

# A revision of *Axinaea* (Melastomataceae)

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A revision of *Axinaea* (Melastomataceae)

## Abstract

The Neotropical genus *Axinaea* (Melastomataceae, *Meranieae*) is revised and 33 of the 38 taxa proposed hitherto are accepted and eight species (*A. alata*, *A. campii*, *A. confusa*, *A. dentata*, *A. disrupta*, *A. luteynii*, *A. minutiflora*, *A. pendula*) are described as new bringing the total number of species in the genus to 41. With the exception of *Axinaea costaricensis*, that grows in Costa Rica and neighboring Panama, species of *Axinaea* grow in the Andes from Venezuela to Bolivia, and the greatest concentration of species is found in southern Ecuador and northern Peru. *Axinaea* belongs to the capsular fruited tribe *Meranieae* in which it stands out by its inflated, spherical or ellipsoidal, anther connective appendages, a character that appears to be a synapomorphy for the genus. Mite domatia are here reported for the first time in an *Axinaea* (*A. macrophylla*) species. Of the species of *Axinaea*, 28 are endemic to one country, nine occur in two countries, three species occur in three countries and a single species - *Axinaea floribunda* - occurs in four countries. The high level of endemism and the threat to its habitats by fire, logging, and clearing for agricultural purposes, makes many species of *Axinaea* severely threatened by extinction.

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*Frederik, Crown Prince of Denmark*

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# Introduction

*Axinaea* is a genus of 41 species of trees and shrubs growing at medium to high elevations in the mountains of Central and South America from Costa Rica to Bolivia. With the exception of *Axinaea costaricensis*, that grows in Costa Rica and neighboring Panama, all *Axinaea* species grow in the Andes from Venezuela to Bolivia, and the greatest concentration of species is in southern Ecuador and northern Peru.

*Axinaea* belongs to the capsular fruited tribe *Merianieae* and has been considered closely related to the genus *Meriania* (Triana 1871, Cogniaux 1891, Wurdack 1973, 1980) based on general morphological similarities, but a detailed study of evolutionary relationships within the *Merianieae* remains to be carried out. Several taxonomic transfers in both directions between *Axinaea* and *Meriania* illustrate the difficulties of defining them morphologically. Traditionally, the only character that has been used to separate the genera is the shape of the anther connective appendage. *Axinaea* is characterized by having anthers with a dorso-basal, inflated, bulbous appendage that can be rounded or more or less apiculate, whereas *Meriania* has anthers with a dorso-basal spur that is never inflated, and occasionally an ascending dorsal appendage. This traditional definition of the two genera is followed in this treatment.

It is interesting to note that observations in the field have shown that the appendages of the anther connective in *Axinaea* are eaten by birds and/or insects. This suggests that this structure, that has traditionally been used as a diagnostic character for the genus *Axinaea*, is possibly linked to functional aspects of its pollination. Nevertheless, once all the genera of the tribe *Merianieae* have been revised, the traditional generic delimitation may change.

The delimitation of species within *Axinaea* has posed many problems over the years and species complexes, such as the *A. macrophylla* - *A. floribunda* - *A. affinis* group, were poorly understood. Several collections were never assigned to any of the known taxa

nor were they formally described as new. Since the latest revision of the genus by Eves (1936), a large number of new collections have become available, making it possible to resolve many of the species delimitation problems mentioned above.

Many species of *Axinaea* grow in populations of only few individuals and more than half of the species are narrow endemics. This situation, coupled with the fact that most of them grow in areas of the Andes that are seriously threatened by fire, logging, or clearing for agricultural purposes, makes many species of *Axinaea* severely threatened by extinction. Strong basic information about their distribution, abundance, and taxonomy is needed to propose realistic conservation measures.

In this study, we present a taxonomic revision of *Axinaea* based on morphological characters. Forty-one species are recognized, eight of which are new. Distribution maps and a key to the species are also included.

Approximately 700 collections from the following herbaria were studied: AAU, BM, BR, F, G, GB, K, LOJA, MA, MO, NY, P, QCA, QCNE, S, US, VEN, and W (herbarium acronyms according Holmgren *et al.* 1990).

## Taxonomic history

The genus *Axinaea* was first described by Ruiz and Pavón in 1794. The characters used to define the genus were the presence of a cyathiform calyx (*i.e.*, shaped as a cup, wider at the top than at the bottom), calcarate (spurred) anthers with one apical pore, and 6-locular capsules almost completely covered by the calyx. The name of *Axinaea* refers to the “axe-shape” of the petals depicted in the illustration of the genus, a shape that in our opinion is not very characteristic. From the start, Ruiz and Pavón included two species with somewhat different floral morphology in their new genus: *Axinaea lanceolata*, described as having an-

thers that were “almost conical, with an obovate spur” and *A. purpurea*, described as having anthers that were “linear, with a conical spur.” The difference in anther connective morphology exhibited by these two species corresponds to the modern definitions of the genus *Axinaea*, to which *A. lanceolata* belongs, and *Meriania*, to which *A. purpurea* has been transferred, as a synonym of *M. radula* (Benth.) Triana.

Other aspects of Ruiz and Pavón’s description added further confusion to the concept of their new genus. Both species described by Ruiz and Pavón have 5-merous flowers, nevertheless, the figure accompanying the original description of the genus shows a 6-merous flower (without designation of which species is shown on the illustration). Furthermore, *Axinaea* was referred to the class *Dodecandria Monogynia*, in spite of the authors’ own notion that the “most common number of stamens in the genus is ten, and five of the other parts of the fructification.” The genus was included in this class only because of a supposed affinity (according to Ruiz and Pavón) with *Blakea* and *Valdesia* (two other 6-merous genera of Melastomataceae). It is, however, possible that the flower dissected for the illustration was an anomalous, 6-merous flower, something that occasionally happens in the genus (see Morphology/Flowers, below).

The uncertainty concerning the generic concept of *Axinaea* introduced by Ruiz and Pavón’s original publication appears to have influenced the way the genus was treated by several authors to follow. David Don (1823) defined *Axinaea* more or less in the same terms as Ruiz and Pavón, but narrowed the circumscription to include only species with anthers with an “elongated calcarate appendage at the base.” In this way Don’s generic concept for *Axinaea* became virtually identical to that of the genus *Meriania*, that had been described by Swartz in 1798 based on a species from Jamaica, *Meriania purpurea* Sw. In spite of his strict circumscription of the genus, Don nevertheless included *A. lanceolata*, *A. glandulosa*, and *A. dependens* in the genus (all three of which have spherical, not calcarate anther appendages), as well as *A. muricata*, a species with subulate anthers and baccate fruit (capsular in *Axinaea*), that rightly belongs to the quite different genus *Miconia*.

The taxonomic concept of Don was largely followed by de Candolle (1828), who, however, added a few characters of his own to the generic diagnosis of *Axinaea*. These included two-pored anthers and a 5-6-denticulate calyx. De Candolle also described a new genus *Chastenea*, dedicated to Victorina de Chastenay and based on a new species, *C. merianiae* from Ecuador, that he considered to be closely related to *Meriania* but distinguished from it by its truncate and entire calyx limb, one-pored anthers, and the inflated, rounded connective appendage. As such, *Chastenea* accommodated the part of *Axinaea* as defined by Ruiz and Pavón that was excluded from the genus in the more strict circumscription applied by Don and de Candolle. As in the case of Don, the five species referred to *Axinaea* by de Candolle mostly did not conform to his generic diagnosis. One species, *A. muricata* [= *Miconia muricata*] had two-pored anthers, but lacked the spur-like anther appendage required in the generic diagnosis. Three species (*A. lanceolata*, *A. glandulosa* and *A. dependens*) had both the wrong type of anther appendage (spherical rather than calcarate) and one-pored anthers. The last species, *A. purpurea*, had the right type of calcarate anther appendage, but one-pored anthers and calyx with minute teeth.

The accumulated confusion resulting from the works of Ruiz and Pavón, Don and de Candolle led Naudin, in 1852, to abandon *Axinaea* altogether, transferring instead *A. lanceolata* and *A. purpurea* to *Chastenea* and *A. dependens* to *Meriania*. This left only three imperfectly known and doubtful taxa in *Axinaea* (*A. purpurea*, *A. muricata* and *A. radula*). Naudin further stated that given the heterogeneity of *Axinaea* and the imperfect knowledge of its taxa, the genus could, in the future, be deleted.

Our current concepts of the genera *Axinaea* and *Meriania* were instated by Triana (1871), who was the first to provide a clear definition of the genera. He wrote: “The genera *Meriania* and *Axinaea* are very close. The species, especially of *Meriania* that have a truncated calyx and the flowers in corymbs, have the same appearance and the same bearing as those of *Axinaea*, so it is that they are really only distinguished by the prolongation of the posterior spur of the connective

that is thick and rounded, instead of straight and acute.” Following the concept of Triana only one of the original two species described in *Axinaea* by Ruiz and Pavón (*A. lanceolata*) was retained in the genus, while the other (*A. purpurea*), was transferred to *Meriania* (as a synonym of *Meriania radula* (Benth.) Triana). *Chastenaea* was reduced to synonymy under *Axinaea*. Finally, Triana described four new species of *Axinaea*, two from Ecuador, one from Colombia and one from Peru, bringing the total number of species in the genus up to 13.

Cogniaux, in 1891, studied *Axinaea* for his treatment of the Melastomataceae in de Candolle’s *Monographiae Phanerogamarum*, and included 18 species in the genus, of which five were new.

The most recent revision of *Axinaea* is that by Eves (1936), who recognized 22 species. Eves studied material from the B, F, G, K, and NY herbaria (about 70 different collections in total) but was unfortunately not able to examine several types of *Axinaea* and *Chastenaea* names kept in the Paris herbarium (P). This, together with the fact that some species at this time were represented only by one or two collections, resulted in a treatment where several of the species could not be delimited with certainty.

After Eves’ treatment, Gleason (1946), Wurdack (1964, 1966, 1976, 1978), Lozano-C. Alvear (2001), Bussmann (2010) and Sagástegui et al. (2010) have published new species of *Axinaea*. Nevertheless, 65 years of intensive exploration in the Andean highlands since Eves revision was completed have resulted in a large number of specimens accumulating in various herbaria around the world. The present revision is thus based on more than 700 different collections, many of them with several duplicates. The number of species recognized is 41, including 19 species from Eves treatment, 12 species published after Eves, two species that have been resurrected from Eves treatment and eight new species that are being described. Since an early version of this manuscript appeared in 2003 as a MSc thesis, four *Axinaea* names have been published. Three of them *Axinaea fernando-cabiesii* Bussmann, Gruhn & Glenn, *A. reginae* Bussmann, Gruhn & Glenn and *A. wurdackii* Sagást., S.J. Arroyo &

E. Rodr are included here and we are fairly certain that they represent new taxa, but our observations are based exclusively on high-resolution photographs of the types and the descriptions accompanying the protologues. A fourth name, *A. ninakurorum* Bussmann & Paniagua, represents a species of *Meriania*, for which we provide a new combination in the list of excluded names and doubtful taxa.

## Morphology

### Growth habit and branching

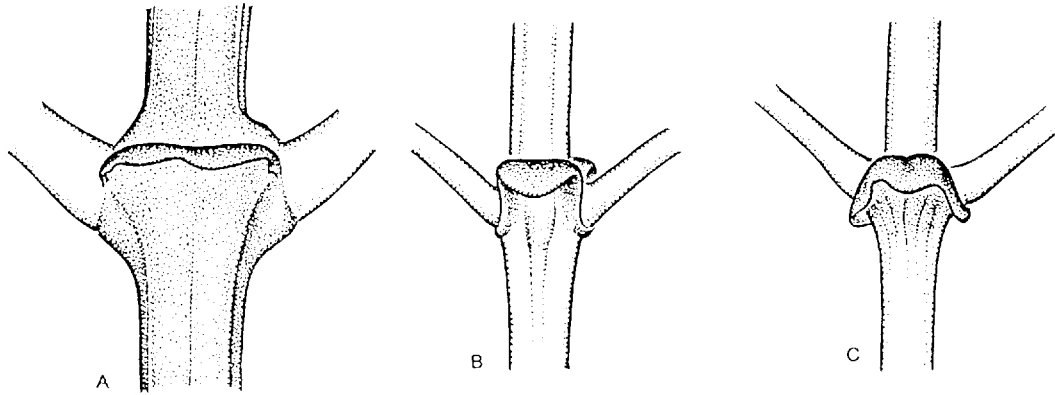
Most species of *Axinaea* are trees or shrubs. Some species show both shrubby and arborescent habits. Species that grow at higher elevations (over 3000 m a.s.l.) are usually shrubby while those found at lower elevations are more frequently trees. Most of the trees are slender and develop a very thin, long stem that only branches at the top. The crowns are normally rounded and can be quite dense.

In most species the young branches are quadrangular or subquadrangular, usually becoming terete with age. In a few cases the angles are sharp (*A. campii*, *A. lanceolata*) or even somewhat alate (*A. alata*, *A. lanceolata*). They are often bright red, magenta or at least reddish in color, and this character seems to be independent of the light conditions under which the plant grows. Older branches, that are three or four nodes (corresponding to growing periods) below the tip, usually decorticate to reveal a slightly orange or ochre bark.

### Nodes and stipuliform flaps

Some species of *Axinaea* have enlarged nodes (Figure 1: A). In this treatment the nodes are called “thickened” when they are at least twice as thick as the middle of the previous adjacent internode. Species with thickened nodes are: *A. crassinoda*, *A. dentata*, *A. dependens*, *A. pendula*, *A. robusta* and *A. sodiroi*.

One third of the species of *Axinaea* have, what has been called, “stipules” or “stipule scars” (Eves 1936), “interpetiolar flaps” or “interpetiolar lines” (Wurdack



**Figure 1.** Nodes and stipuliform flaps in *Axinaea*. A. Thickened node with a well developed, coriaceous stipuliform flap. B. Not thickened node with well developed, coriaceous stipuliform flaps. C. Not thickened node with well developed stipuliform flaps that extend under the point of insertion of the petiole forming a continuous ring around the nodes.

1980), or “stipuliform flaps” (Almeda 2001). These structures resemble stipules even if Melastomataceae have been described in several texts (*e.g.*, Lawrence 1951, Heywood 1993, Judd *et al.* 2002) as not having stipules. Here the term “stipuliform flaps” has been adopted for this structure. The stipuliform flaps can be well developed, coriaceous, and up to 5 mm long (Figure 1: A, B), as in *A. costaricensis*, *A. crassinoda*, *A. dependens*, *A. pendula* and *A. sessilifolia*, or ridge-like, hardened, and raised only 1 mm as in *A. campii*, *A. affinis*, *A. macrophylla* and *A. quitensis*, though in these last three species the ridge may be reduced to a line. In some species stipuliform flaps are present as just a faint interpetiolar line and when so reduced, they have been called a “scar” by Eves (1936) and Wurdack (1973, 1980) but in this treatment the term “stipuliform flaps” is maintained. On occasion the ridge-like stipuliform flap can extend under the petiole forming a continuous ring around the node (Figure 1: C). This continuous ring is most well developed in *A. mertensoides* but is also present to a lesser degree in *A. affinis*.

### Indument

Melastomataceae vary greatly in both type and density of trichomes. Wurdack (1986), studied the hairs of 530 species of Neotropical Melastomataceae, classifying the trichomes into 45 different types. Of the

530 species studied, 18 belonged to the tribe *Merianieae* and of those, only one was an *Axinaea*.

Trichomes in *Axinaea* are restricted to the vegetative parts of the plant and to the external surface of the hypanthium. Petals, filaments, ovaries and styles are consistently glabrous in all species of *Axinaea* though other genera in the tribe *Merianieae* exhibit pubescence or setae in some of these structures.

Typically, all young branches and young leaves in *Axinaea* are moderately to densely covered with short, thick, shaggy or pinoid hairs, evident as a furfureous puberulence on most young, aerial structures of the plants, but it is early caducous. Only the persistent pubescence is of any use as a taxonomic character and of these, *Axinaea* exhibits only the following five types of trichomes:

- a. Short, thick, moderately branched, shaggy or pinoid hairs
- b. Elongated, rugose or shaggy hairs
- c. Squamose, transparent, usually scattered, hairs
- d. Arachnoid hairs forming an indistinct indument
- e. Sessile glands, visible under  $\times 10$  magnification as orange, glandular dots on the abaxial surface of the leaves.

The same type of pubescence is present throughout the plant. There is no mixture of hair types in one plant except for the length of the trichomes, though

the presence of sessile glands may be accompanied by scattered puberulence. *Axinaea colombiana*, *A. crassinoda*, *A. fallax*, *A. flava*, *A. robusta*, *A. sclerophylla* and *A. tomentosa* all have a dense and persistent indument. *Axinaea affinis*, *A. campii*, *A. fernando-cabiesii*, *A. macrophylla*, *A. mertensoides*, *A. quitensis* and *A. reginae* are the only species that present sessile, orange glands on the abaxial surface of the leaf. Only two species have arachnoid pubescence: *A. glauca* and *A. merianiae* and only *A. campii* has squamose, transparent hairs

## Leaves

The leaves in *Axinaea* are always in pairs, isophyllous, entire, oblong, elliptic, ovate, or obovate, usually coriaceous and, in species that grow at higher elevations, often rigid and erect. All but one species of *Axinaea* have petiolate leaves, the exception being *A. sessilifolia*, that has completely sessile leaves. The petioles are often canaliculate and quite commonly bright red or magenta in color. The pubescence on the petioles is usually the same as on the branchlets.

The leaves are often green and lustrous adaxially and less intensely green and matte abaxially. The pubescence is always denser in the abaxial side and the adaxial side is often glabrous. In some species, such as *A. sclerophylla* and *A. dentata* the primary and secondary nerves are sunken abaxially making the surface of the lamina coarsely bullate. In *A. sessilifolia* the primaries are actually shorter than the lamina and the surface therefore becomes subplicate and resembles the surface of a parachute.

## Leaf venation

In the terminology of leaf venation we follow the standards developed by Wurdack (1973, 1978, 1980). All species in *Axinaea* exhibit the acrodromous venation that is typical of Melastomataceae, both as basal venation in which the pairs of primary nerves separate from the main nerve at the base of the lamina, and plinerved venation, where the inner pair(s) of primaries arise some distance above the lamina base. In the case of plinervation the inner pair of primaries can diverge from the main nerve 2–5 millimeters above the

lamina base and then it is referred to as shortly-plinerved, or it can diverge from the main nerve one to several centimeters above the lamina base and then it is referred to as plinerved or strongly plinerved respectively.

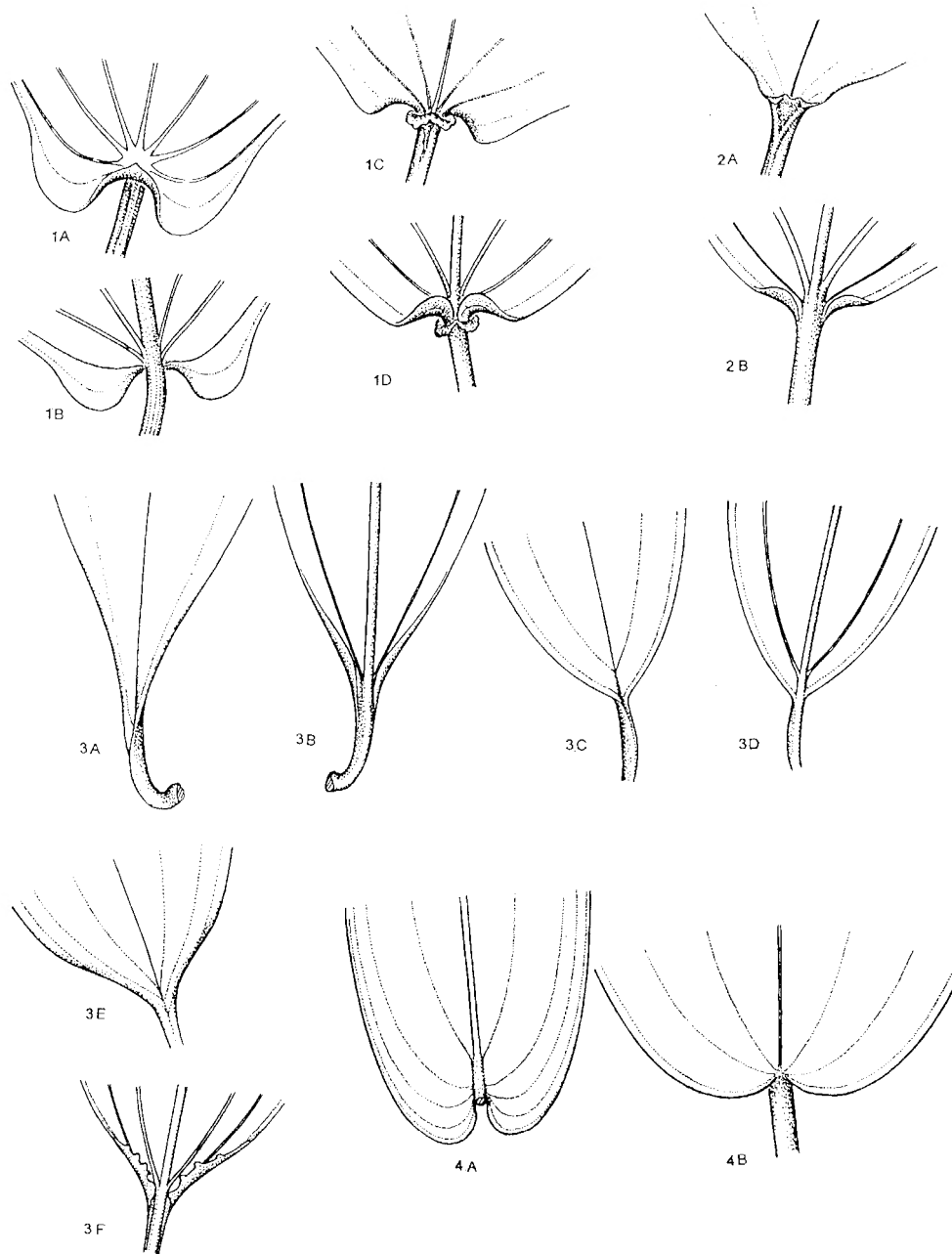
The number of primary nerves in the leaves of *Axinaea* may vary from 3 to 7 with 3-nerved and 5-nerved being the most common. Additionally, there is a pair of faint inframarginal nerves that run at the most 2 mm from the leaf margin. These inframarginal nerves are usually formed by anastomosing secondary venation. Counting the number of primaries can be difficult in some species because occasionally the most external pair of primaries is fainter than the inner pair and could therefore be confused with the inframarginal nerves. It is therefore important to identify the inframarginal nerves adequately in order to establish the number of primaries in the leaf venation.

## Lamina base and auricles

It is quite frequent in *Axinaea* to find auriculate lamina bases (Figure 2: 1A, 1B, 1C, 1D, 2A, 2B, 3E, 3F). The auricles can be as much as 7 mm long or as short as 1 mm long or, with the exception of the cordate based species and *A. weberbaueri*, they are revolute or reflexed. This means that from the adaxial side, the auricles go unnoticed (Figure 2: 1C, 2A, 3E). The shape of the lamina base is described, in this treatment, as seen with the auricles in their revolute or reflexed position since this is the shape that is most evident to observers when trying to identify the plant.

Without considering the basal auricles, the lamina base in *Axinaea* can be attenuate or decurrent (Figure 2: 3A, 3B), cuneate (Figure 2: 3C, 3D, 3E, 3F), rounded, truncate (Figure 2: 1C, 1D), or cordate (Figure 2: 4A, 4B). Few species have cordate lamina bases: *A. sessilifolia*, *A. crassinoda* and *A. sodiroi*. In the case of *A. sessilifolia*, the leaves are also sessile (Figure 2: 4A) and the base of the lamina clasps the stem. Most common in the genus are cuneate, rounded or truncate lamina bases, though six species show attenuate or decurrent lamina bases.

The presence of auricles is common in *Axinaea*. Apart from the four cordate leaved species (*A. crassinoda*



**Figure 2.** Variation of lamina base shape in *Axinaea*. 1A. Auriculate lamina base with well developed knob-shaped scutum, adaxially. 1B. Auriculate lamina base with well developed knob-shaped scutum, abaxially. 1C. Truncate lamina base due to the revolution of the auricles with well developed knob-shaped scutum, adaxially. 1D. Truncate lamina base due to the revolution of the auricles with well developed knob-shaped scutum, abaxially. 2A. Cuneate lamina base due to the revolution of the auricles with an incipient v-shaped scutum, adaxially. 2B. Cuneate lamina base due to the revolution of the auricles with an incipient v-shaped scutum, abaxially. 3A. Attenuate lamina base without scutum, with revolute margins, adaxially. 3B. Attenuate lamina base without scutum, with revolute margins, abaxially. 3C. Cuneate lamina base without scutum, adaxially. 3D. Cuneate lamina base without scutum, abaxially. 3E. Cuneate lamina base due to the revolution of the auricles, adaxially. 3F. Cuneate lamina base due to the revolution of the auricles, abaxially, showing the dentate-undulate margins of the auricles. 4A. Cordate, sessile leaf, abaxially. 4B. Shallowly cordate lamina base, adaxially.

da, *A. sessilifolia*, *A. sodiroi* and *A. weberbaueri*) 13 species do not have auricles and of these, five have revolute base margins. In four species the revolute margins of the lamina base are dentate-undulate (Figure 2: 3F).

#### Scutum

Many species in *Axinaea* exhibit a thick, hard knob at the joint of the lamina base and the petiole adaxially, that resembles a small shield and it is therefore called a scutum. The scutum is formed by the margins of the lamina base that join with the petiole and form a raised ridge. In 13 species the scutum is knob-like, hardened and raised up to 2 mm (Figure 2: 1A, 1C). In three species the margin of the lamina joins with the raised side of the canaliculated petiole forming a v-shaped scutum that is raised less than 1 mm (Figure 2: 2A). The v-shaped scutum is not a constant character.

#### Acarodomatia

Ant domatia are well represented in at least eight genera of melastomes. Both their morphology and their ecological implications have been observed and studied in several occasions (Gleason 1931, Schnell 1967, Whiffin 1972, Roth 1976, Renner & Ricklefs 1998, Svoma & Morawetz 1992, Michelangeli 2000). Even though mite domatia (acarodomatia) were reported already in 1887 in the leaves of a species of *Tilia* (Lundström, cited in Walter 1996), they have only kindled scientific interest in the last 20 years. Acarodomatia have been reported in Melastomataceae in the genera *Blakea*, *Clidemia* and *Topobea* (Almeda 1989, 1990, 2000, 2001) and exist also in *Miconia* (personal observation). One species of *Axinaea*, *A. macrophylla*, exhibits acarodomatia in the form of small pockets at the insertion angle of the inner pair of primaries with the main nerve. Apart from one mention of this character on a herbarium label this is the first time that mite domatia are reported for *Axinaea*.

#### Inflorescences

All species of *Axinaea*, as other species of the tribe *Merianieae*, have terminal inflorescences but sometimes the position of the inflorescence may be obscured by

the growth of a lateral branch, making it seem axillary. Most species have compound dichasia or thyrses but a few species have solitary flowers or at most five flowers such as *A. flava*, *A. lawessonii*, and *A. merianiae*. Almost all *Axinaea* species have pendulous or nodding inflorescences.

The number of flowers per inflorescence can vary from one to several dozen. To ease the identification of the species the inflorescences have been divided into three categories: few-flowered inflorescences (1-10 flowers), moderately-flowered inflorescences (11-25 flowers), and rich-flowered inflorescences with 26 flowers or more.

Three types of inflorescences, with different degrees of reduction, are found in *Axinaea*.

The first type is a synflorescence (Figure 3: A), subtended by a pair of bracts that are identical to the leaves or slightly smaller, composed of several orders of thyrses or dicasia each subtended by an additional pair of persistent bracts similar to the leaves but subsequently smaller. The gradual transition from foliar leaves to bracts makes it very difficult to identify this structure as a single inflorescence and it could just as well be taken for many smaller inflorescences. This type is most evident in *A. ruizteranii*.

The second type is similar to the first one but differs in the number and size of the persistent bracts (Figure 3: C, D). In this type the bracts are often deciduous and smaller making it easier to recognize the inflorescence as a unit. This is the most common type of inflorescence in *Axinaea* and it is found in, e.g., *A. floribunda*, *A. macrophylla*, *A. pauciflora*, and *A. sclerophylla*. The third type is not subtended by a pair of persistent bracts and no bracts are visible in the inflorescence (Figure 3: B). Furthermore, the inflorescence is usually large, pendulous and the flowers are arranged in fascicles at the end of the branches. This type can be seen in *A. costaricensis*, *A. fernando-cabiesii*, *A. pendula*, *A. reginae* and *A. sessilifolia*.

Another interesting feature in the inflorescences of *Axinaea* is that the leaf-like bracts often show a shortly-plinerved or plinerved venation even if the foliar leaves of the plant are basally nerved. Since many herbarium collections include only the flowering branch-



**Figure 3.** Inflorescence types in *Axinaea*. A. Synflorescence composed of thyrses or compound dichasia, subtended by successively smaller pairs of leaf-like bracts. B. Elongated thyrse, rich-flowered, with flowers arranged in fascicles, bracts absent or caducous. C. Compound dichasium subtended by a pair of leaf-like bracts. D. Simple dichasium subtended a pair of leaf-like bracts.

es of the plant, only the plinerved bracts are present in some of the collections. It is also worth noting that the nodes in the main axis of the inflorescence have the same characters as those in the vegetative branches, that is, they are thickened or not and/or exhibit

stipuliform flaps in concordance to the vegetative nodes.

The peduncle and the branches of the inflorescence show the same degree of pubescence and the same type of trichomes as the branchlets.



## Flowers

All flowers in *Axinaea* are diplostemonous, that is, the stamens are twice as many as the petals. The majority of the species have 5-merous flowers, but seven species (*A. colombiana*, *A. crassinoda*, *A. dependens*, *A. fernandocabiesii*, *A. mertensoides*, *A. pendula*, *A. reginae*) are 4-merous. It is not unusual, however, to find some occasional anomalous flowers that are 6-merous, and in these cases, the number of stamens can be somewhat irregular ranging from 11 to 13.

The petals and the stamens are borne on the internal, upper rim of the hypanthium, also called torus. The ovary is completely surrounded by the hypanthium but free from it, being attached only at the base, making all flowers of *Axinaea* perigynous.

The hypanthium length is measured from the base to the torus and its width is the diameter at the torus. The term “cupuliform” is used for those hypanthia where the length and the width are the same or nearly so. The term “cyathiform” is used for those hypanthia where the length is half of its width.

In most species of *Axinaea* the stamens migrate towards the lower side of the flower at anthesis, while the style does not change position.

### *Calyx*

The calyx in *Axinaea* grows on the outer rim of the torus. It is composed of the limb, that is continuous, and exceeds the torus for ca 1 mm, the lobes that are sometimes indistinct or truncate but usually rounded or broadly triangular and 1-2 mm in length, and the teeth. The calyx teeth or external teeth (Wurdack 1973, 1980) are small, teeth-like structures, of unclear origin, that arise from the calyx limb abaxially, in a position that is opposite the calyx lobes. In Melastomataceae calyx teeth are found in many genera and are sometimes the most evident feature of the calyx, exceeding the calyx lobes in length and even covering them almost completely.

The calyx in *Axinaea* is always glabrous and can be a continuation of the hypanthium or it can be flared and almost perpendicular to it. The calyx teeth are most often minute or inconspicuous in the mature

flower, though they can always be seen in the young buds. In *A. dentata*, the external teeth are unusually long and indeed exceed the length of the calyx lobes by ca 1 mm. It is not infrequent to find species where the calyx teeth are reduced to small, hardened, triangular knobs that project perpendicularly from the calyx lobes.

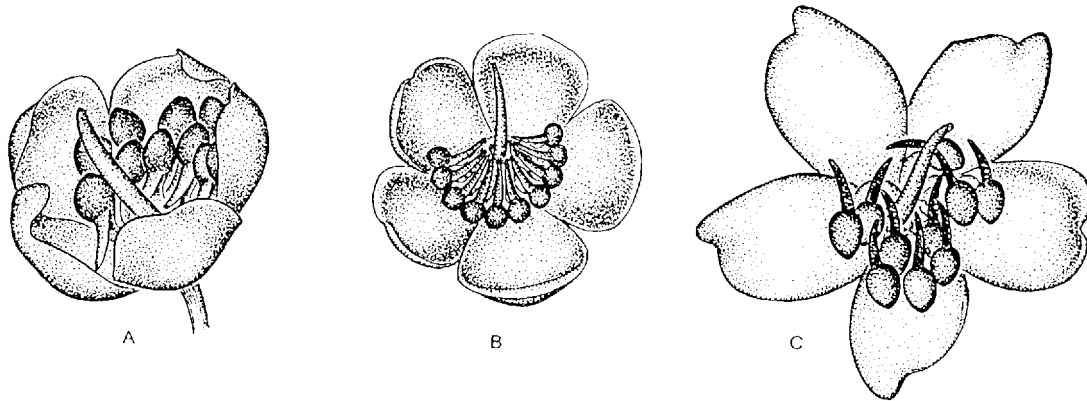
### *Corolla*

Flowers in *Axinaea* often have fleshy, lustrous petals with a waxy look. They are usually concave (cucullate) and asymmetrically bilobed apically. The flowers usually remain half closed even at anthesis though the degree of reflexion of the petals varies (Figure 4: A, B) and only one species, *A. merianiae* has completely reflexed petals at anthesis (Figure 4: C). The petals can be quite varied in color, the most common color being pink or lilac, but white, magenta, red, salmon red, orange, purple-blue and even yellow petals can be found in the genus. The petals are usually darker in color abaxially than adaxially and therefore the large buds always have a more intense color than the flowers at anthesis. This can be due to the fact that the petals in *Axinaea* are not reflexed at anthesis and so the most visible part of the petal is actually the abaxial side.

The petals can be oblong to obovate in shape. The apex is often asymmetrically bilobed but sometimes more or less rounded. Venation can be observed in the petals but this character has not been found to be of any taxonomic significance.

### *Androecium*

The androecium in Melastomataceae can present varied modifications in the number, shape and length of the whorls of stamens, in the absence or presence of connective appendages, in the size and shape of the connective appendage, in the number, size and position of the pores, and in the shape of the anthers. All these have been the source for the delimitation of many of its genera (Cogniaux 1891; Triana 1871; Wurdack 1973, 1980). The androecium in *Axinaea* is composed of two whorls of stamens that are attached to the internal rim of the torus.



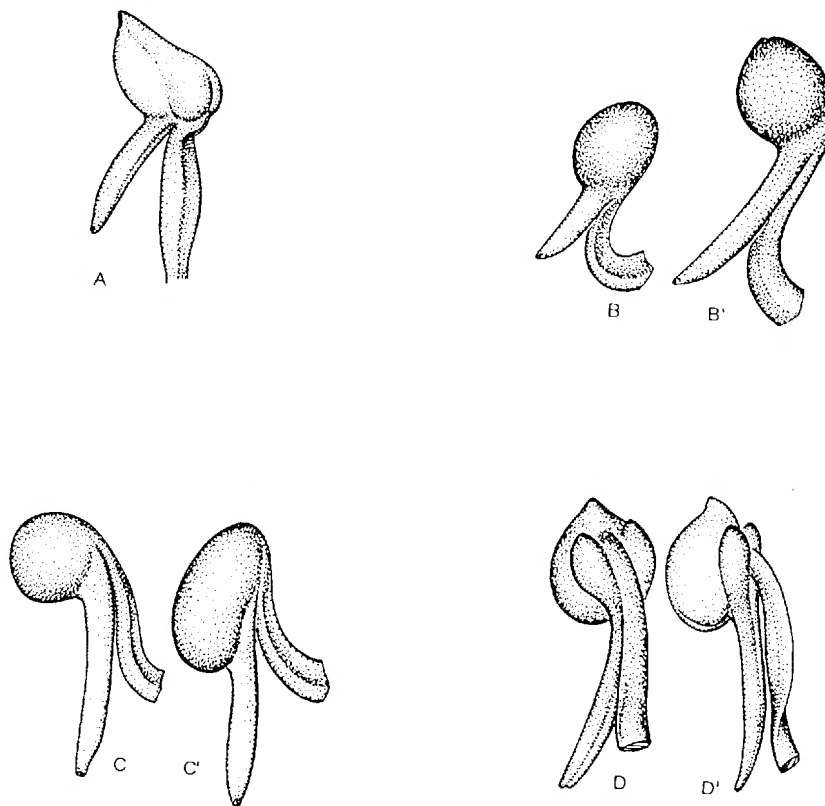
**Figure 4.** Flower types in *Axinaea*. A. Flower at anthesis showing a partly closed corolla of cucullate petals, anisomorphic stamens that have migrated to one side of the flower, and exerted style. B. Flower at anthesis showing a more or less open corolla of cucullate petals, isomorphic stamens that have migrated to one side of the flower, and exerted style. C. Flower at anthesis showing a completely reflexed corolla, anisomorphic stamens that have migrated to one side of the flower, and exerted style.

The morphology of the stamens is characteristic of the genus. In *Axinaea*, the stamens have a flattened, often fleshy filament, a subulate anther with one minute apical or slightly dorsal pore, and an inflated, globular connective appendage that sometimes has a rounded or more or less apiculate base. Commonly, the stamens migrate to the lower part of the flower and rest on the concave petals. The size of the connective appendage is such that it often does not allow for the anther to stand erect. This in turn means that, in most species of *Axinaea*, the anthers rest on the filaments and the connective appendages are actually the most visible part of the androecium. In some species with flowers that open more widely, the stamens are erect and the anthers are positioned in a 90° angle in relation to the filament.

The filaments vary in color from white or cream-colored, through various shades of pink to intense red or magenta. The connective appendages are invariably the most visible part of the androecium and vary in color from cream-colored, various shades of yellow to bright orange or red. The anthers are much less visible than the connective appendages and have often been described in herbarium labels as “a dark appendage.” They vary in color from brown to dark wine-red or dark violet to almost black.

The stamens of the 4-merous species of *Axinaea* have connective appendages that are more ellipsoidal in shape and are acute basally (Figure 5: A) while the stamens of the 5-merous species of the genus have more spherical anther appendages, that can be rounded (Figure 5: B, B') or slightly apiculate (Figure 5: D, D') basally.

The stamens may all be of the same size or, more commonly, the antepetalous stamens are visibly longer than the antesealous ones. In this study some distinctions have been made when referring to the differences in the stamens. Stamens that are similar in size and shape are referred to as being isomorphic. When stamens of one whorl vary only in size in relation to those of the other whorl, they have been referred to as anisomorphic (Figure 5: B, B'). In this case both the filament and the anther size correlate but the size of the connective appendage is usually inversely correlated, meaning that the shorter stamens have actually larger connective appendages. Stamens that in addition to the variation in size, present a variation in the shape of the connective appendage, are referred to as being dimorphic (Figure 5: C, C'). A variation in the intensity of the color both in anthers and connective appendages can also be seen in some anisomorphic and dimorphic stamens but is not a general feature.



**Figure 5.** Stamen types in *Axinaea*. A. Stamen showing the filament, the ellipsoidal connective appendage that is acute at the base, and the anther with a minute slightly dorsal pore. B and B'. Anisomorphic stamens in lateral view, showing the filaments, the spherical connective appendages that are rounded basally, and the anthers with an apical pore each. C and C'. Dimorphic stamens showing the filaments, the spherical or slightly ellipsoidal connective appendages that are rounded basally, and the anthers with an apical pore each. D and D'. Stamen in dorsal and lateral view, showing the filament, the spherical connective appendage that is apiculate basally, and the anthers that are inflated at the base.

On species, *A. lehmannii* has anthers that are inflated at the base, forming two sacs that frame the connective appendage (Figure 5: D, D').

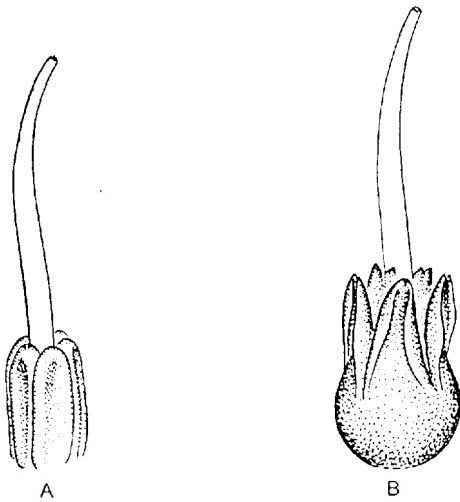
#### *Gynoecium*

The ovary is always free from the walls of the hypanthium and attached to it only at the base. The number of locules corresponds to that of the floral parts so that only 4- and 5-locular ovaries are found in the genus. The ovary is usually more or less costulate and has a lobed apex (Figure 6: A) In *A. weberbaueri* the apex lobes are separated and free (Figure 6: B), later appearing in the mature capsule as hardened extrusions. The style is fleshy, glabrous and often becomes

deflexed at the apex. It continues to grow after anthesis so it is difficult to indicate a specific style length for each species. It varies in color more or less in agreement with the color of the filaments. The stigma is punctiform. Placentation is always axial.

#### Fruits

All *Axinaea* produce dry capsules that dehisce along longitudinal openings (Figure 7). The seeds, as far as known, are always pyramidal or cuneiform in outline. The hypanthium is always persistent and the degree to which the hypanthium covers the mature capsule can be used as a taxonomic character.



**Figure 6.** Ovary types in *Axinaea*. A. Ovary showing the five apical lobes that are not free and barely separated and the style. B. Ovary, showing the free, separated, apical lobes and the style.

### Anatomy

Very little is known about the anatomy of *Axinaea*. The only reference found is the studies made by Welle and Koek-Noorman (1981) on the wood anatomy of Melastomataceae. Two species of *Axinaea*, *A. macrophylla* and *A. nitida*, were included in their study. Due to the fact that the objective of their study was to evaluate the value of wood anatomical characters in order to establish a possible phylogeny of the family, their comments in relation to *Axinaea* are oriented mostly towards this end. Nevertheless, the two species studied presented bands of pseudo-parenchyma composed of fibers, instead of the comparatively constant character found in the rest of the members of the tribe *Merianieae* of a parenchyma arranged in tangential bands.

Within the two species, differences were found in the rays that were heterogeneous in *A. macrophylla* and nearly all homogenous in *A. nitida*.

### Chromosome numbers

The only chromosome counts known for *Axinaea* are those published by Solt and Wurdack (1980). Two specimens of *A. grandifolia* produced chromosome

counts of  $n = 30-31$  and  $n = 31$ , and one specimen of *A. ruizteranii* produced a chromosome count of  $n = 31$ . Some species of *Meriania*, the genus that seems to be most closely related to *Axinaea*, have similar chromosome numbers (*M. grandidens*, *M. macrophylla*, *M. steyermarkii*) but *M. hexamera* has  $n = 23-25$ , *M. leucantha* has  $n = 15-17$  and *M. urceolata* has  $n = 17$ .

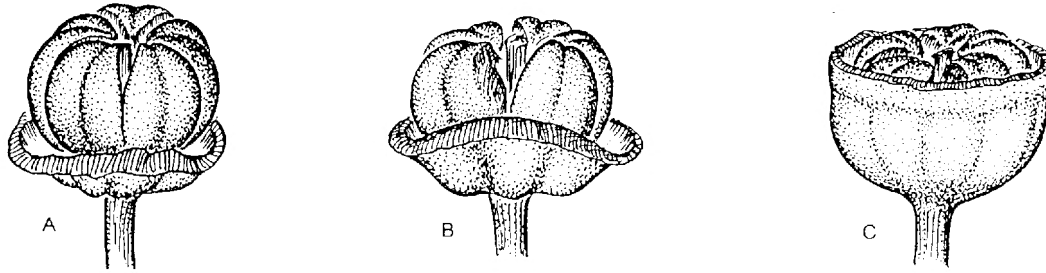
### Species concept

Species are considered as the smallest aggregations of populations that possess either a unique constant character or a unique combination of constant characters (Nixon & Wheeler 1990), which leads to narrowly defined species. Under this definition *A. floribunda*, previously reduced to synonymy by Eves (1936), has been resurrected and eight new species are described. *Axinaea tovarii* Wurdack has been reduced to synonymy under *A. tomentosa*. No sub-specific taxa were described in this study.

### Phylogenetic relationships

The first person to propose an infra-familial classification of the Melastomataceae was José Triana, a Colombian doctor with extensive knowledge of the Melastomataceae both in the field and through work in most of the European herbaria. In 1866, and more extensively in 1871, he proposed the division of the family into two large groups without formal rank, those with indehiscent fruits (berries) and those with capsular fruits. Below these two groups, he created tribes based mainly on geographical separation (Old World *vs.* New World), the presence or absence and position (dorsal or ventral) of connective appendages, and differences in seed shape. Triana placed the genus *Axinaea*, along with nine other genera (*Behuria*, *Huberia*, *Opisthocentra*, *Acanthella*, *Meriania*, *Adelobotrys*, *Graffenrieda*, *Centronia*, and *Calyptrella*), in the tribe *Merianieae*, defined by having a New World distribution, capsular fruits, dorsal connective appendages, and straight seeds.

The first attempt to conduct a phylogenetic analysis of the Melastomataceae (incl. Memecylaceae) using cladistic methods was conducted by Renner



**Figure 7.** Fruit types in *Axinaea*. A. Mature fruit showing the hypanthium leaving the capsule almost completely uncovered. B. Mature fruit showing the hypanthium covering about 1/2 of the capsule. C. Mature fruit showing the hypanthium covering the capsule almost completely.

(1993) based on morphological characters. The study indicated: 1) that the tribe *Merianieae*, with certain modifications, formed a monophyletic group, and 2) that it should be adjusted to encompass all of Triana's genera, with the exception of *Acanthella* and *Opisthocentra*, as well as nine additional genera, mainly from the Guayana Highlands and Brazil, that were undescribed at the time of Triana's publication.

More recently the phylogeny of the family has been analyzed by Clausen and Renner (2001) based on molecular characters. Also this study supported the monophyly of the tribe *Merianieae*, as the three genera sampled (*Adelobotrys*, *Graffenrieda*, and *Meriania*) formed a robust clade. The analysis also indicated that *Merianieae* is in fact a sister group to the *Miconieae*, a large and highly diverse New World tribe that traditionally has been placed far apart from *Merianieae* due to the fact that *Merianieae* have capsular fruits, a character considered to be plesiomorphic in the family, and *Miconieae* have berries, a character considered to be derived. Clausen and Renner's findings have profound implications for the understanding of the evolution of some morphological characters in Melastomataceae, such as, that berries evolved from capsules at least four times within the family and that anther connectives went from dorsally enlarged to basal/ventrally enlarged, giving a whole new perspective to future phylogenetic studies of Melastomataceae.

Ever since Triana's time, *Axinaea* and *Meriania* have been considered closely related genera (Triana 1871; Wurdack 1980) and the two genera are certainly quite similar morphologically to the extent that it is not

possible to assign some species to a genus unless they have mature flowers. But while *Axinaea* species appear to form a monophyletic group, sharing the synapomorphy of a bulbous anther connective appendage, it is more difficult to find a synapomorphy uniting all species of *Meriania*. The connectives in *Meriania* may be prolonged below the thecae or not, have only a dorso-basal spur or sometimes an additional ascending appendage running parallel to the thecae. Some species of *Meriania* have the usual 5-6-lobed calyces and others have calyptrate calyces that rupture irregularly, and the flowers usually have completely reflexed petals. Some species, however, have semi-closed flowers at anthesis similar to those in *Axinaea*. The observed range of variation in essential floral characters may suggest that *Meriania* is in fact not a monophyletic group in its current circumscription. Part of the genus, characterized by connectives with dorso-basal, slightly thickened, spur-like appendages, may form either a sister group to *Axinaea* or a paraphyletic grade in which *Axinaea* forms a nested clade, while other parts of *Meriania* with varying types of ascending appendages in addition to the dorso-basal spur may in fact represent one or more genera that need recognition. As a more complete phylogenetic analysis of the family becomes available it may thus become necessary to adjust of the current generic delimitation within the *Axinaea-Meriania* complex.

Within the genus *Axinaea* phylogenetic relationships remain unknown. Based on morphology some species form groups as reflected in the key, but overall the morphology is insufficient for suggesting a phy-

**Table 1.** List of species of *Axinaea* indicating which ones are new species and their presence in each country from Costa Rica to Bolivia, and in the left column the number of countries in which each species occur.

Species	New Species	Costa Rica	Panama	Venezuela	Colombia	Ecuador	Peru	Bolivia	#
<i>Axinaea affinis</i>				•	•	•			3
<i>Axinaea alata</i>	•							•	1
<i>Axinaea campii</i>	•					•			1
<i>Axinaea colombiana</i>					•				1
<i>Axinaea confusa</i>	•					•	•		2
<i>Axinaea costaricensis</i>		•	•	•					3
<i>Axinaea crassinoda</i>							•		1
<i>Axinaea dentata</i>	•					•			1
<i>Axinaea dependens</i>							•		1
<i>Axinaea disrupta</i>	•					•			1
<i>Axinaea fallax</i>					•				1
<i>Axinaea fernando-cabiesii</i>							•		1
<i>Axinaea flava</i>						•			1
<i>Axinaea floribunda</i>				•	•	•	•		4
<i>Axinaea glandulosa</i>						•	•		2
<i>Axinaea glauca</i>						•			1
<i>Axinaea grandifolia</i>				•	•				2
<i>Axinaea lanceolata</i>							•	•	2
<i>Axinaea lawessonii</i>						•			1
<i>Axinaea lehmannii</i>					•	•			2
<i>Axinaea luteynii</i>	•					•			1
<i>Axinaea macrophylla</i>					•	•			2
<i>Axinaea meriania</i>						•			1
<i>Axinaea mertensioides</i>							•		1
<i>Axinaea minutiflora</i>	•				•				1

<i>Axinaea nitida</i>							•		1	
<i>Axinaea oblongifolia</i>							•	•	2	
<i>Axinaea pauciflora</i>							•		1	
<i>Axinaea pendula</i>	•							•	1	
<i>Axinaea pennellii</i>								•	•	2
<i>Axinaea quitensis</i>							•		1	
<i>Axinaea reginae</i>								•	1	
<i>Axinaea robusta</i>					•				1	
<i>Axinaea ruizteranii</i>				•					1	
<i>Axinaea sclerophylla</i>							•		1	
<i>Axinaea scutigera</i>				•	•	•			3	
<i>Axinaea sessilifolia</i>							•	•	2	
<i>Axinaea sodiroi</i>							•		1	
<i>Axinaea tomentosa</i>								•	1	
<i>Axinaea weberbaueri</i>								•	1	
<i>Axinaea wurdackii</i>								•	1	
	8	1	1	5	10	21	18	3		

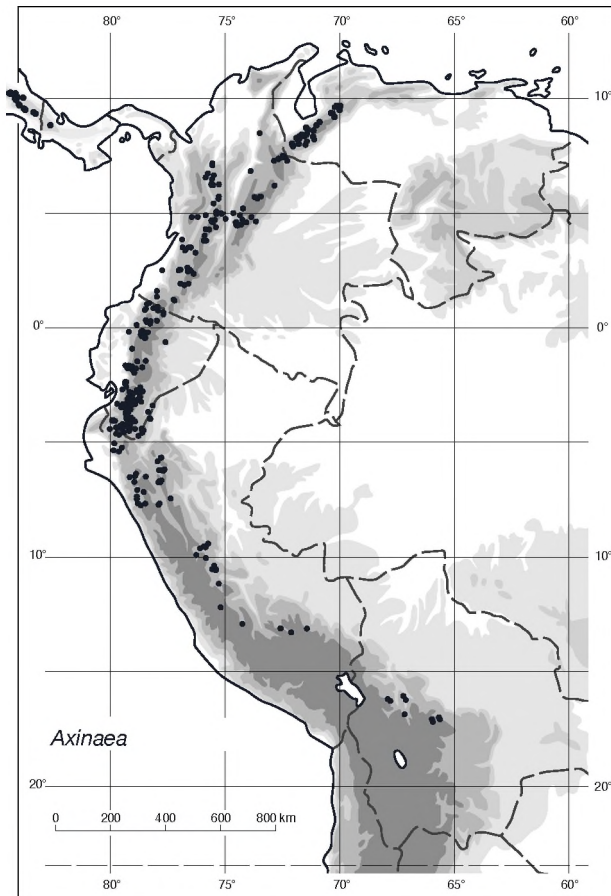
logeny of the genus and molecular data are still not available. The species are therefore arranged alphabetically in the treatment.

## Distribution

*Axinaea* covers a latitudinal range, roughly between 11°N and 18°S (Figure 8). It occupies habitats at 1100–3800 m a.s.l. and most species are found in montane forest. Two species, *A. luteynii* and *A. merianiae*, are found in the drier inter-Andean valleys of Ecuador at altitudes of 3200–3500 m. Of the 41 species recognized in this treatment, only four, *A. affinis*, *A. costaricensis*, *A. floribunda*, and *A. scutigera* are widely distributed both in terms of latitude and in altitude; they range from Ven-

ezuela or Colombia to Ecuador or Peru (Table 1). The rest of the species have narrow distributions and nine of them are known only from the type collection or from a few additional topotypical collections. Twenty-eight species (74%) are endemic to one country, of which two species, *A. grandifolia* and *A. ruizteranii* are endemic to the Venezuelan Andes, four species *A. colombiana*, *A. fallax*, *A. minutiflora* and *A. robusta* are endemic to Colombia, 12 species are endemic to Ecuador, 10 to Peru and one species, *A. alata* is endemic to Bolivia.

No study of the historic biogeography of *Axinaea* has so far been conducted. Nevertheless, evidence from a recent biogeographic study of Melastomataceae in general, coupled with information about the likely phylogenetic position of *Axinaea* as discussed in



**Figure 8.** Distribution of the genus *Axinaea*, based on available herbarium records.

the previous section, provides a certain basis for addressing the questions of the likely origin of the genus and the factors that have determined its current distribution pattern.

The Melastomataceae have traditionally been thought to originate in Gondwanaland (Raven & Axelrod 1974, Gentry 1982, Renner 1993), but recent studies propose otherwise. Using a phylogeny for 91 species in 59 genera, based on gene cpDNA (*rbcL* and *ndhF* genes and *rpl16* intron), Renner *et al.* (2001) proposed a historical biogeography of Melastomataceae using a molecular clock approach. By assigning Melastomataceae fossils of known age to particular nodes in the phylogeny, they were able to calibrate the age of the node and so provide the minimum age of that

clade. They concluded that Melastomataceae most probably originated during the Early Eocene in the tropical belt bordering the northern margin of the Tethys sea (tropical Laurasia) and then spread, during the warmer periods of the Early Eocene, into North America (via Beringia and/or the North Atlantic land bridge) and South East Asia. The earliest fossils of Melastomataceae leaves date from the Early Eocene and Early Middle Eocene (53 Mya) and were found in North America. Both leaf fossils show the acrodromous venation typical of Melastomataceae, numerous densely spaced pairs of secondary veins running in parallel rows, weakly developed drip tips, entire margins, and are of medium size ( $5-9 \times 2.5-5$  cm). These characters are similar to those present in current species of *Meriania/Miconia*. A spread from North America into South America sometime in the Oligocene is suggested by a *Meriania*-like leaf fossil found in northern Colombia dating from the Oligocene (~30 Mya) (Huertas 1977).

The scenario that emerges from these data is that *Merianieae* ancestors enter South America ~30 Mya. It is most probable that *Axinaea* evolution is closely linked to the formation of the Andes, as indicated by the distribution of this genus at 1100–3800 m of elevation, in contrast to the rest of the *Merianieae* that have much broader altitudinal distributions. Such a scenario fits with *Axinaea* being an advanced clade within the *Merianieae*, adapted to high elevations, and possibly nested within *Meriania* itself. Additionally, the high endemism of the genus could be explained by high levels of isolation induced partly by repeated fragmentation of its mountain forest habitat during the Pleistocene climatic fluctuations (Hooghiemstra 1989).

## Reproductive ecology

All species of *Axinaea* are hermaphroditic and reproduce by seeds. Vegetative reproduction has never been observed and cut down trees or treelets were not seen to sprout back. According to our field experience plantlets and young plants are few in most natural populations of *Axinaea*. The seeds, being minute and



light, disperse by wind after the dehiscence of the capsules. Wurdack (pers. comm.) commented on the existence of hybrids in the *Axinaea* populations of northern Peru, but the issue has never been studied in any detail.

So far no studies of the pollination biology of *Axinaea* have been carried out, and speculations concerning this topic and its possible importance for understanding the evolutionary history of the genus must therefore be based on circumstantial evidence. The most widespread pollination system in the Melastomataceae involves the extraction of pollen from poricidal anthers by the vibratory movements of female bees (buzz pollination). This type of pollination occurs in an estimated 98% of the species in the family (Renner 1989). Other mechanisms include pollination by hummingbirds, bats or rodents, so far observed in about 60 species of *Meriania*, *Centronia*, *Tibouchina*, *Brachyotum*, *Miconia*, *Huilaea*, *Chalybea* and *Blakea*.

Non-buzz pollination appears to be almost exclusively associated with nectar producing flowers. Nectar in Melastomataceae is secreted by the filament from a slit-like structure located below the geniculum on the adaxial side of the filament (Renner 1989, Stein & Tobe 1989). Large drops of nectar suspended by adjacent filaments and sliding to the tips of the anthers have been seen in the nectariferous genus *Brachyotum* (Cotton personal observation) pollinated by hummingbirds (Renner 1989, Stein & Tobe 1989). In addition to being nectar-producing, the flowers of non-buzz pollinated members of the family often display a number of other features that may be seen as adaptations to visits by pollinators who are seeking nectar as a reward. The anthers of these species tend to have larger pores, are slightly stiffened at the base, and instead of necessitating the vibration to extrude the pollen, a slight pressure at the base of the anther emits a cloud of pollen, earning them the name of "bellow" anthers (Lagerheim 1899, cited in Renner 1989). In addition to the modifications in the anthers, the flowers of the nectar producing melastomes are usually inclined or pendent, with petals that do not spread at anthesis but remain more or less closed almost like in

bud, and in the case of the bird pollinated ones, usually dark red, deep purple, or bluish to almost black in color.

The morphological characters found in *Axinaea* clearly fit the non-buzz pollination syndrome. A similar conclusion was reached by Renner (1989) who mentioned that, based on their character syndromes, several species of *Meriania*, *Axinaea*, *Centronia* and *Tibouchina* should be expected to have nectar-producing flowers. Even though no observations have been made of pollinators for *Axinaea*, it seems quite possible that their relatively large, pendulous, semi-closed, and often dark pink or red flowers are bird or bumble-bee pollinated. Since it has been proposed by Cruden (1972) that under adverse climatic conditions the homoeothermic birds and mammals may be more reliable pollinators than bees, and these animals have larger energy requirements at high altitudes due to their larger size and to maintain body temperature, it would not be surprising to find, in an Andean-centered genus, a modification from the traditional buzz-pollination system, where the reward for the pollinator is exclusively pollen, to a system that includes nectar (and perhaps also other energy rich food objects - see discussion below), as a reward.

Even though it is not yet clear whether the great diversity of connective appendages in Melastomataceae have a function in the pollination mechanism or are just visual enhancements of the flowers (Renner 1989), we find the connective appendages in *Axinaea* intriguing. These bulbous, often glossy structures are usually in sharp contrast to the color of the corolla and are such a striking part of the flower that it is difficult to avoid thinking that they must somehow be involved in the pollination mechanism of the genus. We have often observed in the field that the connective appendages, and sometimes even the entire anthers, have been partially or completely eaten in many flowers in *Axinaea*. This could suggest that the appendages serves as a type of food-body reward for visiting insects, a syndrome often associated with pollination by beetles (Endress 1994). Studies of the composition of the anther connectives and observa-

tions in the field would be needed to elucidate the adaptive role, if any, of these structures in the pollination mechanism of *Axinaea* and whether the evolution of these unique structures is linked to the increased energy needs of pollinating insects at high elevations.

A recent M.Sc. thesis by Agnes Dellinger from Vienna University on the Floral Structure and Pollination of *Axinaea*, has revealed several interesting details based on field work. The main finding of her investigations, were that instead of a nectar reward, the pollination mechanism of *Axinaea* involved floral food bodies in combination with bird pollination. She also found that a number of tanagers and flower piercers were attracted by the outstanding bulbous connective appendages in the flowers. Nevertheless, these appendages were also an integral part of a complex pollination mechanism which Dellinger called a “bellows-mechanism” in addition to their function as attractants and food reward for the pollinating birds (Dellinger, 2013).

