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## Rhizophores in *Rhizophora mangle* L: an alternative interpretation of so-called “aerial roots”

NANUZA L. DE MENEZES\*

Instituto de Biociências, Universidade de São Paulo, Caixa Postal 11461, 05422-970 São Paulo, SP, Brasil

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### ABSTRACT

*Rhizophora mangle* L., one of the most common mangrove species, has an aerial structure system that gives it stability in permanently swampy soils. In fact, these structures, known as “aerial roots” or “stilt roots”, have proven to be peculiar branches with positive geotropism, which form a large number of roots when in contact with swampy soils. These organs have a sympodial branching system, wide pith, slightly thickened cortex, collateral vascular bundles, polyarch stele and endarch protoxylem, as in the stem, and a periderm produced by a phellogen at the apex similar to a root cap. They also have the same type of trichosclereid that occurs in the stem, with negative geotropism, unlike true *Rhizophora* roots, which do not form trichosclereids at all. On the other hand, these branches do not form leaves and in this respect they are similar to roots. These peculiar branches are rhizophores or special root-bearing branches, analogous to those found in *Lepidodendrales* and other Carboniferous tree ferns that grew in swampy soils.

**Key words:** *Rhizophora mangle* L., rhizophore, “aerial roots”, “stilt roots”.

### INTRODUCTION

One of the few tree species of the Brazilian mangrove is *Rhizophora mangle*, belonging to a widespread genus in the Americas, Africa, Asia, Madagascar and Australia (Juncosa and Tomlinson 1988a). According to Juncosa and Tomlinson (1988b), the generic epithet means “root-bearer”. However, according to Plumier (1703), the name *Rhizophora* was attributed by G. Pisone to the fact that in the propagule of the viviparous plant “the radicle is located at the extremity of an axis, the rhizophore”. In fact, Pisone considered the rhizophore to be the exposed hypocotyl of the viviparous propagule itself.

One of the most striking features of this species

is the presence of structures that expand its supporting base. These structures are defined as aerial roots by most authors, including Warming (1883), Hou (1958), Gill and Tomlinson (1969, 1971a, b, 1977), Sporne (1974), Chapman (1976), Hallé et al. (1978), Ellmore et al. (1983), Tomlinson (1986), Juncosa and Tomlinson (1988a, b), Mauseth (1988), Huang and Huang (1990) and Raven et al. (1992). Some of these authors have carried out extensive anatomical studies on these structures (Gill and Tomlinson 1971a, Chapman 1976, Ellmore et al. 1983), and concluded that they are roots, although they mention that they have detected stem-like characteristics in these organs. They also mention a strong characteristic of roots, which is the presence of a root cap.

Pitot (1951, 1958), in studies on *Rhizophora racemosa*, not only always placed the term “stilt

\*Member Academia Brasileira de Ciências  
E-mail: nanuzalm@usp.br

root" in inverted commas, ("racine échasse"), but also referred to these structures as rhizophores, and advocated that they are part stem and part root. According to Pitot (1951, 1958), the rhizophore grows with a stem-like structure (sometimes as much as several meters) until it reaches the swampy soil, the apex of the rhizophore transforming itself into a root upon contact with the water. According to this author, the submerged portion is, therefore, a root, and all the aerial part, a stem.

On the other hand, Huang and Huang (1990), working with several mangrove species, refer to the fact that "the structure of the aerial root in *Rhizophora mangle* resembles that of the stem", although they do not explicitly refer to the structure as a stem.

The presence of H-trichosclereids in the cortex was observed, in both the stem and root of *Rhizophora mangle*, by Gill and Tomlinson (1971a, b) and in the stem and aerial root, by Warming (1883) and Karsten (1891). The last two authors demonstrate that there is a system of brachiform cells in the submerged root cortex, with a special thickening in the cell walls, which prevents the collapse of the cell due to the large air spaces within it. Referring to these cells observed by Warming (1883), Gill and Tomlinson (1971a) propose that this was a technical flaw, once Warming's observations were made on pickled specimens. Gill and Tomlinson (1971a, p. 63) emphasize that, as their laboratory was directly in front of the mangrove, they were working with recently collected material, and were able to affirm that the root does have H-trichosclereids.

The present study offers an alternative interpretation for the aerial structure system that provides stability to *Rhizophora mangle* in swampy soils, and seeks to understand this structure by comparing it with rhizophores, which are root-bearing organs of the Carboniferous *Lepidodendron* (Stewart 1983), a plant which also grows in swampy soils. In relation to *Lepidodendrales*, Stewart (1983, p. 103) writes that: "these plants have a main axis that grows and branches at both ends. The branches of the aerial part form a three-dimensional system of dichoto-

mous or pseudomonopodial branches, with spirally arranged leaves and terminal cones. The basal end also branches dichotomously to form the anchoring and water-absorption system, which is comprised of rhizophores bearing spirally-arranged roots".

Rhizophores have also been described in *Selaginella* as a *sui generis* organ (Nägeli and Leitgeb 1868 *apud* Jernstedt and Mansfield 1985, Goebel 1905, Jernstedt et al. 1994). Working with *Dioscoreaceae*, Goebel (1905) refers to the "relations between the thickened organ of *Dioscorea* and the root-forming organ of *Selaginella*". According to Goebel (1905), this organ is neither root nor stem, but a *sui generis* organ, half way between stem and root. Ogura (1938), also working with *Dioscoreaceae*, calls these thickened organs rhizophores.

#### MATERIALS AND METHODS

The plant material used was collected from the mangrove on the Rio-Santos highway, at Km 197, in the Municipal District of Bertiooga, next to the Guaratuba River. (Menezes *s.n.*, SPF 124.080) on 02/25/1997.

Free-hand cross-sections were taken from the stem, root and rhizophore of *Rhizophora mangle* L., and stained with astra blue and fuchsin, according to the method described by Roeser (1962). The sections, mounted in 66% glycerine, were photographed using a VANOX model Olympus photomicroscope.

