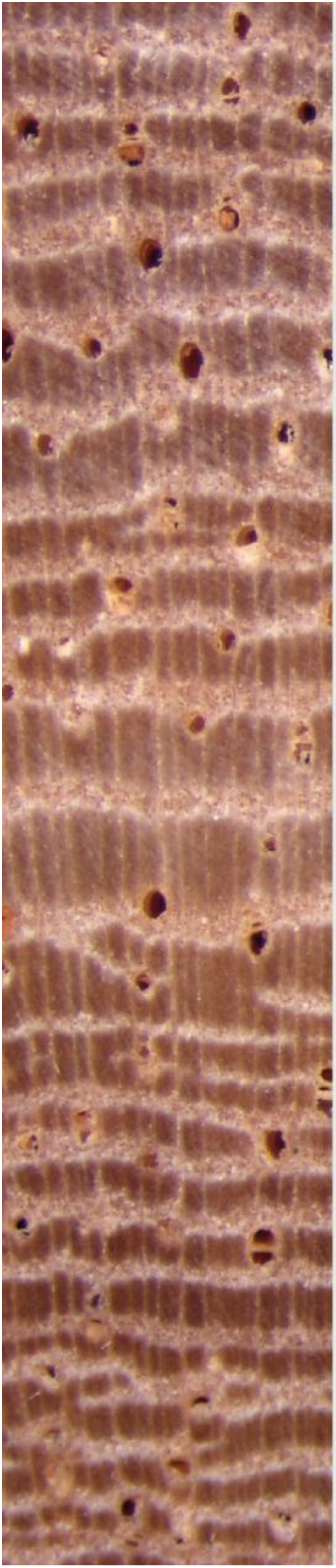

Inferring the hemiepiphytic habit in *Ficus* L. (Moraceae) through wood anatomical characters in modern and fossil woods

Camila Monje Dussán

São Paulo
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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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INDEX

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 distiguish if the fossil wood belong 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 hemiepífito germinam e crescem como epífitas e depois estabelecem ligações com o solo por meio de raízes areas. É possível inferir o hábito hemiepífito 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 oposião 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 hemiepiphyes’ as plants that germinated on the soil, climb into the canopy and later loose their terrestrial connections. Ten years later, Holbrook & Putz (1996) revoked the definition of secondary hemiepiphytes arguing that they are vinelike 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 reestablish contact with the ground, which would make them primary hemiepiphytes, however since they do not geminated 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 trated 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 *Ficu*s, 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.

OBJECTIVES

In this study we address the following major questions:

1) It is possible to infer the hemiepiphytic habit in *Ficus* using wood anatomical characters?
2) Does the fossil woods of *Ficus* and/or *Ficoxylon* belong to an aerial root or a stem?

General objective

Investigate the wood anatomy between trees and hemiepiphytes of *Ficus* L. (Moraceae) in order to seek for features that allow us to distinguish between both habits in modern and fossil woods.

Specific objectives

i) Compare wood anatomical characters of the stem between trees and hemiepiphytes of *Ficus* species.
ii) Compare wood anatomical characters between the stem and the aerial roots within *Ficus* hemiepiphytes.
iii) Analyze wood anatomical characters of the fossil record of woods of *Ficoxylon/ Ficus*
iv) Compare the wood anatomy between modern and fossil species of *Ficus*.
v) Evaluate if it is possible to distinguish the habit and/or the organ to which the fossil wood of *Ficus* belongs.

We worked under the principle that *the present is the key to the past* because we wanted to highlight the importance of integrative studies between botany and paleobotany. We believed that exploring and understanding the present morphology, anatomy and biology of plants we could be able to comprehend the evolutionary history of many plant groups along the geologic time. And, with this study in particulary, we want to understand some of the gaps of hemiepiphytes of the genus *Ficus*.

MATERIAL & METHODS

Sampling

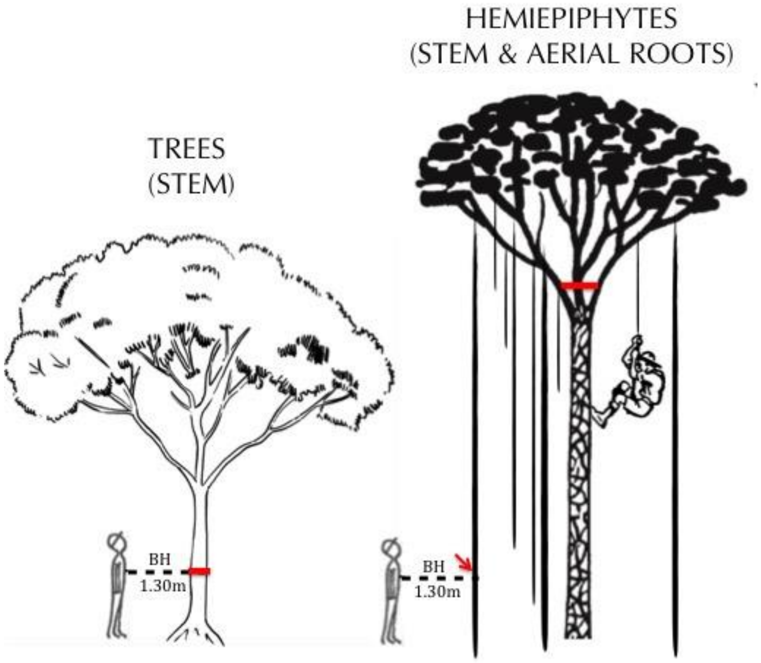
A total of fourteen species were sampled, eight species in arboreal habit and six species in hemiepiphyte habit. These taxa belong to six of the thirteen major clades of *Ficus* L. (Pederneiras *et al*. 2018). Six of the trees belong to the section *Pharmacocysea* (Miq.) Miq., and the other two species belong to the section *Americanae* (Miq.) Corner. The hemiepiphytes belong to all sections of the subgenera *Spherosuke*: *Americanae*, *Cordifoliae* G.Don, *Platyphyllae* Mildbr. & Burret, and *Urostigma* (Endl.) Griseb. For the species names, we followed the latest proposed classification (Pederneiras *et al.* 2015). All studied species were collected in the field and whenever possible, at least three specimens per specie were sampled. Since *Ficus* trees do not possess aerial roots, only stem portions were collected. In the case of hemiepiphytes, stem and aerial roots were sampled. In Table 1 we provide a complete list of species, number of specimens collected, their habit, site of collection, collectors.

Table 1. Studied *Ficus* species, number of specimens collected, their sections, habit, sampling site, collector and accesion number.

Species (number specimens)	*Ficus* section	Habit	Samplig site	Collector
Ficus adhatodifolia Schott ex Spreng (3)	*Pharmacosycea*	Tree	Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil	Monje-Dussán & Pederneiras, 9
Ficus benjamina L. (1)	*Cordifoliae*	Hemiepiphyte	Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil	Monje-Dussán & Pederneiras, 32
Ficus bonijesulapensis R.M. Castro (1)	*Americanae*	Hemiepiphyte	Bom Jesus, Bahia, Brazil	Ceccantini G, 4542
Ficus clusiifolia Schott. (1)	*Americanae*	Tree	Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil	Monje-Dussán & Pederneiras, 16
Ficus crassivenosa W.C. Burger (1)	*Pharmacosycea*	Tree	Estrada da Fazenda, Belém do Pará, Brazil	Monje-Dussán & Devecchi, 28
Ficus elastica Roxb. ex Hornem (3).	*Urostigma*	Hemiepiphyte	Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil	Monje-Dussán & Pederneiras, 04
Ficus maxima Mill. (1)	*Pharmacosycea*	Tree	Estrada da Fazenda Belém do Pará, Brazil	Monje-Dussán, 27
Ficus microcarpa L. f. (1)	*Cordifoliae*	Hemiepiphyte	Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil	Pederneiras & Monje-Dussán, 776
Ficus obtusiuscula (Miq.) Miq. (1)	*Pharmacosycea*	Tree	Museu Nacional, Rio de Janeiro, Brazil	Monje-Dussán & Pederneiras, 13
Ficus pseudomangifera Hutch. (2)	*Platyphyllae*	Hemiepiphyte	Jardim botânico do Rio de Janeiro, Rio de Janeiro, Brazil	Pederneiras & J.P. Basso Alves, 756
Ficus pulchella Schott ex Spreng**.** (1)	*Pharmacosycea*	Tree	Museu Nacional Rio de Janeiro, Brazil	Pederneiras & Monje-Dussán, 570
Ficus tomentella (Miq.) Miq. (1)	*Americanae*	Tree	Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil	Monje-Dussán & Pederneiras, 14
Ficus vermifuga (Miq.) Miq. (1)	*Pharmacosycea*	Tree	Praia Vermelha, Rio de Janeiro, Brazil	Pederneiras & Monje-Dussán 774
Ficus virens Dryand. (1)	*Cordifoliae*	Hemiepiphyte	Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil	Monje-Dussán & Pederneiras, 18

For trees, we sampled adult stem portions of approximately 8 cm^3 at breast height (1.30 m) (Image 1). In the case of hemiepiphytes, there is no a standard protocol for sampling this plants, in fact many studies usually sample the descending roots and included them in liana inventories (Gerwing *et al*. 2006). However, the recommendations for sampling lianas do not applied for hemiepiphytes (Gerwing *et al*. 2006). In this study, we climb the host tree until reaching the adult stem of the hemiepiphyte and removed a portion of approximately 8 cm^3 (Image 1). For aerial roots we removed an entire portion following three criteria: (1) must be an adult individual, (2) should be rooted in the soil and, (3) have a similar diameter of the diameter of the stem (Image 1). All samples of stems and aerial roots were removed with the aid of a saw, a hammer and a chisel.

