Plant hydraulic architecture through time: lessons and questions on the evolution of vascular systems

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ABSTRACT

Studies of anatomically preserved fossils provide a wealth of information on the evolution of plant vascular systems through time, from the oldest evidence of vascular plants more than 400 million years ago to the rise of the modern angiosperm-dominated flora. In reviewing the key contributions of the fossil record, we discuss knowledge gaps and major outstanding questions about the processes attending the evolution of vascular systems. The appearance and diversification of early vascular plants in the late Silurian-Devonian was accompanied by the evolution of different types of tracheids, which initially improved the hydraulics of conduction but had less of a mechanical support function. This was followed in the Devonian and Carboniferous by an increase in complexity of the organization of primary vascular tissues, with different types of steles evolving in response to mechanical, hydraulic, and developmental regulatory constraints. Concurrently, secondary vascular tissues, such as wood, produced by unifacial or bifacial cambia are documented in a wide array of plant

groups, including some that do not undergo secondary growth today. While wood production has traditionally been thought to have evolved independently in different lineages, accumulating evidence suggests that this taxonomic breadth reflects mosaic deployment of basic developmental mechanisms, some of which are derived by common ancestry. For most of vascular plant history, wood contained a single type of conducting element: tracheids (homoxyly). However, quantitative (e.g. diameter and length) and qualitative (e.g. pitting type) diversity of these tracheids allowed various taxa to cover a broad range of hydraulic properties. A second type of conducting elements vessels, is first documented in an extinct late Permian (c. 260 Ma) group. While the putative hydraulic advantages of vessels are still debated, wood characterized by presence of vessels (heteroxyly) would become the dominant type, following the diversification of angiosperms during the Cretaceous.

INTRODUCTION

The term "hydraulic architecture" was first used in the title of a 1978 paper by Martin Zimmermann that compared water flow in different parts of trees with diffuse porous wood. Hydraulic architecture has since received several definitions (see Cruiziat *et al.* 2002 for a review), the simplest and most general of which defines it as "the structure of the water conducting system" (Tyree & Ewers 1991). The functioning of plants as hydraulic systems has always intrigued botanists and the continued development of new techniques to assess and quantify xylem hydraulic properties has provided a wealth of data on the physical laws and structure-function relationships that control water flow in plants (McCulloh *et al.* 2003; Hacke *et al.* 2005; Sperry *et al.* 2006, 2008; Choat *et al.* 2008; Pittermann *et al.* 2011). Understanding the anatomy of vascular tissues, the pipelines of the plant's hydraulic system

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(Cruiziat *et al.* 2002), remains an essential aspect of these studies (e.g., Pittermann *et al.* 2005, 2006a).

Among paleobotanists, the question of the evolution of vascular systems is almost as old as the first observations of fossil plants (e.g., Witham 1831, 1833; Unger 1847; Göppert & Stenzel 1892; Renault 1879). Xylem, the water conducting tissue of vascular plants, typically contains cells with thickened secondary walls (tracheary elements, which are a type of sclerenchyma cells), usually lignified, which are resistant to degradation and, consequently, often well-preserved in the fossil record. The high preservation potential of xylem has underpinned the discovery of major steps in the evolution of vascular tissues, which can be traced back to the appearance of the first vascular plants more than 400 million years ago. The continued discovery of new fossils, combined with the development of new observational techniques and mathematical models, allow access to a steady flow of novel information on the hydraulic architecture of extinct plants, some of which have no living equivalent or were growing in very different environmental conditions (e.g., in terms of climate or atmospheric CO_2 levels). In this review, we summarize the state of the art and main developments in studies of the evolution of vascular systems based on the fossil record, and outline some outstanding questions about the processes that led to the appearance of plant structures that we observe today.

THE FIRST VASCULAR PLANTS

Vascular plants, also known as tracheophytes (Kenrick & Crane 1997; Fig. 1), largely dominate modern terrestrial ecosystems, where they represent over 380 000 species (Willis 2017). Tracheophytes are characterized by the possession of specialized water-conducting cells (tracheary elements) that are longitudinally elongated, non-living at maturity, and have a secondary cell wall laid down in different thickening patterns: annular, helical, scalariform,

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and reticulate or pitted. Pits are cell wall areas without secondary wall (i.e., holes in the secondary wall), through which water can move from one cell to the next, typically through a permeable membrane formed by the primary wall and middle lamella.

Microscopic tubes with internal thickenings found in early Silurian to Early Devonian (c. 440-410 Ma) deposits were initially interpreted as fossil tracheids (Martin 1971). However, the wall ultrastructure of these banded tubes is distinctly different from that of vascular plant tracheary elements (tracheids and vessels) and their role, as well as the organisms they belonged to, remain highly conjectural (Gray & Boucot 1977; Taylor & Wellman 2009). The oldest unequivocal tracheids are a little younger, dating back to the late Silurian-Early Devonian, a little over 400 million years ago (Edwards & Davies 1976). Early Devonian coalified fragments of *Cooksonia* (Paratracheophyta) possess a central strand composed of a few tracheids that are 2-11 µm in diameter (Lang 1937; Edwards *et al.* 1992). Because *Cooksonia* is first recorded in the Silurian (Fig. 2), and tracheids have also been reported from late Silurian sterile axes in a fossil assemblage containing *Cooksonia-type* sporangia (Edwards & Davies 1976), *Cooksonia* is traditionally regarded as the oldest vascular plant. However, the anatomy of Silurian *Cooksonia* specimens is unknown and since recent analyses show that the various species of the genus do not form a monophyletic group (Gonez & Gerrienne 2010), the vascular plant status of the oldest *Cooksonia* remains equivocal.

Investigations of early tracheids with scanning electron microscopy, starting in the 1990s, have led to the recognition of several types that are based on the structure of their wall thickenings (Kenrick & Crane 1991; Friedman & Cook 2000; Edwards 2003; Fig. 3). S-type tracheids have large and simple annular or helical thickenings. The spongy material of the wall thickenings is covered on the lumen side by a thin decay-resistant microporate layer (Kenrick & Crane 1997; Fig. 3B). S-type tracheids, named after the first fossil plant in which

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they were described, *Sennicaulis* (Paratracheophyta, Fig. 1), are also found in a few other fossil plants of Early and Middle Devonian age (Pfeiler & Tomescu 2018). The G-type tracheid, exemplified by the fossil plant *Gosslingia* (Zosterophyllales, Fig. 1), has annular or helical thickenings that can take a scalariform or reticulate aspect through the development of connections between horizontal thickenings. The cell wall between thickenings bears multiple minute perforations (Fig. 3C). G-type tracheids are found in some early representatives of the lycopsids and their extinct precursors, the zosterophylls. Tracheids of the P-type, exemplified by *Psilophyton* (Trimerophyta, Fig. 1), have bordered pits that are scalariform, more rarely almost circular (Edwards 2003). Unlike the bordered pits found in the tracheids of extant plants, their relatively large apertures are covered by a characteristic perforate membrane made of secondary wall material (Fig. 3D). This peculiarity is found in basal members of the euphyllophytes (Kenrick & Crane 1997; Strullu-Derrien *et al.* 2014; Bickner & Tomescu this issue, Fig. 1), the clade that comprises all living non-lycopsid tracheophytes and their extinct relatives, also known as Trimerophyta. The tracheids of some fossil and extant lycopsids also possess a perforated membrane or fimbrils ("Williamson's striations") across the scalariform pit aperture (Cichan *et al.* 1981), but it is unknown whether these structures are homologous to the ones observed in early euphyllophytes (Edwards 2003). Interestingly, some Devonian taxa show a combination of different types of tracheids within a single plant. This is the case for example in an unnamed fossil from the Early Devonian of Norway in which the main axis has G-type tracheids, while the tracheids of lateral branches possess circular to scalariform or reticulate bordered pits (Edwards *et al.* 2006).

