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A revision of *Styrax* L. section *Pamphilia* (MART. ex A.DC.) B.WALLN. (Styracaceae)

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With a contribution to its wood anatomy by B.J.H. ter Welle & W.C. Dickison

Abstract

The former genus *Pamphilia* (Styracaceae) is revised and transferred to *Styrax* as a section of its own, mainly based on similarities in floral and vegetative characters, and co-occurrence of gynodioecy. Section *Pamphilia* comprises two new series: series *Pamphilia* with three species (*S. aureum*, *S. maninul*, *S. pedicellatum*) in southeastern Brazil and one (*S. pefrit*) in northern Colombia, and series *Andinae* with two species (*S. omuk*, *S. vilcabambae*) in the Peruvian Andes. Gynodioecy is reported to occur in all species belonging to section *Pamphilia*, and at least in two species of section *Foveolaria*. Full descriptions of species are provided, including a key for identification, a distribution map, and a list of exsiccatae studied. A chapter on wood anatomy, contributed by B.J.H. ter Welle and W.C. Dickison, is also included.

Key words: Styracaceae, *Styrax*, *Pamphilia*, *Foveolaria*, Flora of South America, Brazil, Colombia, Peru, gynodioecy, wood anatomy.

Zusammenfassung

Die frühere Gattung *Pamphilia* (Styracaceae) wird einer Revision unterzogen und als eigene Sektion zur Gattung *Styrax* gestellt. Dies erfolgt aufgrund von Ähnlichkeiten im Blütenbau und im vegetativen Bereich, als auch wegen des gemeinsamen Auftretens von Gynodiözie. Diese Sektion umfaßt zwei neue Serien: Series *Pamphilia* mit drei Arten (*S. aureum*, *S. maninul*, *S. pedicellatum*) im südöstlichen Brasilien und einer weiteren Art (*S. pefrit*) im nördlichen Kolumbien, sowie Series *Andinae* mit zwei Arten (*S. omuk*, *S. vilcabambae*) in den Anden Perus. Gynodiözie wird für alle Arten der Sektion *Pamphilia*, sowie für zwei Arten der Sektion *Foveolaria* nachgewiesen. Beschreibungen aller Arten, ein Bestimmungsschlüssel, eine Verbreitungskarte und eine Liste der Exsiccatae werden präsentiert. Eine anatomische Beschreibung des Holzes wird von B.J.H. ter Welle und W.C. Dickison beigesteuert.

Introduction and historical overview

Carl F.P. von Martius (1794 - 1868) and his collaborators were the first to collect herbarium specimens of *Styrax* section *Pamphilia* during their famous journey to Brazil (SPIX & MARTIUS 1823 - 1831). The first species was described as *Styrax aureum* in Vol. 2 (page 551) of their travel report. Later, Martius used the generic name *Pamphilia* on the labels of two exsiccatae (for details see under *S. maninul* in the chapter `Taxonomy´) distributed to various herbaria. However, it was Alphonse L.P.P. de Candolle (1806 - 1893), who several years later, provided the first valid description of the new genus, including two species (*P. aurea* and *P. styracifolia*), but he did not transfer *Styrax aureum* (the type

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of which he had never seen) to *Pamphilia*, leaving it as a distinct species within *Styrax* (CANDOLLE 1844: 264). In her monograph of the Styracaceae, PERKINS (1907) described one additional species (*P. pedicellata*) with three varieties. Another species (*P. vilcabambae*), described by SIMPSON (1975), was collected by the late T.R. Dudley in the Andes of Peru, far away from the known distribution of the other species. A recent collection from the border of the Peruvian departments Huánuco and Ucayali turned out to represent another new species and provided the impetus for this revision.

In the present publication the neuter is used as gender for *Styrax*, as did LINNAEUS (compare NICOLSON & STEYSKAL 1976).

As indicated in the title, this revision will ultimately end with the relegation of the genus *Pamphilia* to a section of the genus *Styrax*. To avoid confusion among the readers of this study, the names of species formerly assigned to *Pamphilia* are here juxtaposed to the names resulting from their transfer to the genus *Styrax* (see chapter `Taxonomy´).

Series *Pamphilia*:

Styrax aureum MART. [= *Pamphilia styracifolia* A.DC.]
Styrax maninul B.WALLN., nom.n. [= *Pamphilia aurea* MART. ex A.DC.]
Styrax pedicellatum (PERKINS) B.WALLN., comb.n. [= *Pamphilia pedicellata* PERKINS]
Styrax pefrit B.WALLN., sp.n.

Series *Andinae* B.WALLN., ser.n.:

Styrax omuk B.WALLN., sp.n.
Styrax vilcabambae (D.R.SIMPSON) B.WALLN., comb.n. [= *Pamphilia vilcabambae* D.R.SIMPSON]

The other species of *Styrax* mentioned in the text (sections according to PERKINS [1907]) are:

Section *Styrax*:

Styrax ferrugineum NEES & MART.
Styrax martii SEUB.
Styrax obassia SIEBOLD & ZUCC.
Styrax officinalis L.
Styrax parvifolium POHL
Styrax rotundatum PERKINS

Section *Foveolaria* (RUIZ & PAV.) PERKINS:

Styrax foveolaria PERKINS
Styrax nui B.WALLN.

Growth form and habit

The species of section *Pamphilia* are represented by low shrubs and small trees up to 7 m tall. Trunk diameters are generally less than 10 cm, although *Styrax omuk* (Smith & Pretel 7978) was reported to be a tree of 20 m height with a diameter at breast height (dbh) of 30 cm, and *S. pefrit* (height not reported) to have a dbh of 36 cm (Gentry & Cuadros 64667), and 44 cm (Gentry & Cuadros 55574) respectively.

Styrax maninul and *S. pedicellatum* (and probably also *S. aureum*) develop characteristic ligneous subterranean structures commonly called "xylopodia" (described in LINDMAN 1900: 109; RAWITSCHER & RACHID 1946; RIZZINI & HERINGER 1961; RIZZINI 1965; SARMIENTO & MONASTERIO 1983). Many species growing in the drought- and fire-adapted tropical savannas called "cerrado" and "campo rupestre" (EITEN 1972; SARMIENTO 1983) form xylopodia, which have a strong capacity to develop new sprouts. The xylopodia of *S. maninul* and *S. pedicellatum* are horizontal woody structures reaching a depth of up to ca. 0.5 m, forming one or a few "heads" at their apex, from which sprouts arise (fig. 1). A single-stemmed, juvenile plant of *S. pedicellatum* growing

Fig. 1: Xylopodium of *Styrax maninul*: apical part ca. 0.3 m wide (drawn from a photograph taken from the same plant as Esteves et al. s.n. [CFCR 15472]).

Fig. 2: Xylopodium of *Styrax pedicellatum* growing out of a crevice; woody swelling 25 cm wide and 40 cm high, with an old broken stem on top, and some thin sprouts on lower left side; living stem arising from the back 12 cm thick near base (drawn from a photograph taken near collection site of Esteves et al. s.n. [CFCR 15503]).

between rocks in a place not burned in recent years showed a ligneous, somewhat globose swelling with a diameter of ca. 10 cm, and an irregular surface at the base of the stem above ground level. In two other places, individuals of this species were observed growing out of fissures in rocks never reached by fire. In these cases, aerial parts had not suffered

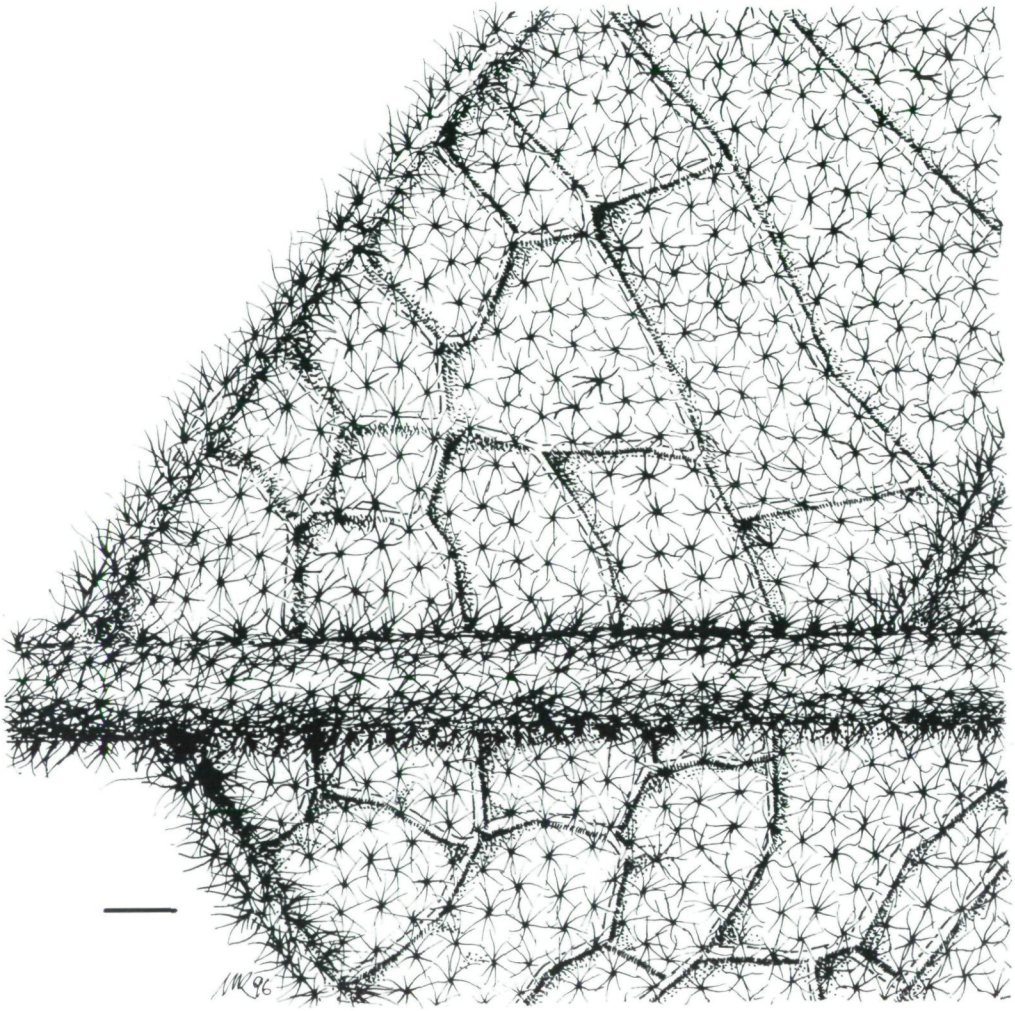

Fig. 3: Indumentum between two secondary veins on abaxial leaf surface of *Styrax aureum* [simplified drawing: hairs in reality much denser, with tightly overlapping branches completely concealing leaf surface; single hairs therefore practically not recognizable; a truly realistic drawing would be completely black because of the large amount of necessary lines] (from Glaziou 17129; Bar = 1 mm).

from combustion and were tree-like. These plants had developed a more or less globose, ligneous swelling above the rocks from which only a single stem had originated. In one case this structure was 25 cm wide and 40 cm high, and the stem was 12 cm thick at the base (fig. 2). Twigs apparently have no, or only a limited capacity to form roots, as observed in an experiment performed with cuttings. All these facts suggest that the growth of xylopodia in these two species is genetically controlled. Many other plant species develop these woody underground structures only after drought- or fire-induced destruction of the aerial parts (RIZZINI & HERINGER 1961). A plant, at the time sterile, belonging to *Styrax* section *Styrax*

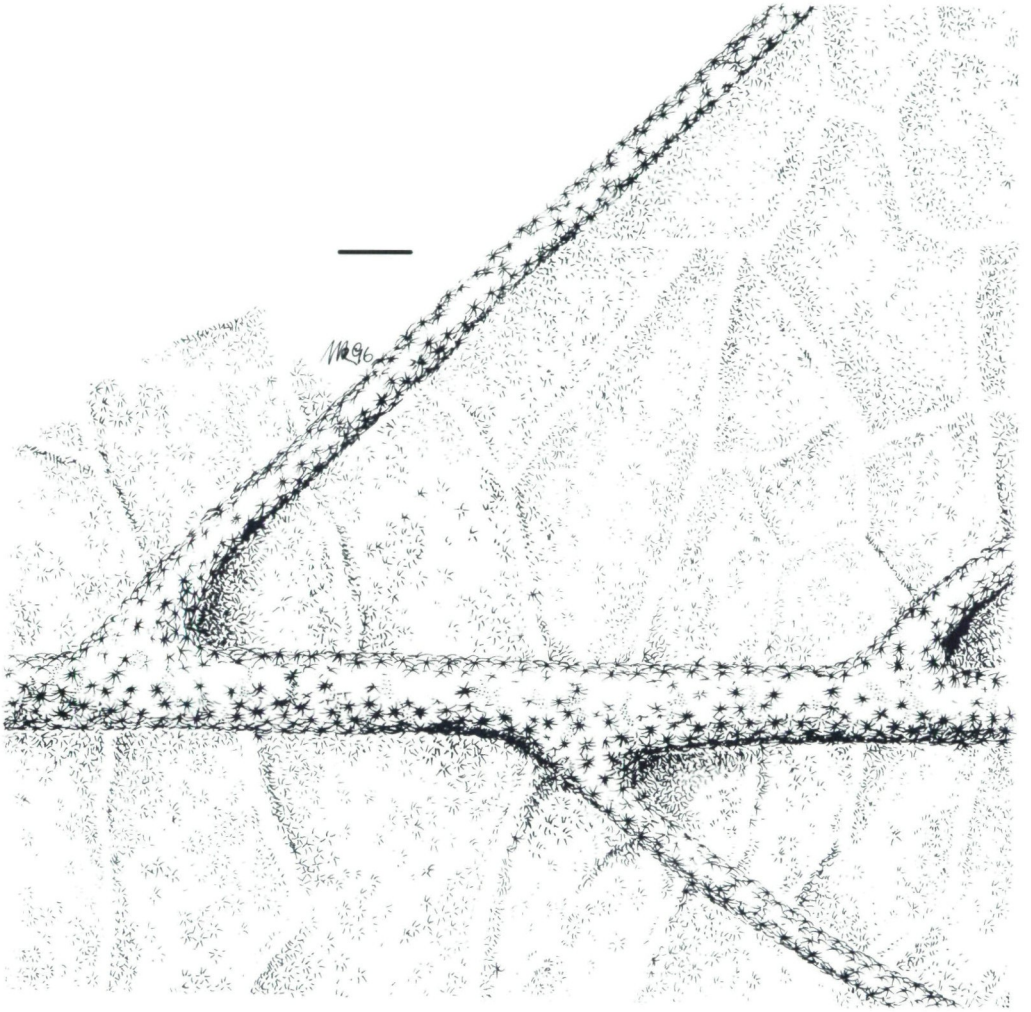

Fig. 4: Indumentum between two secondary veins on abaxial leaf surface of *Styrax pedicellatum* (simplified drawing from Esteves et al. s.n. [CFCR 15503]; Bar = 1 mm).

[according to P. Fritsch (CAS) probably *S. rotundatum* or *S. ferrugineum*], and growing in campo rupestre vegetation near Diamantina, had also developed a xylopodium [Esteves et al. s.n. (CFCR 15514) at LZ, SPF, W]. The growth-form of the other three species of section *Pamphilia* (*S. pefrit*, *S. vilcabambae* and *S. omuk*) occurring in cloud and elfin forests of Peru and Colombia, has not been ascertained. However, since their habitat is quite different, it is most likely that they do not form any unusual underground structures.

