

RHIZOPHORE IN ANGIOSPERMS

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ABSTRACT

RHIZOPHORE IN ANGIOSPERMS

Roots, stems and leaves are present in all vascular plants: pteridophytes, gymnosperms and angiosperms. Rhizophore are shoots that grow downwards with roots in the apex and that are recognised in living *Selaginella* and Carboniferous Lepidodendrales. Recently, rhizophores were also observed in angiosperms. This organ is a stem with positive geotropism and is the sole organ that gives rise to roots in the plant. It can be composed of nodes, internodes and cataphylls protecting lateral buds (*Vernonia psilophylla* D.C., *V. herbacea* (Vell.) Rusby, *Cordyline fruticosa* (L.) Chevalier and *Smilax quinquenervia* Vell.) or it can lack nodes and with only adventitious buds (*Rhizophora mangle* L., *Dioscorea anomala* (Kunth) Gris e *D. filiformis* Griseb L.). The rhizophores grow by apex expansion, without terminal buds. In *R. mangle*, there is a periderm similar to a root cap in the apex. In all species mentioned above, the rhizophore has exogenous origin, and branching sympodially.

Index terms: Rhizophore, *Rhizophora mangle*, *Selaginella*, *Dioscorea*, *Cordyline*, *Vernonia*, *Smilax*.

RESUMO

RIZÓFOROS EM ANGIOSPERMAS

Raiz, caule e folha estão presentes em todas as plantas vasculares: pteridófitas, gimnospermas e angiospermas. Rizóforos são caules que crescem com geotropismo positivo portando raízes na extremidade, e que são reconhecidos nas *Selaginella* atuais e em Lepidodendrales do Carbonífero. Recentemente, rizóforos foram observados também em angiospermas. Esse órgão é um caule com geotropismo positivo e é o único órgão que forma raízes na planta. Pode ser composto de nós, inter-nós e com catafilos protegendo gemas laterais (*Vernonia psilophylla* D.C. e *V. herbacea* (Vell.) Rusby, *Cordyline fruticosa* (L.) Chevalier e *Smilax quinquenervia* Vell. ou então pode não possuir nós e formar apenas gemas adventícias (*Rhizophora mangle* L., *Dioscorea anomala* (Kunth) Gris. e *D. filiformis* Griseb.). Os rizóforos crescem por expansão apical, sem gema terminal. Em *R. mangle*, há uma periderme no ápice, semelhante a uma coifa

de raiz. Em todas as espécies mencionadas acima, o rizóforo tem origem exógena e ramificação simpodial.

Termos para indexação: Rizóforo, *Rhizophora mangle*, *Selaginella*, *Dioscorea*, *Cordyline*, *Vernonia*, *Smilax*.

1. INTRODUCTION

Vascular plants (Pteridophyta and Spermatophyta) present roots, stems and leaves (Bold, 1972; Raven *et al.*, 1999), but there is a structure which is the organ responsible for forming the roots present in Lepidodendrales (arboreal pteridophytes of Carbonifers), and in the present *Selaginella*, which few authors recognize as present in the Spermatophytes. Among those that do so recognize, one can cite Goebel (1905), Ogura (1938), Smith (1955), Pitot (1958), Menezes (1975), Menezes *et al.* (1979), Sajo & Menezes (1986a), Rocha & Menezes (1997), Adreata & Menezes (1999), Machado *et al.* (2004), Martins & Apezato-da-Glória (2006) and Menezes (2006).

When analyzing the so-called “chi-chi” in *Ginkgo biloba*, Barlow & Kurczyńska (2007), also admitted considering them as rhizofores.

For Pitot (1958) in *Rhizophora racemosa*, and for Menezes (2006) in *Rhizophora mangle*, rhizophores are positive geotropic stems, without leaves, and which form roots when reaching the soil.

According to Ogura (1972), in *Selaginella* “it is the basal part of such a root system that is in question. This part is thin and whitish as in other parts, but it is provided with neither root hairs nor rootcap as has been pointed out by Nägelli & Leitgeb (1868 *apud* Ogura 1972) who called it a rhizophore. It elongates until it reaches the substratum, when two points appear endogenously at its tip and elongate in two equal roots provided with root hairs and rootcap” (Ogura 1972, p. 200).