Some of the most emblematic representatives of early vascular plants were found silicified in hydrothermal cherts from the Rhynie area in Aberdeenshire, Scotland (mid-Pragian-?earliest Emsian; Edwards *et al.* 2017). While these cherts preserve the vegetation of unusual environments (volcanic hot springs) (Wellman 2018), they have yielded some of the

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best anatomically preserved fossil plants from the Early Devonian interval. Among them, *Aglaophyton* (Protracheophyta), *Rhynia* (Paratracheophyta), *Asteroxylon* (Drepanophycales), and *Horneophyton* (Horneophyta) are all small plants (<20 cm tall) that lack leaves and true roots and illustrate different stages in the evolution of vascular systems. In *Aglaophyton*, the water conducting cells lack wall thickenings of the kind typically seen in tracheids. Because these cells have a structure intermediate between true tracheids and the hydroids found in bryophytes, *Aglaophyton* is considered a protracheophyte, not a true vascular plant. *Rhynia*, on the other hand, possesses true tracheids with annular to helical thickenings (S-type). The tracheids of *Asteroxylon* are of the G-type. Analyses of fossil cell wall chemistry by Boyce *et al.* (2003) have shown that the tracheids of *Rhynia* were likely unlignified, whereas those of *Asteroxylon* were heavily lignified. A fourth plant found in the Rhynie chert, *Horneophyton,* was regarded as another protracheophyte, but recently Cascales-Miñana *et al.* (2019) documented cells with irregular, annular to helical wall thickenings of putative secondary origin. They interpreted these cells as representing a new intermediate, this time between the simple cells without secondary thickenings found in protracheophytes, such as *Aglaophyton*, and the true tracheids found in *Rhynia* or *Asteroxylon*.

Biomechanical studies by Speck and Vogellehner (1988, 1992) showed that the tracheids of the first vascular plants did not contribute much to the flexural stiffness of axes, of which >80-90% could be attributed to either turgor pressure in the parenchymatous cortex, or to a sclerified hypodermal sterome. The observed increase in the complexity and strength of tracheid secondary wall thickenings is, thus, likely linked to maintenance of their water conducting properties, i.e., improved resistance to inward collapse and cavitation (Carlquist 1975; Hacke *et al.* 2001), in correlation with the trend of increasing tracheid diameters for increased water conductivity that was documented for the Devonian (Niklas 1994). Thus, a first important lesson from the fossil record is that the early evolution of vascular tissues was

in all likelihood not under the constraint of a compromise between hydraulic and mechanical functions.

A significant time interval separates the oldest fossil evidence of land plants (Fig. 1), represented by middle Ordovician spores (Rubinstein *et al.* 2010), and the diversification of vascular plants in the Early Devonian. However, it is important to note that the oldest evidence for plants with vascular tissue consists of late Silurian macrofossils (Kotik *et al.* 2002; Libertin *et al.* 2018) and possibly of hilate/trilete spores of early Silurian age (Gray & Boucot 1977; Steemans *et al.* 2009). The age disparity between these different types of fossils may be a reflection of different biases in taphonomy, geographic sampling, or the nature of the rock record, with respect to different plant parts and fragments. Vascular tissues are known to be quite resistant to degradation, thus, early vascular plants are expected to be better preserved than other types of plants. Kenrick *et al.* (2012) argue that the paucity of their remains before the late Silurian-Early Devonian could be due to biases, including (1) the poor prospection of the supercontinent Gondwana, which corresponded to today's southern continents and where land colonization by plants might have started (Steemans *et al.* 2009), and (2) the paucity of terrestrial deposits that pre-date the latest Silurian and that are exposed today, especially those representing fluvial or lacustrine depositional environments in which most early vascular plant remains are typically found. Until these potential biases are better understood and addressed, the tempo of evolution of plant vascular tissues following the initial colonization of land and the possible underlying processes cannot be assessed with confidence. The most recent timescale of plant evolution using fossil calibrations and genetic data (Morris *et al.* 2018) proposes a middle Cambrian to Early Ordovician age for crown embryophytes and a Late Ordovician to Silurian age for crown tracheophytes.

THE INCREASE IN COMPLEXITY OF THE PRIMARY VASCULAR SYSTEM

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During the Devonian, major innovations, such as the appearance of leaves (Sanders *et al.* 2009; Langdale & Harrison 2008; Tomescu 2009; Galtier 2010), the evolution of root systems (Boyce 2005; Hetherington & Dolan 2018), or the appearance of pseudomonopodial branching - with morphological differentiation of a main axis and subordinate lateral branches (Gensel *et al.* 2001), led to an increase in complexity of plant architecture (Chomicki *et al.* 2017; Bonacorsi & Leslie 2019; Crepet & Niklas 2019). This was paralleled by an increase in complexity of the organization of the primary vascular tissues and the appearance of new types of steles (Figs.4-5). The stele of an axis includes the tissues derived from the procambium. In terms of mature tissues, this translates into vascular tissues (xylem and phloem) and associated ground tissues (such as the pericycle, leaf gaps, interfascicular areas) - these issues are discussed in detail in an upcoming paper by Tomescu (work in progress).

In the most simple type of stele, the protostele, there is no pith and vascular tissues form a central strand. This type of stele, present throughout the entire geologic time scale of tracheophytes, occurs today in some taxa such as *Lycopodium* (Lycopodiales), *Psilotum* (Psilotidae)*,* or *Gleichenia* (Glecheniales). A protostele is also the vascular organization found in the vast majority of roots, independently of their systematic affinities (Esau 1965; Beck 2005). The oldest type of protostele, the haplostele, has circular to elliptical shape in cross-section, with the xylem located in the center (Fig.4A-C). This architecture is typical of the earliest vascular plants (Kenrick & Crane 1997; Fig. 2). Another type of protostele that became common in the Middle Devonian is the actinostele, in which the xylem has a lobed or star-shaped structure in cross-section (Figs.4D-F). Actinosteles are found in many Middle and Late Devonian taxa, including lycopsids, cladoxylopsids (i.e., Iridopteridales and Pseudosporochnales, Fig. 1), progymnosperms, Stenokoleales, and the first spermatophytes (Scheckler 1974, 1976; Beck & Stein 1993; Rothwell & Serbet 1994; Momont *et al.* 2016; Toledo *et al.* 2018; Fig.4F).