Indumentum

The indumentum is composed of whitish, grey or ferrugineous, many-branched stellate hairs as shown in PERKINS 1907: 4, fig. 1A (compare also fig. 95 and 101 in MAGUIRE

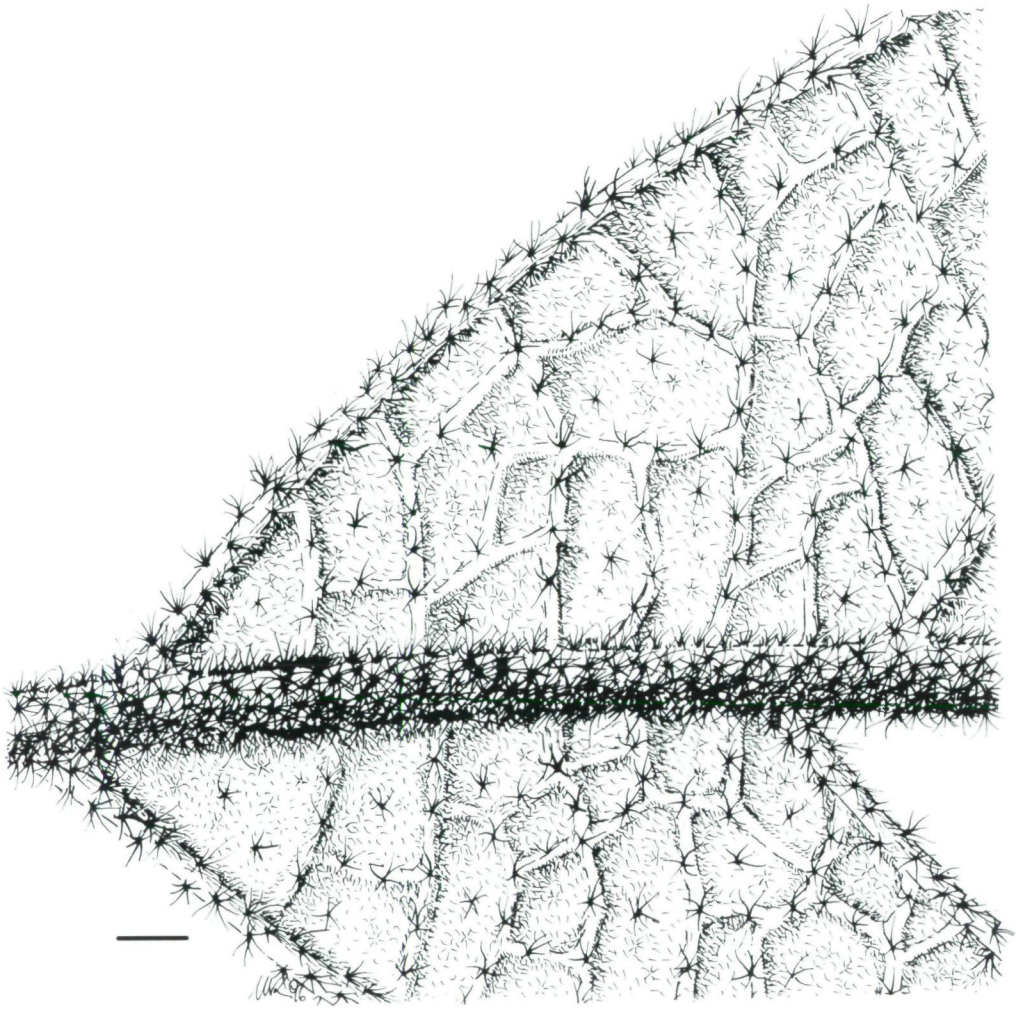

Fig. 5: Indumentum between two secondary veins on abaxial leaf surface of *Styrax maninul* (simplified drawing made from lectotype; Bar = 1 mm).

& HUANG 1978). As a dense layer they cover both surfaces of young leaves, younger parts of twigs, inflorescence axes, bracts, pedicels, calyces and petals. The adaxial surfaces of the mature leaves of all species are glabrescent. The abaxial leaf surfaces, on the other hand, are glabrescent in species of series *Andinae*, but remain covered with a dense indumentum in series *Pamphilia*. It is fairly homogeneous in *S. aureum* (fig. 3) and *S. pedicellatum* (fig. 4) because the hairs are similar in size. In *S. maninul* (fig. 5) and *S. pefrit* two different types of stellate hairs can be observed: the smaller ones form a dense, homogeneous greyish layer (similar to that of *S. pedicellatum*), whereas the larger, more or less ferrugineous hairs, which are mostly located along veins of highest order and only rarely on the intercostal areas, conspicuously exceed the former in length. The apical branches of the larger hairs are several times as long as the basal ones.

Leaf anatomy

The leaf anatomy of Styracaceae has been studied by SCHADEL & DICKISON (1979). They report (p. 18) that "almost all variation observed in the leaf structure of the ten smaller styracaceous genera is encountered among species of the large genus *Styrax*". In *Pamphilia aurea* they observed the presence of "sclerenchymatous supporting sheath cells ... that are perpendicular to the long axis of the veins". They did not find this character in any of the other studied species of *Styrax*. This circumstance was interpreted by these authors as a possible adaptation to dry habitats.

Wood anatomy

B.J.H. ter Welle* & W.C. Dickison**

Growth absent or faint, due to a difference in the lumen diameter - fibre wall thickness ratio (radially flattened fibres). Vessels diffuse, few solitary, but mainly in radial chains and irregular clusters of 2 - 4 (- 6), angular to round in outline, tangential diameter 42 - 68 (33 - 80) µm, 35 - 45 (29 - 48) per sq. mm. Vessel-member length: 680 - 840 (470 - 1380) µm. Perforations scalariform with 8 - 11 (5 - 14) bars per plate. Intervascular pits alternate, round to angular in outline, diameter 3 - 4 µm. Vessel-ray pits similar but half-bordered. Axial parenchyma abundant, apotracheal diffuse, but mainly as uniformly distributed tangential "bands", one cell wide, and 2 - 7 cells long, and some scanty paratracheal cells. Rhombic crystals in chambered axial parenchyma observed in one sample, but lacking in the other sample. Rays heterocellular, 1 - 3-seriate: when uniseriate, composed of erect and square cells, when 2 (- 3)-seriate, composed of a central portion of procumbent cells and (long) uniseriate marginal extensions of square and erect cells. Uniseriate rays up to 9 - 19 cells (= 575 - 1100 µm), multiseriate rays up to 30 - 32 cells (= 1150 - 1500 µm). Number: 15 (13 - 17) per mm. Fibres non-septate, lumen up to 18 µm, walls 3 µm in *Pamphilia pedicellata*, and lumen up to 8 µm, walls up to 8 µm in *P. aurea*, with indistinctly bordered to simple pits, apertures slit-like, mainly on the radial walls. Length: 1250 - 1320 (990 - 1440) µm. F/V ratio: 1.57 - 1.84.

Material studied: *P. aurea* [= *S. maninul*]: Esteves et al. s.n. (CFCR 15453), wood sample at U: UW 34342; *P. pedicellata* [= *Styrax pedicellatum*]: Esteves et al. s.n. (CFCR 15502), wood sample at U: UW 34343.

Discussion: The wood anatomy of the Styracaceae has been described in detail by DICKISON & PHEND (1985). Nearly 100 samples from 9 genera and over 40 species were included in the study. From this work it is clear that the wood anatomy of the Styracaceae is considered as "quantitatively rather uniform". Features present in almost all species include: exclusively scalariform perforation plates, pores occurring as both solitaries and pore multiples, intervessel pits arranged in an opposite to alternate manner, fibres with indistinctly to distinctly bordered pits, both multiseriate and uniseriate heterocellular rays, and axial parenchyma distributed as a combination of diffuse, diffuse-in-aggregates and scanty.

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Table 1: Some quantitative characters of wood of *Bruinsmia*, *Halesia*, *Styrax* (DICKISON & PHEND 1985), and *Pamphilia*.

Genus	mean vessel frequency /mm²	mean vessel diameter (mm)	mean vessel member length (mm)	mean number of bars per perf. plate	mean fibre tracheid length (mm)	mean multis. ray width (cells)	no. samples
Bruinsmia	7	158	1520	15	2469	3	5
Halesia	96-100	50-55	905-963	12-13	1385-1453	3	8
Styrax	11-113	43-111	345-1193	4-13	647-1892	2-5	64
Pamphilia	35-45	42-68	680-840	8-11	1250-1320	2-3	2

Wood samples from species of *Pamphilia* were not available for study to DICKISON & PHEND (1985). From the description presented here it is clear that this taxon belongs to the Styracaceae. However, within the family it is difficult to separate individual genera using qualitative wood anatomical characteristics. One possible exception to this is the occurrence of prismatic crystals, which are restricted to species of *Bruinsmia*, *Halesia* and *Styrax*. In one species of *Pamphilia*, rhombic crystals were observed in chambered axial parenchyma. DICKISON & PHEND (1985) mention that any "report of the absence of crystals may be the result of insufficient sample size".

Further consideration of these four genera regarding quantitative wood anatomical characteristics shows that *Bruinsmia* and *Halesia* can be separated from the genus *Pamphilia* on the basis of a number of features (Table 1). However, there is no quantitative characteristic to separate *Pamphilia* from *Styrax*. Consequently, wood anatomy cannot be used to either support or negate the generic status of *Pamphilia*.

Sexual dimorphism

MIERS (1851 - 1861: 187 - 188) was the first to point out the fact that "the anthers [of species of *Pamphilia*] are sometimes deficient of pollen, in which case they cohere slightly by their margins into a tube, from the bottom [should mean apex] of the anthers to the base; but when polliniferous, they are distinct and free ...", and "I have two specimens of the later species [*P. styracifolia*], one collected by Claussen [= Clausen], the other by Gardner: in the latter the anther-cells are entirely void of pollen, and the filaments below them are united into a monadelphous tube: in Claussen's specimen the filaments are distinct, and free nearly to the base, as shown in Delessert's excellent representation; the anthers are polliniferous. ... It is therefore most probable that in *P. aurea* the union of the filaments for nearly their whole length, as described by Prof. DeCandolle, is a sexual, not a general character". BENTHAM & HOOKER (1873 - 1876) seem to have taken these observations into account in their general description of the "Styraceae": "Flores ... hermaphroditi v. rarius polygamo-dioici". Later authors (GÜRKE 1891, 1897; BAILLON 1892; PERKINS 1907, 1928; MELCHIOR 1964; HUTCHINSON 1967; CRONQUIST 1981) did not mention polygamy in Styracaceae except for *Bruinsmia* (first described in 1893). DICKISON (1993) analyzed flowers of *Pamphilia aurea* (Irwin et al. 29208 at GH), but overlooked the occurrence of gynodioecy. On page 230 he stated: "In my material of

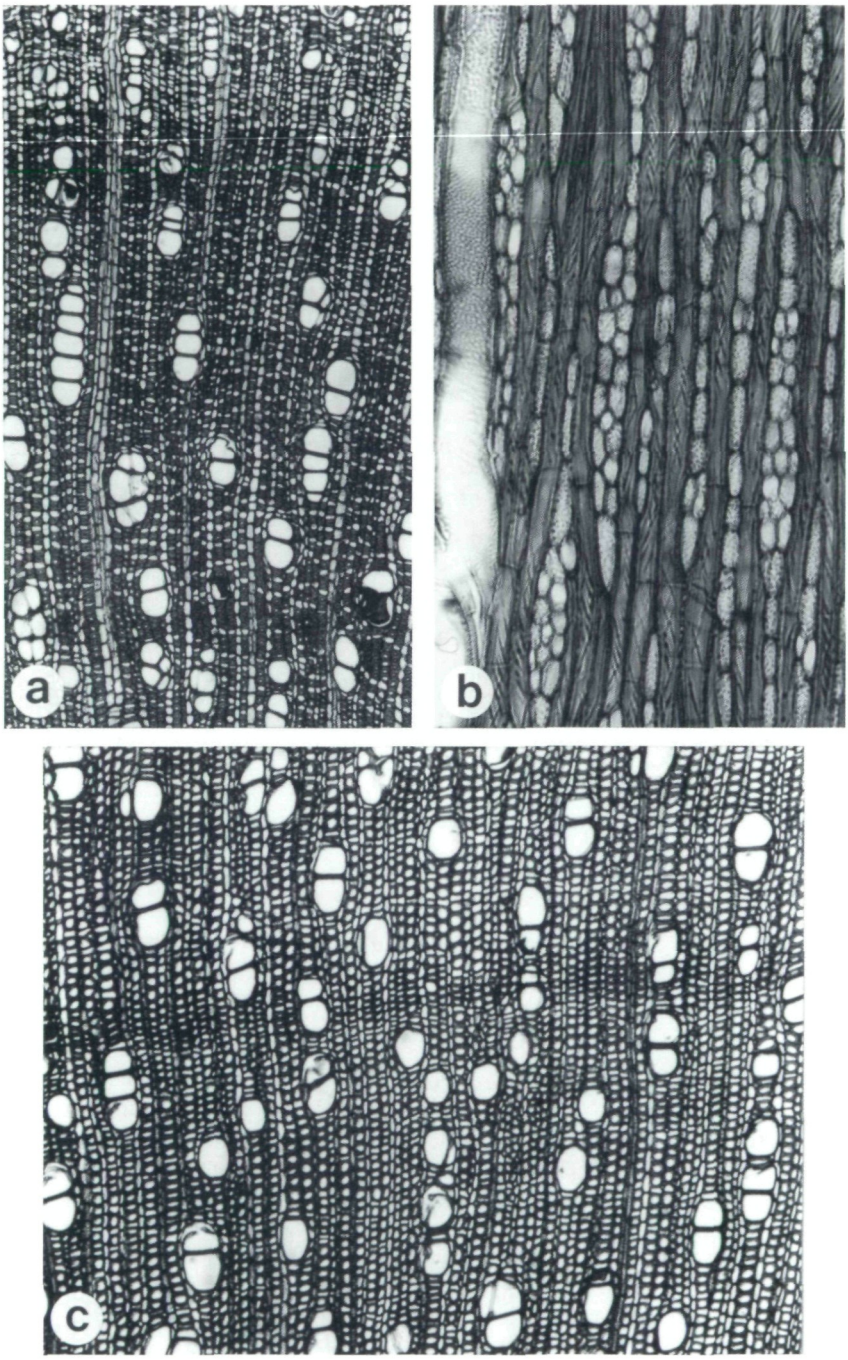


Fig. 6: Wood anatomy: **a - b, *Styrax maninul*** (Esteves et al. s.n. [CFCR 15453], wood sample at U: UW 34342): a, transv. sect., 60x; b, tang. sect., 145x; - **c, *S. pedicellatum*** (Esteves et al. s.n. [CFCR 15502], wood sample at U: UW 34343), transv. sect., 60x.

Pamphilia aurea the locules are small in transsectional area, the sporangial walls thick and the partition between locules shows no evidence of breakdown."

In the course of the present revision it has become clear that gynodioecy (for a general discussion of this topic see FREEMAN & al. 1997) is a normal situation. It occurs in all species of *Styrax* section *Pamphilia*, as well as in *S. foveolaria* and *S. nui*, which belong to *Styrax* section *Foveolaria*. [The type collections of the two latter species show only staminodia. Hermaphroditic flowers of these two species are still not available.]. Bisexual (hermaphroditic) flowers in section *Pamphilia* are slightly larger than unisexual (female) ones. Compared with the stamens of the hermaphroditic flowers, the staminodes of the female flowers (see fig. 187 in MORAWETZ 1993: 404) are quite similar in shape and colour, but slightly smaller. Contrary to the description by MIERS (see above), the filaments of both, staminodia and stamens, are connate for nearly their whole length, forming a tube which is adnate at base to the corolla tube. Only sometimes two (and more rarely several) filaments are connate only towards their bases, so that the tube is not perfect in its upper part. The functionless anthers of staminodia are normally free. Only rarely they are anomalously fused together laterally on their protruding connectives, as observed in *S. pefrit* (see chapter `Taxonomy´) and as described by MIERS (see above). The aborted pollen sacs of staminodia are shorter, narrower, filled only with a spongy tissue and never open by longitudinal slits.

