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Diversity and evolution of the megaphyll in Euphyllophytes: Phylogenetic hypotheses and the problem of foliar organ definition

*Diversité et évolution de la mégaphylle chez les Euphyllophytes : hypothèses
phylogénétiques et le problème de la définition de l'organe foliaire*

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ABSTRACT

Recent paleobotanical studies suggest that megaphylls evolved several times in land plant evolution, implying that behind the single word “megaphyll” are hidden very different notions and concepts. We therefore review current knowledge about diverse foliar organs and related characters observed in fossil and living plants, using one phylogenetic hypothesis to infer their origins and evolution. Four foliar organs and one lateral axis are described in detail and differ by the different combination of four main characters: lateral organ symmetry, abdaxity, planation and webbing. Phylogenetic analyses show that the “true” megaphyll appeared at least twice in Euphyllophytes, and that the history of the four main characters is different in each case. The current definition of the megaphyll is questioned; we propose a clear and accurate terminology in order to remove ambiguities of the current vocabulary. Further analyses of megaphyll evolution need to consider new definitions and descriptors, as well as make use of improved phylogenetic hypotheses.

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RÉSUMÉ

De récentes études paléobotaniques ont suggéré que la mégaphylle est apparue plusieurs fois au cours de l'évolution des plantes terrestres, ceci implique que le mot « mégaphylle » décrit des notions et des concepts très différents. Nous proposons donc une révision des connaissances portant sur les divers organes foliaires ainsi que leurs caractères associés observables chez les fossiles et les plantes actuelles. Les origines et l'évolution de ces organes sont inférées à partir d'une hypothèse phylogénétique issue de la littérature. Quatre organes foliaires et un axe latéral sont décrits en détails et se distinguent par la combinaison différentielle de quatre principaux caractères : la symétrie des organes latéraux, l'abdaxité ainsi que les processus d'aplanissement et de « palmure ». Les inférences phylogénétiques montrent que la mégaphylle dite « vraie » serait apparue au moins deux fois chez les Euphyllophytes et que les caractères impliqués dans sa définition n'évoluent pas de la même manière dans les deux cas. La définition même de la mégaphylle est discutée, nous proposons donc une terminologie claire et précise afin de lever les ambiguïtés du

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vocabulaire. De nouvelles analyses traitant de son évolution sont à entreprendre et nécessiteraient aussi bien l'usage de nouveaux descripteurs et définitions, que de nouvelles phylogénies.

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1. Introduction

Despite a few interesting and key studies combining morphological and molecular evidence (Schneider, 2007; Schneider et al., 2009), within the last few decades, molecular data have been used more often than morphological characters to reconstruct phylogenetic trees in plants; this is particularly illustrated by the well-known current ordinal classification of Angiosperms based only on molecules (APG, 2009). However, in order to take fossils into account in a broader evolutionary context, it is also essential to consider the information provided by morphology and anatomy, and also to rigorously investigate the means by which morphological homologies are assessed. This is required to understand how apomorphic character states are determined and to trace character transformations (Hawkins et al., 1997; Kenrick and Crane, 1997; as also highlighted Schneider, 2007; Schneider et al., 2009). Reproductive features (Endress, 2010; Friis et al., 2011) such as flowers have always received more attention than vegetative features and thus more explicit research on their description and evolution has been carried out. For example, hypotheses on floral homologies in angiosperms have been carried out in greater detail and have been more comprehensively assessed (as reviewed by Soltis et al., 2005, and Ingrouille and Eddie, 2006) than vegetative morphology. In contrast, except for a few studies (Kenrick and Crane, 1997; Pryer et al., 1995; Rothwell, 1999; Schneider, 2007; Schneider et al., 2009), stems, leaves and roots have often been neglected in studies dealing with evolutionary relationships within land plants. The study of these organs, and especially the megaphyll (large branched plagiotropic lateral organ with a developed lamina; see the whole definition in Section 4.1.5), is nevertheless necessary to understand the evolution of Euphyllophyte diversity. Furthermore, understanding timing of foliar organ(s) appearance in evolutionary history is necessary to infer the major evolutionary acquisitions that allowed vascular plants to colonize all the land surface, and thus to understand their history since Silurian time (Beerling et al., 2001; Osborne et al., 2004). The problem is that the three main vegetative organs recognized in vascular plants (stem, leaves and roots) were respectively treated as the same object across the phylogenetic breadth of the plant kingdom (and considered thus as homologous across taxonomic groups) by plant biologists working at the molecular, cellular and physiological levels. This reductive treatment is often applied by taxonomists.

A spruce needle is very different in form, however, from an *Adiantum* (maidenhair fern) frond, from a chestnut tree leaf, or from the leaf of an *Equisetum* (horsetail), not only in anatomy and morphology but also by a distinct history. Currently all these foliar organs are grouped under the general term of megaphyll. However, is it still relevant to use

a single term to describe such different forms observed in living plants, especially taking into account the diversity of fossil species? Can we apply the same concept and name to all the foliar organs in fossil taxa? And a final question: are the diverse megaphylls observed in Euphyllophytes all homologous?

From Devonian to Carboniferous, within Spermatophyte, progymnosperm, fern and horsetail groups, many different types of laminate leaves with multiple kinds of venation and contrasting petiolar anatomy have been described, many of which could have evolved independently (Boyce and Knoll, 2002). Ferns (with horsetails) and Spermatophytes (with progymnosperms) each belong to a distinct lineage in the Euphyllophytes (Pryer et al., 2001, 2004; Qui et al., 2006; Schneider et al., 2009) and the earliest Euphyllophytes (e.g. the early Devonian fossils *Psilophyton* and *Pertica*, Banks et al., 1975; Gerrienne, 1997; Granoff et al., 1976) were leafless. This indeed strongly suggests at least two origins for megaphylls from leafless ancestors: one in the lineage leading to ferns and horsetails (the Monilophytes) and one in the lineage leading to progymnosperms and seed plants (the Lignophytes). Whether or not the megaphyll appeared twice or more than twice (Friedman et al., 2004; Galtier, 2010; Sanders et al., 2009; Tomescu, 2008), the palaeobotanical community agrees with a multiple origin of foliar organs observed in Euphyllophytes.

Therefore, the term “megaphyll” is open to misinterpretation when it is considered as a common and unique descriptor of the whole of the living Euphyllophytes. Moreover, within a defined clade, it is biological nonsense not to take fossil taxa into consideration.

Thus, when taxonomists use megaphyll as a descriptor in their phylogenetic analyses, they are implicitly masking a potential diversity of characters and presenting a primary hypothesis of homology that might be questionable. Furthermore, there is still no available study that combines, firstly, a complete phylogenetic framework involving living plants and fossils; and secondly, accurate rigorous hypotheses on primary homology for foliar characters that takes into account the observed diversity, and proposes alternative scenarios involving potential analogy. The aims of the present study are therefore:

- to provide a critical review of foliar descriptors and definitions traditionally used for the megaphyll, with a focus on anatomical data, in order to improve the megaphyll definition in extinct as well as in living groups;
- to use a land plant phylogenetic hypothesis already published (including fossils and living taxa) to infer hypotheses on the evolution of foliar organs in Euphyllophytes.

This study is preliminary and would lay the ground for further analyses performed on new phylogenetic hypotheses that would integrate more taxa and morpho-anatomical data and/or would focus on particular clades (such as Monilophytes).

2. Material and methods

2.1. Megaphyll definitions

The descriptors traditionally attributed to the megaphyll (Galtier, 2010; Kaplan, 2001; Kenrick and Crane, 1997) (e.g., a distinct lamina, complex venation, large size, leaf gaps – if associated with solenosteles and dictyosteles, etc.) are not always found within living taxa because of numerous cases of reversal and loss (see for Angiosperms the review of Bell, 2008). Therefore if we include fossils, the study will become quite complex.

To define the megaphyll and its diversity, we will consider every type of foliar organ – or more widely photosynthetic organs – observed among land plants (including extinct groups). Twenty-eight genera are thus selected that correspond to representative taxa in Euphyllophytes.

