

Revisional study
of
neotropical *Beilschmiedia* species (Lauraceae)
with special reference to leaf anatomy

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Abstract

Lauraceae contain many species which are important constituents in tropical forests both ecologically and economically, however, taxonomy of the family is still not sufficiently clarified at the genus or species level. *Beilschmiedia* is an example of such a poorly understood genus. Taking advantage of recent intensive collecting of neotropical Lauraceae species, this study revised neotropical *Beilschmiedia* species, with general descriptions of morphology, anatomy, palynology, karyology, distribution, reproductive biology, seed dispersal, systematic position of the species in the family, and the systematic treatment. As a result, 27 species were recognized with four species newly described and two species newly combined in the genus.

Additionally, leaf anatomy of neotropical *Beilschmiedia* species was employed for better understanding of the species relationships. In leaf anatomy, groupings of cuticular characters was accepted as representing the species relationships, which resulted to recognize five groups among the species.

Chapter 1

General Introduction

Lauraceae are the largest family in the order Laurales of the Magnoliidae (sensu Cronquist 1981), with about 50 genera. It is a pantropical family with a few temperate members, and main centers of the diversity are the Indomalayan region and Central to South America (Rohwer 1993 b). All species are trees or shrubs except for the species of *Cassytha* which are herbaceous parasites.

Although the family contains many species which are very important constituents in tropical forests ecologically and economically, taxonomy of the family is still not sufficiently clarified at genus or species level. The number of the species in the family is still difficult to estimate, probably between 2500 and 3500 (Rohwer 1993 b). In the neotropics, Lauraceae have a reputation of being one of the most difficult families in angiosperms (Burger 1988). It is due to the following facts; that the generic concepts are still not clear in some cases, that the species are difficult to recognize, and that the representation in herbarium collections is poor (Burger 1988). Systematic revisions of the family with more intensive collecting is sorely needed.

Beilschmiedia is an example of such a poorly understood genus. This genus is pantropical, distributed from Mexico and southern islands in Japan at the northern limit and to central Chile and New Zealand at the southern limit. It comprises about 250 species and is usually distinguished from the other laurel genera by a combination of the following characters; bisexual and trimerous flowers, six equal to sub-equal tepals, six to nine fertile stamens, 2-celled anthers, staminal glands only in the third whorl, shallow receptacle, and fruit without cupule.

Since Meissner (1864) revised the entire family, no revision for the whole genus *Beilschmiedia* has been made. Regional treatments were made by Liou (1934) for the species in China and Indochina, by Robyns and Wilczek (1951) for the African species, by Fouilloy (1974) for the species in Cameroon, by Li et al. (1982) for the Chinese species, by Wright (1984) for the species in New Zealand, and by Hyland (1989) for the Australian species. For the neotropical species, Kostermans's work (1938) was the most recent comprehensive revision, and Allen (1945) treated the Mexican and Central American species. These revisional works for neotropical *Beilschmiedia* species were not based on abundant material, 7 of 15 species in Kostermans's revision and 4 of 8 species in Allen's revision were known

only from the type collections. And since Kostermans's revision, 15 names have been already described under *Beilschmiedia* in the neotropics. A revision for neotropical *Beilschmiedia* species, being up to date and with more material, is needed for an understanding of the whole genus and also the neotropical Lauraceae.

Fortunately, as Burger (1988) mentions, Latin American botanists are actively collecting neotropical plants including Lauraceae these days. Especially, van der Werff in the Missouri Botanical Garden has been working on a number of projects on a systematic study of Lauraceae coupled with intensive collecting of the family in the neotropics. I had an opportunity to study at Missouri Botanical Garden from fall in 1994 to spring in 1997, and took the advantage to work on neotropical *Beilschmiedia* species under van der Werff's supervision.

In this study I revised neotropical *Beilschmiedia* species in which I recognize 27 species, with general descriptions of morphology, anatomy, palynology, karyology, distribution, reproductive biology, seed dispersal, and systematic position of the species in the family in the second chapter. And for better understanding of relationships of the species, I employed leaf anatomy in the third chapter. Neotropical *Beilschmiedia* species have relatively similar flowers and fruits except for a few species, and it is more reasonable to study vegetative morphology rather than reproductive morphology for systematics of the species. Among neotropical *Beilschmiedia* species, there appear to be two groups, one group of the species alternate leaves and fine ramification (ramification is here defined as ultimate branching patterns in leaf veins), and another group of the species with opposite leaves and coarse ramification. Preliminary observation (Christophel, pers. comm.) indicated that the two groups also differ in characters of the cuticle. Therefore, I investigated leaf anatomical characters (venation patterns, cuticular and leaf section characters) for all the neotropical *Beilschmiedia* species available in order to discuss the following; 1) whether the cuticular and leaf section characters support the grouping based on phyllotaxis and venation patterns, and 2) how we can incorporate leaf-anatomical characters in the classification of neotropical *Beilschmiedia* species. These studies would not only help to know neotropical *Beilschmiedia* species further, but would also give an important step to understand whole *Beilschmiedia*, one of the largest genera in Lauraceae.

Chapter 2

Revisional study of neotropical *Beilschmiedia* species

Introduction - Taxonomic history

The genus *Beilschmiedia* was described by Nees (1831), with two Asian species *B. roxburghiana* and *B. fagifolia*.

Nees (1833) described *Hufelandia* with two neotropical species, *H. pendula* and *H. thomaea*. Since then 12 species had been described under *Hufelandia*. But Hemsley (1882) transferred the type species *H. pendula* (as well as *H. thomaea*) under *Beilschmiedia*. Mez (1889) restored *Hufelandia* to generic rank, but Kostermans (1938) included *Hufelandia* in *Beilschmiedia* again. In this study, I follow Kostermans's sense about the generic treatment, because *Beilschmiedia* in Asia where the type species of the genus occurs is poorly known and it is impossible to clarify the relationship between the neotropical and Asian species before a better understanding of the Asian species.

In addition to *Hufelandia* Nees, *Beilschmiedia* has another synonym, *Bellota* Gay, for the Chilean species. Kostermans (1938) listed other three synonyms, *Boldu* Nees (non Feuillée), *Boldus* O. Kuntze (non Adanson) and *Wimmeria* Nees ex Meissner, but they are not valid or legitimately published. First, *Boldu* Nees is a superfluous name. And *Boldus* is the name which Kuntze did not describe but only reestablished from *Boldus* Molina, and *Boldus* Molina actually belongs to the Monimiaceae. *Wimmeria* is the name written on a specimen label of *B. pendula* and not validly published.

Gay (1849) described a new genus *Bellota* with one species, *Bellota miersii*. The genus Gay described, *Bellota*, was combined in *Beilschmiedia* by Kostermans (1938).

For the palaeotropical species, *Beilschmiedia* has the following synonyms; *Nesodaphne* Hooker f., *Bernieria* Baillon, *Tylostemon* Engler, *Afrodaphne* Stapf, *Thouvenotia* Danguy, *Purkayasthaea* Purkayastha, and *Lauromerrillia* C. K. Allen.

Kostermans (1952) combined a neotropical genus, *Anaueria*, in *Beilschmiedia*. But Richter (1981) found that *Anaueria* differs strongly from *Beilschmiedia* in wood anatomy; this, combined with differences in flower and fruit morphology, resulted in the current recognition of *Anaueria* as a distinct genus.

Materials and Methods

Most of the revisional study was done at Missouri Botanical Garden (MO), St. Louis, U. S. A., where a specialist of Lauraceae, van der Werff, works and a large amount of the neotropical Lauraceae collections are preserved. Loans of neotropical *Beilschmiedia* species were requested from major herbaria (A, B, BM, BR, C, F, IEB, K, LL, MEXU, NY, P, R, RB, S, U, US, VEN). Two major herbaria in Costa Rica (CR, INB) were visited. Some collections obtained by the staffs of Missouri Botanical Garden had been observed before they were sent to the other herbaria (FCME, MEXU, INB, etc.).

Field trips were carried out in Costa Rica in March, 1996. Habit and surroundings of several *Beilschmiedia* species were observed in the field, and the leaves, flowers and fruits were collected for a further study. Most of the specimens collected there are kept at INB and MO.

For the species delimitation I employed morphological species concept. I usually tried to find more than one characters to delimitate the species. If there are a series of intermediate collections, I did not divide the complex even when the extremes appeared distinct enough. The complex should be kept rather than divided before they are studied with more materials or some biological (e.g., genetic) investigations. I avoided infraspecific categories, because I agree with Burger's opinion "we need much more (biological) information to make a subspecies than to make a species" (quoted by Rohwer 1993 a). Neither did I make any infrageneric categories because comprehensive study of the genus *Beilschmiedia* should be made before establishing any infrageneric categories.

In this study I recognized four new species. However, I do not intend to publish these species formally in this dissertation because dissertations are not available to as many people as journals. The formal publication of these new species will be made in a botanical journal.

A description of each species is in the following order; name of the species, a list of basionym and taxonomical synonym, Latin diagnosis if it is a new species, general description, phenology, distribution, common name, economical use, a list of additional specimens examined, and notes. In the list of additional specimens except for type collections, if the specimen is collected by a team, only last name of the first collector on the label is listed. But if the last name of the collector is a common name like "Smith" and "Allen", an initial of the first (and middle, if present) name of the collector might be also listed. For example, if it is a type collection, Berg & Akkermans becomes "Berg &

Akkermans”, if it is not a type, Berg & Akkermans becomes “Berg”, and Caroline K. Allen becomes “C. K. Allen”.

Morphology

Habit. All the neotropical *Beilschmiedia* species are trees, and many of them grow up to about 30 m tall, sometimes up to 40 m tall. There are some species which have been reported as a tree less than 15 m tall (*B. angustieliptica*, *B. angustifolia*, *B. emarginata*, and *B. fluminensis*), but these are the species which are known from only a few collections, and they might be found as a bigger tree when more collections are made in future.

Twigs. Twigs are usually terete, but mostly compressed to angular when they are young. Some species (*B. anay*, *B. brenesii*, *B. immersinervis*, and *B. rigida*) tend to have corky twigs, but this characteristic is not very helpful to delimitate the species because the other species also rarely have corky twigs.

Phyllotaxis. Neotropical *Beilschmiedia* species have two groups of phyllotaxis, one group of species with alternate leaves and another group of species with opposite leaves. Rarely the species with alternate leaves show sub-opposite leaf arrangement near the tip of the twigs. In the group with alternate leaves, there are a few species which appear to have clustered leaves (*B. anay*, *B. alloiophylla*), but the leaves of these species become less clustered when the twigs are getting old. In the group with opposite leaves, *B. brenesii* and some Mexican collections of *B. hondurensis* tend to have some leaves crowded near the tip of the twigs.

Petioles. Petioles are usually canaliculate or flat above. Color of petioles is usually same as the one of twigs, but sometimes slightly darker and making a contrast with the twigs in *B. angustieliptica*, *B. curviramea*, *B. emarginata*, *B. fluminensis*, *B. hondurensis*, *B. rigida* and *B. taubertiana*.

Leaves. Leaf (blade) shape ranges from ovate to obovate. Size and shape of the leaves (leaf blades) vary in some species. Especially, *Beilschmiedia costaricensis* shows variation in leaf size, and *B. towarensis* shows variation in leaf size and shape. *Beilschmiedia pendula* usually

has relatively small and narrow leaves (5-12 x 2-5 cm), but it can have much larger and wider leaves (up to 16 x 9 cm) in some islands like Guadeloupe and Puerto Rico.

Leaves of some species are glaucous on lower surface, appearing whitish. Species known with glaucous leaves are *B. alloiophylla*, *B. anay*, *B. berteroaana*, *B. immersinervis*, *B. latifolia*, *B. miersii*, *B. obovatifolia*, *B. ovalioides*, *B. ovalis* and *B. pendula*. This character is usually consistent within a species, but sometimes exceptional cases occur, e.g., a few collections of *B. pendula* have non-glaucous leaves, and a few collections of *B. mexicana* and *B. riparia* have glaucous leaves although typical collections of these two species do not. The specimens once placed in alcohol may lose the glaucous color. Some Brazilian species, *B. angustifolia*, *B. emarginata*, *B. rigida* and *B. stricta* are not known whether they have glaucous leaves or not because all the collections examined were likely placed in alcohol.

Venation. Venation patterns, especially ramification types, are important characters to delimit neotropical *Beilschmiedia* species. The venation patterns were X-rayed and discussed with other leaf anatomical characters in the third chapter of this study. See the chapter for details.

Domatia. There are no *Beilschmiedia* species reported to have domatia. But in *B. riparia* there are a few collections which have denser pubescence in axils of the secondary veins, appearing to have domatia. See the notes under *B. riparia* for details.

Indument. Pubescence type is an important character to delimitate the species, but one should keep in mind that it sometimes shows a certain variation within a species.

As shown in Fig. 1, Indument of neotropical *Beilschmiedia* species can be divided into three types in orientation (appressed, spreading, erect), and in straightness (straight, wavy, curly). Appressed indument (Fig. 1 A) is always straight and spreading indument (Fig. 1 B) is also usually almost straight, but erect indument can be straight (Fig. 1 C), wavy (Fig. 1 D), or curly (Fig. 1 E). I have classified minutely tomentelose pubescence with short curly hairs (Fig. 1 E) as erect, because orientation of the hairs is not appressed but erect at the base. Appressed indument is strictly appressed on the plant surface, appearing to be somewhat silky and shiny. Spreading indument rarely occurs in *B. berteroaana*, *B. brenesii*, *B. costaricensis* and *B. hondurensis*, all of which usually have appressed indument.

Straightness of the indument sometimes varies on different parts of the plant. For example, indument of the inflorescences is usually erect even in the species with appressed indument on the terminal buds and twigs. Another example is that some collections of *B. alloiophylla* have erect curly indument on the terminal buds and twigs but have erect straight indument on the lower leaf surfaces.

Usually, orientation of indument on terminal buds and twigs are stable enough to use for delimitation of the species, but the straightness is often too variable within a species to use for the delimitation.

Inflorescences. Mostly, inflorescences of neotropical *Beilschmiedia* species are found in axils of the leaves. But *B. brenesii* often has the inflorescences clustered around the terminal buds or on a short leafless shoot in the axils of the leaves.

Inflorescences are usually paniculate (Fig. 2). They consist of a central axis with a number of alternately positioned lateral axes. The lateral axes are usually once or twice branched somewhat cymosely, but actually the ultimate divisions are not strictly cymose (Fig. 3 A). As van der Werff and Richter (1996) indicate, whether ultimate divisions of the inflorescences are strictly cymose (Fig. 3 B) or not is a very helpful character for determination to genus. Most neotropical genera of Lauraceae have the inflorescences with ultimate divisions strictly cymose and differ from *Beilschmiedia* in this character (van der Werff and Richter 1996). Some species like *B. berteriana*, *B. mexicana*, *B. miersii* and *B. pendula* often have the lateral elements scarcely developed and the inflorescences nearly racemose. Inflorescences of *B. stricta* and *B. taubertiana* appear to be racemose, but we have too few collections to confirm that the two species always have racemose inflorescences.

In most species inflorescence bracts are small, early deciduous and often absent at anthesis. Rarely they have foliose bracts (as in *B. miersii*), but the foliose bracts do not occur consistently in a species. Position of the bracts is variable even within an inflorescence, hence length of pedicels above the bracts is often quite variable in a species. Central elements of the ultimate inflorescence divisions usually have much longer flower pedicels than the lateral elements. In a description of each species, pedicel length of the central elements and the lateral divisions is recorded separately. It is not usually practical to use length of the pedicels for delimitation of species, but some species like *B. brenesii* have extremely long pedicels and this character helps to distinguish the species from the others.

Flowers. Flower morphology of some neotropical *Beilschmiedia* species are shown in Fig. 4. Flowers are bisexual, small (ca. 3 mm long) and almost sub-spherical (Fig. 4 A, B, C) except for the ones of *B. linharesensis*, which are depressed-globose (Fig. 4 D). Flowers of neotropical *Beilschmiedia* species appear to be similar to flowers of *Cryptocarya*. But flowers of the former taxon always have shallow receptacles, whereas flowers of the latter have deep, tubular receptacles which cover the fruits after anthesis.

Tepals are six, erect, almost equal and usually ovate to elliptic. Outer surfaces of tepals are pubescent with more or less erect hairs to glabrous, and usually the density is same as on the flower pedicels (but some collections of *B. berteriana* show a contrast between the densely pubescent pedicels and glabrous outer surfaces of the tepals). Inner surfaces of the tepals are usually pubescent with appressed to erect hairs around the center or around the base.

All neotropical *Beilschmiedia* species except for *B. hexanthera* have nine stamens. *Beilschmiedia hexanthera* has six stamens in the outer two whorls and six staminodia in the inner two whorls.

Stamens in the first whorl and the second whorl are similar in size and shape, or stamens in the first whorl are slightly wider than stamens in the second whorl. Stamens in the third whorl are usually slightly longer than the other stamens. Filaments in the first and second whorls are usually much shorter than the anthers, filaments in the third whorl are less so, but still shorter than the anthers. Most of the species have the filaments pubescent, but *B. angustieliptica* and *B. hondurensis* tend to have the filaments only sparsely pubescent to almost glabrous. Anthers in the first and second whorls are ovate, anthers in the third whorl are narrower ovate to almost rectangular. Apex of anthers always more or less protrudes the cells. The apex is obtuse to truncate in most of the species, but more or less acute in *B. angustieliptica* (Fig. 4 B), *B. brenesii* and *B. hondurensis*. Pubescence on the apex of anthers is a discriminating character for some species (*B. anay*, *B. angustifolia*, *B. curviramea*, *B. emarginata*, *B. fluminensis*, *B. linharesensis*, *B. immersinervis*, *B. rigida*, *B. riparia*, *B. stricta* and *B. taubertiana*), but very rarely there are exceptional collections lacking the pubescence in those species. Other species have almost glabrous anthers, and even if the anthers pubescent on the lateral sides, the apex of the anthers is glabrous. Glands of stamens in the third whole are usually globose, slightly shorter than filaments of the stamens or almost as long as the filaments.

Staminodia in the fourth whorl are three, conspicuous, and cordate to triangular in outline. They are pubescent on the abaxial side. In *B. hexanthera*, three staminodia in the third whorl are columnar, different from the innermost three staminodia which are cordate in outline (Fig. 4 C).

Pistil usually has the ovary gradually narrowed into the style. Sometimes pistil is pubescent, but presence of the pubescence is often variable within a species, and the amount of the pubescence is usually small, easy to overlook.

As mentioned above, receptacle is invariably shallow, which is a good character to distinguish neotropical *Beilschmiedia* species from *Cryptocarya*. Pubescence of receptacles ranges from dense to almost glabrous, but many species have the receptacle pubescent only around the base of stamens and staminodia. Pubescence type of receptacle is usually consistent within a species, but it is hard to use for delimitation of the species because even erect hairs sometimes appear to be appressed for being pressed by the ovary.

Fruits. Fruits are not well known for some species, especially the Brazilian species. Among the species of which fruits are known, many species have ellipsoid fruits (Fig. 5 A). But *B. ovalis* (Fig. 5 B) and *B. ovalioides* have spherical fruits, and *B. anay* is reported to have pyriform fruits. Color of fruits is usually green when immature and black or purple-black when mature. Surface of fruits is usually smooth. The collections of *B. curviramea*, *B. fluminensis*, *B. stricta* and *B. taubertiana* have somewhat warty fruit surface, but it is uncertain whether they always have warty surface or not, because most of these species have only a few collections in fruit.

Fruits of *Beilschmiedia* always lack cupules. Fruit pedicels sometimes become slightly thickened below the fruit, especially in the species with spherical fruits, but not so thickened as the pedicels of *Alseodaphne*. In some species, fruit pedicels are constricted at the base and distinguished from the lower part of the axis (Fig. 5 A). The species which have the fruit pedicels constricted at the base are; *B. alloiophylla*, *B. angustieliptica*, *B. latifolia*, *B. mexicana*, *B. pendula* and *B. riparia*. But one should not rely on this character to delimit the species too much, because there are a few exceptional collections in those species, which have the fruit pedicels not constricted, and because some other species like *B. hondurensis* and *B. tovarensis* have the pedicel variable, from constricted to not constricted. Sometimes fruit pedicels have a different texture and color from the lower part of the axis because lenticels cover the infructescence except for the pedicel (Fig. 5 B). This characteristic usually

occurs in the species with fruit pedicels constricted, but rarely it occurs even in the species with fruit pedicels not constricted like *B. brenesii*. And a few species which have the fruit pedicels constricted, like *B. mexicana* and *B. pendula*, do not have different texture or color between the pedicels and axis because the infructescences are not covered with lenticels at all.

Anatomy

Wood anatomy. A comprehensive study on secondary xylem and bark of Lauraceae was made by Richter (1981). According to him, *Beilschmiedia* species, not only neotropical ones but also palaeotropical ones, share the following characters of wood anatomy with most of the other Lauraceae genera; vessels diffuse and not solitary, intervacular pitting alternate, tyloses present in heartwood, fibers libriform and arranged in radial rows, and parenchyma paratracheal.

Richter (1981) recognized three large groups of the Lauraceae genera in wood anatomical characters, one of which includes *Beilschmiedia*, *Endiandra*, *Potameia*, *Triadodaphne*, *Cryptocarya* and *Ravensara*. They are usually distinguished from the other genera by the following characters (some characters are only partly true or exceptional in *Cryptocarya* and *Ravensara*); vessel perforations exclusively simple, fibers non-septate, relatively large and conspicuously bordered, parenchyma more or less vasicentric in combination with multiseriate marginal bands, rays heterogeneous and comprise uniseriate and multiseriate rays, vessel-ray pits extremely variable.

A character which is generally restricted to South American and West African *Beilschmiedia* species (and only occasionally *Endiandra*) is presence of tyloses in fibers (Richter in Metcalfe 1987).

Leaf anatomy. Leaf anatomy of neotropical *Beilschmiedia* species are investigated in the third chapter of this study. See the chapter for details.

Reproductive anatomy. Embryology and pericarp anatomy of *Beilschmiedia* had never been studied before Heo (1995). In his study of reproductive structures and phylogeny of Lauraceae, Heo (1995) observed eight species of *Beilschmiedia*, five of which were neotropical (three samples of the neotropical species are misidentified, i.e., *Haber 9846*

belongs not to *B. ovalis* but to *B. alloiophylla*, *Haber 494* not to *B. pendula* but to *B. costaricensis*, *Cabrera 5252* not to *B. sulcata* but to *B. latifolia*). According to this study, reproductive anatomical characters in *Beilschmiedia* are as follows.

Tapetum is glandular. Number of nuclei in tapetal cells is mostly two. Meiosis in a microspore mother cell is accompanied by successive cytokinesis. Mature pollen grains are two-celled at the time of shedding. Ovule is anatropous and crassinucellate. Archegonium is one-celled. As the ovule being matured, an elongating embryo sac destroys the nucellar tissue on the micropylar side and eventually protrudes from the nucellus. An endothelium is not formed except for *B. costaricensis* (referred as *B. pendula* in his study) where inner epidermal cells of the inner integument are radially elongated so that there appear to be an endothelium. Fertilization is porogamous. Endosperm formation is of Nuclear type. In fruits, pericarp structure is variable. Mesocarp is usually thick and clearly differentiated into the outer and the inner zones, containing sclerotic cells. Endocarp is palisadal (although two palaeotropical *Beilschmiedia* species have the endocarp non-palisadal).

Heo (1995) applied cladistic analyses of Lauraceae with 32 characters from floral and vegetative morphology, pericarp anatomy, embryology, palynology, and wood and bark anatomy. As a result, he recognized five robust clades, one of which included *Beilschmiedia*, *Caryodaphnopsis*, *Cryptocarya*, *Endiandra* and *Potameia*. This clade is supported by an apomorphy in embryology, which is, the mature embryo sac protruding from the nucellus. And all the genera of this clade but *Cryptocarya* share an apomorphy in pericarp anatomy, which is, the mesocarp differentiated into the outer and inner zones.

Palynology

Pollen morphology of *Beilschmiedia* has been studied by several researchers such as Cranwell (1942), Erdtman (1952), Heusser (1971), Macphail (1980), van der Merwe et al. (1988), and Raj & van der Werff (1988). Among these studies, Raj & van der Werff (1988) observed pollen of *B. miersii* and *B. pendula*, and compared them to pollen of the other neotropical Lauraceae genera. The following descriptions are based on their study.

According to Raj & van der Werff (1988), these species share the following pollen characters with the other neotropical Lauraceae genera; pollen grains are inaperturate and spheroidal, exine consists of an extremely thin layer with an ornamentation consisting of

spinules, exine is ectexinous, intine is a dominant layer of the pollen wall and uniformly thick, possibly equally suited for pollen tube egress.

But these species (and *Mezilaurus*) are different from the other genera in size of spinules and in surface of the basal cushions and exine. Size of the spinules is relatively large, 1-1.5 μm long. Surface of the basal cushions and exine is without granular processes.

Grain size of *B. miersii* is reported as the largest of all the species they studied. Density of spinules is reported as one of the lowest in their study.

Karyology

Among neotropical *Beilschmiedia* species, only *B. berteroana* has been reported in chromosome number. The chromosome number is $x = 12$ ($2n = 24$) (Raven 1975), which is common in the Lauraceae species. Polyploid numbers have not been found in *Beilschmiedia*.

Distribution

Beilschmiedia species distributed in the neotropical countries are listed in Table 1.

In the neotropics, *Beilschmiedia* ranges from central Mexico to southern Brazil and Chile. *Beilschmiedia* is absent from Amazon basin and northern Chile, therefore the distribution appears to consist of one large region from central Mexico to western Bolivia, and small regions in northern South America, south-eastern Brazil and central Chile (Fig. 6).

In north-western Latin America, distribution of *Beilschmiedia* ranges from central Mexico to western Bolivia (Fig. 6 A). The country with the highest number of species is Costa Rica, where eight species occur. Six of these species have also represent from Panama, and four of them are also distributed from Venezuela to Ecuador. On the other hand, only two of the Costarican species, *B. ovalis* and *B. pendula*, extend the distribution north of Costa Rica (to Honduras). *Beilschmiedia pendula* is the species with the widest distribution in neotropical *Beilschmiedia* species, which occurs from Honduras to Ecuador, including the West Indies. In Mexico there are six species present, four of which are endemic to Mexico. In the Guianas, there are two species distributed; *B. curviramea* is known from eastern Venezuela to Guyana (Fig. 6 B), and *B. hexanthera* is known only from French Guiana (Fig. 6 C).

Many species occur from premontane wet forests to cloud forests. 11 of 18 species grow in the range of 1000-1800 m alt., while six species are usually known below 500 m alt., and five species are known above 2000 m alt. Two of the last five species (known above 2000 m alt.) are variable species which occur in the range of 600-3000 m alt. (*B. costaricensis* and *B. towarensis*). The species known below 500 m are usually not distributed in the lowlands of the Amazon basin, but in the coastal regions like Osa Peninsula in Costa Rica, Esmeralda in Ecuador, Miranda in Venezuela, or some islands in the West Indies.

In the region of central Chile (Fig. 6 D), there are two *Beilschmiedia* species distributed (*B. berteriana* and *B. miersii*). Both of the species are restricted to the region.

Distribution of *Beilschmiedia* in south-eastern Brazil ranges from Espírito Santo to Parana (Fig. 6 E).

Concerning about endemic species, number of endemic species is high in Mexico and Brazil. Although number of the species is highest in Costa Rica, many species there also occur in South America along the Andes. High percentage of endemic species (100 %) is seen in south-eastern Brazil, the region is one of the centers of endemism in the neotropics (Prance 1982). High number of endemic species in Mexico might be because the collecting has not been intensive in the neighboring countries.

Reproductive biology and seed dispersal

All the neotropical *Beilschmiedia* species are bisexual. Some species of Lauraceae are observed to have a dichogamous outbreeding mechanism (Kubitzki & Kurz 1984), but thus far no report of this mechanism has been made for neotropical *Beilschmiedia* species. About flowering periods, Wheelwright (1985) reported that the Costarican species have very brief flowering periods (1-2 months usually).

Seeds of a few Costarican species are dispersed by birds, especially by *Pharomachrus mocinno* ("Resplendent Quetzal"), *Aulacorhynchus prasinus* ("Emerald Toucanet") and *Procnias tricarunculata* ("Three-wattled Bellbird") (Wheelwright et al. 1984). Fruiting periods of the Costarican species are relatively long (about three months) (Wheelwright 1985). Two interesting facts on their seed dispersal are reported, i.e., that the seeds remain in birds' digestive tracts for more than one hour while seeds of most of the other Lauraceae species remain there for a relatively short time (24-52 minutes) (Wheelwright 1995), and that fruit crops vary greatly from year to year (Wheelwright 1986).

Systematic position of the species in Lauraceae

As mentioned in the introduction, I treated the species studied here as *Beilschmiedia* Nees (1833). Mez (1889) recognized *Hufelandia* distinct from *Beilschmiedia* mainly by absence of an involucre (consisting of scales and subtending young inflorescences), but Kostermans (1938) regarded the involucre character unimportant and combined *Hufelandia* in *Beilschmiedia*. I thus far do not know if the involucre character is taxonomically important and if the species with involucre are distinct enough to be separated from the neotropical species. These questions should be answered after a careful study of palaeotropical *Beilschmiedia* species. In a preliminary observation of the palaeotropical species, the involucre character did not appear consistently and there were several species identified as *Beilschmiedia* apparently congeneric to the neotropical species.

Beilschmiedia had long been placed in the tribe Perseae Nees based on thyrsoid inflorescences without involucre. Kostermans (1957) regarded development or lack of cupules as an important character for the Lauraceae systematics, and placed *Beilschmiedia* closed to the genera such as *Endiandra*, *Mezilaurus*, *Potameia*, *Persea* and *Phoebe*. Hutchinson (1964) regarded number of anther cells as a more important character, and placed *Beilschmiedia* in the tribe Apollonieae Hutchinson with such genera as *Endiandra*, *Aniba*, *Mezilaurus*, *Licaria* and *Endlicheria*.

Richter (1981) published wood and bark anatomy of Lauraceae, in which he found three large groups of genera. He placed *Beilschmiedia* in a group with *Endiandra*, *Potameia*, *Triadodaphne*, *Cryptocarya* and *Ravensara* (see the section *wood anatomy*). *Cryptocarya* has the fruits completely enclosed by cupules and had been regarded a distantly related genus to *Beilschmiedia* by Kostermans (1957).

Van der Werff & Richter (1996) reviewed these classifications and concluded androecial characters such as number of anther cells were not suitable to use in a classification of Lauraceae. Instead they proposed a classification based on the inflorescence structure and the wood and bark anatomy. In their study *Beilschmiedia* was placed in the tribe Cryptocaryeae Nees, distinguished by several characters such as paniculate inflorescences with the ultimate divisions not strictly cymose, marginal parenchyma, non-septate fibers with conspicuously bordered pits, and exclusively simple vessel perforations in secondary xylem.

Although I did not make an intensive study for the systematic position of neotropical *Beilschmiedia* species in Lauraceae, my preliminary comparison of the Lauraceae genera indicated that the closest genus of *Beilschmiedia* in the neotropics might be *Cryptocarya*.

Relationships within neotropical *Beilschmiedia* species

Relationships within neotropical *Beilschmiedia* species is discussed with their leaf anatomy in the third chapter of this study. As the result of the study, they are divided into five groups mainly in their cuticular characters. See the third chapter for detail.

Systematic treatment

Beilschmiedia Nees in Wallich, Pl. Asiat. rar. 2: 61, 69. 1831. TYPE: *Beilschmiedia roxburghiana* Nees.

Hufelandia Nees, Plantarum Laurinarum Secundum Affinitates Naturales Expositio: 11. 1833. TYPE: *Hufelandia pendula* Nees.

Bellota Gay, Historia Fisica y Politica de Chile, Botanica 5: 297. 1849. TYPE: *Bellota miersii* Gay.

Trees or rarely shrubs. Leaves alternate or opposite, rarely clustered, pinnately veined. Inflorescences axillary, paniculate or racemose, terminal branches of the panicles not strictly cymose. Flowers bisexual; tepals 6, equal or subequal, usually deciduous; stamens 9 or 6 (the third whorl staminodial), filaments usually shorter than the anthers; anthers usually 2-locular, the first and second whorls introrse, the third whorl extrose to almost introrse, staminodia 3 in the fourth whorl or absent, or rarely 6 in the third and fourth whorls, the staminodia representing the third whorl columnar, the staminodia representing fourth whorl cordate to triangular in outline; ovary superior; receptacle flat to shallowly cup-shaped. Fruit ellipsoid, pyriform, or spherical, usually purple-black, free on a scarcely thickened pedicel.

Key to neotropical *Beilschmiedia* species.

- 1a. Leaves strictly opposite. Ramification on lower leaf surface coarse, smallest meshes (mesh is defined here as a delicate network of a minor venation) larger than 1.5 mm in diam.
 - 2a. Apex of anthers glabrous. From Central America or Chile.
 - 3a. Leaves roundish-ovate. Leaf apex rounded to retuse. From Chile.
 - 4a. Tepals glabrous outside. Indument on the terminal buds and twigs appressed or spreading, straight. *B. berteroana*.
 - 4b. Tepals pubescent outside. Indument on the terminal buds and twigs erect, curly to wavy. *B. miersii*.
 - 3b. Leaves elliptic. Leaf apex acute or acuminate. From Central America.
 - 5a. Secondary veins more than 14 pairs. Indument on the twigs erect, long and wavy. *B. angustieliptica*.
 - 5b. Secondary veins less than 13 pairs. Indument on the twigs appressed or spreading, or twigs glabrous.
 - 6a. Flower pedicels shorter than 1.5 mm long. *B. hondurensis*.
 - 6b. Flower pedicels longer than 3.0 mm long. *B. brenesii*.
 - 2b. Apex of anthers pubescent. From northern South America or Brazil.
 - 7a. Lower leaf surface pubescent with erect, long and straight hairs. Leaf base obtuse. *B. taubertiana*.
 - 7b. Lower leaf surface glabrous. Leaf base cuneate.
 - 8a. Indument on the terminal buds and twigs rusty, erect, very short and curly. *B. emarginata*.
 - 8b. Indument on the terminal buds and twigs not rusty, appressed, relatively long and straight.
 - 9a. Leaves obovate. Leaf apex round or roundish-obtuse.
 - 10a. Flowers longer than 3 mm, wider than 3 mm. Flowers globose. *B. rigida*.
 - 10b. Flowers shorter than 2.5 mm, narrower than 2.7 mm. Flowers depressed-globose. *B. linharesensis*.
 - 9b. Leaves elliptic. Leaf apex acute (rarely obtuse).
 - 11a. Leaf width less than 1/3 of the leaf length. *B. angustifolia*.
 - 11b. Leaf width more than 1/2 of the leaf length.

- 12a. Inflorescences racemose, more or less densely pubescent. *B. stricta*.
- 12b. Inflorescences paniculate, sparsely pubescent or almost glabrous.
- 13a. Leaf base slightly inrolled. From Brazil. *B. fluminensis*.
- 13b. Leaf base flat. From northern South America. *B. curviramea*.
- 1b. Leaves alternate, rarely sub-opposite. Ramification usually fine, smallest meshes smaller than 0.5 mm in diam. When ramification coarse, leaves still alternate and from Ecuador or Colombia (*B. costaricensis*).
- 14a. Fertile stamens 6. Staminodia 6. From French Guiana. *B. hexanthera*.
- 14b. Fertile stamens 9. Staminodia 3. From Central America, West Indies, or western South America.
- 15a. Indument of the terminal buds and twigs appressed or spreading (when indument spreading, ramification slightly less fine, meshes around 0.5 mm in diam., with free vein lets).
- 16a. Lower leaf surface glabrous on tissue or very rarely pubescent with spreading hairs only along the major veins (when pubescent, ramification square-like with free veinlets).
- 17a. Ramification with few free veinlets. From Mexico. *B. mexicana*
- 17b. Ramification with free veinlets. From Central America north to Nicaragua, West Indies, or South America.
- 18a. Ramification immersed above (although the pattern visible), almost immersed or slightly raised below. Lower leaf surface glaucous. Fruit pedicels constricted at the base. *B. pendula*.
- 18b. Ramification raised above, slightly to conspicuously raised below. Lower leaf surface not glaucous. Fruit pedicels not constricted at the base.
..... *B. costaricensis*.
- 16b. Lower leaf surface pubescent with appressed hairs on tissue. Ramification with few free veinlets.
- 19a. Ramification square-like. Ramification pattern always only partially visible above. Ramification pattern visible above much coarser than the ramification pattern below. *B. pendula*.
- 19b. Ramification finely areolate. Ramification pattern above completely invisible or slightly visible. When ramification pattern visible above, even the finest pattern visible. *B. towarensis*.

- 15b.** Indument on terminal buds and twigs erect.
- 20a.** Apex of anthers pubescent.
- 21a.** Petioles longer than 2.5 cm. Leaves longer than 18 cm, wider than 11 cm.
 *B. anay.*
- 21b.** Petioles shorter than 2 cm. Leaves shorter than 16.5 cm, narrower than 7.5 cm.
- 22a.** Secondary veins conspicuously raised below. Lower leaf surface not glaucous.
 From Mexico. *B. riparia.*
- 22b.** Secondary veins immersed below. Lower leaf surface glaucous. From Costa
 Rica. *B. immersinervis.*
- 20b.** Apex of anthers glabrous.
- 23a.** Leaves narrow elliptic, the width less than 4 cm and less than 1/2 of the length.
 From Guatemala. *B. steyermarkii.*
- 23b.** Leaves broad elliptic, ovate or obovate, the width more than 4 cm and more than
 1/2 of the length. From Mexico, Central America north to Honduras, or South
 America.
- 24a.** Lower leaf surface glabrous when old.
- 25a.** Leaves longer than 14 cm, wider than 7 cm. *B. alloiophylla.*
- 25b.** Leaves shorter than 13 cm, narrower than 7 cm, (or if wider than 7 cm, leaves
 ovate).
- 26a.** Leaves ovate. Secondary veins not strongly percurrent. Inflorescences relatively
 densely pubescent. Fruits spherical. *B. ovalis.*
- 26b.** Leaves obovate. Secondary veins strongly percurrent. Inflorescences glabrous
 or sparsely pubescent. Fruits ellipsoid. *B. obovatifolia.*
- 24b.** Lower leaf surface pubescent when old.
- 27a.** From Mexico. Fruits spherical. *B. ovalioides.*
- 27b.** From southern Central America (Costa Rica, Panama) or western South America
 (Venezuela, Colombia, Ecuador, Peru). Fruits ellipsoid.
- 28a.** Leaves ovate to broadly elliptic. Leaves shorter than 11 cm. Secondary veins
 less than 9 pairs. From higher than 2100 m alt. *B. latifolia.*
- 28b.** Leaves obovate (rarely broadly elliptic). Leaves longer than 14 cm. Secondary
 veins more than 9 pairs. From lower than 1300 m alt. *B. alloiophylla.*

1. *Beilschmiedia alloiophylla* (Rusby) Kostermans, Rec. Trav. Bot. Néerl. 35: 849.

1938. *Ocotea alloiophylla* Rusby, Descript. of three hundred new species of South American plants: 21. 1920. TYPE: Colombia. Santa Marta: mountain forest 5 miles SE of Don Amo, ca. 750 m alt., Mar. 7, 1898-1901 (young fl.), *H. H. Smith 2104* (holotype, NY not seen; isotypes, BM, K, MO, P).

Tree, to 35 m tall. Terminal buds densely pubescent with erect, short to long, straight to curly hairs. Twigs terete, sometimes sulcate or angular, sometimes corky, densely pubescent with erect, long to short, straight to curly hairs. Leaves clustered, rarely almost alternate; petioles (0.7) 1-3.5 (4.5) cm long, canaliculate to flat above, pubescent with erect, short to long, straight to wavy hairs, concolorous with twigs; blades firmly chartaceous, elliptic to obovate, 14-30 x (6) 7-13 (17) cm; base cuneate or obtuse, not inrolled, apex acute to acuminate; upper leaf surface glabrous (sometimes pubescence left mainly on midrib when young), lower leaf surface pubescent with erect to almost appressed, long to short, straight to curly hairs, or glabrous, rarely pubescent only on major veins, lower leaf surface glaucous; midrib and secondary veins slightly impressed or immersed above, raised below, secondary veins 9-16 (19) pairs, tertiary veins percurrent, ramification fine, more or less circle-like, usually without free veinlets, almost immersed (the pattern poorly visible) or slightly raised above, raised below. Inflorescences axillary, paniculate, (4) 8-25 cm long, pubescent with erect, wavy hairs, with (30) 60-250 or more flowers per inflorescence; flower pedicels of the lateral divisions 0.5-0.7 mm long, pedicels of the central flowers up to 2 mm long. Flowers green to creamy, ca. 2.2-3 mm long; tepals 6, equal, ovate to elliptic, 1.5-2.1 x 1-1.5 mm, elliptic to ovate, pubescent with erect, wavy hairs on both surfaces; stamens 9, filaments 0.4-0.5 mm long, pubescent, anthers 0.6-0.7 mm long, all the anthers 2-celled, apex of the anthers roundish to truncate, apex of anthers glabrous, glands of the innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.7 mm long; pistil 1-1.7 mm long, glabrous, ovary longer than and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, purple-black, 3.5-4.5 x 1.5-2.5 cm, the surface smooth; infructescence axis 2.5-3 mm in diam., slightly thickened to 4 mm in diam. near the fruit pedicel, fruit pedicels constricted at the base and remaining narrow (ca. 2.5 mm in diam.), or rarely not constricted, pedicels free from lenticels and darker than the infructescence axis or rarely covered with lenticels and concolorous with the axis.

Phenology: collected in flower from January to July, in mature fruit from September to May.
Distribution: Costa Rica, Panama, western part of Venezuela (Mérida), Colombia, and Ecuador, 35-1400 m alt. (Fig. 7).

Habitat: evergreen lowland forest, Premontane wet forest and montane wet forest.

Economic use: reported as useful wood in Ecuador.

Common name: "Jigua de aguacate" and "María aguacatillo" in Ecuador.

Additional specimens examined: **Costa Rica.** Alajuela: La Paz de Sn. Ramón, Oct. 30, 1973 (sterile), *Poveda 449* (CR). Cartago: Cartago Province, on slopes above Muñeco, 1550 m alt., Mar. 19, 1986 (fr.), *Almeda 5639* (MO); Moravia de Chirripó, Jan. 28, 1977 (fr.), *Poveda 1524* (CR); Muñeco de Cartago, 1000 m alt., Mar. 19, 1986 (fr.), *Zamora 1215* (CR, F, MO (2 sheets)). Guanacaste: Parque Nacional Guanacaste, Estación Pitilla. La Cruz, 10°59'26"N 85°25'40"W, 700-1000 m alt., Apr. 1, 1991 (fl.), *Morega 337* (INB, MO); same park, La Cruz, Santa Cecilia, Estación Pitilla Sendero Orosilito, to the top, 10°58'00"N 85°26'32"W, 900 m alt., May 26, 1990 (immature fr.), *Herrera 3934* (MO); same park, Liberia, Cacao station, 10°55'45"N 85°28'15"W, 1100 m alt., Dec. 17, 1990 (immature fr.), *Chávez 491* (MO). Heredia: Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, 100 m alt., Jul. 25, 1981 (fl.), *Hammel 11049* (MO, NY). Limón: SE region of Lago Dabagré, cross the road to Telire, Nov. 5, 1984 (fr.), *Gómez 23216* (CR), (immature fr.), *Gómez 23227* (CR, MO). Puntarenas: Cantón de Golfito, Corcovado National Park, Sendero Los Patos, 8°34'00"N 83°31'00"W, 200 m alt., Jun. 6, 1994 (young fl.), *Aguilar 3346* (INB, MO); same park, Sirena, Ollas trail, 8°28'N 83°35'W, 1-20 m alt., Sep. 12, 1989 (immature fr.), *Kernan 1269* (CR, MO); Cantón de Osa, Sierpe, Boca Ganado, Estribaciones de Fila ganad, 08°44'50"N 83°36'30"W, 350 m alt., Nov. 24, 1993 (immature fr.), *Herrera 6678* (CR, F, MO); Osa Península, Reserva Forestal Golfo Dulce, Rincón, Aguabuena, 8°42'N 83°31'W, 50 m alt., Sep. 15, 1992 (immature fr.), *Aguilar 1308* (INB, MO); same locality (S, road for Gerico), 50 m alt., Nov. 4, 1992 (immature fr.), *Aguilar 1404* (INB, MO); same reserve forest, ca. 6km NW of campo de aterrizaje de Golfito, 8°41'00"N 83°13'10"W, 100-200 m alt., Jan. 28, 1992 (fl.), *Hammel 18412* (CR, INB, MO); same reserve forest, Rancho Quemado, ca. 15km W of Rincón, 8°42'N 83°33'W, 250 m alt., Jun. 5, 1992 (fl.), *Hammel 18504* (INB, MO); same locality, 250 m alt., Jan. 12, 1993 (fr.), *Hammel 18716* (INB, MO); same locality, 250 m alt., Mar. 14, 1996 (sterile), *Yasuda 1316* (INB, MO); same locality, 8°41'10"N 83°33'20"W, 250 m alt., Nov. 1, 1992 (immature fr.), *Hammel 18575* (INB, MO); Monteverde zone, 1400 m alt., Apr. 13, 1981 (fl.), *Haber 458* (MO); same zone, community Pacific slope, 10°18'N 84°48'W, 1400 m alt., Feb. 27, 1989 (fr.), *Haber 9121* (INB, MO); same zone, Pacific slope, 10°18'N 84°48'W, 1300-1400 m alt., Apr. 5, 1990 (fl.), *Haber 9846* (INB, MO); same locality, 1400-1500 m alt., Jul. 10, 1988 (immature fr.), *Haber 8502* (INB, MO); same zone, Juntas, 10°18'30"N 84°48'30"W, ca. 1400 m alt., Mar. 9, 1996 (fl.), *Yasuda 1308* (INB, MO); Cantón de Golfito, Silvestre, 8°41'10"N 83°11'40"W, 200-300 m alt., Jan. 24, 1995 (fr.), *Martén 849* (MO). San José: Jericó de Deramparados, path to Llano Bonito, near the residual forest, 1750 m alt., Aug. 9, 1992 (immature fr.), *Morales 381* (CR); along Quebrada Tablazo and on

slope S of creek, NE slope of Altos Tablazo, 9°50'N 84°03', 1675-1900 m alt., Apr. 24, 1987 (immature fr.), *Grayum* 8263 (CR, R, MO). **Panama**. Bocas & Chiriquí: Cerro Colorado mine area; in elfin woods on divide road, along trail into Bocas and in woods on Pacific slope; from Chami station to ca. 9 miles along road, 8°35'N 81°54'W, 1100-1750 m alt., Mar. 27-31, 1986 (fr.), *Hammel* 14992 (MO). Darien: Río Pirre, Nov. 16, 1967 (fr.), *Bristan* 1472 (4) (MO). Panama: Cerro Jefe, along summit road and along trail into Chagres Valley, 9°15'N 79°30'W, 900 m alt., Feb. 19, 1988 (fl.), *McPherson* 12122 (MO). **Venezuela**. Merida: Sierra de Perijá, Misión Sabana, 1300 m alt., Mar. 22, 1959 (young fl.), *Bernardi* 7452 (K, NY). **Colombia**. El Valle: Cordillera Occidental, east slope, Río Sanquininí basin, left side, La Laguna, 1250-1400 m alt., Dec. 10-20, 1943, (fr.), *Cuatrecasas* 15619 (F). **Ecuador**. Azuay: Cantón Cuenca, Parroquia Molleturo, Manta Real, 02°34'S 79°23'W, 300-1200 m alt., Jul. 28, 1992 (immature fr.), *Berg* 46 (MO). El Oro: Road between Santa Rosa & Portovelo, Mar. 25, 1921 (immature fr.), *Popenoe* 1304 (US). Esmeraldas: Quininde, Bilsa Biological Station, Mache Mountains, 35km W of Quininde, 5km W of Santa Isabel, 0°21'N 79°44'W, 400-600 m alt., Nov. 14, 1994 (young fl.), *Clark* 248 (MO); same locality, 400-600 m alt., Nov. 21-27, 1995 (immature fr.), *Clark* 1695 (MO); same locality, 400-600 m alt., May. 6, 1996 (fl.), *Clark* 2541 (MO); same locality (third lot W of station following old road to Mono towards Pierdrita), 400-600 m alt., Apr. 8, 1995 (immature fr.), *Clark* 653 (MO); same locality (third lot W of station following old road to Mono towards Pierdrita), 400-600 m alt., May 5, 1995 (fr.), *Clark* 850 (MO); San Antonio, Río Cayapas, 66km NW of Quito, 35 m alt., Nov. 17, 1965 (young fl. & fr.), *Dixon* 21265 (NY, US). Guayas: Cordillera Chongon-Colonche, Loha Alta protected forest, 1°48'S 80°47'W, 600 m alt., Jul. 1995, (immature fr.), *Bonifaz* 3091 (MO). Los Rios: 56km of Quevedo-Santo Domingo, Río Palenque Biological Station, 150-220 m alt., Mar. 25, 1980 (sterile), *Dodson* 9906 (MO); 4km W of Los Angeles, 51km of Quevedo-Santo Domingo, property of Manuel Bravo, 200 m alt., Oct. 7, 1976 (sterile), *Dodson* 6489 (MO). Manabi: Parque Nacional Machalilla, Piñas to the hill Aviión Caído, among R. Piñas & R. Plátano & the hill, 01°35'S 80°41'W, 300 m alt., Sep. 13, 1991 (fr.), *Josse* 714 (MO); P.N. Machalilla, sector San Sebastián, 01°34'S 80°40'W, 520-550 m alt., Nov. 12, 1992 (immature fr.), *Josse* 843 (MO). Pichincha: Along road Nanegal-Palmitopamba, 1200 m alt., Jul. 9, 1991 (immature fr.), *van der Werff* 12256 (MO); same locality, 1200 m alt., Jul. 10, 1991 (fl.), *vanderWerff* 12289 (MO); Santo Domingo de Los Colorados, Via St. Domingo-Quinindé, 41km, La Perla Protected Forest, 00°01'N 79°22'W, 150 m alt., Feb. 24, 1992 (immature fr.), *Tipaz* 652 (MO).

Beilschmiedia alloiophylla has alternate leaves and fine ramification. This species is distinguished from the other species with alternate leaves and fine ramification by a combination of the following characters; erect pubescence on the terminal buds and twigs, large obovate leaves, glabrous anthers and ellipsoid fruits.

Beilschmiedia alloiophylla is a complex species with variable character states in indument. The collections, which I have recognized as this species, might be separated into five groups as follows by the indument structure and the amount of pubescence.

- Group 1. Species with straight to curly hairs on the terminal buds and twigs, and long straight hairs on tissue of the lower leaf surfaces. Many Ecuadorian collections, all the Colombian collections (including the type) and Venezuelan collections, and one Panamanian collection belong to this group. The elevation this group occurs is usually around 1200 m altitude, but there are a few collections from lower than 300 m altitude. Most of the collections in this group have relatively short (1-1.5 cm long) petioles, but one collection, *Dodson 6489*, has long (2.3-2.7 cm long) petioles like the fifth group.
- Group 2. Species with short, curly hairs on the terminal buds and twigs, and sparse, sericeous hairs or almost no hair on the lower leaf surfaces. This group has been collected mainly from relatively low elevation (150-600 m altitude) on the Pacific side of Ecuador, but there is no significant difference in distribution between this group and the first group. Neither is there any significant difference in reproductive characters between them. Length of the petioles is intermediate (1-2 cm long) between the third group and the fifth group.
- Group 3. Species with long straight hairs on the terminal buds, twigs and major veins of the lower leaf surfaces. The lower leaf surfaces of this group have dense pubescence only along the midribs and secondary veins. Only collection from Panama (900 m altitude), *McPherson 12122*, belongs to this group. This collection has rugose leaves, slightly shorter petioles (ca. 0.7 cm long), inflorescences with less flowers (30-40) than the other groups (60-300 or more).
- Group 4. Species with short curly hairs on the terminal buds and twigs, but almost no hair on the lower leaf surfaces (there are sometimes curly hairs on major veins when the leaves are young). This group has been collected from 700-1900 m altitude in Costa Rica and Panama (except for a collection, *Hammel 11049*, from ca. 100 m altitude in Costa Rica). Burger and van der Werff (1990) regarded them as a larger leaved variation of *B. ovalis*, but they can be separated from *B. ovalis* (differences are discussed under *B. ovalis*). Petioles of this group are intermediate in length (1-2.5 cm long) between the third group and the fifth group. Ramification of this group is usually more conspicuously visible (although not so raised) on upper leaf surfaces than in the other groups, but there are some collections even in the second and fifth groups which have more or less conspicuous ramification on upper leaf surfaces like this group.
- Group 5. Species with short curly hairs on the terminal bud, twigs and lower leaf surfaces (although the lower leaf surfaces are sparsely pubescent to almost glabrous). This group has been collected only at lower elevation (below 350 m altitude) in Osa Peninsula, Costa

Rica. This group appears to have relatively longer petioles (1.5-4 cm long) and the smaller flowers (ca. 2 mm long) than the other groups (2.5-3 mm long). A collection (*Kernan 1269*) is slightly different from the other collections of this group, by having a straighter indument on the major veins of the lower leaf surfaces.

Although differences between the groups of *B. alloiophylla* seem strong enough to warrant taxonomic recognition, I decided not to do so for the following reasons. Firstly, a number of collections are, in their indument characters, intermediates between the groups. Secondly, the number of flowering collections is very low (one for each of the first three groups, a few for the latter two groups). Thus, until additional collections show other differences between the groups, I will maintain *B. alloiophylla* as a rather variable species.

2. *Beilschmiedia anay* (Blake) Kostermans, Rec. Trav. Bot. Néerl. 35: 847. 1938.

Hufelandia anay Blake, J. Wash. Acad. Sci. 9: 459. 1919. TYPE: Guatemala.

Suchitepéquez: Mazatenango, Finca Compromiso, ca. 420 m alt., Jan. 17, 1917 (fr., immature), *Popenoe 754* (holotype, US (herb. no. 1011734); isotype, US).

Tree, to 40 m tall. Twigs terete to sulcate, densely pubescent with erect, curly to wavy or rarely almost straight hairs, rarely not so densely, rarely glabrescent with age. Leaves alternate, rather clustered around the terminal buds; petioles 2.5-4 cm long, canaliculate to flat above, pubescent with erect, wavy or almost straight hairs, concolorous with twigs; blades chartaceous, broadly elliptic to ovate, (14) 18-28 x 11-15 cm; base obtuse to round, rarely cuneate, not inrolled, apex acute, rarely cuspidate; upper leaf surface glabrous, or sometimes pubescent with wavy hairs along the midrib, lower leaf surface pubescent with erect, short curly hairs or long wavy hairs, especially densely pubescent along the midrib and secondary veins, lower leaf surface often glaucous; midrib and secondary veins immersed or slightly impressed above, raised below, secondary veins 12-17 pairs, tertiary veins percurrent, ramification immersed above (the pattern partially visible), slightly raised or almost immersed below (the pattern visible), ramification fine, circle-like without free veinlets, the ramification pattern visible on upper leaf surface much coarser than on lower leaf surface. Inflorescences axillary, sometimes in axils of the leaves near the terminal buds, paniculate, 5-10 cm long, pubescent with erect, curly to wavy hairs, with 30-70 flowers per inflorescence; flower pedicels of the lateral divisions 0.5-1 mm long, pedicels of the central flowers up to 4 mm long. Flowers yellowish, 2.5-3.2 mm long, 2.8-3.5 mm in diam.;

tepals 6, equal, elliptic, ca. 2 mm long, 1-1.6 mm wide, more or less densely pubescent with erect, wavy hairs on both sides; stamens 9, outer six filaments ca. 0.4 mm long, innermost three filaments 0.4-0.7 mm long, filaments pubescent, anthers 0.8-1 mm long, all the anthers 2-celled, apex of the anthers roundish to truncate, apex of anthers pubescent, glands of the innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.6-0.8 mm long; pistil 1.3-1.6 mm long, glabrous, ovary as long as or longer than and gradually narrowed into the style; receptacle pubescent with more or less appressed hairs. Fruits ellipsoid to pyriform, deep purple to black, to ca. 1.5 cm long (fide Blake, 1919), the surface smooth; fruit pedicels unknown.