### Conservation status

Many species of *Axinaea* grow in populations consisting of only few individuals and at least one third of the species are narrowly endemic. This situation, coupled with the fact that most of them grow in areas of the Andes which are seriously threatened by fire, logging, or clearing for agricultural purposes, makes many species of *Axinaea* severely threatened by extinction. Two species, *A. robusta* from Colombia, and *A. sodiroi* from Ecuador are only known from the type collections made in 1905 and 1845 respectively. *Axinaea sodiroi* was collected on the Pichincha mountain and by the high level of destruction of the forests of this mountain it could be guessed that the species may have become extinct. It is impossible to make further commentaries about *A. robusta* as the precise locality of collection of this species is impossible to determine.

### Ethnobotany

No special uses have been reported for species of *Axinaea*. They are sometimes used as wood for construction or fire-wood and many farmers do not fell *Axinaea* trees maybe because they appreciate the beauty of their flowers. Some common names reported on herbarium labels for species of *Axinaea* are: *laurelito*, *mortiño*, *mortiño negro* (from Venezuela); *tuno rojo*, *manzanillo* (from Colombia); *palo blanco*, *palo rosa*, *clavelillo*, *cebolleta*, *zarcillo*, *guishle*, *colca*, *guala blanca* (from Ecuador); *torno azul*, *palo blanco*, *naranjillo* (from Peru). No common names have been reported for species of *Axinaea* growing in Bolivia.

### Systematic treatment

#### Generic description

*Axinaea* Ruiz & Pav., Fl. Peruv. Prodr. 68, pl. XII, 1794. – Lectotype: *A. lanceolata* Ruiz & Pav. (Eves 1936). *Chastenea* DC., Prodr. 3: 102. 1828. – Type: *C. meriania* DC.

Trees or shrubs, 0.5–30 m tall; branchlets quadrangular to terete, occasionally winged, glabrous, more or less puberulent or densely pubescent; stipuliform flaps present as a coriaceous flap or a hardened ridge, reduced to a line across the nodes or absent. Leaves usually petiolate, rarely sessile; lamina most commonly elliptic or elliptic-ovate, but also oblong, oblong-elliptic, obovate or ovate, adaxially flat, bullate or subplicate, usually glabrous, abaxially often puberulent to densely pubescent but occasionally glabrous; apex rounded, acute or acuminate; base cuneate, rounded, truncate or cordate, often auriculate, the auricles usually revolute; scutum present, well developed and knob-shaped, incipient and v-shaped or absent; venation 3-, 5- or 7-nerved or plinerved. Inflorescence a few- to many-flowered terminal thyrse often subtended by a pair of leaf-like bracts; pedicels 2–13 mm, often slender. Flowers 4- or 5-merous, diplostemonous, 1–3 cm long; hypanthium terete, cyathiform or cupuliform, 1–10 mm long; calyx lobed or

truncate, external teeth often minute but occasionally well developed, hardened and projecting 1–2 mm; corolla usually in shades of pink, lilac, purple, or red, sometimes white, rarely yellow; petals oblong or oblong-obovate, concave, often fleshy, apex usually asymmetrically bilobed, most commonly not completely reflexed at anthesis; stamens isomorphic or anisomorphic; connective appendage inflated, spheri-

cal or ellipsoidal; anthers subulate with a small apical or slightly dorsal pore. Fruit a capsule; seeds numerous, cuneiform or pyramidal.

A Neotropical genus of 39 species that grow at medium to high elevations in the mountains of Central and South America from Costa Rica to Bolivia, with the greatest concentration of species in southern Ecuador and northern Peru. — Figure 8.

Key to the species

(Parentheses indicate alternative couplets where a species is keyed)

- 1a. Flowers 4-merous; connective appendage elongated, ellipsoid, basally acute . . . . . 2
  - 2a. Stipuliform flaps absent . . . . . 4. *A. colombiana*
  - 2b. Stipuliform flaps present at all nodes, well developed, coriaceous, 1–10 mm long . . . . . 3
    - 3a. Leaf venation basal; leaf base cordate, auricles 1–1.5 cm long; plants densely pubescent, hairs 1–2 mm long . . . . . 7. *A. crassinoda*
    - 3b. Leaf venation short-plinerved or plinerved; leaf base cuneate or rounded, not auriculate; plants sparsely puberulent or dense furfuraceous, hairs under 1 mm . . . . . 4
      - 4a. Leaf venation 7-plinerved . . . . . 28. *A. pendula*
      - 4b. Leaf venation 5-plinerved or shortly 5-plinerved . . . . . 5
        - 5a. Inner pair of primary nerves diverging 1–3 mm above the leaf base . . . 32. *A. reginae*
        - 5b. Inner pair of primary nerves diverging 5–25 mm above the leaf base . . . . . 6
          - 6a. Leaves  $\leq 7 \times 3$  cm; inflorescence 5–10 cm long . . . . . 23. *A. mertensioides*
          - 6b. Leaves  $9\text{--}18 \times 2\text{--}7$  cm; inflorescences 12–75 cm long . . . . . 7
            - 7a. Plants furfuraceous when young, glabrescent with age; inflorescence 12–35 cm long; petals coral-red or pink . . . . 9. *A. dependens*
            - 7b. Plants densely furfuraceous throughout; inflorescence 50–75 cm long; petals magenta outside in bud, turning purple-blue . . . . . 12. *A. fernando-cabiesii*
  - 1b. Flowers 5-merous; connective appendage spherical, not elongated, basally apiculate or rounded . . . . . 8
    - 8a. Branchlets markedly quadrangular, with rigid-coriaceous wings 1–2 mm wide . . . . . 9
      - 9a. Scutum present, well developed, knob-shaped, bilobed; ovary apex lobes free and separated, becoming hard and projecting in the mature capsule; nerves adaxially and abaxially glabrous . . . . . 2. *A. alata*
      - 9b. Scutum absent or, if present, poorly developed and v-shaped; ovary apex lobes not free, not distinguishable in the mature capsule; nerves dense to moderately furfuraceous abaxially (see also 52) . . . . . 17. *A. lanceolata*
    - 8b. Branchlets quadrangular, subquadrangular or terete, not winged . . . . . 10
      - 10a. Scutum present, knob- or v-shaped, though sometimes absent in the leaf-like bracts of the inflorescence . . . . . 11
        - 11a. Stipuliform flaps present across the nodes, either as a coriaceous flap 1–3 mm long, or as a woody ridge, raised 1–2 mm . . . . . 12

- 12a. Stipuliform flaps coriaceous, 1–3 mm long; nodes not thickened; hypanthium 1.5–3 mm long; Costa Rica and Venezuela . . . . . 6. *A. costaricensis*
- 12b. Stipuliform flaps woody, forming a ridge across the nodes, raised 1–2 mm; nodes thickened; hypanthium 3–4 mm long; Colombia . . . . . 32. *A. robusta*
- 11b. Stipuliform flaps absent or reduced to a line across the nodes . . . . . 13
- 13a. Lamina base cordate or shallowly cordate, the auricles not revolute. . . . . 14
- 14a. Ovary lobes free, separated, visible as prolongations at the apex of the ovary . . . . . 39. *A. weberbaueri*
- 14b. Ovary lobes not separated, not prolonged . . . . . 15
- 15a. Lamina subplicate, only the primary nerves sunken adaxially; anthers inflated at the base; Colombia . . . . . 19. *A. lehmannii*
- 15b. Lamina bullate, all venation sunken adaxially and prominent abaxially; anthers not inflated at the base; Ecuador . . . . . 37. *A. sodiroi*
- 13b. Lamina base, in appearance, cuneate, rounded or truncate, in truth the base auriculate but the auricles always revolute . . . . . 16
- 16a. Scutum v-shaped, incipient, often absent in the leaf-like bracts that accompany the inflorescence . . . . . 17
- 17a. Plants glabrous, though the young shoots may be covered by an early caducous a furfuraceous indument; lamina with dentate or denticulate margins, teeth 1–2 mm long; corolla deep red, purple-pink or dark pink; hypanthium covering 1/3 to 1/2 of the mature capsule . . . . . 25. *A. nitida*
- 17b. Plants moderately to densely furfuraceous; lamina with entire or denticulate margins, the teeth, when present, minute; corolla white or light pink, darker abaxially; hypanthium covering 1/2 to 2/3 of the mature capsule (see also 29, 50) . . . . . 13. *A. floribunda*
- 16b. Scutum knob-shaped, well developed, usually present also in the leaf-like bracts that accompany the inflorescence . . . . . 16
- 18a. Plants glabrous throughout or with occasional scattered hairs on the nerves abaxially . . . . . 19
- 19a. Lamina base with auricles 4–8 mm long, auricles with entire margins; lamina apex long acuminate, acumen 1–1.5 cm long; petals purple or pink; Colombia and Ecuador 35. *A. scutigera*
- 19b. Lamina base with auricles 1–3 mm long, auricles with entire or dentate-undulate margins; lamina apex acute; petals coral-red, salmon pink or dark pink; Venezuela and Colombia (see also 21) . . . . . 16. *A. grandifolia*
- 18b. Plants densely to moderately pubescent, puberulent or furfuraceous throughout, the hairs often caducous with age, but persistent abaxially on the lamina and nerves . . . . . 20
- 20a. Plants sparsely puberulent or furfuraceous, the indument usually present only along the leaf venation abaxially . . . . 21
- 21a. Flowers 2 cm long, petals purple; Peru . . 29. *A. pennellii*
- 21b. Flowers 1.2–1.5 cm long, petals coral-red, salmon

- pink or dark pink; Venezuela and  
Colombia (see also 19) . . . . . 16. *A. grandifolia*
- 20b. Plants moderately to densely pubescent, the indument  
present on the whole abaxial surface of the leaf . . . . . 22
- 22a. Inflorescence a pendulous, moderate to densely-  
flowered, terminal thyrse, subtended by a pair of  
leaf-like bracts, occasionally 1 or 2 additional pairs  
of smaller bracts present higher up in the  
inflorescence . . . . . 23
- 23a. Lamina moderately pubescent abaxially, the  
surface of the lamina visible between the hairs . . . . . 22
- 24a. Flowers 2 cm long; corolla light pink or  
white . . . . . 14. *A. glandulosa*
- 24b. Flowers 1.2–1.5 cm long; corolla pink,  
lavender or lilac . . . . . 5. *A. confusa*
- 23b. Lamina densely pubescent abaxially, the  
surface of the lamina completely covered by  
the pubescence . . . . . 38. *A. tomentosa*
- 22b. Inflorescence a synflorescence of several orders of  
few to moderately flowered pendulous thyrses, each  
subtended by a pair of leaf-like bracts; petals lilac to  
dark red- violet; Venezuela . . . . . 33. *A. ruizteranii*
- 10b. Scutum absent . . . . . 25
- 25a. Leaves sessile, the base of the lamina clasping the stem . . . . . 36. *A. sessilifolia*
- 25b. Leaves petiolate . . . . . 26
- 26a. Leaves 3-nerved . . . . . 27
- 27a. Lamina densely pubescent abaxially, the surface of the lamina completely  
covered by the pubescence; petals yellow . . . . . 12. *A. flava*
- 27b. Lamina moderately pubescent to glabrous abaxially, the surface of the  
lamina visible between the hairs . . . . . 28
- 28a. Lamina moderately to sparsely puberulent abaxially . . . . . 29
- 29a. Indument formed of lepidote or arachnoid hairs;  
Ecuador . . . . . 22. *A. merianiae*
- 29b. Indument formed of minute, dendritic or barbellate hairs . . . . . 30
- 30a. Inflorescences many-branched and densely flowered,  
more than 30 flowers per inflorescence  
(see also 17, 49) . . . . . 13. *A. floribunda*
- 30b. Inflorescence few-branched and few to moderately  
flowered . . . . . 31
- 31a. Leaves rigid, erect; petiole 0.5–1 cm long;  
main nerves sunken adaxially, prominent  
abaxial (see also 35) . . . . . 10. *A. disrupta*
- 31b. Leaves not rigid, spreading; petiole 1–4 cm long;  
main nerves not sunken adaxially (see also 34, 44,

- 53) ..... 1. *A. affinis*
- 28b. Lamina glabrous abaxially ..... 32
- 32a. Leaves basally nerved or short-plinerved, with the inner pair of primaries diverging from the main nerve at most 2 mm above the base of the lamina ..... 33
- 33a. Leaf margins dentate; teeth 1-2 mm long, hook-shaped ..... 18. *A. lawessonii*
- 33b. Leaf margins entire or shallowly denticulate ..... 34
- 34a. Leaves obovate or elliptic-obovate ..... 35
- 35a. Leaves elliptic-obovate, coriaceous, rigid, erect, margins entire or at most with a few minute teeth distally; main nerves sunken adaxially, prominent abaxially, secondary venation indistinct (see also 31) ... 10. *A. disrupta*
- 35b. Leaves obovate or elliptic-obovate, subcoriaceous, not rigid, not erect, margins denticulate distally; main nerves not sunken adaxially, secondary venation visibly reticulate (see also 48) ..... 20. *A. luteynii*
- 34b. Leaves oblong-elliptic to elliptic (see also 31, 44, 53) ..... 1. *A. affinis*
- 32b. Leaves plinerved, the inner pair of primaries diverging from the main nerve 3-25 mm above the base of the lamina ..... 26. *A. oblongifolia*
- 26b. Leaves 5-7-nerved ..... 36
- 36a. Leaf venation plinerved or shortly plinerved ..... 35
- 37a. External calyx teeth well developed, projecting, 1-2 mm long ..... 15. *A. glauca*
- 37b. External calyx teeth absent or inconspicuous, not projecting ..... 38
- 38a. Lamina glabrous abaxially ..... 39
- 39a. Leaf venation markedly plinerved, the inner pair of primaries diverging from the main nerve 15-35 mm above the base of the lamina ..... 30. *A. wurdackii*
- 39b. Leaf venation shortly plinerved, the inner pair of primaries diverging from the main nerve 1-3 mm above the base of the lamina (see also 48) ..... 31. *A. quitensis*
- 38b. Lamina sparsely to densely pubescent abaxially ..... 40
- 40a. Plants with moderate to dense, persistent pubescence, present mostly on the branchlets, lamina abaxially, pedicels and hypanthia; hairs dendritic, pinoid or barbellate, not squamose or arachnoid ..... 41
- 41a. Leaves rigid, often bullate, elliptic, elliptic-ovate or elliptic-obovate; flowers 1.5-3 cm long; hypanthium 3-10 mm long; Ecuador ..... 42

- 42a. Petiole 0.5-1 cm long; leaves erect;  
hypanthium 3-4 mm long  
(see also 49) . . . . . 27. *A. pauciflora*
- 42b. Petiole 1.5-3 cm long; leaves spreading;  
hypanthium 6-10 mm long . . . . 34. *A. sclerophylla*
- 41b. Leaves not rigid, not bullate, oblong or elliptic-  
oblong; flowers 1-1.5 cm long; hypanthium 1-2 mm  
long; Colombia (see also 51) . . . . . 24. *A. minutiflora*
- 40b. Plants sparsely puberulent, the indument composed of  
scattered dendritic, pinoid, squamose or arachnoid  
hairs . . . . . 43
- 43a. Indument squamose or arachnoid; base of the lamina  
attenuate or decurrent, not auriculate, revolute;  
stipuliform flaps present as a hardened ridge  
across the nodes, 0.5-1 mm long . . . . . 3. *A. campii*
- 43b. Indument dendritic or pinoid; base of the lamina  
cuneate or rounded, auriculate, the auricles revolute;  
stipuliform flaps absent, only a line visible between  
the nodes . . . . . 44
- 44a. Leaves oblong to oblong-elliptic,  
2-5 × 1.3-2.5 cm; outer pair of primaries  
faint (see also 31, 34, 53) . . . . . 1. *A. affinis*
- 44b. Leaves elliptic to elliptic-ovate, 4-15 × 2.5-7.5  
cm; outer pair of primaries as visible as the  
inner pair (see also 53) . . . . . 21. *A. macrophylla*
- 36b. Leaf venation basal . . . . . 45
- 45a. External calyx teeth visible, hard, pubescent or not, projecting  
1-2 mm . . . . . 46
- 46a. Lamina abaxially densely pubescent, the surface completely  
covered by the indument; calyx teeth projecting 1 mm, densely  
covered with trichomes . . . . . 11. *A. fallax*
- 46b. Lamina abaxially moderately pubescent, the surface clearly  
visible between the indument; calyx teeth projecting about 2  
mm, glabrous . . . . . 8. *A. dentata*
- 45b. External calyx teeth absent or inconspicuous, not projecting . . . . . 47
- 47a. Leaves obovate or elliptic-obovate; lamina base attenuate,  
not auriculate . . . . . 48
- 48a. Stipuliform flaps reduced to a faint line across the nodes;  
flowers 2-2.5 cm long; calyx limb flaring; petals white  
with magenta (see also 35) . . . . . 20. *A. luteynii*
- 48b. Stipuliform flaps present as a hardened ridge across the  
nodes, raised 0.5-1 mm; flowers 1.4-1.8 cm long; calyx  
limb not flaring; petals light pink, lilac or white  
(see also 39) . . . . . 21. *A. quitensis*

- 47b. Leaves elliptic, elliptic-ovate, ovate, oblong, or oblong-elliptic . . . . . 49
- 49a. Leaves rigid, erect, occasionally bullate; petioles 0.5-1 cm long (see also 42) . . . . . 27. *A. pauciflora*
- 49b. Leaves not rigid, spreading, not bullate; petioles 1.5-4 cm long . . . . . 50
- 50a. Inflorescence many-flowered (>25) (see also 17, 30) . . . . . 13. *A. floribunda*
- 50b. Inflorescence moderate to few flowered (<20) . . . . . 51
- 51a. Flowers at most 1.5 cm long; leaves oblong or oblong-elliptic; hypanthium and pedicels moderately to densely pubescent (see also 41) . . . . . 24. *A. minutiflora*
- 51b. Flowers 1.5-2 cm long; leaves elliptic or elliptic-ovate; hypanthium and pedicels glabrous or sparsely puberulent . . . . . 52
- 52a. Leaf margins dentate; teeth 1 mm long; Peru and Bolivia (see also 7) . . . . . 17. *A. lanceolata*
- 52b. Leaf margins entire or shallowly denticulate distally; Venezuela, Colombia and Ecuador . . . . . 53
- 53a. Leaves 2-5 × 1.3-3 cm (see also 31, 34, 44) . . . . . 1. *A. affinis*
- 53b. Leaves 5-11(-15) × 2.5-5(-7.5) cm (see also 44) . . . . . 21. *A. macrophylla*

### Species descriptions

1. *Axinaea affinis* (Naudin) Cogn. in A. DC., Monogr. phan. 7: 449. 1891. — *Chastenea affinis* Naudin, Ann. Sci. Nat. Bot., Sér. 3, 18: 120. 1852. — Type: Venezuela. Trujillo, Agua de Obispo, 2000-2500 m, Aug 1846, *Funck & Schlim 737* (Lectotype: G! [Barbey-Boissier Herb., G Herb.# 8817/1], here designated; isotypes: BR!, BM!, F! [fragment], G [Delessert Herb., n.v.], W!; photo of the G isotype: GH!).

**Shrub or tree**, 1-10(-15)m tall; *branchlets* subquadrate to terete, glabrous to sparsely puberulent; *stipuliform flaps* present as a woody ridge, raised ca 0.5 mm or reduced to a line across the nodes. **Leaves** petiolate; *petiole* 1-4 cm long; *lamina* oblong-elliptic to ellip-

tic, 2-5 × 1.3-3 cm, coriaceous, adaxially glabrous except when young, often lustrous, abaxially glabrous or sparsely puberulent when young, hairs dendritic, short, densely branched, occasionally sparsely gland-dotted with minute orange glands; *apex* broadly acute to shortly acuminate; *base* cuneate or rounded, auriculate; *auricles* minute, less than 1 mm long, revolute, with entire margins; *scutum* absent; *margins* entire or denticulate distally; *venation* 3(-5)-nerved or shortly 3-plinerved, excluding the tenuous inframarginal nerves that run ca 1 mm from the margin, the inner pair of primaries diverging from the main nerve at most 3 mm above the base of the lamina, adaxially glabrous, abaxially glabrous or sparsely puberulent; *secondary nerves* faint, parallel, 1-2 mm apart. **Inflorescence** a pendulous thyrses, 3-25-flowered, terminal, 5-10 cm long, often subtended by a pair of bracts sim-

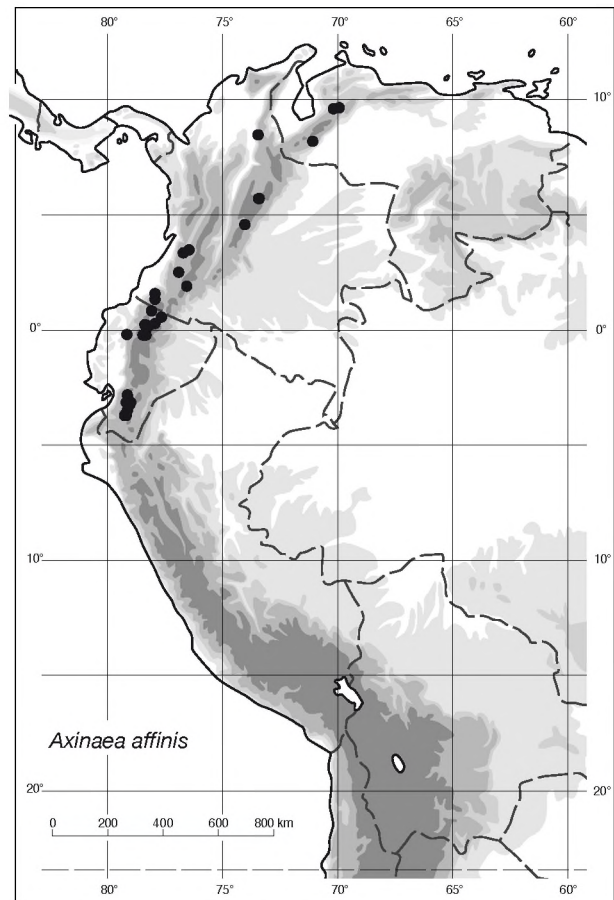


ilar to the leaves but smaller; *pedicels* 4–8 mm long, glabrous. **Flowers** 5-merous, 1.5–2.5 cm long; *hypanthium* cyathiform, 3–5 mm long; *calyx* ca 1 mm long, often flared, obscurely 5-lobed or truncate, external teeth absent or inconspicuous; *petals* pale lilac or pale pink, oblong-obovate, 15–18 × 10–12 cm, apex slightly asymmetric; *stamens* anisomorphic; *filaments* complanate, 8–9 mm long, in the longer stamens, 5–6 mm long in the shorter ones; *connective appendage* spherical, 2 × 2 × 2 mm, rounded or slightly apiculate basally, ochre-brown; *anthers* 5 mm or 7 mm long with one small dorsal pore, dark brown or dark violet; *ovary* oblong, costulate, apex 5-lobed, 5 celled; *style* 15–20 mm long, curved at the apex. **Fruit** a 5-lobed capsule, the hypanthium covering at least 3/4 of the mature capsule; *seeds* cuneiform.

*Axinaea affinis* is distributed in the Andes of Venezuela, Colombia and Ecuador, where it grows at elevations of 2500–3500 m. – Figure 9.

**Additional specimens examined – VENEZUELA:**

**Lara:** close to Las Sabanetas, above Humocaró Bajo, 2600–2800 m, 6 Feb 1944, *Steyermark 55363* (F, NY, VEN). **Mérida:** Páramo de Piñango, 2800 m, 25 May 1944, *Badillo 961* (VEN); crest of La Vagabunda, between El Morro and Aricagua, 2800–1850 m, 11 Oct 1973, *Ruíz-Terán & López-Figueiras 9391* (F, MO, NY). **COLOMBIA:** **Boyacá:** road Arcabuco-Villa de Leiva, 12 Oct 1966, *García-Barriga 18780* (GH); Santuario de Iguaque, 12 km N of Villa de Leiva, 2960 m, 9 Nov 1979, *Melampy 724, 725* (US). **Cauca:** Páramo de Las Papas, between Boquerón and La Hoyola, 3200–3510 m, 7–27 Sep 1958, *Idrobo et al. 3501* (NY). **Cundinamarca:** Bogotá, páramos on road to Calera, 30 May 1926, *Woronow & Juzupczuk 5084* (NY). **Norte de Santander:** Ocaña, Páramos de San Pedro, 3400–3500 m, Jan 1851, *Schlim 304* (BR, G, F, K). **Valle:** Western Cordillera, Los Farallones, Quebrada del Ratón, Mina El Diamante, 2950–3000 m, 29–30 Jul 1946, *Cuatrecasas 21772* (F, NY); El Tambo, Munchique, 3000 m, 9 Nov 1936, *von Sneidern 1194* (NY, S). **ECUADOR:** **Azuay:** Cuenca, Hda. Yanasacha,



**Figure 9.** Distribution of *Axinaea affinis*.

3000–3200 m, 15 Jul 1978, *Boeke & Jaramillo 2436A* (AAU, K, NY); road to Loja, turnoff towards Yanasacha, 15 Jul 1978, *Jaramillo & Boeke 325* (AAU); Cerro Yanasacha, SW of Panamericana Sur, between Baños and Control de Cumbe, ca 20 km from Cuenca, 2600–3000 m, 1 Sep 1984, *Jaramillo 7162* (AAU, MO); Cuenca, S of Cumbe on PanAm Hwy. Pass La Tinajilla, 2700–3150 m, 4 Oct 1995, *Weigend & Horn 3850* (F). **Imbabura:** Eastern Cordillera, Angochagua, 2500–3100 m, 26 Nov 1949, *Acosta-Solís 14607* (F); road Nueva América–Palmira–Mariano Acosta, 3300–3500 m, 30 Dec 1979, *Jaramillo et al. 1735* (AAU); 31 km S of centre of Cuenca on road to Loja, 3000 m, 15 Aug 1996, 3°08'S, 79°2'W, *Gwilym Lewis 2489* (AAU, K, LOJA, NY); Otavalo Cantón, at San Alberto, 3100 m, 29–30 Jun 1989,

0°12'N, 78°22'W, *Morán et al. 16* (AAU, MO specimen of this collection erroneously annotated as *Axinaea quitensis*); Cantón Otavalo, Parroquia San Luis de Quichincha, San Alberto, 3100 m, 29-30 Jun 1989, 0°12'S, 78°22'W, *Morán et al. 17* (AAU), same loc, 2700-2800 m, 21 Oct 1989, *Morán & Paisano 104* (AAU); close to Mariano Acosta, 2950 m, 1-3 Nov 1986, *Ulloa 283* (AAU, F, LOJA, NY, S). **Loja:** Loma de Oro, 10 km S of Saraguro, 3100 m, 24 Sep 1982, 3°40'S, 79°17'W, *Balslev & Steere 3207* (AAU, GH, NY); ca km 5 on road leading to Fierro Urco from Pichig, SSW of Saraguro, 3100-3200 m, 12 Feb 1989, 3°42'S, 79°18'W, *Ollgaard & Madsen 90476* (AAU); San Lucas, Cerro Acacana, 2800 m, 17 Dec 1985, 3°41'14"S, 79°14'51"W, *Vivar & Poma 2634* (AAU, LOJA).

*Axinaea affinis* is very similar to *A. merianiae* but *A. affinis* has the leaves lustrous adaxially (*vs.* leaves matte) and the plants are glabrous or sparsely puberulent when young with dendritic hairs (*vs.* moderately to sparsely pubescent with lepidote hairs). Orange gland dots (lacking in *A. merianiae*) are also present on some leaves abaxially but can only be seen under magnification. The collections made in Azuay by Boeke and Jaramillo, and Weigend have larger stipuliform flaps than the rest of the collections.

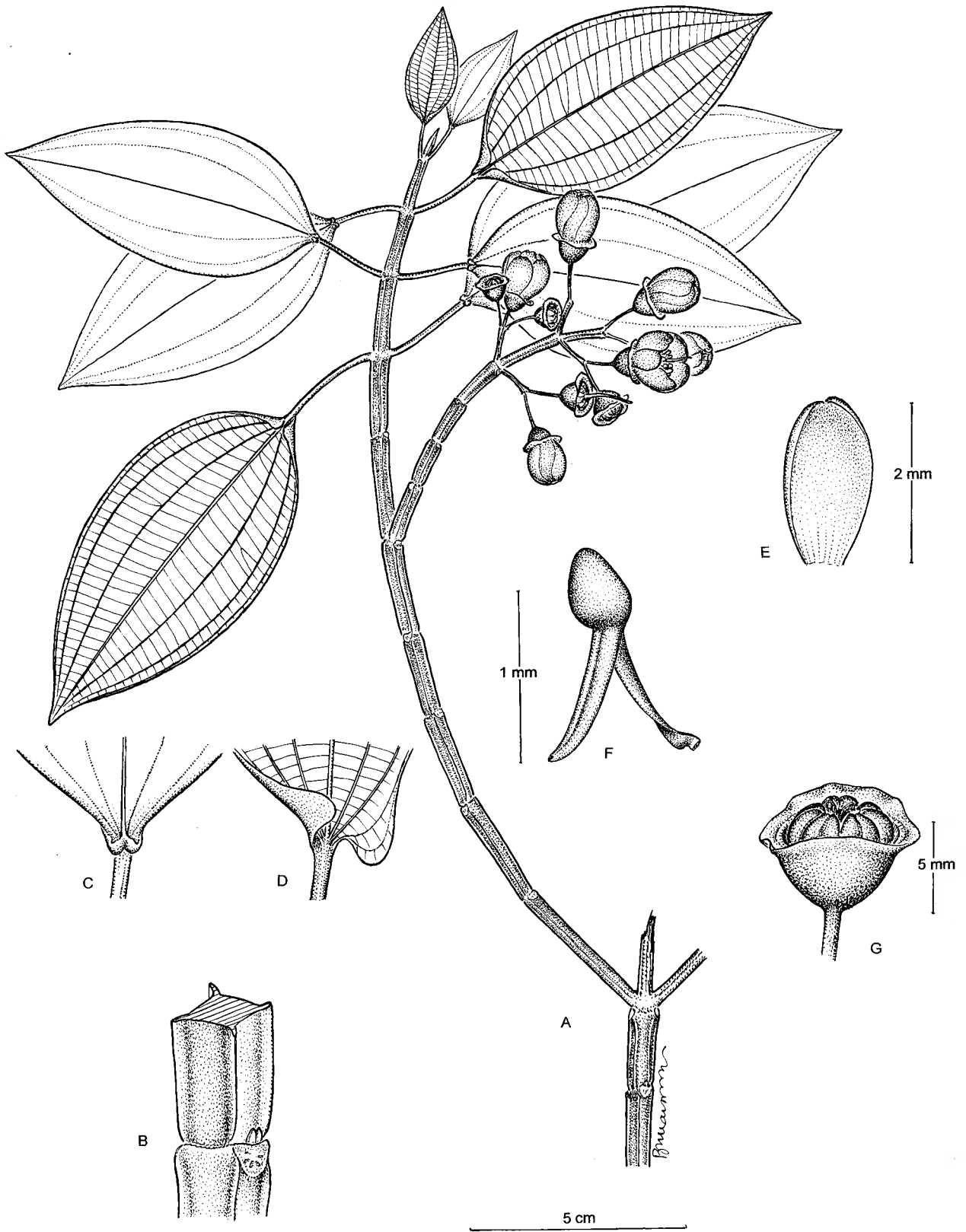
2. *Axinaea alata* E. Cotton, spec. nov. – Type: Bolivia. La Paz: Prov. Inquisivi, slopes below peak of Rancho Cunuhutu, 2 km N of Sita, 6 km N of Inquisivi, 2800 m, 14 Jul 1990, 16°15'S, 67°8'W, *Marko Lewis 37474* (holotype: MO!; isotype: US!). – Figures 10 and 11.

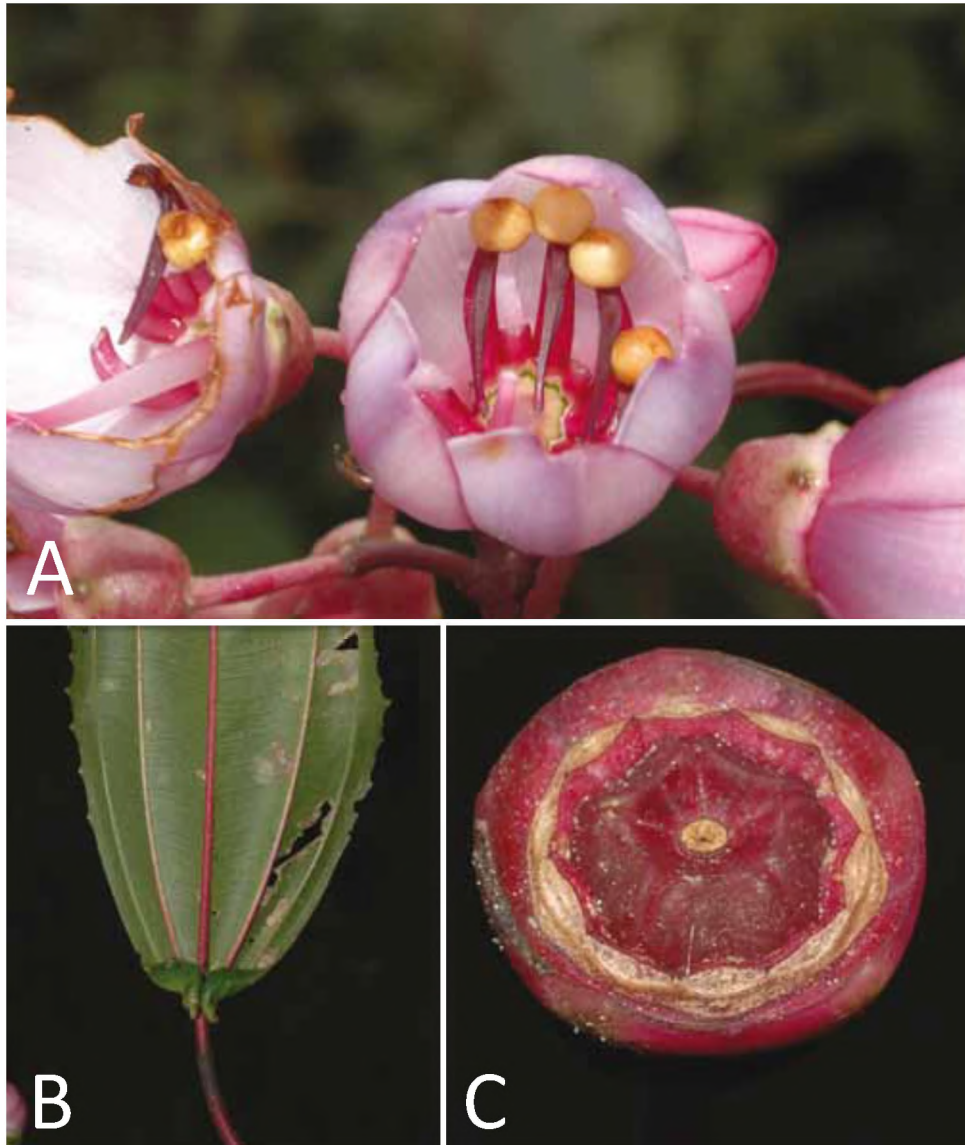
*Species nova a speciebus ceteris generis Axinaeae differt et internodiis anguste alatis, alis rigide coriaceis 1–2 mm latis et scuto gongylode bene evoluto.*

**Tree**, 5–15 m tall; *branchlets* markedly quadrangular, glabrous, narrowly winged, the wings rigid-coriaceous, 1–2 mm wide; *stipuliform flaps* reduced to a thin line across the nodes. **Leaves** petiolate; *petiole* 2.5–3.5 cm long, glabrous; *lamina* elliptic to elliptic-ovate, 9–15 × 4.5–7.5 cm, coriaceous, adaxially glabrous, abaxially sparsely puberulent, hairs dendritic, short, densely branched; *apex* acuminate or acute; *base* strongly auriculate, cuneate or truncate due to revolution of the auricles, auricles 3–6 mm long, often overlapping; *scutum* well developed, knob-shaped, often bilobed; *margins* dentate, the teeth 0.5–1 mm long and 4–6 mm apart; *venation* 5-nerved, excluding the tenuous inframarginal nerves that run ca 1 mm from the margin, adaxially and abaxially glabrous; *secondary nerves* faint, parallel, 2–4 mm apart. **Inflorescence** a somewhat pendulous thyrses, loosely-branched, 3–25-flowered, terminal, 6–10 cm long. **Flowers** 5-merous, 1.5–2 cm long; *hypanthium* cupuliform, 3–4 mm long, glabrous; *calyx* 1–1.5 mm long, truncate or obscurely 5-lobed, external teeth inconspicuous or absent; *petals* pink or pale pink, oblong-obovate, concave, 16–20 × 8–10 mm, apex rounded or asymmetrically bilobed; *stamens* anisomorphic; *filaments* bluish-purple, complanate, 8–9 mm long in the shorter stamens, 9–10 mm long in the longer ones; *connective appendage* spherical, 4 × 3 × 3 mm, rounded basally; *anthers* 8 mm or 9 mm long with one small, slightly dorsal pore; *ovary* oblong, costulate, apex 5-lobed, the lobes free and separated, 5-celled; *style* 2–2.3 cm long, curved at the apex. **Fruit** a 5-lobed capsule, the apical lobes hardened and somewhat project-

*Opposite page:*

**Figure 10.** *Axinaea alata* – A. Habit, showing an inflorescence and leaves, as well as the winged internodes. B. Detail of a node and section of an internode showing the wings, a bud, and a leaf scar. C. Lamina base adaxially showing the bilobed scutum. D. Lamina base abaxially showing one reflexed auricle (usual position) and an extended one. E. Cucullate petal. F. Stamen, showing the filament, the spherical connective, and the anther with a slightly dorsal pore. G. Fruit, showing the hypanthium covering 3/4 of the mature capsule (A, C, D, and F from *Solomon 6034*, US; B, E, and G from *Lewis 37474*, US).





**Figure 11.** *Axinaea alata* – A. Flower. B. Abaxial leaf base. C. Immature fruit, top view. (A. *Nee 55309*. B and C. *Nee 55301*, both from Cochabamba, Bolivia; Photo: Fabián Michelangeli).

ing, hypanthium covering 3/4 of the mature capsule; seeds not seen.

*Axinaea alata* is endemic to the Andes of Bolivia where it grows at 2300–2900 m elevation. – Figure 12.

**Additional specimens examined – BOLIVIA: La Paz:** Nor Yungas, Sacramento, between Yuspipata

and Yolosa, 2360–2370 m, 5 Oct 1985, 16°18'S, 67°48'W, *Gentry & Solomon 52098* (MO); 3 km below Chuspipata on old road, 2900 m, 10 Aug 1981, 16°18'S, 67°48'W, *Solomon 6034* (MO, US).

The presence of the knob-shaped scutum and the free and separated apical lobes of the ovary distinguish *Axinaea alata* from *A. lanceolata*, that also grows in Bo-

livia and is the only other species that occasionally has slightly winged internodes.

The specific epithet refers to the winged internodes.

3. *Axinaea campii* E. Cotton, spec. nov. – Type: Ecuador. Prov. Chimborazo and Cañar border (western escarpment), near Tipococha, 3200–3500 m, *Camp E-4067* (holotype: NY!; isotypes: G!, GH!, K!, MO!, VEN!). – Figure 13.

*Species Axinaeae merianiae (DC.) Triana simulans, a qua differt foliis 5-plinerviis (non 3-plinerviis vel breviter 3-plinerviis), lamina ad basin decurrenti (non cuneati).*

**Shrub or tree**, 1.5–8 m tall; *branchlets* quadrangular often with sharp edges but not winged, moderately arachnoid-puberulent throughout, hairs indistinct; *stipuliform flaps* present as a woody ridge between the nodes, raised 0.5–1 mm. **Leaves** petiolate; *petiole* 0.5–4 cm long, glabrous or with scattered transparent, squamose hairs; *lamina* oblong-elliptic, 4–8 × 2.5–5 cm, subcoriaceous, adaxially glabrous except when very young, abaxially sparsely puberulent with squamose hairs; *base* decurrent, not auriculate, usually revolute; *scutum* absent; *apex* obtuse to rounded; *margins* entire to shallowly denticulate, the teeth less than 1 mm long and 1–3 mm apart; *venation* 5-plinerved, excluding the tenuous inframarginal nerves that run ca 1 mm from the margin, the inner pair of primaries diverging from the main nerve 2–10 mm above the base of the lamina, adaxially and abaxially glabrous; *secondary nerves* parallel, 1–3 mm apart. **Inflorescence** a somewhat pendulous thyrses, loosely-branched, 1–10-flowered, terminal, 5–8 cm long. **Flowers** 5-merous, ca 2.5 cm long; *hypanthium* cupuliform, 4–6 mm long; *calyx* ca 1 mm long, obscurely 5-lobed or truncate, external teeth inconspicuous; *petals* dark pink or purple, lighter at anthesis, oblong-elliptic, concave, 2 × 1 cm, apex asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 4–5 mm long in the shorter stamens, 6–7 mm long in the longer stamens; *connective appendage* dimorphic, spherical, 3–4 × 2 × 2 mm, rounded basally, the apex resting on the thecae in the shorter stamens,

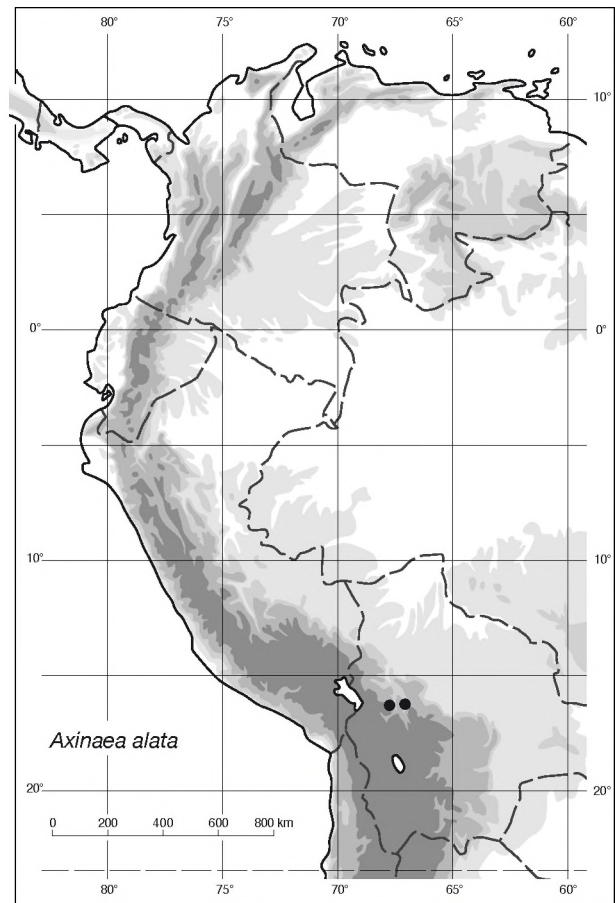
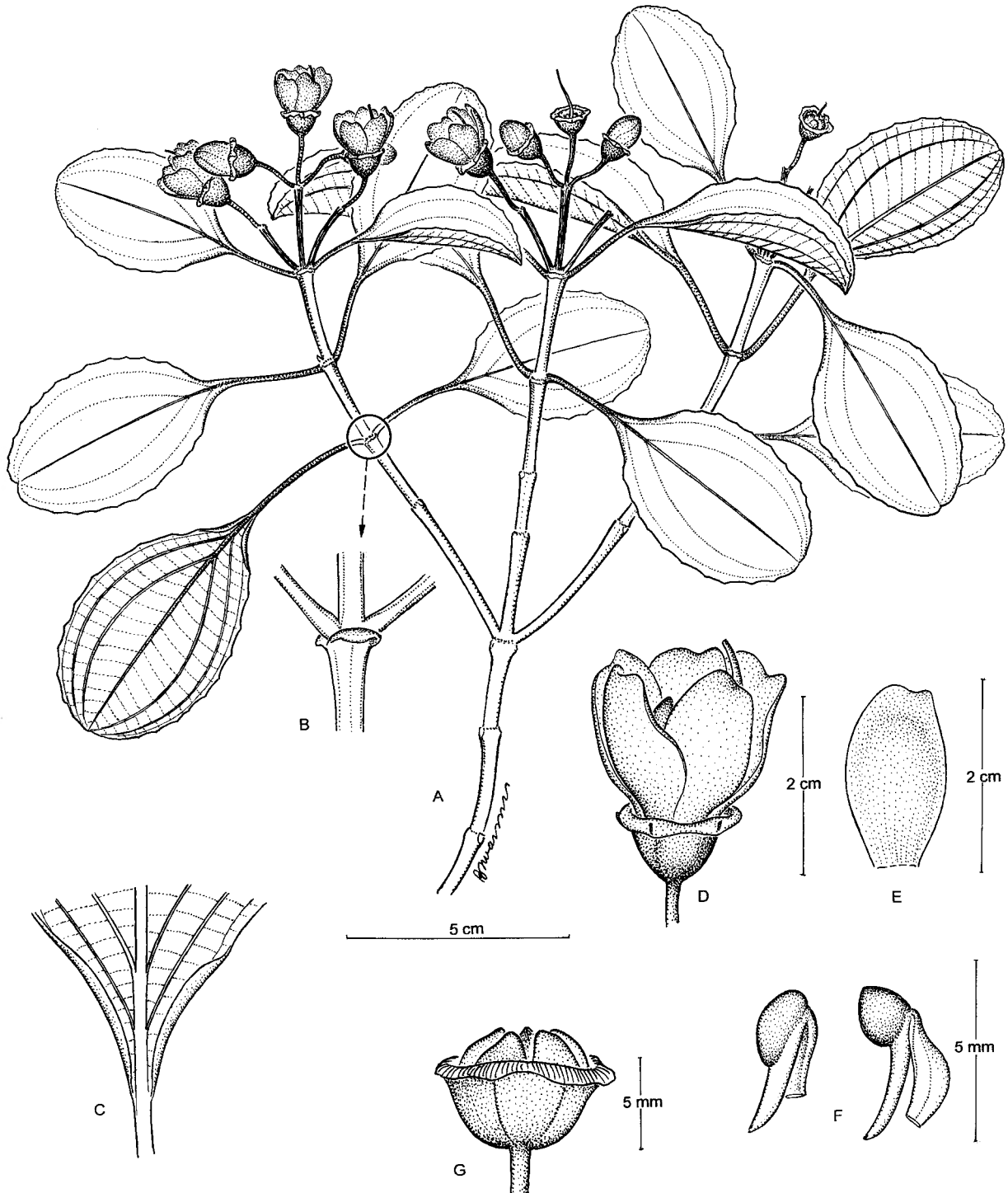


Figure 12. Distribution of *Axinaea alata*.

somewhat acute basally, the apex free from the thecae in the longer ones; *anthers* 5–6 mm or 7–8 mm long with one small, slightly dorsal pore; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* 1.3–2 cm long, often curved distally. **Fruit** a 5-lobed capsule, the hypanthium covering more than 2/3 of the mature capsule; *seeds* cuneiform.

*Axinaea campii* is endemic to the subpáramos and páramos along the border between the Chimborazo and Cañar provinces in the Andes of southern Ecuador where it grows at altitudes between 2700 m and 3400 m. – Figure 14.

**Additional specimens examined – ECUADOR:** **Azuay:** Take-off Llantera-Chiquintal-Saucay, 3130 m, *Or-*



**Figure 13.** *Axinaea campii* – A. Habit, showing three inflorescences, each subtended by a pair of leaf-like bracts. B. Detail of a node showing the stipuliform flap. C. Lamina base abaxially, showing the plinerved venation and the revolute margins. D. Flower at anthesis showing the flared calyx. E. Petal. F. Dimorphic stamens, the antepetalous one longer and with a spherical connective, the antesepalous one shorter and with an ellipsoidal connective. G. Fruit, showing the hypanthium covering  $3/4$  of the mature capsule (From *Camp E-4067*, K).

*tiz* & *Jaramillo 137* (AAU). **Azuay/Cañar**: between Cuenca and Huigra, 2700–3000 m, 12–13 Sep 1923, *Hitchcock 21677* (GH, NY, US). **Chimborazo/Cañar**. Road Alausí–Joyacshic, turn off to Hda. Carmen, 2900–3300 m, 12 Aug 1987, *P. Mena 827* (AAU). **Cañar**: road Alausí–Cañar, between Oyacshic and Hda. El Carmen, 3270 m, 2°33'S, 78°56'W, 12 Aug 1987, *Jaramillo 9792* (LOJA); Tipococha, 3300 m, 10 Jul 1939, *Penland & Summers 1005* (F, NY); turnoff to Oyacshic, Hda. El Carmen, 2900–3270 m, 12 Aug 1987, *Ulloa 424* (AAU, F, NY, S).

*Axinaea campii* is quite similar to *Axinaea merianiaea*, but differs in having the leaves 5-plinerved (not 3-plinerved or short 3-plinerved) and the leaf base which is decurrent (not cuneate). It is also somewhat similar to *A. wurdackii* from northern Peru. Both have plinerved venation and decurrent or attenuate lamina bases, but they differ in the color of the corolla, *A. campii* having pink or purple corolla (*vs.* white in *A. wurdackii*) and in the pubescence that is squamose in *A. campii* (*vs.* glabrous in *A. wurdackii*).

The species is dedicated to Wendell Holmes Camp who collected many unusual species of Melastomataceae in Ecuador.

4. *Axinaea colombiana* Lozano-C. & Alvear, *Caldasia* 23: 148. 2001. – Type: Colombia. Caldas: Mpio. Manizales, trail La Esperanza, Finca Torre Cuatro, near old road to La Elvira and La Línea, 3600–3700 m, 5 Ago 1999, *Alvear & Sánchez 471* (holotype: COL [n. v.]; isotypes: HUA [n.v.], US [n.v.]).

**Tree**, 7–20 m tall; *branchlets* terete or obscurely quadrangular, moderately arachnoid-furfuraceous when young, glabrescent with age, hairs indistinct; *nodes* barely thickened or not at all; *stipuliform flaps* absent. **Leaves** petiolate; *petiole* 5–16 mm long, arachnoid-furfuraceous when young, glabrescent with age; *lamina* elliptic-oblong, 4–8 × 1.6–3.5 cm, coriaceous, adaxially glabrous and lustrous, abaxially densely arachnoid-furfuraceous, the surface of the blade not visible through the hairs, hairs similar to those on the branchlets; *apex* acute; *base* cuneate to slightly rounded, not

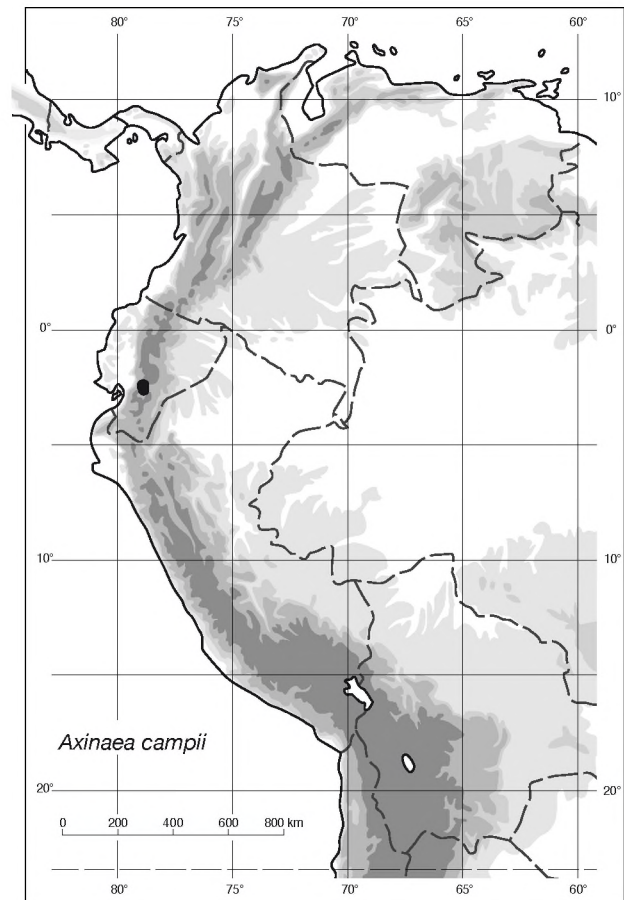


Figure 14. Distribution of *Axinaea campii*.

revolute; *scutum* absent; *margins* entire to shallowly denticulate; *venation* shortly 3-plinerved, excluding the tenuous inframarginal nerves that run 0.5–1.5 mm from the margin, somewhat sunken adaxially, prominent abaxially, glabrous on both surfaces; *secondary nerves* evident, parallel, 1–3 mm apart. **Inflorescence** a pendulous thyrses, loosely branched, 3–25-flowered, terminal, 5–9 cm long, subtended by a pair bracts; *bracts* similar to those on the leaves but smaller, 2–4 × 0.9–1.5 cm; *pedicels* 9–12 mm long, furfuraceous to glabrescent. **Flowers** 4-merous, 1–1.5 cm long; *hypanthium* cyathiform, 2–3 mm long; *calyx* 1–2 mm long, obscurely and irregularly 4-lobed, external teeth minute or absent; *petals* red to dark pink, fleshy, obovate, concave, 8–14 × 10–13 mm wide, apex truncate to rounded; *stamens* isomorphic; *filaments* complanate, 5–8 mm

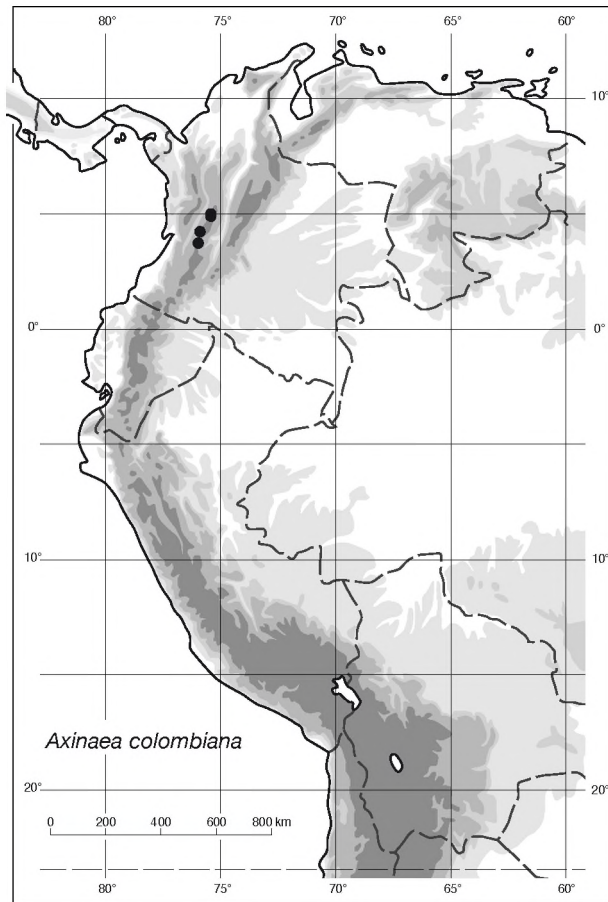


Figure 15. Distribution of *Axinaea colombiana*.

long; *connective appendage* ellipsoidal, 4-4.5 × 3 × 2 mm, acute basally; *anthers* 5 mm long with one small dorsal pore, yellow; *ovary* oblong, costulate, apex 4-lobed, 4-celled; *style* 10-16 mm long, flattened at the apex. **Fruit** a 4-lobed capsule; *seeds* pyramidal or cuneiform.

*Axinaea colombiana* is restricted to the western slopes of the Central Cordillera in the Andes of Colombia where it grows at 3200-3700 m elevation. – Figure 15.

**Additional specimens examined – COLOMBIA:**

**Risaralda:** Mpio. Sta. Rosa de Cabal, trail Termales-finca La Sierra, 3510 m, 3 Apr 1986, *Wolf & de Wilde 910* (US). **Valle:** Mpio. Tuluá, Corr. Santa Lucía, finca Las Nieves, páramo Las Hermosas, 3200 m, 25 Sep 1987, *Devia & Prado 1960* (MO, US); El Crucero, Morro

Bello, 3200 m, 5 Nov 1987, *Devia & Prado 2042* (MO, US).

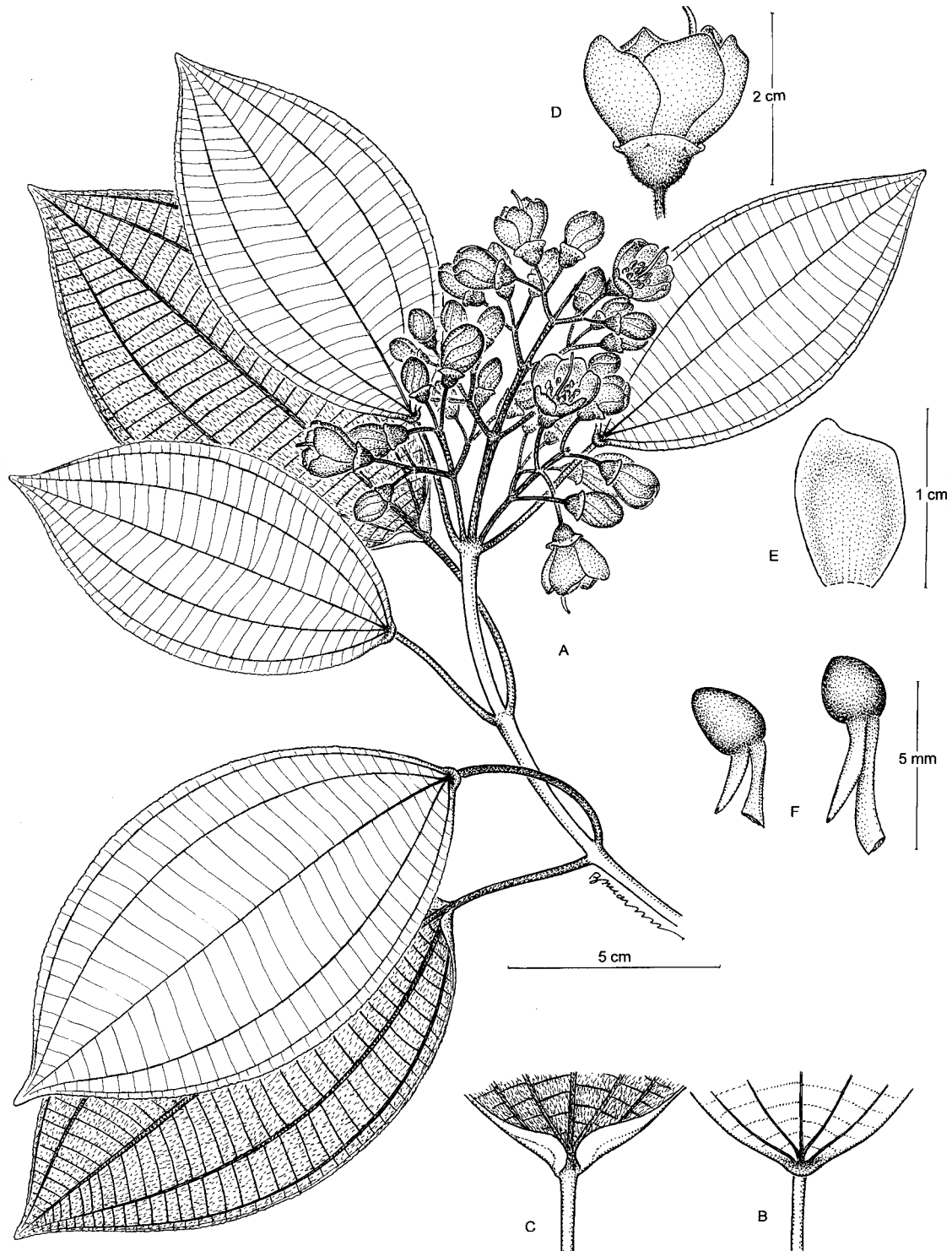
Although *Axinaea colombiana* grows at altitudes over 3000 m, it is a rather large tree, 7-20 m tall. It is surprising to find such large trees at the higher elevations in the Andes. Lozano-C. and Alvear (2001) propose that *A. colombiana* is most closely related to *A. mertensioides*, this species being, at the time, the only other 4-merous species of *Axinaea* known. Apart from being 4-merous, it is difficult to find other similarities between *A. colombiana* and *A. mertensioides*. Instead, *Axinaea colombiana* resembles *A. fallax*, also from Colombia, with which it shares similar pubescence and growth habit, but from which it can be distinguished by its 4-merous (*vs.* 5-merous) flowers and because *A. fallax* is generally a more robust plant than *A. colombiana*.

5. *Axinaea confusa* E. Cotton, spec. nov. – Type: Peru. Ruiz & Pavón *s.n.* (holotype MA!; isotypes: [B destroyed], G!, MA!; photos of the B isotype: F!, MO!, NY!, photo of the MA isotype: NY!). – Figure 16.

