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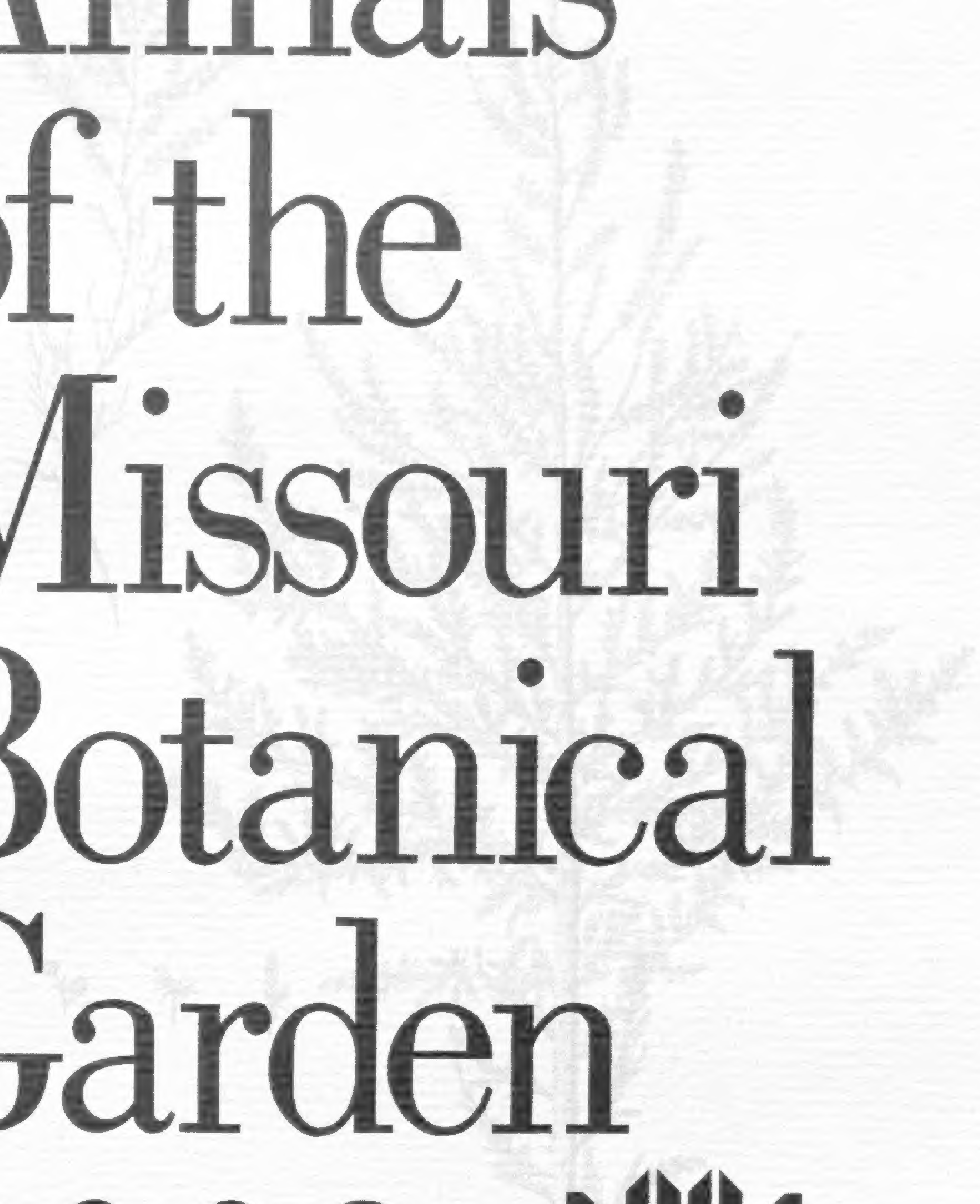

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THE PARAPHYLY OF *CORTADERIA* (DANTHONIOIDEAE; POACEAE): EVIDENCE FROM MORPHOLOGY AND CHLOROPLAST AND NUCLEAR DNA SEQUENCE DATA[1]

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Cynthia M. Morton,[4] *and Mark Lyle*[5]

ABSTRACT

The genus *Cortaderia* Stapf comprises approximately 24 species occurring in South America, New Zealand, and New Guinea. *Cortaderia* is placed in the subfamily Danthonioideae. Several species in the genus are known to be gynodioecious, a feature unusual for the subfamily. The genus has been divided into four sections, two of which are monotypic. This study utilizes nrDNA sequence data from the ITS region and the grass-specific insert in the chloroplast *rpo*C2 gene to elucidate the relationships of 15 species of the genus, including the anomalous *Cortaderia archboldii* (Hitchc.) Connor & Edgar. Results suggest that the genus is not monophyletic, and there are two clades that correspond to continental areas. The South American species of *Cortaderia* (including *Lamprothyrsus* Pilg.) form one clade, while the Australasian species form a second clade. Within *Cortaderia* s. str., section *Bifida* is polyphyletic, while section

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Cortaderia is monophyletic and sister to *Lamprothyrsus*. *Cortaderia archboldii* shows no immediate affinity with either of these two clades, but data indicate a possible relationship with *Danthonia* DC.

Key words: biogeography, *Cortaderia*, ITS, molecular systematics, paraphyly, phylogeny, Poaceae, *rpo*C2, supertrees, Total Evidence.

The grass genus *Cortaderia* (including the ornamental "pampas grass," *C. selloana* (Schult.) Asch. & Graeb) has a Gondwanan distribution, being found in temperate and Andean South America, from Costa Rica to Patagonia (including the Falkland Islands), New Zealand (including Chatham and Pitt Islands), and New Guinea.

Cortaderia is placed in the subfamily Danthonioideae (GPWG, 2001). It was previously included in the polyphyletic subfamily Arundinoideae (Davis & Soreng, 1993; Barker et al., 1995; Clark et al., 1995), and some past classifications place it in its own tribe, the Cortaderieae (Zotov, 1963, emended by Conert, 1987). Results of an initial study based on sequence data from the grass-specific insert in the plastid *rpo*C2 gene (Barker et al., 1999) found no support for the recognition of the tribe Cortaderieae, as *Cortaderia* is included within a large group of genera that approximately agreed with the tribe Danthonieae sensu Watson and Dallwitz (1992). These genera have now been elevated to subfamily status as Danthonioideae (GPWG, 2001). This subfamily is defined by the presence of haustorial synergid cells (Verboom et al., 1994; GPWG, 2001), and all species of *Cortaderia* examined to date possess haustorial synergid cells (Philipson, 1977; Philipson & Connor, 1984).

TAXONOMY

Although no recent species-level taxonomy exists for the entire genus, Connor and Edgar (1974) and Connor (1983a) have reviewed the nomenclature. The New Zealand species have been well studied taxonomically (Connor & Edgar, 1974, 1987; Edgar & Connor, 2000), but the South American species have only been studied on a regional basis (e.g., Davidse & Pohl, 1994; Astegiano et al., 1995, 1996). The number of species in the genus is at present uncertain: Clayton and Renvoize (1986) and Watson and Dallwitz (1992) considered the genus to comprise 24 species, but Lyle (1996) considered there to be only 22 species, and Astegiano et al. (1995) recognized 25 species. However, at least four South American species may not be distinct, and one is considered to be of hybrid origin (*C. sericantha* × *nitida*, Lyle, unpublished). Most species of the genus are found in South America (19 species), but five are known from New Zealand and nearby islands, and the anomalous *C. archboldii* is from New Guinea.

Cortaderia is presently delimited by the presence of a gynodioecious breeding system and floret morphology. The genus is divided into four sections (sects. *Bifida*, *Cortaderia*, *Mutica*, and *Monoaristata*) on the basis of sexual dimorphism and lemma morphology (Conert, 1961; Connor & Edgar, 1974; Clayton & Renvoize, 1986). The latter two sections are monotypic, while section *Bifida* is the most speciose. All New Zealand and several South American species are placed in section *Bifida*, while section *Cortaderia* is restricted to South America.

Morphologically, *Cortaderia* has been considered to intergrade with the New Zealand genus *Chionochloa* Zotov, with the New Guinean *Cortaderia archboldii* intermediate between the two genera (Clayton & Renvoize, 1986). Hitchcock (1936) originally described *Cortaderia archboldii* as a species of *Danthonia*. During the 1960s the broadly circumscribed genus *Danthonia* was broken up into numerous segregate genera. In Africa, all species formerly in *Danthonia* were placed in *Merxmuellera* Conert, *Karroochloa* Conert & Türpe, *Dregeochloa* Conert, and *Pseudopentameris* Conert (Conert, 1966, 1970, 1971; Conert & Türpe, 1969). In New Zealand, *Chionochloa*, *Notodanthonia* Zotov, *Erythranthera* Zotov, and *Pyrranthera* Zotov were erected (Zotov, 1963). In Australia Blake (1972) resurrected *Plinthanthesis* Steud. and *Monachather*, and *Rytidosperma* Steud. was recognized in South America (Nicora, 1973). *Rytidosperma* and *Notodanthonia* have subsequently been synonymized (Connor & Edgar, 1979), although there has been some dispute about the most appropriate name (Veldkamp, 1980; Jacobs, 1982), the validity of recognizing *Rytidosperma* as a genus distinct from *Danthonia* (Conert, 1975; Jacobs, 1982), and the circumscription of *Rytidosperma* (Clayton & Renvoize, 1986). More recently, Linder and Verboom (1996) and Linder (1997) have once again revised the Australasian taxa. *Danthonia archboldii* has not escaped the fragmentation of *Danthonia* as it is clearly not *Danthonia* sensu Zotov. Connor and Edgar (1974) transferred the species to *Cortaderia*, while virtually simultaneously Conert (1975) transferred it to *Chionochloa*. The matter of where this species should be classified has remained unresolved.

Table 1. Known chromosome counts for species of *Cortaderia* and *Lamprothyrsus*.

2*n*	Species	Reference
36	*C. pilosa*	Moore (1967) cited by Connor & Edgar (1974)
72	*C. araucana*	Beuzenberg, pers. comm., cited by Connor & Edgar (1974)
72	*C. archboldii*	Borgmann (1964) cited by Connor & Edgar (1974)
72	*C. colombiana* (published as *C. roraimensis*)	Löve (1967) cited by Connor & Edgar (1974)
72	*C. selloana*	Connor (1965a); Connor & Edgar (1974)
72	*C. speciosa*	H. E. Connor, pers. comm.
90	*C. fulvida*	Hair & Beuzenberg (1966) cited by Connor & Edgar (1974)
90	*C. richardii*	Hair & Beuzenberg (1966) cited by Connor & Edgar (1974)
90	*C. splendens*	Connor (1971); Connor & Edgar (1974)
90	*C. toetoe*	Hair & Beuzenberg (1966) cited by Connor & Edgar (1974)
108	*C. jubata* (published as *C. atacamensis*)	Connor (1965a) cited by Connor & Edgar (1974)
108	*C. rudiuscula*	Connor & Dawson (1993)
~136	*Lamprothysus peruvianus*	Connor & Dawson (1993)

CYTOLOGY AND BREEDING SYSTEM

The reproductive biology of some species of *Cortaderia* has been studied extensively, as they display a gynodioecious breeding system (Connor, 1963, 1965a, b, 1970, 1973, 1979, 1983b, 1987; Robinson, 1984; Connor & Charlesworth, 1989; Connor & Dawson, 1993; Connor et al., 2000). Some species are apomictic (Connor, 1973; Philipson, 1978; Connor et al., 2000). Cytological data exist for several species (summarized in Table 1), and have been used by Connor and Dawson (1993) to suggest that at least some species are related to the South American *Lamprothyrsus*. Connor et al. (2000) also noted that there is incomplete dioecism in *Lamprothyrsus*. On the basis of these chromosome counts, the base chromosome number (x) for *Cortaderia* is considered by some (e.g., Connor & Dawson, 1993; Astegiano et al., 1996) to be nine ($x = 9$).

PHYLOGENETIC RELATIONSHIPS

Early molecular studies indicated the possible polyphyly of *Cortaderia*. Barker et al. (1999) included two species in their study based on sequence data of the grass-specific insert in the chloroplast RNA polymerase subunit C2 gene (*rpo*C2). The South American species was sister to *Lamprothysus* and the New Zealand species was allied to the Australian genera *Notochloe* Domin and *Plinthanthesis*. A subsequent investigation using Internal Transcribed Spacer (ITS) sequence data from a number of species of *Cortaderia* supported the result obtained from the *rpo*C2 study (Barker et al., 2000). A combined analysis was conducted by Barker et al. (2000), but this analysis had numerous taxa with missing data as there was little taxon overlap between the two molecular data sets. Despite this, these results imply either two independent origins of gynodioecy within Danthonioideae, or a single origin and multiple subsequent losses in different genera. These conflicting evolutionary scenarios cannot, however, be readily tested, as the breeding systems of the other genera in the lineage have not been investigated in detail. Also, phylogenies based on plastid genes (such as *rpo*C2) reflect the phylogeny of the organelle and need not reflect organismal phylogeny (Doyle, 1992; Brower et al., 1996). This could explain the unexpected result of a polyphyletic *Cortaderia*.

This study uses evidence from both chloroplast (*rpo*C2) and nuclear (ITS) genes from the majority of the species of *Cortaderia* to test the monophyly of this genus within the context of the seven informal groups of danthonioid genera outlined by Barker et al. (2000). Relationships of *Cortaderia archboldii* are also clarified.

MATERIALS AND METHODS

TAXON SAMPLING, DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

This study includes place-holders of all the seven informal lineages identified by Barker et al. (2000). Table 2 details the taxa sampled in this study, as well as voucher and GenBank information. Leaf material was dried in silica gel (Chase & Hills, 1991). DNA was extracted from these samples using the hot CTAB method of Doyle and Doyle (1987). The entire ITS region was amplified by the Polymerase Chain Reaction (PCR) using the primers 17SE and 26SE published by Sun et al. (1994).

Table 2. Voucher details of species sequenced in this study. The species of *Cortaderia* are presented at the top of the table, sorted according to the section to which they have been traditionally placed. Additional taxa sequenced are listed below those of *Cortaderia.* Note that taxa for which both ITS and *rpo*C2 data have already been published are not included. All those species listed as "ex Cult. New Zealand" were provided by Mr. R. Buxton from the Botanic Garden at Lincoln, New Zealand (G = Garden number). Key: MWC = DNA extract number provided by M. Chase (Jodrell Laboratory, RBG Kew); NPB = collected by N. P. Barker, HPL = collected by H. P. Linder, CHR = Christchurch herbarium.

Genus and species	Section	Voucher, origin & herbarium	*rpo*C2 GenBank No.	ITS GenBank No.
Cortaderia archboldii (Hitchc.) Connor & Edgar	*Bifida*	*J. Marsden* 115 (= MWC 8879) (K)	AF355998	AF367620
Cortaderia bifida Pilg.	*Bifida*	*Lyle 1497;* Ecuador (HBG, BOL)	AF355988	AF367609
Cortaderia colombiana (Pilg.) Pilg.	*Bifida*	*Lyle & Carillo 920;* Venezuela (HBG, BOL)	AF355991	AF367612
Cortaderia fulvida (Buchan.) Zotov	*Bifida*	G 5088; ex Cult. New Zealand (BOL)	Barker et al. (1999)	AF367615
Cortaderia hapalotricha (Phil.) Conert	*Bifida*	*Lyle 1525;* Ecuador (HBG, BOL)	AF355989	AF367610
Cortaderia nitida (Kunth) Pilg.	*Bifida*	*Lyle 1434;* Ecuador (HBG, BOL)	AF355990	AF367611
Cortaderia richardii (Endl.) Zotov	*Bifida*	G 3816; ex Cult. New Zealand (BOL)	AF355996	AF367618
Cortaderia sericantha (Steud.) Hitchc.	*Bifida*	*Lyle 1128;* Ecuador (HBG, BOL)	AF355986	AF367606
Cortaderia splendens Connor	*Bifida*	G 10872; ex Cult. New Zealand (BOL)	AF355994	AF367616
Cortaderia toetoe Zotov	*Bifida*	G 5042; ex Cult. New Zealand (BOL)	AF355997	AF367619
Cortaderia turbaria Connor	*Bifida*	G 17358; ex Cult. New Zealand (BOL)	AF355995	AF367617
Cortaderia araucana Stapf	*Cortaderia*	G 7162; ex Cult. New Zealand (BOL)	AF355993	AF367614
Cortaderia jubata (Lem.) Stapf	*Cortaderia*	*Lyle 1515;* Ecuador (HBG, BOL)	AF355987	AF367608
Cortaderia rudiuscula Stapf	*Cortaderia*	G 11157; ex Cult. New Zealand (BOL)	AF355992	AF367613
Cortaderia selloana (Schult.) Asch. et Graeb.	*Cortaderia*	*Robinson s. n.* (BOL)	Barker et al. (1999)	AF367607
Austrodanthonia auriculata (J. M. Black) Linder		*HPL 5569;* Australia (BOL)	Not sequenced	AF367604
Chaetobromus involucratus (Schrad.) Nees subsp. *involucratus*		*NPB 1715;* South Africa (GRA)	Not sequenced	AF367599
Chionochloa macra Zotov		CHR 475278; ex Cult. New Zealand (BOL)	Barker et al. (1999)	AF367595
Chionochloa pallens Zotov		CHR 475 279; ex Cult. New Zealand (BOL)	Not sequenced	AF267596
Chionochloa rigida (Raoul) Zotov		*HPL 5710;* New Zealand (BOL)	Not sequenced	AF367597
Lamprothyrsus peruvianus Hitch.		G 11154; ex Cult. New Zealand (BOL)	Barker et al. (1999)	AF367605
Merxmuellera cincta (Nees) Conert subsp. *cincta*		NPB 1160; South Africa (BOL)	Barker et al. (1999)	AF367593
Merxmuellera cincta (Nees) Conert subsp. *sericea* N. P. Barker		*NPB 1545;* South Africa (GRA)	AF355985	AF367594
Merxmuellera davyi (C. E. Hubb.) Conert		*NPB 942;* South Africa (BOL)	Barker et al. (1999)	AF367590
Merxmuellera decora (Nees) Conert		*NPB 1168;* South Africa (BOL)	AF355984	AF367592

Table 2. Continued.

Genus and species	Section	Voucher, origin & herbarium	*rpo*C2 GenBank No.	ITS GenBank No.
Merxmuellera disticha (Nees) Conert		*NPB 1002:* South Africa (BOL)	Barker et al. (1999)	AF367600
Merxmuellera lupulina (Thunb.) Conert		*HPL 7004:* South Africa (BOL)	AF355983	
Merxmuellera rufa (Nees) Conert		*NPB 1149:* South Africa (BOL)	Barker et al. (1999)	AF267591
Pseudopentameris macrantha (Schrad.) Conert		*HPL 5470:* South Africa (BOL)	Barker et al. (1999)	AF367598
Notodanthonia gracilis (Kirk) Zotov		*HPL 5683:* New Zealand (BOL)	Not sequenced	AF367603
Tribolium hispidum (Thunb.) Desv.		*NPB 1740:* South Africa (GRA)	Not sequenced	AF367602
Tribolium pusillum (Nees) H. P. Linder & Davidse		*HPL 5402:* South Africa (BOL)	Barker et al. (1999)	AF367601

The grass-specific insert in the chloroplast *rpo*C2 gene was amplified using the primers "*rpo*C2-UP" and "*rpo*C2-DOWN" (details in Barker et al., 1999).

PCR was carried out in a 100 μl volume using PROMEGA Taq and buffer at a concentration range of 1–4 mM magnesium chloride. Thermal cycling conditions were: an initial denaturing stage of 1 min. at 97°C, followed by 30 to 40 cycles (template dependent) using an annealing temperature of 52°C (1 min.), extension at 72°C (3 min.) and denaturation at 97°C (1 min.). A 10-minute extension period at 72°C followed the 30 cycles, prior to cooling at 4°C. The ITS region of *Cortaderia archboldii* was amplified as two separate products, ITS1 and ITS2, by means of the flanking primers and the internal (sequencing) primers described below.

All PCR products were cleaned and concentrated into 20 μl of Tris-EDTA buffer or water using the QIAGEN QIAQuick PCR Product Purification Kit. Sequencing reactions were carried out using the ABI PRISM or ABI PRISM BIG DYE cycle sequencing kit according to the manufacturer's instructions. The ITS PCR product was sequenced completely in both directions, initially using the primers 17SE, 5.8S, 5.8R, and 26SE published by Sun et al. (1994). Owing to primer mismatch, three additional internal primers were used to sequence the PCR product: "ITSL" (Hsiao et al., 1998), "Danth 5.8SF" (5′-GAC TCT CGG CAA CGG-3′), and "Danth5.8SR" (5′-TTT GGC GTG ACG CCC-3′). The *rpo*C2 PCR product was sequenced using the internal primers "*rpo*C2–1" and "*rpo*C2–2" (Barker et al., 1999). Sequencing was carried out on ABI 373, ABI 377, and ABI3100 automated DNA sequencers.

SEQUENCE ALIGNMENT

All component sequences from each PCR product were assembled, checked, and corrected where necessary using Sequencher version 3 (Gene Codes Corporation). Completed sequences were then imported into the existing data set of danthonioid ITS and *rpo*C2 sequences, and aligned using DAPSA (DNA And Protein Sequence Alignment; E. H. Harley, Dept. Chemical Pathology, University of Cape Town). DAPSA was also used to generate data files for subsequent phylogenetic analysis.

PHYLOGENETIC ANALYSIS

The *rpo*C2 and ITS data were analyzed both separately and in a combined analysis using PAUP version 4.0b3a (Swofford, 2000). *Centropodia glauca* (Nees) T. A. Cope and *Merxmuellera rangei* (Pilg.) Conert were used as outgroups in all analyses. These species have previously been shown to be related to the danthonioid lineage (Barker, 1995; Barker et al., 1999, 2000). Two hundred random input order searches were conducted (TKEEP = 1, MULPARS OFF). The most parsimonious trees found using this search were subjected to a full heuristic search (TBR option, MULPARS ON). Fast Bootstrap analyses using 10,000 replicates were conducted on the individual and combined data sets.

Combined molecular data set. Arguments for and against when and how to combine data sets have been discussed at some length (e.g., de Queiroz, 1993; de Queiroz et al., 1995; Huelsenbeck et al., 1996; Nixon & Carpenter, 1996). Mason-Gamer and Kellogg (1996) discussed various ways in which conflict between data sets can be assessed, and advised on when it is suitable to conduct such tests. Following their suggestion, combination of data sets is possible if the trees do not conflict, or if conflict receives low bootstrap support. Thus each node on each of the two trees is tested for congruence against the other tree. Where the nodes are congruent (that is, do not contain conflicting information, even if they are not identical), they are obviously combinable. Where they are incongruent, the bootstrap support for each of the conflicted nodes is examined. If the support is less than 70%, the incongruence is interpreted as being due to chance, and that there is no hard conflict. This logic is derived from Mason-Gamer and Kellogg (1996), and ultimately from Rodrigo et al. (1993) and was recently applied by Eldenäs and Linder (2000). Tests for incongruence (such as that proposed by Farris et al., 1994, 1995) were thus not conducted, as the trees obtained here show no well-supported conflict.

To reduce the amount of missing data in the combined analysis, a combined data set was created from only those taxa for which both ITS and *rpo*C2 data were available. Unfortunately, four genera are not represented by a species common to both data sets, and we thus had to create four "fictive taxa" (Kellogg & Linder, 1995) or "hybrid taxa" (Wiens & Reeder, 1995) that represented the four genera for which different species or subspecies had been sequenced for each gene. These fictive taxa thus represent genera, rather than species. This approach is acceptable when the monophyly of the higher group is known or accepted (Wiens & Reeder, 1995). These fictive taxa represent *Danthonia* (a combination of *D. spicata* (L.) Beauv. ex Roem & Schult. [*rpo*C2] and *D. californica* Bol. [ITS]), *Pentameris* Beauv. (a combination of *P. thuarii* Beauv. [*rpo*C2] and *P. macrocalycina* (Steud.) Schweick. [ITS]), *Chaetobromus* Nees (a combination of *C. involucratus* (Schrad.) Nees subsp. *involucratus* [ITS] and *C. involucratus*. (Schrad.) Nees subsp. *dregeanus* (Nees) Verboom [*rpo*C2]) and *Tribolium* (a combination of *T. uniolae* (L. f.) Renvoize [*rpo*C2] and *T. hispidum* (Thunb.) Desv. [ITS]).

Pentameris has been recently revised (Barker, 1993) and is clearly a monophyletic lineage. However, the monophyly of *Danthonia* has not been examined critically and, for the purposes of this study, it is viewed in a narrow context, comprising mostly Northern Hemisphere species. It is possible that the genus is not monophyletic, but as the two species combined here are both North American, they are considered to be sufficiently closely related to allow data combination. The third fictive taxon represents a single species in a monotypic genus. As suggested by their rank, the two subspecies of *Chaetobromus involucratus* are obviously closely related, and were once considered as distinct species (see Verboom & Linder, 1998, for a summary). The two subspecies share a unique morphological character of a tuft of hairs below each spikelet, corroborating the monophyly of the species. The cytology, ecology, and taxonomy of this genus has been extensively studied (Spies et al., 1990; Verboom & Linder, 1998), and these two entities can be readily combined. *Tribolium* has been recently revised (Linder & Davidse, 1997) and now includes the previously monotypic *Urochlaena* Nees (= *T. pusillum* (Nees) Linder & Davidse). Although data for this latter species are available for both data sets and thus could be used to represent this genus, a broader sampling of *Tribolium* was considered appropriate, hence the combination of the two species of *Tribolium*.

With the use of fictive taxa, the combined data set comprised 45 taxa (including outgroups), and included representatives of all the seven informal lineages recognized by Barker et al. (2000). "Total Evidence" (TE: see de Queiroz et al., 1995; Huelsenbeck et al., 1996) analysis of the combined data set was carried out as described above for the individual data sets.

Supertrees. A supertree approach to combining the results of the ITS and *rpo*C2 analyses was taken to include all species that were sampled for one of these two regions. The supertree was calculated from strict consensus trees of the two molecular data sets, using matrix representation parsimony (MRP; Baum, 1992; Ragan, 1992). Each consensus tree was described as a matrix, with each node constituting a character. Species described by that node were scored as 1, and species not included in the node as 0. Species absent from the tree were scored as unknown (?) for these nodes. In order to reflect the support each node had within its data set, we weighted the characters (nodes) relative to their bootstrap support levels: bootstrap support of 0.7–0.79 was weighted × 3; 0.8–0.89 weighted × 6 and 0.9–1 weighted × 9 (Ronquist, 1996). Since the supertrees search for resolution, and not for nodes supported by all possible trees of a given level of parsimony, we used a semi-strict consensus tree to indicate the result, as semi-strict consensus

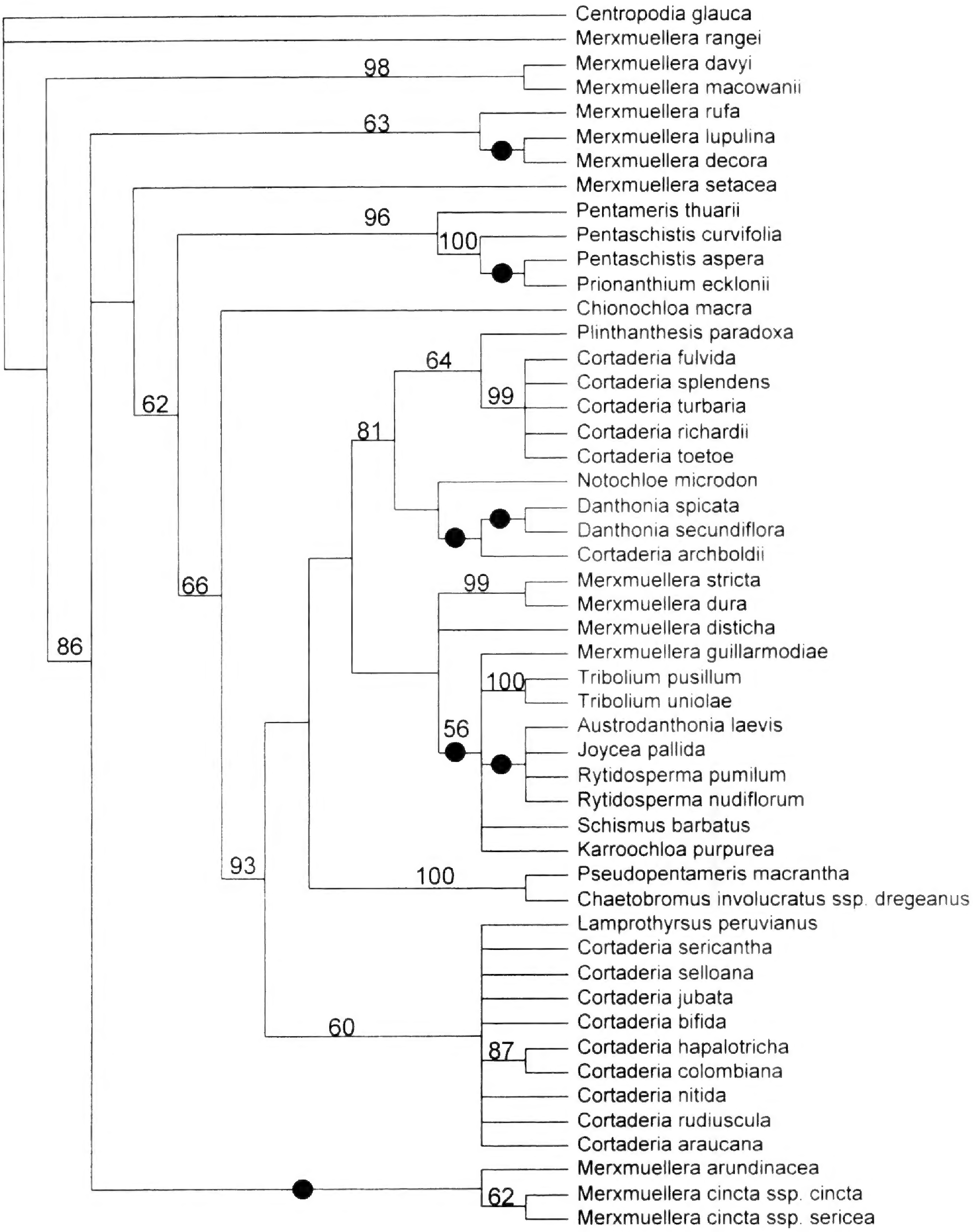

Figure 1. One of the 640 most parsimonious trees obtained from the *rpo*C2 data (length = 555 steps, C.I. = 0.490, R.I. = 0.724). Solid dots indicate nodes that collapse in the consensus tree. Numbers above the nodes are bootstrap values greater than 50% from 10,000 Fast Bootstrap replicates.

trees will retrieve all uncontradicted nodes. We used both Fitch optimization and optimization prohibiting reversals, to prevent shared absences from grouping, as suggested by Bininda-Emonds and Bryant (1998).

MORPHOLOGICAL DATA

As part of a larger study (Barker et al., 2000), morphological and anatomical characters were coded from herbarium specimens. This data set was edited by removing uninformative characters and taxa for which sequence data were unavailable. The data were compiled by HPL from observations of both herbarium and fresh collections. In addition, published revisions and anatomical observations were consulted. These characters and their states are listed in Appendix 2, which also gives literature citations to relevant sources of some data. The data set is provided in Appendix 1. Phylogenetic searches were done using PAUP (200 random taxon-entry replicates were conducted, keeping five trees at most from each search, these trees then used in a second search, in which all most parsimonious trees were kept). This search was limited to 10,000 trees. Further signal was sought by successively weighting the data by the rescaled consistency index, and repeating the above search protocols.

RESULTS

All sequences are deposited in GenBank, and the accession numbers are indicated in Table 2 (or the earlier works indicated there). The morphological data set and alignments are also available from the senior author upon request.

THE *RPOC2* DATA SET

The alignment used in this analysis is identical to that presented by Barker et al. (1999), and the new sequences were placed within the existing alignment without creating any additional insertions. Some of the new sequences did have deletions, but these do not affect the final alignment length. This alignment contained 50 taxa and resulted in 98 phylogenetically informative sites. The maximum parsimony analysis found 9710 equally parsimonious trees of length 165 steps (C.I. = 0.715, R.I. = 0.896). A randomly selected most parsimonious tree is shown in Figure 1, while the strict consensus tree is shown in Figure 3.

THE ITS DATA SET

The ITS sequences from *Chaetobromus* (and to a lesser extent *Pseudopentameris*) were difficult to align in two regions: one at the beginning of the ITS1 region (a deletion in the *Chaetobromus* sequences), the other at the beginning of the ITS2 region (an insertion in the *Chaetobromus* sequences). Alignment of the remaining sequences was unproblematic, but incorporated many small gaps, mostly one to five bases in size. The alignment of 51 sequences produced 168 phylogenetically informative sites. Phylogenetic analysis resulted in 640 most parsimonious trees with a length of 555 steps (C.I. = 0.490, R.I. = 0.724). A randomly selected most parsimonious tree is shown in Figure 2, and the strict consensus tree in Figure 3.

COMBINED DATA SET

The *rpo*C2 strict consensus retrieved 22 nodes and the ITS strict consensus 35 nodes. Of these, nine (40.9% of the *rpo*C2 nodes, 25.76% of the ITS nodes) are identical (Fig. 3). Bootstrap support for these nodes ranges from 63% (*Merxmuellera rufa*, *M. decora*, and *M. lupulina* clade in the *rpo*C2 tree) to 100% (numerous small clades in both trees). Of these nine common nodes, five comprise small clades of two to three taxa, and (with the exception of the *Pentaschistis* clade) none of the nodes in common correspond to the lineages recognized by Barker et al. (2000). There is thus some congruence between the two data sets, and, more importantly, there are no conflicting nodes where bootstrap support is greater than 65%. The data sets were thus considered to be combinable. The TE analysis included 262 phylogenetically informative sites, and analysis of these data resulted in 32 equally parsimonious trees of length 713 steps (C.I. = 0.534, R.I. = 0.737). The strict consensus of these trees is shown in Figure 4.

MORPHOLOGICAL DATA SET

The unweighted analysis located more than 10,000 trees, with a length of 242 steps, consistency index of 0.261, and retention index of 0.644. The strict consensus tree of this set was poorly resolved. The consistency and retention indices stabilized after three rounds of re-weighting, and this weighted data set resulted in 686 trees, with a consistency index of 0.593 and retention index of 0.859. The strict consensus of the most parsimonious trees obtained following re-weighting is shown in Figure 5. Bootstrap support values were not calculated owing to the high degree of homoplasy, poor resolution, and the very high number of initial most parsimonious trees found in the above procedure. Furthermore, because of these reasons, the morphological data were not combined with the molecular data.

In contrast to the molecular trees the consensus tree obtained from the re-weighted analysis shows a single clade for *Cortaderia*, including *C. archboldii* and *Lamprothyrsus*. *Cortaderia* is sister to *Chionochloa*, and both are nested within a large group of *Merxmuellera* species. Although many of the species groups are similar to those obtained from the molecular analyses, the relationships among these groups are quite different. Although no support analyses were conducted, the low resolution in the unweighted trees suggests that there is little support for this particular topology in this data set.

SUPERTREE ANALYSIS

The semi-strict consensus supertree based on the molecular data sets is shown in Figure 6. This has

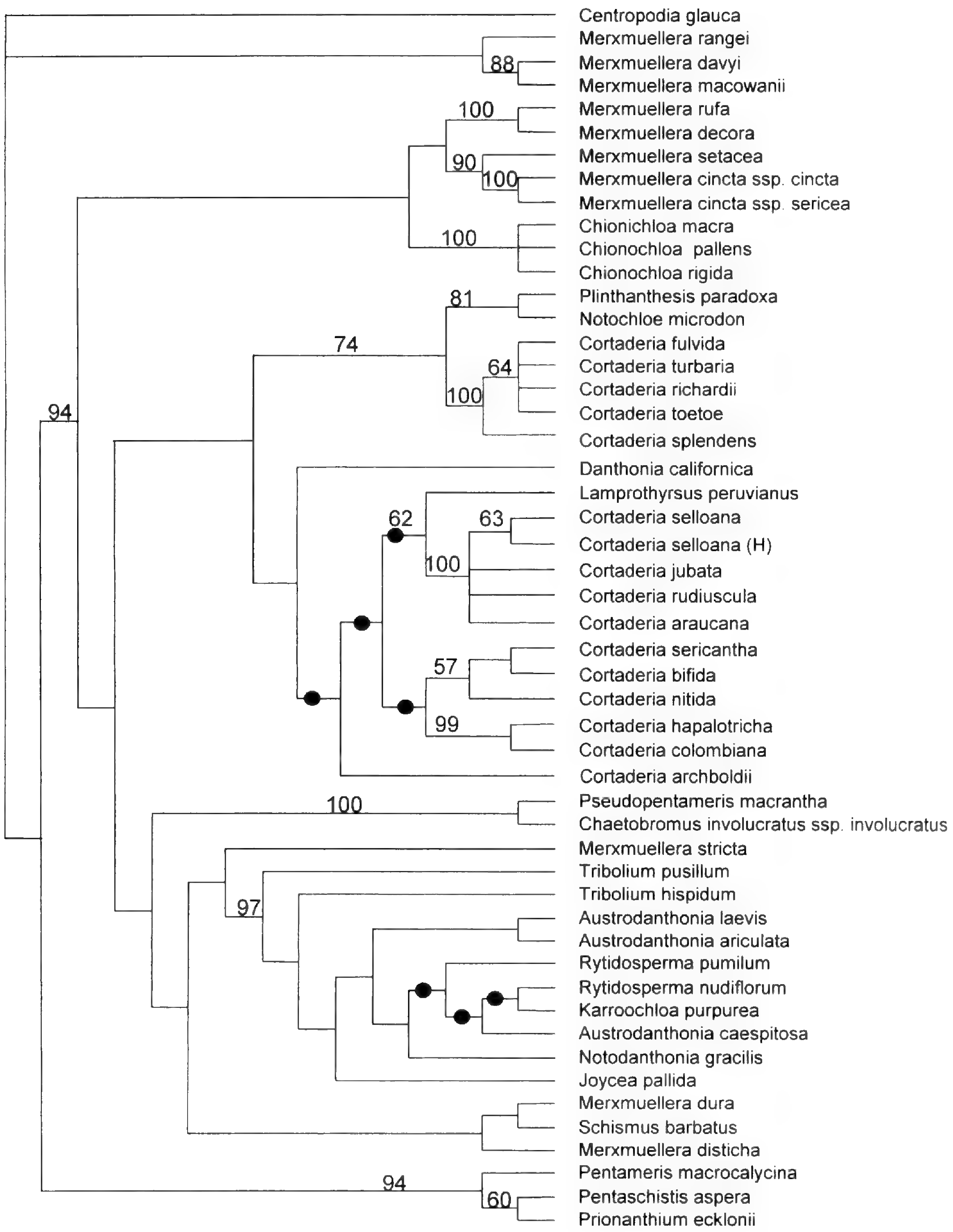

Figure 2. One of the 9710 most parsimonious trees obtained from the ITS data (length = 165 steps, C.I. = 0.715, R.I. = 0.896). Solid dots indicate nodes that collapse in the consensus tree. Numbers above the nodes are bootstrap values greater than 50% from 10,000 Fast Bootstrap replicates. The "H" in parentheses after *Cortaderia selloana* indicates the sequence from Hsiao et al. (1998).

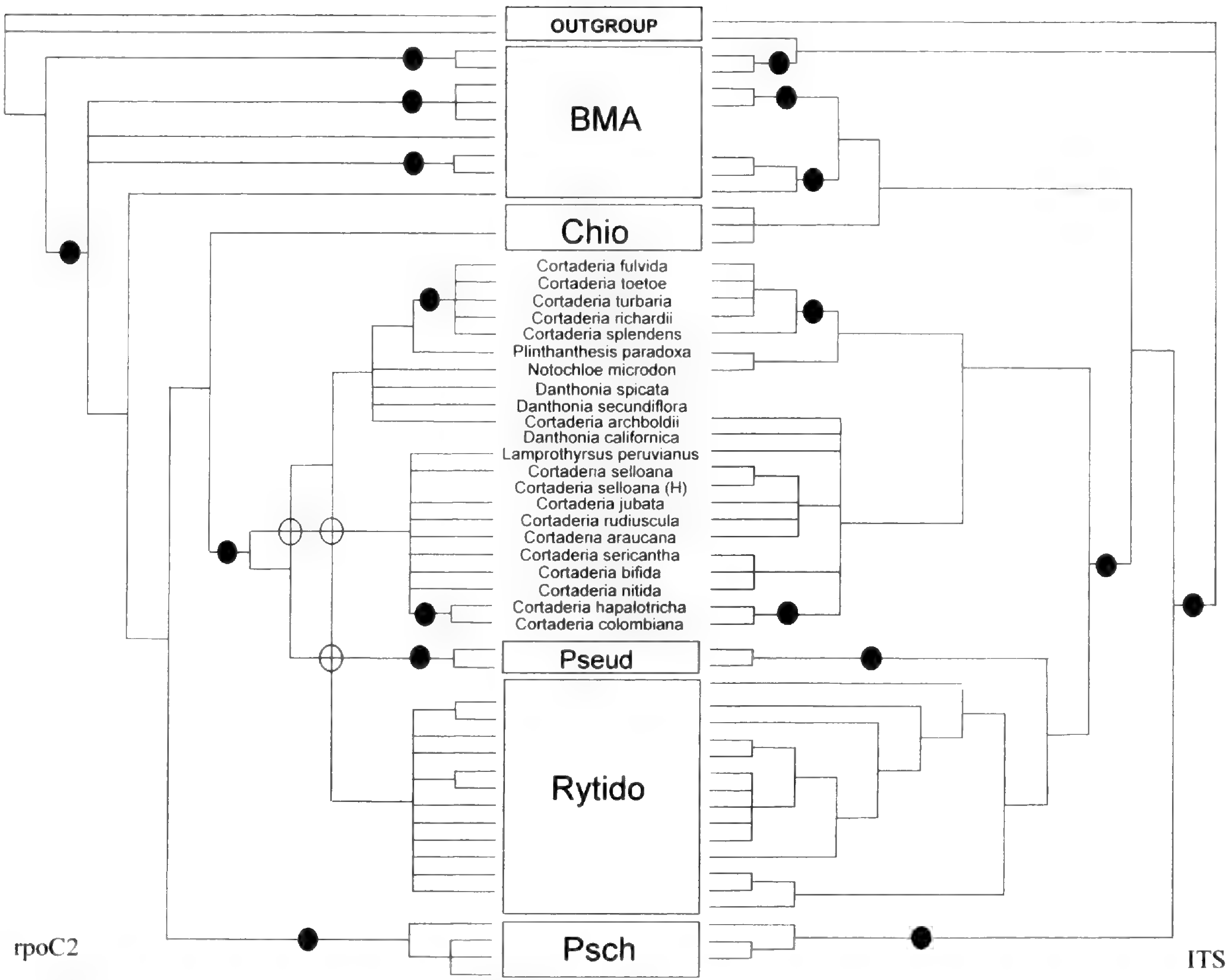

Figure 3. The strict consensus trees from the *rpo*C2 data set (left) and ITS data set (right). Open circles indicate branches that cross in the *rpo*C2 tree to accommodate the topological differences in the ITS tree. Solid dots indicate nodes that are found in both trees; open circles indicate branches that have been crossed or swiveled in the *rpo*C2 topology in order to get the taxa in a common order. The major lineages as outlined by Barker et al. (2000) are indicated in the boxes and labeled as follows: BMA = Basal *Merxmuellera* Assemblage, Chio = *Chionochloa* clade, Pseud = *Psuedopentameris* clade, Rytido = *Rytidosperma* clade, Psch = *Pentaschistis* clade. The "H" in parentheses after *Cortaderia selloana* indicates the sequence from Hsiao et al. (1998).

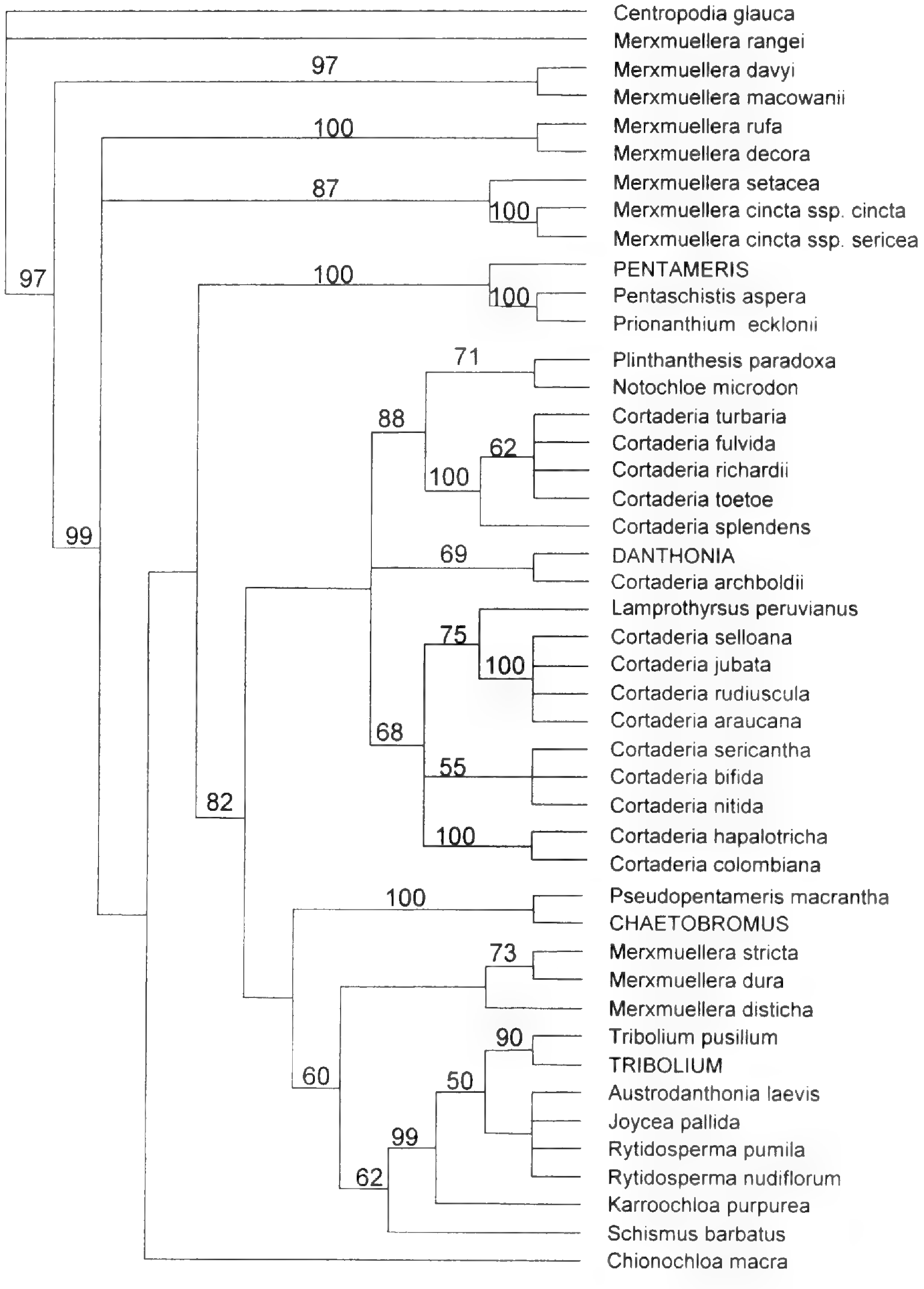

Figure 4. The strict consensus tree of 32 most parsimonious trees (length = 713 steps, C.I. = 0.534, R.I. = 0.737) obtained from the combined *rpo*C2 and ITS data. Taxa in uppercase are fictive taxa. Numbers above the nodes are bootstrap values greater than 50% from 10,000 Fast Bootstrap replicates.

substantially more resolution than the strict consensus tree. Weighting the nodes according to their bootstrap support in the source trees added only a single node in the *Rytidosperma* clade. Treating all characters as irreversible for the unweighted matrix produced the same result as obtained from the weighted matrix with Fitch parsimony, while the weighted matrix with irreversible characters located a further node that links *Plinthanthesis* and *Notochloe*. Including *C. archboldii* leads to the collapse of the three included *Danthonia* species, *C. archboldii*, and the *Plinthanthesis* clade, to form a polytomy with the two *Cortaderia* clades, the *Rytidosperma* clade, and the *Chaetobromus* clade (nodes marked in Fig. 6).

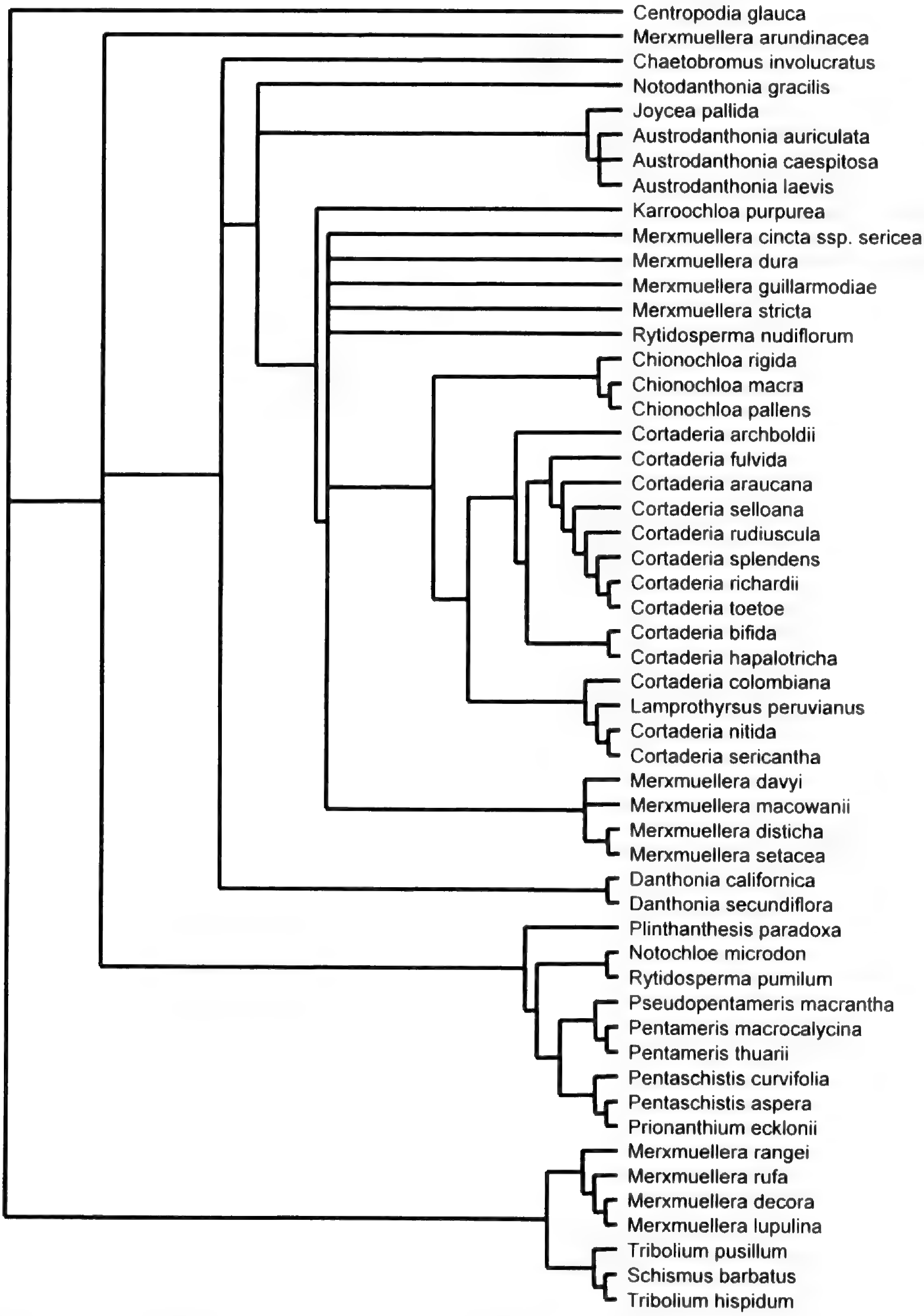

Figure 5. The strict consensus tree derived from the successively re-weighted morphological data. Analysis of the weighted data retrieved 686 most parsimonious trees (C.I. = 0.593, R.I. = 0.859).

DISCUSSION

RPOC2 SEQUENCE DIVERGENCE

As noted above, the alignment used here was identical to that presented by Barker et al. (1999), and no additional indels had to be incorportated into the alignment. Indels correspond to evolutionary events, and as such are a source of phylogenetic information. However, the use of indels in phylogenetic analyses is still somewhat contentious, and numerous coding methods have been proposed (see, for example, Giribet & Wheeler, 1999; Simmons &

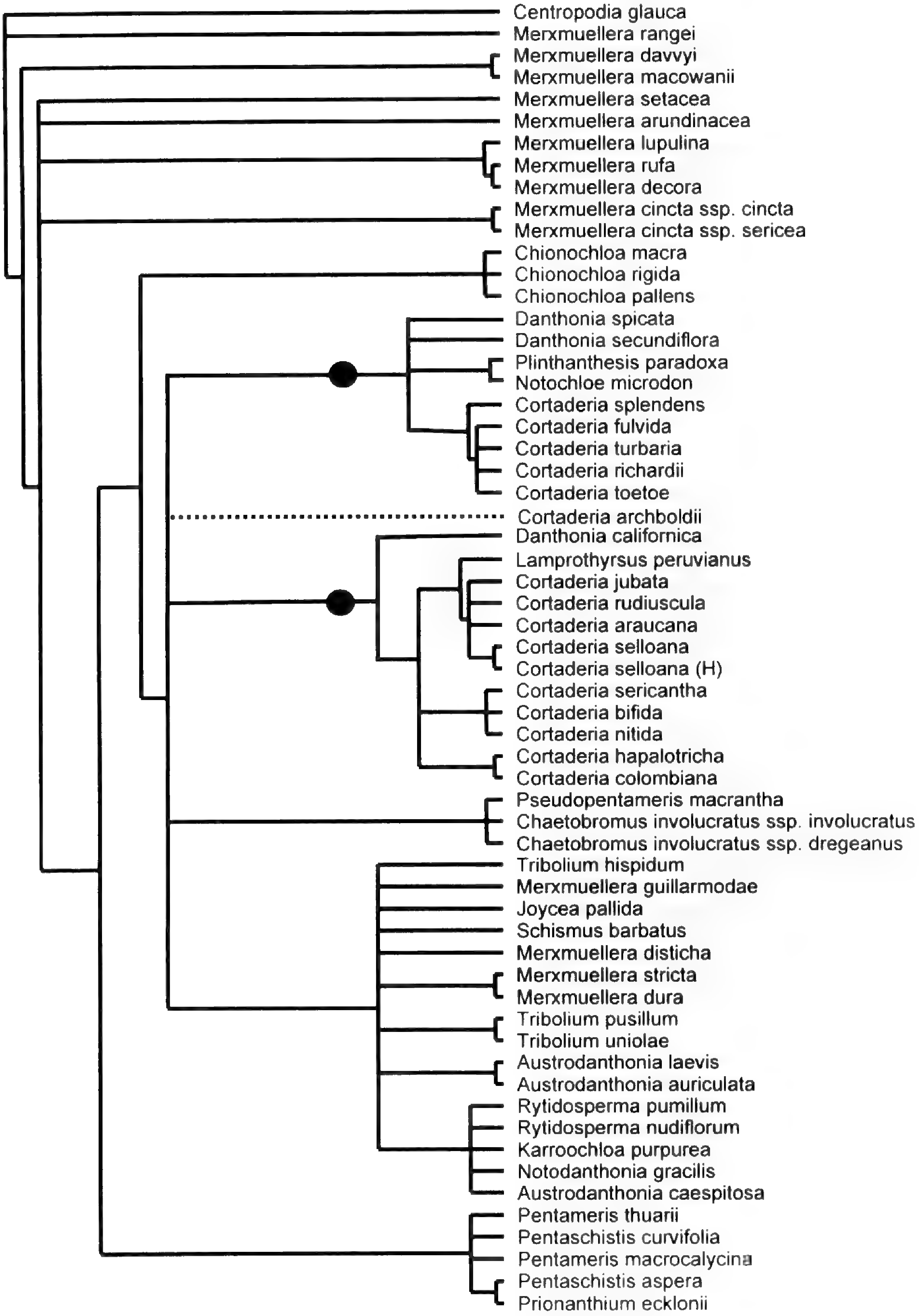

Figure 6. The semi-strict consensus "supertree" as calculated from strict consensus trees of the two molecular data sets, by means of matrix representation using parsimony, weighted according to bootstrap support, with the characters treated as irreversible, and with *Cortaderia archboldii* excluded. Nodes that collapse when *C. archboldii* is included are indicated with solid dots, and the position *C. archboldii* assumes in the tree is indicated by a broken line.

Ochoterena, 2000, and references therein). As described by Igloi et al. (1990), the grass-specific insert in the *rpo*C2 gene comprises a series of 21-base pair repeat motifs (heptameric repeats). Many of the indels in this alignment are thus 21 bases in length, suggesting that the gain and loss of these repeats is under considerable functional constraint. The creation of indels is thus not random as would be expected in a non-coding region of DNA. An initial study on the use of indels as phylogenetic characters for this region at the family level showed high levels of homoplasy, with reversals (deletions of heptameric repeats following insertions) being frequent (Barker, 1995). Because of the possible non-random nature of indel gain and loss, as well as the findings that multiple losses (deletions) follow gains (insertions), indels were not coded for inclusion in these analyses.

The *rpo*C2 sequences for the New Zealand species are identical, with the exception of *C. turbaria*, which has a deletion corresponding to two heptameric repeat motifs. This deletion is in the same region as a deletion in *Lamprothyrsus*, emphasizing the homoplasy of indel data, particularly deletions, for this region. The sequence similarity between *Lamprothyrsus* and *C. turbaria* is 97.4%.

An examination of *rpo*C2 sequences from species in the South American clade (including *Lamprothyrsus*) reveals a similar lack of sequence variation among the species, with similarity ranging from 99.2% to 100%. *Cortaderia colombiana* (Pilg.) Pilg. and *C. hapalotricha* (Phil.) Conert are retrieved as a clade (in all analyses) within the South American group, but these sequences are not identical (99.3% similarity). Among the South American species, *C. sericantha* (Steud.) Hitchc. is unique in having a deletion of 42 bp (two heptameric repeats), but the remaining sequence (i.e., excluding the region with the deletion) is identical to some of the other species, including *Lamprothyrsus*.

The lack of resolution of relationships among the species of *Cortaderia* by these data is disappointing, and is caused by high sequence similarity of species in each of the clades. This may be as a result of recent speciation and radiation within the clade, or that the grass-specific *rpo*C2 insert mutates more readily by slipped strand mis-pairing (producing insertions and deletions) than by substitutions, and that the actual sequence is constrained by the as-yet-unknown function of this region. However, other *rpo*C2 data from species of the African genus *Pentaschistis* (Nees) Spach (Barker & Gilbert, unpublished) suggest that this region may undergo both substitutions and insertion–deletion events. Thus the lack of sequence diversity in both the South American and New Zealand clades of *Cortaderia* may be the result of a recent origin and diversification.

ITS SEQUENCE DIVERGENCE

With the exception of *C. splendens* Connor and *C. turbaria*, sequences of all the species of *Cortaderia* from New Zealand are identical. The former species is 99.5% similar to the remaining taxa, and the latter species identical, but with a two-base pair deletion in the ITS1 region. In addition, this group of species and *Plinthanthesis* and *Notochloe* share a two-base pair insertion in ITS1.

Of the South American taxa, *C. colombiana* and *C. hapalotricha* share a one-base pair insertion in ITS1, and have a sequence similarity of 98.4%. These two species are consistently resolved as sister taxa in all analyses. Field observations indicate that these two species overlap morphologically and geographically: *C. colombiana* is functionally gynodioecious and occupies lower altitudes, while *C. hapalotricha* is apomictic, and is found at higher altitudes. It is possible that these two "species" are extremes of a single species that shows altitudinal variation (M. Lyle, unpublished).

Sequence similarity between *Lamprothyrsus* and the South American *Cortaderia* species ranges from 96.8% (*C. selloana* sequence from Hsiao et al., 1998) to 98.9% (*C. bifida*). The least similar sequences are those of *C. selloana* (Hsiao et al., 1998) and *C. colombiana* (94.2%), and the most similar sequences are 99.8% similar (*C. selloana* (this study)–*C. jubata* (Lem.) Stapf, and *C. jubata–C. araucana* Stapf comparisons).

ITS alignment—problems and implications. The ITS sequences of *Chaetobromus*, and to a lesser extent *Pseudopentameris*, were difficult to align, and were unexpectedly divergent from the remaining data set. This high divergence might indicate an accelerated mutation rate in this lineage or paralogous copies of the gene. Data for *C. involucratus* subsp. *dregeanus* show at least two different copies of the ITS region in the genome, which may reflect the polyploid nature of this subspecies (Spies et al., 1990; Verboom & Linder, 1998). This second subspecies was excluded from the analyses discussed here because of this variation, as the sequences were not usable for a portion of the ITS region. However, in regions where the sequences from these two subspecies are alignable, there is nonetheless a substantial amount of sequence divergence. This suggests that, despite their present status as subspecies (and even their past status as species, for that matter), the ITS region is presently undergoing substantial re-arrangements in this taxon, possibly as a result of ongoing polyploidization events. These events may have been detected here due to the incomplete and/or ongoing process of concerted evolution in these lineages (Arnheim et al., 1980; Zimmer et al., 1980; Arnheim, 1983), the results of which will ultimately be a uniform copy of rDNA loci within the taxon. This has been shown to be possible in other polyploid plants (see, for example, Sang et al., 1995, and Wendel et al., 1995). The danthonioid grasses, and in particular species of *Cortaderia*, are widely known to have varying and sometimes high ploidy levels (Table 1). Despite this there was almost no evidence of polymorphic bases in the sequences from *Cortaderia* or other taxa sampled. This suggests that the ITS region in these taxa has been homogenized through concerted evolution. Thus, although many of these grasses are polyploids or of polyploid origin, they all appear to be stable polyploids (with the exception of the excluded *Chatobromus involucratus* subsp. *dregeanus*). It must, however, be noted that the theoretically exponential nature of PCR amplification would not detect different loci unless they were initially present in approximately equal numbers. Different and rarer loci would only be detectable if a PCR–cloning–sequencing approach were used. The methodological limitations of the approach used here may explain the conflict between the ITS and other (especially chloroplast) data. Only comparison of the ITS-based topologies to those from a second data set derived from a single copy nuclear gene would indicate nodes with conflicting histories possibly caused by problems associated with the ITS data and sequencing methodology used here.

DATA COMBINABILITY

The results from the Total Evidence (TE) analysis contain no nodes that are not found in one or both the trees from the separate analyses. However, there are some noteworthy observations:

1. The ITS data do not retrieve a monophyletic *Tribolium* (< 50% bootstrap support), but the *rpo*C2 data do (100% bootstrap support). The combined analysis resolves this genus as monophyletic with 90% bootstrap support.
2. The ITS data group *Plinthanthesis* and *Notochloe* together (81% bootstrap support) but *rpo*C2 data group *Plinthanthesis* with the New Zealand *Cortaderia* clade (64% bootstrap support). The combined analysis does group *Plinthanthesis* and *Notochloe* as sister genera, but with 71% bootstrap support.
3. The ITS data find a paraphyletic *Cortaderia* (< 50% bootstrap support), and the *rpo*C2 data retrieve a polyphyletic *Cortaderia* (< 50% bootstrap support). The combined analysis agrees with the ITS data, but also at a low (< 50%) bootstrap support.
4. *Cortaderia archboldii* is sister to the fictive *Danthonia* taxon (69% bootstrap support), in agreement with the *rpo*C2 topology, but in conflict with the ITS data.

Fictive taxa. One of the surprises of these analyses is that the position of the fictive "*Danthonia*" taxon appears to be uncertain. As a fictive taxon in the combined analysis, no clear relationship for this entity is retrieved, other than its sister status to *Cortaderia archboldii*. This is seemingly "midway" between the position it occupies in the individual trees: basal to the Australasian *Cortaderia* clade in the ITS analysis (less than 50% bootstrap support), or basal to the Australasian *Cortaderia* and allies clade in the *rpo*C2 analysis. This might indicate that this fictive entity is not a monophyletic construct. There are three possible (and not mutually exclusive) reasons for this:

1. North American *Danthonia* may not be monophyletic.
2. *Danthonia* may be the result of a past hybridization event, and may comprise a maternal lineage (cpDNA) and nuclear lineage with different histories.
3. *Danthonia* may include a polyploid nucleus (possibly of hybrid origin), in which concerted evolution has resulted in the fixation of a single copy of the ITS region, the history of which is independent of the plastid genome.

It seems that even in the restricted sense in which *Danthonia* is regarded now, there might still be taxonomic problems in this genus. However, this seems unlikely from a morphological perspective; apart from a couple of exceptions the basic chromosome number is 36 throughout (Stebbins & Love, 1941; Myers, 1947; De Wet, 1954; Bowden & Senn, 1962; Schwartz & Baessler, 1964), the leaf anatomy is quite uniform, and there is minor variation in the lemma indumentum (Tomlinson, 1985). It is thus difficult to explain the results obtained here pertaining to the relationships of the *Danthonia* taxa sampled, and additional sampling and studies on this genus are warranted.

Supertree. The remarkable degree of resolution in the supertree (Fig. 6) shows the general concordance between the two data sets. However, this resolution is only obtained by weighting nodes according to their bootstrap support, treating characters as irreversible, and calculating a semi-strict rather than a strict consensus tree. The concordance is also borne out by the comparison of the two trees in Figures 1–3. The supertree differs from the TE tree (Fig. 4). Firstly, the TE tree locates much more resolution than the supertree, and some of this resolution is well supported. For example, the *Merxmuellera setacea–M. cincta* clade receives a bootstrap support of 87%, but is not retrieved in the supertree. The supertree is sensitive to any contradictory evidence, resulting in substantial loss of resolution when *C. archiboldii* is included. Of more interest are nodes that conflict between the TE tree and the supertree. For example, the supertree finds (*Pentaschistis* clade, (*Chionochloa*, (*Cortaderia*, *Rytidosperma*))), while the TE tree obtains (*Chionochloa*, (*Pentaschistis* clade, (*Cortaderia*, *Rytidosperma*))). Curiously, neither analysis of individual data sets located the node found in the TE tree, which must thus be regarded as the novel node, suggesting that the supertree might be more conservative than the TE tree. The other conflict involves the node combining *Rytidosperma pumilum* (Kirk) H. P. Linder, *R. nudiflorum* (P. Morris) Connor & Edgar, *Karroochloa purpurea* (L. f.) Conert & Türpe, *Notodanthonia gracilis* (Kirk) Zotov, and *Austrodanthonia caespitosa* (Gaudich.) H. P. Linder: the problem lies with the inclusion of *K. purpurea* within this clade. However, this agrees with the result of the ITS analysis, and again the TE analysis located nodes not found in the individual analyses. There are, however, some positions of uncertainty:

1. The presence of a "*Cortaderia* clade" with *Danthonia*, *Plinthanthesis*, and *Notochloe* included. This is retrieved both by ITS and the combined analysis, but always with less than 50% bootstrap support. However, the conflict of *rpo*C2 and ITS, and the low level of support, indicate that this grouping cannot as yet be taken seriously. Furthermore, the supertree is unable to resolve the relationships of any of the species of *Danthonia*, *Plinthanthesis*, and *Notochloe*.
2. The other fictive taxa survived well: *Pentameris* remained firmly in the *Pentaschistis* clade in the supertree; *Chaetobromus* retains its position as sister to *Pseudopentameris*; and the TE analysis shows *Tribolium* to be monophyletic (the supertree does not).

So is it worth using supertrees? They might be useful as quick summaries of different trees, and also to include all the species that may be missing from many partial data sets. They can also be used as consensus trees to indicate where nodes on the TE trees deviate from the nodes common to the source trees. But there are also shortcomings to this approach. This includes the lack of resolution on some nodes, and, more importantly, the lack of any indication of support for nodes. For example, the supertree places *Chionochloa* in a basal position, just above the *Pentaschistis* node. There is probably little character support for this (and it conflicts with the TE result), but on the supertree it is just another node, the support for which is not known.

MORPHOLOGY

The lack of resolution in the unweighted data set indicates that the morphological data set lacks decisiveness. Yet the main groups extracted are remarkably similar to the molecular trees, although there are numerous differences in detail. There appears to be no morphological support for a biphyletic *Cortaderia*. Parsimony analysis of the morphological data set retrieved a monophyletic *Cortaderia* clade, which includes *Cortaderia*, *Lamprothyrsus*, and *Cortaderia archboldii*. This clade is based on the gynodioecious breeding system.

THE PARAPHYLY OF *CORTADERIA*

All molecular analyses clearly show that *Cortaderia* is not monophyletic. In the TE analysis, *Cortaderia* is retrieved as one clade, but with less than 50% bootstrap support, and with *Danthonia*, *Notochloe*, *Plinthanthesis*, and *Lamprothyrsus* embedded in it. This clade is divided into three subclades: the Australasian clade, the South American clade, and the *C. archboldii*–fictive *Danthonia* clade. The Australasian clade includes *Plinthanthesis* and *Notochloe* (88% bootstrap support in the combined analysis; 74% in ITS analysis; 81% in *rpo*C2 analysis, but also includes *Danthonia*). The South American clade includes *Lamprothyrsus* and receives 68% bootstrap support in the TE (slightly up from 60% in the *rpo*C2 analysis, 51% in the ITS analysis). The *C. archboldii*–fictive *Danthonia* clade receives 69% support in the TE analysis. Relationships between these clades and the *Rytidosperma* lineage (60% bootstrap support in the TE analysis) and the *Pseudopentameris* clade (100% support) are not well supported. There are thus critical nodes in the topology that are poorly supported, and additional data, both molecular and morphological, are required before the relationships of these lineages can be resolved with some certainty. However, it is interesting to note that the resolution of *Cortaderia* into the South American and New Zealand lineages is supported (at least in part) by chemotaxonomic data. Connor and Purdie (1981) reported that Cylindrin, a triterpene methyl ether, was restricted to some species of section *Cortaderia* (excluding *C. selloana*), and absent from the South American *C. bifida* (sect. *Bifida*) and all the New Zealand species tested. Furthermore, the New Zealand species also possessed a range of other triterpene methyl ethers that were not found in any South American species, but which are known from species of *Chionochloa*, another New Zealand grass (Connor & Purdie, 1976).

Within the South American clade, the species from *Cortaderia* sect. *Cortaderia* are more closely related to *Lamprothyrsus* than to species from *Cortaderia* sect. *Bifida*. This result also supports Connor and Dawson's (1993) hypothesis of a close relationship of *Lamprothyrsus* to *Cortaderia* based on cytological and breeding system evidence, and it would seem appropriate to consider synonymizing *Lamprothyrsus* with *Cortaderia*. However, owing to incomplete sampling this step is not taken here.

Within section *Cortaderia*, field observations suggest that currently recognized "species" might well be one dioecious species (*Cortaderia selloana*) and one additional apomictic species, with varying populations in the process of speciation and diversification through loss of sexuality. Both *Lamprothyrsus* and most of the species in section *Cortaderia* are apomictic weeds, inhabiting drier areas and mostly at lower altitudes of southern South America. Only *C. jubata* is widespread, possibly as a result of anthropogenic factors.

The species of *Cortaderia* sect. *Bifida* are all found in perhumid high-altitude areas, are seldom weedy, and share a well-defined biogeographical distribution (páramo). In addition, most species in this section still show some gynodioecious traits, such as large staminodes and the presence of morphologically gynodioecious populations.

Unfortunately, without corroboration from molecular data from the species in the other two sections in *Cortaderia* (sects. *Monoaristata* and *Mutica*), it would be premature to suggest any further conclusions concerning the relationships and composition of the sections of the genus. However, morphological and anatomical evidence indicates that the species of sections *Monoaristata* and *Mutica* are not supported, and that the species in these sections belong in *Cortaderia* sect. *Bifida* (M. Lyle, unpublished). In addition, we feel it would be premature to formalize the status of the New Zealand species of *Cortaderia*, as no morphological synapomorphy has yet been found to unite these species.

THE RELATIONSHIPS OF *CORTADERIA ARCHBOLDII*

The New Guinean *Cortaderia archboldii* is morphologically intermediate between *Cortaderia* and *Chionochloa* (Clayton & Renvoize, 1986). When the species was originally described, it was included in the then much more broadly circumscribed genus *Danthonia* (Hitchcock, 1936). With the break-up of the old, broad *Danthonia* into numerous segregate genera, confusion arose on the correct classification of *D. archboldii*. Connor and Edgar (1974) placed the species in *Cortaderia* sect. *Bifida*, while Conert a year later put it into *Chionochloa* (Conert, 1975). Conert appears to have been unaware of the paper by Connor and Edgar, and did not discuss the possibility that this species could belong in *Cortaderia*. He cited similarities in spikelet and culm anatomy between *D. archboldii* and several species of *Chionochloa*. Tomlinson (1985) used the same arguments to place the species in *Cortaderia*.

Cortaderia archboldii did not group with the three *Chionochloa* species in either molecular analysis. The more extensive morphological data set places *C. archboldii* in *Cortaderia*, and not in *Chionochloa*. Unpublished analyses of Linder show that *Chionochloa* is monophyletic, defined by the unique morphology of the adaxial microhairs with minute apical cells, which are overlapping, restricted to the base of the furrows of the leaf blades. In addition, five other characters, which are also found occasionally in other genera or are variable within *Chionochloa*, can be used. They are disarticulating leaf blades, presence of leaf-margin prickles, glumes shorter than the basal lemmas, the presence of long dense hairs on the palea margins, and the presence of adaxial prickle hairs on the leaf blades. *Cortaderia archboldii* lacks most of these characters, and specifically the adaxial microhairs are "typical," in that they are scattered along the margins of the leaf furrows, are not overlapping, and have relatively large apical cells. In addition, the palea margins are usually glabrous, and leaf prickles are absent. The only derived character shared with *Chionochloa* is the presence of disarticulating leaf blades, a character that also occurs in several species of *Rytidosperma*, *Cortaderia bifida*, *C. jubata*, and *Lamprothyrsus*. In contrast, as pointed out by Tomlinson (1985), there are several characters in common between *Cortaderia archboldii* and at least some other species of *Cortaderia*. The adaxial leaf furrows are much wider than in *Chionochloa*, and have large bulliform cells (a feature in common with *Cortaderia hapalotricha* and *C. pungens* Swallen), especially toward the relatively well-developed midrib. Furthermore, *C. archboldii* also shares a stoloniferous habit with *C. bifida*, a feature that is not found in other species of *Cortaderia*. The gynodioecious breeding system of *C. archboldii* was studied by Connor (1970), who showed that this relatively rare system was found largely in *Cortaderia* (Connor, 1979, 1981). Conert (1975) suggested that similar systems are also found in *Chionochloa*, but a detailed survey (Connor, 1991) documented it only from *Chionochloa bromoides* (Hook. f.) Zotov.

The precise position of *C. archboldii* in the broad *Cortaderia* clade thus remains unclear. *rpo*C2 data suggest an association with *Danthonia* and the Australasian *Cortaderia* clade (including *Plinthanthesis* and *Notochloe*), while ITS data suggest that it is associated with yet other species of *Danthonia* and the South American *Cortaderia* clade. The TE analysis links *C. archboldii* with the fictive taxon *Danthonia*; this could be the result of the rather limited sampling of *Danthonia* species in this study. The result of this conflict is that the supertree loses resolution between the two clades of *Cortaderia* and the species of *Danthonia* when *C. archboldii* is included. Although bootstrap support for the position with the Australian species of *Cortaderia* is stronger in the *rpo*C2 tree than the support for a position with the South American species as suggested by the ITS tree, node support in different parts of the tree indicates that it would be simplistic to suggest that the *rpo*C2 results are more trustworthy. Currently there is therefore strong evidence that *C. archboldii* belongs in the broad *Cortaderia*, rather than *Chionochloa*, clade, but no further progress can be made in determining where in this clade it is best placed.

It is tempting to argue for the recognition of *Cortaderia archboldii* as a monotypic genus, related to the Australasian species of *Cortaderia* and to *Danthonia*. However, the morphological evidence is not strong enough, nor is the molecular evidence currently convincing. Even if *Cortaderia archboldii* finds a position sister to the Australasian segregates of *Cortaderia*, then there would still not be adequate grounds for erecting a separate genus for this geographically isolated species.

MORPHOLOGY: CHARACTERS AND DATA SET CONFLICT

The division of *Cortaderia* into two lineages, with several species of softly herbaceous species of *Danthonia* associated with the one lineage, and the small, heathland genera *Notochloe* and *Plinthanthesis* associated with the other, means that several "typical" characters of *Cortaderia* must have either evolved twice, or been lost twice. These characters include the massive inflorescences, spikelets with linear-lanceolate, 3-veined lemmas with abundant indumentum at the base, the reductions in the lemma setae, parallel loss of bulliform cells and the formation of tough, xerophyllous leaf anatomy, and the rare gynodioecious sexual system. These characters could be clustered into two functional types. The first involves the formation of tough, long-lived plants, with tough leaves. This has happened in parallel in all three southern continents, and has resulted in remarkably convergent leaf anatomies. While it is generally possible to distinguish the leaves of southern African *Merxmuellera* from New Zealand *Chionochloa*, and these from *Cortaderia*, the remaining similarities are still quite convincing. The second character group involves the evolution of the gynodioecious breeding system. Possibly the large inflorescences and long indumentum at the base of the lemmas is associated with this.

Some features are found largely or only in one of the *Cortaderia* segregates. In many South American species of *Cortaderia* there is a variously developed layer of collenchymatous cells below the abaxial epidermis. In some species this can take up almost half of the leaf width, while in other species it may be much narrower. It is sometimes linked to the outer bundle sheath via well-developed extension cells. However, this is also found in one species, *C. fulvida* (Buchan.) Zotov, from New Zealand. The South American species also have characteristically villous inflorescence branches, a character that is remarkably homoplasious in the grasses. A divided phloem is typical of the *C. selloana* clade, but is absent from most other species of South American *Cortaderia*. Abaxial ridging of the leaves has a similar distribution.

Most of the New Zealand *Cortaderia* species possess curious islands of clear cells in the chlorenchyma, a feature also found in *Plinthanthesis* and *Notochloe*. However, this character is missing in *C. splendens*, as well as *C. archboldii*, but this could be interpreted as a secondary reversal. In addition, all New Zealand species of *Cortaderia* have a well-developed and prominent leaf midrib, a feature rare in the danthonioids, but also found in the South American *C. rudiuscula* Stapf.

Over and above these features, it is worth revisiting the cytological data in light of the above results. The New Zealand species all have $2n = 90$ (i.e., are decaploid, if $x = 9$), while the South American species have variable chromosome numbers, ranging from $2n = 36$ (tetraploid), through $2n = 72$ (octoploid), to $2n = 108$ (duodecaploid). Assuming the base chromosome number is $x = 9$, then the South American species can be viewed as having $2n = 4x = 36$, $2n = 8x = 72$, and $2n = 12x = 108$. The chromosome count of the New Zealand species of $2n = 90$ may be a decaploid intermediate between that of $2n = 72$ and $2n = 108$, suggesting that these species could have arisen from an allopolyploid ancestor, which was a hybrid between $2n = 72$ and $2n = 108$ parents. While resorting to an ancient hybridization event as an explanation may be viewed as convenient and possibly undemonstrable, such a history could explain the conflict found here between the nuclear ITS and plastid *rpo*C2 data sets, with morphology reflecting a mixed or mosaic history, further confusing the phylogenetic signal in the analyses of multiple data sets.

SUMMARY

The analyses of the molecular data sets indicate that *Cortaderia* comprises two lineages: one Australasian, the other South American. The relationships of the New Guinea species *C. archboldii* are not satisfactorily resolved, other than to allow us to state that it is not a member of either *Cortaderia* lineage. These relationships are not supported in analyses of morphological data, but the available morphological data are still poor, and it is therefore possible that there are undiscovered morphological markers for these molecular clades. Morphology is thus an area that needs further research. For example, aspects such as caryopsis morphology need investigation. In addition, morphological studies are complicated by the presence of both bisexual and female-only spikelets, creating sampling problems. Having said this, we realize that the molecular sampling is also incomplete, since most of the *Cortaderia* species sampled here are Andean taxa, and the lowland species have not been included. Only once more taxa and samples have been included in the molecular data sets, and an exhaustive field-based taxonomic study of the species (and their breeding systems) in both lineages has been conducted, can any formal nomenclatural changes be made.

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Appendix 1. The data matrix used in the morphological analysis.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Centropodia glauca	0	1	0	0	0	0	0	0	1	0	0	0	0	1	2	2	1	2	
Austrodanthonia auriculata	0	1	0	0	0	0	0	0	1	1	1	1	0	1	2	2	4	0	0
Austrodanthonia caespitosa	0	1	0	0	0	0	0	0	1	0	1	1	0	1	2	2	4	0	0
Austrodanthonia laevis	0	1	0	0	0	0	0	0	1	0	1	1	0	1	2	2	4	0	0
Chaetobromus involucratus	0	1	0	0	0	0	0	0	1	0	1	0	0	1	2	2	5	0	0
Chionochloa macra	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	2	1	0	0
Chionochloa pallens	0	1	?	?	0	0	0	0	1	0	0	0	0	1	1	2	1	0	0
Chionochloa rigida	0	1	?	?	0	0	0	0	1	0	1	0	0	1	?	2	1	0	0
Cortaderia araucana	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	?	2	-
Cortaderia bifida	0	1	2	2	1	0	1	0	1	0	1	0	0	1	0	2	3	0	0
Cortaderia colombiana	0	0	2	1	0	0	1	0	1	0	1	0	0	1	1	1	3	0	0
Cortaderia fulvida	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	3	{12}	0
Cortaderia hapalotricha	0	1	2	2	0	0	1	0	1	0	0	0	0	1	0	2	3	0	0
Cortaderia jubata	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	-		-
Cortaderia nitida	0	1	0	0	0	{01}	1	0	1	0	{01}	0	0	1	1	1	3	0	0
Cortaderia richardiana	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	1	0
Cortaderia rudiuscula	0	1	{01}	0	0	0	1	0	0	0	1	0	0	0	0	0	?	2	-
Cortaderia selloana	0	1	0	0	0	0	1	0	0	0	1	0	0	0	0	0	{35}	2	
Cortaderia sericantha	0	1	0	0	1	1	1	0	1	1	1	0	0	1	1	1	3	1	0
Cortaderia splendens	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Cortaderia toetoe	0	1	?	?	?	0	1	0	0	0	0	0	0	0	0	0	3	1	0
Cortaderia archboldii	0	1	0	0	0	0	1	0	1	0	1	0	0	1	0	2	3	0	0
Danthonia californica	0	1	0	0	1	0	0	1	1	0	0	0	0	1	2	2	5		
Danthonia secundiflora	0	1	0	0	0	0	0	1	1	0	0	0	0	1	2	2	5	0	-
Danthonia spicata	0	1	0	0	0	0	0	1	1	0	0	0	0	1	2	2	5	0	0
Joycea pallida	0	1	0	0	0	0	0	0	1	0	1	0	0	1	2	2	5	0	0
Karroochloa purpurea	0	1	0	0	1	0	0	0	1	0	1	0	0	1	2	2	2	0	0
Lamprothyrsus peruvianus	0	1	1	0	0	0	1	0	1	0	?	0	0	1	1	1	5	0	0
Merxmuellera arundinacea	0	1	0	0	0	0	0	0	1	0	0	0	0	1	2	2	5	1	0
Merxmuellera cincta subsp. *cincta*	0	1	0	0	0	0	0	0	1	0	?	0	0	1	2	2	2	?	0
Merxmuellera cincta subsp. *sericea*	0	1	0	0	0	0	0	0	1	0	?	0	0	1	2	2	2	?	0
Merxmuellera davyi	0	1	0	0	0	0	0	0	1	0	?	0	0	1	2	2	2	{12}	0
Merxmuellera decora	1	1	0	0	0	0	0	0	1	1	0	0	0	1	2	2	6	1	
Merxmuellera disticha	0	1	0	0	0	0	0	0	1	0	1	0	0	1	2	2	-	-	
Merxmuellera dura	0	1	0	0	0	0	0	0	1	0	1	0	0	1	2	2	6	0	
Merxmuellera guillarmodiae	0	1	0	0	0	0	0	0	1	0	?	0	0	1	2	2	2	1	0
Merxmuellera lupulina	1	1	0	0	0	0	0	0	1	1	1	0	0	1	2	2	6	2	0
Merxmuellera macowanii	0	1	0	0	0	0	0	0	1	0	?	0	0	1	2	2	2	0	0
Merxmuellera rangei	0	1	0	0	0	0	0	0	1	1	0	0	0	1	2	2	2	{12}	0
Merxmuellera rufa	1	1	0	0	0	0	0	0	1	1	0	0	0	1	2	2	5	2	0
Merxmuellera setacea	0	1	0	0	0	0	0	0	1	0	?	0	0	1	2	2	2		
Merxmuellera stricta	0	1	0	0	0	0	0	0	1	0	0	0	0	1	2	2	-		-
Notochloe microdon	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	5	1	0
Notodanthonia gracilis	0	1	0	0	0	0	0	0	1	0	0	0	0	1	2	2	6	0	0
Pentameris macrocalycina	0	1	0	0	0	0	0	0	1	0	0	0	1	1	{12}	2	5	0	1
Pentameris thuarii	0	1	0	0	0	0	0	0	1	0	0	0	1	1	{12}	2	5	0	1
Pentaschistis aspera	0	1	0	0	{01}	0	0	0	1	0	1	0	1	1	?	1	5	0	1
Pentaschistis curvifolia	0	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	5	0	1
Plinthanthesis paradoxa	0	1	0	0	0	0	0	0	1	0	0	0	0	1	2	1	5	1	0
Prionanthium ecklonii	0	1	0	0	0	0	0	0	1	0	?	0	1	1	?	1	0	2	-
Pseudopentameris macrantha	0	1	0	0	0	0	0	0	1	0	0	0	1	1	{12}	2	5	0	1
Rytidosperma nudiflorum	0	1	0	0	0	0	0	0	1	0	1	0	0	1	2	2	2	0	0
Rytidosperma pumilum	0	1	0	0	0	0	0	0	1	0	0	0	0	1	1	1	5	2	
Schismus barbatus	0	1	0	0	0	0	0	0	1	1	1	0	0	1	2	0	5	2	-
Tribolium pusillum	0	1	0	0	0	0	0	0	1	1	1	0	0	1	?	0	5	-	
Tribolium hispidum	0	1	0	0	0	0	0	0	1	1	{01}	0	0	1	?	0			

Appendix 1. Extended.

20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
[illegible]		[illegible]			[illegible]	[illegible]	[illegible]	[illegible]	1	1		[illegible]	[illegible]			[illegible]	1	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			[illegible]		
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[illegible]	[illegible]	[illegible]	1	[illegible]	[illegible]						[illegible]					[illegible]	1	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			[illegible]	[illegible]	[illegible]
			[illegible]	[illegible]	[illegible]		[illegible]		[illegible]	[illegible]	[illegible]		[illegible]			[illegible]	1				[illegible]			[illegible]			[illegible]	1	[illegible]
		[illegible]			0	1	0	0	01	[illegible]	0		2	0		1	1	0	1	0	0	[illegible]		[illegible]			[illegible]	[illegible]	[illegible]
[illegible]			1	1		1	0	0	1	[illegible]	0		0	1	[illegible]	1	0	0	0	1	0	[illegible]	1	[illegible]	[illegible]		[illegible]	[illegible]	[illegible]
[illegible]				[illegible]		[illegible]			[illegible]		[illegible]			[illegible]	[illegible]	[illegible]		[illegible]	[illegible]	[illegible]		[illegible]	1	[illegible]			[illegible]	[illegible]	[illegible]
[illegible]						[illegible]			[illegible]					[illegible]		[illegible]			[illegible]	[illegible]			[illegible]					[illegible]	[illegible]
[illegible]		2		[illegible]	[illegible]	?	0	0	1	1	0	1	0	1	[illegible]	[illegible]	1	1	1	1	0	0	0	1	0	0	0	0	[illegible]
[illegible]		1	[illegible]			1	0	0	1	1	0	1	0	1	0	0	0	0	1	1	0	0	0	{01}	1	0	0	0	?
1		[illegible]	[illegible]	[illegible]	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	[illegible]
0		2	[illegible]	[illegible]	[illegible]	1	0	0	1	0	1	1	0	1	0	1	0	0	1	1	1	0	0	1	0	0	0	0	?
1		1	[illegible]	[illegible]	1	1	0	0	1	0	0	1	0	0		1	1	0	0	1	0	0	0	{01}	1	0	0	0	?
[illegible]		2	1	1	[illegible]	?	0	0	?	?	?	?	?	?	[illegible]	?	?	?	?	?	?	0	0	?	[illegible]	?	?	?	?
		1		[illegible]	[illegible]	?	0	0	1	0	0	2	0	1		1	0	1	1	0	0	0	0	1		0	0	0	?
[illegible]			[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		[illegible]			[illegible]		[illegible]	[illegible]	[illegible]			[illegible]			[illegible]					[illegible]
?			[illegible]	[illegible]	[illegible]	?	0	0	1	1	0		0	1	[illegible]	1	[illegible]	1	1	0	1	0	0	1	0	[illegible]		0	?
0	[illegible]	[illegible]	[illegible]		[illegible]	?	0	0	1	1	0	1	0	1	1	1	1	1	1	0	0	0	0	?	?	?	[illegible]	?	0
?	[illegible]	1	[illegible]	[illegible]	[illegible]	?	0	0	0	0	0	2	–	1	0	1	0	0	01}	1	0	0	0	1	1	0	0	0	?
1	0	1	1		[illegible]	?	0	0	1	0	0	[illegible]	[illegible]	1	1	1	1	0	0	0	1	0	0	2	0	0	0	0	?
				[illegible]	[illegible]	?	0	0	1	0	1	[illegible]	[illegible]		1	1	1	0	0	0	1	0	0	0		[illegible]	0	0	[illegible]
[illegible]		[illegible]		[illegible]		[illegible]	[illegible]	[illegible]	[illegible]		[illegible]		[illegible]	[illegible]		1	[illegible]			1	[illegible]	0	(	[illegible]	[illegible]			[illegible]	[illegible]
		[illegible]		[illegible]	1	1	[illegible]	[illegible]	1				[illegible]			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		[illegible]	[illegible]			1		
[illegible]		[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	1	[illegible]			[illegible]			[illegible]	1	[illegible]	?	[illegible]	?	[illegible]	0	[illegible]	[illegible]		[illegible]	[illegible]	[illegible]
0	0	2	[illegible]	[illegible]	1	1	0	0	?	?	[illegible]	[illegible]	?	[illegible]	[illegible]	?	?	?	?	[illegible]	?	?	?	?	?	[illegible]	?	?	?
[illegible]	0			[illegible]	1	1	0	0	1	1	(		2			1	1	0	0	0	0	0	0	2	0	0	1	1	0
[illegible]						[illegible]		[illegible]	[illegible]		[illegible]			[illegible]		[illegible]	[illegible]			1	0	[illegible]		[illegible]			[illegible]		
1				[illegible]	[illegible]	1	0	0	1	1	[illegible]	1				[illegible]	[illegible]	[illegible]	1	1	0	0	0	1	0	0	0	0	?
[illegible]			[illegible]		[illegible]	?	0	0	1	0	[illegible]	0	2			[illegible]	0	0	0	0	0	0	0	0	0	[illegible]	0	0	?
[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]
[illegible]		[illegible]	[illegible]	[illegible]	?	?	0	0	1	0		2	2		–	1	0	0	1	0	2	0	0	1	0	[illegible]	0	0	?
			1	[illegible]	[illegible]	?	?	1	1	0	0	0	2		–	1	0	1	1	0	0	0	0	0	0	0	0	0	?
[illegible]		0	1		?	?	0	0	0	0	0	0	–	[illegible]	–	0	0	0	0	0	2	0	0	1	0	0	0	0	?
		1	1	[illegible]	?	?	0	1	01}	0	0	0	?	[illegible]	–	0	0	0	0	{01}	0	0	0	0	0	0	0	01}	?
		0	1	1	0	0	0	0	1	1	0	0	1	1	0	1	1	0	0	?	2	0	0	0	0	0	0	0	0
		0	[illegible]	?	0	?	0	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
		2	1	0	?	?	0	0	{01}	{01}	0	0	0	0	–	1	1	0	0	1	0	0	0	2	0	0	0	0	?
		?	[illegible]	?	0	1	0	1	1	0	0	0	0	(	[illegible]	1	0	1	1	0	0	0	0	01}	0	0	0	0	?
		1	0	0	?	?	0	0	0	0	0	0	–		–	–	1	0	1	0	0	0	–	2	0	0	0	0	?
[illegible]		2		0	1	01}	0	0	1	0	0	0	2		–	0	0	0	0	1	0	0	0	2	0	0	0	0	[illegible]
[illegible]		[illegible]	[illegible]	[illegible]		?	[illegible]	1	1	[illegible]	0	[illegible]			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		[illegible]	[illegible]
[illegible]	(		1	[illegible]		[illegible]	0	[illegible]	0	0	0	[illegible]		1	[illegible]	[illegible]	1	1	0	[illegible]	0	[illegible]	[illegible]	2	[illegible]	[illegible]		[illegible]	[illegible]
					[illegible]	[illegible]	[illegible]	[illegible]	0	0	1	[illegible]		[illegible]		[illegible]	1	[illegible]	[illegible]	[illegible]	2	0	[illegible]	1	[illegible]	[illegible]	1	[illegible]	[illegible]
1	0	1	1	1	1	{01}	0	0	1	0	0	0	2		–	1	1	0	1	0	0	0	0	1	0	0	1	0	?
0	?	1	1	(	0	1	1	0	1	0	0	0	0		–	1	0	0	1	0	0	0	0	1	0	0	0	0	?
[illegible]	[illegible]	[illegible]	[illegible]			[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]			1	1	[illegible]	1	1	0	0	(	[illegible]	[illegible]		(	[illegible]	[illegible]
?	1	01}	[illegible]	[illegible]	[illegible]	?		0	1	0	0	0	2	0		1	[illegible]	0	0	0	0	1	0	1	0	0	1	0	?
0	1	1	1		?	1		0	1	0	0	0	2	0	–	1	0	0	0	0	0	0	0	2	0	0	0	0	?
?	0	1	[illegible]		1	?	[illegible]	0	1	0	1	0	0	0	–	1	1	0	0	0	0	0	0	0	0	0	0	0	?
0	1	1	[illegible]			1	[illegible]	0	1	0	0	0	2	0	–	1	1	0	0	0	0	1	0	1	0	0	1	0	1
?	0	1						0	1	0	0	0	2		–	1	1	0	1	0	0	0	0	1	0	0	0	0	?
[illegible]								[illegible]	1	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		[illegible]	[illegible]		1	[illegible]	2	[illegible]	[illegible]	1	[illegible]	[illegible]		[illegible]	
	[illegible]	[illegible]						[illegible]		[illegible]	[illegible]						[illegible]		[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]		?
[illegible]		[illegible]	[illegible]	[illegible]	[illegible]				[illegible]	[illegible]	[illegible]					[illegible]	[illegible]	[illegible]	[illegible]	1	0	[illegible]	[illegible]	1	[illegible]		1		0
[illegible]	0	[illegible]			1	[illegible]	0	0	1	0	0	0	2			[illegible]	1	0	0	0	0	0	0	1	0	0	1	1	0
[illegible]	0	[illegible]	[illegible]		1		0	0	1	0	0	0	0			1	1	0	0	0	0	0	0	0	0	0	1	0	0

Appendix 2. Characters and their states used in the morphological analysis. Additional notes and literature citations are provided where necessary.

HABIT, FLORAL, AND FRUIT CHARACTERS

1. *Plants with bulb-like structures*: (0) no; (1) yes. [Swollen underground organs in some danthonioids were described by Linder & Ellis (1990).]
2. *Basal sheaths*: (0) persisting as tangled fibers; (1) not persisting as tangled fibers.
3. *Basal sheaths*: (0) entire; (1) fragmenting transversely; (2) fragmenting lengthwise.
4. *Basal sheath orientation*: (0) straight; (1) spiraling; (2) twisted.
5. *Basal leaf margins*: (0) glabrous; (1) villous.
6. *Leaf apices*: (0) soft; (1) pungent.
7. *Plant sexual system*: (0) bisexual; (1) gynodioecious.
8. *Basal cleistogenes*: (0) absent; (1) present. [Described by Clay (1983) and Dobrenz & Beetle (1966).]
9. *Inflorescence size*: (0) huge (> 30 cm long); (1) smaller (< 30 cm long).
10. *Inflorescences*: (0) paniculate; (1) capitulate.
11. *Inflorescence branches*: (0) glabrous; (1) villous.
12. *Callus relative length*: (0) ca. equaling rachilla; (1) much larger than rachilla.
13. *Number of florets per spikelet*: (0) 3–8; (1) 2.
14. *Lemma shape*: (0) linear-lanceolate; (1) narrowly ovate.
15. *Lemma veins*: (0) 3; (1) 5–7; (2) 9 or more.
16. *Lemma apex*: (0) entire; (1) obscurely bilobed; (2) deeply bilobed.
17. *Lemma indumentum*: (0) absent; (1) longitudinal lines; (2) tufted; (3) scattered at base; (4) tufted in two rows; (5) even felt on back; (6) short in basal half, then row of long hair.
18. *Setae*: (0) substantial; (1) minute; (2) absent.
19. *Setae position on lemma*: (0) terminal on lobes; (1) in sinus between lobe and awn.
20. *Palea marginal hairs*: (0) short or absent; (1) long and dense.
21. *Palea keels*: (0) folded; (1) flat.
22. *Palea length relative to lemma*: (0) taller than lemma; (1) equaling lemma; (2) shorter than lemma.
23. *Lodicule bristles*: (0) absent; (1) present.
24. *Lodicule microhairs*: (0) absent; (1) present.
25. *Caryopsis shape*: (0) linear; (1) obovate.
26. *Caryopsis hilum*: (0) punctate; (1) linear, at least half as long as caryopsis. [This character, for the African members, is largely based on the observations by Barker (1994).]
27. *Fruit apical indumentum*: (0) absent; (1) woolly or with long hairs.

LEAF ANATOMY CHARACTERS

28. *Lamina asymmetrical*: (0) no; (1) yes. [Lamina asymmetry is described in detail by Ellis (1981).]
29. *Adaxial ridging*: (0) absent; (1) present.
30. *Abaxial ridging*: (0) absent; (1) present.
31. *Clear cells in chlorenchyma*: (0) absent; (1) present.
32. *Clear cells under abaxial epidermis*: (0) absent; (1) sparse (1–2 layers); (2) thick (+ 3 layers).
33. *Bulliform cells*: (0) absent; (1) only flanking the midrib; (2) in most furrows.
34. *Adaxial papillae*: (0) absent; (1) present.
35. *Adaxial papillae*: (0) all over; (1) basally on ridges only.
36. *Adaxial prickle hairs*: (0) absent; (1) present.
37. *Abaxial zonation*: (0) absent; (1) present.
38. *Phloem*: (0) entire; (1) divided.
39. *Extension cells*: (0) absent; (1) present.
40. *Vascular bundles*: (0) ± round, or wide; (1) taller than wide.
41. *Midrib*: (0) like other vascular bundles; (1) raised and massive; (2) smaller than other bundles.
42. *Multicellular glands*: (0) absent; (1) present. [Multicellular glands were described by Linder et al. (1990).]
43. *Adaxial microhairs*: (0) not overlapping; (1) overlapping in furrows.
44. *Adaxial sclerenchyma cap*: (0) anchor-shaped; (1) lens-shaped; (2) pyramidal.
45. *Outer bundle sheath of primary vascular bundles*: (0) parenchymatous; (1) thickened.
46. *Scattered large cells in chlorenchyma*: (0) absent; (1) present.
47. *Chlorenchyma spaces (leaf mesic/xeric)*: (0) absent; (1) present.
48. *Cushion-based macrohairs*: (0) absent; (1) present.

CYTOLOGICAL CHARACTERS

49. *Basic chromosome number*: (0) 6; (1) 7.

ENDEMISM IN THE MEXICAN FLORA: A COMPARATIVE STUDY IN THREE PLANT GROUPS[1]

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José Luis Villaseñor Ríos,[2] *and*
Patricia Dávila Aranda[3]

ABSTRACT

Endemism values are not equivalent among the Mexican Musci, Poaceae, and Asteraceae. The number of endemic species varies from one group to the next in various types of vegetation or geographical areas, perhaps in response to age, peculiarities of their life cycle, dispersal ability, and individual response to selective pressures. In Mexico, the three major plant groups include 2373 endemic taxa among which 86 are mosses, 257 are grasses, and 2030 are composites. Cluster analysis of a similarity matrix shows relationships between neighboring states and among geographically related state groups. Along the Neovolcanic Belt there are areas of endemism in western and central Mexico, but the relationship between state pairs does not always have a geographical basis. From the standpoint of the number of endemic species per unit area, Distrito Federal is the richest area in Mexico.

Key words: Asteraceae, endemism, Mexico, Musci, Poaceae.

Although Mexico, with 1,972,544 km², is the fourteenth largest country in the world, it ranks third in biological diversity (Mittermeier, 1988). It harbors approximately 30,000 species of vascular plants, including more than 21,600 in about 2,500 genera of flowering plants (Rzedowski, 1993). Among these, more than 300 genera and between 50 and 60% of the species are endemic to this country (Ramamoorthy & Lorence, 1987). There are 49 Mexican species of pines, representing more than 50% of the total for the world (Styles, 1993), and 900 to 1000 fern species (Riba, 1993). The bryophytes include about 1700 species (cf. Sharp et al., 1994; Fulford & Sharp, 1990), and among them, the mosses compose about 25% of the Neotropical moss flora.

High plant diversity and the large endemic element are features that set apart the flora of Mexico. Information on the number, origin, and distribution of endemics (e.g., Rzedowski, 1978; Sharp, 1953) is still imprecise, but current data suggest their concentration in certain areas such as the Neovolcanic Belt, a mountain range bisecting the country between 19 and 20°N, and the Sierra Madre del Sur, along the southern Pacific coast, which are considered centers of endemism for many groups (Ferrusquía, 1993). Pertinent literature for vascular plants includes contributions by Rzedowski (1962, 1991a, b), in which the endemic taxa and their geographical ranges are identified.

Preliminary observations indicate that the number of Mexican endemics is associated with climate- and geography-dependent factors. Thus, for instance, in the lowland moist areas of southern Mexico the percentage of endemic vascular plant genera is the lowest in the country, while their numbers increase toward the drier (Rzedowski, 1978) and cooler areas. On the highest mountains, the extreme climate may have caused many species to become narrowly adapted to the environment of the alpine meadows and subalpine elevations. Beaman and Andresen (1966), in a survey of the vascular flora of the summit of Cerro Potosí in northern Mexico, detected 27 of 64 species (42.2%) endemic to the Sierra Madre Oriental; 13 of them were restricted to Cerro Potosí. High endemism values have been detected in the dry lands of the Tehuacán Valley (Smith, 1965) where endemism approaches 17% (Villaseñor, 1993).

The significance of these observations cannot be fully evaluated for the entire flora. The main limiting factors are the lack of complete data on the

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geographical ranges of taxa and incomplete inventories or checklists of the major groups in the Mexican flora. Although these will not be attained for many years yet, the use of an alternative strategy may still permit reasonable estimates of endemism, its distribution in Mexico, and how endemism relates to the geography of the country. In this contribution, we make floristic comparisons among taxa for which preliminary lists and geographic ranges are available. As specialists, we have produced and compiled information on the Mexican Musci, Asteraceae, and Poaceae that may serve to illustrate patterns of endemism for the entire country, or for such specific areas as the Neovolcanic Belt of central Mexico where the flora is best known.

For Mexican mosses, in addition to data in a recent flora (Sharp et al., 1994), the number and relative importance of the endemic species have been published in several contributions. In the deciduous forests of eastern Mexico eight species were once considered endemic (Delgadillo, 1979), but further study has shown virtually no endemism in these communities, as is the case of the moss flora of the Yucatan Peninsula (Delgadillo, 1984). In the dry lands of Zacatecas (Delgadillo & Cárdenas, 1987) and the Tehuacán Valley (Delgadillo & Zander, 1984), the proportion of endemics is low, but appears comparatively higher than in the tropical lowlands of southern Mexico. Only five species are recognized as endemic in Zacatecas (4.3% of the moss flora), and four in the Tehuacán Valley (7% of the moss flora). In the alpine areas there are 19 endemic species that account for 17% of the moss flora there (Delgadillo, 1971, 1987).

The studies on the Poaceae of Mexico are mostly floristic in nature, but many contain reliable data on the distribution of species in the country (e.g., Hernández X., 1959, 1964; Johnston, 1940; Miranda, 1960; Rzedowski, 1962, 1965, 1975, 1978, 1993; Sharp, 1953). A valuable discussion on grass endemism was contributed by Valdés and Cabral (1993), who indicated that a total of 272 species (30% of the grass flora) are endemic to Mexico. The Chloridoideae have the highest number of endemics, with 73 species, followed by the Panicoideae with 46, and the Pooideae with 43. According to these authors, the states with the highest numbers of endemic grasses are Jalisco, México, Veracruz, and Oaxaca. Despite the cosmopolitan nature of the Poaceae, their distribution patterns are well defined and are known to be correlated with edaphic and climatic features.

With regard to the Asteraceae, preliminary estimates by Villaseñor (1993) include 1813 endemics out of 2861 species for 63.4% endemism in the Mexican flora; these belong in 371 genera, 67 of which are endemic to Mexico (Villaseñor et al., 1998). The number of species known from Mexico in this family was expected to rise to about 3000 and, with this, an increase in the number of endemic taxa in certain areas; Villaseñor (1993) suggested a trend toward higher endemism values in states located in the drier northern and southern areas or in the mountain region of Mexico. Unpublished data for the Valley of Tehuacán recognize at present, in addition to the taxa endemic to the country, 32 species restricted to the valley out of 358 Asteraceae for the local flora, and in Zacatecas 4 restricted taxa out of the total 488 species. The flora of Nayarit comprises 447 species of Asteraceae, 15 of which are restricted to the state (Ortíz-Bermúdez et al., 1998), while in the Yucatan Peninsula and Tabasco there are 7 restricted endemics from a flora of 252 species (Villaseñor, 1989).

MATERIALS AND METHODS

A Microsoft ACCESS database containing the state distribution and the names of species of Musci, Asteraceae, and Poaceae restricted to the political limits of Mexico was compiled from bibliographic sources and support from herbarium specimens. Sharp et al. (1994) and Delgadillo et al. (1995) were the main sources for mosses. In addition to numerous monographs, information was compiled from publications such as Davidse et al. (1994), McVaugh (1983), and Valdés-Reyna and Dávila (1995) for the Poaceae, and McVaugh (1984), Rzedowski and Calderón (1995), Strother (1999), and Turner (1997), as examples, for the Asteraceae. The main herbarium sources include MEXU for the mosses, and MEXU, ENCB, IBUG, MICH, and US for the Poaceae and the Asteraceae. Specimen data were used to complement the taxon distribution.

Database information was used to compute Jaccard's Index of Similarity and a cluster analysis to determine the floristic relationships of the Mexican states. The database file information was exported to Microsoft EXCEL tables as the first step to use an NTSYSpc version 2.02 software package (Rohlf, 1998). A presence-absence OGUs (Operational Geographical Units, i.e., states) matrix served to calculate the index of similarity and to produce a similarity matrix. The UPGMA (unweighted pair-group arithmetic averages method) dendrograms (Figs. 2–4) were generated by the SAHN-clustering command in NTSYS-pc. Similar procedures were used to review the relationships of individual groups or smaller areas in Mexico, e.g., the Neovolcanic Belt states. As a whole, the present analysis concerns 2373 endemic species, including 15 subspecies and 339 varieties, in the three plant groups studied. The database and the similarity matrices are available on request from the authors.

For reference, the political subdivision of Mexico and the location of certain geomorphological features cited in the text are shown in Figure 1. The Neovolcanic Belt states discussed elsewhere in the text are Nayarit, Jalisco, Colima, Michoacán, Querétaro, Hidalgo, México, Distrito Federal, Morelos, Tlaxcala, Puebla, and Veracruz. The density values shown in Table 2 represent the computation of a simple density index of ecology textbooks, i.e., number of species per unit area.

RESULTS

ENDEMISM IN MEXICO

From our records, there are 86 endemic moss species in Mexico, 4 of which are represented by subspecific taxa. Most endemic species are known from below 2800 m, but there is a group of about 18 species known only from above 3000 m in elevation. Among the species from the higher elevations, *Astomiopsis* × *altivallis* Delgad. is conspicuous for its presumed hybrid origin between *A. amblyocalyx* C. Muell. and *A. exserta* (Bartr.) Snider; *Archidium acauloides* Schwab, a cleistocarpic species, is also of interest because it represents a form with limited dispersal ability. Because of the small number of species involved and their narrow ranges, no distinct geographical trends of state distribution are shown by the cluster analysis. However, most states along the Neovolcanic Belt are grouped together, and harbor, along with Oaxaca and Tamaulipas, more than 10 endemic taxa (Table 1). Despite the disparity in group size, the Poaceae and Asteraceae show similar behavior, i.e., they are best represented in certain adjacent states, in the Neovolcanic Belt states, and in Oaxaca. The values for all three groups seemed to confirm this trend (Table 1).

With respect to the Poaceae, a total of 257 endemic species—including 12 subspecies and varieties—out of 950 grasses, have been registered for Mexico (Tables 1, 3) for 27% endemism. Some species, such as *Festuca hintoniana* Alexeev, are known only from one or a few localities, while others are exclusively known from the type locality, as is the case of *Schaffnerella gracilis* (Benth.) Nash. By contrast, many endemic species, including *Bouteloua scorpioides* Lag., *Muhlenbergia gigantea* (Fourn.) Hitchc., *M. firma* Beal, *Bothriochloa hirtifolia* (J. Presl) Henrard, *Panicum decolorans* Kunth, and *Urochloa meziana* (Hitchc.) Morrone & Zuloaga, are widespread in Mexico. Except for Tabasco, there are endemic grasses known from every Mexican state, mostly distributed at intermediate elevations (ca. 1500–2800 m). The highest number of endemic species is found in Jalisco, México, and Michoacán, with 55 or more species, but the states of Chiapas, Chihuahua, Durango, Guanajuato, Nuevo León, Oaxaca, Puebla, San Luis Potosí, and Veracruz have between 32 and 49 endemic species. In contrast, Baja California, Campeche, Quintana Roo, Tlaxcala, and Yucatán have less than 10 endemic species. In contrast to the results reported by Valdés and Cabral (1993), the present study includes species with a strictly Mexican range only. If the grasses restricted to the southwestern United States (California, Arizona, New Mexico, and Texas) and Mexico were included, the number of endemic species would increase to about 300, with the highest number of them occurring in the semiarid habitats and the alpine grasslands. Endemic Poaceae are present in low numbers in the states of Campeche and Quintana Roo, and are unknown from Tabasco.

The flora of Mexico includes about 3003 Asteraceae; 1972 of them, or 65.7%, are endemic to the country. However, for the analysis, 2030 species, subspecies, and varieties of endemic Asteraceae were accepted, i.e., incorporating 58 taxa not fully documented and increasing the percentage to 67.6 (Table 3). The endemic taxa include 10 subspecies and 328 varieties. The known altitudinal interval for the Mexican Asteraceae places many of the endemic taxa in the intermediate elevations (ca. 1500–2800 m), and their individual ranges are frequently broader than those of mosses and grasses. Some species of Asteraceae have narrow ranges that depend on the presence of special habitats, e.g., *Geissolepis suaedifolia* B. L. Rob. or *Stephanodoria tomentella* (B. L. Rob.) Greene that are endemic to gypsophilous grasslands in San Luis Potosí; other species, such as *Psacalium peltatum* (Kunth) Cass., whose range extends from Chihuahua and Durango south to Puebla and Oaxaca, demonstrate a comparatively broad distribution in Mexico. In terms of the states, those with the largest number of endemic species are Jalisco, México, Michoacán, Oaxaca, and Durango, with 385 to 526 species in each state. A second group, formed by Guerrero and Puebla, contains between 317 and 365 species (Table 1).

Cluster analysis of similarity data for the Asteraceae indicates that many Mexican states are related to their neighbors; the overall analysis for all three groups (Fig. 2) clearly shows this trend at the

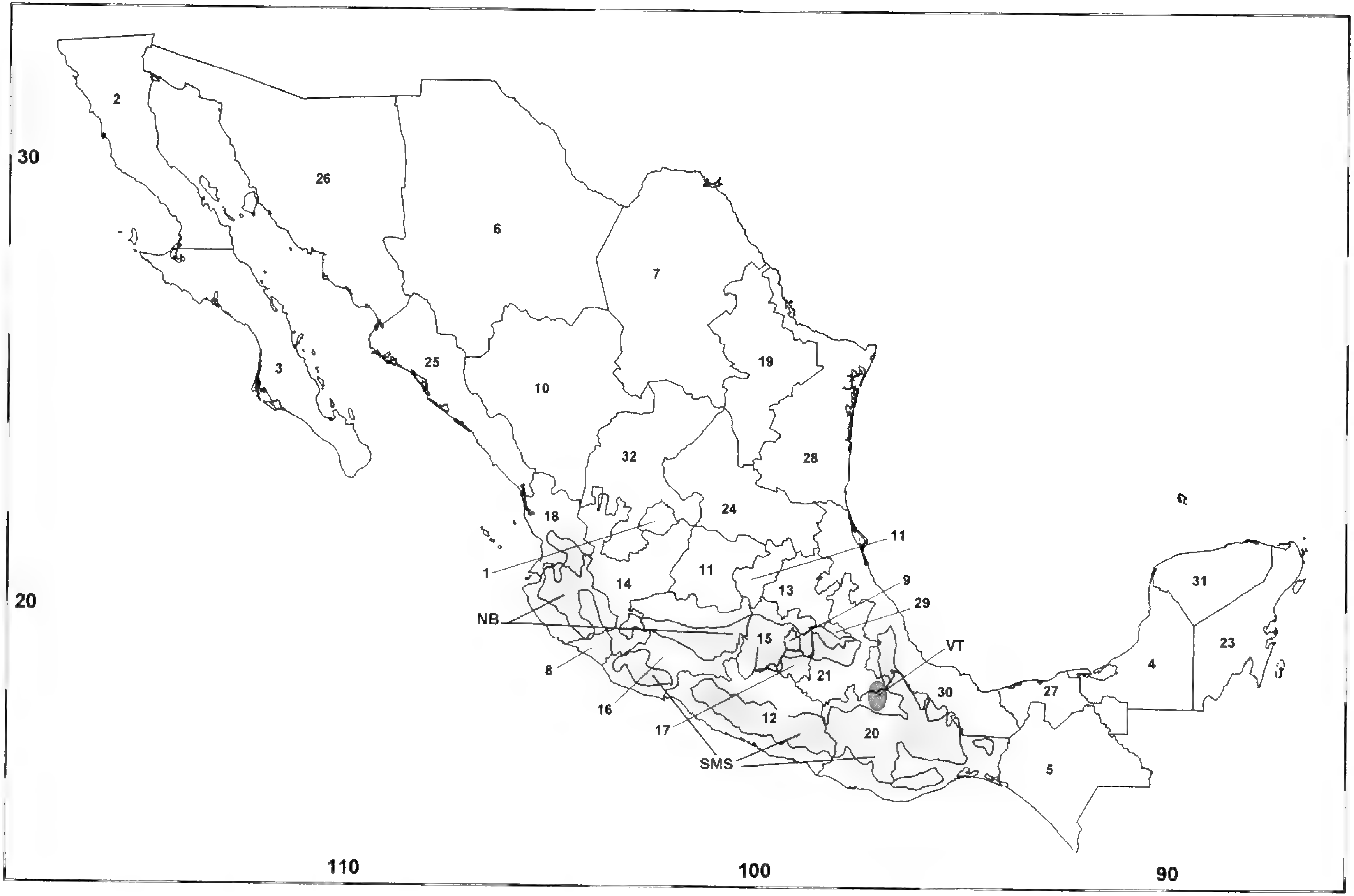

Figure 1. Political subdivision of Mexico. 1 = Aguascalientes (Ags), 2 = Baja California (BC), 3 = Baja California Sur (BCS), 4 = Campeche (Camp), 5 = Chiapas (Chis), 6 = Chihuahua (Chih), 7 = Coahuila (Coah), 8 = Colima (Col), 9 = Distrito Federal (DF), 10 = Durango (Dgo), 11 = Guanajuato (Gto), 12 = Guerrero (Gro), 13 = Hidalgo (Hgo), 14 = Jalisco (Jal), 15 = México (Mex), 16 = Michoacán (Mich), 17 = Morelos (Mor), 18 = Nayarit (Nay), 19 = Nuevo León (NL), 20 = Oaxaca (Oax), 21 = Puebla (Pue), 22 = Querétaro (Qro), 23 = Quintana Roo (QR), 24 = San Luis Potosí (SLP), 25 = Sinaloa (Sin), 26 = Sonora (Son), 27 = Tabasco (Tab), 28 = Tamaulipas (Tamps), 29 = Tlaxcala (Tlax), 30 = Veracruz (Ver), 31 = Yucatán (Yuc), 32 = Zacatecas (Zac), NB = Neovolcanic Belt, SMS = Sierra

Table 1. Number of endemic taxa per state for each major plant group investigated in Mexico. Number of species endemic to a state are given in parentheses; Neovolcanic Belt states are shown in **bold.**

State	Musci	Asteraceae	Poaceae	Σ
Aguascalientes	0 (0)	154 (0)	19 (0)	173 (0)
Baja California	1 (0)	140 (32)	5 (2)	146 (34)
Baja California Sur	1 (0)	103 (48)	12 (4)	116 (52)
Campeche	0 (0)	4 (0)	5 (0)	9 (0)
Chiapas	6 (3)	135 (37)	38 (6)	179 (46)
Chihuahua	2 (0)	275 (58)	44 (8)	321 (66)
Coahuila	1 (1)	223 (46)	41 (10)	265 (57)
Colima	**0 (0)**	**113 (10)**	**20 (6)**	**133 (16)**
Distrito Federal	**12 (3)**	**180 (1)**	**25 (0)**	**217 (4)**
Durango	4 (1)	385 (59)	48 (1)	437 (61)
Guanajuato	0 (0)	213 (2)	38 (0)	251 (2)
Guerrero	2 (1)	365 (54)	29 (0)	396 (55)
Hidalgo	**10 (0)**	**271 (15)**	**28 (0)**	**309 (15)**
Jalisco	**10 (3)**	**526 (64)**	**80 (15)**	**616 (12)**
México	**21 (2)**	**391 (15)**	**67 (7)**	**479 (24)**
Michoacán	**17 (1)**	**460 (25)**	**55 (4)**	**532 (30)**
Morelos	**6 (0)**	**230 (5)**	**22 (0)**	**258 (5)**
Nayarit	**7 (2)**	**277 (15)**	**27 (5)**	**311 (22)**
Nuevo León	4 (2)	257 (41)	32 (4)	293 (47)
Oaxaca	17 (5)	473 (115)	40 (3)	530 (123)
Puebla	**23 (3)**	**317 (13)**	**49 (1)**	**389 (17)**
Querétaro	**1 (0)**	**218 (6)**	**18 (0)**	**237 (6)**
Quintana Roo	0 (0)	6 (0)	2 (0)	8 (0)
San Luis Potosí	8 (1)	249 (23)	48 (5)	305 (29)
Sinaloa	1 (1)	224 (25)	21 (1)	246 (27)
Sonora	1 (0)	160 (27)	23 (0)	184 (27)
Tabasco	0 (0)	6 (0)	0 (0)	6 (0)
Tamaulipas	11 (2)	166 (16)	24 (2)	201 (20)
Tlaxcala	**5 (0)**	**119 (0)**	**9 (0)**	**133 (0)**
Veracruz	**25 (3)**	**271 (21)**	**38 (6)**	**334 (30)**
Yucatán	1 (0)	9 (2)	8 (0)	18 (2)
Zacatecas	5 (0)	208 (5)	22 (1)	235 (6)
TOTAL	86 (34)	2030 (780)	257 (91)	2373 (905)

regional level. Aguascalientes, Zacatecas, Guanajuato, Querétaro, Hidalgo, and San Luis Potosí form the first block of neighboring states that share numerous endemic taxa. The states in the peninsulas of Baja California and Yucatan stay together in the endemism dendrogram (Fig. 2) as do groups of states in northeastern (Coahuila, Nuevo León, and Tamaulipas), northwestern (Chihuahua and Durango), and central Mexico (Distrito Federal, Tlaxcala, Puebla, Veracruz, Guerrero, México, Michoacán, and Morelos). The position of certain states does not conform to geographical vicinity as, for instance, in the case of Oaxaca, which is closer to Morelos and Michoacán than to Puebla and Guerrero, which limit it to the north and west; the endemic flora of Chiapas remotely links that state to the rest of the country. The data set for mosses and grasses modifies the value of the similarity coefficient and the relative position of many states in the dendrogram (Fig. 3). Such states as Aguascalientes, Guanajuato, San Luis Potosí, Zacatecas, Chihuahua, and Durango from the first block in Figure 2 have a different pairing arrangement in Figure 3. Also, individual analyses for mosses and grasses fail to produce reliable dendrograms, as indicated by the lack of similarity among neighboring states, perhaps induced by the low number of records and, in mosses, by the absence of endemic records for about six states.

The number of endemic taxa in the overall analysis seems indirectly related to the size of each state; thus, for instance, Aguascalientes, Colima, and Tlaxcala are among the smallest states in Mexico and have some of the lower numbers (Table 1). By contrast, the low numbers exhibited by the states of the Yucatan Peninsula (Campeche, Yuca-

Table 2. Endemism along the Neovolcanic Belt of Mexico. The second column gives the number of species restricted to a state in parentheses; the last column shows the corresponding density index also in parentheses. Density = Number of endemics/surface area × 100.

State	No. endemics	Surface (km^2)	Density
Colima	133 (16)	5,191	2.56 (0.31)
Jalisco	616 (12)	80,836	0.76 (0.01)
Nayarit	311 (22)	26,979	1.15 (0.08)
Distrito Federal	217 (4)	1,479	14.67 (0.27)
Tlaxcala	133 (0)	4,016	3.31 (0)
Hidalgo	309 (15)	20,813	1.48 (0.07)
Querétaro	237 (6)	11,449	2.07 (0.05)
México	479 (24)	21,355	2.24 (0.11)
Michoacán	532 (30)	59,928	0.89 (0.05)
Morelos	258 (5)	4,950	5.21 (0.10)
Puebla	389 (17)	33,902	1.15 (0.05)
Veracruz	334 (30)	71,699	0.47 (0.04)

tán, and Quintana Roo) may not be dependent on their surface area as each one has between 38,000 and 50,000 km^2. On the other hand, the similarity and relationship among states along the Neovolcanic Belt (Table 1, Fig. 2) suggest areas of endemism that require further analysis.

