
A REVISION OF THE GENUS
PLEUROTHYRIUM
(LAURACEAE)¹

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ABSTRACT

Pleurothyrium, a genus of Lauraceae mostly consisting of trees, ranges from Guatemala to Bolivia and possibly Southern Brazil. The genus is best represented in Peru, Ecuador, and Colombia and mostly occurs at low elevations. In this revision 39 species are included in *Pleurothyrium*, of which 19 are described as new. Taxonomic history, characters, and phylogenetic classification are discussed. Data on phenology, habitat preference, and altitudinal range are presented when available.

In the course of identifying neotropical Lauraceae accumulated in MO or received on loan from other institutions, I found several undescribed species of *Pleurothyrium*. Four of those were published in earlier papers (van der Werff, 1987, 1988), but because the number of novelties kept increasing, I decided that writing a revision of the genus was the best way to deal with the many new species. Notable among those are the collections by J. Cuatrecasas from Chocó and Valle, Colombia, which include three striking, undescribed species. Recent collections by Missouri Botanical Garden staff members have also added significantly to the number of species. In this paper 19 species of *Pleurothyrium* are described, which brings the number of accepted species to 39. Because so many undescribed species were collected recently, I anticipate that the number of *Pleurothyrium* species will continue to grow. Another indication of this future growth is that 12 species are known from the type collection only, and an additional seven are known from two collections. Only three species have been collected more than 20 times. The large number of undescribed species found during this study shows clearly that our knowledge of neotropical Lauraceae is still incomplete. It is not coincidence that the largest percentage of undescribed species comes from Ecuador, a country where an active tree collecting program has been in place during the past seven years. Seven of the 12 *Pleurothyrium* species known from Ecuador are new to science.

There is little information available about economic uses of *Pleurothyrium* species. In central Peru the wood is used as timber and is considered to be of reasonably good quality. The wood of several Colombian species is used for making boards or canoes. It is likely that the wood of other species is also used locally, but because most of these species are rare and several do not grow into tall trees, their use is economically not very important.

MATERIALS

This revision is based on about 300 collections, some with many duplicates, found in many herbaria. A general difficulty with a generic revision in the Lauraceae is that many specimens are not identified to genus and therefore will not be sent when a loan of material of a particular genus is requested. One can solve this problem by personally selecting loans or by having a knowledgeable friend do so. In this case, Jens Rohwer kindly annotated all *Pleurothyrium* specimens in F, NY, and US to genus for me. In addition to these collections, I received loans from B, BM, BR, C, E, INPA, K, L, LE, P, S, U, UC, and VEN. I also had the opportunity to study the specimens of COL, IAN, MG, RB, and SP and thank the curators of these herbaria for loans and assistance during my visits. Recent collections by Missouri Botanical Garden botanists (notably B. Hammel, Costa Rica and Panama; G. McPherson, Panama and Colombia; A. Gentry, Colombia and Peru; C. Dodson, Ecuador;

¹ This study would not have been possible without the collecting efforts of many collectors, especially J. Cuatrecasas and Missouri Botanical Garden staff members, as well as the often large loans I received from several herbaria. I gratefully acknowledge their contributions. J. Crisci's assistance with the cladistic analysis is gratefully acknowledged. I thank several botanists (C. Berg, G. McPherson, R. Moran) who tried out the key and suggested improvements. The illustrations, both older and new ones, were made by J. Myers. The project was supported by National Science Foundation grant BSR-8918096.

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D. Neill, Ecuador; C. Cerón, Ecuador; W. Palacios, Ecuador; R. Vásquez and J. Jaramillo, Peru) have contributed a great deal to this study.

TAXONOMIC HISTORY AND GENERIC RELATIONSHIPS

The genus *Pleurothyrium* was published by Nees in Lindley's *Natural System of Botany*, ed. 2, which appeared in July 1836 fide *Taxonomic Literature* 2, followed soon (October 1836) by a more detailed treatment in Nees's *Systema Laurinarum*. Initially, Nees included two species, *P. chrysophyllum* and *P. bifidum*, in his genus but added in his *Systema Laurinarum* *P. poeppigii* and *P. cuneifolium*. He described the genus as having six staminal glands and characterized it by the large glands and the lateral anther cells, which open back-to-back. Nees did not designate a type species. Bentham & Hooker (1880) expressed the opinion that *P. chrysophyllum* Nees fits the generic description best, and this species has been generally accepted as the lectotype species (Pax, 1889; Kostermans, 1952; Rohwer, 1986). In 1848, Nees described a fifth species of *Pleurothyrium*. Meissner (1864) added three species to *Pleurothyrium*, all of which are now placed in other genera. In his generic description, he mentioned the presence of a hypogynous disk forming a narrow ring on which stamens and glands are inserted. Meissner also stated that only six glands were present at the base of stamens of whorl III and that the staminodia do not possess glands at their base, this in contrast to Nees (1836a, b), who reported glands at the base of the staminodia. Baillon (1870) essentially accepted Meissner's circumscription of the genus; he stated that the disk was situated in the receptacle and that its apex was curved inward. The number of staminal glands remained six. Bentham & Hooker (1880) described *Pleurothyrium* as having a fleshy disk with six lobes alternating with six stamens, this in contrast to earlier authors, who described the disk as a narrow ring. Bentham & Hooker (1880) also mentioned the presence of glands at the base of the stamens of whorl III but did not describe how the glands are placed in relation to the disk. Actually, their description of the disk applies to the glands; the later confusion between disk and glands has its beginning here. Pax's description (1889) is brief and essentially the same as Bentham & Hooker's. Mez (1889) did not mention the presence of a disk in his description of *Pleurothyrium* but stated that all nine stamens had two glands at their base, which were almost always fused. In comparison to Nees's description, two

other differences are noteworthy: Mez did not mention staminodia in his generic description, but Nees included biglandular staminodia in his description; according to Mez, the outer six anthers have two introrse and two extrorse, rarely lateral dehiscing locelli, whereas Nees described the locelli as lateral. Mez was the last person to revise *Pleurothyrium*; he excluded the three species Meissner (1864) described, but added one species described by Meissner (1864) as a *Nectandra*. Mez recognized five species in the genus. In the 1930s, several species of *Pleurothyrium* were described (Ducke, 1930; Smith, 1935; Schmidt, 1928, 1933) without any change in generic circumscription. MacBride (1938) essentially accepted Mez's description of the genus. Lasser (1942) described two Venezuelan species of *Pleurothyrium*, but did not discuss the generic concept. Kostermans (1952, 1957) looked critically at the validity of *Pleurothyrium* as a genus. He found that *Pleurothyrium* only differed from *Ocotea* in the position of the anther cells and the presence of glands at the base of all stamens. In his opinion, these differences were not sufficient for the recognition of *Pleurothyrium* as a genus, and he proposed to treat it as a section (1952) or subgenus (1957) of *Ocotea*. In 1952, he formally transferred all *Pleurothyrium* species to *Ocotea*. Bernardi (1962) followed Kostermans and treated *Pleurothyrium* as a subgenus of *Ocotea*. His description, however, partly followed Meissner: he mentioned a disk in the form of a narrow ring with the stamens inserted on the ring, but differed from Meissner in crediting all stamens with glands at their bases. Hutchinson (1964) fell back on Bentham & Hooker's concept of *Pleurothyrium*, with fleshy disk, this with six teeth alternating with the stamens as well as glands at the base of the inner three stamens. He accepted five species, half the number Kostermans (1952) included. Allen (1966b) discussed the concept of *Pleurothyrium* in detail and concluded that it deserved generic status, characterized by the presence of glands at the base of all stamens and the position of the anther cells. It is worth noting that Kostermans (1952) did not accept that these characters warranted recognition of *Pleurothyrium* as a genus. Kubitzki (1981) expressed the opinion that *Pleurothyrium* is a heterogeneous genus and that its species actually belong to *Ocotea* and *Nectandra*. In contrast to this view, Rohwer & Kubitzki (1985) stated (based on a detailed analysis of *Ocotea* sens. lat.) that *Pleurothyrium* is a valid genus characterized by the lateral position of the locelli and the greatly enlarged glands. They pointed out that in *Pleurothyrium* only the inner three stamens (not all nine

TABLE 1. Distribution records of *Pleurothyrium* species.

Bolivia	<i>P. intermedium</i> , <i>P. poeppigii</i>
Brazil	<i>P. acuminatum</i> , <i>P. amapaense</i> , <i>P. amplifolium</i> , <i>P. cuneifolium</i> , <i>P. insigne</i> , <i>P. intermedium</i> , <i>P. nobile</i> , <i>P. panurense</i> , <i>P. parviflorum</i> , <i>P. poeppigii</i> , <i>P. prancei</i> , <i>P. undulatum</i> , <i>P. vasquezii</i>
Colombia	<i>P. bracteatum</i> , <i>P. crassitepalum</i> , <i>P. cuneifolium</i> , <i>P. glabritepalum</i> , <i>P. grandiflorum</i> , <i>P. marginale</i> , <i>P. poeppigii</i> , <i>P. synandrum</i> , <i>P. tomiwahlii</i> , <i>P. trianae</i>
Costa Rica	<i>P. golfodulcense</i> , <i>P. hexaglandulosum</i> , <i>P. palmanum</i> , <i>P. pauciflorum</i> , <i>P. trianae</i>
Ecuador	<i>P. cinereum</i> , <i>P. cuneifolium</i> , <i>P. giganthum</i> , <i>P. glabrifolium</i> , <i>P. insigne</i> , <i>P. obovatum</i> , <i>P. parviflorum</i> , <i>P. poeppigii</i> , <i>P. tomentellum</i> , <i>P. tomiwahlii</i> , <i>P. trianae</i> , <i>P. williamsii</i>
Guatemala	<i>P. westphalii</i>
Honduras	<i>P. trianae</i>
Nicaragua	<i>P. trianae</i>
Panama	<i>P. hexaglandulosum</i> , <i>P. palmanum</i> , <i>P. pilosum</i> , <i>P. racemosum</i>
Peru	<i>P. acuminatum</i> , <i>P. bifidum</i> , <i>P. brochidodromum</i> , <i>P. cinereum</i> , <i>P. cuneifolium</i> , <i>P. insigne</i> , <i>P. intermedium</i> , <i>P. maximum</i> , <i>P. nobile</i> , <i>P. panurense</i> , <i>P. parviflorum</i> , <i>P. poeppigii</i> , <i>P. vasquezii</i> , <i>P. williamsii</i> , <i>P. tomentellum</i> , <i>P. trianae</i>
Venezuela	<i>P. amapaense</i> , <i>P. costanense</i> , <i>P. steyermarkianum</i> , <i>P. trianae</i>

stamens) have glands at their base, thus accepting Nees's description and rejecting that of Mez and subsequent authors. Rohwer (1986) further discussed and illustrated this concept and accepted eight species groups in *Pleurothyrium*, based on a survey of the types of the published species. Van der Werff (1987, 1988) accepted the circumscription of *Pleurothyrium* given by Rohwer & Kubitzki (1985), as did Burger & van der Werff (1990); in these publications an additional five species are described. However, in recent British literature (Willis, 1973; Mabberley, 1987) only one species is attributed to *Pleurothyrium*; in all likelihood, these authors follow Bentham & Hooker (1880), who wrote that only one species matched Nees's description.

In this study I accept *Pleurothyrium* as a distinct genus, most closely related to *Ocotea* and *Nectandra*. It differs from these two genera in two easy to observe androecial characters. In *Pleurothyrium* the outer six stamens have at least two anther cells in a lateral position (and often all four are lateral), and the six staminal glands are strongly enlarged and always grow outward between the six outer stamens and separate these stamens. In many species the glands become confluent and form a large, pillowlike mass with the anthers embedded in the surface. Other characters that are uncommon or lacking in *Ocotea* and *Nectandra*, but frequently present in *Pleurothyrium*, are the position of the inflorescences in the axils of cataphylls (not or rarely in axils of normal leaves) and the presence of a marginal vein in the leaves. Whether *Ocotea* or *Nectandra* is the closest relative of *Pleurothyrium* is still an open question. This study has not pointed to a particular genus or species group as the closest relative.

Van der Werff (1991) published a key to the

New World genera of Lauraceae, including *Pleurothyrium*.

Although the greatly enlarged and fused glands are unique among neotropical Lauraceae, they also occur in the Asian-Australian genus *Endiandra*. Several Australian species are illustrated in Hyland (1989). The enlarged, fused glands are about the only character *Pleurothyrium* and *Endiandra* have in common. *Endiandra* has only three two-celled stamens and does not have a cupule subtending the fruit; it is closely related to *Beilschmeidia*. Thus, the character of the glands is considered to be an example of convergence and does not indicate a close relationship.

DISTRIBUTION AND ECOLOGY

Pleurothyrium species have been collected from Guatemala, the northernmost extension, to Bolivia and southern Brazil, the southernmost extension. It has been collected in all countries between these extremes with exception of El Salvador and the three Guianas. The genus is absent from the West Indies. Table 1 shows the species present in each country. The greatest concentration of species occurs in Peru, Brazil, Ecuador, and Colombia, while *Pleurothyrium* is represented by only a few species in the other countries. The Brazilian species are, with exception of *P. amplifolium*, Amazonian, and most occur in the upper part of the Amazon basin; only one or two species have been found downstream from Manaus. Most species are only known from lowland forests or the lower foothills of the Andes (below 1,000 m elevation). In Peru, *P. cuneifolium* and *P. poeppigii* occur at 1,800 m near Oxapampa, but these species are better represented in the lowlands. The Ecuadorian *P. obovatum* is only known from three collections at 1,200–1,800 m. In Venezuela, *P. costanense* has been collected

at 2,200 m, but is more common around 1,000 m; the poorly known *P. steyermarkianum* has been collected at 1,400 and 2,000 m.

Our knowledge about the habitat requirements of *Pleurothyrium* species is very poor. Older collections usually do not have habitat information other than "forest" and besides, many species are known from very few collections. For a reliable estimate of the habitat requirements, I would want at least ten collections with the same habitat information. This is only available for *P. parviflorum*, a species restricted to seasonally flooded forests in Peru, Brazil, and Ecuador. It is to be expected in the Amazonian forests of Colombia as well, but it has not yet been collected there. *Pleurothyrium panurense* is known from fewer collections, but all of these were made in flooded forest.

Most of the new or recently described species are from Colombia and Ecuador. For instance, six of the ten species from Colombia are new; for Ecuador these figures are seven out of twelve, but for Brazil it is two out of eleven species. Because of the Projeto Flora Amazonica, Amazonian Brazil has been reasonably well collected, probably better than Colombia, and it seems unlikely that many additional *Pleurothyrium* species will be collected in Brazil. On the other hand, Colombia has at least three additional, but incompletely known species. Taking this into consideration, I expect that the greatest diversity will be in Peru, Ecuador, and Colombia.

MORPHOLOGY AND TAXONOMIC CHARACTERS

At the beginning of this survey of the taxonomic characters of *Pleurothyrium* species, it should be emphasized that about half of the species are known from only one or two collections. This is not enough for a good understanding of the morphological variation within the species, and there are difficulties interpreting differences in degree of pubescence, leaf size, and color of pubescence. Therefore, I decided not to recognize taxa based solely on these characters, even though, for instance, the Peruvian collection of *P. insigne* and the Costa Rican collection of *P. hexaglandulosum* look different from the types. Additional collections of many species are needed for a better understanding and, when available, may well lead to changes in the classification here proposed.

Habit. *Pleurothyrium* species vary from small to tall trees. There is no information about different types of tree architecture represented in the genus, but it is likely that species with clustered leaves have a different growth type than species with evenly spaced leaves.

Habitat. As with habit, label information on habitat is poor. The great majority of the species are restricted to the wet lowlands (below 500 m). *Pleurothyrium cuneifolium* and *P. poeppigii* have been found from the lowlands up to 1,800 m, an unusually wide range of altitude. *Pleurothyrium costanense* is restricted to cloud forest in Venezuela, between 800 and 2,200 m. *Pleurothyrium trianae* occurs occasionally up to 1,200 m, but is most common at elevations between 300 and 600 m. *Pleurothyrium palmanum* is known from four collections in Costa Rica and Panama, between 1,000 and 1,600 m. Finally, there are three montane species known from only three or fewer collections: *P. bracteatum* at 1,000 m in Colombia, *P. obovatum* at 1,200–1,800 m in southern Ecuador, and *P. racemosum* at 900 m in Panama. More detailed habitat preferences are only known for *P. panurense* and *P. parviflorum*: both are restricted to flooded forests in the upper Amazon basin. In the vicinity of Iquitos, Peru, I collected *P. parviflorum* in flooded forests on sandy and clay soils, but never found it outside flooded forests.

Fistulose twigs. Four species, *Pleurothyrium cuneifolium*, *P. obovatum*, *P. parviflorum*, and *P. poeppigii*, have consistently fistulose twigs, while *P. trianae* has rarely fistulose twigs. This is a reliable and readily visible character mentioned by Nees (1836b) in his descriptions. Mez (1889), citing Poeppig (In ramulis revera fistulosis degunt formicarum agmina pessime pungentia), referred to the ants living in the hollow twigs. On several, but certainly not all, labels of these species, the presence of aggressive ants is mentioned; I found *P. parviflorum* sometimes inhabited by aggressive ants and sometimes by timid ones, although each tree was inhabited by one kind only. In Lauraceae fistulose twigs inhabited by ants are not restricted to *Pleurothyrium*, but also occur in *Ocotea javitensis* (HBK) Pitt., *O. dendrodaphne* Mez, the species related to *O. atirrensis* Mez & J. D. Smith, including *Aiouea vextrix* van der Werff, a *Licaria* species from Costa Rica, and an *Aniba* species from Iquitos, Peru. Most Lauraceae with hollow twigs occur in the lowlands, but *P. obovatum*, known only from 1,800 m, has clearly hollow stems with exit holes. An undescribed *Ocotea* species from northern Ecuador, collected at 2,400 m elevation, also had hollow twigs inhabited by ants, as did an undescribed *Cinnamomum* species from central Ecuador, collected at 2,200 m elevation. Both high-elevation species were inhabited by non-aggressive ants, which did not defend the twigs and scarcely left the hollow core when the twigs were broken.

In *Pleurothyrium cuneifolium* and *P. poeppi-*

gii, the main axis of the inflorescences is not rarely fistulose. A good example is the type collection of *P. poeppigii*. These fistulose inflorescences tend to have very short lateral branchlets with the flowers rather densely fasciculate. In the past, all collections with this striking inflorescence shape were annotated as *P. poeppigii*, but floral characters show that this inflorescence shape also occurs in *P. cuneifolium*. In *Ocotea javitensis* the entire inflorescence can be reduced and carry a dense cluster of flowers; such specimens have also been identified as *Pleurothyrium* (for instance, Klug 2908 as *P. densiflorum* Smith). Exactly how the activity of ants induces this peculiar inflorescence shape is not known to me.

Leaf position. Most species have alternate leaves, the predominant arrangement in Lauraceae. About ten species have the leaves clustered at the tips of the branches, potentially a useful character to separate species. However, I found this character not as useful as I hoped, because in some species the leaves are more or less clustered, and in some others the leaves are so large that an herbarium specimen consists of one leaf and an inflorescence and does not show the arrangement of additional leaves. Thus, I used leaf position in the key only when separating relatively small-leaved species.

Leaf shape. Leaf shape ranges from elliptic to strongly obovate. In most species it is rather stable, but I found it difficult to express leaf shape accurately in words and have not used it very much in the key. A few striking leaf shapes should be mentioned: in *Pleurothyrium maximum*, *P. insigne*, and *P. williamsii* the leaves are gradually narrowed toward the base and at the base are abruptly rounded to cordate; in *P. racemosum* and *P. pilosum* the leaves are obtuse or rounded both at the base and apex. *Pleurothyrium tomiwahlii* has a similar leaf shape, but the base is sometimes acute, not obtuse.

Leaf venation. Leaf venation includes both camptodrome and brochidodrome types as well as their intermediates. All species with small flowers and free staminal glands (the first eleven species in the key) have predominantly camptodrome venation, while the species with larger, rotate flowers have camptodrome or brochidodrome venation. Leaf size or shape does not seem to affect venation type strongly; some species with large, obovate leaves have a strongly developed marginal vein (*Pleurothyrium insigne*, *P. maximum*), but others (*P. tomiwahlii*, *P. giganteum*) do not. Among the species with small leaves, *P. marginale* has a strong marginal vein, but *P. golfodulcense*, *P. glabripalium*, and *P. westphalii* do not have a marginal

vein. Although venation type seems characteristic for each species, the various types are hard to describe accurately and have not been used much in the key. A detailed study of the venation types of *Pleurothyrium* is in preparation and will be published separately.

Indument. The type of indument is a very useful character for identification. Because indument on leaves and twigs can be different, I have mostly used the indument on the lower leaf surface, in which I recognize three types. A little more than half the species have glabrous leaves or carry a sparse, appressed indument, which never covers the entire lower surface. A group of ten species has erect straight or tortuous (in *Pleurothyrium racemosum*) hairs, which never cover the entire surface and which, in some species, can be sparse. The third group has a dense (mostly tomentose) pubescence, which completely covers the lower leaf surface. With the exception of three species (*P. crassitepalum*, *P. panurense*, and *P. tomiwahlii*), these pubescence types can easily be recognized. In the three exceptions, it is sometimes difficult to choose between group one (glabrous or sparse, appressed pubescence, the surface visible) or group three (dense pubescence, covering the entire surface). These species are therefore included twice in the key. The three groups based on pubescence types are not natural; sometimes closely related species (for instance, *P. insigne*-*P. maximum*) are placed in different groups. These groups are formed solely to allow easy identification.

Inflorescences. Inflorescences of *Pleurothyrium* are as a rule thyrso-paniculate in the sense of Weberling (1985). They consist of a central axis with a number of alternately positioned lateral axes. The lateral axes are once to several times cymosely branched; the central flower of each cyme flowers before the lateral ones and is usually absent in all but the terminal cymes. Of each cyme, the lateral elements may again be cymosely divided, but the central element always develops into a single flower. Sometimes the lateral elements of the lateral branches fail to develop and then the inflorescence is racemose (as in *P. racemosum*).

In most species inflorescence bracts are early deciduous and absent at anthesis. Exceptions are *Pleurothyrium bracteatum* and *P. golfodulcense*, both of which have rather large bracts at anthesis.

The thyrso-paniculate inflorescence type is very common among neotropical Lauraceae and occurs in all larger genera, such as *Ocotea*, *Nectandra*, *Persea*, *Aniba*, *Licaria*, *Aiouea*, *Endlicheria*, and *Cinnamomum*.

In general, the inflorescences are found in the axils of cataphylls just below the terminal bud.

Although they appear terminal, I have always found them to be lateral. In the species group characterized by erect tepals, inflorescences occur occasionally in the axils of regular leaves, but this is uncommon. In *Pleurothyrium giganteum*, the inflorescences are inserted in the axils of cataphylls below the leaves. However, many species are represented by very few collections and I am not certain that the position of the inflorescences, below or above the leaves, is of any significance.

The nearly consistent presence of inflorescences in the axils of cataphylls is a helpful character for the identification of *Pleurothyrium*. The great majority of species of *Ocotea* and *Nectandra* have inflorescences in the axils of normal leaves, but such species as *O. fasciculata* (Nees) Mez and *N. megapotamica* (Spreng.) Mez are exceptions.

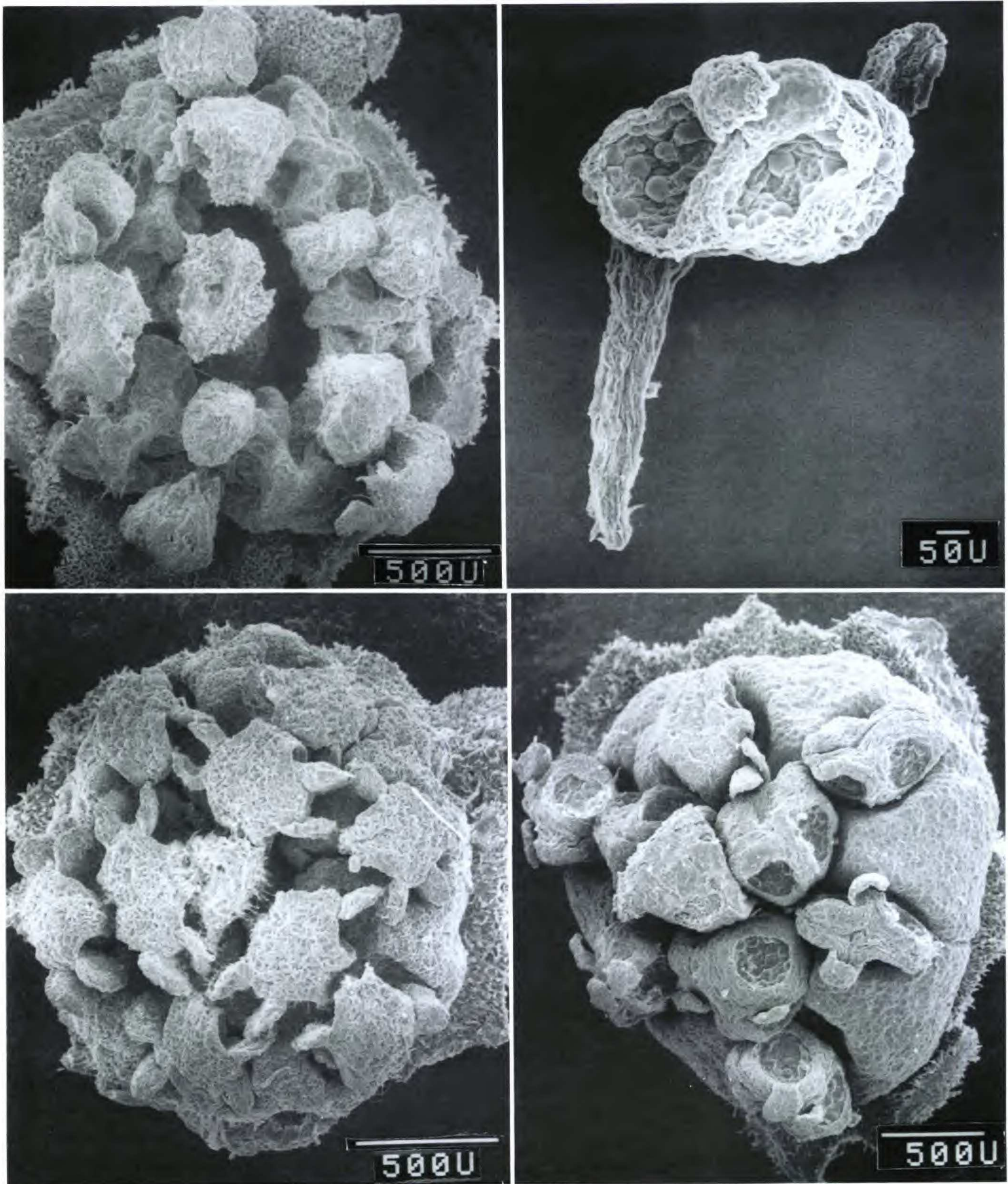
Flowers. The flowers offer a number of discriminating and/or interesting characters. Eight species have more or less erect tepals at anthesis, this in contrast to the remaining species, which have a rotate flower shape. Six of these eight (the exceptions are *Pleurothyrium acuminatum* and *P. amapaense*) also have reflexed margins of the tepals. These reflexed margins are not a result of aging of the flowers; I have seen *P. parviflorum* and *P. trianae* in the field and even young flowers have reflexed margins of the tepals. On herbarium sheets one can see that sometimes buds have already reflexed margins of the tepals. I consider the species with erect tepals, together with *P. cuneifolium* and *P. obovatum*, a closely related group, characterized by flower shape, absence of a marginal vein, similar indument on the pistil, occurrence of fistulose stems, and the rather slender tepals.

Most other species have rotate flowers and broadly ovate to roundish tepals. Species with flowers more than 10 mm in diameter show a tendency toward unequal tepals, with the inner tepals slightly shorter and narrower than the outer ones. The group of species with erect tepals always has equal tepals. In one species, *Pleurothyrium tomiwahlii*, the tepals are strongly reflexed at anthesis and become parallel to the pedicel in older flowers.

The pubescence on the outside of the tepals is frequently much denser or longer on the areas exposed to the outside in bud than on areas protected from the outside. Thus, the outer three tepals and a basal, triangular patch on the inner tepals have a similar pubescence. This is an unusual character in Lauraceae, but is fairly common in the group of species with rotate flowers. It does not occur in the group of species with erect tepals.

The pubescence on the inside of the tepals is variable and is a useful character in separating the taxa. A few species (*Pleurothyrium cuneifolium*, *P. glabrifolium*, *P. glabritepalum*, *P. panurense*, and *P. prancei*) have a glabrous inner surface of the tepals (in *P. prancei* the outer three are glabrous inside, the inner three papillose). Occasionally, some scattered papillae or hairs may be present, especially near the base of the tepals, but a homogeneous cover of papillae or hairs is lacking. The group of species with pubescent inner surfaces of the tepals is also small; it includes *P. bracteatum*, *P. giganteum*, *P. crassitepalum*, *P. tomiwahlii*, *P. grandiflorum*, *P. marginale*, *P. pilosum*, and *P. westphalii*. In *P. racemosum* the inner tepals are pubescent and the outer three have a large, triangular, pubescent patch at the base and are otherwise papillose. The remaining species all have a papillose inner surface.

The different androecial configurations are the most interesting feature of *Pleurothyrium*. In the group of species with erect tepals the enlarged glands grow outward, and the six outer stamens are separated from each other by the glands (Fig. 1). In this flower type the glands do not grow around the outer anthers, and the glands do not touch each other at the periphery of the flower. The stamens have relatively long filaments and the anther cells occupy nearly the entire anther (Fig. 2). The anther is somewhat curved inward, but not horizontal; thus, the anther cells are arranged in an upper and lower pair. The lower pair is always toward the outside in relation to the upper pair. Because of the long filaments, the anthers are clearly raised above the glands. In the next stage, the glands begin to enclose the outer stamens, while the anthers become horizontal, have lateral anther cells, and are not raised above the glands. An example is *P. vasquezii* (Fig. 3). In other species the glands completely surround the outer stamens and appear to form a wall around the stamens. The contact lines between the glands are sometimes clearly visible (Fig. 4) or almost disappear (Fig. 5). In the final stage all stamens are crowded in the center of the flower, surrounded by a broad wall of completely fused glands (Fig. 6). The enlarged glands do not confine the stamens to the center of the flower in all species. In some species the glands grow between the stamens and separate them, especially the stamens of the second whorl (Fig. 7). This configuration is not common; it occurs in *P. golfodulcense*, *P. cinereum*, *P. tomiwahlii*, *P. crassitepalum*, and *P. racemosum*. The species with this flower type also tend to have stamens and

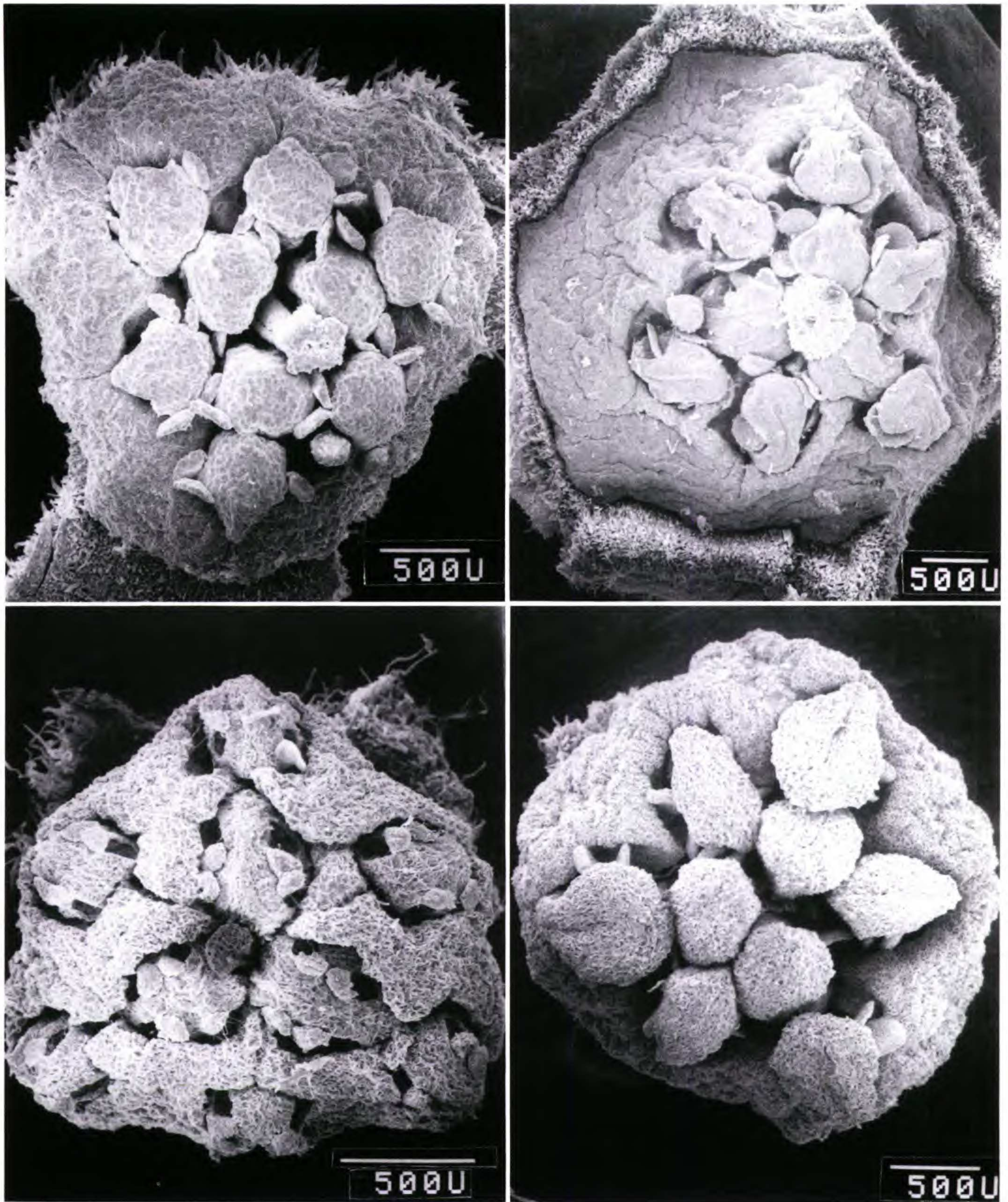


FIGURES 1-4.—1. (Top left.) Flower of *Pleurothyrium poeppigii*, tepals removed (*Palacios 2775*).—2. (Top right.) Stamen (Whorls I-II) of *P. acuminatum* (*van der Werff 9967*).—3. (Bottom left.) Flower of *P. vasquezii*, tepals removed (*Vasquez 7889*).—4. (Bottom right.) Flower of *P. tomentellum*, tepals removed (*Gudiño 12*).

glands forming a taller “dome”; this dome can be as high as its width. In *P. tomiwahlii* the dome is also seated on a short column, thus further raising the androecium. All species with horizontally bent anthers and glands that are (nearly) enclosing the outer stamens have rotate flowers. These species have, on the average, distinctly larger flowers than the species with erect tepals. Unfortunately, no

data on pollination are available, but it seems likely that the species with large, rotate flowers are pollinated by different organisms than those with small flowers with erect tepals.

The indument of the pistil shows considerable variation. Sixteen species were found to have the pistil more or less covered with papillae. Often the lower part of the ovary was glabrous and the density



FIGURES 5-8.—5. (Top left.) Flower of *P. insigne*, tepals removed (*Palacios 4388*).—6. (Top right.) Flower of *P. grandiflorum*, tepals removed (*Juncosa 1675*).—7. (Bottom left.) Flower of *P. golfodulcense*, tepals removed (*Jimenez 648*).—8. (Bottom right.) Flower of *P. brochidodromum*, tepals removed (*Vasquez 7865*).

of the papillae decreased also on the style, but papillae were easily seen on the upper part of the ovary. This condition is present in all species with erect tepals, as well as in *Pleurothyrium bifidum*, *P. brochidodromum*, *P. nobile*, *P. palmanum*, *P. panurense*, *P. vasquezii*, and *P. williamsii*. Ten species have a glabrous pistil: *P. tomiwahlii*, *P. crassitepalum*, *P. glabrifolium*, *P. glabritepa-*

lum, *P. grandiflorum*, *P. marginale*, *P. pilosum*, *P. racemosum*, *P. giganteum*, and *P. westphalii*. The remaining species have a (partly) pubescent pistil. In a few species one finds six bald spots on the upper part of the pubescent ovary corresponding to the contact points between the six glands and the ovary. I have not used the indument of the pistil frequently in the key, because the pu-

bescence is only readily visible on the style in a few species.

Fruits and cupules are unknown for many species. When known, the cupules are relatively deeply cup-shaped and have nearly always conspicuous lenticels or warts. Because of the deep cupules, fruiting collections have sometimes been misidentified as *Aniba* sp., but venation (*Pleurothyrium* has in general more lateral veins and sometimes a distinct marginal vein) and indument (ferruginous tomentum is a good indication for *Pleurothyrium*) help separate the two genera. Frequently, the tepals are persistent on the young cupules. The tepals eventually become damaged and break off or the growing cupule causes the tepals to fall off. In this character, *Pleurothyrium* species differ from *Nectandra*, where the tepals tend to be basally united and fall off as a unit, together with the stamens. Unusual characters are the presence of six large lobes on the cupules of highland populations of *P. poeppigii* in the Selva Central in Peru; the common name "roble zapallo" alludes to this (zapallo = squash). Young cupules of *P. giganteum* are sharply hexangular, a feature not found in other species. In *P. cinereum* the tepals are persistent on the mature cupule, which may be double-rimmed.

Pollen. In a survey of pollen types of neotropical Lauraceae, Raj & van der Werff (1988) found that, with the exceptions of *Cryptocarya* and *Cassytha*, all investigated species had inaperturate, spinulose pollen grains. Pollen of *Pleurothyrium* was found to be very similar to that of *Ocotea*, the main differences being size and ultrastructural details of the sporoderm. Pollen of *Nectandra* is more distinct. Three species of *Pleurothyrium* (*P. parviflorum*, *P. trianae*, and *P. cuneifolium*) were included in this study. Because these three species belong to the group with erect tepals and erect or curved anthers, I checked pollen of two species with rotate flowers and bent anthers (*P. insigne* and *P. racemosum*). These two species have the same inaperturate, spinulose pollen that is present in nearly all neotropical Lauraceae. Because all five investigated *Pleurothyrium* species have the same pollen type, it seems unlikely the pollen will be useful in the classification of *Pleurothyrium* species, and pollen of the other species has not been studied.

CLADISTIC ANALYSIS

A cladistic analysis, based on the principles of phylogenetic systematics as developed by Hennig (1966), was made of *Pleurothyrium*, using the 39 species recognized in this revision as terminal taxa.

Because several species of *Pleurothyrium* are still poorly known, the choice of characters to be used in the analysis was limited to those characters visible on a herbarium sheet. Ideally, one wishes for characters from other fields (such as embryology, anatomy, chemistry) as well as more characters. The characters and the character states used are listed in Table 2; the data matrix is presented in Table 3. The choice of outgroup, and therefore also the polarity of the character states, initially posed considerable problems. Of all genera of Lauraceae, *Nectandra* and *Ocotea* are the closest to *Pleurothyrium*, based on overall morphology. However, neither of the two seems closer to *Pleurothyrium* than the other. Because *Ocotea* and *Nectandra* are very similar in the character states used in this analysis, which of them was chosen as the outgroup seemed relatively unimportant, thus a preliminary analysis was made with the generic concept of *Nectandra* as outgroup. This analysis resulted in 1,988 trees; after successive weighting 293 trees were generated. A strict consensus tree showed as the most derived group of species those species with erect tepals and free, weakly enlarged glands. This topology ran completely counter to my ideas of trends within *Pleurothyrium*. Based on knowledge gained from my nine years of studying Lauraceae, I consider the following character states in *Pleurothyrium* as primitive: free, weakly enlarged glands, stamens with only two of the four anther cells lateral and the anthers raised well above the glands, the occasional presence of inflorescences in the axils of normal leaves, the absence of a marginal vein, and erect tepals. As derived character states, I regard fused, strongly enlarged glands, stamens with four lateral anther cells, anthers that are not or scarcely raised above the glands, inflorescences strictly in the axils of cataphylls, presence of a marginal vein and spreading, rotate (or even reflexed) tepals. These ideas on primitive and derived characters in *Pleurothyrium* are based on my extensive experience with neotropical Lauraceae. Because *Nectandra* and several hermaphroditic species of *Ocotea* (including most South American *Ocotea* species with perfect flowers) have flowers with spreading tepals, the *Pleurothyrium* species with erect tepals ended up as derived in the phylogenetic tree. There are some *Ocotea* species with perfect flowers and erect tepals (for instance, the *O. insularis* group), but various reasons (entirely different indument of anthers, presence of flattened branchlets of inflorescence) make it highly unlikely that *O. insularis* can be considered as outgroup for *Pleurothyrium*.

TABLE 2. Characters and character states used in cladistic analysis of *Pleurothyrium*.

1. Position of tepals	0 = spreading 1 = erect
2. Margin of tepals	0 = plane 1 = inrolled
3. Marginal vein	0 = lacking 1 = present
4. Indument on inner surface of tepals	0 = glabrous 1 = papillose 2 = pubescent
5. Indument of pistil	0 = glabrous 1 = papillose 2 = pubescent
6. Indument of floral tube	0 = glabrous 1 = papillose 2 = pubescent
7. Glands	0 = free, not surrounding stamens 1 = surrounding stamens, \pm fused
8. Stamens	0 = adjacent 1 = separated from each other by glands
9. Twigs	0 = solid 1 = fistulose
10. Number of lateral veins	0 = 5-9 1 = 10-15 2 = 16 or more
11. Tepals	0 = equal 1 = subequal
12. Position of leaves	0 = alternate 1 = clustered
13. Pubescence on lower leaf surface	0 = glabrous or appressed 1 = erect
14. Position of inflorescence	0 = in axils of leaves 1 = in axils of bracts
15. Position of anther cells	0 = 2 lateral 1 = 4 lateral
16. Pubescence of bracts	0 = only on outer surface 1 = on inner and outer surface

Character states of 4, 5, 6, and 10 are unordered.

A second analysis was made with a primitive species of *Pleurothyrium*, *P. acuminatum*, as outgroup. This species was chosen because it lacks the derived characters listed earlier, and it also lacks fistulose twigs and has plane, not inrolled, tepal margins. Analysis of the data matrix using the MHennig* and bb* Wagner parsimony options of Hennig86 (Farris, 1988) produced 540 most parsimonious trees (length 79 steps, consistency index 0.25). A strict consensus tree based on these 540 trees showed an alphabetical listing of 32 species, with only seven species slightly better resolved. The successive weighting procedure on the 540 trees resulted in at least 1,149 trees (overflow) with a length of 110 steps and a consistency index of 0.50. Note that the high value for the length is a function of the weight being scaled up to a value of 10. Although most characters were weighted after the successive weighting procedures, four of the sixteen characters (10, 11, 13, and 14) weight-

ed zero. The analysis was repeated without those characters and resulted in 230 most parsimonious trees with a length of 44 steps and a consistency index of 0.34. After successive weighting, the analysis produced 118 trees with a length of 98 steps and a consistency index of 0.58. As a consequence of deleting the four "weightless" characters, the analysis resulted in a smaller number of trees with fewer steps and a higher consistency index: these four characters must have contributed a great deal of homoplasy to the first analysis.