#### RESULTS

*Rhizophora mangle* almost always grows in swampy soils and has a positive geotropic branching system (Fig. 1 and 2) which is the result of the development of secondary rhizophores, that emerge from the erect stem and grow towards the soil, branching sympodially (exactly like the aerial branch with leaves), and expanding the supporting base of the plant. The hypocotyl of the seedling (Fig. 3) comprises the primary rhizophore, which germinates on the parent plant and generally buries itself when it falls from the tree (Fig. 4). When the secondary rhi-

zophore, protected by an apical periderm (Fig. 5), reaches the water in its positive geotropic growth, it forms roots at its extremities (Fig. 6) or around it (Fig. 7).

A cross-section of the aerial axis of a secondary rhizophore (Fig. 8–9) shows a wide pith and many bundles, in which the protoxylem is in an **endarch** position, surrounded by fiber strands throughout the perimedullary region shown by the arrows in Fig. 8. The metaxylem is external to the protoxylem, where cambium, secondary phloem and secondary xylem can also be seen. The endodermis is external to the vascular system. Even when secondary growth has been fully established (Fig. 10), fiber strands can be seen around the primary xylem. There are H-trichosclereids both in the cortex and in the pith, as shown in longitudinal section in Fig. 11. The root apex in longitudinal section (Fig. 12) shows a root cap formed by layers which separate easily, produced by a calyptragen. In the longitudinal section of the apex of the secondary rhizophore (Fig. 13), a phellogen can be seen, which produces a protective periderm. In a submedian longitudinal section of the secondary rhizophore (Fig. 14) procambial strands can be seen, and in cross-section (Fig. 15), appearing inside the endodermis. These procambial strands present protoxylem in their interior at the level of Fig. 16. Closer to the apex (Fig. 17–18) the primary xylem forms collateral bundles with primary phloem strands. The cambium is formed in the vascular bundle and inside the interfascicular phloem. The bundles show **endarch** differentiation of the primary xylem. There are numerous thickened structures that correspond to H-trichosclereid arms, which are clearly visible in Fig. 11. At the level corresponding to Fig. 19, the cells are already fully lignified around the primary xylem, forming fiber strands.

In the apex of the aerial stem with negative geotropism (Fig. 20–21), a band of primary phloem can be seen, originating from the pericycle, and interspersed with bundles containing protoxylem and metaxylem, as well as primary phloem. At the level corresponding to Fig. 21, the presence of primary

xylem, i.e. proto- and metaxylem, can be seen only inside the secondary xylem, formed by the cambium of procambial origin.

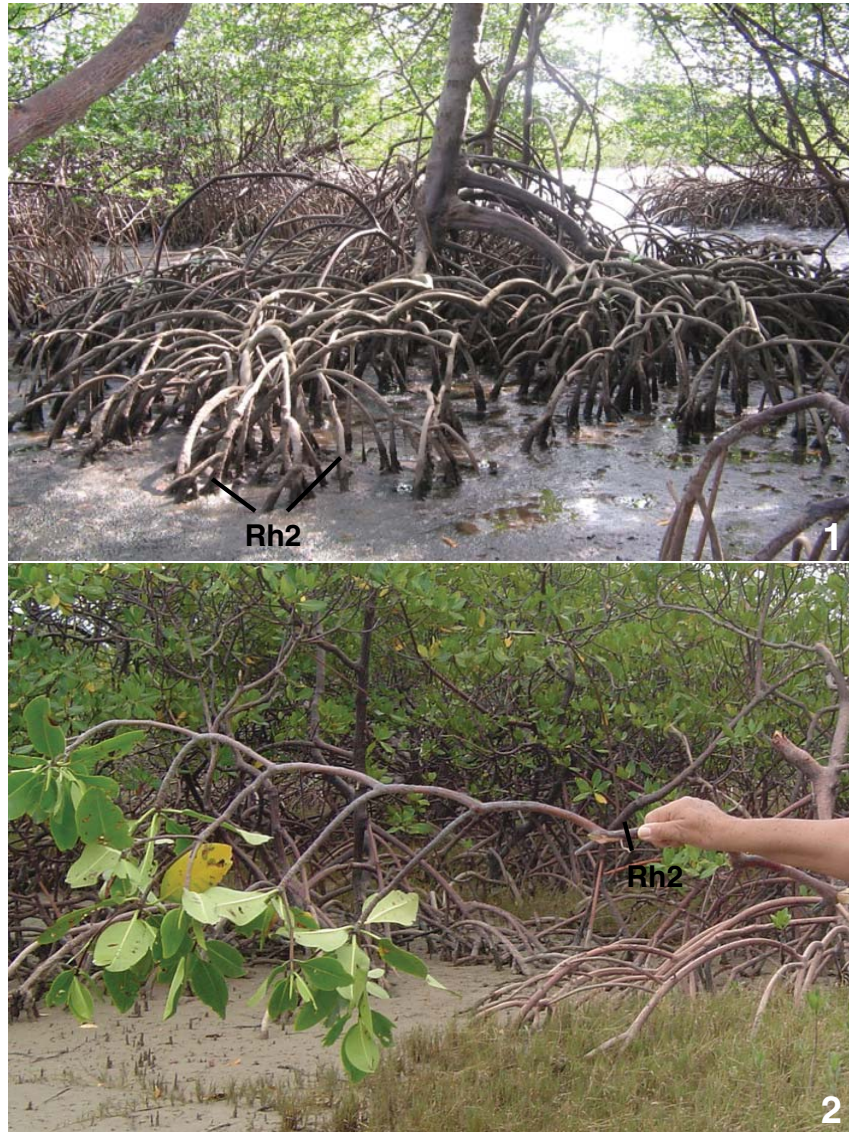
The roots are adventitious, and have a relatively wide pith (Fig. 22) with **exarch** protoxylem (Fig. 23–24). The thickened root cortex (Fig. 22) has brachiform cells with lignified secondary walls (Fig. 25) in certain regions of the cell. In a secondary structure (Fig. 24), parenchymatous rays formed by the cambium of pericyclic origin also can be seen in the root.

## DISCUSSION

Although the branching system that supports *Rhizophora mangle* plants in swampy soils has always been referred to as being composed of “aerial roots” or “stilt roots”, its true identity can only be resolved by means of anatomical studies. Pitot (1958) identified an inversion in the vascular tissues of these organs in *Rhizophora racemosa* G.F.W. Meyer, which he linked to the position of the protoxylem, typically exarch in roots and endarch in these aerial branches, as in stems. He also found another stem characteristic in this organ, namely, the presence of collateral bundles. However, he identified the existence of phloem strands interspersed between these bundles in a radial position, which led him to identify these structures as roots.