Further studies are necessary to survey the occurrence of gynodioecy among other taxa of *Styrax*, and to find out reasons for the maintenance of strict hermaphroditism in most species, but a shift to gynodioecy in only a few others.

Floral anatomy

The floral anatomy of Styracaceae has been studied in detail by DICKISON (1993), who should be consulted for details. According to him the ovules in the genera *Styrax* and *Pamphilia* are bitegmic, although the two integuments are distinct only at the "micropylar end" of the ovule. The ovules of all other genera within Styracaceae are unitegmic except for *Bruinsmia*, which shows an intermediate condition. This is interpreted as a possible evolutionary shift from bitegmic to unitegmic ovules by fusion of the integuments.

DICKISON (1993: 249) also pointed out that the "petals of *Pamphilia aurea* are highly unusual in possessing an extreme form of inverted-eucamptodromous venation. This reduced venation type, in which lower parts of the vein arches have been lost, is highly unusual in dicotyledons, ... This condition appears to be correlated with a reduction in foliage size, presumably in relation to adaptations to xeric habitats." The distribution of this character among species of sections *Pamphilia* (especially those of the elfin forests in the Andes) and *Foveolaria* should be surveyed.

Pollen

The pollen of Styracaceae has been investigated by YUAN-HUI & CHENG-HONG (1985) and MORTON & DICKISON (1992). Especially the second paper should be consulted for details. No significant differences between the pollen of genera *Styrax* and *Pamphilia* have been reported in these papers.

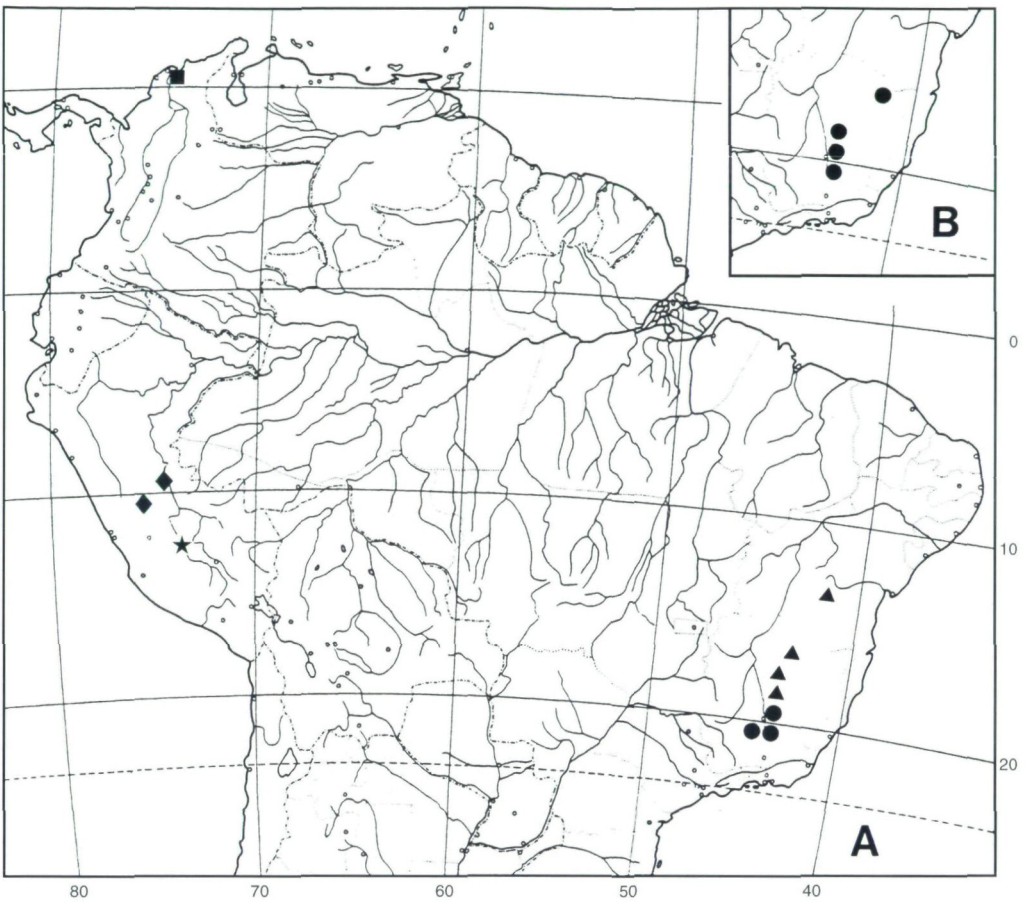


Fig. 7: **A,** Distribution of *Styrax aureum* (●), *S. pedicellatum* (▲), *S. pefrit* (■), *S. omuk* (◆), *S. vilcabambae* (★); - **B,** *S. maninul* (●).

Karyology

MORAWETZ (1991) studied the karyology of two species of *Pamphilia*: *P. aurea* [voucher specimen: Esteves et al. s.n. (CFCR 15453)] and *P. pedicellata* [Esteves et al. s.n. (CFCR 15502)]. According to him, both species are diploid (2n = 16) and do not show any significant karyological differences in comparison with *Styrax* aff. *ferrugineum* and *S. martii*. The majority of chromosome numbers reported for *Styrax* are diploid with 2n = 16 (GOLDBLATT 1981, 1985; LÖVE 1984; for exceptions see GONSOULIN 1974: 200).

Distribution

The distribution (fig. 7) of species of section *Pamphilia* seemingly is of a relict nature and limited to mountainous areas in South America. Three of the four species of series

Pamphilia (*S. aureum*, *S. maninul* and *S. pedicellatum*) occur in the Serra do Espinhaço (between Pico das Almas in Bahia and Ouro Preto in Minas Gerais), in a type of tropical savanna called "campo rupestre" (SARMIENTO 1983). They are confined to the higher parts of the mountains and apparently exhibit an insular distribution comparable to that of other plants of this region (GIULIETTI & PIRANI 1988; HARLEY 1988). Gene flow between isolated populations is, therefore, probably limited. Herbarium specimens of some remote populations are slightly aberrant in some characters, but these differences are trivial with respect to species delimitation. The main area of *S. maninul* overlaps with that of *S. pedicellatum* in the north and with that of *S. aureum* in the south. Some herbarium specimens from these areas of overlap show some intermediate features that could be due to hybridization. It is also possible that *S. maninul* is an ancient hybrid species derived from the other two. This is supported by the intermediate type of indumentum on the abaxial leaf surfaces (compare fig. 3 - 5), and by its geographical distribution (see fig. 7) between the areas of the two other species. *S. pedicellatum* is quite abundant within its area. The other two species are, however, quite rare, probably because they were used as timber and for the production of resin (see under *S. maninul* in the chapter `Taxonomy´). The fourth species (*S. pefrit*) of this series is only known from the cloud forest in the Sierra Nevada de Santa Marta (Dept. Magdalena) in Colombia. The two species (*S. omuk* and *S. vilcabambae*) of series *Andinae* were only collected in three localities in the cloud and elfin forests of the Peruvian Andes (Departments of Huánuco, Pasco, and Cuzco).

Data supporting the inclusion of *Pamphilia* into *Styrax*

The genus *Styrax* (in its present circumscription), comprises three sections (*Styrax*, *Foveolaria* and *Pamphilia*) with ca. 120 species (MELCHIOR 1964), and has been segregated into several separate genera. MIERS (1851 - 1861) recognized five genera (*Cyrta*, *Foveolaria*, *Pamphilia*, *Strigilia* and *Styrax*), whereas PERKINS (1907) only accepted *Styrax* and *Pamphilia*. The latter two genera have traditionally been separated according to the number of stamens per flower (10, respectively 5), and the number of ovules per locule (many, respectively 1).

The inclusion of *Pamphilia* into *Styrax* is supported by the data presented in the following sections 1 and 2, which are then discussed in the third section of this chapter.

1) Variation in the number of floral elements in *Styrax*

Flowers of *Styrax* are actinomorphic and have generally 5 petals, and 5 or 10 stamens. However, the number of stamens and petals per flower is obviously not constant. PERKINS (1907) mentioned irregularities concerning the number of stamens in 10 species, and with regard to the number of petals in 8 species. The quantitative variation of stamens and petals in 400 flowers of *Styrax officinalis* was analyzed by CALDARERA (1905), to demonstrate statistical methods. His results are shown in the following two tables:

Table 2: Variation of number of stamens. A = number of flowers; B = percentage of the total amount (400 flowers); C = Number of stamens per flower.

A	11	58	69	88	80	59	26	9
B	2.75	14.5	17.25	22	20	14.75	6.5	2.25
C	11	12	13	14	15	16	17	18

Table 3: Variation of number of petals. A = number of flowers; B = percentage of the total amount (400 flowers); C = number of petals per flower.

A	5	97	161	112	20	5
B	1.25	24.25	40.25	28	5	1.25
C	5	6	7	8	9	10

To further study this variation I analyzed 170 flowers of *Styrax obassia* as the only living species available to me for this kind of study. I picked them from the ground, below a very richly flowering tree cultivated in the Botanical Garden (HBV) of the University of Vienna [voucher specimens: 4.6.1991 (fl), Wallnöfer 1574, deposited in GZU, LI, W, WU]. 119 flowers (= 70%) were regular, the remaining 51 flowers (= 30%) were irregular, showing different numbers of stamens and petals. My observations are as follows:

Table 4: Variation of number of stamens and petals. A = number of flowers; B = percentage of the total amount (170 flowers); C = number of stamens per flower; D = number of flowers from those in the line A and their respective number of petals in brackets.

A	5	24	119	16	5	1
B	2.9	14.1	70	9.4	2.9	0.6
C	8	9	10	11	12	13
D	2 (4)	9 (4)	119 (5)	5 (5)	5 (6)	1 (6)
	3 (5)	14 (5)		10 (6)		
		1 (7)		1 (7)		

S. officinalis and *S. obassia* are deciduous species. Living, evergreen species of *Styrax* have not been available for study of variation in number of floral elements. To avoid the destruction of too many flowers, only very few of them have been analyzed from herbarium specimens. The following irregularities have been observed: A collection of *S. maninul* (Harley et al. 25258) shows one flower with eight petals and ten superposed stamens, and another flower with six petals and six stamens. A flower of *S. omuk* (Wallnöfer 19-30488) shows six calyx teeth, six petals, six stamens, and a regular ovary. Two flowers of *S. pedicellatum* (Anderson et al 35514) displayed six to seven ovules in their ovaries, three being of normal size, 1 - 2 somewhat smaller, the others very small.

2) Comparison of flowers of *Styrax* section *Pamphilia* and section *Foveolaria*.

The species of section *Pamphilia* share many similarities (shape of flowers, stamens, triovulate ovaries, indumentum, general habit) with *S. foveolaria* (PERKINS 1907: 84, fig. 12A - L) and *S. nui*, which belong to section *Foveolaria*. These two rarely collected species are restricted to the Andes of Peru (WALLNÖFER 1996), and occupy an intermediate position between *Styrax* s.str. and *Pamphilia*. The flowers are of the same shape, although somewhat larger than those of species in section *Pamphilia*. The stamens (PERKINS 1907: 15, fig. 3C - E and 84, fig. 12C) are nearly identical in shape, but differ in their number (9-10 instead of 5). The filaments are broad, thick, flattened, strikingly rigid and connate for most of their length, forming a tube that is attached at base to the short corolla tube. The connectives are flattened and conspicuously exceed the pollen sacs laterally. Stamens are, therefore, almost rigid and densely crowded. As seen from the very few flowers I

boiled up and studied, it seems that the stamens of these two species may not have sufficient space within the relatively small flowers to arrange all the anthers in a regular circle: Many anthers are slightly bent towards the interior of the flowers, obstructing the anthers behind them. This observation needs, however, to be reconfirmed on living flowers.

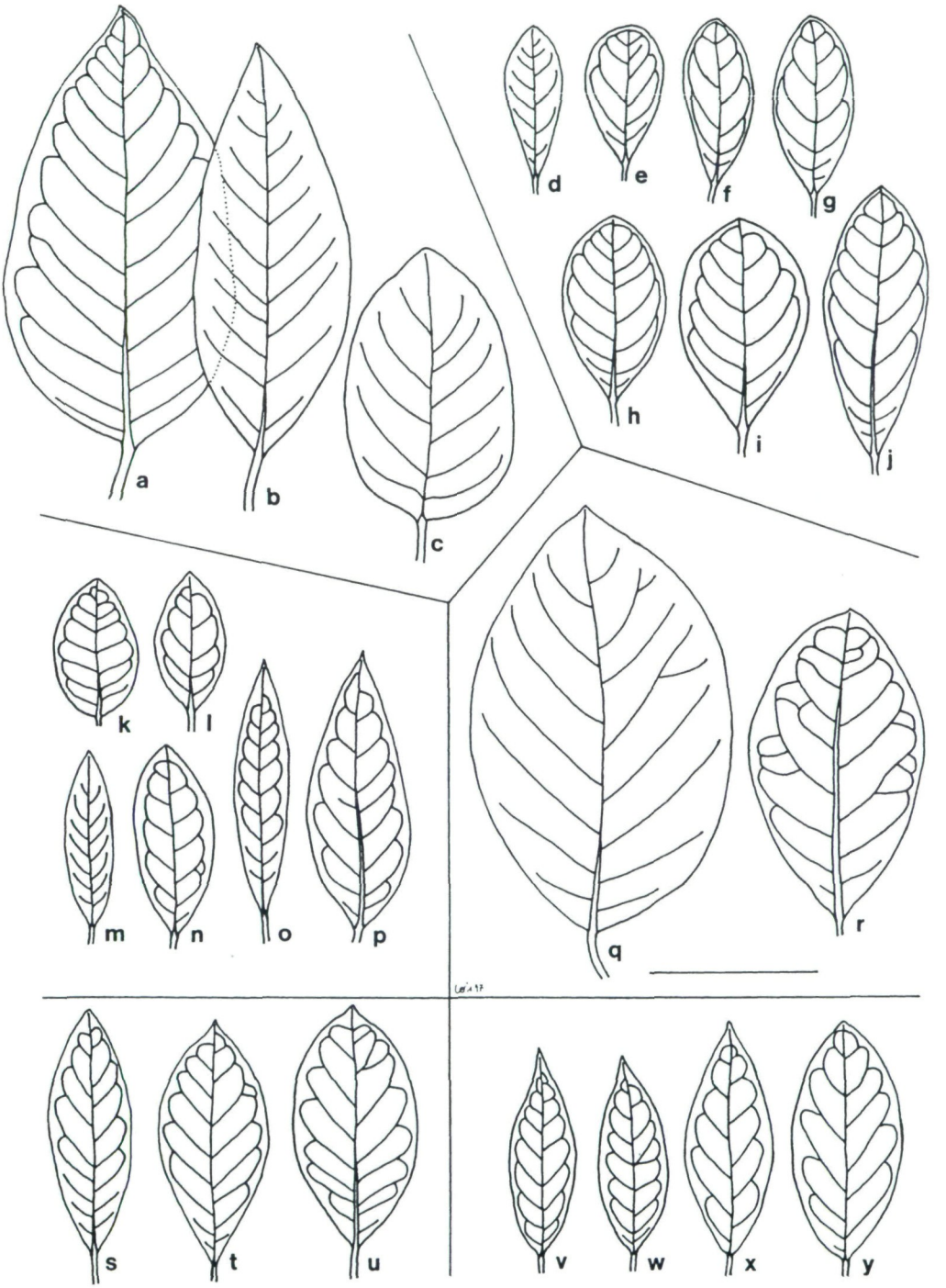
3) Discussion

Species of *Styrax* s. lat. exhibit considerable variability, in flower size, with some groups seemingly having experienced a notable reduction in dimensions of flowers. Among them are the species of section *Foveolaria* with quite small, and those of section *Pamphilia* with the smallest flowers. To avoid an overcrowding of the bulky stamens (see above), and to permit an optimal arrangement of the anthers, three different ways seem hypothetically to have been possible: change of size, change of shape or change of number of stamens. A further decrease in size of the anthers (possessing already narrow pollen sacs!) without a concomitant change of shape would certainly affect fitness, as the amount of pollen per anther would necessarily also have to decrease noticeably. The shape of stamens, on the other hand, is very stable and appears not to be easily modifiable. Considering the remarkable variability in the number of floral elements shown above, a reduction in the number of stamens from 10 in *Styrax* s.str. to 5 in section *Pamphilia* appears to have been the most practicable alternative.

