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A TAXONOMIC REVISION OF THE AMERICAN SPECIES OF AGARISTA (ERICACEAE)[1, 2]

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A GENUS of 30 species occurring in both Africa (including Madagascar) and the Americas, *Agarista* is closely related to several genera in the Andromedeae (Ericaceae) such as *Craibiodendron* W. W. Smith, *Lyonia* Nutt., and *Pieris* D. Don (see Stevens, 1970, 1971; Judd, 1979). In this paper I have reevaluated the limits of the genus and revised the species occurring in the New World; ca. 1900 herbarium specimens have been examined. Usually the African taxa are treated as the genus *Agauria,* and the American species as a section of the eastern Asian–North American genus *Leucothoë* D. Don (see Sleumer, 1938, 1959). The interrelationships and confused taxonomic history of these three groups have been studied by Stevens (1970) and Judd (1979) and are reinvestigated here.

The American species of *Agarista* form a very homogeneous and obviously closely related group, and it has been difficult to delimit phylogenetic groupings of species within this section. However, the taxonomic usefulness of many characters employed in species delimitation (e.g., presence of unicellular hairs and multicellular gland-headed hairs, inflorescence structure, leaf shape) has been reevaluated. I have attempted to employ consistent specific concepts, to compare the taxa and interpret their evolutionary relationships, and to develop practical keys for identification.

PHYLOGENY AND EVOLUTION

GENERIC AND SECTIONAL RELATIONSHIPS

The genus *Agarista* can be divided into two natural and morphologically distinctive groups that are recognized in this treatment as sections. *Agarista*

[1]The third in a series of revisionary studies of genera of the Andromedeae (Ericaceae). Previously studied genera include *Lyonia* (Judd, 1981) and *Pieris* (Judd, 1982).

[2]Florida Agriculture Experiment Station Journal Series no. 4262.

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sect. AGAURIA includes the single widespread and variable species *A. salicifolia*, which is native to central Africa and Madagascar (see Sleumer, 1938). This taxon is characterized by twigs with nonchambered, slightly to very heterogeneous pith; leaves with the abaxial epidermis papillose and the adaxial epidermis having more or less short, usually undivided cells (in cross section); and capsules with basal placentae. In addition, the style is apparently not swollen. *Agarista* sect. AGARISTA includes 29 species (34 taxa) and is most diverse in South America, especially southeastern Brazil. These species are characterized by twigs with non- to clearly chambered, *Calluna*-type pith (i.e., cells small and thick walled toward the outside of the twig, becoming much larger and thinner in the center); leaves with the abaxial epidermis nonpapillose and the adaxial epidermis with usually tall and often divided cells; and capsules with subapical to more or less central placentae. The style is usually swollen toward the apex.

Stevens (1970) has pointed out that the African and American taxa also differ in the development of a hypodermis. *Agarista salicifolia* has a more or less continuous hypodermis, while the American species have at most one or two cells (in cross section) near the larger veins. Additionally, Cox (1948) has reported differences in the anatomy of the xylem.

The sections are very similar in most features. Both are characterized by buds with more than two bud scales; an indumentum of multicellular, multiseriate-stalked, small-headed glandular hairs; leaves usually revolute in bud, with a unifacial midrib bundle and a rather dense vein reticulum in which all orders are more or less equally prominent (Lems, 1964); inflorescences racemose (or paniculate), overwintering within the bud (Lems, 1962); flowers five-merous, with imbricate calyx lobes; stamens lacking appendages, the filaments geniculate (i.e., S-shaped) and with usually long unicellular hairs; and capsules with nonthickened sutures.

Traditionally, *Agarista salicifolia* has almost always been included in the genus *Agauria* (see TABLE 1) and the American species of *Agarista* in *Leucothoë* sect. AGASTIA (see TABLE 1; Sleumer, 1959). However, these two groups are actually very similar phenetically and cladistically and are obviously closely related; neither is close to *Leucothoë* sensu stricto (TABLE 2; Lems, 1964; Stevens, 1970; Judd, 1979). All the characters by which these two sections differ (e.g., pith type, presence of papillae on the abaxial leaf epidermis, placenta position, and presence of a leaf hypodermis) are variable infragenerically—and also sometimes infraspecifically—in at least one closely related genus (*Pieris*, *Lyonia*, or *Craibiodendron*). In addition, the degree of morphological/anatomical divergence between *Agarista salicifolia* and the American species of *Agarista* is comparable to that separating sections within other genera of the Andromedeae (see TABLE 2; Judd, 1969, *fig. 1*), while their differences with *Leucothoë* are of "generic magnitude" (TABLE 2; Judd, 1979). The African and American species also form a monophyletic group (see Judd, 1979, *fig. 2*) based upon the shared derived characters of densely reticulate-veined leaves that are usually revolute in bud. This group is part of a larger monophyletic group that includes *Lyonia*, *Craibiodendron*, and *Pieris* and is characterized by anomocytic stomata, fiber bands in the phloem, usually elongated seed-coat cells,

TABLE 1. **Comparative treatment of Agarista and Leucothoë by various authors.**

AUTHOR	TAXON		
	Agarista sect. **Agarista**	**Agarista** sect. **Agauria**	**Leucothoë** (several sections)
Lamarck (1783)	*Andromeda*	*Andromeda*	*Andromeda*
Michaux (1803), Nuttall (1818)	*Andromeda*	—	*Andromeda*
G. Don (1834)	*Agarista* (but *A. populifolia* placed in *Leucothoë*)	*Agarista*	*Leucothoë*
De Candolle (1839)	*Leucothoë* sect. *Agastia* (but 2 spp. placed in *Amechania*, 2 in *Leucothoë* sect. *Agauria*, 1 in *Leucothoë* sect. *Euleucothoë*)	*Leucothoë* sect. *Agauria*	*Leucothoë* sect. *Euleucothoë* (but 1 sp. placed in *Zenobia*)
Bentham & Hooker (1876)	*Agarista* (but *A. populifolia* placed in *Leucothoë* sect. *Euleucothoë*)	*Agauria*	*Leucothoë* (2 sections)
Gray (1878)	*Leucothoë*	*Agauria*	*Leucothoë* (2 subgenera treated)
Niedenzu (1889)	*Agarista* (2 sections, *A. populifolia* placed in *Leucothoë* sect. *Euleucothoë*)	*Agauria*	*Leucothoë* (2 sections)
Drude (1897)	*Leucothoë* subg. *Agarista* (but *A. populifolia* placed in subg. *Euleucothoë*)	*Agauria*	*Leucothoë* subg. *Euleucothoë* and *Lyonia* subg. *Eubotrys*
Small (1914)	*Leucothoë* (only *A. populifolia* treated)	—	*Eubotrys*, *Leucothoë*, *Oreocallis* (but E Asian spp. not treated)
Sleumer (1938, 1959)	*Leucothoë* sect. *Agastia*	*Agauria*	*Leucothoë* (6 sections)
Stevens (1970, 1971)	*Agarista*	*Agauria*	*Leucothoë*

geniculate and/or spurred filaments, and tendency toward epidermal lignification.

The various generic and infrageneric classifications of the species here considered in *Agarista* are summarized in TABLE 1 (see also Stevens, 1970; Judd, 1979). The generic delimitation adopted here is essentially that of G. Don (1834). Lamarck (1783) described—as species of the then very broadly defined

TABLE 2. **Variation in selected morphological and anatomical characters in Agarista and Leucothoë.**

CHARACTER	TAXON		
	Agarista sect. **Agarista**	**Agarista** sect. **Agauria**	**Leucothoë**
Wood			
Phloem with bands of fibers	+	+	−
Pith	*Calluna*-type (often septate)	Slightly to very heterogeneous	Variable
Plant evergreen	+	+	+/−
Leaves			
Revolute in bud	+(−)	+	−
Margin serrate	−(+)	−	+
Vein reticulum dense	+	+	−
Epidermis lignified	+	+	−
Epidermal cells divided	+(−)	−(+)	−
Abaxial epidermis papillose	−	+	−
Stomata anomocytic	+	+	−
Anthers			
Filaments geniculate	+	+	−
Filaments with unicellular hairs	+	+	+/−
Awns present	−	−	+(−)
Placenta position	Apical (central)	Basal	Apical
Testa cells	Elongated	Elongated	± Isodiametric
Number of species	29	1	8

genus *Andromeda*—the first known species of both sections of *Agarista*: *A. populifolia* of sect. AGARISTA, and *A. salicifolia* of sect. AGAURIA. Important nineteenth-century treatments of the group include those of G. Don (1834), De Candolle (1839), Meissner (1863), and Bentham and Hooker (1876). More recently, Sleumer (1938, 1959) has extensively studied both the African and the American taxa, and Kinoshita-Gouvêa (1980) has included the Brazilian species as part of her floristic study of the Ericaceae of Brazil. Stevens (1970) was the first contemporary botanist to reaffirm the close relationship between the African and American agaristas.

CLADISTIC ANALYSIS

The phylogenetic relationships of the species of *Agarista* sect. AGARISTA were investigated using the method of Wagner (1961, 1962, 1969, 1980). Twenty-seven characters were used and assigned primitive and advanced states. Most of these characters are quantitative, and the states of such characters are necessarily somewhat arbitrarily defined. However, the dividing point of character states was chosen in such a way as to minimize the number of taxa showing

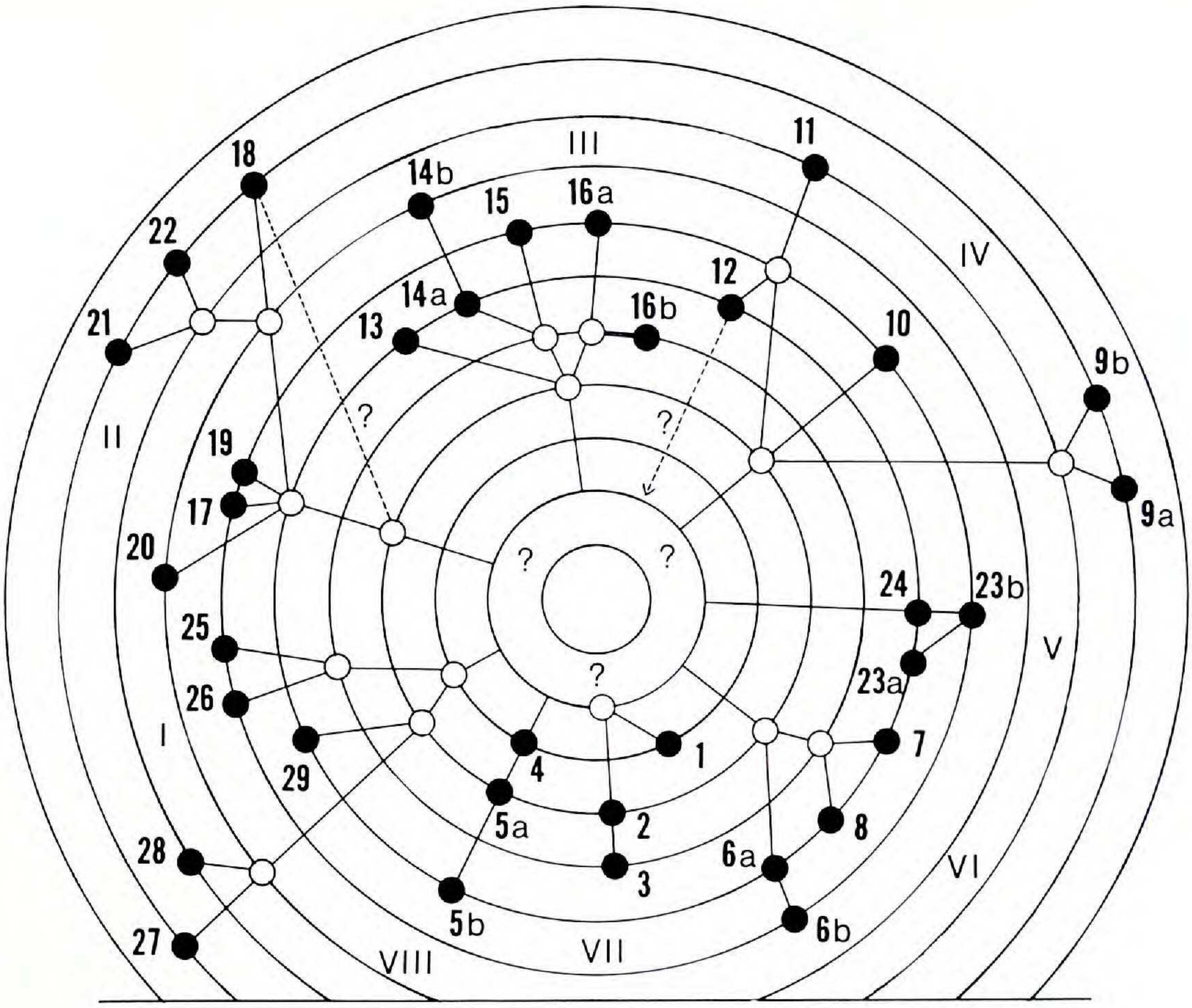


FIGURE 1. Wagner tree for species and varieties of *Agarista* sect. AGARISTA: extant taxa (black circles); hypothetical ancestors showing only derived character states shared by taxa positioned distally on tree (open circles). Taxa indicated by numerals assigned in taxonomic treatment: I = *Agarista eucalyptoides* group, II = *A. hispidula* group, III = *A. oleifolia* group, IV = *A. coriifolia* group, V = *A. niederleinii* group, VI = *A. populifolia* group, VII = *A. albiflora* group, VIII = *A. revoluta* group. (See TABLE 4 for derived character states for each species or variety, and for distinctive features of each species group.)

both conditions. TABLE 3 lists these characters. For each of them, a taxon was scored 0 if primitive and 1 if advanced. When two or more states of a given character were considered derived, each was given a lower-case alphabetic superscript (e.g., 1^a, 1^b). TABLE 4 shows all taxa and their character-state values. For each taxon the total divergence index was determined by adding the individual character-state values. Then mutual groupings of derived characters were determined (by hand), and the taxa were arranged in sequence according to these groupings. In the process, an attempt was made to minimize the number of character-state reversals and parallelisms. The taxa were then plotted graphically (FIGURE 1), with the branching points determined by the mutual grouping of derived characters and the distance by the divergence of each taxon.

The Wagner Groundplan Divergence method, like other cladistic methods,

TABLE 3. **Characters used in the phylogenetic study of the species and varieties of Agarista sect. Agarista.**

CODE	CHARACTER	PRIMITIVE STATE	ADVANCED STATE
A	Habit	± Well-branched shrubs or trees	Subshrubs with rigidly ascending branches
B	Gland-headed hairs	At least sometimes present	Lacking
C	Stem glaucousness	Lacking	At least sometimes present
D	Pith (degree of septation)	Nonseptate to irregularly septate	At least sometimes clearly septate
E	Pith (cellular structure)	Homogeneous	*Calluna*-type
F	Leaf size	Usually > 3 cm	Usually < 2.5 cm
G	Leaf shape	Usually ± ovate to elliptic	a. Often oblong b. ± Linear c. Often ± orbicular
H	Leaf apex	Acute to rounded-mucronate	a. Often acuminate b. Consistently rounded- to retuse-mucronate
I	Leaf base	Not cordate	At least sometimes cordate
J	Abaxial laminar glands	± Lacking or inconspicuous	At least sometimes conspicuous
K	Unicellular hairs on abaxial leaf surface	Lacking to sparse	Usually ± dense
L	Lamina	± Flat to very slightly revolute at margin	a. Slightly to strongly adaxially folded b. Often with strongly revolute margin c. Often clearly curved toward abaxial surface
M	Lamina texture	Coriaceous, ± flexible when dry	Very coriaceous, ± inflexible when dry
N	Leaf margin	Entire (mature leaves)	a. Often crisped/undulate b. Often serrate
O	Petiole length	Short to moderate	Often elongate
P	Inflorescence position	Axillary	Axillary or sometimes terminal
Q	Inflorescence type	Raceme	a. Raceme or panicle b. Sometimes flowers solitary
R	Inflorescence length	> 3 cm	< 3 cm
S	Inflorescence indumentum (unicellular)	Hairs (short, whitish) often present	a. Nearly always lacking b. Hairs ferrugineous c. Hairs long, whitish
T	Calyx lobe length	Usually < 3 mm	Usually > 3 mm
U	Corolla color	White, to pink tinged at apex	Often red

TABLE 3 (*continued*).

CODE	CHARACTER	PRIMITIVE STATE	ADVANCED STATE
V	Corolla size	< 13 mm	Often > 13 mm
W	Corolla pubescence (abaxial surface)	Lacking (or very sparse)	Sparse to dense
X	Ovary pubescence (unicellular)	At least a few hairs	Lacking
Y	Placenta position	± Subapical	± Central
Z	Capsule wall	Not stout	Stout
AA	Seed length	Usually ≥ 2 mm	Usually < 1.5 mm

requires numerous assumptions concerning which is the derived and which the ancestral state of each character. The problems and sources of error associated with each step in the procedure are discussed in Judd (1979), Stevens (1980, 1981), Crisci and Stuessy (1980), Wiley (1981), Watrous and Wheeler (1981), and Wheeler (1981). Although the consensus is that out-group analysis is the most powerful method for determining polarity, Crisci and Stuessy maintain that in-group analysis, if used with care, can be helpful in phylogenetic investigations. The derived state(s) of characters A–G, I–L, N–P, T, U, W, and Y were determined by out-group comparison (using the genera *Craibiodendron* and *Lyonia* as the outgroup; see Judd, 1979), supported by in-group comparison for the character states A, C, F, G, J–L, N–P, T, U, W, and Y. Characters AA and Y are highly correlated. In-group comparison was used in determining the advanced state(s) of H, M, Q–S, V, X, and Z. These decisions were made after careful study of the genus and related groups.

The Wagner Tree resulting from the above procedure (FIGURE 1; see also TABLE 4) indicates that the species of *Agarista* sect. AGARISTA may belong to eight clearly to rather poorly defined phyletic groups: the *Agarista eucalyptoides* group (species 25–29), the *A. hispidula* group (species 17–22), the *A. oleifolia* group (species 13–16), the *A. coriifolia* group (species 9–12), the *A. niederleinii* group (species 23, 24), the *A. populifolia* group (species 6–8), the *A. albiflora* group (species 1–3), and the *A. revoluta* group (species 4, 5). It is also evident that the most advanced taxa—*Agarista coriifolia, A. angustissima, A. glaberrima, A. virgata, A. hispidula,* and *A. ericoides*—are all indigenous to southern Brazil. Most are, in fact, endemic or nearly endemic to Minas Gerais. In contrast, the more primitive taxa—*Agarista albiflora, A. subcordata,* and *A. duckei*—are found in northern South America, the two former in the northern Andes and the latter in the Guayana Highland.

The species of the *Agarista eucalyptoides* group are characterized by their distinctive leaves with often elongate, flexuous petioles (O) and acuminate apices (H^a). These species also have leaves with rounded to narrowly cuneate bases, white flowers with short calyx lobes, and capsules with subapical placentae. *Agarista eucalyptoides* and *A. boliviensis* are likely closely related. Both taxa lack gland-headed hairs (B), have often crisped/undulate leaf margins (N^a), and have leaves that are revolute in bud and more or less flat at maturity. In contrast, the more advanced *A. duartei, A. angustissima,* and *A. glaberrima*

TABLE 4. **Character divergence values for taxa used to construct Wagner Tree.**

Taxon	Character A B C D E F G H I J K L M N O P Q R S T U V W X Y Z AA	Geog.	Total
1	0 0 0 0 1 0 0 0 | 1 | 0 0 0 0 0 0 0 0 0 0 1c0 0 0 0 0 0 0 0 0	A	3
2	0 1 0 0 1 1 0 0 | 1 | 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 ?	A	4
3	0 1 0 0 1 1 0 0 | 0 | 0 0 1b0 0 0 0 0 0 0 0 0 0 0 1 0 0 0	A	5
4	0 | 1 | 0 0 1 0 0 0 0 0 0 0 | 1c0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	G	3
5a	0 | 1 | 0 0 1 0 0 1b0 0 0 | 1c0 0 0 0 0 0 0 0 0 0 0 0 0 0 0	B-N	4
5b	0 | 1 | 0 0 1 0 0 1b0 0 1 | 1c0 0 0 0 0 0 0 0 0 0 1 0 0 ? ?	B-N	6
6a	0 | 1 | 0 | 1 | 1 0 0 | 1a0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 0 1 0 0 0 0	NA	6
6b	0 | 1 | 0 | 1 | 1 0 0 | 1a0 0 1 0 0 0 0 0 0 | 1 | 0 0 0 0 1 0 0 0 0	NA	7
7	0 | 1 | 0 | 1 | 1 0 0 | 1a0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 0 0 1 0 0 0	NA	6
8	0 | 0 | 0 | 1 | 1 0 0 | 1a0 0 0 0 0 1b0 0 0 | 1 | 0 0 0 0 0 1 0 0 0	NA	6
9a	0 | 1 | 1 1 1 0 0 0 1 | 1 | 0 0 | 1 | 0 0 1 1a0 0 0 1 0 0 0 0 0 0	B-N	10
9b	0?| 1 | 1 1 1 0 1a0 0 | 1 | 0 0 | 1 | 0 0 1 1a0 0 0 1 0 0 0 0 0 0	B-N	10
10	0 | 1 | 0 0 1 1 0 0 1 | 1 | 0 0 | 1 | 0 0 0 0 0 0 0 0 0 0 0 0 0 1	B-N	7
11	0 | 0 | 0 0 1 1 0 0 1 | 1 | 1 0 | 1 | 0 0 0 0 0 1c0 1 0 1 0 0 0 0?	B-N	9
12	0 | 1 | 0 0 1 0 1a0 0 | 0 | 1 0 | 0 | 0 0 0 0 0 1c0 0 0 1 0 0 0 0	B-N	6
13	0 0 0 0 1 0 0 0 | 1 | 0 1 0 0 0 0 0 0 0 0 0 0 | 0 | 0 1 0 | 1 | 0 | 1	B-S	6
14a	0 0 0 1 1 0 0 0 | 1 | 0 0 0 0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 | 1 | 0 | 1	B-N	6
14b	0 0 0 1 1 0 0 0 | 0 | 0 0 0 0 0 0 0 0 0 0 1a0 | 1 | 1 0 1 | 1 | 0 | 1	B-N	8
15	0 1 0 1 1 0 1 0 | 0 | 0 0 0 0 0 0 0 0 0 1 0 0 | 0 | 0 0 0 | 1 | 0 | 1	B-S	7
16a	0 0 0 0 1 0 0 0 | 1 | 0 0 0 0 0 0 0 1 1a0 0 0 | 1 | 0 0 0 | 1 | 0 | 1	B-S	7
16b	0 0 0 0 1 1 0 0 | 1 | 0 0 0 0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 | 0 | 0 | 1	B-N	5
17	| 1 | 0 0 0 1 1 1c1b1 | 0 0 | 0 | 0 0 0 0 0 0 0 0 | 1 | 0 0 0 0 0 0 0 0	B-S	7
18	| 1 | 0 0 0 1 1 0 0 | 1 | 0 0 | 0 | 0 0 0 1 1a0 1 | 0 | 0 0 0 1 1 0 1	B-N	10
19	| 1 | 0 0 0 1 1 0 0 | 1 | 0 0 | 1b0 0 0 1 0 0 0 | 1 | 0 0 0 0 0 0 0 0	B-NS	7
20	| 0?| 1 0 1 1 1 0 0 | 1 | 0 0 | 1b0 0 0 0 1b1 0 | 0 | 0 0 0 0 0 0 0 0	B-N	8
21	| 1 | 0 0 0 1 1 0 0 | 1 | 0 0 | 1b0 0 0 0 0 0 0 | 1 | 1 0 1 0 1 0 1	B-N	10
22	| 1 | 0 0 0 1 1 0 0 | 1 | 0 0 | 1b0 0 0 0 0 1 0 | 1 | 1 0 0 0 1 0 1	B-N	10
23a	0 | 1 | 0 | 1 | 1 1 1 0 0 0 0 0 0 0 0 0 0 | 0 | 0 0 0 0 0 0 0 | 1 | 0	B-S	6
23b	0 | 1 | 0 | 1 | 1 0 1 1a0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 0 0 0 0 | 1 | 0	B-S	7
24	0 | 1 | 0 | 1 | 1 0 0 1a0 0 0 0 0 0 0 0 0 | 1 | 0 0 0 0 0 0 0 | 1 | 0	B-N	6
25	0 1 0 0 1 0 0 | 1a0 0 0 | 0 | 0 1a1 | 0 0 1 0 0 0 0 0 1 0 0 0	A	7
26	0 1 0 0 1 0 1a1a0 0 0 | 0 | 0 1a1 | 0 0 0 1b0 0 0 0 0 0 0 0	B-NS	7
27	0 1 0 1 1 0 0 | 1a0 0 0 | 1a0 0 | 1 | 1 1a0 1a0 0 0 0 1 0 0 0	B-N	10
28	0 0 0 0 1 0 1b1a0 0 0 | 1a0 0 | 1 | 1 1a0 1a0 0 0 0 1 0 0 0	B-N	9
29	1 0 0 0 1 0 1b1a0 0 0 | 1a0 0 | 0 | 0 0 1 0 0 0 0 0 0 0 0 0	B-N	6

Explanation of abbreviations: A = Andes, B = Brazilian region (north and south), G = Guayana Highland, NA = North America. Dotted lines separate species groups supported by characters enclosed within rectangular markings. Each taxon indicated by its species number.

have leaf blades that are slightly to strongly adaxially folded. The distinctive linear leaves (G^b) of *A. angustissima* and *A. duartei* have probably evolved convergently. Except for *A. boliviensis*, which occurs in the southern Andes, all species of this phyletic group are limited to the Brazilian region (see geographic analysis). The group is most diverse in Minas Gerais, with only the relatively widespread *A. eucalyptoides* extending southward into the state of Rio Grande do Sul and adjacent Uruguay.

The species of the *Agarista hispidula* group are characterized by their low, more or less sparsely and erectly branched habit (A) and their small, usually cordate-based leaves (F, I). Many species also have strongly revolute leaves (L^b) and elongate calyx lobes (T). The position of the placenta varies from more or less subapical to central, and the group may be derived from extinct, small-leaved members of the *A. oleifolia* group, an assemblage with mainly central placentae (note especially the resemblance in leaf characters to *A. pulchella* var. *cordifolia*). Although *A. hispidula* and *A. ericoides* are probably closely related, both often having red corollas, more or less centrally positioned placentae, and short seeds, the relationships between these species and *A. chlorantha, A. organensis, A. nummularia,* and *A. virgata* are somewhat obscure. Species of the *A. hispidula* group are limited to the Brazilian region. The group is most diverse in the northern subunit of this region, with only *A. chlorantha* and *A. nummularia* occurring as far south as Santa Catarina (the former) or Rio Grande do Sul (the latter).

The *Agarista oleifolia* group is a rather loosely knit assemblage of taxa characterized by often cordate-based leaves (I), and by capsules with central placentae and short seeds (Y, AA). These species tend to have more or less flat leaves and flowers with short calyx lobes. Several taxa have straight-sided or oblong leaves (G^a). The relationships between the taxa comprising this rather weakly defined group are obscure. The group is limited to the Brazilian region (including Paraguay).

The four species of the *Agarista coriifolia* group are characterized by their lack of multicellular gland-headed hairs (B), and by their usually quite coriaceous leaves (M) with often conspicuous abaxial glandular regions along the midvein (J). The leaves tend to be more or less flat, the inflorescences elongate, and the placentae subapical. The calyx lobes are usually short, and the flowers tend to be reddish. The affinities of *A. chapadensis* are probably with *A. subrotunda,* a species with moderately to densely pubescent abaxial leaf and corolla surfaces (K, W). The species of this evolutionary line are limited to the northern portion of the Brazilian region (see phytogeographic discussion).

The *Agarista niederleinii* group includes only three taxa, which are distinguished by their lack of multicellular gland-headed hairs (B), their often septate pith (D), and their large capsules with very stout walls (Z). These taxa also tend to have short racemes (R), subapically positioned placentae, white flowers with short calyx lobes, and flat to slightly revolute leaves. The group is limited to the Brazilian region.

The *Agarista populifolia* group is distinctive due to its often clearly septate

pith (D), its ovate, acuminate leaves (H^a), and its short racemes (R). The members of this lineage frequently have rather large, more or less flat leaf blades with cuneate to rounded bases, white flowers with short calyx lobes, and capsules with subapical placentae. These species are limited to North and Central America, growing in the southeastern United States and east-central Mexico south to Honduras and El Salvador. This group may have originated from extinct members similar to species of the *A. albiflora* group (note especially the resemblance of leaves to those of *A. albiflora*).

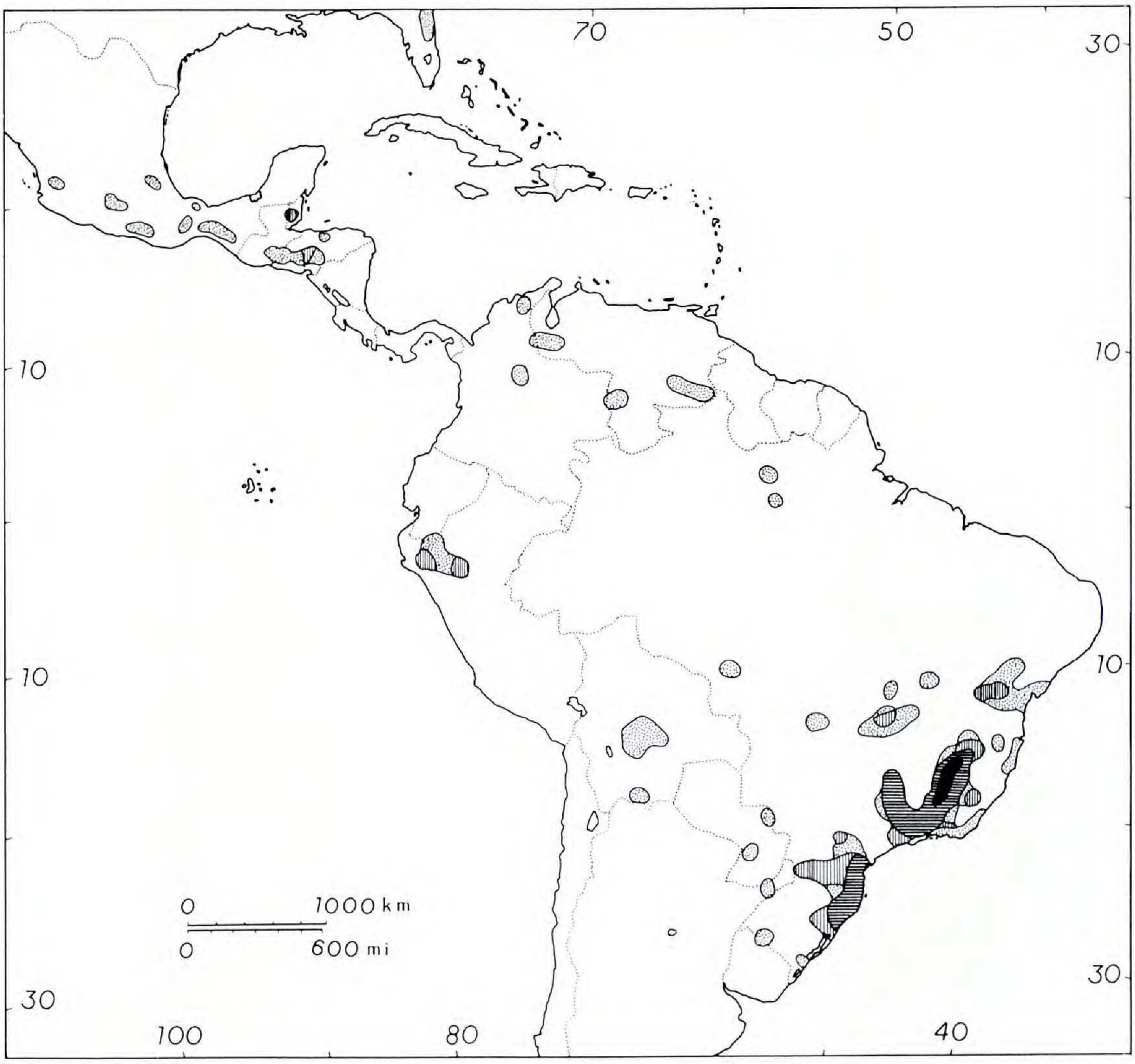
All three species comprising the *Agarista albiflora* group occur in the northern Andes. These species are likely rather primitive, and although it is clear from morphological and geographic evidence that the small-leaved *A. bracamorensis* and *A. subcordata* were probably derived from ancestors similar to the variable and widespread *A. albiflora,* these three species are only weakly linked in at least sometimes having cordate leaves (I).

Finally, the two species comprising the *Agarista revoluta* group (VIII) are characterized by their lack of gland-headed hairs (B; except rarely present on the ovary of *A. duckei*!) and their leaves with the blade often quite variable in extent of abaxial curvature (L^c). The capsules are often ovoid, with the valve margins sometimes slightly differentiated; the placentae are subapical, and the seeds are the longest (2–3.5 mm) of the section. The primitive species, *A. duckei,* occurs chiefly in the Guayana region, while the slightly more specialized *A. revoluta* grows in coastal "restingas" from the state of Bahia south to Estado do Rio in eastern Brazil.

There are insufficient data to determine the evolutionary interrelationships of these eight cladistic groups; all share the derived character-state of *Calluna*-type pith (E). In contrast, the African species, *Agarista salicifolia,* has slightly to strongly heterogeneous pith (Stevens, 1970). The species of *Agarista* sect. AGARISTA are obviously all closely related, although the extensive parallel evolution of characters and the frequency of character-state reversals obscure both intra- and intergroup relationships. Many examples of parallel evolution can be found among the various phylogenetic groups discussed above; these can be determined from FIGURE 1 and TABLE 4. Of the 27 characters used, at least 19 show some degree of intergroup parallelism (and also often intragroup parallelism or reversals), while 2 (O, T) of the remaining 8 show intragroup reversals and 1 (E) is invariant. In groups showing a large amount of homoplasy, such as *Agarista* sect. AGARISTA, the elucidation of cladistic relationships becomes extremely difficult. Thus, the conclusions reached here should be interpreted as very preliminary hypotheses, to be tested by the evaluation of additional characters (including anatomy and chemistry).

DISTRIBUTION AND ECOLOGY

As discussed above, the 30 species of *Agarista* recognized here are divided into two sections. Section AGAURIA, including the single species *A. salicifolia,* occurs in central Africa, Madagascar, Réunion, and Mauritius (Sleumer, 1938), while section AGARISTA, containing the remaining 29 species, occurs mainly in South America (MAP 1). Both sections are composed of basically montane



MAP 1. General distribution of *Agarista* sect. AGARISTA, showing center of diversity in southeastern Brazil. Pattern indicates number of taxa present: stipples, 1; vertical lines, 2; horizontal lines, 3 to 8; solid black, region of greatest diversity.

plants, with *A. salicifolia* occurring between 700 and 3500 m alt. and the many South American species growing from ca. 500 to 2700 m alt. However, *A. duckei,* a species of the Guayana Highland, can be found as low as 100 m, and *A. revoluta,* a taxon of coastal "restingas" in Brazil, frequently occurs near sea level. (*Agarista nummularia* and *A. pulchella* have also occasionally been collected at very low elevations near the coast.) Possible origins of this interesting montane tropical transatlantic distribution pattern shown by *Agarista* are discussed by Stevens (1970).

Section AGAURIA occurs in several widely scattered montane areas of central Africa but reaches its greatest morphological diversity in Madagascar (Sleumer, 1938). Species of section AGARISTA occur in five major geographic areas (see TABLE 5): the Coastal Plain of the southeastern United States (1 sp.—*Agarista populifolia*); the Mexican region—mountainous areas from central Mexico south to Honduras (2 spp.—*A. mexicana* and *A. sleumeri*); the Guayana Highland (1 sp.—*A. duckei*); the Andean region—mountainous areas from Bolivia to

TABLE 5. **Distribution of taxa of Agarista among the nations* of North, Central, and South America.**

1. UNITED STATES (1)
   A. populifolia†
2. MEXICO (3)
   A. mexicana var. *mexicana*
   A. mexicana var. *pinetorum*
   A. sleumeri†
3. GUATEMALA (1)
   A. mexicana var. *mexicana*
4. BELIZE (2)
   A. mexicana var. *mexicana*
   A. mexicana var. *pinetorum*
5. EL SALVADOR (1)
   A. mexicana var. *pinetorum*
6. HONDURAS (2)
   A. mexicana var. *mexicana*
   A. mexicana var. *pinetorum*
7. COLOMBIA (1)
   A. albiflora
8. ECUADOR (1)
   A. albiflora
9. PERU (3)
   A. albiflora
   A. bracamorensis†
   A. subcordata†
10. VENEZUELA (2)
   A. albiflora
   A. duckei
11. BOLIVIA (1)
   A. boliviensis†
12. BRAZIL (25)
   a. Pará (1)
      A. duckei
   b. Bahia (5)
      A. chapadensis
      A. coriifolia var. *coriifolia*
      A. oleifolia var. *glabra*
      A. revoluta var. *revoluta*
      A. revoluta var. *velutina*†
   c. Goiás (2)
      A. chapadensis
      A. oleifolia var. *glabra*
   d. Dist. Federal (2)
      A. chlorantha
      A. oleifolia var. *glabra*
   e. Mato Grosso (2)
      A. duckei
      A. oleifolia var. *glabra*
   f. Minas Gerais (16)
      A. angustissima†
      A. chlorantha
      A. coriifolia var. *coriifolia*
      A. coriifolia var. *bradei*†
      A. duartei†
      A. ericoides†
      A. eucalyptoides
      A. glaberrima†
      A. hispidula
      A. oleifolia var. *glabra*
      A. oleifolia var. *oleifolia*
      A. pulchella var. *cordifolia*
      A. pulchra†
      A. revoluta var. *revoluta*
      A. subrotunda†
      A. virgata†
   g. Estado do Rio/Guanabara (7)
      A. coriifolia var. *coriifolia*
      A. eucalyptoides
      A. hispidula
      A. oleifolia var. *oleifolia*
      A. organensis†
      A. revoluta var. *revoluta*
      A. uleana†
   h. SÃO PAULO (6)
      A. chlorantha
      A. eucalyptoides
      A. hispidula
      A. oleifolia var. *oleifolia*
      A. pulchella var. *cordifolia*
      A. pulchella var. *pulchella*
   i. Paraná (4)
      A. chlorantha
      A. niederleinii var. *acutifolia*
      A. niederleinii var. *niederleinii*
      A. pulchella var. *pulchella*
   j. Santa Catarina (7)
      A. chlorantha
      A. eucalyptoides
      A. minensis
      A. niederleinii var. *acutifolia*
      A. niederleinii var. *niederleinii*
      A. nummularia
      A. pulchella var. *pulchella*
   k. Rio Grande do Sul (5)
      A. eucalyptoides
      A. minensis
      A. niederleinii var. *acutifolia*
      A. niederleinii var. *niederleinii*
      A. nummularia
13. URUGUAY (1)
   A. eucalyptoides
14. PARAGUAY (1)
   A. paraguayensis
15. ARGENTINA (1)
   A. paraguayensis

*Within Brazil, states.