Phenology: collected in flower in April and May, no mature fruit (except for a detached fruit) collected.

Distribution: Mexico, Guatemala, 200- 920 m alt. (Fig. 7).

Habitat: montane mesophyll forest and deciduous forest, on loamy, clayish soil or limestone.

Common name: "Anay", "Keb(?)chii" in Guatemala; "Anaya negra " (Spanish), "Jani'ya" (Totonac) in Mexico.

Economic use: unknown. Reported the fruits to be edible.

Additional specimens examined: **Mexico.** Puebla: Municipio Xochitlán de Vicente Suárez, 19°58'N 97°44'W, 850 m alt., Nov. 22, 1987 (detached fr.), *Pennington*9645 (MEXU); Municipio Zapotitlán de Méndez, along the road to Xochitlán de Vicente Suárez in Zapotitlán, ca. 2.5 km from the town, 20°03'N 97°45'W, ca. 590 m alt., Apr. 18, 1987 (young fl.), *Villalobos* 139 (MEXU), 244 (MEXU). Veracruz: Municipio Tenochtitlan, Colorado, dirt road between Misantla and Tenochtitlan, 920 m alt., Apr. 27, 1976 (fl.), *Pennington* 9265 (F, MO); Misantla, May 6, 1961 (fl.), *Popenoe* 884 (MEXU); Misantla, May 6, 1961 (fl.), *Brigada Dioscoreas* 279 (NY); Carretera Martínez de la Torre -- Misantla, ca. 20km from Martínez de la Torre, 200 m alt., May 20, 1968 (fl.), *Brigada Dioscoreas* 392 (A, K, NY); between Maratinez de la Terre & Misantla, 100 m alt., Oct. 21, 1967 (sterile), *Hernandez* 174 (NY). **Guatemala.** Alta Verapaz: Chamá, ca. 270 m alt., May 6, 1920 (fl.), *Johnson* 170 (F, MO, U, US); Chamá, ca. 270 m alt., Dec. 30, 1919 (sterile), *Villalobos* 138 (US). Escuintla: Río Guacalate, 600 m alt., Dec. 16, 1938 (young fl.), *Standley*60223 (F). Cultivated: Nov. 12, 1947 (sterile), *Popenoe* sn. (1189?) (MEXU).

Kostermans (1938) reported *Beilschmiedia anay* from Guatemala, Costa Rica and Colombia. But he was not sure if the Costarican specimens he cited really belonged to *B.*

anay, and he stated that the Colombian specimen he cited had almost glabrous leaves, which is atypical for *B. anay*. I have not seen those specimens he cited, nor any specimen of *B. anay* from Costa Rica or Colombia. The specimens I recognize as *B. anay* are all from Guatemala and Mexico.

Vegetatively, *Beilschmiedia anay* appears to be similar to *B. alloiophylla*. But in flower, *B. anay* differs from *B. alloiophylla* by its pubescent anthers. Additionally, *B. anay* is reported to have pyriform fruits (Blake 1919), which are quite different from both the ellipsoid fruits of *B. alloiophylla* and the elliptic or roundish fruits of most Neotropical *Beilschmiedia* species. However, I have not seen good fruiting collections of *B. anay*, but only collections with very young or detached fruits. This characteristic for the species should be confirmed through the collections of more and better material.

Indument of the type of *B. anay* is curly, as seen in many collections. But there are a few collections which show less curly to almost straight hairs (*Popenoe 884, Brigada Dioscoreas 279, Brigada Dioscoreas 392* and *Hernandez 174*). Indument of these collections is erect, not appressed, so difference of the indument among them is only straightness of the indument. Since these collections share all the other characters of *B. anay* with curly hairs, straightness of the indument might be variable within the species.

Two collections from Mexico (*Méndez 8233* and *Davidse 29885*) approach *B. anay* in the leaf shape and ramification pattern, but they have glabrous lower leaf surfaces. Additionally, one of these collections (*Méndez 8233*) has glabrous anthers, and another collection (*Davidse 29885*) has a spherical fruit, both of which are atypical for *B. anay*. For the time being, these two collections are classified as indeterminate because more material is needed for their determination.

There are also three collections I have classified as indeterminate although they appear to belong in *B. anay*. They share similar pubescence type and leaf shape with *B. anay*, but show different ramification on the upper leaf surfaces from the typical collections of this species. Usually, *B. anay* has ramification which is only partially visible on the upper leaf surfaces and looks much coarser than the ramification on the lower leaf surfaces. However, the three collections (*Miranda 7793, Reyes 1443* and *1571*) have conspicuously fine areolate ramification even on the upper leaf surfaces. Although ramification on upper leaf surfaces may vary with age or habitat of the plants, the ramification of the three collections are still very different from that of the typical *B. anay*. Since two of the collection are sterile and the other is with only detached fruits, more material is needed for their classification.

3. *Beilschmiedia angustieliptica* Lorea-Hernández, Novon 5: 47. 1995. TYPE:

Mexico. Guerrero: Municipio Atoyac de Alvarez, ca. 2 km S to El Molote, on the trail to El Edén, 1580 m alt., May 19, 1993 (fl. & fr.), Lorea & Lozada 5540 (holotype, FCME not seen; isotype, MO).

Tree, to 7-8 m tall. Terminal buds pubescent with yellowish brown to reddish brown, erect wavy hairs. Twigs terete, compressed when young, densely pubescent with erect, long wavy hairs, less densely to glabrescent when older. Leaves opposite, rarely subopposite; petioles (0.7) 1.1-1.7 mm, flat or slightly canaliculate above, pubescent with erect wavy hairs, soon glabrous, concolorous with twigs or slightly discolored with twigs; blades firmly chartaceous, narrowly elliptic, margin sometimes slightly undulate, (7) 12-20 (24) x (2) 2.5-5 (6) cm, base cuneate, not inrolled, apex acute; leaf surface glabrous on both sides, lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins (13) 14-22 pairs, slightly raised above, raised below, tertiary veins not percurrent, ramification coarse, square-like with free veinlets, slightly raised above, raised below. Inflorescences axillary, paniculate, 2.5-6 (10) cm, pubescent with erect hairs, with 30-60 flowers per inflorescence; flower pedicels of the lateral divisions 1.2-2 mm long, pedicels of the central flowers up to 2.7 mm long. Flowers 2-2.7 mm long, ca. 2.5 mm in diam; tepals 6, equal, ovate, 1.3-1.7 mm long, 0.9-1.3 mm wide, outside pubescent with erect hairs, inside sparsely pubescent with appressed to erect hairs; stamens 9, outer six filaments ca. 0.4 mm, innermost three filaments ca. 0.5 mm long, filaments sparsely pubescent, outer six anthers 0.6-0.8 mm long, innermost three anthers ca. 0.5 mm long, all the anthers 2-celled, apex of the outer six anthers roundish to acute, apex of the innermost three anthers truncate, apex of all the anthers glabrous, glands of the innermost three stamens globose; staminodia 3, cordate in outline, 0.4-0.6 mm long; pistil ca. 1.2 mm long, glabrous or slightly pubescent, ovary slightly longer than and gradually narrowed into the style or sometimes the border between ovary and style conspicuous; receptacle pubescent with more or less erect hairs, less densely toward the bottom. Fruits ellipsoid, black, 2.5-3.5 x 1.5-1.7 cm, the surface smooth; infructescence axis 1.5-2 mm in diam., slightly thickened to 3 mm in diam. near the fruit pedicel, fruit pedicels constricted at the base, free from lenticels and darker than the infructescence axis.

Phenology: collected in flower in May, in mature fruit in April and May.

Distribution: Guerrero, Mexico, collected between 1360 m and 1630 m alt. (Fig. 7).

Habitat: mesophyllous montane forest

Common name: unknown.

Economic use: unknown.

Additional specimens examined: **Mexico.** Guerrero: Municipio Atoyac de Alvarez, El. Molote, in the garden of Margarita Valladares, 1630 m alt., Apr. 15, 1984 (fr.), *Núñez 1159* (MO); Municipio Tecpan, 16 km from path between El Porvenir and San Antonio de Las Tejas, 1360 m alt., May. 31, 1983 (fl.), *Lozano 227* (MO).

Beilschmiedia angustielliptica has opposite leaves and coarse ramification. This species is distinguished from the other species with opposite leaves and coarse ramification by a combination of the following characters; erect pubescence on the terminal buds and twigs, narrowly elliptic leaves with secondary veins more than 14 pairs and glabrous anthers. Lorea-Hernández (1995) adds pubescence of the ovaries as a distinctive character, but I have observed that some ovaries of this species are glabrous, or so sparsely pubescent that one can easily miss the pubescence.

4. *Beilschmiedia angustifolia* Kostermans, Rec. Trav. Bot. Néerl. 35: 857. 1938.

TYPE: Brazil. Rio de Janeiro: Ad cataractam Vargem, Theresopolis, Serra dos Orgãos, Feb. 2, 1838 (fr.), *Miers s.n.* (holotype, BM).

Tree, to 10 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, compressed when young, sparsely pubescent with appressed straight hairs or almost glabrous. Leaves opposite; petioles 0.7-1.3 (1.8) cm long, flat above, glabrous, concolorous with twigs; blades firmly chartaceous, narrowly elliptic, 7-14 x 1.5-3 (4) cm, usually the width less than 1/4 of the length, base acute, slightly inrolled toward the lower surface, apex acute; leaf surface glabrous on both sides, unknown whether lower leaf surface glaucous or not; midrib immersed above, raised or almost immersed below, secondary veins 9-14 pairs, slightly raised or almost immersed on both sides, tertiary veins not percurrent, ramification coarse, square-like with free veinlets, slightly raised or almost immersed on both sides. Inflorescences axillary, paniculate with few branches, 2-3.5 cm long, sparsely pubescent with appressed to erect hairs, with 10-15 flowers per inflorescence;

flower pedicels of the lateral divisions ca. 1 mm long, pedicels of the central flowers up to 3 mm long. Flowers ca. 2.5 mm long, ca. 2.7 mm in diam.; tepals 6, equal, ovate, 1.3-1.7 mm long, ca. 1.3 mm wide, pubescent with appressed to erect hairs outside, sparsely pubescent with appressed hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.4 mm long, filaments pubescent, anthers 0.6-0.8 mm long, all the anthers 2-celled, apex of the anthers roundish to truncate, apex of the anthers pubescent, glands on the innermost three stamens globose, ca. 0.4 mm long; staminodia 3, cordate in outline, ca. 0.5 mm long; pistil ca. 1.8 mm long, pubescent, ovary as long as the style, the border between ovary and style more or less clear; receptacle pubescent with appressed hairs, less densely toward the bottom. Fruits roundish-ellipsoid, ca. 3 x ca. 2.7 cm, the surface smooth; infructescence axis ca. 3 mm in diam., fruit pedicels slightly thickened to 4-7 mm in diam. below the fruit, fruit pedicels not constricted, concolorous with the infructescence axis.

Phenology: collected in flower in October and November, in mature fruit in February.

Distribution: Rio de Janeiro and Guanabara, Brazil (Fig. 7).

Habitat: unknown.

Common name: unknown.

Economic use: unknown.

Additional specimens examined: **Brazil**. Rio de Janeiro: Vista Chinesa, Oct. 13, 1925 (fl.), *Constantino 19914* (RB); Guanabara, forest of Teixeira Borges, Hill Borges, 7°07'S 36°35'W, Nov. 29, 1928 (fl.), *Pessoal do H Florestal 87* (F, NY); Município Magé, Paraiso, Area of Centro de Primatologia de Rio de Janeiro, 190 m alt., Oct. 14, 1984 (fr.), *deLima 2177* (K, NY, RB (fr. missing)). Locality unknown, 1880 (immature fr.), *Binot 81* (NY, P).

Beilschmiedia angustifolia has opposite leaves and coarse ramification, as all the Brazilian species do. Among the Brazilian species, this species is distinguished by its narrow elliptic leaves. Width of the leaves in *B. angustifolia* is usually 1/4, at most 1/3 of the length, while width of the leaves in most of the other species is usually about a half of the length or more (*B. taubertiana* also tends to have narrow leaves, but not narrower than 1/3 of the leaf length, and erect pubescence of the terminal buds, twigs and the lower leaf surface distinguish this species from *B. angustifolia*). However, leaf shape cannot be the best character to define species because it is sometimes variable. In addition to this character, *B.*

angustifolia has pubescent pistils, which is characteristic only for this species and *B. rigida* in Brazil. But I must admit that pubescence on pistils sometimes varies in a species (see notes under *B. angustielliptica* and *B. towarensis*). Since I have only two collections with flowers in this species, I cannot be sure if this characteristic is consistent in *B. angustifolia*. Given that this characteristic is consistent in *B. angustifolia*, one can distinguish *B. angustifolia* from *B. rigida* by its smaller leaves, acute leaf apex and shorter petioles. Additionally, *B. angustifolia* differs from *B. rigida* by its somewhat thinner inflorescence rachises.

5. *Beilschmiedia berteriana* (Gay) Kostermans, Rec. Trav. Bot. Néerl. 35: 858. 1938. *Cryptocarya berteriana* Gay, Historia de Chile, Botanica 5: 301. 1849. TYPE: Chile.: Montibus La Leona, (fl. & immature? fr.), Nov. 1829, *Bertero s.n.* (lectotype designated by Kostermans, P; lectoisotypes, G-DEL not seen, P, GH not seen, W not seen).

Bellota nitida R. A. Philippi, Linnaea 29: 39. 1857-1858. *Boldu nitidum* (R. A. Philippi) Meissner, DC. Prodr. 15: 506. 1964. TYPE: Chili. Depart. Linares: in the Andes, (fr.), *Germain s.n.* (holotype, herbarium not known).

Cryptocarya nitida R. A. Philippi, Linnaea 33: 228. 1864-1865. TYPE: Chile. Santiago: at the foot of the Andes, Nov. 1862 (fl.), *anonymous* (W not seen).

Bellota pauciflora Philippi, Anales Univ. Chile 26: 649. 1865. TYPE: Chile. locality and collected date unknown, (fl.), *Germain. s.n.* (SGO not seen).

Tree, the height unknown. Terminal buds pubescent with appressed to spreading, straight hairs. Twigs terete, slightly compressed when young, densely or rarely sparsely pubescent with appressed to slightly spreading, short straight hairs, less densely when older. Leaves opposite; petioles 0.2-0.5 (0.8) cm long, flat to slightly canaliculate above, pubescent with appressed hairs, concolorous with twigs; blades coriaceous, dried to light green, roundish-ovate, 3-6 x 2-4 cm; base round, not inrolled, apex obtuse to retuse; leaf surface glabrous on both sides, lower leaf surface glaucous; midrib immersed above, slightly raised below, secondary veins 3-7 (9) pairs, almost immersed or slightly raised

above, slightly raised below, tertiary veins not percurrent, ramification very coarse with free veinlets, almost immersed or slightly raised on both sides. Inflorescences axillary, sometimes on a short branchlet (with or without leaves), racemose, rarely paniculate, 0.5-2 cm long, pubescent with erect hairs, rarely only sparsely pubescent, with 3-10 flowers per inflorescence; flower pedicels of the lateral divisions 0.5-1 mm long, pedicels of the central flowers up to 2 (rarely 3) mm long. Flowers 2.5-3 mm long, 3-3.7 mm in diam.; tepals 6, equal, almost round, 1.5-2 mm long, 1.3-1.8 mm wide, glabrous outside, pubescent sparsely to densely with almost appressed hairs at the base inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, anthers 0.7-1 mm long, 2-celled, apex of the anthers obtuse to truncate, apex of anthers glabrous, glands of innermost three stamens globose, 0.3- 0.5 mm long; staminodia 3, cordate in outline, ca. 0.6 mm long; pistil ca. 1.9 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs. Mature fruits unknown.

Phenology: collected in flowers in November and May.

Distribution: Chile (Fig. 8).

Habitat: unknown.

Common name: "Ulmo".

Economic use: unknown.

Additional specimens examined: **Chile**. Colchagua: Cauquenef, etc., (young fl.), *Gay s.n.* (P); San Fernando, (fl. & young fr.), *Gay s.n.* (P). Concepcion: locality unknown, 1855 (fl.), *Germain s.n.* (BM, F, K). Limachi: locality unknown, Oct.-Nov. (immature fr.), *Bertero 760* (BM). Linares: Cordillera de Linares, 1861? (fl.), *Philippi 906* (K). Valparaiso: Mt. la Leona, 1836 (old fl.), *Bertero 4* (BM). cultivated from Chile: Berkeley Botanical Garden, Mar. 20, 1973 (young fl.), *Goldblatt 1231* (MO); U.C. Bot. Garden (which were grown from seed provided by Dr. Carlos Munoz), May. 4, 1973 (fl.), *anonymous (accession no. 55354)* (MO, NY).

Kostermans (1938) recognized one of Bertero's collections in P as the lectotype of this species and stated, "Though Gay (Flora Chilena V, page 301) indicated no type specimen of his *Cryptocarya berteriana* it is evident, that he described the specimens collected by Bertero (n. 4), as he cites the vernacular name: Ulmo and the name: *Adenostemum nitidum* Bertero, both names figuring on the labels of these specimens". I agree with Kostermans's designation, but I suspect that the collection is not *Bertero 4* as he mentioned but *Bertero s.n.*

The specimen with a label saying “*Bertero 4*” is not in P but in BM, and the label of that specimen in BM does not have the vernacular name nor the name *Adenostemum nitidum*. On the other hand, a specimen with Bertero’s label in P has both of these names on its label but without the number “4”. Instead, the label of the specimen in P has a symbol which appears to be “4” at first glance but is actually a planetary symbol meaning “perennial”. I suspect that Kostermans misread the planetary symbol as the number “4”, and since the collection in BM and the collection in P appear to be taken from different trees, I would like to make it clear that the lectotype of this species is not “*Bertero 4*” as present in BM but “*Bertero s.n.*” in P.

I have not seen the types of *Bellota nitida*, *Cryptocarya nitida*, and *Bellota pauciflora*. But considering the descriptions of these species, it is clear that these species are conspecific with *Beilschmiedia berteriana*.

Beilschmiedia berteriana is one of the two species from Chile, with *B. miersii* being the second. These two Chilean species are quite unique among neotropical *Beilschmiedia* species by their opposite, roundish-ovate leaves drying to light green and very coarse ramification. The Chilean species themselves are very similar to one other at first glance, especially in the leaf shape and ramification pattern. But *B. berteriana* has appressed or spreading, straight pubescence on the terminal buds and twigs, and has tepals glabrous outside, while *B. miersii* has erect, curly pubescence on the same region and has tepals densely pubescent outside.

In mature flowers the tepals, which are united at their base, fall off together with the attached stamens and staminodia. Kostermans (1938) considered this characteristic for *B. berteriana*. However, tepals and stamens fall off in a similar way in most, if not all, neotropical *Beilschmiedia* species (see the note on *B. miersii*).

6. *Beilschmiedia brenesii* C. K. Allen, J. Arnold Arbor. 26: 415. 1945. TYPE: Costa Rica. Alajuela: La Palma and El Socorro de San Ramón, July 24, 1928 (fr.), *Brenes 6214* (holotype: F; isotype: NY).

Tree, to 20 (35) m tall. Terminal buds pubescent with spreading or appressed, straight hairs, rarely almost glabrous. Twigs terete, compressed when young, glabrous, rarely pubescent with spreading straight hairs. Leaves opposite, relatively clustered near the terminal buds; petioles 0.5-0.8 cm long, flat or canaliculate, slightly thickened at the base, glabrous, concolorous with twigs; blades coriaceous, elliptic, (4) 6-9 (12) x (1.7) 2.7-4.2 (6) cm; base cuneate, not inrolled, apex acute, rarely obtuse; leaf surface glabrous on both

sides, lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins (7) 8-13 pairs, slightly or conspicuously raised above, raised below, tertiary veins not percurrent, ramification coarse, square-like with free veinlets, slightly raised or almost immersed above, slightly or conspicuously raised below. Inflorescences usually clustered around terminal buds or on short leafless shoots, rarely axillary, paniculate, 3-9 cm long, sparsely pubescent with erect hairs to glabrous, with 20-50 flowers per inflorescence; flower pedicels of the lateral divisions (1.5) 3-5 mm long, pedicels of the central flowers up to 7 mm long. Flowers greenish-yellow to creamy, 2.5-4 mm long, 2.6-3.2 mm in diam.; tepals 6, equal, ovate, 1.3-2.2 mm long, 1-1.5 (1.8) mm wide, almost glabrous or sparsely pubescent with more or less appressed hairs outside, sparsely pubescent with appressed to erect (wavy) hairs inside; stamens 9, outer six filaments 0.4-0.6 mm long, innermost three stamens 0.5-0.8 mm long, filaments pubescent, anthers 0.7-1.1 mm long, all the anthers 2-celled, apex of the anthers obtuse to acute, apex of the anthers glabrous, glands of innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.8 mm long; pistil ca. 1.8 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed or rarely erect hairs, less densely toward the bottom. Fruits ellipsoid, black-purple, ca. 3.3 x ca. 1.8 cm, the surface smooth; infructescence axis 2.5-3 mm in diam., fruit pedicels thickened to 5 mm in diam. below the fruit, fruit pedicels not constricted, without lenticels and darker than the infructescence axis.

Phenology: collected in flower from December to February, in mature fruit in all months except for January and April.

Distribution: Costa Rica (Guanacaste and Puntarenas), Panama, 700-1800 m alt. (Fig. 8).

Habitat: lower montane wet forest.

Common name: "Chanco blanco", "Chanco colorado", "Chanco rosado" in Costa Rica.

Economic use: unknown.

Additional specimens examined: **Costa Rica**. Alajuela: Canton Alfaro Ruiz, 1700 m alt., May. 10, 1941 (sterile), *A. Smith 2717* (F); Reserva Forestal San Ramón, Campamento Río San Lorencito, 10°13'N 84°37'W, 900-1100 m alt., Feb. 17, 1989 (fl.), *Gómez 11772* (FM). Guanacaste: Cantón de Liberia, Parque Nacional Guanacaste, Estación Cacao, 10°55'45"N 85°28'15"W, 1100 m alt., Oct. 3, 1990 (fr.), *Chávez 216* (CR, INB, MO); same locality, 1100 m alt., Nov. 2, 1990 (immature fr.), *Chávez 333* (INB, MO); same locality, 1100 m alt., Apr. 11, 1991 (immature fr.), *Chávez 545* (CR, INB, MO); same locality, 1100 m alt., Jul. 14, 1991 (immature fr.), *Chávez 563* (CR, MO); same locality, 10°55'45"N 85°29'15"W, 1100 m alt., Nov.

23, 1990 (fr.), *Estinoza 45* (CR, INB); same estación, Maritza path, 10°55'43"N 85°28'10"W, 1100 m alt., Feb. 11, 1995 (fl.), *Gamboa 84* (INB); same estación, Cerro Cacao, path to Fran's house, 10°55'43"N 85°28'10"W, 1100 m alt., Feb. 8, 1995 (fr.), *Mora 36* (INB, MO); same park, Estación Las Pailas, path to the volcano, 10°47'50"N 85°21'10"W, 1300 m alt., Sep. 3, 1994 (immature fr.), *García 362* (MO); same park, Estación Mengo, Volcán Cacao, 10°55'N 85°28'W, 1100 m alt., Jul. 17, 1989 (fr.), *anonymous.(INB227)* (CR, F, MO); Cantón de Liberia, Parque Nacional Rincón de la Vieja, Liberia, Range of Guanacaste, Estación Las Pailas, 10°46'40"N 85°21'10"W, 800 m alt., Nov. 8 (immature fr.), *Espinoza 669* (INB, MO); same locality, 10°47'50"N 85°21'10"W, 1300 m alt., Sep. 3, 1994 (fr. immaturred), *García 362* (INB); same park, on the way from Santa Maria to a view point, heading NW, 10°46'N 85°18'W, 1000 m alt., Feb. 28, 1988 (immature fr.), *Herrera 1559* (F, MO); same park, Santa Maria, 10°46'N 85°18'W, 900-1000 m alt., Mar. 4, 1988 (immature fr.), *Herrera 1593* (F, MO, NY); same park, 10°46'05"N 85°17'40"W, Sep. 17, 1990 (immature fr.), *Rivera 612* (CR, MO). Puntarenas: Reserva Biológica Monteverde, Río Veracruz, 10°16'N 84°22'W, 1300 m alt., May. 4, 1991 (fr.), *Bello 2779* (INB, MO); same reserve, Vertiente Pacífica, 10°18'N 84°48'W, 1300-1400 m alt., Jun. 8, 1988 (immature fr.), *Bello 434* (CR, F, MO); same reserve, Altos de Lindora Vertiente Pacífica., 10°18'N 84°50'W, 1300 m alt., Dec. 7, 1988 (fl.), *Bello 580* (INB, MO); same reserve, Río San Luis, a way behind the Estación, Quebrada Cambronero, 10°16'35"N 84°47'45"W, 1060 m alt., Dec. 18, 1992 (fr.), *Fernández 449* (CR, INB); same reserve, vicinity of Pension Quetzal, 10°47'N 84°50'W, 1450 m alt., Aug. 20, 1984 (immature fr.), *Gentry 84-3 48711* (CR, F, MO, NY); same reserve, Cordillera de Tilarán, San Luis, Finca Buen Amigo, 10°16'33"N 84°47'45"W, 1040 m alt., Sep. 1, 1993 (fr. immaturred), *Fuentes 466* (INB, MO); same reserve, Santa Elena, farm of Ricardo Arce, 500 m N from la Escuela, 10°19'N 84°50'W, 1300 m alt., Aug. 10, 1991 (fr.), *Guindon 9* (INB, MO), *10* (INB, MO), *14* (INB, MO); same locality, 1200 m alt., Feb. 11, 1992 (fl.), *Guindon 43* (INB, MO); same reserve, Santa Elena, Los Llanos, Zona Monteverde, 10°18'N 84°49'W, 1150 m alt., Dec. 13, 1991 (young fl.), *Guindon 35* (MO); same reserve, 6 km south of Santa Elena on a road to a highway, Los Cerros, ridge between Río Guacimal and Río Lagarto, 10°17'N 84°49'W, 900-1080 m alt., Jul. 19, 1991 (fr.), *Haber 10749* (F, INB, MO); same reserve, canyon of Río Guacimal, 3 km S of San Luis village, 7 km S of Monteverde, junction of Río Guacimal wit, 10°15'00"N 84°50'00"W, 520-700 m alt., Jul. 8, 1993 (fr.), *Haber 11538* (INB, MO); same reserve, from Santa Elena to San Luis, 10°16'N 84°50'W, 700 m alt., Jun. 16, 1988 (fr.), *Hammel 17042* (CR, MO); same reserve, Guacimal river valley below Monteverde on Pacific slope, 10°20'N, 84°50'W, 1000 m alt., Jan 17, 1986 (fl.), *Haber 4301* (CR, MO), *4322* (CR, F, MO); same valley, below La Lindora, 10°18'N 84°48'W, 1000 m alt., Feb. 19, 1988 (fl.), *Haber 8264* (BM, F, NY, MO), (fr.), *Haber 8282* (INB, MO); same locality, 1350 m alt., Jun. 9, 1988 (fr.), *Haber 8434* (MO); same reserve, Río San Luis valley on Pacific slope, 1000 m alt., Feb. 26, 1985 (fr.), *Haber 1424* (MO); same locality, 10°20'N 84°50'W, 1200 m alt., Dec. 30, 1985 (immature fr.), *Haber 4118* (CR, F, MO, NY); same locality, 1000 m alt., May. 9, 1986 (fr.), *Haber 4974* (CR, MO), *5012* (MO); same locality, 10°17'N 84°48'W, 900 m alt., Jun. 12, 1987 (fr.), *Haber 7216* (F, MO); same locality, 900-1000 m alt., Jul. 14, 1988 (fr.), *Haber 8511* (F, MO); same reserve, 1350 m alt., Jan. 12, 1979 (fl.), *Haber 266* (MO); same reserve, 1550 m alt., Sept. 25, 1985 (fr.), *Haber 2800* (F, MO); same reserve, 10°30'N 85°10'W, 1400 m alt., Jul. 1, 1980 (sterile), *Wheelwright 52* (MO), Jul.,

1980 (detached fr.), *Wheelwright 55* (MO); same reserve, 1400 m alt., Jul. 2, 1980 (immature fr.), *Wheelwright 70* (F, MO); same reserve, 1430 m alt., Feb 2, 1987 (fl.), *Zamora 1321* (F, K, MO); Cantón de Puntarenas, path to La Catarata from Río Sendero Miguel Leitón, 10°16'20"N 84°49'30"W, 1100 m alt., Mar. 11, 1993 (fr.), *Fuentes 251* (INB, MO); Cantón de Buenos Aires, Ujarrás Sabanas Murur Bisuk, towns of Río Ceibo, 9°19'50"N 83°17'20"W, 1800 m alt., Sept. 27, 1989 (immature fr.), *Herrera 3555* (F, MO); along Río Guacinal, 1 km W of Monteverde, 10°18'30"N 84°49'00"W, ca. 1060 m alt., Mar. 10.1996 (immature fr.), *Yasuda 1310* (INB, MO); same locality, ca. 1060 m alt., Mar. 10.1996 (fl.), *Yasuda 1311* (INB); Juntas, 0.5 km N of Monteverde, 10°18'45"N 84°48'35"W, ca. 1400 m alt., Mar. 10.1996 (immature fr.), *Yasuda 1314* (INB, MO). **Panama.** Chiriquí: Near Costa Rican border, c. 13 km from Río Sereno, Finca Hartmann, 8°50'N 82°45'W, 1400-1800 m alt., May. 12, 1991 (fr.), *McPherson 15312* (MO); same locality, 1550-1750 m alt., Oct. 23, 1992 (immature fr.), *McPherson 15961* (MO).

About the distinction between *Beilschmiedia brenesii* and the closest species, *B. hondurensis*, see the notes under *B. hondurensis*.

A few collections from Osa Peninsula, Costa Rica (*Aguilar 1483*, *Thomsen 610*, *1054*, *Yasuda 1319*), share similar leaf arrangement and ramification with *B. brenesii*, but differ from this species by their large leaves (15-23 x 7-9 cm) and long petioles (ca. 1.7 cm long). They were collected from 50-350 m alt, which is much lower than where the typical *B. brenesii* usually grows. Inflorescences of the collections are also different from the typical inflorescences of *B. brenesii* by their densely pubescent rachises and short flower pedicels. These collections might represent a new species. However, I have seen only four collections, only one of which is fertile, with barely mature flowers. I do not think there is enough material to describe the species, hence I decided to keep them as indeterminate and wait for more and better material.

Two collections from Panama (*McPherson 15312*, *15961*) have sometimes alternate leaves and undulate leaf margins, but other characters fit *B. brenesii* well. They appear to have grown abnormally.

7. *Beilschmiedia costaricensis* (Mez & Pittier) C. K. Allen, J. Arnold Arbor. 26: 415. 1945. *Hufelandia costaricensis* Mez & Pittier, Bull. Herb. Boiss. II, 3: 228. 1903. SYNTYPES: Costa Rica. San José: forests of El Copey, 1800 m alt., Feb., 1898 (fl.), *Tonduz 11713* (BM, G-BOIS not seen, K, P, US); forest of Juan Vinas, 1130 m alt., Jan. (fr.), *Pittier 1863* (B not seen, BR not seen).

Beilschmiedia rohliana Lasser, Bol. Acad. Cienc. Fis. Mat. y Nat. Caracas 10: 193. 1946.

TYPE: Venezuela. Aragua: Henri Pittier National Park, a village of Rancho Grande, Feb. 14, 1946 (old fl. & immature fr.), *Lasser 2052* (holotype, VEN).

Cryptocarya kostermansiana C. K. Allen, J. Arnold Arbor. 26: 423. 1945. TYPE: Costa

Rica. Alajuela: Canton Naranjo, Naranjo, Cerro del Espiritu Santo, 1150 m alt., Feb. 24, 1940 (fl.), *Smith P2418* (holotype, A seen on photograph; isotypes, F, US).

Tree, to 30 m tall. Terminal buds pubescent with appressed to spreading, straight hairs. Twigs terete, compressed to angular when young, densely to sparsely pubescent with appressed to spreading, straight, very rarely erect and wavy hairs, less densely when old. Leaves alternate; petioles 0.5-1.5 (2) cm long, flat to canaliculate above, almost glabrous or pubescent with appressed to spreading (very rarely to erect) hairs, concolorous with twigs; blades chartaceous to coriaceous, elliptic, 5-20 (26) x 2.5-9 (14) cm; base cuneate, not inrolled (rarely not only the base but the entire margin slightly inrolled), apex acute to acuminate, rarely obtuse; leaf surface glabrous on both sides, rarely on lower leaf surface sparsely pubescent with appressed to spreading hairs, or very rarely relatively densely pubescent with erect hairs, lower leaf surface not glaucous; midrib almost immersed above, raised below, secondary veins (5) 6-11 (13) pairs, immersed above, raised below, tertiary veins more or less percurrent, ramification fine to intermediate in size, square-like with free veinlets, conspicuously to slightly raised on both sides. Inflorescences axillary, paniculate, (1) 2-14 (16) cm long, sparsely pubescent with erect hairs, with (10) 25-50 (80) flowers per inflorescence; flower pedicels of the lateral divisions (0.3) 0.7-1.5 mm long, pedicels of the central flowers up to 4 mm long. Flowers creamy to whitish, 2-3 mm long, 2.3-2.8 mm in diam.; tepals 6, equal, ovate, 1.3-1.8 mm long, 1-1.4 mm wide, pubescent with more or less erect hairs on both sides; stamens 9, filaments 0.3-0.6 mm long, pubescent, anthers 0.6-0.9 mm long, all the anthers 2-celled, glabrous, apex of the anthers obtuse to truncate, glands of the innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.7 mm long; pistil 1.1-1.8 mm long, glabrous to sparsely pubescent, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs, less densely toward the bottom. Fruits ellipsoid, purple-black, 3-4.5 (5.5) x 1.5-2 (3) cm, the surface smooth; infructescence axis 1.5-3.5 mm in diam., fruit pedicels slightly thickened to 5 mm in diam.

below the fruit, fruit pedicels not constricted at the base, covered with lenticels and concolorous with the infructescence axis.

Phenology: collected in flower in all months except for June, August and November, in mature fruit in all months except for January and April.

Distribution: Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru, (100-) 750-3000 m alt. (Fig. 9).

Habitat: premontane wet forest to cloud forest.

Common name: "Quizarrá", "Chancho" in Costa Rica, "Aguacatillo" in Colombia, "Aguacatillo", "Pacche", "Hevo cuguán", "Malde" in Ecuador, "Palo oso", "Puma" and "Pumapara" in Peru.

Economic use: unknown.

Additional specimens examined: **Costa Rica.** Alajuela: 10°25'N 84°53'W, 900 m alt., Nov. 12, 1986 (fr.), *Haber 6371* (CR, F, MO); Reserva Biológica Monteverde, Río Peñas Blancas, 10°18'N 84°45'W, 900 m alt., Jan. 1, 1987 (young fl.), *Haber 6531* (MO); same river, 10°20'N 84°43'W, 850 m alt., Feb. 6, 1987 (fl.), *Haber 6665* (INB, F, MO); same river, Finca Wilson Badilla, 10°18'N 84°43'W, 860 m alt., Oct. 20, 1987 (immature fr.), *Haber 7514* (CR, MO); same river, Finca Wilson Salazar, 10°18'N 84°43'W, 800 m alt., Nov. 7, 1987 (immature fr.), *Haber 7693* (CR, MO); same river, Finca García, 10°19'N 84°44'W, 850 m alt., Dec. 3, 1987 (fr.), *Haber 7721* (CR, MO); same river, Finca Klaus Stein, 10°18'N 84°45'W, 900 m alt., Aug. 30, 1988 (immature fr.), *Bello 303* (MO); same river, San Carlos, 900 m alt., Jul. 10, 1985 (immature fr.), *Haber 1962* (BM, CR, F, MO, NY); same reserve, San Gerardo, Río Caño Negro, Finca de Chavarría, 10°23'N 84°48'W, 1000 m alt., Jan. 10, 1989 (fl. & immature fr.), *Bello 641* (INB, MO); same reserve, Estación Aleman's, 10°18'N 84°45'W, 950 m alt., May. 7, 1991 (immature fr.), *Bello 2633* (INB, MO); same reserve, Río Negro, Atlantic slope, 10°20'N 84°50'W, 1500 m alt., Oct. 11, 1985 (fr.), *Bello 3212* (F, MO); Road from Zapote to Santa Elena, 1200-1300 m alt., Apr. 16, 1976 (fl.), *Utley 4653* (CR, F, MO, NY); Reserva Forestal San Ramón, San Ramón, Los Angeles, 2 km before the Estación UCR, 10°15'N 84°35'W, 800 m alt., Dec. 9, 1991 (immature fr.), *Herrera 4992* (INB, MO); Reserve Forest of Arenal Quebrada San Gerardo, Río Caño Negro, Rodolfo Quesada, 10°23'N 84°48'W, 800 m alt., Feb. 18, 1990 (fl.), *Bello 1914* (INB, MO); San Ramón, Los Angeles, Reserva de San Ramón, 2 km N. from la Estación, 10°12'40"N 84°36'20"W, 1000 m alt., Oct. 18, 1993 (immature fr.), *Herrera 6605* (F); San Ramón, San Francisco and San Pedro de, Jan. 28, 1929 (fl.), *Brenes 6605* (CR, F, NY); Upala, Bijagua El Pilón, 10°42'00"N 85°02'55"W, 750 m alt., Jul. 21, 1993 (immature fr.), *Herrera 6321* (F, MO); Upala, Bijagua El Pilón, Cerro La Carmela, entre Río Celeste y cabeceras del Río Chimurria, 10°43'15"N 85°00'20"W, 700-800 m alt., Jul. 7, 1988 (immature fr.), *Herrera 2012* (BM, F, MO, NY); Upala, Cordillera de Guanacaste, Bijagua, slope NW of Volcán Tenorio, 10°44'00"N 85°03'00"W, 700-1000 m alt., Aug. 27, 1994

(fl.), *Haber 11837* (MO); La Peña de Zarcero, 1700 m alt., Apr. 4, 1938 (young fl.), *A. Smith H592* (F, MO). Cartago: El Muñeco, on the Río Navarro, 1400-1500 m alt., Mar. 6-7, 1926 (immature fr.), *Standley 51271* (US), (fr.), *Standley 51280* (US), (immature fr.), *Standley 51285* (US); Hills near Navarro Valley, 1800 m alt., Jan. 5, 1928 (young fl. & detached fr.), *Stork 1713* (F). Guanacaste: Parque Nacional Guanacaste, Estación Cacao, 10°55'N 85°29'W, 980 m alt., Dec. 17, 1989 (immature fr.), *Chávez 32* (F); same estación, Liberia, 10°55'45"N 85°28'15", 1100 m alt., Dec. 17, 1990 (immature fr.), *Chávez 490* (MO); same estación, 10°55'38"N 85°29'38"W, 1100 m alt., Jun. 3, 1990 (fr.), *Rojas 28* (INB); same estación, Sendero Mirador (path to a viewpoint), 10°55'43"N 85°28'10"W, 1100 m alt., Feb. 10, 1995 (sterile), *Alfaro 82* (INB, MO); same park, estación Mengo, Volcán Cacao, 10°55'45"N 85°28'20"W, 1100 m alt., Jul. 13, 1989 (fl. detached), *Hammel 17539* (CR); Cantón de Tilarán, mountain range of Tilarán, Palmital, Quebrada Malanga, Río Caño Negro, 10°24'30"N 84°46'30"W, 700 m alt., Mar. 12, 1993 (fl.), *Bello 4882* (MO); Chiripa, Tilarán, 4 km N of La Florida, 10°26'N 84°54'W, 1100 m alt., Jan. 14, 1987 (young fl.), *Haber 6556* (F, MO), *Haber 6559* (MO); Zona Monteverde, San Gerardo, 10°22'N 84°48'W, 1000 m alt., Nov. 21, 1988 (fr.), *Bello 560* (MO); same zone, 10°48'N 84°50'W, 1550 m alt., Jul. 12, 1990 (sterile), *Gentry 71555* (MO); same zone, 5 km N Santa Elena on road to Las Nubes, Finca San Bosco road, Río Negro, Atlantic slope, 10°22'N 84°49'W, 1400 m alt., Nov. 10, 1988 (fr.), *Haber 8746* (CR, F, MO); Parque Rincón de La Vieja, Liberia, The view point following la Fila al Volcán Santa María, 10°46'N 85°49'W, 1100-1200 m alt., Nov. 25, 1987 (fr.), *Herrera 1396* (F (sterile), MO, NY); Zona Protectora Tenorio Tilarán, Cord. V. Tilarán; Tierras Morenas; Río San Lorenzo, 10°36'40"N 84°59'45"W, 1000 m alt., Mar. 23, 1993 (fl.), *Rodríguez 116* (MO); same locality, 10°36'30"N 85°00'W, 1050 m alt., Mar. 24, 1991 (fr.), *Alvarado 126* (MO). Heredia: Cantón Central, 11 km E of Cariblanco, 10°16'N 84°05'W, 1060 m alt., Apr. 18, 1988 (young fl.), *Loiselle 384* (CR); Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, 730 m alt., Apr. 19, 1982 (immature fr.), *Hammel 11766* (MO). Limon: Cordillera de Talamanca, Atlantic slope, Kámuk massif, ridge between the Río Tararia, and the northeastern-most Kámuk páramo, 9°14'-15'N, 82° 59'W, 1900-2300 m alt., Sep. 16, 1984 (immature fr.), *Davidse 29213* (MO); same cordillera, Fila Carbón, ca. 6 km W de Home Creek, 9°40'10"N, 82° 50'35"W, 100 m alt., Feb. 14, 1991 (old fl.), *Hammel 18116* (CR, F, MO); Cordillera de Talamanca, Reserva Biol. Hitoy Cerere Valle del Río La Estrella, siguiendo el camino entre Estación Cerere y el Valle de las Rosas, 9°40'10"N 83°00'40"W, 150 m alt., Oct. 2, 1988 (fl.), *Herrera 2381* (MO). Puntarenas: Cantón de Coto Brus, P. I. La Amistad, Cordillera de Talamanca, Santa Maria de Pittier, 9°01'38"N 82°51'56"W, 1700 m alt., Jun. 10, 1995 (fr.), *González 790* (INB); same cantón, same cordillera, Sendero a Altamira, Río canasta, 09°01'30"N 82°57'40"W, 1700 m alt., Jan. 28, 1995 (fr.), *Villalobos 1* (MO); Reserva Biológica Monteverde, Cantón de Puntarenas, Pacific slope, 10°18'N 84°48'W, 1500 m alt., Apr. 4, 1990 (fl.), *Haber 9838* (INB, MO); E of Monteverde, 10°18'N 84°48'W, 1300-1450 m alt., Jun. 24, 1978 (sterile), *Lawton 1265* (F); same reserve, 1500 m alt., Apr. 7, 1981 (fl.), *Haber 463* (MO); same reserve, 2km SW station, 10°18'N 84°48'W, 1500-1550 m alt., Nov. 5, 1992 (fr.), *Ingram 1666* (CR, MO); same reserve, 1500 m alt., Apr. 24, 1981 (fl.), *Haber 494* (MO); same reserve, 10°20'N 85°10'W, 1500 m alt., Aug. 29, 1980 (immature fr.), *Wheelwright 126B* (F, MO); same reserve, 10°20'N 85°10'W, 1500 m alt., Apr., 1981 (young fl.), *Wheelwright 188/A* (F, MO); same reserve,

10°20'N 85°10'W, 1500 m alt., Mar., 1981 (fl.), *Wheelwright 219* (F, MO); same reserve, 10°48'N 84°50'W, 1550 m alt., Aug. 22, 1984 (sterile), *Gentry48799* (F, MO), *Gentry48804* (F, MO); same reserve, 10°17'50"N 84°48'30"W, 1400m alt., Mar. 9, 1996 (fl.), *Yasuda 1309* (INB, MO); same reserve, in Mata's pasture, 1550 m alt., May. 2, 1974 (fl. & fr.), *Hartshorn 1465* (CR, F, MO); same reserve, Río Ojo de Agua, División Continental, 10°16'N 84°46'W, 1800 m alt., Apr. 23, 1987 (fl.), *Haber 7081* (CR, F, MO); same reserve, San Luis valley, Pacific slope, 10°20'N 84°50'W, 1200 m alt., Nov. 15, 1985 (immature fr.), *Bello 3477* (F, MO); same reserve, Pacific slope, 10°20'N 84°50'W, 1400 m alt., Nov. 1985 (fr.), *Haber 3477* (CR); same reserve, Penas Blancas river valley, Atlantic slope, 10°20'N 84°50'W, 900 m alt., Oct. 27, 1985 (fr.), *Haber3212* (CR); same reserve, Río Guacimal, Comunidad-Reserva, Pacific slope, 10°18'N 84°48'W, 1500 m alt., Mar. 4, 1990 (fl.), *Bello 2112* (INB, MO); same reserve, Cordillera de Tilarán, Comunidad, 1520-1560 m alt., Sep. 2, 1977 (immature fr.), *Dryer 1179* (CR, F); same locality, 1520-1560 m alt., Apr. 5, 1977 (fl.), *Dryer 1334* (CR, F, MO); same reserve, Cordillera de Tilarán, Vert. Pacífico, 1540-1600 m alt., Nov. 16, 1976 (immature fr.), *Dryer 939* (F, MO); same locality, 1520-1580 m alt., Oct. 15, 1976(fr.), *Dryer 1081* (F, MO). San José: Sta. Ma de Dota- El Cedral, Jun. 12, 1975 (sterile), *Póveda1068* (CR, F). **Panama.** Chiriquí: Cerro Horqueta, 2100 m alt., Jul. 24, 1966 (fl.), *Blum 2624* (MO); Near Cerro Colorado, ca. 4.2 miles from Chami Camp, ca. 8°35'N 81°45'W, 1500 m alt., Apr. 16, 1986 (old fl.), *McPherson8973* (MO); Vicinity of Fortuna Dam, in valley S of lake, 8°45'04"N 82°15'04"W, 1200-1300 m alt., Dec. 25, 1986 (immature fr.), *McPherson 10125* (MO). Panama: Cerro Azul, ca. 180 m alt., Jul. 17, 1962 (immature fr.), *Dwyer 2054* (MO). **Venezuela.** Aragua: Henri Pittier Parque Nacional, along road from restaurant towards Rancho Grande and below Biological Station on side towards Guamitas, 1200 m alt., Oct. 24, 1961 (immature fr.), *Steyermark 89880* (NY); same locality, Jun. 16, 1962 (immature fr.), *C. K. Allen 17* (NY); same locality, Jul. 1959 (young fl.), *Kostermans s.n.* (K, NY, U); same locality, 1000-1200 m alt., Jul. 25, 1993 (old fl.), *Lorea5562* (MO), (fl.), *Lorea5563* (MO); same locality, 850 m alt., Jul. 8, 1938 (fr.), *Williams 10253* (F, US); 26 km P. N. Aragua, 950 m alt., Jan. 11, 1939 (immature fr.), *Williams 11073* (F). Mérida: La Chorrera, Carretera Merida-Azulita, Feb. 3, 1987 (fl., sometimes with fr.), *van der Werff 8786* (MO); same carretera, La Azulita. Municipio Zerpa, Distrito Andrés Bello, La Azulita, Nov. 28, 1979 (fr., detached), *Marcano487-979* (BR); Carretera Panamericana, Municipio Jají, Caserío La Chorrera, near bridge of Río Las Gonzalez, Dtto. Campo Elías, Apr. 13, 1966 (fr.), *Marcano820* (U). locality unknown: Feb. 16, 1957 (fl. & immature fr.), *Bernardi s.n. (6256?)* (NY). **Colombia.** Antioquia: Municipio Campamento: Vereda El Alto, 4 km W of mine "Las Brisas", 1 km from gorge "El Niño", 7°03'N 75°19'W, 1810 m alt., Sep. 9, 1989 (fl.), *Callejas 8368* (MO); Municipio de Frontino, region of Murri, ca. 13 km from Nutibara; forest edge E of road, 6°40'N 76°20'W, 2000 m alt., Dec. 9, 1988 (fl.), *McPherson 13370* (MO). Cundinamarca: Laguna Pedro Palo above Finca San Jose, ca. 32 km Mosquera-La Mesa, 2000-2250 m alt., Aug. 1, 1976 (immature fr.), *Gentry17136* (MO, NY). El Valle: Peñas Blancas, cuenca río Pichindé, 1800 m alt., Jun. 11, 1977 (young fl.), *Benalcazar 19* (MO); same locality, 1800 m alt., Jul. 9, 1977 (young fl. & fr.), *Benalcazar 59* (MO); Cordillera Occidental; vertiente occidental: Hoya del río Anchicayá, lado derecho, bosque bajando a La Planta, 400 m alt., Aug. 5, 1943 (fl.), *Cuatrecasas 14876* (F, US); Cordillera Occidental, western slope, Río Digua basin, left side, Piedra de Moler, 900-1180 m alt., Aug. 19-28, 1943 (immature fr.), *Cuatrecasas 15193*

(F); Corr. Ceylán, path La Esmeralda, farm El Diamante, 1600 m alt., May. 13, 1982 (fr.), *Millan 21* (MO); Municipio Sevilla, enroute to Morroazul, stream La Raquelita, 1600 m alt., Feb. 12, 1985 (immature fr.), *Devia 939* (MO, NY); Municipio Sevilla- La Raquelita, to Orilla from stream La Raquelita, 04°00'N 76°00'W, 1500 m alt., Jul. 31, 1985 (immature fr.), *Devia 1050* (MO); Cordillera Occidental, Municipio Yotoco, above Buga, 3°50'N 76°30'W, 1500 m alt., Jul. 14, 1984 (immature fr.), *Gentry 48050* (MO); same municipio, E slope, 18 km W of Buga, 3°52'N 76° 33'W, 1610 m alt., Apr. 29, 1995 (immature fr.), *Silverstone-Sopkin 7493* (MO); same municipio, E. slope, along hightway between Dapa and Loboquerrero at Parque Yotoco, 3°52'N 76°22'W, 1485-1550 m alt., Feb. 17, 1990 (immature fr.), *Croat70684* (MO), (fl.), *Croat70747* (MO); same municipio, Corregimiento Jiguales, garden path, estate of Milan, 1600 m alt., Jan. 16, 1985 (immature fr.), *Devia917* (MO, NY); same municipio, Valle del Cauca, 4°00'N 76°00'W, 1400 m alt., Aug. 6, 1985 (fr.), *Devia 1078* (MO), *Devia 1079* (MO). Magdalena: Sierra de Perijá, E of Manaure, Hacienda Nuevo Horizonte, El Podrido, 1550-1600 m alt., Nov. 16, 1959 (immature fr.), *Cuatrecasas 25413* (US). Narino: 7 km from Chucunés, Planada Natural Reserve, 1°10'N 77°58'W, 1800 m alt., Nov. 16, 1987 (old fl.), *Benavides8964* (MO); same reserve, near Chucunes, trail to La Vieja, ridge of the top in cloud forest, 01°05'N 78°01'W, 1900-2100 m alt., Dec. 23, 1987 (immature fr.), *Gentry59761* (MO); western slope of Cordillera Occidental, same reserve, 1800 m alt., Mar. 23, 1990 (immature fr.), *Beltrán39* (MO). **Ecuador.** Carchi: Gualpí Alto area, 01°02'N 78°23'W, 900-1000 m alt., May. 18-25, 1985 (immature fr.), *Thomsen 58818* (MO); Tulcan, top of Maldonado, border with Colombia, Chilmá site, 00°51'N 78°02'W, 2000 m alt., May. 20, 1991 (young fl.), *Palacios 7304* (MO); same top, Palo bridge, 00°53'N 78°03'W, 1700 m alt., May. 20, 1991 (infl. missing fl. & detached fr.), *Palacios 7350* (MO); Tulcan, Reserva Etnica Awá, Parroquia El Chical, Centro San Marcos, 01°06'N 78°14'W, 900-1100 m alt., Apr. 20-30, 1993 (immature fr.), *Méndez 390* (MO). El Oro: Los Puntos de Guarumal, 1875 (immature fr.), *Poortmann s.n.* (P). Imbabura: Cantón Cotacachi, Carretera Apuela-Cotacachi; above Apuela, Pucará site, Getzemani Forest, 00°25'N 78°32'W, 2000-2100 m alt., Apr. 4, 1990 (immature fr.), *Palacios4842* (MO), (fl.), *Palacios 4852* (MO); Road Otavalo-Apuela, 2000-3000 m alt., Feb. 14, 1989 (fl., sometimes with immature fr.), *van der Werff 10574* (MO); same locality, Jul. 3, 1991 (young fl. sometimes with fr.), *van der Werff 12168* (MO). Loja: El Colorado to 5 km NE of Alamor, 3°59'S 79°58'W, 1200 m alt., Aug. 10, 1975 (immature fr.), *Samaniyo 079* (US). Morona-Santiago: Bomboiza, Misión Salesiana-Shuar and around there, 03°25'S 78°35'W, 800 m alt., Jun. 8-10, 1986 (young fl. & fr.), *Zarcona 485* (MO). Pichincha: Along new road Nanegal-Mindo, 1600-2500 m alt., Mar. 1, 1994 (fl. or fr.), *van der Werff 13368* (MO); same locality, 1600-1800 m alt., Mar. 3, 1994 (immature fr.), *van der Werff 13389* (MO); Cantón de Quito, Reserva Biológica Maquipucuna, 00°8'N 78°35'W, 1200-1700 m alt., May. 20, 1991 (young fl. & immature fr.), *Tipaz 141* (MO); same reserve, Nanegal, 00°10'N 78°40'W, 1500-1700 m alt., May. 17-31, 1991 (fl. & immature fr.), *Quelal 124* (MO), (young fl.), *Quelal 78* (MO). **Peru.** Cajamarca: Cutervo National Park, 12 km NE of San Andres de Cutervo, 06°10'S 78°40'W, 2230 m alt., Sep. 11, 1991 (sterile), *Gentry 74662* (MO); La Palma, 10km NW of Chirinos, 05°25'S 78°53'W, 1780 m alt., Feb. 5, 1988 (fr. immatured), *Gentry61196* (MO), (sterile), *Gentry61198* (MO), *61200* (MO), *61236* (MO), *61255* (MO), *61256* (MO), *61259* (MO), *61260* (MO), *61265* (MO); Provincia San Miguel, Distrito La Florida, Loc. Agua Azúl, 1020 m alt., Oct. 10, 1986 (old fl. & fr.), *Díaz2088* (MO); Santa

Cruz, Road to El Chorro Blanco, 1500 m alt., Oct. 10, 1993 (fl.), *Leiva* 937 (MO); Cajamarca, Chorro Blanco, 1900 m alt., Dec. 19, 1984 (fr.), *Sagastegui* 12408 (MO). Piura: Huancabamba, Distrito Canchaque, Chorro Blanco, 1500-1900 m alt., Apr. 18, 1987 (immature fr.), *Díaz* 2464 (MO); same districto, between Chorro Blanco & War War, 2000-2500 m alt., Jun. 18, 1989 (immature fr.), *Díaz* 3195 (MO). Sapuena: C. I. Jenaro Herrera, Trocha Arboretum Braga, Tahuampa forest, 04°55'S 73°45'W, 120-125 m alt., Sep. 29, 1991 (fr.), *Grandez* 2883 (MO). Huánuco: Prov. Puerto Inca, Dpto. Yuyapichis, 09°40'S 75°02'W, 270 m alt., Nov. 1-15, 1990 (fr.), *Tello* 590 (MO).