ENDEMISM ALONG THE NEOVOLCANIC BELT

Mosses represent an important element in the flora of the Neovolcanic Belt. The Belt occupies portions of the states of Colima, Jalisco, Nayarit, Distrito Federal, Tlaxcala, Hidalgo, Querétaro, México, Michoacán, Morelos, Puebla, and Veracruz, thus extending the width of the country (Fig. 1). About 728 moss species are known from this area. By virtue of this number, the states along the Belt may be considered bryologically diverse, for they include about 74% of the mosses known from Mexico. The Belt states are easily accessible, and their collecting record is better than that of other Mexican states. The percentage of endemism, with about 62 shared endemic moss species in the Belt (8.5%), is nearly as high as that for moss flora of the entire country (8.8%), as shown in Table 3. A distinction must be made between "shared" and "restricted" endemics; in this contribution the former refers to species distributed in two or more states while the latter are known from a single state.

The Asteraceae are represented by 1640 species and infraspecific taxa along the Belt, or nearly 55% of the Mexican Asteraceae. About 1095 of them are endemic to Mexico and 190 are restricted to a single Neovolcanic Belt state (Table 3); the percentage of endemism nationwide (67.6%) is nearly the same as that for the Belt (66.8%). By contrast, there are 222 species of Poaceae (23% of all Mexican grasses) along the Belt states, 162 of which are shared with other states (73% of the Neovolcanic Belt Poaceae), and 44 of them restricted to this mountain range (Table 3). The Neovolcanic Belt may be considered an area of high diversity (4935 in these plant groups) and high endemism (1319 endemics, including 251 narrow endemics, Table 3) and might be recognized, by these criteria, as a separate floristic province. Rzedowski (1978) treated it as part of the Southern Ranges province (see Fig. 1).

The dendrogram in Figure 4 shows the overall relationship of endemism among the states along the Neovolcanic Belt with a general trend in a west-east direction. Jalisco and Nayarit, on the western coast, are very similar to each other, with about 240 shared endemic taxa; the states of México and Michoacán also share numerous taxa (300) and together constitute a separate area of endemism, despite the geographical vicinity with states on the western coast. Colima and Tlaxcala have the lowest endemism numbers along the Belt (Table 2), and this is attributed in part to their small surface area. The latter state, however, is floristically more similar to Distrito Federal (Fig. 4) than to Puebla or Veracruz that surround it. Otherwise, the close flo-

Table 3. Number of endemic species and percentage of endemics among Musci, Asteraceae, and Poaceae in Mexico and in the Neovolcanic Belt.

	Musci	Asteraceae	Poaceae	Total
Mexican species	982	3003	950	4935
Mexican endemics	86	2030	257	2373
Percentage in Mexico	**8.8**	**67.6**	**27**	**48**
Neovolcanic Belt species	728	1640	222	2590
Percentage from total	**74.1**	**54.6**	**23.4**	**52.5**
Shared endemics in Belt states	62	1095	162	1319
Percentage in Belt states	**8.5**	**66.8**	**73.0**	**50.9**
Restricted to one Belt state	17	190	44	251

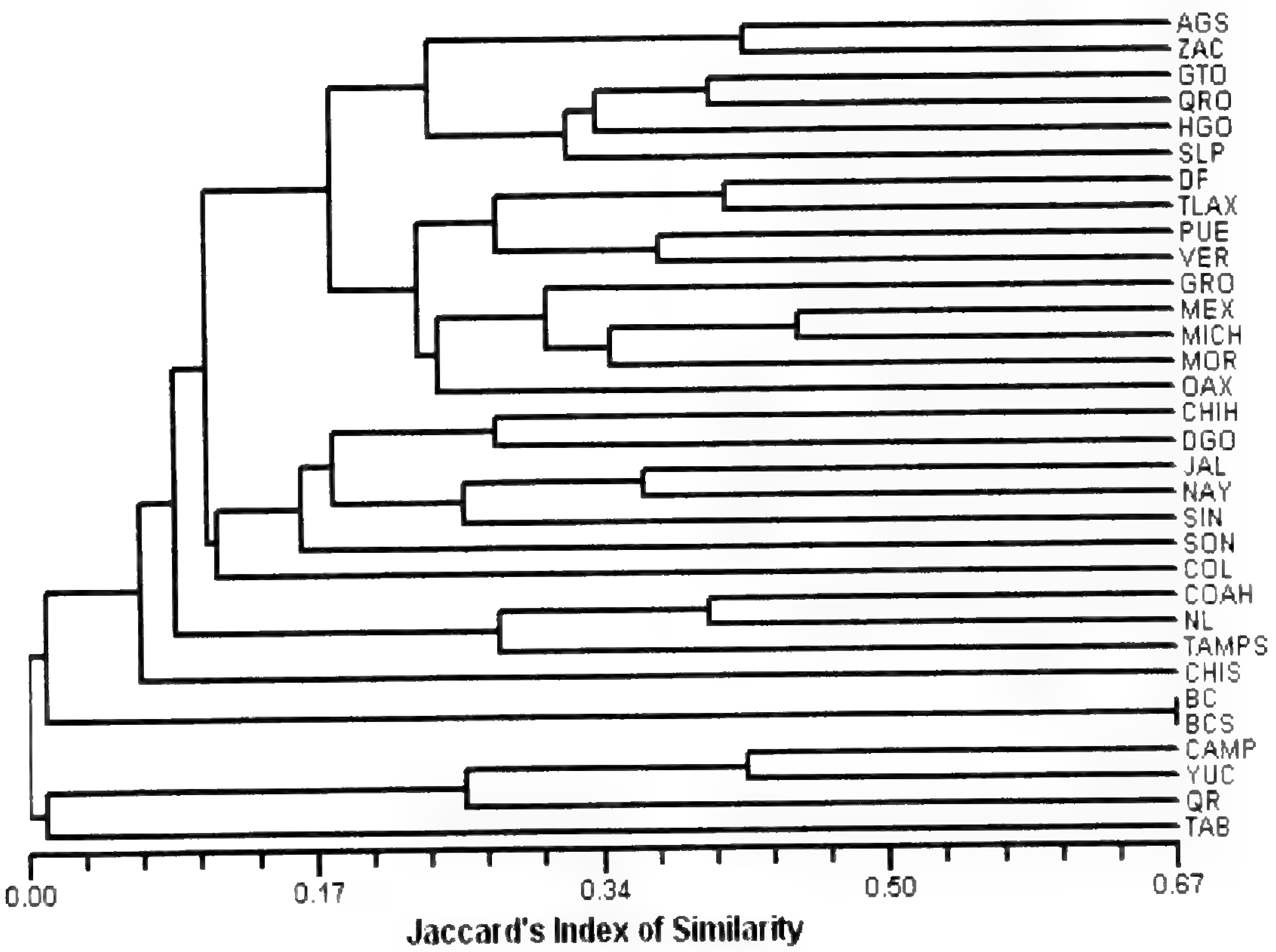

Figure 2. UPGMA dendrogram of the floristic relationships among Mexican states as illustrated by endemic Asteraceae, Poaceae, and Musci.

ristic relationship between members of most state pairs (Fig. 4) may be due to their geographical proximity.

As with the overall analysis, species endemism is only indirectly dependent on size of the area along the Neovolcanic Belt. Geologic history, topographic differences, and climatic regimes may provide better explanations for the number of endemics in a given area. By these measures, the states of Jalisco, Michoacán, and México may be

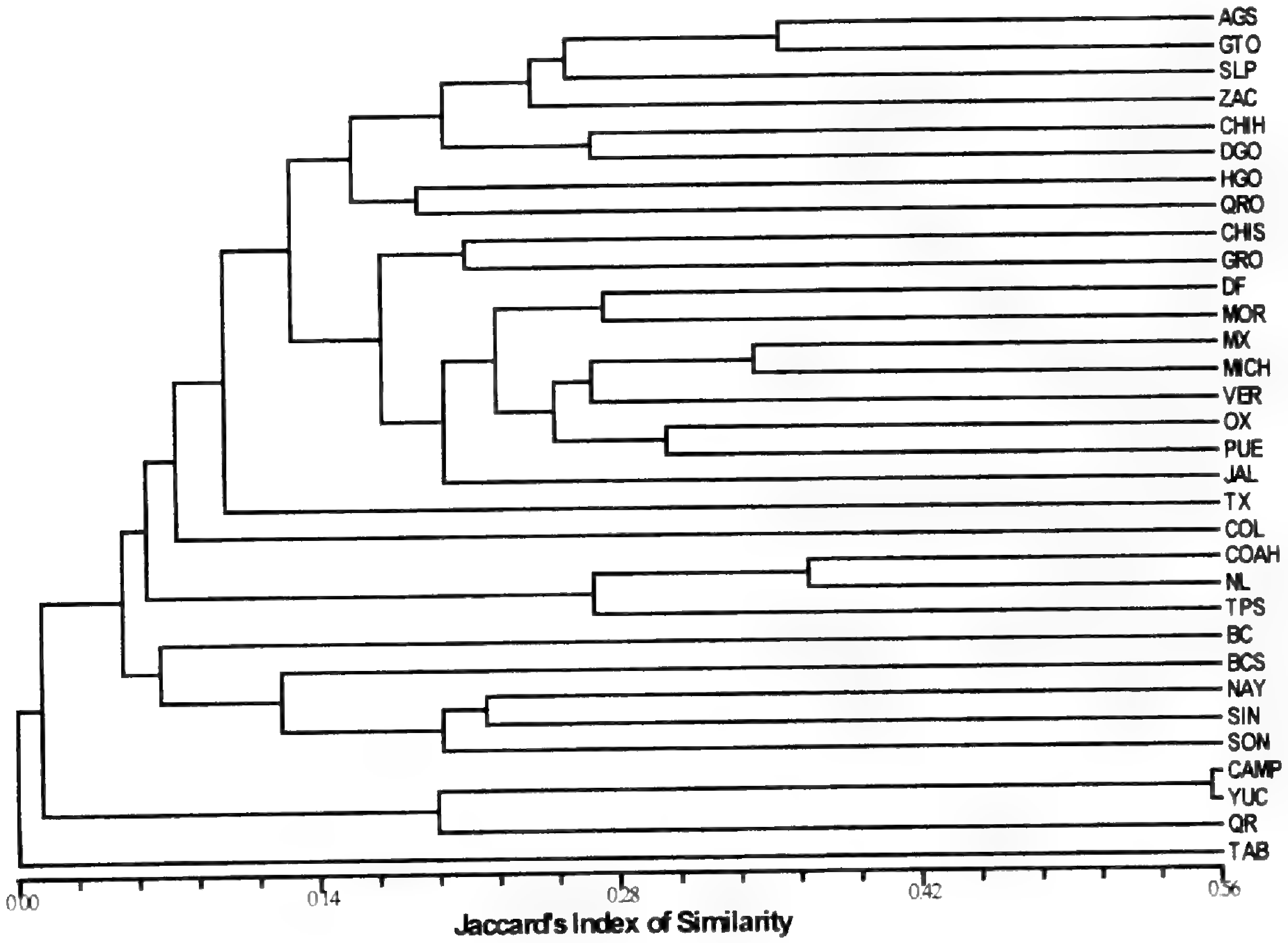

Figure 3. UPGMA dendrogram of the floristic relationships among Mexican states as illustrated by endemic Poaceae and Musci.

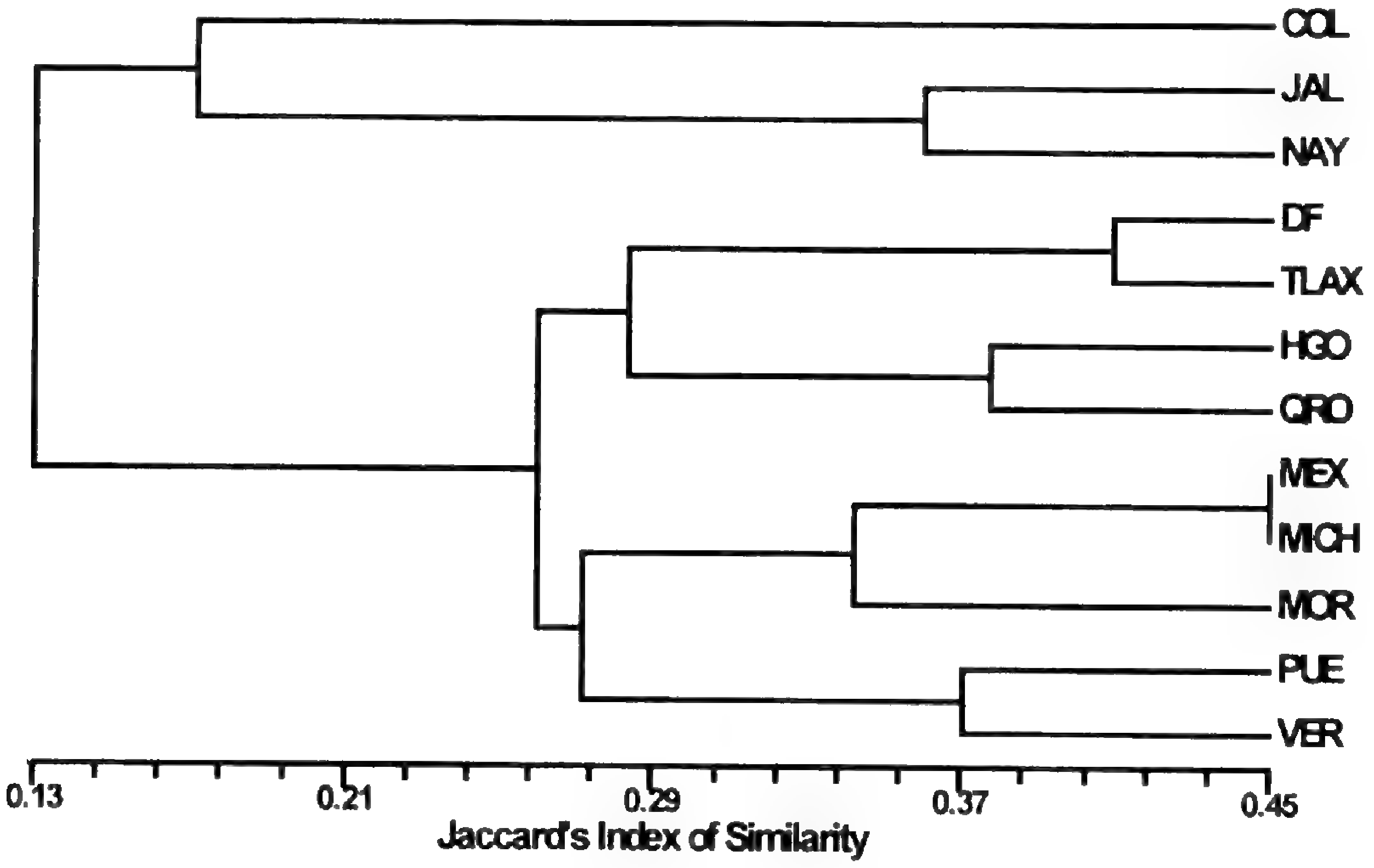

Figure 4. UPGMA dendrogram of the floristic relationships of the states along the Neovolcanic Belt of Mexico as illustrated by endemic Asteraceae, Poaceae, and Musci.

considered the most important areas of endemism along the Neovolcanic Belt. Together these states constitute the largest portion of the Belt, and most endemic taxa in the three major groups are represented in one or the other states. Nevertheless, the computation of the number of endemic taxa per 100 km^2 indicates that Distrito Federal (with a density index of 14.67), Morelos (5.21), and Tlaxcala (3.31, see Table 2) are, by far, the most important areas of endemism in the Belt. A more accurate measure of the relative importance of each state may be obtained by determining the size of the range of endemic taxa and their numbers per unit area. In this study, the density index calculated for the endemic species restricted to each Belt state (Table 2) is not meaningful because their general range size is unknown.

DISCUSSION

The use of a similarity coefficient and cluster analysis has shown that the floristic relationships of states may be established with certain degree of accuracy. The resolution of the analysis, however, depends on the amount of field or herbarium information and an adequate taxonomic background. The input of data from other major plant groups should assist in refining the scheme of relationships among such states, particularly among those that show little similarity with their neighbors. In this contribution, the unusual position of a state may indicate areas of endemism or lack of distributional data, but other explanations may be sought in regional peculiarities or in the biological traits of the plant groups.

The study of endemism by resorting to assemblages of species from widely different plant groups may be advantageous because the combined study of patterns may be a measure of the response of the entire flora to environmental factors that operate over broad geographical areas. The obvious disadvantage of this approach is that the taxa under investigation differ in size, evolutionary history, and biological attributes and, thus, in their response to selective pressures. For these reasons, it could not be assumed that endemism values in mosses would be similar to those of Asteraceae or Poaceae in the same region. Each taxon, by virtue of a differing life cycle or ecological preferences, does not operate under the same selective pressures and, in fact, has differing responses. The dependency on running water for fertilization in mosses contributes to their minor representation in desert areas. Nevertheless, the low number of moss endemics in other habitats may be due to relatively rapid spread of taxa following speciation. Mosses are usually considered to be slow-evolving organisms, but the effect of somatic mutations on evolution and their rates of spread in local populations are unknown. From the standpoint of the life cycle, there are theoretical considerations by which at least some populations may undergo rapid evolutionary change. For instance, if polyploids are produced by diplospory or apospory, or if a somatic mutation is retained in an otherwise haploid organism, with the aid of asexual reproduction these processes may yield an independent and distinct taxon from one generation to the next. Rapid speciation, however, may not be the rule; new taxa may appear by slow evolutionary change and disperse gradually.

Thus, endemic mosses should be comparatively scarce in Mexico and elsewhere. This is supported by current phytogeographic and geologic information suggesting that the moss flora of Mexico has not evolved in isolation. In addition to the examples given in the introduction, a recent study in the lowland areas of Chiapas (Delgadillo & Cárdenas, 2002) reports a single endemic species, *Pylaisiadelpha sharpii* Crum, for the Lacandon Forest and more than 130 species shared with other continental areas. The broad geographical patterns exhibited by Mexican moss species and the age and North–South orientation of mountain ranges agree with the hypothesis of rapid dispersal of newly evolved species in Mexico. The exploration of poorly known areas is not expected to produce a sharp increase in the number of endemic species, but rather the decrease in percentage endemism values as the distribution of described species is better known or as modern taxonomic evaluations result in synonymy. A few years ago, Delgadillo (1994) calculated nearly 11% moss endemism in Mexico; this contribution records only 9%, while the known number of species has increased from 943 in 1994 to about 982 in 2002.

Compared to mosses, grasses and composites represent heterozygote systems where sexual reproduction, the length of the life cycle, and dispersal retard evolutionary events. Assuming similar rates of speciation, but differences in dispersal ability and age of taxa, vascular plants would be expected to be geographically limited, genetically stable, and narrowly distributed, more so than mosses. Long-lived moss species have been documented in the fossil record (Frahm, 2000; Miller, 1984), and broad continental and intercontinental ranges are common among mosses (cf. Sharp et al., 1994). This may not be the case in vascular plants where, in addition, selection does not immediately eliminate mutant genotypes. Phenotypic expressions recognized as endemic taxa may remain for a long time in recombinant diploid populations, even under negative selective pressures. In Mexico, although the number of moss and grass species are similar, the groups differ in their proportion of endemic taxa; the explanation for this difference may be sought among the biological attributes cited above. The present study illustrates how endemism values may not be equivalent between similar taxonomic categories, but does not support such differences in the taxonomic hierarchy.

Local climates certainly act as strong selective forces for every plant group. Mosses, grasses, and composites, however, show differential responses to climate. The distribution of the first group in the drier areas of Mexico does not apparently follow obvious patterns. In fact, there are few endemic species in the desert areas of Zacatecas (e.g., *Curviramea mexicana* (Thér.) Crum and *Jaffuelibryum arsenei* (Thér.) Thér.; Delgadillo & Cárdenas, 1987), but in the alpine areas where mosses are dominant with lichens and grasses, an important endemic element appears. Rzedowski (1962, 1991a) discussed the importance of the dry areas for endemism among vascular plants. In the higher elevations these plant groups may also increase their endemic representation. High UV radiation, daily temperature fluctuation, low organic nitrogen and phosphorus in the substrate of alpine and subalpine areas seem strong selective forces for all plants, including mosses, grasses, and composites.

There are other differences that are evident in the present analysis. Degree of endemism varies among groups, and there are disparities in their altitudinal and latitudinal gradients and in the types of vegetation they occupy. Contributions by Delgadillo (1979, 1984) and Delgadillo and Zander (1984) attest to the uneven distribution of endemic mosses in the deciduous forests of eastern Mexico, in the Yucatan Peninsula, and in the Tehuacán Valley, respectively. Endemism values observed for the Asteraceae and Poaceae also indicate differences among geographical areas, even among those of similar surface area. On a national scale, these preliminary findings may be the basis for the identification of areas of high endemism and the selective forces in operation. They will also assist in unveiling the history of the flora in Mexico and its relationships to other floras in the American tropics. The Neovolcanic Belt, as an example, has been shown to be one such region where portions of the mountain range (Distrito Federal, Jalisco, México, and Michoacán) have higher endemism concentrations than the rest. However, a detailed floristic knowledge of less known or undercollected parts of the country, or even of adjacent areas in other countries, is essential to determine whether the differential distribution of endemics is not an artifact derived from historical collecting preferences.

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YUCCAS, YUCCA MOTHS, AND COEVOLUTION: A REVIEW[1]

Olle Pellmyr[2]

ABSTRACT

The obligate pollination mutualism between yuccas (Agavaceae) and yucca moths (Lepidoptera, Prodoxidae), in which the adult moth pollinates yucca flowers and her progeny feed on developing seeds, is one of the classically cited examples of coevolution. While known since 1872, our understanding of the ecology and evolution of this association has increased dramatically in the past decade. Here I review current information on organismal diversity and phylogenetic relationships, ecological relationships, origin and reversal of the mutualism, and the potential for analyzing patterns of co-speciation and the historical role of coevolution on specific traits in driving diversification in the interaction. Major novel developments in recent years include the recognition of a large species complex of pollinators, previously thought to be one polyphagous species; a majority of all moth species are monophagous. Considerable life history diversity has been unveiled, and mechanisms that maintain a mutualistic equilibrium by preventing overexploitation documented. Phylogenetic and ecological information, including data from other, newly discovered facultative pollinators in the Prodoxidae, have been used to erect a hypothesis for the evolution of obligate mutualism. Application of a molecular clock to phylogenetic data suggests that the plant-moth association arose at least 40 Mya, and that the obligate mutualism evolved very quickly after this event. Two separate events of reversal of mutualism have been identified, involving derived "cheater" moth species that oviposit into fruits resulting from pollination by other pollinator species. This appears to have happened not through selection for cheating, but rather as a byproduct of a phenological shift to an unexploited seed resource, in which case pollination behavior became redundant. Analyses of parallel diversification and character coevolution are hampered by incomplete phylogenetic information at the species level, especially for the plants, but also for the pollinators. Available data indicate considerable deviation from strict co-speciation, and no evident examples of this process. Analyses of the role of coevolutionary processes in driving the diversification of yuccas and yucca moths will be possible once fully resolved phylogenies become available.

Key words: coevolution, *Hesperoyucca*, mutualism, *Parategeticula*, Prodoxidae, *Tegeticula*, *Yucca*, yucca moth.

Coevolution, in the sense of reciprocally induced evolution, is one of the major processes driving diversification and speciation (Farrell & Mitter, 1993; Thompson, 1994, 1999a, b). Since first applied in plant-animal interactions as a hypothesis to explain diversification among butterflies and flowering plants (Ehrlich & Raven, 1964), it has been applied successfully in comparative analyses to test rates of diversification in ecologically defined groups, such as plant-feeding insects and parasitoids (Mitter et al., 1988; Wiegmann et al., 1993; Becerra, 1997; Farrell, 1998; Becerra & Venable, 1999). Several such studies show that plants and plant-feeding insects often have increased rates of diversification compared to sister groups with different life habits; thus one or more life history aspects of these groups appear to be important in driving diversification and speciation. This might involve, for example, chemical, physiological, and morphological arms races between the interacting organisms.

Our understanding of coevolutionary processes at populational and species levels is still in its infancy because identification of proximal factors of diversification relies on strong phylogenetic hypotheses for the interacting organisms (Barraclough et al.,

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[1] I thank the Missouri Botanical Garden for inviting me to speak at the 46th Annual Symposium, and to its archives for providing access to unpublished notes on Riley's experiments. My studies of yuccas and yucca moths have been funded by the National Science Foundation and by the National Geographic Society. This work has been very much a team effort over the years. Collaborators and invaluable information sources outside the lab have included John N. Thompson, Donald Davis, Jerry Powell, Richard Harrison, Jonathan Brown, Karen Clary, and Manuel Balcázar-Lara. A progression of postdocs, graduate students, and undergraduate students in my lab have been wonderful collaborators over the years. They include Jim Leebens-Mack, Deborah Marr, David Althoff, Chad Huth, Kari Segraves, Joshua Groman, Beau Crabb, Mary Ann Feist, Mark Brock, Lindsey Elms, Jeff Keyes, Rachel Roberts, Andrea Farley, Allison Outz, James Goldmeyer, Ansley Grimes, and Eric Weiss. Goggy Davidowitz aided with a reference in Hebrew. Colleagues too numerous to list here have helped greatly in providing samples and locality information over the years. Michael Long provided helpful information on George Engelmann's original observations. Finally, I thank *Annals* editor Victoria Hollowell for her exceptional patience with me during the long gestation of this review. This paper is dedicated to the memory of Ebbe Schmidt Nielsen, who revolutionized our understanding of basal Lepidoptera phylogeny.

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1998; Pagel, 1998, 1999a, b), extensive life history data, and ultimately experimental testing of emerging candidate traits (Armbruster et al., 1997). Often the phylogenetic frameworks are missing, and there are very few instances where all these criteria are met. A recent exception is the study of Becerra (1997), who used data for members of the plant genus *Bursera* (Burseraceae) and a group of specialist herbivorous beetles (*Blepharida*; Chrysomelidae) to suggest that chemical defenses and detoxification traits have been a major evolutionary factor in their diversification.

One of the most often cited cases of coevolution is the obligate mutualism between yuccas (*Yucca* and *Hesperoyucca,* Agavaceae) and yucca moths (*Tegeticula* and *Parategeticula,* Prodoxidae, Lepidoptera). In this association, the plants rely on adult moths for their pollination, while the moth larvae require developing seeds to complete their development. This association was first recognized over a century ago (Anonymous, 1872; Riley, 1872), and then served not only as an example of remarkable pollination mutualism, but also as one of the first and strongest examples of evolution by means of natural selection. Together with a few other models of obligate mutualism that involve seed-eating pollinators, the yuccas and yucca moths form a class of associations that are excellent systems for studies of coevolution, as well as of evolutionary and ecological dynamics of mutualism and its dissolution. This stems in part from the relative simplicity of measuring fitness costs and benefits in these interactions; in most instances both plant cost and benefit can be measured in seeds. Second, in contrast to most other plant-pollinator associations, these are relatively exclusive associations, often with a single pollinator species per plant species, making it easier to measure reciprocal effects than when webs of many, simultaneously interacting taxa have to be analyzed.

Considerable progress has been made in understanding this unusual type of obligate pollination mutualisms in the past 15 years. This is certainly true of the long-recognized yucca-yucca moth and fig-fig wasp associations (Riley, 1872; Weiblen, 2002). The two other documented examples of such obligate associations (*Trollius europaeus* L. [Ranunculaceae] and *Chiastocheta* flies [Diptera: Anthomyidae], and *Lophocereus schottii* (Engelm.) Britton & Rose [Cactaceae] and the moth *Upiga virescens* (Hulst) [Lepidoptera: Pyralidae]) were actually first documented during this period (Pellmyr, 1989, 1992; Fleming & Holland, 1998; Després & Jaeger, 1999; Jaeger et al., 2001). Here I will review our current understanding of the association between yucca moths and yuccas, and discuss its utility in exploring more general questions of coevolution. Since the latest reviews of this interaction, by Baker (1986) and Powell (1992), information on systematics, phylogenetic relationships, and life history has increased dramatically, especially in the moths, and the complexity of the association at different hierarchical levels is now quite different.

Figure 1. *Tegeticula yuccasella* female collected by G. Engelmann on the first night that he observed moths on *Y. filamentosa* flowers. Label likely written by C. V. Riley, who received the moth. From the collections of USNM.

Early History of Study of the Plant-Moth Interaction

The first observation of the yucca moths was made by George Engelmann in St. Louis in 1872 (Engelmann, 1872). Engelmann asked Charles Riley, then state entomologist of Missouri, to explore the relationship between the moths and the plants. Baker (1986) provided a passage from Engelmann's notes written on 13 June 1872 about the initial observations the previous night, and one of the moths observed from that initial set of observations appears to have survived. Riley donated his very large insect collection to the United States National Museum of Natural History (Smithsonian Institution), where it became the nucleus for the creation of the Department of Entomology. Among his yucca moth specimens is one female *Tegeticula yuccasella* (Riley) specimen labeled "found in Yucca flower—Engelm. June 12/72" (Fig. 1). This date coincides with that of Engelmann's original observations at the Missouri Botanical Garden, and is obviously a moth given to Riley by Engelmann. Although this would have been an obvious candidate for holotype, it is not. Riley, a driven and opinionated worker, never bothered to designate or label type material for any of the many species that he described, but instead would mention in his descriptions the number of specimens used for the description (Davis, 1967). A lectotype having already been designated for *T. yuccasella,* the surviving moth from Engelmann's original observations has now been labeled to indicate its historical significance.

Charles Riley was to dominate the field of yucca moth studies up until his sudden death in 1895, despite this being a sideline in his job as the first federal entomologist (Sorensen, 1995). One of his most important contributions was his involvement in the salvation of the French wine industry (Smith, 1992). I mention it here because it indicates Riley's general understanding of the process of plant-insect coevolution. By the early 1870s, North American grape phylloxera aphids (*Daktulosphaira vitifoliae* (Fitch)) accidentally introduced in central Europe caused massive mortality of European grape cultivars by attacking their roots. Riley (1871) reasoned that American *Vitis* species had coevolved with phylloxera, and thus might tolerate them better. A grafting program with European cultivars and American roots proved highly successful in reducing phylloxera impact, and carried the industry to financial survival; Charles Valentine Riley may be the only individual to have received the French Legion of Honor for contributions to coevolution.

An extraordinary observer and able thinker, Riley unfolded the basic natural history of the plant-moth mutualism and documented the life histories of the pollinator *Tegeticula yuccasella* and the bogus yucca moth *Prodoxus decipiens* Riley within a decade of the initial discovery (Riley, 1880, 1881). In contrast to the records of most of his contemporaries, there are very few inaccuracies in his accounts, simply because of his reliance on empirical observation. In this, he arguably belonged in the exclusive group of exceptional naturalists with whom he regularly corresponded, such as Charles Darwin, Alfred Russell Wallace, Henry Walter Bates, Thomas Belt, Fritz and Hermann Müller, and Asa Gray. As one of the early protagonists of evolution by natural selection in the United States, Riley went beyond natural history to use the relationship between the yuccas and the moths in discussing more general issues such as mimicry and animal pollination (Riley, 1871, 1892).

The relationship between yuccas and yucca moths, characterized in an 1877 letter from Charles Darwin as "the most remarkable example of fertilisation ever published" (Burkhardt & Smith, 1994), drew the attention of many other naturalists in the first 15 years after the discovery. Riley was challenged on numerous occasions regarding the accuracy of his observations. This included the argument from P. C. Zeller, a German entomological authority whose experience with yucca moths was limited to three pinned specimens given to him, that it was simply too improbable to be true (Zeller, 1875: 340–342). Others charged not only that Riley was incorrect but that the very phenomenon of insect pollination was a dubious notion in the first place (Boll, 1876; Meehan, 1876); Boll went on to state that active pollination "belongs in the land of fables." Yet other critics challenged that his arguments about exclusivity of moths in pollinating yuccas were overstated (e.g., Hulst, 1886). Riley responded to his critics with experimental results, not always published in full, often with a singularly sharp pen (Davis, 1967). A prolific writer, with some 2400 entries in his bibliography (Ho & Yuille, 1990), Riley used the empirical data as he knew them to rebut and often scold his critics (e.g., Riley, 1877, 1881, 1887), and occasionally even stooped to ridicule.[3]

Following Riley's death, a hiatus arose in the empirical study of the association. Trelease worked with Riley on behavioral and botanical aspects, performing extensive fieldwork, and published detailed observations on pollinator behavior as well as plant morphology and systematics in his works (Trelease, 1893, 1902). Considerable collections of both moths and plants were made by Susan McKelvey for her monographs on southwestern *Yucca* (McKelvey, 1938, 1947). Busck (1947) attempted a reassessment of moth-plant associations based on McKelvey's insect material; his conclusions when correct generally followed those of Riley, but Busck misinterpreted morphological variation that he was the first to document among pollinator yucca moths, cheater yucca moths, and bogus yucca moths.

Since the 1960s, information about the association has accrued at an accelerating pace from several lines of investigation. This includes systematic and phylogenetic studies of the organisms, as well as the ecological and evolutionary studies of the interactions between the moths and the plants.

NATURAL HISTORY

ORGANISMAL DIVERSITY

The yuccas. The yuccas are part of the North and Central American family Agavaceae (Fig. 2). Recent data suggest that the sister group of Agavaceae may be the small family Camassiaceae, confined primarily to mesic habitats of western North America with the exception being one species in eastern North America (Pfosser & Speta, 1999).

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[3] V. T. Chambers, an amateur lepidopterist, mistakenly used the first non-pollinating bogus yucca moth to challenge Riley's description of pollinator yucca moths (Chambers, 1877). In a rebuttal, Riley (1880) untangled the confusion and used Chambers's moth to erect the new genus *Prodoxus* (Gr., "judging of a thing prior to experience").

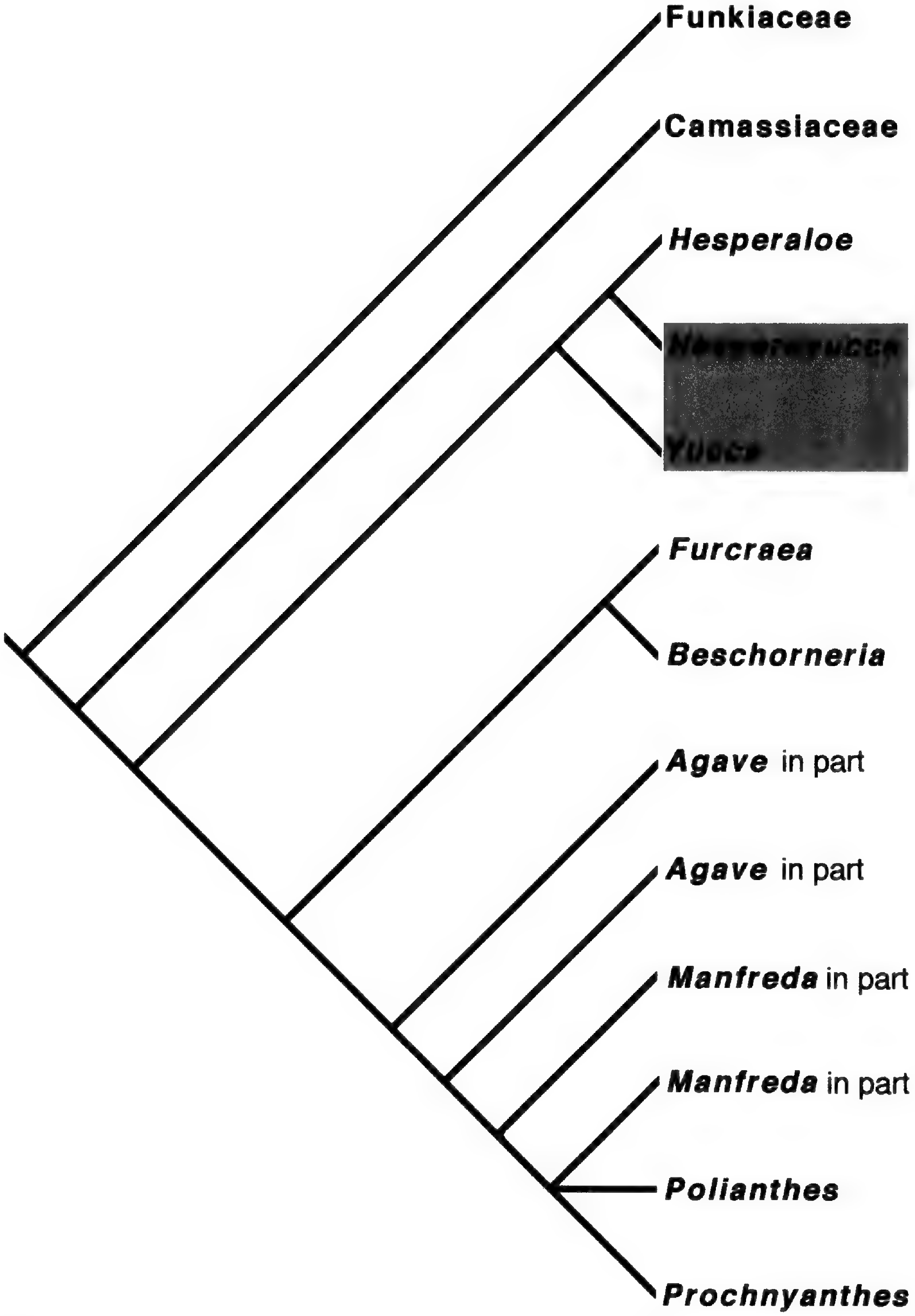

Figure 2. Tentative genus-level consensus phylogeny for Agavaceae and its sister families, adapted from Pfosser and Speta (1999), Bogler and Simpson (1996), and Eguiarte et al. (2000). The only two genera pollinated by prodoxid moths are indicated by gray box.

Generic-level relationships are partly unresolved within the family, but are robust among the taxa involved in the obligate mutualism with yucca moths (Bogler & Simpson, 1996; Clary, 1997). The monobasic *Hesperoyucca*, originally described as a distinct subgenus based on such features as a capitate stigma (Engelmann, 1871), was long considered a section within *Yucca* (Baker, 1986). Recent analyses show *Hesperoyucca* to be the sister group of *Hesperaloe*, a small genus of the Sonoran and Chihuahuan deserts (Bogler & Simpson, 1996). Importantly, *Hesperaloe* taxa are not associated with the yucca moths, and instead rely on hummingbirds (Pellmyr & Augenstein, 1997) and probably bats (Engard, 1980) for their pollination. Jointly, *Hesperoyucca* and *Hesperaloe* constitute the sister group of all remaining yuccas (Bogler & Simpson, 1996).

Yucca is divided into three sections: spongy-fruited section *Clistocarpa*, the fleshy-fruited section *Sarcocarpa*, and the capsular-fruited section *Chaenocarpa*. Section *Clistocarpa* consists solely of *Yucca brevifolia* Engelm., whereas the two other sections consist of no more than 20 to 25 species each (Clary, 1997). Section *Clistocarpa* is characterized by the single autapomorphy of a thickened exocarp, as observed by Trelease (1893). Its position relative to the other yuccas is uncertain but possibly tied to the series *Rupicolae* of capsular-fruited species (Clary, 1997). The longstanding interest in yuccas and their importance in many biological communities notwithstanding, *Yucca* taxonomy and systematics remain in a state of flux, with much need for a modern revision. Revisionary work is complicated by the relative scarcity of herbarium material, caused in part by the logistic problems of preparing specimens from these large, succulent plants. Horticultural interests in the group also have contributed to a plethora of names, with many taxa narrowly delineated using in effect a typological species concept (sensu Mayr, 1963). Observed variation frequently has been attributed to assumed hybridization and introgression (e.g., McKelvey, 1938, 1947; Webber, 1953), but this should be considered speculation as there is only one example where genetic evidence for introgression between two yucca species is provided (Hanson, 1992). Phylogenetic analyses are limited thus far, but appear not to violate assumptions of monophyly of both section *Sarcocarpa* and section *Chaenocarpa* (Clary, 1997). The use of horticultural material or yucca cultivars of unknown origin in some studies may contribute to historical confusion about relationships.

The *Hesperoyucca–Hesperaloe–Yucca* clade is native to North America (Fig. 3), and its contiguous range has been extended into Central America and northern South America through the cultivation of *Y. elephantipes* Regel for their edible flowers (Trelease, 1902; Matuda & Piña Lujan, 1980). Several species have been in cultivation on other continents, including in Europe since the late 1500s (Gerarde, 1633), but yucca moths have never been found either south of Mexico or on other continents. Riley (1881) attempted to establish them by sending batches of pollinator larvae in their cocoons to Darwin and Stainton in England, Planchon in France, H. Müller in Germany, and Asa Gray in Massachusetts, for establishment on cultivated yuccas. Müller (1874) reported that moths hatched, but no local ornamental plants were in flower. Darwin had no yuccas in cultivation, and forwarded his cocoons to Joseph Hooker at Kew, where their subsequent fate is unknown.

The two larger *Yucca* sections, section *Sarcocarpa* and section *Chaenocarpa*, have wide ranges that overlap in areas north and south of the border of Mexico and the United States (Fig. 3). The fleshy-fruited section *Sarcocarpa* is primarily southern, ranging throughout the Megamexico-1 biogeographic region of Rzedowski (1993), and extending in one species northward to southern Colorado. The aberrant *Y. aloifolia* L. occurs in the northern Caribbean and along the U.S. Mexican Gulf and southern Atlantic coasts; it reproduces vegetatively but is not known to have a native pollinator. Its origin is unclear, and I will return to it later. The capsular-fruited yuccas are more northern in distribution, ranging from the northern edge of the Great Plains in southern Canada southward to the Mexican High Plains.

Whereas yuccas generally are associated with shrub desert, chaparral, or grasslands, many Mexican species often grow in pine-oak woodland (Matuda & Piña Lujan, 1980; Gentry, 1982). Packrat midden data from the Wisconsin glacial show that species such as *Y. rostrata* Engelm. ex Trel. that currently inhabit shrub desert grew in pine-oak woodlands in areas such as the Big Bend region of Texas during wetter periods (Van Devender, 1990). The most unusual habitats are those of the southernmost yuccas, *Y. elephantipes* and *Y. lacandonica* G. Pompa & Valdés. Both occur in rainforest, with the former having a terrestrial habit whereas the latter is epiphytic or epilithic (Matuda & Piña Lujan, 1980; C. Beutelspacher, pers. comm.).

The yucca moths. The yucca moths belong to the Prodoxidae, a basal family within Lepidoptera of 78 described species (Davis, 1998; Pellmyr, 2002) and at least 15 additional undescribed spe-

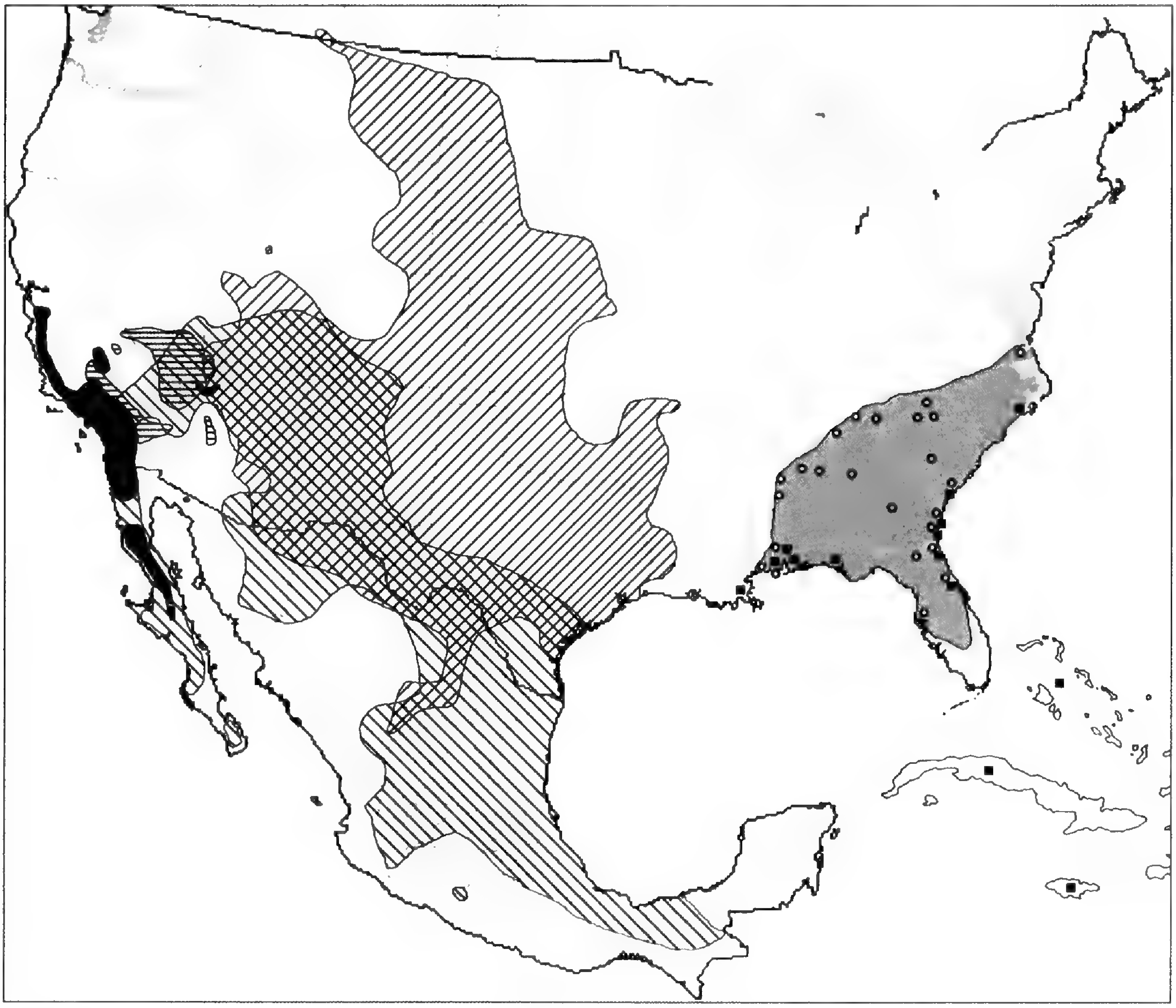

Figure 3. Approximate limits of natural distributions of *Hesperoyucca* and the sections of *Yucca*. *Hesperoyucca*, dark gray (California, Baja California, Arizona); *Yucca* sect. *Clistocarpa*, horizontal lines; section *Chaenocarpa*, diagonal positive-slope lines and medium gray; and section *Sarcocarpa*, diagonal negative-slope lines and black squares (latter along southeast U.S. coast). Only published collection records from the wild, herbarium records from UNAM and MO, and a few records from J. A. Powell and my own fieldwork were included to avoid complications of extensive cultivation and escape. Published sources used were Engelmann (1873), McVaugh (1983), Mohr (1901), McKelvey (1938, 1947), Moss (1959), Steyermark (1963), Powell and Mackie (1966), Great Plains Flora Association (1977), Rowlands (1978), Matuda and Piña Lujan (1980), Turner et al. (1995), and García-Mendoza (1998). Special procedures were made for *Y. filamentosa* and *Y. aloifolia*. *Yucca filamentosa* (s.l.) has been naturalized by European settlers across the eastern U.S. and into adjacent parts of Canada, so I only used records from the oldest comprehensive published sources (Engelmann, 1873; Mohr, 1901; Trelease, 1902) to establish a conservative range (medium gray in southeastern U.S.; open circles give actual sites). For *Y. aloifolia* (black squares), the same sources plus Britton and Millspaugh (1962) were used; for records from the Antilles (Trelease, 1902), specific locations and circumstances of each collection are unknown. Land areas south of Mexico have been excluded.

cies (Frack, 1982; Nielsen, 1982; Pellmyr & Balcázar-Lara, in prep.). The sister family Cecidosidae consists of gall-makers feeding mostly on Anacardiaceae (Nielsen, 1985), and it shows a typical Gondwanan distribution. The presence of sister genera in Africa and South America of these moths, which are highly sedentary, strongly indicates an origin of this family, and by inference the Prodoxidae, before the South Atlantic breakup 95–100 million years ago (Pellmyr & Leebens-Mack, 1999).

Morphological (Nielsen & Davis, 1985) and molecular data (Brown et al., 1994; Pellmyr & Leebens-Mack, 1999) together suggest that the monobasic *Prodoxoides*, the only southern hemisphere prodoxid moth, is the basal genus in the family (Fig. 4). *Greya* is a diverse genus of boreal and temperate humid to semiarid areas of western North America (Davis et al., 1992), with the exception of a few basal members recently documented from easternmost Asia (Kozlov, 1996). *Tetragma* is confined to North America, whereas the large genus *Lampronia* is holarctic in distribution. These gen-

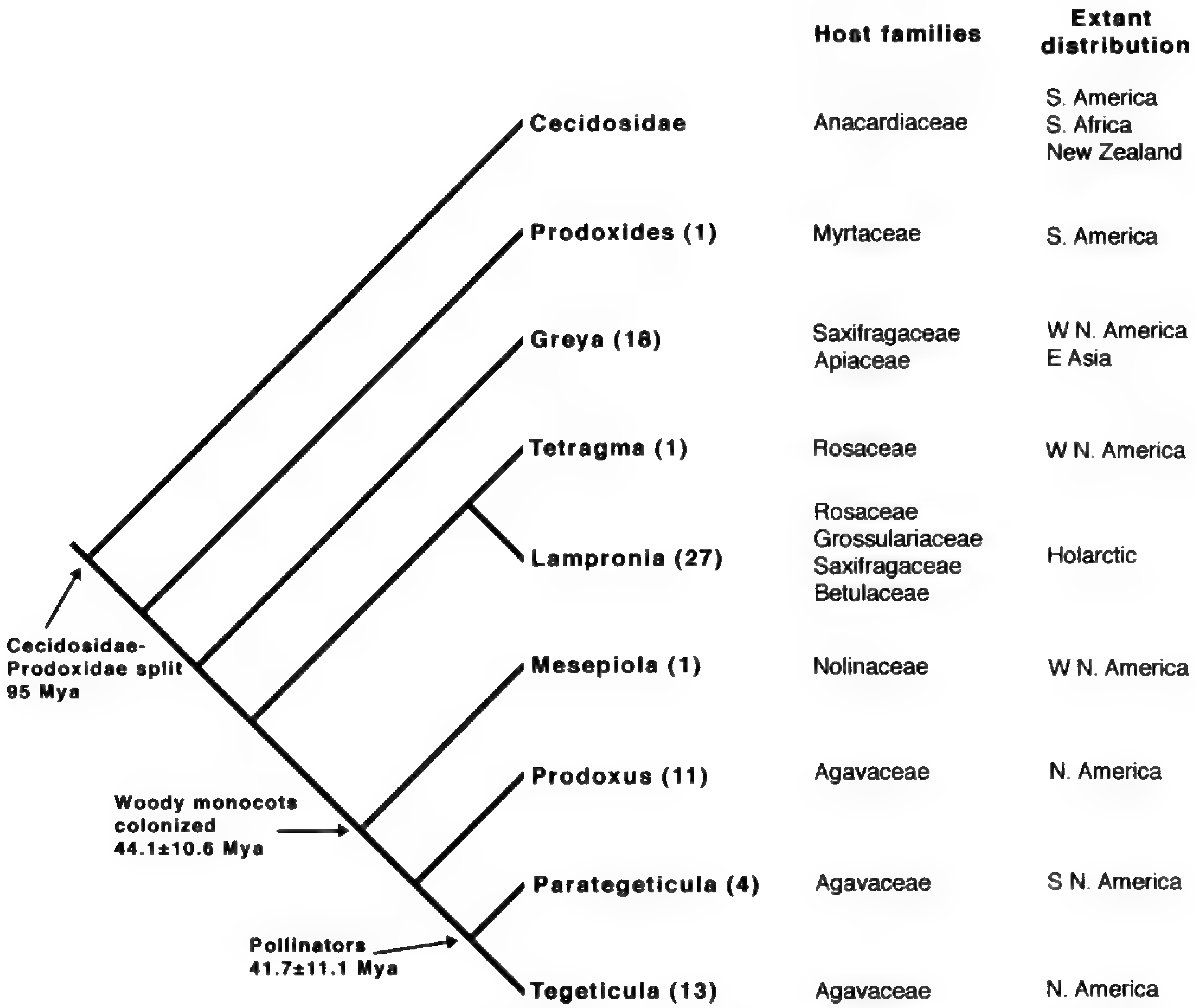

Figure 4. Genus-level phylogeny for Prodoxidae, based on mtDNA and morphological data, with information on plant host families and extant distribution. Estimated minimum dates for seminal events and trait origins are based on a molecular clock, calibrated based on biogeographic data from the sister family Cecidosidae. Tree information and dates from Pellmyr and Leebens-Mack (1999). Numbers in parentheses are numbers of described species.

era use a remarkable variety of host plants, including species of the Myrtaceae, Apiaceae, Rosaceae, Grossulariaceae, and Saxifragaceae, i.e., representatives from four plant orders (APG, 1998). In cases where immature stages are known, the larva feeds inside plant tissue during early instars, and then from the outside while concealed inside folded leaves or cases during the final instars of development (Davis, 1987; Davis et al., 1992).

Colonization of woody monocots, first observed in *Mesepiola*, coincides with colonization of arid habitats and a concurrent change in life habit to having larvae that feed inside host tissue until feeding is complete (Davis, 1967; Frack, 1982). *Mesepiola* feed on members of Nolinaceae, whereas the three yucca moth genera *Prodoxus*, *Parategeticula*, and *Tegeticula* feed on members of Agavaceae. *Prodoxus* (the "bogus yucca moths" of Riley (1880)) coexist with the two other genera, but feed on tissues other than the seeds. They are not involved in pollination. Virtually all yuccas host *Prodoxus* species that feed inside the inflorescence scape, and most fleshy-fruited and spongy-fruited yuccas also host species that feed inside hardening galls in the exo- or mesocarp portion of the fruit. The recently described *Prodoxus phylloryctus* Wagner & Powell is so far unique within the genus in feeding as a communal gall-maker in fleshy yucca leaves (Wagner & Powell, 1988). In addition, the peduncles of at least six *Agave* species are used (Frack, 1982) by some *Prodoxus* species. I will not deal with them further here, as they are not directly involved in the pollination mutualism.

The pollinating yucca moths belong in the genera *Parategeticula* and *Tegeticula*. *Parategeticula*, with four described species (Pellmyr & Balcázar-Lara, 2000), is unique in having lost the linear cutting ovipositor of prodoxid moths used for inserting eggs into plant tissue, and instead their thick blunt ovipositor is used in creating a groove on the surface where eggs are laid (Davis, 1967; Powell, 1984). In species with known biology, they also differ in that the larva bores into the young fruit, where it causes the formation of a gall-like structure ("cyst" of Powell, 1984) formed from modified placental tissue and a few immature seeds that in effect fuse and are consumed from within. *Tegeticula* was until recently held to consist of three species (*T. maculata* (Riley), *T. synthetica* (Riley), and *T. yuccasella*) with broadly similar life histories (Baker, 1986). Morphological variation had long been reported within *T. yuccasella* but considered as intraspecific variation (Busck, 1947; Davis, 1967); Davis (1967: 53) stated that more than one "biological entity" may exist, but refrained from delimitation on the grounds of insufficient information. Miles (1983) used morphometric data to demonstrate the presence of at least three unnamed host-specific entities. Further studies using morphological and molecular tools have so far led to the description of 13 species (Pellmyr, 1999), and several additional taxa remain to be described (Pellmyr & Balcázar-Lara, in prep.). *Tegeticula maculata* is morphologically and molecularly highly divergent and may well consist of several biological species (Powell & Mackie, 1966; Segraves & Pellmyr, 2001), and *T. synthetica* as currently circumscribed contains two species (Pellmyr, in prep.). All species consume seeds as larvae, but there is variation in oviposition timing and location. Pollinators oviposit at the time of flowering, but *Tegeticula* species, sometimes referred to as "cheater yucca moths," delay oviposition to the fruit stage and have independently lost the behavioral and morphological traits of active pollination (Pellmyr et al., 1996a; Pellmyr & Krenn, 2002). Intrageneric phylogenetic information for *Parategeticula* and *Tegeticula* is relatively well established (Pellmyr & Leebens-Mack, 2000), with the major remaining uncertainties revolving around a rapid burst of radiation creating most lineages within the *T. yuccasella* complex and the inclusion of remaining undescribed species primarily from the southern portion of the range. A note of caution about older publications involving the moths of the *T. yuccasella* complex is indicated: because of the historical lumping, many studies must be interpreted very cautiously and are sometimes of little value, as studied species are not identifiable and because as many as three coexisting species may have been treated as one.

Basic ecology of the plant-pollinator interactions. There is considerable variation in the ecological aspects of interactions among both yuccas and the moths, and here I only outline major shared elements. The female yucca moth of both pollinator genera is equipped with unique tentacular mouthparts that she uses for pollen handling (Riley, 1892; Davis, 1967; Fig. 5A). She collects pollen from yucca flowers by dragging her tentacles across the anthers. The pollen is embedded in copious pollen kitt, almost to the point of floating in a semiliquid matrix in *Hesperoyucca*, and often comes off as a unit from the anther. The moth compacts the pollen using the tentacles, and then stores it as a batch underneath her head (Fig. 5A, B). The pollen is kept in place by adhesion alone, and the tentacles play no part in holding it in place. This load can be substantial, reaching nearly 10,000 grains in *Tegeticula yuccasella* females, and constituting nearly 10 percent of the moth's body weight (Pellmyr, 1997). Pollen collection can recur on an occasional basis during the active life of the female, so her pollen load may consist of multiple pollen genotypes. Following pollen collection, the female seeks out flowers of her host species for the purpose of finding suitable oviposition sites. Under most circumstances, only first-night flowers tend to be accepted but under some circumstances older flowers may also be subject to oviposition (Riley, 1889). In *Tegeticula*, the female first walks around the ovary, and her decision whether to oviposit is influenced not only by the flower itself but at least in some species also by its visitation history (Addicott & Tyre, 1995; Huth & Pellmyr, 1999). In *T. yuccasella*, females deposit a host-marking pheromone during oviposition, and subsequent visitors perform a crude estimation of pheromone quantity (Huth & Pellmyr, 1999). Visitors become increasingly unlikely to accept a flower with increasing number of prior visits. In one case of two coexisting pollinators, one species responded to visitation history whereas the other made oviposition choices independent of number of prior visits (Addicott & Tyre, 1995). If the female decides to oviposit, she positions herself in a species-specific location on the ovary and cuts into it (Fig. 5C). Most species penetrate the ovary wall and lay eggs inside the locule, but a few species oviposit very superficially under the epidermis. The female then uses the tips of her tentacles to scrape off a small amount of pollen from her batch, walks up to the stigma, and places the pollen on the papillose internal surfaces of the perforate style using a series of 10–20 bobbing movements (Fig. 5C, E). The only exception in this regard is *T. maculata*, which pollinates the capitate stigma of *Hesperoyucca whipplei* Torr. using the same scraping behavior as is used for pollen col-

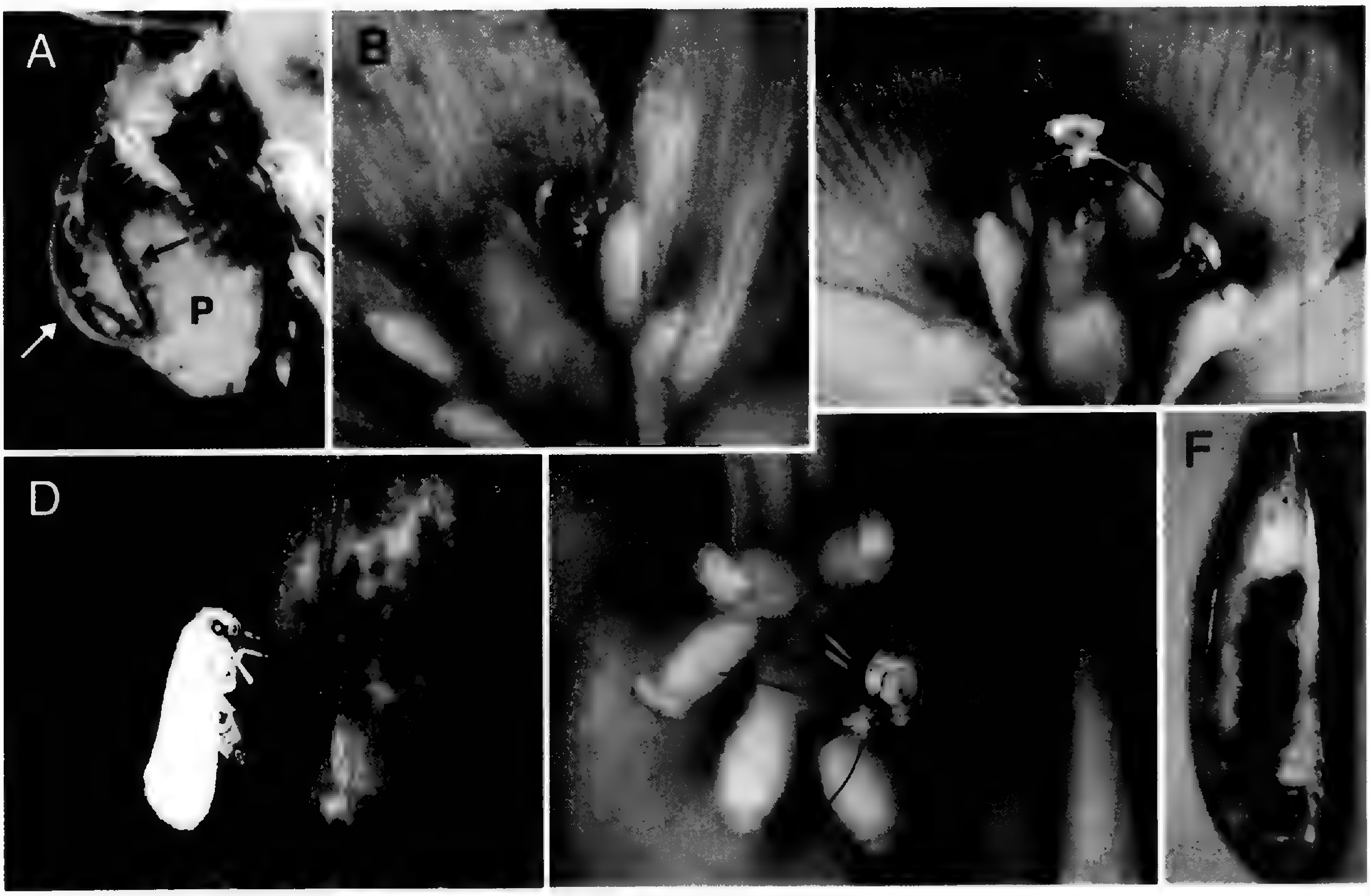

Figure 5. —A. Head of *Tegeticula carnerosanella* female. Large pollen load (P) held below the head, with left tentacle and proboscis indicated by black and white arrows. Cross section of tentacle 1.0 mm. —B. Female *T. yuccasella* compacting pollen just collected from a *Y. filamentosa* stamen. —C. Females of *T. yuccasella* pollinating (top) and ovipositing into (right) a *Y. filamentosa* ovary. —D. Female *T. intermedia* ovipositing into a ca. 8-day-old *Y. filamentosa* fruit; note constriction caused by *T. yuccasella* ovipositions. —E. *T. treculeanella* female pollinating *Y. treculeana* Carrière flower. Moth wing length in panels B–E 10–11 mm. —F. Longitudinal section through locule of mature *Y. carnerosana* (Trel.) McKelv. fruit, showing feeding path of *T. carnerosanella* larva that has destroyed seven seeds; fruit length 73 mm. For a set of color pictures of *T. yuccasella* behavior on *Y. filamentosa*, see Murawski (1997).

lection. A female may repeat oviposition and pollination many times on a flower, especially if she started on a virgin flower. In *T. yuccasella*, pollination almost invariably happens following the first oviposition on a flower, but females then become increasingly likely to skip pollination during subsequent oviposition bouts, and they also deposit less pollen per pollination event (Huth & Pellmyr, 1999). Females of the species that encounter a flower visited by one other female first typically perform about half as many ovipositions and pollinations as the first female (Huth & Pellmyr, 1999), and a smaller yet significant reduction was observed in *T. altiplanella* Pellmyr (Addicott & Tyre, 1995, referred to as "deeps"). Once a female moves on, she usually walks to adjacent flowers and inspects them for suitability, then visits other side branches, and eventually she flies off to other inflorescences. Consequently, females perform both geitonogamous and xenogamous pollinations (Riley, 1892; Fuller, 1990; Dodd & Linhart, 1994; Pellmyr et al., 1997; Marr et al., 2000); there is no experimental evidence of plant self-incompatibility and fruit set readily occurs following both types of pollination, but selfed fruits are highly susceptible to abscission when they develop in competition with outcrossed fruits (Pellmyr et al., 1997; Richter & Weis, 1998; Huth & Pellmyr, 2000).

Eggs of *Tegeticula* hatch within a few days, and larvae of species that lay eggs inside the locule start feeding on seeds immediately. In species that oviposit superficially, the larva first burrows in the ovary wall before entering the locule to feed on seeds (Wilson & Addicott, 1998; Pellmyr & Leebens-Mack, 2000). Larvae consume a variable number of seeds (Fig. 5F), depending on the species and factors such as the presence of abortive seeds that can reduce per capita consumption (Powell, 1984; Ziv & Bronstein, 1996; Bronstein & Ziv, 1997). Upon completion of feeding, the larva creates an exit path. It preferentially exits during rain, either night or day (Whitten, 1894), but perhaps more commonly at night (Groman & Pellmyr, unpublished data), and can spend extended time waiting inside the fruit for optimal conditions (Powell & Mackie, 1966). The larva burrows into the ground, where it creates a silk-lined cocoon covered with soil or sand particles. The exact location in the ground has never been reported, but from lab trials Riley (1873) reported depths of 7.5–10 cm and Rau (1945) 2.5–7.5 cm for *T. yuccasella* and perhaps also *T. intermedia* Pellmyr. Powell (1984) reported depths of 1–3 cm in shallow containers for *T. maderae* Pellmyr. The larvae of five *Tegeticula* species (*T. yuccasella, T. intermedia, T. cassandra* Pellmyr, *T. treculeanella* Pellmyr, *T. carnerosanella* Pellmyr) reared in my lab commonly created their cocoons at a depth of 20 cm where they reached the impenetrable bottom of the rearing canisters. The variation in reported depths among *Tegeticula* species may at least in part reflect depth of rearing canisters.

The larva enters diapause inside the cocoon and pupates a few weeks before emergence. This may happen after a one-year diapause, but the larvae can remain in diapause in lab conditions for at least four years (Riley, 1892). Very high fruit set during mass flowering episodes in yucca populations that then effectively cease flowering almost completely for several years (Pellmyr, unpublished data) suggests that the moth larvae are capable of diapausing for several years in the field as well, and that there are unidentified cues that trigger completion of development and adult moth emergence. This is not to suggest that moth emergence is perfectly synchronized with host flowering—we know it is not (Frack, 1982)—but rather that a sufficient number has remained in diapause to emerge at the time of mass flowering to cause high levels of pollination.

The life history of *Parategeticula* is known in less detail than that of *Tegeticula*, but oviposition and larval biology of one species, *P. pollenifera* Davis, has been described in detail by Davis (1967) and especially Powell (1984). The most obvious difference is that *Parategeticula* females oviposit on pedicels and in petals, rather than into the ovary. In this case, the larva chews its way into the ovary, and then proceeds to feed on partly modified seeds as described above. Larvae of *P. pollenifera* pupated at 1–3 cm in shallow containers (Powell, 1984), and *P. elephantipella* Pellmyr & Balcázar-Lara formed their cocoons at 2–4 cm depth in 15 cm of loose soil (Pellmyr & Balcázar-Lara, 2000). *Parategeticula pollenifera* from southern Arizona invariably required two years to complete development (Powell, 1984), whereas the tropical *P. elephantipella* emerged in the lab without a diapause (Pellmyr & Balcázar-Lara, 2000).

Patterns of host specificity. In the traditional recognition of four species of pollinating yucca moths, three species were monophagous and the fourth species (*T. yuccasella* s.l.) was held to pollinate all other yuccas. This appeared somewhat paradoxical, as most phytophagous insects show relatively high levels of host specificity (Ehrlich & Raven, 1964; Price, 1980; Farrell & Mitter, 1993; Thompson, 1994), especially when the phenological window for the insect to successfully oviposit is very narrow. Yucca moths, which only live for a few days (Kingsolver, 1984; Powell, 1984), must access the plant during the short flowering period, so moth populations would have to be locally adapted for the flowering periods of different hosts. For example, in areas such as the Big Bend region of the Chihuahuan desert, four yucca species coexist and have largely non-overlapping flowering periods spread out from February to early June. If a single pollinator species were to utilize all four species, this would require intraspecific polymorphism in emergence phenology with four distinct peaks in the moths. Busck (1947) and Davis (1967) speculated that *T. yuccasella* may be a complex, but suffered from a dearth of material available for study. The first solid data supporting the hypothesized complex were provided by Miles (1983), who showed that the pollinators of three sympatric yuccas in southern New Mexico differed greatly in morphology. She described the entities but did not formally name them. Addicott (1996) likewise provided morphometric data suggesting the existence of several more host-specific species, and Pellmyr et al. (1996a) provided molecular phylogenetic data indicating the presence of a large complex. Thirteen species, including eleven pollinator species, have since been described (Pellmyr, 1999).

Given the revised moth species delineation, diet breadth among the pollinators is now more uniform (Fig. 6). Using the yucca species delineations used in Pellmyr (1999), members of the *T. yuccasella* complex have been recorded from 17 host species. Seven of the eleven pollinator species within the complex are monophagous, one has two hosts, two have three hosts, and one has six recorded hosts. Thus more than 70% of all pollinator taxa are monophagous, and the most oligophagous species uses six host species. The reason for this level of specificity remains to be explored, but certainly involves phenological specialization on hosts and probably also selection for specialization on plants with critical differences in ovary morphology. Interestingly, the two derived non-pollinating yucca moth species are known to use four and six hosts, respectively, giving them a significantly broader host range than the pollinators with which they coexist (Kruskal-Wallis test, $\chi^2 = 5.68$, $p = 0.017$). Proximal rea-

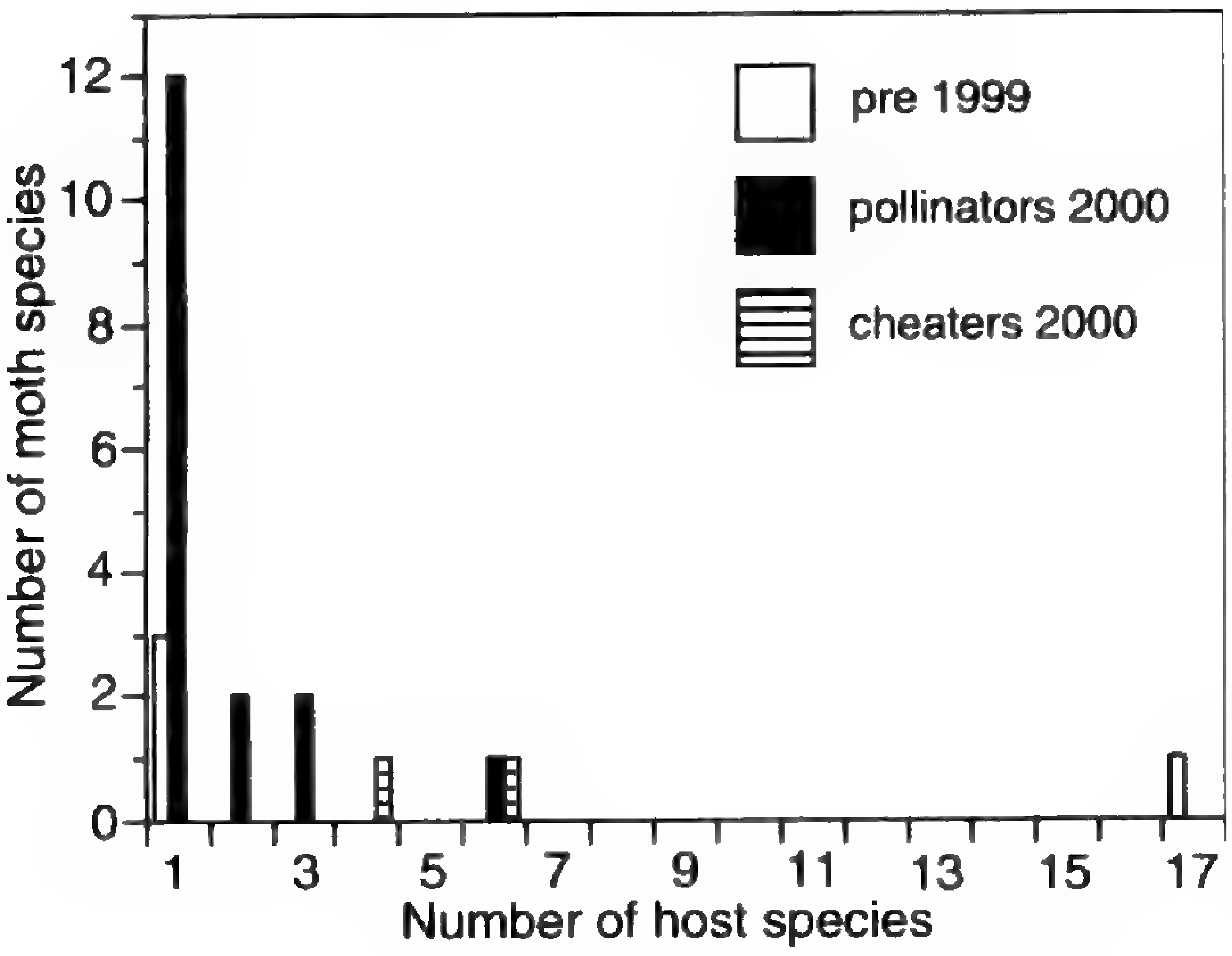

Figure 6. Number of recorded hosts of described *Tegeticula* and *Parategeticula* species. The two open bars give data for the four species recognized before 1999. Black bars give number of hosts for described pollinator species and striped bars derived non-pollinator species as of 2000. Cheater species have significantly more hosts per species than pollinator species (Kruskal-Wallis test, χ^2 = 5.68, p = 0.017).

sons for the wider diet of non-pollinators remain to be explored. Because the non-pollinator larvae feed on seeds side by side with pollinators, diet is an unlikely explanation, but plausible hypotheses to test include a broader phenological window for species that oviposit into fruits, oviposition modes that are less likely to select for specialization, or higher potential for establishment on novel hosts through colonization because of limited resource competition with resident pollinators (Pellmyr & Leebens-Mack, 2000; Marr et al., 2001). Alternatively, it may reflect species age; because the non-pollinators are among the younger species in the complex, they have simply had less time available for potential diversification through host specialization.

The role of copollinators of yuccas. Suggestions of pollinators other than yucca moths appeared shortly after the original description of the plant-moth interaction, and this argument has resurfaced in the last decade, leading one monographer to the unfounded conclusion that "when moth populations are low, the fly *Pseudocalliope* may be an important alternate pollinator [of yuccas]" (Verhoek, 1998). For this reason, it is worth revisiting the support for this untested hypothesis.

I will discuss first all species other than *Yucca aloifolia*, which is a special case in this regard. The earliest claim of copollinators was made by Meehan (1879), who presented fruits resulting from geitonogamous hand-pollination on a cultivated *Y. glauca* Nutt. as evidence that other animals could serve as pollinators. In the absence of hand-pollination, however, no fruit set occurred. Hulst (1886) was the first to use the fallacious argument of abundance of a particular visitor as evidence of pollinator function when stating that honey bees (*Apis mellifera* L.) can be copollinators. Frustrated with such untested hypotheses presumed to be true, Riley used a range of experimental and observational approaches to gather data to test them. Whereas he presented his conclusions in print (Riley, 1887, 1889, 1892), the original data were never published. Tabulated result sheets found in the archives of the Missouri Botanical Garden showed that inclusion experiments using two of the most common flower visitors, *A. mellifera* (25 bees, 72 hr.) and the soldier beetle *Chauliognathus pensylvanicus* de Geer (Cantharidae) (36 beetles, 24 hr.), in separate gauze bags containing single *Yucca filamentosa* L. inflorescences failed to result in any fruit development, whereas control inclusion experiments with yucca moths caused fruit production. Riley (1889, 1892) and Trelease (1893) further argued against copollinators on the basis of extensive visitor behavior observations. For example, honey bees were found to mostly lap the floral exterior for water and honeydew exudates, and when inside the flower probed the ovary base far away from the stigma. Similarly, other visitors also rarely moved close to the stigma. Riley (1881, 1892) also emphasized that plants in areas without moths, for example where plants recently had been put into cultivation, never had been found to set fruit, even though a wide array of other insects were found on the flowers. He also noted that in areas where an introduced yucca species coexisted with a native, moth-inhabited species with different flowering phenology, fruit set was never observed, whereas rare flowering coincidence of individual plants with a native yucca had been known to result in fruit set.

Speculation about copollinators was raised anew by Dodd and Linhart (1994). A lauxaniid fly (*Pseudocalliope* sp.) found in abundance on *Yucca glauca* flowers, with some individuals found to carry modest quantities of pollen on their bodies, was suggested as a possible vector. No attempt was made to test experimentally whether the flies cause pollination. There is reason for skepticism, because, as Riley (1892) first pointed out, lack of fruit set is common in yucca populations for a variety of reasons, yet flower visitors other than moths are often common in those same populations. Further, even if occasional modest pollen transfer were to take place through visitors other than the moths, it would likely be of little or no ecological and evolutionary significance. This follows because flowers that receive small pollen loads or self pollen are highly susceptible to selective abscission (Richter & Weis, 1998; Huth & Pellmyr, 2000); thus a poor vector is expected to contribute minimally to plant fitness. The century-old hypothesis about existence of copollinators could readily be settled by the proper experiments. A simple experimental approach could exploit the size differences between yucca moths and proposed copollinators by using selective screens that permit entry to smaller visitors (such as the lauxaniid fly) but exclude the larger *Tegeticula* moths; this approach worked well in determining contributions to pollination by flies and bumblebees selectively screened on *Trollius europaeus* (Pellmyr, 1989). Given very high levels of genetic diversity in yuccas (Feist, 1995; Massey & Hamrick, 1998), routine genetic analyses of any resulting seed progenies could also provide information about selfing and outcrossing rates.

Yucca aloifolia is the single exception to the lack of evidence for pollinators other than the moths. Introduced as a garden plant in Europe no later than 1596, in Australia by 1885, and in Melanesia by 1880, it has been reported on several occasions to set fruit in locations outside North America even though there never have been any coincident moth reports. For example, Engelmann (1873) saw fruiting plants in Italy, Layard (1880) in gardens of New Caledonia on what undoubtedly was *Y. aloifolia* (MacKee, 1994), Riley (1891) conveyed a report from Australia, and Galil (1969) reported fruit set in a cultivated plant in Israel. The plant historically was scattered along the southeastern North American Atlantic and Gulf coast, especially along sandy shores from central North Carolina to eastern Louisiana (Fig. 3). Occasionally plants set fruit in parts of that range, typically as a result of colonization by *Tegeticula yuccasella* and *T. cassandra* from coexisting and simultaneously flowering *Y. filamentosa* (Engelmann, 1873; Riley, 1873; Pellmyr, 1999), but fruiting plants without oviposition scars or larval damage have also been reported (Riley, 1892; Groman, 1999). Riley hypothesized from floral structure that it may have resulted from autogamy, but Trelease (1893) found that he could prevent fruit set by excluding all floral visitors with a gauze bag in a plant that previously had produced fruit. This is the only reported experiment for any yucca that provides even moderate support for other visitors as copollinators. It needs to be replicated with reasonable sample size, and with inclusion as well as exclusion treatments.

The situation is more complex as *Yucca aloifolia* can have fruiting and non-fruiting inflorescences within populations and even individual plants (Pellmyr, unpublished obs.). In sites with moths on other yuccas, it is generally explained by moths visiting only *Y. aloifolia* inflorescences that coincide with those of the native host (Riley, 1892). Elsewhere this cannot be the case. Conceivable explanations include intrapopulational variation in visitor guilds, and possibility of autogamy or geitonogamy, but they are relatively unlikely explanations in the first place, and no observational or experimental data exist to explore these or any other hypotheses. It is also possible that *Y. aloifolia* is under limited selection for maintaining sexual reproduction, as it reproduces very vigorously by vegetative propagation. This happens both through rapid clonal extension and establishment by broken-off plant parts (Brown, 1959); in coastal North Carolina, local residents disseminate the plant by cutting stems in 10-cm pieces that are tossed on the ground in disturbed sandy sites (J. Groman, pers. comm.). This habit of elevated vegetative propagation, absence of an endemic pollinator, core loss in the fruit, and poorly synchronized flowering spread across many months suggest that *Y. aloifolia* may be an escaped cultivar. Described from European gardens, Trelease (1893) referred to it as a species without a known geographical origin, and this is still the case. It is most closely related to *Y. elephantipes* and *Y. lacandonica*, which are tropical forest dwellers along the Gulf side of Mexico from Veracruz to Yucatan and into northern Belize (Matuda & Piña Lujan, 1980; Davidse et al., 1994); within this range, they set fruit through the actions of a specific yucca moth (Pellmyr & Balcázar-Lara, 2000, unpublished data) whereas plants are sterile elsewhere. This is most evident in *Y. elephantipes*, which is widely cultivated throughout Mexico and southward at least to Panama for its comestible flowers. *Yucca aloifolia* has been reported from Mexico (Matuda & Piña Lujan, 1980), but examination of available herbarium collections at UNAM for their records indicates that these refer to cultivated specimens and to *Y. elephantipes* (Pellmyr & Balcázar-Lara, unpublished data). In addition to its distribution along the shoreline of southeastern North America, *Y. aloifolia* is reportedly also established on Cuba, Jamaica, the Bahamas and Bermuda (Trelease, 1902), where pre-Hispanic cultures are suggested to have used its roots for soap (Engelmann, 1873). This use, together with a disjunct geographic range from the remainder of the genus and traits characteristic of cultivated plants, makes plausible a hypothesis that *Y. aloifolia* originated from *Y. elephantipes* as a cultivar selected for its high vegetative propagation. If correct, phylogeographic studies are predicted to show a genetically depauperate *Y. aloifolia* nested within *Y. elephantipes.* This would be an important analysis to perform from the perspective of the plant-pollinator association, as possible corroboration would imply that occasional fruit set in the absence of moths in *Y. aloifolia* is irrelevant to understanding diversification and coevolution of the plant-moth mutualism.

EVOLUTION OF THE MUTUALISM AND ITS ECOLOGICAL CONTEXT

The origin of the mutualism long remained unknown, and was subject to little speculation for more than a century after its initial discovery. Two limiting factors loom important in this context. First, life history differences and variation in outcomes of yucca-yucca moth interactions had yet to be discovered. The interactions between the four historically recognized yucca moth species (Davis, 1967; Powell, 1992) and yuccas were held to be obligate mutualisms, so there was no apparent transformation series to analyze. Second, and perhaps more important in retrospect, the phylogenetic framework of the yucca moths at the family and genus level was not determined until the 1980s (Frack, 1982; Nielsen & Davis, 1985). At that time, life history data also started to appear for the closely related genera of prodoxid moths (Frack, 1982; Davis et al., 1992).

A timeline for establishment of the yucca-yucca moth mutualism. The fossil record is quite poor for these plants and effectively absent for the moths, providing little assistance in dating the establishment and diversification of the plant-pollinator association. The only pre-Pleistocene yucca macrofossil is a 14-My old trunk segment described as *Protoyucca shadishii* Tidwell & Parker from Nevada, most resembling the extant *Yucca brevifolia* (Tidwell & Parker, 1990). Fossil pollen described as *Agave* has been described from the mid Miocene (Axelrod, 1979; Palacios & Rzedowski, 1993). Bremer (2000) used clocklike behavior in *rbc*L to estimate the minimum age of the Funkiaceae, which is the sister family of Agavaceae + Camassiaceae (Pfosser & Speta, 1999), at 21 My, whereas Eguiarte (1995) provided an independent *rbc*L-based estimate for the Agavaceae of 14 My. For the moths, a mitochondrial DNA sequence data set was used to estimate age of their diversification, using biogeographic events for calibration (Fig. 4; Pellmyr & Leebens-Mack, 1999). Colonization of yuccas as a host was estimated at having occurred about 41.7 Mya, with the diversification of the three genera that inhabit yuccas being so rapid that their dates overlap. Importantly, this narrow time window includes the split between the two pollinator genera as well as the most basal split within *Tegeticula* (between *T. maculata* and all other species), showing that the pollination habit was established in a common ancestor very close in time to the colonization of the yuccas by prodoxid moths. Given this rapid diversification of the moth lineages, we can infer that a basal radiation of yuccas was in existence by this mid Eocene date, pre-dating current independent estimates for the plants. For comparison, there is strong molecular data from several fig wasp lineages suggesting that the obligate mutualism between figs and fig wasps had originated by the late Cretaceous, some 90 Mya (Machado et al., 2001).

PATTERNS OF TRAIT EVOLUTION IN PRODOXIDAE LEADING TO OBLIGATE MUTUALISM

The obligate mutualism between the moths and yuccas could have originated either through extensive trait-level evolution, or it could have been precipitated in interactions where only minor quantitative changes in preexisting traits would be required to switch the outcome from antagonism to mutualism. This would happen, for example, by variation in outcome based on ecological context. Studies of the biology of more basal prodoxid moths that do not feed on yuccas lend support for this model of pre-adaptations, and also reveal two separate origins of pollination mutualism between three members of the genus *Greya* and their saxifragaceous hosts (Pellmyr et al., 1996a).

The first studies were made of *Greya politella* (Walsingham), a specialist of several species of *Lithophragma* (Saxifragaceae) (Pellmyr & Thompson, 1992; Thompson & Pellmyr, 1992). The female moth oviposits into the ovary through the tubular hypanthium, and pollen often is transported on an elongated abdominal segment. Experiments showed that oviposition was a highly effective pollination behavior. At study sites in Washington, an extensive guild of copollinators of mostly bombyliid flies and solitary bees also provided cross-pollination. Although none of the copollinator species was as effective per visit as the ovipositing moths, their relative abundance and far higher rate of visitation made them important contributors to pollination in the study population. In two years of study, *G. politella* was estimated to have contributed 0.8–2% of all seed set in the study population. Their positive effect was effectively masked, as there was no significant effect of moth oviposition on net seed set. Their negative effect through larval seed consumption was also masked by other sources of variation in seed production. The outcome of this moth-plant interaction is thus strongly dependent on copollinator contributions, as there will be no selection on moths for improved pollination efficiency unless it is tied to fitness differences. The same result was found for *Greya enchrysa* Davis & Pellmyr, a highly effective pollinator of its hosts in *Heuchera*, where abundant bumblebee visitors masked beneficial effects on seed set (Pellmyr et al., 1996b). In these interactions, variation in outcomes can be expected across the ranges of the species (Thompson & Pellmyr, 1992; Gomulkiewicz et al., 2000), potentially leading to sustained selection for a stronger mutualistic equilibrium between the moths and plants. The third case and second origin of pollination in *Greya* involves *G. mitellae* Davis & Pellmyr, a species whose larvae feed inside the flowering stalk and in leaf peduncles of *Mitella stauropetala* Piper. Moths pollinate while drinking nectar from the flowers. Whereas virtually all pollination was provided by the moths in study populations, no selection on increased pollination efficiency is expected in this interaction as larval fitness is unaffected by the incidental seed production during adult nectaring bouts. This case indicated that there must be a direct link between female pollination efficiency and progeny fitness to cause selection toward increased pollination efficiency and potentially obligate mutualism (Pellmyr et al., 1996a).

Mapping of several life history traits that were necessary prerequisites for the origin of the mutualistic behavior by yucca moths indicated that most traits were basal to prodoxid moths or at least had evolved before the lineage leading to the common ancestor of the pollinator genera. Hence this supported a scenario in which the life habits of prodoxid moths commonly have states that make pollinator function easy to acquire. At the same time, obligate mutualism that requires novel traits for highly effective pollination has only arisen once in the family, in the true yucca moths. Why did this happen in the yucca-yucca moth association, but not in the others? Pellmyr et al. (1996a) used ancestor reconstruction of the yuccas to erect a hypothesis in which highly effective pollination in the moths evolved first, followed by exclusion of ancestral copollinators through effective cessation of nectar production in the plants. A general feature of the Agavaceae is resource-limited fruit set (Sutherland, 1982), where only a minor fraction of all flowers give rise to mature fruit. As prodoxid moths colonized yucca ovaries, they thus encountered a major new mortality factor for their progeny, because all eggs inside pollinated flowers subsequently abscised will perish. Floral abscission is highly selective, with fertilized flowers resulting from small pollen loads or self pollen having a much elevated risk of abscission (Pellmyr et al., 1997; Richter & Weis, 1998; Huth & Pellmyr, 2000). For this reason, variation in pollination efficiency provided by female yucca moths can result in differential abscission of flowers containing moth eggs, as females providing large amounts of pollen decrease the risk of abortion. Importantly, this trait could evolve in the females against a background of relatively inefficient, nectar- and pollen-consuming floral visitors. In a second step, reciprocal specialization in the plants on the increasingly effective yucca moths is expected as the net fitness contributions attributable to the ancestral nectar-consuming visitors relative to energetic investments in the nectar reward became negative. Both selective abscission as a mortality factor and high cost of nectar production were novel traits to the yucca-yucca moth association in the sense that they are not present in the plant-moth interactions immediately basal to it, and they may point to factors that could facilitate similar transitions in other associations. Consistent with this prediction, much reduced nectar production and low fruit : flower ratio are characteristic of the recently described obligate mutualism in the Sonoran desert between the columnar cactus *Lophocereus schottii* and its pollinating moth, *Upiga virescens* (Holland & Fleming, 1999).

REVERSAL OF MUTUALISM

Mutualistic interactions contain an underlying evolutionary conflict in that the interacting partners are under selection for increased exploitation of each other (Trivers, 1971; Bull & Rice, 1991; Pellmyr & Huth, 1994). In a plant-pollinator relationship, this might manifest as selection for higher efficiency in reward extraction among pollinators, and smaller or more inaccessible rewards in the plants. In facultative relationships, such conflicts may result in arms races that shut out excessive exploiters. For example, a decreasingly rewarding plant species may be abandoned by flower visitors that have a choice, while plant traits that reduce losses to poor pollinators in theory can evolve to complete exclusion. In obligate mutualisms that involve a single pollinator and plant, this conflict has a potentially different dynamic. In such instances, the evolution of a cheating mutant with a fitness advantage over mutualist individuals is expected to lead to reciprocal extinction of the mutualists, at least at the population level and possibly on a species scale, depending on patterns of gene flow. For this reason, obligate mutualisms such as those between yuccas and yucca moths were long considered evolutionary dead ends (Soberon Mainero & Martinez del Rio, 1985; Bull & Rice, 1991). This is clearly not the case under all circumstances, as two distinct species of non-pollinating cheater yucca moths derived from pollinating ancestors have been identified (Pellmyr et al., 1996a). The two described species, *Tegeticula intermedia* and *T. corruptrix* Pellmyr, oviposit directly into fruits at different stages of development, and the larvae consume seeds in coexistence with larvae of the pollinator species (Fig. 5D). Their presence can be very costly for host seed production; in one study of *Y. filamentosa,* seed destruction was tripled in populations where cheater moths coexisted with pollinator moths (Pellmyr et al., 1996a). Ecological data did not reveal any competition between coexisting larvae of the pollinator *T. yuccasella* and the cheater *T. intermedia* (Marr et al., 2001), so coexistence is evidently not a problem, but the separate issue of an evolutionarily stable origin of the cheater life habit remains to be explained.

Phylogenetic analyses based on mitochondrial DNA sequence data suggest that the two species originated separately around 1.26 ± 0.9 Mya; thus these are not ephemeral lineages (Pellmyr et al., 1996a; Pellmyr & Leebens-Mack, 1999). A simple solution to the problem of escaping the evolutionary dead end of obligate mutualism is coexistence of two or more mutualists on a shared partner. For example, if two yucca moths were to coexist on one yucca species, one moth species could evolve the cheater habit without causing failure of sexual reproduction in the yucca. In this situation, reciprocal extinction is only expected if both mutualists independently abandon the pollinator habit. With the recent recognition of a large number of pollinator species, it has become apparent that coexistence of pollinator moth species is not uncommon, with at least five documented instances of two pollinators sharing a host in all or part of its range (Davis, 1967; Powell, 1984; Tyre & Addicott, 1993; Pellmyr, 1999; Pellmyr & Balcázar-Lara, 2000; Pellmyr & Leebens-Mack, 2000). One of those sympatry zones is implicated in the origin of *T. intermedia.* This species is most closely related to the pollinator *T. cassandra,* and available data suggest that it may have evolved where *T. cassandra* came into coexistence with *T. yuccasella* in part of its range. The pollinating sister species of both *T. intermedia* and the other cheater species oviposit in a way that distinguishes them from all other pollinator species, and they have a characteristic ovipositor that allows them to oviposit into either a flower or a young fruit. Thus, these pollinators may be preadapted for a switch to oviposition into fruit once a sympatric pollinator species is available to perpetuate pollination. Because of a selective abscission mechanism in the yuccas that causes flowers with many moth eggs of most pollinator species to be abscised within a few days of pollination, a large proportion of the seeds are simply not accessible for larval consumption by these pollinator species. Hence, a pollinator species that can delay oviposition by a few days and oviposits directly into young fruits can bypass the plant's abscission period and exploit a rich seed resource. In this scenario, the phenological shift can be an adaptive step into a novel niche that precedes the loss of pollination habit, which becomes redundant once fruits become the target of oviposition. Available data thus suggest that the origin of cheater yucca moths from pollinators did not result from selection for cheating per se, but rather as a byproduct of selection for exploitation of a previously untapped seed source (Pellmyr & Leebens-Mack, 2000).

By analogy to evolution of non-cooperative pollinators, it is in theory possible that cheating plants could arise in an obligate mutualism. In the case of yucca plants, that would entail the evolution of mechanisms that maintain pollination but prevent seed destruction by pollinator larvae. This could happen through mechanisms such as prevention of successful oviposition, or killing of the eggs or larvae. If an alternative, cooperative host species exists in the area, such cheating by plants could be evolutionarily stable, whereas evolution of cheating plants in a single plant-single pollinator scenario is predicted to lead to extinction (Bull & Rice, 1991). The only proposed case thus far involves a population of *Yucca baccata* Torr., where Bao and Addicott (1998) reported that the fruits of a substantial proportion of all plants lacked evidence of larval damage, and speculated that this might be evidence of a cheating mechanism in these plants. They did not speculate regarding a mechanistic basis, but mentioned that fruits without larvae had a distinctive shape. Further studies will be needed to determine whether a cheating mechanism indeed is in place.

It should be emphasized that the strongest, most direct evidence for selection for cheating in a mutualism would be direct evidence of individual lifetime fitness gains. Such data are wanting for both yuccas and moths, and it is difficult to accrue such data. The major obstacle in measuring moth lifetime fitness has been difficulty to track them during extended flight; it is likely a matter of time before

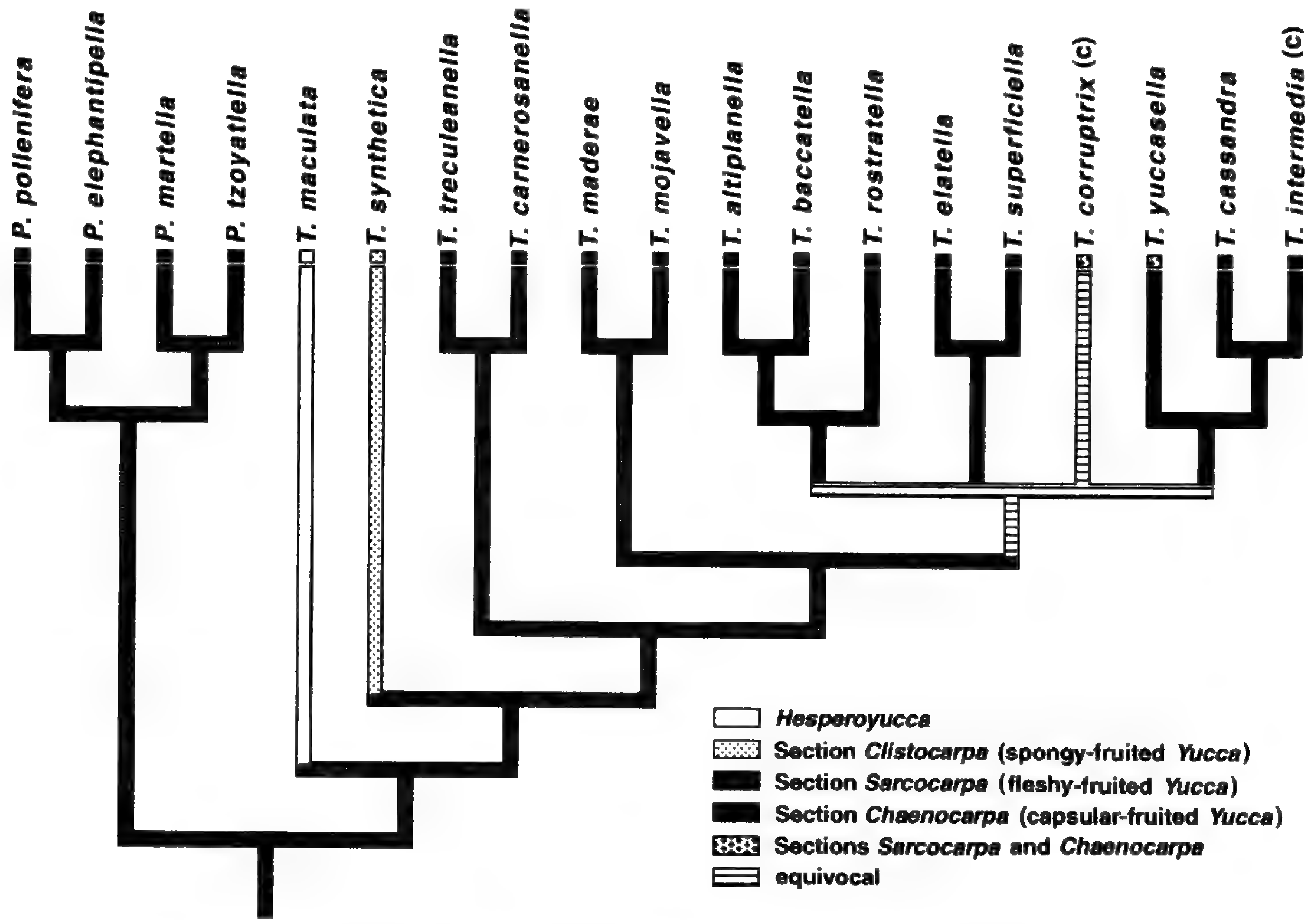

Figure 7. Phylogeny of *Parategeticula* and *Tegeticula*, tracking host use for each species. A "(c)" following the name indicates that it is a cheater species. Two, three, or four origins of *Yucca* sect. *Sarcocarpa* use are indicated and two or three origins of *Y.* sect. *Chaenocarpa* use. Phylogeny from Pellmyr and Leebens-Mack (2000), host records from Pellmyr (1999) and Pellmyr and Balcázar-Lara (2000).

suitable technological tools will be available to solve this problem. In the yuccas, longevity of decades or centuries (McKelvey, 1938; Webber, 1953; Matuda & Piña Lujan, 1980; Webb, 1996; Comanor & Clark, 2000), with iteroparity in all but one species, and also different magnitude and possible plasticity in vegetative propagation, makes it difficult ever to measure lifetime fitness. In consequence, surrogate measures, such as intact seed production in the plants, are the best available option.

PARALLEL SPECIATION AND THE ROLE OF COEVOLUTION IN PLANT-MOTH DIVERSIFICATION

When species are tightly associated, there is a probability that they may co-speciate (Eichler, 1948; Huelsenbeck et al., 2000). Such parallel diversification may result either from vicariance-based divergence or from coevolutionary processes between the species (Page, 1994). For this reason, obligate pollination mutualisms between seed-parasitic pollinators and their hosts should be good candidates for parallel diversification, as potential divergence may derive from linked host specialization in the pollinators and pollen-mediated gene flow in the plants (Bogler et al., 1995; Pellmyr et al., 1996a). The fig-fig wasp associations and yucca-yucca moth associations are sufficiently speciose that analysis of parallel diversification is possible. Analyses of the association between figs and fig wasps have indeed indicated a high level of parallel diversification at the level of fig genera and subgenera (Herre et al., 1996), while there is emerging evidence that this pattern breaks down to a fair degree at lower taxonomic levels (Lopez-Vaamonde et al., 2001; Machado et al., 2001). Analysis for the yuccas and yucca moths is still rudimentary as the yucca phylogeny is incompletely resolved, and the unresolved polytomy in the moth phylogeny also limits analysis (Fig. 7). Given the current unresolved plant relationships, there are no strong candidates for parallel diversification, although this may change with increasing phylogenetic information. Meanwhile, several lines of evidence indicate that there are numerous instances where colonization has occurred. The most obvious instance involves recent colonization by *Tegeticula yuccasella* of *Yucca aloifolia*. Similarly, *T. baccatella* Pellmyr, which feeds on a fleshy-fruited host, is nested amid species that feed on capsular-fruited yuccas (Fig. 7), and thus supports a past shift assuming that monophyly of fleshy-fruited yuccas is upheld. The cheater *T. corruptrix*, also arising from an ancestor on a capsular-fruited yucca (Fig. 7), now utilizes both fleshy-fruited and capsular-fruited species. Second, the coexistence on a host of non-sister taxa of *Tegeticula* pollinators cannot be explained by parallel diversification; in principle, coexistence of a *Parategeticula* and a *Tegeticula* pollinator on a host could reflect two independent parallel diversifications with the hosts, but there is very little support from published host data for this explanation (Fig. 7). Third, instances where a pollinator species utilizes more than one host species (Fig. 6) cannot reflect parallel diversification, although they may possibly reflect an ancestral association with subsequent unilateral diversification in a monophyletic group of hosts.

Co-speciation does not require coevolutionary processes, and coevolution can act on organisms regardless of their history of association; thus the role of coevolution in driving diversification between the plants and the pollinators is an altogether separate matter. Selection on plant and moth traits that vary among species may arise either from the interacting partners or from factors extrinsic to the interaction. For example, traits likely to affect moth oviposition success, such as floral ovary morphology and moth ovipositor morphology, may be strong candidates for reciprocal selection as they directly affect plant and pollinator fitness. Meanwhile, traits such as petal shape and color may be more likely to be under selection based on a wide range of antagonistic interactions with other herbivores, as well as abiotic factors. To determine the historical role of coevolution in the diversification of an interaction, variation in divergent traits must be partitioned to remove extrinsic components, i.e., in essence to remove background evolution in the interacting groups attributable to other factors. This obviously requires groups of plants and pollinators that have coexisted during much or all of their diversification, as is the case for yuccas and yucca moths. It also requires well-resolved phylogenies, preferably with estimates of internal branch lengths. This criterion is not yet met for the yucca-yucca moth association, nor for any other similar plant-pollinator association. Such analyses will be highly useful in evaluating the historical role of coevolution in driving diversification and speciation in plants and pollinators.

CONCLUSION

It may seem a somewhat subdued note on which to end, that we cannot yet perform rigorous tests of the role of coevolution in the diversification of yuccas and yucca moths. But the reason is simply that a large amount of information about morphology, ecology, natural history, and phylogeny is required for any one association before analyses of the historical impact of coevolution can be explored. Most, but not all, of these requirements are now largely met. The last 15 years have seen a dramatic increase in our understanding of organismal diversity, especially among the insects, although much information from the Mexican range of the yucca-yucca moth associations remains to be published. Ecological and evolutionary dynamics have also become far better understood in the last decade, including the expansion into the realm of reversal of mutualism. Phylogenetic information is now arguably the primary limiting factor for analyses of coevolution and several other major questions, but there is reason to hope that robust information soon will be available for both groups. Ongoing parallel projects on subsets of fig-fig wasp associations (e.g., Lopez-Vaamonde et al., 2001; Machado et al., 2001; Weiblen & Bush, 2002) as well as other mutualisms involving seed-parasitic pollinators (Després et al., 2002) also offer possibilities for grander comparisons across mutualisms in the next few years. Whatever generalizations about factors mediating plant-pollinator mutualisms emerge from these highly specific associations can soon be used as a template in analyzing other, more complex plant-pollinator mutualisms.

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CHROMOSOME REPORTS FROM SOUTH AMERICAN *HYPOCHAERIS* (ASTERACEAE)[1]

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ABSTRACT

Eighty-nine new chromosome counts are reported from 85 populations of 15 species of *Hypochaeris* (Asteraceae, Lactuceae) from South America, including first reports from nine taxa (*H. apargioides, H. clarionoides, H. palustris, H. scorzonerae, H. setosa, H. sonchoides, H. spathulata, H. tenuifolia, H. thrincioides*). Most are $2n = 8$ with bimodal and asymmetric karyotypes. Tetraploidy ($2n = 16$) is documented for the first time in some populations of *H. meyeniana, H. scorzonerae*, and *H. tenuifolia.* A summary of previous and new counts reveals that only two uniformly tetraploid species are known (*H. incana* and *H. stenocephala*). Five taxa also show infraspecific polyploidy: *H. chondrilloides, H. meyeniana, H. scorzonerae, H. sessiliflora*, and *H. tenuifolia.* Polyploidy, therefore, occurs in about 10% of the South American taxa. The South American representatives of the genus are all based on $x = 4$ in contrast to more conspicuous karyotypic differences among European taxa ($2n = 6, 8, 10, 12$). This pattern of greater cytological uniformity among many species of the New World (ca. 50 known, 32 now counted chromosomally) suggests that the group was derived from European ancestors rather than the reverse. It appears that *Hypochaeris* in South America radiated explosively into many habitats from sea level to over 3000 m, but that this radiation has not often been accompanied by conspicuous chromosomal change. The absence of aneuploidy and relatively low frequency of polyploidy, plus few known cases of present interspecific hybridization, suggest a weakened role for hybridization as an evolutionary mechanism in the group. Data so far suggest diploid recombinational speciation as the dominant mode accompanied by genetic rather than dramatic cytological alterations, plus occasional polyploid derivatives.

Key words: Asteraceae, chromosome numbers, *Hypochaeris*, karyotype, South America, speciation.

Although much is known about mechanisms of speciation and species-level biogeography in the floras of Europe and North America (e.g., Stebbins, 1971; Stebbins et al., 1953; Grant, 1981), little is understood about these same processes in the flora of South America. To help reveal these dynamics in the temperate regions of southern South America, we have begun a series of investigations on *Hypochaeris* L. (Asteraceae, Lactuceae; *Hypochoeris* L., orthogr. var.). This is a genus of approximately 60 species, with 9 in Europe (DeFillips, 1976) and ca. 50 confined to South America, many of which are localized in the Southern Cone (Bortiri, 1999). *Hypochaeris* is a good genus to extract information on modes of speciation and patterns of biogeography because of the large size and small number of chromosomes (Stebbins, 1971), the diverse morphologies of the taxa varying from small acaulescent alpine forms to broad-leaved large-headed species, and distributions in very different ecological zones ranging from sea level to over 3000 m (Lack, 1979). Apparent rapid and recent speciation of the genus in South America, therefore, combined with favorable karyological aspects, offers a useful system in which to examine evolutionary processes.

Chromosome counts as well as detailed karyological studies have been investigated for European species of *Hypochaeris* (Parker, 1976; Mugnier & Siljak-Yakovlev, 1987; Barghi et al., 1989; Siljak-Yakovlev et al., 1994; Cerbah et al., 1995, 1998a), which appear to possess symmetrical karyotypes, and which show general correlations of different chromosome numbers ($2n = 6, 8, 10, 12$) with taxonomic sections. Molecular phylogenetic studies using ITS regions among these European taxa (Cerbah et al., 1998b), and including four species from South America, have also revealed useful insights on broad evolutionary patterns within the genus that correlate, to some considerable degree, with previous sectional limits.

Despite the large number of species of *Hypochaeris* from South America, they have been poorly studied karyologically. Chromosome numbers, sometimes accompanied by photographs, have been

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Table 1. List of previous chromosome counts of *Hypochaeris* from South America (excluding *H. glabra* and *H. radicata*).

Species	2*n*	*n*	Reference
H. acaulis (Remy) Britton		4	Wulff (1998)
H. arenaria Gaudich.	8		Moore (1981)
H. brasiliensis (Less.) Griseb.[1]	8		Stebbins et al. (1953); Parker (1971); Ruas et al. (1995)
		4	Coleman (1968); Turner et al. (1979)
H. chillensis (Kunth) Hieron.	8		Tomb et al. (1978); Siljak-Yakovlev et al. (1994); Cerbah et al. (1995); Cerbah et al. (1998a)
		4	Wulff (1992, 1998)
H. chillensis × *H. megapotamica*		4	Wulff (1992)
H. chillensis × *H. microcephala* var. *albiflora*		4	Wulff (1992)
H. chondrilloides (A. Gray) Cabrera		4	Cherubini (1982)
		8	Wulff (1998)
H. elata (Wedd.) Griseb.	8		Krapovickas (1951)
		4	Bernardello (1986)
H. foliosa (Phil.) Reiche	8		Stebbins et al. (1953)
H. gardneri Baker		5	Coleman (1968)
H. glauca (Phil.) Reiche[2]	8		Stebbins et al. (1953)
H. halophila (Hauman) Cabrera[2]	8		Schnack & Covas (1947)
H. incana (Hook. f. & Arn.) Macloskie		8	Moore (1981)
H. megapotamica Cabrera	8		Saez (1949); Siljak-Yakovlev et al. (1994); Cerbah et al. (1995); Ruas et al. (1995); Cerbah et al. (1998a)
		4	Wulff (1992, 1998)
H. meyeniana (Walp.) Griseb.	8		Diers (1961)
H. microcephala (Sch. Bip.) Cabrera var. *albiflora* (Kuntze) Cabrera	8		Saez (1949); Siljak-Yakovlev et al. (1994); Cerbah et al. (1995); Ruas et al. (1995); Cerbah et al. (1998a); Wulff (1998)
		4	Wulff (1992)
H. pampasica Cabrera	8		Cerbah et al. (1995); Ruas et al. (1995); Cerbah et al. (1998a)
H. parvifolia H. Kost.	8		Diers (1961)
H. petiolaris (Hook. f. & Arn.) Griseb.		4	Turner et al. (1979)
H. rosengurttii Cabrera	8		Ruas et al. (1995)
H. sessiliflora Kunth		8	Olsen (1980)
		6	Turner et al. (1967)
		4	Jansen & Stuessy (1980)
H. stenocephala (A. Gray ex Wedd.) Kuntze	16		Stebbins et al. (1953); Diers (1961)
H. taraxacoides (Walp.) Benth. & Hook. f.[3]	8		Parker (1971)
H. tweediei (Hook. f. & Arn.) Cabrera[1]	8		Saez (1949)
H. variegata (Lam.) Baker	8		Ruas et al. (1995)

[1–3] Treated as synonyms of *H. chillensis*[1], *H. chondrilloides*[2], and *H. stenocephala*[3] by Bortiri (1999).

published for 23 species (e.g., Saez, 1949; Wulff, 1992; Ruas et al., 1995; Cerbah et al., 1998a; Table 1), but detailed karyotypes exist for far fewer taxa (only ca. 6). Most chromosome numbers so far documented are $2n = 8$ with only two cases of uniform tetraploidy known (*H. incana*, Moore, 1981; *H. stenocephala*, Stebbins et al., 1953; Diers, 1961), and two cases of infraspecific tetraploidy (i.e., *H. chrondrilloides*, Wulff, 1998; *H. sessiliflora*, Olsen, 1980, both 2*n* and 4*n* reports).

To set the stage for additional evolutionary studies on *Hypochaeris*, therefore, the purposes of this paper are to: (1) summarize all available previous chromosome counts for South American species of *Hypochaeris*; (2) report original counts for taxa collected in Chile and other Andean regions (Argentina, Bolivia, Ecuador, Peru, and Venezuela); and (3) comment on the chromosomal variation documented within South America, particularly with reference to the already well known cytological picture of European species. Several populations of each taxon have often been analyzed so that infra-

Table 2. New chromosome counts of *Hypochaeris* from South America [all plants from Chile (regions given by Roman numerals) unless indicated otherwise]. Counts are mostly from mitotic preparations; haploid counts (meiosis I and 1st pollen mitosis) are indicated by *; populations for which both diploid and haploid counts were made are marked with **. Abbreviations of collectors: CB = C. Baeza; DC = D. Crawford; JG = J. Grau; PS = P. Stuessy; TS = T. Stuessy; HF = H. Förther; MW = M. Weigend. Vouchers on deposit in WU and CONC (collections by TS and colleagues and López) and M (all other collections). ++ = first report(s) for taxon; + = new chromosomal level.

Taxon, voucher, and chromosome number
H. acaulis (Remy) Britton 2*n* = 8
VII. Prov. Talca, Laguna del Maule, Laguna sin Puerto, s.d., *JG Hyp-50.* VIII. Termas de Chillán, Valle de las Nieblas, 15 Jan. 1999, *TS et al. 15565.* IX. 20 km E of Chilean Aduana toward Paso Pino Hachado, 20 Jan. 1999, *TS & CB 15587.* ARGENTINA. 1 km E of Paso Pino Hachado, 20 Jan. 1999, *TS & CB 15593.*
++*H. apargioides* Hook. f. & Arn. 2*n* = 8
VIII. Parque Nacional Laguna La Laja, 25 Jan. 1998, *TS & DC 15470;* Las Trancas, 30 Jan. 1998, *TS 15481, 15485,* 13 Jan. 1999, *TS et al. 15549*,* Valle Hermoso, *15551, 15554.* IX. Reserva Nacional Malalcahuello, 12 Feb. 1998, *TS et al. 15509***, 3 km W of Lonquimay, 13 Feb. 1998, *15513;* 10 km E of Puente Lonquimay, *TS et al. 15515*,* 17 km E of Puente Lonquimay, *15516,* 29 km E of Puente Lonquimay, *15517,* 8 km E of Chilean Aduana, 13 Feb. 1998, *15518;* 3 km W of Lonquimay, 19 Jan. 1999, *TS & CB 15576*,* 8 km E of Chilean Aduana, 20 Jan. 1999, *15583,* 3 km W of Chilean Aduana, *15594***, 25 km E of Lonquimay, *15595***, 17 Feb. 2000, *15596,* Volcán Llaima, 21 Jan. 1999, *15602*,* Volcán Villarrica, Piedra de Aquila, 22 Jan. 1999, *15612*,* to Laguna Huinfiucá, 23 Jan. 1999, *15621*,* rd to Lonquimay, 16 Feb. 2000, *15809A.*
++*H. clarionoides* (Remy) Reiche 2*n* = 8
Región Metropolitana de Santiago, 6 km W of La Parva, 18 Feb. 1998, *TS & PS 15527,* 2 km W of La Parva, *15529*, 15531*.*
H. elata (Wedd.) Griseb. 2*n* = 8
BOLIVIA. La Paz, Puerto Pérez, Lake Titicaca, s.d., *Karus Hyp-43.*
+*H. meyeniana* (Walp.) Griseb. 2*n* = 8
PERU. Dept. Cajamarca, Prov. Contumazá, Bosque de Cachil, s.d., *MW 98/554.*
+*H. meyeniana* (Walp.) Griseb. +2*n* = 16
PERU. Dept. Tacna, Prov. Taranta, S of Volcán Tutupaca, 20 km above Candarave, s.d., *MW & HF 97/688.*
++*H. palustris* (Phil.) De Wild. 2*n* = 8
VIII. Valle de Las Nieblas, Termas de Chillan, 15 Jan. 1999, *TS et al. 15566*.* IX. 20 km E of Chilean Aduana, 20 Jan. 1999, *TS & CB 15588*,* Volcán Villarrica, 22 Jan. 1999, *15606, 15607,* rd to Laguna Huinfiucá, 23 Jan. 1999, *15622,* Volcán Casablanca, 24 Jan. 1999, *15628, 15629.*
H. radicata L. 2*n* = 8
VIII. Cerro Ponpón, 21 Jan. 1998, *TS 15450H, 15450J,* Parque Hualpén, Concepción, *15451;* 2 km W of Angol, 24 Jan. 1998, *TS & DC 15454,* 2 km into Parque Nacional Nahuelbuta, *15458*,* Parque Nacional Nahuelbuta, *15461,* Piedra de Aguila, *15465, 15466,* 17 km E of Antuco, 25 Jan. 1998, *15468, 15469*,* Parque Nacional Laguna La Laja, *15471*, 15473;* Lota, Schwager, 27 Jan. 1998, *TS et al. 15477,* Termas de Chillán, 31 Jan. 1998, *15487.* IX. 12 km E of Curacautín, 12 Feb. 1998, *TS et al. 15506,* 5 km S of Lonquimay, 12 Feb. 1998, *15508,* 8 km E of Chilean Aduana, 13 Feb. 1998, *15519;* 14 km E of Cherquenco, 21 Jan. 1999, *TS & CB 15597*,* 1 km W of Pucón toward Volcán Villarrica, 22 Jan. 1999, *15604,* 11 km SE of Aguas Calientes, 24 Jan. 1999, *15626*.* Región Metropolitana de Santiago, Santuario de la Naturaleza Yerba Loca, 18 Feb. 1998, *TS & PS 15533.*
++*H. scorzonerae* (DC.) F. Muell. 2*n* = 8
Region IV. 5 km E of Huentelauquén, 16 Oct. 1999, *Lopez 503,* 3 km N of Puerto Oscuro, *505,* 6 km N of Puerto Oscuro, *507.*
++*H. scorzonerae* (DC.) F. Muell. 2*n* = 16
V. Prov. Quillota, Cerro campana, Mirador de los Guanacos, s.d., *JG 87-29.*
H. sessiliflora Kunth 2*n* = 8
ECUADOR. Quito, Paso Guamani, s.d., *JG Hyp-37;* Carchi, Páramo El Ángel, *38,* Bolívar, Chimborazo, s.d., *MW Hyp-78, 79.*
++*H. setosa* (Wedd.) Rusby 2*n* = 8
VENEZUELA. Mérida, Parque Nacional Sierra Nevada, s.d., *Gaviria 1048.*

Table 2. Continued.

Taxon, voucher, and chromosome number
++*H. sonchoides* Kunth $2n = 8$
ECUADOR. Pichincha, Nono, NW of Quito, s.d., *JG Hyp-36.*
++*H. spathulata* (Remy) Reiche $2n = 8$
IX. N of Pucatrihue, 25 Jan. 1999, *TS & CB 15633**.
H. stenocephala (A. Gray ex Wedd.) Kuntze $2n = 16$
PERU. Dept. Puno, Prov. Puno, Ruins of Sillistani, s.d., *MW & HF 97/119.*
++*H. tenuifolia* (Hook. f. & Arn.) Griseb. $2n = 8$
VII. Prov. Talca, Laguna del Maule, s.d., *JG s.n.* VIII. Prov. Nuble, Nevados de Chillán, Garganta del Diablo, s.d., JG *Hyp*-45; Termas de Chillán, 31 Jan. 1998, *TS et al. 15486, 15490A,* 1 Feb. 1998, *15492C, 15498, 15505.* IX. Volcán Lonquimay, 19 Jan. 1999, *TS & CB 15577-3*;* Volcán Llaima, 21 Jan. 1999, *15600,* Volcán Villarrica, 22 Jan. 1999, *15605.*
++*H. tenuifolia* (Hook. f. & Arn.) Griseb. $2n = 16$
VIII. Termas de Chillán, 31 Jan. 1998, *TS et al. 15489.* IX. 5 km into Reserva Nacional Malalcahuello, 12 Feb. 1998, *TS et al. 15510.*
++*H. thrincioides* (Remy) Reiche $2n = 8$
VIII. Cerro Ponpón near Concepción, 21 Jan. 1998, *TS 154501.* IX. 10 km W into Parque Nahuelbuta, 24 Jan. 1998, *TS & DC 15456**.*

specific euploidy or dysploidy might be revealed and better interpreted.

It must also be stressed that the present taxonomy and nomenclature of *Hypochaeris* in South America needs comprehensive revision. Despite the very helpful treatments on Argentinean species by Cabrera (1971, 1974, 1976, 1978) and more recently Bortiri (1999), there still remains confusion in proper limits and correct names for many taxa. Future studies will have to resolve these important issues.

MATERIALS AND METHODS

MATERIALS

Bud and seed materials of *Hypochaeris* were collected in South America (Table 2). Collections were of populational samples in all instances. Vouchers are on deposit at CONC, M, and WU.

METHODS

For mitotic chromosome counts, root meristems were obtained from surface-sterilized seeds germinated for two days on wet filter paper or from mature plants in cultivation at M.

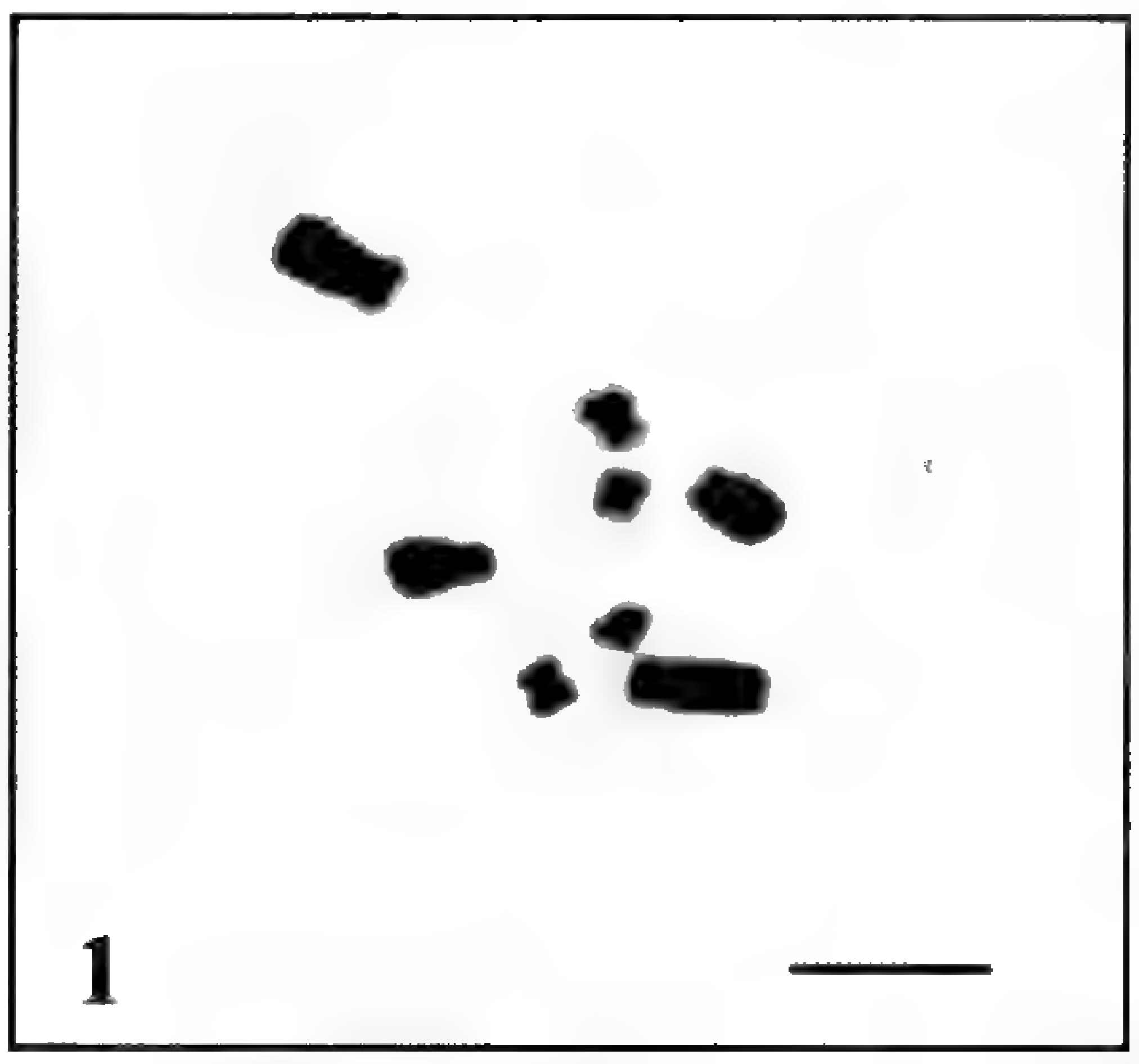
Root tips were pretreated with 0.1% colchicine for 2 hrs at room temperature in darkness, fixed in 3:1 (ethanol : acetic acid) for 24 hr., and stored until use at −20°C. For meiotic chromosome counts flower buds were fixed in modified Carnoy's solution (4:3:1; chloroform : absolute ethanol : glacial acetic acid), transferred to 70% ethanol, and stored at 4°C until examination in the laboratory.

