterized by ultimate appendages with three-dimensional dichotomous branching and recurved tips and ellipsoidal sporangia borne at the tips of ultimate appendage segments (Stein, 1982; Berry et al., 2022).

According to the latest review of the group (Berry et al., 2022) and phylogenetic studies (Durieux et al., 2021; Chu et al., 2024), the Iridopteridales currently include seven genera encompassing nine species (see Supplementary Data 1 and corresponding references in Supplementary Data 2): *Asteropteris noveboracensis* Dawson, 1881; *Arachnoxylon kopfii* Read, 1938; *Arachnoxylon minor* Stein et al., 1983; *Iridopteris eriensis* Arnold, 1940; *Ibyka amphikoma* Skog and Banks, 1973, emend. Berry et al., 2022; *Ibyka vogtii* (Høeg, 1942) Berry, 2005; *Compsocradus laevigatus* Berry and Stein, 2000; *Compsocradus givetianus* Fu et al., 2011; and *Anapaulia moodyi* Berry and Edwards, 1996. In addition, five satellite genera encompassing six species have been considered as closely related or belonging to the Iridopteridales: *Rotoxylon dawsonii* Cordi and Stein, 2005; *Hyenia sphenophylloides* Nathorst, 1915 (according to Berry et al., 2022); *Hyenia banksii* Arnold, 1941 (according to Berry et al., 2022);

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Table 1. Iridopteridales species and characters traditionally defining the group

Species	Type of stele	Permanent protoxylem at rib tips exclusively	Whorled organotaxis (UA or/and branches)	Two type of laterals per node	One vascular trace per lateral emission	Metaxylem tracheids smaller toward the periphery	Spines	3D dichotomous ultimate appendages	Recurved tips of UA	Sporangium shape	References
Anapaulia moodyi Berry and Edwards, 1996	Unknown	Unknown	Yes	Yes	Unknown	Unknown	Yes	Yes/No, planated	Yes	Ellipsoidal	Berry and Edwards, 1996
Arachnoxylon minor Stein et al., 1983	Actinostele	Yes	Yes	Yes	Yes	No	Unknown	Unknown	Unknown	Unknown	Stein et al., 1983
Arachnoxylon kopfii Read, 1938 (according to Stein*)	Actinostele	Yes	Yes	Yes	Yes	No	Unknown	Unknown	Unknown	Unknown	*Stein et al., 1983
Arachnoxylon kopfii Read, 1938 (according to Read†)	Actinostele	Yes	Yes	Yes	Yes	No	Unknown	Unknown	Unknown	Unknown	Arnold, 1935; †Read, 1938; Stein, 1981; Stein et al., 1983
Asteropteris noveboracensis Dawson, 1881	Actinostele	Yes	(?) Yes	(?) Yes	Yes	No	Unknown	Unknown	Unknown	Unknown	Bertrand, 1913
Compsocradus laevigatus Berry and Stein, 2000	Actinostele	Yes	Yes	Yes	Yes	Yes	No	Yes	Yes	Obovate	Berry and Stein, 2000
Compsocradus givetianus Fu et al., 2011	Unknown	Unknown	Yes	Yes	Unknown	Unknown	No	Yes	Yes	Eliptical	D. Wang, 2008; Fu et al., 2011
Ibyka amphikoma Skog and Banks, 1973, emend. Berry et al., 2022	Actinostele	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes	Obovate	Skog and Banks, 1973; Berry et al., 2022
Ibyka vogtii (Høeg, 1942) Berry, 2005	Unknown	Unknown	Yes	Yes	Unknown	Unknown	Yes	Yes	No/Unclear	Unknown	Berry, 2005
Iridopteris eriensis Arnold, 1940	Actinostele	Yes	Yes	Yes	Yes	Yes	No	Unknown	Unknown	Unknown	Stein, 1982
Rotoxylon dawsonii Cordi and Stein, 2005	Partly dissected stele	Yes	Yes	No	Yes (if each trace vascularizes a single lateral)	Yes	Unknown	Unknown	Unknown	Unknown	Cordi and Stein, 2005
Serripteris feistii Rowe and Galtier, 1989	Actinostele	Yes	No	No	Yes	No	Unknown	Unknown	Unknown	Unknown	Rowe and Galtier, 1989
Keraphyton mawsoniae Champreux et al., 2020	Actinostele	Yes but exarch to mesarch	Unknown	Unknown	Unknown	Yes	Unknown	Unknown	Unknown	Unknown	Champreux et al., 2020
Hyenia sphenophylloides Nathorst, 1915	Unknown	Unknown	Yes	Yes	Unknown	Unknown	No	Only singled dichotomy reported	No (inferred from Nathorst‡)	Unknown	‡Nathorst, 1915; Høeg, 1931, 1935, 1945; Berry et al., 2021, 2022
Hyenia banksii Arnold, 1941	Unknown	Unknown	Yes	Yes	Unknown	Unknown	No	Not stated	No	Unknown	Arnold, 1941
Denglongia hubeiensis Xue and Hao, 2008, emend. Xue et al., 2010	Actinostele	Yes	Yes	No	Unknown	Yes	No	No, planated	No	Fusiform	Xue et al., 2010; Xue and Hao, 2008

Keraphyton mawsoniae Champreux et al., 2020; *Serripteris feistii* Rowe and Galtier, 1989; and *Denglongia hubeiensis* Xue and Hao, 2008, emend. Xue et al., 2010. Although the latest phylogenetic studies have not included *Keraphyton* Champreux, Meyer-Berthaud, and Decombeix, 2020 and *Hyenia* Nathorst, 1915, they recovered *Serripteris* Rowe and Galtier, 1989 and *Denglongia* Xue and Hao, 2008, emend. Xue et al., 2010 as a grade transitional between the Iridopteridales and the other cladoxylospid, and *Rotoxylon* Cordi and Stein, 2005 as a cladoxylopsid sensu stricto (Durieux et al., 2021; Chu et al., 2024). In these studies, the Iridopteridales have been recovered as a paraphyletic grade consisting of two clades: an *Ibyka-Anapaulia* clade and a 'core iridopterids' clade, with epidermal extensions and whorled taxis of the ultimate appendages, respectively, as synapomorphies (see Berry et al., 2022 for a different viewpoint).

Cladoxylopsids sensu stricto. The broad group of cladoxylopsids s.s. includes taxa that are not placed in the Iridopteridales or are satellite to that order. This term was first used to replace the traditional Pseudosporochnales after a group referred to as nonpseudosporochnalean cladoxylopsids was segregated from the latter by Y. Wang and Berry (2006) and Meyer-Berthaud et al. (2007). The first hint of the existence of nonpseudosporochnalean cladoxylopsids, not named as such at the time, was provided by Cordi and Stein (2005), who recognized that some taxa (e.g., *Pietzschia* Gothan, 1927; *Metacladoxylon* Z. Wang and Geng, 1997; and *Cladoxylon*) display combinations of characters from both iridopterids and pseudosporochnaleans. Both the Pseudosporochnales and the nonpseudosporochnalean cladoxylopsids have been recovered as monophyletic in the latest phylogenetic studies, in which the latter are referred to as cladoxylalean cladoxylopsids (Durieux et al., 2021; Chu et al., 2024).

The cladoxylopsids s.s. possess deeply lobed and dissected steles with mesarch protoxylem strands located either only at the rib tips, or at the tips as well as along the midplanes of the ribs. Their nodes bear a single type of lateral that is vascularized by traces diverging from multiple xylem ribs (Meyer-Berthaud et al., 2007; Durieux et al., 2021).

Pseudosporochnales. This order, erected by Emberger (1944), currently includes four genera with 11 species (Supplementary Data 1): five species of *Pseudosporochnus*; three species of *Calamophyton* (Weyland, 1925); *Lorophyton goense* Fairon-Demaret and Li, 1993; and two species of *Wattieza* Stockmans, 1968. In addition, the genera *Eospermatopteris* Goldring, 1924 and *Duisbergia* Kräusel and Weyland, 1929 represent the trunk of *Wattieza* and *Calamophyton*, respectively (Stein et al., 2007; Giesen and Berry, 2013). The Early Devonian *Adelocladoxis praecox* Durieux et al., 2021 was recovered as sister to this clade (Durieux et al., 2021) or in a polytomy with the pseudosporochnalean and cladoxylalean clades (Chu et al., 2024). Pseudosporochnalean cladoxylopsids are characterized by the presence of digitately dissected branches (not present in the juvenile specimen of *Lorophyton* Fairon-Demaret and Li, 1993) and regularly arranged sclerenchymatous groups in the cortex, which were recovered as a synapomorphy of the clade. They also possess an irregular arrangement of the ultimate appendages, which are not recurved at the tips, and can be either entirely dichotomous or consisting of a main axis that bears alternate to whorled dichotomous units (Berry and Fairon-Demaret, 1997; Berry, 2000; Y. Wang and Berry, 2006; Meyer-Berthaud et al., 2007).

Cladoxylalean cladoxylopsids. This group, initially referred to as nonpseudosporochnalean cladoxylopsids (Y. Wang and Berry, 2006; Meyer-Berthaud et al., 2007; Durieux et al., 2021), include six genera with 18 species: *Panxia gabata* (Y. Wang and Berry, 2006) emend. Xue et al., 2016; *Rhipidophyton acanthum* Berry and Wang, 2006; *Polypetalophyton wufengenis* (Geng, 1995) emend, Hilton et al., 2003; four species of *Pietzschia*; nine species of *Cladoxylon*; and two species of *Polyxylon* (Read and Campbell, 1939) emend. Chambers and Regan, 1986. Phylogenetic analyses by Durieux et al. (2021) and Chu et al. (2024) have also included in the clade *Metacladophyton ziguinum* (Z. Wang and Geng, 1997) emend. D. Wang and Lin, 2007 (note that *Metacladoxylon tetraxylum* Z. Wang and Geng, 1997 was not included in those analyses); *Rotoxylon dawsonii*; *Rhymokalon trichium* Scheckler, 1975; *Xenocladia medullosina* Arnold, 1940 (Arnold, 1952); and *Paracladoxylon kespekianum* Chu, Durieux, and Tomescu, 2024. As mentioned above, this group possesses a combination of iridopteridalean and pseudosporochnalean characters (Table 2). Its members seem to possess a main axis with dissected stele bearing planar branching systems (Y. Wang and Berry, 2006), recognized as a synapomorphy for the clade including *Panxia* (Y. Wang and Berry, 2006) emend. Xue et al., 2016, *Polyxylon*, and *Pietzchia* (Durieux et al., 2021). In addition, their ultimate appendages, when known, seem to be pseudomonopodial, with a 'central axis' bearing alternately/oppositely arranged dichotomous units (Z. Wang and Geng, 1997; Hilton et al., 2003; Y. Wang and Berry, 2006; Durieux et al., 2026). The 'central axes' of the ultimate appendages have bilateral symmetry and abaxial-adaxial polarity (known in *Cladoxylon taeniatum* [see Durieux et al., 2026], *Metacladoxylon tetraxylum* [see Z. Wang and Geng, 1997]; bilateral symmetry in *Cladoxylon waltoni* Long, 1968 and *Cladoxylon radiatum*). Notably, none of them show evidence of two types of lateral per node or sclerotic nests in the outer cortex (Table 2).