A strict consensus tree based on the 118 trees of the second analysis is presented in Figure 9a, while one of the 118 equally parsimonious trees, selected at random, is presented in Figure 9b. The following comments apply to both cladograms. The changes in character states throughout the cladogram are added to the tree. In both cladograms, the species group I consider primitive forms the basal group. The second, largest group is not well

TABLE 3. Data matrix for cladistic analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Nectandra	?	0	0	1	?	?	0	0	0	1	0	0	?	0	1	?
acuminatum	1	0	0	1	2	0	0	0	0	0	0	0	0	1	0	0
amapaense	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0
amplifolium	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	?
bifidum	0	0	0	1	1	1	1	0	0	1	?	0	1	1	1	0
bracteatum	0	0	1	2	2	2	1	0	0	2	1	0	1	1	1	1
brochidodromum	0	0	1	1	1	0	1	0	0	1	0	1	1	1	1	1
cinereum	0	0	0	1	2	2	1	1	0	1	1	0	0	1	1	0
costanense	0	0	1	1	2	0	0	1	0	1	0	0	1	0	0	0
crassitepalum	0	0	1	2	0	0	1	0	0	1	1	1	0	1	1	?
cuneifolium	1	1	0	0	1	0	0	0	1	?	0	0	?	0	0	1
gigantum	0	0	1	2	0	0	1	0	0	2	1	1	1	1	1	1
glabrifolium	0	0	0	0	0	0	1	0	0	1	0	0	?	1	1	0
glabritepalum	0	0	0	0	0	0	1	0	0	0	1	0	1	1	1	?
golfodulcense	0	0	1	1	2	2	1	0	0	0	0	0	0	1	1	1
grandiflorum	0	0	0	2	0	2	1	0	0	2	1	0	0	1	1	?
hexaglandulosum	0	0	1	0	2	2	0	0	0	2	0	0	0	0	0	?
insigne	0	0	1	1	2	2	1	0	0	2	1	0	1	1	1	0
intermedium	1	1	0	1	0	0	0	0	0	1	0	0	0	1	0	0
marginale	0	0	1	2	0	0	1	0	0	?	1	0	0	1	1	?
maximum	0	0	1	0	2	2	0	0	0	2	0	0	?	1	0	0
nobile	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0
obovatum	0	0	1	1	0	0	0	0	1	2	0	0	?	1	0	?
palmanum	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1
panurense	0	0	1	0	0	0	1	0	0	1	0	1	0	1	1	0
parviflorum	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0
pauciflorum	0	0	1	1	2	2	1	0	0	2	0	0	1	1	1	1
pilosum	0	0	0	2	0	2	1	0	0	0	?	1	1	1	1	?
peoppigii	1	1	0	1	0	0	0	0	1	2	0	0	0	1	0	1
prancei	0	0	1	0	2	2	?	0	0	1	1	0	?	1	1	0
racemosum	0	0	1	2	0	2	1	0	0	0	0	1	1	1	1	0
steyermarkianum	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0
synandrum	0	0	0	1	2	0	0	0	0	2	0	0	1	1	1	0
tomentellum	0	0	0	1	0	2	1	0	0	1	0	0	1	1	1	0
tomihahlii	0	0	1	2	0	0	1	0	0	2	1	1	1	1	1	1
trianae	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0
undulatum	1	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0
vasquezii	0	0	1	1	1	1	0	0	0	1	0	0	1	0	1	0
westphalii	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	?
williamsii	0	0	1	1	1	1	1	0	0	2	1	1	0	1	1	1

resolved; the large number of trees before constructing the consensus tree reflects variation in topology in this group. The cladograms include only four synapomorphies (for characters 1, 2, 7, and 10), indicating that all other changes are changes in unordered states or homoplasies. Although nearly all cladograms include some amount of homoplasy, to have a cladogram for 39 terminal taxa with only four synapomorphies suggests that the data needed for a cladistic analysis were not available.

Reviewing this attempt at making a phylogenetic classification as a byproduct of a taxonomic revision

of *Pleurothyrium*, one may note several problems. First, the number of characters is much lower than the number of terminal taxa. Second, the poor understanding of relationships within Lauraceae makes the choice of an outgroup somewhat arbitrary, and therefore the choice of polarity of the character states cannot be defended very well. Because the choice of outgroup influences the classification strongly, the cladogram cannot be any more reliable than the choice of outgroup. Third, the phylogenetic classification is entirely based on gross morphological characters of herbarium specimens. These characters were not selected because

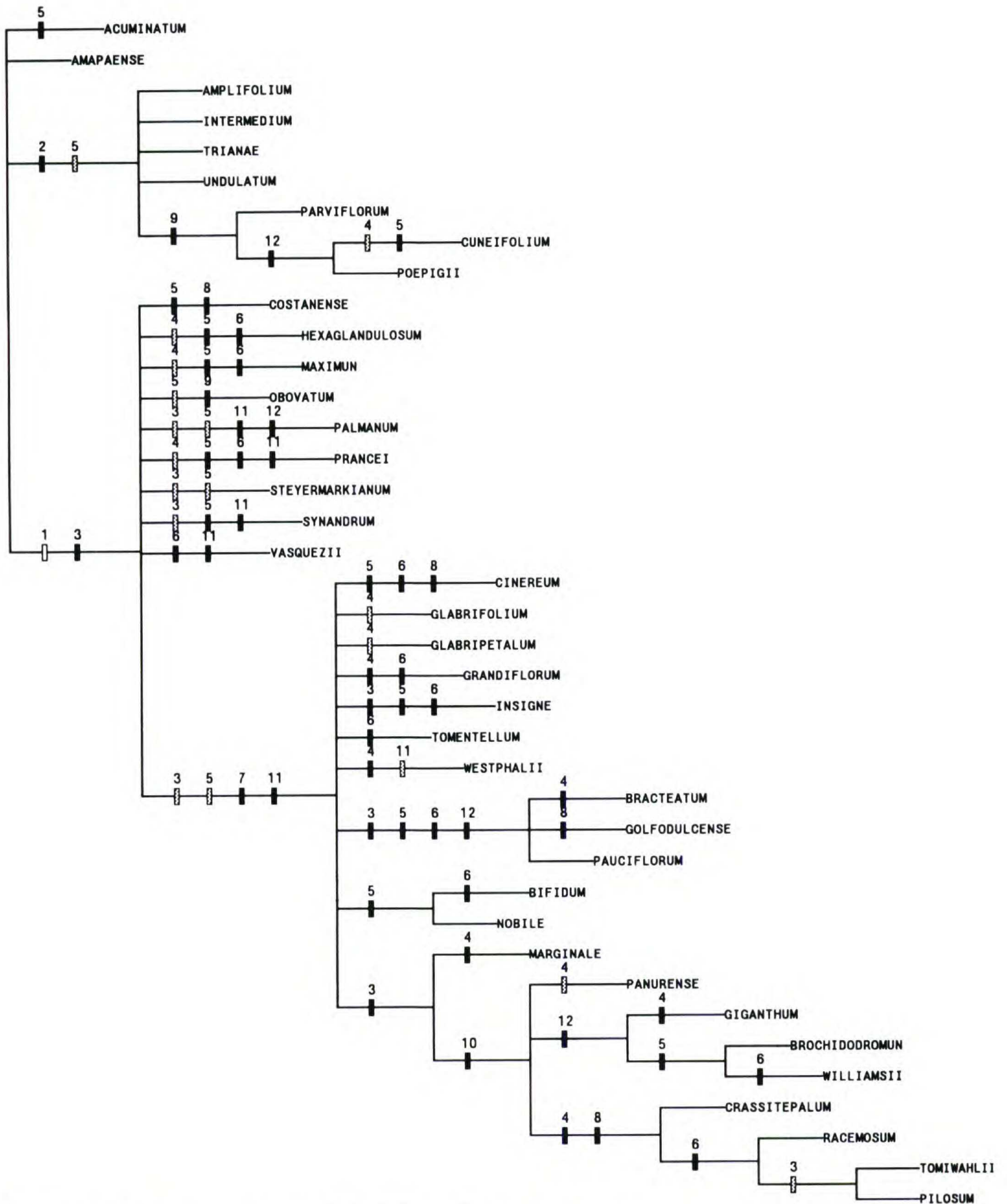


FIGURE 9a. Strict consensus tree of the 118 equally parsimonious trees.

they were regarded as good indicators of phylogenetic relationships, but because they were all that was available. Ideally, one wishes for characters that are regarded as good indicators of phylogenetic relationships. In reality, one does not have much choice about quantity and quality of characters when 19 of the 39 terminal taxa are known from only one or two collections.

In general, a taxonomic classification of a group requires the data needed for the circumscription and identification of the taxa involved. For a phylogenetic classification one needs, in addition to the data for a taxonomic classification, also data showing the evolution within the group over time. Or, to phrase it differently, a phylogenetic classification contains more information than a taxonomic clas-

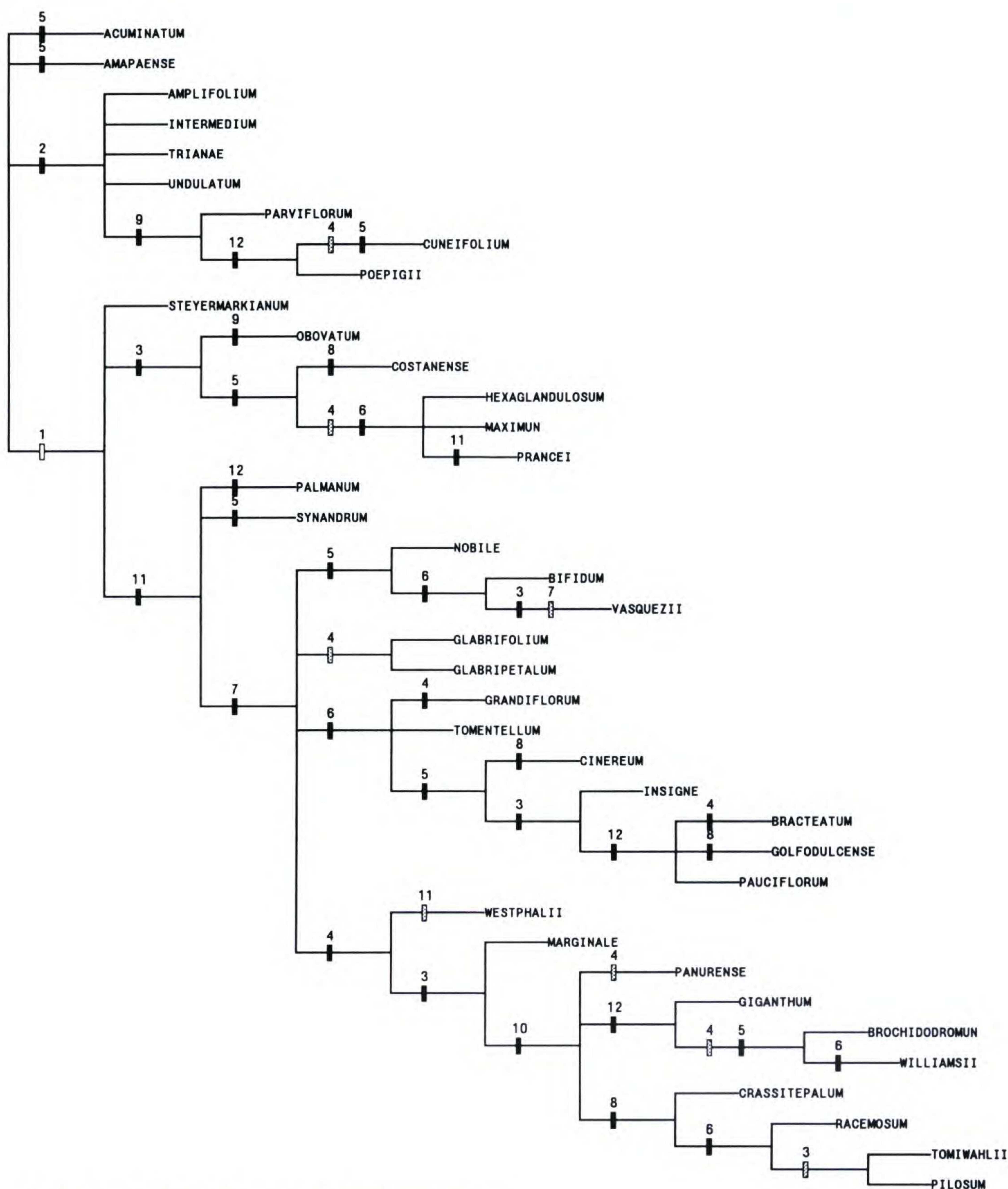


FIGURE 9b. One of the 118 equally parsimonious trees.

sification, and consequently requires a larger input of information. In the case of *Pleurothyrium*, sufficient information is available for taxonomic revision, but not enough for a phylogenetic classification. Obtaining sufficient information for a proper phylogenetic analysis is a project unto itself and making a phylogenetic analysis cannot be merely tacked on to making a taxonomic revision.

Relationships between *Pleurothyrium* species as expressed in the cladogram and as based on morphological similarities show some congruence. For instance, I consider *P. racemosum*, *P. tomiwahlii*, and *P. pilosum* as closely related, a relationship expressed in all cladograms inspected. Likewise, the species with erect tepals, usually with inrolled margin of the tepals, are closely related, as shown

in the cladograms; I would also include *P. obovatum* in this group, a species placed in the more advanced group in the cladograms. Other pairs of closely related species (at least in my opinion) placed well apart in the consensus tree are *P. insigne* and *P. maximum* and, to a lesser degree, *P. costanense* and *P. synandrum*, as well as *P. westphalii* and *P. grandiflorum*.

SPECIES CONCEPT

In preparing this treatment, it was necessary to deal with the number of published species whose distinctiveness was less than convincing. In some cases ample recent collections made it clear that certain taxa (for instance, *P. reflexum* and *P. zilianense*) had to be synonymized. In other cases such collections were not available. In these instances I let myself be guided by the principle to only change the status quo if there was a strong reason for doing so. This means that some species whose distinctiveness I doubt are being maintained (examples are *P. amplifolium*, *P. undulatum*, *P. amapaense*, and *P. intermedium*) and that other taxa, represented by, in my opinion, inadequate collections, are not being described. My reasons for not describing these taxa are twofold: (a) incomplete descriptions make identification of future, complete collections very difficult; (b) the absolute certainty that specimen X (sterile or in fruit) represents an undescribed species of genus A can turn a few weeks later into nagging doubt.

TYPIFICATION

Botanists who described species of *Pleurothyrium* in the nineteenth century never designated holotypes. Usually they cited only a type collection, often indicating in which herbaria they had seen duplicates of the type collection. When only one specimen was cited, I have regarded this as the holotype, even though it was not explicitly annotated as such. If several duplicates exist of the type collection, I have listed them as syntypes. In all cases the syntypes I have seen belonged to the same species, and there cannot be any confusion about the application of the names in question. For this reason it seemed unnecessary to designate lectotypes, and I have therefore not selected lectotypes. Another reason not to select lectotypes is that I very likely have not seen all the existing syntypes, as required by the Code. For instance, I have not seen the specimens at P, and I have no doubt that syntypes of some species are present in other herbaria I did not consult. Lectotypification

would be advisable if two or more collections are cited as types of a given species, but this is not the case for any *Pleurothyrium* species.

TAXONOMIC SECTION

Pleurothyrium Nees, in Lindley, Nat. Syst. Bot.: 422. 1836. *Ocotea* sect. *Pleurothyrium* (Nees in Lindley) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. *Ocotea* subg. *Pleurothyrium* (Nees in Lindley) Kostermans, Comm. Forest Res. Inst. 57: 40. 1957. TYPE: *Pleurothyrium chrysophyllum* Nees (lectotype, selected by Kostermans, 1952).

Trees. Twigs solid or in a few specimens fistulose and inhabited by ants. Leaves alternate or clustered near the tips of branches, mostly elliptic or obovate; venation camptodrome or brochidodrome. Inflorescences in axils of cataphylls, rarely in axils of normal leaves, thyrsopaniculate, rarely by reduction racemose, the ultimate divisions cymose. Flowers rotate at anthesis or in some species with erect tepals. Tepals 6, equal or subequal, then with the inner three a little narrower and shorter. Fertile stamens 9, all 4-celled, the outer 6 with the anthers curved inward or sharply bent inward, the cells mostly lateral, sometimes 2 cells extrorse or introrse; inner three anthers mostly curved outward, with lateral cells. Staminodia frequently present, but small and inconspicuous. Filaments of the inner three stamens each with two glands near the base, these strongly enlarged and growing outward, sometimes fused and enclosing the outer stamens and the anthers embedded in the glandular tissue. Pistil glabrous, papillose or pubescent, largely immersed in the receptacle. Cupule usually deeply cup-shaped, conspicuously warty. Fruit a one-seeded drupe.

KEY TO THE SPECIES OF *Pleurothyrium*

- | | | |
|-------|---|-----------------------|
| 1 | Twigs fistulose | 2 |
| 1. | Twigs solid | 6 |
| 2(1). | Flowers rotate, 7-14 mm diam.; tepals glabrous or papillose on inner surface | 3 |
| 2. | Tepals \pm erect at anthesis, flowers ca. 5 mm diam., tepals papillose on inner surface | 4 |
| 3(2). | Terminal buds, inflorescences, and flowers ferruginous-tomentellous; leaves glabrous below | <i>P. obovatum</i> |
| 3. | Indument, when present, brown; leaves mostly papillose or tomentellous below, rarely glabrous | <i>P. cuneifolium</i> |
| 4(2). | Twigs, inflorescences, and flowers glabrous or minutely puberulent | <i>P. parviflorum</i> |
| 4. | Twigs, inflorescences, or flowers papillose or tomentellous | 5 |

- 5(4). Lateral veins 14–18 on each side; leaves firmly chartaceous to subcoriaceous; always with fistulose twigs *P. poeppigii*
5. Lateral veins 8–12; leaves chartaceous; rarely with fistulose twigs *P. trianae*
- 6(1). Tepals at anthesis erect and sometimes twisted, the margins usually reflexed; staminal glands free, never coalesced; diameter of flowers 5 mm or less; marginal vein lacking, lower leaf surface never with erect hairs 7
6. Tepals at anthesis rotate, plane, the margins not reflexed; staminal glands free or coalesced; diameter of flowers equal to or greater than 8 mm (in *P. glabrifolium*, *P. vasquezii*, and *P. tomentellum* flowers 5–8 mm diam.); marginal vein present or absent, in some species lower leaf surface with erect hairs 12
- 7(6). Leaves ± clustered at tips of branches; pubescence on inflorescences and young twigs ferruginous-tomentellous ... *P. amapaense*
7. Leaves alternate, not clustered; pubescence on inflorescence and young twigs gray or (light) brown, never ferruginous 8
- 8(7). Margin of tepals not reflexed; tepals ± twisted at anthesis; leaf apices acuminate *P. acuminatum*
8. Margin of tepals reflexed; tepals not twisted; leaf apices acute 9
- 9(8). Twigs and inflorescence axes sparsely pubescent; flowers and terminal bud much more densely pubescent *P. intermedium*
9. Degree of pubescence on flowers and terminal bud similar as on inflorescence axes and twigs 10
- 10(9). Flowers subsessile, the pedicels shorter than the flowers *P. undulatum*
10. Flowers with pedicels as long as or longer than the flowers 11
- 11(10). Petioles 8–14 mm long; filaments of stamens longer than anthers, clearly visible in old flowers; leaves 7–10 cm wide; known only from Rio de Janeiro *P. amplifolium*
11. Petioles 10–20 mm long; filaments as long as or shorter than anthers, scarcely exceeding glands and not readily visible in old flowers; leaves usually narrower than 8 cm; northern South America *P. trianae*
- 12(6). Lower leaf surface tomentose or tomentellous, the leaf surface completely hidden by the indument 13
12. Lower leaf surface glabrous or sparsely pubescent, the leaf surface never completely hidden 20
- 13(12). Indument of lower leaf surface whitish, very short, the individual hairs scarcely visible 14
13. Indument of lower leaf surface brown or ferruginous, very short or longer and then individual hairs visible 15
- 14(13). Inner surface of tepals glabrous; inflorescences 5–10 cm long; leaves 15–30 cm long *P. panurense*
14. Inner surface of tepals papillose; inflorescence 15–25 cm long; leaves 30–40 cm long *P. bifidum*
- 15(13). Bracts to 1 cm long present on inflorescence during anthesis; marginal vein present; pubescence on young twigs and inflorescence reddish brown *P. bracteatum*
15. Bracts generally lacking on inflorescences at anthesis (if present, small); marginal veins lacking or present; pubescence on inflorescence brown or yellow-brown 16
- 16(15). Lateral veins 18–24; leaves generally widest below the middle *P. synandrum*
16. Lateral veins to 15–16; leaves widest at or above the middle 17
- 17(16). Tepals subequal, the inner three shorter and narrower than the outer three, both inner and outer surface pubescent; marginal vein present *P. crassitepalum*
17. Tepals equal, the inner surface papillose or puberulous; marginal vein weakly developed or lacking 18
- 18(17). Flowers 10–12 mm diam. 19
18. Flowers to 8 mm diam. *P. tomentellum*
- 19(18). Style gray-pubescent; receptacle pubescent inside; indument of lower leaf surface ± appressed, the hairs very short ... *P. cinereum*
19. Style papillose; receptacle glabrous inside; indument of lower leaf surface tomentellous, the hairs ± erect, curled ... *P. palmanum*
- 20(12). Lower leaf surface with erect hairs, this indument sometimes sparse 21
20. Lower leaf surface glabrous or with appressed hairs 30
- 21(20). Leaves obovate or oblong-obovate, 20–60 cm long, the marginal vein strongly developed from near the base to the apex *P. insigne*
21. Leaves obovate or elliptic (in *P. racemosum* oblong, but less than 15 cm long), a marginal vein lacking or only present in the distal half of the leaf 22
- 22(21). Leaves 30–60 × 15–24 cm, obovate, clustered, marginal vein lacking or weakly developed; flowers large, ca. 2 cm diam. *P. giganteum*
22. Leaves smaller and narrower, alternate or clustered, marginal vein sometimes present; flowers less than 15 mm diam. 23
- 23(22). Tepals reflexed at anthesis; androecium situated on top of a short, pubescent column; pubescence on lower leaf surface sparse; leaves obovate, clustered *P. tomiwahlii*
23. Tepals spreading at anthesis; androecium never raised on a short column; pubescence on lower leaf surface visible; leaves elliptic, oblong, or obovate, alternate or clustered 24
- 24(23). Leaf base and apex obtuse or rounded 25
24. Leaf base and apex not both obtuse or rounded, usually at least apex acute or acuminate 26
- 25(24). Leaves 15–25 cm long, densely pilose below *P. pilosum*
25. Leaves 6–14 cm long, glabrescent with age, indument persisting longest near the base along margin and veins *P. racemosum*
- 26(24). Inflorescences few-flowered (± 7 flowers per inflorescence), 2–5 cm long 27

26. Inflorescences with (many) more than 7 flowers, (8-)10-25 cm long 28
- 27(26). Flowers ca. 8 mm diam., tepals half-erect; leaves 16-35 cm long; ovary and receptacle pubescent *P. pauciflorum*
27. Flowers ca. 13 mm diam.; tepals spreading; leaves 10-18 cm long; ovary and receptacle glabrous *P. glabritepalum*
- 28(26). Pistil pubescent; pubescent style easily visible above the androecium *P. costanense*
28. Pistil papillose; style not pubescent 29
- 29(28). Flowers 5-6 mm diam.; leaves alternate *P. vasquezii*
29. Flowers 9-10 mm diam.; leaves \pm clustered *P. brochidodromum*
- 30(20). Inner surface of tepals glabrous (in *P. prancei* only larger, outer three tepals; inner, smaller ones are papillose) or with a few small lines of papillate hairs 31
30. Inner surface of tepals uniformly pubescent or papillose-pubescent 34
- 31(30). Leaves 30-50 cm long, the base abruptly rounded or cordate; inflorescences 40-65 cm long *P. maximum*
31. Leaves 10-30 cm long, the base acute or obtuse; inflorescences to 20 cm long 32
- 32(31). Leaves clustered at tips of branches; lower leaf surface with minute, appressed, whitish indument, thus lower and upper leaf surface markedly discolorous; inundated forests *P. panurense*
32. Leaves not clustered; upper and lower leaf surface not or scarcely discolorous 33
- 33(32). Inner tepals papillose inside, shorter and narrower than the outer ones, these glabrous inside; inflorescence tomentose *P. prancei*
33. All tepals equal in shape and glabrous inside; inflorescence tomentellous *P. glabrifolium*
- 34(30). Leaves clustered at tips of branches 35
34. Leaves not clustered 37
- 35(34). Leaves at base abruptly cordate, the tip acuminate; petioles to 8 mm long; inner surface of tepals papillose *P. williamsii*
35. Leaves at base attenuate to cuneate, tip obtuse; petioles to 17 mm long; inner surface of tepals tomentellous 36
- 36(35). Tepals spreading at anthesis, subequal; androecium not at top of a short, pubescent column; leaf base cuneate; lower leaf surface covered with very short, \pm hairlike papillae *P. crassitepalum*
36. Tepals reflexed at anthesis, equal; androecium situated on top of a short, pubescent column; leaf base obtuse or (on shade-leaves) acute; lower leaf surface glabrous or with few scattered, erect hairs, never with a cover of papillae *P. tomiwahlii*
- 37(34). Inner surface of tepals pubescent; pistil glabrous 38
37. Inner surface of tepals papillose; pistil papillose or pubescent (in *P. steyermarkianum* pistil glabrous) 40
- 38(37). Marginal vein prominent on lower leaf surface *P. marginale*
38. Marginal vein lacking on lower leaf surface 39
- 39(38). Lateral veins 15-20 on each side; flowers 15-17 mm diam., inner tepals narrower than outer ones *P. grandiflorum*
39. Lateral veins 5-8 on each side; flowers 8 mm diam., tepals equal *P. westphalii*
- 40(37). Leaf base abruptly rounded or abruptly cordate; petioles thick, to 8 mm long 41
40. Leaf bases acute, obtuse or rounded, but never abruptly rounded; petioles 6-30 mm long (*P. nobile*, with rounded leaf bases, has petioles 20-30 mm long) 42
- 41(40). Pedicels ca. 3 mm long; leaves narrowly obovate or oblanceolate; Amazonian Peru and Ecuador *P. williamsii*
41. Pedicels 1.5-2 cm long; leaves obovate; Panama and Costa Rica *P. hexaglandulosum*
- 42(40). Bracts of inflorescences present at anthesis; leaf tips sharply acute to acuminate; upper leaf surface dull *P. golfodulcense*
42. Bracts of inflorescences lacking at anthesis; leaf tips obtuse to acute; upper leaf surface somewhat shiny 43
- 43(42). Style densely gray-pubescent; receptacle pubescent inside *P. cinereum*
43. Style glabrous or brown-papillose; receptacle glabrous inside 44
- 44(43). Lateral veins 7-10 on each side; glands forming a flat, pillowlike mass *P. nobile*
44. Lateral veins 11-16 on each side; glands forming ridges surrounding stamens *P. steyermarkianum*

Pleurothyrium acuminatum van der Werff, sp. nov. TYPE: Peru. Loreto: Prov. Requena, Arboretum Jenaro Herrera, *van der Werff, Vasquez & Jaramillo 9967* (holotype, MO; isotypes, AAU, AMAZ, BR, C, F, G, HBG, K, MEXU, NY, QRS, S, U, US, USM). Figures 10, 11.

Arbor. Ramuli teretes, solidi, dense, minute adpresse pubescentes. Gemma terminalis dense, adpresse pubescens. Folia alterna, tenuiter chartacea, 10-20 \times 3-6 cm, elliptica, basi sensim in petiolum attenuata, apice acuminata, acumine 1-1.5 cm longo, supra glabra, punctata, subtus glabra vel pilis minutis adpressis praedita praecipue secus costam nervosque et ad basim; nervis lateralibus 6-10 utroque costae latere, sursum arcuatis et in dimidio distali parum brochidodromis; venatione supra immersa, subtus costa elevata, nervis et venatione paullo elevata. Petioli 1-2 cm longi, supra applanati, basi paullo incrassati. Inflorescentiae ex axillis cataphyllorum ortae, 8-12 cm longae, graciles, ramulis semel vel bis de modo cymae furcatis, tomentellae, bracteis deciduis. Pedicelli (4-)5(-8) mm longi, tomentelli. Flores albi. Tepala 6, aequalia, per anthesin plerumque erecta, oblonga, 3 \times 1 mm, saepe torta, sed marginibus non reflexis, tres exteriora extus minute puberula vel papillosa, tres interiora extus basi papillosa, demum glabra, omnia intus parum papillosa vel glabra. Receptaculum ad apicem constrictum. Stamina 9, 4-locellata, locellis lateralibus et sursum aperientibus. Filamentis antheris aequantibus; glandulis incrassatis, liberis. Pistillum ca. 1.5 mm longum, ovario ellipsoideo, 1 mm longo, dimidio basale glabro, dimidio distale parum pubescente, stylo pubescente. Fructus ignoti.



FIGURE 10. *P. acuminatum*.—A. Habit.—B. Flower showing abscission line of tepals.—C. Floral detail.—D. Young fruit.—E. Stamens—Whorl I on right, Whorl II in center, Whorl III on left.—F. Branching pattern of inflorescence.

Tree, 15 m. Twigs terete, solid, densely, but minutely appressed gray pubescent, 3 mm diam. ca. 5 cm below the tip. Terminal bud somewhat shiny, densely appressed-pubescent. Leaves alternate, thinly chartaceous, 10–20 × 3–6 cm, elliptic, the base gradually narrowed in the petiole, the tip acuminate, the acumen 1–1.5 cm long, the upper surface glabrous and gland-dotted, this best visible on young leaves, the lower surface glabrous

or with some minute appressed hairs, especially along the veins and near the base; lateral veins 6–10 on each side, arching upward near the margin and weakly loop-connected in the upper half of the lamina; venation immersed on upper surface, midrib raised on lower surface, the lateral veins and tertiary venation less so. Petioles 1–2 cm long, adaxially flattened, somewhat swollen near the base, with a similar indument as the twigs. Inflorescences



FIGURE 11. Distribution of *P. acuminatum* (★), *P. amapaense* (●), *P. amplifolium* (○), and *P. bifidum* (■).

in axils of cataphylls, 8–12 cm long, slender, laxly branched, the branchlets once or twice cymosely branched, minutely tomentose, bracts deciduous at anthesis. Pedicels (4–)5(–8) mm long, minutely tomentellous. Flowers white. Tepals 6, equal, mostly erect at anthesis, oblong, 3×1 mm, often wrinkled, twisted, but the margins not consistently inrolled, the outer 3 minutely puberulous to papillose outside, the inner 3 with a papillose, triangular base, otherwise glabrous, the inside slightly papillose to glabrous. Tepals united at the very base and falling from old flowers as a unit. Receptacle constricted at the tip, the constriction line turning into a dehiscence line in older flowers. Stamens 9, 4-celled, the cells lateral and opening upward, filaments about as long as anthers, glabrous; glands enlarged, protruding between the outer stamens, free. Pistil ca. 1.5 mm long, ovary 1 mm long, the lower half glabrous, the upper half slightly pubescent, style pubescent. Receptacle glabrous inside. Fruit unknown. Flowers: August–September. Elevation range: 100–200 m.

Collections studied. BRAZIL. AMAZONAS: São Paulo de Olivença, *Ducke RB25676* (RB). PERU. LORETO: Requena, Arboretum of Jenaro Herrera, ? (MO), ? *s.n.* (MO), *Castillo 50* (F, MO), *van der Werff 9967* (AAU, AMAZ, BR, C, F, G, HBG, K, MEXU, MO, NY, QRS, S, U, US, USM).

Pleurothyrium acuminatum is only known from a few collections from the Arboretum Jenaro Herrera in Amazonian Peru and one collection from Amazonian Brazil. It is included and illustrated in Spichiger et al. (1989) as *Ocotea undulata* (Meisner) Mez, a species that I place in *Pleurothyrium* and which is closely related to *P. acuminatum*. The erect tepals at anthesis, the relatively small (for *Pleurothyrium*) glands, the shape of the pistil and tepals, and the weakly loop-connected lateral veins all point to the group of species with reflexed margins of tepals as the closest relatives of *P. acuminatum*, even though the margins of the tepals are plane in this species. The other main group of *Pleurothyrium*, characterized among others by rotate flowers, has much broader tepals and usually

larger, fused glands. Within the group of *Pleurothyrium* species with erect tepals, *P. acuminatum* stands apart by its rather long tepals with a plane margin, long, slender pedicels, and the very short, almost papillose indument of the flowers. The acuminate leaves are also a useful character.

Pleurothyrium amapaense Allen, Mem. New York Bot. Gard. 15: 92. 1966. TYPE: Brazil. Amapá: Rio Araguari, *Pires et al.* 51430 (holotype, NY not seen; isotypes, K, S, US). Figure 11.

Tree, 15 m tall. Twigs terete, solid, the young parts ferruginous-tomentellous, older parts glabrous and with pale bark. Terminal bud ferruginous-tomentellous. Leaves clustered at the tips of branches, chartaceous, elliptic-obovate to elliptic, 10–20 × 4–6 cm, the base cuneate, the tip shortly acuminate, glabrous, lateral veins 8–10 on each side, curving upward near the margin and loop-connected in the upper half of the lamina; venation immersed on upper surface, costa and lateral veins raised on lower surface. Petioles ca. 1 cm long, narrowly canaliculate, with similar indument as twigs. Inflorescences in axils of deciduous bracts, ferruginous-tomentellous, to 12 cm long, paniculate, the branches once or twice cymosely branched, bracts lacking at anthesis. Pedicels slender, 4–5 mm long, ferruginous-tomentellous. Flowers greenish brown fide collectors, ca. 5 mm diam. Tepals 6, equal, minutely tomentellous outside, papillose inside, ovate, 2–2.5 mm long, often twisted, spreading or reflexed in old flowers, finally breaking off along a dehiscence line at the base, the margin plane. Stamens 9, 4-celled, the cells lateral, opening upward, anthers glabrous, filaments about as long as anthers; glands enlarged, free, falling off in old flowers. Pistil ca. 2 mm long, ovary ellipsoid, glabrous near base, becoming progressively more papillose toward the tip, style densely papillose, 0.5 mm long, stigma small. Floral tube deeper than wide, glabrous inside. Fruits unknown. Flowers: October. Elevation range: ca. 100 m.

Collections studied. BRAZIL. AMAPA: Rio Araguari, *Pires* 51430 (K, NY, S, US). VENEZUELA. AMAZONAS: Río Negro, upper Río Baria, *Davidse* 27524 (MO, VEN).

Pleurothyrium amapaense is the only *Pleurothyrium* species reported east of Manaus, Brazil. It is only known from the type collections, but as Allen (1966a) already stated, there can be no doubt about its generic position. *Pleurothyrium amapaense* has, for the genus, rather small flowers; it

differs from the other small-flowered species in having tepals with plane, not reflexed, margins, in having clustered leaves, and in its ferruginous indument.

Provisionally included here is *Davidse* 27524 (MO), collected from Depto. Río Negro, Territorio Federal Amazonas, Venezuela. This collection differs in its thinner leaves, shorter pubescence, more elliptic leaves with a less well-developed marginal vein, and its habit (label states it is a liana). The floral characteristics agree reasonably well with those of *Pleurothyrium amapaense*, but it is possible that, once more collections are at hand, it is better recognized as a distinct species.

Pleurothyrium amplifolium (Mez) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 43. 1986. *Nectandra amplifolia* Mez, Arbeiten Königl. Bot. Gart. Breslau 1: 131. 1892. TYPE: Brazil. Rio de Janeiro: Alto Macahé, *Glaziou* 17731 (holotype, B; isotypes, B, G, K, NY, P). Figure 11.

Tree, size unknown. Twigs terete, solid, brown-tomentellous, glabrescent, ca. 4 mm diam. 5 cm below apex. Terminal bud brown-tomentellous. Leaves alternate, chartaceous, elliptic to broadly elliptic, 15–20 × 7–10 cm, the base obtuse or slightly acute, the apex rounded or shortly acute, upper surface glabrous and with venation immersed, the lower surface minutely puberulous when young, soon glabrescent, costa and lateral veins raised, tertiary venation immersed; lateral veins 8–11, arching upward near the margin, not loop-connected. Petioles 8–14 mm long, the upper side flat, with similar pubescence as twigs. Inflorescences in axils of cataphylls, brown-tomentellous, 8–12 cm long, paniculate, the branchlets 1–2 times cymosely branched, flowers more than 30, bracts absent at anthesis. Flowers ca. 4 mm diam. Tepals 6, equal, ± erect at anthesis, the margin reflexed, brown-tomentellous outside, but inner three tepals with papillose margin and tip, all tepals papillose inside. Stamens 9, 4-celled, glabrous, the outer six with one pair of cells lateral and one pair introrse, the inner three with one pair extrose and one pair lateral; filaments clearly visible between glands, ca. 0.5 mm long, longer than anthers; glands enlarged, visible as triangular lobes between the outer stamens, but very low in front of the stamens and not fused. Pistil ellipsoid, ca. 1.5 mm long, ovary glabrous, style papillose. Receptacle glabrous except for a few hairs at the very base. Fruit and cupule unknown. Flowers: October. Elevation range unknown.

Collection studied. BRAZIL. RIO DE JANEIRO: Alto Macahe, *Glaziou 17731* (B, G, K, NY, P).

Pleurothyrium amplifolium is only known from the type and is also, if the label data are correct, the only *Pleurothyrium* species from southern Brazil. It belongs in the group of species with reflexed margins of tepals, small flowers, often with erect tepals and a poorly developed (or without a) marginal vein. It stands apart from the other species in this group by its distribution, broad leaves, and indumentum.

Three isotypes were annotated as *Persea cordata* Mez var. *glabra* Mez, but the holotype does not bear this annotation. *Persea cordata* var. *glabra* is a nomen nudum included in Glaziou's list of determinations, while *Persea cordata* (Vell.) Mez, the correct citation, is a later homonym of *Persea cordata* Meissner.

Pleurothyrium bifidum Nees, Syst. Laur.: 351.

1836. TYPE: Peru. Loreto: Yurimaguas, *Poeppig 2398* (GZU, LE, W destroyed?, holotype not designated). Figure 11.

Tree, to 10 m. Twigs terete, glabrous or nearly so, solid. Terminal bud brown-tomentulose. Leaves alternate, said to be clustered near tips of branches, subcoriaceous, elliptic to obovate-elliptic, 30–40 × 8–13 cm, the base obtuse or acute, the tip acuminate, acumen to 3 cm long, the upper surface glabrous, lower surface covered with a dense, minute, gray-whitish tomentellous indument; venation immersed on upper surface, midrib and lateral veins raised on lower surface, tertiary venation not visible; lateral veins 12–16 on each side, weakly loop-connected in the distal half of leaf. Petioles 3–5 cm long, glabrous. Inflorescences in axils of cataphylls, ferruginous-tomentellous, 15–25 cm long, paniculate, the upper branchlets once or twice cymosely branched, the lower ones racemosely branched, but ultimate divisions cymose; bracts subsistent at anthesis; brown-tomentellous outside, glabrous inside. Flowers white or creamy-white, 10–12 mm diam. Tepals 6, the inner three with a slightly narrower base than the outer ones, broadly elliptic, 4–5 mm long, the outer three ferruginous-tomentellous outside, the inner three with a tomentellous, triangular basal patch, otherwise papillose; inside papillose. Stamens 9, 4-celled, the cells lateral or one pair lateral-extrorse, the valves back-to-back, glands large, completely surrounding stamens, but not fully fused. Ovary ellipsoid, ca. 1 mm long, densely papillose, with 6 glabrous patches near the tip, style short, ca. 0.5 mm long, glabrous, stigma platelike. Floral tube papillose inside. Cupule a rather shallow cup,

ca. 2 cm wide and 1 cm high, verrucose, the pedicel swollen; fruit ellipsoid, 2.5 × 1.5 cm. Fruits: September. Flowers: June–September. Elevation range: 200–500 m.

Collections studied. PERU. AMAZONAS: Río Cenepa, Quebrada Chigka Entsa, *Ancuash 602* (G, MO); Bagua, Cascadas de Mayasi, along Quebrada Tambillo, *Wurdack 2047* (F, GH, K, NY, S, US). LORETO: Yurimaguas, *Poeppig 2398* (GZU, LE).

Pleurothyrium bifidum is an uncommon species, only known from three collections in Amazonian Peru. The type specimens (GZU, LE) are in bud, thus I have not been able to study flowers of the type. A type photograph (A) of the type in W shows that this specimen, probably destroyed in World War II, was also largely in bud. My floral description is based on the two recent collections and agrees with earlier floral descriptions based on the type collection. Nees stated in the original description that the leaves were clustered, but the type specimens at hand have a very short piece of the twig, which does not show if the leaves were clustered or not; the W type had clustered leaves, as can be seen on the type photo. The recent collections have the leaves more or less clustered. However, the recent material differs from the types in having thicker twigs and narrower leaves; in other characters it agrees with the type.

Pleurothyrium bifidum is closely related to *P. panurense* (Meissner) Mez, as is shown by the, for *Pleurothyrium*, very unusual, whitish indument on the lower leaf surface. *Pleurothyrium bifidum* has larger leaves and longer inflorescences and petioles than *P. panurense*; it also has a papillose ovary and floral tube (glabrous in *P. panurense*), and the flowers are slightly larger and have the inner surface of the tepals brown-papillose (glabrous in *P. panurense*). The size differences do not allow easy identification. For instance, *Krukoff 4800* is identified as *P. panurense* based on floral characters; its leaves can be interpreted equally well as large *P. panurense* or small *P. bifidum*.

Kostermans (1952) made combinations for a number of *Pleurothyrium* species in *Ocotea*; he accepted for *Pleurothyrium bifidum* the name *Ocotea bifidum* Poeppig ex Nees. However, *Ocotea bifidum* is a herbarium name cited by Nees as a synonym in the description of *P. bifidum* and is, therefore, not validly published.

Pleurothyrium bracteatum van der Werff, sp.

nov. TYPE: Colombia. Boyaca: El Humbo, ca. 130 mi. N of Bogotá, elev. 3,000 ft., *Lawrance 619* (holotype, MO; isotypes, E, F, UC, US). Figures 12, 13.

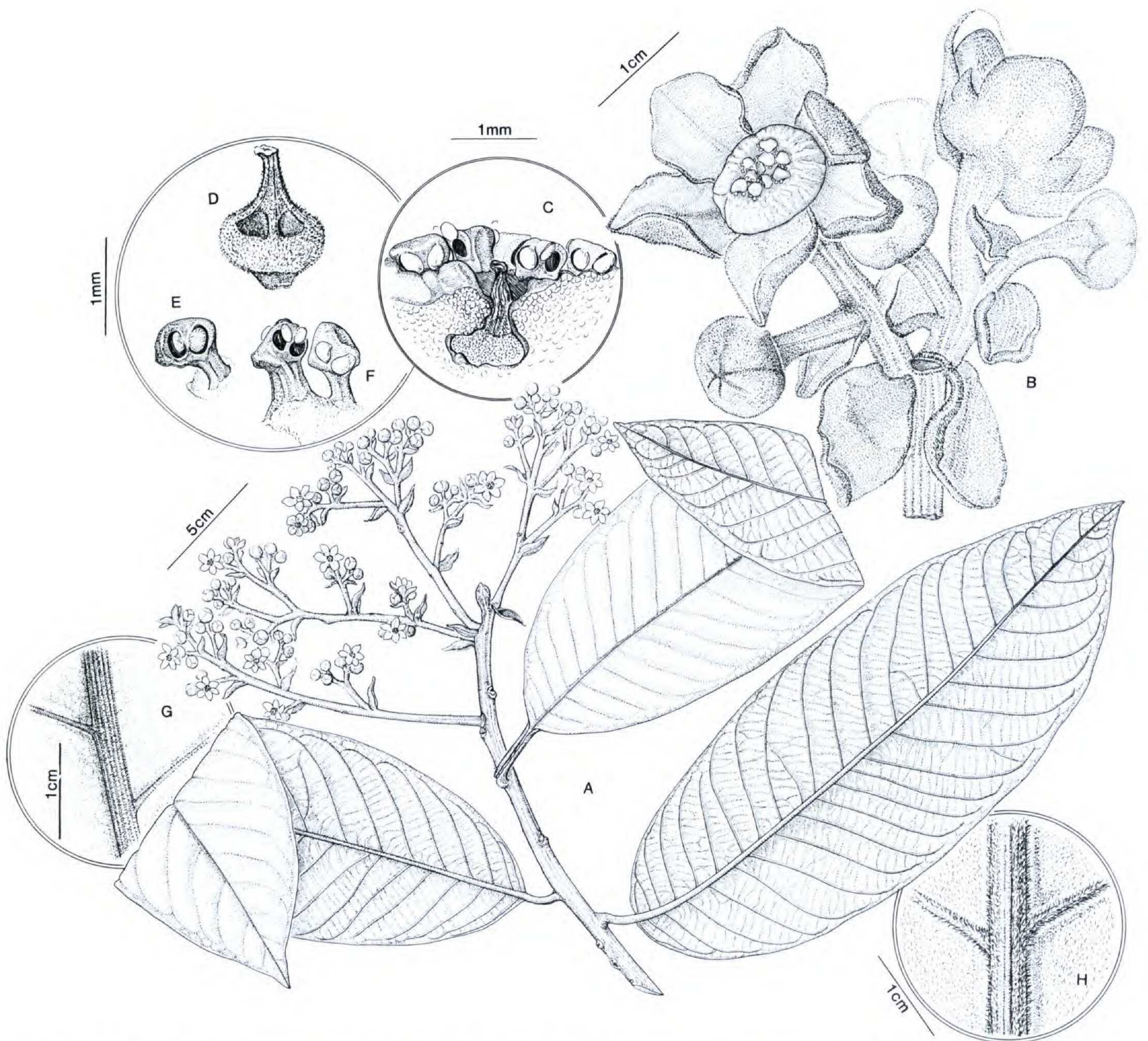


FIGURE 12. *P. bracteatum*. — A. Habit. — B. Detail of inflorescence showing bracts and flower. — C. Cross section through flower, showing pistil and stamens embedded in glands. — D. Pistil. — E, F. Stamens. — G. Detail of upper leaf surface. — H. Detail of lower leaf surface.