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The development of a central pith led to a new major type of stele, in which the vascular tissues form a hollow cylinder (with pith at the center), the siphonostele (Beck *et al.* 1982; Stewart and Rothwell 1993). The vascular cylinder can be interrupted by leaf gaps where vascular traces diverge toward the leaves (Fig.4J-L). Various types of siphonosteles are present from the Late Carboniferous on, especially among the filicopsids (e.g., Phillips 1974; Beck *et al.* 1982; Rothwell 1999; Schneider *et al.* 2002). Late Devonian and Carboniferous lycopsid trees such as *Sublepidodendron* and *Paralycopodites* have vascular tissues arranged in a hollow cylinder in the largest part of their stems (Eggert 1961), but they lack leaf gaps and the question of whether these represent true siphonosteles is still debated. A variation of the siphonostele is the dictyostele, in which leaf gaps are long (tall) and overlap vertically, giving the impression of a dissected vascular system (Fig.5A-C). The oldest dictyosteles date from the Carboniferous, as seen for example in the marattialean tree fern *Psaronius* (Delevoryas 1964; Fig.5C). Today they are found in many ferns, such as *Osmunda* (Osmundales, Fig. 1) or the tree fern *Dicksonia* (Cyatheales) (Bower 1926).

In the eustele, which is typically found in spermatophytes, the vascular tissues are organized as discrete longitudinal sympodia around the pith (Fig.5D-F). The oldest example of this type of organization is seen in the Middle Devonian progymnosperm *Archaeopteris* (Scheckler 1978; Beck 1979; Fig.5F). Eusteles become more common following the diversification of seed plants in the Carboniferous, a period during which they are found in Cordaitales, early conifers (Voltziales), and various families of pteridosperms. Today, eusteles featuring more or less complex connections between the xylem of the stem and that of branches and leaves (Namboodiri & Beck 1968; Beck *et al.* 1982) characterize the gymnosperms and angiosperms. Some monocotyledons have a modified eustele in which the sympodia are arranged in multiple concentric cycles (Beck *et al.* 1982). These multiple sympodia, in combination with the multiple leaf traces diverging from them, produce the

impression of vascular bundles scattered randomly throughout the ground tissue and preclude recognition of a typical pith or cortex (Fig.5G-I). This type of eustele, called an atactostele, is first documented in fossil palm trunks (*Palmoxylon*; Fig.5I) from the Late Cretaceous (Santonian-Campanian, and possibly as old as the Turonian; Crié 1892; Berry 1916).

Several Middle Devonian to Early Carboniferous plants assigned to the extinct group of the cladoxylopsids displayed a vascular system with numerous separate xylem strands of various size and shape in transverse section. The number of strands ranges from a few in some specimens of *Xenocladia* (Pseudosporochnales) (Arnold 1952; Fig.4I) or *Cladoxylon* (Pseudosporochnales) (Bertrand 1935) to over 130 in the Late Devonian tree *Xinicaulis* (Cladoxylopsid) (Xu *et al.* 2017). Stewart and Rothwell (1993) interpreted this organisation as a transition from an actinostele to a plectostele, a type of protostele in which the xylem and phloem are arranged in alternating plates or U or V-shaped bands (in cross section) (Fig.4G-I); in the most extreme cases, the central strands are absent and the architecture resembles that of a eustele.

While the diversity of stelar anatomy and the evolutionary pathways that led from one type of stele to another have been the subject of many hypotheses and discussions, very little is certain regarding the processes driving the diversification of stelar organization in the Devonian and thereafter. Different scenarios involving several categories of factors have been considered.

(1) Increasing mechanical demands. Walter Zimmerman was one of the first proponents of this mechanical hypothesis (Zimmermann 1959). Because the most peripheral tissues of the axis are the ones that have the highest impact on resistance to bending forces, the arrangement of the xylem at the periphery of a pith vs. at the center of the axis provides more stiffness (Speck & Vogellehner 1988). This suggests that the evolution of stelar organizations that

include a pith may have been driven, at least in part, by mechanical constraints associated with increase in size.

(2) Increasing demand of fluid transport. F.O. Bower proposed in 1908 the hypothesis that the stele increased in complexity in order to optimize water transport in plants that were evolving larger sizes and more complex organization (Bower 1908). The development of a central pith and peripheral xylem minimizes the distances between the water conducting cells and other tissues while limiting the amount of energy spent on producing expensive xylem cells (Raven 1994; Roth & Mossbruger 1996). Thus, such hydraulic demands may have represented a different type of driver in the evolution of the pith.

(3) Changes in hormonal signals linked to the evolution of lateral organs. Building on earlier ideas formulated by Wight (1987), Stein (1993) modelled how the evolution of stelar architecture can be linked to the gradients of auxin produced by more complex lateral appendages (branches, leaves). Stein's models support an origin of pith at the center of the stele related to changes in shoot apex geometry under different hormonal gradient regimes, and the dissection of the stele into discrete vascular bundles as a result of changing receptivity to hormonal signaling.

In all likelihood, combinations of these different factors, which are not mutually exclusive, were responsible for stelar evolution in different groups, especially since the increase in complexity of lateral organs has a direct impact on the biomechanical and hydraulic demands of the plant, in addition to driving shifts in hormonal signaling patterns and homeostasis. It is also possible that these factors had different relative importance in shaping the vascular systems of different plant lineages. Leaves evolved independently in the two major tracheophyte groups - the lycopsids and euphyllophytes - and then, again, independently in several euphyllophyte groups (Tomescu 2009; Sanders *et al.* 2009; Galtier 2010). Given their independent origins, as well as differences in their developmental,

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anatomical, and physiological relationships with subtending stems, specific to each lineage, the advent of leaves must have had different impacts on the architecture of the vascular system in each of these lineages. Nevertheless, the evolution of leaves, along with that of roots (also thought to have evolved independently, at least between the lycopsids and euphyllophytes; Boyce 2005; Hetherington & Dolan 2018), and with the general increase in plant size, led to increasingly more complex plant architectures. These are all factors that can be linked to the increase in complexity of the architecture of the primary vascular system.

