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Systematics and Biogeography of the Didymopanax group of Schefflera (Araliaceae)

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Systematics and Biogeography of the Didymopanax group of *Schefflera* (Araliaceae)

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Virginia Commonwealth University.

by

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Abstract

SYSTEMATICS AND BIOGEOGRAPHY OF THE DIDYMOPANAX GROUP OF
SCEFFLERA (ARALIACEAE)

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Schefflera is the largest genus in the angiosperm family Araliaceae, with about
900 species, of which c. 300 belong to five subgeneric groups in the Neotropical region.
Previous phylogenetic studies of Schefflera have been limited to a small number of
species from this region, and very little is know about phylogenetic relationships in the
Brazilian-centered Didymopanax group of this genus. Therefore, to gain a better
understanding of the diversity and evolution of the Didymopanax group of Schefflera, I
investigated the systematics of these plants in the broader context of the entire
Neotropical clade. The main goals were (1) to investigate pollen diversity in Neotropical
species of Schefflera; (2) to test the monophyly of these species; (3) to provide a
taxonomic revision for species of the Didymopanax group of *Schefflera*; and (4) to investigate evolutionary relationships within the Didymopanax group. Pollen morphology exhibits an uneven variability across Neotropical *Schefflera*. For example, pollen characters support the distinctiveness of the Didymopanax group from all remaining groups. Moreover, *S. tremula* has a distinctive pollen morphology compared to remaining species of the Sciodaphyllum group. However, among the remaining groups of Neotropical *Schefflera*, pollen characters are less distinctive. Molecular phylogenetic analyses have confirmed the monophyly of the Neotropical species of *Schefflera*, and helped to identify four major clades. One of these clades includes subclades representing the Didymopanax and Crepinella groups, while another clade includes all species from groups Cotylanthes and Sciodaphyllum, excluding *Schefflera tremula*, a finding that corroborates pollen data. In the formal taxonomic revision of Didymopanax, 37 species are recognized, together with three insufficiently known species. The revision also includes updated species circumscriptions and nomenclatural adjustments for 26 names. Phylogenetic analyses among Didymopanax species recovered four morphologically and geographically coherent clades (Atlantic Forest, Imeri, Five-carpellate and Savannic clades), but their phylogenetic inter-relationships were generally weakly supported. Poorly resolved relationships in the Savannic clade suggests a rapid diversification in the *campos rupestres* vegetation, which accounts for the greatest species richness in the group. The presence of multiple Didymopanax lineages in the Amazonian and Atlantic forests corroborates that these regions may be composite biogeographic areas.
CHAPTER 1

Taxonomic significance of pollen morphology in Neotropical *Schefflera* (Araliaceae)

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Abstract

Pollen grains from 43 species of Neotropical Schefflera were studied under light and scanning electron microscopy to search for variation among species and possible agreement with current taxonomic views. The species investigated are characterized mostly by tri-colporate angulaperturate pollen with lalongate endoapertures and a semitectate sexine, with an ornamentation varying from prominently reticulate to perforate with a psilate to rugulate or rugulate- reticulate surface. Some palynological features support the recognition of a well-defined “Didymopanax” group in Neotropical Schefflera, which can be characterized by unique reticulate-heterobrochate ornamentation. Pollen morphology also supports several additional findings, such as a distinct pollen morphology in S. tremula compared to other species of the “Attenuatae” group of “Sciodaphyllum” (e.g., S. attenuata and S. rodriguesiana), and similar planaperturate pollen grains in S. minutiflora and S. sphaerocoma, despite their placement in different infrageneric groups of “Sciodaphyllum”. Overall, however, sexine patterns alone are not sufficient to place species in the current, informal, classification system. Pollen shape and size also varied greatly among species, but did not appear to be taxonomically informative.

Keywords: Araliaceae, Didymopanax, Neotropics, pollen grains, systematics
Introduction

Recent advances in our understanding of phylogenetic relationships among representatives of Araliaceae have revealed that Schefflera is polyphyletic, with its species forming five independent lineages (Plunkett et al. 2004, 2005). As presently circumscribed, most of the diversity of this genus belongs to two closely related clades (referred to as “Neotropical Schefflera” and “Asian Schefflera”). Both groups belong to the informal “Asian Palmate Clade” of Araliaceae, a mainly Asian group of genera that also includes Brassaiopsis, Dendropanax, Eleutherococcus, Fatsia, Hedera, Trevesia, and Asian Schefflera (among others), as well as the Neotropical genus Oreopanax (Wen et al. 2001, Lowry et al. 2004, Plunkett et al. 2004, 2005, Mitchell & Wen 2005). In the Neotropical Schefflera clade there are about 300 species ranging from Mexico to northern Argentina (Plunkett et al. 2005, Fiaschi & Plunkett, unpubl.). Although a formal infrageneric classification system is not available for these species, they have been grouped into five informal subgeneric groups: “Cephalopanax” (ca. 10 spp., from the Andes), “Cotylanthes” (ca. 15 spp., from Panama to Northern Ecuador), “Crepinella” (ca. 40 spp., mainly from the Guayana Shield in northern South America), “Didymopanax” (ca. 40 spp., mostly from Brazil), and “Sciodaphyllum” (with ca. 200 spp. in the Neotropics, but also currently encompassing unrelated Asian and African lineages). Some of these groups appear to be monophyletic (Fiaschi & Plunkett, unpubl.), but the large, pantropical “Sciodaphyllum” group is clearly polyphyletic (Plunkett et al. 2005). The Neotropical species of “Sciodaphyllum” require further study, but can be rendered monophyletic with the inclusion of species from “Cotylanthes” (Fiaschi & Plunkett, unpubl.).

There have been few studies on the palynotaxonomy of Schefflera, the most comprehensive of which date back to more than 30 years ago (Tseng & Shoup 1978). According
to that study, representatives of *Schefflera* have very distinctive pollen types. However, the taxonomic sampling from Tseng & Shoup’s (1978) study had a strong geographical bias. Among the 48 species they studied, 44 belonged to the lineage now recognized as the Asian clade of *Schefflera*, while only three were from the Neotropical clade and one from the Melanesian *Schefflera* clade [although Melanesian species had been more extensively sampled previously by Tseng (1973) under generic name *Plerandra*]. No representatives from the African-Malagasy *Schefflera* clade or from *Schefflera* sect. *Schefflera* (sensu Plunkett et al. 2005) have been studied. Tseng and Shoup (1978) placed each of the three Neotropical species into distinct pollen groups, implying that there was some palynological variation among Neotropical *Schefflera*. This finding was later corroborated among some eastern Brazilian species of the genus (Fiaschi et al. 2008).

In the present paper, we provide information on pollen morphology from 43 species of Neotropical *Schefflera* using light microscopy (LM) and scanning electron microscopy (SEM). The observed palynological features were used to group species into pollen types, which we then compare to the informal sub-generic groups currently recognized in Neotropical *Schefflera* (Frodin 1995, Plunkett et al. 2005).

**Materials and Methods**

The names of the species sampled in this study are provided in Table 1, together with voucher information. Anthers from hermaphroditic floral buds were taken from herbarium specimens and placed in glacial acetic acid for at least 24 hours before submitting to evacuation by acetolysis (Erdtman 1960).
For light microscopy (LM), pollen grains were mounted in glycerol jelly and sealed with paraffin. Pollen slides were examined and photographed under a Zeiss light microscope, model Axioskop 2 MC80 DS. For scanning electron microscopy (SEM), pollen grains were de-hydrated in alcoholic series following acetalyses. The alcohol solutions with pollen grains were then placed on aluminum stubs, allowed to evaporate, and sputter-coated with 10–12 nm gold palladium in an EMITECH K550X sputter coater. Pollen grains were examined and photographed with either a LEO 1430 VP (Carl Zeiss) microscope or a Hitachi 4500 FESEM (field emission scanning electron microscope).

The pollen terminology adopted here follows Punt et al. (2007). Symmetric plane figures used to characterize endoapertures shape follow Radford (1974, p.119). Size measurements and endoaperture information were based on LM analyses, while pollen grain ornamentation was based on SEM analyses. Ectexine ornamentation patterns were described exclusively based on the mesocolpia surfaces, because the apocolpia sometimes exhibit a distinct pattern.

We attempted to group the analyzed species exclusively according to their pollen features, mostly from the ectexine ornamentation. These groups were then compared to those of D.G. Frodin’s informal classification system of Schefflera (see Plunkett et al. 2005). Inflorescence and floral characters were obtained from herbarium material and the available taxonomic literature (e.g., Cannon & Cannon 1989, Frodin 1993, 1995). Names here proposed for pollen types were based on observed ornamentation patterns.

Results and discussion

General morphology
Pollen of Neotropical *Schefflera* species are usually medium in size (small in *S. diplodactyla*, *S. cf. ternata* and *S. tipuanica*), ranging from P 19–48 x E 16–41 µm. The shapes vary from oblate-spheroidal (Fig. 26, 31, 60, 134, 177) to subprolate (Fig. 67, 78, 100, 215), more commonly oblate- to prolate-spheroidal, and triangular (Fig. 5, 128, 157) to circular (Fig. 119) in polar view (amb), with concave (Fig. 111) to convex (Fig. 64) mesocolpia. Pollen grains present three colpori typically situated at the angular areas of the polar view (angulaperturate, Fig. 92), but some species have planaperturate pollen with apertures in the middle area of the sides in polar view (e.g., *S. minutiflora* and *S. sphaerocoma*, Fig. 46, 55, 64). Ectoapertures can be very long, almost reaching the poles (Fig. 67, 107), or relatively short (Fig. 71). In width, they may be uniform (Fig. 63, 190) or medially constricted (Fig. 67, 222) to enlarged (Fig. 31, 188). The endoapertures are usually lalongate (Fig. 6, 42, 51, 120, 164, 214), and can be laterally fused to form an endocingulum (Fig. 160, 206). The shape of endoapertures is usually elliptic (Fig. 18, 116) to transversely elliptic (Fig. 88) or transversely oblong (Fig. 6, 42, 171), and the latitudinal ends can be continuous with nexine breaks (endocracks), forming H-shaped endoapertures (Fig. 51). Fastigia (Fig. 128, 170) are commonly present. The sexine is usually thicker (Fig. 218, 224) or as thick as nexine (Fig. 68), but the nexine is usually thicker bordering endoapertures (i.e., forming costae) (Fig. 13, 92, 115, 170). Endocracks breaks are rare (Fig. 51). The sexine is usually semitectate, but sometimes eutectate especially bordering apertures (i.e., margines are present) (Fig. 67, 100, 188, 191). The ectexine is reticulate homo- (Fig. 111, 112) or heterobrochate (Fig. 22, 23, 27, 31, 34), microreticulate (Fig. 221, 228), perforate (Fig. 67) or rugulate (Fig. 101, 103, 105) to rugulate-reticulate (Fig. 152, 180), and sometimes less coarse at the apocolpia (Fig. 62, 151, 216). When reticulate, the lumina are isometric, and the muri sometimes have perforations.
The pollen of Neotropical *Schefflera* species fits the general morphology of Araliaceae pollen grains (Erdtman 1952). Many widespread features found across the family were reported among the species studied. The reticulate (or rugulate-reticulate) ectexine ornamentation, and the costae (thickening of nexine along endoaperture border), which are common to *Acanthopanax* (Decne. & Planch.) Witte (= *Eleutherococcus* Maxim.), *Aralia* L., *Panax* L., *Plerandra* A. Gray (= Melanesian *Schefflera*), *Polyscias* J.R.Forst. & G.Forst, *Tetraplasandra* A. Gray and *Tupidanthus* Hook.f. (= Asian *Schefflera*) (Tseng 1971, 1973, Tseng et al. 1983, Henwood 1991, Wen & Nowicke 1999), are also typical of many Neotropical *Schefflera* species. Other commonly observed features, such as the presence of endocracks that sometimes result in H-shaped endoapertures (Tseng 1973, Henwood 1991, Wen & Nowicke 1999) and the presence of an endocingulum (Tseng 1973, Tseng & Shoup 1978) are also found among few representatives of Neotropical *Schefflera* (e.g., *S. sciodaphyllum*, Fig. 51, and *S. quindiuensis*, Fig. 160, respectively).

Pollen ornamentation of the majority of the species studied from Neotropical *Schefflera* can be characterized by a general pattern ranging from perforate (e.g., *S. attenuata*, *S. rodriguesiana*, Fig. 61, 65) to microreticulate, with an almost plane (Fig. 148, 177, 183) or variously undulate surface (Fig. 146, 152, 182, 220), sometimes exhibiting a rugulate to rugulate-reticulate condition with poorly developed muri (e.g., *S. sodiroi*, *S. tamana*, *S. tipuanica*, Figs. 101–105). This same general pattern has been found in many unrelated genera of Araliaceae (Tseng 1971, 1973, 1983, Wen & Nowicke 1999), and appears to be unspecialized in the family. Distinctive ectexine sculpturing in some species and genera has been suggested as being derived from this general pattern, as in *Panax trifolius* L. (Wen & Nowicke 1999), *Schefflera paraensis*
Huber ex Ducke [= *S. decaphylla* (Seem.) Harms] (Tseng & Shoup 1978), some species of *Eleutherococcus* (Tseng et al. 1983), and *Boerlagiodendron* Harms (= *Osmoxylon* Miq.) (Tseng 1974). Among the Neotropical species of *Schefflera*, the only two exceptions to this general ornamentation pattern are exemplified by pollen in which the exine is reticulate homo- (Fig. 111, 112) or heterobrochate (Figs. 20–34).

**Pollen types**

Five main pollen types can be recognized among the species of Neotropical *Schefflera* studied, based mainly on ectexine ornamentation. Two of these types (“Reticulate-heterobrochate” and “Reticulate-homobrochate”) can be easily distinguished from the remaining three (“Perforate”, “Rugulate” and “Perforate-microreticulate, usually rugulate” types), which form a continuum from eutectate-perforate to rugulate-perforate or even rugulate-reticulate ornamentation patterns. Some pollen types are morphologically very homogeneous, and correlate well with Frodin’s system (e.g., the “Reticulate-heterobrochate” type with Frodin’s “Didymopanax” group), but the remaining types are more heterogeneous (e.g., “Perforate” and “Rugulate” types), and sometimes include representatives from several of Frodin’s groups (e.g., “Perforate-microreticulate, usually rugulate” type). A list of the main pollen features of species representing each type is presented in Table 2.

1. **“Reticulate-heterobrochate” type — Figs. 1–34**

   Pollen grains medium in size (P 24.5–32 x E 26.5–34 µm); shape suboblate to oblate-spheroidal (P/E = 0.87–1.00); amb triangular, sub-triangular or sub-circular (Fig. 23), the mesocolpia plane to slightly concave (Fig. 29); ectoapertures long, almost reaching poles (Fig.
29), narrow along length (Fig. 33) to wide at mid-portion (Fig. 31), sometimes enlarged at the poles (Fig. 10, 23, 32), with (Fig. 23) or without margo (Fig. 29, 33); endoapertures lalongate, elliptic (Fig. 18) or rectangular (Fig. 6), usually with diffuse lateral margins (Fig. 14); fastigia and costae (Fig. 7, 13, 19) present; exine semitectate, tectum reticulate-heterobrochate, sometimes with microreticulate areas (Fig. 22); muri plane, sinuous (Fig. 27), sometimes scarcely perforate (Fig. 27, 34); columellae fused laterally in cylindrical units (Fig. 24), nexine thinner than sexine (Fig. 9, 17, 19, 24).

This group is characterized by a very homogeneous pollen morphology, in which the reticulate ornamentation pattern results from the adjacent arrangement of cylindrical units formed by laterally fused columellae, as reported for *S. decaphylla* (Seem) Harms (Shoup & Tseng 1977, Tseng & Shoup 1978). This pattern has also been reported in many species of *Schefflera* from southeastern Brazil (Fiaschi et al. 2008), all of which, together with the ones here included (Table 2), belonging to the “Didymopanax” group of Neotropical *Schefflera* (Frodin 1995, Plunkett et al. 2005). In this case, pollen morphology seems to agree with other morphological features (Frodin 1993, 1995) and molecular data (Fiaschi & Plunkett, unpubl.) on the recognition of “Didymopanax” as a well-defined species group within Neotropical *Schefflera*.

2. “Perforate” type — Figs. 35–75

Pollen grains medium or small (*S. minutiflora*: P 22 x E 19) in size (P 22–33 x E 19–34 µm), agulaperturate or sometimes planaperturate (e.g., *S. minutiflora* and *S. sphaerocoma*, Fig. 46, 55, 64); shape oblate-spheroidal (e.g., *S. sciodaphyllum* and *S. troyana*, Fig. 52, 60, 70, 73) to
subprolate (Fig. 38, 48, 56, 67) \((P/E = 0.97–1.19)\); amb triangular (Fig. 58) to sub-circular or circular (Fig. 41, 62, 64), the mesocolpia plane (e.g., *S. troyana*, Fig. 58) to slightly (Fig. 41, 50) or prominently convex (in planaperturate pollen, Fig. 46, 55, 64); ectoapertures long and almost reaching the poles (e.g., Fig. 51, 61, 63, 67) or relatively short (e.g., Fig. 71), narrow, not enlarged at the poles, with (Fig. 63, 67) or without (e.g., *S. minutiflora*, Fig. 66) margo; endoapertures lalongate, elliptic or rectangular, sometimes H-shaped (*S. sciodaphyllum*, Fig. 51); fastigia (Fig. 41, 58) and costae (Fig. 50, 56) sometimes present; exine eutectate or semitectate, tectum perforate, the perforations variously sized and sparsely distributed; surface plane; columellae very short (Fig. 68); sexine and nexine of similar thickness (Fig. 41, 68), or sexine thicker than nexine (Fig. 48, 56).

Despite sharing a more or less homogeneous pattern of exine ornamentation (i.e., ectexine perforate), species included here show some differences regarding general pollen morphology and aperture type. Three subgroups can be recognized when features other than ornamentation are taken into consideration: (1) *Schefflera minutiflora* and *S. sphaerocoma* share subprolate, planaperturate pollen grains (Fig. 46, 55, 64), with a relatively short ectoaperture (Fig. 66, 71); (2) *Schefflera sciodaphyllum* and *S. troyana* share oblate-spheroidal (Fig. 70, 73), angulaperturate pollen grains (Fig. 50, 58), with more elongate ectoapertures (Fig. 51, 59) and less distinctive perforations; and (3) *Schefflera attenuata* and *S. rodriguesiana* have a somewhat intermediate morphology, characterized by subprolate, angulaperturate pollen grains (Fig. 35, 61) with elongate ectoapertures (Fig. 61, 67).

Although all species included here belong to the “Sciodaphyllum” group (Frodin, 1995), *S. minutiflora* has been placed in the monotypic infrageneric group called “Minutiflorae”,

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whereas the remaining species have been referred to “Sciodaphyllae” (*S. diplodactyla*, *S. sciodaphyllum*, *S. sphaerocoma* and *S. troyana*) and “Attenuatae” (*S. attenuata* and *S. Rodriguesiana*) (Frodin 1995, Plunkett et al. 2005). Pollen data suggest some heterogeneity within the infra-generic group “Sciodaphyllae” (Frodin 1995). Besides the inclusion of *S. sphaerocoma*, which has distinctive pollen morphology (see above), two other species from this sub-group (*S. robusta* and *S. systyla*, D.G. Frodin, pers. comm.) are here listed under the “Perforate-microreticulate, usually rugulate” pollen type due to the presence of a rugulate, rather than a psilate, tectum.

The similarity in pollen morphology between *S. minutiflora* and *S. sphaerocoma* is unexpected (Fig. 44–48, 53–56), especially because they are not similar in several other morphological aspects that are often taxonomically important (e.g., leaf morphology and inflorescence architecture). An evaluation of pollen morphology in other presumably related species, such as *S. chococola* Frodin, *S. magnifolia* Cuatrec., *S. munchiquensis* Ramírez-Padilla and *S. sandiana* Harms, are needed to assess pollen morphological congruence among these taxa.

Similarities of the pollen morphology from *S. attenuata* and *S. Rodriguesiana* agree with the placement of these species in the same infrageneric group (“Attenuatae”, Plunkett et al. 2005), which includes glabrous plants with calyptrate corollas, 2(–3)-carpellate ovaries, and styles that are usually united to form a column (Frodin 1989, 1995). However, the placement of *S. tremula* in “Attenuatae” (Frodin 1989) does not receive palynological support (see discussion under the “Reticulate-homobrochate” type).

3. “Rugulate” type — Figs. 76–89, 98–110
Pollen grains medium or small (S. tipuanica: P 19 x E 16) in size (ca. P 19–40 x E 16–30 µm), angulaperturate or sometimes planaperturate (e.g., S. tamana); subprolate or prolate (S. tamana) (P/E = 1.14–1.46); amb sub-circular, the mesocolpia plane (Fig. 100, 107) to convex (Fig. 84); ectoapertures usually long, almost reaching the poles (Fig. 100, 102, 107), narrow, not enlarged at the poles, with (Fig. 100) or without (Fig. 104, 107) margo; endoapertures lalongate, circular to transversely elliptic (Fig. 88), sometimes almost forming endocingulum (Fig. 81); fastigia (Fig. 78, 92) and costae (Fig. 92) sometimes present; exine semitectate, tectum rugulate (-perforate) (Fig. 99, 108) to rugulate-reticulate with poorly developed muri (Figs. 101–105); surface almost plane (Fig. 101) to undulate (Fig. 105); infratectum as thick as tectum (Fig. 106); sexine and nexine of similar thickness (Fig. 78), or sexine thicker than nexine (Fig. 85, 95).

This type is characteristic of species in which the tectum of the pollen grains is covered with elongated and irregularly arranged sexinous elements; the resulting rugulate pattern is intermediate between striate and reticulate (Punt et al. 2007). Elongated perforations are found scattered among the sexinous elements (Fig. 99, 101, 103), and the muri surface can be almost plane (Fig. 100, 101, 107) to prominently undulate (Fig. 104–105). The shape is usually subprolate, and the endoapertures vary from almost circular (Fig. 76, 82) to prominently lalongate (Fig. 80, 85, 88). The rugulate pattern is shared among presumably unrelated species of Schefflera, all of which belong to the Sciodaphyllum group, but to several distinct infrageneric groups, such as “Bejucosae” (S. tamana), “Cheilodromi” (S. tremuloidea), and “Patulae” (S. patula), as well as the unassigned species S. sodiroi and S. tipuanica.

Frodin (1989, 1995) suggested a possible relationship of groups “Cheilodromi”, “Patulae” and “Bejucosae” to the circum-Caribbean “Attenuatae”. Although this view is not
corroborated by pollen morphology, neither is it rejected by the available data. Despite the remarkable difference in ornamentation between these groups (usually rugulate in “Cheilodromi”, “Patulae” and “Bejucosae” vs. perforate in “Attenuatae”), most species here included share subprolate pollen with relatively elongate ectoapertures (Fig. 61, 67, 69, 102, 107). Schefflera sessiliflora (Fig. 188–189) and S. sipapoensis (Maguire et al. 1984, Fig. 7b-c), both belonging to “Cheilodromii” (Frodin 1995), have prolate-spheroidal pollen with shorter ectoapertures and very distinctive margines (Fig. 188). Schefflera tipuanica has a prominent rugulate ornamentation (Fig. 104), but differs from the remaining species included here. The pollen of this species shows a rugulate ornamentation throughout (even on apocolpia), while in other species, the rugulae are restricted to the mesocolpia and the apocolpia are perforate (Fig. 98, 102, 107).

4. “Reticulate-homobrochate” type — Figs. 90–97, 111–112

Pollen grains medium in size (P 31.2–33 x E 27.5–29 µm), agulaperturate; prolate-spheroidal (P/E = 1.11–1.14); amb triangular, the mesocolpia plane or concave (Fig. 92, 112); ectoapertures long, almost reaching the poles (Fig. 93, 96, 112), narrow, without margo (Fig. 112); endoapertures lalongate (Fig. 94, 96), narrow transversely oblong (Fig. 94), with diffuse lateral ends (Fig. 94); fastigia (Fig. 95) and costae (Fig. 92, 95) present; exine semitectate, tectum reticulate-homobrochate; muri plane, straight to more or less sinuous (Fig. 112), perforate; columellae not seen; sexine thicker than nexine (Fig. 95, 97).

We have decided to separate S. tremula in a distinct group (“Reticulate-homobrochate”) from the “Reticulate-heterobrochate” type (discussed earlier), despite their superficially similar
reticulate ornamentation. Instead of a heterobrochate reticulum resulting from laterally arranged cylindrical units (as in “Didymopanax”), the reticulum of *S. tremula* is homobrochate, and the cylindrical units appear to be missing. Several additional features also serve to distinguish *S. tremula* from the “Didymopanax” group (Frodin 1995), including indumentum (glabrous vs. pubescent plants) and filament length (filament longer vs. usually shorter than the anther).

The placement of *S. tremula* in the “Attenuatae” group of Sciodaphyllum (Frodin 1989, 1995) is not supported by pollen data. Two other species belonging to this group (*S. attenuata* and *S. rodriguesiana*) are characterized by subprolate pollen with a eutectate-perforate tectum, while in *S. tremula* the pollen are prolate-spheroidal with semitectate-reticulate tectum. Other distinctive morphological features of *S. tremula* from “Attenuatae” species include inflorescences usually with tertiary branches present (vs. absent), flowers with free (vs. calyptrate) petals, and fruits with free (vs. variously fused) styles.

5. “Perforate-microreticulate, usually rugulate” type — Figs. 113–230

Pollen grains medium or small (*S. cf. dielsii, S. systyla* and *S. cf. ternata*) in size (P 24–48 x E 20–42 µm), angulaperturate; sub-obl ate to sub-prolate (P/E = 0.84–1.31); amb triangular (Fig. 148, 157), sub-triangular, sub-circular or circular (Fig. 119), the mesocolpia plane (Fig. 128, 157) to slightly concave or convex (Fig. 184, 191, 221, 228); ectoapertures usually long and almost reaching the poles (Fig. 151, 177, 190), sometimes relatively short (Fig. 188, 189), narrow, almost as long as the polar axis (Fig. 143, 154, 181, 190), sometimes with rounded ends (Fig. 222), with (Fig. 177, 188, 190, 222) or without margo (Fig. 143, 181); endoapertures lalongate, elliptic (Fig. 116, 175, 210) to rectangular (Fig. 164, 171, 214), sometimes constricted (Fig. 200) or with bifurcated ends (Fig. 164), or laterally fused forming an endocingulum (Fig.
fastigia (Fig. 115, 126--128, 157, 163, 170) and costae ectocolpi (Fig. 119, 138, 167, 194) sometimes present; exine semitectate, tectum rugulate-peforate, with variously shaped and sized perforations (Fig. 154, 180, 185), or rugulate-microreticulate (Figs. 144, 189, 221, 223, 228, 230), sometimes psilate-peforate (Fig. 177); surface plane or generally undulate in optical section; infratectum as thick as the tectum (Fig. 150, 218, 224); sexine thicker, or as thick as the nexine (Fig. 150, 218, 224).

This pollen type characterizes most of the sampled species, which exhibit great variability in size, shape, and apertural features (Table 2). The ornamentation, however, is very similar and follows a generalized pattern where the tectum is psilate to rugulate, and the perforations (of various sizes and shapes) are found scattered across the sexine surface, which sometimes forms a microreticulum (Fig. 144, 221, 228). Species included here belong to four (of the five) subgeneric groups of Neotropical Schefflera (Plunkett et al. 2005): “Cephalopanax” (2 spp.), “Cotylanthes” (2 spp.), “Crepinella” (4 spp.), and “Sciodaphyllum” (10 spp.). The only group not represented in this type is “Didymopanax”, where ornamentation has a distinctive reticulate pattern (see comments under “Reticulate-heterobrochate” type). Unlike “Didymopanax”, these other groups do not appear to be characterized by unique pollen features.

All sampled species from the “Cephalopanax” and “Crepinella” groups exhibit this generalized pollen type. Both groups are morphologically homogeneous and can be readily distinguishable from other Neotropical species assemblages by features of the leaves, flowers, and fruits. Although there appears to be no diagnostic pollen features for “Cephalopanax” group, both species sampled here (S. jahnii and S. sp. nov. “Cephalopanax”) seem to have somewhat swollen pollen grains (Fig. 151, 191) with convex mesocolpia and very long (Fig. 151, 190, 191)
and laterally curved colpi in E-view (Fig. 133, 190). Among representatives of “Crepinella”, the presence of costae endocolpi is noteworthy even under SEM in *S. harmsii* (Fig. 149), *S. montana* (Fig. 177) and *S. umbellata* (Fig. 227) due to the formation of bulged areas of equatorial exine, as reported in *Schefflera* (Tseng & Shoup 1978), *Hedera* (Van Helvoort & Punt 1984), *Polyscias* (Henwood 1991), and several species of *Panax* (Wen & Nowicke 1999). In Araliaceae, these thickened areas result from increased nexine and decreased sexine deposition bordering the apertures (e.g., Wen & Nowicke 1999, Fig. 35, 42).

The presence of an endocingulum is also noteworthy in the “Perforate-microreticulate, usually rugulate” type, and appears restricted to species from the “Cotylanthes” group (*S. quindiuensis* and *S. sp. nov. “Cotylanthes”, Fig. 159, 160, 196) or presumably related, such as *S. cf. ternata* (Fig. 206) (D.G. Frodin, pers. comm.). Species from this group are usually glabrous or glabrescent, and share membranous leaves, few-branched inflorescences with few-flowered umbellate inflorescence units, and relatively large flowers with calyptrate corollas, free styles, and 5–10-locular ovaries (Frodin 1995).

**General trends in Neotropical Schefflera pollen morphology**

As Tseng & Shoup (1978) suggested, the present study points to high levels of pollen variability among representatives of Neotropical *Schefflera*. Four (or five) of the eight pollen types described for the entire genus *Schefflera* also appear to be found among the Neotropical species. Two pollen types (“Calypttrata” and “Paraensis”) can be assigned with confidence to some of our samples, the first to *S. duidae* (Fig. 146–147), and the second to all “Reticulate-heterobrochate” species (Fig. 20–34). Moreover, a similar structural pattern to Tseng & Shoup’s
“Hoi” type, having eutectate areas along apertures and semitectate areas on remaining sexine, was observed in *S. sodiroi* (Fig. 100) and *S. sessiliflora* (Fig. 188).

The “Thaumiasiantha” type, which was described for pollen with a tectate imperforate sexine thinner than the nexine, was considered to be characteristic of *S. sciodaphyllum* (Tseng & Shoup, 1978). Our sample of *S. sciodaphyllum*, however, seems to be a better fit with the “Leucescens” type due to the presence of perforations in the sexine, even though the size range reported here (*P* 22–33 x *E* 19–34 µm) did not overlap with that mentioned by Tseng & Shoup (1978) for the same species (*P* 12–18 x *E* 12–17 µm).

Taken alone, sexine ornamentation patterns do not suffice to place Neotropical *Schefflera* species in their predicted groups in the current, informal classification system (see Plunkett et al. 2005, Table 1). The presence of a distinct ornamentation may suggest an improper placement of *S. tremula* in the “Attenuatae” group, but several other groups that are well defined morphologically (e.g., “Cephalopanax” and “Crepinella”) do not appear to be characterized by distinctive ornamentation patterns. Apart from the two reticulate patterns (homo- and heterobrochate), the remaining variation observed in pollen morphology does not represent clear-cut patterns. Instead, there seems to be a continuum of pollen surfaces from psilate to rugulate, with perforations that vary in size and shape, sometimes having distinct muri and lumina (microreticulate pattern). The nature of this variation, coupled with the limitations of our sampling, precludes the recognition of taxonomic groupings based on pollen ornamentation alone. This difficulty has resulted in the recognition of a highly variable group (the “Perforate-microreticulate, usually rugulate” type), and is best seen in the large “Sciodaphyllum” subgroup of Frodin’s “Sciodaphyllum” (D.G. Frodin, pers. comm.), where species can have pollen that
ranges from minutely perforate (e.g., *S. sciodaphyllum*, Fig. 70), to perforate (e.g., *S. diplodactyla*, Fig. 62) or rugulate-perforate (e.g., *S. robusta*, Fig. 185, and *S. systyla*, Fig. 220).

Pollen size and shape vary greatly among Neotropical species of *Schefflera*, supporting Tseng & Shoup’s (1978) view of pollen variability in the genus. Pollen size has been regarded as a good predictor of taxonomic relatedness in some genera of Araliaceae (e.g., Tseng 1971, Tseng & Shoup 1978, Henwood 1991, but see Fiaschi et al. 2008). However, such variation in size may be due to changes in chromosome number (Henwood 1991). Pollen shape seems to provide firmer support for the recognition of pollen types in *Schefflera*. Tseng (1973) used pollen shape to distinguish *Tupidanthus* (subprolate to prolate pollen) from *Plerandra* (oblate to spheroidal pollen), and Fiaschi et al. (2008) used shape to distinguish the southeastern Brazilian species of “Didymopanax” (mostly oblate-spheroidal) from “Crepinella” (prolate-spheroidal). We found no unequivocal evidence for the taxonomic utility of pollen shape in Neotropical *Schefflera*, but some of our findings suggest that: (1) oblate-spheroidal pollen predominate in species belonging to the “Didymopanax” group (“Reticulate-heterobrochate” type); (2) both “Perforate” and “Rugulate” types are characterized mostly by subprolate pollen, the only few exceptions being the Jamaican endemics *S. sciodaphyllum* and *S. troyana*; and (3) pollen shape is variable in the “Perforate-microreticulate, usually rugulate” type. Most species have prolate-spheroidal to subprolate pollen, while oblate-spheroidal pollen appear to be found in species with distinctive bulged areas bordering the apertures, such as *S. harmsii* (Fig. 149), *S. montana* (Fig. 177) and *S. umbellata* (Fig. 227).

This study provides further evidence of variability in the pollen morphology of Neotropical *Schefflera*. Although most of the observed variation does not appear to correlate with Frodin’s (1995) informal classification system, the presence of a unique reticulate-
heterobrochate ornamentation in “Didymopanax” supports the recognition of this species group as distinct from the remaining Neotropical species. Future studies of pollen morphology from representatives of Neotropical Schefflera should focus on a broader sampling of species (especially from the “Cephalopanax” and “Sciodaphyllum” groups) and the collection of more detailed information from pollen wall structure. Such studies would also benefit from interpretations in a phylogenetic context, and studies are currently underway to provide this.
CHAPTER 2

Monophyly and phylogenetic relationships of the Neotropical Clade of Schefflera (Araliaceae) based on plastid and nuclear markers

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Abstract — The Pantropical genus *Schefflera* is represented by ca. 300 species in the American tropics, but due to limited sampling in previous phylogenetic studies of the genus, the monophyly of the American species has remained tentative. The monophyly of the Neotropical species of *Schefflera* was tested by expanding a family-wide data set of ITS and *trnL-trnF* sequences, and explored further by assembling an ITS and ETS data set derived from a representative sampling from most of morphological and geographical diversity of the group. Phylogenetic analyses of our expanded data sets confirm the monophyly of Neotropical *Schefflera*, and its broad placement in the Asian Palmate clade of Araliaceae. Four clades were consistently recovered from all analyses, informally called the “Calyptrate,” “Tremula,” “Jahnii,” and “Eastern Andean” clades. The last of these includes species from the Crepinella and Didymopanax groups, and are largely congruent with two geographically centered subclades in the Guayana Shield and Brazil, respectively. The Calyptrate clade agrees to a great extent with the Neotropical species of the Sciodaphyllum group, but excluding *S. tremula*. This Hispaniolan endemic species was instead sister to a Puerto Rican species from the Crepinella group (*S. gleasonii*), a relationship that provides a third example of geographic sub-structuring among Neotropical *Schefflera* species.

Keywords — Didymopanax, external transcribed spacer, Neotropics, Sciodaphyllum, systematics.
Recent efforts towards establishing a phylogenetic classification of Araliaceae have been hindered by an incomplete knowledge of relationships involving *Schefflera* J.R. Forst. & G. Forst., the most speciose genus of the family, comprising ca. 600 described species and perhaps 300 more awaiting description (Plunkett et al. 2004, 2005; Lowry et al. 2004). Moreover, strong molecular evidence indicates that *Schefflera*, as currently circumscribed, is polyphyletic (see Plunkett et al. 2005). Five distinct clades of *Schefflera* s. lat. have been recognized: Pacific, African-Madagaly, Asian, Neotropical, and Section *Schefflera* (which includes *S. digitata* J.R. Forst. & G. Forst., the type of the genus) (Plunkett et al. 2005). The molecular phylogenetic study of Plunkett et al. (2005) placed the Neotropical *Schefflera* clade as a monophyletic group within the larger “Asian Palmate clade” of Araliaceae. However, that study included only 7 samples (from 5 spp.) of Neotropical *Schefflera*. Given the great species and morphological diversity of *Schefflera* in the Neotropics (~ 300 spp.), it is possible that the species from this region may also be polyphyletic. Thus, it is necessary to test relationships in this group with increased sampling, especially from the geographic, morphological, and taxonomic breadth of the group.

Of the 250–300 native species of *Schefflera* in the Neotropics, most are found along the mountain ranges of southern Mesoamerica and northern South America, especially along the Andes and the Guayana Shield (Frodin and Govaerts 2003; Frodin 2004). Frodin divided the Neotropical species of *Schefflera* into five informal subgeneric groups (see Table 1 of Plunkett et al. 2005): “Cephalopanax,” “Cotylanthes,” “Crepinella,” “Didymopanax,” and “Sciodaphyllum.” With the exception of “Sciodaphyllum,” all of these groups are restricted to the Neotropics, and have very coherent morphologies and geographic distributions (Frodin 1995; Plunkett et al. 2005). By contrast, the Pantropical and morphologically diverse “Sciodaphyllum” is now
considered polyphyletic, and its species are placed in three of the five clades of *Schefflera* s. lat. (Plunkett et al. 2005).

The high diversity and widespread occurrence of *Schefflera* in Neotropical rainforests, savannas, and high elevation habitats (e.g., páramos and tepuis) poses interesting questions regarding the morphological diversification of the group. For examples, several species or groups of species exhibit highly similar morphologies, such as epiphytic habits, poplar-like leaflets, capitulate inflorescence units, and calyptrate corollas. However, there are no hypotheses of phylogenetic relationships among Neotropical species of *Schefflera* to test whether such attributes have evolved independently in response to similar selective pressures or if they are the result of common ancestry.

The present study attempts to test the monophyly of Neotropical *Schefflera* by using a sampling drawn from all of the subgroups from Frodin’s informal classification (Plunkett et al. 2005), with a particular emphasis on the morphological and geographical diversity of these species. Where sampling is sufficient, we also attempt to understand phylogenetic relationships among these informal groups of Neotropical *Schefflera*, and even interespecific relationships when that is possible. To accomplish these objectives, we developed a two-tier approach including three molecular markers: nuclear ITS and ETS from the 18S–26S rDNA repeat (White et al. 1990; Baldwin et al. 1995), and the chloroplast *trnL-trnF* (including the *trnL* intron and the *trnL-trnF* spacer). To test the monophyly of Neotropical *Schefflera*, we expanded the ITS + *trnL-trnF* database of Plunkett et al. (2004, 2005), which includes a representative sampling of all but two of the genera of Araliaceae. Because *trnL-trnF* is insufficiently variable at the interspecific level, we then used ITS and ETS to evaluate phylogenetic relationships among species within the Neotropical *Schefflera* clade to improve resolution and branch supports within this group,

**MATERIALS AND METHODS**

**Taxon Sampling** — Sequences from 34 samples of Neotropical *Schefflera* (Table 3) were added to the ITS and *trnL-trnF* data sets from Plunkett et al. (2005), resulting in a data set of 174 terminals to test the monophyly of Neotropical *Schefflera* using a broad sampling from other groups of *Schefflera* and throughout Araliaceae. Three data sets were created for these samples, one for each marker individually, and one combining ITS + *trnL-trnF* into a single matrix.

To evaluate relationships within Neotropical *Schefflera*, a second group of data sets was constructed using a fragment of the nuclear external transcribed spacer (ETS) in addition to ITS data. ETS sequences were obtained from 56 Neotropical *Schefflera* accessions plus five outgroup taxa, and the ITS data set was expanded by the inclusion of additional 18 accessions from Neotropical *Schefflera*. The 56 ingroup samples represent taxa from all five of Frodin’s informal groups of Neotropical *Schefflera* (see Plunkett et al. 2005), including three accessions from Cephalopanax, one from Cotylanthes, six from Crepinella, 14 from Didymopanax and 32 from Sciodaphyllum. Outgroup taxa were chosen on the basis of the ITS + *trnL-trnF* analysis, and included five samples from Asian *Schefflera*, and one each from *Heteropanax* Seem. and *Tetrapanax* (K.Koch) K.Koch. For the Neotropical *Schefflera* samples, all sequences from ITS and ETS were obtained from the same accessions, with the exception of *Schefflera chimantensis* subsp. *rugosifolia* and *S. morototoni* (Table 3). Three data sets were created for these Neotropical *Schefflera* samples, one for each marker individually and one for a combined ITS +
ETS data set. Voucher materials and GenBank accession numbers are provided in Table 3 for new sequences, and in Plunkett et al. (2004, 2005) for previously published sequences.

**DNA Sequencing and Analyses** — Total DNA was extracted using the DNeasy Plant Mini kit (QIAGEN Inc.). The ITS region was amplified using two external primers (ITS5 and C26A) for most samples (White et al. 1990; Downie and Katz-Downie 1996; Wen and Zimmer 1996), but samples derived from Herbarium specimens often required the use of two additional internal primers (ITS3 and ITS2), and sometimes the replacement of C26A by ITS4 (White et al. 1990). The ETS region was amplified using primers 430-f and 18S-2L-r (Tronchet et al. 2005). A novel primer (400-f: 5’--GTT GGT CGG ATC CCT GCT TGT--3’) was designed to amplify ETS from samples that performed poorly using 430-f. The trnL-trnF region was amplified and sequenced using two external primers (“c” from Taberlet et al. 1991, and “f” from Eibl et al. 2001). In some cases, however, internal primers “d” and “e” (Taberlet et al. 1991) were used for both amplification and sequencing reactions.

PCR reactions for ITS region included 3 µL of 10x PCR Buffer (QIAGEN Inc.), 2.4 µL of 10 mM dNTPs, 2.4 µL of 25 mM MgCl₂, 1.2 µL of each primer, 0.6 µL of 5% DMSO, 1.2 µL of spermidine 4 mM, 0.3 µL of Taq DNA polymerase (QIAGEN Inc.), 3 µL of unquantified total DNA, and purified water to a final volume of 30 µL. Herbarium materials were PCR-amplified using 5 µL of JumpStart RedTaq DNA Polymerase (Sigma-Aldrich), 0.5 µL of each primer, 0.5 µL of spermidine 4 mM, 1 µL of total DNA, and purified water to a final volume of 10 µL. PCR recipes for trnL-trnF included 5 µL of 10x PCR Buffer (QIAGEN, Inc.), 4 µL of 10 mM dNTPs, 2 µL of 25 mM MgCl₂, 1 µL of each primer, 2 µL of 5% DMSO, 0.2 µL of Taq DNA polymerase (QIAGEN Inc.), 4 µL of total DNA, and purified water to a final volume of 40 µL.
In samples requiring amplification using internal primers (“d” and “e”), the recipe included 1 µL of 10x PCR Buffer (QIAGEN Inc.), 0.8 µL of 10 mM dNTPs, 0.4 µL of 25 mM MgCl₂, 0.2 µL of each primer, 0.4 µL of 5% DMSO, 0.04 µL of Taq DNA polymerase (QIAGEN Inc.), 0.8 µL of total DNA, and purified water to a final volume of 7.5 µL. Recipes for ETS included 2.5 µL of 10x PCR Buffer (QIAGEN Inc.), 2 µL of 10 mM dNTPs, 2 µL of 25 mM MgCl₂, 1 µL of each primer, 0.25 µL of 5% DMSO, 1 µL of spermidine 4 mM, 0.25 µL of Taq DNA polymerase (QIAGEN Inc.), 2.5 µL of total DNA, and purified water to a final volume of 25 µL. PCR of ETS from herbarium materials was performed using the same recipe as that described for ITS.

Amplification of ITS involved 30 to 40 cycles of 94°C (30 sec), 52°C (1 min), and 72°C (50 sec) for the denaturing, annealing, and extension steps, respectively. For DNA extracted from herbarium material, amplification with internal primers involved 37 to 41 cycles of 94°C (30 sec), 48°C (1 min), and 68°C (1 min) for primers ITS5 and ITS2, and 37 to 41 cycles of 94°C (30 sec), 47°C (1 min), and 68°C (1 min) for primers ITS3 and ITS4. Amplification of trnL-trnF from silica-gel samples involved 35 to 37 cycles of 94°C (30 sec), 48°C (1 min), and 72°C (2 min) using primers “c” + “f”. For herbarium samples, the same region was amplified using combinations of one external primer and one internal (“e” + “d” and “e” + “f”) with 37 cycles of 94°C (30 sec), 47°C (1 min), and 72°C (1 min). Protocols for ETS amplification of silica-gel dried material involved 30 to 40 cycles of 94°C (30 sec), 55°C (1 min), and 72°C (50 sec); ETS from herbarium samples were amplified with 42 cycles of 94°C (30 sec), 52°C (1 min), and 68°C (45 sec).

PCR products were purified using a 1:2 mixture of Exonuclease I and Shrimp Alkaline Phosphatase (USB Corp.) according to manufacturer, and sequenced using the DYEnamic ET Terminator Cycle Sequencing Kit (GE Healthcare Inc.). Sequence products were purified using
the MultiScreen™ – SEQ Filter Plates (Millipore Corp.) and then separated electrophoretically on a MegaBace 1000 DNA Sequencing System (GE Healthcare Inc.). The cleaned sequences were assembled and edited using Sequencher (version 4.1, Gene Codes Corp.), and then aligned manually.

All data sets (ITS, trnL-trnF, ITS + trnL-trnF from Araliaceae) and (ITS, ETS and ITS + ETS from Neotropical Schefflera) were analyzed using maximum parsimony (MP) with PAUP* (version 4.0b10; Swofford 2002), maximum likelihood (ML) using GARLI (version 0.95; Zwickl 2006), and Bayesian inference (BI) using MrBayes (version 3.1.2; Huelsenbeck and Ronquist 2001). Family-wide analyses were performed for ITS and trnL-trnF data sets alone and in a combined matrix. For the more focused analyses on Neotropical Schefflera, the ETS and ITS data sets were also analyzed alone and in combination. Data matrices were combined after being tested for congruence using the partition homogeneity test (100 replicates for the ITS + trnL-trnF data set and 1,000 replicates for the ITS + ETS data set) as implemented in PAUP* (Mickevich and Farris 1981; Farris et al. 1995).

Alignment gaps were treated as missing data in all analyses. All data sets were analyzed using heuristic searches (1,000 replicates with random addition) with TBR branch swapping, ACCTRAN optimization, MULPARS in effect, and saving no more than 100 trees per replicate for individual and combined data sets. To search for additional most parsimonious topologies for two of the family-wide data sets (ITS and ITS + trnL-trnF), trees from this first set of analyses were used as starting trees for an additional heuristic search saving up to 40,000 trees. Finally, the strict consensus from this search was loaded as a topological constraint saving only those trees not agreeing with the constraint, for an additional 1,000 replicates to search for alternative most parsimonious solutions, following the approach of Plunkett et al. (2001, 2004, 2005).
The trnL-trnF data set was not subjected to further analyses because the initial search provided very poorly resolved topologies (see results). Node support was estimated by full heuristic bootstrap (BS) analyses in PAUP*, using 500 replicates for the familial data sets, and 1,000 replicates for the Neotropical Schefflera data sets.

For ML and BI analyses, the model of sequence evolution was selected using ModelTest (Posada and Crandall 1998) for each marker individually. Maximum likelihood analyses were performed with six multiple runs to check for alternative topologies and tree scores, and support values for each node were estimated with 100 bootstrap (BS) replicates using GARLI. Bayesian analyses were performed with one million generations and four chains, sampling trees every 10 generations. Each BI analysis was performed twice to check for alternative topologies. To calculate posterior probabilities (PP), trees sampled during the burn-in stage of each run were discarded, and the remaining trees were used to calculate a 50% majority rule consensus tree in PAUP*.

RESULTS

Data Sets — For the Araliaceae data set, the ITS sequences varied in length from 610 to 635 bp, and included both spacers (ITS1 and ITS2) and the 5.8S coding region. The alignment resulted in a data matrix of 683 characters, of which 267 were constant, 111 variable in a single terminal, and 305 potentially informative. The trnL-trnF sequences included the trnL intron and the trnL-trnF intergenic spacer, and varied from 766 to 996 bp. The alignment, based on the data matrix from Plunkett et al. (2005), yielded 1,097 characters, of which 753 were constant, 167 variable in a single terminal, and 177 potentially informative (Table 4). In the Neotropical Schefflera data set ITS sequence length varied from 615 to 623 bp. The aligned matrix had 626
characters, of which 422 were constant, 92 variable in a single terminal, and 112 potentially informative (Table 4). The ETS sequences varied from 456 to 466 bp in length. The data matrix had 470 characters, of which 302 were constant, 56 variable in a single terminal, and 112 potentially informative (Table 4).

Estimations of sequence divergence for each marker were evaluated with the uncorrected “p” distance using PAUP*. Many pair-wise comparisons of \textit{trnL-trnF} were identical. The greatest distance value (including outgroups) was 9.7%, between \textit{Delarbreana paradoxa} (Lowry 4791) and \textit{Hydrocotyle bowlesioides} (Plunkett 1373). The highest value within Araliaceae was 8.1%, between the same sample of \textit{H. bowlesioides} and \textit{Schefflera aff. lilacina} (Clark 7771). ITS had a wider range of pair-wise sequence variation than \textit{trnL-trnF} and varied from identity (between seven pairs of samples) to 27.7% between \textit{Hydrocotyle vulgaris} (Valiejo-Roman 1998) and \textit{Mackinlaya macrosciadea} (Plunkett 1365). The highest value of ITS sequence divergence within Araliaceae was 23.5%, between the same sample of \textit{H. vulgaris} and \textit{Polyscias ‘orientalis’} Lowry & G.M. Plunkett, ined. (Schatz 3925). In the Neotropical \textit{Schefflera} data set, ITS sequences were identical among seven pairs of samples, such as between \textit{S. minutiflora} and \textit{S. sandiana}, between each of two accessions of \textit{S. sciodaphylum}, and in pair-wise comparisons among \textit{S. burchellii}, \textit{S. botumirimensis}, and \textit{S. cordata}. The highest value, including outgroups, was 13.4% (between \textit{S. tremula} and \textit{Tetrapanax papyrifer}), and among ingroup taxa 11.6% (between \textit{S. tremula} and \textit{S. decaphylla}). Eight pair-wise comparisons of ETS sequences showed no differences. The highest value for ETS sequence divergence including outgroups was 12.5% (between \textit{S. ruschiana} and \textit{S. heptaphylla}), and 10.9% among ingroup taxa, between \textit{S. cf. violacea} and \textit{S. capixaba}. 

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Phylogenetic Analyses — Maximum parsimony analysis of the trnL-trnF resulted in 99,800 most parsimonious trees (Table 4). The strict consensus of these trees was very poorly resolved, where Araliaceae emerged as monophyletic (BS = 96%), comprising 67 clades (of which 48 had only a single terminal) collapsed in a large basal polytomy (tree not shown). Neither the Asian Palmate nor the Neotropical Schefflera clades were recovered in this analysis. When analyzed separately, the ITS data set provided a more resolved tree than trnL-trnF, recovering the Asian Palmate Clade (BS = 74%), but not resolving a Neotropical Schefflera Clade (not shown). The partition homogeneity test indicated that ITS and trnL-trnF were congruent and could be combined in a single matrix (p = 0.53). In analyses based on the combined data set, however, both the Asian Palmate and Neotropical Schefflera clades were recovered (BS = 89% and 58%, respectively), suggesting that the trnL-trnF data set has strengthened phylogenetic signal from ITS characters, as demonstrated by Plunkett et al. (2004). The strict consensus tree recovered from analysis of the combined ITS + trnL-trnF data set is shown in Figure 231 (see table 4 for tree measurements).

ModelTest suggested that the GTR + I + Γ was the best-fit model of molecular evolution for all markers employed in this study (ITS, trnL-trnF, and ETS). Probabilistic analyses (ML and BI) of the combined data set resulted in similar solutions, both of which recovered a Neotropical Schefflera Clade (BS = 84%; PP = 1) within the Asian Palmate Clade (BS = 98%; PP = 1) of Araliaceae. Analyses of the separate trnL-trnF data set failed to recover either the Asian Palmate or the Neotropical Schefflera clades (trees not shown). Maximum likelihood and BI analyses of the combined data matrix (ITS + trnL-trnF) resulted in very similar results, both of which are in general agreement with the MP strict consensus tree. However, unlike the MP trees, the ML and BI analyses did not recover a clade uniting Neotropical Schefflera as sister to a clade comprising
Tetrapanax + Heteropanax + Asian Schefflera. Maximum likelihood recovered the Asian Palmate clade in a broad polytomy uniting 11 lineages (BS = 98%), while BI recovered the Neotropical Schefflera clade plus seven Asian Palmate lineages poorly supported (PP = 0.55) as sister to a clade uniting Asian Schefflera, Heteropanax and Tetrapanax.

Maximum parsimony analysis of the ITS data set from Neotropical Schefflera resulted in 98,206 most parsimonious trees, while the ETS data set resulted in 6,907 most parsimonious trees (see Table 4 for MP trees measurements). The strict consensus trees of these analyses recovered similar results (Fig. 232), but the result of the partition homogeneity test indicated that the ITS and ETS data sets are not congruent with each other (p = 0.001). The utility of the partition homogeneity test as a measure of congruence has, however, been challenged (Dolphin et al. 2000; Barker and Lutzoni 2002), and its use as an indicator of combinability among data sets remains contentious (Cunningham 1997a, 1997b; Barker and Lutzoni, 2002). Thus, to test if the simultaneous analysis of these two data sets would result in a more resolved and better supported tree, we combined them using a “total evidence” approach (Kluge 1989). The analysis of the combined ITS + ETS data matrix yielded 4,174 most parsimonious trees (Table 4), and the strict consensus of these trees (Fig. 233) provided increased resolution and support compared to those derived from the separate analyses.

In Neotropical Schefflera, four major subclades were consistently recovered in trees based on MP analyses of the separate and combined data sets: (1) the Tremula clade (BS = 66–92%); (2) the Jahni clade (BS = 67–100%); (3) the Eastern Andean clade (BS = 79–98%); and (4) the Calyptrate clade (BS = 97–100%) (Figs. 233, 234). Although relationships among these four clades were left unresolved in trees based on the individual data sets (Fig. 232), the trees resulting from the combined data set provided weak support for the Calyptrate clade as sister to
the remaining clades (BS = 51%), and for a sister-group relationship between the Tremula and Jahnii clades (BS = 55%) as sister to the Eastern Andean clade (Fig. 233).

Maximum likelihood and BI analyses yielded very similar results for both individual and combined data sets, all of which corroborated relationships obtained from the MP analyses. ITS data provided a weakly supported sister-group relationship between the Calyptrate clade and the remaining clades (BS = 51%; PP = 0.66). ETS alone recovered a well supported Neotropical Schefflera clade (BS = 95%; PP = 1) with a basal polytomy including the Jahnii (BS = 85%; PP = 1), Tremula (BS = 58%; PP = 0.99), and Calyptrate + Eastern Andean clades (BS = 70%; PP = 0.74). ML and BI analyses of the combined ITS + ETS data matrix recovered trees with poorly supported (BS ≤ 50%) relationships at the base of the tree (Fig. 234). For both analyses, each one of the four major clades received strong support: Tremula (BS = 83%; PP = 1), Jahnii (BS = 100%; PP = 1), Eastern Andean (BS = 99%; PP = 1), and Calyptrate (BS = 100%; PP = 1). Because the combined ITS + ETS data set analyzed with ML and BI yielded topologies with increased resolution and support compared to the separate ITS and ETS data sets, only those trees are shown here (Fig. 234).

**DISCUSSION**

*Placement and Monophyly of Neotropical Schefflera* — The monophyly of Neotropical Schefflera was first suggested by Plunkett et al. (2005) based on molecular phylogenetic analyses from a near-comprehensive sampling of genera from Araliaceae. The seven samples of Neotropical Schefflera included in that study grouped together in a well supported clade (Plunkett et al. 2005). However, because the sampling in that study did not cover the morphological variation and geographical range of the Neotropical species of Schefflera, the
monophyly of this group has remained tentative. This group of species forms several centers of diversity in southern Central America and the West Indies, the Andes, the Guayana Shield, and the Brazilian Plateau (Frodin 1995). By expanding the sample set of ITS + trnL-trnF sequences from among the Neotropical species of Schefflera to include representatives from all five of Frodin’s subgeneric groups, we have been able to confirm the monophyly of these species as the Neotropical Schefflera clade (Fig. 231). Support for this clade was weak based on MP (BS = 58%) but much stronger in the ML and BI trees (BS = 84% and PP = 1, respectively). Moreover, no sample of Schefflera from the Neotropics falls outside the Neotropical Schefflera clade in any of the analyses.

Detailed discussions of inter-generic relationships in Araliaceae have been presented in detail elsewhere (Wen et al. 2001; Lowry et al. 2004; Plunkett et al. 2004, 2005). As Plunkett et al. (2005) indicated, the Neotropical Schefflera clade is part of the broader Asian Palmate clade of Araliaceae, but our data is less consistent with regard to the placement of the Neotropical Schefflera clade. Most separate analyses recovered a broad polytomy at the base of the Asian Palmate clade (trees not shown). In the BI tree, Neotropical Schefflera was left unresolved in a clade that includes all remaining Asian Palmate samples except Tetrapanax, Heteropanax and Asian Schefflera (PP = 0.55) (tree not shown). According to the combined MP analysis, the Neotropical Schefflera clade was weakly supported as sister to a clade including Tetrapanax, Heteropanax and Asian Schefflera (BS < 50%; Fig. 231) as in Plunkett et al. (2005).

Over three quarters of the species diversity of Schefflera s. lat. belongs to the Asian and Neotropical clades of this genus, and both of these are placed in the Asian Palmate clade of Araliaceae. Despite their close relationship in the Asian Palmate clade and their morphological similarity, species from the Neotropical and Asian clades of Schefflera are not direct sister-
groups. Instead, Asian *Schefflera* emerges as successively sister to *Heteropanax* and *Tetrapanax* in the combined MP analysis (Fig. 231; see also Plunkett et al. 2005). While these data could be used to support the union of the two largest *Schefflera* clades into a single, very speciose genus, that genus would also have to encompass both *Heteropanax* and *Tetrapanax*. We do not, however, envision this treatment because *Heteropanax* and *Tetrapanax* are so morphologically distinct from *Schefflera* especially in their leaf morphologies (e.g., 2–4-pinnately compound in *Heteropanax* and palmately lobed in *Tetrapanax*).

Despite this, there are many cases of morphological similarities and even convergence between the Neotropical and Asian clades of *Schefflera*, and no characters or sets of characters have been identified to distinguish these two clades. For instance, both pollen (Tseng and Shoup 1978) and wood anatomical (Oskolski 1995) studies have failed to provide clear-cut differences between species belonging to these clades. Moreover, multiple cases of morphological convergence among Asian and Neotropical species of the genus have been reported (Frodin 1975; Frodin and Govaerts 2003). Examples of this include the hemi-epiphytic habit and calyptrate corollas common to many species from both the of Neotropical “Sciodaphyllum” group and the Asian “Brassaia” group, and the presence of capitulate inflorescence units in several groups from both clades (Frodin 1975). In addition, bundle-compound leaves (having two or more concentric whorls of palmately arranged leaflets) and palmate leaves with pinnate leaflets have been reported in the Neotropical “Didymopanax” group and in species of the “Sciodaphyllum” group from both Asia and the Neotropics (Frodin and Govaerts, 2003; Fiaschi et al. 2008). Some of these features have also been reported from other unrelated clades of *Schefflera*, including bundle-compound leaves in the Pacific clade (P.P. Lowry, pers. comm.),
and a epiphytic habit in some species from the “Sciodaphyllum” group of African *Schefflera* (Bamps 1974).

**Phylogenetic Relationships in the Neotropical *Schefflera* Clade** — The Neotropical species of *Schefflera* appear as a weakly to strongly supported clade on the basis of the family-wide data sets (BS 58–84%; PP = 1). Despite the fact that basal relationships are weakly supported (Fig. 231), the four major clades of Neotropical *Schefflera* were recovered. Among these clades, a sister group relationship between two subclades of mostly Eastern Andean species was recovered (BS = 88–94%; PP = 1). This clade is referred to informally as the Eastern Andean clade (Fig. 231), and includes geographically coherent subclades that correspond closely to two of Frodin’s (1995) subgeneric groups, namely the Guayanan subclade (≈ Frodin’s Crepinella) (BS = 95–96%; PP = 1) and the Brazilian subclade (≈ Frodin’s Didymopanax) (BS = 100%; PP = 1). The three remaining clades (Calyptrate, Jahni, and Tremula clades) were also well supported, but their relationships with the Eastern Andean clade and with each other were weakly supported in the Araliaceae data set (Fig. 231).

Analyses based on an increased sample set of Neotropical *Schefflera* using ITS and ETS sequence data agrees with the overall ITS + *trnL-trnF* topology, but provides a more detailed picture of relationships. The same four major clades (Calyptrate, Tremula, Jahni, and Eastern Andean clades) were consistently recovered in both individual and combined data sets (Figs. 232–234), and are discussed individually below. Whenever possible, these clades are divided further into additional subclades characterized by unique features of their morphologies and/or geographies.
THE CALYPTRATE CLADE — This clade was recovered with strong support from analyses based on individual and combined ITS and ETS data sets (BS = 94–100%; PP = 1). The Calyptrate clade includes nearly all of the species sampled from the Sciodaphyllum subgeneric group (Plunkett et al. 2005), excepting only S. tremula (see below). The species of this clade are largely native to southern Central America (Costa Rica and Panama) and the Andes from Venezuela to Bolivia, but there are also outliers from Jamaica (e.g., S. sciodaphyllum) and the Guayana Shield (e.g., S. quinquestylorum). Although this group is difficult to characterize and possesses no unique apomorphies, all of its species have the petals fused into a calyptrate corolla. This character, however, may be difficult to observe in herbarium material, because the petals are always caducous.

Phylogenetic analyses of the combined data set provided strong support for further dividing the Calyptrate clade into two subclades: the Ligulate subclade (BS = 80–89%; PP = 1) and the Caribbean subclade (BS = 91%; PP = 1) (Figs. 3–4). These two clades were also recovered, although with lower support, in the MP analyses of the individual data sets (Fig. 232), and are discussed in greater detail below.

The Ligulate Subclade — Frodin’s Sciodaphyllum group was envisioned as morphologically generalized and geographically widespread, but molecular data have proved that this subgeneric group is polyphyletic (Plunkett et al. 2005). Most species of the Sciodaphyllum group sampled from the Neotropics appeared together in a single subclade (BS ≤ 50–89; PP = 0.6–1) of the Calyptrate clade in trees based on both separate and combined analyses (Figs. 232–234). This subclade was characterized by a basal polytomy or poorly supported relationships in most analyses, and includes several species with ligulate stipules. Based on morphological characters, we predict that the majority of Neotropical species assigned
to the Sciodaphyllum group will likely belong to this subclade. The only probable exceptions are
the remaining species of Frodin’s Attenuatae infrageneric group (Plunkett et al. 2005) and the ~
16 species of Cheilodromi (Frodin 1993), which are expected to group in the Caribbean subclade
because of the presence of similar morphologies (discussed below).

The Ligulate subclade includes several small and well-supported clades, such as *S.
diplodactyla* + *S. sciodaphyllum* (BS = 81–87%; PP = 1), *S. minutiflora* + *S. sandiana* (BS =
100%; PP = 1), and *S. aff. lilacina* + *S. cf. violacea* (BS = 98–100%; PP = 1). However, the close
relationships of these species must be viewed with some caution because our taxonomic and
character sampling from Sciodaphyllum remains far from comprehensive. In addition, there are
no evident morphological features to distinguish these clades from the remaining species in the
Ligulate subclade.