Image 1. Sampling method for collecting stem (red line) and aerial roots (arrow) of trees and hemiepiphytes. BH= Breast height (1.30 m)



Laboratory procedures and anatomical descriptions

Stems and aerial roots collected in the field were fixed in FAA50 (formalin, acetic acid, and ethanol 50%) and then transferred to 70% ethanol. For both organs we removed a portion of 1 cm^3 of the external portion of secondary xylem, near the vascular cambium. Additionally, for aerial roots we removed a portion of 1 cm^3 of the center of the organ in order to confirm that it belongs to a root. In generally, *Ficus* species studied herein have a very smooth wood, which allows to section without previous boiling. Nevertheless, few aerial roots of hemiepiphytes species were boiled for approximately 2h. Transverse and longitudinal sections were cut with a thickness of 20 to 25 µm, using a sliding microtome. The sections were double-stained in astra blue and safranine (Bukatsh 1972) and permanent slides were mounted with the resin Canada balsam. For macerations, small sections were placed in vials filled with Franklin's solution (1:1 glacial acid and 6% peroxide hydrogen) and heated in the oven at 60ºC for 24-30 hours. Tissues then were rinsed with water and stained in 1% safranine and semi-permanent slides were mounted with glycerol.

Photographs and observations of the slides were obtained using a Leica DMLB photomicroscope with a digital camera DFC310 FX. In order to explore anatomical traits of the secondary xylem of stems and aerial roots, we followed the IAWA List of Features for Hardwood Identification (IAWA Committee, 1989) for microscopic descriptions. Wood anatomical features were measured and counted using the software Image J (Rasband 2012). Quantitative characters were scored as average measurements and, qualitative characters were scored as present or absent. All measurements are presented as the minimum, mean and maximum value for each species (Table 2).
Quantitative features were: a) vessel diameter (µm), b) vessel length (µm), c) vessel density (mm^2), d) solitary vessels index, e) vessel grouping index, f) occupied area of vessels (%), g) diameter of intervessel pit (µm), h) distance between axial parenchyma bands (µm), i) cells wide per axial parenchyma band (number), j) cells per axial parenchyma strand (number), k) occupied area of axial parenchyma (%), l) ray width (µm), m) ray length (µm), n) occupied area of rays (%), o) fibre length (µm), p) fibre wall thickness (µm), q) occupied area of fibres (%). Qualitative features were: r) presence/absence of growth rings, s) vessel arrangement and grouping, t) perforation plate type, u) intervessel pit type, v) vessel-ray pit type, w) presence of septate fibres, x) axial parenchyma type, y) ray composition, z) presence of laticifers, sheath cells and crystals.

Potential hydraulic conductivity

We calculated potential hydraulic conductivity to describe indirectily the water transport efficiency for each species and for habit. We calculated the vessel hydraulic diameter using the equation in Poorter *et al.* (2010):

$$D_h = [(1/n)\ \Sigma\ ^{n}{}_{i=1}\ d^4]^{1/4} \qquad \text{(Eq. 1)}$$

n is the number of vessels and **d** is vessel diameter.

Then, we calculated the potential hydraulic conductivity according to the Hagen-Poiseuille's law (Poorter *et al.* 2010):

$$Kp = (\pi\rho_w/128\eta) \text{ x } Vf \text{ x } D_h^4 \qquad \text{(Eq. 2)}$$

Where ***K*p** is the potential specific stem conductivity (kg m $MPa^{-1}s^{-1}$), $\boldsymbol{\rho_w}$ is the density of the water (998.2 kg m^{-3} at 20ºC), $\boldsymbol{\eta}$ is the viscosity of water (1.002 $x10^{-3}$ Pa s at 20ºC), **Vf** is vessel frequency (m^{-2}) and, $\mathbf{D_h}$ is the vessel hydraulic diameter (m) calculated in equation 1.

Literature review

The name *Ficoxylon* is commonly used for fossil woods that are anatomically like *Ficus* but without sufficient diagnostic characters that allows the assignment in the modern genera *Ficus* (Kaiser, 1880). In this respect, the evaluation of the fossil record started with a literature search of the fossils woods that have been published as having affinities with *Ficus* or *Ficoxylon.* Qualitative and quantitative data was compiled from Inside Wood Database, the Paleobiology Database, and original publications.

Evaluation of fossils

Each one of the fossils was evaluated towards the reliability of its identification. Five criteria were taken into consideration for each fossil, each one evaluated as provided/not provided. The criteria were: [1] full taxonomic description and diagnosis of the fossil, [2] photographs of the specimens, [3] locality, geological formation and age, [4] housing institution, collection number, [5] drawings, or reconstructions of the fossils. To identify the well-supported records we focused on those fossils that fulfilled the first three criteria. These fossils were accepted as representing reliable records. Then, we selected only the ocurrences on the tropical region to avoid misinterpretations on possible environmental variables afecting the anatomical data. Finally, these fossils were analysed using the same qualitative and quantitative features of the modern species.

Statistical analyses

To test differences of anatomical traits of the secondary xylem between trees, hemiepiphytes and fossil woods we performed an analyses of variance (ANOVA) and a Tukey’s test. To evaluated differences in hydraulic conductivity we performed a Kruskal Wallys test and a regression analysis. We used species average values for all traits.

In all statistical analyses, the traits were $\log_{10}$ transformed if necessary to increase normality. And the analyses were performed in R (R Studio Team 2015).

RESULTS

Wood anatomy

Common features present in all analysed *Ficus* species (Figure 1): Wood diffuse porous; vessels solitary combined with multiples of 2 to 4 (Fig. 1A, B); perforation plates simple (Fig. 1C); intervessel pits alternate (Fig. 1D); axial parenchyma banded; parenchyma bands with more than 3 cells wide (Fig. 1A); axial parenchyma paratracheal; scanty to vascicentric (Fig. 1B); multisseriate rays (Fig. 1E), composed of procumbent body cells and one to two rows of square/upright marginal cells (Fig. 1F); prismatic crystals in axial and sometimes radial parenchyma cells (Fig. 1G); sheat cells (Fig. 1H) and laticifers present (Fig. 1H).

Trees (Figure 1 & 3, Table 2): *Ficus adhatodifolia*, *F. clusiifolia*, *F. crassivenosa*, *F. maxima*, *F. obtusiuscula*, *F. pulchella*, *F. tomentella* and, *F. vermifuga*.

All species have indistinct growth rings (Fig. 3A–B). Vessels are solitary combined with multiples of 2–3, with vessel grouping index of 1.4 (Fig. 3A–B). Tangencial diameter of all tree species range from 83 µm to 206 µm, mean 125 µm; vessel element length varies from 324 µm to 454 µm, mean 378 µm; vessel frequency range from 3/mm^2 to 5/mm^2, mean 5/mm^2 (Table 2). Intervessel pits range from medium (8 µm) to large (10 µm), mean 9 µm. Vessels occupie from 3% to 9%, mean 5%, from the total secondary xylem area. Tyloses are rare, observed in *F. clusiifolia* (Fig. 3A) and rarely present in *F. pulchella.*

Axial parenchyma bands are present in all species together with scanty paratracheal parenchyma in vessels that are not immersed within the bands (Fig. 3B); the bands vary from 5 cells to 15 cells wide, mean 11 cells wide (Table 2); radial distance between axial parenchyma bands ranged from 168 µm to 657 µm, mean 307 µm; storied parenchyma is rare, but observed in *F. tomentella* and irregularly storied in *F. obtusiuscula.* Axial parenchyma occupies from 30% to 40%, mean 35%, from the total secondary xylem area.

Rays are heterocellular, composed of procumbent body cells and usually 1 to 2 rows of square and upright marginal cells in all species (Fig. 1F). Rays are multiseriate, ranging from 3 to 7-seriate (Fig. 1E); ray height range from 414 µm to 686 µm, mean 505 µm; sheat cells (Fig. 1H) and radial laticifers (Fig 1H) are present in all species; rays occupie from 18% to 23%, mean 20%, from the total secondary xylem area.

Fibres are non-septate in all species (Fig. 1C, H). Fibres with simple to minutely bordered pits common in radial walls in all species however in *F. tomentella* and *F. clusiifolia* are also common in tangential walls. Fibre length range from 1035 μm to 1795 μm, mean 1372 μm; fibres are thin- to thick walled with average diameter ranging from 5 μm to 7 μm, mean 6 μm; From the total secondary xylem area, fibres occupie 34% to 46%, mean 40%. Gelatinous fibres are observed in *F. crassivenosa.*

Prismatic crystals were observed in non-chambered axial parenchyma cells in *F. adhatodifolia* and *F. tomentella* (Fig. 1G) and rarely present in *F. obtusiuscula* and F. *pulchella* also, prismatic crystals were observed in square marginal cells in *F. tomentella* (Fig. 1G).

Table 2. Wood anatomical features of extant trees and hemiepiphytes. – = absent; + = present; minimum (mean) maximum