Taxa incertae sedis. The classification outlined above is corroborated from published taxonomic placements and those derived from our own inferences, with or without phylogenetic support. However, there remain several taxa with unresolved exact placement. *Xinicaulis lignescens* Xu et al., 2017 and *Jerana modica* Meyer-Berthaud et al., 2024 are two such cladoxylopsids incertae sedis: they can be assigned to the cladoxylopsids s.s. based on their dissected steles, but further taxonomic precision has not been provided in their descriptions, and they have not yet been included in any phylogenetic study. Nevertheless, in the case of *Jerana* Meyer-Berthaud et al., 2024, its numerous similarities with *Pietzschia* suggest that it is a cladoxylalean cladoxylopsid. *Astralocaulis* Hueber, 1971 (see Harris, 1929) was hypothesized to represent part of the root system attached to the stem of an arborescent cladoxylopsid s.s. (Soria and Meyer-Berthaud, 2004). *Dixopodoxylon goense* Fairon-Demaret, 1969 might also represent a cladoxylopsid root, based on its similarity with *Pietzschia* roots (Soria and Meyer-Berthaud, 2004). *Voelkelia refracta* Solms-Laubach, 1896 and *Stenoxylon ludwigii* Solms-Laubach, 1910 can also be included among the cladoxylopsids s.s. based on their dissected stele (see Bertrand, 1935). However, information on these species is so scarce that they will not be included in our discussions further. This also applies to '*Chiasmoxylon hueberii*' Sebby, 1972, a taxon that has some iridopterid characters but has only been reported in an unpublished doctoral dissertation by Sebby (1972). Two Early Devonian plants, *Foozia minuta* Gerrienne, 1992 and *Protohyenia janovii* Ananiev, 1957 (Ananiev and Zakharova, 1986) have been assigned to the cladoxylopsids s.l. based primarily on morphological criteria (see below), but their more precise affinities within the group are not resolved.

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Table 2. Cladoxylalean cladoxylopsids and comparisons using characters traditionally defining pseudosporochnaleans and iridopteridaleans. UA = ultimate appendages

Species	Stele type	Digitate branching or dichotomy of dissected radial stele	Sclerotic nests	Lateral planation/ Bilateral symmetry/ Abaxial-adaxial polarity	Irregular taxis of the of the UA	Whorled organotaxis (branch or/and UA)	Metaxylem tracheids smaller toward the periphery	Recurvation of the vegetative UA tips	References
Typical pseudosporochnalean	Dissected stele	Yes, digitate branching	Yes	Yes, digitate branching	Yes	No	Unclear	No	See Current diversity and classification
Typical iridopteridalean	Actinostele	No	No	None	No	Yes	Yes	Yes	See Current diversity and classification
Cladoxylon mirabile Unger, 1856	Irregulary dissected stele	Unknown/Yes if *Hierogramma* dichotomous	No but sclerotic tissue between ribs	Yes, likely bilateral '*Hierogramma*'	Unknown	No	No	Unknown	Unger, 1856; Bertrand, 1935; Durieux et al., 2026
Cladoxylon radiatum Bertrand, 1935	Irregulary dissected stele	Unknown/Yes if *Hierogramma* dichotomous	No	Yes, bilateral '*Hierogramma*'	Unknown	No	No	Unknown	Unger, 1856; Bertrand, 1935; Taylor et al., 2009
Cladoxylon taeniatum Solms-Laubach, 1896	Dissected stele	Unknown/Yes if *Hierogramma* dichotomous	No	Yes, UA with abaxial-adaxial polarity	No	No	No	Unknown	Unger, 1856; Bertrand, 1935; Galtier, 1970; Durieux et al., 2026
Cladoxylon solmsi Bertrand, 1935	Dissected stele	Unknown/Yes if *Hierogramma* dichotomous	Unknown	Yes, abaxial-adaxial vascular traces	Unknown	No	Unclear	Unknown	Bertrand, 1935
Cladoxylon bakrii Mustafa, 1978b	Dissected stele	Unknown	Yes	Unknown	Unknown	Unknown	No	Unknown	Mustafa, 1978b
Cladoxylon kidstoni Solms-Laubach, 1910	Dissected stele	Not found	Not found	Not found	Not found	Not found	Not found	Not found	Solms-Laubach, 1910
Cladoxylon waltoni Long, 1968	Actinostele to dissected stele	Unknown/Yes if *Hierogramma* dichotomous	No	Yes, bilateral vascular trace. Abaxial-adaxial stele	No	No	No	Unknown	Long, 1968
Cladoxylon edromense Long, 1987	Partially dissected stele	Unknown	No	Abaxial-adaxial stele	No	No	No	Unknown	Long, 1987
Cladoxylon tanaiticum Solms-Laubach, 1896	Dissected stele	Unknown/Yes if *Hierogramma* dichotomous	No (inferred from Snigirevsky and Lyubarova*)	Unknown	Unknown	Unknown	Yes (inferred from Snigirevsky and Lyubarova*)	Unknown	Snigirevsky, 1992; *Snigirevsky and Lyubarova, 2021
Metacladoxylon tetraxylum Z. Wang and Geng, 1997	Actinostele to dissected stele	No	No	Yes, branch with abaxial adaxial polarity	No	Yes	No	Yes	Z. Wang and Geng, 1997
Metacladophyton ziguinum (Z. Wang and Geng, 1997, emend. D. Wang and Lin, 2007	Actinostele to dissected stele	No	No	Yes, potential dichotomy of the UA in the same plane	Yes, on first order/ No, on second order axis	Yes	Yes	Yes	D. Wang and Lin, 2007

(*Continued*)

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Table 2. (*Continued*)

Species	Stele type	Digitate branching or dichotomy of dissected radial stele	Sclerotic nests	Lateral planation/ Bilateral symmetry/ Abaxial-adaxial polarity	Irregular taxis of the of the UA	Whorled organotaxis (branch or/and UA)	Metaxylem tracheids smaller toward the periphery	Recurvation of the vegetative UA tips	References
Panxia gabata (Y. Wang and Berry, 2006) emend. Xue et al., 2016	Irregulary dissected stele	Yes, potential anisotomy of a disected radial stele	No	Yes, planated branching system	No	No	Yes	Yes	Y. Wang and Berry, 2006; Xue et al., 2016
Paracladoxylon kespekianum Chu, Durieux, and Tomescu, 2024	Irregulary dissected stele	Unknown	No	Yes, UA with abaxial adaxial polarity	No	Yes	Yes	Unknown	Chu et al., 2024
Pietzschia polyupsilon (Read and Campbell, 1939) emend. Soria and Meyer-Berthaud, 2003	Dissected stele	Unknown	No but sclerotic tissue between ribs and centraly	Yes, abaxial-adaxial vascular traces	Unknown	Yes	Yes	Unknown	Read and Campbell, 1939; Soria and Meyer-Berthaud, 2003
Pietzschia levis Soria, Meyer-Berthaud, and Scheckler, 2001	Dissected stele	Unknown	No but sclerotic tissue between ribs	Yes, abaxial-adaxial vascular traces	Unknown	No	Yes	Unknown	Soria et al., 2001; Soria and Meyer-Berthaud, 2004
Pietzschia schulleri Gothan, 1927	Dissected stele	Unknown	No but sclerotic tissue between ribs	Yes, abaxial-adaxial vascular traces	Unknown	Yes	Yes	Unknown	Gothan, 1927; Soria and Meyer-Berthaud, 2005
Pietzschia timanica Lepechina, 1968	Dissected stele	Not found	Not found	Not found	Not found	Not found	Not found	Not found	Lepechina, 1968
Polypetalophyton wufengensis (Geng, 1995) emend, Hilton et al., 2003	Dissected stele	No	No	Yes, UA with abaxial-adaxial polarity (Fig 10)	No	No	No	No	Hilton et al., 2003
Polyxylon australe (Chambers and Regan, 1986) emend. Meyer-Berthaud et al., 2007	Dissected stele	Unknown	No	Yes, abaxial-adaxial vascular traces	Unknown	Yes	Yes	Unknown	Chambers and Regan, 1986; Meyer-Berthaud et al., 2007
Polyxylon elegans Read and Campbell, 1939	Dissected stele	Unknown	No	Unknown	Unknown	Unknown	No†	Unknown	Read and Campbell, 1939; †Meyer-Berthaud et al., 2007
Rhipidophyton acanthum Berry and Wang, 2006	Unknown	Yes (potential digitate branching)	No	No, in sterile branches/ Yes, in fertile UA (adaxial sporangia)	No	No	Unknown	Yes	Berry and Wang, 2006
Rhymokalon trichium Scheckler, 1975	Actinostele (central part with parenchyma and tracheids)	Unknown	No	No	Unknown	No	No	Unknown	Scheckler, 1975
Xenocladia medullosina Arnold, 1940	Dissected stele	Unknown	No but high amounth of sclerenchyma in outer cortex surounding the dissected stele	Unknown	Unknown	Unknown	No	Unknown	Arnold, 1940, 1952; Mustafa, 1980; Lemoigne and Iurina, 1983

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Cladoxylopsids, the 'permanent protoxylem group,' and the moniliformopsid conundrum

In a seminal paper, Beck and Stein (1993) proposed a separation of Middle Devonian and younger actinostelic euphyllophytes into two groups, based on their protoxylem architecture. One of these, the 'radiate protoxylem' group, was defined by multiple mesarch protoxylem strands located along the midplanes of the actinostele's xylem lobes plus one strand at the center of the xylem, with all protoxylem strands derived by branching and longitudinal divergence from the central protoxylem. Beck and Stein included in this group the Stenokoleales, early lignophytes (aneurophyte progymnosperms and early seed plants), and some taxa incertae sedis, e.g., *Gothanophyton* Remy and Hass, 1986, which they separated from a second group that included iridopterids, cladoxylopsids, and sphenopsids. They recognized this second group, the 'permanent protoxylem' group, by the lack of a central protoxylem strand and mesarch protoxylem strands located only at the tips of the actinostele's xylem lobes, with little or less conspicuous protoxylem present internally from those (Stein, 1993); the strands at the lobe tips only branched to produce protoxylem strands that departed into the traces to lateral appendages.

Subsequently, in a phylogenetic analysis that included four relevant taxa, Kenrick and Crane (1997) recovered the three genera belonging to the 'permanent protoxylem' group (*Ibyka* Skog and Banks, 1973, emend. Berry et al., 2022; *Pseudosporochnus*; *Rhacophyton* Crépin, 1875) forming a clade; and for the fourth one, the lignophyte (progymnosperm) *Tetraxylopteris* Beck, 1957—a member of the 'radiate protoxylem' group—forming a clade with the basal euphyllophyte *Pertica* Kasper and Andrews, 1972. These results were taken by Kenrick and Crane to provide support for Beck and Stein's separation of the 'permanent' and 'radiate protoxylem' groups, which they named the Moniliformopses and Radiatopses, respectively (although of their two radiatopsids, protoxylem architecture was documented only in *Tetraxylopteris* but not in *Pertica*, the anatomy of which remains unknown).