As discussed above, the composition of the Calyptrate clade agrees in part with the
Neotropical species assigned to Frodin’s (1995) Sciodaphyllum group. Two exceptions to this
pattern were *S. tremula* (see below) and *S. aff. paniculitomentosa* (*Repizzo & Calle* 250), the
only accession sampled from the Cotylanthes group. This species was nested within the Ligulate
subclade based on both the separate and combined analyses of the ETS and ITS data sets (Figs.
232–234). This placement is not unexpected given that all of the features used to define
Cotylanthes such as the few-branched inflorescences, the racemously arranged umbellules with a
few relatively large flowers, the 5 to 10-locular ovaries, and the entirely free styles may also be
found among representatives of Sciodaphyllum (e.g., subgroup “Ternatae”) and Frodin (1995)
suggested that the group “comes near to parts of Sciodaphyllum.” For instance, both *S. brenesii*
and *S. epiphytica* [which were closely related to *S. aff. paniculitomentosa* in the ITS and
combined analyses (Figs. 232–234)] belong to the Ternatae subgroup of Sciodaphyllum (Frodin
Moreover, the geographic distribution of species from Cotylanthes ranges from southern Central America to northern Ecuador (with a minor eastern extension in the Venezuelan coastal mountain range), and is nested completely within the geographic range of the Sciodaphyllum group. Additional sampling of species from the Cotylanthes group would be required to test whether their features have evolved independently or if they were the result of a single evolutionary event.

The Caribbean Subclade — Although the Caribbean subclade received strong support in the analyses of the combined data set (BS = 91%, PP = 1, Figs. 233–234), it was recovered with lower support based on the individual data sets (BS = 58–77%, PP = 0.89–1). Among the species included in this clade are representatives of Frodin’s (1995) circum-Caribbean “Attenuatae” group (e.g., *S. glabrata* and *S. rodriguesiana*). It also included the closely related — and perhaps indistinguishable — *S. patula* and *S. stilpnophylla* from the sandstone plateaus of the Peruvian-Ecuadorian border (Frodin and Govaerts 2003). The inclusion of these two Andean species (from Frodin’s “Patulae” group; Plunkett et al. 2005) in an otherwise entirely circum-Caribbean group in the Caribbean subclade) has not been previously suggested. Despite differences in carpel number (five in “Patulae” vs. two in “Attenuatae”), their overall morphologies seem to agree with this placement (e.g., both groups comprise glabrous plants with calyptrate corollas and more or less well developed stylar columns). Frodin (1995) also suggested that species from the mainly Guayan “Cheilocromi” group might be related to “Attenuatae”, but we were unable to test this hypothesis due to the lack of samples from “Cheilocromi” available for this study.

Species belonging to the Caribbean subclade are almost always terrestrial plants (sometimes with potential for hemi-epiphytism, as in *S. rodriguesiana*) and usually lack an indumentum. They also have leaflets with veins sometimes ending at the margin
(craspedodromous or semi-craspedodromous venation), flowers usually grouped in umbellules (but capitulae in *S. cartagoensis* M. & J. Cannon), calyptrate petals, and styles united to form a column or separated only at the apex. These morphological features mostly also characterize *S. tremula*, a species that Frodin placed in the “Attenuatae” group, but that seems to be unrelated to the remaining species of the Calyptrate clade on the basis of molecular data (Figs. 231–234).

**THE TREMULA CLADE** — The placement of the Hispaniolan endemic *S. tremula* as sister to the Puerto Rican *S. gleasonii* in a clade on their own (Figs. 232–234), and unrelated to the remaining species of the Caribbean subclade, suggests that Frodin’s (1995) “Attenuatae” group is paraphyletic. This finding is corroborated by pollen evidence, which also points to the exclusion of *S. tremula* from “Attenuatae” (Fiaschi et al., in press). In fact, some morphological similarities between *S. tremula* and the remaining species of “Attenuatae” [e.g., *S. attenuata* (Sw.) Frodin and *S. glabrata*] could be the result of convergence due to similarities in the environmental conditions where these species are found. For example, the shared presence of a “poplar-like” leaflet morphology, with long petiolules and a caudate leaf apex in these species could be associated with the windy, high-elevation moist forests where they grow (Frodin 1989). Independent derivation of these features is also known elsewhere in Neotropical species of *Schefflera* (e.g., *S. succinea* Frodin & Fiaschi and *S. tremuloidea* Maguire, Steyerm. & Frodin) and in other genera of Araliaceae, such as *Cheirodendron* [C. platyphyllum (Hook. & Arn.) Seem.] and *Cussonia* (*C. holstii* Harms ex Engl.).

Although the Tremula clade was well supported in the combined analyses (BS = 83–92%; PP = 1), the sister group relationship between *S. tremula* and *S. gleasonii* was unexpected based on morphological grounds, and this was reflected by their placement in different groups of
Neotropical *Schefflera* (Frodin 1995; Plunkett et al. 2005). However, both species are geographically restricted to adjacent islands in the Greater Antilles (*S. tremula* in Hispaniola and *S. gleasonii* in Puerto Rico) and, despite their distinct leaf morphologies, they share inflorescences with branches arranged in whorls, and fruits with free or basally connate and recurved styles.

**THE JAHNII CLADE —** This small clade was consistently recovered as one of the four main clades of Neotropical *Schefflera* in the present study (BS = 67–100%; PP = 1; Figs. 232–234). The Jahnii clade appeared as part of a basal polytomy in Neotropical *Schefflera* (Fig. 232), or poorly supported as sister to the Tremula clade (BS = 55%, Fig. 233), or to a clade including both the Calyptrate and the Eastern Andean clades (BS ≤ 50%; PP ≤ 0.85, Fig. 234).

The Jahnii clade includes two undescribed species presumably related to *S. jahnii* (Harms) Frodin, both of which belong to the Cephalopanax group of Neotropical *Schefflera* (Frodin 1995). These two species are found in high elevation areas (above 2,000 m) across the northern Andes, and are characterized by leaflets where the midrib terminates before it reaches the blade apex, and lateral veins that curve before reaching the margin. The inflorescences are stout, bearing flowers grouped in racemosely arranged capitulae along the main inflorescence axis. The flowers have an obscure calyx rim, free petals, stamens with the filaments longer than the anthers, a bicarpellate ovary, and styles united into a column (Frodin 1995). In future studies, the inclusion of additional, presumably related species, such as the Venezuelan endemics *S. cuatrecasiana* and *S. jahnii*, will be critical to test the extent to which the Jahnii clade agrees with the Cephalopanax group of Frodin (1995) and Plunkett et al. (2005).
THE EASTERN ANDEAN CLADE (EAC) — Analyses of both Araliaceae and Neotropical data sets recovered a clade comprising mostly species of Schefflera east of the Andes (Figs. 233, 234). This Eastern Andean clade is well supported (BS = 75–100%; PP = 0.98–1) but difficult to characterize morphologically, especially because it includes species placed in two very distinctive subgeneric groups: Crepinella and Didymopanax (Frodin 1995). However, these plants do have some similarities, such as their terrestrial habits and short stipules, in contrast with the frequently epiphytic plants with elongate stipules found in most species of the Calyptrate clade. Each of these two groups are morphologically homogeneous, and correspond almost perfectly with the EAC subclades obtained from our analyses, here named the Guayanan (≈ Crepinella) and Brazilian (≈ Didymopanax) subclades (Figs. 233, 234).

The Guayanan Subclade — The Guayanan subclade received moderate to strong support in our phylogenetic analyses (BS = 60–95%; PP = 1, Figs. 232–234). This subclade included species endemic to the tepuis of the Guayana Shield (S. chimantensis subsp. rugosifolia and S. umbellata), as well as one species each from lowland Amazonia (S. spruceana), the sandstone plateaus of southern Ecuador and adjacent Peru (S. harmsii), and the Brazilian Atlantic rainforests (S. aff. varisiana). This same pattern of geographic distribution with most of the diversity centered in the Guayana Shield, but with outliers in the Andes and/or the Atlantic rainforests, has been reported for several other plant taxa, such as Gongylolepis (Asteraceae), Bonnetia (Bonnetiaceae), Caraipa (Clusiaceae), and Pagamea (Rubiaceae) (Berry and Riina 2005).

The Guayanan subclade agrees closely with Frodin’s (1995) Crepinella group, which comprises 35–40 species. This group is characterized mostly by terrestrial plants having leaflets with closely-spaced lateral veins separated by intersecondary veins, inflorescences with whorled
branches, flowers with free petals, and fruits with an often well developed stylar column. The monophyly of the Crepinella group, however, requires the exclusion of *S. gleasonii*, which seems to be more closely related to *S. tremula* than to remaining species of the group (discussed above). Given the morphological homogeneity within the Guayanalan clade (excluding *S. gleasonii*), and our representative sampling from across most of its geographic range, additional sampling from Frodin’s Crepinella group will probably strengthen the identity between Crepinella and this clade.

The Brazilian Subclade — This subclade received strong support from all molecular data sets (Figs. 231–234). Species from the Brazilian subclade occur mostly at low to mid-elevation areas of South America east of the Andes, especially in Brazil and southern Venezuela. These species show a relatively homogeneous morphology, and are distinct from the remaining species of Neotropical *Schefflera*. They are always terrestrial and have a distinctive sericeous indumentum, leaflets with well spaced secondary veins, variously branched inflorescences (but never entirely whorled), filaments that are usually shorter than the anthers, and styles that are usually free and recurved in fruit. Fourteen species in our sampling grouped in the Brazilian subclade, all of which are representatives of Frodin’s Didymopanax group (Frodin 1995; Plunkett et al. 2005). Most of the morphological and geographical variability within this group was represented in our sampling, and is exemplified by the 5-carpellate *S. decaphylla* and the 2-carpellate *S. umbrosa*, both from the Amazonian rainforests, plus several species from the savanna-like vegetation of the Brazilian Plateau (e.g., *S. cordata* and *S. burchellii*) and the Atlantic rainforests (e.g., *S. calva*, *S. capixaba*, and *S. grandigemma*).

Relationships among species of the Brazilian subclade differed slightly in the trees based on the separate and combined data sets. One clade that included species from the Atlantic
rainforests (*S. calva*, *S. capixaba*, *S. grandigemma*, *S. aff. longipetiolata*, and *S. ruschiana*) was sister to all remaining species of the group in trees based on ETS data, and the combined data set (BS = 65–95%; PP = 0.95–1; Figs. 232b, 233). By contrast, the tree based on ITS data did not show this same relationship, but instead suggested a poorly supported placement (BS = 55%) for these Atlantic rainforest species with *S. aurata* (also from the Atlantic forests) and the Amazonian *S. decaphylla* and *S. umbrosa* (Fig. 232a). These conflicting results indicate that further studies with an increased taxonomic sampling and additional markers should be carried out to evaluate relationships within the Brazilian subclade of Neotropical *Schefflera*.

**Comparison with Frodin’s Infrageneric Classification** — The most comprehensive infrageneric classification of Neotropical species of *Schefflera* was provided by Frodin (1995), and later updated by the same author as part of the study by Plunkett et al. (2005). When compared to more traditional classification systems of *Schefflera* (e.g. Harms 1894–1897; Viguier 1909; Hoo & Tseng 1965), Frodin’s proposal relies less heavily on features such as pedicel length, style number, and degree of style fusion, but makes an explicit effort to create geographically coherent groupings based both on vegetative and reproductive features. Initial attempts to classify the Neotropical species of *Schefflera* led Frodin to propose six morphologically distinct and geographically centered groups of species: Attenuatae, Cephaloanax, Cheilodromi, Cotylanthes, Crepinella, Didymopanax, plus a seventh group, Sciodaphyllum, representing a “generalized” or unspecialized morphology, with representatives also in the Paleotropics. In Frodin’s update of this system (Table 1 in Plunkett et al. 2005), minor modifications appeared for the Neotropical groups, such as the inclusion of Attenuatae and Cheilodromi as infrageneric groups within Sciodaphyllum. As it stands, most of the Neotropical...
Schefflera subgroups were defined narrowly and comprise just a few species (between 10 and 40), while the Sciodaphyllum group became increasingly larger and more heterogeneous, with 100–150 species from the Neotropics (plus about as many species from the Old World) (Plunkett et al. 2005).

Our phylogenetic study provides additional evidence for the monophyly of a few of Frodin’s subgroups of Neotropical Schefflera, such as Didymopanax and Crepinella (but requiring the exclusion of S. gleasonii). The Neotropical elements of the widespread and morphologically diverse Sciodaphyllum group is largely congruent with our Calyptrate clade, but requires the exclusion of S. tremula (see also Fiaschi et al., in press) and the inclusion of Cotylanthes to restore monophyly. The monophyly of Cotylanthes itself and Cephalopanax could not be addressed with our sampling, and should be tested in future studies.

Limitations and Future Directions — This study provides further support for the recognition of a Neotropical Schefflera clade based on phylogenetic analyses of molecular data (see also Plunkett et al. 2005) that includes all species of Schefflera native to the New World sampled to date. Our sampling of Schefflera from the Neotropics represents the taxonomic, morphological, and geographic breadth of this species group. Despite this, we have included only ca. 17% of the species diversity of Neotropical Schefflera, and thus, to test the relationships among and within the Neotropical Schefflera subclades, future studies should focus on including additional samples, especially from the Cephalopanax and Cotylanthes groups, as well as several infrageneric groups of Sciodaphyllum (such as Bejucosae and Cheilodromi). Moreover, the use of additional markers, both plastid and nuclear, would be desirable to provide increased resolution and branch support for the phylogenetic hypotheses presented here.
Despite these limitations, our focus on representing the taxonomic, morphological and geographic breadth of the New World species of *Schefflera* makes it very unlikely that the inclusion of additional samples from the Neotropics will uncover additional clades of *Schefflera* s. lat., or of other major clades within Neotropical *Schefflera*. As Plunkett et al. (2005) indicated for the Pacific clade of *Schefflera*, we suggest here that Frodin’s informal classification and our present results represent a good starting point for more intensive studies of subclades towards the ultimate goal of producing a natural classification of Neotropical *Schefflera*. 
Revised by the Didymopanax group of Neotropical *Schefflera* (Araliaceae)
(formatted for submission to *Annals of the Missouri Botanical Garden*)

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ABSTRACT

A taxonomic revision for the species belonging to the Didymopanax group of Neotropical Schefflera is provided here. This informal group is monophyletic and comprises 37 species, most of which are restricted to small areas of lowland to mid-elevation tropical regions across Brazil and adjacent southern Venezuela. Five names are placed in synonymy, and 26 lectotypes are chosen for both accepted (15) and synonymous (11) names. In addition, two new species are here described: Schefflera prancei Fiaschi & Plunkett and Schefflera pubicarpa Fiaschi & Plunkett. We also provide information on the geographic distribution and preferential habitats, diagnostic features, illustrations, maps, a list of examined material, and nomenclatural comments for each of the accepted species. A list with all examined specimens is also provided. Three poorly known taxa are discussed but not formally described; these taxa may deserve taxonomic recognition as additional collections become available.

Key words: Araliaceae, Didymopanax, neotropics, Schefflera, Sciodaphyllum, taxonomy

TAXONOMIC HISTORY

The name Didymopanax was established by Decaisne and Planchon (1854) to accommodate the Neotropical species of Araliaceae having palmately compound leaves (rarely unifoliolate) covered with a sericeous indumentum, panicles of hermaphroditic-flowered umbellules, flowers with a 5-denticulate calyx, free and valvate petals, short stamens, and fruits laterally compressed with 2 persistent styles. Their species list for this genus included 10 taxa, of which four were new [but not validly published due to lack of citation of type-materials (D. argyrophyllum, D. lucumoides, D. marginatum, and D. sericeum)], and six previously recognized
as species of *Panax* (*P. calvum* Cham., *P. chrysophyllum* Poep., *P. chrysophyllum* Vahl., *P. morototoni* Aubl., *P. parviflorum* Mart. et Zucc., and *P. speciosum* Willd.).

Based on Benthan’s (1867) description of *Didymopanax* Decne. & Planch., Seemann (1868) provided an updated list of species, indicating specimens for each of Decaisne and Planchon’s (1854) names. He had cast doubt on the distinctiveness among some of Decaisne and Planchon’s species, but added a few others based on their annotations at the Paris Museum [e.g., *D. calophyllus* Decne. & Planch. ex Seem., *D. claussenianus* Decne. & Planch. ex Marchal, and *D. glabratatus* (Kunth) Decne. & Planch. ex Marchal], as well as several of his own studies (e.g., *D. burchellii* Seem., and *D. gardneri* Seem.). Among the additions to *Didymopanax*, he included a new combination for the overlooked *P. macrocarpus* Cham. & Schltld. [= *D. macrocarpus* (Cham. & Schltld.) Seem.], and created *D. spruceanus* Seem.

Despite Seemann’s (1868) detailed description of *Didymopanax*, his circumscription of the genus considerably increased its morphological heterogeneity. A few unrelated species were included in the genus merely because they possessed bicarpellate ovaries, despite the fact that they did not entirely agree with the description he provided, particularly with regard to flowers with free petals and stamens shorter than the petals (Seemann, 1868). Thus, for example, *D. glabratatus* (= *S. glabrate*, Attenuatae group), with calyptrate petals, and *D. spruceanus* (= *S. spruceana*, Crepinella group), with stamens longer than the petals, were placed in *Didymopanax* (Seemann, 1868). In addition, he also suggested that “*Sciadophyllum rubiginosum* [= *Schefflera rufa* Frodin] is probably a species of *Didymopanax*” (Seemann, 1868), presumably due to the presence of a bicarpellate ovary.

The importance of carpel number as a taxonomic character for placement of Neotropical *Schefflera* species was evident throughout the 19th and early 20th centuries. Based exclusively on
carpel number, several species were accommodated either in *Didymopanax* (mostly bicarpellate) or *Sciodaphyllum* P.Browne (5 or more carpels), regardless of conflicting evidence. For instance, Marchal (1878) recognized both genera, but placed *Sciodaphyllum confusum* Marchal (currently placed in the informal Didymopanax group) and *S. japurense* Mart. et Zucc. ex Marchal (now referred to the informal Crepinella group) together because they share (4-)5(-6) carpels, even though neither fits the protologue of *Sciodaphyllum* by Browne (1756). Moreover, the same author followed Seemann (1868) by including in *Didymopanax* the bicarpellate *D. glabratu*, *D. spruceanus*, and the “true” *Sciodaphyllum* species *D. rubiginosus* Marchal.

During the following decades, the authors of most new species of *Didymopanax* relied on the presence of flowers with bicarpellate ovary as the main criteria for generic placement (Marchal, 1889; Taubert, 1893; Harms, 1894, 1931; Sampaio, 1916). This approach resulted in an extremely heterogeneous genus, which by the first half of the 20th century included several species now assigned to several different informa groups, including the Attenuatae [*D. attenuatus* (Sw.) Marchal, *D. glabratu* (Kunth) Decne. & Planch. ex Marchal, *D. pittier* Marchal ex T.Durand & Pittier, and *D. urbanianus* Marchal ex Urb.], Crepinella [*D. gleasonii* Britton & P.Wilson, *D. montanu* Gleason, and *D. spruceanus* Seem.], and Sciodaphyllum groups (*D. rubiginosu* Marchal). Remarkably, two otherwise very “Didymopanax-like” species having 5(-6)-carpells had consistently been excluded, namely *Sciodaphyllum confusum* Marchal [= *Schefflera confusa* (Marchal) Harms], and *Scid. decaphyllum* [= *Sch. decaphylla* (Seem.) Harms], both of which were at that time placed under *Schefflera* by Harms (1894). Surprisingly, forty years later the same author described a few five-carpellate species under *Didymopanax* (e.g., *D. allocotanthu* Harms), even after stating that the five-lobed fruits essentially contradicted its placement under this genus (Harms, 1931, p. 293).
During the first half of the 20th century, the delimitation of *Schefflera* was broadened to include two Neotropical genera (*Sciodaphyllum* and *Actinophyllum* Ruiz & Pav.) as well as several paleotropical elements, with the conservation of *Schefflera* J.R.Forst. & G.Forst. against the older name, *Sciodaphyllum* P.Browne (Smith, 1941). However, the bicarpellate Neotropical species were maintained as distinct and placed in *Didymopanax* (e.g., *D. ayuantepuiensis* Steyerm., *D. chimantensis* Steyerm., and *D. hitchcockii* Lesser & Maguire) (Lesser & Maguire, 1950; Steyermark, 1967), as were several paleotropical segregates, such as *Agalma* Miq., *Brassaia* Endl., *Dizygotheca* N.E.Br., and *Plerandra* A.Gray. In a global approach to *Schefflera* and related genera, Frodin (1975) pointed to the artificiality of maintaining several segregated genera based on a few highly variable characters, such as bracts number and size, carpel number, and pedicel length. Frodin disregarded the difference in carpel number between *Didymopanax* (mostly two) and *Schefflera* (five or more) in his search for a more natural classification system for the genus, and he suggested that *Didymopanax* should be considered as a synonym under *Schefflera* (Maguire et al., 1984; Frodin, 1989, 1993). This proposal was largely accepted in latter contributions to the taxonomy of the genus, as many newly described species of the former *Didymopanax* have been placed in *Schefflera* (e.g., Fiaschi, 2004; Fiaschi & Pirani, 2005a, 2005b; Fiaschi & Frodin, 2006; Fiaschi et al., 2008).

While studying the Neotropical species of *Schefflera*, Frodin (1989) noted that “*Didymopanax* as traditionally recognized is polyphyletic”, and recognized that most species of *Didymopanax* from the Caribbean Islands form a distinct group (“*S. attenuata* and allies”) from the mainly South American *Didymopanax*. This idea was later presented as part of an informal classification system for the Neotropical species of *Schefflera* (Frodin, 1993, 1995; Plunkett et al., 2005), which included a “Didymopanax group” that excluded *S. attenuata* (and presumably
related species), which were placed under their own group (Attenuatae; Frodin, 1995), or considered as part of the highly diverse and morphological heterogeneous Sciodaphyllum group (Plunkett et al., 2005). Other misplaced species from the genus *Didymopanax* were excluded from the Didymopanax group, and placed in the Crepinella group (e.g., *D. ayuantepuiensis* Steyerm., *D. chimantensis* Steyerm. & Maguire, and *D. hitchcockii* Lasser & Maguire) or elsewhere in Sciodaphyllum (e.g., *D. allocotanthus* and *D. nebularum* Harms). By contrast, the 5(6)-carpellate species *S. confusa* and *S. decaphylla* where for the first time grouped together with their bicarpellate putative relatives under the Didymopanax group.

The current circumscription of the Didymopanax group (Frodin, 1993, 1995) is accepted here as highly coherent morphologically and geographically, and this same group has been corroborated as monophyletic based on molecular evidence (see Chapter 2). The taxonomic revision presented here aims to assess species delimitations in this group. No attempt has been made to provide additional information for taxa with names in *Didymopanax* that do not belong to this group unless they have been erroneously listed as synonyms under any of the 37 species treated here.

**The Didymopanax Group (sensu Frodin, 1995)**

As delimited by Frodin (1995), the Didymopanax group comprises most species formerly described in the segregate genus *Didymopanax* Decne. & Planch., and excludes species that have been transferred to groups Crepinella and Sciodaphyllum (Frodin, 1995).

According to Frodin (1995), the Didymopanax group of *Schefflera* s.l. comprises about 40 species found mostly at low to mid-elevation areas in Brazil. These species share stipules with a bifid apex, the frequent presence of a sericeous indumentum, paniculate inflorescences, flowers
with free petals, stamens with the filaments usually shorter than the anthers, fruits with usually free and recurved styles, and pollen grains with a reticulate-heterobrochate sexine ornamentation. The most comprehensive taxonomic study on this group (Moura, 1983) covered 19 Brazilian species of the formerly recognized *Didymopanax*. Two of those, however, are currently placed in the Crepinella group [*D. rugosus* N.E.Br. = *S. chimantensis* (Steyerm. & Maguire) Maguire, Steyerm. & Frodin, and *D. spruceanus* Seem. = *S. spruceana* (Seem.) Maguire, Steyerm. & Frodin], and six of the remaining 17 are here considered as synonyms. Moreover, this study remains unpublished and is now badly outdated, as 19 new species have subsequently been added to the Didymopanax group (e.g., Maguire et al., 1984; Fiaschi, 2004; Fiaschi & Pirani, 2005a, 2005b; Fiaschi & Frodin, 2006; Fiaschi et al., 2008). More recently, Fiaschi and Pirani (2007) presented a taxonomic study of 21 southeastern Brazilian species of *Schefflera*, all but one of which (*S. aff. varisiana* Frodin, Crepinella) belong to the Didymopanax group. Contrary to Moura (1983), who have largely relied on herbarium samples, Fiaschi and Pirani (2007) carried out extensive fieldwork in poorly collected regions of eastern Brazil, revealing eight previously undescribed species of the Didymopanax group (Fiaschi 2004, Fiaschi & Pirani 2005a, 2005b, Fiaschi & Frodin 2006). That study, however, did not cover the diversity of species in the Amazonian forests or the western and northern areas of the Brazilian Cerrado, and included several species whose delimitation relied on only one (e.g., *S. botumirimensis*, *S. capixaba*) or a few samples (e.g., *S. fruticosa*, *S. grandigemma*, *S. ruschiana*). Moreover, these previous studies lacked nomenclatural comments for most of the accepted names.

The Didymopanax group of *Schefflera* now includes 37 species, most of which are found in forests associated with the Guayana Shield along the borders between Brazil, Venezuela, and Colômbia, and in the southeastern fringes of the Brazilian Plateau, mostly in the Espinhaço
Range in Minas Gerais and the coastal mountains of Rio de Janeiro and Espírito Santo states. Although twenty species of the Didymopanax group from eastern Brazil have already been treated taxonomically by Fiaschi & Pirani (2007), the remaining species are still very poorly known (but see Maguire et al., 1984; Frodin, 1997; Fiaschi et al., 2008). This is especially evident for species from northwestern South America, such as *S. dichotoma* Fiaschi & Frodin, *S. pimichinensis* Maguire, Steyermark & Frodin, *S. plurispicata* Maguire, Steyermark & Frodin, and *S. tamatamaensis* Maguire, Steyermark & Frodin, all of which are known from just a few collections.

Here we provide a first taxonomic revision of species from the Didymopanax group of Neotropical *Schefflera*, as delimited by Frodin (1995). This study includes original or previously published information on the geographic distribution, preferential habitats, diagnostic features, illustrations and nomenclatural comments for all species of the group. For taxonomic studies including species formerly described under *Didymopanax* that do not belong to our concept of the Didymopanax group, Cannon and Cannon (1989), Frodin (1989, 1997), and Frodin and Govaerts (2003) provide useful information.

**MATERIALS AND METHODS**

Materials from the following herbaria were analyzed [acronyms follow Holmgren et al. (1990)]: ALCB, BHCB, BM, BR, C, CEPEC, CESJ, CVRD, ESA, GFJP, HRCB, HUEFS, IAN, INPA, K, LE, M, MBM, MBML, MER, MERF, MG, MO, NY, P, PORT, R, RB, S, SP, SPF, UB, UEC, UPCB, US, VEN, VIES, W e WU. A complete list of examined materials is presented in the list of exsiccatae (see below). Selected materials representing the geographic range and
morphological variation of each species are included after the descriptions. Phenological phases are indicated as flowers (fl), fruits (fr), or sterile (st).

Species circumscriptions were based on the shared presence of a unique combination of morphological features (i.e., character states), following the taxonomic species concept (Davis & Heywood, 1963). Because many species of Didymopanax are known from just a few collections (5 of 37 spp. accounted for about 70% of our data-set entries), we avoided using characters known to be highly variable in well collected species (such as leaflet number and size, and persistence of indumentum) in circumscribing species known from only a few collections. This approach was employed in an attempt to minimize the recognition of species defined by a single character state.

Morphological-descriptive terminology follows Radford et al. (1974), with the exception of leaf venation terminology, which follows Hickey (1979). All measurements of vegetative features are from adult individuals. Unbranched plants without a trunk distinct from the crown were regarded as treelets. Branchlet diameter and leaf measurements were taken, whenever possible, from parts of the plant at least five or more nodes below the inflorescence (if terminal), or the apical meristem (if the inflorescence in pseudolateral). Stipule lengths were measured parallel to the corresponding petiole, and the numbers of secondary veins were based on median leaflets.

Inflorescence measurements were taken exclusively from mature inflorescences, defined as having at least fully developed flower buds. The “peduncle” was defined as the internode between the uppermost leaf and the lowest primary branch of the inflorescence, and the “rachis” as the same axis, but above the lowest inflorescence branch, extending to the terminal whorl of primary branches (Fig. 235). Thus, the “main axis” of the inflorescence refers to the peduncle
plus rachis. Inflorescence branches were regarded as primary, secondary, and so on, according to the branching order. The number of higher order inflorescence branches was counted directly, or estimated based the number of sterile bracts. Ultimate inflorescence units refer to the terminal units of the inflorescence (= flower clusters) (Fig. 235). The number of flowers per ultimate inflorescence unit was based on the distal-most terminal inflorescence units. The units were arbitrarily considered an umbellule when they had up to four sub-terminal accessory flowers (or sterile floral bracts), and a racemule terminating in umbel when the number of accessory flowers (or bracts) was greater than four. In like manner, the terms capitulum and spicule were used for units having sessile flowers. Flowers measurements were obtained from re-hydrated perfect flowers, unless stated that they were from staminate ones. Fruit measurements were based on dry material.

Geographic distribution maps were created using ArcView 9.3 (ESRI) to illustrate the full geographical range of each species. Whenever necessary, geographic coordinates were estimated from herbarium samples by using the following sites:

http://www.fallingrain.com/world/ (Global Gazeteer, version 2.1) and
http://www.ibge.gov.br/cidadesat/

RESULTS

Vegetative morphology

**Habit.** Species of the Didymopanax group of *Schefflera* range in habit from small (c. 1 m tall) and poorly branched treelets (e.g., *S. fruticosa* and *S. lucumoides*) to large trees reaching about 30 m tall (e.g., *S. decaphylla*, *S. morototoni*, and *S. quinquecarinata*). Regardless of size,
most species of Didymopanax are usually sparsely branched, and sometimes branches are lacking entirely (e.g., *S. capixaba*, *S. ciliatifolia*, *S. plurifolia*, and *S. racemifera*). In Didymopanax, many species have been referred to as shrubby, but they always lack basal branches due to a modular growth, and branching (if present) begins after the individuals become reproductively mature. For this reason, we applied the term “treelet” for plants usually lacking branches and reaching up to 8 m tall, and “trees” for plants that are usually branched and taller than 8 m.

The growth patterns exemplified by species of the Didymopanax group follow two of the models characteristic of tropical trees proposed by Hallé et al. (1978) (see also Bell, 2008), referred to as the Leeuwenberg and Chamberlain models. According to the Leeuwenberg model, the first branching occurs after the individual attains reproductive maturity when two (or more) axillary buds develop to replace a terminal bud, that has developed into an inflorescence. Like the original axis, the newly formed branches are also monopodial and monocarpic. This model is characteristic of most species of Didymopanax, and can be seen both in large trees and small treelets (e.g., *S. glaziovii*, *S. vinosa*). The Chamberlain model is similar to Leeuwenberg except that a single axillary bud develops into a new branch to replace the growth axis of the plant. The inflorescence is thus displaced to a pseudolateral position, giving the appearance of an unbranched individual (e.g., *S. longipetiolata* and *S. capixaba*) (see Fiaschi & Pirani, 2007, Fig. 2). In the Didymopanax group, these two models of growth are not mutually exclusive, and different branching patterns following both the Leeuwenberg and Chamberlain models may appear simultaneously on the same individual.
Leaves. Most species of the Didymopanax group have palmately compound leaves, the only exception being *S. lucumoides*, which has unifoliolate leaves (Fig. 244J). In *S. plurifolia*, the leaves are palmately compound and each leaflet is further pinnately compound (Fig. 242H), resulting in twice-compound leaves. In most species, the leaves are usually clustered at the end of each branchlets or stem, but they are sometimes separated by internodes greater than 1 cm long (e.g., *S. distractiflora* and *S. plurifolia*). Leaf size varies greatly in the Didymopanax group and the leaves are often larger in younger individuals, especially in the arborescent species.

Leaf bases are stipulate, and the stipules can vary from very small and almost indistinct to large (up to c. 4 cm long), sometimes almost encircling the stem (e.g., *S. capixaba*, *S. ciliatifolia* and *S. plurifolia*). The stipule apex is usually bifid, sometimes forming well developed apical lobes (Figs. 241C, I, 242C). Petiole lengths range from less than 5 cm (e.g., *S. burchellii*, *S. fruticosa* and *S. lucumoides*) up to more than 80 cm (e.g., in *S. confusa*, *S. morototoni*, and *S. umbrosa*). The petioles are usually cylindrical, striate longitudinally, and slightly thickened at the base. In dry material, there is sometimes a constriction at the petiole base and apex, which is especially evident in *S. ciliatifolia*, *S. plurifolia*, and *S. umbrosa*.

Most species of the Didymopanax group have leaflets arranged in one whorl of three to 14. The median leaflet is always longer than the lateral ones, which are progressively smaller toward the base. In *S. confusa*, *S. prancei*, and some *S. decaphylla*, there are one or two additional concentric whorls of leaflets, and the total number of leaflets per leaf may be as numerous as 25 (in *S. prancei*) or 33 (in *S. confusa*). In these cases, leaflets from the inner (uppermost) whorls are smaller, and have shorter petiolules than those from the outer, lower whorl (Figs. 243A, K, L). In some cases, the basal leaflets differ slightly in shape from the median leaflet, as observed in *S. prancei* (Figs. 243K, L) and *S. umbrosa* (Fiaschi et al., 2008).
The petioles of young leaves are usually ascending, but become horizontal upon maturity. The mature leaflets can be held ascending (e.g., *S. futicosa* and *S. vinosa*, Figs. 244F, N), horizontally (most species) or slightly deflexed (e.g., *S. botumirimensis*, *S. succinea*), and the blades are either plane or conduplicate (e.g., *S. botumirimensis*, *S. glaziovii*). Leaflet blades vary from membranous (in *S. ciliatifolia*, *S. longipetiolata*, *S. plurifolia*, and *S. racemifera*) to strongly coriaceous (e.g., *S. macrocarpa* and *S. malmei*). The young leaves are entirely covered with trichomes, but these typically become restricted to the abaxial surface as the blades mature.

Two main indumentum types have been observed in the Didymopanax group: sericeous (in most species) and villous (in *S. macrocarpa*, *S. malmei*, and *S. villosissima*). The trichomes are mostly malpighiaceous and loosely attached to the epidermis. In *S. ciliatifolia*, the adaxial surface is sparsely covered with hispid trichomes, while the abaxial surface is glabrous. Most species have leaflets with persistent indumentum on the abaxial surface, while in others (e.g., *S. capixaba*, *S. confusa*, *S. decaphylla*, *S. longipetiolata*, and *S. succinea*) the leaflets are glabrescent. The persistence of the indumentum on the abaxial surface of the leaflets has been used to distinguish *S. angustissima* from *S. conspicua* and *S. navarroí*, as well as *S. calva*, *S. clausseniana*, *S. pachycarpa*, and *S. regnelliana* from one another (Moura, 1983; Frodin & Govaerts, 2003). Despite the utility of this feature in characterizing some species, we agree with Fiaschi and Pirani (2007) that a taxonomic distinction based solely on indumentum persistence may result in poor species circumscriptions.

The leaflet petiolules are usually compressed laterally, and sometimes adaxially canaliculate. In *S. succinea*, there is an articulation at the distal point of the petiolule, close to blade base. In other cases, the petiolules are indistinct from the blades due to the attenuation of the blade base [e.g., *S. fruticosa* (Fig. 244G), *S. malmei* (Fig. 248E), and *S. vinosa* (Fig. 244O)].
Blade shapes, bases, and apices are highly variable among species of the Didymopanax group, and provide reliable characters for species identification. The margins are usually entire, but very shallowly lobed blades are found in *S. tamatamaensis* and *S. umbrosa*, and in *S. umbrosa* the blades can also sometimes be trilobed (Fig. 242N). A ciliate margin is typical of *S. ciliatifolia*, while in *S. longipetiolata*, *S. racemifera*, and juvenile forms of *S. angustissima*, *S. calva*, and *S. morototoni* a few minute teeth are sometimes observed at the distal half of the blade. Strongly revolute margins may be observed in *S. burchellii*, *S. distractiflora*, *S. macrocarpa*, and (sometimes) *S. vinosa*.

Leaflet venation in species of the Didymopanax group is brochidodromous, but the secondary veins become thinner distally, resulting in a situation resembling the eucamptodromous pattern (Hickey, 1979). Moreover, the common presence of a dense indumentum on the undersurface of the blades makes it difficult to visualize the venation pattern in some species, such as *S. macrocarpa*, *S. malmei*, and *S. villosissima*. The primary vein (midrib) is sometimes prominent adaxially, and both main and secondary veins are prominent abaxially.

**Reproductive morphology**

**Inflorescence structure.** The inflorescences of species in the Didymopanax group are always ontogenetically terminal, but they may become pseudolateral due to the early development of one or more lateral branches. Inflorescence structure is extremely variable among and within species (Moura, 1983), but always follows a basic plan including a main axis of determinate growth consisting of a peduncle and a rachis (Fig. 235), along which usually two or more primary branches are spirally arranged. The main axis ranges from indistinct (Figs.
235D, 6D) to elongate (e.g., Figs. 239H, 244N, 251H). The primary branches are usually further
divided into higher order secondary branches, which in turn may bear tertiary branches, and so
on (Fig. 235B–F). Most species of the Didymopanax group have flowers grouped in secondary
branches along the primary ones. In S. plurifolia and S. racemifera, the flowers are arranged
along the primary branches (Fig. 235A), while in S. morototoni and some S. burchellii and S.
decaphylla, they are mostly grouped in tertiary (or even quaternary) branches (Figs. 235E, F).

The proximal branches of the inflorescence are sometimes longer and bear a terminal
whorl of higher order branches, while the distal branches are shorter and terminate in one
umbellule (Fig. 235G). Ultimate inflorescence units distally arranged in the inflorescence
branches have a higher number of perfect flowers than the lateral units arranged along the same
branch. For this reason, most fruits of species in the Didymopanax group are found along the
terminal portions of the infructescences, and the fruiting branches often become patent or
pendent. The ultimate inflorescence units (clusters of flowers) are usually umbellules, but the
flowers may be arranged in racemules that terminate in an umbel (e.g., S. cordata, S.
distractiflora, S. plurifolia, S. racemifera, S. umbrosa), spicules (S. plurispicata), or capitula (S.
villosissima). The distinction between umbellules and racemules terminating in umbel is
arbitrary, as in some cases it is common to observe a few accessory lateral flowers attached
below the terminal umbellule. For this reason, we defined as racemules terminating in umbel
those cases where there was five or more accessory lateral flowers (see above).

**Reproductive system.** All species of the Didymopanax group appear to be
andromonoecious, having both perfect (bisexual) and staminate (male) flowers borne on the
same individual. There is no clear spatial separation between these two floral types in the
Didymopanax group, but staminate flowers tend to be grouped in higher order lateral branches and perfect flowers in terminal branches (Figs. 235B, D–G). In the inflorescence units with both perfect and staminate flowers, the perfect flowers are always central (if the units are umbellules) or distal (if racemules terminating in an umbel) relative to the staminate ones. Fiaschi and Frodin (2006) and Fiaschi and Pirani (2007) suggested that *S. longipetiolata* and *S. racemifera* might be androdioecious, based on the presence of either perfect or staminate flowers. This hypothesis remains to be tested, and the apparent androdioecy may merely be an artifact of specimens where one floral type was not fully developed.

Temporally, the species of the Didymopanax group appear to follow the duodichogamous system of andromonoecious species of New Caledonian Araliaceae (Schlessman et al., 1990, 2001), where pollen presentation from perfect flowers is followed by stigma receptivity in the same flowers, and then by a second period of pollen presentation by the staminate flowers. In *S. plurifolia*, duodichogamy seems to be expressed in an alternative way. Floral maturation is acropetal, with the first period of pollen presentation (staminate flowers) followed by a second period of pollen and stigma presentation (protandrous perfect flowers).

**Flower morphology.** Staminate flowers differ from perfect ones in having an abortive ovary, and sometimes very reduced or vestigial styles (e.g., *S. confusa, S. decaphylla, and S. quinquecarinata*). Perfect flowers have regular-sized anthers and pollen grains.

Flowers of the Didymopanax group are epigynous. The calyx is a low rim that covers the insertion of the petals and stamens. The calyx lobes are inconspicuous and toothed (Fig. 247J) or more commonly acuminate to triangular-acuminate (e.g., Figs. 238J, 239E, 244P). The aestivation is valvate, and the petals are thickened. The adaxial surface of the petals is yellow,
greenish, or rarely white (in *S. longipetiolata* and *S. racemifera*) and glabrous, while the abaxial surface is sparsely to densely ochre or light brown to grayish-sericeous, or sometimes glabrescent (Figs. 239N, 251D).

The stamens are epipetalous and isomerous with the petals, and are inserted in grooves between the disc and the corolla. The filaments are usually shorter than the anthers (e.g., Fig. 238K, 240N, 244I), but can be sub-equal or longer than the anthers after anthesis (e.g., *S. angustissima* and *S. calva*; Figs. 237J, T). Due to the typically short filament size, the anthers are either erect (e.g., Figs. 238H, 239D, 241K, 242J) or somewhat reclined (in *S. confusa* and *S. decaphylla*; Figs. 243E, 245F). Anther position might facilitate insect pollination. The nectar reward is accumulated internally to the whorl of stamens, which may promote the transport of pollen by nectar-seeking insects.

The thecae vary from connate (most species) to apically free (e.g., *S. capixaba*) or entirely free above the connective insertion (e.g., *S. longipetiolata*, *S. pimichinensis*, *S. pubicarpa*, *S. racemifera*, and *S. tamatamaensis*). The apex of the anther varies from rounded or slightly retuse (Figs. 243F, 245G) to distinctly apiculate (Figs. 245D, 239D, 240F, 248J).

The gynoecium of Didymopanax consists of one inferior ovary of 2--5(6) carpels, each with one free or basally connate style confluent with the nectariferous disc, which can be plane (Figs. 237I, 241E) or distinctly concave (Figs. 241N, 244P). The styles are involute, their margins creating a more or less channeled adaxial surface when in flower, the adaxial surface becoming fully expanded when in fruit.

**Fruit morphology.** As in most of the Araliaceae, the fruits of the Didymopanax group are drupes. They can vary from laterally compressed (when derived from a bicarpellate ovary, as in
most species), to spheroid or ellipsoid when derived from a 4--6-carpellate ovary (in *S. confusa*, *S. decaphylla*, *S. prancei*, *S. quinquecarinata*, and some *S. angustissima*; Figs. 237L, 243H–I, M, 245I, N).

The styles and calyx rim are persistent on the fruit apex. The styles are usually free or basally connate and recurved (Figs. 238M, 239G, 242Q, 247L), but in *S. succinea*, the styles remain united into a column, and separate only at the stigmatic tips (Fig. 251L). The calyx rim usually retains a dense indumentum or sparsely arranged trichomes, but it can sometimes become glabrous on mature drupes, as in *S. ciliatifolia* and *S. succinea*.

The pericarp can be very fleshy or reduced to a thin layer surrounding the pyrenes, as in *S. longipetiolata*, *S. plurifolia*, and *S. racemifera*. A few curved lines (presumably schizogenous secretory cannals) can sometimes be seen running vertically from fruit base to apex (Figs. 238E, 239L, 241L, 242G, 251L). The 2--6 pyrenes are usually flattened laterally and smooth (but swollen and irregularly crested in *S. tamatamaensis*), with a cartilaginous or crustaceous to indurate texture.

**Palynology.** Information on the pollen of the Didymopanax group has been provided by Salgado-Labouriau (1973), Tseng and Shoup (1978), Maguire et al. (1984), Melhem and Bissa (1985), Pire (1989), and Fiaschi et al. (2008; in press). Pollen morphology is very homogeneous in Didymopanax (see Type 1 in Fiaschi et al., in press). The pollen grains are small to medium in size; the shape is suboblate to oblate-spheroidal, or rarely prolate-spheroidal; the amb is triangular, sub-triangular or sub-circular, angulaperturate; there are three colporate apertures; the ectoapertures are long and narrow or widened at the mid-portion, sometimes enlarged at the poles, with or without margo; the endoapertures are lalongate, usually with diffuse lateral
margins; fastigia and costae are present; the exine is semitectate, with tectum reticulate-
heterobrochate, sometimes with microreticulate areas; the muri are plane, sinuous, and
sometimes scarcely perforate; the columellae are fused laterally in cylindrical units (Shoup &
Tseng, 1977; Tseng & Shoup, 1978), and the nexine is thinner than the sexine (but see Fiaschi et
al., 2008).

Geographic distribution

The Didymopanax group is almost entirely Neotropical, with just a few species (S.
angustissima, S. calva, and S. vinosa) extending into subtropical areas of southern Brazil,
southeastern Paraguay and northeastern Argentina (Fig. 236). All but one species (S. morototoni)
are restricted to South America east of the Andes. The most widespread species is S. morototoni,
which ranges from southern Mexico to tropical South America and throughout the West Indies,
absent only from very dry habitats, such as the Brazilian Caatinga, the Chaco, and the Caribbean
coast of Colombia and Venezuela (Fig. 254G). Other widespread species are S. burchellii (Fig.
252D), S. distractiflora (Fig. 253E), S. macrocarpa (Fig. 254E), and S. vinosa (Fig. 256E) in the
Brazilian Cerrado, S. angustissima (Fig. 252A) and S. calva (Fig. 252E) in the Atlantic
rainforests, S. confusa (Fig. 253A) restricted to western Amazonia, and S. decaphylla (Fig.
253C) from northern Amazonia. Most of the remaining species are known from small regions
south of the Guayana Highlands, along the border of Brazil, eastern Colombia, and southern
Venezuela (e.g., S. dichotoma, S. pimichinensis, S. plurispicata, and S. tamatamaensis), and in
the southeastern fringes of the Brazilian Plateau, either in the Espinhaço Range of Minas Gerais
state (e.g., S. botumirimensis, S. fruticosa, S. gardneri, and S. lucumoides), or in the coastal
mountains of Rio de Janeiro (*S. succinea*) and Espírito Santo states (e.g., *S. capixaba*, *S. grandigemma*, and *S. kollmannii*).

From the species of Didymopanax found in the Cerrado, the high level of narrow endemism (7 of 14 spp., or 50%) in the *campos rupestres* along the Espinhaço Range at Minas Gerais state is remarkable (Fiaschi & Pirani, 2008). In addition, the distribution of some of the remaining species from open physiognomies seem to corroborate the floristic provinces detected by Ratter et al. (1996, 2006) in the Cerrado. Examples are provided by *Schefflera distractiflora* and *S. malmei*, which are mostly restricted to western areas (Figs. 253E, 254F), and *S. burchellii*, which is found mostly in northern/northeastern areas (Fig. 252D). The separation of the Cerrado into western and eastern portions has been previously corroborated by distribution data from *Mimosa* (Simon & Proença, 2000) and *Andira* (Pennington, 2003), and as Pennington (2003, p. 36) suggested “these congruent patterns are suggestive of a common underlying historical factor”.

Among the Atlantic rainforest species of the Didymopanax group, most are found in submontane forests along the eastern fringes of the Brazilian Plateau. Of the 12 species reported from the Atlantic forests, six (50%) are endemic to elevations between 600 and 1800 m in the Espírito Santo and Rio de Janeiro states (Fiaschi & Pirani, 2008). The six remaining species are either more widespread in distribution, or restricted to lowland coastal areas. The geographic separation of a northern lowland species group (including *S. aurata* and *S. selloi*), and a southern (and mostly submontane) species group (including all Espírito Santo and Rio de Janeiro endemic species) corroborate previous hypotheses that the Atlantic forests are a biogeographic unit of composite nature, characterized by an historical separation in northern and southern portions
Fiaschi and Pirani (2008) indicated two centers of endemism for extra-Amazonian Brazilian species of *Schefflera*: the Espinhaço Range at Minas Gerais state and the submontane forests at Espírito Santo state. With the inclusion of the Amazonian species, an additional center of endemism can be recognized along the Upper Negro River in the borders between Brazil, Colômbia, and Venezuelan. This center of endemism (Imeri *sensu* Cracraft, 1985) includes four endemic species of the Didymopanax group (*S. dichotoma*, *S. pimichinensis*, *S. plurispicata*, and *S. tamatamaensis*), and comprises about 30% of the diversity of Amazonian species.

Most species of the Didymopanax group are found in mid-elevation areas of the Brazilian Shield, usually between 600--1200 m. However, a few species are restricted to *restingas* on recent depositional lowland areas along the Brazilian coast (e.g., *S. aurata* and *S. selloi*) or lowland areas of the Amazonian *terra-firme* (e.g., *S.ciliatifolia*, *S. decaphylla*, and *S. umbrosa*) or *campinarana* white-sand forests (e.g., *S. confusa*, *S. dichotoma*, and *S. pimichinensis*).

**TAXONOMIC TREATMENT**


**Didymopanax group (sensu Frodin 1995b)**

Sparsely branched *treelets* (less than 1 m) to *trees* up to c. 30 m tall. *Leaves* spirally arranged, usually densely grouped at the terminal portion of the branchlets (or stem, when
unbranched), but sometimes with internodes up to c. 5 cm long, the blade palmately-compound or unifoliolate (S. lucumoides). Stipules inconspicuous (e.g., S. fruticosa) to well developed (e.g., S. capixaba, Fig. 241C), the apex slightly to deeply bifid; leaflets usually arranged in one whorl, or rarely in 2--3 whorls (S. confusa and S. prancei) and then progressively shorter in the internal whorls, the petiolules unarticulated or with a distal articulation (S. succinea), the blades simple or rarely pinnately compound (S. plurifolia, Fig. 242H), sometimes very shallowly lobed or trilobed (as in some S. umbrosa, Fig. 242N). Venation brochidodromous or nearly so, sometimes obscure due to the dense abaxial indumentum; the secondary veins well spaced, curving toward the margin, sometimes separated by conspicuous intersecondary veins (e.g., S. dichotoma).

Inflorescences terminal or pseudolateral due to the early development of one or more axillary buds; main axis (peduncle plus rachis) absent or very short (e.g., S. ciliatifolia, Fig. 242A) to elongated (up to c. 40 cm long in S. distractiflora); number of branching orders 1--4; primary branches progressively smaller toward the apex, terminating in one inflorescence unit (e.g., S. fruticosa, Fig. 244F) or usually 2--13 higher order branches; tertiary and quaternary branches sometimes present; ultimate inflorescence units umbellules (most species), capitula (S. villosissima), racemules terminating in an umbel (e.g., S. plurifolia, S. racemifera, and S. umbrosa) or spicules (e.g., S. plurispicata), bearing mostly perfect flowers distally and centrally (when umbellules or capitula) or terminally (when racemules or spicules), and mostly of staminate flowers proximally. Reproductive system andromonoecious, each individual bearing both perfect and staminate flowers. Flowers with unarticulated pedicels; calyx rim with (4)5(6) triangular to acuminate teeth; petals thick, valvate, sericeous or glabrescent abaxially, the apex acute or acuminate; the filaments usually shorter than the anthers, more rarely sub-equal in length or longer in S. angustissima and S. calva (Fig. 237J, T); the anthers oblong, elliptic or
ovate, the apex acute, apiculate, rounded or retuse; thecae 2, the portion above the connective connate, apically free, or completely free; the disc more or less plane to distinctly concave, glabrous or pubescent; the styles 2(--6), sometimes pubescent, free or basally connate (most species), sometimes forming a column up to 1.5 mm long (in S. succinea, Fig. 251L), recurved in fruit. Drupes laterally compressed or (3--)5(6)-costate when dry, transversely ellipsoid, obloid, spheroid or broadly ellipsoid, sometimes broadly depressed ovoid (S. tamatamaensis), or depressed to broadly depressed-obovoid (S. publicarpa and S. villosissima), glabrescent to persistently covered with a sericeous indumentum (e.g., S. publicarpa, Fig. 250K); pyrenes 2--5(6), laterally flattened or swollen and irregularly crested (S. tamatamaensis), transversely semi-elliptic or semi-depressed obovate, cartilaginous, crustaceous or indurate.

Species from the Didymopanax group of Schefflera can be distinguished from all of the remaining Neotropical Schefflera species by a unique combination of features, such as the presence (at least in young leaves) of a sericeous or villous indumentum, leaves with a (usually) short and apically bifid stipule, paniculate inflorescences bearing both staminate and perfect flowers (andromonoecious reproductive system), flowers usually pedicellate, free petals, filaments usually shorter than the anthers, and drupes with usually free and recurved styles.

**KEY TO SPECIES OF THE DIDYMOPANAX GROUP OF SCHEFFLERA**

1a. Leaves unifoliolate ................................................................................................................. 20. *S. lucumoides*

1b. Leaves palmately compound.

   2a. Leaflets pinnately compound ......................................................................................... 25. *S. plurifolia*

   2b. Leaflets simple.

      3a. Flowers with 5--6-locular ovaries, drupes 5--6-costate when dry.
4a. Leaflets arranged in 2--3 concentric terminal whorls.

5a. Leaflets membranous, the apex caudate; drupes 15--16 x 13--16 mm ..............

.......................................................................................................................... 9. *S. confusa*

5b. Leaflets chartaceous to subcoriaceous, the apex rounded, obtuse, acute or acuminate; drupes 8--14 x 10--11.5 mm.

6a. Drupes 12.5--14 x 11--11.5 mm; leaflets 10--25, the blade persistently light brown to grayish-sericeous abaxially, the apex acuminate to cuspidate ........

.......................................................................................................................... 27. *S. prancei*

6b. Drupes 8--9 x 10--11 mm; leaflets 10--13, the blade glabrescent, sometimes minutely golden or light brown-sericeous abaxially, the apex usually obtuse to rounded, sometimes acute or acuminate ......................... 11. *S. decaphylla*

4b. Leaflets arranged in one terminal whorl.

7a. Inflorescence terminal; perfect flowers with styles less than 1 mm long; staminate flowers with reduced or vestigial styles; indumentum of light brown or ferrugineous trichomes.

8a. Inflorescence secondary branches mostly restricted to the distal half of the primary ones; leaflets blades light brown to ferrugineous-sericeous abaxially, the apex cuspidate; perfect flowers with pedicel up to c. 1.5 mm long, the styles glabrous ................................................................. 29. *S. quinquecarinata*

8b. Inflorescence secondary branches along the entire length of the primary ones; leaflets blades glabrescent abaxially, the apex usually rounded or obtuse (sometimes acute); perfect flowers with pedicel 5--13 mm long, the styles apically with trichomes ................................................................. 11. *S. decaphylla*
7b. Inflorescence pseudolateral; perfect flowers with styles c. 2 mm long; staminate flowers with well-developed styles; indumentum of ochre or yellowish trichomes ........................................................................................................ 1. *S. angustissima*

3b. Flowers with 2(--4) locular ovaries, drupes flattened laterally (rarely 3--4-costate when dry).

9a. Leaflets with the petiolule articulated distally; inflorescence branches mostly glabrous; tertiary branches usually arranged in two whorls; drupes with styles connate in column c. 1.5 mm long, separating only at the tips ........................................ 33. *S. succinea*

9b. Leaflets with the petiolule not articulated distally; inflorescence branches sparsely to densely pubescent, at least the higher-order ones (sometimes glabrescent in fruit); tertiary branches, if present, racemosely arranged; drupes with styles free or basally connate, recurved in fruits.

10a. Inflorescence terminal (sometimes appearing pseudolateral by time of fruit set).

Cerrado or Amazon rainforest species, except *S. aurata*, *S. selloi*, and some *S. motototoni*.

11a. Leaflet blades with marginal cilia ......................................................... 8. *S. ciliatifolia*

11b. Leaflet blades without marginal cilia.

12a. Leaflets blade with the apex acute, acuminate, cuspidate or caudate; apical extension always present.

13a. Flowers grouped in capitula or umbellules.

14a. Flowers in capitula ............................................................ 7. *S. cephalantha*

14b. Flowers in umbellules.
15a. Blade of median leaflet 3.5--11 x 0.8--5 cm, the petiolules 1--3.8 cm long; flowers with the disc and styles glabrous. Treelets up to 2 m tall, usually growing among rock outcrops in open areas (campos rupestres).

16a. Blade of leaflets up to two and a half times as long as wide ................................................................. 15. S. gardneri

16b. Blade of leaflets more than three times as long as wide.

17a. Inflorescence ochre to light brown-sericeous, fruiting branches becoming patent, the primary branches 2.5--13 cm long, the secondary ones 1--3 cm long; fruiting pedicels 4--8 mm long; leaflet blades with cuneate to attenuate base ..........

................................................................. 16. S. glaziovii

17b. Inflorescence glabrescent, pendent when fruiting, the primary branches 21.5--34 cm long, the secondary ones 4--15 cm long; fruiting pedicels 10--20 mm long; leaflet blades with the base usually rounded (subcordate), sometimes cuneate ..........

................................................................. 3. S. botumirimensis

15b. Blade of median leaflet 12--42 x (2.3--)5.5--20 cm, the petiolules 4--16 mm long; flowers with the disc and/or styles pubescent (glabrous in S. aurata). Treelets to large trees 3--25 m tall, growing in forests on sandy or clayey soils.

18a. Drupes 15--19 x 17.5--20 mm; perfect flowers with ovary c. 3 mm long, the disc and styles glabrous; young leaflets golden-sericeous abaxially ........................................ 2. S. aurata
18b. Drupes 4--13 x 7.5--16 mm (unknown in *S. dichotoma*); perfect flowers with ovary 1--2.5 mm long, the disc and styles pubescent; young leaflets light brown to ferrugineous-sericeous abaxially.

19a. Inflorescence primary branches bearing 2 terminal secondary branches; blade of median leaflet about two times as long as the petiolule; pedicels of staminate flowers distinctly shorter than those of perfect flowers from the same umbellule ..........................

........................................................................................................................................ 12. *S. dichotoma*

19b. Inflorescence primary branches bearing (2)3--6 terminal secondary branches; blade of median leaflet at least two and a half times as long as the petiolule; pedicels of perfect and staminate flowers from the same umbellule sub-equal in length.

20a. Inflorescences with tertiary branches; anthers with thecae connate above the connective insertion; petiole bases noticeably lenticellate ................... 23. *S. morototoni*

20b. Inflorescences without tertiary branches; anthers with thecae free above the connective insertion; petiole bases lacking lenticels.

21a. Terminal primary branches of the inflorescence less than half the length of the proximal ones, terminating in just one umbellule; secondary branches up to 1 cm long; leaflets with distinctive intersecondary veins ...................... 24. *S. pimichinensis*

21b. Terminal primary branches of the inflorescence almost as long as the proximal ones, terminating in (2)3--6 secondary branches 0.9--4 cm long; leaflets without distinctive intersecondary veins.

22a. Leaflets 4--7; inflorescence with secondary branches somewhat reflexed; drupes broadly depressed ovoid, the pyrenes semi broadly depressed-ovoid, with an irregularly sculptured surface ............................................. 34. *S. tamatamaensis*
22b. Leaflets 8--10; inflorescence with secondary branches ascending; drupes obloid or broadly depressed obovoid, the pyrenes semi oblate or semi widely depressed obovate, with a smooth surface ........................................... 28. *S. pubicarpa*

13b. Flowers grouped in spicules or racemules terminating in an umbel.

23a. Ultimate inflorescence units spicules, the flowers grouped along the entire length of the secondary branches; styles c. 0.5 mm long, with a few trichomes ..... 27. *S. plurispicata*

23b. Ultimate inflorescence units racemules terminating in umbel, the flowers mostly grouped along the distal half of the secondary branches; styles 1.4--2 mm long, glabrous.

24a. Stipules c. 3 cm long, the apical lobes c. 10 mm long; leaflet blades ochre to grayish-sericeous abaxially; median leaflet blade 9--18 cm wide, the margin very shallowly lobed to distinctly trilobed; petals 3.6--4.2 x 1.4--1.7 mm ...... 35. *S. umbrosa*

24b. Stipules up to c. 1.5 cm long, the apical lobes up to c. 3 mm; leaflet blades light brown to grayish-sericeous abaxially; median leaflet blade 2--9.5 mm wide, the margin entire; petals 2.2--3 x 1.1--1.5 mm ................................................................. 13. *S. distractiflora*

12b. Leaflet blades with the apex rounded, truncate, retuse or obtuse, rarely acute; apical extension usually absent or at most mucronate.

25a. Blade of leaflets with an attenuate base and thus the petiolules indistinct from the blade.

26a. Inflorescence included within the foliage, the proximal primary branches bearing 1--4 lateral secondary branches, terminating in just one umbellule ................. 14. *S. fruticosa*

26b. Inflorescence usually exceeding the foliage, the proximal primary branches bearing 8--51 secondary branches, terminating in 2--6 umbellules.

27a. Leaflet blades 8--27.5 x 2.6--10.2 cm, the undersurfaces ochre to grayish-villous .... .......................................................... 22. *S. malmei*
27b. Leaflets blades 3.5--14.5 x 1.2--4 cm, the undersurface light brown or ochre to grayish-sericeous ................................................................. 37. *S. vinosa*

25b. Blade of leaflets with a cuneate, obtuse or rounded base, the petiolules distinct from the blade.

28a. Petals glabrescent abaxially; coastal Brazilian *restingas* ......................... 33. *S. selloi*

28b. Petals sericeous abaxially; central Brazilian *cerrados* and *campos rupestres*.

29a. Leaflet blades villous abaxially.

30a. Perfect flowers with pedicel 1--8 mm long, staminate flowers either pedicellate or sessile; leaflet blades light brown or ochre to grayish-villous abaxially; widespread in the Brazilian “cerrados” ................................................................. 21. *S. macrocarpa*

30b. Both perfect and staminate sessile; leaflet blades densely ochre to grayish-villous abaxially; endemic to the Diamantina Plateau ..................... 36. *S. villosissima*

29b. Leaflet blades sericeous abaxially.

31a. Flowers grouped in umbellules; pedicels of fruits 9--14 mm long; branchlets usually with a corky bark ................................................................. 4. *S. burchellii*

31b. Flowers grouped in racemules terminating in an umbel; pedicels of fruits 2--5 mm long; branchlets without a corky bark ................................. 10. *S. cordata*

10b. Inflorescence clearly pseudolateral by anthesis (due to early development of an axillary bud). Atlantic rainforest species.

32a. Stipular apex entire or shortly bifid, the length of apical lobes less than half the basal portion; tall, branched trees or, if treelets, not flowering under the canopy.

33a. Young leaflets and flowers with a light brown or ferruginous indumentum; anthers about three or more times longer than the filaments (in open flowers).
34a. Leaflet blades usually less than three times longer than wide and about three times as long as the petiolules; light brown or ferrugineous-sericeous abaxially.

35a. Petals 2.2--2.7 x 1.1--1.3 mm, sparsely sericeous or glabrescent abaxially; filaments 0.3--0.4 mm long; anthers 1.4--1.5 x 0.7--1 mm; drupes 4.5--7 x 7--9 mm; leaflets 4--7; restinga forests .......................................................... 32. *S. selloi*

35b. Petals 4.6--5.2 x 2.2--2.9 mm, densely sericeous abaxially; filaments c. 1 mm long; anthers 3.1--3.2 x 1.3--1.6 mm; drupes 10--15 x 12--16 mm; leaflets 6--11; submontane forests.

36a. Inflorescences with tertiary branches; secondary branches 16--21; perfect flowers with pedicel 5--10 mm long ..................................................... 31. *S. ruschiana*

36b. Inflorescences without tertiary branches; secondary branches 8--14; perfect flowers with pedicel 2--3(--7) mm long ........................................... 17. *S. grandigemma*

34b. Leaflet blades about four times as long as wide and about four times as long as the petiolules; usually glabrescent abaxially ................................................. 18. *S. kollmannii*

33b. Young leaflets and flowers with an ochre to yellowish or whitish indumentum; stamens with anthers about as long or slightly longer than the filaments (in open flowers).