					Vessels					Axial Parenchyma		
Habit	Species	Growth ring boundaries	Septate fibres	Axial parenchyma cells irregularly storied to storied	Vessel diameter (µm)	Vessel element length (µm)	Vessel frequency (mm^2)	Vessel area (%)	Diameter intervessel pit (µm)	Radial distance between axial parenchyma bands (µm)	Cells per axial parenchyma band (number)	Axial parenchyma area (%)
Tree stem	*F. adhatodifolia*	–	–	–	63 (98) 145	191 (383) 612	4 (5) 10	4 (6) 7	7 (9) 11	127 (169) 239	5 (6) 7	30 (32) 33
	F. clussifolia	–	–	–	66 (135) 193	259 (403) 523	2 (4) 8	3 (4) 6	7 (8) 12	105 (168) 220	3 (5) 6	30 (33) 33
	F. crassivenosa	–	–	–	40 (83) 115	215 (383) 665	2 (4) 5	3 (3) 4	7 (9) 11	215 (383) 665	8 (10) 12	38 (40) 42
	F. maxima	–	–	–	98 (189) 271	320 (454) 592	3 (4) 6	3 (3) 5	6 (8) 10	460 (657) 725	7 (11) 12	27 (30) 31
	F. obtusiuscula	–	–	–	88 (143) 194	236 (344) 464	3 (5) 9	5 (9) 10	7 (8) 13	74 (188) 289	6 (10) 16	33 (34) 36
	F. pulchella	–	–	–	53 (104) 158	262 (381) 475	3 (5) 7	3 (5) 6	7 (8) 11	105 (226) 515	5 (6) 7	30 (33) 35
	F. tomentella	–	–	+	88 (206) 305	229 (324) 437	1 (3) 6	4 (5) 6	7 (10) 15	175 (269) 370	6 (8) 11	35 (37) 41
	F. vermifuga	–	–	–	61 (118) 205	214 (348) 555	4 (5) 8	4 (5) 6	8 (10) 12	255 (340) 478	12 (15) 17	38 (40) 43
Mean for all tree stem					**83 (125) 206**	**324 (378) 454**	**3 (5) 5**	**3 (5) 9**	**8 (9) 10**	**168 (307) 657**	**5 (11) 15**	**30 (35) 40**
Hemiepiphyte stem	*F. benjamina*	+	+	+	90 (151) 225	236 (350) 612	2 (4) 7	2 (2) 3	7 (9) 11	193 (350) 616	5 (7) 8	19 (22) 25
	F. bonijesulapensis	–	–	–	66 (167) 270	206 (357) 587	1 (3) 5	3 (4) 5	6 (11) 12	242 (365) 711	5 (8) 10	26 (30) 31
	F. elastica	+	+	+	116 (230) 331	383 (479) 614	1 (2) 3	3 (5) 6	8 (11) 13	355 (561) 661	5 (6) 7	15 (17) 20
	F. microcarpa	–	–	–	124 (225) 331	241 (400) 580	2 (3) 6	4 (6) 6	7 (10) 12	66 (155) 204	5 (7) 11	33 (35) 37
	F. pseudomangifera	+	+	–	63 (134) 214	173 (292) 425	2 (3) 5	3 (3) 4	6 (9) 11	150 (333) 466	5 (8) 12	21 (24) 26
	F. virens	–	+	+	74 (134) 188	194 (311) 515	2 (3) 4	3 (5) 6	6 (7) 9	132 (195) 263	6 (7) 12	50 (52) 54
Mean for all hemiepiphyte stem					**134 (172) 230**	**292 (365) 479**	**2 (3) 4**	**2 (4) 6**	**7 (9) 11**	**155 (327) 561**	**6 (7) 8**	**17 (30) 52**
Hemiepiphyte aerial roots	*F. benjamina*	–	+	+	88 (147) 206	272 (394) 527	2 (3) 7	2 (3) 5	7 (9) 11	178 (362) 431	5 (7) 9	28 (30) 31
	F. bonijesulapensis	–	–	–	100 (154) 214	233 (355) 601	1 (2) 4	3 (4) 6	7 (9) 12	264 (407) 521	6 (7) 9	33 (35) 36
	F. elastica	+	+	+	98 (159) 232	272 (415) 588	1 (3) 4	3 (4) 6	6 (9) 12	132 (274) 387	4 (5) 7	22 (26) 27
	F. microcarpa	–	–	+	51 (232) 377	181 (302) 421	1 (3) 5	3 (5) 6	8 (9) 11	167 (401) 613	6 (8) 11	16 (19) 20
	F. pseudomangifera	+	+	–	92 (147) 219	267 (354) 503	2 (3) 5	2 (2) 3	6 (9) 11	160 (310) 518	5 (7) 10	24 (26) 29
	F. virens	–	+	+	64 (108) 155	164 (282) 401	2 (4) 5	3 (4) 5	6 (7) 10	164 (286) 419	6 (8) 10	29 (32) 33
Mean for all hemiepiphyte aerial roots					**108 (158) 232**	**282 (350) 415**	**2 (3) 4**	**2 (4) 5**	**7 (9) 9**	**274 (340) 407**	**5 (7) 8**	**19 (28) 35**

(continued on the next page)

Table 2 *continued.*

		Radial Parenchyma			Fibres		
Habit	Species	Ray length (µm)	Ray wide (number of cells)	Ray area (%)	Fibre length (µm)	Fibre wall thickness (µm)	Fibre area (%)
Tree stem	*F. adhatodifolia*	234 (415) 660	3 (5) 7	19 (23) 24	813 (1290) 1774	3 (6) 12	37 (39) 39
	F. clussifolia	248 (445) 701	2 (3) 5	19 (20) 20	1094 (1456) 1910	3 (5) 8	42 (43) 44
	F. crassivenosa	385 (607) 1059	4 (4) 6	18 (19) 22	1368 (1795) 2290	2 (5) 8	35 (37) 38
	F. maxima	322 (686) 1103	4 (7) 7	19 (21) 23	939 (1504) 2036	5 (7) 10	44 (46) 47
	F. obtusiuscula	261 (414) 669	3 (5) 7	17 (19) 24	913 (1221) 1828	2 (5) 8	35 (38) 40
	F. pulchella	303 (518) 846	2 (3) 6	17 (18) 21	762 (1184) 1621	4 (6) 9	43 (44) 45
	F. tomentella	290 (497) 663	4 (4) 6	18 (20) 21	1016 (1492) 2281	5 (6) 9	38 (38) 38
	F. vermifuga	270 (455) 799	3 (4) 7	19 (21) 23	650 (1035) 1380	4 (6) 8	33 (34) 34
Mean for all tree stem		**414 (505) 686**	**3 (4) 7**	**18 (20) 23**	**1035 (1372) 1795**	**5 (6) 7**	**34 (40) 46**
Hemiepiphyte stem	*F. benjamina*	159 (314) 511	2 (4) 7	22 (26) 27	960 (1210) 1974	4 (6) 10	48 (50) 52
	F. bonijesulapensis	220 (488) 737	3 (4) 6	21 (23) 24	879 (1554) 2058	5 (6) 10	40 (43) 47
	F. elastica	403 (630) 1103	2 (4) 6	12 (13) 14	1014 (1297) 1964	5 (9) 11	59 (65) 68
	F. microcarpa	309 (522) 811	5 (6) 7	15 (17) 18	875 (1280) 1858	4 (5) 9	39 (42) 44
	F. pseudomangifera	189 (346) 492	3 (5) 5	16 (17) 17	1003 (1380) 2017	4 (7) 10	54 (56) 58
	F. virens	200 (348) 496	4 (5) 6	12 (12) 14	701 (973) 1215	3 (5) 9	30 (31) 31
Mean for all hemiepiphyte stem		**314 (441) 630**	**4 (5) 6**	**12 (18) 26**	**973 (1282) 1554**	**5 (6) 9**	**31 (48) 65**
Hemiepiphyte aerial roots	*F. benjamina*	380 (612) 1189	3 (4) 6	11 (14) 15	623 (1099) 1257	5 (7) 10	52 (53) 54
	F. bonijesulapensis	174 (587) 1407	3 (3) 7	15 (17) 18	716 (1016) 1420	6 (11) 13	41 (43) 43
	F. elastica	270 (492) 1089	3 (4) 7	14 (16) 19	1024 (1384) 1876	5 (8) 10	52 (54) 57
	F. microcarpa	256 (630) 1324	5 (5) 7	22 (22) 23	795 (1044) 1268	4 (6) 8	50 (53) 57
	F. pseudomangifera	255 (378) 562	3 (5) 6	19 (20) 21	1046 (1463) 1925	4 (6) 9	53 (53) 55
	F. virens	177 (319) 621	3 (5) 6	22 (24) 25	613 (807) 1123	5 (9) 12	39 (40) 43
Mean for all hemiepiphyte aerial roots		**319 (503) 630**	**3 (5) 5**	**14 (19) 24**	**807 (1136) 1463**	**6 (8) 11**	**40 (49) 54**