Kostermans (1938) excluded one of the syntypes, *Pittier* 1863, and classified it as *B. anay*. I have not seen this collection.

Beilschmiedia costaricensis has alternate leaves and fine ramification, but it has relatively coarser ramification than the other species of the same phyllotaxis and ramification. Additionally, this species is distinguished from them by a combination of the following characters; appressed to spreading pubescence on the terminal buds and twigs, ramification with free veinlets, non-glaucous lower leaf surfaces, glabrous anthers and fruit pedicels not constricted at the base. This species is sometimes misidentified as *B. pendula*. About the difference between *B. costaricensis* and *B. pendula*, see the notes under *B. pendula*.

Most of the collections from Colombia and Ecuador appear to be different from the collections from other countries (and some collections from Colombia) by their having coriaceous leaves, coarser and less raised ramification and a sparsely pubescent pistil. Additionally, the former collections tend to have shorter petioles and larger leaves than the latter. However, differences of the leaf texture and ramification size between them are subtle and hard to make a clear separation, and the petiole length and leaf size has no clear gap between them. Pubescence on a pistil in the former collection cannot be a distinctive character because the amount of indument is very small and can be easily missed. Considering that separating those two kinds of collections and making a new species from the former collections would only create a confusion, I decide to keep them in *B. costaricensis*.

Usually, orientation of indument on the terminal buds and twigs is consistent within a species in neotropical *Beilschmiedia* species. But the indument of *B. costaricensis* ranges from appressed to spreading or very rarely to erect. The collections with erect hairs from Costa Rica (*Bello* 560, *Brenes* 6605, *Haber* 6665, 7693, 7721) share the same characters with the other collections of *B. costaricensis* except for the erect indument, hence I keep these collections in *B. costaricensis*. However, the collections with erect hairs from

Colombia (*Cuatrecasas* 22220, 22438) has quite dense pubescence on the lower leaf surfaces, which is very unlikely for *B. costaricensis*. I classified these Colombian collections as “*B. costaricensis* vel. aff.”

Four collections from vicinity of El General, Costa Rica (*Hartshorn* 2159, *Skutch* 4389, 5158, *Stork* 3121), are also regarded as “*B. costaricensis* vel. aff.” Although these collections share similar ramification with *B. costaricensis*, flowers of them have slightly longer tepals and a densely pubescent ovary, and fruits of them have the pedicel constricted at the base. Pubescence of ovary and constriction of fruit pedicel are regarded as characters sometimes inconsistent, so that more material is needed to clarify whether the collections with these characteristics actually represent a new species or the collections are only one of the variations of *B. costaricensis*.

Several collections from Limón, Costa Rica (*Herrera* 2418, 2467, *Gomez* 23614, *Pittier* 16140, *Robles* 2027, 2039, *Stevens* 24491), have the ramification with free veinlets like *B. costaricensis*, but the ramification scarcely raised on the upper surface and the leaves are very large (ca. 30 cm long). I decided to leave them as indeterminate because we have only fruiting material which is not enough for a proper classification. A few of the collections appear to have hollow stems, although it is not certain if they had ants inhabiting inside.

There are a few collections from Panama which have the ramification with free veinlets like *B. costaricensis*, but the ramification almost completely immersed on the upper leaf surfaces (*Correa* 10237, 11035, *Croat* 26947,). Additionally, a few collections from Panama have the ramification totally immersed even on both leaf surfaces (*Gentry* 13789, 14015). I keep all of these collections as indeterminate because more and better material are needed for their proper classification.

8. *Beilschmiedia curviramea* (Meissner) Kostermans, Rec. Trav. Bot. Néerl. 35: 853. 1938. *Aydendron curvirameum* Meissner in D.C., Prodr. XV, 1: 90. 1864. *Hufelandia curviramea* (Meissn.) Mez, Jahrb. Königl. Bot Gart. Berl. 5:19. 1889. SYNTYPES: Guyana. Roraima, 1842-1843 (fl.), *Schomburgk* 1009 (B seen on photograph, BM, BR not seen, G-BOIS not seen, G-DEL not seen, LZ not seen, NY not seen, P, W not seen); Demerara, Apr., 1844 (fl.), *Schomburgk* 1730 (K (3 sheets)).

Tree, to 25 m tall. Terminal buds pubescent with appressed hairs. Twigs terete, compressed when young, almost glabrous or sparsely pubescent with appressed hairs.

Leaves opposite, rarely subopposite; petioles 0.6-1.5 (2.2) cm long, flat or canaliculate above, glabrous, slightly discolored or rarely concolorous with twigs; blades coriaceous, elliptic, (6) 9-20 x (2.5) 4-6.5 (8.5) cm; base cuneate to obtuse, not inrolled, apex acute or rarely cuspidate; leaf surface glabrous on both sides, lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins 8-13 (16) pairs, slightly raised on both sides, tertiary veins not percurrent, ramification coarse, square-like with free veinlets, almost immersed above, slightly raised or almost immersed below. Inflorescences axillary, very rarely clustered on a leafless short shoot in the axils of leaves, paniculate with few branches, 3-7 (12.5) cm long, sparsely pubescent with erect hairs, with 20-30 (50) flowers per inflorescence; flower pedicels of the lateral divisions 1-3 mm long, pedicels of the central flowers up to 5 mm long. Flowers yellow to white, ca. 2 mm long, ca. 2.5 in diam.; tepals 6, equal, ovate to elliptic, 1.5-2 mm long, 1.2-1.7 mm wide, sparsely pubescent with more or less appressed hairs outside, almost glabrous inside; stamens 9, outer six filaments 0.3-0.4 mm long, innermost three filaments 0.4-0.6 mm long, filaments pubescent, anthers 0.8-1 mm long, all the anthers 2-celled, apex of the anthers obtuse to truncate, apex of the anthers pubescent, glands of innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.6 mm long; pistil ca. 1 mm long, glabrous, ovary longer than and gradually narrowed into the style; receptacle pubescent with appressed hairs or glabrous. Fruits ellipsoid, black, 3-5 x 2-4 cm, the surface smooth or rarely slightly warty; infructescence axis ca. 2.5 mm in diam., fruit pedicels thickened to 4-5 mm in diam. below the fruit, fruit pedicels not constricted, covered with lenticels and concolorous with the infructescence axis.

Phenology: collected in flower in February, from April to July, and from September to November, in mature fruit in February and July.

Distribution: western Venezuela, Guyana, (Jamaica?), 10-600 m alt. (Fig. 9).

Habitat: unknown.

Common name: "Aguacatillo moises" in Venezuela.

Economic use: unknown.

Additional specimens examined: **Venezuela**. Bolivar: Cloud forest on summit of southeast-facing escarpment, E of Cerro El Picacho, N of Las Nieves and Las Chicharras, 45kms. N. of Tumeremo, vicinity of Deborah, Nuria Plateau, vicinity of lake-like area, 600-650 m alt., Feb. 5-8, 1961 (fl. & fr.), *Steyermark 89161* (F, NY). Delta Amacuro: E of Rio Grande, EN of El Palmar, near the border of Estado Bolivar, Aug. 19-Sept. 7, 1964 (immature fr. or sterile), *Marcano 387* (F, MO (2 sheets), NY), (sterile), *Marcano 404* (MO); same

locality, Nov. 29- Dec. 18, 1964 (sterile), *Marcano 441* (F, MO, NY), *Marcano 453* (NY, US), (immature fr.), *Marcano 522* (NY). **Guyana.** Cuyuni-Mazaruni: W bank of Essequibo River 0-2 km S of Wolga settlement, 06°27'N 58°38'W, 0-15 m alt., Dec. 24, 1992 (detached fl.), *Henkel 650* (MO). East Demerara-West Coast Berbice: Between the Demerara and Berbice Rivers, ca. 5°50'N, Jul. 15-19, 1922 (fl.), *DeLaCruz 1655* (F, MO, NY). Malali, Demerara River, ca. 5°35'N, Oct. 30-Nov. 5, 1922 (fl.), *DeLaCruz 2725* (F, MO, NY, US); Kaow Isl., Essequibo River, Jul. 26, 1940 (fl.), *anonymous(3261)* (K). Mazaruni-Potaro or East Demerara-West Coast Berbice: Essequibo River, Moraballi Creek, near Bartica, near sea level, Sep. 18, 1929 (fl.), *Sandwith 288* (K, NY (fl. missing), U). Mazaruni-Potaro: Upper Mazaruni River, ca. 60°10'W, Sep. 22-Oct. 6, 1922 (fl.), *DeLaCruz 2249* (F, MO, NY), *DeLaCruz 2379* (F); Mazaruni River, Nov., 1886 (fl.), *Jenman 2439* (K), *Jenman 2515* (K, NY); same locality, Jun. 1889 (fl.), *Jenman 5320* (K); Moorie Island in the Essequibo River, near Bartica, 50-125 m alt., Aug. 18, 1976 (immature fr.), *Mori 8159* (NY); Cuyuni River, Kauri Creek, May 17, 1933 (detached fl.), *Tutin 114* (BM, U, US). Locality unknown ("Lana-balli"?), Jul., 1924 (fl., fr., or detached fr.), *Persaud 70* (F (fr.), NY (fl. & detached fr.)). **Jamaica?** Locality unknown, Sep., 1818 (fl.), *Caley s.n.* (BM).

Beilschmiedia curviramea has opposite leaves and coarse ramification, and is the only species of the phyllotaxis and ramification in northern South America. This species is distinguished from the other species of the phyllotaxis and ramification in Central America and Chile by its pubescent anthers. Instead, this character, pubescence of anthers, is shared with all the species in Brazil. Actually, *B. curviramea* shares very similar leaf and flower structure with a Brazilian species, *B. stricta*. Compared to *B. curviramea*, *B. stricta* tends to have smaller leaves, more conspicuously raised ramification and more pubescent flowers. But since I have seen only one collection of *B. stricta*, I cannot assume that these characteristics occur in *B. stricta* consistently. More material of *B. stricta* is needed in order to clarify the differences between these two species.

Besides *B. stricta*, *B. curviramea* appears to have similar vegetative characters with a Costarican species, *B. brenesii*. But leaves of *B. brenesii* usually tend to cluster near the tip of branches and have the ramification conspicuously raised below, while leaves of *B. curviramea* are usually arranged evenly along the twigs and have the ramification almost immersed on both sides.

A specimen collected by Caley from Jamaica approaches *B. curviramea* very much, although the locality is outside the normal distribution of this species.

9. *Beilschmiedia emarginata* (Meissner) Kostermans, Rec. Trav. Bot. Néerl. 35: 855. 1938. *Cryptocarya emarginata* Meissner, D. C. Prodr. 15: 76. 1864. *Hufelandia*

emarginata (Meissner) Mez, Jahrb. Königl. Bot. Gart. Berl. 5: 18. 1889. TYPE: Brazil. São Paulo: near Lorena, Oct., 1833 (fl.), *Riedel 1585* (holotype, LE; isotypes, G-BOIS not seen, K, NY not seen).

Tree, to 15 m tall. Terminal buds pubescent with rusty erect, short curly hairs. Twigs terete, compressed when young, sparsely pubescent with erect short curly hairs or almost glabrous. Leaves opposite; petioles ca. 0.5 cm long, flat above, sparsely pubescent or glabrous, concolorous with or slightly darker than twigs; blades chartaceous, elliptic, often asymmetrical and sinuate, 6.5-12 x 3-6.5 cm; base cuneate, not inrolled, apex emarginate to round; leaf surface glabrous on both sides, uncertain whether lower leaf surface glaucous or not; midrib immersed above, raised below, secondary veins 7-8 pairs, slightly raised or almost immersed above, raised below, tertiary veins not percurrent, ramification coarse, square-like with free veinlets, slightly raised or almost immersed above, slightly raised below. Inflorescences axillary, paniculate, 3-5 cm long, almost glabrous or sparsely pubescent with erect short curly hairs, with 15-30 flowers per inflorescence; flower pedicels of the lateral divisions 0.5-1.2 mm long, pedicels of the central flowers up to 3 mm long. Flowers 2-2.8 mm long, 2.2-2.8 mm in diam.; tepals 6, equal, ovate, 1.2-1.5 mm long, 0.8-1.2 mm wide, almost glabrous outside, sparsely pubescent with appressed hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, outer six anthers ca. 0.9 mm long, innermost three anthers ca. 0.7 mm long, all the anthers 2-celled, apex of the anthers obtuse to truncate, anthers pubescent, glands of innermost three stamens globose; staminodia 3, ca. 0.7 mm long; pistil 1-1.5 mm long, glabrous, ovary as long as pistil and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits unknown.

Phenology: collected in flower in October and December.

Distribution: São Paulo, Brazil (Fig. 9).

Habitat: unknown.

Common name: unknown.

Economic use: unknown.

Additional specimen examined: **Brazil**. São Paulo: native in Botanical Garden, Dec. 9, 1955 (sterile), *Kuhlmann 3885* (NY).

Among Brazilian *Beilschmiedia* species, *B. emarginata* is distinguished by its rusty, short and erect pubescence on the terminal buds and twigs. Additionally, this species usually has undulate leaves and emarginate leaf apices, both of which are not seen in the other Brazilian species.

Two collections by Hatschbach (2455 & 16310) from Paraná approach to *B. emarginata* in vegetative characters, but have glabrous anthers. Species with pubescent anthers can rarely have exceptional collections which lack the pubescence, so these Hatschbach collections might still belong to *B. emarginata*. But I decided to keep them separated from *B. emarginata* as indeterminate, because the locality and the phenology are different from the other collections (the collections from Paraná were in flower in August and September). Actually, I have seen only two collections which can be identified as *B. emarginata*. More material is needed to clearly delimit this species.

10. *Beilschmiedia fluminensis* Kostermans, Rec. Trav. Bot. Néerl. 35: 865. 1938.

TYPE: Brazil. Rio de Janeiro: Estado Rio G. Portella, Monte Sinai, 1935 (fl.), Nunes 323 (holotype, U not seen; isotypes, RB-2 sheets).

Tree, to 15m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, slightly compressed when young, almost glabrous or sparsely pubescent with appressed hairs. Leaves opposite; petioles 1-2 cm long, canaliculate above, glabrous, slightly darker than twigs; blades firmly chartaceous, elliptic, (10) 13-16 (18) x 4-7 cm; base cuneate, slightly inrolled, apex acute, rarely obtuse; leaf surface glabrous on both sides, rarely lower leaf surface sparsely pubescent with short appressed hairs, lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins 12-14 pairs, raised on both sides, tertiary veins not percurrent, ramification coarse, square-like with free veinlets, slightly raised above, raised below. Inflorescences axillary, paniculate, 4-7 cm long, glabrous to sparsely pubescent with erect hairs, with 20-35 flowers per inflorescence; flower pedicels of the lateral divisions ca. 1 mm long, pedicels of the central flowers up to 2.5 mm long. Flowers greenish, 1.7-2 mm long, 2-2.5 mm in diam.; tepals 6, equal, elliptic to ovate, 1-1.5 mm long, 1.1-1.5 mm wide, glabrous outside, sparsely pubescent with appressed hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three filaments ca. 0.4 mm long, filaments pubescent, anthers 0.7-0.9 mm long, all the anthers 2-celled, apex of the

anthers obtuse to truncate, anthers pubescent, glands of the innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.7 mm long; pistil ca. 1.2 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs around the base of stamens and staminodia. Fruits ellipsoid, 4.5-5 x ca. 3 cm, the surface warty or smooth; fruit pedicels ca. 2.5 mm in diam., thickened to ca. 4 mm in diam., pedicels not constricted at the base, concolorous with the lower part.

Phenology: collected in flower in September and October, in mature fruit in October.

Distribution: Rio de Janeiro, Brazil (Fig. 9).

Habit: unknown.

Common name: unknown.

Economic use: unknown.

Additional specimens examined: **Brazil**. Rio de Janeiro: Malo Breuro, (abras gublich?), Oct. 25, 1927 (fl.), *Auleuis s.n.* (RB); forest of Teixeira, Borges, Horto Florestal, Mar. 20, 1929 (fr.), *Personal do Horto Florestal 85* (RB); Estado da Guanabara, dark forest, Horto Florestal, (fl.), *Personal do Horto Florestal Antenor 102161* (F, NY); locality unknown, Sep. 2, 1959 (fl.), *Duarte 5007* (RB); E. Rio-Tinguá, Oct. 1, 1946 (fr.), *Brade 18642* (RB). Espírito Santo: margin of Rio Paucos, road of Colomia, Colatina, May. 2, 1934 (fr.), *Kuhlmann 292* (RB). Guanabara: road to Pai Ricardo, 510 m alt., Jul. 26, 1973 (fr.), *Sucre 10058* (RB).

Collections of *Beilschmiedia fluminensis* have been sometimes misidentified as *B. taubertiana* or *B. emarginata*. But one can distinguish *B. fluminensis* from the two species by its appressed pubescence on the terminal buds and twigs (*B. taubertiana* has erect, long pubescence and *B. emarginata* has erect, short curly pubescence). Additionally, petioles of *B. fluminensis* are relatively longer than the two species. In fact, *B. stricta*, appears to be most similar to *B. fluminensis*. They share similar indument type, leaf shape and flower structure. Since I have seen only one collection (type) in *B. stricta*, it is hard for me to define the best characters separating these two species. I have observed that the collection of *B. stricta* has the leaves with a flat base and the inflorescences racemose and relatively densely pubescent, while *B. fluminensis* has the leaves with a slightly inrolled base and the inflorescences paniculate and almost glabrous.

11. *Beilschmiedia hexanthera* van der Werff, Brittonia 47 (4): 374. 1995. TYPE:
French Guiana. Vicinity of Eau Claire: near Saül, 200 m alt., Aug. 9-10, 1993 (fl.),

van der Werff et al. 12951 (holotype, MO; isotypes, CAY not seen, NY not seen, U not seen).

Tree, to 20 m tall. Terminal buds pubescent with appressed hairs. Twigs terete, compressed when young, more or less densely pubescent with short appressed hairs, less densely to glabrescent when old. Leaves alternate; petioles (0.6)1-1.3 cm long, flat to canaliculate, sparsely pubescent with short appressed hairs, concolorous with twigs; blades firmly chartaceous, elliptic, (5.5) 8-12 (16) x (2.5) 4-5 (6) cm; base cuneate, not inrolled, apex acute; upper leaf surface glabrous, lower leaf surface pubescent with short appressed hairs, lower leaf surface not glaucous; midrib immersed or slightly raised above, raised below, secondary veins (5) 7-9 pairs, almost immersed above, raised below, tertiary veins not percurrent, ramification fine, areolate without free veinlets, almost immersed on both sides (the pattern visible on both sides, the pattern visible on the upper surface coarser than on the lower surface). Inflorescences axillary, paniculate, (3) 6-11 cm long, sparsely pubescent with short erect hairs, with 25-50 (75) flowers per inflorescence; flower pedicels of the lateral divisions 0.3-0.5 mm long, pedicels of the central flowers up to 2 (rarely 3) mm long. Flowers greenish yellow, ca. 1.5 mm long, 1.7-2.1 mm in diam.; tepals 6, equal, broadly ovate, 0.5-0.8 mm long, 0.6-1 mm wide, sparsely pubescent with short erect hairs outside, sparsely pubescent with appressed hairs inside, or with erect curly hairs at the base inside; stamens 6, representing the outer two whorls, filaments ca. 0.2 mm long, pubescent, anthers ca. 0.4 mm long, all the anthers 2-celled, apex of the anthers obtuse to truncate, apex of the anthers glabrous; staminodia 6, the three staminodia representing the third whorl columnar, 0.5-0.7 mm long, the lower half pubescent, glands on the three staminodia globose to reniform; the three staminodia representing the fourth whorl triangular in outline, ca. 0.5 mm long; pistil 1-1.2 mm long, glabrous, ovary more or less as long as and gradually narrowed into the style; receptacle pubescent with erect curly hairs (upper part of the receptacle) and long appressed hairs (lower part of the receptacle). Fruits unknown.

Phenology: collected in flower in August.

Distribution: French Guiana, 200-400 m alt. (Fig. 10).

Habitat: unflooded forest.

Common name: unknown.

Economic use: unknown.

Additional specimens examined: **French Guiana**. Saül and vicinity: Route of Bélizon, S of Eaux Claires, 3°37'N 53°12'W, ca. 200-400 m alt., Aug. 21, 1993 (fl.), *Mori 23377* (MO).

Beilschmiedia hexanthera is the only neotropical *Beilschmiedia* species with six fertile stamens. This species has been collected only in French Guiana. According to Hyland (1989), there are several *Beilschmiedia* species with six fertile stamens in Australia, but it is unlikely that *B. hexanthera* and the Australian species are closely related (van der Werff 1995). The reduction in the number of stamens occurred probably independently between French Guiana and Australia. I suspect that *B. hexanthera* is close to *B. pendula* due to similar vegetative and floral characters (except for the stamens in the third whorl). One can still separate the two species vegetatively because *B. hexanthera* does not have glaucous leaves like *B. pendula*.

12. *Beilschmiedia hondurensis* Kostermans, Rec. Trav. Bot. Néerl. 35:854. 1938.

TYPE: Belize: Camp 31, British Honduras-Guatemala Survey, 630m alt., April 7, 1934 (fl.), *Schipp 1262* (holotype, K; isotypes, AFS not seen, BM, G-DEL not seen, F, NY).

Tree, to 30 m tall. Terminal buds pubescent with appressed or slightly spreading, straight hairs. Twigs terete, compressed when young, glabrous. Leaves opposite; petioles (0.5) 0.7-1 (1.2) cm, flat or canaliculate above, glabrous, darker than or concolorous with twigs; blades firmly chartaceous, elliptic, (5) 8.3-13.2 (18) x (1.5) 2.9-4.6 (6.5) cm; base cuneate, not inrolled, apex acuminate, rarely acute; leaf surface glabrous on both sides, lower leaf surface not glaucous; midrib immersed above, raised below, secondary veins (7) 9-12 (14) pairs, tertiary veins not percurrent, ramification coarse, square-like with free veinlets, slightly raised above, raised below. Inflorescences axillary or around terminal buds, paniculate with few branches, 3-6 cm long, sparsely pubescent with appressed to erect hairs, sometimes almost glabrous, with 10-30 flowers per inflorescence; flower pedicels of the lateral divisions ca. 0.5 mm long, pedicels of the central flowers up to 1.5 mm long. Flowers ca. 3 mm long, ca. 2.5 mm in diam.; tepals 6, equal, ovate, 1.5-2.1 mm long, 1.3-1.5 mm wide, sparsely pubescent with more or less appressed hairs outside, sparsely pubescent with relatively long appressed to erect hairs inside, sometimes almost glabrous

inside; stamens 9, filaments ca. 0.5 mm long, sparsely pubescent, anthers 0.6-0.8 mm long, sometimes with acute apex, all the anthers 2-celled, apex of the anthers acute or rarely obtuse, apex of the anthers glabrous, glands of innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.5 mm long; pistil ca. 1.3 mm long, glabrous, ovary as long as or longer than and gradually narrower into the style; receptacle sparsely pubescent with erect hairs, less densely toward the bottom. Fruits ellipsoid, black, 2.3-3 x ca. 1.3 cm (immature?), the surface smooth; infructescence axis ca. 2 mm in diam., fruit pedicels slightly thickened to 3 mm below the fruit, fruit pedicels constricted or not constricted at the base, without lenticels and darker than the infructescence axis.

Phenology: collected in flower in February, in relatively mature fruit in April.

Distribution: Chiapas and Veracruz in Mexico, Belize, Guatemala, Honduras, (200) 750-1600 m alt. (Fig. 10).

Habitat: from wet tropical forest to montane forest.

Common name: unknown.

Economic use: unknown.

Additional specimens examined: **Mexico.** Chiapas: Municipio of Cintalapa, SE of Cerro Baul on the border with the state of Oaxaca, 16 km NW of Rizo de Oro along a logging road to Colonia Figaroa, 1600 m alt., Jan. 8, 1973 (immature fr.), *Breedlove 31417* (MEXU, MO, NY); same locality, 1600 m alt., Nov. 3, 1971 (immature fr.), *Breedlove 21817* (MEXU, MO); same municipio, between Colonia Francisco I. Madero and Colonia A. Lopez Mateos, 1250 m alt., Dec. 31, 1980 (immature fr.), *Breedlove 49052* (MEXU, MO). Oaxaca: Municipio San Miguel Chimalapa, Cerro Salomón, ca. 2 km in line to NNO of Cerro Guayabitos, ca. 43 km in a straight line to N of San Pedro Tapanatepec, near the border with Municipio Sat. Maria Chimalapa, 16°45'N 94°11'30"W, 1850 m alt., Dec. 23, 1985 (immature fr.), *Wendt 5151* (MEXU, MO). Veracruz: Municipio Sn. Andres Tuxtla, Laguna Escondida, 3 km N of station of Biología Tropical Los Tuxtlas, 200 m alt., Feb. 21, 1985 (fl.), *Ibarra 2292* (MEXU, MO). **Guatemala.** Peten: La Cumbre, 142/143 km E of the Cadenas Road, May. 11, 1975 (young fl.), *Lundell 19280* (MO). **Belize.** Toledo: SW of Mt. Maya, Columbia River Forest Reserve, Gloreia Camp, 16° 22'N, 89°10'W, 750 m alt., Apr. 13-14, 1992 (immature fr.), *Holst 4435* (BM, MO); Carmelita Camp, Edwards road beyond Columbia, Apr. 21, 1951 (fr.), *Gentle 7292* (F, MO, NY). **Honduras.** Olancho (El Filo): trail between La Chorrera campsite and 1,900 m camp on ridge, 14°59'N, 88°56'W, 1500 m alt., May. 31, 1992 (old fl.), *Thomas 412* (MO), *Thomas 420* (MO).

The type collection of *Beilschmiedia hondurensis* is reported as a shrub, but there are some collections which are described as 30 m.

The closest affinity of *B. hondurensis* is *B. brenesii*. Some, if not all, Mexican collections I placed in *B. hondurensis* approach to *B. brenesii* and make the distinction between *B. hondurensis* and *B. brenesii* difficult. Usually, *B. hondurensis* is distinguished from *B. brenesii* by its petioles darker than twigs, shorter flower pedicels and fruit pedicels constricted at the base. But the Mexican collections have the petioles concolorous with twigs and fruit pedicels not constricted at the base. Typical collections of *B. hondurensis* have acuminate leaf apices, but the Mexican collections sometimes have acute leaf apices, which are similar to the most collections of *B. brenesii*.

Considering distribution of typical *B. hondurensis* (Guatemala, Belize and Honduras) and *B. brenesii* (Costa Rica and Panama), it is unreasonable to combine the Mexican collections and *B. brenesii* into one species with disjunct distribution and to regard *B. hondurensis* as another species which distribution sandwiched between *B. brenesii*. And there are a few collections from Mexico which show an intermediate form between the *B. brenesii*-like Mexican collections and *B. hondurensis*. I consider combining *B. brenesii* and *B. hondurensis* (in this case, *B. hondurensis* has priority) if I had enough flowering material of *B. hondurensis* and if the flowers were similar to *B. brenesii*.

However, I have seen only one collection with good flowers in *Beilschmiedia hondurensis*, which is from 200 m altitude in Mexico, unusually low habitat for both of *B. hondurensis* and *B. brenesii*. And that collection has short flower pedicels (0.5 mm long in the lateral divisions, up to 1.5 mm long in the central flowers), quite different from the long pedicels of *B. brenesii* (3-5 mm in the lateral divisions, up to 7 mm long in the central flowers). There are a few more collections in *B. hondurensis* which appear to have short flower pedicels, but they are too young or too old to compare the length correctly.

Therefore, I decided to keep *B. hondurensis* and *B. brenesii* separate, and to place all the Mexican collections in *B. hondurensis*, because I thought it is more confusing to combine the two species without stronger evidence.

The type collection of *B. zapoteoides* has opposite leaves and coarse ramification like *B. hondurensis*, but has relatively long flower pedicels (ca. 2 mm long in the lateral divisions) and bigger, more or less spherical fruit compared to *B. hondurensis*. And there are two collections from El Salvador, one of which in flower has also long flower pedicels (2.5 mm long in the lateral divisions), and another collection has young fruits, uncertain whether the fruits grow big and spherical or not. I decide to place *B. zapoteoides* in an imperfectly known species, with annotating the two Salvadorian collections "*B. zapoteoides* vel aff.",

because the flowers of the type collection and the Salvadorian collection appear to be abnormal (leaves are diseased, and the number of cells in the third whorled anthers are variable, from two to zero) and one cannot delimitate the species based on such poor material only.

13. *Beilschmiedia immersinervis* Sa. Nishida sp. nov. TYPE: Costa Rica. Puntarenas: Cantón de Puntarenas, Cordillera de Tilarán, Santa Elena, near Cañitas, Zona Monteverde, 10°19'30"N 84°49'30"W, 1400 m alt., Dec. 1, 1992 (fl.), *Guindon & Brenes 56* (holotype, MO; isotypes, CR, INB, MO, USJ).

Beilschmiedia pendula similis, sed pilis erectis et antheris pubescentibus differt.

Tree, to 30m tall. Terminal buds pubescent with erect, short curly hairs. Twigs terete, compressed or sulcate when young, densely to sparsely pubescent with erect curly hairs, less densely to almost glabrous when older. Leaves alternate to sub-opposite, rather clustered near the terminal buds; petioles 0.7-1 (1.5) cm long, flat above, pubescent with erect curly hairs, concolorous with twigs; blades firmly chartaceous, oblanceolate to elliptic, 6-10 (13) x (2) 2.5-4 (6) cm; base attenuate to cuneate, not inrolled, apex acute, rarely obtuse; leaf surface glabrous on both sides, lower leaf surface glaucous; midrib immersed above, slightly raised below, secondary veins 7-10 pairs, immersed on both sides (visible on lower leaf surface), tertiary veins weakly percurrent, ramification fine, areolate without free veinlets, immersed and hardly visible above, almost immersed or very slightly raised below. Inflorescences in axils of the leaves near the terminal buds, paniculate with few branches, 2-6 cm long, pubescent with erect short hairs, with 10-30 (50) flowers per inflorescence; flower pedicels of the lateral divisions ca. 1 mm long, pedicels of the central flowers up to 3 mm long. Flowers greenish-yellow, ca. 2.8 mm long, ca. 2.6 mm in diam.; tepals 6, equal, elliptic to ovate, ca. 2.2 mm long, 1.3-1.7 mm wide, pubescent with erect or appressed hairs on both sides; stamens 9, outer six filaments ca. 0.6 mm long, innermost three filaments ca. 0.8 mm long, filaments pubescent, anthers ca. 0.8-1 mm long, all the anthers 2-celled, apex of the anthers obtuse to truncate, apex of the anthers pubescent, glands of the innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.7 mm long; pistil ca. 1.3 mm long, glabrous, ovary almost as long as and gradually narrowed into the style; receptacle pubescent with appressed to erect hairs. Fruits ellipsoid, shiny black,

2.5 x 1.5 cm, the surface smooth; infructescence axis ca. 2 mm in diam., fruit pedicels rarely slightly thickened to 3 mm in diam., fruit pedicels slightly constricted at the base, or almost not constricted, without or with a few lenticels, slightly darker than the infructescence axis.

Phenology: collected in flower in December and January, in mature fruit in March and June.

Distribution: north-western part of Costa Rica, 300-1400 m alt. (Fig. 10).

Habitat: premontane wet forest.

Common name: unknown.

Economic use: unknown.

Additional specimens examined: **Costa Rica**. Alajuela: along a road between Canas and Upala, lower slopes Volcan Tenorio, 450 m alt., Jan. 23, 1984 (fl.), *Pennington 11416* (CR). Guanacaste: Parque Nacional Guanacaste, Estación Pitilla, La Pasmompa, primary forest remnant beside the road to La Esperanza, 11°02'N 85°25.3'W, 300 m alt., Jun. 17, 1989 (fr.), *Hammel 17502* (INB, MO); Monteverde zone, Cantón de Abangares, Cordillera de Tilarán, from Santa Elena to San Rafael, 10°20'00"N 84°53'00"W, 1200 m alt., Jan. 7, 1992 (fl.), *Guindon 36* (INB, MO); same zone, Los Tornos, Tilarán, Pacific side., 1300 m alt., Apr. 14, 1987 (immature fr.), *Haber 6967* (INB, F, MO); Cantón de Tilarán, San Rafael to El Dos de Tilarán, Pacific slope, 10°22'N 84°53'W, 800-1100 m alt., Mar. 11, 1992 (fr.), *Haber 11070* (INB, MO); San Rafael, 10°21'N 84°52'W, ca. 1010 m alt., Mar. 10, 1996 (immature fr.), *Yasuda 1312* (INB, MO).

Beilschmiedia immersinervis has alternate leaves and fine ramification. This species is distinguished from the other species with alternate leaves and fine ramification by a combination of the following three characters; short curly pubescence on the terminal buds and twigs, secondary veins immersed on both sides of the leaves and pubescent anthers. Some collections of *B. immersinervis* were identified as *B. pendula*, supposedly because *B. immersinervis* has a similar leaf shape as *B. pendula*. But one can separate *B. immersinervis* from *B. pendula* because *B. immersinervis* has erect and curly pubescence on the terminal buds while *B. pendula* has appressed and straight pubescence on the terminal buds.

Beilschmiedia immersinervis has the same pubescence type and ramification pattern as *B. steyermarkii*, but *B. immersinervis* has pubescent anthers and tends to have firmly chartaceous and symmetrical leaves, while *B. steyermarkii* has glabrous anthers and tends to have more coriaceous and asymmetrical leaves.

This species also shares a similar ramification pattern and pubescent anthers with *B. riparia*, but *B. immersinervis* is easily distinguished from *B. riparia* by its immersed secondary veins. Additionally, *B. immersinervis* differs from *B. riparia* by its having glaucous leaves and slightly longer flower pedicels, although there are a couple of exceptional collections with glaucous lower leaf surfaces in *B. riparia*. *Beilschmiedia immersinervis* also tends to have corky twigs which is not seen in *B. riparia*.

14. *Beilschmiedia latifolia* (Nees) Sa. Nishida comb. nov. *Hufelandia latifolia* Nees, *Systema Laurinarum*: 674. 1836. TYPE: Peru. locality unknown, 1835 (fl.), *Matthew 1433* (holotype, E; isotypes, BM, E, K, LE not seen, OXF not seen).

Tree, to 25 m tall. Terminal buds densely pubescent with brown to ferruginous, erect, long, wavy to straight hairs. Twigs terete, angular when young, densely pubescent with erect long hairs, less densely when older. Leaves alternate; petioles 0.5-1 (1.5) cm long, flat above, pubescent with erect long hairs to glabrous, concolorous with twigs; blades coriaceous, ovate to broadly elliptic, (5) 7-11 (18) x 4-8 (11.5) cm; base obtuse to round, not inrolled, apex obtuse; upper leaf surface glabrous, lower leaf surface densely pubescent with long hairs when young, less densely when old, rarely almost glabrous when old, lower surface glaucous; midrib immersed above, raised below, secondary veins 6-9 pairs, immersed or impressed, rarely slightly raised above, raised below, tertiary veins usually percurrent, rarely only weakly percurrent, ramification fine, areolate without free veinlets, immersed above, immersed (the pattern visible) or slightly raised below. Inflorescences axillary, paniculate, 6-11 cm long, densely pubescent with long erect hairs, with 20-40 flowers per inflorescence; flower pedicels of the lateral divisions 0.5-1 mm long, pedicels of the central flowers up to 2 mm long. Flowers (2.3) 2.5-3 mm long; tepals 6, equal, ovate, 1.7-2.2 mm long, 1-1.5 mm wide; pubescent with erect hairs on both sides; stamens 9, outer six filaments ca. 0.3 mm long, innermost three filaments 0.3-0.5 mm long, filaments pubescent, anthers ca. 1 mm long, all the anthers 2-celled, apex of the anthers acute to truncate, apex of the anthers glabrous, glands of the innermost three stamens globose; staminodia 3, cordate in outline, 0.5-0.8 mm long; pistil ca. 1.4 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed long hairs. Fruits ellipsoid, black, 3-5 x (1.5) 2 cm, the surface smooth; infructescence axis 2-3

mm in diam., fruit pedicels not thickened below fruit, fruit pedicels not constricted at the base, with few lenticels and slightly darker than the infructescence axis.

Phenology: collected in flower in April, May and September, in mature fruit in January.

Distribution: Venezuela, Colombia, Ecuador, Peru, 2100- 3000 m alt. (Fig. 10).

Habitat: high montane, cloud forest.

Common name: “Cocoa” and “Curo” in Venezuela, “Roble palta”, “Sacha palta” in Peru.

Economic use: woods used for construction.

Additional specimens examined: **Venezuela.** Mérida: Carbonera, Jan. 22, 1959 (sterile), *Bernardi 10955* (US); El Valle, ca. 6 km from the main road to Páramo Los Conejos, Paddock, 2200 m alt., Jan. 13, 1966 (immature fr.), *Duerto 1* (U); 2 km S of Mérida city, Parque Nacional de Sierra Nevada, c. 0.5 km S of La Montaña Teleférico station, La Montaña study area, 8°35'N 71°07'W, 2450-2650 m alt., Apr. 6, 1995 (fl.), *Kelly 10540* (MO); path above Estación La Montaña del Teleférico from Mérida, 2600-2750 m alt., Sep. 30, 1986 (young fl.), *Tanner 709* (MO); Distrito Campo Elias, La Carbonera, 8°35'N 71°14' W, 2200 m alt., Nov. 23, 1985 (immature fr.), *van der Werff 8224* (MO, NY); same distrito, San Eusebio, 2100-2400 m alt., Sep. 29, 1962, (fl.), *Terran 1065* (MO); Las Coloradas Plateau (Santa Cruz de Mora-El Molino), a path near San Rafael, 2800 m alt., May 27, 1980 (fl.), *Cuatrecasas 29000* (NY, US); La Mucuy, 2040 m alt., Jun. 25, 1962 (sterile), *C. K. Allen 25* (NY). Tachira: from city La Grita to city Pregonero, along path and montane forest, 2300 m alt., Oct. 9, 1965 (old fl. or detached fr.), *Bernardi 10954* (B, C, F, MO, NY); in the skirt of Tamá Plateau, close to the border between Colombia and Venezuela, 2475-2550 m alt., May 18-20, 1967 (old fl. or immature fr.), *Steyermark 98386* (NY), (immature fr.), *Steyermark 98480* (NY). **Colombia.** Antioquia: Municipio Caldas, path La Corrala, estate La Zarza, 2440 m alt., Jun. 22, 1987 (old fl.), *Velásquez 7754* (MO). Cauca: N of Departamento Santander, Cordillera Oriental, above Majuey, on road between Chinácota and Toledo, 7°30'N 72°35'W, 2400-2600 m alt., Mar. 8, 1986 (old fl.), *Stein 3635* (MO, NY). Locality unknown (Merenberg?), Jan. 4, 1980 (fr.), *Cabrera 5252* (MO). **Ecuador.** Loja: between Tambo Cachiyacu, La Entrada, and Nudo de Sabanillas, 2500-3500 m alt., Oct. 7, 1943 (immature fr.), *Steyermark 54404* (F). **Peru.** Amazonas: Province Luya, Camporredondo-Tullanya, short cut to Cerro Huicsocunga, 2350 m alt., Sep. 3, 1989 (sterile), *Díaz 3714* (MO), (immature fr.), *Díaz 3723* (MO). Pasco: Provincia Oxapampa, Río San Alberto valley, E of Oxapampa, W slopes of Cordillera Yanachaga, 10°34'S 75°22'W, 2500 m alt., Jul 24, 1984 (immature fr.), *D. Smith 8004* (MO, NY).

Kostermans (1938) placed *Hufelandia latifolia* Nees and *H. ovalis* Blake under *Beilschmiedia sulcata*. Later, Allen (1945) reestablished *H. ovalis* as *B. ovalis* (Blake) C. K. Allen in her work on the Lauraceae of Central America. But Allen left *H. latifolia* under the

synonym of *B. sulcata*, supposedly because this species is not distributed in Central America. I have studied the type of *H. latifolia* and recognize it as a member of *Beilschmiedia* but different from the type collection of *B. sulcata*. Hence I made a new combination, *B. latifolia*.

Beilschmiedia latifolia has alternate leaves and fine ramification, as *B. sulcata* does. But *B. latifolia* is distinguished from *B. sulcata* by its having erect pubescence, coriaceous leaves and ramification with few free veinlets. The type collection of *B. latifolia* appears to have appressed hairs on the lower leaf surfaces, but it might be only because the leaves have been pressed for long time. One can clearly see the erect hairs on the terminal buds in the type collection.

Beilschmiedia latifolia is actually much more similar to *B. ovalis* than to the type of *B. sulcata*. *Beilschmiedia latifolia* and *B. ovalis* share very similar leaf shape, ramification, inflorescence and flower structure. What distinguishes *B. latifolia* from *B. ovalis* best is its long pubescence on the lower leaf surfaces. Usually, *B. ovalis* has its lower leaf surfaces almost glabrous even when the leaves are young. There are some exceptional specimens in *B. ovalis*, like *Steyrmark 98480*, that have densely pubescent leaves with erect hairs when young, but it is very rare that the leaves remain the pubescence when they are old. But *B. latifolia* has its lower leaf surfaces pubescent with long hairs until the leaves become relatively old. Old leaves of *B. latifolia* sometimes lose the pubescence on the lamina, but leaves of many collections, especially those from Venezuela, remain dense pubescence on the midribs and secondary veins even in old age. The Venezuelan collections tend to have longer, more straight hairs than the collections from other countries, and show a great contrast with the glabrous leaves of *B. ovalis*. Unfortunately, type collection of *B. latifolia* is from Peru, and has relatively short and sparse pubescence on the lower leaf surfaces. In addition to the pubescence, *B. latifolia* differs from *B. ovalis* in fruit shape; *B. latifolia* has elliptic fruits, while *B. ovalis* has roundish fruits. Both species occur in high montane forests, but *B. latifolia* is distributed in Venezuela, Colombia, Ecuador and Peru, while *B. ovalis* has been collected in Honduras, Costa Rica and Panama.

Two collections from Ecuador, *Hurtado 1817* and *Cuatrecasas 16082*, share similar ramification pattern with *B. latifolia*, but they have glabrous and obovate to elliptic leaves. Actually, these collections appear to be very similar to the collections from Costa Rica, *Burger 1218* and *Dayton 3126*, which I mention in the notes under *B. obovatifolia*. I keep these Ecuadorian collections as indeterminate, as I did for the Costarican collections.

15. *Beilschmiedia linharesensis* Sa. Nishida & van der Werff. TYPE: Brazil. Espirito Santo: Linhares, Reserva Florestal da Porto Seguro - CVRD/BA, Aceiro, 2100 km, left side, Oct. 26, 1988 (fl.), *Farias 243* (holotype, MO).

Beilschmiedia rigida similis, a qua floribus minoribus et depresso globosis differt.

Tree, to ca. 30 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, compressed when young, sparsely to densely pubescent with appressed straight hairs. Leaves opposite; petioles 1.5-2 cm long, flat above, slightly darker than twigs, glabrous; blades coriaceous, obovate to elliptic, (5.5) 8-14 x (3) 4-5 cm; base cuneate, inrolled to below (entire margin slightly inrolled to below), apex round to obtuse; leaf surface glabrous on the both sides, not glaucous; midrib immersed or slightly impressed above, raised below, secondary veins 8-12 (14) pairs, slightly raised on both sides, tertiary veins not percurrent, ramification coarse, square-like with free veinlets, almost immersed on both sides. Inflorescences axillary, paniculate with few branching, 2.5-3.5 cm long, relatively densely pubescent with erect straight hairs, with ca. 15 flowers per inflorescence; flower pedicels of the lateral division ca. 0.5 mm long, pedicels of the central flowers up to 1 mm long. Flowers depressed-globose, ca. 1.6 (2) mm long, ca. 2.2 mm in diam.; tepals 6, equal, curved toward inside, broad ovate, ca. 0.5 mm long, ca. 1 mm wide, sparsely pubescent with erect hairs outside, sparsely pubescent with erect hairs to almost glabrous inside, stamens 9, outer six filaments ca. 0.1 mm long, innermost three filaments ca. 0.2 mm long, filaments pubescent, anthers ca. 0.5 mm long, all anthers 2-celled, apex of the anthers obtuse to truncate, apex of the anthers pubescent, glands on innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.3 mm long; pistil ca. 1.2 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed to erect hairs. Fruits unknown.

Phenology: collected in flower in October.

Distribution: Espirito Santo, Brazil (Fig. 11).

Habitat: unknown.

Common name: unknown.

Economic use: unknown.

Additional specimen examined: **Brazil**. Espirito Santo: Reserva Florestal de CVRD. Linhares, Est. CINCO-FOLHAS, 1320 km right side, Sep. 16, 1982 (young fl.), *Folli 409* (MO).

Although I have only one collection in mature flower and two collections in flower buds, the small depressed-globose flowers of this species are unique among neotropical *Beilschmiedia* species and distinguished from the other species clearly. *Beilschmiedia linharesensis* shares similar phyllotaxis, ramification pattern, pubescence type and leaf shape with *B. rigida*.

16. *Beilschmiedia mexicana* (Mez) Kostermans, in Rec. Trav. Bot. Néerl. 35: 846. 1938. *Hufelandia mexicana* Mez, Jahrb. Königl. Bot. Gart. Berl. 5: 20. 1889. SYNTYPES: Mexico. Veracruz: Dos Puentes, Feb. (fl.), *Liebman 712* (= "*Lauraceae N. 20*") (C not seen, K not seen, US not seen); Mirador, Feb., 1842 (fr.), *Liebman 711* (= "*Lauraceae N. 16*" ?) (US), same locality, Mar., 1842 (immature fr.), *Liebman 711* (= "*Lauraceae N. 19*" ?) (C); *Liebman 711* (= "*Lauraceae N. 16*" or "*Lauraceae N. 19*") (P not seen); *Liebman 714* (= "*Lauraceae N. 21*") (C not seen, LE not seen); Totutla, Jan., 1843 (fr.), *Liebman 713* (= "*Lauraceae N. 17, 18*") (C, US). Orizaba, 1853 (fr.), *F. Müller 1460* (B not seen, K-2 sheets, LE not seen, W not seen).

Linociera areolata Lundell, Amer. Midl. Naturalist 23: 176. 1940. TYPE: Mexico. Hidalgo: above Chapulhuacan, 1300 m alt., Jul. 12, 1937 (fr.), *Lundell & Lundell 7165* (holotype, AFS not seen; isotype, F).

Tree, to 25 m tall. Terminal buds pubescent with appressed hairs, rarely almost glabrous. Twigs terete, compressed when young, pubescent with appressed hairs or glabrescent, less densely to glabrous when older. Leaves alternate, petioles 0.5-1.5 (2) cm long, flat to canaliculate above, glabrous, rarely pubescent with appressed hairs, concolorous with twigs; blades chartaceous, elliptic, sometimes asymmetric, 5-13 (19) x 3-8 (10) cm; base cuneate, not inrolled, apex acute to obtuse, rarely acuminate; leaf surface glabrous on both sides, lower leaf surface not glaucous, or very rarely glaucous; midrib and secondary veins almost immersed or slightly raised above, raised below, secondary veins in 6-10 (11) pairs, ramification raised on both size, very rarely immersed above (? see below),

intermediate in size, areolate, usually without free veinlets. Inflorescences in axils of leaves, paniculate, (1) 2-10 (16) cm long, sparsely pubescent with short straight hairs or almost glabrous, with 10-20 (45) flowers per inflorescence; flower pedicels of the lateral divisions (0.3) 1-1.5 mm long, pedicels of the central flowers up to 4 (rarely 5.5) mm long. Flowers 2.5-2.7 mm long, 2.5-3 mm in diam.; tepals 6, equal, ovate to elliptic, 1.3-1.7 mm long, 1.2-1.5 mm wide, sparsely pubescent with erect to appressed hairs on both surfaces. Stamens 9, outer six filaments 0.3-0.5 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, anthers ca. 0.8 mm long, all the anthers 2-celled, apex of the anthers obtuse to truncate, apex of the anthers glabrous, glands of the innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.6 mm long; pistil ca. 1.5 mm long, glabrous, ovary almost as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, purplish-black, 2.5-3 (4) x ca. 1.5 cm, the surface smooth; infructescence axis 1-2.5 mm in diam., fruit pedicels scarcely thickened below the fruits, fruit pedicels slightly constricted at the base, infructescence scarcely covered with lenticels, fruit pedicel almost concolorous with the infructescence axis.

Phenology: collected in flower from March to June and September, in mature fruit from December to February, and June to August.

Distribution: Mexico, 800-1900 m alt. (Fig. 11).

Habitat: montane mesophyll forest with *Liquidambar*, *Quercus*, etc., sometimes with *Pinus*, rarely on limestone.

Common name: "Calanique", "Tzitztez".

Economic use: unknown.

Additional specimens examined: **Mexico**. Chiapas: Municipio Oxchuc, waterfall of Río Mesbiljaz, Jun. 15, 1984 (fr.), *Méndez7686* (MO); Municipio La Trinitaria, 10 km ENE of Dos Lagos, above Santa Elena, 1170 m alt., Dec. 15, 1981 (fr.), *Breedlove56219* (MO, NY). Guerrero: Municipio Atoyac de Alvarez, in Nueva DÍhi, 17 km NE of El Paraíso, 1390 m alt., Mar. 29, 1983 (fl. & immature fr.), *Soto 5122* (MO); same municipio, ca. 1.5 km W of El Molote, 1740 m alt., May. 16, 1993 (fl. & immature fr.), *Lorea5533* (FCME, MO); same locality, 1780 m alt., May. 17, 1993 (fl. & immature fr.), *Lorea 5535* (FCME, MO). Hidalgo: Municipio Tlanchinol, road to Tierra Colorada, 1580 m alt., Apr. 9, 1992 (immature fr.), *Lorea323* (MEXU); same locality, 1480 m alt., May 20, 1992 (immature fr.), *Lorea 363* (MEXU); same locality, 1580 m alt., Aug. 24, 1992 (immature fr.), *Lorea523* (MEXU); same municipio, ca. 7 km E of Tlanchinol, road to Apantlazol, 1330 m alt., Apr. 7, 1992 (young fl.), *Lorea210* (MEXU); Along Hwy 105 between Pachuca & Tampico, along road to San

Cristóbal leaving main Hwy 100.8 mile NE of Pachuca, 1.5 km from San Cristóbal, 10.5 miles S of Santa María; 36.4 miles S of Huejutla, 20°58'N 98°38'W, 1550 m alt., Feb. 28, 1987 (immature fr.), *Croat 65900* (MO); Chapulhuacán, Nov. 27, 1937 (immature fr.), *Kenoyer 980* (F); same locality, 1300 m alt., Jul. 12, 1937 (fr.), *Lundell 7165* (F); same locality (332 km of Mexico City highway), ca. 1140 m alt., Jul. 13, 1943 (fr.), *Lundell 12232* (U); 2 km N of Chapulhuacán around trail to transmission tower, W of road from Chapulhuacán to Hacienda de Cahuazas, ca. 1.5 km E of Mexico Hwy 85, ca. 14 km SW of Tamazunchale, S.L.P., 21°10'N 98°53'W, 1100 m alt., Jun. 26, 1984 (old fl.), *Slheim 1718* (MEXU); Jacala, near (327 km ?) on Hwy between Santa Ana and Chapulhuacán, Jul. 12, 1948 (immature fr. & mature fr.), *Moore 3957* (BM, MEXU). Puebla: Municipio Ahuacatlán, Agua Dulce, 4 km SE of Ahuacatlán, 20°01'N 97°50'W, 1180 m alt., Jun. 12, 1985 (immature fr.), *Tenorio 9000* (MO); same locality, 1425 m alt., Feb. 27, 1987 (detached fr.), *Tenorio 12726* (MO); same locality, 1180 m alt., Feb. 27, 1987 (immature fr.), *Toriz 324* (MO); 3 km SW of Villa Juárez, 1250 m alt., Nov. 2, 1966 (immature fr.), *Rzedowski 23419* (MEXU); 4 km W of Villa Juárez, 1200 m alt., Nov. 26, 1972 (immature fr.), *Rzedowski 29973* (MEXU); near (SW of) Villa Juárez, Apr. 8, 1944 (young fl.), *Miranda 3227* (MEXU); Municipio Xicotepec de Jérez, 5 km NE of Xicotepec, road to La Ceiba, 20°19'N 97°48'W, 1200 m alt., Feb. 24, 1987 (immature fr.), *Tenorio 12612* (MO); same locality, 1200 m alt., Feb. 24, 1987 (immature fr.), *Toriz 297* (MEXU, MO); Municipio Zacapoaxtla, Arroyo Tenaxatena to W of Apulco, 1300 m alt., Apr. 12, 1985 (immature fr.), *Tenorio 8669* (MO (2 sheets)); La Unión, 12 km NE of Tlatlauqui, carr. a Mazatepec, 1670 m alt., Oct. 22, 1987 (immature fr.), *Tenorio 14260* (MO). Queretaro: Municipio Landa, 0.5 km SE of El Aguacate, 1520 m alt., Dec. 19, 1988 (fl., abnormal), *Rubio 362* (IEB, MEXU); same municipio, 1.5 km SE of El Naranjo, 1150 m alt., Nov. 6, 1990 (fl., abnormal), *Rubio 1695* (IEB); same municipio, 1 km SE of El Pemoche, 1320 m alt., May 2, 1989 (fl.), *Rubio 629* (IEB); same locality (near Agua Zarca), 1300 m alt., Dec. 14, 1988 (immature fr.), *Rubio 353* (IEB); same municipio, 1 km to Poniente de El Cerro del Fortín, 1370 m alt., Aug. 2, 1989 (fr.), *Rubio 935* (IEB, MO); same municipio, 2 km NE of Neblinas, 800 m alt., Mar. 31, 1989 (immature fr.), *Rubio 530* (IEB); same municipio, 2 km SE of Neblinas, 700 m alt., Feb. 12, 1991 (immature fr.), *Rubio 2209* (IEB, MO); same municipio, near Neblinas, 1100 m alt., Sep. 14, 1988 (fl. or immature fr.), *Rzedowski 46423* (IEB, MEXU); same municipio, 6 km NE of Agua Zarca, on the way to Neblinas, 1100 m alt., May 12, 1988 (fl.), *Rzedowski 46588* (MO); 2 km W of Neblinas, Canón del Río Tancuilín, 900-950 m alt., Jun. 3, 1993 (fl. & fr.), *Lorea 5553* (FCME, MO); Municipio Jalpan, 3-4 km to N of La Parada, 1250 m alt., Mar. 16, 1990 (fl.), *Servín 27* (MO); same municipio, 3-4 km to Poniente from San Isidro, La Parada, 1150 m alt., Jul. 11, 1990 (fr.), *Servín 339* (MO); same municipio, 3-4 km to E of San Isidro, La Parada, with border of San Luis Potosí, 1400 m alt., Mar. 20, 1991 (fl. & immature fr.), *Servín 900* (IEB, MO); same municipio, 4-5 km to Poniente from La Parada, 1500 m alt., Sep. 11, 1990 (immature fr.), *Servín 484* (IEB); same municipio, N of La Parada, 1140 m alt., Jul. 20, 1988 (immature fr.), *Carranza 832* (IEB, MO); same municipio, 1 km E of El Saucito, between La Parada and Rancho Nuevo, 1100 m alt., Jun. 23, 1988 (immature fr.), *Carranza 653* (MO). San Luis Potosí: Municipio Xilitla, 2 km SE of Ahuacatlán, 1300 m alt., Jun. 27, 1959 (fl.), *Rzedowski 10975* (MEXU); same municipio, 3 km to SE of Ahuacatlán, 1250 m alt., Apr. 10, 1960 (fl. & immature fr.), *Rzedowski 12383* (F, US). Veracruz: Cosalapa, Mar., 1922 (fl.), *Purpus 8745* (MO, NY, US);

same locality, 1400 m alt., Jun. 13, 1991 (immature fr.), *Servin 1329* (F, MO); Municipio Huayacocotla, 17km NNE of center of Huayacocotla, along road to Zontecomatlán, 3.2 NE of Agua de la Calabaza, 20°38'N 98°27'W, 1750 m alt., Jan. 27, 1984 (sterile), *Taylor 260* (NY); Municipio de Totutlá, Rt. 125 ca. 5 km S of Totutlá, way to Orizaba, 1300 m alt., Mar. 9, 1982 (young fl.), *Lorence 3871* (MEXU); same municipio, Totutla, 1250 m alt., May 10, 1975 (fl.), *Ventura 11312* (MEXU); Municipio Yecuatla, below Santa Rita, La Zeta, 19°49'N 96°49'W, 1200 m alt., Oct. 31, 1989 (immature fr.), *Gutierrez 3711* (MEXU); Sierra de Chiconquiaco between Chiconquiaco and Misantla, 1160 m alt., Aug. 13, 1962 (sterile), *Gómez 795* (MEXU); same locality, 1100 m alt., Aug. 13, 1962 (sterile), *Gómez 795* (MEXU). Locality unknown (Rio Jucatusau?), (fl.), *anonymous (438)* (US).