†Taxon endemic to nation or state.

Colombia (4 spp.—*A. albiflora, A. subcordata, A. bracamorensis, A. boliviensis*); and the Brazilian region—mountainous areas of southeastern Brazil (and adjacent Uruguay and Argentina) (22 spp.). With the exception of *A. duckei,* which has many populations in the Guayana Highland and a disjunct locality in western Mato Grosso, all species are endemic to one of these five regions.

The extremely diverse Brazilian region can be divided into northern and southern subunits, with the northern including the mountains of Minas Gerais and the adjacent states of São Paulo (northern part), Rio de Janeiro, Guanabara, Bahia, Goiás, and Mato Grosso, and the southern mountainous regions of the states of São Paulo (southern part) and Paraná south to Rio Grande do Sul and adjacent areas of Uruguay, northeastern Argentina, and Paraguay.

The northern subunit of the Brazilian region has the most species, with eighteen that are indigenous (see MAP 1). Within this area, the state of Minas Gerais has by far the most species, with fourteen (sixteen taxa), of which seven (eight taxa) are endemic; Estado do Rio/Guanabara is next with seven indigenous species (two endemics), followed by São Paulo (northern) with five species (no endemics) and Bahia with four species (one endemic variety). The southern subunit contains only seven indigenous species (eight taxa), of which four species (six taxa) are endemic. Only three species, *Agarista pulchella, A. chlorantha,* and *A. eucalyptoides,* occur in both subunits. TABLE 5 lists the species and varieties of *Agarista* occurring in or endemic to the various countries (and within Brazil, states) of North and South America.

The mountainous region of southeastern Brazil is a major center of diversity for many groups of vascular plants (see L. B. Smith, 1962; Good, 1964; Tryon, 1972). *Agarista* appears to have undergone extensive speciation (probably eco-geographic) in these mountains, since this region supports several groups of very derived taxa such as *A. coriifolia, A. glaberrima, A. angustissima, A. virgata, A. hispidula,* and *A. ericoides.* This concentration of *Agarista* species may be a relatively recent development, formed in response to Tertiary climatic and geologic changes (see Stevens, 1970).

The area of origin of the group is unknown. It is of interest that the primitive species *Agarista duckei* occurs in the floristically diverse Guayana Highland, while two other rather primitive taxa (*A. albiflora* and *A. subcordata*) occur in the geologically recent Andean region.

Agarista populifolia, of the southeastern United States, has its closest affinities with the montane Mexican taxa *A. sleumeri* and *A. mexicana.* There are many similarities between the deciduous forest formations of the eastern United States and the montane temperate forests of Mexico, and a number of species pairs have representatives in the two regions (see Miranda & Sharp, 1950; Dressler, 1954; Martin & Harrell, 1957; Graham, 1964, 1973; Rzedowski, 1965; and Gómez-Pompa, 1973). A similar disjunction pattern is seen in the related genus *Lyonia,* with *L. ferruginea* (Walter) Nutt. and *L. fruticosa* (Michaux) G. Torrey occurring in the southeastern U. S. and *L. squamulosa* Martens & Galeotti in the Sierra Madre Oriental of Mexico (Judd, 1981).

Although a few species such as *Agarista oleifolia, A. albiflora, A. mexicana,* and *A. eucalyptoides* have quite wide distributions, most (e.g., *A. pulchra, A. virgata, A. organensis, A. ericoides, A. angustissima, A. duartei, A. bracamo-*

rensis) are narrowly endemic. Most varieties and closely related species are more or less geographically isolated, but a few taxa, such as the varieties of *A. niederleinii*, seem to be chiefly elevationally/ecologically isolated.

The genus grows in a wide variety of habitats, but most species prefer acid soils and are sun-loving plants of open communities. Most also sprout readily from the base after fire or disturbance. Characteristic habitats include cerrado, rocky or grassy campo, boggy or marshy campo, shrub bogs, gallery forests along rivers or streams, thickets, open scrub, forest or thicket margins, elfin woodland or moist montane forests, rocky crests or slopes, coastal scrub/"restinga," sand dunes, savannas, and pine-oak forests. For detailed discussion of cerrado vegetation (along with lists of characteristic species), see Eiten (1972). Species may occur in iron-rich lateritic soils, sandstone regions, white sands, or highly organic soils.

TAXONOMIC CRITERIA

Because of the extensive parallel evolution and character-state reversals within *Agarista*, different species can be separated only by using sets of vegetative and reproductive characters. Morphological entities that have no major internal discontinuities and that are separated from other, similar entities by consistent morphological gaps are considered to be species. They have definite geographic distributions and ecological preferences. Many species, such as *A. pulchra*, *A. virgata*, *A. organensis*, *A. ericoides*, *A. angustissima*, *A. duartei*, and *A. bracamorensis*, are narrowly endemic. Most species (and varieties) are probably isolated by differences in distribution, ecology, and/or genetic composition. The term "variety" has been used for the morphologically distinctive geographic (or ecological) subunits comprising widespread and/or variable species (see Judd, 1981). Varieties have only very slight morphological gaps between them, may intergrade, and often differ in only one (or very few) aspect(s) of indumentum or leaf morphology.

The taxonomic usefulness of (and the variation within) the various characters used in this revision are discussed below. Characters most useful in species delimitation include: 1) leaf vernation, size, shape, apex and base types, petiole length, and extent to which the margin is revolute; 2) inflorescence length; 3) unicellular indumentum of the abaxial leaf surface and of the inflorescence axes and other reproductive structures (especially calyx, corolla, and ovary); 4) calyx length and, to a lesser extent, corolla color and length; 5) placenta position (in fruit); and 6) seed length.

HABIT

The species of *Agarista* vary from small, sparsely and erectly branched subshrubs such as *A. ericoides*, *A. virgata*, *A. hispidula*, *A. duartei*, and *A. nummularia* to moderate-sized, laxly branched trees up to 6–8(–20) m tall such as *A. populifolia*, *A. sleumeri*, and *A. mexicana*. The branching pattern, including internode length, density of branching, and orientation of branchlets, is quite variable but is sometimes useful in distinguishing between species (e.g., *A.*

virgata and *A. pulchra*; see key). Although the bark is always longitudinally furrowed, it is very poorly developed in the smaller species (e.g., *A. virgata, A. duartei, A. ericoides*). It is occasionally of taxonomic interest, such as in separating *A. populifolia,* in which the bark is thin and shallowly furrowed, from the related *A. mexicana* and *A. sleumeri,* in which it is thick, corky, and deeply furrowed. Cerrado species such as *A. eucalyptoides* tend to have contorted trunks and thick, corky bark, characters very common in this vegetation type (see Eiten, 1972). Most species sprout readily from the base after fire or disturbance.

As in most other members of the Andromedeae, the shoot meristem in *Agarista* has a limited life span, and growth in height is achieved by a succession of equivalent axillary, orthotropic shoots (Lems, 1962). All species show Leeuwenberg's Model of growth (see Hallé, Oldeman, & Tomlinson, 1978, for description) or a slight variation of this architectural pattern. Floral buds are usually produced in the leaf axils of the distal portion of the shoot, although they may be restricted to those at or very near the apex. The shoot apex typically aborts, but in some species (e.g., *A. angustissima, A. coriifolia, A. glaberrima*) it is converted into a terminal inflorescence (with the leaves gradually grading into bracts). The inflorescences overwinter within the buds, with meiosis presumably occurring in the spring (see Lems, 1962).

Twigs

The branchlets vary from terete to slightly angled. Pith is of the *Calluna*-type in all American species and varies from non- to clearly chambered. Its structure is frequently of taxonomic value (see key) and is especially useful in separating *Agarista paraguayensis, A. populifolia,* and *A. sleumeri* from *A. mexicana.*

Indumentum

The indumentum of *Agarista* is of three distinct types: unicellular hairs; multicellular, multiseriate-stalked, gland-headed hairs; and papillae. Although the presence or absence of multicellular, gland-headed hairs has been much used in the taxonomy of the genus (Sleumer, 1959), this character is actually too variable to be of much taxonomic significance. Of the 29 species comprising *Agarista* sect. Agarista, 13 have both glandular-pubescent and nonglandular forms. Only *A. virgata* is consistently glandular-pubescent. However, this taxon has been very poorly collected and nonglandular forms may eventually be discovered. Fifteen species consistently lack glandular hairs. Glandular-pubescent and nonglandular individuals frequently occur intermixed in the same population (e.g., *Judd 2609, A. populifolia*). There is also much variation in density and distribution of multicellular gland-headed hairs. At one extreme are plants with glandular hairs on the young twigs, midvein (or even lamina) of both leaf surfaces, inflorescence axes, pedicels, and calyx lobes; other individuals may have such hairs only on the inflorescence axes, or only along the leaf margins (i.e., leaves ± glandular-ciliate). In a few species such as *A. angustissima* and *A. duartei,* glandular hairs are only present on juvenile plants.

Finally, *A. duckei* is unique because of its occasionally glandular-pubescent capsules. However, because of the extensive intrapopulational (and developmental) variation in glandular indumentum, it has not been possible to use this character at either the specific or the infraspecific level. The several groups of extremely similar taxa (e.g., *A. nummularia* var. *nummularia* and *Leucothoë* (*Agarista*) *nummularia* var. *floccigera*; *A. chlorantha* and *A. serrulata*; *A. hispidula* and *A. intermedia*; *A. ericoides, Leucothoë* (*Agarista*) *lycopodioides*, and *L.* (*Agarista*) *acicularis*; *A. subrotunda* and *A. pistrix*; and *A. oleifolia* var. *oleifolia* and *Leucothoë* (*Agarista*) *oleifolia* var. *hispidula*) that were recognized by Sleumer (1959) and that differ chiefly in the presence or absence of such hairs have been considered conspecific.

All species of *Agarista* have at least a few unicellular hairs, and the distribution and density of such hairs is frequently of taxonomic significance (see keys). Several taxa—*A. mexicana* var. *pinetorum, A. revoluta* var. *velutina, A. subrotunda, A. chapadensis*, and *A. paraguayensis*—have a distinctive dense covering of unicellular hairs on their abaxial leaf surfaces. The unicellular indumentum of the inflorescence axis and other reproductive structures (especially calyx, corolla, and ovary) was found often to be of systematic value. Thus, the inflorescence indumentum is useful in distinguishing *A. glaberrima* from *A. boliviensis* and *A. eucalyptoides, A. virgata* from *A. nummularia, A. oleifolia* var. *oleifolia* from var. *glabra*, and *A. pulchra* from *A. pulchella*. Several taxa (e.g., *A. paraguayensis, A. revoluta* var. *velutina*, and *A. hispidula*) are easily distinguished from related ones due to their abaxially pubescent corollas, and the indumentum of the ovary and calyx is very useful in separating *A. mexicana, A. sleumeri*, and *A. populifolia*. However, such characters must be used with care since many species are quite variable in indumentum. Although the unicellular indumentum of the twigs is usually too variable to be of much taxonomic use, it is distinctive in a few species. For example, the hairs are ferrugineous in *A. eucalyptoides* and elongate in *A. albiflora*.

Abaxially papillose leaves are found only in the African species, *Agarista salicifolia* (sect. AGAURIA); all the American species (sect. AGARISTA) lack such papillae.

LEAVES

Characters of leaf vernation, size, shape, apex and base types, thickness, petiole length, and extent to which the margin is revolute are extremely important in the taxonomy of *Agarista* sect. AGARISTA. Most species of *Agarista* have leaves that are revolute in bud; consequently the mature leaves often have a faint longitudinal "fold" line on each side of the midvein. However, *A. duartei, A. angustissima*, and sometimes *A. glaberrima* have strongly adaxially folded leaves. The mature leaves may be more or less flat with a plane to only very slightly revolute margin (many species), strongly to slightly adaxially folded (*A. duartei, A. angustissima, A. glaberrima*), or clearly abaxially curved with more or less strongly revolute margins (e.g., *A. organensis, A. hispidula, A. chlorantha, A. ericoides*). There is great variation in size and shape of the lamina—from 0.4–1.2 cm long in *A. ericoides* to 4–13 cm long in *A. sleumeri*,

and from linear in *A. angustissima* to often nearly orbicular in *A. nummularia.* Numerous examples of the taxonomic usefulness of leaf shape and size are evident in the key. The petiole ranges from very short (ca. 1.5 mm in *A. ericoides*) to very long (to ca. 40 mm). The often long, slender, flexuous petioles of *A. eucalyptoides, A. glaberrima,* and *A. boliviensis* are especially distinctive. The apex and base of the lamina, although often showing much infraspecific variation, are sometimes useful at the species level. Many species have leaves that vary from acute to rounded with a small mucro at the apex, and from slightly cordate to rounded or cuneate at the base. The leaf apex is useful in distinguishing *A. duckei, A. revoluta,* and *A. albiflora*; the base, in separating *A. minensis* from *A. pulchella* (see key). *Agarista populifolia, A. mexicana,* and *A. sleumeri* are distinctive due to their consistently ovate leaves with acuminate apices. Finally, although most species have moderately coriaceous leaves, *A. coriifolia* and its relatives have thickly coriaceous blades that are rather inflexible when dry.

The leaves of most species are entire but those of *Agarista boliviensis* are distinctive in having crisped/undulate margins, and those of *A. populifolia* are often serrate. In this species each tooth is associated with a multicellular gland-headed hair. The margins of several Brazilian species are sometimes glandular-ciliate due to the presence of multicellular gland-headed hairs.

Many species have glandular "patches" or "dots" along the midvein on the abaxial epidermis. These glandular regions (which should not be confused with the much smaller gland-headed hairs found in some species) seem to be associated with the secondary veins and are variable in size and shape. They are sometimes of taxonomic interest, as in distinguishing the varieties of *Agarista coriifolia.*

All species have reticulodromous venation, with a rather dense vein reticulum and all orders more or less equally prominent (Lems, 1964; Judd, 1979).

Inflorescence

The flowers of *Agarista* are borne in axillary (or, less commonly, terminal) racemes or panicles on branches of the previous season, although in *A. organensis* the inflorescences are often reduced to solitary axillary flowers or few-flowered clusters, and in several species (e.g., *A. minensis*) the axis is so shortened that the inflorescence is nearly a fascicle. There is always a single inflorescence per leaf axil. Terminal flowers are usually lacking, with the apex of the raceme simply aborting, so the inflorescences are polytelic (Weberling, 1965). However, in *A. populifolia* a few of the flowers composing the raceme are rarely replaced by two-flowered clusters—i.e., one of the bracteoles of the pedicel subtends a secondary flower. This also occurs in *A. pulchella* and *A. coriifolia* var. *bradei,* resulting in a small panicle in which the two- to many-flowered inflorescence branches have terminal flowers, although the apex of the primary axis aborts. However, the apices of even the secondary axes (branches) of many panicles abort (see panicles of *A. coriifolia, A. virgata, A. glaberrima*). The few-flowered axillary fascicles (or short racemes) of *A. organensis* also at least sometimes have terminal flowers, and it is probable that

the pedicel of the "solitary axillary flower" with its several bracteoles actually represents a very reduced inflorescence axis (i.e., a terminal-flowered raceme). Thus, monotelic (or partly monotelic) inflorescences occur in a few species of the genus. This inflorescence type is, according to Weberling (1965), more primitive than the polytelic type, and the presence of more or less monotelic inflorescences in this group (along with their variation in position) may indicate its low level of advancement. In reproductive characters most species of *Agarista* are certainly less specialized than those of *Lyonia, Craibiodendron,* or *Pieris* (Judd, 1979).

There is great interspecific variation in inflorescence length—from at most ca. 1.5 cm in *Agarista organensis* or *A. minensis* to over 20 cm in *A. coriifolia.* This character is thus taxonomically useful and has been employed in separating *A. minensis* from *A. pulchella, A. angustissima* from *A. duartei,* and *A. organensis* from *A. chlorantha,* among others.

FLOWERS

All species have actinomorphic, perfect, pendulous flowers, although the pedicel curves upward as the fruits begin to develop, ultimately placing the capsules in an erect position. The flowers of all species are five-merous and quite fragrant. Those of *Agarista populifolia* are visited chiefly by bumblebees (*Bombus*); no information is available on the pollination of the many South American species.

The pedicel varies in length from only 1.5–3 mm in *Agarista bracamorensis* to 14–15 mm in *A. angustissima, A. coriifolia,* and *A. pulchella.* This is not a very useful taxonomic character since the pedicel tends to elongate as the flowers and fruits develop. All species have a clearly developed articulation between the pedicel and the receptacle, its position varying from at to ca. 3 mm below the insertion of the calyx. In all species the pedicel is subtended by a single bract, the size of which is usually too uniform to be of taxonomic importance. Each pedicel in *Agarista* usually has a pair of bracteoles, although there are occasionally three to many in a few taxa. The bracteoles are usually positioned along the pedicel from the base to near the midpoint; they may rarely even be found near its apex. The bracteoles are characteristically minute (see descriptions) and linear to triangular or ovate-triangular; very rarely they subtend secondary flowers. The number, size, and shape of the bracteoles are too uniform to be useful at the species level.

The calyx is composed of five persistent, more or less triangular, imbricate sepals that are connate only at the very base. Stomata are present only on the abaxial surface (Stevens, 1971). The lobes show some interspecific variation in length (e.g., 0.5–1.5 mm in *Agarista bracamorensis,* 3–6 mm in *A. ericoides*). This character is thus frequently of taxonomic significance, and it has been used to distinguish *A. chlorantha* from *A. organensis* and *A. nummularia* from *A. pulchella.* The apex varies from acuminate to acute and is usually too uniform to be of systematic importance. However, *A. chlorantha* typically has acute tips, while those of the related *A. hispidula* are usually acuminate.

The corolla is always sympetalous and deciduous. Stomata are present on

the outer surface but lacking on the inner (Stevens, 1971). In most species the corolla is more or less cylindrical, but in a few such as *Agarista albiflora, A. duckei,* and *A. hispidula* it may be urceolate or nearly so. The corolla is most often white (or greenish white) or white with a pinkish to reddish tinge toward the mouth, but in some species (e.g., *A. revoluta, A. coriifolia* var. *bradei, A. oleifolia* var. *glabra, A. ericoides*) it is frequently red. Its length varies from 5–8 mm in *A. niederleinii* var. *acutifolia* to 10.5–16 mm in *A. oleifolia* var. *glabra.* The shape, size, and color of the corolla are only slightly taxonomically useful in *Agarista,* due both to the overall uniformity of these characters within the genus and to their considerable variation in some taxa.

The flowers of all species of *Agarista* have ten stamens. These are arranged in two whorls and inserted at the base of the corolla; the outer whorl is opposite the corolla lobes. The stamens are always included and are arranged in a tight ring, with the anther pores facing inward. The filaments are slender, flattened, geniculate, nonappendaged, and slightly swollen near the base. They are covered with long unicellular hairs, especially near the base. Filament length varies from 3–4.5 mm in *A. eucalyptoides* and ca. 3.5 mm in *A. subcordata* to 6.5–8.5 mm in *A. oleifolia* var. *glabra.* A white line or triangular patch of disintegration tissue is present on the back of each anther lobe near the apex, but this tissue is only poorly developed in several species. Because of the consistency of the androecial characters within *Agarista,* they have seldom been used at the species level.

The ovary is superior. The placentae are axile and are borne subapically to basally on a central columella. Species with more or less central (e.g., *Agarista oleifolia, A. pulchella, A. paraguayensis*) or basal (e.g., *A. salicifolia*) placentae have very deeply impressed styles. Placenta position is an important taxonomic character and frequently links related groups of species—for example, sect. AGARISTA (subapical to central) vs. sect. AGAURIA (basal), and the *A. oleifolia* species group (± central) vs. the *A. coriifolia* group (± subapical). The ovary shape varies from ovoid to subglobose, but this variation (like that in placenta position) is better expressed in the mature fruit.

FRUITS AND SEEDS

The fruits of *Agarista* are five-valved, subglobose or short-ovoid to ovoid, loculicidal capsules with pale, unthickened (or occasionally very slightly thickened near apex) sutures. Within *Agarista* sect. AGARISTA, the capsules tend to be rather uniform in size and shape, but those of *A. niederleinii* and *A. uleana* are distinctive due to their large size and their thick walls. Placenta position is best observed in mature fruits and, as mentioned above, is a very valuable taxonomic character within the genus. The variation in placental position within *Agarista* sect. AGARISTA is shown in TABLE 4 and in the key.

The seeds are very small, brown, and scobiform, and they have a thin testa composed of very elongate cells. Species with central placentae tend to have short (0.5–1.4(–1.6) mm) seeds, while those with subapical placentae usually have longer (1–3(–3.5) mm) ones. The seeds of *Agarista salicifolia* are 3–4 mm long (Sleumer, 1938).

VEGETATIVE ANATOMY

The vegetative anatomy of the genus has not been studied in detail. However, pith type was found to be an important taxonomic character: it is *Calluna*-type in all American species (see Stevens, 1970) and slightly to very heterogeneous in the African species, *Agarista salicifolia* (Stevens, 1970). In addition, it remains more or less solid in many American species but becomes nearly hollow in *A. paraguayensis,* or irregularly to regularly chambered/diaphragmed in several taxa (see descriptions). The pith is always chambered in *A. populifolia, A. sleumeri,* and *A. minensis*. Stevens (1970) has pointed out that *A. salicifolia* has epidermal cells that are usually not tall and are rarely divided periclinally, and a single-layered hypodermis that is more or less continuous in its leaves. In contrast, the American species of *Agarista* have epidermal cells that are usually tall and with periclinal dividing walls, and a hypodermis of at most one or two cells (in cross section) near the larger veins. The vascular bundles of the midrib and petiole are unifacial, with very prominent bundle-associated fibers (Niedenzu, 1889; Stevens, 1970). The xylem anatomy has been studied by Cox (1948), who placed *A. salicifolia* in his tribe Cassiopeae and retained the species of *Agarista* sect. AGARISTA within the Andromedeae.

TAXONOMIC TREATMENT

Agarista D. Don ex G. Don, Gen. Syst. **3:** 837. 1834. *Leucothoë* D. Don sect. *Agastia* DC. Prodr. **7:** 603. 1839. *Leucothoë* D. Don subg. *Agarista* (D. Don ex G. Don) Drude *in* Engler & Prantl, Nat. Pflanzenfam. IV. **1:** 42. 1889. LECTOTYPE SPECIES: *Agarista nummularia* (Cham. & Schldl.) G. Don.

Leucothoë D. Don sect. *Agauria* DC. Prodr. **7:** 602. 1839. *Agauria* (DC.) J. D. Hooker *in* Bentham & Hooker, Gen. Pl. **2:** 586. 1876. LECTOTYPE SPECIES: *Agauria salicifolia* (Comm. ex Lam.) J. D. Hooker (= *Agarista salicifolia* (Comm. ex Lam.) G. Don).

Amechania DC. Prodr. **7:** 578. 1839. LECTOTYPE SPECIES: *Amechania subcanescens* DC. (= *Agarista chlorantha* (Cham.) G. Don).

Evergreen shrubs or trees with longitudinally furrowed bark and terete to slightly angled branches; pith *Calluna*-type [or slightly to very heterogeneous],[3] nonchambered to clearly chambered. Indumentum of unicellular hairs and often multicellular, multiseriate, long-stalked, gland-headed hairs. Buds conical or slightly flattened and triangular in outline, with 2 to 4 (to 6) imbricate scales. Leaves alternate (to subopposite or nearly 3-whorled at some nodes), simple, petiolate, revolute (or convolute) in bud, often reddish on young shoots, coriaceous, frequently with gland-headed hairs on midvein or along margin (rarely also on lamina), often with unicellular hairs on midvein (and densely covering abaxial surface) [sometimes papillose abaxially]; margin entire (or undulate, to obscurely to clearly serrate, or serrulate/ciliate due to presence of gland-headed hairs); venation reticulodromous, the vein reticulum rather dense and with all

[3]Characters given within brackets apply only to the African species, *A. salicifolia.*

orders more or less equally prominent; petiole vascular bundle unifacial. Inflorescences overwintering within bud with meiosis occurring after emergence, axillary (or terminal) racemes or panicles; flowers perfect, 5-merous, usually fragrant, in axil of small (to rarely large and foliaceous) bract, with 2 (rarely several), bracteoles at or near base to near midpoint of pedicel. Calyx of 5 imbricate lobes, articulate with pedicel, persistent in fruit; corolla cylindrical to urceolate, with 5 short, imbricate lobes, (greenish) white to red, glabrous to densely covered with unicellular hairs abaxially, glabrous adaxially; stamens 10, in 2 whorls, inserted at base of corolla, the filaments flattened, geniculate, with long unicellular hairs, somewhat expanded near base, lacking spurlike appendages, the anthers more or less ovoid, minutely papillose to nearly smooth, lacking apical awns, dehiscing by large, introrse-terminal, elliptic pores, with white line or triangular patch of disintegration tissue on back of each lobe near apex, the pollen tricolporate, in tetrahedral tetrads, without viscin strands; stigma truncate to capitate, obscurely 5-lobed, minutely papillose, the style columnar, slightly swollen [not swollen] near apex, straight, with 5-fluted central canal, slightly to strongly impressed into apex of ovary and usually slightly exserted, the ovary superior, 5-locular, glabrous to densely covered with unicellular hairs (very rarely with few gland-headed hairs), with the placentae axile, subapical to central [basal] on persistent columella, slightly bilobed, bearing numerous anatropous ovules; nectariferous disc an enlargement of base of ovary wall, variously developed and lobed. Capsules loculicidal, subglobose, short-ovoid to ovoid, sutures unthickened (or very slightly thickened near apex), but not separating from valves at dehiscence (margins of valves whitish), placentae persistent on columella. Seeds very small, brown, scobiform, the testa thin, composed of single layer of very much elongated, thin-walled cells; embryo small, straight, more or less allantoid, white, with 2 small cotyledons, central in cross section, surrounded by fleshy endosperm. Germination epigeal(?). $2n = 24$ (*Agarista populifolia*).

The name *Agarista* is taken from Greek mythology—the beautiful daughter of Clisthenes—in reference to the beauty of the flowers (see G. Don, 1834).

DISTRIBUTION. South America—southeastern Brazil (from Bahia and Goiás south to Rio Grande do Sul), Uruguay, northeastern Argentina, and Paraguay, along Andes from Bolivia and northern Peru to Colombia, mountains of southern Venezuela and adjacent Brazil (Pará); Central and North America—mountains of El Salvador and Honduras north to Mexico (Hidalgo, México, Jalisco), and on United States Atlantic Coastal Plain (from Florida to South Carolina); MAP 1. Also in central Africa, Madagascar, Réunion, and Mauritius (Sleumer, 1938, *fig. 1*).

NUMBER OF SPECIES (TAXA): 30 (55).

MEASUREMENTS AND TERMINOLOGY

All measurements (except plant height, which was taken from information included on specimen labels or recorded in the field) included in the descriptions of species have been taken directly from dried herbarium material. The width

of the calyx lobes was measured midway between the apex and the point where they join the adjacent lobes; the width of all other structures was measured at the widest point. The values for inflorescence length refer to the range of variation in the longest inflorescence per specimen (and were determined by surveying total available herbarium material).

As used here, "glabrous" and "pubescent" refer to the presence or absence of unicellular hairs; the presence, distribution, and density of multicellular, gland-headed hairs are described separately.

SPECIMENS EXAMINED

In the citation of specimens, abbreviations of institutions follow the seventh edition of *Index Herbariorum* (Holmgren, Keuken, & Schofield, 1981). In order to conserve space, only selected specimens have been cited. The locations of types cited but not seen have been taken from Sleumer (1959).

KEY TO THE SECTIONS AND SPECIES OF AGARISTA

1. Leaves with abaxial epidermis papillose; capsules with placentae basal; [Africa]; (sect. AGAURIA). . . . . [30.] *A. salicifolia* (for key to infraspecific taxa, see Sleumer, 1938).
1. Leaves with abaxial epidermis nonpapillose; capsules with placentae subapical to central; [Americas]; (sect. AGARISTA).
   2. Leaves moderately to strongly adaxially folded.
      3. Leaves 0.6–2.5(–3) cm wide, narrowly to widely ovate, petiole 10–32 mm long. . . . . 27. *A. glaberrima.*
      3. Leaves 0.1–0.5 cm wide, ± linear, petiole 2–13 mm long.
         4. Stems glabrous; inflorescences axillary or terminal racemes or panicles to 3–6 cm long, axis glabrous; leaves (1.7–)3–7 cm long. . . . . 28. *A. angustissima.*
         4. Stems glabrous to densely pubescent; inflorescences axillary racemes to 0.3–1.5 cm long, axis very slightly to densely pubescent; leaves 1.2–3.5(–4) cm long. . . . . 29. *A. duartei.*
   2. Leaves plane to strongly revolute, always revolute in bud.
      5. Petiole slender, flexuous, elongate, 6–40 mm long.
         6. Inflorescence axis glabrous; capsules 4–8 by 6–8 mm; leaves often slightly adaxially folded. . . . . 27. *A. glaberrima.*
         6. Inflorescence axis moderately to densely pubescent; capsules 3–5 by 4–6.5 mm; leaves ± flat.
            7. Leaves ovate; inflorescence axis with whitish hairs. . . . . 25. *A. boliviensis.*
            7. Leaves oblong to ovate; inflorescence axis with ferrugineous hairs. . . . . 26. *A. eucalyptoides.*
      5. Petiole stout and/or short, not flexuous, 0.5–15(–18) mm long.
         8. Leaves 0.4–2.5(–3.5) by 0.1–1.6(–2) cm.
            9. Leaf margin ± plane (to very slightly revolute, especially near base), lamina ± flat.
               10. Inflorescence axis glabrous.
                  11. Leaf blade with length/width quotient > 1.8; corolla 7.5–13 mm long; filaments 5–6.5 mm long. . . . 16. *A. pulchella.*
                  11. Leaf blade with length/width quotient < 1.8; corolla 6–8.5 mm long; filaments 3.5–5 mm long.
                     12. Multicellular, gland-headed hairs present on leaves and twigs; branches rigidly ascending and wandlike, with internodes usually to only ca. 0.5 cm long; leaves 0.4–1.3 cm wide. . . . . 18. *A. virgata.*
                     12. Multicellular, gland-headed hairs lacking; plants ± widely to erectly branched, with internodes usually to 0.5–2 cm long; leaves 0.8–2.2 cm wide. . . . . 10. *A. pulchra.*
               10. Inflorescence axis sparsely to densely pubescent.
                  13. Abaxial leaf surface ± densely pubescent. . . . . 11. *A. subrotunda.*
                  13. Abaxial leaf surface ± glabrous (but often with few unicellular hairs on midvein).
                     14. Sepals 2.5–5 mm long. . . . . 17. *A. nummularia.*
                     14. Sepals 0.8–2.7 mm long.

15. Capsules with placentae ± central.
    16. Inflorescence axis to 0.5–1.5(–2.5) cm long; leaf blade with length/width quotient usually > 3, cuneate to truncate at base. ..... 15. *A. minensis.*
    16. Inflorescence axis to 2–7(–12) cm long; leaf blade with length/width quotient usually < 3, cordate to rounded at base. ..... 16. *A. pulchella.*
15. Capsules with placentae ± subapical.
    17. Hairs of inflorescence axis to (0.15–)0.2–0.4 mm long, straight to curved. ..... 1. *A. albiflora.*
    17. Hairs of inflorescence axis to 0.05–0.15(–0.17) mm long, curved.
        18. Leaves cuneate to rounded at base; inflorescence axis usually 1.5–3.5 cm long. . . 23. *A. niederleinii.*
        18. Most leaves at least slightly cordate at base; inflorescence axis usually 2–28 cm long.
            19. Stems moderately to densely pubescent; inflorescence axis to (1.5–)2–5.5 cm long. ..... 16. *A. pulchella.*
            19. Stems glabrous to sparsely pubescent; inflorescence axis to 4–28 cm long.
                20. Petioles 1–2.5 mm long, lamina lacking prominent abaxial glands along midvein, margin usually at least slightly undulate and frequently very slightly revolute; [Peru]. ..... 2. *A. subcordata.*
                20. Petioles 1.5–6 mm long, lamina without above combination of characters, with or without conspicuous abaxial glands, margin usually plane; [SE Brazil].
                    21. Leaf blades with length/width quotient (1.5–)1.8–2.5, prominent abaxial glands present along midvein; inflorescence axis moderately to densely pubescent. . . . 9. *A. coriifolia.*
                    21. Leaf blades with length/width quotient 0.9–1.7, usually lacking prominent abaxial glands; inflorescence axis very sparsely to moderately pubescent. ..... 10. *A. pulchra.*

9. Leaf margin slightly to strongly revolute and/or lamina slightly to clearly abaxially curved.
    22. Corolla very sparsely to densely pubescent abaxially.
        23. Calyx lobes 2–5.5 mm long; corolla abaxially sparsely to densely pubescent; seeds ca. 0.6–1.5 mm long; erect shrub 1–2.5 m tall, of inland habitats. ..... 21. *A. hispidula.*
        23. Calyx lobes 0.9–1.6 mm long; corolla abaxially with very few unicellular hairs near apex (or glabrous); seeds ca. 2–3.5 mm long; shrub or gnarled tree to 3(–6) m tall, of coastal scrub. ..... 5. *A. revoluta.*
    22. Corolla glabrous abaxially.
        24. Capsules with placentae ± central; leaves 0.1–0.25 cm wide. ..... 22. *A. ericoides.*
        24. Capsules with placentae ± subapical; leaves 0.15–2.2 cm wide.
            25. Flowers solitary in leaf axils or borne on fasciclelike racemes to 1.5 cm long; plants lacking gland-headed hairs; calyx lobes 1–2 mm long; [Serra dos Orgãos]. ..... 20. *A. organensis.*

25. Flowers in axillary (rarely terminal) racemes to (1–)1.5–9.5 cm long; plants with or without gland-headed hairs; calyx lobes variable; [not of the Serra dos Orgãos].
    26. Calyx lobes 2.5–5.5 mm long; corolla 7–11.5 mm long; leaves clearly cordate at base; inflorescence axis and pedicels with or without gland-headed hairs. ..... 19. *A. chlorantha.*
    26. Calyx lobes 0.5–2.7 mm long; corolla 4.5–9 mm long; leaves cuneate to rounded or slightly cordate at base; inflorescence axis and pedicels lacking gland-headed hairs.
        27. Leaves 0.4–2.2 cm wide, with margins revolute frequently to varying degrees even within single plant; valves of mature capsules frequently ± whitish bordered; capsules ovoid to globose or subglobose; [coastal "restingas"]. ..... 5. *A. revoluta.*
        27. Leaves 0.25–1.3 cm wide, with margins more uniformly revolute within single plant; valves of capsules not obviously bordered; capsules subglobose or short-ovoid; [mountainous habitats].
            28. Capsules robust, 4.5–6.5 by 6.5–8.5 mm; inflorescence axis to 1.5–3.5(–4.5) cm long; [SE Brazil]. .. .. 23. *A. niederleinii.*
            28. Capsules smaller, 4–5 by 4.5–6 mm; inflorescence axis to 5–10 cm long; [Peru].
                29. Leaves 0.25–0.7 by 0.8–1.5 cm, lamina ± strongly revolute, pedicel 1.5–3 mm long. .... 3. *A. bracamorensis.*
                29. Leaves 0.6–1.3 by 1.2–3.1 cm, lamina plane to slightly revolute, pedicel 3.5–7 mm long. .... 2. *A. subcordata.*

8. Leaves 1.5–11.2 by 0.3–4.5(–5) cm.
    30. Lamina clearly to strongly revolute, slightly to strongly abaxially curved.
        31. Inflorescence axis to 0.7–1.5 cm long; leaf apex short-acuminate to elongate-mucronate, mucro usually to 1.5–2 mm long; [Venezuela; Pará and Mato Grosso, Brazil]. ..... 4. *A. duckei.*
        31. Inflorescence axis to 1.5–10 cm long; leaf apex acute- to rounded-mucronate, mucro usually to only 1 mm long.
            32. Leaf apex obtuse- to retuse-mucronate; valves of mature capsules often ± white bordered; [coastal "restingas," E Brazil]. ..... 5. *A. revoluta.*
            32. Leaf apex acute- to obtuse-mucronate; valves of capsules ± unbordered; [mountainous habitats, northern Andes]. .. .. 1. *A. albiflora.*
    30. Lamina plane to only very slightly revolute, ± flat.
        33. Abaxial leaf surface ± densely covered with unicellular hairs, at least parts of surface completely obscured.
            34. Capsules with placentae ± central; seeds 0.9–1.8 mm long; pith ± solid to hollow, often with very sparse, thin septa; [Paraguay, Argentina]. ..... 13. *A. paraguayensis.*
            34. Capsules with placentae ± subapical; seeds 1.3–3 mm long; pith ± solid to irregularly chambered, the septa thick to thin, closely spaced.