*Species Axinaeae glandulosae D. Don simulans, a qua differt floribus longitudine non 1.5 cm excedenti (non 2 cm vel ultra), petalis roseis, lavandulis vel lilacinis (non roseis vel albis).*

**Tree**, 5-15 m tall; *branchlets* sub-quadrangular, moderately to sparsely pubescent when young, almost glabrous with age, hairs multicellular, pinoid, 0.2-0.3 mm; *nodes* slightly thickened, nodal flaps reduced to a thin line across the nodes. **Leaves** petiolate; *petiole* 1.5-4 cm long, moderately pubescent when young becoming glabrous with age, hairs similar to those on the branchlets; *lamina* ovate-lanceolate, 8-20 × 4-9 cm, coriaceous, adaxially glabrous but sparsely pubescent when young, abaxially moderately to densely pubescent, hairs pinoid, 0.3-0.5 mm long; *apex* acute; *base* rounded or cuneate, auriculate, the auricles 1-3 mm long, revolute; *scutum* present, well developed, often absent in the leaf-like bracts that subtend the inflorescence; *margins* entire to shallowly denticulate; *venation* 5-nerved, adaxially faint, glabrous or with scattered





**Figure 16.** *Axinaea confusa* – A. Habit, showing an inflorescence subtended by a pair of leaf-like bracts. B. Lamina base adaxially, showing the knob-shaped scutum. C. Lamina base adaxially, showing the reflexed auricles. D. Flower at anthesis. E. Petal. F. Anisomorphic stamens, the antepetalous stamen longer and with a smaller, spherical connective, the antesealous stamen shorter and with a larger slightly ellipsoidal connective (From Ruiz & Pavón s.n., G).

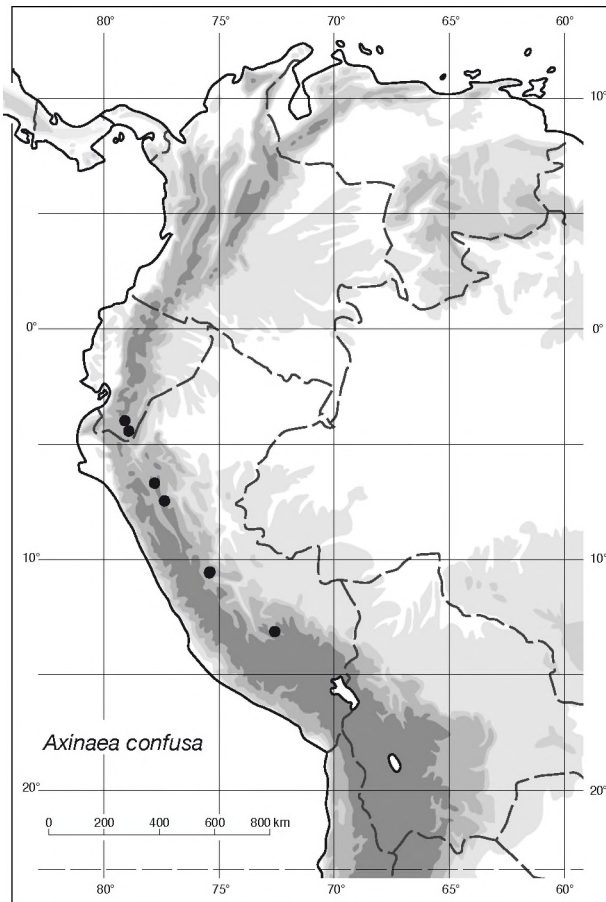


Figure 17. Distribution of *Axinaea confusa*.

pubescence, abaxially prominent and sparsely to moderately pubescent, hairs similar to those on the leaf; *secondary nerves* evident, parallel, 1–3 mm apart. **In-florescence** a thyrse, 11–25-flowered, terminal, 8–15 cm long, often subtended by bracts similar to those on the leaves but smaller; *pedicels* 5–8 mm long, slender, moderately to densely pubescent; *hairs* similar to those on the leaves. **Flowers** 5-merous, 1.2–1.5 cm long; *hypanthium* cupuliform, 2–3(–4) mm long; *calyx* ca 1 mm long, obscurely 5-lobed, apex truncate, external teeth evident, small, hardened; *petals* pink, lavender or lilac, oblong-elliptic, 10–12 × 6–8 mm, apex rounded or irregularly and asymmetrically lobed; *stamens* anisomorphic; *filaments* complanate, 7–8 mm long in the longer stamens, 5–6 mm long in the shorter

ones; *connective appendage* spherical, 2–3 × 2 × 2 mm, rounded or slightly apiculate basally; *anthers* 5–7 mm long with a small apical pore; *ovary* oblong, 5-costulate, 5-lobed at the apex, 5-celled; *style* 13–17 mm long. **Fruit and seeds** not seen.

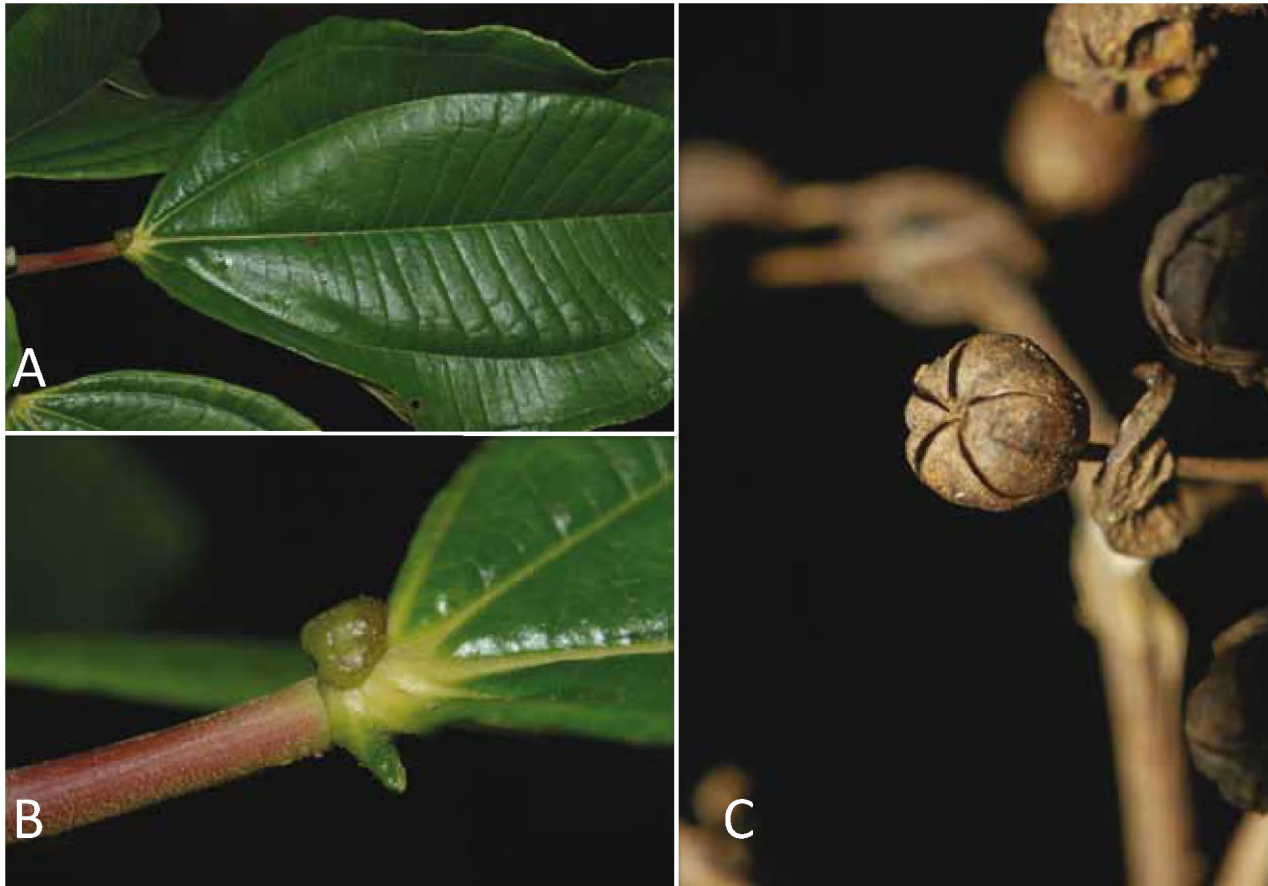
*Axinaea confusa* grows in the montane forests of the Andes of southern Ecuador and northern and central Peru at 1500–3100 m elevation. – Figure 17.

**Additional specimens examined – ECUADOR:**

**Zamora-Chinchipe:** San Francisco Scientific Station, road Loja–Zamora, ca 30 km from Loja, 1910 m, 3°58'S, 79°4'W, 18 Oct 2000, *Homeier 549* (MO); La Canela, 1550 m, 4°25'S, 78°54'W, 15 Sep 1995, *Lozano 224* (LOJA, QCA). **PERU: Amazonas:** Leimebamba–Chilchos trail, near Chilchos, ca 2500 m, 1 Jul 1977, *Boeke 2074* (NY, US). **Cusco:** Machu-Picchu, 2550 m, 7–8 May 1957, *Ellenberg 781* (US). **Pasco:** Oxapampa, Chontabamba, towards Río Chontabamba, 23 Jun 1986, *León et al. 983* (MO); Oxapampa, Palmazú, 1900–2300 m, 10°32'S, 75°23'W, 5 Oct 1984, *D. N. Smith et al. 8713* (MO). **San Martín:** Río Abiseo National Park, 3000–3100 m, 14 Jul 1988, *León et al. 2153* (US); Río Abiseo National Park, between La Playa and Pataten camps, 2500–2600 m, 27 Jul 1985, 7°27'S, 77°21'W, *Young 1341* (MO).

We call this species *A. confusa* due to the confusion that arose because Ruiz and Pavón's collections of this species are mixed with those of the type collection of *Axinaea glandulosa* D. Don. The sheets with the collections of *A. confusa* and *A. glandulosa* that are deposited in MA, lack numbers both for the collector series and for the herbarium itself (see note under *Axinaea glandulosa*). All specimens were studied, but at the time of the visit to MA, no decision had yet been made about the status of the second species and therefore the sheet is not annotated.

*Axinaea confusa* (Figure 16) resembles *A. sclerophylla* (Figure 66) but it has a very evident scutum and the pubescence is not as dense as in that species. In addition the base of the lamina is auriculate and revolute



**Figure 18.** *Axinaea costaricensis* – A. Leaf adaxial surface. B. Leaf base adaxial surface showing the scutum. C. Capsule showing five carpels. (From *Michelangeli 1233*, Costa Rica. Photo: Fabián Michelangeli).

in contrast to *A. sclerophylla* that has only cuneate lamina bases.

6. *Axinaea costaricensis* Cogn. in A. DC., Monogr. phan. 7: 1182. 1891. – Type: Costa Rica. Alajuela: Río Mancaron Island, 2100 m, 15 Feb 1890, *Pittier 2007* (holotype: BR! [mounted on two sheets BR # 843 792 and # 843 793]; isotypes: F!, G!, US!). – Figure 18.

**Shrub or tree**, 2–12 m tall; *branchlets* subquadrangular, densely furfuraceous when young becoming glabrous with age, hairs minute, 0.1–0.2 mm long, dendritic, densely branched; *stipuliform flaps* present, coriaceous, forming a flat outgrowth across the nodes, sometimes bilobed, 1–3 mm long, occasionally reduced to a line.

**Leaves** petiolate; *petiole* 1.2–2.5 cm long, furfuraceous when young but becoming mostly glabrous with age, hairs similar to those on the branchlets; *lamina* elliptic, 8–15 × 5–9 cm, coriaceous, adaxially glabrous, abaxially sparsely furfuraceous, hairs as in the branchlets; *apex* acute; *base* cuneate, ending in two small auricles 1–2 mm long, often revolute; *scutum* knob-shaped; *margins* entire to denticulate; *venation* 5-nerved, excluding the tenuous inframarginal nerves that run ca 0.5 mm from the margin, adaxially glabrous, abaxially furfuraceous, hairs similar to those on the branchlets; secondary nerves evident, parallel, 3–6 mm apart. **Inflorescence** a pendulous thyrse, many-branched, >26-flowered, terminal, 10–30 cm long, flowers arranged in fascicles; *nodal flaps* present in the largest nodes, similar to those on the branches but smaller;

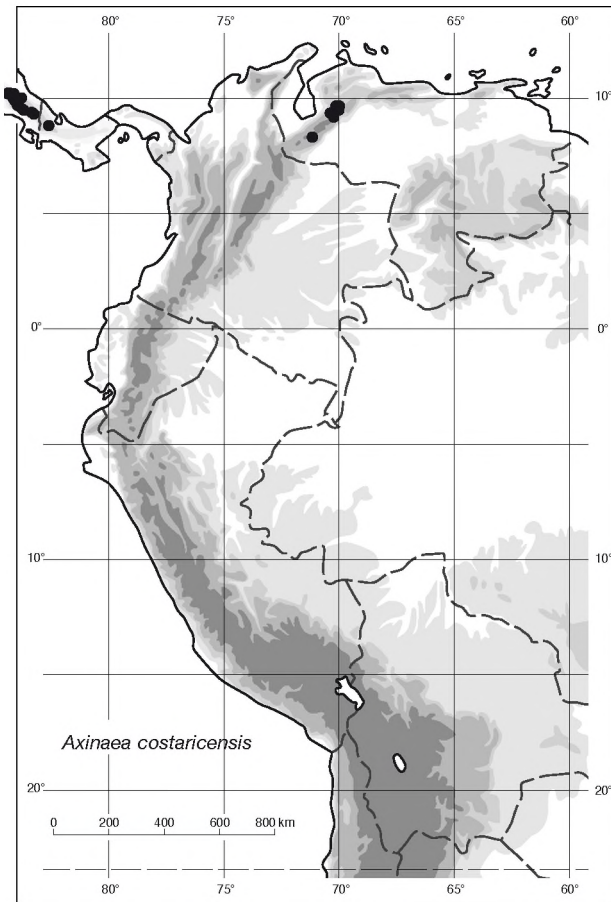


Figure 19. Distribution of *Axinaea costaricensis*.

*pedicels* slender, 7–12 mm long. **Flowers** 5-merous, 1.2–1.8 cm long; *hypanthium* cyathiform, 1.5–3 mm long; *calyx* 1 mm long, obscurely 5-lobed, external teeth minute or absent; *petals* coral red to dark salmon pink, oblong-obovate, concave, 8–12 × 6–7 mm wide, apex broadly and asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 5–6 mm long in the longer stamens, 3–4 mm long in the shorter ones; *connective appendage* spherical, 3–4 × 2 mm, somewhat apiculate basally, white turning brown with age; *anthers* 3–4 mm and 4–5 mm long with one small apical pore, dark red, violet or reddish-maroon; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* 10–13 mm long, curved at the apex. **Fruit** a 5-lobed capsule; *seeds* pyramidal or cuneiform.

*Axinaea costaricensis* is distributed in the mountain of Costa Rica, western Panama and western Venezuela at 1500–2600 m elevation. – Figure 19.

**Additional specimens examined – COSTA RICA:**

**Alajuela:** Finca La Selva, San Rafael de Vara Blanca, NW slope of Volcán Barba, 1720 m, 23 Jun 1963, *Jiménez 829* (F); 892 (US, W); Bajos del Toro Amarillo, 1800 m, 15 Jun 1992, 10°12'N 84°19'W, *Umaña & Chacón 493* (F, MO); slopes of Volcán Poás between edge of crater and 2.5 miles SSE of the rim, 2400–2550 m, 7 Jun 1972, *Wilbur & Almeda 17500* (F, GH, MO, US). **Bocas del Toro:** Robalo Trail, N slopes of Cerro Horqueta, 1800–2100 m, 5–7 Aug 1947, *Allen 4967* (BM, BR, F, G, MO, S). **Cartago:** ca 4–6 km N of Trinidad on S facing slopes of Volcán Turrialba, 1700–1800 m, 4 Jul 1977, *Almeda 2881* (BR); ca 14 km SE of El Empalme, 2600 m, 18 Jul 1977, *Almeda 3106* (F); Prov. Cartago, 5 Aug 1962, *Brown 17512* (F); La Trinidad, SE of El Empalme, 2500 m, 29 Jul 1964, *Jiménez 2196* (F); km 75 Pan-Am Hwy, up Talamanca Range, 2800 m, 2 Aug 1967, *Lent 1178* (F); La Chonta, 2200 m, 15 May 1966, *Schnell 715* (F, US); along Interamerican Hwy ca 4.5 km W of Hwy 222, along gravel road heading NE, 2150–2200 m, 30 Jul 1979, 9°44'N 83°57'W, *Stevens 13456* (F, MO); NE slopes of Volcán Barba, 1700–2000 m, 24 May 1972, *Stone 3268* (F, MO); slopes ca 14 km SE of El Empalme, 2600 m, 18 Jul 1977, *Wilbur et al. 22843* (F). **Cartago/San José:** km 67 S of San José on Pan-Am highway, 20 Mar 1969, *Cowan 2422* (US). **Guanacaste:** Palmira, region of Zarcero, 1900 m, 23 Feb 1938, *Smith 192* (F, MO); 360 (F); Palmira, 2100 m, 1 Jan 1937, *Smith 4212* (F). **Heredia:** Vara Blanca, San Rafael, Parque Nacional Braulio Carrillo, 1800 m, 2 Dec 1992, 10°13'N 84°6'W, *Ballester 189* (F); near Porrosati, S slope of Volcán Barba, 2200 m, 22 Jun 1968, 10°7'N 84°07'W, *Burger 6042* (BM, F, MO); between Georgina and Vara Blanca, 1950 m 11 Jul 1964, *Jiménez 2055* (BM, F, US, W); Volcán Barba, 2200 m, 11 Jun 1966, *Schnell 784* (F, US); Vara Blanca de Sarapiquí, N slope of Central Cordillera, between Poás and Barba volcanoes, 1950 m, 1 Jan 1938, *Skutch 3480* (GH, K, MO, S, US); Juvenal Valerio, Cerro de las Caricias, N of San Isidro, 2000–2400 m, 11 Mar 1926, *Standley 52253* (US);

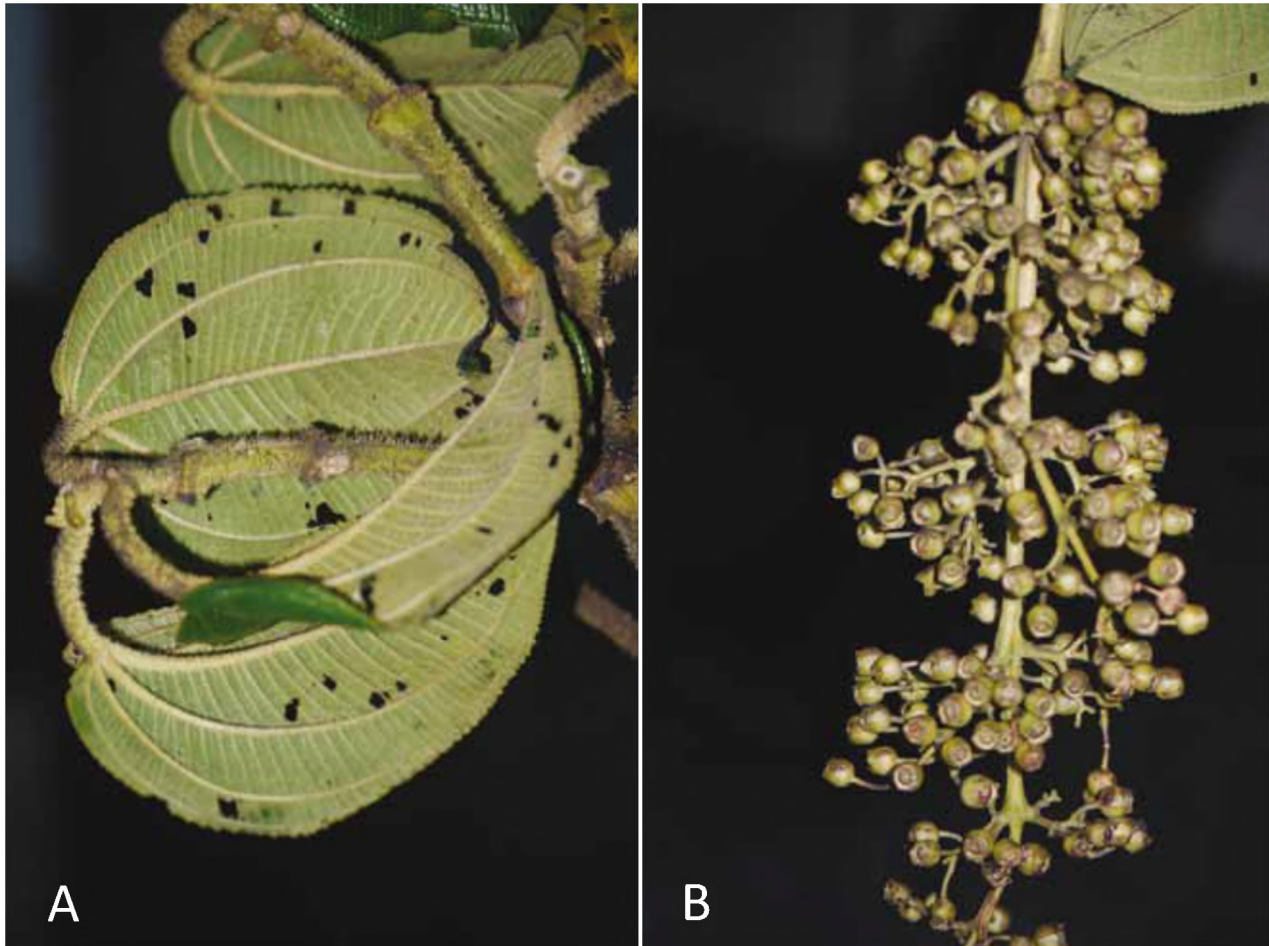
Varablanca, Sarapiquí, Apr 1903, *Wercklé 16687* (F, US). **Limón:** P. N. Cordillera de Talamanca, Quebrada Luisa, trail between Ujarrás and San José de Cabécar, 2160 m, 17 Mar 1993, 9°20'N 83°14'W, *Fernández 703* (MO); trail between Cerro Dúrika and Dúrika sabanas, following the riverbed of Quebrada Intermittente, 2500 m, 21 Oct 1989, 9°24'N 83°19'W, *Herrera 3750* (F, MO). **San José:** Cerros de Zurquí, N of village of San Luis Norte, 1750 m, 23 Apr 1975, 10°03'N 84°01'W, *Crosby 11437* (MO); 17 km NNE of city center of San José. Reserva Forestal Juan Castro Blanco, slopes of Volcán Viejo, 4 km NW of Bajos del Toro, 1700 m, 07 Aug 1988, 10°15'N 84°19'W, *Jiménez et al. 615* (F, MO); 3 km before Empalme coming from Cartago, 12 Jun 1975, *Poveda 1059* (F); La Georgina, S of road to summit of Cerro La Muerte, 28 Aug 1967, *Raven 22087-A* (F, MO). **Province unknown:** *Pittier s.n.* (BR). **PANAMA:** **Chiriqui:** above Guadalupe at STRI cabin, 2200 m, 6 Jun 1986, 8°50'N 82°35'W, *McPherson 9354* (MO). **VENEZUELA:** **Lara:** S- and SW-facing slopes at Palojosco, above Los Aposentos, above Humocaró Bajo, 2375–2530 m, 4 Feb 1944, *Steyermark 55258* (F, NY, US). **Lara/Trujillo:** Páramo de los Ñepes, slopes above La Peña, 2500 m, 24–25 Dec 1959, *Barclay & Jujibioy 10320* (MO, US). **Mérida:** Portachuelo–La India, between El Morro and Arica-gua, 2300 m, 16 Feb 1957, *Bernardi 6199* (G, NY). **Trujillo:** Misisí Mountains, old road Trujillo–Boconó, ca 12 km by air NW of Boconó, 2200–2400 m, 5 Jul 1980, 9°21'N 70°18'W, *Dorr et al. 7274* (NY); 31 Oct 1990, *Dorr et al. 7526* (MO, NY); Páramo de Guaramacal, SE of Boconó, 1500–2600 m, 17 Jul 1990, 9°12'N 70°13'W, *Dorr et al. 7330* (MO, NY); Parque Nacional Dinira, road Carache–Agua de Obispo, 2300–2450 m, 1 Jan 2000, 9°41'N 70°08'W, *Meier et al. 6316* (US); Misisí Mountains, old road Boconó–Trujillo, 2150 m, 21 Sep 1972, *Ruíz-Terán & López-Palacios 7632* (F, NY); Misisí Mountains, old road Trujillo–Boconó, 8.3 km SW of main road Boconó–Flor de Patria, 2200–2400 m, 25–26 Sep 1985, 9°21'N 70°18'W, *Steyermark & Manara 125343* (VEN).

*Axinaea costaricensis* is the only species of the genus that reaches Central America, and actually its occurrence

there represents the largest disjunction in distribution found among any species of *Axinaea*. Nevertheless, we did not find any consistent morphological differentiation between the two populations, and we speculate that the Central American populations may be the result of a recent long distance dispersal event. *Axinaea costaricensis* is most similar to *A. robusta*, from which it differs in the stipuliform flaps that are coriaceous and 1–3 mm long in *A. costaricensis* (*vs.* woody and forming a raised ridge across the nodes in *A. robusta*), the nodes that are not thickened in *A. costaricensis* and thickened in *A. robusta*, and the hypanthium that is 1.5–3 mm long in *A. costaricensis* (*vs.* 3–4 mm long in *A. robusta*.)

7. *Axinaea crassinoda* Triana, Trans. Linn. Soc. London. 28: 69. 1871. — Type: Peru. Chachapoyas: Andes of Peru, no date, *Mathews 3213* (holotype: K!, photo: NY!; isotypes: BM!, F! (fragment), G!, GH!; photo of the BM isotype: NY!; photos of the G isotype: MO!, NY!; photo of the GH isotype: NY!). — Figure 20.

**Tree**, 4–8 m tall; *branchlets* markedly quadrangular, densely pubescent, hairs roughened, 1.4–1.7 mm long; *stipuliform flaps* present, coriaceous, forming a flap outgrowth across the nodes, sometimes bilobed, 1–4 mm long. **Leaves** petiolate; *petiole* 2.8–5.5 cm long, densely pubescent, hairs similar to those on the branchlets; *lamina* obovate, cordiform, 9.5–18 × 6.5–14 cm, coriaceous, adaxially glabrous, abaxially moderately pubescent, hairs roughened, ca 0.2 mm long; *apex* acute; *base* cordate, occasionally rounded or cuneate in young leaves, auricles 1–1.5 cm long; *scutum* absent; *margins* entire to denticulate; *venation* (5–)7-nerved, excluding the tenuous inframarginal nerves that run ca 1 mm from the margin, and disappear into it along the distal 1/3 of the lamina, adaxially glabrous and sunken, abaxially prominent and pubescent, hairs similar to those in the branchlets but shorter, less than 1 mm long; *secondary nerves* evident, parallel, 2–4 mm apart. **Inflorescence** a pendulous thyrse, many-branched, >26-flowered, terminal, 15–35 cm long; *stipuliform flaps* present in the largest nodes; *pedicels* slender, 2–10 mm long. **Flowers** 4-merous, 1–2.8 cm long; *hypanthium* cy-



**Figure 20.** *Axinaea crassinoda* – A. Leafy branch showing the thickened nodes. B. Inflorescence. (No voucher. Photo: Rainer Bussmann).

athiform, 3–5 mm long; *calyx* 2 mm long, 4-lobed, apex rounded, external teeth minute or absent; *petals* pink or white flushed with darker pink, obovate, concave, fleshy, slightly asymmetric, 6–12 × 6–9 mm wide, apex broadly and asymmetrically bilobed; *stamens* isomorphic; *filaments* complanate, 4–7 mm long, light pink; *connective appendage* ellipsoidal, yellow, turning orange, 4–6 × 2–3 × 2 mm, acute basally; *anthers* wine-red, 3–5 mm long with one small apical pore; *ovary* oblong, costulate, apex 4-lobed, 4-celled; *style* 12–17 mm long, curved distally, light pink. **Fruit** a 5-lobed capsule, the hypanthium completely covering the mature capsule; *seeds* numerous, cuneiform.

*Axinaea crassinoda* is endemic to the eastern slopes of the Andes in northern Peru at 2300–3200 m elevation, where it is quite rare. – Figure 21.

**Additional specimens examined – PERU: Amazonas:** Chilchos-Leimebamba trail, Tushpurumbe, 4 Jul 1977, *Boeke 2131* (NY); road Balsas-Calla Calla Páramo-Leimebamba, 50 km from Balsas, 3400–3500 m, 6°44'10''S 77°53'10''W, 3 Jul 2002, *Cotton & Gustafsson 1832* (AAU, CPUN, MO, USM); between Calla Calla and Balsas, 3450 m, 7 Oct 2001, 6°44'S 77°53'W, *I. Sanchez V. & M. Sanchez M. 11074* (AAU); Playapampa, 2700 m, 16–24 Jun 1923 *Macbride 4873* (F); *Mathews s.n.*

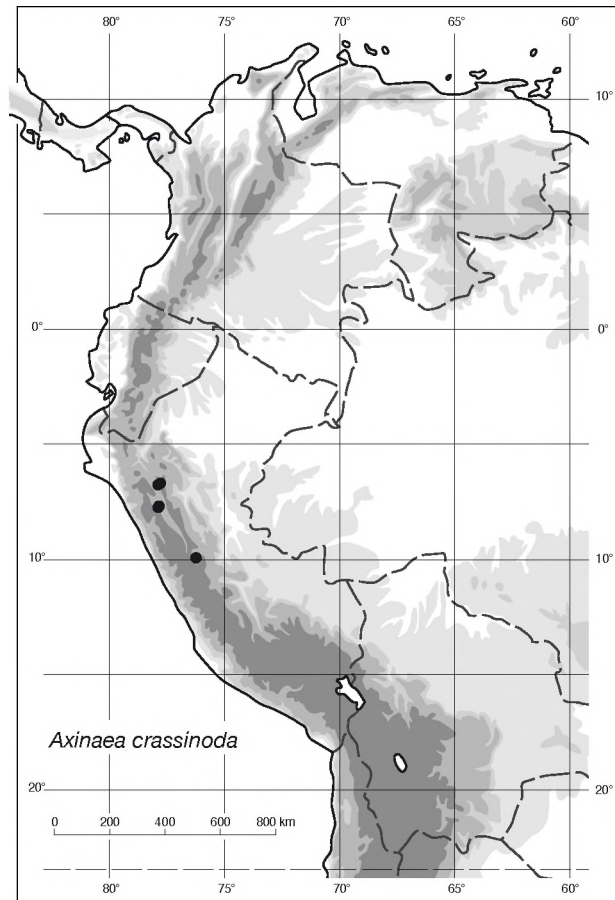
(G, GH, K); upper slopes of Puma-urcu, E-SE of Chachapoyas, 2700–3000 m, 1 Jun 1962, *Wurdack 657* (US); uppermost slopes and summit of Puma-urcu SE of Chachapoyas, 2900–3150 m, 7 Jun 1962, *Wurdack 789* (F, G, GH, K, MO, NY, S, UC).

*Axinaea crassinoda* Triana is easy to recognize by the generally dense pubescence that covers the plant, the incrassate nodes with well developed stipuliform flaps and its long, densely-flowered inflorescences. Though the species is quite distinct, it is possibly most similar to *A. reginae*, another 4-merous species from northern Peru.

**8** *Axinaea dentata* E. Cotton, spec. nov. – Type: Ecuador. Prov. Zamora-Chinchipe, Podocarpus National Park, road Yangana-Valladolid, km 21, 2700 m, 10 Jun 1989, 4°28'S 79°9"W, *Madsen 86050* (holotype: AAU!, isotypes: LOJA!, QCA!). – Figure 22.

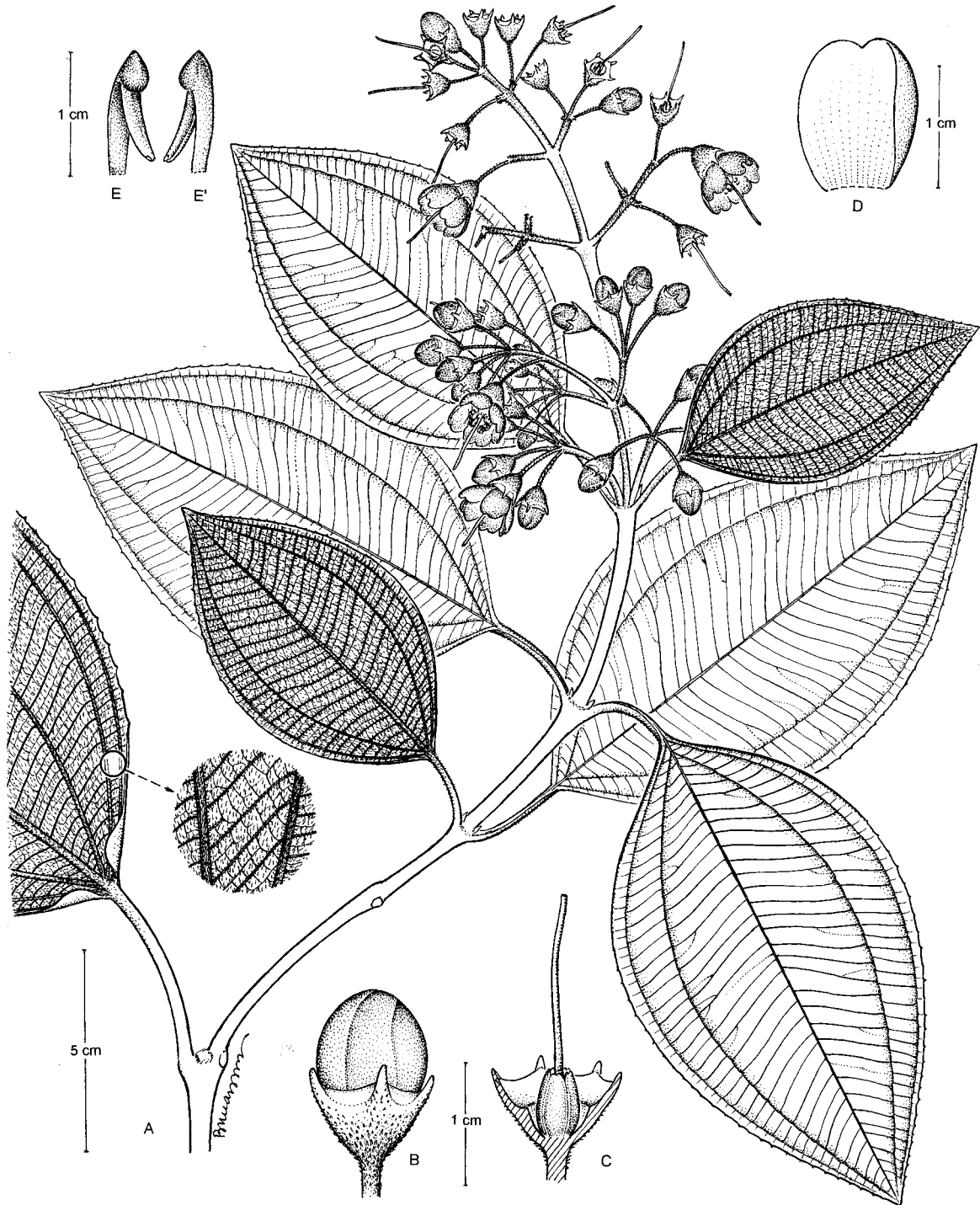
*Species Axinaeae sclerophyllae Triana simulans, a qua differt dentibus calycis bene evolutis (non inconspicuis) a calyce 2–3 mm projectis.*

**Shrub or tree**, 2–? m tall; *branchlets* sub-quadrangular, wider and somewhat flattened at the nodes, moderately to sparsely puberulent when young, becoming glabrous with age, hairs multicellular, thickened, barbellate, 0.3–0.5 mm long; *stipuliform flaps* reduced to a scar across the node. **Leaves** petiolate; *petiole* 1.5–3 cm long, moderately to sparsely pubescent, hairs similar to those on the branchlets; *lamina* elliptic, 5.5–8.5 × 10–15 cm, rigidly coriaceous, often bullate, adaxially glabrous or with scattered pubescence along the nerves, abaxially moderately pubescent, hairs multicellular, thin, barbate, 0.3–0.5 mm long; *apex* acuminate; *base* cuneate or auriculate, with auricles revolute; *scutum* absent; *margins* usually entire on the proximal half of the lamina, denticulate on the distal half, teeth 0.5–1 mm long and 1.5–3 mm apart; *venation* 5-nerved or shortly 5-plinerved, the inner pair of primary nerves diverging from the main nerve 3–6 mm above the leaf base, adaxially sunken, densely to moderately pubescent when young, glabrescent with age, abaxially



**Figure 21.** Distribution of *Axinaea crassinoda*.

prominent and moderately pubescent, hairs similar to those in the branchlets; *secondary nerves* sunken adaxially, prominent abaxially, parallel, 2–4 mm apart. **Inflorescence** a thyrse, 11-many-flowered, terminal, 5–8 cm long, subtended by a pair of bracts that are similar to the ones on the leaves but smaller, 3–5.5 × 6.5–9 cm; *pedicels* 8–10 mm long, densely to sparsely pubescent, hairs similar to those on the branchlets. **Flowers** 5-merous, 12–15 mm long; *hypanthium* cyathiform, 2–3 mm long; *calyx*, 5-lobed, lobes triangular, apex acuminate, external teeth well developed in the shape of hard, triangular keels, 1–2 mm long that protrude from the calyx lobes and are at least 1 mm longer than them; *petals* light red or purple, oblong-elliptic, fleshy, concave, 8–10 × 12–13 mm, apex rounded to irregularly bilobed; *stamens* anisomorphic; *filaments* complanate,



**Figure 22.** *Axinaea dentata* – A. Habit, showing an inflorescence subtended by a pair of leaf-like bracts, and a detail of the abaxial surface of the lamina. B. Bud, showing the well developed calyx teeth. C. Longitudinal section of a flower (petals and stamens removed) showing the superior ovary, the hypanthium, the torus the style and the calyx lobes with the external teeth. D. Petal. E and E'. Stamens showing the filament, the spherical connective appendage that is somewhat apiculate basally, and the anther (From Madsen 86050, AAU).



6–7 mm long in the longer stamens, 5–6 mm long in the shorter ones; *connective appendage* spherical, 1.5–2 × 2 × 2 mm, acuminate basally; *anthers* 5–6 mm or 4–5 mm long with a small apical pore; *ovary* oblong, 5-costulate, apex 5-lobed, 5-celled; style 12–18 mm long. **Fruit** and *seeds* not seen.

*Axinaea dentata* is restricted to the Andes of southern Ecuador, where it grows at 2600–2700 m elevation. – Figure 23.

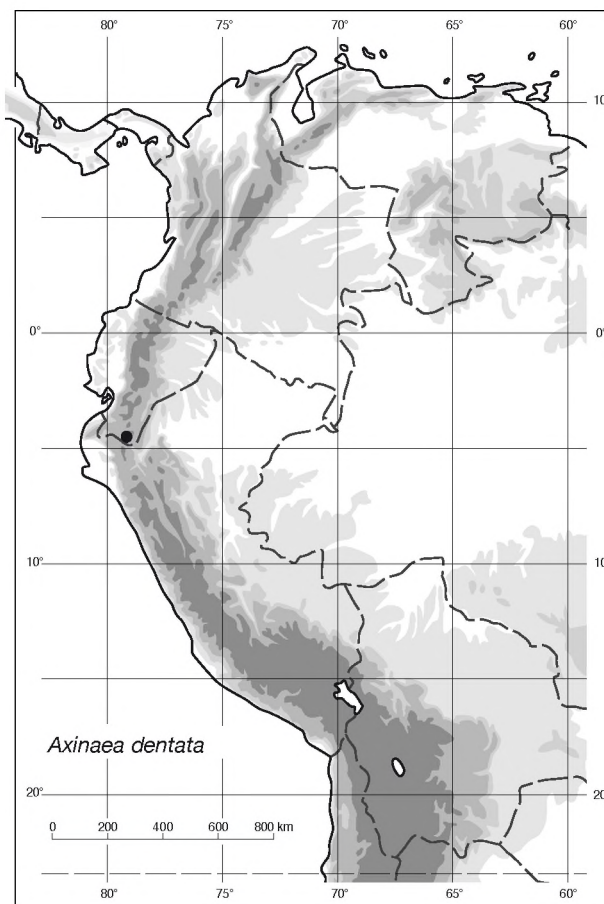
**Additional specimens examined – ECUADOR:**

**Loja:** Yangana–Valladolid road, 5 km N of the pass, 2600 m, 3 Sep 1985, *Larsen 197* (AAU). **Zamora-Chinchipe:** Podocarpus National Park, near the Yangana–Valladolid road, 2700 m, 4°28'S 79°9'W, 7 Jul 1996, *Borgtoft-Pedersen et al. 104396* (AAU, LOJA); Yangana–Valladolid road, km 24, 4°30'S, 79°9'W, 14 Dec 2000, *Madsen & Rosales 7589* (AAU); km 22, 2700 m, 4°27'S 79°9'W, 30 Aug 2001, *Madsen & Chimbo 8359* (AAU); km 21, 4°28'S 79°9'W, 7 Jul 1996, *Madsen 86041* (AAU, LOJA).

*Axinaea dentata* is endemic to the Podocarpus National Park in southern Ecuador. It is vegetatively similar to *A. sclerophylla*, which often also has bullate leaves, but *A. dentata* has 2–3 mm long calyx teeth (vs. not evident in *A. sclerophylla*). Actually, *A. dentata* is the only species in the genus with such long calyx teeth.

9. *Axinaea dependens* D. Don, Mem. Wern. Nat. Hist. Soc. 4: 321. 1823. – *Meriania dependens* (D. Don) Naudin, Ann. Sci. Nat. Bot., Sér. 3, 18: 124, 129. 1852. – Type: Peru. Junín, Vitoc, *Ruiz & Pavón s.n.* [Herbarium Peruvianum Ruiz et Pavón # 23/57], (lectotype: MA!, here designated; photo: NY!; isotype: B (destroyed); photo: F!, GH!, MO!, NY!).

*Axinaea rugosa* Ruiz & Pav., Fl. Peruv. et Chil. 4: 205. 1957. – Type: Peru. Huánuco, Chinchao, *Ruiz & Pavón s.n.* [Herbarium Peruvianum Ruiz et Pavón # 23/55], Lectotype, here designated: MA!; photo: NY!; isotypes: B (destroyed), F!, G!, MA!; photo of the B isotype: F!, GH!, MO!, NY!; photo of the MA isotype: NY!)



**Figure 23.** Distribution of *Axinaea dentata*

**Shrub or tree**, to 12 m tall; *branchlets* quadrangular to obscurely quadrangular, densely to moderately furfuraceous when young, glabrescent with age, hairs minute, 0.5–1 mm long, dendritic, densely branched; *stipuliform flaps* present, coriaceous, forming a flat outgrowth across the nodes, 1–5 mm long. **Leaves** petiolate; *petiole* 1.5–4.5 cm long, densely furfuraceous when young, sparsely so with age, hairs as in the branchlets; *lamina* oblong-elliptic to elliptic-ovate, 11–17 × 5–7 cm, subcoriaceous, adaxially glabrous, abaxially sparsely furfuraceous, hairs similar to those on the branchlets but smaller, 0.2–0.5 mm long; *apex* acute; *base* cuneate or rounded, sometimes asymmetrical, not auriculate, not revolute; *scutum* absent; *margins* denticulate to dentate, the teeth 0.5–1 mm long and 2–3 mm apart; *venation* 5-plinerved, excluding the tenuous inframarginal

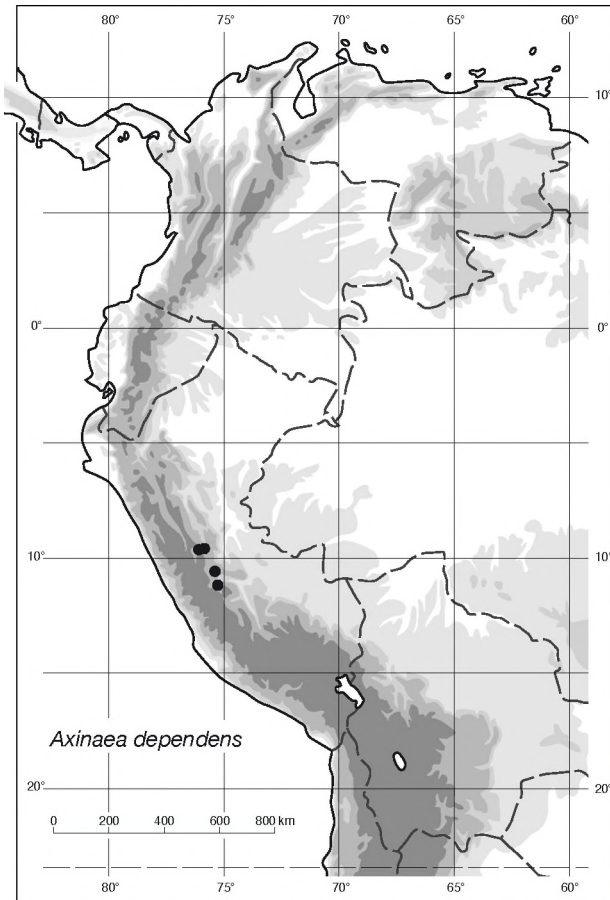


Figure 24. Distribution of *Axinaea dependens*

nerves that run ca 0.5 mm from the margin, the inner pair of primaries diverging 1–2.5 cm above the base of the lamina, sometimes shortly so, and then the inner pair of primaries diverging 0.3–5 mm above the base of the lamina, adaxially glabrous except near the base, abaxially moderately to sparsely furfuraceous; *secondary nerves* evident abaxially, parallel, 2–4 mm apart. **In-florescence** a pendulous thyrse, many-branched, >26-flowered, terminal, 12–35 cm long, flowers arranged in fascicles; *nodal flaps* present in the larger nodes, similar to those on the branches but smaller; *pedicels* slender, 6–10 mm long. **Flowers** 4-merous, 12–18 mm long; *hypanthium* cupuliform, 1.5–3 mm long; *calyx* 1 mm long, obscurely 4-lobed, external teeth obscure or absent; *petals* coral red or pink, widely-obovate, concave, 8–10 × 8–9 mm wide, apex rounded or

truncate; *stamens* isomorphic; *filaments* complanate, 3–4 mm long; *connective appendage* ellipsoidal, 4–5 × 2 × 2 mm, acute basally; *anthers* 4–5 mm long with one small slightly dorsal pore; *ovary* oblong, costulate, apex 4-lobed, 4-celled; *style* 11–14 mm long, curved at the apex. **Fruit** and *seeds* not seen.

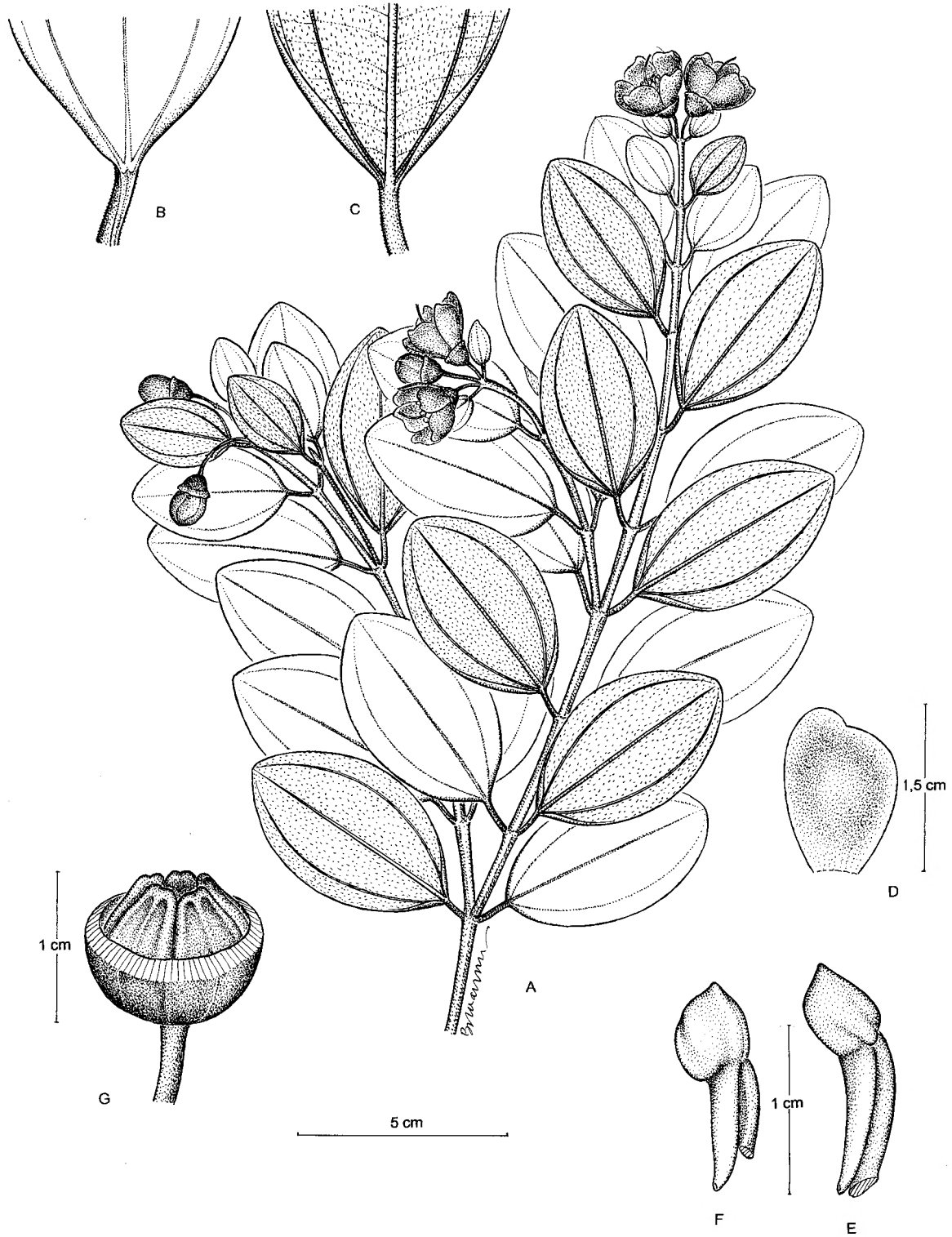
*Axinaea dependens* is endemic to the eastern slopes of the Andes in central Peru, where it grows at 2300–3200 m elevation. – Figure 24.

**Additional specimens examined – PERU: Huánuco:** Prov. Huánuco, summit at Carpish Pass on road between Huánuco and Tingo María, 3200 m, 14 Mar 1945, 10°34'S, 75°22'W, *Hodge 6278* (US). **Pasco:** Prov. Oxapampa, Río San Alberto valley, E of Oxapampa, W slopes of Cordillera Yanachaga, 2300 m, 4 Jul 1984, *D. N. Smith & Pretel 7590* (F, MO, US). **Dept. Unknown:** *Ruiz & Pavón s.n.* (MA).

The lectotype of *Axinaea dependens* in MA, was annotated by Pavón as such, but the name was never formally published since Ruiz and Pavón's *Flora Peruviana et Chilensis 4* did not appear until 1957. The first formal version of this name appears in D. Don (1823). *Axinaea rugosa* Ruiz & Pav., here treated as a synonym of *A. dependens*, was described for the above mentioned Ruiz and Pavón's *Flora Peruviana et Chilensis 4* but based on another specimen. No mention of this name has been found in any published work other than in the original description.

10. *Axinaea disrupta* E. Cotton, sp. nov. – Type: Ecuador. Prov. Loja, Loja–Zamora road, 12 km from Loja, on the farm of Dr. David Espinosa, 2400–2600 m, 17 Nov 1988, *Ellemann 75412* (Holotype: AAU!; isotype: LOJA!). – Figure 25.

*Species Axinaeae merianiae* (DC.) Triana simulans, a qua differt indumento ex trichomatibus dendriticis, ramosissimis (non arachnoideis, indistinctis) et ratio longitudinis/latitudinis 1.75 : 1 (non 2.5 : 1).



**Figure 25.** *Axinaea disrupta* – A. Habit. B. Detail of adaxial leaf base. C. Detail of abaxial leaf base. D. Petal. E, F. Anisomorphic stamens showing the filament, the spherical connective that is basally somewhat apiculate, and the anther. G. Fruit (From *Elleman 75412*).

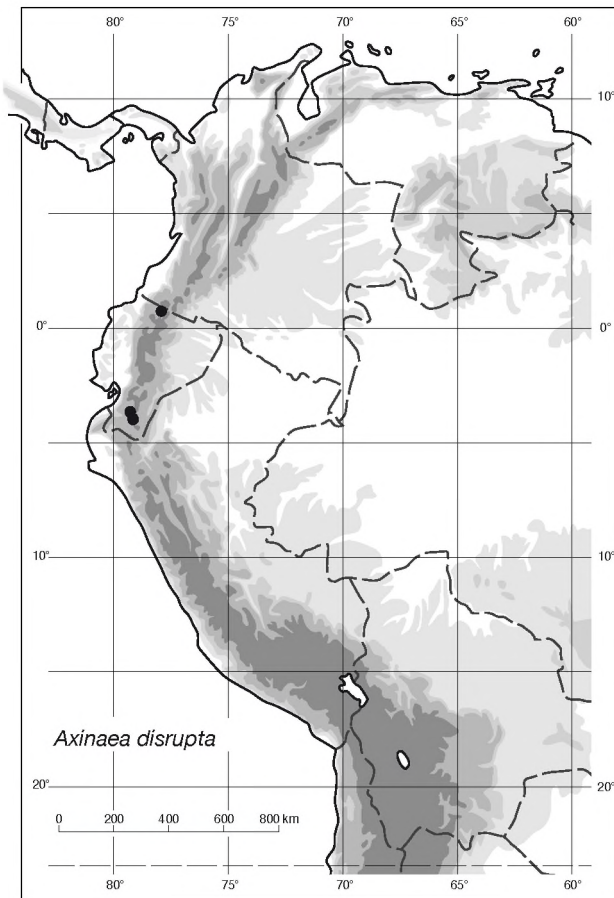


Figure 26. Distribution of *Axinaea disrupta*.

**Shrub or small tree**, 1–6 m tall; *branchlets* sub-quadrangular, moderately to densely puberulent, hairs dendritic, densely branched, under 0.5 mm long; *stipuliform flaps* reduced to a faint, almost indistinct line across the nodes. **Leaves** petiolate; *petiole* 0.5–1 cm long; *lamina* elliptic or elliptic-obovate, 3.5–6 × 2–3.5 cm, coriaceous, rigid, erect, adaxially glabrous, abaxially with scattered puberulence, hairs similar to those on the branchlets; *apex* rounded or obtuse; *base* auriculate, though apparently cuneate due to the revolution of the 1–2 mm long auricles; *scutum* absent; *margins* entire or shallowly and distantly denticulate in the upper half, teeth minute; *venation* 3-nerved, excluding the tenuous inframarginal nerves that run 0.5–1 mm from the margin, adaxially sunken, glabrous, abaxially prominent, sparsely puberulent, hairs similar to those

on the branchlets; *secondary nerves* faint adaxially, parallel, 1–2 mm apart. **Inflorescence** a pendulous, few-flowered, terminal thyrse, 5–8 cm long, subtended by two bracts that are similar to the leaves but smaller, occasionally with additional bracts present in higher nodes of the inflorescence; *pedicels*, 5–6 mm long. **Flowers** 5-merous, 1.5–2 cm long; *hypanthium* cyathiform, 2–4 mm long; *calyx* ca 1 mm long, truncate, external teeth not visible; *petals* lilac, obovate, concave, 1.5–1.8 × 1–1.2 cm, apex broadly and asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 8–10 mm long; *connective appendage* spherical, 3 × 2 × 2 mm, dimorphic, smaller and somewhat apiculate basally on the larger stamens, slightly larger and rounded basally on the shorter ones, yellow-brown; *anthers* 4 mm or 6 mm long with one minute slightly dorsal pore; *ovary* oblong, costulate, apex 5-bilobed, 5-celled; *style* ca 2 cm long. **Fruit** a 5-lobed capsule, lobe apices hardened, thickened and projecting outwards for 0.5–1 mm, hypanthium covering half or less of the mature capsule; *seeds* cuneiform.

*Axinaea disrupta* grows in the Andean montane forests of northern Ecuador in the Carchi province, and disjunctly in southern Ecuador, in the Loja and Zamora provinces, at elevations of 2400–3100 m. – Figure 26.

**Additional specimens examined – ECUADOR:**  
**Carchi:** road Tulcán–Maldonado, Western Cordillera, 3100 m, 15 Jun 1979, *Albert de Escobar & Fallen 1456* (US). **Loja:** road Saraguro–Loma de Oro, 7.8 km from turnoff, 2990 m, 4 Aug 2000, 3°38'S, 79°15'W, *Cotton et al. 1551* (AAU, LOJA, QCNE); 5 km S of Saraguro, on Loja–Cuenca road, 2600–2700 m, 7 Oct 1988, 3°39'S, 79°15'W, *Ellemann 66593* (AAU, LOJA, QCA). **Loja/Zamora-Chinchi:** mountain crest N of road Loja–Zamora, 1 km E of pass, 2800–2900 m, 17 Feb 1989, 3°59'S, 79°08'W, *Ølgaard 90618* (AAU, LOJA). **Zamora-Chinchi:** limit of Parque Nacional Podocarpus, road Loja–Zamora, about 1 km E of pass, 2800–2850 m, 29 Jan 1989, 3°58'S, 79°07'W, *Madsen 85715* (AAU, LOJA); *85720* (AAU, LOJA).

*Axinaea disrupta* is another species that has been separated from the large mix of species previously identified as *A. macrophylla* (see also comments under *A. lawesonii*). The 3-nerved (*vs.* 5-nerved or 5-plinerved) venation, together with the rounded or obtuse (*vs.* widely acute to acuminate) lamina apex, distinguishes this species from *A. macrophylla*. Among the 3-nerved species *A. disrupta* is similar to *A. merianiae*, from which it differs in having a indument of minute, dendritic or barbellate trichomes (not lepidote or arachnoid) and a lamina that is 1.75 times as long as wide (not 2.5 times as long as wide).

The species epithet refers to the disjunct distribution of this species that grows in the montane forests of northern and southern Ecuador and apparently not anywhere in between. The same distribution patterns are found in other completely unrelated species (e.g. *Gleichenia simplex* (Desv.) Hook) and we speculate that the populations may be remnants of a former continued distribution that was interrupted by recent volcanic activity in central Ecuador, forming soils that are unsuited for the growth of some species.

11. *Axinaea fallax* Gleason, Revista Acad. Colomb. Ci. Exact. 6: 551. 1946. — Type: Colombia. Valle: Cordillera Occidental, Los Farallones, north end, eastern slope, Alto del Buey, 3300–3450 m, 13 Oct 1944, *Cuatrecasas 18059* (holotype: NY!; isotypes: F!, [photo: NY!], US! [photo: NY!]).