Beilschmiedia mexicana appears to be close to *B. pendula*, sharing almost same floral characters. But *B. mexicana* usually has the ramification conspicuously raised on both sides, acute leaf apices and non-glaucous lower leaf surfaces, while *B. pendula* usually has the ramification immersed above (although the pattern is visible), acuminate leaf apices and glaucous lower leaf surfaces. Additionally, the ramification is difference between these two species; *B. mexicana* has the ramification circle-like, while *B. pendula* has the ramification square-like. There is a distribution gap between them; *B. pendula* is widely distributed from Nicaragua to Bolivia and the West Indies, but *B. mexicana* is distributed only in Mexico.

There are several collections which I placed in *B. mexicana* with some hesitation (*Breedlove 56219*, *Carranza 653*, *Lorea 5533*, *5535*, *Méndez 7686*, *Servín 27*, *339*). Compared to the typical collections of *B. mexicana*, these collections have firm leaves, immersed ramification on the upper leaf surfaces, and relatively finer ramification on the lower leaf surfaces. And some of the collections have glaucous leaves (*Carranza 832*, *Servín 27*, *339*). They might represent a different species, but we do not have enough material to clarify whether the differences are strong enough to separate them from *B. mexicana*.

17. *Beilschmiedia miersii* (Gay) Kostermans, Rec. Trav. Bot. Néerl. 35: 860. 1938.

Bellota miersii Gay, Historia Física y Política de Chile, Botanica 5: 298. 1849. TYPE: Chile. Aconcagua: (fl.), *Gay 236* (holotype, P).

Tree, to 25 m tall. Terminal buds densely pubescent with erect curly hairs, rarely with erect, slightly wavy hairs. Twigs terete, compressed when young, pubescent with erect, curly to wavy hairs, usually densely so when young, less densely when old. Leaves opposite; petioles 0.3-1 cm long, sulcate to canaliculate or rarely flat to terete above,

pubescent with erect, curly to wavy hairs, concolorous with twigs; blades coriaceous, dried to light green, roundish-ovate, (2.5) 5-12 x (1.5) 2.5-6.5 cm; base round to obtuse, flat or rarely slightly inrolled toward lower surface, apex obtuse to round, sometimes retuse; leaf surface glabrous on both sides, rarely sparsely pubescent along the midrib; midrib immersed above, raised below, secondary veins (5) 7-8 (10) pairs, slightly raised or almost immersed above, slightly to conspicuously raised below, tertiary veins not percurrent, ramification coarse, with free veinlets, slightly raised or almost immersed above, slightly raised below. Inflorescences axillary (sometimes two inflorescence from one axil of the leaf), paniculate with few branches, 2-6 (9) cm long, more or less densely pubescent with erect curly hairs, with 10-25 (35) flowers per inflorescence; flower pedicels of the lateral divisions 0.5-1 mm long, pedicels of the central flowers up to 3.5 mm long. Flowers 2.5-3 mm long, 3.2-3.5 (4.2) mm in diam.; tepals 6, equal, ovate, 1.2-1.5 (2.2) mm long, 1.2-1.7 (2.5) mm wide, more or less densely pubescent with erect curly hairs outside, densely pubescent with erect long hairs inside; stamens 9, outer six filaments ca. 0.2 mm long, innermost three stamens ca. 0.3 mm long, filaments pubescent, outer six anthers 0.7-1 mm long, inner three anthers 0.6-0.8 mm long, all the anthers 2-celled, apex of the anthers obtuse to truncate, apex of the anthers glabrous, glands of the innermost three stamens globose; staminodia 3, triangular in outline, ca. 0.5 mm long; pistil 1.4-1.6 mm long, glabrous or rarely sparsely pubescent, ovary longer than and gradually narrowed into the style; receptacle pubescent with long appressed hairs. Fruits ellipsoid, up to 4 x 3 cm (fide Kostermans, 1938), the surface smooth; fruit pedicels in mature fruit unknown.

Phenology: collected in flower from January to June and October to November, collected with detached mature fruits in January.

Distribution: Chile, 120-900 m alt. (Fig. 11).

Habitat: unknown.

Common name: "Bellota".

Economic use: reported as a useful timber for general construction and shipbuilding by Record and Hess (1942).

Additional specimens examined: **Chile**. Aconcagua: Zapallar, stream of Tigre, Feb. 27, 1952 (fl.), *Boelcke 6466* (F, MO). Santiago: Acules, Apr., 1902 (fl.), *Remy 108* (BM, MO); Quwilá? Norwal, Mar., 1952 (fl.), *R. to. de V.? s.n.* (NY); locality unknown, 1864 (fl.), *Philippi 964* (P). Valparaiso: Chiens, near Concon,

Aug. (immature fr.), *Diar 112* (BM); Concon, (fl.), *J. Miers s.n.* (BM) above Campana, near Limache, Feb. 2, 1964 (young fl.), *Nr547* (B); Cajon de San Pedro, W side of Campana de Quillota, 700-900 m alt., Jan. 19, 1936 (fl & detached fr.), *West 5195* (MO); same locality, Oct. 1829 (young fl.), *Bertero1078* (BM, NY, P); Limache, Mar. 1865 (sterile or fl.), *anonymous* (BM); Quillota, San Pedro, Oct. 1832 (fl.), *Bridge 506* (K); Quillota, stream Alarza near Limache, Nov. 24, 1991 (fl.), *Zöllner 18999* (MO); Quillota, Cerro Granizo, 32°59'S 71°10'W, 300 m alt., Mar. 18, 1967 (fl.), *Schlegel 5927* (B); Granizo, Jan. 15, 1983 (fl. (fl. & detached fr. in MO), *Zöllner 11607* (MO, US); Zapallar, stream Cadillo, 120 m alt., Mar. 27, 1968 (fl.), *Schlegel 6247* (B). Locality unknown, (fl. & leaf in a pocket), *Philippi s.n.* (F). cultivated, Dec. 5, 1991 (young fl.), *Taylor10883* (MO). cultivated in Los Angeles, Jun. 25, 1969 (fl.), *Thorne 38072* (BM, MO, NY).

Beilschmiedia miersii is one of only two *Beilschmiedia* species from Chile. About the difference between *B. miersii* and another Chilean species, *B. berteroana*, see the notes under *B. berteroana*.

Nees (1836) used the name *Boldu chilanum* for this species, but also cited *Boldus chilensis* Molina as a synonym. Therefore, *Boldu chilanum* has the same type as *Boldus chilensis*; this type belongs to the Monimiaceae and hence Nees' name cannot be applied to *Beilschmiedia miersii*.

It is very rare to see persistent tepals in neotropical *Beilschmiedia* species even in young fruit. Most of the species have their tepals fall soon after the anthesis. However, I observed a collection of *B. miersii* in young fruit (*Diar 112*), which showed persistent tepals on the pedicels.

Two collections of this species in flower (*Zöllner 11607*, *anonymous (Nr.? 547)*) have a foliose bract on the rachis, which is also rare for neotropical *Beilschmiedia* species. However, it is not a good character to define this species because it is not consistently present in this species.

18. *Beilschmiedia obovatifolia* Sa. Nishida sp. nov. TYPE: Costa Rica. Guanacaste: Cantón de Tilarán, Cordillera de Tilarán, Las Nubes de Río Chiquito, Mt. Olivo, 10°21'00"N 84°51'00"W, 1450 m alt., Jan. 29, 1992 (fr.), *Guindon & Brenes 40* (holotype, MO; isotypes, CR, INB, MO, USJ).

A Beilschmiedia ovalis foliis obovatis et fructibus ellipsoideis differt.

Tree, to 20 m tall. Terminal buds pubescent with erect short curly hairs. Twigs terete, angular when young, densely pubescent with erect short curly hairs, less denser when old. Leaves alternate; petioles 1-1.5 (2) cm long, almost flat above, sparsely pubescent with erect short curly hairs, concolorous with twigs; blades coriaceous, obovate, rarely elliptic, 6-13 x 4-7 cm; base cuneate, not inrolled, apex obtuse; leaf surface glabrous on both sides, lower leaf surface glaucous; midrib immersed above, raised below, secondary veins 7-11 pairs, almost immersed, rarely impressed above, raised below, tertiary veins percurrent, ramification fine, areolate without free veinlets, immersed above, raised below. Inflorescences axillary, paniculate, 5-12 cm long, sparsely pubescent with erect short curly hairs or almost glabrous, with 20-30 flowers per inflorescence flower pedicels of the lateral divisions 0.5-0.7 (1) mm long, pedicels of the central flowers up to 2 mm long. Flowers creamy, ca. 2.3 mm long, ca. 2.6 mm in diam.; tepals 6, equal, ovate, ca. 1.5 mm long, ca. 1.2 mm wide, sparsely pubescent with erect hairs on both sides; stamens 9, filaments ca. 0.4 mm long, pubescent; anthers ca. 1 mm long, all anthers 2-celled, apex of the anthers obtuse, apex of the anthers glabrous, glands of the innermost three stamens globose; staminodia 3, triangular in outline, ca. 0.7 mm long; pistil ca. 1.5 mm long, glabrous, ovary as long as the style or longer than and gradually narrowed into the style; receptacle sparsely pubescent with appressed hairs. Fruits ellipsoid or obovoid, black, 5.5-6.5 x 2-2.5 cm, the surface smooth; infructescence axis 3-4 mm in diam., fruit pedicels thickened to 4-6 mm in diam. below the fruit; fruit pedicels not constricted at the base, covered with lenticels and almost concolorous with the infructescence axis.

Phenology: Collected in flower in April, with relatively mature fruit in January and March.

Distribution: Costa Rica and Panama, 1000-1600 m alt. (Fig. 11).

Habitat: Premontane forest.

Common name: unknown.

Economic use: unknown.

Additional specimens examined: **Costa Rica.** Alajuela: Cerros de la Palma de San Ramón, 1300-1500 m alt., Jan. 24, 1984 (fr.), *Gomez 9800* (CR, F). Guanacaste: Parque Nacional Guanacaste, Estación Cacao, Liberia, 10°55'45"N 85°28'15"W, 1100 m alt., Dec. 11, 1990 (immature fr.), *Chávez 433* (MO); 1 km N of La Cruz, 10°21'N 84°50'W, ca. 1480 m alt., Mar. 10, 1996 (immature fr.), *Yasuda 1313* (INB, MO). Puntarenas: Cantón de Tilarán 4-5 km NW Monteverde, at and just below Continental Divide, 2-4 km W of Santa Elena between road to Cañitas and upper road to Las Nubes, 10° 20'N 84°49'W, 1400-1500 m alt., Apr. 11, 1992 (fl.),

Haber 11092 (INB, MO); P. I. La Amistad; Cordillera de Talamanca; Estación Biológica Las Altura, 8°57'15"N 83°50'10"W, 1580 m alt., Mar.7.1996 (sterile), *Yasuda 1307* (INB).

Burger and van der Werff (1990) reported that a few collections which he placed in *Beilschmiedia ovalis* had obovate leaves, atypical for *B. ovalis*, and he commented that they might belong to another, undescribed, species. I have also observed several collections which share similar pubescence type and leaf texture with *B. ovalis* but have obovate leaves. They have been collected from lower elevation than where *B. ovalis* occurs, and they consistently have ellipsoid fruits, quite different from the spherical fruits of *B. ovalis*. Although I have not seen a significant difference in flower between these collections and *B. ovalis* (I have seen only one flowering collection with obovate leaves, which has less pubescent inflorescences and slightly smaller flowers than *B. ovalis*), I think obovate leaves and ellipsoid fruits are strong enough characters to distinguish the collections from *B. ovalis*. In addition to the two characters above, this new species has the tertiary veins conspicuously percurrent, which is rarely seen in *B. ovalis*.

Usually, *B. obovatifolia* has the ramification conspicuously raised below and the fruit pedicels slightly thickened below the fruits. There are two collections from Costa Rica (*Burger 12184* and *Dayton 3126*) which have obovate leaves, but I keep the collections separate from this species as indeterminate, because the collections have almost immersed ramification and the fruits of the former collection have narrow pedicels.

19. *Beilschmiedia ovalioides* Sa. Nishida sp. nov. TYPE: Mexico. Oaxaca: Distrito de Ixtlán, Sierra de Juárez, enroute from Xiacui to Talea de Castro, ca. 25 km SSW of Talea from the route, 2750 m alt., Apr. 19, 1982 (fl. & fr.), *Lorence 4078* (holotype, MEXU; isotype, F, MO).

A *Beilschmiedia ovalis* petiolis longioribus et foliis subtus puberulis differt.

Tree, to 35 m tall. Terminal buds densely pubescent with rusty, erect short curly hairs. Twigs terete, slightly angular when young, densely pubescent with rusty, erect short curly hairs. Leaves alternate; petioles (1.7) 2-3 cm long, flat above, rarely slightly canaliculate above, pubescent with rusty short curly hairs, less densely when old, concolorous with twigs; blades coriaceous, broadly elliptic to obovate, sometimes slightly asymmetric, (8) 11-

16 x (5) 6-10 cm; base obtuse to cuneate, not inrolled, apex acute to acuminate; upper leaf surface glabrous, lower leaf surface puberulent with short curly hairs, lower surface usually glaucous; midrib and secondary veins immersed above, raised below, secondary veins (8) 11-14 pairs, tertiary veins percurrent, ramification fine, areolate without free veinlets, immersed above, slightly raised or immersed below (ramification pattern visible below). Inflorescences in the axils of the leaves near the terminal buds, paniculate, (4.5) 6-12 cm long, pubescent with rusty, erect short curly hairs, with 40-80 flowers per inflorescence; flower pedicels of the lateral divisions 0.5-0.7 mm long, pedicels of the central flowers up to 1 mm long. Flowers greenish-yellow, ca. 2.8 mm long, ca. 3 mm in diam.; tepals 6, equal, ovate, 1.8-2.2 mm long, 1.2-1.5 (2) mm wide, densely pubescent with erect hairs outside, sparsely pubescent with erect curly hairs to almost glabrous inside; stamens 9, filaments 0.3-0.5 mm long, pubescent, anthers ca. 0.9 mm long, all the anthers 2-celled, apex of the anthers obtuse to truncate, glabrous, glands of innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.7 mm; pistil ca. 1.5 mm long, glabrous, ovary as long as the and gradually narrowed into the style; receptacle pubescent with long, appressed to erect hairs. Fruits roundish, black, 3-3.5 x 3-4 cm, the surface smooth; infructescence axis ca. 5 mm in diam., fruit pedicels thickened to 10 mm in diam below the fruit; fruit pedicels not constricted at the base, covered with few lenticels and slightly darker than the infructescence axis.

Phenology: collected in flower in May and August, in mature fruit in February, April and November.

Distribution: Mexico, 1850-2750 m alt. (Fig. 12).

Habitat: montane mesophyll forest.

Common name: unknown.

Economic use: unknown.

Additional specimens examined: **Mexico**. Chiapas: Municipio Unión Juárez, in El Volcán Tacaná by a road from Talquián to the top of the volcano, along the border with Guatemala, 2200-2700 m alt., Feb. 4, 1987 (fr.), *Martinez19456* (MO). Oaxaca: Sierra de Juárez, ca. 25km SSW of Talea de Castro, or 3km N of the junction to Yalina, limit of the district of Ixtlán & Villa Alta, 2750 m alt., May 31, 1983 (fl.), *Cedillo2372* (F, MEXU, MO); W of Municipio San Felipe Usila, 8 km straight S from Santa Cruz Tepetotutla, 17°40'06"N 96°33'24"W, 2395 m alt., Mar. 31, 1994 (young fl.), *Gallardo 1007* (MEXU); Distrito Choapam, road from Totontepec to Comaltepec, 5 km NE of Totontepec, 1850 m alt., Nov. 11, 1983 (fr.), *Lorence4376* (F, MEXU, MO); 20 km

SE of Totontepec, 250 m alt.? (mistake for 2500 m ?), Aug. 9, 1977 (fl.), *Sousa 7871* (UC); Distrito Villa Alta, 8.1 km N of Maravillas, road between Talea de Castro and Yalina, 2370 m alt., May 15, 1983 (fl. & a part of fr.), *Torres 2947* (F, MEXU, MO); Municipio San Felipe Usila, 7.3 km S (179°) of Santa Cruz Tepetotutla, 17°40'23"N 96°33'28"W, 2220 m alt., May. 15, 1994 (fr.), *Rincón 419* (MEXU); same municipio, 7.6 km S (179°) of Santa Cruz Tepetotutla, 17°40'13"N 96°33'28"W, 2240 m alt., May. 16, 1994 (fl.), *Rincón 433* (MEXU).

Beilschmiedia ovalioides appears to be close to *B. ovalis*. The two species share very similar pubescence type, ramification, flower structure and fruit shape. But *B. ovalioides* has longer petioles (more than 2.0 cm long), lower leaf surfaces pubescent with curly hairs, secondary veins more than 11 pairs and conspicuously percurrent tertiary veins, while *B. ovalis* has shorter petioles (less than 1.5 cm long), glabrous lower leaf surfaces, secondary veins less than 9 pairs and tertiary veins not conspicuously percurrent. Those characters are not strong individually, but the combination of them separate these two species clearly. Additionally, *B. ovalioides* tends to have larger (more than 11 cm long) and broadly elliptic to obovate leaves, whereas *B. ovalis* usually has smaller (less than 10 cm) and ovate or elliptic leaves. Both of the species occur above 1800 m in elevation, but the distribution has some disjunction; *B. ovalioides* has been collected only in Mexico, whereas *B. ovalis* has been collected in Honduras, Costa Rica and Panama. One specimen of *B. ovalioides* is reported from 250 m alt., but considering the locality, this altitude is likely a mistake for 2500 m alt.

There is a collection from Chiapas which has pubescent lower leaf surfaces, but has shorter petioles (1.5-2.0 cm long) and less secondary veins (8-10) than the typical *B. ovalioides* (*Martínez 19456*). Because the leaves have abnormal apices, I place this collection in *B. ovalioides*, assuming that the leaves are somewhat damaged.

20. *Beilschmiedia ovalis* (Blake) C. K. Allen, *J. Arnold Arbor.* 26: 418. 1945.

Hufelandia ovalis Blake in *Jour. Wash. Acad. Sci.* 9 :461. 1919. TYPE: Costa Rica.

Alajuela: Volcan de Poás, 2300 m alt., (fl.), Mar. 31, 1907, *Pittier 2040* (holotype, US; isotype, F).

Beilschmiedia austin-smithii (Standley) C. K. Allen, *J. Arnold Arbor.* 25: 418. 1945. *Persea*

austin-smithii Standley, *Field. Mus. Publ. Bot.* 18:1552. 1938. Type: Costa Rica.

Alajuela: Cantón de Alfaro Ruiz, Palmira, (fl.), Apr. 30, 1937, *Smith 4168* (holotype: F).

Tree, to 30m tall. Terminal buds pubescent with erect short curly hairs. Twigs terete to angular, densely to sparsely pubescent with short curly hairs, less denser to glabrous when old. Leaves alternate; petioles 1-1.5 cm long, flat above, glabrous or rarely pubescent with short curly hairs, concolorous with twigs; blades coriaceous, ovate to broadly elliptic, (4) 5-10 (14) x (3) 4-8 (10.5) cm; base obtuse to round, not inrolled, apex obtuse; leaf surface glabrous on both sides, rarely partly pubescent with erect curly hairs when young, lower surface glaucous; midrib immersed above, raised below; secondary veins 5-8 (9) pairs, immersed above, raised below; tertiary veins not percurrent or weakly percurrent, ramification fine, areolate without free veinlets, immersed or slightly raised above, slightly to conspicuously raised below. Inflorescences axillary or clustered on the terminal buds, paniculate, (3) 5-15 cm long, pubescent with erect hairs, with 20-50 flowers per inflorescence; flower pedicels of the lateral divisions 0.5-1.2 mm long, pedicels of the central flowers up to 2 mm long. Flowers yellowish, 2.5-3.2 mm long, 2.9-3.7 mm in diam.; tepals 6, equal, ovate to elliptic, (1.4) 1.8-2.3 mm long, 1-1.7 mm wide; pubescent with erect hairs on both sides; stamens 9, outer six filaments 0.3-0.5 mm long, innermost three filaments 0.5-0.7 mm long, filaments pubescent, anthers ca. 1 mm long, all of them 2-celled, apex of the anthers more or less obtuse, apex of the anthers glabrous, glands of the innermost three stamens globose; staminodia cordate in outline, 0.5-1 mm long; pistil 1.3-1.7 mm long, glabrous, ovary almost as long as or longer than and gradually narrowed into the style; receptacle relatively densely pubescent with long, erect to almost appressed hairs. Fruits (known only in immature stage) roundish, green when immature, ca. 3.5 x ca. 3.5 cm (or bigger), the surface smooth; fruit pedicels ca. 5 mm in diam., thickened to ca. 10 mm in diam. below the fruit; pedicels not constricted at the base, concolorous with the lower part.

Phenology: collected in flower from February to May, and in September and November, in mature fruit in November.

Distribution: Honduras, Costa Rica, Panama, in 1800-2800 m alt. (Fig. 12).

Habitat: cloud forest.

Common name: "Aguacate negro" in Costa Rica, "Aguacatillo" in Panama.

Economic use: unknown.

Additional specimens examined: **Honduras.** Comayagua: 10.5 km E of lago Yojoa, Cerro Azul Meámbar, on the ridge leading to the Cerro Azul peak, 14°48'N 87°53'W, 1870 m alt., Mar. 12, 1993 (fr.young), *Thomas 584* (MO). **Costa Rica.** Alajuela: Palmire, 1900 m alt., May 27, 1938 (old fl.), *A. Smith NY675* (F, NY). Heredia: Volcán Barba, 1800-2000 m alt., Nov. 14, 1971 (sterile), *Holdridge 6595* (CR, NY); S slope of Volcan Barba, along road above Porrosatí, 2500 m alt., Mar. 11, 1973 (fl.), *Hartshorn 1127* (CR, F, MO); Parque Nacional Braulio, Carrillo Límite of Volcán Barva, 10°08'05"N 84°06'20", 2800 m alt., Nov. 9, 1989 (fl. & fr), *Rivera 174* (CR, INB, MO). San José: Cantón Aserri, Z. P. Cerros de Escazú, valley of Río Grande de Tárcoles, El Cedral, Alto Hierbabuena, 9°50'30"N 84°06'35"W, 2150 m alt., Nov. 6, 1993 (sterile), *Morales 1952* (INB, MO); same locality, Mar. 1, 1996 (fl.), *Yasuda 1300, 1301* (INB, MO); Finca La Cabana, 3 km W of Rancho Redondo, Highway 6, ca. 1800 m alt., May 29, 1967 (fl. & immature fr.), *Weston 4868* (F). **Panama.** Chiriquí: Cerro Punta, 2000 m alt., May 24, 1946 (fl?, missing), *P. H. Allen 3490* (MO); same locality, 2000 m alt., Sep. 14, 1971 (fl. & immature fr.), *Lao 395* (MO, NY); Around Camp Aguacatal, E slope of Chiriquí Volcano, 2100-2200 m alt., Mar. 10-13, 1911 (fl.), *Pitter 3084* (US); 3.7 km along road through Bajo Grande from bridge NE of Cerro Punta, 8°50'N 82°32'W, 2250-2400 m alt., Nov. 9, 1980 (young fl.), *Sytsma 2148* (MO).

Kostermans (1938) regarded *Hufelandia ovalis* Blake as a synonym of *Beilschmiedia sulcata*. But Allen (1945) reestablished it as *B. ovalis*, because she thought it was difficult to accept Kostermans's conclusion without more widely collected material. Allen did this without seeing the type of *H. ovalis*. And in the same paper, she described a new species, *B. austin-smithii*, based on a collection which is actually conspecific with *B. ovalis*. The type collection of *B. austin-smithii* has more pubescence on the petioles and lower leaf surfaces than the typical collections of *B. ovalis*, probably because the type collection of *B. austin-smithii* has relatively young leaves, and there are no other significant differences between the collection and *B. ovalis*.

Beilschmiedia ovalis has alternate leaves and fine ramification. This species is distinguished from the other species with alternate leaves and fine ramification by its short curly pubescence on the terminal buds and twigs, coriaceous, ovate-broadly elliptic and glabrous leaves, and roundish fruits. This species shares similar leaf shape with *B. latifolia* and *B. towarensis*, similar pubescence type with *B. obovatifolia* and *B. steyermarkii*, and similar reproductive characters with *B. ovalioides*. All the latter five species share similar ramification pattern with *B. ovalis*. About differences between *B. ovalis* and each of the five species, see Table 2 and the notes under the five species respectively.

There are several collections from Costa Rica and Panama, which approach to *B. ovalis* in the pubescence type, ramification pattern on lower leaf surface and flower structure. But they have larger leaves than the typical collections of *B. ovalis*. Burger and van der Werff (1990) accepted them as a large-leaved form of *B. ovalis* at lower elevation. However, those collections also differ from the typical collections of *B. ovalis* in the number of secondary veins, form of tertiary veins, ramification on upper leaf surfaces and fruit shape. These collections are actually very similar to the typical collections of *B. alloiophylla* except for the absence of pubescence on the lower leaf surfaces. I place these collections in *B. alloiophylla* (see the notes under *B. alloiophylla*).

21. *Beilschmiedia pendula* (Swartz) Hemsley, Biol. Cent.-Amer., Bot. 3: 70. 1882. *Laurus pendula* Swartz, Prodr.: 65. 1788. *Hufelandia pendula* (Swartz) Nees, Plantarum Laurinarum Secundum Affinitates Naturales Expositio: 22. 1833. TYPE: Jamaica.: locality unknown, Swartz *s.n.* (BM, C-2 sheets, S not seen).

Hufelandia thomaea Nees, Plantarum Laurinarum Secundum Affinitates Naturales Expositio: 23. 1833. TYPE: St. Thomas. locality and collector unknown (B not seen, P not seen).

Tree, to 35 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, compressed when young, pubescent with appressed straight hairs, less densely to glabrous when old. Leaves alternate; petioles (0.7)1-1.5 (2) cm long, flat or rarely canaliculate above, glabrous or sparsely pubescent with appressed hairs, concolorous with the twigs; blades firmly chartaceous, elliptic to oblanceolate, 4-13 (22) x 2-5 (10.5) cm; base cuneate, not inrolled, apex acuminate or very rarely acute to obtuse; upper leaf surface glabrous, lower leaf surface glabrous or rarely sparsely pubescent with appressed hairs, lower leaf surface glaucous, very rarely not glaucous; midrib immersed above, slightly raised below, secondary veins (5) 7-10 (12) pairs, immersed above, slightly to conspicuously raised or rarely almost immersed below, tertiary veins not percurrent or rarely more or less percurrent, ramification fine, areoles in square or rectangular with a few free veinlets, immersed above (but the pattern partially visible), almost immersed or slightly raised below, the pattern visible on the upper surface much coarser than on the lower surface. Inflorescences axillary, paniculate with few branches, 3-14 (17) cm long, almost glabrous or sparsely pubescent with short appressed hairs, with (5) 10-25 (40) flowers per

inflorescence; flower pedicels of the lateral divisions 0.5-1 (1.5) mm long, pedicels of the central flowers up to 4 mm long. Flowers greenish yellow to whitish, 2-3 mm long, 2.3-2.8 mm in diam.; tepals 6, equal, ovate, 1.2-1.7 mm long, 0.8-1.4 mm wide, sparsely pubescent with appressed to erect hairs on both sides; stamens 9, outer six filaments 0.3-0.4 mm long, innermost three filaments 0.4-0.6 mm long, filaments pubescent, anthers ca. 0.8 mm, all the anthers 2-celled, apex of the anthers obtuse-acute to truncate, glabrous, glands of the innermost stamens globose; staminodia 3, cordate in outline, ca. 0.8 mm long; pistil ca. 1.5 mm long, glabrous or rarely sparsely pubescent, ovary almost as long as and gradually narrower into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, black, shiny, ca. 2-3.5 (4.5) x ca. 1.5 cm, the surface smooth; infructescence axis ca. 2 mm in diam., fruit pedicels constricted at the base, slightly thickened below the fruit, infructescences not covered with lenticels and the fruit pedicel concolorous with the infructescence axis.

Phenology: collected in flower from February to November, in mature fruit from March to November.

Distribution: Honduras, Nicaragua, Costa Rica, Panama, West Indies, Venezuela, Colombia and Ecuador, 0-1680m alt. (Fig. 13).

Habitat: montane broad-leaved forest, tropical wet forest, sometimes on limestone.

Common name: "Mulato" and "Carne de doucella" in Cuba, "Lauries formis" in St. Lucia, "Vacarita" in Panama, "Carabali" and "Cobalongo mach" in Venezuela.

Economic use: reported to be useful as a timber in Dominica, Martinique, Montserrat and St. Lucia.

Additional specimens examined: **Cuba**. Camagüey: Loma del Gato and Vicinity Cobre Range of Sierra Maestra, Jul. 11-Aug. 14, 1921 (immature fr.), *León 10451* (NY). Cienfuegos (Las Villas): SE of Cumanayagua, Sierra de San Juan, 3-400m alt., Jul. 1941, (fl.), *Howard 5695* (F, MO, NY, U). Guatánmo (Oriente): E. Cuba, Monte Verde, 1856-7 (fl. & immature fr.), *Wright 485* (BM, BR, MO, NY); same locality, Sep. 1859-Jan. 1860 (immature fr.), *Wright 1402* (K, MO, NY), (fl.), *Wright 1403* (1402 & 1402, rarely 1414, on same sheets) (K, MO), (immature fr.), *Wright 1414* (BR, MO, NY); Río Purial, 200 m alt., May, 1889 (immature fr.), *Eggers 5434* (P); locality unknown, 1856-7 (fr.), *Wright 486* (BR, NY, MO (sterile)). Holguín (Oriente): Pierra de Nipe, at Río Piedras, 500 m alt., Aug. 24, 1915 (immature fr.), *Ekman 6402* (F, NY, US); Sierra de Nigre (Negro?), at Río Piloto, ca. 350 m alt., Mar. 14, 1915 (sterile), *Ekman 5009* (NY). Sancti Spíritus (El Porvenir): Santa Clara, Mts. Trinidad, 650-750 m alt., Mar. 9, 1910 (fl.), *Britton 5320* (NY). Sancti

Spíritus (Las Villas): same mountains, San Blas-Buenos Aires, Gaviñas, Sep. 18, 1941 (young fr.), *Gonzales 173* (B, BM, NY). Sancti Spíritus (Santa Clara): Mts. Banao, May., 1920 (immature fr.), *Luma?650* (NY); same locality, 950 m alt., Jul. 30, 1918 (immature fr.), *León 7975* (NY); Sierra de Gavilanes, Mts. Sancti-Spiritus, Aug. 1-2, 1916 (immature fr.), *León 6612* (NY). Santiago de Cuba (Oriente): S side of the crest of the Sierra Maestra, La Bayamesa, W of Aserradero San Antonio de los Cumbres, 1400-1500 m alt., Jan. 23-24, 1956 (young fl.), *Morton 9563* (US); Sierra Maestra S of Yara in headwaters of Rio Yara, Alto de Naranjo, Trail to Pico Turquino, 76°52'W, 900-950m alt., Jul. 9, 1985 (fl. & young fr.), *Gentry50952* (MO, NY); S. Oriente and Pico Turquino, Sauks of arroyo del Cristo, Aug. 10, 1922 (immature fr.), *Ekman14826* (NY). Villa Clara (Las Villas): St. Domingo, 600 m alt., May. 24, 1887 (fl.), *Eggers 2087* (NY). Villa Clara (Santa Clara): Buenos Aires, Trinidad Hills, 750-1150 m alt., Mar. 8, 1929 (immature fr.), *Jack 7016* (NY); Buenos Aires, Las Lagunas, ca. 750 m alt., Dec. 5, 1928 (immature fr.), *Jack 6806* (F (2 sheets), NY, US). **Jamaica.** Clarendon, Along road between Ritchies & Balcarres, 900 m alt., Nov. 10, 1973 (immature fr.), *Proctor33607* (MO); same locality, 900 m alt., Apr. 24, 1974 (fl.), *Proctor33791* (NY); same locality, 900 m alt., Oct. 5, 1977 (immature fr.), *Proctor 37316* (MO); same locality, 900 m alt., Jun. 12, 1976 (old fl. & young fr.), *Thorne 48212* (MO, NY); Manchester, Sep. 21-23, 1908 (immature fr.), *Britton 3691* (NY); Manderille, ca. 630 m alt., Sept., 21, 1908 (immature fr.), *Harris10594* (F, NY, US); near Siver Hill, Set. 25, 1894 (sterile), *Harris5286* (BM); Scher Hill Galp., ca. 1050m alt., Aug. 10, 1895 (fl.), *Harris 5843* (BM, F, NY, US); Spanish River, Aug. 24, 1894 (young fr.), *Harris5326* (BM); Troy, Sep. 13-18, 1906 (fl.), *Britton660* (F, NY); Troy, ca. 480 m alt., Sep. 18, 1906 (fr.), *Harris 9447* (NY); Whitfield Hall, Feb. 1, 1895 (immature fr.), *Harris5575* (BM, F). **Haiti.** Ouest: Gros Cheval, Mornes des Commissaires, 1400 m alt., Mar. 17, 1942 (immature fr.), *Holdridge 1053* (BM, F, MO, NY (2 sheets), US). Ouest or Artibonte: Corail, Camp #1, ca. 600 m alt., Jul. 16-17, 1905 (immature fr.), *Nash1035* (NY). Sud: Grand'Anse-Sud limit, Massif de La Hotte, 13.6 km N of Camp Perrin on road between Roseaux and Jérémie, "Tombeau Cheval", 18°23'N 73°53'W, 720 m alt., Nov. 15, 1982 (immature fr.), *Zanoni 24313* (MO); Massif de la Hotte, Pic Macaya National Park, on hills S of Mome Formon, near Ville Formon, 1200-1250 m alt, Feb. 1, 1984 (immature fr.), *Judd3983* (NY); Massif de la Hotte, N Tranchant, near Godet, ca. 1600 m alt., Sep. 19, 1924 (fl.), *EkmanH1950* (K, US). Locality unknown: Jun. 19, 1964 (fl.), *Augusto 1569* (NY). **Dominica.** Barahona: "El Gajo" ca. 7 km from the carretera de Cabral a Polo, through the way to "Entrada de Cortico" ("Monteada Nueva"), 18°07.5'N 71°13.5'W, 1400 m alt., Jan. 18, 1986 (immature fr.), *Zanoni 36009* (MO, NY); "Entrada de Cortico" ("Monteada Nueva"), above the batey de cafe "Monte Nueva", on the peak of la Loma Trocha de Pey, 18°07.5'N 71°13.5'W, 1400 m alt., Jan. 14, 1988 (immature fr.), *Zanoni40676* (MO, NY, U); Mt. Nueva, Caña Brava, 1300 m alt., Apr. 24, 1976 (young fl.), *Liogier 25140* (NY); same locality (S. of Cabral), 1300 m alt., Jun. 15, 1968 (fl.), *Liogier 11658* (NY); Mt. Nueva, 6.3 km from Cruce de El Puerto-Monteado-Nueva, 3.4 km E of Cortico, 18°10'N 71°15'W, 1390 m alt., Apr. 11, 1985 (fr.), *Gentry 50705* (MO); Sierra de Baoruco, Lomas la Trocha de Pey, above Monteada Nueva, 1400 m alt., Oct. 16, 1982 (immature fr.), *Proctor39101* (MO); Sierra de Baoruco; 4 km above a small village "Entrada de Cortico", enroute to El Gajo, 18°07.5'N 71°13.5'W, 1320-1340 m alt., Mar. 25, 1990 (fr.), *Zanoni 44246* (MO, NY); Sierra de Baoruco, on the hill to Morne La Jo, ca. 8 km N of Polo por camino, 18°08'N 71°18'W, 1200-1300 m alt., Feb.

27, 1986 (fl. & immature fr.), *Zanoni 36285* (MO, NY, U). El Seibo: Parque Nacional Los Haitises, El Coco, ca. 5 km along the sea to W of Naranjo Arriba, S border of la Bahía de Samana, 19°05'N 69°38'W, 0-20 m alt., Apr. 24, 1985 (immature fr.), *Zanoni 34216* (MO); same park, ca. 2 km W of la Caseta de Guardaparques in Mt. Bonito, 19°00'N 69°31'W, 200-300 m alt., Aug. 7, 1985 (mature and immature fr.), *Mejía 35524* (MO, NY, U); same park, ca. 20 min. walk from Caseta de Guardaparques de Monte Bonito enroute to Pilacon, 19°00'N 69°30'W, Feb. 20, 1986 (fl.), *Zanoni 36238* (MO, NY). Espaillat: N of Moca, Jamao, La Cumbre, 700-800 m alt., May. 27, 1969 (old fl.), *Liogier 15400* (NY). Jovero: locality unknown, ca. 0 m alt. Feb. 1-7, 1923 (fl. & immature fr.), *Abbot 2529* (US). Juan Santiago: Vicinity of Hondo Valle, at the headwaters of Sonador river, 1100 m alt., Sep. 9, 1968 (immature fr.), *Liogier 12616* (NY). La Vega: 3km W of La Culata on road to Bermúdez Nacional Park, 18°58'N 70°47'W, 1400m alt., Apr. 4, 1981 (immature fr.), *Mejía 12324* (MO, NY); 6 km from Pedregal de Jarabacoa on road to El Río, 19°05'N 70°35.5'W, ca. 900m alt., Apr. 15, 1981 (fl. & immature fr.), *Zanoni 12569* (MO, NY); between Jarabacca and Constanza, Loma de la Sal, vicinity of the forestry house, near Arroyo de la Sal, 1000 m alt., Aug. 7-10, 1968 (detached immature fr.), *Liogier 12016* (NY); Constanza, Río Grande, 1000 m alt., Jul. 6-7, 1973 (fl.), *Liogier 19452* (F, NY), Cordillera Central, 4.5 km SWS of the crosspoint of El Río, on highway to Constanza, stream parallel to the highway, 18°58'N 70°40'W, 1180m alt., Feb. 8, 1984 (immature fr.), *Zanoni 29152* (MO, NY); Cordillera Central, 7 km E from crossroad of El Río enroute in E to Casabito and Carretera Duarte, in a border of Rio Jimenoa, near Arroyo Frio, 19°01'N 70°35'W, 975 m alt., Feb. 25, 1982 (immature fr.), *Zanoni 19410* (MO, NY (sterile)); Cordillera Central, Constanza, El Paragua, 18°58'N 70°44'W, 1680 m alt., Jan. 23, 1986 (immature fr.), *García 952* (MO); Cordillera Central, sone of "El Convento", 8-9 km S of Constanza, enroute to Valle Nuevo and San José de Ocoa, 1500-1550 m alt., Mar. 27, 1990 (fr.), *Zanoni 44284* (MO); Jarabacoa, Manabao, 1000 m alt., Aug. 25, 1973 (detached fr.), *Liogier 20048* (NY); Jimenoa, Jun. 19, 1964 (fl. & immature fr.), *Agosto 1569* (NY); 2km W from La Culata de Constanza on road to Parque Nacional Bermudez, 18°58'N 70°47'W, 1350 m alt., Apr. 4, 1981 (immature fr.), *Zanoni 12311* (MO); property Jarabacoa, 600m alt., Jun. 1912 (fl.), *Fuertes 1617* (NY (2 sheets), U, US). Peravia: Cordillera Central, 9 km SE of San José de Ocoa, El Limón, Loma Punto 3 hour-walk from El Limón, W of source of a stream El Limón, 18°29.5'N 70°28'W, 1350 m alt., May. 29, 1984 (fl. & immature fr.), *Mejía 510* (MO, NY); Cordillera Central, El Manaclar, 18.6 km E of San José de Ocoa, enroute to Los Anones, 18°32'N 70°27'W, 1300 m alt., Mar. 6, 1985 (immature fr.), *Pimentel 242* (MO, NY); Cordillera Central, Los Cateyes, NE of la Loma Valvacoa, to NW of Baní, 18°29'N 70°23'W, ca. 1155 m alt., Nov. 26, 1981 (immature fr.), *Mejía 18334* (MO, NY); "El Manaclar (de Los Anones)", NE of San José de Ocoa, 18°31'N 70°26'W, 1200-1300 m alt., Aug. 12, 1989 (immature fr.), *Zanoni 43103* (NY); San José de Ocoa, Loma del Rancho, SE of Parra, 18°31'N 70°30'W, 1100 m alt., Aug. 16, 1980 (fl.), *Mejía 77* (NY). Puerto Plata: Loaa Isabel de Torres, near the top, 700-800 m alt., Mar. 25, 1969 (fl.), *Liogier 14544* (F, NY). San Cristobal: Cordillera Central, at the foot of la Loma del Casabe, front to the filtration bed of Corporacion de Acueducto and Alcantarrillado de Santo Domingo, in Rio Isa, 18°35'N 70°13'W, ca. 200 m alt., Jul. 25, 1984 (immature fr.), *Mejía 31389* (MO). Santiago: Mt. Colorado near La Placeta, 1000 m alt., Sep. 28, 1958 (immature fr.), *Jiménez 3842* (US). Santo Domingo: Cordillera Leptentrional pro., Puerto Plata, Losúa, near Jagua-mocha, Apr. 3, 1930

(fl.), *Ekman H14565* (MO), Apr. 3, 1930 (fl.), *Ekman 14565* (MO); locality unknown, 600 m alt., May. 24, 1887 (old fl.), *Eggers 2087* (BM). Valverde-Santiago: Cordillera Septentrional, on Loma El Murazo, 19°41'N 70°58'W, 1083 m alt., Dec. 18, 1984 (immature fr.), *Zanoni 32890* (NY). Province unknown: 1 mile E of Laudat, ca. 665 m alt., Mar. 11, 1940 (immature fr.), *Hodge 1958* (US); Sylvania, 600 m alt., Feb. 27, 1946 (immature fr.), *Beard 636* (NY, U). Locality unknown: *Beard 1454* (NY, US). **Puerto Rico.** Adjuntas, in a forest near a stream of Yunro, May. 22, 1886 (fl.), *Sintenis 4398* (B, BM, BR, NY, P, US); Adjuntas, in a forest in Mt. Cienega of La Lucia, Apr. 11, 1886 (fl.), *Sintenis 4137* (B, BM, US); Adjuntas, in a forest in Mt. La Vega, Jun. 24, 1886 (fl. & immature fr.), *Sintenis 4700* (B, BM, F, MO, NY, US); Caribbean National Forest, Highway to Bella Vista Luquillo, Aug. 10, 1950 (immature fr.), *Little 13594* (F, NY); same forest, El Verde Research Station, 18°20'N 65°45'W, 350 m alt., Jun. 19, 1990 (sterile), *Atwell 2* (MO); N. of Yauco, Rubias, ca. 800 m alt., Feb. 11, 1923 (old fl. & fr.), *Britton 7364* (NY); Sierra de Naguabo, in a forest near Rio Blanco, JNov. 4, 1886 (mature & immature fr.), *Sintenis 5317* (B, BM, BR, F, K, MO, NY, P, US); Sierra de Yunros, in a forest in Mt. "Guvuy", Aug. 28, 1885 (sterile), *Sintenis 2678* (NY); locality unknown, Aug. 28, 1940 (fl.), *Gregory 134* (NY); locality unknown, 1886 (fl.), *Sintenis 6523* (B (2 sheets)). **St. Kitt.** Lawnent? estate, Sep. 8-Oct. 5, 1901 (immature fr.), *Britton 634* (NY). **Montserrat.** Centre Hills, 400 m alt., Nov. 7, 1944 (fl.), *Beard 409* (NY, U); Mt. Olveston, 400 m alt., Nov. 14, 1944 (immature fr.), *Beard 438* (NY, U); W of the Soufrière, Feb. 18, 1907 (immature fr.), *Shafer 588* (NY); locality unknown, 1778? (fl.), *Ryan s.n.* (BM). **Guadeloupe** (and dependances). St. Louis: valley of St. Louis, 700 m alt., Sep. 18, 1899 (fl.), *Duss 4014 (4006)* (NY). **Martinique.** Pinte-Notie, 300-700 m alt., 1897 (young fl. & fr.), *Duss 3863* (NY); along Calebass, Monse Martin, 310-600 m alt., 1880 (immature fr.), *Duss 222* (NY); same locality?, 1899 (fl.), *Duss 4096* (on the same sheet with *Duss 222*) (NY); locality unknown, May., 1870 (fr.), *Hahn 1368* (BR, P); locality unknown, (young fl.), *Hahn 1511* (BR); locality unknown, (fr.), *Hahn s.n.* (BM); locality unknown, (sterile), *Plée 204* (P). **St. Lucia.** Fouds St. Laeques, Mar. 26, 1889 (sterile), *anonymous* (BM); locality unknown, 480 m alt., Nov. 11, 1938 (young fl.), *Box 1843* (BM, NY). **West Indies (island unknown).** locality unknown: (fl.), *Richard sn.* (P). **Honduras.** Yoro: road Real de San José Texíquat to Campo Nuevo at a place called Las Letras, W of Cerro Cabeza de Negro, 15°28'00"N 87°26'05"W, 1010 m alt., Apr. 24, 1995 (fr.), *Aguilar 4073* (MO). **Nicaragua.** Matagalpa: Macizos de Peñas Blancas, SE side, drainage of Quebrada El Quebradon, slopes N of Hda. San Martín, ca. 13°14'-15'N 85°39'W, 950-1100 m alt., Nov. 24, 1981, (fr.), *Stevens 20891* (MO). **Costa Rica.** Puntarenas: Buenos Aires, Cordillera de Talamance, Ujarrás, left margin of Quebrada Dorora, enroute to Río Lori, 09°17'50"N 83°15'30"W, 1520 m alt., Mar. 11, 1993 (fl.), *Herrera 5861* (MO); Cantón de Osa, R. F. Golfo Dulce Península de Osa, Rancho Quemado, in line to W of Tierra de Conservación, enroute to Cerro Brujo, 08°46'20"N 83°22'40"W, 200 m alt., Nov. 15, 1993 (fl. & immature fr.), *Aguilar 2619* (MO); same locality, Mar. 14, 1996 (immature fr.), *Yasuda 1317* (INB, MO). San José: Along Pan American Highway, ca. 1 km N of San Isidro del General, ca. 600 m alt., Sep. 9, 1943 (sterile), *Barbour 1019* (F); Cantón de Pérez Seledón San Isidro de El General, El Pilar de Cajón, Sitio Las Parcelas de Las Brisas de Cajón, 9°22'50"N 83°36'45"W, 600 m alt., Apr. 15, 1992 (immature fr.), *Zamora 1817* (MO); same locality, ca. 600 m alt., Mar. 12, 1996 (immature fr.), *Yasuda 1315* (INB, MO). **Panama.** Darién: Bahía de Piñas, slopes of

bordering hills, Jun. 24, 1957 (sterile), *Stern 173* (NY); Cana region, on trail above Cana leading to ridge of Pirre Massif, 7°45'N 77°45'W, 800-900 m alt., May 5, 1990 (immature & mature fr.), *McPherson 15040* (F, MO). Panamá: Sendero de Interpretación, 1km E of camp in the reserveforest of INRENARE, 8°40'N 79°55'W, 800-900 m alt., Mar. 24, 1994 (fl.), *Correa 10408* (MO); same locality, 800-900 m alt., Mar. 30, 1994 (fl.), *Correa 11039* (MO); same locality, 800-900 m alt., Jun. 29, 1995 (immature fr.), *Correa 11164* (MO). **Venezuela.** Merida: Highway Panamericana, between rivers Gavilan & R. Perdido, 150-500 m alt., Jun. 2, 1960 (fr.), *Veillon III12* (MO). Miranda: Distrito Paéz, road between San Juan - Montevideo, 10°04'-06'N, 65°45'-47'W, 400 m alt., Sep. 7, 1977 (young fl.), *González 1363* (MO). **Colombia.** Antioquia: Municipio San Luis, stream "La Cristalina", 6°N 74°45'W, 730-770 m alt., May. 22, 1987 (immature fr.), *Guillermo 933* (MO). Nariño: Espriella, Fumaeo, Jun. 22, 1951 (fr.), *Castaneda 2820* (F). **Ecuador.** Esmeraldas: N of San Lorenzo, Panadero, Silv. Parc. Panadero, 40 m alt., Apr. 30, 1966 (immature fr. or sterile), *Janse 279* (NY, US (sterile)); Río Onzole, 90 m alt., Jul. 14, 1966 (immature fr.), *Játiva 316* (NY), (immature fr.), *Játiva 1096* (NY, US); San Lorenzo, near rail road, right of way 3 km SE, ca. 9 m alt., Apr. 20, 1943 (young fl. & young fr.), *Little, Jr. 6293* (F, NY), US); same locality, 4? m alt., Apr. 20, 1943 (young fl. & young fr.), *Little, Jr. 6294* (MO, NY, US). Napo: 5 km N of Coca, El Chunchu Floristic Reserve, 00°25'S 77°01'W, 250 m alt., May 23, 1993 (young fl.), *Palacios 10794* (MO); Cantón Archidona, S slopes of Volcán Sumaco, Hollín-Loreto road, 40 km, Huamaní, 00°43'S 77°36'W, 1200 m alt., Oct. 19, 1989 (fl.), *Neill 9066* (MO), (fl.), *Palacios 4655* (MO); Estación Biológica Jatun Sacha, Río Napo, 8 km E of Misahuallí, 01°04'S 77°36'W, 200 m alt., Jun. 23-27, 1987 (young fl.), *Cerón 1662* (MO); Orellana, Yasuní National Park, road & pipeline of Maxus in construction, 53-60 km, 0°48'S 76°28'W, 230 m alt., Oct. 6, 1993 (fr.), *Dik 626* (MO).

Beilschmiedia pendula is the only *Beilschmiedia* species distributed in the West Indies. There is actually a collection reported from the West Indies (Jamaica) belonging to another *Beilschmiedia* species (*B. curviramea*). But there is no more collection of this species from the West Indies and I suspect that the locality of the collection was mislabeled.

Beilschmiedia pendula has alternate leaves and fine ramification. Among the species of the same phyllotaxis and ramification, *B. pendula* is one of the most inconspicuous species, often confused with *B. mexicana*, *B. costaricensis*, and *B. towarensis*. These four species share similar pubescence type, leaf shape (except for a group of *B. towarensis* which has ovate-broad elliptic leaves), flower structure and fruit shape.

From *B. mexicana* and *B. costaricensis*, *B. pendula* can be distinguished best by its ramification almost immersed on upper leaf surfaces and glaucous lower leaf surfaces (usually, *B. mexicana* and *B. costaricensis* have conspicuously raised ramification on both leaf surfaces and non-glaucous leaves). However, there are some exceptional collections of *B. pendula* from Costa Rica and Ecuador which have non glaucous leaves (*Janse 279*, *Játiva*

316, 1906, Little Jr. 6293, Aguilar 2619, Yasuda 1315 and 1317), and some exceptional collections of *B. mexicana* which have the ramification almost immersed above or glaucous leaves (about the exceptional collections of *B. mexicana*, see the notes under *B. mexicana*). From *B. costaricensis*, *B. pendula* also differs by its fruit pedicels constricted at the base. And leaf apex of *B. pendula* is usually acuminate and different from the acute to obtuse leaf apex of *B. mexicana* and *B. costaricensis*, but there are some exceptional collections in *B. pendula* with obtuse leaf apex (see below).

About the difference between *B. pendula* and *B. towarensis*, see the notes under *B. towarensis*.

Leaves of *B. pendula* are usually relatively small and narrow elliptic-oblongate, but there are some exceptional collections with large and wide leaves, especially from Puerto Rico and Martinique. Leaf apex of these collections are also different from the typical collections, the typical collections usually have distinctively acuminate leaf apex, but the collections from Puerto Rico and Martinique tend to have obtuse leaf apex.

22. *Beilschmiedia rigida* (Mez) Kostermans, Rec. Trav. Bot. Néerl. 35: 856. 1938. *Hufelandia rigida* Mez in Taubert, Bot. Jahrb. Syst. 17: 519. 1893. SYNTYPES: Brazil. Rio de Janeiro: Alto Macahé de Nova Friburgo, Oct.-Nov. (fl.), *Glaziou 19790* (B not seen, BM, C, F, LE not seen, P); *Glaziou 19793* (B not seen, BR, G-BOIS not seen, K, LE not seen, NY, P, US not seen).