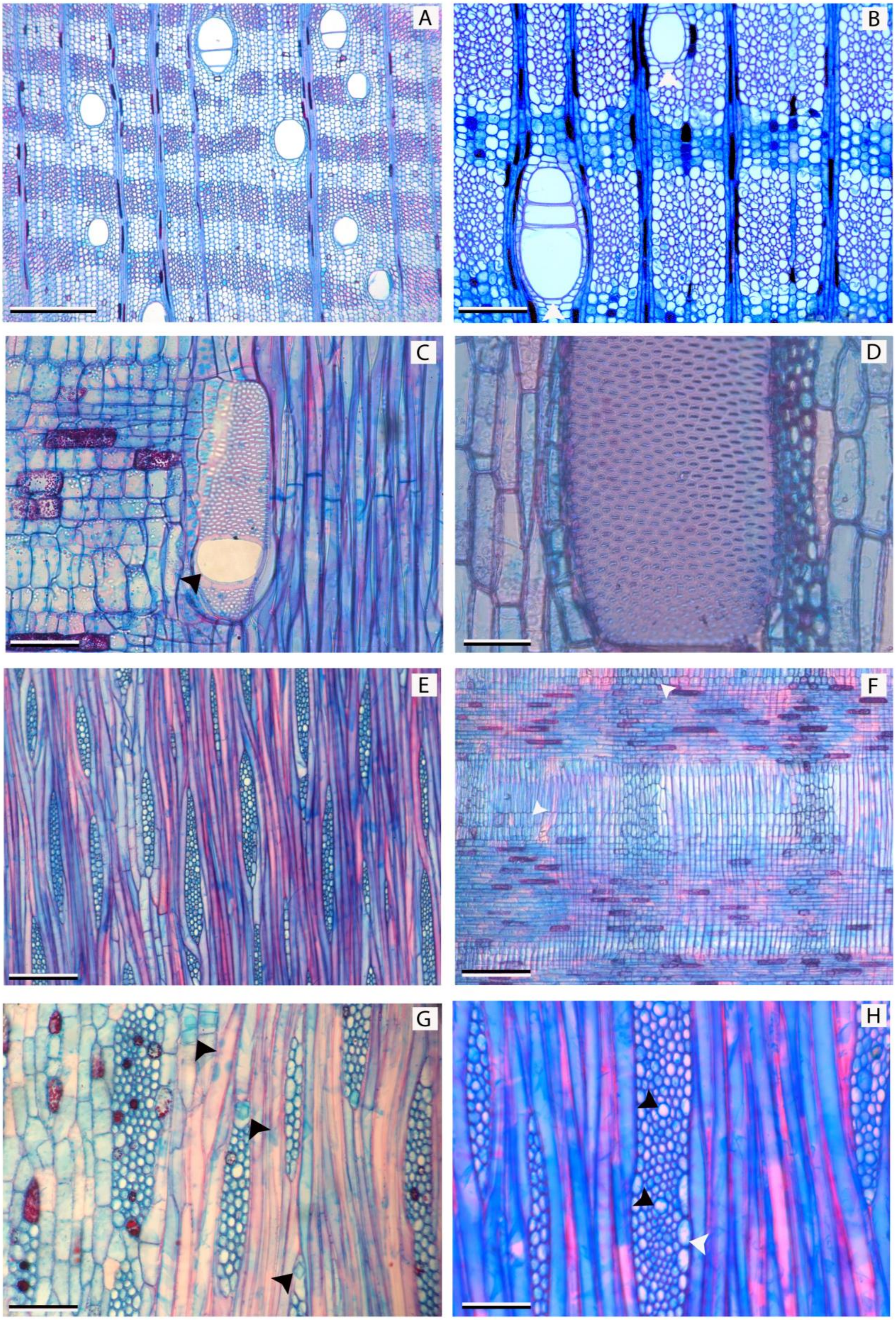

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Figure 1. *Ficus* wood anatomical features**.** –A & B: Transverse sections. - A: Hemiepiphyte *F. virens* stem, diffuse porous; vessels solitary combined with multiples of 2 to 4; banded parenchyma . –B: Hemiepiphyte *F. benjamina* aerial root, banded parenchyma, and scanty to vascicentric parenchyma (arrow). - C: Hemiepiphyte, radial section, *F. virens* aerial root, simple perforation plate (arrow). – D: Tree, tangencial section, *F. clusiifolia* stem, intervessel pits alternate. – E: Tree, tangential section, *F. pulchella* stem, multiseriated rays. – F: Hemiepiphytes, radial section, *F. microcarpa* stem, heterocellular rays composed by procumbent body cells and 1 to 2 (3) rows of square and upright marginal cells (arrows). - G & H: Tangential sections. – G: Tree *F. tomentella* stem, prysmaic crystals in axial and radial parenchyma cells (black arrows). - H: Tree *F. maxima* stem, sheat cells (white arrows) and laticifers (black arrows).– Scale bars: A = 500 µm; B, E, F & G= 200 µm; C & H= 100 µm; D= 50 µm.

Hemiepiphytes (Figure 1–3, Table 2): *Ficus benjamina, F. bonijesulapensis, F. elastica, F. microcarpa, F. pseudomangifera* and, *F. virens.*

Stem and Aerial roots

Xylem anatomy of the aerial roots is similar to the stems. The only way to distinguish both organs is by a) the protoxylem position: xylem exarch in the aerial roots and endarch in the stem; b) the type of stele: protostele in aerial roots and eustele in stems. All studied aerial roots are tetrarch (Fig. 2A).

Stem

Almost all species have indistinct growth rings (Fig. 1A, 3C–D), nevertheless in *F. pseudomangifera, F. elastica* and *F. benjamina* was observed a possible growth ring boundary, marked by a continuous thin band with radially flattened axial parenchyma cells, no more than 3 cells wide, that contrast with rounded axial parenchyma cells (Fig. 2B, Table 2). Vessels are solitary combined with multiples of 2–3 and with vessel grouping index of 1.4 (Fig. 1A, 2B, 3A–D). Tangential diameter of vessel range from 134 µm to 230 µm, mean 172 µm; vessel element length vary from 292 µm to 479 µm, mean 365 µm; vessel frequency range from 2/mm^2 to 4/mm^2, mean 3/mm^2 (Table 2). Intervessel pits are medium (7 µm) to large (11 µm), mean 9 µm; from the total secondary xylem area, vessels occupie 2% to 6%, mean 4%. Tyloses are present in *F. microcarpa* and *F. elastica.*

Axial parenchyma bands are present in all species together with paratracheal scanty parenchyma in vessels that are not immersed within the bands (Fig. 1B, 3B). Axial parenchyma bands vary from 6 to 8 cells wide, mean 7 cells wide (Table 2); radial distance between axial parenchyma bands range from 155 µm to 561 µm, mean 327 µm; from the total secondary xylem area, axial parenchyma occupies 17% to 52%, mean 30%. Axial parenchyma is storied to irregularly storied in *F. benjamina, F. elastica* and *F. virens* see Table 2 and Figure 2C.

Rays are heterocellular, composed of procumbent body cells and usually 1 to 2 rows of square and upright marginal cells in all species. Rays are from 4-seriated to 6-seriated, mean 5-seriate, ray height range from 314 μm to 630 μm, mean 441 μm; from the total secondary xylem area, rays occupie 12% *to* 26%, mean 18%. Sheat cells and radial laticifers are present in all species, however in *F. elastica* sheat cells are very scanty.

Fibres. Septate fibres, with more than one septa per fibre are present in *F. benjamina, F. elastica, F. pseudomangifera* and *F. virens*, see Table 2, and Figure 2D. Fibres with simple to minutely bordered pits common in radial and tangential walls in all species except in *F. benjamina* and *F. virens* which are only common in radial walls. Fibre length range from 973 μm to 1554 μm, mean 1282 μm; fibres are thin- to thick walled with diameter ranging from 5 μm to 9 μm, mean 6 μm; from the total secondary xylem area, fibres occupied 31% to 56%, mean 48%. Gelatinous fibres are observed in *F. benjamina* and *F. pseudomangifera* (Fig. 2E).

Prismatic crystals were observed in non-chambered axial parenchyma cells in *F. bonijesulapensis, F. microcarpa, F. elastica* and *F. benjamina*. Also, prismatic crystals were observed in square marginal cells in *F. microcarpa* and *F. benjamina* and occasionally present in *F. bonijesulapensis*.

Aerial roots

All species have indistinct growth rings (Fig. 1A, 3C–D), nevertheless in *F. pseudomangifera* and *F. elastica* was observed a possible growth ring boundary, marked by a continuous thin band with radially flattened axial parenchyma cells, no more than 3 cells wide, that contrast with rounded axial parenchyma cells (Fig. 2B, Table 2). Vessels are solitary combined with multiples of 2–3 and with vessel grouping index of 1.4 (Fig. 1A, 2B, 3A–D). Tangential diameter of vessel range from 108 μm to 232 μm, mean 158 μm , vessel element length vary from 282 μm to 415 μm, mean 350 μm, vessel frequency range from 2/mm^2 to 4/mm^2, mean 3/mm^2 (Table 2). Intervessel pits are medium (7 μm) to large (9 μm), mean 9 μm; from the total secondary xylem area, vessels occupie 2% to 5%, mean 4%. Tyloses are present in *F. microcarpa* and *F. elastica.*

Axial parenchyma bands are present in all species together with paratracheal scanty parenchyma in vessels that are not immersed within the bands (Fig. 1B, 3B). Axial parenchyma bands vary from 5 to 8 cells wide, mean 7 cells wide (Table 2), radial distance between axial parenchyma bands range from 274 μm to 407 μm, mean 340 μm; from the total secondary xylem area, axial parenchyma occupies 19% to 35%, mean 28%. Axial parenchyma is storied to irregularly storied in *F. benjamina, F. elastica, F. microcarpa* and *F. virens* see Table 2 and Figure 2C.