37a. Leaflet blades with a cuneate or attenuate (rarely obtuse or rounded) base, the mature ones usually ochre or yellowish to grayish-sericeous abaxially (sometimes glabrescent); corolla of mature floral buds sericeous; usually in rainforests east of the Serra do Mar mountain range ................................................................. 1. *S. angustissima*

37b. Leaflet blades with a rounded or truncate base, the mature ones glabrescent or sparsely grayish-sericeous abaxially; corolla of mature floral buds usually glabrescent,
contrasting with the sericeous hypanthium; usually in seasonally dry or gallery forests west of the Serra da Mantiqueira mountain range ............................................. 5. *S. calva*

32b. Stipular apex deeply bifid, the length of apical lobes more than half the basal portion; unbranched or sparsely-branched treelets, flowering under the forest canopy.

38a. Primary branches of the inflorescence 2, 92--97 cm long; flowers light brown-sericeous, the petals yellow-greenish, 4.1--5.2 x 1.8--2.5 mm, the stamens with anthers 2.6--3.2 x 1.6--1.8, the thecae connate above the connective insertion; drupes c. 11 x 14 mm ......................

............................................................................................................................... 6. *S. capixaba*

38b. Primary branches of the inflorescence 2--6, 5.5--33 cm long; flowers ochre-sericeous, the petals whitish, 2.2--2.8 x 0.7--1.2 mm, the stamens with anthers 1.5--2.1 x 0.5--0.8, the thecae free above the connective insertion; drupes 4.8--7 x 9.5--10.5 mm.

39a. Leaflets 7--11, the median blades 9--14 x 1.5--3.8 cm, narrowly elliptic or oblong; flowers grouped in umbels or racemes terminating in an umbel along the secondary branches; drupes with pedicel 3--7 mm long .............................................. 19. *S. longipetiolata*

39b. Leaflets (11-)12--14, the median blades 12--15 x 1.1--1.9 cm, linear to narrowly oblong; flowers grouped in racemes terminating in an umbel along the primary branches; drupes with pedicel 11--14 mm long ...................................................... 30. *S. racemifera*

The remaining two (Riedel & Langsdorff 739, and Glaziou 6558) are morphologically very similar to each other, both fitting the protologue. Because of this similarity, and the fact that Glaziou had several of his numbers added to samples collected by other people, including Riedel (Wurdack 1970), we are suspicious that Glaziou 6558 [K! (3 sheets), LE!, P! (3 sheets)] and Riedel & Langsdorff 739 (LE!) might represent duplicates of the same material. Moreover, several duplicates of what appears to be this same collection have been numbered under two additional of Riedel’s numbers: “1” (LE!), and “ß” [K!, LE! (3 sheets), P!], or left without number (NY!, 2 sheets). Figs. 237A–L and 252A (see also Fiaschi & Pirani, 2007; Fig. 11A–J).

*Didymopanax anomalus* Taub., Bot. Jahrb. Syst. 4: 511. 1893. *Schefflera anomala* (Taub.) Frodin in D. Frodin & R. Govaerts, World Checklist Bibliog. Araliaceae: 323. 2003. TYPE: Brazil, Rio de Janeiro, “Floresta de la Tijuca,” 19 Oct. 1880 (fl, fr), Glaziou 12031 [lectotype, P!, here designated; isolectotypes, F! (photo #3530), K!, P! (2 sheets), R!]. The specimen at B (photo at F!, #3530), used to describe the new species, was probably destroyed in 1943. Among the available duplicates, the one chosen as the lectotype is one of the three sheets at P, which bears an original label and has both flowers and fruits.

603 [G! (2 sheets)], respectively, both of which have Marchal’s annotation. The third, Riedel 1264, has not been annotated by Marchal, but fits well the short diagnosis (based on leaf features), and is the best preserved and distributed of the syntypes. For these reasons, it is here chosen as the lectotype.


*Vernacular names:* Canela-mandioca, mandioqueira, mandioqueiro, pau-mandioca, pau-de-mandioc.

*Trees or treelets* 3--20 m tall. *Branchlets* 6--13 mm diam., smooth or striate longitudinally, whitish to ochre-sericeous, glabrescent. *Leaves* palmately compound, clustered at the end of branchlets, the internodes up to c. 1 cm long. *Stipules* 4--10 mm long, whitish to ochre-sericeous or glabrescent abaxially, glabrous adaxially, apex entire or slightly bifid, the lobes up to c. 1.5 mm long; petiole 6.5--38 cm long, 1.3--4 mm diam., cylindrical, slightly to strongly striate longitudinally, glabrescent; *leaflet* 7--12, grouped in one whorl, held horizontally; the blade
plane, subchartaceous to chartaceous, the adaxial surface glabrous, the abaxial usually ochre-yellowish to grayish-sericeous, sometimes glabrescent. Median leaflet: petiolule 1--6.5 cm long, unarticulated, laterally compressed, canaliculate adaxially; the blade 9--25.5 x 2--6 cm, narrowly oblong or elliptic, symmetrical to falcate, the base cuneate to attenuate, rarely obtuse or rounded, the margin entire, smooth to slightly revolute, sometimes undulate, the apex acute to acuminate, the tip sometimes mucronate. Basal leaflets: petiolule 0.7--4 cm long, the blade 5.3--18 x 1.4--4.3 cm, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially, or only abaxially; secondary veins 8--15, impressed or prominent only abaxially; intersecondary veins absent; higher orders of venation sometimes conspicuous abaxially on mature leaflets. Inflorescence pseudolateral, initially erect, but pendent when fruiting, ochre or grayish-sericeous, glabrescent; peduncle absent or up to c. 1 cm long, rachis absent or up to c. 3.5 cm long; primary branches (2)3--7, of which 2--3 are terminal, 5.5--34 cm long (bracts c. 4 mm long), each bearing 9--31 secondary branches arranged racemosely (3--13 terminal), 1--13.5 cm long, bracts 1--2 mm long; tertiary branches, if present, 7--12, 0.8--4 cm long; ultimate inflorescence units umbellules, with 8--24 flowers, most of which are perfect, sometimes with a few intermixed staminate ones; floral bracts up to c. 1 mm long. Perfect flowers with pedicel 2--8 mm long; hypanthium ochre-sericeous, calyx rim with 5(6) triangular to acuminate teeth; petals 5(6), greenish, 2--3.5 x 1--1.8 mm, elliptic to triangular-ovate, sericeous abaxially, apex acute; filaments 0.6--1.3 mm long; anthers 0.9--2.3 x 0.8--1.4 mm, oblong or ovate, apex acute or apiculate, thecae connate above the connective insertion; ovary 1--2 mm long; disc glabrous; styles 2--3(--6), free or rarely half connate, c. 2 mm long, glabrous, recurved in fruit. Stamine flowers with pedicel 3--4 mm long; styles developed; otherwise similar to perfect ones. Drupes 7--12 x 11--15 mm, transversely ellipsoid, laterally
compressed or 3–6-costate when dry, glabrescent; pedicel 4--8 mm long; pyrenes 2--3(--6), 6--7 x 4--6 mm, flattened, transversely semi-elliptic, indurate.

This species is endemic to the Atlantic rainforests of coastal Brazil, especially east of the Serra do Mar mountain range, from the Serra dos Órgãos mountains (Rio de Janeiro state) to the coastal plain of Santa Catarina state. Several recent collections of the species have been gathered in the montane forests of the Chapada Diamantina and southern Bahia state (Amorim et al., in press), both located far north from the main distributional range of the species (Fig. 252A).

_Schefflera angustissima_ ranges in elevation from sea level to c. 1800 m. It has been collected with flowers throughout the year, and with fruits mostly from August to March.

_Schefflera angustissima_ is characterized by the presence of pseudolateral inflorescences and leaflets with the blade usually narrowly oblong or elliptic, with a cuneate to attenuate base, and an acute to acuminate apex, usually with a persistent indumentum of ochre to yellowish trichomes abaxially. This species is very similar to _S. calva_, and the morphological limits among them are sometimes rather subjective (Fiaschi et al., 2007). In _S. calva_, however, the leaflets blades are usually glabrescent or white to grayish-sericeous abaxially, and have usually a rounded or truncate base. The geographic distribution of these two species is also distinct. While _S. angustissima_ is mostly found in coastal rainforests, with a few incursions in more interior montane forests (e.g., Serra de Ibitipoca and Chapada Diamantina), _S. calva_ is typical of seasonally dry and gallery forests across the Brazilian Cerrado (Fiaschi & Pirani, 2008). For instance, these species are known to co-occur in just a few areas characterized by transitional ombrophilous-seasonally dry vegetation (Fiaschi & Pirani, 2008).

Fiaschi and Pirani (2007) suggested that several species recognized as distinct by Frodin
and Govaerts (2003) should be placed under synonymy in *S. angustissima*, mostly due to the inconsistency of characters that were initially believed to represent unique states in these other species. Thus, the presence of leaflets with a falcate blade (in *S. falcifoliola*), a persistent sericeous indumentum abaxially (in *S. conspicua* and *S. navarroii*), and 4-carpellate ovaries (in *S. anomala*) were considered as part of the variation range of *S. angustissma* by Fiaschi and Pirani (2007).

_Additional selected material. BRAZIL. Bahia:* Camacã, RPPN Serra Bonita, 9,7 km de Camacã, na estrada para Jacareci, 6 km do ramal para a RPPN, 15°23’30’’S, 39°33’55’’W, 850 m, 18 Mar. 2005 (fl), _Fiaschi et al. 2851_ (CEPEC, NY, SPF); Rio de Contas: Mata da base do Pico do Itobira, 13°22’07’’, 41°53’03’’, 1700 m, 29 Jan. 1999 (fl), _Nascimento 119_ (HUEFS, K).

_Minas Gerais:* Catas Altas, Serra do Caraça, Pico do Inficionado, 1850 m, 01 Sep. 1999 (fl), _Vasconcelos s.n._ (BHCB 48899, SPF 152782); Lima Duarte, Parque Estadual da Serra do Ibitipoca, mata da Gruta do Pião, 21°09’S, 43°52’W 1600 m, 18 Jan. 205 (fl), _Forzza et al. 3927_ (RB, SPF). _Paraná:* Antonina, Cacatu, 25 Mar. 1966 (fr), _Hatschbach 14162_ (MBM); Bocaiúva do Sul, Serra Virgem Maria, 11 Nov. 1968 (fl), _Hatschbach 20261_ (MBM); Campina Grande do Sul, Sítio do Belizário, 6 Sep. 1996 (fl), _Silva et al. 1721_ (MBM); Cerro Azul, Morro Grande, 3 Aug. 1973 (fl), _Hatschbach 32624_ (MBM); Guaraqueçaba, aeroporto, 10 Nov. 1995 (fr), _Ziller & Maschio 1381_ (MBM); Morretes, Véu de Noiva, 28 Aug. 1986 (fr), _Silva & Cordeiro 160_ (G, MBM); Paranaguá, Área do BANESTADO, 19 Jan. 1995 (fr), _Ziller & Kuniyoshi 709_ (MBM); Piraquara, Rio Taquary, 29 Sep. 1951 (fl), _Hatschbach 2516_ (MBM); Quatro Barras, Morro Mãe Catira, 20 Sep. 1966 (fl), _Hatschbach & Guimarães 14745_ (MBM); São José dos Pinhais, Serra do Emboque, 1000 m, 29 Aug. 1968 (fl, fr), _Hatschbach 19654_ (MBM). _Rio de Janeiro:* Angra
dos Reis, Praia do Manduri, 23°02’S, 44°38’W, 17 Nov. 1993 (fl), Toniato et al. 30160 (UEC);
Magé, 3º Distrito, Paraíso, Centro de Primatologia do Rio de Janeiro/FEEMA, 200 m, 3 Oct. 1984 (st), Martinelli et al. 9933 (RB, UEC); Nova Friburgo, Reserva Ecológica Municipal de Macaé de Cima, nascente do Rio das Flores, 22°00’S, 42°03’W, 1100 m, 5 Oct. 1987 (fl),
Martinelli et al. 12255 (UEC); Parati, APA Cairuçu, Morro da Pedra Rolada, Córrego do Mico, 23°10’--23°S, 44°30’--51’W, 120--500 m, 19 Oct. 1993 (fl), Moreira 7 (R); Petrópolis, 23 Oct. 1938, Alston-Lutz 183 (BM, R); Rio de Janeiro, Corcovado, 18 Feb. 1871 (fr), Glaziou 1495 (R).

Santa Catarina: Blumenau, Morro Spitzkopf, 950 m, 21 Aug. 1959 (fl), Reitz & Klein 9001 (US); Brusque, Mata do Hoffmann, 10 Feb. 1949 (fl), Klein 187 (MBM); Itajaí, Morro da Fazenda, 12 Aug. 1954 (fl), Klein 799 (MBM); Itapoá, Reserva Volta Velha, 28 Nov. 1991 (fr), Negrelle s.n. (UEC 63644); Joinville, Estrada Dona Francisca, 26°18’00’’S, 48°49’60’’W, 600 m, 21 Jun. 1957 (fl), Reitz & Klein 4399 (US); Palhoça, Pilões, 27°37’60’’S, 48°40’00’’W, 300 m, 6 Sep. 1956 (fl), Reitz & Klein 3620 (US). Rio do Sul, Serra do Matador, c. 700 m, 1 Aug. 1958 (fl), Reitz & Klein 6812 (G); Sabiá, Vidal Ramos, 27 Feb. 1957 (fl), Klein 2283 (MBM).

São Paulo: Bananal, Estação Ecológica de Bananal, Serra da Bocaina, 1100 m, 14 Apr. 2000 (fl), Costa et al. 742 (SP, SPF); Bertioga, Praia de Guaratuba, Rodovia Rio-Santos, km 199, 10 Dec. 2000 (fl), Fiaschi & Lobão 532 (SPF); Biritiba Mirim, Estação Biológica de Boracéia, 23°38’--23°39’S, 45°52’--45°53’W, 890--950 m, 26 Oct. 1983 (fr), Custódio Filho 1742 (IAC, SP); Cananéia, Parque Estadual da Ilha do Cardoso, Restinga do Pereirinha, 9 Apr. 1990 (fr), Sugiyama & Luchii 839 (IAC, SP); Cunha, Parque Estadual da Serra do Mar, Núcleo Cunha, Morro da Marlene, trilha para os campos de altitude, 23°12’44’’S, 45°02’01’’W, s.d. (fl, fr), Ferreti et al. 147 (ESA); Iguape, Estação Ecológica de Chauás, Trilha de Capeava do Mumuna, 24°44’S, 47°41’W, 10 Jan. 1999 (fl, fr), Kozera et al. 805 (ESA); Itanhaém, Parque Estadual da
Serra do Mar, Núcleo Curucutu, entorno do vale do Rio Mambu, 24°02′51″S, 46°49′05″W, 30-100 m, 16 Apr. 2001 (fr), Souza et al. 162 (UEC). Mogi das Cruzes, estrada para Boracéia, 17 Feb. 1950 (fr), Kuhlmann 2365 (IAC, SP); Pariquera- Açu, Estação Experimental do Instituto Agronômico, 24°36′30″S, 47°52′37″W, 1 Oct. 1995 (fl), Ivanauskas 470 (ESA, IAC, UEC); Queluz, 23 Jun. 1899 (fl), Hoehne s.n. (SP 23512); Salesópolis, Estação Biológica de Boracéia, 22 Nov. 1957 (fr), Kuhlmann 4282 (SP); São Luís de Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, trilha para o Salto Grande, 18 Jan. 2001 (fr), Fiaschi & Lobão 540 (SPF); São Miguel Arcanjo, Parque Estadual de Carlos Botelho, 19 Jan. 1995 (fr), Moraes & Ivanauskas 1154 (ESA, IAC); São Paulo, Jardim Botânico, 23 Sep. 1931 (fl), Handro 96 (SP); São Roque, Mata da Câmar, 23°31′26″S, 47°06′45″W, s.d. (st), Cardoso-Leite & Oliveira 348 (ESA, UEC); Sete Barras, estrada de Sete Barras para Juquiá, 24°21′13″S, 47°56′56″W, 13 Feb. 1995 (fr), Rodrigues et al. 33425 (ESA, UEC); Ubatuba, Picinguaba, 23°22′S, 44°48′W, 7 Jan. 1996 (fr), Pedroni & Sanchez 242 (UEC).

2. Schefflera aurata Fiaschi, Brittonia 56(4): 357. 2004. TYPE: Brazil. Bahia: Una, Reserva Biológica de Una, Trilha do Príncipe, 15°10′60″S, 39°04′00″W, 120 m, 5 Feb. 2002 (fr), Fiaschi et al. 988 (holotype, SPF!; isotypes, CEPEC!, HUEFS!, K!, MBM!, NY!). Figs. 238A–E and 252B (see also Fiaschi, 2004; Fig. 1).

Vernacular name. Matataúba.

Trees or treelets 3–15 m tall. Branchlets c. 25 mm diam., longitudinally striate, glabrescent. Leaves palmately compound, clustered at the end of branchlets, the internodes up to
c. 1 cm long. *Stipules* 2.5--4 cm long, glabrescent abaxially, glabrous adaxially, apex deeply bifid, the lobes c. 1 cm long; petiole 30--70 cm long, c. 7 mm diam., cylindrical, slightly striate longitudinally, glabrescent; *leaflet* 5--10, grouped in one whorl, held horizontally; the blade conduplicate, coriaceous, the adaxial surface glabrous, the abaxial persistently golden-sericeous except on the glabrescent primary and secondary veins. *Median leaflet*: petiolule 4.5--12 cm long, unarticulated, cylindrical, canalicate adaxially; the blade 21--42 x 14.5--20 cm, elliptic to widely elliptic or narrowly obovate, the base obtuse to rounded, symmetrical to clearly asymmetrical, the margin entire or slightly undulate, revolute, the apex cuspidate. *Basal leaflets*: petiolule 2.5--6 cm long, the blade 18.5--30 x 11--13 cm, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 8--11, prominent abaxially, impressed to slightly prominent adaxially; intersecondary veins absent; higher orders of venation inconspicuous. *Inflorescence* terminal, erect, whitish to grayish-sericeous, glabrescent; peduncle reduced or up to c. 1.5 cm long, rachis up to c. 8 cm long; primary branches 5--17, of which 3--5 are terminal, 7.5--20 cm long (bracts c. 1.5 cm long), each bearing 10--24 secondary branches arranged racemosely (3--4 terminal), 1--5 cm long, bracts 5--15 mm long; tertiary branches 15--17, up to c. 11 mm long; *ultimate inflorescence units* umbellules, with 8--12 flowers, the peripheral ones staminate, the central ones perfect; floral bracts 1--1.5 mm long. *Perfect flowers* subsessile, pedicel up to c. 3 mm long; hypanthium grayish-sericeous, calyx rim with 5 triangular-acuminate teeth; petals 5, color unknown, 3.9--4 x 1.8--2 mm, ovate, sericeous abaxially, apex acute; filaments c. 1 mm long; anthers c. 2.3 x 1.3 mm, oblong or ovate, apex apiculate, thecae connate above the connective insertion; ovary c. 3 mm long; disc glabrous; styles 2, free, c. 1.5 mm long, glabrous, recurved in fruit. *Staminate flowers* subsessile; styles developed; otherwise similar to perfect ones. *Drupes*
15--19 x 17.5--20 mm, obloid, laterally compressed when dry, glabrescent; pedicel 1--7 mm long; pyrenes 2, 14--16 x 8--8.5 mm, flattened, transversely semi-elliptic, indurate.

*Schefflera aurata* is endemic to restinga forests in southern Bahia state along coastal Brazil. It is known from Itacaré to Canavieiras, and has been collected with flowers in November and February, and with fruits in July and November.

*Schefflera aurata* is a very distinctive species, mainly characterized by the golden indumentum of the leaflets, the large flowers with short pedicels (pedicels up to 3 mm long), and the large fruits (15--19 x 17.5--20 mm). It is partially sympatric with *S. morototoni*, from which can be distinguished by the indumentum, and the subsessile flowers with larger petals (3.9--4 x 1.8--2 mm vs. 2.1--2.7 x 1.1--1.5 mm in *S. morototoni*), an elongated ovary (c. 3 mm long vs. 1--1.5 mm in *S. morototoni*) and the larger drupes (15--19 x 17.5--20 mm vs. 4--7.5 x 7.5--11 mm in *S. morototoni*). *Schefflera aurata* can be distinguished from *S. selloi*, also endemic to restingas, by the golden-sericeous (vs. glabrescent or light brown-sericeous) and larger (21--42 x 14.5--20 cm vs. 4.5--11.5 x 1.5--6.5 cm) leaflet blades, with a cuspidate (vs. obtuse to rounded or retuse) apex, the inflorescences with 5--17 (vs. 2--5) primary branches, and the much larger flowers and fruits.

*Additional selected material.* BRAZIL. Bahia: Canavieiras, Fazenda Gromogô, km 22 da Rod. Canavieiras/Santa Luzia (BA 270), ramal à direita, 15°34’S, 39°01’W, 22 Jul. 1981 (fr), *Mattos-Silva et al.* 1332 (CEPEC); Ilhéus, Estrada que liga a Estação Hidromineral de Olivença ao Povoado de Vila Brasil, 5 km ao Sudoeste de Olivença, 14°59’S, 39°03’W, 8 Feb. 1982 (fl), *Mattos-Silva et al.* 1459 (CEPEC); Itacaré, Estrada de Itacaré para Maraú, pouco após
desembocadura do Rio de Contas, 14°17’S, 38°59’W, 7 Dec. 2002 (st), Fiaschi et al. 1250 (CEPEC); Una, Reserva Biológica do Mico Leão (IBAMA), 46 km on BA 001, between Ilhéus and Una, 15°09’S, 39°05’W, 14 Nov. 1992 (fr), Thomas et al. 9440 (CEPEC, NY).

3. Schefflera botumirimensis Fiaschi & Pirani, Novon 15: 117. 2005. TYPE: Brazil. Minas Gerais: Botumirim, contrafortes orientais da Serra da Canastra, trilha do Cruzeiro, 1280 m, 29 Sep. 1997 (fr), Mello Silva et al. 1475 (holotype, SPF!; isotypes, BHCB!, MO!, NY!). Figs. 239M–P and 252C (see also Fiaschi & Pirani, 2005a; Fig. 1).

Vernacular name unknown.

Treelets up to c. 2 m tall. Branchlets 4–8 mm diam., smooth or slightly striate longitudinally, grayish-sericeous, glabrescent, the very young leaves densely light brown sericeous. Leaves palmately compound, clustered at the end of branchlets, the internodes up to c. 1 cm long. Stipules 4–6 mm long, grayish-sericeous abaxially, glabrous adaxially, apex shortly bifid, the lobes c. 0.5 mm long; petiole 13–23 cm long, 0.9–2 mm diam., cylindrical, slightly striate longitudinally, glabrescent; leaflets 7–11, grouped in one whorl, held horizontally to slightly deflexed; the blade slightly to strongly conduplicate, chartaceous, the adaxial surface glabrous, the abaxial from light brown to grayish-sericeous, glabrescent. Median leaflet: petiolule 1.5–3.8 cm long, unarticulated, laterally compressed, canaliculate adaxially; the blade 5.8–11 x 1–2.7 cm, narrowly elliptic or oblong to ovate, the base usually rounded (subcordate), sometimes cuneate, symmetrical, the margin entire, slightly revolute, the apex acuminate to caudate, the tip mucronate. Basal leaflets: petiolule 0.7–3.2 cm long, the blade 5–10.2 x 1–2.3
cm, the base symmetrical to slightly asymmetrical, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 7--9, slightly prominent abaxially, impressed adaxially; intersecondary veins absent; higher orders of venation inconspicuous to somewhat conspicuous abaxially. *Inflorescence* terminal, initially erect, pendent when fruiting, glabrescent; peduncle absent or up to c. 3.5 cm long, rachis absent or up to c. 8.5 cm long; primary branches 3--4, of which 3 are terminal and 21.5--34 cm long (bracts 2.5--3 mm long), each bearing 7--10 secondary branches arranged racemosely, mostly at the distal half (4--5 terminal), 4--15 cm long, bracts 1.5--2.5 mm long; tertiary branches 5--10, 2.5--4.5 cm long; *ultimate inflorescence units* umbellules, with 10--18 flowers; floral bracts c. 0.5 mm long. *Perfect flowers* not seen. *Staminate flowers* with pedicel 1.5--2 mm long; hypanthium light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5, green-yellowish, 2.1--2.2 x 1--1.4 mm, elliptic to ovate, sericeous abaxially, apex acute; filaments c. 0.3 mm long; anthers c. 1.2 x 0.7--0.8 mm, ovate, apex apiculate, thecae connate above the connective insertion; disc glabrous; styles 2, free, c. 1 mm long, glabrous, recurved in fruit. *Drupes* 4.5--7 x 8.5--10 mm, transversely ellipsoid, laterally compressed when dry, glabrescent; pedicel 1--2 cm long; pyrenes 2(3), 6--7.5 x 4.5--5 mm, flattened, transversely semi-elliptic, indurate.

This species is known from only one area of *campos rupestres* northwest of Botumirim, in the northern portion of the Espinhaço Range in Minas Gerais state (Brazil). Despite its restricted geographic distribution, *S. botumirimensis* is locally abundant. It has been collected mostly with fruits, from July to December.
Schefflera botumirimensis is superficially similar to *S. glaziovii*, from which it can be distinguished by considerably more elongated inflorescences, fruits with long pedicels (10--20 mm long vs. 4--8 mm in *S. glaziovii*), and leaflet blades usually with a rounded (vs. acute to attenuate) base.

This species, together with *S. gardneri* and *S. glaziovii*, forms a group of presumably related species from the campos rupestres of the Espinhaço Range in Minas Gerais that is characterized by leaflets with a somewhat conduplicate blade, and an acute to acuminate or caudate apex.

**Additional selected material.** BRAZIL. **Minas Gerais:** Botumirim, Serra da Canastra. São Domingos. 16°51’13’’--16°51’29’’S, 43°01’58’’--43°02’26’’W, 1219--1332 m, 21 Dez. 2004 (fr), *Mello Silva & Forzza* 2731 (SPF); idem, 16°51’11.5’’S, 43°01’53.2’’W, 1170 m, 13 Jul. 2006 (fl, fr), *Fiaschi et al. 3086* (CEPEC, SPF).


**Vernacular names.** Mandioqueira, mata-menino, quina-brava.
Treelets 1.5--5 m tall. Branchlets 11--16 mm diam., usually with corky bark, sparsely light brown to grayish-sericeous, glabrescent. Leaves palmately compound, clustered at the end of branchlets, the internodes usually indistinct or up to c. 1 cm long. Stipules indistinct or up to c. 6 mm long, sparsely light brown-sericeous abaxially, glabrous adaxially, apex slightly bifid, the lobes no more than 0.5 mm long; petiole 5--24 cm long, 1.5--3.2 mm diam., cylindrical, slightly striate longitudinally, glabrescent; leaflets 6--8, grouped in one whorl, held horizontally; the blade plane or sometimes the entire blade revolute, chartaceous, the adaxial surface glabrescent, the abaxial persistently ochre or light brown to grayish-sericeous, glabrescent. Median leaflet: petiolule 1--7 cm long, unarticulated, slightly compressed laterally, rounded to plane adaxially, glabrescent; the blade 5.2--15.3 x 3--6.6 cm, elliptic to slightly ovate or obovate, the base cuneate to rounded, symmetrical, the margin entire, slightly revolute, the apex rounded to retuse, the tip sometimes mucronulate. Basal leaflets: petiolule 0.9--5 cm long, the blade 3.5--10.3 x 2--4.1 cm, the base sometimes slightly asymmetrical, otherwise similar to the median leaflet.

Venation brochidodromous; main vein prominent abaxially, impressed to slightly prominent adaxially; secondary veins 8--13, prominent abaxially, impressed to slightly prominent adaxially; intersecondary veins present; higher orders of venation sometimes evident adaxially.

Inflorescence terminal, initially erect or bending outwards, then pendent, light brown to grayish-sericeous, glabrescent; peduncle absent or up to c. 0.5 cm long, rachis absent or up to c. 0.5 cm long; primary branches (1)2--5, of which 1--3 are terminal, 4.5--26.5 cm long (bracts 3--4 mm long); each bearing 7--23 secondary branches arranged racemosely, mostly at the distal half (2--5 terminal), 2.5--9.5 cm long, bracts 1--2 mm long; tertiary branches, if present, 3--6, all below the terminal umbel, or up to 15 (3--6 terminal), 1.2--5 cm long; quaternary branches sometimes
present, up to c. 1 cm long; ultimate inflorescence units umbellules, with 12--18 flowers, the peripheral ones staminate, the central ones perfect; floral bracts up to c. 1 mm long. *Perfect flowers* with pedicel 5--7 mm long; hypanthium light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5, yellow-greenish, 2.7--3.2 x 0.9--1.3 mm, ovate to lanceolate, sericeous abaxially, apex acute or acuminate; disc glabrous; filaments 0.3--0.4 mm long; anthers c. 2 x 0.8--1 mm, ovate, apex apiculate, thecae connate above the connective insertion; styles 2, basaly connate, 1.3--1.7 mm long, glabrous, recurved in fruit. *Staminate flowers* with pedicel 0.5--4 mm long; styles developed; otherwise similar to perfect ones. *Drupe* c. 6 x 9.5--10.5 mm, transversely ellipsoid, laterally compressed when dry, glabrescent; pedicel 9--14 mm long; pyrenes 2, c. 7 x 5.5 mm, flattened, transversely semi-elliptic, cartilaginous.

This species can be found in northern areas of the Brazilian Cerrado domain, in the states of Bahia, Goiás, Maranhão, Mato Grosso, Piauí and Tocantins (Fiaschi & Pirani, 2008). It appears to be more common among rocky outcrops in areas usually above 700 m elev. *Schefflera burchellii* has been collected with flowers throughout the year, and with fruits from March to October.

*Schefflera burchellii* may be confused with other species from the Brazilian Cerrado, such as *S. distractiflora* and *S. macrocarpa*. From *S. distractiflora* it differs by the leaflets with a rounded to retuse (vs. acuminate to cuspidate) apex, inflorescences with umbellately arranged primary branches (vs. primary branches usually along an elongated main axis), and flowers grouped in umbellules (vs. flowers in racemules terminating in umbel). From *S. macrocarpa* it differs mostly by the branchlets with corky (vs. loose, exfoliating) bark, and the leaflet blades chartaceous (vs. coriaceaous) and sericeous (vs. villous) abaxially.
Schefflera burchellii was originally described as a variety of *S. vinosa* by Marchal (1878), mostly due to the presence of petiolulate leaflets, in contrast with *S. vinosa*, which has the subsessile leaflets with the blade tapering toward the base. This treatment has not been followed in recent studies (e.g., Frodin & Govaerts, 2003; Fiaschi & Pirani, 2008), which have accepted both taxa as distinct species. Additional features useful in distinguishing *S. burchellii* from *S. vinosa* are the branchlets with a corky (vs. smooth to longitudinally striate) bark and the elliptic to slightly ovate or obovate (vs. obovate to oblanceolate) leaflet blades.

We included in *S. burchellii* several collections of plants with leaflet blades entirely revolute that are known from the Chapada dos Veadeiros mountains north of Brasília, such as Pereira et al. 2776 (IBGE, K), Silva et al. 2080 (IBGE, K), and Souza et al. 24780 (ESA, SPF). Population level studies would be desirable to determine whether the distribution of this character is consistent enough to warrant recognition of these plants as a distinct taxon.

Additional selected material. BRAZIL. Bahia: Campo Formoso, Morro da Antena, 10°30’55”S, 40°18’32”W, 14 Jul. 2004 (fr), Fiaschi et al. 2421 (CEPEC, SPF); Jacobina, Serra de Jacobina, a SE da cidade, 11°10’60”S, 40°31’00”W, 520--770 m, 18 Sep. 1986 (fr), Queiroz et al. 1202 (HUEFS); Senhor do Bonfim, Serra do Barro Amarelo, 10°32’36”S, 40°19’06”W, 900 m, 28 Oct. 2005 (fl), Conceição et al. 349 (HUEFS). Umburanas, Serra do Curral Feio, c. 20 km S de Delfino na estrada para Umburanas, 10°22’S, 41°19’W, 1000--1200 m, 9 Apr. 1999 (fl), Queiroz et al. 5330 (HUEFS, K). Goiás: Alto Paraíso de Goiás, 28 km from Alto Paraíso de Goiás on the road to Teresina de Goiás, 14°02’S, 47°26’W, 1550 m, 27 May 1994 (fl), Ratter et al. 7241 (UB); Chapada dos Veadeiros, c. 7 Km S. of Cavalcante, 1000 m, 8 Mar. 1969 (fr), Irwin et al. 24035 (NY); Chapada dos Veadeiros, c. 65 Km N. of Brasilia, 21 Dec. 1968 (fl),
Harley et al. 11407 (NY, K); Pedro Afonso, Estrada Pedro Afonso/Itacajá, 08°52’S, 47°56’W, 6 Apr. 1984 (fr), Mileski 449 (RB); Teresina de Goiás, Fazenda Hotel Ecológico Alpes Goianos, Rod. GO-118, km 202, 13°53’59.1”S, 47°23’48.9”W, Jul. 2000 (fr), Souza et al. 24780 (ESA, SPF). **Maranhão:** Balsas, 49 km E of Balsas, 07°52’S, 45°50’W, 14 Jul. 1993 (fr), Ratter et al. 6838 (INPA, NY); Mirador, Parque Estadual do Mirador, Galheiro, 21 Mar. 1993 (fl), Montes & Sokolonski 66 (RB); Tasso Fragoso, Próximo a Tasso Fragoso, 10°14’S, 45°49’W, 25 Mar. 1978 (fr), Fonseca 146 (RB). **Mato Grosso:** Barra do Garças: Portal do Roncador, c. 75 km de Barra do Garças, na estrada para Nova Xavantina, c. 15°18’49.7”S, 52°10’22.3”W, Jun. 2006 (fl), Fiaschi et al. 2990 (CEPEC, K, MM, MO, NY, SPF, UB). **Piauí:** 88 km from Gilbués on the road to Santa Filomena, 09°17’S, 45°35’W, 21 Jul. 1997, Ratter et al. 7734 (K). **Tocantins:** 12 km from Rio Sono on the road to Mansinha, 09°24’S, 47°49’W, 150 m, 20 Nov. 1998 (st), Ratter et al. 8136 (K); 69 km from Porto Nacional on the road to Ponte Alta, 10°45’S, 47°58’W, 700 m, 14 Nov. 1998 (st), Ratter et al. 8098 (K); Palmas, Estrada para Aparecida do Rio Negro, Parque Estadual do Lajedo, Fazenda Agronorte, 750 m, Feb. 2001 (fl), Alves et al. 2216 (HTINS, NY, SP, SPF, UB, UFP).

5. **Schefflera calva** (Cham.) Frodin & Fiaschi *in* D. Frodin & R. Govaerts, World Checklist Bibliog. Araliaceae: 328. 2003. *Panax calvus* Cham., Linnaea 8: 332. 1833. *Didymopanax calvus* (Cham.) Decne. & Planch., Rev. Hort. 4(3): 109. 1854. TYPE: Brazil, without locality, without date, Sello 1806 [lectotype, K!, here designated; isolectotype, F! (photo #3531)]. There was no mention of any material accompanying the description of *Panax calvus* (Chamisso, 1833), but we know that it was based on *Sello 1806* because this specimen bears Chamisso’s annotation (“Panax calvus N”). The only fertile material of this collection that we were able to locate was a
photo at F (#3531), taken from a collection at B that was probably destroyed in 1943. One sterile
duplicate from this collection is housed at K and is here chosen as the lectotype because it takes
precedence over the photo at F. Figs. 237M–U and 252E (see also Fiaschi & Pirani, 2007; Fig.
11K–T).

*Didymopanax clausenanus* Decne. & Planch. ex Marchal *in* Mart. & Eichler, Fl. bras. 11(1):
239. 1878. *Schefflera clausenaniana* (Decne. & Planch. ex Marchal) Frodin *in* D. Frodin & R.
Lagoa Santa,” *Warming s.n.*, XI.1863 (fl, fr) [lectotype, C! (6 sheets), here designated;
isolectotypes, K!, P!]. Among the syntypes listed by Marchal (1878), *Warming s.n.* agrees with
the diagnosis and is the best distributed and preserved. For these reasons it is here chosen as the
lectotype.

*Didymopanax pachycarpus* Marchal *in* Mart. & Eichler, Fl. bras. 11(1): 236. 1878. *Schefflera
pachycarpa* (Marchal) Frodin *in* D. Frodin & R. Govaerts, World Checklist Bibliog. Araliaceae:
362. 2003. TYPE: Brazil, Locality not indicated, *Sello s.n.* (lectotype, K!, here designated). Two
specimens were listed by Marchal (1878) as syntypes: *Sello 361* and 1439. The first was housed
at B and was probably destroyed in 1943 (F!, photo #3536), and the second we were unable to
locate. Despite the lack of the collector’s number, *Sello s.n.* (K) is very likely a duplicate of *Sello
361*. It bears an original label from Sello’s collection, as well as Marchal’s annotation, and is
here designated as the lectotype of *D. pachycarpus*. 

**TYPE:** Brazil, “Habitat in provincia Minas Geraës”, Widgren s.n., Regnell III. 214a, Regnell III. 214b. Among the syntypes listed by Marchal (1878), we were able to locate only Widgren s.n. [BR! (2 sheets), PI!]. Because we have not been able to analyze all of the relevant type material, we refrain from designating a lectotype.

**Vernacular names.** Ambay-guású, caixeta, mandiocão, mandioqueiro, pau-mandioca, sapupema.

**Treelets or trees** 5--30 m tall. **Branchlets** 4--15 mm diam, longitudinally striate, ochre-yellow to whitish-seraceous, glabrescent. **Leaves** palmately compound, clustered at the end of branchlets, the internodes up to c. 1 cm long. **Stipules** 8--12 mm long, white to grayish-seraceous or glabrescent abaxially, glabrous adaxially, apex slightly bifid, the lobes 0.5--3 mm long; petiole 12--48 cm long, 3--5.5 mm diam., cylindrical, longitudinally striate, glabrescent or with persistent trichomes at petiolules insertion; **leaflet**s 7--12, grouped in one whorl, held horizontally; the blade plane to slightly conduplicate at the base, subchartaceous to chartaceous, the adaxial surface glabrous, the abaxial surface glabrescent or persistently ochre-yellowish or white to grayish-seraceous, main and secondary veins sometimes glabrescent. **Median leaflet:** petiolule 1.6--8.6 cm long, unarticulated, cylindrical to compressed laterally, slightly to strongly canaliculate adaxially, glabrescent; the blade 8.6--27 x 2--9.8 cm, narrowly oblong or elliptic to obovate, the base acute to rounded or truncate, rarely sub-cordate, symmetrical, the margin entire, smooth to slightly revolute, the apex acute to acuminate, sometimes caudate, the tip
sometimes mucronate. *Basal leaflets*: petiolule 0.7--4 cm long, the blade 5.5--19 x 1.4--8.1 cm, the base symmetrical or slightly asymmetrical, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein prominent abaxially or on both surfaces, more conspicuously so abaxially; secondary veins 8--17, prominent abaxially, impressed adaxially; intersecondary veins sometimes present; higher orders of venation inconspicuous or more or less conspicuous abaxially. *Inflorescence* pseudolateral or rarely terminal, initially erect, becoming patent or pendent when fruiting, white or ochre-sericeous; peduncle obscure or up to c. 2.5 cm long, rachis up to c. 18 cm long; primary branches (2)3--7(--15), 2--3 of which are terminal, (3--)8.5--45 cm long (bracts 4--6 mm long), each bearing 8--36 secondary branches arranged racemosely along the entire length (3--7 terminal), or only 4--11 branches below the terminal inflorescence unit, 1--12 cm long, bracts 2--4 mm long; tertiary branches, if present, 2--16 (3--5 terminal), sometimes all branches below the terminal umbel, 2--18 mm long; *ultimate inflorescence units* umbellules, with 10--37 flowers, mostly perfect, or the peripheral ones staminate, the central ones perfect; floral bracts up to c. 1.5 mm long. *Perfect flowers* with pedicel 2--7 mm long; hypanthium white or ochre-sericeous, calyx rim with 5 acuminate teeth; petals 5, greenish, 2.4--2.8 x 1.1--1.3 mm, elliptic or triangular to ovate, sericeous abaxially, apex acute; filaments 0.3--1.2 mm long; anthers 1--1.8 x 0.7--1 mm, oblong, apex rounded to slightly apiculate, thecae connate above the connective insertion; ovary 1--2 mm long; disc glabrous; styles 2(--4), free or basally connate, 1.2--1.6 mm long, glabrous, recurved in fruit. *Staminate flowers* with pedicel 2--4 mm long; styles developed; otherwise similar to perfect ones. *Drupes* 6--8.5 x 9.5--16.2 mm, transversely ellipsoid, laterally compressed or rarely 3--4-costate when dry, glabrescent; pedicel 3--9 mm long; pyrenes 2--3(4), 5--6 x 3.5--4 mm, flattened, transversely semi-elliptic, indurate.
*Schefflera calva* is widespread in areas west of the Serra da Mantiqueira mountain range, where it has been reported in southeastern and southern Brazil, southeastern Paraguay, and northeastern Argentina (Missiones Province), as well as in gallery forests across the eastern portion of the Brazilian Cerrado (Fig. 252E). It can be considered as a typical element from the Atlantic forests that happens that “invades” the Cerrado (Oliveira-Filho & Ratter, 1995; Fiaschi & Pirani, 2008).

The forests where *S. calva* grows are seasonally dry, such as those across the Paraná Basin (the Paranaense Province of Prado, 2000), or found along streams in planaltine areas surrounded by savannas, such as those along the Espinhaço Range in Minas Gerais state and the *serras* of the Chapada dos Veadeiros, in Goiás state. *Schefflera calva* has been collected with flowers from December to May, and with fruits throughout the year.

*Schefflera calva* is very similar to *S. angustissima*, from which it can be distinguished by the usually longer stipules (8--12 vs. 4--10 in *S. angustissima*), leaflets blades glabrescent or usually white to grayish-sericeous (vs. usually ochre or yellowish-sericeous) abaxially, with a rounded or truncate (vs. usually cuneate to attenuate) base, and floral buds usually with glabrescent (vs. persistently sericeous) petals abaxially.

Moura (1983) proposed that *Didymopanax micranthus* (= *S. regnelliana*) and *D. clausenianus* (= *S. clauseniana*) should be considered synonymous, despite the presence of smaller flowers and fruits in the former. This view was followed by Fiaschi and Pirani (2007), who also suggested that the persistence of the indumentum in the abaxial surface of the leaflets should not be considered as a reliable character for the segregation of *S. clauseniana* from *S. calva*. Moreover, Moura’s (1983) recognition of *S. pachycarpa* as distinct from *S. calva* based on the presence of slightly bifid (vs. entire) anthers and longer styles was not accepted by Fiaschi
and Pirani (2007), who placed *S. pachycarpa* under their expanded circumscription of *S. calva*.

Farinaccio & Campos Filho 228 (HRCB, HUFU, SPF); Sapucai Mirim, Serraria Boa Vista, 27
Oct. 1950 (fr), Kuhlmann 2600 (SPF). Paraná: Candói, Estrada de Paz para Foz do Jordão, c. 8
km de Paz, c. 25.7°S, 52.1°W, 27 Aug. 2006 (st), Fiaschi & Matos 3128 (SPF); Colombo,
Unidade Regional de Pesquisa Florestal Centro-Sul, 27 Jun. 1979 (fr), Rotta 68 (MBM, UEC);
Patrimônio, 13 Mar. 1915 (fr), Dusén 16807 (NY); Near Rio Tigre Preto, c. 25 km S of
Marmeleiro, border of Santa Catarina, 12 May 1966 (fr), Lindeman & de Haas 1318 (NY). Rio
de Janeiro: Visconde de Mauá, Vale das Flores, beira do Rio das Flores, 3 Mar. 2001 (fl),
Lobão 558 (SPF). Rio Grande do Sul: Caxias do Sul, Pinhal, 780 m, 20 Dec. 2001 (fl), Kegler
1212 (US); Vale do Sol, Linha XV de Novembro, 27 Feb. 1993 (fr), Jarenkow 2351 (ESA).
Santa Catarina: Araranguá, Sombrio, 8 Feb. 1946 (fl), Rambo 31803 (NY); Sombrio, Pirão
Umuarama, 22 Nov. 1940 (fl), Kuhlmann et al. 2050 (F, SP); Pedra Bela, do outro lado da
cidade, em estrada de terra, 8 May 1995 (fl), Tamashiro et al. 965 (IAC, UEC); São Paulo,
Parque Alfredo Volpi, Feb. 2000 (fl), Fiaschi et al. 144 (SPF); Teodoro Sampaio, Parque

Cariacica, Reserva Biológica de Duas Bocas, Trilha para o Córrego do Pau Oco, c. 20°17′28′′S,
40°31′20′′–40°31′35′′W, 680–750 m, 8 Mar. 2001, Fiaschi et al. 690 [holotype, SPF! (3
sheets); isotypes K!, MBML!, NY!]. Figs. 241A–G and 252F (see also Fiaschi & Pirani, 2005b;
Fig. 1).
Vernacular name unknown.

Unbranched or sparsely branched treelets 6--7 m tall. Branchlets 9--12 mm diam., longitudinally striate, whitish or ochre-sericeous. Leaves palmately compound, clustered at the end of branchlets, the internodes up to c. 3.5 cm long. Stipules well developed, whitish or ochre-sericeous abaxially, glabrous adaxially, 12--19 mm long at base, apex deeply bifid, the lobes 5--7.5 mm long; petiole (20--)43--59 cm long, 3--4 mm diam., cylindrical, smooth to slightly striate longitudinally, glabrous or glabrescent; leaflets 7--12, grouped in one whorl, held horizontally; the blade plane, chartaceous, the adaxial surface glabrous, the abaxial glabrescent, sparsely sericeous on main and secondary veins. Median leaflet: petiolule 3.8--6.5 cm long, unarticulated, laterally compressed, canaliculate adaxially, the blade 11.2--21.3 x 2.7--6 cm, narrowly elliptic to obovate or oblanceolate, the base obtuse to rounded, symmetrical to slightly asymmetrical, the margin entire, slightly revolute, the apex acuminate to cuspidate, the tip mucronate. Basal leaflets: petiolule 1.4--2.5 cm long, the blade 6.7--14.2 x 3.4--5.2 cm, the base usually asymmetrical, otherwise similar to the median leaflet. Venation brochidodromous, main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 9--12, prominent abaxially, impressed adaxially; intersecondary veins absent; higher orders of venation evident abaxially on mature leaflets. Inflorescence pseudolateral, pendent; peduncle c. 4.5 cm long, rachis reduced, up to c. 3 mm long; primary branches 2, both terminal, 92--97 cm long (bracts caducous, not seen), each bearing 20--24 secondary branches arranged racemosely, mostly at the distal half, 5.5--12.7 cm long, bracts c. 2 mm long; ultimate inflorescence units umbellules, with 20--36 flowers, most of which are perfect; floral bracts c. 1 mm long. Perfect flowers with
pedicel 7--25 mm long; hypanthium light brown-sericeous, calyx rim with 5(6) acuminate teeth; petals 5(6), yellow-greenish, 4.1--5.2 x 1.8--2.5 mm, narrowly ovate, sericeous abaxially, apex apiculate; filaments 0.8--1.2 mm long; anthers 2.6--3.2 x 1.6--1.8 mm, oblong or elliptic, apex acute or slightly apiculate, thecae free just at tips; ovary 1--2 mm long; disc glabrous; styles 2, free, 1--1.8 mm long, glabrous, recurved in fruit. *Staminate flowers* not seen. *Drupe* c. 11 x 14 mm, transversely ellipsoid, laterally compressed when dry; pedicel 11--27 cm long; pyrenes 2, c. 10 x 6.5 mm, flattened, transversely semi-elliptic, cartilaginous.

*Schefflera capixaba* is restricted to the Brazilian Atlantic rainforests of the surroundings of Cariacica (Espírito Santo state), where it is so far known just from the type locality (Fiaschi & Pirani, 2005b, 2007).

*Schefflera capixaba* is distinct from other species of the Didymopanax group by the large stipules with prolonged apical lobes (5--7.5 mm long), the pseudolateral and pendent inflorescence bearing just two elongated (about 1 m long) primary branches, and the large flowers, with pedicels usually more than 1 cm long.

Although Fiaschi and Pirani (2005b, 2007, 2008) suggested that *S. capixaba* is probably related to *S. longipetiolata* and *S. racemifera*, a close relationship among these species is not supported by molecular data, which suggest that *S. capixaba* is related to *S. kollmannii* and *S. ruschiana* (see Chapter 4).

*Additional selected material.* BRAZIL. Espírito Santo: Cariacica, Reserva Biológica de Duas Bocas, Localidade de Alegre, trilha do Pau Oco, 20°17’29’’S, 40°31’10’’, 600 m, 15 Feb. 2008 (fl), Fraga et al. 1845 (MBML, RB).

*Vernacular name* unknown.

Small *trees*. *Branchlets* c. 12 mm diam., ochre-sericeous. *Leaves* palmately compound, clustered at the end of branchlets. *Stipules* c. 8 mm long, ochre-sericeous abaxially, glabrous adaxially, apex slightly bifid; petiole 18.5--27 cm long, c. 3 mm diam., cylindrical, longitudinally striate, glabrescent; *leaflets* 7, grouped in one whorl, held horizontally; the blade plane, sub-leathery, the adaxial surface glabrescent, the abaxial ochre to grayish-sericeous. *Median leaflet*: petiolule c. 1.8 cm long, unarticulated, laterally compressed, canaliculate adaxially, the blade 16.3--17.8 x 5--5.4 cm, narrowly elliptic to slightly obovate, the base cuneate to obtuse, symmetrical to slightly asymmetrical, the margin entire, revolute, the apex acuminate to cuspidate, the tip mucronate. *Basal leaflets*: petiolule c. 1 cm long, the blade 11.8--12.8 x 3.7--4.3 cm, the base usually asymmetrical, otherwise similar to the median leaflet. *Venation* eucamptodromous, main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 9--10, prominent abaxially, impressed adaxially; intersecondary veins sometimes present; higher orders of venation inconspicuous. *Inflorescence* terminal, erect; peduncle c. 7 mm long, rachis absent; primary branches 2, both terminal, c. 32 cm long (bracts
caducous, not seen), each bearing c. 30 secondary branches arranged racemosely along the entire length (5 terminal), 4.5--10.3 cm long, bracts 2--2.5 mm long; tertiary branches present, up to c. 1 cm long; ultimate inflorescence units capitula, with c. 10 flowers, the peripheral ones staminate, the central ones perfect, subsessile; floral bracts not seen. Flowers not seen. Drupes unknown.

*Schefflera cephalantha* is a very poorly known species presumably endemic to the Chapada dos Guimarães, in Mato Grosso state (Brazil). So far it is known just from the type material, which was collected in a cerrado-forest transitional area.

The description above was prepared exclusively based on photos of the type material, available at SPF herbarium. The main diagnostic features of *S. cephalantha* are the flowers grouped in capitula at the end of short (up to c. 1 cm long) tertiary branches. Inflorescence structure in *S. cephalantha* is somewhat reminiscent of that in *S. malmei*, in which the flowers are grouped in umbellules. This species, however, has very distinctive leaflets with the base usually attenuate, the apex truncate or rounded, and the undersurface with a persistent villous indumentum. The leaflets of *S. cephalantha*, on the other hand, are more similar to those of *S. calva*, and have cuneate to obtuse bases, acuminate to caudate apices, and the undersurface with a sericeous indumentum.

It is possible that *S. cephalantha* was described based on an abnormal specimen of *S. malmei* whose leaves had a distinctive shape. This seems to happen when typical savanna species are found growing along forest edges or between rock outcrops. A similar example is *Irwin et al. 12947* (NY!, 4 sheets), which belongs to *S. macrocarpa*, despite having leaflets with an attenuate base, indistinctive petiolules, and the apex acute to acuminate. *Schefflera cephalantha* and *S.
malmei are both commonly found in the Chapada dos Guimarães (Mato Grosso state). Thus, we believe that field exploration in this area would be important to evaluate the extent of morphological variability in S. malmei, and the distinctiveness of this species from S. cephalanthera.

8. Schefflera ciliatifolia Fiaschi & Frodin, Brittonia 60(3): 276. 2008. Type: Brazil. Amazonas: Manaus, c. 90 km N de Manaus, Distrito Agropecuário da SUFRAMA, Rodovia BR 174, km 72, Fazenda Dimona, 2°19’S, 60°05’W, 50–125 m, 16 Jul. 1992 (fl), Nee 43002 (holotype, INPA!; isotypes, NY!, US!). Figs. 242A–G and 252H (see also Fiaschi et al., 2008, Fig. 1).

Vernacular name unknown.

Unbranched treelets 2–3.5 m tall. Young stems 8–9 mm diam., smooth to slightly striate longitudinally, light brown-sericeous. Leaves palmately compound, clustered at the plant apex, the internodes up to c. 1.5 cm long. Stipules c. 15 mm long, light brown-sericeous abaxially, glabrous adaxially, apex bifid, the lobes 1–5 mm long; petiole 17–48 cm long, 1.8–2.3 mm diam., cylindrical to slightly striate longitudinally, glabrous or glabrescent; leaflets 8–11, grouped in one whorl, held horizontally; the blade plane, membranous, the adaxial surface sparsely hispid, the abaxial glabrous. Median leaflet: petiolule 7.5–11 cm long, unarticulated, slightly compressed laterally, plane to canaliculate adaxially; the blade 11–18.2 x 3.8–7.3 cm, narrowly elliptic or elliptic to ovate, the base attenuate to obtuse (rounded), symmetrical, the margin ciliate, smooth to slightly revolute, sometimes very shallowly lobed, the apex acuminate to cuspidate, the tip sometimes mucronate. Basal leaflets: petiolule 0.9–2.5 cm long, the blade
8.7--11 x 3--5.1 cm, the base usually asymmetrical, otherwise similar to the median leaflet.

*Venation* eucamptodromous to clearly brochidodromous; main vein slightly prominent on both surfaces, more conspicuously so abaxially; secondary veins 5--7, prominent abaxially, impressed adaxially; intersecondary veins sometimes present; higher orders of venation inconspicuous.

*Inflorescence* terminal, erect, light brown-sericeous, glabrescent; peduncle obscure, rachis obscure; primary branches 2--9, umbellately arranged, 4--13 cm long (bracts c. 9 mm long); each bearing 2--11 secondary branches arranged racemosely at the distal half (2--4 terminal), 1--4.8 cm long, bracts 3--5 mm long; tertiary branches, if present, 3--6 (2--3 terminal), 1--1.5 cm long; *ultimate inflorescence units* umbellules, with 10--12 flowers, the peripheral ones staminate, the central ones perfect; floral bracts 1--1.5 mm long. *Perfect flowers* with pedicel 2--3.5 mm long; hypanthium ochre-sericeous, calyx rim with 5 triangular-acuminate teeth; petals 5, color unknown, c. 3 x 1--1.2 mm, ovate to lanceolate, glabrescent abaxially, apex acute; filaments c. 0.5 mm long; anthers c. 2 x 1.5 mm, elliptic to ovate, apex apiculate, thecae connate above the connective insertion; ovary c. 1 mm long; disc glabrous; styles 2(3), free, c. 1.5 mm long, glabrous, recurved in fruit. *Staminate flowers* with pedicel 0.5--1.5 mm long; styles developed; otherwise similar to perfect ones. *Drupes* 7--9 x 11--13 mm, depressed ovoid to transversely ellipsoid, laterally compressed or 3-costate when dry, glabrous; pedicel 4--7 mm long; pyrenes 2(3), 7--8 x 5.5--6 mm, flattened, transversely semi-elliptic, cartilaginous.

*Schefflera ciliatifolia* is only known from *terra-firme* forests of Central Amazonian Brazil, largely in the surroundings of Manaus (Amazonas). It has been collected with flowers mostly in June and July, and with fruits from June to October.
This species clearly differs from others in the Didymopanax group by the unbrached habit, and the presence of hispid trichomes on the adaxial surface of leaflets blade and along the margins. The inflorescences of *S. ciliatifolia* have umbellately arranged primary branches, and the bracts of the secondary branches are relatively large when compared with the delicate inflorescence structure.

_{Additional selected material._ BRAZIL. Amazonas: Manaus, c. 90 km N de Manaus, Distrito Agropecuário da SUFRAMA, Rodovia BR 174, km 72, Fazenda Dimona, 02°19’S, 60°05’W, 50--125 m, 14 Jul. 1992 (fl), Dick 209 (INPA, NY); Manaus, Distrito Agropecuário, 90 km NNE de Manaus, Reserva 1501, PDBFF, 02°24’26”--02°25’31”S, 59°43’40”--59°45’50”W, 50--125 m, 10 Sep. 1991 (fr), Oliveira et al. 98 (INPA, SPF, US); Manaus, Estrada Manaus-Itacoatiara, km 80, 9 Jun. 1961 (fr), Rodrigues & Lima 2753 (INPA, NY); Presidente Figueiredo, Rodovia de Manaus a Caracaraí, km 123, ramal vicinal à direita, 01°54’27.6”S, 60°03’18.7”W, 170 m, 4 Aug. 2007, Fiaschi et al. 3213 (SPF); Banks of Rio Urubu, between Cachoeira Iracema and Manaus-Itacoatiara road, 8 Jun. 1968 (fl), Prance et al. 5088 (CGE, INPA, NY).


TYPE: Peru. Loreto: Province Requena, Genaro Herrera, Río Ucayali, non-inundated forest on mixed sand and clay soil, 7 Dec. 1977, Gentry et al. 21225 (holotype, MO!; isotypes, AMAZ not seen, F not seen, INPA!, NY!, USM not seen).

Vernacular names. Morototó, sacha uvilla.

Treelets or trees 3--13 m tall. Branchlets c. 12--18 mm diam., longitudinally striate, light brown-sericeous, glabrescent. Leaves palmately compound, clustered at the end of branchlets, the internodes up to c. 1 cm long. Stipules c. 13 mm long, brown-sericeous abaxially, glabrous adaxially; apex slightly bifid, the lobes c. 2 mm long; petiole 30--85 cm long, 3.5--6 mm diam., cylindrical to laterally flattened when dry, slightly striate longitudinally, light brown-sericeous to glabrescent; leaflets 17--33, grouped in two or three whorls, held horizontally; the blade plane, membranous to sub-chartaceous, the adaxial surface glabrous, the abaxial glabrescent. Median leaflet (of outer whorl): petiolule 13--19.5 cm long, unarticulated, slightly compressed laterally, canalicate adaxially, light brown-sericeous to glabrescent; the blade 18.5--21 x 8--8.5 cm, elliptic to ovate, the base cuneate to rounded, symmetrical to clearly asymmetrical, the margin entire, smooth to slightly revolute, the apex caudate, the tip mucronulate. Basal leaflets (of outer whorl): petiolule 4.8--7 cm long, the blade 14.5--19 x 4.8--6 cm, narrowly elliptic, the base usually cuneate to attenuate, slightly asymmetrical; leaflets from inner whorl(s) progressively...
smaller. *Venation* brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 9--11, prominent abaxially, impressed to slightly prominent adaxially; intersecondary veins sometimes present; higher orders of venation sometimes conspicuous abaxially. *Inflorescence* terminal, initially erect, becoming pendent when fruiting, light brown-sericeous, glabrescent; peduncle absent or up to c. 1 cm long, rachis absent; primary branches (1)2--3, all terminal, 12--36.5 cm long (bracts 5--8 mm long); each bearing 7--24 secondary branches arranged racemously, mostly at the distal half (2--4 terminal), 6.5--16 cm long, bracts 3--5 mm long; tertiary branches 7--13 (2--3 terminal), 1.8--2.6 cm long; *ultimate inflorescence units* umbellules, with 10--12 flowers, the peripheral ones staminate, the central ones perfect; floral bracts up to c. 1 mm long. *Perfect flowers* with pedicel 5--7 mm long; hypanthium light brown-sericeous, calyx rim with 5(6) acuminate teeth; petals 5(6), cream-yellowish, c. 3.5--5 x 1.5--2 mm, elliptic or ovate, sericeous abaxially, apex acute; filaments c. 1.3 mm long; anthers c. 2.2 x 1 mm, oblong, elliptic or ovate, the apex rounded, thecae connate above the connective insertion; ovary 3--4 mm long; disc glabrous; styles 5(6), free, 0.8--1 mm long, apically with trichomes, recurved in fruit. *Staminate flowers* with pedicel 2--4 mm long; styles shorter; otherwise similar to perfect ones. *Drupes* 15--16 x 13--16 mm, broadly ellipsoid, 5(6)-costate when dry, glabrescent; pedicel 8--22 mm long; pyrenes 5(6), c. 11 x 7.5 mm, flattened, transversely semi-elliptic, crustaceous.

*Schefflera confusa* can be found at southeastern Colombia, northeastern Peru, and the western portions of Acre and Amazonas states in Brazil, growing in *terra firme* forests on sandy/clayey soils, or in white-sand *campinarana* forests. It has been collected with flowers in April, May and November, and with fruits from April to January.
Schefflera confusa may be distinguished from other species of the Didymopanax group by the glabrous leaflets, which are grouped in two or three concentric terminal whorls, large 5(6)-costate fruits when dry, flowers with reclined anthers, and styles with apical trichomes. The most similar species is S. prancei, a new species described in this study based on fruiting material (Fig. 243J–M, see below for a detailed discussion of this species).

The characters used by Gentry (1981) to distinguish S. megacarpa A.H. Gentry from S. confusa do not appear to be consistent, and for this reason, Fiaschi et al. (2008) suggested that the former should be considered a synonym of S. confusa. This proposal is formally adopted here.


*TYPE:* Brazil. Minas Gerais, “pr. Biribiry in silvaticis Serrae do Mocotó,” *Glaziou 19413* [lectotype, P!, here designated; isolectotypes, BR!, C!, K!, P!]. The material used by Taubert to describe this species was deposited at B and was presumably destroyed in 1943. Among the available duplicates, the one that better fits the protologue is at P, and is chosen as the lectotype. The remaining sheets are either fragmentary (BR) or lack the leaflets with a cordate base mentioned by Taubert (1893) in the diagnosis (C, K, P). Figs. 244A–E and 253B.

*Vernacular names* unknown.

*Treelets* 0.5–2.5 m tall. *Branchlets* 6–10 mm diam., slightly to strongly striate longitudinally, light brown to grayish-sericeous, sometimes glabrescent. *Leaves* palmately compound, clustered or spacely arranged at the end of branchlets, the internodes up to c. 4 cm long. *Stipules* 3–6 mm long, light brown to grayish-sericeous or glabrescent abaxially, glabrous adaxially; apex slightly bifid, the lobes less than c. 1 mm long; petiole 12–39 cm long, 1.5–3 mm diam., cylindrical, striate longitudinally, grayish-sericeous or glabrescent; *leaflet* (4)5–8, grouped in one whorl, held horizontally; the blade plane or slightly conduplicate, coriaceaous, the adaxial surface glabrescent, the abaxial persistently ochre or light brown to grayish-sericeous,
sometimes villous. *Median leaflet*: petiolule 0.6--7.8 cm long, unarticulated, compressed laterally, flattened to canaliculate adaxially; the blade 5.1--16.5 x 2.3--8 cm, elliptic or oblong, rarely ovate or obovate, the base usually obtuse to rounded (rarely cordate), the margin entire, slightly to strongly revolute, the apex obtuse to rounded (emarginate), the tip mucronate. *Basal leaflets*: petiolule 0.2--4 cm long, the blade 2.2--12.3 x 1--5.1 cm, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 6--13, prominent abaxially, impressed adaxially; intersecondary veins absent or present; higher orders of venation inconspicuous or sometimes conspicuous abaxially on mature leaflets. *Inflorescence* terminal, rarely becoming pseudolateral, erect or with pendent branches when fruiting, ochre or light brown to grayish-sericeous; peduncle up to c. 5 cm long, rachis up to c. 5 cm long; primary branches (1)2--8, of which 1--6 are terminal, (4--)14--35(--76) cm long (bracts 2--3 mm long), each bearing 15--36 secondary branches arranged racemosely along the entire length (3--8 terminal), 2--14.5 cm long, bracts 2--3 mm long; tertiary branches absent; *ultimate inflorescence units* racemules terminating in an umbel, with 15--50 flowers, the proximal ones staminate, the distal ones perfect; floral bracts up to c. 1.5 mm long. *Perfect flowers* with pedicel 1--2 mm long; hypanthium ochre to light brown-sericeous, calyx rim with 5 triangular-acuminate teeth; petals 5, yellow-greenish, 2.2--2.4 x 1.1--1.3 mm, ovate, sericeous abaxially, apex acute; filaments 0.2--0.5 mm long; anthers 1.3--1.9 x 0.8--1.1 mm, ovate, apex apiculate, thecae connate above the connective insertion; ovary c. 1.5 mm long; disc glabrous; styles 2, free or basally connate, 0.6--1.6 mm long, glabrous, recurved in fruit. *Staminate flowers* with pedicel up to c. 0.5 mm long; styles developed; otherwise similar to perfect ones. *Drupes* 6--7 x 10--13 mm, transversely ellipsoid, laterally compressed when dry,
glabrescent; pedicel 2--5 mm long; pyrenes 2, 5.5--7.5 x 4--5.5 mm, flattened, transversely semi-elliptic, indurate.

