

The architecture of *Phyllanthus acuminatus* Vahl: a prelude to understanding the architectural evolution in the Phyllanthaceae

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ABSTRACT

An architectural study was carried out on *Phyllanthus acuminatus* Vahl with the objective to improve our knowledge of the evolution of tree architecture in the genus *Phyllanthus*. The sampled specimens show Roux's model, which is characterized by continuous growth, sylleptic branching, monopodial development and plagiotropic, sometimes phyllomorphic branches. We describe three types of axes (A1, A2 and A3) and the reiteration process. The A1 axes are orthotropic, while the A2 and A3 axes are plagiotropic and limited in their development. Although data are too incomplete to obtain a complete overview of evolution of architecture within the genus, we confirm the hypothesis of basic orthotropic models in *Phyllanthus* s.l. At family level the two clades are congruent with two groups of models, one with continuous growth and the other with rhythmic growth. Also within the group of rhythmic growth, orthotropic models are basic.

KEY WORDS

Tree architecture,
evolution,
Cook model,
Roux model,
Phyllanthaceae,
Phyllanthus acuminatus.

RÉSUMÉ

L'architecture de Phyllanthus acuminatus Vahl: prélude à la connaissance de l'évolution architecturale des Phyllanthaceae.

Une analyse architecturale de *Phyllanthus acuminatus* Vahl a été conduite, afin d'améliorer notre connaissance de l'évolution architecturale dans le genre *Phyllanthus*. Les spécimens étudiés correspondent au modèle de Roux, caractérisé par sa croissance continue, son développement monopodial, sa ramification immédiate et ses branches plagiotropes, parfois phyllomorphiques. Trois types d'axes (A1, A2, A3) ont été décrits, ainsi que le processus de réitération. A1 est orthotrope, alors que A2 et A3 sont plagiotropes et à développement limité. Bien que les informations ne soient pas suffisantes pour acquérir une vue complète de l'évolution architecturale dans le genre, nous confirmons l'hypothèse selon laquelle les architectures orthotropes sont basales dans *Phyllanthus* s.l. Au niveau de la famille, les deux clades sont congruents avec deux groupes de modèles architecturaux, l'un à croissance continue, l'autre à croissance rythmique. Au sein du groupe à croissance rythmique, les architectures orthotropes sont à nouveau basales.

MOTS CLÉS

Architecture des arbres,
évolution,
modèle de Cook,
modèle de Roux,
Phyllanthaceae,
Phyllanthus acuminatus.

INTRODUCTION

Recent publications on phylogenies based on molecular data open the possibility to investigate the evolution of architecture in plants (Kurmman & Hemsley 1999). By comparing phylogenetic trees with information on the architecture of the species within the trees, one can get an idea of how the architecture evolved within a family or genus. In this way one can investigate, for example, the hypothesis that the architectural model is a character fixed in an early state of evolution and changes from one model to another are rare (Hallé & Oldeman 1970; Hallé *et al.* 1978; Vester 2002; Hallé 2004) or the hypothesis that models with orthotropic axes are primitive with respect to models with differentiated axes (Rossignol & Rossignol 1985).

Although there are studies that discuss the evolution in plant architecture (Sanoja 1992; Robson 1993; Vester 1999) the comparison of architectural information with independently obtained phylogenies is rare (Bateman 1999; Johnson 2003) mostly because of the lack both of architectural analyses and of phylogenies of families with architectural information. This gap of architectural analysis is due to the time involved in making observations

on different individuals in the field. In this paper we want to contribute the analysis of *Phyllanthus acuminatus* Vahl in the family Phyllanthaceae and put this analysis in the context of what is known about the architecture of the family and discuss the evolution of architecture in the family.