**Tree**, 15–18 m tall; *branchlets* obscurely quadrangular becoming terete with age, densely furfuraceous-tomentose when young, becoming glabrous with age, hairs minute, 0.2–0.4 mm long, dendritic, densely and finely branched; *nodes* not thickened; *stipuliform flaps* absent. **Leaves** petiolate; *petiole* 7–17 mm long, densely furfuraceous-tomentose when young, moderately so with age, hairs similar to those on the branchlets; *lamina* elliptic-ovate, 7–11 × (3.5–)4.5–6.3 cm, coriaceous, rigid, adaxially glabrous, abaxially densely furfuraceous-tomentose, the pubescence ferruginous, hairs similar to those on the branchlets; *apex* acute to rounded; *base* rounded to shallowly cordate; *scutum* absent; *margins* entire; *venation* 5-nerved, excluding the tenu-

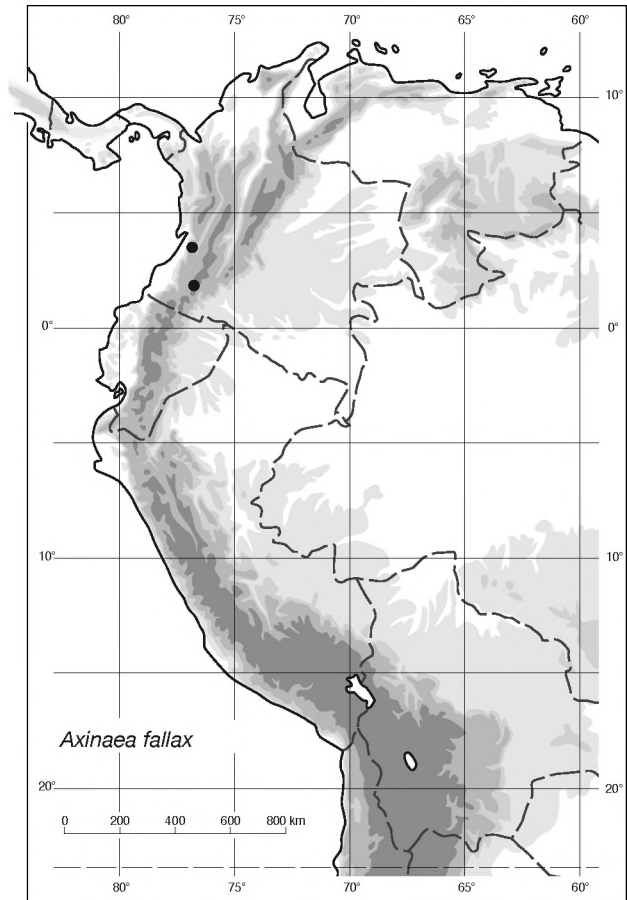


Figure 27. Distribution of *Axinaea fallax*.

ous inframarginal nerves that run ca 0.5 mm from the margin, often made invisible by the pubescence, adaxially glabrous, sunken, abaxially densely furfuraceous-tomentose, prominent, hairs similar to those on the branchlets; *secondary nerves* sunken adaxially, prominent abaxially, parallel, 1–2 mm apart. **Inflorescence** a more or less erect thyrse, few-branched, 3–10-flowered, terminal, 5–8 cm long, subtended by a pair of bracts that are similar to the leaves but smaller, bracts 3.3–7.3 × 1.8–4.5 cm, flowers arranged in dicias; *pedicels* 3–6 mm long, densely tomentose. **Flowers** 5-merous, 1.7–2.5 cm long; *hypanthium* cyathiform, 3–5 mm long, densely to moderately tomentose; *calyx* 2–3 mm long, 5-lobed, lobes rounded, glabrous to moderately tomentose; *external teeth* present as small, hair-covered protuberances, projecting ca 1 mm; *petals* pink to pink-



**Figure 28.** *Axinaea fernando-cabiesii* – A. Flower. (Bussmann *et al.* 15625. Photos: Rainer Bussmann). B. Inflorescence showing flowers and buds.

red, fleshy, widely obovate, concave, 12–14 × 12–14 mm, apex broadly and asymmetrically bilobed or rounded; *stamens* isomorphic; *filaments* (only immature ones seen) 2–3 mm long, complanate; *connective appendage* bulbous, 3–4 × 2 × 2 mm, somewhat apiculate basally; *anthers* 5–6 mm long with one small dorsal pore; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* immature. **Fruit** and *seeds* not seen.

*Axinaea fallax* is restricted to the Western Cordillera of Colombia, where it grows at 2950–3450 m elevation. – Figure 27.

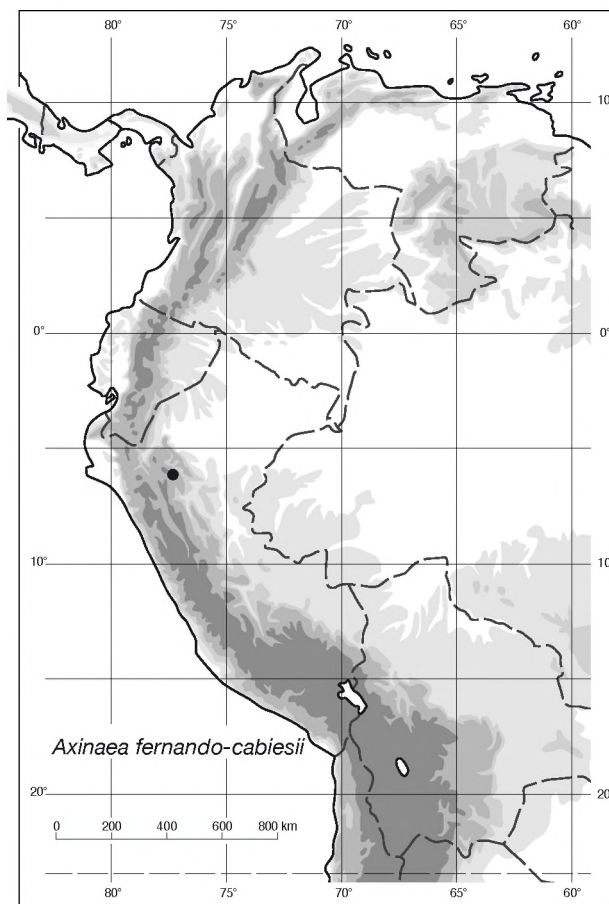
**Additional specimen examined – COLOMBIA:**  
**Cauca:** Mpio. San Sebastián, Cabaña El Hoyuelo, Finca Blanca, towards Peñas Blancas, 2950 m, 6 Oct 1992, Orozco *et al.* 2459 (US).

*Axinaea fallax* is known only from one collection in addition to the type. Both are from the Western Cordillera in Colombia. The type was collected in Dept. Valle and the other specimen in Dept. Cauca, which is a neighboring department. *Axinaea fallax* is quite similar to *Axinaea colombiana* but much larger, more robust and 5-merous (in contrast to *A. colombiana* that is 4-merous).

**12. *Axinaea fernando-cabiesii*** Bussmann, Gruhn & Glenn, in *Nordic Journal of Botany* 28: 518–520. 2010. – Type: Peru. Amazonas: Chachapoyas, Leymebamba, Cordillera Yasgolga, east of peak, close to Refugio 06°41'44"S, 77°41'24"W, 2789 m, 18 Jun 2009, Bussmann, Vega, Glenn, Gruhn & Wagter 15625 (holotype: HUT, isotypes: HAO, MO, NY). – Figure 28.

**Small understory tree**, 4–5 m tall; *branchlets* terete or obscurely quadrangular, densely furfuraceous throughout, hairs pinoid, dendritic, short, thick, densely branched, up to 1 mm long; *nodes* slightly thickened; *stipuliform flaps* well developed, coriaceous, up to 1 cm long. **Leaves** petiolate; *petiole* 6–25 mm long, densely arachnoid-furfuraceous; *lamina* elliptic-lanceolate, 9–18 × 2–5 cm, coriaceous, adaxially sparsely arachnoid-furfuraceous, abaxially densely cream arachnoid-furfuraceous, occasionally gland-dotted with minute orange glands only visible under ×10 magnification; *apex* broadly acute; *base* attenuate, strongly revolute; *scutum* absent; *margins* shallowly denticulate, weakly revolute; *venation* (3-)5-plinerved, excluding the tenuous inframarginal nerves that run ca 0.5 mm from the margin, the inner pair of primaries diverging from the main nerve 1–2 cm above the leaf base, prominent abaxially, sparsely to moderately furfuraceous above, densely furfuraceous abaxially, hairs similar to those on the branches; *secondary nerves* prominent abaxially, parallel, 1–2 mm apart. **Inflorescence** a pedulous, compound thyrse, 60–80-flowered, terminal, 25–75 cm long, subtended by a pair bracts; *bracts* similar to the leaves but smaller; *pedicels* 5–8 mm long, densely furfuraceous, hairs as in the branches but shorter. **Flowers** 4-merous, 1–1.5 cm long; *hypanthium* cupuliform, 4–5 mm long, moderately furfuraceous, hairs as on pedicels; *calyx* 1–2 mm long, obscurely 4-lobed, external teeth inconspicuous or absent; *petals* magenta turning pale neon-blue outside, lighter pink to white inside, fleshy, obovate, concave, 10–12 × 9–11 mm, apex asymmetrically bilobed; *stamens* 8, isomorphic; *filaments* complanate, 9–10 mm long; *connective appendage* ellipsoidal, acute basally, yellow turning red-orange; *anthers* 4–5 mm long with one small slightly dorsal pore, deep reddish-purple; *ovary* oblong, 8-costulate, apex 4-lobed, 4-celled; *style* 10–17 mm long, pale blue. **Fruit and seeds** not seen.

*Axinaea fernando-cabiesii* is known only from the type locality on the eastern slopes of the northern Peruvian Andes in the Leymebamba district. There it grows as an understory tree in slightly disturbed cloud forest,



**Figure 29.** Distribution of *Axinaea fernando-cabiesii*.

at altitudes of 2750–2850 m in an area of less than 20 km<sup>2</sup>. — Figure 29.

*Axinaea fernando-cabiesii* shares the color of the outside of the petals (magenta in bud turning purple-blue in maturity) with *A. mertensioides* also from northern Peru. It shares with *A. dependens* the long pendulous inflorescences but the color of the flowers differs (coral red or pink in *A. dependens*). The pre-eminent student of Melastomataceae during 1950–1990, John Wurdack, commented once based on extensive field observations in northern Peru that hybridization might be an important driver of *Axinaea* diversity. We hypothesize, that *A. fernando-cabiesii* is a hybrid of *A. mertensioides* × *A. dependens*, which would need substantiation by further studies of their breeding ecology.

13. *Axinaea flava* E. Cotton, Bussmann & P. Lozano, in *Nordic Journal of Botany* 23: 51. 2004. — Type: Ecuador. Loja: Amaluza, above Laguna Negra de Jimbura, Cordillera de Sabanilla, 3550–3780 m, 10 Oct 2001, 04°42'46"S, 79°25'41"W, *Lozano & Bussmann 001* (holotype: AAU!; isotype: LOJA [n.v.]). — Figures 30 and 31.

**Shrub or small tree**, 1.5–2 m tall; *branchlets* terete or obscurely quadrangular, densely furfuraceous throughout, hairs dendritic, short, thick, densely branched, 0.25 mm long; *nodes* barely or not at all thickened; *stipuliform flaps* reduced to a line across the nodes. **Leaves** petiolate; *petiole* 4–5 mm long, densely furfuraceous; *lamina* elliptic-ovate, 2.5–3.5 × 2–2.5 cm, coriaceous, rigid, erect, adaxially glabrous and lustrous, abaxially densely white arachnoid-furfuraceous, the surface of the lamina completely covered by the indument, hairs indistinct; *apex* rounded or broadly acute; *base* rounded to truncate, not revolute; *scutum* absent; *margins* entire to shallowly denticulate; *venation* shortly 3-plinerved, excluding the tenuous inframarginal nerves that run ca 0.5 mm from the margin, the inner pair of primaries diverging from the main nerve 2–3 mm above the leaf base, prominent abaxially, glabrous above except at the base, sparsely pubescent abaxially, hairs similar to those on the branches; *secondary nerves* evident abaxially, parallel, 1–2 mm apart. **Inflorescence** an erect thyrse, 3–5-flowered, terminal, 4–6 cm long, subtended by a pair bracts; *bracts* similar to the leaves but smaller, 2–3 × 1.5 cm; *pedicels* 2–4 mm long, densely furfuraceous, hairs as in the branches but shorter. **Flowers** 5-merous, 2–2.5 cm long; *hypanthium* cupuliform, 4–5 mm long, densely furfuraceous, hairs as on pedicels; *calyx* 1–2 mm long, obscurely 5-lobed, external teeth evident, hardened, 0.5–1 mm long; *petals* dark ochre-yellow outside, lighter yellow inside, fleshy, obovate, con-

cave, 1.7–2 × 1–1.2 cm, apex irregularly bilobed; *stamens* 10, isomorphic or with a slight difference in size; *filaments* complanate, 7–8 mm long; *connective appendage* spherical, 4 × 4 × 4 mm, rounded basally, creamy-yellow; *anthers* 6–7 mm long with one small slightly dorsal pore, ochre to dark brown; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* 10–16 mm long, yellow. **Fruit** a (4–)5-lobed capsule, the hypanthium covering 1/2 or less of the mature capsule; *seeds* pyramidal or cuneiform.

*Axinaea flava* is known only from the type locality on the southern slopes of the Ecuadorian Andes, very close to the boundary between Ecuador and Peru. There it grows in slightly disturbed tree-line vegetation and scrub-páramo, at altitudes of 3400–3800 m in a small population with at most 100 individuals. — Figure 32.

**Additional specimens examined — ECUADOR:**

**Loja:** Amaluza, Jimbura, Lagunas Negras, 3400 m, 16 Dec 1995, *N. Aguirre 2* (LOJA); Cordillera de Sabanilla, near road Jimbura-Zumba, páramo above Laguna Negra, 3000–3500 m, 23 Oct 1996, UTM 9479100/674600, *Bussmann & Lange 724* (LOJA, QCA, QCNE).

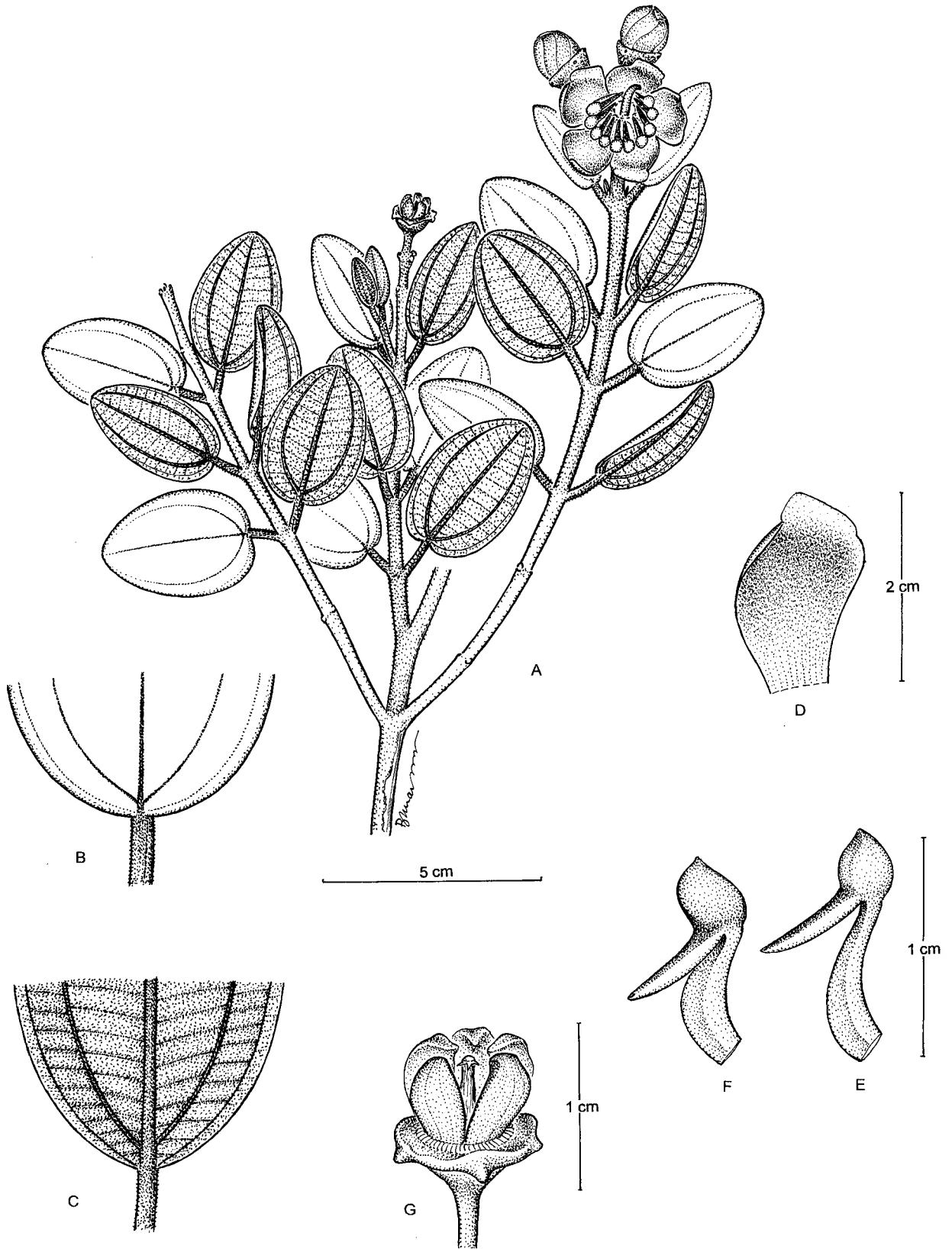
*Axinaea flava* is a scrub páramo species and shows many characteristics of typical high altitude species, such as stunted habit, erect, rigid-coriaceous leaves, and dense pubescence covering the lamina abaxially (Figure 31). It is very easy to identify by the yellow flowers that are quite rare in Melastomataceae and to which the species epithet refers.

14. *Axinaea floribunda* (Naudin) Triana, *Trans. Linn. Soc. London* 28: 69. 1871. — *Chastenaea floribunda* Naudin, *Ann. Sci. Nat. Bot., Sér. 3*, 18: 122. 1852.

*Opposite page:*

**Figure 30.** *Axinaea flava* — A. Habit, showing the erect leaves, a branch with a dichasium, and a branch with a capsule. B. Lamina base adaxially. C. Lamina base abaxially. D. Petal. E and F. Antepetalous and antesepalous stamens respectively, showing the filament, the connective with an apiculate base and the anther with a dorsal pore. G. Fruit, showing the hypanthium covering less than 1/2 of the mature capsule (From *Lozano & Bussmann 001*, AAU).

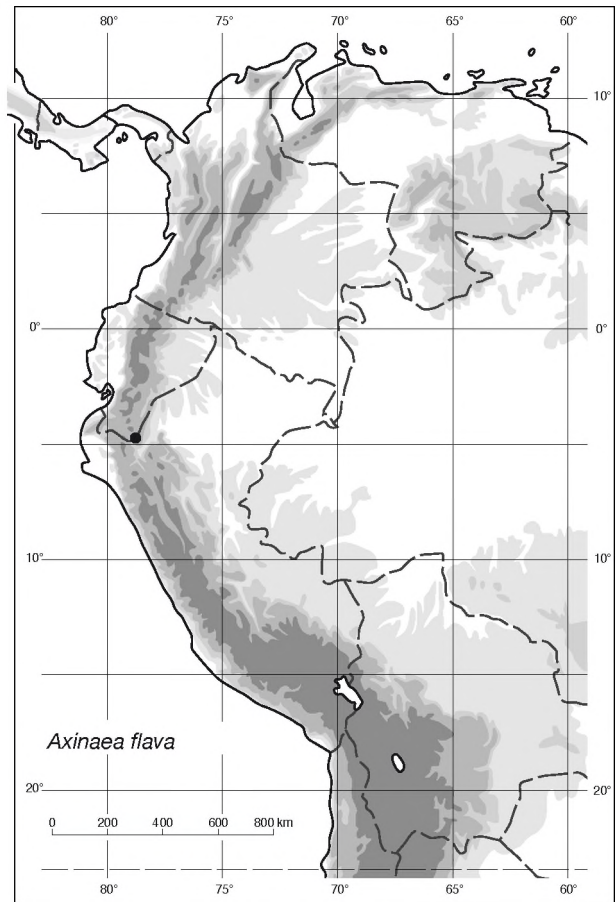






– Type: Colombia: Pamplona, ca 2000 m, *Linden 768* (lectotype: G! [Herb. Delessert], here designated; photos: F!, MO!, NY!; isotypes: BR!, G! [Herb. Barbey-Boissier], P!, W! [2 sheets, W Herb. # 20988, the other sheet unnumbered]; photo of the P isotype: NY!). – Figure 33.

**Tree or large shrub**, 3–12 m tall; *branchlets* subquad-rangular to terete, densely to moderately puberulent when young, becoming glabrous with age, hairs minute, dendritic, shaggy; *stipuliform flaps* reduced to a line across the nodes. **Leaves** petiolate; *petiole* 1.5–4 cm long; *lamina* elliptic, 7–16 × 3–6 cm, coriaceous, adaxially glabrous except when young, abaxially densely to moderately puberulent when young, sparsely so with age, hairs as on the branchlets; *apex* acuminate; *base* cuneate, attenuate, or rounded, shortly auriculate, the auricles up to 3 mm long, revolute, with entire or dentate-undulated margins; *scutum* usually absent but occasionally incipient and v-shaped; *margins* entire to shallowly and distantly denticulate on the upper half; *venation* (3–)5-nerved, or shortly (3–5 mm) plinerved, excluding the tenuous inframarginal nerves that run ca 0.5 mm from the margin, but the second pair of primaries sometimes much fainter, giving the impression of being 3-nerved, adaxially glabrous, abaxially with occasional, short, thick, densely branched, shaggy hairs; *secondary nerves* sometimes faint adaxially, parallel, 2–3 mm apart. **Inflorescence** a pendulous thyrse, many-branched, >26-flowered, terminal, 5–10 cm long, often subtended by two bracts similar to those on the leaves but smaller, occasionally additional, smaller bracts present in higher nodes of the inflorescence; *pedicels* slender, 3–8 mm long. **Flowers** 5-merous, 1–1.5 cm long; *hypanthium* cyathiform, 2–3 mm long; *calyx* ca 1 mm long, flaring, obscurely 5-lobed or the lobes not evident, external teeth not evident; *petals* white or light pink inside, darker outside, oblong to slightly obovate, concave, 6–8 × 9–12 mm, apex asymmetrically bilobed; *stamens* anisomorphic; *filaments* compla-



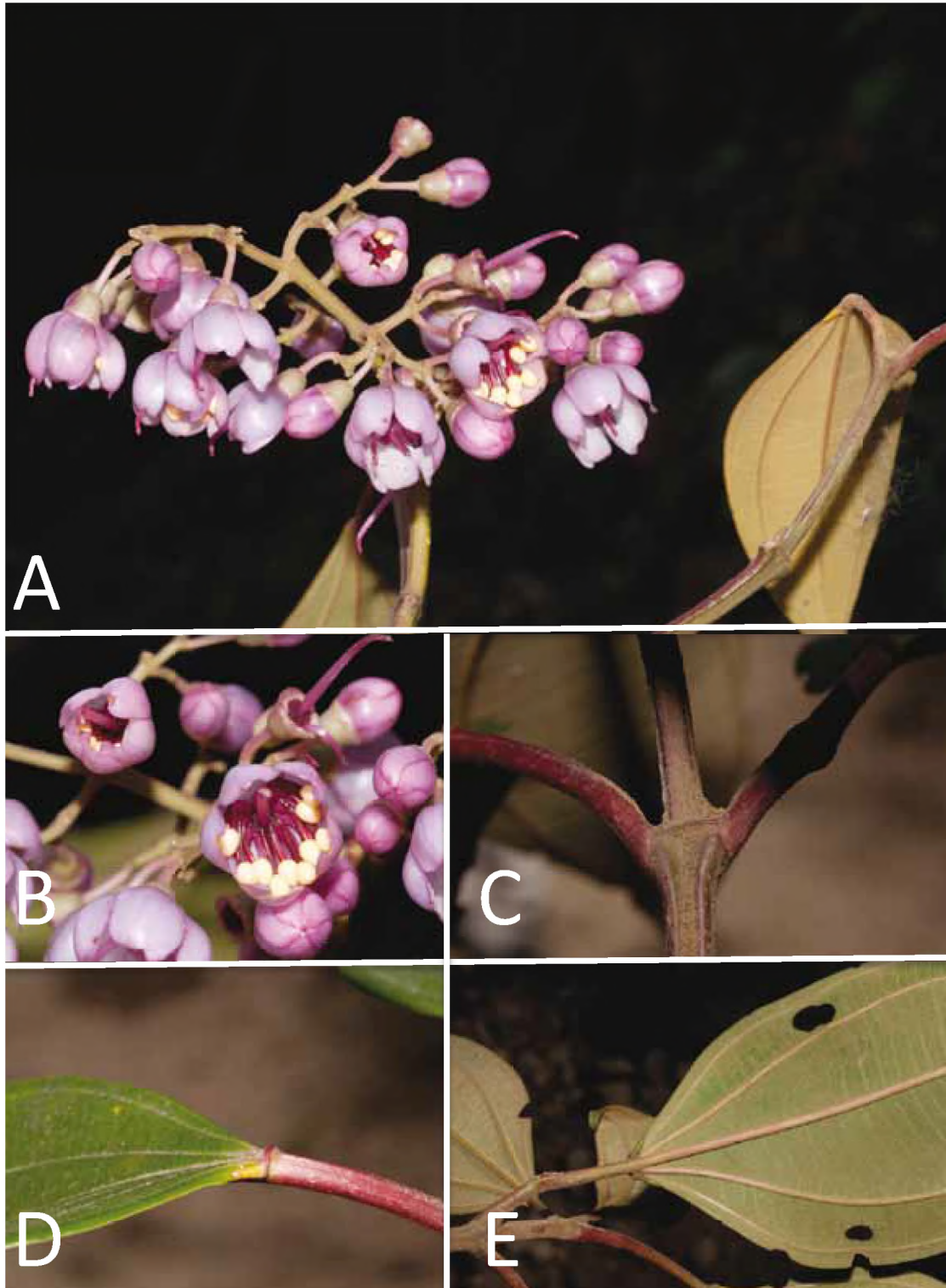
**Figure 32.** Distribution of *Axinaea flava*.

nate, white or pink, 6–7 mm long in the longer stamens, 4–5 mm long in the shorter ones; *connective appendage* spherical, 3 × 2 × 2 mm, somewhat apiculate basally, dark yellow; *anthers* red, dark red, or greenish with a red longitudinal stripe, 4–5 mm long, with one minute slightly dorsal pore; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* ca 1.5 cm long. **Fruit** a 5-lobed capsule, the hypanthium covering 1/2–2/3 of the mature capsule; *seeds* cuneiform.

*Axinaea floribunda* is widely distributed in the Andes from Venezuela over Colombia and Ecuador to Peru,

*Opposite page:*

**Figure 31.** *Axinaea flava* – A. Habit. B. Flower. (Lozano & Bussmann oot. Photos: Rainer Bussmann).

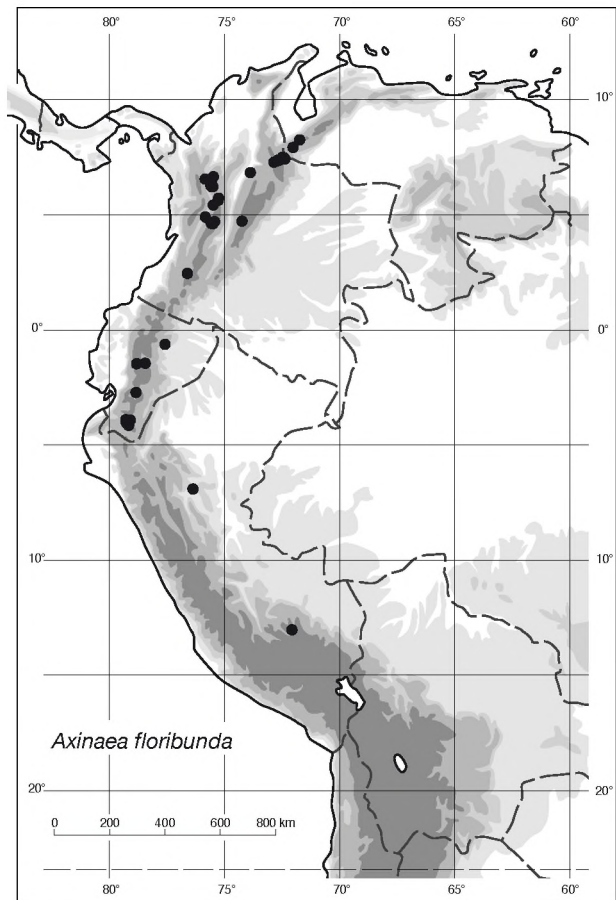


**Figure 33.** *Axinaea floribunda* – A. Inflorescence. B. Flower. C. Node of leafy branch. D. Leaf base adaxial surface showing scutum. E. Leaf base abaxial surface showing the reflexed auricles. (*Michelangeli 1957*, Peru, Cuzco. Photo: Fabián Michelangeli).

where it grows at altitudes of 1500–3000 m. – Figure 34.

**Additional specimens examined – VENEZUELA:**

**Mérida:** 19–21 km S of Tovar along road to Canaguá, 2130 m, 16 Apr 1984, 8°15'N, 71°44'W, *Luteyn & Lebrón-Luteyn 10004* (NY). **Táchira:** Dtto. Junín, between Villa Páez and Betania, close to Colombian border, 2000–2400 m, 15 Nov 1975, *Bunting 4912* (K, NY); right margin of Río Táchira, frontier with Colombia, 2300 m, 13 Nov 1976, *Charpin & Jacquemoud AC 13299* (F, G, US); Río Táchira basin, El Cobre, 2500–2600 m, 15 Jan 1973, *Cuatrecasas et al. 28307* (F, US); Páramo del Zumbador, 2500 m, *Funck & Schlim 1477* (BR, F, G [Herb Barbey-Boissier], G [Herb. Delessert], W), crest of Cobre Pequeño or Chiquito, W of Mountain El Cobre, páramo of Tamá, ca 5.2 km NE of Villa Páez, 2900 m, 13 Dec 1970, *Ruiz-Terán & López-Figueiras 1261* (F, NY); road Zumbador-Queniquea, 2700 m, 25 Nov 1972, *Wurdack et al. 2791* (NY, VEN); below Páramo de Tamá, 2400 m, 28 Nov 1972, *Wurdack et al. 2809* (NY, US, VEN). **COLOMBIA: Antioquia:** Santa Elena, 1500–2000 m, 28 Dec 1930, *Archer 1203* (NY, US); Mpio. Medellín, Las Palmas, El Peñasco, Sitio Manantial, 2330 m, 9 Mar 1990, 6°13.2'N, 75°32.8'W, *Betancur et al. 1784* (MO); Mpio. Sonsón, Chaverras, Quebrada El Padre Sánchez, up towards La Paloma height, 2850–2900 m, 19 Aug 1992, 5°37'N, 75°16'W, *Callejas & Roldán 10626* (NY); Alto Capiro, NW of Sonsón, ca 3000 m, 26 May 1944, *Core 771* (NY, US); San Pedro, Dec 1937, *Bro. Daniel 1469* (F); San Pedro, Dec 1937, *Bro. Daniel & Bro. Thomas 1236* (US); Central Cordillera, road between Medellín and Río Negro, close to Santa Elena, 2000–2500 m, 18 Mar 1946, *Hodge 6756* (F, US); Santa Rosa, 2000–2600 m, *Lehmann 7446* (F, GH, K); Medellín, *Patin s.n.* (NY); San Pedro, Mar 1939, *Bro. Thomas 91* (US); Mpio. Santa Rosa de Osos, km 5–12 of road from Llanos de Cuivá to San Andrés, 2680–2730 m, 10 May 1988, 6°50'N, 75°32'W, *Zarucchi & Betancur 6405* (F, GH, NY). **Caldas:** Central Cordillera, Basin of Río Otún, between Peña Bonita and Las Delicias, 2560 m, 27 Nov 1946, *Cuatrecasas 23360* (F, NY); Laguneta to Magana, old Quindío trail, 3000–3200 m, 1 Aug 1922, *Killip & Hazen 9474* (GH, NY); La-



**Figure 34.** Distribution of *Axinaea floribunda*.

guneta, Salento, 2800 m, 10 Apr 1942, *von Sneidern 3192* (GH, NY, S, US); San Félix, near Salamina, 3000 m, Jul 1945, *Bro. Thomas 2388* (US). **Quindío:** Mariquita, Páramo (Quindío), 3000 m, 1851–1857, *Triana s.n.* (BR, NY [2 sheets], W); Mariquita, Mount Quindío, *Triana s.n.* (BR [fragment]). **Risaralda:** Regional Park Ucumarí, ca 22 km ESE of Pereira, 2100–2670 m, 25 May 1989, 4°40'N, 75°35'W, *Luteyn & Rangel 13182* (AAU, NY); Ucumarí Reserve, La Pastora, 2400–2500 m, 8 Oct 1989, *Rangel et al. 5135* (MO). **Valle del Cauca:** Páramo del Quindío, 2800 m, Jul 1853, *Triana 6171* (BM). **ECUADOR: Sucumbios:** road Julio Andrade-Playón de San Francisco–Santa Bárbara–La Bonita, 24 km from Julio Andrade, 2880 m, 11 Sep 2001, 0°38'W 77°34'N, *Cotton & Rivas 1707* (AAU). **Cañar:** Páramo de Huaira-caja, above Azogues, 2700–3000 m

(from Lehmann's notes), *Lehmann 4653* (F, US); valley of Río Tabacal, ca 15 km NE of Azogues, 3300 m, 27 Sep 1944, *Prieto P-116* (F, NY, S, VEN, W). **Loja:** Cerro Villonaco, ca 7 km W of Loja, 2600–3200 m, 9 Oct 1944, *Camp E-665* (NY [2 sheets], US); road Loja-Zamora, 5 km from Loja, 29 Jul 1982, *Clemants et al. 2239* (NY, US); road Loja-Catamayo, turnoff to Cerro Villonaco, 7.5 km from turnoff, 1500–2500 m, 8 Aug 2000, 3°59'S, 79°16'W, *Cotton et al. 1578* (AAU); 8.4 km from turnoff, 2550 m, *Cotton et al. 1579* (AAU); 1580 (AAU); Villonaco, 2800 m, 5 Oct 1946, *Espinosa 722* (F, LOJA, NY); between La Toma and Loja, 1800–2600 m, 4 Sep 1923, *Hitchcock 21436* (GH, NY, US); road Loja-Zamora, 2400 m, 13 Jun 1999, *Homeier 141* (AAU); Loja-Saraguro, km 25, turnoff towards Buenavista and Taquil, 2400–2500 m, 21 Jul 1990, 3°54'S, 79°16'W, *Jørgensen & Ulloa 91994* (AAU, MO, NY); Cerro de Villonaco, Loja-La Toma, km 13, turnoff towards Chquiribamba, km 2, Hda. La Huangora, 2640 m, 18 Apr 1994, 3°56'52"S, 79°15'52"W, *Jørgensen et al. 324* (MO); old road Catamayo-Loja, km 8.2, 2690 m, 15 Sep 1997, 3°59'S, 79°16'W, *Gwilym Lewis & Bruneau 3540* (AAU, K [2 sheets], NY); road Universidad Nacional de Loja-Las Achira (Uritusinga), km 10, 2800 m, 25 Oct 2001, 4°3'22"S, 79°14'13"W, *Madsen & Chimbo 8605A* (AAU). **Province unknown:** *Ruiz & Pavón s.n.* (F); no locality, *Ruiz & Pavón s.n.* [enumeration on label 14/79], (F); "In Andibus Ecuadorensibus", "Andes Quitenses, Tungurahua", 1857–1859, *Spruce 5831* (BR, F, G, GH, S [3 sheets], W [3 sheets]). **PERU: San Martín:** Province Huallaga, District: Saposoa, near La Canaán, 2000 m, 30 Aug 2001, *Quipuscoa S. & Vilchez T. 2645* (AAU). **Cusco:** Cusco, *Michelangeli 1957* (NY).

Eves (1936) reduced *Axinaea floribunda* to synonymy under *A. macrophylla* (Naudin) Triana. After careful examination of the available type material, we believe *A. floribunda* is a distinct taxon, distinguished from *A. macrophylla* by its >26-flowered (*vs.* 1–25-flowered) inflorescences with flowers at the most 1.5 cm (*vs.* 1.5–2 cm) long.

Specimens from south Ecuador usually have auricles with dentate-undulate margins and hypanthia cover-

ing 2/3 of the mature capsule, while specimens from Venezuela, Colombia and northern Ecuador have auricles mostly with entire margins and the hypanthium covering 1/2 of the mature capsule.

15. *Axinaea glandulosa* D. Don, Mem. Wern. Nat. Hist. Soc. 4: 321. 1823. — Type: Peru. *Ruiz & Pavón s.n.* (lectotype MA!, here designated; isotypes: B [destroyed], BM! [2 sheets], MA! [2 sheets], BR! [fragment], F!, G! 2 sheets [Herb. Barbey-Boissier, G Herb # 8817/14 and 8817/25], US!; photos of the B isotype: F!, MO!, NY!).

**Shrub or tree**, 1–18 m tall; *branchlets* subquadrangular, densely to moderately pubescent when young, less so with age, hairs barbellate, minute; *nodes* slightly thickened; *stipuliform flaps* reduced to a thin line across the nodes. **Leaves** petiolate; *petiole* 1.5–4 cm long, moderately pubescent when young becoming glabrous with age, hairs similar to those on the branchlets; *lamina* ovate-lanceolate, 8–14 × 5–8 cm, coriaceous, adaxially glabrous, abaxially moderately to densely pubescent, hairs roughened, 0.3–0.5 mm long; *apex* acute; *base* rounded, auricles 1–3 mm long, revolute; *scutum* well developed, often absent in the leaf-like bracts that subtend the inflorescence; *margins* entire to shallowly denticulate; *venation* 5-nerved, adaxially faint, glabrous or with scattered pubescence, abaxially prominent and moderately to densely pubescent, hairs similar to those on the leaf; *secondary nerves* evident, parallel, 2–4 mm apart. **Inflorescence** a thyrse, 11–25-flowered, terminal, 5–10 cm long, often subtended by bracts similar to the leaves but smaller; *pedicels* 5–10 mm long, moderately to sparsely pubescent, hairs similar to those on the branchlets. **Flowers** 5-merous, 2 cm long; *hypanthium* cupuliform, 3–4 mm long; *calyx* 1–2 mm long, obscurely 5-lobed, apex truncate, external teeth much reduced or absent; *petals* light pink or white, elliptic-obovate, 14–17 × 10–13 mm wide, apex rounded or irregularly and asymmetrically lobed; *stamens* anisomorphic; *filaments* complanate, 9–10 mm long in the longer stamens, 6–7 mm long in the shorter ones; *connective appendage* spherical, 3–4 × 3 × 3 mm, rounded basally; *anthers* 6–7 mm long with a small apical pore;

*ovary* oblong, 5-costulate, apex 5-lobed, 5-celled; *style* 15–20 mm long. **Fruit** a 5-lobed capsule, the hypanthium covering half of its length; *seeds* cuneiform.

*Axinaea glandulosa* is distributed in the Andes of southern Ecuador and of northern and central Peru at 2400–3100 m elevation. – Figure 35.

**Additional specimens examined – ECUADOR:** **Morona-Santiago:** Sigsig–Gualaquiza road, km 29.3–30, 2950–3070 m, 3 Dec 1990, 3°14'S, 78°38'W, *Jørgensen et al. 92801* (AAU). **PERU:** **Amazonas:** Chachapoyas, S side of the Molinopampa– Diosan pass, 8 Aug 1962, *Wurdack 1624* (F, NY). **Huánuco:** Pampayacu, 2400 m, 4 Feb 1927, *Kanehira 11* (F, GH).

The typification of *Axinaea glandulosa* D. Don has posed problems. The name was to be included in Ruiz and Pavón's *Flora Peruviana et Chilensis 4*, but this work was not published until 1957. The first time the binomial is validly published is by David Don in 1823. During this period Don was working with A. B. Lambert. We have tried to track the Ruiz and Pavón collections from the Lambert herbarium to determine which specimens Don worked with but it is not possible to tell where these specimens went after Lambert's death (Miller 1970). The Ruiz and Pavón collections were sold to different people and could have ended up in any of the following herbaria: BB, GH, F, FI-Webb, LE, BM, G, NY, US. We have therefore decided to select one of the specimens deposited in the herbarium of the *Real Jardín Botánico* in Madrid (MA) as a lectotype as this was the herbarium in which Ruiz and Pavón worked.

To further complicate the issue, most of the Ruiz and Pavón collections of *Axinaea glandulosa* are mixed collections. Duplicates of these collections are deposited in B (destroyed), BM, F, G, MA and US. The second species of the mixed collection is described as new in this revision (see *Axinaea confusa*). In the MA sheets the two species have been labeled with "A" and "B" where "A" corresponds to the new species (*A. confusa*) and "B" corresponds to *A. glandulosa*. All available

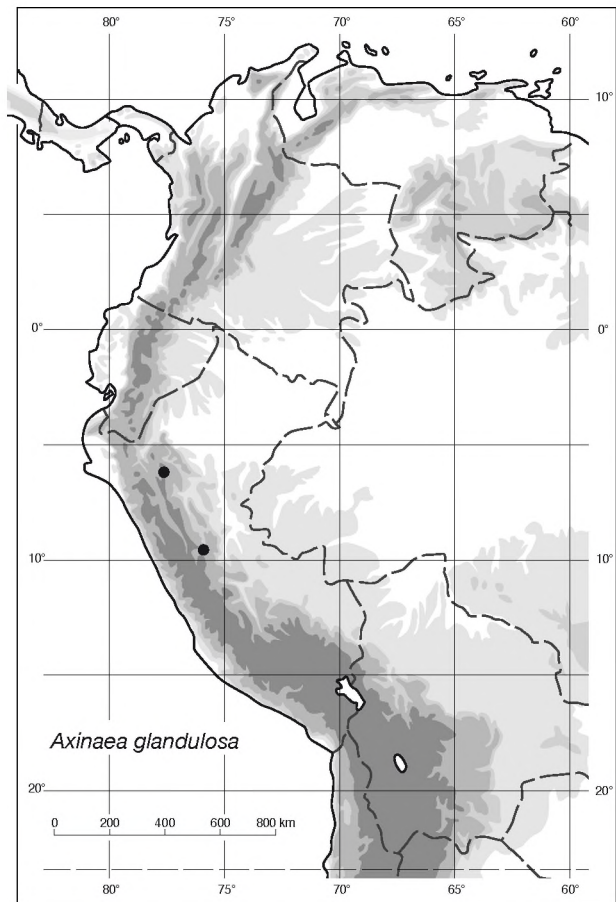


Figure 35. Distribution of *Axinaea glandulosa*.

duplicates and photographs of the duplicates of this collection have also been labeled and annotated using the same convention.

The decision as to which of the two plants in the collections was referred to when *A. glandulosa* was made after reading the Latin description that Ruiz and Pavón made for *Flora Peruviana et Chilensis 4*, published in 1957 as we believe that the original concept of the species must be reflected in their description. The species epithet chosen by Ruiz and Pavón refers to the knob-like scutum present at the base of the lamina that they refer to as a "gland". Since this structure is larger and more evident in one of the species, that species was selected as the one to bear Ruiz and Pavón's name "glandulosa". The MA specimens of *A. confusa* are either sterile fragments or in flower, while those of *A.*

*glandulosa* are in part sterile fragments but almost all are in fruit. The figure that appears in *Flora Peruviana et Chilensis* 4, is most probably a composite of the two species. The vegetative parts and the flowers belong to *A. confusa* and the fruit belongs to *A. glandulosa*.

16. *Axinaea glauca* E. Cotton & P. Lozano, in Cotton, Bussmann & Lozano, *Nordic Journal of Botany* 23: 51. 2004. — Type: Ecuador. Loja: Quilanga, higher part of Gonzanamá, road to El Inca, 2900 m, P. Lozano, A. Mainecke, R. Hofstede & N. Aguirre 1574 (holotype: AAU!; isotype: LOJA). — Figures 36 and 37.

**Shrub**, ca 50 cm tall; *branchlets* obscurely quadrangular to terete, moderately arachnoid-puberulent when young becoming glabrescent with age, hairs indistinct; *stipuliform flaps* reduced to a faint line across the nodes. **Leaves** petiolate; *petiole* 5–10 mm long, hairs similar to those on the branchlets; *lamina* oblong-elliptic, 2.5–3.5 × 1.8–2.5 cm, coriaceous, adaxially with scattered arachnoid puberulence or glabrous, abaxially densely to moderately covered with caducous, arachnoid puberulence; *base* rounded to shallowly cordate, not auriculate, not revolute; *scutum* absent; *apex* obtuse; *margins* shallowly denticulate, teeth 0.5 mm long and 2–3 mm apart; *venation* shortly 5-plinerved, excluding the tenuous inframarginal nerves that run 0.5 mm from the margin, the inner pair of primaries diverging from the main nerve 1–3 mm above the base of the lamina; *secondary venation* faint. **Inflorescence** a somewhat pendulous thyrses, 11–25-flowered, terminal, often subtended by a pair of bracts similar to the leaves but smaller, additional pairs of smaller bracts present higher in the inflorescence; *pedicels* 6–8 mm long, pubescence as in the petioles but denser. **Flowers** 5-merous, 1.5–2 cm long; *hypanthium* cyathiform, 3–4 mm long; *calyx* 1–2 mm long, 5-lobed; *external teeth* present, hardened, projecting perpendicularly ca 1 mm from the calyx lobes; *petals* pale pink or white, darker pink when in bud, oblong-obovate, somewhat asymmetric, 14–18 × 11–13 mm; *stamens* anisomorphic; *filaments* flattened, 9–10 mm long in the longer stamens, 7–8 mm long in the shorter

ones; *connective appendage* slightly dimorphic, 3 × 3 × 4 mm, ellipsoidal in the longer stamens, spherical in the shorter ones; *anthers* 5–7 mm long with one small slightly dorsal pore; *ovary* 10-costulate, apex 5-lobed; *style* 12–15 mm long. **Fruit** and *seeds* not seen.

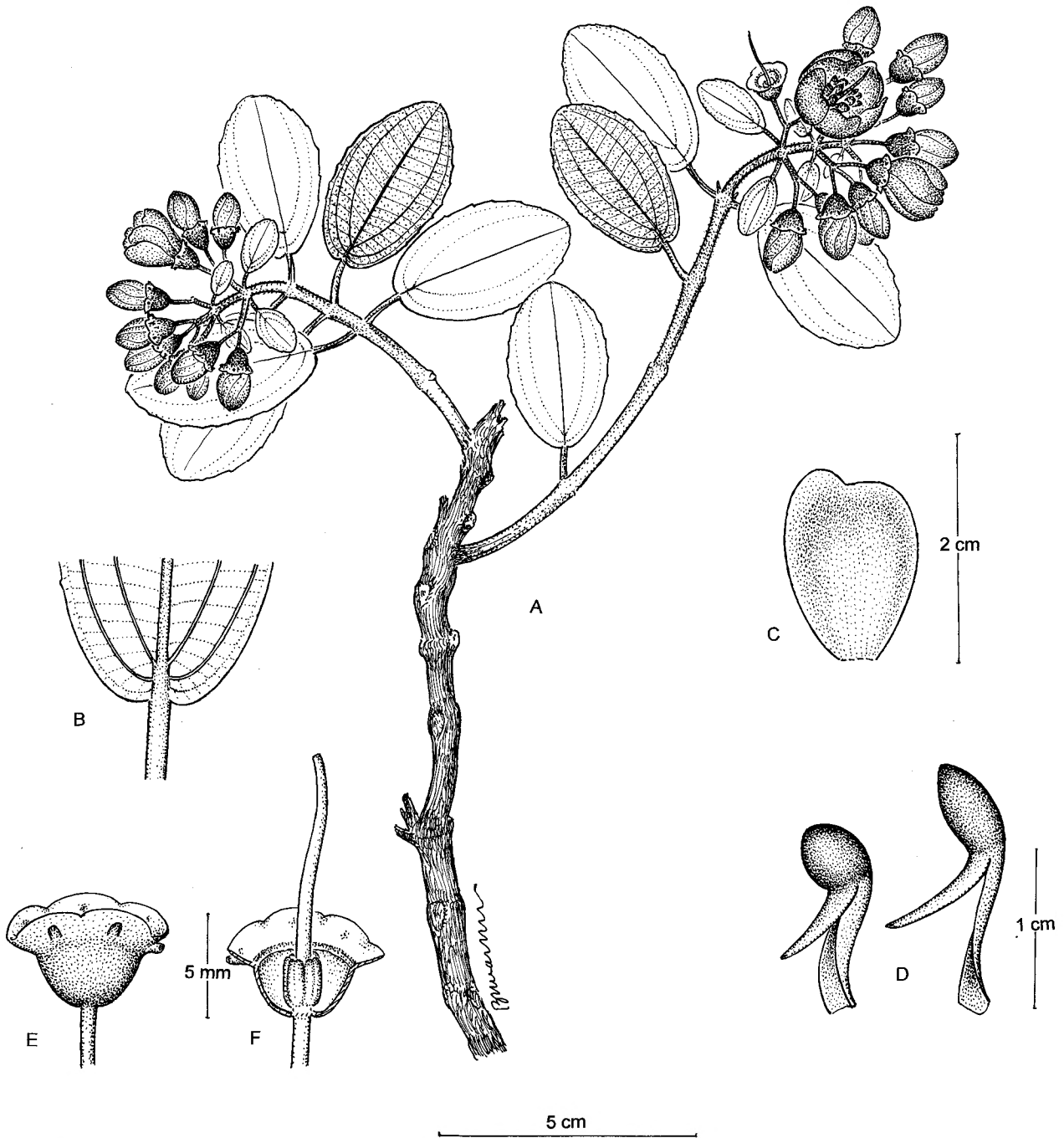
*Axinaea glauca* is known only from the type collection originating in the Andes of southern Ecuador, Loja province, where it grows at an altitude of 2900 m. — Figure 38.

*Axinaea glauca* (Figures 36 and 37) is similar to *Axinaea meriania* (DC.) Triana (Figure 48) from which it can be distinguished mainly in that it has 5-nerved venation. This species, being less than one meter tall, is the smallest *Axinaea* known.

17. *Axinaea grandifolia* (Naudin) Triana, *Trans. Linn. Soc. London* 28: 69. 1871. — *Chastenea grandifolia* Naudin, *Ann. Sci. Nat. Bot., Sér. 3*, 18: 122. 1852. — Type: Venezuela. Táchira: Páramo del Zumbador, 2000–2500 m, Nov 1846, *Funk & Schlim 1254* (holotype: P!; photo: NY!). The original publication cites *Funk & Schlim 1250* as the type specimen, but this must be a printing error as the holotype in Paris (with Naudin's drawings) bears the number 1254. — Figure 39.

**Tree**, 4–20 m tall; *branchlets* subquadrangular, glabrous or sparsely furfuraceous, moderately to densely so when young, hairs minute, 0.1–0.2 mm long, dendritic, densely branched; *stipuliform flaps* reduced to a line across the nodes. **Leaves** petiolate; *petiole* 1.5–3 cm long, furfuraceous when young but becoming glabrous with age, hairs similar to those on the branchlets; *lamina* elliptic to elliptic-ovate, 8–15 × 5–9 cm, coriaceous, adaxially glabrous, abaxially sparsely furfuraceous or glabrous, hairs similar to those of the branchlets; *apex* acute; *base* cuneate, auricles 1–3 mm long, revolute, often with irregularly dentate-undulate margins; *scutum* well developed, knob shaped; *margins* entire to denticulate; *venation* 5-nerved, excluding the tenuous inframarginal nerves that run 0.5–1 mm from the margin, adaxially glabrous, abaxially





**Figure 36.** *Axinaea glauca* – A. Habit. B. Lamina base abaxially. C. Petal. D. Anisomorphic stamens, showing the filaments, the connectives and the anthers with an apical pore. E. Hypanthium showing the somewhat flaring calyx and the external teeth. F. Longitudinal section of a flower (petals and stamens removed) showing the superior ovary, the hypanthium, the torus, the ovary, the style and the calyx (From Lozano et al. 1574).



**Figure 37.** *Axinaea glauca* – Flowers and buds. (Lozano et al. 1574. Photo: Pablo Lozano).

sparsely furfuraceous to glabrous, hairs as in the branchlets; *secondary nerves* evident, parallel, 2–3 mm apart. **Inflorescence** a pendulous thyrse, many-branched, densely-flowered, terminal, 10–20 cm long, often subtended by a pair of bracts similar to the leaves but smaller, additional pairs of smaller bracts present higher in the inflorescence; *pedicels* slender, 4–6 mm long. **Flowers** 5-merous, 1.2–1.5 cm long; *hypanthium* cyathiform, 1.5–3 mm long; *calyx* 0.5–1 mm long, obscurely 5-lobed, external teeth minute or absent; *petals* coral red to dark salmon pink or pink, lighter colored adaxially, oblong-obovate, concave, 8–10 × 6–7 mm wide, apex broadly and asymmetrically bilobed; *stamens* slightly anisomorphic; *filaments* complanate, 4–5 mm long; *connective appendage* spherical, 3–4 × 2 × 2 mm, apiculate basally, yellow; *anthers* 3–4 mm long with one small slightly dorsal pore, dark red or maroon; *ovary* oblong, costulate, apex 5-lobed,

5-celled; *style* 10–15 mm long, curved at the apex. **Fruit** a 5-lobed capsule, the hypanthium covering more than 1/2 of the mature capsule; *seeds* cuneiform.

*Axinaea grandifolia* grows in the Andes of Venezuela at 1800–3500 m elevation (Figure 40). Two specimens, labeled as coming from Colombia, are not indicated in the map, but one, though the label does not indicate it, seems to be cultivated in the Botanical Garden in Bogotá (not mapped). The second specimen is a Wagner number with very poor label data, collected in 1853. It may well be that the species is endemic to the Venezuelan Andes.

**Additional specimens examined –VENEZUELA:**  
**Mérida:** Bosques del Cacique, Mucuquí, 2600 m, 6 Dec 1952, *Bernardi 176* (NY); above Pueblo Nuevo, Páramo de Mucuquí, 2900 m, 7 Dec 1952, *Bernardi 211*

(NY); Páramo del Zumbador, 2500 m, Nov 1846, *Funk & Schlim 1253* (G); El Valle, below Páramo La Culata, 2500 m, 19 Jan 1993, *King et al. 10442* (F, MO); Buena Vista, below Páramo La Culata, NE of Mérida, 2374 m, 20 Jan 1993, *King et al. 10459* (F, MO, S); La Carbonera, 20 km N of Ejido, 2400 m, 30 Sep 1953, *Little 15571* (VEN); La Mucuy, 15 km E of Mérida, 2400 m, 17 Oct 1953, *Little 15750* (VEN); *15751* (VEN); beyond Guaraque along road to Tovar, 2520 m, 24 Sep 1970, *Maguire et al. 62098* (F, GH, NY, VEN); Páramo de Los Colorados, road Tovar-El Molino, 2560 m, 25 Sep 1970, *Maguire et al. 62109* (NY, VEN); San Eusebio, road Mérida-La Azulita, 28 Nov 1979, *Marcano-Berti & Peña 496-979* (BR); Páramo de La Culata, *Moritz 959* (BM, BR, GH); El Valle, NE of Mérida, 2500 m, 14 Nov 1968, *Oberwinkler & Oberwinkler 13439* (VEN); Prado Verde, 7 km N of Mérida, 2000-2300 m, 24 Jun 1963, *Ruíz-Terán 1696* (US); between El Arbolito and crest of Loma Gorda, Piñango slope, 2900-3500 m, 26 Aug 1975, *Ruíz-Terán & Dugarte 12348* (NY); El Tapado-Rincón Chiquito, valley of the Viriguaca Páramo, 2600-2700 m, 30 Nov 1977, *Ruíz-Terán & Dugarte 14769* (NY); between El Delgadito and El Portachuelo, above Bailadores, 2650-2900 m, 2 Dec 1977, *Ruíz-Terán & Dugarte 14871* (NY); La Montaña, Páramo de Las Coloradas, between Santa Cruz de Mora and El Molino, 2850-2900 m, 5 Aug 1970, *Ruíz-Terán & López-Figueras 484* (US); San Antonio village, ca 5 km below El Portachuelo, between Santa Cruz de Mora and El Molino, 1820 m, 28 May 1971, *Ruíz-Terán & López-Figueras 1926* (NY); road El Zumbador-Queniquea, entrance to Páramo de Los Colorados, 2600-2650 m, 31 Jan 1978, *Ruíz-Terán et al. 15132* (NY); above San Isidro Alto, 1820 m, 14 May 1944, *Steyermark 56554* (F, GH, NY, US, VEN); 13 km above La Grita, road to Porqueras, SE of Páramo La Negra, 2500 m, 31 Jul 1973, *Tillett 730-305* (VEN); 2 km above Las Tapias, S of Bailadores, 2275 m, 23 Aug 1973, *Tillett & Hönig 738-379* (US); Bosque San Eusebio, La Carbonera, 2250-2600 m, 1971, *Veillon 32* (US, VEN); road Santa Cruz-Canaguá, 2700 m, 10 Nov 1972, *Wurdack et al. 2735* (NY). **Táchira:** Páramo Zumbador, 14 km S of El Cobre, 2500 m, 31 Mar 1974, *Gentry et al. 11070* (MO, VEN). **COLOMBIA:** Cundinamarca: Bogotá Botanical

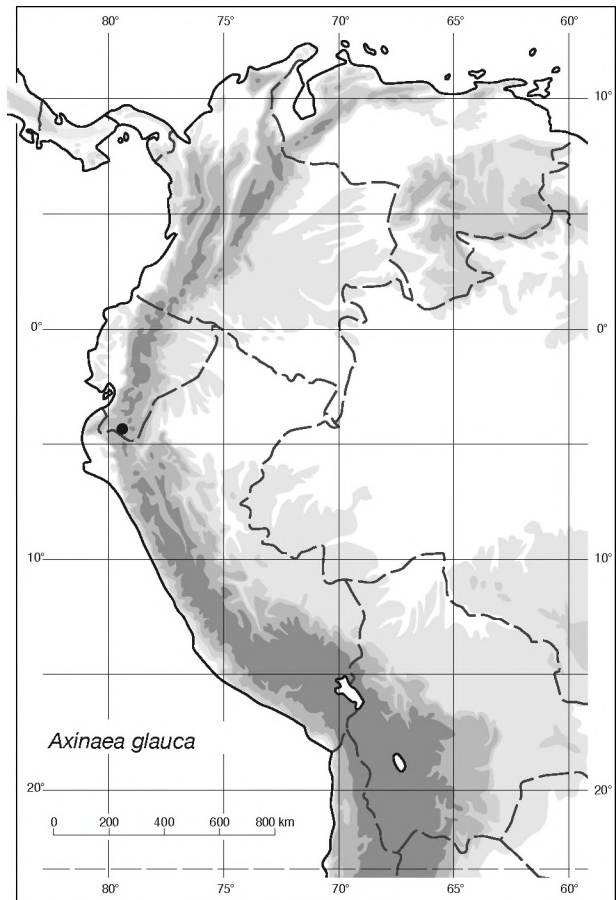
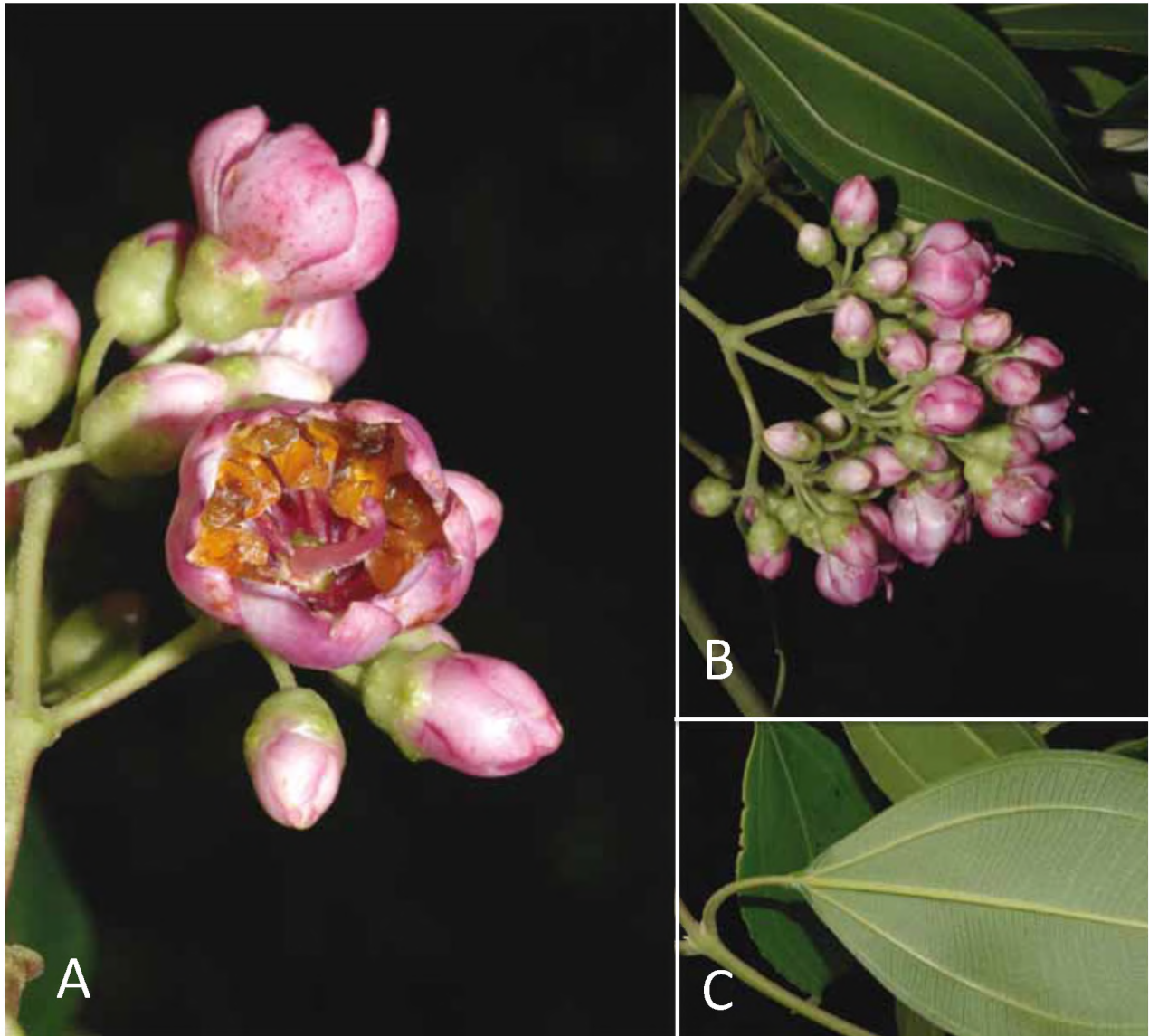


Figure 38. Distribution of *Axinaea glauca*.