The reasons for a reduction in flower size are not clear, but could be associated with changes in breeding system, which still need to be studied. The advent of gynodioecy (see chapter `Sexual dimorphism´) could be one such explanation.

Leaf morphology, wood anatomy, pollen morphology, and karyology do not reveal any significant differences between *Pamphilia* and *Styrax*, and do not contradict their lumping. Furthermore, general morphology, habit, structure and indumentum of vegetative parts in many *Styrax* species are quite similar to those in species of *Pamphilia*. For the non-specialist, herbarium material missing flowers can, therefore, not be assigned to one of the two genera. The gynoecium and its internal structure is nearly identical in species within sections *Foveolaria* and *Pamphilia*. The fact that gynodioecy occurs in both sections further endorses the inclusion of *Pamphilia* into *Styrax*. I also presume that gynodioecy, reduction of flower size, and of number of stamens and ovules are derived characters. Considering all this, I conclude that *Pamphilia* does not deserve generic status, unless *Styrax* itself is segregated into several poorly circumscribed small genera. *Pamphilia* is here reduced into synonymy and kept as a separate section within *Styrax*. Further studies are necessary to reasonably subdivide this large genus, and to determine whether the species of section *Foveolaria* with a triovulate ovary should be transferred to section *Pamphilia*.

Fig. 8: Variation of leaf shapes (leaves with connected secondary veins are shown from abaxial side, others from adaxial side): **a - c, *Styrax aureum*** (a, Glaziou 17129; b, Irwin et al. 19633; c, Gardner 4993); – **d - j, *S. maninul*** (d, Mautone et al. 769; – e, Mello-Silva et al. s.n. [CFSC 10363]; – f - g, Esteves et al. s.n. [CFCR 15472]; – h, Harley et al. 25258; – i, Magalhães 15581; – j, Menezes et al. s.n. [CFCR 119]); – **k - p, *S. pedicellatum*** (k, Glaziou 19616; l, Esteves et al. s.n. [CFCR 15502]; m - n, Irwin et al. 20974; o - p, Esteves et al. s.n. [CFCR 15503]); – **q - r, *S. pefrit*** (q, Romero-Castañeda 7189; r, Romero-Castañeda 7777); – **s - u, *S. omuk*** (s - t Wallnöfer 19-30488; u, Smith & Pretel 7978); – **v - y, *S. vilcabambae*** (v - w, Dudley 10808; x, Dudley 10749; y, Dudley 10802); (Bar = 5 cm, valid for all leaves).



Taxonomy

***Styrax* L.**, Sp. Pl.: 444 (1753).
Type species: *Styrax officinalis* L.

Emendation of the description in PERKINS (1907): smallest flowers 4 mm long; stamens (staminodia) (4 -) 5 - 10 (- 18); petals (4 -) 5 (- 10); all species of section *Pamphilia*, as well as two species of section *Foveolaria* (*S. foveolaria* and *S. nui*), are gynodioecious.

***Styrax* L., sectio *Pamphilia* (MART. ex A.DC.) B.WALLN.**, comb. et stat.n.

≡ *Pamphilia* MART. ex A.DC., Prod. 8: 271 (1844).
Type species: *Pamphilia aurea* MART. ex A.DC. [= *Styrax maninul* B.WALLN.] (designated by HUTCHINSON 1967: 39).

Shrubs or trees up to 7 m (said to attain 20 m, according to one collection); trunk diameter at breast height (dbh) mostly less than 10 cm (on three collections reported to attain 30, 36 and 44 cm, respectively); species growing in campo rupestre-vegetation (tropical savanna) in SE-Brazil develop subterranean woody xylopodia (see chapter `Growth form and habit´); twigs terete, densely stellate-tomentose, later glabrescent; **leaves** (fig. 8) alternate, petiolate; lamina ovate or oblong-elliptic, coriaceous or chartaceous, entire, rarely irregularly crenulate and with some small, remote, mucro-like teeth distally; leaf bases cuneate or rounded, rarely asymmetrical; leaf apices obtuse to acuminate (rarely emarginate or retuse); young leaves adaxially stellate-tomentose, soon glabrescent, but hairs often persisting along veins, rarely on lamina; mature leaves abaxially glabrous (series *Andinae*) or covered with a dense, persistent indumentum of stellate hairs (series *Pamphilia*); in some species domatia present abaxially in axils of secondary veins; **inflorescences** axillary, rarely subterminal or terminal on lateral axes, racemose to subspicate, rarely divaricate, or even more rarely with two racemes arising from the same axil; inflorescence axes, bracts, and pedicels densely stellate-tomentose; flower bracts inconspicuous, mostly shed at anthesis; plants gynodioecious; **flowers** crowded distally and more spaced towards base of inflorescences; anthesis proceeding from proximal to distal parts of inflorescences; flowers sessile or shortly pedicellate (proximal pedicels longer than distal ones), scented, 4 - 8 (- 9) mm long; hermaphroditic flowers up to one third larger than female ones; calyx cup-shaped, nearly truncate or slightly sinuate to dentate at apex, persistent on fruits and mostly irregularly split by one or few longitudinal slits, densely stellate-tomentose outside, nearly glabrous inside (apart from a few, appressed, few-branched hairs); calyx teeth (4 -) 5 (- 6), small, remote (but sometimes up to three closer together); petals white or whitish-yellow, (4 -) 5 (- 8), valvate, connate at base, forming a short tube, covered outside with an extremely dense indumentum of short-branched, apically flattened (somewhat scale-like), stellate hairs (branches of these hairs interlaced into one another and forming a sort of a second, homogenous surface), inside nearly glabrous apart from some hairs near the margins; stamens and staminodia glabrous, (4 -) 5 (- 10), both similar in shape, but the latter about one-third smaller in size; filaments flat, thick and stiff, connate for nearly their whole length, forming a tube that, at the base, is adnate to the corolla tube; distal free part of filaments approximately as long as wide; anthers yellow or greenish-yellow, basifixed, introrse, bithecate; connectives flat, thick and stiff, conspicuously exceeding thecae laterally, rounded but only slightly narrowed apically; thecae linear, close together, those of fertile stamens polliniferous and opening by longitudinal slits, those of staminodia only filled with a spongy tissue

and not opening; pollen solitary, globose, tricolporate; style terminal, narrowly cylindrical or narrowly cone-shaped, glabrous distally, densely stellate-tomentose proximally, dilated at apex into a small, slightly trilobate to slightly capitate stigma, reaching from 2/3 to 3/4 of length of anthers in hermaphroditic flowers and only up to the base of, or 1/2 of length of sterile anthers in female flowers; ovary superior, subglobose, densely stellate-tomentose, tricarpellate, unilocular apically, trilocular basally (septae uncompletely developed); ovules 3 per ovary, rarely more, attached by small funicles at base of ovary; **fruits** subglobose to ellipsoid, ca. 6 - 7 (- 10) mm long and 6 - 7 mm wide, drupaceous, 1 (- 2)-seeded; exocarp covered with a dense indumentum of stellate, sometimes more scale-like hairs; mesocarp slightly fleshy and juicy at maturity; endocarp inconspicuous; seeds ellipsoid, rounded distally, slightly cuneate basally, with a more or less circular hilum on one side near base; testa composed of two distinct, almost completely separated layers of tissue; outer layer lignified, hard, smooth, brown, and proximally on one side with three irregular grooves (impressions of septae; see PERKINS 1907: 15, fig. 3L) and small pits resulting from the aborted seeds; inner layer whitish and membranous; endosperm whitish to brownish, oily, smelling and tasting like nuts; embryo straight, erect within the basifixed endosperm, with radicula near base of endosperm.

Key to series and species

Important note: Some leaves of some collections of *S. maninul* show an atypical indumentum, which makes it necessary to examine leaves of different age.

1 Abaxial surfaces of mature leaves covered with a dense and persistent indumentum of stellate hairs; SE-Brazil, Colombia (series *Pamphilia*) 2

1* Abaxial surfaces of mature leaves glabrous; cloud and elfin forests; Peruvian Andes (series *Andinae*) 5

2 Indumentum on abaxial leaf surfaces not homogeneous: smaller hairs forming a dense whitish-grey layer, larger hairs normally ferrugineous and scattered along veins of highest order (rarely on intercostal areas) (fig. 5) 3

2* Indumentum on abaxial leaf surfaces homogeneous (fig. 3 + 4); campo rupestre-vegetation (tropical savanna) in SE-Brazil 4

3 Leaves (3 -) 4 - 6 (- 8.4) x (1 -) 2 - 3 (- 4.3) cm; inflorescences (2.2 -) 4 - 6 (- 12) cm long, ca. 20-flowered; campo rupestre-vegetation (tropical savanna) in SE-Brazil ..... **2. *S. maninul***

3* Leaves (4 -) 7 - 10 (- 13) x (2.4 -) 4.5 - 6 (- 7.7) cm; inflorescences 0.8 - 2 (- 2.5) cm long, ca. 5 - 7-flowered; cloud forests in northern Colombia ..... **4. *S. pefrit***

4 Longer branches of stellate hairs on abaxial leaf surfaces ca. 0.16 - 0.23 (- 0.58) mm long (fig. 4); single hairs still recognizable; hairs white, grey-green or less frequently some of them ferrugineous; leaves (2.3 -) 3.5 - 5 (- 9) x (0.9 -) 1.5 - 2.5 (- 4.2) cm; petioles 3 - 8 mm long; domatia mostly present and conspicuous in axils of secondary veins on abaxial surfaces of older leaves; pedicels (1 -) 2.5 - 5 mm long ..... **3. *S. pedicellatum***

4* Longer branches of stellate hairs on abaxial leaf surfaces ca. 0.6 - 1 mm long (fig. 3, but in reality hairs much denser, with overlapping branches - single hairs therefore scarcely discernible); hairs always ferrugineous or golden; leaves (4 -) 9 - 12 (- 14)

x (2 -) 4 - 5.7 (- 7.4) cm; petioles (10 -) 13 - 20 mm long; domatia always absent in axils of secondary veins on abaxial leaf surfaces; pedicels 0.5 - 1.5 (- 2) mm long ..... **1. *S. aureum***

5 Inflorescences (2 -) 2.5 - 5.5 cm long, mostly 4 - 7.5 times as long as petioles, 0.5 - 0.7 (- 1) times as long as the subtending leaves (including petioles), (2 -) 6 - 8 (- 10)-flowered; leaves mostly acute at apex, broadest at 1/3 - 1/2 of lamina-length; southern Peru ..... **6. *S. vilcabambae***

5* Inflorescences 0.8 - 2 cm long, mostly 1 - 2 times as long as petioles, ca. 0.25 times as long as the subtending leaves (including petioles), 3 - 5 (- 7)-flowered; leaves mostly obtuse at apex, broadest at 1/2 - 2/3 of lamina-length; central Peru ..... **5. *S. omuk***

Styrax L., sectio *Pamphilia* (MART. ex A.DC.) B.WALLN., series *Pamphilia*

Type species: *Styrax maninul* B.WALLN. (= *Pamphilia aurea* MART. ex A.DC.)

This series is characterized by the persistent, dense indumentum of stellate hairs on abaxial surfaces of mature leaves.

1. *Styrax aureum* MART., Reise Bras. 2: 551 (1828); (fig. 9)

≡ *Strigilia aurea* (MART.) MIERS, Contrib. Bot 1: 185 (1851 - 1861).

Type: Habitat in altis M. Serro Frio ad Tejues et alibis, Maio [1818] (fl, fem*), Martius s.n. [lectotype here designated: M** (photo 1187 at W); isotype: M (photo W 1195); a third sheet at M with the information "Rio San Francisco", (fl, fem), in Herb. Zuccarini, without further information, obviously represents another isotype].

= *Pamphilia styracifolia* A.DC., Prodr. 8: 271 (1844).
Type: Brazil, Minas Gerais, Serra de Ouro Preto, Oct 1839 (fl, her), [information taken from the additional label at P], Claussen 135 [lectotype here designated: G-DEL (photo at W); isolectotype: P ex G-DEL (photo at W)].

Notes on the types of *Styrax aureum* and *Pamphilia styracifolia*: The type locality of *Styrax aureum* is not traceable. According to his itinerary (SPIX & MARTIUS 1823 - 1831: 421 - 422), Martius collected plants in May 1818 in the Serra da Piedade, next to Caeté. Considering the known geographical and altitudinal distribution of this species, this seems to be the only place in which he could have found *S. aureum*.

As to the type of *Pamphilia styracifolia*, CANDOLLE (l.c.) specifies: "Claussen! n. 135 in h. Deless. et DC.". However, only the sheet in G-DEL shows this collection-number. The sheet in his own herbarium (G-DC; see Field Mus. photo 7517 at F, MO, NY, US, and other photo at W), does not indicate neither a collector nor a number. For this reason the sheet in G-DEL is here formally selected as lectotype. Three other sheets in P (dated 1838 [changed by hand to 1841] (fl, fem + her), Claussen 135 n. 12) probably represent isolectotypes of *P. styracifolia*. For problems concerning the Claussen (= Clausen) collections see notes on type material of *S. maninul*.

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* Abbreviations: fem = female flowers; fl = flowering; fr = fruiting; her = hermaphroditic flowers.

** Acronyms of herbaria according to HOLMGREN & al. (1990).

Fig. 9: *Styrax aureum* MART. (lectotype)

Shrub or small tree up to 4 m; structure of subterranean parts unknown, but plants probably develop xylopodia; diameter of stems up to 8 cm; twigs golden-brown, densely stellate-tomentose, slowly becoming glabrous and darker with age, the bark of which mostly shows a few coarse fissures; terminal buds quite large, densely stellate-hispid; petioles (10 -) 13 - 20 x 2.5 - 3 mm, densely stellate-tomentose; young **leaves** on both surfaces ferrugineous to golden, densely stellate-tomentose; mature leaves adaxially almost completely glabrous apart from some hairs on veins, slightly shiny in sicco; abaxially light brown to golden, rarely greyish-brown (veins of same colour or sometimes slightly darker), densely stellate-tomentose (fig. 3, but in reality hairs much denser, with overlapping branches - single hairs therefore scarcely discernible); longer branches of stellate hairs ca. 0.6 - 1 mm long; some hairs in-between the larger ones several orders of magnitude smaller, more papilliform (only visible on closer inspection, after removing larger hairs); lamina coriaceous, broadly ovate to elliptic, rarely oblong (fig. 8a - c), broadest in, or slightly below middle, (4 -) 9 - 12 (- 14) x (2 -) 4 - 5.7 (- 7.4) cm, length to width ratio: (1.5 : 1 -) 2.8 : 1 (- 3.1 : 1); leaf margins entire, mostly flat, sometimes slightly undulate; leaf bases cuneate or rounded (rarely asymmetrical); leaf apices usually tapering gradually (fig. 8b), but sometimes also obtuse or rarely emarginate; secondary veins 7 - 12 per side, curved, flat or only very slightly prominent adaxially, prominent abaxially, where domatia in axils of secondary veins are always absent; **inflorescences** and infructescences (except petals, interior of flowers, and fruits) ferrugineous to golden and densely stellate-tomentose, both (1.5 -) 4.5 - 9.5 cm long, (0.2 -) 0.3 - 0.7 (- 1) times as long as subtending leaves (which are up to 15 cm long, including petioles), ca. 20 - 30-flowered; flower bracts linear, (2 -) 3 - 5 (- 8) mm long; pedicels 0.5 - 1.5 (- 2) mm long; **hermaphroditic flowers** 6.8 mm long (excluding pedicels); calyx 3 mm long, cup-shaped, ferrugineous-green in vivo (Irwin et al. 28764); calyx teeth ca. 0.8 mm long; petals white or cream-coloured, 6 x 2 - 2.8 mm, the proximal parts connate for 2 mm; stamens 5 mm long, the proximal parts connate for 2 mm; free part of filaments ca. 1.3 mm wide; connectives 1.2 mm wide, exceeding thecae laterally by 0.3 mm; thecae 2.3 mm long; style 3 mm long, narrowly cylindrical, glabrous except at base; ovary subglobose, height/width: 1 x 1.5 mm, densely stellate-tomentose; **female flowers** 5 mm, calyx 2.5 mm, calyx teeth ca. 0.5 mm long; petals 4.5 x 2 mm, the proximal parts connate for 1.5 mm; staminodia 3.2 mm long, the proximal parts connate for 1.5 - 1.8 mm; connectives 1 mm wide; aborted thecae 1.2 mm, style 1.8 mm long; **fruits** subglobose, 6 - 7 mm in diameter in sicco, immature greyish in sicco, light green (Irwin & al. 28764) to pale greyish-green (Irwin & al. 19633) in vivo; seeds 6 x 4.5 mm.