Chromosome preparations were made using Feulgen staining with Schiff's reagent following standard methods (Fukui & Nakayama, 1996). Root tips and flower buds were washed in distilled water to remove the fixative, hydrolyzed in 5N HCl for 30 min at 20°C, and washed and stained with Schiff's reagent in darkness for 1–2 hr. Squash preparations were made in a drop of 45% acetic acid. After coverslip removal on dry ice, preparations were dried for 24 hr. at 37°C and mounted in DPX. Chromosome numbers were determined from at least 20 cells of at least two florets for meiotic counts and of at least three seedlings for mitotic observations.

RESULTS AND DISCUSSION

Eighty-nine new chromosome counts are reported from 85 populations of 15 species of *Hypochaeris* from South America (Table 2) including first reports for nine taxa: *H. apargioides, H. clarionoides, H. palustris, H. scorzonerae, H. setosa, H. sonchoides, H. spathulata, H. tenuifolia,* and *H. thrincioides.* All counts give $2n = 8$, with infraspecific tetraploidy ($2n = 4x = 16$) also documented in *H. scorzonerae* and *H. tenuifolia.* A new tetraploid population has also been detected in *H. meyeniana.*

These new data, in correlation with previously published reports for *Hypochaeris* in South America (Table 1), yield 32 species (of ca. 50) now counted from 138 populations. A brief combined analysis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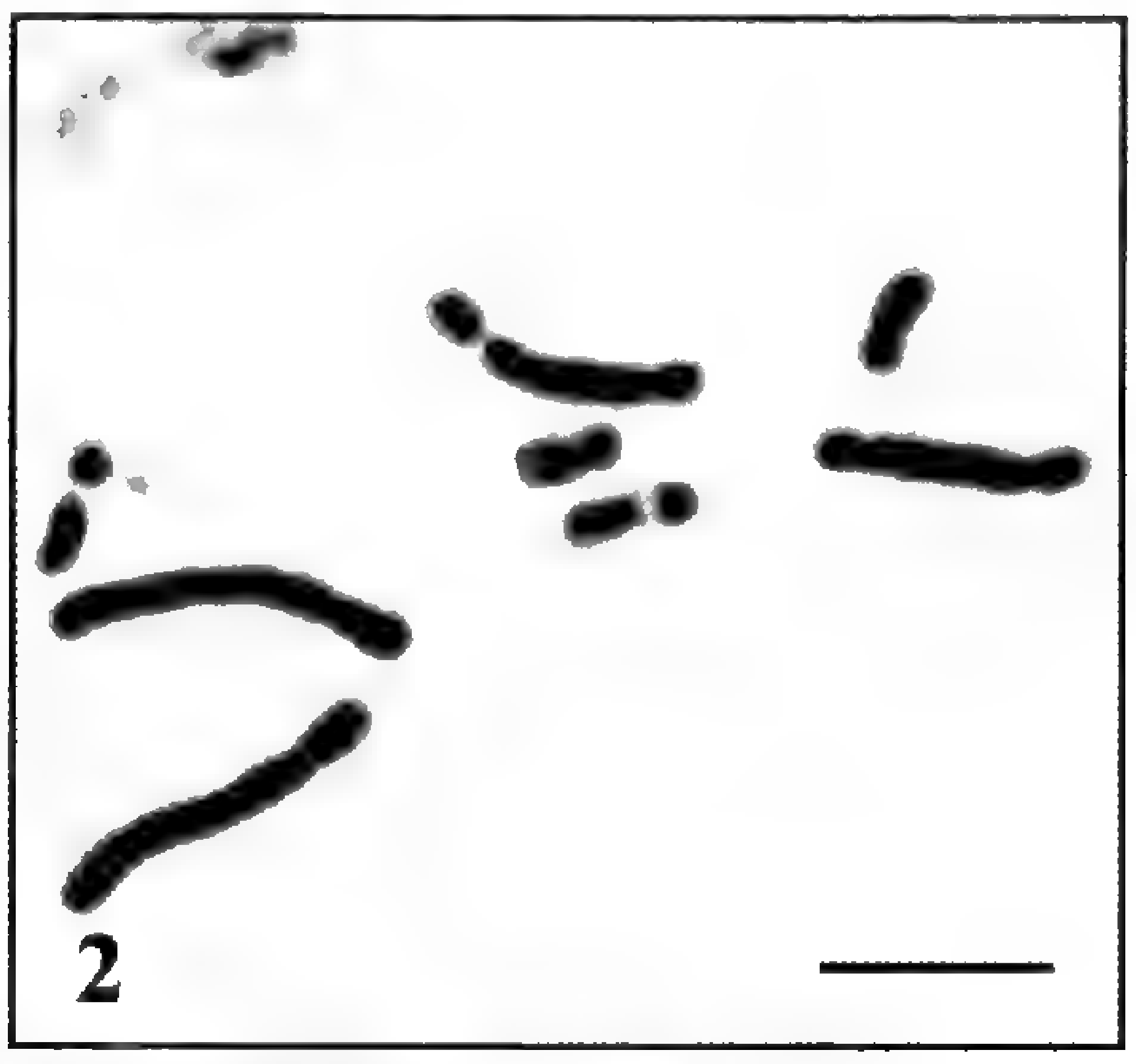
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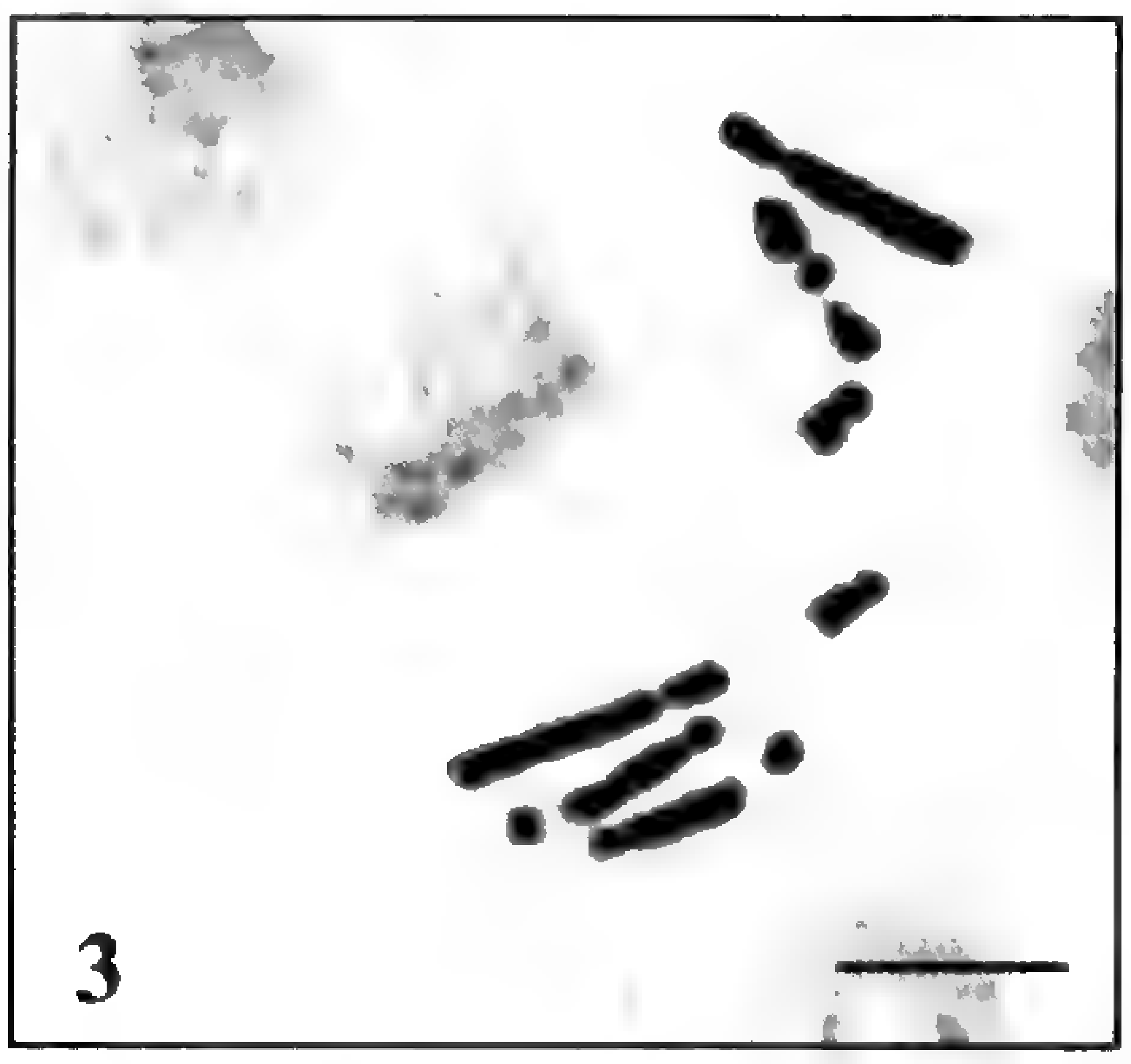
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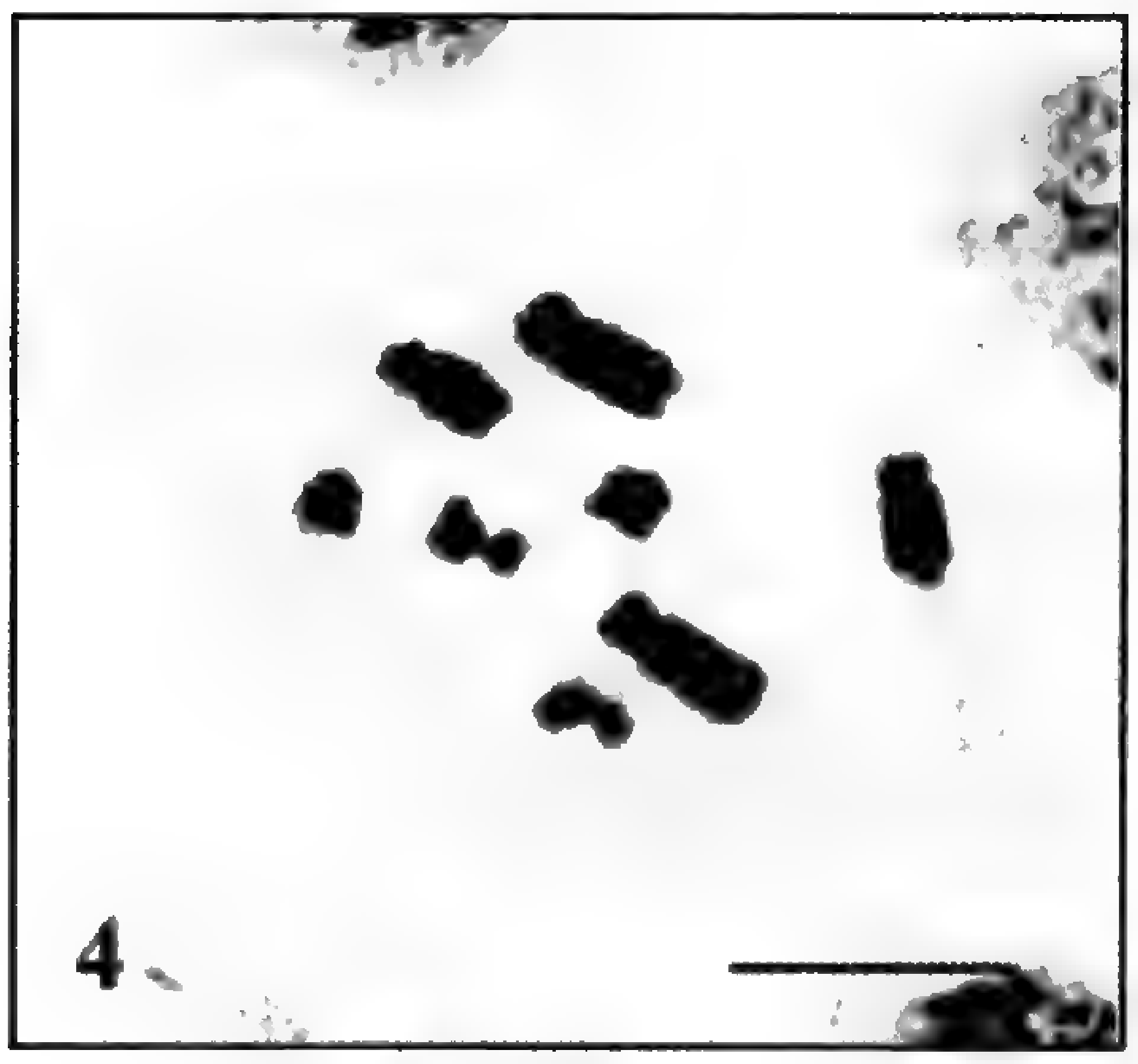
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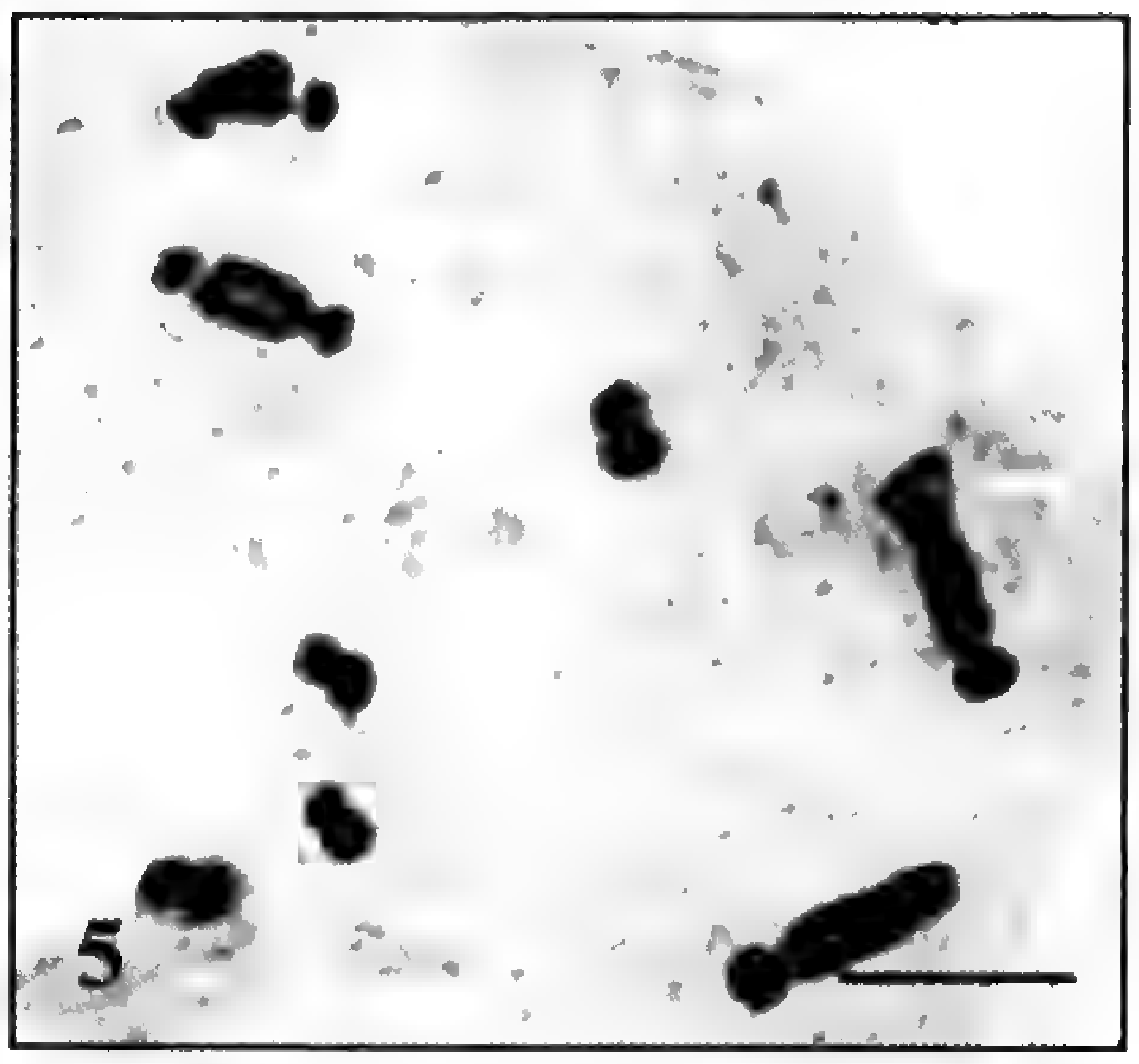
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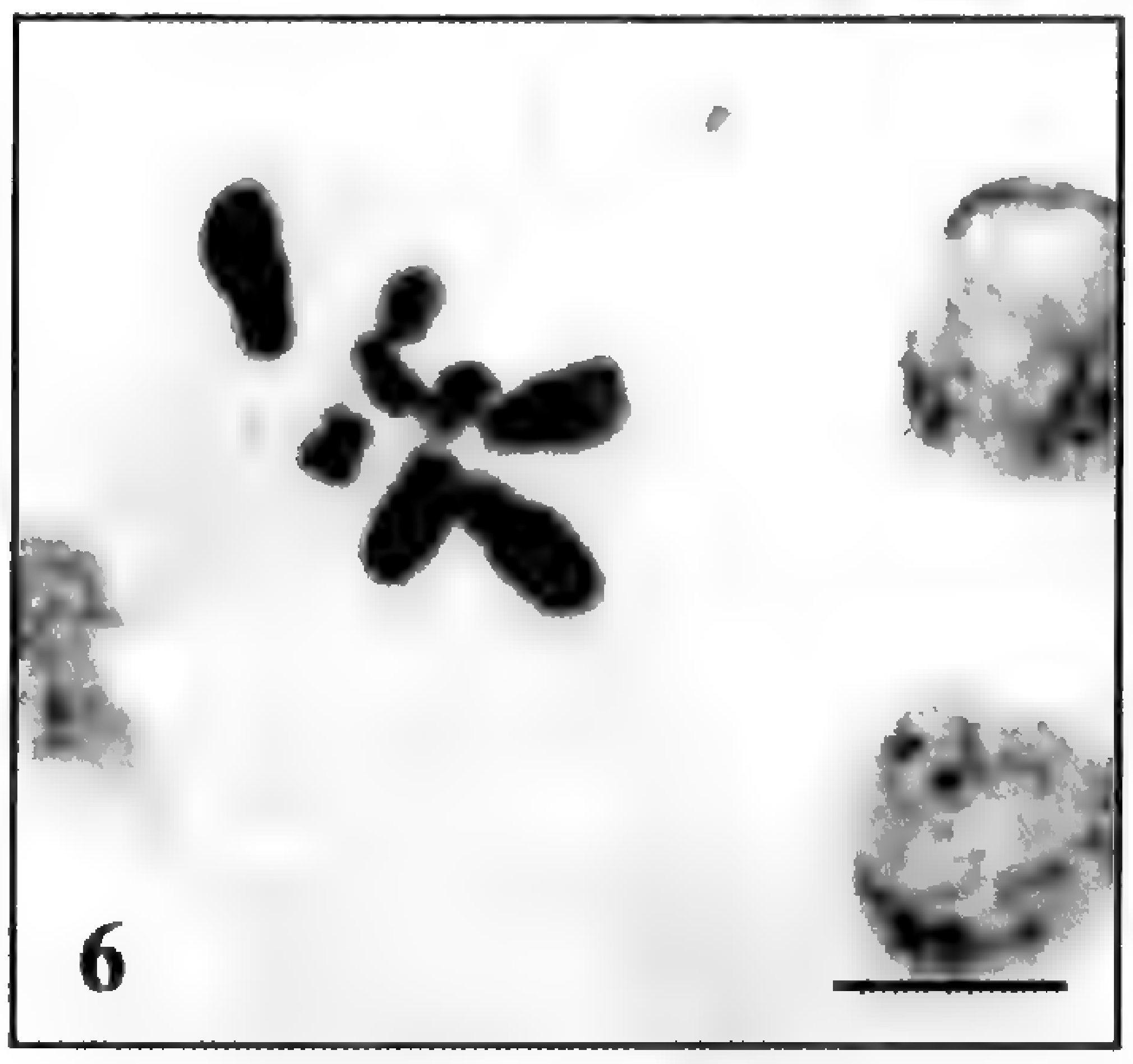
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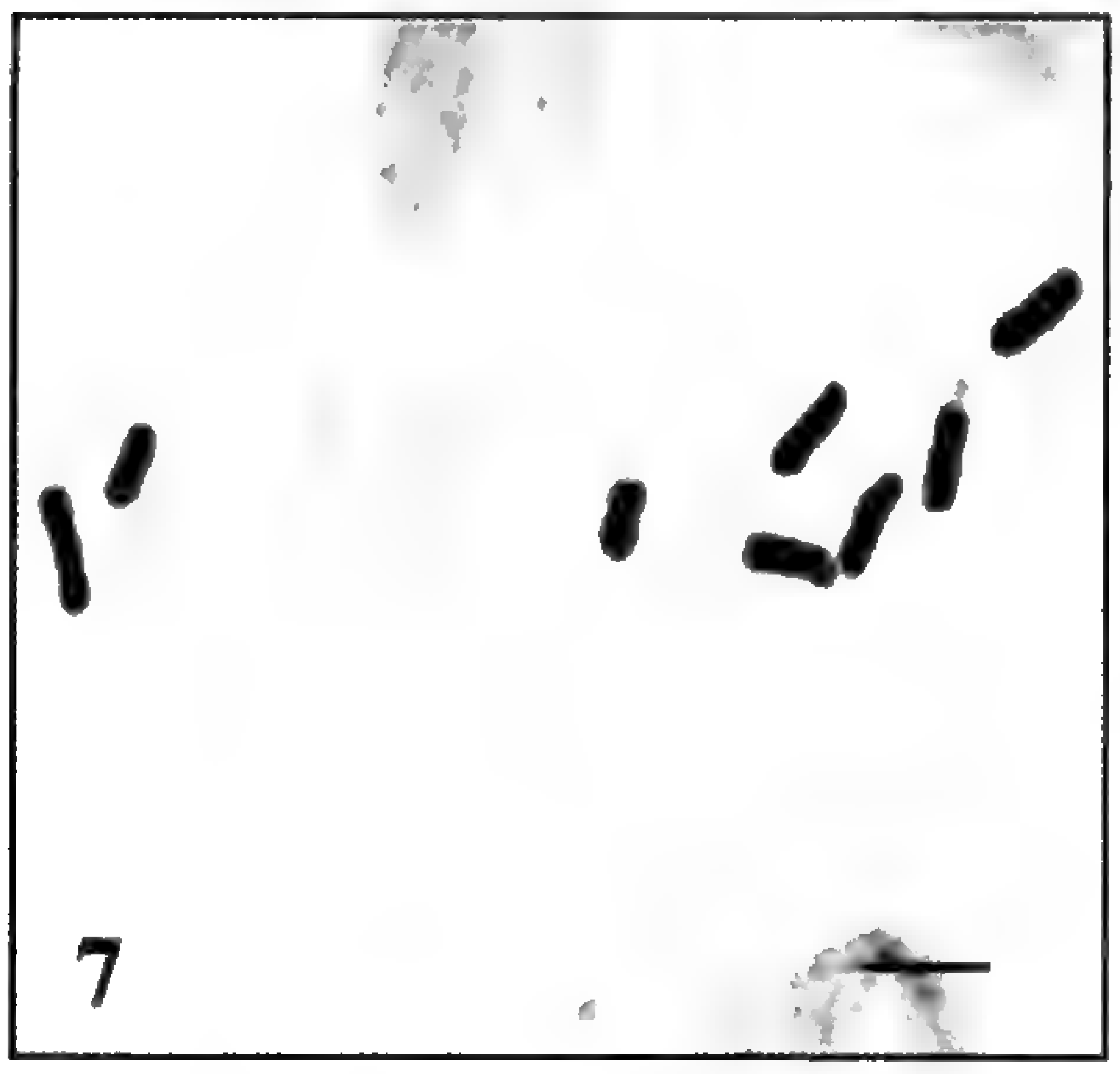
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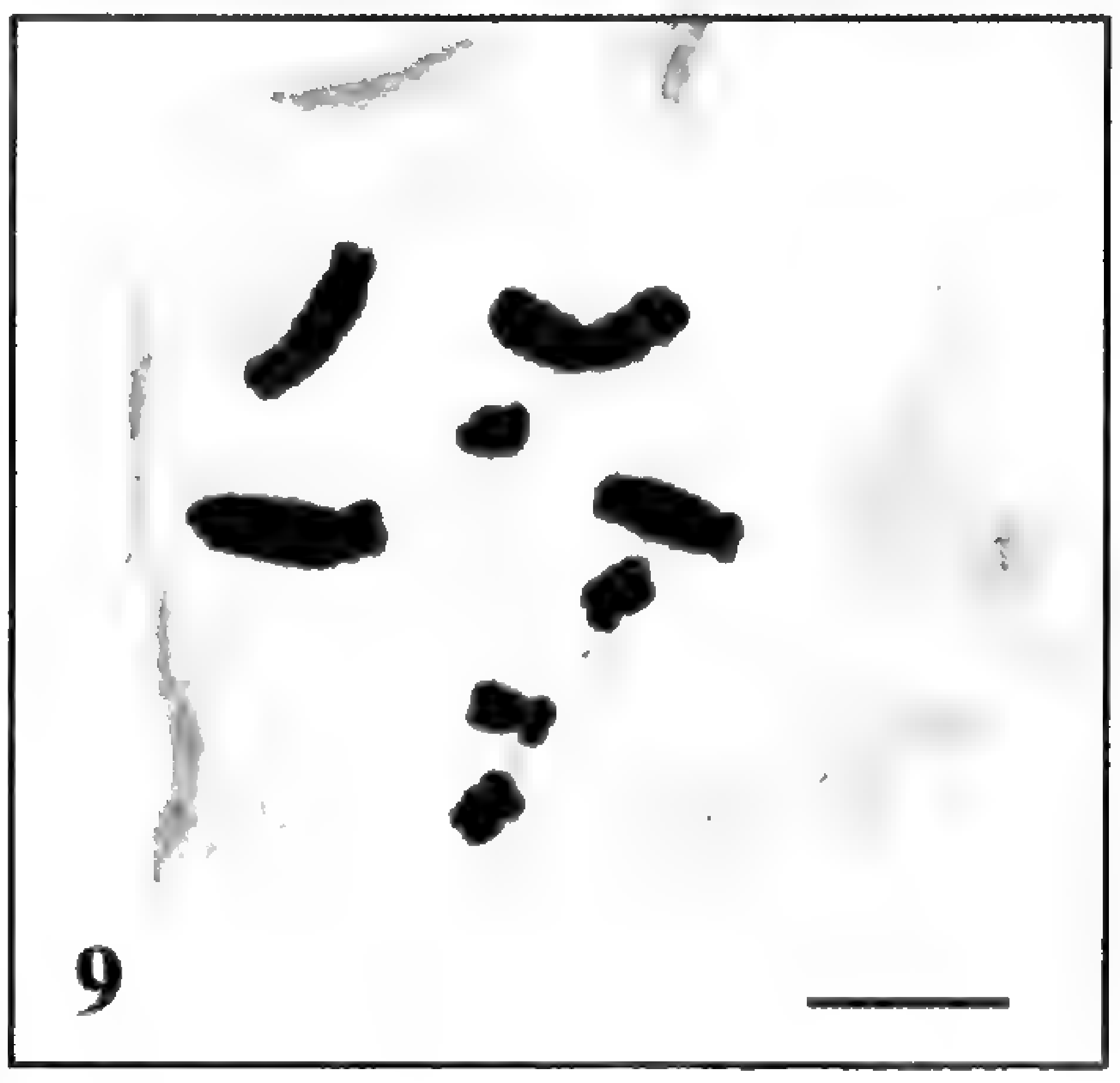
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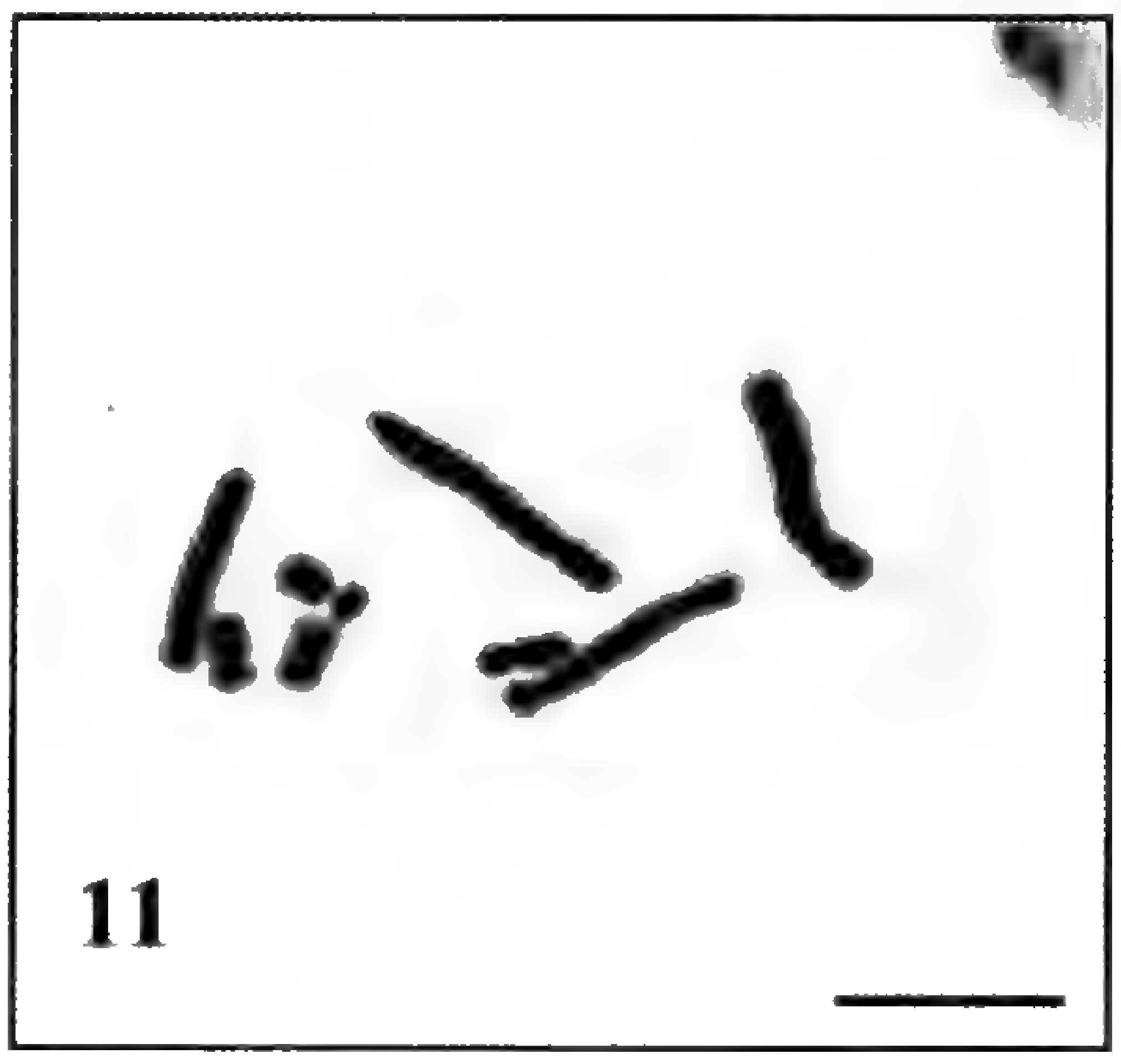
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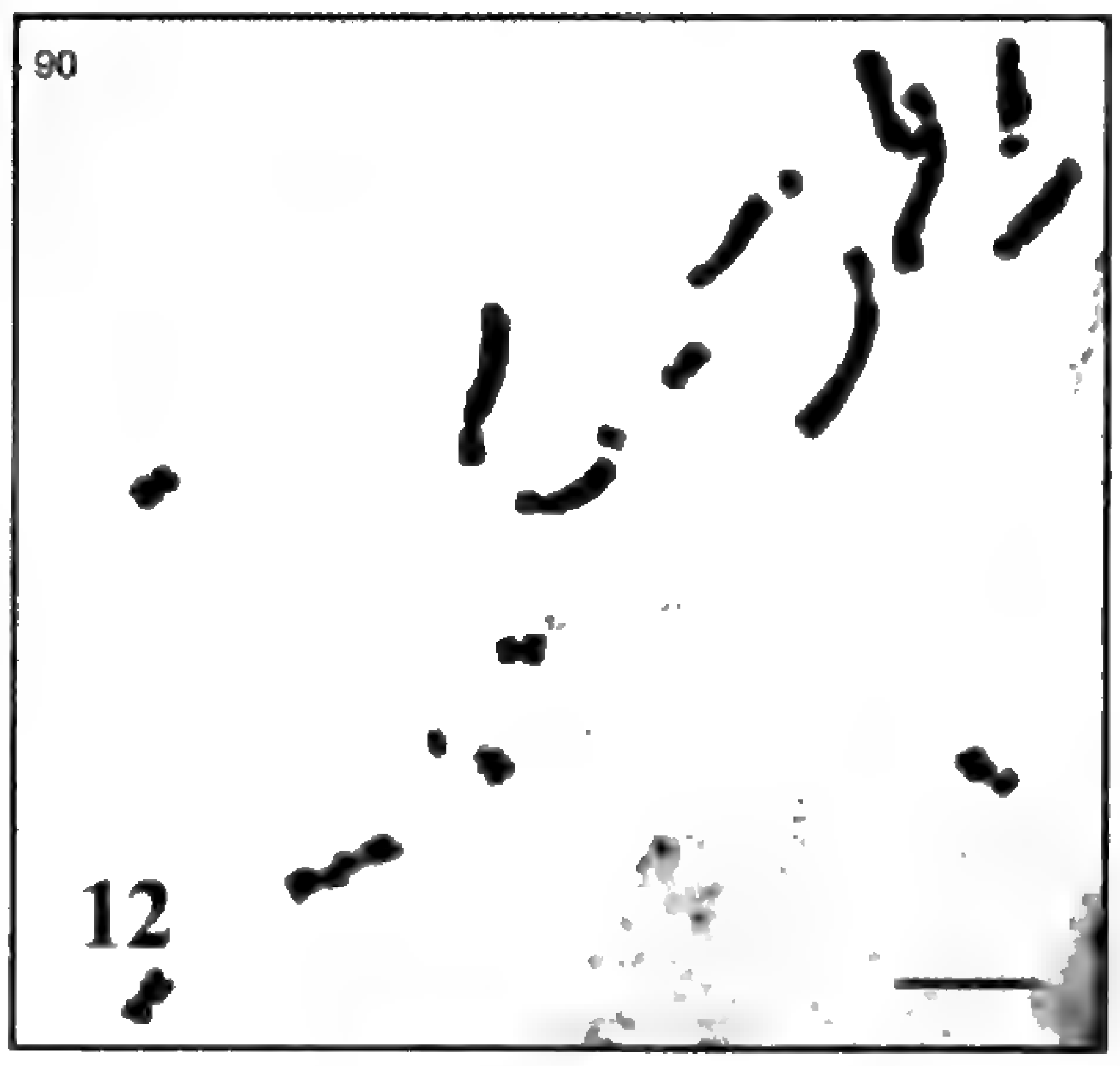

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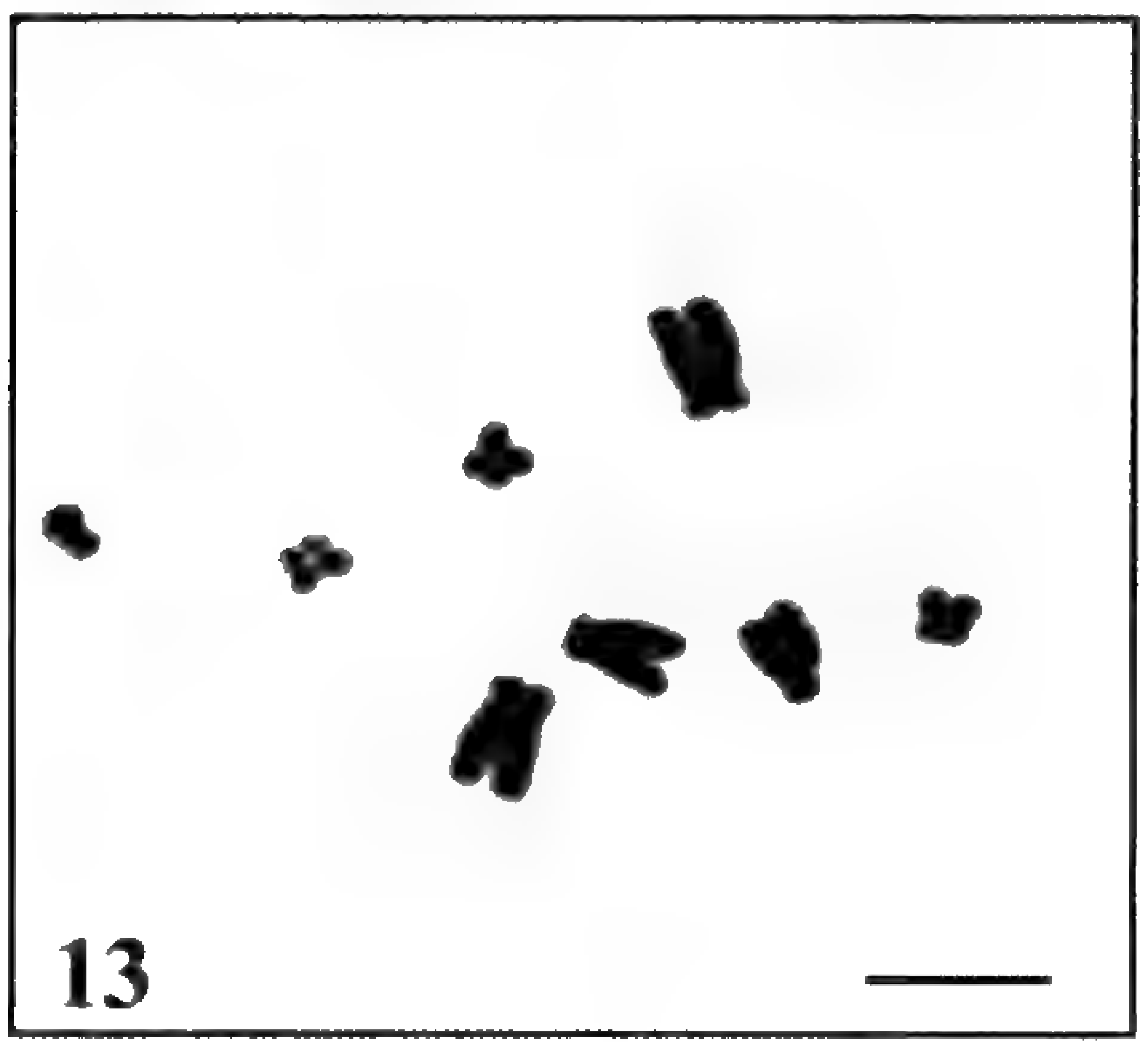
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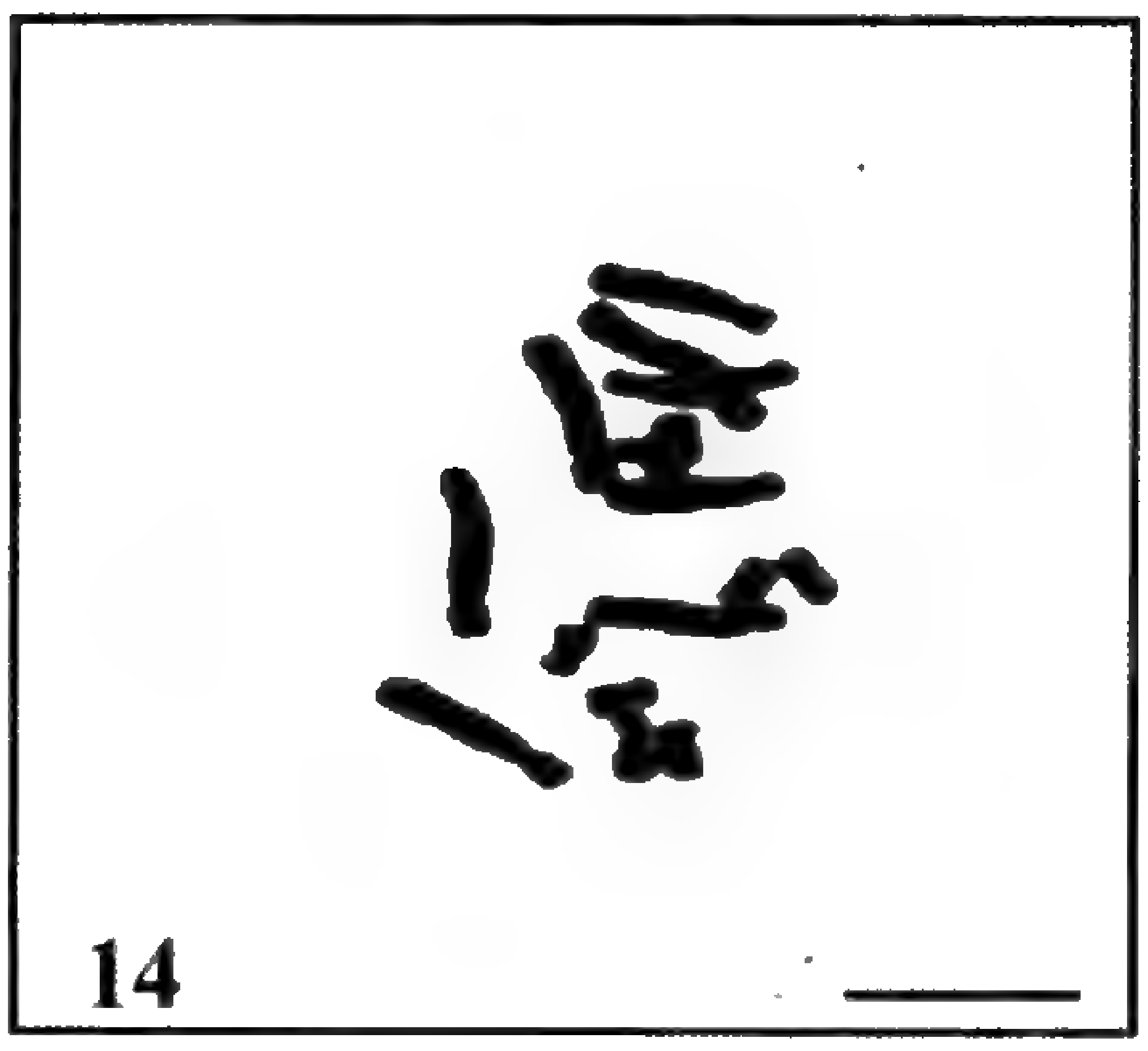
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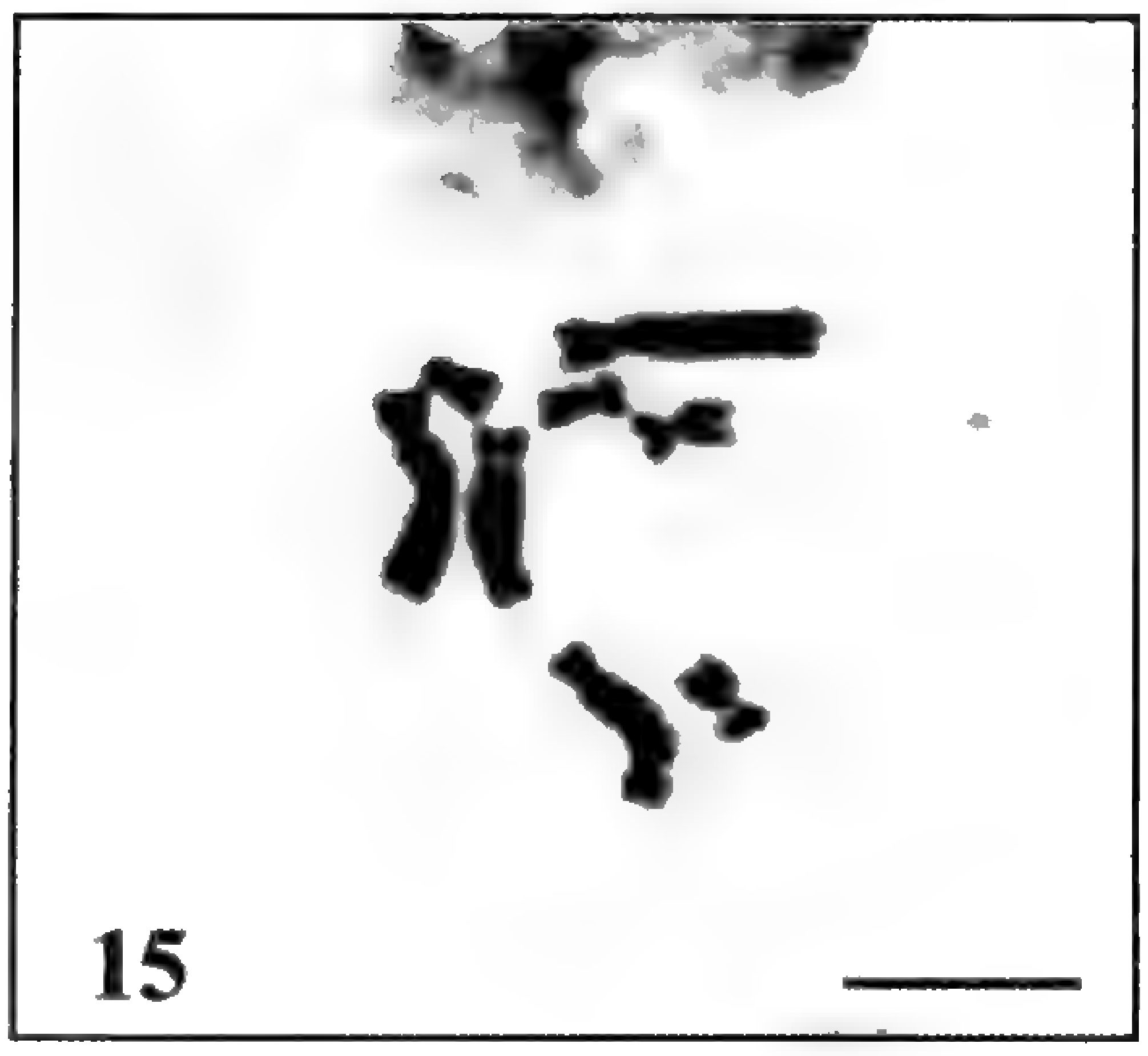
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shows 25 uniformly diploid ($2n = 8$) species, two species uniformly tetraploid ($2n = 16$; *H. incana* and *H. stenocephala*), and five species with both diploid and tetraploid cytotypes (*H. chondrilloides, H. meyeniana, H. scorzonerae, H. sessiliflora,* and *H. tenuifolia*). One species, *H. gardneri,* has been reported previously as $n = 5$ (Coleman, 1968), and another, *H. sessiliflora,* has been documented as $n = 6$ (Turner et al., 1967).

Because of the strong uniformity in chromosome levels among South American species of *Hypochaeris* (all $n = 4$ or $n = 8$), further comments on these two deviating reports are in order. The $n = 6$ report (Turner et al., 1967) for *H. sessilifolia* contrasts with more typical $n = 4$ (Jansen & Stuessy, 1980) or $n = 8$ (Olsen, 1980). Examination of the voucher of *H. sessilifolia* reported by Turner et al. (1967; *Wurdack 437,* TEX) with camera lucida drawing of meiotic bivalents attached, suggests that $n = 4$ is probable, with some homologous chromosomes being pulled apart in metaphase I/early anaphase I earlier than the others. Turner, in fact, wrote in 1977 (handwritten note on the voucher): "In hindsight and with more thought this could be n = 4II!" The voucher for the count of $n = 5$ for *H. gardneri* has not yet been located despite an herbarium search. It is worth mentioning that the European *H. glabra* with $n = 5$ is also known to be adventive in South America (e.g., Matthei, 1995; Bortiri, 1999). Because of the morphological variability of taxa of *Hypochaeris,* and hence difficulties with identification, an examination of the voucher for *H. gardneri* will be essential to reveal whether this represents a new aneuploid level in native species of the continent.

Karyotypes of all newly analyzed South American species of *Hypochaeris* are bimodal and asymmetric and similar in overall morphology to karyotypes of species analyzed previously (Figs. 1–15; see also references in Table 1). In general, they consist of two large and two small chromosome pairs. Two of these pairs, one large subtelocentric and one smaller acrocentric, appear to bear satellites. The other two pairs are most often acrocentric. Despite this general uniformity of karyotype and a reasonably stable chromosome number ($2n = 8$), consistent karyological differences among taxa do exist. The main differentiation of karyotype concerns chromosome size changes and the presence of satellites (Figs. 1–6, 8–15). A detailed analysis of karyotypes of South American *Hypochaeris* and their evolutionary importance will be reported elsewhere.

Although the emphasis in this paper is on new cytological reports of native South American species of *Hypochaeris,* additional reports for the introduced *H. radicata* are also included. This taxon is abundant in Chile (Matthei, 1995; pers. obs.), growing from sea level to over 2000 m and often found intermixed with native species. Because of the possibility of hybridization between *H. radicata* and native congeners, which could confuse interpretations of patterns and processes of evolution, sampling of this taxon was also included (Table 2). Results show the typical chromosome level ($2n = 8$; Fig. 7) for this species and symmetric karyotype and no irregularities, effectively excluding hybridization. Judging by chromosome number, the other weedy species of the genus, *H. glabra,* (distinctive with $2n = 10$, Stebbins et al., 1953), is much less common in South America, at least within Chile, and no representatives of this species have been examined cytologically during this study.

Tetraploidy ($2n = 4x = 16$) has been previously reported for four South American *Hypochaeris* species: *H. chondrilloides* (Wulff, 1998), *H. incana* (Moore, 1981), *H. sessiliflora* (Olsen, 1980), and *H. stenocephala* (Stebbins et al., 1953; Diers, 1961). For *H. chondrilloides* and *H. sessiliflora,* both ploidy levels ($2x$ and $4x$) were reported. The present paper adds three more species, *H. meyeniana* (Fig. 5), *H. scorzonerae,* and *H. tenuifolia* (Figs. 13, 14), in which infraspecific polyploid cytotypes are known. Karyological data provide some suggestions on the mode of origin of these tetraploid cytotypes. The $4x$ races in *H. tenuifolia* and *H. stenocephala* possess karyotypes consisting of four equal-sized sets of chromosomes. It is probable, therefore, that these polyploids are of autopolyploid origin. We suspect this to be the case also in *H. sessiliflora* (Fig. 8) and perhaps also for *H. chondrilloides* that contain both $2x$ and $4x$ cytotypes, although no detailed karyotypes are available for the latter. Understanding the origin of the apparently uniformly tetraploid

←

Figures 1–15. Mitotic chromosomes of South American species of *Hypochaeris.* Scale bar = 5 μm. —1. *H. acaulis, TS et al. 15565.*—2. *H. apargioides, TS 15485.*—3. *H. clarionoides, TS & PS 15527.*—4. *H. elata, RK Hyp-43.*—5. *H. meyeniana, MW 98/554.*—6. *H. palustris, TS et al. 15566.*—7. *H. radicata, TS & PS 15533.*—8. *H. sessiliflora, JG Hyp-38.*—9. *H. setosa, JGa 1048.*—10. *H. sonchoides, JG Hyp-36.*—11. *H. spathulata, TS & CB 15633.*—12. *H. stenocephala, MW & HF 97/119.*—13. *H. tenuifolia, TS & CB 15605.*—14. *H. tenuifolia, TS et al. 15510.*—15. *H. thrincioides, TS 15450I.*

Hypochaeris stenocephala and possibly *H. incana* (only one count known) will be important for documenting evolutionary mechanisms in the group.

Because of the close morphological and karyological similarity and evolutionary relatedness of South American species of *Hypochaeris*, special attention was given to searching for meiotic irregularities that might signal hybridization. Meiotic counts showed exclusively four regular bivalents in all examined populations. Previous reports on meiotic chromosome numbers have shown similar results (Wulff, 1992, 1998). Only experimentally obtained hybrids between *H. chillensis* and *H. megapotamica* showed some irregularities in homologous chromosome pairing with 4II and occasionally 3II + 2I (Wulff, 1992). Presumptive natural hybrids of *H. chillensis* and *H. microcephala* var. *albiflora*, however, showed regular bivalent formation suggesting the possibility of recent origin of these species and high degree of karyotype similarity (Wulff, 1992). Two instances in our own field collections suggested possible hybridization based upon morphological features: *H. apargioides* × *H. tenuifolia* (*TS et al. 15554*) and *H. palustris* × *H. tenuifolia* (*TS & CB 15607*). Because some differences in chromosome size and presence of satellites are obvious in the case of *H. apargioides* (Fig. 2) and *H. tenuifolia* (Fig. 13), hybrid individuals between these taxa should be detectable. These potential hybrids were found to be diploid, however, with no differences in size of chromosomes of the two haploid sets. Based on karyomorphology, possible hybrid origin of these populations is unsupported.

In contrast to broad cytological diversity among nine European species of *Hypochaeris* ($2n$ = 6, 8, 10, 12; Mugnier & Siljak-Yakovlev, 1987; Cerbah et al., 1998a), cytological uniformity of the New World members of the genus suggests several aspects regarding evolution of the group. First, because the karyotype of South American taxa represents only one general pattern, in contrast to several found among European species, it can be hypothesized that the former evolved from out of the latter. This hypothesis is also corroborated by recent molecular phylogenetic studies of nuclear (ITS; Cerbah et al., 1998b; R. Samuel et al., in prep.) and chloroplast (*trn*L; R. Samuel et al., in prep.) genes. Second, the abundance of South American taxa representing so many different growth forms and occurring in so many diverse habitats is strongly indicative of rapid and recent adaptive radiation. Third, the mechanisms of speciation accompanying this explosive evolution have clearly not been driven by gross macro-cytological alterations, such as dysploidy, euploidy, and marked karyotypic change. *Hypochaeris* represents a genus, therefore, in which perhaps more minor amounts of karyotypic, and certainly genetic, change has accompanied speciation. Because of this situation and due to the large and few chromosomes, the genus in South America provides an excellent opportunity to map the genome and determine minor karyotypic changes during speciation, within context of the relatively stable $2n = 8$ karyotype, as has been done successfully for *Helianthus* in North America (Rieseberg et al., 1995; Rieseberg, 2001).

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INVASION BIOLOGY: AN EMERGING FIELD OF STUDY[1]

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Peter S. White[3]

ABSTRACT

Biological invasions are increasingly recognized as a key problem for the conservation of biological diversity. However, the scientific recognition that some species, when introduced outside their native range, cause a decline in indigenous species, goes back to at least the writings of Charles Darwin. In the 1950s another British biologist, Charles Elton, wrote the first book attempting to describe the biology of invasive organisms. It was not until the 1980s, however, that the field of invasion biology as a discipline began to emerge. This emergence has resulted from two forces: the development of the scientific basis for invasion biology based on a substantial and accumulating literature, and the urgency of the invasive species issue because increased world trade and travel are increasing the frequency of invasions.

Key words: invasion biology, scientific history, Systematics Symposium.

THE HISTORICAL CONTEXT

Over the last 20 years biological invasions have gained growing attention from ecologists. From the rapid increase in both scientific and popular articles and books written about invasions one might conclude that invasions are a relatively new phenomenon. In fact, as humans first began to move around the earth, they took familiar plants and animals with them for use as food, medicine, or technology (Fritz, 1994). We know that maize was found in eastern North America when European explorers first arrived in the New World, yet this species is known to have originated in Mesoamerica. Its presence so far from its origin and its common use by Native Americans in eastern North America suggest that it was likely traded and carried by indigenous people to the region prior to the arrival of Europeans. And some species are known to "hitchhike" along with human travelers. The Polynesian rat (*Rattus exulans*) was probably brought to islands by the early Polynesians (Merlin & Juvik, 1992), most likely as an accidental introduction.

Charles Darwin provided the necessary context for understanding the biological invasion problem almost 150 years ago. One of the observations that stimulated Darwin to conceive of evolution by natural selection was that each new continent or island he visited, despite similar environments, had different species. He wrote (Darwin, 1859: 343): "In considering the distribution of organic beings over the face of the globe, the first great fact which strikes us is that neither the similarity nor the dissimilarity of the inhabitants of various regions can be wholly accounted for by climatal and other physical conditions. . . . There is hardly a climate or condition in the Old World which cannot be paralleled in the New . . . [yet] how widely different their organic productions [that is, their species]!" Today we understand fully that the diversity of species on our planet is, in part, the result of continental separation, producing the geography of life that so intrigued Darwin and all biologists since. However, this geography sets up one of the most profound threats to the Earth's diversity. Because the continents differ more in species than climates, each continent has the potential to provide invaders to other places. Humans are a potent force for assisting that invasion.

In their natural settings, species are found with friends and enemies. Darwin realized that this ecological context provided the ultimate check on unfettered population growth. Thus, there is another important perspective to the invasion problem: we

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often transport species without their coevolutionary context. This may result in poor performance (e.g., if a plant lacks a pollinator), but it may also result in the potential for rapid population growth (e.g., if the species is free from natural enemies or other constraints). Darwin (1859: 370) also recognized that some introduced species may threaten native species. In his chapter on geographical distributions he reported, ". . . many European productions cover the ground in La Plata, and in a lesser degree in Australia, and have to a certain extent beaten the natives. . . ." This may be the first scientific comment on invasions.

Although there were studies of invasions in the years since Darwin, biologists and ecologists did not focus on the magnitude of the growing problem until 1958 when Charles Elton ([1958] 2000) published a book that has come to be regarded as the seminal volume in this field of study. *The Ecology of Invasions by Animals and Plants* is a slim book borne from his observations as an animal ecologist. Three 1957 BBC radio broadcasts he developed on the subject of "Balance and Barrier" apparently stimulated Elton to write a book on invasions, aimed at a lay audience, that laid out what are still the fundamental issues in invasion biology: that each continent has its own unique flora and fauna, that human migration and trade were breaking down the barriers that had led to the uniqueness of the biota, and that this breakdown of the barriers could have severe consequences for the maintenance of diversity. The book is amazing in its prescience and yet was in large part underappreciated until the 1980s, when it became widely recognized that the invasion of non-native species was one of the biggest threats to naturally occurring species and ecosystems.

In 1982 the Scientific Committee on Problems of the Environment (SCOPE), a committee of the International Council of Scientific Unions, met in a general assembly in Ottawa. At that meeting the invasive spread of plants, animals, and micro-organisms introduced by humans outside their native ranges was identified as a problem of global concern, amenable to interdisciplinary synthesis. This determination led to a number of symposia held around the world in the mid 1980s and resulted in two important books (MacDonald et al., 1986; Mooney & Drake, 1986) that both address three important questions: (1) What are the factors that determine whether a species will be an invader or not?; (2) What are the site properties that determine whether an ecological system will be relatively prone to, or resistant to, invasion?; and (3) How should management systems be developed using the knowledge gained from answering these questions? Each symposium consisted of distinguished biologists, most of whom worked in related areas of study, though not specifically invasions, attempting to answer these questions from their understanding of the biota of their continent. These volumes (e.g., MacDonald et al., 1986; Mooney & Drake, 1986) serve as "state of the knowledge" documentation and are notable for their general lack of specific data on invasions. This was because there were few studies specifically on invasions from which to draw conclusions. Reading the chapters, it appears that more questions were developed than answered in the course of the symposia and book production. These books fueled the newly emerging field of invasion biology, as a generation of graduate students read the chapters and seized the opportunity to attempt to answer the questions derived during the SCOPE process.

In the approximately 15 years since the publication of the SCOPE books the field of invasion biology has not only influenced the content of many biological journals, but it has also developed its own journal (*Biological Invasions*, Kluwer Press), its own set of terminology, and its own set of raging scientific debates. While the SCOPE volumes provided the initial fuel for the scientific field of invasion biology, it was the mounting evidence of severe environmental degradation that focused the attention of so many people on invasions. For instance, invasive species were identified as significant threats to biodiversity at more Nature Conservancy preserves with completed conservation plans than any other type of threat, including development, fire suppression, and altered hydrology. In fact, 94% of those sites responding as of the summer of 2000 listed invasive species as a serious problem (J. Randall, The Nature Conservancy, pers. comm.). In 1998, a study found that invasive species were second only to habitat destruction and fragmentation in threatening endangered species in the United States (Wilcove et al., 1998). This study reviewed listing information for species proposed as endangered or threatened under the Endangered Species Act and found that 49% of the imperiled species were in that condition at least in part because of invasive species.

FUTURE CHALLENGES

With the recognition that invasive species are one of the most serious conservation concerns today, there has also been the recent realization that the problem is getting worse very rapidly. Globalization of trade and advances in technology mean that species are moving around the earth more frequently and are coming from some places, such as China, that have been closed off from most of the rest of the world during the last several decades. For instance, the Asian long-horned beetle (*Anoplophora glabripennis*), which is native to China and considered to be a pest there, was first detected in the Greenpoint neighborhood of Brooklyn, New York, in 1996. The United States Department of Agriculture subsequently determined that the insect arrived in solid wood packing material on goods imported from China. Not only are new pathways opening, but the journeys that used to take weeks by ship may now take hours by plane, allowing more organisms to survive the trip. Trade agreements and organizations such as the North American Free Trade Agreement (see NAFTA website, 2002), launched in January 1994, and the World Trade Organization (see WTO website, 2002), formed in January of 1995, limit the restrictions that signing countries can place on the entry of trade goods. Many invasive species are introduced either as trade goods themselves, in the case of some plants and animals, or as contaminants of trade goods, such as insects found in shipping dunnage and pallets.

Just as international trade has increased, so has pleasure travel. Tourism has become a major sector of the U.S. economy, with current figures of about $110 billion a year (up from about $26 billion in 1986). Over 46.5 million international visitors entered the United States in 1996, with a projected annual growth of 3–4% (Doggett, 1997), although tourism may decline over the next several years as a result of fears regarding safety in traveling. Travelers often inadvertently carry invasive species as hitchhikers on their person or property, but they also may intentionally bring in species. For instance, 16,997 international passengers checked during one week in May 1990 at the Los Angeles International Airport were found to be carrying 1357 lots of fruits and vegetables and 325 lots of animal products, for a total of 2635 kg of contraband material (U.S. Congress, 1993). They may bring species with them for personal use or as gifts for friends and family.

To address the problems caused by invasive species and the many pathways by which they enter, we must work with the deliberate intention of reducing the entry and impact of such species. As scientists, we will need to ensure that our science is not only viewed by our peers, as is traditional, but that agencies managing invasive species are also aware of our findings. As scientists we must learn from the past, examine the present, and plan for the future. As the field of invasion biology moves into its adolescence, it will continue to test theories basic to ecology and to form new hypotheses to address the novel situations that arise following the introduction of new species. These discoveries, if implemented in management and policy practices, may play a substantial role in lessening environmental degradation through invasions.

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THE THREAT OF INVASIVE ALIEN SPECIES TO BIOLOGICAL DIVERSITY: SETTING A FUTURE COURSE[1]

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ABSTRACT

Over the past decade, mounting evidence has shown the pervasive and escalating harmful impacts of invasive alien species on native species and ecosystems. Thousands of non-native species are established in the United States and many more worldwide. Few areas appear immune to invasions, some of which unfold over decades to centuries as species' ranges slowly expand across the landscape. A plethora of ecological effects have been attributed to invasive species, and other global change processes and widespread habitat destruction will likely multiply these effects. Many conservationists now consider invasive species among the top threats to biological diversity and are grappling with identifying pragmatic, effective solutions. They know that the future will involve mixed assemblages of native and non-native species and have important questions about which invasive species to tackle and which ones to ignore, and even whether to deliberately introduce certain species for restoration. Addressing these issues will push hard against the limits of today's ecological knowledge and our ability to predict the long-term ecological consequences of such decisions. Better envisioning the conservation goals, though, could help to guide the science.

Key words: biological diversity, conservation, global change, invasive species, management, policy, research needs.

> *"Nowadays we live in a very explosive world, and while we may not know where or when the next outburst will be, we might hope to find ways of stopping it or at any rate damping down its force. It's not just nuclear bombs and wars that threaten us, though these rank very high on the list at the moment: there are other sorts of explosions . . . ecological explosions. . . . Ecological explosions differ from some of the rest by not making such a loud noise and in taking longer to happen . . . but they can be very impressive in their effects. . . ."*
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> —Charles Elton ([1958] 1972: 15)

Thus did the British ecologist Charles Elton, in his 1958 book *The Ecology of Invasions by Animals and Plants,* forcefully make the case that species translocations due to human activities are transforming the biological world and help inspire the now burgeoning study of invasion processes and impacts. Elton built a series of revealing case studies, describing, for example, how chestnut blight, *Cryphonectria parasitica* (Murrill) Barr, virtually eliminated the American chestnut from eastern U.S. forests during the early 20th century and how parasitic sea lampreys, *Petromyzon marinus* (L.), native to the Saint Lawrence River and Lake Ontario, migrated up the Welland Canal after 1829 to decimate the Great Lakes' trout fishery.

Today, Elton's case has been bolstered by hundreds of more recent invaders, like common crupina (*Crupina vulgaris* Cass.), Asian tiger mosquito (*Aedes albopictus* Skuse), and the zebra mussel (*Dreissena polymorpha* Pallas) (Craig, 1993; MacIsaac, 1996; Roche & Thill, 2001; Strayer et al., 1999). However, although the quote above may be just as true as it was in 1958, the context of biological invasions has changed significantly.

Rates of species invasions have escalated, and new patterns of species translocation have emerged. For example, the end of the Cold War, globalization of trade, and free trade agreements have connected previously isolated parts of the world and increased rates at which cargoes move among them (e.g., OTA, 1993; McNeely, 2001). Improved transport technologies and increased numbers of species in trade mean that more species are being shipped and shipped more rapidly around the globe and, consequently, that more are surviving in transit and becoming established in new areas. Accelerating rates of habitat destruction, climate change, and

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other global change phenomena are disrupting native species assemblages and creating new invasion opportunities (e.g., Mooney & Hobbs, 2000, and papers therein; Chapin et al., 1997).

At the same time, there is reason for optimism. Worldwide efforts to reduce international transfers of invasive species, particularly those that harm agriculture and other economic interests have grown significantly over the past half century (e.g., McNeely, 2001). A broad commitment to the conservation of biodiversity has emerged as manifested in international treaties such as the Convention on Biological Diversity [see Internet Resources] and in national laws, such as the U.S. Endangered Species Act of 1973 [see Internet Resources]. Reducing the ecological threat that invasive species pose to biodiversity is an important part of these efforts, and our technical capacity to do so has grown. In comparison to the 1950s, today's richer scientific understanding of invasion processes and impacts provides a much stronger basis for targeting efforts and for designing effective prevention and control strategies.

For those engaged in the conservation of biological diversity, then, the picture is one of urgency and hope: Urgency, because the threat is imminent and largely irreversible if left unchecked; Hope, because the opportunities for actions that would contain this threat have never been greater.

IMPACTS OF INVASIVE SPECIES ON BIOLOGICAL DIVERSITY

"Invasive species" here refers to non-native species that become established in new locations, spread, and then cause ecological or economic harm or threaten human health. This definition is consistent with recent uses in U.S. policy, such as Executive Order 13112—*Invasive Species*—signed by President Clinton in 1999 (Clinton, 1999). Note, however, that it differs from strictly ecological definitions of "invasions" and "invasive," such as the ones provided by Richardson et al. (2000) and Rejmanek et al. (2002), which focus on the biological attributes of a species that enable it to spread and become established in new locations.

Rough estimates are that invasive species, as defined here, comprise about 10–20% of the non-native species that have become established outside of human cultivation in free-living populations, or more than 650 to 1750 species of plants, animals, and plant pathogens in the United States (cf. [Williams & Meffee, 1996]; OTA, 1993; Williamson & Fitter, 1996). Their ecological impacts range from local suppression of single native species to species extinction and wholesale changes in the functioning of ecosystems (for detailed summaries of impacts see OTA, 1993; [Williams & Meffe, 1996]; Mack et al., 2000; Ewel et al., 1999; Randall, 2000).

Perhaps the most frequently documented effects of invasive species are their suppression of native species populations through predation, competition, parasitism, or disease. A recent example is the Asian swamp eel, *Monopterus albus* (Zuiew), a fish originally from tropical to warm temperate portions of east Asia that was first detected in Florida and Georgia in 1996, possibly following escape from aquaculture facilities or intentional releases of aquarium specimens [Benson et al., 2001]. Populations of native fishes apparently have declined in areas where this generalist predator has become established [Benson et al., 2001]. The eventual full impacts of the Asian swamp eel in the U.S. are as yet uncertain, but the fish's capacity to tolerate extended periods out of water and at low temperatures suggest its range and associated impacts will expand.

Certain invasive species hybridize with congeneric native species. At a minimum, this alters the gene pool of the native species, sometimes in maladaptive ways. At a maximum, introgression can eventually allow genetic hybrids or the invasive species to completely displace the native species. A recent well-documented example is the invasion of San Francisco Bay salt marshes by smooth cordgrass (*Spartina alterniflora* Loisel.), originally from the Atlantic and Gulf coasts of the United States (Anttila et al., 2000; [San Francisco Estuary Invasive Spartina Project, 2002]; Vila et al., 2000). *Spartina alterniflora* hybridizes with the native *Spartina foliosa* Trin., although rarely, and the resulting hybrids outcompete the native cordgrass, spread clonally, and interbreed with both parental species (Anttila et al., 1998, 2000; Ayres et al., 1999; Vila et al., 2000). Where they have displaced the native cordgrass, the non-native species and the hybrids alter marsh architecture, because, in comparison to the native species, they grow taller, thrive in deeper water, and form denser rhizome mats that trap sediments and raise marsh elevation. These attributes enable the invading species and hybrids to expand into large areas that previously were open mudflats, displacing communities of algae and invertebrates associated with mudflats and reducing foraging resources for certain migratory waterfowl and other animals (Callaway & Josselyn, 1992).

The impacts of certain invasives on native species are indirect—mediated by the altered behavior or other characteristics of intermediary native species that are not themselves harmed. Invasive plants that have showy floral displays, like purple loosestrife (*Lythrum salicaria* L.), have the potential to alter the abundance or behavior of insects that pollinate native plants and thereby indirectly affect native plant reproduction and fitness (Grabas & Laverty, 1999; Brown et al., 2002). Certain invasive shrubs may indirectly reduce the reproductive success of native songbirds, because their architecture and lack of sharp thorns allow predators greater access to songbird nests than do native shrubs (Schmidt & Whelan, 1999).

The most harmful invasive species are those that have system-level impacts, fundamentally altering the ecological processes that structure communities and ecosystems (Vitousek, 1990). A well-known example is melaleuca, *Melaleuca quinquenervia* (Cav.) S. T. Blake, an Australian tree that has spread and become locally abundant in Florida's Everglades. The tree forms dense thickets that trap sediments and debris and elevate the topography. Because of the plant's high rates of evapotranspiration, melaleuca appears to draw down water levels and alter the hydrology of areas where it becomes abundant (Schmitz et al., 1997; Hofstetter, unpublished data). Melaleuca is pyrogenic and increases the temperature and duration of fire. Overall, the tree is fundamentally changing habitats across Florida's "River of Grass" and diminishing recruitment in these wetland habitats of native plants and their associated faunas (e.g., Gordon, 1998).

The zebra mussel, *Dreissena polymorpha*, is another invasive species that is causing broad system-level effects (MacIsaac, 1996; Strayer et al., 1999). The mussel directly suppresses native freshwater bivalves by overgrowing and smothering them. Dense accretions of zebra mussels on hard and soft lake bottoms create new habitat space for benthic invertebrates. Because the mussels' efficient filter feeding clears the water of algae that previously supported pelagic predators, zebra mussels have fundamentally transformed the food web dynamics of places like the Great Lakes. Most production and biomass now occur in benthic parts of these systems, whereas pelagic production and biomass once dominated (MacIsaac, 1996).

Certain invasive species facilitate the establishment of other non-native species or exacerbate their harmful effects. The laurel fig, *Ficus microcarpa* L. f., for example, was introduced into Florida in 1912 as an ornamental tree, but only became invasive about 45 years later when its natural pollinator, a fig wasp specific to *F. microcarpa*, was introduced. The laurel fig has now been reported from 18 of Florida's natural areas, including the Big Cypress National Preserve and the Loxahatchee National Wildlife Refuge (Langeland & Burks, 2000). Simberloff and Von Holle (1999) have hypothesized that "invasional meltdown"—accelerating impacts on native ecosystems—occurs because of the synergistic interactions among repeated species invasions.

By suppressing native species populations and altering habitats and ecosystems, invasive species have contributed to the imperilment of nearly half of the plants and animals now considered rare, threatened, endangered, or extinct in the United States (Wilcove et al., 1998). According to an analysis by Wilcove et al. (1998), non-native species are the second most frequent cause of species imperilment; the most frequent cause is habitat degradation and loss.

In addition to the nearer-term ecological impacts discussed above, species invasions also may be potent drivers of evolutionary change (e.g., Grosholz, 2002; Mooney & Cleland, 2001; Sakai et al., 2001). Some invading species may pass through an evolutionary "bottleneck," for example, if certain phenotypes survive the pathway of species transit or if the receiving environment imposes strong selective pressure on invading populations. Conversely, successful invaders may cause genetic changes in populations of native species by hybridization or by qualitatively or quantitatively altering selection pressures through ecological interactions or through changes in important habitat qualities or ecosystem processes. Many examples exist of hybridization between invasive non-native plants and closely related native species yielding fertile, and in some cases, highly competitive hybrids or new species that are reproductively isolated from both parents by mechanisms such as polyploidy (Vila et al., 2000; Mooney & Cleland, 2001).

Implications for Conservation

Rich case histories and a large body of anecdotal evidence have dominated our understanding of invasive species impacts on native species and ecosystems. Synthesizing this information into a more cohesive picture has proven challenging for conservationists seeking to ensure the long-term survival of native species and ecosystems. This has contributed to the relative slowness with which the environmental community has recognized the importance of invasive species as a major threat to biodiversity, and one whose impacts can be significantly reduced by effective action.

Here we describe how one major conservation organization, The Nature Conservancy (TNC), has developed an overarching assessment of the threat that invasive species pose to biological diversity. TNC is one of the world's largest place-based conservation organizations, working at thousands of locations around the world. The organization's methods for selecting and designing conservation sites have evolved significantly over the past 12 years to include the identification of conservation threats and their solutions at multiple spatial and ecological scales. From this new methodological rigor, a new picture has emerged of how pervasive and significant invasive species are in the organization's work and for biodiversity conservation in general.

The Conservancy selects sites for conservation action through the process of "ecoregional planning"—a stepwise process that uses ecoregions as the basic planning unit (Groves et al., 2002; [TNC, b]). Each ecoregional plan identifies a collection of "conservation areas" required to fully protect the ecoregion's biological diversity. Invasive species were identified as among the top threats to TNC's conservation targets in 15 of 18 completed ecoregional plans for North American ecoregions in a summary completed in 2000 (Groves & Valutis, unpublished data). Habitat destruction was the only other threat that was cited more frequently in the plans.

A site plan is prepared for each of the conservation areas where TNC works or intends to work. Each plan formally assesses the relative severity of known threats to the area's biodiversity—such as unsustainable timber harvest, altered hydrology, second home development, or invasive plants—and sets priorities for actions to abate or mitigate these threats. Examination of plans for 89 conservation areas from 39 North American ecoregions showed the majority (94%) listed invasive species as a critical threat to biodiversity at the site [TNC, a, 2000]. Among these plans, invasive species were the site-level threat most often assigned high priority due to significance and irreversibility.

Implementing a conservation area plan often involves direct ecological management of natural communities. In 1998, The Conservancy's Invasive Species Program conducted a survey of all TNC staff in the U.S. with land management responsibilities [TNC, c]. A total of 110 responses were received from staff working at 916 conservation areas encompassing more than 2 million acres. The managers identified 216 invasive plant species infesting 810 (88%) of the conservation areas covered by the respondents. Table 1 provides an illustrative list of invasive plants considered a serious threat at many of these places or over a large geographical area. The particular invasive plants considered problematic varied greatly among TNC's conservation areas. Of the 216 species, managers identified 175 as a serious threat to at least one conservation area. Most respondents (over 80%) considered invasive plants one of their top 10 management concerns, with 49% of the respondents identifying invasive species as one of their top 3 management concerns.

Table 1. Examples of plant species identified as a serious threat to many sites or across a large geographical area by TNC managers[a].

Lonicera japonica Thunb. (Japanese honeysuckle)
Phragmites australis (Cav.) Trin. ex Steud. (common reed)
Lythrum salicaria L. (purple loosestrife)
Alliaria petiolata (M. Bieb.) Cavara & Grande (garlic mustard)
Cirsium arvense (L.) Scop. (Canada thistle)
Rhamnus cathartica L., *R. frangula* L. (syn. *Frangula alnus* Miller) (buckthorns)
Euphorbia esula L. (leafy spurge)

[a] This Table includes species identified based on the number of conservation areas and acres they affect and by how frequently managers identified them as a serious threat to rare species or habitats. The list is for illustrative purposes only and is not intended to set priorities for conservation actions. The list is biased by the geographic distribution of survey respondents and relative size of different conservation areas. Other highly ranked species included tamarisk (*Tamarix* spp.), reed canarygrass (*Phalaris arundinacea* L.), and spotted knapweed (*Centaurea maculosa* Lam.).

Garlic mustard, *Alliara petiolata* (M. Bieb.) Cavara & Grande, is one example of the kind of invasive species that TNC is tackling. The plant, first detected in 1868 in Long Island, New York, now occurs in 20 eastern and midwestern states and has recently been observed in Washington, Colorado, Idaho, and Alaska (Nuzzo, 1993, [2000]; [Tu & Rice, 2001, 2002]; Rice & Johnson, in press). Garlic mustard invades forest understory, where it apparently displaces native herbaceous species, particularly spring ephemerals, and reduces survival of tree seedlings in some areas (Anderson et al., 1996; McCarthy, 1997). Evidence suggests the weed also reduces the fitness of at least two native butterflies because, although garlic mustard attracts these insects, eggs laid on the plant have lower survivorship than those laid on native host plants (Bowden, 1971; Porter, 1994). Of additional worry to conservationists is that controlling the plant is usually labor-intensive, often difficult, and sometimes impossible [Nuzzo, 2000].

Feral pigs (*Sus scrofa* L.) provide a graphic example of the kinds of problems conservationists face with invasive animals. The pigs cause damage by uprooting and killing native vegetation and thereby opening areas for colonization by invasive plants that further alter the system. Feral pigs cause severe problems in conservation areas across the U.S., ranging from the Great Smoky Mountains

National Park in Tennessee and North Carolina to Santa Cruz Island off the coast of southern California to Haleakala and Hawaii Volcanoes National Parks in Hawaii (Aplet, 1990; Bratton et al., 1982; Hone & Stone, 1989; Hone, 1995; Singer, 1981). In Hawaii, for example, subsequent recruitment of non-native plants, such as the nitrogen-fixing Portuguese fire tree (*Myrica faya* Aiton), into areas disturbed by pigs alters fundamental ecosystem processes and initiates a cascade of other species changes (Aplet et al., 1991; Vtorov, 1993).

The compelling picture emerging from The Nature Conservancy's efforts at all levels is that invasive species are a high-priority threat to biological diversity that must be addressed now. Many in the organization believe that invasive species pose a fundamental risk to the biological diversity that TNC and partner organizations once thought was already successfully conserved on millions of acres and in numerous aquatic and marine systems. In response, TNC is presently mounting a major, multi-year organizational initiative to address the invasive species threat. (For further information see ⟨http://tncweeds.ucdavis.edu/isi.html⟩ or contact the initiative's Executive Director, Ann Bartuska, at abartuska@tnc.org.)

SETTING A FUTURE COURSE

A picture has emerged over the past decade of the full impacts of invasive species on the world's biological diversity, economies, and human health. Paradoxically, the very breadth and depth of these impacts may hold the key to a solution as the many constituencies affected by species invasions—such as conservation, agriculture, forestry, tourism, public health, horticulture, and others—combine their energies in finding common solutions to shared challenges [e.g., National Invasive Species Council, 2001]. Understanding has also grown over the past decade of the potential policy and management strategies for reducing the invasive species threat as well as a set of key questions that can only be solved by scientific research. This section identifies several critical science challenges that lie ahead.

PREVENTION, EARLY DETECTION, AND RAPID RESPONSE

Improved prevention—at scales ranging from the continental to the small nature preserve or sub-watershed—will be the most effective way to minimize the numbers and impacts of future species invasions. This will require scientific and technical advances that enhance our ability to understand and predict invasion pathways, to assess the risks of proposed species introductions, and to detect and manage new incipient species invasions. It also will require national and international policies that flexibly and rapidly integrate these advances into operational practices [e.g., National Invasive Species Council, 2001]. A new level of collaboration among ecologists and other researchers, engineers, and policy experts thus will be essential to the success of future prevention efforts.

Issues related to international trade demonstrate the need for tighter linkages between scientists and policymakers to improve prevention. Because of the dual trends of globalization and trade expansion, incorporating measures to minimize new invasions is both more urgent and more difficult. Inspections, quarantines, and other forms of screening must be rapid and compatible with free-trade agreements already in force or pending. This will require improved technology, transparent rationales for excluding certain species, and control actions that complement any exclusion actions within each nation or trading bloc. Policies under development (e.g., the new U.S. National Management Plan [National Invasive Species Council, 2001]) include science and research agendas specifically designed to meet current and emerging information needs that derive from policy innovations.

Developing criteria and systems for accurately predicting which species are most likely to become harmful invaders if introduced to a given area is one of the most important technical challenges ahead. Weed Risk Assessment systems to evaluate new species proposed for intentional introduction have already been implemented in Australia (Pheloung et al., 1999). In addition, representatives of the U.S. nursery industry and other user groups have recently moved to develop a voluntary "code of conduct" for reducing the risks of new plant introductions (Randall et al., 2002). These and other systems proposed by researchers (e.g., Reichard & Hamilton, 1997; Rejmanek, 1996) are being scrutinized for possible modification and use in Hawaii and other parts of the world (Daehler & Carino, 2000). Further analysis of their performance will help improve these systems and offer insights into how systems for other taxa and other areas could be devised (Kolar & Lodge, 2002).

Even with improved prevention systems, at least some new invasions will continue. Many might be contained or even eradicated if detected early enough, and general agreement exists that better early detection systems are needed [e.g., National Invasive Species Council, 2001]. Research discoveries that improve our ability to search for and detect new invasions will be crucial to making such plans work. For example, spatially explicit models that predict where new invasions are most likely to occur and how they would spread from sites of initial establishment could greatly improve the efficiency of searches (e.g., Higgins et al., 2000; Wadsworth et al., 2000). Easily accessible and networked databases that accept reports of new species and locations and that automatically notify officials in the affected area would allow such information to be acted upon rapidly. Accessible taxonomic keys that have multiple entry points or perhaps even on-line services that can identify species from scanned images would allow many thousands of land managers and other interested citizens to integrate their observations into these early detection systems (e.g., Brooker et al., 1999).

A FUTURE OF MIXED SPECIES ASSEMBLAGES

Even with well-supported prevention programs in place, a need will exist to manage invaders. Many harmful species are already established. Others presently under human cultivation may some day start to spread beyond cultivation, become firmly established in the wild, and cause problems after long lag periods. And at least a few new invaders are likely to elude even the most exemplary prevention efforts. Consequently, invasive species are not a problem that can be "solved" or "engineered away"; rather this is a problem that will require continuous management into the future.

Natural resource managers and conservationists routinely face chronic shortfalls of money and staff time in the face of urgent needs. Since they cannot do everything, they must set priorities and tackle the most important problems first, often leaving lesser problems unaddressed altogether. In many natural areas, the number of established invasive species or the area infested already far exceeds local management resources. Many natural area managers therefore take a "triage" approach and attempt to set priorities by identifying which species, if any, are most detrimental to the native species, communities, and ecosystem processes they are seeking to protect (see, for example, the weed control plan for TNC's Cosumnes River preserve in California available at [TNC, d]).

Several decision-support frameworks are available to help managers set priorities. These frameworks operationalize current ecological knowledge about individual invasive species—their impacts, current and projected distribution range, and ease of management. For example, The Nature Conservancy's Weed Management Plan Template contains guidance on how to set priorities among invasive species and among specific invaded portions of a preserve [TNC, c]. The U.S. National Park Service (NPS) supports an online invasive plant ranking system that calculates a score used for assigning relative management priority to each invasive plant species at a site (Heibert, 2001). Importantly, the NPS system evaluates species' impacts relative to the conservation goals for a specific site and explicitly balances projected impacts of invasive species against management feasibility and costs. These systems warrant further testing and improvement, and similar priority-setting is needed for other groups of invaders (e.g., insect invaders, fish, aquatic invertebrates).

An implicit assumption underlying such priority-setting approaches is that conservation in the future, for some sites, will involve managing mixed assemblages of native and non-native species. Yet the focus of many site managers remains primarily on how to eliminate or sharply reduce the abundance of particularly harmful invaders. In some systems and with some invaders effective control has proven to be extremely difficult and sometimes impossible, however. For example, attempts to control of cheatgrass (*Bromus tectorum* L.) across large expanses of the intermountain West have had very limited success despite many and varied attempts dating back over 50 years (Mack, 1986; Upadhaya et al., 1986; Young & Evans, 1985).

In contrast, we believe conservation practitioners must allocate their resources first toward sustaining native species and communities and retaining, restoring, or mimicking critical ecosystem processes, such as fire regime or periodic flooding (e.g., Randall et al., 1997; Stromberg & Chew, 2002a). Sometimes this may mean allowing certain invasive species to persist. In others, it may even mean managing a non-native species to maximize the conservation value of an area. For example, in some cheatgrass-infested areas, rather than seeking to control the cheatgrass, limited management dollars might better be used for planting other native grasses and shrubs, preventing frequent fires, and scattering seed periodically to ensure reliable, season-long availability of foods required by native rodents and their predators. Modeling, demonstration projects, and monitoring and adaptive management will be necessary for this approach to succeed.

Managers are already using this tactic in Hawai'i Volcanoes National Park, where fire-promoting invasive grasses have converted much of the seasonally dry woodlands to alien grass savanna (Tunison et al., 2001). Rather than seeking to directly control the non-native grasses and restore the original woodlands, management actions emphasize "rehabilitation"—the identification and establishment of fire-tolerant native trees and shrubs that potentially will persist and spread in the savannas now dominated by alien species.

Approaches like these that involve managing mixed assemblages of native and non-native species test the limits of existing ecological knowledge. Practitioners rarely have information about the likely long-term impacts of the management choices they make today on the future structure and function of ecological communities and ecosystems. This is one of the chief shortcomings of current approaches and of the information base that has been supplied by prior research. The field of biological control, a particularly rich discipline in invasion biology, provides an instructive example. Although recent advances in selecting introductions of control agents promise to reduce ecological impacts on non-target species (McEvoy & Coombs, 1999), methods do not yet exist for assessing effects of biocontrol introductions on ecosystem functions, such as the recently documented impacts in Hawaii on food web dynamics (Henneman & Memmott, 2001). An emphasis on long-term research and the development of spatially explicit models and forecasting approaches to predict the long-term ecological impacts of today's management choices and defaults could help to remedy this gap.

CONSERVATION AT LARGE SPATIAL SCALES

An important paradigm shift is under way in the spatial scale of conservation efforts. Increasingly, conservationists are focusing on conserving areas that are large enough to sustain dynamic ecological processes and functioning ecosystems in addition to populations of rare species and examples of natural community types. This shift, from preserves of hundreds of acres to conservation areas that are tens of thousands to millions of acres in extent, brings new challenges in addressing invasive species. For example, controlling local infestations of invasive plants and restoring native vegetation are relatively straightforward for small conservation areas like The Nature Conservancy's 76-acre Blowing Rocks Preserve in Florida where mechanical removal, spot applications of herbicides, and direct planting of native species are standard practices (Randall et al., 1997). Consider how infeasible such approaches are for large areas, such as the 250,000-acre Demonstration Weed Management Area along the Snake River that encompasses parts of Oregon, Washington, and Idaho!

The profound mismatch that currently exists between the large spatial scale required to conserve dynamic ecosystems and the small spatial scale of standard methods for detecting, monitoring, and managing invasive species has and should continue to fuel interest in technologies and management methods that can operate at very large spatial scales. Remote sensing data applied in GIS formats, for example, promise to provide cheaper and more effective ways to detect and track the spread of new weed infestations—and therefore effective ways to eradicate or contain invasions early (e.g., Everitt et al., 1995; Andrews, 2001). Landscape analyses of invasion patterns may help identify emerging pathways of species spread and provide a way for targeting resources to reduce species transit and to monitor for new invasions (Thompson, 1999). Creating "nodes" of native species that serve as source populations and seed banks might enhance the recruitment and persistence of native species in certain systems dominated by invasive species (Tunison et al., 2001). Finally, considerable interest exists in whether or not management prescriptions, such as large-scale patterns of grazing, prescribed fire, or flooding and hydrology, that target abiotic or biotic ecosystem processes will provide cost-effective ways to suppress populations of invasive species and yield conditions that favor native species (e.g., Koebel, 1995; Randall et al., 1997; Thysell & Carey, 2001; Stohlgren et al., 1999; Stromberg & Chew, 2002b).

INTERACTIONS WITH OTHER GLOBAL CHANGE PROCESSES

Ours is a time of dramatic and escalating change in the world's biota. Over the near-term, invasive species and habitat loss and fragmentation due to land use change and changing resource exploitation patterns will continue to be the major drivers of such change (Vitousek et al., 1996; Mooney & Hobbs, 2000, and papers therein). Less well understood, but at least equally important over the long-term, will be the biological changes wrought by nitrogen deposition, enhanced CO_2 levels, and changing temperature and precipitation patterns (e.g., Mooney & Hobbs, 2000). The magnitudes and qualitative details of most global change processes have as yet proven difficult to predict.

Nevertheless, all of these global change processes will interact with one another to yield cumulative impacts on the distribution and abundance of species, the composition of ecological communities, and the functioning of ecosystems. Climate change, nitrogen deposition, and ambient CO_2 levels all will have profound effects on the pool of potential invading species, potential invasion pathways, and the suitability of native habitats for colonization (Mooney & Hobbs, 2000, and papers therein). The shift in CO_2 concentration from the pre-industrial level of 280 ppm to 364 ppm today may already have begun to benefit certain plant invaders like cheatgrass (*Bromus tectorum*), and levels are expected to rise further to 560 ppm within 100 years (Dukes, 2000).

Climate change is expected to result in the disassembly of many terrestrial and aquatic ecological communities as species ranges and abundances shift in response to changing temperature and precipitation patterns and associated changes in fire frequency and other disturbances (e.g., Chapin et al., 1997). This will greatly enhance opportunities for new invasions (e.g., Walther, 2000). The process also is likely to change the ecological impacts of certain invasions, their management potential, and even the possible and desired endpoints of conservation management activities. An important, and largely unanswered, question, in light of the combined impacts of various global change processes, is whether some of the invasive species that we choose to control today will become acceptable or even desired species at some sites tomorrow.

CONCLUSION

Invasive species have emerged as one of the key threats to the world's biological diversity. Today's richer scientific understanding of invasion processes and of management and policy approaches for reducing impacts forms a strong foundation for taking effective action to reduce this threat. Tighter linkages between scientists and policymakers will be essential over the near term to improve the prevention of new invasions and to enable more rapid detection and response to the new invasions that do occur. The critical science challenges ahead include developing ecological forecasting approaches to help set management goals for mixed species assemblages, building methods to effectively address invasive species and promote native species and communities at large spatial scales, and determining how the interactions among various global change processes should alter how conservationists consider and respond to species invasions.

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PLANT NATURALIZATIONS AND INVASIONS IN THE EASTERN UNITED STATES: 1634–1860[1]

Richard N. Mack[2]

ABSTRACT

Plant immigrants to North America arrived from Europe with the first human immigrants, products of the intense incentive early colonists felt to transplant European agriculture into the Western Hemisphere. Among early deliberate and accidental introductions were species that would soon become naturalized in eastern North America: *Artemisia absinthium, Hyoscyamus niger, Plantago lanceolata,* and *Taraxacum officinale.* The naturalized flora grew as species for food, forage, seasonings, and medicine were imported, cultivated, and escaped the bounds of cultivated fields. Importation of what has become the most common category of naturalized species, erstwhile ornamentals, had a modest beginning by the mid 17th century. The first recorded invasion, the spread and proliferation of *Linaria vulgaris* in the Mid-Atlantic colonies, was recognized by the mid 18th century, and *Berberis vulgaris* was rampant in southern New England before 1800. Botanical records, including published floras, became much more common in the first decades of the 19th century and reveal a naturalized flora in the U.S. that was quite similar in composition to the agricultural weed flora of Western Europe. Many ruderals and agricultural weeds were widespread in the eastern U.S., but probably not invasive by 1860, and included *Bromus secalinus, Cynoglossum officinale, Galium aparine,* and *Senecio vulgaris.* Other alien species had, however, become invasive by the 1840s, such as *Echium vulgare* in Virginia. Species that were to form devastating invasions in the United States from 1860 onward (e.g., *Bromus tectorum, Euphorbia esula, Lonicera japonica, Melaleuca quinquenervia*) had either not arrived by 1860, were undetected, or were not reported as having escaped from cultivation. Growth of the naturalized flora and the subsequent number of invasive taxa was certainly facilitated, and probably sparked, by the enormous growth of railroads and rail-borne commerce in the late 19th century.

Key words: *Berberis vulgaris,* biological invasion, John Bartram, *Echium vulgare, Linaria vulgaris,* naturalization, ornamental plants.

> "*. . . Behold, I have given you every herb bearing seed, which is upon the face of all the earth and every tree, in the which is the fruit of a tree yielding seed; to you it shall be for meat.*"
>
> —Genesis 1: 29. Bible, King James version

The first European human immigrants to North America had special reason to believe fervently in these words of Scripture. In transporting their families to a New World about which they knew little, they needed to believe that a Higher Authority would provide for their welfare. Most also firmly believed that God provided through the deliberate planning and industry of the faithful. Each band of European colonists to North America, whether the 16th century Spanish or Portuguese colonists (Crosby, 1972), 17th century English colonists to Maryland (Hall, 1910: 92), or the Pilgrims to New England (Young, 1846: 42), did not trust their survival to the happenstance acquisition of food in the New World. From the outset, each group transferred crops and domesticated animals upon which they based their resolve to establish European agriculture in the New World (Mack, 2001, and references therein).

These determined attempts by European colonists and their American descendants to introduce non-indigenous plants in what was to become the United States have had profound and lasting influence on the floristic composition of North America's natural communities, and have largely determined which species have proved troublesome in agriculture, forests, rangelands, and inland waterways and lakes (Westbrooks, 1998). The size of the current naturalized, i.e., permanent non-indigenous, flora of the U.S. is not known precisely but exceeds 2500 species (Kartesz & Meacham, 1999). Of these, a small minority have become invasive, i.e., prolific and occupying significant new (i.e., non-native)

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ranges. These species, along with many other naturalized species, have caused enormous environmental and economic damage that ranges from threatening native biodiversity to changing the operation of major ecosystems (Mack et al., 2000; Pimentel et al., 2000).

European settlements in North America arose from fledgling colonies of immigrants that stemmed from different countries in western Europe and were established at different times and at widely spaced locales (Quinn, 1990). This mixture of circumstances and events suggests that the current naturalized flora has had a diverse origin and varied circumstances surrounding its eventual persistence. This diversity spawns a series of questions. What has been the chronology of plant naturalizations? More importantly, what can be deduced from that chronology about the circumstances that led some species to become naturalized early in the Europeans' history in North America, while other species became established much later? Which species, if any, formed pre-1860 invasions, and what sparked the demographic transitions among those few naturalized species that became invasive (Crooks & Soule, 1999; Kowarik, 1995)? What role have species introduced long ago into the U.S. continued to play in their new ranges? For instance, have they been supplanted by more recently arriving immigrants (Mack, 1989)? I chose to examine these issues for the period between 1634, the first records I am aware of for plant naturalizations, and 1860, before onset of the American Civil War and the enormous changes in the economy and transportation that so affected the U.S. for the rest of the 19th century and beyond (Kuznets et al., 1960; Meinig, 1986). These questions about plant entry, establishment, and their potential proliferation in new ranges must be considered because species' past immigration histories form part of the information upon which the prediction of future invasions will continue to rely (National Research Council, 2002).

METHODS

Any assessment of species that became naturalized long ago is intrinsically retrospective, and the record is incomplete and often fragmentary. Four general sources that vary substantially in potential accuracy and detail can be used in assembling this record.

(1) Herbarium specimens provide unequivocal evidence for accurate species identifications. Consequently, they may form the best category of evidence, provided the collection dates and locales are accurate. Unfortunately, the number of existing herbarium specimens across the time period under consideration here is meager. Few pre-1860 U.S. specimens still exist; even fewer have survived from pre-1800. Their use remains an unfulfilled goal here.

(2) Pollen records can provide some supplemental information (Brugam, 1978) but are limited in their usefulness because many pollen taxa are impossible to identify with light microscopy and for some families, such as Poaceae, only a few genera are possible to identify in this way (Moore et al., 1991).

(3) Contemporary regional floras became much more common after 1800, e.g., Pursh (1814) and Torrey (1819), and can be enormously informative.

(4) The most common tool examined here consists of contemporary records and correspondence of those who provided first-hand accounts of the species they saw, their ranges, and abundances (e.g., Josselyn, 1672; de Schweinitz, 1832; Dwight, [1821] 1969; Gray, 1842).

Herbarium specimens, floras, and other records vary substantially in accuracy and scope, and until the later part of the 18th century, almost all employed only common names. I have cross-checked the common names (e.g., Fernald, [1950] 1987; Kartesz & Meacham, 1999) and avoided a species citation unless I could be confident of the identification. I have been similarly conservative in assigning an areal extent to any non-indigenous species. Fortunately, the same common names have been used consistently for many European ruderals and medicinal plants for more than 400 years, e.g., elecampane (*Inula helenium* L.), henbane (*Hyoscyamus niger* L.), horehound (*Marrubium vulgare* L.), and St. John's wort (*Hypericum perforatum* L.) (Harvey, 1974). In addition, a surprisingly high percentage (> 75%) of the species encountered in these early records were first described by Linnaeus, and many of these names have been retained in plant systematics. Given the limitations in the information that can be reliably deciphered about pre-1860 naturalizations, the resulting record will, however, remain a minimum estimate of the full scope of plant entry and establishment. Kartesz and Meacham's (1999) *Synthesis* was employed as the nomenclatural standard for plant names and authorities.

FIRST PLANT ARRIVALS: PRE-1700

Preparations for colonization of new lands in North America illustrate the care and forethought that the immigrants placed in the undertaking. Isolated on a continent newly discovered by Europeans, connected to Europe only by infrequent and highly unreliable ship traffic, each colony's planners knew that they needed to become self-sufficient almost from the outset. Acquiring sustained sources of food and medicine figured foremost in their planning (Leighton, 1970). The most reliable early information we have of plans for colonizing North America stems from the establishment of Plymouth Colony, beginning in 1620. Although we do not know which species were in the original manifest, several lists of plants ordered in Britain from 1628 and 1631 have survived. The Endicott expedition in 1628 was to include "Wheat, rye, barley, oats, a hoghead of each in the ear, beans, pease, stones of all sorts of fruits, as peaches, plumes, filberts, cherries, pear, apple, quince, kernels, pomegranates, woad seed, saffron heads, liquorice seed, (roots sent and madder roots,) potatoes, hop roots, hemp seed, flax seeds against winter, coneys, currants plants . . ." (Young, 1846: 42–43).

This intent to send woad seed (*Isatis tinctoria* L.), hemp seed (*Cannabis sativa* L.), and flax seed (*Linum usitatissimum* L.) forms the earliest record we have of the introduction of non-indigenous species that remain in the naturalized or at least the adventive flora of the U.S. Dyer's woad, *Isatis tinctoria*, has not apparently become widely naturalized in New England, despite its exceptionally early arrival (Magee & Ahles, 1999: 552), but it has become invasive in Utah and other arid regions (Farah et al., 1988). *Cannabis sativa* is widely naturalized in the eastern half of the U.S. north of the 37° latitude (Haney & Bazzaz, 1970). In contrast, flax appears commonly as an adventive in abandoned fields but may be naturalized only locally.

In 1631, just three years after the Endicott Expedition, John Winthrop, Jr., bought a detailed group of seeds from a London grocer with the intent of transporting these seeds to the small colony at Plymouth. Winthrop's (Massachusetts Historical Society, 1943: 47–48) list also included species that have since become naturalized, including "Sorrell" (*Rumex crispus* L. or *Rumex acetosella* L., or both), "Tansy" (*Tanacetum vulgare* L.), "Rockett" (*Eruca vesicaria* subsp. *sativa* (P. Mill.) Thellung [*Eruca sativa*]), "Buglos" (e.g., *Anchusa arvensis* (L.) Bieb.), "fennell" (*Foeniculum vulgare* P. Mill.), "dill" (*Anethum graveolens* L.), "sweet maioram" (*Origanum majorana* L. or *Origanum vulgare* L.), and "nipp" (*Nepeta cataria* L.), or adventives, such as "summer sauory" (*Satureja hortensis* L.), "Clary" (*Salvia sclarea* L.), "hysopp" (*Hyssopus officinalis* L.), "marigold" (*Calendula officinalis* L.) and "hollihocks" (*Althaea rosea* L.) (Fernald, [1950] 1987; Magee & Ahles, 1999). The identification of other species on his list is more equivocal, such as "mallow," which may have referred to *Malva moschata* L., *Malva neglecta* Wallr., *Malva verticillata* L., or *Malva parviflora* L. The listing of "popey" (Massachusetts Historical Society, 1943: 47) may refer to *Papaver somniferum* L., the opium poppy, but could also be referring to *Papaver rhoeas* L., which had reputed medicinal properties. Winthrop's list also includes "pursland" or purslane (*Portulaca oleracea* L.). It is often considered non-indigenous to North America (Magee & Ahles, 1999), but appears in the fossil pollen and seed record of Ontario in pre-Columbian levels (Byrne & McAndrews, 1975). Although these species appear to have arrived with the first waves of colonists in New England, the earliest date when they became naturalized or even adventive is not known.

Our most comprehensive picture of the species introduced by 17th century colonists in New England is derived from Josselyn's 1672 publication *New-England's Rarities Discovered* and its 1674 sequel *An Account of Two Voyages to New-England.* Based on Josselyn's accounts of two visits, 1638–1639 and 1663–1671 (Josselyn, [1674] 1988: xiii), he appears to have been a keen observer of the condition of the colonies in New England. Furthermore, he deliberately categorized the species that he encountered in his travels between Massachusetts and Maine, noting those that were apparently native to New England, those species also found in England (and apparently introduced), and even those introduced species that did not thrive in their new locales. Among species that he reported that later became naturalized or at least adventive were many that are not among the manifests of Endicott or Winthrop. The naturalized species include celandine (*Chelidonium majus* L.), goose-grass or "clivers" (*Galium aparine* L.), "Our English Clover-grass" (perhaps *Trifolium repens* L.), speedwell chickweed (*Veronica arvensis* L.), stitchwort (*Stellaria graminea* L.), St. John's wort (*Hypericum perforatum*), sweet brier or eglantine (*Rosa eglanteria* L.), toadflax (*Linaria vulgaris* P. Mill), wormwood (*Artemisia absinthium* L.), and yarrow (*Achillea millefolium* L.). Among species now adventive are blueflowered pimpernel [*Anagallis arvensis* subsp. *foemina* (P. Mill.) Schinz & Thellung], "egrimony" (*Agrimonia eupatoria* L.), herb Robert (*Geranium robertianum* L.), "Oak of Hierusalem" (*Chenopodium botrys* L.), speed-well (*Veronica officinalis* L.), spurge time (*Polygonum persicaria* L.), "Rew" (*Ruta graveolens* L.), watercress (*Rorippa nastur-

tium-aquaticum (L.) Hayek), and wild-mint (*Mentha aquatica* L.) (cf. Magee & Ahles, 1999). Furthermore, Josselyn (1672: 85) took the extraordinary step of noting which species had arrived "... since the English Planted and kept Cattle in New-England" that were already occurring spontaneously without cultivation. In this list, Josselyn provided explicit information on some of the first naturalized species (see below).

The diversity of species in Josselyn's list reveals that by 1671 (his last year in North America), and perhaps much earlier, the small lists of species that Endicott and Winthrop had ordered for the settlers had been expanded severalfold. Most prominent are species that had reputed medicinal value (*Artemisia absinthium, Hypericum perforatum, Inula helenium*), as well as plants for seasonings (*Anethum graveolens, Foeniculum vulgare* P. Mill., *Salvia sclarea*). Perhaps most surprising is that the colonists were beginning to feel confident enough about their survival that they permitted themselves the luxury of importing a few ornamental species, *Linaria vulgaris* and *Rosa eglanteria* (Leighton, 1970). Both of these species would become naturalized, and *L. vulgaris* would become a scourge by the mid 18th century. The arrival of these species is also significant because this early entry of ornamental species signals a trend that would grow substantially over the following 350 years as ornamental species became the largest single functional category of imported species (Mack & Erneberg, 2002).

EMERGENCE OF THE FIRST NATURALIZED SPECIES: PRE-1700

Our ability to detect the earliest naturalizations is severely limited by the fragmentary character of the first accounts of European colonists in North America. For example, the late 16th century Spanish settlements in Florida included gardens and cultivated limes, lemons, and oranges (Lyon, 1996: 55); contemporaneous introductions of oranges soon appear in other Spanish subtropical and even temperate colonies (Gade, 1976). I am, however, unaware of any information on the fate of these species that were cultivated in 16th century Florida. Maine also received European colonists very early: successive temporary settlements were made beginning in 1604. The record referred to as the Edgerton Manuscripts (Lockwood, 1931: 139) is intriguing in describing the author's visit to a long-abandoned settlement in Maine "on the Permaquid River Alderman Alsworth of Bristole settled a co., of people in 1625.... In 1675 I found the Roots and Garden Herbes, and some old walls there when I went first over, which showed it to be the place where they had been." Finding garden herbs many years after the site's abandonment strongly suggests that these species had become naturalized.

The first, admittedly tenuous, records of naturalized species in what was to become the U.S. appear in the decades after establishment of English colonies in New England. Among the praiseworthy features of these English immigrants was their commitment to recording a wide range of information about their nascent settlements, including the fate of their crops. Only 14 years after the first colonists landed in Plymouth Bay, William Wood (Wood, [1634] 1977) had published his account of the "New England's Prospect": a comprehensive report of information that would have proven invaluable to anyone intending to immigrate to New England. Wood's comments entitled "Of the Herbes, Fruites, Woods, Waters and Minerals" prove particularly informative about both the European crops being planted and also those already observed to persist outside cultivation.

Wood's ([1634] 1977: 36) listing of the crops, both native and introduced, reveals species that had already been brought under cultivation and their status: "The ground, affords very good kitchen Gardens, for turneps, Parsnips, Carrots, Radishes, and Pumpkins, Muskmillions, Isquoutersqashes, Coucumbers, Onyons, and whatever grows well in England grows well there, many things being better and larger; there is likewise all manner of Herbes for meate, and medicine, and that not only in planted gardens, *but in the Woods, without eyther the art or the help of man, as sweet Marjoram, Purselane, Sorrel, Peneriall, Yarrow, Mirtle, Saxifarilla, Bayes, etc.*" (italics added). The italicized statement strongly suggests that several of the species that the colonists had planted in the previous decade had already escaped cultivation and were growing freely in the surrounding forest. These species include sorrel (*Rumex acetosa* L. and *Rumex crispus*) and yarrow (*Achillea millefolium*). These are the earliest accounts I am aware of for any naturalizations in North America. Identification of "sweet Marjoram" is equivocal. Wood may have been referring to *Origanum majorana*, which is still referred to as sweet marjoram, but has rarely escaped cultivation and is not considered naturalized in New England today (Magee & Ahles, 1999: 898). Alternatively, he may have seen *Origanum vulgare*, now termed wild marjoram, which is naturalized (Magee & Ahles, 1999: 873). "Peneriall" in Wood's list may refer to the native species *Hedeoma pulegioides* (L.) Pers. rather than the European species, *Mentha pulegium*

L., for which there is no record of naturalization in the U.S.

These earliest references to the naturalized status of some newly arrived European species in New England are substantially corroborated and expanded by Josselyn (1672). His list "Of such Plants as have sprung up since the English Planted and kept Cattle in New-England" is the best account from which to determine the European species that had become naturalized by 1671 and probably much earlier (Josselyn, 1672). Many of the species that he reported in terms indicating their newfound persistence in the New England flora are still prominent today (Magee & Ahles, 1999), such as *Hyoscyamus niger, Stellaria media* (L.) Vill., *Taraxacum officinale* G. H. Webber ex Wiggers, *Senecio vulgaris* L., and *Urtica dioica* L. Josselyn's (1672: 86) report that plantain (*Plantago major* L.) was referred to by Native Americans as "English-Man's foot" has been quoted repeatedly. Plantain was already spreading along paths and roads well ahead of English settlements and served as a harbinger to the aborigines of the coming of the new settlers (Darlington, 1859: 219).

Aside from the immediate needs for importing plants for food and medicine, the early colonists had definite interest in ensuring that their livestock had suitable forage. They soon found, however, that the coastal environments offered their animals little nutritious forage. A common complaint is exemplified by one colonist in Massachusetts who stated that his livestock ". . . grew lousy with feeding upon it, and are much out of heart and likeing . . ." (Hutchinson, [1764] 1972: 483). Help was on the way. These transplanted English farmers and herdsmen were well acquainted with an array of "English grass" that would meet their livestock's needs, and they actively sought seeds of these English pasture species for introduction into their farms. Species identifications in these 17th century accounts are confounded by the common reference to a mixture of grasses and clovers as "English grass," and it is likely that some of these species could have arrived alternatively as seed contaminants in lots of seed or in the ballast or debris off-loaded from ships with livestock, or both (Bidwell & Falconer, 1925). Species that were introduced through the 17th century were *Polygonum aviculare* L., *Holcus mollis* L., *Poa pratensis* L., and possibly *Agrostis capilliaris* L. (Carrier, 1923: 241), and *Holcus lanatus.* Not only were these species becoming naturalized in New England, but they were also being actively spread in colonies to the south. In praising the growth of cattle and other livestock on Long Island (New York), Denton (1670: 5) commented that "the Island likewise [was] producing excellent English grass, the feed of which was brought out of England, which they sometime mow twice a year." And Budd (1685: 10) commented on the practice of using sheep to disperse these grasses "but if we sprinkle a little English grass Hay-Seed on the Land without Plowing, and then feed Sheep on it, in a little time it will so increase, that it will cover the Land with English Grass, like unto our Pastures in England. . . ."

Naturalizations arising from the introduction of forage species were not restricted to grasses. The advantages of sowing pastures with clovers, especially *Trifolium repens* (white clover), were common knowledge in England by the mid 17th century, and this knowledge was widely transferred to North America. As early as 1635 a tract written for those who planned to immigrate to Maryland advised that they bring "Good store of claver grasse seede, to make good meadow" (Hall, 1910: 98). This sound advice had also been followed in New England: Josselyn ([1674] 1988: 131) commented that "Our English clover grass sowen thrives very well." It was both deliberately sown and spread as sheep were moved among fields, as Scot (1685: 187–188) recorded for New Jersey: "As soon as any of the land here comes to be cultivated, it over-runs with small Claver-grass, by the pasturage and dunging of the cattle, and so supplants the naturall grass and hearbs." The movement of livestock and seed among the colonies was extending the new ranges for these European pasture species.

By the mid to late 17th century at least 20 species were observed to have already become naturalized in New England; many of these had likely become established further south in Pennsylvania. The actual number of naturalized species was likely much larger. For example, Josselyn (1672) listed under his category "Of such Plants as are common with us in England" many species that were already in New England and for which we have records of naturalization in the 18th century. How long before 1700 they were naturalized we do not know. Species in this category of 17th century introductions that were to become permanent residents include *Artemisia absinthium, Cannabis sativa, Galium aparine, Hypericum perforatum, Inula helenium, Nepeta cataria,* and *Xanthium strumarium* L.

PLANT ARRIVALS AND NATURALIZATIONS IN THE 18TH CENTURY

Any chronological divisions, such as those between centuries, that could be used to delineate the growth of a naturalized flora are arbitrary. The forces that brought new species to North America and contributed to their naturalization were obviously not so coincidentally partitioned as to conform to even decadal, much less centennial breaks. Nevertheless, there is some justification for distinguishing between the naturalizations in the 17th and the 18th centuries. Leighton (1976: 1) has argued that the necessity of establishing self-sufficient colonies in the 17th century was a powerful incentive to ensure that almost all the species introduced before 1700 were for utilitarian purposes. As noted above, some plants introduced even before 1650 may have had no purpose other than ornamentation, such as *R. eglanteria.* But even *R. eglanteria* may have been deliberately introduced to form hedges (Josselyn, 1672: 90). In contrast, the assurance that the colonies would not only survive but also grow and prosper sparked much incentive in the 18th century for the introduction of species for the widest range of uses, especially for ornamentation. This market in ornamental species grew steadily throughout the 18th century and thereby created opportunity for more naturalizations, and even invasions (Lockwood, 1931: 12; Leighton, 1976).

Perhaps the best single view we have of the growth of this naturalized flora in the 18th century was a retrospective written in the early part of the 19th century but clearly drawn from information gathered in the late 18th century. Rafinesque, an itinerant French botanist, collected plants widely in the new United States. In 1810 he assessed the naturalized flora of the Middle Atlantic states (Rafinesque, 1811). His work appears to be based largely on Muhlenberg's (1793) flora of the area surrounding Lancaster, Pennsylvania, *Index Florae Lancastriensis,* which Rafinesque augmented and annotated to include his own observations for the North American region that stretched south from New York State to Maryland. The most specific location information is given for species occurring near Lancaster, Pennsylvania, and those found in the vicinity of Baltimore, Maryland, Rafinesque's home in the U.S.

In a useful pattern that was to be repeated by other authors in the 19th century, Rafinesque (1811) categorized the species on their mode of introduction: plants introduced by agriculture, plants introduced by gardening, and "totally useless" plants or weeds, i.e., those accidentally introduced. Plants in a fourth category for him had varied modes of introductions and were not native to Europe. A great advantage of this Muhlenberg *cum* Rafinesque list is the consistent use of binomial names, most of which have been retained in modern plant systematics. In addition, Rafinesque gave his assessment of the abundance of the species, making it clear that a few (*Convolvulus arvensis* L., *Leucanthemum vulgare* Lam. [which he termed *Chrysanthemum leucanthemum*], and *Verbascum blattaria* L.) were both widespread and abundant. Among deliberately introduced species are *Cannabis sativa, Hordeum vulgare* L., *Linum usitatissimum, Plantago lanceolata* L., and *Trifolium pratense* L., which were all listed as common to very common, usually in ruderal sites.

Of the more than 300 species in Rafinesque's (1811) list, he considered the largest single group (193 taxa) to have been introduced in gardening, i.e., species grown in small plots and presumably cultivated much more assiduously than field crops (e.g., *Gleochoma hederacea* L., *Sinapis alba* L.). The second category reveals the extensive naturalization of medicinal plants and those used for seasonings in the 18th century: *Asparagus officinalis* L., *Cynoglossum officinale* L., *Digitalis purpurea* L., *Inula helenium, Marrubium vulgare, Nepeta cataria,* and *Tragopogon porrifolius* L. Most of these species were listed as common and confined to roads, near dwellings and gardens. Among this large list of species are also those such as *Cichorium intybus* L. (chicory), which was listed as "very common—in fields, roads, cultivated grounds. . . ," and *Lamium amplexicaule* L., considered, "every where common—in fields."

Many more species had been imported for strictly aesthetic reasons in the 18th compared with the 17th century, and among these were some that soon became naturalized. Ornamental species that had already become naturalized ca. 1800 in Rafinesque's opinion included *Euonymus europaea* L., *Ligustrum vulgare* L., *Rhamnus cathartica* L., and *Syringa vulgaris* L., illustrating that woody ornamental species were also becoming persistent. The remainder of the species noted by Rafinesque were considered accidentally introduced, such as *Bromus secalinus* L., *Echium vulgare* L., which was to become much more conspicuous later, *Agrostemma githago* L., *Chenopodium album* L., *Convolvulus arvensis,* and *Spergula arvensis* L.

Rafinesque (1811) may have applied the appellation "naturalized" rather liberally, as he used it to mean those species that ". . . now grow spontaneously . . . ," not necessarily persistently. For example, he listed some species, such as *Fagopyrum esculentum* Moench (buckwheat), as naturalized and common, yet today it is probably only adventive as an escape from cultivated fields. Alternatively, its status may have indeed changed in the last 200 years (e.g., from diminished cultivation), or he may have been simply noticing volunteer buckwheat that was residual in fields. Another species he considered rare but nonetheless naturalized was *Rubia tinctoria* L. (madder), a species referred to among some of the earliest plant import manifests in the 17th century (Young, 1846: 42) but which is considered as only a rare escape from cultivation today (Magee & Ahles, 1999). Nevertheless, the bulk of the species that he noted as naturalized are indeed persistent today, and his assessments were corroborated by his contemporaries.

EMERGENCE OF THE FIRST PLANT INVASIONS: 18TH CENTURY

The major consequences of non-indigenous species result from the small minority of naturalized species that become prolific in the new range, i.e., these species become invaders. Their abundance and aggressive growth bring about environmental damage to the native species and alteration of native environments (Mack et al., 2000). These species often invade arable fields and pastures and consequently result in severe economic damage (Bridges, 1992). Given the growing array of non-indigenous species that were being introduced both accidentally and deliberately from the early 17th century onward, it is not surprising that a few were eventually reported in terms that we would equate with plant invaders.

The earliest invasion of which I am aware resulted from the introduction of *Linaria vulgaris* P. Mill (yellow toadflax). In the extensive correspondence that John Bartram, the doyen of 18th century American botany, maintained with his colleagues Peter Collinson and Philip Miller in Britain (see Darlington, [1849] 1967), his remarks about *L. vulgaris* are revealing. In a report that both colleagues apparently received accompanying a letter in 1758, Bartram stated, "It was first introduced as a fine garden flower; but it was never more heartily cursed by those that suffer by its encroachment" (Darlington, [1849] 1967: 384). He added, "It is the most hurtful plant to our pastures that can grow in our northern climate. Neither the spade, plough, nor hoe, can eradicate it, when it is spread in a pasture" (Darlington, [1849] 1967: 383). Bartram explained that so desperate were farmers to control yellow toadflax that they would even ignite log piles in a field in the hopes of destroying it in the soil but to no avail. Bartram reported that by 1758 *L. vulgaris* had ". . . spread over great part (sic) of the inhabited parts of Pennsylvania" (Darlington, [1849] 1967: 384)—a clear indication that it was not simply a local problem. *Linaria vulgaris* had formed an invasion. It apparently spread further afield: Pursh (1814) noted that it had become ". . . one of the worst and most troublesome weeds in several parts of Pennsylvania and Virginia." Barton (1818) went even further in his estimation of its spread as he rated it (which he termed as *Antirrhinum linaria*) as ". . . extensively naturalized, in the United States. On roadsides, commons, wastes, and the borders of fields, very common and abundant." Yellow toadflax had reached North Carolina by 1832 because de Schweinitz (1832) reported that a few years after *L. vulgaris* (as *Antirrhinum linaria*) was introduced into a garden it had ". . . contaminated the whole vicinity for many miles."

Other naturalized species were also causing serious problems, although the extent of their new ranges is more difficult to determine. Bartram lived in Philadelphia but had numerous correspondents along the East Coast, so some of his assessments of the damage from naturalized species may have been drawn in part from the reports of others. For example, Bartram in the same 1758 correspondence listed other non-indigenous species in what appears to be a declining order of prominence. He described *Hypericum perforatum* as a "very pernicious weed," which had spread over pastures in eastern Pennsylvania, interfering with the growth of pasture grasses and causing injury to horses and sheep (Darlington, [1849] 1967: 384). This plant was apparently introduced repeatedly in New England and the Middle Atlantic colonies (Josselyn, 1672: 44; Haughton, 1978: 348), so it may well have formed an invasion by the mid 17th century. *Hypericum perforatum* was also proving to be a troublesome plant in fields in New England. Eliot, writing in his fourth essay on agriculture, which was first published in 1753, complained about the difficulty of eliminating St. John's wort in fields (Carman & Tugwell, 1934: 94). Even though Eliot lived in Connecticut, he traveled widely in New England, and his essays were meant to be advice gleaned from decades of observation in the region (Carman & Tugwell, 1934). If *H. perforatum* had not reached the status of an invasion by the mid 18th century, it was at least a widely distributed naturalized species.

Linaria vulgaris and *Hypericum perforatum* bedeviled 18th century farmers across a broad region from Pennsylvania to New England, but these species' prominence appears to have since declined. Darlington (1859: 225) reported that *L. vulgaris* was "extensively naturalized" and a "vile nuisance in our pastures and upland meadows." He described *H. perforatum* as a "rather troublesome weed on our farms," but did not state it in terms that suggest an invasion. He added the intriguing note that in Chester County, Pennsylvania, he noticed that the plant was not detected at all in 1842, and was rare in 1843, but had become "as common as ever" in subsequent years (Darlington, 1859: 55). This statement may allude to the prominence reported by Bartram in the 18th century (Carman & Tugman, 1934).