When only one adventitious root is formed at the apex (as shown in Fig. 6 with two roots at the apex), it simulates a hypocotyl-radicle axis, as a result of tissue continuity, unlike subapical adventitious roots.

On the other hand, an important observation by Pitot (1958) lead the author to admit another possible explanation for the appearance of roots at the apex of the rhizophore. According to Pitot, “*Rhizophora racemosa*, from a morphological point of view, presents two types of root: adventitious fasciculated roots, essentially aquatic, which consist of a fairly dense involucre around a ‘pivot’, forming upon contact with the water; and stabilizing roots, originating from the ‘pivot’ which sink into the mud

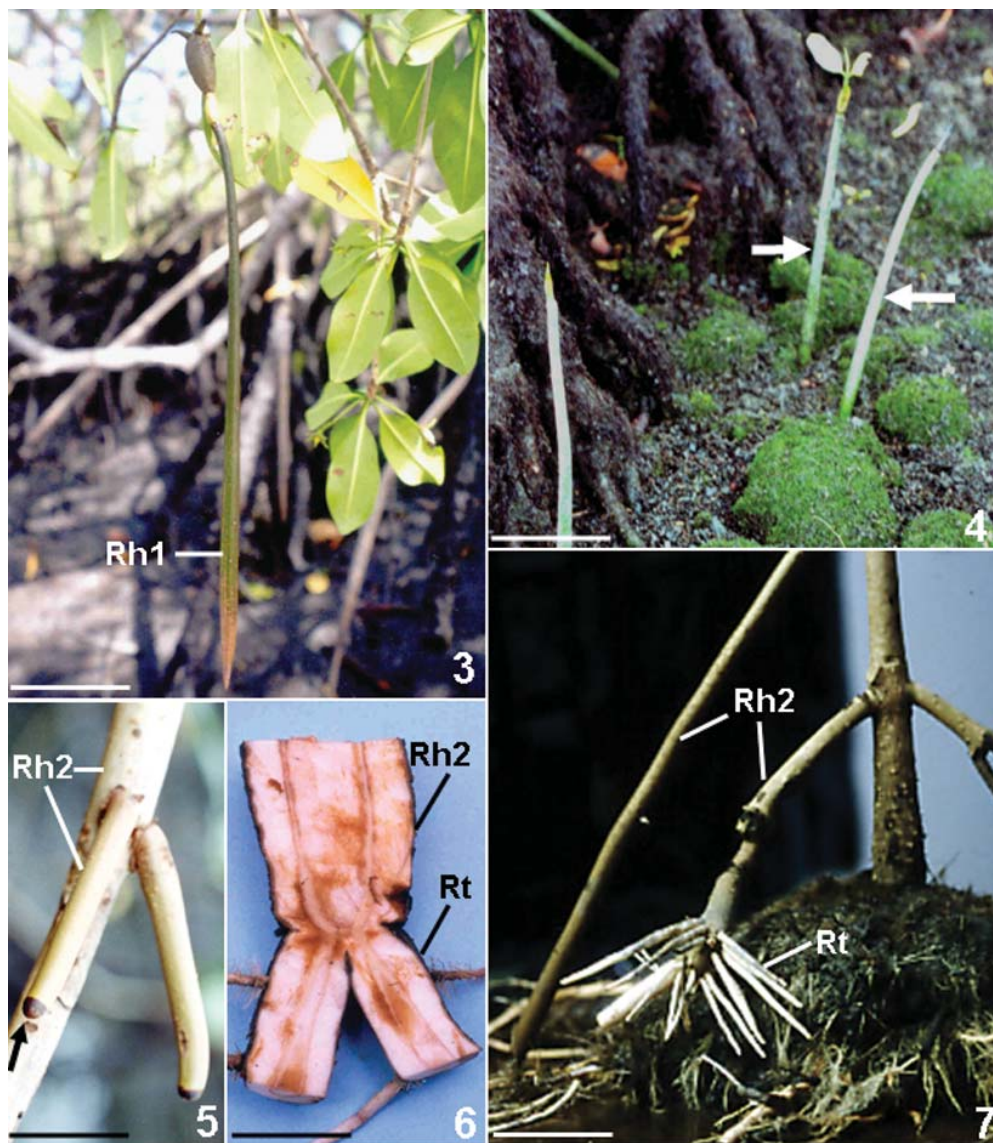


Figs. 1–2 – *Rhizophora mangle* in Porto de Galinhas (Pe, Brazil). Fig. 1 – Entire plant with the secondary rhizophores (Rh2) highlighted, at the base. Fig. 2 – Stem branch with leaves, with the same sympodial branching system as that seen in secondary rhizophores. (Photo Ricardo Sacerdoti)

and transform themselves into roots, upon contact with the swampy soil” (Pitot 1958, p. 1112). Pitot (1958, p. 1118) also states that: “the transformation of an aerial organ into an underground organ is observed; from endarch bundle into alternate exarch

bundle, with a rhizophore root structure. This zone or region of transformation corresponds to the submerged region”. This observation by Pitot (1958) corresponds to what is normally seen in tissue culture, that is, the transformation of organs with the