Illustrations: hairs on leaves (PERKINS 1907: fig. 1A, 1928); twig and several details of flowers [the open flower on tab. 42: fig. 2 is incorrectly drawn: the apices of living petals are normally straight and not incurved] (DELESSERT 1846: tab. 42); twig and several details of flowers [the dense indumentum on twigs and leaves was omitted] (SEUBERT 1868: plate 68); flowers, stamina, cross-sections of the ovary (MIERS 1851 - 1861: plate 29); cross-sections of the ovary (GÜRKE 1891).

Vernacular names: Benjoim falso (specimens: Vitor & Grandi 1964; Siqueira et al. 1903); Benjoeira (Renno 1741).

Distribution (fig. 7A) and habitat: This species occurs only in the southern part of the Serra do Espinhaço around Belo Horizonte and Itabirito in Minas Gerais (Brazil). It grows in campo rupestre-vegetation from 1450 to ca. 1850 m altitude, on steep, rocky slopes and on iron-rich soils.

Specimen examined: **Brazil, Minas Gerais**: **Area around Belo Horizonte**: Belo Horizonte, 1945 (fl, fem), Renno 1741 [BHCB]; Serra do Curral del Rey (now within Belo Horizonte), Sept 1840 (fl, her) [label data ex BM and K], Gardner 4993 [BM, CGE, K 2x, OXF, W]; Nova Lima, Serra do Curral, 4 Sept 1955 (fl, her), Roth 17475 [W ex UFJF]; Serra da Piedade, ca. 35 km E of Belo Horizonte, 1680 m, 19°49'S, 43°40'W, 15 Aug 1985 (fl, her), Siqueira et al. 1903 [BHCB]; same loc., ca. 1850 m, 15 Jan 1971 (fr), Irwin et al. 30431 [C, F, K, NY, SP, US]; same loc., middle and upper slopes, south side, ca. 5 km N of Caeté, ca. 1800 m, 19 Jan 1971 (fr), Irwin et al. 28764 [AAU, MO, NY 2x, UB]; in collibus ficeis prope Caeté, Sept 1824 (fl, fem), Riedel 641 [LE 2x, NY, OXF?]; Serra do Rola Moça, Divisas dos Municípios de Betim e Brumadinho, 1450 m, 28 Jul 1940 (fl, her), Barreto 10847 [UB]; same loc., 28 Jul 1940 (st), Oliveira s.n. [US]; Serra da Moeda, 5 Oct 1985 (fl, fem), Vitor & Grandi 1964 [BHCB]; Serra d'Itabira do Campo, 12 Sep 1887 (label data ex P), (fl, fem), Glaziou 17125 [BR, C, K, LE, P 4x]; Serra do Itabirito ca. 48 km SE of Belo Horizonte, ca. 1750 m, 9 Feb 1968 (fr), Irwin et al. 19633 [F, MO, RB, UB, US 2x]; Pico do Itabirito, "nas áreas de transição da canga", 28 Aug 1993 (fl, fem), Teixeira 22341 [BHCB]; - **without locality**: without year (fl), Claussen 142 [W]; 1840 (fl, fem), Claussen 472 [BM, BR]; 1840 (fl, fem + her), Claussen 702.A [BR, LE]; 1840, (fl, her) Claussen s.n. [BR, CGE, F, K 2x, LE 2x, W]; 1839, (fl, her) Claussen s.n. [P]; sheets lacking specifications, but probably collected by Claussen: (fl), [BR, W].

Atypical collections: Riedel 641 shows atypical inflorescences that are crowded together and only ca. 1.6 cm long. The leaves are small, reaching only 2.6 - 4.5 x 1.2 - 2 cm. Irwin et al. 30431 is also atypical and may perhaps represent a hybrid with *S. maninul*. The leaves are intermediate in shape and size, but more resembling *S. aureum*. The indumentum on abaxial leaf surfaces is somewhat intermediate. The branches of the larger stellate hairs are only 0.3 - 0.45 mm long. The contrast between the colours of lamina and secondary veins is conspicuous, and resembles the pattern in *S. maninul*.

2. *Styrax maninul* B.WALLN., nom.n.; (fig. 10)

≡ *Pamphilia aurea* MART. ex A.DC., Prod. 8: 271 (1844); non *Styrax aureum* MART. (1828).

Type: Brazil, Minas Gerais, Serra do Espinhaço, Cachoeira do Campo [located between Ouro Preto and Itabirito], Aug 1839 (fl, her), Claussen 184 [lectotype here designated: G-DEL (photo W 1190); isolectotypes: G-DC (specimen not seen, but photo at W); NY 2x ex P; P (original label missing)].

The following specimens are also part of the type collection (see note below): Caxoeira [= Cachoeira] do Campo, Aug 1839 (fl, her), [data taken from the additional label sub numero 184 at BR], Martius 902 [isotypes (formally = syntypes): G-DC (specimen not seen, Field Mus. photo 7518 at F, MO, NY; and other photo at W), BM, BR (photo W 1189), G (fem), K, L (fem + her), LE, M, NY, P, S, US, W 2x].

Nomenclatural note: In 1828, Martius described *Styrax aureum*, long before the generic concept of *Pamphilia* was developed. Later, he obtained two new collections from Brazil (see below), which, according to SEUBERT (1868: 186), he recognized as conspecific with his *S. aureum*. He subsequently distributed duplicates of these collections, numbered 902 and 903 (see below), using the unpublished binomial "*Pamphilia aurea* MART.". However, before Martius was able to publish his new genus, it was taken up and validated by CANDOLLE (1844) in his Prodromus. There is no evidence that CANDOLLE has ever seen the type of *S. aureum*, and that he perceived the connection between *Styrax aureum* and *Pamphilia aurea*. Thus, he left *S. aureum* within *Styrax* (CANDOLLE 1844: 264). In the same publication, he also described the new species *Pamphilia aurea* and *P. styracifolia*.

Fig. 10: *Styrax maninul* B.WALLN. (lectotype)

In the course of the present revision, which results in the merger of the two genera, it has become clear, that *S. aureum* is identical with *P. styracifolia*, but not with *P. aurea*. Therefore, a new specific epithet has to be coined for *P. aurea* when transferred to *Styrax*.

Note on type material: Several years after his return from South America, Martius commissioned an unnamed "friend" residing in Brazil to collect plants, and advertised the subscription for a "Herbarium Florae Brasiliensis" (MARTIUS 1835). Descriptions and other information concerning the distributed specimens were subsequently published in several instalments, but only up to collection number 722 (see list in STAFLEU & COWAN 1981: 333). The data for to the collection no. 902 (*P. aurea*) were, therefore, never published. The corresponding specimen in Martius' personal herbarium, now at BR, shows only one twig, but two labels: One with the only information "Martii Herbar. Florae Brasil. N° 902" (which corresponds to all the other labels on specimens distributed to subscribers), and another label numbered 184, which indicates a place and date of collection, but no collectors name. A label ± identical to the latter can also be found on the lectotype here selected (see above), where it is attached to a printed label, which bears the name Claussen. The handwriting on these labels (N° 184) is very characteristic and can be found on several other specimens of Claussen, who dealt with various natural history objects (ANONYMOUS 1842; URBAN 1906: 12 - 13) and repeatedly sold parts of his collections to herbaria in Europe [as documented on additional labels on specimens deposited at G, for example: "3^{e} envoi reçu en janvier 1840"].

The sheet with the label "Martii Herbar. Florae Brasil. N° 903" (see below), also at BR, bears yet another label that can also be assigned to Claussen! Therefore, Martius' unnamed "friend" was obviously Claussen, who evidently send duplicates of some collections to Martius (at Munich) and to Geneva as well! Therefore, Martius 902, and Claussen 184, both belong to the same collection, and all represent in reality isotypes.

Two sheets of the type collection, one at G, one at S, are erroneously numbered 702. Two other sheets, one at LE, one at W, lack a collection number. These misnumbered and unnumbered sheets were distributed by Martius and obviously belong to the type collection, due to the fact that only one set of flowering specimens had been send out.

To date it has generally been assumed that the collection Martius 902 formally represents the type of *Pamphilia aurea*. However, instead of citing one of Martius' specimens, CANDOLLE (l. c.) only refers to an unpublished manuscript of Martius. In the corresponding protologue he cites only two specimens of Claussen, both numbered 184. Of these two specimens, the sheet in G-DEL is here formally selected as the lectotype, because it is first quoted and more informative than the other.

Shrub or small tree up to 4 (- 6) m; xylopodium woody (fig. 1), its phloem and bark red in cross section; diameter of stems up to 6 cm; bark of stems brown with small, contorted, grey fissures; twigs subterete, ferrugineous, densely stellate-tomentose, soon becoming glabrous and dark with age, often finely striate; terminal buds quite small, similar to young twigs in indumentum and colour; petioles 3 - 6 (- 9) x 1 - 1.5 (- 2) mm, ferrugineous, densely stellate-tomentose; very young **leaves** on both surfaces densely stellate-tomentose: indumentum light brown to light green in vivo, ferrugineous in sicco; slightly older leaves flat in vivo, the indumentum light brown to ferrugineous adaxially, abaxially light green to greyish-light brown, with darker hairs along veins; mature leaves adaxially dark green in vivo, slightly shiny in sicco, nearly glabrous or only with a few grey, stellate

hairs, especially along veins; indumentum abaxially dense and persistent, composed of many-branched, stellate hairs of two sizes: light grey hairs with branches 0.09 - 0.2 mm long, forming a dense, homogeneous layer, and ferrugineous hairs with branches up to 0.6, rarely 1 mm long, scattered on lamina, but more dense along veins (fig. 5); from the distance, abaxial leaf surfaces appear to be grey-green or light brown to grey, with darker brown veins; lamina coriaceous, broadly lanceolate, sometimes ovate or obovate (fig. 8d - j), broadest near middle, (3 -) 4 - 6 (- 8.4) x (1 -) 2 - 3 (- 4.3) cm, length to width ratio: (1.5 : 1 -) 2 : 1 (- 2.6 : 1); leaf margins entire, abaxially revolute; leaf bases cuneate, rarely rounded or shortly attenuate; leaf apices mostly obtuse, sometimes shortly acute or rarely retuse; secondary veins 5 - 8 per side, curved, flat or only slightly impressed adaxially, prominent abaxially; domatia in axils of secondary veins rarely present abaxially, and inconspicuous; **inflorescences** and infructescences (except petals, interior of flowers, and fruits) ferrugineous and densely stellate-tomentose, (2.2 -) 4 - 6 (- 12) cm long, (0.5 -) 0.7 - 1 (- 1.5) times as long as subtending leaves (which are up to 8 cm long, including petioles); ca. 20-flowered; flower bracts linear, 1 - 2 (- 7) mm, pedicels 0.5 - 2.5 (- 3) mm long; flowers with a heavy, sweet, but not intense scent (personal observ.); **hermaphroditic flowers** 6 - 7 mm long (excluding pedicels); calyx 3 - 3.5 mm long, cup-shaped; calyx teeth 0.3 - 0.5 mm long; petals (4 -) 5 (- 6 or - 8) per flower, 6 - 7 x 1.7 - 2 mm, the proximal parts connate for 2 mm, white (Irwin et al. 29208, Magalhães s.n. and personal observ.), yellow (Badini 3294), or "branco-creme" (Joly & Semir 3132); stamens 5 (- 10), 4 mm long, the proximal parts connate for 2 mm; filaments white, distally free for ca. 0.5 mm; anthers greenish-yellow or yellow (Magalhães s.n., and personal observ.); connectives ca. 1 mm wide, exceeding thecae laterally by ca. 0.3 mm; thecae 1.5 - 2 mm long; style 2 - 3.7 mm long, narrowly cylindrical, glabrous except at base; ovary subglobose, height/width: 1 - 1.2 x 1.5 - 1.8 mm, densely stellate-tomentose; **female flowers** 4 - 4.5 mm, calyx 2.5 mm, calyx teeth ca. 0.4 mm long; petals 3.8 - 4 x 1 - 1.5 mm, the proximal parts connate for 1.5 - 1.7 mm; staminodia 2.6 mm long, the proximal parts connate for 1.3 mm, yellow (Irwin et al. 29208, and personal observ.); filaments distally free for 0.3 mm; connectives 1 mm wide; aborted thecae ca. 1 mm, style 1.6 mm long; **fruits** subglobose, 6 - 7 mm in diameter in sicco, immature ones light green to slightly greyish in vivo, greyish in sicco; seeds 5 - 6.7 x 4 - 5 mm.

Illustrations: twig and several details of flowers (SEUBERT 1868: plate 67); twig (CORREA 1926, taken from SEUBERT 1868); twig, fruits, seed and embryo (PERKINS 1907, 1928); transverse sections of petiole, lamina and midrib, venation pattern (SCHADEL & DICKISON 1979); flower and stamina (GÜRKE 1891); flower [the connective is not correctly drawn] (BAILLON 1892: 413); several details of flowers (DICKISON 1993); pollen (MORTON & DICKISON 1992); chromosomes (MORAWETZ 1991).

Use: According to CORREA (1926: 298 - 299) the wood of *Pamphilia aurea* has variously been used for constructions and indoor finish. When damaged or cut, the bark of stems exudes a resin which is called "incense of America", and which was used during service in catholic churches, and in domestic medicine (SEUBERT 1868: 198; CORREA 1926).

Vernacular names: Beijoeiro, Benjoeiro, Estoraque, Estoraqueiro [the names have also been used for other species of *Styrax*] (SEUBERT 1868: 198; CORREA 1926).

Epithet: The name has been coined arbitrarily (see GREUTER & al 1994: Art. 23.2).

Distribution (fig. 7B) and habitat: This species occurs in the state of Minas Gerais in Brazil. Most of the specimens seen have been collected in the Serra do Espinhaço, between Ouro Preto and Diamantina. Two apparently isolated populations occur near Jequitinhonha. The species grows in campo rupestre-vegetation, at margins of woods and gallery forests, in rocky ravines and on steep, grassy, shrubby, or wooded slopes with rocky outcrops, at 1000 - 1700 (- 1950) m altitude.