Garden, 27 Apr 1982, *Prance & Barrera 28069* (MO, NY); “Colombie”, 1853, *Wagner N106* [?] (G). **LOCALITY UNKNOWN:** Collector unknown # 105 (G).

18. *Axinaea lanceolata* Ruiz & Pav., Fl. Peruv. Prodr. 68. 1794. — *Chastenaea lanceolata* (Ruiz & Pav.) Naudin, Ann. Sci. Nat. Bot., Sér. 3, 18: 123. 1852. — Type: Peru. “In Panao et Muña silvis”, *Ruiz & Pavón s.n.* (lectotype: MA!, here designated; photo: NY!; isotypes: BM! [leaf fragment mounted with *A. glandulosa* Pav. ex D. Don, BM # 000649745], BR! 2 sheets [BR Herbarium # 843 806 and # 843 824], F!, G! [G Herbarium # 8817/26], MA!; photo of the MA isotype: NY!). *Axinaea lanceolata* is the type species of the genus *Axinaea*. The genus was published by Ruiz and



**Figure 39.** *Axinaea grandifolia* – A. Flower. B. Inflorescence. C. Abaxial leaf base. (*Michelangeli 1247* from Las Porqueras, Táchira, Venezuela: Photo: Fabián Michelangeli).

Pavón in their *Flora Peruviana Prodomus*, in 1794. Both Don (1823) and Macbride (1941) incorrectly cite Ruiz and Pavón's *Systema Vegetabilium Florae Peruviana et Chilensi* (1798) as the place where this species was published.

**Shrub or tree**, 2–18 m tall; *branchlets* sub-quadrangular, sometimes narrowly winged, the wings rigid-coriaceous, sparsely furfuraceous when young becoming

glabrous with age; *stipuliform flaps* reduced to a thin line across the nodes. **Leaves** petiolate; *petiole* 2–4 cm long, sparsely furfuraceous when young, becoming glabrous with age; *lamina* elliptic, 12–15(–19) × 4–6(–12) cm, coriaceous, adaxially glabrous except when very young, abaxially sparsely and caducously furfuraceous; *apex* acute; *base* cuneate or truncate, auricles 2–6 mm long, revolute, sometimes overlapping; *scutum* absent or occasionally incipient and v-shaped;

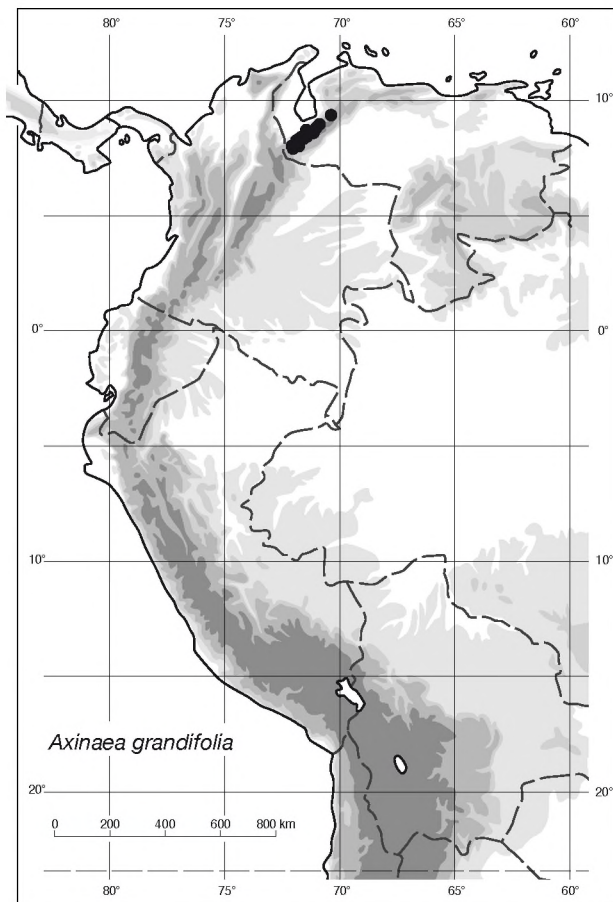


Figure 40. Distribution of *Axinaea grandifolia*.

*margins* dentate, teeth 1 mm long and 4–6 mm apart; *venation* 5(–7)-nerved, excluding the tenuous inframarginal nerves that run ca 1 mm from the margin, adaxially glabrous, abaxially moderate to densely furfuraceous; *secondary nerves* evident, parallel, 3–5 mm apart. **Inflorescence** a somewhat pendulous thyrse, loosely-branched, 1–25-flowered, terminal, 10–20 cm long, often subtended by a pair of bracts similar to but smaller than the leaves and with additional pairs of smaller bracts present higher in the inflorescence; *bracts* occasionally 5-plinerved, the inner pair of primaries diverging from the main nerve 7–10 mm above the base. **Flowers** 5-merous, 1.5–1.8 cm long; *hypanthium* cyathiform, 3–5 mm long, sparsely and caducously furfuraceous; *calyx* 1–1.5 mm long, obscurely 5-lobed, external teeth inconspicuous; *petals* lilac, pink or whitish, ob-

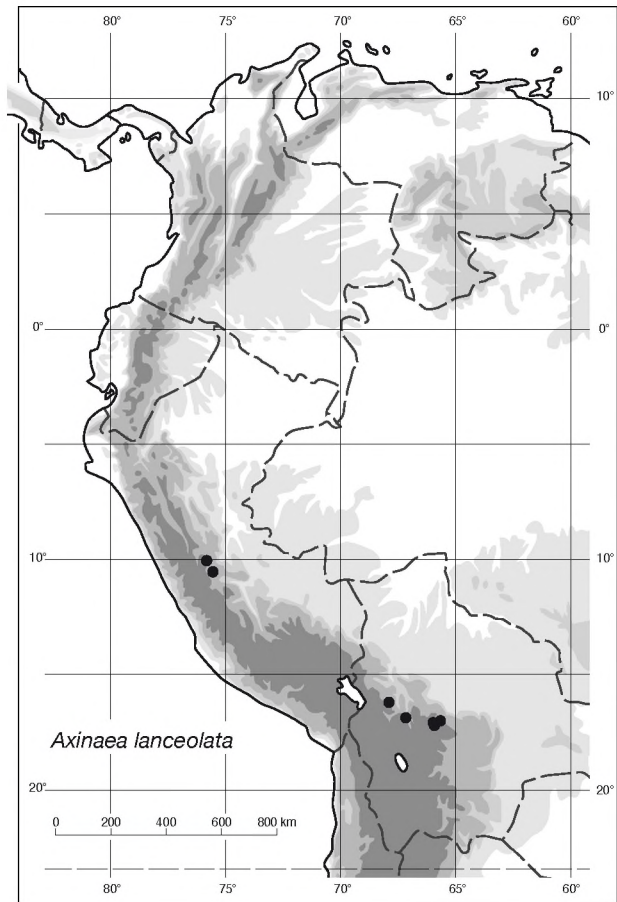
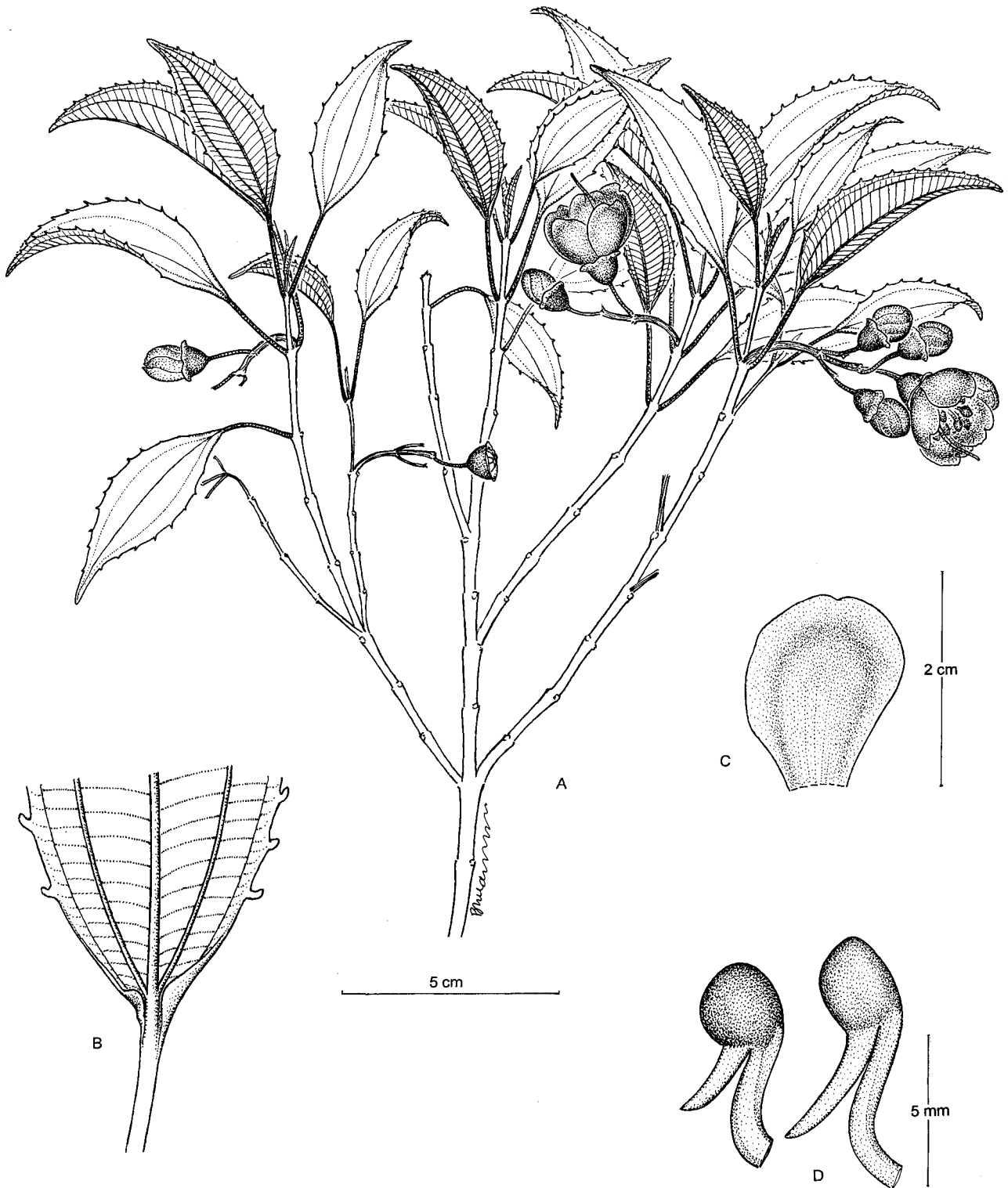


Figure 41. Distribution of *Axinaea lanceolata*.

long-obovate, concave, 12–15 × 6–8 mm wide, apex broadly and asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 6–7 mm long in the longer stamens, 4–5 mm long in the shorter ones; *connective appendage* spherical, 3–4 × 2 × 2 mm, rounded to somewhat acute basally; *anthers* 5–6 mm and 6–7 mm long with one small, slightly dorsal pore; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* 1.3–2 cm long, curved distally. **Fruit** and *seeds* not seen.

*Axinaea lanceolata* grows in the Andes of Peru and Bolivia at 2300–2900 m elevation. – Figure 41.

**Additional specimens examined** – **PERU:** Pasco: Prov. Oxapampa, Río San Alberto Valley, E of Oxapampa, 2700 m, 10°34'S, 75°22'W, 26 Jul 1984, D.



**Figure 42.** *Axinaea lawessonii* – A. Habit. B. Lamina base abaxially, showing the revolute auricles and the hooked margin teeth. C. Petal. D. Anisomorphic stamens showing the filaments, the spherical connectives, rounded basally, and the anthers with a slightly dorsal pore (From Cotton et al. 1529, AAU).

*N. Smith & Poetel 8062* (MO). **BOLIVIA: Cochabamba:** Forested mountain at Incacorral, 2500 m, Jun 1911, *Herzog 2251* (BR, S, W); Prov. Chapare, trail between Laguna Corani and Río Corani Mayu, ca 7.4 km below L. Corani, 2780 m, 4 Jul 1994, *Ritter 1206* (W); Prov. Chapare to Corani Pampa, ca 2 km below highway, 2600 m, 29 Apr 1995, *Ritter 1955* (W); Prov. Chapare, Quebrada Corani, 2400 m, 19 Jun 1929, *Steinbach 9861* (BM, F, G, GH, MO, NY, S); 20 km from the village of Tablas, 2300 m, 17°S 68°W, 8 May 1984, *Krüger M-2* (US). **La Paz:** Loma El Abra (“Abra Sita”), ca 5 km NW from Inquisivi, 2900 m, 16°52’S, 67°10’W, 22 Jun 1988, *Marko Lewis 88875* (MO).

The dentate leaves distinguish *Axinaea lanceolata* from *A. macrophylla* and the absence of scutum distinguishes it from *A. nitida*, both of which it resembles.

19. *Axinaea lawessonii* E. Cotton, in Cotton, Bussmann & Lozano, *Nordic Journal of Botany* 23: 53. 2004. – Type: Ecuador. Loja, road Yangana-Cerro Toledo, Podocarpus National Park, km 16–16.5 km from turnoff to Cerro Toledo, 2800–2900 m, 31 Jul 2000, 4°22’S, 79°8’W, E. Cotton, H. Balslev, M. Gustafsson & P. Lozano 1529 (Holotype: AAU!; isotype: LOJA!). – Figure 42.

**Shrub or slender tree**, 1–8 m tall; *branchlets* subquadrate, glabrous except when young, hairs minute, dendritic (shaggy), thickened, densely branched; *stipuliform flaps* absent or reduced to a line across the nodes. **Leaves** petiolate; *petiole* (1.5–)3–6 cm long; *lamina* narrowly-elliptic, 4–7 × 1.5–3 cm, coriaceous, adaxially glabrous, abaxially glabrous except when young, hairs as on the branchlets; *apex* long-acuminate; *base* attenuate, often auriculate, the auricles revolute, up to 2 mm long; *scutum* absent; *margins* dentate throughout, teeth hook-shaped, 0.5–1 mm long and 1–4 mm apart; *venation* shortly 3-plinerved, or sometimes 3-nerved, excluding the tenuous inframarginal nerves that run ca 1 mm from the margin, the inner pair of primaries diverging from the main nerve up to 8 mm above the base of the lamina, adaxially and abaxially

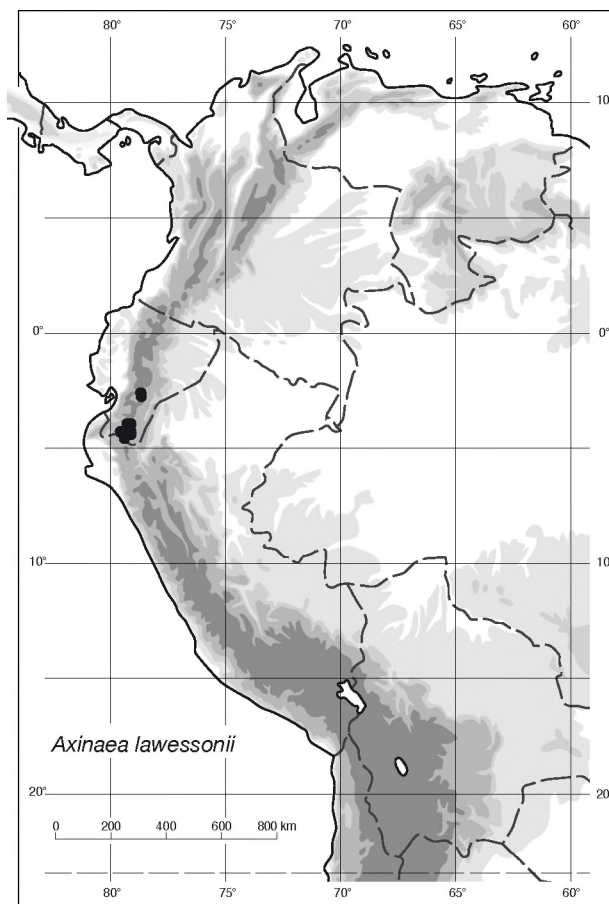


Figure 43. Distribution of *Axinaea lawessonii*.

glabrous; *secondary nerves* faint adaxially and abaxially, parallel, 1–2 mm apart. **Inflorescence** a pendulous thyrse, 1–10-flowered, terminal, 5–10 cm long; often subtended by two bracts that are similar to the leaves but smaller, occasionally additional, smaller bracts present in higher nodes of the inflorescence; *pedicels* 4–10 mm long. **Flowers** 5-merous, 1.5–2.5(–3) cm long; *hypanthium* cupuliform, 4–5 mm long; *calyx* 1–2 mm long, obscurely 5-lobed or truncate, external teeth not evident; *petals* white, lilac or light pink inside, petals oblong to slightly obovate, thickened, strongly concave, 13–18 × 10–13 mm, apex asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, wine-red, 6–7 mm long in the longer stamens, 4–5 mm long in the shorter ones; *connective appendage* spherical, 4 × 3 × 3 mm, rounded basally, bright yellow; *anthers* 4–5 mm

long, wine red, with one minute slightly dorsal pore; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* white ca 1.5 cm long. **Fruit** a 5 lobed capsule, the hypanthium covering half or more of the mature capsule; *seeds* cuneiform.

*Axinaea lawessonii* is endemic to the Andes of southern Ecuador, where it grows in wet montane forest, at altitudes between 2100 m and 3400 m. – Figure 43.

**Additional specimens examined – ECUADOR:**

**Azuay:** Eastern Cordillera, 1–8 km N of Sevilla de Oro, 2500–2750 m, 27 Jul–12 Aug 1945, *Camp E-4533* (F, G, GH, NY, VEN); quebradas leading into the Río Collay, 3–8 km N of Sevilla de Oro, 2100–2500 m, 23 Aug 1945, *Camp E-4891* (F, GH, NY, US, VEN); *4895* (F, MO, NY, S). **Cañar:** Pindilig–Rivera road, km 2 from Pindilig, 2800–3000 m, 8 Jun 1979, 2°36'S, 78°40'W, *Løjtnant & Molau 14325* (AAU); **Loja:** Podocarpus National Park, Cajanuma, trail to Lagunas del Compadre, 3100–3300 m, 13 Jul 1995, 4°5'S, 79°10'W, *Alvarez & Tirado 1523* (AAU, NY), *1525* (AAU, NY); Cajanuma, 2400 m, 7 May 1946, 4°5'S, 79°10'W, *Espinosa 325* (LOJA, NY); road Loja–Zamora, km 15, 2500 m, 16 Aug 1983, *Jaramillo & Winnerskjold 5796* (AAU, NY); Podocarpus National Park, Lagunas de Banderillas, 3400 m, 15 Dec 1994, *Lozano 41* (LOJA); road Yangana–Cerro Toledo, km 20, 3300 m, 29 Nov 2000, 4°24'S, 79°6'W, *Madsen & Leimbeck 7568* (AAU); Podocarpus National Park, above Cajanuma, trail to Lagunas del Compadre, 2900–3100 m, 19 Jan 1989, 4°5'S, 79°10'W, *Madsen 85573* (AAU); Podocarpus National Park, above Nudo de Cajanuma, trail to Mirador, 3000–3150 m, 23 Feb 1989, 4°5'S, 79°10'W, *Madsen 85823* (AAU, LOJA, NY); Podocarpus National Park, Cerro Toledo, 2500–3400 m, 30 Oct 1989, 4°23'S, 79°7'W, *Madsen 86312* (AAU, LOJA); *86313* (AAU, LOJA, MO, NY); Amaluza, 5–10 km ENE of the village, Pasaje del Romerillo, 2400–2700 m, 23 Sep 1976, 4°34'S, 79°23'W, *Øllgaard & Balslev 9737* (AAU, F, MO, NY, US); Muletrack Amaluza–Palanda, W slope nr pass (W of Laguna Chuquiraga), 3100–3400 m, 22 Sep 1976, 4°35'S, 79°20'W, *Øllgaard & Balslev 9645* (AAU – det as *A. cf. lawessonii*); Podocarpus

National Park, S of Loja, above Centro de Información, E of Nudo de Cajanuma, 3050–3300 m, 23 Feb 1985, *Øllgaard et al. 58016* (AAU, LOJA, MO, NY); Podocarpus National Park, Cerro Toledo, road Yangana–Cerro Toledo, 2900 m, Jan 1995, 4°23'S, 79°8'W, *Palacios & Tirado 12911* (AAU, MO, NY); road Loja–Yangana, Podocarpus National Park, E of Nudo de Cajanuma, 2950–3000 m, 14 Mar 1989, *Romoleroux 792* (AAU, NY). **Loja/El Oro:** Zaruma–Sinsao rd. 10 km from Tambillo near Arcos, 2750 m, 21 Feb 1988, *C. Ulloa 589* (AAU). **Loja/Zamora-Chinche:** at pass on road between Loja and Zamora, towards Loma de Los Balcones, 2900 m, 30 Sep 1995, 3°59'38"S, 79°8'40"W, *Garmendia & Paredes 402* (LOJA); Podocarpus National Park, pass on road Loja–Zamora, 2900 m, 8 Jan 1989, 3°58'S, 79°7'W, *Madsen 85466* (AAU, LOJA, MO, NY); *85721* (AAU, LOJA, MO, NY); 2500–3000 m, 26 Sep 1989, 3°57'S, 79°6'W, *Madsen 86204* (AAU, LOJA).

The specimens here referred to *Axinaea lawessonii* had previously been determined by Wurdack, Renner and Cotton as *Axinaea macrophylla* (Naudin) Triana. Until the present treatment, *A. macrophylla* was a name given to almost any Ecuadorian specimen of *Axinaea* which could not be placed in the described taxa for the genus, thus becoming a cauldron of species in dire need for delimitation. *Axinaea lawessonii* can be easily distinguished from *A. macrophylla* by its dentate (*vs.* denticulate) leaf margins and 3-nerved or shortly 3-plinerved (*vs.* 5-nerved or shortly 5-plinerved) venation (Figure 40). The hooked teeth on the margin of the lamina are exclusive to this species. The Azuay population is somewhat serose on the abaxial lamina surface.

The species is named in memory of Jonas Lawesson (†), colleague and friend, who collected extensively in Ecuador.

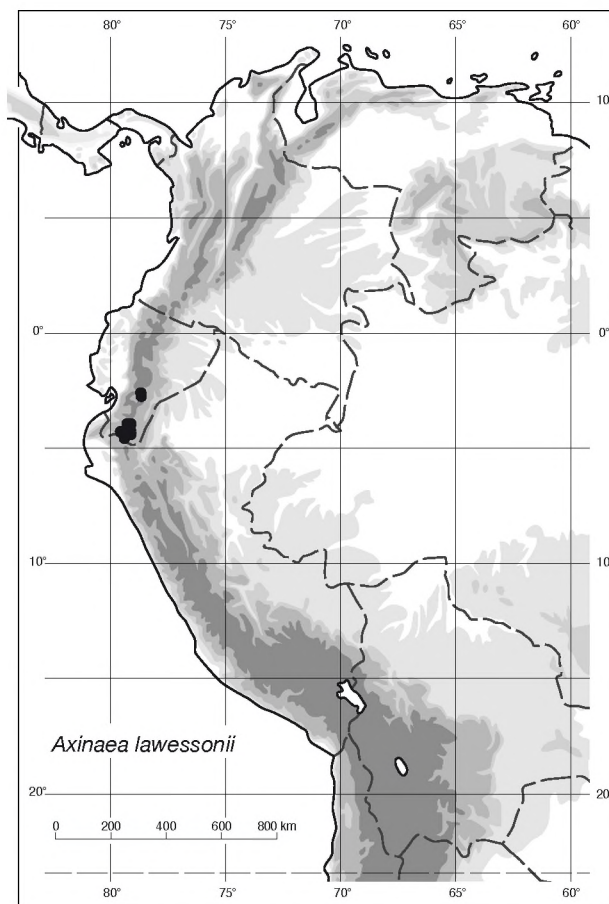
**20. *Axinaea lehmannii* Cogn., Bot. Jahrb. Syst. 8: 20. 1886. – Type:** Colombia. Prov. Cauca, Cerro Munchique, 2400 m, 3 Mar 1884, *Lehmann 3637* (lectotype: G!, here designated; photo: F!, GH!, MO!, NY!; isotype: BR!).



**Shrub or tree**, 5–30 m tall; *branchlets* subquadrangular to terete, usually glabrous but occasionally sparsely furfuraceous when young; *stipuliform flaps* reduced to a thin, often faint line across the nodes. **Leaves** petiole; *petiole* 1–2.5 cm long, usually glabrous, occasionally sparsely furfuraceous when young; *lamina* elliptic to elliptic-ovate, 8–15(–22) × 4.5–10(–15) cm, coriaceous, rigid, adaxially glabrous, lustrous, abaxially usually glabrous, occasionally sparsely and caducously furfuraceous; *apex* broadly acute to bluntly acuminate; *base* shallowly cordate, auricles not revolute; *scutum* well developed, knob-shaped; *margins* entire; *venation* 5–7-nerved, excluding the tenuous inframarginal nerves that run 0.5–1 mm from the margin, adaxially glabrous, sunken, abaxially glabrous, prominent, occasionally sparsely furfuraceous; *secondary nerves* evident, parallel, 3–5 mm apart. **Inflorescence** a somewhat pendulous thyrse, loosely-branched, 3–25-flowered, terminal, 10–20 cm long, often subtended by a pair of bracts similar to the leaves but smaller, bracts occasionally 5-plinerved, the inner pair of primary nerves diverging from the main nerve 5–10 mm above the bract base. **Flowers** 5-merous, ca 1.5 cm long; *hypanthium* cyathiform, shallow, 1–3 mm long; *calyx* ca 1 mm long, obscurely 5-lobed, external teeth inconspicuous; *petals* bright red, oblong-obovate, concave, 12–14 × 6–8 mm wide, apex broadly and asymmetrically bilobed; *stamens* anisomorphic; *connective appendage* spherical, 3 × 2 × 2 mm, apiculate basally; *anthers* 5–6 mm and 6–7 mm long, inflated at the base, with one small, slightly ventral pore; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* 1.3–2 cm long, curved at the apex. **Fruit** a 5-lobed capsule, the hypanthium barely covering the base of the mature capsule; *seeds* cuneiform.

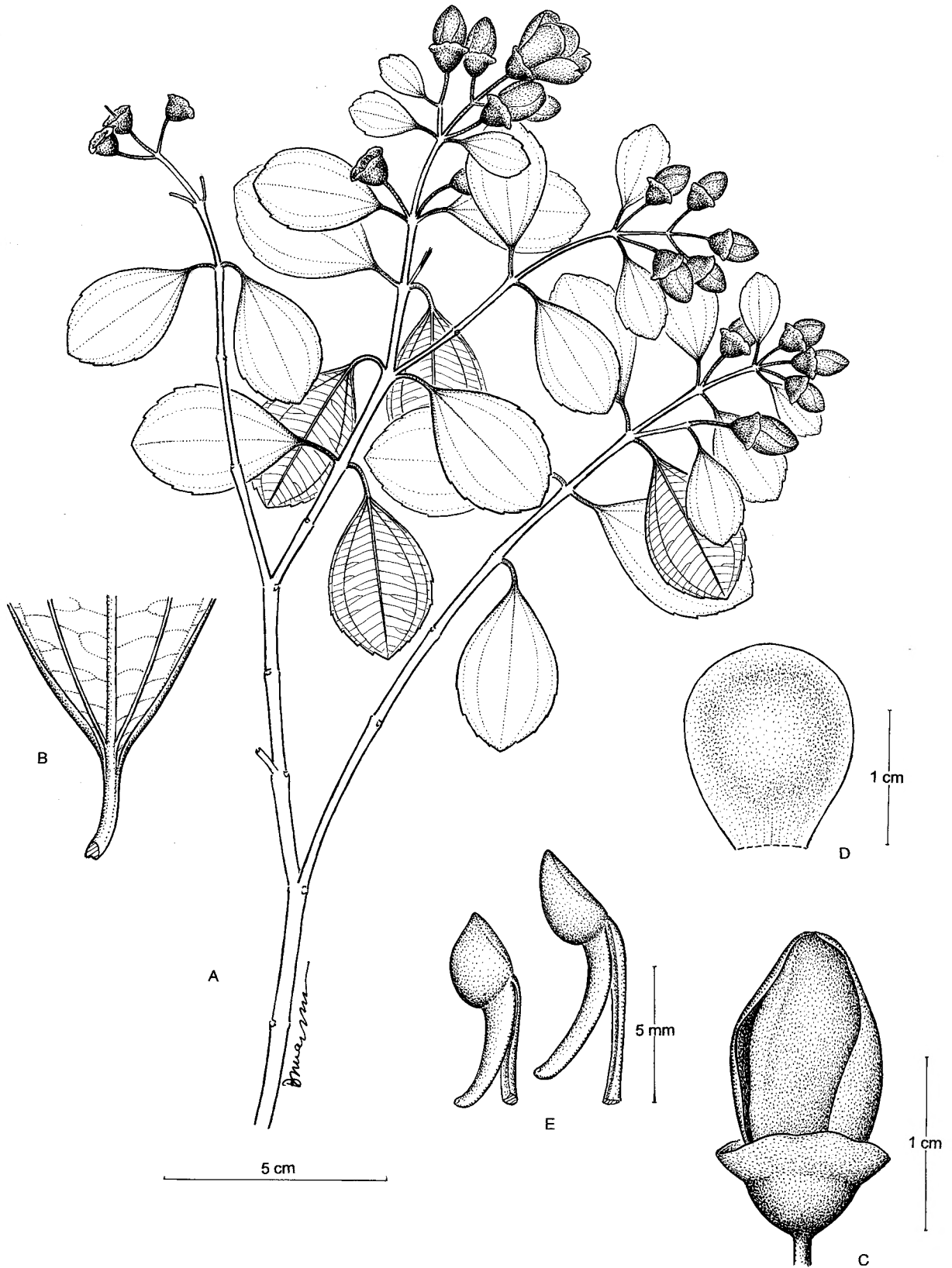
*Axinaea lehmannii* is restricted to the Andes of southern Colombia and northern Ecuador where it grows at altitudes of 1200–2500 m. – Figure 44.

**Additional specimens examined** – **COLOMBIA:** **Antioquia:** Mpio. Briceño, Vereda San Fermín, road Ventanas–Briceño km 2.5, 2100–2300 m, 7°10'N, 75°32'W, *Callejas et al.* 5566 (NY); Mpio. Yarumal/Briceño, road Santa Ana Briceño–Río de Oro, 1800–2000



**Figure 44.** Distribution of *Axinaea lehmannii*.

m, 7°5'N, 7532'W, 19 Dec 1992, *Gómez et al.* 815 (MO). **Cauca:** Mpio. El Tambo, Correg. 20 de Julio, Parque Nacional Munchique, 2200–2300 m, 2°30'N, 77°42'51"W, 4 Jan 1991, *Ruíz et al.* 1118 (MO); El Tambo, La Costa, 2000 m, 26 Jul 1936, *von Sneiderm s.n.* (F, NY). **Chocó:** road Ansermanuevo–San José del Palmar, Alto del Galápago, 2100 m, 27 Aug 1976, *Forero et al.* 2150 (MO, US); 1940 m, 29 Aug 1976, *Forero et al.* 2300 (MO, US); 2000 m, 18 Feb 1977, *Forero et al.* 2853 (MO, NY); Mpio. San José del Palmar, Cerro del Torá, Río Negro, 2200 m, 29 Aug 1988, *Ramos et al.* 1684 (US); 2460 m, 23 Aug 1988, *Silverstone et al.* 4696 (US). **Valle:** Mpio. Cali, Correg. de la Elvira, Western Cordillera, km 18 road Cali–Buenaventura, km 4 towards Dapa, 1900 m, 3°30'N, 76°34'W, 9 Jan 1995, *Giraldo & Olver* 589 (US).



**Loc. unknown:** *Lehmann B. T. 997* (K, NY). **ECUADOR:** **Carchi:** environs of Maldonado, 1450–1650 m, 1 Jun 1978, *Madison et al. 4853* (AAU, F, US); Cantón Mira, N of El Carmen, road to Chical, 2000–2200 m, 0°17'N, 78°13'W, 10 Feb 1992, *Palacios et al. 9855* (NY); ridge N of Gualpí Alto, 1200–1300 m, 1°2'N, 78°23'W, 18–25 May 1985, *Thomsen 58803* (AAU, QCA). **Esmeraldas:** road Lita–El Cristal, 13.5 km S of Lita, 1220–1350 m, 0°49'N, 78°26'W, 2 Nov 1992, *Luteyn et al. 14746* (K, MO, NY, QCA). **Imbabura:** Cantón Cotacachi, Parroquia Plaza Gutiérrez, Tablachupa village, on road to Apuela, NW of Cuicocha, 2800–3000 m, 0°20'N, 78°26'W, 15 May 1992, *Cuamacás et al. 119* (LOJA); 13 Jun 1992, *Cuamacás et al. 158* (LOJA); Río Verde, ca 5 km SW from village of Mani, Río Cachaco, 1700–1740 m, 0°46'N, 78°28'W, 6 Jun 1980, *Sperling & Bleiweis 5071* (QCA).

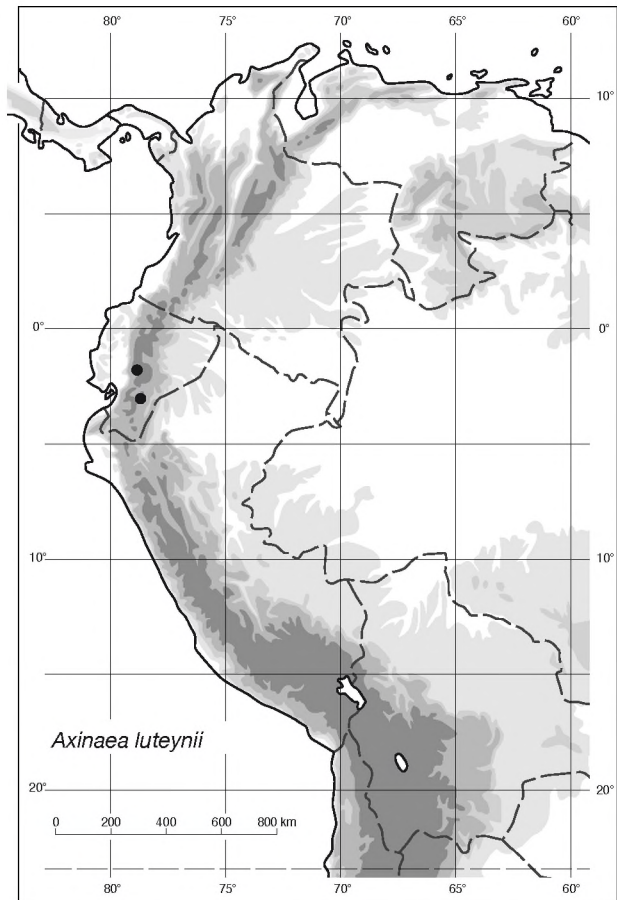
*Axinaea lehmannii* has very distinct stamens with the anthers inflated towards the base forming two sacs that frame the spherical connective appendage. *Axinaea lehmannii* sometimes has several pairs of bracts in the inflorescence and often they are all plinerved.

Cogniaux did not designate a type specimen in the protologue. There is a specimen in G with Cogniaux's handwriting and a fragment of it in BR. All photographs seen of this type specimen indicate that it is deposited in the Paris herbarium (P). Each photograph has been annotated noting the discrepancy. The type specimen is mounted together with flowers of *Miconia* sp. Five of these flowers appear in the photographs of the type.

21. *Axinaea luteynii* E. Cotton, sp. nov. – Type: Ecuador. Prov. Azuay, Gualaceo–Limón road, ca 23 km E of Gualaceo, Páramos de Culebrillas, ca 3477 m, 12 Nov 1990, *Luteyn et al. 14130* (Holotype: NY!; isotypes: F!, MO!, QCA!, VEN!). – Figure 45.

*Opposite page:*

**Figure 45.** *Axinaea luteynii* – A. Habit. B. Detail of leaf base. C. Mature bud. D. Petal. E. Anisomorphic stamens showing the filament, the spherical connective that is basally somewhat apiculate, and the anther (From *Luteyn et al. 14130*).



**Figure 46.** Distribution of *Axinaea luteynii*.

*Species Axinaeae quitensi Benoist simulans, a qua differt linea interpetiolaris inconspicua (non 0.5–1 mm prominenti, indurata), floribus 2–2.5 cm longis (non 1.4–1.8 cm).*

**Shrub or small tree**, to 4 m tall; *branchlets* quadrangular to terete, puberulent when young, becoming glabrous with age; *stipuliform flaps* reduced to a faint line across the nodes. **Leaves** petiolate; *petiole* 5–8 mm long; *lamina* obovate, 3.5–4.5 × 2.5–3 cm, sub-coriaceous, adaxially and abaxially glabrous; *apex* acute; *base* attenuate, not auriculate; *scutum* absent; *margins* entire

and revolute on the lower half, shallowly and distantly denticulate on the upper half; *venation* (3-)5-nerved, excluding the tenuous inframarginal nerves that run ca 0.5 mm from the margin and are nearly invisible due to the revolute margins, adaxially glabrous, abaxially with occasional, thick, densely branched, dendritic hairs growing mostly on the sides of the main nerves; *secondary nerves* faint adaxially, parallel, 2-3 mm apart. **Inflorescence** a pendulous thyse, 1-10-flowered, terminal, 5-8 cm long, subtended by two bracts that are similar to the leaves but smaller, occasionally additional, similar bracts present in higher nodes of the inflorescence; *pedicels* slender, 4-6 mm long. **Flowers** 5-merous, 2-2.5 cm long; *hypanthium* cyathiform, 3-4 mm long; *calyx* 1-2 mm long, flaring, obscurely 5-lobed or the lobes not evident, external teeth inconspicuous; *petals* white with magenta, widely-oblong, concave, 15-18 × 13-15 mm, apex obtuse or rounded; *stamens* anisomorphic; *filaments* complanate, 6-7 mm long in the longer stamens, 5-6 mm long in the shorter ones; *connective appendage* spherical, 5 × 3 × 3 mm, somewhat apiculate basally, yellow; *anthers* 5-6 mm long with one minute slightly ventral pore, cream-colored; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* ca 1.5 cm long. **Fruit** and *seeds* not seen.

*Axinaea luteynii* is known from the type collection in the Páramo de Culebrillas in the Azuay province of southern Ecuador where it grows at 3400-3500 m altitude, and at a locality in Bolivar province at slightly lower elevations. — Figure 46.

**Additional specimens examined – ECUADOR: Bolivar:** Chimbo-Santiago-Totoras rd., 2900-3200 m, *N. Betancourt 474* (AAU), same locality *Betancourt 478* (AAU).

The indistinct stipuliform flaps and rather large (2-2.5 cm long) flowers separate this species from *Axinaea quitensis*. It is also similar to *A. wurdackii* from northern Peru, from which it differs in having basal (*vs.* plinerved) venation.

The species is dedicated to James L. Luteyn with whom we have collected many species of *Axinaea* in both Ecuador and Peru.

22. *Axinaea macrophylla* (Naudin) Triana, Trans. Linn. Soc. London 28: 69. 1871. — *Chastenaea macrophylla* Naudin, Ann. Sci. Nat. Bot., Sér. 3, 4: 55. 1845. — Type: Colombia. Santa-Fé de Bogotá, La Pena Vieja, Dec 1844, *Justin Goudot s.n.* (holotype: P!; photos: F!, MO!, NY!).

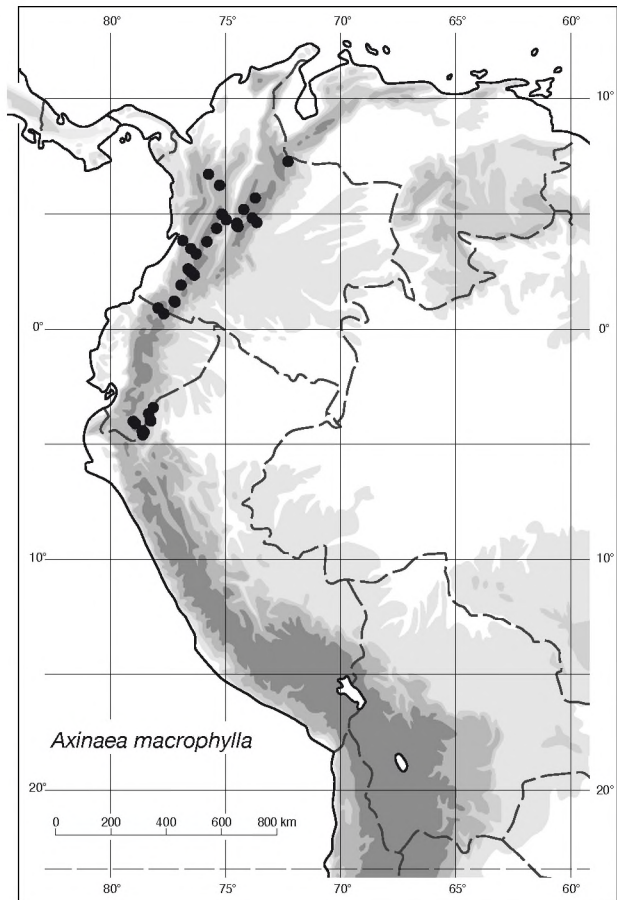
**Shrub or tree**, 3-10(-20)m tall; *branchlets* subquadrangular, glabrous to sparsely puberulent; *stipuliform flaps* present as a hardened ridge, raised ca 0.5 mm, occasionally reduced to a line across the nodes. **Leaves** petiolate; *petiole* 1-3(-4) cm long; *lamina* elliptic, 4-11(-15) × 2.5-5(-7.5) cm, coriaceous, adaxially glabrous except when young, abaxially moderately to sparsely puberulent when young, glabrous with age, occasionally gland-dotted with minute orange glands only visible under ×10 magnification; *apex* broadly acute or shortly acuminate; *base* cuneate, attenuate, or rounded, auricles up to 5 mm long, revolute, with entire or dentate-undulate margins; *scutum* absent; *margins* denticulate especially on the upper half, occasionally entire; *venation* shortly 5-plinerved, or sometimes 5-nerved, excluding the tenuous inframarginal nerves that run ca 0.5 mm from the margin, the inner pair of primaries diverging from the main nerve up to 5 mm above the base of the lamina, adaxially glabrous, abaxially sparsely puberulent or glabrous; *secondary nerves* sometimes faint adaxially, parallel, 1-3 mm apart, raised abaxially, mite domatia sometimes present between the main nerve and the inner pair of primaries. **Inflorescence** a pendulous thyse, 1-25-flowered, terminal, 5-10 cm long, often subtended by two bracts that are similar to the leaves but smaller, additional, smaller bracts occasionally present in higher nodes of the inflorescence; *pedicels* 4-8 mm long. **Flowers** 5-merous, 1.5-2 cm long; *hypanthium* cyathiform, 3-4 mm long; *calyx* ca 1 mm long, obscurely 5-lobed or truncate, external teeth not evident; *petals* white, lilac or light pink adaxially, darker abaxially, oblong to slightly obovate, concave, 7-9 × 12-16 mm, apex asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 6-7 mm long in the longer stamens, 4-5 mm long in the shorter ones; *connective appendage* spherical, 3 × 2 × 2 mm, rounded or somewhat apiculate ba-

sally, dark yellow; *anthers* 4–5 mm long with one minute slightly dorsal pore; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* ca 1.5 cm long. **Fruit** a 5-lobed capsule, the hypanthium covering half or more of the mature capsule; *seeds* cuneiform.

*Axinaea macrophylla* is a widely distributed species that grows in the Andes of Colombia and Ecuador, at altitudes of 2500–3500 m. – Figure 47.

**Additional specimens examined – COLOMBIA:**

**Antioquia:** Páramo de Chaquiro, Western Cordillera, 2800–3000 m, 23 Feb 1918, *Pennell 4259* (NY). **Cauca:** Volcán Puracé, between Pilimbalá and Laguna de San Rafael, 3300 m, 6 Jan 1972, *Cleef & Fernández 524* (US); road between Chapa and Río Blanco, Quebrada Flantots, 2800 m, 13 Jul 1944, *Core 902* (US); Central Cordillera, Puracé páramo, S of the volcano, San Francisco, 3400–3450 m, 23 Jul 1943, *Cuatrecasas 14671* (F, NY); Central Cordillera, headwaters of Río Palo, Alto del Duende, 3300–3350 m, 1–2 Dec 1944, *Cuatrecasas 18894* (F, GH, NY); Eastern Cordillera, headwaters of Río Palo, Quebrada Santo Domingo, 2950–3150 m, 13 Dec 1944, *Cuatrecasas 19267* (F, GH, NY); Central Cordillera, western drainage of Páramo del Puracé, above Quebrada of Río San Juan, 3280–3300 m, 11 Oct 1961, *Cuatrecasas & Willard 26316* (US); Puracé National Park, road Termales San Juan–Cascada San Nicolás, 3100 m, 29 Nov 1985, *Duque 72* (US); “Canaan”, Mt. Puracé, 2900–3100 m, 11–16 Jun 1922, *Killip 6798* (GH, NY, US); above Puracé, 3200 m, 3 Sep 1975, *López-Palacios & Idrobo 3739* (US); “Canaan”, Mt. Puracé, Central Cordillera, 3100–3300 m, 11–13 Jun 1922, *Pennell 6506* (K, NY, US); Central Cordillera, Puracé, 3350 m, Feb 1938, *von Sneidern 1830* (G, S); 1831 (S). **Cundinamarca:** eastern páramos of Guasca, toward Gacheta, 1921, *Bro. Ariste-Joseph s.n.* (F, US); road to Mundo Nuevo, 16 km E of La Calera, side road to La Capilla, 2700 m, 28 Feb 1972, *Barclay et al. 3207* (US); Bogotá massif, Quebrada de Chicó, 2750–2890 m, 8 Jun 1939, *Cuatrecasas 5422* (US); road to Oriente, between Bogotá (San Cristóbal) and Chipaque, 3200–3360 m, 10 Jul 1957, *García-Barriga 15640* (NY); 15645 (NY); Choachí, “in montibus ad orient. Bogotae”, 10 Feb 1854, *Holton 907*



**Figure 47.** Distribution of *Axinaea macrophylla*.

(BR, G, GH, NY); Eastern Cordillera, road between Fómeque and Páramo de Chingaza, 2750 m, 10 Nov 1967, *Jaramillo-Mejía & Acosta 4822* (NY); Central Andes of Popayán, 2900–3300 m, *Lehmann 8649* (G, GH, K, NY, W); Bojacá, San Antonia, La Merced near rd Mosquera-Tena, 2500–2700 m, 25 Oct 1964, *Lozano-C. & Torres R. 174* (AAU); Bogotá road near Villavicencio, 3000–3100 m, 18 Jun 1950, *Schneider 967* (S); Bogotá, *Tracey 299* (K); Sibaté, San Fortunato, 3200 m, 29 Jun 1960, *Uribe-Urbe 3495* (NY); Volcán Puracé, close to Popayán, Central Cordillera, 3180 m, 26 Aug 1956, *Vogel 86* (US). **Huila:** páramo approaching Puracé, 3275 m, *Maguire & Maguire 44215* (GH, NY, VEN). **Nariño:** Andes of Pasto, *Jameson 450* (G); 451 (BR, G, US); road Ipiales–La Victoria, between Cultún and La Victoria, 3200 m, 1 Sep 1962, *Mora 2330* (US); Vereda de

Chires, Hda. de Don Alberto Garzón, 2900 m, 11 Sep 1962, *Mora 2358* (US); Mpio. Pasto, Bosque Botana, 2800–3200 m, 17 Jul 1964, *Soejarto 991* (GH, US). **Quindío:** “Monte Quindío”, 2600 m, 1851–1857, *Triana s.n.* (BM); “Quindío, Mariquita”, 2500 m, 1851–1857, *Triana s.n.* (BR, NY, W). **Santa Fé de Bogotá:** El Salto, Bogotá, 2600 m, 1851–1857, *Triana s.n.* (BR, NY, W). **Santander:** Páramo Rico, 3200 m, 15–19 Jan 1927, *Killip & Smith 17824* (F, GH, NY, S, US). **Valle del Cauca:** Western Cordillera, Los Farallones, Quebrada Las Nieves, 3000–3120 m, 31 Jul 1946, *Cuatrecasas 21833* (F, NY, S). **Department unknown:** Agua Dulce, 40 km from Bogotá, 1917, *Bro. Ariste-Joseph A-109* (US); *B-14* (NY, US); *Linden 212* (BR); *Linden s.n.* (BR); 1760–1808, *Mutis 1263* (US); *2701* (F, G, US, S); *2456* (US); *3405* (US). **ECUADOR:** **Carchi:** Loma El Corazón (Bretaña), SE of Huaca, Río Minas, 3200–3500 m, 2 Jul 1989, 0°35'N, 77°42'W, *Tipaz 29* (MO); *98* (MO). **Cañar:** Cerro Yanguán NE of Pindilig, 3000 m, 13 Dec 1980, 2°36'S, 78°40'W, *Holm-Nielsen et al. 29325* (AAU); Comunidad Charon Ventanas, 3350–3500 m, 17 Jun 1983, 2°40'S 78°50'W, *Brandbyge 42175* (AAU, QCA-sheet erroneously annotated as *A. merianiae*). **Loja:** Finca of the Callderón family at trail NE of Mercadillo towards the c rest, 1800 m, 13 Aug 2000, 4°00'S, 79°57'W, *Cotton et al. 1606* (AAU); Rd Loja-Zamora at border to Zamora-Chinchi, 2600–2800 m, 13 Apr 1974, *Harling & Andersson 13512* (AAU); Podocarpus National Park, Cajanuma, 2850 m, 20 May 1997, 4°6.725'S, 79°10.630'W, *Gwilym Lewis & Cotton 3311* (AAU, K, LOJA, NY); Parque Nacional Podocarpus, E of Nudo de Cajanuma, just N of Centro de Información, 2900 m, 4°05'S, 79°10'W, *Madsen 86146* (AAU). **Loja/Zamora-Chinchi:** Podocarpus National Park, at pass on road Yangana-Valladolid, 2500–3000 m, 10 Dec 1989, 4°28'S, 79°10'W, *Madsen 86663* (AAU); 2800–2900 m, 21 May 1984, 4°27'S, 79°8'W; *Ollgaard & Madsen 74261* (AAU, F, GH, LOJA, NY); road Loja-Zamora, km 18 (El Tiro), 2800 m, 25 Sep 2001, 3°58'57"S, 79°8'43"W, *Madsen 8546* (AAU); pass over Nudo de Sabanilla, 2740 m, 11 May 1985, 4°27'S, 79°10'W, *Stein & D'Alessandro 2732* (AAU, US); El Paso, rd Loja-Zamora, 2450–2600 m, 17 Feb 1988, *Ulloa 557* (AAU). **Morona-Santiago:** Camp San Miguel (along

road in construction Sigsig-Gualaquiza), 3000 m, 8 Apr 1968, *Harling et al. 8034* (F). **Napo:** Rd Quito-Papallacta-Baeza-Tena, 6.6 km after Papallacta, 2760 m, 19 Sep 2001, 0°22'S, 78°04'W, *Cotton et al. 1727* (AAU). Reserva Ecológica Cayambe-Coca, 5 km from Cuyuja on rd. to Quito, slopes of Had La Flor del Bosque, 3050 m, 8–9 May 1991, 0°22'S, 78°56'W, *Gavilanes & Tirira 660* (AAU); same locality, 3350 m, 23 Jun 1991, *Gavilanes et al. 690* (AAU). Paso de Guamaí. Río Chalpi, at the bridge on rd Papallacta-Baeza, 2800 m, 6 May 1967, *Sparre 15942* (AAU); **Zamora-Chinchi:** Podocarpus National Park, at pass on road Yangana-Valladolid, 2800–2900 m, 5 Apr 1985, *Harling & Andersson 23699* (AAU, NY); Podocarpus National Park, at pass on road Yangana-Valladolid, 2500–2680 m, 4°30'S, 79°8'W, 21 Apr 1992, *Luteyn & Romoleroux 14528* (AAU, NY); 10 km outside Loja on road Loja-Zamora, just past the Nudo, 2900 m, 27 Apr 1987, *van der Werff & Palacios 9113* (AAU, NY, US).

*Axinaea macrophylla* is a widely distributed and relatively common species. For many years, the name has been used to identify any *Axinaea* that could not easily fit in any of the other described species. It is interesting to mention that mite domatia are here reported for the first time in the genus *Axinaea* though the character does not seem to be constant. About 50% of the specimens studied from Colombia have mite domatia, whereas none of the Ecuadorian ones do. Considering the disjunct location of the southern Ecuadorian populations (Figure 45) combined with their lack of mite domatia we may have a case of cryptic speciation. *Axinaea macrophylla* is sympatric with and similar to *A. minutiflora*, described as new in this treatment, but the latter differs in its oblong (not elliptic) leaves that are three times (not twice) as long as broad and its smaller flowers < 1.5 cm long.

23. *Axinaea merianiae* (DC.) Triana, Trans. Linn. Soc. London 28: 69. 1871. — *Chastenea merianiae* DC., Prodr. 3: 102. 1828. — Type: Locality not specified, *Bonpland s.n.* (holotype: P! [Herbarium Richard, Herb. Muséum Paris # Poo228675], photo: NY!). — Figure 48.

*Chastenea coriacea* Naudin, Ann. Sci. Nat. Bot., Sér. 3, 4: 55. 1845. — Type: “Mont Saraguru”, *Bonpland, s.n.* (lectotype: P! [Herb. Muséum Paris # Poo228673], here designated; isotype: P! [Herb. Muséum Paris # Poo228674], photo: NY!).

*Chastenea lepidota* Benth., Pl. Hartw. 182. 1845. — *Axinaea lepidota* (Benth.) Triana, Trans. Linn. Soc. London 28: 69. 1871. — Type: Ecuador. Azuay: “In montibus prope Cuenca”, *Hartweg 1014* (holotype: K! [Herb. Benthamianum], photos: F!, GH!, NY!; isotypes: B (destroyed), BR!, E [n.v.], F! [Field Museum Herbarium # 869715] (fragment), F! [Field Museum Herbarium # 937046] (fragment), G!, K! [Herb. Hookerianum], W! (2 sheets), photos of the B isotype: F!, GH!, MO!, NY!, photo of the E isotype: NY!).

**Shrub**, 1–5 m tall; *branchlets* subquadrangular, moderately arachnoid-puberulent when young becoming glabrous with age; *interpeltolar flaps* absent. **Leaves** petiolate; *petiole* 4–17 mm long, hairs similar to those in the branchlets; *lamina* elliptic-oblong to slightly obovate, 2–5 × 0.8–2.2 cm, coriaceous, rigid, erect, adaxially glabrous, abaxially moderately arachnoid-puberulent when young, often becoming glabrous with age; *apex* bluntly acute to rounded; *base* cuneate; *scutum* absent; *margins* shallowly dentate; *venation* 3-nerved or shortly, 3-plinerved, excluding the tenuous inframarginal nerves that run 0.5–1 mm from the margin, the inner pair of primaries diverging from the main nerve 2–3 mm from the base of the lamina; *secondary nerves* faint. **Inflorescence** a terminal dichasium or a reduced thyrses, usually consisting of no more than five flowers and often reduced to one; *bracts* similar to the leaves but smaller; *pedicels* 4–7 mm long, with a pubescence as on the branches. **Flowers** 5-merous, 1.5–2.5 cm long; *hypanthium* cyathiform, 3–5 mm long; *calyx* 1–2 mm long, obscurely 5-lobed; *petals* pale lilac or pale pink, oblong-obovate, 13–18 × 7–12 mm, apex asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 10–12 mm in the longer stamens, 8–9 mm in the shorter ones; *anthers* 7 mm or 8 mm long with one small apical pore; *connective appendage* spherical, 2–3 mm in diameter; *ovary* 10-costulate,

apex 5-lobed; *style* 12–17 mm long, curved at the apex. **Fruit** a 5-lobed capsule, the hypanthium covering 3/4 or more of the mature capsule; *seeds* numerous, cuneiform.

*Axinaea meriania* is endemic to southern Ecuador where it has been found only in a few, intensively collected, populations in the Andean Cordillera elevations of 2500–3000 m. — Figure 49.

**Additional specimens examined — ECUADOR: Azuay:** Gañadel, 3000 m, 23 Sep 1955; *Asplund 17753* (G, K, NY, S); road Oña–Cumbe, 2800–3000 m, 5 Aug 1986; 3°20'S 79°10'W, *Betancourt 366* (F, NY, QCA); road Gualaceo–Macas, 2700–2900 m, 6 Aug 1986, 2°57'S 78°42'W (NY, QCA), *Betancourt 368* (NY, QCA); Cerro Patococha entering through Hda. Tarqui, km 22 Cuenca–Loja road, 2700–3100 m, 8 Aug 1986, 3°3'S 79°5'W, *Betancourt 397* (F, NY, QCA); between Oña and Río León, 2500 m, 2 Aug 1944, *Camp 276* (NY); Cuenca, Parroquia Banos, Had Yanasacha, 3000–3200 m, 15 Jul 1978, *Boeke & Jaramillo 2436B* (AAU). Pan American Highway, 34 km S of Cuenca, 2800 m, 20 Sep 1944, *Camp 452* (GH, NY); Cordillera de Alpachaca, above Río León, 2850 m, 1 Oct 1944, *Camp 527* (K, NY); *528* (NY); *529* (NY); along Río Cumbe 25–30 km S of Cuenca, 2800–3000 m, 7 Mar 1945, *Camp 2079* (NY); road Loja–Cuenca, 2900 m, 1 Oct 1961, 3°22'S 79°12'W, *Dodson 853* (MO, QCA, US); above Bosque de Pongo, 25 km SSW Cuenca, 2900 m, 27 Aug 1986, *Fleming 60* (K); Río Jubones drainage, Hda. Zuzudel, 2 km S of Santa Rosa, S end of Cordillera Alpachaca, 43 km S of Cuenca, 3000 m, 8 Feb 1945, *Fosberg & Giler 22838* (US); Cuenca–Machala highway, km 22.6 on road to Patococha opposite entrance to Hda. Tarqui, 21 Nov 1987, *Grifo & Crespo 461* (AAU, MO); 10 km S of Cumbe, 3000 m, *Harling 5685* (S); S part of Páramo de Tinajillas, Santa Rosa, ca 2 km before the descent to Río León, 3000 m, 2 Nov 1988, 3°20'S 79°25'W, *Harling 25595* (AAU, NY, QCA); 1–2 km N of Nieves, 3000–3100 m, 16 Nov 1988, *Harling 25932* (K, NY); road Cuenca–Loja, upper N slopes of Río León Valley and S parts of Páramo de Tinajillas, 2800–3000 m, 9 May 1974, *Harling & Andersson*



**Figure 48.** *Axinaea meriania* – **A.** Dissected flower showing the petals, the stamens, and a longitudinal section of the hypanthium. **B.** Flower at anthesis, showing the stamens that have migrated to one side of the flower, and the erect style (Luteyn & Cotton 11246; Photos: Elvira Cotton).