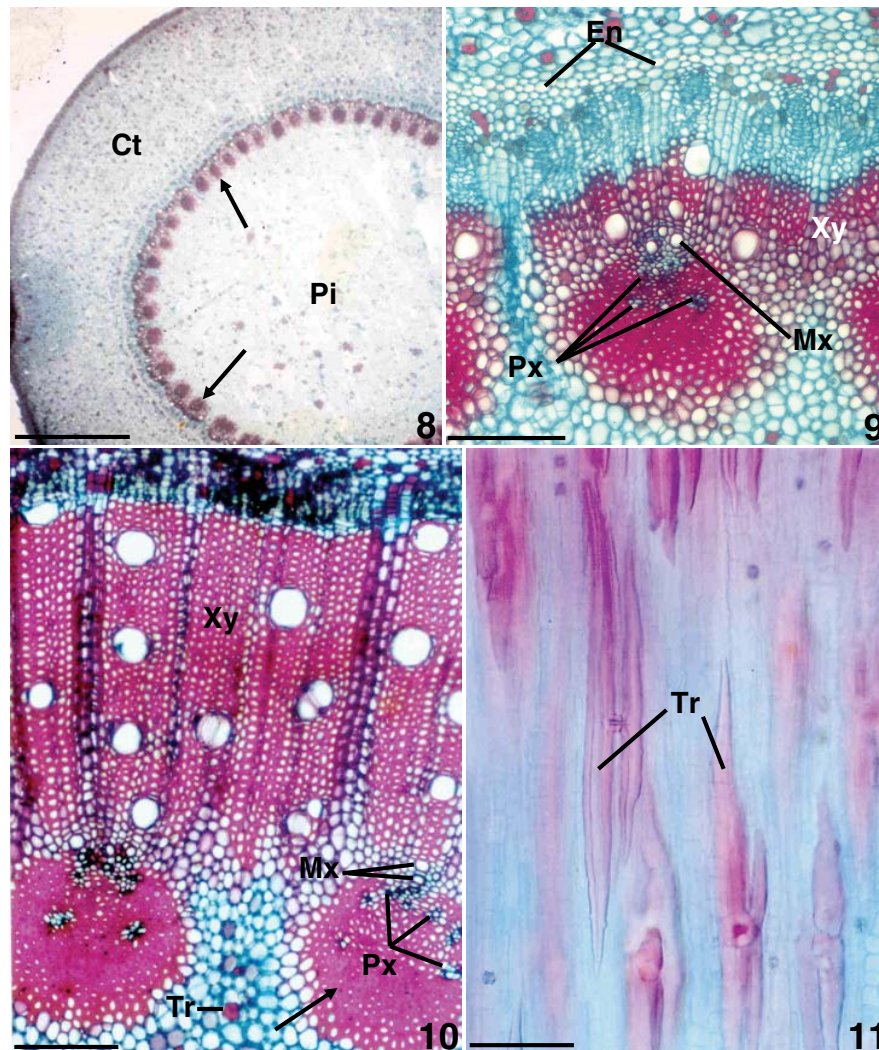




Figs. 3–7 – *Rhizophora mangle*. Fig. 3 – Propagule with well-developed hypocotyl = primary rhizophore (Rh1) still connected to the fruit. Fig. 4 – Two primary rhizophores, partially submerged in the soil of the mangrove (arrows). Fig. 5 – Young branches of secondary rhizophores (Rh2) with apical protection (arrow). Fig. 6. Secondary rhizophore with two adventitious roots (Rt) at the extremity. Fig. 7. Young plant with the adventitious roots at the end of the secondary rhizophore. The bars correspond respectively to: 10 cm, 12 cm, 0.5 cm, 2 cm and 10 cm.

use of hormones. However, as Pitot (1958) demonstrates in his work with *Rhizophora racemosa*, this phenomenon also occurs in nature. The same pro-

cess may also occur in *R. mangle*, but I believe that a single root primordium may also form at the apex of the rhizophore, similar to that seen in this work, with



Figs. 8–11 – Cross-sections (Fig. 8–10) and longitudinal section (Fig. 11) of *Rhizophora mangle* secondary rhizophores. Fig. 8 – Rhizophore with wide pith (Pi) and many fibrous strands (arrows). The vascular cylinder is 2.5 times the width of the cortex (Ct). Fig. 9 – Detail from previous figure, in which the protoxylem (Px), metaxylem (Mx) and secondary xylem (Xy) can be distinguished. Fig. 10 – Rhizophore with the well-developed secondary xylem. The arrow indicates the fibers of procambial origin. Fig. 11 – H-trichosclereids in longitudinal section. The bars correspond respectively to: 2 mm, 250 $\mu$ m, 150 $\mu$ m and 60 $\mu$ m.

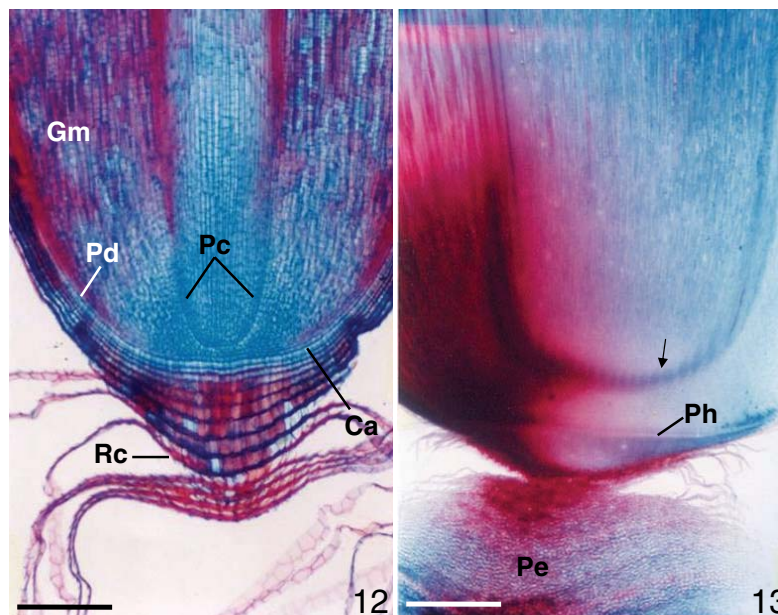
two adventitious roots at the apex of the rhizophore, resulting from two root primordia.

While in this study, only regions with stem characteristics are considered rhizophore, Pitot (1958) considered the whole structure to be a rhizophore (with both stem and root regions), hence,

he referred to it as an “intermediate organ”. However, Pitot did not explain his reasons for labeling the organ a rhizophore.

The presence of interspersed or radial primary phloem strands between the bundles was indicated by Pitot (1958) as being characteristic of roots,





Figs. 12–13 – *Rhizophora mangle*. Longitudinal sections. Fig. 12 – Root apex, showing the procambium (Pc), ground meristem (Gm), protoderm (Pd) and calyptragen (Ca), which gives origin to the root cap (Rc). Fig. 13 – Apex of a secondary rhizophore, where the procambial strands (arrow) and a periderm (Pe) originating from the phellogen (Ph) can be distinguished. The bars correspond respectively to: 250  $\mu$ m and 750  $\mu$ m.