Specimens examined: **Brazil, Minas Gerais: Município de Jequitinhonha:** Serra da Sapucáia, 1000 m, Apr 1959 and 3 Sep 1959 (fl, her), Magalhães 15581 [UB 2x, US]; Serra de Areia ca. 47 km ao sul de Pedra Azul, na estrada para Jequitinhonha 16°22'S, 41°03'W, 1100 m, 20 Oct 1988 (fl, her), Harley et al. 25258 [F, K, W]. - **Area around Diamantina:** Diamantina, 18 Jan 1947 (fr), Eegler 0102 [RB]; Município de Diamantina, ca. 14 km SW of Diamantina on road to Gouveia, 1300 - 1360 m, 5 Feb 1972 (fr), Anderson et al. 35485 [C, F, K, NY, SP, US]; ca. 16 km SW of Diamantina, 1370 m, 19 Jan 1969 (fr), Irwin et al. 22234 [C, F, NY, UB, US]; estrada para Conselheiro Mata, km 190, 18 Jul 1980 (fl, fem), Menezes et al. s.n. (CFCR 119) [W ex SPF]; Rio San Francisco, Curvello, 1837 (fl), Claussen s.n. [L, on same sheet together with Martius 902]; eastern slopes of Pico do Itambé, ca. 1310 m, 13 Feb 1972 (fr), Anderson et al. 35963 [BM, F, MO, NY, UB, US]; near Itambé, Aug 1840 (data from labels in BM and K), (fl, fem), Gardner 4994 [BM, CGE 2x, E, F, G 2x, G-DC, GH, K 2x, NY 2x, OXF, P 3x, SP, US, W 2x; collection heterogeneous: twigs on sheets in OXF, P (1x) and G-DC are different and obviously belong to another individual]; Rio Vermelho, Pedra Menina, Serra do Ambrósio, Espigão do Meio, 1 Aug 1985 (fl, her), Mello-Silva et al. s.n. (CFCR 7851) [W ex SPF]; same area but: Faz. Vargem do Anjo, 13 Oct 1984 (fl, her), Isejima et al. s.n. (CFCR 5425) [W ex SPF]; same area but: Platô Pedra Menina, 1460 m, 9 Sept 1986 (fl, fem), Cavalcanti et al. s.n. (CFCR 10238) [W, WU ex SPF]. - **Serra do Cipó:** Município de Jaboticatubas, km 126 ao longo da rodovia Lagoa Santa-Conceição do Mato Dentro, 8 Jul 1973 (fl), Giulietti 4217 [UEC]; same loc., 10 - 15 Dec 1973 (fr), Semir & Lima 4815 [UEC]; same loc., 3 Sept 1973 (fl), Semir et al. 4335 [UEC]; same area but at km 127, 19 Jul 1972 (fl), Semir & Sazima 27[6?]08 [UEC]; same area but at km 132, 21 Aug 1972 (fl, her), Joly & Semir 3132 [E, UEC]; same area but: Série Itacolomi, 15 Feb 1960 (fl, her), Magalhães s.n. [UB, US]; Município Santana do Riacho, km 127 ao longo da rodovia Belo Horizonte-Conceição do Mato Dentro, 14 Aug 1979 (fl, her), Semir et al. s.n. (CFSC 5589) [W ex SPF]; same area but: região do Congonhas, 22 Nov 1991 (fr), Pereira et al. 981 [BHCB]; same area but at km 135, bifurcação da Rodovia para Morro do Pilar, ca. 1350 m, 19°13'S, 43°30'W, 22 Jul 1987 (fl, her), Mello-Silva et al. s.n. (CFSC 10363) [W ex SPF]; at border of a small patch of wood ca. 0.4 km NE of the junction of the main roads from Conceição do Mato Dentro and Morro do Pilar, ca. 49 km ENE Baldim, 1300 - 1350 m, 19°13'S, 43°30'W, 20 Sept 1990 (fl, fem), Esteves et al. s.n. (CFCR 15472) [B, K, LZ, MO, NY, SPF, U, W]; summit of Serra do Cipó, km 112 - 128 on road from Hotel Chapeu do Sol, 1200 - 1300 m, 7 Aug 1960 (fl), Maguire et al. 49055 [CAS ex NY]; Faz. Cach. da Capivara, 11 Jul 1987 (fl, fem), Andrade & Horta 61 [BHCB]; Serra da Salitreira, 12 Jul 1987 (fl, fem), Andrade & Horta 62 [BHCB]; - without further geographical details: undated (fl), Sena 977 [OUPR]; Aug 1895 (fl buds), Sena s.n. in Herb. Schwacke [RB]. - **Area of Caeté:** Município Caeté, Serra da Pedra Redonda, 26 Nov 1942 (fl buds and fr), Barreto 2301 [UB]; Alegria [next Caraça, fide PERKINS 1907], 9 Jun 1884 (fl buds), Glaziou 15208 [C, K, P]; summit of Serra da Caraça, ca. 1750 - 1950 m, 26 Jan 1971 (fl, fem), Irwin et al. 29208 [F, GH, MO, NY, U, US]. - **Area of Ouro Preto:** Itabira do Campo (Pico), Jun 1910 (fl et fr), Baeta 1806 [EM]; Caxoeira [= "Cachoeira"] do Campo, Feb 1839 (fr), Martius 903 (= Claussen 98, geographical information and date taken from original label at BR), [BR, M, P 2x, W]; same loc., Feb 1839 (fr), Claussen 42 [G]; same loc., Aug 1839 (fl), without collectors name [but probably Claussen] sub no. 701.A [BR]; same loc., but: Puá, (fl, her), Casaretto 2869 [G-DC ex TO]; Serra de Ouro Preto, 22 Aug 1891 (fl, fem), Schwacke 7416 [B, destroyed; BHCB, only with a new label which is dated 1904; RB, number of collection on original label destroyed by insects]; same loc., 1936 (fl), Badini 1846 [OUPR]; same loc., 1937 (fl), Badini 1792 [OUPR]; same loc., 1968 (fl), Badini 20815 [OUPR]; Base do Morro do Cachorro, 26 May 1979 (fl), Badini 25067 [OUPR]; Ouro Preto, Morro de S. Sebastião, 1900 (fl, her), Damazio 250 [G, G-DC]; same loc., undated (fl), Damazio 1030 [EM]; Serra das Camarinhas, 1350 m, 24 Jun 1979 (fl buds), Mautone et al. 769 [RB]; Serra de Lavras Novas, about 20 km S of Ouro Preto, 26 Aug 1960 (fl), Maguire et al. 49296 [NY]; same area, 28 Aug 1938 (fl, fem), Badini 3294 ("3894") [RB]; Serra do Itacolomi, Aug 1824 (fl, her), Riedel 455 [LE, NY 2x]; same loc., 14 Aug 1972 (fl), Lisboa 3141 [EM]; Campo Itacolomy, Jul 1939 (fl),

Badini 24875 [OUPR]; 5 - 8 m tall vegetation (burned shortly before) along a road at the base of the Serra do Itacolomi, Fazenda Manso, 1500 - 1680 m, 17 Sept 1990 (fl, her), Esteves et al. s.n. (CFCR 15453) [B, K, LZ, MO, NY, SPF, U, W; all including wood samples]; same plant and date, Esteves 2287 [SPF, W]; Serra de Ouro Branco, 29 Jul 1988 (fl, her), Attala et al. 13588 [BHCB]; same loc. but ca. 1500 m, 20°29'S, 43°43'W, 24 Jul 198[?] (fl, her), Mello-Silva et al. s.n. (CFCR 11189) [W ex SPF]. - **locality missing or untraceable:** Gaudarela or Gandarela (?), 1570 m, 13 Jul 1972 (fl), Emygdio et al. 3265 [NY ex R]; 1838 (fl, fem), Claussen "30" [P 2x]; 1841 (fr), Claussen 12 [NY ex P]; 1841 (fr), Claussen 21 and 42 [NY ex P]; 1840 (fl), Claussen 305 [G]; 1838, 1839 and 1840 (fl), Claussen s.n. [BM (her), BR 2x, G 2x (fem + her), GH, K, S]; Herb. Martius "43" (most probably collected by Claussen) [BR]; (fl, her), Sellow s.n. [B ex Herb. Baschant, F fragment ex B]; illegible, (fl), Claussen 408 [W]; 1821 - 1824 (fl), Riedel s.n. [NY ex LE].

Atypical collections and variability of indumentum: Sometimes, different leaves on the same twig show variation in the size and distribution of the larger stellate hairs on abaxial leaf surfaces (e.g. Esteves et al. s.n. [CFCR 15472]). In other cases (e.g. Anderson et al. 35963, Gardner 4994 pro maxima parte), all leaves show an atypical indumentum: the branches of the larger hairs are nearly as short as those of the smaller hairs. The larger hairs of some other collections are denser, and the hair branches are very long (exactly as shown in fig. 3), so that there is a certain resemblance with *S. aureum*. But, in these latter cases, these hair branches do not completely cover the abaxial leaf surface, and the layer of smaller, stellate hairs can easily be made out.

The leaf shape of Irwin et al. 29208 resembles *S. maninul*, although the margins are strongly revolute abaxially. The indumentum on abaxial leaf surfaces is, however, very similar to that of *S. pedicellatum*. This collection can only tentatively be determined and may represent a hybrid, although the southernmost known locality of *S. pedicellatum* is situated ca. 140 km (air distance) NNW in the Serra do Cipó (Cordeiro et al. s.n. [CFSC 8152]). Esteves et al. s.n. [CFCR 15453] and Esteves 2287 may represent a hybrid with *S. aureum*, as lowermost leaves are fairly large and resemble those of *S. aureum*. However, the shape and size of uppermost leaves, and especially those on fertile shoots, are more similar to *S. maninul*. The leaves subtending the inflorescences are smaller than those of *S. aureum* and also resemble those in *S. maninul*. The indumentum on abaxial leaf surfaces is similar to that of *S. aureum*, but the larger stellate hairs (branches up to 1 mm long) are more scattered: the smaller stellate hairs (branches up to 0.2 mm long) that cover the leaf surfaces are, therefore, well visible. The leaves on reiterating (resprouting) shoots are missing the characteristic layer of small hairs, and show only the larger and much more scattered, stellate ones. The inflorescences of the collections Martius 902 [LE] and Damazio 250 [G-DC] are branched. The samples of Anderson et al. 35485 show infructescences up to 14 cm long that are composed of 2 - 4 racemes, often subtended by leaves up to 3 cm long.

3. *Styrax pedicellatum* (PERKINS) B.WALLN., comb.n.; (fig. 11)

≡ *P. pedicellata* PERKINS, Pfl.reich IV.241: 17 (1907), var. *salicifolia* PERKINS, Pfl.reich IV.241: 17 (1907).

Type: Diamantina au Perpetua, 11 Apr 1892 (fl, her), Glaziou 19614 [lectotype here designated: F = fragment of destroyed holotype of var. *salicifolia* PERKINS at B (photo W 1196); isolectotypes (= isotypes of var. *salicifolia*): BM ex P (with very small leaves), C 2x, G, K, LE, NY, P 2x (photo W 1203)]. Perkins herself did not select a typical variety, thus this lectotypification is necessary. All preserved syntypes are not annotated by her.

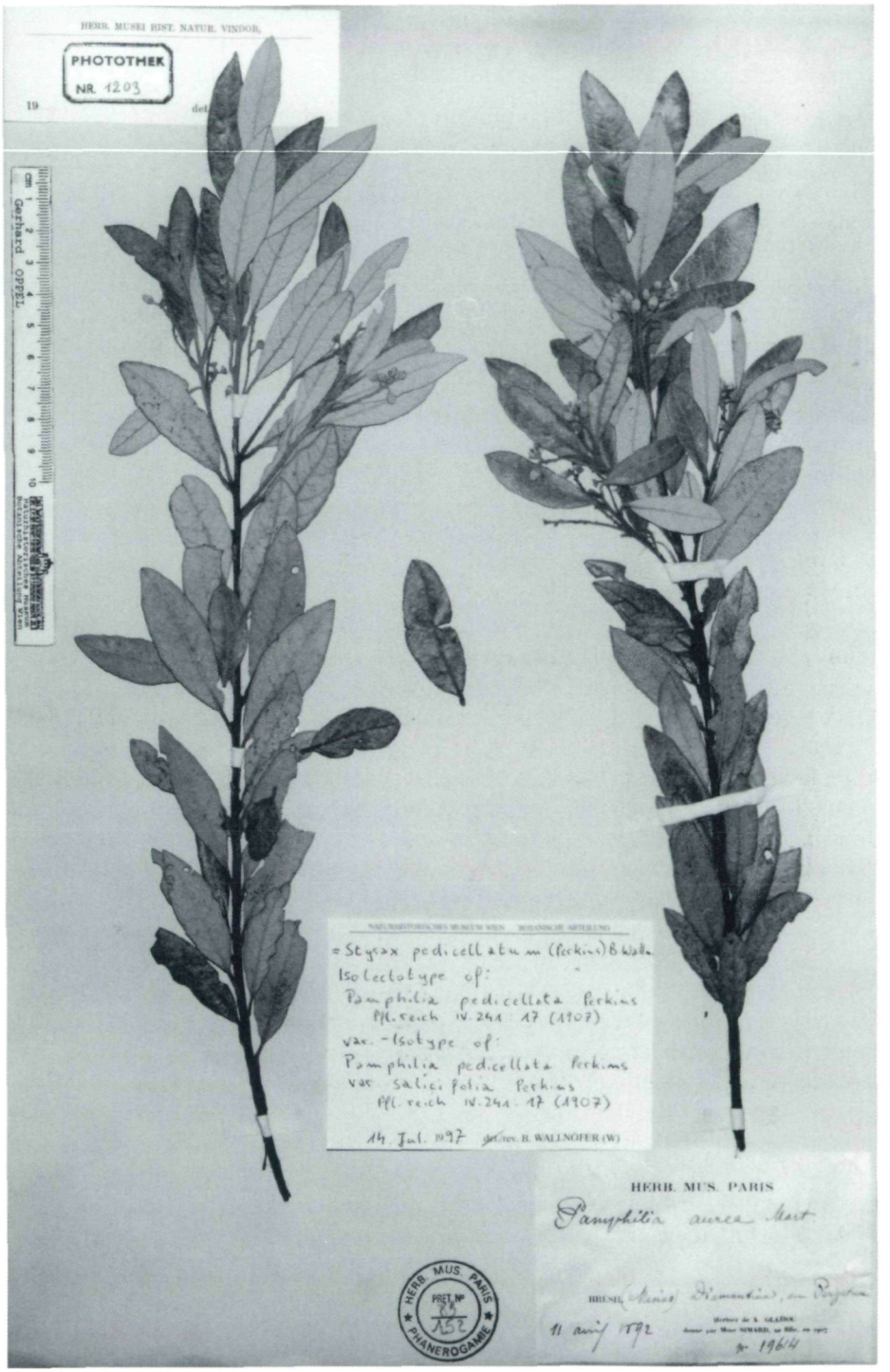

Fig. 11: *Styrax pedicellatum* (PERKINS) B.WALLN. (isolectotype)

= *P. pedicellata* var. *ovalis* PERKINS, Pfl.reich IV.241: 17 (1907).
Type: Près de Diamantina, 6 Apr 1892 (fr), Glaziou 19616 [holotype: B, destroyed; lectotype here designated: P (photo W 1199); isotypes: C, K, P].

= *P. pedicellata* var. *intermedia* PERKINS, Pfl.reich IV.241: 17 (1907).
Type: Diamantina, 9 Apr 1892 (fl, fem), Glaziou 19615 [holotype: B, destroyed; lectotype here designated: P (photo W 1198); isotypes: C, K].

= *P. pedicellata* var. *microphylla* PERKINS, Pfl.reich IV.241: 17 (1907).
Type: Minas Gerais, Serra do Cipó, Apr 1892 (fl, fem), Schwacke 8298 [holotype: B, destroyed; lectotype here designated: BHCB (photo W 1200), as *S. parvifolium* POHL, only a new label present, indicating 1904 as date of collection].