Tree, height unknown. Terminal buds pubescent with appressed short straight hairs. Twigs terete, sparsely pubescent with appressed short straight hairs or almost glabrous. Leaves opposite; petioles 1.5-3.5 cm long, flat above, slightly discolored with twigs, glabrous; blades coriaceous, obovate, 14-22 x 7-11 cm; base decurrent, flat to slightly inrolled to below, apex round to obtuse; leaf surface glabrous on the both sides, not known whether glaucous or not; midrib immersed above, raised below, secondary veins 9-12 pairs, slightly raised above, raised below, tertiary veins not percurrent, ramification coarse, square-like with free veinlets, slightly raised on both sides. Inflorescences axillary or clustered around the terminal buds, paniculate, 4-12 (18) cm long, sparsely pubescent with appressed to erect hairs or almost glabrous, with 10-30 (55) flowers per inflorescence; flower pedicels of the lateral divisions 1.5-2 mm long, pedicels of the central flowers up to 5 mm long. Flowers 3-3.5 mm long, ca. 3.5 mm in diam.; tepals 6, equal, ovate, 1.5-2.3 mm

long, 1.1-1.5 mm wide, pubescent with erect hairs on both surfaces; stamens 9, outer six filaments 0.3-0.5 mm long, innermost three filaments ca. 0.5 mm long, filaments pubescent, anthers 0.9-1.2 mm long, all anthers 2-celled, apex of the anthers obtuse to truncate, anthers pubescent, glands on innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.7 mm long; pistil 1.6-1.9 mm long, pubescent, ovary slightly longer than and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits known only in immature stage, ellipsoid, the surface smooth; infructescence axis ca. 3 mm in diam., fruit pedicels thickened to ca. 5 mm in diam. below the fruit; fruit pedicels scarcely constricted at the base, covered with few lenticels and slightly darker than the infructescence axis.

Phenology: collected in flower from September to November.

Distribution: Rio de Janeiro and Espirito Santo, Brazil (Fig. 13).

Habitat: unknown.

Common name: "Canela-batata".

Economic use: unknown.

Additional specimens examined: **Brazil**. Rio de Janeiro: Alto Macaé de Nova Friburgo, Oct. 8, 1892 (fl.), *Glaziou 19793* (BR, K, NY, P, US); same locality (in Serra Estrela), Oct.-Nov. 1894 (fl.), *Glaziou 20444* (C, K, NY); Nova Friburgo, Reserva Ecológica Municipal de Macaé de Cima, source of Rio das Flores, 22° 00'S 42° 03'W, May. 12, 1988 (immature fr.), *Martinelli 12889* (MO); same reserve, Estrada p/ Hotel Faz. São João, 22° 00'S 42° 03'W, 1200 m alt., Sep. 14, 1989 (fl.), *de Lima 3707* (MO).

Beilschmiedia rigida has opposite leaves and coarse ramification. This species is distinguished from the other species with opposite leaves and coarse ramification by its obovate leaves, round leaf apices and long petioles. Additionally this species tends to have bigger flowers and thicker inflorescence rachises than the other species. In flower, this species has pubescent ovaries, which is also rare for the species with opposite leaves and coarse ramification, only *B. angustielliptica* and *B. angustifolia* share the same character (but see the notes under *B. angustielliptica* and *B. angustifolia* about the inconsistency of this character).

23. *Beilschmiedia riparia* Miranda, Anales Inst. Biol. Univ. Nac. México 24: 75. 1953.

TYPE: Mexico. Chiapas: ca. 7 km SE of Textla Gutierrez, border of the stream of

Cerro Hueco, ca. 700 m alt., Feb. 4, 1951 (fl.), *Miranda 6872* (holotype, MEXU; isotype, F).

Tree, to 40 m tall. Terminal buds pubescent with erect, straight to wavy or rarely curly hairs. Twigs terete, rarely compressed when young, relatively densely pubescent with erect, straight to wavy curly hairs, less densely when old, rarely glabrous when old. Leaves alternate, rarely sub-opposite; petioles 1-2 cm long, flat above, glabrous or pubescent with erect, straight to wavy hairs, densely when young, concolorous with twigs; blades chartaceous, elliptic, rarely ovate, sometimes asymmetric, 7-16.5 x 4-7.5 cm; base cuneate, rarely obtuse, not inrolled, apex acute to obtuse; upper leaf surface glabrous, lower leaf surface pubescent with erect, straight to wavy hairs when young, glabrous when old, or sometimes hairs remaining on the midrib and secondary veins even when old, lower leaf surface not glaucous or very rarely glaucous; midrib and secondary veins immersed above, raised below, secondary veins 8-13 pairs, tertiary veins not percurrent or rarely more or less percurrent, ramifications fine, areolate without free veinlets, immersed (the pattern visible) above, slightly raised below. Inflorescences axillary, rarely clustered on the buds, 2-14 cm long, pubescent with erect, wavy to curly hairs, with 15-100 flowers per inflorescence; flower pedicels of the lateral divisions 0.5-0.7 mm long, pedicels of the central flowers up to 1.5 (rarely 2) mm long. Flowers white to creamy 2-3 mm long, 2.3-3 mm in diam.; tepals 6, equal, ovate to elliptic, ca. 2 mm long, 1.5 mm wide, pubescent with erect, slightly wavy hairs on both sides; stamens 9, outer six filaments 0.3-0.5 mm long, innermost three filaments ca. 0.7 mm long, filaments pubescent; anthers 0.7-1 mm long, all the anthers 2-celled, apex of the anthers obtuse to truncate, pubescent or rarely glabrous, glands of the innermost three stamens globose; staminodia 3, cordate in outline, ca. 0.8 mm long; pistil ca. 1.8 mm long, glabrous to sparsely pubescent, ovary longer than the and gradually narrowed into the style; receptacle pubescent with appressed hairs. Fruits ellipsoid, black, 4 x 1.5 cm, the surface smooth; fruit pedicels ca. 2 mm in diam., scarcely thickened below the fruit, pedicels constricted at the base, concolorous with or rarely darker than the axis.

Phenology: collected in flower from January to May, in mature fruit from May to July.

Distribution: southern Mexico, from Guerrero to Chiapas, 480-1000 m alt. (Fig. 13).

Habitat: often collected along a stream, in semi-deciduous forests with *Andira*, *Albizia*, *Luehea*, *Calycophyllum*, or evergreen forests with *Ficus*, *Bursera*, *Quercus*, *Spondias*, *Lonchocarpus rugosus*, *Hymenaea*, and *Saurauia*.

Common name: “Guaquemico”, “Aguacate de mico”, “Aguacatillo”.

Economic use: reported that the wood is of good quality for timber, easy to polish, but contains a lot of water and needs to be dried quickly to be protected from fungi (Miranda 1953).

Additional specimens examined: **Mexico.** Chiapas: Municipio Villaflores, Depresion Central and Sierra Madre, Finca Ocotlan, 740 m alt., Apr. 21, 1989 (immature fr.), *Bachem 1000* (MO); Los Pinos, Jun. 2, 1904 (fr.), *Goldman 1045* (US); Municipio Acala, 10 m S of México 190 along the road to Acala at Nandaburri, 480 m alt., Feb. 25, 1966 (fl.), *Laughlin 211* (F, NY); Municipio Angel Albino Corzo, 6 km SE of San Nicolas, 15°41'27"N 92°36'07"W, 1000 m alt., Mar. 1, 1988 (fl.), *Martínez 22611* (MEXU, MO); Municipio La Trinitaria, Wooded creek bank 20 miles S of La Trinitaria along Mexican Highway 190, ca. 750 m alt., May 26, 1965 (immature fr.), *Breedlove 10040* (NY); Rancho Lindavista, 24 km E. of Villa Flores, Jan 30, 1950 (fl.), *Miranda 6003* (MEXU). Guerrero: Municipio Chilpancingo, Cañada Las Hamacas, path to Soyatepec, 750 m alt., May. 2, 1988 (fl.), *Rodrigues 374* (FCME, MO); Municipio Mochitlán, a road to Rancho Viejo, ca. 2 km S of Acahuizotla, 750 m alt., Jul. 17, 1992 (fr.), *Lorea5497* (FCME, MO), *Lorea5498* (FCME, MO). Oaxaca: Distrito Putla, Route 125, ca. 2km NE of Putla, Río San Pedro, ca. 800 m alt., May 14, 1981 (immature fr.), *Cedillo 822* (F, MO), *Cedillo828* (F, MEXU, MO); Municipio San Miguel Chimalapa, 2 km N of Col. Rodolfo Figueroa path to Díaz Ordaz and B. Juárez, W of Cerro Baúl, S side of Cordón El Reten, 16°34'N 94°12'W, 1400 m alt., Mar. 28, 1984 (fl.), *Wendt 4338* (MO); same municipio, ca. 36-37 km N of San Pedro Tapanatepec in straight line, 0.5-2 km S of Benito Juárez, near Río Portamoneda, 16°42'N 94°08'W, 900 m alt., Mar. 2, 1985 (fl.), *Maya 1296* (MO); Distrito Juchitán, W of la Col. Benito Juárez, a cattle track below Buenos Aires to Río Porta Monedas, Mar. 19, 1984 (fl.), *Rico 800* (MEXU, MO). Veracruz: Misantla, Jun., 1866 (fr.), *Hahns.n.* (P).

Beilschmiedia riparia has alternate leaves and fine ramification. Among the species of same phyllotaxis and ramification pattern, this species is distinguished from the others by a combination of the following characters; erect pubescence on the terminal buds and twigs, secondary veins raised below, fine ramification, pubescent anthers and elliptic fruits. To separate this species from *B. immersinervis*, which shares some characters with this species, see the notes under *B. immersinervis*.

In fruit, some collections of *B. riparia* are almost identical with *Persea primatogena*, and this fact nearly made me place *P. primatogena* under a synonym of *B. riparia*. But I decided to keep *P. primatogena* separated from *B. riparia*, as an imperfectly known species,

because there is a distribution gap between these two species (*B. riparia* is known only from Mexico and *P. primatogena* is from Honduras and Nicaragua), and because there is no collection of *P. primatogena* in flower to confirm the similarity between the two species in floral characters.

The pubescence of *B. riparia* is always erect, but straightness of the indument and density of the pubescence have some variation within the species. Usually, indument of this species is straight or slightly wavy, but on the terminal buds indument tends to be curly. About the density, this species usually has glabrous leaves, but some collections have the leaves very pubescent on the lower leaf surfaces when the leaves are relatively young and the pubescence remains on the midrib and secondary veins even when the leaves become older.

A few collections of this species have denser hairs in axils of the secondary veins on the lower leaf surfaces, which somewhat look like domatia. Among these collections, *Wendt 4338*, appears to have domatia clearly (additionally, the *Wendt's* collection has glabrous anthers). I decide to keep the collections except for the *Wendt's* collection in *B. riparia* because there is no other characters strong enough to separate them from the species. I keep the *Wendt's* collection as "*Beilschmiedia riparia* aff.", and wait for more material to classify the collection.

There is another collection from Mexico which has glabrous anthers like *Wendt's* collection (*Martínez 22611*). But I keep this collection in *B. riparia*, because this collection shares all the other characters with *B. riparia* and does not have domatia.

24. *Beilschmiedia steyermarkii* C. K. Allen, J. Arnold Arbor. 26: 417. 1945. TYPE. Guatemala. Alta Verapaz: S of Cubilagüitz, 300-400m alt., Mar. 3, 1942(fl.), *Steyermark 44494* (holotype, F).

Tree, to 27 m tall. Terminal buds pubescent with erect, short curly hairs. Twigs terete, slightly angular when young, pubescent with erect, short wavy hairs to glabrous, less densely when older. Leaves alternate; petioles 1-1.7 cm long, flat to canaliculate above, glabrous to pubescent with erect, short curly hairs, concolorous with the twigs; blades coriaceous, elliptic to narrowly ovate, often asymmetric, 5-10 x 1.5-4 cm; base and apex acute, rarely apex obtuse, glabrous on both sides, lower leaf surface uncertain whether glaucous or not; midrib immersed above, raised below, secondary veins in 7-8 pairs, immersed above, slightly raised below, tertiary veins not percurrent, ramification fine,

areolate without free veinlets, immersed above (sometimes the pattern visible above), slightly raised below. Inflorescences axillary, tend to cluster near the top of the branchlets, paniculate, 4-8 cm long, pubescent with erect short wavy hairs, with 25-65 flowers per inflorescence; flower pedicels of the lateral divisions 0.5-1 mm long, pedicels of the central flowers up to 3 mm long. Flowers ca. 2.4 mm long, ca. 2.5 mm in diam.; tepals 6, equal, ovate to elliptical, ca. 1.5 x 1 mm, pubescent with erect wavy hairs outside, pubescent with erect and wavy, or appressed hairs inside; stamens 9, filaments 0.3-0.6 mm long, filaments pubescent, anthers 0.6-0.8 mm long, all anthers 2-celled, apex of the anthers obtuse to truncate, glabrous, glands of the innermost stamens globose, staminodia 3, cordate in outline, ca. 0.8 mm long; pistil ca. 1.4 mm long, glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with erect wavy hairs, less densely to glabrous toward the bottom. Fruits unknown.

Phenology: collected in flower in March (in young flower in December).

Distribution: Guatemala, 300-400 m alt. (Fig. 13).

Habitat: unknown.

Common name: unknown.

Economic use: unknown.

Additional specimen examined: **Guatemala**. State not known: Los Arcos, 149 km of Cadenas Road, Dec. 22, 1969 (young fl.), *Contreras 9448* (C, F, MO).

Beilschmiedia steyermarkii are known to me only by two collections, and the collections appear to be similar to *B. ovalis* in the pubescence type, ramification and floral structure. But the collections are distinguished from *B. ovalis* only by their having narrow leaves. Additionally, the two collections are from 300-400 m altitude, which is too low a habitat for *B. ovalis* (*B. ovalis* occurs above 1800 m altitude). Considering the different altitudinal distributions of *B. steyermarkii* and *B. ovalis*, and about the poor collections available for *B. steyermarkii* (the type collection is only a short branchlet with broken inflorescences, and another collection is only with young flowers), I conclude that it would be better to keep *B. steyermarkii* separate from *B. ovalis* until more material is available to resolve this question.

Beilschmiedia immersinervis also appears to be similar to *B. steyermarkii*. About the difference between them, see the notes under *B. immersinervis*.

As Allen (1945) reported, the type specimen of *B. steyermarkii* has few-flowered inflorescences, but the precise number of flowers in the inflorescences is uncertain because the inflorescences are broken. Another specimen of this species, which was collected after her description, has the inflorescences with relatively many (40-65) flowers.

25. *Beilschmiedia stricta* Kostermans in Rec. Trav. Bot. Néerl. 35: 863. 1938. TYPE: Brazil. Rio de Janeiro: G. Portella, Monte Sinai, 1935 (fl.), *Nunes 313* (holotype, U not seen, isotype, RB).

Tree, height unknown. Terminal buds pubescent with straight appressed hairs. Twigs terete, younger ones compressed, sparsely pubescent with appressed hairs, less densely to glabrous when older. Leaves opposite; petioles ca. 1 cm long, canaliculate to flat above, glabrous, slightly darker than branches; blades firmly chartaceous, elliptic, (5) 8-9 x 2.5-4 cm; base cuneate, not inrolled, apex acute; leaf surface glabrous on both sides, lower leaf surface not glaucous; midrib immersed or impressed above, raised below, secondary veins 9-13 pairs, raised on both sides, tertiary veins not percurrent, ramification coarse, square-like with free veinlets, raised on both sides. Inflorescences axillary, racemose, 1.5-2.5 cm long, pubescent with more or less appressed hairs, with 5-10 flowers per inflorescence; flower pedicels of the lateral divisions 0.5-1.2 mm long, pedicels of the central flowers up to 3 mm long. Flowers ca. 2.5 mm long, ca. 2.7 mm in diam.; tepals 6, almost equal, ovate, ca. 1.8 mm long, 1.2-1.5 mm wide, pubescent with appressed hairs outside, sparsely pubescent with appressed hairs or almost glabrous inside; stamens 9, outer six filaments ca. 0.4 mm long, innermost three filaments ca. 0.5 mm long, pubescent, anthers ca. 1.1 mm long, all anthers 2-celled, apex of the anthers obtuse to truncate, anthers pubescent, glands of innermost three stamens globose; staminodia 3, cordate in outline, ca 0.8 mm long; pistil 1.4-1.6 mm long, glabrous, ovary as long as the and gradually narrowed into the style; receptacle sparsely pubescent with appressed hairs. Mature fruits unknown, young fruit ellipsoid, the surface warty; young fruit pedicels not constricted at the base, covered with lenticels and concolorous with the infructescence axis.

Phenology: unknown.

Distribution: Rio de Janeiro, Brazil (Fig. 14).

Habitat: unknown.

Common name: unknown.

Economic use: unknown.

Beilschmiedia stricta is known to me only by the type collection. This species appears to be similar to *B. curviramea* and *B. fluminensis*. About the difference between *B. stricta* and these two species, see the notes under these two species respectively.

26. *Beilschmiedia taubertiana* (Schwacke & Mez) Kostermans, Rec. Trav. Bot. Néerl. 35: 863. 1938. *Hufelandia taubertiana* Schwacke et Mez, Arb. Bot. Gart. Breslau 1: 108. 1892. TYPE: Brazil. Minas Gerães: Rio Novo, 1890 (fl., collection in B with fl. & fr.), *Alaujo 7047* (holotype, B seen on photograph; isotypes, P, RB).

Tree, height unknown. Terminal buds pubescent with erect long straight hairs. Twigs terete, younger ones compressed, pubescent with erect long straight or slightly wavy hairs, less densely when old. Leaves opposite; petioles 0.8-1 cm long, canaliculate above, pubescent with erect long hairs, slightly discolored with twigs; blades firmly chartaceous, elliptic, 10-14 x 4-5 cm; base obtuse to round, not inrolled, apex acute; upper leaf surface glabrous, lower leaf surface sparsely pubescent with erect, long straight to slightly wavy hairs; midrib immersed above, raised below, secondary veins 9-14 pairs, slightly raised or almost immersed above, raised below, tertiary veins not percurrent, ramification coarse, square-like with free veinlets, slightly raised on both sides. Inflorescences axillary, racemose, ca. 1.5 cm long, pubescent with long erect hairs, with ca. 5 flowers per inflorescence; flower pedicels of the lateral divisions 0.5-1 mm long, pedicels of the central flowers up to 4 mm long. Flowers ca. 3 mm long, ca. 3 mm in diam.; tepals 6, equal, ovate, 1.9-2 mm long, 1.3-1.5 mm wide, pubescent with erect long wavy hairs outside, sparsely pubescent with appressed to erect hairs inside; stamens 9, outer 6 filaments ca. 0.3 mm long, innermost 3 filaments ca. 0.4 mm long, filaments pubescent, outer six anthers 1.2-1.3 mm long, innermost anthers 0.9-1.1 mm long, all the anthers 2-celled, apex of the anthers obtuse to truncate, anthers pubescent, glands of the innermost 3 stamens globose; staminodia 3, cordate in outline, ca. 0.6 mm long; pistil ca. 1.2 mm long, glabrous, ovary shorter than and gradually narrowed into the style; receptacle densely pubescent with erect

hairs. Fruits ellipsoid, ca. 5 x 3 cm, the surface warty; infructescence axis ca. 3 mm in diam., fruit pedicels thickened to ca. 5 mm in diam. below the fruit, fruit pedicels not constricted at the base, covered with lenticels and concolorous with the infructescence axis.

Phenology: unknown.

Distribution: Minas Gerais, Brazil (Fig. 14).

Habitat: unknown.

Common name: unknown.

Economic use: unknown.

Additional specimen examined: **Brazil**. Minas Gerais: Rio Novo, 1889 (sterile), *Araujo 5* (RB).

Beilschmiedia taubertiana has opposite leaves and coarse ramification as all the Brazilian *Beilschmiedia* species do. But this species is easily distinguished from the other Brazilian species by the erect, long straight pubescence on the terminal buds and twigs, and by the lower leaf surfaces sparsely pubescent with same kind of indument.

27. *Beilschmiedia towarensis* (Meissner) Sa. Nishida comb. nov. *Hufelandia towarensis* Meissner, D. C. Prodr. 15: 65. 1864. SYNTYPES: Colombia. locality unknown, *Karsten 88* (B seen on photograph). Venezuela. Aragua: Tovar, ca. 1920 m alt., Aug. 28, 1854 (fl.), *Fendler 1094* (NY).

Aniba pseudo-coto (Rusby) Kostermans, Rec. Trav. Bot. Néerl. 35: 872. 1938. *Ocotea pseudo-coto* Rusby, Bull. Torrey Bot. Club 49: 261. 1922. TYPE: Bolivia. La Paz: mountains S of Huachi, near the Cochabamba River, 750-900 m alt., Sep. 9, 1921 (young fl.), *White 1051* (holotype, NY seen on photograph; isotypes, AFS not seen, C, G-DEL not seen, GH not seen, K, US seen on photograph).

Tree, to 40 m tall. Terminal buds pubescent with appressed straight hairs. Twigs terete, slightly angular when young, pubescent with appressed straight hairs, less densely when older. Leaves alternate; petioles (0.5) 1-4.2 cm long, flat to canaliculate above, glabrous or pubescent with appressed straight hairs, concolorous with twigs; blades coriaceous to firmly chartaceous, ovate to broad elliptic, rarely broad oblanceolate, (5) 8-20

(28) x 4-14 cm; base cordate to obtuse, rarely cuneate, not inrolled, apex acuminate, rarely acute; upper leaf surface glabrous, lower leaf surface pubescent with appressed short straight hairs, lower leaf surface glaucous; midrib immersed above, raised below, secondary veins (5) 6-11 (12) pairs, immersed or slightly raised above, raised below, tertiary veins percurrent, ramification fine, areolate without free veinlets, immersed above (the fine pattern sometimes slightly visible), almost immersed below (the pattern visible). Inflorescences in axils of the leaves near the terminal buds, sometimes in the axils of cataphylls below the leaves near the tips of the twigs, paniculate, 4-16 (23) cm long, pubescent with short, appressed to erect hairs, with 30-100 flowers per inflorescence; flower pedicels of the lateral divisions 0.5-1.5 mm long, pedicels of the central flowers up to 3 mm long. Flowers yellowish white, 2-3 mm long, 2-3 mm in diam.; tepals 6, equal, ovate to elliptic, 1.3-2 mm long, 1-1.5 mm wide, pubescent with appressed to erect hairs on both sides; stamens 9, outer six filaments 0.3-0.4 mm long, innermost three filaments 0.4-0.7 mm long, filaments pubescent, anthers 0.7-1 mm long, all the anthers 2-celled, apex of the anthers obtuse to truncate, glabrous, glands of the innermost three stamens globose, staminodia 3, cordate in outline, ca. 0.7 mm long; pistil ca. 1.3 mm long, sparsely pubescent to glabrous, ovary as long as and gradually narrowed into the style; receptacle pubescent with appressed hairs, less densely toward the bottom. Fruit ellipsoid, purple-black, 2.5-3.5 x 1.5-2 cm, the surface smooth; infructescence axis 2-3 mm in diam., fruit pedicel scarcely thickened below the fruit, fruit pedicel constricted or not constricted at the base, covered with lenticels and concolorous with the infructescence, or free from lenticels and darker than the infructescence axis.

Phenology: collected in flower from July to March, in mature fruit from January to March, from May to June, and from September to October.

Distribution: Costa Rica, Panama, Venezuela, Colombia, Ecuador, Peru and Bolivia, (1-) 600-3000 m alt. (Fig. 14).

Habitat: premontane wet forest to cloud forest.

Common name: "Aguacatillo" in Colombia, "Aguacatillo" and "Aguacatillo de montaña" in Ecuador, "Roble palta", "Palta moena" and "Moena" in Peru, "Coto ordinario" in Bolivia.

Economic use: the bark used as a drug in Bolivia, but medicinally worthless (Rusby 1922).

Additional specimens examined: **Costa Rica.** Heredia: Volcán Barba, Mar. 4, 1983 (fr.), *Peralta sn.* (CR). Puntarenas: Cantón of Golfito Jiménez, Dos Brazos de Río Tigre, enroute between the ravines, Cerro Müeller and Cerro Rincón, 8°30'35"N 83°28'15"W, 782 m alt., Nov. 25, 1990 (fl.), *Herrera4643* (MO); same cantón, Dos Brazos de Río Tigre, head of ravine Patemazo & Cerro Müeller, 8°30'15"N 83°28'20"W, 744 m alt., Nov. 27, 1990 (fl.), *Herrera4658* (MO); Cordillera de Talamanca, Cantón de Coto Brus, P. I. La Amistad, Santa María de Pittier, road to access to the guardplace of Pittier, 09°01'38"N 82°51'56"W, 1700 m alt., Jun. 2, 1995 (immature fr.), *González 800* (MO); Fila El Tigre, SE of Las Alturas, 8°56'N 82°51'W, 1350-1450 m alt., Aug. 29, 1983 (detached immature fr.), *Davidse 24222* (F, MO); foothills of the Cordillera de Talamanca, N of Santa Elena on Fila Contón, S of Agua Caliente, 82°56'N 8°57'W, 1100 m alt., Sep. 4, 1984 (fr.), *Davidse 28226* (MO); Las Alturas de Coto Brus, 8°54'N 82°50'W, 1150-1250 m alt., Mar. 20, 1987 (immature fr.), *Burger 12178* (F, MO, NY), (immature fr.), *Burger 12189* (F, MO); Las Alturas, near Panamanian border, ca. 1250 m alt., Mar. 18, 1978 (immature fr.), *Hartshorn 2166* (F, MO). San José: Cantón Pérez Zeledón San Isidro de El General, El Pilar de Cajón, plots of Las Brisas de Cajón, 9°22'50"N 83°36'45"W, 600 m alt., Apr. 16, 1992 (immature fr.), *Zamora1819* (MO). **Panama.** Barro Colorado Isl.: Lutz Trail cut-off behind Animal house, May 23, 1968 (fr.), *Croat 5813* (F, MO, NY); Near Lutz Stream at base of steep rock slope on Lutz Trail cut off to lab, Jan. 9, 1969 (immature fr.), *Croat7034* (NY); Forest at S edge of clearing along short cut to Lutz Trail, Mar. 7, 1969 (immature fr.), *Croat 8459* (F, NY); Drayton trail, Nov. 23, 1970 (sterile), *Croat 12659 A* (MO); Snyder-Molino trail 125, Dec. 29, 1970 (fl.), *Croat 12928* (F, K, MO); Zetek trail 250, Mar. 26, 1971 (fr.), *Croat 14063* (MO); Snyder-Molino 1.5, Dec. 29, 1970 (fl.), *Foster2053* (F); locality unknown, May. 18, 1944 (sterile), *Zetek 5149* (MO). Canal Zone: Pipeline Road, 6 km N of Gamboa, Dec. 3, 1971 (sterile), *Gentry2829* (MO). Chiriquí: Road from Volcan to Rio Serano, road that turns E 7.2 km from Rio Serano, 1.2 km along the side road, Jun. 29, 1977 (fr.), *Folson 4040* (MO). Los Santos: Coabal, Progrese, W slope above Río Cobachén, 200 m alt., Apr. 19, 1968 (immature fr.), *Holdridge 6209* (MO, (immature fr.?, fr. missing), *Holdridge 6217* (MO). Veraguas: District of Montijo, Cerro Hoya Nacional Park, ca. 900 m alt., Mar. 7, 1993 (immature fr.), *Rivera 324* (MO). **Venezuela.** Aragua: Henri Pittier Nacional Park, Aug. 31, 1990 (fl.), *Cardozo 1549* (MO); same locality, Sep. 20, 1990 (sterile), *Cardozo 1563* (MO), 2 km W of El Junquito, around top of Pozo Negro, 10°27.5'N 67°06.3'W, 2020 m alt., Jan. 18-19, 1992 (young fl.), *Meier 1360* (MO), Cordillera of la Costa, seaward-facing N slopes, El Junquito, 1830-2130 m alt., Jun. 19, 1944 (fl.), *Steyermark 56933* (F). Merida: La Trampa, highway San Juan-Azulita, 2500 m alt., Feb. 2, 1987 (sterile), *van der Werff 8766* (MO); Pueblos del Sur, 1600-2500 m alt., Mar. 31, 1957 (fl. & immature fr.), *Bernardi 6458* (NY). Monagas: Distrito Caripe, forest adjast to the cave of El Guácharo, 1000-1100 m alt., Jul. 16, 1985 (sterile), *Lau 16* (MO); same district, La Laguna, El Paraiso farm, Sep. 12, 1986 (young fl.), *Bosque 22* (MO); same locality, 1100 m alt., Mar. 17, 1987 (fl.), *Bosque 22* (MO). Portuguesa: Distrito Sucre, Concepción division, 9°18'N 70°06'W, 1700 m alt., Oct. 24, 1985 (immature fr.), *vanderWerff7575* (MO). Trujillo: Distrito Carache, road between La Playa (9°37'N 70°8'W), SW of Carache, & Potreritos de Cendé (9°32'N 70°8'W), ca. 10-14 km from La Playa, 2200 m alt., May 11, 1988 (immature fr.), *Dorr 5114* (MO), (fr.), *Dorr 5117* (MO, NY); Quebrada Los Riitos, between Escuque & La Mesa de San Pedro, above Escuque, 1300-1650 m alt., Feb. 20-23, 1971 (fl.), *Steyermark 104700* (NY).

Yaracuy: 7-10 km N of Salom, El Amparo near Candelaria, 1100-1300 m alt., Dec. 27-30, 1972 (young fl.), *Steyermark 106806* (NY). **Trinidad**. Central Highlands, 500 m alt., Jul. 1959 (fl.), *Kostermans A15017* (BR, K, MO, N, P, U). **Colombia**. Antiquia: Municipio of San Luís, canyon of Río Claro, S. sector, right edge, 5°53'N 74°39'W, 325-450 m alt., Jan. 29, 1984 (immature fr.), *Cogolla 1285* (MO). Boyacá: 100m NW of Bogotá, extreme W part of Department Boyaca, region of Mt. Chapon, ca. 1080 m alt., Jul. 23, 1932 (immature fr.), *Lawrance 353* (BM, F, K, NY, U). Caldas: Municipio Risaralda, Quebrada Chovarquía, 1140 m alt., Nov. 14, 1992 (immature fr.), *Vargas 754* (MO). Caramanta: Cordillera Occidental, 9.8 km from Caramanta to Supia, Cerro Viringo, Vereda Hojas Anchas, 5°31.8'N 75°40.69'W, 2420 m alt., Oct. 16, 1988 (fl.), *Betancur 1066* (MO). Cauca: Tierra Odentro, around Huila, Indian village in Río Paez Valley, 1600-1900 m alt., Jan. 1906, (immature fr.), *Pitter 1286* (NY). Cauca & Antiquia: Mt. Ceremanta, Mismis(?) Hill, 1800-2400 m alt., Jul. 1891 (young fl.), *Lehman 7226* (F). El Valle: Cordillera Occidental, valley of Río Cali, suburb of Peffas Blancas, Jan. 23, 1963 (fl.), *Figueiras 8401* (US); Cordillera Occidental, east slope, Río Cali basin, right slope, deep stream, above La Glorieta, road to Miralindo, 2100-2250 m alt., Oct. 31-Nov. 1, 1944 (immature fr.), *Cuatrecasas 18414* (F, U, US); Pacific coast, Río Naya, above Puerto Merizalde, in the branch of Aji Chiquito, left edge, 1-4 m alt., Mar. 1, 1943 (immature fr.), *Cuatrecasas 14299* (F, US); Cordillera Occidental, E slope, basin of Río Cali, Río Pichindé, between Los Cárpatos & El Olivo, 1920-2025 m alt., Jul. 26, 1946 (immature fr.), *Cuatrecasas 21747* (F, U, US); highway from Buga to Darién, forest of los Muertos, 1200 m alt., May 19, 1982 (immature fr.), *Murphy 423* (MO); Municipio Tuluá, Cordillera Central de las Andes, Corregimiento Venus Finca el Paraíso, 2200 m alt., Aug. 4, 1988 (fl.), *Devia 2290* (MO); same municipio, Corregimiento "Monteloro", 1700-2300 m alt., Nov. 9-Dec. 13, 1972 (young fl.), *Jiménez 1816* (NY). Magdalena: region near Santa Marta, 2250 m alt., Mar. 2, 1932 (sterile), *Espina A170* (NY). Medellín: locality unknown, Jan. 22, 1928 (fl.), *Toro 895* (NY). Meta: Sierra de la Macarena, Caño Entrada, 550 m alt., Jan. 13, 1950 (immature fr.), *Philison 2094* (NY); Sierra de la Macarena, central mountains Pico Renjifo, 1700 m alt., Jan. 22, 1950 (fl.), *Philipson 2163* (BM). Department unknown: Jigua, Capilla (sterile), s.c. (*B. T.*) 401 (NY). Locality unknown: (young fl.), *Celestino 1442* (US). **Ecuador**. Bolivar: Road Echandia-Guaranda, 2000 m alt., Jul. 17, 1991 (fl.), *van der Werff 12406* (MO). Esmeraldas: Cantón San Lorenzo, Parroquia Alto Tambo, Sector El Cristal, 01°30'N 78°30'W, 600 m alt., Apr. 13, 1992 (fr.), *Tipaz 792* (MO); same locality, 0°50'N 78°30'W, 600 m alt., Apr. 13, 1992 (immature fr.), *Quelal 459* (MO). Imbabura: Cotacachi, Hda. La Florida, 0°23'S 78°28'W, 1900-2500 m alt., Aug. 28, 1992 (sterile), *Alvarez 625* (MO); Road Otavalo - Apuela, 3000 m alt., Feb. 14, 1989 (immature fr.), *van der Werff 10584* (MO); along same road (not very close to Apuela), Jul. 3, 1991 (fl.), *vanderWerff 12163* (MO). Morona-Santiago: 11.7 km SW of Taisha, 2°32'S 77°44'W, Sep. 11-15, 1976 (sterile), *Ortega 138* (US); Bombia, suburb of la Misión Salesiana-Shuar, 03°25'S 78°35'W, 800 m alt., Nov. 7, 1986 (immature fr.), *Neil 7477* (MO, NY). Napo: Canton Quijos, Chaco, road to Cayambe-Coca Reserve, Río San Juan Chico, following to Río Oyacachi, 00°17'S 77°03'W, 1750 m alt., Jan. 12, 1992, (young fl. & fr.), *Palacios 9554* (MO); Zamora Chinchipe, 52 km NE of Zamora, Estación Experimental "El Padmi.", 3°43'S 78°38'W, 900 m alt., Sept. 13, 1975 (sterile), *Little, Jr. 330* (US). El Oro: 15 km S of Piedras, Ingenio farm, 700-1000 m alt., Jun. 20, 1943 (immature fr.), *Little, Jr. 6657* (NY, US). Pichincha: Along new road Nanegal-Mindo, 1500-1800 m alt., Mar.

2, 1994 (young fl.), *van der Werff 13377* (MO); Cantón Quito, highway Quito-Chiriboga, E skirt of Volcán Pichincha, 78°53'W 00°17'S, 1500 m alt., Mar. 12, 1990 (fl.), *Palacios 4804* (MO); Cantón Quito, Maquipucuna Biological Reserve, 9 km NE of Nanegal, 00°10'N 78°40'W, 1300 m alt., Feb. 1, 1991 (fl.), *Neil 9782* (MO). **Peru.** Amazonas: Luya Province, Jaipe, Fundo "El Paraíso", 1690 m alt., May. 31, 1989 (immature fr.), *Díaz 3587* (MO); Provincia Luya, Ocallí, by Ouispe, property of San Esteban Fernández, found along a stream, 1920-2300 m alt., Jun. 18, 1991 (immature fr.), *Díaz 4355* (MO). Cajamarca: Provincia Jaen, Colasay, hills NW of town, 5°58'S 79°03'W, 2100 m alt., Feb. 21, 1985 (fr.), *Stein 2231* (MO, NY). Chanchamayo: Perene Valley, La Florida, enroute from Villa Rica heading Yurinaki drainage, 10°45'W 75°10'W, 1000 m alt., Oct. 26, 1982 (fr.), *Foster 9460* (MO). Cúberon: locality unknown, (sterile), *Raimondi 6248* (F). Huanco: Provincia Pachitea, Dtto (district?) Honoria, Caserío Leoncio, Aug. 9, 1963 (fl.), *Lao66* (F, NY, US). Madre de Dios: Tambopata Tourist Camp, junction of Ríos la Torre and Tambopata, 12°50'S 69°17'W, 260 m alt., Jun. 6, 1986 (immature fr.), *Gentry 54196* (MO). Pasco: Provincia Oxapampa, 1800 m alt., Mar. 3, 1986 (immature fr.), *vanderWerff8329* (MO), (immature fr.), *vander8333* (MO). San Martín: Provincia Moyobamba, Soritor, 680 m alt., Jul. 23, 1986 (sterile), *Albán 4085* (F); same locality, 670 m alt., Jul. 23, 1986 (sterile), *Albán 4095* (F); same locality, 670 m alt., Jul. 25, 1986 (sterile), *Albán 4142* (F); San Roque, 1350-1500 m alt., Jan.-Feb., 1930 (fr.), *Williams 2077* (F, NY). Locality unknown: Jul. 8, 1878 (sterile), *deJelskii 187* (BR). **Bolivia.** La Paz: Provincia Larecaja, Copacabana (ca. 10km S of Mapiri), 850-950 m alt., Oct. 8 - Nov. 15, 1939 (fl.), *Krukoff 11235* (F, MO, U), (fl.), *Krukoff 11286* (F, US); same province, Tuirí (near Mapiri, on left bank of Río Mapiri), 490-750 m alt., Sep. 12-30, 1939 (fl.), *Krukoff 10784* (F).

Beilschmiedia towarensis has alternate leaves and fine ramification. This species is distinguished from the other species of the same phyllotaxis and ramification pattern by a combination of following characters; appressed pubescence on the terminal buds and twigs, lower leaf surface pubescent with appressed hairs, circle-like ramification, glabrous anthers and ellipsoid fruits. This species is apparently separable into two groups, one group with pubescent ovary and another group with glabrous ovary. The former group tends to have shorter petioles, coriaceous, ovate to broadly elliptic leaves and fruit pedicels not constricted at the base, while the latter group tends to have longer petioles, rigid chartaceous, elliptic leaves and fruit pedicel constricted at the base. However, a careful observation of the leaf morphology revealed that there are many intermediate collections (Fig. 15), so that one cannot make a clear separation between the two groups in petiole length and leaf size. Additionally, there are some exceptional collections in the pubescence of ovaries, which are collections with short petioles, ovate leaves and glabrous ovaries, or collections with long petioles, elliptic leaves and pubescent ovaries. Both groups occur from Venezuela to Bolivia, although the latter group is more distributed in Costa Rica and Panama. I admit that this

species has an unusually wide range in morphology and geographic distribution, but I decide to keep the two groups together in this species, because there are too many intermediate specimens.

The latter group has sometimes been identified as *B. pendula*, but it is usually distinguished from *B. pendula* by its very fine, areolate ramification, longer (1.5-3.5 cm long) petioles and larger (8-20 x 4-14 cm) leaves (although there are some collections in *B. pendula* which have large leaves. See the notes under *B. pendula*).

Several collections from Venezuela, *Bosque 22* (Sep. 12, 1986), *Bosque 22* (Mar. 17, 1987), *Bosque 22* (Jun. 22, 1987), *Lau 5, 16*, *Madrinan 652*, *Marcano 215*, *Meier 1360*, and one collection from Panama, *Duke 10749*, appear to have slightly coarser ramification than typical collections of *B. towarensis*. But I keep them in this species because only the slightly coarser ramification cannot be a characteristic strong enough to separate them as another species.

Imperfectly known species

Persea primatogena Williams, Economic Botany 31:319. 1977. TYPE: Nicaragua.

Matagalpa: Cordillera Central de Nicaragua, finca Sta. María de Ostuma, 1300-1400 m alt., Nov. 30, 1973 (fr.), *Williams & Molina 42575* (holotype, F; isotype, EAP not seen).

Based on the ramification pattern and fruit pedicels, this species belongs in *Beilschmiedia*, and actually, approaches to *B. riparia* very much. However, there are no flowering collections needed for proper determination.

Beilschmiedia sulcata (Ruiz et Pavon) Kostermans, Recueil. Trav. Bot. Néerl. 35: 850.

1938. *Laurus sulcata* Ruiz et Pavon, Flora Peruviana 6: 356. 1802. *Hufelandia sulcata* (Ruiz et Pavon) Nees, Linnaea 21: 494. 1848. *Persea sulcata* (Ruiz et Pavon) Meissner, D. C. Prodr. 15 (1): 54. 1864. TYPE: Peru.: Muña, (immature? fr.), *Ruiz s.n.* (holotype, MA seen on the photograph; isotypes, B not seen, BM, F, G-BOIS not seen,).

In the illustration of Ruiz and Pavon (1802), the anthers are drawn as having 4 cells instead. If this illustration is correct, we need to check whether this species is really a *Beilschmiedia* species, because *Beilschmiedia* has 2-celled anthers, or whether this species actually belongs to another genus. However, the type specimens I have seen have no flower or fruit, but only fruit pedicels. According to Velayos (pers. comm.), there are no flowers in the holotype, either.

There is a collection from Ecuador, which is identified as *B. sulcata* and has 4-celled anthers (*Jaramillo 8165*). But the collection is very different from the type of *B. sulcata* in the pubescence type and ramification pattern. I am not certain if the collection even belongs to *Beilschmiedia*. Like inflorescences of *Beilschmiedia*, inflorescences of this collection appear to have the ultimate division not strictly cymose. But many of inflorescences of the collection are broken and it is hard to confirm the inflorescence structure. Additionally, ramification of the collection is very different from all neotropical *Beilschmiedia* species, by being fine and completely immersed on both surfaces.

Leaves of the type collection have fine ramification, somewhat circle-like, but with free veinlets. They appear to be somewhat similar to *B. costaricensis* or *B. towarensis*, but not identical. There is a collection from Ecuador which approach to *B. sulcata* in the vegetative characters (*A. Gentry et al. 30911*), but it has only immature fruits.

Considering that there has been no way to confirm that the species is one of the *Beilschmiedia* species by itself, identical to another *Beilschmiedia* species, or belongs to another laurel genus, I decide to keep *B. sulcata* as an imperfectly known species.

Beilschmiedia zapoteoides (Lundell) Kostermans, *Reinwardtia* 6 (2): 156. 1962.

Endlicheria zapoteoides Lundell, *Wrightia* 1 (2): 145. 1946. TYPE: Mexico. Chiapas: Cascada near Siltepec, in advanced forest, 1600 m alt., Mar. 1, 1945 (fl. & fr.), *Matuda 5153* (holotype, TEX; isotype, MO, US).

The type collection of *Beilschmiedia zapoteoides* has opposite leaves and coarse ramification like *B. hondurensis*, but has relatively long flower pedicels (ca. 2 mm long in the lateral divisions) and bigger, more or less spherical fruit compared to *B. hondurensis*. And there are two collections from El Salvador, one of which in flower has also long flower pedicels (2.5 mm long in the lateral divisions), and another collection has young fruits, uncertain whether the fruits grow big and spherical or not. I decide to place *B. zapoteoides* in

an imperfectly known species, with annotating the two Salvadorian collections “*Beilschmiedia zapoteoides* vel aff.”, because the flowers of the type collection and the Salvadorian collection appear to be abnormal (leaves are diseased, and the number of cells in the stamens of the third whorls are variable, from two to zero) and one cannot delimitate the species based on such poor material only. If this various number of the anther cells are an ordinary condition for this species, it would be very interesting because the species might be regarded as a transitional stage from the species with 9 fertile stamens to the species with 6 fertile stamens. But it would be judged only after the examination of more and better materials.

Excluded species

Beilschmiedia brasiliensis (Kostermans) Kostermans

= *Anaueria brasiliensis* Kostermans

Beilschmiedia cuneata (Meissner) Kostermans

= *Persea cuneata* Meissner

Beilschmiedia durifolia (Mez) Kostermans

= *Persea durifolia* Mez

Beilschmiedia inaequalis (A. C. Smith) Kostermans

= *Caryodaphnopsis inaequalis* (A. C. Smith) van der Werff & Richter

Beilschmiedia lundelliana Lasser

= *Persea cuneata* Meissner

Beilschmiedia sphaerocarpa H. Winkler (genus unknown)

Table 1. List of the *Beilschmiedia* species in the neotropical countries

Country	Species
Mexico	<i>B. anay</i> , <i>B. angustieliptica</i> *, <i>B. hondurensis</i> , <i>B. mexicana</i> *, <i>B. ovalioides</i> *, <i>B. riparia</i> *
Belize	<i>B. hondurensis</i>
Guatemala	<i>B. anay</i> , <i>B. hondurensis</i> , <i>B. steyermarkii</i> *
Honduras	<i>B. hondurensis</i> , <i>B. ovalis</i> , <i>B. pendula</i>
Nicaragua	<i>B. pendula</i>
Costa Rica	<i>B. alloiophylla</i> , <i>B. brenesii</i> , <i>B. costaricensis</i> , <i>B. immersinervis</i> *, <i>B. obovatifolia</i> *, <i>B. ovalis</i> , <i>B. pendula</i> , <i>B. towarensis</i>
Panama	<i>B. alloiophylla</i> , <i>B. brenesii</i> , <i>B. costaricensis</i> , <i>B. ovalis</i> , <i>B. pendula</i> , <i>B. towarensis</i>
West Indies	<i>B. pendula</i>
Colombia	<i>B. alloiophylla</i> , <i>B. costaricensis</i> , <i>B. latifolia</i> , <i>B. pendula</i> , <i>B. towarensis</i>
Venezuela	<i>B. alloiophylla</i> , <i>B. costaricensis</i> , <i>B. curviramea</i> , <i>B. latifolia</i> , <i>B. pendula</i> , <i>B. towarensis</i>
Guyana	<i>B. curviramea</i>
French Guianas	<i>B. hexanthera</i> *
Ecuador	<i>B. alloiophylla</i> , <i>B. costaricensis</i> , <i>B. latifolia</i> , <i>B. pendula</i> , <i>B. towarensis</i>
Peru	<i>B. costaricensis</i> , <i>B. latifolia</i> , <i>B. towarensis</i>
Bolivia	<i>B. towarensis</i>
Brazil	<i>B. angustifolia</i> *, <i>B. linharesensis</i> *, <i>B. emarginata</i> *, <i>B. fluminensis</i> *, <i>B. rigida</i> *, <i>B. stricta</i> *, <i>B. taubertiana</i> *
Chile	<i>B. berteroana</i> *, <i>B. miersii</i> *

* species endemic to the country

Table 2. Differences between *Beilschmiedia ovalis* and some species morphologically close to *B. ovalis*.

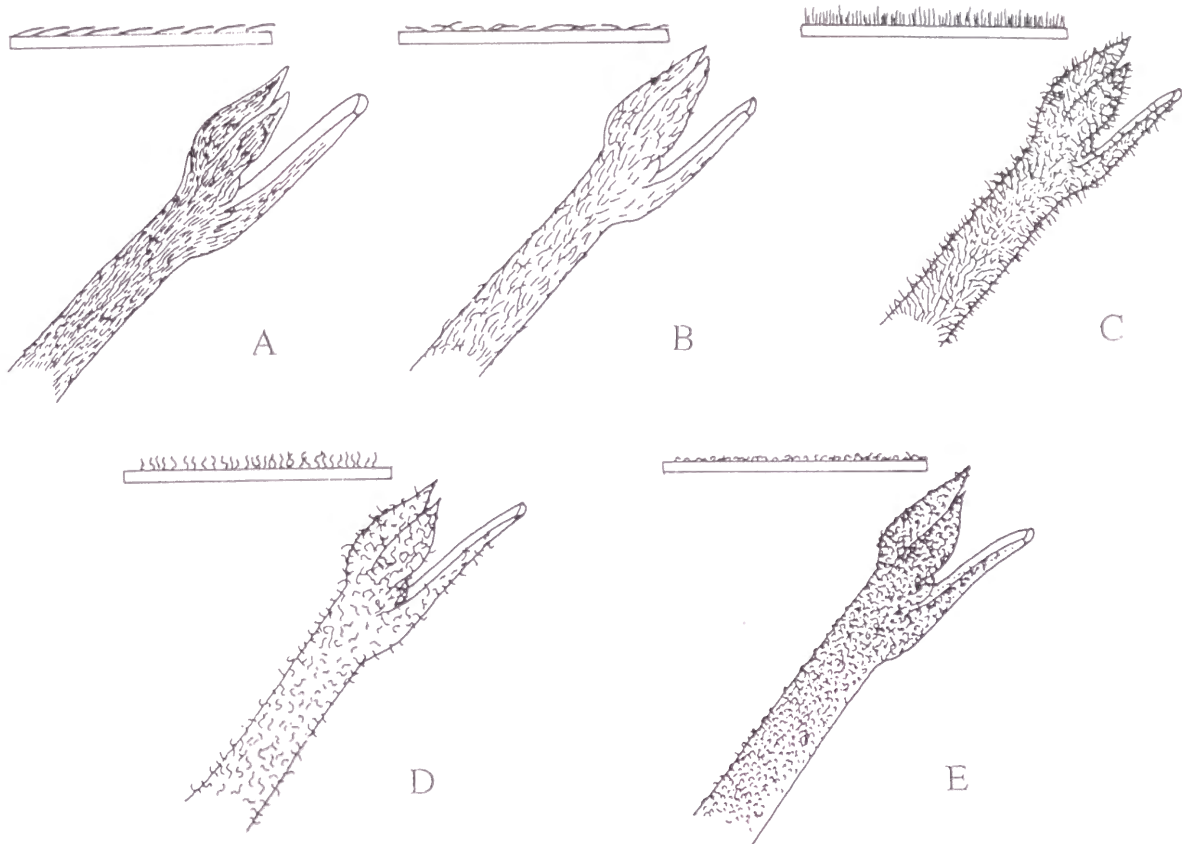
	<i>B. ovalis</i>	<i>B. latifolia</i>	<i>B. obovatifolia</i>	<i>B. ovalioides</i>	<i>B. steyermarkii</i>	<i>B. towarensis</i>
Distribution	Ho, CR, Pa	Ve, Co, Ec, Pe	CR	Me	Gu	CR, Pa, Ve, Co, Ec, Pe, Bo
Altitudal distribution	1800-2800 m	2100-3000 m	1000-1500 m	1850-2750 m	300-400 m	500-3000 m
Pubescence on buds and twigs	erect, short, and curly	erect, long, and straight to curly	erect, short, and curly	erect, short, and curly	erect, short, and curly	appressed, short, and straight
Leaf shape	ovate-broadly elliptic	ovate-broadly elliptic	obovate	obovate-broad elliptic	narrow elliptic	ovate-elliptic-obovate
Leaf length (cm)	5-10	7-11	6-13	11-16	5-10	8-20
Secondary vein number	5-8	6-9	7-11	11-14	7-8	1-11
Pubescence on lower leaf surface	glabrous	pubescent with erect, long, straight to curly hairs	glabrous	pubescent with erect, short, curly hairs	glabrous	pubescent with appressed, short staright hairs
Fruit shape	spherical	ellipsoid	ellipsoid	spherical	unknown	ellipsoid

Country abbreviation, Ho, Honduras; CR, Costa Rica; Gu, Guatemala; Pa, Panama; Ve, Venezuela; Co, Colombia; Ec, Ecuador; Pe, Peru; Bo, Bolivia.

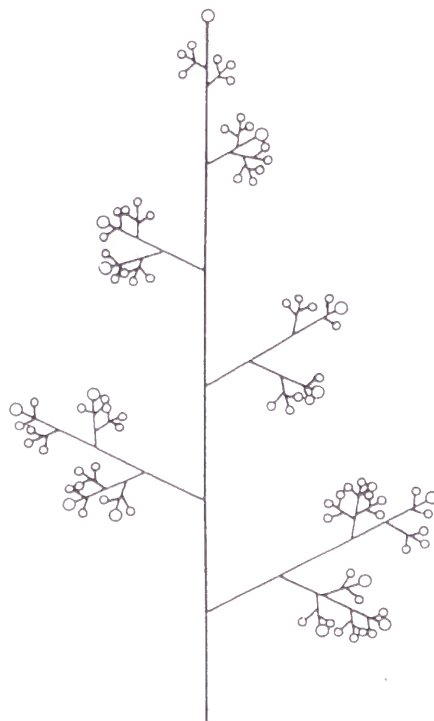
Legends of figures

- Fig. 1. Five types of indument in neotropical *Beilschmiedia* species. A. Appressed. B. Spreading. C. Erect and straight. D. Erect and wavy. E. Erect and curly.
- Fig. 2. Paniculate inflorescence of neotropical *Beilschmiedia* species.
- Fig. 3. Ultimate inflorescence divisions. A. Not strictly cymose. B. Strictly cymose.
- Fig. 4. Flowers of neotropical *Beilschmiedia* species. A. *B. alloiophylla*. B. *B. angustielliptica*. C. *B. hexanthera*. D. *B. linharesensis*. Figure abbreviations, fl, flower; st I, stamen in the first whorl; st II, stamens or staminodia in the third whorl; st IV, staminodia in the fourth whorl; pi, pistil. Scale bars equal 2 mm in flowers, 0.5 mm in stamens, staminodia and pistils.
- Fig. 5. Fruits of neotropical *Beilschmiedia* species. A. *B. pendula*. B. *B. ovalioides*. Scale bars equal 1 cm.
- Fig. 6. Distribution of neotropical *Beilschmiedia* species.
- Fig. 7. Distribution of *Beilschmiedia alloiophylla* (open circles), *B. anay* (pentagrams), *B. angustielliptica* (square), and *B. angustifolia* (dot).
- Fig. 8. Distribution of *Beilschmiedia berteroa* (open circles), *B. brenesii* (pentagrams).
- Fig. 9. Distribution of *Beilschmiedia costaricensis* (open circles), *B. curviramea* (pentagrams), *B. emarginata* (squares), and *B. fluminensis* (dots).
- Fig. 10. Distribution of *Beilschmiedia hexanthera* (open circle), *B. hondurensis* (pentagrams), *B. immersinervis* (square), and *B. latifolia* (dots).
- Fig. 11. Distribution of *Beilschmiedia linharesensis* (open circle), *B. mexicana* (pentagrams), *B. miersii* (square), and *B. obovatifolia* (dots).
- Fig. 12. Distribution of *Beilschmiedia ovalioides* (open circles), and *B. ovalis* (pentagrams).
- Fig. 13. Distribution of *Beilschmiedia pendula* (open circles), *B. rigida* (pentagram), *B. riparia* (squares), and *B. steyermarkii* (dot).
- Fig. 14. Distribution of *Beilschmiedia stricta* (open circle), *B. taubertiana* (pentagrams), and *B. tovarensis* (squares).
- Fig. 15. Leaf morphology of *Beilschmiedia tovarensis*.