The family Phyllanthaceae was earlier treated as subfamily Phyllanthoideae in the Euphorbiaceae s.l. (Webster 1994b). Phenotypic and biochemical studies suggested that the genera of Euphorbiaceae s.l. do not form a monophyletic group. Arguments for separating the family were: 1) two subfamilies (Phyllanthoideae and Oldfieldioideae) presented a trilocular ovary with two anatropous ovules in each locule, while the other three subfamilies (Acalyphoideae, Crotonoideae and Euphorbioideae) present one ovule per locule (Webster 1994a); 2) serological research with the protein Legumin separates Phyllanthoideae from Acalyphoideae and Crotonoideae (Jensen *et al.* 1994); and 3) Phyllanthoideae and Oldfieldioideae have mostly architectural models with indeterminate growth, monopodial axes, and axillary inflorescences such as the models of Attimis and Rauh, while in Acalyphoideae, Crotonoideae and Euphorbioideae, the predominant architectural models have determinate axes and sympodial growth as in



FIG. 1. — Axes A1, A2 and A3 of *Phyllanthus acuminatus* Vahl. The combination of A2 and A3 is clearly similar to a compound leaf (phyllomorphic branch).

the models of Koriba and Leeuwenberg. Moreover in Euphorbioideae one finds the models of Prévost and Nozeran, rarely found in other subfamilies (Webster

1994a). Finally, comparison of *rbcL* shows that Euphorbiaceae *s.l.* is a polyphyletic group (Wurdack & Chase 1996; Wurdack *et al.* 2004) which today is

TABLE 1. — Architectural characterization of the A1, A2 and A3 axes of *Phyllanthus acuminatus* Vahl.

Characteristic	A1	A2	A3
Structure	monopodial	monopodial	monopodial
Growth	continuous	continuous	continuous
Orientation	orthotropic	plagiotropic	plagiotropic
Symmetry	radial	bilateral	bilateral
Chronology	NA	sytleptic	sytleptic
Angle of insertion	NA	nearly 90°	nearly 90°
Type of dermal layer	periderm	epidermis	epidermis
Flowers	no	no	yes, axillary
Phyllotaxis	Fibonacci 2/6	distichous	distichous

separated into the biovulate families Picrodendraceae and Phyllantaceae, and a clade that corresponds to the uniovulate family Euphorbiaceae s.s. (Acalyphoideae + Crotonoideae + Euphorbioideae).

The Phyllanthaceae is a pantropical family with about 2000 species in 59 genera and a wide variety of habits (large trees, xeromorphic shrubs, small herbs and aquatic plants) and of morphology of flowers and fruits (Kathariachchi *et al.* 2005). Based on congruent cladograms of chloroplastic *atpB*, *matK*, *ndhF*, *rbcL* and nucleotic PHYC, Kathariachchi *et al.* (2005) demonstrate two principal clades in the family: F, plants with fasciculate inflorescences and lacking tanniniferous epidermal cells; and T, plants with tanniniferous epidermal cells and elongate inflorescences. Clade F is divided in four subclades (F1, F2, F3 and F4). In this treatment, *Phyllanthus* is grouped in clade F1a with *Breynia cernua*, *B. stipitata*, *Sauropus androgynus*, *S. thorelii*, *Glochidion puberum*, *G. eucleoides* and *Reverchonnia*. But within this clade it seems to be paraphyletic.

Phyllanthus is pantropical and comprises about 700 species, with some important insular endemics (Rossignol & Rossignol 1985) and a large variety of architectural models (Webster 1994a) which makes the genus interesting for architectural study. Hallé (1971) notes that *P. discoideus* (Baill.) Müll.Arg. and *P. mimosoides* Sw. are characterized by their differentiation in plagiotropic secondary axes. Rossignol & Rossignol (1985) propose an evolutionary model for the architecture within the genus based on the degree of orthotropy and plagiotropy of their axes: 1) “generalized orthotropic”, all orthotropic axes and axillary flowers, considered as the most basal

in the phylogeny of the genus and where there is still no differentiation in axes, as in *P. calycinus* Wall., *P. thymoides* (Müll.Arg.) Sieber ex Müll.Arg. and the herbs *P. polygonoides* Nutt. ex Spreng. and *P. lacunarius* F.Muell.; 2) “indecisive plagiotropic”, characterized by an orthotropic principal axis and axillary axes with a certain degree of plagiotropy, represented by *P. grandifolius* L., *P. discoideus* (Baill.) Müll.Arg. and *P. maderaspatensis* L.; and 3) “net plagiotropic”, the most common form in the genus, with an orthotropic main axis and reduced leaves and plagiotropic secondary axes which produce axillary flowers, represented by *P. gunnii* Hook., *P. carolinensis* Walt., *P. odontadenius* Müll.Arg., *P. leonardianus* Lisowski Malaisse & Symoens, *P. emblica* L., *P. carnosulus* Müll.Arg., *P. fluitans* Benth. ex Müll.Arg., *P. hyssopifolioides* Kunth, *P. urinaria* L., *P. aeneus* Baill., *P. epiphyllanthus* L. and *P. angustifolius* (Sw.) Sw.