VASCULAR CAMBIA AND SECONDARY GROWTH

Another major event in plant evolution that occurred during the Devonian is the advent of the vascular cambium, a lateral meristem producing secondary vascular tissues. Two types can be distinguished: unifacial cambium, producing only secondary xylem (wood), and bifacial cambium that produces secondary xylem on one side and secondary phloem on the other side. Like other meristems, the vascular cambium can have permanent activity, leading to indeterminate growth, or can cease functioning at a genetically determined point, leading to determinate growth. Today, all plants with secondary vascular tissue - with the possible exception of the lycopsid *Isoetes* (Isoetales; Fig.6A-B)- are seed plants and have a bifacial cambium with indeterminate growth. In *Isoetes*, a cambial layer (the lateral meristem) produces a "prismatic layer" (consisting of tracheids and sieve cells) toward the inside and a thin layer of parenchymatous tissue toward the outside (Paolillo 1963; Gifford & Foster 1989). Although functionally bifacial, this cambial layer produces vascular tissues only on one of its sides, like the unifacial cambia. Compared to the dearth of lineages exhibiting vascular cambial growth in the modern flora, the fossil record reveals a much broader diversity of modes of secondary growth (Tomescu & Groover 2019; Fig.6).

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To date, the oldest known occurrences of secondary xylem are known from the Early

Devonian euphyllophytes *Armoricaphyton* (Strullu-Derrien *et al.* 2014; Gerrienne and Gensel

2016) from France and *Franhueberia gerriennei* (Hoffman & Tomescu 2013) (Fig. 2) from

Gaspé (Canada), and from a few additional, as yet unnamed, plant types from New Brunswick

and Quebec (Canada) (Gerrienne *et al.* 2011; Gensel 2018). Subsequent to these early

examples, the fossil record has revealed a remarkable diversity of geologically younger

(Middle Devonian and early Carboniferous) plants that produced secondary xylem. This

structural feature has been reported in lycopsids, basal euphyllophytes, cladoxylopsids,

sphenopsids, basal filicopsids such as the zygopterids, stenokoleales, and lignophytes (Figs. 1,

2, 6). Thus, two key lessons are that (1) secondary growth evolved early (possibly earlier than

410 Ma ago) and that (2) the occurrence of secondary xylem in vascular plants is quite

common, even in groups that do not produce wood today, like the lycopsids and sphenopsids.

Lycopsids, basal euphyllophytes, cladoxylopsids, basal filicopsids, and sphenopsids

are all interpreted as having a unifacial cambium (Cichan & Taylor 1990; Fig.6A-E). This

type of cambium usually produced a small amount of wood (a few millimeters to a few

centimeters) and no secondary phloem, but there are examples of Permian sphenopsids in

which the wood cylinder exceeded 30 cm in radial thickness (Rößler & Noll 2006). The

bifacial cambium, producing both secondary xylem and secondary phloem, is considered the

synapomorphy of the lignophyte clade, which includes the spermatophyte plants and their

extinct progymnosperm sister group (Crane 1985; Doyle & Donoghue 1986; Rothwell &

Serbet 1994; Fig. 6G-H). The oldest evidence for this type of cambium dates to the Middle

Devonian, in the aneurophytalean progymnosperms *Tetraxylopteris*, *Triloboxylon*, and

Proteokalon, all of which possess a well preserved complement of secondary phloem in

addition to secondary xylem (Beck 1957; Scheckler & Banks 1971; Stein & Beck 1983; Fig.

2; Fig. 6G). The Stenokoleales, a Late Devonian-Early Carboniferous group of plants

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sometimes associated with the lignophytes (Matten 1992; Toledo *et al.* 2018), have some secondary xylem (Beck & Stein 1993; Momont *et al.* 2016) but there is no evidence to date for secondary phloem, which would indicate the presence of a bifacial cambium in that group. Interestingly, a bifacial cambium is also documented in the Sphenophyllales, an extinct group of sphenopsids from the Late Devonian-Triassic (Taylor *et al.* 2009; Fig. 2). However, unlike that of the lignophytes, their cambium is usually interpreted as having determinate growth and the largest axes of the best known genus, *Sphenophyllum,* are only up to about 1 cm in diameter. Late Carboniferous and Permian representatives of *Sphenophyllum* had wood with a peculiar system of vertical parenchyma cells located at the corners of tracheids and connected to the rays that has no equivalent in other fossil or extant taxa (Cichan & Taylor 1982; Cichan 1985; Fig. 6F). However, older representatives of the Sphenophyllales seem to have possessed a more typical wood anatomy (Terreaux de Felice *et al.* in press).

Among extant plants, the bifacial vascular cambium can show important variations in functioning, which lead to the development of secondary tissue configurations designated as cambial variants (e.g., Angyalossy *et al.* 2012; Pace *et al.* 2018a, b). Evidence for these different types of "anomalous secondary growth" has also been documented in the fossil record (reviewed by Bodnar & Coturel 2012). For example, some members of the Corystospermales, an extinct group of spermatophytes from the Triassic (250-200 Ma), exhibit both centripetal and centrifugal wood development, as well as possible included phloem (Artabe & Brea 2003; Decombeix *et al.* 2014).

As in the case of the first tracheids, the initial role of wood seems to have been hydraulic rather than structural (Gerrienne *et al.* 2011), and the wood of Devonian-Carboniferous plants already exhibited hydraulic properties comparable to those of some modern taxa (Cichan 1986; Wilson *et al.* 2008; Cascales-Miñana *et al.* 2019, this issue; Tanrattana *et al.* 2019, this issue). A role in mechanical support was acquired later and only in

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certain groups (e.g., Rowe & Speck 2004). Today, most trees are gymnosperms or eudicotyledons in which the wood has a dual function: water conduction and mechanical support. However, several plant types, such as palms (monocotyledons) and tree ferns, demonstrate that secondary xylem is not needed to reach arborescence (i.e., the tree habit). Similarly, there are fossil examples of arborescent plants with no secondary xylem or in which the secondary xylem did not contribute much to the stiffness of the stem (Mosbrugger 1990; Meyer-Berthaud & Decombeix 2009). Such is the case of the arborescent lycopsids, like the famous *Lepidodendron* (and related species of Lepidodendrales) of the Carboniferous, in which most of the mechanical support function was filled by a well-developed bark of secondary origin. The small central ring of wood, while very efficient for water conduction (Cichan 1986), played no role in the stem's stiffness (Mosbrugger 1990).

One of the major questions that remains regarding the evolution of secondary xylem is whether vascular cambial growth evolved independently in several tracheophyte lineages or only once, at the base of the clade (Tomescu & Groover 2019). The traditional view, based on records of representatives with secondary growth in multiple lineages that could be traced back to the Middle Devonian (Fig. 2), was that there had been multiple independent evolutionary origins of this important developmental and structural feature. This perspective found support in the more-or-less major perceived differences in the anatomy of secondary tissues between the different lineages.

These traditional views are being reshaped by evidence coming from two directions. One of these is the realization that some mechanisms regulating vascular cambial growth are shared among major tracheophyte lineages spanning both the lycopsids and the euphyllophytes: lepidodendrales, sphenopsids, progymnosperms, and spermatophytes (Rothwell *et al.* 2008; Sanders *et al.* 2011). The other line of evidence is provided by the discovery of multiple euphyllophyte types that demonstrate secondary xylem production in

the Early Devonian (Gerrienne *et al.* 2011; Hoffman & Tomescu 2013; Strullu-Derrien *et al.* 2014; Gensel 2018). These fossils are pushing the documented occurrence of this feature to within a few million-years from the oldest representatives (and, potentially, the origin) of the clade. These data prompted Hoffman and Tomescu (2013) to propose that underlying mechanisms for secondary growth had become part of the euphyllophyte developmental toolkit very early in the evolution of the clade, and to raise the question of whether some of these mechanisms may have originated even earlier, in a common ancestor of euphyllophytes and lycopsids.