Shrub or tree up to 5 (- 7) m; xylopodium woody (fig. 2; for more details see chapter on `Growth form and habit´); diameter of stems near base up to 8 (- 12) cm; bark greyish-brown; twigs subterete, densely stellate-tomentose, light green to greyish or brown in vivo, grey-green in sicco, light brown or brown, soon becoming glabrous and often black with age, the bark of which mostly with small, slightly curved fissures; buds quite small, light brown in vivo and in sicco, densely stellate-tomentose; petioles 3 - 8 x 1.5 - 2 mm, with same indumentum as buds; very young **leaves** on both surfaces with a dense, homogeneous, light green to greyish indumentum of stellate hairs; indumentum of slightly older leaves green or sometimes light brown in vivo, light grey-green to brown in sicco, and less dense adaxially, abaxially whitish-grey, slightly greenish tinged as well in vivo as in sicco; mature leaves adaxially nearly glabrous except along veins, dark green in vivo, slightly shiny in sicco; abaxially covered with a dense, homogeneous and persistent layer (fig. 4) of stellate hairs that are greyish-light brown (slightly greenish tinged) in vivo, and whitish-grey to slightly greenish, or sometimes ferrugineous in sicco; branches of stellate hairs ca. 0.16 - 0.23 (in Harley & al. 26651 up to 0.58) mm long; lamina coriaceous, broadly lanceolate to ovate, rarely obovate or oblong (fig. 8k - p), broadest mostly near middle, (2.3 -) 3.5 - 5 (- 9) x (0.9 -) 1.5 - 2.5 (- 4.2) cm; lamina on reiterating (resprouting) shoots up to 12.5 x 4.6 cm; length to width ratio: (1.6 : 1 -) 2 - 3 : 1 (- 4.5 : 1); leaf margins entire, flat or sometimes slightly revolute; leaf bases cuneate or slightly rounded; apices of early leaves mostly obtuse or sometimes emarginate, those of late leaves acute to acuminate; secondary veins 6 - 12 per side, curved, or sometimes straight, flat or only slightly impressed adaxially, prominent abaxially; domatia in axils of secondary veins mostly present and conspicuous on abaxial surfaces of older leaves; **inflorescences** and infructescences (except petals, interior of flowers, and fruits) densely stellate-tomentose, light green to greyish or brown in vivo, whitish-grey to slightly greenish or sometimes ferrugineous in sicco, 2.5 - 6 cm long, 0.75 - 1 times as long as subtending leaves (including petiole), ca. 15-flowered; flower bracts linear, 1 - 3 mm long; pedicels (1 -) 2.5 - 5 mm; flowers with an intense, sweet fragrance (personal observ.); **hermaphroditic flowers** 7 mm long (excluding pedicels); calyx 2.5 mm long, cup-shaped, ferrugineous; calyx teeth ca. 0.3 mm long; petals white or whitish, 6 - 6.2 x 2 mm, the proximal parts connate for 2 mm; stamens 5 mm long, the proximal parts connate for 2 mm; filaments greenish-white (Anderson et al. 35514) or white in vivo (personal observ.); distal, free part of filaments ca. 1.3 mm wide; anthers slightly greenish-yellow, yellow or dark yellow in vivo (personal observ.: yellow-green anthers with light brown slits after anthesis; dark yellow anthers with dull whitish thecae [the latter belong

probably to staminodia - while in the field I was not yet aware of the occurrence of gynodioecy]); connectives 1.5 mm wide, exceeding thecae laterally by 0.5 mm; thecae 2 mm long; style 3.8 mm long, narrowly cylindrical, glabrous except at base, green in vivo; ovary subglobose, height/width: 1 x 1.2 - 1.5 mm, densely stellate-tomentose, green in vivo; (for abnormal number of ovules see first section of chapter `Data supporting the inclusion of *Pamphilia* into *Styrax*´); **female flowers** 4.8 mm, calyx 2.5 mm, calyx teeth ca. 0.5 mm long; petals 4.5 x ca. 1.5 mm, the proximal parts connate for 2 mm; staminodia yellow (Irwin et al. 28560), 3 mm long, the proximal parts connate for ca. 1.8 mm; distal, free part of filaments ca. 0.8 mm wide; connectives 1 mm wide, exceeding aborted thecae laterally by 0.3 mm; aborted thecae 1.7 mm long; style 2 mm long; immature **fruits** light green, mature ones grey to greenish in vivo, light greyish-green in sicco, smooth but slightly scaly, subglobose, ca. 6 mm in diameter in sicco; inner side of exocarp reddish-brown, violet-tinged at maturity; mesocarp thin, juicy, whitish-grey, with an acid and resinous taste; seeds 5 - 5.5 x 4 mm; endosperm whitish-grey, oily, not very agreeably tasting like nuts, (personal observ.).

Illustrations: twig, flower, stamens, ovary (PERKINS 1907, 1928).

Vernacular name: Bastuzinho do campo (Cordeiro et al. s.n. [CFSC 8152]).

Distribution (fig. 7A), habitat, and ecology: This Brazilian species occurs in the Serra do Espinhaço in Minas Gerais, between Montes Claros, Cristália, Diamantina, and the northern part of the Serra do Cipó. An apparently isolated population has been found in Bahia (Pico das Almas; see STANNARD 1995: 607). The species grows in campo rupestre-vegetation on rocky slopes, on summits of ridges and hills, between grassy or shrubby vegetation, at 1150 - 1500 m altitude. The fruits are eaten by birds, which at first consume the mesocarp and then open the hard part of the testa, peal off the membranous part of it and ingest the seeds (both layers of testa were found on the ground below shrubs!).

Specimens examined: **Brazil, Bahia:** Município Rio de Contas, Pico das Almas, Vertente leste, campo do queiroz ao lado leste, 13°32'S, 41°57'W, 1500 m, 28 Nov 1988 (fl, fem), Harley et al. 26651 [F, K, NY, W].- **Minas Gerais: Município de Cristália:** Morro do Chapéu, ca. 1200 m, 6 Jan 1986 (fl buds), Mello-Silva et al. s.n. (CFCR 8900) [W ex SPF]. - **Itacambira:** 9 km de Itacambira, na estrada para Montes Claros, 1200 m, 29 Nov 1984 (fl, her; fr), Oliveira et al. s.n. (CFCR 6574) [K, MO, W ex SPF]. - **Area of Diamantina:** road to Campo Sampaio ca. 7 km N São João da Chapada, 1150 m, 29 Mar 1970 (fl, fem), Irwin et al. 28560 [F, NY, SP, UB, US]; estrada para São João da Chapada, perto de Sopa, 23 Nov 1985 (fr), Cavalcanti et al. s.n. (CFCR 8635) [NY ex SPF]; estrada Diamantina-Mendanha, km 585, 6 Jun 1985 (young fr), Semir et al. 17546 [UEC, W]; estrada Diamantina-Curvelo a 8 km de Diamantina, 30 Oct 1981 (fr), Giulietti et al. s.n. (CFCR 2294) [W ex SPF]; estrada Diamantina-Gouveia, 10 km de Diamantina, Planalto de Guinda, 18 Apr 1987 (fl, fem), Zappi et al. s.n. (CFCR 10639) [K, W ex SPF]; estrada Diamantina a Corinto até 20 km, 1 Dec 1976 (fl), Shepherd et al. 3945 [NY ex UEC]; estrada para Conselheiro Mata km 189, 2 Aug 1985 (fr), Mello-Silva et al. s.n. (CFCR 7909) [W, WU ex SPF]; same area but: a 2 km do asfalto, 18°16'S, 43°43'W, 11 Apr 1982 (fr), Furlan et al. s.n. (CFCR 3321) [W ex SPF]; same area but: 20 - 26 km WSW Diamantina, camino a Conselheiro Mata, MG 220, 1270 - 1300 m, ca. 18°17'S, 43°49'W, 18 May 1990 (fr), Arbo et al. 4394 [F ex CTES and SPF]; northern slope of a hill south of the kilometre 185 on the road Diamantina-Conselheiro Mata, 15.5 km SW - WSW of the centre of Diamantina, ca. 1360 m, 18°18'S, 43°44'W, 24 Sept 1990 (fl, fem; fr), Esteves et al. s.n. (CFCR 15503) [BM, C, H, LZ, MO, NY, P, SPF, W, US, Z]; rocky place east of the main road and west of the hill "Vaz", ca. 15 km SSW Diamantina, silicate, 1390 m, 18°21'S, 43°41'W, 23 Sept 1990 (fr), Esteves et al. s.n. (CFCR 15502) [AAU, B, CAS, F, G, K, LZ, MO, NY, S, SPF, U, W; all including wood samples]; Município Diamantina, BR 269, km 10, 24 Feb 1975 (fl, her), Hatschbach et al. 36466 [MO ex MBM]; Município de Datas, ca. 15 km S of Diamantina, 1250 m, 5 Feb 1972 (fl, her), Anderson et al. 35514 [F, GH, NY, U, US]; Município Gouveia, Barro Preto, 20 Mar 1987 (fl, her), Hatschbach et al. 51147 [MO ex

MBM]; same area but: estrada Curvelo-Diamantina km 66, Serra do Barro Preto, estr. p/a antena de televisão, 18°36'S, 43°54'W, 9 Apr 1982 (fl, her), Furlan et al. s.n. (CFCR 3229) [F, W ex SPF]; on road to Gouveia ca. 26 km SW of Diamantina, 1300 m, 22 Jan 1969 (fl, her), Irwin et al. 22409 [C, F, K, NY, SP, UB, US]; road between Diamantina and Gouveia, 12 Aug 1960 (fr), Maguire et al. 49176 [NY 2x]; estrada Diamantina-Gouveia, a 73 km em direção a Sete Lagoas, 4 Dec 1981 (fr), Hensold et al. s.n. (CFCR 2709) [W ex SPF]; ca. 18 km N of Sêrro on Road (MG 2) to Diamantina, 1200 m, 27 Feb 1968 (fl, her), Irwin et al. 20974 [C, F, NY, UB, US]; Serra do Rio Grande, 1260 m, 7 May 1931 (fr), Mexia 5778 [A, BM, F, G, GH, K, MO, NA, NY, P 2x, S, U, US]; - Diamantina, 5 Jun 1955 (fr), Pereira 1689 [RB 2x]; 14 Apr 1892 (fl), Schwacke 8297 [RB]. - **Serra do Cipó**: Município Congonhas do Norte, Serra da Mangabeira, prox. à margem direita do rio Preto, 18°50'S, 43°49'W, 23 Apr 1982 (fl, her), Furlan et al. s.n. (CFSC 8460) [W ex SPF]; same area but: retiro do Barbado, morro a esquerda do rio Preto, 18°52'S, 43°46'W, 22 Apr 1982 (fl, fem), Amaral et al. s.n. (CFSC 8413) [W ex SPF]; Santana do Pirapama, Fazenda Inhame, Serra Mineira, 18°55'S, 43°54'W [longitude should be 46'], 23 Mar 1982 (fl, her; fr), Cordeiro et al. s.n. (CFSC 8152) [W ex SPF].

4. *Styrax pefrit* B.WALLN., sp.n.; (fig. 12)

Type: Colombia, Dept. Magdalena, flanco NE de la Sierra Nevada, cima del Cerro de San Lorenzo, 17 Apr 1959 (fl), Romero-Castañeda 7777 [holotype: F (photo W 1188); isotypes: COL n.v., MO, NY]; "arbusto de 4 m; envés foliar amarilento".

Diagnosis: Differt a *Styrace maninul* foliis majoribus, (4 -) 7 - 10 (- 13) cm longis, (2.4 -) 4.5 - 6 (- 7.7) cm latis; inflorescentiis 0.8 - 2 (- 2.5) cm tantum longis, floribus 5 - 7; habitat in silvis humidis montanis Columbiae septentrionalis.

Treelet ("arbusto") to 4 m or tree (height not reported on Gentry collections); trunk dbh up to 36 - 44 cm; bark deeply "ridged", that of twigs grey, splitting into irregular pieces and detaching easily; twigs subterete, densely stellate-tomentose, grey, greyish-brown or brown, later on glabrescent; buds, both surfaces of very young leaves and petioles with similar indumentum as that on young twigs; petioles 6 - 13 x 2 - 3 mm, canaliculate on adaxial side; mature **leaves** glabrescent adaxially, but mostly with some stellate hairs along veins, dull and quite dark in sicco; indumentum abaxially dense and persistent, composed of many-branched, stellate hairs of two sizes: light greyish-green to slightly brownish hairs with branches 0.2 - 0.3 mm long, forming a dense, homogeneous layer, and ferrugineous hairs with branches up to ca. 0.75 mm long, scattered on lamina, but more dense along veins (similar to fig. 5); lamina coriaceous, broadly lanceolate (fig. 8q - r), broadest near middle, (4 -) 7 - 10 (- 13) x (2.4 -) 4.5 - 6 (- 7.7) cm, length to width ratio: 1.6 : 1 - 2.3 : 1; leaf margins flat, rarely revolute abaxially, entire or shallowly and irregularly crenulate, with some small, remote, mucro-like teeth distally; leaf bases cuneate; leaf apices obtuse to short acute; secondary veins 6 - 8 per side, straight, slightly curved distally, slightly impressed adaxially, prominent abaxially; highest order veins slightly prominent on both surfaces; intercostal areas slightly depressed adaxially; domatia in axils of secondary veins always absent abaxially; **inflorescences** (except petals, and interior of flowers) densely stellate-tomentose, greyish, greyish-brown or ferrugineous, 0.8 - 2 (- 2.5) cm long, 0.19 - 0.23 times as long as the subtending leaves (including petiole), ca. 5 - 7-flowered; bracts 2 mm long and ca. 1.5 mm wide at base; pedicels 3 mm long; hermaphroditic flowers not available; **female flowers** at anthesis (only present on Romero-Castañeda 7189) ca. 9 mm long (excluding pedicels); calyx 3 - 3.5 x 3 mm, cup-shaped; calyx teeth (4 -) 5, mucro-like, ca. 0.25 mm long; petals (4 -) 5 per flower, 7 - 7.5 x 1.8 - 2.5 mm, the proximal parts connate for 3 mm, green (Romero-Castañeda 7189) or greenish white (Gentry & Cuadros 64667); stamens (4 -) 5 per flower, 6.5 mm long, the proximal

Fig. 12: *Styrax pefrit* B.WALLN. (holotype)

parts connate for 3 - 3.5 mm and green (Romero-Castañeda 7189); anthers ca. 3 mm long; connectives ca. 1.4 mm wide, exceeding thecae laterally by ca. 0.5 - 0.6 mm; thecae ca. 2.5 x ca. 0.2 mm; style 1.5 - 2 x ca. 0.2 mm, narrowly cylindrical, glabrous; ovary subglobose, 1.5 - 2 mm high and wide, densely stellate-tomentose, gradually narrowed into the style; fruits not available.

Because of the scarce material available for study, only one flower at anthesis and two large buds were dissected. The two buds (Gentry & Cuadros 64667) were 5-merous, showing an irregular androecium. One bud had five shrivelled staminodia, the anthers of which were only ca. 2.5 mm long, and connate laterally. The enclosed style was reaching to 1 mm below apex of the staminodia and strongly adhering or sticking to them. The other bud showed three staminodia of the same shape and behaviour as those in the first bud; the two other stamens were larger, their anthers were 3 mm long and laterally fused in the lower half only. The thecae were filled with a moderate amount of pollen. This mixture of fertile and sterile anthers in one flower seems to be an anomalous exception. The flower at anthesis (Romero-Castañeda 7189) was 4-merous, with four staminodia (thecae void of pollen) the anthers of which were connate laterally in pairs. The entirely free style and stigma reached only to the base of anthers. This species is probably also gynodioecious, but more flowers are needed to elucidate the conditions of sexuality and to exclude any possibility of apomixis.

Epithet: The specimens here cited have been handed over to me for evaluation by Peter Fritsch (CAS). The species is therefore gratefully dedicated to him. The epithet is a compound formed of the two parts of his name.