35. Inflorescence axis to 0.5–2(–4) cm long; leaves ovate, apex acuminate; [Mexico and Central America]. ..... 6. *A. mexicana.*
35. Inflorescence axis to 4–7 cm long; leaves ovate to elliptic or oblong, apex acute- to retuse-mucronate; [E Brazil].
    36. Leaf base cordate; pedicels 5–12.5 mm long. ..... 11. *A. subrotunda.*
    36. Leaf base rounded to cuneate; pedicels 3–7 mm long. ..... 12. *A. chapadensis.*

33. Abaxial leaf surface lacking unicellular hairs to ± sparsely pubescent, surface not obscured.
    37. Capsules with placentae ± central; seeds 0.5–1.5 mm long.
        38. Corolla very sparsely to sparsely pubescent; pith ± solid to hollow or with very sparse, thin septa; [Paraguay, Argentina]. ..... 13. *A. paraguayensis.*
        38. Corolla glabrous; pith ± solid to irregularly or clearly chambered, the septa thin to thick, ± closely spaced; [SE Brazil].
            39. Inflorescence axis to 0.5–1.5 cm long; leaves 0.3–1(–1.7) cm wide, length/width quotient usually > 3, ± straight sided, base cuneate to truncate, apex rounded- to bluntly acute-mucronate (never narrowly acute), petiole 2–6 mm long. ..... 15. *A. minensis.*
            39. Inflorescence axis to 2–12 cm long; leaves various, but without above combination of characters.
                40. Leaves ± ovate, 1.2–4.5(–5) cm long, margin usually convex-curved when viewed from above, base ± cordate, petiole 1.5–5 mm long.
                    41. Lamina with abaxial glands lacking or very inconspicuous along midvein near base, thinly coriaceous and flexible when dry; [Paraná, Santa Catarina, São Paulo]. ..... 16. *A. pulchella.*
                    41. Lamina with prominent abaxial glands along midvein near base, thickly coriaceous and quite inflexible when dry; [Minas Gerais].
                        42. Inflorescence axis ± moderately pubescent. ..... 9. *A. coriifolia.*
                        42. Inflorescence axis glabrous. ..... 10. *A. pulchra.*
                40. Leaves ovate to elliptic or oblong, 2–12.5 cm long, margin often ± straight when viewed from above, base cuneate to slightly cordate, petiole 2–11.5 mm long. ..... 14. *A. oleifolia.*
    37. Capsules with placentae ± subapical; seeds 1–3.2 mm long.
        43. Inflorescence axis usually moderately to densely covered with ferrugineous unicellular hairs. ..... 26. *A. eucalyptoides.*
        43. Inflorescence axis glabrous to densely pubescent, hairs not ferrugineous.
            44. Inflorescence axis to 0.5–3 cm long.
                45. Leaves uniformly ovate, apex acuminate.
                    46. Leaf margin conspicuously crisped/undulate. ..... 25. *A. boliviensis.*
                    46. Leaf entire to serrate, margin not conspicuously crisped/undulate.

47. Capsules (3–)4–6 mm long, with thickened, ± warty/roughened walls; [SE Brazil]. ..... 24. *A. uleana.*
47. Capsules 3–4.5 mm long, with thin, ± smooth walls; [North and Central America].
    48. Ovary very sparsely to densely pubescent; pith nonseptate to septate; bark prominently and deeply furrowed, corky. ..... 6. *A. mexicana.*
    48. Ovary glabrous; pith always clearly septate; bark variable.
        49. Calyx glabrous on abaxial surface; pedicels glabrous; corolla 8.5–13 mm long; leaves entire; bark furrowed, corky; [Mexico]. ..... 7. *A. sleumeri.*
        49. Calyx sparsely to moderately pubescent on abaxial surface; pedicels sparsely to moderately pubescent; corolla 6.5–9.5 mm long; leaves entire or serrate; bark very shallowly furrowed, not corky; [SE United States]. ..... 8. *A. populifolia.*

45. Leaves of single plant varying from ovate to elliptic or oblong (rarely obovate), apex acute- or rounded-mucronate to acuminate.
    50. Capsules roughened/warty; leaves with apex acute- or rounded-mucronate to acuminate, margin convex-curved to ± straight when viewed from above; [SE Brazil].
        51. Leaves ovate to elliptic (rarely oblong), margin very slightly revolute from base to near apex; [Guanabara, Rio de Janeiro]. ..... 24. *A. uleana.*
        51. Leaves ovate to elliptic/oblong, usually at least few per plant ± parallel sided, margin plane to very slightly revolute at base only; [Rio Grande do Sul to Paraná]. ..... 23. *A. niederleinii.*
    50. Capsules ± smooth; leaves with apex elongate-mucronate to short-acuminate, margin convex-curved when viewed from above; [chiefly N South America]. ..... 4. *A. duckei.*

44. Inflorescence axis to 3–15 cm long.
    52. Inflorescence axis with hairs to 0.15–0.4 mm long, straight to curved; calyx lobes 0.7–1.8 mm long; corolla (3.7–)4–9 mm long; leaves thinly coriaceous, flexible when dry; [N Andes]. ..... 1. *A. albiflora.*
    52. Inflorescence axis glabrous or with hairs to 0.05–0.15 mm long, curved; calyx lobes 1–2.7 mm long; corolla 6.5–11 mm long; leaves thickly coriaceous, rather inflexible when dry; [SE Brazil]. ..... 9. *A. coriifolia.*

Agarista D. Don ex G. Don sect. **Agarista**

Leucothoë D. Don sect. *Agastia* DC. Prodr. 7: 603. 1839. *Leucothoë* D. Don subg. *Agarista* (D. Don ex G. Don) Drude *in* Engler & Prantl, Nat. Pflanzenfam. **4**(1): 42. 1889. LECTOTYPE SPECIES: *Agarista nummularia* (Cham. & Schldl.) G. Don.

Agarista D. Don ex G. Don sect. *Leucothoides* Niedenzu, Bot. Jahrb. **11:** 186. 1890. LECTOTYPE SPECIES: *Agarista serrulata* (Cham.) G. Don (= *Agarista chlorantha* (Cham.) G. Don).

Agarista D. Don ex G. Don sect. *Euagarista* Niedenzu, Bot. Jahrb. **11:** 186. 1890, nomen illegit.

Twigs with nonchambered to clearly chambered, *Calluna*-type pith. Leaves with abaxial epidermis nonpapillose, adaxial epidermis usually tall with divided cells (see Stevens, 1970). Style usually swollen toward apex. Capsules with placentae subapical to ± central; seeds 0.5–3(–3.5) mm long.

NUMBER OF SPECIES (TAXA): 29 (35).

1. **Agarista albiflora** (B. Fedtsch. & Basilevsk.) Judd, comb. nov.

FIGURE 2, d.

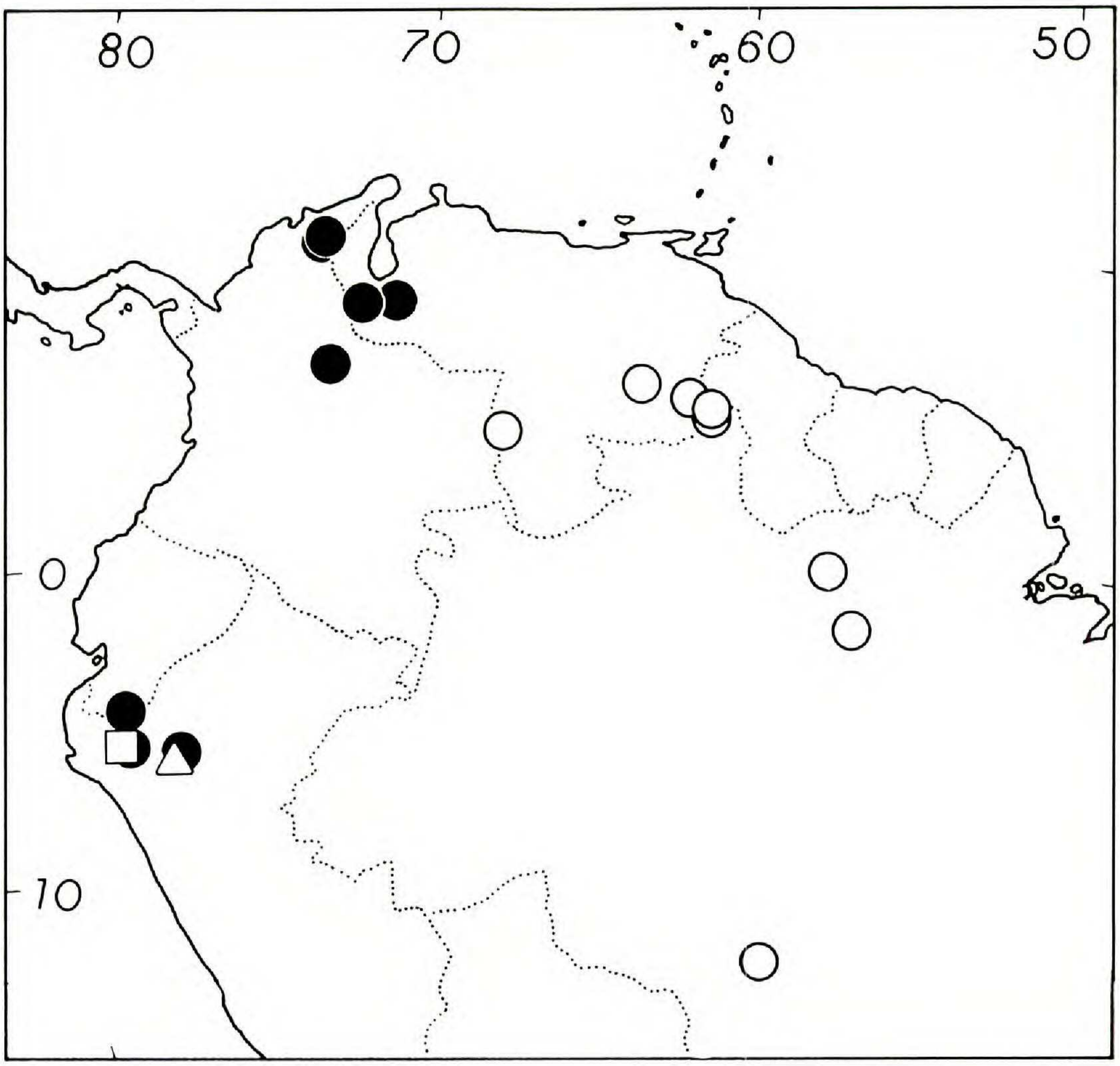
Leucothoë albiflora B. Fedtsch. & Basilevsk. Not. Syst. Herb. Hort. U.S.S.R. **6:** 23. 1926. TYPE: Colombia, Boyacá, near Soatá, April 1843, *Linden 1322* (holotype, LE; isotypes, BR, F!, G, K!, NY!, P!, US!, W).

Leucothoë columbiana Sleumer, Notizbl. Bot. Gart. Berlin **12:** 479. 1935. TYPE: Colombia, Magdalena, Sierra Nevada de Santa Marta, "El Manon," ca. 2100 m alt., 26 Feb. 1928, *Schultze 1113* (holotype, B (destroyed)).

Leucothoë andina Sleumer, *ibid.* 478. TYPE: Peru, Amazonas, Pipos, E of Chachapoyas, 2000 m alt., 19 July 1904, *Weberbauer 4362* (holotype, B (destroyed); isotypes, NY(fragment)!, USM).

Shrub to 3 m tall. Twigs with or without scattered gland-headed hairs, otherwise moderately pubescent, with ± nonchambered pith. Buds to ca. 1.5 mm long. Leaves alternate; petiole 2–8 mm long; blade revolute in bud, ovate to elliptic, 1.6–7 by 0.8–2.7 cm, flat to slightly (strongly) abaxially curved, coriaceous, the apex acute- to rounded-mucronate, the base widely cuneate to cordate, the margin entire (slightly undulate), plane to very slightly (strongly) revolute, the adaxial surface with or without gland-headed hairs on midvein, otherwise sparsely to moderately pubescent on midvein (also sparsely pubescent on lamina and along margin), the abaxial surface with or without gland-headed hairs on midvein, otherwise very sparsely to moderately pubescent on midvein, usually with few to many inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 3–10 cm long, the axis with or without scattered gland-headed hairs, otherwise sparsely to moderately pubescent. Pedicels 2–7.5 mm long, with or without gland-headed hairs, otherwise moderately pubescent; bracteoles 2, opposite to subopposite, basal or nearly so, narrowly triangular, to ca. 0.8 mm long; bracts to 1 mm long. Calyx lobes triangular with acuminate apices, 0.7–1.8 by 0.6–1.1 mm, abaxial surface sparsely to moderately pubescent; corolla cylindrical to urceolate-cylindrical, 4–9 by 2–3.5 mm, white (red tinged at tip, or red), abaxially glabrous; filaments 2.5–5 mm long, anthers 1–1.5 mm long; ovary sparsely to densely pubescent. Capsules

FIGURE 2. a, b, *Agarista mexicana* var. *pinetorum:* a, *Williams & Molina 14000*; b, *Villarreal de Puga 4761,* abaxial leaf surface light due to dense layer of unicellular hairs. c, *A. revoluta* (*Rose & Russell 20687*). d, *A. albiflora* (*Jorgensen & Prieto JP-55*). Scale = 2 cm.



MAP 2. Distribution of *Agarista albiflora* (dots), *A. subcordata* (triangle), *A. bracamorensis* (square), and *A. duckei* (circles).

subglobose to short-ovoid, 3–5.5 by 4–7.5 mm, placentae subapical; seeds 1.5–2 mm long.

DISTRIBUTION AND ECOLOGY. Northern Andes from Venezuela and Colombia south to Peru (MAP 2). Moist montane forests, dwarf forests, rocky areas with scattered shrubs; 1800–2500 m alt. Flowering April to September.

REPRESENTATIVE SPECIMENS. **Colombia.** BOYACÁ: Villa de Leiva, La Candelaria, *Cleef 359* (L). MAGDALENA: San Sebastian de Rabago, *Romero-Castañeda 867* (COL). **Venezuela.** MÉRIDA: San Antonio, *Jahn 1086* (US); Pueblo Nuevo, *López-Palacios 768* (NY). TÁCHIRA: above La Grita, slopes below Páramo de la Negra, *Steyermark 57108* (A, F). **Ecuador.** LOJA: Hacienda Guaycopamba on Río Guaycopamba, 22 km S of Vilcabamba, *Fosberg & Giler 23072* (COL, NY, US); W slope of Cordillera Condor, Huilcabamba, NW of Nudo de Sabinilla, 54 km S of Loja, *Jorgensen & Prieto Jp-55* (FLAS, NY, S). **Peru.** CAJAMARCA: Jaén, El Parco, *Friedberg 665* (L).

Agarista albiflora, a taxon that is rather variable in leaf size and shape, and in the degree to which the margins are revolute, is probably most closely related to *A. subcordata* and *A. bracamorensis.* It can be distinguished from the former

by its often larger leaves and its inflorescence axes with usually elongated, straight to curled, unicellular hairs, and from the latter by its much larger, usually nonrevolute leaves and its often longer pedicels. *Agarista albiflora* may also be confused with *A. revoluta* and *A. duckei*, or *A. mexicana*, *A. sleumeri*, and *A. populifolia* (see key for distinguishing characters).

Agarista albiflora and *A. subcordata* may be slightly sympatric since both have been collected in the Chachapoyas region; the mechanisms isolating these two very similar species are in need of field study.

2. **Agarista subcordata** (Dunal) Judd, comb. nov.

Gaylussacia subcordata Dunal *in* DC. Prodr. **7:** 557. 1839. *Leucothoë subcordata* (Dunal) Sleumer, Bot. Jahrb. **78:** 461. 1959. TYPE: Peru, Amazonas, Chachapoyas, *Matthews s.n.* (holotype, G; fragment and photo of holotype, F!; isotypes, E!, K!, S!).

Shrub. Twigs sparsely to very sparsely pubescent, with ± nonchambered pith. Buds to ca. 1.8 mm long. Leaves alternate; petiole 1–2.5 mm long; blade revolute in bud, ovate to elliptic, 1–3.1 by 0.6–1.3 cm, flat to slightly abaxially curved, coriaceous, the apex acute- to rounded-mucronate, the base rounded to slightly cordate, the margin entire (slightly undulate), the adaxial surface glabrous to sparsely pubescent on midvein, the abaxial surface glabrous to sparsely pubescent on midvein, often with few to several inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 5–10 cm long, axis sparsely to moderately pubescent. Pedicels 3.5–7 mm long, sparsely to moderately pubescent; bracteoles 2, at or near base to within lower ⅓ of pedicel, narrowly triangular, to ca. 1.1 mm long; bracts to 1.5 mm long. Calyx lobes triangular with acuminate apices, 1–1.5 by 0.9–1.5 mm, the abaxial surface glabrous to very sparsely pubescent, especially near base; corolla cylindrical to urceolate-cylindrical, 6–7.5 by 3–3.5 mm, white, abaxially glabrous; filaments ca. 3.5 mm long, anthers ca. 1.3 mm long; ovary glabrous to very sparsely pubescent near apex. Capsules subglobose to short-ovoid, 4–5 by 5.5–6.5 mm, placentae subapical; seeds not seen.

DISTRIBUTION. Andes, endemic to Chachapoyas region of northern Peru, ca. 2700 m alt. (MAP 2).

REPRESENTATIVE SPECIMENS. **Peru.** AMAZONAS: Chachapoyas, Guancas, *Matthews 1635* (E, GH, K, P); Chachapoyas, *Williams 7549* (F).

The poorly known *Agarista subcordata* is probably closely related to both *A. albiflora* and *A. bracamorensis*. All three taxa are limited to the northern Andes, but *A. albiflora* is by far the most widely distributed. *Agarista subcordata* can be readily distinguished from *A. albiflora* by its often smaller leaves and its inflorescence axis with short, curled hairs, and from *A. bracamorensis* by its wider, less strongly revolute leaves and its longer pedicels.

3. **Agarista bracamorensis** (Humb., Bonpl., & Kunth) G. Don, Gen. Syst. **3:** 837. 1834.

Andromeda bracamorensis Humb., Bonpl., & Kunth, Nov. Gen. Sp. Pl. **3:** 225. *t. 263.* 1818. *Leucothoë bracamorensis* (Humb., Bonpl., & Kunth) DC. Prodr. **7:** 603. 1839.

TYPE: Peru, Cajamarca, prov. Bracamora, near S. Felipe and Páramo de Yamoca, ca. 2350 m, *Bonpland 3564* (holotype, P!; fragment and photo of holotype, F!).

Shrub or small tree. Twigs sparsely pubescent, with obscurely chambered pith. Buds to ca. 0.5 mm long. Leaves alternate; petiole 1.5–4 mm long; blade revolute in bud, ovate, 0.8–1.5 by 0.25–0.7 cm, moderately abaxially curved, coriaceous, the apex acute-mucronate, the base rounded, the margin entire, strongly revolute, the adaxial surface sparsely pubescent on midvein, the abaxial surface essentially glabrous, often with few inconspicuous glandular dots along midvein. Inflorescences axillary racemes to ca. 5 cm long, axis sparsely to moderately pubescent. Pedicels 1.5–3 mm long, sparsely to moderately pubescent; bracteoles 2, opposite, nearly basal, narrowly triangular, to ca. 0.6 mm long; bracts to 1 mm long. Calyx lobes triangular with acute to acuminate apices, 0.5–1.5 by 0.4–0.6 mm, abaxial surface glabrous; corolla ± cylindrical, 4.5–6 by 2–3.5 mm, white, abaxially glabrous; filaments ca. 3.5 mm long, anthers ca. 1.3 mm long; ovary glabrous. Capsules short-ovoid, 4–4.5 by 4.5–5.5 mm, placentae subapical; seeds ca. 1.5–2 mm long.

DISTRIBUTION. Andes, northern Peru, Bracamora region, ca. 2350 m alt. (MAP 2).

REPRESENTATIVE SPECIMENS. Known only from type collection.

This rare and little-known species is probably closest to *Agarista albiflora* and *A. subcordata*, two other Andean species. It is readily separated from these allies by its very small, strongly revolute leaves. It is also superficially similar to the revolute-leaved Brazilian species *A. organensis*, *A. chlorantha*, *A. hispidula*, and *A. ericoides* but is quickly distinguished from all of them by its combination of round-based leaves, short pedicels, and short calyx lobes.

4. **Agarista duckei** (Huber) Judd, comb. nov.

Leucothoë duckei Huber, Bull. Soc. Bot. Genève, II. **1:** 246. *fig. 1.* 1909. TYPE: Brazil, Pará, in campis arenosis ad ripam orient. fl. Yamundá, pr. Faro, 27 Aug. 1907, *Ducke 8526* (holotype, MG; fragment and photo of holotype, F!; isotype, G-Boiss.).
Leucothoë venezuelensis A. C. Smith, Contr. U. S. Natl. Herb. **29:** 335. 1950. TYPE: Venezuela, Bolívar, Gran Sabana, Cerro Akurimá, 20 March 1946, *Tamayo 3236* (holotype, US!; photo of holotype, NY!; isotype, F!).

Shrub to tree to 6 m tall, with roughly furrowed bark. Twigs sparsely to densely pubescent, with nonchambered pith. Buds to ca. 1.5 mm long. Leaves alternate; petiole 2–6(–7) mm long; blade revolute in bud, elliptic to slightly ovate (obovate), (1.5–)2–5.7 by 0.5–2.1 cm, nearly flat to strongly abaxially curved, coriaceous, the apex elongate-mucronate to short-acuminate, the base narrowly to widely cuneate or rounded, the margin entire, plane to strongly revolute, the adaxial surface sparsely pubescent on midvein, especially proximal portion (with few scattered hairs on proximal portion of lamina), the abaxial surface sparsely to moderately pubescent on midvein, with few to several very inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 0.5–1.5 cm long, axis densely pubescent. Pedicels 2.5–12 mm

long, moderately to densely pubescent; bracteoles 2, alternate, from nearly basal to within lower ⅓ of pedicel, triangular to narrowly so, to ca. 1.2 mm long; bracts to 1.2 mm long. Calyx lobes triangular with acuminate apices, 0.9–2.3 by 0.7–1 mm, abaxial surface moderately to densely pubescent; corolla urceolate to cylindrical, 6–8 by 3–4.5 mm, white (rarely pink), abaxially glabrous; filaments 3.5–4.7 mm long, anthers 0.9–1.1 mm long; ovary sometimes with scattered gland-headed hairs, otherwise sparsely to densely pubescent. Capsules ovoid to globose or subglobose, 5–6 by 6–8 mm, valves rarely white bordered, placentae subapical; seeds 1.5–3 mm long.

DISTRIBUTION AND ECOLOGY. Southern Venezuela and western Pará and Mato Grosso, Brazil (MAP 2). Thickets and forests on sand, open sandy areas, bush forest and savannas on white sand, river and lake margins, rocky slopes and plateaus; ca. 100–1400 m alt. Flowering May through August (October and December).

REPRESENTATIVE SPECIMENS. **Brazil.** MATO GROSSO: Sararé, Radambrasil, *Pires & Santos 16397* (FLAS, NY). PARÁ: E of Faro, *Ducke 5708* (NY, P, S, US; photos, F, GH); Monte Alegre, Alto de Serra do Ereré, *Lima 53-1609* (K). **Venezuela.** AMAZONAS: Sabanito Morocoto, right bank of Río Orinoco, 2 km below mouth of Río Atabapo, *Wurdack & Adderley 42692* (F, GH, NY, UC, US, VEN). BOLÍVAR: Gran Sabana, Canaima Lagoon, Avensa Camp, *Ehrendorfer 74103-1b* (VEN); Canaima, *López-Palacios 3029* (L, NY); Canaima, between hotel and airport, *Steyermark 106370* (F, MO, NY, VEN); Carretera El Dorado to Santa Elena de Uairén, km 198 S of El Dorado, plateau above Lamá-merú, *Steyermark et al. 106642* (VEN); top of rocky slope, *Steyermark et al. 106634* (NY).

The closest relative of *Agarista duckei* seems to be the geographically separated *A. revoluta* (see MAP 5). The strong similarities between the two species were also noted by Sleumer (1959). In both species the leaf blade is often strongly to moderately abaxially curved. *Agarista duckei* is readily distinguished from *A. revoluta* by its shorter inflorescences, its short-acuminate to elongate-mucronate leaf apices, and its usually white flowers. *Agarista duckei* is also related to (and may sometimes be confused with) the Andean species *A. albiflora*; see key for distinguishing characters.

Albert C. Smith (1950) distinguished *Leucothoë venezuelensis* (populations in Venezuela) from *L. duckei* (populations in state of Pará, Brazil) on the bases of petiole length, leaf shape and base, calyx-lobe apex, and corolla shape. However, the variation in these characters is so slight that separating the plants into two species is quite arbitrary. Thus, the two are considered to be conspecific. The large disjunction separating the Mato Grosso population from similar plants in southern Venezuela is puzzling. Additional localities probably exist; more collecting is evidently needed.

The pollen morphology of this species (Venezuelan populations) has been studied by Maguire, Steyermark, and Luteyn (1978).

5. **Agarista revoluta** (Sprengel) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11**: 236. 1889.

Shrub or small and often gnarled tree to 3(–6) m tall, with roughly furrowed bark. Twigs sparsely to densely pubescent, with nonchambered pith. Buds to

ca. 1.1 mm long. Leaves alternate; petiole 2–7 mm long; blade revolute in bud, ovate to elliptic, 1.3–4.5 by 0.5–2.2 cm, slightly to strongly abaxially curved (rarely nearly flat), coriaceous, the apex obtuse- to retuse-mucronate (rarely acute-mucronate), the base rounded (to very slightly cordate), the margin entire, slightly to strongly revolute, the adaxial surface sparsely to moderately pubescent on proximal portion of midvein (with few hairs on adjacent portion of lamina); abaxial surface sparsely pubescent on midvein or only on proximal portion, or densely pubescent on lamina and midvein, with few inconspicuous glandular dots along midvein. Inflorescences axillary racemes to (1–)1.5–6.5 cm long, axis moderately to densely pubescent. Pedicels 3–11 mm long, sparsely to densely pubescent; bracteoles 2, opposite to alternate, from basal to near midpoint of pedicel, narrowly triangular, to ca. 1 mm long; bracts to 1.3 mm long. Calyx lobes triangular with acuminate apices, 0.9–1.6 by 0.6–1.5 mm, abaxial surface sparsely to densely pubescent; corolla ± cylindrical, 6–9 by 3.5–5 mm, red to white, abaxially glabrous or with very few unicellular hairs near apex to moderately pubescent; filaments 4.5–5.5 mm long, anthers 1–1.2 mm long; ovary very sparsely to densely pubescent. Capsules ovoid to short-ovoid or subglobose, 4–5.5 by 5–7 mm, valves often slightly white bordered, placentae subapical; seeds 2–3.5 mm long.

DISTRIBUTION. Southeastern Brazil, along coast from Bahia south to Estado do Rio.

KEY TO THE VARIETIES OF AGARISTA REVOLUTA

1. Abaxial surface of lamina glabrous, but sparsely pubescent on midvein, especially proximal portion; corolla glabrous or with very few unicellular hairs near apex. . . . . 5a. var. *revoluta*.
1. Abaxial surface of lamina densely pubescent; corolla moderately pubescent, especially near apex. . . . . 5b. var. *velutina*.

5a. **Agarista revoluta** (Sprengel) J. D. Hooker ex Niedenzu var. **revoluta**

FIGURE 2, C.

Andromeda revoluta Sprengel, Neue Entdeck. **2:** 131. 1821. *Agarista sprengelii* G. Don, Gen. Syst. **3:** 837. 1834, nomen superfl. *Leucothoë revoluta* (Sprengel) DC. Prodr. **7:** 604. 1839. *Leucothoë revoluta* (Sprengel) DC. var. *sellowii* Meissner *in* Martius, Fl. Brasil. **7:** 160. 1863, nomen superfl. TYPE: Brazil, Estado do Rio, Restinga de Cabo Frio, *Sellow s.n.* (holotype, B (destroyed); isotype at B! selected as lectotype; remaining isotypes, BM!, BR, E!, G, K!, L!, M!, P!, W; photos of isotype, F!, G, GH!).

Andromeda crassifolia Nees, Flora **4:** 297. 1821. TYPE: Brazil, Estado do Rio, Cabo Frio, *Neuwied 13, 14* (not seen, probably at BR, GOET; see Sleumer, 1959).

Leucothoë bahiensis DC. var. *salzmannii* DC. Prodr. **7:** 604. 1839 (= *L. bahiensis* var. *bahiensis*; chosen as nominate variety by Sleumer, 1959). *Leucothoë revoluta* (Sprengel) DC. var. *salzmannii* (DC.) Meissner *in* Martius, Fl. Brasil. **7:** 160. 1863. TYPE: Brazil, Bahia, 1830, *Salzmann 314* (lectotype, G; isolectotypes, NY(fragment)!, P!; unnumbered Salzmann collections, possible isolectotypes, G, GH!, K!, MO!; photos of unnumbered Salzmann collection, F!, G, GH!).

Leucothoë bahiensis DC. var. *blanchetii* DC. Prodr. **7:** 604. 1839. *Leucothoë revoluta* (Sprengel) DC. var. *blanchetii* (DC.) Meissner *in* Martius, *ibid.* TYPE: Brazil, Bahia, Monte Cerrato, *Blanchet 1680* (holotype, G; isotypes, F!, K!, P!, W).

Andromeda nitida Vell. Conc. Fl. Flum. 174. 1825, a later homonym of *A. nitida* Bartram ex Marsh. Arbust Am. 8. 1785 = *Lyonia lucida* (Lam.) K. Koch. *Leucothoë bahiensis* DC. var. *arrabidae* DC. Prodr. **7:** 604. 1839. *Leucothoë revoluta* (Sprengel) DC. var. *arrabidae* (DC.) Meissner *in* Martius, Fl. Brasil. **7:** 160. 1863. TYPE: lectotype here designated as illustration in Vell. Conc. Fl. Flum. ic. **4:** *t. 94.* 1835.

Twigs sparsely to densely pubescent. Leaves with adaxial surface sparsely pubescent on proximal portion of midvein; abaxial surface sparsely pubescent on midvein, especially proximal portion, otherwise glabrous. Pedicels 3–8.5 mm long, sparsely to densely pubescent. Calyx lobes with abaxial surface sparsely to densely pubescent. Corolla abaxially glabrous or with very few unicellular hairs near apex. Ovary very sparsely to sparsely pubescent.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, along coast from southern Bahia south to Estado do Rio (MAP 5). Coastal scrub on wet to dry sand (sometimes intermixed with sedge meadows), sand dunes; near sea level (rarely inland to 1000 m alt.). Flowering July through October.

REPRESENTATIVE SPECIMENS. **Brazil.** BAHIA: Santa Cruz Cabrália, *Belém & Pinheiro 2544* (C, L, NY); Pôrto Seguro, *Duarte 6144* (L, M, NY, US); between Alcobaça and Caravelas on BA 001, 20 km S of Alcobaça, *Harley 18047* (NY); 7 km NW of Mucuri, *Mori et al., Herb. Cent. Pesquisas do Cacau 10474* (NY). ESTADO DO RIO: Itapuã, *Athayde III-1961* (L); Macahé, Restinga de Cabiuna, *Brade 15781* (B); Cabo Frio, *Duarte & Pereira 5793* (L, S, US); Cabo Frio, along st. to town at jct. with rd. to Arraial do Cabo, *Lems 640317* (M, MO, NY, US); S of Cabo Frio, *Lindeman 6330* (L); Macahé, near Cabo Frio, *Riedel 494* (G, GH, GOET, K, L, NY, S); Arraial do Cabo, Pontal Beach, *Segadas-Vianna et al. I-470* (L); Casimiro de Abreu Co., dist. of Barra de São João, 5 km N of Rio das Ostras, *Segadas-Vianna et al. I-949* (L); Restinga de Itaipu, *Sucre 7611* (NY); Restinga de Cabo Frio, *Ule 4752* (HBG). MINAS GERAIS: Serra Sapucaí, municipio de Jequitinhonha, *Magalhães 17459* (L).

5b. **Agarista revoluta** (Sprengel) J. D. Hooker ex Niedenzu var. **velutina** Judd, var. nov.

Varietas haec ab Agarista revoluta var. revoluta differt in foliis cum pagina abaxiali dense velutina, pedicellis longioribus, corollis et ovariis pubescentibus.

Twigs densely pubescent. Leaves with adaxial surface sparsely to moderately pubescent on midvein and adjacent lamina; abaxial surface velutinous on lamina and midvein. Pedicels 6–11 mm long, densely pubescent. Calyx lobes with abaxial surface densely pubescent. Corolla abaxially moderately pubescent, especially near apex. Ovary ± densely pubescent.

TYPE. Brazil, Bahia, municipio do Salvador, Dunas do Abaeté, 29 Aug. 1976, *J. Silva Araújo et al. 49* (holotype, NY!; isotype, CEPEC).

DISTRIBUTION AND ECOLOGY. Eastern Brazil, on coast near Salvador, Bahia (MAP 5). Coastal scrub. Flowering August and September.

REPRESENTATIVE SPECIMENS. Known only from type collection.

Agarista revoluta, a distinct species with variably revolute, moderate-sized, obtuse- to retuse-mucronate leaves, is probably allied to the geographically

separated *A. duckei* (see MAP 2). It is readily distinguished by its longer inflorescences and its more abruptly and shortly mucronate leaves. Some individuals of *A. albiflora,* an Andean species, may be confused with *A. revoluta*; however, the former taxon has leaves that are usually less abruptly mucronate and only infrequently revolute, inflorescence hairs that are longer, and capsule valves that are never bordered.

Agarista revoluta is divided here into two geographically isolated varieties (MAP 5) separable primarily by the indumentum on the abaxial leaf surface. Variety *velutina,* discovered only recently, may be more widespread, and further collecting is needed along the coast of Bahia.

This taxon is unique in that it is the only species of *Agarista* known to occur in coastal "restingas."

6. **Agarista mexicana** (Hemsley) Judd, Jour. Arnold Arb. **60:** 495. 1979.

Shrub or tree to 8(–11) m tall, with thick, corky, deeply furrowed bark. Twigs very sparsely to densely pubescent, with nonchambered to clearly chambered pith. Buds to ca. 1.5 mm long. Leaves alternate (to subopposite or nearly 3-whorled at some nodes); petiole 2–12.5 mm long; blade revolute in bud, ovate, 2–7.5(–9) by 0.8–2.5(–3.2) cm, flat, coriaceous, the apex acuminate, the base narrowly cuneate to rounded, the margin entire (slightly undulate), plane to very slightly revolute near base, the adaxial surface glabrous to densely pubescent on midvein (with few unicellular hairs on proximal portion of lamina); abaxial surface essentially glabrous to densely pubescent on midvein, otherwise glabrous to densely pubescent, with few to several inconspicuous glandular dots along midvein. Inflorescences (fasciclelike) axillary racemes to 0.5–2.5(–4) cm long, axis sparsely to densely pubescent. Pedicels 2–8 mm long, very sparsely to densely pubescent; bracteoles 2, alternate to opposite, from nearly basal to within lower ⅓ (rarely to midpoint) of pedicel, triangular to narrowly so, to ca. 0.9 mm long; bracts to 1 mm long. Calyx lobes triangular with acuminate apices, 0.9–1.8 by 0.5–2 mm, abaxial surface very sparsely to densely pubescent; corolla cylindrical, 6–9.5 by 2.5–5 mm, white, abaxially glabrous to sparsely pubescent (especially near apex); filaments 4.5–6 mm long, anthers 1–1.8 mm long; ovary very sparsely to densely pubescent. Capsules subglobose to short-ovoid, 3–4.5(–5) by 5–7 mm, placentae subapical; seeds 1.5–2.7 mm long.

DISTRIBUTION. Mountainous areas of Mexico and Central America, from Veracruz and Jalisco south to Honduras and El Salvador.

COMMON NAMES. Cachimbo (Honduras, see Standley & Williams, 1952); quemanote, pellejo de lagarto, nacahuite (Mexico).

KEY TO THE VARIETIES OF AGARISTA MEXICANA

1. Abaxial surface of lamina glabrous to occasionally sparsely pubescent, hairs not obscuring abaxial epidermis. ..... 6a. var. *mexicana.*
1. Abaxial surface of lamina densely to occasionally moderately pubescent, hairs ± obscuring epidermis. ..... 6b. var. *pinetorum.*

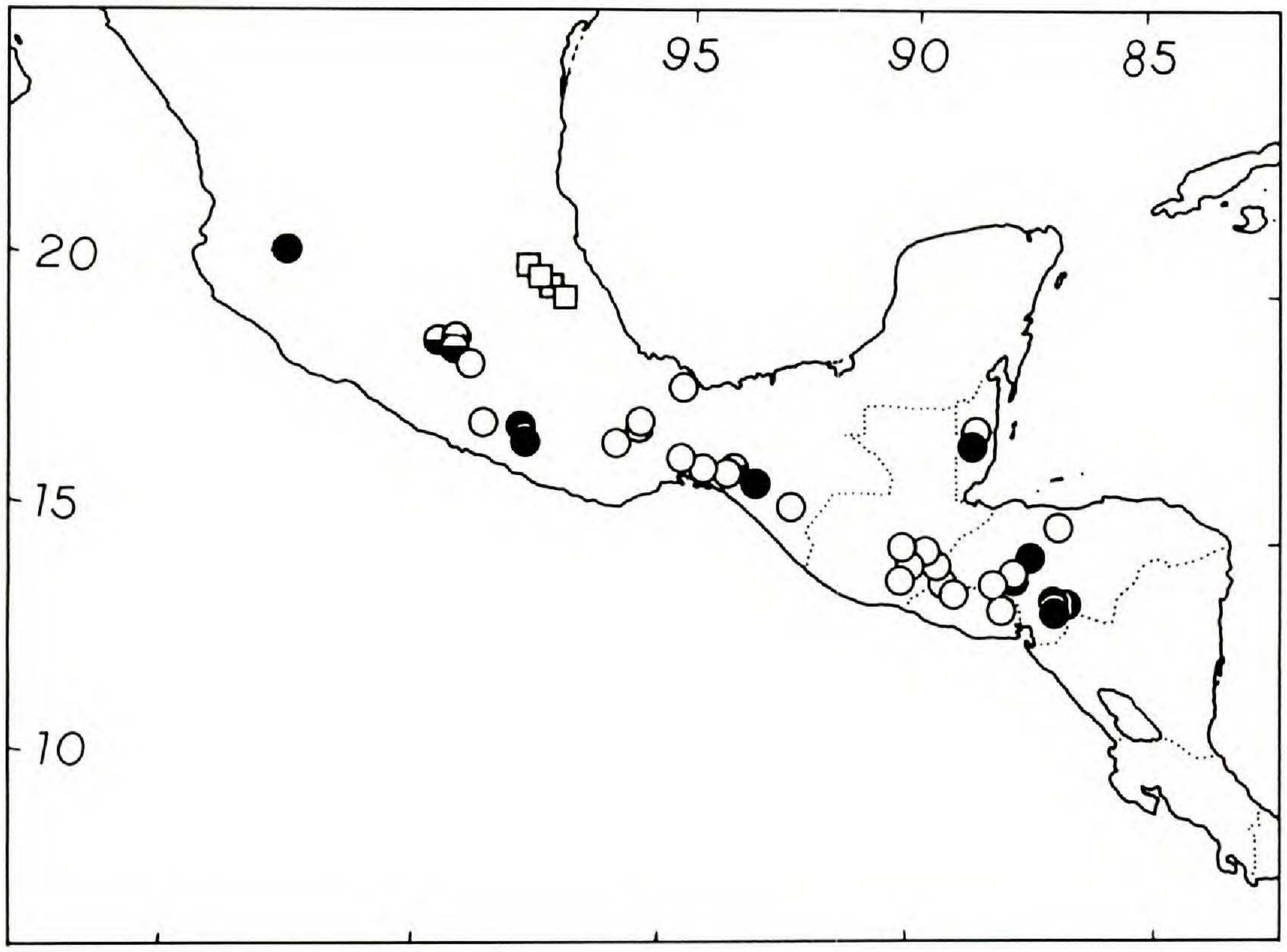
6a. **Agarista mexicana** (Hemsley) Judd var. **mexicana**

Andromeda mexicana Hemsley, Biol. Centr.-Am. Bot. **2:** 282. 1881. *Leucothoë mexicana* (Hemsley) Small, N. Am. Fl. **29:** 57. 1914. TYPE: Mexico, Oaxaca, Sierra San Pedro Nolasco, *Jürgensen 866* (holotype, K; isotype, G!).