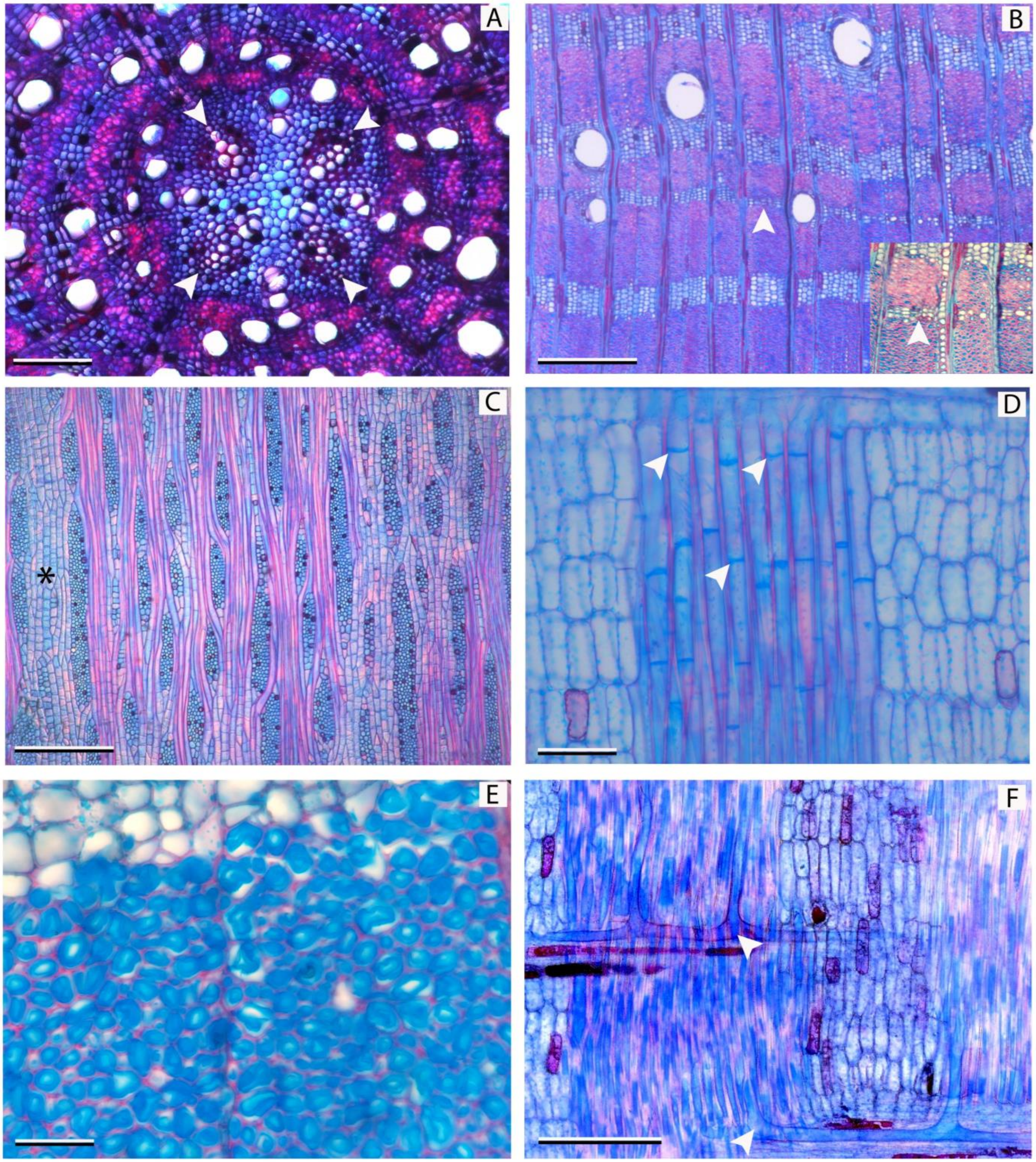


Figure 2. Hemiepiphytes stem and aerial root. –A & B: Transverse sections. – A: Hemiepiphyte *F. elastica* aerial root, tetrach root (white arrows) –B: Hemiepiphyte *F. pseudomangifera* stem, possible growth ring boundary, marked by a continuous thin band with radially flattened axial parenchyma cells (white arrows). - C: Tangential section, hemiepiphyte *F. microcarpa* aerial root, storied axial parenchyma (asterisk). – D: Radial section, hemiepiphyte *F. virens* stem, septate fibres (arrows). - E: Transcerse section, hemiepiphyte *F. benjamina* aerial root, gelatinous fibres. - F: Radial section, hemiepiphyte *F. pseudomangifera* stem, laticifers extending horizontally within the rays and extending in axial direction intruding among the fibres (arrows). – Scale bars: – A & D= 100 μ m; B & C= 500 μ m; E= 50 μ m; F= 200 μ m.

Rays are heterocellular, composed of procumbent body cells and usually 1 to 2 rows of square and upright marginal cells in all species. Rays are from 3-seriated to 5-seriated, mean 5-seriate, ray height range from 319 µm to 630 µm, mean 503 µm, from the total secondary xylem area, rays occupie 14% to 24%, mean 19%. Sheat cells and radial laticifers are present in all species, however in *F. elastica* sheat cells are very scanty. Additionally, is observed that in *F. pseudomangifera* laticifers extended horizontally within the rays and extend in axial direction intruding among the fibres (Fig. 2F).

Fibres. Septate fibres, with more than one septa per fibre are present in *F. benjamina*, *F. elastica*, *F. pseudomangifera* and *F. virens*, see Table 2, and Figure 2D. Fibres with simple to minutely bordered pits common in radial and tangential walls in all species except in *F. benjamina* and *F. virens* which are only common in radial walls. Fibre length range from 807 µm to 1463 µm, mean 1136 µm; fibres are thin- to thick walled with diameter ranging from 6 µm to 11 µm, mean 8 µm; from the total secondary xylem area, fibres occupied 40% to 54%, mean 49%. Gelatinous fibres are observed in *F. benjamina* and *F. pseudomangifera* (Fig. 2E).

Prismatic crystals were observed in non-chambered axial parenchyma cells in *F. bonijesulapensis*, *F. microcarpa*, *F. elastica* and *F. benjamina*. Also, prismatic crystals were observed in square marginal cells in *F. microcarpa* and *F. benjamina* and occasionally present in *F. bonijesulapensis*.

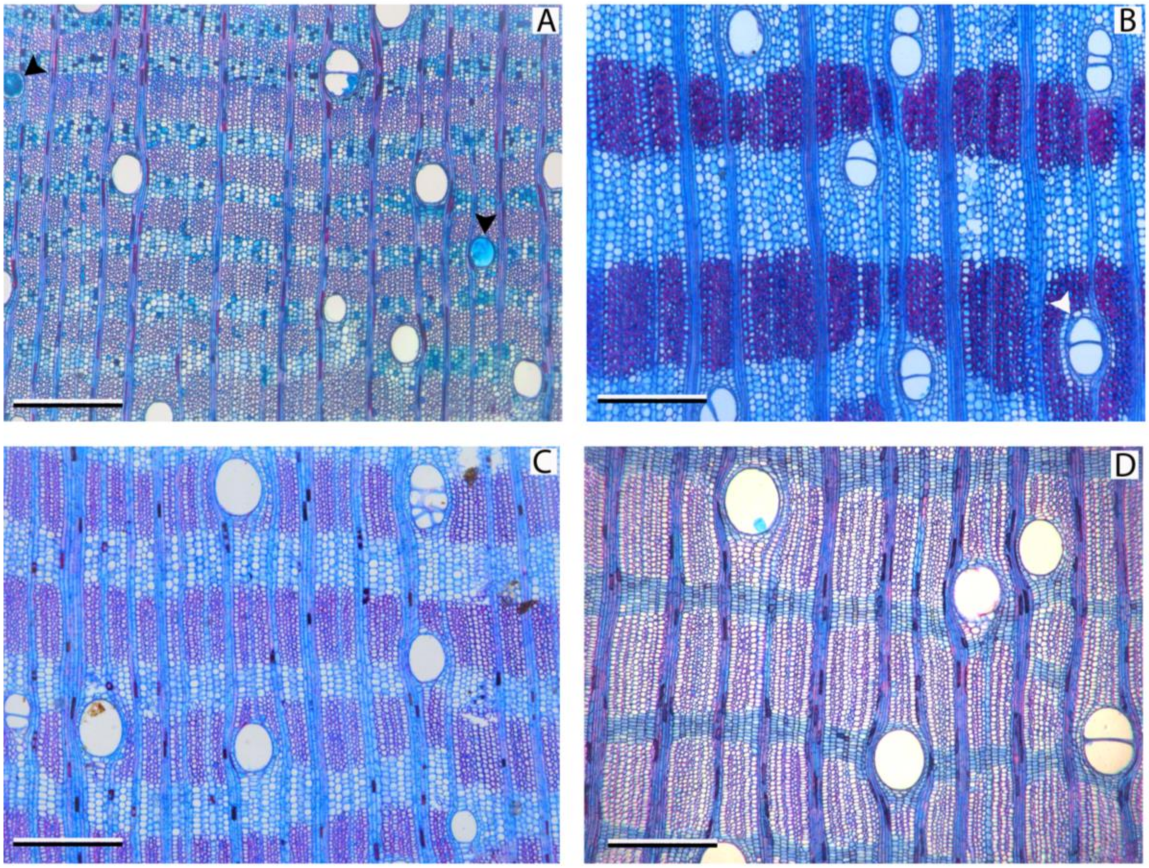


Figure 3. Habit related trait: vessel diameter of trees and hemiepiphytes. –A–D: Transverse sections. – A: Tree *F. clussifolia* stem, tyloses (arrows). – B: Tree *F. crassivenosa* stem, vascicentric parenchyma (arrows). – C: Hemiepiphyte *F. bonijesulapensis* stem. – D: Hemiepiphyte *F. microcarpa* aerial root. – Scale bars: A–D = 500 µm.

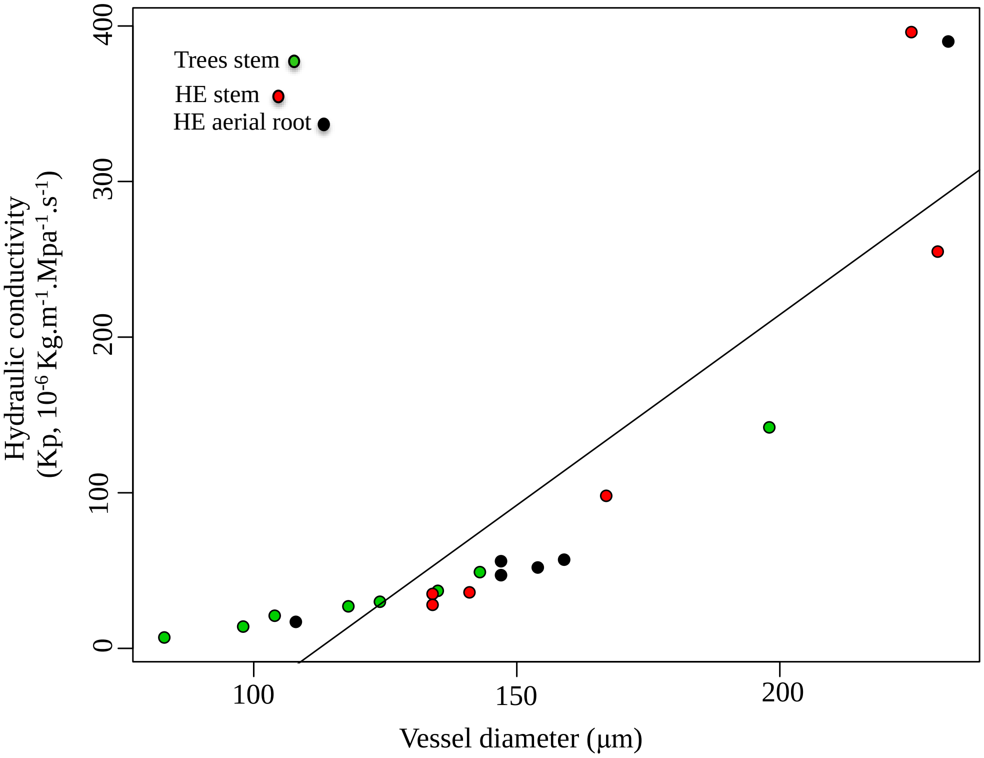
Potential hydraulic conductivity between trees and hemiepiphytes

The mean hydraulic conductivity is significantly higher in hemiepiphytes stem (141±151) and aerial roots (103±141) than in trees (41±43). Besides, the hemiepiphytes stem shows higher hydraulic conductivity than the aerial roots (Table 3, Figure 4).

Table 3. List of potential hydraulic conductivity (Kp) for species and habit.