The basis for architectural analysis is described in many publications, among which is the recent review of Barthélémy & Caraglio (2007). In short, the architectural analysis has the objective to identify and describe the inherited branching pattern of a species. One identifies axes, which may be the trunk, a branch or parts thereof and describes their characteristics with respect to the direction of growth, activity in time and destiny. Within a tree, a species may have different types of axes, which in combination form an architectural model. This model repeats itself by means of the process of reiteration to form larger trees or repair parts of the crown.

Only a limited number of species of *Phyllanthus* have been analyzed for their architecture (Hallé & Oldeman

TABLE 2. — Quantitative characteristics of axes A1, A2 and A3 of *Phyllanthus acuminatus* Vahl, according to four development phases. Ranges and average numbers are given, numbers in bold indicate the largest organ sizes and highest of organ numbers.

Phase	Axis	Length (cm)	Number of leaves	Leaf length	Number of nodes with ramification
Extension	A1	135.5	many	NA	13
	A2	31.3-43.0	14-18	3.6-5.2	6-9
	A3	10.7-15.1	9-13	3.1-4.5	NA
Sexual maturity	A1	300	NA	NA	19
	A2	73.3-86.3	18-27	4.1-4.8	13-20
	A3	19.6-30.6	13-21	3.3-5.3	NA
Amplification	A1	412	NA	NA	19
	A2	57.4-71.2	16-22	3.4-4.5	13-17
	A3	15.8-24.2	13-18	3.3-4.8	NA
Adult	A1	800	NA	NA	10
	A2	19-37	15-23	1.7-2.3	11-16
	A3	10-13	12-16	2.0-3.0	NA

1970; Hallé *et al.* 1978; Vester 2002; Hallé 2004), which is a limitation for the advances in inferences on the evolution in architecture. In view of this lack of architectural studies we supply a detailed analysis of the architecture of *Phyllanthus acuminatus* Vahl., which we put in context of the present knowledge on evolution of architecture in the family.

MATERIALS AND METHODS

Fieldwork was carried out during November 2002 in a patch of medium high semi-evergreen forest near to Chetumal Bay, at km 2 on the highway from Chetumal to Bacalar, Quintana Roo, Mexico. The forest was affected by urbanization and frequent hurricane impacts.

We studied 30 specimens of *P. acuminatus* of different ages and development, which we divided into developmental classes, each one delimited by a significant change in the architecture. The first phases are characterized by the consecutive appearance of lateral axes, which allow the architectural model to be determined. Reiteration and flowering characteristics differentiate the subsequent phases. The following measurements or observations were made on each type of axis in each tree: destiny (determinate or indeterminate), temporality (continuous, rhythmic or diffuse), direction of growth (orthotropic, pla-

giotropic or mixed), symmetry (radial or bilateral), chronology (proleptic or sylleptic), angle of insertion, type of dermal layer (epidermis or periderm), presence and position of flowers, type of phyllotaxis, dimensions of the axes, number of leaves per axis, length of the leaves, number of ramifications.

All observed specimens were schematically drawn to scale respecting the internodal distances. These drawings were digitized on a Wacom® tablet and using the program Canvas 7® for MacIntosh® to record and represent the drawings.

In order to verify the hypotheses mentioned above and to know which architectural characteristics are plesiomorphic or apomorphic, we mapped architectural models of species on the cladogram published by Kathriarachchi *et al.* (2005). This mapping of architectural characteristics is not a preferred method (Bateman 1999) because phylogenies should be made with all available characteristics. This last method is not possible because architectural data are missing for many species of the existing phylogenies. Moreover, it is probably more significant when positive results are obtained in this way.