Although widely naturalized in the northeastern U.S. (Rhoads & Klein, 1993; Magee & Ahles, 1999), neither *H. perforatum* nor *L. vulgaris* appears invasive today. However, these reduced roles are largely the result of active control measures. *Linaria vulgaris* is controlled with the herbicide glyphosate in agricultural fields (Saner et al., 1995), while the abundance of *H. perforatum* has been effectively curbed in much of its new range through biological control (Julien & Griffiths, 1998, and references therein). The difficulty in deciphering from early accounts whether species had become invasive relates to the specific interests of the observer. Eliot and Darlington were primarily interested in species that were hazards to agriculture. Even Bartram's observations appear often influenced by his concern about agriculture. Alien plants that were extensive exclusively in non-agricultural settings may not have been commented on.

As damaging as *L. vulgaris* and *H. perforatum* could be, colonial farmers already had a much greater scourge to cope with—*Berberis vulgaris* L. (common barberry), the alternate host for the stem rust *(Puccinia graminis* f. sp. *tritici*), a devastating parasite of cereal crops (Peterson, 2001). *Berberis vulgaris* had certainly reached the level of impact to qualify as an invader by the late 18th century and had probably reached that status over a century earlier. Our knowledge of its probable entry into North America by the mid 17th century is through a combination of its direct mention and reports of the occurrence and spread of stem rust as it infected wheat across New England. Common barberry was almost certainly introduced deliberately in the 17th century, as it was valued in sauces and as a medicinal plant (Gerard, [1633] 1975: 1326). Josselyn (1672) referred to "barberry trees" in a list of introduced fruit trees and also described the rust (termed "wheat blast" until the 20th century) on wheat in New England in the 1660s. A more detailed account of the incidence of stem rust was provided by John Winthrop in 1668: "generally through all the plantations, both of ye Massacheusetts colony, Plymouth, & this also [the colony of Connecticutt] insomuch that the croppe of wheat hath failed divers yeares in most plantations. The corne flourished well till it came to be eared, and the eares also would appeare faire, and as if full, but no corne in them. There have beene thousands of acres in that maner every yeare. What the cause was, whether naturall, or a blasting fro heaven we know not. Our old husbandmen of England, some of them thought it a meldow . . ." (Bidwell & Falconer, 1925: 13). Given the obligate link between wheat, stem rust, and barberry, it seems a safe inference that where rust was attacking wheat, barberry was nearby.

As further evidence for the spread and impact of *Berberis vulgaris*, Connecticut passed legislation in 1726 to control barberry, followed by Massachusetts and Rhode Island in 1755 and 1772, respectively (Fulling, 1943). These measures failed, as Dwight ([1821] 1969) provided direct observation in 1795 or 1796 of the extent of *B. vulgaris* across much of eastern Massachusetts and coastal New Hampshire. Within the approximately 3000 km^2 area that Dwight circumscribed in his travels he noted ". . . the barberry bush is spread, not universally, but in spots, and those often extensive. In some fields they occupy a sixth, fifth, and even a fourth of the surface" (Dwight, [1821] 1969: 276). Clearly, barberry was exerting a major influence on wheat production across eastern Massachusetts in the 18th century to the point that bread made from wheat had disappeared from farmers' diets in much of New England (Bidwell & Falconer, 1925: 92). Common barberry would later spread much further across the U.S., and by the time control efforts were fully implemented against it early in the 20th century, it was extensive in a 13-state area in the North Central region of the U.S. (Hutton, 1927).

Other biotic invasions were growing in North America by the late 18th century, e.g., the spread of *Trifolium repens*, even if the proliferation of an alien clover does not produce the usual anthropocentric connotations. As stated previously, *T. repens* had been spread both deliberately and accidentally through New England and colonies, such as Pennsylvania and New Jersey, in the 17th century. The resulting transformation of pastures, for which it was valued, represents substantial increases in the soil nitrogen pool in these sites. Such change can precipitate a host of other environmental changes, including a facilitation in the establishment of other alien species. For example, introduction of the nitrogen-fixing Firetree, *Morella faya* (Ait.) Wilbur, so raised the amount of biologically available nitrogen in Hawaiian soils that Firetree has favored the persistence of other non-indigenous species (Vitousek et al., 1996).

GROWTH OF A NEW NATION'S NATURALIZED FLORA: 1800–1860

All the incentives and stimuli that had operated before 1800 for the introduction of non-indigenous plants expanded substantially with the growth of the new nation's commerce and transportation in the 60 years leading up to the Civil War in 1861 (Meyer, 1917). New species were actively sought out that would contribute to the national economy, and for the first time these searches were not left simply to private enterprise. In an often-quoted proclamation, President John Quincy Adams in 1827 instructed U.S. consular offices to gather useful species and U.S. naval ship captains to provide for the transport of these living cargoes to the U.S. (Hodge & Erlanson, 1956). Annual reports of the Commissioner of Patents, who was responsible for federal involvement in agriculture before 1863, routinely chronicled federal interest in introducing new species in the U.S. for potential use (e.g., U.S. 28th Congress 1st Session, 1844: 68; U.S. 36th Congress, 2nd Session, Ex. Doc. 48, 1861).

Federal actions were dwarfed, however, by the private sector's economic incentive to import species new to the U.S. for all manner of use, particularly as ornamentals. Establishment of commercial nurseries and seedsmen in major cities, particularly Philadelphia, even before the American Revolution (Lockwood, 1931: 12), was followed by a huge growth in this cottage industry through the first half of the 19th century (Leighton, 1987: 67; Mack, 1991, and references therein). These seedsmen were remarkably diligent, not only acquiring new species from overseas but also in building clienteles that were not restricted to the immediate vicinity of their businesses and gardens. By 1804 Bernard M'Mahon, a Philadelphia seed merchant, was advertising that he had within his nursery collection species from such far-flung locales as the "South-Sea Islands," Asia, Africa, and Europe (M'Mahon, 1804). The product of such industry was the availability of several hundred species for sale that had not before entered the U.S. (Leighton, 1987; Mack, 1991). Many of these species were to become naturalized by 1900, such as *Casuarina equisetifolia* L., *Cyperus esculentus* L., *Hedychium gardnerianum* Shepard ex Ker-Gawl., *Lonicera japonica* Thunb., *Lysimachia nummularia* L., *Morella faya*, *Tamarix* spp., and *Ulex europaeus* L. (Mack, 1991).

Occasionally, single events are recorded that may have spawned a naturalization. *Cytisus scoparius* (L.) Link, Scotch broom, is a notorious sprawling shrub that rapidly covers new range through a combination of vegetative propagation and local seed dispersal from explosive capsules. Once it occupies a site, it can form an impenetrable thicket that reduces the prevalence of other plants and interferes with the movement of livestock (Peterson & Prasad, 1998). Although there are apocryphal reports of earlier introductions (Lockwood, 1934: 32), the earliest clear reference to the shrub in Virginia arises in a letter (Anonymous, 1921) detailing the misguided generosity of J. M. Galt, a visitor to the farm of John Cocke in Mount Pleasant, Virginia, in 1803. Learning that Cocke intended to introduce an unidentified species to his farm as sheep fodder, Galt wrote with news about what he deemed a superior choice: "When I was at your house you mentioned your Intention of Cultivating the Pride of China for feeding sheep. This will answer for the winter months very well. It did not occur to me then to recommend to your notice the cultivation of Scotch Broom, which affords an ample food for between two or three summer months for sheep and hogs. . . ." Dr. Galt gave more than advice; he also sent along seeds of *C. scoparius*: "I have sent you seed sufficient to plant all your hill sides that you do not mean to cultivate in grain." The seeds had been imported by Galt from a farm in Warwick, England, a few years earlier. His account of the plant's behavior on the Warwick farm seems particularly ominous in retrospect ". . . it was originally planted as a hedge by an old Englishman—from which it has spread over some hundreds of acres of land by the Birds." To ensure that the spread of Scotch Broom would be complete, Dr. Galt helpfully added the following tip: "in England they have a method of Expediting Vegetation of Broom—Hawthorn and Holl—by mixing the seeds with the feed of their horn'd Cattle & keeping the Cattle up until they have passed the seed—they then sprinkle this over their Land & plough it in, in the fall season, in the spring the seed will vegetate . . ." (Anonymous, 1921). Unknown is whether the land owner, John Cocke, actually sowed the seeds given by Galt. However, *C. scoparius* remains naturalized in Virginia in scattered locales (Harvill et al., 1992).

Records of the escapes and naturalizations of these new immigrant species, as well as confirmation of the naturalized status of many other species imported much earlier, are established through the proliferation of published local and regional floras along much of the East Coast of the U.S. and even at newly established inland settlements (Sullivant, 1840). Pursh (1814) and Torrey (1824) exemplified ambitious early attempts to record floras that were not confined to urban seaports. Their records are invaluable because these early U.S. botanists confidently assigned Latin binomials to their collections and often reported in unambiguous terms whether these species were naturalized. Thus, Pursh (1814) was able to describe the noxious alien grass *Eleusine indica* (L.) Gaertn. as occurring in sandy soil from New Jersey to Florida, *Festuca elatior* [probably *Lolium pratense* (Huds.) S. J. Darbyshire] as occurring in wet meadows in Pennsylvania and New England, and *Urtica dioica* as found from Canada to the Carolinas. Even if the geographic range was restricted, the notes on the status of these species is nonetheless valuable, e.g., Barton's (1818) *Compendium florae philadelphicae,* which was restricted to sites within 10 miles of Philadelphia. For example, Barton (1818) described *Ranunculus bulbosus* L. as so abundant that "... whole fields are often rendered yellow by the profusion of the plant" and *Allium vineale* L. as common, pestiferous, and "... impossible to eradicate."

As valuable as published floras of the early 19th century are in tracing the earliest record and fate of non-indigenous species, authors such as Pursh, Torrey, and Barton were not concerned specifically with these species and their effect in the U.S. Coming approximately 30 years apart, the accounts of de Schweinitz (1832) and Darlington (1859) provide extraordinarily valuable benchmark accounts that deal explicitly with the scope and status of non-indigenous species along the East Coast of the U.S. Although the detail of their investigations and observations differ in geographic range, these two accounts provide perhaps the best guides we have on the growth of the naturalized flora across the first half of the 19th century.

De Schweinitz (1832) explicitly dealt with species that had become naturalized in the U.S., including a grouping of species by their mode of introduction: those introduced deliberately for cultivation and those ostensibly introduced as seed contaminants ("Introduced fortuitously with agricultural seeds") (de Schweinitz, 1832: 151). De Schweinitz provided a separate list of plants that he considered naturalized in smaller areas, e.g., individual states or urban areas. Furthermore, he provided an unambiguous definition for "naturalized" species: "... which are regularly reproduced, and gradually extending themselves, without present cultivation ..." (de Schweinitz, 1832: 149). His list of deliberately introduced species included many that had been introduced at least a century earlier: *Anthoxanthum odoratum* L., *Nepeta cataria, Plantago major, Taxaracum officinale,* and *Verbascum thapsus* L. But this category also included apparent newcomers, such as *Barbarea vulgaris* Ait. f., *Poa annua* L., and *Raphanus raphanistrum* L. His list of accidentally introduced species included *Allium vineale, Cerastium vulgatum* [probably *Cerastium fontanum* subsp. *vulgare* (Hartman) Greuter & Burdet], and *Lolium perenne* L. These species may have been introduced in the 18th century as there is no mention of them before 1700. Species that were naturalized locally, i.e., without the extensive new range occupation he observed for others, included *Anagallis arvensis* L., *Briza media* L., *Bromus hordaceus* L., *Dactylis glomerata* L., and *Inula helenium.* Unfortunately, de Schweinitz did not describe these species in terms of their abundance and impact, especially in terms that would allow evaluation of any invasive role.

Darlington's (1859) *American Weeds and Useful Plants* provides probably the best overview we have of the composition and impact of the non-indigenous flora ca. 1860. Darlington was explicitly concerned with those species that were troublesome in agriculture; then as now most agricultural weeds are non-indigenous (Bridges, 1992). He recorded about 400 non-indigenous taxa that were established in the eastern third of the country, but it is clear that his collections and observations are drawn from the Middle Atlantic States, the collecting area of Rafinesque 50 years earlier. Darlington repeatedly referred to species as "naturalized" (e.g., *Sisymbrium officinale* (L.) Scop.), in contrast to other species that were merely present in the U.S. by the 1850s. For other species, it certainly appears that he also considered them as naturalized, e.g., in referring to the Scotch thistle *Onopordum acanthium* L. as "... very common along road-sides and in waste places in New England" (Darlington, 1859: 199). Interesting in this regard is his assessment of all *Galium* species, which he dismissed as "... not sufficiently important even as weeds to require notice" (Darlington, 1859: 164). He reported that the flax dodder *Cuscuta epilinum* Weihe had become quite rare because of the decline in the cultivation of *Linum usitatissimum,* its host. He also recognized that some species, such as *Ailanthus altissima* (P. Mill.) Swingle (tree-of-heaven), had both beneficial and detrimental qualities: providing urban shade but also escaping to vacant lots and even emerging from pavement.

PLANT INVASIONS BY THE MID 19TH CENTURY

An invasion is commonly dependent on the immigrant species being transported to many suitable localities in the new range (Moody & Mack, 1988). The disseminules of some species are readily carried by wind, water, or animals (Ridley, 1930) and can rapidly fill a new range with little or no human assistance. But the spread of many others within a potential new range is greatly facilitated by human agencies. Consequently, as the network of roads, canals, and railroad routes grew in the 19th century U.S., the spread of non-indigenous species also expanded. Some of these routes or pathways were being developed even before 1800. For example, there was a comprehensive network of national postal roads that linked the country from north to south by 1804 (Paullin, 1932). Additional roads, supplemented by canals and established barge traffic along major rivers, such as the Hudson, the Ohio, and the Delaware, extended this network (Meyer, 1917). Even by the early 19th century, commerce, including seeds and seed-contaminated cargo, was moving routinely throughout the new nation.

The extent of the American commercial network, as well as the volume of goods moved in the interior of the country, increased markedly with the growth of railroad lines. The first U.S. railroad routes were built in the 1830s. New lines were added rapidly, and most importantly, these lines became linked, so that goods could be moved hundreds of miles in days, not the weeks or months that were needed even along the national trunk roads. From 1830 to 1850, the total length of the railroad system grew from 117 to more than 14,200 km in 27 states in the eastern half of the nation (Meyer, 1917: 573). Growth over the following ten years would dwarf even this total (Meyer, 1917, plate 5).

At least one plant invasion appears to have been added in the early 19th century to those that had begun earlier. Asa Gray, who was to become the doyen of American botany in the second half of the 19th century, was by his estimation the first botanist to explore the Shenandoah Valley (Gray, 1842). Upon reaching Winchester, Virginia, at the northern end of the valley in June 1841, he traveled south. Throughout the broad valley for over a hundred miles Gray was amazed to see immense amounts of *Echium vulgare* L. (viper's bugloss), a Eurasian biennial, occupying many sites, including cultivated fields. Arriving in late June Gray saw viper's bugloss in full flower and described how it formed a "... broad expanse of brilliant blue" (Gray, 1842: 13). Gray's account of the geographic spread and prominence of *E. vulgare* at this time leaves little doubt that he was describing an invasion. He was surprised that farmers had allowed the plant to overrun their fields. Their reluctance to remove it may have stemmed in part from the difficulty of handling it, as it causes contact dermatitis (Magee & Ahles, 1999). Gray (1842) further reported that in the northern states he had seen it only as an occasional roadside plant. Darlington (1859: 242) later reported that he had seen it in "considerable quantities" in Maryland and in abundance in New York. Viper's bugloss may have been introduced deliberately among these widely separated sites because it was valued as a medicinal plant (Parsons & Cuthbertson, 1992: 332).

It is intriguing that this plant, which was so prominent in the mid 19th century in Virginia and elsewhere, would be viewed today as locally abundant but not invasive anywhere in the U.S. (Lorenzi & Jeffrey, 1987: 245). The abundance of a plant invader can decline precipitously, e.g., *Agrostemma githago* in Britain (Clement & Foster, 1994), through a change in agricultural practices. Given the need to control plant invasions, understanding the demise of invaders such as *E. vulgare* in Virginia becomes an important topic for experimentation. The ability to identify this species' pollen in 19th-century sediments could aid in this investigation (cf. McGlone & Basher, 1995).

The list of invasions under way by 1860 likely included more species than *Cytisus scoparius* and *Echium vulgare*, although the strength of evidence for the others is more circumstantial. Darlington (1859) was concerned primarily with the spread and damage of weedy species in agriculture and only incidentally with those species' occupation of other sites. Nevertheless, he did describe the range and impact of several dozen species in such terms that suggest these were invaders. In fact, he described *Aegopodium podagraria* L. (goutweed) as an invader that "... should be carefully watched and its spread arrested" (Darlington, 1859: 151). The strength of the descriptors he used for a few species is a guide to their impact. For example, Darlington (1859: 197) referred to *Cirsium arvense* (L.) Scop. as "... perhaps, the most execrable weed that has yet invaded the farms of our country." Similar language was applied to the spread and impact of *Cyperus rotundus* L. in its role on cultivated ground in the South, especially in sandy fields and sand drifts and along the seacoast. *Leucanthemum vulgare* Lam. (which he termed as *Chrysanthemum leucanthemum*) may have also reached the status of an invader because Darlington (1859: 189) described it not only as a "great nuisance in our country" but also as having "in some districts ... exclusive possession of their pasture fields." It is apparent in Darlington's description of the status of *Echium vulgare* and *Berberis vulgaris* that these two earlier recognized invaders had maintained their role until at least the mid 19th century.

Collectively these invasions had already sparked attention and admonishments to farmers to apply diligence in keeping their fields free of these pests and to sow and trade crop seeds that were free of these damaging contaminants (Darlington, 1859: 242). Even if farmers had universally accepted the advice, it would have been difficult to carry it into practice. Threshing equipment in the early 19th century was a poor match against the seed mimics (e.g., *Avena fatua* L., *Bromus secalinus*) that contaminated crop seeds, and a great wave of new introductions were headed to the U.S. (Mack, 1991). As a result, many of the naturalized species that were to become ruderals in the U.S. were not only in the country by 1800, they had been spread throughout much of the eastern half of the U.S. by 1860. In contrast, many other species that have become invaders in the U.S. were just being detected by this date, such as *Bromus tectorum* L. (Bartlett et al., 2002) and *Lonicera japonica* (Schierenbeck et al., 1994) or had yet to be detected (e.g., *Salsola kali* L.). In a sense, the damage caused by plant invaders in the first 200 years or more of European colonization along the eastern coast of the United States would be far outweighed by the damage brought about by species introduced or deliberately spread post-1860.

CONCLUSIONS

Several timely observations can be gleaned from tracing the growth of the naturalized flora in the U.S. between the early 17th and mid 19th centuries. From the beginnings of European colonization in North America, the list of plants that became naturalized was shaped strongly by the species human immigrants selected for their transplanted agriculture. Even if a naturalized species did not owe its new status to deliberate introduction, it likely arrived as a contaminant in the seed of a deliberately selected species; Pursh (1814) maintained that *Anthoxanthum odoratum* and *Festuca elatior* [probably *Lolium pratense* (Huds.) S. J. Darbyshire] arrived in this manner. Although the link between naturalization and the deliberate introduction of species for food, forage, and medicinal use continued, even in the 17th century some species appear to have been imported for aesthetic reasons. The list of species selected as ornamentals has expanded ever since; in fact, it dwarfed the number of new immigrant species in more utilitarian categories by at least 1860, if not earlier (Mack & Erneberg, 2002).

The link between agriculture in western Europe and the establishment of colonial agriculture was so strong that by ca. 1850, the weed and ruderal floras of western Europe and eastern North America were quite similar. Through a combination of deliberate introductions and seed contaminants in imported seed and other cargo, Europe's colonizing flora had been largely transplanted to form much of North America's naturalized flora. Although formed by happenstance, this link remains.

As introduced species were traded or accidentally spread in commerce among the eastern colonies beginning in the 17th century, a few species became so widespread and naturalized that they formed invasions. Although the known list of apparently invasive species by 1800 is modest, other species were probably playing that role but were not described in terms that we can decipher as invasions. The frequency with which widespread and perhaps invasive species were reported through the first half of the 19th century suggests that these species' opportunity to spread and consequently proliferate was tied to the growth of all forms of commerce and the forms of transportation that fostered the spread of commerce.

Furthermore, the connection between which species received cultivation in their new range and those that became naturalized appears high (Mack & Erneberg, 2002). This historic link between cultivation and naturalization (Mack, 2000) provides an important harbinger for the future. If the history of plant naturalization between 1634 and 1860 is any guide, future naturalizations will be largely shaped by (1) the often idiosyncratic human motivations for importing alien species, (2) the degree of cultivation provided to these species upon their entry, and (3) human industry in transporting those species to many new locales and habitats in new ranges, thereby enhancing the opportunities for establishment on sites where they can persist without further human assistance.

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INVASIVE ANTS: UNWANTED PARTNERS IN ANT-PLANT INTERACTIONS?[1]

Lori Lach[2]

ABSTRACT

As invasive ants spread, their interactions with plants are inevitable and have potentially great implications for agriculture and conservation. When considered in the context of pre-existing models of ant-plant interactions, the higher abundance, aggressive nature, and attraction to high-carbohydrate resources typically associated with invasive ants lead to hypotheses about how invasive ants may differ from native ants in protecting plants from herbivores, tending of Homoptera, and interactions affecting plant reproduction. Examples demonstrate that all three of these traits common to invasive ants can influence the outcome of interactions between invasive ants and plants, but ant biology and attributes of other organisms also determine the consequences for the plant. Drawing from these examples and considering traits of the invasive ants, plants, and other organisms that interact with the plant, I offer predictions for the contexts in which plants will be at high and low risk of adverse outcomes or may benefit from interacting with an invasive ant. The potential for effects of invasive ants on plants to counteract, and the complexity and context-dependency that are hallmarks of ant-plant interactions generally, preclude drawing simple conclusions about the net impacts of invasive ants on plants. Further research on interactions between invasive ants and plants will contribute directly to conservation and agriculture, and provide insights to invasion ecology and our understanding of ant-plant interactions.

Key words: abundance, aggression, byproduct mutualism, carbohydrates, context-dependent outcomes, extrafloral nectaries, Homoptera, invasive ants.

Interactions between ants and plants range from facultative, loose associations to species-specific, obligate mutualisms, and innumerable questions have been posed about the costs, benefits, and evolutionary implications of these relationships (Beattie, 1985; Bronstein, 1994; Jolivet, 1996). As invasive ants spread, their interactions with plants are inevitable and have potentially great implications for agriculture and conservation. To what extent are ant-plant interactions altered by the introduction of these novel partners?

Invasive ants possess a distinct combination of traits relative to native ants (Holway et al., 2002). In this paper, I hypothesize that some of these traits will affect how invasive ants associate with plants and provide a basis for predicting the outcome of these novel interactions. I focus on the potential for differences between native and invasive ants in the way they protect plants from herbivory, tend Homoptera, and interfere with plant reproduction. These examples encompass the more facultative, ubiquitous interactions in which invasive ants are increasingly likely to participate as they spread around the globe.

Although I explore the differences between native and invasive ants for each type of interaction separately, the same ant can interact directly and indirectly with the same plant in multiple ways. Invasive ants that benefit the plant in one interaction may be detrimental to the plant in another. The net outcome for the plant will depend on the relative balance of a range of interactions, all of which in turn will be influenced by the same set of variables that typically influence ant-plant interactions. Ultimately, we will want to know whether invasive ants have the ability to tip the balance of interactions toward consistently positive or negative outcomes for the plants, and how these outcomes can be manipulated to achieve land management goals.

INVASIVE ANTS

Of the approximately 10,000 species of ants in the world, about 150 have been introduced around the world with the help of humans; these may be termed exotic, or tramp ants (McGlynn, 1999). Invasive ants are the small subset of introduced ants that are able to establish and penetrate areas outside of human-modified habitats (Holway et al., 2002). Well-known examples in the United States include the red imported fire ant, *Solenopsis invicta,*

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and the Argentine ant, *Linepithema humile.* The little fire ant, *Wasmannia auropunctata,* the big-headed ant, *Pheidole megacephala,* and long-legged ant, *Anoplolepis gracilipes,* also appear to be highly successful invaders, although they are far less studied. See Table 1 for a summary of distributions.

One hallmark of invasive ants is their ability to become extremely abundant in their new habitats. Pitfall traps in areas invaded by *Solenopsis invicta* (Porter & Savignano, 1990), *Linepithema humile* (Holway, 1998), and *Pheidole megacephala* (Hoffman et al., 1999) have all shown that the number of invasive ant workers greatly exceeds that of native ants in nearby un-invaded areas. Several mechanisms are likely contributing to invasive ants' achievement of numerical superiority including escape from natural enemies and competitors and changes in colony structure toward multi-queened, multi-nest supercolonies that lack intraspecific aggression (Holway et al., 2002).

The physiology and behavior of invasive ants also likely play a role in their tendency to achieve high abundance (Holway et al., 2002). Ecologically dominant ants, including invasive ants such as *Linepithema humile,* have modified crops that allow them to take in more liquid foods, including floral and extrafloral nectar and homopteran honeydew (Eisner, 1957; Davidson, 1998). The ability to harvest these carbohydrate-rich resources may be especially important in fueling the high tempo activity of a large workforce, thereby maintaining a high dynamic density (ants/area/time) (Tennant & Porter, 1991; Davidson, 1997; Davidson, 1998). Individual nests can be highly vagile, allowing invasive ants to move in response to the availability of resources (Passera, 1994). Even *Solenopsis invicta,* which nests in mounds, will create satellite nests at the base of plants when tending aphids (Kaakeh & Dutcher, 1992). A high level of aggression is another character common to invasive ants and likely enhances their success as predators (Holway et al., 2002). Access to prey and carbohydrate-rich resources and a large workforce are both the cause and effect of superior exploitative and interference competition abilities through which native ants and other competitors may be displaced (Holway et al., 2002).

Displacement of native ants is the most commonly documented consequence of an invasive ant introduction (Holway et al., 2002). *Linepithema humile,* for example, has displaced several species of epigaeic ants in California (Erickson, 1971; Ward, 1987; Holway, 1995; Human & Gordon, 1996), Portugal (Cammell et al., 1996; Way et al., 1997), and South Africa (Donnelly & Giliomee, 1985). *Wasmannia auropunctata* has expanded its territory

Table 1. Native and introduced ranges of some invasive ants.

Species	Common name	Native range	Introduced range	References
Anoplolepis gracilipes (F. Smith)	long-legged or crazy ant	in dispute	Asia, Australia, Pacific and Indian Ocean islands	Fluker & Beardsley (1970), Haines & Haines (1978), Veeresh & Gubbaiah (1984), Fellowes (1999), Green et al. (1999), Young et al. (2001)
Linepithema humile (Mayr)	Argentine ant	Argentina and Brazil	Mediterranean-type climates of all continents, Hawai'i, Bermuda	Haskins & Haskins (1965), Fluker & Beardsley (1970), Majer (1994), Suarez et al. (2001)
Pheidole megacephala (Fabricius)	big-headed ant	tropical Africa	South America, Asia, Australia, U.S., Pacific Ocean islands, Bermuda	Haskins & Haskins (1965), Greenslade (1971), Room (1975), Fluker & Beardsley (1970), Majer (1985), Fowler et al. (1990), Fellowes (1999), Deyrup et al. (2000)
Solenopsis invicta (Buren)	red imported fire ant	Brazil	U.S., Australia	Vinson & Greenberg (1986), Holway et al. (2002)
Wasmannia auropunctata (Rogers)	little fire ant	neotropics	Africa, continental U.S., Hawai'i, Galapagos Islands, New Caledonia	Spencer (1941), Entwistle (1972), Fabres & Brown (1978), Williams (1994), Conant & Hirayama (2000)

at the expense of native ants on the Galapagos Islands (Lubin, 1984). *Pheidole megacephala* has diminished the native ant populations of several habitats in Australia (Majer, 1985; May & Heterick, 2000; Hoffman et al., 1999; Vanderwoude et al., 2000). *Solenopsis geminata* (F.) and other ants native to the southern U.S. have become much less common following invasion by *S. invicta* (Porter & Savignano, 1990; Gotelli & Arnett, 2000).

Invasive ants also affect other invertebrates and even vertebrates, usually negatively. *Anoplolepis gracilipes* is blamed for diminished populations of various invertebrates in the Seychelles (Haines & Haines, 1978) and is generating ecosystem-level changes through its impact on the red land crab on Christmas Island (Green et al., 1999). *Linepithema humile* is associated with decreases in some insects in California and Hawai'i (Cole et al., 1992; Bolger et al., 2000). The great reduction in endemic insects in lowland Hawai'i at the end of the 1800s has been attributed to invasion by *Pheidole megacephala* (Zimmerman, 1970). *Solenopsis invicta* has been linked to declines in a number of terrestrial invertebrates, birds, and mammals in the southern United States (Holway et al., 2002). *Wasmannia auropunctata* has eliminated or reduced terrestrial invertebrate populations in the Galapagos Islands (Lubin, 1984) and New Caledonia (Jourdan, 1997). The mechanisms for these effects are not always clear but likely involve some combination of predation and competition, via direct or indirect interactions (Holway et al., 2002).

PREDICTING THE NATURE AND OUTCOMES OF INVASIVE ANT-PLANT INTERACTIONS

A wealth of studies has established that the nature of ant-plant interactions is dependent on many variables including ant behavior, ant colony size and stage, host plant attributes, and the abundance and behavior of other organisms in the system (Buckley, 1982; Beattie, 1985; Keeler, 1989; Cushman, 1991; Davidson & McKey, 1993; Bronstein, 1994, 1998; Jolivet, 1996). As explained above, invasive ants tend to have larger colonies and exhibit more aggressive behavior than native ants. Moreover, invasive ants appear to have a stronger predilection than many native ants for carbohydrate resources, which are invariably obtained directly or indirectly from plants. Since native ants are frequently displaced when invasive ants enter a new habitat, it will be traits of the invaders that influence future outcomes for the plants. Applying existing models of ant-plant interactions, I develop hypotheses about how invasive ants' elevated abundance, aggression, and affinity for carbohydrate-rich food affect how they might protect plants from herbivores, tend Homoptera, and interfere with plant reproduction.

ANT PROTECTION FROM HERBIVORES

Protection of plants from herbivores is perhaps the oldest recognized effect of ants on plants. As long ago as A.D. 304, Chinese citrus growers facilitated the spread of the yellow citrus ant, which preyed on herbivores in their orange orchards (Huang & Yang, 1987). Since then, ants' ability to prey on, or simply harass, would-be herbivores has been noted in many systems (Beattie, 1985; Hölldobler & Wilson, 1990). In some cases, plants entice ants by offering food or shelter. For example, it is thought that one of the primary reasons for the presence of extrafloral nectaries is to attract ants in exchange for protection from herbivores (Bentley, 1977).

A number of traits associated with invasive ants have been linked to plant defense: large colony size, high levels of worker activity, and aggressiveness (Davidson & McKey, 1993; Bronstein, 1998). A large number of very active workers may result in increased plant visitation by ants leading to decreased herbivory (Gaume et al., 1997; Bronstein, 1998; Gaume et al., 1998; Linsenmair et al., 2001) because herbivores are located more rapidly and have a shorter residence time on the plant (Duarte Rocha & Godoy Bergallo, 1992). Benefits to the plant probably level off or even decline at some colony size, however. An extremely large colony may impose a cost on the plant if the ants are stealing floral nectar, tending Homoptera, interfering with the natural enemies of herbivores, or excavating the plant's root system. Research to determine where the cost-benefit trade-offs lie with respect to ant colony size has yet to be done.

Aggressive behavior also aids in protecting the plant from herbivores (Fiala et al., 1989; Letourneau, 1983; Bronstein, 1998). Bentley (1977) related ant aggression on plants to three factors: predatory behavior, ownership behavior or the defense of territorial boundaries (Way, 1963), and swarming behavior or the ability to rapidly recruit workers. All three behaviors may be enhanced at the colony level by having a large workforce. Aggression is also negatively correlated with proximity to an ants' nest; disturbance near an ants' nest or food source will elicit a stronger response than a threat encountered farther away (Way, 1963). The vagile, polydomous nesting behavior of invasive ants may allow them to nest in closer proximity than a native

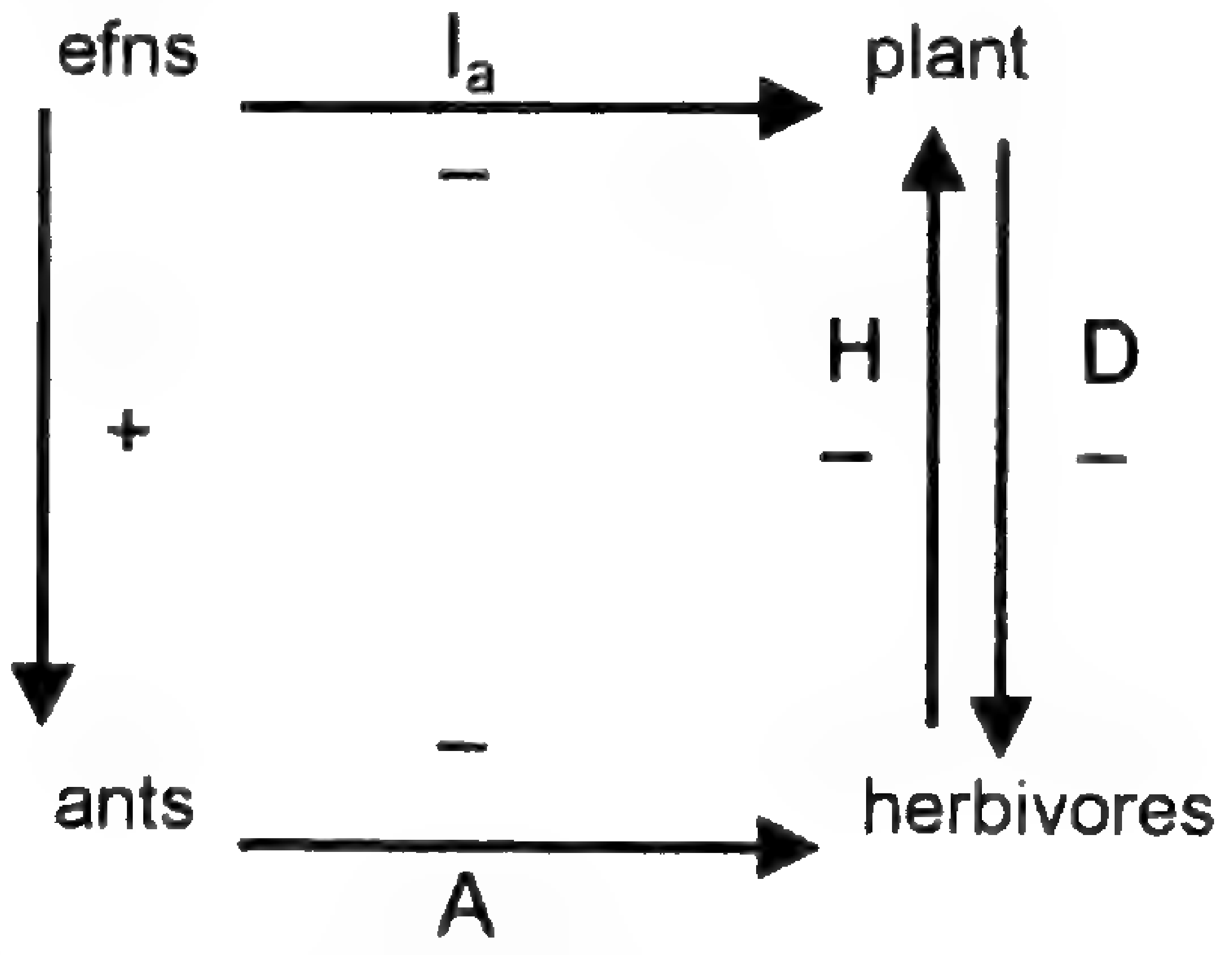

Figure. 1. A schematic of the food-for-protection mutualism between ants and extrafloral nectaries. The extrafloral nectaries provide ants with food and the ants deter herbivores. The direction of the arrows indicates the direction of the effect and the positive and negative signs show the type of effect. A = effectiveness of ant-defense, D = effectiveness of other defenses, H = intensity of herbivory, I_a = investment in nectar and nectaries, and efns = extrafloral nectaries.

ant would, possibly facilitating a greater aggressive response.

Some ants provide protection from herbivores while collecting extrafloral nectar. Keeler (1981: 490) modeled the conditions under which the mutualism is favored:

$$p[A(1 - D)H] > I_a$$

where p = probability that ants will find the plant, A = effectiveness of ant-defense, D = effectiveness of other defenses, H = intensity of herbivory, and I_a = investment in nectar and nectaries. From the plants' perspective, the mutualism is maintained when the left side of the equation, the benefits to the plant, exceeds the right side, the costs of attracting the ants (Keeler, 1981). A schematic of the relationship is shown in Figure 1.

Given the numerical superiority, attraction to carbohydrate resources, and aggressive character of invasive ants, we might expect that $p_{invasive} > p_{native}$ and $A_{invasive} > A_{native}$. Since D is primarily a factor of the plant and the herbivore(s), $D_{invasive}$ and D_{native} are not likely to differ. $H_{invasive}$ may exceed H_{native} if intraguild predation is a factor, i.e., if ants prey on or interfere with the natural enemies of herbivores (Eubanks, 2001). However, $H_{invasive}$ may be less than H_{native} if invasive ants diminish herbivore populations via direct or indirect interactions that affect herbivore eggs, larvae, pupae, or adults away from the plant. If extrafloral nectar production is an inducible defense (Koptur, 1989; Ness, 2001) I_a will increase with H. For example, if H_{native} is greater than $H_{invasive}$, then extrafloral nectaries will be induced more often when native ants are present, and $I_{a\ native}$ will be greater than $I_{a\ invasive}$.

If on balance, the left side of the equation increases and I_a stays the same, then there will be a greater benefit margin for the plant when invasive ants are present. If, however, the presence of invasive ants lowers the left side of the equation, then to maintain the mutualism, $I_{a\ invasive}$ may also need to be less than $I_{a\ native}$. For invasive ants that are aggressive, abundant, and attracted to carbohydrate-rich resources, the model predicts maintenance of the mutualism if the potential for herbivory is not diminished (e.g., through interactions away from the plant).

ANT TENDING OF HOMOPTERA

Ant tending of honeydew-producing Homoptera, including scale, mealybugs, aphids, and membracids, is a common indirect ant-plant interaction (Way, 1963; Carroll & Janzen, 1973; Buckley, 1987; Hölldobler & Wilson, 1990; Davidson & McKey, 1993). Homoptera extract phloem from the host plants and excrete it as honeydew. Ants feeding on the honeydew often protect these Homoptera from parasites and predators (Way, 1963; Buckley, 1987). The ant-Homoptera mutualism may be detrimental for the plant, robbing it of phloem and sometimes leading to mold accumulation (Bach, 1991; Lewis et al., 1976) or phytopathogen transmission (e.g., pineapple mealybug wilt disease (Beardsley et al., 1982), *Phytophthora* pod rot (Evans, 1973), swollen shoot virus (Taylor & Adedoyin, 1978)) while conferring no benefits in exchange (Buckley, 1987). Less commonly, the interaction may benefit the plant if ants deter other herbivores while tending Homoptera (Carroll & Janzen, 1973; Messina, 1981; Compton & Robertson, 1988).

As with plant protection from herbivores, the characters common to many invasive ants will affect their Homoptera-tending abilities and consequently the outcome for the plant. The need for carbohydrate resources and ability to harvest copious amounts of liquid provides the basis for the attraction of invasive ants to Homoptera. Ant aggression, particularly ownership behavior, is an effective deterrent to most would-be parasites and predators of Homoptera (Way, 1963). Polydomy and nest vagility may allow invasive ants to reside in closer proximity to these carbohydrate resources than would native ants.

Ant abundance, however, may be the primary trait affecting invasive ant-Homoptera mutualisms, as it may affect the interaction through several mechanisms. Higher ant numbers may translate into a higher probability of locating the tendees,

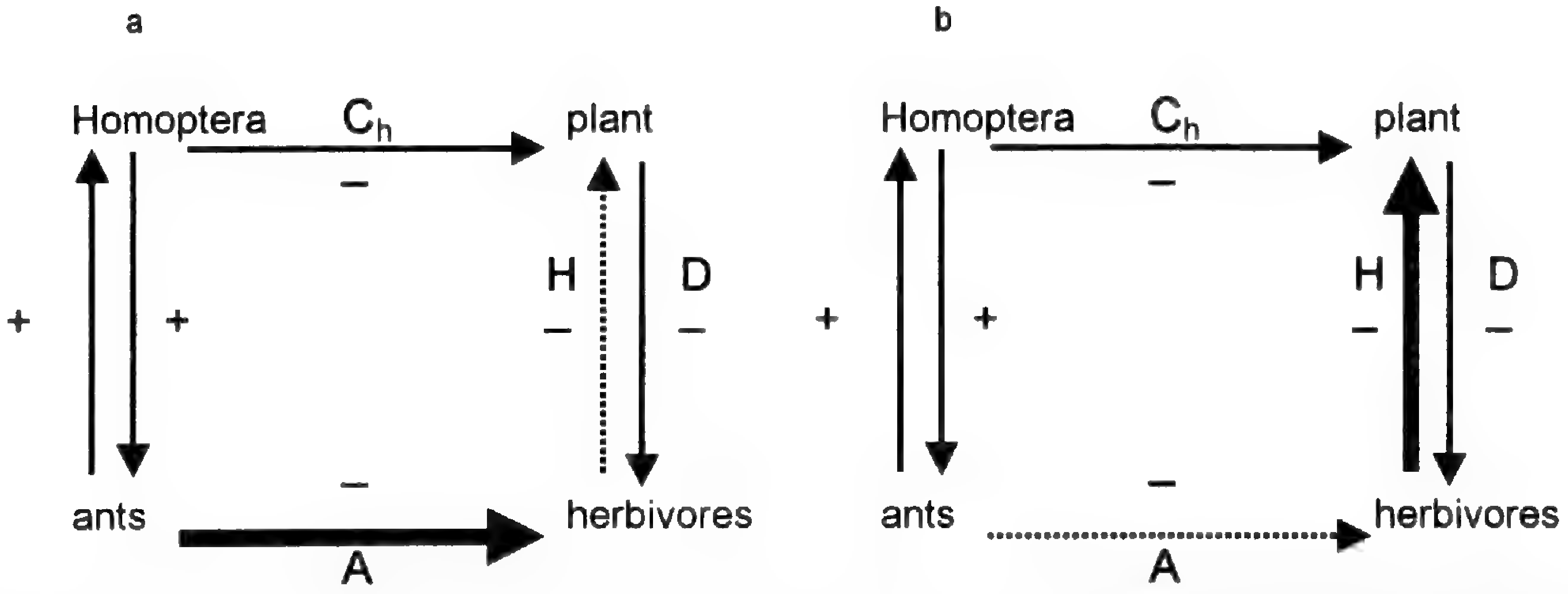

Figure 2. The ant-Homoptera mutualism when it results in a byproduct mutualism with the plant (2a) and when it is a parasite on the plant (2b). The direction of the arrows indicates the direction of the effect and the positive and negative signs show the type of effect. The thickness of the arrow indicates the strength of the effect. Dotted lines illustrate weak or no effect. C_h = the cost of hosting the Homoptera. H, A, and D are as defined in Figure 1. In 2a, the detrimental effect of the ants on the herbivores and subsequent decline in herbivore attack outweighs the cost to the plant of hosting the Homoptera. In 2b, the ants fail to deter herbivores so the plant bears the cost of hosting the Homoptera and attack by other herbivores.

and a higher ant:homopteran ratio may make ants more effective at deterring their partners' enemies (Steyn, 1955). Tending ants are a limiting resource to honeydew-producing Homoptera in many systems (Addicott, 1978; Sudd, 1987; Cushman & Addicott, 1989; Breton & Addicott, 1992; Fischer et al., 2001), and well-tended Homoptera may grow faster, reproduce more rapidly, and produce more young than untended ones (Way, 1963; Bristow, 1984; Morales, 2000). Where the ant:Homoptera ratio becomes too low, Homoptera may become ant prey or be more easily parasitized or preyed upon by natural enemies (Way, 1963, and references therein; Breton & Addicott, 1992; Sakata, 1994; Jolivet, 1996). The superabundance achieved by invasive ants may keep the tender:tendee ratio from falling below this threshold. In such a case, we would expect limits to the abundance of both mutualists to be imposed by the host plant.

Impacts on the plant, however, also may depend on whether the ants tending Homoptera deter other herbivores. In this byproduct mutualism (Yu, 2001), the plant benefits indirectly from the ants' presence; the ants benefit from the Homoptera hosted by the plant and possibly the herbivores, if they are captured as prey. In this scenario, Homoptera are analogous to extrafloral nectaries and Keeler's model (1981) can be modified as:

$$p[A(1 - D)H_{\text{non-Homoptera}}] > C_h$$

The right side of the equation (formerly the investment in nectar and nectaries, I_a) becomes the cost to the plant of hosting the Homoptera, C_h, including direct effects of lost phloem and indirect consequences such as mold accumulation and susceptibility to phytopathogens. Other terms remain the same: p = probability that ants will find the plant, A = effectiveness of ant-defense against (non-homopteran) herbivores, D = effectiveness of other defenses, H = intensity of (non-homopteran) herbivory. Considering the traits of invasive ants that favor high homopteran populations, it is probable that in many cases $C_{h\text{-invasive}}$ will be greater than $C_{h\text{-native}}$. The probability that the ant finds the plant, p, may vary not only with the abundance of the ant, but possibly with the ability of different Homoptera to recruit ants (Del-Claro & Oliveira, 1996). It is unclear, though, whether invasive ants may respond to attractant cues differently than native ants. Hypothesized differences in A, D, and H for native and invasive ants would be as explained above. As with the food-for-protection mutualism involving extrafloral nectaries, the byproduct mutualism will only be maintained if the benefits, in terms of deterred non-homopteran herbivores denoted on the left side of the equation, exceed the costs exacted on the plant by the Homoptera, the right side of the equation (Fig. 2a). If costs to the plant exceed benefits, the ant-Homoptera interaction will tend toward a parasitic relationship with its host (Fig. 2b), possibly resulting in reduced fitness of the plant. Studies that fail to detect any change in plant fitness with Homoptera outbreaks associated with invasive ants may be observing a balance between the two types of outcomes. As with interactions involving extrafloral nectaries, for invasive ants that are aggressive, abundant, and attracted to carbohydrate-rich resources, the model predicts maintenance of the byproduct mutualism if the potential for herbivory is not diminished (i.e., through interactions away from the plant).

ANT IMPACTS ON PLANT REPRODUCTION

Seed set. With few exceptions (e.g., Yano, 1994; Puterbaugh, 1998), ants commonly have been regarded as unwanted guests in flowers (Kerner, 1878; Buckley, 1982). Attracted by floral nectar, ants may damage floral structures, and depress pollen viability with their antibiotic secretions (Kerner, 1878; Peakall et al., 1991; Galen, 1999). As with Homoptera and extrafloral nectary tending, superabundance and an affinity for carbohydrate resources combined with high levels of aggression would lead to the expectation that invasive ants would be exceptional at recruiting colony members to flowers and exploiting floral nectar.

If numerous aggressive ants are present in flowers, their presence may affect other floral visitors. Pollinators may be forced to reposition frequently to avoid attack by the ants, and this may result in increased transfer of pollen and consequently higher seed set. Alternatively, pollinators may avoid the flower altogether, or reposition too superficially for effective pollen transfer, ultimately resulting in decreased seed set (Wyatt, 1980). A plethora of floral antagonists, including pollen consumers, and other florivores, however, may also be deterred, perhaps compensating for any adverse effects on pollinators.

The ants' ultimate impacts on seed set will be dependent on the attraction and availability of floral nectar in the context of the ants' seasonal diet preferences, activity patterns, and abundance, the number of pollinators and floral antagonists and their susceptibility to ant deterrence, floral structure and defenses against ants, and the pollination requirements of the plant (Kerner, 1878; Koptur, 1979; Vinson & Greenberg, 1986; Huxley & Cutler, 1991; Klinkhamer & de Jong, 1993; Lanza et al., 1993; Koptur & Truong, 1998; Puterbaugh, 1998), as well as the relative difference between ants' effects on pollinators and floral antagonists. For example, I would expect nectar-robbing by invasive ants to have little effect on seed set across a plant population in an invaded area if there is little competition for the resource, e.g., if nectar is available in excess of demand by pollinators. I would expect invasive ants to be more likely to decrease seed set in a plant species that has few floral antagonists and is dependent on a few species of small pollinators, than in a species that suffers from many floral antagonists and has a diverse pollinator guild. Moreover, flowers in which nectaries are in close proximity to the stigma and anthers relative to the ants' body size may be more affected by nectarivorous ants than those in which nectaries are farther away.

Seed predation and harvesting. Impacts of ants on seed dispersal and seed predation have received more attention than impacts on seed set. In myrmecochorous mutualisms, ants disperse seeds away from the parent plant, often burying them in their nest, in exchange for the lipid-rich eliaosome attached to the seed (Buckley, 1982; Beattie, 1985). The dispersed seeds therefore may escape competition with siblings and parents and are less susceptible to predation and other threats, such as fire (Buckley, 1982; Beattie, 1985). Ants may also be seed harvesters, consuming the seed itself. Seed harvesters, however, do not eat all the seeds they collect, and therefore may act as accidental seed dispersers (Buckley, 1982; Hölldobler & Wilson, 1990).

Various species of ants may be attracted to eliaosomes and opportunistically take part in myrmecochorous mutualisms, whereas harvester ants tend to have special adaptations for harvesting, consuming, and storing seeds (Hölldobler & Wilson, 1990; Keeler, 1989). In both cases, the ants need to (a) discover the seed, (b) recognize the seed as a resource, and (c) be able to carry the seed back to the nest. Seed discovery will be dictated by ant foraging patterns, seasonal and temporal overlap between ant activity and seed availability, and the attractiveness of the eliaosome, if present (Beattie, 1985; Keeler, 1989). Seeds are typically high in lipids and proteins; recognition of the seed as a desirable resource may depend on the relative abundance and composition of other food sources in the environment and the dietary requirements of the colony when the seeds are available (Beattie, 1985). In every myrmecochorous system studied, seed-dispersing ants comprise only a small subset of the ant species present, and their behavior toward seeds can vary from one day to the next (Beattie, 1985), suggesting that recognition of the seed as a valuable food resource is not constant among ant species or over time for a single species. The ability to carry the seed back to the nest will depend on the ants' foraging behavior and size and shape complementarity between seed and ant (Keeler, 1989). Harvester ants must also have the mandibular strength and agility to ingest the seeds (Beattie, 1985).

How do we expect invasive ants to compare to native ants in these requirements? Traits of invasive ants that have formed the basis for hypotheses about other types of interactions discussed in this paper, namely elevated abundance, aggression, and attraction to carbohydrates, may not have as much influence on seed predation and dispersal. Numerical superiority of invasive ants may increase the probability that they will discover seeds. However, common traits of invasive ants offer little capacity for predicting how invasive ants will respond to the seeds they encounter. Other traits that may be linked to seed discovery and dispersal may not vary consistently between invasive and native ants. *Solenopsis invicta* and *Pheidole megacephala* are attracted to oily, lipid-rich food sources (Vinson & Greenberg, 1986; Sanders et al., 1992), and seed harvesters occur in both genera (Hölldobler & Wilson, 1990). Thus, we might expect these invaders to be attracted to seeds, and even have some of the mandibular adaptations helpful for ingesting seeds, but perhaps no more so than native ants.

OTHER VARIABLES AFFECTING ANT-PLANT INTERACTIONS

As noted above, numerical superiority, aggressive behavior, and resource acquisition abilities of the ants are unlikely to account for all differences between invasive and native ant-plant interactions. Other biological traits that may vary substantially among ants, but are unlikely to vary consistently among invasive and native ants such as temperature tolerance, daily activity patterns, colony cycles, and seasonal preferences for food types will certainly affect ants' relationships with plants. Even for a single ant species, associations with plants may change spatially or temporally. For example, the degree of plant protection is largely linked to ant foraging patterns, which may change depending on the nutritional requirements of the colony (e.g., in relation to reproductive cycles), and the availability of carbohydrate and protein resources that require less foraging effort than those on the plant of interest (Ali & Reagan, 1985; Vinson & Greenberg, 1986; Stein et al., 1990; Rapp & Salum, 1995; Cornelius & Grace, 1997).

Attributes of the potential prey items, Homoptera, and the host plant will also play roles in defining ant interactions with these organisms (Way, 1963; Cushman, 1991; Huxley & Cutler, 1991; Bronstein, 1994), and invasive and native ants may diverge in their responses to these variables as well. Many herbivores (Van Der Goot, 1916; Kaakeh & Dutcher, 1992; Pavis et al., 1992; Gunawardena & Bandumathie, 1993; Cornelius & Bernays, 1995; Montgomery & Wheeler, 2000; Brinkman et al., 2001) and flowers (Kerner, 1878; Willmer & Stone, 1997; Ghazoul, 2000) have effective chemical or physical defenses against ants. Whether differences in ant size, recruitment ability, or tolerance to phytotoxins, for example, will enable certain groups of ants to evade these defenses is yet to be seen. In cases where herbivores and flowering plants have no evolutionary history with ants and therefore might lack specific defenses against ants (e.g., Hawai'i), invasive ants might not need to be especially aggressive or adept at thwarting defenses to deter herbivores or steal floral nectar.

TESTING THE PREDICTIONS WITH FIELD EVIDENCE

Do observations of invasive ant-plant interactions support predictions that the distinct combination of invasive ant traits will affect the outcome of their interactions with plants? Specifically, because of their combination of traits, are invasive ants more likely than native ants to deter herbivores, tend Homoptera to the detriment of host plants, and interfere with plant reproduction? There have been few direct tests. Most research on ant interactions with herbivores has been done in agroecosystems, has focused on how pest populations and crop yields are affected by changes in ant fauna, and has not explored any particular ant attributes influencing the interactions. Still less is known about how invasive ants affect seed set, predation, and dispersal. Nonetheless, examples below provide some evidence of the importance of the common traits of invasive ants while also underscoring the influence of ant biology and the role of other organisms in the system in determining the outcome of these interactions for the plant.

ANT PROTECTION FROM HERBIVORES

There are dozens of examples of invasive ants preying on or harassing would-be herbivores (see Holway et al., 2002, for a review). Almost none of these compare invasive to native ants, however, and rarely do they pinpoint any particular characteristic of the ant responsible for effects on herbivores. Some insights can be gained from cases in which the invader fails to deter herbivores. For example, *Anoplolepis gracilipes* affords protection from the sucking bug, *Amblypelta cocophaga* (China), in Solomon Islands coconut when it reaches high abundance in the trees. But when prey are abundant on the ground, *A. gracilipes* fails to forage in the trees and premature nutfall ensues due to *A. cocophaga* damage (Greenslade, 1971). In Keeler's (1981) terms, in this case a high A, ability to deter herbivores, is inconsequential if the probability of foraging on the plant (p) is low.

Extrafloral nectaries may serve to increase p.

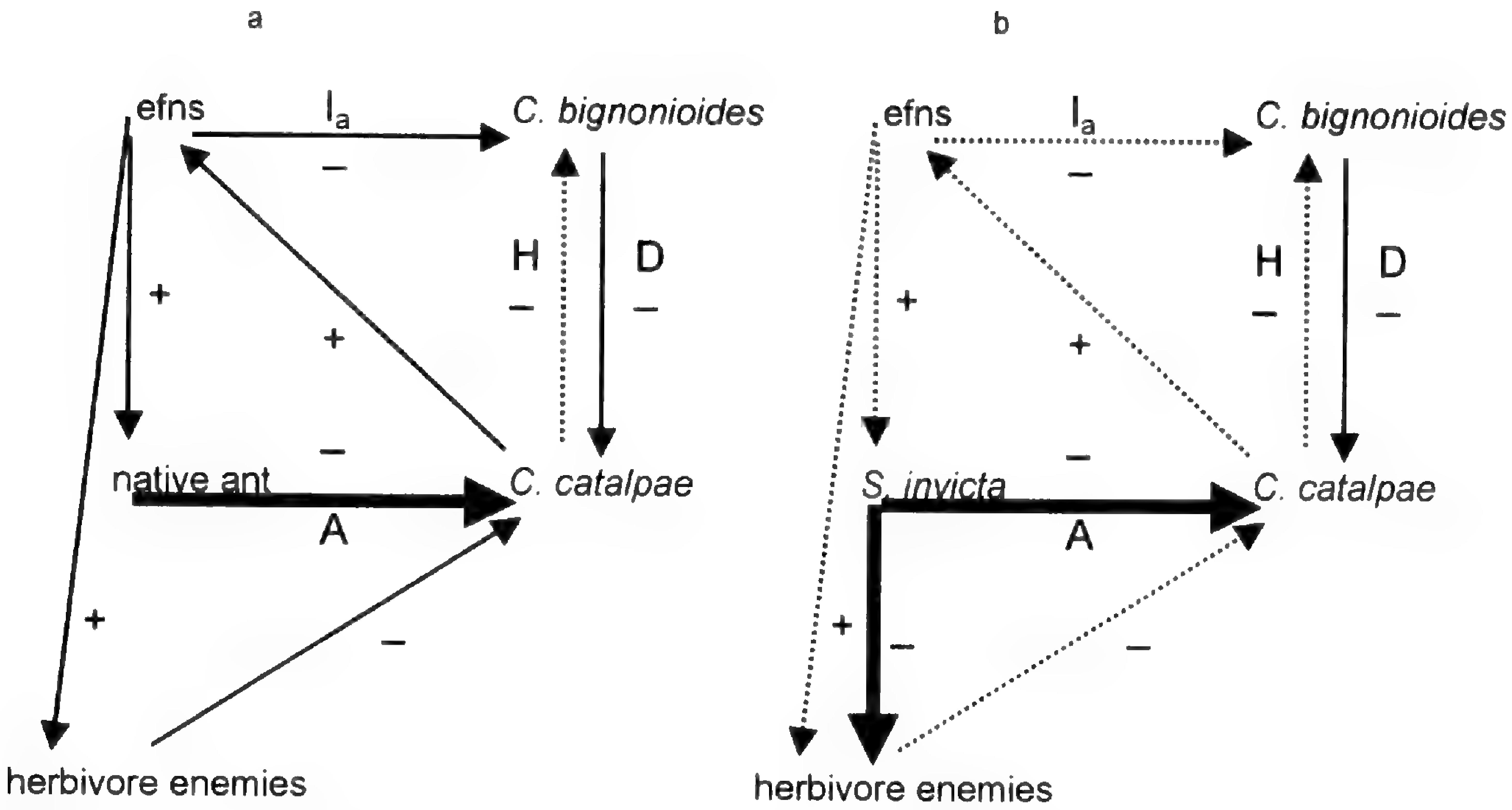

Figure 3. The food-for-protection mutualism between the tree *Catalpa bignonioides* and the dominant native ant (3a) and with *Solenopsis invicta* (3b). The direction of the arrows indicates the direction of the effect and the positive and negative signs show the type of effect. The thickness of the arrow indicates the strength of the effect. Dotted lines illustrate weak or no effect. I_a, H, A, and D are as described in Figure 1, efns = extrafloral nectaries. In 3a, the native ant and other enemies of the main herbivore, *Ceratoma catalpae*, are attracted to extrafloral nectar and are effective in reducing the herbivore attack on the plant. In 3b, *S. invicta* is not attracted to the extrafloral nectaries, deters *C. catalpae*'s other natural enemies, but still decreases the impact of the herbivore on the plant. In both scenarios, the extrafloral nectaries are induced by herbivory. See text for references.

Several studies have shown that different invasive ants are attracted to extrafloral nectar and can decrease herbivory on extrafloral nectar-bearing plants (see Holway et al., 2002, for a review). The high population density of *Pheidole megacephala* and its tending of extrafloral nectaries are blamed for the difference in populations of shrubs between *P. megacephala* and native ant-inhabited sites in Australian rainforest. The native *Urena lobata* L. and the introduced *Senna obtusifolia* (L.) H. S. Irwin & Barneby occur in dense stands and suffer little from folivory in areas invaded by *P. megacephala*, whereas in areas with native ants, the shrubs are small, isolated, and heavily attacked by herbivores (Hoffman et al., 1999). Other studies demonstrate that *Solenopsis invicta* (Fleet & Young, 2000), *Linepithema humile* (Koptur, 1979), and *Wasmannia auropunctata* (Meier, 1994) also are attracted to extrafloral nectaries on plants in their introduced habitats, sometimes to the benefit of the plant. But these studies, as with most, do not compare the behavior of invasive ants to that of native ants, nor do they explore specific attributes of invasive ants that may be influencing the interaction or its outcome.

Research exploring the interactions of *Solenopsis invicta* with *Catalpa bignonioides* Walter provides an interesting case study because it compares the invasive to native ant's interactions with the tree and reveals specific attributes of the invader that are responsible for the differences. The production of extrafloral nectar is an inducible defense in this system; extrafloral nectar production increases in response to herbivory, thereby attracting native ants and parasitic wasps (Ness, 2001). Field experiments have shown that *S. invicta* displaces native ants and preys on the parasitic wasps of the predominant herbivore in the system, the caterpillar *Ceratoma catalpae* (Boisduval). Moreover, *S. invicta* visits extrafloral nectaries much less frequently than native ants, most likely due to peak extrafloral nectar production coinciding with the stage of colony cycle when workers prefer protein-rich resources. *Solenopsis invicta* is apparently as effective a predator of *C. catalpae* as are the native ants because it preys on pupae and pre-pupal instars as well as larvae, and because of its exceptional aggressiveness when prey are encountered. Thus, while *S. invicta* disrupts the mutualism by preventing other natural enemies of *C. catalpae* from visiting extrafloral nectaries and protecting *Catalpa bignonioides*, it does not do so at the cost of increased herbivory (Ness, 2001).

Putting the example in the context of Keeler's (1981) model (Fig. 3), even without the lure of extrafloral nectar, A_{Sinv} equals or exceeds A_{native}. $I_{a\ Sinv}$

need not be as high as $I_{a\,native}$; when *Solenopsis invicta* is present, neither the invasive ant nor the parasitic wasps visit the extrafloral nectaries as much as they are visited when native ants are present. In fact, because the extrafloral nectar is inducible, if *S. invicta* decreases the herbivore load more than native ants do, $I_{a\,Sinv}$ will be lower than $I_{a\,native}$. The difference between the benefits of reduced herbivory and the investment in extrafloral nectar production will be higher when *S. invicta* is present than when native ants are present.

It is worth noting that p, the probability of locating and foraging on the plant, may be influenced both by the abundance of the ant and its attraction to the nectar reward offered. As such, an extremely high density of *Solenopsis invicta* may offset its weak attraction to extrafloral nectar (Agnew et al., 1982). Indeed, high abundance of *S. invicta* has been offered as an explanation for the lack of any difference in its foraging frequency between nectaried and nectariless isolines of cotton (Agnew et al., 1982). Analogously, it is possible that high density of *S. invicta* in the invaded *Catalpa bignonioides* stand (Ness, 2001) facilitated the ants' foraging on the plant, notwithstanding the absence of its attraction to extrafloral nectar. In these cases, if abiotic or other conditions ever result in diminished abundance of *S. invicta*, the invader may become less effective at deterring herbivores than ants that may not be as abundant, but are lured to the plants by the nectar reward.

ANTS TENDING HOMOPTERA

Anoplolepis gracilipes, Linepithema humile, Pheidole megacephala, and *Wasmannia auropunctata* all have been noted for their ability to cause Homoptera outbreaks in various parts of the world (Holway et al., 2002). *Solenopsis invicta* may sometimes obtain carbohydrates directly from plant tissue (Vander Meer et al., 1995), but also has been associated with increased Homoptera populations (Lofgren, 1986; Holway et al., 2002). The data collected in these studies often fail to discern any particular trait of invasive versus native ants that are responsible for Homoptera outbreaks. While some evidence of the importance of abundance, aggression, and attraction to carbohydrate resources in invasive ant interactions with plants is seen in the examples below, evaluation of my prediction that these common invasive ant traits play a major role in determining their interactions with plants will be enhanced by further detailed study. However, some studies do allow us to examine the relative impact on the plant of the invasive ant as Homoptera tender versus herbivore deterrent. These studies reveal that both types of outcomes outlined above occur, those in which the ant-Homoptera mutualism is parasitic toward the plant and those in which the ants tending Homoptera enter into a byproduct mutualism with the plant by deterring non-homopteran herbivores.

Linepithema humile's abundance, aggression, and tending of aphids have all been related to its ability to control populations of the pine processionary moth (*Thaumetopoea pityocampa* Den. & Schiff.) in Portugal pine plantations (Way et al., 1999). The aphids attract foraging *L. humile* to pine tree crowns. Later in the season, pine processionary moth larvae on trees with *L. humile* are fiercely attacked, whereas those on native ant-occupied trees are ignored. Consequently, parts of plantations that are inhabited by *L. humile* escape the severe defoliation caused by *T. pityocampa* in native ant-inhabited areas. Figures 4a and b contrast the interactions with the plant when native ants versus *L. humile* are present in terms of Keeler's (1981) modified model derived above.

Reviewing interactions of invasive ants and Homoptera in cacao (*Theobroma cacao* L.) is a study in contrasts, and illustrates the possibility for different outcomes to occur between the same plant and ant. In West Africa, *Wasmannia auropunctata* is actively spread among cacao plantations because it effectively deters pestiferous mirid bugs despite its association with high levels of scale and psyllids (Entwistle, 1972). In contrast, in its native Brazil, *W. auropunctata* tends the mealybug *Planococcus citri* (Risso) and many other Homoptera in cacao and fails to control pest herbivores possibly because it does not always achieve dominance in the ant mosaic (De Medeiros et al., 1995; De Souza et al., 1998). In the parlance of the modified Keeler (1981) model, in West Africa, C_h, the cost to the plant of hosting the Homoptera associated with *W. auropunctata*, is outweighed by the high A, the ability of *W. auropunctata* to deter key herbivores, and the ant can be said to have entered a byproduct mutualism with cacao. But in Brazil, *W. auropunctata* tending *P. citri* imposes a high C_h and a small A, resulting in a cost to the plant that exceeds the benefit.

Similarly, *Pheidole megacephala* in its native West Africa tends the mealybugs, *Planococcus citri* and *P. njalensis* (Laing), which are associated with swollen shoot virus in cacao (Taylor & Adedoyin, 1978; Campbell, 1994). As part of its tending behavior, *P. megacephala* transports soil from the ground to create tent shelters for the homopterans and thereby acts as a vertical vector of *Phytophtho-*

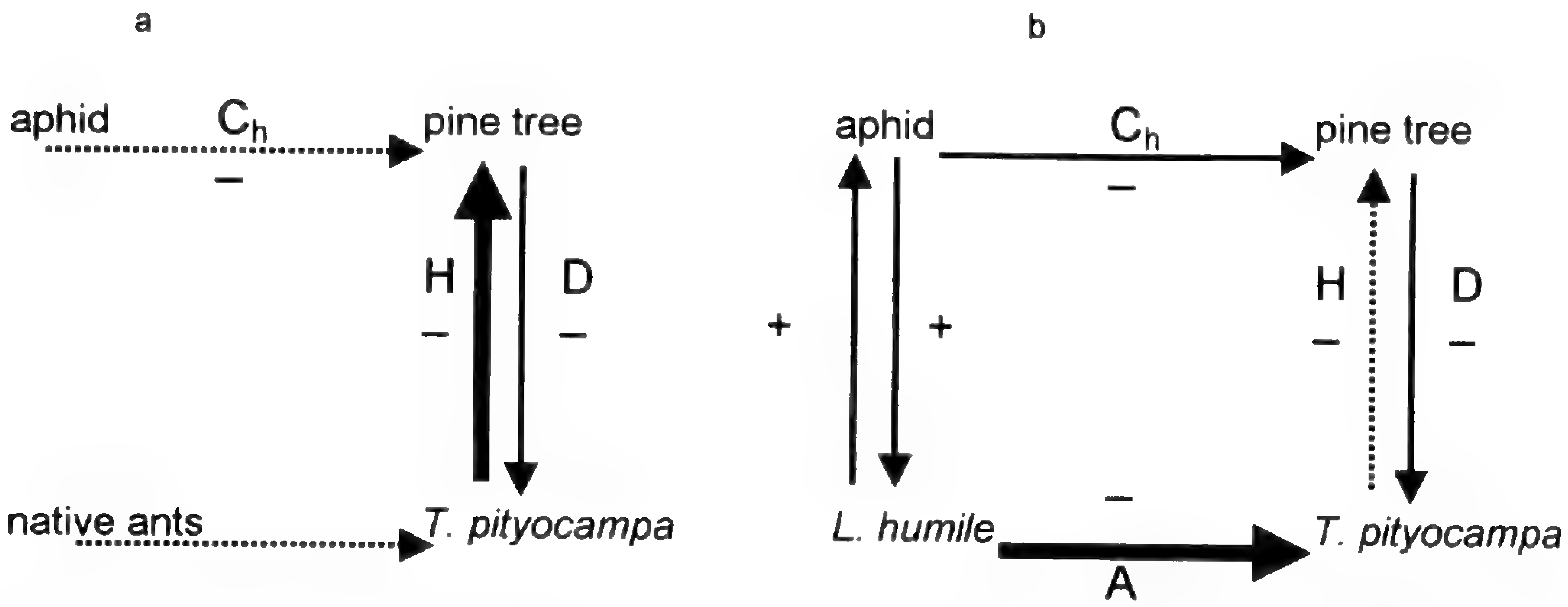

Figure 4. The native ant–*Thaumetopoea pityocampa*–pine tree relationship (4a) and the *Linepithema humile–T. pityocampa*–pine tree relationship (4b). The direction of the arrows indicates the direction of the effect and the positive and negative signs show the type of effect. The thickness of the arrow indicates the strength of the effect. Dotted lines illustrate weak or no effect. C_h, H, A, and D are as described in Figures 1 and 2. In 4a, the native ant is not attracted to the tree by aphids, fails to prey on the major herbivore, *T. pityocampa*, and the pine trees suffer from severe defoliation. Figure 4b illustrates the byproduct mutualism between *L. humile* and the pine tree. *Linepithema humile* is attracted to the trees by aphids and preys on *T. pityocampa* to the benefit of the plant. See text for references.

ra spores, the etiologic agent of black pod rot (Evans, 1973). In this case, C_h comprises not only the direct cost of hosting the mealybugs, but also the associated increased likelihood of being infected with two of the worst diseases of cacao. While no cacao studies have ever reported relationships between *P. megacephala* and non-homopteran herbivores, it is unlikely that strong deterrence of herbivores (a high A) would have gone unnoticed by farmers intimately aware of any effect on their yields. *Pheidole megacephala*'s frequent association with high Homoptera outbreaks to the detriment of plant fitness places it firmly in the pest category in West Africa (Taylor & Adedoyin, 1978).

In contrast, a low C_h and high A characterize the interaction between Homoptera, cacao, and *Anoplolepis gracilipes* in Papua New Guinea. The ant relies on honeydew-producing Homoptera to maintain its abundance (Baker, 1972). It displaces the native tent-building ants that facilitate transmission of black pod rot (Room & Smith, 1975; McGregor & Moxon, 1985; Way & Khoo, 1992). Moreover, unlike the ants it displaces, *A. gracilipes* harasses adult cocoa weevils and persistently disrupts egg laying and foraging of several mirid and coreid bugs, all of which are major pests (Entwistle, 1972; McGregor & Moxon, 1985; Way & Khoo, 1992). But the same ant fails to forage in trees in Malaysian cacao and so is not effective against herbivores (Way & Khoo, 1989), indicating that a low p, probability of finding and foraging on the plant, can undermine any ability to deter its herbivores.

The examples above suggest that ant-Homoptera mutualisms that are parasitic on the host plant are more likely to occur in the invaders' native range, and those in which the mutualism benefits the plant may be more likely in the introduced range. If this were the case, we would expect that studies that report on invasive ant-Homoptera mutualisms but do not explicitly evaluate the effects of the ants on herbivores, would nonetheless observe improved plant fitness. But this is not the case; when plant fitness is noted, it is usually reported as decreasing (Beattie, 1985; Holway et al., 2002), suggesting that in most cases the invasive ant-Homoptera mutualism is parasitic for its host plant. Beattie (1985) further points out that the vast majority of data describing homopteran damage to plants is from agroecosystems, or other heavily manipulated environments where the population of natural enemies of Homoptera may be quite depauperate. Discerning whether there are differences in how the invasive ant-Homoptera mutualism affects plants in the ants' native versus introduced habitats and in agricultural versus less manipulated environments is worth additional research.

ANT IMPACTS ON PLANT REPRODUCTION

Even more so than with invasive ant interactions with extrafloral nectaries and Homoptera, the dearth of research into invasive ant impacts on seed set, seed dispersal, and seed predation precludes attempts to test the predictions outlined above at present. A brief review of the current state of knowledge can, however, point to early trends and identify areas for future research.

Although several species of invasive ants have been observed to forage in various flowers (Adams, 1986; Lofgren, 1986; Buys, 1990; Hara & Hata, 1992; Nicolson, 1994; Hata et al., 1995), little research has explored invasive ants' attraction to flowers and their interactions with pollinators. *Linepithema humile* is known to exploit floral nectar otherwise taken by bees (Buys, 1987), is associated with lower insect diversity in *Protea nitida* Mill. flowerheads (Visser et al., 1996), and is hypothesized to reduce seed set by deterring pollinators from some crops (Potgieter, 1937; Durr, 1952). But to date, no studies have been published that compare *L. humile,* or any other invasive ant, to native ants with respect to their attraction to flowers, interactions with floral visitors, and any subsequent impacts.

The impact of invasive ants on seed predation and dispersal has received a little more research attention. *Linepithema humile* in the South African fynbos is slower to discover eliaosome-bearing seeds than the native ants that it displaces (Bond & Slingsby, 1984). Moreover, when the seeds are found, the invasive ants eat the eliaosomes but fail to disperse and bury the seeds, leaving them vulnerable to predation and fire, and resulting in reduced seedling emergence in invaded sites (Bond & Slingsby, 1984). A recent experiment reported that the disruption of this myrmecochorous mutualism results in plant community changes (Christian, 2001), but this study did not take into account other potential effects of the ant on the plants (e.g., pollination) that also might have been responsible for the observed differences between invaded and uninvaded sites. In Corsica, *L. humile* is more likely to find and remove *Anchusa crispa* Viv. seeds with eliaosomes than without, whereas the dominant native ants do not show a preference between seeds with and without eliaosomes in the seeds they remove. It is unclear what impact the differences in behavior between the invasive and native ants may have on *A. crispa* population dynamics (Quilichini & Debussche, 2000).

Pheidole megacephala and *Solenopsis invicta* also appear to be attracted to seeds in their adopted habitats. *Pheidole megacephala* collects seeds of *Acacia concurrens* Pedley in Australia with unknown consequences for the tree (Majer, 1985). *Solenopsis invicta* is a predator of seeds of numerous crops and other plants (Ready & Vinson, 1995; Morrison et al., 1997) and is attracted to most eliaosome-bearing seeds, but often destroys or scarifies them (Zettler et al., 2001). *Wasmannia auropunctata* is a poor seed disperser in its native Mexico (Horvitz & Schemske, 1986), but there are no published studies that examine its seed harvesting or dispersal tendencies in the habitats it has invaded. As with *Linepithema humile,* further study is necessary to determine the impacts of *P. megacephala, S. invicta,* and *W. auropunctata* on seeds relative to native ants, and any implications for plant community dynamics.

WHY SHOULD WE STRIVE FOR PREDICTIVE CAPACITY?

The ability to predict the nature and outcomes of interactions between invasive ants and plants has the potential to yield many rewards. Agriculturalists and conservationists, in particular, may benefit by knowing whether a potential invader is likely to have impacts that will thwart their management goals. This foresight may provide further impetus for putting policies in place to prevent the invasion.

In cases where the invasive ant is already present, identification of the specific ant traits that influence the outcomes of invasive ant interactions with plants may reveal options for mitigating undesirable effects. If a key to many effects of invasive ants is their extreme abundance and penchant for carbohydrates, complete eradication from an area may not be necessary to prevent outcomes that are counter to land management goals. Agriculturalists have realized the link between invasive ants and Homoptera outbreaks, for example (Flanders, 1951; Prins et al., 1990; Reimer et al., 1990). Preventing the ants from foraging in trees via use of sticky barriers or other means decreases the Homoptera population below pest levels and deprives ants of this source of carbohydrates (Samways, 1990). Therefore, although the ants may still be present they no longer contribute to yield loss via their relationship with homopterans. Deprived of their carbohydrate source, they may not be abundant enough to effect other outcomes on the plants or native ant community (Addison & Samways, 2000).

Foraging conditions can also be manipulated naturally so that the ants are less pestiferous, or even aid in achieving management goals. In Zanzibar coconut, *Pheidole megacephala* is a pest because it does not prey on the primary agent causing premature nutfall, the bug *Pseudotheraptus wayi* (Brown), as much as the native weaver ant it displaces. *Pheidole megacephala* is attracted to the palm crown by nectar, pollen, and various homopterans. Retaining ground vegetation in palm plantations provides *P. megacephala* with enough foraging opportunity that it does not ascend the palm trees in search of food. The weaver ant is then free to inhabit the canopy and prey on *P. wayi* (Rapp & Salum, 1995). Similarly, in Louisiana sugar cane, allowing broadleaf weeds to grow in the early part

Table 2. Hypothesized contexts under which an individual plant may have a high or low risk of an adverse outcome or may benefit from association with an invasive ant for five types of ant-plant interactions.

	Protection from herbivores	Homoptera tending	Seed set	Seed dispersal	Seed predation
High risk of adverse outcome for plant	Invasive ant: —is not attracted to plant, or —does not recognize herbivore as an enemy, and —displaces other ants that are effective protectors; and/or Herbivore: —is abundant, or —has defenses against ants; and Plant: —is lacking other effective defenses against herbivores	Invasive ant is: —present in high numbers, and —seeking carbohydrates, and —an effective deterrent of Homoptera natural enemies; and Homoptera: —produce honeydew, and —benefit from invasive ant tending; Plant: —is vulnerable to Homoptera-associated phytopathogens or other effects of Homoptera abundance	Invasive ant is: —present in high numbers, and —seeking carbohydrates, and —attracted to the flower, and —an effective deterrent of pollinators; and Pollinators are: —not abundant, or —vulnerable to attack by aggressive ants; and Plant: —has no floral defenses against ants, and —has attractive nectar of medium availability, and —is pollen-limited	Invasive ant: —is not attracted to seeds and has completely displaced seed dispersing native ants, or —is attracted to seeds and is poor at seed handling and dispersing; and Plant: —is dependent on ants for seed dispersal	Invasive ant: —is attracted to seeds and is capable of damaging them; and Plant: —produces seeds without effective defenses against ant granivory, and —is seed-limited
Low risk of adverse outcome for plant	Invasive ant: —does not displace other ants that are effective protectors; and/or Herbivore is: —rare, or —vulnerable to ant attack; and/or Plant: —has other effective defenses against herbivores	Invasive ant: —has access to a carbohydrate source that is more attractive or requires less foraging effort, or —is not seeking carbohydrates, or —is not an effective deterrent of homopteran enemies; or Homoptera: —are not attractive to ants, or —do not increase with ant-tending	Invasive ant: —has access to a carbohydrate source that is more attractive or requires less foraging effort, or —is not seeking carbohydrates, or —does not deter pollinators from transferring pollen; or Pollinators are: —abundant and diverse, or —still able to transfer pollen in the presence of invasive ants; or Plant: —has broadly effective floral defenses against ants, or —has unpalatable or too little nectar to attract ants, or —produces copious nectar so that ants and pollinators do not compete, or —is not pollen-limited	Invasive ant: —is not attracted to seeds, and has not completely displaced seed-dispersing native ants, or Plant: —is not entirely dependent on ants for seed dispersal	Invasive ant is: —not attracted to seeds, or —not capable of damaging seeds; or Plant: —produces seeds with defenses against ant granivory, or —is not seed-limited

Table 2. Continued.

	Protection from herbivores	Homoptera tending	Seed set	Seed dispersal	Seed predation
Potential for plant to benefit	Invasive ant: —is highly attracted to plant, and —is effective at displacing herbivores	Invasive ant: —displaces other ants that are better Homoptera tenders; or —enters a byproduct mutualism with the plant (see text)	Invasive ant: —displaces other ants that are better nectar-robbers and pollinator deterrents, or —is seeking carbohydrates, and —is attracted to the flower, and —does not deter pollinators from transferring pollen; and Pollinators —transfer more pollen in the presence of the invasive ant (i.e., through increased repositioning frequency)	Invasive ant: —is attracted to seeds, and —is able to disperse and shelter them more effectively than any displaced ants	Invasive ant: —is not attracted to seeds, or —is not capable of damaging seeds; and —displaces other ants that are seed harvesters

of the season facilitates an increase of *S. invicta* populations because it provides abundant prey (Ali et al., 1984). As the weeds die back with the closing of the sugarcane canopy, the ants transfer their foraging to the sugarcane where they are effective predators against the sugarcane borer, *Diatrea saccharalis* (F.) (Ali & Reagan, 1985).

SYNTHESIS AND CONCLUSIONS

Traits associated with invasive ants, namely elevated abundance, aggression, and attraction to high-carbohydrate resources directly and indirectly affect outcomes of interactions with plants. Abundance of invasive ants tends to be higher than native ants, but as shown in the examples, it is where, how, and when the bulk of these abundant workers tend to forage that ultimately influences interaction outcomes. As described above, while both *Anoplolepis gracilipes* and *Pheidole megacephala* can be abundant in coconut palm plantations, outcomes for coconut palms are quite different depending on whether conditions favor ground or arboreal foraging of the ants. However, the relative scarcity of *Solenopsis invicta* on *Catalpa bignonioides* appears not to be a factor in the protection of the plant from its main herbivore because it is offset by the ant's foraging efficiency. Invasive ant colony cycles and needs for a particular resource play a major role in determining foraging behavior, and may or may not coincide with plants' or Homoptera carbohydrate production and need for protection. In the case of *S. invicta* on *C. bignonioides,* had it been the time of year when *S. invicta* seeks carbohydrate-rich resources, or had the extrafloral nectar contained a profusion of amino acids, perhaps visitation frequency would have been higher and an even greater decline in herbivory witnessed (Ness, 2001). For host plants that suffer from a less palatable or vulnerable dominant herbivore or interact with a less aggressive ant, phenological overlap between ants' and plants' needs and rewards may be more critical to the outcome of the interaction (Bronstein, 1998).

The other invasive ant traits that I have focused on, aggression and attraction to carbohydrates, also deserve further examination. In predicting effects of invasive ants on plants, it will be useful to know what biochemical or other cues trigger the ants' aggressive behavior. Why, for example, does *Anoplolepis gracilipes* displace the coconut bug *Amblypelta cocophaga* in Solomon Islands coconut (Greenslade, 1971), but fail to deter the coconut bug *Pseudotheraptus wayi* in Zanzibar coconut (Way, 1953)? Likewise, carbohydrate resources can vary greatly in composition and therefore in their attraction of ants. In any plant community, an ant may have the opportunity to choose among various floral nectars, extrafloral nectars, or homopteran exudates. The options and preferences may vary over the season and result in different outcomes for the individual plants and the plant community as a whole. For example, aphids attract *Solenopsis invicta* to nectaried cotton plants early in the season, but later in the season extrafloral nectar is preferred and the ants are seldom observed tending aphids (Agnew et al., 1982). The amount and types of amino acids and sugars, and the balance among them have all variously been suggested as affecting attraction of ants to nectar and homopteran exudates (Lanza, 1991; Lanza et al., 1993; Koptur, 1979; Vander Meer et al., 1995; Koptur & Truong, 1998). Further research may reveal whether invasive ants are attracted to certain carbohydrate sources more than native ants, and why an invasive ant may be more attracted to one carbohydrate source over another, as well as how any observed preferences change with other variables (e.g., availability of other resources, ant colony needs).

Elucidating the attractiveness and availability of different carbohydrate resources is likely the key to predicting when and where invasive ants will be found on plants and, therefore, the potential for a host of subsequent effects. Of the three attractants, Homoptera, extrafloral nectar, and floral nectar, it appears Homoptera are the most important lures for the invaders because of their near ubiquity and broad attractiveness to most invasive ants. Extrafloral nectar, while considered generally attractive to ants (Carroll & Janzen, 1973), is not as widely available. Moreover, plants that possess inducible extrafloral nectaries may offer nectar too inconsistently to appease the sweet tooth of invasive ants. Floral nectar is certainly common, but is perhaps not as universally attractive to ants unless floral defenses can be thwarted (Guerrant & Fiedler, 1981; Ghazoul, 2000). Once attracted to the plant, the invasive ant may deter herbivores, as part of the food-for-protection mutualism with extrafloral nectaries, or as part of a byproduct mutualism, an indirect effect of the ants' association with Homoptera. But an analogous byproduct parasitism, although not yet reported in the literature, is not implausible; invasive ants lured to plants by Homoptera or extrafloral nectaries may deter pollinators or a key herbivore enemy. Since evolution did not play a role in shaping the interactions between invasive ants and plants in their adopted habitats, we should not limit ourselves to considering only those outcomes that would be evolutionarily plausible.

That invasive ants can exert both positive and negative effects on plants precludes any generalization about the ultimate impact of invasive ants on plants. Indeed, the same ant may affect different parts and processes of the same plant in different ways at different times (Lofgren, 1986). Nonetheless, the existing data offer a starting point for predicting the context in which one outcome may be more likely than another for each type of interaction. In Table 2 I offer predictions about under what conditions an individual plant may face a high or low risk of an adverse effect or may benefit from association with an invasive ant for interactions involving plant protection, Homoptera tending, seed set, seed dispersal, and seed predation. A plant may simultaneously have a high risk of adverse outcomes in some categories and a low risk or potential to benefit in others. Net effects will depend on whether impacts combine or compensate for each other. For example, the reproductive capacity of a plant may be severely curtailed if an invasive ant both disrupts pollination and interferes with seed dispersal. Alternatively, there may be no net effect on a plant's reproductive success in the presence of an invasive ant that increases seed set and interferes with seed dispersal (e.g., Horvitz & Schemske, 1984). Plants may have their own compensatory mechanisms; angiosperms that rely on a few specialized pollinators may be clonal or extremely long-lived, thereby decreasing dependence on seed production (Bond, 1994).

The innumerable combinations of effects and vastly different potential net outcomes demonstrate the need for research that takes into account the multiple mechanisms through which invasive ants may affect plants, and the consequences for the plant at population and community levels. The complexity and context-dependency of ant-plant interactions make predicting the net effects of invasive ants on plants a formidable challenge. Nonetheless, incorporating characteristics common to invasive ants into pre-existing models of ant-plant interactions provides a framework for generating testable hypotheses about how invasive ants may interact with plants and the consequences for the plant. Testing these hypotheses will contribute directly to conservation and agriculture, and provide insights applicable to both invasion ecology and our understanding of ant-plant interactions.

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MOLECULAR SYSTEMATICS AND THE CONTROL OF INVASIVE PLANTS: A CASE STUDY OF *TAMARIX* (TAMARICACEAE)[1]

John F. Gaskin[2]

ABSTRACT

The invasion of habitats by non-native organisms is considered, behind habitat destruction, the second largest threat to biodiversity worldwide. Consequently, control of invasive organisms is now an integral part of ecosystem stewardship. Effective control may require explicit characterization of the invasion at the family, species, and/or population levels. *Tamarix* is considered one of the worst plant invasions in the United States. A synopsis of molecular systematic advances at the family and species levels is presented, and the impact on the control of *Tamarix* is discussed. Also, a preliminary population-level analysis of *T. ramosissima* is performed using chloroplast DNA sequence data. This analysis investigates origins of invasive haplotypes and tests for the presence of cultivated haplotypes in the invasion. Advances in understanding invasions through molecular systematic and population-level studies will prove to be powerful tools in many control scenarios.

Key words: biodiversity, biological control, conservation, invasion, molecular systematics, population structure, phylogeny, tamarisk, *Tamarix*, saltcedar.

The invasion of habitats by non-native organisms is considered the second largest threat to biodiversity worldwide behind habitat destruction (Wilson, 1997). In the United States exotic plants now represent 17.3% of the flora (Kartesz & Meacham, 1999), and approximately 400 of the 972 plants and animals listed by the Endangered Species Act are at risk primarily due to competition with and predation by non-native species (Stein & Flack, 1996). For these reasons, the control of invasives is becoming an integral part of ecosystem stewardship.

Methods of controlling invasive plants include manual removal, fire, herbicides, biological control, and legislation of import and sale. Effective control of invasive plants often requires explicit characterization of the invasion at the family, species, and/or population levels.

Several species of the genus *Tamarix* L. (common name: saltcedar or tamarisk, family Tamaricaceae) are, as a group, considered one of the worst plant invasions in the southwestern U.S. (TNC, 2002). This invasion is the subject of localized manual, chemical, and legislative control efforts and a large-scale biological control project conducted by the United States Department of Agriculture. Additional legislative control may be required, as cultivars of *Tamarix* are still available from numerous horticultural suppliers. The effective implementation of biological control projects of *Tamarix* (e.g., DeLoach et al., 2000) has been influenced by phylogenetic concerns at the following levels:

(1) FAMILY LEVEL

Phylogenetic relationships of the invasive plant's family are important when biological control is proposed. Control agents must be tested for their risk of host-switching by confronting the control agent with plant species from closely related plant families. In the past, Tamaricaceae usually were placed in the plant order Violales of the Dilleniidae (e.g., Cronquist, 1981), but recent molecular sequence data analyses have altered the traditional ordinal placement of many plant families, and Tamaricaceae are now included in the Caryophyllales (APG, 1998). These changes will alter the plant taxa to be

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Table 1. Putative U.S. *Tamarix* invasives complied from McClintock (1951), Baum (1967), and Crins (1989).

Putative U.S. invasive	Taxonomic and morphological notes
T. africana Poir.	morphologically similar to *T. canariensis* and *T. gallica* in aestival floral form (Baum, 1978)
T. aralensis Bunge	rarely cultivated, not extensively naturalized (Baum, 1967)
T. aphylla (L.) H. Karst.	morphologically dissimilar to all other U.S. *Tamarix*
T. canariensis Willd.	morphologically similar to *T. gallica* (Crins, 1989)
T. chinensis Lour.	morphologically similar to *T. ramosissima* (Crins, 1989)
T. gallica L.	morphologically similar to *T. canariensis* (Crins, 1989)
T. juniperina Bunge	synonym of *T. chinensis* (Baum, 1978)
T. parviflora D.C.	morphologically dissimilar to all other invasive U.S. *Tamarix*
T. pentandra Pall.	synonym of *T. ramosissima* (Baum, 1978)
T. ramosissima Ledeb.	morphologically similar to *T. chinensis* (Crins, 1989)
T. tetrandra Pall.	U.S. invasive specimens with this name considered to be *T. parviflora* (Baum, 1967)
T. tetragyna Ehrenb.	naturalized in eastern U.S., not yet invasive (Crins, 1989)

tested in the risk analysis of biological control agent host-switches.

(2) SPECIES LEVEL

The *Tamarix* invasion consists of many species, some of which are morphologically very similar. The specific identities of taxa involved in the invasion are controversial (Crins, 1989), in part, because most *Tamarix* species cannot be distinguished without flowers or fruit present. Precise species identity is needed to determine the geographic origin of the invasive species and its coevolved biological control agents. *Tamarix* is one of the more taxonomically challenging genera among the angiosperms (Baum, 1978), and intermediate states exist for some morphological characters used in species identification. These character states can often vary on a single individual from season to season (Rusanov, 1949), and hybridization may play a role in the taxonomic confusion (Rusanov, 1949; Wilken, 1993). Improper species identification could lead to searches for biological control agents perhaps outside the native range of the invasive plant. The failure of morphological data to elucidate the identities of invasive *Tamarix* species necessitates the use of molecular data as an additional source of taxonomic information.

(3) POPULATION LEVEL

Population-level investigation of any of the invasive *Tamarix* may be necessary if the biological control agents are extremely host-specific, and if the invasive plant species has widespread origins. Initial biological control tests show that imported insects have differential effectiveness on what putatively appears to be a single species of *Tamarix* (*T. ramosissima* Ledeb.) collected from different regions of the U.S. (DeLoach & Tracy, 1997), raising the issue of infraspecific geographical variation. Many species of *Tamarix* are widespread in Eurasia (Baum, 1978), and it is unlikely that much of the genetic diversity of any one species was imported to the United States. Historical records do not reveal precise origins or genetic information concerning the introductions (Horton, 1964). The control agents being tested (e.g., saltcedar leaf beetle, *Diorhabda elongata*) may not have evolved with the invasive, and thus might result in ineffective or sub-optimal control. For these reasons, it would be useful to know how many genotypes are represented in the U.S. invasion, and to what degree we can pinpoint their Eurasian origins.

Additionally, *Tamarix* is still being horticulturally distributed in the United States. Policy makers need to determine if the genotypes currently being promoted predominate in the invasive populations. Based on their similar morphology, invasive *Tamarix* is often indistinguishable from cultivars. Molecular evidence of contemporary cultivars contributing to the *Tamarix* invasion could greatly influence future policy decisions regarding the sale and distribution of these plants.

BACKGROUND

Tamarix is an Old World genus of approximately 54 species (Baum, 1978). Eight to twelve of these (Table 1) were imported to the United States from southern Europe or Asia in the 1800s to be used for shade and erosion control (Baum, 1967), and an aggressive subset has overtaken more than 1,000,000 riparian acres (Brotherson & Field, 1987). This infestation is expanding by 40,000 acres per year (DiTomaso, 1998), eroding the biodiversity of many western U.S. natural areas, including major river systems and national parks.

Tamarix species initially invade by germinating during wet periods or in riparian areas. Once established, they can tolerate drought by utilizing deep groundwater sources. They also exude excess salt from salinized water sources from glands in their scale-like leaves (Neill, 1985), which are seasonally dropped, forming a thick saline duff on the soil surface that inhibits the germination of other plants. In the U.S., *Tamarix* species are avoided by most avian frugivores and insectivores (Brotherson & Field, 1987), and only two mammal species (the desert wood rat and desert cottontail) are known to feed upon them, with minimal damage to the plants (DiTomaso, 1998). *Tamarix* invasions lower biodiversity levels by displacing typical Southwestern riparian vegetation such as cottonwood and willow (Hughes, 1993), as well as the insects, birds, and mammals that these native trees support (Neill, 1985). Their profuse growth alters stream and river dynamics by narrowing channel width (Robinson, 1965), and invasions can extend over 1 km on each side of a river (e.g., Gila River, southwestern Arizona, and Colorado River south of Blythe, California, U.S.; J. Gaskin, pers. obs.). Dense stands of *Tamarix*, with their high rates of transpiration, can substantially lower the water table, and have caused perennial springs and creeks to dry up, in some cases threatening regionally rare or federally listed species such as the desert pupfish and the desert slender salamander (Kerpez & Smith, 1987).

Tamarix invasions have proven difficult to control. These plants cannot be killed easily by fire, by cutting at ground level, or by herbicide applied to the foliage alone. Effective removal is both expensive and potentially damaging to the habitat, requiring mechanical uprooting, or cutting at ground level with application of a systemic herbicide to the stump. Repeated treatments are often necessary (Neill, 1985). Control is possible on a small scale, but land managers are often forced to live with large invasions due to prohibitive control costs (Stein & Flack, 1996). For these reasons biological agents were proposed as an alternative means of control.

Well-researched biological control projects often come under heavy public scrutiny due to the potentially dire effects of control agent host-switches (Thomas & Willis, 1998). Therefore, biological control researchers must unambiguously know the identity of the invasive *Tamarix* and its relationships to native species. Improper taxonomic identification may lead to searches for control agents outside the native range of the invasive species and thus wasted efforts or less-effective biocontrol agents. Improper identification of the invasive could also lead to the collection of biological control agents that have historic ties to sympatric congener plant species or to genotypes with a different phenology or developmental timing, again yielding ineffective biological control. Considering that the average biological control research program spans many years at a cost of hundreds of thousands to millions of dollars (Gillot, 1995), it is logical and economical to predicate a biological control project with precise taxonomic knowledge of the invasive plant.

Knowing the genotype of an invasive plant is especially important when choosing a fungal, bacterial, or viral control agent involved in a gene-for-gene resistance/virulence interaction (Kerr, 1987). Even insects are often species-specific, and in some cases, host-specificity can reach to the level of the plant genotype. An example is the differential herbivory of the Hessian fly (*Mayetiola destructor*) on different genotypes of wheat (*Triticum aestivum* L.) (Schoonhoven et al., 1998). Also, differential herbivory on plant populations has been detected in willow trees (*Salix*) under natural conditions (Rank, 1991).

The saltcedar leaf beetle (*Diorhabda elongata*) from western China is already being investigated as a potential *Tamarix* control agent in quarantined and field releases (C. J. DeLoach, pers. comm.). In no-choice tests, newly hatched *D. elongata* larvae were placed in vials, each with leaf material from a different plant specimen. The plants were collected from different areas of the United States and grown in common garden plots. Using morphology, all specimens were determined to be the same species (*T. ramosissima*). Observations on the feeding and life span of the insects were recorded, and survival of the insects to adulthood on different plant specimens varied from 34% to 0% (DeLoach & Tracy, 1997). The reduced survival on several of the *T. ramosissima* plants may have in part been caused by less than optimal physiological condition of some of the plants (DeLoach & Tracy, 1997), but genotypic differences in the plants also may have influenced the results.

The search for *Tamarix* biological control agents continues, as the Agricultural Research Service of the United States Department of Agriculture does not expect that the current control agents will achieve satisfactory control of saltcedar in all areas, and perhaps as many as 8 to 12 additional insects as specific herbivores will be required (DeLoach & Tracy, 1997). This is based on biological control of other invasive plants, such as cacti, lantana, and leafy spurge, which have required up to 15 or more insect species introductions (DeLoach & Tracy, 1997) for effective control.

CULTIVARS

Tamarix ramosissima is commonly sold today as an ornamental plant. Cultivars of *T. ramosissima* include 'Pink Cascade', 'Rosea', 'Rubra', and 'Summer Glow'. The most common of these is *T. ramosissima* 'Pink Cascade', known for its dense, dark pink plumes of flowers (due to mostly compound, not simple, inflorescence racemes) and finely textured bluish foliage. These cultivars and invasive populations are almost identical in floral and vegetative structures, and may only differ in the intensity of flower color, density of inflorescences, and foliage color. Invasive *T. ramosissima* is highly variable in flower color within some populations, ranging from deep red to white. On a single invasive plant, both simple and compound racemes can be found, making the density of inflorescences also highly variable. Invasive foliage color can vary within populations from dark green to the blue-gray found in the *T. ramosissima* 'Pink Cascade' cultivar (J. Gaskin, pers. obs.).

As a weedy species, the *Tamarix* cultivars are easy to grow and tolerant of poor soils. They are available through many nurseries, catalogs, and from internet sales (e.g., Gertens Online Shop, www.gertens.com). *Tamarix ramosissima* is not legally available in Colorado, Nevada, Washington, and Wyoming, where it is listed as a noxious weed (USDA, 2002).

MOLECULAR SYSTEMATICS AND THE CONTROL OF *TAMARIX*

FAMILY LEVEL

Biological control agents are assessed for their risk of host-switching by placing them on U.S. native plants that are closely related to *Tamarix*. Tamaricaceae, along with the sister family Frankeniaceae, had historically been placed in the order Violales (Cronquist, 1981). Therefore, U.S.D.A. researchers tested if the *Tamarix* control agents would feed and reproduce on plants from other families in this order, such as Frankeniaceae and Fouquieriaceae (DeLoach & Tracy, 1997). Recent DNA sequence data analyses strongly suggest that Tamaricaceae and Frankeniaceae actually belong together in the order Caryophyllales (APG, 1998), closely aligned with families such as Droseraceae and Polygonaceae (Lledó et al., 1998). This phylogenetic rearrangement requires a substantially different set of test plants in the greenhouse, which may provide significantly different assessments of the risk of host-switching.

SPECIES LEVEL

A recent study used DNA sequence data to determine how many invasive *Tamarix* species were naturalized in the United States and to see if the molecular data were congruent with the morphological distinctions currently used to segregate taxa (Gaskin & Schaal, in press). The taxonomy and morphology of the 12 putative U.S. naturalized *Tamarix* species were investigated (Table 1). Three of the species names had been designated as synonyms, and two were not yet considered invasive, leaving seven putative invasive taxa. A molecular phylogenetic analysis of these and other selected species in the genus was performed from samples collected in the western U.S., Argentina, and wild native populations across Eurasia and southern Africa (voucher information is listed in Appendix 1).

Phylogenies from both nuclear ribosomal ITS and chloroplast *trn*S-*trn*G intergenic spacer sequence data were constructed and compared. Portions of the final phylogenies presented in Figure 1 illustrate incongruence with earlier taxonomic understanding of the genus. For example, note that *T. chinensis* Lour. and *T. ramosissima,* thought to belong in different sections of the genus (sects. *Oligadenia* and *Tamarix,* respectively), have identical placement on both phylogenies. Additionally, the most recent sectional classification of the genus (Baum, 1978) was not significantly similar to either the chloroplast or nuclear topologies found in Gaskin and Schaal (in press).

For many samples there was incongruence between the chloroplast and nuclear evolutionary histories. For example, in the nuclear phylogeny of Figure 1, *T. ramosissima* specimen *Schulte 1* was in a clade with all of the other *T. ramosissima,* but in the chloroplast phylogeny it appeared in a clade with *T. canariensis* Willd. (*Gaskin 3049*) and *T. gallica* L. (*Gaskin 3039*). Similarly, a *T. canariensis* specimen (*Kirk 2*) was in a chloroplast clade with another *T. canariensis* (*Gaskin 3020*), but in the nuclear phylogeny it was found far from specimen *Gaskin 3020,* as the sister to the *T. ramosissima* clade. These incongruences of chloroplast and nuclear evolutionary histories, which were significant based on the Templeton test (Templeton, 1983), supported a hypothesis of hybridization (Whittemore & Schaal, 1991; Soltis & Kuzoff, 1995).

The study concluded that morphology within *Tamarix* is often misleading as a means of identifying specimens. Also, though not all putative invasive species could be distinguished with molecular data, there was enough phylogenetic resolution to recognize four invasive *Tamarix* entities in the U.S.:

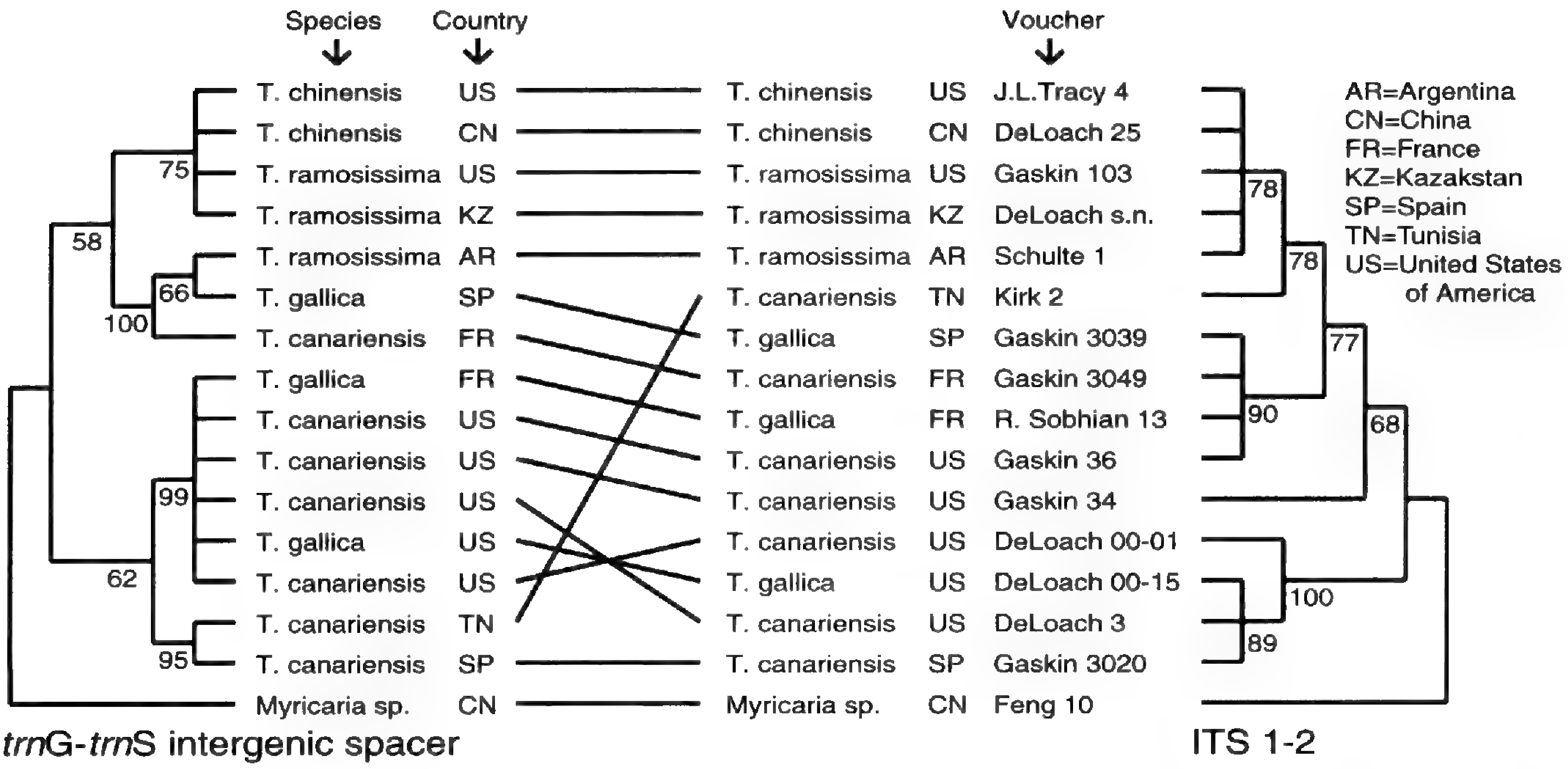

Figure 1. Chloroplast and nuclear marker phylogenies. On the left is the single most parsimonious tree for the chloroplast sequence marker (*trn*S–*trn*G intergenic spacer), 218 steps in length, with a C.I. of 0.99 and an R.C. of 0.95. On the right is the strict consensus of the 30 most parsimonious trees for the nuclear sequence marker (ITS1–2), 179 steps in length, with a C.I. of 0.95 and a R.C. of 0.88. Numbers below lines are bootstrap values. The same specimens were used in each analysis, and are connected by lines in between the two phylogenies. Adapted from Gaskin and Schaal (in press).

(1) *T. aphylla* (L.) H. Karst, (2) *T. parviflora* DC., (3) *T. canariensis*/*T. gallica*, and (4) *T. chinensis*/*T. ramosissima*. Additionally, there was evidence of introgression between *T. ramosissima*, *T. canariensis*, and *T. gallica*, which is a likely source of confusion in the characterization of some *Tamarix* invasions (Gaskin & Schaal, in press).

POPULATION LEVEL

To examine the Eurasian origins and relationships of *T. chinensis* and *T. ramosissima* invasive genotypes, and to investigate the presence of cultivated haplotypes in the invasion, the highly variable 1001 bp chloroplast *trn*S-*trn*G intergenic spacer is analyzed using the primers of Hamilton (1999). A gene tree, which infers genealogical relationships of DNA sequence haplotypes (alleles), is constructed to represent the populations and their relationships (see Fig. 2).

A total of 59 cultivated, invasive, and native *T. ramosissima* or *T. chinensis* specimens was collected, with 33 samples from the New World and 26 from the Old World. The identities of most specimens were determined using Baum's (1978) morphological descriptions and keys. Voucher information is listed in Appendix 1.

In the chloroplast sequence aligned data set, 93 (9.3%) of the sites are variable. There are 12 (1.2%) single bp changes, three single base insertion/deletions, one 2-bp indel, and three prominent indels that vary from 8 to 55 bp in length. All indels are treated as a single event (a fifth base). A most parsimonious gene tree (or minimum spanning network) of 22 steps was assembled by hand, representing the fewest mutations that explain the relationships of the specimens (Fig. 2).

The molecular analysis presents population-level information that is unobtainable using morphology alone. For example, the *T. ramosissima* species is represented by a total of seven haplotypes, marked A through G, on the gene tree (Fig. 2). The specimens and their origins are also presented in the boxes. The lines separating the gene tree boxes represent single point mutations or indel events. The small circles represent inferred intermediate haplotypes that may be extinct, may not have been collected during sampling, or may not have ever existed if mutations did not accumulate in single steps. Interesting results include the following:

(1) Of the seven haplotypes found, four are represented in the western U.S. *Tamarix* invasion. Haplotype A is very common, representing 46 (78%) of the specimens sampled. The native haplotype A specimens were collected in the Republic of Georgia, Iran, Turkmenistan, Kazakstan, China, and South Korea. The naturalized U.S. specimens were collected from California, east to Texas, north to Kansas, and west to Washington. The widespread nature of this haplotype will not facilitate pinpointing its invasive origins in Eurasia. Finer resolution

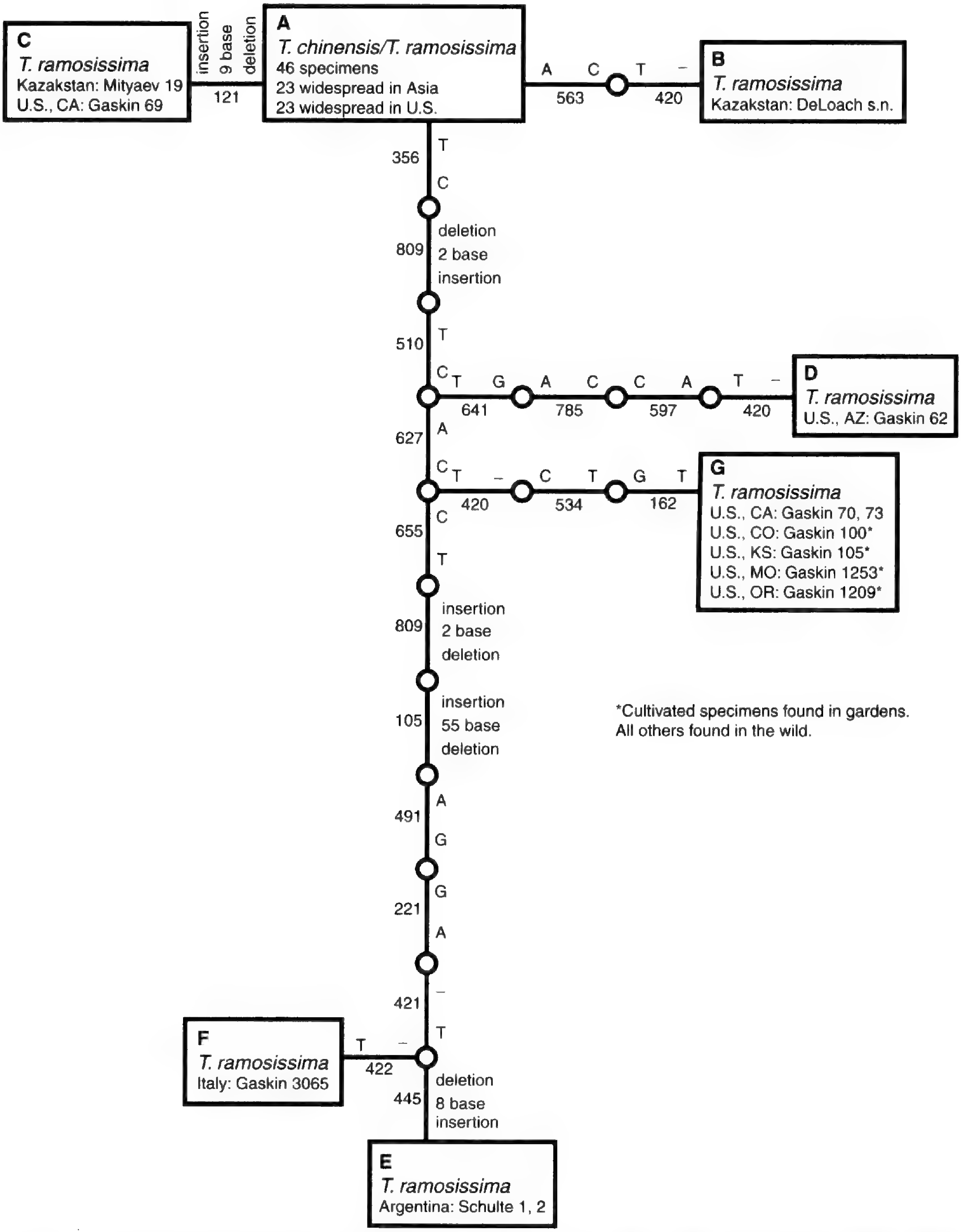

Figure 2. Single most parsimonious gene genealogy of the chloroplast sequence marker *trnS–trnG* intergenic spacer for *T. ramosissima* and morphologically similar species. The gene tree is 22 steps (mutations) in length. The haplotype (allele) designation is in each box, along with information on the number and distribution of specimens with that haplotype. The lines separating the haplotype boxes are single point mutations or insertion/deletion events. The small circles represent intermediate haplotypes not recovered in this analysis. The gene tree is interpreted in the following manner: Haplotype A differs from haplotype B by two mutations. One of these is a single nucleotide mutation at site #563 along the *trnS–trnG* intergenic spacer, where haplotype A has an adenine (A) and haplotype B has a cytosine (C). The other difference is at site #420, where haplotype A has a thymine (T), and haplotype B has lost this thymine in a deletion event (-).

markers are needed to distinguish if there is unrevealed population structure or if the haplotype A plants are genetically similar across Eurasia. If these plants are genetically similar across the native range, collection of insects from any area of Eurasia will be equally likely to find control agents that have evolved with this haplotype.

(2) Haplotype C is rarer than A, representing only two of the specimens (Fig. 2), and was found once in southern California and once in Kazakstan. This haplotype is only one mutation different from the common A haplotype, but that mutation is a prominent 9 bp indel event that was not found in any other samples. This presents evidence that at least a small part of the invasion may have its origins in Kazakstan.

(3) Haplotype D was found once, in Arizona. The plant containing this haplotype (*Gaskin 62*) morphologically resembled *T. ramosissima.* In a different study, this haplotype was found to be common in another species, *T. parviflora* (Gaskin & Schaal, in press). *Tamarix parviflora* is an invasive species with tetramerous floral structure, morphologically very distinct from the pentamerous floral structure of *T. ramosissima* and *T. chinensis.* This incongruence between morphology and haplotype may be due to hybridization, as was found in the genus-wide study (Gaskin & Schaal, in press).

(4) Haplotype E was found twice in Argentina invasions by *Tamarix,* but never in the U.S. This haplotype is genetically quite distinct from the common A haplotype, differing by 11 mutations, including two notable 8 and 55 bp indel events. This genotype has not been found in Eurasia, indicating that further sampling of native *Tamarix* populations is needed.

(5) All cultivated U.S. specimens of *Tamarix* contain haplotype G. This haplotype was not recovered in Eurasian sampling. Haplotype G differs from the common haplotype A by at least seven mutation events. The haplotype G, as representative of cultivar introgression, was found once, as an invasive, near the Salton Sea in California (*Gaskin 70*). Even though the presence of this genotype is not common in the invasion, its ability to invade is now confirmed. Any presence of cultivar haplotypes in invasions should serve as a strong forewarning in future policy decisions regarding the horticultural use of invasive taxa.

The preceding chloroplast sequence marker data allow us to begin to delve into the genetic structure of the *T. ramosissima*/*T. chinensis* invasion. This preliminary analysis is of a small sample size, and a more in-depth population analysis is in preparation, using highly variable nuclear DNA sequence markers such as phosphoenolpyruvate carboxylase introns. I plan to continue sequencing selected *Tamarix* that exhibit resistance to biological control agents. If they are determined to be genotypically distinct from the susceptible *Tamarix,* their Eurasian origins will be provided to the biological control exploration project. Knowing the number of haplotypes that comprise a plant invasion, their origins, and the ability of cultivars to contribute to the invasion are powerful tools to document and control problematic exotic plant species.

CONCLUSION

Molecular analyses will have an increasing role in invasive plant control efforts. At the family level they will enable more accurate risk assessments of biological control host-switching. At the species level, molecular systematics will help elucidate invasive species identities and any morphologically cryptic hybridization events. At the population level, molecular systematics will allow the unprecedented characterization of invasive taxa as genotypes, allowing precise matching of biological control agents with their targets, and elucidating links between cultivars and invasions of plants. These advances in understanding plant invasions will enhance control efforts and contribute to the protection of native biodiversity.

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Appendix 1. Vouchers for exemplars used in DNA sequencing, and corresponding GenBank accession numbers. (*) = USDA-ARS Grassland Soil and Water Research Lab, Temple, Texas, U.S.A. OW = Old World, NW = New World.

trn S-*trn*G haplotype	Species	Origin	Collection #	DNA specimen #	GenBank accession *trn* S–*trn*G	GenBank accession ITS 1–2
A	*Tamarix* cf. *ramosissima* Ledeb.	OW: China	*DeLoach s.n.* (*)	164	AF490798	
A	*Tamarix chinensis* Lour.	OW: China	*DeLoach 00-13* (*)	0.13	AF490798	
A	*Tamarix chinensis* Lour.	OW: China	*DeLoach 25* (*)	23	AF490798	AF484770
A	*Tamarix chinensis* Lour.	OW: China	*DeLoach s.n.* (*)	140	AF490798	
A	*Tamarix chinensis* Lour.	OW: China	*USDA 00-45* (*)	2011	AF490798	
A	*Tamarix chinensis* Lour.	OW: S. Korea	*Gaskin 202* (MO)	202	AF490798	
A	*Tamarix chinensis* Lour.	NW: U.S., TX	*DeLoach 00-14* (*)	0.14	AF490798	
A	*Tamarix chinensis* Lour.	NW: U.S., TX	*J. L. Tracy 4* (*)	22	AF490798	AF484776
A	*Tamarix* cf. *ramosissima* Ledeb.	OW: China	*DeLoach s.n.* (*)	141	AF490798	
A	*Tamarix* cf. *ramosissima* Ledeb.	OW: Turkmenistan	*Gaskin 1107* (MO)	1107	AF490798	
A	*Tamarix ramosissima* Ledeb.	OW: Georgia	*Gaskin 229* (MO)	292	AF490798	
A	*Tamarix ramosissima* Ledeb.	OW: Georgia	*Gaskin 505* (MO)	310	AF490798	
A	*Tamarix ramosissima* Ledeb.	OW: Georgia	*Gaskin 508* (MO)	315	AF490798	
A	*Tamarix ramosissima* Ledeb.	OW: Kazakstan	*I. D. Mityaev 20* (*)	33	AF490798	
A	*Tamarix ramosissima* Ledeb.	OW: Kazakstan	*V. Ivlev s.n.* (MO)	419	AF490798	
A	*Tamarix ramosissima* Ledeb.	OW: Kazakstan	*V. Ivlev s.n.* (MO)	422	AF490798	
A	*Tamarix ramosissima* Ledeb.	OW: Kazakstan	*V. Ivlev s.n.* (MO)	423	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., KS	*DeLoach 00-21* (*)	0.21	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., NM	*DeLoach 00-23* (*)	0.23	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., CA	*DeLoach 00-24* (*)	0.24	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., CA	*DeLoach 00-25* (*)	0.25	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., NM	*DeLoach 00-26* (*)	0.26	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., NV	*DeLoach 00-27* (*)	0.27	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., NM	*DeLoach 00-38* (*)	0.38	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., TX	*DeLoach 00-41* (*)	0.41	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., TX	*DeLoach 00-42* (*)	0.42	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., TX	*DeLoach 00-43* (*)	0.43	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., CO	*Gaskin 103* (MO)	55	AF490798	AF484774
A	*Tamarix ramosissima* Ledeb.	NW: U.S., CO	*Gaskin 99* (MO)	59	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., TX	*Gaskin 41* (MO)	72	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., CA	*Gaskin 85* (MO)	77	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., CA	*Gaskin 88* (MO)	80	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., CA	*Gaskin 72* (MO)	87	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., NM	*Gaskin 50* (MO)	94	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., WA	*Gaskin 1204.1* (MO)	1204.1	AF490798	

Appendix 1. Continued.

trn S-*trn*G haplotype	Species	Origin	Collection #	DNA specimen #	GenBank accession *trn* S–*trn*G	GenBank accession ITS 1–2
A	*Tamarix ramosissima* Ledeb.	NW: U.S., OK	*Gaskin 1251* (MO)	1251.1	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., TX	*DeLoach 00-51* (*)	2009	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., TX	*DeLoach 00-46* (*)	2012	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., CO	*DeLoach 00-48* (*)	2013	AF490798	
A	*Tamarix ramosissima* Ledeb.	NW: U.S., WY	*DeLoach 00-49* (*)	2014	AF490798	
A	*Tamarix* cf. *ramosissima* Ledeb.	OW: Georgia	*Gaskin 753* (MO)	345	AF490798	
A	*Tamarix* cf. *ramosissima* Ledeb.	OW: Iran	*Gaskin 962* (MO)	962	AF490798	
A	*Tamarix* cf. *ramosissima* Ledeb.	OW: Iran	*Gaskin 964* (MO)	964	AF490798	
A	*Tamarix* cf. *ramosissima* Ledeb.	OW: Turkmenistan	*Gaskin 1087* (MO)	1087	AF490798	
A	*Tamarix* cf. *ramosissima* Ledeb.	OW: Turkmenistan	*Gaskin 1116* (MO)	1116	AF490798	
A	*Tamarix* cf. *ramosissima* Ledeb.	NW: U.S., TX	*DeLoach 00-12A* (*)	448	AF490798	
B	*Tamarix ramosissima* Ledeb.	OW: Kazakstan	*DeLoach s.n.* (*)	431	AF490776	AF484748
C	*Tamarix ramosissima* Ledeb.	OW: Kazakstan	*I. D. Mityaev 19* (*)	31	AF490796	
C	*Tamarix ramosissima* Ledeb.	NW: U.S., CA	*Gaskin 69* (MO)	84	AF490796	
D	*Tamarix ramosissima* Ledeb.	NW: U.S., AZ	*Gaskin 62* (MO)	110	AF539998	
E	*Tamarix ramosissima* Ledeb.	OW: Argentina	*Schulte 1* (MO)	449	AF490789	AF484761
E	*Tamarix ramosissima* Ledeb.	OW: Argentina	*Schulte 2* (MO)	454	AF490789	
F	*Tamarix ramosissima* Ledeb.	OW: Italy	*Gaskin 3065* (MO)	3065	AF490837	
G	*Tamarix ramosissima* Ledeb.	NW: U.S., KS	*Gaskin 105* (MO)	53	AF490782	
G	*Tamarix ramosissima* Ledeb.	NW: U.S., CO	*Gaskin 100* (MO)	57	AF490782	
G	*Tamarix ramosissima* Ledeb.	NW: U.S., CA	*Gaskin 70* (MO)	89	AF490782	
G	*Tamarix ramosissima* Ledeb.	NW: U.S., CA	*Gaskin 73* (MO)	90	AF490782	
G	*Tamarix ramosissima* Ledeb.	NW: U.S., OR	*Gaskin 1209* (MO)	1209	AF490782	
G	*Tamarix ramosissima* Ledeb.	NW: U.S., MO	*Gaskin 1253* (MO)	1253	AF490782	
	Tamarix gallica L.	OW: Spain	*Gaskin 3039* (MO)	3039		AF484807
	Tamarix canariensis Willd.	OW: France	*Gaskin 3049* (MO)	3049		AF484808
	Tamarix gallica L.	OW: France	*R. Sobhian 13* (*)	25		AF484775
	Tamarix canariensis Willd.	NW: U.S., LA	*Gaskin 36* (MO)	68		AF484802
	Tamarix canariensis Willd.	NW: U.S., LA	*Gaskin 34* (MO)	65		AF484801
	Tamarix canariensis Willd.	NW: U.S., LA	*DeLoach 3* (*)	24		AF484752
	Tamarix gallica L.	NW: U.S., TX	*DeLoach 00-15* (*)	0.15		AF484781
	Tamarix canariensis Willd.	NW: U.S., TX	*DeLoach 00-01* (*)	438		AF484778
	Tamarix canariensis Willd.	OW: Tunisia	*Kirk 2-Tunisia* (MO)	1276		AF484796
	Tamarix canariensis Willd.	OW: Spain	*Gaskin 3020* (MO)	3020		AF484806
	Myricaria alopecuroides Schrenk	OW: China	*Wang Jian Feng 10* (*)	18		AF484746

WEEDS IN PARADISE: THOUGHTS ON THE INVASIBILITY OF TROPICAL ISLANDS[1]

Julie S. Denslow[2]

ABSTRACT

Tropical island ecosystems appear to be especially vulnerable to invasive species as indicated by the often high numbers and percentages of exotic species on oceanic and continental islands. Here I reexamine hypotheses offered to account for the apparently high invasibility of tropical islands and suggest a simple synthesis based on resource availability, propagule supply, and relative competitive abilities of exotic and island species. This review suggests that fundamentally two interacting processes—high net resource availability and poor ability of native species to preempt those resources—make island communities vulnerable to the establishment and spread of alien species. In addition, historically high rates of introduction have provided opportunity in the form of a diverse and abundant propagule rain of exotic species. The combination produces a scenario that is not an optimistic one for island ecosystems. It suggests that these native ecosystems on islands are particularly vulnerable to naturalizing exotics growing on their borders, and that while disturbance from a variety of causes, including pigs, fire, grazing, and natural dieback of the canopy dominants, increases the opportunities for exotic incursions, even intact forests are not immune. Unless these forests are aggressively managed and alien propagule pressure reduced, they will be highly modified by expanding exotic plant populations. Tropical islands are an effective early warning system of the impacts that successive waves of exotic species invasions may cause to isolated ecosystems. As mainland natural areas become fragmented, degraded and depauperate, they acquire many of the ecological attributes of islands, including limited habitat area, missing functional groups, declining species diversity, and disturbed habitats. A better understanding of invasions on islands may improve our attempts to protect both mainland and island ecosystems from the impacts of exotic species.