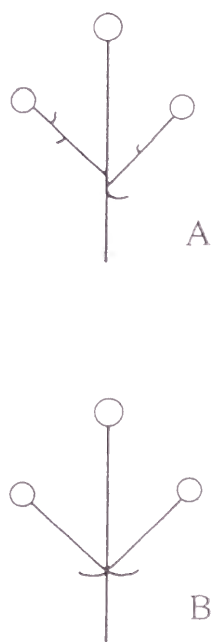
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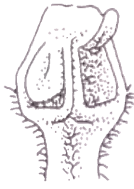
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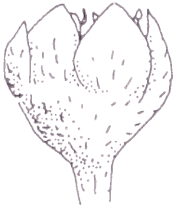
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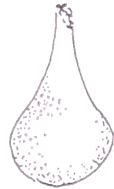
4



A



B



C



D



fl



st I



st III

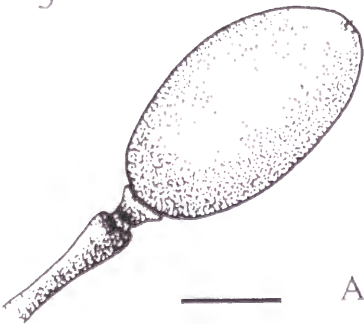


st IV

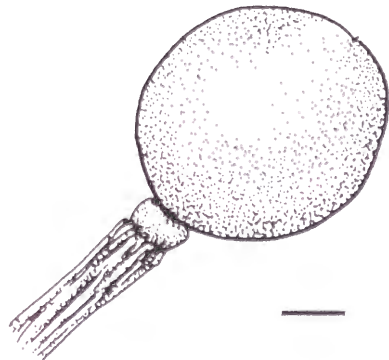


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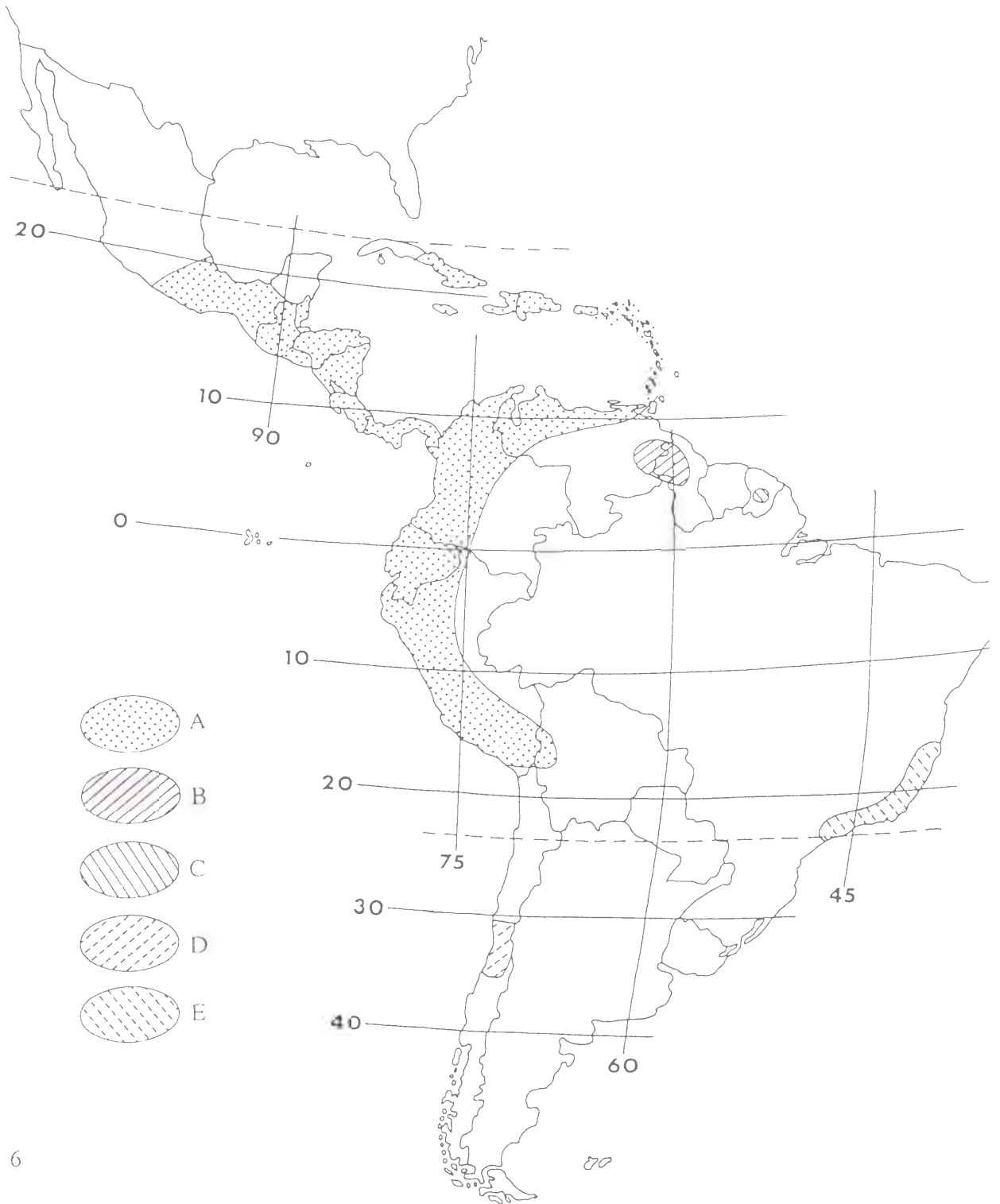
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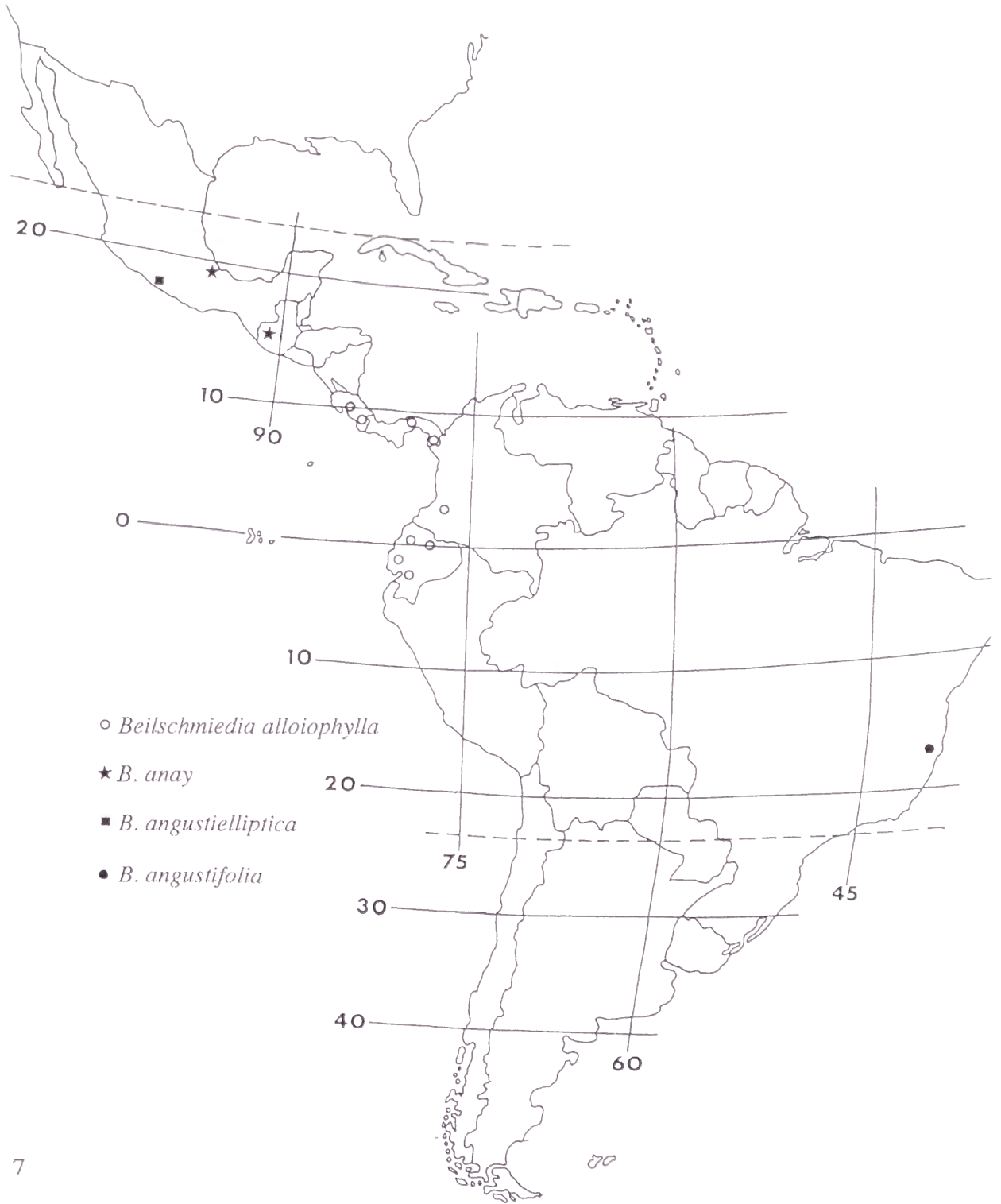
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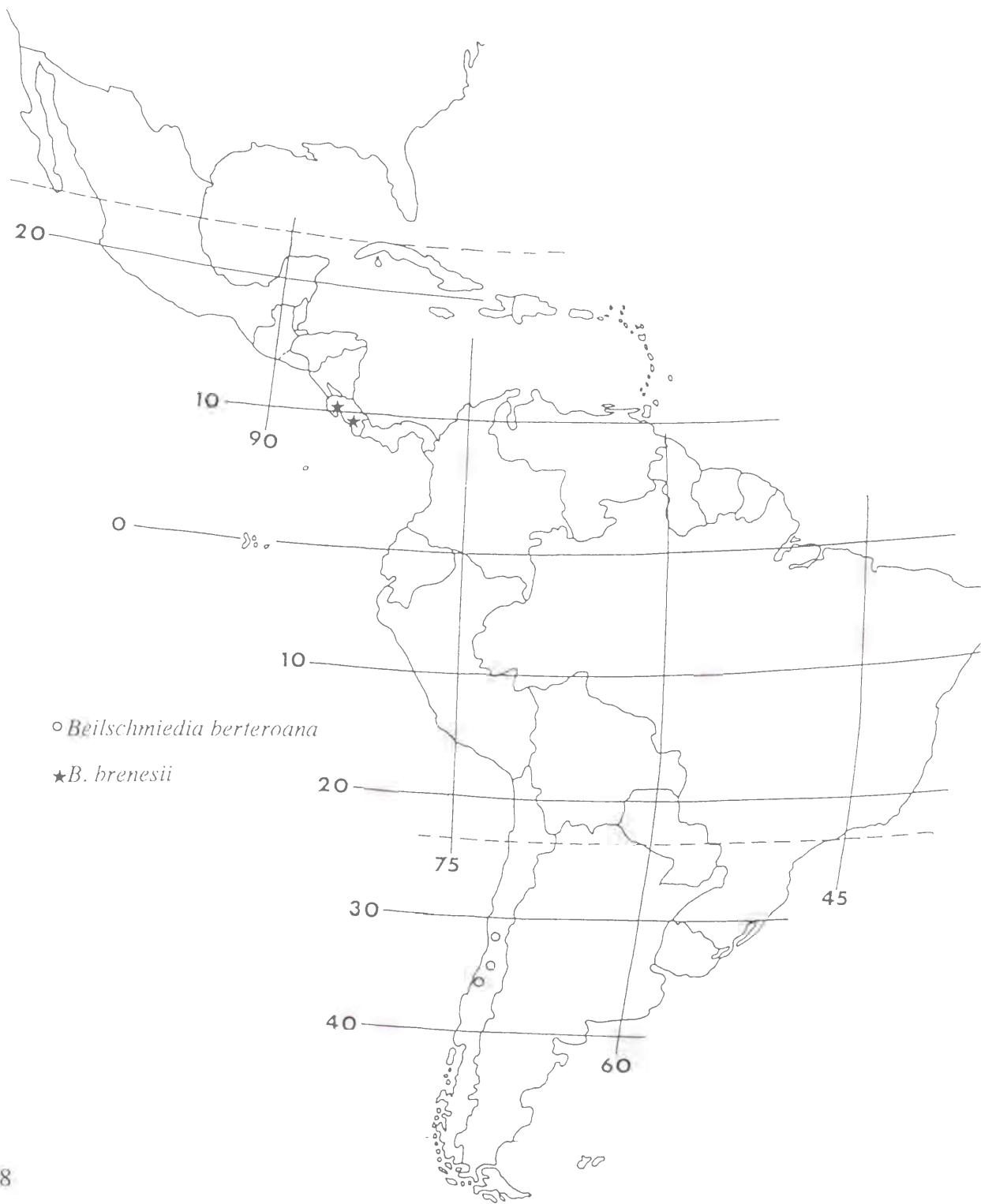


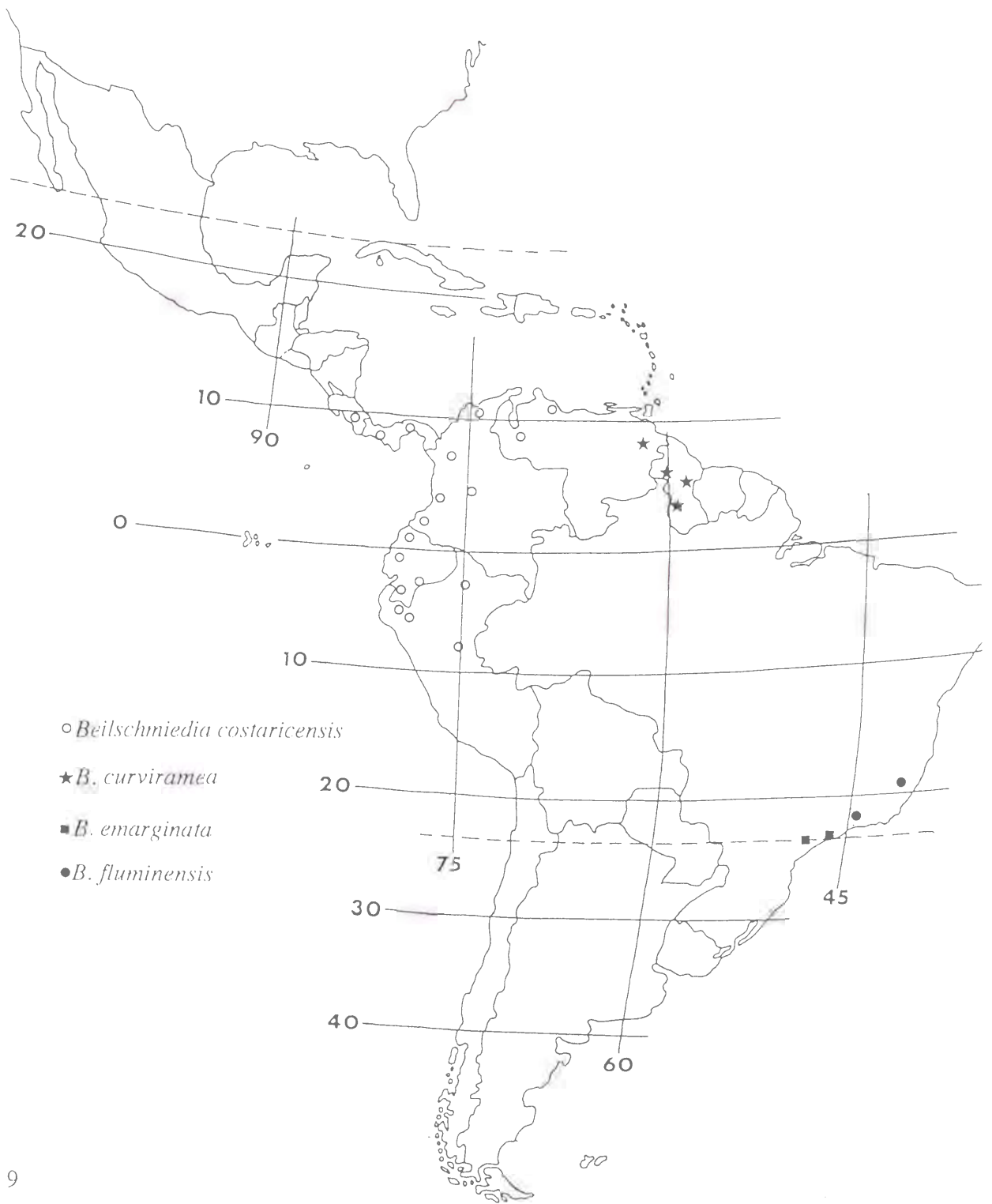
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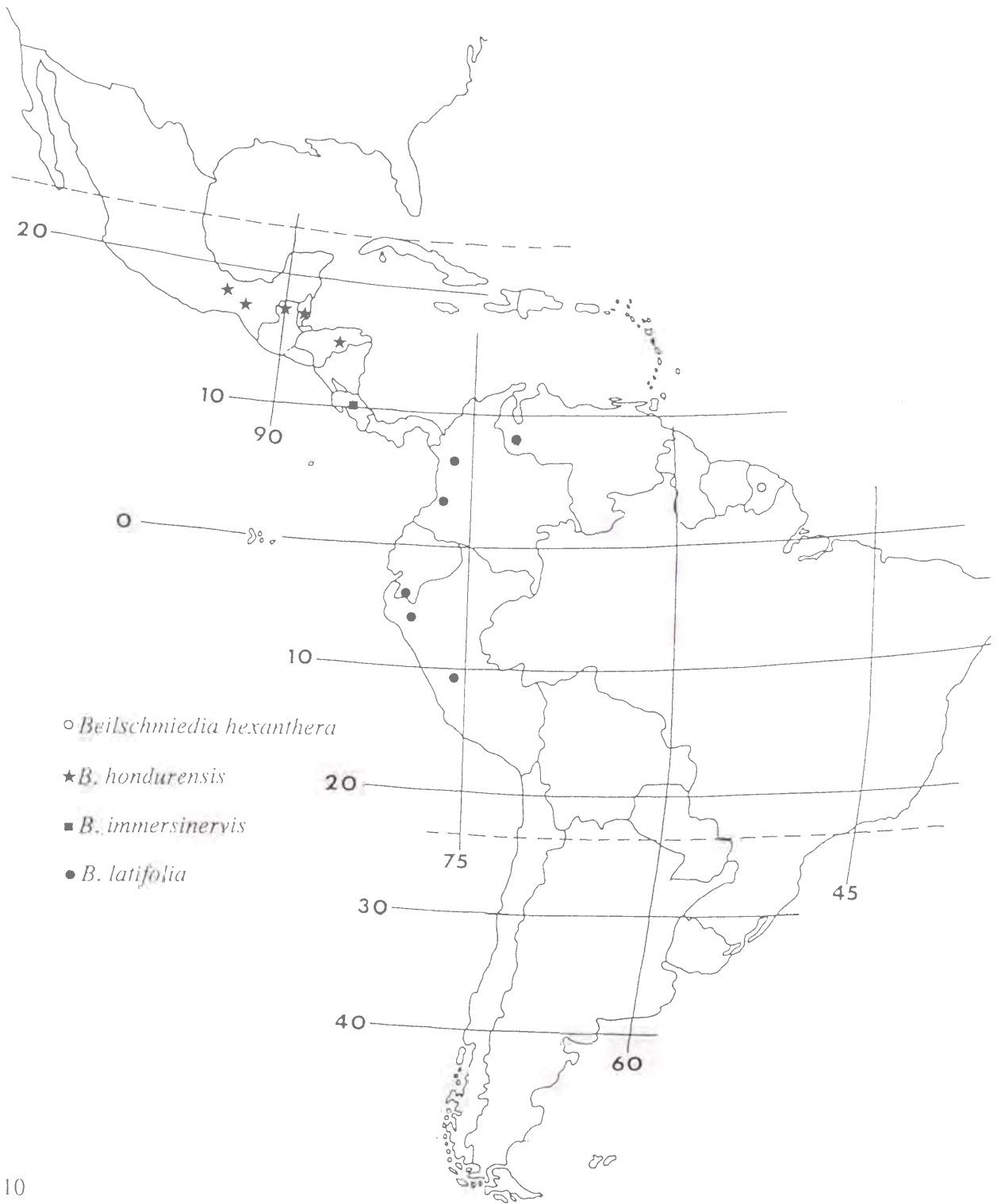


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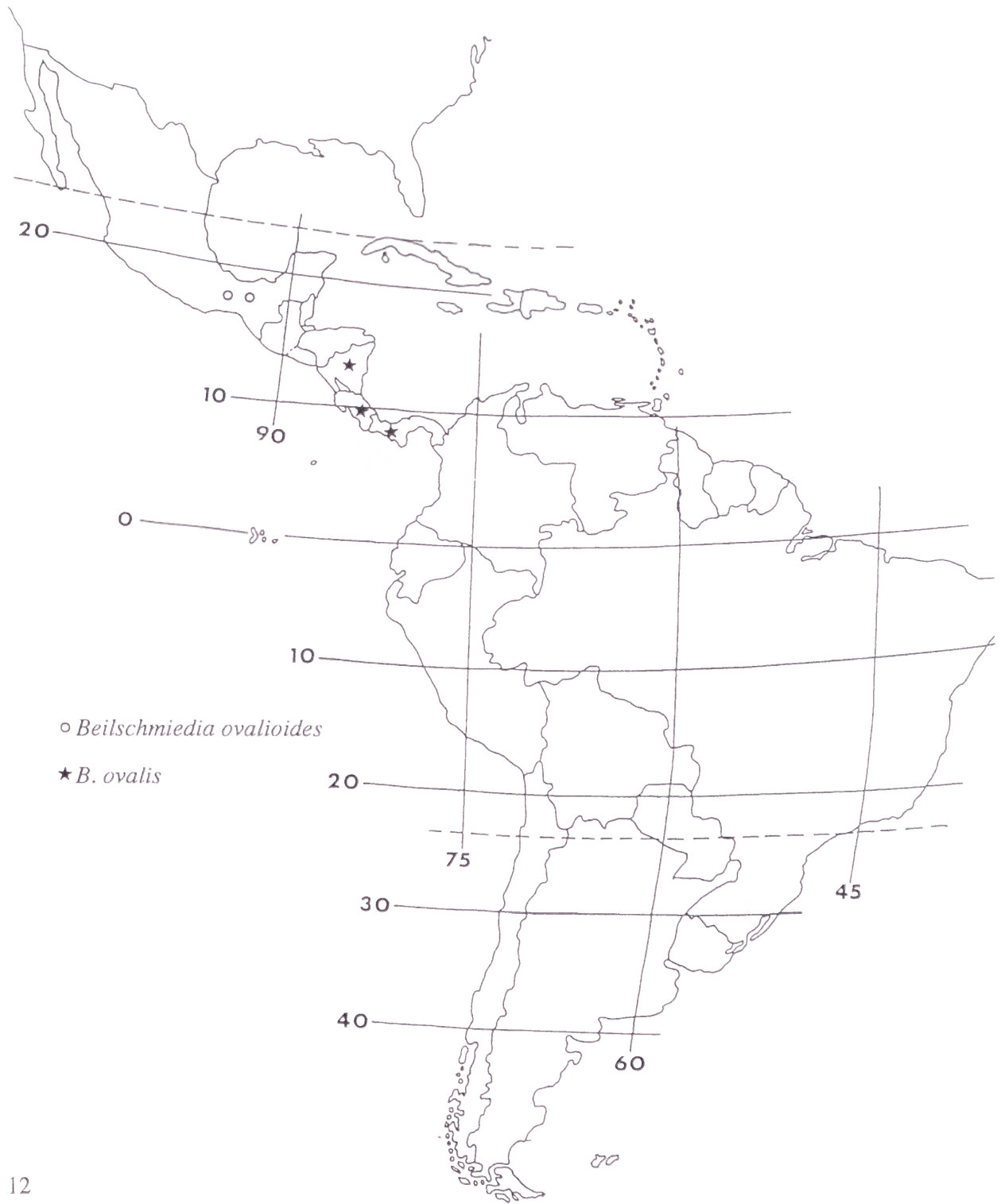


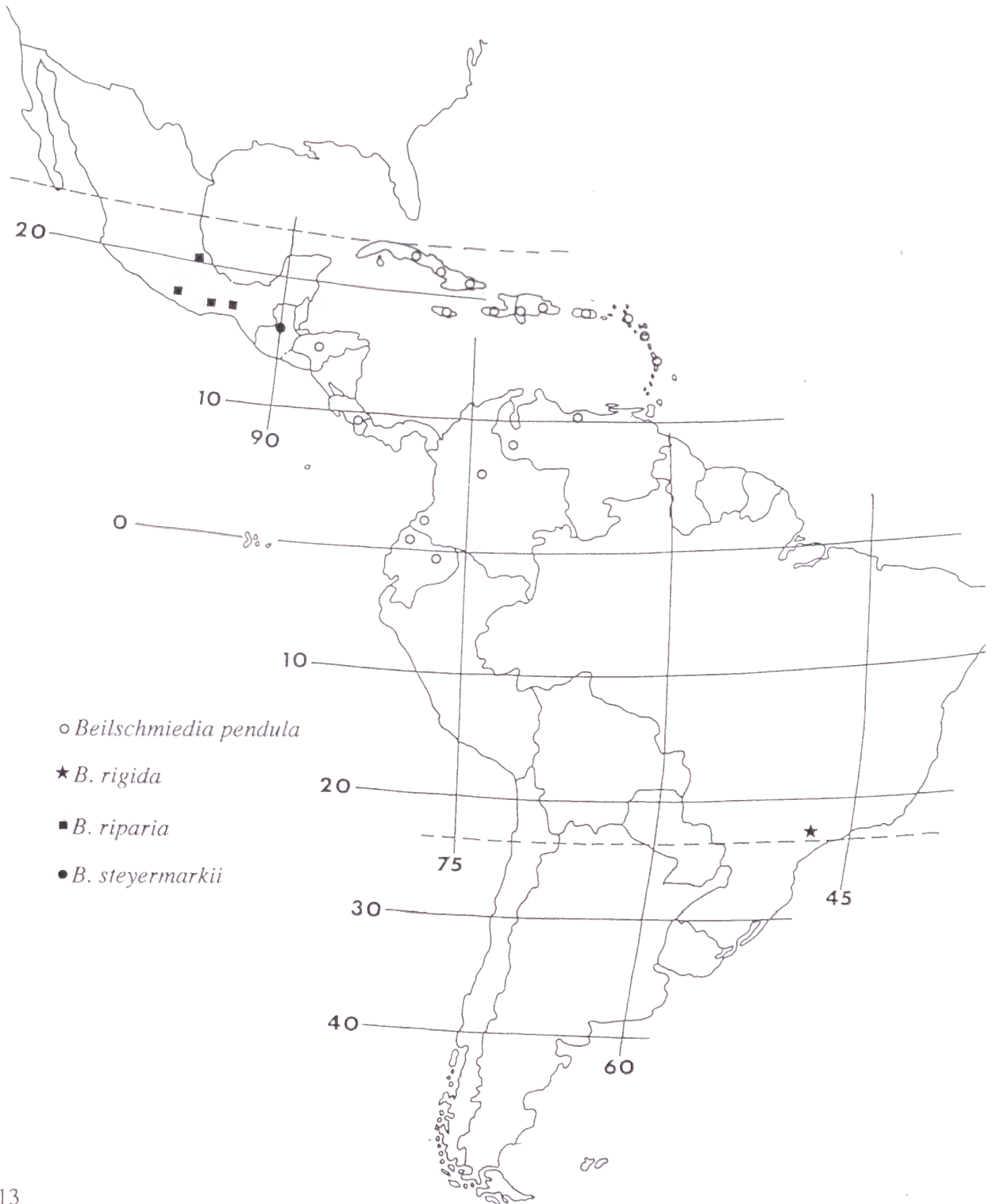


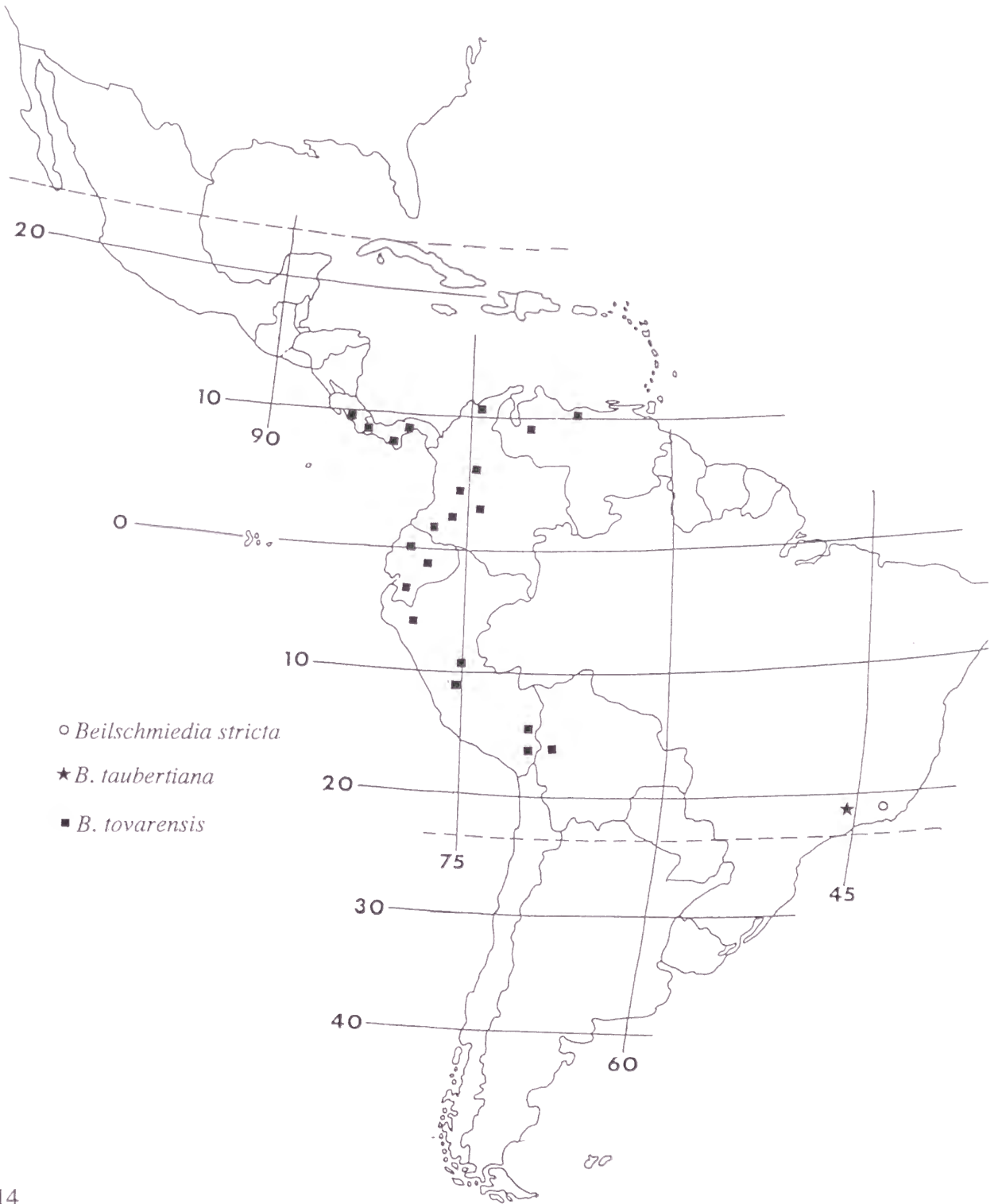




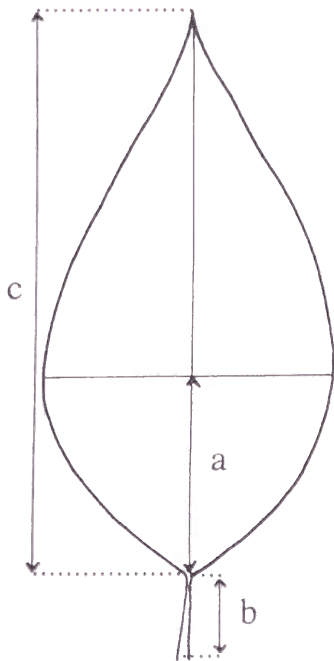
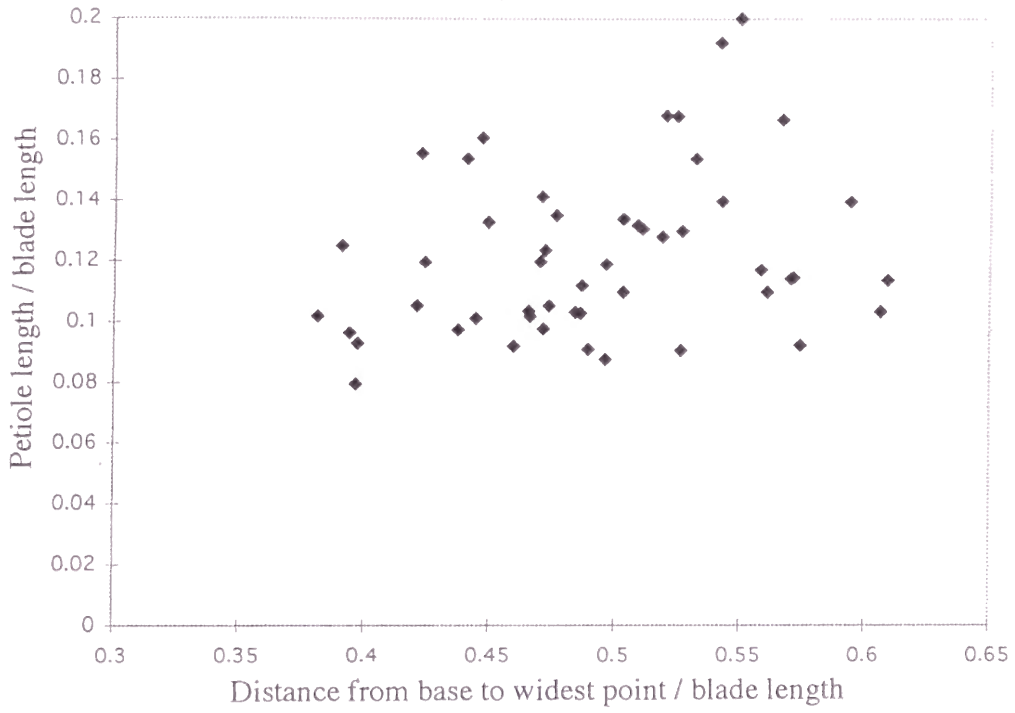








Leaf morphology of *Beilschmiedia towarensis*



a: Distance from base to widest point

b: Petiole length

c: Blade length

Chapter 3. Leaf Anatomy of neotropical *Beilschmiedia* species

Introduction

Neotropical *Beilschmiedia* species have, with a few exceptions, quite similar flowers and fruits. Thus, it is extremely difficult to discuss their relationships solely based on the reproductive characters. Considering this difficulty, I investigated leaf anatomy, especially the venation pattern, cuticular characters and leaf section, for this revisional study.

Leaf anatomy of Lauraceae has been studied for more than a century and is still energetically studied especially in Australia. Christophel and Rowett (1996) recently published a leaf and cuticle atlas of Australian Lauraceae, which include the leaf architecture and cuticular study for all the Australian Lauraceae except for *Cassytha*. Christophel et al. (1996) proposed the use of cuticular characters in the taxonomic study of Lauraceae based on their investigation of the Australian species.

On the other hand, there are few studies in which leaf anatomy of neotropical *Beilschmiedia* species was examined intensively. There is a study by Petzold (1907) in which he observed the epidermis, hypodermis, and mesophyll characters of some neotropical Lauraceae species. But he did not mention any character which could distinguish *Beilschmiedia* (referred as *Bellota* and *Hufelandia* in that study) from other genera, nor did he suggest any subdivision within the genus.

As mentioned in the general introduction, a survey of the specimens indicated that neotropical *Beilschmiedia* species appear to be divided into two groups based on phyllotaxis and venation pattern, one characterized by alternate leaves and fine ramification (ramification is defined here as ultimate branching patterns in leaf veins), and the other by opposite leaves and coarse ramification. This grouping was supported by the preliminary observations of cuticular characters by Christophel (pers. comm.).

To examine this in more details, I investigated the venation patterns, cuticular characters and leaf section for all the neotropical *Beilschmiedia* species available. With these results, I discuss the following articles; 1) whether the cuticular and leaf section characters support the grouping system based on the phyllotaxis and venation patterns, and 2) how we can recognize relationships within neotropical *Beilschmiedia* species based on their leaf anatomical characters.

Materials and Methods

The specimens used for this study are listed in Table 1 with their exsiccatae data.

1. Venation Patterns

To avoid destruction of the leaves and to retain a clear picture of the venation patterns, I employed an X-ray technique proposed by Wing (1992). See his study for the details.

Leaves from the specimens were placed on a sheet of SR5 Kodak film in a vacuum press, where the distance from the leaf to the film was reduced. Then low-voltage X-rays (10-12 kv) with about 3 milliamps were exposed to the films in the press with about 60 cm distance for 3-4 minutes. The films were then developed immediately.

2. Cuticular characters

For the cuticular study, I basically employed a technique described by Christophel and Rowett (1996). About the number of the samples, I firstly used three samples from two different collections (if available) for several species. After confirming the consistency of the characters of the samples in a collection, I used two samples from two different collections whenever available for the rest of the species.

The 1-cm² samples were taken from the near basal margin on the left side (with the adaxial surface upward) of the mature leaf. The sample were placed into test tubes and soaked in 90% ethanol for about 18 hours. Then the ethanol was poured off and ca. 1 ml of 30% H₂O₂ and ca. 0.5 ml of 90% ethanol were added instead. The test tubes were then heated in a hot water bath for 3 to 10 hours.

When color of the samples turned light yellow to white, the samples were transferred from the tube to a petri dish with water. Then the cellular contents of the samples were brushed away with fine artists' brushes to clean the cuticles on both surfaces of the samples. Some of the samples were returned to a test tube of 90% ethanol for about 12 hours to clean the cuticles completely.

The cuticles of the samples were then rinsed in 2% ammonia to adjust pH, and stained in 0.1% Crystal Violet for around 50 seconds. The stained cuticles were placed in phenol glycerin jelly on a slide and a cover glass mounted. After removing the excess jelly, the mounts were ringed with nail varnish to retard dehydration.

3. Leaf sections

The technique used here is a modification of the methodology by Keating (1996).

Dried leaves were soaked in water with some detergent for more than two weeks. The samples were then cleaned with water, placed on a plastic board and sliced by hand with a thin razor blade. The sliced samples were mounted in about 30% calcium chloride, with a cover glass.

Results

1. Venation patterns

All neotropical *Beilschmiedia* species except *B. emarginata* were X-rayed. *Beilschmiedia emarginata* could not be X-rayed because there is no sample free from the specimen sheet, but seen and compared with the other species. *Beilschmiedia ovalioides* were only partially X-rayed (for close up) because an entire leaf free from the specimen sheet was not available. The X-ray pictures are shown in Fig. 1-25 for an entire leaf and Fig. 26-51 for the close up. The terminology of Hyland (1989) and Christophel & Rowett (1996) is employed for descriptions of the basic pattern, secondary veins and tertiary veins, and the terminology of Roth (1996) is employed for the mesh description, unless especially mentioned.

Basic pattern. In venation patterns of Lauraceae, there are two basic patterns which were referred as penninerved and triplinerved by Hyland (1989). All the neotropical *Beilschmiedia* species have penninerved leaves.

Secondary vein pattern. Hyland (1989) considered the midrib to be just that and the lateral veins to be primary veins. I rather follow the terms used by Christophel & Rowett (1996) (originally used by Hickey 1979), calling the midrib a primary vein, the lateral veins secondary veins (secondaries), and so forth.

According to Christophel & Rowett (1996), the secondary vein patterns in Lauraceae include brochidodromous (in which the secondaries bend upward and form a loop with the super-adjacent secondaries), eucamptodromous (in which the secondaries do not meet the adjacent ones and curve towards the margin of the leaf without ever reaching it), and

pseudo-brochidodromous (in which the leaf appears brochidodromous but actually the loops are formed by strengthened tertiaries, not by the secondaries themselves).

Most neotropical *Beilschmiedia* species have pseudo-brochidodromous leaves. But the leaves of these species sometimes have the secondaries near the leaf apex, forming loops by themselves and appearing partly brochidodromous. Leaves of *B. angustifolia* (Fig. 4) and *B. linharesensis* (Fig. 14) in the X-ray pictures appear to be entirely brochidodromous, but the larger leaves of these species often have pseudo-brochidodromous (and partly brochidodromous). A few species such as *B. ovalis* (Fig. 18) and *B. steyermarkii* (Fig. 22) appear to have eucamptodromous leaves, but even in these species margins of the secondaries curve inwards and some of the tertiaries reach to the adjacent veins, appearing pseudo-brochidodromous.

Tertiary vein pattern. In the tertiaries, Christophel and Rowett (1996) recognized two patterns; 1) percurrent, in which the tertiaries directly connect to adjacent secondaries, 2) reticulate, in which tertiaries anastomose with other tertiary or secondary veins and do not run directly to secondaries. The former category, percurrent, can be divided into two further categories; 1) strongly percurrent, having a ladder-like appearance, 2) weakly percurrent, appearing to meander or arch in their course. The latter category can be also divided into two further categories, 1) orthogonal, meaning that they form mainly right-angled anastomoses, 2) random, meaning they are either curved or form a variety of anastomoses.

Some neotropical *Beilschmiedia* species, such as *B. alloiophylla* (Fig. 1), *B. anay* (Fig. 2), *B. latifolia* (Fig. 13), *B. obovatifolia* (Fig. 17), *B. ovalioides*, and *B. riparia* (Fig. 21), have strongly percurrent tertiaries. Most of these species have mostly simple tertiaries, but *B. latifolia* and *B. riparia* often have branched tertiaries. Weakly percurrent tertiaries often occur in *B. costaricensis* (Fig. 7), *B. hexanthera* (Fig. 10), *B. immersinervis* (Fig. 12), *B. ovalis* (Fig. 18), *B. steyermarkii* (Fig. 22) and *B. towarensis* (Fig. 25). But *B. costaricensis*, *B. hexanthera*, *B. immersinervis* and *B. ovalis* sometimes have reticulate rather than percurrent tertiaries. The tertiaries in these species are mostly branched even if percurrent.

Reticulate tertiaries occur in *B. angustieliptica* (Fig. 3), *B. angustifolia* (Fig. 4), *B. berteriana* (Fig. 5), *B. brenesii* (Fig. 6), *B. costaricensis* (Fig. 7), *B. curviramea* (Fig. 8), *B. emarginata*, *B. fluminensis* (Fig. 9), *B. hexanthera* (Fig. 10), *B. hondurensis* (Fig. 11), *B. immersinervis* (Fig. 12), *B. linharesensis* (Fig. 14), *B. mexicana* (Fig. 15), *B. miersii* (Fig.

16), *B. ovalis* (Fig. 18), *B. pendula* (Fig. 19), *B. rigida* (Fig. 20), *B. stricta* (Fig. 23) and *B. taubertiana* (Fig. 24). Most of these species have the tertiaries random reticulate.

Ramification. Roth (1996) called an area surrounded by a delicate network of a minor venation “mesh”. Meshes are various in size and shape, sometimes divided into smaller meshes. She recognized two types of meshes, “open” meshes and “closed” meshes. In open meshes the bundle ramifications terminate freely within the meshes, while in closed meshes no free endings are developed within the meshes.

In neotropical *Beilschmiedia* species, the most discriminating character of the ramification is the extent of the hierarchy of mesh subdivision, rather than whether meshes are open or closed.

In most species, larger meshes are divided further into smaller meshes, and the smallest meshes can be open or closed even in the same leaf (but see below).

Compared to the difference between the open and closed meshes, two patterns are more clearly recognizable in the degree of their mesh division. In some species the larger meshes are divided several times and the smallest meshes formed by the veins in the sixth or higher order. In other species larger meshes are divided only once or twice, and the smallest meshes are formed by the veins in the fourth and fifth order. The appearance of the leaf in the former case is “fine ramification”, whereas the appearance in the latter case is “coarse ramification” (these terms are original for this study). The appearances are so different that one can recognize them with the unaided eye.

Fine ramification occurs in *B. alloiophylla* (Fig. 26) *B. anay* (Fig. 27), *B. costaricensis* (Fig. 32, but see below), *B. hexanthera* (Fig. 35), *B. immersinervis* (Fig. 37), *B. latifolia* (Fig. 38), *B. mexicana* (Fig. 40), *B. obovatifolia* (Fig. 42), *B. ovalioides* (Fig. 43), *B. ovalis* (Fig. 44), *B. pendula* (Fig. 45), *B. riparia* (Fig. 47), *B. steyermarkii* (Fig. 48) and *B. towarensis* (Fig. 51). The smallest meshes are less than 0.5 mm in diam. Among the species, *B. costaricensis* and *B. pendula* usually have slightly coarser (c.a. 0.5 mm in diam.) ramification than the other species (c.a. 0.2 mm in diam.). These species also have the ramification square-like with angular meshes, whereas the other species have the one areole with more or less roundish meshes. And in *B. costaricensis* there are some collections which appear to have coarser ramification (but see the discussion). Many species with fine ramification have their smallest meshes more or less closed, whereas *B. costaricensis*, *B. hexanthera* and *B. pendula* have the smallest meshes open.

The coarse ramification occurs in *B. angustieliptica* (Fig. 28), *B. angustifolia* (Fig. 29), *B. berteroana* (Fig. 30), *B. brenesii* (Fig. 31), *B. curviramea* (Fig. 33), *B. emarginata*, *B. fluminensis* (Fig. 34), *B. hondurensis* (Fig. 36), *B. miersii* (Fig. 41), *B. rigida* (Fig. 46), *B. stricta* (Fig. 49) and *B. taubertiana* (Fig. 50). The smallest meshes are more than 1.5 mm in diam., and usually open, with the terminal veinlets free, dendroid or like cock's tread.

2. Cuticular characters

The cuticles studied here are in fact the cuticular membrane on the epidermis or the stomatal complex which remained through the preparation, and that the cuticular characters described here are mostly the characters of the epidermal cells or the stomatal complex whose impression is preserved in the membrane (Fig. 52). An exception to this is a description of the stomatal ledges, which protrude from the cuticular membrane and often referred as cuticular ledges. Sometimes walls of the cells under epidermis are also cutinized and remain the impression (e.g., black lines of the adaxial surface in *B. curviramea*, Fig. 60), but the impression of these cells was not taken in consider in this study because the presence was not consistent among the species.

Twenty-two out of 27 species were examined. Samples were unavailable of *B. anay*, *B. emarginata*, *B. fluminensis*, *B. stricta* and *B. taubertiana*. The cuticular pictures are shown in Fig. 53 (SEM, abaxial surface), Fig. 54-75 (adaxial surfaces), Fig. 76-97 (abaxial surfaces), Fig. 98-119 (stomata). The terminology of Christophel et al. (1996) is employed unless otherwise mentioned.

Neotropical *Beilschmiedia* species are hypostomatic, as Christophel et al. (1996) suspected for most of the Lauraceae. In addition to presence/absence of stomata, cuticles of either side of the leaves vary in shape and size of epidermal cells. According to Christophel et al. (1996), useful cuticular characters are 1) ornamentation on periclinal walls of the epidermal cells, 2) uniformity of thickness of the anticlinal walls, 3) straightness of the anticlinal walls, 4) uniformity of cell size and maximum dimension of the epidermal cells, 5) variation in cell size and shape between the adaxial and abaxial cuticles, 6) cell size and characters of subsidiary cells, 7) the nature of the stomatal ledges, 8) presence/absence and characters of various specialized cells.

1) *Ornamentation on periclinal walls of the epidermal cells.* In the majority of neotropical *Beilschmiedia* species, the periclinal walls on both (adaxial/abaxial) epidermal surfaces are

smooth. However, in *B. angustieliptica* (Fig. 55, 77), *B. brenesii* (Fig. 53, 58, 80) and *B. hondurensis* (Fig. 62, 84), the periclinal walls of both surfaces protrude outwards along the anticlinal walls and appear to be somewhat dotted. In *B. angustifolia*, *B. curviramea*, *B. linharesensis* and *B. rigida*, the periclinal walls appear dotted on the adaxial epidermis, but irregularly thickened (granular) on the abaxial epidermis (Fig. 78, 82, 87, 94).

2) *Uniformity of thickness of the anticlinal walls.* Christophel et al. (1996) described anticlinal walls as smooth, irregularly thickened, regularly uneven (beaded), or sinuous in outline (buttressed). According to them, the most common state in Lauraceae is smooth, but *Beilschmiedia* is characterized by some degree of uneven anticlinal wall thickening (buttressing or beading).

Many of neotropical *Beilschmiedia* species have some degree of uneven anticlinal walls. Several species have almost smooth anticlinal walls, but the walls are sometimes slightly beaded, which makes it difficult to draw a clear borderline between smooth walls and beaded walls. Generally, the walls are too variable to be placed into a clear-cut category except for the extremes. The anticlinal walls in the extreme states are: 1) the ones strongly buttressed in *B. angustieliptica* (Fig. 55, 77), *B. brenesii* (Fig. 58, 80) and *B. hondurensis* (Fig. 62, 84) on both surfaces; and 2) the ones in which the walls themselves are only slightly sinuous but the outline appears buttressed because the walls are “branched” (original term for this study, the state having an extended cuticle from the walls, see the arrow in Fig. 56) in *B. angustifolia* (Fig. 56) only on the adaxial surface, *B. curviramea* (Fig. 60, 82) and *B. linharesensis* (Fig. 65, 87) on both surfaces.

3) *Straightness of the anticlinal walls.* Christophel et al. (1996) scored anticlinal walls with another character, straightness of the walls; “angular” for the straight walls, “rounded” (regularly or irregularly) for the slightly curved walls, “undulate” for the walls one trough and peak per cell wall, or “sinuous” for the walls in which more than one peak and trough per wall.

Many neotropical *Beilschmiedia* species have almost angular anticlinal walls, but with corners of the cells somewhat roundish. Rounded walls occur on the abaxial epidermis in *B. hexanthera* (Fig. 83), *B. mexicana* (Fig. 88), *B. pendula* (Fig. 93), *B. rigida* (Fig. 94) and *B. tovarensis* (Fig. 97), but the difference between angular walls and rounded walls are very little. Undulate walls occur on abaxial epidermis in *B. alloiophylla* (Fig. 76), *B. angustifolia*

(Fig. 78), *B. curviramea* (Fig. 82). Sinuous walls occur on either side of the epidermis in *B. angustieliptica* (Fig. 55, 77), *B. brenesii* (Fig. 58, 80) and *B. hondurensis* (Fig. 62, 84). Anticlinal walls on the adaxial epidermis in *B. angustifolia* (Fig. 56), on both surfaces in *B. curviramea* (Fig. 60, 82) and *B. linharesensis* (Fig. 65, 87), are hard to be categorized by the scoring of Christophel et al. (1996), in which the center of the walls is almost angular or rounded but the entire walls appear sinuous because the walls are branched.

4) *Uniformity of cell size and maximum dimension of the epidermal cells.* Generally, the cell size is variable within an epidermis in neotropical *Beilschmiedia* species. The variation is greater on the abaxial epidermis than on the adaxial epidermis.

The maximum dimension of the cells is rather small (ca. 15-25 μm on the adaxial epidermis, ca. 25-35 μm on the abaxial epidermis) in many species, while it is larger (ca. 30-40 μm on the adaxial epidermis, ca. 35-50 μm) in *B. angustieliptica* (Fig. 55, 77), *B. angustifolia* (Fig. 56, 78), *B. berteroaana* (Fig. 57, 79), *B. brenesii* (Fig. 58, 80), *B. curviramea* (Fig. 60, 82), *B. hondurensis* (Fig. 62, 84), *B. linharesensis* (Fig. 65, 87), *B. miersii* (Fig. 67, 89) and *B. rigida* (Fig. 72, 94).

5) *Variation in cell size and shape between the adaxial and abaxial cuticles.* Most neotropical *Beilschmiedia* species have epidermal cells of equivalent size and shape on the adaxial and abaxial cuticles. The species which have a great variation in cell size (not in shape) between the two cuticles are *B. latifolia* (Fig. 64, 86), *B. miersii* (Fig. 67, 89), *B. obovatifolia* (Fig. 68, 90), *B. ovalioides* (Fig. 69, 91), and *B. towarensis* (Fig. 75, 97). Among them *B. miersii* is especially distinct with its adaxial cells larger than the abaxial cells. *Beilschmiedia latifolia*, *B. obovatifolia*, *B. ovalioides* and *B. towarensis* have the adaxial cells smaller than the abaxial cells. The species with much variation in cell shape between the two cuticles are *B. angustifolia* (Fig. 56, 78), *B. curviramea* (Fig. 60, 82), *B. linharesensis* (Fig. 65, 87) and *B. rigida* (Fig. 72, 94).

6) *Cell size and characters of subsidiary cells.* Stomata of neotropical *Beilschmiedia* species are paracytic, more or less uniformly distributed within areoles and randomly oriented. Stomata of Lauraceae are reported to be mostly sunken (Christophel et al. 1996) (Fig. 52), and those of neotropical *Beilschmiedia* species are not exceptional. Christophel & Rowett (1996) mentioned that a characteristic of the Australian *Beilschmiedia* is possession of

uneven-sized subsidiary cells. This is also true of neotropical *Beilschmiedia* species. Distinct subsidiary cells, whose periclinal walls are irregularly thickened and appear granular, occur in *B. angustifolia* (Fig. 100), *B. curviramea* (Fig. 104), *B. linharesensis* (Fig. 109) and *B. rigida* (Fig. 116).

7) *The nature of the stomatal ledges.* Many neotropical *Beilschmiedia* species have narrow stomatal ledges. Slightly wider stomatal ledges are seen in *B. angustifolia* (Fig. 100), *B. curviramea* (Fig. 104), *B. linharesensis* (Fig. 109) and *B. rigida* (Fig. 116). Extremely wide stomatal ledges occur in *B. angustielliptica* (Fig. 99), *B. brenesii* (Fig. 102), *B. hondurensis* (Fig. 106), whose inner stomatal ledges protrude between the guard cells and the subsidiary cells, forming “butterfly-shape” (termed in Christophel et al. 1996). *B. berteriana* also has very different stomata from the other species, in which the inner stomatal ledges protrude in parallel to the outer ledges, forming rectangular “box-shape” (termed by Christophel, pers. comm.) and the ledges themselves are scarcely stained (Fig. 101).

8) *Presence/absence and characters of various specialized cells.* The specialized cells mostly seen in neotropical *Beilschmiedia* species are trichomes, which are same as all the trichomes of Lauraceae thus far reported (Christophel et al. 1996). The trichomes of neotropical *Beilschmiedia* species are simple, with their basal bases (e.g., Fig. 86). Although the trichomes themselves are various among the species (see the section *indument* in the second chapter), basal cells of trichomes are relatively uniform. Giant stomata, referred as “hydathodes” in Christophel et al. (1996), are sometimes present in neotropical *Beilschmiedia* species (e.g., Fig. 97), but there is no significant difference among the species.

3. Leaf sections

Twenty-two of 27 species were examined for the leaf section study. *Beilschmiedia anay*, *B. emarginata*, *B. fluminensis*, *B. stricta* and *B. taubertiana* could not be studied because of the lack of material. Pictures of the petiole sections are shown in Fig. 120-121, midrib sections in Fig. 122-143.