Arbor, 20–25 m alta. Ramuli solidi, teretes vel paullo angulati, rufo-tomentosi. Gemma terminalis ad 7 mm crassa, rufo-tomentosa. Folia alterna, subcoriacea, 15–30 × 8–12 cm, oblonga vel oblongo-elliptica, basi rotundata, apice paullo acuta, supra glabra, subtus rufo-tomentosa, nervis lateralibus 14–20 utroque costae latere, prope marginem sursum curvantibus, vena marginale in dimidio distale praesente, venatione supra immersa, subtus costa nervisque lateralibus elevatis, venatione tertia paullo elevata. Petioli rufo-tomentosi, valde canaliculati, 10–15 mm longi. Inflorescentiae ex axillis bractearum ortae, rufo-tomentosae, 10–15 cm longae, paniculatae, ramulis vulgo duplo cymae more ramosis; bracteis sub anthesi praesentibus, rufo-tomentosis, eis ad ramulorum inferiorum basim ovatis, 12–15 mm longis, eis ad cymarum terminalium basim ca. 5 mm longis. Pedicelli florum apertorum ca. 8 mm longi. Flores cremei, saltem 13 mm diametro. Tepala 6, subaequalia, late ovata, ca. 5 mm longa, intus tomentella. Stamina 9, glabra, 4-locellata, locellis lateralibus, glandulis permagnis, coalitis, stamina cingentibus. Ovar-

ium ellipsoideum, ca. 1.3 mm longum, basi glabrum, parte media tomentellum, parte superiore tomentellum 6 maculis nudis praeditum; stylum glabrum, ca. 1 mm longum. Tubus floralis intus tomentellus. Fructus ignotus.

Tree, 20–25 m tall. Twigs solid, terete or slightly ridged, reddish-brown-tomentose, 5–6 mm diam. 5 cm below the tip. Terminal buds to 7 mm thick, rufous-tomentose. Leaves alternate, subcoriaceous, 15–30 × 8–12 cm, oblong to oblong-elliptic, the base rounded, the tip slightly acute, glabrous above, rufous-tomentose below, venation immersed on upper surface, midrib and lateral veins raised on lower surface, the tertiary venation slightly raised; lateral veins 14–20 on each side, curving upward near the margin and united with the superior vein, forming a marginal vein in the upper half of the lamina.



FIGURE 13. Distribution of *P. bracteatum* (★), *P. brochidodromum* (●), *P. cinereum* (○), and *P. costanense* (■).

Petioles rufous-tomentose, strongly canaliculate, 10–15 mm long. Inflorescences in axils of cataphylls, rufous-tomentose, 10–15 cm long, paniculate, the branchlets usually twice cymosely branched; bracts present at anthesis, those at the base of the lower branchlets 12–15 mm long, ovate, rufous-tomentose, gradually reduced in size toward the ultimate divisions, the bracts at the base of the ultimate cymes ca. 5 mm long. Pedicels of open flowers ca. 8 mm long, rufous-tomentose. Flowers creamy white inside, at least 13 mm diam. (none of the flowers had all tepals spreading). Tepals 6, \pm equal, broadly ovate, ca. 5 mm long, the outer three tomentose on the outside, the inner three with a tomentose, basal triangular patch, otherwise tomentellous; all tepals tomentellous inside. Stamens 9, glabrous, 4-celled, the cells lateral and opening back-to-back, the glands strongly enlarged and forming a thick wall surrounding the stamens, fused. Ovary ellipsoid, ca. 1.3 mm long, the very base glabrous, the middle part brown-tomentellous, the upper part tomentellous with 6 bare spots where

glands touched the ovary; style ca. 1 mm long, glabrous. Floral tube rather deep, brown-tomentellous inside. Fruit unknown. Flowers: February. Elevation range: ca. 1,000 m.

Collection studied. COLOMBIA. BOYACA: El Humbo, Lawrance 619 (E, F, MO, UC, US).

Pleurothyrium bracteatum is only known from the type collection from the El Humbo region in Boyaca, Colombia; this area also yielded *Aiouea angulata* Kostermans, another Lauraceae only known from the type collected by Lawrance.

This new species can be readily identified by the large bracts of the inflorescence, which persist during anthesis. Other useful characters are the rufous pubescence (described by the collector as burnt sienna), the rounded leaf bases, and large flowers. It can be confused with *Pleurothyrium costanense* from similar elevation in Venezuela, but the latter species lacks bracts at anthesis, has smaller flowers, a distinctly pubescent style, and an almost glabrous ovary.

The collector noted that the stamens were in the form of a button. The wood is said to be soft and has no economic uses.

Pleurothyrium brochidodromum van der Werff, sp. nov. TYPE: Peru. Loreto: Maynas, km 32 of Carretera Iquitos-Nauta, *Vasquez & Jaramillo 7865* (holotype, MO; isotypes, AMAZ, F, G, HBG, NY, USM). Figures 13, 14.

Arbor, 16 m alta. Ramuli teretes, solidi, ferrugineo-tomentosi, glabrescentes. Gemma terminalis fusco-tomentosa, magna, ad 5 mm diametro. Folia ad ramulorum apices conferta, chartacea, 12–22 × 4–7 cm, elliptica vel obovato-elliptica, basi acuta, apice acuminata, supra glabra sed costa pilis parvis praedita, subtus pilis dispersis, erectis praedita (secus costam nervosque indumento densiore); supra venatione immersa, subtus costa nervisque elevata, venatione tertia paullo elevata; nervis utroque costae latere 12–15 in vena marginale terminantibus. Petioli 1.5–2 cm longi; teretes, indumento illo ramuli simile. Inflorescentiae ex axillis bractearum ortae, 8–14 cm longae, ferrugineo-tomentosae, paniculatae, ramulis 1–2-plocymae more divis. Flores 9–10 mm diametro. Tepala 6, aequalia, 3–4 mm longa, oblonga, intus ferrugineo-papillosa, extus ferrugineo-tomentella (tepala interiora margine et apice papillosa). Stamina 9, 4-locellata, locellis lateralibus, minute papillosa; glandulae magnae, stamina cingentes, coalitae. Ovarium parvum, ovoideum, in stylum attenuatum, stigmathe antheris oblecto. Fructus ignotus.

Tree, 16 m tall. Twigs terete, solid, ferruginous-tomentose, but soon glabrescent, 3–4 mm diam. 5 cm below tip. Terminal bud large, 5 mm thick, fuscous tomentose. Leaves clustered near tips of branches, chartaceous, 12–22 × 4–7 cm, elliptic to obovate-elliptic, the base acute, the tip acuminate, the upper surface glabrous except for some short hairs on midrib, the lower surface with scattered, brown, erect hairs, these denser along main veins and midrib; venation immersed on upper surface, midrib, lateral veins, and to a lesser degree tertiary venation raised on lower surface; lateral veins 12–15 on each side, the lower 2–3 arching upward, the other ones ± straight and ending in a well-developed marginal vein. Petioles 1.5–2 cm long, terete, with similar indument as twig, ca. 2 mm diam. Inflorescences in axils of cataphylls, 8–14 cm long, ferruginous-tomentose, paniculate, the branchlets 1–2 times cymosely branched, ca. 40-flowered, bracts often persisting at anthesis, ferruginous-tomentose on both surfaces, to 4 mm long (but bracts subtending flowers smaller), elliptic. Flowers green fide collectors, 9–10 mm diam. Tepals 6, equal, 3–4 mm long, oblong, spreading to slightly reflexed at anthesis, the inner surface ferruginous papillose, the outer tepals ferruginous-tomentellous on the outside, the inner three with

papillose margin and tip, otherwise tomentellous. Stamens 9, all 4-celled, finely papillose, the cells lateral; stamens ca. 1 mm long, the filaments short and nearly as wide as the anthers; glands conspicuously enlarged, completely surrounding the stamens, fused. Ovary small, ovoid, the very base glabrous, situated in the glabrous, shallow receptacle, with a band of coarse papillae near the middle, the upper part gradually narrowed into the style, finely papillose, pistil ca. 1.4 mm long; stigma in all flowers seen not exposed, but covered by the anthers. Floral tube glabrous. Fruits unknown. Flowers: August. Elevation range: ca. 150 m.

Collection studied. PERU. LORETO: Maynas, Carretera Iquitos-Nauta, km 32, *Vásquez 7865* (AMAZ, F, G, HBG, MO, NY, USM).

Pleurothyrium brochidodromum, only known from the type collection made near Iquitos, Peru, is easily identified by its sparse, erect pubescence on the lower leaf surface, clustered leaves, and floral size. Other *Pleurothyrium* species from Amazonian Peru with an erect pubescence on lower leaf surface include *P. insigne* and *P. vasquezii*. *Pleurothyrium insigne* differs in its much larger, obovate leaves, while *P. vasquezii* differs in its alternate (not clustered) leaves and smaller flowers (5–6 mm vs. 9–10 mm in *P. brochidodromum*).

A brochidodromous venation type is relatively common in *Pleurothyrium*, but is particularly clearly visible in *P. brochidodromum*. However, in such species as *P. maximum* and *P. williamsii* the brochidodromous venation is equally well developed.

Although the type collection has good young and old flowers, the stigma is hidden in all flowers seen. This is unusual in *Pleurothyrium*; normally in the species with large flowers and greatly enlarged glands the stigma is large, almost platelike, and easily visible.

Pleurothyrium cinereum van der Werff, sp. nov. TYPE: Ecuador. Esmeraldas: Panadero, 5 km from the river, *Játiva & Epling 2039* (holotype, MO; isotypes, NY, US). Figures 13, 15.

Arbor ad 32 m. Ramuli angulares, fusco-tomentelli, glabrescentes, solidi. Folia alterna, firme chartacea, 13–20 × 6–10 cm, elliptica, basi obtusa, apica acuta, raro obtusa, supra venatione impressa, subtus costa nervisque (10–14 utroque costae latere) elevatis, reticulatione paullo elevata, venatione in dimidio distale brochidodroma, supra glabra, subtus pilis parvis adpressis praedita. Petioli canaliculati, 1.5–2.5 cm longi. Inflorescentiae e axillis cataphyllorum ortae, fusco-tomentellae, 10–15 cm longi, ramulis semel vel bis cymae more divis. Pedicelli ca. 5

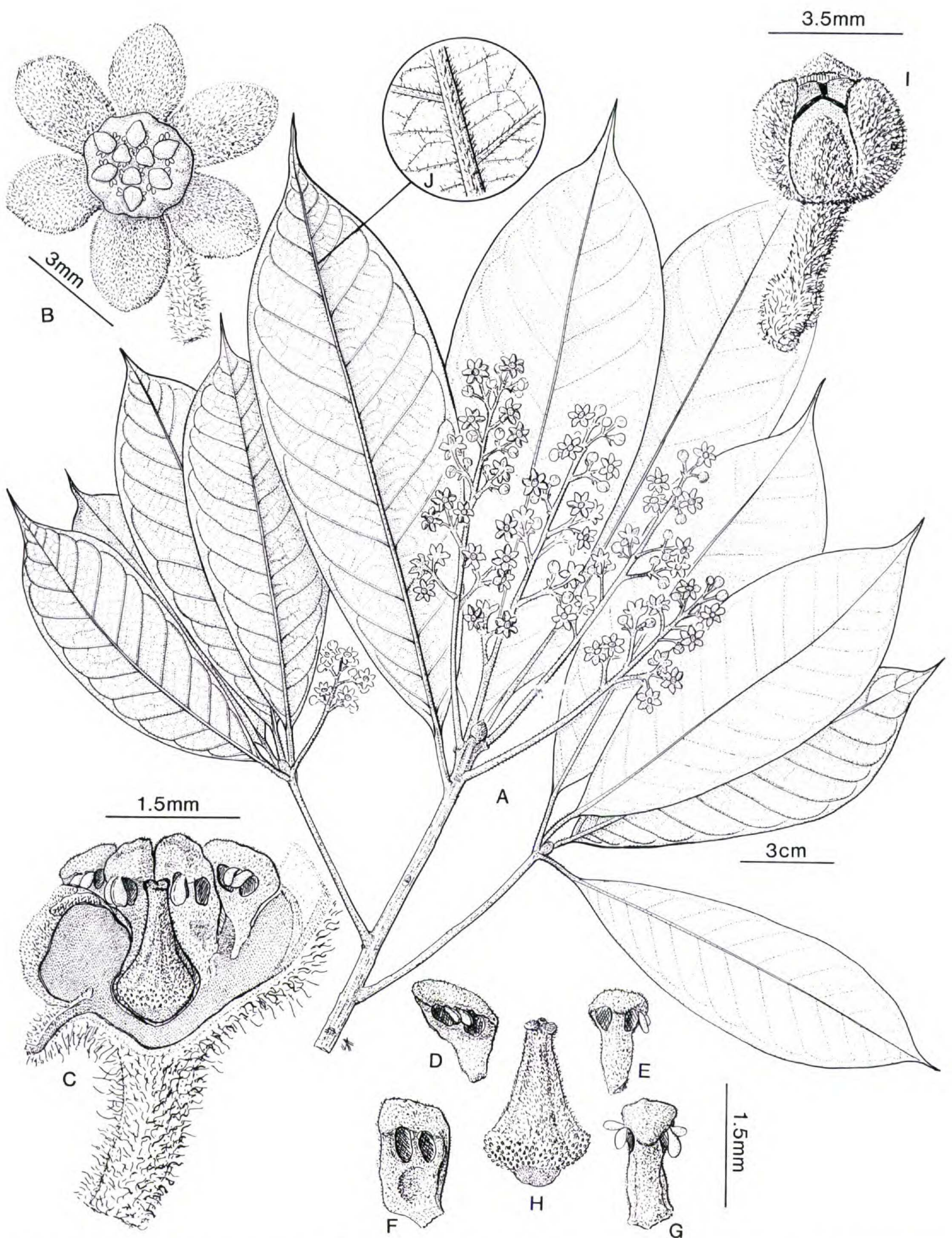


FIGURE 14. *P. brochidodromum*. — A. Habit. — B. Flower. — C. Cross section through flower. — D, E. Lateral and frontal views of outer stamen. — F, G. Lateral and frontal views of inner stamen. — H. Pistil. — I. Bud, showing indument on inner and outer tepals. — J. Detail of lower leaf surface.

mm longi. Flores rotati, 11 mm in diametro. Tepala 6, subaequalia, 3 exteriora late elliptica vel rotundata, 4 × 4 mm, extus cinereo-pubescentia, 3 interiora elliptica, 4 × 3 mm, secus basim angustata, extus cinereo-puberuli

sed basi cinereo-pubescenti, omnia intus papillosa basi cinereo-pubescenti. Stamina 9, 4-locellata, locellis dorsali-lateralibus; glandulis per dilatatis, fere stamina cingentibus, connatis. Pistillum ad 2 mm longum, cinereo-pubescenti,

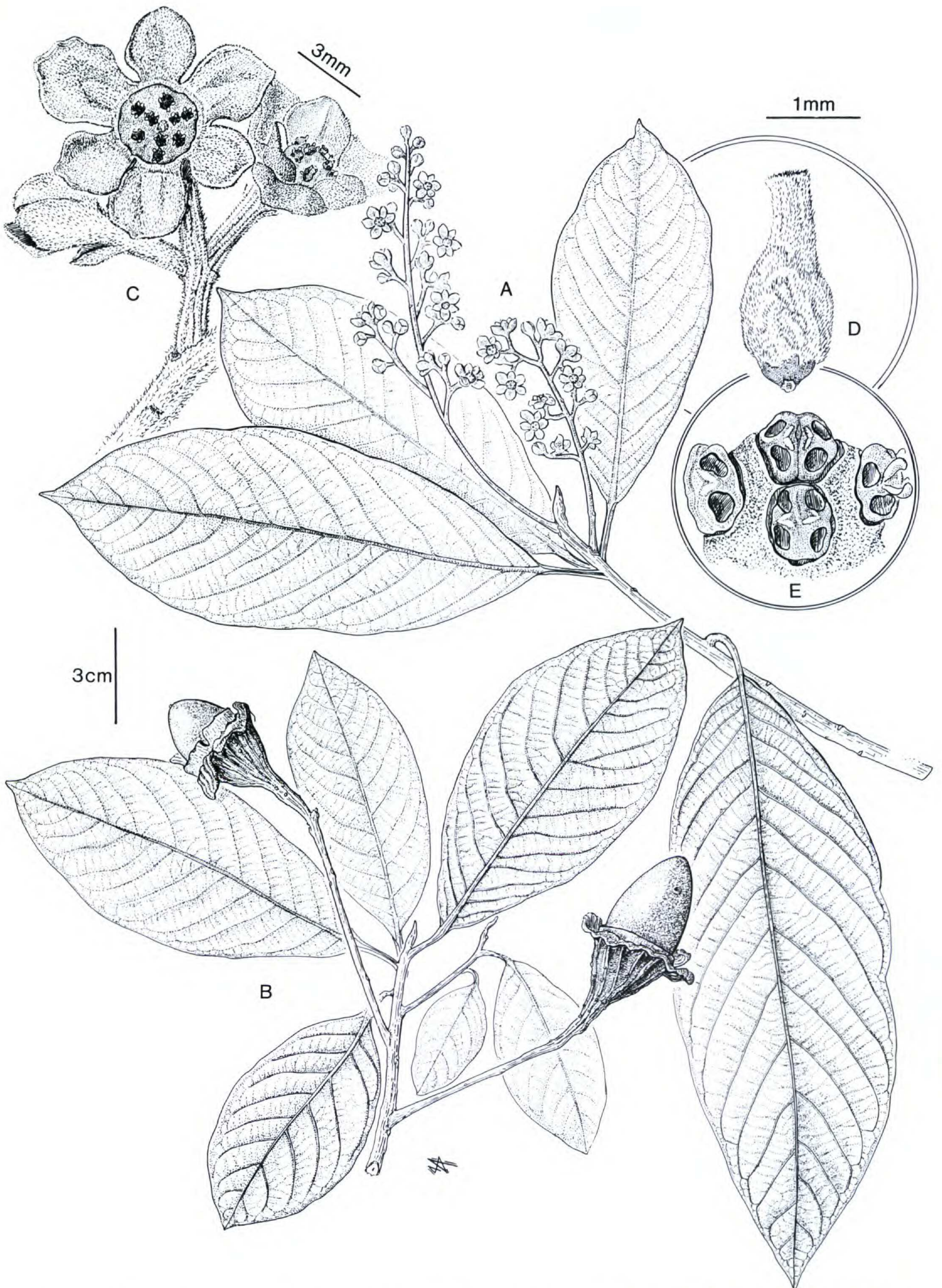


FIGURE 15. *P. cinereum*. — A. Habit, flowering. — B. Habit, fruiting. — C. Flower. — D. Pistil. — E. Detail of flower, showing embedded anthers. B from *Gentry & Smith 45117*, others from *Neill 8954*.

ovario ellipsoideo, sensim in stylum attenuato. Receptaculum intus cinereo-pubescentibus. Cupula profunda, lenticellata, tepalis persistentibus. Fructus ellipsoideus, ad 6 cm longus.

Tree, to 32 m tall, with buttresses. Twigs angular, brown-tomentellous, becoming glabrous with age, solid, 4 mm diam. ca. 5 cm below apex. Terminal bud brown-tomentellous, about as wide as the twig. Leaves alternate, firmly chartaceous, 13–20 × 6–10 cm, elliptic, the base obtuse, the tip acute, rarely obtuse, venation impressed on upper surface, midrib and lateral veins (10–14 on each side) raised on lower surface, tertiary venation slightly raised, lateral veins weakly loop-connected in the distal half of lamina, upper surface glabrous, the lower surface with varying amounts of minute, appressed hairs. Petioles canaliculate, 1.5–2.5 cm long, with similar indument as twigs. Inflorescences in axils of cataphylls, brown-tomentellous, 10–15 cm long, the branchlets once or twice cymosely branched, bracts deciduous at anthesis. Pedicels ca. 5 mm long. Flowers rotate, 11 mm diam. described as creamy-white, yellowish-ferruginous or brick-red. Tepals 6, subequal, the outer three broadly ovate to rounded, 4 × 4 mm, gray-pubescent outside, the inner three elliptic, 4 × 3 mm, narrowed toward the base, gray-puberulent outside except for a basal, triangular, gray-pubescent patch; all tepals papillose inside except for the gray-pubescent base. Stamens 9, all 4-celled, the cells dorsal-lateral and opening back-to-back; glands strongly enlarged, almost completely surrounding the outer stamens, fused. Pistil ca. 2 mm long, gray-pubescent, ovary ellipsoid and gradually narrowed into the style, the gray-pubescent style in dried flowers visible above the androecium. Floral tube gray-pubescent inside. Cupule deeply cup-shaped, lenticellate, 2 × 2.5 cm, tepals persisting on the margin of the cupule. Fruit an ellipsoid berry, to 6 cm long. Fruits: February–May. Flowers: May, July. Elevation range: sea level to 1,600 m.

Collections studied. ECUADOR. ESMERALDAS: Río Onzole, *Jativa 1104* (NY); Panadero, N of San Lorenzo, *Janse 280* (MO, NY, US); Panadero, 5 km from river, *Jativa 2039* (MO, NY, US); Panadero, *Little 21359* (MO, QAME). NAPO: Archidona, S slopes of Volcán Sumaco, *Neill 8954* (MO). PERU: LORETO: Florida, mouth of Río Zubineta in Río Putumayo, *Klug 2122* (A, F, G, GH, K, MO, S, US); Pongo de Manseriche, mouth of Río Santiago in Marañon, *Tessmann 4634* (G). SAN MARTIN: *A. Gentry & D. N. Smith 45117* (MO).

Pleurothyrium cinereum is known from several rather widely separated localities. The type collection is from the coast near Esmeraldas, Ecuador. *Little et al. 21359* was collected the same day at

the same locality and likely came from the same tree. *Janse 280*, a fruiting collection, is also from Esmeraldas. *Neill et al. 8954* was collected on the slopes of volcano Sumaco 1,150 m elevation, Napo province, Ecuador. This collection, with flowers and a fruit, has slightly smaller and more pubescent leaves than the Esmeraldas specimens and has the pleasant odor commonly encountered in *Aniba*. The third locality is along the Río Putumayo, Dept. Loreto, Peru, at 180 m elevation. The specimens from Esmeraldas have creamy-white flowers, from volcano Sumaco yellowish-ferruginous, and from Peru brick-red flowers. The collections all possess a slightly shiny upper leaf surface, a pubescent style, very slight difference in pubescence on outer surface of tepals between inner and outer tepals (much less than common in the genus), and frequently an obtuse leaf base. Visibly pubescent styles are very uncommon in *Pleurothyrium* and are an important reason for placing these collections in one species. *Pleurothyrium cinereum* is included in Little & Dixon (1969) as *Pleurothyrium* sp.

Vegetatively *P. cinereum* strongly resembles *P. steyermarkianum*. The latter species has quite different flowers (with glands forming ridges, not a central dome, and a glabrous style), and its pedicels are strongly triangular in cross section.

The common name used by the Huitot Indians, cited by Klug, is Naime-ey.

The epithet *cinereum* refers to the gray-pubescent style, one of the most distinctive features of this species.

Provisionally placed here is a fruiting collection from the San Martin Province, 20 km NW from Rioja, elevation 1,000 m (*Gentry & Smith 45117*, MO). This collection has the denser indument also found in the Neill collection from Ecuador. In leaf characters it is a good match for *P. cinereum*. The fruit is large (4 × 2–2.5 cm) and the cupule has a double margin. The outer margin is formed by the persistent tepals and the inner margin is erect, ca. 0.5 cm taller than the outer one. Such a pronounced double margin has not been seen in other collections of *Pleurothyrium*. Remnants of stamens found on the cupule clearly point to *Pleurothyrium*; they have four lateral anther cells. The Neill collection includes one weakly double-margined cupule; cupules from Esmeraldas are less mature and do not show a double margin. If the Gentry collection is not an aberration, *P. cinereum* is the only *Pleurothyrium* species with a double-rimmed cupule.

Pleurothyrium costanense van der Werff, Ann. Missouri Bot. Gard. 74: 408. 1987. TYPE:

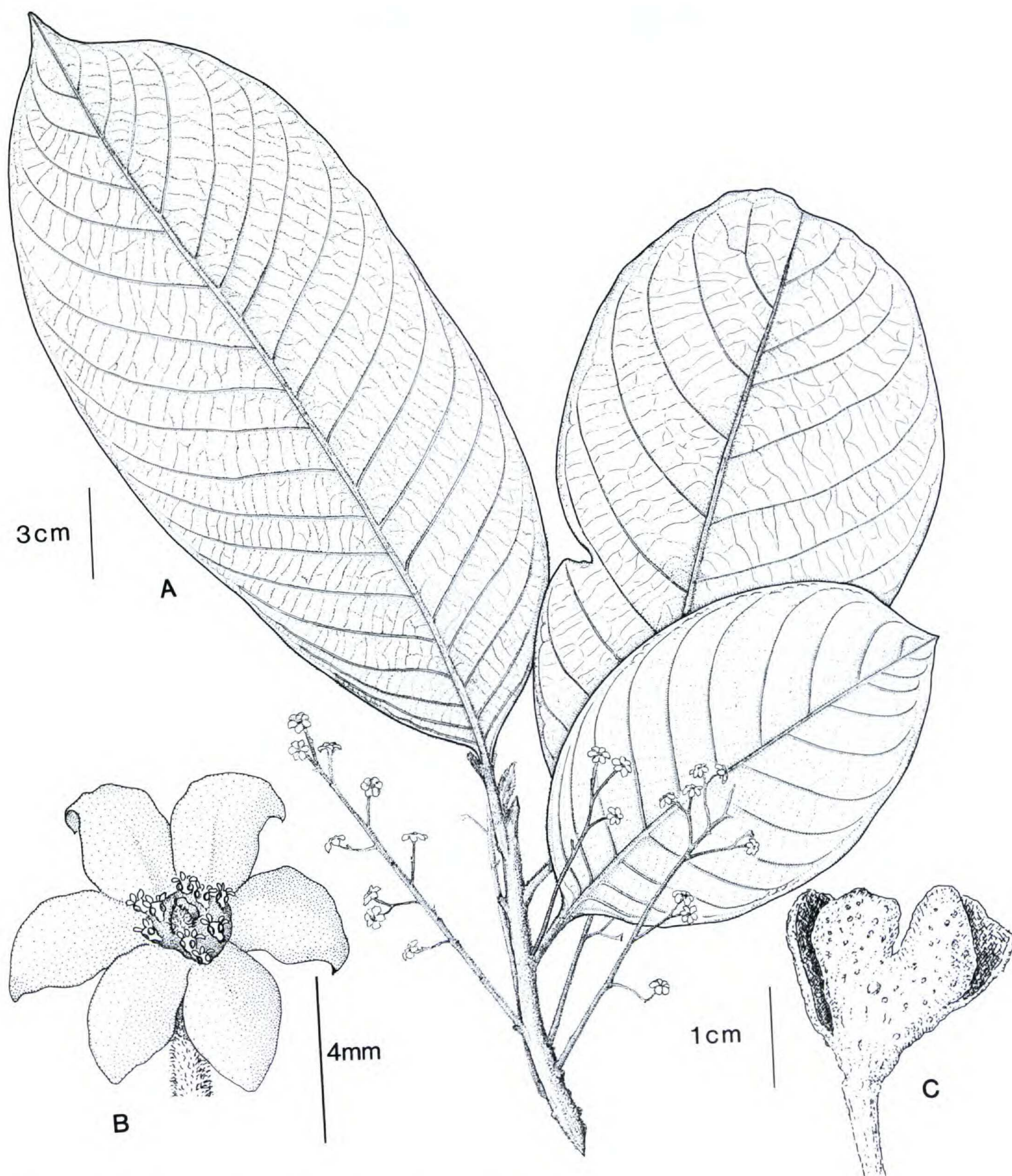


FIGURE 16. *P. costanense*.—A. Habit.—B. Flower.—C. Cupule.

Venezuela. Falcón: Sierra de San Luis, above La Chapa, *van der Werff* 3654 (holotype, U; isotype, CORO). Figures 13, 16.

Tree, to 20 m tall. Twigs somewhat angular, ferruginous tomentose, but glabrescent with age, ca. 6 mm diam. 5 cm below apex, solid. Terminal bud ferruginous tomentose. Leaves alternate, chartaceous, 20–35 × 8–17 cm, elliptic to broadly elliptic, the base obtuse or acute, the apex rounded

to shortly acuminate; upper surface with variable amounts of tomentose pubescence on midrib and lateral veins, otherwise glabrous; lower surface with a ± dense cover of erect, ferruginous hairs, this becoming tomentose on midrib and lateral veins. Venation immersed on lower surface, but midrib, lateral veins, and tertiary venation raised on lower surface; lateral veins 10–17 on each side, arching near the margin toward the tip and becoming loop-connected in the distal half of the lamina. Petioles

1.7–3 cm long, ferruginous tomentose. Inflorescences in the axils of foliage leaves or cataphylls, ferruginous tomentose, 10–20 cm long, the branchlets 2–3 times cymosely branched. Flowers white or buff, 6–9 mm diam. Tepals 6, equal, spreading at anthesis, the outer 3 ferruginous pubescent outside, inner 3 puberulous outside except for a basal, triangular pubescent patch; all tepals papillose inside, elliptic, to 4 mm long. Stamens 9, all 4-celled, the outer 6 with the lower pair lateral-extrorse, the upper pair lateral-introrse, the inner 3 with extrorse or extrorse-lateral (upper pair) cells; filaments short, glabrous. Glands conspicuous, partly enclosing the outer stamens, but not fused. Ovary ellipsoid, with 6 longitudinal lines of hairs, otherwise glabrous, gradually narrowed in the conspicuously pubescent style; pistil ca. 2.8 mm long. Receptacle glabrous inside. Cupule large, warty. Fruits: March–August. Flowers: July–September. Elevation range: 700–2,200 m.

Collections studied. VENEZUELA. *Bernardi* 6879 (G, MER, NY). ANZOATEGUI: Cerro Peonia, NE of Bergantin, *Steyermark* 61393 (F). DISTRITO FEDERAL: mountain slope above Puerto Cruz, *Whitford* 49 (A). FALCON: Sierra de San Luis, above la Chapa, *van der Werff* 3654 (CORO, U). MERIDA: Andres Bello, La Carbonera, *Marcano Berti* 1123 (MER, MO); Andres Bello, San Eusebio, *Quintero* 11 (MER). MIRANDA: Paez, Fila La Tigra, 18 km SO de Cupira, *González & Ortega* 1215 (G, MO). MONAGAS: Pueblo de Yucucual, *Lau* 10 (MO); Montaña de Aguacate, *Steyermark* 62230 (F); Caripe, Juasjuillar, *Bosque J-03* (MO), *Bosque J-03A* (MO), *Bosque J-12* (MO). SUCRE: Cerro Espejo, peninsula de Paria, *Steyermark & Rabe* 96072 (G, K, NY, US).

Pleurothyrium costanense is known from the Cordillera de La Costa, the Sierra de San Luis in Edo. Falcón, and the Venezuelan Andes, where it occurs between 700 and 2,200 m elevation. Most collections are from about 1,000 m. Only one other *Pleurothyrium* species, *P. steyermarkianum* Allen, is known from the Venezuelan Andes, but this species lacks the erect-tomentose pubescence on the lower leaf surface and the young twigs. *Pleurothyrium trianae* is not uncommon at the base of the Andes and Cordillera de La Costa, but this species differs greatly from *P. costanense* in the reflexed margins of the tepals and the dense, but short tomentellous indument on the lower leaf surface, which completely covers the leaf surface.

There is a good deal of variation in the color of the indument in *P. costanense*. Especially the type and *Steyermark* 96072 have a light color of indument, whereas some of the other collections are dark ferruginous. In other characters, such as leaf shape, type of indument, raised tertiary venation, and the short, densely pubescent style, these col-

lections agree with each other, and consequently all are placed in the same species.

Pleurothyrium crassitepalum van der Werff, sp. nov. TYPE: Colombia. Valle: Río Naya near Puerto Merizalde, elev. 5–20 m, *Cuatrecasas* 13986 (holotype, F; isotype, US). Figures 17, 18.

Arbor magna. Ramuli teretes vel subangulares, foliorum cicatibus magnis praediti, hornotini dense, minute, adpresse fusco-pubescentes, annotini glabrescentes. Gemma terminalis dense, adpresse avellino-pubescentis. Folia ad apices ramulorum congesta, firme chartacea, elliptica vel elliptico-obovata, 10–17 × 6–9 cm, basi attenuata vel cuneata, apice rotundata vel obtusa, supra glabra, subtus indumento minuto, fere papilloso, praedita; nervis lateralibus 13–16 utroque costae latere, versus marginem sursum curvatis et in dimidio distale folii venam superiorem junctis; supra venatione immersa, subtus costa, nervis lateralibus et venatione tertia elevata. Petioli 11–17 mm longi, ca. 3 mm diametro. Inflorescentiae ex axillis bractearum ortae, dense fusco-tomentulosae, 7–14 cm longae, plerumque racemosae, aliquando ramulis cymae more divisas. Pedicelli 5–11 mm longi, fusco-tomentulosi. Flores extus rufescentes, intus albidis fide coll., ca. 13 mm diametro. Tepala 6, subaequalia, late ovata, exteriora ca. 5 mm longa, interiora ca. 4 mm longa, dense fusco-tomentella in sicco, crassa. Stamina 9, 4-locellata, locellis lateralibus, antheris papillosis, glandulis magnis connatis stamina cingentibus. Ovarium glabrum, ellipsoideum, ca. 1 mm longum, style glabro, ca. 1.5 mm longo, stamina non superante. Tubus floralis glaber. Fructus ignotus.

Large tree, Twigs solid, terete or somewhat angular, with large scars of old leaves, the tips densely, but minutely, brown appressed pubescent, glabrescent on older parts, 5–6 mm diam. 5 cm below apex. Terminal bud with a dense, appressed tan pubescence. Leaves clustered near the tips of branches, firmly chartaceous, elliptic to elliptic-obovate, 10–17 × 6–9 cm, the base attenuate or cuneate, the tip rounded or obtuse, the upper surface glabrous, the lower surface covered with a short, minute, almost papillose indument; lateral veins 13–16 on each side, arching upwards near the margin and connected with the superior vein in the upper half of the lamina, the marginal vein well-developed; venation immersed on the upper surface, but midrib, lateral veins and tertiary venation raised on lower surface. Petioles 11–17 mm long, flattened on the upper side, ca. 3 mm in diameter, with a similar indument as twigs. Inflorescences in axils of cataphylls near the tips of branches, densely brown-tomentulose, 7–14 cm long, mostly racemose, but occasionally with branchlets once cymosely branched, with 10–20 flowers, bracts not present at anthesis. Pedicels 5–11 mm long, densely brown tomentulose. Flowers dark reddish brown outside, white inside fide collector, ca. 13 mm diam. Tepals 6, subequal, all

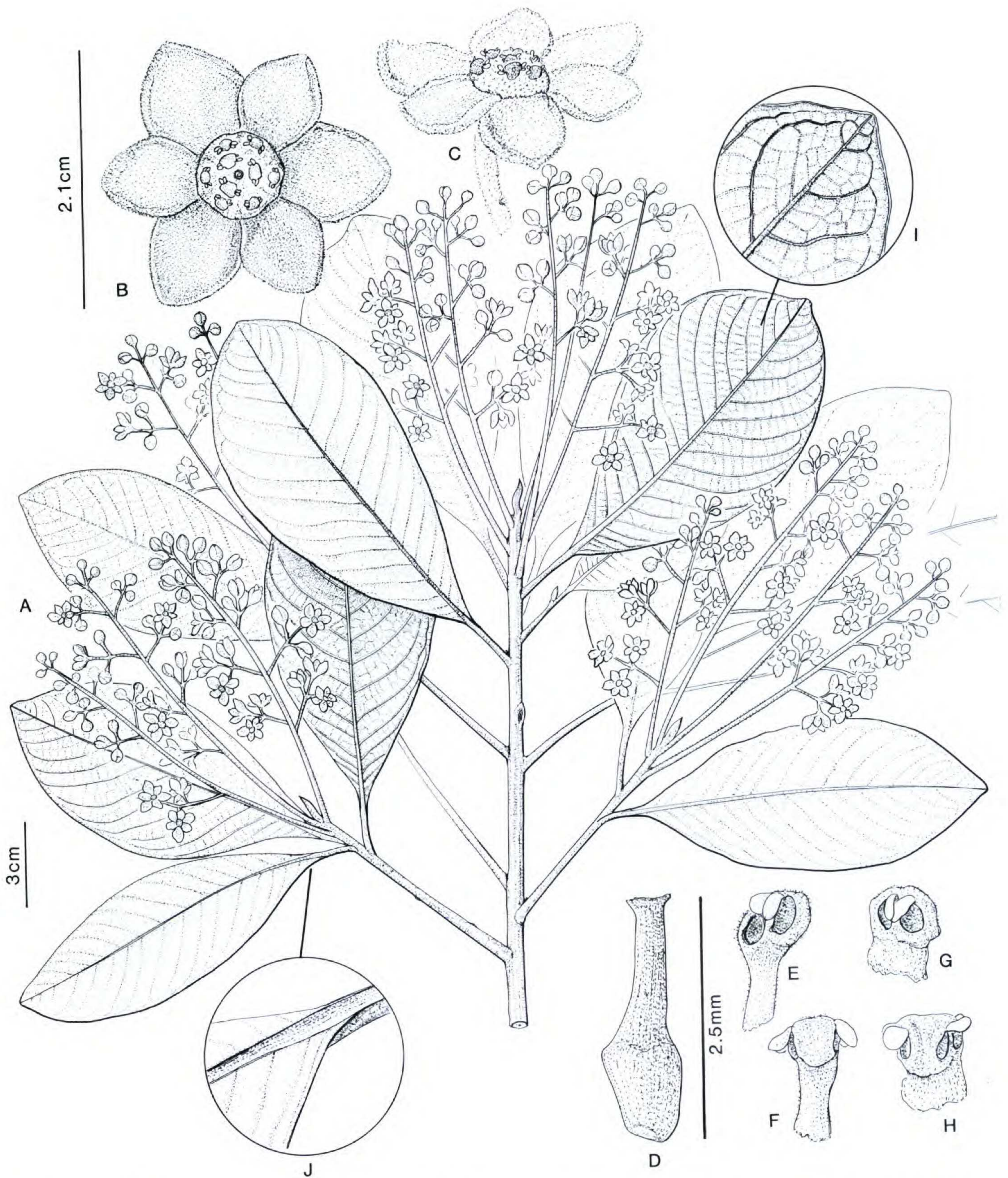


FIGURE 17. *P. crassitepalum*.—A. Habit.—B, C. Flowers.—D. Pistil.—E, F. Lateral and frontal view of outer stamen.—G, H. Lateral and frontal view of inner stamen.—I. Detail of lower leaf surface.—J. Base of leaf.

broadly ovate, the outer 3 ca. 5 mm long, the inner 3 ca. 4 mm long, all on both surfaces densely brown tomentellous, thick. Stamens 9, all 4-celled, the cells lateral and opening back-to-back, the anthers papillose; glands strongly enlarged, forming a central dome, enclosing the outer anthers and fused. Ovary glabrous, ellipsoid, ca. 1 mm long, style glabrous, ca. 1.5 mm long, not surpassing stamens; stigma not or hardly enlarged. Floral tube

glabrous. Fruit unknown. Flowers: February. Elevation range: 5–20 m.

Collection studied. COLOMBIA: VALLE: Puerto Merizalde, Río Naya, Costa del Pacifico, Cuatrecasas 13986 (F, US).

Pleurothyrium crassitepalum is one of several *Pleurothyrium* species known only from the type. Distinctive characters are the thick tepals, which



FIGURE 18. Distribution of *P. crassitepalum* (★), *P. giganteum* (●), *P. glabrifolium* (○), and *P. golfodulcense* (■).

appear almost double-margined, the very short and dense pubescence on the leaves, which is unusual in the group of species with large flowers and relatively few-flowered inflorescences, and the raised tertiary venation on the lower leaf surfaces. The clustered leaves with rounded tips are also useful characteristics. Common names for this species are *nadde*, *nande*, and *palo blanco*. The wood is used for making boards.

Pleurothyrium cuneifolium Nees, Syst. Laur.: 352. 1836. *Ocotea triangulata* Kostermans, J. Sci. Res. (Jakarta) 1: 122, 1952. TYPE: Brazil. Amazonas: Tefé (Ega), *Poeppig* 2908 (holotype not designated; B, G—2 sheets, GZU, LE). Figures 19, 20.

Pleurothyrium chrysophyllum Nees, Syst. Laur.: 351. 1836. SYNTYPES: Peru. Cuchero, *Poeppig* 1718 (B, as no. 1719, GZU, LE, US); Peru. Chachapoyas, Yambasbamba, *Matthews* 1432 (E, K).

Pleurothyrium macranthum Nees, Linnaea 21: 512.

1848. SYNTYPES: Peru. *Poeppig* 1790 (not seen); *Poeppig* 2125 (G, LE).

Tree, to 20–25 m. Twigs angular or ridged when young, becoming ± terete with age, often fistulose, often lenticellate, the young parts minutely tomentellous, glabrescent with age; diameter of young twigs 4–8 mm, depending on how strongly fistulose the twigs are. Terminal bud densely brown tomentellous. Leaves alternate, chartaceous, (narrowly) elliptic to (narrowly) elliptic-obovate, 15–30 × 7–15 cm, the base cuneate, acute or abruptly rounded, the tip obtuse or acute, lateral veins 12–18 on each side, arching upward near the margin and weakly loop-connected in the distal half of the lamina, immersed on the upper surface, midribs and lateral veins raised on lower surface, upper surface glabrous or nearly so, lower surface glabrous, papillose or tomentellous, the indument wearing off with age. Petioles 1.3–2.0 cm long, canaliculate, with similar indument as twigs. Inflorescences in axils of cataphylls, or infrequently in



FIGURE 19. *P. cuneifolium*. — A. Habit. — B. Detail of normal inflorescence. — C. Stunted inflorescence with main axis inhabited by ants. — D. Androecium and glands. — E. Pistil. — F. Young fruits. — G. Hollow twig, showing holes used by ants.



FIGURE 20. Distribution of *P. cuneifolium* (★) and *P. glabritepalum* (●).

axils of normal leaves, brown-tomentellous, 10–27 cm long, the lateral branchlets to four times cymosely branched but sometimes (when inflorescence fistulose) reduced to short spurs with clustered flowers, many-flowered, bracts often persistent during anthesis, ovate, to ca. 5 mm long, tomentellous on both surfaces. Pedicels of variable length, the lateral flowers of a cyme often nearly sessile, but flowers on fistulose inflorescences with pedicels of up to 7 mm long, with same indument as inflorescence. Flowers white, yellow to yellowish red, from 7 to 14 mm diam. Tepals 6, equal, \pm erect, elliptic or elliptic-ovate, 3–7 mm long, the outer 3 (minutely) tomentellous outside, inner 3 with a basal, triangular, (minutely) tomentellous patch, otherwise glabrous, all tepals glabrous inside (rarely papillose), the margins plane or inrolled, not reflexed. Stamens 9, 4-celled, the lower 2 cells lateral-extrorse, the upper 2 lateral-introrse; glands strongly enlarged, surrounding the base of the outer stamens, fused. Pistil 2–3 mm long, the ovary about as long as the style or slightly shorter, sometimes well defined, sometimes gradually narrowed

into the style, the lower $\frac{1}{3}$ – $\frac{2}{3}$ glabrous, the remainder (and the style) papillose, the stigma often platelike. Floral tube glabrous inside, rarely pubescent. Cupule cup-shaped, (sometimes?) with 6 thick lobes, warty, ca. 2 cm wide, 1 cm high. Fruit ovoid, ca. 2 cm long. Fruits: February–March. Flowers: nearly year-round. Elevation range: 100–1,800 m.