In the following text, taxonomic names follow the classification of Chase and Reveal (2009) with some exceptions concerning some extinct lineages not treated in this publication. In these latter cases, we follow Taylor et al. (2009). The main clades are: Monilophytes (including Polypodiidae or leptosporangiate ferns, Ophioglossidae and Marattiidae representing eusporangiate ferns, Equisetiidae or Sphenophytes or horsetails, Psilotidae or whisk ferns, “cladoxyloids” and other extinct fern groups such as “zygopterids”, “botryopterids” and “anachoropterids”), “progymnosperms” and Spermatophytes, the monophyly of taxa in “quotes” being still debated. Polypodiidae (Bierhorst, 1971; Gifford and Foster, 1989; Kramer and Green, 1990) are represented by the living *Osmunda* (Osmundales) and *Polypodium* (Polypodiales), Ophioglossidae (Bierhorst, 1971; Gifford and Foster, 1989; Kramer and Green, 1990) by *Ophioglossum* and *Botrychium* (Ophioglossales), Marattiidae (Bierhorst, 1971; Gifford and Foster, 1989; Kramer and Green, 1990) by *Marattia* (Marattiales) and the extinct *Psaronius* (Marattiales), and Psilotidae (Bierhorst, 1971; Gifford and Foster, 1989; Kramer and Green, 1990) by living *Tmesipteris* and *Psilotum*. The extinct fern lineages are represented by *Zygopteris* (“zygopterid” ferns, Phillips and Galtier, 2005) and *Rhacophyton* (Rhacophytales, Leclercq, 1954), *Botryopteris* (“botryopterid” ferns, Galtier, 1981; Rössler and Galtier, 2003; Rothwell, 1991) and *Psalixochlaena* (“anachoropterid” ferns, Holmes, 1981, 1989). For convenience, Polypodiidae, Ophioglossidae, Marattiidae, Psilotidae, “zygopterids”, *Rhacophyton*, “botryopterids” and “anachoropterids” all will be considered ferns. Equisetidae are represented by living *Equisetum* (Equisetales), extinct *Sphenophyllum* (Sphenophyllales, Reed, 1949; Yao et al., 1999) and *Archaeocalamites* (Calamitales, Mamay and Bateman, 1991). Extinct “cladoxyloids” are represented by *Pseudosporochnus* (Pseudosporochnales, Berry and Fairon-Demaret, 1997, 2002; Leclercq and Banks, 1962; Stein and Hueber, 1989) and *Ibyka* (Iridopteridales,

Skog and Banks, 1973), extinct “progymnosperms” by *Aneurophyton* (Aneurophytales, Serlin and Banks, 1978) and *Archaeopteris* (Archaeopteridales, Beck, 1971; Fairon-Demaret and Leponce, 2001; Meyer-Berthaud et al., 1999) and Spermatophytes by extinct *Elkinsia* (Elkinsiales, Serbet and Rothwell, 1992), extinct *Medullosa* (Medullosales, Smoot and Taylor, 1981), living *Cycas* (Cycadales) and living *Pinus* (Pinales). Euphyllophytes are also represented by the traditional extinct and leafless *Psilophyton* (Banks et al., 1975; Gerrienne, 1997; Trant and Gensel, 1985) and *Pertica* (Granoff et al., 1976), traditionally belonging to “trimerophytes”, which would be paraphyletic according to Kenrick and Crane (1997) and Schneider (2007). Outside Euphyllophytes, *Lycopodium* (Kramer and Green, 1990; Thomas, 1992) represents Lycopodiidae or Lycophytes. In addition, leafless *Aglaophyton* (non vascular Polysporangiophytes, Remy and Hass, 1996) and *Rhynia* (“rhyniopsids”, Edwards, 1980) have been selected, essentially as extragroups for the phylogenetic analyses. All these taxa represent as well the diversity among Euphyllophytes (and also Tracheophytes) as the selected taxa *pro parte* present in the phylogenetic hypothesis used here (see below). Some other Devonian plants, such as *Foozia*, should be added in further analysis because of the originality of their morpho-anatomy.

The precise description of lateral organs resulted from observations on specimens in several collections (National Museum of Natural History, Paris, France; University Montpellier 2 and UMR AMAP, CIRAD, Montpellier, France; National Museum and Charles University Prague, Czech Republic; Pilsen Museum, Czech Republic) in addition to published data (see below).

2.2. Diversity of lateral branch systems and/or foliar organs in Tracheophytes

2.2.1. *Psilophyton* lateral branching system (Banks et al., 1975; Gerrienne, 1997; Trant and Gensel, 1985)

Psilophyton is a “trimerophyte” from the Early Devonian. Main cauline axes display both dichotomous and pseudomonopodial branching as lateral branching systems. First and second order branches bear dichotomous ultimate appendages (twice to thrice isotomous) that are non-planated (Fig. 1A). Lateral branching systems (LBS) are cauline and display radial symmetry. Thus, *Psilophyton* exhibits a primitive model of LBS and other kinds of LBS may have been derived from it.

2.2.2. *Pseudosporochnus* lateral branching system (Berry and Fairon-Demaret, 1997, 2002; Leclercq and Banks, 1962; Stein and Hueber, 1989)

Pseudosporochnus is a “cladoxyloids”; this extinct group was very diverse and widespread during the Devonian. These tree-like plants displayed a cauline erect axis-trunk bearing photosynthetic branches (LBS) in an apical crown (Fig. 1B). The first-order branches were helically arranged and probably deciduous; both first and second order branches dichotomized (“digitate branching”) with helically arranged ultimate units that were tridimensional and several times dichotomous. The primary branches displayed a radial symmetry but the anatomy of other division