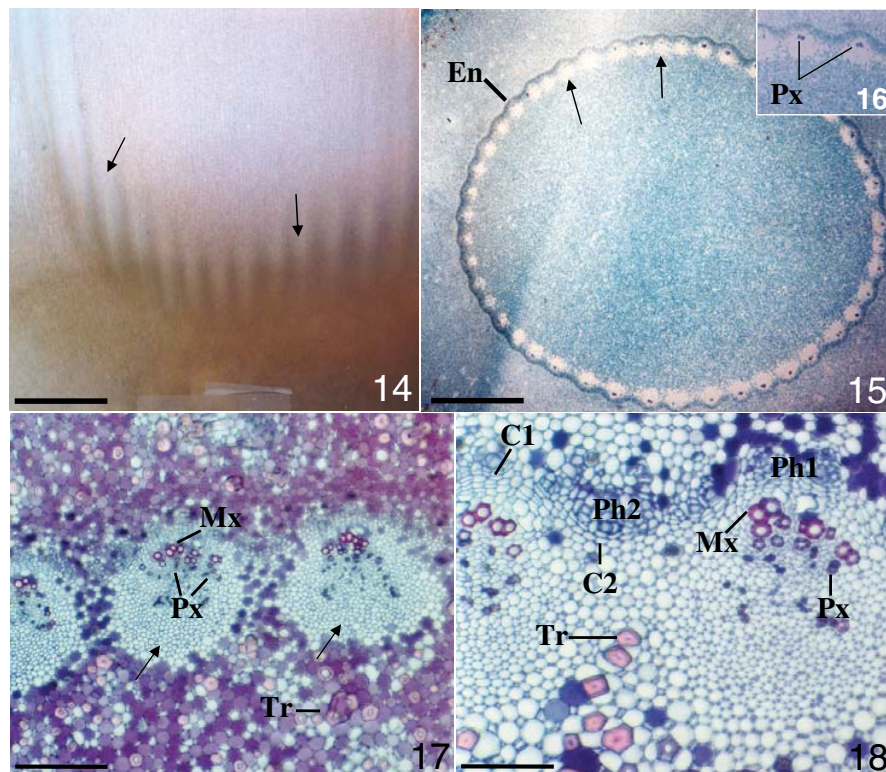
but these strands are usually found in young shoots. In the stem of *Rhizophora mangle*, Behnke and Richter (1990) prove the existence of several primary phloem strands without their corresponding primary xylems, between bundles of the young shoot apex, exactly as shown in this paper. It should be noted, as demonstrated in the present work, that on the inner side of the secondary xylem, in the areas corresponding to the intercalary phloem, there are no protoxylem elements in the adult stem.

Subsequent to Pitot's studies (1958), Gill and Tomlinson (1969) and Chapman (1976) made a series of important observations on the adventitious origin of these rhizophores, which they refer to as "aerial roots". In other words, unlike roots (except for the radicle), they are not endogenous in origin. According to these authors, these branches are clearly adventitious because the primary xylem does not have a vascular connection with the primary xylem of the stem that originated it. Ac-

cording to Chapman (1976), "there are no prior root primordia, neither can continuity with the primary xylem" be observed between the root and its generator axis. Therefore, like the stem, they are exogenous in origin. Gill and Tomlinson (1969) demonstrate that while all roots have a monopodial branching system, the "aerial roots" of *Rhizophora* have a sympodial branching system (a characteristic shared with stems) which is also demonstrated in this work.

Gill and Tomlinson (1971a, b) also observe that earlier authors questioned the root nature of these branches due to the presence of trichosclereids. They believe mainly owing to the presence of wide pith and polyarch stele, the structure is also rather different from the characteristic structure of other dicotyledonous roots. Gill and Tomlinson (1971a, b) also mention that in these organs, the protoxylem is on the inner side of the metaxylem and they believe that this condition led



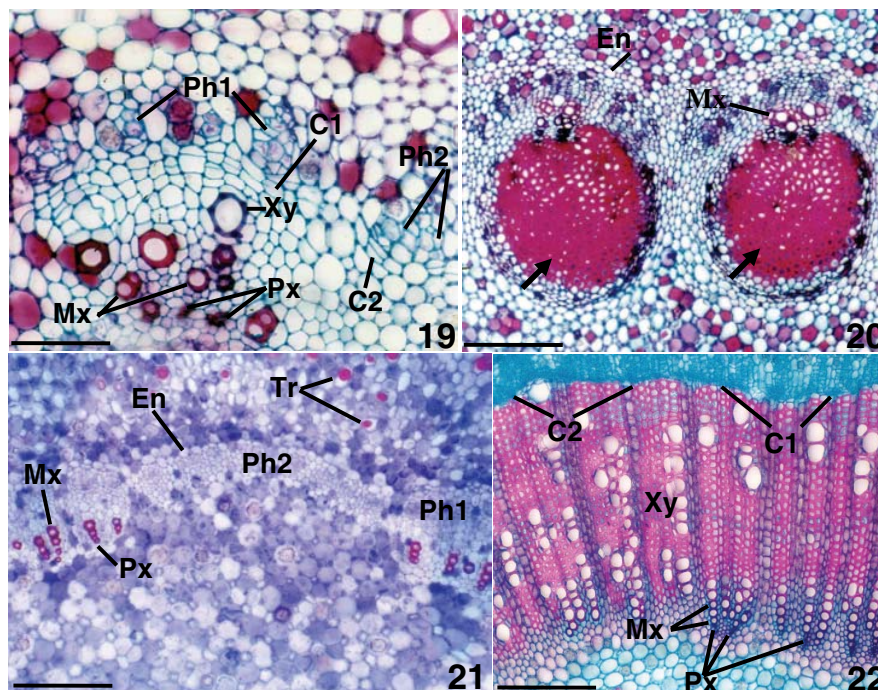


Figs. 14–18 – *Rhizophora mangle*. Fig. 14 – Submedian longitudinal section of the secondary rhizophore where procambial strands (arrows) can be seen. Fig. 15–16. Cross-sections, where the arrows indicate the procambial strands and protoxylem (Px) already differentiated. Fig. 17 – Cross-section with protoxylem and metaxylem (Mx) perfectly differentiated. Fig. 18 – Differentiated fascicular cambium (C1) between the fascicular phloem (Ph1) and the metaxylem; interfascicular cambium (C2) and the interfascicular phloem (Ph2) can also be observed. En – endodermis; Tr – trichosclereid. The bars correspond respectively to: 750 $\mu$ m, 750 $\mu$ m, 150 $\mu$ m and 60 $\mu$ m.

to confusion among earlier anatomists, as to whether or not it was a root. The authors conclude their study by emphasizing features which are not found in dicotyledonous roots, and which are considered exceptions in the roots of *Rhizophora mangle*: pol-yarch stele, wide pith, the collateral position of the vascular tissues, and endarch protoxylem. In a later study, Gill and Tomlinson (1977) also mention that these “aerial roots” originate in the trunk, or in other “aerial roots”, sympodially, but never in underground (or submerged) roots.

