



**Inferring the hemiepiphytic habit in
Ficus L. (Moraceae) through wood
anatomical characters in modern and
fossil woods**

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The present is the key to the past
Charles Lyell

*Um dia de chuva é tão belo
como um dia de sol.
Ambos existem; cada um como é.*
Fernando Pessoa

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ABSTRACT

Plant habits are easily recognized not only by morphological aspects but also by a combination of anatomical characters, which have been essential to the understanding of the evolution of plant habits in the fossil record. Hemiepiphytes germinate and grow as epiphytes and later produce roots to the ground and connect with the soil. It is possible to infer the hemiepiphytic habit using wood anatomical characters? To address this question, we choose the genus *Ficus* L. from the family Moraceae, because exhibits a wide range of habits including small to large trees, lianas and about 60% of its species are hemiepiphytes. In this study, we compare the wood anatomy of the stem between trees and hemiepiphytes and, between the stems and aerial roots within hemiepiphytes species. Then, we analyse the wood anatomy of the fossil woods with affinities to *Ficus/Ficoxylon* and evaluate if was possible to distinguish the habit and/or the organ to which the fossil wood of *Ficus* belongs. Wood samples of aerial roots and stems of trees and hemiepiphytes were collected at breast height and prepared according to standard wood anatomical techniques. Qualitative and quantitative anatomical features were analysed to determine variance among habits and potential hydraulic conductivity was calculated to compare efficiency of water transport. We performed a literature search for the fossil woods of *Ficus/Ficoxylon*. Each of the fossils was evaluated as to the reliability of its identification and the accepted fossils were compared with modern species. Our results show that the stem and the aerial roots of hemiepiphytes presented wider vessels and higher hydraulic conductivity than trees. Within the hemiepiphytes, the only way to distinguish between stem and aerial roots is by the exarch xylem of the aerial roots in opposition to the endarch xylem of the stem. In fossil woods we found that it is not possible to distinguish if the fossil wood belongs to an aerial root or to a stem, however our data suggests that the fossils share more anatomical features with modern species of hemiepiphytes than with trees.

Keywords: Habit, Secondary xylem, Stem, Aerial root, section *Pharmacosycea*, subgenera *Spherosuke*, *Ficoxylon*

RESUMO

Os diferentes hábitos que as plantas apresentam na natureza são facilmente reconhecíveis não apenas pelo seu aspecto morfológico, mas também por uma combinação de caracteres anatômicos. Esses caracteres tem sido fundamentais para entender a evolução dos hábitos das plantas no registro fóssil. As plantas de hábito hemiepífita germinam e crescem como epífitas e depois estabelecem ligações com o solo por meio de raízes aéreas. É possível inferir o hábito hemiepífita usando caracteres anatômicos? Para abordar esta questão, escolhemos o gênero *Ficus* L. da família Moraceae porque possui uma grande diversidade de hábitos incluindo, arbustos, árvores, lianas e mais do 60% das espécies são hemiepífitas. Neste estudo, comparamos a anatomia da madeira do caule entre espécies arbóreas e hemiepífitas, adicionalmente entre as espécies hemiepífitas comparamos a anatomia da madeira entre raízes aéreas e o caule. Posteriormente, analisamos a anatomia do lenho de fósseis com afinidade a *Ficus* / *Ficoxylon* e avaliamos se é possível distinguir o hábito ou o órgão ao qual a lenho fóssil de *Ficus* pertence. Amostras de madeira de raízes aéreas e caules de árvores e hemiepífitas foram coletadas na altura do peito e preparadas de acordo com técnicas anatômicas da madeira. Características anatômicas qualitativas e quantitativas da madeira foram analisadas para determinar a variação entre hábitos, e a condutividade hidráulica hipotética foi calculada para comparar a eficiência no transporte hídrico. Foi realizado um levantamento bibliográfico referente aos lenhos fósseis de *Ficus* / *Ficoxylon* e cada um dos fósseis foi avaliado quanto à confiabilidade de sua identificação. Os fósseis aceitos foram posteriormente comparados com as espécies modernas estudadas. Nossos resultados mostram que o caule e as raízes aéreas das espécies hemiepífitas apresentam vasos de maior diâmetro e maior condutividade hidráulica hipotética do que as espécies arbóreas. Das plantas hemiepífitas, a única forma de distinguir as raízes aéreas do caule é pela posição do protoxilema, isto é, o xilema exarco nas raízes em oposição ao xilema endarco do caule. Nos lenhos fósseis, observamos que não é possível distinguir se o lenho fóssil pertence a uma raiz aérea ou a um caule, no entanto, nossos dados sugerem que os fósseis compartilham mais características anatômicas com espécies hemiepífitas do que com espécies arbóreas.