Hypodermis. According to Metcalfe (1987), a single-layered hypodermis has been recorded beneath the adaxial epidermis in species of *Beilschmiedia*.

Many neotropical *Beilschmiedia* species have a single-layered or double-layered adaxial hypodermis. A single-layered hypodermis was observed in *B. berteriana*, *B. costaricensis*, *B. curviramea*, *B. hexanthera*, *B. latifolia*, *B. linharesensis*, *B. miersii*, *B. obovatifolia*, *B. ovalis*, *B. pendula*, *B. riparia*, *B. steyermarkii* and *B. towarensis*. Double-layered hypodermis occurs in *B. angustifolia*, *B. ovalioides* and *B. ovalis*. But some of the species have a double-layered hypodermis near the midrib and a single-layered hypodermis toward the margin. A three-layered hypodermis was observed in *B. rigida*.

Mesophyll. Most neotropical *Beilschmiedia* species have 1-2 layered palisade tissue. The species with well developed palisade tissue (three-layered) are *B. latifolia*, *B. miersii*, *B. obovatifolia*, *B. ovalis* and *B. pendula*. It is sometimes difficult to count the palisade layers because some palisade tissue does not appear elongated enough in dried leaves, which makes it hard to distinguish the palisade tissue from the spongy parenchyma. Oil cells are often observed in the palisade tissue.

Bundle sheaths. Bundle sheaths are sclerenchymatous in neotropical *Beilschmiedia* species. The sclerenchyma is 2-3 layered, and some of the sheaths extend to both sides of the epidermis, forming "bundle sheath extensions". This bundle sheath extension was usually observed in *B. alloiophylla*, *B. costaricensis*, *B. hexanthera*, *B. immersinervis*, *B. latifolia*, *B. mexicana*, *B. obovatifolia*, *B. ovalioides*, *B. ovalis*, *B. pendula*, *B. riparia*, *B. steyermarkii* and *B. towarensis*. The other species studied do not usually have the bundle sheath extension. *Beilschmiedia angustielliptica* rarely has the bundle sheath thick and somewhat extending to the epidermis.

Nodes and petioles. As Metcalfe (1987) reported for the general features of Lauraceae nodes and petioles, the nodes are three-trace unilacunar (3:1) in neotropical *Beilschmiedia* species. Metcalfe (1987) mentioned that where there are three bundles at the base of the petiole they may branch half-way along the length of the petiole to give five or seven bundles which commonly reunite at the petiole's distal end. This is also true of neotropical *Beilschmiedia* species. Most of the species have the bundles of the petioles arranged in a flattened arc, but the ends of the arc tends to curve inwards (Fig. 120-121) in the species which have the bundles of the midrib arranged in a ring.

Midrib. The most distinct character which discriminate neotropical *Beilschmiedia* species is arrangement of the vascular bundles. The vascular bundles of the midrib are arranged in a ring (with the upper part flattened) in *B. alloiophylla* (Fig. 122), *B. angustifolia* (Fig. 124), *B. costaricensis* (Fig. 127), *B. curviramea* (Fig. 128), *B. hexanthera* (Fig. 129), *B. immersinervis* (Fig. 131), *B. latifolia* (Fig. 132), *B. linharesensis* (Fig. 133), *B. mexicana* (Fig. 134), *B. obovatifolia* (Fig. 136), *B. ovalioides* (Fig. 137), *B. ovalis* (Fig. 138), *B. pendula* (Fig. 139), *B. rigida* (Fig. 140), *B. riparia* (Fig. 141), *B. steyermarkii* (Fig. 142) and *B. tovarensis* (Fig. 143), while the bundles are arranged in a flattened arc in *B. angustielliptica* (Fig. 123), *B. berteroaana* (Fig. 125), *B. brenesii* (Fig. 126), *B. hondurensis* (Fig. 130) and *B. miersii* (Fig. 135).

Most of the bundles arranged in a flattened arc are united. On the other hand, most of the bundles in a ring are diffuse to some degree. Less diffused bundles (into about two units in the upper part, one in the lower part) occur in *B. angustifolia* (Fig. 124), *B. curviramea* (Fig. 128), *B. linharesensis* (Fig. 133), *B. rigida* (Fig. 140) and *B. riparia* (Fig. 141), while highly diffused (into more than ten parts) occur in the other species.

Metcalf (1987) mentioned that medium-sized and small veins are often made vertically transcurrent by sclerenchymatous elements, and that the sclerenchymatous sheath in a few species of *Persea* spreads out beneath the adaxial epidermis. This is also seen in the midribs of neotropical *Beilschmiedia* species. The vascular bundles are surrounded by sclerenchymatous cells in all the species (e.g., Fig. 126), and the sclerenchymatous sheath spreads out in *B. angustielliptica* (Fig. 123), *B. costaricensis* (Fig. 127), *B. hexanthera* (Fig. 129), *B. hondurensis* (Fig. 130), *B. pendula* (Fig. 139), *B. riparia* (Fig. 141) and *B. steyermarkii* (Fig. 142). The sclerenchymatous sheath in *B. berteroaana* and *B. miersii* is not spread out, but thickened to more than eight layers.

The vascular bundles with sclerenchymatous sheaths are then surrounded by spongy tissue, and gradually by collenchymatous tissue. In most of the species oil or mucilage cells occur in the spongy tissue or collenchymatous tissue.

Discussion

To understand relationships within neotropical *Beilschmiedia* species with their leaf anatomical characters, one of the most important prerequisites is that characters informative for the systematics are carefully selected. Therefore, which characters are informative is

discussed first, followed by groupings of venation patterns, cuticles and leaf sections respectively. Discussion of relationships with consideration of total characters then follows.

1) venation patterns

Considering how consistently the character states occur within each species, the most informative character in venation patterns is the ramification. Usually, ramification of neotropical *Beilschmiedia* species is clearly divided into two patterns, fine ramification or coarse ramification, and the character state is consistent in each species. The distinctly exceptional species is *B. costaricensis*, in which coarse ramification occurs to the individuals from Colombia and Ecuador. However, shape of the meshes and structure of the smallest veinlets of *B. costaricensis* from these countries are basically similar to the same species from the other countries rather than the species with coarse ramification. Therefore the coarse ramification in *B. costaricensis* might be interpreted as modification of the fine ramification and should not be grouped in the species regularly with coarse ramification.

The mesh pattern (open/closed) is also informative to some extent, but not as well as fine/coarse ramification. Open meshes in the species with fine ramification consist of the veinlets in a different order from the veinlets in the species with coarse ramification, and the meshes in the former species are not homologous with the ones in the latter species. Thus mesh pattern should be discussed within each group defined by the ramification pattern.

The secondary vein pattern (brochidodromous/eucamptodromous/pseudo-brochidodromous) sometimes shows some variations even within an individual. Thus it is a less-informative character. The basic tertiary vein pattern (percurrent/reticulate) is relatively consistent within each species and of some value for the systematics, while the more detailed character states (strongly percurrent/weakly percurrent, orthogonal reticulation/random reticulation) are less consistent and of less value.

As a result, two major groups are recognized as follows in venation patterns of neotropical *Beilschmiedia* species; 1) group with fine ramification, and 2) group with coarse ramification. Species belonging to group 1 are: *B. alloiophylla*, *B. anay*, *B. costaricensis*, *B. hexanthera*, *B. immersinervis*, *B. latifolia*, *B. mexicana*, *B. obovatifolia*, *B. ovalioides*, *B. ovalis*, *B. pendula*, *B. riparia*, *B. steyermarkii* and *B. towarensis*. Species belonging to group 2 are: *B. angustieliptica*, *B. angustifolia*, *B. berteroana*, *B. brenesii*, *B. curviramea*, *B. emarginata*, *B. fluminensis*, *B. hondurensis*, *B. linharesensis*, *B. miersii*, *B. rigida*, *B. stricta* and *B. taubertiana*.

This grouping is more or less supported by the mesh pattern and the tertiary vein pattern. In group 2 all the species share open meshes and reticulate tertiaries. In group 1 many species have closed meshes, but some species are exceptions. The exceptional species which have open meshes are *B. costaricensis*, *B. hexanthera*, and *B. pendula*. Some species of the group 1 are distinguished from others by the strongly percurrent tertiary veins. The other species have weakly percurrent or reticulate tertiary veins, and some of these have both types of the tertiary veins within a species. Since the mesh patterns and tertiary vein patterns have no correspondence among the species of group 1, relationships within group 1 species can not be determined only with the venation pattern.

2) cuticular characters

The characters observed in cuticles here are mostly regarded as informative characters by Christophel et. al. (1996). The character which should be used carefully is size of the epidermal cells. Roth (1984) reported that size of the epidermal cells tend to be larger in xeric habitat. Therefore dimension of the epidermal cells might be affected by the environmental change. Instead, variation of the cell size between adaxial and abaxial surfaces is preferred for the systematic use.

In the overall similarity of the cuticular characters, neotropical *Beilschmiedia* species are divided into five groups as following;

Group 1: *Beilschmiedia alloiophylla*, *B. costaricensis*, *B. hexanthera*, *B. immersinervis*, *B. latifolia*, *B. mexicana*, *B. obovatifolia*, *B. ovalioides*, *B. ovalis*, *B. pendula*, *B. riparia*, *B. steyermarkii* and *B. towarensis*.

Members of this group share smooth periclinal walls on both surfaces, smooth-beaded and angular-roundish anticlinal walls on both surfaces, cell shape more or less similar between the two surfaces, and narrow stomatal ledges. *Beilschmiedia latifolia*, *B. obovatifolia*, *B. ovalioides* and *B. towarensis* differ from the other members in their variation in cell size between the two surfaces, but the variation is less distinct than the one of *B. miersii*, which I recognize as forming a different group.

Group 2: *Beilschmiedia angustifolia*, *B. curviramea*, *B. linharesensis* and *B. rigida*.

Members of this group share dotted periclinal walls on the adaxial surface, granular periclinal walls on the abaxial surface, more or less buttressed anticlinal walls, a variation in cell shape between the two surfaces, and relatively wide stomatal ledges. *Beilschmiedia*

rigida differs from the other members in thickness and straightness of the anticlinal walls, and might be interpreted as less closely related to the other members.

Group 3: *Beilschmiedia angustielliptica*, *B. brenesii* and *B. hondurensis*.

Members of this group share dotted periclinal walls on the both surfaces, buttressed and strongly sinuous anticlinal walls on both surfaces, similar cell size and shape, butterfly-shaped stomatal ledges.

Group 4: *Beilschmiedia miersii*.

This species share more or less similar characters with the members of group 1, but it is distinguished from them by the great variation in cell size, which is, having larger cells on the adaxial surface than the abaxial surface. Members of group 1 usually have the epidermal cells similar in size between both surfaces or the epidermal cells larger on the abaxial surfaces.

Group 5: *Beilschmiedia berteriana*.

This species is distinguished from the other species by its box-shaped and scarcely stained stomatal ledges.

Most of the groups recognized above are quite different from each other, while they share the character states consistent within each group. Group 2 has some similarities with group 1, and a few species of group 1 or *Beilschmiedia rigida* of group 3 have some differences from the other members. These facts are evaluated in conjunction with the other leaf anatomical characters.

3) leaf section

The most and only useful character in leaf sectional study for the systematics of neotropical *Beilschmiedia* species is vascular bundle arrangement in the midrib. Hypodermis and palisade tissues are sometimes variable within a species, and especially palisadal tissues are not easily distinguished from the spongy parenchyma in dried samples since shape of the tissues is sometimes modified. Presence/absence of bundle sheath extension is usually consistent within each species except for *B. angustielliptica*. However, this character is reported to have a relation with density of the bundles for some temperate plants by Wylie (1951), and there is a possibility that this character is not independent from fine/coarse ramification.

In leaf sectional study, neotropical *Beilschmiedia* species are divided into two groups only by vascular bundle arrangement in the midrib (from now, mentioned only bundle arrangement): 1) group with bundle arrangement in a ring, and 2) group with bundle arrangement in a flattened arc. Species belonging to group 1 are: *B. alloiophylla*, *B. angustifolia*, *B. costaricensis*, *B. curviramea*, *B. hexanthera*, *B. immersinervis*, *B. latifolia*, *B. linharesensis*, *B. mexicana*, *B. obovatifolia*, *B. ovalioides*, *B. ovalis*, *B. pendula*, *B. rigida*, *B. riparia*, *B. steyermarkii* and *B. towarensis*. Species belonging to group 2 are: *B. angustielliptica*, *B. berteroana*, *B. brenesii*, *B. hondurensis* and *B. miersii*. There are some variations seen within each group, especially within group 1, like diffused/united bundles. But they are not always consistent within a species and cannot be used for dividing the groups further.

Relationships within neotropical Beilschmiedia species

Distribution of the character states which are recognized as informative for the systematics of neotropical *Beilschmiedia* is summarized in Table 2.

As a result, groupings of neotropical *Beilschmiedia* species of phyllotaxis agree with groupings of venation pattern, but do not perfectly agree with cuticular characters or bundle arrangement. Cuticular characters divide the phyllotaxis groups further into five groups, and bundle arrangement contradicts the phyllotaxis grouping. Therefore, our expectation that groupings of phyllotaxis and venation pattern might be supported by the other leaf anatomical characters is not perfectly right.

Instead, the five groups defined by cuticular characters has no conflict with the phyllotaxis, venation pattern, or bundle arrangement. Additionally, groupings of cuticular characters have some correspondence with the geographical distributions. Therefore, groupings of cuticular characters is accepted as representing relationships among neotropical *Beilschmiedia* species.

In groupings of cuticular characters, there are several species which have some uncertainty whether they should be separated from the other members of the group (*B. latifolia*, *B. miersii*, *B. obovatifolia*, *B. ovalioides*, *B. rigida* and *B. towarensis*). Among them, separation of *B. miersii* from cuticular group 1 as a distinct group is supported by the other leaf anatomical characters, while separation of the other species is not well supported.

In conclusion, the leaf anatomical characters studied here recognize five groups in neotropical *Beilschmiedia* species as follows:

Group 1: *Beilschmiedia alloiophylla*, *B. anay**, *B. costaricensis*, *B. hexanthera*, *B.*

immersinervis, *B. latifolia*, *B. mexicana*, *B. obovatifolia*, *B. ovalioides*, *B. ovalis*,
B. pendula, *B. riparia*, *B. steyermarkii* and *B. tovarensis*.

Group 2: *Beilschmiedia angustifolia*, *B. curviramea*, *B. emarginata**, *B. fluminensis**, *B.*
linharesensis, *B. rigida*, *B. stricta** and *B. taubertiana**.

Group 3: *Beilschmiedia angustielliptica*, *B. brenesii* and *B. hondurensis*.

Group 4: *Beilschmiedia miersii*.

Group 5: *Beilschmiedia berteroa*.

The species with asterisk are temporally placed by the characters thus far known. Leaf anatomical characters, species name, and geographical distributions of the groups are summarized in Table 3.

Group 1

Species of group 1 have leaves alternate, ramification fine, cuticular characters belonging to group 1, and bundle arrangement in a ring. Most of the species are distributed in Central America and/or the Andes, one of which ranges to northern South America and West Indies, and another is endemic to French Guiana.

Within group 1, some species are recognized as different from the others in mesh pattern, tertiary vein pattern, or variation in cell size between the two surfaces. But groupings of these characters have little correspondence with one another. Therefore relationships within group 1 cannot be determined with these characters. In floral characters, *B. hexanthera* is distinguished from the other species by its six fertile stamens, and *B. anay*, *B. immersinervis* and *B. riparia* are by their pubescent anther apices. Since *B. hexanthera* has a disjunct distribution from all the other neotropical *Beilschmiedia* species, it might be reasonable to think that this species has some distinct position in relationships within group 1. But no character has been found to distinguish the species from the other in leaf anatomy. There is no character holding *B. anay*, *B. immersinervis* and *B. riparia* as a distinct group in leaf anatomy.

Group 2

Species of group 2 have leaves opposite, ramification coarse, cuticular characters belonging to group 2, and bundle arrangement in a ring. Most of the species are endemic to the southern Brazil, while one species, *B. curviramea*, is endemic to Guianas (Venezuelan Guiana and Guyana).

Geographical distribution distinguishes *B. curviramea* from the other species, but leaf anatomy shows its close relationships to the south-eastern Brazilian species. In floral characters, pubescence of anther apices is present in all the members of this group, and outside this group only in *B. anay*, *B. immersinervis* and *B. riparia*.

Group 3

Species of group 3 have leaves opposite, ramification coarse, cuticular characters belonging to the group 3, bundle arrangement in a flattened arc. All the three species are distributed in Central America.

Among the three species, *B. angustieliptica* is distinguished from the other by its long leaves. The other two species share many morphological characters, and their identities are discussed in the systematic treatment of the second chapter. All the three species have anther apices obtuse to acute, which distinguish the species from all the other neotropical *Beilschmiedia* species.

Group 4

Only member of group 4 is *B. miersii*, which has leaves opposite, ramification coarse, cuticular characters belonging to group 4, and bundle arrangement in a flattened arc. This species is endemic to central Chile.

As mentioned above, this species has some common cuticular characters with group 1. But the variation in cell size between the two surfaces distinguishes the species from the members of group 1. The phyllotaxis, ramification and bundle arrangement support this differentiation. This species shares many macromorphological characters with the species of group 5, *B. berteriana*, even their geographical distribution is common. In leaf anatomy, the two species share same characters in phyllotaxis, ramification and bundle arrangement. However, cuticular characters clearly distinguish one from the other. An interesting fact is that *Cryptocarya alba* (Mol.) Looser, which is also endemic to central Chile, appears to share vegetative macromorphological characters with the two Chilean *Beilschmiedia* species, but that it has quite different ramification pattern and cuticular characters from them. Bundle

arrangement of *C. alba* is in a flattened arc like the two Chilean *Beilschmiedia* species, but all the *Cryptocarya* species examined in my preliminary research have bundle arrangement in a flattened arc. Similarity of these three species might be due to their adaptation to the subtropical, xeric habitat.

Group 5

Group 5 consists of only one species, *B. berteriana*, which has leaves opposite, ramification coarse, bundle arrangement in a flattened arc. This species is endemic to the central Chile.

Similarity between group 4 and group 5 is mentioned above.

These five groups are firstly delimited by the cuticular characters. But they are well supported by phyllotaxis, venation pattern and bundle arrangement. Additionally, they mostly correspond to the geographical distributions, and some of the groups share same floral characters within the group. Thus, the five groups are likely to be natural groups. Since it is unknown which character state is close to the other, what we can recognize in leaf anatomy is groupings among the species, and relationships between the groupings should be discussed with other studies such as molecular systematics.

This study shows that leaf anatomy, especially cuticular characters, is informative for the systematics of neotropical *Beilschmiedia* species as a grouping system. *Beilschmiedia* is a large genus, putatively containing about 250 species. It is so far difficult to carry out the phylogenetic analysis using all the species as terminal taxa. Thus it is more reasonable to recognize some natural groups in the genus first and then study the phylogeny of the groups. For this purpose, leaf anatomy provides valuable information to recognize natural groups. In future study, leaf anatomy would contribute to a better understanding of the genus *Beilschmiedia*, including the systematic position of neotropical species in the genus.

Table 1. List of samples for venation study of neotropical *Beilschmiedia* species.

Species	Exsiccatae data of samples for X-ray	Exsiccatae data of samples for cuticular studies	Exsiccatae data of samples for leaf section
<i>B. alloiophylla</i>	Clark 850 (MO)	Clark 850 (MO), Dodson 6489 (MO)	Haber 9121 (MO), Bristan 1472 (MO), Hammel 18504, Yasuda 1308 (MO), 1316 (MO)
<i>B. anay</i>	Popenoe 754 (U)	-	-
<i>B. angustieliptica</i>	Lorea 5540 (MO)	Lozano 227 (MO), Núñez 1159 (MO)	Lorea 5538 (MO), Núñez 1159 (MO)
<i>B. angustifolia</i>	Constantis 19914 (RB)	Constantino 19914 (RB)	Lima 2177 (NY)
<i>B. berteriana</i>	anonymous (MO)	anonymous (MO)	anonymous (MO)
<i>B. brenesii</i>	Guindon 35 (MO)	Guindon 35 (MO), Bello 580 (MO)	Guindon 35 (MO), Yasuda 1314 (MO)
<i>B. costaricensis</i>	Bello 4882 (MO)	Bello 4882 (MO), Lorea 5563 (MO), van der Werff 12168 (MO), 13368 (MO)	Benavides 8964 (MO), Yasuda 1309 (MO)
<i>B. curviramea</i>	Tutin 114 (US)	Persaud 70 (NY)	Marcano 387 (MO)
<i>B. emarginata</i>	-	-	-
<i>B. fluminensis</i>	Brade 18642 (RB)	-	-
<i>B. hexanthera</i>	van der Werff 12951 (MO)	van der Werff 12951 (MO)	van der Werff 12951 (MO)
<i>B. hondurensis</i>	Gentle 7292 (MO)	Gentle 7292 (MO), Lundel 19280 (MO)	Gentle 7292 (MO), Thomas 420 (MO)
<i>B. immersinervis</i>	Haber 11070 (MO)	Haber 11070 (MO), Hammel 17502 (MO)	Hammel 17502 (MO), Yasuda 1312 (MO)
<i>B. latifolia</i>	Tanner 709 (MO)	Steyermark 98386 (NY)	Steyermark 98386 (NY)
<i>B. linharesensis</i>	Forias 243 (MO)	Folli 409 (MO)	Folli 409 (MO)
<i>B. mexicana</i>	Rubio 2209 (MO)	Croat 65900 (MO), Lorea 5553 (MO)	Croat 65900 (MO), Lorea 5553 (MO)
<i>B. miersii</i>	Zöllner 18999 (MO)	Taylor 10883 (MO)	Taylor 10883 (MO), West 5195 (MO)
<i>B. obovatifolia</i>	Guindon 40 (MO)	Chávez 443 (MO), Guindon 40 (MO)	Guindon 40 (MO), Yasuda 1307 (INB), 1313 (MO)
<i>B. ovalioides</i>	Lorence 4078 (MO)	Lorence 4376 (MO), Martínez 19456 (MO)	Lorence 4376 (MO), Martínez 19456 (MO)
<i>B. ovalis</i>	Sytsma 2148 (MO)	Lao 395 (MO), Sytsma 2148 (MO)	Yasuda 1300 (MO), 1301 (MO)
<i>B. pendula</i>	Gonzales 173 (NY)	Herrera 5861 (MO), Zanoni 36009 (MO)	Proctor 39101 (MO), Zanoni 19410 (MO)
<i>B. rigida</i>	Glaziou 19790 (C)	Martinelli 12889 (MO)	Martinelli 12889 (MO)
<i>B. riparia</i>	Lorea 5498 (MO)	Lorea 5498 (MO), Maya 1296 (MO)	Lorea 5498 (MO), Rodríguez 374 (MO)
<i>B. styermarkii</i>	Contreras 9448 (MO)	Contreras 9448 (MO)	Contreras 9448 (MO)
<i>B. stricta</i>	Nunes 313 (U)	-	-
<i>B. taubertiana</i>	Araujo (U)	-	-
<i>B. towarensis</i>	van der Werff 10584 (MO)	Croat 14063 (MO), Devia 2290 (MO), Díaz 3587 (MO), van der Werff 13377 (MO)	Devia 2290 (MO), van der Werff 10584 (MO)

Table 2. Leaf anatomical characters of neotropical *Beilschmiedia* species.

Species	Phyllotaxis	Venation pattern			Cuticular characters			
		Ramification	Mesh	Tertiary vein	Periclinal wall		Anticlinal wall thickness	
					Adaxial	Abaxial	Adaxial	Abaxial
<i>B. alloiophylla</i>	alternate	fine	closed	percurrent	smooth	smooth	beaded	irregular
<i>B. anay</i>	alternate	fine	closed	percurrent	-	-	-	-
<i>B. angustieliptica</i>	opposite	coarse	open	reticulate	dotted	dotted	buttressed	buttressed
<i>B. angustifolia</i>	opposite	coarse	open	reticulate	dotted	granular	branched	irregular
<i>B. berteroa</i>	opposite	coarse	open	reticulate	smooth	smooth	beaded	beaded
<i>B. brenesii</i>	opposite	coarse	open	reticulate	dotted	dotted	buttressed	buttressed
<i>B. costaricensis</i>	alternate	fine	open	percurrent/reticulate	smooth	smooth	beaded	beaded
<i>B. curviramea</i>	opposite	coarse	open	reticulate	dotted	granular	branched	branched
<i>B. emarginata</i>	opposite	coarse	open	reticulate	-	-	-	-
<i>B. fluminensis</i>	opposite	coarse	open	reticulate	-	-	-	-
<i>B. hexanthera</i>	alternate	fine	open	percurrent/reticulate	smooth	smooth	beaded	beaded
<i>B. hondurensis</i>	opposite	coarse	open	reticulate	dotted	dotted	buttressed	buttressed
<i>B. immersinervis</i>	alternate	fine	closed	percurrent/reticulate	smooth	smooth	beaded	smooth
<i>B. latifolia</i>	alternate	fine	closed	percurrent	smooth	smooth	smooth	beaded
<i>B. linharesensis</i>	opposite	coarse	open	reticulate	dotted	granular	branched	branched
<i>B. mexicana</i>	alternate	fine	closed	reticulate	smooth	smooth	beaded	smooth
<i>B. miersii</i>	opposite	coarse	open	reticulate	smooth	smooth	beaded	beaded
<i>B. obovatifolia</i>	alternate	fine	closed	percurrent	smooth	smooth	beaded	beaded
<i>B. ovalioides</i>	alternate	fine	closed	percurrent	smooth	smooth	smooth	beaded
<i>B. ovalis</i>	alternate	fine	closed	percurrent/reticulate	smooth	smooth	smooth	beaded
<i>B. pendula</i>	alternate	fine	open	reticulate	smooth	smooth	beaded	beaded
<i>B. rigida</i>	opposite	coarse	open	reticulate	dotted	granular	beaded	irregular
<i>B. riparia</i>	alternate	fine	closed	percurrent	smooth	smooth	smooth	beaded
<i>B. steyermarkii</i>	alternate	fine	closed	percurrent	smooth	smooth	beaded	smooth
<i>B. stricta</i>	opposite	coarse	open	reticulate	-	-	-	-
<i>B. taubertiana</i>	opposite	coarse	open	reticulate	-	-	-	-
<i>B. tovarensis</i>	alternate	fine	closed	percurrent	smooth	smooth	smooth	irregular

Table 2. Continued.

Species	Cuticular characters					Leaf section
	Anticlinal wall straightness		Variation in cell size	Variation in cell shape	Stomatal ledges	Bundle arrangement
	Adaxial	Abaxial				
<i>B. alloiophylla</i>	angular	undulate	absent	absent	narrow	ring
<i>B. anay</i>	-	-	-	-	-	-
<i>B. angustielliptica</i>	sinuous	sinuous	absent	absent	butterfly-shape	flattened arc
<i>B. angustifolia</i>	branched	undulate	absent	present	narrow	ring
<i>B. berteriana</i>	angular	angular	absent	absent	box-shape	flattened arc
<i>B. brenesii</i>	sinuous	sinuous	absent	absent	butterfly-shape	flattened arc
<i>B. costaricensis</i>	angular	angular	absent	absent	narrow	ring
<i>B. curviramea</i>	branched	undulate	absent	present	narrow	ring
<i>B. emarginata</i>	-	-	-	-	-	-
<i>B. fluminensis</i>	-	-	-	-	-	-
<i>B. hexanthera</i>	angular	rounded	absent	absent	narrow	ring
<i>B. hondurensis</i>	sinuous	sinuous	absent	absent	butterfly-shape	flattened arc
<i>B. immersinervis</i>	angular	angular	absent	absent	narrow	ring
<i>B. latifolia</i>	angular	angular	present	absent	narrow	ring
<i>B. linharesensis</i>	branched	branched	absent	present	narrow	ring
<i>B. mexicana</i>	angular	rounded	absent	absent	narrow	ring
<i>B. miersii</i>	angular	angular	present	absent	narrow	flattened arc
<i>B. obovatifolia</i>	angular	angular	present	absent	narrow	ring
<i>B. ovalioides</i>	angular	angular	present	absent	narrow	ring
<i>B. ovalis</i>	angular	angular	absent	absent	narrow	ring
<i>B. pendula</i>	angular	rounded	absent	absent	narrow	ring
<i>B. rigida</i>	angular	rounded	absent	present	narrow	ring
<i>B. riparia</i>	angular	angular	absent	absent	narrow	ring
<i>B. steyermarkii</i>	angular	angular	absent	absent	narrow	ring
<i>B. stricta</i>	-	-	-	-	-	-
<i>B. taubertiana</i>	-	-	-	-	-	-
<i>B. towarensis</i>	angular	rounded	present	absent	narrow	ring

Table 3. Groupings of neotropical *Beilschmiedia* species.

	Phyllotaxis	Venation pattern	Cuticular characters	Vascular bundle arrangement	Species name	Rough geographical distribution
Group 1	alternate	fine	group 1	ring	<i>B. alloiophylla</i> <i>B. anay*</i> <i>B. costaricensis</i> <i>B. hexanthera</i> <i>B. immersinervis</i> <i>B. latifolia</i> <i>B. mexicana</i> <i>B. obovatifolia</i> <i>B. ovalioides</i> <i>B. ovalis</i> <i>B. pendula</i> <i>B. riparia</i> <i>B. styermarkii</i>	C. America, the Andes C. America C. America, Andes French Guiana C. America the Andes C. America C. America C. America C. America C. America, West Indies, northern S. America, the Andes C. America C. America
Group 2	opposite	coarse	group 2	ring	<i>B. angustifolia</i> <i>B. curviramea</i> <i>B. emarginata*</i> , <i>B. fluminensis*</i> , <i>B. linharesensis</i> <i>B. rigida</i> <i>B. stricta*</i> <i>B. taubertiana*</i>	Brazil the Guianas Brazil Brazil Brazil Brazil Brazil Brazil
Group 3	opposite	coarse	group 3	flattened arc	<i>B. angustielliptica</i> <i>B. brenesii</i> <i>B. hondurensis</i>	C. America C. America C. America
Group 4	opposite	coarse	group 4	flattened arc	<i>B. miersii</i>	Chile
Group 5	opposite	coarse	group 5	flattened arc	<i>B. berteroaana</i>	Chile

* species temporarily placed with thus far know characters.

Legends of figures

Fig. 1-25. Venation patterns of neotropical *Beilschmiedia* species. 1. *B. alloiophylla*. (Clark 850). 2. *B. anay* (Popenoe 754). 3. *B. angustielliptica* (Lorea 5540). 4. *B. angustifolia* (Constantis 19914). 5. *B. berteroa* (anonymous). 6. *B. brenesii* (Guindon 35). 7. *B. costaricensis* (Bello 4882). 8. *B. curviramea* (Tutin 114). 9. *B. fluminensis* (Brade 18642). 10. *B. hexanthera* (van der Werff 12951). 11. *B. hondurensis* (Gentle 7292). 12. *B. immersinervis* (Haber 11070). 13. *B. latifolia* (Tanner 709). 14. *B. linharesensis* (Forias 243). 15. *B. mexicana* (Rubio 2209). 16. *B. miersii* (Zöllner 18999). 17. *B. obovatifolia* (Guindon 40). 18. *B. ovalis* (Sytsma 2148). 19. *B. pendula* (Gonzales 173). 20. *B. rigida* (Glaziou 19790). 21. *B. riparia* (Lorea 5498). 22. *B. steyermarkii* (Contreras 9448). 23. *B. stricta* (Núñez 313). 24. *B. taubertiana* (Araujo s.c.). 25. *B. towarensis* (van der Werff 10584). Scale bars equal 2 cm in all figures.

Fig. 26-51. Venation patterns (closed up) of neotropical *Beilschmiedia* species. 26. *B. alloiophylla*. (Clark 850). 27. *B. anay* (Popenoe 754). 28. *B. angustielliptica* (Lorea 5540). 29. *B. angustifolia* (Constantis 19914). 30. *B. berteroa* (anonymous). 31. *B. brenesii* (Guindon 35). 32. *B. costaricensis* (Bello 4882). 33. *B. curviramea* (Tutin 114). 34. *B. fluminensis* (Brade 18642). 35. *B. hexanthera* (van der Werff 12951). 36. *B. hondurensis* (Gentle 7292). 37. *B. immersinervis* (Haber 11070). 38. *B. latifolia* (Tanner 709). 39. *B. linharesensis* (Forias 243). 40. *B. mexicana* (Rubio 2209). 41. *B. miersii* (Zöllner 18999). 42. *B. obovatifolia* (Guindon 40). 43. *B. ovalioides* (Lorence 4078). 44. *B. ovalis* (Sytsma 2148). 45. *B. pendula* (Gonzales 173). 46. *B. rigida* (Glaziou 19790). 47. *B. riparia* (Lorea 5498). 48. *B. steyermarkii* (Contreras 9448). 49. *B. stricta* (Núñez 313). 50. *B. taubertiana* (Araujo s.c.). 51. *B. towarensis* (van der Werff 10584). Scale bars equal 2 mm in all figures.

Fig. 52. Diagrams of transverse section (upper) and overlook (lower) of typical Lauraceae cuticle (abaxial surface). Figure abbreviations, c, cuticular membrane; sc, subsidiary cell; g, guard cell; ol, outer cuticular ledge; il, inner cuticular ledge; aw, anticlinal wall; pw, periclinal wall.

Fig. 53. Scanning Electron Micrograph of abaxial cuticular surface of *Beilschmiedia angustielliptica*. Scale bar equals 50 μm .

Fig. 54-75. Adaxial cuticles of neotropical *Beilschmiedia* species. 54. *B. alloiophylla*. (Clark 850). 55. *B. angustielliptica* (Núñez 1159). 56. *B. angustifolia* (Constantis 19914). 57. *B. berteroa* (anonymous). 58. *B. brenesii* (Bello 580). 59. *B. costaricensis* (Lorea 5563). 60. *B. curviramea* (Tutin 114). 61. *B. hexanthera*

(van der Werff 12951). 62. *B. hondurensis* (Lundel 19280). 63. *B. immersinervis* (Hammel 17502). 64. *B. latifolia* (Steyermarkii 98386). 65. *B. linharesensis* (Folli 409). 66. *B. mexicana* (Croat 65900). 67. *B. miersii* (Taylor 10883). 68. *B. obovatifolia* (Guindon 40). 69. *B. ovalioides* (Lorea 4376). 70. *B. ovalis* (Sytsma 2148). 71. *B. pendula* (Herrera 5861). 72. *B. rigida* (Martinelli 12889). 73. *B. riparia* (Maya 1296). 74. *B. steyermarkii* (Contreras 9448). 75. *B. towarensis* (Díaz 3587). Scale bars equal 50 µm in all figures. Figure abbreviation, t, trichome or its base.

Fig. 76-97. Abaxial cuticles of neotropical *Beilschmiedia* species. 76. *B. alloiophylla*. (Clark 850). 77. *B. angustieliptica* (Núñez 1159). 78. *B. angustifolia* (anonymous). 79. *B. berteroaana* (anonymous). 80. *B. brenesii* (Bello 580). 81. *B. costaricensis* (Lorea 5563). 82. *B. curviramea* (Tutin 114). 83. *B. hexanthera* (van der Werff 12951). 84. *B. hondurensis* (Lundel 19280). 85. *B. immersinervis* (Haber 11070). 86. *B. latifolia* (Steyermarkii 98386). 87. *B. linharesensis* (Folli 409). 88. *B. mexicana* (Croat 65900). 89. *B. miersii* (Taylor 10883). 90. *B. obovatifolia* (Chávez 443). 91. *B. ovalioides* (Lorea 4376). 92. *B. ovalis* (Sytsma 2148). 93. *B. pendula* (Herrera 5861). 94. *B. rigida* (Martinelli 12889). 95. *B. riparia* (Maya 1296). 96. *B. steyermarkii* (Contreras 9448). 97. *B. towarensis* (Díaz 3587). Scale bars equal 50 µm in all figures. Figure abbreviations, t, trichome or its base; s, specialized cell; gs, giant stoma.

Fig. 98-119. Stomata of neotropical *Beilschmiedia* species. 98. *B. alloiophylla*. (Clark 850). 99. *B. angustieliptica* (Núñez 1159). 100. *B. angustifolia* (anonymous). 101. *B. berteroaana* (anonymous). 102. *B. brenesii* (Bello 580). 103. *B. costaricensis* (Lorea 5563). 104. *B. curviramea* (Tutin 114). 105. *B. hexanthera* (van der Werff 12951). 106. *B. hondurensis* (Lundel 19280). 107. *B. immersinervis* (Haber 11070). 108. *B. latifolia* (Steyermarkii 98386). 109. *B. linharesensis* (Folli 409). 110. *B. mexicana* (Croat 65900). 111. *B. miersii* (Taylor 10883). 112. *B. obovatifolia* (Chávez 443). 113. *B. ovalioides* (Lorea 4376). 114. *B. ovalis* (Sytsma 2148). 115. *B. pendula* (Herrera 5861). 116. *B. rigida* (Martinelli 12889). 117. *B. riparia* (Maya 1296). 118. *B. steyermarkii* (Contreras 9448). 119. *B. towarensis* (Díaz 3587). Scale bars equal 20 µm in all figures.

Fig. 120. Petiole section (middle position) of *Beilschmiedia mexicana* (Croat 65900). Scale bar equals 500 µm. Figure abbreviations, p, phloem; x, xylem.

Fig. 121. Petiole section (near blade) of *Beilschmiedia mexicana* (Croat 65900). Scale bar equals 500 µm. Figure abbreviations, p, phloem; x, xylem.

Fig. 122-143. Midrib sections of neotropical *Beilschmiedia* species. 122. *B. alloiophylla*. (Clark 850). 123. *B. angustieliptica* (Núñez 1159). 124. *B. angustifolia* (anonymous). 125. *B. berteriana* (anonymous). 126. *B. brenesii* (Bello 580). 127. *B. costaricensis* (Lorea 5563). 128. *B. curviramea* (Tutin 114). 129. *B. hexanthera* (van der Werff 12951). 130. *B. hondurensis* (Lundel 19280). 131. *B. immersinervis* (Haber 11070). 132. *B. latifolia* (*Steyermarkii* 98386). 133. *B. linharesensis* (Folli 409). 134. *B. mexicana* (Croat 64900). 135. *B. miersii* (Taylor 10883). 136. *B. obovatifolia* (Chávez 443). 137. *B. ovalioides* (Lorea 4376). 138. *B. ovalis* (Sytsma 2148). 139. *B. pendula* (Herrera 5861). 140. *B. rigida* (Martinelli 12889). 141. *B. riparia* (Maya 1296). 142. *B. steyermarkii* (Contreras 9448). 143. *B. towarensis* (Díaz 3587). Scale bars equal 500 μm in Fig. 122, Fig. 124, Fig. 141, and Fig. 143; 200 μm in Fig. 123, Fig. 125-129, Fig. 131-139, and Fig. 141-142; 100 μm in Fig. 130. Figure abbreviations, p, phloem; s, sclerenchymatous cells; sv, secondary vein; x, xylem.



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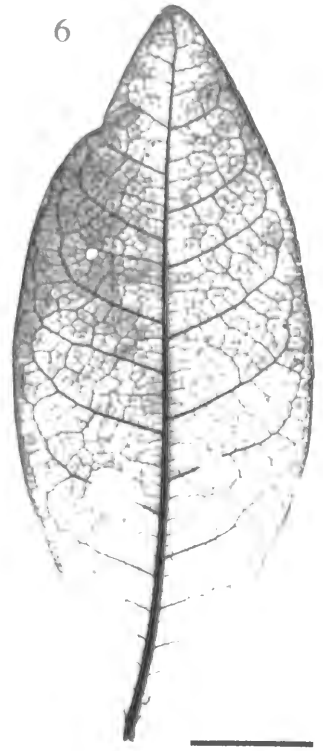
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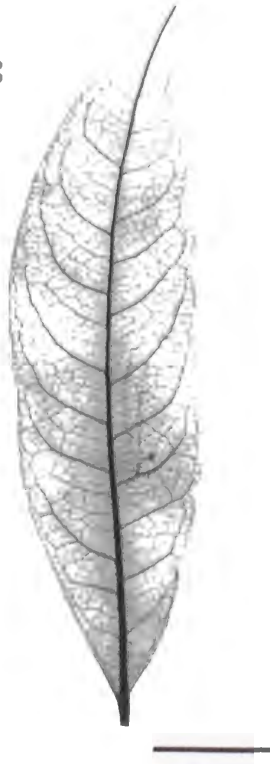
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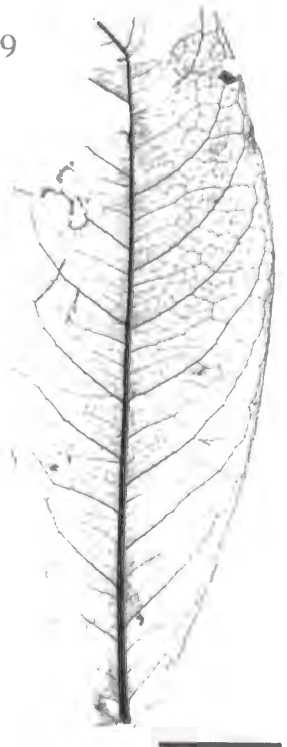
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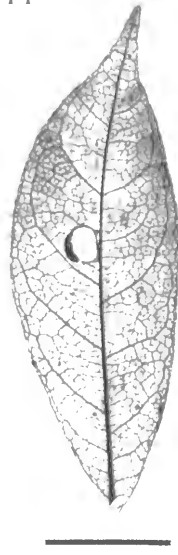
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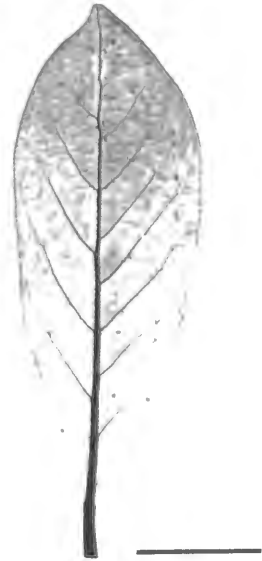
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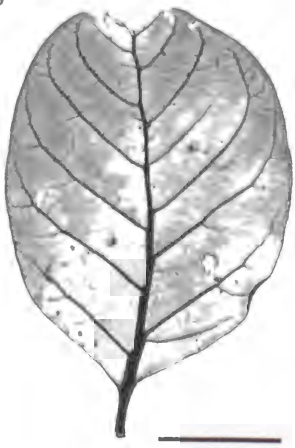
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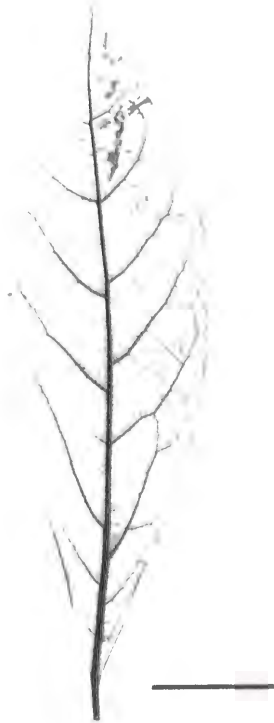
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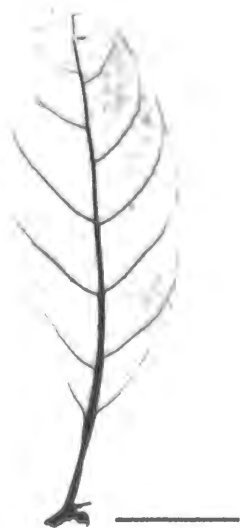
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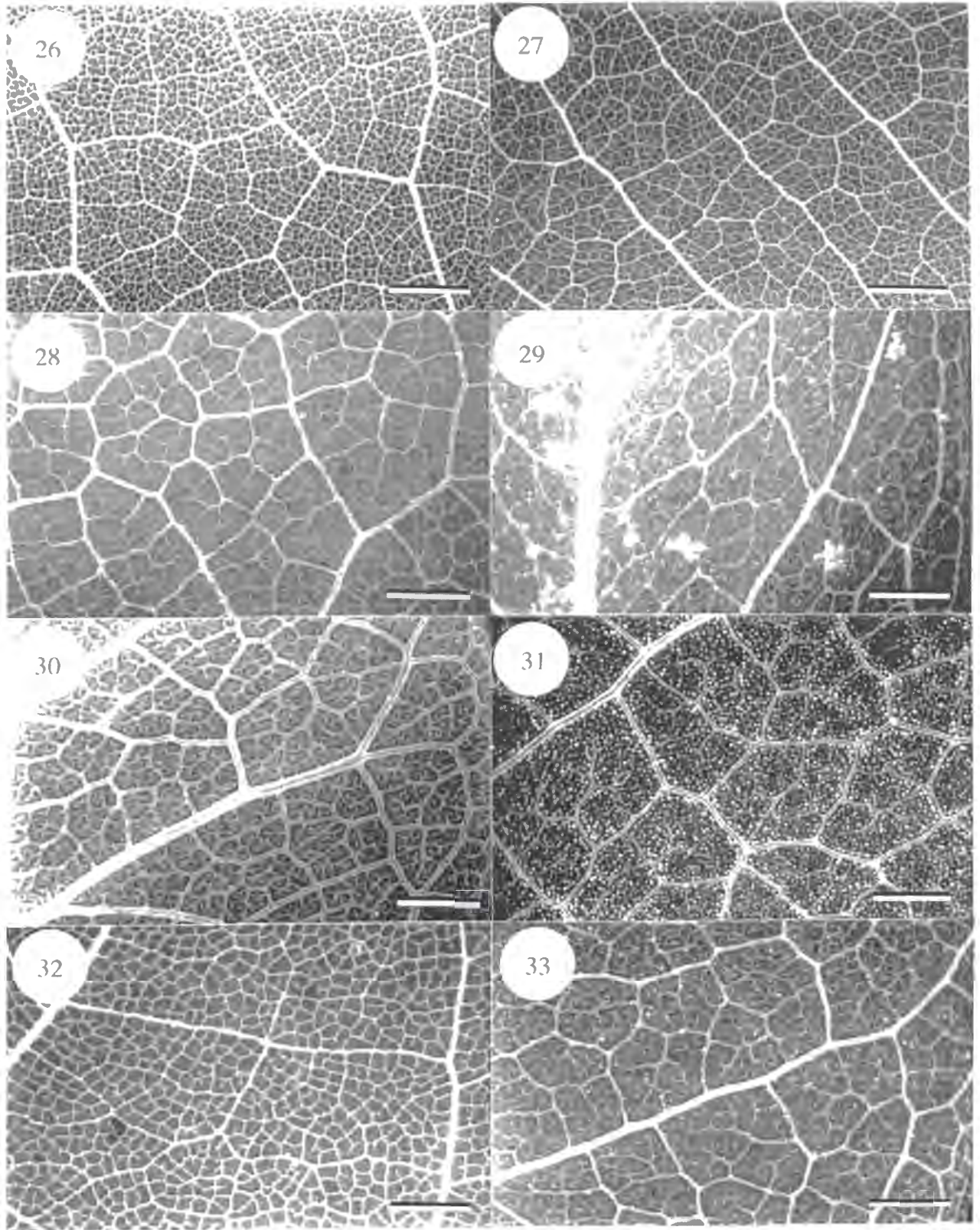


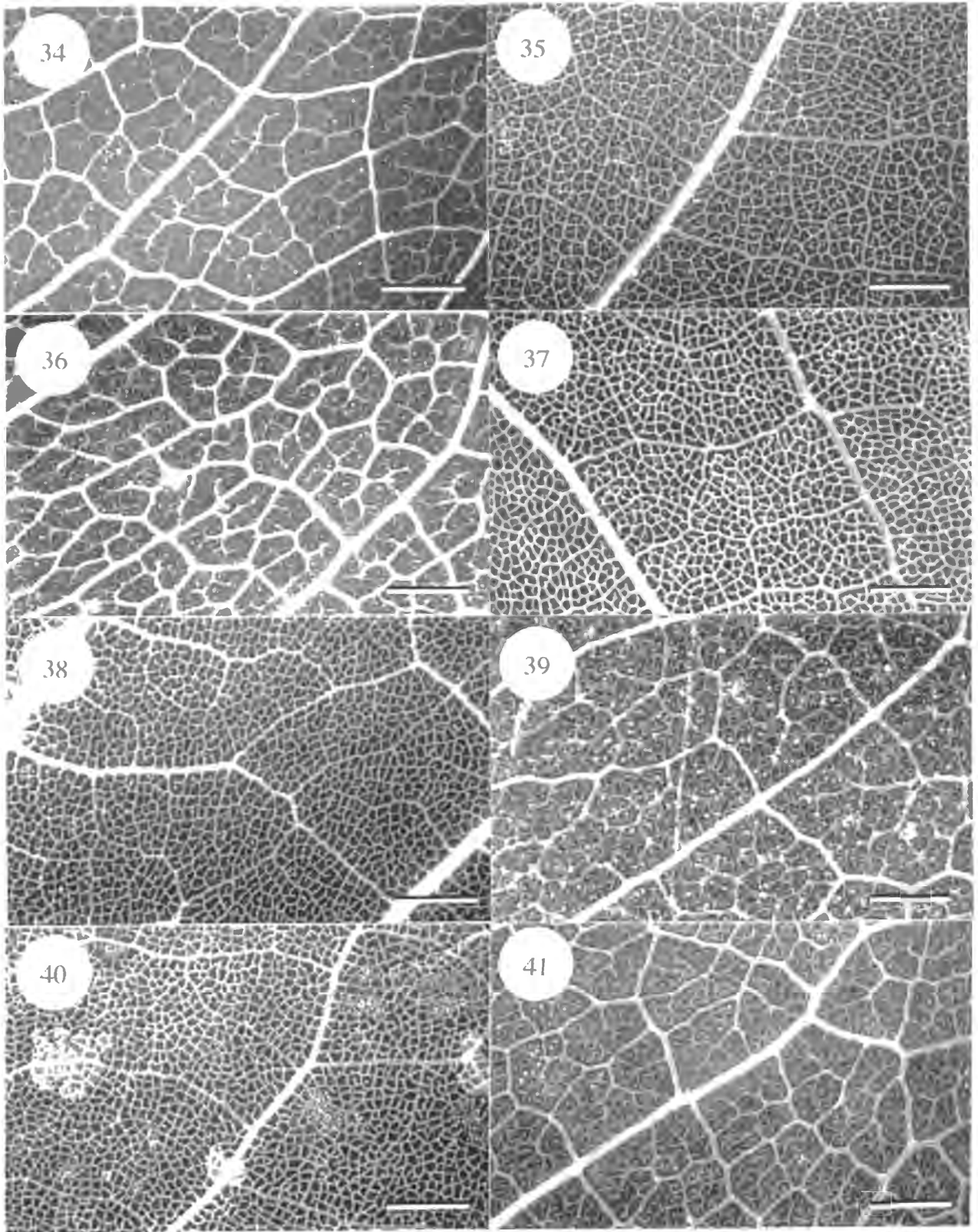
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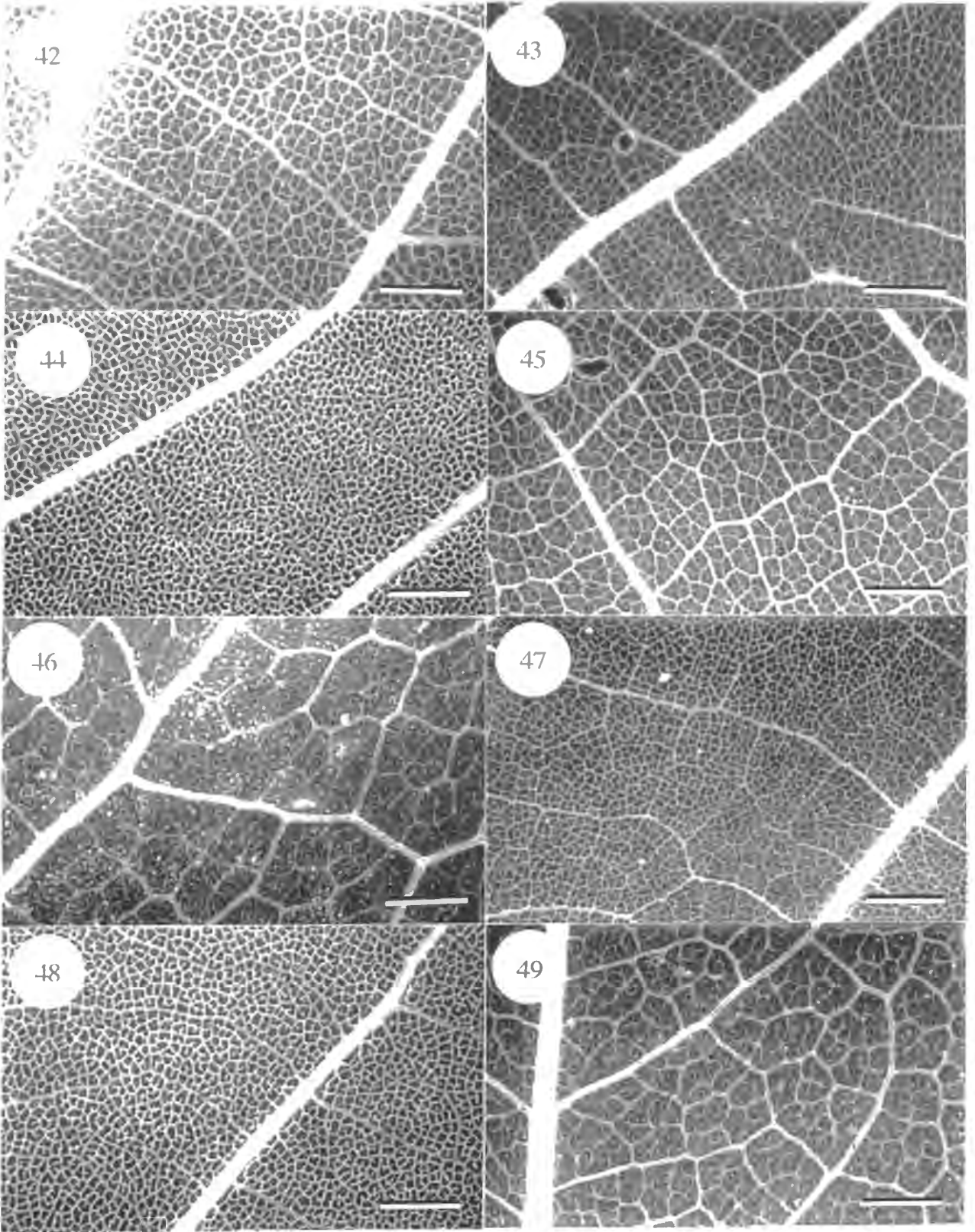