Further, and according to Ogura (1972), “the rhizophore in *Selaginella* and the root, are similar in form and structure, but the rhizophore possesses multicellular hairs but no root cap” (Ogura 1972, p. 134). The author also states that “the root-like organ of *Selaginella*, which comes of a dichotomously branched part of the stem, is called a rhizophore, and on its tip a pair of true roots is produced”.

Both Goebel (1905) and Ogura (1938) called attention to what would be homology between these organs, in *Selaginella* and in species of Dioscoreaceae, for which Ogura (1938) used the nomenclature rhizophore, in particular when referring

to the thickened organ of *Dioscorea batatas*, *D. altissima* and *Tamus communis*. Goebel (1905) not only related the thickened organs of *Dioscorea* species with the root formers of *Selaginella*, but also mentioned that other angiosperms could present the same type of structure, amongst these *Cordyline*, *Dracaena* and *Yucca*.

Well before perceiving that the so-called aerial roots of *R. mangle* were really stems, Menezes (1975), Menezes *et al.* (1979) and Sajo & Menezes (1986a and b), described the underground system of species of *Vernonia* as being a positive geotropic stem system, denominated rhizophore by Menezes (1975). Later, in *Dioscorea kunthiana* (Rocha & Menezes 1997), in *Smilax quinquenervia* (Andreato & Menezes, 1999), in *Smilax polyantha* (Martins & Appezzato-da-Gloria 2006) the authors noted the presence of rhizophores in these species, demonstrating in the case of *S. quinquenervia* (Andreato & Menezes 1999), its origin in the cotyledonary node, as was also demonstrated by Sajo and Menezes (1986a) in *Vernonia psilophylla*.

For Goebel (1905) the tubercularized structures of Dioscoreaceae could be the result of the transformation of other organs (stem or root) or could be new formations, “sui generis” organs which exhibit in part stem characteristics and in part those of roots.

In a recent article (Menezes, 2006), the author also establishes a relationship among the characteristics presented by *R. mangle* with those presented by Lapidodendrales that lived in the Carboniferous, and which, according to Stewart (1983 pg. 103), “these plants had a main axis that grew and branched at both ends. The branches of the aerial part formed a three-dimensional system of dichotomous or pseudomonopodial branches with spirally arranged leaves and terminal cones. The basal end also branched dichotomously to form the anchoring and water-absorbing system comprised of rhizophores bearing spirally arranged roots”.

In *R. mangle*, the basal branches were always described as being aerial roots, but, as demonstrated by Menezes (2006), the authors called attention to the fact of dealing with a root with various accomplishments through being of exogenous origin, possessing endarch protoxylem and primary vascular tissues organized in bundles, and presenting sympodial braching, besides other stem characteristics, but with a pronounced root characteristic, which is the presence of rootcap (Gill & Tomlinson, 1971a and b; Chapman, 1976; Ellmore *et al.*, 1983).

In the same work Menezes (2006) demonstrates that the tissue protecting the apex of these basal branches, which she calls rhizophores, is a cork produced by phellogen. Thus one is dealing with a peridermis.

Pitot (1958), when working with *R. racemosa*, uses the term rhizophore for the structure that he himself denominates “supporting root” (“raiz échasse”) between apostrophes, demonstrating that an internal cauline structure (not corresponding to its external morphology of aerial root) with positive geotropism, on touching water is transformed into an internal radical structure by modification of the apical meristem.

Through the present paper, it is intention to present evidence of the existence of rhizophores in angiosperms, based on already published or unpublished works.