_Schefflera cordata_ is endemic to the _campos rupestres_ of the Diamantina Plateau, Minas Gerais state (Brazil), where it is especially common among rock outcrops along the road from Diamantina to São João da Chapada. It has been collected with flowers along the year, and with fruits from October to July.

In the original description of _S. cordata_, Taubert (1893) pointed to a putative similarity to _S. morototoni_. This view was followed by Moura (1983), who suggested that _S. cordata_ “is probably one of the variations of _S. morototoni_” (p. 163). Fiaschi and Pirani (2007) disagreed with this hypothesis, and proposed that _S. cordata_ is similar and probably more closely related to _S. macrocarpa_ and _S. vinosa_, both of which are commonly found in the _campos rupestres_ of the Espinhaço Range in Minas Gerais. _Schefflera cordata_ is very similar to _S. macrocarpa_ and _S. vinosa_ in many respects, and it is sometimes difficult to establish morphological limits among the three species. The fruits of _S. cordata_ are somewhat similar to those of _S. macrocarpa_, but _Schefflera cordata_ can be distinguished from _S. macrocarpa_ by the unbranched (vs. branched) habit, the usually smooth to longitudinally striate (vs. loose) branchlets bark, the leaflet blades usually sericeous (vs. villous) abaxially, and the flowers grouped in racemules terminating in umbel (vs. umbellules). These two species may rarely be found growing together (e.g., on the road to Mendanha, Diamantina), but _S. cordata_ grows mostly in areas of the Diamantina Plateau above 1100 m, while _S. macrocarpa_ is more common in lowland _cerrados_ (Fiaschi & Pirani, 2008), and usually found below 900 m.

To distinguish _S. cordata_ from _S. vinosa_, one can rely on the presence of leaflets with
distinct petiolules and a cuneate to rounded or rarely cordate base, and the flowers grouped in racemose ultimate inflorescence units. In *S. vinosa* the leaflets are usually sessile, with an attenuate to cuneate base, although sometimes they may be petiolulate, and the flowers are grouped in umbellate ultimate inflorescence units (see below for a discussion on the morphological variability of *S. vinosa*).

Although the protologue of *S. cordata* makes special reference to the presence of leaflets with a cordate base (Taubert, 1893), this feature is very rare and, to our knowledge, has been recorded only from the type collection.

*Additional selected material*. **BRAZIL. Minas Gerais**: Diamantina, estrada para Conselheiro Mata, 18°17’55”’S, 43°50’17’’W, 1150 m, 12 Jan. 1998 (fl, fr), *Pirani et al. 3932* (SPF); idem, estrada para Mendanha a 15 km de Diamantina, 18°07’S, 43°30’W, 1200–1225 m, 31 Oct. 1988 (fl), *Harley et al. 25474* (K, SPF); idem, c. 3 km N of São João da Chapada, c. 1200 m, 24 Mar. 1970 (fl), *Irwin et al. 28247* (NY, UB); idem, estrada para Biribiri, 18°10’S, 43°37’W, 8 Apr. 1982 (fl, fr), *Hensold et al. CFCR3194* (SPF); idem, perto de Sentinela, 18°10’56”’S, 43°37’08”’W, 1200 m, 28 Feb. 1998 (fl), *Pirani et al. 4035* (SPF); Gouveia, Fazenda Contagem, 13 km à direita na Rodovia Curvelo-Diamantina, 29 Aug. 1981 (fl), *Giulietti et al. CFCR1755* (SPF).

K!, P! (6 sheets), W!]. The sheet chosen as lectotype is the only one that bears Seemann’s annotation. Figs. 245A–I and 253C.

*Schefflera paraensis* Huber ex Ducke, Arch. Jard. Bot. Rio de Janeiro 3: 228. 1922. TYPE: Brazil. Pará. 1. Belém do Pará, 24.III.1915 (fl), *Ducke 15743* (G!, MG!, R not seen); 2. Prope Santa Izabel viae ferreæ inter Belém et Bragança, 12.II.1909 (fr), *Pessoal do Museu 10175* [G!, MG! (2 sheets), R not seen]. These two specimens (*Pessoal do Museu 10175* and *Ducke 15743*) were listed as syntypes in the protologue, and are mounted on the same sheet at G. Because we have not been able to examine all of the relevant material, we have refrained from designating a lectotype.

_Vernacular names._ Hebeoballi, karahora, karahore, and karahoro (Suriname, Arawak), ilikoro, morototó branco, parapará, tobitoutou (French Guiana, Paramaka).

_Treellets or trees_ 6--32 m tall. *Branchlets* 11--15 mm diam., longitudinally striate, ochre to grayish-sericeous, glabrescent. *Leaves* palmately compound, clustered at the end of branchlets, internodes indistinct, or up to c. 1 cm long. *Stipules* 5--10 mm long, ochre to grayish-sericeous abaxially, glabrous adaxially, apex bifid, the lobes up to c. 1 mm long; petiole 11.5--56.5 cm long, 2.5--3.5 mm diam., cylindrical, longitudinally striate, golden to grayish-sericeous or glabrescent; _leaflets_ 7--13, grouped in one (or rarely two) whorls at the verticil, held horizontally; the blade plane, chartaceous to subcoriaceous, the adaxial surface glabrous or glabrescent, sometimes very shiny, the abaxial glabrescent, always dull. _Median leaflet:_ petiolule 3--11 cm long, unarticulated, slightly compressed laterally, usually canaliculate adaxially; the
blade 9.2--16.6 x 2.8--7.7 cm, elliptic to oblong or sometimes slightly obovate, the base obtuse to rounded, sometimes cuneate, symmetrical, the margin entire, smooth to slightly revolute, the apex usually rounded or obtuse, if acute or acuminate, the tip is blunt-ended or slightly retuse. 

*Basal leaflets:* petiolule 1--2.7 cm long, the blade 5.6--12.5 x 1.6--5.1 cm, the base sometimes asymmetrical, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein prominent abaxially, almost impressed adaxially; secondary veins 6--10, prominent abaxially, impressed adaxially; intersecondary veins sometimes present; higher orders of venation inconspicuous. *Inflorescence* terminal, initially erect, pendent when fruiting, ochre to grayish-sericeous, glabrescent; peduncle absent or up to c. 1.5 cm long, rachis absent; primary branches (1)2(3), all terminal, 7--25.5 cm long (bracts 4--6 mm long), each bearing 6--32 secondary branches arranged racemously at the distal half (3--7 terminal), 0.8--11 cm long, bracts 1--1.5 mm long; tertiary branches, if present, 5--14, 0.5--3 cm long; quaternary branches rarely present; *ultimate inflorescence units* umbellules with 10--20 flowers, all of which are staminate, or with a few central perfect ones, sometimes with up to 5 subtending lateral flowers; floral bracts up to c. 1 mm long. *Perfect flowers* with pedicel 5--13 mm long; hypanthium ochre-sericeous, calyx rim with 5 acuminate teeth; petals 5, cream-yellowish, 3.2--3.6 x 1.3--1.5 mm, elliptic, sericeous abaxially, apex acute; filaments c. 1.2 mm long; anthers c. 2.3 x 1.2 mm, oblong, apex rounded to slightly retuse, thecae connate above the connective insertion; ovary c. 2.5 mm long; disc glabrous; styles 5, free, 0.5--0.7 mm long, apically with trichomes, recurved in fruit. *Staminate flowers* with pedicel 2--6(--21) mm long; styles vestigial; otherwise similar to perfect ones. 

*Drupes* 8--9 x 10--11 mm, 5-costate when dry, obloid or spheroid, glabrescent; pedicel 6--15 mm long; pyrenes 5, 8.2--8.5 x 5.5--5.8 mm, flattened, transversely semi-elliptic, indurate.
Schefflera decaphylla occurs in lowland Amazonian rainforests at Brazil (east of Manaus), the Guianas (Guyana, French Guiana and Suriname), and southern Venezuela. This species can be found growing in terra firme forests on loamy soils. It has been collected with flowers from December to March, and with fruits from December to September.

Schefflera decaphylla is distinct from other species of the Didymopanax group by the terminal inflorescence with a short main axis and a few (1--3) primary branches, the flowers with reclined anthers and styles apically with trichomes, and the 5-costate fruits. It can be distinguished from S. confusa by the number of leaflets (7--13 vs. 17--33), which are usually arranged in one whrol (vs. always in 2--3 whrols in S. confusa), the chartaceous to sub-coriceous (vs. membranous to sub-chartaceous) blades, and the smaller fruits (8--9 x 10--11 mm vs. 15--16 x 13--16 mm). Leaflet shape is also distinctive between these two species. In S. decaphylla, the blade apex is usually rounded or obtuse (Fig. 245B) and, if acute or acuminate, the tip is blunt-ended or slightly retuse, while in S. confusa the apex is caudate, with a very pointy tip (Fig. 243B). To distinguish S. decaphylla from S. prancei and S. quinquecarinata, see comments under these species below.

Mosqueiro, 15 Jul. 1971 (st), *Oliveira* 5775 (IAN); Vigio, c. 14 km ESE of Vigio, Campina do São Benedito, 0°53’S, 48°04’W, 50 m, 1 Apr. 1980 (fr), *Davidse et al.* 17719 (IAN, INPA, MG).


**Rondônia**: Vilhena, Estrada para Aripuanã, 15 km de Vilhena, Faz. Flor da Serra, 22 May 1884 (fr), *Rosário et al.* 476 (MG). FRENCH GUIANA. Sinnamary, Station Recherche Expérimentale de Paracou, Parcelle 16, 5°15’N, 52°56’W, 20--80 m, 24 Feb. 2004 (fl), *Poncy et al.* 1729 (P); Route de Cayenne, Km 10, 12 Feb. 1957 (fl) *French Guiana Forest Service s.n.* (NY); Saül, 3°37’N, 53°12’W, Carbet Maïs Trail, c. 200--300 m, 6 Jun. 1986 (fr), *Mori & Gracie* 18364 (NY); Sinnamary River, above Petit Saut, between Crique Plomb and Crique Tigre, 500 m above Saut Tigre, 05°N, 53°01’W, 87 m, 2 Sep. 1993 (fr), *Mori et al.* 23529 (NY). GUYANA. E. Berbice-Corentyne, left bank Canje River, c. 0.75 km N or Ekwaram River, 05°20’N, 57°38’W, 0--25 m, 10 Apr. 1987 (fr), *Pipoly et al.* 11376 (INPA, NY, P); Amacura River, Northwest district, 08°10’N, 60°W, 23--30 Mar. 1923 (fl), *de La Cruz* 3502 (NY); Near township of Mabura, 05°15’N, 58°45’W, 0--100 m, 14 Mar. 1991 (fr) *Polak* 250 (NY). SURINAME. without loc., 7 Mar. 1917 (fl), *HAB. Sectie O, Arbor no. 847, Herb no. 2702* (K). VENEZUELA.

**Amazonas**: Rio Negro, 9 Km, aguas arriba del Río Orinoco, 02°26’N, 65°58’W, 380 m, Feb. 1991 (fl, fr), *Marin* 1471 (NY).

Vernacular name unknown.

Trees c. 25 m tall. Branchlets c. 12 mm diam., slightly striate longitudinally, light brown-sericeous. Leaves palmately compound, clustered at the end of branchlets, the internodes up to c. 1 cm long. Stipules 10--15 mm long, light brown-sericeous abaxially, glabrous adaxially, apex bifid, the lobes 1--2 mm long; petiole 31--37 cm long, c. 2.5 mm diam., cylindrical, slightly striate longitudinally, light brown-sericeous, glabrescent; leaflets 6--9, grouped in one whorl at the verticil, held horizontally; the blade plane, chartaceous, the adaxial surface glabrous, the abaxial persistently light brown to grayish-sericeous. Median leaflet: petiolule 7.5--8 cm long, unarticulated, striate longitudinally, flattened adaxially; the blade 15--16.5 x 7.5--8.7 cm, elliptic, the base obtuse to rounded, symmetrical, the margin entire, smooth to slightly revolute, the apex caudate, the tip mucronulate. Basal leaflets: petiolule 4--5 cm long, the blade c. 16 x 7 cm, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 11--15, impressed on both surfaces; intersecondary veins present, progressively more similar to secondary ones toward the apex; higher orders of venation inconspicuous. Inflorescence terminal, initially erect, branches patent, presumably becoming pendent when fruiting, light brown-sericeous; peduncle c. 1 cm long, rachis c. 1 cm long; primary branches 3, of which 2 are terminal, 29.5--35.5 cm long (bracts not seen), each bearing 8--11 secondary branches arranged racemosely at the distal half (2 terminal), 11.5--14.5 cm long, bracts 2.5--3 mm long; tertiary branches 8--10, 0.7--2 cm long; ultimate inflorescence units umbellules, with 8--12 flowers, the peripheral ones staminate, the central ones perfect; floral bracts up to c. 1 mm long. Perfect flowers with pedicel 5--8 mm long;
hypanthium light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5, green-yellowish, 2.8--3 x 1.2--1.5 mm, triangular-ovate, glabrescent abaxially, apex acute; filaments c. 0.5 mm long; anthers c. 2.2 x 1--1.2 mm, ovate, apex retuse, thecae free above the connective insertion; ovary c. 2.5 mm long; disc pubescent; styles 2, free, c. 1 mm long, pubescent, presumably recurved in fruit. *Staminate flowers* with pedicel 3.5--4 mm long; styles shorter; otherwise similar to perfect ones. *Drupes* unknown.

This species is known from only a few collections from white-sand forests at the Upper Negro River, close to the borders between Brazil, Colombia and Venezuela. It has been collected with flowers in May; fruiting collections are not yet known.

The main distinctive feature of *S. dichotoma* is the inflorescence, which has a few elongated secondary branches per primary branch, each terminating in 2 secondaries; each of these secondary branches also terminate in just 2 tertiaries. Other diagnostic features include the pubescent nectariferous disc, the few-flowered umbellules (8--10 flowers), the elliptic leaflets with a caudate apex, and the leaf venation, with distinctive intersecondary veins.

*Shefflera dichotoma* is somewhat similar to *S. pimichinensis*, from which it can be distinguished mostly by the inflorescence structure. In *S. dichotoma*, there are just three primary branches, each bearing elongated secondaries (11.5--14.5 cm long), and tertiary branches are present. In *S. pimichinensis*, the inflorescences have 10--14 primary branches, each bearing short secondaries (0.5--1 cm long), but no tertiary branches.

*Additional selected material.* BRAZIL. **Amazonas:** São Gabriel da Cachoeira. Rio Içana, arredores da Comunidade Assunção do Rio Içana, Sítio Santana, c. 01°01’N, 67°31’W, 80 m, 2
Aug. 2008 (st), Fiaschi et al. 3276 (SPF). VENEZUELA. Amazonas: 1 to 2 km E of San Carlos de Rio Negro; c. 20 km S of confluence of Rio Negro and Brazo Casiquiare, 01°56’N, 67°03’W, 120 m, 22 Apr. 1979 (st), Liesner 6884 (VEN).


Didymopanax distractiflorus Harms, Notizl. Bot. Gart. Berlin-Dahlem 11: 488. 1932. TYPE: Brazil. Mato Grosso, “Serra da Chapada,” 2 June 1903, Malme 3439 [lectotype, S!, here designated; isolectotypes, S!]. Among the syntypes listed by Harms (1932), the sheet chosen as the lectotype bears an entire inflorescence and multiple leaves showing both upper and lower surfaces. Figs. 240H–O and 253E.


Treelets 1--3.5 m tall. Branchlets 4.5--20 mm diam., slightly striate longitudinally, light brown to grayish-sericeous, glabrescent. Leaves palmately compound, usually not clustered at the end of branchlets, the internodes more than 1 cm long. Stipules 4--15 mm long, light brown to grayish-sericeous abaxially, glabrous adaxially, apex bifid, the lobes up to c. 3 mm long; petiole 12--47 cm long, 1.5--5.5 mm diam., cylindrical or flattened laterally, slightly striate longitudinally, light brown to grayish-sericeous, glabrescent; leaflets (4)5--10, grouped in one
whorl, held horizontally; plane or slightly conduplicate, subcoriaceous to coriaceous, the adaxial surface glabrescent, the abaxial light brown to grayish-sericeous. Median leaflet: petiolule 1.7--10.2 cm long, slightly compressed laterally, canalicate adaxially; the blade 5.3--19.5 x 2--9.5 cm, narrowly elliptic or oblong to slightly obovate, the base obtuse to rounded, sometimes cuneate, symmetrical, the margin entire, usually revolute, sometimes undulate, the apex acuminate to cuspidate, sometimes acute, the tip sometimes mucronate. Basal leaflets: petiolule 0.4--4.7 cm long, the blade 5.5--18.3 x 2.5--8.1 cm, the base sometimes slightly asymmetrical, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 7--15, prominent abaxially, impressed to slightly prominent adaxially; intersecondary veins sometimes present; higher orders of venation usually inconspicuous, sometimes conspicuous abaxially on mature leaflets.

Inflorescence terminal, light brown to grayish-sericeous, initially erect, fruiting branches becoming patent to pendent; peduncle up to c. 2 cm long, rachis obscure or 1.5--37.5 cm long; primary branches 3--28, of which (2)3--4 are terminal, 6--31 cm long (bracts 2.5--5 mm long); each bearing 9--55 secondary branches arranged racemously along the entire length (2--7 terminal), or only 4--5 branches below the terminal inflorescence unit, 0.5--11 cm long, bracts 2--5 mm long; tertiary branches lacking; ultimate inflorescence units racemules terminating in umbel, with 10--30 flowers, most of which are staminate, or the proximal ones staminate, and the distal ones perfect; floral bracts 1--2 mm long. Perfect flowers with pedicel 1.5--4 mm long; hypanthium light brown-sericeous, calyx rim with 5 triangular-acuminate teeth; petals 5, greenish, 2.2--3 x 1.2--1.5 mm, ovate, sericeous abaxially, apex acuminate; filaments 0.2--0.4 mm long; anthers 1.3--1.8 x 0.4--1 mm, oblong or elliptic, apex apiculate, thecae connate above the connective insertion; ovary 1--2 mm long; disc glabrous; styles 2, free, c. 1.5 mm long,
glabrous, recurved in fruit. *Staminate flowers* with pedicel up to c. 2 mm long; styles developed; otherwise similar to perfect ones. *Drupes* 5--6 x 8.5--11.5 mm, laterally compressed when dry, transversely ellipsoid, glabrescent; pedicel 2--8 mm long; pyrenes 2, 5--7 x 4.5--5 mm, flattened, transversely semi-elliptic, cartilaginous or indurate.

*Schefflera distractiflora* is commonly found in the Brazilian Cerrado at Mato Grosso and Rondônia states, as well as in neighbor areas at southern Pará and Amazonas states (Brazil), eastern Bolivia, and in the Llanos de Moxos along River Beni valley (northern Bolivia). The habitat of this species ranges from open to dense *cerrado*, edges of dry forests and *cerradão* forests. It has been collected with flowers along the entire year, and with fruits from June to December.

*Schefflera distractiflora* can be readily distinguished from the remaining species of the Didymopanax group by leaflets with relatively elongated petiolules, coriaceous blades with typically strongly revolute margin and an acuminate to cuspidate apex, and the long terminal inflorescences, with flowers grouped in racemose ultimate inflorescence units.

Several samples of this species have been previously identified as *S. morototoni*. This is most likely because they share a similar leaflet morphology, despite the fact that they are generally smaller in *S. distractiflora* (5.3--19.5 x 2--9.5 cm, vs. 12.5--40 x 2.3--16.5 cm in *S. morototoni*). Other features that can be used to distinguish these species are habit (treelets up to 3.5 m tall, vs. trees 5--30 m tall in *S. morototoni*), inflorescences without (vs. usually with) tertiary branches, flowers grouped in racemose (vs. umbellate) ultimate inflorescence units, and glabrous (vs. usually pubescent) nectariferous disc.
A few collections from Niquelândia and Chapada da Contagem (Distrito Federal, Brazil) appear conspecific with *S. distractiflora* (e.g., Oliveira et al. 827, Irwin & Soderstrom 6236, Irwin et al. 15615, 15734). However, these localities are at least 400 km away from the geographic range of *S. distractiflora*, and a few morphological differences appear consistent enough to recognize these populations as a distinct taxon (see below in poorly known species).

Additional selected material. BOLIVIA. Bení: Itenez, Serranía San Simón, 14°25’S, 62°03’W, 200 m, 19 Jul. 1994 (fl), Quevedo et al. 925 (K, MO). La Paz: Iturralde, 12°27’S, 67°37’W, 180 m, 8 Jun. 1987 (fl), Solomon 16988 (K, MO). Santa Cruz: Chiquitos, South slope of the Serranía de Santiago, 18°23’S, 59°30’W, 800--950 m, 20 Jul. 1983 (fr), Daly et al. 2170 (NY); Velasco, Estacion Flor de Oro, 14°35’00’’S, 60°51’00’’W, 30 Jun. 1993 (fl, fr), Saldías et al. 2807 (MO); idem, 13°35’9’’S, 61°03’43’’W, 200m, 28 Jun. 1998 (fl, fr), Ritter et al. 4399 (MO); idem, Serranía de Huanchaca, Parque Nacional Prof. Noel Kempff Mercado, 13°59’S, 60°43’W, 800 m, 3 Dec. 1987 (fr), Thomas et al. 5587 (NY); Parque Nacional Noel Kempff, 14°35’00’’S, 60°50’29’’W, 230 m, 12 Jun. 1994 (fl), Killen & Gonzales 6386 (MO). Vaca Diez: 35 Km E of Riberalta on the road to Guayaramerín, 11°05’S, 65°45’W, 230 m, 12 Sep. 1981 (fl), Solomon 6232 (MO, NY). BRAZIL. Amazonas: Humaitá, Estrada Humaitá-Lábrea, km 17, 10 Jun. 1982 (fl, fr), Teixeira et al. 1056 (INPA, NY); Estrada Manaus-Porto Velho, BR 319, km 540, 21 Apr. 1976 (fl), Monteiro & Ramos 827 (INPA); Estrada do Estanho, road to Igarapé Preto, c. 60--62 Km SE of Transamazon Tallway, 3 Jul. 1979 (fl), Calderon et al. 2762 (NY). Mato Grosso: Campo Verde, estrada Nova Brasilândia-Campo Verde, c. 32 km de Nova Brasilândia, 15°07’S, 55°06’W, 8 Oct. 1997 (fr), Souza et al. 20418 (SPF); Chapada dos Guimarães, Fazenda Morro dos Lajes, 600 m, 14 Jul. 1984 (fr), Mori et al. 16799 (CEPEC);
Comodoro, Chapada dos Parecis, estrada BR-364, c. 1--2 km N de Comodoro, 622 m, 24 Jul. 2000 (fr), Vicentini 1657 (INPA); Juruena, Cachoeira São Simão, 21 May 1977 (fl), Rosa & Santos 1965 (INPA, NY); Nobres, 1,5--2 km E of BR-163, 18 km S of Rio Celeste (c. 70 km S of Sinop), 12°27’S, 55°40’W, 19 Sep. 1985 (fl), Thomas et al. 3882 (NY, SPF); Nova Ubiratã, Cachoeira do rio Teles Pires, 13°34’60”S, 55°16’10”W, 4 Jun. 1997 (fl), Nave et al. 1394 (SPF); Novo Aripuanã, Rodovia do Estanho, km 120, entrocamento das estradas das minerações Igarapé Preto e São Francisco, 08°40’S, 61°25’W, 20 Apr. 1985 (fl), Cid Ferreira 5652 (INPA, NY); Nobres, BR-163, a 125 km ao S de Sinop, 10 km de Primavera, 12°55’S, 55°53’W, 18 Sep. 1985 (fl), Cid Ferreira et al. 6105 (INPA, SPF); Pontes e Lacerda, a mais ou menos 23 km da BR na estrada dos Parecis, atravês da Fazenda Sapé, 18 Jul. 1985 (fl), Souza et al. 1404 (SPF); Sararé, Campo Base do RADAMBRASIL, 15°10’S, 59°40’W, 2 Aug. 1978 (fr), Pires & Santos 163 (MG, NY); Serra de São Vicente, Cascata do Rio das Mortes, 600 m, 27 Sep. 1988 (fr), Kral et al. 75106 (SP); Serra do Roncador, 5 Km South of Xavantina, 26 Sep. 1964 (fr), Prance et al. 59136 (NY); Tapurah, Estrada do Capixaba, 20 km ENE de Tapurah, 12°37’25’’S, 56°21’51’’W, 11 Jun. 1997 (fl), Souza et al. 17665 (SPF); Vila Bela da S.S. Trindade BR-174, área de Pantanal, mais ou menos 30 km da cidade de Vila Bela, 18 Jul. 1985 (fl), Souza et al. 1330 (SPF); vicinity of Xavantina, 2 Km N. of Xavantina, 14°40’S, 52°20’W, 300--400 m, 26 Sep. 1964 (fr), Irwin & Soderstrom 6363 (NY); vicinity of Garapú, c. 5 Km South of Garapú, 13°12’S, 52°34’W, 300--400 m, 2 Oct. 1964 (fr), Irwin & T.R. Soderstrom 6590 (NY); vicinity of Barra do Garças, c. 50 km on road to Xavantina, 15°53’S, 52°15’W, 300--400 m, 14 Oct. 1964 (fr), Irwin & Soderstrom 6832 (NY); Xavantina, 1.5 km S. of Xavantina, 14°44’S, 52°20’W, 500 m, 17 Aug. 1967 (fr), Ratter & Ramos 373 (NY); idem, c. 270 Km N. of Xavantina, 12°54’S, 51°52’W, 24 Jun. 1968 (fr), Ratter et al. 1928 (NY). Pará: Perto do Rio


*Vernacular names* unknown.

*Treelets* 1--1.5 m tall. *Branchlets* 3--5 mm diam., slightly striate longitudinally, ochre-yellowish or grayish-sericeous, glabrescent. *Leaves* palmately compound, sometimes clustered at
the end of branchlets, the internodes up to c. 2.5 cm long. Stipules c. 3 mm long, glabrescent abaxially, glabrous adaxially, apex entire or slightly bifid, the lobes indistinct; petiole 3--13 cm long, 0.8--1.5 mm diam., cylindrical, slightly striate longitudinally, glabrescent; leaflets (1--)3--8, grouped in one whorl, ascending; the blade plane, chartaceous, the adaxial surface glabrous, the abaxial ochre-yellowish to grayish-sericeous, glabrescent. Median leaflet: petiolule 1--2.5 cm long, unarticulated, plane adaxially; the blade 3.5--11 x 0.7--2.7 cm, oblanceolate, the base narrowly cuneate to attenuate, accompanying the petiolule, the margin entire, revolute, the apex acute to rounded (truncate), the tip mucronate. Basal leaflets: petiolule up to c. 6 mm long, the blade 2.2--7 x 0.5--1.3 cm, the base symmetrical to clearly asymmetrical, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 6--9, prominent only abaxially; intersecondary veins absent; higher orders of venation inconspicuous or sometimes conspicuous abaxially on mature leaflets. Inflorescence terminal, erect, included within the foliage, ochre-yellowish to grayish-sericeous, glabrescent; peduncle up to c. 5 mm long, rachis absent or up to c. 5.5 cm long; primary branches (2)3--7, all but 1(2) of which are terminal, these 2.5--13 cm long (bracts 1--2 mm long); each bearing 1--4 secondary branches arranged racemosely mostly at the distal half, all branches below the terminal inflorescence unit, 0.3--5.5 cm long, bracts 1--2 mm long; tertiary branches, if present, up to c. 6 mm long; ultimate inflorescence units umbellules, with 7--18 flowers; floral bracts c. 1 mm long. Perfect flowers with pedicel 4--10 mm long; hypanthium ochre to yellowish-sericeous, calyx rim with 5 acuminate teeth; petals 5, green yellowish, c. 3 x 1.5 mm, elliptic to ovate, sericeous abaxially, apex acute; filaments c. 0.7 mm long, anthers 1.8--2 x 0.8--1 mm, oblong, apex rounded or apiculate, thecae connate above the connective insertion; ovary c. 1 mm long; disc glabrous; styles 2(3), basally connate, c. 2.2 mm long, glabrous,
recurved in fruit. *Staminate flowers* with pedicel 1--2 mm long; styles developed; otherwise similar to perfect ones. *Drupes* 6--7.2 x 10--11.5 mm, laterally compressed or 3-costate when dry, transversely ellipsoid, glabrous; pedicel 5--8 mm long; pyrenes (1)2(3), 5.5--8 x 4.5--6 mm, flattened, transversely semi-elliptic, indurate.

*Schefflera fruticosa* is endemic to the *campos rupestres* of the Serra do Cipó mountain range in Minas Gerais (Brazil), where it grows mostly among rock outcrops. The species has been collected with flowers in February, June, and July, and with fruits from June to September.

*Schefflera fruticosa* can be readily distinguished from other species of the Didymopanax group by the narrow and ascending ob lanceolate leaflets with a narrowly cuneate to attenuate base. The short inflorescences included within the foliage (Fig. 244F), with just a few (1--4) secondary branches along each primary branch are also distinctive of this species.


Seemann’s annotation and an original label. This material is the best match to the protologue, which includes the habit information (“a shrub about 4 feet high”) from Gardner’s label. Figs. 239A–G and 253G (see also Fiaschi & Pirani, 2007; Fig. 8A–E).

*Vernacular names* unknown.

*Treelets* 0.6--3 m tall. *Branchlets* 4.5--6 mm diam, longitudinally striate, light brown to grayish-sericeous, sometimes glabrescent. *Leaves* palmately compound, clustered at the end of branchlets, the internodes up to c. 1 cm long. *Stipules* 3--4 mm long, light brown to grayish-sericeous abaxially, glabrous adaxially, apex slightly bifid, the lobes up to c. 1 mm long; petiole 9--15.5 cm long, 0.7--1.8 mm diam., cylindrical, smooth to slightly striate longitudinally, light brown or grayish-sericeous, glabrescent; *leaflets* 5--8, grouped in one whorl, held horizontally; the blade basally conduplicate, chartaceous to subcoriaceous, the adaxial surface glabrescent or glabrous, sometimes conspicuously lustrous, the abaxial surface persistently light brown to grayish-sericeous, glabrescent. *Median leaflet*: petiolule 1--3 cm long, unarticulated, cylindrical, canaliculate adaxially; the blade 3.5--7 x 1.5--5 cm, elliptic or oblong to suborbicular, the base rounded to truncate, symmetrical, the margin entire, slightly revolute, the apex acuminate to caudate, the tip mucronate. *Basal leaflets*: petiolule up to c. 1 cm long, the blade 3--6 x 1.3--3.2 cm, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein impressed to slightly prominent adaxially, prominent abaxially; secondary veins 4--6, similar to main vein; intersecondary veins sometimes present; higher orders of venation inconspicuous or sometimes conspicuous abaxially on mature leaflets. *Inflorescence* terminal, erect or with patent branches when fruiting, ochre to light brown or grayish-sericeous; peduncle up to c. 1.5 cm long, rachis up
to c. 13.5 cm long; primary branches (5--7)--19, of which 4--5 are terminal, these 2.3--12.5 cm long (bracts 1.5--2 mm long), each bearing 7--26 secondary ones arranged racemosely along the entire length or mostly at the distal half (3--6 terminal), or only 2--8 branches below the terminal inflorescence unit, 0.5--4.5 cm long, bracts c. 1 mm long; tertiary branches, if present, up to c. 8 mm long; ultimate inflorescence units umbellules, with 10--30 flowers, most of which are perfect (terminal umbel), or staminate (lateral umbels); floral bracts c. 0.5 mm long. Perfect flowers with pedicel 1--7.5 mm long; hypanthium ochre to light brown-sericeous, calyx rim with 5(6) acuminete teeth; petals 5(6), green-yellowish, 2--2.7 x 1.2--1.5 mm, ovate, sericeous abaxially, apex acute or acuminate; filaments 0.2--0.5 mm long; anthers 1.4--1.9 x 0.7--1.1 mm, ovate, apex apiculate, thecae connate above the connective insertion; ovary c. 1 mm long; disc glabrous; styles 2, basally connate, 1--2 mm long, glabrous, recurved in fruits. Staminate flowers with pedicel 2--3.5 mm long; styles developed; otherwise similar to perfect ones. Drupes 4--7 x 6.5--9.5 mm, transversely ellipsoid, laterally compressed when dry, glabrescent; pedicel 3--7.5 mm long; pyrenes 2(3), 4.5--6.5 x 4--5 mm, flattened to slightly swollen, transversely semi-elliptic, indurate.

_Schefflera gardneri_ is endemic to the campos rupestres of the Espinhaço Range in Minas Gerais (Brazil), where it can be found in several localities north of the Serra do Cipó, mostly growing among rock outcrops. It has been collected with flowers from May to January and with fruits throughout the year.

_Schefflera gardneri_ can be distinguished from other species of the Didymopanax group by leaflets with distinct petiolules, an elliptic or oblong to suborbicular and basally conduplicate blade, and an acuminate to caudate apex. The young leaflets are sometimes adaxially grayish due
to the presence of sparse sericeous trichomes, while the mature leaflets have a shiney upper surface.

In earlier studies, Frodin and Govaerts (2003) and Fiaschi and Pirani (2007) had rejected *Didymopanax gardneri* var. *ellipticus* Marchal as distinct from the typical variety based on leaflet number and shape (Marchal, 1878), and placed it under synonymy in *S. gardneri*. However, after examining the type collection of *D. gardneri* var. *ellipticus* (Riedel 1070, LE), collected in the Serra da Lapa (= Serra do Cipó), we now believe that both morphology and geographic distribution indicate that this specimen (and thus the variety) is referable to *S. glaziovii* (see comments below).

**Additional selected material.** **BRAZIL.** **Minas Gerais:** Couto de Magalhães de Minas, Chapada do Couto, 17 Jun. 1984 (fr), Varanda et al. CFCR4651 (K, SP, SPF); Itacambira, Serra da Itacambira, estrada para Juramento, 17°04’57”S, 43°18’45”W, 1300 m, 17 May 1998 (fl, fr), Pirani et al. 4383 (SPF); Joaquim Felício, Serra do Cabral, 31 Aug. 1985 (fl, fr), Cavalcanti et al. CFCR8073 (SPF); Juramento, Rodovia de Juramento para Itacambira, km 2, 17°04’53.8”S, 43°18’39.6”W, 1320 m, 13 Jul. 2006 (fl, fr), Fiaschi et al. 3090 (CEPEC, SPF).

**16. Schefflera glaziovii** (Taub.) Frodin & Fiaschi in D. Frodin & R. Govaerts, World Checklist Bibliog. Araliaceae: 340. 2003. *Didymopanax glaziovii* Taub., Bot. Jahrb. Syst. 4: 510. 1893. TYPE: Brazil, Minas Gerais, “in Serro do Cipó,” 23 Apr. 1892 (fl), Glaziou 19410 [lectotype, P!, here designated; isolectotypes: BR!, CI!, F! (photo #3533), K!, LE!, P!]. The collections at K and LE do not fit well with the protologue, and seem to be supplementary. Among the remaining material, the specimen at B (photo at F! #3533), used to describe the new species, was probably
destroyed in 1943. From the available duplicates, the one chosen as the lectotype is one of the sheets at P, which is in good condition and bears an original label. Figs. 239H–L and 253H (see also Fiaschi & Pirani, 2007; Figs. 8F–K).

*Didymopanax gardneri* var. *ellipticus* Marchal in Mart. & Eichler, Fl. bras. 11(1): 236. 1878.

Syn. nov. TYPE: Brazil. Minas Gerais, “In rupibas S. da Lapa,” May (or Nov.) 1824 (fl) *Riedel 1070* (lectotype, LE!, here designated). We have not been able to examine *Riedel et Langsdorff s.n.*, which was mentioned by Marchal (1878) as one of two syntypes for this name. *Riedel 1070* (LE) is in very good condition and fits well with the short diagnosis provided by Marchal, but does not carry Marchal’s annotation. This was the only material we were able to locate, and it is here chosen as the lectotype.

*Vernacular names* unknown.

*Treelets* 1--3 m tall. *Branchlets* 4--8 mm diam., slightly striate longitudinally, ochre to grayish-sericeous, sometimes glabrescent. *Leaves* palmately compound, usually not clustered at the end of branchlets, the internodes up to c. 2 cm long. *Stipules* 2--4 mm long, ochre to grayish-sericeous abaxially, glabrous adaxially, apex usually bifid, the lobes less than 1 mm long; petiole 7.5--21 cm long, 1--2 mm diam., cylindrical, slightly striate longitudinally, ochre to grayish-sericeous, glabrescent; *leaflet* 6--10, grouped in one whorl, held horizontally; conduplicate entirely or just at base, chartaceous, the adaxial surface glabrous, the abaxial persistently ochre to grayish-sericeous or glabrescent. *Median leaflet*: petiolule 1--3.5 cm long, unarticulated, slightly compressed laterally, canaliculate adaxially; the blade 5--14 x 1--4.5 cm, narrowly elliptic or
oblong to oblanceolate, the base cuneate to attenuate, symmetrical, the margin entire, slightly revolute, somewhat undulate, the apex acuminate to caudate, the tip sometimes mucronate. Basal leaflets: petiolule 0.9--2.5 cm long, the blade 4.6--9 x 0.8--2.5 cm, the base symmetrical or slightly asymmetrical, otherwise similar to the median leaflet. Venation brochidodromous; main vein impressed to slightly prominent adaxially, prominent abaxially; secondary veins 6--10, similar to main vein; intersecondary veins sometimes present; higher orders of venation inconspicuous or sometimes conspicuous at both surfaces. Inflorescence terminal, initially erect, fruiting branches becoming patent, ochre to light brown-sericeous; peduncle up to c. 4.5 cm long, rachis 5--12.5 cm long; primary branches 4--19, of which 3--5 are terminal, these 2.5--13 cm long (bracts 1--2 mm long), each bearing 6--21 secondary branches racemously arranged along the entire length, sometimes restricted to distal half (3--8 terminal), or 2--25 branches below the terminal inflorescence unit, 1--3 cm long, bracts c. 0.5 mm long; tertiary branches, if present, up to c. 2 cm long; ultimate inflorescence units umbellules, with 10--21 flowers, most of which are perfect (terminal umbel), or staminate (lateral umbels); floral bracts c. 0.5 mm long. Perfect flowers with pedicel 1--4 mm long; hypanthium ochre to light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5, greenish, 2.2--3 x 1.1--1.5 mm, ovate, sericeous abaxially, apex acuminate, thecae connate above the connective insertion; filaments 0.2--0.8 mm long; anthers 1.4--2 x 0.7--1 mm, oblong, apex apiculate; ovary 1--1.5 mm long; disc glabrous; styles 2, basally connate, 1.2--1.5 mm long, glabrous, recurved in fruit. Staminate flowers with pedicel up to c. 2 mm long; styles developed; otherwise similar to perfect ones. Drupes 4.5--7 x 8.5--10 mm, transversely ellipsoid, laterally compressed when dry; pedicel 4--8 mm long; pyrenes 2(3), 6--7.5 x 4.5--5 mm, flattened, transversely semi-elliptic, indurate.
Schefflera glaziovii is endemic to the campos rupestres of the northern part of the Serra do Cipó, in the Espinhaço Range of Minas Gerais (Brazil), where it grows mostly among rock outcrops. It has been collected with flowers from January to June, and with fruits from March to July.

Schefflera glaziovii can be distinguished from other species of the Didymopanax group endemic to the campos rupestres of Minas Gerais by leaflets with distinct petiolules, the usually conduplicate, narrowly elliptic or oblong to oblanceolate blades with an acuminate to caudate apex, and the inflorescences with a distinctive main axis.

Frodin and Govaerts (2003) and Fiaschi and Pirani (2007) placed Didymopanax gardneri var. ellipticus Marchal under synonymy in S. gardneri. After analyzing the type collection of this variety (Riedel 1070, LE), we realized that the narrow and conduplicate leaflets of this specimen fit better the ones of S. glaziovii than those of S. gardneri. Thus, because leaflet shape is the main feature to distinguish these two species, D. gardneri var. ellipticus is considered here synonymous under S. glaziovii.


*Vernacular names* unknown.

*Trees* 8--14 m tall. *Branchlets* 13--17 mm diam., longitudinally striate, white to light brown sericeous. *Leaves* palmately compound, clustered at the end of branchlets, the internodes up to c. 1 cm long. *Stipules* 5--10 mm long, white to ochre or grayish-sericeous abaxially, glabrous adaxially, apex entire or slightly bifid, the lobes indistinct; petiole 9--30 cm long, 2--3.5 mm diam., cylindrical, longitudinally striate, glabrescent; *leaflet* 6--9, grouped in one whorl, held horizontally; the blade plane, chartaceous to somewhat coriaceous, the adaxial surface glabrescent, the abaxial light brown, becoming grayish-sericeous. *Median leaflet*: petiolule 3--6.5 cm long, unarticulated, laterally compressed, plane to slightly canaliculate adaxially; the blade 7.5--12.6 x 3--6 cm, narrowly elliptic to obovate, the base cuneate to obtuse (rounded), symmetrical to slightly asymmetrical, the margin entire, revolute, the apex usually obtuse to rounded (retuse), sometimes acute, the tip mucronate. *Basal leaflets*: petiolule 0.8--2.7 cm long, the blade 4--8 x 1.8--4 cm, the base usually asymmetrical, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein prominent abaxially, impressed to slightly prominent adaxially; secondary veins 8--13, prominent only abaxially; intersecondary veins usually present; higher orders of venation inconspicuous. *Inflorescence* pseudolateral, erect, fruiting branches becoming pendent, glabrescent; peduncle obscure or up to c. 1.5 cm long,
rachis obscure or up to c. 2 cm long; primary branches 3--5, of which 3 are terminal, these 7.5--14 cm long (bracts caducous, not seen), each bearing 8--14 secondary branches arranged racemosely along the entire length (5--9 terminal), 1.5--4.5 cm long, bracts 2--3 mm long; tertiary branches lacking; ultimate inflorescence units umbellules, with 9--16 flowers, most of which are perfect; floral bracts up to c. 1 mm long. Perfect flowers with pedicel 2--3(--7) mm long; hypanthium light brown to brownish-sericeous, calyx rim with 5 acuminate teeth; petals 5, yellow-greenish, 4.6--5.2 x 2.2--2.9 mm, ovate, sericeous abaxially, apex acute; filaments c. 1 mm long; anthers 3.1--3.2 x 1.3--1.6 mm, oblong, apex rounded, thecae connate above the connective insertion; ovary c. 2.5 mm long; disc glabrous; styles 2, free, 0.8--1.3 mm long, glabrous, recurved in fruit. Stamine flowers not seen. Drupes 10--15 x 13--16 cm, transversely ellipsoid, laterally compressed when dry, glabrescent; pedicel 2--7 mm long; pyrenes 2, 8--9.2 x 5.5--6.3 mm, flattened, transversely semi-elliptic, indurate.

*Schefflera grandigemma* is endemic to submontane rainforests of the surroundings of Santa Teresa, Espírito Santo state (Brazil). It has been collected with flowers in September, October, and March, and with fruits from January to April.

*Schefflera grandigemma* can be distinguished from other species of the Didymopanax group by the combination of leaflets persistently light brown to grayish-sericeous abaxially, with an apex usually obtuse to rounded, the inflorescences without tertiary branches, and the large floral buds and fruits (10--15 x 13--16 mm). *Schefflera grandigemma* most closely resembles *S. ruschiana*, from which it can be distinguished by the leaves with 6--9 (vs. 9--11) leaflets with a typically obtuse to rounded (vs. acute or acuminate, rarely obtuse or rounded) apex, and the erect (vs. pendent) inflorescences without (vs. with) tertiary branches.
Additional selected material. **BRAZIL. Espírito Santo:** Santa Teresa, 2 Mar. 1993 (fl, fr), *Thomaz 1303* (HRCB, MBML, SPF); idem, Santo Antônio, Terreno do Boza, 9 Mar. 1999 (fl, fr), *Kollmann et al. 2046* (MBML, SPF); idem, Terreno do Boza, 26 Oct. 1999 (fl), *Demuner et al. 169* (MBML); idem, 750 m, 14 Jan. 1999 (fr), *Kollmann & Bausen 1548* (MBML, SPF).


*Treelets or trees* 6--16 m tall. **Branchlets** 11--17 mm diam., longitudinally striate, glabrescent. **Leaves** palmately compound, clustered at the end of branchlets, the internodes up to c. 1.5 cm long. **Stipules** 5--12 mm long, glabrescent abaxially, glabrous adaxially, apex entire or slightly bifid, the lobes up to c. 1 mm long; petiole 27--55 cm long, 1.3--5 mm diam., cylindrical, slightly striate longitudinally, glabrescent; **leaflets** (11)12--13, grouped in one whorl, held horizontally; the blade plane, chartaceous, the adaxial surface glabrous, the abaxial light brown-sericeous, glabrescent. **Median leaflet:** petiolule 2.7--6.5 cm long, unarticulated, laterally compressed, plane to canaliculate adaxially; the blade 10--25 x 2.7--5.9 cm, narrowly oblong or elliptic to slightly oblanceolate, the base rounded to truncate, sometimes cuneate, symmetrical to slightly asymmetrical, the margin entire, slightly revolute, the apex acute or acuminate, the tip mucronate. **Basal leaflets:** petiolule 1.5--4.5 cm long, the blade 6.7--14 x 2.1--4 cm, otherwise similar to the median leaflet. **Venation** brochidodromous; main vein prominent on both surfaces,
more conspicuously so abaxially, or only abaxially; secondary veins 8--12, prominent abaxially, impressed adaxially; intersecondary veins absent; higher orders of venation usually conspicuous abaxially. Inflorescence generally pseudolateral, sometimes terminal, with pendent branches when fruiting, sparsely light brown-sericeous; peduncle reduced or up to c. 2 cm long, rachis up to c. 2.5 cm long; primary branches 2--4, of which 2--3 are terminal, these 10--25.5 cm long (bracts up to c. 5 mm long), each bearing 12--16 secondary branches arranged racemosely along the entire length (3--5 terminal), 2.5--10.5 cm long, bracts c. 2 mm long; tertiary branches 8--12, 1--2.5 cm long; bracts c. 1 mm long; ultimate inflorescence units umbellules, with 6--14 flowers, most of which are perfect; floral bracts up to c. 1 mm long. Perfect flowers with pedicel 3--9 mm long; hypanthium light brown to ferrugineous-sericeous, calyx rim with 5 acuminate teeth; petals 5, yellowish, c. 3.5 x 1.8--2.2 mm, elliptic to ovate, sericeous abaxially, apex acute; filaments 0.8--1.1 mm long; anthers c. 2.4 x 1.3--1.7 mm, oblong, apex apiculate, thecae connate above the connective insertion; ovary 1.5--2 mm long; disc glabrous; styles 2, basally connate, 1.2--1.5 mm long, glabrous, recurved in fruit. Stamine flowers with pedicel 1--2 mm long; styles developed; otherwise similar to perfect ones. Drupes 6.5--9 x 11.5--16.2 mm, transversely ellipsoid to obloid, laterally compressed when dry, glabrescent; pedicel 4--7 mm long; pyrenes 2, 5--6 x 3.5--4 mm, flattened, transversely semi-elliptic, cartilaginous.

*Schefflera kollmannii* is endemic to submontane forests of the surroundings of Santa Teresa, Espírito Santo state (Brazil). It has been collected with flowers from May to July, and with fruits from August to December.

*Schefflera kollmannii* can be readily distinguished from other species of the Didymopanax group by the leaves with (11)12--13 narrow leaflets with a glabrescent blade, rounded or truncate
bases, acute or acuminate apices, and usually pseudolateral inflorescences bearing tertiary branches terminating in umbellules with 6--14 flowers.

Fiaschi and Pirani (2007) suggested that \textit{S. kollmannii} might be related to \textit{S. angustissima}. However, molecular data points to a close relationship of this species to \textit{S. capixaba} and \textit{S. ruschiana} (see Chapter 4). \textit{Schefflera kollmannii} may be distinguished from \textit{S. capixaba} by the stipules with a shortly bifid apex (lobes c. 1 mm vs. 5--7.5 mm in \textit{S. capixaba}), and the inflorescences with short primary branches (10--25.5 vs. 92--97 in \textit{S. capixaba}), tertiary branches present (vs. absent), and umbellules with 6--14 (vs. 20--36) flowers. It differs from \textit{S. ruschiana} by leaflets with shorter petiolules (2.7--6.5 vs. 6.5--7.5 cm long), blades about four times (vs. about two times) as long as the petiolules, and usually rounded or truncate (vs. cuneate) bases.

\textit{Additional selected material.} BRAZIL. \textbf{Espírito Santo}: Santa Leopoldina, Rio do Norte, Ribeirão Timbui, Cachoeira do Cravo, 600 m, 18 Aug. 1998 (fr), \textit{Kollmann et al. 366} (MBML); Santa Teresa, Dois Pinheiros, mata do Banestes, 700 m, 31 Jun. 1998 (fl), \textit{Kollmann et al. 149} (MBML, SPF); idem, Penha, sítio do Zurlo, 700 m, 9 Jul. 1998 (fl), \textit{Kollmann et al. 200} (MBML, SPF); idem, Valsugana Velha, Estação Biológica de Santa Lúcia, Trilha Bonita, 5 Sep. 2001 (fr), \textit{Kollmann & Bausen 4517} (MBML, SPF); idem, São Antônio, sítio do Boza, 700 m, 12 Jul. 2001 (fl), \textit{Kollmann et al. 4168} (MBML, SPF).

M!, here designated; isolecotypes G!, F! photo #8063, NY! photo). The material chosen as the lectotype bears both an inflorescence and the terminal portion of a branch, with both young and fully developed leaves. Figs. 241H–L and 254C (see also Fiaschi & Pirani, 2007; Fig. 4K–O).

*Sciadophyllum burchellianum* Baill., Adansonia 12: 147. 1878. TYPE: Brazil. Rio de Janeiro, “Organ Mts, near the town of Magé,” s.d. (fl), *Burchell 2690* (lectotype, P!, here designated; isolecotype, K!). We have chosen as the lectotype material that annotated by Baillon, which is in good condition and bears an original label.

*Vernacular names* unknown.

*Treelets* 0.5--3.5 m tall. *Branchlets* 2--6 mm diam., slightly striate longitudinally, ochre-sericeous, glabrescent. *Leaves* palmately compound, sometimes clustered at the end of branchlets, the internodes up to c. 2 cm long. *Stipules* 4.5--7.5 mm long, ochre-sericeous abaxially, glabrous adaxially, apex bifid, the lobes 2--3 mm long; petiole 14--31.5 cm long, 1.5--2 mm diam., cylindrical, smooth or slightly striate longitudinally, ochre-sericeous or glabrescent; *leaflets* 7--11, grouped in one whorl, held horizontally; the blade plane, membranous, the adaxial surface glabrous, the abaxial glabrescent. *Median leaflet*: petiolule 3.2--5.5 cm long, unarticulated, compressed laterally, canaliculate adaxially; the blade 9--14 x 1.5--3.8 cm, narrowly elliptic or oblong, the base cuneate to rounded, symmetrical to clearly asymmetrical, the margin entire, sometimes with denticules c. 1 mm long, smooth to slightly revolute, the apex acuminate to caudate, the tip mucronate. *Basal leaflets*: petiolule 0.4--1.4 cm long, the blade 4.9--10 x 1.2--2.2 cm, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein
prominent on both surfaces, more conspicuously so abaxially; secondary veins 5--11, prominent abaxially, impressed adaxially; intersecondary veins sometimes present; higher orders of venation usually inconspicuous. *Inflorescence* pseudolateral, flowering and fruiting branches pendent, ochre to light brown-sericeous, glabrescent; peduncle obscure, up to c. 0.5 cm long, rachis obscure or up to c. 9 cm long; primary branches 2--5, of which 2 are terminal, these (5.5--14--33 cm long (bracts caducous, not seen), each bearing 8--17 secondary branches arranged racemosely along the entire length (3--4 terminal), 1.5--7 cm long; bracts 2--4 mm long; tertiary branches, if present, 1.3--1.9 mm long; *ultimate inflorescence units* umbellules or racemules terminating in an umbel, with 10--17 flowers, the peripheral and lateral ones staminate, the central ones perfect; floral bracts 0.5--1 mm long. *Perfect flowers* with pedicel 1--4 mm long; hypanthium ochre-sericeous, calyx rim with 5 triangular-acuminate teeth; petals (4)5, whitish, 2.2--2.8 x 0.7--1.2 mm, triangular to ovate, sericeous abaxially, apex acute or acuminate; filaments 0.6--0.8 mm long; anthers 1.6--2.1 x 0.6--0.8 mm, oblong, apex apiculate, thecae free above the connective insertion; ovary c. 1 mm long; disc glabrous; styles 2, basally connate, c. 0.8 mm long, glabrous, recurved in fruit. *Staminate flowers* with pedicel up to c. 1 mm long; styles developed; otherwise similar to perfect ones. *Drupes* 4.8--7 x 9.5--10.5 mm, transversely ellipsoid, laterally compressed when dry, glabrescent; pedicel 3--7 mm long; pyrenes 2, 4.7--5.3 x 6.1--6.3 mm, flattened, transversely semi-elliptic, cartilaginous.

*Schefflera longipetiolata* is endemic to the Atlantic rainforests of southeastern Brazil, where it has been found in Rio de Janeiro and eastern Minas Gerais states. A few collections from Espírito Santo state (e.g., *Hatschbach 46679* and *Fiaschi et al. 3117*) possibly represent a
closely related, as yet undescribed species (Fiaschi & Frodin, 2006) (see poorly known taxa, *Schefflera* sp. B).

*Schefflera longipetiolata* can readily be distinguished from most species of the Didymopanax group by the short and unbranched habit, stipules deeply bifid apically, membranous leaflets, pseudolateral and pendent inflorescences, and flowers having white petals and anthers with thecae free above the connective insertion. It is very similar to *S. racemifera*, from which it can be distinguished by the leaves with 7--11 [vs. (11)12--14] leaflets, narrowly oblong (9--14 x 1.5--3.8 cm) vs. linear (12--15 × 1.1--1.9 cm) leaflet blades, and inflorescences with (vs. without) secondary branches.


the syntypes listed by Marchal (1878), *Claussen 188* is the best fit to the original description of this species. The lectotype is the sheet with a flowering branch. Figs. 244J–M and 254D (see also Fiaschi & Pirani, 2007; Fig. 5 A–E).

*Treelets* 0.5--2 m tall. *Branchlets* 3--7 mm diam., slightly striate longitudinally, sparsely ochre to grayish-sericeous, glabrescent. *Leaves* unifoliolate, appearing simple (rarely palmately compound with 2--3-leaflet when sterile), the internodes up to c. 3.5 cm long. *Stipules* up to c. 1.5 mm long, ochre-sericeous abaxially, glabrous adaxially, apex entire or slightly bifid, the lobes up to c. 1 mm long; petiole 0.5--5.3 cm long, 1.2--2.5 mm diam., cylindrical, smooth to slightly striate, glabrescent; the blade plane, coriaceous, the adaxial surface glabrescent, the abaxial light brown to ochre or grayish-sericeous or villose; 7.5--13 x 1.8--5.3 cm, elliptic or oblong to ovate, the base cuneate to attenuate, symmetrical, the margin entire, revolute, the apex obtuse to rounded, sometimes truncate or retuse, the tip mucronate. *Venation* brochiododromous; main vein impressed to prominent adaxially, prominent abaxially; secondary veins 8--13, prominent abaxially, impressed adaxially; intersecondary veins sometimes present; higher orders of venation inconspicuous. *Inflorescence* terminal, erect, ochre or light brown-sericeous; peduncle absent or up to c. 1 cm long; rachis 2.4--9 cm long; primary branches 8--32, of which 2--5 are terminal, these 0.9--4 cm long (bracts 1.5--3 mm long); secondary branches, if present, 1--2, arranged racemosely along the entire length, all branches below the terminal umbel, 0.5--1.3 cm long, bracts c. 1 mm long; tertiary branches lacking; *ultimate inflorescence units* umbellules, with 12--26 flowers, most of which are perfect; floral bracts c. 0.5 mm long. *Perfect flowers* with pedicel up to c. 3 mm long; hypanthium ochre to light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5, greenish, c. 2.5 x 1.5 mm, narrowly ovate, sericeous abaxially,
apex acute, thecae connate above the connective insertion; filaments 0.2--0.5 mm long; anthers 1.5--1.9 x 0.8--1.1 mm, oblong, apex apiculate; ovary c. 1 mm long; disc glabrous; styles 2(3), basally connate, c. 1.4 mm long, sometimes with a few trichomes, recurved in fruit. *Staminate flowers* with pedicel c. 1 mm long; styles developed; otherwise similar to perfect ones. *Drupes* 4.5--7 x 7--9 mm, transversely ellipsoid, laterally compressed or 3-costate when dry, glabrescent; pedicel 2--4 mm long; pyrenes 2(3), c. 5.5 x 4 mm, flattened, transversely semi-elliptic, indurate.

*Schefflera lucumoides* is endemic to the *campos rupestres* of the Espinhaço Range south of Belo Horizonte, in Minas Gerais state (Brazil). It grows among rock outcrops, and has been collected with flowers in March and from July to November, and with fruits from November to February.

*Scheffera lucumoides* is the only species of Didymopanax that has unifoliolate leaves. Other species of Neotropical *Schefflera* with unifoliolate leaves include *S. hitchcockii* (Lasser & Maguire) Maguire, Steyerm. & Frodin and *S. montana* (Gleason) Maguire, Steyerm. & Frodin, both from the Crepinella group, and *S. epiphytica* A.C. Sm., from the Sciodaphyllum group.

*Didymopanax simplicifolius* Hoehne was included under synonymy in *Didymopanax lucumoides* (= *S. lucumoides*) by Moura (1983), but this decision was rejected by Frodin and Govaerts (2003) and Fiaschi and Pirani (2007) based not only on morphological but also geographical evidence, since *D. simplicifolius* is only known from the Amazonian forests of northern Mato Grosso (Brazil). Moreover, there seems also to be strong evidence for the transfer of *D. simplicifolius* from *Didymopanax* (= *Schefflera*) to *Dendropanax* Decne. & Planch. (Fiaschi & Pirani, 2007), due to the absence of trichomes, presence of articulated inflorescence branches, cuculate petals, and four connate styles free just apically.
Additional selected material. BRAZIL. Minas Gerais: Itabira do Campo, Serra de Itabira do Campo, Sep. 1887 (fl), Schwacke s.n. (R 34554); idem, Serra do Itabirito, 24 Oct. 1994 (fl), Teixeira s.n. (BHC B 26039); idem, c. 45 km de Belo Horizonte, 1600 m, 12 Feb. 1968 (fr), Irwin et al. 19893 (K, NY, UEC); idem, km 14, 20°14’S, 43°48’W, 1300 m, 14 Nov. 1987 (fl), Pinto s.n. (BHCB 11726); idem, Serra de Ouro Preto para Belo Horizonte, 27 Nov. 1964 (fr), Duarte 8618 (RB, SPF); Rio Acima, Rodovia de Ouro Preto para Belo Horizonte, próximo ao Pico do Itabirito, 20°12’08”S, 43°50’33”W, 1230 m, 12 Jul. 2001 (fl), Fiaschi et al. 908 (SPF).


Didymopanax macrocarpus (Cham. & Schltdl.) Seem., J. Bot. 6: 132. 1868. TYPE: Brazil. “In Brasilia tropica,” Sellow s.n. [lectotype, K!, here designated; isolectotypes, K!, LE! (3 sheets), P!]. The protologue of Panax macrocarpus mentions the absence of flowers in the type material (“Flores non visi”). The specimen here chosen as the lectotype is the only fruiting material known to us among the duplicates of Sellow s.n. and agrees with the original description of the species. Figs. 248A–D and 254E (see also Fiaschi & Pirani, 2007; Fig. 5F–I).

Didymopanax macrocarpus var. capitatus Marchal in Mart. & Eichler, Fl. bras. 11(1): 238. 1878. TYPE: Brasil. “loco speciati ignoto”, Martius s.n. (holotype, M!).
**Vernacular names.** Fruto-de-tucano, imbaubinho-do-campo, mandioca, mandioca-brava, mandiocão, mandioqueiro-do-cerrado, mandioquinha, unha d’anta, verga d’anta, tucaneiro, tukano.

**Treelets or trees** 0.5--5(--9) m tall. **Branchlets** 9--14 mm diam., usually with loose bark falling apart when dry, light brown or ochre to grayish-villose. **Leaves** palmately compound, clustered at the end of branchlets, the internodes up to c. 1.5 cm long. **Stipules** 5--13 mm long, light brown or ochre-villose abaxially, glabrous adaxially, apex bifid, the lobes c. 0.5 mm long; petiole 5.5--37 cm long, 2--3 mm diam., cylindrical, slightly striate longitudinally, densely villose to glabrescent; **leaflet**s (3--)5--9, grouped in one whorl, held horizontally; the blade plane to slightly conduplicate, coriaceous, the adaxial surface glabrescent (sometimes proximally villose on main vein), the abaxial persistently light brown or ochre to grayish-villose. **Median leaflet:** petiolule 0.1--4.5 cm long, unarticulated, compressed laterally, canaliculate adaxially, ochre to grayish-villose; the blade 4--20 x 1.5--9 cm, elliptic or oblong, sometimes slightly obovate, the base cuneate to rounded, the margin entire, revolute, sometimes undulate, the apex usually rounded or retuse to truncate, rarely acute, the tip mucronate. **Basal leaflets:** sub-sessile or with petiolule up to c. 1 cm long, the blade 2.1--14.2 x 1--6.4 cm, otherwise similar to the median leaflet. **Venation** brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 4--12, prominent abaxially, impressed to slightly prominent adaxially; intersecondary veins sometimes present; higher orders of venation inconspicuous. **Inflorescence** terminal (rarely pseudolateral when fruiting), erect or with decumbent branches, becoming pendent when fruiting, densely ochre to grayish-villose; peduncle up to c. 5 cm long, rachis up to c. 4.5 cm long; primary branches 2--8, of which 2--3
are terminal, these 9--35 cm long (bracts 6--8 mm long), each bearing 7--36 secondary branches arranged racemously along the entire length (2--6 terminal), 1.5--16.5 cm long, bracts 2--6 mm long; tertiary branches, if present, 0.8--3 cm long; ultimate inflorescence units umbellules, with 7--20 flowers, most of which are perfect; floral bracts 1--1.5 mm long. Perfect flowers with pedicel 1--8 mm long; hypanthium ochre-villose, calyx rim with 5 acuminate teeth; petals 5, yellowish, 3--3.5 x 1.3--1.6 mm, ovate to narrowly ovate, tomentose abaxially, apex acute; filaments 0.5--0.9 mm long; anthers 1.7--2 x 1--1.2 mm, elliptic or ovate, apex apiculate, thecae connate above the connective insertion; ovary 1--1.5 mm long; disc glabrous; styles 2(3), free, 1.5--2 mm long, glabrous, recurved in fruit. Staminate flowers with pedicel up to c. 1.5 mm long; styles shorter; otherwise similar to perfect ones. Drupes 4.5--8 x 8--15 mm, transversely ellipsoid, laterally compressed or rarely 3-costate when dry, glabrescent; pedicel 3--11 mm long; pyrenes 2(3), 5--8 x 4.5--7.5 mm, flattened, transversely semi-elliptic, sometimes adaxially thickened, indurate or cartilaginous.