Collections studied. BRAZIL. AMAZONAS: ad Ega (= Tefé), *Poeppig* 2908 (G); near Rio Chipurana, *Huber* 1557 (G). COLOMBIA: ANTIOQUIA: Anori, Planta Providencia, *Shepherd* 537 (MO); Mpio. de San Carlos, near ISA hydro-electric dam, *McPherson* 13365 (MO); Mpio. de San Luis, sector Río Samana–Río Claro, vereda Tulipan, *Cogollo* 170 (MO). BOYACA: El Humbo, 130 mi. N of Bogotá, *Lawrance* 780 (A, F, G, UC, US). HUILA: *Little* 8488 (A). ECUADOR: MORONA-SANTIAGO: along new road Mendez–Morona, *van der Werff* 11157 (MO). NAPO: 8 km Río abajo de Misahualli, *Neill* 7019 (F, K, MO), *Neill* 7128 (MO). PERU: CUCHERO: *Poeppig* 1718 (US); Peruvia subandina, *Poeppig* 1845 (G), *Poeppig* 2125 (G). AMAZONAS: Quebrada de Bashuchunuk, *Kayap* 145 (F, G, MO); Quebrada Kayamas, Río Cenepa, *Kayap* 648 (MO). CHACHAPOYAS: Yambrasbamba, *Matthews* 1432 (E, K). CUZCO: Hda. Santa Rosa (Convención), *Soukop* 910

(F). JUNIN: Chanchamayo, Mina Pichita, above San Ramon, *van der Werff* 8673 (MO); Oxapampa, Chontabamba, *Smith* 3061 (MO). LORETO: Quistocochas, *Ayala* 574 (MO); Fortaleza, near Yurimaguas, *Klug* 2779 (A, F, G, GH, K, MO, S, US); Balsapuerto, *Klug* 2931 (A, F, G, GH, K, S); Cachipuerto, Río Cachiyacu, *Klug* 3116 (A, F, G, GH, K, MO, S, US); Pumayacu, between Balsapuerto and Moyabamba, *Klug* 3195 (A, F, G, GH, K, MO, NY, S), *Klug* 3228 (A, F, G, GH, K, MO, NY, S, US); La Victoria on the Amazon River, *Williams* 2715 (F). MADRE DE DIOS: Tambopata, *Gentry* 45760 (MO); Tambopata Nature Reserve, *Gentry* 57817 (MO); Tambopata, Cuzco Amazonico Lodge, *Nuñez* 12207 (MO). PASCO: Palcazu Valley, *Hartshorn* 2631 (MO); Palcazu Valley, Buenos Aires, *Hartshorn* 2937 (MO); Oxapampa, Huancabamba, *Reynel* 102 (MO); Oxapampa, Chontabamba valley, 2–8 km W of Oxapampa, *Gentry* 39902 (MO); Oxapampa, Distr. Iscozacín, Palcazu valley, *Pariona* 63 (MO); Oxapampa, Chontabamba, 2 de Mayo, *Smith* 1743 (G, MO), *Smith* 1756 (G, MO); Oxapampa, Villa Rica, *van der Werff* 8266 (MO), *van der Werff* 8287 (MO); Oxapampa, Villa Rica, Santa Polonia Alta, *van der Werff* 8291 (MO); Oxapampa, near Oxapampa, *van der Werff* 8346 (MO). SAN MARTIN: Zepalacio, near Moyabamba, *Klug* 3567 (F, G, GH, MO, NY, S, US). UCAYALI: Distrito Inahuaya, Comunidad de Santa Rosa, *Campos* 364 (MO); 65 km NE of Pucallpa, *Gentry* 58574 (MO).

As accepted here, *P. cuneifolium* is a wide-ranging species, known from Colombia, Ecuador, Peru, and Brazil, and occurs in the Amazonian lowlands and up to 1,800 m in the Peruvian Andes. Given its wide distribution and presence in different habitats, it is not surprising to find that it is a variable species. The two species placed in synonymy under *P. cuneifolium*, *P. chrysophyllum* and *P. macranthum*, were not published at the same time by Nees and he did not discuss the characters that separate the three species. Meissner (1864) regarded *P. chrysophyllum* as scarcely more than a variety of *P. cuneifolium*, differing in a denser indument, slightly smaller flowers, shorter pedicels, more branched inflorescences, and flowers with a linear bract near their base. *Pleurothyrium macranthum* differed, fide Meissner (1864), in its larger flowers. Mez (1889) placed *P. macranthum* under *P. cuneifolium*, but kept *P. chrysophyllum* apart; he separated the two on the relative length of the style and ovary: the style longer than the ovary in *P. cuneifolium* and shorter in *P. chrysophyllum*. I found this not a reliable character: in most flowers I dissected the style was about as long as the ovary, and it seemed that often in old flowers the apical part of the style and the stigma had fallen off, which makes it unsuitable as a character to separate two taxa. MacBride (1938) did not mention *P. macranthum* and separated *P. cuneifolium* and *P. chrysophyllum* by the density of their indument on the leaves. The denser indument occurs mostly on specimens from

higher elevations, such as the syntypes of *P. chrysophyllum* and several collections from the Oxapampa area (1,500–1,800 m), but *Ayala* 574 (Quistacochas, near Iquitos, 140 m) is equally tomentellous. Because minutely tomentellous specimens have been collected near Oxapampa and in the lowlands, and no other characters are restricted to the collections with denser indument, I reduce *P. chrysophyllum* to synonymy. The larger number of collections now available show that there are no discontinuities in flower size, and thus *P. macranthum* cannot be recognized as a distinct taxon. The largest flowers, with tepals to 7 mm long, are found on three Klug collections (3195, 3228, and 3567), which have strongly fistulose branches and fistulose inflorescences. The branchlets of the inflorescences have, in these collections, been reduced to short spurs bearing a cluster of flowers. This inflorescence shape is quite similar to that of the type of *P. poeppigii* and, indeed, the Klug collections had in some herbaria been annotated as *P. poeppigii*. However, the flowers of *P. cuneifolium* are clearly larger, lack reflexed margins of their tepals, and are glabrous on the inner surface of the tepals.

Included in *P. cuneifolium* are a few collections with entirely glabrous leaves, for instance, *Lawrance* 780. *Neill* 7019 provides the link between the collections with glabrous leaves and tomentellous leaves; it has young, tomentellous and older, glabrous leaves.

Unfortunately, fruiting material of this species is not well known. A common name in the Oxapampa region is roble zapallo, because the cupule has six thick ribs, like the ribs on a squash. This is both unusual for Lauraceae and easy to see on fresh material, but disappears largely on dried specimens. It seems that this cupule type also occurs in lowland populations (Palcazu valley). Flowering material of the roble zapallo fits very well in *P. cuneifolium*.

Infrequently found in Lauraceae are the strikingly lenticellate twigs of many collections of *P. cuneifolium*; other useful characters for *P. cuneifolium* are the fistulose twigs, tomentellous inflorescences, (usually) glabrous inner face of tepals, and the more or less erect tepals (especially the inner ones) at anthesis. Although *P. cuneifolium* lacks reflexed margins of the tepals, I do not think its closest relatives are among the other species with plane tepals. Leaf shape, venation, the more or less erect tepals, and indument of the pistil all suggest a relationship with the species with reflexed margins of tepals, such as *P. trianae* and *P. poeppigii*. Probably also closely related is *P. obovatum*,

a species with fistulose twigs (and sometimes fistulose inflorescences), more or less erect tepals at anthesis, and some lenticels on the small piece of twig I have seen.

A few specimens of *Pleurothyrium cuneifolium* lacked a fistulose stem and would key to *P. trianae*, while very few collections of *P. trianae* had a fistulose stem and would key to *P. cuneifolium*. Apart from the characters used in the key, these two species can be separated as follows: *P. cuneifolium* has longer tepals (3–7 mm vs. ca. 2 mm), larger and more persistent bracts protecting the flower buds, and has the inner surface of the tepals usually glabrous (papillose in *P. trianae*).

Pleurothyrium giganthum van der Werff, sp. nov. TYPE: Ecuador. Los Ríos: Río Palenque Science Center, km 56 Quevedo–Sto. Domingo, *Dodson 18217* (holotype, QCNE). Figures 18, 21.

Arbor, ad 30 m alta. Ramuli angulares, solidi, fusco-tomentosi, cicatricibus conspicuis et plerumque cataphyllis adpressis praeediti. Cataphylla 1–2.5 cm longa. Gemma terminalis fusco-tomentosa, ad 7 mm longa. Folia ad apices ramulorum aggregata, chartacea, 30–60 × (10–)15–24 cm, obovata vel obovato-elliptica, sensim versus basim attenuata, basi rotundata, apice apiculata vel rotundata; supra costa nervisque fusco-pubescentibus, lamina pilis paucis erectis, maturitate deciduis praedita, infra costa nervisque fusco-tomentosis, lamina pilis erectis praedita; nervis lateralibus 15–20 utroque costae latere, supra immersis, subtus costa nervisque elevatis, reticulatione minus elevata; venatione in dimidio distale brochidodroma. Petioli crassi, fusco-tomentosi, 5–10 mm longi. Inflorescentiae ex axillis cataphyllorum ortae, foliis perbreviores, fusco-tomentosae, racemosae. Flores virides. Tepala 6, subaequalia, tres interiora basi magis angustata, omnia margine albida, intus et extus pubescentia. Stamina nova, glandulis magnis connatis stamina cingentibus. Ovarium et receptaculum glabrum. Fructus immaturus in cupula inclusus; cupula immatura hexangularis, lenticellata, sensim in pedicello attenuata.

Tree, to 30 m tall. Twigs roundly angular, solid, brown-tomentose, diameter 7–9 mm ca. 5 cm below the tip with conspicuous scars of fallen leaves, often with cataphylls at the base of the most recent growth, these cataphylls appressed and 1–2.5 cm long. Terminal bud brown-tomentose, ca. 7 mm long, narrower than the twig. Leaves clustered near the tips of the branches, chartaceous, 30–60 × (10–)15–24 cm, obovate or obovate-elliptic, gradually narrowed toward the base, the base abruptly rounded, the tip shortly acute to rounded, lateral veins 15–20 on each side, immersed on the upper surface, the midrib strongly raised on the lower surface, lateral veins and tertiary venation also raised on lower surface; lateral veins arching upward near the margin and becoming loop-con-

nected in the distal half; upper surface drying dark green, with brown-tomentose pubescence along the midrib, less so along the lateral veins, the lamina with scattered, erect hairs, which wear off with age; lower surface with brown-tomentose midrib and lateral veins, the lamina with erect hairs, which leave the surface readily visible. Petioles brown-tomentose, 5–10 mm long and 4–6 mm thick. Inflorescences racemose, in the axils of cataphylls below the leaves, ca. 6 cm long, much shorter than the leaves, brown-tomentose, the flowers subtended by brown-tomentose bracts ca. 5 mm long. Pedicels ca. 1.2 cm long, brown-tomentose, gradually widened toward the buds, 3-angled, the ridges continuing as a low keel on the 3 outer tepals. Flowers ca. 2 cm diam., light green with whitish margins. Tepals 6, subequal, the outer 3 ca. 10 × 9 mm, the inner 3 ca. 7 × 7 mm, more constricted at their base than the outer 3, broadly ovate to broadly elliptic, pubescent on both surfaces. Stamens 9, the valves back to back, glands strongly enlarged, completely enclosing the stamens and fused. Ovary (in young fruit) subglobose, glabrous; floral tube glabrous inside. Young fruits fully enclosed in cupule, this lenticellate, gradually narrowed into pedicel, ca. 2.5 cm long, and strongly 6-angled. Fruits: May. Flowers: January, September.

Collections studied. ECUADOR. LOS RÍOS: Río Palenque Science Center, *Dodson 10181* (MO), *van der Werff 12362* (MO); Río Palenque Science Center, *Dodson 13632, 18217* (both QCNE), *Dodson 6302, van der Werff 9471* (both MO).

Pleurothyrium giganthum is only known from one or two trees at the Río Palenque Science Center. Characteristic for this species are the large, clustered leaves, the conspicuous cataphylls, and the erect pubescence on the lower leaf surface. This species was first collected flowering in January 1983, but the collected flowers were later lost. Immature fruits were collected in May 1987, also indicating January–February as the flowering season. Since 1987, C. Dodson regularly checked the only known tree for flowers and finally, in September 1990, the tree became deciduous and flowered briefly when the new foliage developed.

The specific epithet is based on the Greek words *gigas* (giant) and *anthos* (flower) and refers to the very large flowers of this species.

This species was included in the *Flora of Río Palenque* (Dodson & Gentry, 1978) as *Ocotea* sp. nov.

Pleurothyrium glabrifolium van der Werff, sp. nov. TYPE: Ecuador. Napo: Río Payamina, 2–10 km S of the road Coca–Loreto, *Cerón*

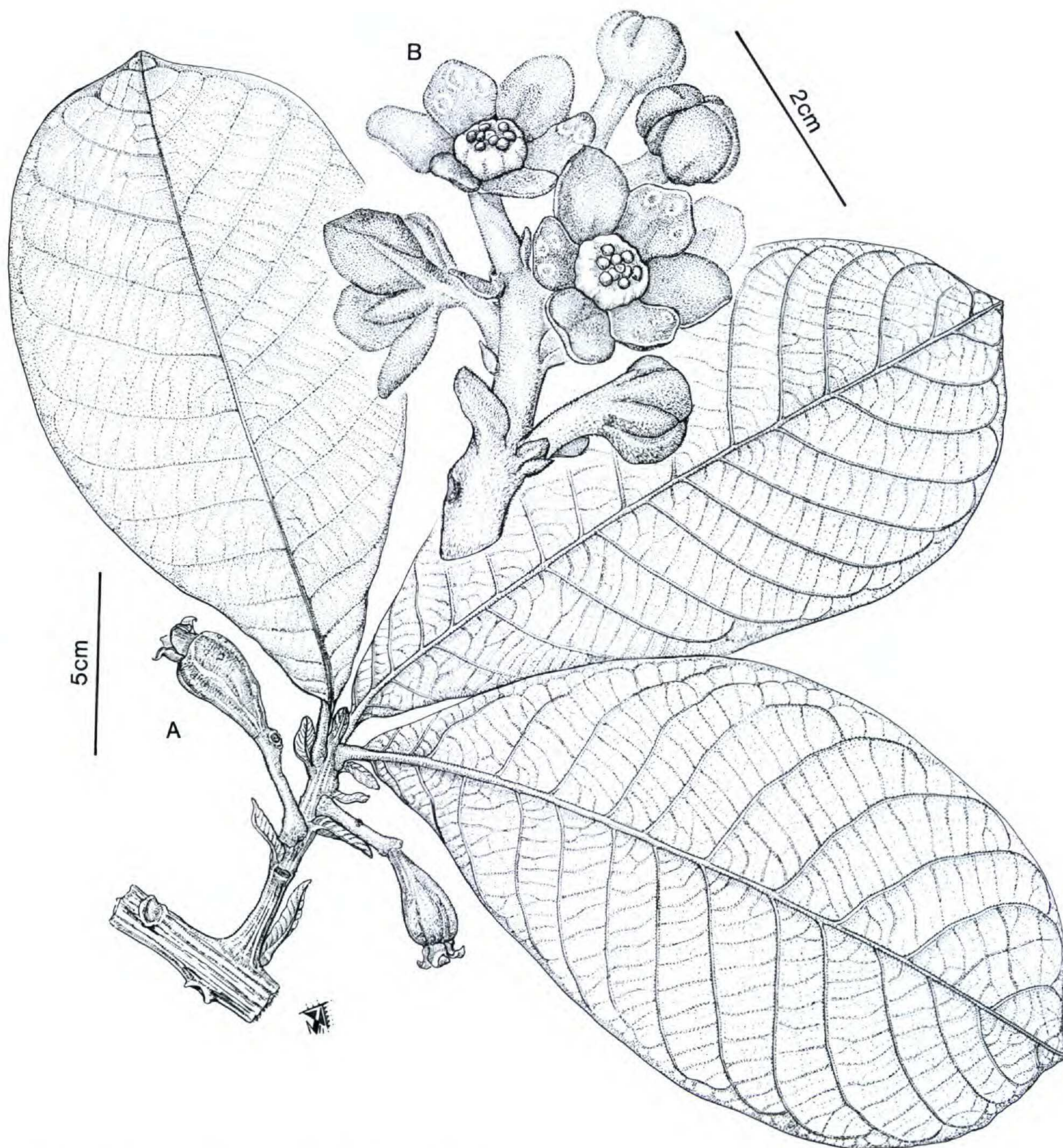


FIGURE 21. *P. giganthum*. —A. Habit.—B. Inflorescence.

& Palacios 3017 (holotype, MO; isotypes, AAU, C, COL, G, HBG, K, LE, NY, QAME, QRS, U, US). Figures 18, 22.

Arbor, ad 15 m. Ramuli teretes, solidi, ad apicem brunneo-tomentosi, glabrescentes. Gemma terminalis brunneo-tomentosa. Folia alterna, subcoriacea, elliptica, 14–25 × 6–9 cm, basi acuta, apice acuminata, glabra; supra glanduloso-punctata, venatione immersa; subtus costa nervisque elevatis, reticulatione paullo elevata; nervis utroque costae latere 12–16, in dimidio distale venatione brochidodroma. Petioli 1.5–3 cm longi, canaliculati, indumento ramulis similes. Inflorescentiae ex axillis bractearum ortae, 7–16 cm longae, brunneo-tomentellae, paniculatae, bracteis ad anthesim deciduis. Flores 6–7 mm diametro. Tepala 6, aequalia, ovata, ca. 3 mm longa, 3 exteriora extus tomentella, intus glabra, 3 interiora extus basi tomentella, demum glabra, intus glabra. Stamina 9, 4-locellata, locellis lateralibus, filamentis quam antheris brevioribus; glandulis magnis, connatis, stamina cingen-

tibus. Pistillum glabrum, 1 mm longum, stylo breve, stigmatate peltata. Receptaculum glabrum. Fructus ignoti.

Tree, to 15 m tall. Twigs terete, solid, the very tip and terminal bud brown-tomentose, older parts becoming glabrous, ca. 4 mm diam. 5 cm below apex. Leaves alternate, subcoriaceous, elliptic, 14–25 × 6–9 cm, the base acute, tip acuminate, glabrous on both surfaces, the upper surface gland-dotted, venation immersed on upper surface, costa and lateral veins raised on lower surface, the tertiary venation less so; lateral veins 12–16 on each side, curving upward near the margin and becoming loop-connected in the distal half of the lamina. Petioles 1.5–3 cm long, canaliculate, with similar tomentum as the twig. Inflorescences in axils of cataphylls, 7–16 cm long, brown-tomentellous, pa-



FIGURE 22. *P. glabrifolium*. — A. Habit. — B. Flower. — C. Cross section of flower. — D. Detail of inflorescence. — E. stamen. — F. Pistil.

niculate, many-flowered, the branchlets 1–2 times cymosely branched, bracts mostly deciduous at anthesis. Pedicels 2–3 mm long, brown-tomentellous. Flowers 6–7 mm diam., whitish. Tepals 6, equal, ovate, ca. 3 mm long, tomentellous outside, but inner 3 with glabrous margin and tip; glabrous inside. Stamens 9, glabrous, 4-celled, the cells lateral; filaments shorter than the anthers, ca. 0.2 mm long; glands enlarged, fused, completely enclosing the stamens. Pistil glabrous or nearly so, ca. 1 mm long, the style very short, stigma plate-like. Floral tube shallow, glabrous; ovary largely covered by the enlarged glands. Fruits unknown. Flowers: December. Elevation range: 250–300 m.

Collections studied. ECUADOR. NAPO: Río Payamino, 2–10 km S of Carretera Coca–Loreto, *Ceron & Palacios 3017* (AAU, C, COL, G, HBG, K, LE, MO, NY, QAME, QRS, U, US); El Chunchu, 6 km from Río Payamino, *Palacios 2288* (MO).

Pleurothyrium glabrifolium is only known from two collections, made in the same area in the lowlands of eastern Ecuador. The combination of glabrous inner surface of tepals, glabrous and alternate leaves is characteristic for this species. The only other Amazonian species with the inner surface of the tepals glabrous is *P. panurense*, but that species has clustered leaves with a minute, whitish, and dense indument on the lower leaf surface. The completely glabrous stamens and pistil of *P. glabrifolium* are an uncommon character in *Pleurothyrium*.

Pleurothyrium glabritepalum van der Werff, sp. nov. TYPE: Colombia. Choco: hills behind Bahia Solano (Puerto Mutis), *Gentry & Forero 7201* (holotype, MO; isotypes, HBG, U). Figures 20, 23.

Arbor, ad 8 m alta. Ramuli solidi, teretes, porphyreo-tomentosi, glabrescentes. Gemma terminalis parva, porphyreo-tomentosa. Folia alterna, subchartacea, elliptica, 10–18 × 3.5–6 cm, basi acuta, apice acuminata, acumine 1–2 cm longo, supra glandulo-punctata et pilis dispersis praedita sed secus costam nervosque laterales indumento densiore, subtus pilis subdispersis arrectis praedita, indumento paginam non tegente, sed secus costam nervosque tomentoso. Nervi laterales 5–8 utroque costae latere, venatione brochidodroma in dimidio distale, supra immersa subtus costa nervisque elevatis, venatione tertia paullo elevata. Petioli 10–15 mm longi, teretes. Inflorescentiae ex axillis bractearum ortae, 2–4 cm longae, 1–3-florae, porphyreo-tomentosae, sub anthesi bracteis deciduis. Flores ca. 13 mm diametro. Tepala 6, subaequalia, ovata, 3 exteriora 5.5 mm longa, extus tomentulosa, intus glabra, 3 interiora 4.5 mm longa, extus basi tomentulosa, demum glabra, intus glabra. Stamina 9, glabra, 4-locellata, locellis lateralibus, glandulis incrassatis stamina cingenti-

bus, coalitis, ovarium depresso globosum, glabrum, ca. 1 mm diametro, tubus floralis glaber. Fructus ignotus.

Tree, at least 8 m tall fide collectors. Twigs solid, terete, brown-tomentose when young, glabrescent, 2–3 mm diam. ca. 5 cm below the tip. Terminal bud small, brown-tomentose. Leaves alternate, thinly chartaceous, elliptic, 10–18 × 3.5–6 cm, the base acute, the tip acuminate, the acumen 1–2 cm long, the upper surface with gland dots and scattered brown hairs, these much denser along midrib and lateral veins, the lower surface with a rather sparse, erect pubescence, the hairs somewhat wrinkled and not covering the leaf surface; indument brown-tomentose along midrib and lateral veins; lateral veins 5–8 on each side, venation immersed on upper surface, midrib and lateral veins raised on lower surface, the tertiary venation slightly so, lateral veins arching upward near the margin and weakly loop-connected in the distal half of the lamina. Petioles 10–15 mm long, terete, with similar pubescence as twigs. Inflorescences in axils of cataphylls, 1–3-flowered, 2–4 cm long, brown-tomentose, bracts lacking at anthesis. Pedicels 4–5 mm long, tomentose. Flowers green with tan center (fide collectors), ca. 13 mm diam. Tepals 6, subequal, the outer three 5.5 mm long, the inner three 4.5 mm long, the outer three tomentulose outside, inner three with a basal, triangular tomentulose patch, otherwise glabrous; all tepals with a glabrous inner surface. Stamens 9, 4-celled, glabrous, the cells lateral and opening back-to-back, glands strongly enlarged, surrounding the stamens, fused; ovary depressed globose, glabrous, ca. 1 mm diam., receptacle glabrous inside. Fruit unknown. Flowers: January. Elevation range: below 250 m.

Collection studied. COLOMBIA. CHOCO: hills behind Bahia Solano (Puerto Mutis), *Gentry & Forero 7201* (HBG, MO, U).

Pleurothyrium glabritepalum, named after the glabrous inner surface of the tepals, is only known from the type collection. Useful characters for its identification are the following: the more or less erect pubescence, which is also present on the upper leaf surface, the gland dots on the upper leaf surface, the alternate, acuminate thin leaves, the few-flowered inflorescences, and the glabrous inner surface of the tepals. The leaves have, for the genus, few lateral veins and a marginal vein is weakly developed.

Pleurothyrium golfodulcense Burger & Zamora, *Fieldiana Botany*, New Series, 23: 115.

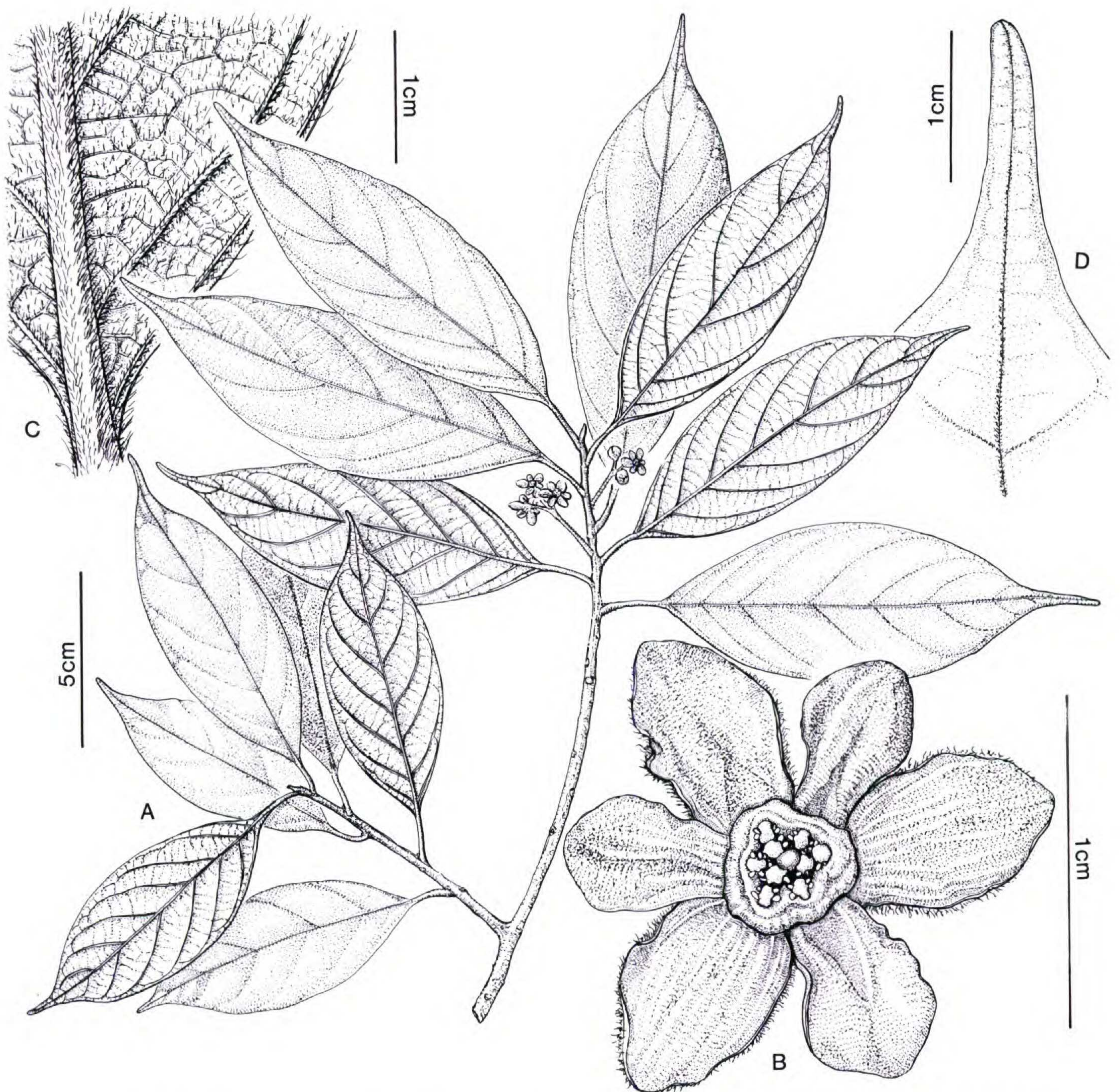


FIGURE 23. *P. glabritepalum*.—A. Habit.—B. Flower.—C. Leaf base, showing indument.—D. Leaf apex.

1990. TYPE: Costa Rica. Puntarenas: Alto de las Mogas, Sanchez, Zamora & Brenes 1228 (holotype, CR not seen; isotype, F not seen). Figures 18, 24.

Tree, to 15 m tall. Twigs terete, solid, gray pubescent, 2–3 mm diam. ca. 5 cm below tip. Terminal bud densely gray-pubescent. Leaves alternate, thinly chartaceous to coriaceous, 10–20 × 4–7 cm, elliptic to elliptic-obovate, base acute or obtuse, apex acuminate, acumens to 2 cm long, upper surface glabrous, except for the ± pubescent midrib, gland-dotted, lower surface glabrous or with minute appressed hairs, but midrib and to a lesser degree lateral veins pubescent; lateral veins 6–9; loop-connected in distal half of lamina, venation

immersed on upper surface, midrib and lateral veins raised on lower surface. Petioles 6–22 mm long. Inflorescences in axils of cataphylls or normal leaves, to 10 cm long, racemose, ferruginous pubescent, the lateral branches often subtended by an elliptic bract, to 6 mm long, pubescent on both surfaces; pedicels to 14 mm long, often with a bracteole halfway between inflorescence axis and flower. Flowers white, rotate, 9–12 mm diam. Tepals 6, equal, elliptic, 4–6 mm long, ca. 3 mm wide, gray to ferruginous pubescent outside, papillose inside. Stamens 9, 4-celled, the cells lateral to apical, opening back-to-back, the glands strongly enlarged and, together with the stamens, forming a dome 2.5 mm wide and 1 mm high, the glands enclosing the stamens, but not fully fused. Pistil 2.2 mm

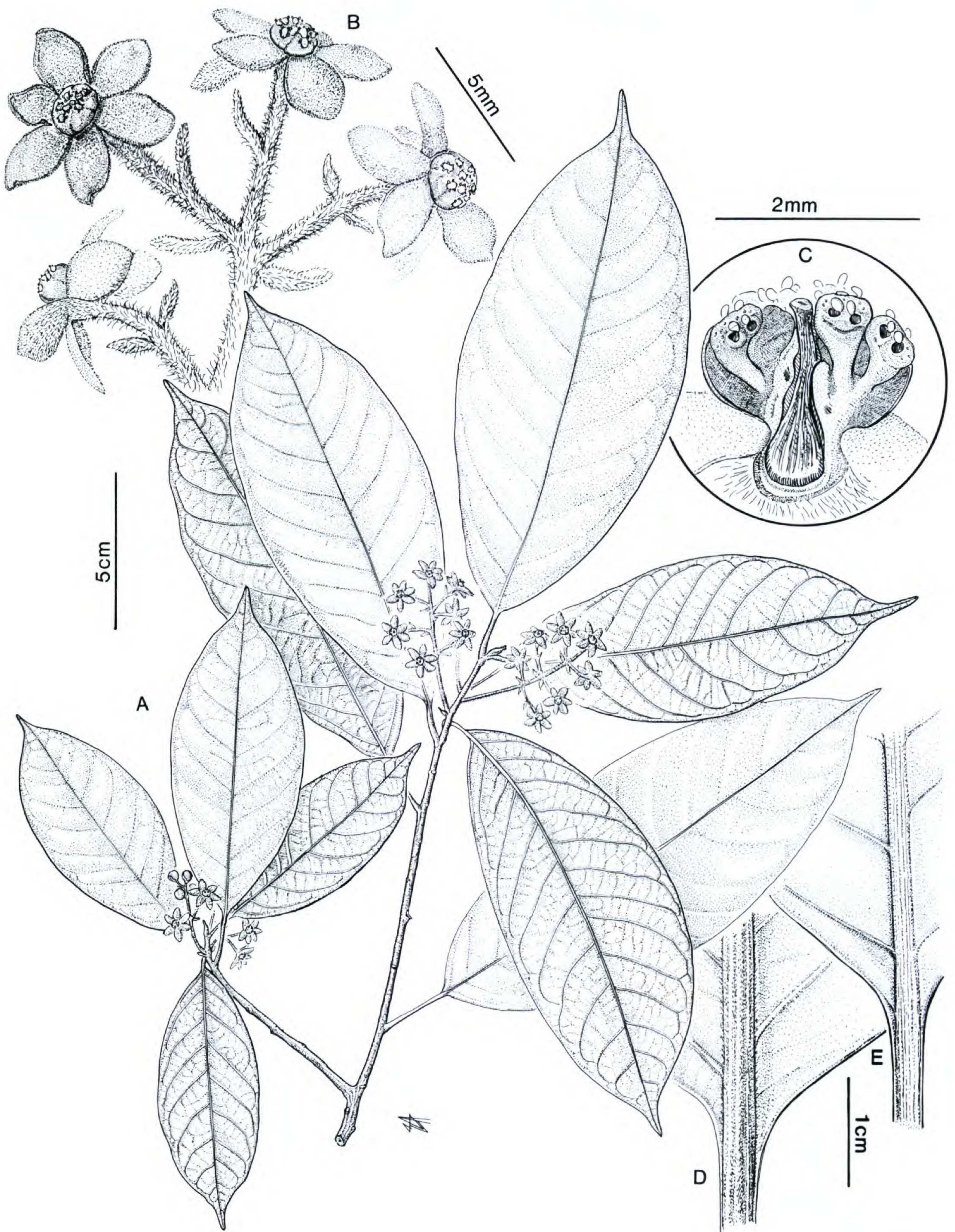


FIGURE 24. *P. golfodulcense*. — A. Habit. — B. Part of inflorescence. — C. Cross section of flower. — D, E. Lower and upper surface of leaf base.

long, ovary ca. 1 mm long, pubescent, style sparsely pubescent. Receptacle pubescent inside. Cupule with coarse warts, 2 cm tall, 2 cm wide. Fruit unknown. Flowers: January–February. Elevation range: 200–800 m.

Collections studied. COSTA RICA. PUNTARENAS: forested slopes above Golfito, *Burger 4690* (CR, F, MO). PUNTARENAS: forested hills above Palmar Norte, *Allen 5885* (GH, UC); Parque Nacional Corcovado, Los Patos Forest, *Kernan 184* (CR, MO), *Kernan 187* (CR, MO); Osa, Rancho Quemado, *Jimenez 648* (MO).

Pleurothyrium golfodulcense is restricted to the Osa peninsula and adjoining area in Costa Rica. I have accepted a rather wide concept of this species and include here, for instance, *Kernan 184*, which differs from typical *P. golfodulcense* in its thinner leaves, shorter petioles and gray vs. ferruginous pubescence. In leaf size and shape, venation, pubescent pistil and receptacle, gland-dotted leaves, petiole length, and bracts pubescent on both surfaces it fits in *P. golfodulcense*, and because it was collected together with typical *P. golfodulcense* (*Kernan 187*) and young leaves of *Allen 5885* are as thin as those of *Kernan 184*, I prefer to include *Kernan 184* in *P. golfodulcense*.

The closest relatives of *Pleurothyrium golfodulcense* are probably the Panamanian species *P. racemosum* and *P. pilosum* and the Ecuadorian-Colombian *P. tomiwahlii* (see discussion under *P. tomiwahlii*).

Pleurothyrium grandiflorum van der Werff, *Ann. Missouri Bot. Gard.* 74: 408. 1987. TYPE: Colombia. Chocó: Río Mecana, *Juncosa 1675* (holotype, MO). Figures 25, 26.

Tree, 15 m. Twigs ridged, becoming terete, solid, very finely appressed puberulent, ca. 3 mm diam. 5 cm below the tip. Terminal bud appressed puberulent, shiny. Leaves alternate, thinly chartaceous, 15–24 × 4–7 cm, elliptic or narrowly elliptic, the base sharply acute or slightly decurrent on petiole, the tip acute, the upper surface nearly glabrous, but with some fine appressed hairs, especially on the midrib; the lower surface with scattered, minute, appressed hairs, these more numerous along lateral veins and midrib; venation on upper surface immersed, but slightly raised on lower surface; lateral veins 15–20 on each side, arching upward near the margin and becoming loop-connected in the upper half of the lamina. Petioles 1–1.5 cm long, with same kind and density of pubescence as twigs. Inflorescences to 10 cm long, with same kind and density of pubescence as twigs, racemose, few-flowered (usually 2 flowers present

on each inflorescence), bracts not present at anthesis. Pedicels to 6 mm long, appressed puberulous. Flowers yellow, 1.5–1.7 cm diam., fragrant (same odor as in some euglossine bee-pollinated flowers, fide collector). Tepals 6, subequal, the inner three narrower than the outer three, the inner surface with a dense, short pubescence. Stamens 9, 4-celled, the outer six with lateral cells, the inner three with extrorse cells, anthers glabrous, filaments not discernible in the glandular mass. Pistil 1.3 mm long, glabrous, the ovary partly sunken in the pubescent floral tube and covered by the glabrous glandular mass. Staminal glands strongly enlarged, fused, forming a thick wall outside the stamens. Fruit unknown. Flowers: January. Elevation range: below 100 m.

Collection studied. COLOMBIA. CHOCO: Río Mecana, *Juncosa 1675* (MO).

Pleurothyrium grandiflorum represents the extreme in the tendency toward large flowers and few-flowered inflorescences in the genus. Its venation type, with a rather weakly developed marginal vein, is not specialized and its pubescence type is also rather nondescript, quite unlike the brown-tomentose pubescence which is common in *Pleurothyrium*, but rarely found in the closely related *Ocotea* and *Nectandra*. *Pleurothyrium grandiflorum* is only known from the type collection in the Chocó, an area known to be rich in endemic species.

Pleurothyrium hexaglandulosum van der Werff, *Ann. Missouri Bot. Gard.* 75: 417. 1988. TYPE: Panama. Colón: Río Guanche, 5 km upstream from road to Portobelo, *Hammel & Trainer 14781* (holotype, MO; isotypes, BR, PMA). Figures 26, 27.

Small tree, to 5 m tall. Twigs terete, densely tomentellous, solid, diameter 5 cm below tip 5 mm. Leaves alternate, chartaceous, 30–45 × 10–15 cm, obovate, gradually narrowed toward the base, the base abruptly rounded to subcordate, the tip acuminate, the upper surface glabrous, the lower surface with some small appressed hairs, especially along midrib and lateral veins; lateral veins 14–18 on each side, immersed on upper surface, raised on lower surface, the veins arching toward the tip near the margin and prominently loop-connected in the upper two-thirds of the lamina. Petioles tomentellous, ca. 5 mm long, swollen, to 5 mm thick. Inflorescences in axils of cataphylls, to 65 cm long, brown puberulous, paniculate, the branchlets 3–4 times cymosely branched, the basal

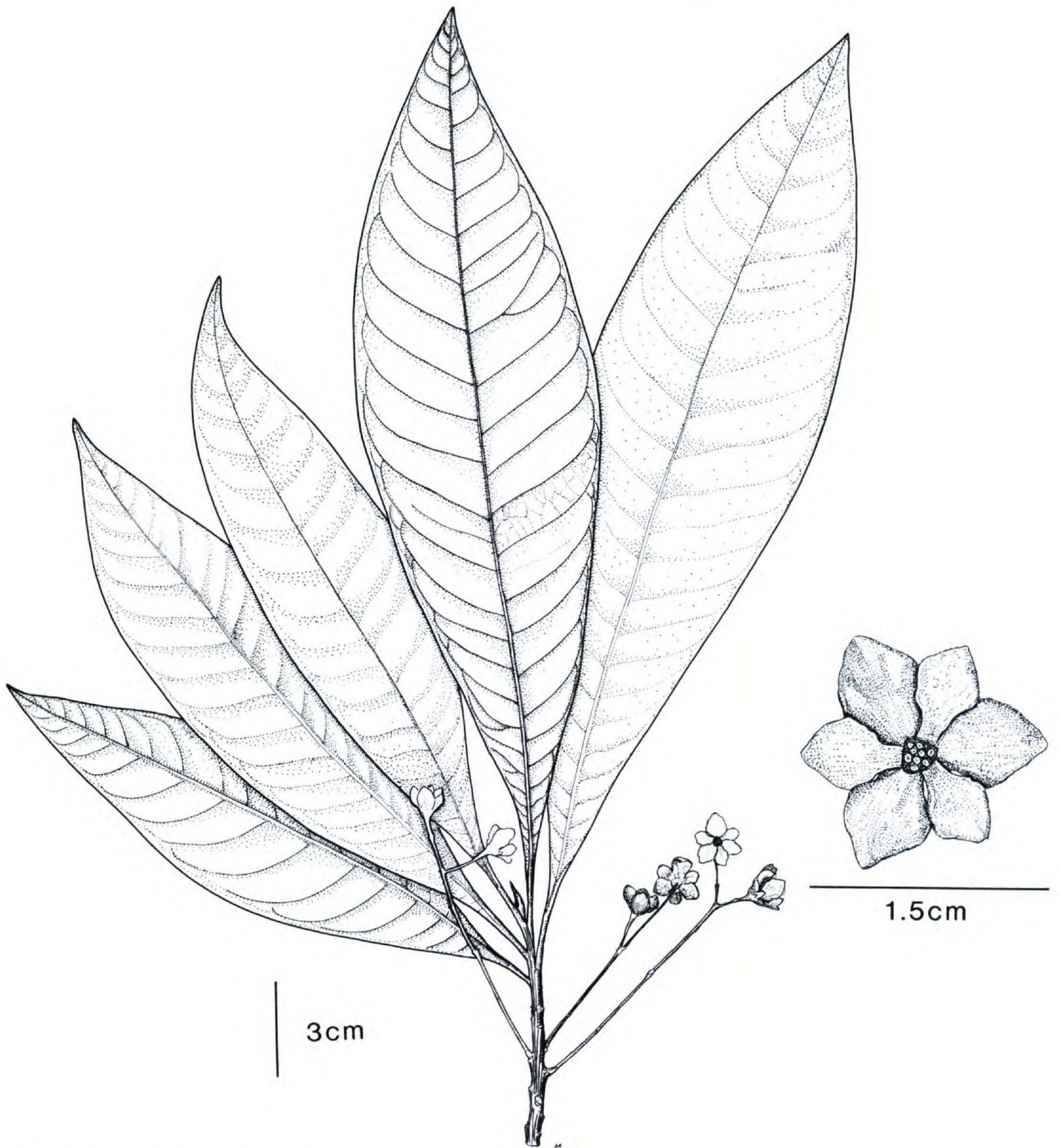


FIGURE 25. *P. grandiflorum*. Habit and flower.

branchlets to 25 cm long, the upper ones gradually shorter. Bracts absent at anthesis. Pedicels 1.5 (-2) cm long, densely gray-pubescent. Flowers ca. 10 mm diam., green, turning yellow. Tepals 6, equal, ca. 4 mm long, glabrous inside except where glands and stamens were not pressed against tepals, thus showing a narrow line of hairs in the center of the lower part of the tepal, this expended in a diamond-shaped pattern in the upper part; margin of tepals flat. Stamens 9, 4-celled, the outer six with introrse-lateral cells, the inner three with ex-

trorse-lateral cells; in young flowers the anthers bent down and not raised above the glandular mass, but stamens becoming straight in older flowers with anthers clearly raised above the glands; filaments pubescent on the back. Glands conspicuously enlarged, but not fused, although enclosing the outer stamens. Ovary broadly ovoid, 1 × 1.5 mm, with short, gray pubescence, partly enclosed in the pubescent floral tube. Style ca. 0.5 mm long, with some gray pubescence. Glands and stamens deciduous in older flowers, leaving the ovary fully ex-



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FIGURE 26. Distribution of *P. grandiflorum* (★), *P. hexaglandulosum* (●), *P. insigne* (○), and *P. intermedium* (■).

posed. Fruits unknown. Flowers: March. Elevation range: 150–200 m.

Collections studied. COSTA RICA. PUNTARENAS: Osa Peninsula, *Croat & Grayum 59792* (MO). PANAMA. COLON: Rio Guancho, ca. 5 km upstream from road to Portobelo, *Hammel & Trainer 14781* (BR, MO, PMA).