14494 (US); about 3 km SE of Jima on road towards San Miguel de Cuyes, 3000 m, 27 Apr 1985, 2°48'S 78°48'W, Harling & Andersson 24696 (AAU, F, NY, QCA); between Saraguro and San Pablo de Tenta, 2950 m, 21 Feb 1993, 3°34'S 79°06'W, Harling & Ståhl 26568 (QCA); 10–20 km S of Cumbe, Páramo de Tinajillas, 3000–3300 m, 3 Feb 1982, 3°13'S 79°02'W, Harling et al. 20141 (QCA); km 91, Pan American Highway N of Loja, 2900 m, 5 May 1973, 3°25'S 79°10'W, Holm-Nielsen et al. 5121 (AAU, MO, NY, S); above Cumbe, 2500–3000 m, Mar 1979, 3°5'S 79°5'W, Holm-Nielsen 18778 (AAU); between Oña and Urdaneta, 3100 m, 3 Apr 1980, 3°31'S 79°11'W, Holm-Nielsen 22774 (AAU, QCA); heights of Tarqui, near Cuenca, 2700

m, Jameson 15 (K); between Saraguro and San Lucas, 8 Sep 1865, Jameson 143 (K); take-off Llantera-Chiquintad-Saucay-Guandum, 3000 m, 27 May 1979, 2°51'S 79°1'W, Jaramillo 1061 (AAU); Gualaceo-Limón, W side of pass, 3000 m, 19 Aug 1987, 3°0'S 78°42'W, Jørgensen 61891 (AAU); Cuenca-Machala, km 22, turnoff towards Patachoca, km 7, 3000 m, 18 Jul 1990, 3°6'S 79°5'W, Jørgensen et al. 91844 (AAU, QCA, QCNE); “Páramo de Tinajillas, Prov. of Cuenca”, 2900–3300 m, Lehmann 4924 (F, GH, K, S, US); 67 km S of centre of Cuenca on road to Loja, 2890–3090 m, 16 Aug 1996, 3°14'S 79°7'W, Gwilym Lewis 2507 (AAU, K, LOJA, NY, QCA); Cuenca-Loja, km 30 from outskirts of Cuenca, km 14 from road junction Girón-Cuenca-



Loja, 3100 m, 7 Apr 1996, 3°8'S 79°2'W, *Gwilym Lewis & Klitgaard 2229* (AAU, K, LOJA, QCA); Páramo de Tinajillas. 12.5–32 km S of Cumbe, 3100–3400 m, 26 Jan 1985, 3°10'S 79°5'W, *Luteyn & Cotton 11230* (AAU, NY, QCA, QCNE); 11238 (AAU, K, NY, QCA, QCNE); 11239 (AAU, NY, QCA, QCNE); 11240 (AAU, NY, QCA, QCNE); ca 55 km S of Cumbe and 71 km N of Saraguro, 2960 m, 27 Jan 1985, 3°15'S 79°12'W, *Luteyn & Cotton 11246* (AAU, BR, NY, QCA, QCNE, W); Cuenca-Cumbe-Jima, road, ca 4 km above Jimá, towards Palcurcu, 2920 m, 4 Dec 1990, 3°14'S 78°55'W, *Luteyn et al. 14303* (AAU, MO, NY, S); Baños at Cuenca, 2800 m, 21 Nov 1981, 2°55'S 79°5'W, *Madsen 36650* (AAU); 100 km from Loja along Pan American Highway to Cuenca, 2800 m, 10 Sep 1969, *Maguire & Maguire 61678* (F, GH, NY); below Patacocha, 4–5 km by trail S of Hda. Tarqui at Irquis on the main Cuenca-Machala road, 2900–3000 m, 29 Jan 1988, 3°7'S 79°2'W, *Molau et al. 2740* (QCA); E of Charqui sector, El Paso, E of Nabón, 27 Dec 1981, *Ortiz s.n.* (NY); 56 km S of the intersection of the roads to Loja and Girón on road to Loja, 2950 m, 7 Jul 1992, *Panero & Clark 2951* (NY); Cuenca, 3400 m, 12 Sep 1973, *Rauh & Barthlott 35124* (US); Nabón, 25 Sep 1918, *Rose et al. 22992* (NY, US); vicinity of Tablón de Oña, 27 Sep 1918, *Rose et al. 23116* (NY, US); road Cuenca-Loja, ca 20 km N of Oña, 2900 m, 11 Jul 1976, 3°22'S 79°11'W, *Ståhl & Knudsen 2801* (AAU, QCA); between km 67 and S towards Oña, 3715 m, 3 Aug 1943, *Steyermark 53689* (F, NY, US); road Cuenca-Oña, between 5–15 km S of Cumbe, 2700–3250 m, 8 Apr 1987, 3°9'S 79°3'W, *Zak 1861* (AAU, QCA). **Azuay/Loja:** node of Cordillera Oriental and Cordillera Occidental, between Oña and Rancho Ovejero; 2900 m, 1 Aug 1959, *Barclay & Juajibioy 8467* (AAU, MO, US). **Cañar:** road Cañar-Azuay, take-off to comunidad Molobog-Ventanas, between Molobog and Ventanas, 3200–3450 m 14 Aug 1987, 2°30'S 78°54'W, *Romoleroux 400* (QCA). **El Oro:** Manu-Guanasán, km 17, 3150 m, 6 Nov 1997, 3°27'S 79°28'W, *Gwilym Lewis et al. 3685* (AAU, K, LOJA, NY). **Loja:** Cuenca-Loja road, 26 km N of Saraguro, 3060 m, 28 Jul 1982, 3°25'S 79°8'W, *Clemants et al. 2227* (NY, QCA, QCNE); Saraguro, ca 50 km N of Loja, 2500 m, 3°37'S 79°14'W, *Espinosa 1413* (LOJA, NY); above Gua-

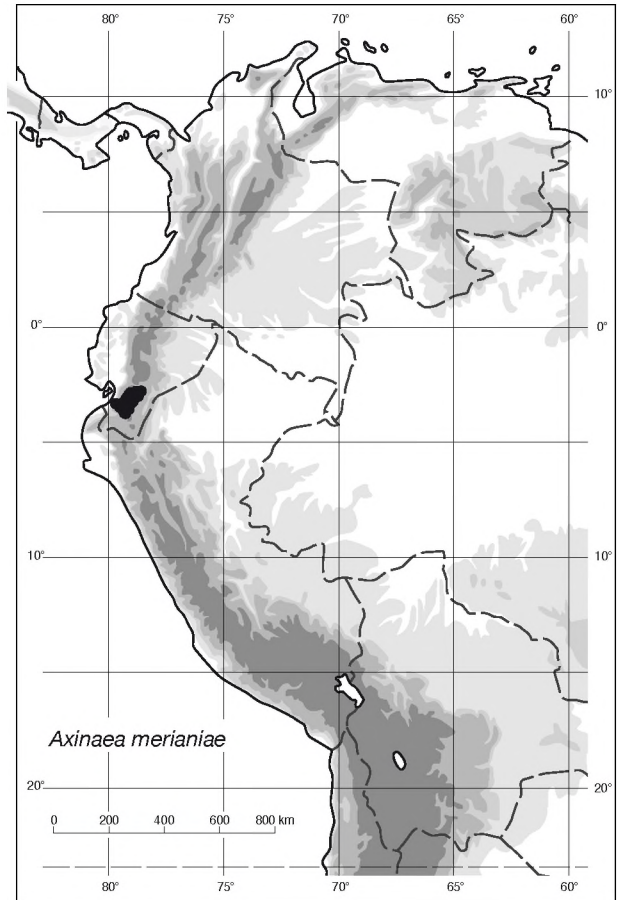


Figure 49. Distribution of *Axinaea merianiae*.

nazán, N of Zaruma, 2700 m, 9 Sep 1947, *Espinosa 2177* (NY); between San Lucas and Oña, 2200–3100 m, 7 Sep 1923, *Hitchcock 21573* (GH, NY, US); road Saraguro-Tenta, 2500–2800, 16 Sep 1980, 3°37'S 79°15'W, *Jaramillo 3825* (AAU, MO, NY); road Saraguro-Tenta, cerro Pichanga, 2900–3050 m, 6 Sep 1984, 3°36'S 79°12'W, *Jaramillo 7261* (AAU, NY, QCA); Saraguro-Tenta, Tentacruz, 25 Feb 1979, 3° 37'S 79°15'W, *Jaramillo & Jaramillo 837* (AAU, NY, QCA, QCNE); Cerro de Chilla, Saraguro-Manú, km 7, 2970 m, 2 May 1994, 3°36'S 79°15'W, *Jørgensen et al. 662* (LOJA, QCA, QCNE); along main road 1–5 km N of entrance to Refugio Carboncillo, 2900 m, 26 Jun 1998, 3°33'S 79°15'W, *Lægaard 18948* (AAU, LOJA); 17 km N of Saraguro, 2865 m, 2 Jan 1979, 3°31'S 79°10'W, *Luteyn et al. 6689* (AAU, F, K, MO, NY, QCA, S); ca 5

km S of Tablón, 2820 m, 27 Jan 1985, 3°16'S 79°12'W, *Luteyn & Cotton 11255* (NY); road to San Pablo de Tenta, 6.4 km W of Saraguro, 2800 m, 27 Jan 1985, 3°30'S 79°20'W, *Luteyn & Cotton 11262* (AAU, NY, QCA, QCNE); km 113 en route to Loja, 3000 m, 26 Sep 1959, *Maguire & Maguire 44317* (GH, NY); summit of road Saraguro-Tenta, 2900 m, 12 Feb 1989, 3°37'S 79°16'W, *Ollgaard & Madsen 90529* (AAU, LOJA, MO, NY, QCA); Saraguro, Manú, Moras, 26 Jun 1994, *Vivar et al. 4256* (AAU, LOJA). **Morona-Santiago**: trail Sevilla de Oro-Méndez, between Páramo del Castillo-Cerro Negro-Dominguillos, 3000-3250 m, 6 Aug 1983, 2°47'S 78°34'W, *Jaramillo 5530* (AAU, QCA). **Province unknown**: "Amérique équatoriale", *Bonpland s.n.* (F); *Jameson s.n.* (F).

*Axinaea meriania* (Figure 48) is easily recognized by its arachnoid or lepidote indument that gives the plants a waxy appearance. It has been abundantly collected, as one of the few populations of the species grows right beside the road that leads from Cuenca to Loja where it grows in a rather large population forming part of a scrub forest.

24. *Axinaea mertensioides* Wurdack, *Phytologia* 9: 409, 1964. — Type: Peru. Amazonas: Prov. Chachapoyas, Río Ventilla, 1-2 km W of Molinopampa, 2100 m, 23-25 Jul 1962, *Wurdack 1467* (holotype: US!; isotypes: F!, G!, GH!, MO!, NY!, P!, S!).

**Shrub**, 2-5 m tall; *branchlets* markedly quadrangular, sparsely puberulent to glabrous; *stipuliform flaps* present, coriaceous, forming a continuous flat outgrowth that surrounds the nodes, 1-3 mm long across the nodes, 0.5-1 mm long under the place of insertion of the petioles. **Leaves** petiolate; *petiole* 5-10 mm long; *lamina* elliptic-oblong, 4.5-7 × 2-3 cm, more or less coriaceous, adaxially glabrous, abaxially sparsely puberulent and dotted with minute orange glands; *apex* acute; *base* cuneate, neither auriculate nor revolute; *scutum* absent; *margins* entire; *venation* 5-plinerved, excluding the tenuous inframarginal nerves that run ca 0.5 mm from the margin, the inner pair of primaries diverging from the main nerve 5-10 mm from the base

of the lamina, the outer pair faint and diverging ca 1 mm above the base of the lamina, adaxially glabrous, abaxially sparsely puberulent to glabrous; *secondary nerves* evident abaxially, parallel, 0.5-2 mm apart. **Inflorescence** a pendulous thyrse, many-branched, >26-flowered, terminal, 6-10 cm long, flowers arranged in fascicles; *nodal flaps* present in the largest nodes, similar to those on the branches but smaller; *pedicels* slender, 8-13 mm long. **Flowers** 4-merous, 1.3-1.5 cm long; *hypanthium* cupuliform, 2.5-3 mm long; *calyx* 0.5-1 mm long, obscurely 4-lobed, external teeth inconspicuous or absent; *petals* pink in bud turning purple-blue at anthesis, obovate, concave, 12-14 × 8-10 mm, apex broadly and asymmetrically bilobed; *stamens* isomorphic; *filaments* complanate, 4-5 mm long; *connective appendage* ellipsoidal, 5 × 3 × 2 mm, acute basally, burnt orange; *anthers* 4-5 mm long with one minute slightly dorsal pore, purple-brown; *ovary* oblong, costulate, apex 4-lobed, 4-celled; *style* 13-15 mm long, curved distally. **Fruit** a 4-lobed capsule, the hypanthium completely covering the mature capsule; *seeds* not seen.

*Axinaea mertensioides* is known only from the type specimen that was collected close to Molinopampa, in the central cordillera of the Andes of Peru, at 2350-2400 m elevation. — Figure 50.

In the protologue to *Axinaea mertensioides*, Wurdack mentions that the species is frequent. It is therefore surprising that it has not been collected again.

25. *Axinaea minutiflora* E. Cotton, spec. nov. — Type: Colombia. Dpto. Valle, Mpio. Tuluá, Corr. Barragán, Hda. La Florida, road Barragán-Santa Lucía, 2850 m, 25 Jun 1983, *Devia 207* (holotype: MO!; isotype: US!). — Figure 51.

*Species Axinaeae macrophyllae (Naudin) Triana simulans, a qua differt foliis oblongis usque ad oblongo-ellipticis (non ellipticis) triplo longioribus quam latis (non duplo), floribus minoribus, 1-1.5 cm longis (non 1.5-2 cm).*

**Tree**, 10–20 m tall; *branchlets* subquadrangular to terete, densely puberulent when young, moderately so with age, hairs minute, dendritic; *stipuliform flaps* reduced to a faint line across the nodes. **Leaves** petiolate; *petiole* 1.5–4 cm long; *lamina* oblong to oblong-elliptic, 8–12 × 3–4 cm, coriaceous, adaxially glabrous, except when young, abaxially moderately puberulent, hairs similar to those on the branchlets; *apex* acute or rounded; *base* cuneate or attenuate, shortly auriculate, the auricles up to 2 mm long, revolute, with entire margins; *scutum* absent; *margins* entire to shallowly and distantly denticulate on the upper half; *venation* 5-nerved, or shortly (3–5 mm) plinerved, excluding the tenuous inframarginal nerves that run ca 0.5 mm from the margin, adaxially glabrous, abaxially glabrous to moderately puberulent; *secondary nerves* faint adaxially and abaxially, parallel, 1–2 mm apart. **Inflorescence** a pendulous thyrses, 11–15-flowered, terminal, 5–10 cm long, often subtended by two bracts that are similar to the leaves but smaller, occasionally with additional, smaller bracts present in higher nodes of the inflorescence, bracts 5-plinerved; *pedicels* slender, 3–7 mm long. **Flowers** 5-merous, 1–1.5 cm long; *hypanthium* cyathiform, 1–2 mm long; *calyx* ca 1 mm long, obscurely 5-lobed or the lobes not evident, external teeth minute; *petals* white or light purple, oblong to obovate, concave, 10–11 × 6–7 mm, apex asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 5–6 mm long, in the longer stamens, 4–5 mm long in the shorter ones; *connective appendage* spherical, 3 × 2 × 2 mm, slightly larger in the shorter stamens, somewhat apiculate basally; *anthers* 3 mm or 4 mm long with one minute dorsal pore; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* ca 1.5 cm long. **Fruit** a 5-lobed capsule, the hypanthium covering less than half of the mature capsule; *seeds* numerous, cuneiform.

*Axinaea minutiflora* is restricted to the Western Cordillera of the Andes in Colombia where it grows at elevations of 2850 m. – Figure 52.

This species is most similar to *Axinaea macrophylla* from which it differs in having oblong leaves (not elliptic) that are three times (not twice) as long as broad and

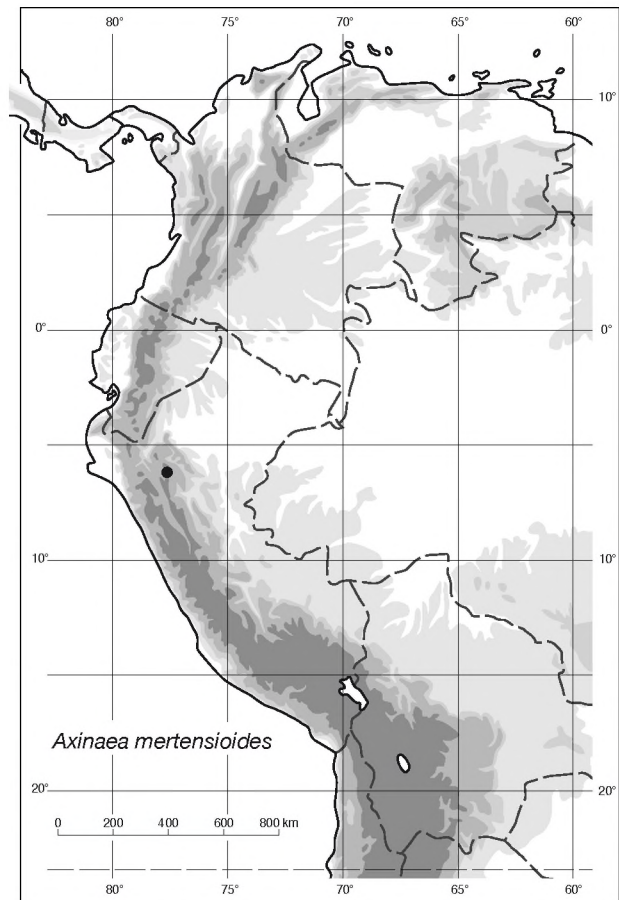
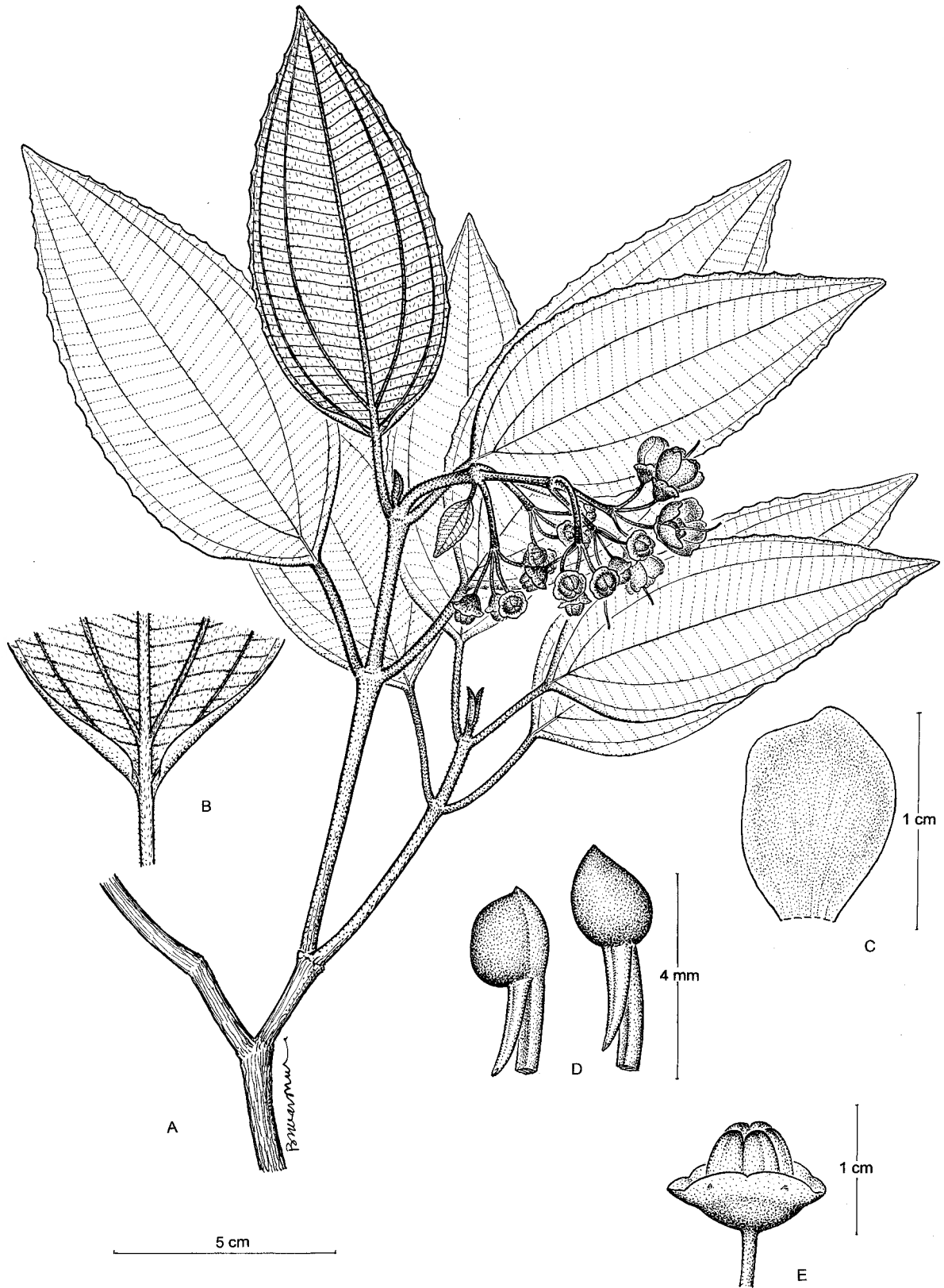


Figure 50. Distribution of *Axinaea mertensioides*.

its smaller flowers, 1–1.5 cm long (not 1.5–2 cm). It is also reminiscent of *Axinaea floribunda*, that also has quite small flowers, but the inflorescences are 11–25-flowered (*vs.* >26-flowered in *A. floribunda*) and the flowers tend to be, in average, smaller than those of *A. floribunda*.

26. *Axinaea nitida* Cogn., Bot. Jahrb. Syst. 42: 138. 1908. – Type: Peru. Amazonas, Molinopampa, E of Chachapoyas, 2000–2300 m, Jul 1904, *Weberbauer* 4355 (holotype: B [destroyed], photo: NY!; lectotype, here designated: BR! [fragment]). – Figure 53 and 54.

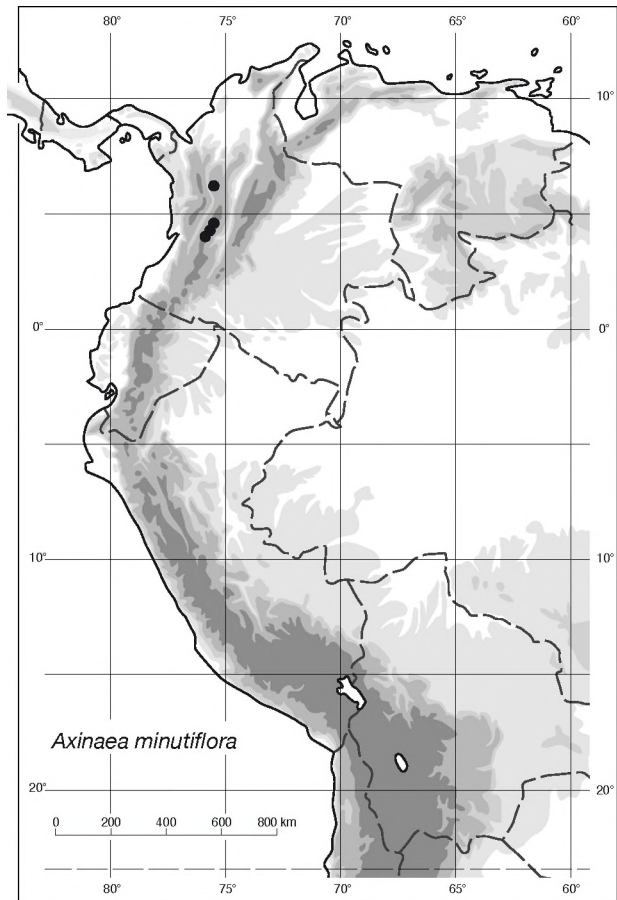
**Treelet or tree**, 3–20 m tall; *branchlets* subquadrangular to terete, glabrous, usually lustrous and bright



red; *stipuliform flaps* absent. **Leaves** petiolate; *petiole* 1.5–5 cm long, glabrous, bright red; *lamina* ovate to elliptic-ovate, 7–12(–15) × 4–6 cm, coriaceous, adaxially and abaxially glabrous; *apex* acute to acuminate; *base* cuneate, auriculate, auricles 1–3 mm long, revolute; *scutum* usually present, v-shaped, occasionally much reduced or absent; *margins* denticulate to dentate, teeth 1–2 mm long and 2–3 mm apart; *venation* 5–7-nerved, excluding the tenuous inframarginal nerves that run 0.5–1 mm from the margin, adaxially and abaxially glabrous; *secondary nerves* evident though not prominent, parallel, 1–3 mm apart. **Inflorescence** a pendulous thyrses, many-branched, >26-flowered, terminal, 8–15 cm long, often subtended by a pair of bracts that are similar to the leaves but smaller; *pedicels* 3–7 mm long. **Flowers** 5-merous, 12–15 mm long; *hypanthium* cyathiform, 1.5–3 mm long; *calyx* 0.5–1 mm long, obscurely 5-lobed, external teeth minute or absent; *petals* deep red, purple-pink or dark pink, oblong-obovate, concave, 10–12 × 6–7 mm, apex broadly and asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 5–6 mm long in the longer stamens, 3–4 mm long in the shorter ones; *connective appendage* spherical, 3–4 × 2 × 2 mm, rounded basally, yellow; *anthers* 3–5 mm long with one small slightly dorsal pore, dark red or maroon; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* 10–15 mm long. **Fruit** a 5-lobed capsule, hypanthium covering 1/2 to 1/3 of the mature capsule; *seeds* cuneiform.

*Axinaea nitida* grows in the montane forests of the Andes in Peru at altitudes of 2000–3100 m. — Figure 55.

**Additional specimens examined** — **PERU: Amazonas:** road Pedro Ruiz Gallo–Florida de Pomacocha–Rioja, 48 km after Florida, 2000–2100 m, 6 Jul 2002, 5°40′48″S, 77°46′38″W, *Cotton & Gustafsson 1864* (AAU, CPUN, HUT); road Balsas–Leimebamba–Chachapoyas, 72 km from Balsas, Cerros Calla-Calla, 2600–



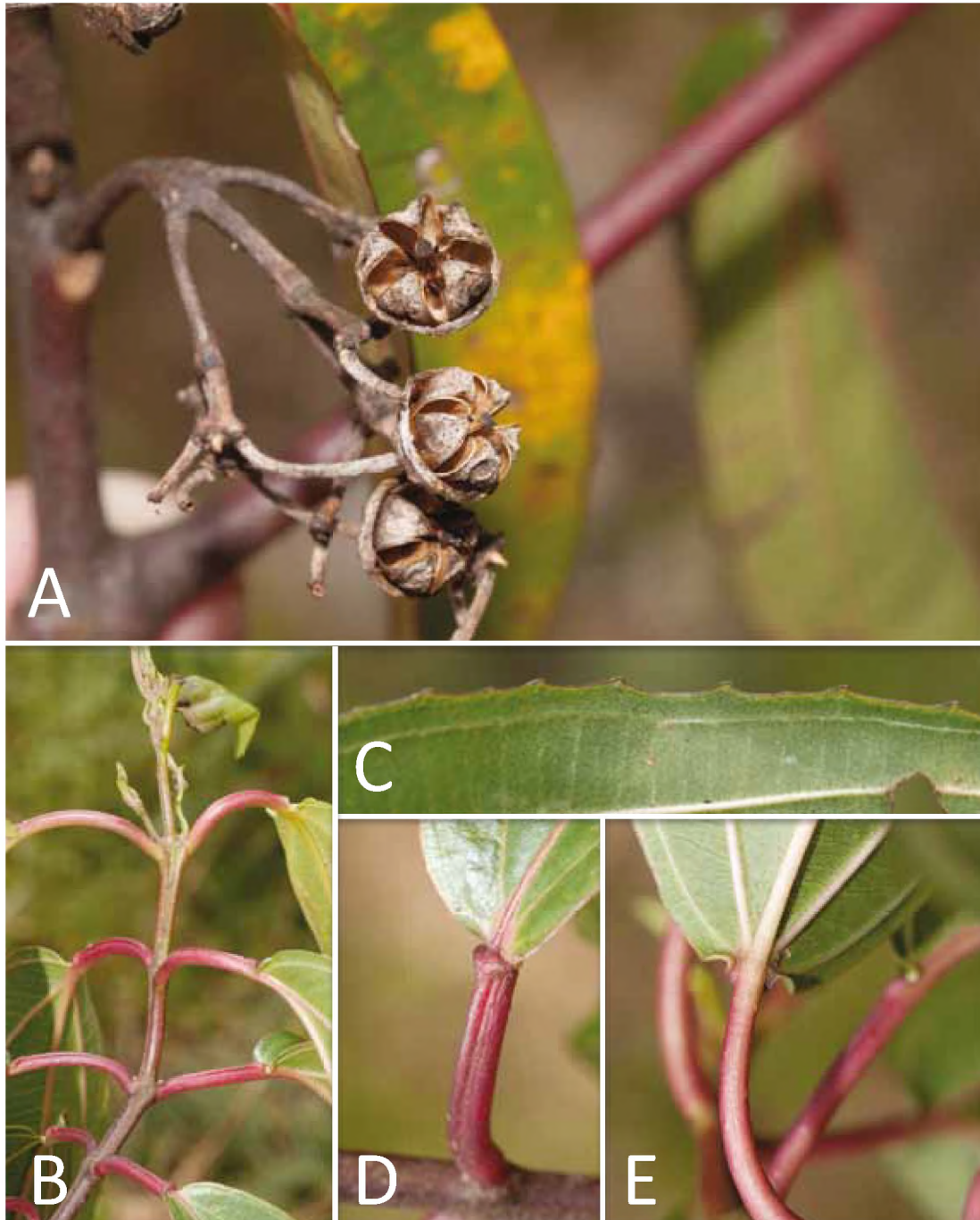
**Figure 52.** Distribution of *Axinaea minutiflora*.

2700 m, 3 Jul 2002, 6°42′S, 77°51′W, *Cotton & Gustafsson 1834* (AAU, CPUN, HUT); 1837 (AAU, CPUN, HUT); Cerros Calla-Calla, 19 km above Leimebamba on road to Balsas, 3100 m, 7 Jun 1964, *Hutchison & Wright 5590* (BR, F, G, GH, MO, NY, S, US); 18 km SW of Leimebamba along road to Balsas, 3000 m, 13 Feb 1985, 6°45′S, 77°48′W, *Luteyn & Cotton 11385* (NY); 15 Feb 1985, *Luteyn & Cotton 11432* (NY); Cochabamba, 2800 m, 23 Jul 1995, *Quipuscoa & Schjellerup 202* (F); 3 km S of Pomacocha, E of Shipasbamba trail, 2400 m, 20 Jun 1962, *Wurdack 954* (F, G, GH, NY, S); middle eastern

*Opposite page:*

**Figure 51.** *Axinaea minutiflora* — A. Habit. B. Detail of leaf base. C. Petal. D. Anisomorphic stamens showing the filament, the spherical connective that is basally somewhat apiculate, and the anther. E. Fruit (From *Devia 207*).





**Figure 54.** *Axinaca nitida* – A. Capsule. B. Habit showing typical red petioles. C. Dentate leaf margin. D. Leaf base adaxial surface showing the scutum. E. Leaf base abaxially showing the auricles (From *Michelangeli 1722*, Peru, Cuzco. Photo: Fabián Michelangeli).

*Opposite page:*

**Figure 53.** *Axinaca nitida* – A. Flower. B. Inflorescence. (Peru 2010, No voucher. Photo: Rainer Bussmann).

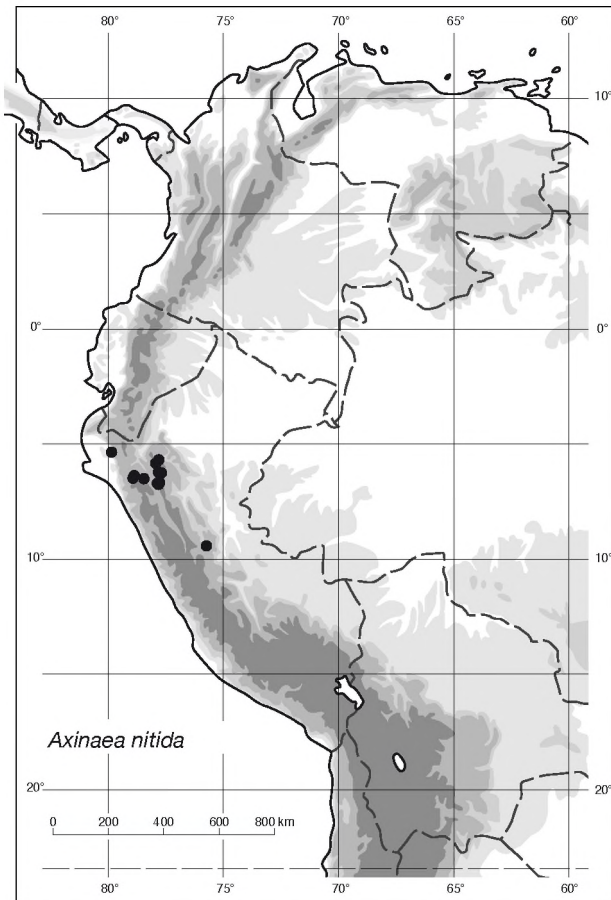


Figure 55. Distribution of *Axinaea nitida*.

Calla-Calla slopes, km 416-419 of Leimebamba-Balsas road, 2900-3100 m, 9 Jul 1962, *Wurdack 1259* (F, NY, US). **Cajamarca:** Parque Nacional Cutervo, Pajonal village, towards Jaén, 2600 m, 10 Aug 1987, *Díaz & Osorio 2586* (F, MO, NY, W); Hda. Taulis, road between La Playa and Palmito, 2900 m, 5 Sep 1964, *Hutchison & von Bismarck 6532* (F, K, MO, NY); Taulis Recorco (Calquis), 2740 m, 3 Aug 1986, *Mostacero et al. 1163* (AAU, F, MO, NY, US); between El Molino and La Pucarilla, *J. G. Sánchez-Vega 332* (NY, US); Parque Nacional San Andrés, La Pucarilla, 2500 m, 24 Jun 1988, *J. G. Sánchez-Vega 448* (F); 26 Jun 1992, *I. Sánchez-Vega & Miranda 6359* (MO, NY); Prov. Chota, Rejo Pampa, 2600 m, 21 Jul 1993, *J. G. Sánchez-Vega 836* (F). **Huánuco:** Pucallpa, western part of Sira mountains, 26-28 km ESE from Puerto Inca, 2240 m, 19 Jun 1988, 9°25'S, 74°43'W, *Wallnöfer 19-19688* (US).

The Berlin (B) type of *Axinaea nitida* was destroyed during World War II. There is a fragment of the B type deposited in BR consisting of a leaf and a couple of flowers that are here designated as lectotype.

27. *Axinaea oblongifolia* (Cogn.) Wurdack, *Phytologia* 20: 373. 1970. — *Meriania oblongifolia* Cogn. in A. DC. *Mon. Phan.* 7: 429. 1891. — Type: "Ecuador vel Peruvia," *Grisar s.n.* (lectotype, here designated: P!, photo: F!; isotypes: BR!, F, LE [n.v., cited by Cogniaux]).

**Shrub or small tree**, 1.5-8 m tall; *branchlets* subquadrate to terete, glabrous; *stipuliform flaps* reduced to a line across the nodes. **Leaves** petiolate; *petiole* 1-3 cm long; *lamina* elliptic-oblong to elliptic-ovate, 6-12 × 1.5-4.8 cm, sub-coriaceous, adaxially and abaxially glabrous; *apex* acute to bluntly acute; *base* cuneate to long-attenuate, not auriculate, often revolute; *scutum* absent; *margins* dentate, teeth minute-2 mm long and 3-5 mm apart; *venation* 3-plinerved, excluding the tenuous inframarginal nerves that run 0.5-2 mm from the margin, the inner pair of primaries diverging from the main nerve 3-25 mm from the base of the lamina, adaxially glabrous, abaxially glabrous; *secondary nerves* faint abaxially, parallel, 1-3 mm apart. **Inflorescence** a pendulous thyrse, 11-many-flowered, terminal, 5-12 cm long, subtended by two bracts that are similar to the leaves but smaller, 5-9 × 1.8-3.5 cm; *pedicels* slender, 6-10 mm long. **Flowers** 5-merous, 1-1.3 cm long; *hypanthium* shallowly cyathiform, 1-2 mm long, obscurely 5-lobed or the truncate, external teeth inconspicuous, appearing just as a small protuberance 0.5 mm long; *petals* lavender or violet abaxially, white adaxially, obovate, concave, 10-15 × 6-11 mm, apex broadly and asymmetrically bilobed; *stamens* isomorphic; *filaments* complanate, 4-5 mm long; *connective appendage* spherical, 4 × 3 × 3 mm, rounded basally, yellow; *anthers* 4-5 mm long with one minute slightly dorsal pore, dark purple; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* ca 1 cm long. **Fruit** a 5-lobed capsule, hypanthium completely covering the mature capsule; *seeds* not seen.



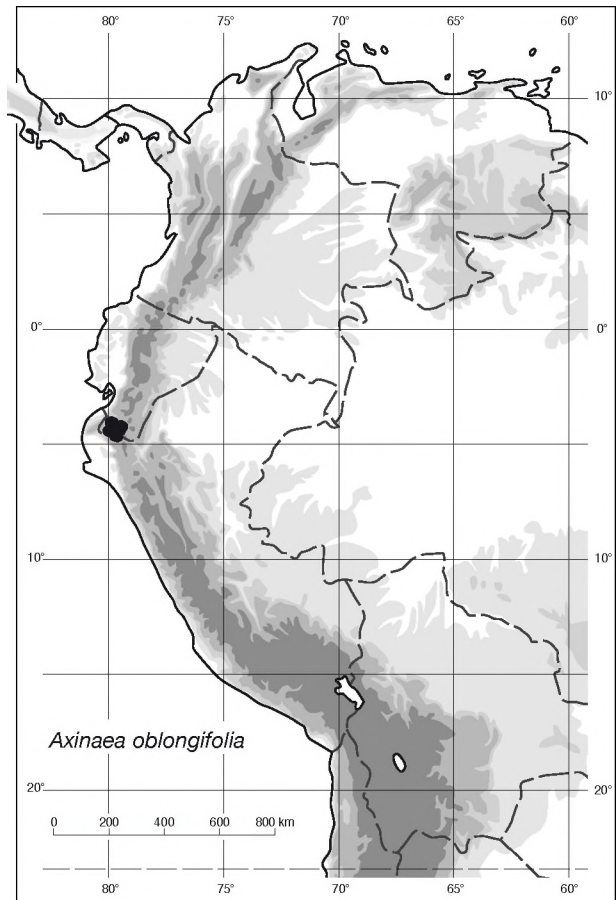
*Axinaea oblongifolia* is restricted to a small area on the border between Ecuador and Peru, where it grows in the montane forest, at 1400–3050 m elevation. – Figure 56.

**Additional specimens examined – ECUADOR:**

**Loja:** Loma Larga, Hda. La Hamaca, Cantón Catacacha, 2200–2400 m, 15 Apr 1944, *Acosta-Solís 7817* (F); Quilanga, Bosque Protector de Santa Rosa, 2600 m, 5–7 Aug 1997, 4°23'31"S 79°27'53"W, *Aguirre et al. 135* (LOJA); Road Sapotepamba-Celica-Guachanamá, 1600–2600 m, 26 Feb 88, *Jaramillo 10312* (AAU); Cerro Celica, Celica-Guachanamá, km 14, 2430 m, 15 Apr 1994, 4°3'50"S 79°54'16"W, *Jørgensen et al. 252* (LOJA, MO, NY); Guachanamá, Cerro Guachaurcu, km 0–6, 2800–3050 m, 25 Jul 1990, 4°2'S 79°52'W, *Jørgensen et al. 92144* (AAU, MO, NY); 13.5 km before Sozoranga, 2300 m, 15 Jul 1998, 4°21'S 79°43'W, *Lozano et al. 1113* (LOJA); Loja-Macará road, 2200 m, 30 Sep 1959, *Maguire & Maguire 44378, 44379* (NY); Gonzanamá, cerro Colombo, 2700 m, 1966, 4°14'S 79°23'W, *Vivar et al. 493* (LOJA); Gonzanamá, Cuenca of Río Tinajones, 6 Aug 1994, 4°12'11"S 79°27'27"W, *Vivar & Merino 4309* (AAU, LOJA). **PERU: Piura:** Prov. Ayabaca, around Ayabaca, 2760 m, 27 May 1971, *López et al. 7795* (MO, US); 2742 m, 7 Aug 1954, *Soukup 4321* (F, US); Cerro Chacas, 2800 m, 8 Jul 2000, *Sagástegui 16245* (AAU); Bosque del Toldo, 2700–2800 m, 11 Jul 2000, *Sagástegui 16251* (AAU); 2650 m, 10 Sep 1976, *Sagástegui & Cabanillas 8717* (F, MO, NY); 2900 m, May 1912, *Weberbauer 6371* (F, GH, NY, US); Quebrada Los Molinos, Tacalpo, 1500–2000 m, 28 May 1996, 4°39'58"S 79°35'51"W, *Quipuscoa et al. 693* (NY); Prov. Huancabamba, Cixse, Talaneo-Cachaco, 2700 m, 5 Sep 1976, *Sagástegui & Cabanillas 8641* (AAU, F, MO, NY). **LOCALITY UNKNOWN:** "Amérique équatoriale," *Bonpland s.n.* (P)

*Axinaea oblongifolia* has somewhat variable leaves that can be oblong or more oblong-ovate. The plinervation is also variable, with the primaries arising from 3 mm to 25 mm above the lamina base.

Cogniaux cites two of Grisar's collections in the protologue, one duplicate deposited in Paris and the other one in "Herb. Petropol." It is assumed that this



**Figure 56.** Distribution of *Axinaea oblongifolia*.

last specimen is now in Leningrad and was not seen, so the Paris duplicate has been designated as the lectotype.

- 28. *Axinaea pauciflora*** Cogn. in A. DC., Monogr. phan. 7: 448. 1891. Type: "Ecuadore vel Peruvia," *Grisar s.n.* (holotype: P!, photo: F!, NY!; isotype: BR! [fragment]).

**Shrub or tree**, 1–6 m tall; *branchlets* subquadrangular, densely to moderately pubescent when young, glabrescent with age, hairs dendritic, thick, densely branched, 0.2–0.6 mm long; *stipuliform flaps* absent or reduced to a faint line across the nodes. **Leaves** petiolate; *petiole* 0.5–1 cm long, moderately to densely pubescent, hairs similar to those on the branchlets; *lami-*

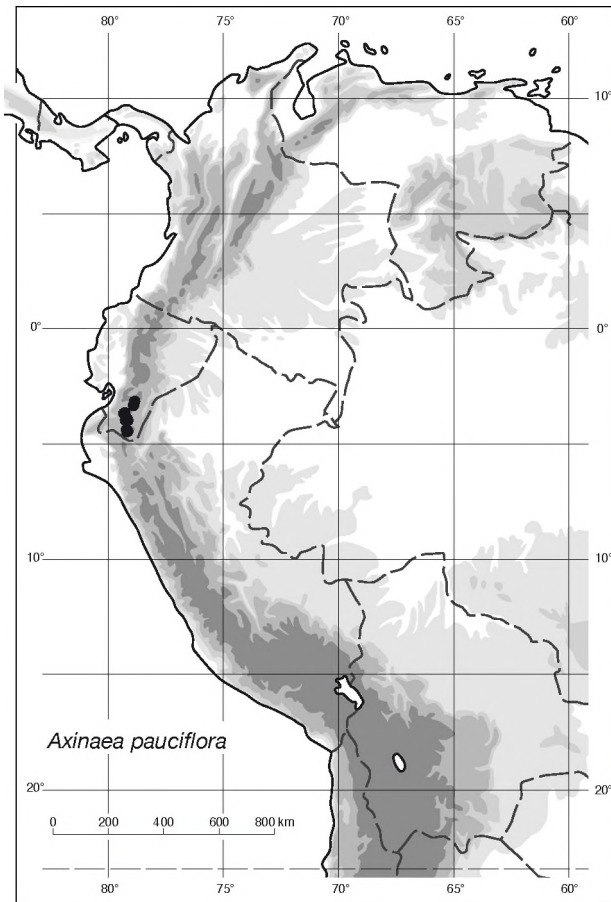


Figure 57. Distribution of *Axinaea pauciflora*.

*na* elliptic to elliptic-ovate, 6–11 × 3–7 cm, coriaceous, hardened, sometimes bullate, adaxially glabrous or with scattered pubescence along the nerves, abaxially sparsely to densely pubescent, hairs similar to those on the branchlets but more slender; *apex* acute or rounded; *base* rounded or truncate, auricles to 1 mm long, revolute; *scutum* absent; *margins* entire to shallowly denticulate; *venation* 5-nerved or shortly 5-plinerved, the inner pair of primaries diverging from the main nerve 3–10 mm above the leaf base, nerves adaxially sunken, glabrous or with scattered pubescence, abaxially prominent and moderately to densely pu-

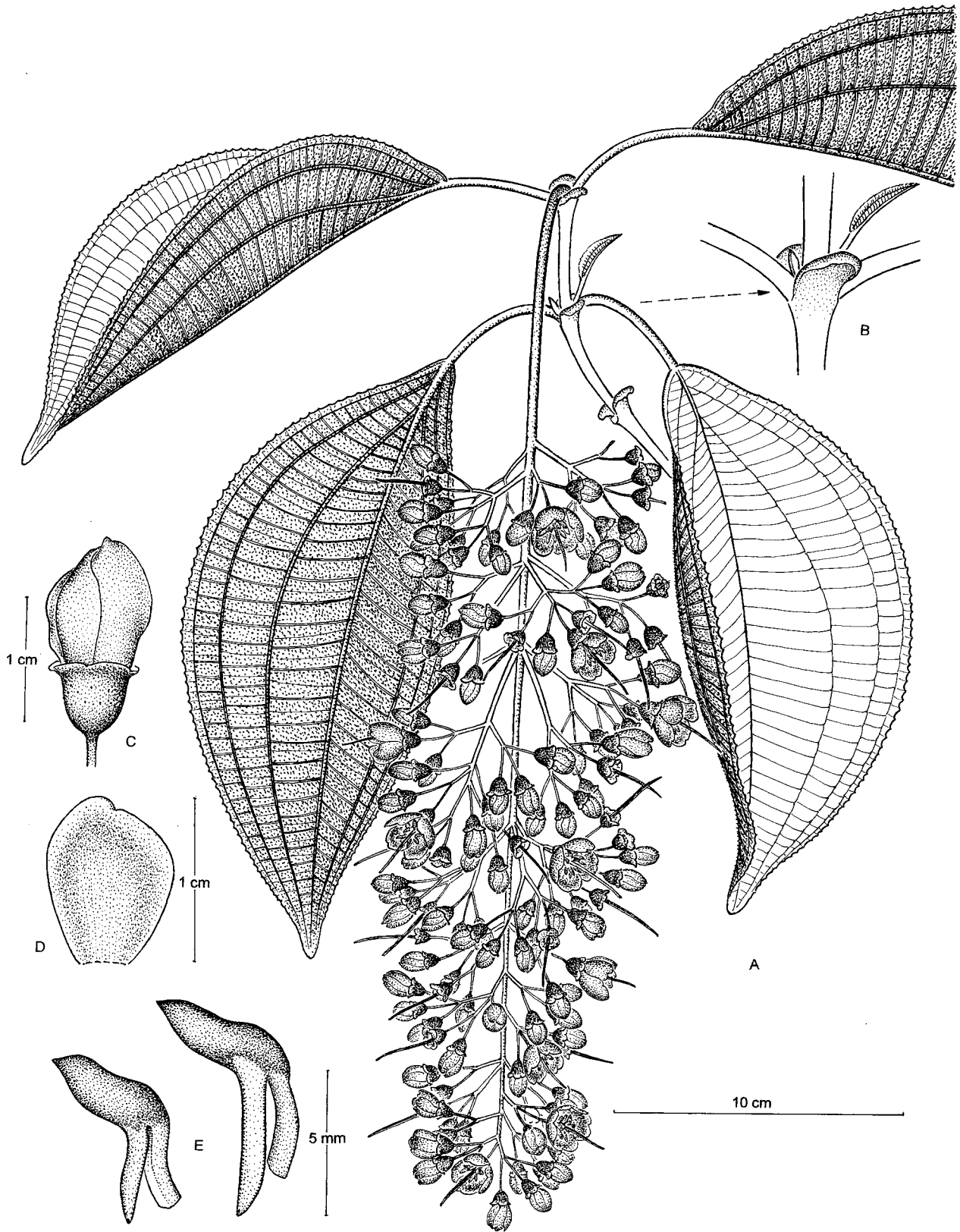
bescent, hairs similar to those in the branchlets but more slender; *secondary nerves* evident, parallel, 3–4 mm apart. **Inflorescence** a few-flowered thyrse, terminal, 5–8 cm long; *pedicels* 4–10 mm long, densely to moderately pubescent, hairs similar to those on the branchlets but more slender. **Flowers** 5-merous, 1.5–2 cm long; *hypanthium* cupuliform, 3–4 mm long, densely to sparsely pubescent, hairs similar to those on the branchlets; *calyx* ca 1 mm long, obscurely 5-lobed, apex truncate, external teeth minute or absent; *petals* pink, purplish-violet or pale lilac, elliptic-obovate, 12–14 × 8–10 mm wide, apex rounded or asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 7–8 mm long in the longer stamens, 5–6 mm long in the shorter ones; *connective appendage* spherical, 3–4 × 2–3 × 2–3 mm, somewhat apiculate basally; *anthers* 4–5 mm or 6–7 mm long with a small apical pore; *ovary* oblong, 5-costate, apex 5-lobed, 5-celled; *style* 10–18 mm long. **Fruit** a 5-lobed capsule, 5-celled, the hypanthium never covering more than a half of the capsule; *seeds* numerous, cuneiform.

*Axinaea pauciflora* is restricted to the Andes of southern Ecuador, where it grows at 2400–3400 m elevation. — Figure 57.

**Additional specimens examined – ECUADOR: Azuay:** Road Sigsig–Molón–Cuchil, near Molón, 2800 m, 3°9'S 78°50'W, 6 Aug 1986, *Betancourt 376* (F, NY, US); Fierro-Urco, Loja–Saraguro, km 12.4, turnoff towards Fierro-Urco, km 6, 3360 m, 8 Dec 1994, 3°42'S, 79°18'W, *Jørgensen et al. 1327* (MO); 22–25 km S of Sigsig along road towards Gualaquiza, Páramos de Matanga, 3040–3340 m, 3°20'S 78°53'W, 21 Jan 1985, *Luteyn & Cotton 11147* (NY); **Loja:** 58.6 km N of Loja, ca 5 km S of Saraguro, 2875 m, 3°39'S 79°15'W, 4 Mar 1992, *Croat 72670* (MO); Loja–Zamora, 12 km from Loja, farm of Dr. David Espinosa, 2600 m, 3°55'S 79°9'W, 1 Oct 1988, *Ellemann 66539* (AAU, LOJA, QCA); Parque

Opposite page:

**Figure 58.** *Axinaea pendula* – A. Habit. B. Detail of the node showing the stipuliform flaps. C. Mature bud. D. Petal. E. Anisomorphic stamens showing the filament, the ellipsoidal connective, basally acute, and the anther (From *Sánchez-Vega & Miranda 6320*).





**Figure 59.** *Axinaea pendula* – A. Habit. B. Inflorescence. (From *Sánchez-Vega & Miranda 6320*. Photo: Michael Dillon).

Nacional Podocarpus, Cerro Toledo, E of Yangana, 2700–3000 m, 4 May 1987, *van der Werff & Palacios 9311* (AAU, K, NY, S). **Loja/Zamora-Chinchipe:** road Yangana-Valladolid, entrance of Parque Nacional Podocarpus, 2500–3000 m, 10 Dec 1989, 4°28'S, 79°10'W, *Madsen 86684* (AAU). **Zamora-Chinchipe:** road Loja-Zamora, km 17, 2400 m, 16 Apr 1973, 3°59'S, 79°08'W, *Holm-Nielsen et al. 3557* (AAU); along new road Loja-Zamora, 2500 m, 25 Apr 1987, *van der Werff & Palacios 9025* (AAU, K, NY, US).

*Axinaea pauciflora* is most similar to *A. sclerophylla* from which it can be distinguished by its petioles that are 0.5–1 cm long (*vs.* 1.5–3 cm), its erect (*vs.* spreading) leaves, and its hypanthium that is 3–4 mm long (*vs.* 6–10 mm).

The holotype of *A. pauciflora* in the Paris herbarium was annotated by Cogniaux so, no doubt exists about its validity.

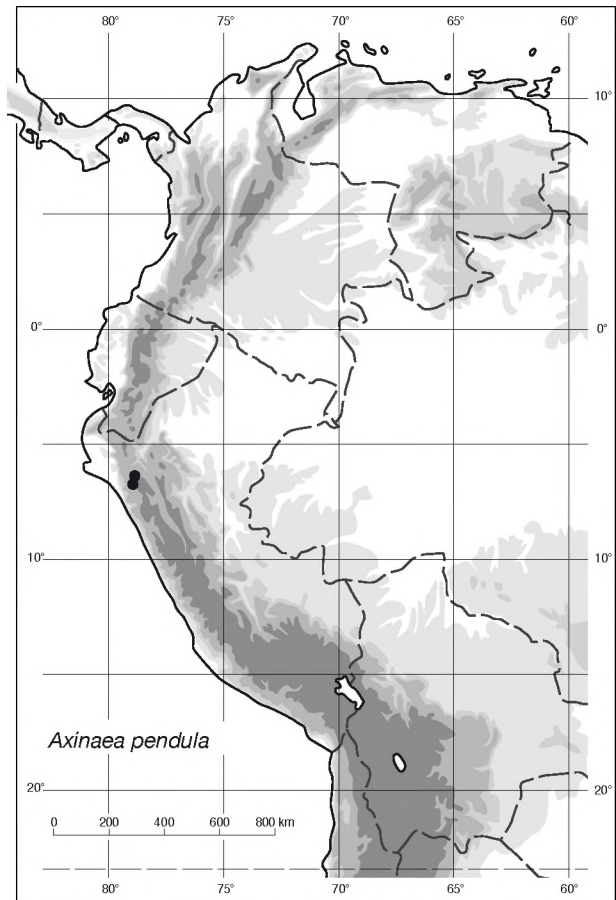
**29. *Axinaea pendula*** E. Cotton, spec. nov. – Type: Peru. Prov. Cutervo, Madre Mía, between El Suro and La Flor, NE of the Parque Nacional Cutervo, 2400 m, 25 Jun 1992, *I. Sánchez Vega & Miranda 6320* (holotype: F!; isotypes: AAU!, US!). – Figures 58 and 59.

*Species Axinaeae crassinodae Triana simulans, a qua differt ramulis sparse puberulentis usque ad glabris (non dense pubescentibus) foliis 7-plinerviis (non 5–) 7-nerviis, petalis clare rubris (non roseis vel albotinctis).*

**Tree**, 10–12 m tall; *branchlets* quadrangular to subquad-rangular, sparsely puberulent when young, glabrous with age, hairs minute, 0.5–1 mm long, thick, dendritic, densely branched; *stipuliform flaps* present, coriaceous, forming a flat outgrowth across the nodes, up to 7 mm long. **Leaves** petiolate; *petiole* 4–4.5 cm long, moderately furfuraceous when young, glabrous with age, hairs similar to those on branchlets; *lamina* broadly elliptic or elliptic-ovate, 13–18 × 7–10 cm, sub-coriaceous, bullate, adaxially glabrous, abaxially sparsely puberulent, hairs similar to those of branchlets but only 0.2–0.5 mm long; *apex* acuminate; *base* rounded or cuneate, not auriculate, not revolute; *scutum* absent; *margins* denticulate to dentate, teeth 0.5–1 mm long and 2–3 mm apart; *venation* 7-plinerved, excluding the tenuous inframarginal nerves that run ca 0.5 mm from the margin, with the inner pair of primaries diverging 1–1.5 cm above the base of the lamina, adaxially somewhat sunken, glabrous, except near the base, abaxially prominent, moderately to sparsely furfuraceous; *secondary nerves* evident sunken adaxially, prominent abaxially, parallel, 3–6 mm apart. **Inflorescence** a pendulous thyrses, many-branched, >26-flowered, terminal, 20–40 cm long, flowers arranged in loose fascicles; *pedicels* slender, 8–10 mm long. **Flowers** 4-merous, 1.2–1.5 cm long; *hypanthium* cupuliform, 3–4 mm long; *calyx* 0.5–1 mm long, 4-lobed, external teeth obscure or absent; *petals* bright red outside, whitish-red inside, obovate, concave, 10–11 × 7–8 mm wide, apex asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 4 or 5 mm long; *connective appendage* ellipsoidal, elongated, 4 × 1 × 1 mm, acute basally; *anthers* 4 or 5 mm long with one small slightly dorsal pore; *ovary* oblong, 4-lobed at the apex, 4-celled; style 12–18 mm long, curved distally. **Fruit** and *seeds* not seen.

*Axinaea pendula* is endemic to the Andes of northern Peru, where it grows at 2400–3300 m elevation. — Figure 60.

**Additional specimens examined** — PERU: **Cajamarca**: Prov. Santa Cruz, Dtto. Pulán, Quebrada Cocán, 3280 m, 2 Nov 2001, *Sánchez-Vega & Sánchez* 11108 (AAU, F).



**Figure 60.** Distribution of *Axinaea pendula*.

The long pendulous inflorescence and the red corolla make *Axinaea pendula* particularly beautiful. It is similar to *A. crassinoda* but differs in having 5-merous (not 4-merous) flowers, glabrous to only sparsely pubescent branchlets (not densely pubescent), in having leaves 7-plinerved (not 5–7 nerved), and bright red petals (not pink or white flushed with darker pink). *Axinaea pendula* also has some resemblance to *A. dependens*, which is also 4-merous.

30. *Axinaea pennellii* Gleason, Bull. Torrey Bot. Club 54: 28. 1927. — Type: Peru. Dept. Cusco, forested hills above Pillahuata, 2300–2400 m, 3–6 May 1925, *Pennell* 14003 (holotype: NY!; photo: BM!, GH!, MO!, NY!; isotypes: F!, GH!, S!, US!; photo of the GH isotype: NY!; photo of the US isotype: NY!).

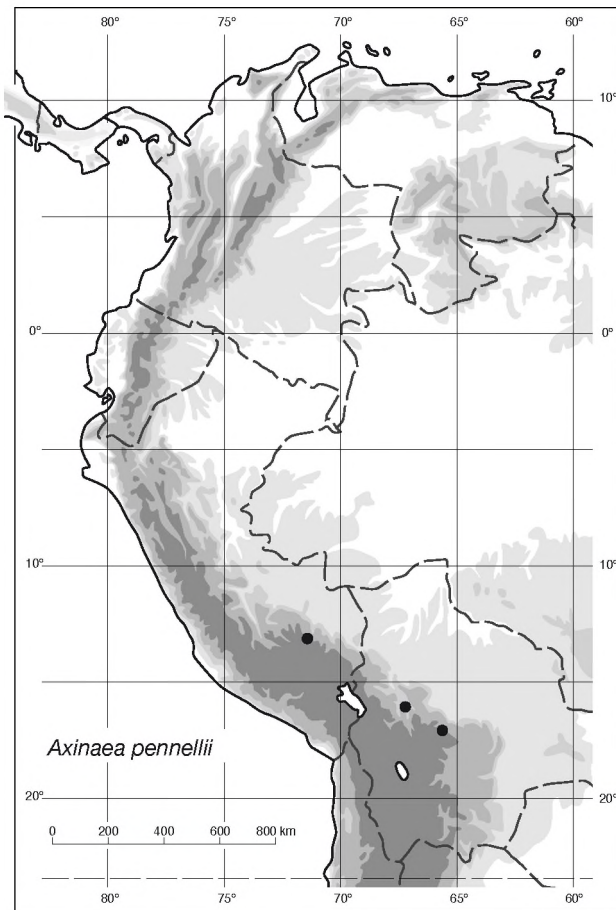


Figure 61. Distribution of *Axinaea pennellii*.