In discussing their results, Kenrick and Crane (1997) suggested that (1) their radiatopsid clade (*Pertica-Tetraxylopteris*) also includes the seed plants, due to their lignophyte clade membership alongside progymnosperms (*Tetraxylopteris*); and (2) their moniliformopsid clade (*Ibyka-Pseudosporochnus-Rhacophyton*) is a sphenopsid-fern clade (p. 241), with *Ibyka* more closely related to sphenopsids and *Pseudosporochnus* and *Rhacophyton* more closely related to the living ferns. However, Kenrick and Crane (1997) were also careful to point out (p. 241) that for solid support, the relationships that they recovered among early euphyllophytes would require a more detailed treatment than theirs, and (p. 139) that rigorous testing of their assumptions of close relationships between sphenopsids, living ferns, and the members of their moniliformopsid clade, and between the latter and their radiatopsids require more detailed analyses including a broader sampling of early fossil taxa. Indeed, no phylogenetic analysis to date has included all of the taxa discussed in Kenrick and Crane's (1997) hypothesis; the only analyses currently available have included only some of the taxa discussed there. A recent analysis by Rastier et al. (2025) has found support for a sister-group relationship between *Ibyka*—plus another iridopterid, *Compsocradus* (Berry and Stein, 2000) emend Fu et al., 2011—and the sphenopsid clade. However, that analysis focused on the evolution and systematics of sphenopsids and did not include *Rhacophyton* or any fern-grade taxon, to (1) test for the latter's relationships with *Pseudosporochnus*, and (2) test for the potential(ly disruptive) effects that the polarization of characters associated with inclusion of fern taxa would have on the pattern of relationships supported in their absence. Likewise, Rothwell's (1999) analysis that included *Cladoxylon* (a close relative of *Pseudosporochnus*, which was not included in that analysis) and *Rhacophyton* alongside living and extinct sphenopsids and ferns, recovered those two taxa in a clade that was more closely related to sphenopsids and, together with the latter, to the lignophytes, than they were to the living ferns. Thus, to date, Kenrick and Crane's (1997) hypothesis remains untested empirically, and it is still unclear how closely related iridopterids are to sphenopsids, and the pseudosporochnalean cladoxylopsids and the rhacophyte 'ferns' are to the living ferns. Therefore, the relationships between the fossil taxa that form the 'permanent protoxylem' group/moniliformopsids and the 'radiate protoxylem' group/radiatopsids, and different living euphyllophyte lineages remain unresolved to date due to an absence of studies deliberately focused on them.

For the cladoxylopsids s.l., a well-sampled study—i.e., including as outgroups representatives of multiple lineages of noncladoxylopsid euphyllophytes (e.g., rhacophyte, zygopterid and stauropterid 'ferns,' stenokolealeans, and lignophytes)—has yet to be conducted to test their monophyly, which has been taken for granted based on their membership in the 'permanent protoxylem' group/Moniliformopses. However, the 'permanent protoxylem'-'radiate protoxylem' group dichotomy is not as well defined as Beck and Stein (1993) saw it. On one hand, some cladoxylopsids have protoxylem strands also along the midplanes of the lobes of xylem, or strands located in a central position (Bertrand, 1935; Lemoigne and Iurina, 1983; Stein, 1993; Leclercq and Lele, 1968; Soria and Meyer-Berthaud, 2005; Chu et al., 2024), as in the radiatopsids; however, unlike in radiatopsids, the strands seem to have entirely independent trajectories and do not originate from each other by branching. On the other hand, some radiatopsids do not have a central protoxylem strand (May and Matten, 1983; Scheckler et al., 2006; Rothwell et al., 2022), as proposed in the definition of the group. All of these introduce uncertainty in the circumscription of the two groups, thus questioning their utility and validity—along with those of the radiatopsid and moniliformopsid concepts—as taxonomic or phylogenetic entities.

Despite the caveats outlined above, Kenrick and Crane's (1997) moniliformopsid concept was revisited, from a different perspective, by Pryer et al. (2001). Finding support in molecular data for a clade that included living ferns and *Equisetum* Linnaeus, 1753, to the exclusion of seed plants, Pryer et al. (2001) applied to that clade the same name—Moniliformopses (or moniliforms)—that Kenrick and Crane (1997) defined for the *Ibyka-Pseudosporochnus-Rhacophyton* clade. However, to date, it is still unclear how closely related iridopterids are to sphenopsids, and the pseudosporochnalean cladoxylopsids and the rhacophytalean 'ferns' are to the living ferns. The phylogenetic relationships between *Ibyka* and the sphenopsids (including *Equisetum*) have never been tested, and the only analyses that have included *Rhacophyton* and *Cladoxylon* (a close relative of *Pseudosporochnus*; Durieux et al., 2021) do not recover them in the same clade as the living ferns (Rothwell, 1999; Rothwell and Nixon, 2006). In other words, the relationships between *Ibyka*, *Pseudosporochnus*, and *Rhacophyton* on one hand, and the living ferns and *Equisetum* on the other hand, are either unexplored or not of close relatedness. Thus, it is unfortunate that the same name (Moniliformopses) has been used for two groups that are entirely different in terms of membership and not even closely related phylogenetically, based on current knowledge. Even more unfortunate is that forgoing any consideration of this situation, the plant systematics community in the 21st century has uncritically

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embraced Pryer et al.'s (2021) nomenclature, perpetuating the application of a name (Moniliformopses/moniliforms/monilophytes) to a group (living ferns and *Equisetum*) different from and not clearly related to that for which the name was formally defined.

Rise and spread of cladoxylopsids

Earliest cladoxylopsids. The earliest cladoxylopsids recognized to date are Emsian. The oldest of them, *Foozia minuta*, was described from the lower Emsian of Belgium based on adpressions with some cellular preservation in the xylem. Similar to *Foozia* Gerrienne, 1992, *Protohyenia janovii* (see Ananiev and Zakharova, 1986) is known from adpressions with cellular preservation in the xylem documented in the upper Emsian of southern Siberia (Russia). Both of these early representatives share xylem interpreted as multifasciculate (although it could have been just deeply lobed; see below), with tracheids bearing scalariform to circular bordered pits, and fine filiform lateral appendages more-or-less isotomously branched bearing terminal, paired fusiform sporangia. *Koeppenia eifeliensis* Schweitzer, 2000, an adpression from the lower Emsian of Germany, is very similar to both *Foozia* and *Protohyenia* Ananiev, 1957, even though it has not been discussed as a cladoxylopsid.

Two anatomically-preserved cladoxylopsids have been described from mid- to upper Emsian rocks in Quebec (Canada). One of them, *Adelocladoxis praecox* (see Durieux et al., 2021), is an actinostelic form with dichotomously branched filiform appendages bearing terminal fusiform sporangia (although it is unknown whether the sporangia were paired). The other one, *Paracladoxylon kespekianum* (see Chu et al., 2024) has complex dissected xylem and lateral appendages that might have had pseudomonopodial organization and dorsiventral polarity. Both *Adelocladoxis* Durieux et al., 2021 and *Paracladoxylon* Chu, Durieux, and Tomescu, 2024 have tracheids with circular bordered pits, and they are both recovered in phylogenetic analyses (Durieux et al., 2021; Chu et al., 2024) among the cladoxylopsids s.s. (and *Paracladoxylon* specifically as a cladoxylalean cladoxylopsid). The same rock layers that yielded *Adelocladoxis* and *Paracladoxylon* also host a few other forms of cladoxylopsid affinity that are currently studied by one of us (AMFT; e.g., Frazier and Tomescu, 2023). Upper Emsian strata in Poland have yielded another, as yet unnamed, anatomically-preserved plant with complex dissected xylem (Filipiak et al., 2022) assignable to the cladoxylopsids s.s.

Throughout the Early Devonian, the euphyllophytes formed a plexus of taxa that, although generally regarded as structurally simple, populate an ample morphospace. It is thus notable that the cladoxylopsids are the only group to stand out with its own individuality among these earliest euphyllophytes. In adpressions, they have been recognized by their multifascicular xylem—which could have been just simply deeply lobed, because its architecture is not known from direct anatomical observations and is only inferred from the pronounced and consistent longitudinal striations present on axes—and by their filiform lateral appendages that are much thinner than the subtending axes and bear terminal paired fusiform sporangia (Ananiev and Zakharova, 1986; Gerrienne, 1992). Judging by the lateral appendage criterion, an even older adpression from Wyoming (USA) dated to the latest Lochkovian–earliest Pragian and bearing lateral branches significantly thinner than the main axis (see Tomescu and Whitewoods, 2024, fig. 9H, p. 15), might also be an early cladoxylopsid. When anatomically preserved, the xylem architecture and 'permanent' mesarch protoxylem strands are diagnostic of cladoxylopsids. Also notable is the fact that all the early cladoxylopsids in which the secondary wall thickenings of tracheids have been documented have bordered pits (like all of the younger members of the group), which set them apart from all of the other coeval early euphyllophytes (characterized by *Psilophyton*-type tracheids; Kenrick and Crane, 1997) and could represent another diagnostic feature useful especially for recognizing early representatives of the group.

Geography and ecology of the cladoxylopsid expansion. The presence as early as the Early Devonian, in the mid- to late Emsian (Fig. 1.1), of derived members of the cladoxylopsid plexus—*Adelocladoxis* (a cladoxylopsid s.s.) and *Paracladoxylon* (a cladoxylalean cladoxylopsid; Chu et al., 2024)—indicates that distinct groups were already present in Laurussia (as also supported by other Emsian occurrences). These, along with the Siberian *Protohyenia*, show that by Emsian time, the cladoxylopsids had already populated at least two paleocontinents, on either side of the Equator (Fig. 1.1). Together, these earliest occurrences indicate that the Cladoxylopsida originated before the Emsian and underwent a currently undetected pre-Emsian phase of diversification (Durieux et al., 2021, p. 2091).

Cladoxylopsids reached their maximum geographic expansion in the Middle Devonian (Fig. 1.2). The Pseudosporochnales were the most widely distributed; from north to south, they occupied Siberia, Kazakhstan, and West Junggar (present-day records located in central Kazakhstan and Xinjiang; for detailed analyses of the paleogeography of the Kazakhstan terranes and Junggar basin during the Paleozoic, see Domeier and Torsvik, 2014 and Xu et al., 2014), Laurussia (numerous localities in Europe and North America), and northwestern Gondwana (Venezuela, Morocco). They appear to have been absent in the east, unless the *Astralocaulis* collected in Queensland (represented as a cladoxylopsid incertae sedis in Fig. 1.2) corresponds to the root system of a pseudosporochnalean cladoxylopsid, and its Middle Devonian age, assigned by Harris (1929), is correct (Supplementary Data 3). Thus, the Pseudosporochnales straddled a wide climatic gradient, ranging from arid to tropical and warm temperate climates (Capel et al., 2023, fig. 5). They also played a major role in the establishment of the first forest ecosystems, which had delayed but far-reaching effects across the Earth's biomes (Li et al., 2026). Eifelian forests in Germany (Lindlar) and Somerset were occupied by *Calamophyton* trees < 3 m tall (Giesen and Berry, 2013; Davies et al., 2024). Although they exceeded this height, the contemporary *Pseudosporochnus* forests in Belgium (Goé) remained of moderate size (Berry and Fairon-Demaret, 2002). The detailed structure (composition and spatial organization) of these Eifelian forests is poorly understood. To date, the first forest communities that were complex and composed of tall trees have been identified in the Givetian localities of New York State (Stein et al., 2012, 2020). Their composition varied depending on local environmental conditions. In the poorly-drained and disturbed environments represented at Riverside quarry near Gilboa, *Wattieza-Eospermatopteris*, which reached heights of 10 m or more, were the only canopy trees, alongside rare lycopsids. The known understory consisted of woody aneurophytalean progymnosperms (Stein et al., 2012). By contrast, in the drier landscapes represented at a quarry near Cairo (Egypt), *Wattieza-Eospermatopteris* formed a forest in association with even larger archaeopterids (Stein et al., 2020). The composition of its understory is unknown. Cladoxylopsids representing groups other than the pseudosporochnalean clade are known from a smaller number of localities in the Middle Devonian, but the presence of cladoxylalean cladoxylopsids in South China, where both the Pseudosporochnales and the Iridopteridales are absent, is worth noting.