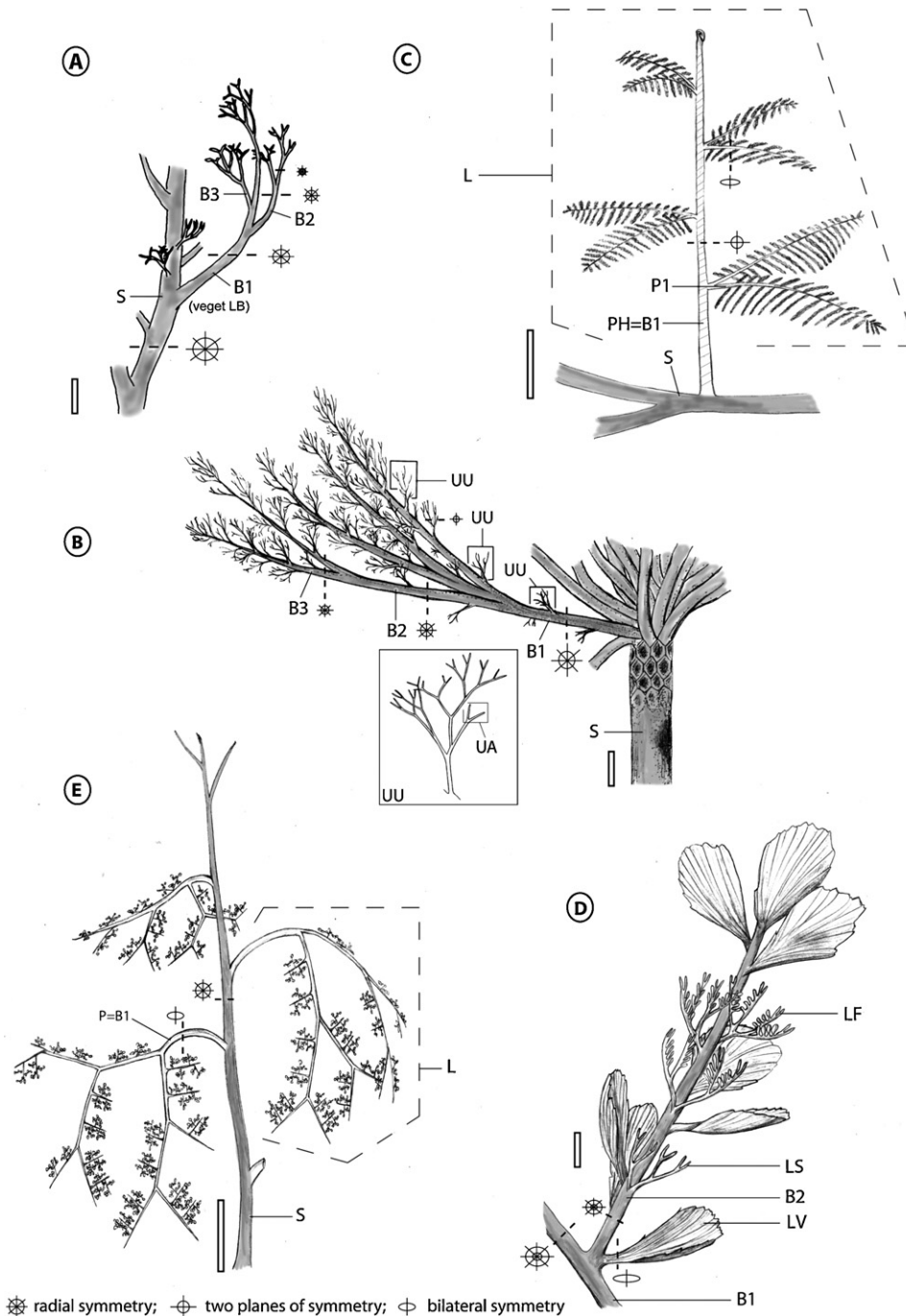


Fig. 1. Diversity of lateral branching systems (LBS). A. *Psilophyton*: stem (S) bearing a lateral system constituted of successive orders of pseudomonopodial branches (B1, B2, B3) and terminating with isotomous ultimate units (UU) bearing ultimate appendages (UA). The whole system (drawn in grey) shows a radial symmetry (redrawn from Banks et al., 1975). Bar = 1 cm. B. *Pseudosporochnus*: one lateral branch system borne at the top of a trunk (S), the branching of B1 and B2 is digitate; all branches are bearing ultimate units (UU) terminating as ultimate appendages (UA) (Redrawn from Berry and Fairon-Demaret, 2002). Scale bar = 10 cm. C. *Zygopteris*: horizontal stem (S) bearing a modified LBS with the B1 in the form of a petiole or phyllophore (PH) showing two planes of symmetry and B2 as paired pinnae (P1) with bilateral symmetry. The ultimate divisions borne on the pinnae are small laminate pinnules, not visible on the figure. The whole system is interpreted as a single large leaf/frond (L) (redrawn from Phillips and Galtier, 2005). Scale bar = 10 cm. D. *Archaeopteris*: detail of the LBS, the whole B1 is not represented but only one attached penultimate branch (B2), which is bearing bilaterally symmetrical UA interpreted as small leaves (L) either unwebbed or laminate. LV = vegetative leaf; LS = sterile leaf; LF = fertile leaf (redrawn from Phillips et al., 1972). Scale bar = 5 mm. E. *Elkinsia*: erect slender stem (S) bearing a modified LBS with the B1 in the form of a petiole (P) showing a single plane of symmetry and dichotomous branching then distichous arrangement of successive orders (= pinnae) bearing ultimate divisions as small laminate pinnules. The whole system is interpreted as a single large leaf (L) (redrawn from Serbet and Rothwell, 1992). Scale bar = 5 mm. Grey = cauline Axes with radial symmetry; Hatched = phyllophore with two perpendicular planes of symmetry.

orders is not well known. Ultimate appendages (UA) are distal ramifications of ultimate units (UU) and divide isotomously (Fig. 1B); they are more or less planated according to Stein and Hueber (1989) but are interpreted as definitely three-dimensional by Berry and Fairon-Demaret (1997) (p.369). Webbing as well as the presence of a lamina are absent. We decided to treat the lamina as absent and planation as present in this case. Berry and Fairon-Demaret (1997) described *Pseudosporochnus* LBS but their terminology is different as from the one proposed here: their “LBS” correspond to our “ultimate units – UU” and their “ultimate branching units – UBU” correspond to our “ultimate appendage – UA”. We decided to follow our terminology in order to improve the homogeneity of vocabulary.

2.2.3. Sphenophyte leaf (Gifford and Foster, 1989; Mamay and Bateman, 1991; Reed, 1949; Yao et al., 1999)

Equisetum is the only living genus belonging to Equisetidae (or Sphenophytes). *Equisetum* leaves are narrow, inserted in whorls around the cauline axis and fused into nodal sheaths. They are neither ramified nor circinate. They possess hydathodes and a single central vein. The latter character is confusing and may explain why the *Equisetum* leaf has often been described as a microphyll, but one that is not homologous of the microphyll of Lycopodiidae, also named lycophyll (Schneider et al., 2002). *Sphenophyllum* is an extinct sphenophyte genus belonging to Sphenophyllales. In contrast to that of *Equisetum*, the *Sphenophyllum* leaf is broad with a well developed lamina. Leaves are heterophyllous, spatulate and present wide ranges of variation in leaf size. Two veins are often present at the base of the leaf and bifurcate several times. *Archaeocalamites* is a late Devonian member of the Calamitaceae displaying leaves arranged in whorls on the distal branches and dichotomizing one to three times (Jennings, 1970).

2.2.4. Zygopteris leaf (Galtier, 2003; Phillips and Galtier, 2005)

The leaves of “zygopterid” ferns were helically borne on a creeping rhizome (Fig. 1C); they show a quadriseriate arrangement of pinnae (i.e. the pinnae were inserted as alternating pairs on either side of the primary rachis). The frond was up to four times divided and pinnules were small. Petiole anatomy (i.e. phyllophore type) is remarkable, the foliar trace presenting two perpendicular planes

of bilateral symmetry. This anatomy is not present in any living fern group.

2.2.5. Botryopteris leaf (Galtier, 1981; Rössler and Galtier, 2003; Rothwell, 1991)

“Botryopterid” ferns, from the Early Carboniferous to the beginning of the Permian, exhibited an important foliar diversity. The leaves, helically borne on the stem, were at least six times pinnate. The petiole trace had bilateral symmetry and exhibited a unique anatomy, characteristic of the genus. The oldest species, *Botryopteris antiqua*, showed a quite narrow lamina (almost absent) whereas *B. forensis* displayed small pinnules.

2.2.6. Osmunda leaf (Gifford and Foster, 1989; Kramer and Green, 1990)

Osmunda presents a short erect stem bearing roots and erect circinate leaves with persistent bases. The leaf is once to twice pinnate and is representative of the standard fern megaphyll, also called a frond. The frond is divided into opposite pinnae inserted on a primary central rachis, more or less in a single plane, and possesses bilateral symmetry. Each pinna has determinate growth and is composed of a number of pinnules, which are the laminate distal appendages. We propose here that the diversity of fronds observed in living ferns represents variation from this standard: extreme reduction in water ferns, such as *Azolla* spp. (Azollaceae), or more divided fronds in many species, such as the bracken fern, *Pteridium aquilinum* (Dennstaedtiaceae), or non divided leaves with an entire broad lamina as in *Asplenium (Phyllitis) scolopendrium* (Aspleniaceae), or with a peculiar indeterminate growth as in *Lygodium* (Lygodiaceae), or with a pseudodichotomous branching in Gleicheniaceae (Smith et al., 2006), etc.

2.2.7. Archaeopteris (“progymnosperms”) lateral branching system (Beck, 1971; Fairon-Demaret and Laponce, 2001; Meyer-Berthaud et al., 1999)

Archaeopteris is an extinct tree that lived during the Late Devonian. It was the main species of the first widespread Devonian forests. It has been interpreted as one of the earliest known modern trees with trunks showing massive wood and secondary phloem. The trunk produced deciduous LBS consisting of two orders of branches. Laminate or dichotomous non-laminate photosynthetic ultimate appendages – traditionally interpreted as small leaves (Beck, 1971) – were helically borne on ultimate (B2)

Fig. 1. Diversité des systèmes de ramification latéraux (LBS). A. *Psilophyton* : tige (S) portant un système latéral constitué d'ordres successifs de ramification pseudomonopodiales (B1, B2, B3) qui sont terminées par des unités ultimes isotomes (UU) portant des appendices ultimes (UA). L'ensemble du système (en gris) présente une symétrie radiale (adapté de Banks et al., 1975). Échelle = 1 cm. B. *Pseudosporochnus* : le système de ramification latéral s'insère à l'extrémité du tronc (S), le mode de ramification de B1 et B2 est de type digité et toutes les branches portent des unités ultimes (UU) se terminant en appendices ultimes (UA) (d'après Berry et Fairon-Demaret, 2002). Échelle = 10 cm. C. *Zygopteris* : la tige horizontale (S) porte un LBS modifié dont le premier ordre de ramification (B1) correspond à un pétiole ou phyllophore (PH) avec deux plans de symétrie. Les B2 sont organisés en paires de pennes (P1) à symétrie bilatérale. Les divisions terminales portées par les pennes sont de petites pinnules laminées (non visibles sur la figure). L'ensemble du système est interprété comme une unique grande feuille/fronde (L) (d'après Phillips et Galtier, 2005). Échelle = 10 cm. D. *Archaeopteris* : détail du LBS, B1 n'est pas représenté mais seulement une branche pennultime (B2) portant des UA à symétrie bilatérale interprétés comme de petites feuilles (L), laminées ou non. LV = feuille végétative ; LS = feuille stérile ; LF = feuille fertile (d'après Phillips et al., 1972). Échelle = 5 mm. E. *Elkinsia* : tige grêle érigée (S) portant un LBS modifié avec B1 qui correspond à un pétiole (P) présentant un seul plan de symétrie et un mode de ramification dichotome. Puis se succèdent des ordres de ramifications (= pennes) arrangés de façon distique et portant des divisions ultimes telles des petites pinnules laminées. L'ensemble du système est interprété comme une unique grande feuille (L) (d'après Serbet et Rothwell, 1992). Échelle = 5 mm. En gris = axes caulinaires à symétrie radiale ; en hachuré = phyllophore avec deux plans de symétrie perpendiculaire.

and penultimate branches (B1) (Fig. 1D). B1 and B2 display radial symmetry whereas laminate or non-laminate ultimate appendages exhibit bilateral symmetry and a complex dichotomous venation.