**Shrub or tree**, 2-? m tall; *branchlets* quadrangular or subquadrangular, furfuraceous when young becoming glabrous with age, hairs minute, 0.1-0.2 mm long, dendritic, densely branched; *stipuliform flaps* reduced to a thin line across the nodes. **Leaves** petiolate; *petiole* 2-3.5 cm long, furfuraceous when young but becoming glabrous with age, hairs similar to those on the branchlets; *lamina* ovate-lanceolate, 12-18 × 5.5-7 cm, coriaceous, adaxially glabrous except when very young, abaxially moderately to sparsely furfuraceous, hairs similar to those on the branchlets, caducous with age; *apex* acute; *base* cuneate or truncate, auricles 4-8 mm long, revolute, often overlapping; *scutum* well developed, knob-shaped; *margins* dentate, teeth 1 mm long, and 4-6 mm apart; venation 5(-7)-nerved, excluding the tenuous inframarginal nerves that run ca

1 mm from the margin, adaxially glabrous, abaxially moderately to densely furfuraceous, hairs similar to those on the branchlets; *secondary nerves* parallel, 3-5 mm apart. **Inflorescence** a somewhat pendulous thyrs, loosely-branched, 3-25-flowered, terminal, 10-20 cm long. **Flowers** 5-merous, ca 2 cm long; *hypanthium* cyathiform, 2-4 mm long; *calyx* ca 1 mm long, obscurely 5-lobed, external teeth inconspicuous; *petals* purple, oblong-obovate, concave, 12-15 × 6-8 mm wide, apex broadly and asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 6-7 mm long in the longer stamens, 4-5 mm long in the shorter ones; *connective appendage* spherical, 3-4 × 2 × 2 mm, rounded to somewhat apiculate basally; *anthers* 5-6 mm and 6-7 mm long with one small, slightly dorsal pore; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* 3-2 cm long, curved distally. **Fruit** a 5-lobed capsule; *seeds* cuneiform.

*Axinaea pennellii* grows on the the eastern slopes of the Andes in Peru and Bolivia at altitudes of 2300-2900 m. — Figure 61.

**Additional specimens examined — BOLIVIA:**  
**Cochabamba:** Incachaca, 2000 m, Mar 1941, *Cárdenas* 2222 (US); Yungas of Espíritu Santo, 2400 m, Nov 1976, *Cárdenas* 3751 (S).

*Axinaea pennellii* closely resembles *A. lanceolata* from which it can be distinguished by the presence of a well developed, knob-shaped scutum.

31. *Axinaea quitensis* Benoist, Bull. Soc. Bot. France 81: 326. 1934. — Type: Ecuador. "Páramos de San Juan," 26 Feb 1931, *Benoist* 3941 (holotype: P!; photos: BR!, F!, GH!, MO!, NY!, S!).

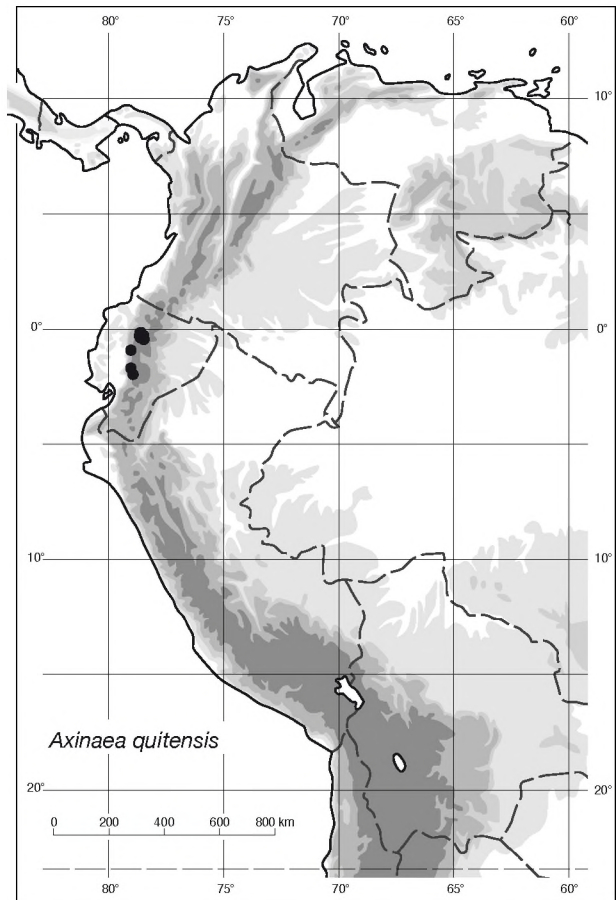
**Tree**, (3-)6-20 m tall; *branchlets* subquadrangular or terete, glabrous; *stipuliform flaps* present as a hardened ridge, raised ca 0.5-1 mm. **Leaves** petiolate; *petiole* 0.5-2.5 cm long; *lamina* elliptic-obovate, 5-12 × 2-5 cm, coriaceous, glabrous, abaxially moderately to sparsely covered with minute, orange glands, visible only under ×10 magnification; *apex* acute or acuminate; *base*

long attenuate, not auriculate; *scutum* absent; *margins* entire or sometimes denticulate on the upper half, revolute, dentate-undulate or occasionally entire in the lower 1/3; *venation* 5-nerved or shortly 5-plinerved, excluding the tenuous inframarginal nerves that run very close to the margin, the outer pair of primaries much fainter than the inner pair and running 1–3 mm from the margin, the inner pair diverging up to 5 mm above the lamina base but this is often obscured by the attenuation of the base, adaxially and abaxially glabrous; *secondary nerves* faint adaxially and abaxially, parallel, 2–4 mm apart. **Inflorescence** a pendulous thyrse, moderately-flowered, terminal, 5–12 cm long, often subtended by two bracts that are similar to the leaves but smaller; *pedicels* 5–10 mm long. **Flowers** 5-merous, 14–18 mm long; *hypanthium* cupuliform, 3–4 mm long; *calyx* ca 1 mm long, 5-lobed, lobes rounded or broadly triangular, external teeth not evident; *petals* light pink, lilac or white inside, darker outside, oblong to slightly obovate, concave, 6–8 × 11–13 mm, apex asymmetrically bilobed; *stamens* anisomorphic; *filaments* light violet, complanate, 5–6 mm long in the longer stamens, 4–5 mm long in the shorter ones; *connective appendage* spherical, 2 × 2 × 2 mm, somewhat apiculate basally, dark yellow; *anthers* 4–5 mm long with one minute slightly dorsal pore, dark violet; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* ca 1.5 cm long. **Fruit** a 5-lobed capsule, the hypanthium covering only half or less of the mature capsule; *seeds* cuneiform.

*Axinaea quitensis* is restricted to the Andes of northern and central Ecuador, where it grows at altitudes between 2600 m and 3900 m. — Figure 62.

**Additional specimens examined — ECUADOR:**

**Carchi:** Cerro Golondrinas, N ridge, 2880–2950 m, 24 Jul 1994, 0°51'30"N, 78°8'20"W, *Boyle et al. 3407* (MO); above Maldonado, border with Colombia, at Chilmá, 2000 m, 20 May 1991, 0°51'N, 78°2'W, *Palacios & Rubio 7293* (MO); Espejo, El Gualtal, summit of Cerro Golondrinas Hembra, 3000 m, 21 Aug 1994, 0°51'N, 78°8'W, *Palacios & Clark 12542* (AAU). **Chimborazo:** Pallatanga, community Jesús del Gran Poder,



**Figure 62.** Distribution of *Axinaea quitensis*.

from Panza Redonda 2 km S, ca 4 km NE of Pallatanga, 2800–3200 m, 12–14 Jul 1995, 1°58'S, 78°56'W, *Clark et al. 1296* (AAU, NY). **Cotopaxi:** road Latacunga–Pilaló–Quevedo, 5–15 km E of Pilaló, 2700–3350 m, 22 May 1988, 0°55'S, 79°1'W, *Cerón et al. 3792* (AAU, NY). **Imbabura:** Hda. Rosa Pamba, Otavalo Canton, 2850–3000 m, 15 May 1944, *Acosta-Solís 8074* (F); Angochagua, Eastern Cordillera, 2500–3150 m, 26 Nov 1949, *Acosta-Solís 14594* (F); Rd Otavalo–Laguna Mojanda, 3350 m, 29 Jun 1983, 0°11'N, 78°17'W, *Brandbyge 42210* (AAU); Quebrada San Isidro, road Otavalo–Laguna Mojanda, 3000–3070 m, 15 Apr 1983, 0°10'N, 78°16'W, *Brandbyge 42124* (AAU, MO, NY); Laguna Mojanda–Cajas, road between Otavalo and the lake, 3100 m, 24 Jun 1984, *Jaramillo 6691* (AAU); 2600–3100 m, 12 Jul 1989, 0°12'N, 78°30'W, *Morán et al. 53* (MO);



**Figure 63.** *Axinaea reginae* – A. Flower. B. Habit. (Bussman et al. 15926. Photo: Rainer Bussmann).

12 km W of Otavalo on road to San José de Minas, Hda. Pisabo, 2800 m, 25 Apr 1991, 0°14'N, 78°21'W, Neill et al. 9853 (MO, US); Cordillera de Quichinche, Hda. San Alberto, SW of Otavalo, 3200–3500 m, 12 Mar 1989, 0°15'N, 78°25'W, Palacios 4007 (AAU, MO). **Pichincha:** below San Juan towards Chiriboga, 2600 m, 2 Aug 1955, Asplund 17164 (F, G, K, NY, S); road to Yanacocha, NW side of Cerro Pichincha, 30 Sep 1982, 0°5'S, 78°33'W, Balslev & Steere 3258 (AAU, NY); Bosque Protector Pasochoa, 30 km SE of Quito, 2850–3900 m, 25 May 1986, 0°27'S, 78°28'W, Betancourt 241 (US); 14 Jun 1986, 250 (F, NY); 253 (NY); Jaramillo 8601 (AAU); 8621 (AAU); Yanacocha, NW slopes, 3700 m, 22 Mar 1987, Jaramillo 9576 (AAU, QCA); Quito–Nono, turnoff to Yanacocha, 3600 m, 22 Mar 1987, 0°9'S, 78°35'W, Jørgensen 61741 (AAU, MO); Lloa Valley, Hda. Las Palmas, Lloa–Mindó, km 14, 2900 m, 21–23 Jan 1989, 0°10'S, 78°38'W, Jørgensen 61845 (AAU); 18–21 Sep 1988,

65481 (AAU); 65521 (AAU, MO); 21–23 Jan 1989, 65845 (AAU, NY); 21–23 Jan 1989, 65864 (AAU); 7 Feb 1989, 65907 (AAU, MO, NY); 65973 (AAU, NY); 24–28 Sep 1990, 0°50'S, 78°38'W, Jørgensen et al. 92502 (AAU, MO); 20–21 Oct 1990, 92608 (AAU, MO, NY); 92610 (AAU, MO); 92612 (AAU); 92614 (AAU); 7 Apr 1991, 93084 (AAU); Bosque Protector Pasochoa, 3225–3310 m, 26 Aug 1986, 0°27'S, 78°27'W, Jørgensen & Valencia 61498 (AAU, MO, NY); 26–28 Oct 1986, 61551 (AAU, F, GH, MO, NY); 61554 (MO, NY); 18 Nov 1986, 61577 (MO, NY); Volcán Pasochoa, 3000–3200 m, 27 Apr 1985, Larsen 41 (AAU); La Cocha, near San Juan towards Chiriboga, 3360 m, 19 Mar 1976, Oldeman 3412 (US); Mt. Corazón, 3200 m, Sep 1873, Sodiro 483 (AAU); Volcán Atacazo, 3300 m, Aug 1903, Sodiro s.n. (BR); Volcán Pasochoa, SW of Quebrada Monjas, 3225–3310 m, 5 Mar 1987, Valencia 75 (AAU); road Chillogallo–San Juan–Chiriboga–Empalme, near San Juan, 3100–3260



m, 9–10 Sep 1985, 0°18'S, 78°39'W, Zak & Jaramillo 652 (AAU, NY); 663 (AAU, NY).

All studied specimens of *A. quitensis* have orange glandular dots on the abaxial surface of the lamina. Also the stipuliform flaps are hardened and slightly raised.

32. *Axinaea reginae* Bussmann, Gruhn & Glenn, in Nordic Journal of Botany 28: 520–522. 2010. – Type: Peru. Amazonas: Chachapoyas, Leymebamba, Río El Jardín, tall *Escallonia/Weinmannia* forest with high amount of *Ichroma* in understory, 06°56'44"S, 77°41'54"W, 3090 m, 30 Jun 2009, Bussmann, Gruhn, Wägener, Briones & Espinoza 15926 (holotype: HUT (nv), isotypes: HAO, MO, NY). – Figure 63.

**Tree**, 3–5 m tall in the forest understory; *branchlets* terete or obscurely quadrangular, densely furfuraceous throughout, hairs cream-coloured, pinoid, dendritic, with a well developed axis and few short terete branches, up to 0.75 mm long; *nodes* strongly thickened; *stipuliform flaps* well developed, up to 1 cm long. **Leaves** petiolate; *petiole* 17–30 mm long, densely furfuraceous; *lamina* elliptic-ovate, 7–10 × 3.5–4.5 cm, coriaceous, adaxially sparse indument with long and short hairs, abaxially dense indument with medium-length hairs cream, sparsely dotted with minute orange glands; *apex* broadly acute; *base* rounded to broadly acute, not auriculate; *scutum* absent; *margins* narrowly dentate, weakly or not at all revolute; *venation* shortly (3-)5-plinerved, excluding the tenuous inframarginal nerves, the inner pair of primaries diverging from the main nerve 1–3 cm above the leaf base, prominent abaxially, sparsely to moderately furfuraceous above, densely furfuraceous abaxially, hairs similar to those on the branches; *secondary nerves* evident adaxially and abaxially, parallel, 1–2 mm apart. **Inflorescence** a pedunculate, compound thyrse, 115–150-flowered, terminal, 30–40 cm long including the 9–12 cm long peduncle; *pedicels* 5–8 mm long, densely furfuraceous, hairs as in the branches but shorter. **Flowers** 4-merous, 1–1.5 cm long; *hypanthium* cupuliform, 3–4 mm long, with a sparse indument of short hairs; *calyx* 1–2 mm long, ob-

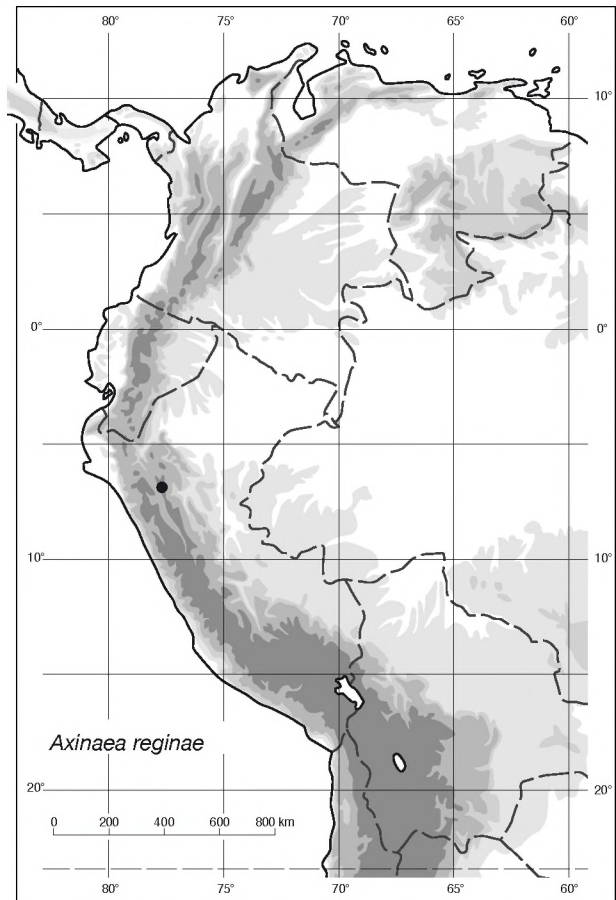


Figure 64. Distribution of *Axinaea reginae*.

scurely 4-lobed, lobes bilobed, external teeth inconspicuous or absent; *petals* white with pale purple margins outside, white inside, fleshy, spherical, concave, 6–12 × 9–14 mm, apex asymmetrically bilobed; *stamens* 8, isomorphic; *filaments* complanate, 6–7 mm long; *connective appendage* ellipsoidal, acute basally, deep yellow; *anthers* 3–4 mm long with one small slightly dorsal pore, deep reddish-purple; *ovary* oblong, 8-costulate, apex 4-lobed, 4-celled; *style* 7–15 mm long, white turning purple at tip. **Fruit** and *seeds* not seen.

*Axinaea reginae* is known only from a restricted area of less than 10 km<sup>2</sup> at the type locality on the eastern slopes of the northern Peruvian Andes in the Leymebamba district, where it grows in tall *Escallonia/Weinmannia* forest, at altitudes of 2900–3100 m. – Figure 64.

*Axinaea reginae* shares the pendulous inflorescences and the plinerved leaves with *A. dependens* but differs from it in the more dense and persistent pubescence (*vs* glabrescent with age in *A. dependens*). It shares with *A. crassinoda* the thickened nodes and the type of pubescence, as well as the colour of the flowers and the pendulous inflorescences. As commented before under *A. fernando-cabiesii*, hybridization may be an important driver of *Axinaea* diversity. We hypothesize, that *A. reginae* is a hybrid of *A. crassinoda* x *A. dependens*, which again would need substantiation by further studies of their breeding ecology.

33. *Axinaea robusta* Eves, Bull. Torrey Bot. Club 63: 221. 1936. — Type: Colombia. “Mont del Moro,” Dec 1845, *Purdie s.n.* (holotype: K!, photos: F!, GH!, NY!; isotype: K!, photos: F!, GH!, NY!).

**Shrub**, ? m tall; *branchlets* quadrangular, densely to moderately furfuraceous when young, less so with age, hairs minute, 0.5–1 mm long, dendritic, thickened, densely branched; *nodes* thickened; *stipuliform flaps* present, hardened, forming a woody ridge across the nodes, raised up to 2 mm. **Leaves** petiolate; *petiole* 3–3.5 cm long, densely furfuraceous when young, moderately so with age, hairs similar to those on the branchlets; *lamina* ovate to elliptic-ovate, 9–16 × 5–10 cm, coriaceous, adaxially glabrous, abaxially sparsely furfuraceous, hairs similar to those of the branchlets but only 0.2–0.5 mm long; *apex* acuminate; *base* cuneate or rounded, auricles revolute; *scutum* well developed, knob-shaped; *margins* entire to obscurely denticulate; *venation* 5-nerved, excluding the tenuous inframarginal nerves that run ca 0.5–1 mm from the margin, adaxially glabrous, except near the base, abaxially densely to moderately furfuraceous; *secondary nerves* evident and somewhat prominent abaxially, parallel, 3–6 mm apart. **Inflorescence** a pendulous thyrses, many-branched, densely-flowered, terminal, 20–40 cm long, flowers arranged in fascicles; *nodes* thickened; *stipuliform flaps* present at the larger nodes, similar to those on the branches but smaller; *pedicels* slender, 10–12 mm long, densely to moderately furfuraceous. **Flowers** 5-merous, 12–15 mm long; *hypanthi-*

*um* cupuliform, 3–4 mm long; *calyx* 1 mm long, obscurely 5-lobed or truncate, external teeth not evident; *petals* oblong-obovate, concave, 10–12 × 6–7 mm wide, apex obscurely and asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 5–6 mm long in the longer stamens, 4–5 mm long in the shorter ones; *connective appendage* spherical to slightly ellipsoidal, 3–4 × 2–3 × 2–3 mm, somewhat apiculate basally; *anthers* 6–7 mm or 5–6 mm long, with one small slightly dorsal pore; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* 15–17 mm long. **Fruit** and *seeds* not seen.

*Axinaea robusta* is known only from the type locality in Mount del Moro, Colombia.

It has been impossible to locate the place called “Mont del Moro” in Colombia. It could be a locality in Venezuela, instead of Colombia, called “Monte del Morro,” in Mérida State, where two other species of *Axinaea*, *A. affinis* and *A. costaricensis*, also grow.

34. *Axinaea ruizteranii* Wurdack, Acta Bot. Venez. 13: 136–138. 1978. — Type: Venezuela. Táchira: San Rafael, between El Molino and El Portachuelo, Dtto. Chacón, 2840 m, 8 Apr 1966, *Ruiz-Terán 3057* (holotype: US!, photo: NY).

**Shrub or tree**, 3–22 m tall; *branchlets* subquadrangular, densely setulose-furfuraceous when young sparsely so with age, hairs minute, 0.2–0.5 mm long, dendritic, densely branched; *stipuliform flaps* absent. **Leaves** petiolate; *petiole* 1.2–3 cm long, densely setulose-furfuraceous, hairs similar to those on the branchlets; *lamina* suborbicular to broadly-ovate, 5–11 × 3.5–8 cm, coriaceous and rigid, adaxially glabrous, abaxially sparsely pinoid-furfuraceous, hairs similar to those of the branchlets; *apex* bluntly acute to obtuse; *base* rounded to widely obtuse, revolute; *scutum* knob-shaped, sometimes obscure; *margins* entire to obscurely denticulate; *venation* 5-nerved, excluding the tenuous inframarginal nerves that run ca 0.5 mm from the margin, adaxially pinoid furfuraceous towards the base of the lamina, abaxially densely to

sparingly pinoid-furfuraceous, hairs similar as those on the branchlets; *secondary nerves* evident, parallel, 2–3 mm apart. **Inflorescence** a 8–15 cm long synflorescence composed of several orders of 1–15-flowered, pendulous thyrses or dicasia, each 3–5 cm long and subtended by a pair of bracts similar to the leaves; *pedicels* slender, 3–5 mm long. **Flowers** 5-merous, 1.2–1.5 cm long; *hypanthium* cupuliform, ca 3 mm long; *calyx* ca 1 mm long, obscurely 5-lobed, external teeth minute; *petals* lilac to dark red-violet abaxially, lighter adaxially, fleshy, oblong-obovate, concave, 12–15 × 10–12 mm wide, apex truncate or broadly and asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 5 mm long in the longer stamens, 4 mm long in the shorter ones; *connective appendage* spherical or slightly ellipsoidal, 2.5–3 × 1.5–2 × 1.5–2 mm, apiculate basally, orange-yellow; *anthers* 4 mm and 5–6 mm long with one small apical pore, dark red-purple; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* 10 mm long, slightly curved at the apex. **Fruit** (immature) a 5-lobed capsule, the hypanthium covering at least half of the capsule; *seeds* not seen.

*Axinaea ruizteranii* is restricted to the Andes of Venezuela, where it grows at 2700–3200 m elevation. – Figure 65.

#### Additional specimens examined – VENEZUELA:

**Mérida:** La Porquera, Bailadores, 25 May 1966, *López-Palacios 1234* (US); La Montaña, after El Portachuelo, between Santa Cruz and El Molino, 2850–2900 m, 6 Aug 1970, *Ruíz-Terán & López-Figueiras 555* (NY); Quirorá, or Chacantá, Páramo, 3000–3200 m, 22 Apr 1971, *Ruíz-Terán & López-Figueiras 1693* (NY, US); road to Mesa de Bustamante, 5 km S of La Playita on highway Bailadores–Páramo La Negra, 2700 m, 24–25 Aug 1973, *Tillett & Hömig 738-391* (US). **Táchira:** Portachuelo–Pregonero road, 2900 m, 24 Nov 1972, *Wurdack et al. 2787* (F).

*Axinaea ruizteranii* is known only from Mérida and Táchira. It has almost round leaves although in some plants they may be somewhat elliptic-ovate. Most of the plant is hairy, especially the young branches and the petioles and nerves abaxially. Wurdack cites only

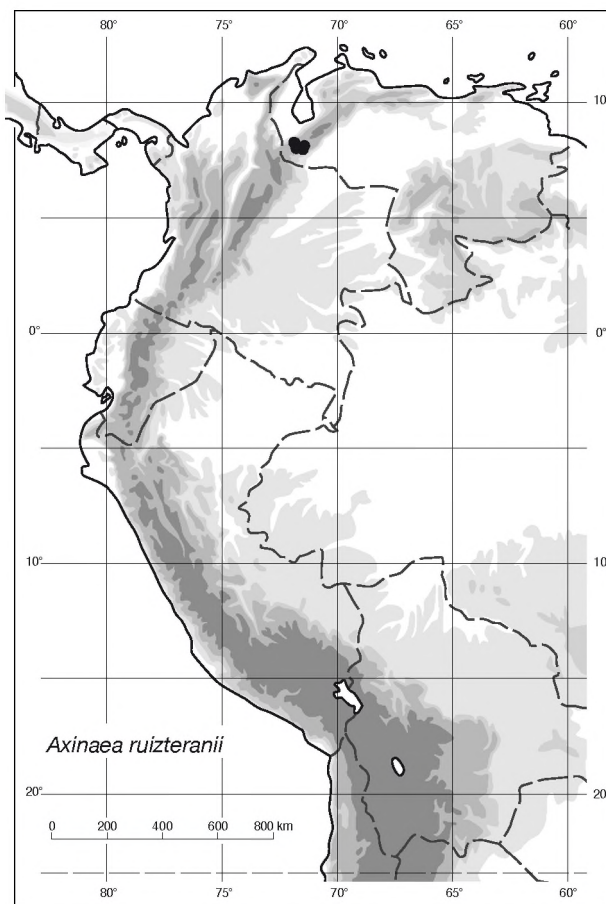


Figure 65. Distribution of *Axinaea ruizteranii*.

one specimen in the protologue, but additional isotypes may be deposited in one of the Mérida herbaria (MER, MERC or MERF).

35. *Axinaea sclerophylla* Triana, Trans. Linn. Soc. London 28: 68. 1871. Type: Ecuador. “Loxa”, August 1847, *Seemann 765* (holotype: K!, photos: F!, GH!, NY!; isotype: GH!; photo of the BM isotype: NY!; photos of the G isotype: MO!, NY!; photo of the GH isotype: NY!). – Figure 66.

**Shrub or tree**, 3–12 m tall; *branchlets* quadrangular to subquadrangular, moderately to densely pubescent when young, becoming glabrous with age, hairs barbellate, 0.1–0.5 mm long; *nodal flaps* absent or reduced to a line across the nodes. **Leaves** petiolate; *petiole* 1.5–



**Figure 66.** *Axinaca sclerophylla* (Ecuador, Loja, 22 Aug 1977, *Lewis 3511*: Photo: G. Lewis).

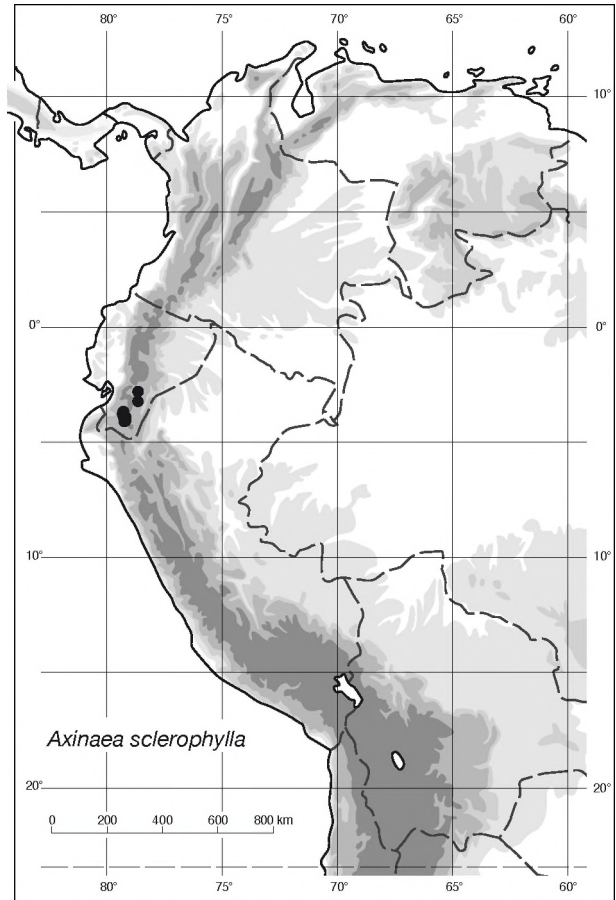
3 cm long, moderately to densely pubescent, hairs similar to those on the branchlets; *lamina* elliptic, elliptic-ovate or elliptic-obovate, (6-)8-15(-23) × (3.5-)6-9(-14) cm, coriaceous, rigid, often bullate, adaxially glabrous and often lustrous, abaxially moderately to densely pubescent, hairs barbellate, 0.3-0.5 mm long; *apex* acute or abruptly acuminate; *base* cuneate; *margins* entire to denticulate; *venation* shortly 5-plinerved, the inner pair of primaries diverging from the main nerve 3-6(-10) mm above the leaf base, adaxially sunken, glabrous or with scattered pubescence, abaxially prominent and moderately to densely pubescent, hairs similar to those of the branchlets, caducous; *secondary nerves* evident, parallel, 2-4 mm apart. **Inflorescence** a pendulous thyrse, 1-25-flowered, terminal, 7-12 cm long, often subtended by bracts that are similar to the leaves but smaller; *pedicels* 2-5 mm

long, densely pubescent, hairs similar to those found on the branchlets. **Flowers** 5-merous, 1.5-3 cm long; *hypanthium* cupuliform, 6-10 mm long, moderately to sparsely pubescent, hairs similar to those of the branchlets, caducous; *calyx* 1-2 mm long, obscurely 5-lobed, apex rounded or truncate, external teeth not evident; *petals* light pink, white or white suffused with pink, fleshy, oblong-elliptic, 16-24 × 11-14 mm, apex asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 11-13 mm long in the longer stamens, 8-9 mm long in the shorter ones, red; *connective appendage* dimorphic, yellow-orange or dark yellow, spherical, 3-4 mm in diameter in the longer stamens, ellipsoidal, 6 × 4 × 4 mm, with the apex resting on the anther in the shorter ones, rounded or slightly apiculate basally; *anthers* dark red or brown-red, often lighter in the longer stamens, 8 mm or 11 mm long with a

small apical pore; *ovary* oblong, 5-costate, apex 5-lobed, 5-celled; *style* 12–18 mm long. **Fruit** a 5-lobed capsule, the hypanthium covering at least half of the mature capsule; *seeds* numerous, cuneiform.

*Axinaea sclerophylla* is restricted to the Andes of southern Ecuador where it grows at 1700–3400 m elevation. – Figure 67.

**Additional specimens examined – ECUADOR:** **Azuay:** 1–8 km N of Sevilla de Oro, 2400–2700 m, 27 Jul 1945, *Camp E-4332* (F, NY, S, US); *E-4371* (F, G, GH, MO, NY, US, W); *E-4584* (F, GH, NY, US). **Loja:** Uritusinga, 2800 m, 4° 6' S 79° 14' W, 13 Feb 1995, *Aguirre et al. 4426* (LOJA); Loma de Oro, 10 km S from Saraguro, 3100 m, 3° 40' S 79° 17' W, 24 Sep 1982, *Balslev & Steere 3200* (AAU, NY, QCA); road Loja-Saraguro, km 28, Bosque Protector La Cofradía, 2680–2840 m, 3° 50' S 79° 13' W, 4 Aug 2000, *Cotton et al. 1539* (AAU); Loja-Zamora, 12 km from Loja, finca of Dr. David Espinosa, 2600 m, 3° 55' S 79° 9' W, 17 Nov 1988, *Ellemann 75398* (AAU, LOJA, QCA, QCNE); Zamora-Huaico (6 km SE of Loja), 2300–2400 m, 4° 2' S 79° 11' W, 3 Jul 1947, *Espinosa 1553* (F, LOJA, NY, US); Loja-Saraguro, km 25, 1730 m, 22 Apr 1994, 3° 52' S, 79° 17' W, *Jørgensen et al. 504* (MO); track from Universidad Nacional to Uritusinga, km 10.5, 2900 m, 4° S 79° 12' W, 22 Aug 1997, *Gwilym Lewis 3511* (AAU, K, LOJA, NY, QCA); road Loja-Las Achira (Uritusinga), km 9–10 from Universidad Nacional de Loja, 2750–2800 m, 22 Sep 2001, 4° 3' S, 79° 14' W, *Madsen & Rosales 8461* (AAU); 25 Oct 2001, *Madsen & Chimbo 8609* (AAU); Parque Nacional Podocarpus, above Cajanuma, trail from Centro de Información towards Lagunas de Compadre, 2900–3100 m, 4° 5' S 79° 10' W, 19 Jan 1989, *Madsen 85578* (AAU, LOJA, MO, NY, QCNE); Parque Nacional Podocarpus, E of Nudo de Cajanuma, just N of Centro de Información, 2900 m, 4° 5' S 79° 10' W, 16 Aug 1989, *Madsen 86144* (AAU, LOJA, MO, NY, QCA); new road Loja-Saraguro, km 17, 2600–2650 m, 3° 55' S 79° 15' W, 19 Mar 1989, *Øllgaard & Feil 91108* (AAU, K, LOJA, MO, NY, QCA, QCNE); Villonaco, *Poortmann 67* (BR, F, P); about 26 km from Loja on road to Saraguro, ca 6 km before Santiago, 2750–2800 m, 3° 50' S 79° 17' W, 11



**Figure 67.** Distribution of *Axinaea sclerophylla*.

Jun 1996, *Ståhl et al. 2630* (AAU, LOJA, QCA); San Lucas, Loma del Oro, 2800 m, 3° 40' S 79° 15' W, 18 May 1966, *Vivar 403* (LOJA); Santiago, El Sauce, 9 Apr 1983, *Vivar, 1763A* (LOJA); Mountains of Santiago, 3° 47' S 79° 17' W, 1 Dec 1988, *Vivar 3326* (LOJA). **Zamora-Chinche:** road Loja-Zamora, km 16, near the pass, 2700 m, 20 May 1967, *Sparre 16499* (AAU, S, US); road Yangana-Valladolid, S and E of pass, Nudo de Sabanilla, Parque Nacional Podocarpus, 2750–2950 m, 14 Mar 1989, 4° 27' S, 78° 8' W, *Øllgaard 91097* (AAU).

All specimens of *Axinaea sclerophylla* from Azuay, have larger leaves and less dense pubescence all over. The slight differences in this population, however, do not seem to merit taxonomic recognition.

36. *Axinaea scutigera* Triana, Trans. Linn. Soc. London 28: 69. 1871. — Type: Colombia. Antioquia: 2500 m, Nov 1846, *Triana s.n.* (holotype: K!, photos: GH!, K!, NY!; isotypes: COL (n.v.), P! [2 sheets], photos of the COL isotype: F! NY!, photos of the P isotype: MO!, NY!).

*Axinaea scutigera* Triana ssp. *ecuadorensis* Wurdack, Mem. New York Bot. Gard. 16: 7. 1967. — Type: Ecuador. Loja: Hda. Anganuma, headwaters of Río Cachi-yacu, W slopes of Cordillera Cóndor, about 46 km S of Loja, 3200 m 13–16 Jul 1944, *Prieto JP-50A* (holotype: US! [US Herb. # 2404649], photo: NY!; isotype: NY!).

**Shrub or tree**, 1–10 m tall; *branchlets* subquadangular, glabrous and lustrous, often bright red or magenta; *stipuliform flaps* absent. **Leaves** petiolate; *petiole* 2–5.5 cm long, glabrous, often red or magenta; *lamina* ovate, 6–15 × 4–8 cm, coriaceous, glabrous except for a few short, dendritic hairs alongside the abaxial main nerves; *apex* long acuminate, acumen 1–1.5 cm long; *base* cordate, auricles 4–8 mm long, revolute, often overlapping; *scutum* present; *margins* usually entire, occasionally shallowly denticulate; *venation* 5-nerved, excluding the tenuous inframarginal nerves that run 0.5 mm from the margin, often 1(–2) additional pair(s) of nerves present in the auricles but they soon disappear in the margins, adaxially and abaxially glabrous; *secondary nerves* slightly prominent on both surfaces, parallel, 2–4 mm apart. **Inflorescence** a more or less pendulous thyse, densely to moderately-flowered, terminal, 5–12 cm long, often subtended by bracts similar to the leaves but smaller; *pedicels* 5–10 mm long. **Flowers** 5-merous, ca 1.5 cm long; *hypanthium* cyathiform, 1.5–3 mm long; *calyx* 0.5–1 mm long, obscurely 5-lobed, external teeth absent; *petals* purple, pink or purple-pink, lighter inside, oblong-obovate, concave, 10–12 × 6–7 mm wide, apex broadly and asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 4–5 mm long; *connective appendage* spherical to slightly ellipsoidal, 3–4 × 2–3 × 2–3 mm, rounded basally, yellow; *anthers* 3–5 mm long with one small slightly dorsal pore, dark red or dark purple; *ovary* ob-

long, costulate, apex 5-lobed, 5-celled; *style* 10–15 mm long, curved distally. **Fruit** a 5-lobed capsule, the hypanthium always covering less than 1/2 of the mature capsule; *seeds* cuneiform.

*Axinaea scutigera* is widely distributed though relatively rare. It grows in the Andes of Colombia, Ecuador and northern Peru at 1100–3000 m elevation. — Figure 68.

**Additional specimens examined — COLOMBIA:** **Antioquia:** Mpio. Caldas, Vereda La Corrala, finca La Zarza, 2440 m, 24 May 1985, *Albert de Escobar & Giraldo 5261* (NY); 22 Jun 1987, *Albert de Escobar et al. 7751* (US). **Boyacá:** Santuario de Iguaque, Cañón de Mamarra-mos, 12 km N of Villa de Leyva, 2800 m, 2 May 1981, *Melampy 1336* (US). **Chocó:** Cerro del Torrá, crest, 2700–2800 m, 21 Aug 1988, *Silverstone Sopkin et al. 4655* (US). **Cundinamarca:** road La Mesa–San Javier, 1100–1300 m, 20 Jun 1976, *García-Barriga 21030* (F, US); Dintel, between Facatativá and La Vega, 2300–2700 m, 4 Jun 1939, *Pérez Arbeláez & Cuatrecasas 5287* (F, MO, NY); Alto de San Miguel, Sibaté, 2800 m, 28 Sep 1968, *Uribe 6171* (NY). **Santander:** road Páramo de Guántiva–Onzaga, 2970 m, 1 Dec 1967, *R. Jaramillo & van der Hammen 4431* (US). **ECUADOR:** **Loja:** Parque Nacional Podocarpus, road Loja–Zamora, E of Cerro Yanacocha, 2550–2650 m, 26 Nov 1988, 3°59'S, 79°7'W, *Madsen 75566* (AAU); Parque Nacional Podocarpus, road Yanguana–Cerro Toledo, 2800–2850 m, 27 Feb 1985, 4°23'S, 79°7'W, *Øllgaard et al. 58291* (AAU, MO, NY). **PERU:** **Pasco:** Oxapampa, trail to summit of Cordillera Yanachaga via Río San Daniel, 2700–3000 m, 13 Jul 1984, 10°23'S, 75°27'W, *D. N. Smith 7765* (F, MO, NY, US); 2600 m, 18 Jul 1984, *D. N. Smith 7897* (F, US).

The position of the scutum in *A. scutigera* is rather high on the petiole, making the leaf look truncate due to the reflexed position of the auricles. When Wurdack (1967) described *A. scutigera* ssp. *ecuadorensis* he had only available a fragment of the type specimen of the typical subspecies. Now, with many more collections available, the differences mentioned, e.g., primary nerves only 1–2 mm (not 3–4 mm) from the margin and the marginal teeth raised at most 0.2 mm (not

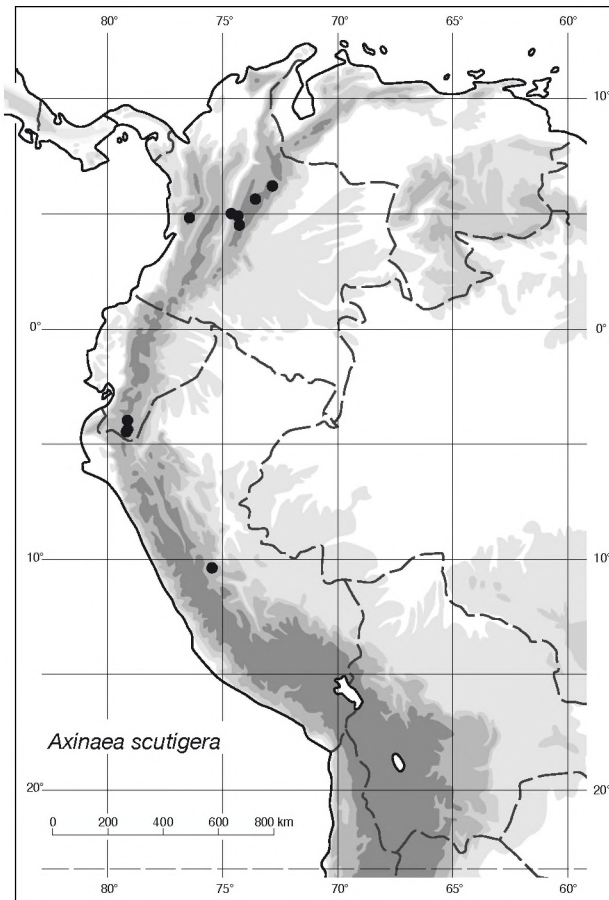


Figure 68. Distribution of *Axinaea scutigera*.

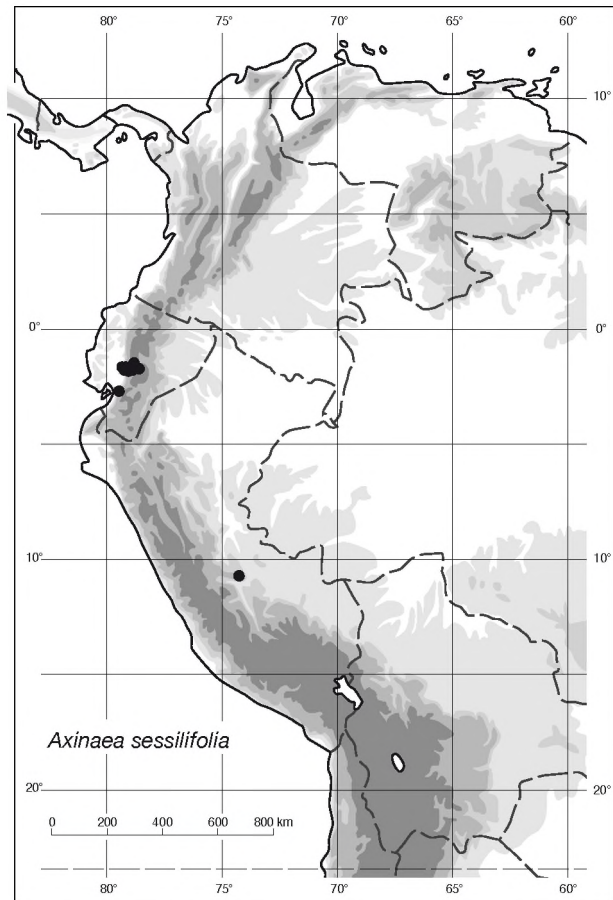


Figure 69. Distribution of *Axinaea sessilifolia*.

1–1.5 mm), do not hold up. Also this species is now known from a disjunct population in central Peru (Figure 66).

37. *Axinaea sessilifolia* Triana, Trans. Linn. Soc. London 28: 68, pl. 5, figure 57c. 1871. – Type: Ecuador. Los Ríos: western slopes of Mount Chimborazo, Río Tablas, 2000–2300 m, Jun 1860, *Spruce 6174* (holotype: K!, photo: F!, GH!, NY!; isotypes: K!, W!; photos of the K isotype: F!, GH!, NY!; photos of the W isotype: F!, MO!, NY!). – Front cover. *Meriania simsiana* Gleason, Bull. Torrey Bot. Club 63: 533. 1936. – Type: Ecuador. Bolívar: Western Cordillera, between Chimbo and Balsapampa, 2600 m, 14 Sep 1934, *Rimbach 211* (holotype NY!; isotypes F!, GH!, US!).

**Tree**, 4–15 m tall; *branchlets* quadrangular, sparsely puberulent when young, glabrous with age; *stipuliform flaps* present, coriaceous, forming a ridge across the nodes, raised 1–2 mm. **Leaves** subplicate, sessile; *lamina* ovate-oblong, 15–28 × 6.5–11.5 cm, coriaceous, adaxially glabrous, abaxially sparsely puberulent when young, glabrous with age; *apex* rounded to acute; *base* cordate, the auricles 1–1.5 cm long; *margins* entire to denticulate; *venation* markedly 5(–7)-plinerved, excluding the tenuous inframarginal nerves that run 0.5–1 mm from the margin, often 2–3 additional pairs of nerves visible in the auricles but they soon disappear in the margins, prominent abaxially, the inner pair of primaries diverging from the main nerve 1–3 cm above the lamina base; *secondary nerves* evident, parallel, 0.4–1 mm apart. **Inflorescence** a pendulous

thyrses, loosely-branched, >26-flowered, terminal, 15–50 cm long, bracts filiform, 0.5–1 mm long, early caducous; *pedicels* slender, (3–)5–15 mm. **Flowers** 5-merous, 1.5–2.5 cm long; *hypanthium* cyathiform, 3–6 mm long; *calyx* 2 mm long, somewhat flared, obscurely lobed, margins somewhat irregular; *petals* deep red to violet, oblong-obovate, symmetric, 13–18 × 7–12 mm wide, apex emarginate; *stamens* isomorphic; *filaments* complanate, 8–12 mm long; *connective appendage* ellipsoidal, dimorphic, 7 × 3 × 3 mm, with apex resting on the anthers in the shorter stamens, 5 × 2 × 2 mm, in the longer ones, somewhat apiculate basally; *anthers* 10–13 mm long with one small apical pore; *ovary* oblong, costate, apex 5-lobed; *style* 10–20 mm long, curved at the apex. **Fruit** a 5-lobed capsule, the hypanthium covering 1/4 of the mature capsules; *seeds* numerous, cuneiform.

*Axinaea sessilifolia* grows in Ecuador and Peru, where it has been found only in a few populations on the western slopes of the Andes at 1800–2700 m elevation. – Figure 69.

**Additional specimens examined – ECUADOR:** **Azuay:** Road Cuenca-Molleturo-Naranjal, Bajo Molleturo, 79°27'W, 02°42'S, 2000 m, 3 Aug 1990, *Palacios & Cerón 13830* (AAU, NY). **Bolívar:** Forest of Chillanes, external side of the Cordillera Occidental, 2400 m, 4 Nov 1943, *Acosta-Solis 6679* (F); Liso road San Vicente-Santiago, banks of Río Tatahuaso, 79°05' W, 01°47' S, 2500 m, 23 Feb 1987, *Betancourt 480* (AAU, F, NY); Road Balsapamba-San Miguel, Las Guardias, 79°05' W, 01°45' S, 2100 m, 16–17 May 1968 *Harling et al. 9555* (F, GB, MO, NY, QCA, US, WIS); 0–3 km SW of Las Guardias on San Miguel-Balsapamba road, 79°10' W, 01°45' S, 2000–2200 m, 17 Jan 1985, *Luteyn & Cotton 11088* (AAU, NY, QCNE); 7–9 km NE of Las Guardias on San Miguel-Balsapamba road, 79°10' W, 1°39' S, 2400–2500 m, 17 Jan 1985, *Luteyn & Cotton 11090* (AAU, NY, QCNE, US), *11092* (NY, QCA); *Rimbach 513* (S); first 15 km of road Chillanes-El Tambo, 2400 m, 18 Jul 1991, *van der Werff 12466* (MO). **Chimborazo:** Road Pallatanga-San Juan Llimbe, 78°51' W, 01°47' S, 2300–2700 m, 26 Feb 1987, *Betancourt 493* (AAU, F, NY); Vol-

cán Chimborazo, *Cross (Veitch) 80* (K). **PERU:** **Junín:** Vitoc, *Ruiz & Pavón s.n.* (MA).

*Axinaea sessilifolia* is easily distinguished from the other species of the genus by its sessile leaves and strongly plinerved venation. There is a Spruce specimen in Vienna (W) that has no number. It is most probably *Spruce 6174* or part of it and most possibly an isotype. Wurdack has also indicated this on the specimen. There is also a fragment in Cogniaux's herbarium (BR) without a collector or a number. As seemed to be his habit, Cogniaux may have taken a fragment from *Spruce 6174* so this could be a fragment of the type specimen, but it could also be a fragment of the Ruiz and Pavón collection from Peru. The latter is the only known collection from that country.

**38. *Axinaea sodiroi*** Wurdack, *Phytologia* 35: 8. 1976.  
– Type: Ecuador. “In silv. occ. suband. m. Pich.,” Aug 1905, *Sodiro s.n.* (holotype: BR! [2 sheets]; photos: F!, GH!, MO!, NY!, S!; isotype: P!).

**Tree**, 6–8 m tall; *branchlets* obtusely quadrangular, densely furfuraceous when young, less so with age, hairs minute, 0.3–0.5 mm long, dendritic, thickened, densely branched; *nodes* somewhat thickened; *stipuliform flaps* absent or reduced to a faint line across the nodes. **Leaves** petiolate; *petiole* 2–3(–11) cm long, densely furfuraceous when young, moderately so with age, hairs similar to those in the branchlets; *lamina* elliptic-ovate, 11–18(–28) × (6–)9–14(–25) cm, coriaceous, adaxially glabrous, abaxially sparsely furfuraceous, hairs similar to those in the branchlets but smaller; *apex* rounded or obtuse; *base* cordate, not auriculate; *scutum* knob-shaped; *margins* entire to obscurely denticulate; *venation* 5(–7)-nerved, excluding the tenuous inframarginal nerves that run ca 0.5–1 mm from the margin, adaxially glabrous, abaxially moderately to sparsely furfuraceous; *secondary nerves* immersed adaxially, prominent abaxially, parallel, 4–6 mm apart. **Inflorescence** a pendulous thyrses, loosely branched, 11-many-flowered terminal, 15–25 cm long; *pedicels* slender, 7–10 mm long, glabrous. **Flowers** 5-merous, ca 2 cm long; *hypanthium* cupuli-



form, 4–5 mm long; *calyx* 1 mm long, obscurely 5-lobed or truncate, external teeth not evident; *petals* oblong-ovate, concave, 15–17 × 9–10 mm, apex obscurely and asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 10–11 mm long in the longer stamens, 7–8 mm long in the shorter ones; *connective appendage* spherical, 3–4 × 2–3 × 2–3 mm, somewhat apiculate basally; *anthers* 10 mm or 13 mm long, with one small, slightly dorsal pore; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* 15–17 mm long. **Fruit** and **seeds** not seen.

*Axinaea sodiroi* is known only from the type locality on Mount Pichincha, Ecuador. — Figure 70.

*Axinaea sodiroi* has only been collected in the Pichincha Volcano close to Quito in 1905, and since it has never been collected again. The high level of destruction of the forests growing on the Pichincha volcano may have extinguished this species.

39. *Axinaea tomentosa* Cogn. in A. DC. Monogr. phan. 7: 451. 1891. — Type: Peru. Chachapoyas, *Mathews s.n.* (lectotype, here designated: G! [Herb. Barbey-Boissier, G Herb. # 8817/52; isotypes: BR!, F! [fragment], G! [Herb. Delessert, 2 sheets, G Herb. # 8817/50 and 8817/51], NY!; photos of the G isotype: F!, MO!, NY!)

*Axinaea tovarii* Wurdack, *Phytologia* 13: 80. 1966. — Type: Peru: Huancavelica, Prov. Tayacaja, Marcavalle, between Huachocolpa and Tintay, 2700 m, 20 Apr 1964, *Tovar 4753* (holotype: US! [US Herb. # 2446955]).

**Shrub or tree**, 3–7 m tall; *branchlets* subquadrangular, moderately to densely puberulent when young, less so with age, hairs multicellular, barbellate, 0.2–0.8 mm long; *stipuliform flaps* reduced to a faint line across the nodes. **Leaves** petiolate; *petiole* 0.5–3 cm long, moderately to densely pubescent, hairs similar to those on the branchlets; *lamina* elliptic, 6–18 × 4–10 cm, coriaceous, adaxially glabrous or with scattered pubescence along the nerves that is more dense towards the base, abaxially densely pubescent, hairs

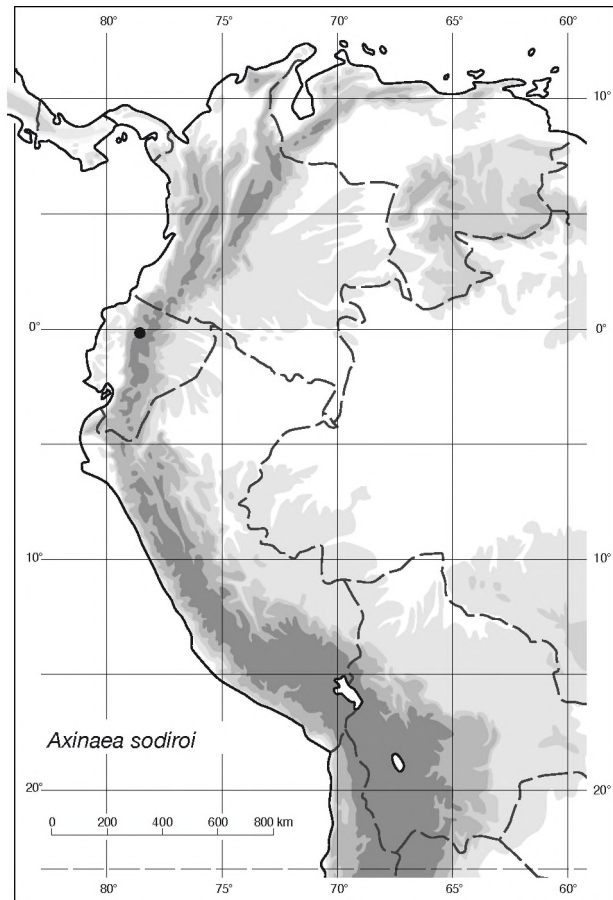


Figure 70. Distribution of *Axinaea sodiroi*.

barbellate, 0.3–0.5 mm long; *apex* acuminate; *base* rounded, auriculate, auricles 2–3 mm long, revolute; *scutum* well developed, knob-shaped, often absent in the leaf-like bracts that subtend the inflorescence; *margins* entire or denticulate; *venation* 5-nerved or shortly 5-plinerved, the inner pair of primaries diverging from the main nerve 2–4 mm above the leaf base, adaxially sometimes sunken, glabrous or with scattered pubescence towards the base, abaxially prominent and densely pubescent, hairs similar to those in the branchlets but shorter; *secondary nerves* evident, parallel, 1–4 mm apart. **Inflorescence** a thyrses, >26-flowered, terminal, 5–12 cm long, often subtended by a pair of leaf-like bracts that usually bear no scutum; *pedicels* 2–5 mm long, densely pubescent, hairs similar to those on the branchlets. **Flowers** 5-merous, 1.2–2

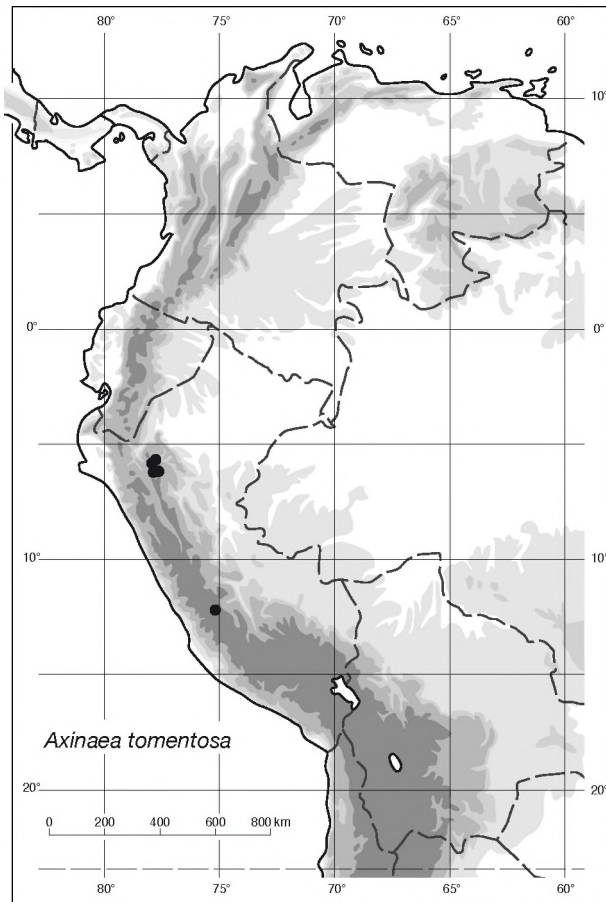


Figure 71. Distribution of *Axinaea tomentosa*.

cm long; *hypanthium* cupuliform, 3 mm long, densely and caducously pubescent, hairs as in the branches; *calyx* 1–2 mm long, 5-lobed, apex bluntly acute, external teeth present, small; *petals* pink, pale pink or reddish-lilac, oblong-elliptic, 12–16 × 6–8 mm wide, apex rounded, somewhat irregular; *stamens* anisomorphic; *filaments* complanate, 5–6 mm long in the longer stamens, 4–5 mm long in the shorter ones; *connective appendage* spherical, 3 × 2 × 2 mm, somewhat apiculate basally; *anthers* 4–6 mm long with a small slightly dorsal pore; *ovary* oblong, 5-costate, apex 5-lobed, 5-celled; *style* 12–18 mm long. **Fruit** and *seeds* not seen.

*Axinaea tomentosa* is endemic to the Andes in northern and central Peru where it grows at altitudes of 2300–3400 m. — Figure 71.

**Additional specimens examined** — PERU: **Amazonas:** Bongará, Jumbilla–San Carlos, 2500–2600 m, Jun 1915, *Weberbauer 7150* (F, GH); NW of Pomacocha, 2300–2700 m, 19 Jun 1962, *Wurdack 907* (F, G, GH, NY, S, US); S of Molinopampa–Diosan pass, 2700–3100 m, 8 Aug 1962, *Wurdack 1623* (F, GH, NY, S).

*Axinaea tomentosa* is very similar to *A. sclerophylla* but differs in the presence (*vs.* absence) of a well developed scutum. The flowers in *A. tomentosa* are also smaller (1.2–2 cm long) in average than those in *A. sclerophylla* (1.5–3 cm long).

40. *Axinaea weberbaueri* Cogn., Bot. Jahrb. Syst. 50. Beibl. III: 32. 1913. — Type: Peru. Dept. Ayacucho, Prov. Huanta, between Tambo and the Apurimac: Yanamonte, 2700–3000 m, Jun 1910, *Weberbauer 5648* (holotype: B [destroyed], photos: F!; GH!; lectotype, here designated: F!, photo: NY!; isotypes: BR!, GH!, S!, US!, photo of the US isotype: NY!).

**Tree**, 4–9 m tall; *branchlets* quadrangular, furfuraceous when young becoming glabrous with age, hairs minute, barbellate; *stipuliform flaps* reduced to a faint line across the nodes. **Leaves** petiolate; *petiole* 2.5–3.5 cm long, furfuraceous when young becoming glabrous with age, hairs similar to those on the branchlets; *lamina* elliptic-lanceolate to ovate-lanceolate, 10–20 × 4–9 cm, coriaceous, adaxially glabrous, abaxially moderately to sparsely furfuraceous, hairs pinoid, 0.2–0.3 mm long, caducous with age; *apex* acuminate; *base* cordate, auricles 1–3 mm long, not revolute; *scutum* well developed, knob-shaped; *margins* entire or shallowly denticulate; *venation* 5-nerved, excluding the tenuous inframarginal nerves that run ca 1 mm from the margin, adaxially glabrous, abaxially moderately to sparsely furfuraceous, hairs similar to those of the abaxial leaf surface; *secondary nerves* parallel, 1–3 mm apart. **Inflorescence** a somewhat pendulous thyrs, loosely-branched, 3–25-flowered, terminal, 10–15 cm long. **Flowers** 5-merous, ca 1.5 cm long; *hypanthium* cyathiform, 2–3 mm long; *calyx* ca 1 mm long, obscurely

5-lobed, external teeth inconspicuous; *petals* violet-pink, oblong-obovate, concave, 12–13 × 6–7 mm wide, apex broadly and asymmetrically bilobed; *stamens* anisomorphic; *filaments* complanate, 6–7 mm long in the longer stamens, 4–5 mm long in the shorter ones; *connective appendage* spherical, 3 × 2 × 2 mm, light yellow, rounded to somewhat apiculate basally; *anthers* 4–5 mm and 6–7 mm long with one small, slightly dorsal pore; *ovary* oblong, costulate, apex with 10 fleshy lobes, the lobes free and separated, 5-celled; *style* 1.3–2 cm long, curved at the apex. **Fruit** and *seeds* not seen.

*Axinaea weberbaueri* is endemic to the Andes of southern Peru (Ayacucho and Cusco Departments) at 2700–3000 m elevation. – Figure 72.

**Additional specimens examined – PERU: Cusco:** Urubamba, Machu Picchu, 1.5 km downriver along Urubamba River from km 88 of the Urubamba railroad, 2820 m, 28 Jun 1982, *Peyton & Tilney Peyton 674* (MO, US); 0.5 km N of the union of Sayacmarca and Aobamba Rivers, 2285 m, 11 Oct 1982, *Peyton & Tilney Peyton 1463* (MO, US).

This species can be distinguished from all other known species of *Axinaea* by the ten apical lobes of the ovary that are free and separated.