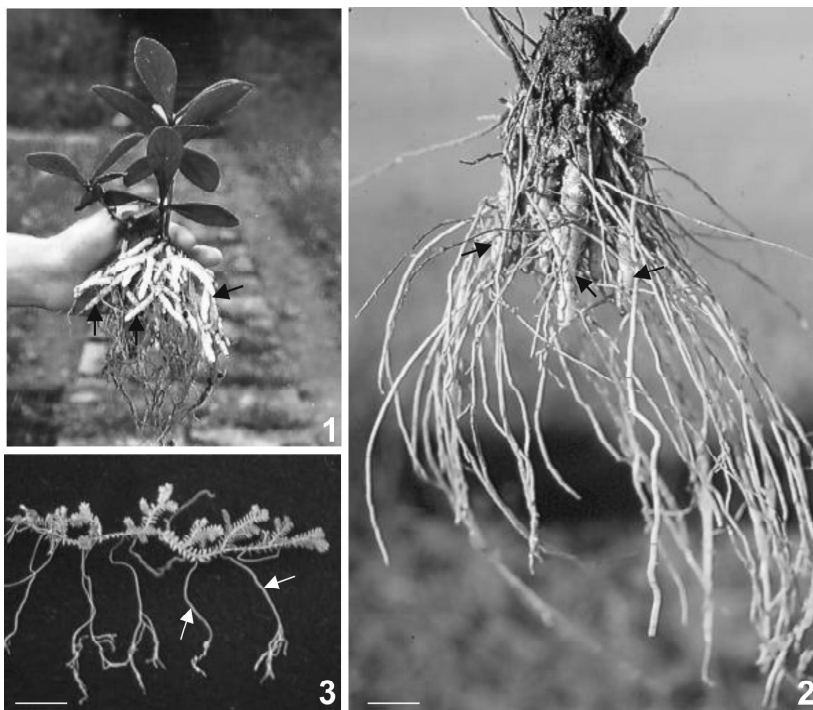
2. MATERIAL AND METHODS

The material presented in this work mainly corresponds to papers already published by the author and collaborators (Figure 4–11). The remaining figures are unpublished: *Vernonia herbacea* (Vell.) Rusby (photographed in the Botanical Institute of SMA, São Paulo, Brazil), *V. psilophylla* D.C. (photographed in the Serra do Cipó – MG), *Selaginella* sp and *Cordyline fruticosa* (L.) Chevalier, collected and photographed in the gardens of the Instituto de Biociências (Universidade de São Paulo, Brazil), and those of *R. mangle* L., on Muro Alto beach (Porto de Galinhas – PE).