Plant Part	**Specie**	**Kp ($p<0.05$)**
Tree stem	*Ficus adhatodifolia*	14
Tree stem	*Ficus clusiifolia*	37
Tree stem	*Ficus crassivenosa*	9
Tree stem	*Ficus maxima*	30
Tree stem	*Ficus obtusiuscula*	49
Tree stem	*Ficus pulchella*	21
Tree stem	*Ficus tomentella*	142
Tree stem	*Ficus vermifuga*	27
Mean for all trees		**41±43**
Hemiepiphyte stem	*Ficus bonijesulapensis*	98
Hemiepiphyte stem	*Ficus benjamina*	36
Hemiepiphyte stem	*Ficus elastica*	256
Hemiepiphyte stem	*Ficus microcarpa*	396
Hemiepiphyte stem	*Ficus pseudomangifera*	36
Hemiepiphyte stem	*Ficus virens*	28
Mean for all hemiepiphytes stems		**141±151**
Hemiepiphyte aerial root	*Ficus bonijesulapensis*	52
Hemiepiphyte aerial root	*Ficus benjamina*	56
Hemiepiphyte aerial root	*Ficus elastica*	57
Hemiepiphyte aerial root	*Ficus microcarpa*	390
Hemiepiphyte aerial root	*Ficus pseudomangifera*	47
Hemiepiphyte aerial root	*Ficus virens*	17
Mean for all hemiepiphytes aerial roots		**103±141**

Figure 4. Potential hydraulic conductivity between hemiepiphytes (HE) and trees



The fossil wood record of Ficus

A total of eighteen fossils woods described as *Ficus or Ficoxylon* were identified (Table 4). Despite the huge diversity of *Ficus* today, the fossil record of woods is still very scarce. From the eighteen records only seven fossil woods fullfill our first three criteria, which include: taxonomic description, photographs, and age and locality (Table 4). These seven fossils represent reliable records of fossil woods for *Ficus*, however from those seven reliable records only four fossil woods posses a complete anatomical description that allow us to compare with modern species (Table 5).

Table 4. Fossil woods attributed to *Ficoxylon* or *Ficus.* Accepted fossils are the ones that fulfill the first three criteria.

Fossil taxon	**Age**	**Locality**	**Reference**	**Accepted**
Ficoxylon angustiparenchymatosum	Miocene	Asia	Shimakura, 1937	no
Ficoxylon bajacaliforniense	Miocene	Central America	Martínez-Cabrera *et al*. 2006	yes
Ficoxylon blanckenhorni	Oligocene-Miocene	Africa	Krausel, 1939	no
Ficoxylon bohemicum	Oligocene (?)	Europe	Kaiser, 1880	no
Ficoxylon cretaceum	Oligocene–Pliocene	Africa, South America	Schenk, 1883	yes
Ficoxylon guettarense	Oligocene (?)	Africa	Fessler-Vrolant, 1972	yes
Ficoxylon helictoxyloides	Miocene-Pliocene	North America	Platen, 1908	no
Ficoxylon kalagarhensis	Miocene	Asia	Prasad, 1993	no
Ficoxylon? melahense	Miocene	Asia	Louvet, 1971	no
Ficoxylon mougaungense	Eocene	Asia	Licht *et al*. 2014	yes
Ficoxylon saurinii	?	Asia	Boureau, 1950	no
Ficoxylon schenki	Oligocene-Miocene	Africa	Blanckernhorn, 1901	no
Ficoxylon sp.	Pliocene	Africa	Jolly-Saad *et al.* 2010	yes
Ficoxylon tropicum	Oligocene	Europe	Felix, 1883	no
Ficoxylon zirkelii	?	?	Hofmann, 1884	no
Ficus brachylepis	Pliocene	Africa	Dechamps, 1983	no
Ficus koek-noormaniae	Miocene	Central America	Jud & Dunham, 2017	yes
Ficus vallis-choudae	Pliocene	Africa	Dechamps, 1983	no

Table 5. Fossil woods attributed to *Ficoxylon* or *Ficus* that possess a complete anatomical description that allow us to compare with modern species.

Fossil taxon	Vessel diameter (µm)	Vessel length (µm)	Vessels.mm^2	Diameter of intervessel pit (µm)	Size of parenchyma bands (number cells)	Ray width (number cells)	Ray height (µm)
Ficus koek-noormaniae	208	311	2	7	5	3	422
Ficoxylon bajacaliforniense	154	290	3	5	9	6	632
Ficoxylon mougaungense	115	185	9	5	6	3	405
Ficoxylon sp.	220	262	5	6	5	4	776

Comparison of anatomical features between modern and fossil woods

From the sixteen anatomical characters that we explored in extant species (see Table 2 and 5), only seven characters were present in the fossils that allow us to compare with the modern trees and hemiepiphytes (see Table 6).

Vessel diameter. The stem (174 µm) and aerial roots (157 µm) of hemiepiphytes, and fossil woods (165 µm) have significant widest vessels than stem of trees (126 µm).

Vessel length. Vessel element length is significantly shorter in fossil woods (262 µm) compared to extant trees (378 µm) and hemiepiphytes (stem: 368 µm, aerial root: 350 µm)

Vessel frequency. No statistical difference was found in vessel frequency between extant trees and hemiepiphytes and fossil woods.

Size of intervessel pit. Intervessel pit is significant smaller in fossil woods (6 µm) compared to extant trees (9 µm) and hemiepiphytes (stem:10 µm, aerial root: 9 µm)

Size of axial parenchyma bands. No statistical difference was found for the size of parenchyma bands between extant trees and hemiepiphytes and fossil woods.

Ray width. No statistical difference was found for ray width between extant trees and hemiepiphytes and fossil woods.

Ray height. No statistical difference was found for ray height between extant trees and hemiepiphytes and fossil woods.

Table 6. Statistical comparison (ANOVA) between trees, hemiepiphyte stems, hemiepiphytes aerial roots, and fossils woods.

Feature	**Habit**	**Mean (±SD)**	**$F_{3,20}$**	**p-value (<0.05)**
Vessel diameter (µm)	Trees	126 (±38)	4.29	**0.037**
	Hemiepiphyte stem	174 (±44)		
	Hemiepiphyte aerial roots	157 (±41)		
	Fossils	165 (±36)		
Vessel lenght (µm)	Trees	378 (±41)	2.68	**0.054**
	Hemiepiphyte stem	368 (±75)		
	Hemiepiphyte aerial roots	350 (±51)		
	Fossils	262 (±67)		
Vessels.mm^2	Trees	4 (±0.7)	1.92	0.158
	Hemiepiphyte stem	3 (±1.0)		
	Hemiepiphyte aerial roots	3 (±0.6)		
	Fossils	5 (±3.1)		
Diameter of intervessel pit (µm)	Trees	9 (±0.9)	10.61	**0.0002**
	Hemiepiphyte stem	10 (±1.5)		
	Hemiepiphyte aerial roots	9 (±0.8)		
	Fossils	6 (±1.2)		
Size of parenchyma bands (number cells)	Trees	11(±4.1)	1.54	0.235
	Hemiepiphyte stem	7 (±1.5)		
	Hemiepiphyte aerial roots	7 (±0.8)		
	Fossils	5 (±1.7)		
Ray width (number cells)	Trees	4 (±1.3)	0.70	0.566
	Hemiepiphyte stem	5 (±0.8)		
	Hemiepiphyte aerial roots	5 (±0.8)		
	Fossils	3 (±1.3)		
Ray height (µm)	Trees	505 (±97)	0.71	0.557
	Hemiepiphyte stem	441 (±125)		
	Hemiepiphyte aerial roots	503 (±130)		
	Fossils	559 (±154)		

DICUSSION

Wood anatomy of Ficus

Trees vs hemiepiphytes

Some of the wood characters here described are referred in previous literature as diagnostic for *Ficus:* diffuse porous wood, vessels solitary combined with multiples of 2 to 4, simple perforation plates, intervessel pits alternate, axial parenchyma banded, parenchyma bands wide, sheat cells and laticifers present (Koek-Noorman *et al*. 1984).

Growth rings–Possible growth rings marked by a continuous thin band with radially flattened axial parenchyma cells no more than 3 cells wide, are present in the hemiephytes: stem of *F. benjamina,* and in the stem and aerial roots of *F. elastica* and *F. pseudomangifera*. Growth rings have not been reported yet in previous literature for the mentioned species, although they are documented in the hemiepiphyte *Ficus rumphii* Blume from India (Ajmal & Iqbal, 1987) and in the tree *Ficus boliviana* C.C. Berg from Bolivia (Lopez *et al*. 2012). Acording to Schweingruber (1996), growth rings are a predictor of tree performance in a changing environment. Changes in environmental conditions are transformed into physiological and metabolic reactions resulting in tree rings (Fichtler & Worbes 2012). Hydric seasonality, dry periods, temperature, light intensity and hormone gradients, especially auxines related to growth, are some of the variables for the formation of growth rings in tropical trees (Alves & Angyalossy, 2000; Giraldo *et al*. 2020). These factors can affect species in the same forest differently (Giraldo *et al.* 2020).

Vessels–Vessel diameter vary between the stem of trees and hemiepiphytes, with the widest range observed in the hemiepiphytes. As has been documented in a considerable body of literature, mean vessel diameter varied across plant habits (Gasson & Dobbins, 1991; Dong & Baas, 1993; Chen *et al*. 1993; Li *et al*. 1995; Ewers *et al*. 1997; Dias Leme, 2000; Lahaye *et al*. 2002; Wheeler *et al*. 2007; Isnard *et al*. 2012; Pace & Angyalossy 2013; Olson *et al*. 2014; Wagner *et al*. 2012; Gerolamo & Angyalossy, 2017). Lianas are notably well known to have wider vessels than self supporting plants like shurbs and trees (Alfondillo *et al*. 2013; Olson *et al*. 2014). Mean vessel diameter at the stem base is gerenerally wider in taller plants as a result of maintaining a constat hydraulic resistance as plants grow in size (Alfondillo *et al*. 2013; Olson *et al*. 2014).

In the case of hemiephytes this relationship it not very well understood. With our results we observed that *Ficus* species with vessel diameters close to 200 µm occurs in hemiepiphytes rather than trees (mean: 125 µm).

Nevertheless, this pattern was not observed in previous studies with other hemiepiphytes taxa (Esserman de Quadros, 2001). In *Clusia criuva* (Clusiaceae, Esserman de Quadros, 2001), the mean vessel diameter was similar between the stem of trees and hemiepiphytes.