Palavras-chave: Hábito, Xilema secundário, Caule, Raiz aérea, seção *Pharmacosycea*, subgênero *Spherosuke*, *Ficoxylon*

INTRODUCTION

Evolution of habits along the geologic time

What would have driven the evolution of growth habits? A variety of possibilities may have contributed in several ways to form a shrub, a tree, a liana, an epiphyte or a hemiepiphyte. Some of the most widely accepted selective pressures favouring the evolution of those habits are light availability, wind for dispersal of propagules and rooting systems for anchoring and for water and nutrients acquisition (Kenrick & Davis, 2004; Taylor *et al.* 2009; Boyce *et al.* 2017).

If we look back to the geologic timescale, lianas and trees have an evolutionary history that dated back to the Paleozoic era and are present in all major groups of vascular plants. Trees are well known since the Devonian (ca. 410 Myr) and the Carboniferous (ca. 358 Myr) with the Cladoxylopsids (rosette trees) and archaeopterid progymnosperms (Taylor *et al.* 2009; Meyer-Berthaud *et al.* 2010; Boyce *et al.* 2017). Lianas were abundant and diverse since the early Carboniferous, with several groups of Pteridosperms (seed ferns) like the Lyginopteridales and Medullosales (Burnham & Johnson, 2004; Burnham, 2009). Phylogenetically, hemiepiphyte plants are found in twenty families of angiosperms (Putz & Holbrook, 1986) and recently it has been documented in at least five families of ferns (Watts *et al.* 2019). Within the ferns they are present in the Polypodiaceae (Testo & Sundue, 2014), Dryopteridaceae (Lagomarsino *et al.* 2012), Hymenophyllaceae (Nitta & Epps, 2009), Aspleniaceae and Lomariopsidaceae (Watts *et al.* 2019). In the angiosperms, they are present among monocotyledons (e.g. Araceae, Cyclantaceae) and are commonly represented in major groups of Rosids (e.g. Clusiaceae, Moraceae, Melastomataceae) and Asterids (e.g. Araliaceae, Solanaceae, Marcgraviaceae). Some authors have suggested that it is possible that when the tropical rainforests was established, near the Eocene (ca. 56 Myr) and when the canopy became dense, many plants adopted different mechanisms in order to survive to the scarceness of light in the forest floor (Ramirez, 1997). Epiphytic habits, seeds capable of germinating in the upper layers of the forest and production of fast-growing aerial roots were some of the key innovations that possibly allowed plants like hemiepiphytes to occupy niches that most plants like trees and shrubs did not readily occupy (Ramirez, 1997). The evolutionary history of hemiepiphytes is still a mystery, which can be attributed to the lack of detailed morphological and anatomical studies capable of identifying this habit in extant and fossil records. To date we don't know if all kinds of hemiepiphytes are homologous, and if this habit evolved

independently in ferns and angiosperms or if, by contrary, it appears early in the ferns and was lost in other groups.

Are there means to recognize the hemiepiphytic habit in the fossil record? The fossil record provides fragments of pieces instead of complete individuals, then, the inference of the plant habit is almost made on temporary sources (Burnham, 2009). For example, the pteridosperm *Lyginopteris oldhamia* from the early Carboniferous, possess adventitious roots that are borne on the stem, up to 7 mm in diameter and apparently some of them produce secondary xylem (Taylor *et al.* 2009). Some authors suggested that it was a climbing liana (Potonie, 1899), whereas others reconstructed this plant as a freestanding shrub (Retallac & Dilcher 1988). Others, support the hypothesis of a not self-supporting plant based on biomechanical analyses, arguing that this plant had a sophisticated, climbing stem architecture (Speck, 1994; Masselter *et al.* 2017). It is possible that this plant was a hemiepiphyte? To answer this question is important to first define a hemiepiphyte.