Key words: alien species, exotic species, extinctions, invasive species, invasibility, island ecosystems, plant communities, tropical islands.

> *"He who admits the doctrine of the creation of each separate species, will have to admit that a sufficient number of the best adapted plants and animals were not created for oceanic islands; for man has unintentionally stocked them far more fully and perfectly than did nature"*
>
> —C. Darwin ([1859] 1972: 347–348)

Island ecosystems appear to be especially vulnerable to invasive species. Reviews cite the high numbers and percentages of exotic species on heavily visited oceanic and continental islands (e.g., Vitousek et al., 1997), and invasive species often are implicated in species extinctions in island ecosystems (Simberloff, 1995; D'Antonio & Dudley, 1995). Tropical islands as well often are characterized by high alien species densities, unlike tropical mainland ecosystems where the incidence of alien species is low (Rejmánek, 1996). The apparently high invasibility of islands might suggest that island ecosystems hold few lessons for the prevention and management of exotic species in continental ecosystems. However, as mainland natural areas become fragmented, degraded, and depauperate, they acquire many of the ecological attributes of islands, including limited habitat area, missing functional groups, declining species diversity, and disturbed habitats (Laurance & Bierregaard, 1997). A better understanding of invasions on islands may improve our attempts to protect both mainland and island ecosystems from the impacts of exotic species.

Here I reexamine hypotheses offered to account for the apparently high invasibility of tropical islands and suggest a simple synthesis based on resource availability, propagule supply, and relative competitive abilities of exotic and island species. My focus is on invasions of exotic terrestrial plants into native island ecosystems. In the following discussion, I describe some of the hypotheses proposed to account for variation in community invasibility; however, in developing the synthesis I have relied on few assumptions about the presence of vacant niches or the strength of competitive interactions in equilibrium communities. Rather, I assume that ecological communities are open to the

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establishment and evolution of new species and that they are constantly changing with variation in the environment and in the abundance of competitors, mutualists, diseases, and predators (Hubbell, 2001). The composition and structure of plant communities seem largely attributable to differential responses of individual species to resource availability, habitat conditions, and pest pressures. Beyond these individualistic patterns, assembly rules for plant communities are poorly understood and difficult to demonstrate (Wilson, 1999). Thus, I assume that some degree of invasibility characterizes all communities and that our challenge is to understand why some communities appear to be more open to the establishment of new species than others.

As D'Antonio and Dudley (1995) observed, generalizations about the vulnerability of islands to invasive species often fail to distinguish among invasibility, opportunity, and impact, any or all of which may contribute to observed patterns: (1) island communities may be more *invasible,* that is, with similar opportunity exotic species may be more likely to establish new populations in island than in mainland communities; (2) the *opportunity* for new colonists may be greater on islands because islands may be exposed more frequently to inputs of seeds and other propagules than mainland habitats; and (3) the *impact* of exotic invasions on island species and ecosystems may be more substantial than on similar mainland communities.

Both opportunity and impact are high on many tropical islands. Because islands often lack critical sources of food, forage, and fiber, colonists from early Polynesian voyagers to modern government agencies have promoted plant introductions, including pasture grasses, timber trees, food crops, ornamentals, and sources of fuel and fiber (Mueller-Dombois & Fosberg, 1998). In addition, rates of unintentional introductions are often high because islands have been important provisioning stations for transoceanic shipping traffic, exposing island habitats to species from wide and heterogeneous sources. Moreover, invasive species have strong impacts on islands, because the spatial extent of ecosystems and the population sizes of species are necessarily small and thus vulnerable (Simberloff, 1995, 2000; Sakai et al., 2002). Here I focus on the *invasibility* of tropical island ecosystems and ask whether community processes on islands make them particularly vulnerable to the establishment and spread of alien species and, if so, whether these observations have broader implications for our understanding of invasion ecology.

ARE ISLAND COMMUNITIES MORE INVASIBLE?

Ecological and evolutionary theorists have suggested several factors that may make island communities particularly vulnerable to the establishment of novel species. Communities with low native species diversity, missing functional groups, disharmonic community composition, poorly competitive species, and low pest pressures are seen to provide few barriers to the establishment of mainland species adapted to ecosystems with higher pressures from competitors, predators, and pests (Rejmánek, 1996; Simberloff, 2000; Mack et al., 2000).

LOW DIVERSITY ON ISLANDS

The effect of native species diversity on the invasibility of island communities is predicated on two hypotheses: (1) that there are fewer species on islands than in mainland habitats of comparable size, and (2) that high species richness is a deterrent to the establishment of alien species (Elton, 1958). The proposition that islands are less diverse than mainland areas of comparable size comes largely from island biogeography theory (MacArthur & Wilson, 1967), which proposes that two interacting processes affect species richness on islands: The distance of islands from mainland source pools affects immigration rates of new species, and island size affects the number of species of minimum viable population sizes that can be accommodated. Thus diversity on small and/or remote islands is likely to be lower than in mainland habitats of comparable size (MacArthur & Wilson, 1967).

Island–mainland comparisons of native plant species diversity are scant, however. Frequently cited support for the pattern of low plant diversity on islands is still MacArthur and Wilson's original treatise, although often the generalization is regarded as sufficiently widely recognized as to need no documentation. However, many factors affect native plant diversity on islands, and their effects are not easily separated (Carlquist, 1974). Geological age, latitude, elevation, habitat diversity, productivity, and proximity to source pools all affect rates of immigration and diversification as well as patterns of species coexistence (Ricklefs & Schluter, 1993; Simberloff, 2000). Early human settlers on oceanic islands not only brought new species, but caused such widespread extinction and habitat alteration that native lowland floras in particular are difficult to reconstruct (Steadman, 1995; Kirch & Hunt, 1997; Mueller-Dombois & Fosberg, 1998). These factors interact to produce high variation in species richness among islands and mainland sites and to obscure effects of isolation and area on diversity. At least one study suggests that islands may not be significantly less rich than mainland sites. Lonsdale (1999) found no difference in the species richness of island and mainland native floras from 104 island and mainland sites after area was taken into account. Similarly, syntheses of earlier studies suggest little difference between species-area curves for island and mainland sites (Rosenzweig, 1995), and low regression coefficients in species-area plots of island plants suggest that correlates of species diversity are more varied than can be accounted for by area and isolation alone (Gilbert, 1980). Island floras may not always be more species poor than those of mainland habitats.

If species diversity is assessed at the patch or stand level where most ecological interactions take place, low diversity may be a salient aspect of island ecosystems nevertheless. Island floras often are characterized by high levels of endemism. Even within archipelagos, ranges of congeneric species are often distinct and restricted to single islands, mountains, or valleys (Carlquist, 1974; Eliasson, 1995; Wagner et al., 1999). Although a few species are widespread and polymorphic, many have highly restricted, non-overlapping ranges. For example, speciation within Hawaiian *Cyrtandra* (53 species, Gesneriaceae), a genus of deep ravines and gulches, appears to have been driven by the isolation produced by the dissected topography of highly eroded islands (Carlquist, 1974). In most mainland tropical and subtropical forests, in contrast, within-stand diversity is high (e.g., Heaney & Proctor, 1990), characterized by high diversity within families and co-occurrence of many congeneric species (Croat, 1978; Hartshorn & Hammel, 1994). Thus at a stand level, if not at a regional level, species diversity is likely to be low in island ecosystems.

The thesis that species-rich communities are less invasible than species-poor communities was first suggested by Elton (1958) and has become a central tenet of invasion ecology (e.g., Mack et al., 2000). However, empirical support for this hypothesis seemingly has been ambiguous. At the landscape and regional scales, several recent analyses have shown that the most diverse communities often also have the largest number of exotic species. Analyses of islands (Lonsdale, 1999), riparian ecosystems (Levine, 2000), and rangelands (Stohlgren et al., 1999) all show strong positive correlations between native and exotic species diversity. The authors conclude that likely the same factors that promote a rich assemblage of native species—largely availability of limiting resources—also facilitate the establishment of exotics. In contrast, experimental manipulations of species in plots or microcosms suggest that more diverse assemblages may exploit resources more efficiently and resist establishment of new species (e.g., Levine & D'Antonio, 1999; Levine, 2000; Naeem et al., 2000; Tilman et al., 2001; Kennedy, 2002). These apparently inconsistent results from experimental and observational studies may be resolved by considering process and scale (Levine & D'Antonio, 1999). Both net resource availability and species richness may increase along a resource supply gradient if supply increases faster than uptake by the community (Fig. 1). Thus the effect of diversity on biotic resistance to invasions should be assessed in the context of resource supply and demand; net resource availability rather than species richness *per se* likely determines community invasibility (Shea & Chesson, 2002). For example, low diversity forests at Semliki Forest Reserve, Uganda, were found to be no more invasible than high diversity stands (Rejmánek, 1996). Similarly, observations of Davis et al. (1998) showed that competition intensity between tree seedlings and herbaceous vegetation was correlated with net resource supply rather than biomass or gross resource supply. These studies suggest two correlates of community invasibility: (1) new species are most likely to become established where limiting resources are available; (2) more resources are likely to be used or preempted when species richness is high than when it is low. Under conditions of constant resource supply, high species richness may reduce invasibility (e.g., Levine & D'Antonio, 1999; Tilman et al., 2001). On oceanic islands, low stand-level diversity likely contributes to low levels of resource use, high resource availability, and poor resistance to the establishment of new individuals (e.g., Kitayama, 1996; Kitayama & Itow, 1999).

DISHARMONIC FLORAS

In addition to their effects on species diversity, long-distance oceanic dispersal and novel environmental conditions constitute a strong ecological filter on island biota. As a result, insular floras are often depauperate in certain taxonomic lineages, functional groups, life forms, dispersal characteristics, or environmental adaptations, a pattern that Carlquist (1974) described as disharmonic. For example, rain forests on oceanic islands may lack tall, large-seeded, shade-tolerant canopy trees that dominate many mainland rain forests. In Hawaii, native palms are confined to a single genus (*Pritchardia*); in contrast, dwarf, understory, climbing, and clonal palms are common in mainland forests. Similarly,

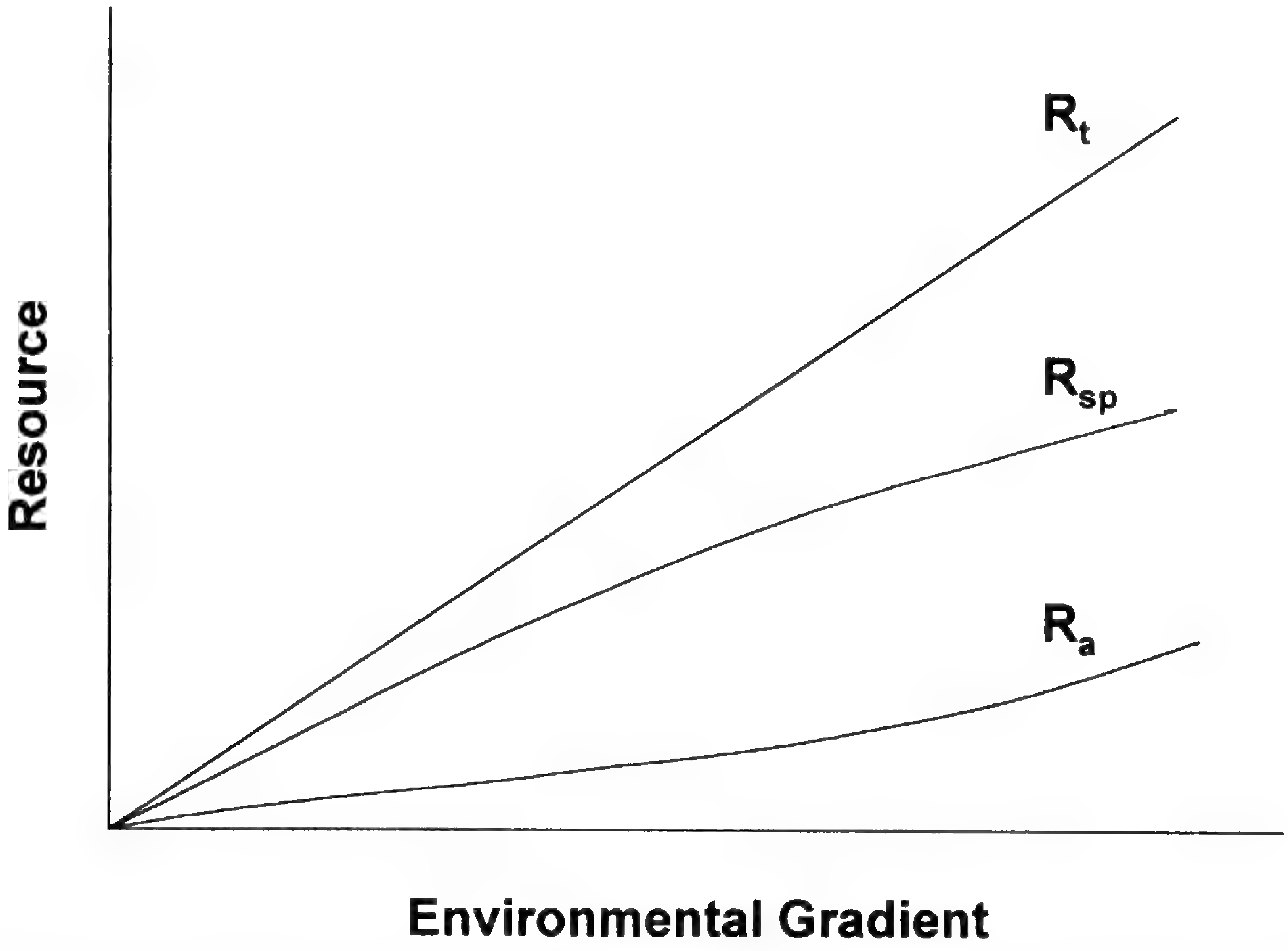

Figure 1. Hypothetical patterns of resource supply and demand across an environmental gradient. R_t = total resource availability; R_{sp} = resources consumed or preempted by species present. The increased resource demand reflects combined effects of all co-occurring species, which may often, but not always, be associated with an increase in species richness, functional group diversity, and/or redundancy within functional groups. R_a = available or net unused resources; these may remain unused or be exploited by additional native or alien species.

there are few species of native lianas in Hawaii. In mainland ecosystems, both of these functional groups can have important effects on forest structure and regeneration processes (Dewalt et al., 2000; Schnitzer et al., 2000; Farris-Lopez et al., ms.).

The availability of vacant niches arising from this disharmony in the structure of island biota is cited frequently as providing opportunity for invasive species (e.g., Mack et al., 2002; Shea & Chesson, 2002). Among plants, however, the concept of functional groups may be a more useful model than niches, since unique habitat and resource requirements are difficult to describe among plants. Species in a functional group share traits that similarly affect ecosystem and community processes (Fownes, 1995; Denslow, 1996). For example, *Myrica faya* Aiton (Myricaceae) is an alien, N-fixing tree that invades recent lava flows in Hawaii. Addition of its N-rich litter increases nutrient supply rates to other species and thus alters successional dynamics on this new substrate (Vitousek et al., 1987). The scarcity of native species that fill this role suggests that this functional group is missing in Hawaii (Fownes, 1995), although the presence of widespread N-fixing shrubs in the fossil record (James, 1995) indicates that this role once may have been filled. Indeed the ability of alien invasive species to alter nutrient supply, disturbance regimes, light environments, productivity, and other ecosystem properties may be taken as evidence of unexploited opportunity and missing or poorly represented functional groups. Similarly, Kitayama (1996) and Kitayama and Itow (1999) suggested that low stand productivity and low above-ground biomass in spite of high resource availability were linked to low species diversity and missing functional groups in Hawaii and the Galapagos. However, a deterrent effect of native species on the establishment of alien species with similar habitat requirements, resource needs, and growth forms may be difficult to demonstrate. In Hawaii, for example, much of the diversity among woody plants resides in understory shrubs, yet this group of plants also is well represented in the naturalized exotic flora.

High levels of apparent functional redundancy among plants in mainland rain forests suggest that there may be few barriers to the coexistence of many species playing similar functional roles. For example, about 1700 species of vascular plants have been recorded in 1536 ha at the La Selva Biological Station, Costa Rica, of which there are 44 species of *Piper* (Piperaceae), 39 species of *Psychotria* (Rubiaceae), and 25 species of *Miconia* (Melastomataceae) (Wilbur, 1994), almost all of which are understory shrubs and small trees. There are 107 species of lianas and 323 species of trees (Hartshorn & Hammel, 1994; Wilbur, 1994). Differences among these species, for example, in light requirements, growth form, or climbing mechanisms, are small, suggesting strong overlap among them in habitat requirements. In addition, studies on the 50-ha permanent plot in Panama fail to reveal significant habitat differences among the majority of coexisting trees and shrubs there (Hubbell et al., 1999; Harms et al., 2001). These patterns in relatively homogeneous forests suggest that the presence of many ecologically similar species is not a strong deterrent to the occurrence and persistence of plant species in mainland tropical forest. In this context, it also seems unlikely that the presence of native species would be a significant barrier to the establishment of ecologically similar alien species in island ecosystems.

NATIVE SPECIES ARE POOR COMPETITORS

Native species on islands often appear to be poor competitors (Darwin, [1859] 1972; Carlquist, 1974). For example, wet and mesic forests throughout the Hawaiian archipelago are dominated by a single highly polymorphic species, *Metrosideros polymorpha* Gaud. (Myrtaceae). These *Metrosideros* forests are characterized by relatively open canopies, widely spaced crowns, and inefficient light absorption (Cordell & Goldstein, 1999). As a result, considerable light reaches the forest understory (Cordell & Goldstein, 1999), where native and alien grasses, herbs, and shrubs are able to establish. In addition, net CO_2 assimilation, leaf turnover, and growth rates of *M. polymorpha* are generally low (Burton, 1982; Burton & Mueller-Dombois, 1984), and *M. polymorpha* shows little plasticity in response to increases in light or nutrient supply (Cordell et al., 2001; Austin & Vitousek, 2000). Where growth or carbon fixation rates have been compared, lower rates are often measured in native Hawaiian than in comparable alien species (Pattison et al., 1998; Baruch & Goldstein, 1999; Durand & Goldstein, 2001). Similarly, the exotic Himalayan raspberry, *Rubus ellipticus* Sm., is replacing the native ʻakala, *Rubus hawaiiensis* A. Gray, in the treefall gaps both require for establishment in montane rain forest. Although the two species have similar dispersal mechanisms and habitat requirements, the alien *R. ellipticus* exhibits faster growth rates, a more efficient canopy configuration, and greater seed production increasing the likelihood that it eventually will replace the native species in these forests (Denslow, unpublished data).

The reasons why island species should be poor competitors are various. Loss of resilience in the gene pool may be a consequence of founder effects, inbreeding depression, small population sizes, strong post-establishment selection, drift, and low vagility of pollinators and dispersers (Carlquist, 1974; Loope & Mueller-Dombois, 1989; Kaneshiro, 1995). The steep environmental gradients over short distances that characterize high tropical islands may constrain development of specialized adaptations. For example, Kitayama (cited in Denslow, 2001) has suggested that the dominance of oceanic island forests by species with wide ecological ranges may be linked to their low productivity and high invasibility. In his study of Hawaiian and Bornean rain forests (Kitayama, 1996), he found that species on Borneo had narrower elevation ranges than did species in Hawaii. He suggested, therefore, that the Bornean species may be better adapted to their environments and thus present stronger barriers to alien species than the more broadly adapted species in Hawaii. The links among adaptive ranges, competitive ability, and resistance to invasion deserve further exploration in this regard. A large proportion of island endemics are threatened or endangered due in part to their small ranges (Simberloff, 2000; Sakai et al., 2002), and the positive correlation between range size and local abundance has been widely acknowledged (e.g., Brown & Maurer, 1984; Kelly, 1996). These studies suggest that on islands, depauperate and disharmonic floras and poorly competitive species may result in low productivity and high ecosystem invasibility.

Loss of dispersal efficiency in island species may contribute to their poor competitive abilities. The generality of this pattern in many unrelated plant groups (Carlquist, 1974) suggests that selective pressure to avoid loss of reproductive output and reduce investment in dispersal mechanisms is strong on islands. Compounding the evolutionary loss of dispersability has been the historic loss of avian frugivores in Hawaii (James, 1995), loss of pollinators, and lack of a persistent seed bank in many native species (Drake, 1998), all of which contribute to low seed availability. As a result, population growth of native species may be strongly dispersal-limited in some habitats. Indigenous species thus may be less likely to fully occupy suitable habitats than aliens with better dispersal mechanisms, greater seed output, and larger seedbanks, and less likely to reach and occupy critical, but ephemeral, establishment sites such as treefall gaps and nurse logs. Dispersal limitation contributes to less-than-full exploitation of limiting resources in all ecosystems (Hubbell, 2001), but may be particularly important on islands.

EFFECTS OF LOW PEST LOADS

The enemy release hypothesis proposes that alien plant species in their introduced ranges experience lower pest loads than co-occurring native species and than they do in their native ranges (Keane & Crawley, 2002). As a result, populations of exotic species may be released from control by natural enemies, enhancing their competitive positions relative to native species, which may remain under pressure from specialist and generalist enemies. There have been few appropriate tests of this hypothesis and in a few cases only were significant impacts of either generalist or specialist herbivores on the exotic plant species recorded (Keane & Crawley, 2002). Classical biological control—the introduction of specialist pests and pathogens to control invasive species in their introduced ranges—is based on this premise. There are several examples of intentional and accidental introductions of pests limiting the populations of their hosts (Louda et al., 1997; Strong & Pemberton, 2000), and Louda (1982) and DeWalt et al. (unpublished ms.) offer evidence that pests limit both growth and habitat distributions of weedy plants. In addition, data presented by DeWalt et al. (unpublished ms.) suggest that survival of *Clidemia hirta* (L.) D. Don (Melastomataceae) is more strongly affected by insect and pathogen impacts in its native than in its introduced range. The role of pest and pathogen pressure in island plant invasions is still poorly understood.

Furthermore, indigenous island species, which also originated as waifs, are thought to be under low pressure from natural enemies as well (Carlquist, 1980). In the process of dispersal to new and isolated habitats, insular floras are thought to have left their specialized pests behind. While subsequent diversification has produced many specialized associations of plants and their natural enemies (Swezey, 1954), the common lack of defensive compounds and structures among indigenous island species suggests that plant pathogen and herbivore impacts are not high. As a result, island plants may be particularly vulnerable to the introduction of exotic pests such as ungulates (Mueller-Dombois & Fosberg, 1998; Richardson et al., 2000). If islands are depauperate in natural enemies or dominated by specialist herbivores, both exotic and native species may be under little control by their natural enemies. The net effect of low pest loads on native and alien plant species on islands is then difficult to predict. We lack critical information on the role of natural enemies in limiting plant population growth, abundance, and distribution in both mainland and island habitats. On balance, however, the more rapid growth rates and plastic physiological responses of alien species may result in their greater population growth where pest pressures are low (Keane & Crawley, 2002).

SYNTHESIS

Net resource availability is an important component of community invasibility. The role of resource pulses in the spread of alien species has been noted widely (Vitousek et al., 1997; D'Antonio et al., 1999; Mack et al., 2002). The generality of this relationship can be extended usefully to include chronic as well as temporary resource availability, such as that provided by disturbances, and to affect native as well as alien species. Seedlings of both native and alien species are likely to become established where resources are chronically or temporarily under-used, as following natural or anthropogenic disturbance; under conditions of naturally high levels of resource supply; where resources are incompletely exploited by the existing community; or where resource supply has been augmented. For example, it is widely recognized that both natural and anthropogenic disturbances facilitate the establishment of alien species (Rejmánek, 1989; Horvitz et al., 1998; D'Antonio et al., 1999), in part because disturbance reduces competition and increases local resource availability. In intact native communities, ant mounds, treefall gaps, and riparian habitats are important sites for seedling establishment (Platt, 1975; Denslow, 1987; Levine, 2000). Similarly, where disturbances are ecologically novel or unusually frequent or intense, we can expect that some native species as well as some exotic species may find suitable environmental conditions. Diversity and abundance of both alien and native species also are often highest in resource-rich habitats (e.g., Stohlgren et al., 1999), and, conversely, communities characterized by resource limitation (in Hawaii, alpine and subalpine ecosystems, communities on young lava flows, and dryland forests) are often notable for scarcity of exotic invasives. Other attributes proposed to increase community invasibility, such as vacant niches, novel anthropogenic disturbances, or disequilibrium conditions, also address the availability of resource availability, but might be seen as special examples of a more general phenomenon.

In isolated tropical island habitats, resource availability likely is high because indigenous species do not effectively use or preempt them. Low local species richness, low diversity of functional groups, and low redundancy within functional groups suggest that few species may be available to take advantage of establishment opportunities or unused resources. Dispersal limitation, characteristic of all plant communities, may be particularly strong on islands, reducing the occupancy rate of suitable habitats and leaving sites and resources available for others. Where propagule pressures are high, the vulnerability of island communities to establishment of exotic species will be particularly apparent (Rejmánek, 1989; Drake, 1998; Levine, 2000).

Invasibility, however, is not a unilateral function of habitat characteristics, but rather the interaction of habitat and species. Limiting resources are available relative to the physiological and morphological capacity of plants to exploit them. Low growth plasticity in response to resource availability in many native species contributes to the underutilization of resources and thus invasibility of some island communities, and exotic species with more plastic growth responses may compete more effectively for natural establishment sites such as treefall gaps and decaying logs and take better advantage of novel disturbances such as pig foraging sites.

Assuming that fundamental tradeoffs between rapid growth rate in high light environments and persistence in shaded environments characterize alien and native species (Reich et al., 1997; Hubbell, 2001), both alien and native species should be able to thrive across a full spectrum of environments. Invasive species often are assumed to have characteristics of disturbance-adapted species (e.g., rapid growth in resource-rich environments and copious production of well-dispersed seeds); however, in part this pattern may reflect historic pathways of introduction associated with development of agriculture and rangelands (Mack, 1992), rather than inherent characteristics of invasive species. A rising global horticultural trade is introducing species that are shade-tolerant, spread vegetatively, and/or have large seeds (Reichard & Hamilton, 1997) and thus are potentially invasive in intact forest ecosystems.

This review suggests that fundamentally two interacting processes—high net resource availability and poor ability of native species to preempt those resources—make island communities vulnerable to the establishment and spread of alien species. Historically high rates of introduction have provided opportunity in the form of a diverse and abundant propagule rain of exotic species. The combination produces a scenario that is not an optimistic one for island ecosystems. It suggests that these native ecosystems on islands are particularly vulnerable to naturalizing exotics growing on their borders, and that while disturbance from a variety of causes, including pigs, fire, grazing, and natural dieback of the canopy dominants, increases the opportunities for exotic incursions, even intact forests are not immune. Unless these forests are aggressively managed and alien propagule pressure reduced, they will be highly modified by new exotic introductions.

There are implications of this scenario for mainland ecosystems as well. With rising human populations, increased incursions into wilderness areas, and global environmental change, mainland preserves will assume many island-like characteristics. Habitat fragmentation and large-scale habitat loss will increase habitat isolation, reduce the extent, and increase the edges. Fragmentation of forests is widely associated with increased disturbance, alteration of edge and sometimes interior habitats, loss of species, and increased invasibility (e.g., Laurance & Bierregaard, 1997). Effects of population reductions and species extinctions will simplify ecosystem structure, reduce population sizes, produce disharmonies in species assemblages, and reduce functional redundancy. Loss of higher trophic levels, in particular, may result in increased populations of herbivores and edge species. Increased intensities and rates of exploitation will free resources (light, space, nutrients) and increase opportunities for exploitation by novel species. Rising rates of human traffic through suburban expansion, road extensions, global trade, ecotourism, and population movements will provide rising and repeated exposure to a diverse seed rain from exotic species. Tropical islands are an effective early warning system of the impacts successive waves of exotic species invasions may cause to isolated ecosystems. As island managers develop strategies for preventing and controlling these invasions, they will be watched by many on the mainland.

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Cover illustration. *Tamarix pentandra.* Plate LXXIX in *Flora Rossica*, edited by P.S. Pallas, K.F. Friedrich, and J.J. Weitbrecht and published by Petropoli, Leningrad, 1784–1788. A book of hand-colored copper engravings of plants indigenous to European and Asian areas of the Russian Empire, and one of a large collection of such books in the library of the Missouri Botanical Garden.

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PHYLOGENETIC ANALYSES AND PERIANTH EVOLUTION IN BASAL ANGIOSPERMS[1]

Michael J. Zanis,[2] Pamela S. Soltis,[3] Yin Long Qiu,[4] Elizabeth Zimmer,[5] and Douglas E. Soltis[6,7]

ABSTRACT

Using a compartmentalization approach, we conducted phylogenetic analyses of the basalmost extant angiosperms using sequences from six genes (over 12,000 bp per taxon) from all three genomes (chloroplast—*atp*B, *rbc*L; nuclear—18S rDNA, 26S rDNA; mitochondrial—*mat*R, *atp*A). Trees resulting from parsimony and maximum likelihood analyses of the compartmentalized data are identical. We find strong support (100% for each node) for the earliest-branching angiosperms: Amborellaceae, Nymphaeaceae, and an Austrobaileyales clade (Illiciaceae, Schisandraceae, Trimeniaceae, Austrobaileyaceae). Whereas most recent studies using multiple genes provided poor resolution and support for relationships among the remaining basal angiosperms (Ceratophyllaceae, Chloranthaceae, Canellales (= Winterales), Piperales, monocots, Magnoliales, Laurales), with compartmentalization, we find high levels (> 90%) of bootstrap support for relationships among these clades. Canellales and Piperales form a strongly supported (100%) sister group that is, in turn, sister to a well-supported (100%) clade of Laurales and Magnoliales. Canellales + Piperales and Magnoliales + Laurales form a well-supported magnoliid clade. Ceratophyllaceae are strongly supported (100%) as sister to the monocots; the monocot/Ceratophyllaceae clade is well supported (86%) as sister to all remaining angiosperms (Chloranthaceae, the magnoliid clade, and eudicots). The addition of entire 26S rDNA sequences clearly contributed to this increased internal support. We examined the diversification of perianth phyllotaxis, merosity, and differentiation using our phylogenetic hypothesis for angiosperms. Ancestral perianth phyllotaxis and merosity are equivocal for each node of the Amborellaceae, Nymphaeaceae, Austrobaileyales grade; however, an undifferentiated perianth is reconstructed

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as the ancestral state for the angiosperms. Trimery and whorled perianth phyllotaxis have played a major role in basal angiosperm perianth evolution and represent the ancestral states for the large clade comprising all angiosperms other than *Amborella*, Nymphaeaceae, and Austrobaileyales. A differentiated perianth has apparently evolved multiple times.

Key words: basal angiosperms, floral evolution, merosity, perianth, phylogeny.

Understanding phylogenetic relationships among extant basal angiosperms is critical for reconstructing the evolution of numerous traits, including wood anatomy, chromosome numbers, pollen morphology, and floral morphology (Endress, 1986, 1994a; Endress & Hufford, 1989; Endress & Igersheim, 1997; Igersheim & Endress, 1997; Qiu et al., 2000; P. Soltis et al., 1999a; Thorne, 1992; Walker & Walker, 1984). In recent classifications, most basal angiosperms have been recognized as subclass Magnoliidae (Cronquist, 1981; Takhtajan, 1969, 1997; Thorne, 1992). However, these groups have typically formed a grade (Donoghue & Doyle, 1989; Doyle, 1994; Nandi et al., 1998; Savolainen et al., 2000; D. Soltis et al., 2000; P. Soltis et al., 1999a), and only rarely a clade (Chase et al., 1993; Qiu et al., 1993), in phylogenetic analyses of angiosperms.

Previous analyses of relationships among basal angiosperms based on morphology have generally provided conflicting results regarding the early branches of angiosperm phylogeny. Phylogenetic analyses of morphological data (Donoghue & Doyle, 1989) suggested that Magnoliales were sister to all other angiosperms, although in trees only one step longer Nymphaeaceae appeared in this position. In that same study, paleoherbs (Piperales, Nymphaeaceae, and monocots) formed a clade, Chloranthaceae and Austrobaileyaceae were nested within Laurales, and Winteraceae were allied with Austrobaileyaceae. In contrast, Loconte and Stevenson's (1991) phylogenetic analysis of morphological data placed Calycanthaceae as sister to all remaining angiosperms; as in Donoghue and Doyle (1989), Chloranthaceae were nested within Laurales, and Winteraceae were included within Illiciaceae and Schisandraceae, but Austrobaileyaceae appeared within Magnoliales.

There have been several attempts to analyze phylogenetic relationships among basal angiosperms using both RNA and DNA sequence data. Phylogenetic analyses using 18S rRNA sequences (Hamby & Zimmer, 1992) suggested that Nymphaeaceae, Piperales, and monocots were successive sister groups to all remaining angiosperms. In agreement with the broad analysis of 500 *rbc*L sequences from seed plants (Chase et al., 1993), Qiu et al.'s (1993) analyses of *rbc*L sequences focusing on basal angiosperms suggested that Ceratophyllaceae were sister to all other angiosperms, with the remaining basal angiosperms forming a clade sister to the eudicots. Qiu et al. (1993) also recovered four major lineages within this large basal angiosperm clade: Magnoliales, Laurales, Piperales, and Nymphaeaceae. Combined analyses using morphological and rRNA sequence data (Doyle et al., 1994) found Nymphaeaceae, monocots, Piperales, and Aristolochiaceae to be successive sisters to the remaining angiosperms; the rest of the Magnoliidae formed a clade sister to the eudicots. Analyses of complete 18S rDNA sequences with greater taxon sampling than employed by Hamby and Zimmer (1992) placed Amborellaceae, Austrobaileyaceae, Illiciaceae, Schisandraceae, and Nymphaeaceae as the earliest-branching angiosperms (D. Soltis et al., 1997). The analysis of a large *atp*B data set (Savolainen et al., 2000) also placed Amborellaceae, Nymphaeaceae, and Austrobaileyales as the earliest-branching angiosperms. In all of these analyses, internal support (as measured by bootstrap values) at deep levels within the phylogenies was low (less than 50%). In addition, some of the above studies may have experienced long-branch attractions of highly divergent taxa or clades.

By combining data from multiple genes and, in some cases, sampling numerous taxa, recent studies have greatly enhanced our understanding of relationships among basal angiosperms. Recent studies not only agree on the same groups of early-branching angiosperms, but also provide strong internal support for many relationships (Graham & Olmstead, 2000; Mathews & Donoghue, 1999, 2000; Parkinson et al., 1999; Qiu et al., 1999, 2000; D. Soltis et al., 2000; P. Soltis et al., 1999a). These investigations used sequences from a variety of genes representing the chloroplast, mitochondrial, and nuclear genomes. In addition, different approaches were employed, including parsimony, maximum likelihood, and a duplicate gene rooting strategy (Mathews & Donoghue, 1999, 2000). These analyses reveal that Amborellaceae, Nymphaeaceae (comprising Cabombaceae and Nymphaeaceae s. str., the two families constituting Nymphaeales following Les et al., 1999), and a clade of Illiciaceae, Schisandraceae, Austrobaileyaceae, and Trimeniaceae (hereafter referred to as Austrobaileyales) are successive sisters (with strong internal support) to the rest of the angiosperms. However, despite generally strong support for this branching order, an analysis employing RASA (Lyons-Weiler et al., 1996) indicated that Nymphaeaceae + Amborellaceae may form a clade sister to all other angiosperms (Barkman et al., 2000). In contrast, analyses of a large multigene data set found strong bootstrap support for *Amborella* as sister to all other angiosperms using both maximum parsimony and maximum likelihood methods, and a hypothesis test using parsimony rejected the *Amborella* + Nymphaeaceae topology; however, a hypothesis test using maximum likelihood could not reject the *Amborella* + Nymphaeaceae topology (Zanis et al., 2002).

Although recent studies have clarified the early branches of the angiosperm tree, relationships among the remaining basal angiosperms remain uncertain. As reviewed above, the remaining basal angiosperms form a number of very strongly supported clades: Piperales, Winteraceae/Canellaceae (Canellales; referred to as Winterales by some), Magnoliales, monocots, Laurales, and Chloranthaceae (ordinal composition sensu APG II, 2003). Relationships among these clades were uncertain in many previous studies, but are becoming clearer (e.g., Qiu et al., 1999, 2000; Zanis et al., 2002): a magnoliid clade comprises Magnoliales + Laurales and Canellales + Piperales, although the positions of the monocots and Chloranthaceae relative to this magnoliid clade are not well supported. The placement of Ceratophyllaceae has varied among studies. Ceratophyllaceae were sister to all other angiosperms in analyses based on *rbc*L sequences (Chase et al., 1993; Qiu et al., 1993; Savolainen et al., 2000); however, in the three-gene, 567-taxon analysis (D. Soltis et al., 2000; P. Soltis et al., 1999a), Ceratophyllaceae appeared as sister to the eudicots (with 53% jackknife support). Other studies have placed Ceratophyllaceae closer to the monocots (Qiu et al., 1999, 2000; Savolainen et al., 2000; Zanis et al., 2002) or as sister to Winteraceae (Parkinson et al., 1999).

A clear understanding of relationships among basal angiosperms has obvious major implications for interpreting the morphology of the early angiosperms and subsequent patterns of floral evolution. Early hypotheses proposed that the first angiosperms had large, *Magnolia*-like, flowers (Arber & Parkin, 1907; Bessey, 1897, 1915; Cronquist, 1981, 1988; Takhtajan, 1969, 1997). However, Stebbins (1974) stressed that the concept of the earliest flower as large, strobiloid, and *Magnolia*-like was not consistent with the amount of specialization that occurs within the Magnoliaceae. Stebbins (1974) proposed that the earliest flowers were moderate in size. Using a combination of information from both extant and fossil Magnoliidae, Endress (1987c) suggested that the earliest angiosperm was bisexual, but that the transition to unisexuality was relatively easy, the perianth was undifferentiated and could be easily lost, and the number of floral parts was labile.

Early phylogenetic studies focused attention on paleoherbs (Nymphaeaceae, Piperaceae, and Chloranthaceae) as possible first-branching extant angiosperms (Donoghue & Doyle, 1989; Doyle et al., 1994; Hamby & Zimmer, 1992), suggesting that early flowers were small, with a trimerous perianth, and with few stamens and carpels. Recent topologies (Doyle & Endress, 2000; Graham & Olmstead, 2000; Mathews & Donoghue, 1999, 2000; Parkinson et al., 1999; Qiu et al., 1999, 2000; D. Soltis et al., 2000; P. Soltis et al., 1999a; Zanis et al., 2002) that place *Amborella* as sister to other angiosperms suggest instead that the earliest flowers were small to moderate in size, with an undifferentiated perianth, stamens lacking a well-differentiated filament, and a gynoecium composed of one or more unilocular ovaries. The diverse array of early angiosperm fossils is consistent with this hypothesis (Crane, 1985; Crane et al., 1995; Friis et al., 1994, 1997, 2000).

Patterns of evolution of specific floral characters in basal angiosperms have also been examined using a phylogenetic framework (e.g., Hufford, 1996; Albert et al., 1998). Using the topologies of Donoghue and Doyle (1989) and Chase et al. (1993), Hufford (1996) found that the laminar stamen may have evolved independently several times in the Magnoliidae. Using the *rbc*L topology for angiosperms (Chase et al., 1993), Albert et al. (1998) reconstructed perianth architecture to elucidate the evolution of the bipartite whorled perianth found in the eudicots. Albert et al. (1998) found that the single whorled perianth optimized as the ancestral character state for the angiosperms, based on a placement of Ceratophyllaceae as sister to all angiosperms in the *rbc*L tree.

To explore relationships among basal angiosperms further, we added a sixth gene, 26S rDNA, to the data set of Qiu et al. (1999). A compartmentalization approach (Donoghue, 1994; Mishler, 1994; Rice et al., 1997) for these six genes was employed; this method facilitated the use of maximum likelihood and more thorough parsimony methods of phylogenetic inference. Using our six-gene phylogenetic tree for basal angiosperms as a framework, we subsequently investigated the evolution of perianth (1) phyllotaxis, (2) merosity (merism), and (3) differentiation.

MATERIALS AND METHODS

26S rDNA SEQUENCING

The utility of entire 26S rDNA sequences for reconstructing angiosperm phylogeny has recently been demonstrated (Fan & Xiang, 2001; Fishbein et al., 2001; Kuzoff et al., 1998). Although partial 26S rRNA and rDNA sequences have occasionally been used to infer phylogeny (Buchheim & Chapman, 1991; Hamby & Zimmer, 1992; Ro et al., 1997), the great length of the gene (over 3200 bp) had, until recently, precluded the use of its entire sequence for phylogeny reconstruction. The gene comprises both conserved core regions and more rapidly evolving expansion segments, thus enhancing the utility of the gene for phylogenetic inference across several phylogenetic levels, from the angiosperms as a whole (Kuzoff et al., 1998) to smaller clades such as Saxifragales (Fishbein et al., 2001), Cornales (Fan & Xiang, 2001), and Ranunculales (Kim et al., submitted).

We generated and analyzed entire 26S rDNA sequences for 44 angiosperms representing Magnoliales, Laurales, Chloranthales, Piperaceae, Aristolochiaceae, Nymphaeaceae, Canellales, Austrobaileyales, monocots, and eudicots. The following gymnosperms served as outgroups: *Ginkgo*, *Gnetum*, *Ephedra*, and *Larix*. All species for which 26S rDNA sequences were included in this analysis are listed in Table 1; voucher information and GenBank numbers are also provided. We attempted to use the same species, and in many cases the same DNAs, used by Qiu et al. (1993) and D. Soltis et al. (1997, 2000). Familial and ordinal circumscriptions mostly follow those given in APG II (2003).

Amplification and sequencing of 26S rDNA generally followed the methods of Kuzoff et al. (1998). For PCR amplification, we used either ITS3 or N-nc26S1 as the forward primer and 3331rev for the reverse primer. In some cases we amplified 26S rDNA in two portions. The 5' half of the gene was amplified using either ITS3 or N-nc26S1 as the forward PCR primer and 1839rev as the reverse primer. The 3′ half of 26S rDNA was amplified using N-nc26S7 as the forward primer and 3331rev as the reverse primer. For the sequencing of 26S rDNA, the following primers were used: N-nc26S1, N-nc26S3, N-nc26S5, N-nc26S7, N-nc26S9, N-nc26S11, N-nc26S13, N-nc26S14, 268rev, 641rev, 950rev, 1229rev, 1499rev, 1839rev, 2134rev, 2782rev, 3058rev, and 3331rev (Kuzoff et al., 1998).

The vast majority of 26S rDNA sequence is easily aligned by eye; however, several small portions of some of the expansion segments were more difficult to align visually. Clustal X (Thompson et al., 1997), with gap opening set to 10 and gap extension set to 0.2, was therefore used to obtain an initial 26S rDNA alignment, which was further refined by eye.

PHYLOGENETIC ANALYSES USING COMPARTMENTALIZATION

Mishler (1994) proposed compartmentalization as a method to reduce a large data set to a smaller, more manageable size, to decrease the effect of "spurious homoplasy," and to maximize the amount of information used in phylogenetic analyses by allowing different data sets to be used for the local and global analyses. This approach also facilitates the application of maximum likelihood to the compartmentalized data, an approach that could not be employed with the large, more complete data set. In brief, an initial global analysis is performed on the large data set. Well-supported clades (compartments) are identified from the global analysis using bootstrap, jackknife, or decay values (Bremer, 1988; Farris et al., 1996; Felsenstein, 1985). Smaller, focused analyses are then performed to establish relationships within each of the compartments. Upon completion of the smaller analyses, relationships within compartments can be constrained and relationships among compartments can be inferred, or a hypothetical ancestor for each compartment can be reconstructed using parsimony or maximum likelihood methods (Yang et al., 1995) and used to infer relationships among compartments (Donoghue, 1994; Mishler, 1994; Rice et al., 1997).

Using the five-gene data set of Qiu et al. (1999), we conducted a global parsimony analysis with 100 replicates of random taxon addition to search for multiple islands of most parsimonious trees (Maddison, 1991) and TBR branch swapping. Internal support was estimated using the bootstrap (Felsenstein, 1985) with 100 replicates with 100 random taxon addition replicates, MULPARS, and TBR branch swapping. Each of the following compartments appeared well supported in our global parsimony analysis, receiving greater than 90% bootstrap support (see also Qiu et al., 1999; Parkinson et al., 1999; P. Soltis et al., 1999a): Nymphaeaceae, Austrobaileyales, Magnoliales, Laurales, Piperales, Canellales, Chloranthaceae, monocots, and eudicots. For each compartment we then reconstructed a hypothetical ancestral sequence for each of the

Table 1. Voucher information and GenBank Accession numbers for the 26S rDNA sequences used in this study.

Family	Species	Voucher	GenBank Accession number
Acoraceae	*Acorus gramineus* Aiton	Kuzoff (1998)	AF036490
Amborellaceae	*Amborella trichopoda* Baill.	Plunkett, G.	AY095449
Annonaceae	*Asimina triloba* (L.) Dunal.	*Qiu 15*	AY095451
Araceae	*Spathiphyllum wallisii* Hort.	*Chase 201* (NCU)	AY095473
Aristolochiaceae	*Aristolochia macrophylla* Lam.	*Qiu 91019*	AY095450
Lactoridaceae	*Lactoris fernandeziana* Phil.	*Stuessy et al. 11784* (OS)	AY095463
Asphodelaceae	*Bulbine succulenta* Compton	*UCI Arb. 7174*	AY095471
Austrobaileyaceae	*Austrobaileya scandens* C. T. White	*Qiu 90030*	AY095452
Berberidopsidaceae	*Berberidopsis corallina* Hook. f.	*Chase 555* (K)	AF389242
Buxaceaee	*Buxus sempervirens* L.	*Chase 203* (NCU)	AF389244
Cabombaceae	*Cabomba* sp.	*Qiu 97027*	AY095453
Calycanthaceae	*Calycanthus occidentalis* Hook. & Arn.	Cult. WSU	AY095454
Canellaceae	*Canella winterana* (L.) Gaertn.	*Qiu 90017*	AY095455
Ceratophyllaceae	*Ceratophyllum demersum* L.	*Qiu 95003*	AY095456
Chloranthaceae	*Chloranthus multistachys* Pei	*K. Wurdack 920010*	AY095457
Chloranthaceae	*Hedyosmum bonplandianum* L.	*Endress 97-102*	AY095461
Eupteleaceae	*Euptelea polyandra* Sieb. & Zucc.	*Qiu 9001* (NCU)	AF389249
Fumariaceae	*Dicentra eximia* Torrey	*Reznicek 9756* (MICH)	AF389262
Ginkgoaceae	*Ginkgo biloba* L.	Cult. WSU	AY095475
Gnetaceae	*Gnetum gnemon* L.	Kuzoff et al. (1998)	AF036488
Ephedraceae	*Ephedra distachya*	Kuzoff et al. (1998)	AF036489
Gomortegaceae	*Gomortega keule* (Molina) I. M. Johnston	K. Ueda	AY095460
Hamamelidaceae	*Hamamelis virginiana* L.	*Hoot 910*	AF036495
Hernandiaceae	*Hernandia nymphaeifolia* L.	Univ. Zurich Bot. Gard.	AY095462
Himantandraceae	*Galbulimima belgraveana* (F. Muell.) Sprague	*P. H. Weston 929*	AY095459
Magnoliaceae	*Magnolia denudata* Desr.	*S. Kim 1010* (NPRI)	AF389256
Magnoliaceae	*Liriodendron chinense* (Hemsl.) Sarg.	*Qiu 28*	AY095464
Menispermaceae	*Tinospora caffra* Miers	*Jaarsveld 2131* (NGB)	AF389258
Monimiaceae	*Peumus boldus* Molina	Strybing Arb.	AY095466
Nelumbonaceae	*Nelumbo lutea* (Willd.) Pers.	*Hoot 9212* (UWM)	AF389259
Nymphaeaceae	*Nymphaea* sp.	*Qiu 91029*	AY095465
Pinaceae	*Larix* sp.	Cult. WSU	AY095476
Piperaceae	*Piper betle* L.	*Qiu 91048*	AY095467
Platanaceae	*Platanus occidentalis* L.	*Qiu P90005* (NCU)	AF274662
Poaceae	*Oryza sativa* L.	Sugiura et al. (1985)	M11585
Ranunculaceae	*Ranunculus keniensis* Milne-Redhead & Turrill	*Chase 573* (K)	AF389269
Sabiaceae	*Sabia swinhoei* Hemsl.	*Wagner 6518* (HAST)	AF389272
Saururaceae	*Saururus cernuus* L.	*Suh 128* (US)	AY095468
Taccaceae	*Tacca chantieri* André	*Chase 175* (NCU)	AY095474
Tofieldiaceae	*Pleea tenuifolia* Michx.	*Chase 152* (NCU)	AY095472
Trimeniaceae	*Trimenia moorei* (Oliv.) Philipson	*ANBG 701680*	AY095470
Trochodendraceae	*Trochodendron aralioides* Siebold	*Qiu 90026* (NCU)	AF274670
Winteraceae	*Drimys winteri* J. R. & G. Forster	*Nickrent 3013* (SIU)	AF036491
Winteraceae	*Tasmannia insipida* DC.	*Qiu 90032*	AY095469

five genes analyzed by Qiu et al. (1999) and our 26S rDNA data set using a maximum likelihood approach as implemented in Phylogenetic Analysis using Maximum Likelihood (PAML) (Yang, 1997); we employed a general time-reversible model with rate heterogeneity as our model of molecular evolution. In addition to the ancestral sequence for each of the compartments noted above, our final compartmentalized data set also included *Ceratophyllum* and *Amborella*, critical individual taxa that were not members of any compartment.

Maximum likelihood represents an alternative to the parsimony method of reconstructing ancestral sequences (Yang et al., 1995), employing information from a model of substitution and branch length estimates. Comparing both parsimony and maximum likelihood methods for inferring ancestral sequences, Yang et al. (1995) revealed that when sequences were from closely related species, both maximum likelihood and parsimony methods were accurate. Thus, when dealing with invariant sites, or less variable sites, both parsimony and maximum likelihood methods often produced identical results, and both had high levels of accuracy in reconstructing ancestral sequences. In contrast, both methods may be unreliable at reconstructing ancestral sequences for highly variable sites (Yang et al., 1995).

All of the hypothetical ancestral sequences for the six genes analyzed (five from Qiu et al., 1999, plus the 26S rDNA data set presented here) were ultimately combined for subsequent parsimony and maximum likelihood analyses; we will hereafter refer to this as the compartmentalized data set. Both parsimony and maximum likelihood estimation methods were performed using PAUP* 4.0 (Swofford, 1998). Parsimony analyses of the compartmentalized data set were conducted using the branch-and-bound search strategy with the initial upper bound computed via stepwise addition with furthest sequence addition.

Maximum likelihood parameter values were estimated from the single most parsimonious tree obtained from the parsimony analysis described. We used the general time-reversible model of molecular evolution, accounting for invariant sites and rate heterogeneity (Swofford et al., 1996). The choice of model of molecular evolution was done using MODELTEST 3.0 (Posada & Crandall, 1998). Fifty-six models were compared using the Akaike information criterion (AIC). The AIC model comparsion method does not require models to be nested and selects models for good fit but penalizes models for unnecessary parameters (Posada & Crandall, 1998). The –ln likelihood score for the single most parsimonious tree was 39743.36269, the proportion of invariant sites was estimated to be 0.516797, and the gamma shape parameter was estimated to be 0.744558. These estimates along with estimates for the general time-reversible model and base frequencies were used in maximum likelihood analysis using heuristic searches similar to the parsimony analyses. Internal support for both maximum likelihood and parsimony analyses was estimated using bootstrap analysis with 100 replicates with 100 random taxon additions per replicate, with TBR branch swapping.

CHARACTER ANALYSES

Perianth character states were mapped assuming equally weighted parsimony using MacClade 3.0 (Maddison & Maddison, 1992). We employed the "all most parsimonious states" trace option. A synthetic phylogenetic tree was used to expand the tree in regions that were not sampled thoroughly in the analysis of basal angiosperms. That portion of the topology dealing with relationships among the basal angiosperms was generated here (see below); eudicot relationships are those from the jackknife consensus tree of P. Soltis et al. (1999a) and D. Soltis et al. (2000). Phylogenetic relationships depicted within Nymphaeaceae follow Les et al. (1999). Relationships depicted within the monocots are a portion of one of the shortest trees obtained from a combined morphological and *rbc*L data set analyzed by Chase et al. (1995).

CHARACTER DEFINITIONS

Because definitions for the perianth vary (Endress, 1994a; Greyson, 1994; Weberling, 1989), we refer to the perianth as the sterile structures above the bract(s) if present, and immediately below the spore-producing organs in a flower. The organs of a perianth (i.e., sepals and petals) share similarities with bracts, a scale-like leaf subtending the organs of a flower, as well as staminodes, structures that represent sterilized stamens. For example, sepals have many features in common with bracts: both are green and lack clear anatomical differentiation into palisade and spongy parenchyma. Petals and staminodes share several characteristics as well (Esau, 1965). Both are laminar in shape and usually colorful (due to chromoplasts or pigments) (Esau, 1965). Descriptions of the perianth characters and states followed previous workers' interpretations for each of the groups studied and are presented in the Appendix.

Perianth phyllotaxis is the arrangement of perianth organs (i.e., sepals and petals) on an axis (Endress, 1994a). The states we coded are: absent (i.e., there is no perianth), a single whorl, two whorls, multiple whorls, and spiral. We also explored alternative character-state coding by reducing the different forms of whorled phyllotaxis (i.e., single whorl, two whorls, multiple whorls) into a single character state, whorled. Phyllotaxis is difficult to divide into states because it is labile in many groups (Doust, 2000, 2001; Endress, 1987b). Furthermore, the distinction between spiral and whorled is not always clear. That is, spiral and whorled may not be fundamentally different forms of phyllotaxis. Spiral and whorled perianth phyllotaxis likely represent a continuous (quantitative) character rather than a discrete (qualitative) character (Stevens, 1991). Perianths with whorled phyllotaxis appear to have organs arranged in the same plane. These organs appear equally spaced and also appear to have been initiated simultaneously (Endress, 1987b). However, ontogenetic investigations have indicated that in some cases floral organs typically identified as being whorled actually result from the presence of long plastochrons [the time interval between the initiation of two consecutive organ primordia; (Endress, 1994a; Tucker, 1960)] inserted between a number of small plastochrons [e.g., Huber (1980) for Solanaceae; Erbar & Leins (1985) for Apiaceae]. Thus, both spiral and whorled phyllotaxis may have the organs developing in a spiral sequence (Endress, 1987b, 2001).

Perianth merosity refers to the number of perianth parts present within each whorl. We recognized five character states: three organs per whorl, two or four organs per whorl, five organs per whorl, or an indeterminate number of organs per whorl. Indeterminate refers to a range with no fixed number of parts; typically, these are perianths with numerous spirally arranged parts.

Differentiated perianths are those having an outer whorl (or series) that is clearly differentiated from the inner whorl(s) (series). A differentiated perianth is commonly referred to as being composed of sepals and petals. In contrast, an undifferentiated perianth is one that lacks clear distinction between the outer and inner whorls; these have been traditionally recognized as tepals (Cronquist, 1988; Takhtajan, 1997). Albert et al. (1998) suggested that there must be at least two whorls present for unambiguous interpretation of sepals and petals, that is, an outer whorl that is clearly distinguishable from the inner whorl. Often, when only a single-whorled perianth is present, it is referred to as a calyx as a matter of convention (Cronquist, 1981, 1988). For example, those Aristolochiaceae characterized by a single-whorled perianth are referred to as having sepals (Cronquist, 1988; Takhtajan, 1997; Tucker & Douglas, 1996); developmental data for *Asarum* (Leins & Erbar, 1985) and *Aristolochia* (González & Stevenson, 2000) support this interpretation.

Perianth differentiation can often be difficult to score in those taxa having a perianth of a single whorl. We used the following character states in our analysis of perianth differentiation: undifferentiated (no clear distinction into outer and inner whorls), differentiated (clear distinction between inner and outer whorls), single whorl, and absent.

CHARACTER-STATE CAVEATS

Several studies have considered the treatment of polymorphic characters (Mabee & Humphries, 1993; Maddison, 1993; Nixon & Davis, 1991; Wiens, 1999). There are three options: (1) code the polymorphic state as "missing," (2) code polymorphic taxa with a putative ancestral state, by reconstructing the ancestral state from a phylogeny of the taxa in question, and (3) code the polymorphic taxa as polymorphic. We coded several taxa as polymorphic. For example, Canellaceae are coded as trimerous, tetramerous, or pentamerous (Wilson, 1966). We tested the robustness of our results by using alternative codings (Donoghue & Ackerly, 1996; Weller et al., 1995).

In addition to uncertainty in scoring taxa, due either to difficulty in interpreting structures or to polymorphism, there is uncertainty in the tree topology and the impact that alternative tree topologies may have on ancestral character-state reconstructions (Donoghue & Ackerly, 1996). We examined the sensitivity of our character-state reconstructions by examining reconstructions on alternative trees. For example, we examined character-state reconstructions on trees that placed Chloranthaceae sister to the clade containing the monocots and *Ceratophyllum*, and on trees that had *Amborella* and Nymphaeaceae as a clade sister to the rest of the angiosperms.

We omitted outgroups from our analysis of perianth evolution. Previous morphological analyses that included both extant and fossil seed plants indicated that the angiosperms were part of an anthophyte clade containing the Gnetales, Bennettitales, and *Pentoxylon*. This anthophyte clade was sister to the seed fern *Caytonia* (Donoghue & Doyle, 2000; Doyle, 1996, 1998). Recent analyses (e.g., Bowe et al., 2000; Chaw et al., 2000; P. Soltis et al., 1999b) indicate that gymnosperms are monophyletic, with the Gnetales nested within the conifers or as the sister clade to the conifers. Furthermore, it is difficult to assess the homology of the angiosperm perianth with perianth-like structures in the gymnosperms (e.g., Crane, 1988; Hufford, 1996). Nevertheless, we explored the effect of assuming different plesiomorphic states for the angiosperms on our inferences of perianth evolution.

RESULTS

PHYLOGENETIC ANALYSES

The compartmentalized data set had 14 hypothetical taxonomic units and three additional taxa with aligned sequences of 12,215 bp of sequence data per taxon. Of these sites, 9658 were constant, 1239 were parsimony-uninformative, and 1318 were parsimony-informative. Parsimony analysis of the compartmentalized data resulted in a single most parsimonious tree of 4218 steps (CI = 0.741 and RI = 0.694). The topology obtained from the maximum likelihood analysis of the compartmentalized data set had a –ln likelihood score of 39,743.36269. Both parsimony and maximum likelihood analyses of the compartmentalized data resulted in identical trees that are also entirely consistent with the shortest tree of Qiu et al. (1999), as well as the tree we obtained in our first global analysis. The same early-diverging angiosperms are present in the same order: *Amborella*, Nymphaeaceae, and an Austrobaileyales clade of Austrobaileyaceae/Trimeniaceae/Illiciaceae/Schisandraceae. Bootstrap support for these relationships is 100%.

In recent studies of basal angiosperm phylogeny (e.g., Qiu et al., 1999, 2000; Zanis et al., 2002), bootstrap or jackknife support > 70% has been observed for relationships among the major remaining clades of basal angiosperms (i.e., Piperales, Canellales, Magnoliales, monocots, Laurales, and Chloranthaceae). However, some relationships, such as the sister group of the monocots or the position of the Chloranthaceae, remain uncertain. In the compartmentalized analysis, bootstrap support for relationships among the compartments (clades) is much higher (> 90%) for most nodes than the internal support found in both our global analysis and in the recent corresponding parsimony analyses (Qiu et al., 1999, 2000; Zanis et al., 2002). Canellales and Piperales form a strongly supported (100%) sister group that is, in turn, sister to a well-supported (100%) Laurales/Magnoliales clade. This magnoliid clade is also strongly supported (100%). Ceratophyllaceae are strongly supported (100%) as sister to the monocots. There is also strong support (86%) for the placement of the monocot/Ceratophyllaceae clade as sister to a large clade comprising Chloranthaceae, Canellales, Piperales, Magnoliales, Laurales, and eudicots. The only relationship that remains uncertain is the placement of Chloranthaceae within this clade. Although Chloranthaceae appear as the sister group to the large clade of eudicots and magnoliids (Piperales, Canellales, Laurales, and Magnoliales), this placement receives bootstrap support < 50%.

The complete 26S rDNA sequences have made an important overall contribution to the increase in internal support. For example, in a bootstrap analysis of the compartmentalized data set using parsimony with 26S rDNA sequences removed, support for the Ceratophyllaceae + monocot clade is only 56% (Fig. 2). Phylogenetic analyses of the 26S rDNA data alone (tree not shown) reveal a topology highly similar to, although less resolved than, that obtained for basal angiosperms based on three (D. Soltis et al., 2000; P. Soltis et al., 1999a), five (Qiu et al., 1999, 2000), or more genes (Zanis et al., 2002).

CHARACTER ANALYSES

All perianth characters were mapped onto the synthetic tree described above. Table 2 lists the minimum and maximum number of changes between states for each of the characters examined. Much of the tree is equivocal when examining perianth phyllotaxis as a five-state character (Fig. 3). By combining all the whorled character states (i.e., single whorl, two whorls, and multiple whorls) into a single state, less of the reconstruction is equivocal (Fig. 4). Each node of the Amborellaceae/Nymphaeaceae/Austrobaileyales grade is equivocal with whorled or spiral perianth being equally parsimonious states for the base of the angiosperms. However, the ancestral state for the large clade containing the magnoliid clade, Chloranthaceae, Ceratophyllaceae, monocots, and eudicots is a whorled perianth (Fig. 4). The mapping of number of perianth parts onto our topology indicates that it is equally parsimonious to have an ancestral perianth with parts in threes or indeterminate (Fig. 5). The ancestral condition for the large clade containing the magnoliid clade, Chloranthaceae, Ceratophyllaceae, monocots, and eudicots is a trimerous perianth (Fig. 5).

Mapping of perianth differentiation results in much of the tree being equivocal with multiple most parsimonious scenarios for the evolution of perianth differentiation (Fig. 6). Clearly a differentiated perianth evolved multiple times in the angiosperms. Our analyses indicate that there may have been as few as two to as many as six changes to a differentiated perianth from an undifferentiated perianth (Table 2). Futhermore, some differentiated perianths may have evolved from spirally arranged perianths, whereas other differentiated perianths, such as in *Saruma* (Aristolochiaceae), may have evolved from ancestors that had a perianth composed of a single whorl.

We also conducted analyses to assess the sensitivity of our reconstructions to alternative topologies. Our analysis of perianth phyllotaxis and number of perianth parts is robust (little effect on ancestral reconstructions) to alternative topologies (data not shown). However, the analysis of perianth

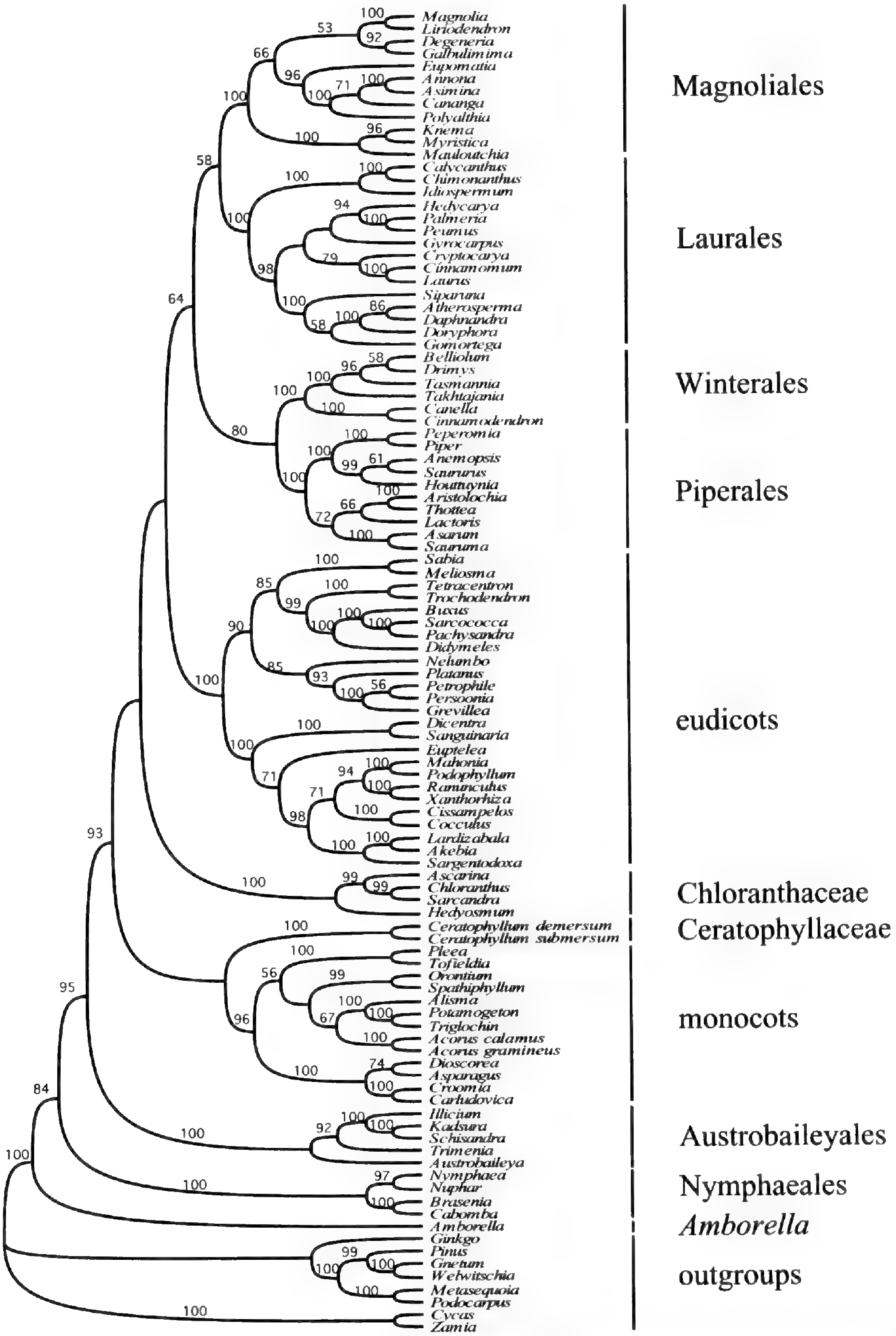

Figure 1. Single most parsimonious tree from global analysis. Numbers above the branches indicate bootstrap values.

differentiation is sensitive to alternative topologies. For example, if Chloranthaceae are sister to the clade containing the monocots and *Ceratophyllum*, then the ancestral state for the clade containing the eudicots, Canellales, Piperales, Magnoliales, and Laurales is reconstructed as having a differentiated perianth (data not shown). In addition to examining the sensitivity of our character analyses to alternative topologies, we examined the effect of coding terminal taxa as monomorphic versus polymorphic.

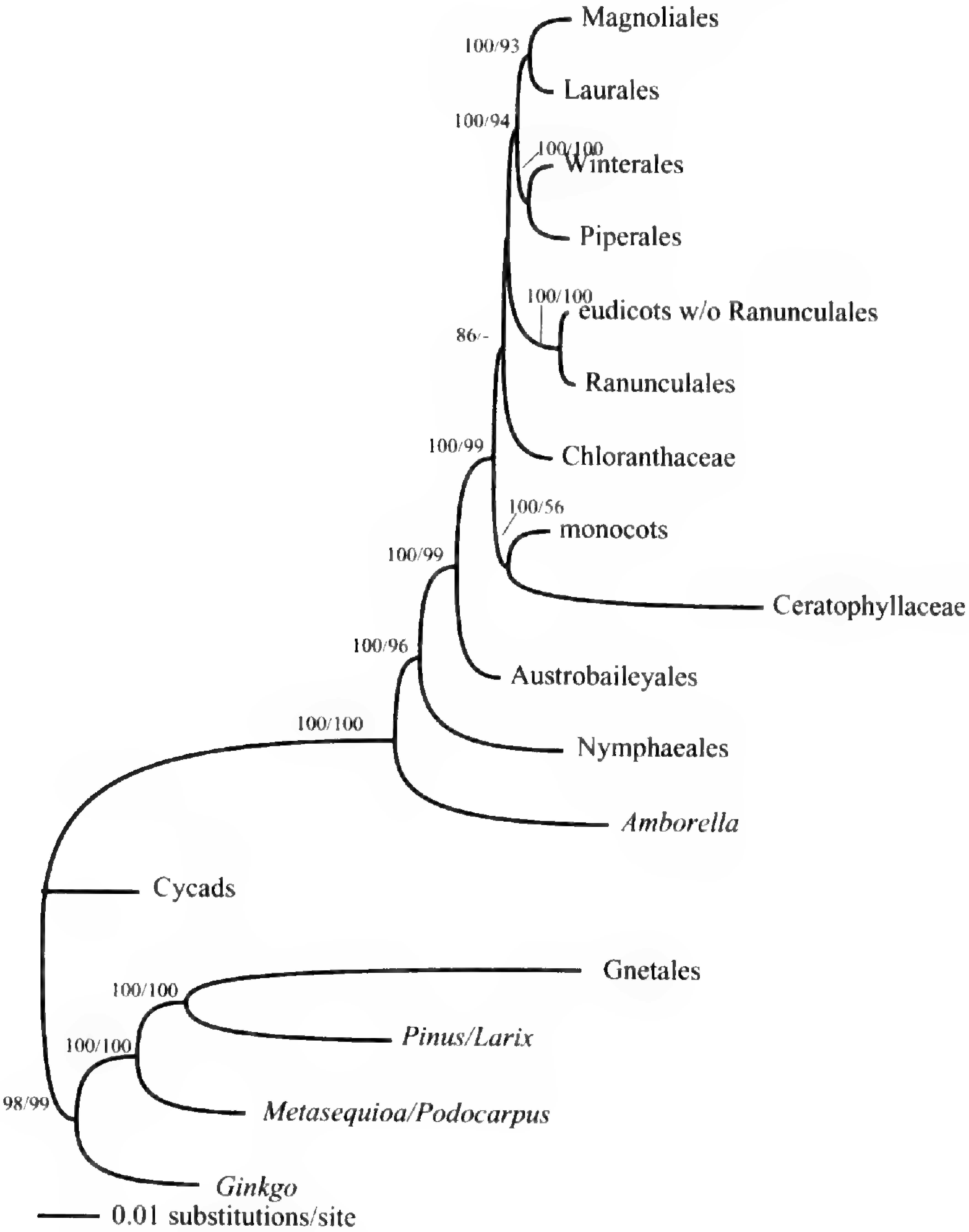

Figure 2. Single most parsimonious tree from compartmentalization analyses. Numbers above branches indicate bootstrap values. First value above branch indicates bootstrap support using six genes; second value indicates bootstrap support obtained from five genes (without 26S rDNA). Branch lengths calculated using the general time-reversible model of molecular evolution accounting for invariant sites and rate heterogeneity.

The results indicate that our analyses are not affected by changes from polymorphic to a fixed character state. Lastly, assuming different plesiomorphic states for the angiosperms does affect our inference of ancestral character-state reconstruction. Thus, if we assume that the trimerous perianth is the plesiomorphic state for the angiosperms, then the trimerous perianth maps as the ancestral state for the deepest nodes of the tree. However, assuming that the plesiomorphic state was a perianth with an indeterminate number of parts does not differ from what is shown in Figure 4. If we assume that lacking a perianth is the plesiomorphic state for the angiosperms, we then find that there have been multiple origins of both a differentiated and undifferentiated perianth. Assuming other plesiomorphic character states for perianth differentiation had little impact on our inferences of perianth evolution.

DISCUSSION

COMPARTMENTALIZATION

The compartmentalization approach allowed us to reduce the number of taxa from 105 in the Qiu et al. (1999) data set to 14 hypothetical (ancestral) taxonomic units and three operational taxonomic units so that we could employ both a more thorough parsimony analysis and the maximum likelihood method. The topology that resulted from the compartmentalized analysis is entirely consistent with respect to the phylogenetic placement of basal angiosperms with the trees obtained in both our initial global analysis and the five-gene analysis of Qiu et al. (1999) (Fig. 1). Identical topologies were obtained using the entire data set of Qiu et al. (1999) or the hypothetical ancestral sequences using both maximum likelihood and maximum parsimony

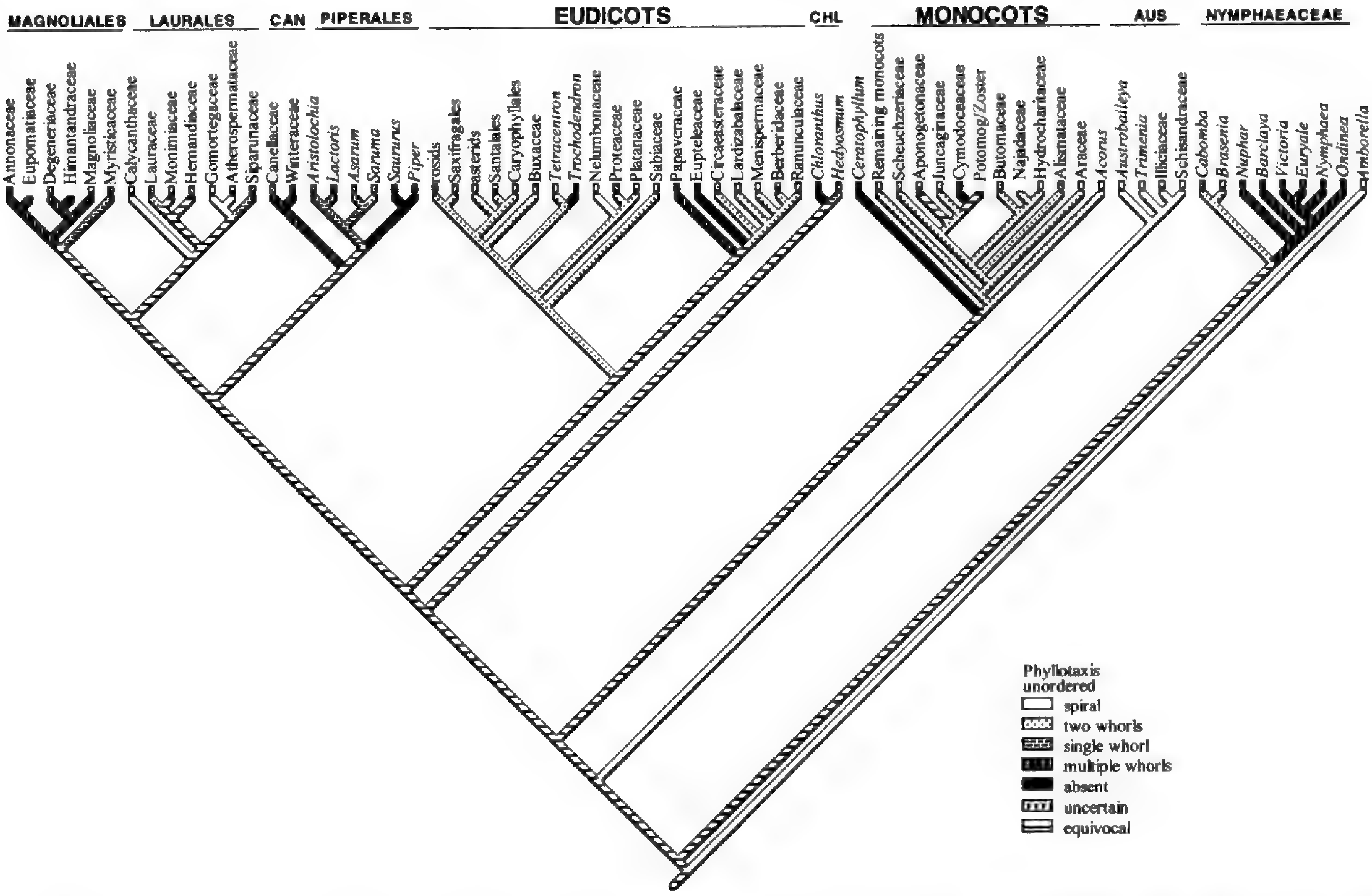

Figure 3. Synthetic cladogram showing parsimony reconstruction of perianth phyllotaxis using MacClade 3.03. Five character states are employed with the whorled phyllotaxis state divided into three separate character states: two whorls, single whorl, and multiple whorls. Potomog/Zoster = Potomogetonaceae/Zosteraceae; CAN = Canellales; CHL = Chloranthaceae; AUS = Austrobaileyales.

methods on the final compartmentalized data set (Fig. 2). Nevertheless, further work is needed to understand the limits and biases associated with compartmentalization analyses.

Phylogenetic analyses of the 26S rDNA sequence data alone yielded topologies with the same early-branching angiosperms, as well as the same major clades of basal angiosperms (i.e., Piperales, Chloranthales, Magnoliales, Laurales, Canellales, monocots) observed in analyses of three-gene (D. Soltis et al., 2000; P. Soltis et al., 1999a), five-gene (Qiu et al., 1999), and larger (Zanis et al., 2002) data sets. The addition of 26S rDNA sequences to the five-gene data set played an important role, increasing bootstrap support for relationships. For example, the addition of 26S rDNA sequences provided high bootstrap support for the placement of the monocots among the basal angiosperm lineages and the placement of *Ceratophyllum* as the sister group to the monocots (Fig. 2). However, compartmentalization of the three-gene data set (D. Soltis et al., 2000; P. Soltis et al., 1999a) did not lead to greater resolution or support among basal angiosperms (P. Soltis et al., 2000). Thus, it is not the analytical approach alone that accounts for the improvement in resolution and support, but the use of additional data.

Our six-gene topology reveals the same order of early-branching angiosperms observed in other recent studies (Mathews & Donoghue, 1999; Parkinson et al., 1999; Qiu et al., 1999, 2000; D. Soltis et al., 2000; P. Soltis et al., 1999a; Zanis et al., 2002): Amborellaceae, followed by Nymphaeaceae, and the Austrobaileyales clade (Austrobaileyaceae/Trimeniaceae/Illiciaceae/Schisandraceae).

We found high levels of bootstrap support (> 90%) in the compartmentalized analysis for all nodes, except the node supporting Chloranthaceae as sister group to the clade of Magnoliales, Laurales, Canellales, Piperales, Aristolochiales, and eudicots. Our analyses show strong support for the sister relationship of Canellales and Piperales (100%); Laurales are sister to Magnoliales (100%); Laurales/Magnoliales and Canellales/Piperales also form a well-supported magnoliid clade (100%); Ceratophyllaceae are sister to the monocots (100%).

The increase in bootstrap support between the initial global analysis (as well as the broad analysis of Qiu et al., 1999) and the compartmentalized

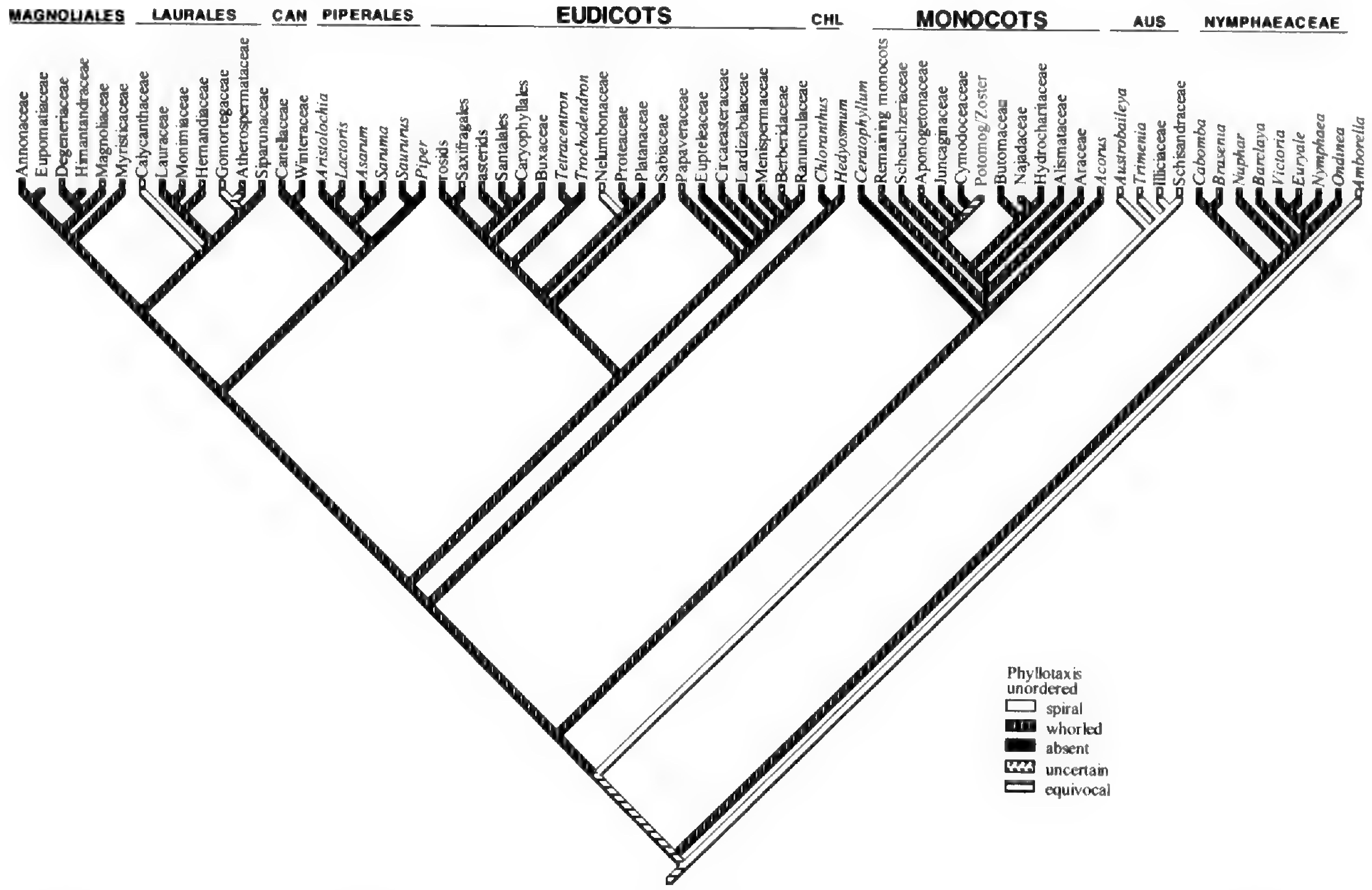

Figure 4. Synthetic cladogram showing parsimony reconstruction of perianth phyllotaxis using MacClade 3.03. Three character states are employed (spiral, whorled, absent), with two whorls, single whorl, and multiple whorl character states (from Fig. 3) combined into a single character state—whorled. Potomog/Zoster = Potomogetonaceae/Zosteraceae; CAN = Canellales; CHL = Chloranthaceae; AUS = Austrobaileyales.

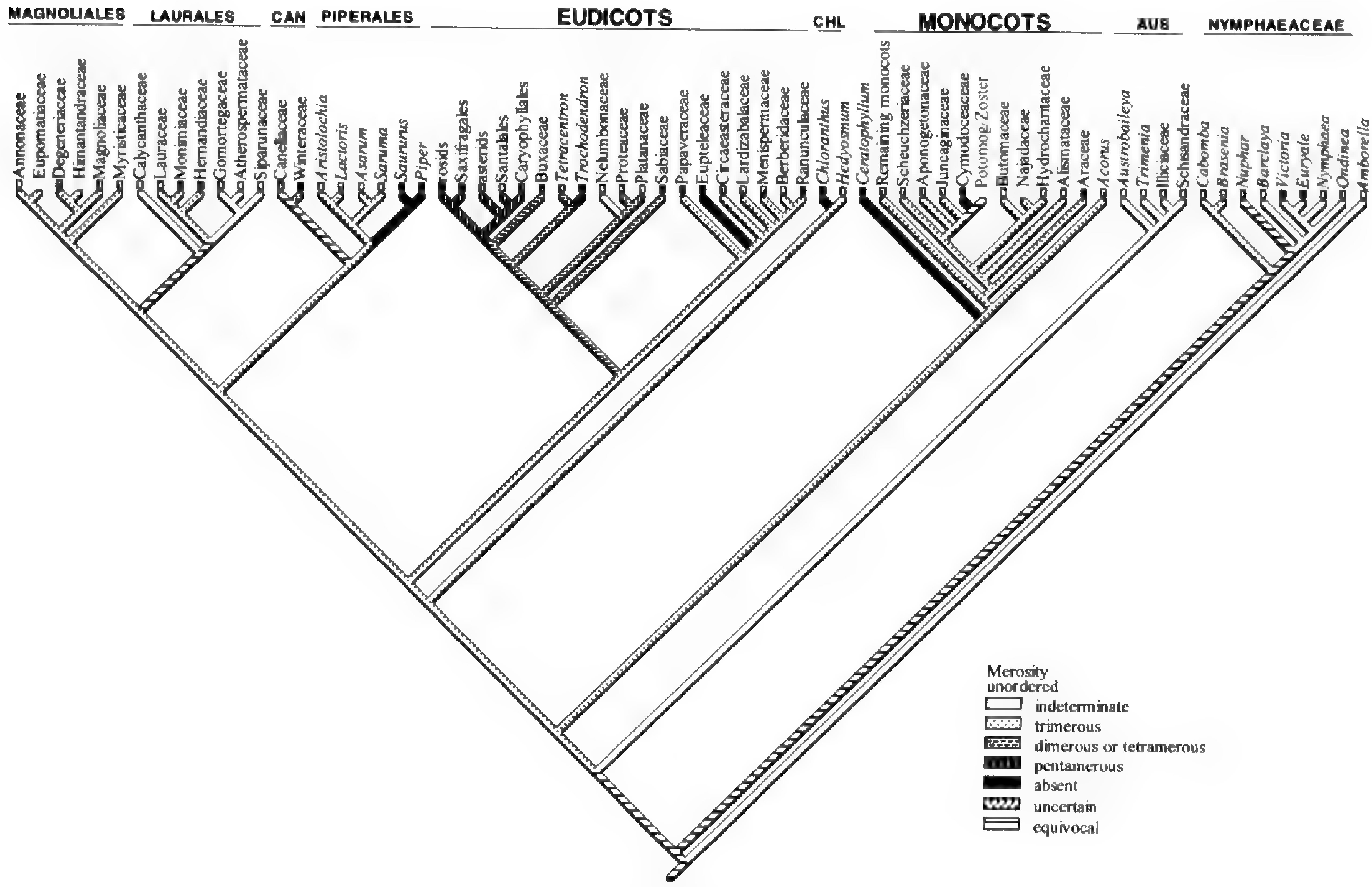

Figure 5. Synthetic cladogram showing parsimony reconstruction of perianth merosity using MacClade 3.03. Potomog/Zoster = Potomogetonaceae/Zosteraceae; CAN = Canellales; CHL = Chloranthaceae; AUS = Austrobaileyales.

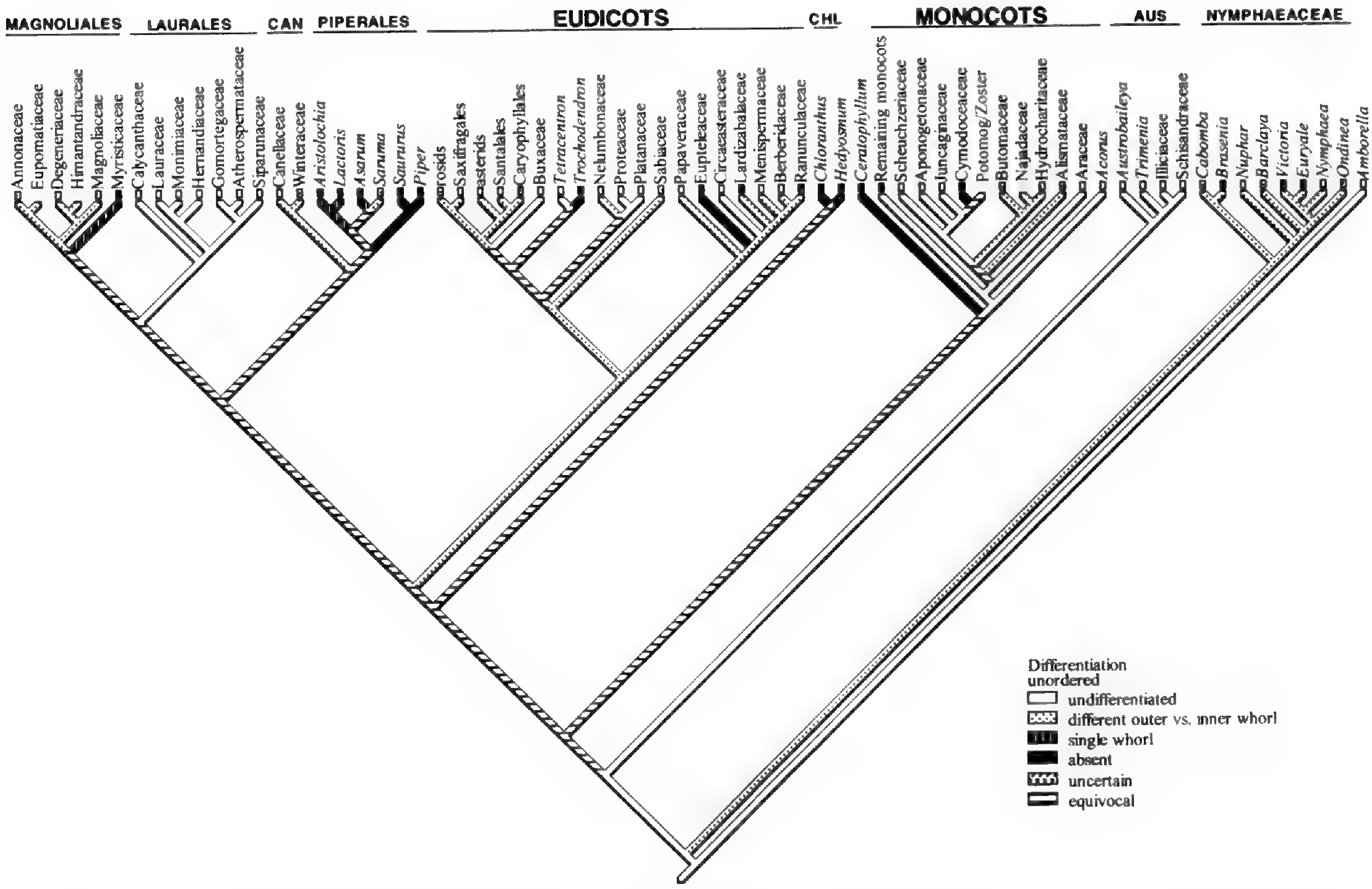

Figure 6. A synthetic cladogram showing parsimony reconstruction of perianth differentiation using MacClade 3.03. Potomog/Zoster = Potomogetonaceae/Zosteraceae; CAN = Canellales; CHL = Chloranthaceae; AUS = Austrobaileyales.

analysis is most likely due to both the minimization of homoplasy as a result of the construction of the hypothetical ancestral sequences (Mishler, 1994) and, as noted, the addition of 26S rDNA sequences. However, some areas of the phylogeny remain poorly resolved and supported despite the use of data for six genes and approximately 12,000 base pairs of sequence data per taxon. For example, the node supporting the placement of the Chloranthaceae is weakly supported in both the Qiu et al. (1999) analysis and our compartmentalized analyses of the six-gene data set. The low bootstrap support for this node is likely the result of short internal branch lengths. For example, the branch leading to the Chloranthaceae and all remaining angiosperms is only 17 steps with ACCTRAN optimization. The uncertainty surrounding the placement of the Chloranthaceae supports Mathews and Donoghue's (1999) suggestion that after the appearance of the Amborellaceae, Nymphaeaceae, and Austrobaileyales lineages, there was a rapid radiation of the remaining basal angiosperm lineages. The hypothesis of a rapid radiation is plausible and consistent with long-standing hypotheses on the origin and divergence of the angiosperms especially given that fossils of Chloranthaceae, Laurales, Magnoliales, and eudicots are all common by the mid Cretaceous (Crane et al., 1995; Friis et al., 1997).

CHARACTER ANALYSES

The origin of the perianth is uncertain, and various hypotheses have been proposed. Weberling (1989) outlined four views regarding the origin of the perianth: (1) the whole perianth is derived from foliage leaves (following Glück, 1919; Prantl, 1887; Velenovsky, 1910); (2) the perianth is derived from sporophyll structures (Celakovsky, 1900; Nemejc, 1956); (3) the calyx is derived from bracts and the corolla is derived from modified stamens (Drude, 1887; Goethe, 1790; Naegeli, 1884); and (4) the calyx is derived from bracts and the corolla has a different origin, neither calyx nor staminal (Weberling, 1989). Features of the perianth that have attracted attention are perianth phyllotaxis (Endress, 1987c), the number of parts (Kubitzki, 1987), differentiation of the perianth (Albert et al., 1998), and, recently, patterns of symmetry in asterids (Donoghue et al., 1998; Ree & Donoghue, 1998). We have examined here the evolution of phyllotaxis, number of parts (merosity), and differentiation, characters that are not necessarily independent.

Table 2. Parsimony based character analyses: The minimum and maximum number of changes between states for each of the perianth characters examined using the chart changes option in MacClade 3.03 (Maddison & Maddison, 1992).

Perianth phyllotaxis: Five states

	To: Spiral	Two whorls	Single whorl	Multiple whorls	Absent
From: Spiral	—	0–3	0–2	0–2	0–1
Two whorls	1–4	—	0–4	0–3	2–5
Single whorl	0–2	1–4	—	0–2	0–3
Multiple whorls	0–1	0–3	0–2	—	0–2
Absent	0–1	0–3	0–3	0–3	—

Perianth phyllotaxis: Two states

	To: Spiral	Whorled	Absent
From: Spiral	—	0–2	0
Whorled	3–5	—	6
Absent	0	0	—

Number of perianth parts

	To: Indeterminate	Threes	Twos	Fives	Fours	Absent
From: Indeterminate	—	0–4	0	0–1	0	0
Threes	1–5	—	0–1	0	1–2	5
Twos	0	0	—	1	0	1
Fives	0	0	0	—	0	0
Fours	1	0	1	0	—	0
Absent	0	0	0	0	0	—

Perianth differentiation

	To: Undifferentiated	Differentiated	Single whorl	Absent
From: Undifferentiated	—	2–6	0–1	2–4
Differentiated	2–6	—	0–4	1–4
Single whorl	0–1	0–4	—	0–2
Absent	0–2	0–2	0–2	—

For example, Kubitzki (1987) discussed the origin of the trimerous perianth from a spiral (indeterminate) ancestor. Thus, merosity and phyllotaxis are sometimes intertwined. Moreover, perianth differentiation is dependent on having more than a single-whorled perianth (Albert et al., 1998).

Our analysis indicates that when perianth phyllotaxis is considered a five-state character (spiral, two whorls, single whorl, multiple whorls, absent), ancestral reconstruction is ambiguous for many of the internal branches (Fig. 3). However, the analysis of perianth phyllotaxis as a three-state character (absent, spiral, whorled) indicates that while the ancestral state for the angiosperms is ambiguous, the ancestral state for the large clade containing the magnoliid clade, Chloranthaceae, Ceratophyllaceae, monocots, and eudicots is a perianth based on a whorled ground plan (Fig. 4). However, we have treated perianth phyllotaxis as a discrete character rather than a continuous character (Stevens, 1991), and interpretation of our results should reflect this treatment. For example, the transition from a spiral to a whorled arrangement brings floral parts closer together through the gradual shortening of the floral axis (Takhtajan, 1980).

Perianth merosity has been of particular interest with regard to the origin of the trimerous flower (Kubitzki, 1987). Our analysis of perianth merosity indicates that the ancestral condition for the angiosperms is equivocal. However, the ancestral character state for the large clade containing the magnoliid clade, Chloranthaceae, Ceratophyllaceae, monocots, and eudicots is a trimerous perianth (Fig. 5). There may have been as many as four origins of the trimerous perianth from a perianth with an indeterminate number of parts, based on our topology (Fig. 5). Also, the indeterminate perianth may have originated as few as two or as many as five times (Fig. 5). Kubitzki (1987) suggested that the amount of morphological change required in the transition from a spiral (indeterminate) perianth to a trimerous perianth could be small; moreover, he suggested that the trimerous condition is a morphological constraint and that the return from a trimerous perianth to a spiral (indeterminate) perianth or pentamerous perianth is not possible. Significantly, however, our analysis of perianth merosity indicates that there have been from one to five transitions from trimery to an indeterminate perianth (Fig. 5 and Table 2). Some of the changes from a trimerous perianth to an indeterminate perianth occur in Laurales. For example, the perianth of Calycanthaceae, which has an indeterminate number of parts, may have evolved from an ancestor with a trimerous perianth. However, Laurales are unique among basal angiosperms due to the presence of a hypanthium, which may affect the development and arrangement of the perianth.

Perianth differentiation has long been studied (Eames, 1931; Hiepko, 1965; Kosuge, 1994). Recent investigations of the evolution of perianth differentiation have come from both phylogenetic and developmental genetic perspectives (Albert et al., 1998; Kramer & Irish, 1999, 2000). Differentiated perianths have been proposed to have evolved multiple times from different structures in different groups (Hiepko, 1965; Kosuge, 1994; Takhtajan, 1991). Our analysis of perianth differentiation indicates that there may have been as few as two to as many as six changes to a differentiated perianth from an undifferentiated perianth (Fig. 6) (Table 2). Thus, our results agree with earlier interpretations that a differentiated perianth (Hiepko, 1965; Kosuge, 1994; Takhtajan, 1991) evolved multiple times. Some differentiated perianths may be those in which the calyx is derived from bracts and the corolla derived from modified stamens, a corolla composed of "andropetals" (Kozo-Poljanski, 1922; Takhtajan, 1980). Other differentiated perianths may have a corolla that is derived from modified bracts, referred to as "bracteopetals" (Kozo-Poljanski, 1922; Takhtajan, 1980). The ontogeny of petals and sepals (Kosuge, 1994) and the number of vascular traces (Carlquist, 1969; Melville, 1969; Puri, 1951; Smith, 1928) have been used as criteria for deciding if petals are staminal in origin or sepal/bract in origin. Thus, the differentiated perianth found in Nymphaeaceae, Ranunculales, and Caryophyllales is considered to be staminal in origin, whereas the petals of Magnoliales and Austrobaileyales are considered to be bract in origin (Takhtajan, 1980). These are just two of several scenarios for organ differentiation.

CONCLUSION

Compartmentalization of a six-gene data set yielded trees congruent with many recent phylogenetic analyses (Graham & Olmstead, 2000; Mathews & Donoghue, 1999, 2000; Qiu et al., 1999, 2000; D. Soltis et al., 2000; P. Soltis et al., 1999a; Zanis et al., 2002). We also observed high levels of bootstrap support for most of the nodes in the compartmentalized tree; the values we obtained were higher than those in any previous study. However, these values should be interpreted cautiously as the potential biases of compartmentalization analyses are unknown.

The ancestral states for perianth phyllotaxis and merosity are unclear. However, the ancestral state for the large clade containing the magnoliid clade, Chloranthaceae, Ceratophyllaceae, monocots, and eudicots is a whorled perianth, with reversals to spiral phyllotaxis and an indeterminate number of parts in some lineages. These results support the hypothesis of floral lability ("open organization") for basal angiosperms; intricate synorganization occurred with the origin of eudicots (e.g., Albert et al., 1998; Endress, 1987c, 2001). Our analysis of perianth evolution across basal angiosperms indicates that there are multiple most parsimonious reconstructions of perianth phyllotaxis and perianth differentiation. However, the trimerous perianth occurred early in angiosperm evolution. In fact, the ancestral state for the clade containing the magnoliid clade, Chloranthaceae, Ceratophyllaceae, monocots, and eudicots is trimery. Much of our mapping of perianth differentiation is equivocal for the deepest nodes of the tree, although a differentiated perianth has clearly originated multiple times. Some differentiated perianths may have evolved from spirally arranged perianths, whereas other differentiated perianths, such as that of *Saruma* (Aristolochiaceae), may have evolved from ancestors that had a perianth composed of a single whorl.

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APPENDIX 1. DESCRIPTIONS AND REFERENCES FOR PERIANTH CHARACTERS USED IN THIS STUDY.

Outgroup. With the exception of *Gnetum*, none of the extant gymnosperms has a perianth. The extinct Bennettitales have a perianth. However, Crane (1985) suggested that the perianth found in the Bennettitales is not homologous to the angiosperm perianth. Moreover, phylogenetic analyses suggest that neither Bennettitales nor *Gnetum* is sister to the angiosperms (e.g., Doyle, 1996, 1998). Thus, we have scored the perianth in the outgroup as absent.

Amborellaceae. Bailey and Swamy (1948) described the male and female flowers in detail, noting that the perianth is not differentiated into calyx and corolla, but instead composed of tepals. The perianth is arranged in a cyclic or spiral arrangement, and the number of tepals ranges from six to eight in the female flower. This work was further corroborated by recent work done by Endress and Igersheim (2000) which shows a spirally arranged undifferentiated perianth; the number of tepals ranges from 9 to 11 in male flowers and is 7 or 8 in female flowers.

Aristolochiaceae. All genera of Aristolochiaceae have a trimerous perianth that consists of a single whorl, with the exception of *Saruma*, which has two whorls that are differentiated (Huber, 1993; Leins & Erbar, 1985). In some species of *Asarum*, petals apparently begin to develop, but the only traces are small, threadlike structures (Leins & Erbar, 1985). González and Stevenson (2000) demonstrated that the uniseriate perianth in *Aristolochia* is derived from the outer whorl of a biseriate perianth.

Austrobaileyales. Austrobaileyales are composed of Austrobaileyaceae, Trimeniaceae, Schisandraceae, and Illiciaceae (APG II, 2003). These families have all been scored as having an undifferentiated, spirally arranged perianth with an indeterminate number of parts (Endress, 1983; Endress & Sampson, 1983; Robertson & Tucker, 1979).

Buxaceae. Buxaceae have unisexual flowers. The staminate flowers have a perianth consisting of two or three whorls of dimerous tepals (Drinnan et al., 1994). The pistillate flowers typically have a spirally arranged perianth with 6 to 20 tepals (Drinnan et al., 1994). However, Drinnan et al. (1994) noted that the tepals in the pistillate flowers are similar to the tepals of the staminate flowers and are basically bracts with a morphology identical to the bracts of the inflorescence. The flower of Buxaceae is described as dimerous and cyclic (e.g., Drinnan et al., 1994; von Balthazar & Endress, 2002). We coded the perianth of Buxaceae as being undifferentiated and dimerous, with the number of whorls being polymorphic (two or three whorls).

Canellaceae. Canellaceae have a differentiated, whorled perianth; the number of whorls varies from two to multiple. The perianth is composed of three fleshy sepals; the number of petals ranges from 4 to 12, with each whorl being either trimerous, tetramerous, or pentamerous (Wilson, 1966). We coded the perianth as differentiated and polymorphic for the number of whorls and the number of parts.

Ceratophyllaceae. *Ceratophyllum* has a whorl of scales that subtend the reproductive organs, and these scales have been variously interpreted as a perianth or bracts (Aboy, 1936; Endress, 1994b; Les, 1988). Some reports suggest the presence of additional flowers between these scales, indicating that the scales may best be interpreted as bracts (Aboy, 1936). In our analysis we coded Ceratophyllaceae as lacking a perianth, following Aboy (1936) and Les et al. (1993).

Chloranthaceae. Within the Chloranthaceae only the female flowers of *Hedyosmum* have a structure regarded as a perianth (Endress, 1987a). Thus, we scored *Chloranthus* as lacking a perianth and *Hedyosmum* as having a single, trimerous, whorled perianth.

Lactoridaceae. Lactoridaceae have a single-whorled, trimerous perianth.

Laurales. Laurales consist of seven families: Atherospermataceae, Calycanthaceae, Gomortegaceae, Hernandiaceae, Lauraceae, Monimiaceae, and Siparunaceae. The perianth is complex within this clade. Also, many members of this group have a hypanthium. Atherospermataceae have an indeterminate number of undifferentiated perianth parts that are spiral or whorled. Calycanthaceae have an undifferentiated perianth that is spirally arranged; the number of parts is indeterminate (Dengler, 1972). Gomortegaceae have a spiral, undifferentiated perianth with an indeterminate number of parts (Brizicky, 1959). Hernandiaceae have a perianth with one or two whorls of three to five undifferentiated parts (Kubitzki et al., 1993). Lauraceae have an undifferentiated perianth of two whorls, each whorl consisting of three parts. Monimiaceae have a complex perianth, with some members having a well-developed perianth and others having an enlarged receptacle and diminutive perianth. The perianth in all Monimiaceae is undifferentiated and varies in number of parts; some taxa have a spiral perianth (e.g., *Hortonia*, Endress, 1980; however, see Doyle & Endress, 2000) and others have a whorled perianth. Siparunaceae have a perianth of a single whorl and a variable number of parts (Doyle & Endress, 2000).

Magnoliales. Magnoliales are composed of six families: Annonaceae, Degeneriaceae, Eupomatiaceae, Himantandraceae, Magnoliaceae, and Myristicaceae. Annonaceae have a trimerous, whorled, differentiated perianth (following Doyle & Endress, 2000; Doyle & Le Thomas, 1996). Degeneriaceae have a differentiated, trimerous, spirally arranged perianth (Swamy, 1949). Eupomatiaceae have a calyptra; however, it is uncertain if this structure is sepal or bract in origin (Endress, 1977); thus, we coded it as "?". Himantandraceae have two sepal-like structures that surround the bud; however, it is uncertain if these structures are perianth or bracts (Endress, 1977). Thus, we coded Himantandraceae as "?". Some Magnoliaceae have a perianth with numerous parts (apparently indeterminate; e.g., *Magnolia*), but in *Liriodendron* and certain species of *Magnolia*, the perianth is in three trimerous whorls (Erbar & Leins, 1981, 1983; Tucker, 1960). Myristicaceae have a perianth of a single, trimerous, whorl (Armstrong & Tucker, 1986; Armstrong & Wilson, 1978).

Monocots. Monocots have members that lack a perianth and other taxa that have either a differentiated or an undifferentiated perianth. In nearly all taxa that have a perianth, the perianth is whorled and trimerous; only a few taxa have a pentamerous perianth (Chase et al., 1995;

Dahlgren et al., 1985). We have used the basal lineages of the monocots as placeholders for our analyses.

Nelumbonaceae. Nelumbonaceae have been considered to have a spirally arranged perianth with two (to five) sepals and 10–30 petals (Hayes et al., 2000).

Nymphaeaceae. Nymphaeaceae are composed of two clades, sometimes treated as the distinct families Cabombaceae and Nymphaeaceae s. str. (APG II, 2002; Les et al., 1999). Les et al. (1999) considered the two families to constitute Nymphaeales. Cabombaceae have either a differentiated (Endress, 2001; Les et al., 1999; Moseley et al., 1984) or undifferentiated (Doyle & Endress, 2000) perianth; the phyllotaxis is considered to be whorled. Within Nymphaeaceae, perianth phyllotaxis has been regarded alternatively as spiral (Albert et al., 1998; E. Schneider, pers. comm.) or whorled (Doyle & Endress, 2000; Endress, 2001; Moseley, 1961, 1972). *Nuphar* and *Barclaya* each has a differentiated perianth, whereas in *Nymphaea* and *Victoria* the differentiation is gradual. The number of petals and sepals varies throughout the family and even within genera. *Nuphar* is considered to have a perianth with five, six, or nine sepals (Padgett et al., 1999). Those *Nuphar* species with six and nine sepals may be based on a trimerous ground plan; the number of petals ranges from 10 to 25. *Barclaya* has 8 to 20 sepals, and 8 to 14 petals, *Ondinea* has four sepals, and four or five petals, and *Nymphaea*, *Victoria*, and *Euryale* have four sepals, with the number of petals ranging from 8 to 40 in *Nymphaea* and from 50 to 70 in *Victoria*. Cabombaceae are scored as having a trimerous, whorled perianth, and are scored as polymorphic for perianth differentiation. In Nymphaeaceae, each taxon was scored as polymorphic for phyllotaxis and for number of perianth parts (see text for discussion).

Piperaceae. Piperaceae lack a perianth.

Platanaceae. The architecture of the perianth of *Platanus* is uncertain (Drinnan et al., 1994). Cronquist (1981) defined the perianth as composed of three or four poorly developed sepals that alternate with small petals. Hufford and Crane (1989) coded *Platanus* as having an undifferentiated perianth. Doyle and Endress (2000) coded Platanaceae as having a one- or two-whorled, undifferentiated perianth, with the number of parts two, four, or five. Studies of fossilized Platanaceae indicate that the perianth was diverse, with some members having a well-developed undifferentiated perianth and others having staminate flowers composed of a single perianth whorl composed of four tepals (Magallón-Puebla et al., 1997; Magallón et al., 1997, 1999; Manchester, 1986; Pigg & Stockey, 1991). We coded Platanaceae as having an undifferentiated perianth, polymorphic for number of whorls (one or two whorls), and polymorphic for the number of parts (trimerous, pentamerous, dimerous/tetramerous).

Proteaceae. The perianth in Proteaceae consists of four petaloid tepals (Douglas & Tucker, 1996a, 1996b), sometimes referred to as sepals, and two to four scales, sometimes referred to as petals (Takhtajan, 1997). We coded Proteaceae as polymorphic for the number of whorls (a single whorl of tepals, or as having two whorls of two tepals). We coded the perianth as undifferentiated; we also considered the option of coding perianth differentiation as uncertain. The merosity of Proteaceae has been interpreted as either dimerous or tetramerous (Douglas & Tucker, 1996a, 1996b). These different codings have no impact on our conclusions (see also D. Soltis et al., 2003). The family is coded as tetramerous in Figure 5.

Ranunculales. We used seven families of Ranunculales in our analysis. The perianth is complex within this group in terms of merosity, phyllotaxis, and differentiation (Drinnan et al., 1994; Kosuge, 1994). In Papaveraceae, the perianth contains one dimerous whorl of sepals and two dimerous petal whorls (Hoot et al., 1997). Trimerous flowers are found in some genera of Papaveraceae, and some genera contain species in which both dimerous and trimerous perianths are present (Hoot et al., 1997). Moreover, some taxa in Papaveraceae lack petals (Hoot et al., 1997). Eupteleaceae lack a perianth, although the lower flowers in the inflorescence may have two small prophylls (Endress, 1986). Circaeasteraceae have flowers in which there is no clear differentiation of the perianth, and the perianth varies from dimerous to trimerous (Foster, 1963). Lardizabalaceae have flowers with a two-whorled, undifferentiated, trimerous perianth (Drinnan et al., 1994). Menispermaceae have a whorled, differentiated, trimerous perianth (Kessler, 1993). Berberidaceae usually have a two-whorled perianth that is undifferentiated and either trimerous or dimerous (Meacham, 1980). Ranunculaceae exhibit extremely variable perianths (Kosuge, 1994). Petals appear to have evolved multiple times within this family, and petals/nectaries are usually interpreted as derived from stamens (Erbar et al., 1999; Kosuge, 1994). Sepals range from five to eight and when petals are present they range from five to seven. We coded many families of the order as polymorphic for all three characters.

Rosids, asterids, Santalales, and Caryophyllales. For each of these groups, we followed the character coding of Nandi et al. (1998). Thus, we coded the perianth of the rosids and asterids as two whorled, pentamerous, and differentiated. Santalales and Caryophyllales are coded as either being composed of a single whorl or two whorls, and differentiated or single-whorled. Caryophyllales are coded as having a perianth that is pentamerous. Santalales are coded as having a perianth that is trimerous, pentamerous, or tetramerous.

Sabiaceae. Sabiaceae have a two-whorled perianth that is composed of three to five sepals and four or five petals (Drinnan et al., 1994). Van Beusekom (1971) suggested that the flowers of Sabiaceae are pentamerous and that trimery has arisen through a series of reductions.

Saxifragales. Saxifragales are a small, early-diverging group of eudicots (Fishbein et al., 2001). The perianth morphologies in this group vary, and we coded the group polymorphic for each of the perianth characters analyzed here. Perianth merosity is coded as absent, indeterminate, tetramerous, and pentamerous. Perianth differentiation is coded as absent, differentiated, and undifferentiated. Phyllotaxis is coded as absent or in two whorls.

Saururaceae. The family comprise five genera and only seven species. The flowers are perfect and without a perianth.

Trochodendraceae. Trochodendraceae comprise two genera, *Trochodendron* and *Tetracentron*. The perianth of *Tetracentron* has two whorls, each composed of two tepals. *Trochodendron* is usually considered to lack a perianth; however, Endress (1986) noted several small scales that may be interpreted as a perianth, between prophylls and stamens on lateral flowers. We coded *Tetracentron* as having two whorls of undifferentiated, dimerous tepals and *Trochodendron* as lacking a perianth.

Winteraceae. The phylogeny of Winteraceae indicates that *Takhtajania*, *Tasmannia*, and *Drimys* are successive sisters to the rest of the family (Karol et al., 2000). Patterns of variation in perianth structure and organization in Winteraceae are complex, with some members having a differentiated, whorled, dimerous, perianth and others a perianth with spiral phyllotaxis (Doust, 2000, 2001; Vink, 1970, 1977). *Takhtajania* has a perianth that begins as dimerous, then changes to tetramerous, and eventually becomes pentamerous (Endress et al., 2000). *Tasmannia* has a perianth that has four sepals and four petals in a whorled arrangement. *Drimys* has a perianth that varies in terms of phyllotaxis as well as number of sepals and petals. In fact, phyllotaxis in *Drimys* may vary on the same plant (Doust, 2001). We coded the family as having a differentiated perianth. Because all of the early-branching members of the family have a whorled phyllotaxis, we coded Winteraceae as whorled for phyllotaxis and polymorphic for the number of perianth parts.

MOLECULAR SYSTEMATICS, EVOLUTION, AND POPULATION BIOLOGY IN THE MUSTARD FAMILY (BRASSICACEAE)[1]

Marcus Koch,[2] Ihsan A. Al-Shehbaz,[3] and Klaus Mummenhoff[4]

ABSTRACT

The present review summarizes results from the past decade on the systematics, population genetics, and evolutionary biology of the mustard family, Brassicaceae (Cruciferae). The research of various authors is discussed and presented in the context of ongoing and accumulating studies. The review is useful in view of the immensely increasing work on *Arabidopsis thaliana,* the model species of plant molecular biology, and on important crop plants such as species of *Brassica.* Traditional and molecular-based phylogenies are critically discussed, new generic alignments are proposed, and groups in need of molecular studies are identified. Unfortunately, knowledge obtained from molecular genetics and development of *A. thaliana* is only very slowly creeping into the systematics of Brassicaceae. Future directions of research should move beyond assessing generic relationships or limits, and should also address character development and evolution, the molecular basis of various homoplastic characters, the nature of the genome, and many other new challenges that are emerging from detailed molecular studies of *A. thaliana.*

Key words: *Arabidopsis,* Brassicaceae, Cruciferae, evolution, literature review, molecular systematics, polyploidy, population biology, speciation.

The Brassicaceae are an important family for three primary reasons. First, the family includes several crop plants grown worldwide, some of which have been cultivated since prehistoric times. Various species are grown for oil, mustard condiments, forage and fodder for animals, or as vegetables (Crisp, 1976; Simmonds, 1986). The most important members belong to the genus *Brassica* L., including varieties of *B. oleracea* L. (broccoli, brussels sprouts, cabbage, cauliflower, kale, kohlrabi, savoy), *B. juncea* (L.) Czern. (Indian mustard), *B. nigra* (L.) W. D. J. Koch (black mustard), *B. napus* L. var. *napobrassica* (L.) Rchb. (rutabaga), *B. napus* var. *napus* (rape), and *B. rapa* L. (summer turnip rape, Chinese mustard, Chinese cabbage). Other locally important crops are *Lepidium sativum* L. (cress), *L. meyenii* Walp. (maca), *Armoracia rusticana* P. Gaertn., B. Mey. & Scherb. (horseradish), *Raphanus sativus* L. (radish), *Sinapis alba* L. and *B. juncea* (both used in the manufacture of table mustard), *Nasturtium officinale* R. Br. (watercress), *Cochlearia officinalis* L. and *Cardamine amara* L. (bittercress), *Eruca vesicaria* (L.) Cavan. var. *sativa* (Mill.) Thell. (rucola or erugula), and *Eutrema wasabi* (Siebold) Maxim. (wasabi). Second, many species of the genera *Aethionema* R. Br., *Alyssum* L., *Arabis* L., *Aubrieta* Adans., *Draba* L., *Erysimum* L., *Hesperis* L., *Iberis* L., *Lobularia* Desv., *Lunaria* L., and *Matthiola* R. Br. are cultivated as ornamentals (Al-Shehbaz, 1984). Third, *Arabidopsis thaliana* (L.) Heynh. (thale cress) is considered to be the most important flowering plant for conducting experimental work in various fields of biology, including plant genetics, physiology, development, pathology, genetic engineering, and related fields. In recent years, *A. thaliana* has become a model system for plant molecular biology, which has culminated in the recent publication of its complete genomic sequence (The Arabidopsis Genome Initiative, 2000), also available via the World Wide Web (⟨http://www.nature.com/genomics/papers/a_thaliana.html⟩). *Arabidopsis thaliana* has a small genome, is fast growing, easy to cultivate with minimal space and care demands, and self-pollinating

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with a high fecundity (Meyerowitz, 1989; Patrusky, 1991). Moreover, genetic modifications by transformation are routinely accomplished to generate mutants or to over-express particular genes. Stock centers distribute seeds of different accessions and mutants, mapping populations, DNA libraries, YACs (yeast artificial chromosomes), and BACs (bacterial artificial chromosomes) for molecular analysis in genetics and development. A central question for this research program is how to apply knowledge gained from the model system (i.e., laboratory lines/strains of *A. thaliana*) to wild plant species. A wealth of information on *A. thaliana* is being assembled electronically (⟨http://www.aspb.org/publications/arabidopsis⟩), and it should be consulted by biologists from all fields.

In order to understand the evolutionary processes and interactions of plants with their environment, it is necessary to work with wild species and populations. Representatives of the mustard family show remarkable variability in certain characters. Important variable traits include resistance to insects and fungi, tolerance to heavy metals and salt, apomixis, annual versus perennial life cycles, and morphological characters such as leaf architecture, fruit diversity, development of woody tissue, seed production, and trichome morphology. Therefore, an increasing number of molecular and evolutionary biologists are focusing on the study of the wild relatives of *A. thaliana* (e.g., Pennisi, 2000a, 2000b; Nasrallah et al., 2000).

As traditionally delimited, the Brassicaceae include about 340 genera and some 3350 species distributed worldwide, especially in temperate regions of the Northern Hemisphere (Al-Shehbaz, 1984; Appel & Al-Shehbaz, 2002). The family, which has long been recognized as a natural group, is well defined morphologically and has a fairly uniform flower structure. The flowers are radially symmetrical and consist of four almost always free sepals in two whorls, four free petals (though sometimes lacking), often six, free, tetradynamous stamens (outer 2 shorter than inner 4; though many species of the large genus *Lepidium* L. have four or only two stamens), and a bicarpellate ovary almost always with a false septum (a partition dividing the ovary into two locules). On the other hand, fruits of Brassicaceae exhibit enormous diversity in size, shape, and structure. They are the source of the most important diagnostic characters for the delimitation and identification of taxa at various ranks. The fruits are often dehiscent, 2-valved capsules divided longitudinally by a septum, though in many genera the fruits are indehiscent and/or the septum is totally lacking. Some groups are characterized by angustiseptate fruits (compressed at a right angle to the septum), such as the members of tribe Lepidieae sensu Schulz (1936), while in the majority of the family the fruits are either latiseptate (compressed parallel to the septum) or not flattened (terete or angled in cross section). On the basis of length/width ratio, the fruits have been traditionally divided into silicles (length less than three times width) or siliques (length more than three times width), but such division, though useful for identification, is arbitrary and has limited phylogenetic utility (Al-Shehbaz, 1984; Appel & Al-Shehbaz, 2002). Additional important taxonomic characters include embryologic features (position of cotyledons in relation to radicle), nectar-gland morphology, trichome types, growth forms, chromosome number, and seed-coat anatomy and surface.