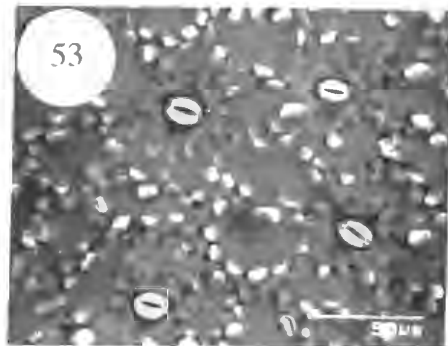
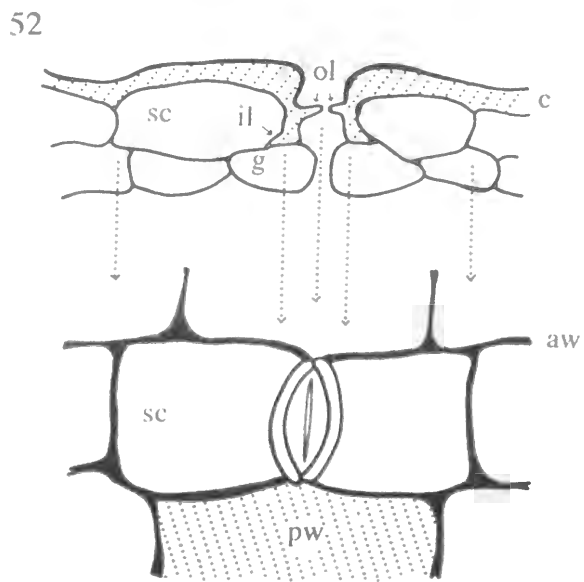
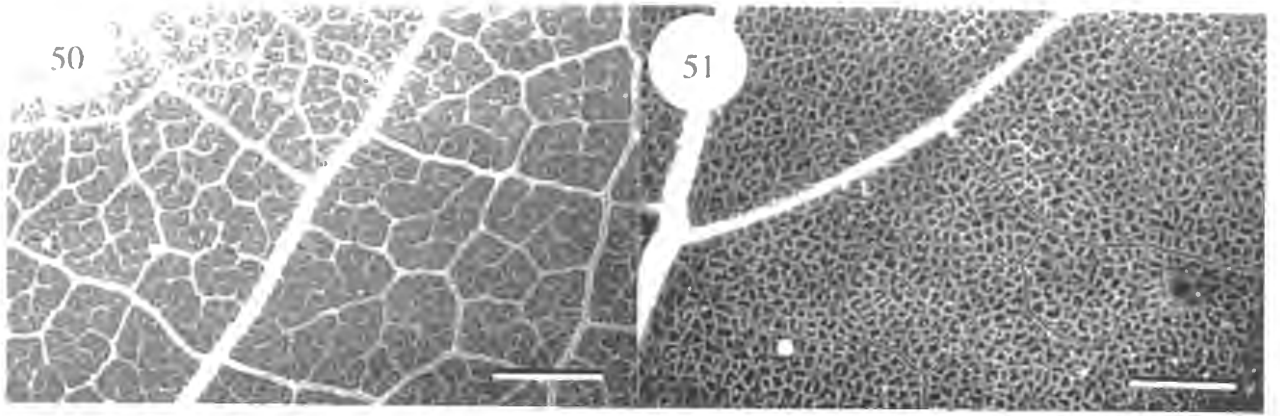
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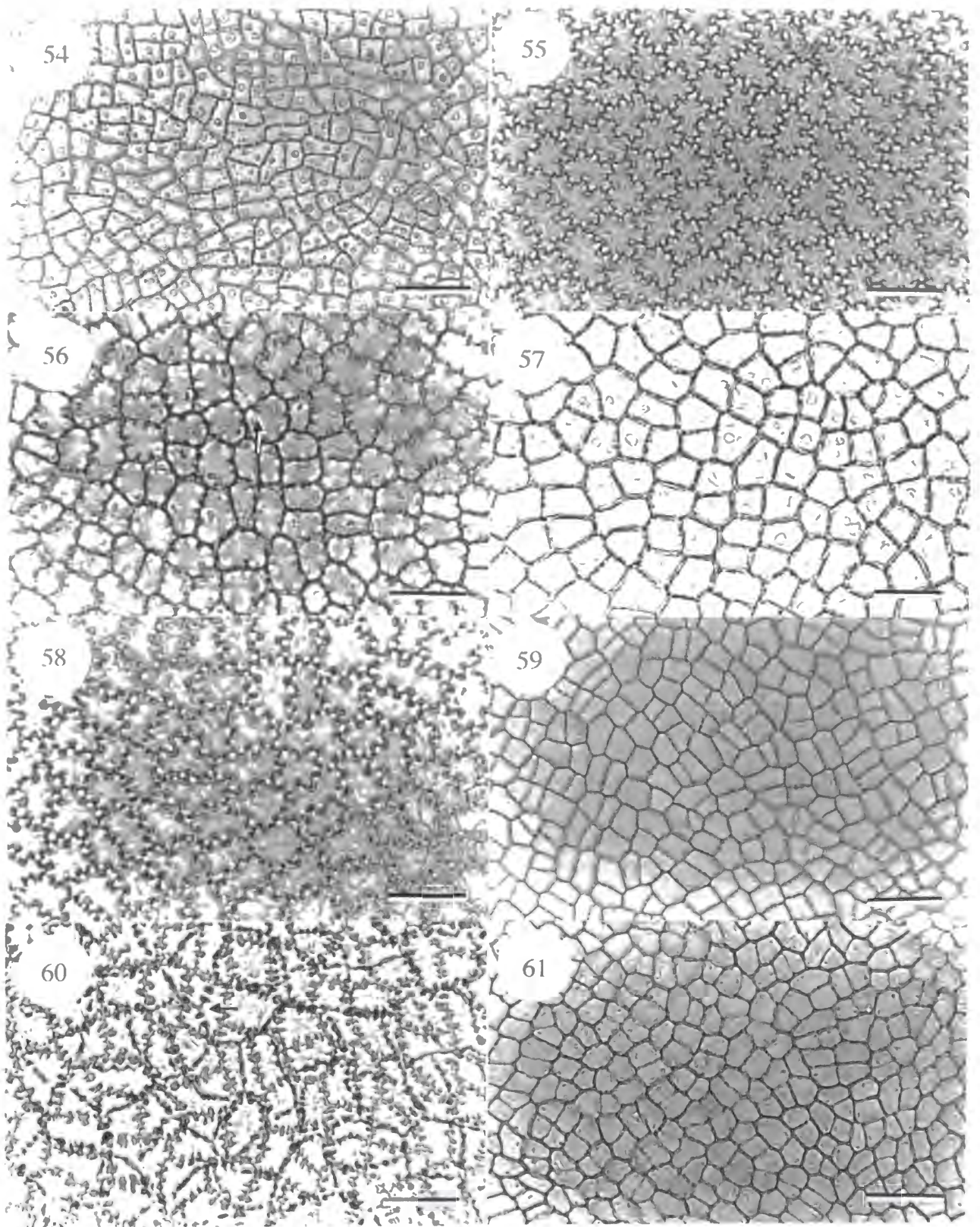


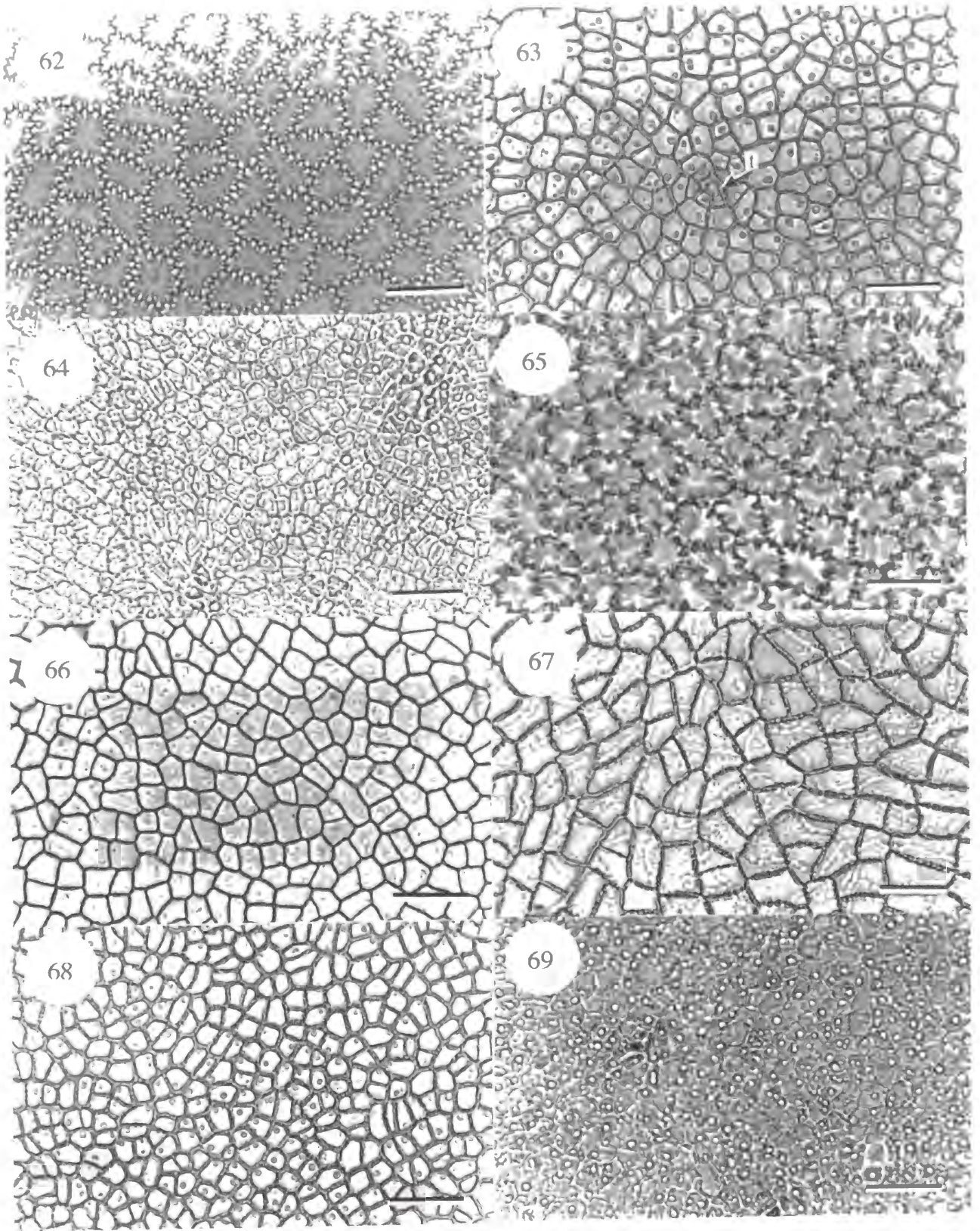


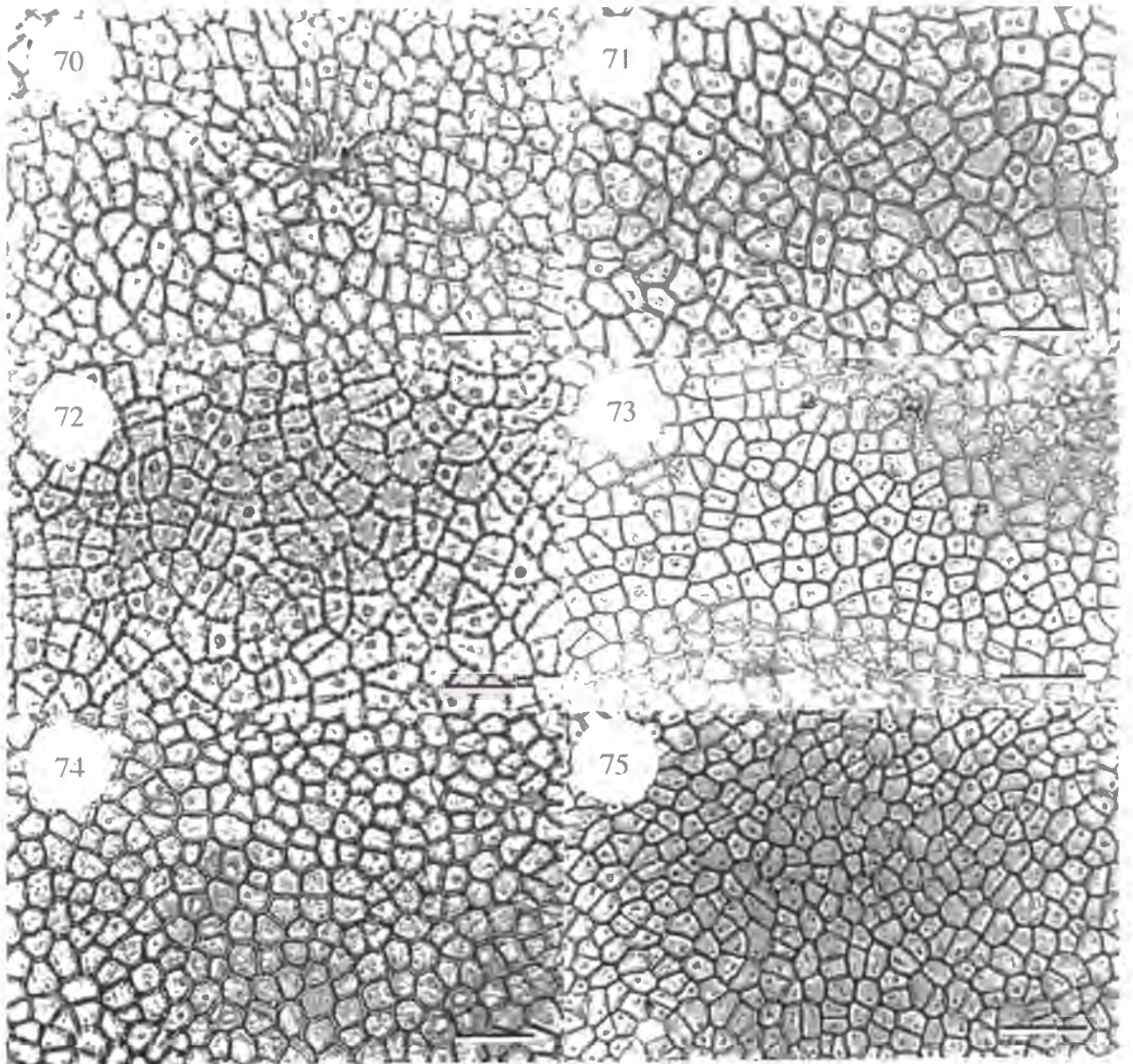


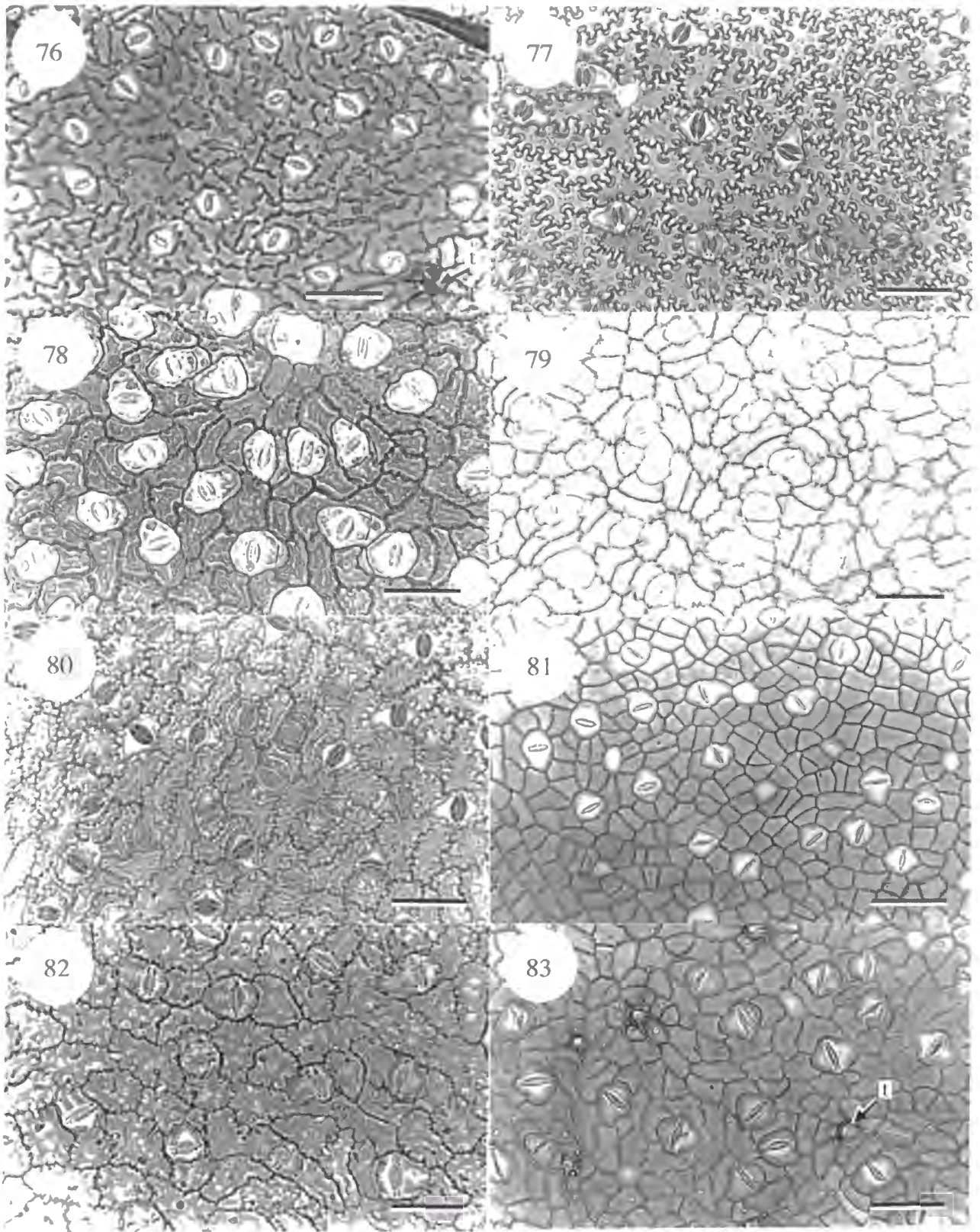


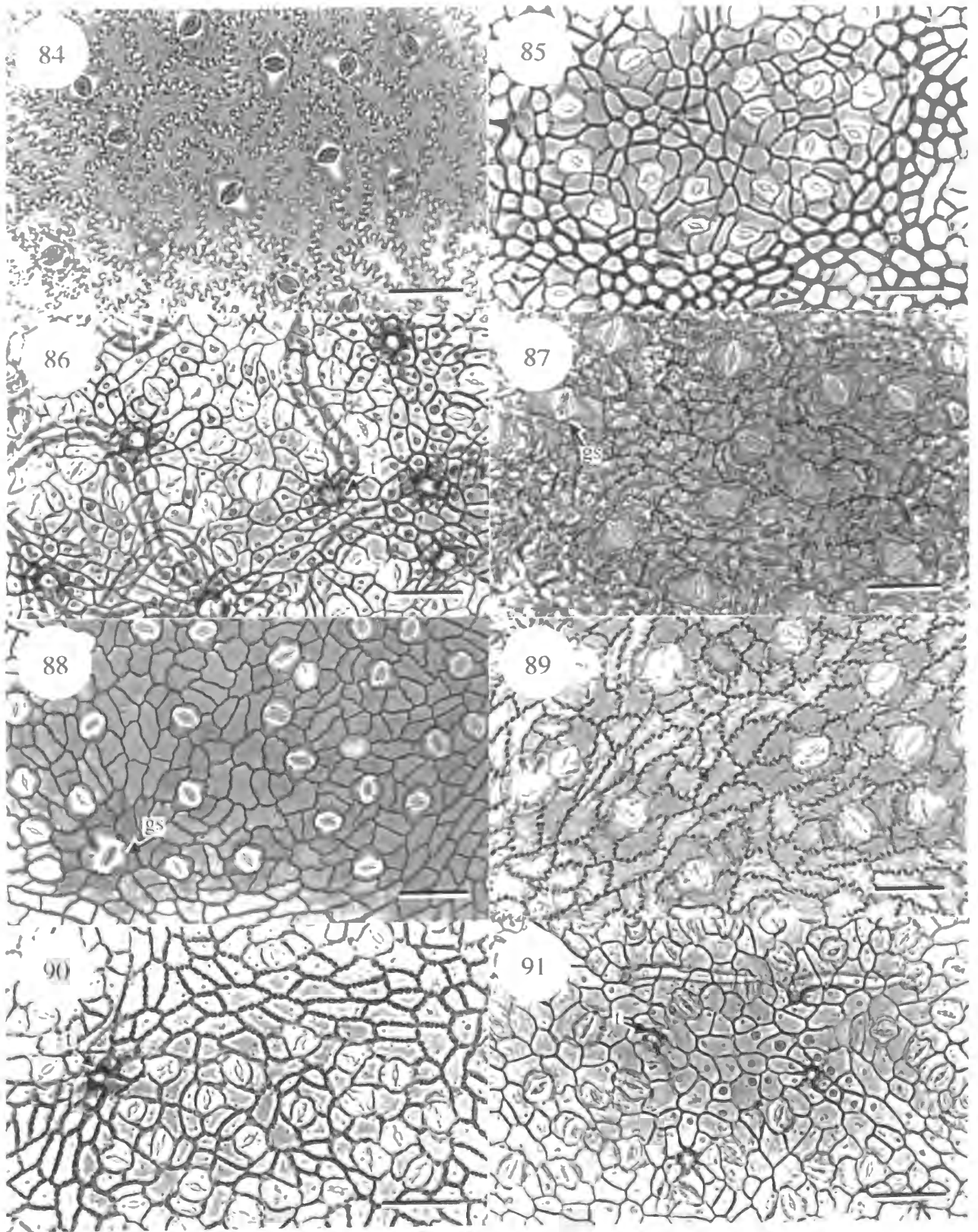


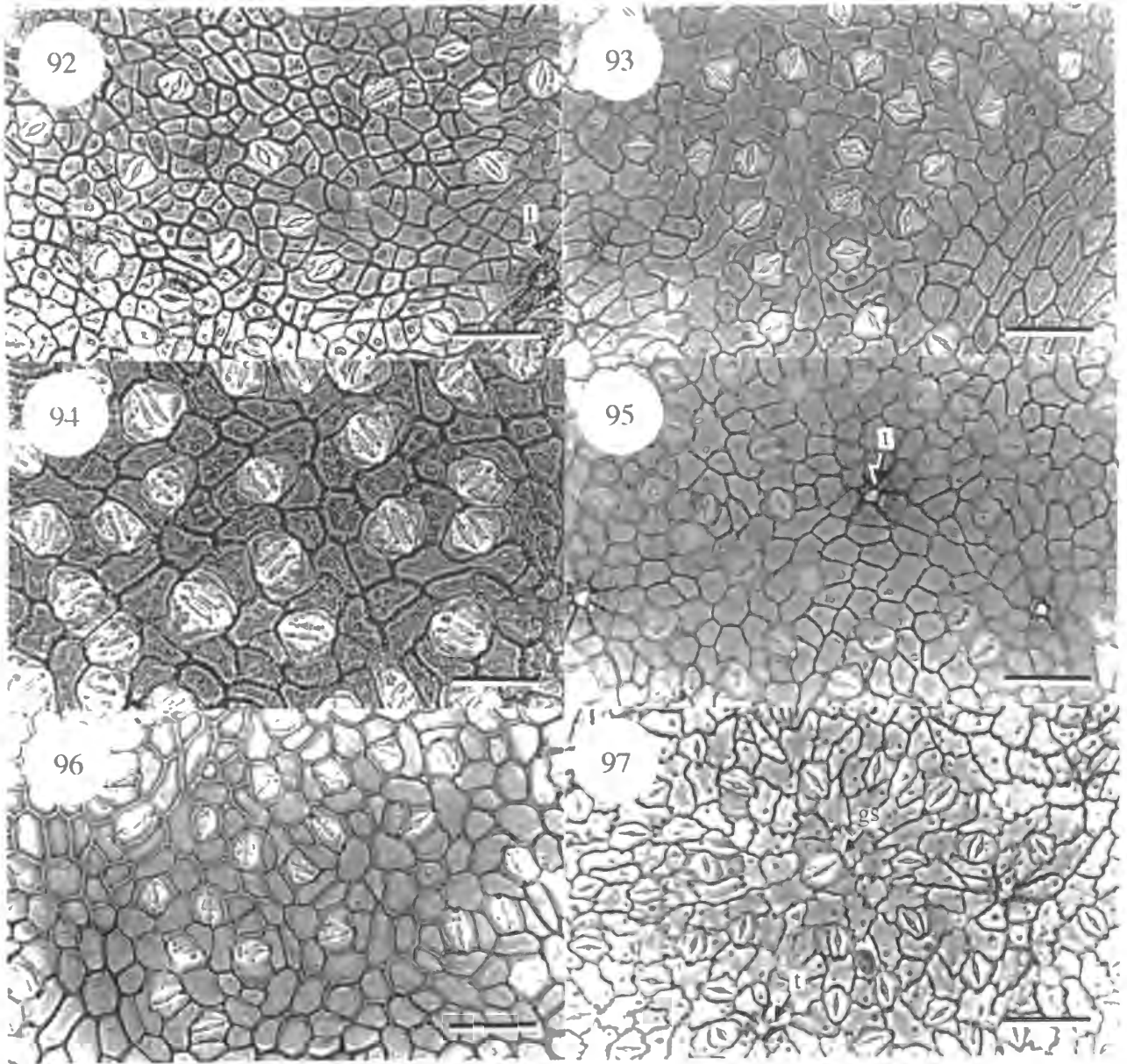


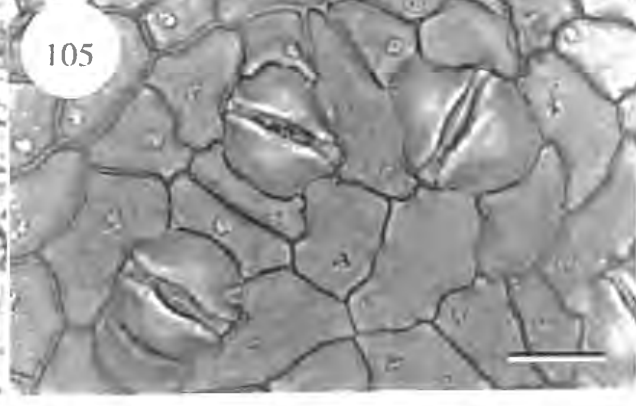
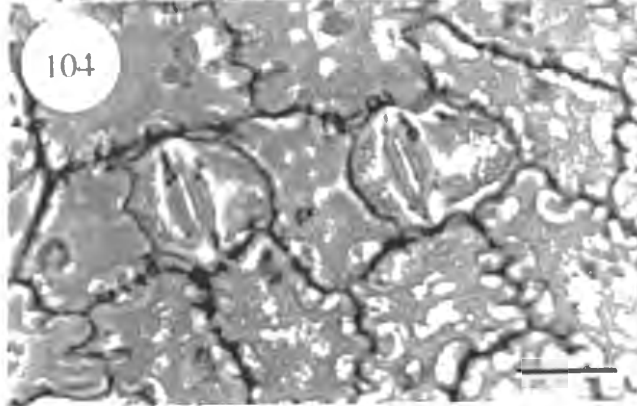
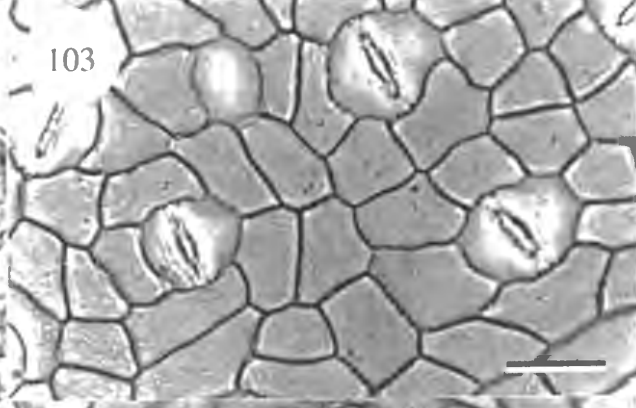
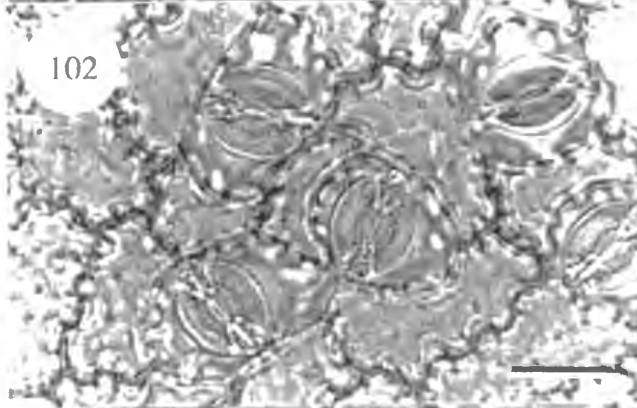
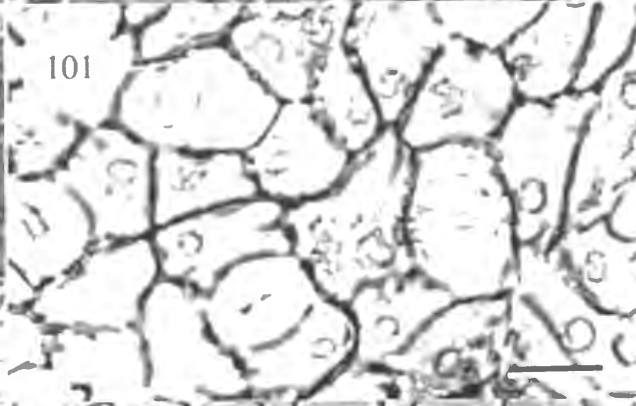
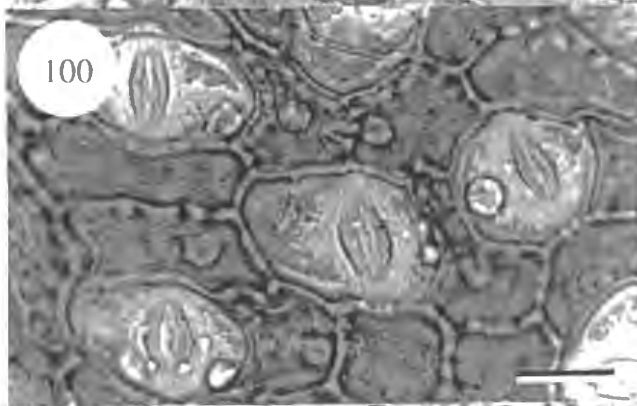
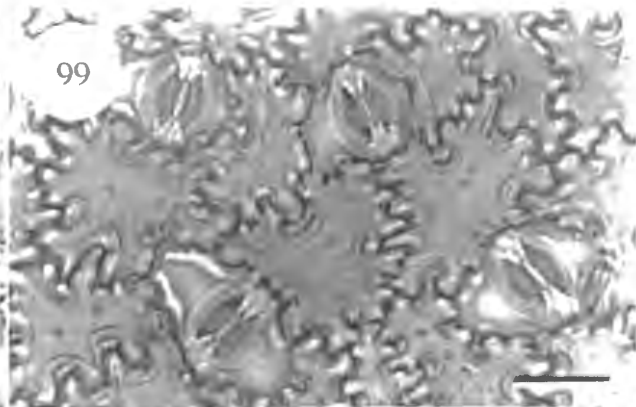
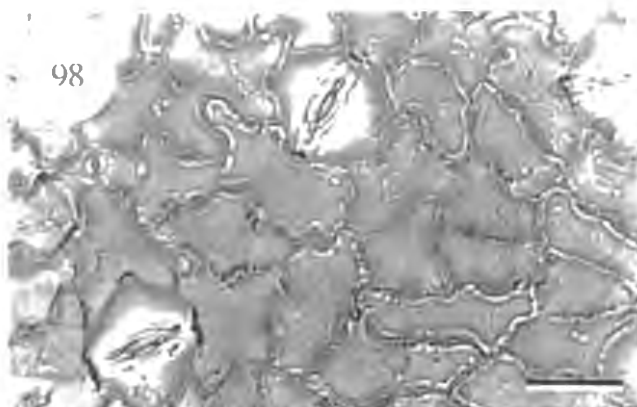


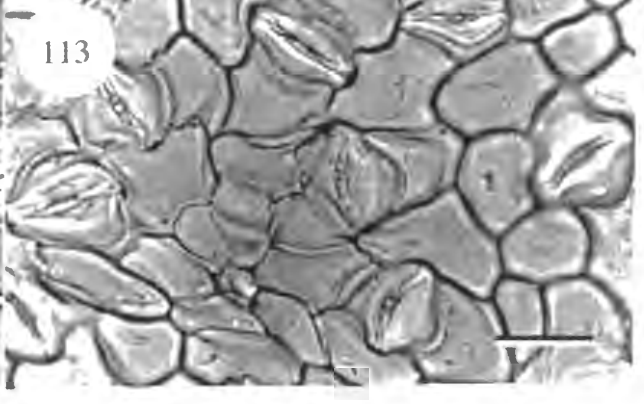
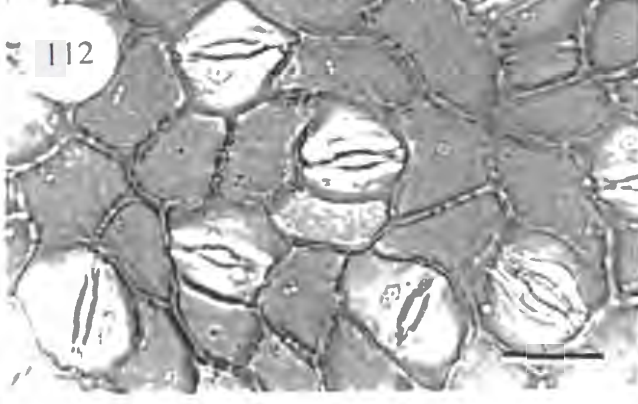
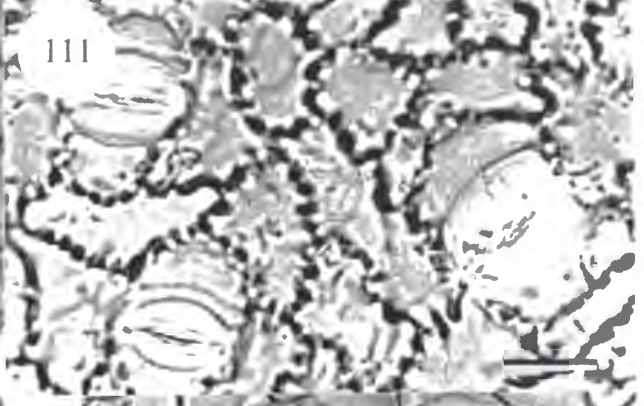
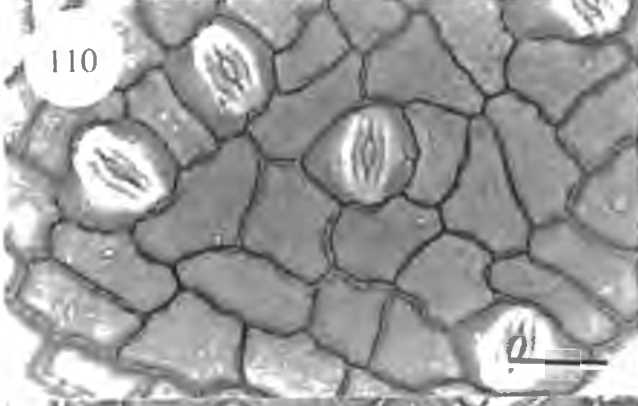
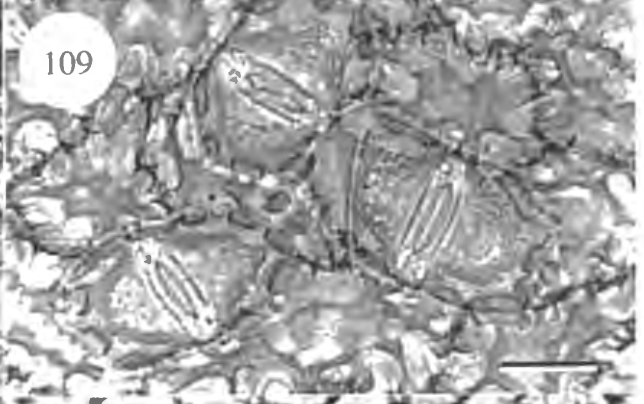
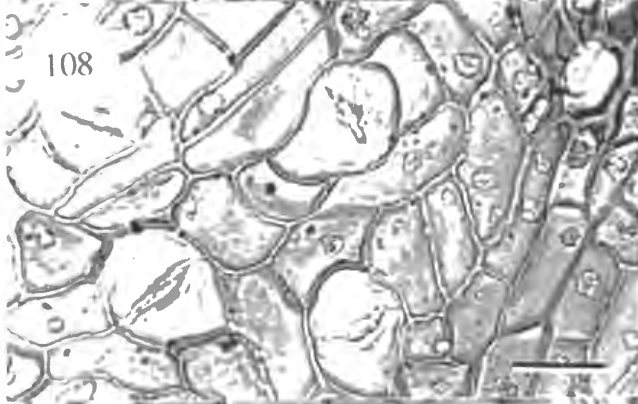
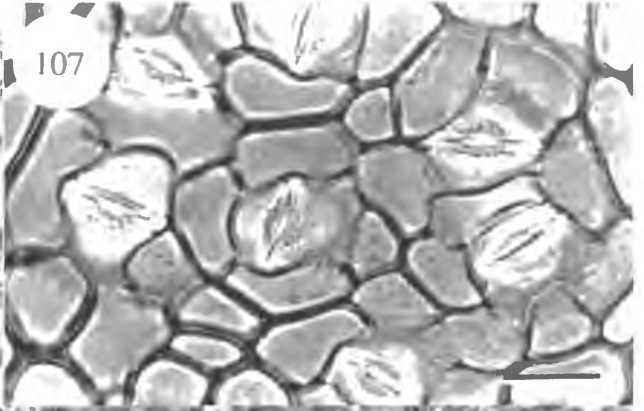
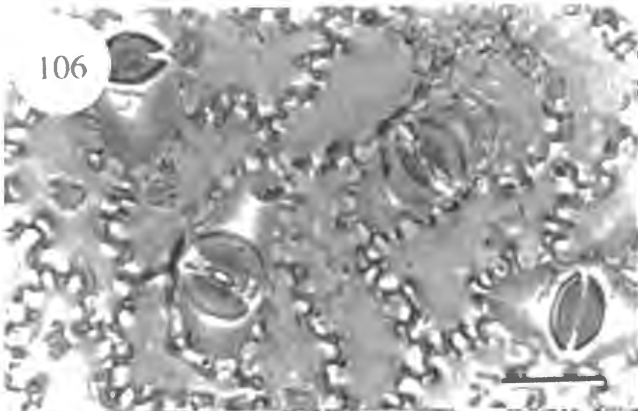


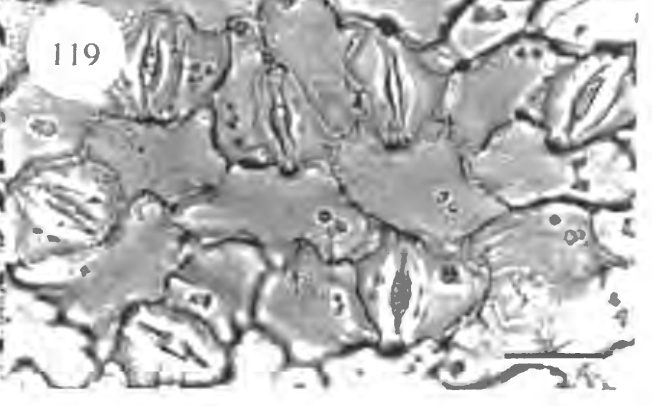
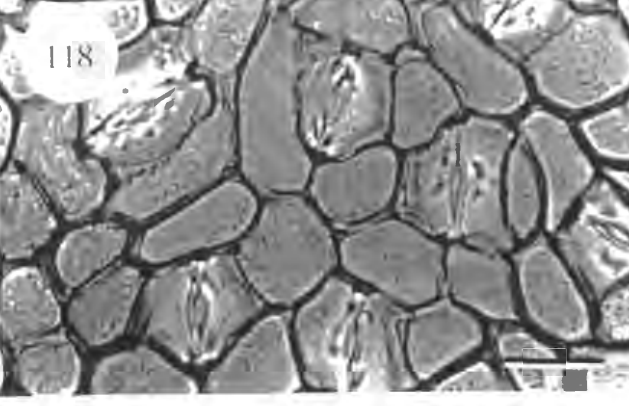
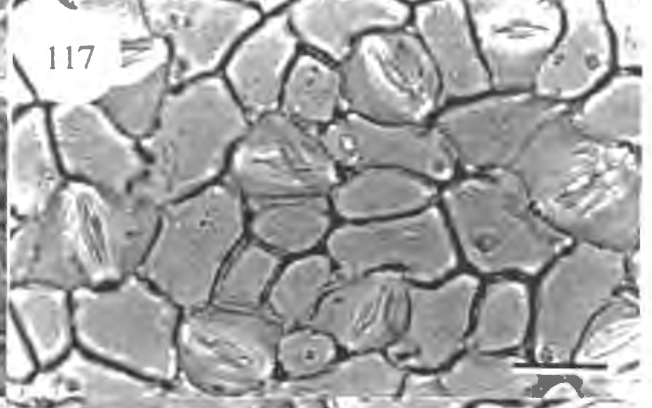
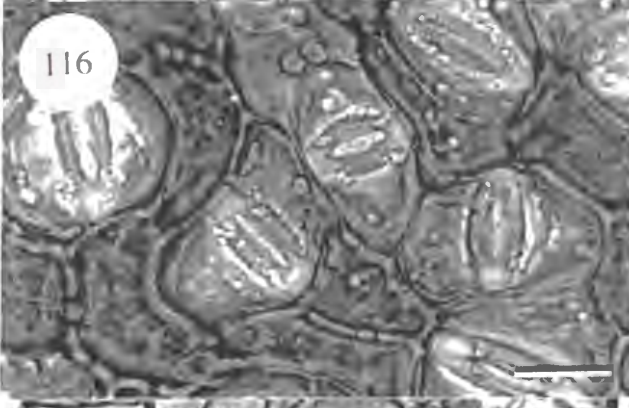
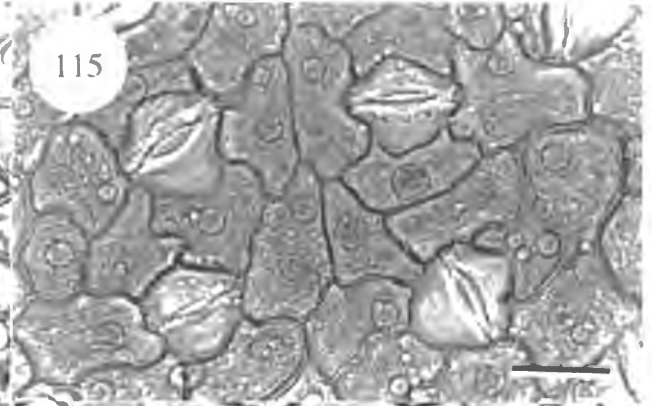
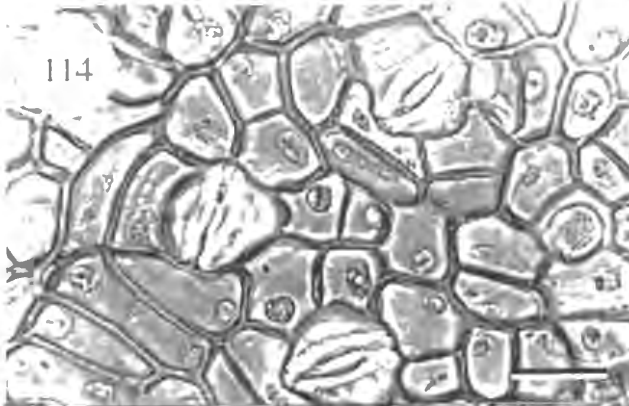










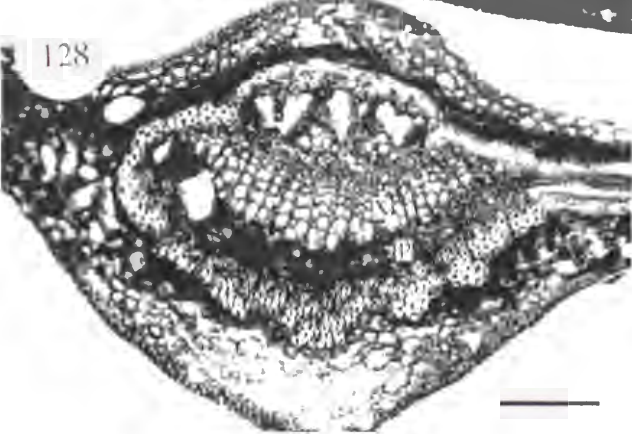
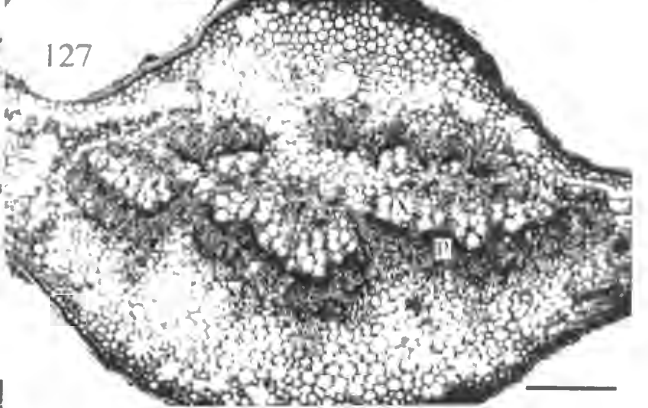
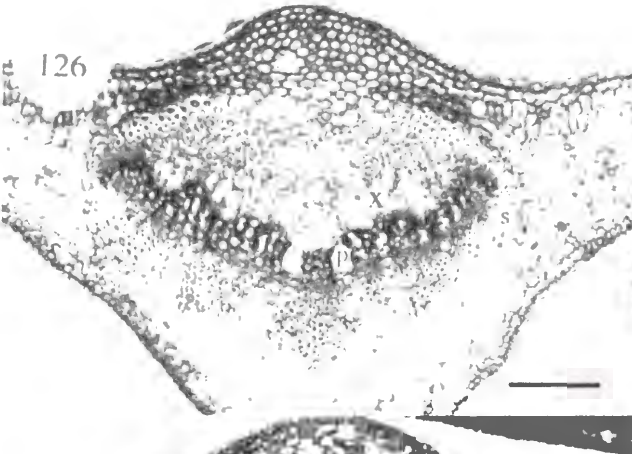
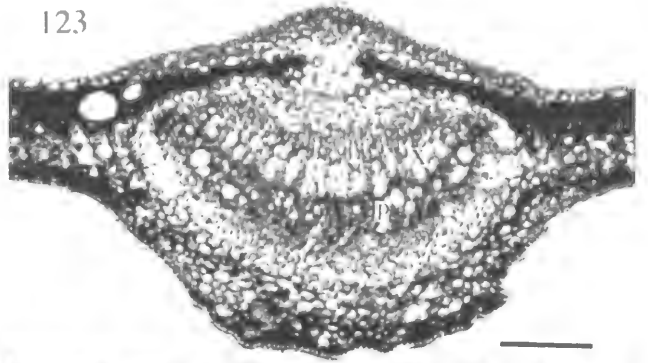
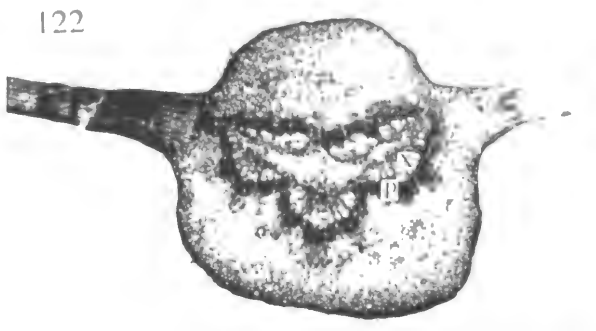


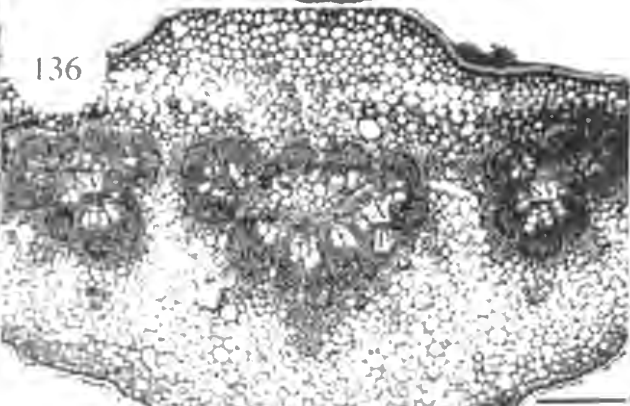
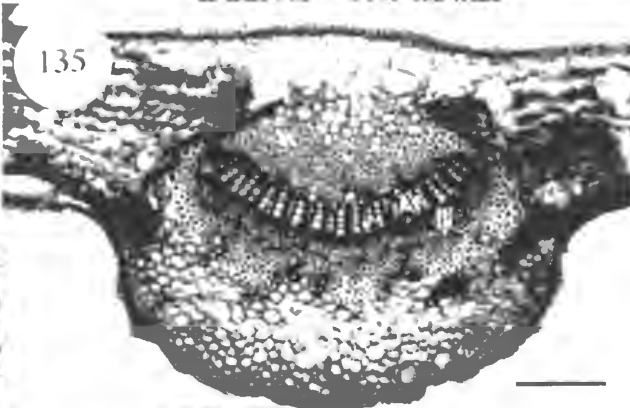
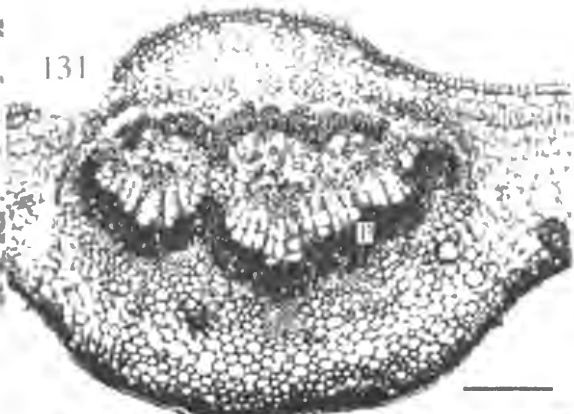
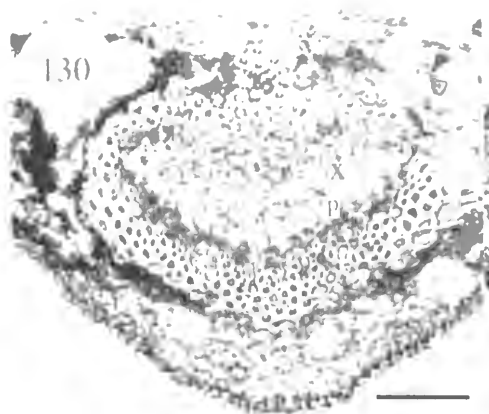
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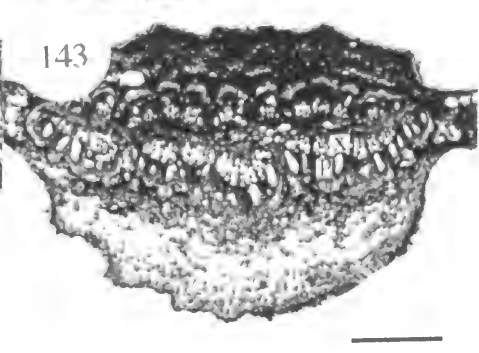
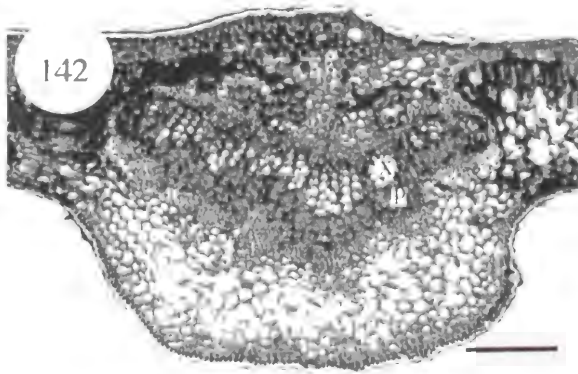
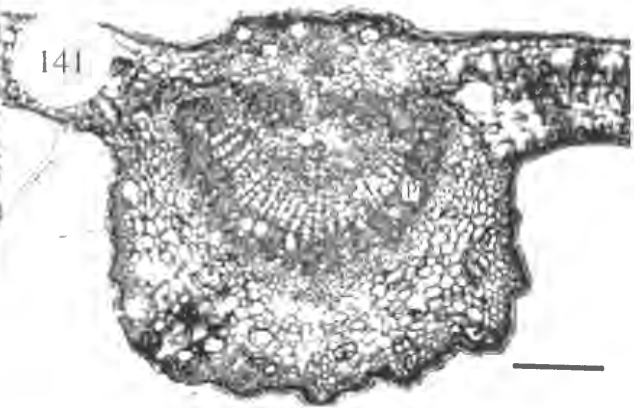
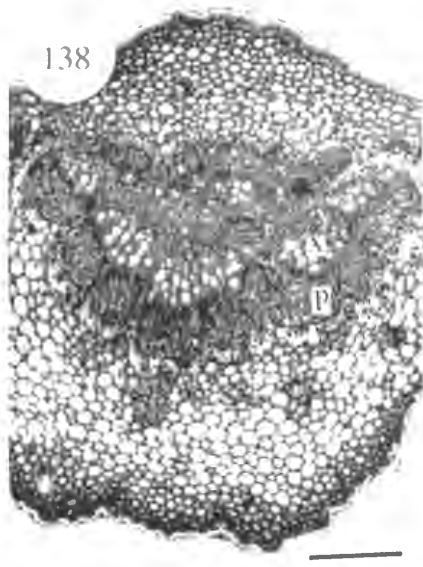
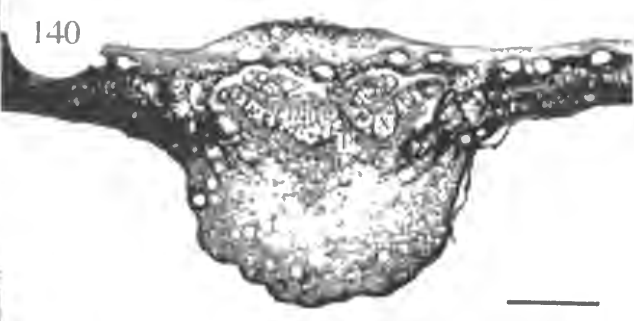
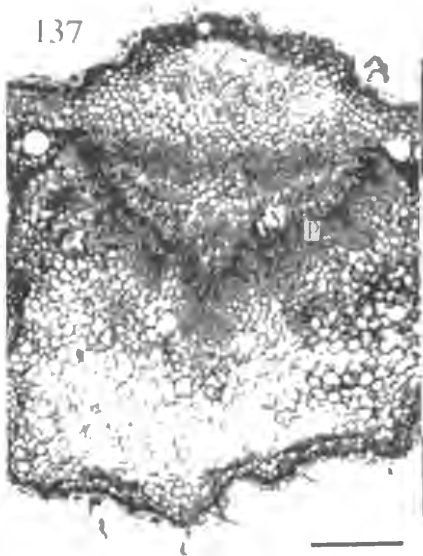


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