The results presented in this study indicate that the aerial branch system of *Rhizophora mangle*, with

positive geotropism, is, in fact, a rhizophorous system which is very similar to a stem system with negative geotropism, as perfectly demonstrated in Table I of the present work. All the characteristics which are considered exceptions in roots, define the rhizophore as a stem system: to these characteristics, one can add the presence of H-trichosclereids identical to those found in rhizophores and negative geotropic stems, and distinct from Warming root cells, with phi-thickenings (Haas et al. 1976). Another major difference between the rhizophore and the root, as demonstrated in this work, is that while in the true root of *Rhizophora mangle* there



Figs. 19–22 – *Rhizophora mangle*. Fig. 19 – Cross-section of the rhizophore, showing vascular bundle with endarch protoxylem (Px), and elements of the secondary xylem (Xy) already differentiated and the fascicular cambium (C1). Fig. 20 – Fibres (arrows) resulting from the procambial strands represented in Fig. 15–18. The elements of the protoxylem appear obliterated. Fig. 21 – First internode of a stem with negative geotropism in cross-section, showing the presence of an interfascicular phloem (Ph2) between the original bundles with primary xylem. Fig. 22 – Eighth internode of the same stem, without protoxylem inside the secondary xylem formed by the interfascicular cambium (C2). En – endodermis; Mx – metaxylem; Ph1 – fascicular phloem; Tr – trichosclereid. The bars correspond respectively to: 60 $\mu$ m, 150 $\mu$ m, 150 $\mu$ m and 150 $\mu$ m.

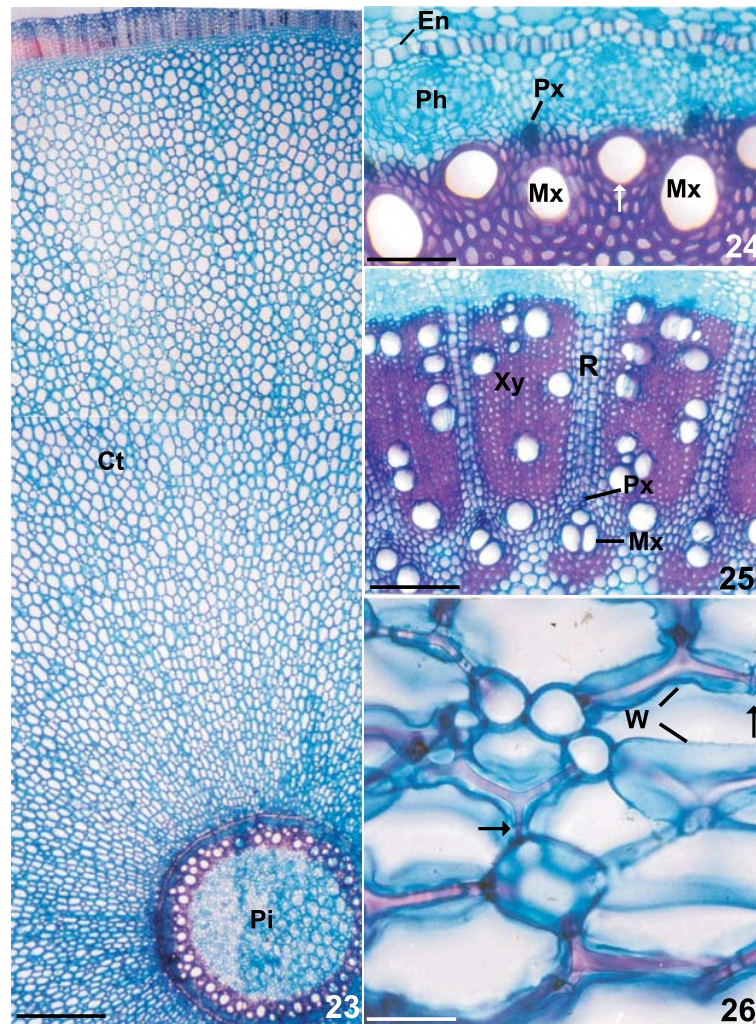
is a root cap, formed by the calyptragen, in the rhizophore, the apical protection is a periderm formed by a phellogen. Above all, attention is drawn to the fact that the root has a subapical meristem similar to all mono- and dicotyledonous roots, while the rhizophore does not present the same type of subapical region. It grows as an extension of the apex, in which vascular tissues are formed from the procambial strands.

I agree almost entirely with the statement of Pitot (1958, p. 1136) that: “This study of the anatomic transformation of the rhizophore leads us to conclude that the internal structure of the rhizophore known as the “stilt root” of *Rhizophora racemosa* does not correspond to its external mor-

phology, which is that of an aerial root with positive geotropism, and a root cap at the extremity. Due to its anatomical structure, the rhizophore is not a root in the exact sense”. The only point with which I disagree is his affirmation that there is a root cap at the extremity of the rhizophore in fact, a periderm. However, the absence of leaves and nodes, which are characteristics of roots, supports the idea of a rhizophore as an intermediate organ between root and stem (Goebel 1905).

An analogy with Carboniferous *Lepidodendrales* (Stewart 1983, Gifford and Foster 1988) clarifies the relationship between the rhizophore and the stem. An interesting point is the similarity of the *Lepidodendron* reconstruction with my Fig. 2,





Figs. 23–26 – Cross-sections of the roots of *Rhizophora mangle*. Fig. 23 – Adventitious root with a well-developed pith (Pi) and cortex (Ct) with a thickness of 3 times the diameter of the vascular cylinder. Fig. 24 – Region of the root in primary structure with exarc protoxylem (Px); white arrow indicates secondary xylem. Fig. 25 – Region of the root in secondary structure. Fig. 26 – Warty cells (W) with a special type of thickness, lignified; the arrows indicate regions rich in plasmodesmata, in the contact between two cells. En – endodermis; Mx – metaxylem; Ph – phloem; R – parenchymatous ray; Xy – secondary xylem. The bars correspond respectively to: 2 mm, 100 $\mu$ m, 150 $\mu$ m and 60 $\mu$ m.