Pleurothyrium hexaglandulosum is only known from the type collection. The collection *Croat & Grayum 59792*, from the Osa Peninsula, Costa Rica, is tentatively placed here, although it differs in a number of minor characters. The twigs are almost glabrous, the inflorescences much shorter (to 15 cm long) and less pubescent, the tepals papillose, not pubescent, and the pedicels are shorter. On the other hand, the Costa Rican collection has the short, swollen petioles, the leaf shape, the pattern on the inner face of the tepals (though not as sharply outlined), and the androecial structure of the type of *P. hexaglandulosum*. Because the differences are quantitative and the leaf shape,

thick petioles, and lax inflorescences are unmatched in *Pleurothyrium*, I place the Costa Rican collection in *P. hexaglandulosum*. However, if future collections show that the differences between the Panamanian and Costa Rican populations are consistent and not individual variation, it might be best to describe the Costa Rican material as a new taxon.

Pleurothyrium insigne van der Werff, sp. nov.

TYPE: Ecuador. Napo: Reserva Biológica Jatun Sacha, tree, 12 m, tepals red outside, creamy-white inside, 13 Feb. 1987, *Palacios 1332* (holotype, MO; isotypes, AAU, C, COL, G, HBG, K, KUN, LE, NY, QAME, QRS, U). Figures 26, 28.

Arbor, ad 12 m alta. Ramuli teretes, solidi, ferrugineo-tomentosi, vetustiores glabrescentes. Folia alterna, firme chartacea, 20–60 × 7–15 cm, obovata vel anguste obovata, apice breviter acuminata vel rotundata, basi (acuta)

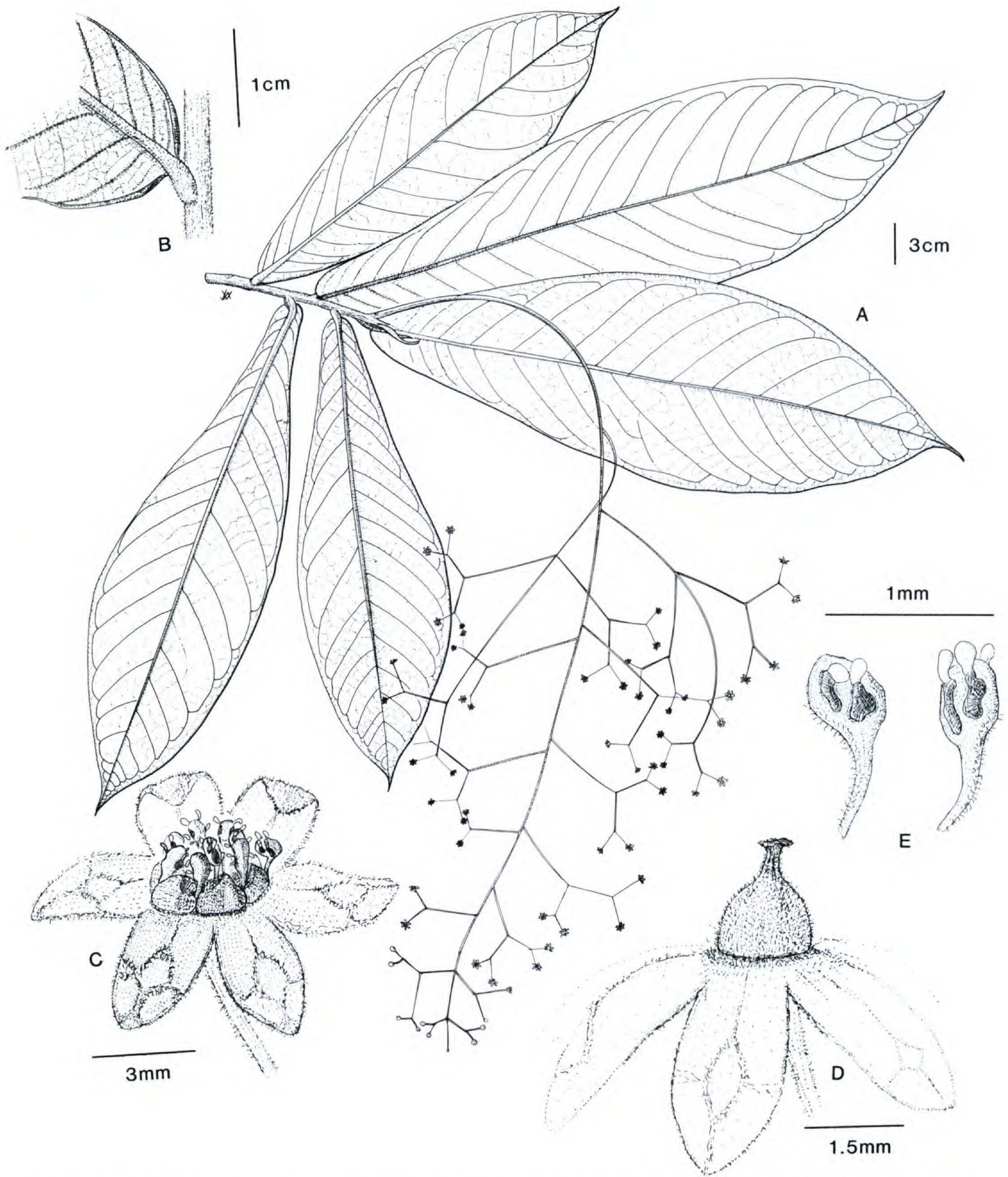


FIGURE 27. *P. hexaglandulosum*.—A. Habit.—B. Base of leaf.—C. Flower.—D. Old flower with androecium fallen off.—E. Stamens.

obtusa vel abrupte rotundata (cordata), supra praeter costae basem pubescentem glabra, subtus pilis erectis parvis praedita, indumento secus costam nervosque densiore castaneoque, venatione supra immersa, subtus costa nervisque elevatis; nervis (14-)18-26(-28) utroque costae latere, ad marginem in venam conspicuam marginalem terminantibus. Petioli 1.5-4 cm longi, ferrugineo-tomentosi. Inflorescentiae ad apices ramulorum ex axillis bractearum ortae, ferrugineo-tomentosae, ad 40 cm longae, paniculatae. Pedicelli ad 1 cm longi. Flores rotati, 12-

15 mm diametro. Tepala 6, subaequalia, tres exteriora late elliptica, 5-6 × 4-5 mm, extus tomentella, intus minute papillosa; tres interiora 4-5 × 2.5 mm, extus basi tomentella, demum papillosa, intus papillosa. Stamina 9, 4-locellata, locellis lateralibus, glandulis permagnis, stamina cingentibus, staminodia parva, 3. Ovarium (depresso) globosum, ca. 1.5 mm diametro, basi glabrum, demum ferrugineo-tomentellum; stylo ca. 1 mm longo. Receptaculum intus tomentellum. Cupula verrucosa, 1.5 × 2.5 cm; fructus ellipsoideus, 2.5 × 2 cm.

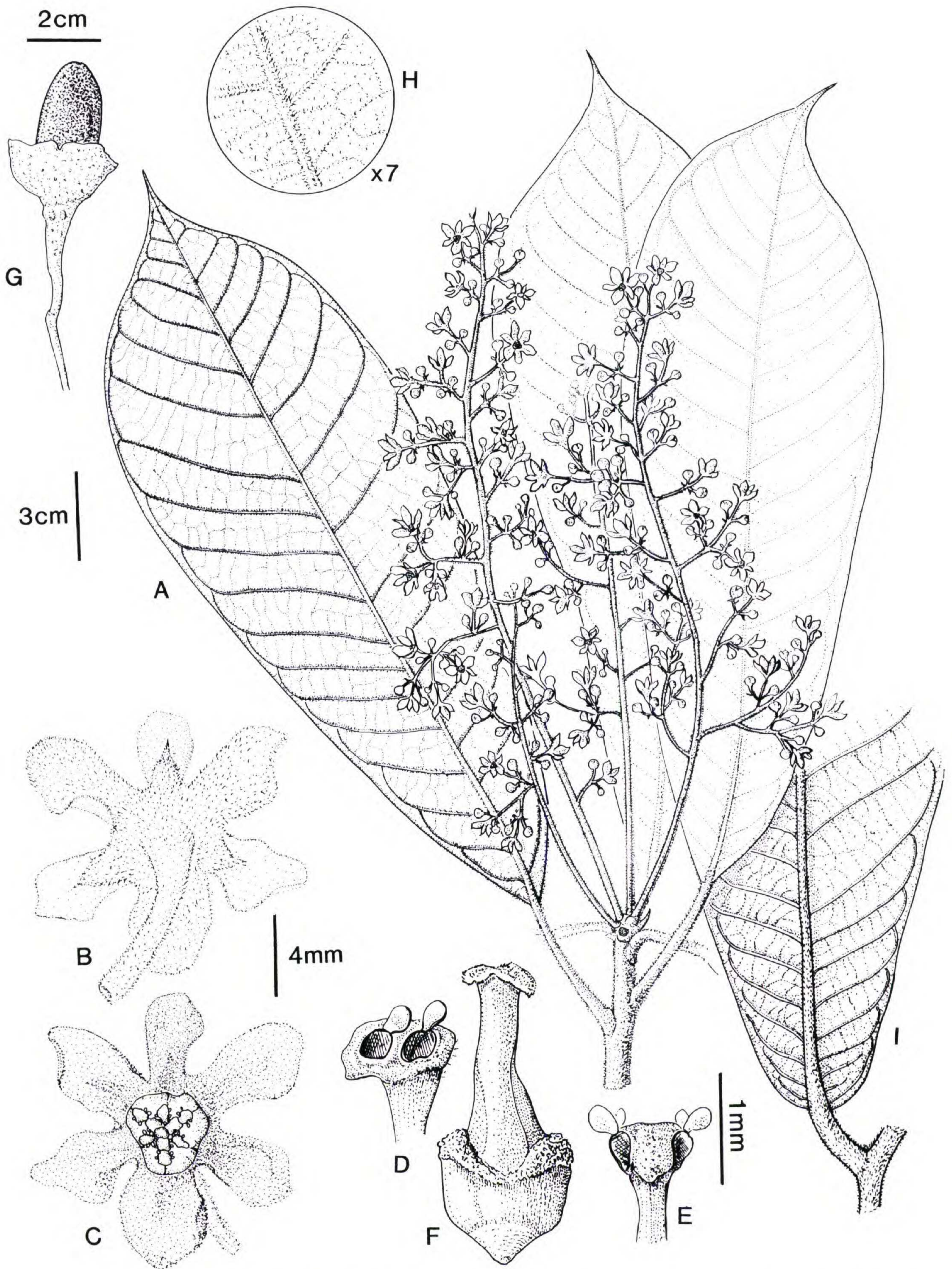


FIGURE 28. *P. insigne*.—A. Habit.—B, C. Flower.—D, E. Outer and inner stamen.—F. Pistil.—G. Fruit.—H. Indument on lower leaf surface.—I. Leaf base.

Small tree, to 12 m tall. Twigs solid, terete, 5–9 mm diam. 5 cm below the tip, ferruginous tomentose, but glabrescent with age. Leaves alternate, firmly chartaceous, 20–60 × 7–15 cm (narrowly) obovate, the base (acute) obtuse, abruptly rounded or cordate, the tip rounded or shortly acuminate; upper surface with some pubescence at the base of the midrib, otherwise glabrous, lower surface with an indument of erect hairs, this much denser on midrib and lateral veins; venation immersed on upper surface, midrib, lateral veins and marginal vein prominently raised on lower surface; lateral veins (14–)18–26(–28), connected by a conspicuous marginal vein. Petioles 1.5–4.0 cm long, to 5 mm diam., castaneous tomentose. Inflorescences clustered near tips of branches in axils of cataphylls, rarely along leafless short-shoots, 15–40 cm long, paniculate, ferruginous tomentose. Bracts of inflorescences, if present, to 4 mm long, ovate, tomentose outside, nearly glabrous inside. Pedicels to 1 cm long. Flowers reddish outside, greenish white inside, the tepals spreading, 12–15 mm diam. Tepals 6, subequal, outer 3 elliptic, 5–6 × 4–5 mm, tomentose outside, papillose inside, inner 3 elliptic, ca. 5 × 2.5–3 mm, outside with a basal, triangular, tomentose patch, otherwise papillose; inside papillose. Stamens 9, 4-celled, the cells lateral; staminodia 3, minute, linear, ca. 0.3 mm long, hidden by stamens and glands. Glands of inner stamens strongly enlarged and enclosing the outer stamens, forming a large mass, but not fully fused. Ovary (depressed) globose, ca. 1.5 mm diam., the base glabrous, upper part pubescent. Style ca. 1 mm long. Floral tube shallow, pubescent within. Cupule 1.5 × 3.5 cm or smaller, warty. Fruit ellipsoid, ca. 2.5 cm long, well exerted from cupule. Fruits: August–February. Flowers: June–November. Elevation range: 100–450 m.

Collections studied. BRAZIL. AMAZONAS: Humaita, near Tres Casas, *Krukoff* 6232 (A, G, K, MO, NY, S, US). ECUADOR. MORONA-SANTIAGO: Pozo petrolero “Garza” de Tenneco, 35 km NE of Motalvo, *Zak* 4511 (MO). NAPO: Jatun Sacha, 8 km downstream from Misahualli, *Palacios* 1332 (AAU, C, COL, G, HBG, K, KUN, LE, MO, NY, QCNE, QRS, U, US); Jatun Sacha Biological Station, *Neill & Alvaredo* 9033 (MO, QAME), *Palacios* 1518 (MO), *Palacios* 4388 (MO). PERU. LORETO: Varadero de Mazan, *Croat* 19439 (MO, NY); Iquitos, Santa Maria del Ojeal on Río Amazonas, *Davidson* 5336 (MO, NY); Maynas, Buena Suerte (Río Itaya), *Vásquez & Jaramillo* 8444 (MO); Maynas, *Vásquez* 9365 (MO); Requena, Sinchicuy, *Vásquez et al.* 7823 (MO). PASCO: Oxapampa, Iscozacín, Arboretum, *Pariona* 49 (MO). SAN MARTIN: San Martín, *Knapp & Mallet* 8205 (MO).

Pleurothyrium insigne is a striking species, easily recognized by its large, obovate leaves with a

pronounced marginal vein, the castaneous-tomentose indument of twigs, and the erect hairs on the lower leaf surface. Initially, I divided the specimens included in *P. insigne* between two species, one with abruptly rounded or cordate leaf base and short petioles (to 2 cm long), the other with an obtuse leaf base and longer (3–4 cm) petioles. Because some collections (for instance, *Krukoff* 6232) include specimens with obtuse and abruptly rounded leaf bases and the difference in petiole length is not consistent, I decided to place all specimens in one species, even though the extremes look quite different. The specimens with an abruptly rounded to cordate leaf base are very similar to *P. maximum*; the latter differs only in its glabrous lower leaf surface, smaller flowers, equal tepals, and relatively smaller glands. *Pleurothyrium maximum* is largely recognized because of the floral differences. I consider such differences as fundamental in *Pleurothyrium* and expect that additional collections of *P. maximum* will show that these differences will be consistent.

Pleurothyrium insigne is known from several widely scattered localities in Ecuador, Peru, and Brazil. The best collections are from the Jatun Sacha Biological Station, where the species is locally common. All collections from that area have leaves with an obtuse base; Peruvian collections and the sole Brazilian collection can have obtuse or abruptly rounded/cordate leaf bases.

***Pleurothyrium intermedium* (Mez) Rohwer,** *Mitt. Inst. Allg. Bot. Hamburg* 20: 43. 1986. *Nectandra intermedia* Mez, *Repert. Spec. Nov. Regni Veg.* 16: 308. 1920. TYPE: Brazil. Acre: Seringal São Francisco, *Ule* 9408 (holotype, B; isotype, K). Figure 26.

Tree or shrub, 5–20 m tall. Twigs terete, solid, sparsely pubescent to glabrous, diameter 5 cm below the apex ca. 3 mm. Terminal buds densely appressed yellowish pubescent, the bud contrasting with the dark twig. Leaves alternate, chartaceous, elliptic to obovate-elliptic, 9–16 × 3–5 cm, the base acute, the tip obtuse, upper surface glabrous, the venation immersed, the lower surface glabrous or nearly so, the midrib raised, lateral veins weakly raised; lateral veins 10–12 on each side, arching upward near the margin, not or very weakly connected with the superior vein. Petioles ca. 1.5 cm long, with similar tomentum as twigs. Inflorescences in axils of deciduous bracts, ca. 12 cm long, paniculate, the branchlets with racemosely arranged cymes, often the two lateral flowers of a cyme missing; main axis sparsely pubescent, the

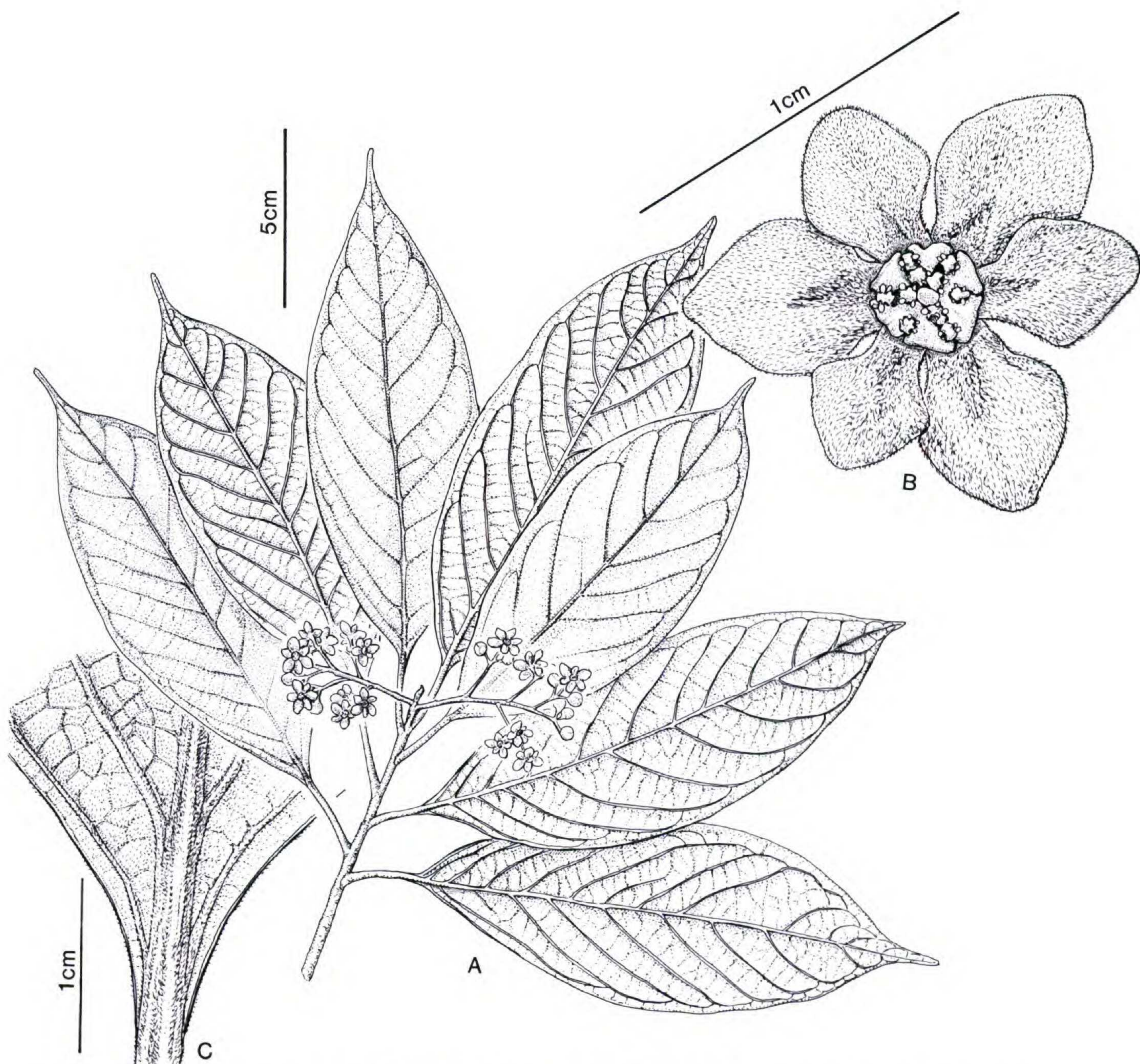


FIGURE 29. *P. marginale*.—A. Habit.—B. Flower.—C. Base of leaf underside, showing indument.

branchlets denser pubescent, pedicels almost white pubescent, 2–3(–5) mm long. Flowers yellowish green, ca. 3 mm diam., the tepals \pm erect at anthesis. Tepals 6, equal, ovate, ca. 2 mm long, puberulous outside, papillose inside, the margin reflexed. Stamens 9, 4-celled, the cells lateral, filaments glabrous, about as long as the anthers, glands enlarged, but not fused and not surrounding the outer stamens, but visible as large lobes separating the outer stamens; anthers raised above the level of the glands. Ovary glabrous, ovoid, gradually narrowed into the short style, stigma platelike; pistil 1.8 mm long. Floral tube glabrous inside. Fruit unknown. Flowers: August. Elevation range: 100–200 m.

Collections studied. BOLIVIA. SANTA CRUZ: Ichilo, Reserva Forestal Chore, Camp. Arroyo Perdido, Neill 9435 (MO, QCNE), Neill 9439 (MO, QCNE). BRAZIL.

AMAZONAS: Seringal São Francisco, Ule 9408 (B, K). PERU. MADRE DE DIOS: Tambopata, Hermosa Chica, Pasha 10 (MO).

Pleurothyrium intermedium is only known from the type collection, two recent collections from Bolivia, and one recent collection from Peru. It belongs to the group of species with erect tepals at anthesis and is most closely related to two other, equally poorly known, species from Brazil (*P. amplifolium* and *P. undulatum*). More collections are needed for a better understanding of the status of those three species.

Pleurothyrium marginale van der Werff, sp. nov. TYPE: Colombia. Valle: Río Cajambre near Barco on the Pacific coast, elev. 5–80 m, Cuatrecasas 17196 (holotype, US; isotype, F). Figures 29, 30.



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FIGURE 30. Distribution of *P. marginale* (★), *P. maximum* (●), *P. nobile* (○), and *P. obovatum* (■).

Arbor, ad 20 m. Ramuli teretes, solidi, minute fusco-puberuli, glabrescentes. Folia alterna, firme chartacea, elliptica, 8–14 × 3–5 cm, basi acuta vel attenuata, apice acuminata, supra glabra vel paucis pilis adpressis munita, subtus sparse adpresse strigosa, indumento densiore secus costam nervosque laterales; nervis lateralibus 8–12 utroque costae latere. Venatio brochidodroma, supra immersa, subtus costa, nervis lateralibus et venatione tertia elevata. Petioli 15–22 mm longi. Inflorescentiae ex axillis bractearum ortae, fusco-tomentulosae, 4–6 cm longae, racemosae, uni- vel biflorae, bracteis sub anthesi absentibus. Pedicelli ca. 4 mm longi, pedunculi ca. 9 mm longi, fusco-tomentulosi. Tepala 6, subaequalia, 3 exteriora late ovata, ca. 5 mm longa, 3 interiora rhomboidea, basi late et breviter stipitata, ca. 4 mm longa, in sicco utrinque fusco-tomentella. Stamina 9, 4-locellata, locellis laterali-bus, antheris glabris, glandulis incrassatis, coalitis, stamina cingentibus. Ovarium ellipsoideum, glabrum, ca. 0.8 mm longum; stylum glabrum, ca. 1 mm longum, stigma pel-tatum. Tubus floralis glaber. Fructus perjuvenalis in tubo florale inclusus; fructus adultus ignotus.

Tree, 20 m tall. Twigs terete, solid, minutely brown-puberulous, glabrescent, ca. 3 mm diam. 5 cm below the tip. Leaves alternate, not clustered, firmly chartaceous, elliptic, 8–14 × 3–5 cm, the base acute to attenuate, the tip acuminate, the

upper surface glabrous or with some minute hairs, especially near the base of the midrib, the lower surface with scattered, minute, appressed hairs, these denser along midrib and lateral veins; venation brochidodromous, immersed on upper surface, midrib and lateral veins raised on lower surface, a marginal vein well developed; lateral veins 8–12 on each side. Petioles 15–22 mm long, flattened on upper surface, pubescence similar to that of twigs. Inflorescences in axils of cataphylls, brown-tomentulose, 4–6 cm long, racemose, 1–2-flowered (but probably several flowers fallen off), bracts absent at anthesis. Flowers yellow fide collector, ca. 12 mm diam. Pedicel ca. 4 mm long, peduncle ca. 9 mm long, brown-tomentulose. Tepals 6, subequal, the outer three broadly ovate, ca. 5 mm long, the inner three mostly rhombic with a short, broad stalk, ca. 4 mm long; both inside and outside brown tomentellous in sicco. Stamens 9, 4-celled, the cells lateral, opening back-to-back, anthers glabrous; glands enlarged, fused, enclosing the stamens. Ovary ellipsoid, ca. 0.8 mm long, glabrous, style glabrous, ca. 1 mm long, stigma platelike. Floral tube

glabrous inside. Very young fruit fully enclosed in the enlarged floral tube; mature fruit unknown. Flowers: April. Elevation range: below 100 m.

Collection studied. COLOMBIA. VALLE: Costa del Pacifico, Río Cajambre, *Cuatrecasas 17196* (F, US).

A species only known from the type collection, *Pleurothyrium marginale* derives its name from its well-developed marginal vein. This species can be readily identified also by the sparse, appressed indument on the lower leaf surface and the few-flowered inflorescences. The collector indicated that the tree had tall buttresses (as in *Cecropia*) and canary-yellow wood. Buttresses are rare among neotropical Lauraceae: I have only seen them in a *Caryodaphnopsis* species from Peru. Yellow wood is a common feature in *Aniba*, but is infrequent outside this genus. The wood is used for making boards and canoes; the common name is palo blanco.

Pleurothyrium maximum O. C. Schmidt, Notizbl. Bot. Gart. Berlin-Dahlem 10: 235. 1928. *Ocotea maxima* (O. C. Schmidt) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Peru. Amazonas: mouth of Río Santiago, Pongo de Manseriche, terra firma forest, 160 m elev., *Tessman 4040* (holotype, B; isotypes, G, NY). Figure 30.

Small tree, 4–6 m tall. Twigs terete, solid, ferruginous tomentose, glabrescent in age, 5–6 mm diam. a few cm below the tip. Leaves alternate, chartaceous or firmly chartaceous, 30–50 × 7–15 cm, obovate to narrowly obovate, gradually narrowed toward the base, the base abruptly rounded to cordate, the tip acute to acuminate, glabrous above, the lower surface with a few scattered, minute, appressed hairs, otherwise glabrous; midrib and lateral veins immersed on upper surface, prominently raised on lower surface, the tertiary venation weakly raised. Lateral veins 20–30 on each side, near the margin connected by a conspicuous marginal vein. Petioles 1–2 cm long, 4–5 mm diam., with similar pubescence as the twigs. Inflorescences slender, lax, 40–65 cm long, ferruginous tomentose, the branchlets once or twice cymosely branched, in axils of cataphylls at tips of twigs, bracts mostly lacking at anthesis. Pedicels 5–9 mm long, ferruginous tomentose. Flowers rotate, ca. 8–9 mm diam. dark green-red-brown outside, dark green inside, the glands bright green, stamens yellowish. Tepals 6, equal in shape and size, 2.5 × 1.5 mm, the margin flat, the outer three ferruginous tomentellous outside, the inner three with a

basal, triangular, tomentellous patch, otherwise glabrous; all tepals glabrous inside except for a narrow line of short hairs in the center of the lower part, this expanded into a diamond-shaped outline in the upper part. Stamens 9, 4-celled, the outer six with 2 cells lateral and 2 cells introrse, the inner three with one pair lateral and one extrorse; glands enlarged, protruding between and ± enclosing the outer stamens, but definitely free. Immature ovary globose to ovoid, 1–1.5 mm long, covered with short brown hairs; style glabrous. Floral tube inside covered with short reddish hairs. Fruit and cupule unknown. Flowers: September–November. Elevation range: below 200 m.

Collections studied. PERU. AMAZONAS: mouth of Río Santiago, Pongo de Manseriche, *Tessmann 4040* (B, G, NY), *Tessmann 4529* (B, G, NY).

Pleurothyrium maximum is only known from two collections from the area where the Río Santiago joins the Río Marañon, in northern Peru. It is vegetatively similar to *P. insigne*, which see for further discussion. *Pleurothyrium maximum* also resembles *P. williamsii*, which differs in its narrower leaves (5 cm above the base, 2–3.5 cm wide vs. 5–6 cm wide), shorter indument on twigs (or glabrous) and inflorescences, thinner leaves that dry dark green, and shorter inflorescences (but few inflorescences are known). In *P. maximum* the glands of the stamens are free and do not form a wall surrounding the stamens, while in *P. williamsii* the glands do form a wall, with only a faint line indicating the boundaries of the individual glands.

Pleurothyrium nobile A. C. Smith, Phytologia 1: 120. 1935. *Ocotea nobilis* (A. C. Smith) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Brazil. Amazonas: near mouth of Rio Embira, *Krukoff 5121* (holotype, NY not seen; isotypes, A, B, G, K, MO, S, US). Figure 30.

Tree, 25 m tall. Twigs solid, terete or ridged, glabrous, 6–7 mm diam. 5 cm below the apex. Terminal bud brown-tomentellous. Leaves alternate, stiffly chartaceous, elliptic, 15–30 × 6–12 cm, the base obtuse to rounded, the tip acute, glabrous on both surfaces, venation immersed on upper surface, midrib and lateral veins raised on lower surface, tertiary venation weakly raised on lower surface, lateral veins 7–10 on each side, arching upward near the margin, but not or very weakly connected with the superior vein. Petioles 2–3 cm long, glabrous, canaliculate. Inflorescences in axils of cataphylls, to 12 cm long, minutely

puberulous, glabrescent, paniculate, the branchlets 3–4 times cymosely branched, few-flowered, bracts not present at anthesis. Pedicels 3–4 mm long. Flowers ca. 10 mm diam. Tepals 6, equal, brown-puberulous on outside, minutely brown-papillose to glabrous inside, ovate, ca. 4 mm long. Stamens 9, 4-celled, the cells lateral, anthers and upper part of filaments brown-papillose, glands large, completely surrounding the stamens but not fully fused. Ovary ovoid, ca. 2 mm long, the lower part glabrous, the upper part brown-papillose, except for six large glabrous spots, where glands were in contact with ovary; style poorly differentiated, brown-papillose, 0.2 mm long. Floral tube glabrous inside. Cupule and fruits unknown. Flowers: June–July. Elevation range: 200–300 m.

Collections studied. BRAZIL. AMAZONAS: mouth of Rio Embira, *Krukoff 5121* (A, B, G, K, MO, NY, S, US). PERU. HUANUCO: Puerto Inca, Dtto. Lullapichis, *Kroll 285* (MO), *Kroll 422* (MO). LORETO: Coronel Portillo, Km 98 carretera Pucallpa–Huanuco, *M. Castillo 12* (F, K, MO, NY, US, WIS), *M. Castillo 15* (F, K, US).

Pleurothyrium nobile is rarely collected and is known only from five collections. The type collection was made in varzea forest, two later collections (both from the same tree) in dry tropical forest, and two from wet forest. The recent collections have smaller, less-branched inflorescences, but the collections agree well in leaf shape, type of indumentum, and floral characteristics. Smith (1935) cited *Krukoff 4800* as a paratype of *P. nobile*. Because this collection has a whitish, very short appressed indument on lower leaf surface, acuminate leaf tips, and slender inflorescences, I include it in *P. panurense* (Meissner) Mez. The common name for the species in Peru is *lobo moena*.

Pleurothyrium obovatum van der Werff, sp. nov. TYPE: Ecuador. El Oro: 15 km NW of Paccha on the road to Pasaje, 1,800 m elev., *Brandbyge 42366* (holotype, AAU). Figures 30, 31.

Arbor parva, ad 10 m alta. Ramuli teretes, fistulosi. Gemma terminalis ferrugineo-tomentella. Folia alterna, perobovata, 40–45 × 16–20 cm, firme chartacea, basi acuta, apice rotundata vel breviter acuminata, glabra. Nervi laterales ca. 20 utroque costae latere, venatione leviter brochidodroma. Inflorescentiae ex axillis bractearum ortae, interdum fistulosae, ferrugineo-tomentelli, 20–30 cm longae, paniculatae. Flores ca. 11 mm diametro. Tepala 6, aequalia, elliptica, dense tomentella vel papillosa. Stamina 9, 4-locellata, locellis interioribus extrorsis, superioribus lateralibus, antheris erectis, super glandulas prominentibus. Glandulae liberae. Ovarium ellipsoideum, glabrum, stylo ca. 1 mm longo, papillis ferrugineis praedito. Tubus floralis glaber. Fructus ignoti.

Small tree, to 10 m tall. Twigs terete, fistulose, with scattered small, erect ferruginous hairs, diameter of twigs 5 cm below tip ca. 9 mm. Terminal bud minutely, but densely, ferruginous tomentelous. Leaves alternate, strongly obovate, 40–45 × 16–20 cm, firmly chartaceous, gradually narrowed to the acute base, the tip blunt or with a very short acumen, glabrous on both surfaces, midrib slightly raised or immersed, otherwise venation immersed on upper surface, midrib prominently raised on lower surface, lateral veins and tertiary venation progressively less raised. Lateral veins ca. 20 on each side, near the margin arching upward and in the distal half of the lamina connected with the superior vein, but a marginal vein not well developed. Petioles ca. 2 cm long, glabrous or with some scattered ferruginous hairs, 5 mm diam. Inflorescences in axils of cataphylls, sometimes fistulose, ferruginous-tomentelous, 20–30 cm long, paniculate, the lateral branches 2–3 times cymosely branched, many-flowered, bracts deciduous at anthesis. Pedicels ca. 3 mm long, gradually widened in floral tube. Flowers outside ferruginous brown, inside whitish, ca. 11 mm diam., rotate. Tepals 6, equal, 4 mm long, elliptic, densely tomentelous or papillose on both surfaces, the margins plane. Stamens 9, 4-celled, the lower pair extrorse, the upper pair lateral, the cells large; anthers erect and raised well above the glands. Glands not completely enclosing the outer stamens, not fused. Ovary ellipsoid, ca. 1.5 mm long, glabrous, gradually narrowed into the style, this ca. 1 mm long and with some ferruginous papillae; stigma platelike. Floral tube glabrous inside. Very young fruit fully enclosed in floral tube. Fruits and cupules unknown. Flowers: September. Elevation range: 1,000–1,800 m.

Collections studied. ECUADOR. AZUAY: Cuenca, El Sillado, Parque Molleturo, *Ortiz-Proyecto Molleturo 192* (MO). EL ORO: Pasaje, 15 km NW of Paccha on road to Pasaje, *Brandbyge 42366* (AAU). LOJA: 15 km E of Alamor on road to Celica, *Brandbyge 42343* (AAU).

Pleurothyrium obovatum is only known from three recent collections in southern Ecuador. The fistulose (lenticellate?) branches, relatively small glands of the stamens, and floral shape indicate a close relationship to the *P. cuneifolium* group. *Pleurothyrium obovatum* is, however, easily recognized by the ferruginous indument, which becomes floccose on older twigs, and obovate, glabrous leaves. The large, erect anthers are another character of this species. The leaves of the two Brandbyge collections are more narrowed toward the base than the Ortiz collection, and it is likely

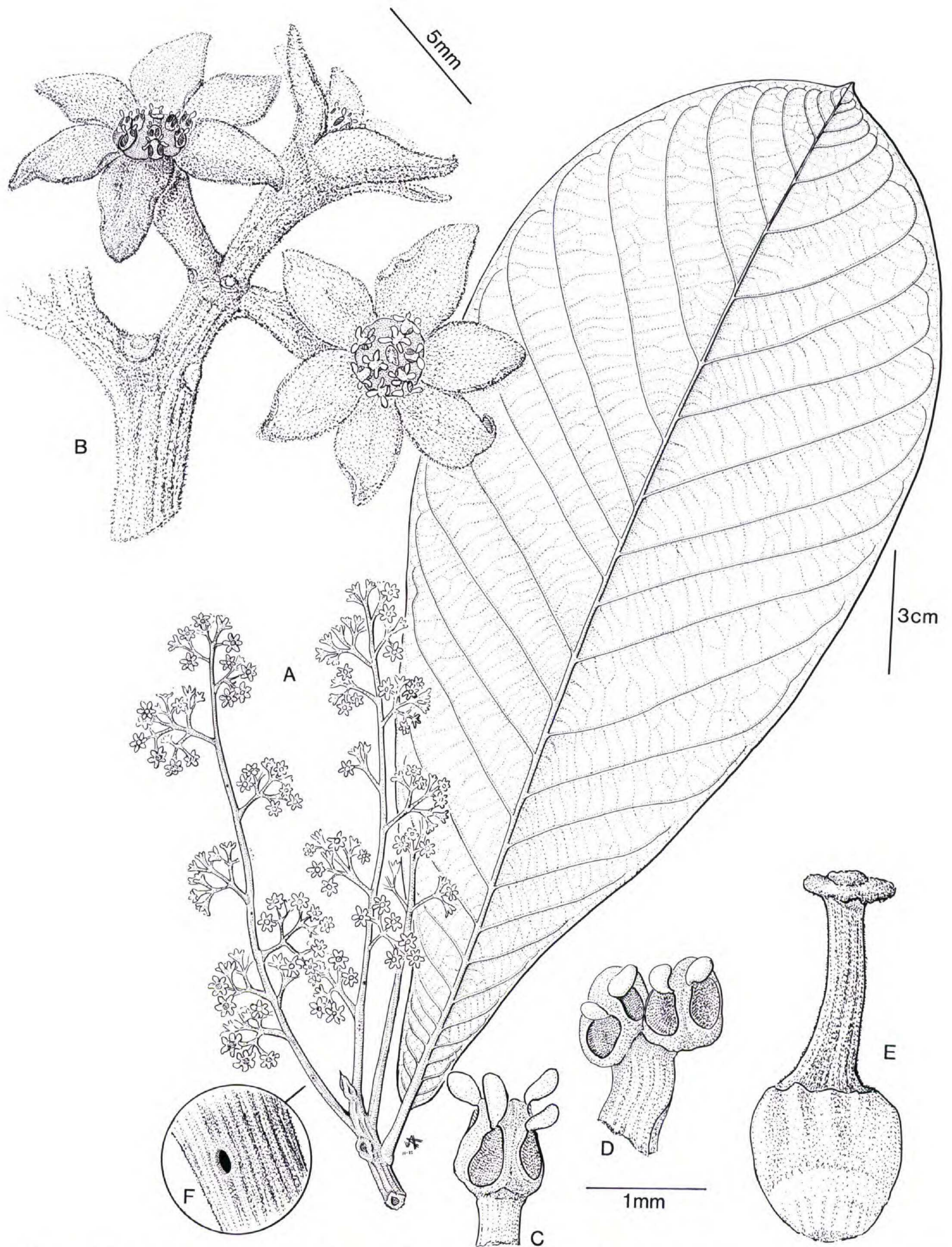
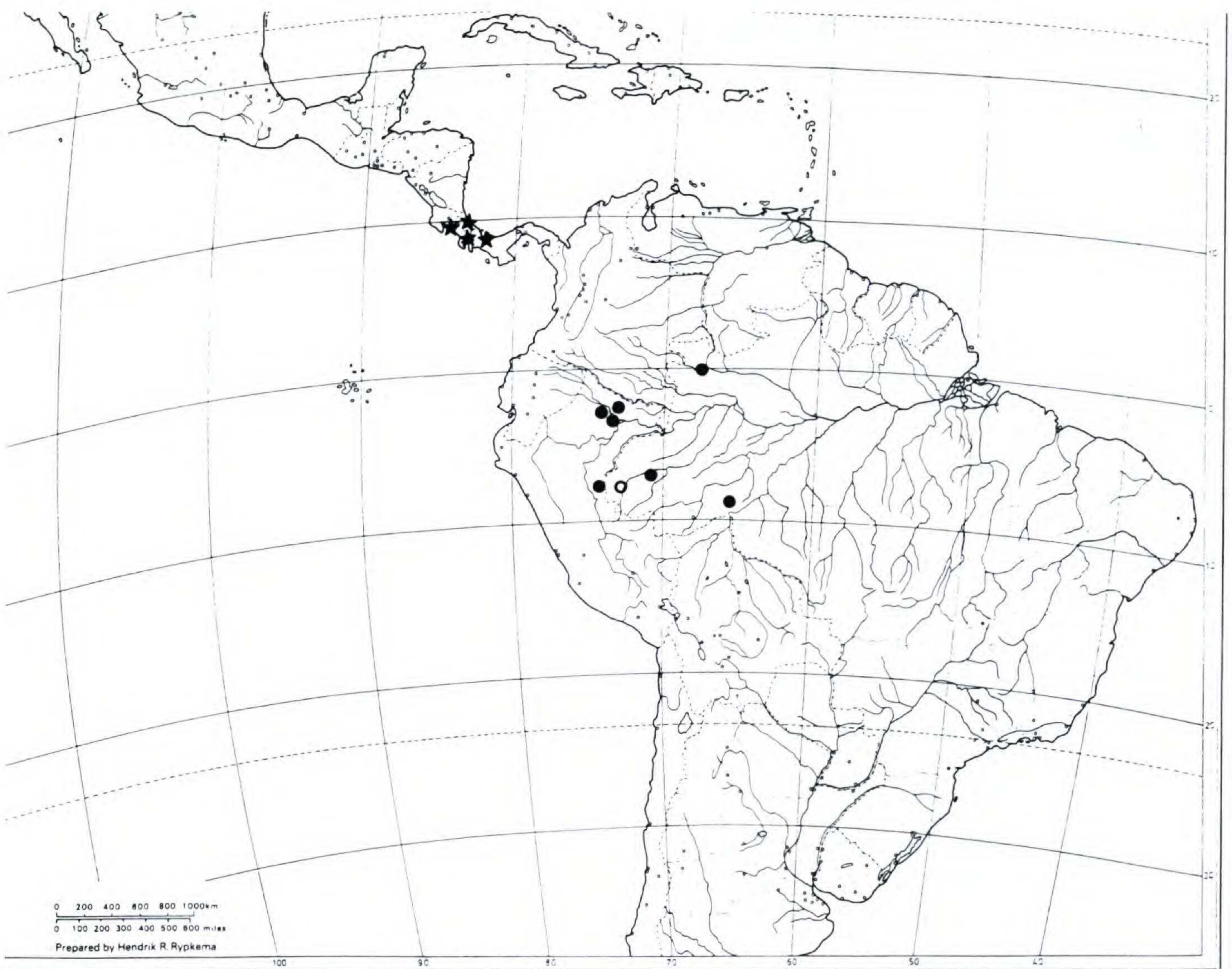


FIGURE 31. *P. obovatum*.—A, Habit.—B, Flowers.—C, Stamen (Whorl I).—D, Stamens (Whorls I and III) with fused filaments.—E, Pistil.—F, Detail of inflorescence axis, showing hole used as passage by ants.



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FIGURE 32. Distribution of *P. palmanum* (★), *P. panurense* (●), and *P. prancei* (○).

that the few collections do not show the full range of morphological variation.

Pleurothyrium palmanum (Mez & J. D. Smith) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 41. 1986. *Ocotea palmana* Mez & J. D. Smith, Bot. Gaz. (Crawfordsville) 33: 258. 1902. TYPE: Costa Rica. San José: La Palma, *Tonduz CR 12652* = *J. D. Smith Herb. 7374* (B, GH, US; also reported in K, M; holotype not designated). Figure 32.