2.2.8. *Elkinsia* lateral branching system (Serbet and Rothwell, 1992)

Elkinsia is an early Spermatophyte from the Upper Devonian; the slender erect stem bore helically arranged LBS interpreted as dimorphic leaves branching dichotomously to pinnately and presenting a diversified morphology (Fig. 1E). Fertile leaves were tridimensional whereas the vegetative ones displayed very small laminate pinnules at their distal ends. Fertile leaves seemed to have an apical location on the main axis. We have to specify that the reconstruction of *Elkinsia* is based on dispersed elements but we assume the presence of pinnules on vegetative leaves.

2.3. Methods

2.3.1. Selected characters

Foliar characters have already been used several times in phylogenetic analyses, especially in ferns (Kenrick and Crane, 1997; Pryer et al., 1995; Rothwell, 1999; Schneider, 2007; Schneider et al., 2009; Stevenson and Loconte, 1996). However, because of an unequal distribution of taxonomic sampling (including or not fossil taxa and/or modern lineages), the treatment of foliar organs (i.e., selection of descriptors and coding of states) is also quite biased or contrasts among studies.

The term megaphyll was described by Kenrick and Crane (1997) as leafy appendages of seed plants, ferns and basal Equisetiidae. True megaphylls are characterized by a developed lamina and complex venation patterns. Although they are typically of large size with a pinnate organization, megaphylls show an extreme diversity in terms of form and size (Kenrick and Crane, 1997).

Some foliar characters traditionally used in the literature are not used in the present study. For example, circinate venation is a character considered as the main criterion defining extant ferns (Polypodiidae, Marattiidae and Ophioglossidae). However, circination is not a character common to the whole of ferns: for instance there is no standard circinate venation in Ophioglossidae (Smith et al., 2006). Furthermore, the rarity of young crossers in fossils makes it difficult to confirm circinate development in extinct taxa (Schneider et al., 2009).

To discuss the foliar organ concept, we propose that all lateral photosynthetic organs (including leaves) be considered to be lateral branching systems (LBS, Fig. 1). The comparison of their characters will allow a better discrimination between different kinds of foliar organs (from unwebbed lateral branches to megaphylls). However, the anatomical description of some of these lateral branching systems remains unclear. The variability of foliar organs thus must be described in detail in order to collect as much information as possible. In this respect, we propose to focus principally on four anatomical characters of importance regarding foliar organs (versus cauline axis). Some have been already discussed in previous studies

(Galtier, 2010; Sanders et al., 2009). We have to point out that phyllotaxy is also a major criterion characterizing leaves. We have chosen, however, not to use it in our consideration of the LBS concept. Indeed, this character describes developmental reiteration of leaves on the cauline axis; because it can often be difficult to distinguish foliar from cauline organs on fossils, we thought that the use of this character would have been misleading. To be rigorous, we should have considered the insertion of ramifications on each order of the LBS (B1, B2, . . . Fig. 1) for which the distinction between cladotaxy and phyllotaxy is unclear.

Symmetry of lateral branching systems: The presence of one or two planes of symmetry characterizes bilateral symmetry (Fig. 2). Bilateral versus radial symmetry is defined from the cross section of vegetative organs depending of the position of protoxylem strands and of the global shape of the vascular supply of the LBS or the leaf (Galtier, 2010). Comparing symmetry of stem, LBS and leaf permits identification – or not – of an anatomical distinction between organs. It is difficult to distinguish between a foliar or cauline nature of lateral ramifications, especially in putative basal groups like “cladoxyloids”. We also must note that the bilateral symmetry of lateral branching systems is not homologous with the dorsiventrality of rhizomes, which results in their prostrate subterranean habit. Symmetry of LBS is defined here for the first-order branches (B1 in Fig. 1).

Abdaxity: Fig. 2 brings to light differences between bilateral symmetry and abdaxity with the examples of fern and seed plant petioles. In the ferns *Osmunda* and *Psali-xochlaena* and in the seed plant *Elkinsia*, the leaf trace possesses a single plane of symmetry with a clear distinction between abaxial (inferior) and adaxial (superior) faces. This differentiation is supported by an adaxial concavity on the rachis. In contrast, there are two perpendicular planes of symmetry in the petiole or phyllophore of *Zygopteris* preventing the differentiation of abaxial from adaxial face; in this case there is no abdaxity. Recognition of this aspect of lateral-appendage organization also depends on determination of the position of the protoxylem strand, which is adaxial (abdaxity S) in ferns versus abaxial (abdaxity I) in seed plants and *Archaeopteris*. Abdaxity is a new term, introduced here, for a character similar but more complete than the “abaxial/adaxial identity” of Sanders et al. (2009), it is defined conjointly by:

- the presence of a single plane of symmetry;
- the position of protoxylem poles;
- eventual petiole trace concavity.

Furthermore, bilateral symmetry and abdaxity are defined for the first-order branch of the leaf in this study, but they can be different in the more distal branching orders. That is why these characters generally vary along leaf ramification divisions. Notice that the “leaves” of *Tmesipteris* lack a petiole and thus the character is not applicable.

In this study, we described the lamina through two characters: planation and webbing (Zimmermann, 1938). However, caution is required in the observation of these

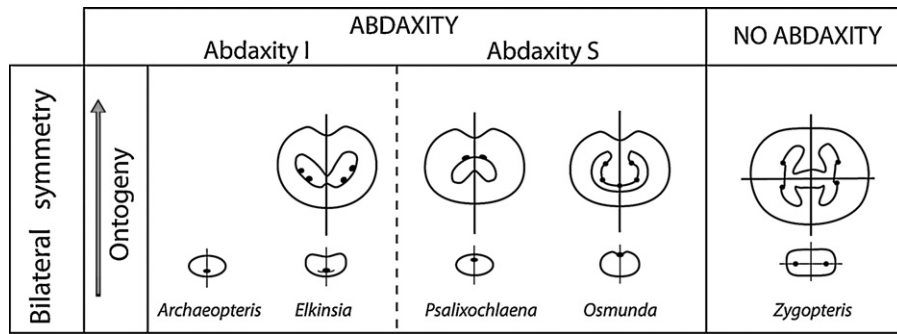


Fig. 2. Two types of abdoxity observed in Euphyllophytes. Black dots = protoxylem strands, lines = symmetry planes. Abdoxity I: Protoxylem on abaxial side, Abdoxity S: protoxylem on adaxial side.

Fig. 2. Deux types d'abdoxité observés chez les Euphyllophytes. Points noirs = fibres de protoxylème ; lignes = plans de symétrie. Abdoxité I : protoxylème sur la face abaxiale, Abdoxité S : protoxylème sur la face adaxiale.

descriptors on fossils because taphonomic processes attendant fossilization can confer the appearance of flattened and webbed morphology (Chaloner, 1999). For the present study, the absence or presence of planation and webbing is coded for the whole LBS: it can as well be borne on first-order branches as on ultimate appendages.

Planation: planation is the transition from three-dimensional to bi-dimensional terete segments. Planate organs are thus flattened branching axes organized into a single plane (Beerling and Fleming, 2007).

Webbing: webbing consists of filling in flattened branches with laminar tissue. In developmental terms, the webbing of telomes to produce a laminate leaf blade involves, first, the production of lateral outgrowths and, second, fusion of adjacent branches (Beerling and Fleming, 2007). The acquisition of planation then webbing induces the development of the lamina.

2.3.2. Phylogenetic hypotheses

It is necessary to rely on relevant phylogenetic analysis to understand megaphyll evolution and especially to define one or several kinds of foliar organs among Euphyllophytes. Consequently, we propose to use one phylogenetic tree illustrating the main consensus hypotheses published by Schneider (2007). The tree presented and used here (Figs. 3 and 4) is synthetic, meaning it is not exactly the same as any of the published ones, in order to provide a larger and summarized view of recent phylogenetic knowledge and hypotheses on the subject (see below). The characters tested (symmetry, abdoxity, planation and webbing) were added after the fact by the authors in order to permit discussion of their evolution.