Several classification systems were proposed from the early 19th to the mid 20th century, the most notable of which are those of de Candolle (1821), Prantl (1891), Hayek (1911), Schulz (1936), and Janchen (1942). According to these systems, the Brassicaceae can be divided into anywhere from 4 to 19 tribes and 20 to 30 subtribes. Recent molecular studies (e.g., Koch et al., 2001a) suggest that these taxonomic subdivisions mostly do not reflect phylogenetic relationships. Molecular data strongly support a sister relationship between Cleomoideae (Capparaceae) and Brassicaceae (Rodman et al., 1994). On the basis of a little generic sampling, Judd et al. (1994) proposed merging Brassicaceae and Capparaceae in one family, but recent molecular data (J. C. Hall et al., 2002) clearly support the maintenance of Brassicaceae, Capparaceae, and Cleomaceae as three distinct but closely related families.

A better understanding of evolution within Brassicaceae can be achieved only by a comprehensive review of studies ranging from the population level to analyses from the infraspecific level to the entire family. This should take into account data from anatomy, morphology, chorology, cytology, population biology, ecology, and molecular systematics, including results from studies of *A. thaliana*. The present paper summarizes several important aspects of evolution within Brassicaceae and reviews relevant literature from the past decade on molecular marker systems used to reach a better understanding of phylogeny, evolutionary trends, and patterns of variation at the population level and above. The review specifically identifies new challenges in the systematics and phylogeny of Brassicaceae, proposes a few generic alignments and groupings, and determines groups most in need of studies.

1. SPECIATION PROCESSES: POLYPLOIDY AND HYBRIDIZATION

The origin of polyploids and the mechanisms behind the establishment of newly evolved populations and taxa are among the many challenging questions in plant sciences (Ramsey & Schemske, 1998; Thompson & Lumaret, 1992; Petit et al., 1999; Soltis & Soltis, 1993, 1999). Recent studies of the overall genome structure of hybrid and polyploid taxa provide new insights about the dynamic nature of complete genomes. The data obtained in these studies were generated on the basis of artificial hybrids or by comparative mapping (Rieseberg et al., 1999; Rieseberg & Linder, 1999; Lagercrantz, 1998; Kowalski et al., 1994; Axelsson et al., 2000). Comparative genome analysis of some Brassicaceae (Acarkan et al., 2000) has shown that structural rearrangements occurred with a significantly higher frequency in polyploid *Brassica* than in diploid *Arabidopsis thaliana* or *Capsella rubella* Reut. By contrast, Axelsson et al. (2000) have shown that the genome of *B. juncea* remained almost unchanged since the species originated as an allopolyploid hybrid between *B. nigra* and *B. rapa*. Unfortunately, such studies are based only on a few cultivated species of *Brassica* and on *A. thaliana*, and hardly anything is known about other polyploids in the family, especially those with very high chromosome numbers such as *Cardamine diphylla* (Michx.) A. Wood ($2n = 256$), which has the highest known number in Brassicaceae (see Al-Shehbaz, 1984). Polyploidy is widespread in the Brassicaceae, occurring in at least 37% of the species (Appel & Al-Shehbaz, 2002); some genera (e.g., *Crambe* L., *Moricandia* DC., *Vella* L.) appear to be exclusively polyploid (Al-Shehbaz, 1984). If we consider the diploid species of *Brassica* and other genera (e.g., *Physaria* (Nutt. ex Torr. & A. Gray) A. Gray, including *Lesquerella* S. Watson) as "palaeopolyploids" (see below), the percentage of polyploid taxa in the family will be at least 50% (authors' compilation). Allopolyploidy is probably the most common mode of hybrid speciation in the Brassicaceae and accounts for the majority of polyploid species (authors' compilation). However, phylogenetic studies are needed to determine if speciation in polyploids occurred at rates higher than in diploids.

Molecular methods have helped to elucidate the complex evolutionary history of many allopolyploid groups in the family. *Arabidopsis suecica* (Fr.) Norrl. ($n = 13$), an allopolyploid species derived from *A. thaliana* ($n = 5$) and *A. arenosa* (L.) Lawlrée ($n = 8$) (Mummenhoff & Hurka, 1994, 1995; Kamm et al., 1995; O'Kane et al., 1997; Comai et al., 2000), is one of the best studied species of hybrid origin. Other studies include *Brassica* (Palmer et al., 1983; Erickson et al., 1983; Lagercantz & Lydiate, 1996), *Arabis holboellii* Hornem. (Sharbel & Mitchell-Olds, 2001; Koch et al., 2003a), *Capsella* Medik. (Mummenhoff & Hurka, 1990; Hurka & Neuffer, 1997), *Cardamine ×insueta* Urbanska and *C. schulzii* Urbanska (Urbanska et al., 1997; Franzke & Mummenhoff, 1999), *Cardamine ×enriquei* Marhold et al. (Marhold et al., 2002b), *Diplotaxis* DC. (Mummenhoff et al., 1993), *Draba* (Brochmann et al., 1992a, 1992b, 1992c; Widmer & Baltisberger, 1999a), *Nasturtium* R. Br. (Bleeker et al., 1999), and *Rorippa* Scop. (Bleeker & Hurka, 2001). More recently, research focusing on hybridization and polyploidization among cruciferous plants has been attributed additional importance because of the successful crosses between the model organism *Arabidopsis thaliana* and its wild relative *A. lyrata* (L.) O'Kane & Al-Shehbaz subsp. *petraea* (L.) O'Kane & Al-Shehbaz ($n = 8$) (see Nasrallah et al., 2000).

A knowledge of the patterns of speciation and species relationships within a group of plants is critical for the understanding of its morphological evolution. *Lepidium*, which exhibits more floral diversity than any other genus of Brassicaceae, shows that more than half of its species lack the lateral stamens and most of these also have reduced petals. The species with reduced flowers are distributed primarily in the Americas and Australia/New Zealand. Previous phylogenetic studies with noncoding regions of cpDNA and rDNA ITS showed incongruences in most New World species relationships (Bowman et al., 1999; Mummenhoff et al., 2001a). This, combined with the presence of many polyploid species, implied a reticulate history of the genus, but did not provide enough information to infer the evolutionary pattern of flower structures. To address this question more thoroughly, sequences of the first intron of a single copy nuclear gene, *PISTILLATA* (*PI*), were determined from 43 *Lepidium* species. The phylogenetic analysis of the *PI* intron suggests that many species in the New World might have originated from allopolyploidization correlated with floral reduction. Interspecific hybrids were generated to test this hypothesis, and the phenotypes of F_1 flowers indicate allelic dominance of the absence of lateral stamens. This suggests that propagation of dominant alleles through interspecific hybridization could account for the abundance of the allopolyploid species without lateral stamens (Lee et al., 2002).

Hybridization and reticulation have been extensively analyzed at the molecular level on the North American *Arabis* ×*divaricarpa* A. Nels. focusing on concerted evolution of the internal transcribed spacer regions 1 and 2 (Koch et al., 2003b). In this case study it is remarkable that apomixis also played an important role in speciation and differentiation.

Polyploidy also played an important role in the evolution of species complexes, particularly during time periods greatly influenced by glaciation and deglaciation. This holds true for *Arabidopsis suecica* in Scandinavia (Mummenhoff & Hurka, 1994, 1995; O'Kane et al., 1997), the *Cardamine pratensis* complex (Franzke & Hurka, 2000), *Cardamine amara* (Marhold et al., 2002a), and *Cochlearia* L. in Europe (Koch et al., 1996, 1998a; Koch, 2002). Furthermore, diversification of most species of *Draba* (Koch & Al-Shehbaz, 2002; Brochmann et al., 1992a, 1992b) is best interpreted by reticulation and polyploidization during the last few million years. In the absence of significant glacial influence, however, hybridization, reticulation, and polyploidy apparently have played an important role in the evolution of old species complexes in the genera *Yinshania* Ma & Y. Z. Zhao in China (Koch & Al-Shehbaz, 2000) and *Microthlaspi* F. K. Mey. in the Balkans (Koch et al., 1998c; Koch & Hurka, 1999).

We now have the molecular tools to unravel the origin of (alloploid) hybrid taxa. But techniques such as genome mapping and QTL analysis will allow us to study many details of hybridization and speciation (Bradshaw et al., 1995; Rieseberg et al., 1995). It is also important to measure in future studies the relative fitness of hybrids and parental taxa in a range of habitats to further elucidate the role of natural hybridization (Arnold, 1997). Furthermore, to test the evolutionary importance of hybridization in a given species complex, it is critical that findings from greenhouse/population cage experiments be tested in the field (Arnold et al., 2001).

2. POPULATIONAL DIFFERENTIATION, PHENOTYPIC PLASTICITY, AND ADAPTATION

In order to elucidate speciation processes and phylogenetic relationships between species, it is necessary to understand intra-population dynamics and genetics. Numerous phenotypic traits have been analyzed in Brassicaceae, including local adaptation across climatic gradients in *Arabis fecunda* Rollins (McKay et al., 2001) and *Capsella* (Hurka, 1990; Hurka & Neuffer, 1997; Neuffer & Hurka, 1999; Neuffer & Hoffrogge, 1999), survivorship in *Arabis laevigata* (Muhl. ex Willd.) Poir. (Bloom et al., 2001), glucosinolate accumulation during plant/insect interaction in *Arabidopsis thaliana* (Kliebenstein et al., 2001), and herbivore resistance and pollination in *Brassica rapa* (Strauss et al., 1999). *Capsella bursa-pastoris* (L.) Medik. was studied for maternal effects upon germination behavior (Neuffer & Koch, 1996), mechanical stress (Neuffer & Meyer-Walf, 1996), flowering time (Neuffer & Hurka, 1986; Neuffer & Bartelheim, 1989; Neuffer, 1990), and leaf morphology (Neuffer, 1989). Detailed analysis of host-pathogen interaction and their coevolution have been analyzed in Brassicaceae (Constantinescu & Fatehi, 2002), particularly in *Arabis* (Roy, 2001), and studies have focused on phenotypic plasticity, reaction norm, and its evolution in *A. thaliana* (Pigliucci & Byrd, 1998; Pigliucci & Schmitt, 1999; Pigliucci et al., 1999; Pigliucci & Marlow, 2001; Pigliucci, 2002; Pollard et al., 2001). Many of these investigations have also used molecular markers, isozymes, or RAPDs to study intra- and interpopulational differentiation (see Appendix 1, parts II and III).

The majority of these investigations have, however, neglected the genetic diversity stored in the soil seed bank. Depending on the type of seed bank and the reproductive biology of the selected species, the seed bank may play an essential role in the recruitment and establishment of new generations. The spatial genetic structure of the subpopulations (surface and aboveground populations) represented by seeds may account for significant changes in the genetic constitution of plant populations during their history. The soil seed bank not only reduces the rate of genetic erosion (e.g., via genetic drift), but also may compensate environmental changes in space and time. Of the seven known studies focusing on seed-bank genetics (Tonsor et al., 1993; Alvarez-Buylla & Garay, 1994; McCue & Holtsford, 1998; Mahy et al., 1999; Cabin, 1996; Evans et al., 2000; Koch et al., 2003a), the last three were conducted on members of the Brassicaceae.

3. CONVERGENT EVOLUTION OF MORPHOLOGICAL CHARACTERS: MOLECULAR PHYLOGENETIC STUDIES CONTRADICT TRADITIONAL SYSTEMS OF TRIBAL CLASSIFICATION

Traditionally, the Brassicaceae have been divided into tribes and subtribes on the basis of relatively few characters (morphology, embryology). Major disagreements are readily observed by comparison of the systems of Hayek (1911), Schulz (1936), and Janchen (1942). Molecular data demonstrate that morphological variation used traditionally in these three classification systems does not provide phylogenetically informative characters to distinguish several groups (Koch et al., 2001a). The major drawback of all the classification systems proposed thus far is their almost complete failure to accommodate convergence of morphological characters. In fact, molecular studies reveal homoplasy in almost every conceivable morphological character in the Brassicaceae (Price et al., 1994; Zunk et al., 1996; Mummenhoff et al., 1997a; Koch & Mummenhoff, 2001; Mummenhoff et al., 2001a, 2001b). For example, gamosepaly, which is rare in the family, has recently been shown to have evolved independently in at least 12 genera (Al-Shehbaz, 2001). As for fruit morphology and cotyledon position in relation to the radicle, which are extensively used in every facet of taxonomy in the family, convergence is so widespread that extreme care should be taken in classification and delimitation of taxa solely based on these characters. A classic example is demonstrated by the genera *Arabis* and *Arabidopsis* Heynh., both of which are characterized by linear and narrow fruits, branched trichomes, and cotyledons that are primarily accumbent. Recent molecular studies (Koch et al., 1999a, 2000, 2001a; Al-Shehbaz & O'Kane, 2002a; O'Kane & Al-Shehbaz, in prep.) have provided ample evidence that both genera are polyphyletic, and an overemphasis on these homoplastic characters is the main reason for their artificial delimitation. Conversely, taxa that appear to be quite different morphologically may in fact be very closely related. For example, *Draba* exhibits enormous morphological diversity in habit, trichome type, flower color, chromosome number, and fruit morphology, but molecular data clearly support its monophyly (Koch & Al-Shehbaz, 2002). For *Thlaspi* L., molecular data (Mummenhoff & Koch, 1994; Zunk et al., 1996; Mummenhoff et al., 1997a, 1997b; Koch & Mummenhoff, 2001) provide strong support for the recognition of several segregates as proposed by Meyer (1973, 1979) based on seed-coat anatomy. The molecular phylogeny of *Thlaspi* is not congruent with the traditional classification of Schulz (1936) based on fruit form. Several lineages in the molecular tree include *Thlaspi* species with diverse fruit types, whereas species with the same fruit type belong to different clades, thus providing strong evidence for convergence in fruit traits. As for *Lepidium*, the cpDNA sequence phylogeny once again demonstrates the widely artificial nature of the traditional classification schemes, and it shows that fruit morphology (e.g., thickening, compression, and union of valves) is not a reliable phylogenetic marker in this genus (Brüggemann, 2000; Mummenhoff et al., 2001a). Numerous other examples of homoplasy in almost every conceivable morphological character can be demonstrated in *Cochlearia* L. (Koch et al., 1999b; Koch & Al-Shehbaz, 2000), *Arabis* and *Arabidopsis* (Koch et al., 1999a), *Draba* (Koch & Al-Shehbaz, 2002), *Cardamine* L. (including *Dentaria* L.: Franzke et al., 1998; Sweeney & Price, 2000), *Microthlaspi* (Koch & Mummenhoff, 2001), and the halimolobine clade (Bailey et al., 2002).

Some traditionally recognized tribes have been shown to be polyphyletic, including Arabideae and Lepidieae (Koch et al., 1999a, 2000, 2001a) and Sisymbrieae (Koch et al., 2001a; Bailey et al., 2002). Moreover, boundaries between the tribes Lepidieae, Lunarieae, Sisymbrieae, Euclidieae, and Alysseae are highly artificial (Zunk et al., 1993; Price et al., 1994). The tribes Brassiceae, Thelypodieae, and Lepidieae have long been thought to be natural groups (Al-Shehbaz, 1973, 1984; Zunk et al., 1999), but the results of Koch et al. (2001a) strongly suggest that the Lepidieae are polyphyletic. This tribe is based solely on the presence of angustiseptate fruits (Schulz, 1936), a feature that in fact evolved independently within Lepidieae, Brassiceae (e.g., *Psychine* Desf., *Schouwia* DC.), and Thelypodieae (*Caulanthus californicus* (S. Watson) Payson). Moreover, *Capsella, Lepidium,* and *Thlaspi* s.l., which have been placed in Lepidieae in every system of classification of the family, are clearly unrelated, and *Capsella* shows more affinities to *Arabidopsis* than to either *Lepidium* or *Thlaspi* (Koch et al., 2001a; O'Kane & Al-Shehbaz, in prep.).

Monophyly of the Brassiceae is shown in a series of studies summarized in Warwick and Black (1997a, 1997b). Members of this tribe are characterized by having segmented (heteroarthrocarpous) fruits and/or conduplicate cotyledons (Appel & Al-Shehbaz, 2002), and there is strong evidence that reversals in one or both characters have taken place. Segmented fruits and conduplicate cotyledons are among a few characters in the family where convergent evolution apparently has not occurred.

The Heliophileae, a tribe comprising six South African genera that mostly have diplecolobal cotyledons (Appel & Al-Shehbaz, 1997), are also likely monophyletic. Preliminary ITS sequence data (Mummenhoff et al., unpublished) strongly support the monophyly of *Heliophila* L. and related genera. However, the phylogenetic relationships within Heliophileae are unresolved, and the smaller genera *Brachycarpaea* DC., *Cycloptychis* E. Mey. ex Sond., *Schlechteria* Bolus, *Silicularia* Compton, and *Thlas-*

peocarpa C. A. Sm. are all well nested within *Heliophila* and might not be taxonomically distinct from it. The last genus exhibits far more diversity in habit, leaf morphology, flowers, fruits, and seeds than any other genus in Brassicaceae.

Outside of the Brassiceae and Heliophileae, the cotyledonary position is unreliable in tribal delimitation. Within several genera (e.g., *Erysimum*) or even species (e.g., *Lepidium virginicum* L.) one finds both accumbent and incumbent cotyledons, the most common types in the family. In summary, it appears that except for these two tribes, the remainder of the family is not readily divided into large monophyletic groups based solely on single morphological characters. Critical re-examinations of morphology, anatomy, and palynology, in the light of molecular phylogenies, are needed to subdivide the family into monophyletic groups based on character combinations rather than individual characters. Such studies have already identified some monophyletic clades, including the polycolpate, cardaminine, and halimolobine clades (see below).

4. Advances in Molecular Systematics

Critical phylogenetic relationships within the tribe Brassiceae have identified six reasonably well-defined groups corresponding to subtribes. However, traditional taxonomy (e.g., Gómez-Campo, 1999; Gómez-Campo & Prakash, 1999) did not take into consideration the overwhelming molecular data that have accumulated over the past decade, and *Brassica*, *Diplotaxis*, *Erucastrum*, and *Sinapis* continue to be artificially delimited following Schulz (1936). The characters separating these genera (e.g., seeds uniseriate vs. biseriate, valves 1-veined vs. more than 1-veined, racemes bracteate vs. ebracteate) exhibit enormous homoplasy throughout the family, yet they are taken in these genera as reliable characters. According to molecular data (Warwick & Black, 1997b), species of all four genera fall into two monophyletic groups, the nigra and rapa clades, that also include many smaller or monotypic genera. In our opinion, taxa within the rapa and nigra clades need extensive studies to establish monophyletic groups and to redefine generic boundaries based on critical re-evaluation of morphology. Warwick and Black (1997a) also clearly demonstrated that *Cakile* Mill., *Didesmus* Desv., and *Erucaria* Gaertn. form an unresolved clade. *Cakile* is distinguished primarily by having corky (instead of non-corky) fruits and obsolete (vs. distinct) styles. Corky fruits evolved independently in some species of *Crambe* and *Raphanus*, and this feature is unreliable for generic delimitation, as is the style length. Although all three genera were maintained by Appel and Al-Shehbaz (2002), further studies may prove that they are congeneric.

Molecular data (Warwick & Black, 1994; Crespo et al., 2000) provided ample evidence that *Boleum* Desv. and *Euzomodendron* Coss. are nested within *Vella*, which prompted Warwick and Al-Shehbaz (1998) and Appel and Al-Shehbaz (2002) to recognize one genus, *Vella*. Of the entire Brassiceae, these are the only three genera with united inner staminal filaments and a base chromosome number of $x = 17$. However, Gómez-Campo (1999: 19) maintained all three because they “exhibit very distinct sets of adaptive characters . . . for seed dispersal.” These “adaptive characters” (presence of distinct vs. vestigial seed wing, seed number, fruit dehiscence) are also homoplastic elsewhere in the family and, therefore, should not be overemphasized at the expense of the extensive molecular data now available. In fact, fruit indehiscence evolved independently numerous times not only within Brassiceae but in the entire family (Appel & Al-Shehbaz, 2002; Mummenhoff et al., 2001a). Of the 337 genera of Brassicaceae recognized by Appel and Al-Shehbaz (2002), 125 are monotypic and about an additional 100 contain two to four species (oligotypic). Molecular studies show that several of the monotypic genera are indistinguishable from other larger genera. For example, both *Agallis* Phil. and *Twisselmannia* Al-Shehbaz are nested within and should be united with *Tropidocarpum* Hook., whereas *Hugueninia* Rchb. should be united with *Descurainia* Webb & Berthel. (Price & Al-Shehbaz, 2003). Other examples include the union of *Lycocarpus* O. E. Schulz with *Sisymbrium* and *Neobeckia* Greene with *Rorippa* (Price, pers. comm.), *Boleum* and *Euzomodendron* with *Vella* (Warwick & Black, 1994; Crespo et al., 2000), *Iti* Garn.-Jones & P. N. Johnson with *Cardamine* (Mitchell & Heenan, 2002), *Pachyphragma* (DC.) Rchb. and *Gagria* M. Král with *Thlaspi* s. str. (Mummenhoff et al., 2001b), and *Drabopsis* K. Koch with *Draba* (Al-Shehbaz & Koch, in prep.). We believe that upon a combination of molecular studies and critical evaluation of morphology the vast majority of monotypic or oligotypic genera will eventually be merged with other genera.

Molecular data indicate that the largest genera of the family, including *Draba* (350 spp.), *Lepidium* (ca. 220 spp.), *Cardamine* (200 spp.), *Erysimum* (180 spp.), and *Physaria* and *Lesquerella* combined (100 spp.), are monophyletic. Studies are needed to demonstrate monophyly of *Alyssum* (170–190 spp.), including *Meniocus* Desv. and *Ptilotrichum* C.

A. Mey., and *Rorippa* Scop. (75 spp.). *Erysimum* is taxonomically one of the most difficult genera of the family, and it is much in need of extensive phylogenetic studies. Phylogenetic studies on *Sisymbrium* (Warwick et al., 2002) show that the genus is polyphyletic, that it should consist of 43 Old World and 1 New World species, and that the remaining 46 species in the New World belong to other genera allied to the Thelypodieae sensu Al-Shehbaz (1973).

As for *Arabis*, molecular studies (Koch et al., 1999a, 2000; O'Kane & Al-Shehbaz, in prep.; Price, pers. comm.) clearly demonstrate that it is polyphyletic and that most of the species recognized by Rollins (1993) should be assigned to *Boechera* A. Löve & D. Löve, *Turritis* L., *Pennellia* Nieuwl., and *Arabidopsis*, whereas some of the European species (sensu Jones & Akeroyd, 1993) should be assigned to *Fourraea* Greuter & Burdet and *Arabidopsis*. *Arabis* has been traditionally delimited solely by having branched trichomes, flat and linear fruits, and accumbent cotyledons, a combination of characters found in many other genera of Brassicaceae. The entire *Arabis* complex is much in need of further morphological and molecular studies, but all of these segregates do not appear to be closely related to the core of *Arabis* that includes the type species, *A. alpina* L.

Extensive studies on *Lepidium* (Brüggemann, 2000; Mummenhoff, 1995; Mummenhoff & Hurka, 1991; Mummenhoff et al., 1992, 1995, 2001a; Zunk et al., 1999) have clearly demonstrated the genus should include *Cardaria* Desv., *Coronopus* Zinn, and *Stroganowia* Kar. & Kir. and that the last two genera are polyphyletic. Based on such data and on a critical re-evaluation of morphology, Al-Shehbaz et al. (2002) united all three with *Lepidium*. Although *Lepidium* shows more diversity in the reductions of petals and stamens than any other genus in the family (Bowman & Smyth, 1998; Bowman et al., 1999), it is well defined by having angustiseptate (rarely terete or 4-angled) fruits and two subapical ovules one in each locule. Other genera that show this combination of characters (e.g., *Acanthocardamum* Thell., *Delpinophytum* Speg., *Stubendorffia* Schrenk ex Fisch., C. A. Mey. & Avé-Lall., *Winklera* Regel) should also be studied, and it is quite possible that they, too, might be congeneric with *Lepidium*.

The polycolpate clade (Al-Shehbaz & O'Kane, 2002b; O'Kane & Al-Shehbaz, 2002) is a monophyletic New World group readily distinguished from the remaining 96% of Brassicaceae by having 4–10-colpate instead of strictly 3-colpate pollen. The clade comprises *Physaria* (including *Lesquerella*), *Dimorphocarpa* Rollins, *Dithyrea* Harv., *Lyrocarpa* Hook. & Harv., *Nerisyrenia* Greene, *Paysonia* O'Kane & Al-Shehbaz, and *Synthlipsis* A. Gray. Sequence data of this group (O'Kane & Al-Shehbaz, unpublished) in GenBank have recently been taken by Kropf (2002) in his comprehensive ITS tree. The results support the monophyly of the *Physaria* clade and place it between *Arabidopsis* and *Olimarabidopsis* Al-Shehbaz et al.

Although no comprehensive study has been conducted on the cardaminine clade, a compilation of various works (Bleeker et al., 2002a, 2002b; Franzke et al., 1998; Les, 1994; Mitchell & Heenan, 2000; Sweeney & Price, 2000; Price & Sweeney, pers. comm.) shows that it consists of *Cardamine* (including *Dentaria* and *Iti*), *Nasturtium*, *Rorippa* (including *Neobeckia*), *Barbarea* R. Br., *Armoracia*, *Iodanthus* (Torr. & A. Gray) Steud., *Leavenworthia* Torr., *Planodes* Greene, and *Selenia* Nutt. The vast majority of taxa in this clade occupy wet or mesic habitats, are glabrous or rarely have simple trichomes, and have dissected or compound leaves, elongated fruits, and mostly accumbent cotyledons. A few exceptions occur, but this is a well-defined group that perhaps includes the genera *Lignariella* Baehni, *Neomartinella* Pilger, *Ornithocarpa* Rose, *Pegaeophyton* Hayek & Hand.-Mazz., *Raphanorynchа* Rollins, *Subularia* L., *Taphrospermum* C. A. Mey., and *Yinshania*. The analysis of Kropf (2002) appears to be erroneous because it shows *Rorippa* nested within *Cardamine* and *Iti* (New Zealand) forming a sister group with the unrelated *Bivonaea* DC. (Mediterranean) instead of being nested within *Cardamine* (Mitchell & Heenan, 2000).

The halimolobine clade is an exclusively New World group that consists of *Halimolobos* Tausch, *Mancoa* Wedd., *Pennellia* Niewl., *Sphaerocardamum* Schaur, and, yet to be described, a new segregate genus (Bailey et al., 2002). Almost all members of this clade have dendritic trichomes, plump seeds, incumbent cotyledons, entire or dentate leaves, and small white flowers with subtetradynamous stamens. The clade is related to other North American genera with branched trichomes, including *Boechera*, *Cusickiella* Rollins, and *Beringia* Price et al., but some South American species of *Sisymbrium* that have dendritic trichomes, all excluded from the genus (Warwick et al., 2002), should also be tested.

A morphologically well-defined group of primarily central Asian genera (e.g., *Chartoloma* Bunge, *Glastaria* Boiss., *Goldbachia* DC., *Isatis* L., *Litwinowia* Woronow, *Pachypterygium* Bunge, *Pugionium* Gaertn., *Sameraria* Desv., *Schimpera* Hochst.

& Steud., *Spirorhynchus* Kar. & Kir., *Tauscheria* Fisch. ex DC.) has not been studied phylogenetically, and it probably forms a monophyletic clade. All members are characterized by having indehiscent, 1- or 2-seeded, primarily angustiseptate fruits, yellow or rarely whitish flowers, sessile often auriculate cauline leaves, and simple or no trichomes (Appel & Al-Shehbaz, 2002). Only ITS data for *Isatis* are available, and the genus appears to be related to those with angustiseptate fruits and simple or no trichomes (Kropf, 2002).

Based on ITS data (Warwick et al., 2002), most of the New World American genera with simple or no trichomes, as well as *Pringlea* (six islands in the South Indian Ocean), form a large unresolved clade that includes members of the Thelypodieae sensu Al-Shehbaz (1973). This clade encompasses taxa with enormous fruit diversity, and extensive molecular and morphological studies are needed to resolve its generic limits. Among the genera that fall in this clade are most of the South American *Sisymbrium, Dryopetalum* A. Gray, *Hesperidanthus* (B. L. Rob.) Rydb., *Mostacillastrum* O. E. Schulz, *Sibara* Greene, and *Werdermannia* O. E. Schulz. Other genera that should be studied are *Chilocardamum* O. E. Schulz, *Dictyophragmus* O. E. Schulz, *Eremodraba* O. E. Schulz, *Neuontobotrys* O. E. Schulz, *Phlebiophragmus* O. E. Schulz, *Phlebolobium* O. E. Schulz, *Polypsecadium* O. E. Schulz, and *Sarcodraba* Gilg & Muschl. Pepper and Norwood (2001) have shown *Caulanthus* S. Watson to be polyphyletic and, together with *Guillenia* Greene, is nested within *Streptanthus* Nutt. In our opinion, these three genera, plus *Streptanthella* Rydb. and *Sibaropsis* S. Boyd & T. S. Ross, are perfectly at home in the more inclusive *Streptanthus*.

Trichome type is a feature used extensively in the delimitation of genera of Brassicaceae. Branched trichomes apparently evolved independently at least two or three times in the family (Galloway et al., 1998; Koch et al., 2001a; Kropf, 2002). However, little is known about the genetic background behind the shift in trichome morphology. Knowledge of the molecular basis of trichome development in *Arabidopsis thaliana* (see the excellent review of Szymanski et al., 2000) is rapidly expanding. Once the genes coding for the development of various trichomes are identified and sequenced, we should be able to use these markers as potentially powerful tools in phylogenetic studies in the family. Such knowledge will also help in understanding the origin of glabrous from the pubescent state, or vice versa.

Similarly, fruit type in the family is also essential in generic delimitation. Once the developmental and molecular bases of various fruit and seed characters (e.g., segmented vs. unsegmented fruits, corky vs. non-corky ones, dehiscent vs. indehiscent, seeded vs. seedless segments, winged vs. wingless seeds, flattened vs. terete valves) are understood, the taxonomy of the family could be based on more solid foundations. The differences in fruit characters often are overemphasized at the expense of more useful features that are largely ignored. Two examples demonstrate that. First, *Twisselmannia* was shown by Price and Al-Shehbaz (2003) to be identical to *Tropidocarpum* in their chloroplast gene *ndh*F and nuclear ITS. *Twisselmannia* has short (4–5 mm long), obtriangular, 4- to 8-seeded fruits superficially resembling those of *Capsella bursa-pastoris*, whereas *Tropidocarpum* has longer (10–70 mm) narrowly linear or oblong, 16–70-seeded fruits. These genera are indistinguishable in every aspect of habit, leaf, raceme, flower, and seed morphology. Second, based on nuclear and chloroplast DNA sequences, Mummenhoff et al. (2001b) have clearly demonstrated that *Alliaria* (with linear, wingless, subterete to 4-angled fruits) is nested within *Thlaspi* s. str. (obcordate, winged, strongly angustiseptate fruits). Traditional taxonomy (e.g., Schulz, 1936) places *Alliaria* in the tribe Sisymbrieae and *Thlaspi* in the Lepidieae. Both genera have concentrically striate seeds, a character not known elsewhere in the Brassicaceae, and molecular data strongly indicate that they should be united, a position with which we agree. In this context, it is important to note that fruit dehiscence (also a diagnostic character for generic delimitation; see above) and the relative length of fruit are controlled in *A. thaliana* by only few MADS-box genes, i.e., *SHATTERPROOF* and *FRUITFULL* (Liljegren et al., 2000; Ferrandiz et al., 2000). We conclude that fruit characters alone may well lead to erroneous taxonomic conclusions, and that such characters should be critically evaluated in light of molecular and other morphological data.

Arabidopsis represents a classic example where molecular studies have contributed to a better understanding of its taxonomy and generic delimitation. The approximately 60 binomials previously assigned to the genus are now placed in 14 genera (Al-Shehbaz et al., 1999) and, as presently circumscribed (O'Kane & Al-Shehbaz, 1997; Al-Shehbaz & O'Kane, 2002a), *Arabidopsis* includes only nine species. Support for the new segregate genera proposed by Al-Shehbaz et al. (1999) comes from ITS sequences (Koch et al., 1999a; O'Kane & Al-Shehbaz, 2002, and in prep.), chalcone synthase (Koch et al., 2001a), *mat*K (Koch et al., 2001a), and alcohol dehydrogenase (Miyashita et al., 1998).

Perhaps the most surprising finding from molecular data is the basal position of the genus *Aethionema* R. Br. in relation to the rest of Brassicaceae (Zunk et al., 1993, 1996, 1999; Galloway et al., 1998; Koch et al., 2001a). Although only the highly variable *A. grandiflorum* Boiss. & Hohen. ($n = 14$) has been studied, the basal position of the genus poses several challenging questions. First, *Aethionema,* which is a highly polymorphic genus of 50–60 species (primarily Turkey and the Middle East), is much in need of detailed systematic and phylogenetic studies (Appel & Al-Shehbaz, 2002). Second, fruit morphology in the genus (angustiseptate, 2- to 8-seeded) has traditionally been considered as specialized (Schulz, 1936). Third, *Aethionema* exhibits enormous diversity in chromosome numbers (n = 7, 8, 11, 12, 14, 16, 18, 21, 22, 24, 30; see Appel & Al-Shehbaz, 2002). Without critical phylogenetic studies of *Aethionema* and several other southwestern Asian genera, it is premature to speculate as to what an ancestral mustard might look like. It is interesting to note that members of the Thelypodieae (New World) were considered at one point as primitive (Al-Shehbaz, 1973) but now are treated as relatively specialized (Galloway et al., 1998).

Although substantial molecular data have accumulated during the past ten years, only data on ITS sequences are somewhat more extensive than those of other markers. Such data are being synthesized by Bailey et al. (pers. comm.), and it is premature to make any generalizations. The compilation by Kropf (2002) of largely unpublished sequences from GenBank is far from adequate. It would be rewarding to assemble similar large data sets on chloroplast genes and compare them with those of ITS sequences. Most studies have concentrated on North American and European taxa, and except for the work of Mitchell and Heenan (2000) and Hurka et al. (unpublished) on the mustards of New Zealand and Australia, respectively, hardly any studies exist on the South American, African, Himalayan, and central Asian genera of the family. Molecular studies on disjunctions, especially in cosmopolitan genera such as *Cardamine, Lepidium,* and *Rorippa,* which occur on all continents except Antarctica, are needed, though the works of Mummenhoff et al. (2001a), Lee et al. (2002), and Mummenhoff et al. (in prep.) on *Lepidium* are ideal studies to follow.

The vast majority of molecular studies in Brassicaceae involved sequences of single markers, but it is far more important to study multiple markers separately and combined, as was done by Bailey et al. (2002) and Koch et al. (2001a). Now that the entire genome of *Arabidopsis* is well known and the function of many of its genes has been identified, it is highly desirable that phylogenetic studies be based on sequences of genes with definite functions, especially those controlling the development of trichomes, leaves, and fruits, structures that offer the taxonomic characters most frequently used. Equally important is to determine on the basis of molecular data the evolution of individual characters and the distribution of their homoplasy on a family-wide basis. For example, we have no idea if the presence of multicellular multiseriate glands represents a synapomorphy within the family, and the evolution of many other characters (e.g., schizocarpic or samaroid fruits, palmately compound leaves, decurrent stigmas with united lobes, stellate trichomes with webbing and numerous rays, segmented fruits, conduplicate or diplecolobal cotyledons, production of garlic smell, to name a few) needs critical studies. A good example illustrating this aspect is the determination of evolutionary changes in leaf development (Bharathan et al., 2002) and floral structure in *Lepidium* (Bowman et al., 1999; Lee et al., 2002) and fruit convergence in *Thlaspi* (Mummenhoff et al., 1997a), but studies such as these are needed on many other characters. The absence of a given feature in *Arabidopsis thaliana* should also stimulate research to trace if this species still has at least part of the genome responsible for that character. The studies of self-incompatibility in *Brassica* and its homolog in *Arabidopsis* (Conner et al., 1998; Kusba et al., 2001) are excellent examples to follow.

5. *Arabidopsis* and Its Wild Relatives: Genome Synteny and Comparative Molecular Approaches

Molecular markers are widely used to study the organization of plant genomes, and genetic-linkage maps based on molecular markers have been assembled for many plant species (Schmidt, 2000). The use of identical sets of markers can lead to the construction of comparative genetic maps of species. Such experiments give an idea about the degree of conservation of gene repertoire and structure of markers among different species. Additional information about genome regions between markers can be obtained by cloning and characterizing these regions using information from the flanking regions. If there are high levels of genome co-linearity, as well as of the gene level (microsynteny), comparative genome-mapping experiments can serve as an efficient tool for transferring information and resources from well-studied genomes, such as that of *Arabidopsis,* to related plants. Sequencing the entire genome of *Arabidopsis thaliana* (The Arabidopsis Genome Initiative, 2000; Blanc et al., 2000; Vision et al., 2000; Simillion et al., 2002) have shown that at least 70% of the genome is duplicated and that the original haploid number of its ancestors was probably four, doubled to eight, and reduced to five as a result of extensive chromosomal rearrangements, fusion, and loss.

Brassica has been thoroughly studied using comparative mapping experiments (Lagercrantz & Lydiate, 1996; Kowalski et al., 1994; Lagercrantz, 1998). Other studies (Kowalski et al., 1994; Lagercrantz, 1998; Grant et al., 1998; Lagercrantz et al., 1996; Cavell et al., 1998; Jackson et al., 2000; O'Neill & Bancroft, 2000; Axelsson et al., 2001; Quiros et al., 2001) have focused on the *Arabidopsis–Brassica* comparison. These results have substantiated the view that "diploid" species of *Brassica, B. nigra* ($n = 8$), *B. oleracea* ($n = 9$), *B. rapa* ($n = 10$), have largely triplicated genomes and most likely have descended from a polyploid ancestor. Comparative mapping experiments have demonstrated that approximately 90 rearrangements occurred since the divergence of *Arabidopsis* and *B. nigra*, estimated to have occurred 14–20 million years ago (Koch et al., 2000, 2001a; Vision et al., 2000). Higher degrees of genome co-linearity have been observed in comparisons between *A. thaliana* and *A. lyrata* subsp. *petraea* (diverged ~5 MYA; De Haen et al., 1999) and *A. thaliana* and *Capsella rubella* (diverged ~6.2 to 9.8 MYA; Schmidt et al., 2001; Acarkan et al., 2000). Co-linearity on a small scale (microsynteny) has been detected in several regions in *Arabidopsis* and *Brassica* (Sadowski et al., 1996; Sadowski & Quiros, 1998; Conner et al., 1998; Osborn et al., 1997), although no general conclusions can be drawn from these studies. However, similar homologous segments with drastically increased fragment sizes were found. Nevertheless, genome co-linearity is extensive enough to permit the application in *Brassica* species of a lot of information assembled in the framework of the *Arabidopsis* genome project. For the first time, a combinatorial approach of analyzing microsynteny (based on DNA sequence information) and function (gene expression analysis) has been performed on a large set of cruciferous plants using promoter regions of APETALA3, and CHS (Koch et al., 2001b). This analysis among distantly related species may help to predict gene and promoter functions and specificity, and may also help achieve a deeper understanding of the evolutionary significance and consequences of mutations in coding regions (Stotz et al., 2000; Bishop et al., 2000). Comparative genome studies are essential for understanding genome co-linearity, duplications, deletions, and rearrangements, as well as for determining the evolution of duplicated genomes through time and the unification of genomes within polyploids (A. E. Hall et al., 2002). In our opinion, more studies of this kind, though both labor intensive and rather costly, are needed, especially for understanding the evolution of major clades of Brassicaceae and the role polyploidy played during their evolution.

6. MIGRATION AND PHYLOGEOGRAPHY

Molecular markers have been utilized as a tool to assess geographic distribution patterns in groups whose diversification has not substantially been influenced by the environment. Maternally inherited DNA markers (e.g., the plastome of most angiosperms; see Harris & Ingram, 1991; Reboud & Zeyl, 1994) can be used to trace the maternal lineages. A variety of nuclear markers are used in such studies: either "co-dominant" such as isozymes and microsatellites, or dominant such as "RAPDs" (random amplified polymorphic DNAs) or "AFLPs" (amplified fragment length polymorphisms), as well as DNA sequences of nuclear regions such as the frequently used internal transcribed spacers of nuclear ribosomal DNA (ITS-1 and ITS-2) (Franzke et al., 1998; Francisco-Ortega et al., 1999; Bleeker et al., 2002b). These nuclear markers serve as tools to detect patterns of genetic diversity that are inherited maternally and paternally. By using molecular markers, biogeographical (source areas of genetic diversity, vicariant patterns, migration routes, hybridization zones, secondary contact zones, etc.) and related evolutionary questions (speciation processes, polytopic origin, etc.) can be addressed, and the data obtained serve to develop more appropriate models that explain present-day distribution and diversity. A recent example for such analyses is the coordinated effort to develop a deeper understanding of distribution patterns, group differentiation, and the evolution of plants in the arctic and alpine regions (Stehlik et al., 2001). Both *Biscutella* L. (Dannemann, 2000; Tremetsberger et al., 2002) and *Cochlearia* (Koch, 2002) include some species of alpine plants that have been subjected to such studies. Other studies on European *Arabis alpina* L. (Plantholt, 1995), *Cardamine* (Franzke & Hurka, 2000), and Eurasian *Microthlaspi* (Koch et al., 1998c; Koch & Hurka, 1999) helped to elucidate colonization routes from refugial areas into formerly glaciated areas of northern and central Europe. The analyses of *Arabidopsis thaliana* have demonstrated distribution patterns of genetic diversity that are congruent with those found in other plant and animal species, all of which demonstrate that the Iberian Peninsula, Italy, and the Balkans represented three major refugial areas during glaciation in central Europe (Sharbel et al., 2000). A complex speciation and migration scenario in *Draba* was elaborated for North, Central, and South America (Koch & Al-Shehbaz, 2002). *Draba* also shows strong affinities to high alpine regions (e.g., in the Alps, Scandinavia, the Himalayas, Rocky Mts., Andes) and, therefore, its evolution appears to have been influenced by glaciation and deglaciation periods throughout the Pleistocene. Studies on the Chinese *Yinshania* elucidated migration over long distances and extensive reticulation during migration (Koch & Al-Shehbaz, 2000). It is remarkable that, in all cases analyzed to date, polyploidization played an important role in migration and phylogeography, and this seems also to be the case in *Lepidium*. Comprehensive molecular studies of the biogeographic history of *Lepidium* and *Rorippa* on a worldwide scale were conducted by Mummenhoff et al. (2001a) and Bleeker et al. (2002a), respectively. The easily dispersible mucilaginous seeds of species of *Lepidium* and the widespread occurrence of autogamous breeding systems suggest a rapid radiation of the genus by long-distance dispersal during the Pliocene/Pleistocene, an interpretation supported by estimates of divergence times based on cpDNA sequence divergence. Climatic changes resulted in the establishment of arid/semiarid areas, thus providing favorable conditions for the radiation of *Lepidium* that led to its current worldwide distribution.

Lepidium is represented in Australia and New Zealand by 19 and 7 native species, respectively. ITS and cpDNA phylogenies gave strongly conflicting signals and provided evidence for bicontinental hybrid genomic constitution in *Lepidium* in these areas (Mummenhoff et al., submitted). Seventeen Australian/New Zealand species share a Californian cpDNA type. As for ITS, nine species appear to harbor a Californian type and eight species share a South African type. This pattern is most likely explained by two trans-oceanic dispersals of *Lepidium* from California and Africa into Australia/New Zealand and subsequent hybridization followed by homogenization of the ribosomal DNA either to the Californian or South African ITS type in the two different lineages.

Some future directions of research should focus on the origin and early diversification of Brassicaceae. There are two contradicting hypotheses: a western North American and Irano-Turanian origin (Hauser & Crovello, 1982). Molecular and morphological studies at the family level are needed to understand the early evolutionary history and dispersal of Brassicaceae. Other research directions should focus on the range extension of species, as recent global climatic changes and human activities will lead to the spread of species beyond their natural ranges or the reduction of their ranges (Walther et al., 2002). Studies on *Arabidopsis* and *Teesdalia* R. Br. demonstrate the influence of climate on the global ranges of species (Hoffmann, 2000, 2002). Such studies may provide information about the ecogeographic amplitude of species. Species of some genera (e.g., *Nasturtium*, *Cardamine*) have been cited as examples where hybridization may serve as a stimulus for the evolution of invasiveness (Ellstrand & Schierenbeck, 2000).

7. Molecular Clock Estimates from DNA Sequence Variation and the Age of Brassicaceae

The reliability of molecular clock estimates of evolutionary divergence has been the subject of much debate (Sanderson, 1998; Soltis & Soltis, 2001). Questions largely involve: (1) the possibility of varying substitution rates within a lineage, (2) differing substitution rates between lineages, and (3) the lack of accurate evidence to calibrate the molecular clock (e.g., missing fossil evidence) (Sanderson, 1998, 2002; Britton et al., 2002; Syvanen, 2002). Estimates from *Chs* (chalcone synthase), *Adh* (alcohol dehydrogenase), and *mat*K (maturase K) indicate that the Brassicaceae appeared approximately 50 million years ago (MYA) (Koch et al., 2001a). Synonymous substitution rates of 1.5×10^{-8} at *Chs* and *Adh*, and 1.7×10^{-9} at *mat*K were estimated (Koch et al., 2000, 2001a). Substitution rates obtained from these studies were used to calculate that *Arabidopsis thaliana* diverged from its *Cardaminopsis*-like common ancestor approximately 5 MYA, while the most recent common ancestor of polymorphic *A. thaliana* accessions occurred roughly 1.5 MYA (the average divergence time between *Brassica* and *Arabidopsis* has been calculated to be 14–20 MYA; Koch et al., 2000). These results correspond to findings obtained from divergence time estimates of the mitochondrial gene for NADH subunit 4 (*nad*4) in *Brassica* species by Yang et al. (1999b). These data also help to calibrate other molecular clocks of more widely used markers in Brassicaceae, such as the ITS or *trn*L intron and *trn*L-F spacer region (Mummenhoff et al., 2001a; Bleeker et al., 2002b). Despite the inherent uncertainties associated with rate and time estimates outlined by Sanderson (1998), this procedure has been found to be useful in many studies of plant evolution and biogeography (Böhle et al., 1996; Kim et al., 1998; Vargas et al., 1998). Meanwhile, an approach to estimate divergence times in the absence of rate constancy has been developed (Sanderson, 1997). As for Brassicaceae, it would be desirable to calibrate substitution rates of widely used nuclear, cpDNA, and mtDNA marker systems by reference to alternative/more substantiated fossil records, geological history/events, and palaeoclimatic data (Baldwin & Sanderson, 1998; Richardson et al., 2001).

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APPENDIX 1. MOLECULAR MARKERS IN THE STUDY OF SYSTEMATICS AND EVOLUTION OF BRASSICACEAE: A LITERATURE SURVEY

The following list summarizes studies in which various methods have been used to study the evolution and systematics of Brassicaceae. The compiled literature is sorted according to the marker systems used, listed alphabetically by taxa and then by authors. The list is restricted to studies at the populational level or above.

I. Isoelectric focusing of ribulose-1,5-bisphosphate carboxylase (IEF-Rubisco):

Arabidopsis including *Cardaminopsis* (C. A. Mey.) Hayek (Mummenhoff & Hurka, 1994).
Capsella bursa-pastoris (Mummenhoff & Hurka, 1990).
Diplotaxis (Mummenhoff et al., 1993).
Erysimum (Mummenhoff & Jentzsch, 1994).
Lepidium (Mummenhoff, 1989, 1995; Mummenhoff & Hurka, 1991; Mummenhoff et al., 1992).
Thlaspi (Koch et al., 1993; Mummenhoff & Zunk, 1991).

II. Isozyme analysis:

Arabidopsis including *Cardaminopsis* (Mummenhoff & Hurka, 1995).
A. lyrata subsp. *petraea*, as *Arabis petraea* L. (Schierup, 1998).
Arabis (Roy & Rieseberg, 1989).
A. fecunda (McKay et al., 2001).
A. serrata Franch. & Sav. (Oyama et al., 1993).
Biscutella (Tremetsberger et al., 2003).
Boechera A. & D. Löve, as *Arabis* (Roy, 1995; Roy & Rieseberg, 1989).
Brassica (Chevre et al., 1995; Simonsen & Heneen, 1995a, 1995b).
B. insularis Moris (Petit et al., 2001).
Brassicaceae (Chevre et al., 1995).
Brassiceae (Anderson & Warwick, 1999; Simonsen & Heneen, 1995a, 1995b).
Capsella (Hurka, 1990; Hurka & Düring, 1994; Hurka & Neuffer, 1997; Neuffer & Hurka, 1999).
C. bursa-pastoris (Neuffer, 1996; Neuffer & Hoffrogge, 1999; Neuffer & Hurka, 1999; Neuffer et al., 1999).
C. rubella (Neuffer & Hoffrogge, 1999).
Cardamine (Urbanska et al., 1997).
C. amara (Koch et al., 2003a; Marhold et al., 2002a).
C. pratensis L. agg. (Franzke & Hurka, 2000).
Cochlearia (Koch et al., 1998a; Koch, 2002).
Draba (Brochmann, 1992; Brochmann et al., 1991, 1992a, 1992b, 1992c; Scheen et al., 2002).
Lesquerella fendleri (A. Gray) S. Watson (Cabin, 1996).
Microthlaspi (Koch & Hurka, 1999).
Nasturtium (Bleeker et al., 1999).
Raphanus sativus (Huh & Ohnishi, 2001).
Rorippa (Bleeker & Hurka, 2001).
Streptanthus Nutt. (Mayer et al., 1994).
Thlaspi caerulescens J. & C. Presl (Koch et al., 1998b).
Warea carteri Small (Evans et al., 2000).
III. Restriction fragment length polymorphism of
(a) chloroplast (cp) DNA:
Arabidopsis, including *Cardaminopsis* (Mummenhoff & Hurka, 1995; Price et al., 1994).
Arabideae (Price et al., 1994).
Brassica (Song et al., 1995; Warwick & Black, 1991, 1993, 1994, 1997a, 1997b; Warwick et al., 1992).
Brassicinae (Warwick & Black, 1991, 1993, 1994, 1997a, 1997b).
Brassiceae (Pradhan et al., 1992; Warwick & Black, 1994, 1997a).
Cakilinae (Warwick & Black, 1997a).
Cardamine (Urbanska et al., 1997).
Diplotaxis (Warwick et al., 1992).
Draba (Brochmann et al., 1992c).
Lepidieae (Zunk et al., 1993; Zunk et al., 1999).
Lepidium (Mummenhoff et al., 1995).
Microthlaspi (Koch et al., 1998c).
Moricandiineae (Warwick & Black, 1994).
Raphaninae (Warwick & Black, 1997a).
Savignyinae (Warwick & Black, 1994).
Sisymbrieae (Price et al., 1994).
Streptanthus (Mayer & Soltis, 1994).
Thelypodieae (Zunk et al., 1996).
Thlaspidineae (Zunk et al., 1996).
Thlaspi (Mummenhoff & Koch, 1994; Mummenhoff et al., 1997a, 1997b; Zunk et al., 1996).
Vellinae (Warwick & Black, 1994).
Zillinae (Warwick & Black, 1994).
(b) nuclear ribosomal DNA:
Brassica (Delseny et al., 1990; Maluszynska & Heslop-Harrison, 1993; Waters & Schaal, 1996).
Eruca Mill. (Lakshmikumaran & Negi, 1994).
Microthlaspi (Koch et al., 1998c).
(c) total nuclear DNA:
Brassica (Song et al., 1995).
(d) mitochondrial DNA:
Brassica (Song et al., 1995).
IV. Random amplified polymorphic DNA (RAPD):
Capsella bursa-pastoris (Neuffer, 1996; Neuffer et al., 1999; Yang et al., 1998).
Cardamine (Neuffer & Jahncke, 1997; Urbanska et al., 1997).
C. amara (Lihová et al., 2000).
C. pratensis agg. (Franzke & Hurka, 2000).
Cochlearia (Koch et al., 1996).
Draba (Scheen et al., 2002).
Lepidium meyenii (Toledo et al., 1998).
V. Amplified fragment length polymorphism (AFLP):
Arabidopsis thaliana (Sharbel et al., 2000).
Cardamine amara (Marhold et al., 2002b).
Cheesemania O. E. Schulz, *Pachycladon* Hook. f. (Mitchell & Heenan, 2002).
VI. repetitive DNA and microsatellites:
Alliaria petiolata (M. Bieb.) Cavara & Grande (Meekins et al., 2001).
Arabidopsis, including *Cardaminopsis* (Kamm et al., 1995; Van der Zwan et al., 2000).
A. lyrata subsp. *petraea* (van Treuren et al., 1997).
Brassica (Harrison & Heslop-Harrison, 1995; Saal et al., 2001).
Diplotaxis (Martin & Sanchez-Yelamo, 2000).
VII. DNA Sequencing of
(a) coding plastid genes:
maturase K:
Brassicaceae (Koch et al., 2001a).
***ndh*F:**
Cardamine, including *Dentaria* (Les, 1994; Sweeney & Price, 2000).
***rbc*L:**
Arabidopsis (Price et al., 1994; Tsukaya et al., 1997).
Capparales (Rodman et al., 1993, 1996).
Armoracia, *Nasturtium*, *Neobeckia*, *Rorippa* Les (1994).
(b) non-coding plastid *trn*L intron and spacer:
Arabis (Roy, 2001).
A. holboellii (Sharbel & Mitchell-Olds, 2001).
Boechera (Roy, 2001).
Brassica (Lannér, 1998).
Cardamine, including *Dentaria* (Franzke et al., 1998; Sweeney & Price, 2000; Bleeker et al., 2002b).
C. pratensis agg. (Franzke & Hurka, 2000).
Caulanthus S. Watson, including *Guillenia* Greene (Pepper & Norwood, 2001).
Cochlearia (Koch et al., 1999b).
Draba (Koch & Al-Shehbaz, 2002).
Halimolobos Tausch (Bailey et al., 2002).
Lepidium (Mummenhoff et al., 2001a).
Mancoa Wedd. (Bailey et al., 2002).
Pennellia Nieuwl. (Bailey et al., 2002).
Rorippa (Bleeker & Hurka, 2001; Bleeker et al., 2002a).
Sphaerocardamum Schauer (Bailey & Doyle, 1999; Bailey et al., 2002).
Streptanthus (Pepper & Norwood, 2001).
Yinshania (Koch & Al-Shehbaz, 2000).
(c) nuclear coding alcohol dehydrogenase (ADH):
Arabidopsis (Miyashita et al., 1996, 1998).
A. thaliana (Hanfstingl et al., 1994; Innan et al., 1996).
Arabis (Miyashita et al., 1996, 1998).

Brassicaceae (Koch et al., 2000).
Leavenworthia Torr. (Charlesworth et al., 1998).
(d) nuclear coding S-alleles:
Arabidopsis lyrata (Charlesworth et al., 2000).
A. thaliana (Charlesworth et al., 2000).
Brassica (Charlesworth et al., 2000; Uyenoyama, 2000).
(e) nuclear coding chalcone synthase (CHS):
Brassicaceae (Koch et al., 2000, 2001a).
(f) nuclear coding arginine decarboxylase (ADC):
Brassicaceae (Galloway et al., 1998).
(g) nuclear coding 2S albumin:
Arabidopsis, Brassica (Boutilier et al., 1999).
(h) nuclear coding myrosinase:
Arabidopsis, Brassica (Rask et al., 2000).
(i) nuclear coding acidic chitinase:
Arabidopsis thaliana (Kawabe et al., 1997).
Arabis (Bishop et al., 2000).
(j) nuclear coding chalcone isomerase:
Arabidopsis, including *Cardaminopsis* (Kuittinen & Aguade, 2000).
(k) nuclear coding floral homeotic genes (APETALA, PISTILLATA, CAULIFLOWER):
Arabidopsis thaliana (Lowman & Purugganan, 1999; Purugganan & Suddith, 1998, 1999).
Brassica (Lowman & Purugganan, 1999; Purugganan et al., 2000).
(l) nuclear non-coding internal transcribed spacer of ribosomal DNA (ITS):
Arabidopsis (O'Kane et al., 1997; Yang et al., 1999a).
Arabis (Koch et al., 1999a; Roy, 2001).
Boechera (Roy, 2001; Koch et al., 2003b).
Brassica (Yang et al., 1999a, 1999b; Warwick et al., 2002).
Brassicaceae (Heenan et al., 2002; Mitchell & Heenan, 2000).
Cardamine, including *Dentaria* (Franzke & Mummenhoff, 1999; Franzke et al., 1998; Bleeker et al., 2002b).
C. pratensis agg. (Franzke & Hurka, 2000).
Caulanthus, including *Guillenia* (Pepper & Norwood, 2001; Warwick et al., 2002).
Cochlearia (Koch et al., 1999b).
Crambe (Francisco-Ortega et al., 1999).
Descurainia Webb & Berthel. (Bricker et al., 2000).
Draba (Beilstein & Windham, 2002; Koch & Al-Shehbaz, 2002; Widmer & Baltisberger, 1999a, 1999b).
Dryopetalum A. Gray (Warwick et al., 2002).
Erucastrum C. Presl (Warwick et al., 2002).
Halimolobos (Bailey et al., 2002).
Hornungia (Kropf, 2002).
Hymenolobus (Kropf, 2002).
Lepidium (Bowman et al., 1999).
Mancoa (Bailey et al., 2002).
Mostacillastrum O. E. Schulz (Warwick et al., 2002).
Neotorularia Hedge & J. Léonard (Warwick et al., 2002).
Pachyphragma (DC.) Rchb. (Mummenhoff et al., 2001b).
Pennellia (Bailey et al., 2002).
Pringlea W. Anderson ex Hook. f. (Warwick et al., 2002).
Pritzelago (Kropf, 2002).
Romanschulzia O. E. Schulz (Warwick et al., 2002).
Rorippa (Yang et al., 1999a; Bleeker et al., 2002b).
Schoenocrambe Greene (Warwick et al., 2002).
Sibara Greene (Warwick et al., 2002).
Sisymbrium (Warwick et al., 2002).
Sphaerocardamum (Bailey & Doyle, 1999; Bailey et al., 2002).
Stanleya Nutt. (Warwick et al., 2002).
Streptanthella Rydb. (Warwick et al., 2002).
Streptanthus (Pepper & Norwood, 2001; Warwick et al., 2002).
Thelypodiopsis Rydb. (Warwick et al., 2002).
Thelypodium Endl. (Warwick et al., 2002).
Thlaspi (Koch & Mummenhoff, 2001; Mummenhoff et al., 1997a, 1997b, 2001b).
Vellinae (Crespo et al., 2000).
Warea Nutt. (Warwick et al., 2002).
Yinshania (Koch & Al-Shehbaz, 2000).
(m) chalcone synthase promoter region:
Brassicaceae (Koch et al., 2001b).
(n) alcohol dehydrogenase promoter region:
Arabidopsis halleri (L.) O'Kane & Al-Shehbaz subsp. *gemmifera* (Matsum.) O'Kane & Al-Shehbaz (Miyashita, 2001).
A. thaliana (Miyashita, 2001).
(o) *apetala3* promoter region:
Brassicaceae (Koch et al., 2001b).
(p) pistillata-intron:
Halimolobos (Bailey et al., 2002).
Mancoa (Bailey et al., 2002).
Pennellia (Bailey et al., 2002).
Sphaerocardamum (Bailey & Doyle, 1999; Bailey et al., 2002).
Lepidium (Lee et al., 2002).
(q) coding mitochondrial *nad4*:
Arabidopsis (Yang et al., 1999a).
Brassica (Yang et al., 1999a, 1999b).
VIII. Comparative mapping approaches, segregation analysis:
Arabidopsis (Acarkan et al., 2000; Vision et al., 2000).
Brassica or *Brassica-Arabidopsis* (Axelsson et al., 2000, 2001; Bohuon et al., 1996; Cavell et al., 1998; Conner et al., 1998; Lagercrantz, 1998; Lagercrantz et al., 1996; Lan & Paterson, 2000, 2001; Lan et al., 2000; Rossberg et al., 2001; Ryder et al., 2001; Schmidt, 2000; Schmidt et al., 2001; Sillito et al., 2000).
Capsella bursa-pastoris (Linde et al., 2001).
Capsella rubella (Acarkan et al., 2000; Rossberg et al., 2001).
Review (Schmidt, 2000; Schmidt et al., 2001).
IX. Short interspersed elements (SINE):
Brassiceae (Lenoir et al., 1997).

HOW BIG IS THE GLOBAL WEED PATCH?[1]

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ABSTRACT

Invasive species are a major global threat to both biodiversity and agriculture and thus are a high priority for conservation science. Governments recognize this and are devoting increasing resources toward solving the problem. Even so, there is inadequate information on where invasives occur and thus where society can best use these resources. Disturbed areas tend to be very favorable to invasives, especially the weedy species. We map the world's disturbed areas, the global weed patch, using maps of original and current landcover. At least 29.4 million km^2 (ca. 23%) of the world's ice-free land area is disturbed and thus favorable for invasive species. This weed patch map corresponds well to known locations of some of the world's worst weeds, lending support to our approach. Our results should help in setting geographic priorities for actions against invasive species.

Key words: disturbance, global change, invasive species, landcover, weeds.

Organisms have moved—and been moved—around the planet for millennia, but never in the numbers and with such speed as today. Most are benign, but a dangerous few cause major environmental problems. Invasive species may thrive in their new environment and dramatically change the dynamics and composition of the ecosystem. Because of our lack of vigilance, we now suffer large economic losses in agriculture (Pimentel et al., 2000), suffer disrupted water supply and riverine transport (e.g., zebra mussel (*Dreissena polymorpha*) and Asian clam (*Corbicula fluminea*), Pimentel et al., 2000), and witness the degradation or even replacement of entire ecosystems (e.g., purple loosestrife (*Lythrum salicaria* L.), Thompson et al., 1987; Pimentel et al., 2000). Growth of the global trade network results in a concomitant growth in the problem, and this is unlikely to change in the near future. As the problem is inherently global, we must develop a global strategy to solve it.

Much invasive species research focuses on identifying characteristics of species that enable them to invade. The idea is to identify who will invade and then restrict their movement around the world. That is certainly a vital approach to solving the problem, but it need not be the only one. This paper takes an alternative approach. We attempt to identify where they will invade rather than who the invaders will be.

WHERE DO SPECIES INVADE?

The simplest answer to this question is "everywhere"! Consider the flora of Britain: It includes *Polygonum amplexicaule* D. Don from the Himalayas, *Dianthus caryophyllus* L. from southern Europe, *Papaver somniferum* L. from western Asia, *Coronopus didymus* (L.) Sm. from South America, *Rubus spectabilis* Pursh from North America, and *Acaena novae-zelandiae* T. Kirk from New Zealand (Blamey & Grey-Wilson, 1989). These examples show that when a flora is well known it is likely to include species from around the world. Britain's species-poor native flora now accommodates a global flora. Species can be introduced from anywhere to anywhere, it would seem. That said, it is clear that some species are more likely to be introduced than others, and some areas are more likely to receive invasive species than others.

Our argument is that disturbed areas are the prime habitats for invasive species. Recognizing the absence of an ideal database, we selected a set of species from the World's Worst Invasive Alien Species list compiled by Lowe et al. (2001) to see if they occur predominantly in disturbed areas. The top three plants, and the number of countries in which they occur, were *Lantana camara* L. [51], *Chromolaena odorata* R. M. King & H. Rob. [38], and *Leucaena leucocephala* (Lam.) de Wit [37].

The counts of countries are a little misleading in

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that they are dominated by small, usually Pacific island nations. Nonetheless, all three species have invaded large areas. *Chromolaena odorata,* native to tropical America and the Caribbean (Holm et al., 1977: 212–216; Holm et al., 1979: 85), invades pastures and croplands in much of tropical Africa and Asia, the Southeast Asian island nations, and Australia. *Lantana camara,* native to Central and South America (Holm et al., 1977: 299–302; Holm et al., 1979: 207), is a widespread invader of pasturelands in Southeast Asia, Australia (where it is a Weed of National Significance), parts of southern Africa and Madagascar, the Mediterranean, and extreme southern parts of the United States. *Leucaena leucocephala* is native to tropical America (Holm et al., 1979: 214; Lowe et al., 2001), but in its non-native range can form dense, almost monospecific stands that render large areas unusable. Currently it occurs in China, most of the Pacific Rim islands, and Australia.

All three species occur in heavily disturbed areas, as do many other widely distributed invasive species, such as *Mimosa pigra* L., various species of *Opuntia,* and *Ricinus communis* L. Another way to view this problem is to survey disturbed areas. Throughout the tropics, it is our experience that disturbed habitats will have at least one and often several of these listed species. Often they will be common; sometimes they will be the dominant species. Searching for "worst weeds" on the World Wide Web produces a list of repeat offenders that cause economic harm to croplands and pastures. Most are exotics, but not all.

In short, these and other examples suggest that invasive species occur predominantly in disturbed ecosystems. By "disturbed," we mean major ecosystem changes, such as conversion to croplands, grazing lands, urban areas, or anthropogenic ones, such as grasslands where there was once forest.

We will not further belabor this connection between invasive species and human-modified habitats, for it is well-established and not obviously controversial. Rather, we accept the connection and move to the problem of estimating how large a fraction of the Earth's land surface humans have modified. Since invasive species in these disturbed habitats are often deemed to be weeds, we can rephrase our question to: How big is the global weed patch?

We proceed by estimating the size of the weed patch at first global, then regional levels. Globally, the area of disturbed habitats is large. Regionally, we find that our global estimates are too small, for there is much disturbance that they miss. It is not surprising that invasive species are such an ecological problem.

A First Assessment of the Size of the Weed Patch

Global assessments of landcover change provide a series of somewhat overlapping estimates of disturbed habitats. A rough estimate of the size of the weed patch comes from combining the areas of (1) croplands, with (2) degraded grazing lands, and (3) the areas of cleared forests that are not in productive use.

(1) Of the ice-free land surface of about 129 million km^2, croplands cover about 15 million km^2 of the planet. All but 4 million km^2 were converted from naturally wooded or forested ecosystems (Pimm, 2001).

(2) The world's drylands cover roughly 61 million km^2—an estimate that includes deserts, grasslands, shrublands, and savannas. The area varies from author to author depending on what one means by "dry" (Pimm, 2001; Vitousek et al., 1986; Olson et al., 1983).

Most of the world's drylands suffer from desertification—a large portfolio of mostly human-caused problems that depress plant productivity. Some 23 million km^2 of the drylands have damaged vegetation (Dregne, 1986). This often means the spread or increase of unpalatable plant species following overgrazing by cattle, goats, and other livestock (Young & Longland, 1996; Archer, 1994; Bahre & Shelton, 1993; Van Auken, 2000). Those will sometimes be native species. For instance, mesquite (native *Prosopis* spp.) has dramatically increased in density over much of the southwestern United States (Bahre & Shelton, 1993; Archer, 1994; Van Auken, 2000). More often, the weeds will be exotic invasives such as *Opuntia* in Australia and Africa.

(3) Another 40 million km^2 of the land surface has forests or woodlands of one kind or another, another 8 million km^2 are tundras, and the remainder includes wetlands and urban areas (Olson et al., 1983).

The conversion of forests to other habitats is more complicated, since most of the world's croplands were once forests—and so have already been counted above as croplands. Most of the converted forests are in temperate regions. About 2 million km^2 of these forests have also been converted to grazing lands (Pimm, 2001).

Modern human actions have shrunk the world's tropical humid forests from an original area of from 14 to 18 million km^2 to about 7 million km^2 at present (Myers et al., 2000; Pimm, 2001). Again, the exact numbers depend somewhat on what one means by "humid." Yet only about 2 million km^2 of croplands are in what was formerly humid forests. Some 5–9 million km^2 of humid forests have been converted to nominally grazing land, though much of it has very low stocking rates (Pimm, 2001).

Summing these three pieces suggests that 15 million km^2 of present-day croplands, 23 million km^2 of drylands, 2 million km^2 of temperate forest converted to grazing lands, and from 5 to 9 million km^2 of additional forested land not producing crops have sustained sufficient changes to their vegetation to make them target areas for invasive species. The combined total is just under half the ice-free land surface. The potential weed patch is huge.

This approach is inevitably approximate and must miss many details. In particular, it does not map where these disturbed lands are. To both refine these estimates and provide a check on their accuracy, we will now explore detailed estimates of landcover. We do so first at a global scale, then at regional scales. Our analyses relate primarily to the once-forested half of the planet since the remote sensing imagery on which we rely does not so readily detect the damage to drylands.

A Spatially Explicit Global Assessment of Converted Forests

For the global analysis, we use a Geographic Information System (ERDAS Imagine v 8.5) to combine a map of presumed original vegetation with an estimate of current landcover. The result is a global map where each pixel has information about its original vegetation and if it has changed, or not changed, into a different type of landcover.

The original vegetation map is from the Integrated Model to Assess the Global Environment (IMAGE) project (Leemans & van den Born, 1994; Alcamo et al., 1998; IMAGE team, 2001). In their Terrestrial Vegetation Model, the IMAGE team uses a modified BIOME model to estimate potential natural vegetation using climate and soil characteristics. For a detailed description of this model, see Prentice et al. (1992) and Leemans and van den Born (1994). The resolution of this map is one-half degree of latitude and longitude. Color maps are available from Alcamo et al. (1998) and IMAGE team (2001).

The current landcover map is from the Global Land Cover Characterization (GLCC) (Loveland et al., 2000). A digital version is available at ⟨http://edcdaac.usgs.gov/glcc/glcc.html⟩. This project used a one-year sequence of AVHRR satellite imagery to identify landcover in ca. 1992. As the primary concern of our study is disturbance (i.e., areas vulnerable to invasion), we focus on the disturbed classes of the GLCC (croplands, mosaics of croplands and natural vegetation, and urban areas). The resolution of this map is approximately one km^2 at the equator.

We also identify areas that have changed landcover, but not necessarily into croplands or urban areas. For example, the conversion of forests into grasslands for grazing will not appear as disturbed, but it obviously is. (Grasslands are a natural type of vegetation, but not where the original vegetation was a humid tropical forest.) We do this to assess potential error causes and means of improving on our main analysis.

The current data sets are not adequate for a complete and detailed analysis of landcover changes of all ecosystem types. The BIOME and GLCC maps use different classification schemes for vegetation that make matching corresponding classes between them somewhat arbitrary. For example, the GLCC map has an "open shrubland" class that corresponds to some grassland in the BIOME map. However, open shrubland also includes areas that are obviously not grassland, such as central Australia, which the BIOME map classifies as hot desert. It is uncertain that these changes represent land degradation: more likely, they represent differences in classification schemes.

Results and Discussion

Not surprisingly, the global analysis confirms that humanity has disturbed a large fraction of the world (Fig. 1). Of the ca. 129 million km^2 of ice-free land, ca. 27 million km^2 appear to have been converted to croplands, mosaics of croplands and natural areas, and urban areas. Table 1 shows the total disturbed area originating from each vegetation type (rightmost column). Of the total disturbed area, 80% comes from just six vegetation types (bold numbers in Table 1) that originally covered 47% of the land. Disturbance concentrates in temperate climates (temperate forests, warm mixed forest, grassland/steppe) and the drier subtropical and tropical vegetation (scrubland, savanna). Again, not surprisingly, most of this disturbance coincides with the world's human population and croplands, mostly in the Northern Hemisphere.

Grasslands, scrublands, and savannas have lost from a fourth to a third of their original area (Table 1), but these numbers may be misleading. Disturbance from livestock grazing on such ecosystems is difficult to detect by satellite. Most of the very cold

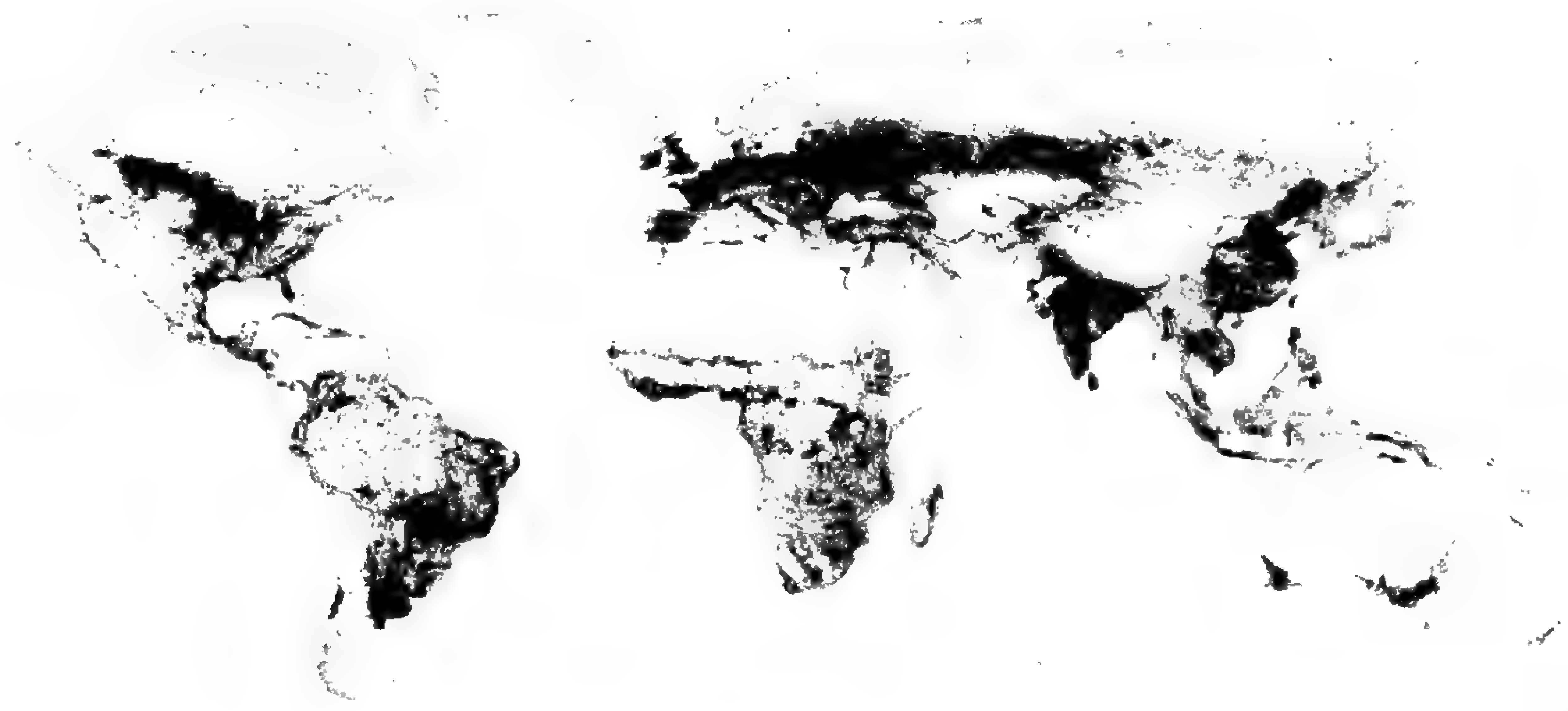

Figure 1. Map of global disturbed areas. Black areas include croplands, mosaics of croplands and natural vegetation, urban areas, and original tropical woodlands and forests that are now grassland, savanna, or woody savanna. Original vegetation is from the BIOME map and current landcover is from the GLCC map. This map uses a geographic projection and is not equal area.

areas (tundra and boreal forest) and the very dry (deserts) escape major disturbance.

Of the combined disturbed areas, 14.2 million km^2 are from once-forested areas (Table 1, sum of disturbed boreal forest, cool conifer, temp. mixed and decid. forest, warm mixed forest, and tropical woodland and forest). This seems to be a low estimate, for we should compare it with the 11 million km^2 of forests that are now croplands plus a further minimum estimate of 5 million km^2 of cleared tropical forests not converted to croplands (above and Pimm, 2001).

However, the GLCC data do not include separate categories for dry habitats (such as grasslands) that are purported to originally have been forest (Loveland et al., 2000). What happens if we assume that these are also converted landscapes? We approximate the area of forest to dryland conversion by identifying tropical woodlands and forests that are now grasslands, savannas, or woody savannas. The area is about 2.4 million km^2. Adding in this piece suggests that 16.6 million km^2 of forest have been converted. This is close to the lower estimate of 16 million km^2 based on combining independent es-

Table 1. Original area of each vegetation type, the area disturbed as croplands, mosaics of croplands and natural vegetation, and as urban areas. Drylands are areas that were originally tropical woodlands or tropical forests (BIOME map), but are now grasslands, savannas, or woody savannas (GLCC map). All areas are expressed as 1000s of square kilometers. Totals may be different from the sum of the parts because of rounding.

	Area (1000 sq. km.)					
Vegetation type	Original	Croplands	Mosaic	Urban	Drylands	Total disturbed*
Tundra	6096	7	13	0		20
Wooded tundra	2586	5	6	0		11
Boreal forest	16,144	399	119	6		523
Cool conifer	3809	686	378	10		1074
Temp. mixed forest	6471	2151	1706	67		**3924**
Temp. decid. forest	4677	1842	837	62		**2741**
Warm mixed forest	6189	1503	1185	31		**2719**
Grassland/steppe	17,800	1975	2078	32		**4085**
Hot desert	23,006	274	232	6		512
Scrubland	9745	2013	1356	19		**3387**
Savanna	15,926	2775	1962	11		**4748**
Tropical woodland	7485	830	842	10	1629	1682
Tropical forest	8893	718	843	7	767	1569
Total	128,824	15,178	11,556	260	2397	26,995

* Does not include drylands.

Table 2. Area disturbed through deforestation and through edge effects in the Amazon example. The area within 300 meters of an edge includes 4986 km² of "natural" edge forest (see text). All areas are expressed as square kilometers.

Year	Area of forest	Total area deforested	Area <300 m from edge	Total area disturbed
Original	112,919	0	4986	0
1992	100,974	11,945	17,801	24,760

timates of forest converted to croplands (11 million km²) and tropical forests converted to grazing lands (5 million km²); see above and Pimm (2001).

This broad agreement is encouraging, but it also points to the difficulty in translating landcover maps, with their inevitably arbitrary classifications of vegetation cover, into ecologically sensitive measurements of human impacts. That is a conclusion on which we now expand by considering two areas of forest conversion in more detail.

A Fine-Scale Analysis of Tropical Forests

We selected two tropical forest areas in Brazil with different disturbance histories to try to identify what the global analysis is missing.

The Amazon is relatively intact but has had high rates of recent deforestation (i.e., within the last 30 years, Skole & Tucker, 1993). Northern Mato Grosso state, in the southeastern Amazon Basin, is our example of such recent anthropogenic disturbance. In contrast, most of the Atlantic Forest was deforested more than 30 years ago (Fundação SOS Mata Atlântica, 1998). The state of Rio de Janeiro and the surrounding area is our example of such historic disturbance.

For the Amazon example, we calculate deforestation using forest cover maps from the Tropical Rain Forest Information Center (TRFIC, 2002). We use maps for 1992 to match the year of the GLCC map. We also simulate the undisturbed condition by replacing the deforested class in the 1992 map with forest.

Table 2 shows the deforestation statistics for the Amazon example. Comparison of TRFIC maps shows that as of 1992, 100,974 km² of the original 112,919 km² of forest remained, yielding 11,945 km² of deforested (disturbed) area.

The global analysis significantly underestimates disturbance in this region. According to the GLCC, the Amazon example shows just 3943 km² of disturbed area. That is only about a third of the regional estimate in the previous paragraph. Another 3582 km² is grassland, savanna, or woody savanna. Including these as disturbed brings the total to 7525 km², which is still less than two-thirds of the TRFIC estimate. Even after correcting the GLCC map for unnatural drylands, it still misses a third of the disturbed area.

For the Atlantic Forest example, we map forest cover in 1999 using Landsat 7 ETM+ satellite imagery. Using standard supervised classification techniques, we classify seven Landsat images into forest and non-forest classes. We do not distinguish between natural and plantation forests, but monospecific plantations (e.g., eucalyptus) are not a large proportion of remaining forest in this area (pers. obs.). The World Wildlife Fund ecoregion map provides an estimate of original forest cover (Olson & Dinerstein, 1998).

In the Atlantic Forest example, the analyses of Landsat imagery show that 91,993 km² of forest, of an original 127,850 km², has been lost to deforestation. The area of disturbed lands in the GLCC map is just 51,851 km², 56% of the Landsat-derived estimate. However, adding in forests converted to drylands increases the area to 111,000 km², an overestimate of disturbance.

In both examples, the best fit of estimates from GLCC data to detailed regional estimates comes only when we recognize the conversion of forests to obviously disturbed habitats (such as croplands) and less obvious categories (such as grasslands and savannas) that could be natural ecosystems, but are not.

Two factors contribute to these deficiencies of the GLCC map. One, the AVHRR imagery used in making the GLCC has limited ability to discriminate vegetation types. The AVHRR sensor's spectral bands are too wide and poorly positioned for mapping vegetation, yielding inevitable errors. This appears to contribute to the overestimation of deforestation in the Atlantic Forest example. The remaining forest is simply misclassified. The second factor is that the resolution of the regional analyses (0.0009 km²) is much finer than the GLCC data (1 km²) in the global analysis. This finer resolution enables better detection of small areas of deforestation. This likely contributes to the underestimate in the Amazon example, where there are many small patches of deforestation.

We do not know if these error rates are general for the global analysis. These are only two examples from relatively small areas. What they do indicate is a need for better global mapping of landcover. At the time of writing, the GLCC was the best global data set available, but good prospects exist for refining our results. Efforts are under way using

MODIS ⟨http://geography.bu.edu/landcover/index.html⟩ and Landsat ⟨http://www.geocover.com⟩ satellite imagery to map the world at 250-meter and 30-meter resolutions, respectively. Vegetation mapping is a primary consideration in these sensor's designs, so the resulting maps should better discriminate vegetation types and their level of disturbance. The improved spatial resolution should also better detect small areas of disturbance.

THE MISSING EDGES

We have mapped disturbed areas as best possible using current data sets, but another part of the weed patch is still missing from our estimates. Laurance (1997) found forest edges to be vulnerable to invasives because of "edge effects" disturbing the forest community. Although we cannot assess how much edge forest contributes to the global weed patch, the one km² resolution is too coarse; we can estimate it for the Amazon and Atlantic Forest examples.

The regional forest maps have some errors that we must first correct. They have small gaps of non-forest, some of which may be natural, but many of which are small classification errors. These are insignificant for the earlier analyses, but can cause large areas of forest to appear to be near an edge, even if that edge is a single 30-m pixel. To account for this, we replace patches of non-forest smaller than 2 hectares with forest. The use of 2 hectares is conservative. It is larger than the presumed classification errors, but may also include some truly deforested areas and natural gaps. The result is a probable underestimate of edge forest.

In the Amazon example, 17,801 km² of forest is within 300 meters of an edge (Table 2), the distance that Laurance et al. (1998, 2000) detected community changes in Amazonian forest fragments. However, in the original state this region already had 4986 km² of natural edge forest due to rivers and savannas. Adding the edge forest, minus natural edge, to the earlier estimate of disturbed area yields 24,760 km² of disturbed area (Table 2), approximately twice the original estimate.

In the Atlantic Forest example, 29,373 km² of the remaining forest is within 300 meters of an edge. Adding this to the deforested area yields 121,366 km² of disturbed area, leaving just 6484 km² of undisturbed forest. The map of original forest (WWF ecoregion) is too general to reliably calculate a "natural" amount of edge as done for the Amazon.

When we incorporate these regional estimates of edges into the calculations of disturbed area, then the GLCC estimates are both too small. In short, much disturbance—and much habitat for invasive species—occurs on a scale too small to detect with global landcover maps.

CONCLUSIONS

Invasive species are a growing problem for the world, both ecologically and economically. In response to the problem, governments are devoting increasing amounts of resources toward the prevention, control, and eradication of invasives in many parts of the world. To enable efficient use of these resources, the scientific community needs to identify where invasives are likely to be a problem or become a problem in the future.

Disturbed ecosystems are often favorable for invasives, a conclusion confirmed by comparing our map of disturbed areas with the distributions of some of the worst invaders. These disturbed areas, the global weed patch, occupy at least 29.4 million km² (23%) of the ice-free land surface. Other than the overgrazed drylands, which our analyses are unable to detect, the numbers broadly agree with independent estimates of disturbed area.

The advantage of our approach is that it shows where those disturbed areas are and thus where the invaders are likely to be. Combining this with information on who the invaders are likely to be should help in efficiently allocating resources to solve the invasive species problem.

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REVISION OF *ARDISIA* SUBGENUS *AURICULARDISIA* (MYRSINACEAE)[1]

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ABSTRACT

A taxonomic revision of the Neotropical *Ardisia* subg. *Auriculardisia* (Lundell) Ricketson & Pipoly is presented, and a key to the Neotropical subgenera of *Ardisia* is provided. The group comprises taxa formerly placed by Lundell in his segregate genera *Auriculardisia, Amatlania,* and *Valerioanthus. Ardisia* subg. *Auriculardisia* is defined by its unique calyx lobes, which are asymmetrical, usually notched just below the apex, and always auriculate basally. Six sections are recognized within *Ardisia* subg. *Auriculardisia,* comprising 75 taxa: sect. *Auriculardisia* (Lundell) Ricketson & Pipoly (4 species), sect. *Pleurobotryae* Ricketson & Pipoly (1 species), sect. *Fagerlindia* Ricketson & Pipoly (7 species), sect. *Wedelia* Ricketson & Pipoly (8 species), sect. *Amatlania* (Lundell) Ricketson & Pipoly (3 species, including 6 subspecies), and sect. *Palmanae* Ricketson & Pipoly (47 species, including 2 subspecies). Thirteen new species and two new subspecies are described and illustrated. The new combinations *Ardisia pellucida* Oerst. subsp. *pectinata* (Donn. Sm.) Ricketson & Pipoly, *Ardisia liebmannii* Oerst. subsp. *jalapensis* (Lundell) Ricketson & Pipoly, and *Ardisia croatii* Lundell subsp. *correae* (Lundell) Ricketson & Pipoly are proposed. *Ardisia carchiana* and *Ardisia zakii* are transferred to *Geissanthus* as *Geissanthus carchianus* (Lundell) Ricketson & Pipoly and *Geissanthus zakii* (Pipoly) Ricketson & Pipoly.

Key words: Ardisia section *Amatlania, Ardisia,* section and subgenus *Auriculardisia,* section *Fagerlindia,* Myrsinaceae, Neotropics, section *Palmanae,* section *Pleurobotryae,* section *Wedelia.*

RESUMEN

Se presenta una revisión taxonómica del subgénero neotropical *Ardisia* subg. *Auriculardisia* (Lundell) Ricketson & Pipoly y una clave para separar a los subgéneros neotropicales de *Ardisia.* El grupo comprende taxones anteriormente segregados por Lundell en sus géneros *Auriculardisia, Amatlania* y *Valerioanthus. Ardisia* subg. *Auriculardisia* se define por el caracter único de sus lóbulos calicinos asimétricos, normalmente incisos justo debajo del ápice y siempre auriculados en la base. Se reconocen seis secciones dentro del *Ardisia* subg. *Auriculardisia,* que comprenden 75 taxones, listados a continuación: *Auriculardisia* (Lundell) Ricketson & Pipoly (4 especies), sect. *Pleurobotryae* Ricketson & Pipoly (1 especie), sect. *Fagerlindia* Ricketson & Pipoly (7 especies), sect. *Wedelia* Ricketson & Pipoly (8 especies), sect. *Amatlania* (Lundell) Ricketson & Pipoly (3 especies, incluyendo 6 subespecies) y sect. *Palmanae* Ricketson & Pipoly (47 especies, incluyendo 2 subespecies). Se describen e ilustran trece especies y dos subespecies como nuevas para la ciencia. Se proponen tres combinaciones nuevas: *Ardisia pellucida* Oerst. subsp. *pectinata* (Donn. Sm.) Ricketson & Pipoly, *Ardisia liebmannii* Oerst. subsp. *jalapensis* (Lundell) Ricketson & Pipoly y *Ardisia croatii* Lundell subsp. *correae* (Lundell) Ricketson & Pipoly. Se transfieren *Ardisia carchiana* y *Ardisia zakii* al género *Geissanthus,* como *Geissanthus carchianus* (Lundell) Ricketson & Pipoly y *Geissanthus zakii* (Pipoly) Ricketson & Pipoly.

The pantropical *Ardisia* Sw. is the largest genus in the family Myrsinaceae, containing perhaps as many as 500 species (Chen & Pipoly, 1996). Its circumscription has been problematic owing to a lack of comprehensive treatment since that of Mez (1902) in Engler's *Das Pflanzenreich* a century ago.

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The genus has traditionally been separated from all others in the Myrsinaceae by what were interpreted as free filaments, and pluriseriate ovules (Mez, 1902). Pipoly and Ricketson (1998a), however, found that the stamens in all *Ardisia* are actually connate basally by their filaments to form a hyaline, inconspicuous tube, but that the tube is free from the corolla. While only a few groups within *Ardisia* s.l. have been segregated as separate genera in the Paleotropics (*Sadiria* Mez (1902), *Afrardisia* Mez (1902), *Tetrardisia* Mez (1902), *Hymenandra* A. DC. (1834), *Parardisia* Nayar & Giri (1986)), there has been an enormous increase in separation of species groups from *Ardisia* to new genera in the Neotropics, starting with Aublet's (1775) description of *Icacorea* (against which *Ardisia* is conserved) followed by Alphonse de Candolle (1841), Ducke (1930), and finally Lundell (1963, 1964, 1981a, 1981b, 1981c, 1981d, 1982). Lundell's contribution was clearly the most extensive, consisting of the segregation of *Amatlania* Lundell (= *Ardisia* subg. *Auriculardisia* sect. *Amatlania* (Lundell) Ricketson & Pipoly), *Auriculardisia* Lundell (= *Ardisia* subg. *Auriculardisia* (Lundell) Ricketson & Pipoly), *Chontalesia* Lundell (= *Hymenandra* A. DC., p.p.), *Yunckeria* Lundell (= *Ctenardisia* Ducke), *Gentlea* Lundell, *Graphardisia* Lundell (= *Ardisia* subg. *Graphardisia* Mez, Pipoly & Ricketson, 1998a), *Ibarrea* Lundell (= *Ardisia* subg. *Ardisia*), *Oerstedianthus* Lundell, *Synardisia* (Mez) Lundell, *Valerioanthus* Lundell (= *Ardisia* subg. *Auriculardisia* sect. *Auriculardisia* (Lundell) Ricketson & Pipoly), and *Zunilia* Lundell (= *Ardisia* subg. *Graphardisia* Mez, Pipoly & Ricketson, 1999b). Because the group is comprised of over 800 names, it will be some time before each species has been reviewed and the entire group revised. In the meantime, we suggest using the key to the Mesoamerican genera that we recently published (Pipoly & Ricketson, 1999a) to identify specimens to generic levels (*Ardisia* vs. *Ctenardisia*, *Hymenandra*, *Gentlea*, and *Synardisia*). Lundell (1981d: 342) separated his genus *Auriculardisia* from *Ardisia* s.l. using the following key:

1\. Plants glabrous or pubescent, not scaly; sepals symmetrical, ovate, longer than wide, usually thick; flowers strictly racemose or subspicate .... *Ardisia*

1\. Plants conspicuously scaly, furfuraceous or rarely lepidote; sepals asymmetrical, depressed-orbicular, elliptic or broadly ovate, and mostly wider than long, auriculate; flowers in heads, subcorymbose, or rarely umbellate or spicate, the rachis sometimes accrescent with the fruits becoming racemose .... *Auriculardisia*

Our concept of the *Auriculardisia* group of species as a part of the larger genus *Ardisia* includes another group, *Amatlania*, segregated from *Ardisia* by Lundell (1982). Lundell stated that *Amatlania* resembles another segregate genus, *Oerstedianthus* Lundell, because both have filaments with gland-tipped hairs [a character Pipoly and Ricketson (1998a, 1999b) observed in *Ardisia* subg. *Graphardisia*], but differs notably in the nature of the indument.

We also discovered that Lundell's (1982) genus *Valerioanthus* belonged to the *Auriculardisia* group, based on its auriculate, asymmetric calyx lobes with subapical notches. Lundell (1982) defined *Valerioanthus* by its coarse red hirsute indument, with trichomes up to 2 mm long. During the course of this study, we noted with interest that the species Lundell (1982) included in the group, including *Valerioanthus nevermannii* (Standl.) Lundell (= *Ardisia nevermannii* Standl. in sect. *Fagerlindia*), *V. ursinus* (Lundell) Lundell (= *Ardisia ursina* Lundell in sect. *Auriculardisia*), and *V. hirsutissima* (Lundell) Lundell (which we have placed in synonymy under *Ardisia ursina*) have strikingly distinct vestiture that in no way serves as a uniting character state. As defined in this treatment, *Ardisia* subg. *Auriculardisia* represents the largest group of *Ardisia* species in the Neotropics and is comparable in size and taxonomic complexity only to subgenus *Acrardisia*, which ranges from Southeast Asia and the Pacific to Mesoamerica and the Caribbean.

While preparing a treatment of *Ardisia* subg. *Auriculardisia* for inclusion in the Myrsinaceae for *Flora Mesoamericana*, we saw the need to present a full account of the group with detail not possible in the format of *Flora Mesoamericana*, and as a precursor to our eventual *Flora Neotropica* treatment. Herein we formally propose a new taxonomy for *Ardisia* subg. *Auriculardisia* to include six sections, of which four, sect. *Fagerlindia*, sect. *Pleurobotrya*, sect. *Wedelia*, and sect. *Palmanae*, are new; we reduce the genus *Amatlania* to a section of *Ardisia* subg. *Auriculardisia*; and finally, we circumscribe the type section *Auriculardisia*. Delimitation of sections, while admittedly artificial, is designed to facilitate identification and to illustrate the salient character states of each group of species within the subgenus. Unfortunately, it was not possible to conduct a phylogenetic analysis, so the extent to which each section is monophyletic is currently unknown.

Ardisia subg. *Auriculardisia* sect. *Amatlania* contains three species and eight taxa. *Amatlania* was described as a separate genus by Lundell (1982: 38), based largely on the "reddish glandular pubescence" of the branchlets and inflorescences. We have determined (see Morphology, Vestiture) that the vestiture found among this suite of species is actually composed of papillae or papillae mixed with uniseriate, multicellular glandular villous trichomes (Fig. 3A). Other features that define the section include the various toothing to serration of the leaf margins and the dense yellow glandular-granules within the corolla tube and on the filaments. Recognition of this group of species as a separate genus would leave *Ardisia* undefined. In all species of *Amatlania*, the stamens are united basally by their filaments to form an inconspicuous tube free from the corolla tube, clearly placing them within *Ardisia*. In addition, all species in *Amatlania* have asymmetric calyx lobes with a subapical notch and an (albeit more imperfectly formed) auricle on one side, which also indicates that this group of species belongs to *Ardisia* subg. *Auriculardisia*. We therefore reduce *Amatlania* from generic to sectional status within *Ardisia* subg. *Auriculardisia*.

Ardisia subg. *Auriculardisia* sect. *Auriculardisia*, containing four species, is defined by the combination of its terminal inflorescence with branches terminating in congested, glomerate corymbs, each of which is subtended by a persistent, enlarged inflorescence branch bract, and finally, the individual flowers subtended by a persistent, enlarged floral bract as long as the flowers. This section includes the rare and very interesting species *Ardisia dodgei*, which has unique red to pink floral bracts and is visited by hummingbirds. The section includes two species placed in the genus *Valerioanthus* by Lundell (1982) based on his misinterpretation of their vestiture (now considered synonyms of *A. ursina*), along with *A. dodgei*, *A. glomerata*, and *A. nervosissima*.

Ardisia subg. *Auriculardisia* sect. *Fagerlindia* contains seven species and is defined by exhibition of Fagerlind's Architectural Model (see Morphology), combined with terminal, pendent inflorescences. Because the vegetative and reproductive shoot leaves are dimorphic, many herbarium specimens are incomplete, containing the flowering shoot only, or with a vegetative shoot flowering precociously. This has led to taxonomic over-description and a fundamental lack of understanding of the developmental dynamics of these plants. Members of section *Fagerlindia* are normally inconspicuous elements of the understory.

Ardisia subg. *Auriculardisia* sect. *Palmanae* is clearly the largest section in the subgenus, with 47 species. The section is admittedly artificial and is defined by the subsessile to sessile inflorescences. Whether this feature has arisen several times within subgenus *Auriculardisia*, or whether section *Palmanae* represents a group without any other distinguishing character state, is unknown at this time and will require more rigorous study.

Ardisia subg. *Auriculardisia* sect. *Pleurobotryae* is monotypic, containing only *Ardisia pleurobotrya* Donn. Sm., and is defined by the strictly lateral inflorescences, long naked peduncles to 6.2 cm long, dense, overlapping chocolate brown lepidote scales on most plant parts, and pendent flowers on long, usually sigmoid pedicels. The lateral inflorescences and chocolate brown lepidote scales are unique within subgenus *Auriculardisia*, and within the genus as a whole are otherwise frequent only in subgenus *Akosmos* Mez of Asia.

Ardisia subg. *Auriculardisia* sect. *Wedelia* is defined by a subshrubby to small arborescent habit, and terminal, columnar to sub-columnar and often pendent inflorescences, on peduncles at least ⅓ the length of the inflorescence and subtended by large, foliaceous bracts. Like species of section *Fagerlindia*, these plants are inconspicuous members of the forest understory. The most salient feature of the section is the columnar to sub-columnar inflorescences, similar to the branches found in the basally branched, pyramidal inflorescence of *Ardisia pseudoracemiflora* (sect. *Palmanae*).

MORPHOLOGY

HABIT AND ARCHITECTURE

Species of *Ardisia* subg. *Auriculardisia* are terrestrial, small trees and shrubs, rarely subshrubs (*A. pellucida*). The vast majority of taxa (sect. *Amatlania*, sect. *Auriculardisia*, sect. *Palmanae*, and sect. *Wedelia*) display Scarrone's Architectural Model (Hallé et al., 1978; Bell, 1991), which is defined by an orthotropic monopodial, rhythmically growing principal axis (stem or trunk) differentiated from the branches, which are produced in pseudoverticillate tiers. The branches are composed of orthotropic shoots that produce terminal inflorescences; thus branching is sympodial by substitution. In a mature individual, there is often a dense canopy crown whose ultimate units may appear plagiotropic by gradual bending as they develop, a phenomenon documented by Fisher and Stevenson (1981).

Species of *Ardisia* subg. *Auriculardisia* sect. *Pleurobotryae* exhibit Rauh's Architectural Model, which is characterized by a monopodial, rhythmically growing, readily distinguishable trunk that develops pseudoverticillate tiers of branches morphogenetically identical to itself. All branches are orthotropic and monopodial, with lateral inflorescences that do not affect development of branches.

The most unusual model we found was that of *Ardisia* subg. *Auriculardisia* sect. *Fagerlindia*, described herein, which exhibits Fagerlind's Architectural Model (Hallé et al., 1978). Fagerlind's Model is defined by its monopodial, rhythmically growing trunk, with tiers of modular, plagiotropic branches that branch sympodially. The modular branches form sylleptically and sympodially, often by apposition, and with spiral phyllotaxy. First, a trunk ("vegetative shoot") develops rhythmically, producing successive pseudoverticels of "vegetative" leaves until the apex loses dominance and latent lateral ("axillary") buds are released, producing successive, monopodial pseudoverticels of shoots, each of which is sylleptic, with a long hypopodium and exhibiting rapid extension growth. The sylleptic branch shoots produce first a prophyll, then pseudoverticels of "reproductive shoot" leaves (similar to the leaves of the "vegetative shoot" but notably smaller), and then may either lose dominance and once again produce "vegetative shoot" leaves, branch sympodially by apposition growth (repeating the module) without flowering, or produce a terminal or pseudoterminal (acting as a terminal) inflorescence, followed by sympodial branching by substitution. The pseudoterminal inflorescences are lateral and form just below the branchlet apex. While the terminal bud is visible, it appears that the shoot does not grow significantly until the inflorescence is in late fruit. While not taxonomically significant, it is interesting that all members of the recently discovered Mesoamerican component of the boreotropical genus *Hymenandra* also exhibit Fagerlind's Model and fused anthers (Pipoly & Ricketson, 1999a). However, members of *Ardisia* subg. *Auriculardisia* sect. *Fagerlindia* may be readily distinguished from *Hymenandra* by their free anthers.

TRUNK AND BRANCHLETS

In this treatment, the principal axis formed by a negatively geotropic shoot is termed a "trunk" if it attains a diameter greater than or equal to 2.5 cm diameter at breast height (DBH); if it does not, it is termed a "stem." Branchlets are defined as the upper 10 cm of any branch. Branchlets may be stout or slender, straight or flexuous, terete, subterete, somewhat angulate with longitudinal ridges, or bearing well-developed interpetiolar ridges. The branchlets always bruise blue-purple when cut, due to the few to numerous lyso-schizogenous resin canals present in the secondary phloem. The resin canals of the pith in the primary growth region near the apex gradually coalesce into a poorly defined resinous area during secondary xylem formation and branchlet thickening. The bark is mostly smooth, or is rarely exfoliating (*Ardisia vesca* Lundell).

VESTITURE

The vestiture of the stems or branchlets, the petioles, leaves, and peduncle is normally uniform within a given species. Much confusion is evident in the literature regarding the term "furfuraceous-lepidote" because the structure of the covering scales of the leaves had not been thoroughly investigated. While a study of the covering scales for the entire family is clearly warranted, we here define the principal types of scales and other vestiture found in *Ardisia* subg. *Auriculardisia.*

The most striking type of trichome found in the subgenus is the cupuliform scale, which is sessile to subsessile, with small lobes to arms, composed of one cell each, variously connate to the next to form a deep cup or a small cup with radiating arms (Fig. 1A–1D). These trichomes are quite large, ranging in size from 200 to 300 μm in height. The cupuliform scales may be mixed with much smaller scales of the same type or translucent subentire scales, here referred to as minutely furfuraceous-lepidote scales, composed of 8 to 12 cap cells and one stalk cell, approximately 30–50 μm in diameter, shown in the middle left area of Figure 1C and throughout in Figure 1D.

Furfuraceous-lepidote scales are those that do not form a discernible cup and which may be entire to subentire but never with radiating arms, and range in size from 200 to 300 μm in diameter (Fig. 2B). The apparent thickness of the cap cells, owing to their respective lignification, varies greatly, from extremely thin, almost translucent (Fig. 2B) to appearing opaque (Fig. 2A, 2D).

In many taxa of the subgenus, varying quantitites of hydropotes may be present, mostly on the abaxial leaf surface (Fig. 2A). They are often confused with lepidote scales, but their obvious subsidiary cells and unusual cap morphology easily distinguish them. A good example is seen on the left side of Figure 2A, found in *Ardisia panamensis* Lundell. Hydropotes ("water drinkers") were described by Mayr (1915), then Grüss (1927a, 1927b), and finally, Gessner and Volz (1951), all of whom reported these structures from studies of submerged aquatic plants. They were first reported for the Myrsinaceae by Pipoly (1987) in *Cybianthus* Mart. subg. *Grammadenia* (Benth.) Pipoly, but are now

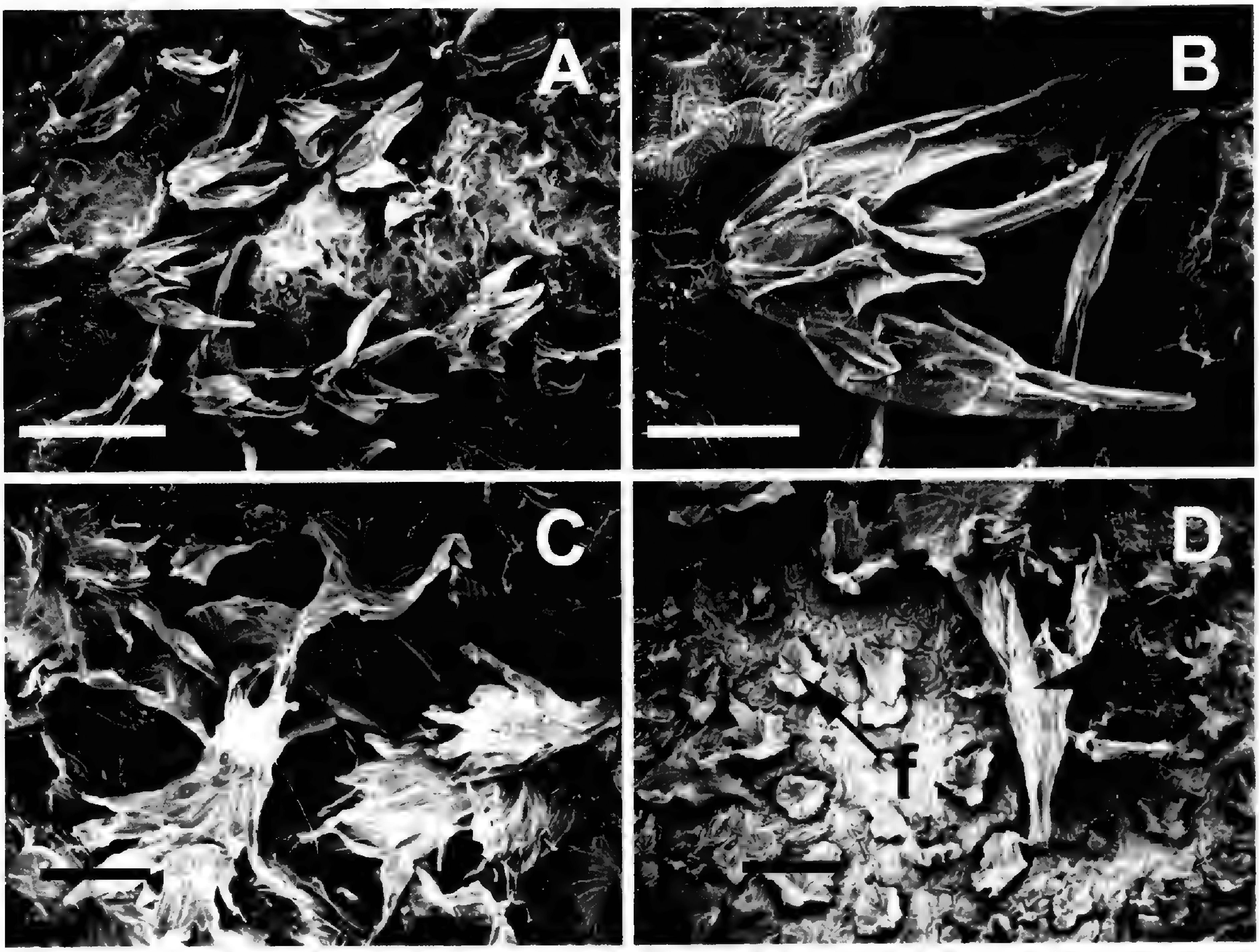

Figure 1. Cupuliform scales in *Ardisia* subg. *Auriculardisia.* —A, B. Cupuliform scales of *A. brenesii*; note semi-reclined habit. —C. Close-up of cupuliform scales, *A. crassiramea*, showing cup opened and flattened at maturity. —D. Cupuliform scales (c) above furfuraceous-lepidote scales (f), *A. furfuracea.* Note that cupuliform scales resemble those of *A. brenesii*, but are more stipitate. (A, B from *W. Haber & W. Zuchowski 9358* (MO); C from *W. Haber & W. Zuchowski 9128* (MO); D from *B. Boyle & C. Godt 932* (FTG).) Scale bars: A, C: 200 μm; B, D: 50 μm.

known for most subgenera of *Cybianthus* (Pipoly, 1998), *Hymenandra* (A. DC.) A. DC. ex Spach (Pipoly & Ricketson, 1999a), and *Wallenia* Sw. (Panfet, 2002). These structures may easily be distinguished from lepidote scales by their 5 to 7 subsidiary cells, a central foot cell, a basal cell, a stalk cell, and up to 12 cap cells. In early ontogeny, a mucilaginous substance accumulates around the basal cell. Later the cap breaks off, leaving a mucilaginous ring around the basal cell, whereupon they function as hydathodes in water regulation. Based on elegant ultrastructural and chemical studies by Lüttge (1964) and Lüttge and Krapf (1972), we now know that these structures actively transport minerals into the leaf through the mucilaginous substance secreted around the stalk. The mucilaginous substance stains easily with Sudan IV (Pipoly, 1987). Given the nutrient-poor, moist to pluvial tropical life zones inhabited by most Myrsinaceae, we expect to find that these structures are ubiquitous within the family. Hydropotes are easily distinguished from translucent lepidote scales by their subsidiary cells.

Ardisia nevermannii Standl. is unique within *Ardisia* subg. *Auriculardisia* sect. *Fagerlindia* because of its ferrugineous hirtellous vestiture, composed of stiff trichomes less than 2 mm long. These densely packed hairs are apparently unicellular, with subulate apices and bulbous bases (Fig. 2C). Lundell (1982) did not adequately distinguish the hirtellous tomentum of *Ardisia nevermannii* from the rufous multicellular, stipitate-stellate trichomes such as those of *Ardisia ursina*, which consist of a uniseriate row of glandular cells that terminate in a stellate cluster of arms (Fig. 3C, 3D). If they are dense, the vestiture is referred to as stipitate-stellate tomentose, or if they are less so, it is termed stipitate-stellate tomentellous. The arms frequently break off, leaving an apparent glandular-villous trichome, indistinguishable from those found on the branchlets and inflorescences of section *Amatlania*, such as *Ardisia pellucida* (Fig. 3A). While we can-

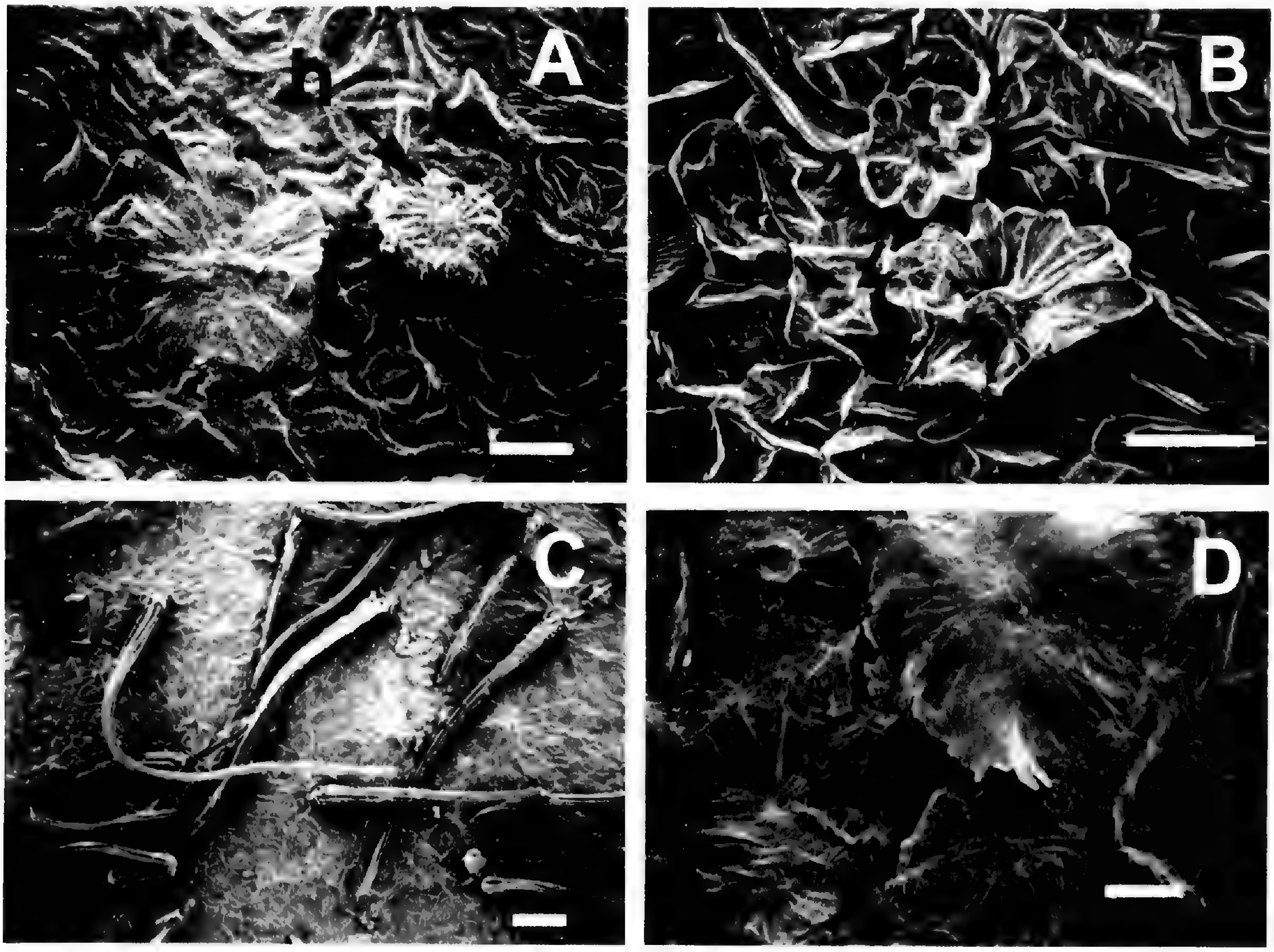

Figure 2. Leaf vestiture in *Ardisia* subg. *Auriculardisia.* —A. Minute furfuraceous-lepidote scale (f), hydropote (h), *A. panamensis.* Note that scale is small and opaque. —B. Minute furfuraceous-lepidote scales, *A. auriculata.* Note that scale is thin-walled and translucent. —C. Hirtellous trichomes, *A. nevermannii.* —D. Furfuraceous-lepidote scales, *A. pleurobotrya.* Note relatively large size and thickness greater than the other species. (A from *J. Pipoly 7065* (FTG); B from *B. Hammel et al. 19091* (FTG); C from *P. Acevedo 6875* (FTG); D from *G. Herrera 3626* (FTG).) Scale bars: A, D: 50 μm; B: 250 μm; C: 300 μm.

not dismiss the possibility that the glandular-villous trichomes of section *Amatlania* (Fig. 3A) are derived from the glandular stipitate-stellate trichomes found in section *Palmanae* (Fig. 3C), we have not found any remnant arms on the villous trichomes of any member of section *Amatlania.* At times, the stipitate-stellate trichomes form a layer of vestiture above the minute, subsessile translucent scales indistinguishable from those sometimes co-occurring with cupuliform-lepidote scales.

The inflorescence vestiture among members of *Ardisia* subg. *Auriculardisia* sect. *Amatlania* is particularly notable for the well-developed glandular-papillae (Fig. 3A), which in *Ardisia pellucida* subsp. *pellucida* are also accompanied by glandular villous trichomes. These trichomes preserve poorly and detach easily during the pressing and drying process, so many specimens lose most of the indument with time and handling. The papillae are very similar to those found in *Cybianthus* subgenera *Grammadenia* (Pipoly, 1987) and *Microconomorpha* (Pipoly, 1983), are epidermal in origin, and are somewhat sticky to the touch when alive. The chemical substance they contain is unknown.

LEAVES

The leaves of all species of *Ardisia* subg. *Auriculardisia* are alternate or pseudoverticillate, exstipulate, and simple. Given that all branching is sylleptic, rapid extension growth of each shoot is followed by production of one or two prophylls, followed by fully formed leaves. In those species exhibiting Fagerlind's Model, the easily distinguishable "vegetative shoot leaves" are much larger than the "reproductive shoot leaves" and have a smaller length-to-width ratio. While the leaves of the principal axis and the branches have spiral phyllotaxis, the leaves of the branches are reoriented in a plane (dorsiventral) through a twisting of the internodes rather than by distichous phyllotaxis. The blades are mostly chartaceous to coriaceous, or rarely

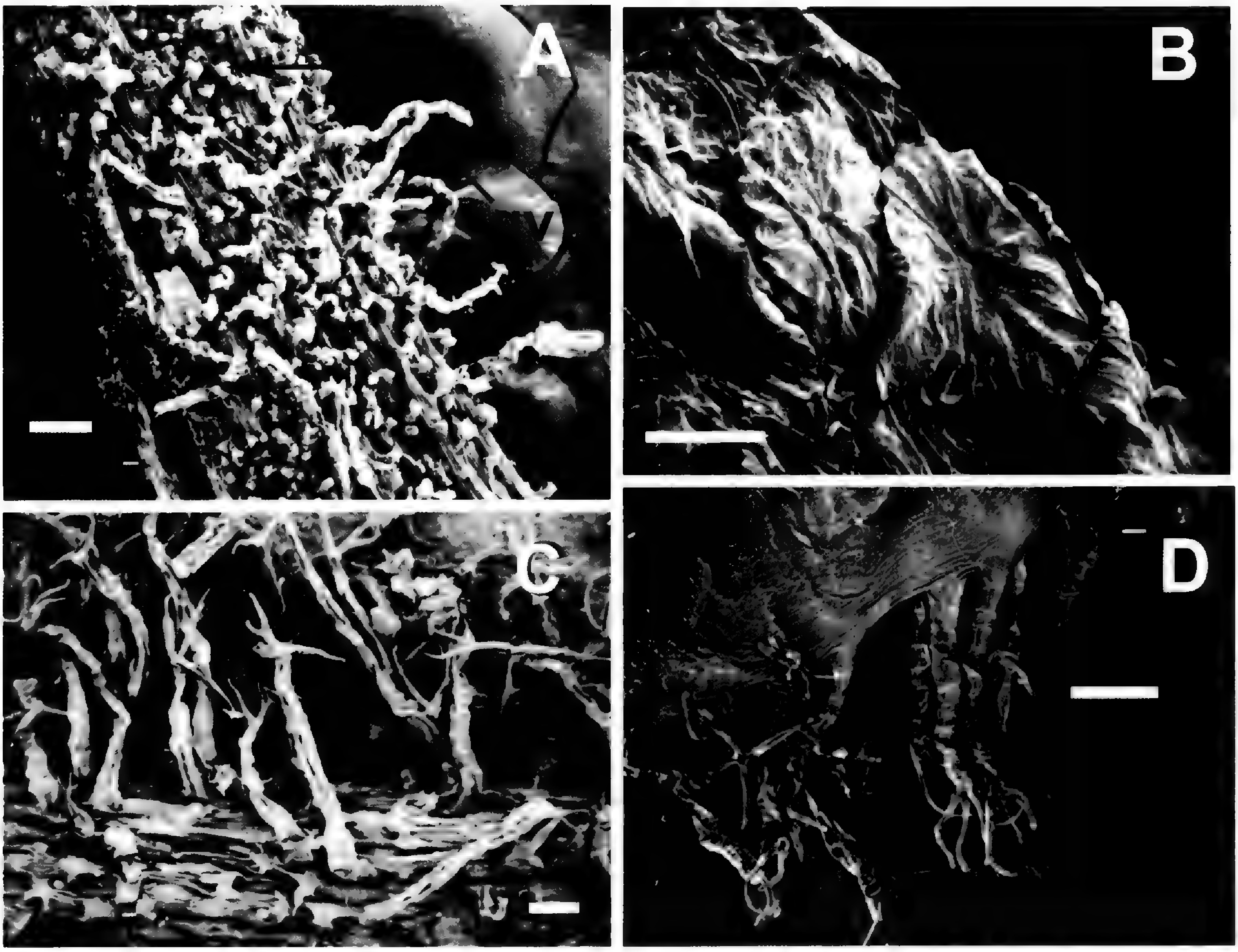

Figure 3. Vestiture in *Ardisia* subg. *Auriculardisia.* —A. Inflorescence rachis with glandular-papillae (gp) and glandular-villous (gv) trichomes, *A. pellucida* subsp. *pellucida.* This is representative of section *Amatlania.* —B. Inflorescence rachis with minute, overlapping furfuraceous-lepidote scales, *A. wedelii.* —C. Abaxial leaf surface near midvein, *A. ursina,* showing the glandular, stipitate-stellate trichomes. —D. Inflorescence bract margin with glandular, stipitate-stellate trichomes, *A. ursina.* (A from *C. Martinez* 1074 (FTG); B from *P. Moreno 7716* (MO); C, D from *G. McPherson 14042* (FTG).) Scale bars: A–C: 200 μm; D: 50 μm.

membranaceous, elliptic, oblanceolate or oblong, apically acute to long-acuminate, basally cuneate, to obtuse or rounded, or rarely auriculate.

The blades may also be decurrent on the petiole or not, conspicuously or inconspicuously (visible but not raised) or prominently (raised) punctate or punctate-lineate, variously furfuraceous- or cupuliform-lepidote, hirtellous-tomentose, villous glandular tomentose, or stipitate-stellate tomentose. The margins may be entire, crenate, serrate, pectinate, dentate, flat, or revolute. The petioles may be obsolete or subobsolete, canaliculate or marginate.

INFLORESCENCES AND FLOWERS

Within *Ardisia* subg. *Auriculardisia,* the most common inflorescence is a panicle, with flowers arranged in corymbs or glomerules at the end of the branches, rarely appearing subracemose. The inflorescence is a terminal panicle except in section *Pleurobotryae,* which has obviously lateral inflorescences on long peduncles terminating in corymbs. The panicles are normally pyramidal and much broader than long. However, an exception is found in section *Wedelia,* where the panicles are columnar (much longer than broad) to sub-columnar (longer than broad). The rachis may be straight, flexuous, or rarely geniculate. The inflorescence bract is normally early caducous; the inflorescence branch bracts may be foliaceous, large, and often envelop the terminal flower cluster, at least in early ontogeny.

The flowers can be 4-, 5-, or 6-merous, with asymmetric calyx lobes that have a subapical notch and a prominent auricle on one side, a feature that defines the subgenus. The corollas are usually white to pink. The corolla lobes may be ovate, elliptic, or oblong, symmetric to asymmetric, apparently epunctate, pellucid, black or orange punctate, and/or lineate. The stamens are fused basally by their filaments to form a hyaline, inconspicuous tube, and the filaments may be flat or terete, straight or gradually broader toward the base. The anthers may be ovate, lanceolate, linear-lanceolate, or oblong, apically apiculate, subulate, caudate, mucronate, acute, or acuminate, basally cordate to subcordate or sagittate, dehiscent by subapical pores opening into wide longitudinal slits, with the connective inconspicuously to conspicuously or prominently punctate dorsally. The pistil is most often obturbinate but may be obnapiform or ellipsoid; the ovary is globose, subglobose, ellipsoid, ovoid, or oblong. The placenta may be globose, subglobose, or ellipsoid, with apparently uniseriate (few ovules in a high anthotactic spiral), biseriate or pluriseriate, few to many ovules.

FRUIT

The fruit is a one-seeded drupe that may be globose to subglobose, inconspicuously (pellucid) punctate, or prominently black punctate and/or lineate.

NOTES ON KEYS, TAXONOMIC CONCEPTS, NOMENCLATURE, AND TERMINOLOGY

The keys are artificial and designed to expedite identification of herbarium specimens. An attempt has been made to emphasize vegetative characters to increase their usefulness with sterile material. Quantitative and qualitative data presented in keys and descriptions for floral parts and bracts were taken from organs rehydrated from herbarium specimens by boiling in water. Measurements from these range from 10% to 15% greater than those measurements taken directly from dried material. Data regarding stem diameters, inflorescence rachises, pedicels, and leaf and fruit shape and size were taken from dried herbarium specimens. A List of Species and Subspecies and an Index to Exsiccatae are provided in Appendices 1 and 2, respectively. The numbering system of Appendix 1 has been used for the species and subspecies in the text to help the reader locate taxa within the article. These numbers are also used in the sectional keys. Any correlations with phylogenetic relationships are coincidental.