Twigs very sparsely to densely pubescent. Leaf blades with abaxial surface glabrous to occasionally sparsely pubescent, epidermis not obscured. Ovary very sparsely to densely pubescent.

DISTRIBUTION AND ECOLOGY. Mountainous areas of Mexico and Central America, from states of México, Guerrero, Oaxaca, and Veracruz south to Honduras and El Salvador (MAP 3). Dry ridges, *Pinus* and/or *Quercus* forests, *Pinus, Quercus,* and *Liquidambar* forests with *Ulmus, Zinowiewia, Weinmannia,* and *Styrax,* montane mixed forests, disturbed openings, and forest margins; frequently in sandy soil; 170–2500 m alt. Reported from forests of *Pinus teocote, P. rudis,* and *P. oocarpa* by Gómez-Pompa (1973). Flowering mid-February through April (early May).

REPRESENTATIVE SPECIMENS. **Mexico.** CHIAPAS: SE of Cerro Baul on border with Oaxaca, 16 km NW of Rizo de Oro, municipio de Cintalapa, *Breedlove & Smith 31375* (MEXU, MO); SW of Tal-tenango, along rd. to Finca Pousia, *Miranda 6945* (MEXU, US). GUERRERO: Agua de Obispo, near 17°20′N, 99°34′W, *Kruse 630* (ENCB, MEXU); Taxco, *Miranda 3074* (MEXU). MÉXICO: dist. Temascaltepec, Guayabal, *Hinton 3377* (GH, NY, US); Nanchititla, *Hinton 3415* (GH, NY, US); Temascaltepec, *Hinton 3528* (GH, NY, UC, US); dist. Sultepec, Almoloya, *Hinton et al. 7450* (BM, F, G, GH, MO, NY, US); Cerro de Mamatla, Zacualpan, *Matuda 30563* (F, MEXU); Puerto del Embocadero, 7 km W of Luvianos, municipio de Tejupilco, *Rzedowski 22122* (WIS). OAXACA: Zempoaltepetl, between Santa María and Mitla, *Camp 2761* (GH, NY, S, UC); Chavela, *Mell 14* (F, NY, US); dist. Choapam, Yaveo, trail to Arroyo Culebras, *Mexia 9157* (B, F, G, GH, MO, NY, S, UC, US); Teotalcingo to Choapan, *Reko 4080* (US); Choapan to Comaltepec, *Reko 4116* (US); between Río Grande and Niltepec, *Xolocotzi X-1230 & Sharp 46232* (GH, MEXU). VERACRUZ: Cerro Monte de Oro, *Dorantes et al. 856* (F, MEXU); Falda del Cerro Azul, transecto Punta Limon–Cerro Azul, *Dorantes et al. 1114* (MEXU); along trail to Santa Marta, 2 km N of San Fernando, municipio Soteapan, *Nee et al. 24729* (F, FLAS); Ocozotepec, 6 km NW of Soteapan, *Sousa 3253* (F, MEXU); 1 km SW of Ocozotepec, *Sousa 3532* (F, MEXU). **Belize:** Hidden Valley Falls Rd., *Poppleton s.n.,* 26 Dec. 1973 (FLAS). **Guatemala:** Zamorora, dept. Santa Rosa, *Heyde & Lux 4530* (F, G, GH, NY, US); Sierra de las Minas, near San Gerónimo, dept. Baja Verapaz, *Kellerman 6636* (F, US); above Morazán, El Progreso, *Sharp 4633* (GH, MEXU); between Finca San José and Montaña Nube, 1.5 mi SE of Concepción de las Minas, dept. Chiquimula, *Steyermark 30857* (F, NY); Montaña Castilla, vic. of Montaña Cebollas, 3 mi SE of Quezaltepeque, dept. Chiquimula, *Steyermark 31303* (F); Sierra de las Minas, dept. Zacapa, Volcán de Monos, *Steyermark 42317* (F, NY); Sierra de las Minas, near Finca Piamonte, dept. El Progreso, *Steyermark 43427* (F, NY); Aguacate, dept. Jalapa, *Williams 13172* (F, GH); near Soledad, dept. Jalapa, *Williams 14239* (F). **Honduras:** dept. Comayagua, near Siguatepeque, *Allen 6219* (F); dept. Intibuca, Cascada de Yamaranguilla, *Molina 6362* (F); dept. Yoro, above Los Flores, vic. of Coyoles, *Yuncker et al. 8172* (BM, F, G, GH, NY, US). **El Salvador:** dept. Chalatenango, La Reina, *Calderón* (F, US); dept. Santa Ana, Cerro Miramundo, NE of Metapán, *Carlson 956* (F, UC); dept. Chalatenango, S of La Palma, *Lagos & Weberling 256* (L, M); dept. Morazán, easternmost peak, Montes de Cacaguatique, lat. 13°46′N, long. 88°13′W, *Tucker 698* (G, NY, P, UC, US).



MAP 3. Distribution of *Agarista mexicana* var. *mexicana* (circles), *A. mexicana* var. *pinetorum* (dots), and *A. sleumeri* (squares). Localities with both *A. mexicana* var. *mexicana* and intermediates between this taxon and var. *pinetorum* indicated by half-closed circles.

6b. **Agarista mexicana** (Hemsley) Judd var. **pinetorum** (Standley & Williams) Judd, Jour. Arnold Arb. **60:** 495. 1979. FIGURE 2, a, b.

Leucothoë pinetorum Standley & Williams, Ceiba **3:** 54. 1952. *Leucothoë mexicana* (Hemsley) Small var. *pinetorum* (Standley & Williams) Sleumer, Bot. Jahrb. **78:** 466. 1959. TYPE: Honduras, El Paraíso, Manzaragua, 1400 m alt., 4 April 1948, *Williams & Molina 14000* (holotype, US!; photos of holotype, F!, GH!, NY!, UC!; isotypes, GH!, MEXU!, MO!, US!).

Twigs moderately to densely pubescent. Leaf blades with abaxial surface densely (to moderately) pubescent, epidermis obscured or nearly so. Ovary moderately to densely pubescent.

DISTRIBUTION AND ECOLOGY. Mountainous areas of Mexico (states of Jalisco, Guerrero, and Chiapas), Belize, and Honduras (MAP 3). Rocky, brushy hillsides, *Pinus* and/or *Quercus* forests, *Pinus* savannas, *Pinus, Quercus,* and *Liquidambar* forests, and montane mixed forests; often in sandy soil; 500–2000 m alt. Flowering March through April (early May).

REPRESENTATIVE SPECIMENS. **Mexico.** CHIAPAS: E base of Cerro Tres Picos near Cerro Bola, logging rd. SW of Colonia Agronomos Méxicanos, municipio Villa Corzo, *Breedlove & Thorne 30037* (DUKE, ENCB, F, MEXU, MO). GUERRERO: Mina, Manchon dist., *Hinton 10082* (C, F, G, GH, M, MO, NY, UC); Armenia-Zoyate, Mina, *Hinton 10159* (C, ENCB, F,

G, GH, M, MO, NY, UC, US); Chilacayote–La Soledad, Mina, *Hinton et al. 14199* (F, GH, MO, NY, UC, US); Petlacala, Mina, *Hinton 14205* (F, MO, NY, US). JALISCO: La Venta, municipio de Zapopan, *Diáz-Luna 87* (ENCB); Venta del Astillero, La Primavera, *Villarreal de Puga 150* (ENCB); Sierra de la Venta, 18 km W of Guadalajara, *Villarreal de Puga 531* (ENCB). **Belize:** Augustine, 16°34′N, 88°54′W, *Hunt 438* (BM, US); El Cayo dist., 17 km S of Georgeville, *Liesner & Dwyer 1612* (MO, NY); El Cayo dist., San Agustín, *Lundell 6792* (F, NY, US). **Honduras:** Las Jagnas, Minas de Oro, Comayagua dist., *Edwards P-180* (A); El Paraíso, rd. from Zamoras to Güinope, *Webster et al. 11988* (F, GH, MO, US); dept. Morazán, Rd. Valle de Angeles near San Antonio, *Molina 389* (F, GH, MEXU, MO, UC, US); dept. El Paraíso, between Galeras and Las Casitas, *Molina 10765* (F, US); dept. Comayagua, La Piramide, *Molina 14393* (F); dept. Morazán, San Antonio de Oriente, *Rodríguez 3133* (F, GH, NY); dept. El Paraíso, NW of Güinope, *Standley et al. 2047* (F, NY, US); dept. Morazán, vic. of Agua Amarilla, *Standley 12297* (F); dept. El Paraíso, above Galeras, *Williams & Molina 10246* (F, GH); dept. Comayagua, 5 km N of Siguatepeque, *Williams & Molina 18128* (F, GH, US).

Agarista mexicana is closely allied to *A. sleumeri* and *A. populifolia*; all three species are characterized by ovate leaves with acuminate apices and rounded to cuneate bases, and by short inflorescences of white flowers. *Agarista mexicana* can be differentiated from both taxa by its pubescent ovary, from *A. populifolia* by its corky, prominently furrowed bark, and from *A. sleumeri* by its pubescent calyx and pedicels and its smaller corollas and leaves.

Agarista mexicana is a widely distributed taxon (see MAP 3) that is extremely variable in its unicellular indumentum. Populations of this species are here divided into two weakly differentiated geographic varieties on the basis of the density of unicellular hairs on the abaxial leaf surface. However, some populations are variable in leaf pubescence, and intermediate specimens are known, mostly in the state of México. Representative intermediate material includes:

Mexico. CHIAPAS: near Fenia, *Purpus 294* (US); E of Monserrate, *Purpus 10156* (A, F), *Purpus 10518* (A, NY). MÉXICO: dist. Temascaltepec, Ypericones, *Hinton 3899* (GH, NY, US); 5 km SW of Nanchititla, Tejupilco, *Medrano et al. 5030* (MEXU); Puerto del Embocadera, 7 km W of Luvianos, municipio de Tejupilco, *Rzedowski 22122* (ENCB, MEXU); La Cienaga, 4 km S of Sultepec, *Rzedowski 30392* (ENCB).

Agarista mexicana var. *mexicana* has been illustrated by Standley and Williams (1952, *fig. 30*).

7. **Agarista sleumeri** Judd, sp. nov. FIGURE 3, a.

Frutex vel arbor ad 6(–20) m alta. Ramuli hornotini glabri cum medulla septata. Folia ovata, 4–11.5(–13) cm longa, 1.6–4.5(–5.3) cm lata, coriacea, ad apicem acuminata, ad basin cuneata vel rotundata; margo ± planiuscula, integra; pagina abaxialis glabra; petioli 6.5–13 mm longi. Inflorescentiae axillares, racemosae, ad 0.5–2.5(–4) cm longae; axis glaber vel leviter pubescens. Pedicelli glabri, 3.5–8.5 mm longi. Flores 5-merus. Calyx lobis 1.2–2.6(–3) mm longis, 0.7–2 mm latis, abaxialiter glabris. Corolla cylindrica, 8.5–13 mm longa, 3–7.5 mm lata, alba, abaxialiter glabra. Filamenta 5–7.5 mm longa; antherae 1.3–1.7 mm longae. Ovarium glabrum. Capsula subglobosa vel brevissime ovoidea, 3–4.5 mm longa, 5–8 mm lata, placentis subapicalibus. Semina 1.5–2.4 mm longa.

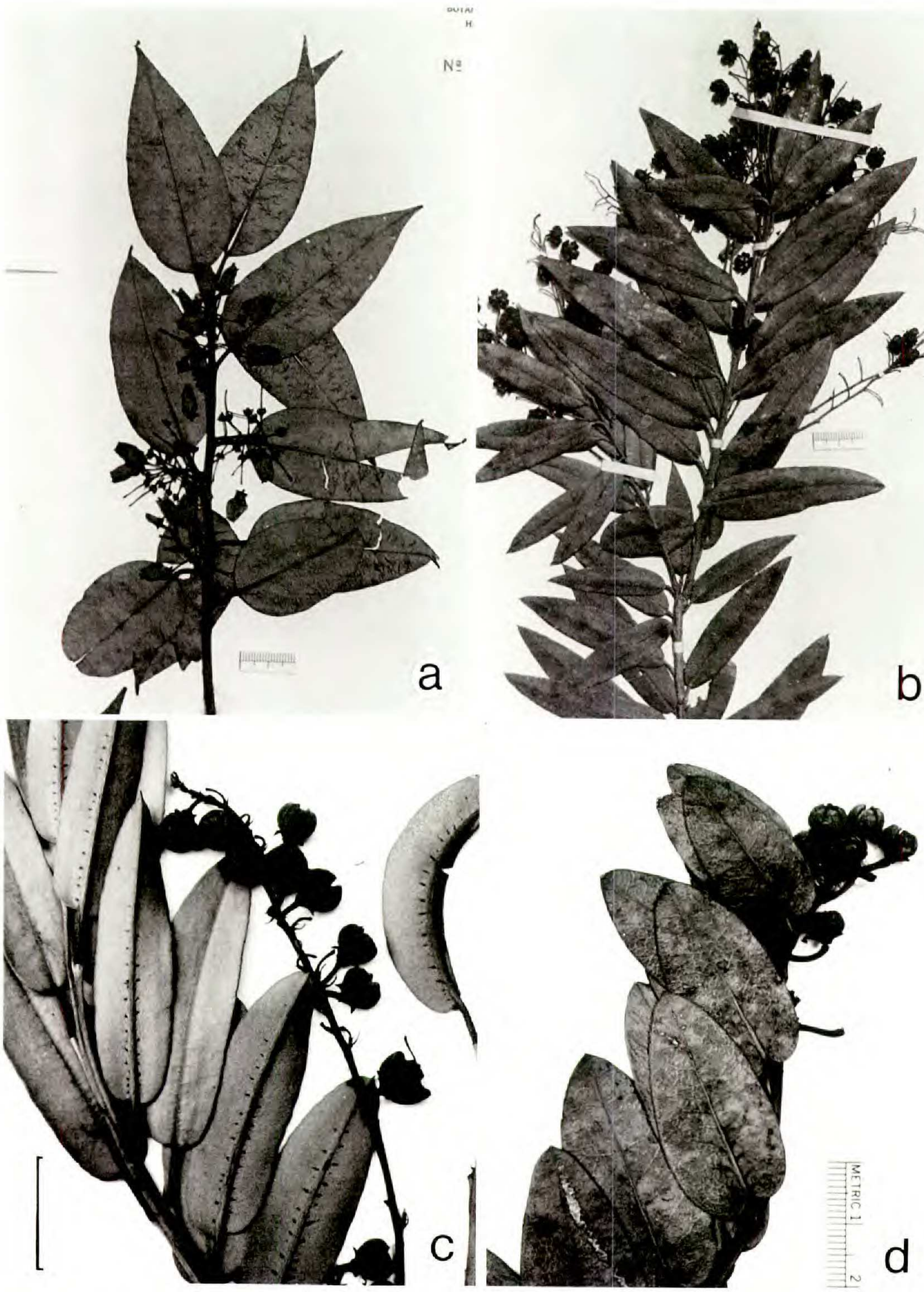


FIGURE 3. a, *Agarista sleumeri* (*Koch & Garcia 76103*). b, *A. oleifolia* var. *oleifolia* (*Glaziou 15171*). c, *A. coriifolia* var. *bradei* (*Irwin et al. 28486*): note round-based leaves with conspicuous glandular dots extending along midvein on abaxial surface. d, *A. coriifolia* var. *coriifolia* (*Duarte 2044*): note cordate-based leaves with glandular dots less well developed. Scale = 2 cm.

Shrub or tree to 6(–20) m tall, with corky, longitudinally furrowed bark. Twigs glabrous, with clearly chambered pith. Buds to ca. 1.2 mm long. Leaves alternate (to rarely subopposite at few nodes); petiole 6.5–13 mm long; blade revolute in bud, ovate, 4–11.5(–13) by 1.6–4.5(–5.3) cm, flat, coriaceous, the apex acuminate, the base cuneate to rounded, the margin entire (slightly undulate), plane to very slightly revolute near base, the adaxial surface glabrous to very slightly pubescent near extreme proximal portion of midvein, the abaxial surface glabrous, with few to several inconspicuous glandular dots along midvein. Inflorescences (fasciclelike) axillary racemes to 0.5–2.5(–4) cm long, axis essentially glabrous to sparsely pubescent. Pedicels 3.5–8.5 mm long, glabrous; bracteoles 2, alternate, nearly basal to within lower ¼ of pedicel, triangular to narrowly so, to ca. 0.8 mm long; bracts to 1.3 mm long. Calyx lobes triangular with acuminate apices, 1.2–2.6(–3) by 0.7–2 mm, abaxial surface glabrous; corolla cylindrical, 8.5–13 by 3–7.5 mm, white, abaxially glabrous; filaments 5–7.5 mm long, anthers 1.3–1.7 mm long; ovary glabrous. Capsules subglobose to short-ovoid, 3–4.5 by 5–8 mm, placentae subapical; seeds 1.5–2.4 mm long.

TYPE. Mexico, Hidalgo, municipio de Tenango de Doria, 30 km NE of Tulancingo, rd. between Metepec and Tenango de Doria, 19 km N of Metepec, 22 May 1976, *S. D. Koch & J. García P. 76103* (holotype, ENCB!; isotypes, MEXU!, MO!).

DISTRIBUTION AND ECOLOGY. Mexico, limited to small area of Hidalgo, Veracruz, and Puebla in Sierra Madre Oriental (MAP 3). *Pinus* and/or *Quercus* forests, *Pinus* and *Liquidambar* forest, mixed forest of *Pinus, Quercus, Alnus,* or *Cupressus*, and *Lyonia* and *Cupressus* forest; 1220–2250 m alt. Flowering April and May (June).

REPRESENTATIVE SPECIMENS. **Mexico.** HIDALGO: 2 km SW of Tutotepec, *Gimante 608* (ENCB); municipio de Tenango de Doria, El Estribo, *Gimante 950* (ENCB, MEXU, WIS); NE of Honey, *Hernandez 767* (MEXU); municipio de Tenango de Doria, 25 km NE of Tulancingo, *Perino 3353* (NY); border of Hidalgo and Veracruz, Puente Agapito Barranco, *Gómez-Pompa 4354* (F, GH). PUEBLA: N of Tlatlanqui, *Boege 1713* (MEXU); Necaxa, *Miranda 3421* (MEXU); Pahuatlán, *Miranda 3641* (MEXU); along Río Tenango, near Tenango, *Sharp 45353* (MEXU); 1 km from Tlaxpanaloya, Naupan, *Vela 455* (ENCB). VERACRUZ: La Capilla, 3 km from Huayacocotla, *Calzada & Horritz 2628* (F, MEXU, NY); SW entrance to Huayacocotla on rd. from Palo Bendito, *Diggs & Nee 2957* (F, FLAS); El Paraje, Huayacocotla, *Hernandez & Cedillo 817* (F, GH, MEXU, MO); municipio Huayacocotla, *Hernandez 1150* (MEXU); between La Cruz del Ataque and Zacualpan, *Vela 618* (ENCB).

Agarista sleumeri is most closely related to *A. populifolia* and *A. mexicana,* differing from both in its abaxially glabrous calyx and glabrous pedicel (vs. very sparsely to densely pubescent calyx and pedicel) and its larger corolla. It can also be distinguished from the latter species by its glabrous (vs. very sparsely to densely pubescent) ovary, its clearly septate pith, and its usually larger leaves. These three species form a well-marked subgroup of the genus and can be separated from the South American species by their ovate leaves with cuneate

FIGURE 4. *Agarista populifolia* (*Judd 2609*): a, segment of twig, × .5; b, longitudinal section of twig, showing chambered pith, × 2; c, cross section of older stem, showing hollow central portion, × 1; d, margin of leaf, × 10; e, multiseriate-stalked, gland-headed hair of pedicel, × 130; f, unicellular hairs of pedicel, × 130; g, flower, × 5; h, stamen, × 10; i, anther, × 25; j, capsule and portion of pedicel, × 5; k, columella with placentae, × 6.5; l, seed with elongated testa cells, × 10.

to rounded bases and acuminate apices, their white flowers, and their short racemes. The three species are geographically isolated (MAPS 3, 4).

It is a pleasure to name this distinctive species for Dr. H. Sleumer, who has done so much to increase our taxonomic understanding of *Agarista* and various other ericad groups.

8. **Agarista populifolia** (Lam.) Judd, Jour. Arnold Arb. **60:** 195. 1979.
FIGURE 4.

Andromeda populifolia Lam. Encycl. Méth. Bot. **1:** 159. 1783. *Andromeda laurina* Michaux, Fl. Bor.-Am. **1:** 253. 1803, nomen superfl. *Lyonia populifolia* (Lam.) K. Koch, Dendrol. **2:** 123. 1872. *Leucothoë populifolia* (Lam.) Dippel, Handb. Laubh. **1:** 356. 1889. TYPE: United States, South Carolina, *Fraser s.n.* (holotype, P-LA; photo of holotype, GH!).

Andromeda lucida Jacq. Collect. **1:** 95. 1786, non *Andromeda lucida* Lam. Encycl. **1:** 157. 1783 (= *Lyonia lucida* (Lam.) K. Koch).

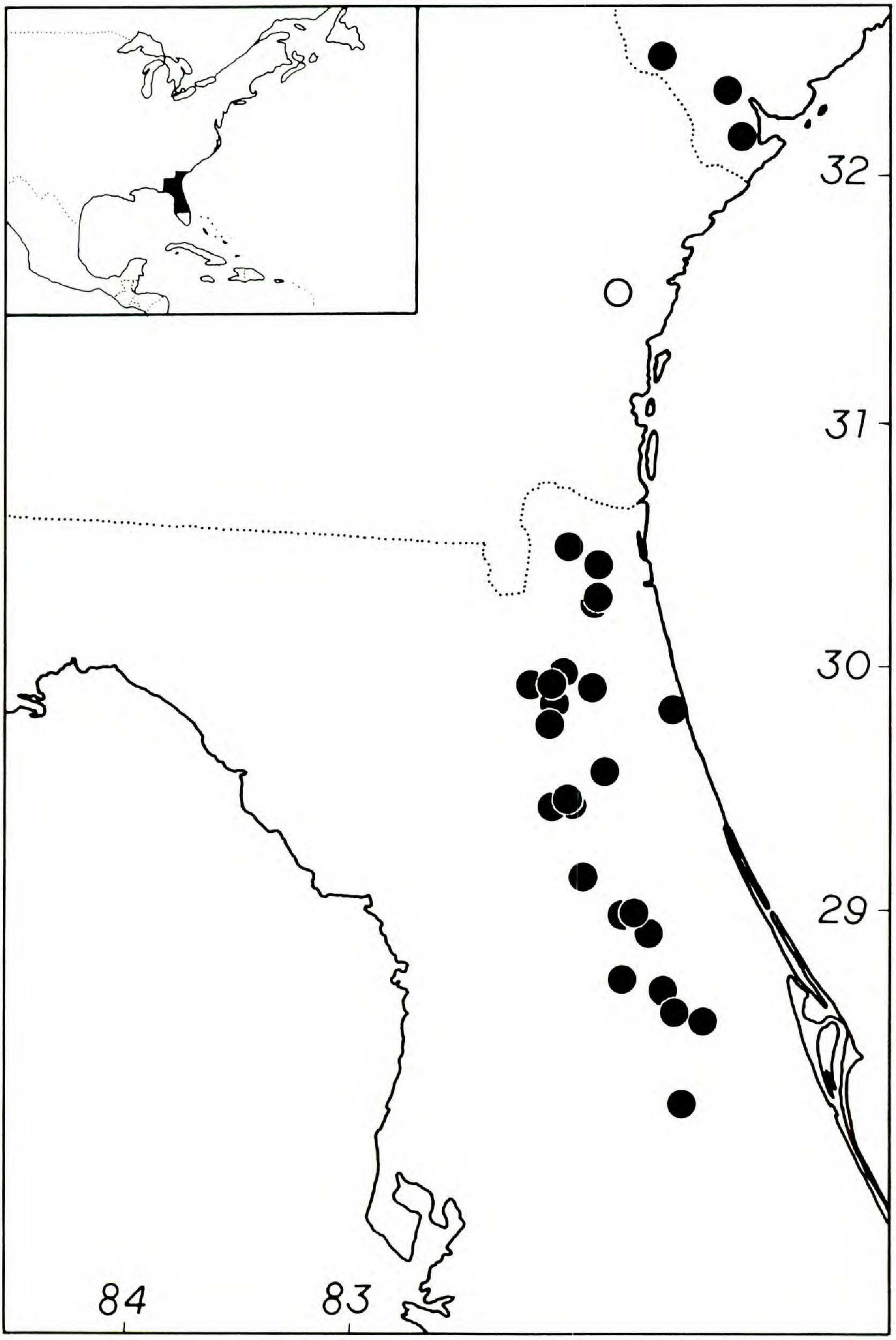
Andromeda reticulata Walter, Fl. Carolin. 137. 1788. TYPE: not seen.

Andromeda acuminata Aiton, Hortus Kew. **2:** 70. 1789. *Andromeda acuminata* Lodd. ex C. F. Ludwig, Neue Wilde Baumz. 4. 1783, nomen nudum. *Leucothoë acuminata* (Aiton) G. Don, Gen. Syst. **3:** 832. 1834. TYPE: cultivated, "introduced by Mr. John Cree" (not seen).

Andromeda formosissima Bartram, Travels N. S. Carol. **5:** 24, 172, 303. 1791, nomen nudum.

Shrub or small tree to 7 m tall, with shallowly furrowed bark. Twigs with or without scattered gland-headed hairs, otherwise glabrous to sparsely pubescent, with clearly chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 3–12 mm long; blade revolute in bud, ovate, 2.6–9(–11.2) by 0.9–4(–5) cm, flat, coriaceous, the apex acuminate (to nearly acute), the base narrowly cuneate to rounded, the margin entire to obscurely or sharply serrate (serrations, when present, each associated with gland-headed hair) (undulate), plane to very slightly revolute near base, the adaxial surface with or without scattered gland-headed hairs, otherwise sparsely pubescent on midvein, especially proximal portion, the abaxial surface with or without gland-headed hairs along midvein (and proximal portion of lamina), otherwise glabrous or with very few unicellular hairs at base of midvein, with few to several inconspicuous glandular dots along midvein. Inflorescences (fasciclelike) axillary racemes to 1–2.5(–3.5) cm long, the axis with or without scattered gland-headed hairs, otherwise sparsely to densely pubescent. Pedicels 5.5–11.5 mm long, with or without gland-headed hairs, otherwise sparsely to moderately pubescent; bracteoles 2 (rarely 3), alternate, nearly basal to within lower ⅓ (rarely to midpoint) of pedicel, triangular or narrowly so, to ca. 1.2 mm long, very rarely subtending an axillary flower; bracts to 1.2 mm long. Calyx lobes triangular with acuminate apices, 0.9–2 by 0.6–1.5 mm, the abaxial surface with or without gland-headed hairs, otherwise sparsely to moderately pubescent; corolla cylindrical, 6–9.5 by 3–5 mm, white, abaxial surface glabrous; filaments 4–5.5 mm long, anthers 1.1–1.4 mm long; ovary glabrous. Capsules subglobose to short-ovoid, 3–4 by 4.5–6.5 mm, placentae subapical; seeds 1.4–2 mm long. $2n = 24$ (Wood, 1961).

DISTRIBUTION AND ECOLOGY. Southeastern U. S. Atlantic Coastal Plain from southern South Carolina to eastern Florida (MAP 4). Acidic swamps in pine



MAP 4. Distribution of *Agarista populifolia* (open circle = unspecified Georgia locality).

flatwoods, mixed hydric hammocks (hardwood swamps) of *Fraxinus, Quercus, Nyssa, Sabal, Acer, Liquidambar, Persea, Gordonia, Carpinus,* and *Pinus,* riverine swamps, swamp forests of *Taxodium* or *Chamaecyparis* (along with various hardwoods), bayheads and lake margins, frequently along streams or in ravines; near sea level to 55 m alt. Flowering chiefly late March through early May.

COMMON NAMES. Pipe-plant, pipe-stem wood.

REPRESENTATIVE SPECIMENS. **United States.** FLORIDA. Clay Co.: ravine at Goldhead Branch St. Park, NE of Keystone Heights, *Arnold s.n.,* 5 May 1940 (FLAS); Rte. 21, 4.8 mi N of jct. with Rte. 16, along Mill Creek, S22, T5S, R24E, *Judd 2541* (FLAS); 5 mi W of Penny Farms, S15, T6S, R24E, *Ward 5521* (FLAS). Duval Co.: near Jacksonville, *Curtiss 1692* (A, G, GH, K, M, MO, NY, UC, US). Lake Co.: Alexander Springs, *Ford & West s.n.,* 11 July 1958 (FLAS, UNC). Marion Co.: just N of Orange Springs, near jct. of Orange Creek and Rte. 21, S25, T11S, R23E, *Judd 2609* (FLAS, FSU, GH, MO, S, UNC); Juniper Springs, *Murrill s.n.,* 5 May 1940 (FLAS, MO). Nassau Co.: near Callahan, *E. J. Palmer 38293* (A, MO, S). Orange Co.: Rock Springs, S15, T20S, R28E, *Moore s.n.,* 1 April 1961 (FLAS, MO, UNC). Osceola Co.: near Kissimmee, *Hunnewell 8707* (GH). Putnam Co.: S1, T11S, R24E, center of section, *Cooper 697* (FLAS). Seminole Co.: 5 mi W of Oviedo, S23, T21S, R30E, *Lotspeich & Perkins 472* (FLAS). St. Johns Co.: near St. Augustine, *Reynolds s.n.,* May–June 1875 (MO, NY). GEORGIA: without definite locality, *Le Conte s.n.* (MO); *Feay s.n.* (NY). SOUTH CAROLINA. Beaufort Co.: Bluffton, *Mellichamp s.n.,* 1876 (GH, NY). Hampton Co.: Garnett, *Lawton s.n.,* 28 Sept. 1931 (NCU). Jasper Co.: Elliott (1817) reported it from near the "Black Swamp, on the road from Coosawhatchie to the Sisters Ferry."

Agarista populifolia, the northernmost-ranging species of the genus, is very closely related to *A. sleumeri.* The two species are distinguished by calyx and pedicel indumentum, corolla size, and bark characters, and they are geographically separated, with *A. populifolia* occurring on the Atlantic Coastal Plain from South Carolina to Florida and *A. sleumeri* in the Sierra Madre Oriental of Hidalgo, Veracruz, and Puebla. *Agarista populifolia* is also allied with *A. mexicana,* from which it is easily distinguished by its glabrous (vs. pubescent) ovary, its shallowly (vs. corky and prominently) furrowed bark, and its more consistently septate pith. It is puzzling that *A. populifolia* has consistently been misclassified despite the many characters linking it to its South and Central American relatives (see TABLE 1).

Agarista populifolia is rather variable in glandular indumentum and in the size and margin of the leaves. Leaves of some plants are sharply (to obscurely) serrate, while those of others are entire; the two forms are commonly found intermixed within the populations. In addition, some plants have gland-headed hairs on the inflorescences and frequently also on the stems and/or leaves, while others completely lack them. Most populations contain plants with such hairs and plants without them.

This species is locally common in eastern Florida (MAP 4) from Osceola County to Nassau County but is apparently extremely rare in Georgia and South Carolina. In fact, the presence of the taxon in Georgia is somewhat questionable since no exact localities are known, although Bartram (1791)

reported it growing along the St. Marys River. The species is occasionally cultivated (Ingram, 1961, *fig. 26*; Melvin, 1981).

Andromeda serratifolia (see DC. Prodr. **7:** 602, 609. 1839) and *A. serrata* (see *ibid.* 602) are horticultural names (of no nomenclatural standing) that were occasionally used for *Agarista populifolia* in the late eighteenth or early nineteenth century.

9. **Agarista coriifolia** (Thunb.) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889.

Shrub (to tree) to 2(–5) m tall. Twigs glabrous to moderately pubescent (glaucous), with nonchambered to clearly chambered pith. Buds to ca. 1.8 mm long. Leaves alternate to subopposite or nearly 3-whorled at some nodes; petiole 2–18 mm long; blade revolute in bud, ovate to elliptic or oblong, 1.8–10.5 by 0.6–3.5(–5) cm, ± flat, very coriaceous, the apex acute- to rounded-mucronate to acuminate, the base cordate to cuneate, the margin entire, plane (slightly revolute near base, rarely slightly undulate), the adaxial surface glabrous to sparsely pubescent on midvein, especially proximal portion, the abaxial surface glabrous to very sparsely pubescent along proximal portion of midvein, with glandular dots absent, or few to many and inconspicuous to conspicuous along midvein. Inflorescences axillary or terminal racemes or panicles, to (2.5–)4.5–28 cm long, axis glabrous to densely pubescent. Pedicels 2–14 mm long, glabrous to densely pubescent; bracteoles 2 (rarely to 4), alternate to opposite, from nearly basal to near middle of pedicel, triangular to narrowly so, to ca. 1.6 mm long; bracts to 4 mm long. Calyx lobes triangular with acuminate apices, 1–2.7 by 0.6–2.2 mm, abaxial surface glabrous to sparsely (moderately) pubescent; corolla cylindrical to urceolate-cylindrical, 6.5–11 by 3–6.5 mm, white or greenish white to red, abaxially glabrous (rarely with very few unicellular hairs near apex); filaments 4–6 mm long, anthers 1.3–2.3 mm long; ovary glabrous to moderately pubescent. Capsules short-ovoid to subglobose, 3–6 by 4.5–8 mm, placentae subapical (rarely ± central); seeds 1–2.6 mm long.

DISTRIBUTION. Eastern Brazil, Bahia, Minas Gerais, and Estado do Rio.

KEY TO THE VARIETIES OF AGARISTA CORIIFOLIA

1. Leaves usually ovate (to ± elliptic), base usually cordate to rounded, abaxial surface with glandular dots lacking to limited to proximal half of blade; calyx lobes abaxially glabrous to sparsely (moderately) pubescent. ..... 9a. var. *coriifolia.*
1. Leaves ± oblong to slightly elliptic (slightly ovate), base usually cuneate to rounded, abaxial surface with glandular dots usually extending along midvein to near apex of blade; calyx lobes abaxially glabrous. ..... 9b. var. *bradei.*

9a. **Agarista coriifolia** (Thunb.) J. D. Hooker ex Niedenzu var. **coriifolia**

FIGURE 3, d.

Andromeda coriifolia Thunb. Pl. Brasil. Decas 1, p. 9. 1817. *Leucothoë coriifolia* (Thunb.) DC. Prodr. 7: 605. 1839. TYPE: Brazil, Minas Gerais, Villa Rica, *Freyreiss s.n.* (holotype, UPS).

Leucothoë neriifolia Cham. & Schldl. Linnaea **1:** 522. 1826. *Agarista neriifolia* (Cham. & Schldl.) G. Don, Gen. Syst. **3:** 838. 1834. *Leucothoë laxiflora* Meissner var. *sellowii*

Meissner *in* Martius, Fl. Brasil. **7:** 157. 1863 (= var. *laxiflora*), nomen superfl. TYPE: Brazil, Minas Gerais, without definite locality, *Sellow s.n.* (holotype, B (destroyed); fragment of holotype, NY; photos of holotype, F!, G!, GH!; isotypes, E!, K!).

Andromeda crassifolia Pohl, Pl. Brasil. **2:** 34. 1828/29, non Nees, Flora **4:** 297. 1821.

Agarista pohlii G. Don, Gen. Syst. **3:** 837. 1834, nomen novum. *Leucothoë crassifolia* (Pohl) DC. Prodr. **7:** 605. 1839. *Leucothoë crassifolia* (Pohl) DC. var. *subevenia* Meissner *in* Martius, Fl. Brasil. **7:** 158. *t. 59, fig. 1.* 1863 (= var. *crassifolia*), nomen superfl. *Leucothoë pohlii* (G. Don) Sleumer, Bot. Jahrb. **78:** 463. 1959. TYPE: Brazil, Minas Gerais, Diamantina, Pico Itambé, Nov. 1821, *Pohl 3506* (holotype, W; fragment of holotype, NY!).

Leucothoë laxiflora Meissner var. *martii* Meissner *in* Martius, Fl. Brasil. **7:** 157. 1863. TYPE: Brazil, Estado do Rio, near Paraiba, *Martius 1118* (holotype, M!; fragment of holotype, NY!; photos of holotype, F!, GH!; isotypes, M!).

Leucothoë laxiflora Meissner var. *subcordata* Meissner *in* Martius, *ibid.* TYPE: not seen.

Leucothoë laxiflora Meissner var. *hookeriana* Meissner *in* Martius, *ibid.* 158. TYPE: cultivated in England, in garden of Mr. Cunningham (see Hooker & Smith, 1851, *t. 4593*) (holotype, K!).

Leucothoë crassifolia (Pohl) DC. var. *subreticulata* Meissner *in* Martius, *ibid.* TYPE: Brazil, Minas Gerais, Itambé, Aug. 1840, *Martius 836* (holotype, M!; fragment of holotype, NY!; isotypes, BR, G!, K!, P!, W; photos of isotype, F!, GH!).