We arbitrarily added some fossil representatives not present in Schneider (2007) (such as “cladoxyloids”, “zygopterids”, “botryopterids” and “anachoropterids”) in order to increase the diversity of fossil foliar forms. We also removed some living taxa to reduce the sampling and to focus our study on basal lineages. Our synthetic tree proposes the monophyly of Monilophytes, but with paraphyletic “cladoxyloids” (*Pseudosporochnus* and *Ibyka*) as sister to a clade including Equisetidae and ferns. In Schneider's supertree (fig. 2 in Schneider, 2007), *Ibyka*

appears as closely related to Equisetidae, confirming a traditional view (Stewart and Rothwell, 1993). We prefer the hypothesis of Taylor et al. (2009) who proposed that Iridopteridales (including *Ibyka*) share more characters with Pseudosporochnales (“cladoxyloids”) than with Equisetidae. In the study of Schneider (2007), other “cladoxyloids” are lacking, and relationships of *Ibyka* with traditional “cladoxyloids” were thus not tested. In the maximum parsimony analysis combining fossils and living taxa (Fig. 1A in Schneider, 2007), Equisetidae display an unresolved position within the Monilophytes. We propose to regroup Equisetidae with ferns in order to keep the hypothesis that horsetails would be embedded within ferns in accordance with other phylogenies focused on living taxa and including molecular data (Qui et al., 2006; Schneider et al., 2009). Furthermore, a clade that groups together some Paleozoic extinct ferns (*Botryopteris* and *Psalixochlaena*) is proposed to be related to *Osmunda* and *Polypodium*, and represents extinct Polypodiidae or leptosporangiate ferns (Taylor et al., 2009). In addition, the Euphyllophytes are rooted by extinct *Aglaophyton* (non vascular Polysporangiophyte), extinct *Rhynia* (“rhyniopsids”) and living *Lycopodium* (Lycopodiidae), which together represent the basal Tracheophytes. We also added *Psilophyton* to the Euphyllophyte sample because this genus is a key taxon when considering early LBS diversity. Lignophytes are represented in Schneider's tree by *Archaeopteris*, *Pinus* and *Cycas*; we propose to insert the additional *Aneurophyton*, *Elkinsia* and *Medullosa* to increase fossil representatives. The positions of extinct Spermatophytes are in accordance with Hilton and Bateman (2006).

2.3.3. Phylogenetic inference of character evolution

In order to study the evolution of the selected supposed foliar organ characters within Euphyllophytes we used Mesquite version 2.74 software (Maddison and Maddison, 2010), which allows the inferred history of each selected character to be traced on the phylogenetic hypothesis by applying the maximum parsimony (MP) criterion and by treating characters as unordered and unweighted. If inference for a character on the tree provides several character

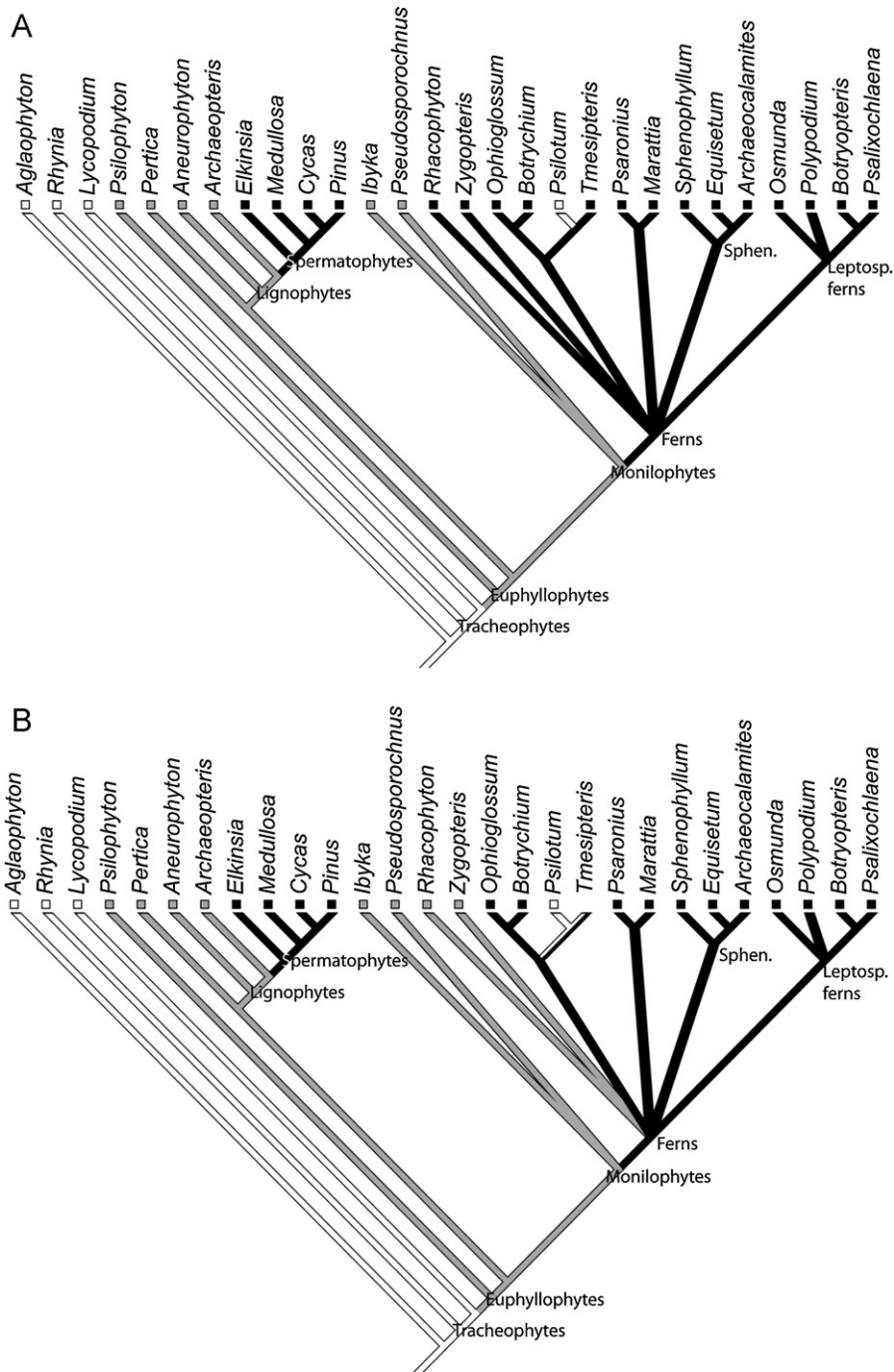


Fig. 3. Inferred evolution of bilateral symmetry and abdxity of lateral branching systems (LBS). A. Evolution of bilateral symmetry, white = non-applicable, grey = radial, black = bilateral. B. Evolution of abdxity, white = non-applicable, grey = absent, black = present. For details on phylogenetic hypotheses, see text. Sphen. = Sphenophytes, Leptospor. Ferns = Leptosporangiate ferns.

Fig. 3. Inférence de l'évolution de la symétrie bilatérale et de l'abdxité des LBS. A. Évolution de la symétrie bilatérale, en blanc = non applicable, en gris = radial, en noir = bilatéral. B. Évolution de l'abdxité, en blanc = non applicable, en gris = absent, en noir = présent. Pour les détails des analyses phylogénétiques, se référer au texte. Sphen = Sphénophytes, Leptospor. ferns = fougères leptosporangiées.

distributions (resulting in an ambiguous state for some nodes), all optimizations (including ACCTRAN and DELTRAN) are tested. The four characters of interest were coded as follows:

- symmetry of LBS: non-applicable, radial, bilateral;
- abdxity: non-applicable, absent, present;
- planation: absent, present;
- webbing: absent, present.