*Schefflera macrocarpa* is very common and widespread in eastern areas of the Brazilian Cerrado (Fiaschi & Pirani, 2008). It can be found in the states of Bahia, Goiás, eastern Mato Grosso, Minas Gerais, São Paulo, and the Distrito Federal, growing mostly in open habitats and, occasionally, in cerradão forests. Some collections from Mato Grosso and Mato Grosso do Sul listed by Moura (1983) under *S. macrocarpa* belong, in our opinion, to *S. malmei* (see below). *Schefflera macrocarpa* has been collected with flowers and fruits throughout the year.

*Schefflera macrocarpa* can be readily distinguished from other species of the Didymopanax group by the frequent presence of a loose exfoliating bark in dry material, leaflets with coriaceous blades and persistently light brown or ochre to grayish-villose indumentum
abaxilly, an usually rounded or retuse to truncate apex, and large (4.5--8 x 8--15) and very fleshy fruits.

Fiaschi & Marcato 136 (SPF); Cristalina, Serra dos Cristais, 12 km N de Cristalina, 1600 m, 3 Apr. 1973 (fr), Anderson 8012 (UEC); Formosa, Área do Exército, Córrego Tapetinga, c. 15°34’S, 47°18’W, 30 Nov. 1997 (fr), Oliveira 801 (IBGE, K); Itameri, rodovia de Campo Alegre de Goiás para Catalão, 17°03’15’’S, 47°45’02’’W, 900 m, 31 Jan. 2000 (fl), Fiaschi & Marcato 140 (SPF); Luziânia, BR-040, estrada que liga Luziânia a Cristalina, 16°27’17’’S, 47°48’22’’W, 905 m, 10 Jun. 2002 (fr), Mendonça et al. 4783 (IBGE, SPF); Mozarlândia, estrada entre Mozarlândia e Rubiataba, 15°00’14’’S, 50°00’58’’W, 590 m, 26 Jan. 2000 (fl, fr), Fiaschi & Marcato 114 (SPF); Niquelândia, c. 8 km S de Niquelândia, 750 m, 23 Jan. 1972 (fr), Irwin et al. 34869 (K, NY); Pirenópolis, Rio Maranhão, 27 Jul. 1952 (fr), Macêdo 3686 (SP); São João da Aliança, Serra Geral do Paraná, 7 km S da estrada de São João da Aliança, 1100 m, 22 Mar. 1973 (fr), Anderson 7652 (UEC). Mato Grosso: Rio Turvo, c. 210 km N of Xavantina, 29 May 1966 (fl, fr), Irwin et al. 16279 (K). Minas Gerais: Alegre, rodovia de Guarda-Mor para Alegre, 18°06’13’’S, 47°03’41’’W, 730 m, 1 Feb. 2000 (fl), Fiaschi & Marcato 143 (SPF); Belo Horizonte, Fazenda Baleia, 19 Jan. 1943 (fl), Viegas & Barreto s.n. (SP 268165); Botumirim, trilha para Campina do Palmital, c. 16°54’S, 43°02’W, 23 Mar. 2000 (fl), Fiaschi et al. 182 (SPF); Conceição do Mato Dentro, 7 km E-NE de São José de Almeida, 19°26’S 43°48’W, 10 Feb. 1991 (fr), Arbo et al. 4775 (SPF); Corinto, c. 5 km W de Corinto, 725 m, 4 Mar. 1970 (fl), Irwin et al. 26945 (K, NY, UEC); Coromandel, Serra dos Óculos, c. 70 km N de Patrocínio, 1050 m, 1 Feb. 1970 (fl), Irwin et al. 25847 (UEC); Couto de Magalhães de Minas, 5 km NE de Couto de Magalhães de Minas, 960--1000 m, 13 Apr. 1973 (fl, fr), Anderson et al. 8736 (UB); Cristália, ramo vicinal de acesso ao Morro do Chapéu, c. 16°44’S, 42°55’W, 23 Mar. 2000 (fr), Fiaschi et al. 178 (SPF); Diamantina, rodovia para Couto de Magalhães de Minas, ramo vicinal à esq. c. 1,5 km da ponte sobre o córrego Carrapato, c. 18°07’S, 43°32’W, 18 Jun. 2000 (fr),
Fiaschi & Costa 313 (SPF); Joaquim Felício, Serra do Cabral, estrada de Joaquim Felício para Augusto de Lima, c. 17°45’S, 44°12’W, 25 Mar. 2000 (fr), Fiaschi et al. 205 (SPF); Lavras, Serrinha, estrada de acesso à Retransmissão da CEMIG, 7 Dec. 1983 (fr), Leitão Filho et al. 15365 (UEC); Mato Verde, estrada para Rio Pardo de Minas, c. 6 km do trevo, 15°23’00’S, 42°45’32’’W, 985 m, 11 May 1998 (fr), Pirani et al. 4256 (SPF); Monte Alegre de Minas, rodovia para Uberlândia, 18°53’10’S, 48°27’28’’W, 810 m, 30 Jan. 2000 (fl), Fiaschi & Marcato 135 (SPF); Ouro Branco, Serra do Ouro Branco, 20°30’11’S, 43°39’24’’W, 1400 m, 28 May 1997 (fr), Mello-Silva 1395 (SPF); Ouro Preto, Bairro Saramenha, Estrada Real, c. 100 m da bifurcação Lavras Novas-Chapada, 27 Mar. 2001 (fl, fr), Groppo Jr. & Unwin 660 (SPF); Paracatu, Serra da Anta, c. 2 km N de Paracatu, 700 m, 3 Feb. 1970 (fl), Irwin et al. 25916 (K, NY, UEC); Sabará, Jan. 1916 (fl, fr), Hoehne s.n. (SP 32004); Santana de Pirapama, Fazenda Inhame, 21 Mar. 1982 (fl), Pirani et al. CFSC8030 (SPF); Santana do Riacho, PARNA da Serra do Cipó, caminho da base do IBAMA do Rio Cipó para o Capão dos Palmitos, 900 m, 25 Mar. 1991 (fr), Pirani et al. CFSC12032 (SPF); São João del Rei, Serra do Lenheiro, 16 Feb. 1985 (fl), Krieger 20368 (CESJ); São Roque de Minas, Parque Nacional da Serra da Canastra, trilha para a parte inferior da Casca d’Anta, 900--1200 m, 30 Sep. 1999 (fr), Mello-Silva et al. 1687 (SPF); Serro, estrada para Gouveia, 10 Dec. 1996 (fr), Marcondes-Ferreira et al. 13211 (UEC); Tiradentes, 1 May 1985 (fr), Krieger et al. 20552 (CESJ, SPF). São Paulo: Alumínio, 3 Dec. 1998 (fr), Tozzi et al. 308 (UEC); Caieiras, 4 May 1945 (fl, fr), Hoehne s.n. (SPF 141035); Campinas, Campo Grande, 12 Dec. 1940 (fr), Viegas & Lima s.n. (SP 48961); Campos de Cunha, Estrada de Campos de Cunha para os Campos da Bocaina, 22°52’15.2’’S, 44°47’21.1’’W, 21 Jun. 2006 (fr), Fiaschi et al. 3040 (CEPEC, K, MBM, MO, NY, RB, SP, SPF, UB); Franco da Rocha, Parque Estadual do Juquery, 23°18’S, 46°48’W, 24 Mar. 2002 (fr),


Mato Grosso, “Santa Anna da Chapada,” 14 Jun. 1903, Malme 3501 (S!, 3 sheets); 10 Aug. 1902, Malme (S not seen); 27 May 1903, Malme (S not seen). Among the syntypes mentioned by Harms (1932), the only one that we were able to see was Malme 3501. This material fits the original description, but none of the sheets are individually satisfactory for typification. Until we have the opportunity to examine all of the relevant material, we refrain from designating a lectotype. Figs. 248E and 254F (see also Fiaschi & Pirani, 2007; Fig. 5 J–L).

Vernacular name unknown.

Treelets 1--5 m tall. Branchlets 15--20 mm diam., smooth, densely ochre to grayish-villose. Leaves palmately compound, clustered at the end of branchlets, the internodes indistinct or up to c. 1.5 cm long. Stipules c. 1 cm long, light-brown or ochre to grayish-villose abaxially, glabrous adaxially, apex slightly bifid, the lobes up to c. 1 mm long; petiole 12--42 cm long, 2.2-5 mm diam., cylindrical, striate longitudinally, glabrescent; leaflets 6--10, grouped in one whorl,
held horizontally; the blade plane, coriaceous, the adaxial surface glabrous, sometimes proximally villose, the abaxial persistently ochre to grayish-villose, sometimes glabrescent on main and secondary veins. Median leaflet: sessile or petiolule up to c. 2 cm long, unarticulated, glabrescent; the blade 8--27.5 x 2.6--10.2 cm, oblanceolate (rarely narrowly elliptic), the base attenuate to cuneate, the margin entire, revolute, the apex truncate and retuse or rounded, rarely obtuse, the tip mucronate. Basal leaflets: subsessile; the blade 5.3--16.5 x 1.9--6.5 cm, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 8--12 pairs, prominent abaxially, impressed adaxially; intersecondary veins absent; higher orders of venation inconspicuous. Inflorescence terminal or rarely pseudolateral, erect, persistently ochre to grayish-villose or glabrescent; peduncle obscure to c. 3 cm long, rachis obscure to c. 2 cm long; primary branches 2--4, all or most of which are terminal, these (3--)9--30 cm long (bracts 5--8 mm long), each bearing 9--23 secondary branches arranged racemosely along the entire length (2--3 terminal), (1--)5.5--20 cm long, bracts 2--3 mm long; tertiary branches, if present, 7--13, 0.5--3 cm long; ultimate inflorescence units umbellules, with c. 15 flowers, the peripheral ones staminate, the central ones perfect; floral bracts up to c. 1.5 mm long. Perfect flowers with pedicel up to c. 7 mm long; hypanthium ochre to light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5, yellowish, 2.9--3 x 1.3--1.5 mm; filaments 0.3--0.7 mm long; anthers c. 1.7--1.8 x 0.8--1 mm, elliptic or ovate, apex apiculate, thecae connate above the connective insertion; ovary c. 2 mm long; disc glabrous; styles 2(3), free, 1.2--1.4 mm long, glabrous, recurved in fruit. Staminate flowers subsessile, with pedicel c. 1 mm long; styles developed; otherwise similar to perfect ones. Drupes 5--8 x 11--13 mm, transversely ellipsoid, laterally compressed or rarely 3-costate
when dry, glabrescent; pedicel 4--8 mm long; pyrenes 2(3), c. 7.5 x 5.5--6.5 mm, flattened, transversely semi-elliptic, indurate.

*Schefflera malmei* is found in western areas of the Brazilian Cerrado (Fiaschi & Pirani, 2008), where it has been collected in Goiás, Mato Grosso, Mato Grosso do Sul and São Paulo states. Individuals of this species grow mostly in open areas, but occasionally are found in *cerradão* forests. It has been collected with flowers from May to February, and with fruits from December to June.

*Schefflera malmei* is very similar to, and sometimes considered under synonymy in *S. macrocarpa* (Moura, 1983), but Frodin and Govaerts (2003) and Fiaschi and Pirani (2007) accepted these species as distinct, mostly because of the presence of oblanceolate leaflets in *S. malmei*, and usually elliptic or oblong leaflets in *S. macrocarpa*. Moreover, the geographic distribution ranges of *S. malmei* and *S. macrocarpa* overlap only in the small region at southwestern Goiás and eastern Mato Grosso states. Moreover, individuals of both species can be distinguished morphologically even when precise locality information is lacking.

*Additional selected material. BRAZIL. Goiás:* Chapadão do Céu/Mineiros, Parque Nacional das Emas, 17°49’--18°28’S, 52°39’--53°10’W, 10 Dec. 1998 (fl, fr), *Batalha 2394* (SPF); Serranópolis, Rodovia Jataí (GO) - Aporé (MS), km 115, 18°43’52.5”S, 52°04’18.5”W, 700 m, 1 Jun. 2006 (fr), *Fiaschi & Filho 2972* (MO, SPF). *Mato Grosso:* Alto Araguaia, BR 364, 10 km W of Alto Araguaia, 2 Feb. 1978 (fr), *Pedersen 12156* (MBM); Chapada dos Guimarães, MT 020, between Buriti and Água Fria, 15°23’S, 55°47’W, 1 Feb. 1995 (fl), *Dubs 1824* (E, ESA, K, Z); Cuiabá, Rio Caxipozinho, próximo à Cachoeira Véu de Noiva, c. 15°--
16°S, 55°-56°W, 21 Oct. 1985 (fl), Cid Ferreira et al. 6558 (SPF, UEC); Diamantino, Faz. Pequeno Figueiredo, c. 4 km N de Diamantino, 14°20’S, 56°27’W, 22 May 1997 (fl, fr), Souza et al. 16840 (ESA); Tangará da Serra, próximo ao Rio Verde (Chapada dos Parecis), 14°23’S, 58°18’W, 1 Sep. 1986 (fl), Santos 203 (IBGE, MBM); Nova Xavantina, 7 km S of Xavantina, on Aragarças road, 14°38’S, 52°15’W, 15 Nov. 1968 (fl), Harley & Souza 11080 (K, P); Tangará da Serra, Próximo ao Rio Verde (Chapada dos Parecis), 3 Sep. 1986 (fl), Santos 203 (IBGE, INPA, RB). **Mato Grosso do Sul:** Coxim, 1 km ao Norte, 9 Feb. 1975 (fr), Hatschbach et al. 36016 (MBM); Camapuã, W of Rio Verde, Fazenda Ponte de Lobo, 64 km from Camapuã, on the road to Paraíso (BR 060), 19°23’S, 53°36’W, 13 Nov. 1996 (fl), Ratter et al. 7686 (K); Nova Andradina, 21°48’S, 53°06’W, 28 Oct. 1981 (fl), Dambrós 227 (RB). **Rondônia:** Vilhena, 4 km próximo de Vilhena, 12°45’S, 60°10’W, 26 Oct. 1979 (fl), Vieira et al. 677 (INPA, MG, RB). **São Paulo:** Rancharia, Rodovia SP-4, 13 May 1970 (fr), Hatschbach 24224 (MBM).


(presumably at C, not seen; P!, 2 sheets). We have not been able to examine all of the relevant type material, so we refrain from designating a lectotype.


*Panax spinosus* Poir. in J.B.A.M. de Lamarck, Encycl., Suppl. 2: 778. 1812. This name seems to be the result of Poiret’s misspelling of Willdenow’s *Panax speciosus*. This is evident because Poiret attributed *P. spinosus* to Willdenow, and also because the description he provided for *P. spinosus* was reproduced from that of *P. speciosus*, including the same type information given by Willdenow, despite the lack of the collector’s name (*Bredemeyer*).


Didymopanax morototoni var. poeppigii Marchal in Mart. & Eichler, Fl. bras. 11(1): 240. 1878. TYPE: Peru. “Maynas Alto, silvae ad Mission,” July 1930, Poeppig 1959 [lectotype, W!, here designated; isolectotypes, LE! (3 sheets), P!]). The sheet at W is the only known to us that bears Marchal’s annotation, and is here chosen as the lectotype.


Vernacular names. Aceite-caspi (Peru), aguaita camino (Venezuela), ankú ká (Venezuela, Panare), árbol-lenteja (Ecuador), botador (Venezuela), caixeta, cajete (Colombia), casavahout (Suriname), guitarrero (Bolivia), huármí-huármí (Peru), imbaubão, imbaubarana, kanahoire (Guyana), karahoro (Suriname, Arawak), kuyuwiyu (Venezuela, Yekuna), lenguig bru (Venezuela), majei (Venezuela, Yanomami), malamala (French Guiana, Wayana), mandiocaím, mandiocão, mandiocão-da-mata, mandioqueiro, marupá, marupaúba, matataúba,
molototo (Wayapi), morototó, morototó-da-mata, mountain trumpet (Honduras), mucutuba, murucututú, naij (Bolivia), paragua caspi (Peru), parapará, pata-gallo (Dominican Republic), pau-caixeta, pau-de-jangada, pau-mandioca, paunayek (Venezuela, Pemón), sambacuim, sambacuíma, sambaquim, seniush (Peru), sentus (Peru), suntuch (Peru, Huambisa), sun sun (Venezuela), tagrume macho (Puerto Rico), tobitoutou (French Guiana, Paramaka), tumba-maco (Colombia), utucuro de monte alto (Peru), wede hi rāti (Brazil, Xavante)

Treelets or trees 5--30 m tall. Branchlets 13--25 mm diam., striate longitudinally, light brown or ochre to grayish-sericeous. Leaves palmately compound, clustered at the end of branchlets, the internodes up to c. 5 mm long. Stipules 1.4--3 cm long, light brown to grayish-sericeous abaxially, glabrous adaxially, apex bifid, the lobes 2--6 mm long; petiole 27--90.5 cm long, 2.5--8 mm diam., cylindrical, slightly striate longitudinally, ochre to grayish-sericeous, glabrescent; leaflets 7--13, grouped in one whorl, held horizontally; the blade plane to slightly conduplicate at base, chartaceous to subcoriaceous, the adaxial surface glabrous, the abaxial light brown or ochre to grayish-sericeous, except sometimes on the glabrescent main and secondary veins. Median leaflet: petiolule 4--12 cm long, unarticulated, cylindrical to compressed laterally, slightly canaliculate adaxially; the blade 12.5--40 x 2.3--16.5 cm, oblong to obovate or elliptic, sometimes narrowly elliptic, the base usually rounded or truncate, sometimes cuneate or cordate, symmetrical to asymmetrical, the margin entire, slightly revolute, sometimes undulate, the apex acuminate to caudate, the tip sometimes mucronate. Basal leaflets: petiolule 1.3--5 cm long, the blade 8.5--19 x 2.3--7 cm, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 8--16 pairs, similar to the median leaflet; intersecondary veins absent; higher orders of venation
generally inconspicuous. *Inflorescence* terminal, sometimes pseudolateral when fruiting, erect, becoming pendent when fruiting, light brown or ochre to grayish-sericeous; peduncle up to c. 3 cm long, rachis 3.5--11 cm long; primary branches 2--24, of which 2--5 are terminal, these 5.5--46.5 cm long (bracts 7--14 mm long), each bearing 6--36 secondary branches arranged racemously along the entire length [(2)3--5 terminal], 1.5--33 cm long, bracts 2--6 mm long; tertiary branches usually present, 13--33, 0.8--6.5 cm long; quaternary branches, if present, 4--11 mm long; *ultimate inflorescence units* umbellules, with 10--40 flowers, the peripheral ones staminate, the central ones perfect; floral bracts c. 1 mm long. *Perfect flowers* with pedicel 1--4 mm long; hypanthium light-brown or ochre to grayish-sericeous, cayx rim with 5 acuminate teeth; petals 5, greenish, 2.1--2.7 x 1.1--1.5 mm, ovate, sericeous abaxially, apex acute; filaments 0.2--0.6 mm long; anthers 1.2--1.5 x 0.7--0.9 mm, oblong or ovate, apex apiculate, thecae connate above the connective insertion; ovary 1--1.5 mm long; disc pubescent; styles 2(3), free, 0.8--1.3 mm long, glabrous, recurved in fruit. *Staminate flowers* with pedicel 0.5--3 mm long; styles developed or sometimes vestigial; otherwise similar to perfect ones. *Drupes* 4--7.5 x 7.5--11 mm, transversely ellipsoid, laterally compressed or rarely 3-costate when dry, glabrescent; pedicel 3--16 mm long; pyrenes 2(3), 5--7.5 x 3.5--5.5 mm, flattened, transversely semi-elliptic, indurate.

*Schefflera morototoni* is the most widely distributed species of *Schefflera* in the Neotropical region, ranging from southern Mexico and the Greater Antilles to southern Brazil. It is largely absent from the main areas of dry vegetation in South America, such as the Brazilian Caatinga, the Chaco, and the Caribbean coast of Colombia and Venezuela (Fig. 254G), and is
especially common as a pioneer species in disturbed forests. *Schefflera morototoni* has been collected with flowers and fruits throughout the year.

*Schefflera morototoni* can be distinguished from the remaining species of the Didymopanax group mostly by the terminal and well-branched inflorescences, with as many as 24 primary branches bearing both secondaries and (almost always) tertiaries along the entire length. The flowers have a pubescent disc and a bicarpellate ovary, and the fruits are relatively small (4--7.5 x 7.5--11) and glabrescent.

Several names have been applied to plants now placed under *S. morototoni* during the late 18th and the 19th centuries, and many of these do not seem to merit specific recognition (see Frodin & Govaerts 2003 for a current list of synonyms). Among the most distinctive taxa described under *S. morototoni* are *S. morototoni* var. *sessiliflora* and *S. morototoni* var. *angustipetala*, both created and validly published under *Didymopanax* by Marchal (1878).

*Schefflera morototoni* var. *sessiliflora* was treated as distinct from the typical variety by Fiaschi et al. (2007), who suggested that it could have resulted from hybridization between *S. macrocarpa* and *S. morototoni*. Here, however, we refrain from recognizing infraspecific taxa under *S. morototoni* because such distinctions become much less clear when the total morphological variability of the species is taken into consideration across its entire geographic range.

Marchal (1878) established *Didymopanax morototoni* var. *angustipetalus* (= *S. morototoni* var. *angustipetala*) based on the presence of petals three or more times longer than wide, and umbels with reflexed peduncles (= secondary branches). Frodin and Govaerts (2003) indicated that this variety “may merit specific rank but [is] so far known from only two collections, neither fruiting” (p. 358). In our opinion, *S. morototoni* var. *angustipetala* is
indistinguishable from *S. tamatamaensis*, which was described based exclusively on fruiting material (see comments after this species, below).

*Additional selected material.* 

**BOLÍVIA.** 

**Beni:** Vaca Diez, 25 km E of Riberalta on the road to Guayaramerín, 11°05’S, 65°50’W, 230 m, 23 Sep. 1981 (fr), *Solomon 6406* (MO, NY).  

**Cochabamba:** Carrasco, km 240 en carretera Santa Cruz-Villa Tunari, 17°00’S, 64°46’W, c. 290 m, 10 Jul. 1989 (fr), *Smith et al. 13657* (MO, NY).  

**La Paz:** Iturralde, Comunidad de Buena Vista, 14°22’S, 67°33’W, 180 m, 18 Apr. 1995 (fl), *de Walt et al. 189* (K).  

**Pando:** 74 km SW Cobija, Puerto Oro, 11°25’S, 69°05’W, c. 250 m, 17 Aug. 1988 (fr), *Pennington et al. 135* (K);  

**Santa Cruz:** Velasco, Campamento Toledo, 1550 m SW de la casa, 14°42’S, 61°09’W, 180 m, 11 Jun. 1994 (fl), *Guillen & Chore 1844* (MO, K).  

**BRAZIL.**  


**Bahia:** Camamu, Acarai, estrada ao lado S, 1 Jul. 1971 (fl), *Santos 1715* (CEPEC); Ilhéus, Mata da Esperança, estrada a 2 km a partir da antiga ponte do Rio Fundão, 14°46’55’’S,
(SPF); Araraquara, beira da Rodovia Washington Luiz, 15 May 1995 (fr), *Bernacci et al. 1603* (HRCB, SPF); Cajuru, Fazenda Santana, área 2, 3 Oct. 1999 (fr), *Nicolau et al. 1809* (SP);


**ECUADOR.** **Napo:** Yasuni National Park, Adjacent to km 47 of Maxus-built Pompeya Sur-Iro road, 00°42’01”S, 76°28’05”W, 210--330 m, 17 Sep. 1996 (fl), *Bass 371* (MO, NY, QCA). **Pastaza:** Pastaza Canton, Parroquia Villano, 01°25’S, 77°20’W, 400 m, 26 Sep. 1991 (fr), *Espinoza & Gualinga 841* (K, MO). **Zamora-Chinchipe:** Zamora Canton, Jambo Bajo,


Carabobo: c. de Bejuma, sector El Rincón, Finca La Calceta, ladera Sur de Fila Las Mesas, cabeceras del Río Bejuma, 10°12’N, 68°13’W, 800 m, Nov. 1996 (fr), Riina et al. 236 (VEN).

Cojedes: Hato El Socorro, 100 m, Feb. 1981 (st), Delascio 9246 (VEN). Delta Amacuro: Departamento Tucupita, mountain area c. 13 km by road ESE of the town of Sierra Imata, 08°23’N, 62°23’W, 400 m, Apr. 1979 (fr), Davidse & González 16582 (VEN). Miranda: Cerros
de Bachiller, above Quebrada Bachiller, south of Caño Rico and Bachiller, 10°06’N, 65°53’W, 20–690 m, Mar. 1978 (fr), Steyermark & Davidse 116982 (VEN). **Portuguesa:** Guanare, Entre Boquemonte y El Algarrobo, 500 m, 27 Sep. 1981 (fl), Ortega & Stergios 1314 (NY). **Sucre:** Distrito Sucre, 8 km south of Santa Fe by road, 10°16’N, 64°24’W, 230 m, Nov. 1981 (fr), Davidse & González 19087 (VEN). **Zulia:** Cerro Los Manantiales, east of Río Guanare, west of Hacienda Los Manantiales, 12 km west of Corpozulia Campamento Carichuano, 11°01’00”N, 72°20’30”W, 600 m, Jun. 1980 (st), Steyermark et al. 123275 (VEN). Collón, alrededores de Casigua El Cubo, setor Las Cruces, vía Casigua-El Carmelo- Pozo T-218, Aug. 1979 (fl), Bunting & Fucci 7840 (VEN).

24. **Schefflera pimichinensis** Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 55. 1984. TYPE: Venezuela. Amazonas: Sabana El Venado, on left bank of Caño Pimichín, above Puerto Pimichín, 140 m, 14 Apr. 1953 (fl), Maguire & Wurdack 35635 [holotype, NY! (2 sheets); isotype, K! (4 sheets), VEN! (3 sheets)]. Figs. 249A–E and 254H (see also Frodin, 1997; Fig. 17).

_Treelets or trees_ 5–8 m tall. _Branchlets_ c. 13 mm diam., striate longitudinally, light brown-sericeous. _Leaves_ palmately compound, the internodes not seen. _Stipules_ c. 20 mm long, light brown-sericeous abaxially, glabrous adaxially, apex slightly bifid, the lobes c. 1 mm long; petiole 25–48 cm long, c. 3.5 mm diam., cylindrical, longitudinally striate, light brown to grayish-sericeous, glabrescent. _Leaflets_ 5–7, grouped in one whorl, held horizontally; the blade plane, chartaceous to subcoriaceous, the adaxial surface glabrescent, the abaxial light brown to grayish-sericeous. _Median leaflet:_ petiolule 4–6 cm long, slightly compressed laterally,
canaliculate adaxially; the blade 12--24 x 6--10 cm, elliptic to ovate, the base obtuse to rounded, symmetrical, the margin entire, smooth to strongly revolute, the apex cuspidate to caudate, sometimes shortly acuminate, the tip mucronulate. Basal leaflets: petiolule 1.5--3.8 cm long, the blade 10.5--16 x 5.8--7.5 cm, the base usually asymmetrical, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent abaxially, slightly prominent or impressed adaxially; secondary veins 16--20, prominent abaxially, impressed adaxially; intersecondary veins distinctive; higher orders of venation inconspicuous. Inflorescence terminal, erect, ferrugineous-sericeous; peduncle up to c. 1.5 cm long, rachis 10--30 cm long; primary branches 10--14, of which 3--4 are terminal, these 13--23 cm long (bracts c. 5 mm long), each of which with 2--15 secondary branches below the terminal umbel, or up to 40 (4 terminal) along the proximal primary branches, 5--10 mm long, bracts c. 3 mm long; tertiary branches lacking; ultimate inflorescence units umbellules, with 15--25 flowers, the peripheral ones staminate, the central ones perfect; floral bracts up to c. 1 mm long. Perfect flowers with pedicel c. 2 mm long; hypanthium ferrugineous or light brown-sericeous, calyx rim typically tearing among the 5 acuminate teeth; petals 5, color unknown, c. 2.8 x 1.3 mm, ovate, sericeous abaxially, apex acute; filaments c. 0.5 mm long; anthers c. 1.3 x 0.8 mm, oblong, apex rounded, thecae free above the connective insertion; ovary 1--1.5 mm long; disc glabrous; styles 2(3), free, c. 1.2 mm long, with a few trichomes, recurved in fruit. Staminate flowers with pedicel 1--2 mm long; styles shorter; otherwise similar to perfect ones. Drupes c. 5 x 8 mm, transversally ellipsoid, laterally compressed or 3-costate when dry, glabrescent; pedicel 5--9 mm long; pyrenes 2(3), not measured, flattened.
Schefflera pimichinensis can be found in southwestern Venezuela, where it is known only from the type locality, at Sabana El Venado, close to the border with Brazil and Colombia. The vegetation of this area, popularly known as savanna, is more probably an Amazonian caatinga forest on white-sand (Anderson, 1981). This species was collected with flowers and fruits in April.

Schefflera pimichinensis can be readily distinguished from other species of the Didymopanax group by the terminal light brown to ferrugineous-sericeous inflorescences with an elongated main axis (10--30 cm long), bearing very elongated proximal primary branches (up to c. 42 cm long), along which the umbellules are arranged on short (up to c. 1 cm long) secondary branches. The flowers have short pedicels (not longer than 2 mm long), the styles have a few trichomes and the anthers have free thecae above the insertion of the connective. The leaflets of S. pimichinensis are reminiscent of those from S. dichotoma, with distinctive intersecondary veins, and a (usually) caudate apex.

Maguire et al. (1984) suggested that S. pimichinensis was probably closely related to S. tamatamaensis, an opinion that is shared here. Schefflera plurispicata and S. pubicarpa might be other closely related species. Schefflera pimichinensis differs from S. tamatamaensis and S. pubicarpa by having shorter secondary branches (5--10 vs. 9--28 mm long), and smaller fruits (c. 5 x 8 vs. 11--13 x 13--16 mm). From S. plurispicata it differs mostly by having flowers grouped in umbellules (vs. spicules), smaller flowers, and the leaflets with distinctive intersecondary veins (vs. intersecondary veins absent), and an obtuse to rounded (vs. cordate) base.

Additional selected material. VENEZUELA. Amazonas: Sabana El Venado, left bank of Caño Pimichín, 140 m, 14 Apr. 1953 (fl), Maguire & Wurdack 35636 (NY).
25. *Schefflera plurifolia* Fiaschi & Frodin, Brittonia 60(3): 280. 2008. TYPE: Brazil. Rondônia: Estrada de Vilhena para Juína (BR 174), km 10. Estrada vicinal à esquerda. Ramo de acesso à sede da Fazenda, a c. 3 km. 12°39'52.7''S, 60°07'52.9''W, 563 m, 8 Jun. 2006 (fl), Fiaschi & Geremias 3027 [holotype, SPF! (3 sheets); isotypes, CEPEC!, INPA!, K!, MBM!, MO!, NY!]. Figs. 242H–K and 255A (see also Fiaschi et al., 2008; Fig. 3).

Treelets 1.5--8 m tall. Branchlets 7--9 mm diam., slightly striate longitudinally, whitish to light-brown or grayish-sericeous. Leaves palmate-pinnately compound, the internodes 1--2.5 cm long; first-order leaflet units 5--7, palmately arranged, the median leaflet with 5--9 imparipinnately arranged leaflets, the lateral first-order units with a progressively smaller number of leaflets, sometimes simple. Stipules 12--20 mm long, whitish to light brown or grayish-sericeous abaxially, glabrous adaxially, apex bifid, the lobes 3--7 mm long; petiole 16.5--37 cm long, cylindrical, slightly striate longitudinally, glabrescent. Leaflets held horizontally; the blade plane, membranous, adaxially glabrous, abaxially glabrescent. Median first-order leaflet units: petiolule 10--19 cm long, cylindrical; rachilla 11.5--18 cm long, sometimes with the proximal pair of leaflets further pinnately compound; terminal leaflet: petiolule 1.5--4.6 cm, the blade 6--13 x 2.5--4.8 cm, obovate, elliptic or ovate, the base slightly to abruptly attenuate, symmetrical to strongly asymmetrical, the margin entire, smooth, the apex acuminate or long-acuminate to caudate; lateral leaflets: size progressively smaller and with shorter petioles, except the basal pair, which is sometimes reduced and sessile. Venation (of terminal leaflet) brochidodromous; main vein prominent on both surfaces, more conspicuously abaxially; secondary veins 5--7, slightly prominent on both surfaces; intersecondary veins absent, higher
orders of venation inconspicuous. *Inflorescence* terminal, erect, becoming pendent when fruiting, grayish-sericeous, glabrescent; peduncle up to c. 1 cm long, rachis 1.5--3.5 cm long; primary branches 7--10, of which 3--4 are terminal, these 15--26 mm long (bracts 2.5--5 mm long); secondary branches lacking; ultimate inflorescence units racemules, with 35--45 flowers, the proximal ones staminate, the terminal ones perfect; floral bracts 1--1.5 mm long. Perfect flowers with pedicel 4--18 mm long; hypanthium grayish-sericeous, calyx rim with 5 acuminate teeth; petals 5, greenish, 2.5--3 x 1.2--1.5 mm, ovate, sericeous abaxially, apex acute; filaments 0.3--0.7 mm long; anthers 1.5--2 x 0.7--0.8 mm, oblong, apex rounded, thecae connate above the connective insertion; ovary c. 1.5 mm long; disc glabrous; styles 2, free, 1.2--1.5 mm long, glabrous, recurved in fruit. Staminate flowers with pedicel 1--2(--5) mm long; styles developed; otherwise similar to perfect ones. Drupes 7--8 x 12.5--13 mm, transversally ellipsoid, laterally compressed when dry, glabrescent; pedicel 1.2--3 cm long; pyrenes 2, 7--9 x 6.5--7 mm, flattened, transversely semi-elliptic, cartilaginous.

*Schefflera plurifolia* occurs in southern Amazonian rainforests, especially in ecotonal areas with the Brazilian Cerrado, where it has been collected in the Brazilian states of Amazonas, Rondônia and Mato Grosso. It grows on sandy or clayey soils, and is usually found along streams. It has been collected with flowers from May to October, and with fruits from May to August.

*Schefflera plurifolia* is unique among species of the Didymopanax group in having palmate leaves with pinnately compound leaflets. The inflorescence morphology of this species is somewhat similar to that of *S. racemifera*, with racemules terminating in umbel along the primary branches. Staminate and perfect flowers are spatially separated within each
inflorescence unit, and there also seems to be a temporal separation in the development of these flower types, with staminate ones opening earlier than the perfect, and becoming detached from the inflorescences by the time the perfect flowers reach anthesis (Fiaschi et al., 2008).

*Additional selected material.* **BRAZIL.** **Amazonas:** Humaitá, Estrada Humaitá-Jacarecanga, Km 64, a 1 Km ao Norte, 07°45’S, 62°32’W, 18 Jun. 1982 (fl), *Teixeira et al. 1212* (INPA, NY). **Mato Grosso:** Comodoro, Fazenda Dolce Vitta, 12°44’19”‘S, 60°03’04”‘W, 1 Aug. 1997 (fr), *Árbocz et al. 4389* (ESA, MT). **Rondônia:** Vilhena, BR 364, Rodovia Porto Velho-Cuiabá, Km 18, 12°13’S, 60°61’W, 10 Jun. 1984 (fr), *Cid et al. 4501* (INPA, NY); estrada Vilhena (RO) a Juína (MT), ramo vicinal à esq., c. 10 km de Vilhena, 12°38’33.4”‘S, 60°08’58.4”‘W, 593 m, 8 Jun. 2006 (fr), *Fiaschi & Geremias 3026* (SPF); a 38 Km de Vilhena, 12°45’S, 60°10’W, 29 Oct. 1979 (fl), *Vieira et al. 779* (INPA, NY); 1 km W from BR 364, c. 1 km N of road to São Sebastião, 24 May 1984 (fl), *Frame et al. 164* (INPA, NY).

**26. Schefflera plurispicata** Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 52. 1984. TYPE: Brazil. Amazonas: Serra da Neblina, Serra Pirapucú, 1250--1300 m, 29 Jan. 1966 (fl), *Silva & Brazão 60941* [holotype, NY! (3 sheets); isotype, IAN!, K! (2 sheets), MG!, VEN! (2 sheets)]. Figs. 246F–K and 255B (see also Maguire et al., 1984; Fig. 6).

*Vernacular names* unknown.

*Trees* c. 25 m tall. *Branchlets* not seen. *Leaves* palmately compound, the internodes not seen. *Stipules* c. 13 mm long, light brown-sericeous abaxially, glabrous adaxially, apex bifid, the
lobes c. 3 mm long; petiole 25--65 cm long, 3.5--7 mm diam., cylindrical, slightly striate longitudinally, glabrescent; leaflets 7--9, grouped in one whorl, held horizontally; the blade plane, chartaceous or subcoriaceous, the adaxial surface glabrescent, the abaxial light brown-sericeous. Median leaflet: petiolule 5--10 cm long, unarticulated, slightly compressed laterally, slightly canaliculate adaxially; the blade 13.4--28 x 7.8--13 cm, ovate, the base cordate, symmetrical to slightly asymmetrical, the margin entire, slightly revolute, the apex cuspidate, the tip mucronulate. Basal leaflets: petiolule 0.8--3.2 cm long, the blade 10.3--24.2 x 6.8--11.5 cm, the base asymmetrical, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent abaxially, slightly prominent to impressed adaxially; secondary veins 10--14, prominent abaxially, impressed adaxially; intersecondary veins absent; higher orders of venation evident abaxially. Inflorescence terminal, presumably erect, light brown-sericeous; peduncle and rachis not seen; primary branches of unknown number, 15.5--42 cm long (bracts c. 15 mm long), each bearing 45--65 secondary branches arranged racemosely (3--4 terminal), 2--3.5 cm long, bracts 4--6 mm long; tertiary branches lacking; ultimate inflorescence units spicules, with 25--30 flowers, the proximal ones staminate, the terminal ones perfect; floral bracts c. 1 mm long. Perfect flowers with pedicel up to c. 1 mm long; hypanthium light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5, color unknown, c. 4 x 1.8--2 mm, ovate, sericeous abaxially, apex acute; filaments 1--1.5 mm long; anthers c. 3 x 1.5 mm, oblong, apex rounded, thecae connate above the connective insertion; ovary 2--2.5 mm long; disc glabrous; styles 2, free, c. 0.5 mm long, with a few trichomes, presumably recurved in fruit. Staminate flowers sessile; styles vestigial; otherwise similar to perfect ones. Drupes unknown.
Schefflera plurispicata is known from a single collection in montane rainforests of the Serra Pirapucú, in the Neblina massif on the Brazilian-Venezuelan border.

Schefflera plurispicata is a distinctive species due to the presence of spiculate ultimate inflorescence units, leaflets with relatively short petiolules (the blade at least two and a half times longer than the petiolules), and blades with a cordate base.


Vernacular names unknown.

Species nova a S. confusa lamina foliorum anguste elliptica ad oblanceolata (vs. elliptica ad ovata), abaxialiter castanea sericea (vs. glabrescenti), chartacea ad subcoriacea (vs. membranacea ad subchartacea), apice acuminato vel cuspidato (vs. apice caudato) differt; a Schefflera decaphylla foliolis 10--25 (vs. 7--15) in 2--3 verticillis [vs. in 1(2) verticillis], lamina abaxialiter castanea sericea (vs. vulgo glabrescenti), fructibus maioribus (12.5--14 x 11--11.5 vs. 8--9--10--11 mm) differt.

Trees 14--15 m tall. Branchlets 1.5--2 cm diam., longitudinally striate, light brown-sericeous. Leaves palmately compound, clustered at the end of branchlets, the internodes barely noticeable. Stipules 10--13 mm long, light brown-sericeous abaxially, glabrous adaxially, apex slightly bifid, the lobes c. 2 mm long; petiole 26--36 cm long, cylindrical to compressed laterally,
longitudinally striate, persistently light brown to grayish-sericeous or glabrescent; leaflets 10--25, grouped in two or three whorls, held horizontally; the blade plane, chartaceous to subcoriaceous, the adaxial surface glabrous, the abaxial surface light-brown to grayish-sericeous. Median leaflet (of outer whorl): petiolule 8.5--11.5 cm long, compressed laterally, canaliculate adaxially; the blade 12--17 x 4--5.4 cm, narrowly elliptic, the base cuneate to attenuate, symmetrical, the margin entire, revolute, the apex acuminate to cuspidate, the tip sometimes mucronulate. Basal leaflets (of outer whorl): petiolule 2.5--7 cm long, the blade 13.7--14.5 x 3.5--4.6 cm, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent abaxially, impressed to slightly prominent adaxially; secondary veins 12--14, prominent abaxially, impressed adaxially; intersecondary veins sometimes present; higher orders of venation inconspicuous. Inflorescence terminal, initially erect(?), becoming pendent when fruiting, light brown to grayish-sericeous; main axis minute (c. 5 mm long); primary branches 2, both terminal, 17.5--20 cm long (bracts c. 5 mm long); each bearing 9--10 secondary branches (2--3 terminal), 4.8--8.4 cm long, bracts c. 2.5 mm long; tertiary branches 1.3--2.7 cm long; ultimate inflorescence units umbellules, number of flowers unknown; floral bracts not seen. Flowers unknown. Drupes 12.5--14 x 11--11.5 mm, broadly ellipsoid, 5-costate when dry, glabrescent; pedicel 6--11 mm long; pyrenes 5, c. 12--12.5 x 6 mm, flattened, transversely semi-elliptic, cartilaginous.

*Schefflera prancei* is known only from the type locality, at the western-most tip of Brazil (Serra do Divisor National Park). This species very likely also occurs in adjacent Peru, but no collections have been made in this country. *Schefflera prancei* grows in terra-firme rainforests on sandy-clayey soils. It was collected with fruits in April.
Schefflera prancei can be readily distinguished from the remaining species of the Didymopanax group by bundle-compound leaves with leaflets grouped in 2--3 whorls, and the flowers with a 5-carpellate ovary. It is named after Sir Ghilean T. Prance, for his enormous contribution to the knowledge of the Amazonian flora. This species is very similar to *S. confusa*, from which it can be distinguished by leaflets with a narrowly-elliptic to slightly oblanceolate (vs. elliptic to ovate) blade, the acuminate to cuspidate (vs. caudate) blade apex, and the light brown-sericeous (vs. glabrescent) undersurface. In addition, the fruits appear to be smaller in *S. prancei* (12.5--14 x 11--11.5 vs. 15--16 x 13--16), but this may be due the fact that they were unripe in the type collection. Unlike *S. confusa*, which grows mostly on white-sand forests (campinarana), *S. prancei* grows in terra firme forests on sandy-clayey soils.

From *S. decaphylla*, the new species can be distinguished by a combination of characters, including leaflets arranged in 2--3 [vs. 1(2) whorls], blades that are light brown-sericeous (vs. glabrescent) abaxially and with an acuminate to cuspidate (vs. usually rounded or obtuse) apex, and the larger fruits (12.5--14 x 11--11.5 vs. 8--9 x 10--11 mm). A few collections of *S. decaphylla*, however, do have either leaflets arranged in two whorls, a persistently sericeous undersurface, or blades with an acuminate apex (e.g., Ferreira et al. 6597 and 7055, INPA), but the geographic distributions of the two species do not overlap. *Schefflera decaphylla* does not appear to be distributed west of 66°W longitude, whereas *S. prancei* is found only west of 73°W (Figs. 253C and 255C).

Additional selected material. BRAZIL. Acre: Mâncio Lima, PARNA Serra do Divisor, Trilha para a Cachoeira Formosa, 07°26’47.4”S, 73°39’27.4”W, 225 m, 22 Aug. 2008 (st), Fiaschi et al. 3309 (NY).
28. *Schefflera pubicarpa* Fiaschi & Plunkett, sp. nov. TYPE: Brazil. Amazonas. Rodovia de Manaus (AM) a Porto Velho (RO), trecho entre os rios Castanho e Tupana, na altura do km 158. Hotel Tupana. 04°04’26”S, 60°40’11”W, 25 m alt., 18 July 2007 (fr), *Fiaschi 3187* [holotype, SPF! (3 sheets); isotypes to be distributed to CEPEC!, INPA!, K!, MO!, NY!, RB!]. Figs. 250 and 255D.

*Vernacular names* unknown.

Species nova a *Schefflera morototoni* fructibus maioribus (12--13 x 15--16 mm vs. 4--6.5 x 7.5--11 mm) persistenter pubescenti (vs. fructibus glabrescenti), inflorescentiis sine ramiis tertiaris (vs. ramiis tertiaris vulgo praesentibus) differt; a *Schefflera tamatamaensis* habitu arboris magnae (vs. habitu arbusculae), foliis 8--10 (vs. 4--7)-foliolatis, floribus stylis pubescenti (vs. floribus stylis glabris), fructibus transverse late ellipticis vel latissime obovatis (vs. latissime ovatis), pyrenis laevigatis compressis semi-oblatis vel semi late depressis-obovatis (vs. semi late depressis-ovoideis) differt.

*Trees* 15--25 m tall. *Branchlets* 2.8--3.5 cm diam., longitudinally striate, light brown-sericeous. *Leaves* palmately compound, clustered at the end of branchlets, the internodes up to c. 1 cm long. *Stipules* c. 2 cm long, light brown-sericeous abaxially, glabrous adaxially, apex bifid, the lobes c. 2 mm long; petiole 21.5--55 cm long, 2.5--5 mm diam., cylindrical, slightly striate longitudinally, glabrescent; *leaflet* 8--10, grouped in one whorl, held horizontally; the blade plane to slightly conduplicate, chartaceous to subcoriaceous, the adaxial surface glabrescent, the
abaxial light-brown to grayish-sericeous when mature. *Median leaflet:* petiolule 4--8.5 cm long, unarticulated, slightly compressed laterally, slightly canalicate adaxially; the blade 14.5--26.5 x 3.8--8 cm, narrowly elliptic or oblong to lanceolate, the base rounded, symmetrical to slightly asymmetrical, the margin entire, revolute, sometimes slightly undulate, the apex acuminate to caudate, the tip mucronulate. *Basal leaflets:* petiolule 1.8--3.7 cm long, the blade 10--20 x 2.5--6.5 cm, asymmetrical, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 9--12, prominent abaxially, impressed adaxially; intersecondary veins sometimes present; higher orders of venation inconspicuous, sometimes conspicuous adaxially. *Inflorescence* terminal, initially erect, branches becoming patent when fruiting, light brown-sericeous; peduncle 0.5--1.5 cm long, rachis 5--8.5 cm long; primary branches 3--40, 2--6 of which are terminal, these 8.7--36 cm long (bracts 4--6 mm long), each bearing one terminal hermaphroditic umbel, or 22--75 secondary branches arranged racemosely (4--6 terminal), 9--28 mm long, bracts 2--3 mm long; tertiary branches lacking; *ultimate inflorescence units* umbellules, number of flowers unknown; floral bracts c. 1 mm long. *Perfect flowers* with pedicel 2--3 mm long; hypanthium light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5, yellowish, 3.7--3.8 x 1.3--1.8 mm, narrowly ovate to ovate, sericeous abaxially, apex acute or acuminate; filaments 0.8--1 mm long; anthers c. 1.8 x 1--1.1 mm, oblong, apex rounded, thecae free above the connective insertion; ovary 1--1.5 mm long; disc pubescent; styles 2(3), free, c. 1.2 mm long, pubescent, recurved in fruit. *Staminate flowers* not seen. *Drupes* 12--13 x 15--16 mm, obloid or broadly depressed obovoid, compressed laterally or rarely 3-costate when dry, pubescent; pedicel 4--6 mm long; pyrenes 2(3), 10.5--12.5 x 6.5--7.5 mm, flattened, semi-oblate or semi widely depressed-ovoiate, cartilaginous.
*Schefflera pubicarpa* grows in central Amazonian *terra-firme* forests on sandy-clayey soils. It is known only from the type locality, where it is a rather common species. This species has been collected with fruits in July. Flowering materials are unknown — the flowers analyzed here were pickled from the type collection, and are deposited at the spirit collection at SPF.

*Schefflera pubicarpa* resembles *S. tamatamaensis*, from which it can be distinguished by the habit (large trees, vs. unbranched treelets up to 6 m tall), leaves with 8--10 (vs. 4--7) leaflets, the inflorescences with reflexed (vs. ascending) secondary branches, the flowers with trichomes along the styles (vs. styles glabrous), and the obloid or broadly depressed obovoid (vs. broadly depressed ovoid) drupes with laterally flattened and smooth (vs. swollen and irregularly sculptured) pyrenes.

One of the specimens included in *S. pubicarpa* (*Silva et al. 852*) was collected about 100 km north of the type locality. In this specimen, the leaflets have smaller (c. 15 x 4, vs 21--26.5 x 7--8) and narrowly elliptic (vs. lanceolate) blades, and obloid (c. 13 x 13 mm) (vs. broadly depressed obovoid, 11--13 x 14--16 mm) fruits. The inflorescences may have only 3 primary branches bearing 19--20 secondary branches (INPA 36943), or up to 16 primary branches, each bearing one terminal hermaphroditic umbel and 5--6 lateral sterile bracts (MO 3499822). These features may be sufficiently distinctive to recognize this collection as another new species, but we believe that these differences may prove to represent intraspecific variation as more collections become available.

Several fragmentary samples from the Amazonian white-sand forests of northeastern Peru (Iquitos region), southeastern Colombia, and eastern Ecuador appear to belong here. However, we consider it premature to place them under *S. pubicarpa* before additional
collections become available, especially considering the geographic distance separating these collections from *S. pubicarpa* (more than 1000 km). Because there is no data supporting a continuous distribution over the western Amazon, these fragmentary specimens are thus treated as a poorly known species (see *Schefflera* sp. C, below).

*Additional selected material.* **BRAZIL.** **Amazonas:** Estrada Manaus-Porto Velho, trecho entre os rios Castanho e Tupana, 20 Jul. 1972 (fr), *Silva et al.* 964 (INPA); Estrada Manaus-Porto Velho, km 50, estrada Castanho-Tupana, 18 Jul. 1972 (fr), *Silva et al.* 852 (INPA, MO).


**Vernacular names.** Poy-no-yek (Arekuna).

**Trees** 12–30 m tall. **Branchlets** 20–30 mm diam., longitudinally striate, light brown or ferrugineous-sericeous. **Leaves** palmately compound, clustered at the end of branchlets, the
internodes up to c. 5 mm long. Stipules c. 15 mm long, light brown to ferrugineous-sericeous abaxially, glabrous adaxially, apex bifid, the lobes 2--3 mm long; petiole 32--53 cm long, cylindrical to compressed adaxially, slightly striate longitudinally, light brown to ferrugineous-sericeous; leaflets 7--10, grouped in one whorl, held horizontally; the blade usually conduplicate, chartaceous to coriaceous, the adaxial surface glabrescent, the abaxial light brown to ferrugineous-sericeous. Median leaflet: petiolule 5--11.5 cm long, compressed laterally, slightly canaliculate adaxially; the blade 15--39 x 7--11.5 cm, elliptic to slightly ovate or obovate, symmetrical, the base obtuse to rounded, sometimes truncate, the margin entire, smooth to slightly revolute, the apex cuspidate, the tip sometimes mucronate. Basal leaflets: petiolule 0.5--3.5 cm long, the blade 12.5--22.5 x 5.2--9.6 cm, slightly asymmetrical, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent abaxially, almost impressed adaxially; secondary veins 12--14, prominent abaxially, impressed adaxially; intersecondary veins sometimes present; higher orders of venation inconspicuous. Inflorescence terminal, erect, becoming pendent when fruiting, light brown to ferrugineous-sericeous; penduncle up to c. 1 cm long, rachis obscure or up to 1 cm long; primary branches 2--4, most terminal, these 6--16.5 cm long (bracts 3--9 mm long), each bearing 4--14 secondary branches arranged racemosely (4--8 terminal), 2--9.5 cm long, bracts 3--4 mm long; tertiary branches, if present, 10--20 (4--8 terminal), up to c. 4 cm long; ultimate inflorescence units umbellules, with 10--15 flowers, the peripheral ones staminate, the central ones perfect; floral bracts up to c. 1 mm long. Perfect flowers subsessile, the pedicel up to c. 1.5 mm long; hypanthium light brown to ferrugineous-sericeous, calyx rim with 5 acuminate teeth; petals 5, color unknown, 2--3 x 1.3--1.4 mm, triangular to ovate, sericeous abaxially, apex acute; filaments 0.3--0.5 mm long; anthers 1.5--2.2 x 1 mm, ovate, apex acute to obtuse, thecae connate above the connective insertion; ovary c. 1.5
mm long; disc glabrous; styles (4)5(6), free, c. 0.5 mm long, glabrous, recurved in fruit.  

Staminate flowers subsessile, the pedicel up to c. 1 mm long; styles vestigial; otherwise similar to perfect ones. Drupes c. 10--15 x 10--17 mm, obloid, (4)5(6)-costate when dry, glabrescent; pedicel 2--17 mm long; pyrenes (4)5(6), 8.5--13 x 6--9 mm, flattened, transversely semi-elliptic, indurate or cartilaginous.

*Schefflera quinquecarinata* is found in montane forests (1000--1500 m) of the Guayana Shield. It has probably a widespread occurrence in this area, and is rather common at Sierra de Lema, southeastern Venezuela. However, it has not been widely collected and may have been overlooked by plant collectors because of its resemblance to *S. morototoni*, and thus undercollected due to the large size of mature individuals (usually 20--30 m tall). *Schefflera quinquecarinata* has been collected with flowers from January to March, and with fruits in March and July.

*Schefflera quinquecarinata* can be readily distinguished from the remaining species of the Didymopanax group by the flowers with (4)5(6)-locular ovaries, the leaflet blades with a light brown to ferrugineous-sericeous undersurface and a cuspidate apex, and the flowers with short (up to c. 1.5 mm long) pedicels. *Schefflera quinquecarinata* resembles *S. decaphylla*, from which it is distinct by the leaflets (usually glabrescent and with an obtuse or rounded apex in *S. decaphylla*), and the subsesille (vs. distinctly pedicellated) flowers with glabrous (vs. apically with trichomes) styles. Moreover, these two species do not appear to co-occur, as *S. decaphylla* is mostly found at lowland forests (below 300 m) and *S. quinquecarinata* is found exclusively at areas above 1000 m.
Schefflera yutagensis does not appear to merit specific rank, and is here considered under S. quinquecarinata. The inflorescences with tertiary branches, short pedicels, and glabrescent fruits, mentioned by Steyermark & Holst (1988) as diagnostic to the former, do not appear to warrant recognition at the species level. For example, the degree of inflorescence branching is often variable within species of the Didymopanax group (Moura, 1983), as the secondary branches can bear only one terminal hermaphroditic umbel (e.g., Tillet et al. 44849 and Steyermark & Nilsson 483) or 10--20 tertiary branches arranged racemosely (e.g., Prance et al. 10159 and Steyermark et al. 92954).

Additional selected material. BRAZIL. Roraima: Serra dos Surucucus, NW of Mission station, 02°42--47’N, 63°33--36’W, 21 Feb 1969 (fl), Prance et al. 10159 (MG, NY, VEN).
GUYANA. Upper Mazaruni River Basin, Merume Mountain, 1140 m, 7 Jul. 1960 (fr), Tillet et al. 44849 (NY).
VENEZUELA. Bolivar: Cerro Venamo, afluen te izquierdo del Río Venamo desde el campamento cerca de la unión con el afl uente derecho, 950--1000 m, 10 Jan. 1964 (fl), Steyermark et al. 92954 (NY, VEN). Drenaje del Río Cuyuní, a lo largo del Río Anawaray-Parú, vecinidades del km 134 y campamento 134 al sur de El Dorado, 1300--1350 m, 25 Dec. 1970 (fr), Steyermark & Dunsterville 104451 (MER, VEN).

30. Schefflera racemifera Fiaschi & Frodin, Kew Bull. 61(2): 188. 2006. TYPE: Brazil, Espírito Santo, Santa Maria de Jetibá, Belém, Terreno de Paulo Seick, 700 m, 18 Mar. 2003, Kollmann & Berger 6057 (holotype, MBML!). Figs. 241M--N and 255F (see also Fiaschi & Frodin, 2006; Fig. 1).
Vernacular name unknown.

Treelets 2--4 m tall. Branchlets 5.5--7 mm diam., longitudinally striate, ochre-sericeous, glabrescent. Leaves clustered at the end of stem, the internodes up to c. 5 mm long. Stipules 6--10 mm long, ochre-sericeous abaxially, glabrous adaxially, apex bifid, the lobes 4--5 mm long; petiole 14--23.5 cm long, 1.2--1.8 mm diam., cylindrical, smooth to slightly striate longitudinally, glabrescent; leaflets 11--14, grouped in one whorl, held horizontally; the blade plane, membranous, the adaxial surface glabrous, the abaxial glabrescent. Median leaflet: petiolule 2.4--3.5 cm long, compressed laterally, canaliculate adaxially; the blade 12--15 × 1.1--1.9 cm, linear to narrowly oblong, the base rounded to obtuse, symmetrical, the margin entire or sometimes with small denticules toward the apex, smooth, the apex acuminate to caudate, the tip mucronate. Basal leaflets: petiolule 8--10 mm long, the blade 7--10 x 1--1.2 cm, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 10--15, prominent abaxially, impressed adaxially; intersecondary veins sometimes present, higher orders of venation inconspicuous. Inflorescence usually pseudolateral (rarely terminal), erect or patent, becoming pendent when fruiting, ochre-sericeous; peduncle reduced, up to c. 5 mm long, rachis 1--4 cm long; primary branches 3--6, of which 2--3 are terminal, these 13--27 cm long (bracts 3--5 mm long); secondary branches lacking; ultimate inflorescence units racemules terminating in umbel, with 45--50 flowers, the proximal ones staminate, the 30--35 distal ones perfect; floral bracts 1--3 mm long. Perfect flowers with pedicel 4--6 mm long; hypanthium ochre-sericeous, calyx rim with 5 acuminate teeth; petals 5, whitish, c. 2.5 x 1 mm, ovate, sericeous abaxially, apex acuminate; filaments c. 0.8 mm long; anthers c. 1.5 x 0.5 mm, oblong, apex acute, thecae free above the
connective insertion; ovary c. 1 mm long; disc glabrous; styles 2(3), free, c. 1.2 mm long, glabrous, recurved in fruit. Staminate flowers not seen. Drupes c. 7 x 9.5--10 mm, transversely ellipsoid, compressed laterally or rarely 3-costate when dry, glabrescent; pedicel 11--14 mm long; pyrenes 2(3), 6--6.5 x 4.5--5 mm, flattened, transversely semi-elliptic, cartilaginous.

*Schefflera racemifera* is known from just a single population, growing in semideciduous forests at Espírito Santo state (Brazil). It has been collected with flowers from December to March, and with fruits in March.

*Schefflera racemifera* resembles *S. longipetiolata*, from which it can be distinguished by leaves with (11)12--14 (vs. 7--11) leaflets, blades linear (12--15 x 1.1--1.9 cm) vs. narrowly oblong (9--14 x 1.5--3.8 cm), the number of secondary veins (11--17, vs. 5--11), inflorescences lacking secondary branches (vs. secondary branches present), flowers racemosely (vs. umbellately) arranged, and with longer (4--6, vs. 1--4 mm) pedicels.

*Additional selected material.* BRAZIL. Espírito Santo: Santa Maria de Jetibá, Belém, Terreno de Paulo Seick, 700 m, 3 Dec. 2002 (fl), Kollmann et al. 5800 (MBML, SPF); idem, 14 Jan. 2003 (fl), Kollmann et al. 5893 (MBML).

Trees 9--10 m tall. Branchlets 14--18 mm diam, longitudinally striate, whitish to ochre or light brown-sericeous. Leaves palmately compound, clustered at the end of branchlets, the internodes up to c. 1 cm long. Stipules c. 8 mm long, whitish to ochre or light brown-sericeous abaxially, glabrous adaxially, apex slightly bifid, the lobes up to c. 1 mm long; petiole 30--42 cm long, cylindrical, longitudinally striate, glabrescent; leaflets 9--11, in one whorl, held horizontally; the blade plane, chartaceous, the adaxial surface glabrescent, the abaxial surface light brown or ferrugineous to grayish-sericeous. Median leaflet: petiolule 6.5--7.5 cm long, laterally compressed, slightly canalicate adaxially; the blade 14--16.5 x 4.8--5.7 cm, narrowly elliptic to obovate, symmetrical, the base cuneate, the margin entire, slightly revolute, sometimes undulate, the apex acute or acuminate, rarely obtuse or rounded, the tip mucronate. Basal leaflets: petiolule 3.2--4.2 cm long, the blade 9--11.7 x 2.7--4.5 cm, otherwise similar to the median leaflet. Venation brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 8--12, prominent abaxially, impressed adaxially; intersecondary veins sometimes present; higher orders of venation inconspicuous. Inflorescence pseudolateral, pendent, light brown-sericeous to glabrescent; peduncle up to c. 2 cm long, rachis obscure or up to c. 5 mm long; primary branches 3, of which two are terminal, these 23--24 cm long (bracts 6--9 mm long), each bearing 16--21 secondary branches arranged racemosely along the entire length (8--9 terminal), 3--6.5 cm long, bracts c. 3 mm long; tertiary branches 6--8, up to 1--3 cm long; ultimate inflorescence units umbellules with 10--15 flowers; floral bracts up to c. 1 mm long. Perfect flowers with pedicel 5--10 mm long; hypanthium light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5, yellow-greenish, c. 4.6 x 2.2--2.5 mm, ovate, sericeous abaxially, apex acute; filaments c. 1 mm long; anthers yellow, 3.1--3.2 x 1.6 mm, oblong, apex rounded, thecae connate above the connective insertion; styles 2, free, c. 2 mm
long, glabrous, recurved in fruit. *Staminate flowers* with pedicel 2--3 mm long; styles developed; otherwise similar to perfect ones. *Drupes* 10--11 x 12--13 mm, obloid, laterally compressed when dry, glabrescent; pedicel 8--12 mm long; pyrenes 2, c. 8.2--8.5 x 5.5--5.8 mm, flattened, transversely semi-elliptic, indurate.

*Schefflera ruschiana* is known only from a few collections from submontane rainforests near Santa Teresa, Espírito Santo state (Brazil). It has been collected with flowers in January, and with fruits in April.

*Schefflera ruschiana* is very similar to *S. grandigemma*, from which it can be distinguished by leaves with (9)10--11 (vs. 6--9) leaflets, the blades with a usually acute to acuminate (vs. usually obtuse to rounded) apex, the pendent inflorescences with (vs. without) tertiary branches, and the flowers with longer pedicels [5--10 vs. 2--3(--)]. The morphological limits between these two species are not clear, and additional collections may provide evidence to unite these two taxa.

*Additional selected material. BRAZIL. Espírito Santo:* Santa Teresa. Estação Biológica de Santa Lúcia, 19°57′59″S, 40°32′16″W, c. 600 m, 11 Apr. 2003 (fr), *Fiaschi et al. 1457* (CEPEC, MBML, NY, SPF), idem, Trilha do Sagui, 650--800 m, 14 Apr. 1994 (fr), *Thomaz 741* (MBML, VIES).

K!, here designated). Among the syntypes listed by Marchal (1878), we were able to examine  
*Riedel 803* [K! LE! (3 sheets), P! (2 sheets), W!] and *Talbot 985* (K!). *Sello 840* and *1020* (both B) were probably destroyed in 1943, and duplicates are unknown to us. Despite the wide 
distribution of duplicates of *Riedel 803*, and the fact that 2 sheets were annotated by Marchal in LE, the specimens are in bad condition. *Talbot 985* was examined by Marchal and is in very 
good condition, despite the lack of locality information or Marchal’s annotation. Because it 
matches closely to the original description and plate (Marchal 1878, p. 67), it is here chosen as 
the lectotype. Figs. 251A–G and 255H (see also Fiaschi & Pirani, 2007; Fig. 7A–D).

*Vernacular names.* Imbaubão-do-nativo (ES), matataúba.