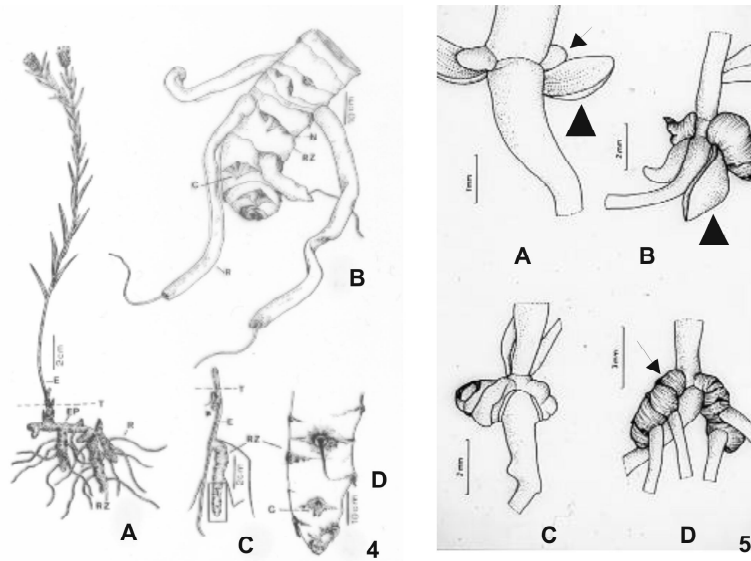
3. RESULTS

The rhizophores of *V. herbacea* are structures that grow with positive geotropism (Figure 1) in the same way as in *V. psilophylla* (Figure 2) and in *Selaginella* sp (Figure 3). It can be observed that the positive geotropism of these rhizophores, besides of nodes, internodes and cataphylls (Figure 4 A–D), is also the origin in the cotyledonary node (Figure 5 A–D). The same origin in the cotyledonal knot, can be seen in *S. quinquenervia* (Figure 6), and in an adult plant the number of adventitial roots which leave the rhizophore, are also visible (Figure 7 A–B), besides the aerial cauline axis. In *Dioscorea anomala* (Figure 8), one can note that the rhizophore is the hypocotyl itself, which thickens and forms lateral expansions (Figure 9) In *Dioscorea filiformis*, a thin cauline branch grows from the seed, with positive geotropism (Figure 10 and 11), reaching different depths and forming thickened structures in the nodes, which turn out to be adventitial root formers. When the underground cauline branch stops

growing, it forms a more succulent structure with adventitious roots on the extremity (Figure 10). Arrow "a" in Figure 10 and the arrow in Figure 11, indicate the position in which the seed originally was. *C. fruticosa* presents rhizophore development arising from the cotyledonary bud (Figure 12). In *R. mangle*, those rhizophores presenting sympodial branching can be observed (Figure 13 and 14), besides new branches first present negative geotropic growth, before curving towards the soil (Figure 15). A structure similar to an aerial rootcap can be seen on the extremities of the new rhizophores (Figure 16).



Figures 1, 2 and 3. — **1.** *Vernonia herbacea* (Photo from Maria Ângela de Carvalho). **2.** *Vernonia psilophylla*. **3.** *Selaginella* sp. The arrows indicate rhizophores, with positive geotropism, from which adventitious roots arise. Bars in Fig. 2 and 3 correspond to 2 cm.



Figures 4 and 5. — 4. Rhizophores (RZ) of *Vernonia psilophylla* (Menezes et al., 1979). 5. *V. psilophylla*, showing the origin of rhizophores (arrows) from cotyledon sprouts. Arrow heads indicate the cotyledon leaf. (Sajo & Menezes 1986a).