RESULTS

Phyllanthus acuminatus Vahl shows an architectural development (Table 1), which follows the model



FIG. 2. — Leaves and inflorescences of *Phyllanthus acuminatus* Vahl.

of Roux (formerly Cook, Hallé *et al.* 1978; Hallé 2004). It is a tree of approximately 10 m height, which grows in forest gaps, along roads and in secondary vegetation, although with less frequency it can be found in shaded conditions under higher trees. Multi-stemmed individuals were the result of trees having been cut at ground level.

We distinguish three types of axes described as A1, A2 and A3 (Fig. 1; Tables 1, 2). Axis A1 is the first axis formed and is orthotropic, monopodial, with continuous growth, without inflorescences but with rudimentary leaves. In the axils of the rudimentary leaves, A2 axes are borne. Ramification starts in a very early stage of development, so that it is difficult to find specimens without branches. The A2 axes are plagiotropic and monopodial, with continuous growth and with leaves but without flowers. The

axillary meristems of the A2 axes produce A3 axes by syllepsis: these are plagiotropic, monopodial with continuous growth, and bear leaves and flowers (Table 1; Fig. 2). Flowers and fruits are formed in the axils of the leaves (one fruit per axil and from one to seven fruiting axils on each axis). Both the A2 and A3 axes have limited secondary growth, no bark formation and shed like leaves, leaving a scar. Microscopic survey showed no formation of periderm in mature A3 axes (Fig. 3).

Reiterated axes (A1') can be the result of adaptation or trauma. Adaptive reiterates surge from supernumerary axillary buds on A1 or A1' in the same axils where A2 axes are formed. Traumatic reiterations originate from supernumerary axillary buds, cambium or dormant buds. In all observed trees, these reiterates were total, i.e. showing the

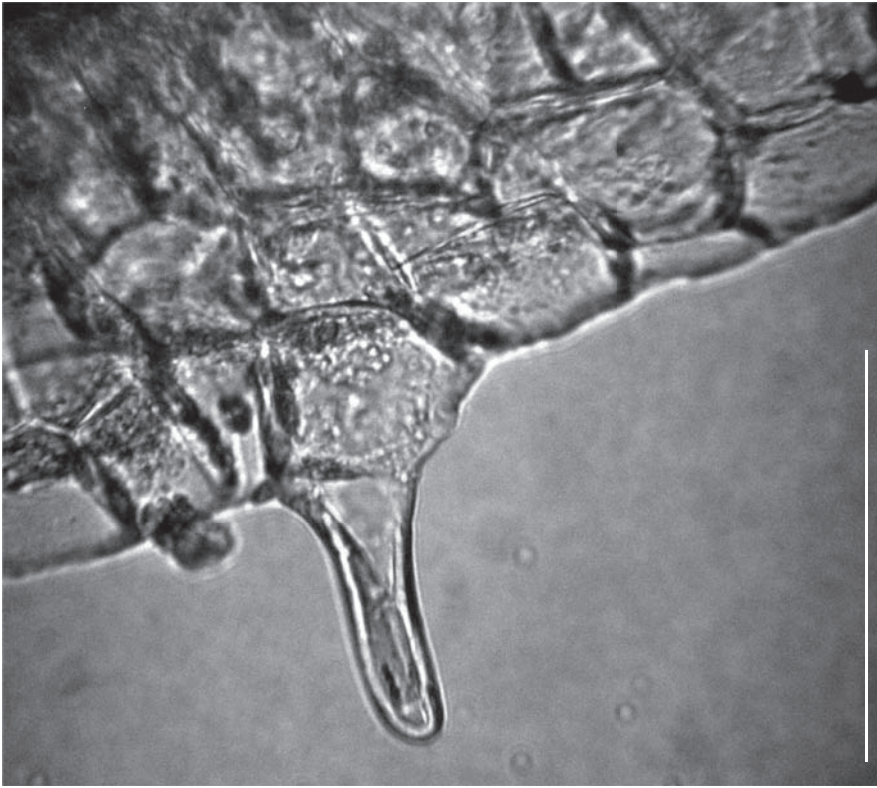


FIG. 3. — Microscopic transversal section of mature A2 axis of *Phyllanthus acuminatus* Vahl. Beneath the epiderm there is no sign of phellogen. Photo by L. F. Cabrera. Scale bar: 64 μ m.

complete architectural model; there only seems to be a decrease in vigour with age.