*Treelets or trees* 2--10 m tall. *Branchlets* 6--14 mm diam., slightly striate longitudinally, 
light brown to grayish-sericeous, glabrescent. *Leaves* palmately compound, clustered at the end 
of branchlets, the internodes up to c. 1 cm long. *Stipules* 5--6 mm long, sericeous abaxially, 
glabrous adaxially, apex slightly bifid, the lobes inconspicuous, up to c. 1 mm long; petiole 9.5-- 
40 cm long, cylindrical, slightly striate longitudinally, glabrescent; *leaflets* 4--7, grouped in one 
whorl, held horizontally; the blade plane, chartaceous to subcoriaceous, the adaxial surface 
glabrous, the abaxial light brown to grayish-sericeous, glabrescent. *Median leaflet*: petiolule 3--
7.5 cm long, unarticulated, cylindrical to slightly compressed laterally, canaliculate adaxially; the 
blade 6--16 x 3--8.5 cm, elliptic to obovate, the base attenuate to cuneate, symmetrical to slightly 
asymmetrical, the margin entire, slightly revolute, the apex obtuse to rounded or retuse, the tip 
mucronulate. *Basal leaflets*: petiolule 0.2--3.5 cm long, the blade 4.5--11.5 x 1.5--6.5 cm, 
otherwise similar to the median leaflet. *Venation* brochidodromous; main vein impressed to
slightly prominent adaxially, prominent abaxially; secondary veins 4--9, prominent abaxially, impressed adaxially; intersecondary veins sometimes present; higher orders of venation inconspicuous, or sometimes conspicuous abaxially on mature leaflets. *Inflorescence* terminal or pseudolateral, initially erect, becoming pendent when fruiting, grayish-sericeous to glabrescent; peduncle up to c. 2.5 cm long, rachis obscure or up to c. 3 cm long; primary branches 2--5, of which 2--3 are terminal, these 14.5--70 cm long (bracts 3--4 mm long), each bearing 12--35 secondary branches arranged racemosely along the entire length or restricted to the distal half (2--5 terminal), 2--19 cm long, bracts 1--2 mm long; tertiary branches, if present, 12--19 (2--4 terminal), or 1--7 branches below the terminal inflorescence unit, 4--9 mm long; *ultimate inflorescence units* umbellules, with 12--17 flowers, most of which are perfect (terminal umbels) or staminate (lateral umbels), or sometimes with just a few perfect flowers on terminal-most branches; floral bracts c. 0.5 mm long. *Perfect flowers* with pedicel 1--2 mm long; hypanthium ochre to light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5(6), greenish, 2.2--2.7 x 1.1--1.3 mm, elliptic or ovate, sparsely sericeous to glabrescent abaxially, apex acuminate or acute; filaments 0.3--0.4 mm long; anthers 1.4--1.5 x 0.7--1 mm, oblong, apex rounded or apiculate, thecae connate above the connective insertion; ovary c. 1 mm long; disc glabrous; styles 2(3), free or connate at base, 0.5--0.8 mm long, glabrous, recurved in fruit. *Staminate flowers* with pedicel up to c. 2 mm long; styles developed; otherwise similar to perfect ones. *Drupes* 4.5--7 x 7--9 mm, transversely ellipsoid, laterally compressed or rarely 3-costate when dry, glabrescent; pedicel 2--12 mm long; pyrenes 2(3), c. 5.5--6 x 4--4.5 mm, flattened, transversely semi-elliptic, indurate.
Schefflera selloi is endemic to the restingas of coastal Brazil, with occurrence data ranging from Itacaré (Bahia state) to Guarapari (Espírito Santo state). Small individuals (sometimes less than 3 m tall) are usually found in open areas called campos nativos and mussunungas, while trees up to 10 m tall are known from forest habitats. This species has been collected with flowers from November to March and with fruits from November to May.

Schefflera selloi can be distinguished from other species of the Didymopanax group by the glabrescent leaflets with an obtuse to rounded or retuse apex, the inflorescences with a short main axis bearing a few (2--5) primary branches, and tertiary branches usually present, and the flowers with petals glabrescent abaxially.

This species is very distinctive from all remaining species of the Didymopanax group from the Brazilian Atlantic forests, and appears to be more closely related to species from the cerrados of the Brazilian Plateau, such as S. burchelli and S. vinosa.

Additional selected material. BRAZIL. Bahia: Alcobaça, rodovia de Alcobaça para Prado, c. 500 m do entroncamento com estrada para Teixeira de Freitas, 17°30’S, 39°13’W, 17 May 2000 (fr), Fiaschi et al. 269 (SPF); Belmonte, Barrolândia, Estação Experimental Gregório Bondar, 48 km E of BR 101, on road to Belmonte, 16°08’S, 39°15’W, 12 May 1993 (fr), Thomas et al. 9869 (CEPEC); Camacan, estrada para Canavieiras, 25 km de Camacan, Faz. Santa Terezinha, 26 Nov. 1968 (fl), Almeida 242 (CEPEC); Maraú, 75 km de Ubaitaba, na estrada para Campinhos, 14°00’S, 38°58’W, 1 Feb. 1993 (fr), Kallunki & Pirani 416 (SPF); Mucuri, km 6 da rodovia de Mucuri para Nova Viçosa, ramal à esq., 10 m, 20 May 1980 (fr), Mattos Silva & Santos 776 (CEPEC, UEC); Nilo Peçanha, km 1 a 4 da Rodovia Nilo Peçanha/Cairu, 20 Feb. 1975 (fl), Santos 2873 (CEPEC); Nova Viçosa, km 9 da estrada para Mucuri, 2 Jan. 1991 (fl),

Vernacular names unknown.

Treelets or trees 3--12 m tall. Branchlets 9--12 mm diam., longitudinally striate, light brown sericeous to glabrescent. Leaves palmately compound, clustered at the end of branchlets, the internodes up to c. 5 mm long. Stipules 5--8 mm long, glabrescent abaxially, glabrous
adaxially, apex slightly bifid, the lobes less than c. 1 mm long; petiole 9--16 cm long, 1.5--2 mm diam., cylindrical or slightly flattened dorsiventrally, striate longitudinally, glabrous; *leaflets* 5--8, grouped in one whorl, held horizontally; the blade plane to slightly conduplicate, chartaceous, both surfaces glabrous. *Median leaflet:* petiolule 4.5--6.8 cm long, articulated distally, slightly compressed laterally, canaliculate adaxially; the blade 9--14 x 4.7--6.3 cm, elliptic to ovate, the base obtuse or cuneate to attenuate, symmetrical to slightly asymmetrical, the margin entire, undulate, the apex caudate with a mucronulate tip. *Basal leaflets:* petiolule 3.8--6 cm long, the blade 6.2--11.7 x 2.9--5.2 cm, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein impressed to slightly prominent adaxially, prominent abaxially; secondary veins 8--13, impressed on both surfaces; intersecondary veins absent; higher orders of venation conspicuous abaxially. *Inflorescence* pseudolateral, branches patent, becoming pendent when fruiting, glabrous; peduncle up to c. 1 cm long, rachis obscure; primary branches 2, both terminal, 16--26 cm long (bracts caducous, not seen), each bearing 5--10 secondary branches arranged racemously (2--3 terminal), 2.5--10.5 cm long, bracts not seen; tertiary branches 6--8, 1--2 cm long, usually arranged in two whorls; *ultimate inflorescence units* umbellules, with 9--17 flowers, the peripheral ones staminate, the central ones perfect; floral bracts c. 1 mm long.

*Perfect flowers* with pedicel c. 2 mm long; hypanthium light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5, color unknown, 2.4--2.5 x 1--1.2 mm, ovate, sericeous abaxially, apex acute; filaments c. 0.5 mm long; anthers c. 1.4 x 0.8 mm, oblong, apex apiculate, thecae connate above the connective insertion, just the tips free; ovary 1--1.5 mm long; disc glabrous; styles 2, connate into a column, c. 1.5 mm long, glabrous, tips recurved in fruit. *Staminate flowers* with pedicel up to c. 2 mm long; styles developed; otherwise similar to perfect ones. *Drupes* 6--7.5 x
8--9.5 mm, obloid to transversely ellipsoid, laterally compressed when dry, glabrous; pedicel 5--7 mm long; pyrenes 2, c. 5.5 x 4 mm, flattened, transversely semi-elliptic, indurate.

*Schefflera succinea* is known from only a few locations in the montane rainforests at Rio de Janeiro state. This species has been collected with flowers and fruits in March, June to August, and November.

*Schefflera succinea* can be readily distinguished from the remaining species of the Didymopanax group by the presence of glabrous leaflets with petiolules distally articulated, blades about two times longer than the petiolules and with a caudate apex, the inflorescences with glabrous branches, the tertiary branches mostly arranged in two whorls, and the glabrous fruits with styles connate into a short (c. 1.5 mm long) column.

*Additional selected material.* **BRAZIL. Rio de Janeiro:** Nova Friburgo, distrito de Macaé de Cima, nascente do Rio das Flores, 22°00’S, 42°03’W, 1100 m, 26 Nov. 1986 (fl, fr), *Martinelli 11929* (SP); Santa Maria Madalena, Parque Estadual do Desengano, Pedra do Desengano, 1800 m, vertentes NE e SE/S, 30 Jun. 1989 (fl, fr), *Martinelli et al. 13395* (RB).

34. *Schefflera tamatamaensis* Maguire, Steyerm. & Frodin, Mem. New York Bot. Gard. 38: 55. 1984. Type: Venezuela. “Unbranched tree 2.5--5 m tall, fruit brown, occasional in Caño Tama-Tama, a blackwater caño just above Tama-Tama, right bank Río Orinoco, 150 m, Territorio Amazonas, Venezuela, 23 June 1969, *Wurdack & Adderley 43148* [holotype, NY!; isotypes, K!, MG!, VEN!, US!]. Figs. 249F–L and 256B (see also Maguire et al., 1984; Fig. 8).


Vernacular names unknown.

Treelets 2.5--6 m tall. Branchlets c. 15 mm diam., longitudinally striate, light brown-sericeous. Leaves palmately compound, the internodes not seen. Stipules c. 17 mm long, light brown-sericeous abaxially, glabrous adaxially, apex bifid, the lobes c. 2 mm long; petiole 15--60 cm long, 3.5--4.5 mm diam., cylindrical, or laterally flattened when dry, longitudinally striate, glabrescent; leaflets 4--7, grouped in one whorl, held horizontally; the blade plane or slightly conduplicate, chartaceous, the adaxial surface glabrescent, the abaxial light brown to grayish-sericeous. Median leaflet: petiolule 7.5--16 cm long, unarticulated, cylindrical to slightly compressed laterally, slightly canaliculate adaxially; the blade 15--30 x 5.5--15 cm, elliptic, the base obtuse to rounded, symmetrical, the margin entire or very shallowly lobed, smooth to slightly revolute, the apex acute or acuminate to caudate, the tip sometimes mucronulate. Basal leaflets: petiolule 2--5 cm long, the blade 10.5--14.3 x 3--6 cm, symmetrical to slightly asymmetrical, similar to the median leaflet. Venation brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 12--14, prominent abaxially, impressed to slightly prominent adaxially; intersecondary veins sometimes present; higher orders
of venation inconspicuous. *Inflorescence* terminal, pendent(?), light brown-sericeous; peduncle obscure, rachis obscure; primary branches 3(-more?), 22.5--50 cm long (bracts not seen), each bearing 20--47 secondary branches arranged racemously [(2)3--4 terminal], 2--4 cm long, bracts 3--4 mm long; tertiary branches lacking; *ultimate inflorescence units* umbellules with 10--30 flowers, the peripheral ones staminate, the central ones perfect; floral bracts c. 1 mm long. *Perfect flowers* with pedicel up to c. 3 mm long; hypanthium light brown-sericeous, calyx rim with 5 acuminate teeth; petals 5, greenish, 3.8--4 x 1.5--1.6 mm, elliptic to ovate, sericeous abaxially, apex acute; filaments c. 0.6 mm long; anthers c. 2.1 x 1.2 mm, oblong, apex rounded, thecae free above the connective insertion; ovary c. 1 mm long; disc glabrous; styles 2, free, c. 1.2 mm long, glabrous, recurved in fruit. *Staminate flowers* with pedicel 1--2.5 mm long; styles vestigial; otherwise similar to perfect ones. *Drupes* 13--16 x 16--18 mm, broadly depressed ovoid, laterally compressed when dry, sparsely pubescent; pedicel 2--8 mm long; pyrenes 2, 15--15.5 x 8.5 mm, swollen, semi broadly depressed-ovoid, cartilaginous.

*Schefflera tamatamaensis* is known from only a few collections from the southern Venezuelan Amazon, in the Upper Orinoco River. It has been found growing in seasonal *igapó* forests (periodically flooded with black or clear water; Prance, 1979) with *Leopoldinia piassaba* (Palmae), *Micrandra* spp. and *Hevea* spp. (Euphorbiaceae). The presence of swollen and irregularly sculptured pyrenes is unique to *S. tamatamaensis*, and might be an adaptation for buoyancy in the periodically flooded forests where this species grows, as fruit-set appears to occur during the flooding period (between May and September, see Goulding et al., 2003). *Schefflera tamatamaensis* has been collected with flowers in February and March, and with fruits in June.
Schefflera tamatamaensis can be distinguished from other species of the Didymopanax group by a combination of features including the leaves with 4--7 leaflets, the inflorescences with elongated (37.5--50 cm long) primary branches bearing reflexed secondaries along the entire length in flower, flowers with petals about two and a half as long as wide, the glabrous nectariferous disc, stamens with thecae free above the connective insertion, and the broadly depressed, ovoid, glabrescent fruits, and swollen pyrenes with an irregularly sculptured surface.

Schefflera tamatamaensis was originally described exclusively on fruiting material from Caño Tama-Tama (Maguire et al., 1984). Frodin (1997) accepted S. tamatamaensis, and suggested that it could be related to Didymopanax morototoni var. angustipetalus (Marchal, 1878), which he believed was distinct at the species level from the type variety. The same opinion was put forward by Frodin & Govaerts (2003), who mentioned that S. morototoni var. angustipetalifer was “may merit specific rank, but [is] so far known from only two collections, neither fruiting”. We agree with Frodin (1997) and Frodin & Govaerts (2003) that S. morototoni var. angustipetala should be recognized as a different species from S. morototoni, but not as a new species. Instead we believe that it is conspecific with S. tamatamaensis, sharing with this species the same morphology and restricted geographical area, in the Upper Orinoco River.


Aug. 1993 (fr), *Ribeiro et al. 1150* (holotype, INPA!; isotype, NY!). Figs. 242L–Q and 256C (see also Fiaschi et al. 2008; Fig. 4).

*Vernacular name:* morototó.

*Treelets* 3--8 m tall. *Branchlets* 15--20 mm diam., smooth to slightly striate longitudinally, ochre to grayish-sericeous. *Leaves* palmately compound, clustered at the end of branchlets, the internodes up to c. 1 cm long. *Stipules* 2.5--3 cm long, ochre-sericeous abaxially, glabrous adaxially, apex bifid, the lobes c. 1 cm long; petiole 38--84 cm long, cylindrical, smooth to slightly striate longitudinally, ochre-sericeous, glabrescent; *leaflets* 8--10, grouped in one whorl, held horizontally; the blade plane, sub-chartaceous to chartaceous, the adaxial surface glabrescent, the abaxial persistently ochre-sericeous. *Median leaflet:* petiolule 7--14.5 cm long, unarticulated, slightly compressed laterally, canalicate adaxially, the blade 17--30 x 9--18 cm, elliptic or narrowly elliptic to ovate or lanceolate, the base obtuse to rounded (subcordate), symmetrical to slightly asymmetrical, the margin sometimes very shallowly lobed to distinctly trilobed above the median portion, smooth to slightly revolute, the apex (of both median portion of blade and lobes) caudate, the tip sometimes mucronate. *Basal leaflets:* petiolule 1--3.5 cm long, the blade 12--24 x 5--8 cm, always entire and usually asymmetrical, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein slightly prominent on both surfaces, more conspicuously so abaxially; secondary veins 11--13, prominent abaxially, impressed to slightly prominent adaxially; intersecondary veins usually present; higher orders of venation inconspicuous or sometimes conspicuous adaxially. *Inflorescence* terminal, erect, ochre to light brown-sericeous; peduncle up to c. 1 cm long, rachis up to c. 7 cm long; primary branches 10--
30, of which 3--4 are terminal, these 13--42 cm long (bracts 10--20 mm long), each bearing 20--55 secondary branches racemously arranged (4--5 terminal), 1.5--4.5 cm long, bracts 2--9 mm long; tertiary branches lacking; ultimate inflorescence units racemules terminating in umbel, with 15--25 flowers, the proximal ones staminate, the terminal ones perfect; floral bracts 0.7--1.3 mm long. Perfect flowers with pedicel 2--4 mm long; hypanthium ochre-sericeous, calyx rim with 5 acuminate teeth; petals 5, greenish, 3.6--4.2 x 1.4--1.7 mm, elliptic or slightly ovate, apex acute, sericeous abaxially; filaments 0.8--1 mm long; anthers 1.8--2.2 x 1.2--1.6 mm, oblong, apex apiculate, thecae connate above the connective insertion; ovary c. 1 mm long; disc glabrous; styles 2, basally connate, 1.4--2 mm long, glabrous, recurved in fruit. Staminate flowers with pedicel 1--2.5 mm long; styles developed; otherwise similar to perfect ones. Drupes 6.5--8 x 11.5--13.5 mm, transversely ellipsoid, laterally compressed when dry, glabrescent; pedicel 3--8 mm long; pyrenes 2, 6.5--7.5 x 5.5--6.5 mm, flattened, transversely semi-elliptic, cartilaginous.

*Schefflera umbrosa* is found in the rainforests of central Brazilian Amazon, where it grows both on *terra firme* and *campinarana* (white-sand) forests. This species is especially common in the surroundings of Manaus (Amazonas state), and has been collected with flowers and fruits throughout the year.

*Schefflera umbrosa* can be readily distinguished from the remaining species of the Didymopanax group by stipules with apical lobes c. 1 cm long, median leaflets with the blade varying from very shallowly lobed to distinctly trilobed, the ochre-sericeous inflorescences with large bracts, and flowers grouped in racemules terminating in umbel along the secondary branches. Other species of the Didymopanax group with similar ultimate inflorescence units are *S. cordata* and *S. distractiflora*, both of which may be distinguished from *S. umbrosa* by the
shorter stipules (up to c. 1.5 cm, vs. 2.5--3 cm) with shorter apical lobes (up to c. 3 mm, vs. c. 10 mm), and the flowers with smaller petals (2.2--3 x 1.1--1.5 mm, vs. 3.6--4.2 x 1.4--1.7 mm) and generally shorter styles (0.6--1.6 vs. 1.4--2 mm) in *S. cordata* and *S. distractiflora*.

36. Schefflera villosissima Fiaschi & Pirani, Novon 15: 120. 2005. TYPE: Brazil. Minas Gerais: Serra do Espinhaço, at Lapinha, c. 19 km N of Serro, on road (MG 2) to Diamantina, c. 1200 m, 24 Feb. 1968 (fl), Irwin et al. 20809 [holotype, K! (2 sheets); isotypes, NY!, UBI!]. Figs. 248F–K and 256D (see also Fiaschi & Pirani, 2005a; Fig. 3).

Vernacular names unknown.

Treelets to 4 m tall. Branchlets c. 12 mm diam., longitudinally striate, densely ochre to yellowish-villose, glabrescent. Leaves palmately compound, clustered at the end of branchlets, the internodes up to c. 5 mm long. Stipules 8--10 mm long, villous abaxially, glabrous adaxially, apex slightly bifid, the lobes up to c. 1.5 mm long; petiole 11--23 cm long, cylindrical, ochre or yellowish to grayish-villous or glabrescent; leaflets 6--9, grouped in one whorl, held horizontally; the blade plane, leathery, the adaxial surface glabrescent, the abaxial densely ochre to yellowish-villose. Median leaflet: petiolute 2.2--5.5 cm long, unarticulated, compressed laterally, canaliculate adaxially, villose or glabrescent; the blade 12--14.5 x 6.2--8 cm, elliptic or oblong, the base obtuse to rounded, the margin entire, revolute, the apex retuse to rounded, the
tip mucronate. *Basal leaflets*: petiolule 5--15 mm long, the blade 8--9 x 2.5--4 cm, otherwise similar to the median leaflet. *Venation* brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 10--12, prominent abaxially, impressed adaxially; intersecondary veins absent; higher orders of venation inconspicuous. *Inflorescence* terminal, erect, densely ochre to yellowish-villose; peduncle c. 1 cm long, rachis c. 4 mm long; primary branches 4, of which 2 are terminal, these 15--43 cm long (bracts c. 7 mm long), each bearing with 25--57 secondary branches arranged racemosely along the entire length (3--5 terminal), 2.5--9.5 cm, bracts 2--4 mm long; tertiary branches sometimes present; *ultimate inflorescence units* capitula or spicules terminating in capitula, with 20--25 flowers; floral bracts c. 1.5 mm long. *Perfect flowers* sessile; hypanthium densely ochre to yellowish-villose, rim with 5 acuminate teeth; petals 5, yellowish, 2.5--3.7 x 1.3--2.1 mm, ovate or elliptic, the apex acute, villose abaxially; filaments 0.3--0.5 mm long; anthers 2.2--2.4 x 1.1--1.2 mm wide, oblong, apex apiculate, thecae connate above the connective insertion; ovary c. 1.5 mm long; disc glabrous; styles 2(3), free, c. 1.5 mm long, glabrous, recurved in fruit. *Staminate flowers* sessile; styles developed; otherwise similar to perfect ones. *Drupes* 6--7 x 9--11 mm, depressed obovoid, laterally compressed or rarely 3-costate when dry, glabrescent, apically villose; pedicel c. 1 mm long; pyrenes 2, not measured.

*Schefflera villosissima* is endemic to the *campos rupestres* of the Diamantina Plateau, in Minas Gerais state (Brazil). This species is known from only a few localities growing among rock outcrops, and has been collected with flowers in August and November, and with fruits from January to April.

*Schefflera villosissima* is very similar to *S. macrocarpa*, from which it can be
distinguished by the presence of flowers grouped in capitula or spicules terminating in capitula (vs. flowers grouped in umbellules), and the dense villous indumentum that covers the undersurface of leaflets, inflorescence branches and flowers (vs. indumentum less dense in *S. macrocarpa*). These differences, however, may be hard to detect due to the frequent presence of flowers with short pedicels in *S. macrocarpa*. Despite this, we accept both species as distinct because *Schefflera villosissima* is geographically restricted to high-elevation areas of the Diamantina Plateau, while *S. macrocarpa* has not been found in those areas and appears to be more common at lower elevations (see *S. cordata*, above).

*Additional selected material.* **BRAZIL. Minas Gerais:** Carbonita, Chapada dos Columbus, estrada Diamantina - Virgem da Lapa (BR-367), 76 km NE da ponte sobre o Rio Jequitinhonha, 17°38’18”S, 43°15’03”W, 965 m, 17 Nov. 2007 (fl), *Forzza et al. 4880* (NY, RB, SPF); Couto de Magalhães de Minas, 5 km by road NE of Rio Manso and Couto de Magalhães, 960--1000 m, 13 Apr. 1973 (fr), *Anderson 8736* (UB); Diamantina, Serra do Mourão, 24 Jan. 1978 (fr), *Hatschbach 40869* (MBM); Felisberto Caldeira, Curtidor, 16 Feb. 1973 (fr), *Hatschbach & Ahumada 31681* (MBM); Rio Vermelho, Pedra Menina, Serra do Ambrósio, Espigão do Meio, 1 Aug. 1985 (fl), *Mello-Silva et al. CFCR7870* (SPF).

5620 (B not seen, F! photo #3541) is also part of the original material, and was probably destroyed in 1943. Figs. 244N–Q, 256E (see also Fiaschi & Pirani, 2007; Fig. 7E–I).

_Panax sericeus_ Pohl ex DC., Prodr. 4: 254. 1830. _Didymopanax sericeus_ (Pohl ex DC.) Decne. & Planch., Rev. Hort. IV, 3: 109. 1854. TYPE: Brazil, locality unknown, _Pohl 3041_. Because we have not been able to examine all of the relevant material, we have refrained from designating a lectotype.

_Panax parviflorus_ Mart. & Zucc., Abh. Math.-Phys. Cl. Konigl. Bayer. Akad. Wiss. 1: 319. 1832. TYPE: Brazil. Minas Gerais, _Martius s.n_. Because we have not been able to examine all of the relevant material, we have refrained from designating a lectotype.

_Didymopanax vinosus_ var. _attenuatus_ Marchal in Mart. & Eichler, Fl. bras. 11(1): 239. 1878. TYPE: Brazil. Without locality information, _Martius s.n_. Because we have not been able to examine all of the relevant material, we have refrained from designating a lectotype.

**Vernacular names.** Cinco-folhas, mamoneiro, mandioqueiro-pequeno, mandioqueiro-do-campo, matataúba.

**Treelets** 0.8--5 m tall. **Branchlets** 4--10 mm diam., slightly striate longitudinally, light brown or ferrugineous to grayish-sericeous, glabrescent. **Leaves** palmately compound, clustered at the end of branchlets, the internodes up to c. 5 cm long. **Stipules** 2--6 mm long, light brown to grayish-sericeous abaxially, glabrous adaxially, apex bifid, the lobes up to c. 0.5 mm long; petiole 4.5--25 cm long, 0.8--3 mm diam., unarticulated, cylindrical to slightly compressed laterally, slightly striate longitudinally, glabrescent; **leaflets** 3--11, grouped in one whorl, held horizontally or ascending, the blade plane, chartaceous to coriaceous, the adaxial surface glabrescent, the abaxial persistently light brown or ochre to grayish-sericeous. **Median leaflet:** sessile or with petiolule up to c. 3 cm long, unarticulated; the blade 3.5--14.5 x 1.2--4 cm, obovate to oblanceolate, sometimes narrowly oblong, the base attenuate to cuneate, the margin entire, slightly to strongly revolute, the apex obtuse to rounded or truncate (emarginate), very rarely acute or acuminate, the tip mucronate. **Basal leaflets:** petiolule up to c. 1 cm long, the blade 2--9 x 0.3--3 cm, otherwise similar to the median leaflet. **Venation** brochidodromous; main vein prominent on both surfaces, more conspicuously so abaxially; secondary veins 5--11, prominent abaxially, impressed adaxially; intersecondary veins absent or present; higher orders of venation inconspicuous, sometimes conspicuous abaxially. **Inflorescence** terminal, rarely becoming pseudolateral when fruiting, erect or with decumbent branches when fruiting, light brown or ochre to grayish-sericeous; peduncle reduced or up to c. 11 cm long, rachis reduced or up to c. 31 cm long; primary branches 2--32, of which 2--6 are terminal, these 3.2--29 cm long (bracts 2--6 mm long), each with 8--51 secondary branches arranged racemosely along the entire
length (2--6 terminal), 0.7--14.5 cm long, bracts 2--4 mm long; tertiary branches, if present, 4--15 mm long; *ultimate inflorescence units* umbellules, sometimes racemules terminating in umbel, with 10--40 flowers, most of which are perfect, or the peripheral ones staminate and the central ones perfect; floral bracts 0.5--1 mm long. *Perfect flowers* with pedicel 1--7 mm long; hypanthium light brown-sericeous, calyx rim with 5(6) acuminate teeth; petals 5(6), green-yellowish, 2.2--2.8 x 0.9--1.4 mm, elliptic to ovate, sericeous abaxially, apex acute or acuminate; filaments 0.3--0.7 mm long; anthers 1.3--1.7 x 0.6--0.9 mm, oblong or ovate, apex apiculate, thecae connate above the connective insertion; ovary 1--1.5 mm long; disc glabrous; styles 2, free or up to half connate, 1.3--1.7 mm long, glabrous, recurved in fruit. *Staminate flowers* with pedicel up to 2 mm long; styles developed; otherwise similar to perfect ones. *Drupes* 4.5--7.5 x 7--11 mm, transversely ellipsoid, laterally compressed when dry, glabrescent; pedicel 2--10 mm long; pyrenes 2(3), 5--6.5 x 4--5.5 mm, flattened to somewhat swollen, transversely semi-elliptic, indurate.

*Schefflera vinosa* is a widespread and common species of the Brazilian Cerrado. The geographic distribution of *S. vinosa* ranges from northern Paraná and southwestern Goiás to northern Bahia state, where it grows on high-elevation areas (*serras*) of the Chapada Diamantina (Fig. 256E). The high elevations along the Espinhaço Range provide suitable habitats for the occurrence of *S. vinosa* in more northern geographical areas (Fiaschi & Pirani, 2008). These mountains retain more humidity than the surrounding lowland areas covered by the seasonally dry *caatingas* (Harley, 1995), where none of the drought-intolerant species of the Didymopanax group appear to be able to grow.
Schefflera vinosa is more commonly found in savannah habitats of the Cerrado domain, and in campos rupestres, where it usually grows among rock outcrops. It can also be found growing along the edges of gallery forests and Eucalyptus plantations. This species has been collected with flowers and fruits throughout the year.

Schefflera vinosa can typically be distinguished from other species of the Didymopanax group by leaflets with an obovate to oblanceolate blade, an attenuate to cuneate base (the leaflets usually appearing sessile), and a usually obtuse to rounded or truncate apex. Other than leaf morphology, few characters are useful in distinguishing S. vinosa from other species of the Didymopanax group from the cerrados and campos rupestres of the Brazilian Plateau, especially S. burchellii, S. cordata and S. fruticosa. It differs from S. burchellii by the inflorescence, which usually has a distinctive main axis (vs. primary branches usually umbellately arranged), the smooth to longitudinally striate (vs. corky) bark, and the leaflets, which usually lack distinctive petiolules. From S. cordata, S. vinosa can be distinguished by the presence of flowers usually grouped in umbellules (vs. racemules terminating in umbel in S. cordata), and the usually sessile leaflets with an attenuate to cuneate base (vs. leaflets clearly petiolulate with a usually obtuse to rounded base). Schefflera fruticosa differs from S. vinosa by having shorter inflorescences included within the foliage (vs. usually exceeding the foliage), with just a few (1--4) (vs. 8--51) secondary branches along each primary one, and the young leaflets with the blade grayish (vs. light brow to ochre-sericeous) abaxially.

Schefflera vinosa is a highly polymorphic species, especially regarding its habit, leaflet number and shape, and inflorescence structure. The morphological variation exhibited in S. vinosa does not appear to be sufficiently correlated with the geographic distributions of different populations to justify the recognition of intraspecific taxa, which prompted Fiaschi & Pirani
(2007) to describe it as an ochlospecies (White, 1962, 1979). This opinion is here followed, but we suggest that further studies using intraspecific molecular markers (e.g., microsatellites) and morphometric analyses might provide some evidence for the recognition of a few groups of populations as distinct taxa.

Additional selected material. BRAZIL. Bahia: Abaíra, caminho Jambreiro- Belo Horizonte, 13°17’S, 41°52’W, 1150–1300 m, 5 May 1994 (fl), Ganev 3208 (SPF); Água Quente, Pico das Almas, vertente W, entre Paramirim das Crioulas e a face N/NW do pico, 13°31’S, 42°00’W, 1250 m, 16 Dec. 1988 (fl), Harley et al. 27198 (SPF); Barreiras, rodovia Barreiras- Brasília, km 90, 12°05’S, 45°48’W, 800 m, 8 Jul. 1983 (fr), Coradin et al. 7424 (SPF); Correntina, Fazenda Jatobá, 13°58’51.3”S, 45°59’40.6”W, 845 m, 28 Jul. 2004 (fr), Fonseca et al. 5567 (IBGE, SPF); Lençóis, BR 242, c. 3 km da estrada para Utinga, 12°33’38”S, 41°23’29”W, 1000 m, 10 Mar. 1996 (fl), Conceição et al. PCD2218 (SPF); Morro do Chapéu, Estrada de Morro do Chapéu para Utinga, ramal à direita, acesso à torre, 11°37’S, 41°10’W, 24 Feb. 2003 (fl, fr), Fiaschi & Rapini 1366 (CEPEC, SPF); Mucugê, caminho para Guiné, 12°56’23”S, 41°28’31”W, 1040 m, 15 Feb. 1997 (fr), Saar et al. PCD5697 (SPF); Piatã, c. 9 km de Piatã, 1250 m, 15 Feb. 1987 (fl), Harley et al. 24249 (SPF); Rio de Contas, 6–10 km de Rio de Contas, estrada para o Pico das Almas, 1000 m, 13°32’S, 41°53’W, 21 Jul. 1979 (fr), Mori et al. 12452 (CEPEC, UEC); São Desidério, Estrada para Sítio Grande, 12°38’S, 45°02’W, 690 m, 4 Apr. 1984 (fr), Collares & Fernandez 135 (K, NY); Umburanas, Serra da Empreitada, 10°24’11”S, 41°19’21”W, 975 m, 16 Jul. 2004 (fl), Fiaschi et al. 2463 (CEPEC, NY, SPF); Vitória da Conquista, Rodovia BA-265, de Vitória da Conquista para Barra do Choça, 9 km E de Vitória da Conquista, 4 Mar. 1978 (fl), Mori et al. 9462 (CEPEC, UEC). Distrito Federal:
Fercal, NE de Brasília, 1200 m, 13 Jul. 1976 (fr), Davis 60265 (UB). **Goiás:** Chapadão do Céu/Mineiros, PARNA das Emas, 17°49’--18°28’S, 52°39’--53°10’W, 6 Jan. 1999 (fl), Batalha 2733 (SPF); Itumirim, entre Serranópolis e Aporé, c. 25 km S de Itumirim, 18°51’03”S, 52°07’21”W, 723 m, 22 Jan. 2001 (fl, fr), Pirani et al. 4789 (SPF); Posse, Rio da Prata, c. 6 km de Posse, 800 m, 7 Apr. 1966 (fl), Irwin et al. 14500 (UB). **Mato Grosso do Sul:** Selvíria-Três Lagoas, Fazenda Matão, 4 Sep. 1984 (fr), Martins et al. 16255 (UEC); Estrada de Campo Grande para Presidente Prudente, c. 90 km do Rio Paraná, 24 Jul. 1997 (fl), Gibbs et al. 5477 (UEC).

**Minas Gerais:** Antônio Carlos, 7 Jan. 1972 (fl), Krieger s.n. (CESJ 11435); Arinos, Invernada, c. 70 km de Arinos, na estrada para a Vila dos Gaúchos, 15°28’S, 45°47’W, 900 m, 5 Aug. 1998 (fr), Ratter et al. 8067 (UB); Campo do Meio, 30 Feb. 1982 (fl), Briter et al. s.n. (ESA 3931, UEC 42794); Casa Branca, Fazenda 4 mil réis, Rod. SP-340, km 47.5, sentido Vargem Grande do Sul-Casa Grande, 21°47’06.2”S 47°02’18.9”W, 7 Apr. 2002 (fl, fr), Magenta & J.E.M. Neto 433 (SPF); Datas, c. 15 km S de Diamantina, 1250 m, 5 Feb. 1972 (fr), Anderson et al. 35523 (UB); Diamantina, estrada para Milho Verde, c. 2 km N de Milho Verde, 18°27’S, 43°29’W, 10 Apr. 1982 (fl, fr), Menezes et al. CFCR3310 (SPF); Formoso, PARNA Grande Sertão Veredas, estrada Belém- Bahia, c. 21.4 km da sede da Funatura, 15°18’09”S, 45°56’34”W, 725 m, 19 May 1998 (fl), Oliveira et al. 1038 (IBGE, K); Francisco Sá, Serra do Calixto, 15 km da estrada de Francisco Sá para Grão Mogol, 26 Nov. 1984 (fr), Harley et al. CFCR6464 (SPF); Gouveia, rodovia de Gouveia para Diamantina, na altura do km 605, 18 Jun. 2000 (fl, fr), Fiaschi & F.N. Costa 320 (SPF); Grão Mogol, Rio Itacambiruçu, c. 15 km N de Grão Mogol, 950 m, 18 Feb. 1969 (fr), Irwin et al. 23522 (UB); Itambé do Mato Dentro, estrada para Carmo, c. 2 km de Itambé do Mato Dentro, 8 Aug. 1992 (fr), Stehmann & Sobral 1154 (UEC); Jaboticatubas, Serra das Bandeirinhas, 1400--1500 m, 27 Jul. 1991 (fl, fr), Giulietti et al. CFSC12541 (SPF); João...
1983 (fl, fr), *Ratter et al. 4828* (K); Araraquara, Bairro do Serraial, 29 Nov. 1951 (fr), *Hoehne s.n.* (SPF 141036); Assis, 24 Jul. 1991 (fl), *Chiea et al. 653* (SP); Avaré, Rodovia SP 255, km 284, Fazenda Caldeira, 3 Sep. 1984 (fr), *Pirani et al. 883* (SPF); Bauru, Bairro Samambaia, à beira da Rodovia Marechal Rondon (SP 300), 7 Jul. 1994 (fl), *Pirani et al. 3287* (SPF); Botucatu, estrada para Fazenda Lagoa Negra e Porto Said., 22°42’54”S, 48°19’42”W, 520 m, 6 Jun. 1996 (fl, fr), *Souza & Souza 11303* (ESA, SPF); Bragança Paulista, 14.6 km W da estrada de Bragança Paulista, 24 Sep. 1960 (fr), *Mattos & Mattos 8410* (SP); Campinas, cerrado próximo ao Aeroporto Viracopos, 26 Nov. 1994 (fr), *Leitão Filho et al. 32286* (UEC); Cristália, rodovia de Bauru para Paulistânia, alt. do km 270, 8 Jul. 2000 (fl, fr), *Fiaschi & Christianini 350* (SPF); Indaiatuba, 8 Sep. 1956 (fl, fr), *Grotta s.n.* (SPF 15724); Itapeva, estrada de Itapeva para Itararé, 24°02’54”S, 49°00’05”W, 765 m, 6 May 2001 (fl), *Fiaschi & Marcato 801* (SPF); Itararé, rodovia de Itararé para Itapeva, próximo ao Rio Verde, 24°06’S, 49°13’W, 5 Jun. 1994 (fr), *Souza et al. 6230* (SPF); Itirapina, estrada entre Itirapina e São Carlos, c. 9 km de Itirapina, 22°10’49”S, 47°52’59”W, 17 Apr. 1994 (fl, fr), *Souza et al. 5792* (SPF); Itu, Área de Proteção Ambiental, 12 Jul. 1987 (fl), *Souza & Britez 25182* (UEC); Lençóis Paulista, estrada de Lençóis Paulista para Águas de Santa Bárbara, 26°39’04”S, 48°52’03”W, 12 Jun. 1995 (fl), *Tamashiro et al. 1058* (SPF); Moji-Guaçu, estrada de acesso ao viveiro de mudas da Faz. Campininha, 11 Jul. 1997 (fr), *Lopes & Nuñez 92* (SPF); idem, Pádua Sales, Fazenda Campininha, 24 May 1965 (fl), *Mattos 11250* (SP); Moji-Mirim, km 153, 8 Dec. 1943 (fr), *Lima s.n.* (SP 51774); Novo Horizonte, estrada Novo Horizonte-Sales, c. 20 km de Novo Horizonte (SP-304, km 438), 21°23’28”S, 49°23’38”W, 440 m, 7 Jun. 1996 (fl), *Souza & Souza 11359* (ESA, SPF); Pirassununga, Cerrado de Emas, 2 Jul. 1943 (fl, fr), *Rachid s.n.* (SPF 17067); Pitangueiras, 3 Aug. 1940 (fr), *Fonseca s.n.* (SP 43045); Presidente Bernardes, rodovia de Pirapozinho para o
Mirante do Paranapanema (SP 272), entre km 22 e 23, 22°01’S, 51°34’W, 400–500 m, 10 Mar. 1996 (fl), Pietrobom-Silva 3171 (SJRJ, SPF); Santa Rita do Passa Quatro, A.R.I.E. Cerrado Pé-de-Gigante, 21°36–44’S, 47°34–41’W, 3 Oct. 1995 (fr), Batalha 780 (SPF); São Pedro do Turvo, Faz. São Sebastião, 31 Jul. 1962 (fl), Válvio 272 (SP); São Simão, 20 May 1941 (fl), Lima s.n. (SP 48962); Tatuí, 6 km de Tatuí, via Itapetininga, 3 Apr. 1960 (fl), Campos 228 (SP, SPF); Teodoro Sampaio, Parque Estadual do Morro do Diabo, estrada para Estreito, 21 Jun. 1994 (fr), Baitello 684 (SPF).

POORLY KNOWN SPECIES

Schefflera sp. A

This species is morphologically similar to S. distractiflora. The inflorescences, however, appear to have a shorter main axis, tertiary branches present (vs. absent in S. distractiflora), and flowers in umbellules (vs. racemules terminating in umbel). The leaflet blades are also distinctive, with an ochraceous indumentum (vs. usually light brown to grayish-sericeous), and a rounded to acute (vs. usually conspicuously acuminate) apex.

Schefflera sp. A is a small treelet, 1–5 m tall. It has been collected growing at the edge of gallery forests or capões de mata (natural patches of forest on high elevation areas). Fiaschi (2006) included some materials of this species as S. aff. burchellii; however, they seem to differ from S. burchellii by the absence of corky branches, the leaflets without intersecondary veins (vs. present in S. burchellii), and the inflorescences with a distinctive (vs. reduced) main axis.
Representative collections. BRAZIL. Distrito Federal: C. 15 km NE of Brasilia, lower slopes of Chapada da Contagem, c. 1000 m alt., 4 May 1966 (fr), Irwin et al. 15615 (K).

Schefflera sp. B

This species is morphologically intermediate between S. longipetiolata and S. racemifera. It shares with both the unbranched habit, stipules deeply bifid apically, membranous leaflets, a pseudolateral and pendent inflorescence, and flowers with white petals. The leaflets are very narrow (10.8--16 x 0.8--1.5 cm), and resemble those of S. racemifera; the inflorescences, however, bear secondary branches, along which the flowers are grouped in racemules terminating in umbel (in S. racemifera the flowers are racemosely arranged along the primary inflorescence branches). It differs from S. longipetiolata mostly by the narrow leaflets and the flowers with less distinctive calyx laciniae.

Schefflera sp. B is a short treelet 1.5--4 m tall. It grows under the canopy of sub-montane rainforests, and is so far known from only a single population. Collections available so far have staminate flowers and immature perfect flowers. Mature perfect flowers and fruits are needed to determine if it is conspecific with S. longipetiolata or belong to an as yet undescribed species.

Representative collections. BRAZIL. Espírito Santo: Ibatiba, c. 22 km de Ibatiba, na estrada para Vitória. Ramal à esquerda, c. 1.5 km, 20º13’49’’S, 41º20’36.3’’W, 1050 m, 19 July.
Schefflera sp. C

This arboreal species (25--32 m tall) is very similar to *S. pubicarpa*, but the available material is too fragmentary to place it with confidence. The leaves have very long petioles (70--75 cm long) bearing 11--12 large leaflets in one whorl (the median leaflet 27--31 x 10--16 cm long). The leaflets blades are chartaceous to subcoriaceous and persistently light brown to grayish-sericeous abaxially, with a caudate apex and an obtuse to truncate base. The inflorescence primary branches are about 50 cm long, and the umbels are terminal to short secondary branches (1--2.5 cm long). The flowers have a pubescent disc and anthers with thecae free above the connective insertion, and the fruits are reminiscent of those from *S. pubicarpa*.

Unfortunately most of the materials of this species available so far are either fragmentary or represent sterile voucher materials from ecological studies (most Peruvian samples). *Schefflera* sp. C can be distinguished from *S. pubicarpa* by the leaves with 11--12 (vs. 8--10) leaflets, and the larger leaflets blades, but they might prove to be conspecific with *S. pubicarpa* should additional fertile samples from both species become available. As discussed above, the geographic distance separating *S. pubicarpa* from *S. sp. C* is very large, but this apparent disjunction may be explained by the dearth of botanical knowledge in intermediate areas (e.g., the Purus-Juruá interfluve, Hopkins, 2007).

*Representative collections. COLOMBIA. Caquetá:* Región de Araracuara, alrededores de la pista aérea, c. 0°25’S, 72°30’W, 5 Nov. 1991 (fl), Restrepo & Matapi 370 (NY); Rio
Apaporis, Soratama (above mouth of Rio Kananari) and vicinity, c. 0°5’N, 70°40’W, 300 m, 26 Mar. 1952 (fr), Schultes & Cabrera 16010 (US). ECUADOR. Pastaza: Cantón Arajuno, Campamentos temporales 11 y 12, 01°25’S, 77°39’W, 785 m, 15--20 Sep. 1998 (fl), Freire et al. 3394 (MO). PERU. Loreto: Maynas, Iquitos, Río Nanay, trail from caserio of Nina Rumi, 21 June 1977 (fl); Rimachi Y. 3116 (MO); Mishana, Río Nanay half-way between Iquitos and Santa Maria de Nanay, 180 m, 30 May 1978 (st), Gentry et al. 22440 (MO); idem, 3°50’S, 73°30’W, 140 m, 23 Mar. 1979 (st), Gentry et al. 26110 (MO); Mishana, trail from village to Campamento 1, 140 m, 22 Jul. 1980 (st), Gentry et al. 28930 (MO); Pena Negra, 25 km southwest of Iquitos, 1 Aug. 1972 (st), Croat 18642 (MO); Puerto Almedras, 3°45’S, 73°25’W, 122 m, 7 Dec. 1982 (fr), Vásquez & Jaramillo 3507 (K, MO, US).

LIST OF NAMES (boldfaced names are accepted in this study):

*Aralia L.*

*A. micans* Willd. ex Schult.

*Didymopanax* Decne. & Planch.

*D. acuminatus* Marchal

*D. angustissimus* Marchal

*D. angustissimus* var. *conspicuus* Marchal

*D. anomalus* Taub.

*D. burchellii* Seem.

*D. calvus* (Cham.) Decne. & Planch.
D. *macrocarpus* var. *capitatus* Marchal

D. *cephalanthus* Harms

D. *chrysophyllus* (Vahl) Decne. & Planch.

D. *claussenianus* Decne. & Planch. ex Marchal

D. *cordatus* Taub.

D. *distractiflorus* Harms

D. *falcatus* Marchal

D. *gardneri* Seem.

D. *gardneri* var. *ellipticus* Marchal

D. *glaziovii* Taub.

D. *longipetiolatus* (Pohl ex DC.) Marchal

D. *lucumoides* Decne. & Planch. ex Marchal

D. *macrocarpus* (Cham. & Schltdl.) Seem.

D. *macrocarpus* var. *capitatus* Marchal

D. *malmei* Harms

D. *micans* (Willd. ex Schult.) Krug & Urb.

D. *micranthus* Marchal

D. *morototoni* (Aubl.) Decne. & Planch.

D. *morototoni* var. *angustipetalus* Marchal

D. *morototoni* var. *poeppigii* Marchal

D. *morototoni* var. *sessiliflorus* Marchal

D. *navarroii* A. Samp.

D. *pachycarpus* Marchal
D. poeppigii Decne. & Planch.

D. selloi Marchal

D. sericeus (Pohl ex DC.) Decne. & Planch.

D. simplicifolius Hoehne

D. speciosus (Willd.) Decne. & Planch.

D. splendens (Kunth) Decne. & Planch. ex Seem.

D. undulatus (Aubl.) Whright

D. utiarityensis Hoehne

D. venulosus Taub.

D. vinosus (Cham. & Schltldl.) Marchal

D. vinosus var. attenuatus Marchal

D. vinosus var. burchellii (Seem.) Marchal

Oreopanax Decne. & Planch.

O. morototoni (Aubl.) Pittier

Panax L.

P. calvus Cham.

P. chrysophyllus Poep.

P. chrysophyllus Vahl

P. longipetiolatus Pohl ex DC.

P. macrocarpus Cham. & Schltldl.

P. morototoni Aubl.
P. parviflorus Mart. et Zucc.

P. sericeus Pohl ex DC.

P. speciosus Willd.

P. spinosus Poir.

P. splendens Kunth

P. undulatus Aubl.

P. vinosus Cham. & Schltldl.

Schefflera J.R.Forst. & G.Forst.

1. S. angustissima (Marchal) Frodin

S. anomal a (Taub.) Frodin

2. S. aurata Fiaschi

3. S. botumirimensis Fiaschi & Pirani

4. S. burchellii (Seem. ) Frodin & Fiaschi

5. S. calva (Cham.) Frodin & Fiaschi

6. S. capixaba Fiaschi

7. S. cephalantha (Harms) Frodin

8. S. ciliatifolia Fiaschi & Frodin

S. clausseniana (Decne. & Planch. ex Marchal) Frodin

9. S. confusa (Marchal) Harms

S. conspicua (Marchal) Frodin

10. S. cordata (Taub.) Frodin & Fiaschi

11. S. decaphylla (Seem.) Harms
12. *S. dichotoma* Fiaschi & Frodin

13. *S. distractiflora* (Harms) Frodin

*S. falcatifolia* Frodin

14. *S. fruticosa* Fiaschi & Pirani

15. *S. gardneri* (Seem.) Frodin & Fiaschi

16. *S. glaziovii* (Taub.) Frodin & Fiaschi

17. *S. grandigemma* Fiaschi

18. *S. kollmannii* Fiaschi

19. *S. longipetiolata* (Pohl ex DC.) Frodin & Fiaschi

20. *S. lucumoides* (Decne. & Planch. ex Marchal) Frodin & Fiaschi

21. *S. macrocarpa* (Cham. & Schltldl.) Frodin

22. *S. malmei* (Harms) Frodin

*S. megacarpa* A.H. Gentry

23. *S. morototoni* (Aubl.) Maguire, Steyermark & Frodin

*S. morototoni var. angustipetala* (Marchal) Frodin

*S. morototoni var. sessiliflorus* (Marchal) Frodin

*S. navarroii* (A. Samp.) Frodin

*S. pachycarpa* (Marchal) Frodin

*S. paraensis* Huber ex Ducke

24. *S. pimichinensis* Maguire, Steyerm. & Frodin

25. *S. plurifolia* Fiaschi & Frodin

26. *S. plurispicata* Maguire, Steyerm. & Frodin

27. *S. prancei* Fiaschi & Plunkett
28. *S. pubicarpa* Fiaschi & Plunkett

29. *S. quinquecarinata* Steyerm.

30. *S. racemifera* Fiaschi & Frodin

*S. regnelliana* Frodin

31. *S. ruschiana* Fiaschi & Pirani

32. *S. selloi* (Marchal) Frodin & Fiaschi

*S. splendens* (Kunth) Frodin ex Lindeman

33. *S. succinea* Frodin & Fiaschi

34. *S. tamatamaensis* Maguire, Steyerm. & Frodin

35. *S. umbrosa* Frodin & Fiaschi

*S. venosa* Frodin

36. *S. villosissima* Fiaschi & Pirani

37. *S. vinosa* (Cham. & Schltldl.) Frodin & Fiaschi

*S. yutagensis* Steyerm. & Holst

*Sciodaphyllum* P.Browne

*S. burchellianum* Baill.

*S. confusum* Marchal

*S. paniculatum* Britton

**LIST OF EXSICCATAE**

In the list previously published by Fiaschi & Pirani (2007) the number 7 refers to *S. villosissima* (instead of *S. macrocarpa*), 8 refers to *S. macrocarpa* (instead of *S. malmei*), and 9
refers to *S. malmei* (instead of *S. villosissima*). The only exception is *Irwin 20889*, which in fact belongs to *S. villosissima*. Moreover, *S. capixaba* (4) and *S. longipetiolata* (5) had their numbers shifted in that list.


Burchell, W.J.: 1842 (23), 2690 (19), 4885 (37), 4896 (37), 5144 (21), 8425 (4).


Irwin, H.S.: 2152 (5), 5088 (21), 5280 (Sch. sp. A), 6236 (Sch. sp. A), 6363 (13), 6590 (13), 6832 (13), 7964 (21), 9268 (21), 9341 (4), 9349 (4), 11511 (5), 12478 (21), 12623 (5), 12850 (21), 12902 (4), 12947 (21), 13349 (21), 13561 (5), 13667 (21), 13926 (21), 14500 (37), 14683 (37), 14728 (37), 14812 (37), 14865 (37), 14865 (37), 14877 (37), 15326 (21), 15511 (5), 15615 (Sch. sp. A), 15734 (Sch. sp. A), 16070 (23), 16279 (13), 16591 (23), 16720 (13), 16870 (13), 16948 (13), 17139 (13), 17269 (4), 17767 (21), 18149 (21), 18934 (21), 19893 (20), 20147 (5), 20446 (21), 20809 (36), 21721 (23), 21815 (5), 21833 (37), 22316 (5), 22387 (37), 22446 (10), 22634 (37), 22635 (10), 22656 (10), 22955 (21), 23522 (37), 23907 (21), 24482 (4), 24914 (21), 25134 (21), 25387 (5), 25847 (21), 25916 (21), 26107 (21), 26431 (21), 26945 (21), 27035 (21), 27437 (37), 27438 (37), 27779 (37), 28247 (10), 28422 (21), 28954 (37), 29658 (37), 30913 (37), 32268 (37), 32473 (37), 32962 (21), 33046 (5), 34869 (21), 47776a (23), 48459 (23). Ivanauskas, N.M.: 20 (1), 470 (1), 551 (23), 559 (1), 1606 (23), 1972 (23), 2079 (13).


Young, K.: 1051 (23).

CHAPTER 4

Phylogenetics, biogeography and the distributional diversity of the Didymopanax group of Neotropical *Schefflera* (Araliaceae)

(formatted for publication in Taxon)

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Abstract

The Didymopanax group of *Schefflera* is a clade of c. 40 species almost entirely restricted to tropical South America east of the Andes, with centers of diversity in the Atlantic rainforests, the *cerrados* of the Brazilian Plateau, and the western Amazon. Here we investigate interspecific phylogenetic relationships in the Didymopanax group using three molecular markers from the nrDNA (ITS, ETS and 5S-NTS) and a small morphological data set. The resulting phylogenies were subjected to dispersal-vicariance analysis to reconstruct the biogeographic history of the Didymopanax group in South America. Using alternative diversity measures (species richness and phylogenetic diversity), we tested whether those areas having greater diversity and endemism for Didymopanax species resulted from diversification within specific lineages, or to the presence of unrelated species in the same areas. Four main clades were consistently recovered from the phylogenetic analyses, each with coherent morphologies and geographic distributions, and are informally refered to as the Atlantic Forest (centered in the Parana subregion), Savannic (centered in the Chacoan subregion), Imeri, and Five-carpellate clades (the latter two entirely restricted to the Amazonian subregion). However, interrelationships among these four clades were weakly supported. A recent diversification within the Savannic clade of the Didymopanax group appears to have occurred in the *campos rupestres* vegetation of the Brazilian Plateau, resulting in sites across this region with high species richness but relatively low phylogenetic diversity. Other than the main clades of Amazonian (Imeri and Five-carpellate clades) and Parana (Atlantic Forest clade) forests, a few additional lineages (*S. aurata*, *S. ciliatifolia* and *S. plurifolia* + *S. umbrosa*) and some savannic species (e.g., *S. selloi*) contribute to the species assemblage of these two forest blocks. The presence of species from unrelated clades in the Amazonian and Parana subregions support their recognition as composite
biogeographic areas, and point to the importance of these regions in the conservation of phylogenetic diversity for the Didymopanax group.

KEYWORDS: biogeography, Didymopanax, phylogenetic diversity, Schefflera, South America, systematics

Short title: Systematics of the Didymopanax group of Schefflera

Introduction

The Neotropical Schefflera clade of Araliaceae comprises about 300 species (Plunkett & al., 2005), most of which occur along the mountain ranges of southern Mesoamerica and northern South America, especially along the Andes and the Guayana Shield (Frodin, 1995, 2004). Within this clade, most of the species of Schefflera east of the Andes belong to two sister groups: the Guayanan and Brazilian subclades (see Chapter 2). The composition of the Brazilian subclade agrees perfectly with Frodin’s (1995) concept of the “Didymopanax” group of Schefflera, which includes most of the species previously described in the segregate genus Didymopanax Decne. & Planch. This group is exceptional among Neotropical Schefflera in the fact that most of its 37 species occur in low- to mid-elevation (up to 1,000 m) habitats in Brazil and southernmost Venezuela (Frodin, 1995; Fiaschi & Pirani, 2007; see Chapter 3), regions where the remaining subgeneric groups of Schefflera are either far less common (Crepinella and Sciodaphyllum) or entirely absent (Cephalopanax and Cotylanthes) (Frodin, 1995; Fiaschi & Pirani, 2008). Species from the Didymopanax group can be distinguished from other Neotropical
Schefflera species by the presence of a unique combination of features, which includes sericeous or villous indumentum of malpighiaceous trichomes, secondary veins usually widely spaced and without distinctive intersecondaries, paniculate inflorescences usually twice or thrice compound, flowers with free petals, stamens with short filaments, and mostly bicarpellate drupes, usually with free and recurved styles (Frodin, 1995; see Chapter 3).

The taxonomy of species from the Didymopanax group has been recently updated in a series of papers dealing with new species (Fiaschi, 2004; Fiaschi & Pirani, 2005a, 2005b; Fiaschi & Frodin, 2006; Fiaschi & al., 2008), regional taxonomic studies (Maguire & al., 1984; Frodin, 1997; Fiaschi & Pirani, 2007), and an overview of the geographic distributions of the extra-Amazonian species from Brazil (Fiaschi & Pirani, 2008). Moura (1983) carried out a revision of the Brazilian species of the former segregate genus Didymopanax, but this study was incomplete and remains unpublished. The first complete revision of the Didymopanax group in more than 150 years has now become available (see Chapter 3), establishing species delimitations and geographic distribution for a total of 37 species (plus three additional entities for which too little is known to recognize them as distinct). However, interspecific relationships in the Didymopanax group are largely unknown, and until recently most of its species have never been included in phylogenetic studies. In a preliminary study of Neotropical Schefflera (see Chapter 2), 14 species of the Didymopanax group were sampled, and the monophyly of this group as currently circumscribed by Frodin (1995) was corroborated. Moreover, Fiaschi & Plunkett (see Chapter 2) also detected that some species of the Didymopanax group had slightly different phylogenetic placements based either on ITS or ETS sequence data, and recommended that more comprehensive studies with representatives from this group should be carried out.
In the present study, we investigate phylogenetic relationships in the Didymopanax group of *Schefflera* using three nuclear ribosomal DNA (nrDNA) markers and a small morphological data set. Two of the molecular markers (ITS and ETS) are transcribed spacers. The ITS region includes the internal transcribed spacers ITS1 and ITS2, plus the intervening 5.8S ribosomal RNA gene (White & al., 1990; Baldwin & al., 1995), while the external transcribed spacer (ETS) is located upstream from 18S, and is also included in the 18S–26S nrDNA repeat (Baldwin & Markos, 1998; Linder & al., 2000). This nrDNA unit is tandemly repeated, often in many thousands of copies (Baldwin & al., 1995), but rapid concerted evolution via unequal crossing-over and gene conversion promote uniformity among repeat units (Zimmer & al., 1980; Appels & Dvorak, 1982; Hillis & al., 1991, Wendel & al., 1995; Kovarik & al., 2005). This property of nrDNA spacers makes them reliable markers of evolutionary relationships (Zimmer & al., 1980; Baldwin & al., 1995), except in cases when concerted evolution fails to homogenize paralogous copies (Sanderson & Doyle, 1992), as in Melanesian *Schefflera* (Plunkett & al., 2009).

Moreover, ITS and ETS can be easily amplified, and have been successfully employed in interspecific phylogenetic studies throughout Araliaceae (e.g., Tronchet & al., 2005; Mitchell & Wen, 2005; Plunkett & al., 2001, 2004a, 2004b, 2005; Plunkett & Lowry, 2001, 2009; Costello & Motley, 2007). The third marker used was the non-transcribed spacer associated with the unlinked rDNA 5S gene (5S-NTS), which is found in hundreds to thousands of tandemly arrayed copies at one or more loci in the nuclear genome (Kellogg & Appels, 1995; Crisp & al., 1999). The genes are small (ca. 120 bp) and highly conserved, whereas the non-transcribed spacers have variable lengths (100–600 bp) and evolve rapidly (Crisp & al., 1999). In contrast to ITS and ETS, where concerted evolution efficiently homogenizes the repeat units, homogenization in the 5S units is less efficient, and does not necessarily occur among loci (Kellogg & Appels, 1995),
increasing the concern of sampling from paralogous copies for phylogenetic inference (see Sanderson & Doyle, 1992). The 5S-NTS has successfully provided useful characters for interspecific relationships in Araliaceae (Eibl & al., 2001; Mitchell & Wen, 2005; Costello & Motley, 2001, 2007), as well as other angiosperm families, such as Asteraceae (Morgan & al., 2009), Fabaceae (e.g., Crisp & al., 1999; Saini & Jawali, 2009), Myrtaceae (e.g., Udovicic & al., 1995), Poaceae (Cox & al., 1992), and Rubiaceae (e.g., Persson, 2000).

Because molecular markers can provide a large number of useful characters in a relatively short amount of time, there have been some attempts to disregard the use of morphological characters for plant phylogenetic inference, presumably because of their higher levels of homoplasy when compared to molecular data (Givnish & Sytsma, 1997; Scotland & al., 2003; but see Hillis & Wiens, 2000). However, there is increasing evidence that adding morphological characters to a mostly molecular data set can result in phylogenies with greater resolution and/or higher support (e.g., Donoghue & Sanderson, 1992; Pennington, 1996; Kress & al., 2001). The morphological characters that have traditionally been used in the classification of Araliaceae have been shown to be extensively homoplasious at the infrafamilial level (Plunkett & al., 2004b), but few studies have investigated the utility of morphology on infrageneric phylogenies in this family (e.g., Costello & Motley, 2007). Carpel number is very labile at the infrafamilial level (Plunkett & al., 2004b) but among the species of the Didymopanax group, Fiaschi and Pirani (2008) suggested that carpel number seems to justify its division into two subgroups, one including the 5(6)-carpellate Amazonian species, and the other comprising the usually 2(3)-carpellate species. In the present study, the consistency of this character (carpel number) and a few other morphological characters was tested in the Didymopanax group by
assembling and analyzing a small morphological data set using a “total evidence” framework (Kluge, 1989).

The Didymopanax group is almost entirely Neotropical, with just a few species occurring in adjacent subtropical regions of South America (see Chapter 3). The Neotropical flora comprises about 34% of worldwide plant species (Janovec & al., 2003), yet there have been very few phylogenetic and biogeographic studies of plant groups centered in tropical South America. Among recent biogeographic studies including South American plants, most involve either intercontinental disjunctions (e.g., Chanderbali & al., 2001; Davis & al., 2002; Zerega & al., 2005; Muellner & al., 2006; Trénel & al., 2007; Cuenca & al., 2008) or groups centered in subtropical areas (e.g., Crisci & al., 1991, 2001; Sanmartín & Ronquist, 2004). Moreover, few studies have investigated the historical biogeography of tropical South America east of the Andes using interspecific plant phylogenies, and of those available, most are concerned with temporal diversification (Richardson & al., 2001; Kay & al., 2005; Erkens & al., 2007; Rapini & al., 2007), habitat specialization (e.g., Fine & al., 2005), and the biogeography of specific areas (e.g., Fritsch & al., 2004; Pennington & al., 2004; Frasier & al., 2008). Among those few studies that have employed objective historical biogeographic methods to interpret the diversification of tropical South American plants, we are unaware of any that has investigated widespread groups that span most tropical areas of the continent (e.g., Perret & al., 2006; Antonelli & al., 2009).

Based on insect data, Morrone (2006) defined three main biogeographic subregions in tropical South America east of the Andes: Amazonian, Chacoan and Parana (Fig. 257b), all belonging to the broader Neotropical Region, and each further divided into several provinces (Fig. 257a). The Amazonian Subregion is the largest of the three, and is separated from the Parana Subregion by a “diagonal of open formations” (Prado & Gibbs, 1993) that corresponds to
the Chacoan Subregion (Morrone, 2006). Species of the Didymopanax group are distributed in most of the tropical regions of South America east of the Andes, with the exception of vast areas of the Caatinga and Chaco provinces of the Chacoan Subregion (Fig. 257a), which are covered with seasonally dry vegetation (Morrone, 2006). The greatest diversity in the Didymopanax group is centered in the Brazilian Atlantic forests, the *campos rupestres* (high elevation open vegetation on rocky substrates of the Cerrado Province), and the Amazonian forests of the Upper Negro River, at the Brazil-Colombia-Venezuela border (Imeri Province) (Fiaschi & Pirani, 2008; see Chapter 3). This distributional pattern, with several species endemic to these three different subregions of tropical South America (Amazonian, Chacoan and Parana; Morrone, 2006), suggests that the Didymopanax group may provide a useful comparison to explore biogeographic histories in subregions defined largely on the basis of insect distributions.