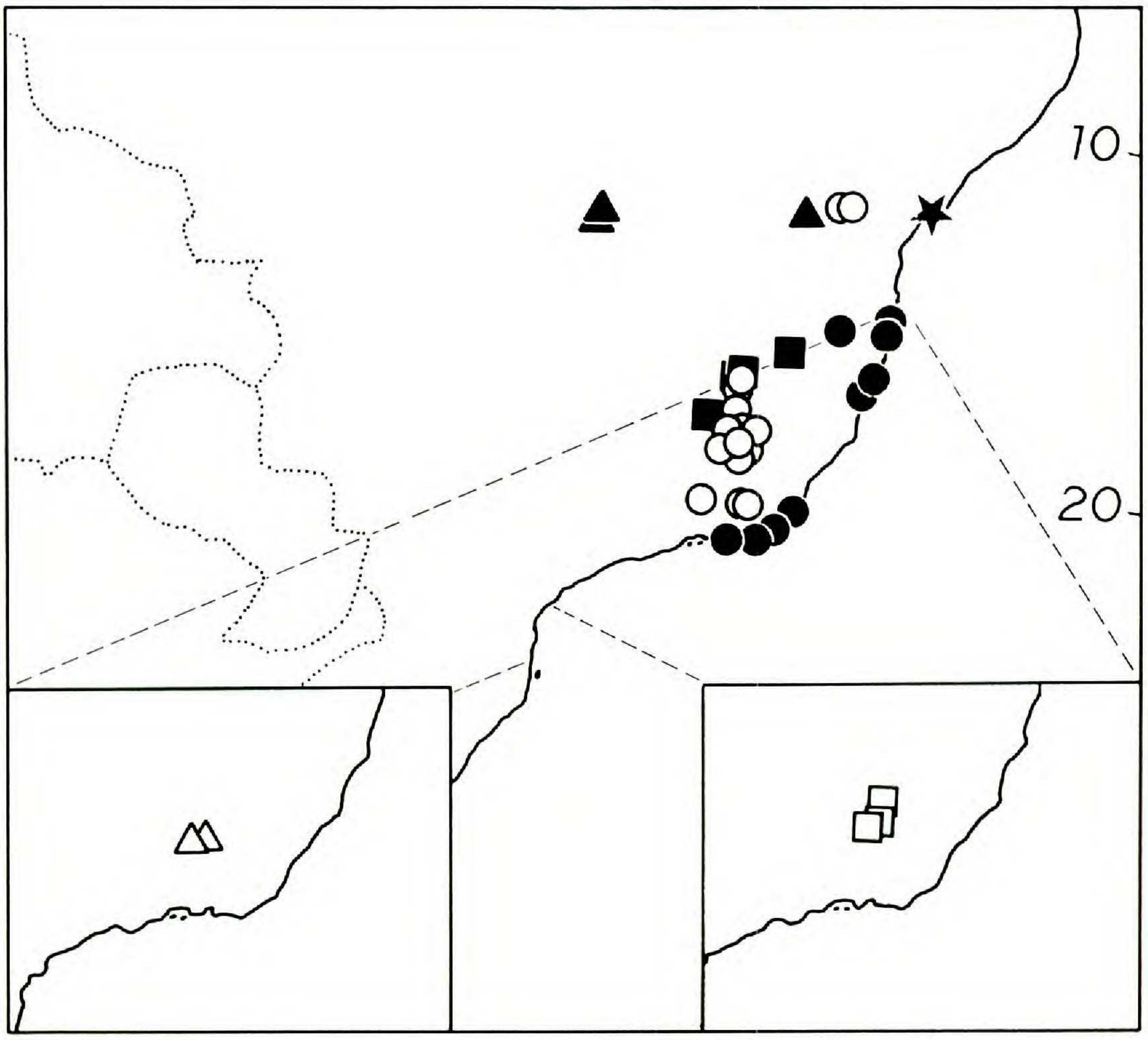
Leucothoë crassifolia (Pohl) DC. var. *reticulata* Meissner *in* Martius, *ibid.* TYPE: Brazil, Minas Gerais, without definite locality, *Claussen 535* (holotype, BR; fragment of holotype, NY!).

Leucothoë crassifolia (Pohl) DC. var. *macrophylla* Meissner *in* Martius, *ibid.* TYPE: Brazil, Serra da Paraca, fl. Paraiba, *Martius s.n.* (holotype, M!; photos of holotype, F!, GH!).

Shrub (or tree) to 2(–5) m tall. Twigs glabrous to moderately pubescent. Leaves with petiole 2–18 mm long; blade ovate (to ± elliptic), 1.8–10.5 by (0.6–)1–3.5(–5) cm, base usually cordate to rounded, abaxial surface with glandular dots absent to limited to proximal half. Inflorescence axis to 6–28 cm long, glabrous to densely pubescent. Pedicels glabrous to densely pubescent. Calyx lobes abaxially glabrous to sparsely (or moderately) pubescent; corolla 6.5–10.5 mm long, red to white; ovary glabrous to sparsely pubescent.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, from Bahia to southern Minas Gerais and adjacent Estado do Rio (MAP 5). Open rocky and/or grassy campo, open scrub, thickets and forests, frequently along streams; usually in sandy soil, with sandstone or manganese outcrops; 500–1950 m alt. Flowering chiefly June through September (to January or February).

REPRESENTATIVE SPECIMENS. **Brazil.** BAHIA: Lençóis, *Duarte 9337* (L); Serra do Sincorá, by Rio Cumbuca, ca. 3 km S of Mucugê, *Harley et al. 15911* (E, L, MO, NY, US); 10 km S of Andaraí on rd. to Mucugê, *Harley 18758* (NY); 3 km S of Mucugê, *Mori et al. 12578* (NY); between Lençóis and Itaberaba, *Pereira 2040* (L); Serra do Sincorá, *Ule 7336* (HBG, L). MINAS GERAIS: E slopes of Pico do Itambé, *Anderson et al. 35887* (C, F, L, NY, US); Serra do Taquaril, Belo Horizonte, *Barreto 528* (F); Serra do Cipó, km 131, Palacio, Santa Luzia, *Barreto 9253* (F); Cachoeira do Campo, *Claussen 54* (G); Palmeira, Rio Carandaí, *Duarte 4314* (L); Caraça, *Emygdio et al. 3525* (NY); Furnas, Alvinópolis, *Emygdio et al. 3588* (NY); Ribeirão das Capidalas, *Emygdio 3623* (NY); Diamantina, *Gardner 4990* (E, G, GH, K, NY, P, US); Serra do Palmital, near São Bartholomeu, *Glaziou 15172* (C, K, L, P); Serra do Itacolomy, *Gomes 2846* (F); Pico Itambé, São Antonio do Itambé, *Hatschbach 30123* (C, L, MO, UC); Serra do Caraça, *Irwin et al. 29067* (L, MO,



MAP 5. Distribution of *Agarista coriifolia* var. *coriifolia* (circles), *A. coriifolia* var. *bradei* (solid squares), *A. pulchra* (open squares), *A. subrotunda* (open triangles), *A. chapadensis* (solid triangles), *A. revoluta* var. *revoluta* (dots), and *A. revoluta* var. *velutina* (star).

NY), *St.-Hilaire s.n.*, 1816–1821 (P); Serra do Cipó, Mato Dentro, *Macedo 3757* (NY, S, US); Serro Frio, *Martius s.n.* (M); Serra do Curral d'El Rey, *Reinhardt s.n.*, Sept. 1855 (C); Serra d'Uro Branco, *St.-Hilaire 234* (P); Itambé, *St.-Hilaire 395* (P); Serra do Ouro Prêto, *Ule s.n.*, Feb. 1892 (HBG); Casa Branca, Ouro Prêto, *Williams 8130* (GH).

9b. **Agarista coriifolia** (Thunb.) J. D. Hooker ex Niedenzu var. **bradei** (Sleumer) Judd, comb. et stat. nov. FIGURE 3, c.

Leucothoë bradei Sleumer, Notizbl. Bot. Gart. Berlin **13:** 213. 1936. TYPE: Brazil, Minas Gerais, Diamantina, June 1934, *Brade 13614* (holotype, RB; fragment of holotype, LIL; photos of isotype, B (destroyed), s!).

Shrub to 2 m tall. Twigs glabrous to very sparsely pubescent. Leaves with petiole 4–11 mm long; blade ± oblong to slightly elliptic (slightly ovate), (2.4–)3–7.5 by 0.6–2.5(–3) cm, base usually cuneate to rounded, abaxial surface with glandular dots usually extending along midvein from base to near apex. Inflorescence axis to (2.5–)4.5–15(–20) cm long, glabrous to sparsely pubescent.

Pedicels glabrous to sparsely pubescent. Calyx lobes abaxially glabrous; corolla 8–11 mm long, red; ovary glabrous to moderately pubescent.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais (MAP 5). Rocky or grassy campo, shrubby cerrado, gallery forest, sometimes on termite mounds; ca. 1200–1410(?) m alt. Flowering September and October.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Serra do Espinhaço, 13 km SW of Rio Jequiti and Mendanha, on rd. to Diamantina, *Anderson 8992* (C, F, L, MO, NY); between Diamantina and Guinda, *Archer 4103* (A, NY); Diamantina, *Duarte 8927* (L); Guinda, Diamantina, *Hatschbach 27371* (C, L, NY, S, UC, US); 27 km SW of Diamantina on rd. to Gouveia, *Irwin et al. 22043* (F, L, NY); 3 km N of São João da Chapada, rd. to Campo do Sampaio, *Irwin 28486* (F, L, NY); Chapada, *St.-Hilaire, Cat. B*[1], *n. 2048* (P).

Agarista coriifolia is probably closely related to *A. pulchra* and *A. subrotunda*. It can be separated from the former by its larger, narrower leaves with a length/width quotient of (1.5–)1.8–6 (vs. 0.9–1.7) and its glabrous to densely pubescent inflorescence axes, and from the latter by its abaxially glabrous leaves. This species may also be confused with *A. pulchella* var. *pulchella* or *A. oleifolia* (both varieties), but these taxa have more or less central placentae and usually less coriaceous leaves that always lack conspicuous abaxial glands (see key for other distinguishing features).

Agarista coriifolia is extremely variable in unicellular indumentum, shape and size of the leaves, development of abaxial laminar glands, and color of the corolla. This variation has led to the description of numerous species and varieties (e.g., *A. neriifolia, A. pohlii, A. bradei,* or the various varieties of *A. laxiflora*) that cannot be maintained when the total pattern of variation is analyzed. Plants with glabrous inflorescence axes and often large leaves lacking abaxial glandular dots along the midvein have often been considered as *A. neriifolia* or *A. coriifolia* sensu stricto, while individuals with pubescent inflorescence axes, and small to large leaves with few to many, conspicuous to inconspicuous abaxial glands along the midvein have been treated as *A. pohlii*. However, these characters are not consistently correlated, and intermediate specimens—e.g., *Harley 15911* (E, L, MO, NY, US), *Harley 18758* (NY), *St.-Hilaire s.n.*, 1816–1821 (P), *St.-Hilaire 234* (P), *Claussen 5* (BM), *Claussen 214* (G), *Barreto 528* (F), *Williams 8130* (GH), and *Pereira 2040* (L)—are common. In addition, both morphological extremes, along with intermediates, grow in the same geographic regions. Thus, these plants are here considered as representatives of a single variable species. Yet specimens previously referred to *A. bradei* (occurring in Minas Gerais, from Diamantina to Chapada in the Serra do Espinhaço) are distinctive due to their leaves that are more or less oblong to slightly elliptic, with cuneate to rounded bases and numerous very conspicuous glandular dots along the midvein abaxially. These populations are here maintained as a weakly delimited variety of *A. coriifolia*. The remaining more variable populations are all treated under var. *coriifolia* due to the lack of any internal discontinuities in the pattern of variation. The two varieties are, at least in part, geographically separate (MAP 5), but both may occur together in the Diamantina region, and the factors isolating them are in need of field investigation.

10. **Agarista pulchra** (Cham. & Schldl.) G. Don, Gen. Syst. **3:** 837. 1834.

Andromeda pulchra Cham. & Schldl. Linnaea **1:** 521. 1826. *Leucothoë pulchra* (Cham. & Schldl.) DC. Prodr. **7:** 604. 1839. *Andromeda sellowii* Steudel, Nomencl. Bot. **2:** 89. 1841, nomen superfl. TYPE: Brazil, without definite locality, *Sellow s.n.* (holotype, B (destroyed); fragment of holotype, NY; isotypes, E!, G!, K!).

Gaylussacia leptobotrys DC. Prodr. **7:** 560. 1839. TYPE: Brazil, Minas Gerais, Serra de Piedade, Nov. 1834, *Lund s.n.* (holotype, G-DC; fragment of holotype, NY; isotypes, C!).

Leucothoë pulchra (Cham. & Schldl.) DC. var. *parvifolia* Meissner *in* Martius, Fl. Brasil. **7:** 161. 1863. TYPE: Brazil, Minas Gerais, without definite locality, 1843, *Claussen 159* (lectotype (selected by Sleumer, 1959), BR; isolectotypes, G!, NY!).

Shrub to ca. 1 m tall. Twigs glabrous to very sparsely pubescent, with nonseptate pith. Buds to ca. 1.3 mm long. Leaves alternate; petiole 1–5 mm long; blade revolute in bud, ovate to elliptic, 1.3–3.5(–4.3) by 0.8–2(–2.5) cm, ± flat, usually very coriaceous, the apex acute- to rounded- or retuse-mucronate, the base cordate to rounded, the margin entire, plane, the adaxial surface glabrous to sparsely pubescent on proximal portion of midvein, the abaxial surface glabrous, usually with few to several inconspicuous to conspicuous glandular dots along midvein. Inflorescences axillary racemes to 4–12 cm long, axis glabrous to very sparsely (moderately) pubescent. Pedicels 3.5–7(–8) mm long, glabrous to sparsely (rarely moderately) pubescent; bracteoles 2, alternate to subopposite, from nearly basal to within lower ⅓ (to near middle) of pedicel, triangular to narrowly so, to ca. 1.2 mm long; bracts to 1.7 mm long. Calyx lobes triangular with acuminate apices, 1.2–2 by 0.6–1.3 mm, abaxial surface glabrous (to rarely sparsely to moderately pubescent); corolla cylindrical, 6–8.5(–9) by 2.5–4 mm, white (to reddish), abaxially glabrous; filaments 3.5–5 mm long, anthers 1.1–1.3 mm long; ovary glabrous (rarely sparsely to moderately pubescent). Capsules subglobose to short-ovoid, 3.5–4.5 by 5–7 mm, placentae subapical (to occasionally ± central); seeds 1–1.5 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, small region of south-central Minas Gerais (MAP 5). Open campo and slopes, low, dense woodland and thickets; iron-rich soil. Flowering September through January.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Camarinhas, Serra do Ouro Prêto, *Barreto 9065* (F); Morro de Santa Anna, Ouro Prêto, *Barreto 9070* (F); Serra da Piedade, *Damazio 1240* (G), *Glaziou 20390* (C, G, K), *Riedel 2666* (G, L, NY); Serra de José d'El Rey and Ouro Prêto, Campo de São Sebastião, *Glaziou 15173* (C); Caeté, Serra da Piedade, *Ianna & Strang 1975/1486* (L); Serra da Piedade, ca. 40 km E of Belo Horizonte, near BR-31, *Irwin et al. 30468* (NY, US); Serra de Ouro Branco, *St.-Hilaire s.n.*, 1816–1821 (NY, P).

Agarista pulchra is apparently closely related to *A. coriifolia* and *A. subrotunda*. It can be distinguished from the former by its usually glabrous (vs. glabrous to densely pubescent) inflorescence axis and its usually smaller, broader leaves with a length/width quotient of 0.9–1.7 (vs. ca. 1.8–6), and from the latter by its glabrous abaxial leaf surface and corolla. The factors isolating these taxa are in need of field study. See illustration in Hooker (1847, *t. 4313*).

Several specimens—for example, *St.-Hilaire s.n.*, 1816–1821—are unusual

because of their rather large leaves and their capsules with central placentae. These plants are tentatively placed here, although they also show similarities to *Agarista coriifolia*.

11. **Agarista subrotunda** (Pohl) G. Don, Gen. Syst. **3:** 837. 1834.

Andromeda subrotunda Pohl, Pl. Brasil. **2:** 32. *t. 121.* 1828/29. *Leucothoë subrotunda* (Pohl) DC. Prodr. **7:** 603. 1839. TYPE: Brazil, Minas Gerais, São João d'El Rey, Oct. 1819, *Pohl s.n.* (not seen).

Andromeda pistrix Cham. Linnaea **8:** 508. 1833. *Agarista pistrix* (Cham.) G. Don, Gen. Syst. **3:** 838. 1834. *Leucothoë pistrix* (Cham.) DC. Prodr. **7:** 604. 1839. *Leucothoë subrotunda* (Pohl) DC. var. *pistrix* (Cham.) Meissner *in* Martius, Fl. Brasil. **7:** 161. 1863. TYPE: Brazil, Minas Gerais, Serra do Lenheiro, *Sellow s.n.* (holotype, B (destroyed); fragment of holotype, NY).

Shrub to ca. 2.5 m tall. Twigs with or without scattered gland-headed hairs, otherwise densely pubescent, with nonseptate pith. Buds to ca. 1.2 mm long. Leaves alternate; petiole 2–4.5 mm long; blade revolute in bud, ovate to elliptic or nearly orbicular, 1–3.5(–4) by 0.7–2.5(–3.7) cm, flat to slightly abaxially curved, very coriaceous, the apex acute- to rounded- or retuse-mucronate, the base cordate, the margin entire (ciliate due to gland-headed hairs), ± plane, the adaxial surface sparsely pubescent on lamina and midvein, often glabrescent, the abaxial surface with or without gland-headed hairs on midvein, otherwise moderately to densely pubescent on lamina and sparsely to densely pubescent on midvein, with few to several inconspicuous to conspicuous glandular dots along midvein (although these often obscured by dense pubescence). Inflorescences axillary racemes to 4–7 cm long, the axis with or without scattered gland-headed hairs, otherwise densely pubescent. Pedicels 5–12.5 mm long, with or without gland-headed hairs, otherwise densely pubescent; bracteoles 2, alternate to subopposite, from nearly basal to near middle of pedicel, narrowly triangular, to ca. 1.3 mm long; bracts to 2 mm long. Calyx lobes triangular to ovate, with acuminate apices, 1.5–2.5 by 1–2 mm, the abaxial surface sometimes with few gland-headed hairs, otherwise densely pubescent; corolla cylindrical, 6.5–9 by 3–4.5 mm, red, abaxially sparsely to densely pubescent; filaments 3.5–4.5 mm long, anthers 1.5–2 mm long; ovary densely pubescent. Capsules short-ovoid, 4–5 by 6–7 mm, placentae subapical; seeds 1.3–2 mm long (probably also larger).

DISTRIBUTION. Brazil, southern Minas Gerais, region surrounding São João d'El Rey (MAP 5). Circa 1065–1675 m alt. Flowering July and August.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Serra de Tiradentes, *Barreto 4787* (L); Serra do Lenheiro, *Glaziou 17110* (C, P); São João d'El Rey, *Sellow s.n.* (E, G, K), *Stephan s.n.*, Aug. 1876 (K).

Agarista subrotunda is likely closely allied with *A. pulchra* and *A. coriifolia*. All of these species have thickly coriaceous, at least occasionally conspicuously gland-dotted leaves, and usually subapical placentae. This species is easily separated from both *A. coriifolia* and *A. pulchra* by its conspicuous abaxially pubescent leaves and corollas. *Agarista chapadensis* has similar abaxially pu-

bescent leaves and flowers and may also be closely related; it can be distinguished from *A. subrotunda* by leaf-base shape (cuneate to rounded vs. cordate) and pedicel length. *Agarista paraguayensis, A. mexicana* var. *pinetorum,* and *A. revoluta* var. *velutina* also have abaxially pubescent leaves, but these taxa differ in many other characters and are not closely related to *A. subrotunda. Agarista subrotunda* appears to be geographically separated from all of the above-mentioned species except *A. pulchra* (MAPS 3, 5, and 6). The taxon has been poorly collected and is in need of field investigation.

12. **Agarista chapadensis** (Kinoshita-Gouvêa) Judd, comb. nov.

Leucothoë chapadensis Kinoshita-Gouvêa, Rev. Brasil. Bot. **4:** 127. *fig. 2.* 1981. TYPE: Goiás, Chapada dos Veadeiros, 20 km N of Alto Paraíso, 1600 m alt., 6 March 1983, *Anderson et al. 6502* (holotype, UNB; isotype, NY!).

Shrub or small tree to ca. 3 m tall. Twigs moderately to densely pubescent, with nonseptate pith. Buds to ca. 1 mm long. Leaves alternate; petiole 2–6 mm long; blade revolute in bud, oblong or elliptic to slightly ovate, 2.4–6 by 0.7–2.2 cm, flat, coriaceous, the apex acute- to rounded-mucronate, the base cuneate to rounded, the margin entire, plane, the adaxial surface sparsely pubescent on midvein, the abaxial surface densely pubescent on lamina and midvein (hairs frequently ferrugineous, at least when young) (with few ± inconspicuous glandular dots along midvein, these obscured by dense pubescence). Inflorescences axillary racemes to 4–6 cm long, axis densely pubescent. Pedicels 3–7 mm long, sparsely to densely pubescent; bracteoles 2, alternate to subopposite, from nearly basal to near middle of pedicel, narrowly triangular, to ca. 1 mm long; bracts to ca. 1.3 mm long. Calyx lobes triangular with acuminate apices, 1–2 by 0.7–1.5 mm, abaxial surface moderately to densely pubescent; corolla cylindrical, 6–8 by 3–4.5 mm, white, abaxially moderately to densely pubescent; filaments 4–6 mm long, anthers 1.1–1.4 mm long; ovary densely pubescent. Capsules subglobose to short-ovoid, 4.5–6 by 6–7 mm, placentae subapical; seeds 1.5–3 mm long.

DISTRIBUTION AND ECOLOGY. Central Brazil, Goiás and Bahia (MAP 5). Sandy or rocky campo, rocky (sandstone) open cerrado, moist woods along streams; ca. 1000–1600 m alt. Flowering February and March.

REPRESENTATIVE SPECIMENS. **Brazil.** BAHIA: 4 km N of Rio de Contas, *Mori et al. 12412* (NY). GOIÁS: Chapada dos Veadeiros, ca. 10 km W of Veadeiros, *Irwin et al. 12862* (FLAS, L, NY).

Agarista chapadensis is probably allied with *A. subrotunda*; however, both taxa have been poorly collected and their relationship will remain somewhat obscure until additional material has been collected. The two taxa are distinctive due to their abaxially conspicuously pubescent leaves. Among the South American species of *Agarista,* only *A. paraguayensis* also has similarly pubescent leaves. *Agarista chapadensis* is easily distinguished from *A. subrotunda* by its rounded- to cuneate- (vs. cordate-)based, often longer leaves and by its shorter pedicels; the taxa are geographically separated (MAP 5).

13. **Agarista paraguayensis** (Sleumer) Judd, comb. nov.

Leucothoë paraguayensis Sleumer, Bot. Jahrb. **78:** 465. 1959. TYPE: Paraguay, Paraguarí, Piribebuy, Salto Piravetá, 23 Nov. 1950, *Sparre & Vervoorst 501* (holotype, LIL; isotypes, C!, K!, S!).

Leucothoë paraguayensis Sleumer var. *calva* Sleumer, Bot. Jahrb. **78:** 465. 1959. TYPE: Paraguay, Amambay, Sierra de Amambay, Cerro Corá, Aug. 1933, *Rojas 6189* (holotype, SI).

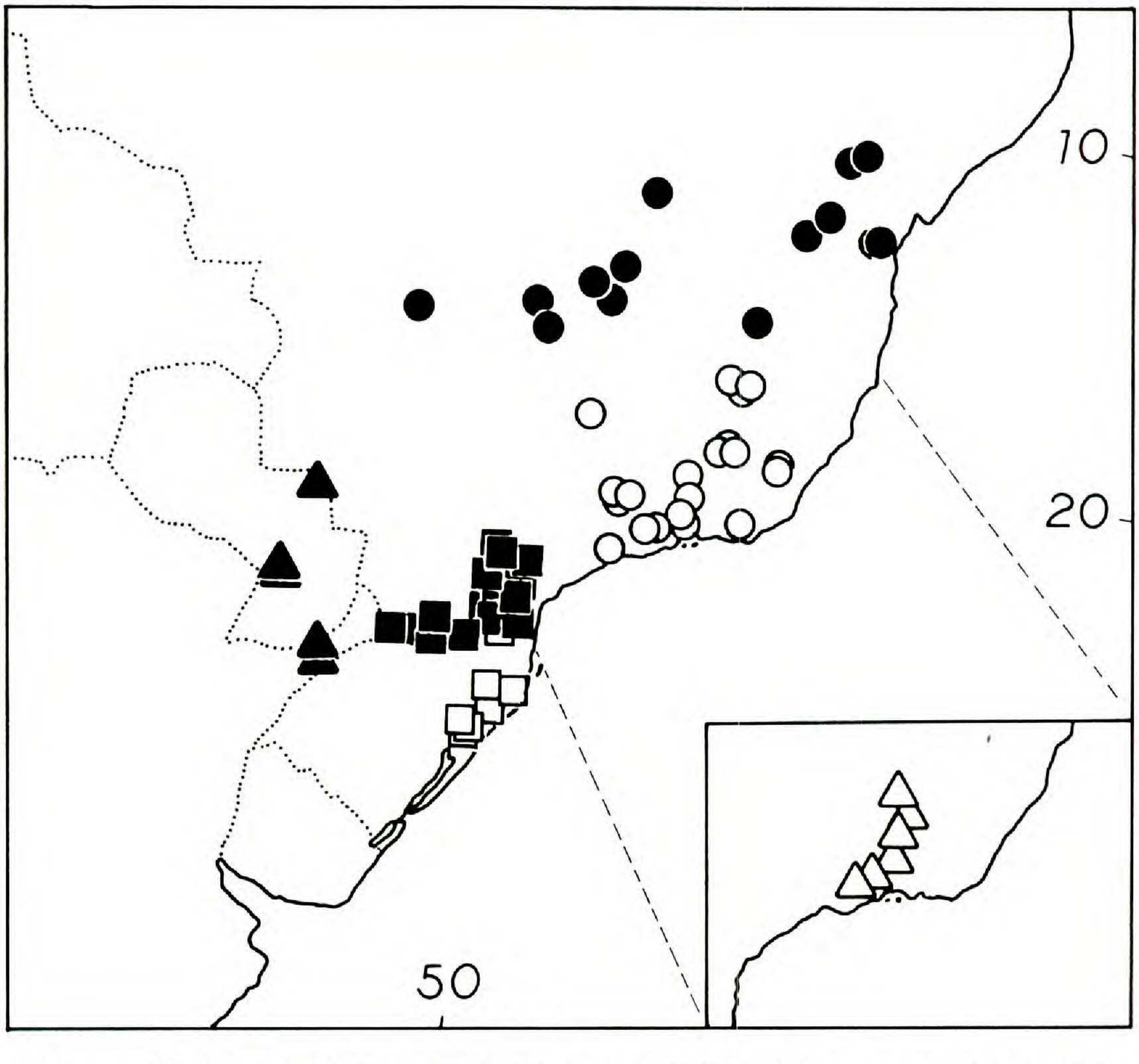
Shrub to ca. 3 m tall. Twigs with or without scattered gland-headed hairs, otherwise sparsely to densely pubescent, with nonchambered to hollow or very sparsely septate pith. Buds to ca. 2.5 mm long. Leaves alternate; petiole 2.5–6 mm long; blade revolute in bud, ovate, 1.8–5.2 by 0.7–2.2 cm, ± flat, coriaceous, the apex acute- to rounded-mucronate or slightly acuminate, the base rounded to cordate, the margin entire (slightly undulate), plane to very slightly revolute, especially near base, the adaxial surface pubescent on midvein (also with few unicellular hairs on lamina), the abaxial surface densely to irregularly and sparsely pubescent on midvein and lamina (glabrous or with pubescence limited to midvein), often with inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 1.5–9 cm long, the axis with or without scattered gland-headed hairs, otherwise moderately to densely pubescent. Pedicels 3–9 mm long, with or without gland-headed hairs, otherwise densely to moderately (sparsely) pubescent; bracteoles 2, opposite to alternate, from nearly basal to within lower ⅓ of pedicel, narrowly triangular, to ca. 1.5 mm long; bracts to 1.5 mm long. Calyx lobes triangular with acuminate apices, 0.9–2.5 by 0.9–1.8 mm, the abaxial surface sometimes with few gland-headed hairs, otherwise sparsely to densely pubescent; corolla cylindrical, 6.5–9 by 3–4 mm, red to white(?), abaxially slightly to very slightly pubescent (to glabrous?); filaments 4.5–5.5 mm long, anthers 1.1–2 mm long; ovary nearly glabrous to densely pubescent. Capsules subglobose, 3.5–4.5 by 5–6.5 mm, placentae ± central; seeds 0.9–1.8 mm long.

DISTRIBUTION AND ECOLOGY. Eastern Paraguay and adjacent Argentina (MAP 6). Rocky areas, steep slopes, ravine slopes along arroyos. Flowering August to December.

REPRESENTATIVE SPECIMENS. **Paraguay:** Campt. Yagin, *Chodat s.n.*, 1914 (G); Cordillera Tobaty, Cerro Tobaty, *Schinini 7920* (L). **Argentina:** Misiones, dept. San Ignacio, Teyucuaré, Peñón Reina Victoria, *Schinini 5499* (F, L, MO); Teyucuaré, *Medan et al. 108* (BAA).

This poorly known species is the only taxon of *Agarista* known to occur in either Paraguay or Argentina. It is probably allied with *A. oleifolia* and *A. pulchella,* from which it can be distinguished by its distinctive combination of often abaxially pubescent leaves and corollas and more or less hollow pith. *Agarista paraguayensis* is superficially similar to *A. mexicana* var. *pinetorum, A. revoluta* var. *velutina, A. chapadensis,* and *A. subrotunda,* all of which have abaxially pubescent leaves. However, it differs from them in placenta position, seed length, and pith structure.

This taxon is variable in leaf indumentum. The leaves of many individuals



MAP 6. Distribution of *Agarista oleifolia* var. *oleifolia* (circles), *A. oleifolia* var. *glabra* (dots), *A. paraguayensis* (solid triangles), *A. minensis* (open squares), *A. pulchella* var. *pulchella* (solid squares), and *A. pulchella* var. *cordifolia* (open triangles).

have a more or less moderate to dense layer of unicellular hairs on the abaxial surface, but those of some plants (e.g., *Sparre & Vervoorst 501*) are essentially glabrous beneath. The taxonomic significance of this variation will remain unknown until the taxon is better known and has been studied in the field.

14. **Agarista oleifolia** (Cham.) G. Don, Gen. Syst. **3:** 838. 1834.

Shrub (to small tree) to 3(–6) m tall, with thickly furrowed bark and often tortuous branches. Twigs with or without scattered gland-headed hairs, otherwise glabrous to sparsely pubescent, with nonchambered to clearly chambered pith. Buds to ca. 1 mm long. Leaves alternate (to nearly 3-whorled); petiole 2–11.5 mm long; blade revolute in bud, (very narrowly) ovate to elliptic or oblong, (2–)2.5–10(–12.5) by 0.4–3.3 cm, ± flat, coriaceous, the apex acute- to rounded-mucronate (slightly acuminate), the base cuneate to rounded or slightly cordate, the margin entire (slightly undulate), plane to very slightly revolute, especially near base, the adaxial surface nearly glabrous to sparsely pubescent on midvein, especially proximal portion, the abaxial surface glabrous to sparsely pubescent

on midvein, usually with inconspicuous glandular dots along midvein. Inflorescences axillary racemes to (2.5–)3–13 cm long, the axis with or without scattered gland-headed hairs, otherwise glabrous to densely pubescent. Pedicels 2.5–15 mm long, with or without gland-headed hairs, otherwise glabrous to densely pubescent; bracteoles 2 (rarely 3), alternate to subopposite, from nearly basal to near midpoint of pedicel (rarely with 1 near apex), to ca. 1.5 mm long; bracts to 2 mm long. Calyx lobes triangular with acuminate apices, 1.4–2.7(–3) by 0.8–2.1 mm, the abaxial surface with or without gland-headed hairs, otherwise glabrous to moderately pubescent; corolla cylindrical, 7.5–16 by (2.5–)3–6.5 mm, red to white, abaxially glabrous; filaments 5.3–8.5 mm long, anthers 1–2.2 mm long; ovary glabrous to sparsely pubescent. Capsules subglobose to short-ovoid, 2.5–5.5 by 4–8 mm, placentae ± central; seeds 0.5–1.3 mm long.

DISTRIBUTION. Southeastern Brazil, from Bahia, Goiás, and extreme southeastern Mato Grosso south to Estado do Rio and São Paulo.

KEY TO THE VARIETIES OF AGARISTA OLEIFOLIA

1. Inflorescence axis sparsely to densely pubescent; corolla 7.5–12 mm long. ..... 14a. var. *oleifolia*.
1. Inflorescence axis glabrous or essentially so; corolla 10.5–16 mm long. ..... 14b. var. *glabra*.

14a. **Agarista oleifolia** (Cham.) G. Don var. **oleifolia** FIGURE 3, b.

Andromeda oleifolia Cham. Linnaea **8:** 504. 1833. *Leucothoë oleifolia* (Cham.) DC. Prodr. **7:** 605. 1839. TYPE: Brazil, Minas Gerais, Itambé, *Sellow s.n.* (holotype, B (destroyed); fragments of holotype, F!, NY; photos of holotype, F, GH!; isotypes, E!, G!, K!, L!).

Leucothoë ambigua Meissner var. *tomentella* Meissner *in* Martius, Fl. Brasil. **7:** 156. 1863 (= *L. ambigua* var. *ambigua*; chosen as nominal variety of *A. ambigua* by Sleumer, 1959, since Meissner described six named varieties of this taxon at the same time). *Agarista ambigua* (Meissner) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. TYPE: Brazil, Minas Gerais, *Martius 837* (lectotype, M! (= holotype of *L. ambigua* var. *tomentella*); fragment of lectotype, F!; isolectotypes, G!, GH!, K!, L!, M!, MO!, NY!, W; photos of isotype, B (destroyed), G!, GH!).

Leucothoë ambigua Meissner var. *hispidula* Meissner *in* Martius, Fl. Brasil. **7:** 156. 1863. *Leucothoë oleifolia* (Cham.) DC. var. *hispidula* (Meissner) Sleumer, Bot. Jahrb. **78:** 476. 1959. TYPE: Brazil, Minas Gerais, Carunhanha R., Sertão do Paranán, *Martius 2000* (holotype, M!).

Leucothoë ambigua Meissner var. *peduncularis* Meissner *in* Martius, Fl. Brasil. **7:** 156. 1863. TYPE: Brazil, Minas Gerais, Serra do Frio, July 1846, *Gardner 4987* (holotype, BM (destroyed?); fragment of holotype, NY!; isotypes, E!, F!, G!, GH!, K!, NY!, P!, S!, US!, W).

Leucothoë stenophylla Loesener, Flora **72:** 77. 1889. *Agarista stenophylla* (Loesener) Niedenzu, Bot. Jahrb. **11:** 236. 1889. TYPE: Brazil, Estado do Rio, Serra dos Orgãos, 21 Jan. 1887, *Glaziou 16232* (holotype, B (destroyed); isotype at B! here designated as lectotype; isolectotypes, C!, F!, K!, P!).

Leucothoë rivularis Sleumer, Notizbl. Bot. Gart. Berlin **12:** 481. 1935. TYPE: Brazil, Minas Gerais, Serra do Itatiaia, 2100 m, 27 Dec. 1895, *Ule 3737* (holotype, B (destroyed); fragment of holotype, F!; photos of holotype, F!, GH!; isotype, HBG!).

Shrub (to small tree) to 3(–6) m tall. Twigs glabrous to sparsely pubescent. Leaves with petiole 2–8 mm long; blade (2–)2.5–8.5(–10.5) by 0.4–2.8 cm, base cuneate, abaxial surface glabrous to sparsely pubescent on midvein. Inflorescences (2.5–)3–12 cm long, axis sparsely to densely pubescent. Pedicels glabrous to densely pubescent. Corolla 7.5–12 mm long, red to white; filaments 5.3–6.8 mm long, anthers 1–1.5 mm long; ovary glabrous to sparsely pubescent. Capsules 2.5–4 by 4–6.5 mm.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, southern and central Minas Gerais and adjacent portions of Estado do Rio and São Paulo (MAP 6). Margins of forests and thickets, frequently along rivers or streams, bogs, open rocky campo; 800–2100 m alt. Flowering chiefly August through October.

REPRESENTATIVE SPECIMENS. **Brazil.** ESTADO DO RIO: Itatiaia, *Brade 21265* (L); Novo Friburgo, *Capell s.n.*, 26 Nov. 1953 (L); Serra do Itatiaia, Retiro, *Dusén 529* (S); Montserrat, *Dusén 2124* (GH, S); Parque Nacional do Itatiaia, margins Rio Campo Belo, *Maas & Martinelli 3162* (NY); Itatiaia, Abrigo Rebouças, *Santos 5755* (L). MINAS GERAIS: Andrelândia, Fazenda da Parahyba, *Barreto 5276* (F, L, NY); Rio Viravinha, *Burchell 5495* (GH, K); Cachoeira do Campo, *Casaretto 2861* (G); Curvello and Rio San Francisco, *Claussen s.n.*, 1837 (L); Fazenda de Manoel José, *Damazio 960* (G); Tiradentes, *Duarte 35505* (F, G, L, S); Rio das Velhas, Itabirito, *Glaziou 15171* (C, G, US); Pico Itambé, S. Antonio do Itambé, *Hatschbach 27511* (C, L, S, UC); Poços de Caldas, Morro do Ferro, *Leoncini & Roppa 206* (L); Caldas, *Regnell II-179* (C, NY, S, US); Uberaba, *Regnell III-835* (C, NY, S, US); near Villa Rica, Itacolumi, *Riedel 408* (G, GOET, K, L); Pico da Bandeira, near Caparaó, *Shepherd et al. 5799* (F, L); Serra de Curimataí, *St.-Hilaire, Cat. B[1], n. 1997* (P); Serra do Caparaó, Macieiras (Grotão), *Strang 220* (L); Serra do Ouro Prêto, *Ule 2619* (HBG); Tejuco [Diamantina], *Vauthier 5* (G, GH, P). SÃO PAULO: Moóca camp, *Brade 5667* (S, SP); rd. from São Bernardo to São Paulo, *Burchell 4054* (K); Butantan, *Gehrt, SP n. 2083* (SP); Cidade Jardim, *Kuhlmann, SP n. 35241* (SP); Campos do Jordão, *Leite 3615* (A, GH); Serra da Bocaina, S of Itatiaia, *Markgraf & Aparicio 10418* (L).