We distinguish four development phases: 1) extension growth; 2) sexual maturation; 3) broadening; and 4) adult (Fig. 4). These phases correspond to potential trees, trees with the potential of future expansion within the forest patch (Hallé *et al.* 1978) and trees of the present, trees which have reached their maximum expansion within the forest mosaic (Hallé *et al.* 1978), because we did not find trees of the past, senescent trees, which are about to be eliminated from the forest (Hallé *et al.* 1978). We neither found saplings (with just one axis). From the 30 analyzed individuals, two correspond to the extension phase, eight to the sexual maturation, seven to the broadening and 13 to the adult phase.

EXTENSION PHASE

This phase is characterized by the absence of flowers and a vigorous, erect development between 0.5 and 2.3 m. The A1 axis has A3 branches and only some A2 ones in the apical region (Fig. 5B). During this phase, the length of every new axis is larger than the former, and also the number of leaves per axis increases (Table 2).

SEXUAL MATURATION PHASE

During this phase flowers and fruits appear, and adaptive reiteration starts (Fig. 5; Table 2). Growth of the main axis is still erect and trees measure 2.3-3.8 m in height. The lower branches (A2) are shed and leave marks that look like leaf scars formed by an abscission zone. In this phase the largest leaves are formed, as well as the biggest branches (A2, A3).



FIG. 4. — Aspect of the adult plant *Phyllanthus acuminatus* Vahl.

BROADENING PHASE

The tree presents two to four well developed reiterations, and flowers and fruits are abundant. Trees are erect and 3.5-4.5 m high (Fig. 5D, E). The dimensions of axes, number of leaves per axis and number of nodes with developing A3 axes is lower than during the sexual maturation phase (Table 2). The A2 axes on A1 axes usually abscise before development of the supernumerary bud into an A1', although there are exceptions (Fig. 5D).

ADULT

The phase is characterized by vigorous reiterations on the A1 and A1' (Figs 4; 5F-H) in a tree which is between 5 and 10 m high. In this phase the A2 and A3 axes are relatively small in comparison with earlier phases, but on traumatic A1' they may be

larger again. There is abundant flowering and fruiting. The number and size of the leaves is reduced in concert with the size of the A2 and A3 axes and with increasing number of adaptive A1'.

EVOLUTION OF ARCHITECTURE

The mapping of architectural models on the cladogram produced by Kathriarachchi *et al.* (2005) results in three observations:

- 1) the two principal clades, denominated "fasciculate" and "tanniniferous" correspond with two groups of models with a clear distinction. The clade "fasciculate" presents only models with continuous ramification and the clade "tanniniferous" presents only models with rhythmic ramification (Table 3; Fig. 6);
- 2) in both clades appears the model of Troll in positions away from the root, which is a clear argument