Distribution (fig. 7A) and habitat: This species has been collected only in cloud forests of the Sierra Nevada de Santa Marta (Dept. Magdalena, Colombia) at 2580 - 2620 m altitude.

Paratypes: Colombia, Dept. Magdalena, Sierra Nevada de Santa Marta, Cerro Kennedy, 11°5'N, 74°1'W, 2620 m, 14 Jan 1989 (fl), Gentry & Cuadros 64667 [MO 2x]; "montane cloud forest; tree 36 cm dbh, single flower greenish white, mostly in bud, bark deeply ridged". - same loc., but: Cerro Kennedy near top of highest peak in N massif, 11°5'N, 74°1'W, 2580 - 2590 m, 14 Aug 1986 (st), Gentry & Cuadros 55574 [MO]; "tree 44 cm dbh". - same area but: Páramo a Cebolleta, 2400 - 3100 m, 31 Jan 1959 (fl), Romero-Castañeda 7189 [COL n.v., NY]; "arbusto de 4 m; corolla y tubo estaminal verdes".

Styrax L., sectio *Pamphilia* (MART. ex A.DC.) B.WALLN., series *Andinae* B.WALLN., ser.n.

Type: *Styrax omuk* B.WALLN.

Diagnosis: Differt a serie typica foliis adultis subtus glabris.

This series is characterized by the glabrous abaxial surfaces of mature leaves.

5. *Styrax omuk* B.WALLN., sp.n.; (fig. 13)

Type: Peru, Dept. Huanuco, Prov. Pachitea, Sira mountains, elfin forest along the crest of a peak (9°25'S, 74°43'W) of the main range near watershed at 2250 m, ca. 26 - 28 km ESE Puerto Inca, 30 Apr 1988 (fl, fem), (all samples were collected from the same individual!), Wallnöfer 19-30488 [holotype: W (photo W 1192); isotypes: G, K, LZ, NY, USM].

Fig. 13: *Styrax omuk* B.WALLN. (holotype)

Diagnosis: Differt a *Styrace vilcabambae* inflorescentiis 0.8 - 2 cm longis, plerumque petiolis aequilongis usque ad duplo longioribus, foliis eas gerentibus (petiolis inclusi) quadruplo brevioribus, floribus tantum 3 - 5; foliis obtusis, prope medium vel ad tertiam partem superiorem latissimis; nervis ultimi ordinis magis prominentibus; habitat in silvis humidis montanis Peruviae centralis.

Treelet 2 - 3 m high; trunk dbh ca. 5 cm (but a "tree of 20 m, dbh 30 cm" according to Smith & Pretel 7978); twigs subterete, carinate below leaf insertions, densely stellate-tomentose and ferrugineous, later glabrescent, with a greyish-brown to blackish bark; terminal buds quite small, covered with a similar indumentum; petioles 6 - 8 x 1.2 mm, densely stellate-tomentose and ferrugineous; young **leaves** ferrugineous, on both surfaces sparsely (sometimes more densely) and minutely, stellate-tomentose, soon glabrescent; mature leaves glabrous on both surfaces, except along primary and secondary veins (these densely covered adaxially with minute, ferrugineous, stellate hairs, but only scarcely hairy abaxially); lamina chartaceous, broadly lanceolate to obovate (fig. 8s - u), broadest at 1/2 - 2/3 of length of lamina, (1.9 -) 4 - 7 (- 7.8) x (1.9 -) 2.5 - 3.3 (- 3.7) cm; length to width ratio: 1.2 : 1 - 2.7 : 1; leaf margins entire, flat; leaf bases cuneate; leaf apices abruptly acute or sometimes obtuse; secondary veins 6 - 8 per side, straight, slightly impressed adaxially, prominent abaxially; reticulum of smallest veins (on dry leaves) markedly regular and conspicuous, prominent on both surfaces; intercostal areas depressed on both surfaces; domatia in axils of secondary veins present and conspicuous abaxially; **inflorescences** (except petals, and interior of flowers) densely stellate-tomentose, greenish-brown in vivo, ferrugineous in sicco, 0.8 - 2 cm long, mostly 1 - 2 times as long as petioles, ca. 0.25 times as long as subtending leaves (including petiole), 3 - 5 (- 7)-flowered; flower bracts 2 - 2.5 mm long, mostly shed at anthesis; pedicels 1 - 2 mm long; hermaphroditic flowers not available; **female flowers** 5 - 6 mm long (excluding pedicels); calyx 2 x 1.5 mm, cup-shaped, ferrugineous in vivo; calyx teeth ca. 0.2 - 0.3 mm long; petals 4.5 - 5.5 x 1 - 1.5 mm, the proximal parts connate for ca. 1.5 mm, beige (Wallnöfer 19-30488) or white (Smith & Pretel 7978) in vivo; staminodia 3.8 - 4.5 mm long, white in vivo, the proximal parts connate for 1.5 - 2.5 mm; free part of filaments 0.2 - 0.8 x ca. 0.8 - 1 mm; connectives 0.8 - 1 mm wide, exceeding aborted thecae laterally by ca. 0.2 - 0.4 mm; aborted thecae ca. 1.8 mm long; style 1.8 - 2.3 mm long, at base 0.5 mm wide, gradually narrowed towards apex, the proximal half densely stellate-tomentose, the distal part glabrous, greenish in vivo; ovary subglobose, height/width: 1 x 1 - 1.4 mm, densely stellate-tomentose, greenish in vivo; fruits not available.

Illustrations: twig and flowers from type collection (MORAWETZ 1993: 404, Abb. 187). This illustration is not accurately in all details, and was published without my consent: the petals are in fact valvate and not turbinate, the calyces are symmetrical, and the venation on abaxial leaf surfaces is more finely reticulate.

Epithet: The name has been coined arbitrarily (see GREUTER & al 1994: Art. 23.2).

Distribution (fig. 7A) and habitat: This species is known only from two collections gathered in the central part of the Peruvian Andes, were it occurs in "high montane primary forests on ridges" and in elfin forests at 2250 - 2500 m altitude (for more information concerning the vegetation at the type locality in the Sira mountains, see TERBORGH & WESKE [1975] and RAINER [1995]).

Paratypes: Peru, Dept. Pasco, Prov Oxapampa, Rio San Alberto Valley, E of Oxapampa, W slopes of Cordillera Yanachaga, 10°34'S, 75°22'W, 2500 m, 24 Jul 1984 (fl, fem), Smith & Pretel 7978 [G 3x, W, all ex MO].

6. *Styrax vilcabambae* (D.R.SIMPSON) B.WALLN., comb.n.; (fig. 14)

≡ *Pamphilia vilcabambae* D.R.SIMPSON, Phytologia 30: 315 - 316 (1975).

Type: Peru, Dept. Cuzco, Prov. La Convencion, Cordillera Vilcabamba, 12°38'S, 73°34'W, ca. 2400 - 2655 m, 6 Jul 1968 (fl, her), Dudley 10808 [holotype: F (photo W 1191); isotypes: MO, NA, USM n.v.].

Small trees or shrubs 2 - 7 m high; trunk dbh 5 - 10 cm, either one- or multi-trunked, "very stiff and strict"; crown rounded, 1 - 2 m across, with "greatly congested" leaves; bark of stems lustrous and rufous-coppery in vivo; twigs subterete, carinate below leaf insertions, densely stellate-tomentose and ferrugineous, later glabrescent, with a grey-brown to blackish bark; terminal buds quite small, covered with a similar indumentum; petioles 4 - 10 x 1.2 - 1.5 mm, densely stellate-tomentose and ferrugineous; young **leaves** ferrugineous, sparsely and minutely stellate-tomentose on both surfaces; mature leaves glabrous on both surfaces (except a few minute, ferrugineous, stellate hairs, mostly along primary and secondary veins), dull in sicco, in vivo "glossy green" or dark green adaxially, abaxially yellowish-green or brownish-coppery in vivo; lamina chartaceous, broadly lanceolate to ovate (fig. 8v - y), broadest at 1/3 - 1/2 of length of lamina, (1.4 -) 4 - 6.5 (- 7.6) x (0.7 -) 1.5 - 3 (- 3.8) cm; length to width ratio: 2 : 1 - 3.3 : 1; leaf margins entire, flat in sicco, "curled" in vivo; leaf bases cuneate; leaf apices markedly acute, rarely short-acute; secondary veins 6 - 8 per side, straight, slightly impressed adaxially, prominent abaxially; reticulum of the smallest veins (on dry leaves) irregular and not clearly visible, moderately prominent on both surfaces; intercostal areas inconspicuous and even; domatia in axils of secondary veins present and conspicuous abaxially (stellate hairs with long branches); **inflorescences** (except petals, and interior of flowers) densely stellate-tomentose, "lustrous and rufous-coppery" in vivo, ferrugineous in sicco, (2 -) 2.5 - 5.5 cm long, mostly 4 - 7.5 times as long as the petioles, 0.5 - 0.7 (- 1) times as long as the subtending leaves (including petiole), mostly (2 -) 6 - 8 (- 10)-flowered; pedicels 2 - 4 mm long; flower bracts 2 mm long, usually shed at anthesis; **hermaphroditic flowers** 8 - 8.5 mm long (excluding pedicels); calyx 2.5 x ca. 2.5 mm, cup-shaped; calyx teeth ca. 0.2 mm long; petals ca. 8 x 1.5 mm, the proximal parts connate for 2 - 2.5 mm, deep yellow in bud, greenish-yellow, yellowish or yellowish-white in vivo at anthesis; stamens 6.5 mm long, the proximal parts of filaments connate for 3 mm (the proximal 2 mm adnate also to the corolla tube); free part of filaments 0.8 mm long and 1 mm wide, with some scattered, long-branched, stellate hairs; connectives 1 mm wide, exceeding thecae laterally by 0.2 mm; thecae 3 mm long; style 3 mm long, 0.5 mm wide at base, gradually narrowed towards apex, densely covered with stellate hairs on lower 2/3 of its length; ovary subglobose, height/width: 1 x ca. 1.5 mm, densely covered with stellate hairs; **female flowers** ca. 6.5 mm, calyx 2 mm, calyx teeth ca. 0.3 mm long; petals ca. 6 x 1.5 mm, the proximal parts connate for 1.8 mm; staminodia 5 mm long, the proximal parts connate for ca. 3 mm; distal, free part of filaments ca. 0.8 mm long; connectives 0.8 - 1 mm wide, exceeding the aborted thecae by 0.1 - 0.3 mm laterally; aborted thecae 1.2 mm long; style ca. 2.6 mm long, ca. 0.7 mm wide at base; **fruits** ellipsoid, brown or yellow to golden in vivo, brownish in sicco, ca. 10 x 7 mm, covered with a dense layer of scale-like emergences with an irregular, erose margin (derived from stellate hairs with rudimentary branches), (only one slightly squashed fruit available in the capsule of Dudley 10802 at NA).

Fig. 14: *Styrax vilcabambae* (D.R.SIMPSON) B.WALLN. (holotype)

Distribution (fig. 7A) and habitat: This species is only known from four collections made in the Serra de Vilcabamba in the southern Peruvian Andes. According to the labels, it occurs "in more or less open & exposed, depauperate cloud forest, becoming elfin forest (monte chico) ... on ridges (cejas) & rounded cumbres & on the slopes (steep) ..." and "in very dense, dark, high cloud forest ..." between 2300 - 2750 m altitude (for more information concerning the vegetation of this mountain range, see TERBORGH [1971]).

Specimens examined: Peru, Dept. Cuzco, Prov. La Convencion, Cordillera Vilcabamba, 12°37'S, 73°32'W, ca. 2600 - 2750 m, 5 Jul 1968 (fl, fem), Dudley 10802 [F, MO, NA, USM n.v.]; same loc., 5 Jul 1968 (st), Dudley 10802C [NA, USM n.v.]; same area but at 12°37'S, 73°33'W, ca. 2660 m, 4 Jul 1968 (fl, her), Dudley 10749 [NA, USM n.v.].

List of exsiccatae

Number in brackets: 1 = *S. aureum*; 2 = *S. maninul*; 3 = *S. pedicellatum*; 4 = *S. pefrit*; 5 = *S. omuk*; 6 = *S. vilcabambae*.

Amaral et al. s.n. [CFSC 8413] (3);
Anderson et al. 35485 (2),
35514 (3),
35963 (2);
Andrade & Horta 61 (2),
62 (2);
Arbo et al. 4394 (3);
Attala et al. 13588 (2);
Badini 1792 (2),
1846 (2),
3294 ("3894") (2),
20815 (2),
24875 (2),
25067 (2);
Baeta 1806 (2);
Barreto 2301 (2),
10847 (1);
Casaretto 2869 (2);
Cavalcanti et al. s.n. [CFCR 8635] (3),
s.n. [CFCR 10238] (2);
Claussen 12 (2),
21 (2),
"30" (2),
42 (2),
98 (2),
135 (1),
135 n. 12 (1),
142 (1),
184 (2),
305 (2),
408 (2),
472 (1),
702.A (1),
s.n. (1, 2);
Cordeiro et al. s.n. [CFSC 8152] (3);
Damazio 250 (2),
1030 (2);
Dudley 10749 (6),
10802 (6),
10802C (6),
10808 (6);
Eegler 0102 (2);
Emygdio et al. 3265 (2);
Esteves 2287 (2);
Esteves et al. s.n. [CFCR 15453] (2),
s.n. [CFCR 15472] (2),
s.n. [CFCR 15502] (3),
s.n. [CFCR 15503] (3);
Furlan et al. s.n. [CFCR 3229] (3),
s.n. [CFCR 3321] (3),
s.n. [CFSC 8460] (3);
Gardner 4993 (1),
4994 (2);
Gentry & Cuadros 55574 (4),
64667 (4);
Giulietti 4217 (2);
Giulietti et al. s.n. [CFCR 2294] (3);
Glaziou 15208 (2),
17125 (1),
19614 (3),
19615 (3),
19616 (3);
Harley et al. 25258 (2),
26651 (3);
Hatschbach et al. 36466 (3),
51147 (3);
Hensold et al. s.n. [CFCR 2709] (3);
Irwin et al. 19633 (1),
20974 (3),
22234 (2),
22409 (3),
28560 (3),
28764 (1),
29208 (2),
30431 (1);

Isejima et al. s.n. [CFCR 5425] (2);
Joly & Semir 3132 (2);
Lisboa 3141 (2);
Magalhães 15581 (2),
s.n. (2);
Maguire et al. 49055 (2),
49176 (3),
49296 (2);
Martius 902 (2),
903 (2),
s.n. (1);
Mautone et al. 769 (2);
Mello-Silva et al. s.n. [CFCR 7851] (2),
s.n. [CFCR 7909] (3),
s.n. [CFCR 8900] (3),
s.n. [CFSC 10363] (2),
s.n. [CFCR 11189] (2);
Menezes et al. s.n. [CFCR 119] (2);
Mexia 5778 (3);
Oliveira s.n. (1);
Oliveira et al. s.n. [CFCR 6574] (3);
Pereira 1689 (3);
Pereira et al. 981 (2);
Renno 1741 (1);
Riedel 455 (2),
641 (1),
s.n. (2);
Romero-Castañeda 7189 (4),
7777 (4);
Roth 17475 (1);
Schwacke 7416 (2),
8297 (3),
8298 (3);
Sellow s.n. (2);
Semir & Lima 4815 (2);
Semir & Sazima 27[6?]08 (2);
Semir et al. 4335 (2),
17546 (3),
s.n. [CFSC 5589] (2);
Sena 977 (2),
s.n. (2);
Shepherd et al. 3945 (3);
Siqueira et al. 1903 (1);
Smith & Pretel 7978 (5);
Teixeira 22341 (1);
Vitor & Grandi 1964 (1);
Wallnöfer 1574 (*S. obassia*),
19-30488 (5);
Zappi et al. s.n. [CFCR 10639] (3).

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