To reconstruct the biogeographic history of the Didymopanax group, we used dispersal-vicariance analysis (DIVA; Ronquist, 1997). DIVA uses a taxon cladogram together with current distributions of each taxon to reconstruct the ancestral range of areas at each node. To reconstruct these ancestral areas, a cost matrix is applied where vicariance and duplications (i.e., speciation without vicariance) are favored over dispersals and extinction events. The most parsimonious solution (minimizing the cost and thus favoring vicariance and duplications) is taken as the most likely biogeographic scenario to explain the given taxon-area cladogram (Ronquist, 1997; Sanmartin, 2007). DIVA is a taxon-based historical biogeographic method, and does not attempt to evaluate the hierarchical relationships among areas, which is the main objective of other approaches to historical biogeography, such as cladistic biogeography (Humphries & Parenti, 1999) and panbiogeography (Craw & al., 1999). However, DIVA can be used to find general relationships of areas, especially when these have a reticulate history.
(Morrone, 2009). DIVA also does not require individual area cladograms to conform to a general area cladogram, allowing the evaluation of biogeographic scenarios when general area cladograms are lacking (Crisci & al., 2003; Sanmartín, 2007). For these reasons, we chose DIVA as an appropriate method to reconstruct the biogeographic history of the Didymopanax group in South America east of the Andes.

In addition to providing insights into the evolutionary and biogeographic histories of organisms, phylogenetic information can also serve as a tool for the selection of priority areas for the conservation of biodiversity (Mace & al., 2003). Currently, highly threatened areas with the greatest species richness (total number of species) are typically chosen as the most appropriate units for biodiversity conservation at a worldwide scale (Myers & al., 2000). In South America, five areas that concentrate endemic species and are experiencing exceptional levels of habitat loss have been recognized as biodiversity hotspots (Myers & al., 2000; Mittermeier & al., 2005), two of which (Atlantic Forest and Cerrado) harbor a large number of narrowly endemic species of the Didymopanax group of Schefflera (Fiaschi & Pirani, 2008). However, biodiversity assessments based merely on species counts do not take into account the degree of distinctiveness among those species (Faith, 1992), and may not be the best criteria for the conservation of biodiversity, which has an important (but often ignored) genetic component. Recent efforts towards the selection of priority areas for the conservation of highly diverse biotas have been made using a measure called phylogenetic diversity or “PD” (Faith, 1992; Faith & Baker, 2006) such as the study by Jaramillo (2006). By incorporating both the number of species and the degree of distinctiveness among them (based on genetic differences), this measurement can be useful to identify areas that harbor species that are more distantly related (and thus carry greater genetic diversity) rather than areas with a large number of closely related species that are
not as different genetically. Because the Didymopanax group has been recently monographed (see Chapter 3) and there is a phylogenetic hypothesis for almost all of their species (this chapter), it can be used to identify priority areas for conservation in South America east of the Andes based on a combination of species counts and PD criteria. Thus, areas containing the greatest species richness can be compared to those having greater phylogenetic diversity to determine whether these measures coincide in identifying the same regions as priorities for conservation, or if they include several closely related species that are genetically less distinctive.

In the present study, phylogenetic relationships in the Didymopanax group of Schefflera were reconstructed, and these hypotheses were used as the starting point to investigate the morphological diversification, historical biogeography, and phylogenetic diversity of the Didymopanax group in South America. These phylogenies were also used to reconstruct the biogeographic history of the Didymopanax group in tropical South America east of the Andes, and to help identify priority areas for the conservation of species from this group.

Materials and Methods

Taxonomic sampling — DNA sequence data were obtained from samples of 33 of the 37 species from the Didymopanax group of Schefflera, plus two (of three) undescribed species currently considered as poorly known taxa (see Chapter 3) (Table 5). Five species from this total group of 40 were missing in our data set: *S. cephalantha* (Harms) Frodin, *S. pimichinensis* Maguire, Steyerm. & Frodin, *S. plurispicata* Maguire, Steyerm. & Frodin, *S. tamatamaensis* Maguire, Steyerm. & Frodin, and *Schefflera* sp. A (see Chapter 3). We chose three representatives from the Guayanan subclade of Neotropical Schefflera (see Chapter 2) as the outgroup taxa for the ITS
and ETS data sets (Table 5). We were unable to amplify 5S-NTS from these outgroup taxa, and thus used *Oreopanax capitatus* (Jacq.) Decne. & Planch. as the sole outgroup. Among the ingroup taxa, we attempted to obtain sequence data from each marker using the same set of samples.

**Data sets and congruence** — Data sets were initially created maximizing taxon sampling for each of three nuclear markers (ITS, ETS and 5S-NTS) and analyzed individually as means of data exploration (see Lecointre & Deleporte, 2005). Because there was incomplete overlap in the sampling among data sets, we assembled a reduced data set with identical ingroup taxon sampling from 30 accessions (plus the same outgroup taxa from previous analyses) to eliminate sampling error and thus provide a more comparable assessment of congruence among these three molecular markers, following the approach of Eibl & al. (2001). Congruence was assessed by inspection of the resulting topologies and through use of the incongruence length difference (ILD) test (Farris & al., 1995) (1,000 replicates) as implemented in PAUP* (as the partition homogeneity test) for all pair-wise marker combinations (ITS + ETS, ITS + 5S-NTS and ETS + 5S-NTS), as well as a combined data set with all three markers (ITS + ETS + 5S-NTS). The partition homogeneity test was implemented after excluding uninformative characters, as recommended for data partitions where such characters occur at different proportions (Cunningham, 1997a; Lee, 2001).

To create a data matrix including both molecular and morphological characters, we reduced the number of terminals from the individual molecular data sets by calculating consensus sequences for each of the species included (35 spp., plus 3 outgroup taxa). The use of consensus sequences was adopted to summarize information from those species for which we
had multiple DNA accessions. Consensus sequences were calculated using both plurality and inclusivity criteria using Sequencher (version 4.7, Gene Codes Corp.). When assembled by plurality, consensus sequences use the most frequent nucleotide at each site from sequences being compared, and when assembled by inclusivity, IUPAC ambiguity codes are used for nucleotide polymorphism, thus providing a more conservative consensus of multiple sequences. A data set of consensus sequences was created for all molecular markers together, and for a combined data set that also included ten meristic morphological characters (see Table 6). These morphological characters were included to verify whether they are consistent with molecular clades recovered from the phylogenetic analyses, or if they would be better interpreted as homoplasious in the Didymopanax group. We have prioritized the inclusion of meristic characters due mostly to difficulties in coding continuously varying characters (Thiele, 1993). Species showing variation in the morphological characters were coded as having all represented character states (polymorphic coding; Wiens, 1999; Table 7).

**DNA sequencing and analyses** — Total DNA was extracted using the QIAGEN DNeasy Plant Mini kit or following a modification of the protocol of Alexander & al. (2007). The ITS region was amplified using two external primers (ITS5 and C26A) for most samples, but herbarium samples often required the use of two additional internal primers (ITS3 and ITS2), and sometimes the replacement of C26A by ITS4 (White & al., 1990; Downie & Katz-Downie, 1996; Wen & Zimmer, 1996). The ETS region was amplified using primers 430 F and 18S-2L R (Linder & al., 2000; Tronchet & al., 2005). An additional primer (400 F: 5′–GTT GGT CGG ATC CCT GCT TGT–3’) was designed to sequence reactions that performed poorly using 430 F. The 5S region was initially amplified using primers 5S-R and 5S-Ful (Udovicic & al., 1995),
which preferentially amplified a large band (~1,200 bp) and in some cases one or two additional smaller bands (about 900 and 200 bp). Sequences derived from this large band were used to design new primers after comparisons to published 5S-NTS sequence data from the Asian Palmate Clade of Araliaceae available at GenBank (Mitchell & Wen, 2005). These primers (F: 5’–GYC WYG TTA GTG GYG GTA CGR TCG–3’ and R: 5’–GTG ACC CCC TGG GAA GTC CTC G–3’) preferentially amplified either both or just the shortest of the two smaller products. To obtain sequence data from as many taxa as possible, the shortest bands (~200 bp) were either sequenced directly or purified from the gel, re-amplified with the same primers, and sequenced. Using those sequences obtained from the external primers 5S-Ful and 5S-R (Udovicic & al., 1995) as a reference, two additional, more-specific primers were designed. One was located internal to 5S-Ful and just external to primer F (Didy 5S-F: 5’–GGT ACG GTG GCA CCC GTT AGG–3’), and the second was located internal to primer R (Didy 5S-R: 5’–CCT GGG AAG TCC TCG CGC–3’). These primers amplified the shorter products and allowed for direct sequencing of these amplicons.

PCR reactions for the ITS region included 3 µL of QIAGEN 10X PCR Buffer, 2.4 µL of 10 mM dNTPs, 2.4 µL of 25 mM MgCl₂, 1.2 µL of each primer, 0.6 µL of DMSO, 1.2 µL of 4 mM spermidine, 0.3 µL of QIAGEN Taq DNA polymerase, 3 µL of unquantified total DNA, and purified water to a final volume of 30 µL. An alternative recipe was adopted for some samples, using 5 µL of REDTaq ReadyMix PCR Reaction mix (Sigma-Aldrich), 0.5 µL of each primer, 0.5 µL of 4 mM spermidine, 1 µL of unquantified total DNA, and purified water to a final volume of 10 µL. Recipes for ETS included 2.5 µL of QIAGEN 10X PCR Buffer, 2 µL of 10 mM dNTPs, 2 µL of 25 mM MgCl₂, 1 µL of each primer, 0.25 µL of DMSO, 1 µL of 4 mM spermidine, 0.25 µL of QIAGEN Taq DNA polymerase, 2.5 µL of total DNA, and purified water.
to a final volume of 25 µL, or the same alternative recipe used for ITS. The recipe for 5S-NTS amplification included 5 µL of REDTaq ReadyMix PCR reaction mix (Sigma-Aldrich) or GoTaq Green Master Mix (Promega, Inc.), 0.5 or 1 µL of each primer, 1 µL of unquantified total DNA, and purified water to a final volume of 10 µL.

Amplification of ITS involved 30 to 40 cycles of 94°C (30 sec), 52°C (1 min), and 72°C (50 sec), for the denaturing, annealing and extension steps, respectively. For DNA extracted from herbarium material, amplification with internal primers involved 37 to 41 cycles of 94°C (30 sec), 48°C (1 min), and 68°C (1 min) for primers ITS5 and ITS2, and 37 to 41 cycles of 94°C (30 sec), 47°C (1 min), and 68°C (1 min) for primers ITS3 and ITS4. ITS amplification yielded a double-banding pattern for a few samples. In those cases, the two bands were separated electrophoretically, and those that comigrated with the single-banded products from other samples were isolated and re-amplified using the same PCR conditions. Protocols for ETS amplification of silica-gel dried material involved 30 to 40 cycles of 94°C (30 sec), 55°C (1 min), and 72°C (50 sec); ETS from herbarium samples was amplified using 42 cycles of 94°C (30 sec), 52°C (1 min), and 68°C (45 sec). Initial protocols for 5S-NTS amplification involved 32 cycles of 93°C (10 sec), 62°C (10 sec), and 72°C (20 sec), using the primers from Udovicic & al. (1995). To amplify preferentially the short bands, we used primers Didy 5S-F and Didy 5S-R and a protocol of 45 cycles of 93°C (10 sec), 60°C (10 sec), and 72°C (6 sec). PCR products were purified using a 1:2 mixture of Exonuclease I and Shrimp Alkaline Phosphatase (USB Corp.) according to manufacturer, and sequenced using the DYEnamic ET Terminator Cycle Sequencing Kit (GE Healthcare Inc.) with the following recipe: 1 µL of primer, 1 µL of ET Terminators, 1.5 µL of 2.5X Buffer and 3.5 µL of purified PCR product. Sequencing reaction products were purified using the MultiScreen384 – SEQ Filter Plates (Millipore Corp.) and then
separated electrophoretically on a MegaBace 1000 DNA Sequencing System (GE Healthcare Inc.). The resulting sequences were assembled and edited using Sequencher (version 4.7, Gene Codes Corp.), and then aligned manually. Pair-wise distances for each molecular data set were calculated (including and excluding outgroup taxa) using the uncorrected “p” distance with PAUP* (version 4.0b10; Swofford, 2002).

**Phylogenetic analyses** — All data sets were analyzed using maximum parsimony (MP) with PAUP* (version 4.0b10; Swofford, 2002), maximum likelihood (ML) with GARLI (version 0.95; Zwickl, 2006), and Bayesian inference (BI) with MrBayes (version 3.1.2; Huelsenbeck & Ronquist, 2001). For MP of both combined and separate data sets, alignment gaps were treated as missing data in all analyses, and analyses used heuristic searches (1,000 replicates with random addition) with TBR branch swapping, ACCTRAN optimization, and MULPARS in effect, saving no more than 100 trees per replicate. Node support was estimated by bootstrap (BS) analyses in PAUP* using 1,000 replicates (Felsenstein, 1985).

For ML and BI analyses, the model of sequence evolution was selected using ModelTest (Posada & Crandall, 1998) for each marker individually. ML analyses were performed with eight multiple runs to check for alternative topologies and scores. Support values for the ML tree branches were estimated with 100 bootstrap (BS) replicates using GARLI. Bayesian analyses were performed with one million generations and four chains, sampling trees every 100 generations. Each BI analysis was performed twice to check for alternative topologies. To calculate posterior probabilities (PP), trees sampled during the burn-in stage of each run were discarded, and the remaining trees were used to calculate a 50% majority rule consensus tree in PAUP*.
Biogeographic analyses — Biogeographic analyses were carried out using a three-step approach that included the delimitation of areas of endemism, the construction of individual area cladograms, and the interpretation of biogeographic patterns (Morrone, 2009). Because our focus was the biogeographic subdivision of tropical South America east of the Andes, occurrence data of *S. morototoni* in the Caribbean islands and Central America were excluded from the analyses.

We attempted to employ two approaches for the delimitation of areas of endemism in South America, namely parsimony analysis of endemicity (PAE) with quadrats (Morrone, 1994; Crisci & al., 2003), and a previously defined biogeographic division of South America into subregions and provinces (Morrone, 2006; modified in Nihei, 2008). PAE searches for a hierarchical classification of area units, which are grouped according to the shared presence of taxa (treated as characters) using a maximum parsimony approach (Crisci & al., 2003; Morrone, 2009). Clusters of areas supported by the presence of at least two exclusive (= endemic) taxa (non-homoplasious synapomorphies) are considered as areas of endemism, which are spatially delimited by the distribution of the taxa defining each cluster. Two data sets were employed in this study, the first including specimens from all species from the Didymopanax group (1,460 records from 40 species), and the second excluding *S. morototoni* (1,148 records from 39 species), to test for the effect of including a widespread species in the analyses. For each data set, we built presence/absence matrices based on 1 x 1° and 2 x 2° quadrats, testing the effect of geographic-unit size on the analyses (Morrone & Escalante, 2002). For the data matrix that included *S. morototoni*, there were 570 areas using 1° quadrats, and 237 areas using 2° quadrats. Excluding this species, the numbers were reduced to 355 areas (1° quadrats) and 155 areas (2° quadrats). A hypothetical area with all zeros was included in the matrices as the sole outgroup.
for each parsimony analysis. Maximum parsimony analyses of the data sets were carried out with PAUP* (version 4.0b10; Swofford, 2002), using heuristic searches (1,000 replicates with random addition) saving no more than 10 trees per replicate.

We used the dispersal-vicariance analysis (DIVA; Ronquist, 1997) to assess the extent to which dispersal and vicariance have contributed to the current distribution of species in the Didymopanax group. For the phylogenetic tree, we used fully resolved trees resulting from the ML analyses of data sets including only one terminal from each species (32 spp., plus three outgroup taxa). Sequence data for these samples were obtained from consensus sequences assembled by inclusivity (see above). Because the ITS + ETS data set and the ITS + ETS + 5S-NTS data set recovered slightly different topologies (see results), both were used as the input file in separate DIVA analyses to explore alternative biogeographic scenarios. DIVA uses a tree supplied from a phylogenetic analyses and a geographic data matrix in which each terminal is coded for its presence/absence in each of the defined areas. In defining geographic areas, we attempted PAE as an empirical approach, but this analysis did not provide satisfactory results for delimitation of areas of endemism in South America. Thus, the geographic data matrix was created exclusively from a previously defined biogeographic division of South America (Morrone, 2006). Two sets of areas were used for DIVA. The first set included 15 areas (Fig. 257a), excluding two mostly subtropical provinces (Pampa and Chaco) and the Yungas Province, the latter of which has biogeographic affinities with the Andean biota and is occupied only by S. morototoni. The second set included a total of five areas from three South American subregions east of the Andes (Morrone, 2006): Amazonian, Chacoan and Parana (Fig. 257b). The Amazonian and Parana subregions were each separated in two blocks following other biogeographic studies (Amazonian: Nihei, 2008; Parana: Amorim & Pires, 1996). For both sets
of areas, we performed an unconstrained analysis and a constrained analysis limiting the maximum number of areas for ancestral distributions to two.

**Conservation and phylogenetic diversity measures** — A database including 1,460 specimens of 40 species of the Didymopanax group was assembled from materials deposited at the following herbaria: ALCB, BHCB, BM, BR, C, CEPEC, CESJ, CVRD, ESA, GFJP, HRCB, HUEFS, IAN, INPA, K, LE, M, MBM, MBML, MG, MO, NY, P, R, RB, S, SP, SPF, UB, UEC, UPCB, US, VIES, W and WU (acronyms following Holmgren & al., 1990). Two measures of diversity were calculated: species richness (Gotelli & Colwell, 2001; Magurran, 2003) and phylogenetic diversity (Faith, 1992). To calculate species richness, we created a 1 x 1° grid map of South America using ArcView 9.3 (ESRI) and counted the number of species in each quadrat using Hawth’s tools (http://www.spatialecology.com/htools/download.php). For phylogenetic diversity, the same map was used, but the five species for which we do not have sequence data (see taxonomic sampling) were excluded from the database, resulting in 1,449 specimens. All quadrats having at least two species were selected, and the phylogenetic diversity at each quadrat was calculated from rooted subtrees as the sum of branch lengths among species (see Jaramillo, 2006). To provide reliable estimates of branch lengths, we used the maximum likelihood tree from a combined data set (ITS + ETS + 5S-NTS) of consensus sequences from one terminal of each species using GARLI (version 0.95; Zwickl, 2006). Among species, branch lengths per quadrat were obtained by pruning the ML tree to leave only the present taxa using the PRUNE feature in PAUP* (see Jaramillo, 2006).

**Results**
**Data sets** — ITS sequences included both spacers (ITS1 and ITS2) and the 5.8 S coding region and varied in length from 617 to 621 bp. The alignment resulted in a data matrix of 623 characters, of which 503 were constant, 30 variable in a single terminal, and 90 potentially informative (Table 8). The ETS sequences varied from 456 to 459 bp in length, and the alignment had 460 characters, of which 344 were constant, 38 variable in a single terminal, and 78 potentially informative (Table 8). The 5S-NTS sequences varied from 194 to 199 bp in length, and the alignment had 200 characters, of which 99 were constant, 28 variable in a single terminal, and 73 potentially informative (Table 8).

Estimations of sequence divergence for each marker were evaluated with the uncorrected “p” distance using PAUP*. ITS sequences varied from identity (between 75 pair-wise ingroup comparisons) to 6% between Schefflera confusa (Cid Ferreira 10955) and S. selloi (Amorim 6009). ETS sequences showed no differences among 243 pair-wise ingroup comparisons. The highest value for ETS sequence divergence including outgroups was 8.1% between S. umbrosa (Fiaschi 3185) and S. umbellata (Fiaschi 3199), and 7.8% between S. longipetiolata (Fiaschi 617) and S. umbrosa (Fiaschi 3185) among ingroup taxa. 5S-NTS sequences varied from identity (for 128 pair-wise comparisons) to 21.3% between S. distractiflora (Fiaschi 3007) and S. pubicarpa (Fiaschi 3187).

**Phylogenetic analyses** — Maximum parsimony analyses of the separate data sets with all available samples yielded trees with either unresolved (ITS, Fig. 258) or poorly supported (ETS and 5S-NTS; Figs. 259–260) relationships at the base of the tree. The analysis of ITS sequences yielded 39,672 most parsimonious trees with 132 steps (see Table 8 for MP trees statistics). The strict consensus tree recovered a basal polytomy that included four well supported clades, herein
named the “Atlantic Forest” clade (BS = 89%), “Savannic” clade (BS = 98%), “Plurifolia + umbrosa” clade (BS = 85%) and *S. ciliatifolia* (BS = 100%), plus a weakly supported clade (BS = 63%) including species from the “Five-carpellate” and “Imeri” clades, and three clades of *S. aurata* samples (Fig. 258). The Savannic clade was further divided in two well supported sister subclades, the first including species from the *campos rupestris* clade (recovered with ETS data) plus two accessions of *S. burchellii* (BS = 92%), and the second grouping all samples of *S. distractiflora, S. malmei, S. morototoni*, and *S. selloi*, plus one sample of *S. burchelli* (*Fiaschi 2421*) (BS = 81%). Within the Atlantic Forest clade, a well supported subclade including *S. capixaba, S. kollmannii* and *S. ruschiana* was recovered (BS = 87%) (Fig. 258).

The MP analysis of ETS sequences yielded 98,700 most parsimonious trees, each with 124 steps (Table 8). In this phylogeny (Fig. 259), most early diverging nodes received BS support lower than 50%, while the more distal nodes received stronger BS support (Fig. 259). The Atlantic Forest and Imeri clades emerged as sister groups (BS < 50%), and sister to the remaining of species of the Didymopanax group (BS = 100%). Within the Atlantic Forest clade (BS = 73%), a subclade including species restricted to forests at Espírito Santo state, *S. capixaba, S. kollmannii* and *S. ruschiana* (“ES endemic” subclade; BS = 100%), was sister to the remaining species (“Calva” subclade; BS = 71%), which included a well supported subclade with *S. longipetiola, S. aff. longipetiola* and *S. racemifera* (BS = 84%). Four samples of *S. aurata* grouped together (BS = 97%) as sister to a poorly supported clade characterized by a large polytomy (BS < 50%). The Savannic clade was left unresolved as part of this polytomy, which also included *S. ciliatifolia* (BS = 98%), the Plurifolia + umbrosa (BS = 82%) clade, and a moderately supported *campos rupestris* subclade (BS = 67%). Contrary to the ITS phylogeny, this subclade excluded all samples of *S. burchellii*, and included samples of other endemic
species from the *campos rupestres* for which ITS sequences were unavailable, such as *S. lumumoides* and *S. villosissima*. Other moderately supported clades from this broad polytomy grouped two accessions of *S. burchellii* with *S. distractiflora* and *S. morototoni* (BS = 63%), and all four accessions of *Schefflera selloi* (BS = 63%) (Fig. 259).

Maximum parsimony analysis of 5S-NTS sequences yielded 87,300 most parsimonious trees, each with 150 steps (Table 8). Two main clades were recovered in this analysis (Fig. 260). The first clade (BS = 96%) comprised a strongly supported Imeri clade (BS = 100%) as sister to a clade (BS = 61%) uniting all samples from the Atlantic Forest clade (BS = 54%) and a strongly supported “Five-carpellate” clade (BS = 96%) (Fig. 260) that was not recovered either in the ITS or the ETS trees (Figs. 258--259). The other major clade had lower support (BS = 83%) and was characterized by a basal polytomy including *S. ciliatifolia* (BS = 100%), *S. aurata* (BS = 83%), and a moderately supported clade including all remaining samples (BS = 66%) (Fig. 260). This latter clade was further divided into a subclade with the *campos rupestres* species plus *S. burchellii* and *S. malmei* (BS = 56%), and a strongly supported subclade (BS = 85%) including *S. distractiflora*, *S. morototoni*, *S. plurifolia*, and *S. umbrosa* (Fig. 260). The sister group relationship between *S. plurifolia* and *S. umbrosa* (recovered from ITS and ETS sequence data) was not supported by 5S-NTS, which placed *S. plurifolia* (BS = 100%) as sister to a strongly supported clade including *S. distractiflora*, *S. morototoni*, and *S. umbrosa* (BS = 96%) (Fig. 260). We were unable to obtain 5S-NTS sequences from *S. selloi*, presumably due to mutations at the priming sites.

Visual inspection of the topologies revealed incongruence among the trees derived from the separate analyses of different markers (Figs. 258--260). To assess congruence among data sets, maximum parsimony analyses were carried out for reduced data sets with identical taxon
sampling (Fig. 261) (see Table 9 for MP tree metrics). Several poorly supported relationships were unique to trees resulting from analyses of the separate data sets, such as: (1) the inclusion of the Imeri clade in the Five-carpellate clade in the ITS tree (BS = 65%; Fig. 261a); (2) the inclusion of Plurifolia + umbrosa and \textit{S. ciliatifolia} in the Savannic clade (BS < 50%), and the Imeri clade as sister to the Atlantic Forest clade (BS < 50%) in the ETS tree (Fig. 261b); and (3) the placement of the Five-carpellate clade as sister to the Atlantic Forest clade (BS = 60%) with 5S-NTS data (Fig. 261c).

Results from the partition homogeneity tests indicated a high degree of incongruence among the molecular data sets (see Table 9), suggesting that they should not be combined into a single matrix. The use of the ILD test as a measure of congruence among data sets has been challenged by some authors (e.g., Dolphin \& al., 2000; Barker \& Lutzoni, 2002). Moreover, its use as an indicator of combinability remain contentious, and even when separate data sets appear to be incongruent, simultaneous analyses may be justified (Cunningham, 1997a, 1997b; Barker \& Lutzoni, 2002). Visual inspection of the trees resulting from separate analyses reveals that most examples of incongruence were poorly supported (< 65%) in all three trees (Figs. 261a--c), suggesting that the ILD results may have been due to “soft” incongruence among separate data sets. Therefore, we assembled pair-wise combined data sets with this reduced taxonomic sampling following the “total evidence” approach (Kluge, 1989). Simultaneous analyses of three pair-wise combinations of data sets (ITS + ETS, ITS + 5S-NTS, and ETS + 5S-NTS) resulted in trees that are better supported, but apparently less resolved than those from analyses of separate data sets (Figs. 261d--f). The combined ITS + ETS tree had equal or higher bootstrap values for almost all internal branches compared to those from individual ITS and ETS trees, except for the placement of \textit{S. burchellii} and \textit{S. malmei} (Fig. 261d). Incongruence between the ITS and 5S-NTS
data sets was apparent in both separate and combined trees. In the separate trees, incongruence was detected in the placement of *S. umbosa*, either as sister to *S. plurifolia* (ITS; BS = 79%, Fig. 261a) or unresolved in a clade with *S. distractiflora* and *S. morototoni* (5S-NTS; BS = 100%, Fig. 261c). In the combined tree, this incongruent placement resulted in the collapse of the Plurifolia + umbrosa clade (Fig. 261e). Incongruence was also detected in the placement of *S. malmei* (Figs. 261a, c) and of *S. burchellii* either nested in the campos rupestres clade (Figs. 261a, c) or sister to *S. distractiflora + S. morototoni* (Fig. 261b), albeit with weak support (BS = 64%). The combination of ETS with 5S-NTS yielded a more resolved and better supported tree than those from separate analyses. *Schefflera umbrosa* was sister to *S. plurifolia* in most separate trees and in the ITS + ETS tree (Figs. 261a, b, d), but grouped with *S. distractiflora* and *S. morototoni* in the 5S-NTS tree (BS = 100%; Fig. 261c) and in the ETS + 5S-NTS tree (BS = 90%; Fig. 261f). The tree obtained from all three molecular data sets analyzed simultaneously was similar to that obtained from the combined ITS + ETS data set, and all internal branches from the Atlantic Forest, Imeri, and Five-carpellate clades received higher BS support after the inclusion of the 5S-NTS data set (Fig. 262). Two areas of disagreement between these topologies remained: (1) the placement of *S. malmei*, either as sister to the campos rupestres clade + *S. burchellii* (BS = 70%, all markers) or as sister to *S. distractiflora + S. morototoni* (BS = 82%, ITS + ETS), and (2) the successive placement of *S. ciliatifolia* and the Plurifolia + umbrosa clades as sister to the Savannic clade appeared in a different order (Figs. 261d, 262).

Based on these initial searches, *Schefflera burchellii*, *S. malmei* and *S. umbrosa* were identified as the cause of most of the incongruence among the three data sets. The exclusion of *S. burchellii* from the ITS + ETS data set resulted in a considerably higher score for the ILD test (from 0.01 to 0.043), but heterogeneity between the two data sets was still significant (Table 9).
The placement of *Schefflera malmei* was very unstable. In the ITS and ITS + ETS trees, it was sister to *S. distractiflora + S. morototoni* (Figs. 261a, d); in the 5S-NTS, ITS + 5S-NTS and ETS + 5S-NTS trees, it was sister to the *campos rupestres* clade + *S. burchellii* (Figs. 261c, e, f), and in the ETS tree, it was left unresolved with *S. ciliatifolia, Umbrosa + plurifolia, S. burchellii + S. distractiflora + S. morototoni*, and the *campos rupestres* clade (Fig. 261b). Based on morphological evidence, it appears that *S. malmei* may be of hybrid origin between *S. macrocarpa* and *S. vinosa* (see Chapter 3). This view is also substantiated by the presence of a double-banding pattern in the ITS samples from *S. malmei*, and therefore this species was removed from the data set (Seelanan & al., 1997; Vriesendorp & Bakker, 2005; Soltis & al., 2008). Finally, *S. umbrosa* was recovered either as sister to *S. plurifolia* (BS = 79--96%, ITS and ETS) or in a clade that also includes *S. ditractiflora* and *S. morototoni* (BS = 100%, 5S-NTS). The removal of all three of these species from the combined data sets resulted in minimal increases in the consistency and retention indices (not shown), and considerably improved the *p* values from the partition homogeneity tests for most pair-wise combinations (Table 9). Incongruence remained significant only in the data set where all three markers were combined (*p* = 0.002).

To construct combined data sets that maximized sampling, we removed all accessions from the three species that caused most of the observed incongruence among the three molecular data sets (i.e., *S. burchellii, S. malmei, and S. umbrosa*), following the approach of Seelanan & al. (1997), and analyzed the combined data sets. In the resulting trees, topologies obtained from separate analyses remained largely unaltered after the removal of problematic taxa (trees not shown), but the trees resulting from the MP analyses of the combined data sets were generally better resolved and had greater support than those derived from individual markers. Analyses of
the combined ITS + ETS and ITS + ETS + 5S-NTS data sets had better resolution and support trees than those from ITS + 5S-NTS and ETS + 5S-NTS data sets, and are shown in Figure 263. These topologies (Fig. 263) depict different sets of relationships among the main clades of Didymopanax from the trees resulting from separate analyses (Figs. 258--260), but here most basal branches were also poorly supported (BS < 50% to 65%; Fig. 263). In addition, the inclusion of 5S-NTS data resulted in the collapse of the well supported Savannic clade (BS = 100%), and the loss of the strongly supported sister-group relationships between the “ES endemic” and “Calva” subclades in the Atlantic Forest clade, and between *S. distractiflora* + *S. morototoni* and *S. selloi* in the Savannic clade (Fig. 263b).

ML and BI analyses were performed for the ITS + ETS and ITS + ETS + 5S-NTS combined data sets before and after the exclusion of *S. burchellii*, *S. malmei*, and *S. umbrosa*. As with the MP trees, the removal of these three species yielded greater resolution and better supported nodes, and thus only these trees are shown. For the ITS + ETS data set, ML and BI trees recovered very similar solutions, which were largely congruent with the MP results (Fig. 264). However, in contrast to the MP topology, which recovered the Five-carpellate and *S. aurata* clades as poorly supported successive sister groups to the Atlantic Forest + Imeri clades (Fig. 263a), the ML and BI trees recovered these same clades but in a different order, as successive sister groups to the Savannic clade plus *S. ciliatifolia* and *S. plurifolia* (Fig. 264). The inclusion of 5S-NTS data resulted in the collapse (ML) or decreased support (BI; PP = 0.85) for the Atlantic Forest clade (trees not shown), while the remaining relationships largely agreed with the MP analysis of the same data set (Fig. 263b). The only exception was that the ML and BI analyses of the ITS + ETS + 5S-NTS data set resolved the placement of *S. selloi* as sister to *S.
distractiflora + S. morototoni, as suggested by the ML and BI analyses of the ITS + ETS data set (Fig. 264).

Maximum parsimony analyses of the separate and combined molecular data sets were also performed on consensus sequences derived from multiple accessions of the same species, excluding S. burchellii, S. malmei, and S. umbrosa. As with the analyses based on maximized taxon sampling, those using consensus sequences had greater resolution and higher node support for trees resulting from combined analyses than from separate ones. The use of consensus sequences instead of the observed sequences from individual samples reduced the levels of homoplasy, but this is due largely to the decrease in taxon sampling and the increase in the number of ambiguous character states (Sanderson & Donoghue, 1989). The morphological data set (Table 7) was combined with the data set based on consensus sequences assembled by inclusivity. Maximum parsimony analyses of this combined data set resulted in 70,061 most parsimonious trees, each with 236 steps (CI = 0.775; RI = 0.921). This “total evidence” hypothesis of relationships separates the Didymopanax group in two weakly to moderately supported clades (Fig. 265), which coincide with those from the separate analysis of 5S-NTS (Fig. 260). The first of these clades (BS = 68%), included the Atlantic Forest clade (BS = 99%), and the Five-carpellate (BS = 99%) and Imeri (BS = 100%) clades as weakly supported sister groups (BS < 50%) (Fig. 265). The second clade (BS = 74%) included S. aurata, S. ciliatifolia, S. plurifolia, and the Savannic clade (BS = 94%) (Fig. 265).

Parsimony analyses of endemicity (PAE) — All PAE trials resulted in a large number of most parsimonious trees, which were used to calculate strict consensus trees (see Table 10 for MP trees statistics). The resulting trees were very poorly resolved and few areas of endemism could
be detected. For the 1 x 1° grid, only two adjacent quadrats were supported by two or more endemic taxa (quadrats N’33 and N’34, Fig. 266a) for data sets including (Fig. 266b) and excluding (Fig. 266c) *Schefflera morototoni*. These two quadrats are located in the Espírito Santo rainforests (Parana Subregion), and were named Atlantic Forest 1 and Atlantic Forest 2 (Fig. 266). For the 2 x 2° grid, two areas of endemism were detected, corresponding to clades “Cerrado” (quadrats S16 and T16) and “Brazilian Atlantic Forest” (quadrats U16 and U17) (Fig. 267). Both quadrats from the “Brazilian Atlantic Forest” clade were individually supported as smaller areas of endemism, and each was supported by two endemic species (synapomorphies) (Fig. 267c, Table 11). A list of the endemic species supporting areas of endemism recovered from both PAE trials is provided in the Table 11.

**Dispersal-vicariance analyses (DIVA)** — DIVA optimizations based on the ITS + ETS and ITS + ETS + 5S-NTS topologies and the coding of 15 areas resulted in biogeographic scenarios required 32 dispersal and extinction events using unconstrained analyses and 41 dispersal and extinction events using constrained analyses. Alternative ancestral reconstructions for internal nodes varied from 1 to 65 using unconstrained analyses, and from 1 to 11 using constrained analyses with this set of areas, but the biogeographic scenario recovered from this optimization was unclear because the distributions of several species of the Didymopanax group do not agree with the delimited areas (Fig. 257a). Because the data set with only five areas is a simplification of this larger data set and provides a much clearer picture of the biogeographic pattern observed, results form the DIVA with 15 areas are not discussed. Reconstructions using the data set with five areas required 21 dispersal and extinction events for both ITS + ETS and ITS + ETS + 5S-NTS topologies (Figs. 268, 269). Alternative ancestral reconstructions for internal nodes varied
from 1 to 6 in the unconstrained analysis and 1 to 4 in the constrained analysis (Figs. 268, 269). Using the constrained analysis, both topologies recovered northwestern Amazon (area A) as the sole ancestral area for the Didymopanax group (Figs. 268, 269). Internal branches of the Imeri + Atlantic Forest, and the Five-carpellate clades were characterized by speciation without vicariance, and the few instances of dispersal required by the optimization were restricted to terminal branches (Figs. 268, 269). In the Savannic clade, dispersal events were invoked for several terminal branches (S. distractiflora, S. macrocarpa, S. morototoni, and S. vinosa), as well as some internal nodes and all nodes leading to its closest successive sister groups (S. ciliatifolia, S. plurifolia, and S. aurata), all of which are restricted to areas other than the Chacoan Subregion (area C) (Figs. 268, 269). The two topologies disagreed only in poorly supported relationships in the Savannic clade and in the placement of S. ciliatifolia and S. plurifolia, but optimization in the ITS + ETS tree (Fig. 268) had fewer alternative reconstructions for ancestral distributions than in the ITS + ETS + 5S-NTS tree (Fig. 269).

Conservation and phylogenetic diversity measures — 570 quadrats from the 1 x 1° grid had between one and nine species (Fig. 270a). The majority of those quadrats (378, representing c. 66.3% of the total) had just one species, and only 13 quadrats (c. 2.3%) had five or more species. Most of the quadrats with five or more species were situated in the Brazilian Atlantic forests in Espírito Santo and Rio de Janeiro states (Parana Subregion) and the Cerrado Province, especially along the Espinhaço Range in Minas Gerais and the Federal District (Fig. 270a). The majority of sites with five or more species of the Didymopanax group were located in eastern Brazil, and only a single of those sites (T17, Fig. 270a) was located in the Amazon. The quadrat with the
highest diversity (9 spp.) was located in the southern portion of the Espinhaço Range in Minas Gerais (K'32, Fig. 270a).

Maximum likelihood analysis of a combined data set of consensus sequences from all molecular markers (ITS + ETS + 5S-NTS) yielded a tree with likelihood score of $\ln = -4,142.17$ (Fig. 271). This tree recovered the same clades from the other phylogenetic analyses of the Didymopanax group discussed above: Atlantic Forest, Imeri, Five-carpellate, Savannic, Plurifolia + umbrosa, $S. \text{aurata}$, and $S. \text{ciliatifolia}$ (Fig. 15). Phylogenetic diversity (PD) was calculated for 192 quadrats (1 x 1°) with at least two species, and ranged from 0.0534 to 0.1447 (c. 17.7--48% of the total PD). Nine of ten quadrats with the highest PD values were located in the Amazonian Subregion, and the remaining one was in the Brazilian Atlantic forests (N'33, Fig. 270b). The quadrat with the highest PD was located in the surroundings of Manaus (T17), followed by one in the Atlantic forests of Espírito Santo state (N'33) and one in the border between Bolivia and the Brazilian states of Mato Grosso and Rondônia (T26, Fig. 270b). Another quadrat with a high PD was situated at southeastern Colombia, close to the Peruvian border (H14, Fig. 270b).

**Discussion**

*Separate analyses and congruence among molecular data sets* — Phylogenetic trees recovered from the separate analyses of molecular data sets with an identical sampling suggest that most discrepancies among the markers are due either to low support among basal branches (ITS and ETS, Figs. 261a, b) or to poor resolution (5S-NTS; Fig. 261c). In poorly resolved trees with low node support, relationships can be obscured by the presence of low phylogenetic signal (insufficient character evidence), signal derived from excessively homoplasious substitutions,
and rate heterogeneity among markers, and alternative topologies often result from “soft”
incongruence among markers (Barrett & al., 1991; Seelanan & al., 1997; Wenzel & Siddall,
1999; Smith, 2000). Such soft incongruence is the most likely explanation for the observed
differences among topologies derived from analyses of separate molecular data sets in the
Didymopanax group (Figs. 258–260, 261a–c). When these data sets are analyzed in
combination, most branches exhibit an increase in node support (Figs. 261d–f), suggesting that
the noise from individual data sets is overcome by the additivity of phylogenetic signal present in
each separate data set (Barrett & al., 1991; Olmstead & Sweere, 1994). However, simultaneous
analyses of the combined data sets also suggest some cases of “hard” incongruence, resulting
from markers that track different evolutionary histories (Bull & al., 1993; Seelanan & al., 1997).
Hard incongruence may be found when including taxa with reticulate histories, which may result
from hybridization, polyploid speciation, and/or lineage sorting of ancestral polymorphisms
(Sanderson & Doyle, 1992; Wendel & Doyle, 1998). Among the three likely cases of hard
incongruence detected in our data sets (S. burchellii, S. malmei, and S. umbrosa), we only have
circumstantial evidence for the hybrid origin of S. malmei from S. macrocarpa and S. vinosa (see
Chapter 3). Nevertheless, when all three of those species are removed from the pair-wise
combined data sets, there is a marked increase in the ILD values (Table 9), suggesting that these
taxa are sources of the incongruence.

**Phylogenetic relationships in Didymopanax** — Most of our phylogenetic analyses
supported the recognition of four main clades within the Didymopanax group of Schefflera: the
Atlantic Forest clade, the Five-carpellate clade, the Imeri clade, and the Savannic clade. Two
additional monospecific lineages (S. aurata and S. ciliatifolia) were also recovered from all
analyses, as well as the species pair of *S. plurifolia* and *S. umbrosa* (Plurifolia + umbrosa clade). The 5S-NTS data set (Fig. 260) and the “total evidence” combined analysis (Fig. 265) also supported the separation of the Didymopanax group into two sister clades, one uniting the Five-carpellate, Imeri, and Atlantic Forest clades, and the other uniting the Savannic clade, *S. aurata*, *S. ciliatifolia*, and *S. plurifolia*. The combined ITS + ETS data set recovered a similar solution (Fig. 263a), except that *S. aurata* was placed as sister to the clade uniting the Five-carpellate, Imeri, and Atlantic Forest clades.

The four main clades of the Didymopanax group are morphologically and geographically coherent, and are discussed individually below. Whenever internal subclades or species pairs were recovered, these groups are also discussed, as are clades comprising *Schefflera aurata* and *S. ciliatifolia*, and the Plurifolia + umbrosa clade.

**The Atlantic Forest clade.** — The Atlantic Forest clade groups most of the species of the Didymopanax group that are endemic to the Atlantic forests of eastern Brazil, as well as *S. calva*, which is also found in gallery forests and seasonally dry forests of the Cerrado Province, northeastern Argentina, and southeastern Paraguay (see Chapter 3). All species from the Atlantic Forest clade have pseudolateral inflorescences, which are laterally displaced due to the early growth of one or more axillary buds (Fiaschi & Pirani, 2007; see Chapter 3). Another common feature of most species in this clade are leaflets typically having an acute or acuminate to caudate apex, although the leaflet apex is obtuse to rounded in *S. grandigemma* and sometimes in *S. ruschiana*. The Atlantic Forest clade was recovered with moderate to strong support in most separate and combined MP analyses (Figs. 258--260, 263--265). Maximum likelihood analyses of the combined data set (ITS + ETS + 5S-NTS) failed to recover this clade (not shown), but it was well supported in the BI tree (PP = 0.97, not shown). Based on the separate data sets, the
placement of the Atlantic Forest clade was left unresolved (ITS, Fig. 258) or poorly supported as sister to the Imeri clade (ETS, Fig. 259). However, when molecular markers were analyzed together, this clade emerged either with weak support (BS < 50) as the sister group to all remaining species of the Didymopanax group (Fig. 263b), or as sister to a weakly supported clade of Amazonian species including the Five-carpellate and Imeri clades (Fig. 265). If supported by further studies, the close relationship of the Atlantic Forest clade to an entirely Amazonian clade could indicate strong niche conservatism in Didymopanax, as species from this entire clade (Atlantic Forest + Five-carpellate + Imeri) are restricted to rainforest habitats.

Both ETS and most of the combined data sets recovered a moderately to strongly supported sister-group relationship between two subclades in the Atlantic Forest clade: “ES endemic” and “Calva” subclades (Figs. 259, 263a). These two groups were also consistently recovered by most analyses using reduced data sets and consensus sequences (Fig. 265). The ES endemic subclade includes four species (*S. capixaba*, *S. grandigemma*, *S. kollmannii*, and *S. ruschiana*) whose distributions are entirely restricted to the submontane forests of Espírito Santo state, mostly in the surroundings of Santa Teresa (Fiaschi & Pirani, 2008). The forests where these species grow harbor at least seven species of *Schefflera* (5 of which are endemic), and have been considered an important center of diversity for the genus in Brazil (Fiaschi & Pirani, 2008; see Chapter 3). No unequivocal morphological feature seems to be shared by all species of the ES endemic subclade, but the presence of light brown trichomes in the young leaves, inflorescences, and flowers is common. The ES endemic subclade was strongly supported based on ETS (BS = 100%) and ITS (BS = 87%) data, but 5S-NTS placed these species in a moderately supported clade together with accessions from *S. angustissima* and *S. calva* (BS = 76%, Fig. 260). A close relationship between *S. grandigemma* and *S. ruschiana* had previously
been suggested by Fiaschi & Pirani (2005b, 2007) based on morphological data, but the morphological limits between these two species are not very clear (see Chapter 3). The remaining species from the ES endemic subclade (S. capixaba and S. kollmannii) are morphologically more distinctive from S. grandigemma and S. ruschiana, and phylogenetic data contradicts the relationships suggested by Fiaschi & Pirani (2005b, 2007). According to those authors, Schefflera capixaba was probably related to S. longipetiolata, due largely to the presence of stipules having deeply lobed apices and the Chamberlain architectural growth model (Hallé & al., 1978), while S. kollmannii was placed near to S. angustissima, despite sharing with S. ruschiana and S. grandigemma inflorescences that have a distinctive light brown indumentum. Our phylogenetic analyses placed both S. longipetiolata and S. angustissima in a distinct subclade of the Atlantic Forest clade (“Calva” subclade), providing further evidence for the recognition of a highly geographically structured clade of species endemic to Espírito Santo state.

The remaining samples of the Atlantic Forest clade were either left unresolved (ITS and 5S-NTS) or sister to the ES endemic subclade as the weakly supported (ETS, BS = 71%) “Calva” subclade based on the maximized taxon sampling (Figs. 258--260). Analyses of the ITS + ETS combined data set recovered this subclade with strong support (BS = 86--88%, PP = 0.98; Figs. 263a, 264). The Calva subclade includes five species, four of which (S. angustissima, S. longipetiolata, S. racemifera, and S. succinea) are endemic to the Brazilian Atlantic forests (Parana Subregion; Fig. 257) and one (S. calva) is also found in forest habitats of the Cerrado Province (Fig. 257a). These species do not appear to share any evident morphological features but they have an ochre or yellowish to grayish indumentum rather than the light brown indumentum of the ES subclade, and their flowers are typically smaller (see Chapter 3).
Interspecific relationships in the Calva subclade were mostly left unresolved (Figs. 258, 259, 263), especially among samples of *S. angustissima* and *S. calva*, the two most widespread and morphologically variable species of the subclade. These two species are very similar, and their morphological limits are somewhat subjective, due mostly to large variation in leaflet shape and degree of indumentum persistence on the leaflets undersurface (Fiaschi & al., 2007; see Chapter 3). *Schefflera succinea*, which was nested among accessions of *S. angustissima* and *S. calva* (Figs. 258--259, 263--264), is a rather distinctive species that has been previously linked to the Guayanan endemic Cheilodromi group of *Schefflera* (Frodin, 1989); however, the placement of *S. succinea* in the Didymopanax group based on both morphological (see Chapter 3) and molecular data suggests that its poplar-like leaflet morphology (unique among species of the Didymopanax group) is more likely the result of convergent evolution than evidence for a close relationship to other species with a similar leaflet morphology, such as *S. tremuloidea* Maguire, Steyerm. & Frodin and *S. tremula* (Krug & Urb.) Alain (see Chapter 2).

Both separate and combined analyses suggested a close relationship among *S. longipetiolata*, *S. racemifera*, and *S. aff. longipetiolata* (Figs. 258--259, 263--264). These species share several morphological features, such as an unbranched habit derived from the Chamberlain growth model (Hallé & al., 1978), stipules with a deeply bifid apex, membranous leaflets, flowers with white petals, anthers with thecae free above the insertion of the connective, and fruits with a very thin pericarp (Fiaschi & Frodin, 2006; Fiaschi & Pirani, 2007; see Chapter 3). Based on the morphological similarity of *S. longipetiolata* and *S. racemifera* to young individuals of *S. angustissima* and *S. calva*, Fiaschi & Frodin (2006) suggested that those species could have had a neotenic origin from arboreal ancestors, but this hypothesis requires corroboration.
The Five-carpellate clade. — The Five-carpellate clade includes all Amazonian species of the Didymopanax group whose carpel number is typically five, sometimes with a few intermixed four- or six-carpellate flowers (see Chapter 3). This clade received support from separate (5S-NTS; Fig. 260) and combined analyses (Figs. 263--265), and a few morphological characters provide further evidence for its recognition, such as the presence of leaves with two or three concentric whors of leaflets (in *S. confusa*, *S. prancei*, and rarely *S. decaphylla*), inflorescences with a very short main axis and usually only 2(3) primary branches, perfect flowers with reclined anthers and styles with apical trichomes (in *S. confusa* and *S. decaphylla*), and staminate flowers with vestigial styles (in *S. decaphylla* and *S. quinquecarinata*) (see Chapter 3). The presence of additional whors of leaflets is shared between *S. confusa* and *S. prancei* and appears to be derived in the Five-carpellate clade. In addition, these species are restricted to western Amazonian forests, while *S. decaphylla* and *S. quinquecarinata* are widespread in central-eastern areas and the Guayana Shield, respectively (see Chapter 3).

The Imeri clade. — The Imeri clade included three (5S-NTS) or four (ITS and ETS) accessions of Amazonian species of the Didymopanax group, and was well supported in both separate and combined analyses of molecular data (Figs. 258, 260, 263--265). Two species from this clade were recently described and are known from just a few collections: *S. dichotoma* (Fiaschi & al., 2008) and *S. pubicarpa* (see Chapter 3), and the remaining accessions (*Restrepo & Matapi 370* and *Fine s.n.*) may represent an undescribed species (*S. aff. pubicarpa*; see Chapter 3). Species from this clade share several morphological features, such as the arboreal habit, leaflets grouped in one whorl and with a cuspidate to caudate apex, terminal inflorescences covered with a light-brown sericeous indumentum, flowers with pubescent disc and styles, anthers with thecae free above the connective insertion, and bicornellate fruits (see Chapter 3).
Several other species not sampled in this study share the same set of morphological features and thus may also belong to this clade, including *S. pimichinensis* Maguire, Steyerl. & Frodin, *S. plurispicata* Maguire, Steyerl. & Frodin, and *S. tamatamaensis* Maguire, Steyerl. & Frodin. Because our taxonomic sampling lacks several species presumably belonging to the Imeri clade, discussion of interspecific relationships within this clade must await future study.

With the exception of *S. pubicarpa* and *S. aff. pubicarpa*, which are found respectively in central Brazilian Amazon and western Amazonian sites in Peru, Ecuador and Colombia, most species of the Imeri clade appear to be endemic to the forests of northern Brazil, southern Venezuela, and southeastern Colombia, which have been collectively recognized as an important area of endemism in the Amazon ("Imeri" *sensu* Cracraft, 1985). This area harbors four endemic species of the Didymopanax group, and has been considered one of three centers of diversity for the group (see Chapter 3). According to Morrone’s (2006) biogeographic system, the Imeri Province extends to the surroundings of Manaus (thus including *S. pubicarpa*), but does not cover the geographic range of *S. aff. pubicarpa*, which extends west into the Napo Province (Fig. 257a; see Chapter 3).

**The Savannic clade.** — The Savannic clade includes all species from the Didymopanax group that grow in open areas of the Cerrado Province (Fig. 257a), which is the largest continuous area of savanna-dominated vegetation in South America (Pennington & al., 2006), together with *S. morototoni* (widespread in the Neotropics) and *S. selloi*, which is endemic to *restingas* of eastern Brazil (Fiaschi & Pirani, 2008). This clade was strongly supported with ITS data (BS = 98%; Fig. 258), and the ITS + ETS combined data set (Figs. 263a, 264), but collapsed in the separate analyses of ETS and 5S-NTS sequence data (Figs. 259, 260). In sharp contrast with the Atlantic Forest clade, where species have pseudolateral inflorescences, all species of the
Savannic clade have terminal inflorescences. In species with terminal inflorescences, the subtending axillary buds remain dormant until the infructescence is fully developed (Fiaschi & Pirani, 2007). In the ETS tree, a poorly supported clade (BS < 50%) closely approximated the composition of the Savannic clade, but also included two Amazonian lineages, *S. ciliatifolia* (BS = 98%), and the Plurifolia + umbrosa clade (BS = 82%) (Fig. 259). The 5S-NTS tree also supported the placement of *S. plurifolia* and *S. umbrosa* together with the Savannic clade, but not as sister species (Fig. 260). Several smaller subclades were recovered in the Savannic clade, and are discussed individually below.

*Schefflera distractiflora* and *S. morototoni* form a well defined subclade (BS = 86--90%, PP = 1; Figs. 263a, 264). These two species share similar leaf morphologies, although the leaves are generally smaller in *S. distractiflora* (see Chapter 3). *Schefflera distractiflora* is also distinct from *S. morototoni* by the shorter habit (treelets up to 3.5 m, vs. trees 5--30 m tall), the inflorescences without (vs. usually with) tertiary branches, flowers grouped in racemose (vs. umbellate) inflorescence units, and glabrous (vs. usually pubescent) nectariferous disc (see Chapter 3). The geographic distribution of *S. distractiflora* shows a complete overlap with that of *S. morototoni*, and both species occur in sympatry across their ranges. The first, however, is restricted to open savannas, while the later occurs mostly in disturbed forests. There is no evidence from molecular data to suggest that these species are distinct, perhaps due to recent divergence, but population-level studies are needed to test whether these species are distinct or merely different growth forms associated with different habitats.

Earlier studies (Frodin, 1997; Frodin & Govaerts, 2003) and a taxonomic revision of the Didymopanax group (see Chapter 3) suggested that *S. morototoni* var. *angustipetala* Marchal is not closely related to the typical variety, and that it is better placed as a synonym under *S.*
tamatamaensis Maguire, Steyerm. & Frodin (see Chapter 3). Although we were unable to include S. tamatamaensis in our phylogenetic analyses, several morphological attributes suggest that it would be better placed in the Imeri clade than with the remaining samples of S. morototoni (see comments under the Imeri clade).

The four samples of Schefflera selloi formed their own subclade within the Savannic clade in the trees resulting from most separate and combined analyses, and sometimes emerged with strong support as sister to S. distractiflora + S. morototoni (BS = 85--92%, PP = 1; Figs. 263a, 264). Schefflera selloi is the only species of the Savannic clade that is entirely restricted to the Brazilian Atlantic forests (Parana Subregion; Morrone, 2006), where it grows on restingas at sea-level sandy areas (see Chapter 3). In contrast to most of the remaining endemic species from the Atlantic forests, which typically have pseudolateral inflorescences and leaflets with an acute or acuminate apex (see discussion under the Atlantic Forest clade), S. selloi is morphologically more similar to S. burchellii and S. vinosa, both from the cerrados of the Brazilian Plateau (see Chapter 3). Schefflera selloi and S. burchellii share leaflets with distinctive petiolules and elliptic to slightly ovate or obovate blades with a rounded to retuse apex, and terminal inflorescences with a short main axis and flowers grouped in umbellules.

The campos rupestres subclade includes species mostly associated with eastern areas of the Cerrado Province (e.g., S. macrocarpa and S. vinosa, see Fiaschi & Pirani, 2008), and all of the endemic species of Schefflera from the campos rupestres vegetation (S. botumirimensis, S. cordata, S. fruticosa, S. gardneri, S. glaziovii, S. lucumoides, and S. villoissima) (Fiaschi & Pirani, 2005a, 2008). The campos rupestres are found in high elevations (usually above 900 m) and are characterized mostly by herbaceous and shrubby plants growing on sandy or stony soils (Giulietti & Pirani, 1988; Harley, 1995). Although the species from this subclade do not seem to
share unique morphological features, a few sub-groups have been recognized on morphological
grounds (Fiaschi & Pirani, 2007, 2008). For example, Fiaschi & Pirani (2007) suggested that S. 
*botumirimensis*, *S. gardneri*, and *S. glaziovii* could be closely related due to the shared presence 
of leaflets with a conduplicate blade and acuminate or caudate to cuspidate apices, features that 
are not found in other *campos rupestres* endemic species. The same authors also suggested a 
species group uniting *S. cordata* and *S. villosissima* to the widespread *S. macrocarpa* due to the 
common presence of a villous indumentum (Fiaschi & Pirani, 2008). In the phylogenetic 
hypotheses presented here, we were unable to gain any insights into interspecific relationships 
within the *campos rupestres* subclade (Figs. 258--260, 263--265), and the sequences from most 
samples in this clade were identical. This result could be suggestive of a recent and rapid 
radiation of *Schefflera* in the eastern Brazilian Cerrado Province, as previously indicated for 
other angiosperm groups (see discussion under biogeography), or possible hybridization among 
species.

Most separate and combined analyses placed *S. plurifolia* and *S. umbrosa* as sister 
species in the Didymopanax group. An alternative placement of *S. plurifolia* as sister to a clade 
uniting *S. umbrosa*, *S. distractiflora*, and *S. morototoni* was strongly supported by 5S-NTS data 
(BS = 85%; Fig. 260). *Schefflera plurifolia* and *S. umbrosa* share a similar stipular morphology, 
as well as the Chamberlain growth model (Fiaschi & al., 2008), but can be easily distinguished 
from each other by vegetative and reproductive features (see Chapter 3). Pinnately compound 
leafletlets are unique to *S. plurifolia* among species of the Didymopanax group, while in *S. umbrosa* trilobed median leaflets are sometimes observed (Fiaschi & al., 2008). In addition, both 
species are endemic to the Amazonian Subregion, although their geographic distributions do not 
overlap (see Chapter 3).
Most phylogenetic analyses recovered the four samples of *Schefflera aurata* as a single clade, which was placed either in a broad basal polytomy in the Didymopanax group or as sister to a clade that includes *S. ciliatifolia*, the Plurifolia + umbrosa clade, and the Savannic clade (Figs. 259, 263b, 264). Maximum parsimony analysis of the ITS + ETS data set recovered a poorly supported placement for *S. aurata* as sister to the Atlantic Forest + Imeri + Five-carpellate clades (Fig. 263a). *Schefflera aurata* has no evident morphological affinities with any other species of the Didymopanax group, but Fiaschi (2004) suggested that it might be closely related to *S. morototoni* mostly on the basis of vegetative features, such as the presence of large and broad leaflets. However, our data suggests that the shared presence of terminal inflorescences in *S. aurata* and *S. morototoni* is symplesiomorphic, and that large and broad leaflets appear to have evolved independently. Moreover, floral and fruit characters clearly distinguish these two species (see Chapter 3) and, despite their geographic sympatry, they are ecologically separated, with *S. aurata* restricted to restinga forests on sandy soils, and *S. morototoni* more common, found as a pioneer species in disturbed areas (see Chapter 3).

The four samples of *S. ciliatifolia* also consistently formed a single lineage, placed either in a broad polytomy, or as sister to the Savannic clade (Figs. 263a, 264) or to the Savannic clade plus *S. plurifolia* (Figs. 263b, 265). *Schefflera ciliatifolia* is unique among species in the Didymopanax group in having leaflets with hispid trichomes on the adaxial surface of the blades and a ciliate margin (Fiaschi & al., 2008). Moreover, there are no morphological features that suggest a close relationship to any known species in the Didymopanax group, and thus its isolated placement does not seem to be an artifact of taxonomic sampling.
**Systematic implications of morphological diversity in the Didymopanax group** — Species of the Didymopanax group share a unique combination of morphological features not found together among other Neotropical species of *Schefflera* (see Chapter 3). Within Frodin’s (1995) subgeneric “Didymopanax” group, he recognized three lineages on the basis of leaf morphology: *Schefflera confusa* (with up to three concentric whorls of leaflets), *S. plurifolia* (with pinnately compound leaflets), and the remaining species, with palmately compound leaves. Most species have two carpels (as the prefix *didymo* suggests), but the earlier placement of two 5-carpellate species (*S. confusa* and *S. decaphylla*) in the segregate genus *Sciodaphyllum* P.Browne (Seemann, 1865; Marchal, 1878) is artificial, and these species are better placed with the remaining species of the Didymopanax group (Frodin, 1995; see Chapter 3). Despite the morphological homogeneity observed across the group, some characters analyzed here were synapomorphistic for individual subclades and are discussed below.

The presence of palmate leaves with more than a single whorl of leaflets is not uncommon in *Schefflera* s. lat. This feature characterizes a few of the Neotropical species from the “Sciodaphyllum” subgeneric group (Frodin, 1995) (e.g., *S. robusta* and *S. sciodaphyllum*), and some species from the Asian clade (e.g., *S. metcalfiana*), as well as an undescribed species from the Melanesian clade (Porter Lowry, pers. comm.). In the Didymopanax group, two species from the Five-carpellate clade have leaves with one or two additional whorls of leaflets (*S. confusa* and *S. prancei*), while in *S. decaphylla* the presence of one additional whorl is sometimes observed (see Chapter 3). The distribution of this character in the phylogeny suggests that it is derived within the Five-carpellate clade (Fig. 265). Another morphological feature that appears to be restricted to this clade is the presence of anthers that are reclined in open flowers, which are known from *S. confusa* and *S. decaphylla* but have not yet been recorded from *S.*
prancei and *S. quinquecarinata* due to the lack of material with open flowers (see Chapter 3). All remaining species of the Didymopanax group, even those where the filaments are longer than the anthers (e.g., *S. angustissima* and *S. calva*) have open flowers with erect anthers. Two other morphological characters common in the Five-carpellate clade each appear to have evolved independently among species of the Didymopanax group. For example, the presence of mostly 5-carpellate ovaries has also been recorded in some populations of *S. angustissima* (Atlantic Forest clade) from Rio de Janeiro state, while the presence of trichomes on the styles is shared by species of the Five-carpellate (*S. confusa* and *S. decaphylla*) and Imeri (*S. pimichinensis*, *S. plurispicata* and *S. pubicarpa*) clades.

The presence of pseudolateral inflorescences in the Didymopanax group is unique to species from the Atlantic Forest clade. All of the remaining species are characterized by terminal inflorescences, which may become pseudolateral only after fructification. Thus, while inflorescence position is not commonly used as a character of systematic significance in Araliaceae, it appears to be of phylogenetic importance in the Didymopanax group. Depending on the topology under consideration, differences in inflorescence position characterizes two main sister clades (Atlantic Forest and remaining species of the Didymopanax group; Fig. 263b) or helps to define a subclade of species with pseudolateral inflorescences in a more inclusive clade that is otherwise characterized by terminal inflorescences (Figs. 263a, 265). Within the Atlantic Forest clade, two other morphological characters help to support the recognition of a subclade uniting *S. longipetiolata*, *S. aff. longipetiolata*, and *S. racemifera* (Figs. 259--260, 263--265), namely the presence of white petals and anthers with thecae free above the insertion of the connective. White petals are are found only in this small subclade, while the remaining species of the Didymopanax group have yellow or greenish petals (see Chapter 3). By contrast, the
anther character is shared between this clade and the Imeri clade, suggesting an independent origin of this character state in the two clades. The Imeri clade also appears to be supported by the presence of pubescent discs, but there are important exceptions, including *S. tamatamaensis*, which lacks this feature but presumably belongs to the Imeri clade, and *S. morototoni*, which shares this character but belongs to the unrelated Savannic clade.

**Biogeography of *Didymopanax*** — The Didymopanax group of *Schefflera* is limited mostly to tropical areas east of the Andes mountain range, with just one species extending into Central America, Mexico, and the West Indies (*S. morototoni*). Other widespread species are known from the Amazonian Subregion (e.g., *S. decaphylla*), the Cerrado Province (e.g., *S. macrocarpa*) and the Parana Subregion (e.g., *S. angustissima* and *S. calva*), while most of the remaining species are typically restricted to much smaller small areas (see Chapter 3).

The areas of endemism defined by PAE using our data agree largely with those suggested by Fiaschi & Pirani (2008) on the basis of geographic distribution maps. These authors pointed to two centers of endemism for *Schefflera* in extra-Amazonian Brazil: the Espinhaço Range of Minas Gerais and the coastal mountains of Rio de Janeiro and Espírito Santo states, which are largely congruent with the “Cerrado” and “Brazilian Atlantic Forest” areas of endemism recovered from the PAE using 2 x 2° quadrats (Fig. 267c). The Imeri Province has also been suggested as a third center of species diversity for the Didymopanax group (see Chapter 3), but there is no support to recognize an Imeri area of endemism based on PAE. The lack of an Imeri area of endemism may result from the fact that the four species endemic to this region do not fall in the same grid square units, and may be an artifact of the poor knowledge of their geographic
distribution limits (see Chapter 3), and of the flora of eastern Colombian lowlands in general, which is known to be one of the most poorly documented in the entire Amazon (Hopkins, 2007).