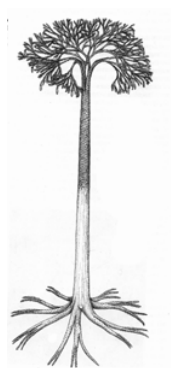
a sympodial branching with leaves and the basal system of rhizophores, also with sympodial branching. Despite the difficulties involved in studying fossilized plants, Stewart (1983) reconstituted these basal organs in *Lepidodendron*, demonstrating that they also have a cauline structure. Ac-

cording to Stewart (1983), Stigmarian systems are comprised of roots linked to a root-bearing axis, the rhizophores. These rhizophores are known as anchoring systems, and form the absorption system of *Lepidodendrales*.

I have already identified rhizophores in many

TABLE I  
Comparison of the anatomical characteristics of the rhizophore with those of the stem  
and root of *Rhizophora mangle*.

	Stem	Rhizophore	Root
Endarch Protoxylem	▲	▲	–
Exarch Protoxylem	–	–	▲
Cortex thickness 1/3 of vascular cylinder	▲	▲	–
Cortex thickness 3 x vascular cylinder	–	–	▲
Collateral bundles	▲	▲	–
Exogenous origin	▲	▲	–
Endogenous origin	–	–	▲
Vascular connection with the primary xylem of the shoot absent	▲	▲	–
Vascular connection with the primary xylem of the shoot present	–	–	▲
Method of monopodial branching	–	–	▲
Method of sympodial branching	▲	▲	–
Leaves	▲	–	–
Nodes	▲	–	–
H-Trichosclereids present	▲	▲	–
Warming cells present	–	–	▲
Root cap	–	–	▲



Reconstruction of *Lepidodendron* sp. (Stewart 1983)

other angiosperm families. When I first observed a second cauline system, with positive geotropism in the Asteraceae genus *Vernonia* (Menezes 1975, Menezes et al. 1979) I assumed it to be a mutation and, in an analogy with *Selaginella* (Selaginel-

laceae), I chose the term **rhizophore**. In choosing this label, I took into account the fact that angiosperms have roots, stem and leaves, like Pteridophyte, and so rhizophore seemed an appropriate choice. Later, while studying members of Dioscoreaceae (Rocha and Menezes 1997) and Smilacaceae (Andreata and Menezes 1999), a comparative analysis of these two families led the discovery that the tuberized structures are indeed rhizophores, as in *Vernonia*. Our work on Dioscoreaceae (Rocha and Menezes 1997) led us to a study by Goebel (1905), who lamented the fact that up until then, morphologists had failed to notice the existence of what he referred to as “an intermediate organ between root and stem in the Dioscoreaceae, analogous to *Selaginella*’s root-bearing organ”. It was only after studies on *Dioscorea* (Rocha and Menezes 1997) and *Smilax* (Andreata and Menezes 1999)



had been published, that we became aware of Ogura's study (1938), which contained the same considerations on Dioscoreaceae as ours, i.e., analogies with *Selaginella* and Lepidodendrales, and a reference to Goebel.

I consider the possibility of the rhizophore, by evolution, gives rise to the rhizome, rather than the latter originating from an aerial stem, as is currently assumed. Although the rhizophores in *Rhizophora* are above the surface, as in Lepidodendrales, in other angiosperms this organ is normally found under the ground. Tomlinson (1962, p. 211), in his studies on the phylogeny of Scitamineae, makes an interesting statement. Referring to the species *Phenakospermum*, he writes: "It is one of the dogmas of elementary botany that the rhizome is morphologically equivalent to a stem modified as a horizontal, storage and propagating organ. Can this long-accepted idea be challenged? The rhizome, or its equivalent, already exists in primitive monocotyledons. This might suggest that it is an organ *sui generis* and not homologous with the aerial stem. One is tempted to compare the rhizome in the Scitamineae with Stigmarian axis of *Lepidodendron* and the rhizophores of *Selaginella* similar organs, the morphology of which is unexplained".

I propose here that *Rhizophora mangle* has a rhizophore system. Juncosa and Tomlinson (1988b) state that the genus name *Rhizophora* means "root-bearer". However, I believe that *Rhizophora* should mean "one that has rhizophores" and that rhizophore is a "root bearing" branch.

At first, I did not believe that Pisone's rhizophore (according to Plumier 1703) bore any relation to the rhizophore I was describing. However, it is the very first rhizophore of *Rhizophora mangle*, hence it is referred to in this paper as the primary rhizophore (Rh1), i.e., with well-developed hypocotyl, unlike the secondary rhizophores (Rh2), which appear later in *R. mangle* from adventitious buds.

According to Chapman (1976), no primary root appears to develop in *Rhizophora mangle*. In a study which is not yet published, I intend to demonstrate that this is, in fact, true.

#### ACKNOWLEDGMENTS

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#### RESUMO

*Rhizophora mangle* L., uma das mais comuns espécies do mangue, tem um sistema de estruturas aéreas que lhe fornecem estabilidade em solo permanentemente alagado. De fato, essas estruturas, conhecidas por "raízes aéreas" ou "raízes suportes" demonstraram tratar-se de ramos especiais com geotropismo positivo, que formam grande número de raízes quando em contato com o solo. Esses órgãos apresentam um sistema de ramificação simpodial, medula ampla, córtex pouco espesso, feixes vasculares colaterais, estelo poliarco e protoxilema endarco, como no caule, e uma periderme produzida por um felogênio no ápice, semelhante a uma coifa. Esses ramos apresentam, também, o mesmo tipo de tricoesclereídes que ocorrem no caule com geotropismo negativo, diferente das verdadeiras raízes de *Rhizophora*, que não formam tricoesclereídes. Por outro lado, esses ramos não formam folhas e nesse aspecto são semelhantes às raízes. Esses ramos especiais são rizóforos, isto é, ramos portadores

de raízes, com geotropismo negativo e análogos àqueles encontrados em Lepidodendrales e outras pteridófitas arbóreas do Carbonífero que, usualmente, cresciam em solos alagados.