To provide an empirical framework for addressing such questions, Tomescu and Groover (2019) proposed an updated perspective that approaches vascular cambial growth as a complex developmental process of modular nature. Their view explains the diverse anatomies of secondary growth seen in different lineages (referred to as modes of secondary growth) as a mosaic pattern of expression of distinct developmental-regulatory modules (responsible for different component processes of secondary growth) among different lineages, living and extinct. This view emphasizes patterns of shared processes and developmental regulation, and accommodates a hypothesis-testing approach to address questions about the evolutionary origins of secondary growth.

FURTHER EVOLUTION OF HOMOXYLOUS WOODS IN SEED PLANTS (SPERMATOPHYTES)

From its first appearance in the basal euphyllophytes, through the lignophytes and all the way to the extant conifers, wood has fulfilled both its functions - conduction and mechanical support - with only one type of cell, the tracheid. The structure of wood that has only tracheids as conducting cells is referred to as homoxylous (Fig. 7). For example, in most conifers the tracheids have a small diameter (<50 μm) and the rays are small - short and

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uniseriate. Wood of this type is known as picnoxylic (Fig. 7A). In contrast, extant cycads, as well as many Paleozoic pteridosperms have manoxylic wood, characterized by large tracheids with diameters up to 150 μm and large rays (more than 5 cells wide and up to 200 cells tall) (Galtier 1992; (Fig. 7B-C).

The first spermatophytes that appeared in the Late Devonian are represented by small axes with only a small amount of wood (Serbet & Rothwell 1992), but significant patterns of anatomical disparity can be observed in the wood of homoxylous spermatophytes as soon as the early Carboniferous. For example, ray size in early Carboniferous spermatophytes ranged from uniseriate rays only one or two cells high in some taxa (such as like *Bilignea*) to multiseriate rays up to a hundred cells high in *Calamopitys* or *Pitus* (Galtier 1992; Galtier & Meyer-Berthaud 2006; Dunn 2006; Fig.7B-C). A combination of very large rays and small tracheids (<50 μm in diameter) occurs in several early Carboniferous taxa, but is extremely rare in the rest of the fossil record prior to the appearance of vesselless angiosperms, toward the end of the Mesozoic (Philippe *et al.* 2010; Boura *et al.* 2019, this issue). Ray tracheids and axial parenchyma are present since at least the Late Devonian-early Carboniferous (Beck & Wight 1988; Galtier & Meyer-Berthaud 2006) (Fig. 7A).

Secondary xylem tracheids range widely between 15 and 97 μm in diameter in *Elkinsia,* one of the best known Late Devonian spermatophytes (Serbet & Rothwell 1992). In the Carboniferous and Permian, taxa with tangential tracheid diameters exceeding 100 μm are found among several groups of pteridosperms, including the Calamopityales, Lyginopteridales, and Medullosales, while the Cordaitales, the first conifers, and other spermatophytes such as the Glossopteridales, had smaller tracheids (Cichan 1986; Pigg & Taylor 1993; Vozenin-Serra et al. 1991). Tracheid length is less well documented, in part because the longest tracheids exceed the size of thin-section slides that have been prepared from fossil material. Tracheid length reaches at least 1 cm in *Callistophyton*

(Callistophytales), and several centimeters in *Medullosa*, both of which are late Carboniferous spermatophytes.

Reconstructions of the hydraulic properties of selected fossil plants by Cichan (1986) and Wilson & Knoll (2010) suggest that the wide, long, and densely pitted tracheids of the Carboniferous pteridosperms *Medullosa*, *Callistophyton*, and *Lyginopteris* occupied an area of tracheid morphospace that is not populated by any younger or extant seed plant taxa. Those authors hypothesized that the unusually high conductivity of these tracheids was related to the combination of a non-selfsupporting growth habit, in which tracheids do not play a role in mechanical support, and growth in a warm wetland environment in which there is little risk of embolism (air bubbles in the vascular system) caused by drought or frost. It is interesting to note that such high-conductivity tracheids are to date unknown in the Mesozoic pteridosperms, despite the existence at that time of broadly similar conditions.

The pitting of secondary xylem tracheids in the earliest spermatophytes typically consists of crowded multiseriate oval to oblique pits with oval aperture (Serbet & Rothwell 1992), similar to most representatives of their sister group, the progymnosperms (Beck & Wight 1988; Fig. 7D). A different type of pitting, with uniseriate circular pits possessing circular apertures, is documented in three Late Devonian-early Carboniferous woods belonging to progymnosperms or spermatophytes (Beck & Wight 1988; Prestianni *et al.* 2010; Decombeix *et al.* 2011). Scalariform pits in secondary xylem tracheids are first documented in progymnosperms, such as *Rellimia* and *Protopitys* (Beck & Wight 1988; Fig. 7E), and occur afterwards throughout the history of spermatophytes, for example, in the putative Permian conifer *Xuanweioxylon scalariforme* (He *et al.* 2013), and some cycads, bennettitales, and angiosperms, as well as in some Mesozoic taxa of uncertain affinities, such as *Sahnioxylon* or *Ecpagloxylon* (Philippe *et al.* 2010). Wilson & Knoll (2010) hypothesized that the tracheids with scalariform pitting of the Cretaceous bennettitale *Cycadeoidea* had pit

area resistances similar to those of extant vesselless angiosperms, such as *Trochodendron*, but the evolutionary history and hydraulic properties of homoxylous woods with scalariform pitting have yet to be properly understood.

One of the major events in the evolution of homoxylous woods was the advent of torus-margo pit membranes with a highly permeable water-porous marginal region, the margo, and a thickened central zone impermeable to water, the torus. Under normal and favorable conditions, water moves from one tracheid to the adjacent one through the margo while the torus is centrally located in the pit chamber allowing water flow. In the case of an embolism, the pit membrane is aspirated against the pit border, such that the torus blocks the pit aperture, preventing the spread of air through the xylem (Bailey 1916). Torus-margo pit membranes ensure, thus, both a high efficiency of water conduction when environmental conditions are hydraulically safe, and a high degree of hydraulic safety when conditions are degraded (Pittermann *et al.* 2005, 2006b; Sperry *et al.* 2006).