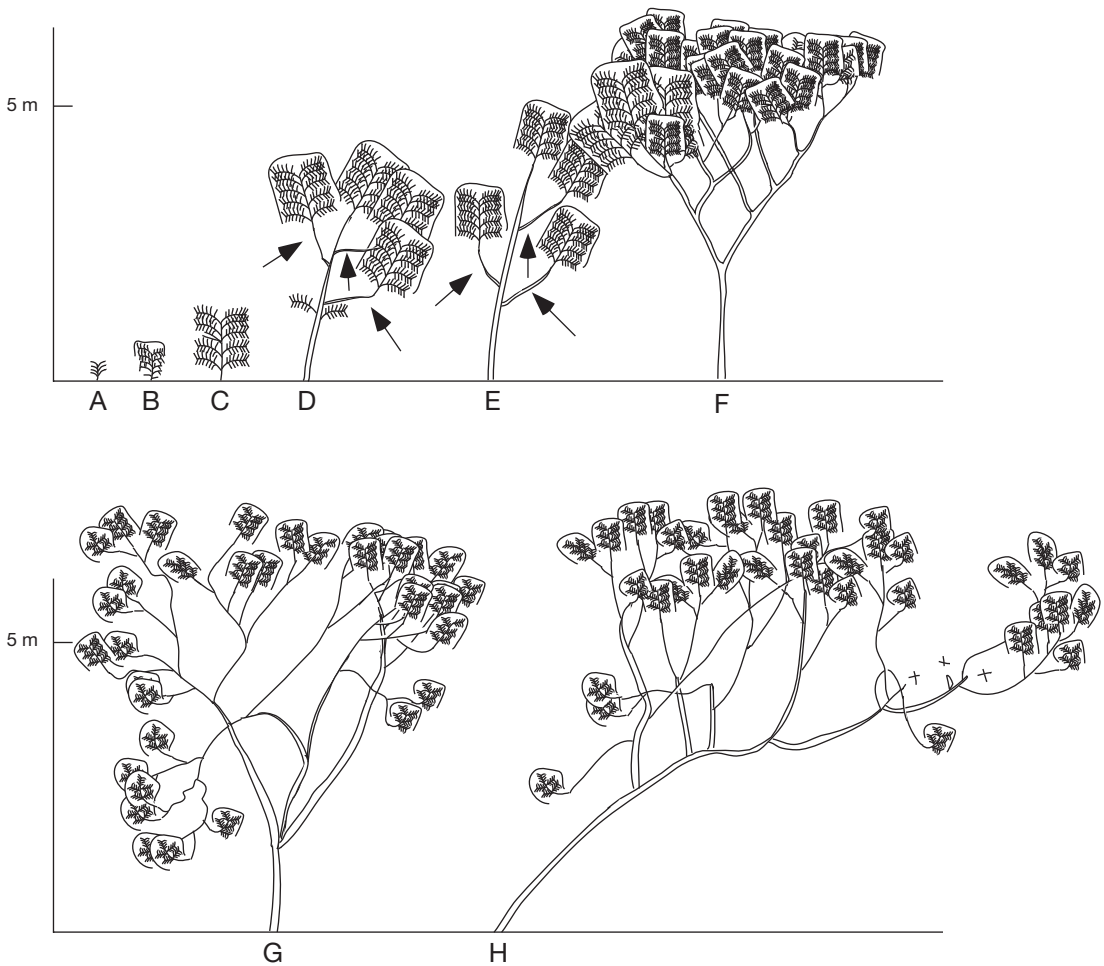


FIG. 5. — Phases of development of *Phyllanthus acuminatus* Vahl: **A**, seedling (not observed); **B**, branching of A1 with A3 and some A2; **C**, sexual maturation with axes A1, A2 and A3, also development of A1'; **D**, **E**, crown broadening with reiterated A1' (arrows); **F-H**, adults. Crosses indicate dead or broken axes.

for considering this model as derived from different original models (homoplasly);
3) in both clades orthotropic models (Rauh, At-tims) are nearest to the root.

DISCUSSION

The most remarkable architectural phenomenon, which this species presents is the phyllomorphic branch, a characteristic that led Hallé & Oldeman (1970) to consider species with this characteristic

in a separate model, the model of Cook, which recently Hallé (2004) reconsidered and united with the model of Roux.

This integration into the model of Roux is justified because the differences between Cook and Roux are only a matter of degree. The model of Roux has a monopodial, orthotropic main axis with continuous growth and branching, the branches are plagiotropic (never by apposition), and flowering does not influence the model (Hallé *et al.* 1978). The difference in Cook's model is that the branches are phyllomorphic, they have limited growth and

TABLE 3. — Architectural models within the two principal clades distinguished by Kathriarachchi *et al.* (2005). *, taxa mentioned by Kathriarachchi *et al.* (2005), but not included in their analysis. Data on the models is from Hallé *et al.* (1978), Bancelhon (1971) and personal observations of F. Hallé.