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The Upper Devonian saw the disappearance of cladoxylopsids from Siberia and a marked decline in the global distribution of the Pseudosporochnales, the last records of which date to the Frasnian, in North Timan (Russia) and New York State (USA) (Stein and Hueber, 1989; Orlova et al., 2016; Fig. 1.3). The Iridopteridales also declined and were no longer present in Xinjiang (West Junggar). Only the genus *Keraphyton* (Champreux et al., 2020) recorded in the Famennian of Australia might represent the group in the Late Devonian, although, despite sharing characters with the iridopterids, the affinities of *Keraphyton*, which is based on a single axis, are not unequivocally resolved. By contrast, it is at the end of the Devonian, during the Famennian, that the cladoxylalean cladoxylopsids reached the eastern part of Gondwana (present-day Australia) for the first time (Meyer-Berthaud et al., 2021; Fig. 1.3). This group persisted beyond the Devonian-Carboniferous boundary and, together with *Serripteris* and *Voelkelia* Solms-Laubach, 1896 (both recorded as cladoxylopsids s.s. in Fig. 1.4), they are the last known representatives of the Cladoxylopsida, in the lower Carboniferous (Solms-Laubach, 1910; Long, 1968, 1987; Rowe and Galtier, 1989), at which time they occurred exclusively in the Southern Hemisphere, close to the Equator.

Trends in morphological evolution

Stelar architecture. Stelar architecture encompasses a broad range of diversity among cladoxylopsids, ranging from actinosteles with few lobes seen among iridopterids to much-dissected steles with up to 100 ribs or vascular segments, as seen among cladoxylopsids s.s. Arnold (1952) was the first to formulate hypotheses on the evolution of the steles in this group, proposing a transition from a terete protostele toward an actinostele (as exemplified by *Asteroxylon* Kiston and Lang, 1920), followed by dissection of the latter. Within this framework, Lemoigne and Iurina (1983) hypothesized gradual stele dissection starting with only some of the ribs disconnected from the central xylem region, and progressing toward a stele with completely disconnected vascular segments. The latter are arranged radially around a central parenchymatous region with or without discrete central vascular bundles, a hypothesis reiterated by Stewart and Rothwell (1993, p. 222–224). Lemoigne and Iurina (1983) nevertheless pointed out that such supposed evolutionary transitions could also either represent, or be recapitulated in, successive developmental stages of cladoxylopsids like *Xenocladia* Arnold, 1940.

These hypotheses are generally supported by phylogenetic studies of the cladoxylopsid plexus (Durieux et al., 2021; Chu et al., 2024). Thus, the circular to elliptical basal shape of appendage traces that become H-shaped (actinostelic) distally in the iridopterid *Arachnoxylon kopfii* (Sebby, 1972; Stein, 1981, 1982; Stein et al., 1983), which is part of a basal grade of cladoxylopsids, supports the hypothesized evolutionary transition from haplostele to actinostele in the group. The second step of the evolution of the stele in the cladoxylopsids is the gradual dissection of the actinostele and the increase in the number of ribs. This is supported by the phylogenetic placement of the actinostelic taxa, which form a basal grade among cladoxylopsids s.l., and by the distribution of stele architecture among the cladoxylalean cladoxylopsids (Fig. 2; Table 2). The earliest diverging cladoxylalean cladoxylopsids possessed incompletely dissected steles, i.e., wherein some of the ribs are connected at the center of the stele (e.g., *Cladoxylon mirabile*, *Cladoxylon radiatum*, *Rotoxylon*, *Metacladoxylon*, *Panxia*, *Paracladoxylon*). By contrast, the most derived members of the clade

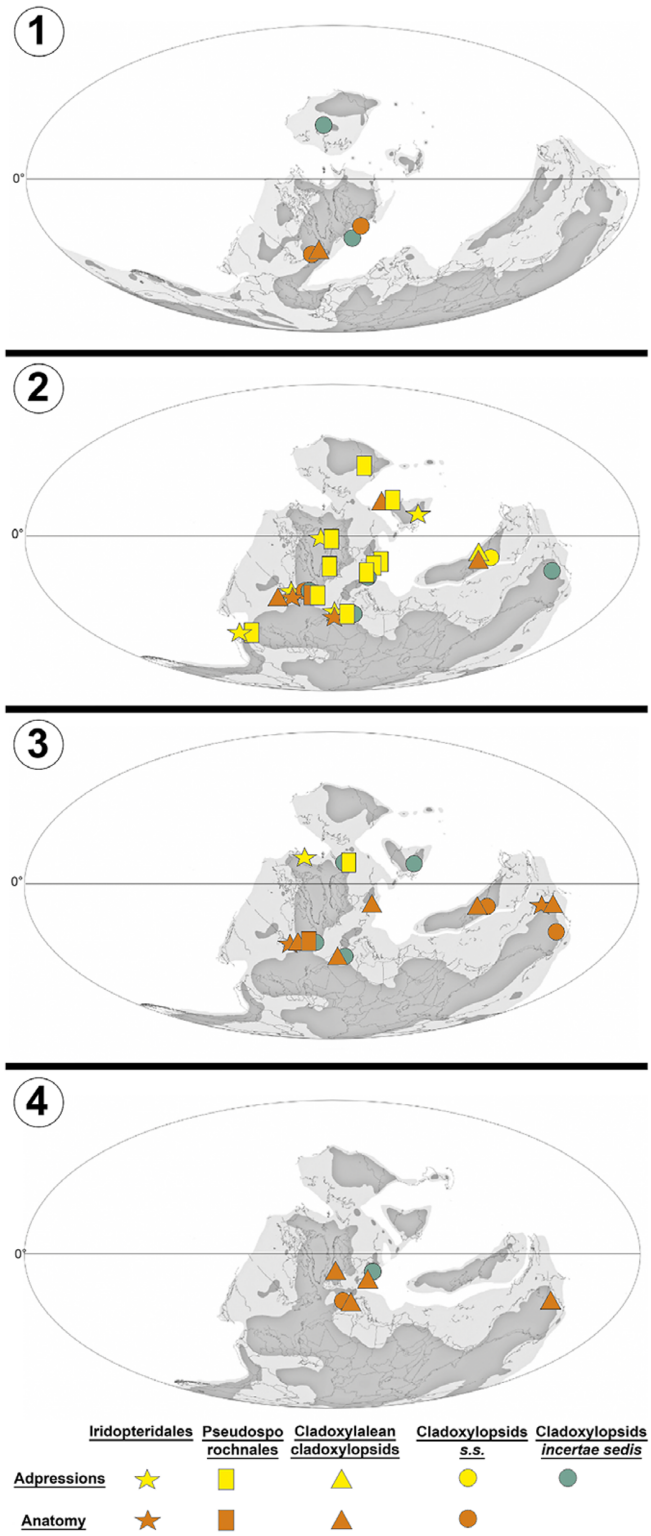


Figure 1. Paleogeographic distribution of the Iridopteridales, the Pseudosporochnales, and the cladoxylalean cladoxylopsids from their first record in the Lower Devonian until their last one in the Visean: (**1**) Emsian; (**2**) Middle Devonian; (**3**) Upper Devonian; (**4**) lower Carboniferous. Maps modified from Kocsis and Scotese (2021). The cladoxylopsids that do not belong to any of these groups in the phylogenies of Durieux et al. (2021) and Chu et al. (2024) (i.e., *Adelocladoxis* Durieux et al., 2021; *Denglongia* Xue and Hao, 2008, emend. Xue et al., 2010; *Serripteris* Rowe and Galtier, 1989) are simply referred to as cladoxylopsids s.s. All others (e.g., *Protohyenia* Ananiev, 1957; *Foozia* Gerrienne, 1992; and *Dixopodoxylon* Fairon-Demaret, 1969) are listed as 'cladoxylopsids incertae sedis.'

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(i.e., *Xenocladia*, *Polyxylon*, *Pietzschia*) possessed entirely dissected steles with large central parenchymatous areas that host central vascular bundles, corresponding to the most derived condition of cladoxylopsid steles (Fig. 2). Additionally, the transition from actinostele to a dissected stele is observed in the development of *Cladoxylon waltonii* (see Long, 1968) and *Metacladophyton* (Z. Wang and Geng, 1997) emend. D. Wang and Lin, 2007, and the increase in the number of ribs has been observed in epidogenetic phases of *Pietzschia levis* Soria, Meyer-Berthaud, and Scheckler, 2001 (Soria and Meyer-Berthaud, 2004) and *Xinicaulis lignescens.*

In summary, an evolutionary sequence of stelar architecture among cladoxylopsids s.l. is supported by the pattern of phylogenetic relationships in the group and is recapitulated in the ontogeny of some of the taxa. Interestingly, the evolutionary transitions in stelar architecture are paralleled by an increase in plant diameter (Fig. 3) as well as by transitions in the lateral organ morphology (see below). These correlations are consistent with hypotheses that have proposed as a driver in the evolution of cladoxylopsid stelar architectures the redistribution of a 'vascular identity specifier' (i.e., auxin) modulated by changes in apical meristem size and in lateral organ size and complexity (Wight, 1987; Stein, 1993; Tomescu, 2021; Durieux et al., 2021).

Ultimate appendages. All cladoxylopsids possess as their highest orders of branching axes that are either (1) branching more-or-less isotomously in their entirety, or (2) small pseudomonopodial systems consisting of a 'central axis' that bears lateral isotomous ultimate segments. These small branching systems of the highest orders are typically referred to as ultimate appendages, especially if entirely isotomously branched, but the second type has been termed 'lateral branching systems' in pseudosporochnaleans (Berry and Fairon-Demaret, 1997; Berry, 2000). However, the term 'lateral branching system' can be confusing, because it can apply to any branch (and its offshoots) that is borne on an axis of the next lower order (e.g., the digitate branches, which bear ultimate appendages, of the pseudoporochnaleans). Additionally, the co-occurrence of isotomous and pseudomonopodial small branching systems of the highest orders on the same plant (e.g., in *Pseudosporochnus*; Berry and Fairon-Demaret, 1997) suggests that they are organographically equivalent. Consequently, here we refer to both of these two types of small branching systems of the highest orders as 'ultimate appendages.' It is then worth noting that in plants in which the anatomy of ultimate appendages of the pseudomonopodial type is known, it suggests that their base was petiole-like (see Cladoxylalean cladoxylopsids in the Current diversity and classification section; Durieux et al., 2026).

The homology of ultimate appendages across the cladoxylopsid plexus has been articulated by Durieux et al. (2021). Approaching the question for phylogenetic purposes (character construction and scoring), they pointed out the vexing nature of recognizing ultimate appendages, i.e., determining where, in going along the successive orders of branching from lowest to highest, the base of an ultimate appendage starts. Durieux et al. (2021) proposed that ultimate appendages are recognized by their determinate development; the fact that they are reiterated, with consistent morphology, throughout the plant body (and sometimes on different orders of branching); and their possession of the simplest anatomy among the different orders of branching recognized in a plant.