14b. **Agarista oleifolia** (Cham.) G. Don var. **glabra** (Meissner) Judd, comb. nov. FIGURE 5, a, b.

Leucothoë ambigua Meissner var. *glabra* Meissner *in* Martius, Fl. Brasil. **7:** 156. 1863. *Leucothoë oleifolia* (Cham.) DC. var. *glabra* (Meissner) Sleumer, Bot. Jahrb. **78:** 476. 1959. TYPE: Brazil, Bahia, ca. Moritiba, Serra da Jacobina, 1842–1845, *Blanchet 3562* (holotype, W; isotypes, BR, C!, F(specimen and photo)!, G!, GH(specimen and photo)!, K!, MO!, P!).

Leucothoë ambigua Meissner var. *longifolia* Meissner *in* Martius, Fl. Brasil. **7:** 156. 1863. *Leucothoë oleifolia* (Cham.) DC. var. *longifolia* (Meissner) Sleumer, Bot. Jahrb. **78:** 476. 1959. TYPE: Brazil, Goiás, Arrayas, 1841, *Gardner 3876* (holotype, BM; isotypes, E!, F!, G!, K!, NY!, P!, W).

Leucothoë martii Meissner var. *puberula* Meissner *in* Martius, Fl. Brasil. **7:** 155. 1863. TYPE: Brazil, Minas Gerais/Pernambuco, Rio Fermo, *Martius s.n.* (holotype, M!; fragment of holotype, NY; photo of holotype, GH!; isotypes, G!, M!).

Leucothoë martii Meissner var. *glabra* Meissner *in* Martius, *ibid.* 156. TYPE: Brazil, Minas Gerais/Pernambuco, Rio Fermo, *Martius s.n.* (holotype, M!; isotype, M!).

Leucothoë spectabilis Meissner *in* Martius, *ibid.* 159. *Agarista spectabilis* (Meissner) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. TYPE: Brazil, Goiás, banks of S. Bartholomeo, Chapada de S. Marcos, Aug. 1834, *Riedel 2484* (holotype, LE; isotype, NY!).

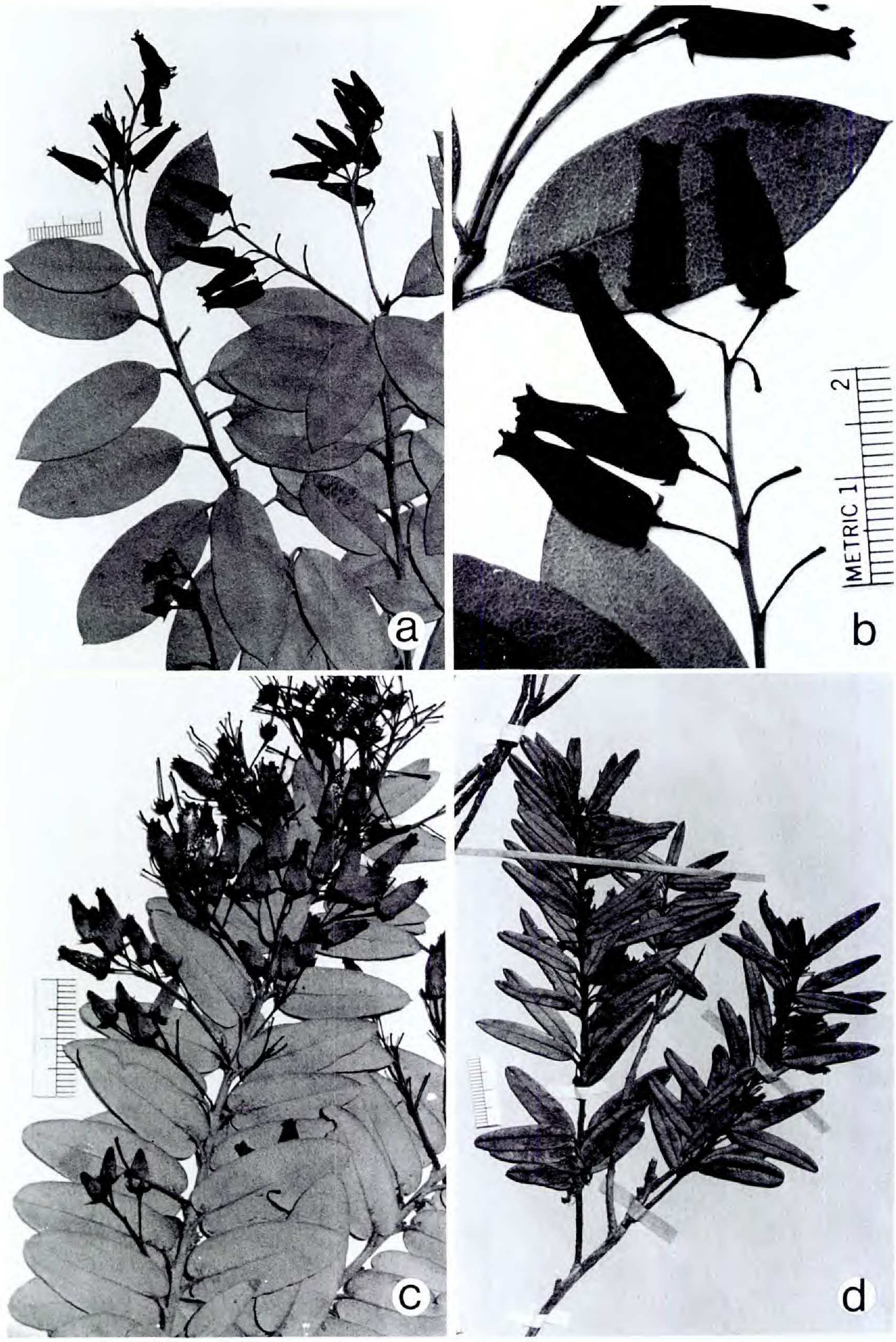


FIGURE 5. a, b, *Agarista oleifolia* var. *glabra* (*Irwin & Soderstrom 5830*): in b note glabrous inflorescence axis and flowers articulated with pedicels. c, *A. pulchella* var. *pulchella* (*Hatschbach 19703*): note elongate racemes and cordate-based leaves. d, *A. minensis* (*Ule 1840*): note short racemes and round-based leaves. Scale = 2 cm.

Leucothoë varnhageniana Reichardt, Verh. Zool.-Bot. Ges. Wien **33:** 323. 1884. *Agarista varnhageniana* (Reichardt) Niedenzu, Bot. Jahrb. **11:** 236. 1889. TYPE: Brazil, Goiás, Villa Formosa do Imperatriz, *Seguro 68* (holotype, w; fragment of holotype, F!; photos of holotype, A!, F!).

Shrub (to small tree) to 3(–4) m tall. Twigs glabrous. Leaves with petiole 4–11.5 mm long; blade (2.5–)3.5–10(–12.5) by 0.9–3.3 cm, base cuneate to rounded, abaxial surface glabrous. Inflorescences 6–13 cm long, axis glabrous or essentially so. Pedicels glabrous. Corolla 10.5–16 mm long, red (rarely white); filaments 6.5–8.5 mm long, anthers 2–2.2 mm long; ovary glabrous. Capsules 3.5–5.5 by 5.5–8 mm.

DISTRIBUTION AND ECOLOGY. South-central Brazil, from Bahia and northern Minas Gerais east to Goiás and southeastern Mato Grosso (MAP 6). Scrub vegetation over sandstone, woodland and thickets, especially along rivers or streams; ca. 700–1700 m alt. Flowering chiefly August through October.

REPRESENTATIVE SPECIMENS. **Brazil.** BAHIA: Serra do Rio de Contas, 3 km N of town of Rio de Contas, *Harley et al. 15383* (E, L, NY, US); Serra do Sincorá, by Rio Cumbuca, 3 km N of Mucugê on rd. to Andaraí, *Harley 18705* (NY); Serra do Tombador, 18 km E of Morro do Chapéu, Rio Ferro Doido, *Irwin et al. 32626* (FLAS, NY); Lençóis, rd. to Barro Branco, *Mori & Funch 13349* (NY). DISTRITO FEDERAL: Parque Municipal do Gama, ca. 20 km S of Brasília, *Irwin & Soderstrom 5830* (C, F, L, MO, NY, SP, US). GOIÁS: Meia Ponte, near Rio das Almas, *Glaziou 21690* (C, K, P, S); ca. 5 km S of Cristalina, *Irwin et al. 9852* (F, NY); along Rio de Passa Quatro, Joaquim Diaz, *St.-Hilaire, Cat. C, n. 869* (L, P). MATO GROSSO: Rib. Claro, Alto Araguaia, *Hatschbach 35079* (L). MINAS GERAIS: near Grão Mogol, *Williams & Assis 8190* (GH).

Agarista oleifolia is probably most closely related to *A. pulchella, A. minensis,* and *A. paraguayensis.* All four species have moderate to large, flat leaves and capsules with more or less centrally positioned placentae. *Agarista oleifolia* is easily distinguished from *A. paraguayensis* by its abaxially glabrous corollas and leaves and its solid to chambered pith, and from *A. minensis* by its longer inflorescences and often wider leaves. *Agarista oleifolia* is geographically separated from both of these species. It can be distinguished from the very similar but geographically separated *A. pulchella* var. *pulchella* by its differently shaped leaves and its often longer petioles; in addition, the sympatric *A. pulchella* var. *cordifolia* can be readily distinguished by its usually subapical placentae and its smaller leaves. Individuals of *A. oleifolia* are also sometimes confused with *A. uleana, A. niederleinii* var. *acutifolia,* and *A. coriifolia*; see distinguishing characters in key.

Populations of *Agarista oleifolia* are separable into two morphologically distinctive and geographically separate varieties. The more northern, var. *glabra,* is best distinguished from var. *oleifolia* by its glabrous (vs. sparsely to densely covered with short unicellular hairs) inflorescence axis and its usually larger, more frequently red corollas. Variety *oleifolia* has been illustrated by Meissner (1863, *t. 58*).

Both taxa are variable in glandular indumentum and leaf shape, which has led to the description of numerous species and varieties (see synonymy) that cannot be maintained when the entire range of variation is considered. Indi-

viduals with small, very narrowly ovate, acute-apexed leaves are frequent in the Serra do Itatiaia (and also occur in the Serra dos Órgãos). Such plants were described as *Leucothoë stenophylla* by Loesener (1889) and maintained as a distinct species by Sleumer (1959); however, this form intergrades completely with more typical *A. oleifolia* (see *Dusén 2124* (GH, S), *Dusén s.n.*, 15 June 1902 (S), *Dusén s.n.*, 22 July 1902 (S)). Such narrow-leaved plants have occasionally been confused with *A. minensis.*

Several specimens from São Paulo (i.e., *Hoehne, SP no.* (SP), *Lutz 770* (NY, US), *Lutz 1920* (L)) have small, ovate, ± revolute, abaxially curved leaves, and *Lutz 770* has robust capsules with ± subapical placentae. These individuals may be hybrids between *Agarista oleifolia* and a species with small, strongly revolute leaves such as *A. hispidula* or *A. chlorantha. Leite 3615* (A, GH) has slightly ferrugineous hairs on its inflorescence axes and may represent a hybrid with the sympatric *A. eucalyptoides.*

15. **Agarista minensis** (Glaz. ex Sleumer) Judd, comb. nov. FIGURE 5, d.

Leucothoë minensis Glaz. Bull. Soc. Bot. France **57:** 129. 1910, nomen nudum. *Leucothoë minensis* Glaz. ex Sleumer, Notizbl. Bot. Gart. Berlin **12:** 480. 1935. TYPE: Brazil, Minas Gerais, Biribiry, Mocotó, near Diamantina, 28 March 1892, *Glaziou 19572* (holotype, B (destroyed); isotype at K! here designated as lectotype; isolectotype, P!).

Shrub to 4 m tall. Twigs glabrous to sparsely pubescent, with clearly chambered pith. Buds to ca. 0.8 mm long. Leaves alternate; petiole 2–6 mm long; blade revolute in bud, slightly and narrowly ovate to narrowly oblong, (1–)1.6–5.6 by 0.3–1(–1.7) cm, ± flat, coriaceous, the apex acute- to rounded-mucronate, the base cuneate to truncate, the margin entire, plane to very slightly revolute, especially near base, the adaxial surface sparsely to very sparsely pubescent on proximal portion of midvein, the abaxial surface glabrous (with few very inconspicuous glandular dots along midvein). Inflorescences (fascilelike) axillary racemes to 0.5–1.5(–2.5) cm long, axis sparsely to densely pubescent. Pedicels 4–10 mm long, very sparsely to moderately pubescent; bracteoles 2, alternate to subopposite, from nearly basal to near midpoint of pedicel, narrowly triangular to linear, to ca. 1.6 mm long; bracts to 1.2 mm long. Calyx lobes triangular with acuminate (to acute) apices, 1.4–2.6 by 0.8–1.4 mm, abaxial surface glabrous to sparsely pubescent; corolla cylindrical, 6.5–11 by 2.5–4.5 mm, white, abaxially glabrous; filaments 5–5.5 mm long, anthers ca. 1.2 mm long; ovary glabrous to very slightly pubescent near apex. Capsules short-ovoid to subglobose, 3–5 mm by 4.5–7.5 mm, placentae ± central; seeds 1–1.5 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Santa Catarina and Rio Grande do Sul (MAP 6). Scrub and forests along streams and rivers; 900–1300 m alt. Flowering November through December (January).

REPRESENTATIVE SPECIMENS. **Brazil.** RIO GRANDE DO SUL: Bom Jesus, Fazenda Bernardo Velho, *Rambo 34939* (MO, S); Cambará, near S. Francisco de Paula, *Rambo 36728* (US); Taimbé, near S. Francisco de Paula, *Rambo 49306* (S); Jaquirana, near S. Francisco de

Paula, *Rambo 51933* (S, US); Passo do Inferno, near Canela, *Rambo 56563* (B). SANTA CATARINA: Bom Jardim, São Joaquim, *Reitz & Klein 7968* (L); Campo Alegre, Pinheiral, Morro Iquererim, *Smith & Klein 7968* (L); 2 km W of Rio Capetinga on rd. to Dionísio Cerqueira, *Smith et al. 9622* (US); Serra Geral, Campos de Capivari, *Ule 1840* (HBG, L).

Although this taxon was included in *Agarista niederleinii* by Sleumer (1959), the two species differ greatly in capsule morphology and inflorescence length and are probably not closely related. *Agarista minensis* is actually closely related to *A. pulchella* var. *pulchella,* from which it is distinguished by its shorter inflorescences and its different leaf shape (length/width quotient (2.5–)3–6 vs. (1.4–)1.6–3(–3.5), base cuneate to truncate vs. cordate). (See Emrich & Rambo, 1949, *fig. 20,* and Marques & Klein, 1975, *pl. 6, fig. 9.*) The ranges of the two taxa overlap only slightly (MAP 6). However, some hybridization may be occurring between them because a few specimens of *A. pulchella* (e.g., *Smith & Klein 8470* (L, US), from Santa Catarina) show some *A. minensis*-like characters. *Agarista minensis* is also allied to *A. oleifolia* and can easily be confused with especially small and narrow-leaved individuals of *A. oleifolia* var. *oleifolia.* The two can be distinguished by the length of the inflorescences and shape of the leaves—especially the apex, which is never narrowly acute in *A. minensis* but is usually so in narrow-leaved variants of *A. oleifolia* var. *oleifolia.*

The provenance of the type (*Glaziou 19572*) is very uncertain. These specimens are identical with *Ule 1840* (HBG, L) and *1841* (see Sleumer, 1959), collected in the state of Santa Catarina. However, *Glaziou 19572* was supposedly collected in Minas Gerais near Diamantina! *Glaziou 19572* is the only collection of *A. minensis* from Minas Gerais, an area separate from the major portion of the species' range, Santa Catarina and Rio Grande do Sul. It is very probable that the specimens represented by *Glaziou 19572* were actually sent to Glaziou by Ule, and that the label information was altered by Glaziou; see discussion in Wurdack (1970).

16. **Agarista pulchella** Cham. ex G. Don, Gen. Hist. **3:** 838. 1834.

Shrub to 2(–3) m tall. Twigs with or without scattered gland-headed hairs, otherwise essentially glabrous to densely pubescent, with nonchambered to irregularly chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 1.5–5 mm long; blade revolute in bud, ± ovate, 0.5–4(–5) by 0.4–2(–2.8) cm, ± flat, coriaceous, the apex rounded- to acute-mucronate (short-acuminate), the base cordate (to rarely truncate), the margin entire (to serrulate due to gland-headed hairs) (undulate), plane to very slightly revolute, especially near base, the adaxial surface glabrous to sparsely pubescent on midvein, especially proximal portion, the abaxial surface with or without few gland-headed hairs on midvein, otherwise glabrous to sparsely pubescent (with few very inconspicuous glandular dots) on midvein. Inflorescences axillary racemes (axillary panicles, or terminal racemes or panicles) to (1.5–)2–7(–12) cm long, the axis with or without scattered gland-headed hairs, otherwise glabrous to densely pubescent. Pedicels 4–15 mm long, with or without gland-headed hairs, otherwise glabrous to densely pubescent; bracteoles 2 (to 5), alternate to subopposite, from nearly basal to near midpoint (or rarely apex) of pedicel, narrowly

triangular to linear, to ca. 2.2 mm long, occasionally with 1 or more subtending axillary flowers; bracts to 3 mm long. Calyx lobes triangular with acuminate (to acute) apices, 1.4–2.6 by 0.8–1.5 mm, the abaxial surface with or without gland-headed hairs, otherwise glabrous to densely pubescent; corolla cylindrical, 6.5–13 by 3–5.5 mm, white with reddish apex to red throughout, abaxially glabrous to sparsely pubescent; filaments 4–6.5 mm long, anthers 1.2–1.5 mm long; ovary glabrous to densely pubescent. Capsules short-ovoid to subglobose, 3–5 by 4.5–8 mm, placentae central to subapical; seeds 0.8–1.7 mm long.

DISTRIBUTION. Southeastern Brazil, from Paraná and Santa Catarina, and disjunctly to the north in Minas Gerais and adjacent São Paulo.

KEY TO THE VARIETIES OF AGARISTA PULCHELLA

1. Capsules with placentae usually ± central; leaves with length/width quotient (1.4–)1.6–3(–3.5), margin not (rarely slightly) undulate; [Paraná, Santa Catarina, and adjacent portion of São Paulo]. ..... 16a. var. *pulchella*.
1. Capsules with placentae usually subapical; leaves with length/width quotient 0.8–2, margin often clearly undulate; [Minas Gerais and adjacent northern portion of São Paulo]. ..... 16b. var. *cordifolia*.

16a. **Agarista pulchella** Cham. ex G. Don var. **pulchella** FIGURE 5, C.

Andromeda pulchella Cham. Linnaea **8:** 509. 1833, a later homonym of *Andromeda pulchella* Salisb. Prodr. 289. 1796, nomen superfl. (*A. mariana* L. = *Lyonia mariana* (L.) D. Don cited in synonymy). *Leucothoë pulchella* (Cham. ex G. Don) DC. Prodr. **7:** 604. 1839. TYPE: Brazil, Minas Gerais, Antônio Pereira (see Meissner *in* Martius, 1863; locality very questionable since nearly all collections from Paraná or Santa Catarina), *Sellow 4830* (holotype, B (destroyed); fragments of holotype, F!, NY; photos of holotype, F!, GH!).

Shrub to 2(–3) m tall. Twigs glabrous to densely pubescent. Leaves with petiole 1.5–5 mm long; blade 1.2–4(–5) by 0.4–1.8(–2.8) cm, margin not (rarely slightly) undulate; adaxial and abaxial surfaces glabrous to sparsely pubescent on midvein. Inflorescences axillary racemes (axillary panicles, or terminal racemes or panicles) to 2–7(–12) cm long, axis glabrous to densely pubescent. Corolla 7.5–13 by 3–5 mm; filaments 4.8–6.5 mm long. Capsules 3–4 by 5.5–6 mm, placentae ± central (to rarely subapical); seeds 0.8–1.3 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Paraná, Santa Catarina, and adjacent regions of São Paulo (MAP 6). Gallery forests along rivers or streams, bogs, thickets or thicket-margins, sandy or rocky campo; (110–)780–1500 m alt. Flowering (August) September through November (December).

REPRESENTATIVE SPECIMENS. **Brazil.** PARANÁ: Rio dos Papagaios, *Dombrowski 3009 & Kuniyoshi 2489* (L); Palmeira, *Dombrowski 6596* (L); Serrinha, *Dusén 6955* (F, GH, MO, S); Villa Velha, *Dusén 7272* (S); Jaguariaíva, *Jönsson 372*[a] (A, S); Lapa, Rio São Vicente, Serrinha, *Hatschbach (Curial) 518* (L, S); Lapa, Rio Passa Dois, *Hatschbach 5097* (US); Arapoti, Rio das Cinzas, Barra do Perdizes, *Hatschbach 7223* (L); Palmeira, Rod. do Café, *Hatschbach 10158* (B); Pôrto Amazonas, Fazenda São Luís, *Hatschbach 10243* (L); Ponta Grossa, Passo do Pupo, *Hatschbach 17380* (L, UC); Balsa Nova, Barra Rio Papagaios, *Hatschbach 19703* (MO, UC); Estr. do Cerne, Serra das Furnas, Piraí do Sul,

Hatschbach & Guimarães 24761 (K, MO, S, UC, US); Morro da Baliza, Lageadinho, Palmas, *Hatschbach 30747* (C, L, UC, US); Serra da Canha, Cerro Azul, *Hatschbach 32608* (C, L, UC); Rod. dos Mineiros, Almirante Tamandaré, *Hatschbach 37224* (L); Estr. Curitiba to Ponta Grossa, km 38, Serra São Luís do Purunã, *Pabst 5909 & Pereira 6082* (L). SANTA CATARINA: Fazenda Carneiros, Caçador, *Klein 3543* (L); Morro do Iquererim, Campo Alegre, *Reitz & Klein 4766* (L, NY, US); 11 km E of Mafra on rd. to Tinguí, *Smith & Klein 8470* (L, US); Irani, Campo de Irani, *Smith & Klein 13030* (GH, L, MO, UC, US, WIS); Fazenda Campo São Vicente, 24 km W of Campo Erê, *Smith & Klein 13832* (L, NY, US). SÃO PAULO: Itararé, Campos de São Pedro, near Serra de Bom Sucesso, Fazenda Ventania, *Mattos 14108* (SP).

16b. **Agarista pulchella** Cham. ex G. Don var. **cordifolia** (Meissner) Judd, comb. nov.

Leucothoë cordifolia Meissner *in* Martius, Fl. Brasil. **7:** 162. *t. 60, fig. 2.* 1863. *Agarista cordifolia* (Meissner) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. *Leucothoë pulchella* (Cham. ex G. Don) DC. var. *cordifolia* (Meissner) Sleumer, Bot. Jahrb. **78:** 473. 1959. TYPE: Brazil, Minas Gerais, Serra do São João d'El Rey and Serra de São José, June 1824, *Riedel 308* (holotype, LE; isotype, NY!).

Shrub to 1.5 m tall. Twigs moderately to densely pubescent. Leaves with petiole 1.5–3 mm long; blade 0.5–3.5 by 0.4–2 cm, margin often clearly undulate; adaxial and abaxial surfaces ± sparsely pubescent on midvein. Inflorescences axillary racemes to (1.5–)2–5.5 cm long, axis densely pubescent. Corolla 6.5–10 by 3.5–5.5 mm; filaments 4–4.5(?) mm long. Capsules 2.5–5 by 4.5–8 mm, placentae usually subapical; seeds ca. 0.8–1.7 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais and adjacent São Paulo (MAP 6). Dry, rocky campo; ca. 1600–1700(?) m alt. Flowering March, June, July, and October through December.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Serra de Tiradentes, *Barreto 17476* (NY); São José d'El Rey and Ouro Prêto, *Glaziou 17109* (B, C, NY); Serra do Ibitipoca, *St.-Hilaire, Cat. D, n. 238* (P). SÃO PAULO: Serra da Bocaina, *Brade & Duarte 21179* (L); Serra da Bocaina, Vacca Cahio, *Glaziou 8236* (C, G, P, US); Barreiro Co., Serra da Bocaina, Lageado Farm, *Segadas-Vianna 2800* (L); Silveiras Co., Serra da Bocaina, Jardim Farm, *Segadas-Vianna 3256* (L).

Agarista pulchella is most closely related to *A. minensis* and *A. oleifolia.* It can be distinguished from the former by its longer inflorescences and by the length/width quotient (usually 1.6–3 vs. 3–6) and the bases (cordate vs. cuneate to truncate) of its leaves; from the latter, by its often shorter, more consistently ovate, cordate-based leaves with often shorter petioles. The ranges of *A. pulchella* and *A. minensis* overlap slightly (in northern Santa Catarina), and a few intermediate specimens are known (e.g., *Smith & Klein 8470,* L, US); thus, some hybridization may be occurring. *Agarista oleifolia* is geographically separated from the southern *A. pulchella* var. *pulchella,* but it occurs sympatrically with the northern var. *cordifolia. Agarista pulchella* var. *cordifolia* is easily separable from *A. oleifolia* by the characters given above, as well as by its subapical placentae. Intermediate specimens are apparently unknown. Specimens of *A. pulchella* are occasionally identified as *A. niederleinii, A. subcordata,* or *A. coriifolia*; see distinguishing characters given in key.

Populations of *Agarista pulchella* are divisible into two geographically separate varieties (see illustration of var. *pulchella* in Marques & Klein (1975, *pl. 7*), and of var. *cordifolia* in Meissner (1863, *t. 60, fig. 2*)). Variety *pulchella* has been widely collected in Paraná and Santa Catarina, while var. *cordifolia* seems to be uncommon and limited to a small portion of Minas Gerais and adjacent São Paulo (MAP 6). Sleumer (1959) first recognized the close relationship between these two taxa. Although the capsules of *A. pulchella* var. *pulchella* usually have ± central placentae, plants with subapical placentae (e.g., *Jönsson 224*[a], S)—the typical condition in var. *cordifolia*—are known. *St.-Hilaire, Cat. D, n. 238* is here placed in *A. pulchella* var. *cordifolia*; this specimen is aberrant in having moderately pubescent corollas and capsules with central placentae. However, *A. pulchella* var. *cordifolia* sometimes has slightly pubescent corollas (see *Riedel 308*, NY), and individuals with atypical placenta position occur very occasionally in the southern populations of this species. The unusual placenta position could possibly indicate that this specimen is a hybrid with *A. hispidula*, a species with central placentae and conspicuously pubescent corollas that grows sympatrically with *A. pulchella* in southern Minas Gerais. Field studies are necessary to determine the placement of this unusual specimen conclusively.

Agarista pulchella var. *pulchella* is quite variable in the shape and the length/width quotient of its leaves. At one extreme are plants with short, rather broad, clearly cordate-based leaves, and at the other are those with longer, narrower, and only slightly cordate ones. The former plants are vegetatively rather similar to var. *cordifolia* and have often been identified as such, while the latter are easily confused with *A. minensis*.

17. **Agarista nummularia** (Cham. & Schldl.) G. Don, Gen. Syst. **3:** 837. 1834. FIGURE 6, a, b.

Andromeda nummularia Cham. & Schldl. Linnaea **1:** 520. 1826. *Leucothoë nummularia* (Cham. & Schldl.) DC. Prodr. **7:** 603. 1839. TYPE: Brazil, Rio Grande do Sul, Pôrto Alegre (see Meissner *in* Martius, 1863), *Sellow 1229* (holotype, B (destroyed); fragment of holotype, F!; photos of holotype, F!, G!, GH!; isotype, G-DC).

Leucothoë nummularia (Cham. & Schldl.) DC. var. *floccigera* Sleumer, Bot. Jahrb. **78:** 460. 1959. TYPE: Brazil, Rio Grande do Sul, Povo Novo, near Pelotas, 12 Nov. 1901, *Malme 401* (holotype, S!; isotypes, GH!, S!).

Erect shrub or subshrub to 2 m tall, with bark usually not well developed. Twigs with or without scattered gland-headed hairs, otherwise sparsely to densely pubescent, with hollow to irregularly chambered pith. Buds to ca. 1.2 mm long. Leaves alternate; petiole 0.5–2.5 mm long; blade revolute in bud, ovate to elliptic or orbicular, 0.5–1.5(–2.3) by 0.5–1.6(–2) cm, ± flat, coriaceous, the apex obtuse- to retuse-mucronate (rarely short-acuminate), the base cordate to ± truncate (rounded), the margin entire to serrulate due to gland-headed hairs (slightly undulate), plane to very slightly revolute near base, the adaxial surface with or without gland-headed hairs, otherwise sparsely pubescent on proximal portion of midvein, the abaxial surface with or without gland-headed hairs on midvein and blade, otherwise glabrous to sparsely pubescent on proximal portion of midvein (with few very inconspicuous glandular dots along midvein).

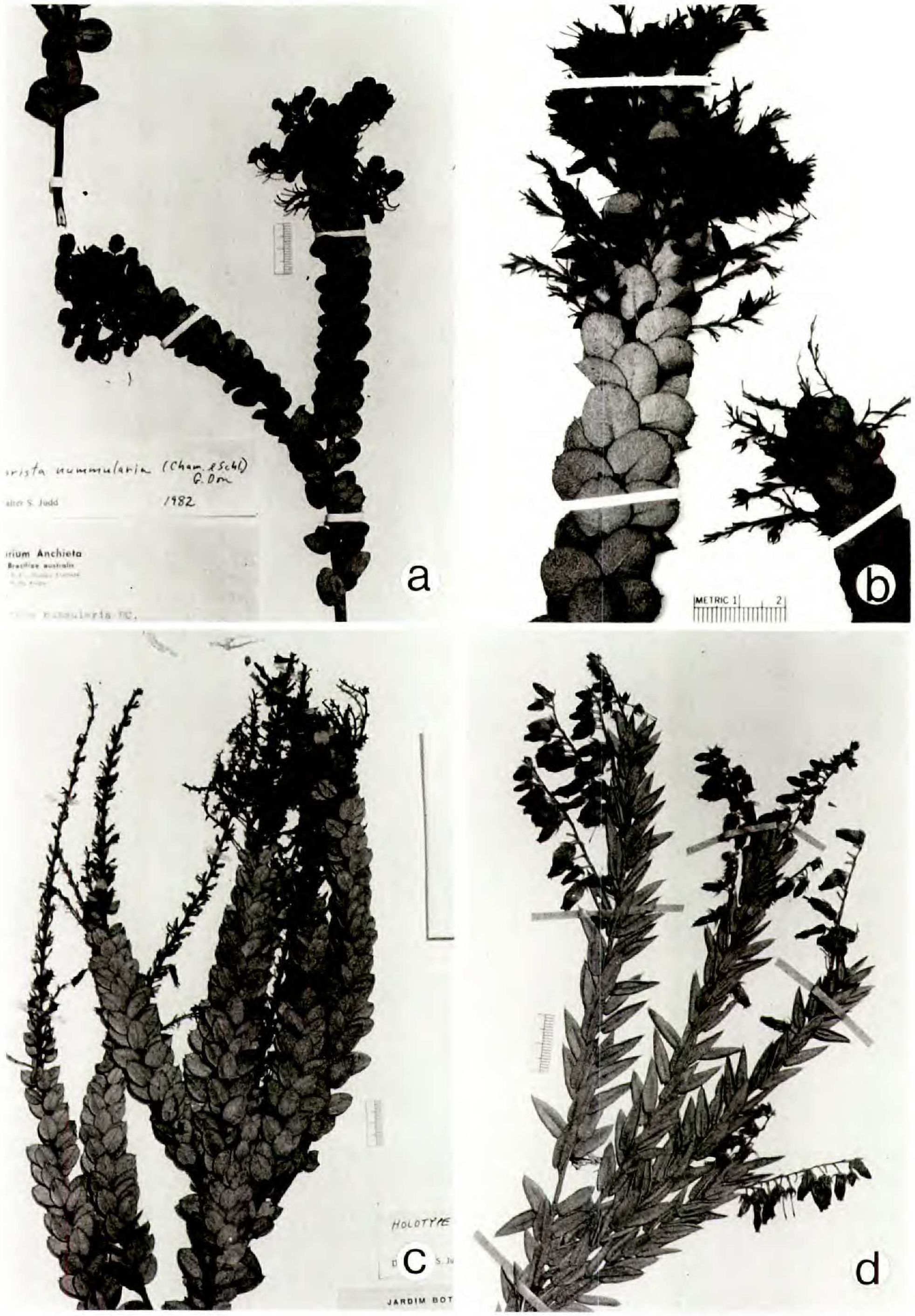


FIGURE 6. a, b, *Agarista nummularia:* a, *Rambo 53881*; b, *Rambo 48695*. c, *A. virgata* (*Duarte 8098*): note wandlike, rigidly ascending branches. d, *A. chlorantha* (*Ratter et al. 3384*). Scale = 2 cm.

Inflorescences axillary racemes to 1.5–8 cm long, the axis with or without scattered gland-headed hairs, otherwise densely pubescent. Pedicels 4–11 mm long, with or without gland-headed hairs, otherwise densely pubescent; bracteoles 2, alternate to opposite, from nearly basal to within lower ⅓ of pedicel, narrowly triangular to linear, ovate, or elliptic, to ca. 2.5 mm long; bracts to 3 mm long. Calyx lobes triangular with acuminate to acute apices, (2.1–)2.5–5 by 0.7–1.7(–2.2) cm, the abaxial surface with or without gland-headed hairs, otherwise sparsely to densely pubescent; corolla cylindrical, 7–10.5 by 2.5–5 mm, white, abaxially glabrous; filaments 4.5–5.5 mm long, anthers 1–1.7 mm long; ovary densely pubescent. Capsules short-ovoid to subglobose, 3.5–5 by 5–7 mm, placentae subapical; seeds 1.2–2.3 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Santa Catarina and Rio Grande do Sul (MAP 7). Rocky areas, bogs, wet forests, and moist thickets; 10–1650 m alt. Flowering (August) September through December (January).

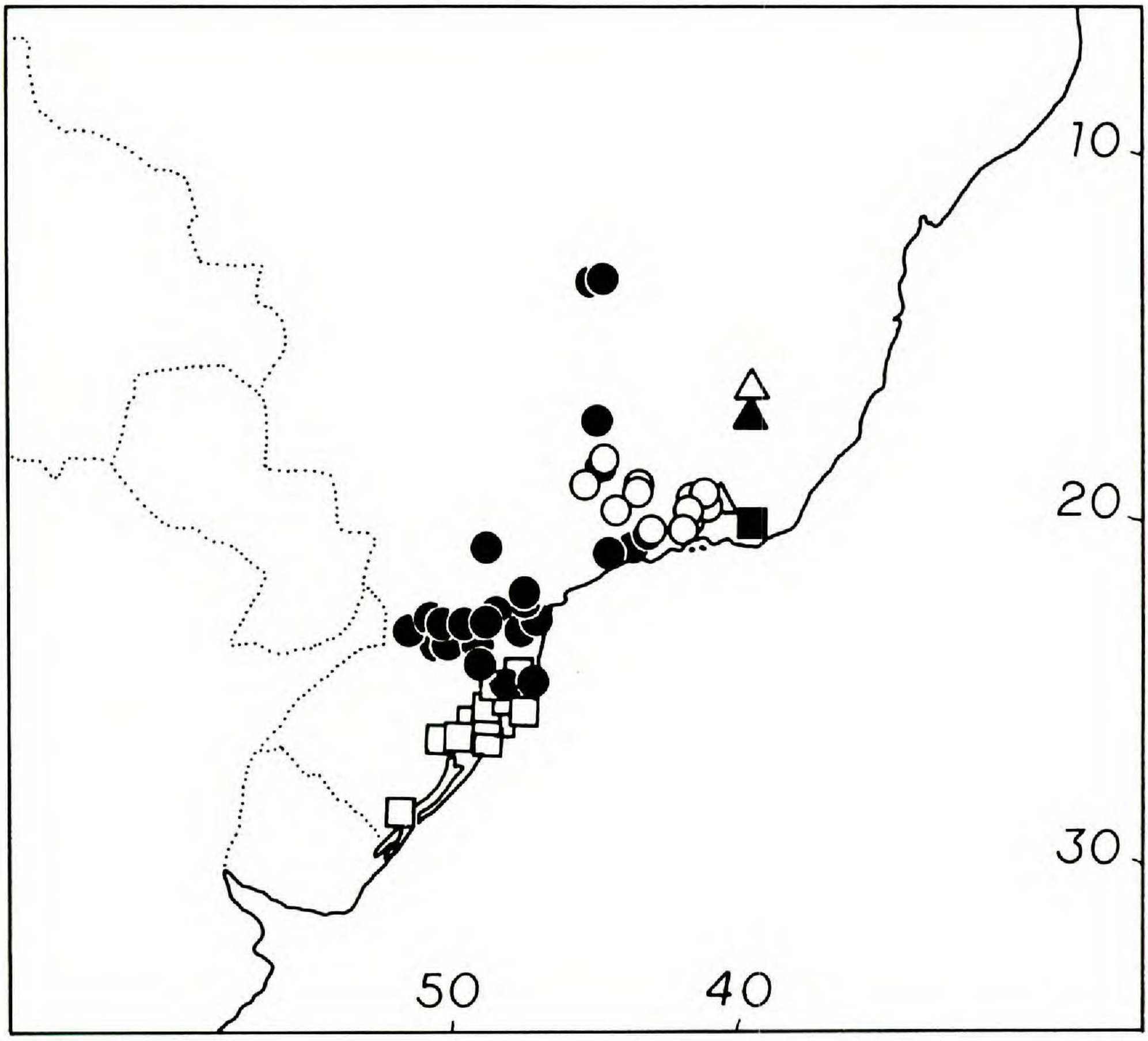
REPRESENTATIVE SPECIMENS. **Brazil.** RIO GRANDE DO SUL: Montenegro, *Camargo 1786* (B); Morro Sapucaia, São Leopoldo, *Leite 3257* (GH); Cachoeira, *Malme 401a* (S); Aparados da Serra, *Pabst 6301 & Pereira 6474* (L); Cambará, S. Francisco de Paula, *Rambo 36724* (B, MO, NY, US); Gravataí, summit Monte Sapucaia, *Rambo 42757* (B, L, US); Sapucaia, São Leopoldo, *Rambo 48695* (B, US); S. Francisco de Paula, *Rambo 52951* (S); Serra da Roçinha, near Bom Jesus, *Rambo 53881* (B); Fazenda Englert, near S. Francisco de Paula, *Rambo 54674* (B); Canela, *Richter 7837* (L). SANTA CATARINA: Serra do Oratório, Bom Jardim, São Joaquim, *Reitz & Klein 7456* (L); Bom Retiro, Fazenda Santo Antônio, Campo dos Padres, *Smith & Reitz 10333* (US); Sombrio, *Reitz 1926* (G, S, US).