Defining a hemiepiphyte

Hemiepiphytes constitute a special category of plants because they share characteristics of terrestrial and epiphytes during different stages of their development (Watts *et al.* 2019). The term hemiepiphyte has been used in different contexts, and consequently it is a confusing term (Zotz, 2013). Went (1895) distinguish hemiepiphytes from epiphytes because only hemiepiphytes produce roots that reach the ground. A similar definition was given by Shimper (1903); he defined hemiepiphytes as structural dependent plants that share germination with epiphytes but later establish contact with the ground via aerial roots. In 1925 Pessin, introduces a completely different definition, he used the term hemiepiphyte for facultative epiphytes, which derived water and nutrients either from the ground or the canopy. Raunkier (1937) defined hemiepiphytes as ‘pseudolianas’. He used the term for plants that germinate on other plants and later establish contact with the ground through aerial roots or plants that germinate on the soil and later climb on other plants to reach the canopy. Mueller-Dombois (1974), defined hemiepiphytes as ‘pseudolianas’ or as ‘epiphytic lianas’, depending on their stage of development. Later, Putz & Holbrook (1986) divided the hemiepiphytes in two groups; ‘primary hemiepiphytes’ as those plants that begin with an epiphytic stage and have root connections with the soil. And ‘secondary hemiepiphytes’ as plants that germinated on the soil, climb into the canopy and later lose their terrestrial connections. Ten years later, Holbrook & Putz (1996) revoked the definition of secondary hemiepiphytes arguing that they are vine-like in physiology and morphology and reserved the term hemiepiphyte only for plants that begin with an epiphytic stage. Luttge (1997) considered that

the term secondary hemiepiphytes is not convincing, arguing that many aroid species produces adventitious roots that re-establish contact with the ground, which would make them primary hemiepiphytes, however since they do not germinate on other plants they cannot be defined as primary hemiepiphytes. In 2000, Moffett introduces the term ‘nomadic vine’ for secondary hemiepiphytes, however this term was never used in any publication. Due to the abundance of terms, defining habits has turned a complex matter (Sperotto *et al.* 2020). In the case of hemiepiphytes the term ‘secondary hemiepiphytes’ continues to be a matter of debate (Watts *et al.* 2019).

Recently, Sperotto *et al.* (2020) support the suggestion of Moffet (2000) that plants that germinate on the ground and later become epiphytic (secondary hemiepiphytes) would be treated as ‘nomadic climbers’ emphasizing the relationship and proximity of strategies to the climbing habit. And, suggest that term ‘hemiepiphyte’ would be exclusive to ‘primary hemiepiphytes’ *sensu* Putz & Holbrook (1986). This reduce the ambiguity associated with the term ‘hemiepiphyte’ that is often seen in the literature (Sperotto *et al.* 2020). Therefore, for this study, we follow the most recent terminology proposed by Sperotto *et al.* (2020) in which the term ‘hemiepiphyte’ refers exclusively to plants that begin with an epiphytic stage and have root connections with the soil.

Secondary xylem between habits

Aside from morphological aspects defining a hemiepiphyte requires also an understanding of the anatomical structure associated to this kind of habit. The secondary growth is formed by the vascular cambium, which is a lateral meristem with two types of initials, fusiform initials, which are vertically elongated, and ray initials, which are radially elongated (Evert, 2006). Together these initials differentiate into secondary xylem and secondary phloem (Evert, 2006). The secondary vascular growth allowed the formation of different plant forms, ranging from huge trees like the sequoia (*Sequoiadendron giganteum* (Lindl.) J. Buchholz; Cupressaceae), to woody lianas like many members of the Bignoniaceae family. Most extant shrubs and trees are characterized by develop a single bifacial cambium that produces secondary phloem externally and secondary xylem internally (Evert, 2006).

However, previous studies on different angiosperm families that compare the secondary xylem between habits (Ter Welle *et al.* 1981; Gasson & Dobbins, 1991; Dong & Baas, 1993; Chen *et al.* 1993; Li *et al.* 1995; Ewers *et al.* 1997; Dias Leme, 2000; Esemann de Quadros, 2001; Lahaye *et al.* 2002; Isnard *et al.* 2012; Wagner *et al.* 2012; Gerolamo & Angyalossy, 2017), have highlight that lianas, shrubs and trees exhibit a combination of anatomical characters that allow to distinguish these habits in the absence of morphological aspects. Most lianas, for example, share a group of anatomical