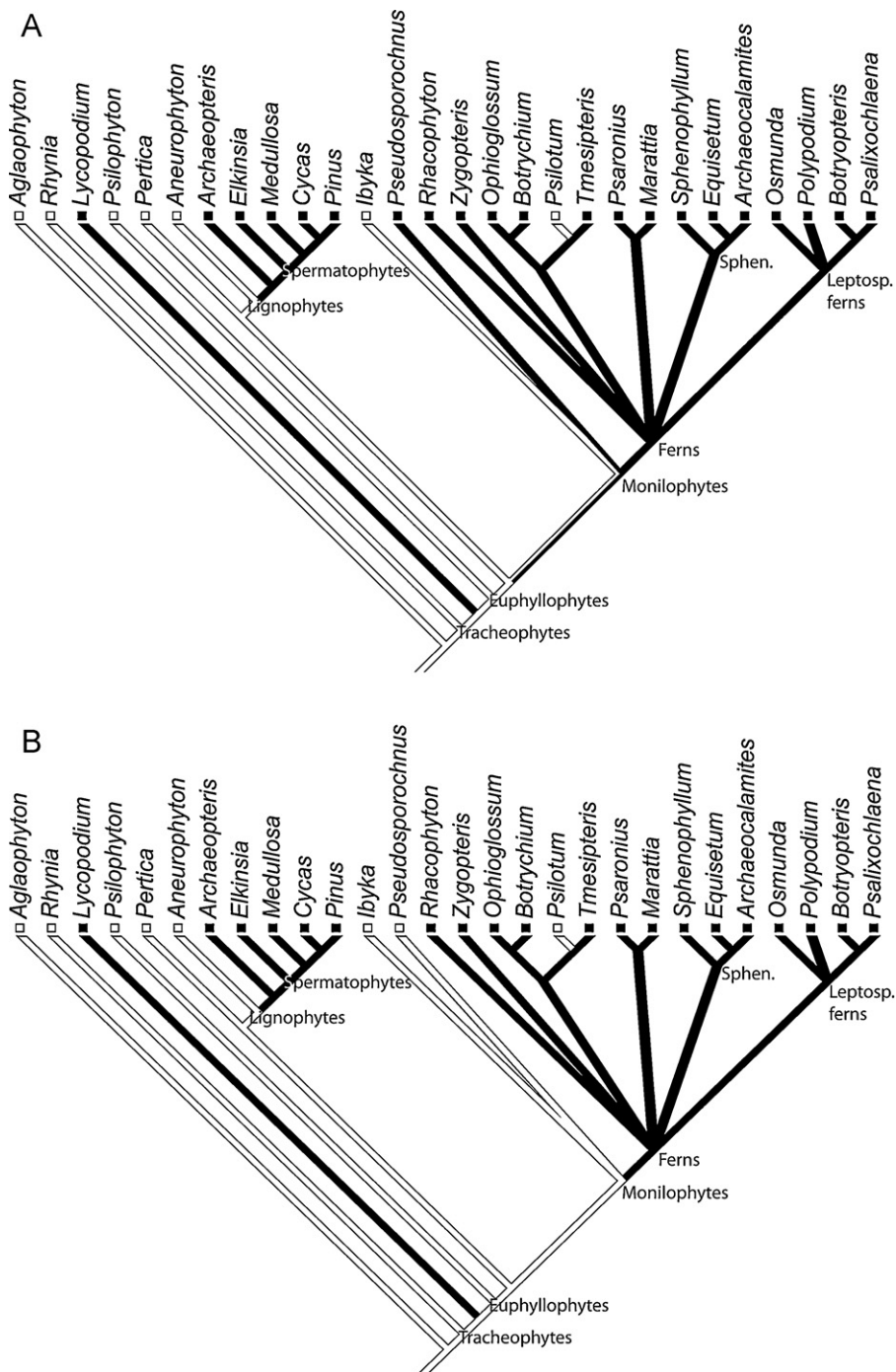


Fig. 4. Inferred evolution of planation and webbing. A. Evolution of planation. B. Evolution of webbing. For details on phylogenetic hypotheses, see text. White = absent, black = present. Sphen. = Sphenophytes, Leptosp. Ferns = Leptosporangiate ferns.

Fig. 4. Inférence de l'évolution de l'aplanissement et de la palmure. A. Évolution de l'aplanissement. B. Évolution de la palmure. Pour les détails des analyses phylogénétiques, se référer au texte. En blanc = absent, en noir = présent. Sphen = Sphénophytes, Leptosp. ferns = fougères leptosporangées.

Symmetry and abaxity are defined for differentiated lateral branches (related to pseudomonopodial growth). Outside Euphyllophytes, both characters are coded as non-applicable because taxa do not have pseudomonopodial

growth. Coding of the selected characters for all the taxa is reported in Table 1, determined by personal observations on Paris, Liège and Montpellier collections and from the published data mentioned above.

Table 1

Character coding.

Tableau 1

Codage des caractères.

	Symmetry of LBS	Abdaxity	Planation	Webbing
<i>Aglaophyton</i> ^a	Non-applicable	Non-applicable	Absent	Absent
<i>Rhynia</i> ^a	Non-applicable	Non-applicable	Absent	Absent
<i>Lycopodium</i>	Non-applicable	Non-applicable	Present	Present
<i>Psilophyton</i> ^a	Radial	Absent	Absent	Absent
<i>Pertica</i> ^a	Radial	Absent	Absent	Absent
<i>Aneurophyton</i> ^a	Radial	Absent	Absent	Absent
<i>Archaeopteris</i> ^a	Radial	Absent	Present	Present
<i>Elkinsia</i> ^a	Bilateral	Present	Present	Present
<i>Medullosa</i> ^a	Bilateral	Present	Present	Present
<i>Cycas</i>	Bilateral	Present	Present	Present
<i>Pinus</i>	Bilateral	Present	Present	Present
<i>Ibyka</i> ^a	Radial	Absent	Absent	Absent
<i>Pseudosporochnus</i> ^a	Radial	Absent	Present	Absent
<i>Rhacophyton</i> ^a	Bilateral	Absent	Present	Present
<i>Zygopteris</i> ^a	Bilateral	Absent	Present	Present
<i>Ophioglossum</i>	Bilateral	Present	Present	Present
<i>Botrychium</i>	Bilateral	Present	Present	Present
<i>Psilotum</i>	Non-applicable	Non-applicable	Absent	Absent
<i>Tmesipteris</i>	Bilateral	Non-applicable	Present	Present
<i>Psaronius</i> ^a	Bilateral	Present	Present	Present
<i>Marattia</i>	Bilateral	Present	Present	Present
<i>Sphenophyllum</i> ^a	Bilateral	Present	Present	Present
<i>Equisetum</i>	Bilateral	Present	Present	Present
<i>Archaeocalamites</i> ^a	Bilateral	Present	Present	Present
<i>Osmunda</i>	Bilateral	Present	Present	Present
<i>Polypodium</i>	Bilateral	Present	Present	Present
<i>Botryopteris</i> ^a	Bilateral	Present	Present	Present
<i>Psalixochlaena</i> ^a	Bilateral	Present	Present	Present

LBS: lateral branching systems.

^a Fossil taxon.

3. Results

3.1. Inferred evolution of characters

3.1.1. Symmetry of lateral branching systems (LBS)

Radial symmetry is inferred as ancestral in Euphyllophytes.

The Maximum Parsimony (MP) proposes a single scenario (Fig. 3A): one appearance of bilateral symmetry in Spermatophytes and one appearance in ferns within Monilophytes. The non-applicable status for *Psilotum* suggests a secondary loss of the LBS rather than illustrating a plesiomorphic state preceding the acquisition of pseudomonopodial growth.

3.1.2. Abdaxity

Absence of abdaxity is inferred as ancestral in Euphyllophytes.

A single MP scenario proposes two appearances of abdaxity (Fig. 3B): once in Spermatophytes and once in ferns with reversal in *Rhacophyton* and *Zygopteris*. The inclusion of *Tmesipteris* and *Psilotum* in ferns suggests that abdaxity was present in ancestors but can no longer be observed. Peculiar foliar features or absence of leaves in, respectively, *Tmesipteris* and its close relative *Psilotum* are proposed as the result of reduction (minimization), which can thus be interpreted as an evolutionary reversion.

3.1.3. Planation

Absence of planation is inferred as ancestral in Polysporangiophytes (Fig. 4A).

Planation would have appeared in *Lycopodium* (with the appearance of the lycophyll), in a clade grouping *Archaeopteris* and Spermatophytes and in Monilophytes with two equally parsimonious scenarios: one appearance in Monilophytes with one reversal in *Ibyka* (ACCTRAN optimization) or one appearance in *Pseudosporochnus* and one appearance in ferns (DELTRAN optimization). The absence of planation in *Psilotum* is explained by a regressive loss of the leaf.

3.1.4. Webbing

Absence of webbing is inferred as ancestral in Polysporangiophytes.

Webbing would have appeared three times in Tracheophytes (Fig. 4B): in *Lycopodium* (resulting in the lycophyll), in a clade grouping *Archaeopteris* and Spermatophytes, and in ferns (the absence of webbing in *Psilotum* is again explained by a regressive loss of the leaf).

4. Discussion

Phylogenetic trees allow us to define different kinds of foliar organs in the Euphyllophytes. The successive branching orders (B1, B2, . . . UA) of LBS can display both cauline and foliar nature; therefore, it can be very difficult to

distinguish stems from leaves. The way in which the concept of a “lateral branching system” is defined allow us to identify which kinds or parts of LBS display cauline features and which ones exhibit foliar features.

4.1. Vocabulary and hypotheses

Searching for accurate definitions of foliar organs is important for taxonomists and perhaps even more for phylogeneticists. Indeed, the term “leaf” is satisfactory as a descriptor for a diagnosis (i.e. descriptive term without any implied homology sense, *sensu* Lebbe, 1991) but insufficient to emphasize the primary homology assessments included in a phylogenetic “character” concept. For this reason, the terms described below have to be considered as a sum of characters and not a combination of descriptors.

4.1.1. Cauline lateral branches

Cauline lateral branches result from anisotomous branching of the main axis. They are not plagiotropic and are not necessarily specialized for the same functions as extant leaves (photosynthesis, respiration, evapotranspiration), and are thus distinct from the next trait, lateral branching systems (LBS). For instance, lateral systems of *Psilophyton* (Fig. 1A) are branched cauline axes that end in ultimate appendages. They correspond to the cauline ramified system *sensu* Gerrienne (1997).

4.1.2. Lateral branching system (LBS)

Although this term has been widely used in the literature, we propose here a new meaning in order to permit comparison of the different kinds of foliar organs within the Euphyllophytes. “LBS” encompasses every organ involved in the principal functions of leaves within extant organisms (photosynthesis, respiration, evapotranspiration) regardless the morpho-anatomy, except for the case of organs with a radially symmetrical stele. Plagiotropic ramifications, possibly deciduous, as for instance, the penultimate branches of *Archaeopteris*, typically belong to this latter category. The lateral branching system is a ramification borne lateral to a main axis, with cauline and/or foliar parts, and possibly bearing ultimate appendages on distal extremities. This LBS definition encompasses the different kinds of foliar organs and facilitates the comparison between homologous structures. LBS can encompass true stems bearing leaves. For example, B1 of *Pseudosporochnus* are true stems/branches and ultimate appendages of *Archaeopteris* are true megaphylls (with or without lamina). The organs described below (quadriseriate leaf, pinnate leaf, ...) are subsets of LBS.