Today, torus-margo pit membranes are found in all extant conifer families (Bauch *et al.* 1972; Dute 2015), as well as in other gymnosperm taxa, such as extant *Ginkgo* (Wilson & Knoll 2010) or the gnetales (*Ephedra*, *Gnetum* and *Welwitschia*) (Carlquist 2012), but are absent in the cycads (Bauch *et al.* 1972). Torus-margo pit membranes have also been reported in the fern genus *Botrychium* (Ophioglossidae) (Morrow & Dute 1998). Most angiosperms lack a torus and have homogeneous membranes with smaller size pores randomly distributed. However, in a few angiosperm families (Ericaceae, Oleaceae, Thymeleaceae, Rosaceae, Ulmaceae, Cannabaceae, Schisandraceae), the fine mesh of the typical intervascular pit membrane is associated with a centrally thickened area that resembles a torus (Ohtani & Ishida 1978; Ohtani 1983; Wheeler 1983; Jansen *et al.* 2004; Dute 2015; Nguyen *et al.* 2017).

In 1967, Schmid pointed out that because of the small number of records of torus-margo pit membranes in the fossil record, the evolution of this character has been inferred

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largely based on data from living plants. Fifty years later this is still the case (Pittermann *et al.* 2010; Wilson & Knoll 2010; Wilson 2016) and the timing of the evolution of torus-margo pit membranes remains an enigma. It is possible that this character evolved independently in different lineages, in response to environmental pressures, contributing to the optimization of the balance between safety and efficiency of the secondary xylem (Wilson 2013; Pittermann *et al.* 2010). All Paleozoic conifers have bordered pits with simple pit membranes, i.e., devoid of a torus (Wilson & Knoll 2010). Pre-Cretaceous occurrences of fossil wood with a well-defined torus-margo are very rare and sometimes questionable (Holden 1915), but the presence of torus-margo pit membranes is documented in many coniferous fossil woods from the Cretaceous on (Schmid 1967). Nevertheless, there are recent reports of torus-margo pit membranes from the middle Triassic of Argentina (Bodnar *et al.* 2015) and the basal Jurassic of France (Moreau *et al.* 2019) (Fig. 2).

In sum, the combination of fossil data and modelling thus shows that homoxylous woods in fossil seed plants displayed a wide range of hydraulic properties resulting from (1) a rapid increase in anatomical diversity in the Carboniferous, and (2) the advent of torus-margo pit membranes possibly as early as the Triassic.

VESSELS AND EARLY ANGIOSPERM EVOLUTION

Vessels are water-conducting units consisting of several non-living cells (vessel elements) that are connected vertically by perforated end walls (perforation plates). Unlike the pits found on the lateral walls of tracheids, perforation plates lack a pit membrane and are complete holes through both primary and secondary walls. The end wall can have one (simple perforation plate) or several perforations (multiple perforation plate). In the latter case, the perforations can be scalariform, reticulate, or foraminate (grouped circular) (Esau 1965; IAWA Committee 1989). Vessel elements are thought to have evolved by dissolution of the

primary wall in certain areas of the end wall of tracheids. Vessels range from a few

millimeters to several meters in length and can exceed 500 μm in diameter, in some

angiosperm lianas (e.g., Angyalossy *et al.* 2015; Apgaua *et al.* 2017).

The presence of vessels is generally associated with the wood of angiosperms and the

evolution of vessels has often been cited as one of the main reasons for the evolutionary

success of angiosperms, due to the putative increase in hydraulic conductivity that it entailed

(e.g., Bailey 1944; Carlquist 1975; Bond 1989). However, not all angiosperm have vessels

and vessels have also been reported in other living and extinct plant groups. Among free-

sporing vascular plants, vessels have been reported in the primary xylem of lycopsids, such as

Selaginella, of the sphenopsid *Equisteum*, and of several filicopsids, such as *Pteridium*

(Duerden 1934; Bailey 1944; Bierhorst 1958; Carlquist & Schneider 1997; Schneider &

Carlquist 2000; Fig. 8A-C). It is generally agreed that the vessels of these plants have evolved

independently from those found in spermatophytes.

In the spermatophytes, vessels are present in the angiosperms, the gnetales (Fig. 8E-

G) and the extinct Gigantopteridales (Li *et al.* 1996; Li & Taylor 1999; Figs. 2, 8D). The

oldest occurrence of vessels in spermatophytes was reported in small stems of late Permian

age (ca. 270 Ma) assigned to the Gigantopteridales, a group of unclear affinities from the

Permian-Triassic (Li *et al.* 1996; Li & Taylor 1999; Fig. 1; Fig. 8D). Vessels in the wood of

Vasovinea tiannii are 150-250 μm in diameter, more rarely up to 500 μm, and each vessel

element is 4.5-5 mm long. The perforation plates superficially resemble those commonly

found in gnetales (foraminate perforation plates, Fig. 8G) but can be distinguished from the

latter by a few characters, including the high number of pores (about 14 rows) and the

presence of pores that bear remnants of primary wall. One putative vessel observed in the

primary xylem shows a scalariform perforation plate more similar to those found in

angiosperms. Tian and Li (1992) also reported the presence of "scalariform-reticulate

perforation plates" in some primary xylem tracheary elements of *Guizhouoxylon*, another

possible gigantopterid from the Late Permian of China. Currently, no other evidence is

available for vessels in the secondary xylem of spermatophytes prior to the Cretaceous,

almost 150 million years after the Gigantopteridales (Fig. 2).

Permian and Triassic polyplicate pollen grains reminiscent of gnetalean pollen are the

oldest putative evidence for the Gnetales. By the Cretaceous they are well represented in the

fossil record by pollen, charcoalified seeds, and impressions/compressions of reproductive

and vegetative structures (Friis *et al.* 2011). There is, however, no convincing record of fossil

gnetalean wood and hypotheses about wood evolution in this group (e.g., Carlquist 2012) are

based exclusively on extant taxa. Vessel diameters are broadly variable within the group, from

around 15 μm in the desert plant *Welwitschia* to >400 μm in some lianescent *Gnetum* species

(Fischer & Ewers 1995).

Despite recent claims of Jurassic angiosperms and even older pollen exhibiting

angiospermous features (reviewed by Herendeen *et al.* 2016), the oldest widely accepted

fossil evidence for angiosperms consists of pollen from the Early Cretaceous (Hauterivian, ca

130 Ma; Brenner & Bickoff 1992). Macrofossil evidence in the form of flowers and leaves

documents significant diversification of the group throughout the Cretaceous (see Friis *et al.*

2011 for a review of the angiosperm fossil record). The oldest unequivocal angiosperm woods

with vessels date to the Albian, 110-100 million years ago (Herendeen *et al.* 1999). The

vessels in these woods have either simple (e.g., *Paraphyllanthoxylon*) or scalariform (e.g.,

Icacinoxylon) perforation plates, with some taxa having both types of perforations (Baas &

Wheeler 1996; Wheeler & Baas 2019, this issue). Whereas wide vessels (>200 μm) occur in

some of the earliest angiosperm woods (Albian-Cenomanian), mean tangential vessel

diameter is <100 μm in most Cretaceous angiosperm woods (Wheeler & Baas 2019, this

issue). In one Late Cretaceous (Maastrichtian) assemblage with ten wood types, maximum

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vessel diameters ranged from 80–250 µm (Olmos Formation, Mexico; Martinez-Cabrera & Estrada-Ruiz 2014..