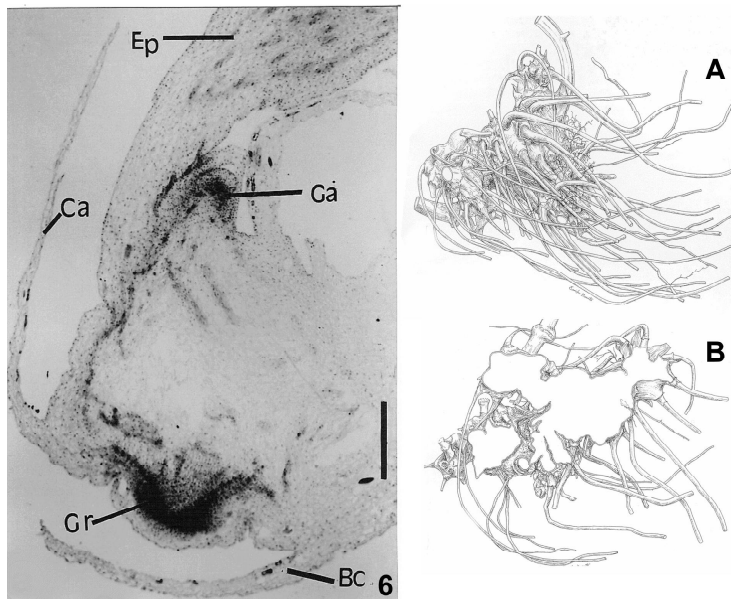
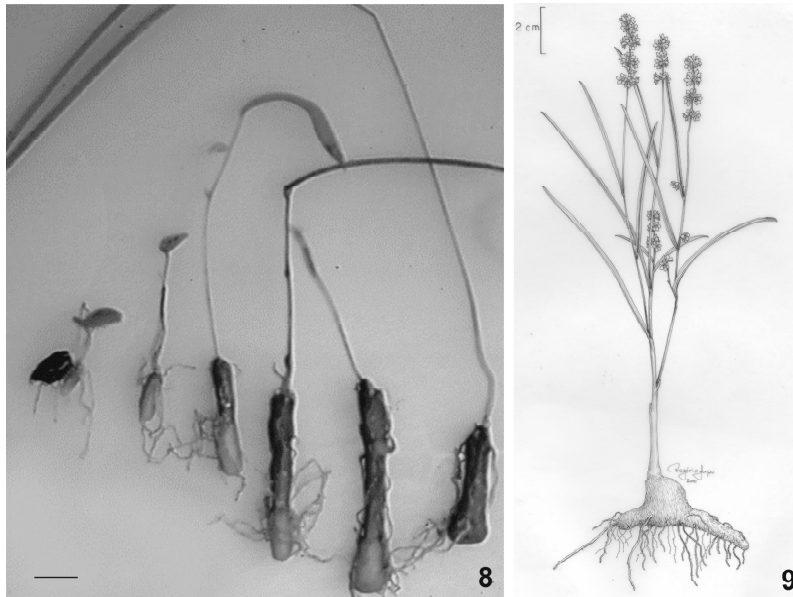
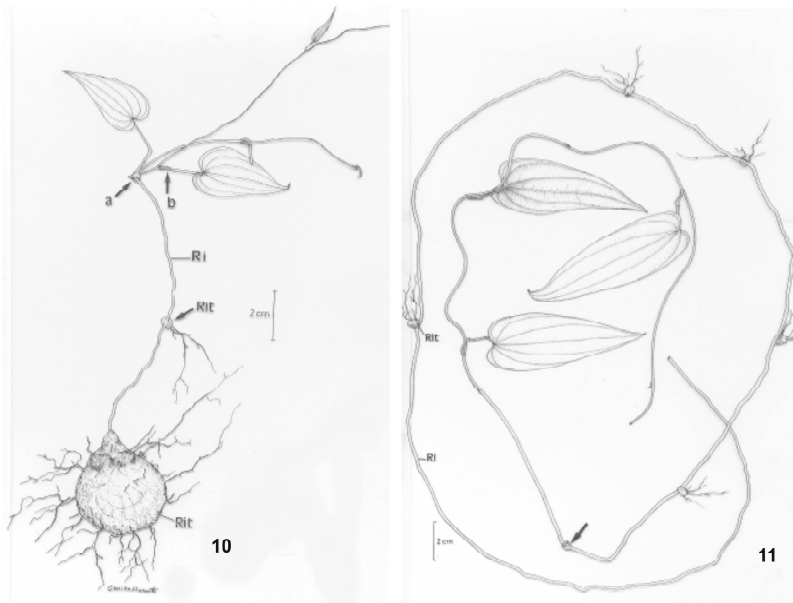


Figure 6 and 7. — 6. *Smilax quinquevria*, showing the origin of the rhizophore bud (Gr), protected by the cotyledonary leaf sheath (Bc). (Andreatta & Menezes 1999). The bar on the left corresponds to 800 μ m. 7. *Smilax quinquevria* Rhizophores (Ri) – from an adult plant, outer-view (A) and in longitudinal section (B) with inumerous adventitious roots (R) (Andreatta & Menezes 1999). Cv – rising aerial stem.



Figures 8 and 9. — *Dioscorea anomala*. Rhizophore of hypocotyl origin. **8.** Development of the hypocotyl from a seed (arrow). **9.** Hypocotyl with side expansion (Cardoso, 2001). The bar in Fig. 8 corresponds to 0.8 mm.



Figures 10 and 11. — *Dioscorea kunthiana*. Arrow “a” of Figure 10 and the arrow of Figure 11 indicate the position where the seed is to be found (Rocha & Menezes 1997). Ri – non-thickened rhizophore; Rit – tuberculized rhizophore, with adventitial roots.



Figure 12. — *Cordyline fruticosa*. Origin of the rhizophore with positive geotropism from the cotyledonary node (arrow). The bar corresponds to 2 cm.



Figures 13 and 14. — *Rhizophora mangle*. Rhizophores with sympodial branching. In Figure 14, the white arrow indicates a rhizophore branch curving towards the ground. The black arrow indicates self-buried propagulum.