Agarista nummularia is probably closely related to *A. chlorantha* and *A. virgata*; it can be separated from the former by its more or less flat, nonrevolute leaves, and from the latter by its sparsely to densely pubescent inflorescence axis, pedicels, and ovaries, and its capsules with more or less subapical placentae. These species are essentially geographically isolated. *Agarista nummularia* may also be confused with small-leaved individuals of *A. pulchella*, a species with shorter calyx lobes that grows to the north of the range of *A. nummularia* (MAPS 6, 7).

The species has been illustrated by Marques and Klein (1975, *pl. 10*).

18. **Agarista virgata** Judd, sp. nov. FIGURE 6, C.

Frutex erectus ad ca. 1 m altus. Ramuli hornotini pilis glandulosis praediti, aliter glabri, cum medulla non septata. Folia ovata vel elliptica, 0.7–1.8 cm longa, 0.7–1.7 cm lata, coriacea, ad apicem brevissime acuminata, acuta vel obtusa cum mucrone brevi, ad basin rotundata vel cordata; margo planiuscula, integra vel minute serrulata; pagina abaxialis pilis glandulosis praedita (praecipue in nervo primario), aliter glabra. Inflorescentiae axillares vel terminales, racemosae vel paniculatae, ad 5–16 cm longae; axis pilis glandulosis praeditus, aliter glaber. Pedicelli 2–7 mm longi, pilis glandulosis praediti, aliter glabri. Flores 5-merus. Calyx lobis 1.4–3 mm longis, 0.6–1.6 mm latis, cum pilis glandulosis in pagina abaxiali. Corolla cylindrica, 6–7 mm longa, 2–3 mm lata, alba, glabra in pagina abaxiali. Filamenta ca. 4 mm longa; antherae ca. 1 mm



MAP 7. Distribution of *Agarista nummularia* (open squares), *A. virgata* (solid triangle), *A. chlorantha* (dots), *A. organensis* (solid square), *A. hispidula* (circles), and *A. ericoides* (open triangles).

longae. Ovarium glabrum. Capsula subglobosa vel brevissime ovoidea, 4–5.5 mm longa, 5.5–7.5 mm lata, cum placentis ± centralibus. Semina 1.2–1.6 mm longa.

Erectly branched shrub to ca. 1 m tall. Twigs with scattered gland-headed hairs, otherwise glabrous, with nonchambered pith. Buds to ca. 2.8 mm long. Leaves alternate; petiole 1–2 mm long; blade revolute in bud, ovate to elliptic, 0.7–1.8 by 0.4–1.3 cm, ± flat, coriaceous, the apex acute- to obtuse-mucronate to short-acuminate, the base cordate to rounded, the margin entire or serrulate due to gland-headed hairs, plane, the adaxial surface with gland-headed hairs, otherwise very sparsely pubescent on extreme proximal portion of midvein, the abaxial surface with gland-headed hairs especially on midvein, otherwise glabrous, usually with few very inconspicuous glandular dots along midvein. Inflorescences axillary racemes or terminal racemes or panicles, to 5–16 cm long, the axis with scattered gland-headed hairs, otherwise glabrous. Pedicels 2–7 mm long, with gland-headed hairs, otherwise glabrous; bracteoles 2, alternate to opposite, from near apex to midpoint of pedicel, narrowly triangular

to ovate, to ca. 2.3 mm long; bracts to 5 mm long (grading into leaves). Calyx lobes triangular with acuminate apices, 1.4–3 by 0.6–1.6 mm, the abaxial surface with gland-headed hairs, otherwise glabrous; corolla cylindrical, 6–7 by 2–3 mm, white, abaxially glabrous; filaments ca. 4 mm long, anthers ca. 1 mm long; ovary glabrous. Capsules subglobose to short-ovoid, 4–5.5 by 5.5–7.5 mm, placentae ± central; seeds 1.2–1.6 mm long.

TYPE. Brazil, Minas Gerais, Serra do Cipó, km 140, 22 June 1964, *A. P. Duarte 8098* (holotype, F!; isotypes, L!, S!).

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais, Serra do Cipó (MAP 7); ca. 1400 m alt. Flowering in June.

REPRESENTATIVE SPECIMEN. **Brazil.** MINAS GERAIS: Serra do Cipó, km 131, *Duarte 2682* (G, L).

This distinctive species is easily recognized by its rigidly ascending, wandlike branches (from which the specific epithet is derived) with small, more or less flat, densely overlapping leaves. It is most easily confused with the geographically separated *Agarista nummularia* (see MAP 7). However, *A. virgata* is easily separated from *A. nummularia* by its twigs, inflorescence axis, pedicels, and ovaries that completely lack unicellular hairs, and by its capsules with more or less centrally located placentae. This species is also allied with *A. hispidula* and *A. chlorantha*.

It is of interest that both known collections of this taxon have gland-headed hairs; further collecting may reveal plants lacking these hairs, since their presence is variable in all other species in which they occur.

19. **Agarista chlorantha** (Cham.) G. Don, Gen. Syst. **3:** 838. 1934.

FIGURE 6, d.

Andromeda chlorantha Cham. Linnaea **8:** 508. 1833. *Leucothoë chlorantha* (Cham.) DC. Prodr. **7:** 604. 1839. TYPE: Brazil, without definite locality, *Sellow s.n.* (holotype, B (destroyed); fragment of holotype, F!; photos of holotype, F!, G!, GH!; fragment of isotype, NY!).

Amechania subcanescens DC. Prodr. **7:** 579. 1839. *Leucothoë subcanescens* (DC.) Meissner *in* Martius, Fl. Brasil. **7:** 163. *t. 62, fig. 1.* 1863. *Leucothoë chlorantha* (Cham.) DC. var. *subcanescens* (DC.) Sleumer, Bot. Jahrb. **78:** 454. 1959. TYPE: Brazil, São Paulo, Batatais, June 1834, *Lund s.n.* (holotype, G-DC; fragment of holotype, NY; isotype, C!).

Andromeda serrulata Cham. Linnaea **8:** 506. 1833. *Agarista serrulata* (Cham.) G. Don, Gen. Syst. **3:** 838. 1834. *Leucothoë serrulata* (Cham.) DC. Prodr. **7:** 604. 1839. TYPE: Brazil, São Paulo (see Meissner *in* Martius, 1863), *Sellow s.n.* (holotype, B (destroyed); fragments of holotype, F!, NY; photo of holotype, GH!; isotypes, E!, G!, K!).

Erectly branched shrub or subshrub to 1.5 m tall, with bark usually not well developed. Twigs with or without scattered gland-headed hairs, otherwise moderately to densely pubescent, with ± nonchambered to hollow pith. Buds to ca. 0.6 mm long. Leaves alternate; petiole 1–4 mm long; blade revolute in bud, ovate or narrowly ovate to orbicular or even suborbicular, 0.7–2.5 by 0.25–1.3(–1.7) cm, strongly to slightly abaxially curved (rarely ± flat), coriaceous,

the apex acute- to rounded-mucronate, the base cordate, the margin entire, often undulate (serrulate due to gland-headed hairs), strongly to slightly revolute (rarely ± plane), the adaxial surface sparsely pubescent on midvein, especially proximal portion, the abaxial surface with or without gland-headed hairs on midvein, otherwise glabrous to sparsely pubescent on proximal portion of midvein, often with few very inconspicuous glandular dots along midvein. Inflorescences axillary (rarely terminal) racemes to (1–)1.5–8.5 cm long (very rarely flowers solitary, axillary), the axis with or without scattered gland-headed hairs, otherwise moderately to densely pubescent. Pedicels 3.5–13 mm long, with or without gland-headed hairs, otherwise moderately to densely pubescent; bracteoles 2 (rarely several), alternate to subopposite, from nearly basal to within lower ⅓ of pedicel (rarely to near apex), triangular to linear (ovate), to ca. 2.5 mm long; bracts to 3 mm long. Calyx lobes triangular to ovate, with ± acute apices, 2.5–5.5 by 0.8–1.7 mm, the abaxial surface with or without gland-headed hairs, otherwise very sparsely to densely pubescent; corolla cylindrical, 7–11.5 by 3–6.5 mm, white (reddish toward apex), abaxially glabrous; filaments 5.5–6.5 mm long, anthers 1–1.6 mm long; ovary sparsely to densely pubescent. Capsules short-ovoid to subglobose, 3–5 by 4.5–7 mm, placentae subapical; seeds 1–2.1 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, from Distrito Federal south to Minas Gerais and São Paulo, and disjunctly from Paraná south to Santa Catarina (MAP 7). Wet, boggy or marshy campo, with grasses, sedges, and *Xyris,* open rocky and/or grassy areas, gallery forest; 700–1650 m alt. Flowering late August through December (January).

REPRESENTATIVE SPECIMENS. **Brazil.** DIST. FEDERAL: Córrego Samambaia, near Taguatinga, *Irwin et al. 8151* (NY, SP, UC, US); Rio Torto, N of Brasília, *Irwin et al. 8433* (NY); Fazenda Água Limpa, near Vargem Bonita, 18 km SSW of Brasília TV tower, *Ratter 3050* (E). PARANÁ: Campos do Capão da Imbuia, Curitiba, *Dombrowski 408 & Saito 227* (A, L); Colônia Orleães, Curitiba, *Dombrowski 3088* (L); Pinhaes, *Dusén 7082* (GH, MO, NY, S); Piraquara, Rio Palmital, *Hatschbach 781* (L); Palmas, Sta. Barbara, *Hatschbach 15005* (F, L, NY, UC, US, WIS); Rio Pequeno, S. José dos Pinhais, *Hatschbach 22815* (C, L, UC); S. João do Triunfo, *Hatschbach 17748* (L, UC); Clevelandia, *Hatschbach 22714* (L, UC); S. Jerônimo da Serra, Rio S. Jerônimo, *Hatschbach & Guimarães 24777* (C, S, UC); Rio Atuba, Curitiba, *Hatschbach 32738* (L); Rio Palmital, Colombo, *Hatschbach 32792* (L, MO, UC); União da Vitória, *Koczicki 48* (L, UC); Tatuquara, Curitiba, *Kummrow 692* (L). MINAS GERAIS: Uberaba, *Lund s.n.,* 1843 (C). SANTA CATARINA: Fazenda Carneiros, Caçador, *Klein 3546* (L); Planalto Catarinense, *Pereira 6290 & Pabst 6117* (L); Morro do Iquererim, Campo Alegre, *Reitz & Klein 5220* (L, US); Serra da Boa Vista, São José, *Reitz & Klein 5418* (L, US); Ponte Alta do Norte, Curitibanos, *Reitz & Klein 13386* (L); Valões, *Reitz & Klein 13549* (L); Fazenda Frei Rogério, Pôrto União, *Reitz & Klein 13609* (L); Campo do Areão, Santa Cecília, *Reitz & Klein 14196* (L); Fazenda Ernesto Scheide, Campo Alegre, *Reitz & Klein 5324* (L, US); Bom Retiro, falls of Rio Canoas, Campo dos Padres, *Smith & Klein 7861* (US); Chapecó, Fazenda Campo São Vicente, 24 km W of Campo Erê, *Smith et al. 9525* (L, US); Bom Retiro, Fazenda Santo Antônio, Campo dos Padres, *Smith & Reitz 10331* (L, US); Irani, Campo de Irani, *Smith & Klein 13032* (US); Água Doce, Campos de Palmas, 3 km NW of Herciliópolis, *Smith & Klein 13634* (GH, L, NY, UC, US); 6 km W of Campo Erê, *Smith & Klein 13708* (L, NY, US). SÃO PAULO: Campos do Jordão, *Hashimoto 286* (SP), *Leite 3942* (A, GH); Butantan, *Hoehne,*

SP n. 467 (SP), *572* (SP); Salesópolis, near Rio Coruja, *Mattos, SP n. 157944* (NY); Araramara, *St.-Hilaire, Cat. C*[1] *n. 1004* (P); Urupunga, *St.-Hilaire, Cat. C*[1] *n. 1048* (P).

Agarista chlorantha is most similar to (and easily confused with) *A. hispidula* and *A. organensis*; all three taxa are characterized by more or less erect branches with small, usually ovate, clearly revolute leaves. This species is easily separated from *A. hispidula* by its abaxially glabrous (vs. pubescent) corollas and its more or less acute (vs. acuminate) calyx lobes. It can be distinguished from *A. organensis* by its longer calyx lobes, corollas, and inflorescences, although a few specimens (e.g., *Dombrowski 408, Leite 3942, Mattos, SP n. 157944, Reitz & Klein 5220*) have very short inflorescences or rarely even solitary flowers and thus somewhat approach the latter species. *Agarista chlorantha* is geographically separated from *A. organensis* (see MAP 7), although it grows together with *A. hispidula* in the northern portion of its range (MAP 7). Specimens intermediate between *A. chlorantha* and *A. hispidula* are apparently unknown, but field studies in their area of overlap would be of interest. *Agarista chlorantha* appears to be more common (or at least much better collected) in the southern portion of its range (Paraná and Santa Catarina).

Agarista chlorantha occurs sympatrically with *A. pulchella* over much of its range, and *Hatschbach 17748* (L, UC) may represent a hybrid between these species. This specimen is unusual in its large (to 3.7 by 2 cm) nonrevolute leaves.

Like many other *Agarista* species, *A. chlorantha* is variable in its glandular indumentum. There may be many to few multicellular, gland-headed hairs on the twigs, leaves, inflorescence axis, pedicels, and calyx lobes, or these hairs may be lacking. The plants are alike in all other features, and both indument forms may be found in a single locality (e.g., *Smith & Klein 13634*; *Hoehne, SP n. 467, 572*). Thus, *A. serrulata* and *A. chlorantha,* the former characterized by Sleumer (1959) as being glandular-hairy and the latter as lacking such hairs, are considered to be conspecific. Leaves of *Agarista chlorantha* are also somewhat variable in extent of marginal revolution: those near the base of the plant are frequently less strongly revolute than those toward the distal part of the shoots. In a few plants many of the leaves are only very slightly revolute and more or less orbicular; such plants are easily confused with the closely related *A. nummularia,* a species with consistently plane and widely ovate to elliptic or nearly orbicular leaves.

The species has been illustrated several times—see Meissner (1863, *t. 1, fig. 1*; *t. 62, fig. 1*; *t. 63, fig. 1*) and Marques and Klein (1975, *pl. 9*).

20. **Agarista organensis** (Gardner) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. FIGURE 7, C.

Leucothoë organensis Gardner *in* W. J. Hooker, London Jour. Bot. **4:** 132. 1845. TYPE: Brazil, Estado do Rio, Serra dos Órgãos, ca. 1675 m alt., May 1837, *Gardner 475* (lectotype, K!; isolectotypes, F(fragment)!, G, GH!, NY!, P!; photos of isolectotype, F!, G, GH!).

Erect shrub to ca. 2 m tall. Twigs very sparsely to moderately pubescent, with nonchambered to clearly chambered pith. Buds to ca. 0.7 mm long. Leaves

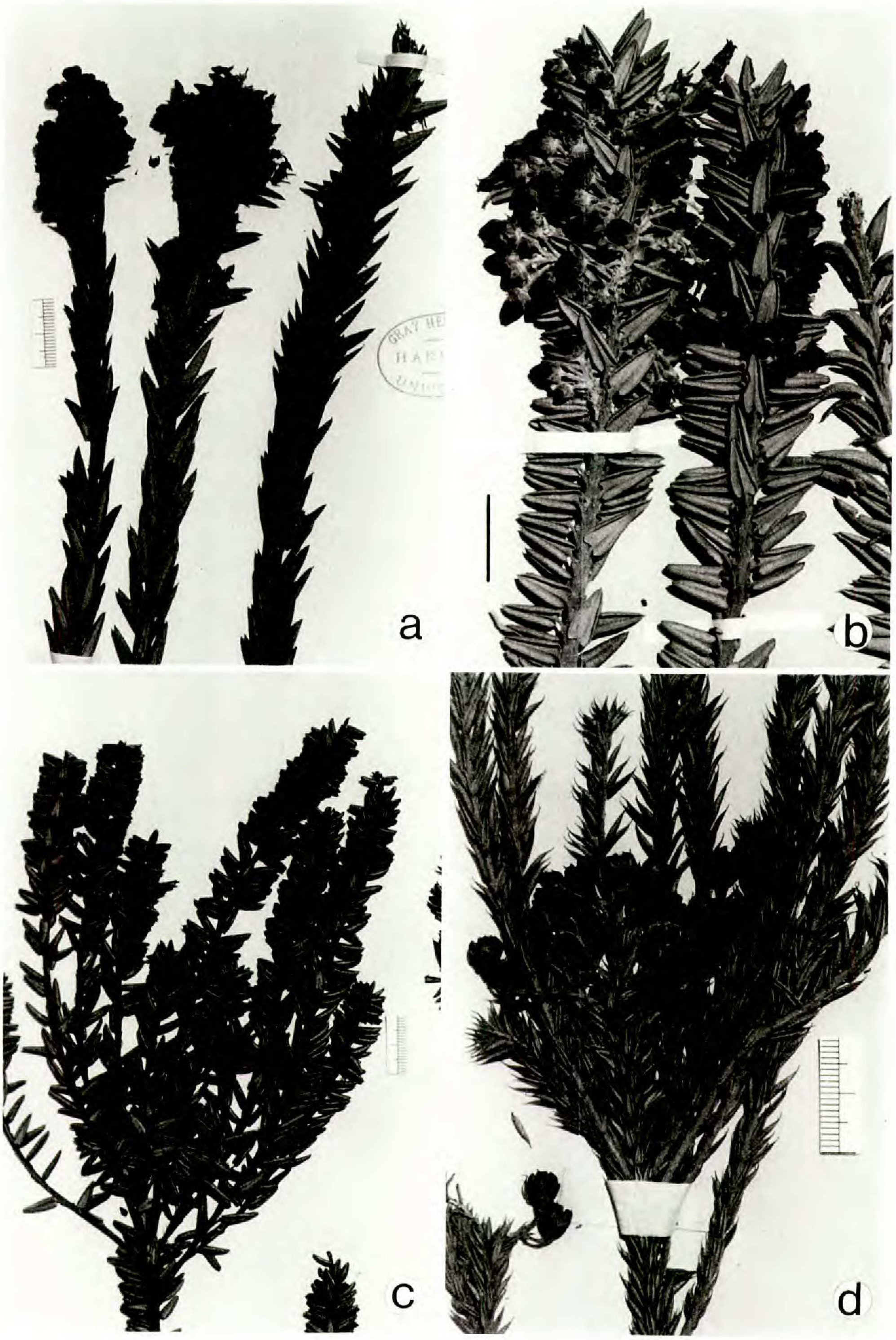


FIGURE 7. a, b, *Agarista hispidula:* a, *Leite 3477*; b, *Dusen s.n.*, 22 June 1902 (s). c, *A. organensis* (*Glaziou 17119*). d, *A. ericoides* (*Glaziou 19577*). Scale = 2 cm.

alternate; petiole 1.5–4 mm long; blade revolute in bud, ovate (to elliptic), 0.5–1.7 by 0.15–0.8 cm, strongly abaxially curved, coriaceous, the apex acute- to rounded-mucronate, the base cordate to truncate, the margin entire, strongly revolute, the adaxial surface glabrous to sparsely pubescent on midvein, especially proximal portion, the abaxial surface glabrous to sparsely pubescent on midvein, usually with few very inconspicuous glandular dots along midvein. Inflorescences axillary, fasciclelike, often only few flowered racemes to 0.3–1.5 cm long, or flowers solitary and axillary, axis moderately to densely pubescent. Pedicels 4–8 mm long, sparsely to densely pubescent; bracteoles 2 to several, alternate to subopposite, from near base to near midpoint of pedicel, narrowly triangular, to ca. 0.9 mm long; bracts to ca. 1 mm long. Calyx lobes triangular with acuminate apices, 1.1–2 by 0.5–1.2 mm, abaxial surface sparsely to moderately pubescent; corolla cylindrical, 6–7.5 by 2–4 mm, white to red(?), abaxially glabrous; filaments 4–4.5 mm long, anthers 1–1.3 mm long; ovary sparsely to moderately pubescent. Capsules short-ovoid, 3–5 by 4.5–6 mm, placentae subapical; seeds 1–3 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Estado do Rio, Serra dos Órgãos (MAP 7). Shrub bogs with *Sphagnum*; ca. 1500–1830 m alt. Flowering November through January.

REPRESENTATIVE SPECIMENS. **Brazil.** ESTADO DO RIO: Serra dos Órgãos, *Gardner 5802* (K, NY), *Glaziou 3763* (C, K, L), *Glaziou 16231* (A, B, C, F, NY, P), *Glaziou 17119* (A, C, F, K, NY, UC, US), *Guillemin 948* (P).

Agarista organensis is very closely related to (and easily confused with) *A. chlorantha*. Both species are shrubs with more or less rigidly ascending branches bearing small, more or less ovate, usually moderately to strongly revolute, cordate-based leaves. *Agarista organensis* can be distinguished from *A. chlorantha* by its short calyx lobes and its very short fasciclelike racemes or its solitary flowers. However, some fasciculate or solitary-flowered variants of *A. chlorantha* are known, and additional collections are necessary in order to clarify the taxonomic value of this character. *Agarista organensis* is geographically isolated; within the genus only *A. oleifolia* also occurs in the Serra dos Órgãos.

21. **Agarista hispidula** (DC.) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. FIGURE 7, a, b.

Amechania hispidula DC. Prodr. **7:** 579. 1839. *Leucothoë hispidula* (DC.) Meissner *in* Martius, Fl. Brasil. **7:** 164. *t. 62, fig. 2.* 1863. TYPE: Brazil, São Paulo, Batatais, June 1834, *Lund s.n.* (holotype, G-DC; fragment of holotype, NY; isotype, C!).

Leucothoë breviflora Meissner *in* Martius, *ibid.* 165. *t. 63, fig. 2. Agarista breviflora* (Meissner) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889. TYPE: Brazil, Minas Gerais, Caldas, Oct. 1854, *Lindberg 418* (holotype, BR; fragment of holotype, NY!; isotype, s!).

Leucothoë intermedia Meissner *in* Martius, Fl. Brasil. **7:** 163. *t. 60, fig. 1.* 1863. TYPE: Brazil, Minas Gerais, Caldas, 1845, *Widgren 329* (lectotype (here designated), BR; fragment of lectotype, NY!; possible isolectotype, s!).

Usually erect shrub to 2.5 m tall (but often only ca. 1 m tall), with bark often not well developed. Twigs with or without scattered gland-headed hairs, otherwise sparsely to densely pubescent, with nonchambered to irregularly chambered or sometimes hollow pith. Buds to ca. 0.8 mm long. Leaves alternate; petiole 1–4 mm long; blade revolute in bud, ovate to narrowly ovate, 0.8–2.5(–3.3) by 0.15–1.2 cm, strongly to slightly abaxially curved, coriaceous, the apex acute- to rounded-mucronate (short-acuminate), the base cordate, the margin entire (slightly undulate) (serrulate due to gland-headed hairs), strongly to moderately (only slightly) revolute, the adaxial surface sparsely to densely pubescent on midvein and often with scattered hairs on lamina, the abaxial surface with or without gland-headed hairs on midvein, otherwise sparsely to densely pubescent on midvein and often also sparsely pubescent on lamina (with few very inconspicuous glandular dots along midvein). Inflorescences (very short, fasciclelike) axillary racemes (rarely terminal racemes or panicles) to 0.5–6.5 cm long, axis with or without scattered gland-headed hairs, otherwise densely pubescent. Pedicels 5–13 mm long, with or without gland-headed hairs, otherwise moderately to densely pubescent; bracteoles 2 (rarely 3), alternate to subopposite, from nearly basal to near midpoint of pedicel, narrowly triangular, to ca. 1.8 mm long; bracts to 2.3 mm long. Calyx lobes triangular to ovate with acuminate (to rarely ± acute) apices, 2–5.5 by 0.8–2 mm, abaxial surface with or without gland-headed hairs, otherwise sparsely to densely pubescent; corolla cylindrical to urceolate-cylindrical, 6.5–8.5 by 3–6 mm, red to pink (or white), abaxially sparsely to densely pubescent (rarely also with few gland-headed hairs); filaments 4–5 mm long, anthers 1.4–1.8 mm long; ovary densely pubescent. Capsules short-ovoid, 2.5–5 by 4–7.5 mm, placentae subapical to central; seeds 0.6–1.4 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, southern Minas Gerais and adjacent São Paulo and Estado do Rio, with one specimen from Goiás (MAP 7). Elfin woodlands, thickets, thicket margins, shrubby grassland, rocky sites, open boggy areas; 1000–2500 m alt. Flowering (June) September through December (February).

REPRESENTATIVE SPECIMENS. **Brazil.** ESTADO DO RIO: Retiro, *Dusén 51* (S); Itatiaia, *Glaziou 8787* (C, L, P); Serra do Itatiaia, W of Retiro de Ramos, *Hemmendorf 586* (S); summit, Mt. Itatiaia, Estação Biologica, *L. B. Smith 1504* (GH, S); Planalto of Itatiaia, 150 km WNW of Rio de Janeiro, *R. & A. Tryon 6696* (NY); Serro do Itatiaia, *Ule 3410* (HBG); Parque Nacional de Itatiaia, *Veloso 304* (NY). GOIÁS: Corumbá, *Glaziou 21621* (P). MINAS GERAIS: Fazenda da Parahyba, Andrelândia, *Barreto 5304* (L); São Thomé das Letras, Baipendi, *Brade 20428* (F, M, US); Pocos de Caldas, *Emmerich 2140* (L); Camanducaia, Vila Monte Verde, *Filho 1869* (L); Caldas, Cervo, *Regnell III-838* (S); Caldas, between Rio Pardo and Corcovado, *Regnell III-839* (P, S); Plateleiras, Agulhas Negras, *Sucre 5767* (F). SÃO PAULO: Campos do Jordão, Reserva do Inst. Forestal, São José dos Alpes, *Davis 3036* (E); São Carlos, *Handro 401* (US); Campos do Jordão, *Kuhlmann 32477* (SP), *Leite 3477* (A, GH, S); Moji-Guaçu, Fazenda Campininha, 3 km NNW of Pádua Sales, *Mattos & Mattos 8214* (K).

Agarista hispidula is most closely related to *A. chlorantha, A. organensis,* and *A. ericoides*; it can be distinguished from all of these species by its abaxially pubescent corollas. In addition, it differs from *A. organensis* in its elongated

calyx lobes, from *A. chlorantha* in its acuminate (vs. acute) calyx lobes, and from *A. ericoides* in its larger leaves.

Sleumer (1959) separated the plants lacking gland-headed hairs as *Leucothoë intermedia,* but these plants are identical in all other characters to the glandular-hairy plants, and both pubescence forms can be found in the same locality (population?) (see *Widgren 329* (BR, S), *Widgren 668* (C, NY, S), *Lindberg 418* (NY, S), *Leoncini & Roppa 341* (L); *Regnell I-186* (F, M, NY, S, US), *Regnell III-838* (S), *Regnell III-839* (S), *Emmerich 2140* (L)).

22. **Agarista ericoides** Taubert, Bot. Jahrb. **17:** 512. 1893. FIGURE 7, d.

Leucothoë ericoides (Taubert) Glaz. Bull. Soc. Bot. France **57**(Mém. 3): 430. 1910. TYPE: Brazil, Minas Gerais, Serra dos Cristais, near Diamantina, 1892, *Glaziou 19577* (holotype, B (destroyed); fragment of holotype, F!; photos of holotype, F!, GH!; isotypes, BR, C!, G!, K!, P!).

Leucothoë lycopodioides Sleumer, Bot. Jahrb. **78:** 450. 1959. TYPE: Brazil, Minas Gerais, Serra de Ibitipoca (43°53′, 21°40′), 11 Aug. 1896, *Schwacke 12360* (holotype, P!; photo of holotype, S!).

Leucothoë acicularis Sleumer, *ibid.* 451. TYPE: Brazil, Minas Gerais, without definite locality, 1816–1821, *St.-Hilaire, Cat. B*[1], *n. 2986* (holotype, P!; isotype, P!).

Erect shrub to ca. 0.5(?) m tall. Twigs with or without scattered gland-headed hairs, otherwise glabrous to densely pubescent, with nonchambered pith. Buds to ca. 0.5 mm long. Leaves alternate; petiole 0.5–1.5 mm long, with or without gland-headed hairs adaxially; blade revolute in bud, narrowly ovate to nearly linear, 0.4–1.2 by 0.1–0.25 cm, strongly abaxially curved, coriaceous, the apex minutely acuminate, the base slightly cordate to truncate, the margin entire (to appearing serrulate/ciliate due to presence of many gland-headed hairs), strongly revolute, the adaxial surface with or without gland-headed hairs on extreme proximal portion of midvein, otherwise glabrous to very sparsely pubescent on proximal portion of midvein, the abaxial surface with or without gland-headed hairs along midvein, otherwise glabrous to very sparsely pubescent on extreme proximal portion of midvein, lacking or with few very inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 1.5–3 cm long, the axis with or without scattered gland-headed hairs, otherwise densely pubescent. Pedicels 3.5–11 mm long, with or without gland-headed hairs, otherwise densely pubescent; bracteoles 2, alternate to opposite, from within lower ¼ to near middle of pedicel, narrowly triangular to ovate, to ca. 3 mm long; bracts ca. 3.5 mm long. Calyx lobes narrowly triangular, with long-acuminate apices, 3–6 by 0.4–0.7 mm, the abaxial surface with or without conspicuous gland-headed hairs, otherwise sparsely to densely pubescent; corolla cylindrical, 8–9.5 by 3.5–4 mm, pink to red, abaxially glabrous; filaments ca. 5.7–6 mm long, anthers ca. 1.5 mm long; ovary densely pubescent. Capsules short-ovoid, 3.5–4.5 by 4–5 mm, placentae ± central; seeds 0.7–1.2 mm long.

DISTRIBUTION. Southeastern Brazil, Minas Gerais (MAP 7).

REPRESENTATIVE SPECIMENS. Known only from type collections.

This distinctive but poorly collected species is immediately recognizable due to its small, extremely revolute leaves. It is probably most closely related to

FIGURE 8. a, *Agarista niederleinii* var. *niederleinii* (*Reitz & Klein 5889*). b, *A. niederleinii* var. *acutifolia* (*Hatschbach & Guimarães 25598*). c, *A. boliviensis* (*Steinbach 8568*): note crisped/undulate leaf margins. d, *A. eucalyptoides* (*Williams & Assis 7503*): note elongate, flexuous petioles. Scale = 2 cm.

three species from which it is geographically separated: *Agarista hispidula, A. organensis,* and *A. chlorantha.*

Like many other species of *Agarista,* this taxon is quite variable in glandular indumentum. Some plants are densely covered with multicellular gland-headed hairs on stems and leaves, while others have only a few of these hairs or none at all. This variation thus cannot be used to delimit species, and *Leucothoë lycopodioides* and *L. acicularis* of Sleumer (1959) are reduced to synonymy under *A. ericoides.*

23. **Agarista niederleinii** (Sleumer) Judd, comb. nov.

Shrub to small tree to 5 m tall with longitudinally furrowed bark. Twigs nearly glabrous to moderately pubescent, with nonchambered to clearly chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 1.5–8 mm long; blade revolute in bud, ovate to elliptic or oblong, 0.6–5.7 by 0.3–1.7(–1.9) cm, flat to moderately abaxially curved, coriaceous, the apex acuminate or acute- to retuse-mucronate, the base cuneate to rounded (rarely very slightly cordate), the margin entire, plane to revolute, the adaxial surface glabrous, but sparsely pubescent on midvein, the abaxial surface glabrous (very sparsely pubescent along proximal portion of midvein), usually with few very inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 1–3.5(–4.5) cm long, axis moderately to densely pubescent; bracteoles 2, alternate to opposite, from nearly basal to near midpoint of pedicel, triangular to linear, to ca. 1.5 mm long; bracts to ca. 1.7 mm long. Calyx lobes triangular with acuminate apices, 0.8–2.7 by 0.6–1.8 mm, abaxial surface glabrous to moderately pubescent; corolla cylindrical, 5–8 mm long, 2–4 mm wide, white, abaxially glabrous; filaments 4–5 mm long, anthers 0.9–1.5 mm long; ovary glabrous to sparsely pubescent (with few hairs at apex and around base). Capsules short-ovoid to subglobose, 4.5–7 by 5.5–10 mm, very thick walled, placentae subapical; seeds 1.5–3.2 mm long.

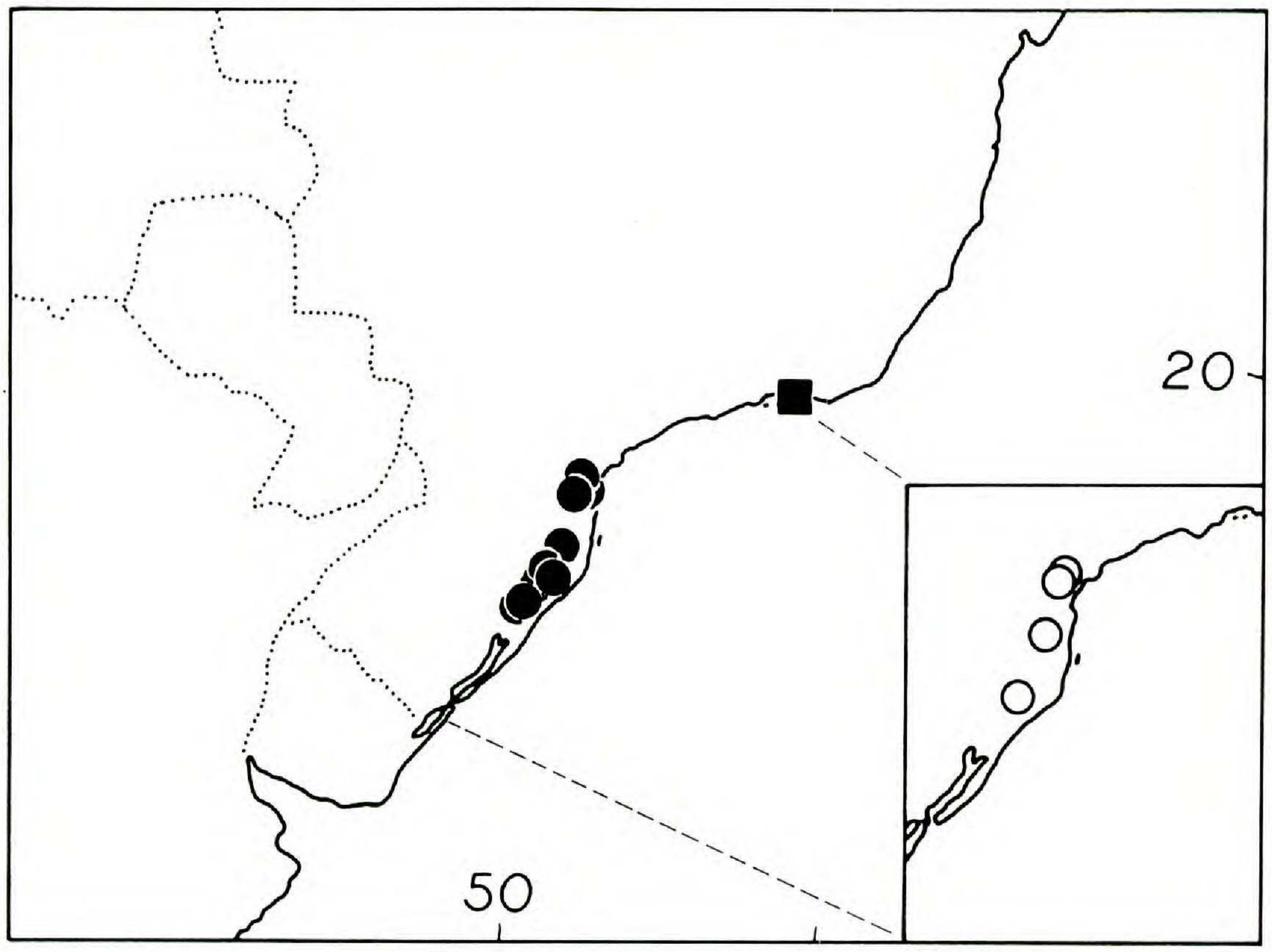
DISTRIBUTION. Southeastern Brazil, from Paraná south to Rio Grande do Sul in the Serra do Mar. Various habitats; 350–2000 m alt.

KEY TO THE VARIETIES OF AGARISTA NIEDERLEINII

1. Leaves with blade 0.6–2.8 by 0.3–0.9 cm, apex usually obtuse- to rounded- or retuse-mucronate; petiole 1.5–4.5 mm long. ..... 23a. var. *niederleinii.*
1. Leaves with blade 2–5.7 by 0.5–1.7(–1.9) cm, apex usually acute-mucronate to acuminate; petiole 3–8 mm long. ..... 23b. var. *acutifolia.*

23a. **Agarista niederleinii** (Sleumer) Judd var. **niederleinii** FIGURE 8, a.

Leucothoë niederleinii Sleumer, Notizbl. Bot. Gart. Berlin **12:** 480. 1935. TYPE: Brazil, Santa Catarina, Campos de los Rios Chopim y Chapecó, Palmas Altas, Jan. 1887, *Niederlein 2006* (holotype, B (destroyed)). The following neotype is here designated: Santa Catarina, Monte Cristo, Garuva, S. Francisco do Sul, *Reitz & Klein 5889* (s!; isoneotypes, B!, L!, NY!, UC!, US!).



MAP 8. Distribution of *Agarista niederleinii* var. *niederleinii* (dots), *A. niederleinii* var. *acutifolia* (circles), and *A. uleana* (square).