Fasciculate		Tanniniferous	
Species	Model	Species	Model
<i>Phyllanthus mimosoides</i> *	Roux (Cook)	<i>Antidesma montanum</i> *	Troll
<i>P. muellerianus</i> *	Roux	<i>Martretia quadricornis</i>	Massart
<i>P. urinaria</i> *	Roux (Cook)	<i>Aporosa</i> sp.*	Massart
<i>P. amarus</i> *	Roux	<i>Richeria grandis</i>	Aubréville
<i>P. discoideus</i> *	Roux	<i>Spondianthus preussii</i>	Rauh
<i>P. koghiensis</i> *	Roux (?)	<i>Protomegabaria stapfiana</i>	Rauh
<i>P. gunnii</i> *	Roux (Cook)	<i>Uapaca bojeri</i> *	Rauh
<i>P. odontadenius</i> *	Roux (Cook)	<i>U. guineensis</i> *	Rauh
<i>P. pantheranus</i> *	Roux (Cook)		
<i>P. aeneus</i> *	Roux (Cook)		
<i>P. debilis</i> *	Roux (Cook)		
<i>P. niruri</i> *	Roux (Cook)		
<i>P. alpestris</i> *	Troll		
<i>P. caroliniensis</i> *	Troll		
<i>P. myrtifolius</i> *	Troll		
<i>P. lacunarius</i> *	Attims		
<i>P. polygonoides</i> *	Attims		
<i>P. calycinus</i> *	Attims		
<i>P. maderaspatensis</i> *	Attims		
<i>Breynia patens</i> *	Troll		
<i>Glochidion laevigatum</i> *	Roux		

“behave” like leaves, being deciduous (Hallé & Oldeman 1970; Hallé *et al.* 1978). Thus, these phyllomorphic branches are just more differentiated than the already differentiated plagiotropic branches in Roux’s model, which does not merit a different model.

Species with phyllomorphic branches were considered of recent evolution by Rossignol & Rossignol (1985). In order to prove that this phenomenon is really the result of recent evolution within the genus, species with phyllomorphic branches need to be in a clade which is clearly away from the root of the cladogram.

The genus *Phyllanthus* in the analysis of Kathriarachchi *et al.* (2005) is polyphyletic, separated into three groups: group 1 including *P. epiphyllanthus*, *P. juglandifolius* and *P. polyphyllus* and which are related to the genera *Breynia*, *Glochidion* and *Saururus*; group 2 which consists of *P. liebmannianus*, *P. arenaria*, *P. lokohensis* and *P. nummularifolius*, related to *Reverchonnia*; and group 3 which consists of *P. calycinus* and *P. cf. fuscoluridus*, although these groups do not have sufficient support to consider

them clades and meanwhile are gathered in the clade F1a, which can be considered as *Phyllanthus* s.l.

From these groups, the most alleged from the root is group 1 (Fig. 6). In group 1 we find species with Roux’s model (*Glochidion* and *P. epiphyllanthus*), but also the model of Troll (*Breynia*), which as earlier mentioned frequently recurs as a homoplasy. *Phyllanthus epiphyllanthus* is the type of the subgenus *Xylophylla* (Webster 1956), which in his key is characterized by “phyllanthoid” branching (model of Roux). Probably part of the species in this group show the model of Cook, but there are not enough data to confirm this, or to corroborate with recent evolution. Of group 2 there are no species of which the models are identified, but it is probable that there are at least some species with Roux’s model. *Phyllanthus acuminatus* could belong either to group 1 or group 2.

On the other hand, group 3 is the most basal to the root of the three groups and contains *P. calycinus* which Webster (1956) groups in the section *Isocladius* together with *P. polygonoides*, *P. lacunarius* and *P. maderaspatensis*, all growing according to the