Trees, to 20 m tall. Twigs solid, ridged or terete, tomentulose with brown or yellow-brown hairs. Terminal bud tomentulose. Leaves alternate, clustered near the tips of branches, chartaceous, 15–28 × 7–15 cm, obovate or broadly obovate, the base cuneate or acute, the tip rounded or with a very short, blunt acumen, upper surface with short, brown pubescence along midrib, otherwise glabrous, lower surface densely yellow-brown to brown-tomentulose, sometimes with taller hairs mixed in,

lateral veins 5–9 on each side, these arching toward the tip and becoming weakly loop-connected in the distal half of the lamina; venation immersed on the upper surface or the midrib slightly raised, midrib and lateral veins elevated on lower surface, tertiary venation slightly raised. Petioles 1–2 cm long, terete, with similar pubescence as twigs. Inflorescences in axils of cataphylls, 4–10 cm long, paniculate, the branchlets once cymosely branched, rarely depauperate and racemose, with up to 20 flowers, brown-tomentellous, bracts subtending flowers sometimes persisting, these elliptic, to 4 mm long, tomentellous on both surfaces. Pedicels ca. 3 mm long, tomentellous. Flowers ca. 10–12 mm diam. Tepals 6, equal in size, ca. 5 mm long, elliptic, the outer three tomentellous outside, inner three papillose except for the tomentellous base; all tepals papillose inside. Stamens 9, 4-celled, the cells lateral, the valves nearly back-to-back; filaments and anthers each ca. 1 mm long, papillose; glands large, partially fused, but not enclosing all outer stamens. Style ca. 1.5 mm long, papillose;

ovary globose, glabrous, ca. 1 mm long, enclosed in the glabrous floral tube. Cupule and fruit unknown. Flowers: November. Elevation range: 1,000–1,600 m.

Collections studied. COSTA RICA. LA PALMA: *Rowlee 233* (F, US), CARTAGO: *Barbour 1011* (F, MO). PUNTARENAS: Reserva Biológica Monteverde, Powell Trail, Pacific slope, *Haber 9526* (MO). SAN JOSE: La Palma, *Tonduz 12652* (B, GH, US). PANAMA. CHIRIQUI: Palo Alto, just E of Boquete, *Stern et al. 1064* (MO).

Pleurothyrium palmanum is a rarely collected species. The concept of this species accepted here is different from that in Burger & van der Werff (1990); one of the two flowering collections cited in that publication (*Barbour 1012*) is here excluded from *P. palmanum*. It differs in its indument (lower leaf surface is nearly glabrous, not entirely covered by a brown-tomentellous indument) and flower structure (glands are fused and enclosing stamens, not only partly fused and not enclosing stamens). The only flowering collections I have seen are the type and *Haber 9526*. The glands in *P. palmanum* are not strongly enlarged and the stamens are erect, with the lower pair of locelli lateral and the upper introrse. The available collections are quite variable in leaf size. The type has large (18–28-cm-long) leaves; *Barbour 1011*, a sterile collection, has leaves to 15 cm long, while *Stern et al. 1064* (from Chiriquí, Panama) and *Haber 9526* have even smaller leaves, to 10 cm long. Because *Haber 9526* and the type have the same flower type, leaf shape (\pm obovate), and indument, I attach no taxonomic value to the striking variation in leaf size. The collection *Barbour 1012* remains unplaced. As mentioned earlier, I exclude it from *P. palmanum*, but the specimens (a MO and a US sheet) have few flowers, some of which had been dissected by earlier botanists and were unrecognizable, while others were covered with fungus or were otherwise damaged. Vegetatively, *Barbour 1012* somewhat resembles *P. golfodulcense*.

Pleurothyrium panurense (Meissner) Mez, *Jahrb. Bot. Gart. Berlin* 5: 468. 1889. *Nectandra panurensis* Meissner, D.C. *Prodr.* 15(1): 157. 1864. *Ocotea panurensis* (Meissner) Kostermans, *J. Sci. Res. (Jakarta)* 1: 122. 1952. TYPE: Brazil. Amazonas: near Panure along the Rio Uaupés, *Spruce 2449* (B, BM, BR, E, G, K; holotype not designated). Figures 32, 33.

Tree, to 20 m tall. Twigs solid, terete, minutely brown-tomentellous, ca. 4 mm diam. 5 cm below the apex. Terminal bud brown-tomentellous. Leaves

clustered near tips of branches, chartaceous, 15–30 \times 6–10 cm, elliptic to elliptic-obovate, the base obtuse or rounded, the tip acuminate; upper surface glabrous, lower surface covered with a very fine, almost appressed whitish tomentum, this partially wearing off on older leaves; lateral veins 12–16, arching upward near the margin and loop-connected in the upper half of the laminae, venation immersed on upper surface, costa and lateral veins raised on lower surface. Petioles 5–14(–24) mm long, with similar indument as twigs. Inflorescences in the axils of cataphylls, brown-tomentellous, 5–10 cm long, paniculate, the branchlets 1–2 times cymosely branched, 15–30-flowered, bracts deciduous at anthesis. Pedicels to 5 mm long. Flowers white, ca. 8 mm diam. Tepals 6, equal, outer three gray-tomentellous outside, inner three with a basal triangular tomentellous patch, otherwise glabrous, elliptic, ca. 3 mm long. Stamens 9, 4-celled, all with 2 cells extrorse, the other pair lateral; stamens scarcely raised above the glandular mass that completely surrounds the stamens; ovary glabrous, globose, ca. 1.3 mm long, enclosed mostly in the rather deep, glabrous floral tube, the upper part covered by the glands; style ca. 0.5 mm long, papillose; stigma platelike. Cupule deeply cup-shaped, 2–2.5 cm wide, ca. 1.5 cm long, warty, gradually narrowing into the pedicel. Fruit ellipsoid, ca. 2.3 cm long, 1.4 cm wide. Fruits: December–April. Flowers: May–June. Elevation range: 100–200 m.

Collections studied. BRAZIL. AMAZONAS: near mouth of Rio Embira, *Krukoff 4783* (G, NY); mouth of Rio Embira, tributary of River Tarauaca, *Krukoff 4800* (A, F, G, MO, NY); Rio Apitua tributary of Rio Purus, 120 km S of Labrea, *Prance 13927* (NY); Panure ad Rio Uaupés, *Spruce 2449* (B, BM, BR, E, G, K). PERU. LORETO: Maynas, Mishana, Río Nanay, *Ayala 5734* (MO); Maynas, vicinity of Iquitos, *Revilla 3687* (MO); Maynas, Pto. Almendras, *Vásquez 10233* (MO); San Antonio, Río Pintuyacu, *Vásquez et al. 7468* (MO). UCAYALI: Coronel Portillo, Leoncio Prado (Yarina Cocha), *Vásquez 4970* (MO).

Pleurothyrium panurense is a rarely collected species, known with certainty from six collections: the type collection, four recent collections from Peru, and a collection from Brazil. All collections, including the type (indicated on the K sheet), come from inundated forest. Allen (1964) listed two additional collections of *P. panurense*, *Froes 20526* and *21295* (both NY), and presented a description of cupule and fruit based on *Froes 20526*. I assign these collections to *P. vasquezii* because the pubescence on the lower leaf surface consists of scattered, erect hairs (not a finely appressed, whitish indument) and because the leaves are not clustered.

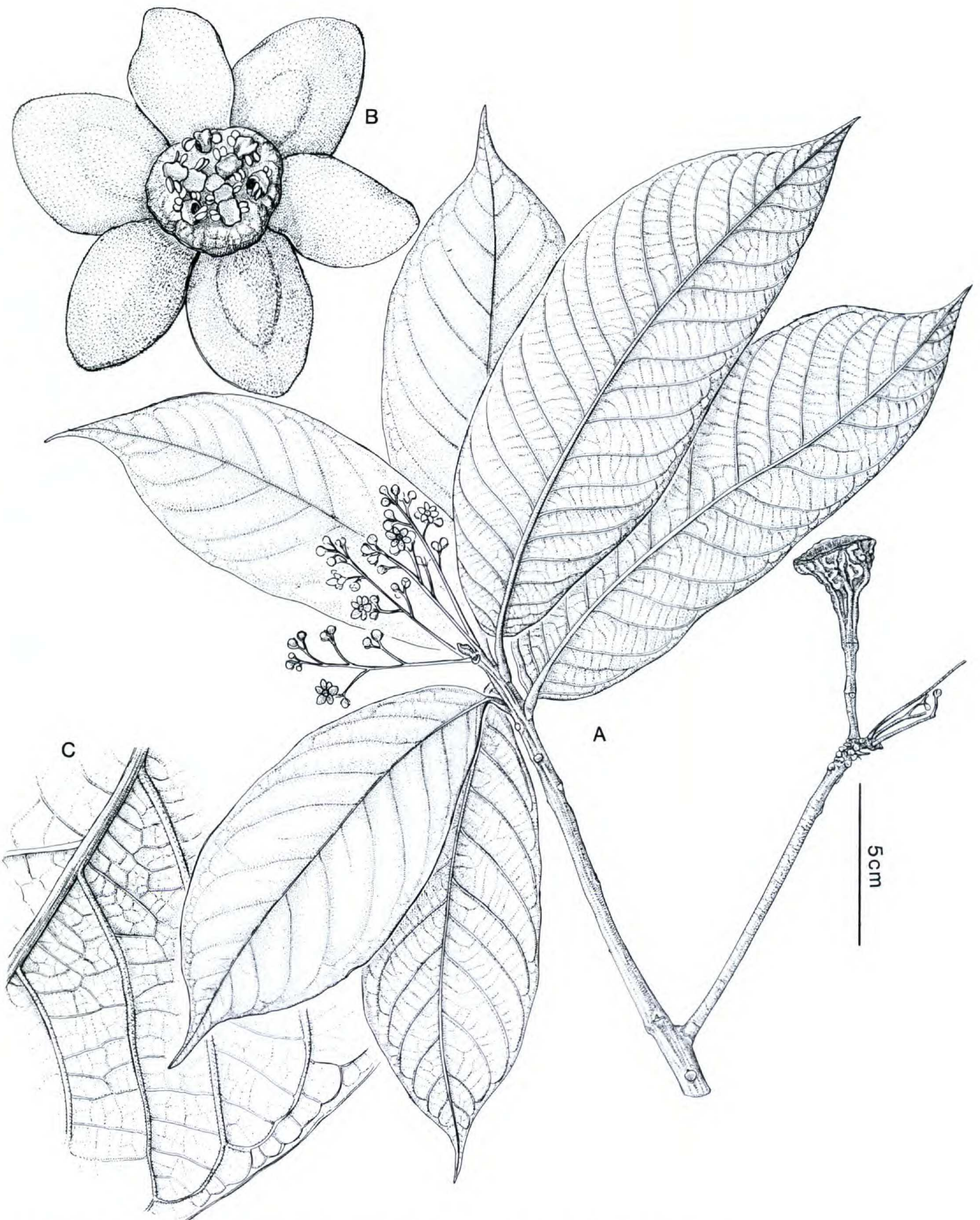


FIGURE 33. *P. panurense*.—A. Habit.—B. Flower.—C. Detail of lower leaf surface.

Also, the marginal vein is more strongly developed, and the pubescence on the young twigs is ferruginous-tomentose rather than light-brown tomentellous. Thus, Allen's description of cupules and fruits of *P. panurense* should be ignored.

Actually, *Pleurothyrium panurense* can be readily identified by the following combination of

characters: short (to 10-cm-long) inflorescences, inner face of tepals glabrous, leaves clustered, leaves with an obtuse or rounded base, and leaves with a whitish indument on lower leaf surface. The flower size is normal for the genus and the glands are well developed.

It is likely that *Prance et al.* 13927 (NY) be-



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FIGURE 34. Distribution of *P. parviflorum* (★), *P. pauciflorum* (●), and *P. pilosum* (○).

longs here, too. However, the leaves are rather narrow and not clustered; the indument agrees with *Pleurothyrium panurense*. Unfortunately, the specimen is sterile.

Krukoff 4800 and *Vasquez 4970* are provisionally placed here. They differ from *P. panurense* in their acute leaf bases and longer petioles (18–24 mm vs. 5–13 mm in typical *P. panurense*), but agree well in inflorescence and floral characters. Both collections were made in flooded forest. Although it is possible that future collections will show these collections to be different from *P. panurense*, I prefer to include them for the time being in *P. panurense*. *Krukoff 4800* was cited by A. C. Smith as a paratype of *P. nobile*, but it differs from that species in its indument.

Pleurothyrium parviflorum Ducke, Arch. Jard. Bot. Rio de Janeiro 5: 114. 1930. *Ocotea parviflora* (Ducke) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Brazil. Amazonas: Igarapé do Lago de Serpa prope Itacoatiara, ad ripas inundatas, *Ducke RB 19935*

(holotype, RB; isotypes, B, U). Figures 34, 35.

Pleurothyrium densiflorum A. C. Smith, Bull. Torrey Bot. Club 58: 109. 1931. *Ocotea compactiflora* Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Peru. Loreto: Mishuyacu, *Klug 1372* (holotype, NY not seen; isotype, US).

Tree, to 30 m tall, but usually not exceeding 20 m. Twigs slightly angular or terete, fistulose, glabrous or nearly so, ca. 5 mm diam. a few cm below the tip. Terminal bud covered with gray, fine appressed hairs. Leaves alternate, chartaceous, 10–20 × 3.5–9 cm, elliptic, the base acute to truncate, apex acute, glabrous or nearly so on both surfaces. Lateral veins 10–15 on each side, curving toward the tip near the margin, but not uniting with the superior veins; veins immersed on upper surface, midrib and lateral veins raised on lower surface. Petioles 10–15 mm long, glabrous, somewhat canaliculate. Inflorescences in axils of leaves or cataphylls, glabrous or with some minute appressed pubescence, 5–15 cm long, the branches up to 4 times cymosely branched, frequently flat-

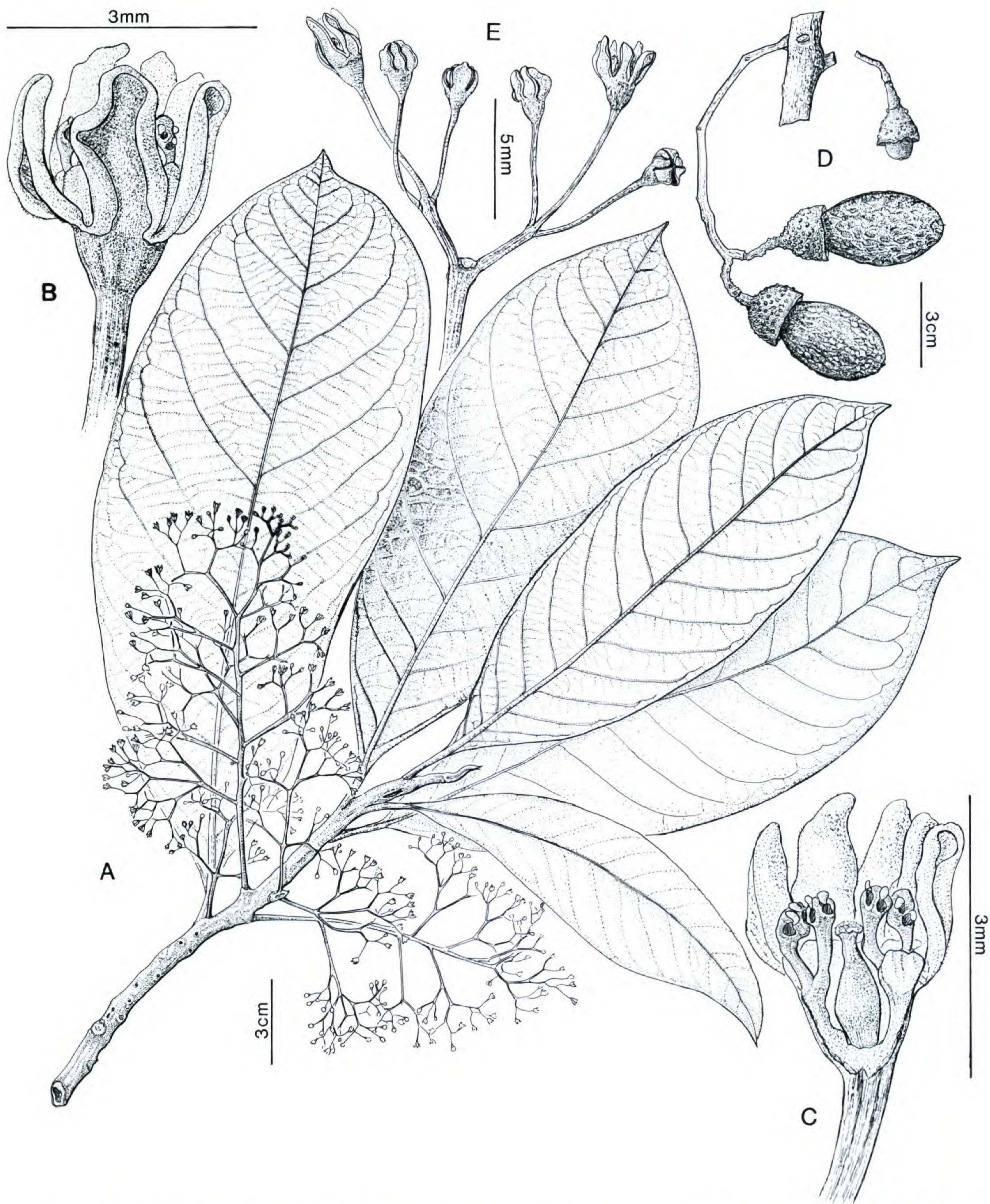


FIGURE 35. *P. parviflorum*.—A. Habit.—B. Flower.—C. Cross section of flowers.—D. Fruit.—E. Part of inflorescence.

tened, many-flowered; bracts absent at anthesis, but present in younger parts of inflorescences, linear, to 2.5 mm long, glabrous or with some minute appressed pubescence, the margin ciliate. Pedicels 3–5(–7) mm long. Flowers green or greenish white, ca. 5 mm diam. Tepals 6, equal, narrowly elliptic, ca. 2 mm long, the margins reflexed, glabrous or

minutely papillose outside, papillose on inner surface. Stamens 9, ca. 0.9 mm long, 4-celled, the cells lateral, filaments glabrous, as long as anthers. Glands almost completely encircling the outer stamens, but not fused. Ovary glabrous, ellipsoid, ca. 0.7 mm long, gradually narrowed into the 0.4-mm-long, glabrous style. Floral tube deep, fully en-

closing the ovary, glabrous. Cupule with large lenticels, completely enclosing the fruit when young, at maturity bowl-shaped, 2.5 cm wide, 1 cm high, sometimes smaller and shallower; fruit ellipsoid, 3.6 × 2.7 cm, well exerted. Fruits: December–April. Flowers: April–August. Elevation range: 100–300 m.

Collections studied. BRAZIL. ACRE: Rio Moa, 10 km from Maita, *Prance et al.* 11970 (K, NY). AMAZONAS: Itacoatiara, Igarape de Serpa, *Ducke RB* 19935 (B, RB, U); Rio Jutahy, *Froes* 21036 (F, NY); Rio Asapinus, Tapajos, *Miranda Bastos* 17 (RB); delta of Rio Jauaperi, *Mori* 20470 (MO, NY); mouth of Rio Ica along Rio Solimões, *Mori et al.* 9074 (K, MO, NY); Mun. Jutai, Est. Ecologica Jutai-Solimões, *Cid Ferreira et al.* 7292 (MO, NY). ECUADOR. NAPO: Río Cuyabeno, *Berg & Akkermans* 1050 (F, K, MO, U); Aguarico, Parque Nacional Yasuni, Garza Cocha, *Ceron* 4982 (MO). PERU. Soledad, *Tessmann* 5175 (NY). UCAYALI: Coronel Portillo, Yarinacocha, Nueva Esperanza de Panaillo, *Vásquez* 10500 (MO). LORETO: Manfinfa on upper Río Nanay, *Llewelyn Williams* 1090 (F); Caballo-Cocha, *Llewelyn Williams* 2273 (F, G); Maynas, Caballo-Cocha, *Ayala* 3386 (MO, NY); Maynas, *Croat* 17593 (F, MO, NY); Maynas, Puerto Almendras, *Díaz* 241 (MO); Maynas, E of Pto. Alegria, *Gentry & Daly* 18317 (MO, NY); Maynas, Río Mazan, ca. 35 km above Mazan, *Gentry & Revilla* 16627 (F, MO, NY); Maynas, Tamshiyacu, *Gentry et al.* 25807 (F, MO, NY); Maynas, Mishana, *Gentry et al.* 25914 (MO, NY); Maynas, Río Nanay, *Gentry et al.* 28959 (MO); Maynas, Quebrada Yahuasyacu, Caserio Portugal, *Grandez* 1732 (MO); Maynas, Mishuyacu, *Klug* 1301 (F, NY, US), *Klug* 1372 (NY, US); Maynas, Mishana, *López* 8634 (NY); Maynas, Río Nanay below Bellavista, *McDaniel* 15243 (F, NY); Maynas, Río Momon above Bellavista, *McDaniel* 20716 (MO, NY), *McDaniel* 20753 (MO); Maynas, Río Atacuari, *Mori et al.* 9227 (F, MO, NY); Maynas, Río Yaguasyaco, affluent of Río Ampiyaco, *Plowman* 6908 (F); Maynas, Leticia, Isla Rondina, *Plowman et al.* 6410 (F, GH); Maynas, Río Nanay, cerca a Santa Clara, *Revilla & Froehner* 2532 (F, MO); Maynas, Río Yahuasyacu, *Revilla* 742 (F, G, MO); Maynas, Alberque Selva Tours Río Momon, *Ruiz* 1438 (MO); Maynas, Yanamono Explorama Tourist Camp, *van der Werff* 9956 (MO); Maynas, Yanamono-Explorama Lodge, *Vásquez & Jaramillo* 9138 (MO); Maynas, Iquitos, Caseria Nueva Jerusalem, Isla Iquitos, *Vásquez* 11507 (MO); Requena, Jenaro Herrera, *Freitas* 55 (MO); Requena, Río Tapiche, *Gentry et al.* 21284 (MO); Requena, Jenaro Herrera, *Lamotte* 0200 (MO), *Lamotte* 085 (MO); Requena, Jenaro Herrera, Quebrada Iricahua, *Peters & Hammond* 52/84 (F, MO, NY); Requena, Jenaro Herrera, *van der Werff* 10050 (MO), *van der Werff* 10066 (MO); Requena, Cocha Paucate, Río Ucayali near Pto. Peru, *Vásquez & Jaramillo* 896 (F, G, MO, NY); Requena, Yarina (Río Tapiche), *Vásquez et al.* 4858 (MO, NY); Ucayali, Yarinacocha (near Pucallpa), *Vásquez & Jaramillo* 1520 (MO); Ucayali, Jenaro Herrera, Quebrada Supay, *Vásquez* 12284 (MO).

Pleurothyrium parviflorum is one of the most frequently collected *Pleurothyrium* species. It is apparently a common tree in seasonally flooded forest (tahuampa) in Amazonian Peru and has been

reported also from Brazil (Estado Acre and Amazonas) and Ecuador. This species can be easily identified by its habitat preference, and the combination of hollow stems (sometimes inhabited by ants), nearly glabrous inflorescence, glabrous leaves, and the reflexed margin of the tepals. There are a few other *Pleurothyrium* species with hollow twigs and tepals with reflexed margin and of those, *Pleurothyrium poeppigii* Nees can be confused with *P. parviflorum*. However, *P. poeppigii* has a dense, minute cover of hairs on the lower leaf surface, stiffer leaves, pubescent flowers and inflorescences, and smaller glands that do not enclose the outer stamens. One collection, *Nuñez* 5901 (MO), is intermediate between the two. It resembles *P. parviflorum* in the lack of pubescence and the texture of the leaves and size of the glands, but has the stiffer, narrower inflorescences and pubescence of the flowers found in *P. poeppigii*. Common name: Yacu Moena (= Moena del agua).

Pleurothyrium pauciflorum van der Werff & Hammel, sp. nov. TYPE: Costa Rica. Puntarenas: Cantón de Osa, ca. 2 km NE of the union of Río Pavón and Río Rincón, tree, 30 m, fl., *Hammel et al.* 17909 (holotype, MO; isotypes, BM, CR, MEXU, USJ). Figures 34, 36.

Arbor, ad 35 m. Ramuli teretes, solidi, ferrugineo-tomentelli. Gemma apicalis ferrugineo-tomentella. Folia alterna, firme chartacea, 16–35 × 7–12 cm, oblonga vel elliptica, basi acuta vel obtusa, apice acumine ad 2 cm longo praedita, nervis lateralibus 14–20 utroque costae latere, brochidodroma in dimidio distale, supra glabra vel basi sparse tomentella, subtus pilis plus minusve erectis praedita, indumento secus nervos densiore, secus nervos majores tomentello; supra nervis immersis, subtus costa nervisque lateralibus prominenter elevatis, reticulatione paullo elevata. Petioli 1.8–3.2 cm longi. Inflorescentiae in bractorum axillis ortae, ad 3 cm longae, pauciflorae. Pedicelli ad 2 mm longi. Flores ad 8 mm diametro, tepalis semi-erectis. Tepala 6, aequalia, crassa, 4–5 mm longa, ca. 4 mm lata, intus paullo papillosa, tres exteriora extus tomentella, tres interiora basi tomentella, demum papillosa. Stamina 9, 4-locellata, locellis lateralibus, glandulis peraeuctis, staminibus cingentibus. Pistillum ca. 3 mm longum, ovario pubescente sensim in stylum glabrum attenuato; receptaculo pubescente. Infructescentiae 2.5–4.5 cm longae; cupulae crassae, verrucosae, 2 cm longae, 3 cm latae, 1.5 cm profundae, tepalis frequenter persistentibus. Fructus ellipsoideus, 3 × 1.5 cm.

Tree, to 35 m tall. Twigs terete, solid, ferruginous-tomentellous, 4–6 mm diam. ca 5 cm below apex. Terminal buds ferruginous-tomentellous. Leaves alternate, grouped near tips of branches, firmly chartaceous, 16–35 × 7–12 cm, oblong or elliptic, the base acute or obtuse, tip acuminate, acumen to 2 cm long, but frequently damaged,



FIGURE 36. *P. pauciflorum*.—A. Habit.—B. Inflorescence with flower.—C. Fruit.

lateral veins 14–20 on each side, curving strongly upward near the margin and becoming loop-connected in upper half of the leaf, upper leaf surface glabrous or with traces of a tomentellous indument along midrib, the lower surface with \pm erect hairs, this indument denser along veins and becoming tomentellous along major veins; veins immersed on upper surface, midrib and lateral veins prominently raised on lower surface, the tertiary venation slightly raised, but readily visible because of its indument. Petioles 1.8–3.2 cm long, upper surface flat, with similar indument as on twigs. Inflorescences in axils of (tardily) deciduous bracts, to 3 cm long, with up to 7 flowers (usually 3 or 1), ferruginous-tomentellous, bracts at base of inflorescences frequently present at anthesis, ovate or elliptic, to 5 mm long, pubescent on both surfaces. Pedicels ca. 2 mm long, ferruginous-tomentellous. Flowers ca. 8 mm diam., the tepals half-erect or somewhat spreading, never fully rotate; in old flowers tepals erect. Tepals 6, equal in size and shape, thick, 4–5 mm long, ca. 4 mm wide, all tepals inside slightly papillose, the outer 3 outside ferruginous-tomentellous, inner 3 with a basal triangular tomentellous area, otherwise slightly papillose. Stamens 9, all 4-celled, the cells lateral, glands strongly enlarged, enclosing stamens and fused. Pistil ca. 3 mm long, the pubescent ovary gradually narrowed into the glabrous style; receptacle \pm pubescent. Infructescences 2.5–4.5 cm long, usually with 1 fruit; cupule thick, warty, ca. 2 cm tall, 3 cm wide and 1.5 cm deep, the tepals often persisting on the margin; fruit ellipsoid, ca. 3 \times 1.5 cm. Fruits: June. Flowers: October. Elevation range: 50–200 m.

Collections studied. COSTA RICA. PUNTARENAS: Osa, Hammel 17009 (MO); Osa, Reserva Indigena Guaimi, Hammel 17909 (BM, CR, MEXU, MO, US).

Pleurothyrium pauciflorum can be readily identified by the ferruginous-tomentellous branchlets and the short, few-flowered inflorescences. Depauperate specimens of *P. golfodulcense* may also have short inflorescences, but this species has twigs covered with more or less appressed, ascending hairs, lacks erect hairs on the lower leaf surface, and has rotate flowers. It is uncommon to find a *Pleurothyrium* species with strongly enlarged glands that has half-erect tepals instead of rotate flowers. The androecium was, in all flowers seen, more or less covered by the tepals. Also, the tepals were, in comparison to other *Pleurothyrium* species, quite thick and fleshy. It would be interesting to discover

what insect might pollinate this species; the arrangement of tepals suggests a beetle.

Pleurothyrium pilosum van der Werff, sp. nov.

TYPE: Panama. San Blas: Cangandi, 9°24'N, 70°24'W, hills near village, *de Nevers*, *Herrera & Charnely* 7520 (holotype, MO; isotypes, CAS, PMA). Figure 34.

Arbor. Ramuli angulares, lateritio-tomentosi, cicatricibus conspicuis praediti. Gemma terminalis brevis, crassa, lateritio-tomentosa. Folia ad apices ramulorum congesta, chartacea, 15–25 \times 7–13 cm, obovata, basi obtusa vel rotundata, apice rotundata vel breviter acuminata, nervis lateralibus 6–9 utroque costae latere, basalibus sub angulo acutiore quam venis distalibus abeuntibus, supra costa nervisque immersis, subtus elevatis, reticulatione paullo elevata; supra glabra, subtus dense pilosa, indumento secus costam nervosque tomentoso. Petioli 1.5–3 cm longi, lateritio-tomentosi. Inflorescentiae axillis cataphyllorum ortae, ad 15 cm longae, lateritio-tomentosae. Flores non visi. Tepala 6, late elliptica, 3 mm longa, intus et extus pubescentia. Stamina pubescentia, 9, 4-locellata, locellis lateralibus, glandulis magnis, stamina fere cingentibus, liberis. Pistillum glabrum, receptaculum pubescens. Fructus immaturus in cupula profunda, hexangulare inclusus.

Tree. Twigs angular, reddish brown tomentose, with conspicuous scars of old leaves, solid, 6 mm diam. ca. 5 cm below the tip. Terminal bud short, thick, reddish brown tomentose. Leaves clustered near tips of branches, chartaceous, 15–25 \times 7–13 cm, obovate, the base obtuse to rounded, tip rounded or very shortly acuminate, lateral veins 6–9 on each side, the lowest pair leaving the midrib at the very base of the lamina and under a smaller angle than the more distal lateral veins, lateral veins approaching the leaf margin very closely and strongly arching upward, but only the upper 2 or 3 veins loop-connected, midrib and lateral veins immersed on upper leaf surface, but prominently raised on lower surface, the tertiary venation slightly raised; upper surface glabrous or with very few scattered reddish hairs, lower surface densely covered with erect, reddish hairs, these not obscuring the surface, the indument becoming tomentose along lateral veins and midrib. Petioles flattened above, 1.5–3 cm long, reddish brown tomentose. Pubescence on twigs and veins on lower leaf surface described by collectors as orange. Inflorescences in axils of cataphylls, at tips of branches, to 15 cm long, reddish brown tomentose, branchlets once cymosely branched or flowers racemosely arranged. Open flowers not seen. Tepals (based on remnants on young fruits) broadly elliptic, densely pubescent on both surfaces, 3 mm long. Stamens pubescent, 9, 4-celled, cells lateral; glands en-

larged, forming a dome and largely enclosing stamens, free (the glandular mass is broken up in fruiting stage). Ovary and style glabrous; receptacle pubescent inside. Young fruits enclosed in cupule, cupule with 6 ribs, to 1.5 cm long. Young fruits: March. Elevation range: ca. 30 m.

Collection studied. PANAMA. SAN BLAS: Cangandi, de Nevers *et al.* 7520 (CAS, MO, PMA).

Pleurothyrium pilosum, only known from the type collection from San Blas, Panama, is closely related to *P. racemosum*, another Panamanian species only known from the type. These two species have in common a glabrous ovary and style, pubescent receptacle, clustered leaves, the basal lateral vein leaving the midrib under an acute angle at the very base of the lamina, and lateral veins that approach the leaf margin very closely. Although some of these characters occur also in other *Pleurothyrium* species, the ascending basal lateral veins are unique to these two species. *Pleurothyrium pilosum* differs from *P. racemosum* in its larger leaves (to 25 vs. 14 cm), in its leaf shape (obovate vs. oblong), indument of lower leaf surface (pilose vs. with scattered curled hairs or subglabrous) and indument of twigs (longer, red-brown vs. shorter plain brown).

Unfortunately, the only collection of *Pleurothyrium pilosum* is in young fruit. The description of floral parts is based on dried remnants on the young fruits, and I am not certain that the dimensions are correct. Because the type collection was made from a marked tree in a permanent quadrat, it is likely that the tree will be recollected in the future.

Pleurothyrium poeppigii Nees, Syst. laur.: 349.

1836. *Octoea poeppigii* (Nees) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Peru. Maynas: *Poeppig addenda* 301 (B, G, GZU, L, holotype not designated). Figure 37.

Pleurothyrium krukovii A. C. Smith, Phytologia 1: 121.

1935. *Ocotea krukovii* (A. C. Smith) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Brazil. Acre: near mouth of Rio Macauhan, *Krukoff* 5563 (holotype, NY not seen; isotypes A, G, K, MO).

Tree to 30 m tall. Twigs terete or subangular, fistulose, minutely brown-tomentellous or glabrous, 4–7 mm diam. ca. 5 cm below the tip. Terminal bud minutely brown-tomentellous. Leaves alternate, firmly chartaceous or subcoriaceous, 20–30 × 6–10 cm, (narrowly) elliptic to slightly (narrowly) obovate, the base acute, tip rounded or shortly

acute, the upper surface glabrous, lower surface minutely tomentellous, papillose or rarely glabrous, lateral veins 14–18 on each side, arching upward near the margin, not or very weakly loop-connected, venation immersed on the upper surface, midrib and lateral veins raised on the lower surface. Petioles 1.5–2 cm long, with similar indument as on twigs, canaliculate. Inflorescences in axils of deciduous bracts, or infrequently in axils of regular leaves, to 18 cm long, minutely tomentellous or subglabrous, the branchlets complanate, to two times cymosely branched, the flowers often appearing densely clustered; bracts deciduous at anthesis. Pedicels 2–3 mm long. Tepals 6, equal, ± erect at anthesis, the margin reflexed, elliptic, ca. 2 mm long, the outer three minutely tomentellous outside, the inner three with a minutely tomentellous, triangular, basal patch, otherwise papillose; all tepals papillose on inner surface. Flower color described as white, green, and dull orangish; odor of melon. Stamens 9, all 4-celled, glabrous, 2 cells ± extrorse, the other 2 ± introrse, filaments about as long as anther, outer stamens separated by the enlarged glands, but glands not surrounding stamens and remaining free. Ovary ellipsoid, mostly included in the glabrous receptacle, glabrous or papillose near the tip, the style about as long as ovary, papillose; pistil ca. 2 mm long. Cupule cup-shaped, ± warty, ca. 1.5 cm high, 1.8 cm wide. Fruits: January, August, and November. Flowers: March, April, August, and December. Elevation range: 400–1,800 m.

Collections studied. BOLIVIA. COCHABAMBA: Totora, Yungas of Janamayú, *Cardenas* 3966 (F, US). BRAZIL. ACRE: mouth of Rio Macauhan (tributary of Rio Yaco), *Krukoff* 5255 (A, F, G, MO, NY, S, US); near mouth of Rio Macauhan (tributary of Rio Yaco), *Krukoff* 5263 (S); mouth of Rio Macauhan (tributary of Rio Yaco), *Krukoff* 5563 (A, G, K, MO), *Krukoff* 5722 (A, NY). COLOMBIA. PUTUMAYO: along Rumiaco River, above confluence with Rio Mocoa, *Soejarto* 1268 (GH). ECUADOR. NAPO: road to Puerto Napo–Tena, *Lugo* 320 (S); 7–16 km E of Puerto Napo, *Neill* 6555 (F, MO, NY); along road to Tena, 2 km from Misahualli, *Palacios* 2775 (MO); Jatun Sacha, 8 km abajo de Puerto Misahualli, *Palacios* 982 (MO); Tena, *Neill* 7603 (MO). PERU. *Ruíz & Pavón s.n.* (F). LORETO: Maynas, Yurimaguas, *Poeppig Addenda* 301 (B, G, GZU, LE). MADRE DE DIOS: Cocha Cashu Biological Station, Manu National Park, *Gentry* 43560 (MO, NY); Manu, Río Manu, Cocha Cashu Station, *Davidson* 85-19 (F); Manu, Cerro de Pantiacolla, Río Palatua, *Foster* 10642 (MO); Manu, Río Manu, *Foster* 3153 (F, MO); Manu, Cocha Cashu uplands, Manu Park, *Nuñez* 5901 (MO). PASCO: around Oxapampa, *van der Werff* 8343 (MO), *van der Werff* 8345 (MO); Oxapampa, 5 km SE of Oxapampa, *Smith* 2793 (MO); Oxapampa, around Villa Rica, *van der Werff* 8288 (MO).



FIGURE 37. Distribution of *P. poeppigii* (★), *P. racemosum* (●), *P. steyermarkianum* (○), and *P. synandrum* (■).

As accepted here, *P. poeppigii* is a wide-ranging species occurring in Amazonian Brazil, Bolivia, Peru, Ecuador, and Colombia. Its nearest relative is *P. parviflorum* Ducke, from which it differs in the tomentellous flowers and inflorescences, the narrower inflorescences, the tomentellous lower leaf surfaces, and the more coriaceous and generally larger leaves. The type specimens of *P. poeppigii* and *P. krukovii* are both somewhat atypical for this species. *Poeppig addenda* 301, the type of *P. poeppigii*, has strongly fistulose twigs and even some of the inflorescences are fistulose. These inflorescences are shorter and more compact than nonfistulose inflorescences on other specimens. The flowers of *Poeppig addenda* 301 are slightly larger than on the other specimens, and the pedicels are slightly thicker. However, I feel that these differences do not warrant the recognition of two species, and I am inclined to accept most of these differences as a consequence of the strongly fistulose character of twigs and inflorescences. Oddly enough, none of the labels indicate that the twigs were inhabited by ants, although the hollow twigs and

the exit holes along the twigs strongly suggest that ants colonize the twigs. See also discussion under *P. cuneifolium*.

The type of *P. krukovii* has, for this species, rather thin and glabrous leaves, characters found in *P. parviflorum*. The inflorescence and the flower buds have, however, the indumentum of *P. poeppigii*. In spite of the fact that A. C. Smith described flowers of *P. krukovii*, none of the isotypes I have seen had flowers, and the microfiche photo of the NY holotype does not show flowers either. *Krukoff* 5722, a paratype, also has glabrous leaves, but has tomentellous flowers. *Krukoff* 5255 has stiffer leaves and tomentellous leaves and flowers; it fits my concept of *P. poeppigii* very well. These observations allow two approaches. One is to define three species narrowly: *P. poeppigii*, only known from its type; *P. krukovii*, with very few collections (excluding, for instance, *Krukoff* 5255) and defined by its glabrous, chartaceous leaves and subglabrous inflorescence axes; and a third, undescribed species occurring in Brazil, Peru, Ecuador, and Colombia with subcoriaceous, tomentellous leaves and rather

lax inflorescences. The other approach is to accept *P. poeppigii* in a wider sense, defined by its fistulose stems, tomentellous flowers, narrow inflorescences, and similar floral structure. I take this approach rather than recognizing three poorly defined and hard to identify taxa.

For the same reason, the collection *Cardenas 3966* (F, US) is included in *Pleurothyrium poeppigii*, although its obovate leaves are aberrant for this species. In other characters, such as flower size and structure, fistulose and tomentellous twigs, it fits in *P. poeppigii*, and I am not willing to describe a new taxon with only one collection based solely on a different leaf shape. This is the only collection of *P. poeppigii* from Bolivia.

In addition to *Pleurothyrium parviflorum* Ducke and *P. poeppigii*, *P. cuneifolium* Nees can also have fistulose twigs. This latter species can be recognized by its angular, lenticellate twigs, larger flowers, and tepals that are glabrous on the inner surface.

Although most collections of *Pleurothyrium poeppigii* are from lowland sites, I include here three collections from the Oxapampa area in central Peru from ca. 1,800 m elevation.

Pleurothyrium prancei van der Werff, sp. nov.

TYPE: Brazil. Acre: vicinity of Serra de Moa, varzea forest, stilt-rooted tree, 8 m tall, *Prance et al. 12392* (holotype, F; isotypes, F, MO, NY, S). Figure 32.

Arbor, ad 8 m. Ramuli parum angulati, cinnamomeo-tomentelli; glabrescentes. Gemma terminalis cinnamomeo-tomentosa. Folia alterna, chartacea, 15–30 × 4.5–9 cm, anguste obovata vel anguste elliptica, basi acuta, apice acuminata, acumine ad 1.5 cm longo, supra glabra, subtus costa et nervis tomentellis, laminis glabris vel paucis pilis praeditis, supra venatione immersa, subtus costa nervisque elevatis, reticulatione paullo elevata; nervis 9–12 utroque costae latere, sursum arcuatis, venatione brochidodroma in dimidio distale. Petioli 2–3 cm longi. Inflorescentiae axillis cataphyllorum ortae, in apicibus ramulorum congestae, cinnamomeo-tomentellae, 10–20 cm longae, ramulis semel, raro bis cymae more furcatis, bracteis sub anthesi deciduis. Pedicelli 5–10 mm longi. Flores intus virides, 8–9 mm diametro. Tepala 6, subaequalia, patentia, margine plano, tres exteriora late elliptica 4 × 3 mm, extus cinnamomeo-tomentella, intus maxime basi pubescentia et zona peranguste centrali papillosa, demum glabra; tres interiora elliptica, 3 × 2 mm, extus parte triangulari basali tomentella, demum glabra, intus dense papillosa. Stamina 9, 4-locellata, locellis lateralibus, filamentis stamina aequantibus, glabris; glandulis incrassatis, vix stamina cingentibus, liberis. Pistillum ca. 2 mm longum, pubescens, ovario sensim in stylum brevem attenuato, stigmatem incrassato. Fructus ignotus.

Tree, to 8 m tall, with stilt roots fide collectors. Twigs slightly angular, brown-tomentellous, gla-

brescent, 4 mm diam. ca. 5 mm below tip. Terminal bud brown-tomentellous. Leaves alternate, chartaceous, 15–30 × 4.5–9 cm, narrowly obovate to narrowly elliptic, the base acute, the apex acuminate, acumine to 1.5 cm long, but usually broken off, glabrous above, midrib and to a lesser degree lateral veins tomentellous below, the lamina glabrous or with a few scattered hairs near the base, venation immersed on upper surface, midrib and lateral veins raised on lower surface, tertiary venation slightly raised; lateral veins 9–12 on each side, arching upward near the margin and loop-connected in the distal half. Petioles 2–3 cm long, ± terete, with a similar indument as on twigs. Inflorescences in axils of cataphylls near tip of twigs, brown-tomentellous, 10–20 cm long, the branchlets once or rarely twice cymosely branched, bracts deciduous at anthesis, those subtending buds ca. 2 mm long, tomentellous outside, glabrous inside. Pedicels 5–10 mm long, brown-tomentellous. Flowers green inside, 8–9 mm diam. Tepals 6, subequal, spreading, the margin plane, the outer 3 broadly elliptic, 4 × 3 mm, brown-tomentellous outside, glabrous inside, except for some hairs near the very base and a narrow, median, papillose strip; inner 3 elliptic, 3 × 2 mm, the outside with a basal, triangular, tomentellous patch, otherwise glabrous, the inside densely papillose. Stamens 9, 4-celled, the cells lateral, opening back-to-back, filaments about as long as anther, glabrous; glands enlarged, protruding between the outer stamens and touching adjoining gland in front of outer stamens, but free. Pistil ca. 2 mm long, the ovary pubescent, gradually narrowed into the short style, stigma enlarged. Floral tube pubescent inside. Fruits unknown. Flowers: April. Elevation range: ca. 100 m.

Collection studied. BRAZIL. ACRE: Cruzeiro do Sul, vicinity of Serra da Moa, *Prance 12392* (F, MO, NY, S).

Pleurothyrium prancei, only known from the type collection, occurs in varzea (flooded forest) and reportedly has stilt roots, very unusual for a Lauraceae. It is characterized by the combination of glabrous, alternate leaves, a pubescent pistil, and flowers with the outer tepals glabrous inside, and inner tepals papillose inside. *Pleurothyrium prancei* does not seem to have close relatives. *Campbell et al. 8057*, from the upper Rio Moa in Acre, Brazil is possibly this species; the specimen is, however, sterile and hence the identification tentative.

It is a pleasure to name this species after Ghilleen Prance, who has contributed so widely to the knowledge of the Amazonian flora.

Pleurothyrium racemosum van der Werff, sp. nov. TYPE: Panama. Panama: Cerro Jefe, along summit road and trail into Chagres Valley, elev. 900 m, *McPherson 12120* (holotype, MO; isotypes, BM, F, HBG, MEXU, PMA). Figures 37, 38.