Ultimate appendages are isotomous and three-dimensional in iridopterids, in which they can be borne on all orders of branching, as well as in the pseudosporochnaleans *Lorophyton* and *Calamophyton* (Leclercq and Andrews, 1960; Fairon-Demaret and Li, 1993; Fairon-Demaret and Berry, 2000; Berry, 2000; Berry et al., 2022). Ultimate appendages of the pseudomonopodial type, with dichotomous segments arranged alternately or in whorls, are found in two other pseudosporochnaleans, *Wattieza* and *Pseudosporochnus*; in the latter, they co-occur with isotomous ultimate appendages (Berry and Fairon-Demaret, 1997; Berry, 2000). Whether isotomous or pseudomonopodial, the ultimate appendages of pseudosporochnaleans lack regular taxis. When they are known in the cladoxylalean cladoxylopsids, the ultimate appendages have regular taxis; they are pseudomonopodial, with alternate to opposite dichotomous units, and their stalks have bilateral to abaxial-adaxial polarity, except in *Metacladophyton ziguinum* (Z. Wang and Geng, 1997) emend. D. Wang and Lin, 2007 (Fig. 2; Table 2).

The specific features and distribution of the different types of ultimate appendages across the phylogeny of the group (Fig. 2) provide the elements for outlining a hypothesized evolutionary sequence. This sequence starts with the transition from an exclusively isotomous lateral appendage with determinate growth and progresses toward pseudomonopodial appendages, involving the advent of bilateral symmetry, and then of abaxial-adaxial polarity. This sequence has already been hypothesized for the independent evolution of leaves in other euphyllophyte groups (Sanders et al., 2009; Tomescu, 2009; Galtier, 2010; Tomescu and Whitewoods, 2024). In the lignophyte clade, for instance, seed-plant leaves evolved from determinate lateral organs that became subsequently bilaterally and abaxial-adaxially polarized starting from their proximal ends (Sanders et al., 2009; Galtier, 2010). Thus, the ultimate appendages of cladoxylopsids represent a new example among euphyllophytes of an independent (and incomplete, in this case) pathway of evolution of lateral appendages toward true leaf structure and identity, from precursors consisting of lateral branching systems (Kenrick and Crane, 1997).

In parallel with the stepwise evolution of ultimate appendages toward leaf identity, the cladoxylopsids also show the acquisition of planation and of abaxial-adaxial polarity elsewhere in their branching systems. Although the iridopterids possess three-dimensional branches, the pseudosporochnaleans have digitate branches that divide in the same plane (planation) and some cladoxylalean cladoxylopsids have branches with abaxial-adaxial polarity, e.g., plants in the genus *Pietzschia* (Soria and Meyer-Berthaud, 2005) and possibly *Cladoxylon waltonii* and *Cladoxylon edromense* Long, 1987 (Long, 1968, 1987). However, in the latter two species, it is unclear what position abaxial-adaxially polarized branches occupy in the hierarchy of their branching architecture.

An evolutionary scenario can also be proposed for the positioning and taxis of the cladoxylopsid ultimate appendages. The phylogenetic distribution of these characters suggests that ultimate appendages evolved from being produced on axes of all orders to produced only on higher orders of branching and possibly only on branches of the highest order in the cladoxylalean cladoxylopsids. In terms of ultimate appendage taxis, it seems to be regular at least in some of the iridopterids, in which they co-occur with branches at nodes, whereas in the cladoxylopsids s.s., it is irregular in pseudosporochnaleans and regular in the cladoxylaleans. Thus, the basal iridopterids possess regularly arranged ultimate appendages on axes of all orders; transitional cladoxylopsids bear only branches on their main axis and, when known (i.e., *Denglongia* [Xue and Hao, 2008]), ultimate appendages have regular taxis on branches of multiple orders; the pseudosporochnaleans also bear ultimate appendages on branches of all orders, with irregular taxis (Stein and Hueber, 1989; Berry and Fairon-Demaret, 1997; Berry, 2000), and the cladoxylalean cladoxylopsids likely bear ultimate

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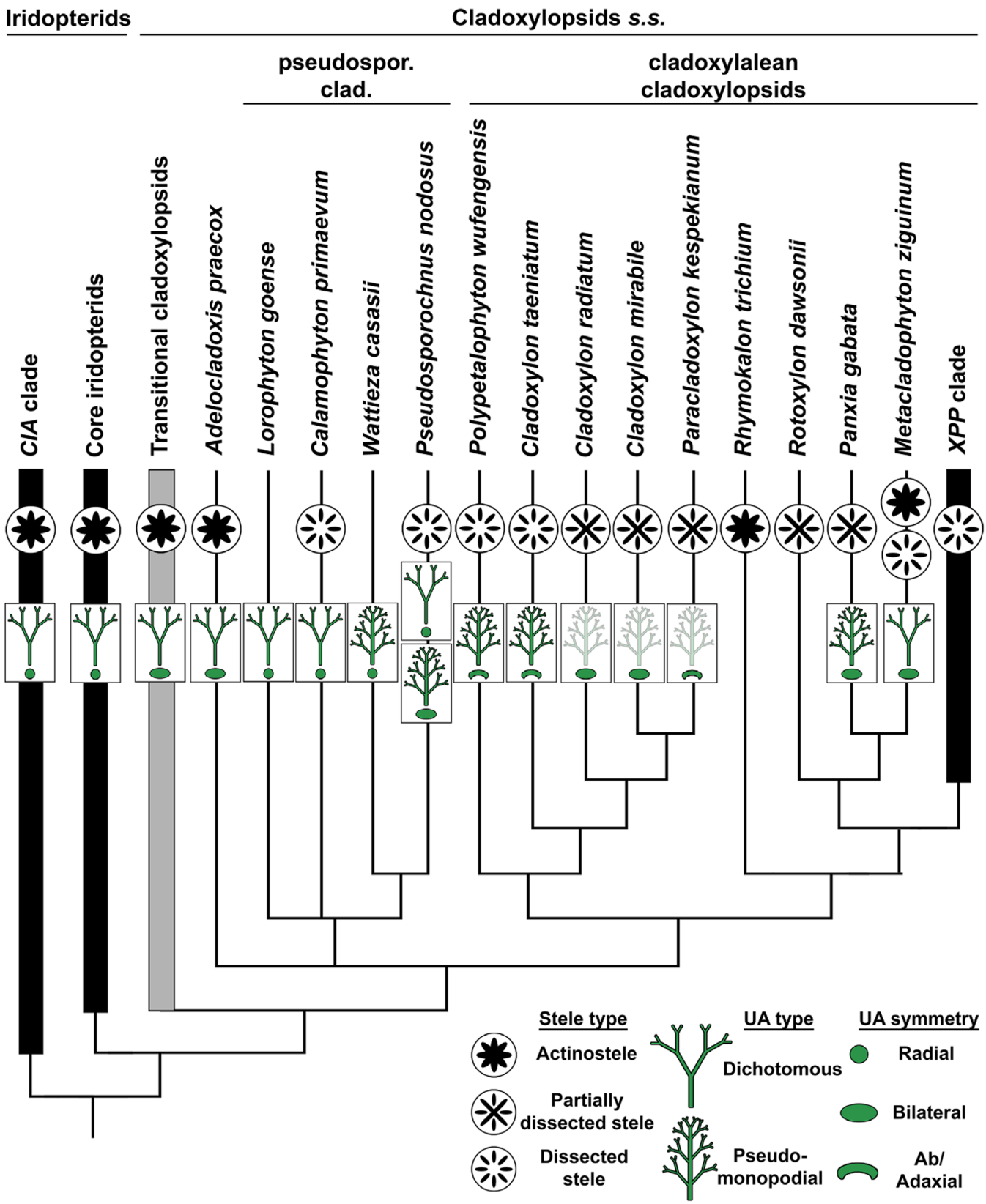


Figure 2. Simplified phylogenetic tree of the cladoxylopsids from Chu et al. (2024, fig. 51) with discussed stele and ultimate appendages characters mapped. Large black branches represent monophyletic groups, and the large gray branch represents a paraphyletic grade. 'CIA clade' includes *Compsocradus givetianus* Fu et al., 2011; *Ibyka amphikoma* Skog and Banks, 1973, emend. Berry et al., 2022; and *Anapaulia moodyi* Berry and Edwards, 1996. 'Core iridopterids' includes *Arachnoxylon minor* Stein, Wight, and Beck, 1983; *Arachnoxylon kopfii* Read, 1938; *Asteropteris noveboracensis* Dawson, 1881; *Compsocradus laevigatus* Berry and Stein, 2000; and *Iridopteris eriensis* Arnold, 1940. 'Transitional cladoxylopsids' includes *Denglongia huebeiensis* Xue and Hao, 2008, emend. Xue et al., 2010 and *Serripteris feistii* Rowe and Galtier, 1989. 'XPP clade' includes *Xenocladia medullosina* Arnold, 1940; *Pietzschia schulleri* Gothan, 1927; *Pietzschia levis* Soria, Meyer-Berthaud, and Scheckler, 2001; *Pietzschia polyupsilon* (Read and Campbell, 1939) emend. Soria and Meyer-Berthaud, 2003; and *Polyxylon australe* (Chambers and Regan, 1986) emend. Meyer-Berthaud et al., 2007. UA = ultimate appendages. Translucent UA mapped on the tree represents the UA from taxa for which there is no definitive evidence about their types (i.e., dichotomous or pseudomonopodial).

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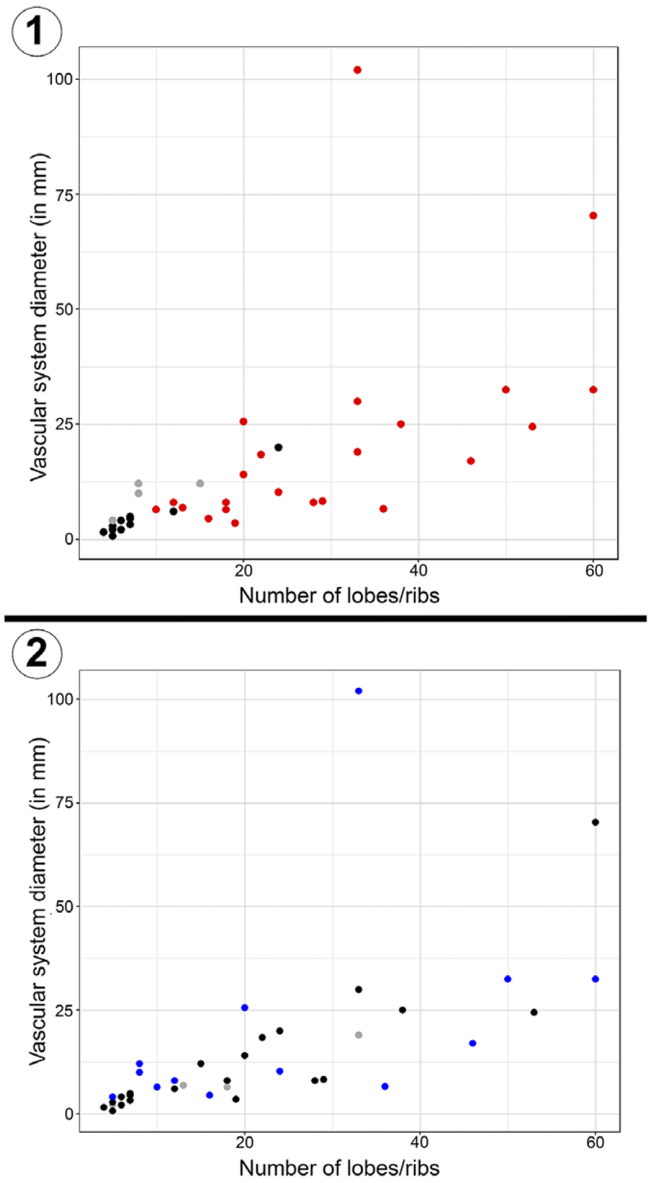