4.1.3. Ultimate appendages

Ultimate appendages are small, dichotomous, ultimate branches, mostly non-planated and unwebbed (Fig. 1B, UA). They are borne on ultimate units (Fig. 1B, UU) that are helically arranged along and up to the distal extremities of proximal appendages (= LBS) in “cladoxylospids” and “progymnosperms”. Anatomy of ultimate appendages is distinct from the stem anatomy and their morphology can be variable in “cladoxylospids”. Some of them are similar to terete cylindrical cauline (telomic) axes (*Ibyka*) whereas

others can be flattened (*Pseudosporochnus*) or even possess bilateral symmetry and a lamina varying from small to broad, as in *Archaeopteris*; in this latter case they are currently interpreted as leaves or “small megaphylls” (Galtier, 2010). The term ultimate appendages also encompasses dichotomously branched, “megaphyll precursors” (*sensu* Kenrick and Crane, 1997) present in basal Euphyllophytes.

4.1.4. Quadriseriate leaf

This term defines the case where secondary axes are inserted in pairs alternately on the main rachis revealing the existence of two planes of bilateral symmetry but no abaxity (Fig. 1C). A lamina may be present on distal divisions of the organ in the form of generally narrow pinnules, as in *Zygopteris* (Galtier, 2010). Such organization has not yet been observed in Lignophytes.

4.1.5. “True” megaphylls

We define this as a large branched plagiotropic lateral organ with a developed lamina (not only restricted to distal appendages). This corresponds to the lateral, webbed appendages found in all living Euphyllophytes. Applied to living organisms, the megaphyll is a vascular organ with determinate growth, bilateral symmetry (and abaxity) definitely organized on the stem in some kind of phyllotaxy (Sanders et al., 2009; Tomescu, 2008). Taking into account fossil taxa and additional anatomical characters, we will be able to check the validity of this megaphyll concept within the whole Euphyllophyte clade, or show that this concept hides a diversity that is rather explained by various character combinations illustrating contrasting histories and processes. Characters discussed in the present study are insufficient to distinguish Lignophyte leaves and Monilophyte leaves on the basis of major anatomical differences (Fig. 2) between abaxity S (Monilophytes) and abaxity I (Lignophytes). However, the literature suggests some differences, which can be summarized as follows:

- megaphyll: Lignophyte leaves in which the adaxial face is associated with a lateral cauline meristem and in which both cellular differentiation and tissue maturation are basipetal (Tomescu, 2008). This pattern differs from that found in other Euphyllophyte groups;
- megafrond (new term): Monilophyte leaves in which development generally is circinate but may be revolute in some taxa and in which both cellular differentiation and tissue maturation are acropetal (Tomescu, 2008). This form of leaf is characteristic of ferns. In those ferns with stelar architecture more complex than a protostele, the stem stele possesses leaf gaps (Gifford and Foster, 1989), a feature absent in Lignophytes.

4.1.6. Lycophylls

The lycophyll (Kaplan, 2001; Schneider et al., 2009) is a Lycophyte apomorphy, not observed in Euphyllophytes. It is a lateral organ with simple venation and limited development of laminar tissue, straight or forked, with one vein or, in some instances, two running in parallel. The so-called “microphyllous leaf” of Sphenophytes is not homologous with the lycophyll and must be studied in the context of frond evolution in Monilophytes. It is generally accepted

that the “unbranched microphyllous leaf” of *Equisetum* and advanced calamitean fossils evolved by reduction from the dichotomous leaf of archaeocalamiteans (Stanich et al., 2009).

4.1.7. Necessary and dispensable characters defining foliar organs

The different types of organs defined above exhibit the combination of anatomical and morphological traits as summarized in Table 2, with corresponding taxa noted. All of the characters proposed are observable on both fossil and/or living plants. The presence of a megaphyll or a megafond is often supported by the presence of a lamina, and consequently by the presence of planation and webbing. We propose here to overcome this viewpoint, defining the presence of a leaf by, at least, the presence of planation (such as the ultimate appendages of *Pseudosporochnus*). Conversely, bilateral symmetry is a necessary criterion but not sufficient to define megaphyll or megafond. Abdaxity is an important anatomical character to identify modern leaves but we showed that some flattened and laminate leaves (such as quadriseriate leaves of “zygopterids”) do not display abdaxity. As with abdaxity, the presence of a webbed lamina is not sufficient to define a foliar organ in a broad sense even if abdaxity and webbing are required to identify megaphyll and megafond. Finally, bilateral symmetry and planation are necessary to define a leaf *sensu lato*; abdaxity and webbing are necessary to characterize megaphyll and megafond (even if they can be reduced in some derived taxa) (Table 2). The four characters discussed are essential to define the leaf concept but we must not lose sight that to be considered leaves, LBS have to be repeated over and over in an orderly arrangement on the stem, initiated by apical meristematic activity (phyllotaxy).

Considering the origins of the leaf *sensu lato*, the question is: would those characters have appeared simultaneously or not during the land plant evolution? By inferring evolution of anatomical and morphological traits, independently of the organs, we thus have the possibility to examine evolutionary relationships and/or potential pathways between the diverse observed organs.

4.2. Evolution of lateral organs

4.2.1. Symmetry

The appearance of bilateral symmetry of lateral branching systems is a first important stage regarding the differentiation of cauline and foliar organs. The presence of bilateral symmetry reveals a modification of LBS anatomy in Monilophytes. Indeed from the radial symmetry of cauline axes, lateral ramifications developed one or two bilateral symmetry planes (as observed in extinct “zygopterids” and Rhacophytales for the second case; Phillips and Galtier, 2005). In addition to the bilateral state, the number of symmetry planes should also be taken into account. In the present state of knowledge, the “zygopterids” and Rhacophytales appear to be the earliest ferns, and likely sisters to other ferns (Galtier, 2010). This could suggest that the symmetry in one plane was derived from the model with two planes, likely by the reduction of the phyllophore. In this hypothesis, the “true” megafond

in ferns would thus be derived from quadriseriate lateral organs. Such an interpretation implies that relationships of “zygopterid” ferns and Rhacophytales to the other ferns (particularly early botryopterids) are better known than they actually are. Phylogeny in Monilophytes, and especially in ferns, including fossil taxa needs to be improved. The genetic background for morpho-anatomical characters already may have been present in some groups even if the morphological expression of that genetic background had not yet been expressed or was not yet clearly observable (Endress, 2010). Consequently, the previous hypothesis can be tempered because the first appearance of bilateral state can occur earlier than the base of the fern clade.

If we define the megaphyll by its symmetry, then the megaphyll *sensu lato* would have appeared twice: once (the megaphyll) in Spermatophytes and once (the megafond) in ferns. However, the study of this character needs to be improved because it was, up to now, mainly defined for first-order branches. Indeed, some taxa (e.g. *Pseudosporochnus*) have no anatomical distinction between first-order branches and the cauline axis. Rather, a bilateral symmetry is observed in second order branches (Stein and Hueber, 1989). Thereby, it is necessary to distinguish branch orders in order to discuss the evolution of this character and avoid misinterpretation.

4.2.2. Abdaxity

Abdaxity is an essential character to understand the evolution of leaf anatomy. Evolution of abdaxity and symmetry is fully congruent in Spermatophytes. Besides, we can notice that abdaxity is absent from first-order branches in *Archaeopteris* but present in its ultimate appendages (abdaxity 1) as shown in Fig. 2, suggesting that anatomical changes first occurred in the last-order branch systems. For this reason, we can assert that *Archaeopteris* leaves are not homologous with Spermatophyte megaphylls. Interpretation of the evolution of abdaxity in ferns depends on the phylogenetic position of the “zygopterids” and the Rhacophytales. Because of phylogenetic irresolution, the absence of abdaxity in “zygopterids” and Rhacophytales is interpreted as two independent reversals. However, if such taxa are sisters to other ferns, as already suggested here above, abdaxity would have appeared in a clade grouping all ferns but excluding “zygopterids” and Rhacophytales, and thus after the appearance of bilateral symmetry. This suggests that the megaphyll could be defined by the strict combination of both these anatomical features only in Lignophytes but not in Monilophytes. Here again, new phylogenetic hypotheses including fossils are needed to clarify the evolution of abdaxity and its relation to symmetry in ferns.