In general, the low degree of resolution using both quadrat sizes (1 x 1° and 2 x 2°) in our study resulted from the small number of species (40) and the large number of quadrats (from 238 to 571) used in the PAE. Using the 1 x 1° grid, a larger number of quadrats clusters were recovered from the maximum parsimony analysis, but most lacked the minimum number of endemic species to be considered areas of endemism. Only two individual quadrats were supported by two or more endemic species, and could thus be recognized as areas of endemism for the Didymopanax group (Fig. 266). Analyses using larger quadrats (2 x 2° degrees) recovered a smaller number of quadrat clusters, but more of those had at least two endemic species (Fig. 267). Morrone and Escalante (2002) investigated the influence of quadrat size in PAE, and concluded that larger quadrats tend to have an additive number of endemic species to support their recognition as areas of endemism. Moreover, they concluded that smaller quadrat sizes yield less resolved trees because there are more “terminals” but the same number of “characters.” Although this conclusion is intuitive, there is a trade-off between quadrat size and the number of detected areas of endemism because larger quadrats may include greater habitat heterogeneity, and consequently may lead to confusion in the biological interpretations of the hierarchical clustering of areas (Sigrist & Carvalho, 2008).

Trees resulting from PAE including S. morototoni resolved clusters of areas that were not recovered when this species was excluded (Figs. 266b, 267b), because the presence of this species may have provided homoplasious synapomorphies for some clades. However, the inclusion of S. morototoni also resulted in a considerable increase in the number of terminals (from 355 to 570 using 1 x 1° quadrats, and 155 to 237 using 2 x 2° quadrats), and, consequently,
in the time required to complete the parsimony analyses. When *S. morototoni* was excluded from the data sets, similar results were obtained (Figs. 266c, 267c), but no additional areas of endemism could be recognized, because the number of such areas increases proportionally with the number of species included in the analyses (Morrone, 1994, 2009).

Our phylogenetic analyses did not recover a single and strongly supported set of relationships among the species of the Didymopanax group, especially due to the poor support and/or resolution among the basal branches (see above). Despite this, the same four main clades were consistently recovered in most trees, and the geographic distribution of the species in these clades can provide insights into the diversification of this group in South America. Because the DIVA optimization based on the ML topology obtained from consensus sequences of ITS + ETS + 5S-NTS data (Fig. 269) provided a more conservative biogeographic scenario (i.e., with more alternative ancestral area reconstructions, see results) than the optimization from the topology excluding 5S-NTS data (Fig. 268), the topology based on all three data sets (i.e., also including 5S-NTS data; Fig. 269) was chosen to discuss the biogeography of the Didymopanax group. The ML tree resulting from ITS + ETS along (i.e., excluding 5S-NTS) recovered a very similar set of relationships except for some poorly supported relationships within the *campos rupestres* subclade and the placement of *S. ciliatifolia* and *S. plurifolia*, and did not provide a significantly different biogeographic history for species of the Didymopanax group. Based on DIVA, a biogeographic scenario for the species of Didymopanax group from tropical South American east of the Andes [as defined by Morrone’s (2006) biogeographic subregions] is discussed in the following paragraphs (Fig. 272).

Possibly because early attempts to understand the biogeographic history in the Amazon have emphasized the diversification of its biota *in situ* (see Garzón-Orduña & Miranda-Esquivel,
2007; Haffer, 2008) instead of the origin of its lineages, Amazonia has traditionally been viewed as a single biogeographic unit in which its organisms were thought to share the same biogeographic history (Cabrera & Willink, 1973; Prance, 1982; Siva & Oren, 1996; Bates & al., 1998; Morrone, 2001, 2006). However, several more recent biogeographic studies based on quantitative biogeographic approaches have suggested that the Amazonian Subregion (sensu Morrone, 2006) may be a “composite biogeographic area”, whose different subdivisions represent different biogeographic histories. In particular, studies of several groups of insects and birds have suggested that the northwestern portion of Amazonia may be more closely related to the Caribbean Subregion, while its southeastern portion is more closely related to the Chacoan and Parana subregions of eastern Brazil (e.g., Amorim, 2001; Hall & Harvey, 2002; Ribas & Miyaki, 2004; Nihei & Carvalho, 2007). These two hypotheses (biogeographic unit vs. composite area) may not be mutually exclusive, depending on the group under consideration. For example, the same area may be considered a single biogeographic unit if all species of the group derive from a common exclusive ancestor (as may be the case with several Amazonian endemic genera), or as a composite biogeographic unit if representatives from the same genus in the area descend from more than one ancestor.

Four Amazonian-centered clades of the Didymopanax group were recovered in our phylogenetic analyses, each of which have distinctive morphologies and geographic distributions: Imeri, Five-carpellate, Plurifolia + umbrosa, and S. ciliatifolia (Figs. 258--260, 262). Together, these clades did not form a monophyletic group in any of the recovered trees, and their phylogenetic placement varied between MP topologies including and excluding the 5S-NTS data (Fig. 263). Among these Amazonian clades of the Didymopanax group, two are better represented in northern and western Amazonian areas [(1) Imeri and (3) Five-carpellate clades,
Fig. 272], while the *S. plurifolia* and *S. ciliatifolia* clades are entirely restricted to central and southeastern areas (Figs. 268, 269, 272). With the exception of a few samples of *S. decaphylla* (Fig. 268, 269), the Imeri and Five-carpellate clades are restricted to northwestern Amazonia, as delimited by Nihei (2008) (Figs. 257b, 272). These two clades (Imeri and Five-carpellate) appeared either as sister groups (Fig. 265) or as successive sisters to a mostly eastern clade [either the Atlantic Forest clade (Fig. 263a) or a clade uniting *S. aurata*, the Savannic clade, *S. ciliatifolia*, and *S. plurifolia* (Fig. 263b)], and did not group together with any of the remaining Amazonian subclades (Plurifolia + umbrosa and *S. ciliatifolia*). *Schefflera plurifolia* and *S. ciliatifolia*, on the other hand, were consistently placed in a clade that also included the central-eastern Brazilian species of the Savannic clade (Figs. 263--265, 268, 269). The relationships among the Amazonian-centered clades of the Didymopanax group agree with several phylogenetic studies of other Neotropical organisms that have also pointed to a closer biogeographic connection of the southeastern Amazonian forests to the Brazilian Atlantic forests (Parana Subregion), and the Chacoan Subregion then to the northwestern Amazonian forests (Amorim & Pires, 1996, 2001; Hall & Harvey, 2002; Nihei & Carvalho, 2004, 2007), thus providing further evidence for the recognition of the Amazonian Subregion of Morrone (2006) as a composite biogeographic area.

The separation of the Amazonian biota into two groups (northwestern and southeastern) has been explained in terms of several vicariance events that may have separated the Guayanan and Brazilian shields at different times throughout the Late Cretaceous and Tertiary (Amorim & Pires, 1996; Nihei & Carvalho, 2004; Wesselingh & Salo, 2006; Hoorn, 2006; Antonelli & al., 2009; Wesselingh & al., in press). Among the currently advocated episodes of such separation are the formation of a lake along the rivers Amazonas, Madeira and Mamoré during the Late
Cretaceous (Amorim & Pires, 1996; Nihei & Carvalho, 2004) and the western Amazonian Lake Pebas (or Pebasian Sea) during the early and middle Miocene (Wesselingh & Salo, 2006; Hoorn, 2006; Antonelli & al., 2009; Wesselingh & al., in press). The biogeographic pattern resulting from these multiple episodes of separation is “pseudocongruent” (Donoghue & Moore, 2003), as the spatial congruence among different organisms has been achieved at different geological times (Nihei & Carvalho, 2007).

Compared to the Amazonian Subregion, the Cerrado Province has a much smaller area but nearly the same diversity of Didymopanax species. There are 14 species of the Didymopanax group in the Cerrado Province (Fig. 257a), half of which are restricted to the campos rupestres vegetation of the Espinhaço Range in Minas Gerais (Fiaschi & Pirani, 2008). Excluding S. morototoni, which is a widespread species associated mostly with disturbed forests, and S. calva, which is a typical element of the Parana Subregion that “invades” the Cerrado Province (Fiaschi & Pirani, 2008), all remaining species from the cerrados are endemic to open savannic areas. Our phylogenetic hypotheses consistently recovered a clade that groups all (but not only) these endemic savannic species (the Savannic clade, Figs. 258, 263--265, 268). This result contrasts with findings from Prance (1992), who indicated that most savannic species of Chrysobalanaceae are probably the result of independent habitat shifts from forest species. By contrast, in Didymopanax, there seems to be a high degree of phylogenetic niche conservatism, which predicts that closely related species are likely to be found within the same habitat, rather than in different habitats (Wiens, 2004; Donoghue, 2008). The only exception to the niche conservatism observed in the Savannic clade is provided by S. selloi, a species restricted to coastal sandy areas of recent deposition, called restingas, in the Brazilian Atlantic forests (see Chapter 3). The placement of S. selloi in the Savannic clade is also supported by morphological data (see above),
and corroborates a well documented series of geographic disjunctions in the Brazilian flora between the Espinhaço Range (Brazilian Plateau) and the coastal *restingas* (Giulietti & Pirani, 1988; Alves & al., 2007).

High levels of plant endemism have been reported in the *campos rupestres* flora of the Espinhaço Range in Minas Gerais (Joly, 1970; Giulietti & Pirani, 1988; Harley, 1995; Rapini & al., 2002). The Didymopanax group has seven species endemic to this region (Fiaschi & Pirani, 2008), all of which formed a well supported subclade within the Savannic clade (*campos rupestres* subclade; Figs. 259, 263, 265, 268). The lack of resolution in this subclade may point to a rapid diversification of *Schefflera* in the *campos rupestres* vegetation. The same biogeographic pattern of several closely related species endemic to the *cerrados* and *campos rupestres* of eastern Brazil has been reported for other angiosperm groups, such as *Viguiera* (Compositae) (Schilling & al., 2000), *Microlicieae* (Melastomataceae) (Fritsch & al., 2004), and *Minaria* (Apocynaceae) (Rapini & al., 2007). These studies have suggested recent (3--4.7 mya) diversification events in high-altitude clades that include *campos rupestres* endemic species.

Among the plant groups studied so far, diversification of endemic plants from the Cerrado Province seem to have been associated with the evolution of drought tolerance (Fritsch & al., 2004) and plant-defense strategies, such as the development of mutualistic associations with nectar-seeking ants (Marazzi & al., 2006). Further phylogenetic studies of the endemic flora of the Cerrado Province could provide additional data to evaluate whether it has resulted mostly from recent radiations as suggested by Pennington & al. (2006).

Our study also provides strong evidence for the recognition of an Atlantic Forest clade of Didymopanax (Figs. 258--260, 263--265) that includes most of the endemic species from the Parana Subregion plus *S. calva*, which has a western expansion in the gallery forests of the
Cerrado Province (Fiaschi & Pirani, 2008). Species from this clade are found mostly in submontane and montane forests of the eastern fringes of the Brazilian Plateau, especially along the Serra do Mar and Serra da Mantiqueira mountain ranges, and only *S. angustissima* can be found occasionally at lowland sea-level forests from Rio de Janeiro to Santa Catarina states (Fiaschi & Pirani, 2008). The geographic distribution of species of the Didymopanax group from the Atlantic Forest clade stands in sharp contrast to that of the two remaining endemic species from the Parana Subregion, *S. aurata* and *S. selloi*, both of which belong to lineages exclusive to restingas at Espírito Santo and Bahia states (see Chapter 3).

The South American Atlantic forests comprise a continuous strip of rainforests along the Atlantic coast of Brazil, from c. 5–30ºS (Oliveira-Filho & Fontes, 2000; Silva & Casteleti, 2003). Due to their isolation from the remaining areas of rainforests in South America, the Atlantic forests have been also traditionally treated as a single biogeographic unit (e.g., Müller, 1973; Rizzini, 1997; Morrone, 2001, 2006). However, like the Amazonian Subregion, some studies have suggested that the Atlantic forests (Parana Subregion sensu Morrone, 2006) may also represent a composite biogeographic area, in which it is possible to recognize distinct histories for groups of organisms occurring in northern and southern portions (Cracraft, 1985; Soderstrom & al., 1988; Costa, 2003; Silva & al., 2004). The biogeographic scenario reconstructed from DIVA shows that species of the Didymopanax group from the Parana Subregion are separated into a well supported and mostly southern group (Atlantic Forest clade), and three unrelated northern lineages, namely *S. aurata* (Fig. 272), *S. macrocarpa*, and *S. selloi*, the latter two of which belong to the Savannic clade (Figs. 268, 269, 272). The geographic structuring of the Atlantic Forest clade in southern forests, and the presence of multiple unrelated lineages in the northern forests of the Parana Subregion (Fig. 272) provides an additional line of
evidence that the Brazilian Atlantic Forest is a composite biogeographic unit (Costa, 2003; Perret & al., 2006; Nihei & Carvalho, 2007; Santos & al., 2007; Sigrist & Carvalho, 2008).

Several studies have suggested that there may be an historical separation between the northern and southern portions of the Atlantic forests, whose limits are more or less coincident with the Rio Doce valley (northern Espírito Santo state) (Cracraft & Prum, 1988; Amorim & Pires, 1996; Costa, 2003; Silva & al., 2004). These two forest blocks are highly differentiated in their floras (e.g., Oliveira-Filho & Fontes, 2000; Oliveira-Filho & al., 2005) and relatively few cases of exchange between them have been reported in previous phylogenetic studies (e.g., Perret & al., 2006). Among species of the Didymopanax group, the occurrences of *S. angustissima* and *S. calva* as far north as southern Bahia montane forests and the Chapada Diamantina forests (Amorim & al., 2009; see Chapter 3) provide rare examples of the northern migration of two otherwise entirely southern species (Fig. 272).

Despite the lack of a temporal scale for the diversification of the Didymopanax group in the Atlantic forests, our data suggest that species of this group diversified from at least three independent lineages. The first lineage is a speciose clade restricted mostly to the eastern fringes of the Brazilian Plateau (Atlantic Forest clade, 10 spp.). Species from this clade seem to have diversified locally in the Espírito Santo submontane rainforests, where four closely related species co-occur (Fiaschi & Pirani, 2008). This species group (ES endemic subclade) is well supported as sister to the remaining species from the Atlantic Forest clade (the Calva subclade; Figs. 259, 263a, 264, 265), which did not show the same degree of geographic structure. Among the species of the Calva subclade, some appear to have evolved to occupy specific habitats, such as wind-exposed montane rainforests at hilltops (*S. succinea*) and the dim sub-canopy of rainforest habitats (e.g., *S. longipetiolata* and *S. racemifera*). The remaining Atlantic forest
endemic lineages (S. aurata and S. selloi) are likely to be at least evolutionary as young as the restingas they inhabit, which were formed during the Quaternary (Lacerda & al., 1993; Scarano, 2002). Moreover, the occurrence of S. morototoni in the Atlantic forests is probably the result of multiple additional dispersals, but an extensive sampling of this species and population-level studies would be required to test this hypothesis. Schefflera macrocarpa and S. vinosa represent dispersals of Savannic species that occasionally occupy marginal habitats in patches of cerrado across the Parana Subregion (Fig. 272, lineage 4.1).

Conservation and phylogenetic diversity measures — The two different measures of species diversity in the Didymopanax group of South America provided very different results. The species richness approach indicated that the campos rupestres of the Espinhaço Range in Minas Gerais is the area of maximum species diversity, with three contiguous quadrats having 7 to 9 species (Fig. 270a). Seven species from quadrat K'32, which had the greatest richness (9 spp.), belonging to a single clade characterized by very short branch lengths (Fig. 271), and probably represents a recent radiation of the Didymopanax group in the campos rupestres (see above). Of these nine species, five are endemic to this vegetation type (Fiaschi & Pirani, 2008). Despite the large number of species in this region, these quadrats were not identified as the most diverse when using PD as the measure of diversity (Fig. 270b).

One quadrat from the Atlantic forests located in the state of Espírito Santo showed high values for both species richness and phylogenetic diversity (quadrat N'33; Figs. 270a, b). This quadrat had seven species, five of which are placed in the Atlantic Forest clade of Didymopanax (S. calva, S. grandigemma, S. kollmannii, S. ruschiana and S. aff. longipetiolata). Three of these species (S. grandigemma, S. kollmannii and S. ruschiana) belong to the ES endemic subclade
(Fig. 271), while the remaining two belong to the Calva subclade (Fig. 271). In addition, the presence of two species from the Savannic clade (S. morototoni and S. selloi) resulted in the high PD value observed in this quadrat (PD = 0.123). Another quadrat with high PD (but only 4 spp.) was observed in the Atlantic forests in southern Bahia (quadrat O'30; Fig. 270b). In this quadrat, the occurrence of S. calva (from the Atlantic Forest clade) contributed significantly to the increase of the PD value derived from the combined presence of S. aurata, S. morototoni, and S. selloi, all of which are more closely related to plants from the Brazilian cerrados and southeastern Amazonian forests than to species from the Atlantic Forest clade (Fig. 271). These two quadrats (N'33 and O'30) in the Atlantic forests marked by high PD values appear to result from the joint contribution of a mostly southern species (S. calva) in a northern site (quadrat O'30), and a mostly northern species (S. selloi) in a southern site (quadrat N'33).

The most surprising result from the diversity measures of the Didymopanax group involves a small number of Amazonian sites. Nine of ten quadrats with the highest PD values were located in the Amazon (T17, T26, T16, U16, U17, H14, T27, U26, U27), even though most of these sites had relatively few species. Quadrat T17, from the surroundings of Manaus, had the highest PD value, but only five species contribute to the richness at this specific site. The diversity of this quadrat reflects the many different clades represented in this site (Fig. 271). With the exception of the Atlantic Forest clade, each of the other main clades had one species represented in this quadrat: S. pubicarpa from the Imeri clade, S. decaphylla from the Five-carpellate clade, and S. morototoni from the Savannic clade (Fig. 271). In addition, two taxa from minor clades, S. umbrosa and S. ciliatifolia (both represented by long branches in the phylogeny; Fig. 271), contributed to the estimate of PD at this specific quadrat. More frequent sampling in the Manaus area compared to other Amazonian sites (Nelson & al., 1990) could
provide a satisfactory explanation for the high PD observed in this quadrat. However, we believe that this result is not an artifact but instead reflects the history of this region as a crossroad of distinct phytogeographic regions (Oliveira & Daly, 1999). For example, the five species of the Didymopanax group found in this site represent different patterns of Amazonian geographic distribution, including species that are widespread in the Amazon (S. decaphylla and S. morototoni), species endemic to the Manaus region (S. ciliatifolia), and elements of mostly western (S. pubicarpa) and central (S. umbrosa) regions. As such, this region (represented in our analysis by quadrat T17) represents an important repository for phylogenetic diversity of the Didymopanax group.

Two other Amazonian sites had PD values higher than most of the remaining areas (Fig. 270b). The first (T26) was located in an ecotonal region between the southeastern Amazon and the western Brazilian Cerrado and is characterized by a mosaic of savannas and forests (Ratter, 1992). Among the four species observed in this quadrat (Fig. 270a), two are unrelated Amazonian species (S. decaphylla and S. plurifolia; Fig. 271), while two others, S. distractiflora and S. malmei, grow in open savannic areas. The identification of this quadrat as one of those having the highest PD scores corroborates earlier studies that suggested the importance of areas with habitat heterogeneity for the conservation of biodiversity (e.g., Kreft & Jetz, 2007). For instance, the phylogenetic niche conservatism observed in the Didymopanax group (discussed above) suggests that species occupying different habitats tend to belong to different clades, which leads to an increased level of PD in areas with habitat heterogeneity. Another site with a surprisingly high PD value but a relatively low number of species (only three) was situated in the Amazonian forests at southeastern Colombia (H14; Fig. 270b). This region comprises remnant outliers from the Guayana Shield, and is characterized by an edafic mosaic of clay and sandy
soils where rainforest and campinarana white-sand forest species can co-occur (Arbeláez & Duivenvoorden, 2004). In fact, S. aff. pubicarpa and S. confusa appear to be typical of forests on sandy soils, while S. morototoni is usually found in forests on clayey soils (see Chapter 3). A few species from the Imeri Province (Fig. 257a) were unavailable for this study (e.g., S. pimichinensis, S. plurispicata and S. tamatamaensis) and they could help to identify additional Amazonian quadrats with high PD along the borders between of Brazil, Colombia, and Venezuela, where these three species appear to co-occur (see Chapter 3).

Species richness and PD measures point to different areas as those having the highest diversity of Didymopanax. The area with greatest richness (quadrat K'32; Fig. 270a) carries a low phylogenetic diversity, whereas a few Amazonian areas with a relatively low richness (e.g., quadrats T17, T26, H14) are among the most phylogenetically diverse. To maximize the conservation of this group we recommend that both approaches should be taken into consideration because they provide complementary tools for biodiversity assessment. In addition to the widespread use of species richness as an important biodiversity indicator, phylogenetic hypotheses of tropical organisms can provide valuable information for decision-making strategies regarding the conservation of the highly threatened but poorly known tropical biota (e.g., Faith, 1992; Faith & Baker, 2006; Jaramillo, 2006).

**Limitations and future directions**

In this study, we used three nrDNA markers and a morphological data set to infer interspecific relationships in the Didymopanax group of Neotropical Schefflera. An almost complete sampling was obtained, but five species were lacking and thus could not be placed in the phylogenetic trees. The trees we did recover had weak support at most of the basal nodes.
Moreover, trees resulting from combined data sets yielded contrasting topologies due to “soft” incongruence and three significant examples of “hard” incongruence. Future studies should focus on the use of plastid markers and low-copy-number nuclear markers to test and enhance the phylogenetic relationships presented here. Those clades that were strongly supported in the Didymopanax group correlate well with biogeographic areas of South America east of the Andes, and seem to corroborate the composite biogeographic nature of the Atlantic and Amazonian forests. However, the biogeographic scenario derived from these phylogenies requires further corroboration before it can be adopted to explain current distribution patterns among the species of the Didymopanax group.

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Milton Groppo, Rosângela Melo, Serginho Sant’Ana, and Thayná Mello provided help during fieldwork. Financial assistance for this research was provided by the National Science Foundation (DEB 0613728).
Table 1: Species and voucher information of the specimens used for this study. Subgeneric and infrageneric group names follow Plunkett et al. (2005). Sciod. = Sciodaphyllum. Pollen sample techniques: LM = light microscopy only, SEM = scanning electron microscopy only (if both LM and SEM were used on the same sample, the technique is not indicated). Herbarium acronyms follow Holmgren et al. (1990).

<table>
<thead>
<tr>
<th>Species</th>
<th>Pollen sample</th>
<th>Informal Group</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>S. attenuata</em> (Sw.) Frodin</td>
<td>Beard 1289 (MO)</td>
<td>Sciod., Attenuatae</td>
</tr>
<tr>
<td><em>S. chimantensis</em> (Steyermark &amp; Maguire) Maguire, Steyermark &amp; Frodin</td>
<td>Steyermark 128475 (MO)</td>
<td>Crepinella</td>
</tr>
<tr>
<td><em>S. ciliatifolia</em> Fiaschi &amp; Frodin</td>
<td>Nee 43002 (NY) – SEM</td>
<td>Didymopanax</td>
</tr>
<tr>
<td><em>S. confusa</em> (Marchal) Harms</td>
<td>Prance 3010 (NY)</td>
<td>Didymopanax</td>
</tr>
<tr>
<td><em>S. decaphylla</em> (Seem.) Harms</td>
<td>Ducke 1929 (US) – SEM</td>
<td>Didymopanax</td>
</tr>
<tr>
<td><em>S. cf. dielsii</em> Harms</td>
<td>Neill 15066 (MO)</td>
<td>Sciod., unassigned</td>
</tr>
<tr>
<td><em>S. diplodactyla</em> Harms</td>
<td>Asplund 18527 (US)</td>
<td>Sciod., unassigned</td>
</tr>
<tr>
<td><em>S. distractiflora</em> (Harms) Frodin</td>
<td>Ferreira 5695 (NY)</td>
<td>Didymopanax</td>
</tr>
<tr>
<td><em>S. duidae</em> Steyermark</td>
<td>Steyermark 107285 (MO)</td>
<td>Sciod., unassigned</td>
</tr>
<tr>
<td><em>S. epiphytica</em> A.C.Sm.</td>
<td>Kirkbride 1067 (NY) – LM</td>
<td>Sciod., unassigned</td>
</tr>
<tr>
<td><em>S. harmsii</em> J.F.Macbr.</td>
<td>Fuentes 1183 (MO)</td>
<td>Crepinella</td>
</tr>
<tr>
<td><em>S. jahnii</em> (Harms) Steyermark</td>
<td>Terán 13263 (MERF)</td>
<td>Cephalopanax</td>
</tr>
<tr>
<td><em>S. lasiogyne</em> Harms</td>
<td>Tipaz &amp; Quelal 203 (MO)</td>
<td>Sciod., Lasiogynes</td>
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<td></td>
<td>– LM</td>
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</tr>
<tr>
<td></td>
<td>Zak 1289 (MO) – SEM</td>
<td></td>
</tr>
<tr>
<td><em>S. longipetiolata</em> (Pohl ex DC.)</td>
<td>Lima &amp; Martinelli 1831</td>
<td>Didymopanax</td>
</tr>
<tr>
<td>Frodin &amp; Fiaschi</td>
<td>(RB) – SEM</td>
<td></td>
</tr>
</tbody>
</table>
S. minutiflora Harms Vega 9515 (US) Sciod.,

Minutiflorae

S. montana (Gleason) Maguire, Steyerm & Frodin Cowan & Wurdack 31129 Crepinella

(NY)

S. patula (Rusby) Harms Waytkowski 8333 (US) Sciod. Patulae

S. pentandra (Pav.) Harms Harling 3875 (NY) Sciod. Pentandrae

S. pimichinensis Maguire, Steyerm & Frodin Maguire & Wurdack 35636 Didymopanax

(NY)

S. cf. quindiuensis (Kunth) Callejas 3730 (MO) Cotylanthes

Harms

S. quinquecarinata Steyermark Prance 10159 (NY) Didymopanax

S. robusta (A.C.Sm.) A.C.Sm. Maas 7813 (MO) Sciod., unassigned

S. rodriguesiana Frodin Burger & Liesner 6441 Sciod. Attenuatae

(MO) – SEM

S. rufa Frodin Bautista 3834 (MER) Sciod., unassigned

S. ruschiana Fiaschi & Pirani Fiaschi 956 (SPF) – SEM Didymopanax

S. sciodaphyllum (Sw.) Harms Britton 3869 (NY) Sciod.,

Sciodaphyllum

S. sessiliflora Frodin Steyermark 124075 (VEN) Sciod., unassigned

S. sodiroi Harms Palacios & Werff 3909 Sciad., unassigned

(MO)

S. sp. nov. ‘Cephalopanax’ Homeier 1582 (MO) Cephalopanax

S. sp. nov. ‘Cotylanthes’ Palacios 6411 (MO) Cotylanthes

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<thead>
<tr>
<th>Species</th>
<th>Collection Details</th>
<th>Identification Notes</th>
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<tr>
<td>S. sp. nov. ‘Sciodaphyllum’</td>
<td>Steyermark 100789 (VEN)</td>
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<td>S. sphaerocoma (Benth.) Harms</td>
<td>Zarucchi 5097 (MO)</td>
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<td>S. systyla (Donn.Sm.) R.Vig.</td>
<td>Quesada 760 (MO)</td>
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<td>S. tamana Steyermark</td>
<td>Steyermark &amp; Dunsterville 98539 (MO)</td>
<td>Sciod., Bejucosae Sciodaphyllum</td>
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<td>S. tamatamaensis Maguire, Steyermark &amp; Frodin</td>
<td>Aymard &amp; Delgado 8430</td>
<td>Didymopanax</td>
</tr>
<tr>
<td>S. aff. tamatamaensis Maguire, Steyermark &amp; Frodin</td>
<td>Restrepo &amp; Matapi 370</td>
<td>Didymopanax</td>
</tr>
<tr>
<td>S. cf. ternata Cuatrec.</td>
<td>Werff 11947 (MO)</td>
<td>Sciod., unassigned</td>
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<tr>
<td>S. tipuanica Harms</td>
<td>Valenzuela 4046 (MO)</td>
<td>Sciod., unassigned</td>
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<tr>
<td>S. tremula (Krug &amp; Urb.) Alain</td>
<td>Holdridge 1876 (US) – LM</td>
<td>Sciod., Attenuatae Jimenez 1080 (NY)</td>
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<td>S. tremuloidea Maguire, Steyermark &amp; Frodin</td>
<td>Nee 30614 (NY) – SEM</td>
<td>Sciod., Cheilodromi</td>
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<td>S. troyana (Urb.) A.C.Sm.</td>
<td>Harris 10876 (NY)</td>
<td>Sciod., Sciodaphyllum</td>
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<td>S. umbellata (N.E.Br.) R.Vig.</td>
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<td>Crepinella</td>
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<td>S. cf. violacea Cuatrec.</td>
<td>Quizhpe 1593 (MO)</td>
<td>Sciod., unassigned</td>
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</table>
Table 2. Comparison of Neotropical *Schefflera* pollen types with other reproductive features and geographic distributions. Geographic areas: BOL (Bolivia), BRA (Brazil), COL (Colombia), COS (Costa Rica), ECU (Ecuador), GUY (Guyana), HIS (Hispaniola), JAM (Jamaica), LAN (Lesser Antilles), PAN (Panama), PER (Peru), VEN (Venezuela). ‘raceme’ refers to “racemes terminating in an umbel”. Missing information (–). SEX:NEX (relative thickness of sexine and nexine layers).

<table>
<thead>
<tr>
<th>Species</th>
<th>Size (P x E, µm*)</th>
<th>Ornamentation</th>
<th>Shape</th>
<th>SEX: NEX</th>
<th>Inflorescence terminal unit</th>
<th>Petals</th>
<th>Carpel number</th>
<th>Geographic distribution</th>
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<td><strong>1. “Reticulate-heterobrochate” type</strong></td>
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<td></td>
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<tr>
<td><em>S. confusa</em></td>
<td>32 x 34</td>
<td>reticulate-heterobrochate</td>
<td>oblate-spheroidal</td>
<td>≥</td>
<td>umbel</td>
<td>free</td>
<td>5</td>
<td>BRA, COL, PER</td>
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<tr>
<td><em>S. distractiflora</em></td>
<td>24.5 x 26.5</td>
<td>reticulate-heterobrochate</td>
<td>oblate-spheroidal</td>
<td>≥</td>
<td>‘raceme’</td>
<td>free</td>
<td>2</td>
<td>BRA, BOL</td>
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<td><em>S. pimichinensis</em></td>
<td>27 x 29</td>
<td>reticulate-heterobrochate</td>
<td>oblate-spheroidal</td>
<td>≥</td>
<td>umbel</td>
<td>free</td>
<td>2</td>
<td>VEN</td>
</tr>
<tr>
<td><em>S. quinquecarinata</em></td>
<td>28 x 28</td>
<td>reticulate-heterobrochate</td>
<td>oblate-spheroidal</td>
<td>≥</td>
<td>umbel</td>
<td>free</td>
<td>5</td>
<td>BRA, VEN</td>
</tr>
<tr>
<td><em>S. tamatamaensis</em></td>
<td>29 x 33</td>
<td>reticulate-heterobrochate</td>
<td>oblate-spheroidal</td>
<td>≥</td>
<td>umbel</td>
<td>free</td>
<td>2</td>
<td>VEN</td>
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<tr>
<td><strong>2. “Perforate” type</strong></td>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td><em>S. attenuata</em></td>
<td>29 x 23</td>
<td>perforate</td>
<td>subprolate</td>
<td>=</td>
<td>umbel</td>
<td>calyptrate</td>
<td>2</td>
<td>LAN</td>
</tr>
<tr>
<td><em>S. diplodactyla</em></td>
<td>26 x 22</td>
<td>perforate</td>
<td>subprolate</td>
<td>=</td>
<td>umbel</td>
<td>calyptrate</td>
<td>5</td>
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<td><em>S. minutiflora</em></td>
<td>22 x 19</td>
<td>perforate</td>
<td>subprolate</td>
<td>≥</td>
<td>umbel</td>
<td>calyptrate</td>
<td>5</td>
<td>COL, ECU, PER</td>
</tr>
<tr>
<td><em>S. rodriquesiana</em></td>
<td>36 x 27</td>
<td>perforate</td>
<td>subprolate</td>
<td>=</td>
<td>umbel</td>
<td>calyptrate</td>
<td>2</td>
<td>COS, PAN</td>
</tr>
<tr>
<td><em>S. sciodaphyllum</em></td>
<td>29 x 30</td>
<td>minutely perforate</td>
<td>subprolate</td>
<td>=</td>
<td>umbel</td>
<td>calyptrate</td>
<td>5</td>
<td>JAM</td>
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<tr>
<td><em>S. sphaerocoma</em></td>
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<td>oblate-spheroidal</td>
<td>≥</td>
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<td><em>S. patula</em></td>
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4. “Reticulate-homobrochate” type

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5. “Perforate-microreticulate, usually rugulate” type

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<td>S. duidae</td>
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<td>S. sessiliflora</td>
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<td>calyptrate</td>
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* Average (n = 25).
Table 3. Names, sources and GenBank accession numbers of Neotropical *Schefflera* samples used in this study (plus 5 new sequences of ETS for outgroup taxa). Sources from remaining samples analyzed in this study are provided in Plunkett et al. (2004, 2005). DNA extracted from herbarium samples indicated by (*). ¹Infrageneric groups of Sciodaphyllum follows Frodin (1995) and Plunkett et al. (2005).

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Table 4. Comparisons among data sets and maximum parsimony trees statistics obtained for this study. * Indicates MP trees shown in the paper. MP = most parsimonious.

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Table 5. List of species, voucher information and GenBank accession numbers for the samples included in this study. Specific epithets in quotation marks refer to undescribed species. Vouchers followed by an asterisk had DNA extracted from herbarium material. Herbarium acronyms follow Holmgren & al. (1990).

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P. Fine 1462 (UC); French Guiana  
Schefflera dichotoma Fiaschi & Frodin  
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Fiaschi 3009 (SPF); Brazil, Rondônia
Schefflera distractiflora  
M. Santos 364 (SPF); Brazil, Mato Grosso
Schefflera distractiflora  
P. Viana 2718 (INPA); Brazil, Amazonas
Schefflera fruticosa Fiaschi & Pirani  
Fiaschi 3109 (CEPEC); Brazil, Minas Gerais
Schefflera gardneri (Seem.) Frodin & Fiaschi  
Fiaschi 3090 (SPF); Brazil, Minas Gerais
Schefflera gardneri  
J. Pirani 5306 (SPF); Brazil, Minas Gerais*
Schefflera glaziovii (Taub.) Frodin & Fiaschi  
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Schefflera glaziovii  
J. Pirani 5192 (SPF); Brazil, Minas Gerais*
Schefflera grandigemma Fiaschi  
Fiaschi 1475 (CEPEC); Brazil, Espírito Santo
Schefflera kollmannii Fiaschi  
Fiaschi 1474 (CEPEC); Brazil, Espírito Santo
Schefflera longipetiolata (Pohl ex DC.) Frodin & Fiaschi  
Fiaschi 617 (SPF); Brazil, Minas Gerais
Schefflera longipetiolata  
R. Forzza 2877 (RB); Brazil, Rio de Janeiro*
Schefflera aff. longipetiolata  
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Schefflera lucumoides (Decne. & Planch. ex Marchal) Frodin & Fiaschi  
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Schefflera macrocarpa (Cham. & Schltldl.) Frodin  
Fiaschi 2397 (SPF); Brazil, Bahia
Schefflera macrocarpa  
Fiaschi 3039 (SPF); Brazil, São Paulo
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Fiaschi 3040 (SPF); Brazil, São Paulo
Schefflera macrocarpa  
Fiaschi 3087 (SPF); Brazil, Minas Gerais
Schefflera macrocarpa  
L. Assis 1191 (SPF); Brazil, Bahia
Schefflera malmei (Harms) Frodin  
Fiaschi 2972 (SPF); Brazil, Mato Grosso

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Schefflera malmei  
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Schefflera malmei  
M. Santos 362 (SPF); Brazil, Mato Grosso
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin  
B. Hammel 22506 (MO); Costa Rica
Schefflera morototoni  
D. Neill 13999 (MO); Ecuador, Napo
Schefflera morototoni  
Fiaschi 888 (SPF); Brazil, Bahia
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Fiaschi 1121 (SPF); Brazil, Bahia
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Fiaschi 2376 (SPF); Brazil, Bahia
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Fiaschi 3370 (NY); Brazil, Acre
Schefflera “pubicarpa” Fiaschi & Plunkett, ined.  
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Schefflera quinquecarinata Steyerm.  
E. Sanoja 9092 (GUYN); Venezuela, Bolivar
Schefflera racemifera Fiaschi & Frodin  
L. Kollmann 7090 (MBML); Brazil, Espírito Santo
Schefflera ruschiana Fiaschi & Pirani  
Fiaschi 956 (NY, SPF); Brazil, Espírito Santo
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A. Amorim 4117 (CEPEC); Brazil, Bahia
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* Inflorescences are pseudolateral when displaced by the early growth of one or more axillary buds (see Chapter 3).
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“publicarpa”
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Schefflera ruschiana  | 0 1 0 1 0 0 0 0 0 0 0
Schefflera selloi  | 0 0/1 0 1 0 0 0 0 0 0 0
Schefflera succinea  | 0 1 0 ? 0 ? 0 0 0 0 0
Schefflera villosissima  | 0 0 0 1 0 0 0 0 0 0 0
Schefflera vinosa  | 0 0 0 1 0 0 0 0 0 0 0
Table 8. Comparisons among data sets and maximum parsimony (MP) trees derived from data sets with maximized taxon sampling. Asterisks (*) indicate the combined data sets after removal of *S. burchellii*, *S. malmei*, and *S. umbrosa*.

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Table 9. Comparisons among data sets with an identical, reduced taxon sampling and trees resulting from maximum parsimony (MP) analyses. Asterisks (*) indicate ILD p values $\geq 0.05$.

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<td>110</td>
<td>98</td>
<td>159</td>
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<tr>
<td><strong>Parsimony trees measurements</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Number of MP trees</td>
<td>4</td>
<td>6</td>
<td>54</td>
<td>8</td>
<td>450</td>
<td>48</td>
<td>121</td>
</tr>
<tr>
<td>Length of MP trees</td>
<td>89</td>
<td>72</td>
<td>81</td>
<td>167</td>
<td>177</td>
<td>153</td>
<td>258</td>
</tr>
<tr>
<td>Consistency Index (CI)</td>
<td>0.764</td>
<td>0.833</td>
<td>0.778</td>
<td>0.766</td>
<td>0.706</td>
<td>0.765</td>
<td>0.717</td>
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<tr>
<td>Retention Index (RI)</td>
<td>0.908</td>
<td>0.935</td>
<td>0.935</td>
<td>0.906</td>
<td>0.896</td>
<td>0.921</td>
<td>0.893</td>
</tr>
<tr>
<td>ILD p value</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.01</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td>ILD p value excluding S.</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>0.043</td>
<td>0.001</td>
<td>0.001</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>ILD p value excluding S. malmei</td>
<td>ILD p value excluding S. umbrosa</td>
<td>ILD p value excluding three spp.</td>
<td></td>
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<tr>
<td>burchellii</td>
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<tr>
<td></td>
<td>0.007</td>
<td>0.001</td>
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<tr>
<td></td>
<td>0.03</td>
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<tr>
<td></td>
<td>0.1*</td>
<td>0.216*</td>
<td>0.063*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>0.216*</td>
<td>0.063*</td>
<td>0.002</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>
Table 10. Comparison among data sets and most parsimonious trees obtained from PAE.

<table>
<thead>
<tr>
<th></th>
<th>All species</th>
<th>Without <em>S. morototoni</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1 x 1°</td>
<td>2 x 2°</td>
</tr>
<tr>
<td><strong>Number of terminals</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(including outgroup)</td>
<td>571</td>
<td>238</td>
</tr>
<tr>
<td><strong>Parsimony trees measurements</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of MP trees</td>
<td>6,120</td>
<td>9,300</td>
</tr>
<tr>
<td>Length of MP trees</td>
<td>110</td>
<td>107</td>
</tr>
<tr>
<td>Consistency Index (CI)</td>
<td>0.364</td>
<td>0.374</td>
</tr>
<tr>
<td>Retention Index (RI)</td>
<td>0.910</td>
<td>0.807</td>
</tr>
</tbody>
</table>
Table 11. Areas of endemism detected from PAE, and their synapomorphic species for the 1 x 1° and 2 x 2° quadrats.

<table>
<thead>
<tr>
<th>Quadrat number</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1° x 1° quadrats</strong></td>
<td></td>
</tr>
<tr>
<td>N’33 (Atlantic Forest 1)</td>
<td><em>Schefflera grandigemma</em></td>
</tr>
<tr>
<td></td>
<td><em>Schefflera ruschiana</em></td>
</tr>
<tr>
<td>N’34 (Atlantic Forest 2)</td>
<td><em>Schefflera capixaba</em></td>
</tr>
<tr>
<td></td>
<td><em>Schefflera racemifera</em></td>
</tr>
<tr>
<td><strong>2° x 2° quadrats</strong></td>
<td></td>
</tr>
<tr>
<td>S16, T16 (Cerrado)</td>
<td><em>Schefflera cordata</em></td>
</tr>
<tr>
<td></td>
<td><em>Schefflera fruticosa</em></td>
</tr>
<tr>
<td></td>
<td><em>Schefflera glaziovii</em></td>
</tr>
<tr>
<td>U16, U17 (Brazilian Atlantic Forest)</td>
<td><em>Schefflera kollmannii</em></td>
</tr>
<tr>
<td></td>
<td><em>Schefflera aff. longipetiola</em></td>
</tr>
<tr>
<td>U16</td>
<td><em>Schefflera grandigemma</em></td>
</tr>
<tr>
<td></td>
<td><em>Schefflera ruschiana</em></td>
</tr>
<tr>
<td>U17</td>
<td><em>Schefflera capixaba</em></td>
</tr>
<tr>
<td></td>
<td><em>Schefflera racemifera</em></td>
</tr>
</tbody>
</table>
Fig. 1–19. “Reticulate-heterobrochate” type, LM. – Fig. 1–3. S. confusa. — 1, 2, P-view, LO-analysis. — 3, P-view, optical section. Fig. 4–7. S. distractiflora. — 4, P-view, surface. — 5, P-view, note costa. — 6, E-view, surface, note lalongate endoaperture. — 7, E-view, note fastigia. Fig. 8–11. S. pimichinensis. — 8, P-view, surface. — 9, P-view, optical section. — 10, E-view, note lalongate endoaperture. — 11, E-view, optical section. Fig. 12–15. S. quinquecarinata. — 12, P-view, surface. — 13, P-view, optical section. — 14, E-view, surface, note lalongate endoaperture. — 15, E-view, showing exine layers. Fig. 16–19. S. tamatamaensis. — 16, P-view surface. — 17, P-view, optical section. — 18, E-view, note circular endoaperture. — 19, E-view, optical section. Scale bars = 10 µm.
Fig. 20–34. “Reticulate-heterobrochate” type, SEM. — Fig. 20–21. S. ciliatifolia. — 20, P-view. — 21, detail of apocolpium. — Fig. 22. S.confusa, detail of mesocolpium. — Fig. 23–24. S. decaphylla. — 23, P-view. — 24, detail of wall. — Fig. 25–27. S. distractiflora. — 25, P-view. — 26, E-view, — 27, detail of apocolpium. — Fig. 28. S. longipetiola, P-view. — Fig. 29. S. pimichinensis, E-view. — Fig. 30. S. quinquecarinata, detail of apocolpium. — Fig. 31. S. ruschiana, E-view. — Fig. 32. S. aff. tamatamaensis, P-view. Fig. 33–34. S tamatamaensis. — 33, E-view. — 34, detail of apocolpium.
Fig. 61–75. “Perforate” type, SEM. — Fig. 61. *S. attenuata*, E-(left) and P-(right) views. — Fig. 62–63. *S. diplodactyla*. — 62, P-view. — 63, E-view. — Fig. 64–66. *S. minutiflora*. — 64, P-view. — 65, view of mesocolpium. — 66, E-view, note relatively short ectoaperture. Fig. 67–69. *S. rodriguesiana*. — 67, E-view, note margo. — 68, detail of wall. — 69, view of mesocolpium. — Fig. 70. *S. sciodaphyllum*, E-view. — Fig. 71–72. *S. sphaerocoma*. — 71, E-view, note relatively short ectoaperture. — 72, view of mesocolpium. — Fig. 73–75. *S. troyana*. — 73, E-view. — 74, view of mesocolpium. — 75, detail of mesocolpium.
Fig. 76–97. “Rugulate” and “Reticulate-homobrochate” types, LM. — Fig. 76–78. S. patula. — 76, E-view, note relatively long ectoaperture. — 77, E-view, surface. — 78, E-view, optical section. — Fig. 79–81. S. sodiroi. — 79, E-view, optical section. — 80, E-view, note long ectoaperture. — 81, E-view. — Fig. 82–83. S. tamana, E-views, note long ectoaperture and circular endoaperture. — Fig. 84–85. S. tipuanica. — 84, P-view, note circular outline. — 85, E-view, optical section. — Fig. 86–89. S. sp. nov. “Sciodaphyllum”. — 86, 87, P-view, LO-analysis. — 88, E-view, surface. — 89, E-view, optical section. — Fig. 90–95. S. tremula (Holdridge 1876). — 90, 91, P-view, LO-analysis. — 92, P-view, note costa. — 93, E-view, surface. — 94, E-view, note H-shaped endoaperture. — 95, E-view, optical section. — Fig. 96–97. S. tremula (Jimenez 1080). — 96, E-view, surface. — 97, E-view, optical section. Scale bars = 10 µm.
Fig. 98–112. “Rugulate” and “Reticulate-homobrochate” types, SEM. — Fig. 98–99. *S. patula.* — 98, detail of apocolpium. — 99, detail of mesocolpium. — Fig. 100–101. *S. sodiroi.* — 100, view of mesocolpium, note margo. — 101, detail of mesocolpium. — Fig. 102–103. *S. tamana.* — 102, E-view. — 103, detail of mesocolpium. — Fig. 104–106. *S. tipuanica.* — 104, E-view. — 105, detail of mesocolpium. — 106, detail of wall. — Fig. 107–108. *S. tremuloidea.* — 107, E-view, note relatively elongate ectoaperture. — 108, detail of apocolpium. — Fig. 109–110. *S. sp. nov. “Sciodaphyllum”.* — 109, 110, views of mesocolpium. — Fig. 111–112. *S. tremula.* — 111, P-view. — 112, E-view.
Fig. 140–154. “Perforate-microreticulate, usually rugulate” type, SEM. — Fig. 140–142. S. chimantensis. — 140, P-view. — 141, detail of apocolpium. — 142, E-view. — Fig. 143–145. S. cf. dielsii. — 143, E-view. — 144, detail of apocolpium. — 145, detail of wall. — Fig. 146–147. S. duidae. — 146, E-view. — 147, detail of apocolpium. — Fig. 148–150. S. harmsii. — 148, P-view. — 149, E-view. — 150, detail of wall. — Fig. 151. S. jahnii, P-view. — Fig. 152–154. S. lasiogyne. — 152, P-view. — 153, detail of apocolpium. — 154, E-view.
Fig. 177–191. “Perforate-microreticulate, usually rugulate” type, SEM. — Fig. 177–178. S. montana. — 177, E-view. — 178, view of mesocolpium. — Fig. 179–181. S. pentandra. — 179, view of mesocolpium. — 180, E-view. — 181, detail of apocolpium. — Fig. 182. S. quindiuensis, E-view. — Fig. 183–185. S. robusta. — 183, E-view. — 184, P-view. — 185, detail of mesocolpium. — Fig. 186–187. S. rufa. — 186, E-view. — 187, view of mesocolpium. — Fig. 188–189. S. sessiliflora. — 188, E-view, note margo. — 189, P-view. — Fig. 190–191. S. sp. nov. “Cephalopanax”. — 190, E-view, note long ectoaperture. — 191, P-view.
Fig. 216–230. “Perforate-microreticulate, usually rugulate” type, SEM. — Fig. 216–218. S. sp. nov. “Cotylanthes”. — 216, P-view. — 217, E-view. — 218, detail of wall. — Fig. 219–220. S. systyla. — 219, view of mesocolpium. — 220, detail of mesocolpium. — Fig. 221–224. S. cf. ternata. — 221, P-view. — 222, E-view. — 223, detail of mesocolpium. — 224, detail of wall. — Fig. 225–227. S. umbellata. — 225, view of mesocolpium. — 226, detail of apocolpium. — 227, E-view. — Fig. 228–230. S. cf. violacea. — 228, P-view. — 229, E-view. — 230, detail of apocolpium.
Fig. 231. Strict consensus of 3,600 trees (length = 2,478 steps) resulting from the MP analysis of the combined data matrix of 174 ITS and trnL-trnF sequences (CI = 0.461; RI = 0.745). Support values are provided from all three analyses above the branches in the following order: bootstrap (BS) from MP/BS from ML/posterior probability (PP) from BI. BS percentages < 50%, and PP < 0.85 are represented by <, while values equal to 100% (BS) and 1.0 (PP) are represented by *. Dashed lines represent alternative placements of taxa in the BI tree. Names of major clades follow Plunkett et al. (2004, 2005).
Fig. 232. Strict consensus trees resulting from separate parsimony analyses of ITS and ETS data, each with an identical 61-taxon sampling. Bootstrap percentages are provided above the branches. A. ITS analysis: strict consensus of 98,206 shortest trees resulting from the MP analysis of 626 characters (CI = 0.611; RI = 0.880). B. ETS analysis: strict consensus of 6,907 shortest trees resulting from the MP analysis of 470 characters (CI = 0.712; RI = 0.885). Bootstrap percentages < 50% are represented by <, and values equal to 100% are represented by *.
Fig. 233. Strict consensus of 4,174 trees (length = 480 steps) resulting from MP analysis of the combined data set of Neotropical Schefflera (ETS + ITS) (CI = 0.592; RI = 0.867). Bootstrap percentages < 50% are represented by <, and values equal to 100% are represented by *. Names next to brackets refer to clades and subclades discussed in the text.
Fig. 234. Maximum likelihood tree of the combined data set of Neotropical *Schefflera* (ETS + ITS). Support values are provided for both ML and BI analyses above or below the branches in the following order: bootstrap from ML/posterior probability from BI. Bootstrap percentages < 50%, and posterior probabilities < 0.85 are represented by <, and values equal to 100% (BS) and 1.0 (PP) are represented by *. Names next to brackets refer to clades and subclades discussed in the text.
Figure 235. Schematic drawings illustrating the variation of inflorescence structure in Didymopanax showing terminal inflorescence units rather than individual flowers. A–F. All branches with similar branching degree. --A. Primary branches terminating in bisexual units (e.g., S. plurifolia). --B. Same as in A, but with lateral secondary male branches (e.g., S. fruticosa). --C. Primary branches terminating in whorl of secondary ones, presence of lateral secondary branches (e.g., S. capixaba). --D. Same as in C, but with lateral tertiary male branches (e.g., S. angustissima). --E. Secondary branches terminating in whorl of tertiary ones, with lateral secondary and tertiary branches (e.g., S. kollmannii). --F. Same as in E, but tertiary branches bearing lateral male quaternary ones (e.g., S. morototoni). --G. Proximal branches with higher branching degree than distal ones (e.g., S. gardneri). ★ = peduncle, r = rachis, 1--4 = primary to quaternary branches, ● = mostly bisexual inflorescence unit, ○ = mostly male inflorescence unit. Leaves and bracts are represented by solid triangular shapes.
Figure 236. Geographic distribution of the Didymopanax group of *Schefflera*. 
Figure 237. A–K. *Schefflera angustissima*. --A. Flowering branch. --B. Stipule, lateral view. --C–G. Median leaflets. --H. Flower, one petal and two stamens removed. --I. Flower, two stamens removed. --J. Stamens, abaxial (left) and adaxial (right) views. --K. Fruit with two pyrenes. --L. Fruit with four pyrenes (A: Fiaschi 725, SPF; B, F, H: Fiaschi 745, SPF; C, K: Vidal II-4563, SP; D: Gonçalves & Pereira s.n., SPF72929; E: Glaziou 17018, R; G: Fiaschi & Lobão 558, SPF; I–J: Wesenberg 558, SPF; L: Kuhlmann 4047, SPF). M–U. *S. calva*. --M. Fruiting branch. --N. Stipule, lateral view. --O–R. Median leaflets. --S. Flower, stamens removed. --T. Stamens, abaxial (left) and adaxial (right) views. --U. Fruit, lateral view (M: Fiaschi 291, SPF; N: Fiaschi 354, SPF; O: Fiaschi 664, SPF; P: Itaipú Binacional 604, MO; Q: Curran 702, NY; R: Fiaschi 880, SPF; S–T: Kollmann 2495, SPF; U: Kollmann 274, SPF)
Fig. 248. A–D. *S. macrocarpa*. --A. Flowering branch. --B. Umbel. --C. Flower, one petal removed. --D. Fruit, lateral view (A: Harley CFCR14228, SPF; B: Diacui & Esteves CFSC9134, SPF; C: Sakuragui CFCR15220, SPF; D: Arbo 4775, SPF). E. *S. malmei*. Median leaflet on petiole apex (from Cid Ferreira 6558, SPF). F–K. *S. villosissima*. --F. Leaf. --G. Detail of blade underside. --H. Terminal inflorescence unit. --I. Longitudinal section of flower. --J. Stamens, adaxial (left) and abaxial (right) views. --K. Fruit, lateral view (F–G: Mello-Silva CFCR7870, SPF; H–I: Irwin 20809, UB; J: Forzza 4880 (36); K: Anderson 8736, UB).
Figure. 256. A–F. Geographic distribution maps. --A. S. succinea. --B. S. tamatamaensis. --C. S. umbrosa. --D. S. villoissima. --E. S. vinosa. --F. Schefflera sp. A. --G. Schefflera sp. B. --H. Schefflera sp. C.
Fig. 257. A. Biogeographic subdivision of South America east of the Andes, adapted from Morrone (2006). The Parana Subregion (provinces not shown) is bounded west and south by the Chacoan Subregion (Caatinga, Cerrado, Chaco and Pampa provinces), and separated from the Amazonian Subregion (remaining provinces). Dashed lines separate provinces within subregions, and continuous lines separate subregions. B. Limits among subregions from A, showing the separation of the Amazonian and Parana subregions in two blocks each (adapted from Nihei, 2008 and Amorim & Pires, 1996). The asterisk (*) indicates the approximate location of Manaus.
Fig. 258. Strict consensus of 39,672 most parsimonious trees resulting from the analyses of 84 ITS sequences (623 characters); tree length = 132 steps; consistency index = 0.75; retention index = 0.951. Names of clades discussed in the text are provided next to brackets (dashed brackets indicate clades resolved in other analyses but left unresolved here). Bootstrap percentages are provided above the branches; those < 50% are represented by < and those equal to 100% are represented by *.
Fig. 259. Strict consensus of 98,700 most parsimonious trees resulting from the analyses of 97 ETS sequences (460 characters); tree length = 124 steps; consistency index = 0.774; retention index = 0.95. Names of clades discussed in the text are provided next to brackets (dashed brackets indicate clades resolved in other analyses but left unresolved here). 1 = “ES endemic” subclade; 2 = “Calva” subclade. Bootstrap percentages are provided above the branches; those < 50% are represented by < and those equal to 100% are represented by *.
Fig. 260. Strict consensus of 87,300 most parsimonious trees resulting from the analyses of 91 5S-NTS sequences (200 characters); tree length = 147 steps; consistency index = 0.680; retention index = 0.952. Names of clades discussed in the text are provided next to brackets (dashed brackets indicate clades resolved in other analyses but left unresolved here). Bootstrap percentages are provided above the branches; those ≤ 50% are represented by < and those equal to 100% are represented by *.
Fig. 261. Strict consensus trees resulting from separate and pair-wise combinations of the data sets based on ITS, ETS and 5S-NTS data, each with an identical sampling of 30 ingroup taxa. Bootstrap percentages are provided above the branches; those < 50% are represented by < and those equal to 100% are represented by *. Clade labels: 1 = Atlantic Forest; 2 = 5-carpellate; 3 = Imeri; 4 = Plurifolia + umbrosa; 5 = Savannic; dashed bars indicate when clades were left unresolved. The placement of S. burchelli, S. malmei, and S. umbrosa is highlighted with dashed branches. A. ITS: strict consensus of 4 MP trees; tree length = 89 steps (CI = 0.764; RI = 0.952). B. ETS: strict consensus of 6 MP trees; length = 72 steps (CI = 0.833; RI = 0.935). C. 5S-NTS: strict consensus of 54 MP trees; length = 81 steps (CI = 0.778; RI = 0.935). D. ITS + ETS: strict consensus of 8 MP trees; length = 167 steps (CI = 0.766; RI = 0.906). E. ITS + 5S-NTS: strict consensus of 450 MP trees; length = 177 steps (CI = 0.765; RI = 0.896). F. ETS + 5S-NTS: strict consensus of 48 MP trees; length = 153 steps (CI = 0.765; RI = 0.921).
Fig. 262. Strict consensus of 121 most parsimonious trees resulting from analysis of the combined data set including ITS + ETS + 5S-NTS sequences (1,282 characters) and a reduced sampling of 30 taxa; tree length = 258 steps (CI = 0.717; RI = 0.893). Names of clades discussed in the text are provided next to brackets. The placement of *S. burchellii*, *S. malmei*, and *S. umbrosa* is highlighted with dashed branches. Bootstrap percentages are provided above the branches; those < 50% are represented by < and those equal to 100% are represented by *.
Fig. 263. Strict consensus trees resulting from MP analyses of the ITS + ETS and ITS + ETS + 5S-NTS combined data sets after exclusion of *S. burchellii*, *S. malmei*, and *S. umbrosa*. Names of clades discussed in the text are provided next to brackets (dashed brackets indicate clades that were left unresolved). Bootstrap percentages are provided above the branches. A. ITS + ETS analysis: strict consensus of 8 shortest trees resulting from the MP analysis of 1,083 characters (CI = 0.766; RI = 0.906). B. ITS + ETS + 5S-NTS analysis: strict consensus of 121 shortest trees resulting from the MP analysis of 1,282 characters (CI = 0.717; RI = 0.893). Dashed branches represent nodes that collapse with the inclusion of ETS sequences from *S. burchellii* and 5S-NTS sequences from *S. umbrosa* coded with missing data. Bootstrap percentages < 50% are represented by < and equal to 100% by *.
Figure 264. Maximum likelihood tree of the ITS + ETS data set of the Didymopanax excluding *S. burchellii*, *S. malmei*, and *S. umbrosa*. Support values are provided along the branches in the following order: bootstrap from ML/posterior probability from BI. Bootstrap percentages < 50%, and posterior probabilities < 0.85 are represented by <, and values equal to 100% (BS) and 1 (PP) are represented by *. Names next to brackets refer to clades discussed in the text.
Figure 265. Strict consensus of 70,061 most parsimonious trees resulting from MP analysis of the combined molecular and morphological data set; tree length = 236 steps (CI = 0.775; RI = 0.921). Names of clades discussed in the text are provided next to brackets. Bootstrap percentages are provided above the branches; those < 50% are represented by < and those equal to 100% are represented by *. 

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Figure 266. PAE results based on 1 x 1° quadrats. A. Map of tropical South America divided into 1 x 1° quadrats; asterisks (*) indicate quadrats for which clades were resolved. Two quadrats that were identified as areas of endemism (N’33 and N’34) are indicated with bold squares. B. Informative part of the strict consensus cladogram obtained with all species; branches representing a massive basal polytomy are not shown (dashed line) C. Informative part of the strict consensus cladogram obtained after exclusion of *Schefflera morototoni* (basal polytomy not shown). Terminal branches represent quadrats from the map. Number of endemic species provided above branches. OG = outgroup (all zero terminal).
Figure 267. PAE results based on 2 x 2° quadrats. A. Map of tropical South America divided in 2 x 2° quadrats. Quadrats from the resolved part of the trees are numbered. Quadrats and groups of quadrats recovered as areas of endemism are delimited with squares. B. Informative part of the strict consensus cladogram obtained with all species (basal polytomy not shown). The Brazilian Atlantic Forest quadrats U16 and U17 are supported by two endemic species each, but are not resolved in the cladogram (dashed branches). C. Informative part of the strict consensus cladogram obtained after exclusion of *Schefflera morototoni* (basal polytomy not shown). Terminal branches represent the quadrats from the map. Number of endemic species provided above branches. OG = outgroup (all zero terminal).
Figure 268. Maximum likelihood tree of the ITS + ETS data set used for reconstructing biogeographic history using DIVA. Ancestral areas of each clade are indicated above the branches and known areas of occurrence are provided next to each species name. Areas recovered from constrained analysis are boldfaced. Names and numbers (see Fig. 272) of major clades are provided next to brackets (OG = outgroup). ML bootstrap values greater than 50% are provided below the branches. Included areas: A = Northwestern Amazon; B = Southeastern Amazon; C = Chacoan; D = Northern Parana; E = Southern Parana. The map (reproduced from Fig. 257b) indicates limits among areas. Dashed lines indicate area limits within the same subregion.
Figure 269. Maximum likelihood tree of the ITS + ETS + 5S-NTS data set used for reconstructing biogeographic history using DIVA. Ancestral areas of each clade are indicated above the branches and known areas of occurrence are provided next to each species name. Areas recovered from constrained analysis are boldfaced. Names and numbers (see Fig. 272) of major clades are next to brackets (OG = outgroup). ML bootstrap values greater than 50% are provided below the branches. Included areas: A = Northwestern Amazon; B = Southeastern Amazon; C = Chacoan; D = Northern Parana; E = Southern Parana. The map (reproduced from Fig. 257b) indicates limits among areas. Dashed lines indicate area limits within the same subregion.
Figure 270. Maps depicting the diversity of the Didymopanax group using two different approaches. A. Species richness. B. Phylogenetic diversity (PD). Numbered quadrats follow terminology from PAE using 1 x 1° quadrats (Fig. 266a).
Figure 271. Maximum likelihood tree from combined ITS + ETS + 5S-NTS data set of Didymopanax using consensus sequences. Bootstrap percentages are provided above the branches. Those < 50% are represented by <, and those equal to 100% by *. Names next to brackets refer to clades discussed in the text.
Figure 272. Simplified biogeographic scenario for Didymopanax derived from the DIVA reconstruction (Fig. 269). The asterisk (*) indicates the cladogram root (but not necessarily the geographic origin). Black circles indicate the four main clades of Didymopanax [(1) Imeri, (2) Atlantic Forest, (3) 5-carpellate and (4) Savannic]. Lineages within the Savannic clade are: 4.1. *Campos rupestres* subclade, 4.2. *S. distractiflora + S. morototoni*, 4.3. *S. selloi*. Other indicated lineages correspond to *S. aurata* (a), *S. ciliatifolia* (c), and *S. plurifolia* (p). Lines terminating in a blunt end represent lineages not dispersed over biogeographic areas boundaries, while those terminating in arrow heads represent lineages crossing area boundaries (see Fig. 257b for areas names). Nodes placement correspond to their presence in a given area, but not their precise location. Dispersals of *S. morototoni* across all areas are not represented.
Literature Cited
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Costello, A. & T. J. Motley. 2001. Molecular systematics of Tetraplasandra,
*Munroidendron* and *Reynoldisia sandwicensis* (Araliaceae) and the evolution of superior ovaries in *Tetraplasandra*. Edinburgh J. Bot. 58: 229--242.


Pennington, R. T. 1996. Molecular and morphological data provide phylogenetic resolution at different hierarchical levels in Andira. Syst. Biol. 45: 496--515.


Pennington, R. T., J. E. Richardson & M. Lavin. 2006. Insights into the historical construction of species-rich biomes from dated plant phylogenies, neutral


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