Figure 3. Scatter plots of the vascular system diameter (in mm) as a function of the number of lobes/ribs measured on anatomically preserved cladoxylopsids (N = 38). Note that Spearman correlation = 0.84, suggesting a high correlation between these two characters. (**1**) Scatter plot with black = actinostelic taxa; gray = taxa showing actinostelic and dissected stele; red = taxa with a dissected stele. (**2**) Scatter plot with black = taxa without secondary xylem; red = taxa with secondary xylem; gray = taxa with tissues not officially recognized as secondary xylem but sharing numerous similarities. For details of the data, see Supplementary Data 4.

appendages exclusively on axes of the highest order with regular organotaxis (e.g., *Panxia* [Y. Wang and Berry, 2006], *Polypetalophyton* (Geng 1995) emend, Hilton et al., 2003, *Cladoxylon taeniatum* [see Durieux et al., 2026]; in *Pietzschia*, the main axis and its branches bear no ultimate appendages, which suggests that they might also have been borne only on axes of the highest order) (Table 2). A notable exception to the latter is the cladoxylalean *Metacladophyton ziguinum* (see D. Wang and Lin, 2007), in which ultimate appendages have regular taxis, but they can also have irregular taxis—like the pseudosporochnaleans—depending on the axis order that bears them. If the ultimate appendages of pseudosporochnaleans and *Metacladophyton ziguinum* have irregular taxis, that would imply that this feature, typically used to identify a lateral appendage as a leaf (Sanders et al., 2009; Tomescu, 2009) and proposed as the most plesiomorphic uniting feature of leaf precursors (Tomescu and Whitewoods, 2024), shows a reversal in these derived cladoxylopsid s.l. taxa.

Sporangia. Consistent with their early euphyllophyte identity, the plesiomorphic sporangium condition in cladoxylopsids consists of ellipsoidal to fusiform sporangia borne in pairs at the tips of the ultimate segments of fertile ultimate appendages. When documented, the dehiscence of these sporangia proceeds along a single longitudinal opening, similar to those of the basal euphyllophyte *Psilophyton* Dawson, 1859 (e.g., Banks et al., 1975). This plesiomorphic condition seems to have persisted all across the iridopterids and through the pseudosporochnalean cladoxylopsids, with differences among genera being related to the morphology of the fertile ultimate appendages rather than to the morphology of the sporangia themselves (Berry and Edwards, 1996; Berry, 2000; D. Wang and Lin, 2007; Xue and Hao, 2008; Fu et al., 2011). The few cladoxylalean cladoxylopsids in which sporangia are known suggest that sporangial characters evolved away from the plesiomorphic form: the sporangia are terminal and fusiform but not paired in *Polypetalophyton* (Hilton et al., 2003), and they are not fusiform and probably not paired in *Panxia* (Y. Wang and Berry, 2006).

Cladoxylopsid architecture

Iterative versus hierarchized architecture: a debatable taxonomic dichotomy. Devonian cladoxylopsids display morphologies, the diversity and complexity of which can be appreciated from the numerous reconstructions now available. Architectural analysis (Barthélemy and Caraglio, 2007) allows this complexity to be organized by defining the different types of morphological components of the plants, their sequence of production, and their topological arrangement, as well as various aspects of their geometry (e.g., dimensions, branching angle). Architectural analysis also records the changes in form during growth, particularly those due to branching.

This type of analysis is particularly useful for recognizing two types of architectural features that have been used to separate systematic groups within the Cladoxylopsida: the repetition of architectural elements and their co-occurrence. Thus, the Iridopteridales have been traditionally thought to be distinguished by (1) their so-called 'iterative' architecture, i.e., one that repeats the same branching pattern in different orders of axes; (2) their whorled to pseudowhorled organotaxy; and (3) the presence of both branches and ultimate appendages within the same nodes (Berry and Stein, 2000; Meyer-Berthaud et al., 2007). By contrast, the cladoxylopsids s.s., particularly the Pseudosporochnales, have been regarded as possessing a 'hierarchized' architecture (Meyer-Berthaud et al., 2007), wherein each order of branching has distinctive features that do not repeat those of the other orders.

Architectural analysis demonstrates that the structural dichotomy between iridopterids and pseudosporochnaleans, as traditionally conceived, is not as clear-cut and is, therefore, debatable (to facilitate comparisons below we refer to the axes of all taxa as first-order, second-order, third-order, and, eventually, fourth-order axes; Figs. 4, 5). Take, for example, three taxa with iridopterid affinities that are unanimously accepted—*Ibyka*, *Anapaulia* Berry and Edwards, 1996, and *Compsocradus* Berry and Stein, 2000,

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emend. Fu et al., 2011 (Durieux et al., 2021; Chu et al., 2024). Of these, *Ibyka* is the only taxon that clearly shows the three iridopterid characters listed above (Fig. 4.1). In *Compsocradus*, laterals are arranged in loose whorls on the first- and second-order axes, whereas the ultimate appendages do not exhibit any precise pattern along the third-order axes (Fu et al., 2011, p. 719; Fig. 4.2). In *Anapaulia*, both the first- and second-order axes exhibit a whorled branching pattern (Fig. 4.3), but ultimate appendages have not been documented on the second-order axes, which consequently cannot be considered repeated structures.

In *Metacladophyton*, a taxon with possible iridopterid affinities according to Berry and Stein (2000), each order of axes has its own characteristics: the first-order axis is the only one to produce lateral axes in whorls, and only axes of the most distal order bear ultimate appendages (Fig. 4.4). Similarly, in *Denglongia*, another taxon with iridopterid features interpreted as a transitional cladoxylopsid by Durieux et al. (2021), both the first- and second-order axes exhibit a whorled branching pattern and produce adventitious roots (Fig. 4.5). However, the second-order axes bear ultimate appendages, whereas the first-order axes do not. These two orders of axes cannot therefore be considered as repeated structures. Together, these comparisons show that the concept of 'iterative' architecture does not apply to the majority of Iridopteridales and related taxa, and it does not account for the entire breadth of morphological diversity observed within taxa assigned to this group.

In the cladoxylopsids s.s., particularly the Pseudosporochnales, the first-order branches differ significantly from the massive stem (trunk) that supports them, consistent with the idea that they have a 'hierarchized' architecture (Meyer-Berthaud et al., 2007). However, pseudosporochnalean branches divide dichotomously, producing a sequence of orders of axes that are similar from one order to the next—a pattern that can be described as iterative (Fig. 5.1). The ultimate appendages of the Pseudosporochnales, which are also dichotomous, developed along all the orders of axes that make up the branches. Those of the genus *Rhipidophyton* Berry and Wang,

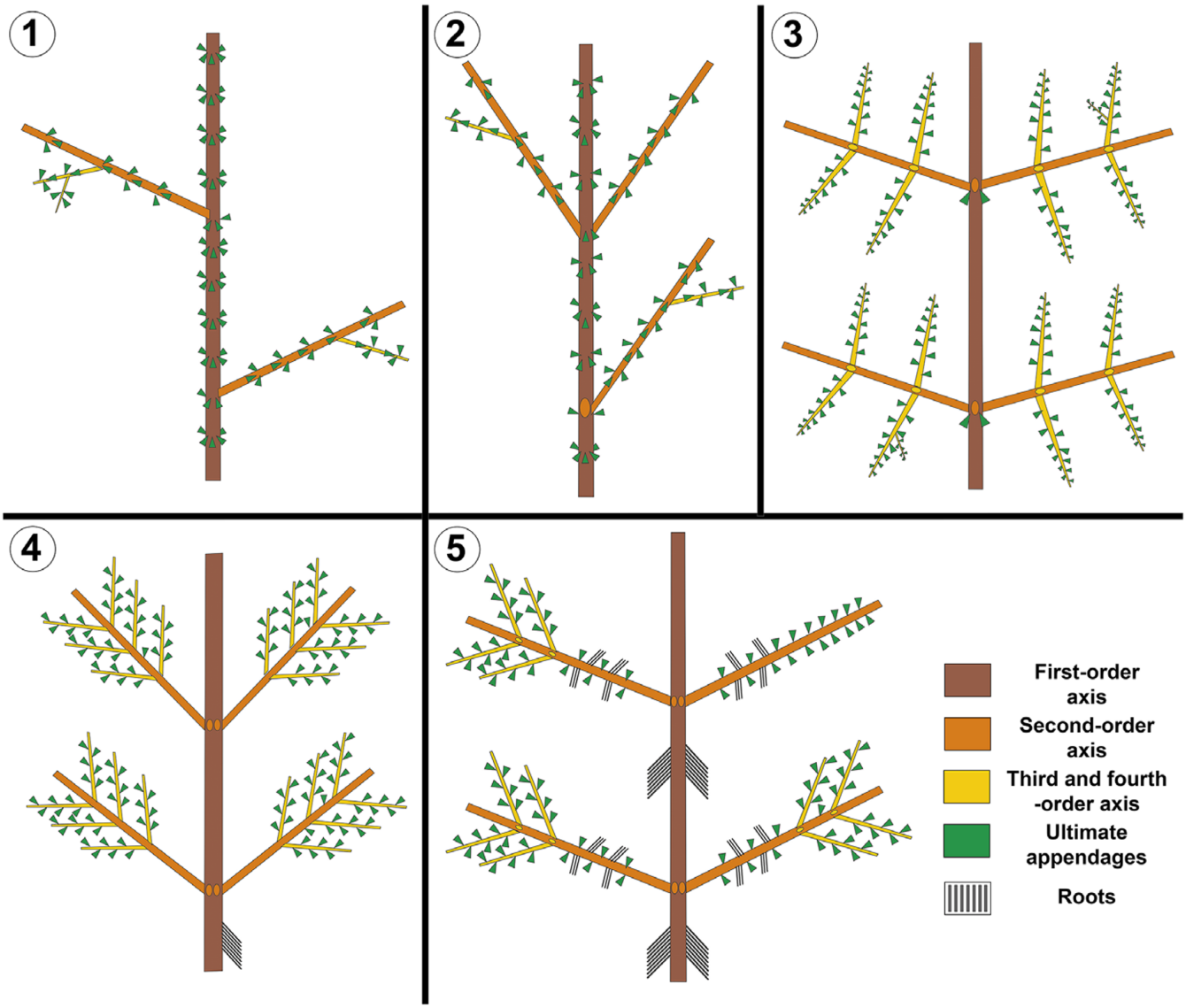


Figure 4. Compared architectural models of three Iridopteridales (**1–3**) and two cladoxylopsids s.s. showing some iridopteridalean features (**4, 5**): (**1**) *Ibyka amphikoma* Skog and Banks, 1973, emend. Berry et al., 2022; (**2**) *Compsocradus* (Berry and Stein, 2000) emend Fu et al., 2011; (**3**) *Anapaulia* Berry and Edwards, 1996; (**4**) *Metacladoxylon tetraxylum* Z. Wang and Geng, 1997 (cladoxylalean cladoxylopsid); (**5**) *Denglongia* Xue and Hao, 2008, emend. Xue et al., 2010 (transitional cladoxylopsid).