**Palavras-chave:** *Rhizophora mangle* L, rizóforo, “raízes aéreas”, “raízes suporte”.

#### REFERENCES

- ANDREATA RHP AND MENEZES NL DE. 1999. Morfoanatomia do embrião, desenvolvimento pós-seminal e origem do rizóforo de *Smilax quinquenervia* Vell. (Smilacaceae). Bol Bot Univ São Paulo 18: 33–37.
- BEHNKE HD AND RICHTER K. 1990. Primary phloem development in the shoot apex of *Rhizophora mangle* L. (Rhizophoraceae). Bot Acta 103: 296–304.
- CHAPMAN V J. 1976. *Mangrove vegetation*. Vaduz: J. Cramer.
- ELLMORE GS, LEE SC AND NICKERSON NH. 1983. Plasticity expressed by root ground tissues of *Rhizophora mangle* L. (Red Mangrove). Rhodora 85: 397–403.
- GIFFORD EM AND FOSTER AS. 1988. Morphology and evolution of vascular plants. W.H. Freeman Co., New York, 3<sup>rd</sup> ed.
- GILL AM AND TOMLINSON PB. 1969. Studies of the growth of Red Mangrove (*Rhizophora mangle* L.) 1. Habit and general morphology. Biotropica 1: 1–9.
- GILL AM AND TOMLINSON PB. 1971a. Studies of the growth of Red Mangrove (*Rhizophora mangle* L.) 2. Growth and differentiation of aerial roots. Biotropica 3: 63–77.
- GILL AM AND TOMLINSON PB. 1971b. Studies of the growth of Red Mangrove (*Rhizophora mangle* L.) 3. Phenology of the shoot. Biotropica 3: 109–124.
- GILL AM AND TOMLINSON PB. 1977. Studies of the growth of Red Mangrove (*Rhizophora mangle* L.) 4. The adult root system. Biotropica 9: 145–155.
- GOEBEL K. 1905. Morphologische und biologische Bemerkungen. 16. Die Knollen der Dioscoreen und die Wurzelträger der Selaginellen, Organe, welche zwischen Wurzeln und Sprossen stehen. Flora 95: 167–212.
- HAAS DL, CAROTHERS ZB AND ROBBINS RR. 1976. Observations on phi-thickenings and casparian strips in *Pelargonium* roots. Am J Bot 63: 863–867.
- HALLÉ F, OLDEMAN RAA AND TOMLINSON PB. 1978. Tropical trees and forests – An Architectural Analysis. Springer-Verlag, Berlin.
- HOU D. 1958. Rhizophoraceae. Flora Malesiana ser 1. 5: 429–493.
- HUANG G AND HUANG Q. 1990. Studies on the structure of plant organs and ecological adaptation of Mangrove in China (II). Acta Sci Nat Univ Sunyatseni.
- JERNSTEDT JA AND MANSFIELD MA. 1985. Two dimensional gel electrophoresis of polypeptides from stems, roots, leaves and rhizophores of *Selaginella kraussiana*. Bot Gaz 146: 460–465.
- JERNSTEDT JA, CUTTER EG AND LU P. 1994. Independence of organogenesis and cell pattern in developing angle shoots of *Selaginella martensi*. Ann Bot 74: 343–355.
- JUNCOSA AM AND TOMLINSON PB. 1988a. A historical and taxonomic synopsis of Rhizophoraceae and Anisophylleaceae. Ann Missouri Bot Gard 75: 1278–1295.
- JUNCOSA AM AND TOMLINSON PB. 1988b. Systematic comparison and some biological characteristics of Rhizophoraceae and Anisophylleaceae. Ann Missouri Bot Gard 75: 1296–1318.
- KARSTEN G. 1891. Über die Mangrove-vegetation in Malayischen Archipel Bibl Bot 22: 1–71.
- MAUSETH JD. 1988. Plant Anatomy. The Benjamin/Cummings Publishing Company, Inc. California.
- MENEZES NL DE. 1975. Presença de rizóforo em espécies de *Vernonia* da Serra do Cipó. XXVI Congresso Nacional de Botânica, Rio de Janeiro, RJ. Temas Livres – Resumos, p. 31.
- MENEZES NL DE, MULLER C AND SAJO MG. 1979. Um novo e peculiar tipo de sistema subterrâneo em espécies de *Vernonia* da Serra do Cipó (Minas Gerais) Brasil. Bol Bot Univ São Paulo 7: 33–38.
- OGURA Y. 1938. Problems in morphology (13) Botany and Zoology 6: 139–148.
- PITOT A. 1951. Les “Racines-échasses” de *Rhizophora racemosa* G.F.W. Meyer. Bull Inst Fr Afr Noire 13: 978–1010.

- PITOT A. 1958. Rhizophores et racines chez *Rhizophora* sp. Bull Inst Fr Afr Noire 20: 1103–1138.
- PLUMIER C. 1703. Nova Plantarum americanarum Genera. Paris II.
- RAVEN PH, EVERT RF AND EICHHORN SE. 1992. Biology of Plants. Worth Publishers, Inc. New York.
- ROCHA DC AND MENEZES NL DE. 1997. O sistema subterrâneo em *Dioscorea kunthiana* Uline and R. Knuth (Dioscoreaceae). Bol Bot Univ São Paulo 16: 1–11.
- ROESER KR. 1962. Die Nadel der Schwarzkiefer – Massenprodukt und Kunstwert der Natur. Mikrokosmos 61: 33–36.
- SPORNE KR. 1974. The Morphology of Angiosperms. Hutchinson and Co. (Publishers) Ltd., London, England.
- STEWART WN. 1983. Paleobotany and the evolution of plants. Cambridge University Press, London, England.
- TOMLINSON PB. 1962. Phylogeny of the Scitamineae – Morphological and Anatomical Considerations. Evolution 16: 192–213.
- TOMLINSON PB. 1986. The botany of Mangroves. Cambridge University Press, Cambridge.
- WARMING E. 1883. Tropische Fragment II. *Rhizophora mangle* L. Bot Jahrb 4: 519–548.