features known as the “lianescent vascular syndrome” (Angyalossy *et al.* 2015). These features include, vessels dimorphism, high amounts of soft tissues as parenchyma and phloem, and tall and wide rays (Angyalossy *et al.* 2012, 2015; Gerolamo & Angyalossy, 2017). By the other hand, trees and shrubs have much higher percentage of fibres and narrower vessels as a result for mechanical support and water transport (Baas *et al.* 2004; Rowe *et al.* 2004; Gerolamo & Angyalossy, 2017). These show us that morphological changes have been accompanied by anatomical modifications. Besides, these contributions on wood anatomy have been essential to the understanding of plant habits in the fossil record and anatomical characters have even been used to identify habits like lianas and trees in fossil assemblages (Martínez-Cabrera *et al.* 2006; Burnham 2009, 2015; Rodriguez *et al.* 2014; Jud & Dunham 2017; Rozefeld & Pace 2018). Nevertheless, little attention has been paid to the differences between hemiepiphytes. To date, the anatomy of hemiepiphytes has been little explored (Esemann de Quadros 2001). Within Clusiaceae family, Esemann de Quadros (2001) compared the secondary xylem between stem and aerial roots of the hemiepiphyte *Clusia criuva*. Interestingly, she found that aerial roots possess anatomical characters very similar to that of lianas, like high amounts of axial parenchyma and vessel dimorphism (Esemann de Quadros, 2001).

Study group

We chose *Ficus* L., the largest genus of the family Moraceae and one of the most emblematic and important components of lowland tropical forests, to study anatomical characters and to distinguish plant habits. *Ficus* contains more than 800 species and exhibit a wide range of habits including small to large trees, lianas and about 60% of *Ficus* species are hemiepiphytes (Berg & Corner, 2005; Pederneiras & Romaniuc, 2019; Li *et al.* 2019). The evolutionary history of *Ficus* suggests that *Ficus* originated at the beginning of the Cenozoic and the major clades radiated during the Eocene (Pederneiras *et al.* 2018). Jousselin *et al.* (2003) suggest that there might be repeated evolution of hemiepiphytism in the genus and the ancestral condition is ambiguous. The oldest records assigned to *Ficus* are based on fossil fruits (Eocene; Collinson, 1989) and *Ficus* wasps (Oligocene; Compton *et al.* 2010), but the fossil record of woods attributed to *Ficus* dates back to the Middle Eocene (Licht *et al.* 2014). Nevertheless, there is no information about the habit of the fossils described for *Ficus*, which can be attributed not only to the scarcity of anatomical studies in modern species but also the lack of studies comparing between wood anatomy and habits within *Ficus*. Indeed, many studies on *Ficus* have focus on stem and leaf functional traits between hemiepiphytes and non-hemiepiphytes (Li *et al.* 2019). Previous studies on *Ficus* have demonstrated that hemiepiphytes compared to non-hemiepiphytes

exhibit drought-tolerant traits such as stronger stomatal control, smaller leaf size, smaller xylem vessel lumen diameter and lower stem conductivity (Patiño *et al.* 1995; Holbrook & Putz 1996; Hao *et al.* 2011; Li *et al.* 2019). However, little attention has been done investigating the wood anatomy diversity in the context of habits and organs for the genus.

GENERAL CONCLUSIONS

According to the results presented here, we concluded from our research questions:

(i) It is possible to infer the hemiepiphytic habit in *Ficus* using wood anatomical characters?

- The wood anatomy between *Ficus* species is very similar. However, between trees and hemiepiphytes we found that hemiepiphytes has statistically wider vessels (close to 200 μm) than trees (close to 120 μm).
- Within the hemiepiphytes, the only way to distinguish between stem and aerial roots is by the exarch xylem of the aerial roots in opposition to the endarch xylem of the stems.
- The potential hydraulic conductivity is higher in hemiepiphytes than trees. And, within the hemiepiphytes, stems have higher potential hydraulic conductivity than their aerial roots.

(ii) Do the fossil woods of *Ficus* and/or *Ficoxylon* belong to trees or hemiepiphytes?

- It is not possible to distinguish if the fossil wood belongs to an aerial root or to a stem, however our data suggest that the fossils share more anatomical features with modern species of hemiepiphytes rather than trees.
- Intervessel pit size and vessel element length were significantly smaller in fossils than in modern species while, vessel diameter was similar in size with modern hemiepiphytes.
- We can infer that an isolated piece of fossil wood with vessel diameters close to 200 μm likely would be a hemiepiphyte.

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