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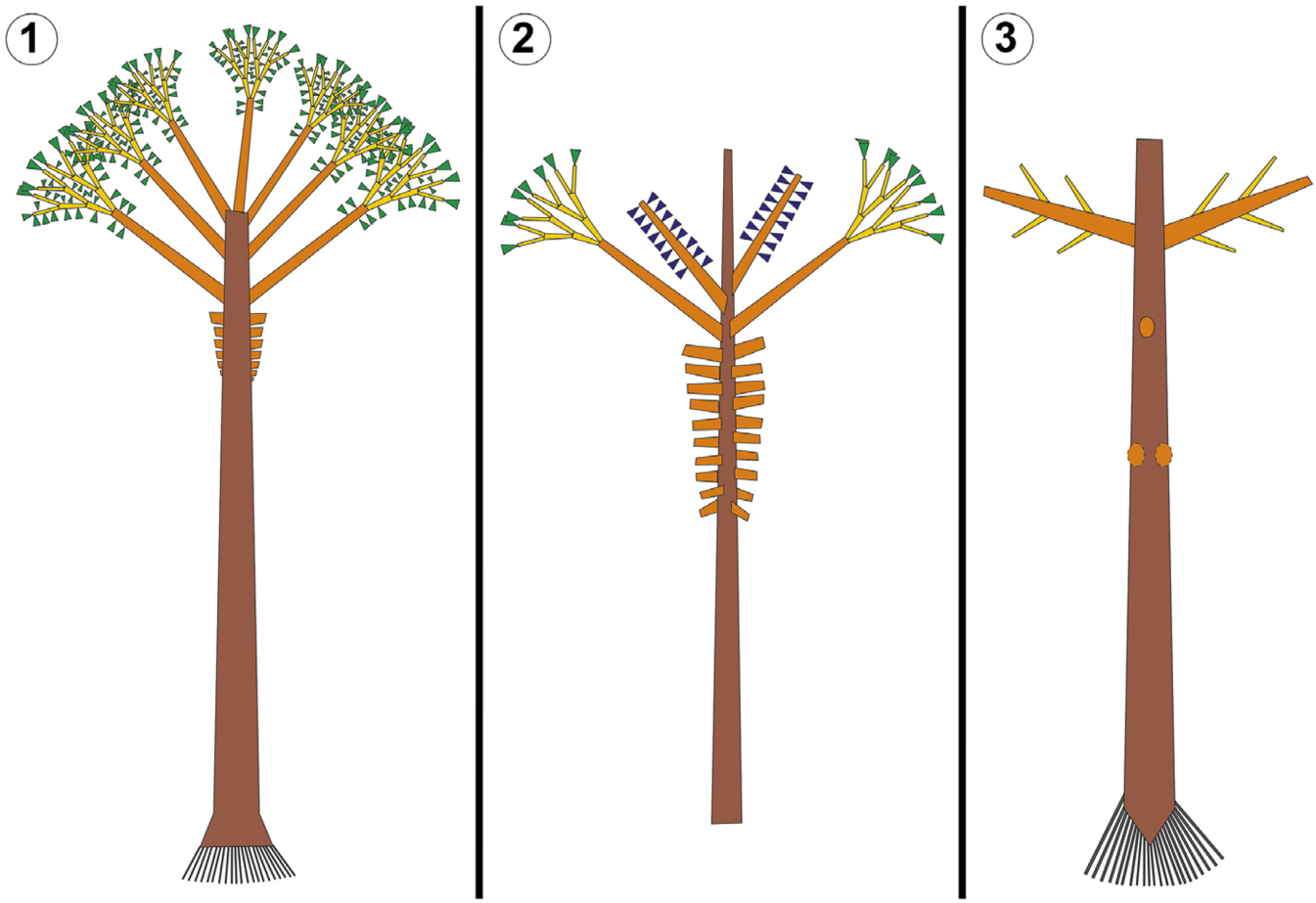


Figure 5. Compared architectural models of cladoxylopsids with a distinctive first-order axis, i.e., a trunk: (**1**) *Calamophyton* Kräusel and Weyland, 1926 (Pseudosporochnales); (**2**) *Rhipidophyton* Berry and Wang, 2006 (cladoxylopsid of uncertain affinities); (**3**) *Pietzschia* Gothan, 1927 (cladoxylalean cladoxylopsids). The *Pietzschia* model combines traits of *Pietzschia levis* Soria, Meyer-Berthaud, and Scheckler, 2001 for the epidogenetic stem base and traits of *Pietzschia schulleri* Gothan, 1927 for the rest of the plant. Most colors as in Figure 4; dark blue = fertile ultimate appendages.

2006, which shares some, but not all, architectural characteristics of the Pseudosporochnales, are the sole exceptions (Fig. 5.2). Additionally, there is no clear gradation from a branching pattern that would be lateral proximally and dichotomous distally; instead, lateral and dichotomous branching patterns are intermixed in pseudosporochnalean branches. Thus, the 'hierarchized' architecture traditionally thought to characterize the cladoxylopsids s.s., particularly the Pseudosporochnales (Meyer-Berthaud et al., 2007), is also debatable.

Growth models and habits. The ontogenetic approach initiated by Eggert (1961, 1962) on Paleozoic lycophytes and sphenophytes, and applied to other groups (e.g., progymnosperms and pteridosperms; Scheckler, 1976; Masselter et al., 2006), represents another way of investigating the complexity of plant structures. It highlights the links between anatomy and external morphology at various stages in the development of entire plants or individual organs. Depending on the size and complexity of the primary body, or of its proxy represented by the primary vascular system (i.e., stele), Eggert distinguished three ontogenetic stages. Epidogenesis corresponds to an expansion of the primary body in parallel with elongation. It characterizes the earlier development of a plant, and can also occur at branch bases. Menetogenesis corresponds to a phase when the size of the primary body remains constant longitudinally. Apoxogenesis corresponds to a decrease in size and complexity of the primary body with elongation. These stages, which characterize primary growth, are associated with variable amounts of secondary tissues in the taxa that exhibit secondary growth. In the cladoxylopsids, the ontogenetic approach is particularly useful for comparing the developmental patterns of large growth forms, e.g., trees, and for hypothesizing about the growth habits of taxa represented only by isolated anatomical sections of fragmentary specimens.

The ontogenetic approach has been applied to a few species of cladoxylopsids s.s., but rarely to the Iridopteridales, for which the available relevant information is scarce—to our knowledge, only one case of epidogenesis has been reported in *Arachnoxylon* Read, 1938 (Stein et al., 1983). Within the cladoxylopsids s.s., attention has mainly focused on the largest species, reconstructed as trees (Berry and Fairon-Demaret, 2002; Soria and Meyer-Berthaud, 2004; Meyer-Berthaud et al., 2010; Giesen and Berry, 2013; Xu et al., 2017). Despite sharing the same habit, the arboreous cladoxylopsids differ in several ways in their morphology and growth pattern.

Morphologically, the four major taxa of Pseudosporochnales—*Pseudosporochnus*, *Calamophyton-Duisbergia*, *Wattieza-Eospermatopteris*, and *Lorophyton*—are reconstructed as tree-sized plants ranging from 2–>10 m in height, the type specimen of *Lorophyton* corresponding to a juvenile (Fairon-Demaret and Li, 1993; Berry

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and Fairon-Demaret, 2002; Stein et al., 2007; Giesen and Berry, 2013). They all possess an orthotropic trunk bearing a crown of digitate branches (Fig. 5.1) arranged differently in the four taxa: broadly offset rows in *Pseudosporochnus*, vertical ranks in *Duisbergia* and *Wattieza*, and helically in *Lorophyton.* As the plant grows in height, the oldest branches are shed, from their base in *Pseudosporochnus* or distal to it in *Calamophyton* (Berry and Fairon-Demaret, 2002; Giesen and Berry, 2013). The branches bear ultimate appendages lacking regular taxis that dichotomize three-dimensionally and can bear erect (*Pseudosporochnus* model [Berry and Fairon-Demaret, 2002]) or recurved sporangia (e.g., in *Calamophyton*, *Lorophyton*, and *Wattieza* [see Berry, 2000]) at the tips. Numerous adventitious roots with little or no branching are present on the underside and around the swollen base of the trunks.

The growth patterns of pseudosporochnalean trees have been hypothesized based on morphological features and not on patterns of anatomical change, which have, however, been used in characterizing the growth patterns of their branches. Indeed, the determinate growth of pseudosporochnalean branches, inferred from their multiple dichotomies and ephemeral lifespan has been validated by anatomical analyses performed on the branches of *Calamophyton primaevum* Kräusel and Weyland, 1926 (previously *Cladoxylon scoparium* Kräusel and Weyland, 1926) and *Pseudosporochnus hueberi* Stein and Hueber, 1989. The branches of these taxa lack secondary tissues and show an acropetal decrease in the amount of primary xylem, indicating their apoxogenetic character.

Several ontogenetic models that emphasize different aspects of trunk growth have been proposed for the Pseudosporochnales (Giesen and Berry, 2013; Xu et al., 2017). Berry and Fairon-Demaret (2002) hypothesized a significant role of the secondary xylem that surrounds the individual xylem ribs in increasing trunk girth. By contrast, Meyer-Berthaud et al. (2010) proposed a model inspired by that of *Pietzschia* (see below) in which the maximum size of the trunk is determined by primary growth, following a short epidogenetic phase. In this model, the trunk has a determinate growth characterized by a long apoxogenetic phase; the secondary xylem, which is not accompanied by the development of a secondary cortex, remains within the boundaries of the primary body and does not contribute to the enlargement of the trunk. The base of the trunk, covered by the root mantle, is enlarged by diffuse proliferation in the parenchymatous central region. In the *Calamophyton* model proposed by Giesen and Berry (2013), the trunk has an indeterminate growth characterized by an extended epidogenetic phase followed by a menetogenetic phase of primary growth, and by the production of secondary xylem—supported by the presence of secondary xylem in an anatomically preserved trunk of *Duisbergia* (Mustafa, 1978a)—at all levels of the trunk below the apex. This model of growth has been expanded to *Eospermatopteris-Wattiezza* (Giesen and Berry, 2013) and has received support from the anatomy of *Xinicaulis* Xu et al., 2017, a genus of cladoxylopsids with uncertain affinities, but that shares the anatomical structure inferred for *Eospermatopteris* (Xu et al., 2017). Based on *Xinicaulis* and *Eospermatopteris* trunk base casts (Boyer, 1995), the largest pseudosporochnalean cladoxylopsid trees are hypothesized to have grown a large body by an extensive phase of epidogenesis involving the acropetal dissection of the xylem ribs and by the production of significant amounts of secondary xylem, accompanied by "diffuse secondary growth in ground and inner cortical tissues" (Xu et al., 2017, p. 12013).