Arbor parva, ad 7 m alta. Ramuli teretes, hornotini castaneo-tomentosi, annotini cinereo-tomentosi. Folia ad apices ramulorum aggregata, firme chartacea, 6–14 × 2.5–4 cm, oblonga vel leviter obovata, basi truncata vel acuta, apice obtusa vel breviter acuta, supra glabra vel basi costae nervorumque paullo castaneo-tomentosa, subtus pilis castaneis praedita basi costae nervorumque et margine tomentosa. Nervi laterales utroque costae latere 6–9, venatione brochidodroma in dimidio distale. Inflorescentiae ex axillis bractearum ortae, castaneo-tomentosae, 3–7 cm longae, ob abortionem florum lateralium racemosae. Tepala 6, aequalia, elliptica, ca. 4.5 mm longa, rotata vel paullo reflexa. Stamina 9, 4-locellata, antheris introrsum flexis, locellis lateralibus, filamentis pubescentibus. Glandulae stamina exteriora cingentes, liberae. Ovarium anguste ellipsoideum, glabrum; stylus glaber, stigmatate peltato. Tubus floralis profundus, pubescens. Fructus ignoti.

Small tree, to 7 m tall. Twigs terete, solid, brown-tomentose when young, the tomentum turning gray on older twigs, the demarcation between brown and gray tomentum sharp, diameter of the young twigs ca. 3 mm. Terminal bud brown-tomentose. Leaves clustered near tips of branches, firmly chartaceous, 6–14 × 2.5–4 cm, oblong or somewhat obovate, the base truncate or acute, the tip obtuse or slightly acute, the upper surface glabrous or with some scattered brown hairs, these concentrated along the base of the midrib and lateral veins, the lower surface with more brown hairs becoming tomentose along the base of the midrib, lateral veins and margin. Venation, including midrib, immersed on upper surface, raised on lower surface; lateral veins 6–9 on each side, curving toward the tip near the margin and venation becoming brochidodromous in the distal half of the laminae. Basal veins leaving midrib under a more acute angle than more distal veins, and situated at the very base of the lamina. Petioles brown tomentose, 9–12 mm long. Inflorescences in the axils of cataphylls at the tip of the branches, brown tomentose, 3–7 cm long, racemose, 4–10 flowers per inflorescence; individual flowers representing a dichasium with the lateral flowers undeveloped, this indicated by 2 bracts at the transition from peduncle to pedicel. Peduncle to 10 mm long, pedicel to 3 mm long, both brown tomentose. Flowers brown outside, creamy-white inside, 9 mm diam. Tepals 6, equal in size, 4.5 mm long, elliptic, spreading to reflexed at anthesis; outer tepals brown-tomentose outside, with a triangular, gray-tomentose patch inside, otherwise

papillose; inner tepals with a triangular, brown-tomentellous patch, otherwise glabrous outside, gray-tomentellous inside. Stamens 9, all 4-celled, the anthers curved inward, the cells lateral; filaments pubescent. Bases of filaments united, forming a ridge carrying the free parts of the stamens and the glands. Staminal glands enclosing the outer stamens, but not fused. Ovary narrowly ellipsoid, glabrous, 1 mm long; style glabrous, 1 mm long; stigma peltate. Floral tube deep, densely pubescent inside. Fruits and cupule unknown. Flowers: February.

Collection studied. PANAMA. PANAMA: Cerro Jefe, *McPherson 12120* (BM, F, HBG, MEXU, MO, PMA).

The type (and only) collection of *Pleurothyrium racemosum* was made on Cerro Jefe in Panama, a low mountain about 800 m high, which has yielded many endemics. The indument on the lower leaf surface can be rather sparse, especially on older leaves, but remnants of the characteristic curled hairs are always present near the base of the leaf and along the major veins. This species is closely related to *P. pilosum*, where differences between these species are discussed.

Pleurothyrium steyermarkianum Allen, Mem. New York Bot. Gard. 15: 93. 1966. TYPE: Venezuela. Mérida: La Azulita, forest above Hacienda Agua Blanca, elev. 1,310–1,340 m (fl), *Steyermark 56077* (holotype, F not seen; isotype, VEN). Figures 37, 39.

Tree, to about 20 m tall. Twigs angular, solid, minutely tomentellous when young, becoming glabrous with age, 4–5 mm diam. about 4 cm below apex. Leaves alternate, coriaceous, 12–25 × 5–10 cm, elliptic to broadly elliptic, base acute or obtuse, apex acute or acuminate, glabrous and somewhat shiny above, with scattered, appressed hairs or glabrous below, lateral veins 11–16 on each side, curving upward near the margin and weakly loop-connected in the distal half of lamina, midrib and lateral veins immersed on upper surface, raised on lower surface, tertiary venation scarcely visible on upper surface, slightly raised on lower surface. Petioles canaliculate, 1.1–2.5 cm long. Inflorescences in axils of deciduous bracts, to 16 cm long, minutely and laxly brown-tomentellous, the branchlets 2–3 times cymosely branched, bracts subtending the flower buds broadly ovate, boat-shaped, tomentellous outside and glabrous inside. Pedicels to 2 mm long, tomentellous, thick, acutely triangular in cross section, the three ribs continuing as keels on the outer 3 tepals.

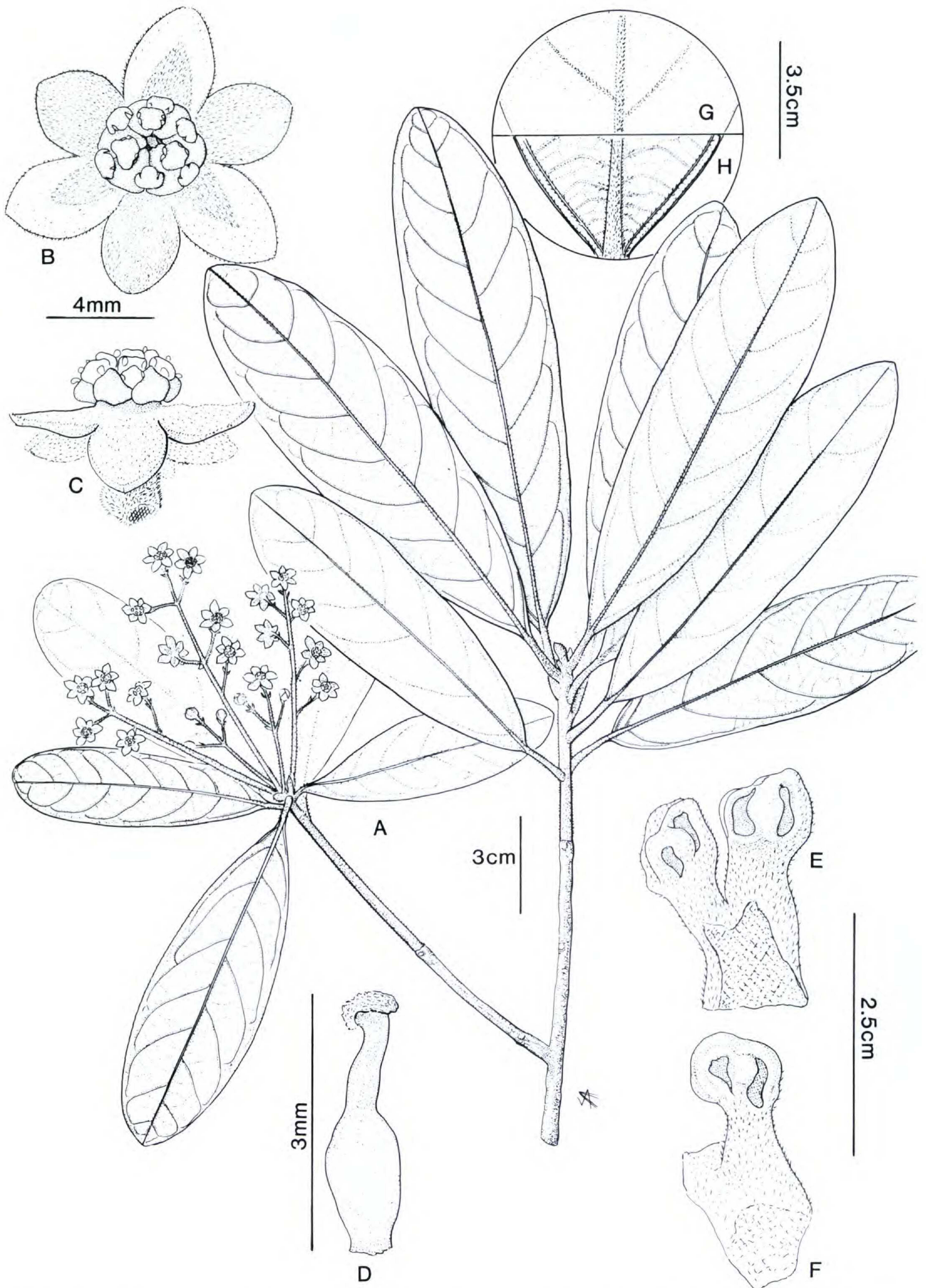


FIGURE 38. *P. racemosum*. — A. Habit. — B. Flower. — C. Flower, side view. — D. Pistil. — E. Stamens I and III. — F. Stamen II. — G. Detail of upper leaf surface. — H. Detail of lower leaf surface.



FIGURE 39. *P. steyermarkianum*.—A. Habit.—B. Flower.—C, D. Stamens.—E. Pistil.—F. Petiole.—G. Reticulation pattern on leaf.—H. Part of inflorescence.—I. Underside of leaf base.—J. Detail of lower leaf surface.

Flowers ca. 8 mm diam., pale yellow-green and fragrant fide collectors. Tepals 6, elliptic, 3–3.5 mm long, papillose inside, the outer 3 tomentellous outside, the inner 3 with a central tomentellous strip, otherwise glabrous outside. Stamens 9, 4-celled, the cells lateral; glands enlarged, forming ridges surrounding the stamens, fused. Pistil and receptacle glabrous, ovary ellipsoid. Cupule cup-shaped, 2 cm wide, 1 cm high; fruit ellipsoid, ca. 2 × 1.5 cm. Flowers: April. Elevation range: 1,300–2,000 m.

Collections studied. VENEZUELA. MERIDA: Selva nublada de la Zona La Trampa, *Bernardi* 2169 (G, MER, NY); La Azulita, *Steyermark* 56077 (VEN).

Pleurothyrium steyermarkianum is only known from two collections made in the Andes of Venezuela. The floral structure, especially the way in which the enlarged glands form ridges surrounding the stamens, the triangular or three-ribbed pedicels, and broad bracts of the inflorescence suggest a relationship with *P. cuneifolium* and its allies. However, *P. steyermarkianum* has a characteristic leaf

indument, lacks fistulose twigs, and differs in floral dimensions from *P. cuneifolium*.

When publishing *Pleurothyrium steyermarkianum* (as *P. steyermarkiana*), Allen indicated that the holotype was deposited in NY. This is an error. The holotype was at F and no isotype was found at NY. The F holotype was sent on loan from F to MO, but unfortunately never arrived and presumably is lost. The only specimen of the type collection studied is the VEN isotype.

Allen also indicated the collection *Bernardi 2169* had flowers and fruits. All sheets I have seen, however, have floral buds and fruits; thus, the only specimen of *P. steyermarkianum* with flowers is the VEN isotype.

Pleurothyrium synandrum van der Werff, sp. nov. TYPE: Colombia. Valle: Río Calima, La Trojita, *Cuatrecasas 16656* (holotype, F; isotypes, U, US). Figures 37, 40.

Arbor, ad 30 m. Ramuli teretes, ferrugineo-tomentulosi, glabrescentes. Gemma terminalis dense ferrugineo-pubescentis. Folia alterna, coriacea, elliptico-ovata vel elliptica, 15–25 × 6–8 cm, basi et apice acuta, supra glabra, subtus ferrugineo-tomentosa vel tomentella, paucis pilis longioribus secus costam et venas laterales praedita; supra venatione immersa, subtus costa venisque lateralibus elevatis; venis lateralibus 18–24 utroque costae latere, marginem versus arcuatis, sed non connexis. Petioli ca. 1 cm longi, ferrugineo-tomentulosi. Inflorescentiae ex axillis bractearum ortae, 8–15 cm longae, ferrugineo-tomentulosae, paniculatae, ramulis 2–3 plo cymae more divisae. Flores pallide flavi, 11–12 mm diametro. Tepala 6, aequalia, 5 mm longa, intus papillosa, exteriora extus pubescentia, interiora minute puberula praeter basim pubescentem. Stamina 9, 4-locellata, 6 exteriora duobus locellis extrorsis, duobus lateralibus, 3 interiora locellis extrorsis, filamentis staminum exteriorum dorsaliter pubescentibus; interiora arcte stylum pubescentem cingentia. Glandulae dilatatae sed stamina exteriora vix ambientes. Cupula 4–5 cm late, 2.5 cm alta, verrucosa; fructus ovoideus, 4 × 2.5 cm.

Tree, 30 m tall. Twigs terete, solid, the tip with brown slender spreading hairs, brown-tomentulose on older parts, the indument wearing off on older parts, diameter of twig 6–8 mm 5 cm below tip. Terminal bud densely brown pubescent. Leaves alternate, coriaceous, elliptic-ovate to elliptic, 15–25 × 6–8 cm, base and apex acute, the upper surface glabrous, lower surface ferruginous-tomentulose or tomentulose with some longer hairs along midrib and lateral veins; venation immersed on upper surface, midrib and lateral veins raised on lower surface; lateral veins 18–24, closely spaced, arching toward apex near the margin, but not connected with their superior vein. Petioles ca. 1 cm long, brown-tomentulose, broadly canaliculate, ca. 4 mm diam. Inflorescences in the axils of cataphylls, 5–15 cm long, paniculate, the branchlets

2–3 times cymosely branched, brown-tomentulose, 40–60 flowers per inflorescence, bracts mostly deciduous at anthesis, ca. 3 mm long, elliptic, brown-pubescent outside, glabrous inside. Flowers pale yellow, 11–12 mm diam. Tepals 6, equal, elliptic, 5 mm long, papillose on inside, outer tepals pubescent outside, inner ones minutely puberulous except for the pubescent base. Stamens 9, 4-celled, the outer 6 with one pair of cells extrorse, the other pair introrse; inner stamens with extrorse cells; filaments of outer stamens dorsally pubescent; filaments and anthers of inner 3 stamens poorly differentiated, the stamens forming a tight cylinder around the brown-pubescent style. Glands enlarged, protruding between the outer stamens, but these scarcely enclosing, free. Receptacle pubescent inside. Cupule, when pressed, 4–5 cm diam., ca. 2.5 cm tall, warty fruit ovoid, 4 × 2.5 cm when dry. Flowers and fruits: March. Elevation range: ca. 50 m.

Collection studied. COLOMBIA. VALLE: Río Calima, La Trojita, *Cuatrecasas 16656* (F, U, US).

Pleurothyrium synandrum is only known from the type collection from near the coast in Depto. Valle, Colombia. This species can immediately be recognized by its ovate-elliptic leaves with the numerous lateral veins close together and its unusual floral structure. In other *Pleurothyrium* species with strongly enlarged glands, not only do the glands grow outward, but also sideways and somewhat inward and the inner three stamens are therefore separated from each other by glandular tissue. Frequently, the glandular mass covers the upper part of the ovary and surrounds the style, while the lower part of the ovary is sunk in the floral tube. In *P. synandrum* the inner three stamens completely surround the style and the glandular tissue does not take part in protecting the pistil. The androecium of this species contains much mucilage, which makes the dried flowers very hard and brittle, whereas after boiling the flowers the parts become soft and slimy; I could therefore not make sure whether the inner stamens were actually (partly) fused or merely tightly pressed together. Another unusual feature of *P. synandrum* is that the basal pair of locelli on the outer stamens has virtually become extrorse. The glandular mass in this species shrinks strongly upon drying, and the outer stamens are raised much higher above the glands in dried flowers than in boiled flowers.

Pleurothyrium tomentellum van der Werff, sp. nov. TYPE: Ecuador. Pastaza: Pozo petrolero "Golondrina" de Petro-Canada, 30 km NW of Curaray, elev. 400 m, tree, 15 m, 10

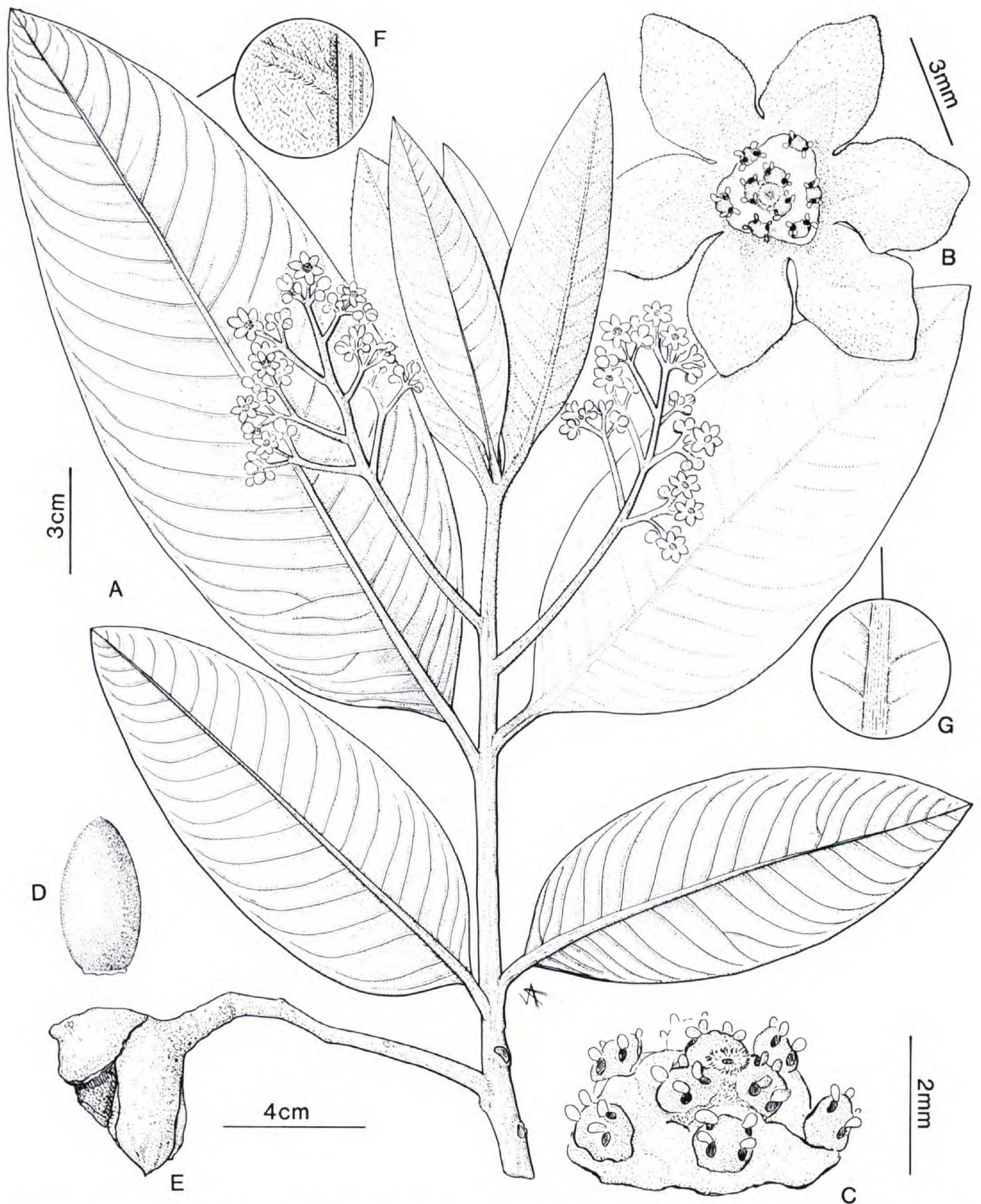


FIGURE 40. *P. synandrum*.—A. Habit.—B. Flower.—C. Androecium.—D. Fruit.—E. Cupule.—F. Detail of lower leaf surface.—G. Detail of upper leaf surface.

July 1989, *Gudiño 12* (holotype, MO; isotypes, AAU, COL, G, HBG, K, LE, MEXU, NY, QCNE, QRS, US). Figure 41.

Arbor, ad 30 m alta. Ramuli teretes, tomentelli. Gemma terminalis tomentella. Folia alterna, coriacea, 13–35 × 6.5–13 cm, (late) elliptica vel oblonga, apice et basi acuta vel obtusa, supra glabra, subtus ferrugineo-tomentella;

nervis lateralibus 9–14 utroque costae latere, costa nervisque supra immersis, subtus elevatis; reticulatione subtus paullo elevata, supra non evidente. Petioli 1.7–3.6 cm longi, canaliculati. Inflorescentiae in axillis bractearum (raro foliorum) ortae, 7–15 cm longae, tomentellae. Flores albi, 6–8 mm diametro. Tepala 6, intus papillosa, oblonga, 2.5–3 mm longa, statura et forma aequalia. Stamina 9, 4-locellata, locellis lateralibus, filamentis ca. 0.8 mm lon-



FIGURE 41. Distribution of *P. tomentellum* (★), *P. tomiwahlii* (●), *P. undulatum* (○), and *P. westphalii* (■).

gis, glandulis incrassatis, stamina cingentibus, contiguis, non connatis. Ovarium glabrum, in stylo attenuatum; tubo florale intus tomentello. Fructus ellipsoideus, 3×1.5 cm, cupula verrucata, 2 cm lata, 1 cm profunda.

Tree, to 30 m tall. Twigs terete, smooth or finely ridged, brown-tomentellous, solid, 4–7 mm diam. ca. 5 cm below tip. Terminal bud brown-tomentellous. Leaves alternate, coriaceous, $13\text{--}35 \times 6.5\text{--}13$ cm, elliptic, broadly elliptic or oblong, the tip and base acute or obtuse, upper surface glabrous, opaque, lower surface densely rufous-tomentellous or coarsely papillose, the surface completely covered by the indument; lateral veins 9–14 on each side, arching upward near the margin, but not loop-connected; midrib and lateral veins immersed on upper surface, raised on lower surface; tertiary venation (very) weakly raised on lower surface, not visible on upper surface. Petioles 1.7–3.6 cm long, canaliculate to deeply canaliculate, with similar indument as twigs. Inflorescences in axils of deciduous bracts, rarely in axils

of leaves, to 7–15 cm long, the branchlets to 4 times dichotomously branched, rufous-tomentellous, bracts mostly deciduous at anthesis, if present tomentellous outside and subglabrous or tomentellous inside. Pedicels 2–6 mm long, rufous-tomentellous. Flowers 6–8 mm diam. Tepals 6, white, papillose-puberulous on inside, oblong, 2.5–3 mm long, equal in size and shape. Stamens 9, 4-celled, the cells lateral, the filaments ventrally pubescent, filaments ca. 0.8 mm long. Glands strongly enlarged, completely surrounding the stamens, but not fused. Pistil glabrous, 1.5 mm long, ovary gradually narrowed into the style, style and ovary of the same length; floral tube densely tomentellous within. Fruit ellipsoid, 3×1.5 cm, cupule cup-shaped, warty, 2 cm wide, 1 cm tall. Flowers: January–July. Fruits: January.

Common name (Huaorani): Ontumo.

Collections studied. ECUADOR. MORONA-SANTIAGO: 35 km NE from Montalvo, Zak 4459 (MO, QCNE). PASTAZA:

30 km NWE of Curaray, *Gudiño 12* (AAU, COL, G, HBG, LE, K, MEXU, MO, NY, QCNE, QRS, US); 30 km NE from Curaray, *Gudiño 17* (MO, QCNE); 115 km S of Coca, near Río Tiguino, *Hurtado 1464* (MO, QCNE); Via Auca, 115 km S of Coca, *Neill 8741* (MO, QCNE); 115 km S of Coca, near Río Tiguino, *Neill & Hurtado 8783* (MO, QCNE), *Rubio 56* (MO, QCNE); 110 km S of Coca, 10 km from Río Tiguino, *Palacios 3416* (MO, QCNE). PERU. HUANUCO: Pachitea, Pucallpa region, 24 km SE of Puerto Inca, *Wallnoefer 18-29788* (MO).

Pleurothyrium tomentellum is a species with a limited distribution, known only from the Amazonian lowlands of Ecuador, from areas that recently became accessible due to oil exploration, and one collection from Amazonian Peru. According to the label data of *Neill & Hurtado 8783*, the species is locally very common. *Pleurothyrium tomentellum* can be readily identified by the combination of its tomentellous leaves and small (6–8-mm-diam.) flowers. Noteworthy are also the glabrous pistil, pubescent receptacle, and rather small cupule. In leaf characters (texture, indument, lack of marginal vein) and its short inflorescence it resembles *P. palmanum* from Costa Rica, but that species has larger flowers, broader, more or less obovate leaves, and a glabrous receptacle. Most collections have tomentellous lower leaf surfaces and inflorescence bracts that are tomentellous on both surfaces. The type collection has a shorter indument on the leaves, approaching the papillose condition, and the inner surface of the inflorescence bracts is subglabrous. In floral characters the collections are identical (only the sole Peruvian collection has a sparser indument on inner surface of tepals), and the differences mentioned are too weak for recognition of two taxa. Moreover, the type was collected together with a specimen with the slightly longer indument (*Gudiño 12, 17*).

Pleurothyrium tomiwahlii van der Werff, sp. nov. TYPE: Ecuador. Los Ríos: Centinela Ridge, elev. 600 m, 16 July 1991, *van der Werff et al. 12365* (holotype, MO; isotypes, AAU, B, BR, C, COL, E, F, G, GH, HBG, K, KUN, LE, MEXU, MY, QCNE, QRS, S, SEL, U, US). Figures 41, 42.

Arbor, 20 m. Ramuli crassi, teretes, juvenales ferrugineo-tomentosi, vetustiores glabrescentes. Gemma terminalis tomentosa. Folia ad apices ramulorum aggregata, chartacea, laminis 11–40 × 6–17 cm, basi obtusis vel acutis, apice rotundatis, obtusis vel breviter acuminatis, (late) obovatis vel (late) ellipticis, utrinque glabris vel paucis pilis erectis praeditis; nervis lateralibus 8–10 utroque costae latere. Petioli 2.5–6 cm longi, base incrassati, canaliculati. Inflorescentiae ex axillis bractearum ortae, tomentosae, paniculatae ramulis semel (raro bis) cymose ramosis, 7–12 cm longae, bracteis sub anthesi deciduis. Tepala 6, aequalia, extus pubescentia, 3 interiora intus

pubescentia, 3 exteriora intus praeter partem triangularem basalem glabra vel papillosa, sub anthesi reflexa, ca. 4 mm longa, elliptica. Stamina 9, 4-locellata, locellis lateralibus, filamentis pubescentibus, parte basale in tubo coalitis; glandulis magnis inter stamina exteriora protrudentibus. Ovarium gracile, glabrum, sensim in stylum attenuatum; receptaculo et tubo filamentorum intus pubescente. Fructus ignotus.

Tree, to 20 m tall. Twigs ± terete, solid, with pale bark, the young growth ferruginous-tomentose, soon glabrescent, ca. 8 mm diam. 5 cm below tip. Terminal bud brown tomentose. Leaves clustered near tips of branches, alternate, chartaceous, laminae 11–40 × 6–17 cm, the base obtuse or acute, the tip rounded, obtuse or shortly acuminate, (broadly) obovate, or (broadly) elliptic; glabrous on both surfaces or with scattered erect hairs, these mostly along the major veins or near base of the lamina; lateral veins 8–10 on each side; venation immersed on upper surface or weakly raised, midrib and lateral veins raised on lower surface. Petioles 2.5–6 cm long, strongly canaliculate, the base swollen, with similar indument as on the twig. Inflorescences in the axils of cataphylls near the tips of branches, tomentose, paniculate, the lateral branchlets once cymosely branched, 7–12 cm long, bracts deciduous at anthesis. Flowers cream-colored, fragrant. Tepals 6, equal in shape, densely pubescent outside, the inner three densely pubescent inside, outer three with a basal, triangular, pubescent patch, otherwise glabrous or finely papillose; at anthesis reflexed, ca. 4 mm long, elliptic. Stamens 9, all 4-celled, the cells lateral, filaments of the outer 6 stamens dorsally pubescent; glands at base of inner stamens strongly enlarged and separating the outer stamens from each other; bases of filaments fused into a pubescent column, ca. 1 mm long. Ovary slender, glabrous, gradually narrowed into the style; inside of the floral tube and column formed by the stamens densely pubescent. Fruit unknown. Flowers: July and December. Elevation range: 600–1,400 m.

Collections studied. COLOMBIA. ANTIOQUIA: Amalfi, Salazary Marengo, *Callejas 9143* (MO). ECUADOR. LOS RÍOS: Centinela Ridge, *van der Werff et al. 12365* (AAU, B, BR, C, COL, E, F, G, GH, HBG, K, KUN, LE, MEXU, MO, NY, QCNE, QRS, S, SEL, U, US), *van der Werff et al. 12367* (AAU, QRS, MO, QCNE). PICHINCHA: Cima de las Montañas de Ila, *Dodson 14531* (MO).

Pleurothyrium tomiwahlii is readily identified by its clustered, obovate leaves, long petioles with swollen base, its flowers with reflexed tepals, and the base of the filaments united in a column, giving the flower the appearance of a gonoloboid Asclepiadaceae species. Its closest relatives are the Costa Rican *P. golfodulcense*, in which the androecium

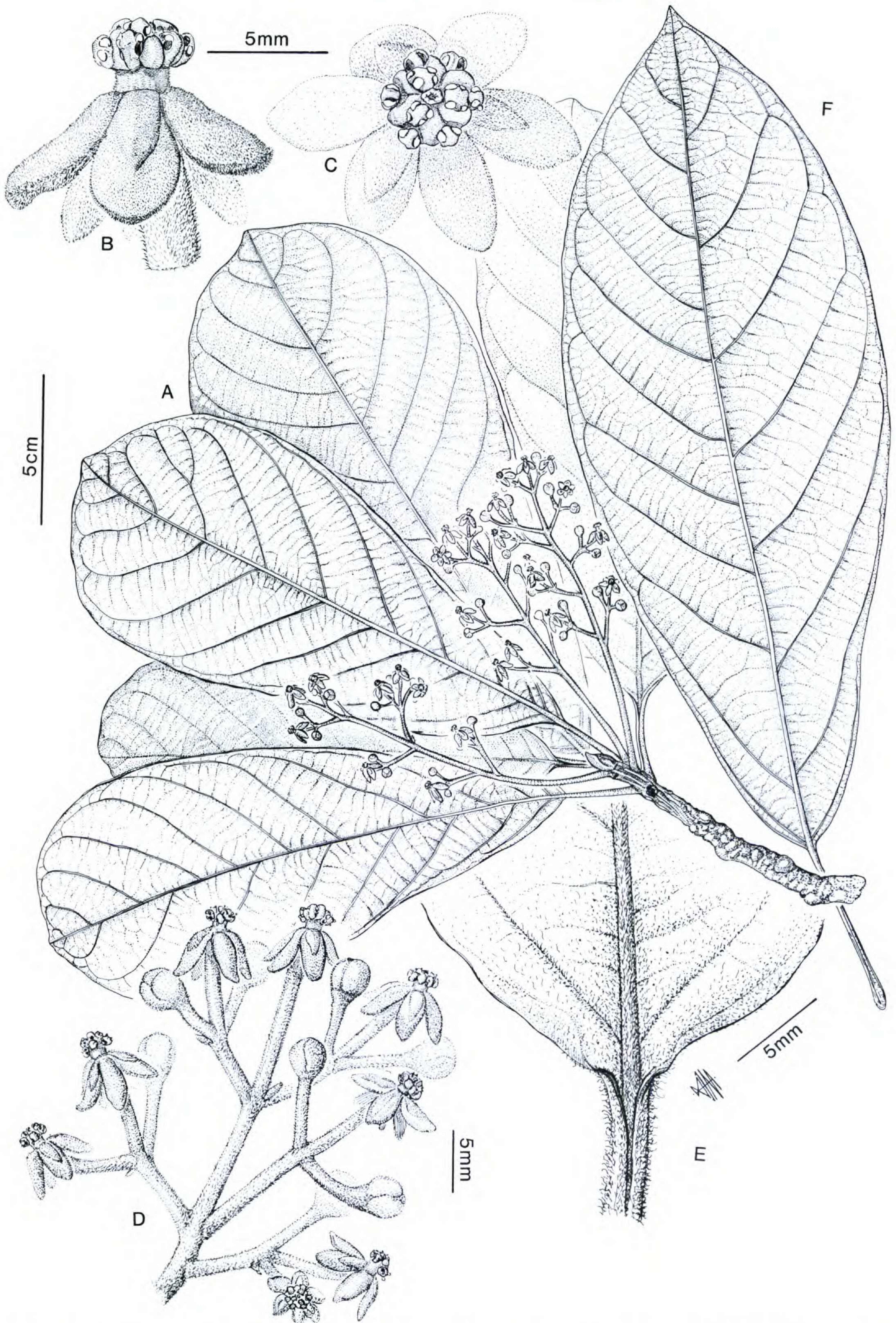


FIGURE 42. *P. tomiwahlii*. — A. Habit. — B, C. Flower sideways and seen from above. — D. Part of inflorescence. — E. Leaf base. — F. Shade leaf, showing less obovate shape and more acute leaf base.

forms a dome (without a column) and in which the glands separate the outer stamens just as in *P. tomiwahlii*; and the Panamanian species *P. racemosum* and *P. pilosum*, with similar floral structure as in *P. golfodulcense*, and with relatively long petioles, obtuse leaf bases and apices, and clustered leaves as in *P. tomiwahlii*. Details of indument, leaf shape and size as mentioned in the species descriptions, as well as the reflexed tepals, characterize *P. tomiwahlii*.

There is considerable variation in leaf size among the few available collections, probably a result of exposure to sunlight. The type tree, with rather small leaves, was free-standing in a pasture, while *van der Werff et al.* 12367 was an understory tree in a forest patch. The Dodson collection has the largest leaves and was growing in forest. *Pleurothyrium tomiwahlii* is a rare species; during a day-long search at Centinela only three individuals were seen. Although the single Colombian collection represents a great range extension, *P. tomiwahlii* is such a distinctive species that I have no doubt about its identification.

The specific epithet honors the Wahl family, in recognition of their keen interest in conservation of tropical forests.

Pleurothyrium trianae (Mez) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 43. 1986. *Nectandra trianae* Mez, Jahrb. Bot. Gart. Berlin 5: 439. 1889. TYPE: Colombia. *Triana* 1037 (holotype, P not seen; isotypes, BM, NY). Figure 43.

Pleurothyrium zulianense Lasser, Bol. Tecn. Minist. Agric. 3: 18. 1942. *Octoea zulianense* (Lasser) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Venezuela. Zulia: en selvas claras del Río Lora, *Pittier* 10947 (holotype, VEN not seen; isotypes, G, GH, US).

Pleurothyrium reflexum Lasser, Bol. Tecn. Minist. Agric. 3: 18. 1942. *Ocotea reflexa* (Lasser) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Venezuela. Lara: entre San Isidro y Guarico, *Tamayo* 1094 (holotype, VEN not seen; isotypes, F, US).

Large trees, becoming more than 20 m tall. Twigs roundly angular or terete, solid (rarely fistulose), glabrous, but the tips minutely brown-tomentellous, ca. 3 mm diam. 5 cm below the apex. Terminal buds minutely brown-tomentellous. Leaves alternate, chartaceous, elliptic, 9–25 × 3–10 cm, the upper surface glabrous, the lower surface minutely papillose to glabrous, the base acute, the tip shortly acuminate. Lateral veins 8–12 on each side, arching upward near the margin, not loop-connected, venation immersed on upper surface, midrib and lateral veins raised on lower surface.

Petioles 10–20 mm long, shallowly canaliculate. Inflorescences in axils of cataphylls, minutely brown-tomentellous, paniculate, the branchlets once or twice cymosely branched, bracts deciduous at anthesis. Pedicels 2.5–4.5 mm long, minutely brown-tomentellous. Flowers white, ca. 4 mm diam., the tepals at anthesis erect or halfway spreading. Tepals 6, equal, ca. 2 mm long, the margin reflexed, minutely tomentellous outside, papillose inside. Stamens 9, glabrous, 4-celled, the cells mostly lateral and opening upward; filaments about as long as the anther, glands enlarged, visible as large lobes between the outer stamens, free. Ovary ellipsoid, glabrous or slightly papillose near the tip, style papillose, pistil 1.5–2.0 mm long. Receptacle glabrous inside. Cupule warty, to 15 mm wide, 10 mm tall, the pedicel not thickened; fruit ellipsoid, to 22 × 16 mm. Fruits: February–June. Flowers: collected in every month except June–July. Elevation range: 10–1,400 m.

Collections studied. COLOMBIA: *Triana* 1037 (BM, NY). ANTIOQUIA: Frontino, Murri, 20–28 km from Nutibara, *McPherson* 12999 (MO). CHOCO: Quebrada Taparal, hoyá del Río San Juan, *Forero* 4135 (MO); Taparalito, Quebrada Taparal, N of Palestina, *Gentry* 53812 (MO), *Gentry* 53833 (MO); Palo Gordo, *Triana* 2042 (K); basin of Río San Juan, tributary Río Taparal, *van Rooden* 650 (MO, U), *van Rooden* 681 (MO, U); hoyá del Río San Juan, Río Bicordo, arriba de Noanama, *Forero* 4693 (MO); Quibdo, Río Cabi, *Prance* 28012 (NY). NORTE DE SANTANDER: Sarare, Río Cubugon, junto a la quebrada de Gibraltar, *Cuatrecasas* 13227 (F, US). VALLE: Río Calima, La Trojita, *Cuatrecasas* 16321 (F, US), *Cuatrecasas* 16321A (F, U, US), *Cuatrecasas* 16781 (F, US); lower Río Calima near junction with Río San Juan, *Gentry* 53758 (MO); Río Calima, *Cuatrecasas* 16675 (F), *Cuatrecasas* 16864 (F, US). COSTA RICA. ALAJUELA: San Carlos, Refugio Cano Negro, Los Chiles, *Zamora* 1363 (MO). PUNTARENAS: Osa, Reserva Florestal Golfo Dulce, *Hammel* 18152 (MO). ECUADOR. LOS RIOS: Río Palenque Biological Center, *Dodson* 6419 (MO). MORONA-SANTIAGO: Pozo Petrolero “Garza” de TENNECO, *Zak* 4608 (MO). NAPO: Reserva Florestica El Ahuano, Estación INIAP, *Palacios* 2094 (MO); 3 km from entrance to Jatun Sacha toward Río Arajuno, *Palacios* 2804 (MO); Archidona, S slope of Sumaco, Comunidad El Pacto, *Palacios* 4727 (MO); Tena, Estación Biológica Jatun Sacha, *Ceron* 7416 (MO), *Palacios* 4273 (MO), *Palacios* 4334 (MO), *Palacios* 4436 (MO, QCNE). HONDURAS. ATLANTIDA: Refugio Nacional de Vida Silvestre, *Soto* 613 (MO). NICARAGUA: along Río San Juan, *Bunting* 872 (F, NY, US). PERU. LORETO: Maynas, Indiana, Explorama Reserve, *Vásquez* 12921 (MO). VENEZUELA. Ticoporo Forest Reserve, *Breteler* 3517 (NY, U, US); El Vigia, *Mocquerys* 1002 (K, NY, U). BARINAS: banks of Río Bumbun, *Aristeguieta* 1584 (NY, VEN); near Ciudad Bolivia (Pedraza), *Aristeguieta* 1647 (NY, VEN); Reserva Forestal de Ticoporo, *Aristeguieta* 6978 (VEN); Pedraza La Vieja, Río Pedraza, *Bernardi* 1137 (G, MO); Ticoporo Forest Reserve, bank of Río Bumbun, *Breteler* 3667 (NY, US); Distr. Pedraza, *Dorr* 4720 (MO, NY, PORT); Reserva Forestal de Caparo, *Jimenez* 1289 (NY), *Marcano* 2913

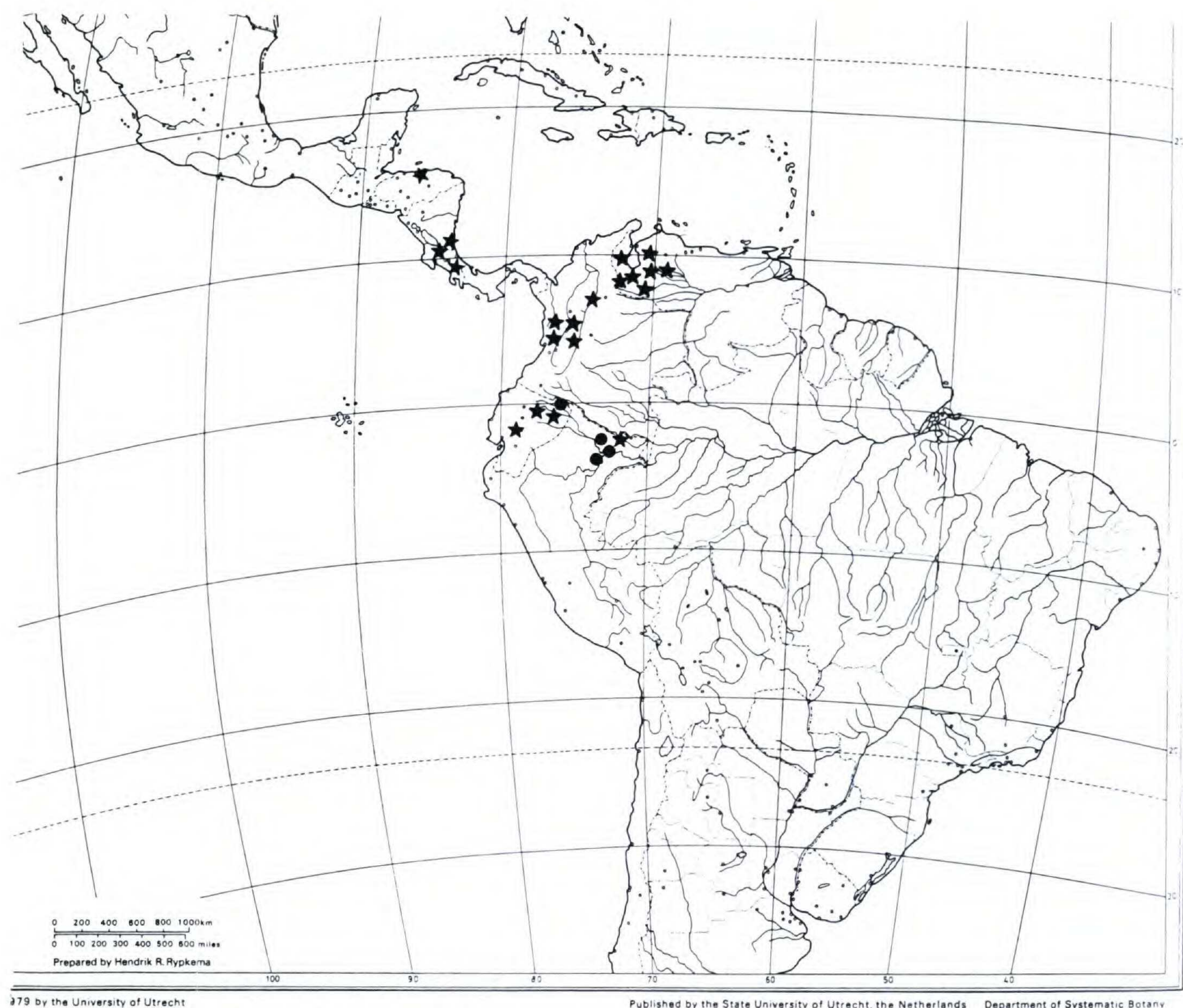


FIGURE 43. Distribution of *P. trianae* (★) and *P. williamsii* (●).