One long-standing matter of debate has been the single vs. multiple origin of vessels in the seed plants. Classical studies from the 1900's and the first cladistic analyses based on morphological characters (e.g., Doyle & Donoghue 1986) have interpreted the occurrence of vessels in both gnetales and angiosperms as a synapomorphy supporting a close relationship between the two groups. On the other hand, detailed anatomical studies have suggested independent origins of the vessels in the two groups: the foraminate perforations typical of gnetaleans (Fig. 8G) thought to have evolved from tracheids with circular bordered pits on the end walls, and the angiosperm perforation plate from tracheids that had scalariform pits on the end walls (see Thompson 1918; Bailey 1944, 1953). Other authors (Muhamad & Sattler 1982) have suggested that both types of perforation plates occur in the gnetales and, thus, that the two types of vessels are homologous. More recently, Fischer and Ewers (1995) and Carlquist (1996) have taken the view that the apparent similarities between gnetales and angiosperm vessels are the result of convergence. If convergent evolution is, indeed, the explanation for the vessels of angiosperms and gnetales, then the secondary xylem vessels of the Permian Gigantopteridales, with their distinctive perforation plates, could represent another instance of convergence.

Another key question is that of the putative advantage provided by vessels over tracheids and their roles in angiosperm evolution. Vessels have often been considered a key element in the success of the angiosperms (e.g., Bailey 1944; Carlquist 1975; Bond 1989). However data from both extant and fossil angiosperms suggests a more nuanced situation. First, ecophysiological studies comparing the hydraulic capacity in extant angiosperms and gymnosperms show that at small lumen diameters, below 60-70 µm, tracheids can be as efficient hydraulically as vessels (e.g., Hacke *et al.* 2005; Sperry *et al.* 2006; Brodribb *et al.*

2012). Pitterman *et al.* (2005) showed that the hydraulic efficiency of conifer wood for a

given sapwood-area exceeds that of angiosperm wood for the same average conduit diameter,

in part thanks to the presence of torus-margo pits (see above). As a result, if vessel diameter is

limited (as the result of selection pressures, because narrower vessels are less sensitive to

embolism caused by freeze-thaw events or by drought), conifer wood can be more efficient.

However, vessels have the advantage of reaching a given conductivity with lower investment

in wood conduit area (Tyree et al. 1994; Feild & Arens 2007). It is possible that the earliest

angiosperm vessels did not provide a significant hydraulic advantage. If they did, it might

have also caused a decreased embolism tolerance compared to contemporaneous vesselless

seed plants, according to Feild and Wilson (2012). A recent study of rainforest angiosperms

from New Caledonia shows that taxa bearing vessels with scalariform plates and vesselless

taxa have comparable (low) hydraulic efficiency and safety (Trueba *et al.* in press).

The importance of vessels in angiosperm diversification, at least in its early stages, is

also challenged by several lines of evidence suggesting that the earliest angiosperms were

vesselless (Baas & Wheeler 1996; Herendeen *et al.* 1999). Recent phylogenetic analyses of

extant angiosperms place the vesselless genus *Amborella* (ANA grade, Fig. 1) as sister-group

to all other angiosperms. Several other vesselless taxa occur in relatively basal angiosperm

groups (e.g., Winteraceae; Fig. 7H), although loss of vessels in some of the latter cannot be

excluded (Baas & Wheeler 1996; Herendeen *et al.* 1999; Feild *et al.* 2002; see also Boura *et

al.* 2019, this issue). On the other hand, the fossil record provides a counterpoint to the

hypothesis of initially vesselless early angiosperms, as the oldest known angiosperm woods

have vessels. Nevertheless, the oldest evidence for angiosperms, represented by pollen,

predates the oldest angiosperm wood (Hickey & Doyle 1977; Friis *et al.* 2011), indicating that

the oldest angiosperm wood has yet to be found. Furthermore, the distinction between

vesselless early angiosperm woods and non-angiosperm homoxylous woods in the fossil

record can be problematic, especially since potentially useful characters appear to be plesiomorphic or convergent within seed plants (see discussion in Philippe *et al.* 2010). Several Mesozoic fossil woods with homoxylous structure, like *Lhassoxylon aptianum* (Vozenin-Serra & Pons 1990; Fig. 7F), *Ecpagloxylon mathiesenii* (Philippe *et al.* 2010) or one of the specimens described in Neraudeau *et al.* (2017; Fig. 7G), also show unusual features (respectively tangential lines of axial parenchyma, scalariform intertracheary radial pits, or very abundant axial parenchyma) compared to extant conifer taxa, so that they are sometimes described and considered as an early stage of the evolution that led to angiosperm wood types.

The high hydraulic efficiency of vessels led to a significant increase in wood anatomical diversity among angiosperms by allowing the diversification of other cell types devoted to distinct functions (Hudson *et al.* 2010). This diversity likely contributed to the diversification of angiosperm growth forms. The diversification of angiosperm lianas, for example, has been associated to heteroxyly (e.g., Isnard & Feild 2015), although there are also many examples of lianas in homoxylous fossil seed plants (Burnham 2015). The fossil record suggests that Early Cretaceous (120-110 Ma) angiosperms were small-sized (see Philippe *et al.* 2008; Coiffard *et al.* 2012), with the first large angiosperm trees found in the Cenomanian and Turonian (about 100-90 Ma) (Coiffard *et al.* 2012; Jud *et al.* 2018; Saulnier *et al.* 2018). However, this is based mostly on high-latitude localities and more investigations of lower latitude floras are needed. Evidence of angiosperm-dominated forests with a significant diversity can be found in latest Cretaceous-Paleocene wood assemblages from India (Wheeler *et al.* 2017); such assemblages become more common and similar in composition to extant communities during the Eocene (Licht *et al.* 2014; 2015; Woodcock *et al.*, 2019, this issue). While vessels certainly played a role in the increasing diversity of angiosperms throughout the Cretaceous, many questions remain on the evolution of their wood anatomy, especially in the context of whole-plant physiology and environmental factors.