Our concept of a subgenus is here defined as: a group of species that comprises a major basal phylogenetic subdivision within a monophyletic genus, whose formal recognition enables better understanding of the phylogeny of the entire genus. A corollary to that is our concept of the section, defined as: a group of species within a formally recognized subgenus that appears to share a common ancestry, based on the fact that they share unique character states. We should emphasize that our work has thus far produced only preliminary cladograms, and that all homologies have not been worked out. However, we believe it is more appropriate to formulate a preliminary phylogenetic hypothesis rather than have no working framework until the final analysis is done. By definition we advocate the use of sectional rank only within formal subgenera.

Our concept of subspecies follows that of Pipoly (1987: 46), who defined a subspecies as: "groups of populations within a single lineage of ancestor-descendant populations that show variation by unique combinations of plesiomorphies, or homoplasic apomorphies, correlated with biogeography and/or ecology. This rank is primarily used to convey information regarding variation in the life histories of these populations and character state differences hypothesized to be the result of this variation. The subspecific rank in no way attempts to predict speciation events."

Morphological terms in this treatment follow Lindley (1848) and Pipoly (1987, 1992) for the inflorescence, rachis pedicels, and floral parts. Description of leaf morphology follows Hickey (1984), trichome description follows Theobald et al. (1984), and basic cell and tissue terminology follow Metcalfe (1984).

Lundell (1981b, 1986) published 68 new names and combinations for binomials in *Ardisia* and *Myrsine* L. In both papers, he indicated that he was opposed to placement of the taxa involved in those genera and that the combinations and new names were provided in anticipation of future circumscriptions of the genera. We agree with Morales (1997) that in doing so, Lundell inadvertently invalidated his new names and combinations, according to the *International Code of Botanical Nomenclature,* Article 34.1 (Greuter et al., 2000). For *Ardisia* species, we (Pipoly & Ricketson, 1998b) corrected this situation by making 27 combinations and 9 new names, of which 14 belong to members of *Ardisia* subg. *Auriculardisia.* In this monograph, we cite Lundell's invalid combinations solely for the purposes of clarity, given the preponderance of nomenclatural synonyms complicated by the fact that the same epithets have been used for *Ardisia* as well as for many species in the segregate genera. While we are cognizant of the fact that these Lundell names have no nomenclatural status, we felt it was important to summarize all relevant nomenclatural matters in one place to avoid confusion.

TAXONOMIC TREATMENT

Ardisia Sw., Prodr. 3: 48. 1788. TYPE [conserved]: *Ardisia tinifolia* Sw.

Trees or shrubs, rarely suffrutescent or herbs. Leaves simple, exstipulate, alternate or pseudoverticillate, normally punctate or punctate-lineate, petiolate or sessile. *Flowers* bisexual, 4- to 5(to 6)-merous; perianth with imbricate or quincuncial aestivation (either dextrorse or sinistrorse), the lobes shortly connate; stamens included, the filaments connate into an inconspicuous tube, always free from the corolla tube, the anthers free, often 3 times longer than wide, dehiscent by apical or subapical pores, subapical pores opening into longitudinal slits or simple longitudinal slits, rarely transversely septate; pistil obturbinate, the ovary ovoid or oblong, the ovules few to numerous on a basal placenta, at times appearing uniseriate, sometimes biseriate, most commonly pluriseriate, the style elongate, normally exserted at anthesis. *Fruits* drupaceous, 1-seeded, punctate or punctate-lineate, sometimes longitudinally costate, with a somewhat fleshy exocarp and crusty or slightly bony endocarp; seeds covered by membranous remnants of placenta.

Distribution. About 400 to 500 species, pantropically distributed but with the highest diversities in central Malesia and southern Mesoamerica. For Mesoamerica, we expect that of the nearly 800 names for the group, we will recognize approximately 120 species.

For groups within *Ardisia* native to or naturalized in Mesoamerica, we present the following key to the subgenera:

KEY TO THE SUBGENERA OF *ARDISIA* IN THE NEOTROPICS

1a. Leaf blade margins crenate with a translucent vascularized nodule in the sinus of each crenation; ovules few, appearing uniseriate .... subg. *Crispardisia*
1b. Leaf blades entire, crenate, serrate or pectinate, but never with nodules in the sinus of each crenation or indentation; ovules numerous, pluriseriate.
  2a. Calyx and corolla lobes dextrorsely imbricate; apically free portions of the filaments less than ⅓ as long as the anthers.
    3a. Inflorescence a short-peduncled, terminal panicle; anthers widely ovate, dehiscent by wide longitudinal slits subconfluent apically at anthesis .... subg. *Acrardisia*
    3b. Inflorescence a long-peduncled lateral umbel; anthers lanceolate, dehiscent by narrow longitudinal, non-confluent slits .... subg. *Tinus*
  2b. Calyx and corolla lobes sinistrorsely imbricate or quincuncial; apically free portions of the filaments longer than ⅓ as long as the anthers.
    4a. Anthers yellow or white, rarely light pink, not concolorous, dehiscent by longitudinal slits or subapical pores opening into longitudinal slits, the pores not wider than the corresponding slits.
      5a. Inflorescence branches racemose to spicate; branchlets mostly glabrous; calyx lobes usually glandular-granulose basally adaxially, without a subapical notch along the margin, symmetrical, longer than wide, not auriculate basally .... subg. *Ardisia*
      5b. Inflorescence branches corymbose to glomerate; branchlets mostly scaly or variously tomentose; calyx lobes usually glabrous adaxially, with a subapical notch along the margin, asymmetrical, auriculate basally .... subg. *Auriculardisia*
    4b. Anthers concolorous (drying gray), deshiscent by terminal to subterminal pores, the open pore wider than the theca area below it.
      6a. Branchlets and inflorescence rachises glabrous or rarely sparsely glandular-granulose; leaf blades, inflorescence, floral bracts, and perianth densely and prominently black or red punctate and/or punctate-lineate; calyx lobes accrescent, usually clasping the developing fruit .... subg. *Graphardisia*
      6b. Branchlets and inflorescence rachis furfuraceous-lepidote; leaf blades rarely conspicuously but never prominently punctate-lineate, the inflorescence and floral bracts mostly orange, rarely black, punctate, the perianth mostly orange, or rarely black punctate; calyx lobes not accrescent, never clasping the developing fruit .... subg. *Icacorea*

Treatments of *Ardisia* subg. *Graphardisia* were published by Pipoly and Ricketson (1998a, 1999b) and of *Ardisia* subg. *Acrardisia* by Pipoly and Ricketson (2000). Treatment of the other subgenera (subg. *Ardisia*, subg. *Icacorea*, subg. *Tinus*, and subg. *Crispardisia*) are now under way (Ricketson & Pipoly, in prep.).

TAXONOMIC TREATMENT OF *ARDISIA* SUBG. *AURICULARDISIA*

Ardisia Sw. subg. **Auriculardisia** (Lundell) Ricketson & Pipoly, comb. et stat. nov. Basionym: *Auriculardisia* Lundell, Phytologia 49: 341. 1981. TYPE: *Ardisia glomerata* Lundell.

Valerioanthus Lundell, Wrightia 7: 50. 1982. TYPE: *Ardisia nevermannii* Standl., [≡ *Valerioanthus nevermannii* (Standl.) Lundell].

Subshrubs or small trees. Stems or branchlets and leaves furfuraceous-lepidote (the scales tawny, or rarely chocolate brown in color, appressed or flat, thin, without veins visible), cupuliform-lepidote (chocolate or rufous, like a bowl with lobes, or arms, stiff yet translucent, with prominent venation visible), mixed lepidote, hirtellous-tomentose (the hairs simple, apparently one-celled, long and somewhat stiff), rufous stellate-tomentose, the trichomes on multicellular, uniseriate stalks (the star section frequently breaking off and the hairs then seeming villous), minutely glandular-papillate (normal rufous), or villous-tomentose (indistinguishable from stipitate-stellate with star arms broken off). *Inflorescences* terminal or rarely (*A. pleurobotrya*) lateral panicles that are pyramidal, or rarely (sect. *Wedelia*) columnar to sub-columnar, the branches bearing flowers in corymbs, glomerules or rarely pseudoracemes; pedicels stout to almost obsolete. *Flowers* with the perianth sinistrorsely imbricate or quincuncial; calyx lobes essentially free, subapically notched, basally auriculate on one side; corolla lobes often slightly asymmetric, conspicuously or prominently punctate and/or punctate-lineate; the hyaline and inconspicuous staminal tube elobate, the apical free portions of the filaments mostly longer than ⅓ anther length, at times subequaling to slightly longer than the anthers, the anthers narrowly ovoid or lanceoloid, apically apiculate, caudate-apiculate, subulate-apiculate or rarely mucronate-apiculate, basally subcordate, cordate, or sagittate, dehiscent by subapical pores opening into longitudinal slits, the pores not wider than the slits; pistil obturbinate, the ovary globose to subglobose to oblongoid, the style slender, at times punctate and/or punctate-lineate, the placenta globose or ovoid, the ovules few to numerous, in 2 or more series, when few, at times appearing uniseriate. *Fruits* subglobose to globose, conspicuously or prominently punctate and punctate-lineate, smooth or costate.

Distribution. *Ardisia* subg. *Auriculardisia* is known from San Luis Potosí, Hidalgo, Pueblo, Veracruz, and Oaxaca, Mexico, south throughout Mesoamerica to Colombia, Ecuador, and in parts of Peru and Venezuela. It grows from sea level to 3300 m in elevation.

Ecology. *Ardisia* subg. *Auriculardisia* occurs in a wide variety of moist or humid, wet and pluvial habitats in primary, secondary, remnant, and disturbed areas, oak-pine woodlands, premontane, montane, cloud, and elfin forests.

The subgenus contains 70 species, including 75 taxa, and is defined by asymmetric calyx lobes that are usually subapically notched and always basally auriculate.

Key to the Sections of *Ardisia* subg. *Auriculardisia*

1a. Individual flowers subtended by a persistent foliaceous floral bract, equal to the size of the flowers; inflorescence with each flower subtended by a persistent, foliaceous inflorescence branch bract .... sect. *Auriculardisia*

1b. Individual flowers often subtended by persistent or caducous, non-foliaceous floral bracts much smaller than the flowers; inflorescence with flowers not subtended by a foliaceous inflorescence branch bract.

  2a. Inflorescences lateral (axillary) .... sect. *Pleurobotryae*

  2b. Inflorescences strictly terminal or pseudoterminal.

    3a. Leaf blades dimorphic, those of the reproductive shoots usually smaller and often a different shape from those of the vegetative ones .... sect. *Fagerlindia*

    3b. Leaf blades monomorphic, the shoots not specialized into vegetative and reproductive shoots, and the leaves all of the same general shape and size.

      4a. Peduncles at least ⅓ the length of the inflorescence .... sect. *Wedelia*

      4b. Peduncles less than ⅓ the length of the inflorescence.

        5a. Pedicels and inflorescence rachis minutely rufous glandular papillate or mixed with scattered uniseriate multicellular glandular villous hairs .... sect. *Amatlania*

        5b. Pedicels and inflorescence rachis furfuraceous-lepidote and/or cupuliform, and/or rufous stipitate-stellate villous, the trichomes with uniseriate, multicellular stalks below a stellate group of arms, the terminal arms often breaking off, leaving an apparently villous trichome, the indument normally persistent .... sect. *Palmanae*

Taxonomic Treatment of *Ardisia* subg. *Auriculardisia* sect. *Amatlania*

Ardisia subg. **Auriculardisia** sect. **Amatlania** (Lundell) Ricketson & Pipoly, comb. et stat. nov. Basionym: *Amatlania* Lundell, Wrightia 7: 38. 1982. TYPE: *Ardisia liebmannii* Oerst. [≡ *Amatlania liebmannii* (Oerst.) Lundell].

Shrubs or small trees. *Branchlets* slender, terete, densely and minutely rufous glandular papillate or mixed with scattered uniseriate multicellular glandular villous hairs, often glabrescent with age. *Leaves* monomorphic; blades membranous to coriaceous, elliptic to oblong or obovate to oblanceolate, mostly inconspicuously or conspicuously but often prominently punctate and punctate-lineate; petioles slender, terete. *Inflorescences* terminal, erect, bipinnately to quadri-pinnately paniculate, pyramidal, shorter or longer than the leaves, usually loosely congested corymbs; inflorescence bracts foliaceous, usually caducous; inflorescence branch bracts and floral bracts often caducous, margins variously toothed, usually with irregularly finely serrate "pectinate" teeth, or regularly dentate or serrate, or rarely entire; pedicels slender, terete. *Flowers* 5-merous, white, light pink, light purple, red, or blue-violet; calyx lobes essentially free, membranous to chartaceous, ovate to lanceolate, basally auriculate; corolla membranous, the lobes ovate to lanceolate, inconspicuously to conspicuously and usually prominently punctate and punctate-lineate, densely yellow glandular-granulose within the corolla tube; stamens connate; the filaments apically free, connate basally into an elobate tube, free from the corolla tube, epunctate, densely yellow glandular-granulose, the anthers ovoid to lanceoloid, apically apiculate, basally sagittate to cordate, dehiscent by subapical pores, opening into wide, longitudinal slits, the connective punctate; pistil glabrous, the ovary oblong, the style slender, erect, epunctate to inconspicuously punctate, the ovules pluriseriate. *Fruits* globose, inconspicuously or conspicuously, often prominently punctate and punctate-lineate, costate.

Distribution. *Ardisia* subg. *Auriculardisia* sect. *Amatlania* is found from San Luis Potosí, Hidalgo, Pueblo, Veracruz, and Oaxaca, throughout the Mesoamerican region. In South America it is found from Venezuela, Colombia, Ecuador, and Peru. It grows from 10 to 1700 m in elevation.

Ecology. Members of *Ardisia* subg. *Auriculardisia* sect. *Amatlania* grow in a variety of humid habitats, including tall moist, humid, wet and pluvial forests, and lowland, premontane, and montane elevations. There are a few species that occur in gallery forest in seasonally dry areas as well. They generally have broad ecological tolerance for disturbance as long as water is not scarce.

Ardisia subg. *Auriculardisia* sect. *Amatlania* is defined by (1) its vestiture of sparse to dense minute papillae or those papillae mixed with dense to sparse uniseriate, multicellular villous hairs; (2) leaf margins variously toothed, usually with irregularly finely serrate "pectinate" teeth, or regularly dentate or serrate, or rarely entire; (3) dense yellow glandular-granules within the corolla tube and on the filaments, similar to those found in *Ardisia* subg. *Graphardisia*.

KEY TO THE TAXA OF *ARDISIA* SUBG. *AURICULARDISIA* SECT. *AMATLANIA*

1a. Leaf blade margins irregularly finely serrate, the teeth 7 to 12 per cm, "pectinate" .... *Ardisia pellucida*

2a. Vestiture of the branchlets, inflorescence rachis, branches, and pedicels with a mixture of densely minutely rufous glandular papillose and scattered erect uniseriate multicellular glandular villous hairs; calyx sparsely to densely and prominently punctate and punctate-lineate.

3a. Calyx lobes ovate, 1.7–1.9 × 0.9–1.4 mm; corolla lobes 2.2–2.7 mm long; anthers ovoid, 1.2–1.4 mm long .... 5. *Ardisia pellucida* subsp. *pellucida*

3b. Calyx lobes ovate to lanceolate, 3.1–3.2 × 1.5–1.7 mm; corolla lobes 4.3–4.5 mm long; anthers lanceoloid, 3–3.1 mm long .... 3. *Ardisia pellucida* subsp. *lancetillensis*

2b. Vestiture of the branchlets, inflorescence rachis, branches, and pedicels densely minutely papillose only; calyx sparsely, inconspicuously punctate and punctate-lineate.

4a. Leaves oblanceolate; calyx lobes ovate, 2.1–2.2 × 1.4–1.5 mm; corolla lobes 5–5.2 × 2.8–2.9 mm; anthers lanceoloid, 3–3.1 × 0.8–1 mm; pistil 4.7–4.8 mm long; style 3.2–3.3 mm long .... 4. *Ardisia pellucida* subsp. *pectinata*

4b. Leaves elliptic; calyx lobes lanceolate, 2.5–2.6 × 0.9–1 mm; corolla lobes 3.6–3.8 × 2.4–2.6 mm; anthers ovoid, 0.9–1 × 0.6–0.7 mm; pistil 3.8–3.9 mm long; style 2.7–2.9 mm long .... 6. *Ardisia pellucida* subsp. *thomascroatii*

1b. Leaf blade margins entire to regularly dentate to serrate, the teeth 3 to 5 per cm.

5a. Corolla lobes 5.6–5.8 × 2.6–2.9 mm; anthers lanceoloid, apically subulate-apiculate, 2.5–2.6 mm long; styles 4.6–4.7 mm long .... 7. *Ardisia schippii*

5b. Corolla lobes 2.7–3.2 × 1.6–2 mm; anthers linear-lanceoloid, apically apiculate, 1.9–2.2 mm long; styles 3.1–3.6 mm long .... *Ardisia liebmannii*

6a. Vestiture of branchlets and inflorescence branches glabrescent, or of scattered to densely and minutely rufous glandular papillose, or with a mixture of densely and minutely rufous glandular papillose and scattered erect uniseriate multicellular glandular villous trichomes; vestiture of leaves usually glabrous above, scattered minutely papillose below; corolla lobes 2.7–2.8 × 1.9–2 mm; anthers 2.1–2.2 mm; styles 3.1–3.2 mm long .... 2. *Ardisia liebmannii* subsp. *liebmannii*

6b. Vestiture of branchlets and inflorescence branches with a mixture of densely and minutely rufous glandular papillose and densely erect uniseriate multicellular glandular villous trichomes; vestiture of leaves usually glabrous above or sparsely and minutely papillose especially along the midrib, glabrous below or sparsely and minutely papillose, the indument of the midrib with a mixture of densely and minutely papillose and densely simple multicellular hairs; corolla lobes 3.1–3.2 × 1.6–1.9 mm; anthers 1.9–2 mm long; styles 3.5–3.6 mm long .... 1. *Ardisia liebmannii* subsp. *jalapensis*

Ardisia liebmannii Oerst., Vidensk. Meddel. Dansk Naturhist. Føren Kjøbenhavn 1861: 129. 1862. *Icacorea liebmannii* (Oerst.) Standl., Contr. U.S. Natl. Herb. 23: 1110. 1924. *Amatlania liebmannii* (Oerst.) Lundell, Wrightia 7: 40. 1982. TYPE: Mexico. Veracruz: prope Amatlan [de los Reyes], July 1842 (fl), *F. Liebmann 7A* (holotype, C!).

Shrubs 0.3–6.1 m tall. *Branchlets* 1–4 mm diam., glabrescent, or of scattered to densely and minutely rufous glandular papillose, or with a mixture of densely and minutely rufous glandular papillose and scattered to densely erect uniseriate multicellular glandular villous trichomes. *Leaves* with blades chartaceous, oblong to elliptic, 4.8–21.5 × 2.5–9.1 cm, apically acuminate to long acuminate, with an acumen 0.6–4.2 cm long, basally acute to cuneate, decurrent on the petiole, inconspicuously punctate and punctate-lineate, usually glabrous above or sparsely and minutely papillose especially along the midrib, glabrous below or sparsely to scattered minutely papillose, the indument of the midrib often with a mixture of densely and minutely papillose and densely simple multicellular hairs, the midrib impressed above, conspicuously raised below, the secondary veins 10 to 19 pairs, prominulous above and below, the margins regularly dentate to serrate, flat; petioles slender, marginate, 0.6–2.7 mm long, vestiture as in the leaves. *Inflorescences* erect, bi- to tripinnately paniculate, 2.5–14 × 2–13 cm, pyramidal, shorter to longer than the leaf blades, the rachis with vestiture like the branchlets, the branches terminating in 4- to 10-flowered corymbs; peduncles 0.4–3.4 cm long, the lower branches often subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts membranous, oblong, 1.2–7.5 × 0.2–3 mm, apically acute, basally sessile, midvein obscure to impressed above, prominulous below, prominently punctate and punctate-lineate, papillate and/or villous as in the leaves, the margins regularly entire, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but ovate or deltate, 0.6–2 × 0.2–0.8 mm, usually glabrous above or sparsely and minutely papillose, glabrous below or with scattered minute papillae; petioles slender, terete, 2.8–6 mm long, inconspicuously punctate and punctate-lineate, papillate and/or villous like the branchlets. *Flowers* 5-merous, pink to light purple or red; calyx lobes chartaceous, ovate, 1.4–1.9 × 0.9–1.3 mm, apically acute to acuminate, nearly epunctate to sparsely and conspicuously or inconspicuously to prominently punctate and punctate-lineate, glabrous adaxially, sparsely and minutely papillate abaxially, the margins erose, hyaline, sparsely glandular ciliolate; corolla membranous, 3.6–4 mm long, the tube 0.4–0.6 mm long, the lobes ovate to lanceolate, 2.7–3.2 × 1.6–2 mm, apically acute, few inconspicuous and prominently punctate and punctate-lineate, glabrous throughout, but densely yellow glandular-granulose adaxially, apically above staminal tube as well as between the junction of the corolla tube and the lobes, the margins entire, hyaline; stamens 3.4–4 mm long, the filaments 1.6–2 mm long, the tube 0.3–0.6 mm long, the apically free portions 1–1.7 mm long, epunctate, densely yellow glandular-granulose, the anthers lanceoloid, 1.9–2.2 × 0.6–0.8 mm, apically long acuminate apiculate, basally cordate, the connective epunctate to few conspicuous and prominently punctate; pistil 4–4.5 mm long, the ovary oblong, 0.8–1 mm long, the style 3.1–3.6 mm long, epunctate, the ovules 8, biseriate. *Fruits* globose, 3.6–5 mm diam., usually apically inconspicuously punctate and punctate-lineate, prominently costate.

Distribution. *Ardisia liebmannii* is found from Hidalgo, Pueblo, Oaxaca, Veracruz, and Chiapas, Mexico, growing from 550 to 1700 m in elevation.

Ecology. *Ardisia liebmannii* occurs in primary and secondary lower montane forests, montane rain forests, and evergreen wet forests.

Within *Ardisia* subg. *Auriculardisia* sect. *Amatlania*, *Ardisia liebmannii* appears to be most closely related to *A. schippii* based on its entire to regularly dentate or serrate (not pectinate) leaf margins. However, *A. liebmannii* may be distinguished from *A. schippii* by its smaller corolla lobes to 3.2 × 2 mm, shorter linear-lanceoloid anthers to 2.2 mm long with apiculate apices, and the shorter styles to 3.6 mm long.

During the 1930s, J. F. Macbride of the Field Museum of Natural History photographed Neotropical types and "authentic specimens" of European herbaria. Unfortunately, the widely circulated photograph of *Ardisia liebmannii*, F neg. 22951, is from *F. Liebmann 7* (C), not of the type specimen, *F. Liebmann 7A*, and should only be considered a paratype.

1. **Ardisia liebmannii** subsp. **jalapensis** (Lundell) Ricketson & Pipoly, comb. et stat. nov. Basionym: *Ardisia jalapensis* Lundell, Wrightia 6: 104. 1980. *Amatlania jalapensis* (Lundell) Lundell, Wrightia 7: 40. 1982. TYPE: Mexico. Veracruz: Mpio. de Xalapa [Jalapa], km 7 carr. San Andresito, 1320 m, 4 Aug. 1976 (fr), *M. Zola B. 610* (holotype, LL!; isotypes, F!, MEXU!, XAL!). Figure 4.

Shrubs 1–6 m tall. *Branchlets* 1–3 mm diam., with a mixture of densely and minutely rufous glandular papillose and densely erect uniseriate multicellular glandular villous trichomes. *Leaves* with blades 5.4–15.8 × 2.5–6 cm, with an acumen 0.6–2.3 cm long, usually glabrous above or sparsely and minutely papillose especially along the midrib, glabrous below or sparsely and minutely papillose, the indument of the midrib with a mixture of densely and minutely papillose and densely simple multicellular hairs; petioles 0.8–1.7 mm long, vestiture as in the leaves. *Inflorescences* 3–10.5 × 3–12 cm, vestiture as in the branchlets, the branches terminating in 4- to 8-flowered corymbs; peduncles 0.8–1.7 cm long; inflorescence branch bracts 2–6 × 0.3–1.4 mm, densely glandular papillose and/or villous; floral bracts 0.8–1.3 × 0.2–0.4 mm; petioles 4–4.3 mm long. *Flowers* pink to violet; calyx lobes 1.4–1.5 × 0.9–1 mm; corolla 3.6–3.8 mm long, the tube 0.5–0.6 mm long, the lobes 3.1–3.2 × 1.6–1.9 mm; stamens 3.4–3.5 mm long, the filaments 1.6–1.7 mm long, the staminal tube 0.5–0.6 mm long, the apically free portions 1–1.2 mm long, the anthers lanceoloid, 1.9–2 × 0.6–0.7 mm; pistil 4.4–4.5 mm long, the ovary 0.9–1 mm long, the style 3.5–3.6 mm long. *Fruits* 4.2–4.8 mm diam.

Distribution. *Ardisia liebmannii* subsp. *jalapensis* is found in Hidalgo, Pueblo, and Veracruz, Mexico, growing from 800 to 1700 m in elevation.

Ecology and conservation status. *Ardisia liebmannii* subsp. *jalapensis* occurs in montane oak and pine forests. It apparently has some ecological tolerance because it has been collected in secondary forests, and data suggest that it is currently under threat.

Within *Ardisia* subg. *Auriculardisia* sect. *Amatlania*, *Ardisia liebmannii* subsp. *jalapensis* is most closely related to *A. liebmannii* subsp. *liebmannii* by its leaf blade margins regularly dentate to serrate, corolla lobes to 3.2 × 2 mm, linear-lanceoloid anthers to 2.2 mm long with apiculate apices, and styles to only 3.6 mm long. *Ardisia liebmannii* subsp. *jalapensis* may be easily distinguished from subspecies *liebmannii* because of the vestiture of the leaves usually glabrous above or sparsely and minutely papillose especially along the midrib, glabrous below or sparsely and minutely papillose, the indument of the midrib with a mixture of densely and minutely papillose and of densely simple multicellular hairs along the midrib and the vestiture on its branchlets and inflorescence branches with a mixture of densely and minutely rufous glandular papillose and densely erect uniseriate multicellular glandular villous trichomes, the longer corolla lobes to 3.2 × 1.9 mm, the shorter anthers to 2 mm long, and the longer styles to 3.6 mm long.

Specimens examined. MEXICO. **Hidalgo**: Mpio. Tenang de Doria, 5 km NE of Tenango de Doria, toward Huehuetla, 5 July 1979 (fr), *R. Hernández M. 3338* (MO); Mpio. Tenango de Doria, 9.5 km N of Tenango along road to San Bartolo Tutotepec, 9 Aug. 1987 (fl, fr), *S. Koch 8772* (LL). **Pueblo**: Cañada del Río Apulco N of Zacapoaxtla, 21 June 1977 (fl), *M. Martínez et al. 90* (MEXU, MO); Mpio. de Pahuatlan, Xopanapa 8 km al SW de Pahuatlan, 22 May 1986 (fl), *P. Tenorio L. & C. Romero de T. 11375* (MEXU, MO); Mpio. Ahuacatlán, path to Zapotitlán, Agua Dulce, 4 km SE of Ahuacatlán, 2 July 1987 (fl), *G. Toriz A. et al. 584* (FTG, MEXU). **Veracruz**: Mpio. Huatusco, trail to Tepampa, 4 km from the Huatusco–Coscomatepec Hwy., 1 Aug. 1979 (fl), *S. Avendaño R. & J. Calzada 403* (F, LL); Mpio. Huatusco, Cerro Cercano, Río Seco, along Huatusco–Coscomatepec Hwy., 7 Nov. 1979 (fr), *S. Avendaño R. 556* (F, LL); Mpio. Juchique de Ferrer, Cerro de Villa Rica, 6 May 1981 (fl), *G. Castillo C. et al. 1764* (F, LL, XAL); Mpio. Juchique Ferrer, between Las Hayas & Pena Colorada, 21 June 1972 (fl), *R. Hernández M. & I. Calzada 1536* (F, MEXU); Mpio. Juchique Ferrer, La Cima, Las Hayas, 21 June 1972 (fl), *R. Hernández M. 1565* (F, MEXU); Mpio. Tlapacoyan, ca. 6 km by air S of Tlapacoyan on road to Altotonga, 11 July 1982 (fr), *M. Nee & G. Diggs 24883* (F).

2. **Ardisia liebmannii** subsp. **liebmannii.** Figure 5.

Ardisia crenipetala Mez, in Engl., Pflanzenr. IV. 236 (Heft 9): 91. 1902. Syn. nov. *Icacorea crenipetala* (Mez) Standl., Contr. U.S. Natl. Herb. 23: 1110. 1924. *Amatlania crenipetala* (Mez) Lundell, Wrightia 7: 41. 1982. TYPE: Mexico. Veracruz: Orizaba, 1856 (fl), *M. Botteri 146* (lectotype, designated by C. Lundell (1982), G!; isolectotypes, GH!, LL!, US!).

Ardisia rekoi Lundell, in Schultes, Bot. Mus. Leafl. 9: 185. 1941. Syn. nov. TYPE: Mexico. Oaxaca: Dtto. Teotitlán, barranca Nin-du-da-gé, San Antonio Eloxochitlán, 18°21′N, 096°45′W, 1100 m, 24 July 1938 (fl), *R. Schultes & B. Reko 273* (holotype, MICH!, LL neg. 1971-12!; isotype, GH!).

Amatlania elliptica Lundell, Phytologia 56: 19. 1984. Syn. nov. *Ardisia ellipitifolia* Lundell, Phytologia 61: 63. 1986, non *Ardisia elliptica* Thunb., Nov. Gen. Pl. 8: 119. 1798. TYPE: Mexico. Oaxaca: Mpio. de Comaltepec, km 149 carr. Tuxtepec, Sierra Juárez, Puerto Eligio, 800 m, 17 June 1966 (fr), *G. Martínez-Calderón 884* (holotype, XAL not seen; isotype, MO!).

Shrubs 0.3–6.1 m tall. *Branchlets* 1.5–4 mm diam., glabrescent, or of scattered to densely and

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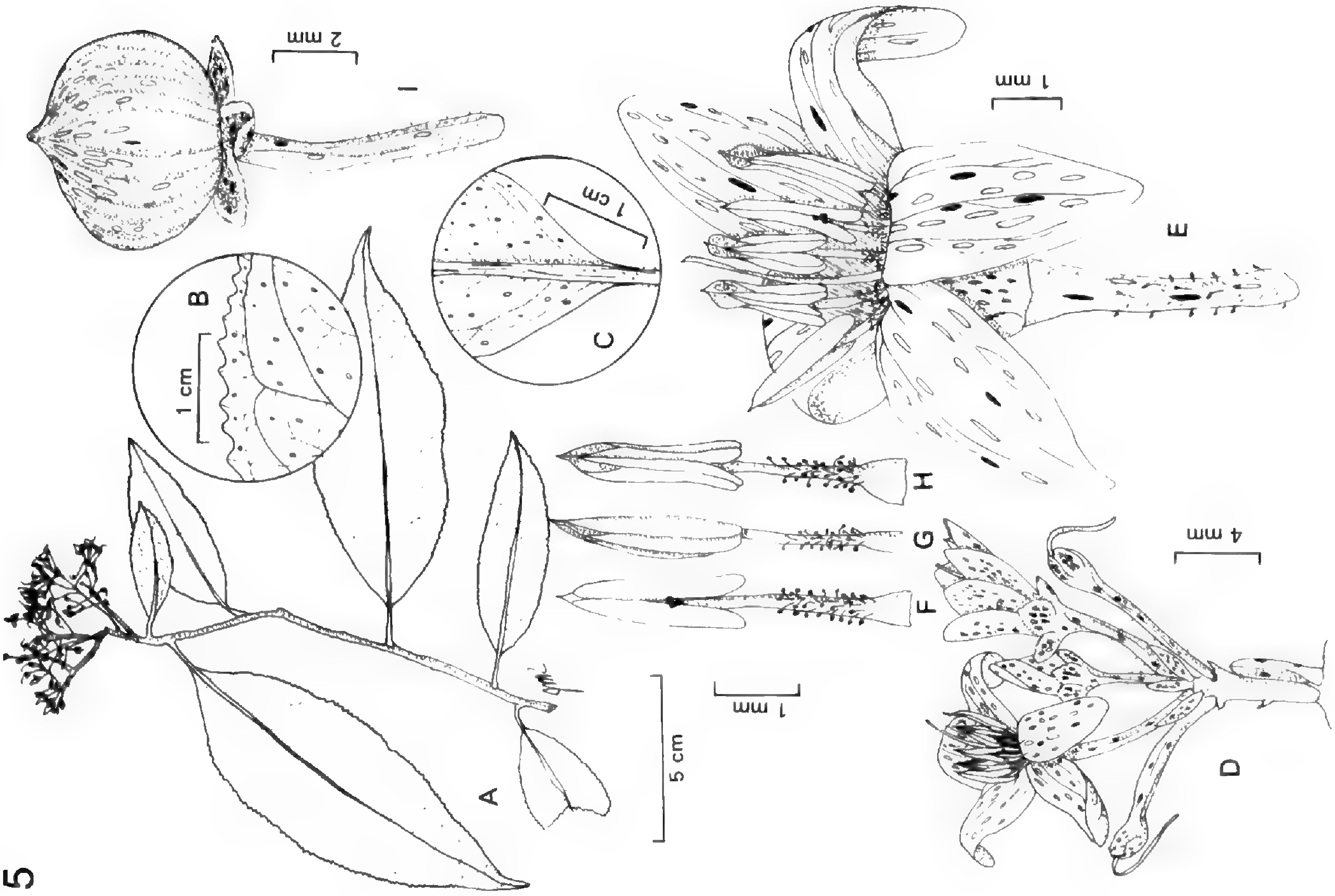
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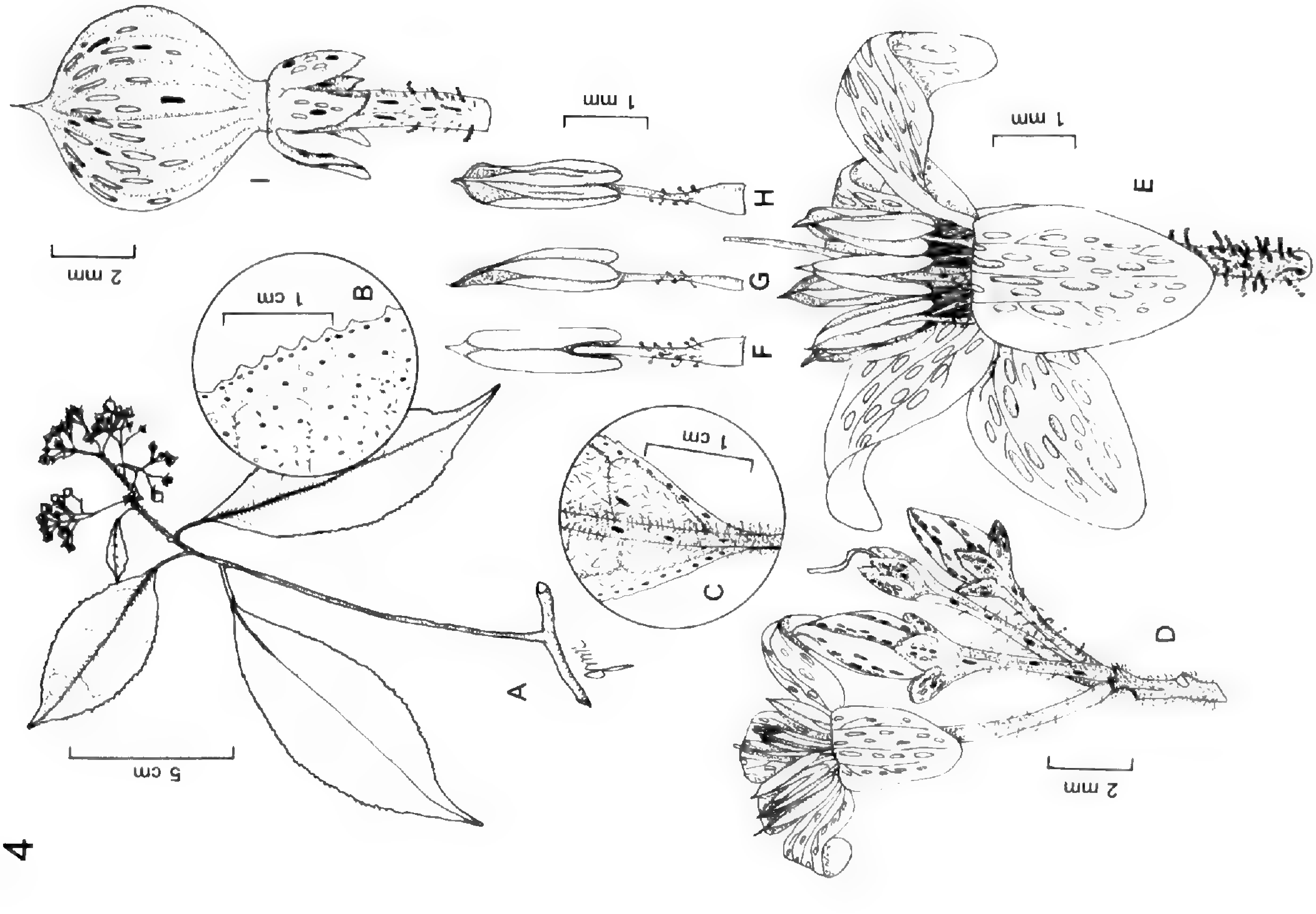
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minutely rufous glandular papillose, or with a mixture of densely and minutely rufous glandular papillose and scattered erect uniseriate multicellular glandular villous trichomes. *Leaves* with blades 4.8–21.5 × 2.5–9.1 cm, with an acumen 1–4.2 cm long, usually glabrous above, scattered minutely papillose below; petioles 0.6–2.7 mm long, vestiture as in the leaves. *Inflorescences* 2.5–14 × 2–13 cm, with the vestiture like the branchlets, the branches terminating in 4- to 10-flowered corymbs; peduncles 0.4–3.4 cm long; inflorescence branch bracts membranous, 1.2–7.5 × 0.2–3 mm, with scattered minute papillae; floral bracts 0.6–2 × 0.3–0.8 mm; petioles 2.8–6 mm long, papillose or villous as in the branchlets. *Flowers* lavender or pink to light purple or red; calyx lobes 1.5–1.9 × 1–1.3 mm; corolla 3.9–4 mm long, the tube 0.4–0.5 mm long, the lobes 2.7–2.8 × 1.9–2 mm; stamens 3.9–4 mm long, the filaments 1.9–2 mm long, the staminal tube 0.3–0.4 mm long, the apically free portions 1.5–1.7 mm long, the anthers 2.1–2.2 × 0.7–0.8 mm; pistil 4–4.1 mm long, the ovary 0.8–0.9 mm long, the style 3.1–3.2 mm long. *Fruits* 3.6–5 mm diam.

Distribution. Ardisia liebmannii subsp. *liebmannii* is restricted to Chiapas, Oaxaca, and Veracruz, Mexico, growing from 550 to 1680 m in elevation.

Ecology and conservation status. Ardisia liebmannii subsp. *liebmannii* occurs in primary and secondary lower montane forests, montane rain forests, and evergreen wet forests. Because it is relatively uncommon, it should be considered threatened.

Within *Ardisia* subg. *Auriculardisia* sect. *Amatlania, Ardisia liebmannii* subsp. *liebmannii* is most closely related to *A. liebmannii* subsp. *jalapensis* (see under that subspecies for a discussion). *Ardisia liebmannii* subsp. *liebmannii* may be easily distinguished from subspecies *jalapensis* because the vestiture of the leaves is usually glabrous above, with scattered minute papillae below, and the vestiture on its branchlets and inflorescence branches is glabrescent, or of scattered to densely and minutely rufous glandular papillose, or with a mixture of densely and minutely rufous glandular papillose and scattered erect uniseriate multicellular glandular villous trichomes, the shorter corolla lobes to 2.8 × 2 mm, the longer anthers to 2.2 mm long, and the shorter styles to 3.2 mm long.

Populations corresponding to the type of *Ardisia crenipetala* are unique only for the more scattered and slightly longer multicellular glandular villous hairs in the inflorescence; otherwise it matches *Ardisia liebmannii* subsp. *liebmannii* in all other respects. In Mez's (1902) original description of *Ardisia crenipetala,* he listed three syntypes, *Botteri 146, 481,* and *Conzatti 169,* from G-DC, P, and GH. Standley (1924) did not list any specimens in his treatment for Mexico. Lundell (1982), however, indirectly lectotypified the *Botteri 146* collection at G as the lectotype in his treatment of *Amatlania.*

Ardisia rekoi was originally described as being related to *Ardisia nigrescens* Oerst. However, study of the type shows that it has auriculate calyx lobes, which clearly place it in *Ardisia* subg. *Auriculardisia.* The type of *Amatlania elliptica* was collected in fruit and represents populations unique for their slightly wider leaves with shallow dentate margins.

Specimens examined. MEXICO. **Chiapas:** Mpio. of Tenejapa, slope at the sumidero at the market place of Yochib, paraje of Kotol Te', 16 July 1965 (fl), *D. Breedlove 11081* (LL); Chiapas Highlands, 6 km NE, by road, of Bochil on hwy. 195, 10 Aug. 1965 (fr), *K. Roe et al. 1145* (F). **Oaxaca:** Mpio. of San Felipe Usila, Cerro Verde, 7 km al NNE de San Felipe Usila, 30 Sep. 1992 (fr), *G. Ibarra M. et al. 3720* (MO); Mirador, 1843 (fl), *F. Liebmann 7* (C, F neg. 22951); Mpio. of Valle Nacional, Cerro Mirador, 15 km NNW de Valle Nacional, 16 Oct. 1992 (fr), *J. Meave del Castillo et al. 1514* (MO); Mpio. Angel Albino Corzo, slope near Rancho Viejo of the Finca Prusia, 23 Jan. 1968 (fr), *A. Shilom T. 3567* (F, LL, NY). **Veracruz:** Cerro del Borrego, Oct. 1856 (fl), *M. Botteri 481* (G, K, P); Cantón de Cordoba, Colonia Melchor Ocampo, 19 June 1896 (fl), *C. Conzatti 169* (GH); Orizaba, 1855 (fl), *M. Cuming s.n.* (G); Mpio. Misantla, El Haya, camino Naolinco, Misantla, 27 June 1971 (fl), *J. Dorantes 242* (MEXU); Orizaba, May 1905 (fl), *C. Purpus 1242* (F, GH, MO, NY); El Paso Berero between Atzacan and Dos

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Figure 4 (left). *Ardisia liebmannii* subsp. *jalapensis.* —A. Flowering branch. —B. Detail of margin of abaxial leaf surface. —C. Detail of basal area of abaxial leaf surface. —D. Detail of inflorescence. —E. Flower. —F. Stamen, abaxial surface. —G. Stamen, lateral margin. —H. Stamen, adaxial surface. —I. Fruit. (A, B drawn from holotype, *M. Zola B. 610* (LL); C, E–H from *M. Martínez et al. 90* (MEXU); D from *R. Hernández M. 1565* (MEXU); I from *S. Avendaño R. 556* (F).)

Figure 5 (right). *Ardisia liebmannii* subsp. *liebmannii.* —A. Flowering branch. —B. Detail of margin of abaxial leaf surface. —C. Detail of basal area of abaxial leaf surface. —D. Detail of inflorescence. —E. Flower. —F. Stamen, abaxial surface. —G. Stamen, lateral margin. —H. Stamen, adaxial surface. —I. Fruit. (A–C drawn from the holotype, *F. Liebmann 7A* (C); D from *F. Liebmann 7* (C); E–H from *S. Sohmer 9517* (F); I from *A. Shilom T. 3567* (F).)

Ríos about 10 km N of Orizaba, 15 July 1974 (fl), *S. Sohmer 9517* (F, MEXU); Tenango al N Río Blanco, 11 July 1983 (fl), *R. Torres C. & H. Hernández 3261* (MEXU), *3262* (MO).

Ardisia pellucida Oerst., Vidensk. Meddel. Dansk Naturhist. Føren Kjøbenhavn 1861: 130. 1862. *Icacorea pellucida* (Oerst.) Standl., Contr. U.S. Natl. Herb. 23: 1110. 1924. *Amatlania pellucida* (Oerst.) Lundell, Wrightia 7: 40. 1982. TYPE: Mexico. Veracruz: prope Pital, (fl), *F. Liebmann 29C* (holotype, C!, F neg. 22955!).

Shrubs or *subshrubs* 0.3–5(–10) m tall, 2.5–6 cm diam. *Branchlets* 2–9 mm diam., scattered to densely and minutely rufous glandular papillose, or with a mixture of densely minutely rufous glandular papillose and scattered erect uniseriate multicellular glandular villous hairs. *Leaves* with blades membranous to chartaceous, elliptic, obovate to oblanceolate, 6.5–64.2 × 3–20.6 cm, apically acute to acuminate, with an acumen 0.4–4.8 cm long, basally obtuse to cuneate or oblique or auriculate, usually decurrent on the petiole, inconspicuously or conspicuously and usually prominently punctate and punctate-lineate, glabrous above, sparsely and minutely papillose, denser along the midveins and secondary veins, the midrib impressed above, conspicuously raised below, the secondary veins 12 to 39 pairs, prominulous above and below, the margins irregularly finely serrate, the teeth 7 to 12 per cm, "pectinate," flat; petioles slender, marginate, 0.9–3.6 cm long, glabrous above, sparsely to densely and minutely papillose. *Inflorescences* erect, bi- to quadri-pinnately paniculate, 2.8–28.2 × 2.6–22.7 cm, pyramidal, shorter or longer than the leaves, vestiture of the rachis similar to the branchlets, the branches terminating in 5- to 19-flowered corymbs; peduncles obsolete to 2.1 cm long, the lower branches often subtended by leaves; inflorescence bracts obsolete; inflorescence branch bracts membranous, linear or oblong to elliptic, 2.8–12.9 × 0.2–2.9 mm, apically acute to attenuate, sparsely to densely and conspicuously or prominently punctate and punctate-lineate, the margins entire except minutely erose apically, hyaline, sparsely glandular ciliolate or irregularly finally serrate "pectinate," the midvein obscure to impressed above and raised below, the secondary veins obscure, floral bracts membranous, linear, 0.6–3.3 × 0.2–0.8 mm, apically acute, basally sessile, the veins obsolete, sparsely to densely inconspicuously or conspicuously or prominently punctate and punctate-lineate, the margins entire except minutely erose apically, hyaline, sparsely glandular ciliolate; pedicels slender, terete, 3.1–12.5 mm long, inconspicuously punctate and punctate-lineate, sparsely to densely minutely papillose. *Flowers* 5- or 6-merous, lavender to red-violet or blue-violet to deep purple; calyx lobes essentially free, membranous to chartaceous, ovate to lanceolate, 1.7–3.2 × 0.9–1.7 mm, apically acute to long acuminate, notched below the apex, rarely lacking a notch, basally auriculate, sparsely to densely and inconspicuous or conspicuously punctate or punctate-lineate, and often prominently punctate and punctate-lineate, glabrous adaxially, sparsely minutely papillose, the margins erose, hyaline, sparsely glandular ciliolate; corolla membranous, 3.5–6.1 mm long, the tube 0.7–1.4 mm long, the lobes ovate to lanceolate, 2.2–5.2 × 1.8–2.9 mm, apically acute, epunctate to bearing a few inconspicuous or conspicuous punctations and punctate-lineations, glabrous adaxially, or densely yellow glandular-granulose apically above the staminal tube as well as between the junction of the corolla tube and lobe, glabrous outside or sparsely minutely papillose medially, the margins entire, hyaline; stamens 2.3–4.8 mm long, the filaments 1.3–2.5 mm long, the staminal tube 0.2–0.8 mm long, the apically free portions 1–1.8 mm long, epunctate to slightly punctate, glabrous to densely yellow glandular-granulose, the anthers ovoid to lanceoloid, 0.9–3.1 × 0.6–1 mm, apically apiculate, basally cordate to sagittate, the connective epunctate to inconspicuously punctate; pistil 2.5–4.8 mm long, the ovary oblong, 0.9–1.5 mm long, epunctate or conspicuously punctate and punctate-lineate, the style 1.5–3.3 mm long, epunctate or inconspicuously punctate, the ovules 9 to 37. *Fruits* globose, 3.9–5.8 mm diam., inconspicuously punctate and punctate-lineate, costate.

Distribution. *Ardisia pellucida* is found from San Luis Potosí, Pueblo, Veracruz, Oaxaca, Tabasco, and Chiapas, Mexico, and throughout Mesoamerica. In South America it is found from Venezuela, Colombia, Ecuador, and Peru, growing from 35 to 1650 m in elevation.

Ecology. *Ardisia pellucida* occurs in primary or secondary humid, moist, wet, or pluvial tropical forests from the lowlands to premontane levels, rarely in cloud forests where it occurs on low, isolated mountain peaks.

Ardisia pellucida is a highly variable species within *Ardisia* subg. *Auriculardisia* sect. *Amatlania*. From the other species in section *Amatlania*, it may be recognized by its leaf blade margin irregularly finely serrate with teeth 7 to 12 per cm, "pectinate," whereas the leaf blade margins in *Ardisia schippii* and *A. liebmannii* are regularly dentate to serrate with teeth 3 to 5 per cm or, very rarely, entire.

3. **Ardisia pellucida** subsp. **lancetillensis** Ricketson & Pipoly, subsp. nov. TYPE: Honduras. Atlántida: hills above Lancetilla, 1500 ft. [457 m], 15 July 1934 (fl), *T. Yuncker 4588* (holotype, MO!; isotypes, A!, F!, NY!). Figure 6.

Subspecies haec a subsp. *pellucida,* lobulis calycinis 3.1–3.2 (nec 1.7–1.9) mm longis 1.5–1.7 (nec 0.9–1.4) mm latis, lobulis corollinis 4.3–4.5 (non 2.2–2.7) mm longis, denique antheris 3.0–3.1 (non 1.2–1.4) mm longis praeclare distat.

Shrubs 1–3 m tall. *Branchlets* 5–9 mm diam., sparsely to densely minutely rufous glandular papillose, or with a mixture of rufous glandular papillae and uniseriate multicellular glandular villous trichomes. *Leaves* with blades oblanceolate, 13.7–64.2 × 3.9–20.6 cm, with an acumen 0.7–3.6 cm long, the secondary veins 21 to 29 pairs; petioles 0.9–3.6 cm long. *Inflorescences* bi- to tripinnately paniculate, 8.5–28.2 × 5.6–22.7 cm, shorter or longer than the leaves, the peduncle, vestiture of the rachis, and branches similar to the branchlets, the branches terminating in 11- to 19-flowered corymbs; peduncles obsolete to 4.8 cm long; inflorescence branch bracts linear, 3.8–12.9 × 0.8–2.9 mm, densely and prominently punctate and punctate-lineate, the veins obscure, the margins minutely erose, hyaline, sparsely glandular ciliolate; floral bracts 1.5–3.3 × 0.2–0.6 mm, densely and prominently punctate and punctate-lineate; pedicels 3.1–12.5 mm long, inconspicuously punctate and punctate-lineate, densely minutely papillose. *Flowers* 5-merous, lilac, blue-violet, violet-purple to deep purple; calyx lobes ovate to lanceolate, 3.1–3.2 × 1.5–1.7 mm, apically acute to long acuminate, without notch below the apex, sparsely to prominently punctate and punctate-lineate; corolla 5.4–5.5 mm long, the tube 0.9–1 mm long, the lobes 4.3–4.5 × 2.2–2.3 mm, sparsely but conspicuously punctate and punctate-lineate, densely yellow glandular-granulose adaxially, apically above the staminal tube, as well as between the corolla tube and lobe junction, sparsely and minutely papillose medially outside; stamens 3.8–4 mm long, the filaments 1.3–1.6 mm long, the staminal tube 0.2–0.5 mm long, the apically free portions 1.1–1.2 mm, inconspicuously punctate, densely yellow glandular-granulose, the anthers lanceoloid, 3–3.1 × 0.9–1 mm; pistil 3.1–3.2 mm long, the ovary 0.9–1 mm long, conspicuously punctate and punctate-lineate, the style 2.1–2.2 mm long, inconspicuously punctate, the ovules 35 to 37. *Fruits* 5.5–5.8 mm diam.

Distribution. *Ardisia pellucida* subsp. *lancetillensis* is endemic to the area around the Lancetilla Valley, near Tela and the Jardín Botánico Lancetilla Biological Reserve in Atlántida, Honduras, growing between 10 and 600 m in elevation.

Ecology and conservation status. *Ardisia pellucida* subsp. *lancetillensis* occurs in disturbed primary and secondary rain forests, which receive up to 4500 mm annual precipitation. An exhaustive search was conducted to look for this subspecies, without success, so we may assume the subspecies is threatened.

Etymology. The subspecies is named for the Lancetilla Valley region, near Tela, Atlántida, on the north coast of Honduras. We are very grateful to Ing. Ciro Navarro, Director of the Jardín Botánico de Lancetilla, who brought this subspecies to our attention and helped Pipoly look for it in the field.

Within *Ardisia* subg. *Auriculardisia* sect. *Amatlania, Ardisia pellucida* subsp. *lancetillensis* shares with subspecies *pellucida* a similar vestiture with a mixture of densely minutely papillose and scattered, erect, long, simple multicellular hairs on the upper branchlets and throughout the inflorescence branches, but subspecies *lancetillensis* may be distinguished by its larger ovate to lanceolate calyx lobes to 3.2 mm long, larger corolla lobes to 4.5 mm long, and larger lanceoloid anthers to 3.1 mm long.

Paratypes. HONDURAS. **Atlántida**: Reserva del Jardín Botánico de Lancetilla, Sep. 1979 (fl), *M. Antonio V. 15* (MO); Lancetilla Valley, Lancetilla, 22 June–27 July 1929 (fl), *A. Chickering 200* (F); Lancetilla Valley, ca. 10 mi. SE of Tela, in forest preserve along Río Lancetilla, on trail to water reservoir, 3 Aug. 1977 (fl), *T. Croat 42632* (MO); along road for municipal water supply of Tela, Lancetilla Botanical Gardens, on road ca. 2 mi. WSW of Tela and S of main hwy., 9 Feb. 1987 (fr), *T. Croat & D. Hannon 64637* (MO); basin in front of old dam, 21 Aug. 1999 (fl), *R. Cruz 225* (HJBL); permanent Plot area, Lancetilla Reserve, 12 Nov. 1978 (fr), *D. Hazlett 2984* (HJBL); Lancetilla, 10 Aug. 1978 (fl), *D. Hazlett 3058* (HJBL); upper dam, Lancetilla Valley, 29 July–10 Aug. 1951 (fl), *R. Howard et al. 500* (A); Tela, Lancetilla Valley, above Experiment Station, along stream and slopes above stream but below the dam, 4 Nov. 1988 (fr), *J. MacDougal et al. 3170* (MO); trail between arboretum and Nuevo San Francisco, 18 Jan. 1994 (fr), *C. Nelson 17325* (HJBL); vicinity of San Alejo, at base of hills S of San Alejo near Río San Alejo [ca. 15 km SW of Tela], 22–27 Apr. 1947 (ster.), *P. Standley 7729* (F); Lancetilla Valley, near Tela, 6 Dec. 1927–20 Mar. 1928 (fr), *P. Standley 52692* (F, US), *53157* (F, US), *53322* (F, US); Lancetilla Valley, ca. 3 mi. S of Tela, 30 July 1962 (fl), *G. Webster et al. 12681* (F, LL); Lila River 2 mi. above Puerto Sierra, 18 Jan. 1903 (fr), *P. Wilson 79* (NY, US).

4. **Ardisia pellucida** subsp. **pectinata** (Donn. Sm.) Ricketson & Pipoly, comb. et stat. nov.

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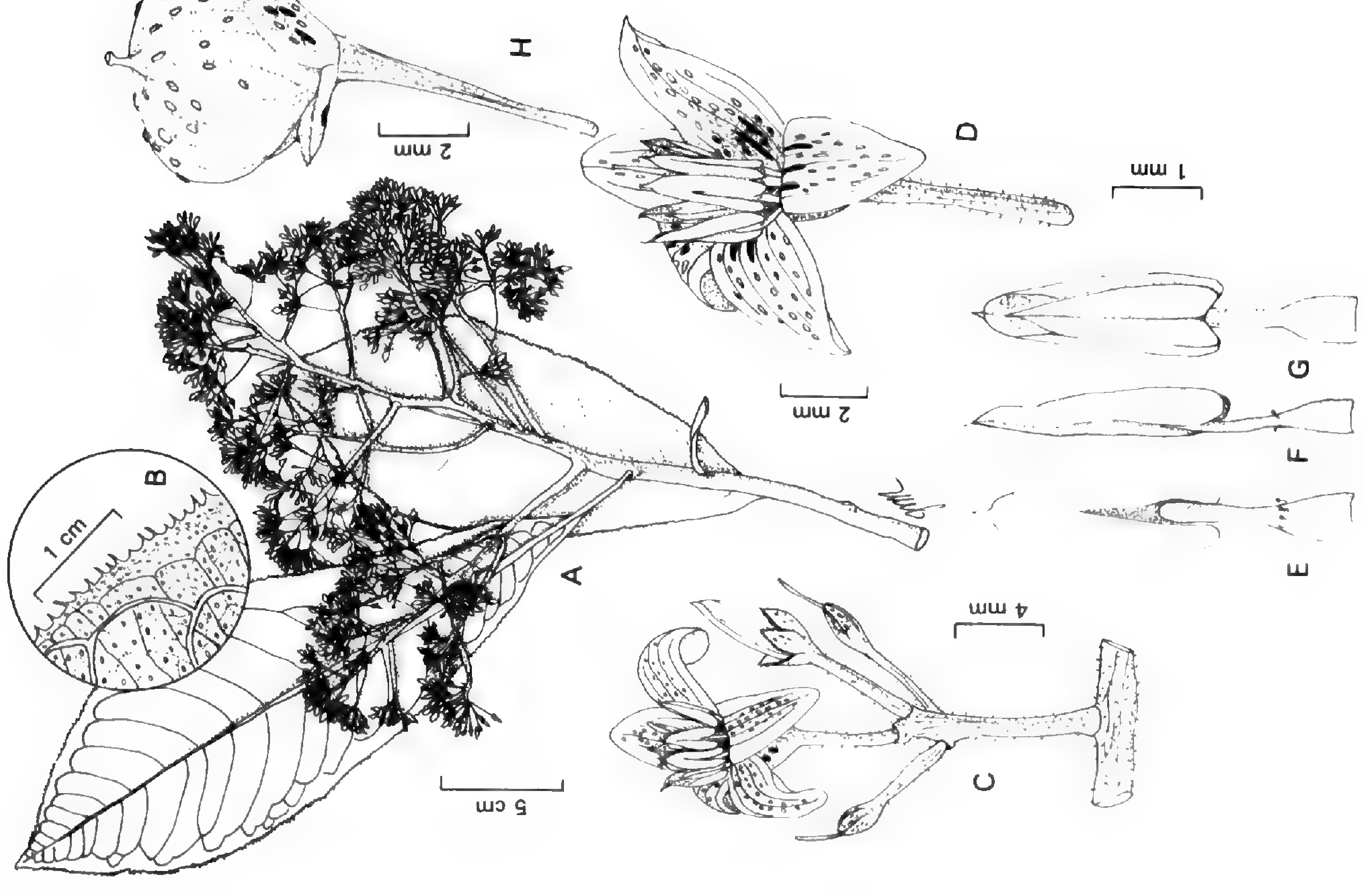
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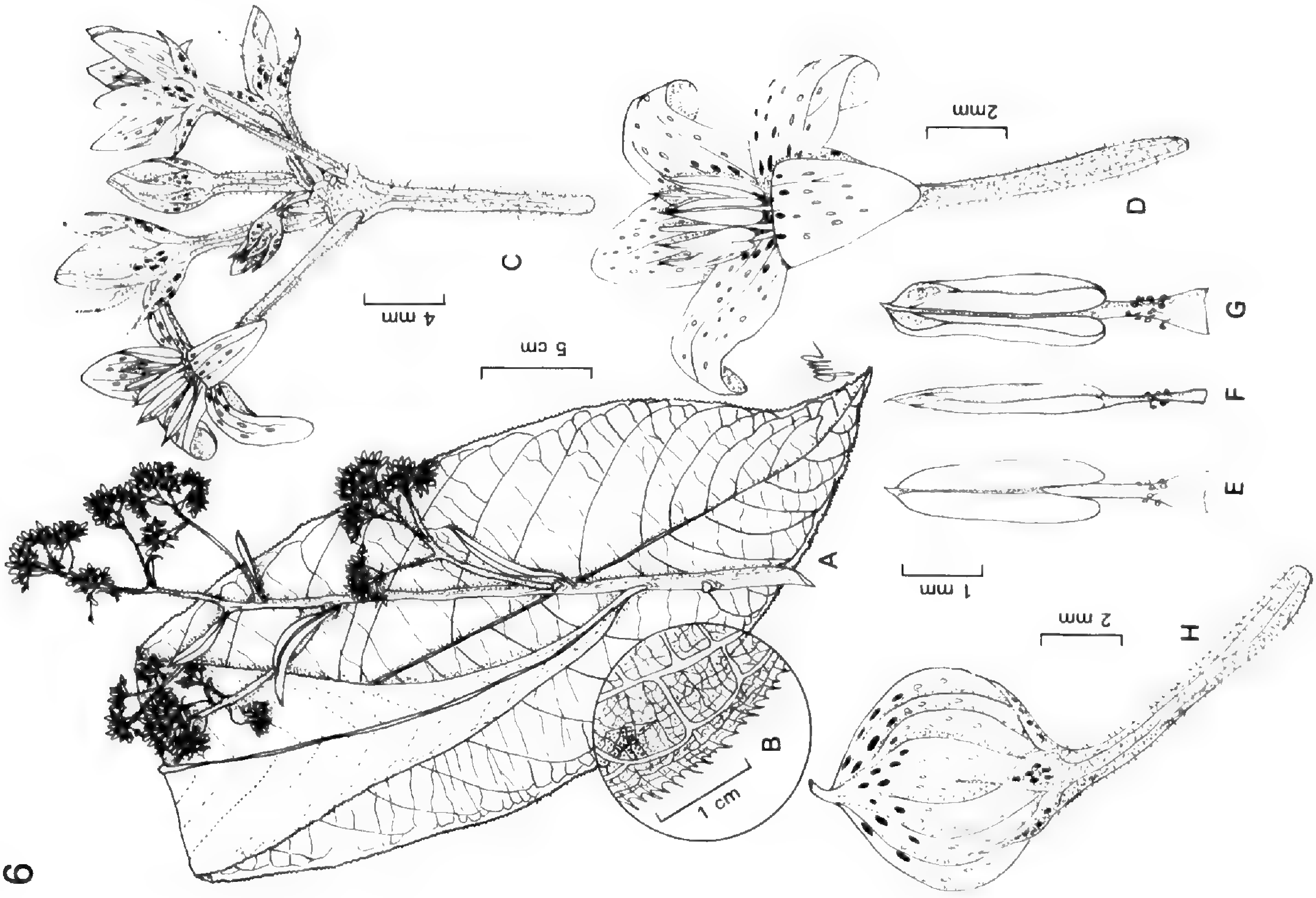

A
B
1 cm
5 cm
C
4 mm
D
2mm
E
F
G
1 mm
H
2 mm

Basionym: *Ardisia pectinata* Donn. Sm., Bot. Gaz. 12: 132. 1887. *Icacorea pectinata* (Donn. Sm.) Standl., Contr. U.S. Natl. Herb. 23: 1110. 1924. *Ardisia pellucida* Oerst. var. *pectinata* (Donn. Sm.) Lundell, Wrightia 3: 99. 1964. *Amatlania pellucida* (Oerst.) Lundell var. *pectinata* (Donn. Sm.) Lundell, Wrightia 7: 40. 1982. *Amatlania pectinata* (Donn. Sm.) Lundell, Phytologia 55: 235. 1984. TYPE: Guatemala. Alta Verapaz: Pansamalá, 3800 pp [1158 m], June 1886 (fl), *H. von Türckheim 942* (holotype, US!, US neg. 2381!; isotype, GH!). Figure 7.

Shrubs 3–5 m tall. *Branchlets* 4–7.5 mm diam., scattered to densely rufous glandular papillose. *Leaves* with blades oblanceolate, 6.5–41 × 3–12.3 cm, with an acumen 0.7–4.2 cm long, the secondary veins 12 to 31 pairs; petioles 0.9–2.1 cm long. *Inflorescences* tri- to quadri-pinnately paniculate, 6.2–20.1 × 6.1–22.5 cm, shorter or longer than the leaves, vestiture of the rachis, branchlets, abaxial bract surfaces, and pedicels similar to the branchlets, the branches terminating in 5- to 16-flowered corymbs; peduncles obsolete to 2.1 cm long; inflorescence branch bracts linear, 3.2–4.9 × 0.2–0.8 mm, sparsely and inconspicuously punctate and punctate-lineate, the veins obsolete, the margins minutely erose, hyaline, sparsely glandular ciliolate; floral bracts 1.5–2.6 × 0.2–0.6 mm, sparsely and inconspicuously punctate and punctate-lineate; pedicels 6.2–7.8 mm long, inconspicuously punctate and punctate-lineate. *Flowers* 5- or 6-merous, lavender to red-violet; calyx lobes ovate, 2.1–2.2 × 1.4–1.5 mm, apically acute, sparsely inconspicuously punctate and punctate-lineate; corolla 5.9–6.1 mm long, the tube 0.7–1.1 mm long, the lobes 5–5.2 × 2.8–2.9 mm, mostly epunctate, rarely or sparsely with glandular-granulose papillae around the top of the corolla tube inside, sparsely and minutely papillose medially outside; stamens 4.3–4.8 mm long, the filaments 1.8–2.2 mm long, the staminal tube 0.5–0.7 mm long, rarely or sparsely with glandular-granulose papillae on the staminal tube and filaments, the apically free portions 1.1–1.7 mm long, epunctate, the anthers lanceoloid, 3–3.1 × 0.8–1 mm, basally subcordate; pistil 4.7–4.8 mm long, the ovary 1.4–1.5 mm long, epunctate, the styles 3.2–3.3 mm long, epunctate, the ovules 21 to 22. *Fruits* 5.5–5.8 mm diam.

Distribution. *Ardisia pellucida* subsp. *pectinata* is found from Mpio. Rayón in Chiapas, Mexico, to Baja Verapaz and Izabal, Guatemala, growing at (50–)1158–1851 m elevation.

Ecology and conservation status. *Ardisia pellucida* subsp. *pectinata* occurs in primary premontane and montane wet forests. Because of its restricted distribution, it should be considered threatened.

Etymology. The specific epithet was derived from the Latin, meaning "with narrow closely-set divisions, like a comb" referring to the teeth on the leaf blade margins.

Within *Ardisia* subg. *Auriculardisia* sect. *Amatlania*, *Ardisia pellucida* subsp. *pectinata* shares a similar vestiture with subspecies *thomascroatii*, sparsely to densely, minutely, rufous glandular papillose throughout. However, *Ardisia pellucida* subsp. *pectinata* may be distinguished by its oblanceolate leaves, smaller but wider ovate calyx lobes to 2.2 × 1.5 mm, larger corolla lobes to 5.2 × 2.9 mm that are sparsely and minutely papillose medially outside and sparsely glandular-granulose inside around the corolla tube and filaments, the larger lanceoloid anthers to 3.1 × 1 mm, the larger pistil to 4.8 mm long, and the longer style to 3.3 mm long.

Specimens examined. MEXICO. **Chiapas**: Mpio. Rayón, near Puerto del Viento, 9 mi. NW of Pueblo Nuevo Solistahuacán along road to Tapiula, 20 Aug. 1965 (fl), *D. Breedlove 11998* (F, LL, NY); Selva Negra 10 km above Rayón mezcalapa along road to Jitotol, 10 Jan. 1981 (fr), *D. Breedlove & B. Keller 49317* (LL, MO, NY). GUATEMALA. **Baja Verapaz**: along dirt road 4 mi. NE of Purulhá, 17 July 1977 (fl), *T. Croat 41325* (MO). **Izabal**: Río Juyamá, SE of Cheyenne, about 15 mi. SW of Bananera, 8 Apr. 1940 (fl, fr), *J. Steyermark 39114* (F [inflorescence galled]).

5. Ardisia pellucida subsp. **pellucida.** Figure 8.

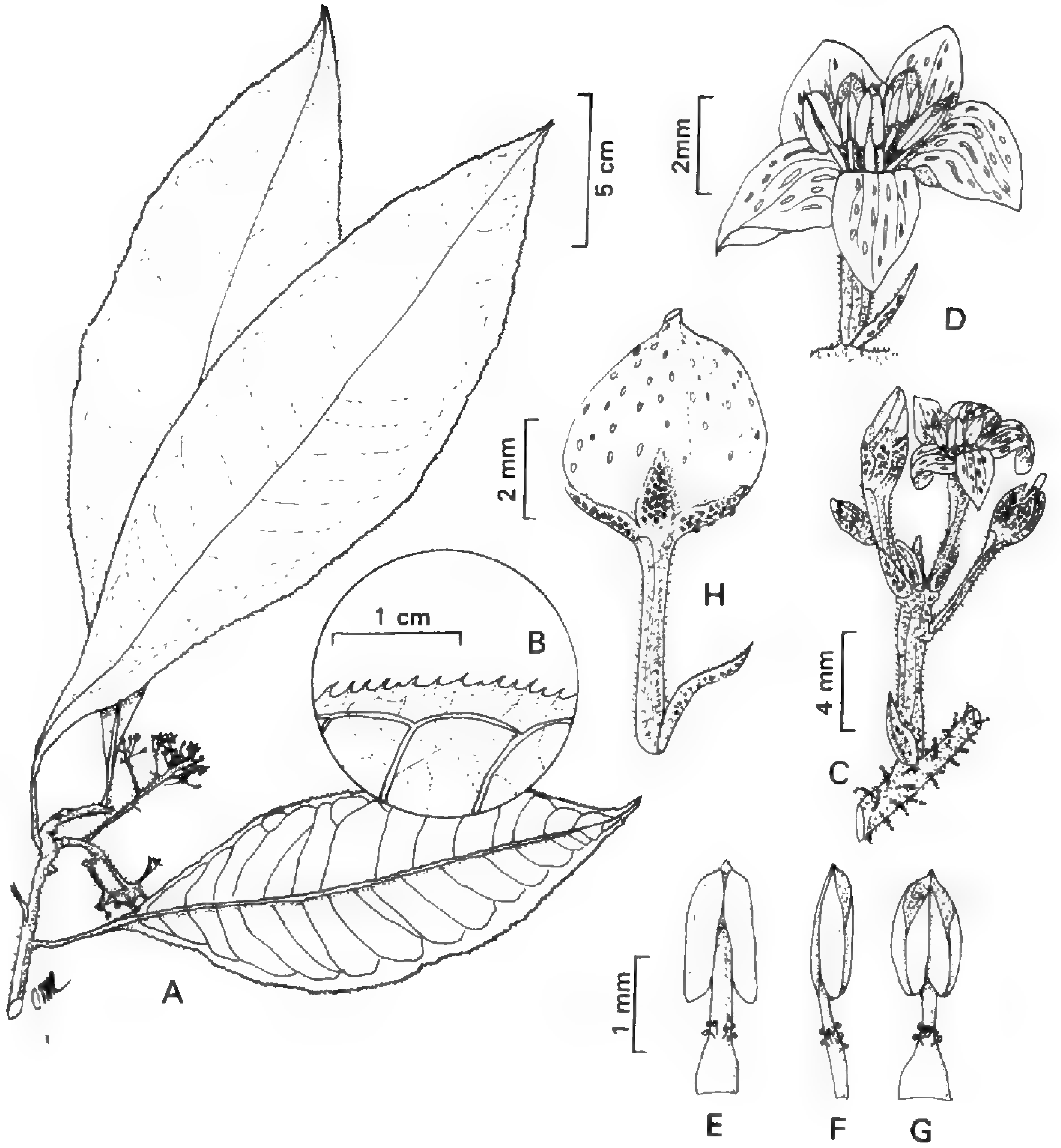
Ardisia myriodonta Standl., J. Wash. Acad. Sci. 17: 13. 1927. Syn. nov. *Amatlania pellucida* (Oerst.) Lundell

←

Figure 6 (left). *Ardisia pellucida* subsp. *lancetillensis.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, adaxial surface. —G. Stamen, lateral margin. —H. Fruit. (A (inflorescence) & C drawn from isotype, *T. Yuncker 4588* (GH); A (leaf) & B from isotype, *T. Yuncker 4588* (F); D–G from *G. Webster et al. 12681* (LL); H from *P. Standley 53322* (F).)

Figure 7 (right). *Ardisia pellucida* subsp. *pectinata.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, adaxial surface. —G. Stamen, lateral margin. —H. Fruit. (A, B drawn from holotype, *H. von Türckheim 942* (US); C from isotype, *H. von Türckheim 942* (GH); D–G from *D. Breedlove 11998* (F); H from *D. Breedlove & B. Keller 49317* (NY).)

8



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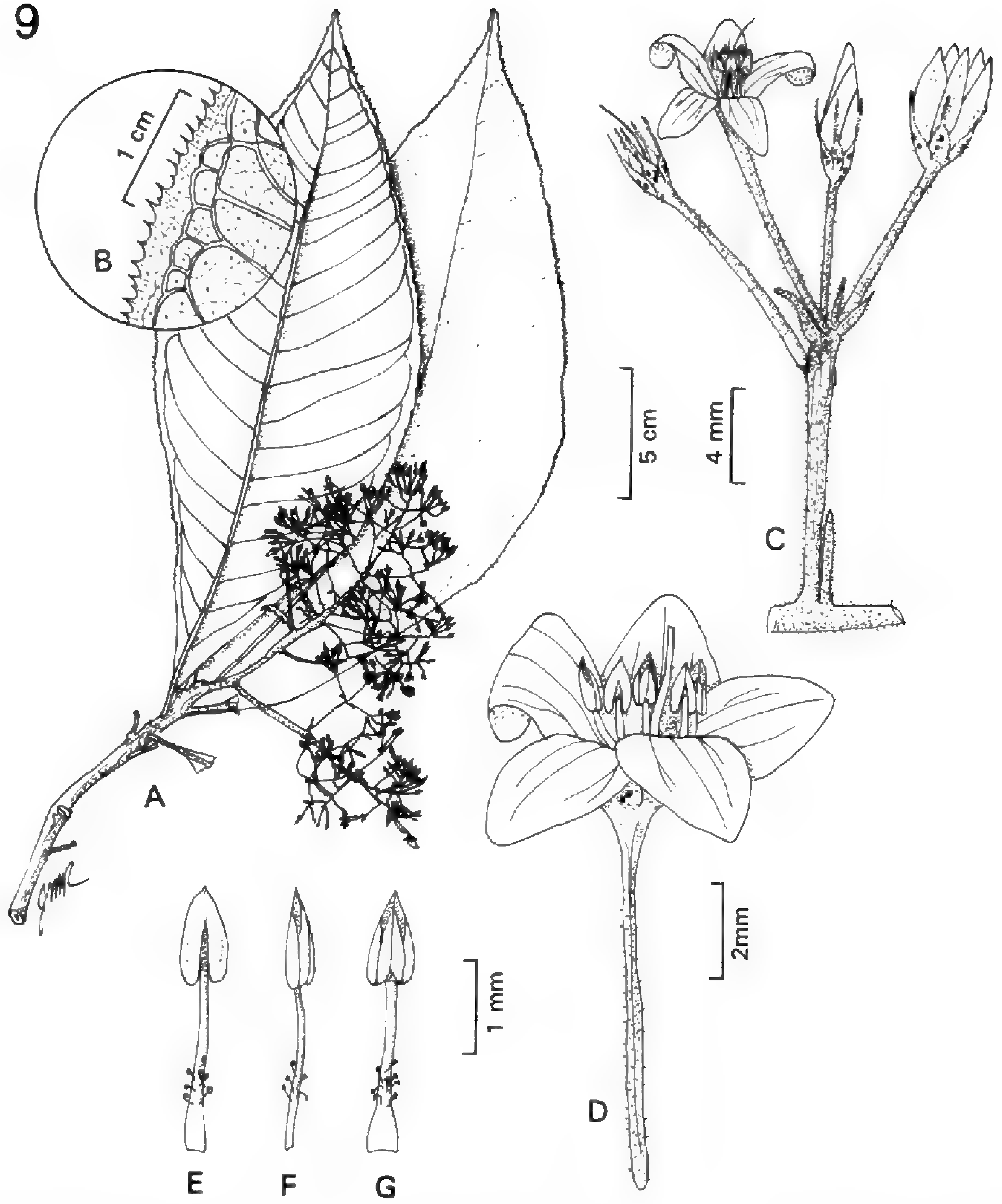

Figure 8 (left). *Ardisia pellucida* subsp. *pellucida.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, adaxial surface. —G. Stamen, lateral margin. —H. Fruit. (A, B drawn from holotype, *F. Liebmann 29C* (C); C from *R. Foster 870* (DUKE); D–G from *B. Hammel 8480* (DUKE); H from *M. Vázquez T. et al. 1055* (LL).)

Figure 9 (right). *Ardisia pellucida* subsp. *thomascroatii.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, lateral margin. —G. Stamen, adaxial surface. (A–G drawn from holotype, *T. Croat 35270* (MO).)

var. *myriodonta* (Standl.) Lundell, Wrightia 7: 40. 1982. TYPE: Panama. Panamá: Canal Zone, Barro Colorado Island in Gatún Lake, ca. 120 m or less, 18–24 Nov. 1925 (fr), *P. Standley 40848* (holotype, US!, US neg. 2376!).

Subshrubs 0.3–3(–10) m tall, 2.5–6 cm diam. *Branchlets* 2–6.5 mm diam., sparsely or densely rufous glandular papillose, or with a mixture of rufous glandular papillae and uniseriate multicellular glandular villous hairs. *Leaves* with blades 8.7–42.9 × 3.7–14.6 cm, with an acumen 0.4–4.8 cm long, the secondary veins 14 to 29 pairs; petioles 1.1–3.1 cm long. *Inflorescences* bipinnately paniculate, 2.8–15.2 × 2.6–10.2 cm, shorter than the leaves, vestiture of the rachis, branches, abaxial bract surfaces, and pedicels similar to the branchlets, the branches terminating in 9- to 16-flowered corymbs; peduncles obsolete to 2 cm long; inflorescence branch bracts linear or oblong to elliptic, 2.8–11.2 × 0.6–2.6 mm, midvein obscure to impressed above and raised below, densely and prominently punctate and punctate-lineate, the margins minutely erose, hyaline, sparsely glandular ciliolate or irregularly finally serrate "pectinate"; floral bracts 1–3.2 × 0.2–0.8 mm, densely and prominently punctate and punctate-lineate; pedicels 3.2–4.3 mm long, inconspicuously punctate and punctate-lineate. *Flowers* lavender, red-violet to deep purple; calyx lobes ovate, 1.7–1.9 × 0.9–1.4 mm, apically acute, slightly notched below the apex, prominently punctate and punctate-lineate; corolla 3.5–3.8 mm long, the tube 0.7–1.3 mm long, the lobes 2.2–2.7 × 1.8–2.2 mm, with few but conspicuous punctations and punctate-lineations, densely yellow glandular-granulose adaxially, apically above the staminal tube as well as between corolla tube and lobe junction, sparsely and minutely papillate medially outside; stamens 2.3–2.5 mm long, the filaments 1.3–1.5 mm long, the staminal tube 0.3–0.4 mm long, the apically free portions 1–1.1 mm, densely yellow glandular-granulose, the anthers ovoid, 1.2–1.4 × 0.6–0.8 mm, pistil 2.5–2.8 mm long, the ovary 0.9–1.2 mm long, conspicuously punctate and punctate-lineate, the style 1.5–1.7 mm long, epunctate or inconspicuously punctate, the ovules 9 to 22. *Fruits* 3.9–5.7 mm diam.

Distribution. *Ardisia pellucida* subsp. *pellucida* is found from San Luis Potosí, Pueblo, Veracruz, Oaxaca, Tabasco, and Chiapas, Mexico, through Belize, Guatemala, Honduras, Nicaragua, Costa Rica, and Panama. In South America it is found from Venezuela, Colombia, Ecuador, and Peru. It grows from 35 to 1650 m in elevation.

Ecology and conservation status. *Ardisia pellucida* subsp. *pellucida* occurs in moist, humid, wet, or rain forest, especially at the margins of natural gaps, and at the forest edge along watercourses. It can tolerate moderate to deep shade, but not compaction of soil. At this time we see no immediate threat to this subspecies.

Common Names. "Tapacajete" (*L. Williams 8314*).

Within *Ardisia* subg. *Auriculardisia* sect. *Amatlania, Ardisia pellucida* subsp. *pellucida* appears to be more closely related to subspecies *lancetillensis* than to the other subspecies because of the mixed vestiture on the vegetative parts consisting of minute papillae and villous trichomes. However, subspecies *pellucida* may be distinguished from subspecies *lancetillensis* by its smaller ovate calyx lobes to 1.9 mm long, smaller corolla lobes to 2.7 mm long, and smaller ovoid anthers to 1.4 mm long.

The type of *Ardisia myriodonta* is in fruit; however, because of its similar vestiture and small ovate calyx lobes it matches *A. pellucida* subsp. *pellucida* in all respects.

Specimens examined. MEXICO. **Chiapas**: Mpio. Ocozocoautla de Espinosa, 32 km N of Ocozocoautla along road to Mal Paso, 19 Oct. 1965 (fr), *D. Breedlove & P. Raven 13562* (LL); Mpio. Palenque, 6–12 km S of Palenque on road to Ocosingo, 27 July 1972 (fl), *D. Breedlove 26511* (LL). **Oaxaca**: Mpio. Santa María Chimalapa, ca. 5 km SW of Santa María along road to Lázaro Cárdenas, 17 July 1984 (fl), *H. Hernández G. 211* (MO); Dtto. Juchitán, Los Angeles 20 km NW of intersection with Matías Romero–Acayucan Road, on path before Martín Dehesa, 23 Oct. 1987 (fr), *C. Martínez 1074* (FTG, MEXU, MO). **Puebla**: Mesa de San Diego, Mar. 1951 (fr), *H. Bravo H. 268* (MEXU); Mpio. Piedras Negras, El Salto, 9 km NE of La Ceiba, 25 Feb. 1987 (fr), *A. Campos et al. 64* (FTG, MEXU). **San Luis Potosí**: Mpio. Xilitla, Poblado Xumchiaio, 12 Aug. 1976 (fr), *J. Calzada 2572* (MEXU); 10 mi. NW of Tamazunchale, 3 July 1940 (fl), *C. Hitchcock & L. Stanford 6930* (F). **Tabasco**: Mpio. Teapa, vicinity of Teapa, along road between Teapa and Tacotalpa, 3.1 mi. E of Teapa along stream and cliffs ca. ¼ mi. S of hwy., 19 Feb. 1987 (fr), *T. Croat & D. Hannon 65343* (LL, MO). **Veracruz**: Mpio. Catemaco, Arroyo Basuras, Sontecomapan, 10 July 1971 (fl); Misantla, July 1912 (fl, fr), *R. Hernández M. 1227* (F), *C. Purpus 5959* (BM, F, GH [2], LL, MO); Mpio. Hidalgotitlan, La Escuadra, 17°18′N, 094°38′W, 16 Sep. 1974 (fr), *M. Vazquez T. et al. 1055* (LL, MEXU). BELIZE. **Toledo**: headwaters Río Grande, 21 Apr. 1933 (fl), *W. Schipp S-559* (F). GUATEMALA. **Alta Verapaz**: near Tactic, 5 Apr. 1939 (ster.), *P. Standley 70506* (F, LL). **Escuintla**: barranco of Río Burrión, NE of Escuintla, 16 Mar. 1941 (fl, fr), *P. Standley 89600* (F). **Huehuetenango**: along Río Lacandon, between Ixcan and Río Ixcan, Sierra de los Cuchumatanes, 23 July 1942 (fr), *J. Steyermark 49320* (F). **Izabal**: between Virginia and Laguna Izabal, Montaña del Mico, 4 Apr. 1940 (fl), *J. Steyermark 38745* (F, LL). **Petén**: Chinchila, 10 km from San Luís on Sebol Road, 9 Oct. 1966 (fr), *E. Contreras 6348* (LL [3]); La Cumbre, 4 km E on Río Purula Road, 21 Sep. 1975 (fr), *C. Lundell & E. Contreras 19914* (LL). **Santa Barbara**: Sololá, Aug. 1891 (fl), *W. Shannon*

1256 [*J. Donnell Smith 170*] (US). HONDURAS. **Atlántida**: vicinity of La Ceiba, lower slopes of Mt. Cangrejal, June–Aug. 1938 (fr), *T. Yuncker et al. 8832* (F, G, MO, NY, TEX, US). NICARAGUA. **Boaco**: Cerro Mombachito, SE of Boaco, 30 Sep. 1980 (fr), *P. Moreno 3193* (MO); upper SW slope of Cerro Mombachito, S of road between Boaco and Camoapa, 3 Oct. 1979 (fr), *W. Stevens et al. 14591* (MO, NY). **Jinotega**: Caño Litutus, Río Bocay, 9 Mar. 1980 (fr), *W. Stevens 16651* (MO). **Rivas**: Hacienda Fátima, Montaña La Victoria, N of the house of Hacienda Fátima, SW of Sapoá, 12 Sep. 1982 (fr), *J. Sandino 3575* (MO, NY). **Zelaya**: along the banks of Río Prínzapolka, ca. 2 km S of Waní, 16 Mar. 1979 (fr), *J. Pipoly 4713* (MO, NY); Mpio. de Waspám, Reserva Bosawás, between Cerro la Francia and the summit of Hill Tara (Asang, nuhni), 20 Jan. 1996 (fr), *R. Rueda et al. 3974* (MO). COSTA RICA. **Alajuela**: about 5 km S of Canalete near the Río Zapate and along the new road to Upala, 12 Nov. 1975 (fr), *W. Burger & R. Baker 10008* (F); Llanura de San Carlos, 21 Feb. 1966 (fr), *A. Molina R. et al. 17638* (F). **Cartago**: Río Reventazón behind main building of CATIE, Turrialba, 30 July 1985 (fl), *M. Grayum & B. Hammel 5754* (MO). **Guanacaste**: N of Río Las Flores, ca. 1 km E of Río Tenorio, Hacienda Montezuma, 24 Jan. 1985 (fr), *M. Grayum & G. Herrera 4832* (LL, MO); vicinity of Tilarán, 10–31 Jan. 1926 (fr), *P. Standley & J. Valerio 44443* (US). **Heredia**: finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, along W River Road, 4 June 1978 (fl), *M. Grayum 1353* (DUKE), 7 Apr. 1980 (fl), *B. Hammel 8480* (DUKE). **Limón**: near Bratsi ca. 30 mi. SE of Limón along Río Sixaola, 12 Aug. 1977 (fr), *T. Croat 43275* (LL, MO); Cantón de Talamanca, Reserva Indígena Talamanca, Valle de Talamanca, Amubri, Soki, 17 June 1994 (fr), *G. Gallardo 256* (FTG, MO). **Puntarenas**: along Quebrada Bonita, Carara Reserva, 25 July 1985 (fr), *M. Grayum et al. 5718* (MO); along N Fork (known locally as "Quebrada Mona"), of Quebrada Bonita, Carara Reserva, 11 June 1986 (fl), *M. Grayum et al. 7602* (LL, MO [2]). PANAMA. **Colón**: Achiote, 2 June 1973 (fl), *R. Dressler 4403* (MO). **Darién**: vicinity of Tortí, 38.6 mi. E of Bayano Dam Bridge, near Río Tortí, 17 May 1980 (fr), *T. Antonio 4640* (LL, MO); Cana, near Río Setigandi, 18 Apr. 1980 (fl), *A. Gentry et al. 28551* (MO); vicinity of Paya, Río Paya, trail between Paya & Payita, 10 June 1959 (fl), *W. Stern et al. 395* (MO). **Panamá**: Canal Zone, Barro Colorado Island, Wheeler at jct. with Armour, 1 Apr. 1970 (fl), *T. Croat 9257* (MO); Armour 6, 24 May 1969 (fl, fr), *R. Foster 870* (DUKE); Maumee Station, 6 June 1862 (fl, fr), *S. Hayes s.n.* (BM). VENEZUELA. **Zulia**: Sierra de Perijá, along Río Yasa, near "Guasáma," above Kasmera, Biological station of the Universidad del Zulia, al SW of Machiques, 26–27 Aug. 1967 (fr), *J. Steyermark & J. Fernández 99746* (NY). COLOMBIA. **Magdalena**: Alto Río Buritaca, Alto de Mira, on the trail to Quebrada Julepia, 13 July 1989 (fl), *S. Madriñán & C. Barbosa 192* (GH, MO). **Risaralda**: Mpio. Pereira, Hacienda Malabar, 4 km from Cerritos along Cerritos–Pereira Hwy., 27 Nov. 1989 (fr), *P. Silverstone-Sopkin et al. 5709* (MO). ECUADOR. **Napo**: Cantón Archidona, Carretera Hollín–Loreto, entre Avila y Loreto, Huiruno, comunidad Quichua, 24 Nov. 1989 (fr), *C. Cerón 7699* (MO); NW, Nuevo Rocafuerte, a 1–2 km al N de la población en línea recta, aguas arriba del Río Napo, caserio Quichua, 26 Feb. 1981 (fr), *J. Jaramillo & F. Coello 4254* (QCA), *4274* (QCA). PERU. **Madre de Dios**: Prov. Manu, Río Alto Madre de Dios, forest near chacra of Sr. Carpio, halfway between Shintuya & Manu, 10–11 Aug. 1974 (fr), *R. Foster et al. 3253* (MO). **Ucayali**: near Peru–Brazil border, Quebrada Sapallal, tributary of Quebrada Shesha, base of Cerro Las Cachoeiras, 19 June 1987 (fr), *A. Gentry & C. Diaz 58457* (MO).

6. **Ardisia pellucida** subsp. **thomascroatii** Ricketson & Pipoly, subsp. nov. TYPE: Costa Rica. San José: about 1 mi. beyond divide between San Isidro del General and coastal town of Dominical, 900 m, 22 May 1976 (fl), *T. Croat 35270* (holotype, MO!). Figure 9.

Propter ramulos, rhachides inflorescentiarum, pedicelos dense minuteque papillosos, atque lobis calycinis inconspicue punctatis et lineato-punctatis, a subsp. *pectinata* similans, sed ab ea lobulis calycinis 2.5–2.6 (non 2.1–2.2) mm longis 0.9–1.0 (nec 1.4–1.5) mm latis, lobulis corollinis 3.6–3.8 (nec 5.0–5.2) mm longis, anteris ovoideis ad apices acutis (non lanceolatis ad apices caudatis) perfacile recognoscitur.

Shrubs 1 m tall. *Branchlets* 4.5–5 mm diam., scattered to densely minutely rufous glandular papillose. *Leaves* with blades elliptic, 13.5–28.5 × 5–11 cm, with an acumen 1.5–1.7 cm long, the secondary veins 20 to 23 pairs; petioles 1.2–1.7 cm long. *Inflorescences* tripinnately paniculate, 12–12.5 × 14–14.5 cm, shorter than the leaves, vestiture of the rachis and branches similar to the branchlets, the branches terminating in 5- to 7-flowered corymbs; peduncles 1.6–1.7 cm long; inflorescence branch bracts linear, 3.5–7.3 × 0.4–0.6 mm, inconspicuously punctate and punctate-lineate, below sparsely and minutely papillose, the veins obsolete, the margins entire, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts 0.6–3.2 × 0.2–0.4 mm, inconspicuously punctate and punctate-lineate; pedicels 5–7.3 mm long, inconspicuously punctate and punctate-lineate, sparsely and minutely papillose. *Flowers* 5-merous, lavender; calyx lobes lanceolate, 2.5–2.6 × 0.9–1 mm, apically long acuminate, without a notch below the apex, inconspicuously punctate and punctate-lineate; corolla 4.8–5 mm long, the tube 1–1.4 mm long, the lobes 3.6–3.8 × 2.4–2.6 mm, mostly epunctate, densely yellow glandular-granulose adaxially, apically above the staminal tube, as well as between the corolla tube and the lobe junction, glabrous outside; stamens 3.2–3.3 mm long, the filaments 2.4–2.5 mm long, the staminal tube 0.7–0.8 mm long, the apically free portions 1.7–1.8 mm long, epunctate, densely yellow glandular-granulose, the anthers ovoid, 0.9–1 × 0.6–0.7 mm; pistil 3.8–3.9 mm long, the ovary 0.9–1 mm long, conspicuously punctate and punctate-lineate, the style 2.7–2.9 mm long, epunctate, the ovules 26 to 29. *Fruits* unknown.

Distribution. *Ardisia pellucida* subsp. *thomas-*

croatii is known only from the type collection and is endemic to San José, Costa Rica, growing at 900 m in elevation.

Ecology and conservation status. *Ardisia pellucida* subsp. *thomascroatii* occurs in tropical moist forest. Unfortunately, no further ecological data are available from the label. Given the accessibility of the site, and lack of collections, this subspecies should be considered threatened.

Etymology. It is an honor to dedicate this taxon to Thomas B. Croat of the Missouri Botanical Garden, scholar, gentleman, and preeminent authority on the systematics and ecology of Neotropical Araceae and the genus *Anthurium* in particular.

Within *Ardisia* subg. *Auriculardisia* sect. *Amatlania*, *Ardisia pellucida* subsp. *thomascroatii* shares a similar vestiture with subspecies *pectinata*, sparsely to densely, minutely, rufous glandular papillose throughout. However, subspecies *thomascroatii* may be distinguished by its elliptic leaves, longer but thinner lanceolate calyx lobes to 2.6 × 1 mm, smaller corolla lobes to 3.8 × 2.6 mm that are glabrous outside and densely glandular-granulose inside around the corolla tube and filaments, the smaller ovoid anthers to 1 × 0.7 mm, the smaller pistil to 3.9 mm long, and the shorter style to 2.9 mm long.

7. **Ardisia schippii** Standl., Field Mus. Nat. Hist., Bot. Ser. 12: 412. 1936. *Amatlania schippii* (Standl.) Lundell, Wrightia 7: 40. 1982. TYPE: Belize. Toledo: Temash River, 200 ft. [61 m], 8 Aug. 1935 (fl, fr), *W. Schipp 1365* (holotype, F!, F neg. 68249!, LL neg. 1971-99!; isotypes, A!, BM!, G!, GH!, K!, MICH!, MO!, NY!). Figure 10.

Ardisia izabalana Lundell, Wrightia 5: 88. 1975. Syn. nov. *Amatlania izabalana* (Lundell) Lundell, Phytologia 53: 413. 1983. TYPE: Guatemala. Izabal: El Estor, 6 km S, 30 Jan. 1975 (fr), *C. Lundell & E. Contreras 18898* (holotype, LL!, F neg. 55616!; isotypes, LL!, F neg. 55617!, LL!).

Shrubs or small trees 4–10.7 m tall, 5–26 cm diam. *Branchlets* 3–4.5 mm diam., scattered to densely minutely rufous glandular papillose, often glabrescent with age. *Leaves* with blades coriaceous, elliptic, 7.8–25.9 × 2.6–9.1 cm, apically acute, with an acumen to 1 cm long, basally acute to obtuse, often oblique, decurrent on petiole, inconspicuously punctate and punctate-lineate, glabrous above, sparsely and minutely papillate along the midrib, often on the blade, usually glabrous, the midrib impressed above, conspicuously raised below, the secondary veins 11 to 22 pairs, prominulous above and below, the margins entire to regularly dentate or serrate, the teeth 3 to 5 per cm when present, flat; petioles slender, marginate, 1.2–2.8 cm long, glabrous above, papillose below. *Inflorescences* erect, tripinnately paniculate, 7.5–24 × 9–23 cm, pyramidal, mostly longer than the leaf blades, peduncle, branches, and pedicels minutely papillose, the branches terminating in 5- to 10-flowered corymbs; peduncles 1.1–3.3 cm long, the lower branches often subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts membranous, oblong, 2.1–2.4 × 0.9–1.1 mm, apically acute, basally sessile, scattered, inconspicuously punctate and punctate-lineate, the veins obscure, the margins minutely erose, hyaline, sparsely glandular ciliolate; floral bracts membranous, ovate to deltate, 1.8–1.9 × 0.9–1.1 mm, apically acute, scattered inconspicuously punctate and punctate-lineate, the veins obscure, the margins minutely erose, hyaline, sparsely glandular ciliolate; pedicels slender, terete, 3.8–6.3 mm long, inconspicuously punctate and punctate-lineate. *Flowers* 5-merous, lilac to purple; calyx lobes chartaceous, ovate, 1.7–1.8 × 1.2–1.3 mm, apically acute to acuminate, few prominently punctate and punctate-lineate, glabrous adaxially, sparsely and minutely papillose, the margins erose, hyaline, sparsely glandular ciliolate; corolla membranous, 6.6–6.8 mm long, the tube 1–1.2 mm long, the lobes ovate to lanceolate, 5.6–5.8 × 2.6–2.9 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, but densely yellow glandular-granulose adaxially, apically above staminal tube, as well as between the corolla tube and the lobe junction, the margins entire, hyaline; stamens 4.4–4.6 mm long, the filaments 2.5–2.6 mm long, the staminal tube 0.8–0.9 mm long, the apically free portions 1.6–1.8 mm, epunctate, densely yellow glandular-granulose, the anthers lanceoloid, 2.5–2.6 × 0.7–0.8 mm, apically long subulate-apiculate, basally cordate, the connective inconspicuously punctate; pistil 5.9–6 mm long, the ovary oblong, 1.3–1.4 mm long, prominently punctate and punctate-lineate, the styles 4.6–4.7 mm long, epunctate, the ovules 28 to 32. *Fruits* globose, 3.7–6.5 mm diam., prominently punctate and punctate-lineate, conspicuously costate.

Distribution. *Ardisia schippii* is found in Cayo and Toledo, Belize, and Alta Verapaz, Izabal, and Petén, Guatemala, growing from 61 to 1900 m in elevation.

Ecology and conservation status. *Ardisia schippii* occurs in primary rain forests. While it is certainly not common, at this time there are no data to suggest that the species is threatened.

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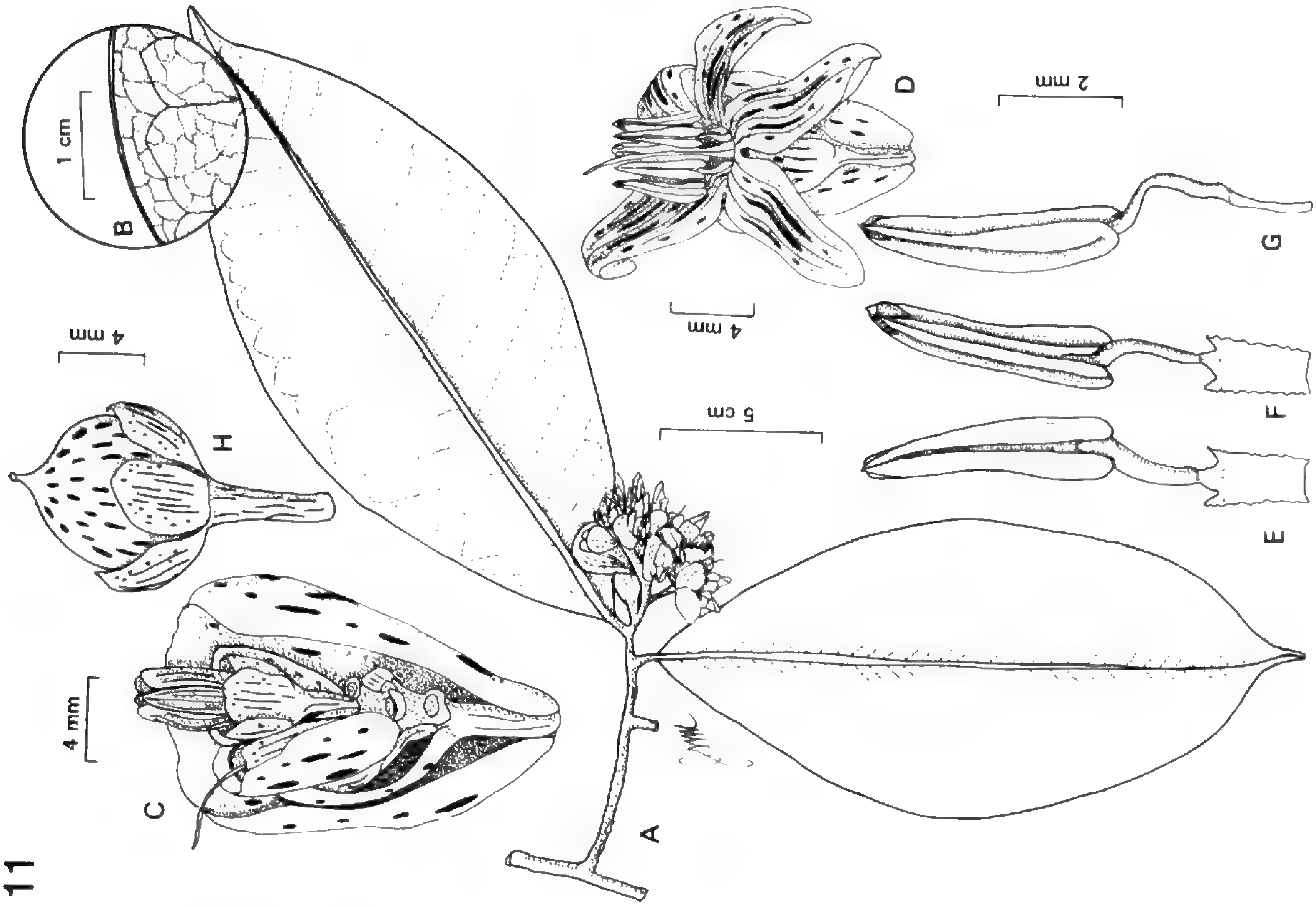
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Within *Ardisia* subg. *Auriculardisia* sect. *Amatlania, Ardisia schippii* appears to be most closely related to *A. liebmannii* (see under that species for similarities). However, *A. schippii* may be distinguished from *A. liebmannii* by its larger corolla lobes to 5.8 × 2.9 mm, longer lanceoloid anthers to 2.6 mm long with subulate-apiculate apices, and the longer styles to 4.7 mm long.

The populations corresponding to the type of *Ardisia izabalana* are unique only for their narrow leaf blades with more entire margins. The vestiture is sparser than in *A. schippii,* but otherwise they match perfectly. The type of *Ardisia izabalana* is in late fruit.

Specimens examined. BELIZE. **Cayo:** vicinity of Cuevas S of Millionario, 29–30 May 1973 (fl), *T. Croat 23587* (F, FTG, LL, MO); Valentin, June–July 1936 (fr), *C. Lundell 6204* (F, LL, NY), (fl), *C. Lundell 6277* (F, GH, LL, NY, TEX). GUATEMALA. **Alta Verapaz:** Rubelsanto, betw. Pozo #4 and laguneta Los Lagartos, 29 July 1975 (fr), *C. Lundell & E. Contreras 19576* (LL [2], MO). **Izabal:** Puerto Mendez, Cadenas, on new Izabal Road, about 2.5 km from village, 17 Aug. 1969 (fr), *E. Contreras 8964* (LL [2], TEX); Cadenas, 6 km SW, 9 July 1970 (fl), *E. Contreras 10154* (DUKE, LL [3], NY), (fr), *10164* (F, LL [3], NY); Puerto Mendez, on Río Dulce Road about 10 km, 6 Sep. 1970 (fr), *E. Contreras 10217* (DUKE, LL [3], NY); El Estor, 23 Mar. 1972 (fr), *E. Contreras 11491* (LL [2]). **Petén:** Julec, km 51 of road between Santo Toribio and Santa Ana, 26 July 1961 (fl, fr), *E. Contreras 2675* (DUKE, LL [2], TEX); La Cumbre, W of km 142/143, 500 m from the road, 10 Sep. 1975 (fr), *C. Lundell & E. Contreras 19838* (LL [2], MO).

TAXONOMIC TREATMENT OF *ARDISIA* SUBG. *AURICULARDISIA* SECT. *AURICULARDISIA*

Ardisia subg. **Auriculardisia** sect. **Auriculardisia.**

Subshrubs or small trees to 20 m tall, 10 cm diam. *Branchlets* stout, terete, densely furfuraceous-lepidote, cupuliform-lepidote (the scales with varying number of lobes or arms, at times of two sizes), mixed furfuraceous- and cupuliform-lepidote, or stipitate-stellate tomentose, the terminal star often breaking off, leaving an apparently villous trichome, the indument normally persistent. *Leaves* monomorphic; blades membranaceous to coriaceous, elliptic, obovate to oblanceolate, prominently, inconspicuously (pellucid) or conspicuously punctate and punctate-lineate, the margins entire, flat; petioles at times obsolete, or slender or stout and much longer, then canaliculate or marginate. *Inflorescences* terminal, erect, pinnately to tripinnately paniculate, pyramidal, shorter than the leaves, the flowers on the secondary or tertiary branches glomerate, corymbose or of congested corymbs, rarely pseudoracemose; inflorescence bracts, inflorescence branch bracts, and floral bracts membranaceous to coriaceous, usually persistent, floral bracts white, light pink to red, 3.7–9.7 × 1–8.5 mm; pedicels stout, terete, often recurved and accrescent or incrassate with maturity. *Flowers* 5- or 6-merous, green to white or pink to purple in hues; calyx lobes membranaceous to coriaceous, the margins entire, hyaline; corolla membranaceous to coriaceous, the lobes variously connate, ovate to lanceolate, the margins entire, hyaline; stamens with obvious filaments, connate basally into an elobate inconspicuously hyaline tube, the anthers free, narrowly ovoid to linear-lanceoloid, lanceoloid, to ovoid, apically apiculate, basally cordate to subcordate, dehiscent by subapical pores, opening into wide, longitudinal slits, the connective inconspicuously to conspicuously punctate dorsally; pistil glabrous, the ovary oblong, the style slender, erect, inconspicuously or conspicuously, or prominently punctate, the ovules few to numerous, in 2 to numerous verticels. *Fruits* globose to depressed-globose, often conspicuously to prominently punctate and punctate-lineate.

Distribution. Four species, from Puntarenas and San José in Costa Rica, southward to Coclé, Panamá, and San Blas in Panama, to Antioquia and Vaupés in Colombia. They grow in habitats from 5 to 1400 m in elevation.

Ecology and conservation status. Members of section *Auriculardisia* occur in primary premontane, cloud and elfin forests and pluvial forests. All members are considered threatened.

←

Figure 10 (left). *Ardisia schippii.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, lateral margin. —G. Stamen, adaxial surface. —H. Fruit. (A–C drawn from holotype, *W. Schipp 1365* (F); D–G from *C. Lundell 6277* (GH); H from *E. Contreras 10217* (LL).)

Figure 11 (right). *Ardisia dodgei.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence, inflorescence branch bract, and floral bracts. —D. Flower and floral bract. —E. Stamen, abaxial surface. —F. Stamen, adaxial surface. —G. Stamen, lateral margin. —H. Fruit. (A, B drawn from isotype, *C. Dodge & V. Goerger 9881* (MICH); C–G from *F. Quesada 530* (F); H from *R. Aguilar 354* (MO).)

Ardisia subg. *Auricülardisia* sect. *Auricülardisia* is defined by the combination of its terminal inflorescence with branches terminating in congested, glomerate corymbs, each of which is subtended by a persistent, enlarged inflorescence branch bract, and finally, the individual flowers subtended by a persistent, enlarged floral bract, as long as the flowers.

KEY TO THE TAXA OF *ARDISIA* SUBG. *AURICULARDISIA* SECT. *AURICULARDISIA*

1a. Plants with a mixture of minute, sessile translucent scales, the scales often early caducous, and tomentose or villous to hirsute rufous stipitate-stellate trichomes, the stellate branches on uniseriate, multicellular stalks to 1.5 mm long, the apical stellate arms often caducous, the hairs then appearing glandular-villous; calyx lobes narrowly lanceolate, 7.2–8.2 mm long, apically attenuate .... 11. *Ardisia ursina*
1b. Plants with a mixture of primarily furfuraceous-lepidote scales and cupuliform scales and/or stipitate-stellate trichomes, when present the stipitate-stellate trichomes less than 0.4 mm and inconspicuous, barely discernable from the scales; calyx lobes ovate, oblate or orbicular to suborbicular, 1.8–5.7 mm long, apically rounded to truncate, often slightly emarginate.
  2a. Floral bracts red or pink; calyx lobes coriaceous, 5.4–5.7 × 4.8–5.2 mm; corolla lobes 8.3–8.5 × 3.2–3.5 mm; anthers linear-lanceoloid, 4.5–5.7 × 0.9–1.1 mm, basally subcordate .... 8. *Ardisia dodgei*
  2b. Floral bracts white to light pink, not red; calyx lobes membranaceous to chartaceous, 1.8–2.7 × 1.9–4.7 mm; corolla lobes 4.5–5.7 × 2.1–2.7 mm long; anthers ovoid to lanceoloid, 2.6–4.1 × 1.2–1.5 mm, basally cordate to sagittate.
    3a. Petioles canaliculate, 3–4.5 cm long; leaf blades flat above, the secondary veins prominulous above and below; perianth blue-gray or lavender; calyx lobes chartaceous, oblate, 2.3–2.7 × 4.3–4.7 mm; corolla 8–8.4 mm long, the lobes 5.3–5.7 mm long; anthers 3.8–4.1 mm long, the filaments broadest at the base .... 9. *Ardisia glomerata*
    3b. Petioles marginate to nearly auriculate, subsessile to 0.3 cm long; leaf blades bullate above, the secondary veins deeply impressed above, prominent below; perianth light green to pink; calyx lobes membranous, orbicular to suborbicular, 1.8–2.2 × 1.9–2.1 mm; corolla 6.8–7 mm long, the lobes 4.5–4.8 mm long; anthers 2.6–2.8 mm long, the filaments not basally broadened .... 10. *Ardisia nervosissima*

8. Ardisia dodgei Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 888. 1938. *Auricülardisia dodgei* (Standl.) Lundell, Phytologia 49: 343. 1981. TYPE: Costa Rica. San José: low hills above Río Paquita, 5–50 m, 15 Aug. 1936 (fl), *C. Dodge & V. Goerger 9881* (holotype, F!, F neg. 68147!, LL neg. 1971-45!; isotypes, CR!, GH!, MICH!, LL neg. 1971-15!, MO!, LL neg. 1971-46!, NY!, PH!, UC!, US!, US neg. 2371!). Figure 11.

Shrubs or small trees to 20 m tall, 10 cm diam. *Branchlets* 3–7 mm diam., densely tomentose with a mixture of furfuraceous-lepidote and cupuliform scales and with scattered stellate and stipitate-stellate trichomes. *Leaves* with blades chartaceous to coriaceous, elliptic, 12.7–25.2 × 5.2–11.3 cm, apically acute to acuminate, with an acumen 0.8–2.4 cm long, basally acute to obtuse, decurrent on the petiole, mostly inconspicuously (pellucid) punctate and punctate-lineate, glabrate above, furfuraceous-lepidote below, occasionally with cupuliform scales along the midrib, the midrib impressed above, prominently raised below, the secondary veins 22 to 64 pairs, prominulous above and below; petiole stout, marginate, 4–12 mm long, mostly glabrate above, below with a mixture of dense furfuraceous-lepidote and cupuliform scales and with sparse stellate and stipitate-stellate trichomes. *Inflorescences* bipinnately or tripinnately paniculate, 2–7.5 × 2.5–7 cm, the rachises densely tomentose with a mixture of furfuraceous-lepidote and cupuliform scales with scattered stellate and stipitate-stellate trichomes, the branches terminating in 5- to 10-flowered glomerate corymbs; peduncle 0.4–1.4 cm long; inflorescence bract caducous, membranous, widely ovate to oblong, 1.1–2.6 × 0.8–1.6 cm, apically rounded to truncate, prominently punctate and punctate-lineate, glabrate above, furfuraceous-lepidote below, the midrib inconspicuous, the margins entire, flat; inflorescence branch bracts similar to the inflorescence bracts, but persistent, ovate, 0.8–2.1 × 0.6–1.6 cm; floral bracts similar to the inflorescence bracts, but red to light pink, usually persistent, 8–9.7 × 5.2–8.5 mm, enveloping the flower; pedicels 3.6–4.2 mm long, inconspicuously punctate-lineate, with scattered furfuraceous-lepidote scales. *Flowers* 5-merous, white or light pink; calyx lobes coriaceous, very widely ovate to suborbicular, 5.4–5.7 × 4.8–5.2 mm, apically rounded or truncate, conspicuously and somewhat prominently punctate and punctate-lineate, glabrous adaxially, scattered furfuraceous-lepidote abaxially; corolla chartaceous, 10.3–10.5 mm long, the tube 2–2.2 mm long, the lobes ovate, 8.3–8.5 × 3.2–3.5 mm, apically obtuse to rounded, conspicuously punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially; stamens

9.6–9.8 mm long, the filaments 5.2–5.4 mm long, the staminal tube 2.5–2.6 mm long, the apically free portions 2.7–2.8 mm long, pellucid punctate, the anthers linear-lanceoloid, 4.5–5.7 × 0.9–1.1 mm, basally subcordate, the connective conspicuously punctate; pistil 7–8.4 mm long, the ovary 0.9–1 mm long, the style 6.1–7.4 mm long, conspicuously punctate and punctate-lineate, the ovules 36 to 39. *Fruits* depressed-globose, 6.8–7.2 mm diam., conspicuously punctate.

Distribution. *Ardisia dodgei* was considered endemic to the area of the Osa Peninsula in San José and Puntarenas, Costa Rica, until Pipoly (1991a) reported disjunct populations from Antioquia and Vaupés, Colombia, growing from 5 to 700 m in elevation.

Ecology and conservation status. *Ardisia dodgei* occurs in primary wet or pluvial forests. Because of its restricted distribution, it should be considered threatened.

Etymology. *Ardisia dodgei* was named in honor of the late Carroll William Dodge (1895–1988), lichenologist, mycologist, and staff member at the Missouri Botanical Garden from 1931 to 1963.

Within *Ardisia* subg. *Auriculardisia* sect. *Auriculardisia*, *Ardisia dodgei* is distinguished by its red or pink persistent floral bracts to 9.7 mm long and to 8.5 mm wide, the large corolla to 10.5 mm long with lobes to 8.5 mm long, and linear-lanceoloid anthers to 5.7 mm long.

Specimens examined. COSTA RICA. **Puntarenas**: Cantón de Osa, Reserva Forestal Golfo Dulce, Los Mogos, Golfito, 5 Sep. 1991 (fr), *R. Aguilar 354* (CR, INB, MO); Rincón de Osa, Quebrada Banegas, 25 Sep. 1991 (fr), *R. Aguilar 469* (CR, MO); Cuenca Térraba-Sierpe, Bahía Chal, La Parcela, 24 Sep. 1996 (ster.), *R. Aguilar 4699* (INB, MO); 25 km W de Chacarita by road, between Rincón and Chacarita, 29 June 1991 (fl), *B. Hammel & M. Nepokroeff 18251* (CR, FTG, INB, MO); Cortés, Los Mogos, headwaters of Quebrada Taboga, 24 Nov. 1991 (fl), *G. Herrera 4977* (CR, FTG, INB, MO); Península de Osa, Rancho Quemado, SE Sector, 16 Sep. 1992 (fr), *J. Marín & D. Marín 520* (CR, FTG, INB, MO); Cantón de Golfito, Parque Nacional Corcovado, Península de Osa, Corcovado, 26 May 1995 (fl), *E. Alfaro 249* (CR, INB, MO); Esquinas Forest, area betw. Río Esquinas and Palmar, 11 July 1951 (fl), *P. Allen 6258* (CAS, F [2], GH); road to Puerto Jiménez, Osa, 40 km W of I.A. route 2, s.d. (fl), *L. Gómez P. 19496* (LL [2], MO); Cantón de Osa, Sierpe, Los Mogos, upper drainage of Río Sierpe, affluent of Quebrada Taboga, 15 Dec. 1990 (fl), *G. Herrera 4791* (CR, FTG, INB, MO); Parque Nacional Corcovado, Upper Ollas Trail, 27 June 1988 (fl), *C. Kernan & P. Phillips 629* (CR, MO); Cantón de Osa, Rancho Quemado, 5 July 1991 (fl), *F. Quesada 530* (CR, F, FTG, INB, MO); Cantón de Golfito, Refugio Nacional de Fauna Silvestre Golfito, 28 Feb. 1994 (fr), *G. Rivera et al. 2237* (CR, K); betw. Golfo Dulce and Río Térraba, Dec. 1947 (fl), *A. Skutch 5310* (F, MICH [2], US); Cantón de Osa, Rincón de Osa, Entrance to Chocuaco, 27 Aug. 1992 (fr), *N. Zamora et al. 1861* (CR, INB, MO). COLOMBIA. **Antioquia**: highway to the sea, near Villa Arteaga, 6 Dec. 1948 (fl), *F. López & M. Sánchez M. 28* (COL, US). **Vaupés**: Río Kananarí and Cerro de Isibukuri, district along river and mountain summit, 30 Nov. 1951 (fl), *H. García-Barriga 13766A* (COL).

9. Ardisia glomerata Lundell, Amer. Midl. Naturalist 29: 486. 1943. *Auriculardisia glomerata* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Panama. Coclé: hills N of El Valle de Antón, trail to La Mesa, ca. 1000 m, 2 Sep. 1941 (fl), *P. Allen 2741* (holotype, MO!, LL neg. 1971-51!; isotypes, A!, US!). Figure 12.