Additionally, as vessel diameter increses, vessel frequency decreases (see Wheeler *et al*. 2007). This inverse relationship between diameter and frequency was observed in *Ficus* species and it is one aspect of examining tradeoffs between transport efficiency and safety from cavitation (Carlquist 1977; Wheeler *et al*. 2007; Poorter *et al*. 2009). This will be explored further in this discussion.

Axial and radial parenchyma– From the total xylem area, axial and radial parenchyma occupied more than 50% in all *Ficus* species studied herein. Xylem parenchyma has been recognized as having function of storage, embolism repair and as a defense mechanism against pathogens (Tyree *et al*. 1999; Salleo *et al*. 2004; Wheeler *et al*. 2007; Zheng & Martinez-Cabrera 2013). *Ficus* anatomy is characterized by having axial parenchyma bands more than three cells wide (Koek-Noorman *et al*. 1984). According to Wheeler *et al*. (2007) wide bands have a rare occurrence with only 9% of the world's wood having this characteristic and are more common in tropical than in temperate regions.

Species with wide bands have been associated with absent or indistinct growth rings, indicating that perhaps in the absence of growth rings, parenchyma may act as a defensive function (Wheeler *et al*. 2007; Morris & Steven 2016). Wider bands, implied higher contact between axial and radial parenchyma systems, and probably the more efficient the photosynthate conduction between the two systems (Carlquist 2001). In the species studeid herein, we observed that the occupied area of axial parenchyma (AP) have a tendency to be higher than the proportion of radial parenchyma (RP) in trees (AP: 35%, RP: 20%) and hemiepiphytes (stem AP: 30%, RP: 18%; aerial roots AP: 28%, RP: 19%). Both types of xylem parenchyma are important for water transport since they act as water reservors to prevent embolism formation (Salleo *et al*. 2004; Zheng & Martinez-Cabrera 2013). In addition, it has been documented that in some species higher amounts of parenchyma are associated with higher xylem vulnerability (Zheng & Martinez-Cabrera 2013).

Additionally, Carlquist (2001) mentioned the presence of storied structure in axial parenchyma for *Ficus* species. However, we observed irregularly to regularly storied axial parenchyma cells in few species, as in the tree stem of *F. tomentella* and in the stem and aerial roots of the hemiepiphytes *F. benjamina*, *F. elastica*, *F. virens* and in the aerial roots of *F. microcarpa*.

Fibres– Septate fibers are living fibers, whose function may be regarded as like that of axial parenchyma (Carlquist 2001; Wheeler *et al*. 2007). Carlquist (2001) suggested that woods with septate fibers are associated with less abundant axial parenchyma, which was supported by Wheeler *et al* (2007) and Pace & Angyalossy (2013). In the species studied herein in, we observed presence of septate fibers in the stem and aerial roots of the hemiepiphytes: *F. elastica, F. pseudomangifera*, *F. benjamina* and *F. virens*. We noticed that the stem of *F. benjamina* and the stem and aerial roots of *F. elastica* and *F. pseudomangifera* have less axial parenchyma area compared to other species with non-septate fibers. Although, this is not the case for *F. virens* in which more than 50% of the total xylem area corresponds to axial parenchyma. Also, we observed that some species with non-septate fibers like the aerial roots of the hemiepiphyte *F. microcarpa* have less than 20% of the total area of the xylem corresponding to axial parenchyma. Septate fibers are a rare ocurrence in *Ficus.* Previous descriptions never mention presence of septate fibers for the genus (Koek-Noormanie *et al*. 1984). However, it was recently reported in the fossil *F. koek-noormanie* from the Miocene of Panamá (Jud & Dunham, 2017). And, interestingly septate fibers are a diagnostic character for its sister group tribe Castillae (Clement & Weiblen, 2009) and present in other members of the Moraceae family (Metcalfe & Chalk, 1950; Carlquist, 2001). This leave open the question if having septate fibers could be an ancestral condition for *Ficus*.

Laticifers: We observed latificers in all trees and hemiepiphytes species studied herein. Laticifers in *Ficus* are well documented in the literature (Metcalfe & Chalk 1950; Koek-Noorman *et al*. 1984; Carlquist 2001; Palhares *et al*. 2007; Kajii *et al*. 2014). Various studies point out that the latex of *Ficus* contains ficin (cysteine protease), which has a role of protection against herbivores and phatogens (Konno 2011; Zare *et al*. 2013). We observed non-articulated laticifers extending horizontally within the rays and in one case the laticifer extend from radial to axial direction intruding among the fibres in the stem and the aerial roots of the hemiepiphyte, *F. pseudomangifera.* Axial non-articulate laticifers have not been reported yet in previous literature for *F. pseudomangifera*, although they are known to exist in the secondary xylem and secondary phloem of *F. carica* (Kajii *et al*. 2014) and in the secondary xylem of *Artocarpus* species (Moraceae, Topper & Koek-Noorman 1980). It is suggested that lineages that have laticifers become more species-rich that their sister lineages (Farrel *et al*. 1991). *Ficus* is without a doubt a very species-rich genus that have laticifers, and it is the most species genus of the family Moraceae. However its sister group tribe Castillae also posses laticifiers and within the family, tribes Artocarpeae and Dorstenieae also posses laticifers and are not as species-rich as *Ficus*. Therefore, laticifers probably may not played an important role in the diversification of *Ficus* in particularly. But, possible the presence of laticifers influenced the diversification of the family Moraceae as a whole, since it is one of the most diverse angiosperms families in the neotropics.

Hemiepiphytes: Stem vs aerial roots

Hemiepiphytes of *Ficus*, germinate and grow as epiphytes and later produce roots to the ground and connect with the soil (Putz & Holbrook 1986). These plants benefit from growth in a higher light environment but with lower water and nutrient availability (Putz & Holbrook 1986; Patiño *et al.* 1999). To relieve water stress, hemiepiphytes make connections to the ground through the production of aerial roots (Patiño *et al*. 1999). Such a connection is crucial for these plants since they will not reproduce until they are rooted in the soil (Putz *et al.* 1995). Aerial roots produce secondary growth upon reaching the ground, producing tension wood that makes them contract (Zimmerman 1968).

Eventually, these woody aerial roots serve essentially like a stem giving support to branches (Zimmerman 1968). In the studied hemiepiphytes of *Ficus*, we found that the wood anatomical characters analysed for the stem and aerial roots are very similar and show no statistical significant differences. The only way to distinguish the aerial roots from the stem in *Ficus* species is by the exarch position of the xylem in the aerial roots. In many respects aerial roots are anatomically more similar to stems than to roots (Kapil & Rustagi 1966). Considering the anatomy of roots in general, it has been reported in a considerable body of literature, that stem and subterranean roots wood show several differences with respect to diameter of vessels, amount of parenchyma and fibres (Palhares *et al*. 2007). For instance, subterranean roots tend to have wider vessels than stems, which has been related to higher water potential in the roots (Aloni & Zimmermann, 1983), larger amounts of parenchyma and thinner-walled, septate fibres (Lebedenko 1962; Patel 1965; Aloni & Zimmermann, 1983; Sieber 1985; Ewers *et al*. 1997; Machado *et al*. 1997, 2007; McElrone *et al*. 2004; Psaras & Sofroniou 2004; Palhares *et al*. 2007; Pratt *et al*. 2007; Goulart & Marcati 2008). Additionaly, in previous studies with hemiepiphytes, Esserman de Quadros (2001) found wider vessels in aerial roots than in stems of *Clusia criuva* together with higher amounts of parenchyma, resembling the anatomy of a liana. Contrary, to our expectations, in *Ficus* hemiepiphytes studied herein we found that the stem tend to have wider vessels (mean: 172 µm) than the aerial roots (mean: 158 µm), similar amounts of parenchyma and similar fibres features.

Additionally, we observed gelatinous fibers in the aerial roots of the hemiepiphytes. Zimmerman (1968), Fisher (1982) and Abasolo *et al*. (2009) reported presence of gelatinous fibres in the aerial roots of hemiepiphytes species of *Ficus*. Esserman de Quadros (2001) also observed gelatinous fibres in the aerial roots of hemiepiphytes species of *C. criuva*. Gelatinous fibres lack lignin on its cell wall, possess flexible properties (Tomlinson 2003) and are associated to tension wood commonly found in eudicotiledons (Carlquist 2001). The formation of tension wood in aerial roots is related to geotropism as a response of secondary growth (Zimmerman 1968). Tension wood differs from normal wood in that fibres possess extremely thick walls in which one or more layers are unlignified (Zimmerman 1968). Nevertheless, we also observed gelatinous fibers in the stem of hemiepiphytes and in some tree species, implying that this character is not exclusively from aerial roots. However in stems, the presence of gelatinous fibres is thought to bring recovery of leaning stems, mainting the position of the trunk or the branch despite possible factors tending to change their position (Zimmerman 1968, Carlquist 2001).

Potential hydraulic conductivity between trees and hemiepiphytes

In the species studied herein the potential hydraulic conductivity is higher in hemiepiphytes than trees. And, within the hemiepiphytes, stems have higher potential hydraulic conductivity that their aerial roots.

The potential hydraulic conductivity (Kp) has been associated to anatomical structures, mainly with characteristics of the xylem. The xylem posses multiple functions, like the balance (trade-off) between efficiency and safety of water transport (Tyree & Zimmermann 2002; Baas *et al*. 2004; Poorter *et al*. 2010; Fichtler & Worbes 2012; Gerolamo & Angyalossy 2017). One possible strategy to increase the efficiency of water transport is either increase the area of the xylem or change anatomical features that are directly related to the potential hydraulic conductivity, like the diameter of the vessels (Ewers, 1985). Previous studies with other plant habits showed that plants with larger Kp possess wider vessels (Tyree & Zimmermann 2002; Baas *et al*. 2004; Poorter *et al*. 2010; Fichtler & Worbes 2012; Gerolamo & Angyalossy 2017). In our study, hemiepiphytes (stem and aerial roots) have significantly wider vessels than trees. As seen in the present study, the stem and aerial roots of the hemiepiphytes *Ficus elastica* and *F. microcarpa* posseses significantly wider vessels than the other hemiepiphyte *Ficus* species, which is also associated with their highest hydraulic conductivity.