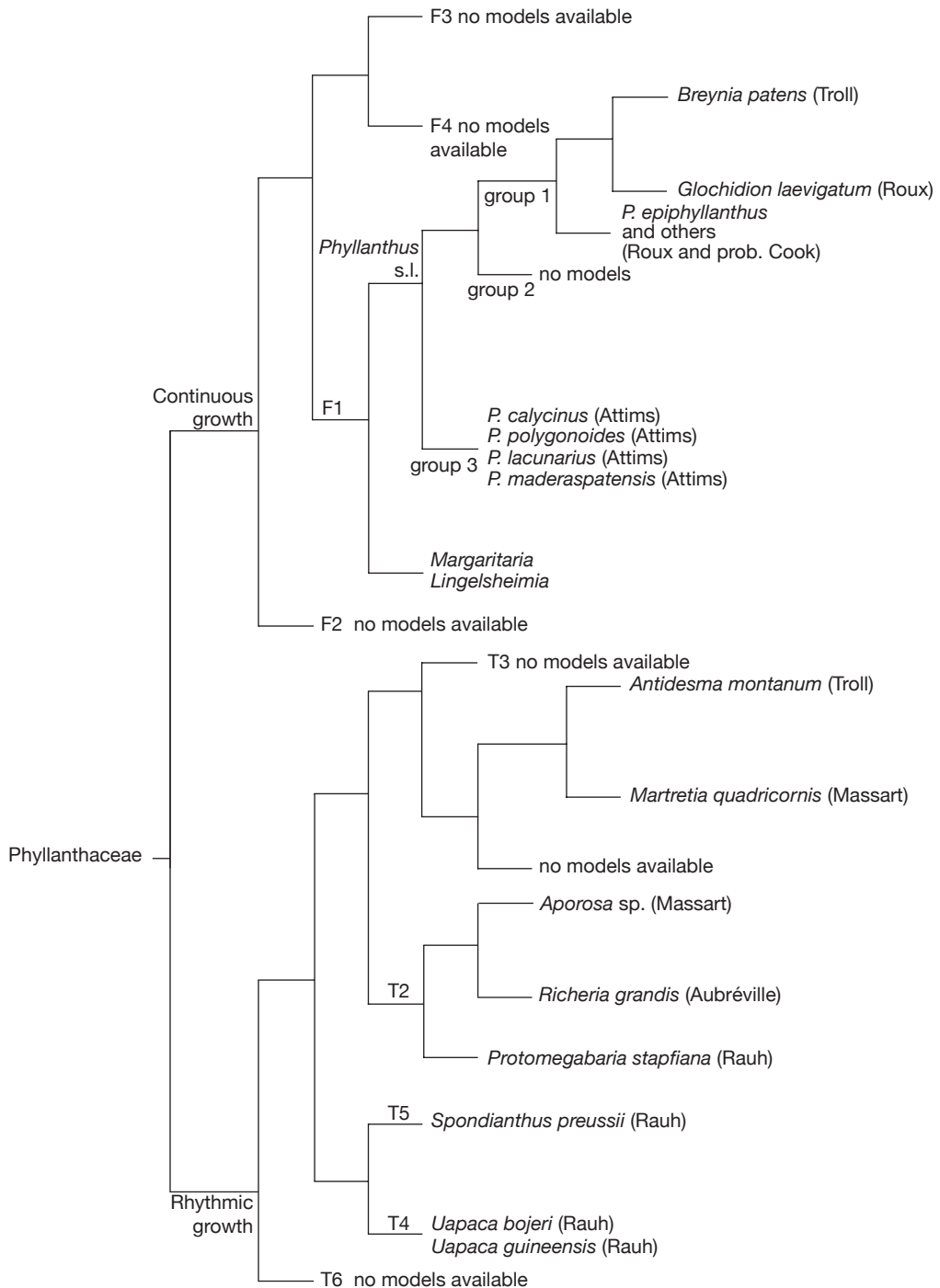


FIG. 6. — Mapping of architectural models on a synthesis of the phylogeny of Phyllanthaceae according to Kathriarachchi *et al.* (2005); clades T1-6 and F1-4 correspond with their clades and are firmly supported by their analysis.

model of Attims, a strong support for the hypothesis of Rossignol & Rossignol (1985) that the ancestral model in *Phyllanthus* has orthotropic axes.

Within the Rhythmic clade we find a similar position of orthotropic models near to the root, in this case the model of Rauh (T4, T5 and T2 in Fig. 6), and again Troll's model as a homoplasy (T1 in Fig. 6).

The architectural analysis of *Phyllanthus acuminatus* yields another suggestion, that the type of reiteration for amplification of the crown is adaptive. Hallé (1986) hypothesizes that species with automatic reiteration, also called metamorphosis (Hallé & Ng 1981; Edelin 1984) are of more recent evolution than species which do not show reiteration, like palms. Probably intermediate to these species are species with adaptive reiteration as the here presented one. In order to prove this hypothesis within the genus *Phyllanthus* it will be necessary to know the way of reiteration in the crown of many more species.

The separation of the family Phyllanthaceae in two groups (tanniniferous and fasciculate) and their correspondence with tree architecture, and the partial confirmation of the hypothesis of Rossignol & Rossignol (1985) confirms the value of architectural characteristics and the urgency for obtaining more information on these characteristics in order to improve our knowledge on the evolution of plants.

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