Figure 15 and 16. — *Rhizophora mangle*. 15. Three new rhizophores growing with negative geotropism. 16. the apical peridermis, similar to a rootcap, is noted.

4. DISCUSSION

The first time that the author removed a specimen of *V. psilophylla* from the soil and perceived the presence of cauline branches with positive geotropism (besides the aerial roots with negative geotropism), and the profusion of adventitial roots formed by these branches, she associated them with what she had seen in *Selaginella* and decided to name them rhizophore, as in the pteridophytes.

A report (Menezes, 1975) was presented in a congress of the same year, stating the presence of rhizophores in species of *Vernonia* from Serra do Cipó (MG), to be later published in the paper Menezes *et al.* (1979). At the time, the author was unacquainted with the works of Goebel (1905) and Ogura (1938), these only being detected on undertaking studies with Dioscoreaceae (Rocha & Menezes, 1997). Both authors related the thickened organ of Dioscoreaceae with the root-bearing organ of *Selaginella*, which Ogura (1938) calls rizophore, based on the proposal of Nägelli and Leitgeb (1867 apud Ogura 1938). When the author became acquainted with the works of Goebel (1905) and Ogura (1938), she considered it an incredible coincidence her having chosen the same name (rhizophore), as had Ogura, an idea which, furthermore, appeared to her very propitious on obtaining this authors work, which,

although entirely written in Japanese, besides a beautiful figure of *Lepidodendron* of the Carboniferous, presented all the figures of species of *Selaginella* and *Dioscorea*, together with latin names. The idea was the same! Above all, Ogura (1938) also cited Goebel (1905).

According to Goebel (1905), who undertook an exclusively morphological study of the development of tuberculated organs of Dioscoreaceae, these root-bearing organs would be “sui generis” organs, for they were neither stems nor roots, but possessed the characteristics of both. Furthermore, this author stated that this organ appears in the plântula of *Dioscorea*, in the region of the cotyledonary node, and that this could be an aerial stem which has completely lost the ability to form leaves.

Furthermore, and also according to Goebel (1905), “these organs are so similar to roots that eminent researchers have considered them, unbelievably, as roots”. For this author, these “sui generis” organs are primarily root-bearing which make it possible to form a much richer root system than that which would be available for the plant”. Goebel (1905) also noted that these organs without leaves in *Dioscorea* could sprout aerial branches on removing the aerial stem with leaves or when the growth of this is hindered.

Another interesting aspect, as has already been stated, is that Goebel (1905) says that he believes that other angiosperms should present this type of organ, citing as an example the genera *Cordyline*, *Yucca* and *Dracaena*. In this work not only is it confirmed that *Cordyline* forms rhizophores, as also that this originates from the cotyledonary node, as seen in *Smilax* (Andreato & Menezes, 1999; Martins & Appezzato-da-Gloria, 2000). In the above mentioned genera, Goebel (1905), found these organs to be root-bearing, an also firmer soil-anchorage than would be possible, above all, seeing that these plants, even with arboreal habits, have no firm rooting at the base of the trunk, as occurs in *Arecaceae* and *Pandanus*. This is exactly what one can say regarding *R. mangle*.

Regarding this same structure herein, denominated rhizofore, in *Cordyline terminalis*, Fisher (1972) and Fisher & Tomlinson (1972) named this “vertical rhizome”, without knowing of (or without referring to) the work of Goebel (1905). This same observation was presented by Sajo & Menezes (1986a), which demonstrates that the first rhizophores originated from cotyledonary node in species of *Vernonia*.