41. *Axinaea wurdackii* Sagást., S. J. Arroyo & E. Rodr., Rev. peru. biol. 17(2): 145–150. 2010. – Type: Peru. Dept. Cajamarca, Prov. Contumazá, Molino de Singarrán (Cascas), 1800 m, 11 Jun 1981, *A. Sagástegui, E. García, S. López & J. Mostacero 9972* (Holotype: HUT (n.v.); isotypes: MO!, NY!, US!). – Figure 73.

**Shrub or tree**, 3–35 m tall; *branchlets* subquadrangular, glabrous; *stipuliform flaps* reduced to a line across the nodes. **Leaves** petiolate; *petiole* 1.5–2.5 cm long; *lamina* obovate, 7–11 × 3.5–6.5 cm, sub-coriaceous, adaxially and abaxially glabrous; *apex* acuminate or rounded; *base* long-attenuate, occasionally only cuneate, not auriculate, not revolute; *scutum* absent; margins dentate or denticulate, teeth minute–1 mm long and 2–3 mm

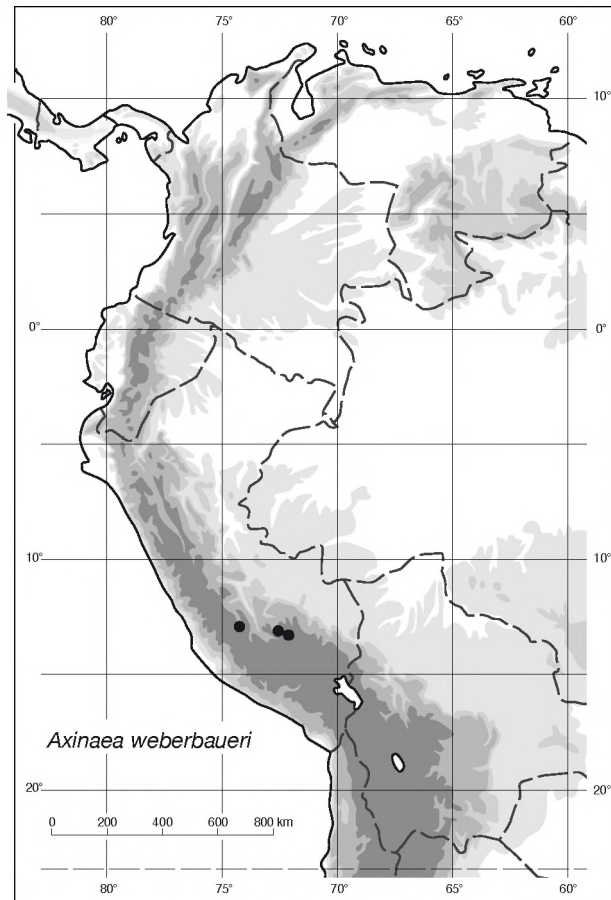
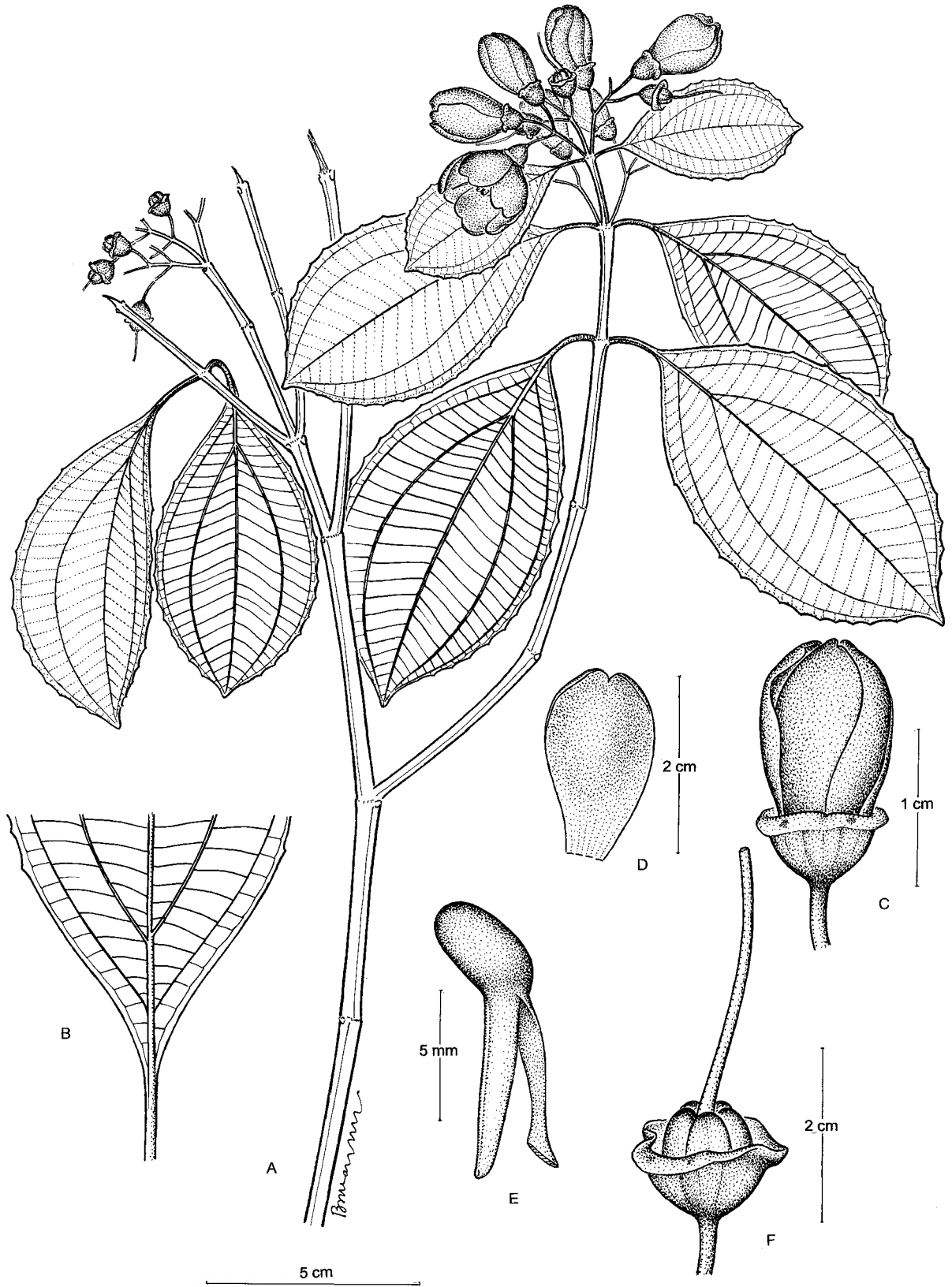


Figure 72. Distribution of *Axinaea weberbaueri*.

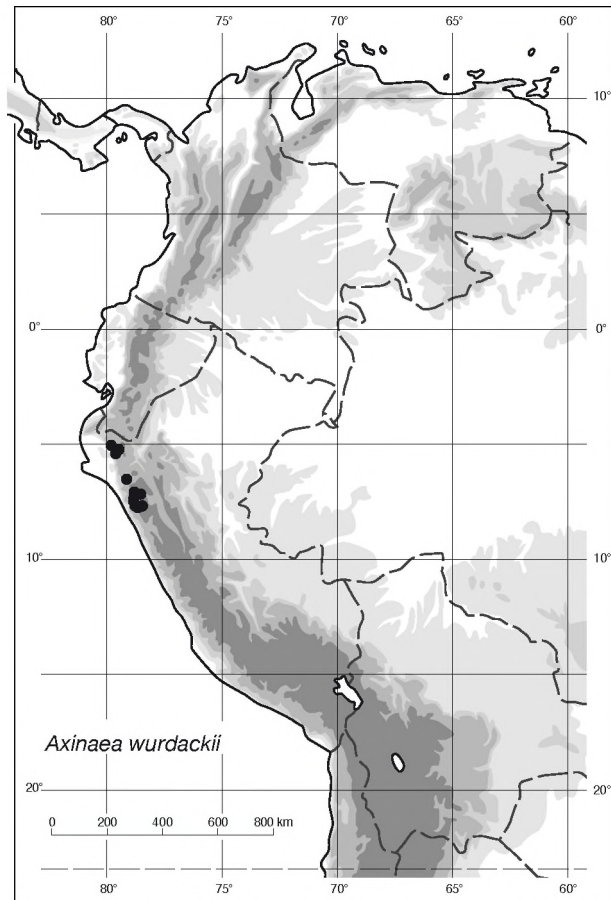
apart; *venation* 5-plinerved, excluding the tenuous inframarginal nerves that run 0.5–1 mm from the margin, the inner pair of primaries diverging from the main nerve 1.5–3.5 cm from the base of the lamina, adaxially and abaxially glabrous; *secondary nerves* faint adaxially, parallel, 2–4 mm apart. **Inflorescence** a pendulous thyrses, 1–25-flowered, terminal, 5–15 cm long, subtended by two bracts similar to the leaves but smaller, occasionally additional bracts present in higher nodes of the inflorescence; *pedicels* slender, 5–10 mm long. **Flowers** 5-merous, 1–2 cm long; *hypanthium* cupuliform, 3–5 mm long; *calyx* 1–2 mm long, obscurely 5-lobed or the lobes not evident, external teeth inconspicuous; *corolla* light pink or light violet abaxially, white adaxially, petals obovate, concave, 2–2.3 × 1–1.2 cm, apex broadly and asymmetrically bilobed; *stamens*



isomorphic; *filaments* complanate, 8–10 mm long; *connective appendage* somewhat ellipsoidal,  $5 \times 3 \times 3$  mm, rounded basally, bright yellow-orange; *anthers* 7 mm long with one minute slightly dorsal pore, dark nigrescent-purple; *ovary* oblong, costulate, apex 5-lobed, 5-celled; *style* ca 2 cm long. **Fruit** a 5-lobed capsule, the hypanthium covering half of the mature capsule; *seeds* not seen.

*Axinaea wurdackii* is restricted to the western slopes of the Andes in northern Peru, where it grows at altitudes of 1400–3050 m. – Figure 74.

**Additional specimens examined – PERU:** **Cajamarca:** Prov. Cajamarca, around Cajamarca, 2700 m, 10 Jun 1989, *Becker & Terrones 10* (AAU); La Posada, Las Quinuas–Huatum, 2800 m, 14 Jun 1981, *Sagástegui et al. 10131* (MO, US); Prov. Contumazá, Bosque de Cachil (Cascas–Contumazá), 2200 m, 3 Jun 1975, *A. López 8311* (NY); Molino de Singarrón, Cascas, 1800 m, 29 Jun 1983, *Sagástegui et al. 10891* (MO, US); Bosque de Cachil, 2500 m, 11 Oct 1992, *Sagástegui & Leiva 14811* (AAU, US); 2440 m, 28 Sep 1993, *Sagástegui et al. 14929* (AAU); 2500 m, 31 Jul 1995, *Sagástegui et al. 15802* (AAU); 2700 m, 2 Jul 1983, *I. Sánchez-V. 3164* (NY, US); Llama, Cutervo, 2500 m, Jul 1943, *Sandeman 4198* (K); Prov. Santa Cruz, Bosque Monteseco, 1400 m, 25 May 1987, *Sagástegui et al. 13010* (US); ca 3 km ENE Monteseco, 1750 m, 5 Jun 1987, *Santisteban & Guevara 138* (US). **La Libertad:** Prov. Morropón, Chalaco, road towards Las Pircas, 2200–2750 m, 17 Oct 1988, *Díaz & Vásquez 2983* (MO, US); Prov. Otuzco, *A. López et al. 2499* (NY); above Succhabamba, 2600 m, Jun 1914, *Weberbauer 6997* (F, GH, US). **Piura:** Prov. Huancabamba, ca 21 km E of Canchaque on route to Huancabamba, SW facing slopes, 2250 m,  $5^{\circ}24'S$ ,  $79^{\circ}36'W$ , 20 Jul 1991, *Dillon & I. Sánchez-V. 6274* (AAU); ca 12 km E of



**Figure 74.** Distribution of *Axinaea wurdackii*.

Canchaque on route to Huancabamba, 1800 m,  $5^{\circ}24'S$ ,  $79^{\circ}36'W$ , 21 Jul 1991, *Dillon & I. Sánchez-V. 6285* (AAU, US); above Jumbe, 1750 m, 13 Sep 1981, *A. López et al. 8820* (MO); Canchaque–Minas Turmalina, 2200 m, 23 Jul 1975, *Sagástegui 8286* (MO, NY).

*Axinaea wurdackii* is similar to *A. quitensis* but its plinervation is more marked, the secondary veins arising 15–35 mm from the base of the lamina (*vs.* 0–5 mm).

*Opposite page:*

**Figure 73.** *Axinaea wurdackii* – A. Habit. B. Detail of leaf base. C. Mature bud. D. Petal. E. Anisomorphic stamens showing the filament, the somewhat ellipsoidal connective, basally rounded, and the anther (From *Lopez M. et al. 9071*).

## Doubtful names and excluded taxa

*Axinaea drakei* Cogn. in A. DC. Monogr. phan. 7: 447. 1891. – Type: Ecuador. Loja: near Loja, *Poortmann 149* (holotype: P) = *Meriania drakei* (Cogn.) Wurdack, Mem. New York Bot. Gard. 16: 3. 1967.

*Axinaea integrifolia* Ruiz & Pav., Fl. Peruv. et Chil. 4: 205. 1957. – Type: Peru. “Chinchao.” *Ruiz & Pavón s.n.* (type: MA) = *Meriania* sp. – A specimen annotated by Ruiz and Pavón bearing this name and deposited in the MA herbarium is not an *Axinaea* sp. but a *Meriania* sp.

*Axinaea muricata* D. Don, Mem. Wern. Nat. Hist. Soc. 4: 321. 1823. – Type: Peru. *Ruiz & Pavón s.n.* (type: MA) = *Miconia muricata* (D. Don) Triana, Trans. Linn. Soc. London 28: 102. 1871.

*Axinaea ninakurorum* Bussmann & Paniagua, Arnoldia 19(1): 23–27. 2012. – Type: Peru. Amazonas, Hualaga, Bolívar, cloud forest surrounding Pampa Hermosa around old Chacha and Inca settlements with high amount of old *Cedrela*, 6°59'31.9”S, 77°39'16.3”W, 2400 m, 24 May 2011. *R. W. Bussmann, N. Y. Paniagua Z., C. Vega & L. Cotrina 17076* (holotype HAO, isotypes MO, NY) = *Meriania ninakurorum* (Bussmann & Paniagua) Cotton & Balslev, comb. nov. This species of *Meriania* is closely related to *M. franciscana* C. Ulloa & Homeier, described in 2008 from southern Ecuador.

*Axinaea purpurea* Ruiz & Pav., Fl. Peruv. Prodr. 68. 1794. – Type: Peru. *Ruiz & Pav. s.n.* (type: MA) = *Meriania radula* (Benth.) Triana, Trans. Linn. Soc. London 28: 66. 1871.

*Axinaea radula* Benth., Pl. Hartw. 130. 1844. – Type: Ecuador. Loja, near Cerro de San Francisco, *Hartweg s.n.* (type: K) = *Meriania radula* (Benth.) Triana, Trans. Linn. Soc. London 28: 66. 1871.

*Axinaea speciosa* Britton, Bull. Torrey Bot. Club. 17: 57. 1890. – Type: Bolivia. Mapiri, 830 m, *Rusby 2328* (holotype: NY; isotypes: B [destroyed], F, G, GH, MO, NY, P, US) = *Meriania brittoniana* Wurdack, Phytologia 13: 70. 1966.

*Axinaea tetragona* Cogn., Bot. Jahrb. Syst. 42: 137. 1908. – Type: Peru. Amazonas, E of Chachapoyas, between Tambo Almirante and Tambo Bagazán,

2700–2800 m, Jul 1904, *Weberbauer 4430* (types: B [destroyed], BR [fragment]) = *Meriania tetragona* (Cogn.) Wurdack, Phytologia 9: 411. 1964.

*Chastenaea (Axinaea) furfuracea* Klotzsch & H. Karst., in *schedis*. Photographs of a specimen from the Berlin herbarium (B) destroyed during World War II, show a collection by *Karsten s.n.* from Colombia annotated with this name. No published references to the name have been found in the literature. The quality of the photograph and the condition of the collection do not permit positive identification but the specimen does not seem to match any of the current species of *Axinaea*, and we believe it is a species of *Meriania*.

*Chastenaea (Axinaea) macropoda* Klotzsch, in *schedis*. Photographs of a specimen from the Berlin herbarium (B) destroyed during World War II, show a collection by *Karsten s.n.* annotated with this name. No published references to the name have been found in the literature. The quality of the photograph and the condition of the collection do not permit positive identification but the specimen does not seem to match any of the current species of *Axinaea*, and we believe it is a species of *Meriania*.

## Acknowledgements

Field work was possible thanks to a generous grant from His Royal Highness Crown Prince Frederik's Fund (Hans Kongelige Højhed Kronprins Frederik's Fond) to Henrik Balslev. Visits to European Herbaria were funded by Engineer and Mrs. Svend G. Fiedler's Fund (Ingeniør Svend Fiedler og Hustrus Legat). We are grateful to the curators of the AAU, BM, BR, F, G, GB, K, LOJA, MA, MO, NY, P, QCA, QCNE, S, US, VEN, and W herbaria for their help with the loans of *Axinaea* material. Mats Gustafsson and James Luteyn provided opportunities for field work in Ecuador and Peru. Our thanks go also to Rainer Bussmann, Michael Dillon, Jürgen Homeier, Gwilym Lewis, Pablo Lozano and Fabián Michelangeli for letting us use their photographs of *Axinaea*. Bruno Manara did the beautiful line drawings and Benjamin Øllgaard generously translated the diagnoses into Latin. Special

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### List of Exsiccatae

- Acosta-Solís 6679 (F) = *A. sessilifolia*  
 Acosta-Solís 7817 (F) = *A. oblongifolia*  
 Acosta-Solís 8074 (F) = *A. quitensis*  
 Acosta-Solís 14594 (F) = *A. quitensis*  
 Acosta-Solís 14607 (F) = *A. affinis*  
 Aguirre et al. 135 (LOJA) = *A. oblongifolia*  
 Aguirre et al. 4426 (LOJA) = *A. sclerophylla*  
 Aguirre, N. 2 (LOJA) = *A. flava*  
 Albert de Escobar & Fallen 1456 (US) = *A. disruipta*  
 Albert de Escobar & Giraldo 5261 (NY) = *A. scutigera*  
 Albert de Escobar et al. 7751 (US) = *A. scutigera*  
 Allen 4967 (BM, BR, F, G, MO, S) = *A. costaricensis*  
 Almeda 2881 (BR), 3106 (F) = *A. costaricensis*  
 Alvarez & Tirado 1523 (AAU, NY), 1525 (AAU, NY) = *A. lawessonii*  
 Alvear & Sánchez 471 (holotype: COL [n. v.]; isotypes: HUA [n.v.], US [n.v.]) = *A. colombiana*  
 Archer 1203 (NY, US) = *A. floribunda*  
 Asplund 17164 (F, G, K, NY, S) = *A. quitensis*  
 Asplund 17753 (G, K, NY, S) = *A. merianiae*
- Badillo 961 (VEN) = *A. affinis*  
 Ballester 189 (F) = *A. costaricensis*  
 Balslev & Steere 3200 (AAU, NY, QCA) = *A. sclerophylla*  
 Balslev & Steere 3207 (AAU, GH, NY) = *A. affinis*  
 Balslev & Steere 3258 (AAU, NY) = *A. quitensis*  
 Barclay & Juajibioy 8467 (AAU, MO, US) = *A. merianiae*  
 Barclay & Juajibioy 10320 (MO, US) = *A. costaricensis*
- Barclay et al. 3207 (US) = *A. macrophylla*  
 Becker & Terrones 10 (AAU) = *A. wurdackii*  
 Benoist 3941 (holotype: P!; photos: BR!, F!, GH!, MO!, NY!, S!) = *A. quitensis*  
 Bernardi 176 (NY), 211 (NY) = *A. grandifolia*  
 Bernardi 6199 (G, NY) = *A. costaricensis*  
 Betancur et al. 1784 (MO) = *A. floribunda*  
 Betancourt 241 (US); 250 (F, NY); 253 (NY) = *A. quitensis*  
 Betancourt 366 (F, NY, QCA), 368 (NY, QCA), 397 (F, NY, QCA) = *A. merianiae*  
 Betancourt 376 (F, NY, US) = *A. pauciflora*  
 Betancourt 474 (AAU) = *A. luteynii*  
 Betancourt 478 (AAU) = *A. luteynii*  
 Betancourt 480 (AAU, F, NY), 493 (AAU, F, NY) = *A. sessilifolia*  
 Boeke 2074 (NY, US) = *A. confusa*  
 Boeke 2131 (NY) = *A. crassinoda*  
 Boeke & Jaramillo 2436A (AAU, K, NY) = *A. affinis*  
 Boeke & Jaramillo 2436B (AAU) = *A. merianiae*  
 Bonpland s.n. (holotype: P! [Herbarium Richard, Herb. Muséum Paris # Poo228675], photo: NY!) = *A. merianiae* (Type of *Chastenea merianiae* DC.)  
 Bonpland, s.n. (lectotype: P! [Herb. Muséum Paris # Poo228673], here designated; isotype: P! [Herb. Muséum Paris # Poo228674], photo: NY!) = *A. merianiae* (Type of *Chastenea coriacea* Naudin)  
 Bonpland s.n. (F) = *A. merianiae*  
 Bonpland s.n. (P) = *A. oblongifolia*  
 Borgtoft-Pedersen et al. 104396 (AAU, LOJA) = *A. dentata*  
 Boyle et al. 3407 (MO) = *A. quitensis*  
 Brandbyge 42124 (AAU, MO, NY) = *A. quitensis*  
 Brandbyge 42175 (AAU, QCA-sheet erroneously annotated as *A. merianiae*) = *A. macrophylla*  
 Brandbyge 42210 (AAU) = *A. quitensis*  
 Bro. Ariste-Joseph A-109 (US); B-14 (NY, US), s.n. (F, US) = *A. macrophylla*  
 Bro. Daniel 1469 (F) = *A. floribunda*  
 Bro. Daniel & Bro. Thomas 1236 (US) = *A. floribunda*  
 Bro. Thomas 91 (US), 2388 (US) = *A. floribunda*  
 Brown 17512 (F) = *A. costaricensis*  
 Bunting 4912 (K, NY) = *A. floribunda*  
 Burger 6042 (BM, F, MO) = *A. costaricensis*

- Bussmann & Lange 724 (LOJA, QCA, QCNE) = *A. flava*
- Bussmann et al. 15625 (holotype: HUT; isotypes: HAO, MO, NY) = *A. fernando-cabiesii*
- Bussmann et al. 15926 (holotype: HUT; isotypes: HAO, MO, NY) = *A. reginae*
- Callejas & Roldán 10626 (NY) = *A. floribunda*
- Callejas et al. 5566 (NY) = *A. lehmannii*
- Camp 276 (NY), 452 (GH, NY), 527 (K, NY), 528 (NY), 529 (NY), 2079 (NY) = *A. merianiae*
- Camp E-665 (NY [2 sheets], US) = *A. floribunda*
- Camp E-4067 (holotype: NY!; isotypes: G!, GH!, K!, MO!, VEN!) = *A. campii*
- Camp E-4332 (F, NY, S, US); E-4371 (F, G, GH, MO, NY, US, W); E-4584 (F, GH, NY, US) = *A. sclerophylla*
- Camp E-4533 (F, G, GH, NY, VEN), E-4891 (F, GH, NY, US, VEN), E-4895 (F, MO, NY, S) = *A. lawessonii*
- Cárdenas 2222 (US), 3751 (S) = *A. pennellii*
- Cerón et al. 3792 (AAU, NY) = *A. quitensis*
- Charpin & Jacquemoud AC 13299 (F, G, US) = *A. floribunda*
- Clark et al. 1296 (AAU, NY) = *A. quitensis*
- Cleef & Fernández 524 (US) = *A. macrophylla*
- Clemants et al. 2227 (NY, QCA, QCNE) = *A. merianiae*
- Clemants et al. 2239 (NY, US) = *A. floribunda*
- Core 771 (NY, US) = *A. floribunda*
- Core 902 (US) = *A. macrophylla*
- Cotton & Gustafsson 1832 (AAU, CPUN, MO, USM) = *A. crassinoda*
- Cotton & Gustafsson 1834 (AAU, CPUN, HUT), 1837 (AAU, CPUN, HUT), 1864 (AAU, CPUN, HUT) = *A. nitida*
- Cotton & Rivas 1707 (AAU) = *A. floribunda*
- Cotton, H. Balslev, M. Gustafsson & P. Lozano 1529 (Holotype: AAU!; isotypes: LOJA!) = *A. lawessonii*
- Cotton et al. 1539 (AAU) = *A. sclerophylla*
- Cotton et al. 1551 (AAU, LOJA, QCNE) = *A. disrupta*
- Cotton et al. 1578 (AAU), 1579 (AAU), 1580 (AAU) = *A. floribunda*
- Cotton et al. 1606 (AAU) = *A. macrophylla*
- Cotton et al. 1727 (AAU) = *A. macrophylla*
- Cowan 2422 (US) = *A. costaricensis*
- Croat 72670 (MO) = *A. pauciflora*
- Crosby 11437 (MO) = *A. costaricensis*
- Cross (Veitch) 80 (K) = *A. sessilifolia*
- Cuamacás et al. 119 (LOJA), 158 (LOJA) = *A. lehmannii*
- Cuatrecasas 5422 (US), 14671 (F, NY), 18894 (F, GH, NY), 19267 (F, GH, NY), 21833 (F, NY, S) = *A. macrophylla*
- Cuatrecasas 18059 (holotype: NY!; isotypes: F!, [photo: NY!], US! [photo: NY!]) = *A. fallax*
- Cuatrecasas 21772 (F, NY) = *A. affinis*
- Cuatrecasas 23360 (F, NY) = *A. floribunda*
- Cuatrecasas & Willard 26316 (US) = *A. macrophylla*
- Cuatrecasas et al. 28307 (F, US) = *A. floribunda*
- Devia 207 (holotype: MO!; isotype: US!) = *A. minutiflora*
- Díaz & Osoreo 2586 (F, MO, NY, W) = *A. nitida*
- Devia & Prado 1960 (MO, US), 2042 (MO, US) = *A. colombiana*
- Díaz & Vásquez 2983 (MO, US) = *A. wurdackii*
- Dillon & I. Sánchez-V. 6274 (AAU), 6285 (AAU, US) = *A. wurdackii*
- Dodson 853 (MO, QCA, US) = *A. merianiae*
- Dorr et al. 7274 (NY), (7330 (MO, NY), 7526 (MO, NY) = *A. costaricensis*
- Duque 72 (US) = *A. macrophylla*
- Ellemann 66539 (AAU, LOJA, QCA) = *A. pauciflora*
- Ellemann 66593 (AAU, LOJA, QCA) = *A. disrupta*
- Ellemann 75398 (AAU, LOJA, QCA, QCNE) = *A. sclerophylla*
- Ellemann 75412 (Holotype: AAU!; isotype: LOJA!) = *A. disrupta*
- Ellenberg 781 (US) = *A. confusa*
- Espinosa 325 (LOJA, NY) = *A. lawessonii*
- Espinosa 722 (F, LOJA, NY) = *A. floribunda*
- Espinosa 1413 (LOJA, NY), 2177 (NY) = *A. merianiae*
- Espinosa 1553 (F, LOJA, NY, US) = *A. sclerophylla*
- Fernández 703 (MO) = *A. costaricensis*
- Fleming 60 (K) = *A. merianiae*
- Forero et al. 2150 (MO, US), 2300 (MO, US), 2853 (MO, NY) = *A. lehmannii*
- Fosberg & Giler 22838 (US) = *A. merianiae*



- Funck & Schlim 737 (Lectotype: G! [Barbey-Boissier Herb., G Herb.# 8817/1]; isotypes: BR!, BM!, F! [fragment], G [Delessert Herb., n.v.], W!; photo of the G isotype: GH!) = *A. affinis*
- Funck & Schlim 1253 (G) = *A. grandifolia*
- Funck & Schlim 1254 (holotype: P!; photo: NY!) = *A. grandifolia*
- Funck & Schlim 1477 (BR, F, G [Herb Barbey-Boissier], G [Herb. Delessert], W) = *A. floribunda*
- García-Barriga 15640 (NY); 15645 (NY) = *A. macrophylla*
- García-Barriga 18780 (GH) = *A. affinis*
- García-Barriga 21030 (F, US) = *A. scutigera*
- Garmendia & Paredes 402 (LOJA) = *A. lawessonii*
- Gavilanes & Tirira 660 (AAU) = *A. macrophylla*
- Gavilanes et al. 690 (AAU) = *A. macrophylla*
- Gentry & Solomon 52098 (MO) = *A. alata*
- Gentry et al. 11070 (MO, VEN) = *A. grandifolia*
- Giraldo & Olver 589 (US) = *A. lehmannii*
- Gómez et al. 815 (MO) = *A. lehmannii*
- Goudot, J. s.n. (holotype: P!; photos: F!, MO!, NY!) = *A. macrophylla*
- Grifo & Crespo 461 (AAU, MO) = *A. merianiae*
- Grisar s.n. (lectotype: P!, photo: F!; isotypes: BR!, F, LE [n.v., cited by Cogn.]) = *A. oblongifolia*
- Grisar s.n. (holotype: P!, photo: F!, NY!; isotype: BR! [fragment]) = *A. pauciflora*
- Harling 5685 (S), 25595 (AAU, NY, QCA), 25932 (K, NY) = *A. merianiae*
- Harling & Andersson 13512 (AAU) = *A. macrophylla*
- Harling & Andersson 14494 (US) = *A. merianiae*
- Harling & Andersson 23699 (AAU, NY) = *A. macrophylla*
- Harling & Andersson 24696 (AAU, F, NY, QCA) = *A. merianiae*
- Harling & Ståhl 26568 (QCA) = *A. merianiae*
- Harling et al. 8034 (F) = *A. macrophylla*
- Harling et al. 9555 (F, GB, MO, NY, QCA, US, WIS) = *A. sessilifolia*
- Harling et al. 20141 (QCA) = *A. merianiae*
- Hartweg 1014 (holotype: K! [Herb. Benthamianum], photos: F!, GH!, NY!; isotypes: B (destroyed), BR!, E [n.v.], F! [Field Museum Herbarium # 869715] (fragment), F! [Field Museum Herbarium # 937046] (fragment), G!, K! [Herb. Hookerianum], W! (2 sheets), photos of the B isotype: F!, GH!, MO!, NY!, photo of the E isotype: NY!) = *A. merianiae* (Type of *Chastenea lepidota* Benth.)
- Herrera 3750 (F, MO) = *A. costaricensis*
- Herzog 2251 (BR, S, W) = *A. lanceolata*
- Hitchcock 21436 (GH, NY, US) = *A. floribunda*
- Hitchcock 21573 (GH, NY, US) = *A. merianiae*
- Hitchcock 21677 (GH, NY, US) = *A. campii*
- Hodge 6278 (US) = *A. dependens*
- Hodge 6756 (F, US) = *A. floribunda*
- Holton 907 (BR, G, GH, NY) = *A. macrophylla*
- Holm-Nielsen 18778 (AAU), 22774 (AAU, QCA) = *A. merianiae*
- Holm-Nielsen et al. 3557 (AAU) = *A. pauciflora*
- Holm-Nielsen et al. 5121 (AAU, MO, NY, S) = *A. merianiae*
- Holm-Nielsen et al. 29325 (AAU) = *A. macrophylla*
- Homeier 141 (AAU) = *A. floribunda*
- Homeier 549 (MO) = *A. confusa*
- Hutchison & von Bismarck 6532 (F, K, MO, NY) = *A. nitida*
- Hutchison & Wright 5590 (BR, F, G, GH, MO, NY, S, US) = *A. nitida*
- Idrobo et al. 3501 (NY) = *A. affinis*
- Jameson 15 (K), 143 (K), s.n. (F) = *A. merianiae*
- Jameson 450 (G); 451 (BR, G, US) = *A. macrophylla*
- Jaramillo 1061 (AAU), 3825 (AAU, MO, NY), 5530 (AAU, QCA) = *A. merianiae*
- Jaramillo 6691 (AAU) = *A. quitensis*
- Jaramillo 7162 (AAU, MO) = *A. affinis*
- Jaramillo 7261 (AAU, NY, QCA) = *A. merianiae*
- Jaramillo 8601 (AAU), 8621 (AAU) = *A. quitensis*
- Jaramillo 9576 (AAU, QCA) = *A. quitensis*
- Jaramillo 9792 (LOJA) = *A. campii*
- Jaramillo 10312 (AAU) = *A. oblongifolia*
- Jaramillo & Boeck 325 (AAU) = *A. affinis*
- Jaramillo & Jaramillo 837 (AAU, NY, QCA, QCNE) = *A. merianiae*
- Jaramillo & Winnerskjold 5796 (AAU, NY) = *A. lawessonii*

- Jaramillo et al. 1735 (AAU) = *A. affinis*  
 Jaramillo-Mejía & Acosta 4822 (NY) = *A. macrophylla*  
 Jaramillo, R. & van der Hammen 4431 (US) = *A. scutigera*  
 Jiménez 829 (F); 892 (US, W), 2055 (BM, F, US, W),  
 2196 (F) = *A. costaricensis*  
 Jiménez et al. 615 (F, MO) = *A. costaricensis*  
 Jørgensen 61741 (AAU, MO), 61845 (AAU), = *A. quitensis*  
 Jørgensen 61891 (AAU) = *A. merianiae*  
 Jørgensen 65481 (AAU), 65521 (AAU, MO), 65845  
 (AAU, NY), 65864 (AAU), 65907 (AAU, MO,  
 NY), 65973 (AAU, NY) = *A. quitensis*  
 Jørgensen & Ulloa 91994 (AAU, MO, NY) = *A. flori-  
 bunda*  
 Jørgensen & Valencia 61498 (AAU, MO, NY); 61551  
 (AAU, F, GH, MO, NY); 61554 (MO, NY); 61577  
 (MO, NY) = *A. quitensis*  
 Jørgensen et al. 252 (LOJA, MO, NY) = *A. oblongifolia*  
 Jørgensen et al. 324 (MO) = *A. floribunda*  
 Jørgensen et al. 504 (MO) = *A. sclerophylla*  
 Jørgensen et al. 662 (LOJA, QCA, QCNE) = *A. meri-  
 aniae*  
 Jørgensen et al. 1327 (MO) = *A. pauciflora*  
 Jørgensen et al. 91844 (AAU, QCA, QCNE) = *A. meri-  
 aniae*  
 Jørgensen et al. 92144 (AAU, MO, NY) = *A. oblongifolia*  
 Jørgensen et al. 92502 (AAU, MO), 92608 (AAU,  
 MO, NY), 92610 (AAU, MO), 92612 (AAU), 92614  
 (AAU) = *A. quitensis*  
 Jørgensen et al. 92801 (AAU) = *A. glandulosa*  
 Jørgensen et al. 93084 (AAU) = *A. quitensis*
- Kanehira 11 (F, GH) = *A. glandulosa*  
 Killip 6798 (GH, NY, US) = *A. macrophylla*  
 Killip & Hazen 9474 (GH, NY) = *A. floribunda*  
 Killip & Smith 17824 (F, GH, NY, S, US) = *A. macro-  
 phylla*  
 King et al. 10442 (F, MO), 10459 (F, MO, S) = *A. grandifolia*  
 Krüger M-2 (US) = *A. lanceolata*
- Larsen 41 (AAU) = *A. quitensis*  
 Larsen 197 (AAU) = *A. dentata*  
 Lægaard 18948 (AAU, LOJA) = *A. merianiae*  
 Lehmann 997 (K, NY) = *A. lehmannii*
- Lehmann 3637 (lectotype: G!, here designated; photo:  
 F!, GH!, MO!, NY!; isotype: BR!) = *A. lehmannii*  
 Lehmann 4653 (F, US) = *A. floribunda*  
 Lehmann 4924 (F, GH, K, S, US) = *A. merianiae*  
 Lehmann 7446 (F, GH, K) = *A. floribunda*  
 Lehmann 8649 (G, GH, K, NY, W) = *A. macrophylla*  
 Lent 1178 (F) = *A. costaricensis*  
 León et al. 983 (MO), 2153 (US) = *A. confusa*  
 Lewis, Gwilym 2489 (AAU, K, LOJA, NY) = *A. affinis*  
 Lewis, Gwilym 2507 (AAU, K, LOJA, NY, QCA) = *A.  
 merianiae*  
 Lewis, Gwilym 3511 (AAU, K, LOJA, NY, QCA) = *A.  
 sclerophylla*  
 Lewis, Gwilym & Bruneau 3540 (AAU, K[2 sheets],  
 NY) = *A. floribunda*  
 Lewis, Gwilym & Cotton 3311 (AAU, K, LOJA, NY) =  
*A. macrophylla*  
 Lewis, Gwilym & Klitgaard 2229 (AAU, K, LOJA,  
 QCA) = *A. merianiae*  
 Lewis, Gwilym et al. 3685 (AAU, K, LOJA, NY) = *A.  
 merianiae*  
 Lewis, Marko (holotype: MO!; isotype: US!) = *A. alata*  
 Lewis, Marko 88875 (MO) = *A. lanceolata*  
 Linden 212 (BR), s.n. (BR) = *A. macrophylla*  
 Linden 768 (lectotype: G! [Herb. Delessert]; photos:  
 F!, MO!, NY!; isotypes: BR!, G! [Herb. Barbey-  
 Boissier], P!, W! [2 sheets, W Herb. # 20988, the  
 other sheet unnumbered]; photo of the P isotype:  
 NY!) = *A. floribunda*  
 Little 15571 (VEN), 15750 (VEN), 15751 (VEN) = *A. gran-  
 difolia*  
 Løjtant & Molau 14325 (AAU) = *A. lawessonii*  
 López, A. 8311 (NY) = *A. wurdackii*  
 López, A. et al. 2499 (NY), 8820 (MO) = *A. wurdackii*  
 López et al. 7795 (MO, US) = *A. oblongifolia*  
 López-Palacios 1234 (US) = *A. Ruizteranii*  
 López-Palacios & Idrobo 3739 (US) = *A. macrophylla*  
 Lozano 41 (LOJA) = *A. lawessonii*  
 Lozano 224 (LOJA, QCA) = *A. confusa*  
 Lozano & Bussmann 001 (holotype: AAU!; isotype:  
 LOJA [n.v.]) = *A. flava*  
 Lozano et al. 1113 (LOJA) = *A. oblongifolia*  
 Lozano et al. 1574 (holotype: AAU!; isotype: LOJA) =  
*A. glauca*

- Lozano-C. & Torres H. 174 (AAU) = *A. macrophylla*  
 Luteyn & Cotton 11088 (AAU, NY, QCNE), 11090 (AAU, NY, QCNE, US), 11092 (NY, QCA) = *A. sessilifolia*  
 Luteyn & Cotton 11147 (NY) = *A. pauciflora*  
 Luteyn & Cotton 11230 (AAU, NY, QCA, QCNE), 11238 (AAU, K, NY, QCA, QCNE), 11239 (AAU, NY, QCA, QCNE), 11240 (AAU, NY, QCA, QCNE), 11246 (AAU, BR, NY, QCA, QCNE, W), 11255 (NY), 11262 (AAU, NY, QCA, QCNE) = *A. merianiae*  
 Luteyn & Cotton 11385 (NY), 11432 (NY) = *A. nitida*  
 Luteyn & Lebrón-Luteyn 10004 (NY) = *A. floribunda*  
 Luteyn & Rangel 13182 (AAU, NY) = *A. floribunda*  
 Luteyn & Romoleroux 14528 (AAU, NY) = *A. macrophylla*  
 Luteyn et al. 6689 (AAU, F, K, MO, NY, QCA, S) = *A. merianiae*  
 Luteyn et al. 14130 (Holotype: NY!; isotypes: F!, MO!, QCA, VEN!) = *A. luteynii*  
 Luteyn et al. 14303 (AAU, MO, NY, S) = *A. merianiae*  
 Luteyn et al. 14746 (K, MO, NY, QCA) = *A. lehmannii*
- Macbride 4873 (F) = *A. crassinoda*  
 Madison et al. 4853 (AAU, F, US) = *A. lehmannii*  
 Madsen 8546 (AAU) = *A. macrophylla*  
 Madsen 36650 (AAU) = *A. merianiae*  
 Madsen 75566 (AAU) = *A. scutigera*  
 Madsen 85466 (AAU, LOJA, MO, NY), 85573 (AAU) = *A. lawessonii*  
 Madsen 85578 (AAU, LOJA, MO, NY, QCNE) = *A. sclerophylla*  
 Madsen 85715 (AAU, LOJA), 85720 (AAU, LOJA) = *A. disrupta*  
 Madsen 85721 (AAU, LOJA, MO, NY), 85823 (AAU, LOJA, NY) = *A. lawessonii*  
 Madsen 86041 (AAU, LOJA) = *A. dentata*  
 Madsen 86050 (holotype: AAU!, isotypes: LOJA!, QCA) = *A. dentata*  
 Madsen 86144 (AAU, LOJA, MO, NY, QCA) = *A. sclerophylla*  
 Madsen 86146 (AAU) = *A. macrophylla*  
 Madsen 86204 (AAU, LOJA) = *A. lawessonii*
- Madsen 86312 (AAU, LOJA); 86313 (AAU, LOJA, MO, NY) = *A. lawessonii*  
 Madsen 86663 (AAU) = *A. macrophylla*  
 Madsen 86684 (AAU) = *A. pauciflora*  
 Madsen & Chimbo 8359 (AAU) = *A. dentata*  
 Madsen & Chimbo 8605A (AAU) = *A. floribunda*  
 Madsen & Chimbo 8609 (AAU) = *A. sclerophylla*  
 Madsen & Leimbeck 7568 (AAU) = *A. lawessonii*  
 Madsen & Rosales 7589 (AAU) = *A. dentata*  
 Madsen & Rosales 8461 (AAU) = *A. sclerophylla*  
 Maguire & Maguire 44215 (GH, NY, VEN) = *A. macrophylla*  
 Maguire & Maguire 44317 (GH, NY), 61678 (F, GH, NY) = *A. merianiae*  
 Maguire & Maguire 44378, 44379 (NY) = *A. oblongifolia*  
 Maguire et al. 62098 (F, GH, NY, VEN), 62109 (NY, VEN) = *A. grandifolia*  
 Marcano-Berti & Peña 496-979 (BR) = *A. grandifolia*  
 Mathews 3213 (holotype: K!, photo: NY!; isotypes: BM!, F! (fragment), G!, GH!; photo of the BM isotype: NY!; photos of the G isotype: MO!, NY!; photo of the GH isotype: NY!) = *A. crassinoda*  
 Mathews s.n. (G, GH, K) = *A. crassinoda*  
 Mathews s.n. (lectotype: G! [Herb. Barbey-Boissier, G Herb. # 8817/52; isotypes: BR!, F! [fragment], G! [Herb. Delessert, 2 sheets, G Herb. # 8817/50 and 8817/51], NY!; photos of the G isotype: F!, MO!, NY!) = *A. tomentosa*  
 McPherson 9354 (MO) = *A. costaricensis*  
 Meier et al. 6316 (US) = *A. costaricensis*  
 Melampy 724, 725 (US) = *A. affinis*  
 Melampy 1336 (US) = *A. scutigera*  
 Mena, P. 827 (AAU) = *A. campii*  
 Molau et al. 2740 (QCA) = *A. merianiae*  
 Mora 2330 (US), 2358 (US) = *A. macrophylla*  
 Morán & Paisano 104 (AAU) = *A. affinis*  
 Morán et al. 16 (AAU, MO-sheet erroneously annotated as *A. quitensis*) = *A. affinis*  
 Morán et al. 53 (MO) = *A. quitensis*  
 Morán et al. 17 (AAU) = *A. affinis*  
 Moritz 959 (BM, BR, GH) = *A. grandifolia*  
 Mostacero et al. 1163 (AAU, F, MO, NY, US) = *A. nitida*  
 Mutis 1263 (US); 2701 (F, G, US, S); 2456 (US); 3405 (US) = *A. macrophylla*

- Neill et al. 9853 (MO, US) = *A. quitensis*
- Oberwinkler & Oberwinkler 13439 (VEN) = *A. grandifolia*
- Oldeman 3412 (US) = *A. quitensis*
- Orozco et al. 2459 (US) = *A. fallax*
- Ortiz s.n. (NY) = *A. merianiae*
- Ortiz & Jaramillo 137 (AAU) = *A. campii*
- Palacios 4007 (AAU, MO) = *A. quitensis*
- Palacios & Cerón 13830 (AAU, NY) = *A. sessilifolia*
- Palacios & Clark 12542 (AAU) = *A. quitensis*
- Palacios & Rubio 7293 (MO) = *A. quitensis*
- Palacios & Tirado 12911 (AAU, MO, NY) = *A. lawessonii*
- Palacios et al. 9855 (NY) = *A. lehmannii*
- Panero & Clark 2951 (NY) = *A. merianiae*
- Patin s.n. (NY) = *A. floribunda*
- Penland & Summers 1005 (F, NY) = *A. campii*
- Pennell 4259 (NY), 6506 (K, NY, US) = *A. macrophylla*
- Pennell 14003 (holotype: NY!; photo: BM!, GH!, MO!, NY!; isotypes: F!, GH!, S!, US!; photo of the GH isotype: NY!; photo of the US isotype: NY!) = *A. pennellii*
- Pérez Arbeláez & Cuatrecasas 5287 (F, MO, NY) = *A. scutigera*
- Peyton & Tilney Peyton 674 (MO, US), 1463 (MO, US) = *A. weberbaueri*
- Pittier 2007 (holotype: BR! [mounted on two sheets BR # 843 792 and # 843 793]; isotypes: F!, G!, US!) = *A. costaricensis*
- Pittier s.n. (BR) = *A. costaricensis*
- Poortmann 67 (BR, F, P) = *A. sclerophylla*
- Poveda 1059 (F) = *A. costaricensis*
- Prance & Barrera 28069 (MO, NY) = *A. grandifolia*
- Prieto P-116 (F, NY, S, VEN, W) = *A. floribunda*
- Prieto JP-50A (holotype: US! [US Herb. # 2404649], photo: NY!; isotype: NY!) = *A. scutigera* (Type of *A. scutigera* ssp. *ecuadorensis*)
- Purdie s.n. (holotype: K!, photos: F!, GH!, NY!; isotype: K!, photos: F!, GH!, NY!) = *A. robusta*
- Quipuscoá & Schjellerup 202 (F) = *A. nitida*
- Quipuscoá & Vilchez T. 2645 (AAU) = *A. floribunda*
- Quipuscoá et al. 693 (NY) = *A. oblongifolia*
- Ramos et al. 1684 (US) = *A. lehmannii*
- Rangel et al. 5135 (MO) = *A. floribunda*
- Rauh & Barthlott 35124 (US) = *A. merianiae*
- Raven 22087-A (F, MO) = *A. costaricensis*
- Rimbach 211 (holotype NY!; isotypes F!, GH!, US!) = *A. sessilifolia* (Type of *Meriania simsiana*)
- Rimbach 513 (S) = *A. sessilifolia*
- Ritter 1206 (W), 1955 (W) = *A. lanceolata*
- Romoleroux 400 (QCA) = *A. merianiae*
- Romoleroux 792 (AAU, NY) = *A. lawessonii*
- Rose et al. 22992 (NY, US), 23116 (NY, US) = *A. merianiae*
- Ruiz & Pavón s.n. (holotype MA!; isotypes: [B destroyed], G!, MA!; photos of the B isotype: F!, MO!, NY!, photo of the MA isotype: NY!) = *A. confusa*
- Ruiz & Pavón s.n. [Herbarium Peruvianum Ruiz et Pavón # 23/57], (lectotype: MA!; photo: NY!; isotype: B (destroyed); photo: F!, GH!, MO!, NY!) = *A. dependens*
- Ruiz & Pavón s.n. [Herbarium Peruvianum Ruiz et Pavón # 23/55], Lectotype, here designated: MA!; photo: NY!; isotypes: B (destroyed), F!, G!, MA!; photo of the B isotype: F!, GH!, MO!, NY!; photo of the MA isotype: NY!) = *A. dependens* (Lectotype of *A. rugosa*)
- Ruiz & Pavón s.n. (MA) = *A. dependens*
- Ruiz & Pavón s.n. (F), s.n. [numeration on label 14/79], (F) = *A. floribunda*
- Ruiz & Pavón s.n. (lectotype MA!; isotypes: B [destroyed], BM! [2 sheets], MA! [2 sheets], BR! [fragment], F!, G! 2 sheets [Herb. Barbey-Boissier, G Herb # 8817/14 and 8817/25], US!; photos of the B isotype: F!, MO!, NY!) = *A. glandulosa*
- Ruiz & Pavón s.n. (lectotype: MA!, here designated; photo: NY!; isotypes: BM! [leaf fragment mounted with *A. glandulosa* D. Don, BM # 000649745], BR! 2 sheets [BR Herbarium # 843 806 and # 843 824], F!, G! [G Herbarium # 8817/26], MA!; photo of the MA isotype: NY!) = *A. lanceolata*
- Ruiz & Pavón s.n. (MA) = *A. sessilifolia*
- Ruiz et al. 1118 (MO) = *A. lehmannii*
- Ruiz-Terán 1696 (US) = *A. grandifolia*
- Ruiz-Terán 3057 (holotype: US!, photo: NY) = *A. ruiz-teranii*

- Ruíz-Terán & Dugarte 12348 (NY), 14769 (NY), 14871 (NY) = *A. grandifolia*  
 Ruíz-Terán & López-Figueiras 484 (US), 1926 (NY) = *A. grandifolia*  
 Ruíz-Terán & López-Figueiras 555 (NY), 1693 (NY, US) = *A. ruizteranii*  
 Ruíz-Terán & López-Figueiras 1261 (F, NY) = *A. floribunda*  
 Ruíz-Terán & López-Figueiras 9391 (F, MO, NY) = *A. affinis*  
 Ruíz-Terán & López-Palacios 7632 (F, NY) = *A. costaricensis*  
 Ruíz-Terán et al. 15132 (NY) = *A. grandifolia*
- Sagástegui 8286 (MO, NY) = *A. wurdackii*  
 Sagástegui 16245 (AAU), 16251 (AAU) = *A. oblongifolia*  
 Sagástegui & Cabanillas 8641 (AAU, F, MO, NY), 8717 (F, MO, NY) = *A. oblongifolia*  
 Sagástegui & Leiva 14811 (US) = *A. wurdackii*  
 Sagástegui et al. 9972 (holotype: HUT; isotypes: MO!, NY!, US!) = *A. wurdackii*  
 Sagástegui et al. 10131 (MO, US), 10891 (MO, US), 13010 (US), 14929 (AAU), 15802 (AAU) = *A. wurdackii*  
 Sánchez-Vega, I. 3164 (NY, US) = *A. wurdackii*  
 Sánchez-Vega, I. & Miranda 6320 (holotype: F!; isotypes: AAU!, US!) = *A. pendula*  
 Sánchez-Vega, I. & Miranda 6359 (MO, NY) = *A. nitida*  
 Sánchez-Vega, I. & Sánchez 11074 (AAU) = *A. crassinoda*  
 Sánchez-Vega, I. & Sánchez 11108 (AAU, F) = *A. pendula*  
 Sánchez-Vega, J. G. 332 (NY, US), 448 (F), 836 (F) = *A. nitida*  
 Sandeman 4198 (K) = *A. wurdackii*  
 Santisteban & Guevara 138 (US) = *A. wurdackii*  
 Schlim 304 (BR, G, F, K) = *A. affinis*  
 Schneider 967 (S) = *A. macrophylla*  
 Schnell 715 (F, US), 784 (F, US) = *A. costaricensis*  
 Seemann 765 (holotype: K!, photos: F!, GH!, NY!; isotype: GH!; photo of the BM isotype: NY!; photos of the G isotype: MO!, NY!; photo of the GH isotype: NY!) = *A. sclerophylla*  
 Silverstone Sopkin et al. 4655 (US) = *A. scutigera*  
 Silverstone et al. 4696 (US) = *A. lehmannii*  
 Skutch 3480 (GH, K, MO, S, US) = *A. costaricensis*  
 Smith 192 (F, MO), 360 (F), 4212 (F) = *A. costaricensis*  
 Smith, D. N. 7765 (F, MO, NY, US), 7897 (F, US) = *A. scutigera*  
 Smith, D. N. & Poetel 7590 (F, MO, US) = *A. dependens*  
 Smith, D. N. & Poetel 8062 (MO) = *A. lanceolata*  
 Smith, D. N. et al. 8713 (MO) = *A. confusa*  
 Sodiro s.n. (BR) = *A. quitensis*  
 Sodiro s.n. (holotype: BR! [2 sheets]; photos: F!, GH!, MO!, NY!, S!; isotype: P!) = *A. sodiroi*  
 Sodiro 483 (AAU) = *A. quitensis*  
 Soejarto 991 (GH, US) = *A. macrophylla*  
 Solomon 6034 (MO, US) = *A. alata*  
 Soukup 4321 (F, US) = *A. oblongifolia*  
 Sparre 15942 (AAU) = *A. macrophylla*  
 Sparre 16499 (AAU, S, US) = *A. sclerophylla*  
 Sperling & Bleiweiss 5071 (QCA) = *A. lehmannii*  
 Spruce 5831 (BR, F, G, GH, S [3 sheets], W [3 sheets]) = *A. floribunda*  
 Spruce 6174 (holotype: K!, photo: F!, GH!, NY!; isotypes: K!, W!; photos of the K isotype: F!, GH!, NY!; photos of the W isotype: F!, MO!, NY!) = *A. sessilifolia*  
 Ståhl & Knudsen 2801 (AAU, QCA) = *A. merianiae*  
 Ståhl et al. 2630 (AAU, LOJA, QCA) = *A. sclerophylla*  
 Standley 52253 (US) = *A. costaricensis*  
 Stein & D'Alessandro 2732 (AAU, US) = *A. macrophylla*  
 Steinbach 9861 (BM, F, G, GH, MO, NY, S) = *A. lanceolata*  
 Stevens 13456 (F, MO) = *A. costaricensis*  
 Steyermark 53689 (F, NY, US) = *A. merianiae*  
 Steyermark 55258 (F, NY, US) = *A. costaricensis*  
 Steyermark 55363 (F, NY, VEN) = *A. affinis*  
 Steyermark 56554 (F, GH, NY, US, VEN) = *A. grandifolia*  
 Steyermark & Manara 125343 (VEN) = *A. costaricensis*  
 Stone 3268 (F, MO) = *A. costaricensis*
- Thomsen 58803 (AAU, QCA) = *A. lehmannii*  
 Tillett 730-305 (VEN) = *A. grandifolia*  
 Tillett & Hönic 738-379 (US) = *A. grandifolia*  
 Tillett & Hönic 738-391 (US) = *A. ruizteranii*  
 Tipaz 29 (MO); 98 (MO) = *A. macrophylla*  
 Tovar 4753 (holotype: US! [US Herb. # 2446955]). = *A. tomentosa* (Type of *A. tovarii*)

- Tracey 299 (K) = *A. macrophylla*  
 Triana 6171 (BM) = *A. floribunda*  
 Triana s.n. (BR, NY [2 sheets], W), s.n. (BR [fragment]) = *A. floribunda*  
 Triana s.n. (BM), s.n. (BR, NY, W) = *A. macrophylla*  
 Triana s.n. (holotype: K!, photos: GH!, K!, NY!; isotypes: COL (n.v.), P! [2 sheets], photos of the COL isotype: F! NY!, photos of the P isotype: MO!, NY!) = *A. scutigera*
- Ulloa 283 (AAU, F, LOJA, NY, S) = *A. affinis*  
 Ulloa 424 (AAU, F, NY, S) = *A. campii*  
 Ulloa 557 (AAU) = *A. macrophylla*  
 Ulloa 589 (AAU) = *A. lawessonii*  
 Umaña & Chacón 493 (F, MO) = *A. costaricensis*  
 Uribe 6171 (NY) = *A. scutigera*  
 Uribe-Uribe 3495 (NY) = *A. macrophylla*
- Valencia 75 (AAU) = *A. quitensis*  
 van der Werff 12466 (MO) = *A. sessilifolia*  
 van der Werff & Palacios 9025 (AAU, K, NY, US) = *A. pauciflora*  
 van der Werff & Palacios 9113 (AAU, NY, US) = *A. macrophylla*  
 van der Werff & Palacios 9311 (AAU, K, NY, S) = *A. pauciflora*  
 Veillon 32 (US, VEN) = *A. grandifolia*  
 Vivar 403 (LOJA), 1763A (LOJA), 3326 (LOJA) = *A. sclerophylla*  
 Vivar & Merino 4309 (AAU, LOJA) = *A. oblongifolia*  
 Vivar & Poma 2634 (AAU, LOJA) = *A. affinis*  
 Vivar et al. 493 (LOJA) = *A. oblongifolia*  
 Vivar et al. 4256 (AAU, LOJA) = *A. merianiaae*  
 Vogel 86 (US) = *A. macrophylla*  
 von Sneidern s.n. (F, NY) = *A. lehmannii*  
 von Sneidern 1194 (NY, S) = *A. affinis*  
 von Sneidern 1830 (G, S); 1831 (S) = *A. macrophylla*  
 von Sneidern 3192 (GH, NY, S, US) = *A. floribunda*
- Wagner N106 [?] (G) = *A. grandifolia*  
 Wallnöfer 19-19688 (US) = *A. nitida*  
 Weberbauer 4355 (holotype: B [destroyed], photo: NY!; lectotype: BR! [fragment]) = *A. nitida*  
 Weberbauer 5648 (holotype: B [destroyed], photos: F!; GH!; lectotype: F!, photo: NY!; isotypes: BR!, GH!, S!, US!, photo of the US isotype: NY!) = *A. weberbaueri*  
 Weberbauer 6371 (F, GH, NY, US) = *A. oblongifolia*  
 Weberbauer 6997 (F, GH, US) = *A. wurdackii*  
 Weberbauer 7150 (F, GH) = *A. tomentosa*  
 Weigend & Horn 3850 (F) = *A. affinis*  
 Wercklé 16687 (F, US) = *A. costaricensis*  
 Wilbur et al. 22843 (F) = *A. costaricensis*  
 Wilbur & Almeda 17500 (F, GH, MO, US) = *A. costaricensis*  
 Wolf & de Wilde 910 (US) = *A. colombiana*  
 Woronow & Juzupczuk 5084 (NY) = *A. affinis*  
 Wurdack 657 (US), 789 (F, G, GH, K, MO, NY, S, UC) = *A. crassinoda*  
 Wurdack 907 (F, G, GH, NY, S, US), 1623 (F, GH, NY, S) = *A. tomentosa*  
 Wurdack 954 (F, G, GH, NY, S), 1259 (F, NY, US) = *A. nitida*  
 Wurdack 1467 (holotype: US!; isotypes: F!, G!, GH!, MO!, NY!, P!, S!) = *A. mertensioides*  
 Wurdack 1624 (F, NY) = *A. glandulosa*  
 Wurdack et al. 2735 (NY) = *A. grandifolia*  
 Wurdack et al. 2791 (NY, VEN) = *A. floribunda*  
 Wurdack et al. 2787 (F) = *A. ruizteranii*  
 Wurdack et al. 2809 (NY, US, VEN) = *A. floribunda*  
 Young 1341 (MO) = *A. confusa*
- Zak 1861 (AAU, QCA) = *A. merianiaae*  
 Zak & Jaramillo 652 (AAU, NY); 663 (AAU, NY) = *A. quitensis*  
 Zarucchi & Betancur 6405 (F, GH, NY) = *A. floribunda*
- Øllgaard 90618 (AAU, LOJA) = *A. disrupta*  
 Øllgaard 91097 (AAU) = *A. sclerophylla*  
 Øllgaard & Balslev 9645 (AAU) = *A. cf. lawessonii*  
 Øllgaard & Balslev 9737 (AAU, F, MO, NY, US) = *A. lawessonii*  
 Øllgaard & Feil 91108 (AAU, K, LOJA, MO, NY, QCA, QCNE) = *A. sclerophylla*  
 Øllgaard & Madsen 74261 (AAU, F, GH, LOJA, NY) = *A. macrophylla*  
 Øllgaard & Madsen 90476 (AAU) = *A. affinis*  
 Øllgaard & Madsen 90529 (AAU, LOJA, MO, NY, QCA) = *A. merianiaae*

- Øllgaard et al. 58016 (AAU, LOJA, MO, NY) = *A. lawessonii*  
 Øllgaard et al. 58291 (AAU, MO, NY) = *A. scutigera*

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