Wide vessels are the most efficient water conductors because the water conductivity increases with the fourth power of vessel diameter (Tyree & Zimmermann 2002; Poorter *et al*. 2010; Fichtler & Worbes 2012). Efficiency in water transport allows for higher stomatal conductance, and photosynthetic rates (Poorter *et al*. 2010). Also, larger leaf area can be supplied with water, and wood properties that facilitate high water flow therefore contribute positively to carbon gain and growth (Poorter *et al*. 2010). The ecological disadvantage of wide vessels is their vulnerability against cavitation (Choat *et al.* 2005). In fact, in some tree species has been demonstrated that wider vessels are less safety because they posses higher pit membrane porosity and largest pit area per vessel (Wheeler *et al*. 2005; Hacke *et al*. 2006). As a hydraulic strategy regarding lower safety, vessel diameter is negatively correlate with vessel density, since a small number of wide vessels is much safer in terms of vulnerability (Carlquist 1977; Poorter *et al*. 2010). This trade-off can be observed in *Ficus* species. In our data, tree species possess significantly smaller vessels and higher vessel frequency opposite to hemiepiphytes. The species *F. tomentella* was the only tree species that posses similar vessel diameter to that of hemiepiphytes. It is interestingly to mention that *F. tomentella* belongs to the subgenera *Spherosuke*, the same as the hemiepiphytes species.

In addittion to the size and density of vessels, previous studies have demostrated that pit morphology could also be an important factor influencing the trade-off between hydraulic safety and hydraulic efficiency (Baas *et al*. 2004; Wheeler *et al*. 2005; Hacke *et al*. 2006; Jansen *et al*. 2009; Pfautsch *et al*. 2018; Li *et al*. 2019). In general it is known that small intervessel pit area increases cavitation resistance of water transport, while larger pit area, larger aperture and lower pit density have found to increase hydraulic conductivity (Wheeler *et al*. 2005; Hacke *et al*. 2006; Li *et al*. 2019). Also, pit shape is known to be correlated with embolism resistance, commonly, species with narrower and elliptical apertures are more resistance to cavitation (Wheeler *et al*. 2005; Hacke *et al*. 2006; Li *et al*. 2019).

Our data showed the size of intervessel pit to be similar among trees and hemiepiphytes (stem and aerial roots). However, Li *et al*. (2019) observed larger pit size and pit aperture size and lower pit densities in hemiepiphytes than non-hemiepiphytes species of *Ficus*, suggesting that hydraulic efficiency is more crucial than hydraulic safety for hemiepiphytes (Li *et al*. 2019). In fact, some studies point out that dehydratation is the main cause of death of hemiepiphytes, especially in the epiphytic phase (Zotz & Andrade 2002) and that water is important to determine abundance and diversity of *Ficus* species in seasonal environments (Coelho *et al*. 2014). Together, it seems, that having wider vessels, lower vessel density and larger pit size suggests that water availability is a major factor limiting growth and development of hemiepiphytes species.

Comparison of anatomical features between modern and fossil woods

The fossil record of woods assigned, as *Ficus* or *Ficoxylon* is very sparse. The oldest published record is *Ficoxylon mogaungense* sp. nov. from the Eocene of Myanmar (Licht *et al*. 2014), and the youngest record is *Ficoxylon* sp. from the Pliocene of Ethiopia (Jolly Saad *et al*. 2010). In the Neotropical region the occurrence of fossil woods belongs to the Oligocene (Jud & Dunham, 2017), and Miocene (Martinez-Cabrera *et al*. 2006), which is consistent with the hypothesis that neotropical sections arrive in the neotropics between the Late Oligocene and the Lower Miocene (Machado *et al*. 2018).

After the comparison conducted between modern and fossils species, the main anatomical features that varied were: vessel diameter, intervessel pit and vessel element length. In general intervessel pit size and vessel element length were significant smaller in fossils than in modern species, while vessel diameter was similar in size with modern hemiepiphytes. According to the results obtained herein it is not possible to distiguish if the fossil wood belong to an aerial root or to a stem. However, our data suggest that the fossils woods share more anatomical features with modern species of hemiepiphytes rather than trees. We can infered that an isolated piece of fossil wood with vessel diameters close to 200 µm likely would be a hemiepiphyte.

Ficoxylon bajacaliforniense is similar in vessel diameter with the aerial roots of *F.elastica, F. bonijesulapensis, F. pseudomangifera* and *F. benjamina* all of which are hemiepiphytes. Additionally, other features such as vessel element length and vessel density are also similar with the stem and aerial roots of the hemiepiphytic species. *Ficus koek-noormaniae* is similar in vessel diameter with the stem of the tree *Ficus tomentella.* However, vessel element length, vessel density and intervessel pit size is similar with the stem and aerial roots of *F. virens, F. microcarpa* and *F. bonijesulapensis* which are hemiepiphytes. *Ficoxylon* sp. is similar in vessel diameter with the stem and aerial roots of *F. microcarpa* and with the stem of *F. elastica,* both hemiepiphytes. The size of intervessel pit and the size of vessel element length differ from the modern species. However, vessel density is similar with both, trees and hemiepiphytes.

F. koek-noormaniae and *F. bajacaliforniense* from the Oligocene and Miocene of Panama and Mexico, respectively, and *Ficoxylon* sp. from the Pliocene of Africa share anatomical features similar to hemiepiphytes of the subgenera *Sperosuke* rather than with the trees of *Pharmacosycea.*

Today, tropical Africa is characterized by a high diversity of *Ficus* section *Platyphyllae* from the subgenera *Sperosuke* (Pederneiras *et al*. 2018). While the Neotropical region is composed of sections *Americanae* and *Pharmacosycea* (Machado *et al*. 2018; Pederneiras *et al*. 2018). According to the last proposed biogeographic scenario for the main lineages of *Ficus* (Pederneiras *et al*. 2018), the section *Pharmacosycea* move to tropical regions of southern North America and northern South America in the Oligocene (*c*. 28 Mya). This section is endemic to the Neotropical region and is composed entirely by trees (Machado *et al*. 2018; Pederneiras *et al*. 2018). By the oher hand, the *Sperosuke* lineage, composed mainly of hemiepiphytes species, probably reached South America from Africa via the Atlantic Ocean during the Eocene, giving rise to the *Americanae* lineage in South America and the *Platyphyllae* lineage in Africa from an event of vicariance (Pederneiras *et al*. 2018).

According to this, we suggest that *F. koek-noormaniae* and *F. bajacaliforniense* support the hypothesis of the arrival of the *Americanae* lineage in the Americas during the Oligocene and *Ficoxylon* sp. probably represents relicts from section *Platyphyllae* linage in Africa.

By the other hand, *Ficoxylon mougaungagense* is similar in vessel diameter with the stem of *F. vermifuga*, which is a tree. However, vessel length, vessel density and diameter of intervessel pit differ from all modern trees and hemiepiphytes species. According to our results *F. mougaungagense* from the Eocene of Myanmar share more anatomical characters with trees than with hemiepiphytes. Neverthless, many of the anatomical features of this fossil differ from the modern species studied herein. Still, Licht *et al* (2014) suggested that *F. mougaungagense* resemble the extant *F. benghalensis*, which is an evergreen to deciduous tree common in sub-Himalayan forests (not analysed here).

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 have 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 that their aerial roots.

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

- It is not possible to distiguish if the fossil wood belong 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 significant 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.

Future research directions

Aerial roots–Aerial roots of hemiepiphytes are the most conspicuous organ of these plants. Despite the apparent importance of aerial roots, little is known about their ontogeny and morphoanatomical diversity.

It is known, for example, that upon reaching the soil, aerial roots often grew across the soil surface before penetrating the soil or producing lateral roots. Whether particular soil moisture conditions or other environmental cues are necessary for roots to penetrate is unknown (Patiño et al. 1999). This, leave open questions such as: How does the morphoanatomy of the aerial root change when it penetrates in the soil? which morphological and anatomical characters help them cope with the different environments?

As observed by Patiño et al. (1999) aerial roots grew faster in wet than dry seasons, suggesting that water stress may limit the growth of aerial roots. In this respect, it would be interesting to measure survival rates in hemiepiphytes of different root growth strategies.

In synthesis, future research is needed in search for morphological, developmental and anatomical characters of aerial roots.

Phylogenetic approaches within Ficus lineages–The systematic of *Ficus* has been controversial because phylogenetic results have not corroborated the morphological classification (Pederneiras *et al*. 2018). *Pharmacosycea* and *Spherosuke* are subgenera that have always been recovered as paraphyletic (Pederneiras *et al*. 2018). From the eight tree species that we studied herein, two of them (*F. clusiifolia* and *F. tomentella*) belong to the subgenerea *Spherosuke*, the same lineage of all the studied hemiepiphytes. The other six tree species belong to the subgenera *Pharmacosycea.*

Our results show no phylogenetic signal between the studied species. However, future studies should increase the number of species to investigate the wood anatomy of major lineages of *Ficus* in search for anatomical sinapomorphies for clades. Additionally, it will be very interesting to map the anatomical characters explored in the present study of both fossils and modern species onto a robust phylogeny of *Ficus* to: i) depict the pattern of wood evolution; ii) support the hypothesis that vessel diameter could be a habit-related trait and; iii) investigate if septate fibers are an ancestral condition for *Ficus* species.

Hemiepiphyte plants–Hemiepiphyte plants can be found only in two groups within the vascular plants; the angiosperms (Putz & Holbrook, 1986) and the ferns (Watts *et al*. 2019). Within the ferns they are present in 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). This leave open the question if hemiepiphytism evolved independently in ferns and angiosperms or if by contrary it may have appeared way before the angiosperms in the evolutionary history of land plants. However, not enough evidence has accumulated in the fossil record and to date, studies with modern hemiepiphytes are very scarce. Therefore, we suggest that to understand the evolutionary history of the hemipiphytism, future studies on morphology, ontogeny and anatomy of hemiepiphytes are needed.

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