4.2.3. Lamina

Lamina is traditionally defined as the result of planation and webbing processes (Zimmermann, 1938). It is a planated two-dimensional structure likely to be present on the whole leaf or restricted to distal portions. Phyllods and cladods of cauline origins but with foliar function are essentially defined by their planate form converging on being a lamina (Bell, 2008). Thus a lamina or a lamina-like structure does not necessarily mean the presence of a leaf in absence

Table 2

Lateral organ definition in Euphyllophytes.

Tableau 2

Définition des organes latéraux chez les Euphyllophytes.

Lateral organs	Characters	Taxa
Cauline lateral branches	No bilateral symmetry No abaxity No planation No webbing	“Trimerophytes”
Ultimate appendages	Bilateral symmetry No abaxity (except in Archaeopteridales) No planation (except in Archeopteridales and some Pseudosporochnales) No webbing (except in Archeopteridales)	Aneurophytales Archeopteridales “Cladoxylopsids”
Quadriseriate leaf	Bilateral symmetry No abaxity Planation present Webbing present	“Zygopterids”
“True” megaphyll and megafond	Bilateral symmetry Abaxity Planation present Webbing present	Living Euphyllophytes Ferns (including Sphenophytes) Spermatophytes

of other evidence. Present data (Stein and Boyer, 2006) suggest that the development of veins and laminae and the transition from axes to veins are progressive. There is no word to designate a structure displaying planation without webbing as in *Pseudosporochnus*. Furthermore, where is the limit between a broad lamina and slightly webbed appendages? To address these issues, further phylogenetic analysis will be required in order to better define the concept of “lamina” and understand its evolution. Leaves are usually defined by the presence of a lamina, an interpretation based on observations that can be quite subjective (Sattler and Rutishauser, 1997). A standard megafond is a compound leaf with numerous branching orders and a narrow distal lamina. In this case, it is often difficult to distinguish between a real absence of a lamina (i.e. a structure that does not yet exist) and an absence of a lamina that has secondarily disappeared. There are numerous examples of living ferns with fronds that lack laminae, the result of regressive loss, interpreted as hygrophilous adaptive strategies (e.g. in Hymenophyllaceae and the genus *Abrodia*; Ebihara et al., 2006). It is thus important to compare in detail the organisms without laminae with their putative relatives in order to examine the possibility that the character has been lost.

4.2.4. The foliar organ as a combination of anatomical and morphological characters

Bilateral symmetry of first-order branches would have appeared after planation within Lignophytes and Monilophytes (with the ACCTRAN optimization): the progymnosperm *Archaeopteris* displays planation and webbing only for its ultimate appendages (= vegetative leaves) and *Pseudosporochnus* exhibits planation only at distal ends of ramifications. Therefore, in these examples, the appearance of planation and bilateral symmetry was concomitant only in last-order branching (ultimate appendages). However, planation would have appeared together with webbing in a clade grouping *Archaeopteris* and Spermatophytes. The evolution of these characters is

different in Monilophytes: both are present for the whole of ferns and horsetails but are not present in “cladoxylopsids” (*Ibyka* and *Pseudosporochnus*). Indeed, planate ultimate appendages are present in *Pseudosporochnus* but not in *Ibyka*. Webbing is absent in “cladoxylopsids” and seems to appear once in the clade grouping horsetails and ferns. With the ACCTRAN optimization, planation would have been acquired before webbing (with reversal in *Ibyka*). With the DELTRAN optimization, the planation observed in some “cladoxylopsids” would be not homologous with planation observed in ferns and horsetails (it would be an example of a convergence). The “cladoxylopsid” planation is restricted to ultimate appendages, whereas planation is observed on the whole lateral organ in most ferns (except Rhacophytales and “zygopterids”) and horsetails, supporting the hypothesis of absence of homology. In this case, the combination of webbing and planation defines the megafond only in the ferns and horsetails and not in the “cladoxylopsids”. The form of the leaves in “cladoxylopsid” makes this group key for understanding the evolution of the lamina, at least in Monilophytes. In available phylogenies, these taxa, whose monophyly is still questioned, are under-represented. Further studies should integrate additional “cladoxylopsids” in order to refine our understanding of their relationships, and to determine more accurately the phylogenetic location of planated structures in this lineage.

Phylogenetic inferences show that the definition of a “true” leaf, as a combination of anatomical changes and planation and webbing processes, cannot be easily applied in Lignophytes because the laminar surface would have appeared before the anatomical changes necessary to support it functionally. Actually, this observation is due to the character coding of *Archaeopteris*: bilateral symmetry and abaxity have been coded as absent because these characters were defined for first-order branches of LBS. However, if we had considered only the vegetative leaves of *Archaeopteris* (Fig. 1D), bilateral symmetry and abaxity would have been coded as present. Finally, the combination

of anatomical changes and planation and webbing processes were concomitant in vegetative leaves of ultimate branches of LBS, at least in *Archaeopteris*.

In Monilophytes, bilateral symmetry could have appeared concomitantly with webbing and planation processes in ferns (including horsetails), if we suppose that planation observed in some “cladoxyloids” is not homologous with that observed in ferns. This evolution suggests that, among the four discussed characters, planation is the first necessary step through the emergence of the leaf at the Euphylliphyte scale. Furthermore, bilateral symmetry combined with appearance of the lamina (planation and webbing) was present before the appearance of abaxity, at least in “zygopterids” and Rhacophytales, if we assume that both of these taxa are sisters to other ferns (as we discussed here above).

Concerning *Tmesipteris*, the symmetry of the lateral organ was *a priori* coded bilateral because of the planate shape and the single central vein, but we cannot exclude here that this organ could be, in fact, given its absence of clear abaxity, a cladod (i.e. a planate stem with a foliar function). *Tmesipteris* and its relative *Psilotum* are now well recognized as true ferns, but exhibiting particular morphology illustrating numerous regressive processes (loss of roots and reduction of leaves) (Smith et al., 2006).

In this review we emphasized that Lignophytes and Monilophytes do not display homologous leaves even if both are traditionally called megaphylls (Tomescu, 2008). In order to remove ambiguities about foliar differences between Monilophytes and Lignophytes, we proposed to distinguish the two kinds of leaves by use of the terms megafond, the leaf observed in Monilophytes, and megaphyll, now restricted to the Lignophytes, (as suggested here above). Besides, in the absence of megaphyll or megafond, some ultimate appendages of extinct “progymnosperms” and “cladoxyloids” display distinct and various forms, also suggesting analogy rather than homology. We note that the term megafond could be *a priori* not appropriate for narrow leaves of Sphenopsids even though phylogenetic analysis shows that leaves of Sphenophytes and ferns are homologous. Sphenophyte leaves are thus interpreted as regressed megafonds.

Galtier (2010) argued that leaves evolved from two complex and concomitant processes. On one hand there is a transition from radial to bilateral symmetry, linked to abaxity. On the other hand, the blade resulted from planation and webbing. The independent evolution of the two processes would be illustrated by the morphology of “zygopterids” and some “botryopterids”, and also of *Elkinsia* and early seed plants. This interpretation is based mainly on paleobotanical studies without any phylogenetic considerations. Our inferences do not contradict this hypothesis by suggesting the scenario in which lamina (defined *sensu lato*) did not necessarily evolve concomitantly with anatomical changes in Euphylliphytes. Hypotheses proposed by our phylogenetic inferences encourage additional evolutionary studies that could benefit from more complete phylogenies and the new vocabulary proposed here. For example, it would allow examination of the independence between planation processes and anatomical changes in distinct clades, especially

in Monilophytes. It would also emphasize the necessity to treat phyllotaxy as a combination of branching patterns of different ramification orders. Indeed, this character should be one of the first of importance involved in the origin of leaves.

5. Conclusion

The definition of a new terminology to describe precisely the various kinds of lateral photosynthetic organs is a first step to clarify the origins of foliar organs in Euphylliphytes. This vocabulary should now be used in a phylogenetic analysis, the results of which will allow the usefulness of these new terms to be evaluated. Development of a lamina remains a necessary condition for the definition of a megaphyll or a megafond but alone it clearly appears insufficient. It is essential to combine this character with anatomical criteria in order to fully characterize the megaphyll and the megafond. We showed in this study that appearances of the four discussed characters are neither fully successive nor concomitant, but seem to develop first on last-order branches. We saw that the location of anatomical characters on the lateral branching systems is also very important for understanding the evolution of foliar forms. Therefore, it would be very interesting to add some new characters (such as location of planation, size of webbed surfaces, ...) in further analyses in order to distinguish possible different kinds of megaphylls and megafonds. One question remains: is bilateral symmetry or abaxity the main anatomical character required to improve the definition of the leaf? Is it still relevant to speak about the “megaphyll”, if this concept is highly homoplastic? It will be very difficult to abandon this word for many historical academic reasons. We propose in this study to limit the use of “megaphyll” to modern true leaves of Spermatophytes. If we persist in using this word in inappropriate ways, misinterpretation and incorrect use will continue in the field.

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