Whereas in *Vernonia* (Menezes, 1975; Menezes *et al.*, 1979; Sajo & Menezes, 1986a and b), *Smilax* (Andreato & Menezes, 1999; Martins & Appezzato-da-Gloria, 2006), *Cordyline* (Goebel, 1905) and *Dioscorea kunthiana* (Rocha & Menezes, 1999),

the rhizophore originates in the cotyledonary node, in *Dioscorea debilis* and *D. anomala* the rhizophore is the hypocotyl itself, which thickens and presents sympodial branches formed from adventitial sprouts (Cardoso, 2001). After this discovery, Menezes (2006) decided to denominate “primary rhizophore” that which represents the hypocotyl itself, which in *R. mangle* would be the propagulum which buries itself in the swampy soil of the mangrove. On the other side, as to rhizophores arising from cotyledonal sprouts, as already seen, or adventitial sprouts from the erect caulinar axis, as in *R. mangle*, this same author decided to call these “secondary rhizophores”.

In all plants that present rhizophores, all water and nutrients only penetrate through adventitial roots formed in these rhizophores

In Dioscoreaceae, the hypocotyledonal rhizophores or those formed at the extremities of special underground branches are normally eatable, going under the vernacular denomination of “inhame” (Correa, 1984).

With the work on *R. mangle*, Menezes (2006) intended to demonstrate that, what all authors call “supporting root” in *R. mangle* (ever since its description by G. Plumier 1703), is really, anatomically, a stem with positive geotropism characteristics, similar to those of the rhizophores of a *Lepidodendron*, an arboreal pteridophyte, which lived in swampy soils in the Carboniferous period. Furthermore, according to Stewart (1983), “*Lepidodendron* had bipolar growth, that is, the main axis that grew and branched at both ends”.

With the overlapping of an aerial branch, with leaves, and the rhizophores at the base of *R. mangle*, Menezes (2006) intended to demonstrate the same type of sympodial branching, which only the stem presents, at both ends of the plant.

Appraisal of the apex of a rhizophore in long section, according to Menezes (2006), permits perceiving two different, important aspects of the root: the occurrence of procambium strands which will give origin to vascular bundles, and that the protective structure of the rhizophore apex, is really a peridermis of phellogen origin and not a rootcap originating from the calyptragen, as stated by Gill & Tomlinson (1971a and b and 1977).

In an anatomical study on the so-called “chi-chi” in *G. biloba*, Barlow & Kurczyńska (2007), came to the conclusion that the type of apical growth (through the activity of a cambium which extends from side to apical) and the absence of a rootcap, suggests that these structures would not be roots but rhizophores. Even though the authors refer to the work of Menezes (2006) as if the author had called “shoot-born roots of mangrove”, rhizophore, in reality the author (Menezes, 2006)

demonstrated this organ in rhizophore to be a caulinar structure, with exactly the same type of apical growth (meristematic tissues extending from lateral to apical without stopping), but not through a cambium as in “chi-chi”, but through procambium strands. This same organ in *G. biloba* has been called “stalactite-like” branches by Li & Lin (1991).

In *Curcuma zedoaria* (Zingiberaceae), even though not having been represented, the same type of caulinar system with positive geotropism was observed. As regards another genus of the same family, Holtum (1955) made a curious statement: “I saw at Kew a very remarkable dwarf species of *Costus* (Zingiberaceae) from Rhodesia, *C. spectabilis*. The rhizomes, instead of growing horizontally, grow vertically downwards. This habit reminds me very much of downward-growing tubers of some species of *Dioscorea*. The *Dioscorea* tubers are not morphologically exactly equivalent to the downward-growing rhizome of *Costus spectabilis*, but perhaps, the *Costus* gives an indication of the way tuber-evolution in *Dioscorea* may have started”.

In a work on the phylogeny of Scitamineae, Tomlinson (1962 p. 211) literally said, when referring to the genus *Phenakospermum*: “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 the 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 *Lepidodendrons* and the rhizophores of *Selaginella*, similar organs, the morphology of which is unexplained”.

The question which appears is the following: if the angiosperms possess, as do the pteridophytes, root, stem and leaves, why can they not present rhizophores?

It is important to remember here that the rhizophore of a Dioscoreaceae cannot be confounded with a tubercule, such as that which is formed in *Solanum tuberosum*. The tubercule only forms a root when detached from the mother plant. In the rhizophore, as already seen, all water and nutrients enter the plant through those adventitial roots that only the rhizophore forms.

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