(BR, G, MO); Caserio Barragan, *Salcedo 225* (G, US); Cacao, Barinitas, *Valverde 15* (MO). LARA: *Tamayo 1094* (F, US); Iribarren, Parque Nacional Terepaima, Fila San Esteban, *Smith 7463* (MO); Iribarren, Parque Nacional Terepaima, Represa Río Claro, *Smith 9021* (MO); Iribarren, Loma de los Naranjos, Montana de Macanillal, *Steyermark 111580* (G, NY, U, VEN). MERIDA: *Little 15822* (NY), *Marcano 1177* (MO). PORTUGUESA: Guanare, 17 km NW of Tucupido, N slope of Fila Las Palmas, *Davidse 21459* (MO, NY), *Davidse 21467* (MO, NY). PORTUGUESA/BARINAS: Represa de Bocono, *Aymard 1747* (MO). TACHIRA: La Fria, *Little 16121* (VEN). TRUJILLO: Carretera Campo Elias-Bocono, *van der Werff 8887* (MO). ZULIA: near Mission de Tukukos, Perija, *Aristeguieta 2085* (NY); road Machiques-Colon, near Río Caratumbo, *de Bruijn 1422* (MO, NY, US, VEN); along Río Lora, above Camp 2, Perija, *Pittier 10947* (G, GH, US).

Pleurothyrium trianae is, as treated here, a wide-ranging and variable species. It has been recorded from Honduras to Ecuador and Venezuela, but the records are not evenly distributed over this area. Only two collections are known from Central America. Nearly all South American collections come from the following three areas = (a) Pacific

lowlands of Colombia (type locality of *P. trianae*), (b) Andean foothills in Venezuela (type localities of *P. zulianense* and *P. reflexum*), and (c) the Oriente of Ecuador, while almost no collections are known from the intervening areas. It is therefore not surprising to find local differentiation. The Colombian collections tend to have almost glabrous leaves, a rather sparse indument on twigs, and pedicels that are 3.5–4.5 mm long. The Venezuelan plants have more indument on twigs and leaves and have pedicels 2–2.5 mm long. The Ecuadorian plants agree with the Colombian specimens in their indument, have variable length of pedicels (2–4 mm), and have smaller leaves (9–14 × 3–5 cm) than the other populations (*Palacios 2094* has larger leaves). These differences are nearly all quantitative and form an insufficient basis for the recognition of separate taxa. The length of pedicels cannot be relied on for the separation of taxa because the lateral flowers of a cyme nearly always have shorter pedicels than the central flower and young flowers tend to have slightly shorter pedicels than old flow-

ers. I expect that once collections of *P. trianae* become available from other areas, the differences between populations as described above will disappear. For example, a collection from Antioquia at 1,050 m elevation (*McPherson 12999*) has the denser indument and shorter pedicels commonly found in Venezuelan collections; it also has stiffer leaves than usual for *P. trianae*.

The relationships of *P. trianae* are with a small group of poorly defined species that is characterized by small flowers with erect, more or less inrolled tepals, solid twigs, and chartaceous leaves. This group consists of *P. acuminatum*, *P. amapaense*, *P. amplifolium*, *P. intermedium*, and *P. undulatum*. *Pleurothyrium acuminatum* differs in its relatively long pedicels ((4–)5(–8) mm), and long tepals (3 mm long); *P. amplifolium* has broad leaves, while *P. intermedium*, *P. undulatum*, and *P. amapaense* have a different indument. It is possible that, once more material is available, some of these species will be placed in synonymy.

More distantly related are *P. parviflorum* and *P. poeppigii*, which both have fistulose twigs. Additionally, *P. parviflorum* differs in its glabrous flowers and *P. poeppigii* in its coriaceous leaves. A few collections of *P. trianae* have fistulose stems, and the differences cited above help separate these specimens from *P. parviflorum* and *P. poeppigii*. Differences between *P. trianae* and *P. cuneifolium* are discussed under the latter species.

Pleurothyrium undulatum (Meissner) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 44. 1986. *Oreodaphne undulata* Meissner, DC. Prodr. 15(1): 115. 1864. *Ocotea undulata* (Meissner) Mez, Jahrb. Bot. Gart. Berlin 5: 278. 1889. TYPE: Brazil. Amazonas: Prov. Rio Negro, *Riedel 1412* (holotype, LE not seen; isotypes, B, G, K, L, NY). Figure 41.

Tree of unknown size. Twigs terete, solid, minutely brown-tomentellous, glabrescent with age. Terminal bud brown-tomentellous. Leaves alternate, chartaceous, elliptic to narrowly elliptic, 10–17 × 2–5 cm, base and tip acute, glabrous on upper surface, glabrous or minutely papillose on lower surface, venation immersed on upper surface, midrib raised on lower surface, the lateral veins (12–15 on each side) poorly visible and less elevated; marginal vein poorly developed or lacking. Petioles ca. 1.5 cm long, with similar pubescence as twigs. Inflorescences in axils of cataphylls or leaves, brown-tomentellous, especially the ultimate branches, 8–12 cm long, paniculate, the branchlets 2–3 times cymosely branched, the flow-

ers close together; bracts present, ovate, to 2 mm long, tomentellous outside, minutely so inside. Pedicels to 1 mm long, tomentellous. Flowers ca. 3 mm diam., the tepals ± erect at anthesis. Tepals 6, equal, ca. 2 mm long, tomentellous outside, papillose inside, the margin reflexed. Stamens 9, 4-celled, the cells lateral, glands enlarged and protruding between the outer stamens, but not enclosing them and not fused. Ovary globose, glabrous, enclosed by the glabrous receptacle; style papillose. Fruits unknown.

Collection studied. BRAZIL. *Riedel 1412* (B, G, K, L, NY).

Pleurothyrium undulatum is only known from the type collection made by Riedel in 1824–1825. Meissner (1864) gave as locality only Amazonas, Prov. Rio Negro; the isotype in NY gives as locality Barra, an old name for Manaus. *Pleurothyrium undulatum* was placed by Mez (1889) in *Ocotea*; he considered that the presence of glands at the base of all stamens was typical for *Pleurothyrium*, and although he noted that in respect of anther shape this species resembled *Pleurothyrium*, he treated it in *Ocotea* because of the presence of only six glands. *Pleurothyrium undulatum* belongs to a small group of species characterized by tepals with reflexed margins, often erect tepals at anthesis, marginal vein lacking or weakly developed, small flowers (less than 5 mm diam.) and inflorescences sometimes present in axils of leaves and not restricted to axils of cataphylls. Within this group, the narrow, almost glabrous leaves and the tomentellous pubescence of the inflorescences characterize this species.

Pleurothyrium vasquezii van der Werff, sp. nov. TYPE: Peru. Loreto: Maynas, km 32 along carretera Iquitos-Nauta, elev. 150 m, primary forest, *Vasquez & Jaramillo 7889* (holotype, MO; isotypes, AAU, AMAZ, F, G, NY). Figures 44, 45.

Arbor, 20 m alta. Ramuli teretes, solidi, fusco-tomentosi. Folia alterna, firme chartacea vel coriacea, elliptica vel late elliptica, 15–30 × 5–10 cm, basi acuta vel obtusa (rotundata), apice acuminata, supra glabra, subtus pilis erectis praedita, venatione supra immersa, subtus elevata, in dimidio distali brochydroma, venis lateralibus 9–13 utroque costae latere. Petioli 1.5–3 cm longi, canaliculati. Inflorescentiae ex bractearum axillis ortae (raro ex foliorum axillis), fusco-tomentosae, 10–17 cm longae, paniculatae. Pedicelli 3–4 mm longi. Flores 5–6 mm diametro, rotati. Tepala 6, aequalia, oblonga, ca. 2 mm longa, margine plano, extus tomentella, intus papillosa. Tubus floralis ad ostium constrictus. Stamina 9, 4-locellata, locellis lateralibus vel extrorso-lateralibus, minute papillosa; glandulis magnis, staminibus exterioribus cingentibus, libe-



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FIGURE 44. Distribution of *P. vasquezii* (★).

ris. Ovarium ellipticum, papillosum, ca. 1 mm longum, in receptaculo profundo, papilloso inclusum. Cupula verrucosa, 1 cm alta, 1.3 cm lata.

Tree, to 20 m tall. Twigs solid, terete, fuscous-tomentose, glabrescent, 3–4 mm diam. 5 cm below the tip. Terminal bud fuscous-tomentose. Leaves alternate, stiffly chartaceous to coriaceous, elliptic to broadly elliptic, 15–30 × 5–10 cm, the base acute to obtuse, rarely rounded, the tip shortly acuminate, the upper surface glabrous and with immersed midrib and lateral veins, the lower surface with erect hairs, the surface well visible, the elevated midrib and, to a lesser degree, lateral veins tomentose, tertiary venation also raised, lateral veins 9–13 on each side, curving upward near the margin, a marginal vein quite well developed in the distal half. Petioles 1.5–3 cm long, canaliculate, with same kind of tomentum as twig. Inflorescences in axils of cataphylls, rarely in axils of leaves, fuscous-tomentose, 10–17 cm long, paniculate, the branchlets 2–3 times cymosely branched, many-

flowered, bracts lacking at anthesis. Pedicels 3–4 mm long, tomentose. Flowers yellow or green, 5–6 mm diam., the tepals spreading at anthesis. Tepals 6, equal, oblong, ca. 2 mm long, the margin plane, tomentellous outside, papillose inside. Floral tube constricted just below tepals. Stamens 9, 4-celled, the cells lateral or one pair lateral-extrorse, opening back-to-back, filaments and anthers minutely papillose; glands enlarged, almost completely enclosing the outer stamens, but not fused. Ovary elliptic, papillose, ca. 1 mm long, enclosed in the papillose, deep receptacle, the upper part covered by the enlarged glands, style ca. 0.5 mm long, papillose; stigma not enlarged, partly hidden by the longer stamens. Cupule cup-shaped, warty, ca. 1 cm tall, 1.3 cm wide (but probably not fully mature). Fruits: February. Flowers: August–October. Elevation range: 100–600 m.

Collections studied. BRAZIL. ACRE: Rio Jurua, 1 km upstream from Colonia Rodrigues Alvez, *Campbell 10852* (MO, NY); Reserva INCRA Santa Luzia, km 40 BR-364,

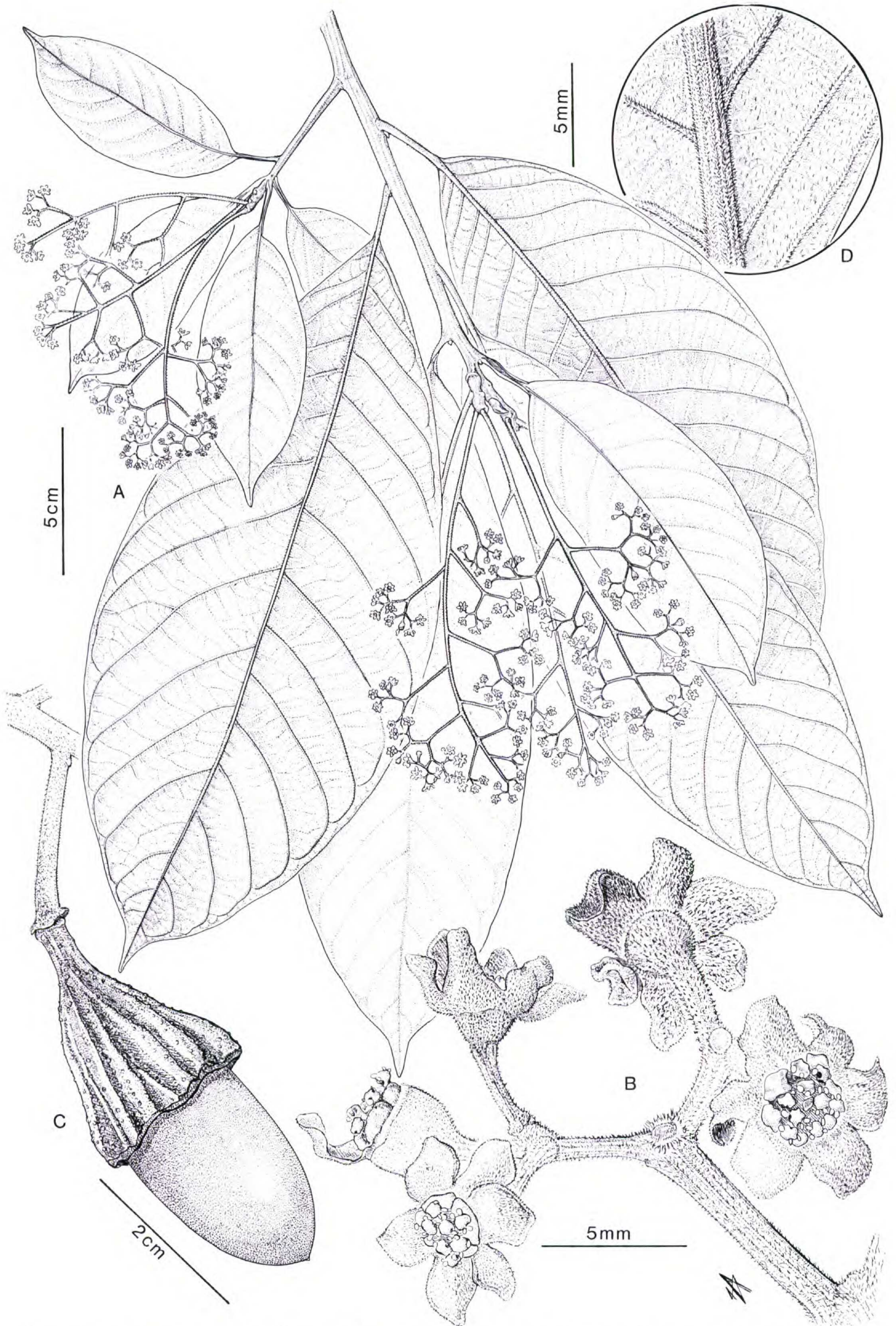


FIGURE 45. *P. vasquezii*. — A. Habit. — B. Part of inflorescence with flowers. — C. Fruit. — D. Detail of lower leaf surface.

Campbell 6887 (MO, NY). AMAZONAS: Mun. de Itapiranga, Rio Uatuma, *Cid 859* (MO, NY); Manaus, *Froes 20526* (NY, US); Rio Negro, Vaupes, Jauarete, *Froes 21235* (NY); Rio Negro, Rio Jauapari, Estirão Tacuera, *Santos 78* (NY). RONDONIA: Mun. Porto Velho, Usina Hidroelectrica Samuel, *Thomas 6476* (MO, NY). PERU. LORETO: Maynas, Alpahuayo, *Grandez 1376* (MO); Maynas, Mishana, halfway between Iquitos and Sta. Maria de Nanay, *Ramirez 61* (HBG, MO); Pto. Almendras, *Vásquez & Jaramillo 5469* (MO); Maynas, Carretera Iquitos-Nauta, km 32, *Vásquez & Jaramillo 7889* (AAU, AMAZ, F, G, MO, NY); Requena, Arboretum Jenaro Herrera, without data (MO). MADRE DE DIOS: 39 km SW of Puerto Maldonado, *Smith & Jaramillo 384* (MO, US); Manu, Parque Nacional Manu, Rio Sotileja, *Foster 11719* (MO); Tambopata, Tambopata Nature Reserve, *Gentry 58103* (MO). SAN MARTIN: Mariscal Caceres, Tocache Nuevo, Quebrada de Mantención, *Schunke 13643* (MO); Mariscal Caceres, Distr. Campanillo, near Caserio de Sion, *Schunke 3475* (F). UCAYALI: Coronel Portillo, Bosque Nacional Alexander von Humboldt, *Oliveira 21* (MO).

Pleurothyrium vasquezii is known from several collections in Amazonian Peru and adjacent Brazil, as far downstream as Manaus. It is the only *Pleurothyrium* species in this area with a sparse, erect pubescence on the lower leaf surface and alternate leaves. *Pleurothyrium brochidodromum* has a very similar indument on the lower leaf surface, but differs in having larger flowers (9–10 vs. 5–6 mm diam.) and in its clustered leaves. A few collections placed in *P. vasquezii* were earlier identified as *P. panurense* (Allen, 1964), but this species has clustered leaves, a very short, appressed indument on the lower leaf surface that completely covers the surface, and flowers ca. 8 mm in diameter.

Two Froes collections (20526, 21235) from Brazil have somewhat more coriaceous leaves and roundish leaf bases. However, these collections are fruiting, which may explain their stiffer leaf texture. Because *Ramirez 61* from Peru also has roundish leaf bases and agrees in floral characters with *P. vasquezii*, I placed the Brazilian collections here. Spichiger et al. (1989) reported this species as *Nectandra amplifolia* Mez (= *P. amplifolium* (Mez) Rohwer) from the Arboretum at Jenaro Herrera, Peru (tree 159 in parcela 1). This latter species differs in its puberulous indument on the lower leaf surface, and in its more or less erect tepals with reflexed margins. The same tree is also cited under *Ocotea undulata* (Meissner) Mez (= *P. undulatum* (Meissner) Rohwer), which also has a different indument on the lower leaf surface, and more or less erect tepals with reflexed margins at anthesis.

Pleurothyrium vasquezii is named after Rodolfo Vasquez, whose fine collections have added much to our knowledge of the trees in Amazonian Peru.

Pleurothyrium westphalii van der Werff, Ann. Missouri Bot. Gard. 74: 410. 1987. TYPE: Guatemala. Alta Verapaz: Sacté, *Kunkel 9* (holotype, BR). Figures 41, 46.

Tree, to 20 m tall. Twigs solid, terete, young ones with brown, dense appressed pubescence, older ones glabrous. Terminal bud densely brown-pubescent. Leaves alternate, membraneous, 15–20 × 4–7 cm, elliptic or narrowly elliptic, the base acute, the margin somewhat decurrent, apex acute, glabrous and gland dotted on the upper surface (except for some appressed hairs near the base of the midrib), lower surface with few appressed hairs, more so near the base; lateral veins 5–9 on each side, arching upward near the margin, but not loop-connected; venation immersed on upper surface, midrib, lateral veins and tertiary venation weakly raised on lower surface. Petioles to 1 cm long, with similar pubescence as twigs. Inflorescences in axils of deciduous bracts, attached below the leaves, ca. 8 cm long, densely gray-brown pubescent, the lowest branches once cymosely branched, otherwise inflorescence racemose. Flowers ca. 8 mm diam. Pedicels ca. 4 mm long. Tepals 6, equal, ovate, 3–4 mm long, densely pubescent on both surfaces. Stamens 9, 4-celled, the cells lateral, anthers glabrous, filaments brown-pubescent; glands strongly enlarged, completely enclosing outer stamens; ovary ellipsoid, glabrous, ca. 1 mm long, enclosed by the glabrous receptacle; stigma platelike. Fruits unknown. Flowers: April. Elevation range: 900–1,100 m.

Collections studied. GUATEMALA. ALTA VERAPAZ: Sacté, *Kunkel 9* (BR), *Kunkel 17* (MO).

Pleurothyrium westphalii, known only from two collections in Guatemala, is the northernmost representative of the genus. The species can be readily identified by its appressed, gray-brown pubescence, the pubescent tepals (also inner surface is pubescent), pubescent filaments, the few-flowered inflorescences, the membraneous leaves, and the absence of a marginal vein.

Pleurothyrium williamsii O. C. Schmidt, Rept, Spec. Nov. Regni Veg. 31: 189. 1933. *Ocotea williamsii* (O. C. Schmidt) Kostermans, J. Sci. Res. (Jakarta) 1: 122. 1952. TYPE: Peru. Loreto: Pebas on the Amazon River, *Llewelyn Williams 1766* (holotype, F probably lost; isotype, B, fragment G). Figure 43.

Shrub or small tree, to 8 m tall. Twigs angular, solid, becoming terete in age, brown-tomentellous to glabrous, 4–5 mm diam. 5 cm below apex.

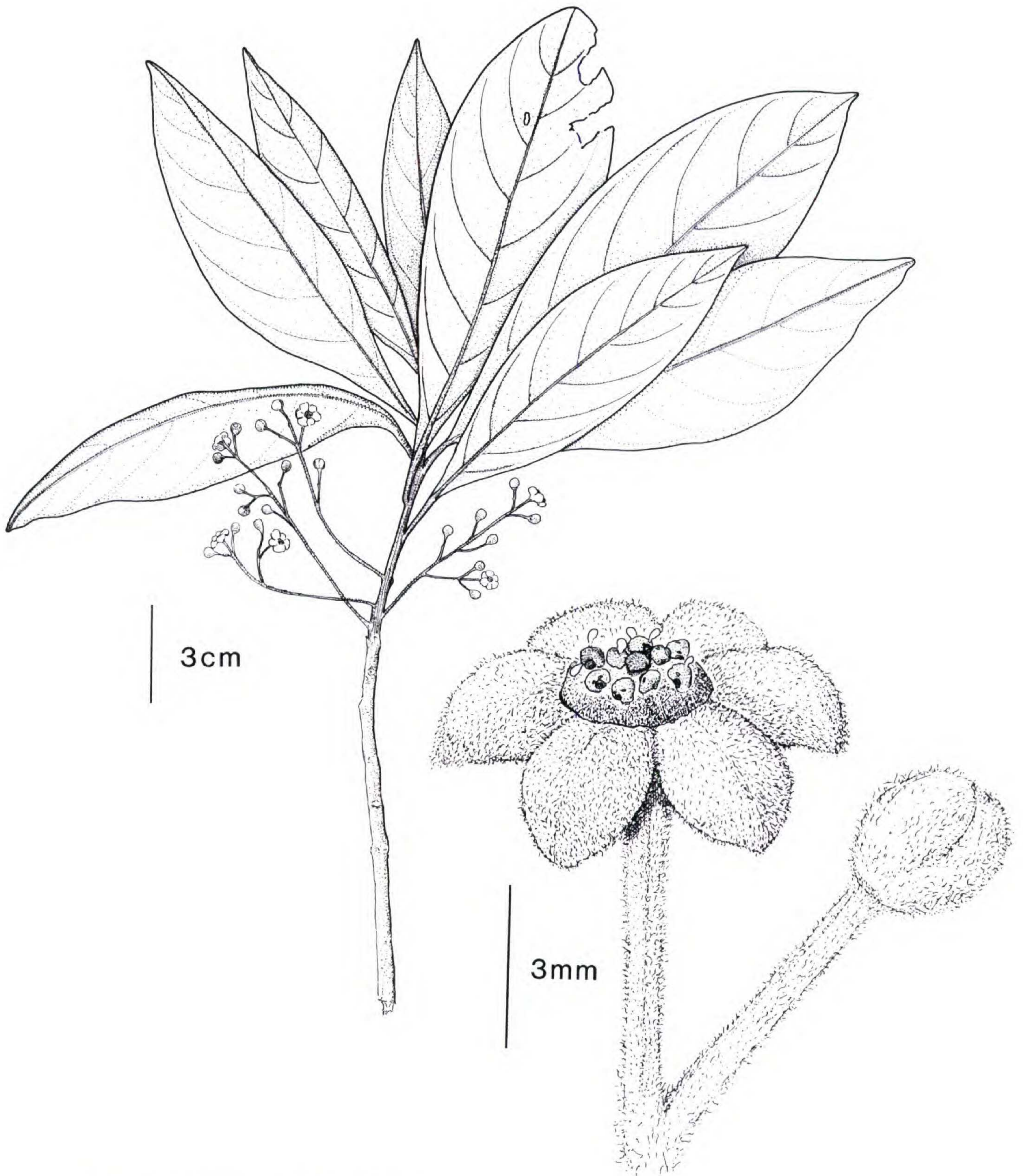


FIGURE 46. *P. westphalii*. Habit and flower.

Leaves clustered, rarely alternate, chartaceous, 30–40 × 6–11 cm, oblanceolate or narrowly obovate, the base cordate, the tip acuminate, acumen to 3 cm long, both surfaces glabrous, but with varying amounts of minute hairs on midrib and lateral veins; venation immersed on upper surface, midrib and lateral veins raised on lower surface, the tertiary venation weakly raised; lateral veins 20–25 on each side, curving upward near the margin and prominently loop-connected in the upper $\frac{2}{3}$ of the lamina. Petioles to 8 mm long, with similar indu-

ment as twig. Inflorescences in axils of deciduous bracts, pendent, to 20 cm long, rufous-tomentellous, the branchlets 2–3 times cymosely branched, bracts present at anthesis, ovate, tomentellous, to 4 mm long. Flowers white, 8–9 mm diam. Pedicels 3 mm long. Tepals 6, subequal, the outer three slightly wider than the inner three, the outer three tomentellous outside, inner three with a basal triangular tomentellous patch, otherwise papillose, inside of all tepals papillose. Stamens 9, 4-celled, the cells lateral, anthers minutely papillose, glands

of stamens greatly enlarged, surrounding the stamens, fused. Ovary and style densely brown-papillose, floral tube brown-papillose inside; ovary globose, ca. 0.7 mm long, the style distinct, ca. 0.5 mm long. Cupule of young fruit cup-shaped, ca. 2 cm wide and 1 cm tall; young fruit ellipsoid, ca. 1.5 cm long. Fruits: July–October. Flowers: June–July.

Collections studied. ECUADOR. NAPO: Aguarico, Reserva Faunística Cuyabeno, *Palacios 7667* (MO). PERU. LORETO: Quebrada Sucursari, tributary of Río Napo, *Gentry 54300* (MO); Pebas on the Amazon River, *Williams 1766* (B); Maynas, Iquitos, Asociación Agraria Paujil, *Vásquez 10877* (MO); Maynas, Explornapo Camp, Río Sucursari, *Vásquez 8119* (MO), *Vásquez 13078* (MO).

Pleurothyrium williamsii is only known from the type collection, four collections, all from Peru in the area north of the Río Napo–Río Amazonas, and one collection from Ecuador. Unfortunately, the holotype, which was requested from the Field Museum, disappeared, together with other *Pleurothyrium* types, while being sent to St. Louis. Of the type collection, only a duplicate in B (with buds) and some inflorescence fragments in G (with a few flowers) exist. The recent collections are a good match as far as floral characters and leaf shape are concerned, but there are some differences. The B specimen has alternate leaves, while the recent specimens and the photo of the holotype (in NY and F) show clustered leaves. The phototypes have the inflorescences alternate along a leafless twig, the recent specimens have the inflorescences near the tip of the stem, while the B specimen has a detached inflorescence. The B specimen is also more tomentulose. However, the similarities in leaf shape and flowers outweigh these differences, and I do not hesitate to assign the two recent collections to *P. williamsii*.

A close relative of this species is *Pleurothyrium panurense* (Meissner) Mez, a species with elliptic-obovate leaves, an obtuse leaf base and similar flowers. It differs, however, in its smaller leaves, the whitish indument on the lower leaf surface, its glabrous ovary, and longer petioles. *Pleurothyrium insigne* differs from *P. williamsii* in its larger leaves, the leaves not so gradually narrowed toward the base, erect indument on lower leaf surface, and its larger flowers. All three species occur in Amazonian Peru and/or adjacent Brazil. Another close relative is *P. maximum*, which see for further discussion.

IMPERFECTLY KNOWN SPECIES

Among the collections were found a number of specimens that do not belong to any of the treated

species and which very likely represent undescribed species. Because these specimens are incomplete (sterile or fruiting), they are not formally described, but only listed below so as to call attention to their existence. I hope that in the near future material adequate for their description will become available.

G. Proctor Cooper 539, Panama, Bocas del Toro, region of Almirante (F, NY, US).

A fruiting collection with large (to 35 cm), elliptic to elliptic-oblong, acuminate leaves. Leaves are glabrous below and have a strongly developed marginal vein; the twigs are solid, glabrous or nearly so. A distinct species, included in Burger & van der Werff (1990) as *Pleurothyrium* sp. A.

Gentry 57004, Colombia, Valle, Bajo Calima (MO).

A sterile specimen with gigantic leaves, according to the label ca. 1 m long. The specimen has leaves 60–70 cm long and 30–35 cm wide, densely rusty-tomentose below.

Monsalve 1651, Colombia, Valle, Bajo Calima (MO).

A species with clustered leaves, dark ferruginous-tomentose below, ca. 15 × 6 cm. Young inflorescences and infructescences are very short, ca. 1 cm long, and carry only one bud or fruit. There are five collections of this species, but none with flowers.

López & H. Triana 24, Colombia, Antioquia, Parque Nacional de las Orquideas (MO).

Characterized by its obovate to obovate-elliptic leaves, glabrous below, with 15–20 pairs of lateral veins and an obtuse to rounded leaf base. The young cupules are covered with many small lenticles.

Vasquez 3220, Peru, Loreto, Requena (MO).

Leaves glabrous, whorled, narrowly oblong with abruptly rounded base. Related to *P. williamsii*, but with narrower, oblong leaves and much smaller inflorescences.

EXCLUDED SPECIES

Pleurothyrium bahiense (Meissner) Barroso = *Urbanodendron bahiense* (Meissner) Rohwer

Pleurothyrium chrysothyrsus Meissner = *Rhodostemonodaphne*

Pleurothyrium cowanianum C. K. Allen = *Rhodostemonodaphne kunthiana* (Nees) Rohwer

Pleurothyrium ferrugineum Meissner = *Ocotea arnottiana* (Nees) van der Werff
Pleurothyrium glandulosum (Lundell) Lundell = *Nectandra*
Pleurothyrium velutinum Meissner = *Ocotea calophylla* Mez

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List of species recognized. New species are in boldface.

1. ***Pleurothyrium acuminatum*** van der Werff
2. *Pleurothyrium amapaense* Allen
3. *Pleurothyrium amplifolium* (Mez) Rohwer
4. *Pleurothyrium bifidum* Nees
5. ***Pleurothyrium bracteatum*** van der Werff
6. ***Pleurothyrium brochidodromum*** van der Werff
7. ***Pleurothyrium cinereum*** van der Werff
8. *Pleurothyrium costanense* van der Werff
9. ***Pleurothyrium crassitepalum*** van der Werff
10. *Pleurothyrium cuneifolium* Nees
11. ***Pleurothyrium giganthum*** van der Werff
12. ***Pleurothyrium glabrifolium*** van der Werff
13. ***Pleurothyrium glabritepalum*** van der Werff
14. *Pleurothyrium golfodulcense* Burger & Zamora
15. *Pleurothyrium grandiflorum* van der Werff
16. *Pleurothyrium hexaglandulosum* van der Werff
17. ***Pleurothyrium insigne*** van der Werff
18. *Pleurothyrium intermedium* (Mez) Rohwer
19. ***Pleurothyrium marginale*** van der Werff
20. *Pleurothyrium maximum* O. C. Schmidt
21. *Pleurothyrium nobile* A. C. Smith
22. ***Pleurothyrium obovatum*** van der Werff
23. *Pleurothyrium palmanum* (Mez & J. D. Smith) Rohwer
24. *Pleurothyrium panurense* (Meissner) Mez
25. *Pleurothyrium parviflorum* Ducke
26. ***Pleurothyrium pauciflorum*** van der Werff & Hammel

27. ***Pleurothyrium pilosum*** van der Werff
28. *Pleurothyrium poeppigii* Nees
29. ***Pleurothyrium prancei*** van der Werff
30. ***Pleurothyrium racemosum*** van der Werff
31. *Pleurothyrium steyermarkianum* Allen
32. ***Pleurothyrium synandrum*** van der Werff
33. ***Pleurothyrium tomentellum*** van der Werff
34. ***Pleurothyrium tomiwahlii*** van der Werff
35. *Pleurothyrium trianae* (Mez) Rohwer
36. *Pleurothyrium undulatum* (Meissner) Rohwer
37. ***Pleurothyrium vasquezii*** van der Werff
38. *Pleurothyrium westphalii* van der Werff
39. *Pleurothyrium williamsii* O. C. Schmidt

Specimens studied. If collected by a team, only last name of the first collector on the label is listed. Thus, Berg & Akkermans becomes Berg.

Allen 5885 (14); *Ancuash* 602 (4); *Aristeguieta* 1584 (35); *Aristeguieta* 1647 (35); *Aristeguieta* 2085 (35); *Aristeguieta* 6978 (35); *Ayala* 574 (10); *Ayala* 3386 (35); *Ayala* 5734 (24); *Aymard* 1747 (35).

Barbour 1011 (23); *Berg* 1050 (25); *Bernardi* 1137 (35); *Bernardi* 2169 (31); *Bernardi* 6879 (8); *Bosque J-03* (8); *Bosque J-03A* (8); *Bosque J-12* (8); *Brandbyge* 42343 (22); *Brandbyge* 42366 (22); *Breteler* 3517 (35); *Breteler* 3667 (35); *Bunting* 872 (35); *Burger* 4690 (14).

Callejas 9143 (34); *Campbell* 6887 (37); *Campbell* 10852 (37); *Campos* 364 (10); *Cardenas* 3966 (28); *Castillo* 12 (21); *Castillo* 15 (21); *Castillo* 50 (1); *Ceron* 3017 (12); *Ceron* 4982 (25); *Cid* 859 (37); *Cid Ferreira* 7292 (25); *Cogollo* 170 (10); *Croat* 17593 (25); *Croat* 19439 (17); *Croat* 59792 (16); *Cuatrecasas* 13227 (35); *Cuatrecasas* 13986 (9); *Cuatrecasas* 16321A (35); *Cuatrecasas* 16656 (32); *Cuatrecasas* 16675 (35); *Cuatrecasas* 16781 (35); *Cuatrecasas* 16864 (35); *Cuatrecasas* 17196 (19).

Davidse 21459 (35); *Davidse* 21467 (35); *Davidse* 27524 (2); *Davidson* 5336 (17); *de Bruijn* 1422 (35); *de Nevers* 7520 (27); *Díaz* 241 (25); *Dodson* 6302 (11); *Dodson* 6419 (35); *Dodson* 10181 (11); *Dodson* 13632 (11); *Dodson* 14531 (34); *Dorr* 4720 (35); *Ducke RB19935* (25); *Ducke RB25676* (1).

Forero 4135 (35); *Forero* 4693 (35); *Foster* 3153 (28); *Foster* 10642 (28); *Foster* 11719 (37); *Freitas* 55 (25); *Froes* 20526 (37); *Froes* 21036 (25); *Froes* 21235 (37).

Gentry 7201 (13); *Gentry* 16627 (25); *Gentry* 18317 (25); *Gentry* 21284 (25); *Gentry* 25807 (25); *Gentry* 25914 (25); *Gentry* 28959 (25); *Gentry* 39902 (10); *Gentry* 43560 (28); *Gentry* 45117 (7); *Gentry* 45760 (10); *Gentry* 53812 (35); *Gentry* 53833 (35); *Gentry* 54300 (39); *Gentry* 57817 (10); *Gentry* 58103 (37); *Gentry* 58574 (10); *Glaziou* 17731 (3); *González* 1215 (8); *Grandez* 1376 (37); *Grandez* 1732 (25); *Gudiño* 12 (33); *Gudiño* 17 (33).

Haber 9526 (23); *Hammel* 14781 (16); *Hammel* 17009 (26); *Hammel* 17909 (26); *Hammel* 18152 (35); *Hartshorn* 2631 (10); *Hartshorn* 2937 (10); *Huber* 1557 (10); *Hurtado* 1464 (33).

Janse 280 (7); *Jativa* 1104 (7); *Jativa* 2039 (7); *Jimenez* 648 (14); *Jimenez* 1289 (35); *Juncosa* 1675 (15).

Kayap 145 (10); *Kayap* 648 (10); *Kernan* 184 (14); *Kernan* 187 (14); *Klug* 1301 (25); *Klug* 1372 (25); *Klug* 2122 (7); *Klug* 2779 (10); *Klug* 2931 (10); *Klug*

3116 (10); *Klug* 3195 (10); *Klug* 3228 (10); *Klug* 3567 (10); *Knapp* 8205 (17); *Kroll* 285 (21); *Kroll* 422 (21); *Krukoff* 4783 (24); *Krukoff* 4800 (24); *Krukoff* 5121 (21); *Krukoff* 5255 (28); *Krukoff* 5263 (28); *Krukoff* 5722 (28); *Krukoff* 6232 (17); *Kunkel* 9 (38); *Kunkel* 17 (38).

Lamotte 085 (25); *Lamotte* 0200 (25); *Lau* 10 (8); *Lawrance* 619 (5); *Lawrance* 780 (10); *Little* 8488 (10); *Little* 15822 (35); *Little* 16121 (35); *Little* 21359 (7); *Llewelyn Williams* 1090 (25); *Llewelyn Williams* 2273 (25); *López* 8634 (25); *Lugo* 320 (28).

Marcano Berti 1123 (8); *Marcano Berti* 1177 (35); *Marcano Berti* 2913 (35); *Matthews* 1432 (10); *McDaniel* 15243 (25); *McDaniel* 20716 (25); *McDaniel* 20753 (25); *McPherson* 12120 (30); *McPherson* 12999 (35); *McPherson* 13365 (10); *Miranda Bastos* 17 (25); *Mocquerys* 1002 (35); *Mori* 9074 (25); *Mori* 9227 (25); *Mori* 20470 (25).

Neill 6555 (28); *Neill* 7019 (10); *Neill* 7128 (10); *Neill* 7603 (28); *Neill* 8741 (33); *Neill* 8783 (33); *Neill* 8954 (7); *Neill* 9033 (17); *Neill* 9435 (18); *Neill* 9439 (18); *Nuñez* 5901 (28); *Nuñez* 12207 (10).

Oliveira 21 (37); *Ortiz* 192 (22).

Palacios 982 (28); *Palacios* 1332 (17); *Palacios* 1518 (17); *Palacios* 2094 (35); *Palacios* 2288 (12); *Palacios* 2775 (28); *Palacios* 2804 (35); *Palacios* 3416 (33); *Palacios* 4273 (35); *Palacios* 4334 (35); *Palacios* 4388 (17); *Palacios* 4436 (35); *Palacios* 4727 (35); *Palacios* 7667 (39); *Pariona* 49 (17); *Pariona* 63 (10); *Peters* 52/84 (25); *Pires* 51430 (2); *Pittier* 10947 (35); *Plowman* 6410 (25); *Plowman* 6908 (25); *Poeppig* Addenda 301 (28); *Poeppig* 1718 (10); *Poeppig* 1845 (10); *Poeppig* 2125 (10); *Poeppig* 2398 (4); *Poeppig* 2908 (10); *Prance* 11970 (25); *Prance* 12392 (29); *Prance* 13927 (24); *Prance* 28012 (35).

Quintero 11 (8).

Ramírez 61 (37); *Riedel* 1412 (36); *Revilla* 742 (25); *Revilla* 2532 (25); *Revilla* 3687 (24); *Reynel* 102 (10); *van Rooden* 650 (35); *van Rooden* 681 (35); *Rowlee* 233 (23); *Rubio* 45 (33); *Ruíz* 1438 (25); *Ruíz* s.n. (28).

Salcedo 225 (35); *Santos* 78 (37); *Schunke* 3475 (37); *Schunke* 13643 (37); *Shepherd* 537 (10); *Smith* 384 (37); *Smith* 1743 (10); *Smith* 1756 (10); *Smith* 2793 (28); *Smith* 3061 (10); *Smith* 7463 (35); *Smith* 9021 (35); *Soejarto* 1268 (28); *Soto* 613 (35); *Soukop* 910 (10); *Spruce* 2449 (24); *Stern* 1064 (23); *Steyermark* 56077 (31); *Steyermark* 61393 (8); *Steyermark* 62230 (8); *Steyermark* 96072 (8); *Steyermark* 111580 (35).

Tamayo 1094 (35); *Tessmann* 4040 (20); *Tessmann* 4529 (20); *Tessmann* 4634 (7); *Tessmann* 5175 (25); *Thomas* 6476 (37); *Tonduz* CR 12652 (23); *Triana* 1037 (35); *Triana* 2042 (35).

Ule 9408 (18); *Unknown* s.n. (37).

Valverde 15 (35); *Vásquez* 896 (35); *Vásquez* 1520 (25); *Vásquez* 4858 (25); *Vásquez* 4970 (24); *Vásquez* 5469 (37); *Vásquez* 7468 (24); *Vásquez* 7823 (17); *Vásquez* 7865 (6); *Vásquez* 7889 (37); *Vásquez* 8119 (39); *Vásquez* 8444 (17); *Vásquez* 9138 (25); *Vásquez* 9365 (17); *Vásquez* 10233 (24); *Vásquez* 10500 (25); *Vásquez* 10877 (39); *Vásquez* 11507 (25); *Vásquez* 12284 (25); *Vásquez* 12921 (35); *Vásquez* 13078 (39).

Wallnoefer 18-29788 (33); *van der Werff* 3654 (8); *van der Werff* 8266 (10); *van der Werff* 8287 (10); *van der Werff* 8291 (10); *van der Werff* 8343 (28); *van der Werff* 8345 (28); *van der Werff* 8346 (10); *van der*

Werff 8673 (10); *van der Werff* 8887 (35); *van der Werff* 9471 (11); *van der Werff* 9956 (25); *van der Werff* 9967 (1); *van der Werff* 10050 (25); *van der Werff* 10066 (25); *van der Werff* 11157 (10); *van der Werff* 12362 (11); *van der Werff* 12365 934); *van der Werff* 12367 (34); *Whitford* 49 (8); *Williams* 1090 (25); *Williams* 1766 (39); *Williams* 2273 (25); *Williams* 2715 (10); *Wurdack* 2047 (4).

Zak 4459 (33); *Zak* 4511 (17); *Zak* 4608 (35); *Zamora* 1363 (35).

Note added in proof.

At the very last moment, the collection *Herrera & Fallas* 4638 was received for identification. This collection represents an undescribed species, which could not be incorporated in the manuscript. The description of this species and a discussion of its affinities are presented in this note.

Pleurothyrium immersum *van der Werff*, sp. nov.

TYPE: Costa Rica. Punarenas: Cantón de Golfito, Dos Brazos de Río Tigre, Fila Puriscal Rico (fls), *Herrera & Fallas* 4638 (holotype, MO; isotypes, BM, CR, HBG, INB, MEXU, QRS, US, USJ).

Haec species *P. golfodulcense* proxima, sed foliis floribusque minoribus, reticulatione immersa, tepalis intus pubescentibus et inflorescentia paniculato-cymosa differt.

Tree, 20 m tall. Twigs terete, solid, finely gray appressed-pubescent, 1–2 mm diam. ca. 5 cm below the tip. Terminal bud densely appressed-pubescent. Leaves alternate, firmly chartaceous, 5–9 × 1.5–2.5 cm, elliptic, base acute, tip acuminate or acute, upper surface glabrous, gland dotted, lower surface with scattered appressed hairs, these more dense along midrib, or glabrous; midrib slightly raised on both surfaces, otherwise venation immersed and scarcely visible; lateral veins 5–6, not loop-connected. Petioles 4–9 mm long, finely appressed-pubescent. Inflorescences in axils of normal leaves or cataphylls, paniculate-cymose, the lateral branchlets once or

twice cymosely branched, densely gray-pubescent, bracts often present at anthesis, narrowly elliptic, to 1.5 mm long, pubescent on both surfaces. Flowers yellow-green, the tepals spreading to bent downward, ca. 5 mm diam. Pedicels 2–4 mm long. Tepals 6, equal or nearly so, pubescent on both surfaces, the margin plane, elliptic, ca. 2 mm long, the inner 3 ca. 1.5 mm wide, outer 3 ca. 1 mm wide. Stamens 9, all 4-celled, fully immersed in the glandular mass, with only the cells and valves recognizable; glands strongly enlarged, fused, and forming a pillowlike mass; stamens, especially those of whorl II, separated from each other by the glandular tissue and not restricted to the center of the glandular mass. Pistil ca. 1.2 mm long, the moderately pubescent ovary gradually narrowed into the glabrous style. Receptacle pubescent inside. Cupule and fruit unknown. Flowers: November. Elevation range: ca. 700 m.

Pleurothyrium immersum is only known from the type collection made on the Osa Peninsula, collected in the same general area as *P. golfodulcense*; these two species are closely related. Characters shared by both are the position of the stamens in the glandular mass (not crowded together in the center, but stamens of whorl II separated from the others by the glandular tissue), position of inflorescences (not infrequently in axils of normal leaves), the reflexed tepals in older flowers, and the acute-acuminate leaf tips. However, the two species differ in the following characters: *P. immersum* has much smaller leaves (5–9 vs. 10–20 cm), the lateral veins are immersed and not raised on lower leaf surface, flowers are much smaller (4–5 vs. 9–12 mm diam.), tepals are pubescent (not papillose) on inner surface, and the inflorescences are paniculate-cymose, not racemose.

In the key, *Pleurothyrium immersum* would run to couplet 37, where the combination in *P. immersum* of pubescent inner surface of tepals and a pubescent pistil will cause a problem. However, *P. immersum* differs from all other *Pleurothyrium* species with glabrous or appressed-pubescent lower leaf surfaces in its small leaves with immersed venation. The glandular dots on the upper leaf surface are also a good indicator for this species.