Among the nonpseudosporochnalean cladoxylopsids, the genus *Pietzschia* also includes tree-sized individuals, the largest of which exceeded 2 m in height (*Pietzschia schulleri* Gothan, 1927; Soria and Meyer-Berthaud, 2005). *Pietzschia* is represented by numerous anatomically preserved specimens, which have enabled detailed ontogenetic analyses, and the proposal of a growth model for the genus (Soria et al., 2001; Soria and Meyer-Berthaud, 2004, 2005; Meyer-Berthaud et al., 2010). *Pietzschia* plants had a short obconical base, covered by a mantle of adventitious roots (Soria and Meyer-Berthaud, 2004; Fig. 5.3), that shows acropetal increase in the amount of primary xylem, corresponding to an epidogenetic phase of growth. Above that, the trunk can show a short menetogenetic phase of growth, but soon becomes conical, tapering apically and showing acropetal reduction in the cross-sectional area of vascular tissues (apoxogenetic growth). The orthotropic trunk bore planated branches produced starting shortly before the end of the epidogenetic phase and arranged helically in *Pietzschia levis* or in whorls in *Pietzschia polyupsilon* (Read and Campbell, 1939) emend. Soria and Meyer-Berthaud, 2003 and *Pietzschia schulleri* (Soria et al., 2001; Soria and Meyer-Berthaud, 2003, 2004, 2005). The width and amount of primary xylem in the first-order branches decrease distally. This, along with the apoxogenesis of the main trunk, indicates that the growth model of *Pietzschia* consists mainly of determinate units (Meyer-Berthaud et al., 2010). The branches were probably shed in *Pietzschia schulleri* (see Soria and Meyer-Berhaud, 2005), in which two orders of branching have been preserved, with distichously arranged second-order branches (preserved only at their very base). No ultimate appendages are known in *Pietzschia*, which does not possess secondary tissues or evidence of branch dichotomy.

Recently, the first architectural model of a nonarborescent cladoxylopsid was proposed for *Cladoxylon taeniatum.* This model is based on detailed analyses of anatomical changes during ontogeny in a large number of isolated axes, some of which bear laterals (Durieux et al., 2026). *Cladoxylon taeniatum* is reconstructed with a main axis bearing helically arranged ultimate appendages possessing adaxial-abaxial polarity and pseudomonopodial architecture (with alternate to opposite isotomous lateral segments). The structure of the primary body (i.e., the number, size, and arrangement of the primary xylem ribs) and the amount of secondary tissues indicate a basal epidogenetic phase followed by an extended apoxogenetic phase of growth in the main axes of *Cladoxylon taeniatum.* This ontogenetic model can underpin two hypotheses about the growth habit of the plant. One hypothesis is that *Cladoxylon taeniatum* was an erect, self- to semiself-supporting plant resembling *Pietzschia*, but comprising secondary tissues. An alternative hypothesis is that *Cladoxylon taeniatum* had rhizomatous growth. This latter hypothesis is supported by an ontogenetically older specimen that has a significant amount of secondary tissues, including periderm, and a root trace that diverges from the vascular trace of an aerial organ; those two traces diverge at very different angles and have differently positioned secondary xylem, consistent with the inference that the subtending axis was a horizontal rhizome with aerial branches and adventitious roots growing in opposite directions, as is typical in plants with unipolar rhizomatous growth.

In summary, as discussed above, the cladoxylopsids s.l. encompass a significant amount of diversity from an architectural standpoint. However, some relationships among anatomical variables seem to hold true across the entire group, independent of architecture. Thus, in all cladoxylopsids with a dissected stele: (1) apoxogenesis and epidogenesis phase of growth are associated with, respectively, increase or decrease of the number of ribs or of the amount of primary xylem inside each ribs; (2) the number of ribs changes between axes of different orders; (3) the largest axes of tree-sized cladoxylopsids possess a stele with a large central

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parenchymatous zone surrounded by numerous radially elongated xylem ribs; (4) exclusively isotomous ultimate appendages/dichotomous units are supplied by a vascular trace that diverges from a single stele rib; and (5) in axis segments immediately basal to a dichotomy, the organization is altered with some ribs crossing the axis through its center or by the radial or tangential elongation of the central bundles.

Outstanding questions

Current understanding of cladoxylopsids has gaps, large and small. Major unanswered questions regard the ontogeny and architecture of these plants, e.g., the characterization of the different stages of growth of a pseudosporochnalean trunk, its associated rooting structures, and their corresponding anatomy, or the characterization of the growth and habit of iridopteridaleans. Speaking of roots, although cladoxylopsid roots are among the oldest euphyllophyte roots known in the fossil record (Giesen and Berry, 2013; Hetherington et al., 2020), our understanding of their anatomy is limited to but a few instances (Harris, 1929; Soria et al., 2001; Meyer-Berthaud et al., 2024; Xu et al., 2017; and intriguing structures published recently by Stein et al., 2023). Their development, especially in relation to the ontogeny of the whole plants has never been addressed.

The autapomorphic vascular architecture of cladoxylopsids raises functional questions, like those related to the possible advantages and constraints conferred by the dissected vascular system: did it offer mechanical or hydraulic advantages that could explain the evolutionary success of the group in the Devonian and its broad morphological diversification? If so, how could it have contributed to the construction of the first cladoxylopsid trees, mechanistically and in comparison to the vascular systems of living plants with analogous monocaulous arboreous habits (tree ferns and palms)?

The 'permanent protoxylem' of cladoxylopsids raises questions related to development and architecture: how does the distribution of protoxylem strands in the axes of different taxa relate to the vascular supply of their lateral appendages? And how might homeostasis and the distribution of hormones and morphogens in and around apical meristems be involved in the specification and early development of these appendages? When integrated in an evo-devo framework with equivalent data from other euphyllophyte lineages, e.g., those traditionally associated with the evolution of seed plants (Toledo et al., 2021), which are themselves in a similar state of incomplete exploration, the cladoxylopsid data will provide key insights on the evolution of leaves and, more generally, of euphyllophyte organography.

The reproductive biology of cladoxylopsids is another poorly developed area of knowledge. Sporangia have been documented in only about one-quarter of the known taxa and we know little about them beyond their overall shape, (sometimes) dehiscence pattern, and positioning on the plants. We also know virtually nothing about sporangium-wall anatomy and the spore content. It is notable that all cladoxylopsids s.l., except for the cladoxylalean cladoxylopsids, seem to have retained until the Late Devonian and longer than other euphyllophyte groups (e.g., progymnosperms), the plesiomorphic trimerophyte condition with terminal paired sporangia. This raises questions about whether this and any aspects of reproductive biology associated with it could have influenced the evolutionary trajectory of different cladoxylopsid lineages, e.g., the fact that most of those with plesiomorphic sporangia seem to have gone extinct by Famennian time. And, because we know so little about their sporangia and spores, could any members of the group (especially among cladoxylalean cladoxylopsids, the sporangia of which are the least well known but seem to have been different from those of other cladoxylopsids) have evolved heterospory, which is known to have originated independently multiple times among the vascular plants (Bateman and DiMichele, 1994)?

Beyond ontogeny, form, and function, key questions regard the phylogeny of and within the cladoxylopsid plexus. First, the monophyly of all the lineages and taxa considered as part of the cladoxylopsid plexus—which was never tested explicitly and thoroughly in a cladistic framework—needs to be addressed by targeted studies that include enough of the relevant outgroups to provide unassailable answers. Other important questions should be addressed by more broadly sampled studies aimed at clarifying with good levels of support (1) the relationships between the different cladoxylopsid lineages, and (2) the relationships between cladoxylopsids, other Devonian-Carboniferous pteridophytic euphyllophyte lineages (zygopterids, rhacophytaleans, stauropterids), and equisetophyte lineages (including basal sphenophytes, e.g., *Rotafolia* D.-M. Wang, Hao, and Wang, 2005, as well as Pseudoborniales, Sphenophyllales, Calamitales), and including crown-group fern lineages (eusporangiate and leptosporangiate). Answers to all of these questions will provide critical insights on hotly debated issues in plant phylogeny. Such issues include the ancestry and deep relationships of ferns (extinct and living) and equisetophytes, the phylogenetic position of *Equisetum*, and its relationships with the different fern lineages. Answers to these questions will help address the meaning and usefulness of the monilophyte concept and will provide sounder foundations for understanding the overall pattern of relationships between all of the major euphyllophyte lineages, including the relationships between different pteridophytic lineages, on one hand, and the seed plants and related lignophyte lineages, on the other hand.

Future fossil discoveries and their integration into renewed studies of the group have the potential to answer many of the questions above, but while waiting for them, we should not neglect the much more immediate untapped potential of known, previously described specimens. Reassessed in light of the knowledge accumulated over the last 40 yr of discovery and using improved or new methods of imaging and investigation, these specimens have the potential to provide answers to many of the critical questions regarding cladoxylopsid anatomy, morphology, phylogeny, and evolution.

Conclusions

Despite having been recognized >150 yr ago, substantial progress in our understanding of cladoxylopsids was made over the last 30 yr. First, taxonomically, we now recognize three main groups among the cladoxylopsids s.l.: the Iridopteridales, which probably form a grade basal to the cladoxylopsids s.s. clade, within which the pseudosporochnalean cladoxylopsids and cladoxylalean cladoxylopsids form two distinct clades. However, the sets of defining characters discussed for each of these three cladoxylopsid groups do not apply universally within each group, a situation that reflects gaps in our understanding of the morphology of these groups of their relationships. Second, the application of architectural models led to improved understanding of the morphology and development of cladoxylopsids in each group, especially those that had evolved the tree habit. These advances, combined with improved comprehension of phylogenetic relationships, suggest hypotheses

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on the evolution of cladoxylopsid stele architecture (toward increased dissection of the xylem volume) and ultimate appendages (toward pseudomonopodial and dorsiventral organization). Currently, cladoxylopsids are known from all around the world, spanning the Early Devonian to the early Carboniferous. Available data reveal a previously unrecognized feature of cladoxylopsid evolutionary history—they were the earliest group to acquire morphological identity from among the plexus of early euphyllophytes, in the Early Devonian, >400 Myr ago and probably before the Emsian. This makes them the oldest recognizable euphyllophyte lineage. They are also the earliest euphyllophyte lineage to have evolved by the Emsian tracheids with bordered pits of modern aspect, and include some of the oldest (Emsian) euphyllophytes with regular taxis of ultimate appendages. The group radiated throughout the Early Devonian and thereafter, generating a broad diversity of Middle Devonian and younger representatives. However, as early as the end of the Early Devonian, cladoxylopsids already covered a considerable span of morphological disparity, especially in terms of stele architecture and branching patterns. Their ultimate appendages provide some of the oldest (Emsian) evidence for a euphyllophyte group that had already made big strides along pathways leading to the evolution of leaves. The group was widely spread geographically by the Middle Devonian, during which cladoxylopsids reached worldwide distribution and were the first group of plants that evolved the tree habit. Their geographic distribution started shrinking in the Late Devonian and the group went extinct sometime during the early Carboniferous. Despite the large body of knowledge accumulated about cladoxylopsids, critical questions remain to be addressed for reaching a fuller understanding of their structure, development, and taxonomy. Additionally, the monophyletic status of the cladoxylopsids needs to be thoroughly tested by studies based on broader taxon sampling. Such studies should also resolve the phylogenetic placement of the different cladoxylopsid groups among the euphyllophytes and address the issue of the 'permanent' versus 'radiate' protoxylem groups and, thus, shed light on the origin and deep relationships of plant lineages that are still present in the modern flora.

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