CONCLUSIONS

Since the first observations of anatomically preserved plants in the XIXth century, paleobotany has contributed significant - and sometimes unexpected - data to our understanding of the evolution of plant vascular systems. Important among these is the realization that many key features of the vascular systems that we observe today appeared very early in plant evolution (i.e., in the Paleozoic, >250 million years ago, Fig. 2). This is true at various levels, from the organisation of vascular tissues within plant axes (stelar architecture, secondary tissues), to the types of conducting cells (tracheids, vessel elements), and even the fine elements of cell structure (pitting type, variation in conduit diameter). Furthermore, current advances in the methods used to model water flow in the xylem of fossil plants suggest that, as a result of these early evolutionary developments, significant differences in hydraulic properties existed as early as the Carboniferous. Another important lesson from the fossil record is that features related to xylem hydraulic properties might have ranked among the main drivers of the diversification of vascular plants in the late Silurian-Early Devonian and the evolution of secondary xylem (wood) in the Early Devonian. Finally, consideration of the rich data provided by the fossil record in a phylogenetic context raises numerous questions about the perceived homoplastic nature vs. potential single origin of major features of the vascular system, such as the presence and functional details of a vascular cambium or of vessels. Understanding the developmental mechanisms and the evolutionary and environmental constraints that led to the anatomies observed today will undoubtedly require continued study of the anatomy and physiology of extinct and extant plants. The fossil record will play an important role in these studies, as an irreplaceable source of (1) chronostratigraphic data as calibration points for the timing of main evolutionary events, and

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(2) examples of character combinations that do not exist today and can be used to test

hypotheses formulated based on extant taxa or can be incorporated in such hypotheses.

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FIGURE LEGENDS

Fig. 1. Simplified phylogenetic tree of embryophytes and stratigraphic ranges of the main lineages. The tree topology is composite, based on several studies from the recent literature. Observed stratigraphic ranges (as documented by unambiguous fossils) shown by continuous lines. Dashed lines represent ranges hypothesized based on phylogenetic analyses or molecular dating. Extinct groups in blue; taxa in quotation marks are considered paraphyletic. Geologic time scale as adopted by the International Commission on Stratigraphy (v2018/08).

Fig. 2. First occurrences and stratigraphic ranges of main characters in vascular plant evolution discussed in this paper. Sections 1-5 correspond to the text sections. Stratigraphic ranges of early tracheid types based on Edwards (2003, Fig.1). "Modern tracheids" include both those of lycopsids and of euphyllophytes. A cambial layer in extant lycopsids is present in *Isoetes* (see text and Fig. 6A, B). Taxa in blue are extinct groups. Taxon names and geologic time scale as in Fig. 1.

Fig. 3. Water-conducting cells in early land plants (top) with details of their wall structure (bottom). A. Bryophyte hydroid; B. S-type tracheid (fossil) typical of rhyniopsids; C: G-type tracheid (fossil) typical of zosterophyllophytes; D: P-type tracheid (fossil) typical of trimerophyte grade plants (basal euphyllophytes). From Kenrick & Crane 1997

Fig. 4. Stelar diversity part 1. Dotted line = epidermis, white = ground tissues, grey = primary phloem, black = primary xylem. Ts = transverse section.
A-C. Protostele; B. Ts of *Gleichenia* sp. stem (extant); C. Ts of *Lepidodendron esnostense* stem, early Carboniferous, France.

D-F. Actinostele; E. Ts of *Psilotum* sp. axis (extant); F. Ts of *Tristichia longii*, early

Carboniferous, France.

G-I. Plectostele; H. Ts of *Selaginella* sp. stem (extant); I. Ts of *Xenocladia medullosina*,

Middle Devonian, Kazakhstan.

J-L. Solenostele; K. Ts of *Adiantum* sp. rhizome (extant); L. Ts of *Tempskya* sp. rhizome,

middle Cenomanian, France.

Scale bars: E = 250 μm; B, H, K = 500 μm; C, L = 1 mm; F, I = 2 mm.

Fig. 5. Stelar diversity part 2. Dotted line = epidermis, white = ground tissues, grey = primary

phloem, black = primary xylem. Ts = transverse section.

A-C. Dictyostele; B. Ts of *Polypodium* sp. rhizome (extant); C. Ts of *Psaronius brasiliensis*

stem (MNHN.F.1445 picture. R. Thomas), Permian, Brazil.

D-F. Eustele; E. Ts of *Vitis vinifera* stem (extant); F. Ts of *Callixylon zalessky*, Late

Devonian, USA.

G-I. Atactostele; H. Ts of *Oenocarpus* sp. stem (extant); I. Ts of *Palmoxylon* sp., Oligocene,

France.

Scale bars: E = 500 μm; B, I = 1 mm; F = 2 mm; H = 5 mm; C = 5 cm.

Fig. 6. Secondary growth. Ts = transverse section.

A-B. Secondary growth from a bifacial cambium in *Isoetes* sp. stem (extant); A. Ts, cambium

located at the periphery of lighter, vacuolated area around the central tissues; B. Radial

longitudinal section, cambium located along the vertical boundaries between the lighter,

vacuolated layers and the dark-nucleated layers that border them externally.

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C-E. Unifacial cambial growth; C. Ts of *Lepidodendron serratum*, late Carboniferous, USA;

D. Ts of *Cladoxylon* sp., early Carboniferous, Germany; E. Ts of *Arthropitys* sp., late

Carboniferous, USA.

F. Bifacial cambium in *Sphenophyllum* sp., Permian, France.

G-H. Bifacial cambium with well-preserved secondary phloem; G. Ts of *Tetraxylopteris* sp.,

Middle Devonian, USA; H. Ts of *Stanwoodia* sp., early Carboniferous, Scotland.

 Scale bars: A, G, H = 250 μm; B, E, F = 500 μm; D=1.5 mm; C = 5 mm.

Fig. 7. Homoxylous wood. Ts = transverse section.

A. Ts; Picnoxylic wood in *Callixylon* sp., Late Devonian, USA.

B. Ts; Manoxylic wood in *Calamopitys schweitzeri*, early Carboniferous, France.

C. Tangential longitudinal section (Tls); Multiseriate rays up to 100 cells high in *Eristophyton*

waltonii, early Carboniferous, Scotland.

D. Radial longitudinal section (Rls); Crowded multiseriate oval to oblique bordered pits with

oval aperture in *Callixylon* sp., Late Devonian, USA.

E. Rls; Scalariform pits in *Protopitys* sp., early Carboniferous, France.

F-G. Ts; Unusual homoxylous wood structure in *Lhassoxylon aptianum* (UPMC 10468) and

in a specimen from Neraudeau et al. (2017).

H. Ts; Homoxylous wood structure in *Drimys* sp. (Winteraceae; extant)

Scale bar D, E = 100 μm, A, B = 200 μm, F, G = 250 μm, C, H = 500 μm.

Fig. 8. Vessels and heteroxylous woods.

A-C. Vessels in the primary xylem A-B. *Pteris sp.* (extant) C. *Tempskya sp.* rhizome, middle

Cenomanian, France.

D. Ts. Vessels in *Vasovinea tianii* (Gigantopteridales)

E-G. Heteroxylous wood in *Ephedra* sp. (extant) (Gnetales), E-F. Ts, G. Rls. foraminate

perforation plate.

Scale bar G = 50 μm, B, C = 100 μm A, F = 200 μm D, E = 1 mm.

Figure 2 Main events

Figure 3_draft Kenrick & Crane fig

Figure 4 Stele types part 1

Figure 5 Stele types part 2

Figure 7 Homoxylous woods

Figure 8 Vessels & heteroxylous woods