Leaves with petiole 1.5–4.5 mm long; blade 0.6–2.8 by 0.3–0.9 cm, flat to moderately abaxially curved, apex usually obtuse- to rounded- or retuse-mucronate, margin plane to revolute. Inflorescences to 1.5–3.5(–4.5) cm long; bracteoles narrowly triangular to linear.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, from Paraná south to Rio Grande do Sul in Serra do Mar (MAP 8). Cloud forests, thickets, and open, rocky crests and slopes; 850–2000 m alt. Flowering November and December (to February).

REPRESENTATIVE SPECIMENS. **Brazil.** PARANÁ: Guaratuba, Serra de Araçatuba, *Hatschbach 6493* (L, UC). RIO GRANDE DO SUL: Taimbesinho, *Araujo 1279* (L); S. Francisco de Paula, Cambará, *Rambo 36724* (NY); Serra da Rocinha, Bom Jesus, *Rambo 53824* (B). SANTA CATARINA: São Joaquim, Serra do Oratório, *Lourteig 2149* (C, P, S, US); Bom Retiro, Campo dos Padres, *Reitz 2338* (B, L, NY, UC, US); Curral Falso, Bom Jardim, São Joaquim, *Reitz & Klein 7794* (L); Morro do Campo Alegre, S. Francisco do Sul, *Reitz & Klein 10322* (L, US); Campo Alegre, Morro Iquererim, *Smith & Klein 8522* (L, US); São Joaquim, Serra do Oratório, 10 km E of Bom Jardim da Serra, *Smith & Reitz 10159* (L, US).

23b. **Agarista niederleinii** (Sleumer) Judd var. **acutifolia** Judd, var. nov.

FIGURE 8, b.

Varietas haec ab Agarista niederleinii var. niederleinii differt in foliis grandioribus 2–5.7 cm longis, 0.5–1.7(–1.9) cm latis, apicibus plerumque acuminatis vel acutatis, mucronibus brevibus, et petiolis longioribus 3–8 mm longis.

Leaves with petiole 3–8 mm long; blade 2–5.7 by 0.5–1.7(–1.9) cm, ± flat, apex usually acuminate to acute- (obtuse-)mucronate, margin plane to very slightly revolute at base. Inflorescences to 1–2.8 cm long; bracteoles triangular.

TYPE. Brazil, Paraná, Campina dos Tavares, Bocaiúva do Sul, 21 Nov. 1970, *G. Hatschbach & O. Guimarães 25598* (holotype, US!; isotypes, C!, M!, MO!, NY!, S!, SP!, UC!).

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, from Paraná south to Rio Grande do Sul in Serra do Mar (MAP 8). Thickets and thicket margins adjacent to grassy campo, stream margins; 350–1000(?) m alt. Flowering November and December.

REPRESENTATIVE SPECIMENS. **Brazil.** PARANÁ: Rio Pequeno, São José dos Pinhais, *Hatschbach 22818* (L, UC, US); Campina dos Tavares, Bocaiúva do Sul, *Hatschbach 23443* (L, NY, US); Guaricana, São José dos Pinhais, *Hatschbach 34903* (NY). RIO GRANDE DO SUL: Taimbesinho, S. Francisco de Paula, *Rambo 54121* (S). SANTA CATARINA: Morro Spitzkopf, *Klein 2318* (L, US), *Reitz 2260* (NY, US); Alto Matador, Rio do Sul, *Reitz & Klein 8303* (L).

Agarista niederleinii is most closely related to *A. uleana,* a geographically isolated species of the Pico da Tijuca region in Guanabara. Both species have distinctive, large, thick-walled capsules with subapical placentae, but they can be distinguished by leaf shape and size, and the extent to which the margins are revolute. The species is also easily confused with *A. minensis* and *A. pulchella,* both of which have smaller, thinner-walled capsules with usually more or less central placentae. In addition, *A. pulchella* has cordate-based leaves and usually longer racemes. It is of interest that Sleumer's (1959) concept of *A. niederleinii* was quite broad, including all of the plants here referred to *A. minensis* and even a few here considered to belong to *A. pulchella.* Although these three species are quite similar in leaf shape and size, they cannot be maintained as a single species because of the great variation in reproductive structures (especially inflorescence and fruit).

Populations of *Agarista niederleinii* are separable into two morphologically distinctive and more or less elevationally isolated varieties. Variety *niederleinii* can usually be separated from var. *acutifolia* by its smaller, usually more or less obtuse-mucronate (vs. acute to acuminate) leaves. Variety *niederleinii,* from the specimens now available, seems to occur at higher and/or more exposed sites than var. *acutifolia,* and it is thus likely that the two taxa are ecologically isolated. However, the two may occasionally grow in close proximity, as they do near Taimbesinho, São Francisco de Paula, and a few more or less intermediate specimens (e.g., *Rambo 54523,* B) are known. These intermediate plants appear to be highly fertile (most pollen grains stain darkly with cotton blue in lactophenol).

Rambo 49305 (S; collected in Taimbe, São Francisco de Paula, Rio Grande do Sul) contains several somewhat aberrant twigs with small, more or less flat, cordate-based leaves. Sleumer (note on sheet) suggested that these plants possibly represent hybrids between *Agarista niederleinii* (var. *niederleinii*) and *A. pulchella* var. *cordifolia* (a taxon with small, cordate-based leaves). However, *A. pulchella* var. *cordifolia* is limited to Minas Gerais and São Paulo and thus

does not occur anywhere near the state of Rio Grande do Sul. These plants are completely fertile (pollen grains stain darkly with cotton blue in lactophenol) and more likely represent merely a cordate-leaved extreme of *A. niederleinii* var. *niederleinii*. Field studies are needed in order to clarify this situation.

24. **Agarista uleana** (Sleumer) Judd, comb. nov.

Leucothoë uleana Sleumer, Notizbl. Bot. Gart. Berlin **12:** 481. 1935. TYPE: Brazil, Guanabara, Rio de Janeiro, Pico da Tijuca, 1000 m alt., Nov. 1897, *Ule 4576* (holotype, B (destroyed); isotype at HBG! here designated as lectotype; isolectotype, R).

Leucothoë ambigua Meissner var. *parvifolia* Meissner *in* Martius, Fl. Brasil. **7:** 156. 1863. TYPE: Brazil, Guanabara, Rio de Janeiro, *Riedel s.n.* (holotype, Herb. Sonder; fragment of holotype, NY!).

Shrub to small tree to 3 m tall. Twigs very sparsely to moderately pubescent, with nonchambered to clearly chambered pith. Buds to ca. 1.3 mm long. Leaves alternate; petiole 4–10 mm long; blade revolute in bud, ovate to elliptic (rarely oblong), 2–6 by 0.6–2.1 cm, ± flat, coriaceous, the apex acuminate, to acute with small mucro, the base cuneate to rounded, the margin entire, very slightly revolute (± plane), the adaxial surface glabrous, but sparsely pubescent on proximal portion of midvein, the abaxial surface glabrous (but sparsely pubescent along midvein), usually with few inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 1–2.5(–4) cm long, axis moderately to densely pubescent. Pedicels 3–8 mm long, sparsely to densely pubescent; bracteoles 2, alternate to ± opposite, nearly basal, triangular to narrowly so, to ca. 1 mm long; bracts to ca. 1.5 mm long. Calyx lobes triangular with acuminate apices, 1–2 by 0.6–1.2 mm, abaxial surface glabrous to moderately pubescent; corolla cylindrical, 6.5–10 by 2–4.5 mm, white, abaxially glabrous; filaments 4.5–5.2 mm long, anthers 1–1.6 mm long; ovary glabrous to sparsely pubescent, especially near apex and base. Capsules short-ovoid to subglobose, (3–)4–6 by (5–)5.5–8 mm, very thick walled, placentae subapical; seeds 1.5–2.8 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Guanabara, chiefly limited to Pico da Tijuca region (MAP 8). Low forest and scrub, sunny open areas; ca. 700–1020 m alt. Flowering September through November.

REPRESENTATIVE SPECIMENS. **Brazil.** GUANABARA: Pico da Tijuca, *Araujo & Almeida 519* (F), *Duarte 8462* (L, M, NY, S, US); Morro Queimado, *Brade 11108* (GH), *Glaziou 6620* (C, F, NY, P, S); Pedra do Conde, Tijuca, *Lems s.n.*, 22 March 1964 (F, L, M, MO, NY, S). ESTADO DO RIO: see Sleumer (1959).

Agarista uleana is most closely related to *A. niederleinii* and is especially easily confused with *A. niederleinii* var. *acutifolia*. Both species have distinctive, large, thick-walled capsules with subapical placentae. *Agarista uleana* can be separated from *A. niederleinii* var. *niederleinii* by its much larger leaves with acute to acuminate (vs. obtuse- to rounded-mucronate) apices, and from var. *acutifolia* by its slightly different range of leaf shapes and by the extent to which its leaf margins are revolute. The two taxa are geographically separated. Nonfruiting specimens may be confused with *A. oleifolia*, *A. populifolia*, or *A.*

mexicana, but none of these species occurs in the Pico da Tijuca region; see key for distinguishing characters.

25. **Agarista boliviensis** (Sleumer) Judd, comb. nov. FIGURE 8, c.

Leucothoë boliviensis Sleumer, Notizbl. Bot. Gart. Berlin **12:** 131. 1934. TYPE: Bolivia, Dept. Santa Cruz, valley of Comarapa, 2000 m alt., 26 Oct. 1928, *Steinbach 8568* (holotype, B (destroyed); fragment of holotype, US!; isotypes, BM, E!, F!, G, GH!, K!, LIL, MO!, NY!, S!, UC!; photos of isotype, F!, G, GH!).

Shrub or small tree to ca. 5 m tall. Twigs glabrous, with obscurely chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole (5–)8–17 mm long, frequently slender and flexuous; blade revolute in bud, ovate, 2–5.5 by 0.9–2.2 cm, ± flat, coriaceous, the apex acuminate, the base rounded and often slightly asymmetric, the margin entire and minutely undulate, ± plane, the adaxial surface glabrous, but usually very sparsely pubescent on midvein, the abaxial surface glabrous, but usually very sparsely pubescent along midvein, with or without inconspicuous to conspicuous glandular dots along midvein. Inflorescences axillary racemes to 1–2.5 cm long, axis moderately pubescent with ± whitish hairs. Pedicels 4–8 mm long, sparsely to moderately pubescent; bracteoles 2, opposite to alternate, from basal to within lower ⅓ of pedicel, narrowly triangular to linear, to ca. 1.1 mm long; bracts to ca. 1.4 mm long. Calyx lobes triangular with acuminate apices, 0.9–1.7 by 0.5–1.5 mm, abaxial surface glabrous to moderately pubescent; corolla cylindrical, 6–9.5 by 3–5 mm, white, abaxially glabrous; filaments 3.5–4.5 mm long, anthers 1–1.1 mm long, ovary glabrous to sparsely pubescent near apex. Capsules subglobose to ovoid, 3.5–4.5 by 5–6.5 mm, placentae subapical; seeds 2–2.5 mm long.

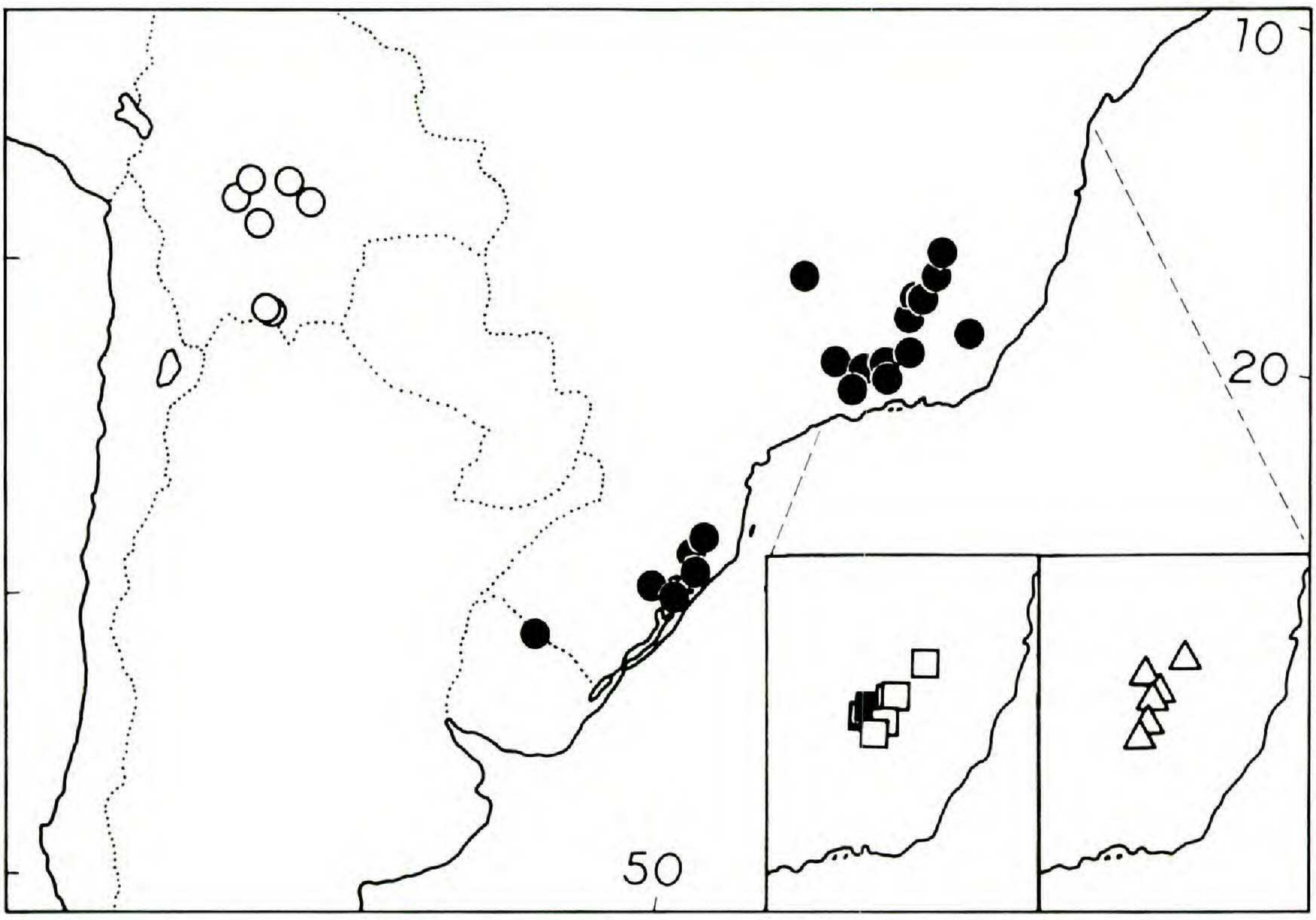
DISTRIBUTION AND ECOLOGY. Bolivia (MAP 9). Mountainous areas ca. 1200–2500 m alt. Flowering September and October.

REPRESENTATIVE SPECIMENS. **Bolivia:** Charcas, San Pedro, Pasopaya, *Anonymous 3400* (GH); Cochabamba, Rosal, below pumping station, *Brooke 5702* (F, NY); Santa Cruz, Tres Cruces, *Herzog 1634a* (L); Sucre, Alto de Aguas Blancas, *Troll 1249* (B); Tarija, Lomas peladas, Alto de las Cañas, *Troll 359* (B, M); Camino de Emborozú, La Mamora, *Türpe et al. 4777* (BAA).

Agarista boliviensis is most closely related to *A. eucalyptoides,* from which it is easily distinguished by its more consistently ovate leaves and its inflorescence axis with whitish (vs. ferrugineous) hairs. Both taxa are distinctive due to their moderate-sized leaves with often elongate and flexuous petioles. *Agarista boliviensis* has consistently crisped/undulate leaf margins, whereas in *A. eucalyptoides* this character is variable. The two species are completely allopatric since *A. eucalyptoides* is limited to southeastern Brazil and Uruguay.

26. **Agarista eucalyptoides** (Cham. & Schldl.) G. Don, Gen. Syst. **3:** 837. 1834. FIGURE 8, d.

Andromeda lanceolata Vell. Conc. Fl. Flum. 175. 1825, later homonym of *A. lanceolata* Wallich, Asiatic Res. **12:** 391. 1820 = *Lyonia ovalifolia* (Wallich) Drude. TYPE: "Cabinet d'Histoire naturelle de Rio de Janeiro" (not seen).



MAP 9. Distribution of *Agarista boliviensis* (circles), *A. eucalyptoides* (dots), *A. glaberrima* (triangles), *A. angustissima* (open squares), and *A. duartei* (closed squares).

Andromeda eucalyptoides Cham. & Schldl. Linnaea **1**: 518. 1826. *Leucothoë eucalyptoides* (Cham. & Schldl.) DC. Prodr. **7**: 605. 1839. *Leucothoë multiflora* (Pohl) DC. var. *eucalyptoides* (Cham. & Schldl.) Meissner *in* Martius, Fl. Brasil. **7**: 155. 1863. TYPE: Brazil, Rio Grande do Sul, *Sellow s.n.* (holotype, B (destroyed); fragment of holotype, NY; isotypes, BR, E!, G!, K!).

Andromeda multiflora Pohl, Pl. Brasil. **2**: 33. *t. 122.* 1828/29. *Agarista multiflora* (Pohl) G. Don, Gen. Syst. **3**: 837. 1834. *Leucothoë multiflora* (Pohl) DC. Prodr. **7**: 605. 1839. *Leucothoë multiflora* (Pohl) DC. var. *pohlii* Meissner *in* Martius, Fl. Brasil. **7**: 155. 1863, nomen superfl. TYPE: Brazil, Minas Gerais, Rancho Novo, Serra da Mantiqueira, Sept./Oct. 1819, *Pohl s.n.* (holotype, W (destroyed?); isotypes, BR, M!).

Andromeda longepetiolata Fenzl ex Ettingsh. Blatt-Skel. Dikot. 94. *fig. 56.* 1861. TYPE: not seen.

Leucothoë multiflora (Pohl) DC. var. *petiolaris* Meissner *in* Martius, Fl. Brasil. **7**: 155. 1863. TYPE: Brazil, Minas Gerais, Serra de Cural d'El Rey, ca. 1841–1842, *Gardner 4986* (holotype, BM; isotypes, E!, F!, G!, GH!, K!, NY!, P!, US!, W).

Leucothoë multiflora (Pohl) DC. var. *brevipes* Meissner *in* Martius, *ibid.* TYPE: Brazil, Minas Gerais, Tejuco (= Diamantina), *Martius 1337* (holotype, M!; isotype, M!).

Shrub or small tree to ca. 4(–8) m tall, with often contorted trunks and thick, corky, furrowed bark. Twigs glabrous to sparsely pubescent, with ± nonchambered pith. Buds to ca. 1.5 mm long. Leaves alternate to subopposite or ± whorled, often variable even within single twig; petiole 6–40 mm long, frequently slender and flexuous; blade revolute in bud, ovate to oblong, 2.5–8 (–9.3) by 0.8–2.6 cm, ± flat, coriaceous, the apex acute to acuminate or shortly

so, to nearly rounded-mucronate, the base rounded to truncate and often slightly asymmetric, the margin entire (undulate), plane to very slightly revolute, especially near base, the adaxial surface glabrous (sparsely pubescent on midvein), the abaxial surface glabrous (very sparsely pubescent on midvein near base), with usually at least few inconspicuous (to conspicuous) glandular dots along midvein. Inflorescences axillary racemes to 1–6 cm long, axis moderately to densely ferrugineous/crisped-pubescent. Pedicels 2–6 mm long, sparsely to densely ferrugineous-pubescent; bracteoles 2, opposite to alternate, from nearly basal to near midpoint of pedicel, narrowly triangular, to ca. 1.1 mm long; bracts to ca. 1.7 mm long. Calyx lobes triangular with acuminate (to acute) apices, 1–1.8 by 0.5–1.2 mm, abaxial surface essentially glabrous; corolla cylindrical, 6–10.5 by 2.5–5 mm, white (to reddish), abaxially glabrous; filaments 3–4.5 mm long, anthers 0.8–1.1 mm long; ovary glabrous to sparsely pubescent. Capsules ovoid to short-ovoid, 3–5 by 4–5 mm, placentae subapical; seeds 1.8–2.5 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil (Minas Gerais and adjacent regions of Estado do Rio and São Paulo; Santa Catarina, Rio Grande do Sul) and Uruguay (MAP 9). Cerrado vegetation, open, rocky thickets and thicket margins, or rocky hillsides; (250–)800–2300 m alt. Flowering chiefly late August through November (December).

REPRESENTATIVE SPECIMENS. **Brazil.** ESTADO DO RIO: Nova Friburgo to Pedra do Cônego, *Glaziou 12927* (C, P). MINAS GERAIS: Itatiaia, *Brade 14086* (F, L); Serra do Caparaó, *Brade 16987* (F, L); São Thomé das Letras, Baipendí, *Brade 20429* (F, M); Serra do Cipó, km 131, *Duarte 2693* (F, L); Serra da Moeda, *Duarte 8897* (L, M); Serra do Itatiaia, *Dusén 2011* (G, GH, S); Serra da Mutuca, Belo Horizonte, *Markgraf 3523* (F); 35 km from Lambari, *Pereira 7153* (B); Uberava, *Regnell III-837* (S, US); Pico da Bandeira, near Caparaó, *Shepherd et al. 5795* (L); Caldas, *Widgren 327* (S); Serra da Calveira, Betim, *Williams & Assis 7503* (F, GH, MO, NY, S, SP, US). RIO GRANDE DO SUL: Pôrto Alegre, Morro da Policia, *Malme 608* (S); São Leopoldo, *Rambo 132* (S, SP); Montenegro, Zimmerberg, *Rambo 8309* (B); S. Francisco de Paula, Vila Oliva, *Rambo 31063* (F, MO, S); Pôrto Alegre, Morro da Glória, *Rambo 40072* (B, MO); Passo do Socorro, Vacaria, *Rambo 51626* (S, US). SANTA CATARINA: 16 km E of Lajes on rd. to Painel, *Smith & Reitz 10103* (L, US). SÃO PAULO: Campos do Jordão, *Leite 3614* (A, GH). **Uruguay:** Rivera, Cuñapirú, *Berro 4973* (G); Rivera, Galgo, *Herter 1859* (B, F, G, L, M, MO, NY, S).

Agarista eucalyptoides is a distinctive species easily recognizable by the moderately to densely ferrugineous/crisped pubescence of its inflorescence axis and pedicels. It is most closely related to *A. boliviensis*, a geographically separated species with more consistently ovate leaves and an inflorescence axis with whitish hairs. Both of these species (along with *A. glaberrima* and—to a lesser extent—*A. angustissima*) frequently have slender, flexuous, elongate petioles. Sleumer (1959) considered *A. glaberrima* to be only varietally distinct from *A. eucalyptoides*, but the two taxa differ in leaf shape, degree of adaxial folding of the lamina, inflorescence indumentum (lacking in *A. glaberrima*), and—to a lesser extent—capsule size. The morphological gap separating these taxa is thus comparable to that between most *Agarista* species. *Agarista glaberrima* is considered here to be a distinct species that is probably more closely related to *A. angustissima* than it is to *A. eucalyptoides*.

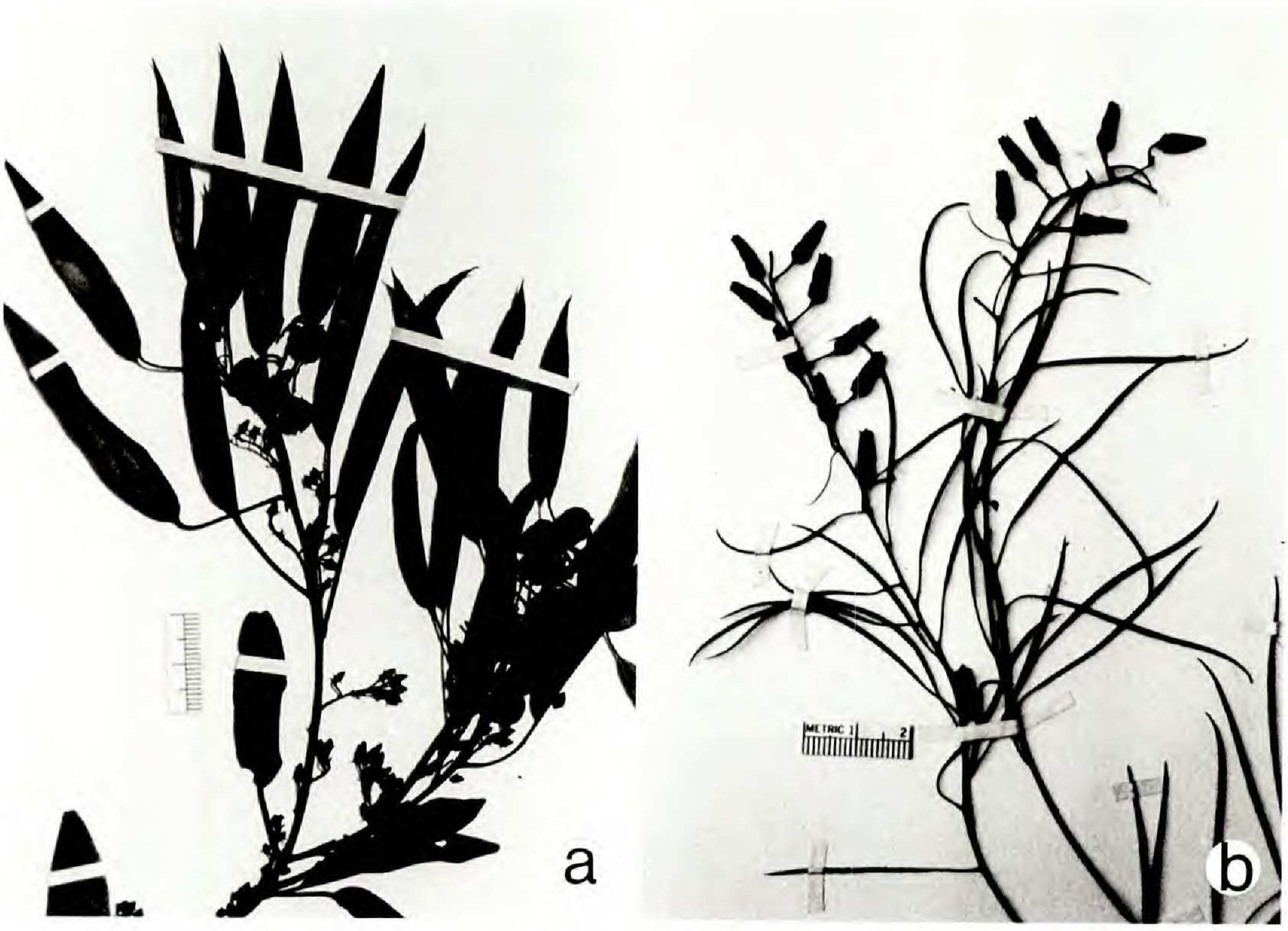


FIGURE 9. a, *Agarista glaberrima* (*Hatschbach, Smith, & Ayensu 28814*). b, *A. angustissima* (*Hatschbach 27988*, UC): note terminal racemes. Scale = 2 cm.

27. **Agarista glaberrima** (Sleumer) Judd, comb. et stat. nov. FIGURE 9, a.

Leucothoë eucalyptoides (Cham. & Schldl.) DC. var. *glaberrima* Sleumer, Bot. Jahrb. **78:** 458. 1959. TYPE: Brazil, Minas Gerais, Santa Lúcia, Serra do Cipó, km 135, 4 Feb. 1938, *Barreto 8921* (holotype, F!; photo of holotype, F!).

Shrub or small tree to 4 m tall. Twigs glabrous, with nonchambered to clearly chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 10–32 mm long, frequently slender and flexuous; blade revolute to conduplicate(?) in bud, ovate to narrowly ovate, 2.3–8.5 by 0.6–2.5(–3) cm, flat to strongly adaxially folded, coriaceous, the apex acuminate, the base cuneate to rounded and often slightly asymmetric, the margin entire (slightly undulate), plane, the adaxial surface glabrous (very sparsely pubescent on proximal portion of midvein), the abaxial surface glabrous, with few to many inconspicuous to conspicuous glandular dots along midvein. Inflorescences axillary racemes, or terminal racemes or panicles, to 1–9.5 cm long, axis glabrous. Pedicels 2.5–8 mm long, glabrous; bracteoles 2, opposite to alternate, from nearly basal to near midpoint of pedicel, narrowly triangular, to ca. 0.9 mm long; bracts to ca. 1.4 mm long. Calyx lobes triangular with acuminate (to nearly acute) apices, 0.8–1.7 by 0.5–1.3 mm, abaxial surface glabrous; corolla ± cylindrical, 6–10 by 2.7–4.5 mm, white or greenish white, abaxially glabrous; filaments 3.5–4.5 mm long, anthers 1.1–1.3 mm long; ovary glabrous or nearly so. Capsules subglobose to short-ovoid, 4–8 by 6–8 mm, placentae subapical to nearly central; seeds 2–2.5 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais (MAP 9). Sandy to rocky cerrado vegetation, margins of woods, rocky and/or disturbed thickets, rocky hillsides; 900–1500 m alt. Flowering chiefly November through February.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Serra do Espinhaço, Gouvêa, km 258 on M. G. 259, *Anderson et al. 35627* (F, L, NY); Serra dos Cristais, Diamantina, *Barreto 9562* (F); Boa Vista–Extracção, Diamantina, *Barreto 9647* (F); Serra do Cabral, Joaquim Felício, *Davis et al. 2374* (E); Diamantina, *Duarte 10526* (L); Serra do Cipó, Jaboticatuba, *Hatschbach et al. 28814* (C, L, MO, NY, S, UC); Serra do Espinhaço, Lapinha, 19 km N of Cêrro on road to Diamantina, *Irwin et al. 20802* (NY); 12 km NE of Diamantina on rd. to Mendanha, *Irwin et al. 22758* (ENCB, F, GH, K, NY); Serra Grão Mogul, *Maguire et al. 49269* (NY); Serra Negra, *St.-Hilaire, Cat. D, n. 94* (L, P).

Agarista glaberrima is most closely related to the sympatric *A. angustissima,* another Minas Gerais endemic (MAP 9) from which it can easily be distinguished by its ovate and wider leaves with usually longer petioles and less strongly adaxially folded blades. Although Sleumer (1959) considered this species to be a variety of *A. eucalyptoides,* the two taxa are quite distinct and can be separated by inflorescence indumentum (lacking vs. moderate to dense and ferrugineous), leaf shape (ovate vs. ovate to oblong), and degree of adaxial folding of the lamina.

28. **Agarista angustissima** Taubert, Bot. Jahrb. **17:** 513. 1893. FIGURE 9, b.

Leucothoë angustissima (Taubert) Sleumer, Bot. Jahrb. **78:** 451. 1959. TYPE: Brazil, Minas Gerais, Pinheiro, near Biribiri, 26 March 1892, *Glaziou 19582* (holotype, B (destroyed); fragment and photo of holotype, F!; photo of holotype, GH!; isotypes, BR, F!, G!, K!, MO!, NY!, P!).

Shrub to ca. 2 m tall. Twigs with or without gland-headed hairs, otherwise glabrous, with nonchambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 5.5–13 mm long, often slender and flexuous; blade conduplicate in bud, linear and curved, to narrowly ovate in juvenile leaves, (1.7–)3–7 by 0.1–0.5 cm but often appearing narrower, strongly adaxially folded and thus obscuring adaxial surface, coriaceous, the apex narrowly acute to short-acuminate, the base narrowly cuneate, the margin entire, to serrulate in juvenile leaves due to presence of gland-headed hairs, plane, the adaxial surface glabrous, the abaxial surface with or without gland-headed hairs, otherwise glabrous, lacking or with few inconspicuous glandular dots along midvein. Inflorescences axillary racemes, or terminal racemes or panicles, to 3–6 cm long, axis glabrous. Pedicels 4.5–14 mm long, glabrous; bracteoles 2, alternate to opposite, from nearly basal to within lower ¼ of pedicel, narrowly triangular to linear, to ca. 1 mm long; bracts to ca. 3 mm long, grading into leaves. Calyx lobes triangular with acuminate apices, 1–1.5 by 0.5–1.1 mm, abaxial surface glabrous; corolla cylindrical, 6.5–10.5 by 2.5–3.5 mm, white, abaxially glabrous; filaments 4–5 mm long, anthers 1–1.7 mm long; ovary glabrous. Capsules short-ovoid to subglobose, 3.5–5.5 by 5–7 mm, placentae subapical to nearly central; seeds 1.5–2.9 mm long.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais (MAP 9). Cerrado vegetation, moist rocky areas; ca. 1200–1400 m alt. Flowering November.

REPRESENTATIVE SPECIMENS. **Brazil.** MINAS GERAIS: Diamantina, *Barreto 10132* (F); Biribiri, Diamantina, *Hatschbach & Pelanda 27988* (C, L, NY, S, UC); Serra do Cipó, Fazenda Palacio, Jaboticatuba, *Hatschbach & Ahumada 31564* (L); Chapada, *St.-Hilaire, Cat. B*[1], *n. 2057* (L, P).

Agarista angustissima is a very distinctive species recognizable by its very narrow, more or less linear/curved leaves that are strongly adaxially folded and ca. 3–7 cm long, its glabrous stems, and its often terminal inflorescences. Most closely related to *A. glaberrima* and *A. duartei,* it can be distinguished from the former by its narrower, linear leaves, and from the latter by its glabrous stems and its more elongated, terminal inflorescences. All three species are limited to the Serra do Espinhaço region of Minas Gerais.

29. **Agarista duartei** (Sleumer) Judd, comb. nov.

Leucothoë duartei Sleumer, Bot. Jahrb. **78:** 451. 1959. TYPE: Brazil, Minas Gerais, Serra do Cipó, km 137 da Estrada de Conceição, 1300 m alt., 6 Dec. 1949, *Duarte 2103* (holotype, RB; isotypes, L!, LIL).

Subshrub to ca. 0.5 m tall, with bark not well developed. Twigs ± glabrous to densely pubescent, with nonchambered to irregularly chambered pith. Buds to ca. 1 mm long. Leaves alternate; petiole 2–6.5 mm long, not flexuous; blade conduplicate in bud, linear and ± curved, 1.2–3.5(–4) by 0.2–0.4 cm but often appearing narrower, strongly adaxially folded and thus obscuring adaxial surface, coriaceous, the apex narrowly acute to short-acuminate, the base narrowly cuneate, the margin entire, to serrulate in juvenile leaves due to presence of gland-headed hairs, plane, the adaxial surface sparsely pubescent, the abaxial surface with or without gland-headed hairs, otherwise glabrous to very sparsely pubescent on proximal portion of midvein, lacking or with few inconspicuous glandular dots along midvein. Inflorescences axillary racemes to 0.3–1.5 cm long, axis very slightly to densely pubescent. Pedicels 2–7.5 mm long, glabrous to densely pubescent; bracteoles 2, subopposite to alternate, from nearly basal to near midpoint of pedicel, narrowly triangular, to ca. 1 mm long; bracts to ca. 1 mm long. Calyx lobes triangular with acuminate apices, 1–1.5 by 0.6–1 mm, abaxial surface essentially glabrous; corolla cylindrical, 7–8 by 2.5–3.5 mm, white, abaxially glabrous; filaments 4.5–5 mm long, anthers 1.1–1.2 mm long; ovary glabrous to moderately pubescent, placentae ± subapical(?). Capsules not seen.

DISTRIBUTION AND ECOLOGY. Southeastern Brazil, Minas Gerais (MAP 9). Open sandy or rocky areas; ca. 1300 m alt. Flowering October to December.

REPRESENTATIVE SPECIMEN. **Brazil.** MINAS GERAIS: Serra do Cipó, Sta. Ana do Riacho, *Hatschbach & Koczicki 35379* (L).

This rare and little-collected species is most closely related to *Agarista angustissima* and *A. glaberrima.* It is easily distinguished from both of these species by its often pubescent stems and inflorescence axis, its shorter petioles, and its shorter and exclusively axillary racemes. Its leaves, like those of *A. angustissima,* are linear and very strongly adaxially folded. *Agarista duartei*

has only been collected in the Serra do Cipó, a region where the genus shows a large amount of diversity. Fruiting material has not been seen.

Agarista D. Don ex G. Don sect. **Agauria** (DC.) Judd, comb nov.

Leucothoë D. Don sect. *Agauria* DC. Prodr. **7:** 602. 1839. *Agauria* (DC.) J. D. Hooker *in* Bentham & Hooker, Gen. Pl. **2:** 586. 1876. LECTOTYPE SPECIES: *Agarista salicifolia* (Comm. ex Lam.) G. Don.

Twigs with nonchambered, slightly to very heterogeneous pith. Leaves with the abaxial epidermis papillose, the adaxial epidermal cells short, usually not divided. Style apparently not swollen. Capsules with placentae basal; seeds 3–4 mm long.

DISTRIBUTION. Central Africa, Madagascar, Réunion, and Mauritius (see Sleumer, 1938, *fig. 1*).

NUMBER OF SPECIES (TAXA): 1 (20).

This section is not treated here; see Sleumer (1938) for a revision of the group and a key to the many infraspecific taxa comprising the widespread and variable *Agarista salicifolia* (species no. 30).

SPECIES EXCLUDED FROM AGARISTA

Agarista anastomosans G. Don, Gen. Syst. **3:** 838. 1834, nomen superfl. = **Gaultheria glomerata** (Cav.) Sleumer (Sleumer, 1959).
Agarista ciliata (Nees) J. D. Hooker ex Niedenzu, Bot. Jahrb. **11:** 236. 1889 = **Gaylussacia brasiliensis** (Sprengel) Meissner (Sleumer, 1959).
Agarista coccinea (Schrader) J. D. Hooker ex Niedenzu, *ibid.* = **Gaylussacia brasiliensis** (Sprengel) Meissner (Sleumer, 1959).
Agarista eriophylla (Pers.) G. Don, Gen. Syst. **3:** 838. 1834 = **Gaultheria eriophylla** (Pers.) Sleumer ex Burtt (Sleumer, 1959).
Agarista ilicifolia (Pers.) G. Don, Gen. Syst. **3:** 838. 1834 = **Gaultheria phillyreifolia** (Pers.) Sleumer (Sleumer, 1959).
Agarista itatiaiae (Wawra) Wawra, Itin. Princ. Coburgi **1:** 73. 1883 = **Gaultheria itatiaiae** Wawra (Sleumer, 1959).

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