Small trees to 8.5 m tall. *Branchlets* 6.5–11 mm diam., densely tomentose with a mixture of furfuraceous-lepidote and cupulate scales and stipitate-stellate tomentellous on multicellular stalks to 0.7 mm long, appearing glandular-villous as in *A. ursina* with the stellate portion broken off. *Leaves* with blades membranous to chartaceous, elliptic, 31.5–39.5 × 9.6–16.2 cm, apically acute to acuminate, with an acumen 0.7–2.3 cm long, basally acute or acuminate, decurrent on the petiole, mostly inconspicuously punctate, but with a few punctate-lineations above and below, glabrate above, below with a mixture of dense furfuraceous-lepidote and scattered cupulate scales, except densely so along midrib, the midrib impressed above, prominent below, the secondary veins 25 to 75 pairs, prominulous above and below; petioles stout, canaliculate, 3–4.5 cm long, glabrous above, below with a mixture of dense furfuraceous-lepidote and scattered cupulate scales. *Inflorescences* bipinnately or tripinnately paniculate, 12–24 × 6–16 cm, the rachis densely tomentose as in the branchlets, the branches terminating in 5- to 9-flowered glomerate corymbs; peduncle 1.7–3.8 cm long; inflorescence bract unknown; inflorescence branch bracts often persistent, membranous, oblong, 0.9–1.2 × 0.4–0.7 cm, apically acute, inconspicuously (pellucid) punctate and punctate-lineate, glabrate above, furfuraceous-lepidote and stellate-tomentose below, the midrib inconspicuous, the secondary veins inconspicuous, the margins entire, flat, glandular-ciliolate; floral bracts similar to the inflorescence branch bracts, white to light pink, but ovate to oblong, 4.5–7.2 × 3.8–4.5 mm; pedicels 3.4–6.7 mm long, inconspicuously punctate-lineate, furfuraceous-lepidote and stellate-tomentose. *Flowers* 5- or 6-merous, blue-gray or lavender; calyx lobes chartaceous, oblate, 2.3–2.7 × 4.3–4.7 mm, apically truncate and slightly emarginate, conspicuously punctate and punctate-lineate, glabrous ada-

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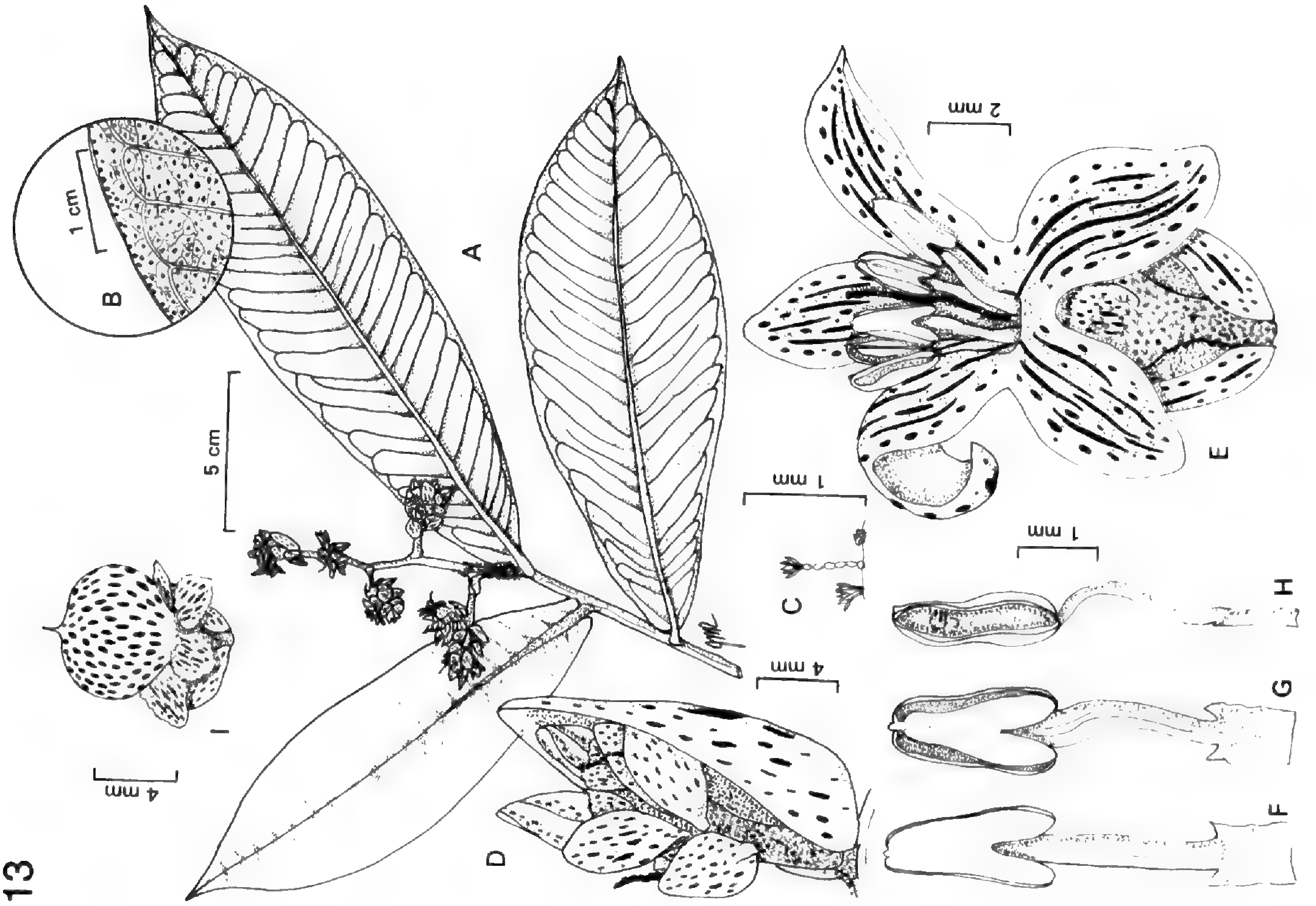
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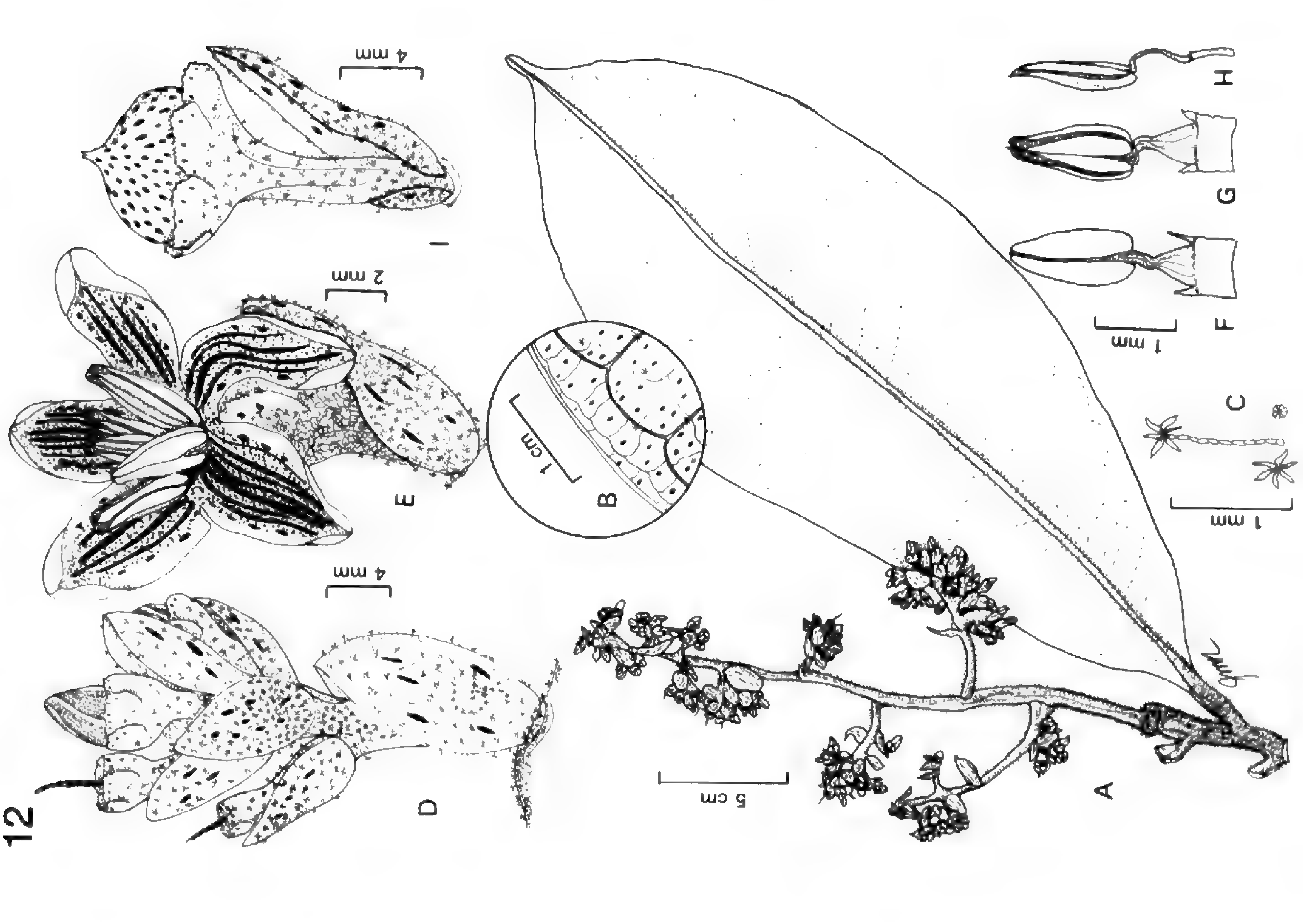
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xially, furfuraceous-lepidote abaxially; corolla coriaceous, 8–8.4 mm long, the tube 2.7–2.8 mm long, the lobes ovate, 5.3–5.7 × 2.4–2.7 mm, apically obtuse to rounded, cucullate, conspicuously punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially; stamens 6.6–6.9 mm long, the filaments 3–3.2 mm long, basally widened above the junction with the tube, the staminal tube 1.4–1.6 mm long, the apically free portions 1.4–1.6 mm long, the anthers lanceoloid, 3.8–4.1 × 1.3–1.5 mm, basally cordate, the connective conspicuously punctate dorsally; pistil 5.4–6.2 mm long, the ovary 0.9–1.1 mm long, the style 4.5–5.1 mm long, conspicuously punctate and punctate-lineate, the ovules 19 to 21. *Fruits* depressed-globose, 6.2–8.2 mm diam., densely and conspicuously punctate.

Distribution. *Ardisia glomerata* is endemic to Cerro Pilón and adjacent areas near El Valle in Coclé, Panama, from 600 to 1000 m in elevation.

Ecology and conservation status. *Ardisia glomerata* is found in cloud forests, a life zone that is rapidly disappearing in Panama. Because of its restricted distribution, it should be considered threatened.

Etymology. The specific epithet was derived from the Latin *glomer,* meaning to form or collect closely together into a sphere, and refers to the congested flowers of the inflorescence.

Within *Ardisia* subg. *Auriculardisia* sect. *Auriculardisia, Ardisia glomerata* is most closely related to *A. nervosissima* because of their small oblate or orbicular to suborbicular calyx lobes, which are apically rounded to truncate, and chartaceous to coriaceous corollas. However, *A. glomerata* can easily be separated from *A. nervosissima* because of its canaliculate petioles to 4.5 cm long, flat leaf blades, chartaceous, oblate calyx lobes to 2.7 mm long and to 4.7 mm wide, and coriaceous corolla with lobes to 5.7 mm long and to 2.7 mm wide and sparsely furfuraceous-lepidote abaxially, and anther to 4.1 mm long.

Specimens examined. PANAMA. **Coclé:** betw. Cerro Pilón and El Valle, 15 Aug. 1967 (fl), *J. Duke & J. Dwyer 13964* (LL, MO); foothills of Cerro Pilón near El Valle, 5 Oct. 1967 (fl), *J. Duke & M. Correa A. 14692* (LL); Cerro Pilón, El Valle, 4 Jan. 1968 (fr), *J. Duke & B. Lallathin 14989* (FTG, LL, MO); El Valle de Antón at the foot of Cerro Pilón, 15 Aug. 1967 (fl), *J. Dwyer & M. Correa A. 7938* (FTG, LL, MO); La Mesa, Cerro Pilón area, 19 Jan. 1968 (fl), *J. Dwyer 8321* (MO); woods adjacent to chicken farm, La Mesa above El Valle, 3 Jan. 1974 (fr), *J. Dwyer 11866* (LL, MO).

10. Ardisia nervosissima Lundell, Wrightia 4: 62. 1968. *Auriculardisia nervosissima* (Lundell) Lundell, Phytologia 49: 345. 1981. TYPE: Panama. Coclé: El Valle, 800–1000 m, 28 June 1967 (fl), *J. Duke 13150* (holotype, LL!, F neg. 55645!; isotypes, GH!, LL!). Figure 13.

Shrubs or small trees to 10 m tall. *Branchlets* 3.5–8.5 mm diam., densely furfuraceous-lepidote, the scales persistent. *Leaves* with blades chartaceous, elliptic, obovate or oblanceolate, 9.2–26.5 × 3.2–9.6 cm, apically acuminate, with an acumen 0.3–1.7 cm long, basally acute to nearly auriculate, decurrent on the petiole, prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote above, more densely so below along midrib and toward base, strongly bullate above, the midrib impressed above, prominent below, the secondary veins 22 to 35 pairs, deeply impressed above, prominent below; petioles stout, marginate to nearly auriculate, subsessile to 3 mm long, densely furfuraceous-lepidote. *Inflorescences* pinnately to bipinnately paniculate, 6.2–12.5 × 4–8.5 cm, tomentose with rufous translucent cupuliform scales, at times with arms, the scales 0.1–0.6 mm long, and with flat furfuraceous-lepidote scales below, the branches terminating in 3- to 7(or 9)-flowered glomerate corymbs; peduncle 0.5–1.4 cm long; inflores-

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Figure 12 (left). *Ardisia glomerata.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Trichome types, sessile stellate (left), stipitate-stellate on a multicellular stalk with the rays terminally rotate (center), and a sessile, flat scale (right). —D. Detail of inflorescence, showing inflorescence branch bract and floral bracts. —E. Flower, showing floral bract. —F. Stamen, abaxial surface. —G. Stamen, adaxial surface. —H. Stamen, lateral margin. —I. Fruit. (A–C & E–H drawn from holotype, *P. Allen 2741* (MO); D from isotype, *P. Allen 2741* (US); I from *J. Dwyer 11866* (MO).)

Figure 13 (right). *Ardisia nervosissima.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of vestiture types showing sessile (left) or multicellular stipitate (center) scales, the scales terminally rotate, usually cupulate with age and drying, and sessile flat (right) scales. —D. Detail of inflorescence, showing inflorescence branch bract and floral bracts. —E. Flower and floral bract. —F. Stamen, abaxial surface. —G. Stamen, adaxial surface. —H. Stamen, lateral margin. —I. Fruit. (A–I drawn from *S. Knapp et al. 6058* (MO).)

cence bracts unknown; inflorescence branch bracts usually persistent, membranous to chartaceous, lanceolate to elliptic, 0.5–4.1 × 0.3–1.4 cm, acropetally smaller, apically acute to obtuse, densely and prominently punctate and punctate-lineate, tomentose as in the rachis, glabrescent, the midrib conspicuously impressed above and prominent and conspicuous below, the secondary veins inconspicuous, the margins entire, sparsely glandular-ciliolate; floral bracts similar to the inflorescence branch bracts, but white to light pink, widely ovate, 4.8–5.7 × 3.4–4.3 mm; pedicels 0.5–5.1 mm long, tomentose like the inflorescence rachis. *Flowers* 5-merous, light green to pink; calyx lobes membranous, orbicular to suborbicular, 1.8–2.2 × 1.9–2.1 mm, apically broadly rounded to truncate, prominently punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially; corolla coriaceous, 6.8–7 mm long, the tube 2.2–2.3 mm long, the lobes ovate, 4.5–4.8 × 2.1–2.3 mm, apically flat, rounded to obtuse, prominently punctate and punctate-lineate, glabrous throughout; stamens 5.8–6 mm long, the filaments 3.7–3.9 mm long, not widened above the tube junction, the staminal tube 1.3–1.5 mm long, the apically free portions 2.3–2.5 mm long, 0.4–0.6 mm diam., epunctate, the anthers ovoid, 2.6–2.8 × 1.2–1.4 mm, basally sagittate, the connective inconspicuously punctate dorsally; pistil 5.3–5.8 mm long, the ovary 0.9–1.1 mm long, the style 4.4–4.7 mm long, prominently punctate, the ovules 19 to 21. *Fruits* globose, 6.4–7.2 mm diam., densely and prominently punctate and punctate-lineate, glabrous.

Distribution. *Ardisia nervosissima* is endemic to Panama, in Coclé (Cerro Caracoral, Cerro Pilón, La Mesa, and El Valle) and Panamá (Cerro Campana and Cerro Trinidad), growing from 800 to 1100 m in elevation.

Ecology and conservation status. *Ardisia nervosissima* is found in elfin and cloud forests. Because of its restricted distribution, it should be considered threatened.

Etymology. The specific epithet refers to the strongly nerved leaves.

Within *Ardisia* subg. *Auricalardisia* sect. *Auricalardisia*, *Ardisia nervosissima* is most closely related to *A. glomerata* (see under that species for similarities). However, *A. nervosissima* can easily be separated from *A. glomerata* because of its subsessile, marginate to auriculate petioles to 3 mm long, bullate leaf blades, membranous and orbicular to suborbicular calyx lobes to 2.2 mm long and to 2.1 mm wide, and coriaceous corolla with lobes to 4.8 mm long and to 2.3 mm wide and glabrous abaxially, and anther to 2.8 mm long.

Specimens examined. PANAMA. **Coclé:** Cerro Pilón, El Valle, 4 Jan. 1968 (fr), *J. Duke & B. Lallathin 14968* (LL, MO), *15004* (LL, MO); Cerro Caracoral, 19 Jan. 1968 (fr), *J. Duke & J. Dwyer 15132* (LL, MO); Cerro Pilón, 14 Sep. 1968 (fl), *J. Dwyer & B. Lallathin 8677* (FTG, MO); N of El Valle, between Cerro Caracoral and Cerro Gaital, 18 July 1982 (fl), *S. Knapp et al. 6058* (LL, MO); Cerro Pilón, Sep. 1968 (fl, fr), *B. Lallathin 8-2* (FTG [2], MO); divide SW of La Mesa at end of logging road, 26 Dec. 1982 (fl, fr), *B. Stein & C. Hamilton 972* (LL, MO, NY); La Mesa, 2 km W of Cerro Pilón, 22 July 1976 (fl), *G. Sullivan 519* (FTG, LL [3], MO). **Panamá:** Parque Nacional Altos de Campana, near summit of Cerro Campana, 23 June 1994 (fl), *M. Correa A. & E. Montenegro 10638* (MO, PMA); Cerro Campana, forest beyond Motel Su-Lin, 8 Sep. 1966 (fr), *J. Duke 8650* (MO); Capira, NE side of Cerro Trinidad, 4 Feb. 1971 (fr), *R. Foster 2097* (DUKE, MO); Cerro Campana, 23 July 1983 (fl), *C. Hamilton et al. 4105* (LL, MO, NY); Cerro Campana, 31 Dec. 1985 (fl, fr), *G. McPherson 7904* (LL, MO).

11. Ardisia ursina Lundell, Wrightia 6: 92. 1979. *Valerioanthus ursinus* (Lundell) Lundell, Wrightia 7: 50. 1982. *Auricalardisia ursina* (Lundell) Lundell, Phytologia 57: 450. 1985. TYPE: Panama. Panamá: El Llano–Cartí Road, 10 km from Inter-American Hwy., 5 Oct. 1974 (fl), *S. Mori & J. Kallunki 2314* (holotype, MO!, LL neg. 1979-5!). Figure 14.

Ardisia hirsutissima Lundell, Phytologia 61: 64. 1986. Syn. nov. *Valerioanthus hirsutissima* (Lundell) Lundell, Phytologia 63: 78. 1987. TYPE: Panama. Coclé: Continental Divide above El Copé, 08°38′N, 080°39′W, 650–750 m, 27 Nov. 1985 (fr), *G. de Nevers, A. Henderson, H. Herrera, G. McPherson & L. Brako 6408* (holotype, LL!; isotypes, BM!, CAS!, CR!, MEXU!, MO!, NY!, PMA!).

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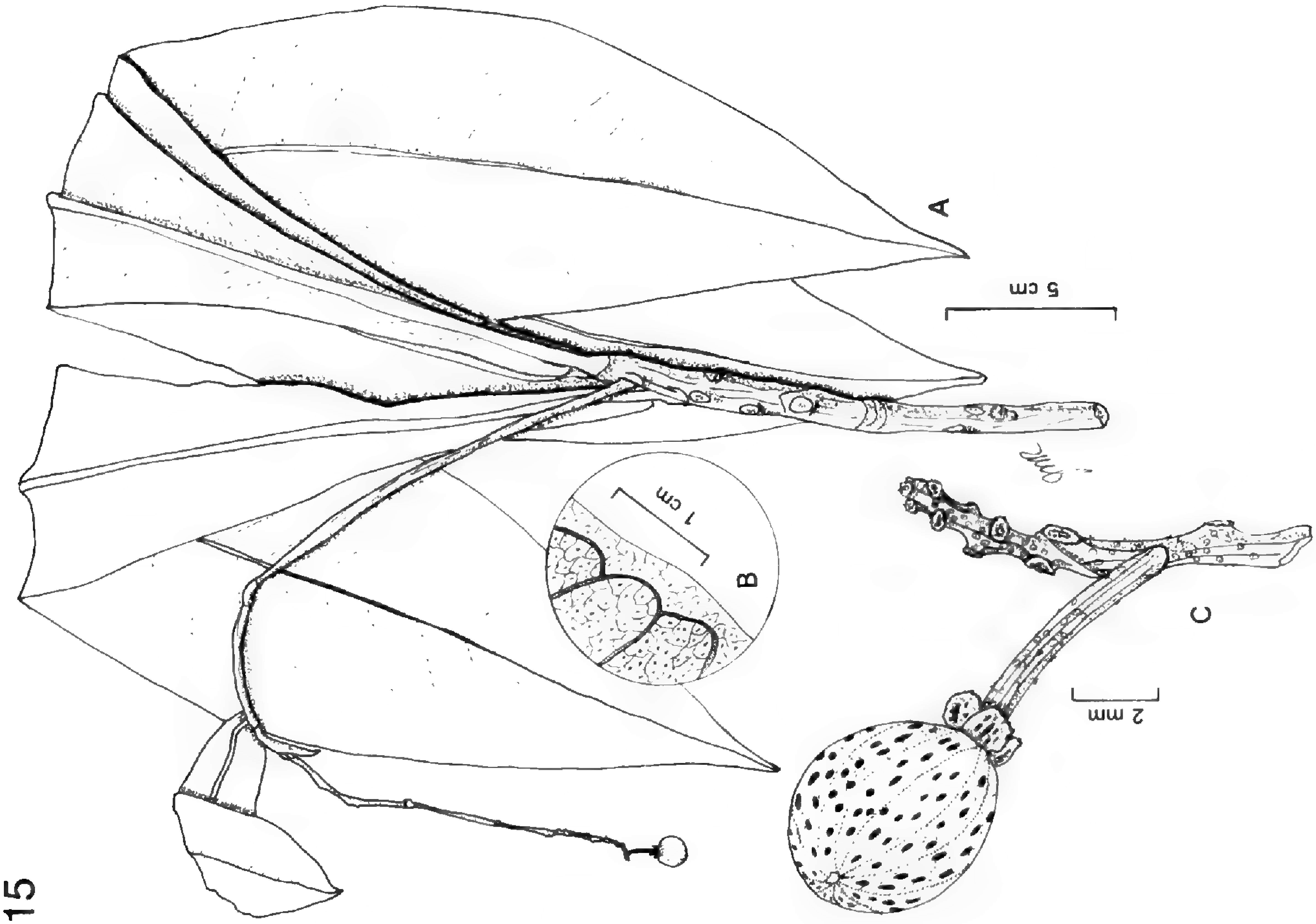
Figure 14 (left). *Ardisia ursina.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, lateral margin. —G. Stamen, adaxial surface. —H. Fruit. —I. Detail of stipitate-stellate trichome with long arms, uniseriate on multicellular stalks. (A, B & I drawn from holotype, *S. Mori & J. Kallunki 2314* (MO); C–G from *G. McPherson 14042* (MO); H from *G. de Nevers et al. 6408* (MO isotype of *Ardisia hirsutissima* Lundell).)

Figure 15 (right). *Ardisia apoda.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence with mature fruit. (A–C drawn from holotype, *J. Steyermark 41923* (F).)



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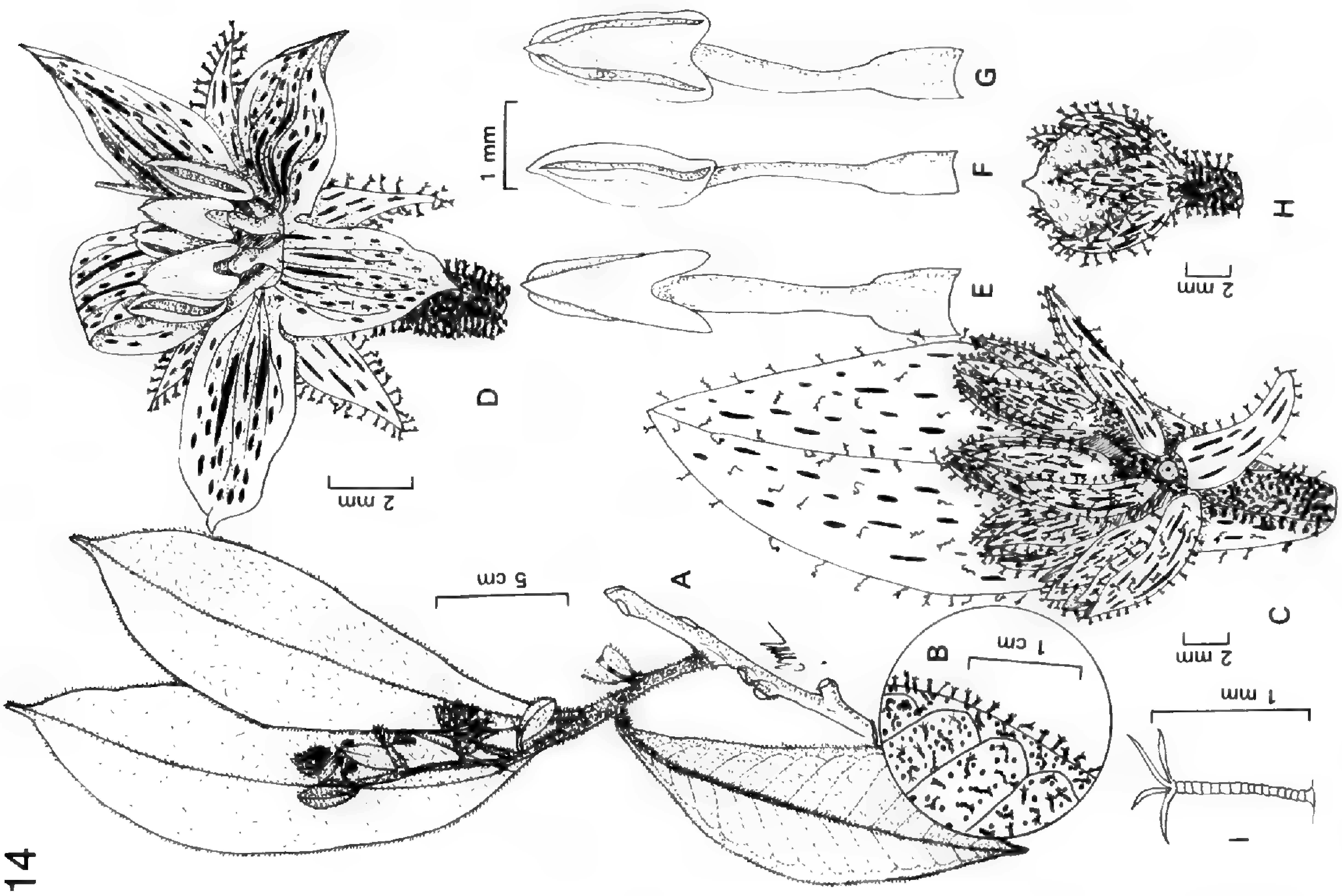

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Trees to 6 m tall. *Branchlets* 3–7 mm diam., with a mixture of scattered minute, sessile translucent scales, the scales often early caducous, and densely tomentose or villous to hirsute rufous stipitate-stellate trichomes throughout, the stellate branches on uniseriate, multicellular stalks to 1.5 mm long, the apical stellate arms often caducous, the hairs then appearing glandular-villous. *Leaves* with blades membranous, elliptic to narrowly obovate, 6.3–23.7 × 2.2–6.9 cm, apically acuminate, with an acumen 3–16 mm long, basally acute, decurrent on the petiole, prominently punctate and punctate-lineate, above and below with a mixture of sparse to scattered, minute, sessile translucent scales, the scales often early caducous, and with scattered villous or hirsute rufous stipitate-stellate trichomes, denser along midvein, otherwise as in the branchlets, the midrib impressed above, prominently raised below, the secondary veins 21 to 35 pairs, prominulous above and below; petioles slender, canaliculate, 2–6 mm long, with a mixture of scattered minute, sessile translucent scales, the scales often early caducous, and scattered to densely tomentose or villous to hirsute rufous stipitate-stellate trichomes above and below. *Inflorescences* bipinnately paniculate, 4.2–8.4 × 2.3–4.7 cm, with a mixture of scattered minute, sessile translucent scales, the scales often early caducous, and densely tomentose or villous to hirsute rufous stipitate-stellate trichomes, otherwise like the branchlets, the branches terminating in 3- to 9-flowered glomerate corymbs; peduncles 0.2–1.5 cm long; inflorescence bracts early caducous, unknown; inflorescence branch bracts persistent, membranous, ovate to elliptic, 0.6–4.2 × 0.4–1 cm, apically and basally acute, conspicuously and prominently punctate and punctate-lineate, with a mixture of scattered minute, sessile translucent scales, the scales often early caducous, and scattered villous or hirsute rufous stipitate-stellate trichomes as in the inflorescence rachis, the midrib impressed above, prominently raised below, the secondary veins 9 to 15 pairs, prominent above and below, the margins entire; floral bracts similar to the inflorescence branch bracts but white to light pink, 3.7–6.9 × 1–1.7 mm, sessile, the veins inconspicuous; pedicels 1.5–3.1 mm long, inconspicuously punctate and punctate-lineate, vestiture as in the inflorescence rachis. *Flowers* 5-merous, white with a pink tinge; calyx lobes membranous, narrowly lanceolate, 7.2–8.2 × 2–2.3 mm, apically attenuate, prominently punctate and punctate-lineate, glabrous adaxially, with a mixture of sparse minute, sessile translucent scales, the scales often early caducous, and scattered villous or hirsute stipitate-stellate trichomes abaxially; corolla membranous, 9–9.4 mm long, the tube 2.1–2.7 mm long, the lobes ovate, 6.7–6.9 × 3.6–4.2 mm, apically acute to acuminate, prominently punctate and punctate-lineate, glabrous throughout; stamens 6.6–6.8 mm long, the filaments 3.9–4.1 mm long, the staminal tube 1.3–1.7 mm long, the apical free portion 2.4–2.6 × 1–1.4 mm, the anthers ovoid, 3.8–4 × 1.5–1.7 mm, basally subcordate, the connective inconspicuously punctate dorsally; pistil 7.4–7.7 mm long, the ovary 1.7–1.9 mm long, the style 5.5–5.6 mm long, inconspicuously punctate, the ovules 24 to 29. *Fruits* globose, 5–5.8 mm diam., prominently punctate and punctate-lineate.

Distribution. *Ardisia ursina* is endemic to Panamá, Coclé, and San Blas, Panama, growing from 300 to 1400 m in elevation.

Ecology and conservation status. *Ardisia ursina* occurs in primary, premontane rain forests. Because it is relatively uncommon, it should be considered threatened.

Etymology. The specific epithet, meaning "of the bear," refers to the rufous stipitate-stellate indument of the branchlets, leaves, and inflorescence that resembles the fur coat of a bear.

Ardisia ursina is unique within *Ardisia* subg. *Auricülardisia* sect. *Auriculardisia* because its branchlets, leaves, and inflorescence branches have an indument with a mixture of minute, sessile translucent scales, the scales often early caducous, and tomentose or villous to hirsute rufous stipitate-stellate trichomes, the stellate branches on uniseriate, multicellular stalks to 1.5 mm long, the apical stellate arms often caducous, the hairs then appearing glandular-villous. Although the branchlets and inflorescence branches of *Ardisia dodgei*, *A. glomerata*, and *A. nervosissima* also can have stipitate-stellate trichomes, they are considerably smaller, to only 0.4 mm long, and inconspicuously mixed with both furfuraceous-lepidote and cupuliform scales. *Ardisia ursina* is also the only member of the section with narrowly lanceolate calyx lobes to 8.2 mm long with an attenuate apex. The type of *Ardisia hirsutissima* was collected in fruit, and except for a slightly darker and thicker vestiture, it is identical to *A. ursina*.

Specimens examined. PANAMA. **Coclé**: above El Potroso sawmill at Continental Divide, 24 Oct. 1980 (fl), *K. Sytsma 1821* (LL, MO). **Panamá**: along El Llano–Cartí road, along creek E of road, 8 Sep. 1989 (fl), *G. McPherson 14042* (F, FTG, MEXU, MO, PMA). **San Blas**: Cerro Obu, 25 June 1986 (fl), *G. de Nevers et al. 8046* (LL, MO); Nusagandi, Sendero Wedar, 19 July 1986 (fl), *J. McDonagh et al. 202* (MO); Cerro Habú, trail from Río Sidro, 20 Dec. 1980 (fr), *K. Sytsma et al. 2770* (LL, MO).

TAXONOMIC TREATMENT OF *ARDISIA* SUBG. *AURICULARDISIA* SECT. *FAGERLINDIA*

Ardisia subg. **Auriculardisia** sect. **Fagerlindia** Ricketson & Pipoly, sect. nov. TYPE here designated: *Ardisia brenesii* Standl.

Quoad sepala asymmetrica ad bases auriculata atque ramulos furfuraceo-lepidotos ad *Ardisiam* subg. *Auriculardisiam* pertinet. Ab aliis sectionibus subgeneris foliis dimorphicis, atque planta exemplar architecturalem Fagerlindii exhibente praeclare distat.

Small *subshrubs* or *trees* exhibiting Fagerlind's Architectural Model (Hallé et al., 1978), to 7 m tall, 3 cm diam. *Trunk, vegetative shoots,* and *reproductive shoots* slender, terete, hirtellous-tomentose, or furfuraceous-lepidote and/or with cupuliform scales. *Leaves* dimorphic; vegetative shoot leaves with blades membranous, often glabrous above, usually similar to the shoots below; petioles stout, obsolete to petiolate; reproductive shoot leaves with blades similar to the vegetative shoot leaf blades, but usually smaller. *Inflorescences* terminal or pseudoterminal, pendent, pinnately to tripinnately paniculate, pyramidal, usually longer than the leaves, the branches terminating with flowers in loosely congested corymbs; inflorescence bracts usually persistent, foliaceous; inflorescence branch bracts and floral bracts caducous, the floral bracts much smaller than the flowers; pedicels slender, terete. *Flowers* 5-merous, white, light pink, light purple or red; calyx lobes essentially free, membranous to chartaceous, ovate to suborbicular, basally auriculate; corolla membranous, the lobes ovate to lanceolate, conspicuously and often prominently punctate and punctate-lineate; stamens with the filaments apically free, connate basally into an elobate tube, free from the corolla tube, epunctate, the anthers ovoid or narrowly ovoid to lanceoloid or linear-lanceoloid, apically apiculate, cuspidate, subulate, mucronate or caudate, basally sagittate or cordate, dehiscent by subapical pores, opening into wide, longitudinal slits, the connective punctate; pistil glabrous, the ovary oblong, the style slender, erect, inconspicuously or conspicuously, rarely prominently punctate, the ovules pluriseriate. *Fruits* globose, inconspicuously or conspicuously, often prominently punctate and punctate-lineate, often costate.

Distribution. Seven species, including one population from Veracruz, Mexico, and one population in Izabal, Guatemala, then southward from Nicaragua (Río San Juan) throughout Costa Rica to Bocas del Toro, Panama, with a disjunct population in the Chocó of Colombia. They grow between sea level and 1500 m in elevation.

Ecology. Species of *Ardisia* subg. *Auriculardisia* sect. *Fagerlindia* occur in primary, secondary, and remnant, premontane wet and pluvial forests and in evergreen *Liquidambar–Quercus* forests.

Etymology. The name "fagerlindia" is derived from the architectural model exhibited by the members of this section.

Ardisia subg. *Auriculardisia* sect. *Fagerlindia* is defined by the species' exhibiting Fagerlind's Architectural Model (Hallé et al., 1978), and its terminal, pendent inflorescences. One of the outstanding features exhibited by Fagerlind's Model is that the flowering shoots bear leaves markedly different in shape and size from those of the vegetative shoots.

KEY TO THE TAXA OF *ARDISIA* SUBG. *AURICULARDISIA* SECT. *FAGERLINDIA*

1a. Trunks and shoots, leaf blades, and inflorescence rachises hirtellous-tomentose, the trichomes apparently unicellular, 0.8–1.8 mm long .... 16. *Ardisia nevermannii*

1b. Trunks and shoots, leaf blades, and inflorescence rachises furfuraceous-lepidote and/or with cupuliform scales sessile to 0.9 mm long.

  2a. Indument of lower leaf surface a mixture of scales, flat furfuraceous-lepidote and/or erect cupuliform scales; corolla lobes 4.5–4.8 mm long; anthers 3.1–3.4 mm long .... 14. *Ardisia brenesii*

  2b. Indument of lower leaf surface of strictly furfuraceous-lepidote scales; corolla lobes 1.3–4.2 mm long; anthers 1.2–3.1 mm long.

    3a. Vegetative shoot leaf blades 7.5–21.5 × 1.9–7.6 cm.

      4a. Leaf blades broadly elliptic, acute basally, not gradually tapering toward the base; petioles conspicuous, 12–27 mm long; inflorescence bracts unknown (early caducous); corolla lobes pellucid punctate and punctate-lineate; anthers apically mucronate-apiculate .... 13. *Ardisia bastonalensis*

      4b. Leaf blades narrowly elliptic to oblanceolate or spathulate, gradually tapering to an auriculate base; petioles obsolete to 2.5 mm long; inflorescence bracts persistent; corolla lobes black punctate and punctate-lineate; anthers not mucronate, merely apiculate.

        5a. Leaf blades crenate to dentate; peduncles 0.4–1.7 cm long; calyx lobes 1–1.1 × 0.6–0.7 mm; corolla lobes 1.6–1.9 × 1.2–1.3 mm; anthers 1.2–1.3 mm long, on apically free filaments 0.6–0.7 mm long; fruits 6.0–6.5 mm diam., prominently punctate, somewhat costate .... 17. *Ardisia tilaranensis*

        5b. Leaf blades entire; peduncles

5.5–15.5 cm long; calyx lobes 1.3–1.5 × 0.8–1.0 mm; corolla lobes 3.2–3.4 × 1.9–2.0 mm; anthers 1.8–2.0 mm long, on apically free filaments 0.7–0.9 mm long; fruits 7.0–7.5 mm diam., inconspicuously pellucid-punctate, not costate .... 15. *Ardisia gordonii*

3b. Vegetative shoot leaf blades 25.2–42.6 × 9.4–11.1 cm.
  6a. Branchlets 7.5–8.5 mm diam.; vegetative shoot leaf blades 39.8–42.6 cm long, apically long attenuate; petioles of reproductive shoot leaves sessile to 0.3 cm long; inflorescences 12.4–12.8 cm long; calyx lobes 1–1.2 mm long .... 12. *Ardisia apoda*
  6b. Branchlets 4.5–5.4 mm diam.; vegetative shoot leaf blades 25.2–34.6 cm long; apically abruptly acuminate; petioles of reproductive shoot leaves 0.2–0.7 cm long; inflorescences 9.2–11.5 cm long; calyx lobes 1.3–1.5 mm long .... 18. *Ardisia tortuguerensis*

12. Ardisia apoda Standl. & Steyerm., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 219. 1947. *Icacorea apoda* (Standl. & Steyerm.) Lundell, Phytologia 49: 347. 1981. *Auriculardisia apoda* (Standl. & Steyerm.) Lundell, Wrightia 7: 266. 1984. TYPE: Guatemala. Izabal: Cerro San Gil, 300–900 m, 25 Dec. 1941 (fr), *J. Steyermark 41923* (holotype, F!, F neg. 68130!, LL neg. 1971-18!). Figure 15.

Small trees to 6.1 m tall. *Trunk and vegetative shoots* 7.5–8.5 mm diam., densely furfuraceous-lepidote; *reproductive shoots* similar, but 3–4.2 mm diam. *Leaves* dimorphic; vegetative shoot leaves with the blades membranous, elliptic to slightly oblanceolate, 39.8–42.6 × 9.4–9.8 cm, apically long attenuate to an indistinct acumen, basally auriculate, inconspicuously punctate and punctate-lineate, glabrous above, sparsely furfuraceous-lepidote below except denser along the midrib, the midrib impressed above, prominently raised below, the secondary veins 28 to 36 pairs, slightly depressed above, prominulous below, the margins entire to slightly crenulate, flat or revolute; petioles stout marginate, obsolete to 0.3 cm long, furfuraceous-lepidote; reproductive shoot leaves with the blades similar to the vegetative ones but 9.3–12.9 × 3.4–3.6 cm, the secondary veins 9 to 21 pairs; petioles similar to the vegetative ones. *Inflorescences* pinnately or bipinnately paniculate, 12.4–12.8 cm long, longer than the leaves, the rachis, branches, and pedicels densely furfuraceous-lepidote, the branches terminating in 7- to 12-flowered corymbs; peduncle 3.1–6.5 cm long; inflorescence bracts persistent, oblong, 1.4–1.6 × 4.8–5.4 mm, apically acute to rounded, midrib prominulous above and below, prominently punctate and punctate-lineate, the margins entire, flat; inflorescence branch bracts similar to the inflorescence bracts, but 1.7–2.2 × 0.4–0.9 mm; floral bracts unknown, early caducous; pedicel 7.4–9.1 mm long, prominently punctate and punctate-lineate. *Flower* color unknown; calyx lobes chartaceous, suborbicular to oblate, 1–1.2 × 1.1–1.3 mm, apically acute, prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote, the margins minutely erose, hyaline, sparsely glandular-ciliolate; corolla, stamens, and pistil unknown. *Fruits* 7.4–8.5 mm diam., prominently punctate and punctate-lineate, slightly costate.

Distribution. *Ardisia apoda* is only known from Cerro San Gil, Izabal, Guatemala, growing from 300 to 900 m in elevation.

Ecology and conservation status. *Ardisia apoda* is found on damp, forested slopes and ravines. Because it is only known from the type collection, it should be considered threatened.

Etymology. The specific epithet refers to the sessile leaves.

Because this species is only known from the type, the relationships of *Ardisia apoda* are uncertain. However, within *Ardisia* subg. *Auriculardisia* sect. *Fagerlindia*, *Ardisia apoda* may be most easily confused with *Ardisia tortuguerensis* by virtue of its large vegetative shoot leaves to 42.6 × 11.1 cm, gradually tapering to the base, the relatively thick stems to 8.5 mm in diameter and pedicels to 9.1

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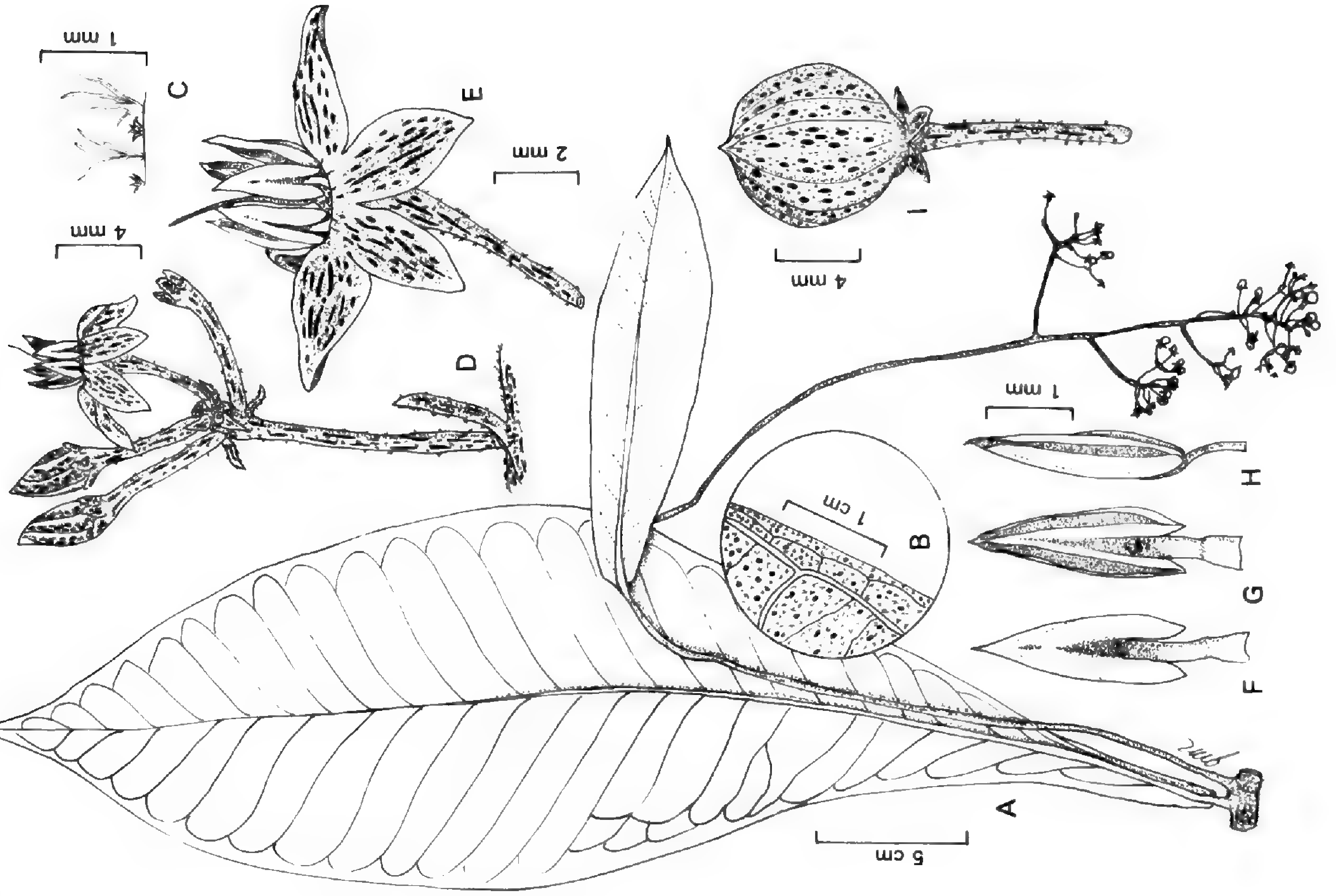
Figure 16 (left). *Ardisia bastonalensis.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, lateral margin. —G. Stamen, adaxial surface. (A–G drawn from holotype, *R. Cedillo T. & G. Higareda 2890* (MEXU).)

Figure 17 (right). *Ardisia brenesii.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of vestiture consisting of a mixture of short, sessile flat or cupulate scales and longer erect cupulate scales. —D. Detail of inflorescence. —E. Flower. —F. Stamen, abaxial surface. —G. Stamen, adaxial surface. —H. Stamen, lateral margin. —I. Fruit. (A, B drawn from *R. Riviere 358* (MO); C–H from *M. Grayum et al. 8993* (MO); I from *W. Burger & T. Antonio 11183* (F).)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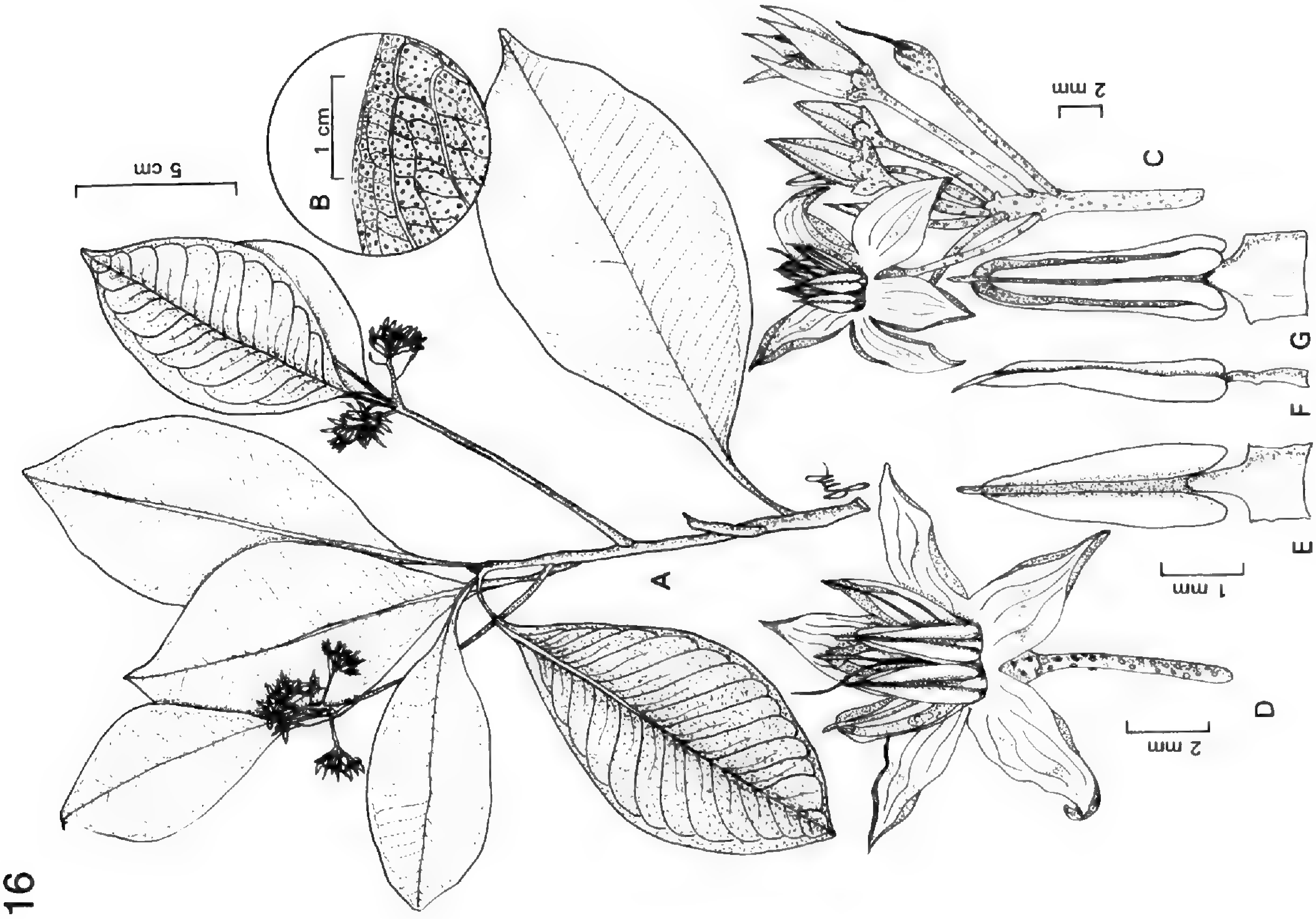
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16

mm long. However, *Ardisia apoda* is easily separated from *A. tortuguerensis* by its much thicker branchlets to 8.5 mm in diameter, much longer vegetative shoot leaves to 42.6 cm long with attenuate-acuminate apices, longer inflorescences to 12.8 cm long and larger calyx lobes to 1.2 × 1.3 mm.

13. Ardisia bastonalensis Ricketson & Pipoly, sp. nov. TYPE: Mexico. Veracruz: Mpio. De Catemaco, Rancho La Chingada, 10 km al SE de Tebanca, camino a Bastonal, 22 Nov. 1984 (fl), *R. Cedillo T. & G. Higareda 2890* (holotype, MEXU!; isotype, US!). Figure 16.

Propter folia dimorpha etiam inflorescentiam terminalem ad *Ardisiam* sectionem *Fagerlindiam* pertinet. Species haec ab aliis speciebus sectionis laminis foliaribus ellipticis ad bases acutis, petiolis conspicuis 12–27 mm longis, pedunculis longioribus, perianthiis pellucido-punctato-lineatis denique antheris mucronatis statim separabilis.

Subshrubs 0.9 m tall. *Trunk and vegetative shoots* 3–7 mm diam., sparsely and minutely furfuraceous-lepidote; *reproductive shoots* similar, but 1–2 mm diam. *Leaves* dimorphic; vegetative shoot leaves with the blades membranous, elliptic, 8.8–15.1 × 3.8–7.6 cm, apically acuminate, with an acumen 5–9 mm long, basally acute, slightly decurrent on the petiole, conspicuously punctate and punctate-lineate, glabrous above, sparsely furfuraceous-lepidote below, glabrescent, the midrib impressed above, prominently raised below, the secondary veins 40 to 45 pairs, slightly raised above and below, the margins entire, flat; petiole slender, marginate, 12–27 mm long, glabrous above, sparsely furfuraceous-lepidote below, glabrescent; reproductive shoot leaves with the blades similar to the vegetative ones, but 3.2–9.4 × 2.2–5.1 cm, the secondary veins 23 to 29 pairs; petioles similar to the vegetative ones, but 4–12 mm long. *Inflorescences* pinnate, 1.6–4 × 0.8–5 cm, shorter than the leaves, the rachis and pedicels with densely furfuraceous-lepidote scales, the branches terminating in 11- to 17-flowered corymbs; peduncles 4–9 mm long; inflorescence bracts and branch bracts unknown (early caducous); floral bracts membranous, oblong, 2–2.6 × 0.4–0.6 mm, apically acute, inconspicuously punctate and punctate-lineate, the margins minutely erose, apically hyaline, sparsely glandular ciliolate; pedicels 5.2–11.2 mm long, inconspicuously punctate and punctate-lineate, with scattered to dense minute furfuraceous-lepidote scales. *Flowers* white; calyx lobes membranous to chartaceous, suborbicular to widely ovate, 1.4–1.6 × 1.1–1.3 mm, apically acute to rounded, prominently punctate and punctate-lineate, pellucid, glabrous adaxially, glabrous or sparsely furfuraceous-lepidote, the margins minutely erose, hyaline, sparsely glandular ciliolate; corolla 5.4–5.6 mm long, the tube 1.2–1.4 mm long, the lobes narrowly ovate to ovate, 4–4.2 × 2.2–2.4 mm, apically acute, prominently punctate and punctate-lineate, pellucid, glabrous throughout, the margins entire, hyaline; stamens 4.3–4.4 mm long, the filaments 1.4–1.6 mm long, the staminal tube 1.2–1.3 mm long, the apically free portions 0.2–0.3 mm long, epunctate, the anthers lanceoloid, 2.9–3.1 × 1.2–1.6 mm, apically mucronate-apiculate, basally sagittate, the connective inconspicuously punctate; pistil 5.6–5.9 mm long, the ovary 1.6–1.9 mm long, the styles 3.8–4 mm long, epunctate, the ovules 10 to 12. *Fruits* unknown.

Distribution. Ardisia bastonalensis is endemic to the area around Bastonal, in the Mpio. de Catemaco, Veracruz, Mexico, growing at around 500 m in elevation.

Ecology and conservation status. Ardisia bastonalensis occurs in tall evergreen *Liquidambar–Quercus* forests on clay soils. Because of its restricted distribution, it should be considered threatened.

Etymology. The specific epithet refers to the type locality, around Bastonal, Veracruz, Mexico.

Within *Ardisia* subg. *Auriculardisia* sect. *Fagerlindia, Ardisia bastonalensis* is most closely related to *A. tilaranensis* and *A. gordonii* by their smaller vegetative shoot leaves less than 21.5 cm long and 7.6 cm wide. However, the elliptic leaves with acute bases, conspicuous petioles to 2.7 cm long in the vegetative shoot leaves and long peduncles to 9 mm long, the pellucid (not black) punctate-lineate perianth, and the markedly mucronate-apiculate anthers clearly set it apart from these other two species.

Paratype. MEXICO. **Veracruz:** Mpio. de Catemaco, Cumbres de Bastonal, 19 Nov. 1974 (fl), *R. Cedillo T. 424* (MEXU, US).

14. Ardisia brenesii Standl., Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 855. 1938. *Auriculardisia brenesii* (Standl.) Lundell, Phytologia 49: 342. 1981. TYPE: Costa Rica. Alajuela: Cataratas (Los Angeles) de San Ramón, vicinity of San Ramón, 17 Apr. 1935 (fl), *A. Brenes 20537* (holotype, F!, F neg. 68135!, LL neg. 1971-23!; isotypes, NY! [2]). Figure 17.

Ardisia limonensis Lundell, Wrightia 6: 79. 1979. Syn. nov. *Auriculardisia limonensis* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Costa Rica. Limón: 29 air km W of Tortuguero, S border Hacienda La

Suerte, E of sentry gate, 10°30′N, 083°47′W, 40 m, 15 Mar. 1978 (fl, fr), *C. Davidson, A. Kaminer, L. Middleton & B. Rasnow 7009* (holotype, MO!, F neg. 55677!; isotypes, F!, F neg. 68446!, LL!).

Shrubs or small trees 2–7 m tall, 1–3 cm diam. *Trunk and vegetative shoots* 4–11.5 mm diam., indument with a mixture of dense ferrugineous-lepidote and scattered erect cupuliform scales, 0.1–0.9 mm long, the scale margins lobed or with 2 to 8 arms; *reproductive shoots* similar, but 1.2–3.5 mm diam. *Leaves* dimorphic; vegetative shoot leaves with the blades membranous, elliptic to oblanceolate, 22.5–53.7 × 5.4–22.6 cm, apically acuminate, with an acumen 1.3–3.2 cm long, basally auriculate, prominently punctate and punctate-lineate, glabrous above, indument with a mixture of dense ferrugineous-lepidote and scattered erect cupuliform scales, 0.1–0.9 mm tall, the scale margins lobed or with 2 to 8 arms, the midrib impressed above, prominently raised below, the secondary veins 23 to 36 pairs, slightly depressed above, prominulous below, the margins entire or regularly crenate, flat or revolute toward the base; petioles stout, marginate, 0.3–0.8 cm long, indument similar to the vegetative shoots; reproductive shoot leaves with the blades similar to the vegetative shoots but oblong, 4.9–23.9 × 0.7–8.8 mm, the secondary veins 3 to 30 pairs; petioles similar to the vegetative ones but 0.1–0.5 cm long. *Inflorescences* bipinnately or tripinnately paniculate, 9.2–35.5 cm long, longer than the leaves, indument as in shoots, the branches terminating in 7- to 19-flowered corymbs; peduncle 3.1–19.4 cm long; inflorescence bracts early caducous, oblong, 1.5–8.6 × 0.5–2.4 cm, apically acute to rounded, prominently punctate and punctate-lineate, glabrous above, indument below similar to the vegetative shoot leaves, the midrib prominulous above and below, the margins entire, flat or revolute toward the base; inflorescence branch bracts similar to the inflorescence bracts, but 1.1–3.3 × 0.5–14.9 mm; floral bracts similar to the inflorescence bracts, but 0.8–1.2 × 0.2–0.5 mm; pedicels 5.4–10.2 mm long, pellucid punctate and punctate-lineate, indument similar to the vegetative shoots. *Flowers* pink, purple, or red; calyx lobes membranous to chartaceous, ovate to suborbicular, 1.2–1.4 × 0.9–1.2 mm, apically acute, prominently punctate and punctate-lineate, with sparsely ferrugineous-lepidote or cupuliform scales, the margins minutely erose apically, hyaline, sparsely glandular-ciliolate; corolla 5–5.3 mm long, the tube 0.5–0.7 mm long, the lobes widely ovate, 4.5–4.8 × 2.2–2.4 mm, apically acute, prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote abaxially, the margins entire; stamens 3.8–4.1 mm long, the filaments 1–1.2 mm long, the staminal tube 0.3–0.7 mm long, the apical free portions 0.3–0.7 mm long, the anthers narrowly ovoid to lanceoloid, 3.1–3.4 × 1.1–1.2 mm, apically apiculate, basally sagittate, the connective punctate; pistil 2.9–4 mm long, the ovary 1–1.2 mm long, the style 1.7–2.8 mm long, inconspicuously punctate, the ovules 12 to 14. *Fruits* 6.4–7.6 mm diam., prominently punctate and punctate-lineate, costate.

Distribution. *Ardisia brenesii* occurs from Río San Juan, Nicaragua, through Alajuela, and Heredia to Limón, Costa Rica, with a disjunct population in San Blas, Panama, growing at 0 to 1500 m in elevation. This is the first report of the species from Panama.

Ecology and conservation status. *Ardisia brenesii* occurs in primary, secondary, and remnant premontane wet forests. Fieldwork by Pipoly in Alajuela, Costa Rica, revealed that the species occurs at a density of less than a dozen individuals per hectare, normally on slopes beside small watercourses. While it is certainly not common, at this time there are no data to suggest that the species is threatened.

Etymology. This species was named in honor of Alberto M. Brenes of the Museo Nacional de Costa Rica.

Ardisia brenesii is unique within *Ardisia* subg. *Auriculardisia* sect. *Fagerlindia* because of the mixture of ferrugineous-lepidote and cupuliform scales present throughout the plant, although it clearly belongs to the section because of the dimorphism between the leaves of the vegetative and reproductive shoots. *Ardisia brenesii* may be most easily confused with *A. tortuguerensis* because of its large, strikingly dimorphic leaf blades to 53.7 cm long, those of the vegetative shoots elliptic to oblanceolate with obvious acumen to 3.2 cm long, and gradually tapering toward the base. However, *Ardisia brenesii*, with its mixed vestiture, apiculate-subulate anthers, much larger calyx lobes to 1.4 mm long, and corolla lobes furfuraceous-lepidote abaxially, is easily recognized.

The type of *Ardisia limonensis* is identical to populations of *A. brenesii*, except it is more robust. It is important to note that the MO holotype of *A. limonensis* is made of two vegetative shoot leaves and an inflorescence, and both the F and LL isotypes are made up of reproductive shoot leaves with an attached inflorescence.

Specimens examined. NICARAGUA. **Río San Juan**: near Río San Juan at "El Relos," ca. midpoint between El Castillo and Delta de San Juan, 23 Mar. 1961 (fl), *G.*

Bunting & L. Licht 791 (F [2], LL, NY); Buena Vista 1 km W of mouth of Río San Juan, 13 Sep. 1983 (fl, fr), *E. Martínez & R. Riviere 2072* (MEXU, US); trail between el Castillito or Caño de Oro, toward Cerro el Gigante, 15 Sep. 1982 (fr), *E. Martínez S. 2159* (MEXU); Río San Juan, El Castillito, 14 Sep. 1982 (fr), *R. Riviere 358* (MO); along Fish and Top House Creek branches of Río Indio, 5 July 1994 (fr), *R. Rueda et al. 1798* (HULE, MO); Reserva Indio-Maíz, slopes facing mouth of Río San Carlos, on the Río San Juan, 11 Feb. 1996 (fl), *R. Rueda et al. 4054* (HULE, MO); Mpio. San Juan del Norte, Reserva Indio-Maíz, Cerro El Gigante, 5 km del Río San Juan, 21 Sep. 1998 (fl), *R. Rueda et al. 8877* (HULE, MO). COSTA RICA. **Alajuela**: on Caribbean slope between San Lorenzo and Los Angeles de San Ramón, above the Río San Lorenzo, 20 Sep. 1978 (fr), *W. Burger & T. Antonio 11183* (F); Cantón de San Ramón, Reserva Forestal San Ramón, Cordillera de Tilarán, trail to the Station, 6 Mar. 1995 (fl), *G. Carballo 514* (CR, FTG, INB, MO); Reserva Biológica Monteverde, valley of Río Peñas Blancas, 24 Apr. 1987 (fl), *W. Haber & E. Cruz 6997* (CR, INB, MO, US); Reserva Forestal de San Ramón, ca. 10 km W of Lagitos along Río San Lorencito, 30 May–1 June 1986 (fl, fr), *B. Hammel et al. 15261* (LL [2], MO [2]); Cantón de San Ramón, Reserva Forestal San Ramón, Volcán Muerto Ridge, El Sahino Trail, 26 Apr. 1993 (fl), *E. López et al. 42* (CR, F, FTG INB, MO); Reserva Biológica Monteverde, Estación Eladio's, 2 Oct. 1990 (fl), *N. Obando et al. 201* (CR, INB, MO); Los Angeles de San Ramón, 20 July 1984 (fr), *J. Pipoly 7113* (CR, NY, TEX, US). **Heredia**: Cantón de Sarapiquí, Cuenca del Sarapiquí, Sardinal Hills, ca. 15 km N of Puerto Viejo, 11 Jan. 1997 (fr), *B. Hammel 20661* (INB, MO). **Limón**: hills 3.5 airline km S of Isla Buena Vista in the Río Colorado, 16 airline km SW of Barra del Colorado, 15–16 Sep. 1986 (fl, fr), *G. Davidse & G. Herrera 31185* (MO); Refugio Barra del Colorado, between Río Chirripocito and Río Sardina, "sardinal" on Chirripó Atlántico quadrangle, 11 Nov. 1988 (fl), *M. Grayum et al. 8993* (CR, MO); Cantón de Pococí, R.N.F.S. Barra del Colorado, Llanura de Tortuguero, Sector Cocorí, 4 Jan. 1991 (fr), *E. Rojas 206* (CR, INB, MO); El Cedral, 26 km N of Cariari, on the farm of Mario Chavarría P., 13 Sep. 1994 (fl), *K. Thomsen 1024* (C, MO). PANAMA. **San Blas**: trail from Río Esadí to Cerro Banega, 21 Dec. 1985 (fl, fr), *G. de Nevers & H. Herrera 6646* (MO [2]).

15. Ardisia gordonii Ricketson & Pipoly, sp. nov. TYPE: Panama. Bocas del Toro: above Chiriquí Grande, 08°55′04″N, 082°10′04″W, 300 m, 26 Dec. 1986 (fl), *G. McPherson & J. Aranda 10163* (holotype, MO!; isotype, LL!). Figure 18.

Ob laminam secus margines integerrimam lobos calycinos 1.3–1.5 mm longos 0.8–1.0 latosque lobos corollinos 3.2–3.4 mm longos 1.9–2.0 mm latos denique antheras 1.8–2.0 mm longas 1.0–1.1 mm latas, *A. bastonalensi* valde arcte affinis, sed ab ea habitu fruticoso (non suffruticoso) lobulis calycinis 0.8–1.0 (non 1.1–1.3) mm latis, antheris 1.8–2.0 (non 2.9–3.1) mm longis 1.0–1.1 (nec 1.2–1.6) mm latis, denique pistillo 4.2–4.4 (non 5.6–5.9) longo facile distinguitur.

Small trees to 4 m tall. *Trunk and vegetative shoots* 3–4.5 mm diam., densely furfuraceous-lepidote, the scales flat, pallid, *reproductive shoots* similar to the vegetative shoots, but 1.5–2.5 mm diam. *Leaves* dimorphic; vegetative shoot leaves with the blades membranous, narrowly elliptic to oblanceolate or spathulate, 11.5–21.5 × 3.2–5.6 cm, apically acuminate, with an acumen 5–14 mm long, gradually tapering to an auriculate, amplexicaul base, prominently punctate and punctate-lineate above and below, glabrous above, densely furfuraceous-lepidote, more scattered on the midrib, the midrib impressed above, prominently raised below, the secondary veins 37 to 45 pairs, prominulous above and below, the margins entire, flat; petioles obsolete; reproductive shoot leaves with the blades similar to the vegetative shoot leaf blades, but 6.4–8.8 × 1.5–3.4 cm. *Inflorescences* bipinnately paniculate, 10–22 × 5.5–8 cm, longer than the leaves, densely furfuraceous-lepidote, the branches terminating in 5- to 12-flowered corymbs; peduncles 5.5–15.5 cm long; inflorescence bracts similar to the vegetative shoot leaf blades, but oblanceolate or oblong, 1.8–4.3 × 0.4–0.8 cm; inflorescence branch bracts persistent, membranous, oblong, 4.5–5.6 × 1.4–2.1 mm, apically acute, the veins absent, prominently punctate and punctate-lineate, glabrous above, sparsely furfuraceous-lepidote below, the margin minutely erose, hyaline; floral bracts similar to the inflorescence branch bracts, but 0.7–2.1 × 0.4–0.8 mm; pedicels 0.6–1.1 cm long, prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote. *Flowers* pink; calyx lobes membranous, ovate, 1.3–1.5 × 0.8–1 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote

→

Figure 18 (left). *Ardisia gordonii.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, lateral margin. —G. Stamen, adaxial surface. —H. Fruit. (A, B & H drawn from holotype, *G. McPherson & J. Aranda 10163* (MO); C–G from *G. McPherson 8753* (MO).)

Figure 19 (right). *Ardisia nevermannii.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of indument, stiff, mostly erect modified hairs. —D. Detail of inflorescence. —E. Flower. —F. Stamen, abaxial surface. —G. Stamen, adaxial surface. —H. Stamen, lateral margin. —I. Fruit. (A, B drawn from *M. Grayum et al. 7925* (MO); C–H from *C. Barbosa 6591* (MO); I from *L. Poveda A. et al. 4174* (F).)

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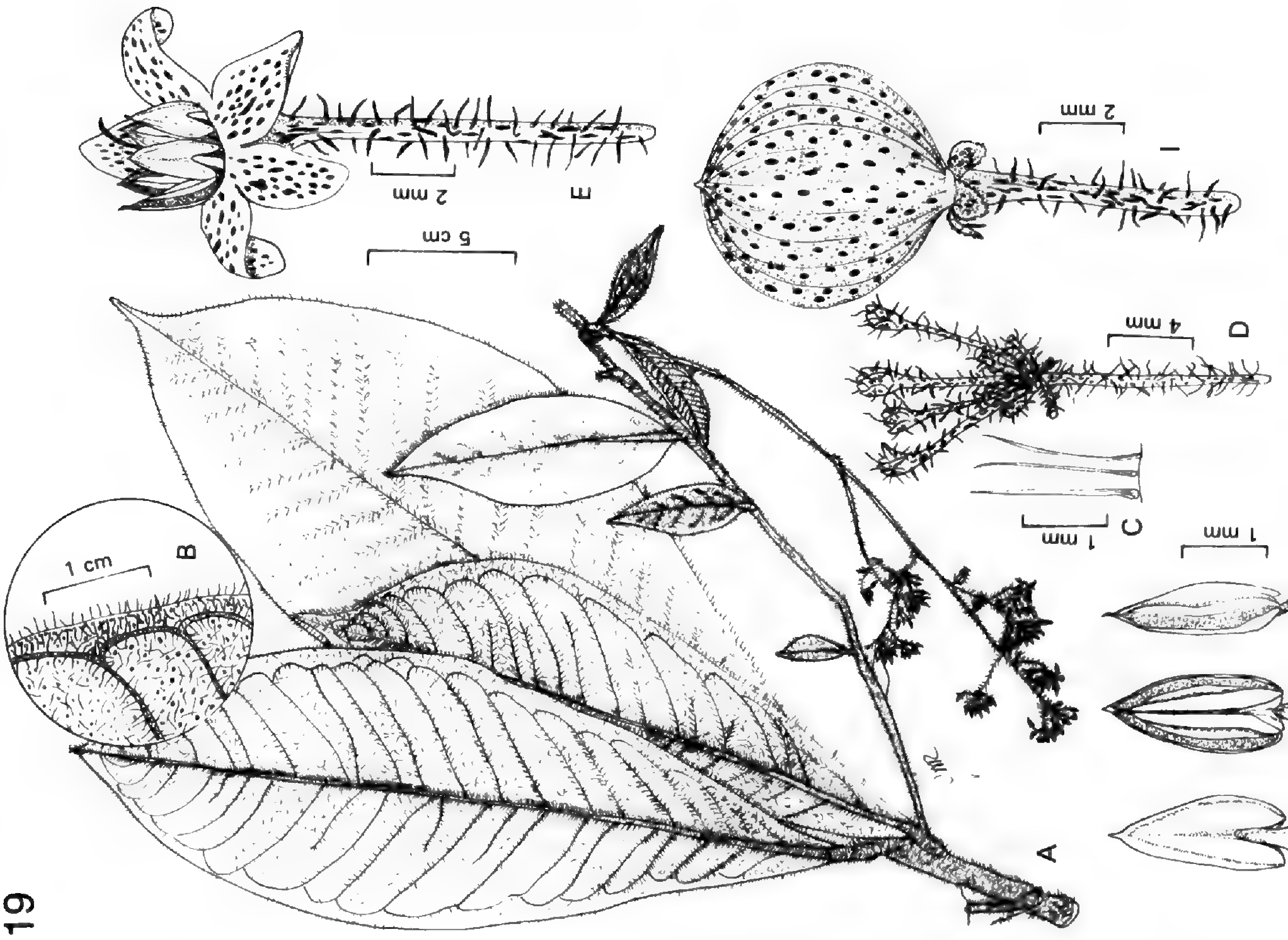
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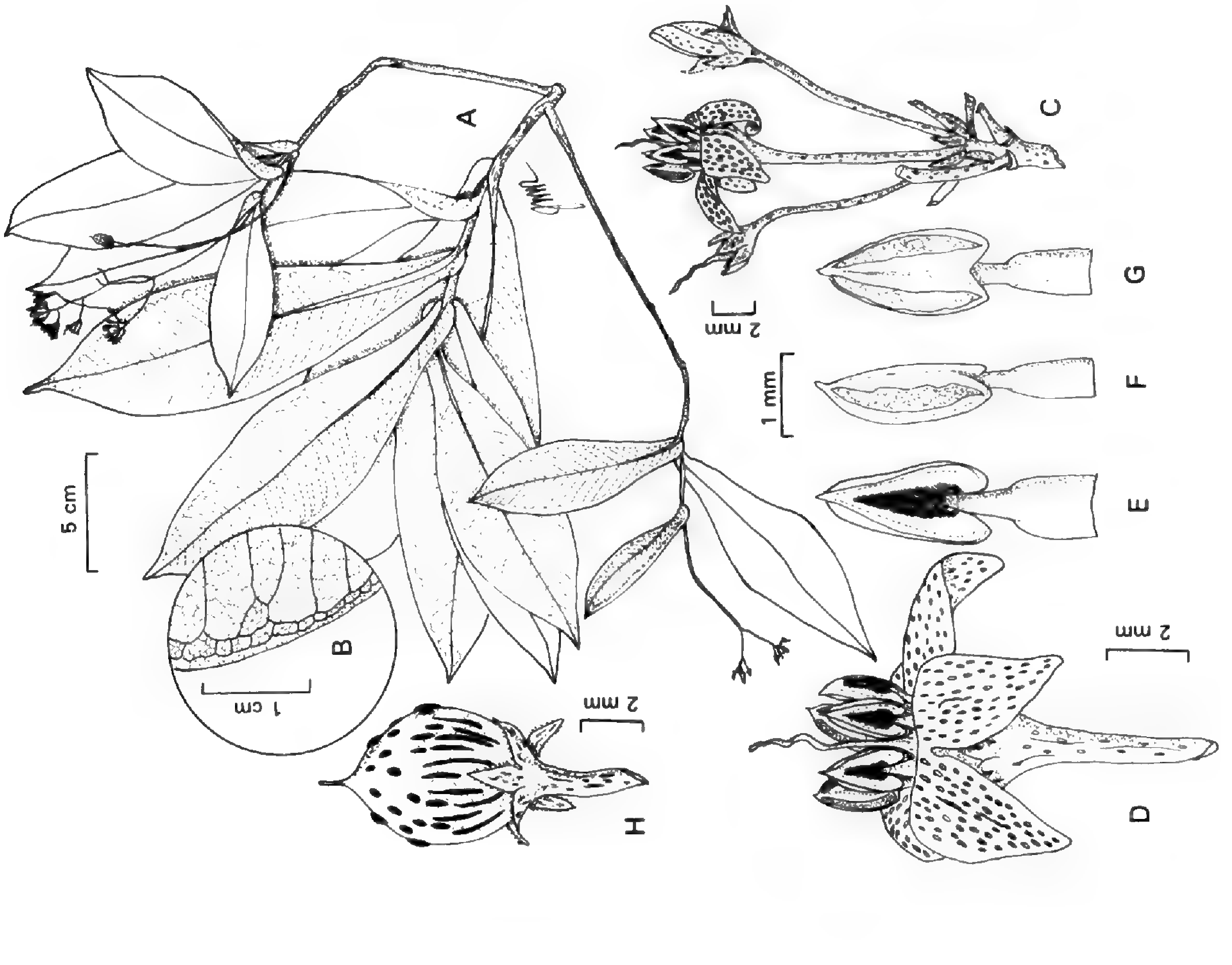
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2 mm

abaxially, the margins minutely erose, hyaline, sparsely glandular ciliolate; corolla 4.4–4.6 mm long, the tube 1–1.4 mm long, the lobes ovate, 3.2–3.4 × 1.9–2 mm, apically acute, prominently black punctate, glabrous throughout, the margins entire, hyaline; stamens 2.5–2.8 mm long, the filaments 1.7–1.8 mm long, the staminal tube 0.9–1 mm long, the apically free portions 0.7–0.9 mm long, epunctate, the anthers ovoid, 1.8–2 × 1–1.1 mm, apically apiculate, basally deeply cordate, the connective inconspicuously punctate; pistil 4.2–4.4 mm long, the ovary 1–1.1 mm long, the styles 3.1–3.4 mm long, inconspicuously punctate, the ovules 8 to 11. *Fruits* 7–7.5 mm diam., inconspicuously pellucid-punctate.

Distribution. *Ardisia gordonii* is endemic to the area above Chiriquí Grande around the area of Cerro Pila de Arroz, in Bocas del Toro, Panama, growing at 300–500 m in elevation.

Ecology and conservation status. *Ardisia gordonii* occurs on slopes of premontane wet forest. Because of its restricted distribution it should be considered threatened.

Etymology. It is an honor to dedicate this species to Gordon McPherson, a curator at the Missouri Botanical Garden. Gordon is an indefatigable collector, prodigious floristician, a noted specialist in African and Central American floras, and above all, a scholar and gentleman.

Within *Ardisia* subg. *Auriculardisia* sect. *Fagerlindia, Ardisia gordonii* appears to be most closely related to *A. tilaranensis* by the narrowly elliptic to oblanceolate or spatulate leaf blades gradually tapering to an auriculate base, the very short or obsolete petioles, persistent inflorescence bract, black punctate corolla lobes, and apiculate anthers. However, *Ardisia gordonii* can easily be separated from *A. tilaranensis* by the entire leaf blades, calyx lobes to 1.5 × 1 mm, much larger, black punctate corolla lobes to 3.4 × 2 mm, larger anthers to 2 × 1.1 mm on longer apically free filaments to 0.9 mm long, and larger non-costate fruit to 7.5 mm in diameter.

Paratype. PANAMA. **Bocas del Toro**: along road to Chiriquí Grande, 10 road mi. from Continental Divide and 2 mi. along pipeline access road E of hwy., on Cerro Pila de Arroz, 10 Mar. 1986 (fl, fr), *G. McPherson 8753* (LL, MO).

16. Ardisia nevermannii Standl., J. Wash. Acad. Sci. 17: 524. 1927. *Valerioanthus nevermannii* (Standl.) Lundell, Wrightia 7: 50. 1982. *Auriculardisia nevermannii* (Standl.) Lundell, Phytologia 57: 450. 1985. TYPE: Costa Rica. Limón: Finca Montecristo, on the Río Reventazón, below El Cairo, ca. 25 m, 18–19 Feb. 1926 (fl), *P. Standley & J. Valerio 48603* (holotype, US!, LL neg. 1971-73!, US neg. 2377!). Figure 19.

Shrubs or subshrubs 3 m tall. *Trunk and vegetative shoots* 6–9 mm diam., hirtellous-tomentose, the trichomes apparently unicellular, the hairs 1.4–1.8 mm long; *reproductive shoots* similar, but 2.5–4.5 mm diam. *Leaves* dimorphic; vegetative shoot leaves with the blades membranous, narrowly oblong to oblanceolate, 34.2–42.5 × 10.2–13.9 cm, apically acuminate, with an acumen 1.3–2.9 cm long, basally obtuse or slightly auriculate, prominently punctate and punctate-lineate, hirtellous-tomentose above and below, the hairs 0.8–1.8 mm long, much denser along the midribs, the midrib impressed above, prominently raised below, the secondary veins 26 to 42 pairs, slightly impressed above, prominulous below, the margins entire, flat; petioles stout, canaliculate, 0.7–1.8 cm long, hirtellous-tomentose above and below, the hairs 1.4–1.8 mm long; reproductive shoot leaves with the blades similar to the vegetative ones but 5.5–27.5 × 2.7–8.9 mm, the secondary veins 13 to 31 pairs; petioles similar to the vegetative ones but 0.2–1.2 cm long. *Inflorescences* pinnately or bipinnately paniculate, 11–22.5 cm long, longer than the leaves, hirtellous-tomentose, the hairs 1.4–1.8 mm long, the branches terminating in 3- to 8-flowered corymbs; peduncle 4.1–12.7 cm long; inflorescence bract unknown; inflorescence branch bracts early caducous, oblong, 0.5–2.6 × 1.1–8.2 mm, apically acute to rounded, prominently punctate and punctate-lineate, hirtellous-tomentose, the hairs 0.8–1.8 mm long, the midrib prominulous above and below, the secondary veins inconspicuous, the margins entire; floral bracts similar to the inflorescence branch bracts but 0.4–1.6 × 0.2–0.4 mm, basally sessile; pedicel 6.2–7.6 mm long, conspicuously punctate, hirtellous-tomentose, the hairs 1.2–1.8 mm long. *Flowers* white or light pink; calyx lobes membranous to chartaceous, ovate to suborbicular, 1–1.2 × 1.1–1.4 mm, apically acute, prominently punctate and punctate-lineate, sparsely hirtellous abaxially, the hairs 0.3–0.8 mm long, glabrous adaxially, the margins irregular, minutely erose, hyaline, sparsely glandular-ciliolate; corolla 4.3–4.6 mm long, the tube 0.3–0.7 mm long, the lobes widely ovate, 3.9–4.3 × 2.1–2.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire; stamens 3.1–3.3 mm long, the filaments 0.9–1 mm long, the staminal tube 0.3–0.7 mm long, the apically free portions 0.3–0.6 mm long, the anthers narrowly ovoid to lanceoloid, 2.4–2.7 × 0.9–1.1 mm, apically caudate, basally sagittate, the connective punctate dorsally; pistil 3.1–3.3 mm long, the ovary 0.5–0.6 mm long, the style 2.5–2.7 mm long, inconspicuously punctate, the ovules 7 to 9. *Fruits* 7.2–7.9 mm diam., prominently punctate and punctate-lineate, costate.

Distribution. *Ardisia nevermannii* occurs in San José and Limón, Costa Rica, and the Chocó of Colombia. It is not known from Panama, but should be expected in the Darién, growing from sea level to 850 m in elevation.

Ecology and conservation status. *Ardisia nevermannii* occurs in wet and pluvial forests. While it is certainly not common, there are no data to suggest the species is threatened at this time.

Etymology. Standley (1927: 524) stated that "the species is named for Mr. Ferdinand Nevermann, a keen student of Costa Rican *Coleoptera* . . . ."

Ardisia nevermannii is unique among all the members of *Ardisia* subg. *Auriculardisia* sect. *Fagerlindia* because of its hirtellous-tomentose vestiture throughout the plant and the caudate apices of the anthers.

Specimens examined. COSTA RICA. **Limón**: Hamburg, 9 km down river from Reventazón, 2 May 1930 (fl), *G. Cufodonti 685* (W); Zona Protectora Barbilla, W side of plateau separating headwaters of N fork of Río Dantas from headwaters of Quebrada varreal, Río Barbilla drainage, SE of Siquirres, 11 Jan. 1987 (fl), *M. Grayum et al. 7925* (CR, MO, TEX); Cerro Muchilla, Fila Matamá, Cordillera de Talamanca, 6 Apr. 1989 (fr), *R. Robles & A. Chacón 2683* (CR, FTG, INB, MO); Río Reventazón drainage basin, 23 Oct. 1951 (fr), *P. Shank & A. Molina R. 4412* (F); Finca Montecristo, on the Río Reventazón, below Cairo, 18–19 Feb. 1926 (fl), *P. Standley & J. Valerio 48484* (US); Hamburg Finca, on the Río Reventazón, below Cairo, 19 Feb. 1926 (fl), *P. Standley & J. Valerio 48754* (US), *48824* (US). **San José**: Carrillo Station, Braulio Carrillo, 19 Apr. 1984 (fr), *L. Gómez et al. 21159* (LL, MO); Parque Nacional Braulio Carrillo, Estación Carrillo, 27 Nov. 1986 (fr), *L. Poveda A. et al. 4174* (F); Laguna on hills along Río Corinto, Parque Nacional Braulio Carrillo, 16 Aug. 1984 (fr), *P. Sánchez & N. Zamora 561* (MO). COLOMBIA. **Chocó**: Mpio. de Nuquí, Corregimiento Termales, N of Quebrada Piedra, Piedra, 8 Sep. 1994 (fr), *P. Acevedo-Rdgz. et al. 6875* (FTG, US); trail on Morro de Mico to the scenic lookout, along "jurubidá" path, southward and then on "Copete de Pava" trail northward, 15 May 1990 (fl, fr), *C. Barbosa 6591* (CHOCO, FTG [2], MO [2]); NW of Alto Curiche, 20 May 1967 (fr), *J. Duke & J. Idrobo 11248* (LL); Mpio. Bahía de Solano, Parque Nacional Natural Ensenada de Utría, trail between Punta Diego and Caída Cocalito, 18 Apr. 1990 (fr), *J. Espina et al. 3639* (CHOCO, MO); Mpio. Bahía de Solano, Parque Nacional Natural Ensenada de Utria, trail between the cove and Cocalito beach, 23 Apr. 1990 (fr), *J. Espina et al. 3827* (CHOCO, MO).

17. Ardisia tilaranensis Standl., J. Wash. Acad. Sci. 17: 524. 1927. *Auriculardisia tilaranensis* (Standl.) Lundell, Phytologia 49: 345. 1981. TYPE: Costa Rica. Guanacaste: Quebrada Serena, SE of Tilarán, ca. 700 m, 27 Jan. 1926 (fr), *P. Standley & J. Valerio 46169* (holotype, US!, US neg. 2389!, LL neg. 71-115!). Figure 20.

Subshrubs to 3 m tall. *Trunk and vegetative shoots* 2.5–5 mm diam., densely appressed furfuraceous-lepidote, *reproductive shoots* similar to the vegetative shoots, but 1.5–3.5 mm diam. *Leaves* dimorphic; vegetative shoot leaves with the blades membranous, narrowly elliptic, 7.5–17.2 × 1.9–4.2 cm, apically attenuate to acuminate, with an acumen 0.7–1.4 cm long, gradually tapering to an auriculate base, prominently punctate and punctate-lineate, essentially glabrous above, sparsely appressed furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 21 to 34 pairs, slightly depressed above, prominulous below, the margin crenate to dentate, flat; petioles stout, marginate, subobsolete to 2.5 mm long, glabrous above, densely furfuraceous-lepidote below; reproductive shoot leaves with the blades similar to the vegetative ones, but 3.5–14.7 × 1.1–4.3 cm. *Inflorescences* bipinnately to tripinnately paniculate, 5.4–9.2 × 2.5–5.6 cm, longer than the leaves, the rachis and pedicels densely furfuraceous-lepidote, the branches terminating in 7- to 13-flowered corymbs; peduncles 0.4–1.7 cm long; inflorescence bracts persistent, membranous, ovate to lanceolate, 0.4–3.7 × 0.3–0.9 cm, apically acuminate, otherwise as in the reproductive shoot leaf blades; inflorescence branch bracts caducous, membranous, ovate, 1.5–3.2 × 1.4–2.6 mm, apically acute, basally auriculate, prominently punctate and punctate-lineate, essentially glabrous above, sparsely furfuraceous-lepidote below, the midrib impressed above, slightly prominent below; pedicels 4.5–6.2 mm long, prominently punctate and punctate-lineate, densely furfuraceous-lepidote. *Flowers* pink; calyx lobes membranous to chartaceous, ovate, 1–1.1 × 0.6–0.7 mm, apically acute, prominently punctate, sparsely furfuraceous-lepidote, the margins minutely erose, hyaline, sparsely glandular-ciliolate; corolla 2.8–2.9 mm long, the tube 1–1.1 mm long, the lobes ovate, 1.6–1.9 × 1.2–1.3 mm, apically acute, prominently black punctate and punctate-lineate, glabrous throughout, the margins entire; stamens 2.1–2.2 mm long, the filaments 1–1.1 mm long, the staminal tube 0.4–0.6 mm long, the apically free portions 0.6–0.7 mm long, epunctate, the anthers ovoid, 1.2–1.3 × 0.4–0.5 mm, apically apiculate, basally cordate, the connective inconspicuously

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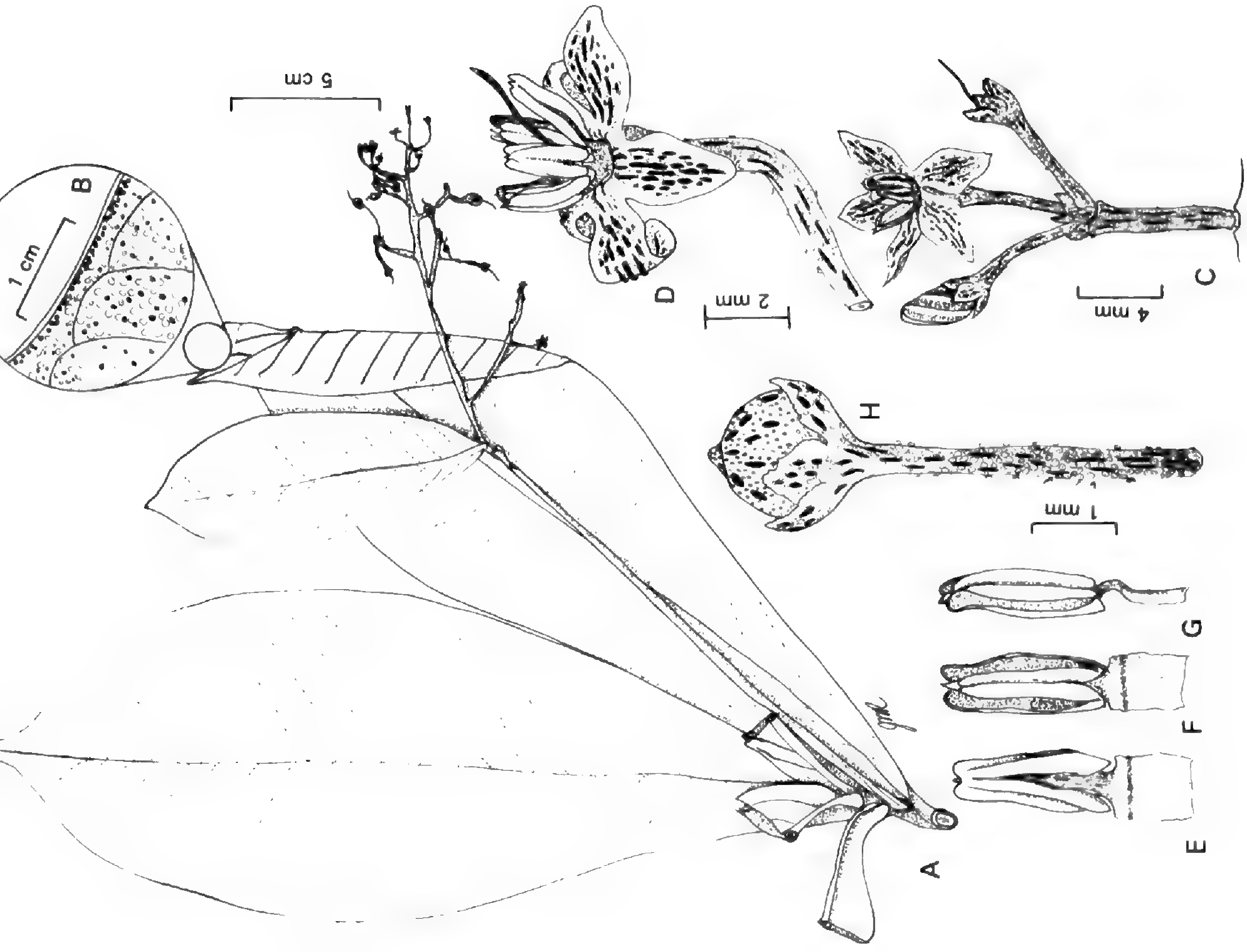

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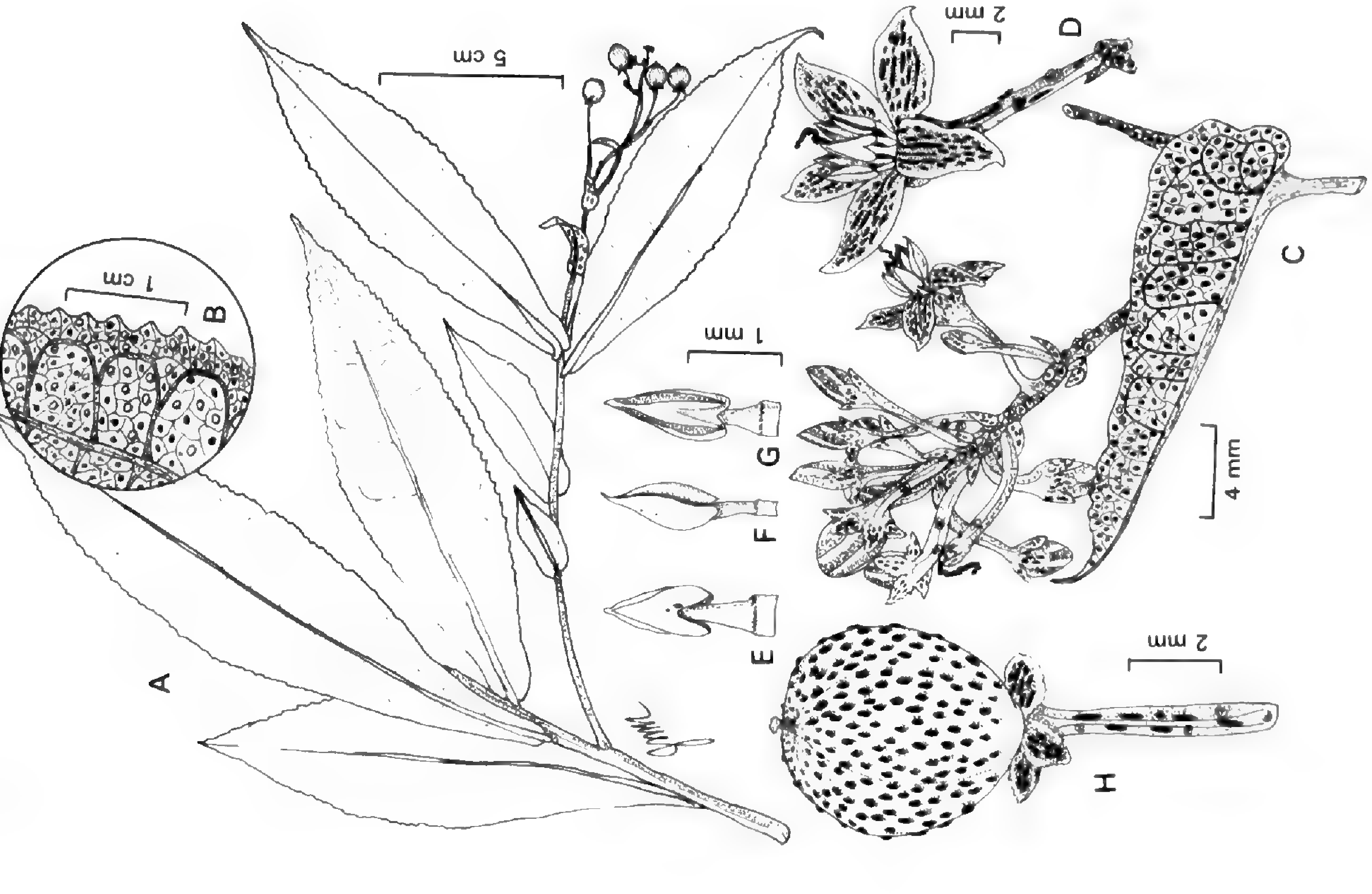

punctate; pistil 2.9–3 mm long, the ovary 0.6–0.7 mm long, the style 1.8–2.1 mm long, prominently and conspicuously punctate, the ovules 10 to 12. *Fruits* 6–6.5 mm diam., prominently punctate, slightly costate.

Distribution. *Ardisia tilaranensis* is endemic to the Cordillera de Tilarán, located in Guanacaste and Alajuela, Costa Rica, growing from 600 to 1400 m in elevation.

Ecology and conservation status. *Ardisia tilaranensis* occurs in premontane humid forests. We believe that the protected status of the areas where this species has been recorded is enough to protect it for the time being.

Etymology. The specific epithet referred to the type locality, along the Cordillera de Tilarán in Cantón Guanacaste, Costa Rica.

By virtue of its subsessile leaf blades gradually tapering to an auriculate base and apiculate anthers, *Ardisia tilaranensis* is most closely related to *A. gordonii* within *Ardisia* subg. *Auriculardisia* sect. *Fagerlindia.* However, *Ardisia tilaranensis* can be easily separated from *A. gordonii* by its crenate to dentate leaf blade margins, the smaller calyx to 1.1 mm long and corolla lobes to 1.9 mm long, shorter, apically free portions of the filaments to 0.7 mm long, and the smaller fruits to 6.5 mm in diameter.

Specimens examined. COSTA RICA. **Alajuela**: Reserva Biológica Monteverde, Bosque Eterno de los Niños, Quebrada Agua Gata, 25 Jan. 1990 (fr), *E. Bello C. 1810* (CR, FTG, INB, MO); forest trail from Macadamia Village to summit of Cerro Chato, 3 Oct. 1991 (fr), *V. Funk et al. 10984* (US); Reserva Monteverde, Poco Sol, 13 km S Fortuna, 20 Aug. 1989 (fl), *W. Haber & W. Zuchowski 9358* (CR, INB, MO); Cantón Upala, Bijagua, El Retiro, slopes of Cerro Montezuma, 23 July 1993 (fl), *G. Herrera 6341* (CR, F); S slope of Cerro Chato, 25 Feb. 1989 (fr), *G. Russell et al. 976* (US). **Guanacaste**: hills on way to Laguna de Arenal, 18 July 1962 (fl), *C. Brown 17416A* (F, LSU); Quebrada Grande, Tilarán, Esperanza–Las Nubes Trail, on Continental Divide, 24 Feb. 1987 (fl, fr), *W. Haber & E. Bello C. 6710* (MO); El Silencio, near Tilarán, 13 Jan. 1926 (fr), *P. Standley & J. Valerio 44729* (US), *44763* (US); Los Ayotes, near Tilarán, 21 Jan. 1926 (fr), *P. Standley & J. Valerio 45422* (US).

18. Ardisia tortuguerensis Ricketson & Pipoly, sp. nov. TYPE: Costa Rica. Limón: Parque Nacional Tortuguero, Lomas de Sierpe, 4 km NE of gate at Parque Nacional, along the Río Sierpe, 10°24′N, 083°33′W, 100 m, 15 Aug. 1988 (fl, fr), *R. Robles, G. Herrera, L. Flores & M. Rojas 2052* (holotype, MO!; isotype, CR!). Figure 21.

Ob laminam foliarem ad basim gradatim contractam, ramulos crassos atque pedicellos longos cum ad *A. apoda* saepenumero confusus erat, sed ab ea ramulis 4.5–5.4 (non 7.5–8.5) mm diametro, laminis foliaribus 25.2–34.6 (non 39.8–42.6) cm longis ad apices abrupte acuminatis (nec attenuato-acuminatis), inflorescentiis 9.2–11.5 (non 12.4–12.8) cm longis, denique lobulis calycinis 1.3–1.5 (non 1–1.2) mm longis praeclare distat.

Small shrubs, height unknown. *Trunk and vegetative shoots* 4.5–5.4 mm diam., dense furfuraceous-lepidote to short cupuliform scales, the scales sessile or slightly stalked, 0.1–0.2 mm tall, lobed or with 2 to 8 arms, very similar to those of *A. brenesii* but of one size instead of two; *reproductive shoots* similar, but 1.5–2.3 mm diam. *Leaves* dimorphic; vegetative shoot leaves with the blades membranous, oblanceolate, 25.2–34.6 × 9.6–11.1 cm, apically abruptly acuminate, with an acumen 0.3–0.5 cm long, basally gradually tapering to an auriculate base, prominently punctate and punctate-lineate, furfuraceous-lepidote, the scales sparse above, denser below, much denser basally below and along the midrib, the midrib impressed above, prominently raised below, the secondary veins 28 to 37 pairs, slightly depressed above, prominulous below, the margins entire, flat or revolute; petioles stout, marginate, subobsolete to 0.3 cm long, densely furfuraceous-lepidote; reproductive shoot leaves with the blades similar to the vegetative ones but 10.3–19.4 × 4–7.4 cm, the secondary veins 25 to 32 pairs; petioles similar to the vegetative ones but 0.2–0.7 cm long. *Inflorescences* bipinnately or tripinnately paniculate, 9.2–11.5 × 6.1–8.5 cm, longer than the leaves, indument as in the vegetative shoots, the branches terminating in 5- to 9-flowered corymbs; peduncles 0.5–1.5 cm long; inflorescence bracts and branch bracts early caducous, unknown; floral bracts chartaceous, oblong, 1.4–1.7 × 0.5–0.6 mm, apically acute, prom-

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Figure 20 (left). *Ardisia tilaranensis.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, lateral margin. —G. Stamen, adaxial surface. —H. Fruit. (A–H drawn from *W. Haber & E. Bello C. 6710* (MO).)

Figure 21 (right). *Ardisia tortuguerensis.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, adaxial surface. —G. Stamen, lateral margin. —H. Fruit. (A–H drawn from holotype, *R. Robles et al. 2052* (MO).)

inently punctate and punctate-lineate, glabrous above, densely furfuraceous-lepidote below, midrib and secondary veins inconspicuous, the margins entire, hyaline; pedicels 4.3–8.1 mm long, conspicuously punctate, indument as in the vegetative shoots. *Flowers* light purple; calyx lobes membranous to chartaceous, ovate to suborbicular, 1.3–1.5 × 1.1–1.3 mm, apically acute or rounded, prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote, the margins entire, minutely erose, hyaline, sparsely glandular-ciliolate; corolla 3.1–3.4 mm long, the tube 0.5–0.6 mm long, the lobes ovate, 2.6–2.8 × 1.6–1.9 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margin entire; stamens 2.9–3 mm long, the filaments 1.1–1.3 mm long, the staminal tube 0.6–0.8 mm long, the apically free portions 0.5–0.7 mm long, epunctate, the anthers narrowly ovoid to lanceoloid, 1.9–2.1 × 0.7–0.8 mm, apically apiculate-cuspidate, basally sagittate, the connective punctate; pistil 3.2–4 mm long, glabrous, the ovary 1–1.2 mm long, the style 2–2.4 mm long, inconspicuously punctate, the ovules 8 to 10. *Immature fruits* 3–4.2 mm diam., prominently punctate and punctate-lineate, appearing non-costate.

Distribution. *Ardisia tortuguerensis* is known only from the type in Limón, Costa Rica, growing at 100 m in elevation.

Ecology and conservation status. *Ardisia tortuguerensis* occurs on fairly steep, densely forested slopes with well-drained soils. Because it is only known from the type, it should be considered threatened.

Etymology. The specific epithet refers to the area in which it is found, Parque Nacional Tortuguero, along the east coast of Costa Rica in Limón.

Within *Ardisia* subg. *Auriculardisia* sect. *Fagerlindia*, *Ardisia tortuguerensis* most closely resembles *A. apoda*, because of the large vegetative shoot leaves 25.2–42.6 × 9.4–11.1 cm. *Ardisia tortuguerensis* is easily separated from *A. apoda* by the narrower branchlets to only 5.4 mm in diameter, smaller vegetative shoot leaf blades to 34.6 cm long with abruptly acuminate apices, shorter petioles of reproductive shoot leaf blades to 0.7 cm long, shorter inflorescences to 11.5 cm long, and smaller calyx lobes to 1.5 mm long.

TAXONOMIC TREATMENT OF *ARDISIA* SUBG. *AURICULARDISIA* SECT. *PALMANAE*

Ardisia subg. **Auriculardisia** sect. **Palmanae** Ricketson & Pipoly, sect. nov. TYPE here designated: *Ardisia palmana* Donn. Sm.

Quoad lobulos calycinos fere liberos asymmetricos sub apicibus subincises ad bases auriculatos ad *Ardisiam* subg. *Auriculardisiam* pertinet. Ab aliis sectionibus subgeneris inflorescentiis terminalibus pedunculis obsoletis (versus breves) insidentibus perfacile cognoscitur.

Shrubs or small trees. Branchlets straight or flexuous, slender to stout, terete, subterete, with fine longitudinal ridges, or angulate, with densely furfuraceous-lepidote and/or cupuliform scales, rarely stipitate-stellate tomentellous (*A. liesneri*), the vestiture mostly persistent, but at times glabrescent. *Leaves* monomorphic, with blades membranous to coriaceous, elliptic to oblong or obovate to oblanceolate, at times inconspicuously punctate and/or punctate-lineate, the margins flat or revolute. *Inflorescences* terminal, mostly pendent, sometimes erect, pinnately to tripinnately paniculate, pyramidal, or obpyramidal, mostly shorter than the leaves, the branches loosely to tightly congested into corymbs; peduncle short to obsolete, inflorescence bracts usually early caducous, inflorescence branch bracts and floral bracts often small and early caducous; pedicels slender to stout, terete, obsolete to short. *Flowers* 5- or 6-merous; calyx lobes essentially free, membranous to coriaceous, asymmetric, widely ovate, oblate to ovate, subapically notched, basally auriculate; corolla membranous to coriaceous, the lobes narrowly ovate, lanceolate, or oblong, inconspicuously to conspicuously or prominently punctate and/or punctate-lineate; stamens connate, the filaments connate basally into an elobate tube, free from the corolla tube, epunctate, glabrous, the anthers ovoid to lanceoloid, basally lobate or cordate, dehiscent by longitudinal slits, the connective punctate; pistil glabrous, the ovary ovoid, the style slender, erect, epunctate or punctate and/or punctate-lineate, the ovules pluriseriate. *Fruits* globose to depressed globose, inconspicuously or conspicuously to prominently punctate.

Distribution. Forty-seven species from Belize and Guatemala, southward through Mesoamerica to the Chocó Floristic Province of Panama, Colombia, and western Ecuador, from sea level to 2200 m in elevation.

Ecology. The majority of the species of *Ardisia* subg. *Auriculardisia* sect. *Palmanae* are very localized, occurring in montane and cloud forest habitats, occasionally in premontane pluvial forest and rarely in tall, lowland wet forest.

Ardisia subg. *Auriculardisia* sect. *Palmanae* is defined by the terminal, sessile to subsessile inflorescences. In the absence of phylogenetic studies, we cannot be sure if this character arose more than once, so we cannot be sure about the monophyly of the section.

KEY TO THE TAXA OF *ARDISIA* SUBG. *AURICULARDISIA* SECT. *PALMANAE*

1a. Abaxial leaf surface with a dense mixture of cupuliform and furfuraceous-lepidote scales.

2a. Inflorescences pendent; pedicels 6–14 mm long; corolla tube sparsely furfuraceous-lepidote abaxially; anthers 4–4.1 mm long; styles 9.1–9.4 mm long .... 51. *Ardisia lundelliana*

2b. Inflorescences erect; pedicels 0–4 mm long; corolla tube glabrous abaxially; anthers 1.6–2.6 mm long; styles 2.1–5.2 mm long.

3a. Branchlets straight; leaf blades elliptic to oblanceolate, calyx lobes 0.9–1.4 mm wide; corolla lobes 1.9–3.7 mm long.

4a. Branchlets without longitudinal ridges, with large petiole scars; inflorescences obpyramidal, bipinnately paniculate; pedicels obsolete to 1.2 mm long; calyx lobes obtuse to broadly rounded, 0.9–1.2 mm wide; corolla lobes 1.9–2.1 × 0.8–1 mm; anthers ca. 1.6 × 0.6 mm .... 31. *Ardisia conglomerata*

4b. Branchlets angulate, with longitudinal ridges, the petiole scars small, inconspicuous; inflorescences pyramidal, tripinnately paniculate; pedicels 2–4 mm long; calyx lobes acute, 1.3–1.4 mm wide; corolla lobes 3.5–3.7 × 1.9–2.2 mm; anthers 2.1–2.4 × 0.6–0.8 mm .... 34. *Ardisia crassiramea*

3b. Branchlets flexuous; leaf blades oblong to narrowly elliptic; calyx lobes 1.4–1.9 mm wide; corolla lobes 3.7–4.3 mm long.

5a. Calyx lobes 1.7–1.9 mm wide; corolla lobes oblong, apically acuminate, 1–1.2 mm wide; stamens 3.2–3.6 mm long; anthers 2.4–2.6 × 1–1.2 mm; styles 2.1–2.3 mm long .... 52. *Ardisia mcphersonii*

5b. Calyx lobes 1.4–1.7 mm wide; corolla lobes ovate, apically acute, 2.3–2.5 mm wide; stamens 5.8–6 mm long; anthers 2–2.2 × 0.8–1.1 mm; styles 4.5–5.2 mm long 43. *Ardisia furfuracea*

1b. Abaxial leaf surface with only one type of scale, either of densely cupuliform or furfuraceous-lepidote scales, or occasionally with glandular stipitate-stellate hairs.

6a. Calyx lobes 1.7 mm long or longer.

7a. Petioles slender, 1–3 mm diam.

8a. Calyx lobes as wide as long or wider than long, deeply notched below the apex.

9a. Pedicels 4.5 mm or longer.

10a. Corolla lobes 6.1–6.4 mm long; anthers 3.7–4.3 mm long.

11a. Branchlets with furfuraceous-lepidote scales; leaf blades coriaceous; calyx lobes oblate, 2.4–3 × 4–4.5 mm; corolla lobes 2.8–3.4 mm wide; anthers 3.7–3.8 × 1.2–1.4 mm; styles 5.1–5.3 mm long 32. *Ardisia crassipedicellata*

11b. Branchlets with cupuliform scales and stalked glandular-stellate trichomes; leaf blades chartaceous; calyx lobes orbicular, 1.7–1.9 × 1.7–1.9 mm; corolla lobes 2.5–2.7 mm wide; anthers 4.2–4.3 × 1–1.1 mm; styles 5.7–5.9 mm long .... 50. *Ardisia liesneri*

10b. Corolla lobes 3.1–5.2 mm long; anthers 1.8–3 mm long.

12a. Abaxial leaf punctations inconspicuous, not prominent, the quaternary venation flat; calyx lobes 1.7–2 mm long; corolla lobes 3.1–4.1 × 1.6–2.2 mm .... 65. *Ardisia unguiensis*

12b. Abaxial leaf punctations prominently raised, the quaternary venation prominulous; calyx lobes 2–2.9 mm long; corolla lobes 4.5–5.2 × 3–3.8 mm.

13a. Furfuraceous-lepidote scales on the branchlets, leaves and inflorescence ferrugineous; secondary leaf venation prominulous above and below; calyx lobes ovate to orbicular, apically acute to obtuse, 2.3–2.5 mm wide; anthers 2.6–2.8 × 1.2–1.3 mm .... 46. *Ardisia glandulosomarginata*

13b. Furfuraceous-lepidote scales on the branchlets, leaves and inflorescence rufous; secondary leaf venation impressed above, prominently raised below; calyx lobes oblate, apically broadly rounded to truncate, 2.5–3 mm wide; anthers 3–3.4 × 1.4–1.7 mm .... *Ardisia croatii*

14a. Petioles 4–13 mm long; calyx lobes 2–2.5 mm long; corolla lobes 3.4–3.6 mm wide; anthers 3–3.1 × 1.5–1.7 mm .... 36. *Ardisia croatii* subsp. *croatii*

14b. Petioles 15–24 mm long; calyx lobes 2.6–2.8 mm long; corolla lobes 3–3.2 mm wide; anthers 3.3–3.4 × 1.4–1.5 mm .... 35. *Ardisia croatii* subsp. *correae*

9b. Pedicels 4.5 mm long or shorter.

15a. Styles less than 5 mm long.

16a. Branchlets subterete; leaf blades coriaceous; calyx lobes ovate; anthers 0.8–1 mm wide; styles 3–3.5 mm long .... 59. *Ardisia ruedae*

16b. Branchlets terete; leaf blades chartaceous or membranous; calyx lobes suborbicular to orbicular; anthers 1.1–2.1 mm wide; styles 4–4.7 mm long.

17a. Leaf blades chartaceous; calyx coriaceous; corolla chartaceous, the tube glabrous outside; anthers 1.9–2.2 mm long; styles 4–4.2 mm long; plants of Ecuador ..... 25. *Ardisia awarum*

17b. Leaf blades membranous; calyx chartaceous; corolla membranous, the tube sparsely furfuraceous-lepidote outside; anthers 2.2–2.7 mm long; styles 4.4–4.7 mm long; plants of Costa Rica ..... 39. *Ardisia dunlapiana*

15b. Styles 5 mm long or longer.

18a. Calyx lobes 3.5–3.7 mm wide; corolla lobes 5.3–5.6 mm long; anthers 3.6–3.8 mm long; styles 6.9–7.1 mm long ..... 47. *Ardisia hagenii*

18b. Calyx lobes 1.8–3 mm wide; corolla lobes 4.5–5.2 mm long; anthers 2.2–3.2 mm long; styles 5–5.7 mm long.

19a. Leaf blades 5.2–12.6 × 1.4–3.2 cm; pedicels 0–1.2 mm long; corolla lobes 1.8–2 mm wide; anthers 2.2–2.4 × 0.9–1 mm ..... 26. *Ardisia blepharodes*

19b. Leaf blades 12.6–34.8 × 4–9.7 cm; pedicels 1.8–3.5 mm long; corolla lobes 2.3–3 mm wide; anthers 2.6–3.2 × 1.1–1.5 mm.

20a. Trees 3–25 m tall; blades inconspicuously punctate and punctate-lineate on the upper surface; flowers white or light yellow; calyx lobes coriaceous, 2.2–3 mm wide; anthers 2.6–2.9 × 1.3–1.5 mm ..... 42. *Ardisia fimbrillifera*

20b. Trees 30–40 m tall; blades prominently punctate and punctate-lineate on the upper surface; flowers white to light pink; calyx lobes chartaceous, 1.8–2 mm wide; anthers 3.1–3.2 × 1.1–1.2 mm ..... 57. *Ardisia pseudoracemiflora*

8b. Calyx lobes longer than wide, rarely deeply notched below the apex.

21a. Calyx lobes 3–5 mm long.

22a. Calyx lobes 4.8–5 × 3.9–4.1 mm; styles 5.9–6.4 mm long ..... 37. *Ardisia darienensis*

22b. Calyx lobes 3–3.7 × 2.6–3.4 mm; styles 5–5.6 mm long.

23a. Leaf blades 16.4–32.8 × 4.4–9.8 cm; inflorescence 8.2–32.4 × 4.8–31.5 cm; flowers mostly 5-merous, rarely 6-merous; calyx lobes 3–3.4 × 2.6–3.2 mm; corolla lobes 5.8–6 × 2.8–3.2 mm; anthers 3.2–3.5 × 1.3–1.5 mm; styles 5–5.2 mm long ..... 27. *Ardisia capitellata*

23b. Leaf blades 4.8–11.5 × 1.7–4.2 cm; inflorescence 4.8–7.2 × 3–4.5 cm; flowers all 5-merous; calyx lobes 3.4–3.7 × 3.2–3.4 mm; corolla lobes 4.4–4.7 × 2.2–2.5 mm; anthers 3–3.1 × 1.2–1.3 mm; styles 5.4–5.6 mm long ..... 44. *Ardisia generalensis*

21b. Calyx lobes 1.7–2.9 mm long.

24a. Leaf blades basally auriculate; petioles subobsolete to 5 mm long ..... 24. *Ardisia auriculata*

24b. Leaf blades basally obtuse, acute or cuneate; petioles 4–19 mm long.

25a. Calyx lobes 2.7–2.9 × 2.4–2.7 mm; fruits 4–5 mm diam. ..... 22. *Ardisia angucianensis*

25b. Calyx lobes 1.7–2.4 × 1.2–2 mm; fruits 5–9 mm diam. ..... 54. *Ardisia nigropunctata*

7b. Petioles thick, more than 3 mm diam.

26a. Calyx lobes 2.6–2.8 mm long; corolla lobes 5.4–5.5 mm long; anthers 3.1–3.3 mm long; styles 5.4–5.6 mm long ..... 53. *Ardisia megistophylla*

26b. Calyx lobes 2.1–2.6 mm long; corolla lobes 4–4.5 mm long; anthers 2.3–3 mm long; styles 2–5.1 mm long.

27a. Leaf blades longer than 51 cm long; branchlets 15–20 mm diam.; peduncles 4–6.3 cm long; corolla lobes 1.5–1.7 mm wide ..... 19. *Ardisia aguirreana*

27b. Leaf blades shorter than 51 cm long; branchlets 5–10.5 mm diam.; peduncles nearly sessile to 3.5 cm long; corolla lobes 1.9–2.6 mm wide.

28a. Calyx lobes ovate, 2.5–2.6 × 1.8–1.9 mm; anthers 2.3–2.6 × 1.3–1.5 mm; styles 2–2.2 mm long; fruits 8–9.8 mm diam. ..... 29. *Ardisia cogolloi*

28b. Calyx lobes orbicular to oblate, 2.1–2.3 × 2.1–3.1 mm; anthers 2.8–3 × 0.9–1.1 mm; styles 4.6–5.1 mm long; fruits 4.5–6 mm diam.

29a. Leaf blades coriaceous, rufous furfuraceous-lepidote above and below; petioles 4–5 mm diam.; calyx lobes 2.8–3.1 mm wide; corolla lobes 4.4–4.5 × 2.2–2.3 mm; styles 5–5.1 mm long ..... 33. *Ardisia crassipes*

29b. Leaf blades membranous, glabrous above and below; petioles 3–4 mm diam.; calyx lobes 2.1–2.4 mm wide; corolla lobes 4–4.2 × 1.9–2.7 mm; styles 4.6–4.7 mm long ..... 28. *Ardisia cartagoana*

6b. Calyx lobes less than 1.7 mm long.

30a. Pedicels 3.5 mm long or longer.

31a. Branchlets 8–10 mm in diam.; leaf blades 45.8–46.6 × 15.7–21.5 cm; inflorescences ca. 32 × 25–28 cm; calyx lobes 3.3–3.6 mm wide .... 45. *Ardisia gigantea*

31b. Branchlets 1–6 mm diam.; leaf blades 2–16.6 × 0.6–5.7 cm; inflorescences 3–24 × 2–19 cm; calyx lobes 0.7–3.2 mm wide.

32a. Corolla lobes 1.2–1.8 mm wide; anthers 1–1.9 mm long.

33a. Calyx lobes 1–1.4 mm long.

34a. Branchlets with interpetiolar ridges forming up to 5 angles, 3–5 mm diam.; calyx lobes 1.2–1.4 mm long; corolla lobes 2.8–3 × 1.6–1.7 mm; anthers 0.7–0.9 mm wide; styles 3–3.1 mm long; fruits 3–5 mm diam. .... 61. *Ardisia tarariae*

34b. Branchlets terete or angled, but without interpetiolar ridges, 1–3(–3.5) mm diam.; calyx lobes 0.9–1.2 mm long; corolla lobes 2.3–2.6 × 1.2–1.5 mm; anthers 0.5–0.7 mm wide; styles 1.3–2.9 mm long; fruits 4.3–8 mm diam.

35a. Branchlets angled, sparsely and minutely ferrugineous furfuraceous-lepidote; calyx lobes 1–1.3 mm wide; corolla lobes 2.4–2.6 × 1.2–1.4 mm; anthers 1.8–1.9 mm long; styles 1.3–1.5 mm long; fruits 7–8 mm diam. .... 62. *Ardisia tenuicaulis*

35b. Branchlets terete, densely cupuliform and furfuraceous-lepidote; calyx lobes 0.7–0.8 mm wide; corolla lobes 2.3–2.4 × 1.4–1.5 mm; anthers 1–1.1 mm long; styles 2.6–2.9 mm long; fruits 4.3–4.7 mm diam. .... 63. *Ardisia tenuis*

33b. Calyx lobes 1.4–1.7 mm long.

36a. Branchlets 3–6 mm diam.; petioles 1.1–2.4 mm long; calyx lobes 1.6–1.9 mm wide .... 30. *Ardisia coloradoana*

36b. Branchlets 1–3 mm diam.; petioles 4–7 mm long; calyx lobes 0.8–1 mm wide.

37a. Branchlets 2–3 mm diam.; pedicels 3.6–4.8 mm long; corolla lobes 2.4–3.1 × 1.7–1.8 mm; anthers 1.6–1.7 × 0.6–0.7 mm; styles 3.1–3.3 mm long .... 41. *Ardisia eucuneata*

37b. Branchlets 1–2 mm diam.; pedicels 7.2–16.3 mm long; corolla lobes 1.7–1.8 × 1.2–1.3 mm; anthers 1.8–1.9 × 0.8–0.9 mm; styles 1.6–1.8 mm long .... 23. *Ardisia atropurpurea*

32b. Corolla lobes 1.9–3.3 mm wide; anthers 2.2–4.2 mm long.

38a. Branchlets 1–3.5 mm diam.; pedicels 12–15 mm long .... 56. *Ardisia panamensis*

38b. Branchlets (2–)4–5 mm diam.; pedicels 4–9 mm long.

39a. Leaf blades coriaceous; pedicels 4–5 mm long; calyx lobes coriaceous, oblate, 2.8–3.2 mm wide, apically rounded; corolla lobes chartaceous, 5–6 × 2.3–3.3 mm; anthers 3.2–4.2 × 1.2–1.4 mm; styles 4.9–5 mm long; fruits 8–9.8 mm diam. .... 40. *Ardisia dwyeri*

39b. Leaf blades membranous; pedicels 6–9 mm long; calyx lobes membranous to chartaceous, 1.1–1.2 mm wide, apically acute; corolla lobes membranous, 3.3–3.4 × 1.9–2 mm; anthers 2.3–2.4 × 0.8–0.9 mm; styles 3.4–3.5 mm long; fruits 4–5 mm diam. .... 66. *Ardisia vesca*

30b. Pedicels 2.5 mm long or shorter.

40a. Calyx lobes as long as or much longer than wide.

41a. Leaf blades more than 18 cm long.

42a. Leaf blades 24.5–51 × 9.2–15.4 cm; calyx lobes 1.4–1.6 × 1.3–1.5 mm; corolla lobes 3.8–4 × 1.8–2 mm; anthers 2.3–2.4 × 1–1.1 mm; styles 3.7–3.9 mm long .... 49. *Ardisia knappii*

42b. Leaf blades 18.5–20 × 6.7–7.9 cm; calyx lobes 1.2–1.3 × 0.7–0.8 mm; corolla lobes 1.7–1.8 × 1–1.2 mm; anthers 1.1–1.2 × 0.6–0.7 mm; styles 1.2–1.4 mm long .... 58. *Ardisia pulverulenta*

41b. Leaf blades less than 15 cm long.

43a. Branchlets 3–5 mm diam.; calyx lobes 0.9–1 mm wide; corolla lobes 3–3.2 × 2–2.2 mm; anthers 1.7–1.8 mm long; styles 3.1–3.2 mm long .... 20. *Ardisia albisepala*

43b. Branchlets 5–8 mm diam.; calyx lobes 1.4–1.6 mm wide; corolla lobes 2.9–3 × 1.6–1.9 mm; anthers 2.2–2.4 mm long; styles 1.9–2 mm long .... 64. *Ardisia tysonii*

40b. Calyx lobes wider than long.

44a. Leaf blades coriaceous.

45a. Branchlets horizontally checking and exfoliating; leaf blades 23–23.5 × 5–5.6 cm; petioles stout, marginate, 1–1.3 mm long; calyx lobes membranous, orbicular to oblate, 0.8–1 × 0.6–1.1 mm .... 60. *Ardisia smurfitana*

45b. Branchlets smooth; leaf blades 11.3–14.9 × 2.9–4.4 cm; petioles slender, canaliculate, 3–6 mm long; calyx lobes chartaceous, ovate, 1.3–1.6 × 1.3–1.8 mm .... 48. *Ardisia hugonensis*

44b. Leaf blades membranous to chartaceous.

46a. Calyx lobes 0.9–1.1 × 1.1–1.3 mm; styles 1–3 mm long .... 38. *Ardisia dukei*
46b. Calyx lobes 1.1–1.5 × 1.4–2 mm; styles 3.5–5.4 mm long.
    47a. Calyx lobes 1.4–1.5 mm long; corolla lobes 4.1–4.4 mm long; anthers 2.8–2.9 mm long; styles 5.3–5.4 mm long .... 21. *Ardisia anchicayana*
    47b. Calyx lobes 1.1–1.4 mm long; corolla lobes 2.7–3.7 mm long; anthers 1.9–2.5 mm long; styles 3.5–3.6 mm long .... 55. *Ardisia palmana*

19. Ardisia aguirreana Pipoly, Caldasia 17: 419. 1995. TYPE: Colombia. Chocó: area of Baudó, on left bank of river Baudó, about 1.5 km upstream of estuary, practically opposite the E-most houses of Puerto Pizarro, about 20 m inland from the shoreline of the bay in front of Estero del medio, ca. 5 m above shoreline, [0–100 m], 11 Feb. 1967 (fl, fr), *H. Fuchs & L. Zanella 21851* (holotype, COL!; isotypes, F!, US! [2]).

For illustration, see Pipoly (1995: 419, fig. 1).

Small shrubs ca. 3 m tall. *Branchlets* stout, terete, 15–20 mm diam., densely appressed rufous furfuraceous-lepidote. *Leaves* with blades chartaceous, oblanceolate, 51.5–67 × 12–17.5 cm, apically acuminate, with an acumen 0.5–1.2 cm long, basally cuneate, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above, densely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 75 to 85 pairs, nitid above, prominently raised below, the margins entire, revolute; petiole stout, 3–5.5 cm long, 5–8 mm diam., glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, tripinnately paniculate, 12–22 × 6–12 cm, pyramidal, shorter than the leaves, the rachis, branches, abaxial bract surfaces, and pedicels furfuraceous-lepidote, the branches loosely congested into 6- to 11-flowered corymbs; peduncles 4–6.3 cm long; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, ovate to lanceolate, 1.5–4.2 × 0.9–1.5 mm, apically acute, conspicuously punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins entire, sparse glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 2–2.5 × 0.2–0.3 mm; pedicels stout, subobsolete to 2.5 mm long, conspicuously punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, light violet gray; calyx lobes chartaceous, ovate, 2.1–2.6 × 1.2–1.4 mm, apically acute, conspicuously punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins entire, erose, hyaline, sparse glandular ciliolate; corolla chartaceous, 6–6.2 mm long, the tube 1.9–2.2 mm long, the lobes narrowly lanceolate, 4–4.1 × 1.5–1.7 mm, apically acute, conspicuously punctate and punctate-lineate, glabrous throughout, the margin entire, hyaline; stamen 4.9–5 mm long; the filament 2.9–3 mm long, the staminal tube 1.1–1.4 mm long, the apically free portions 1.6–1.8 mm long, the anthers lanceoloid, 2.4–2.6 × 0.8–1 mm, apically broadly apiculate, basally lobate, the connective conspicuously punctate; pistil 4.8–5 mm long, glabrous, the ovary ovoid, 1–1.1 mm long, styles 3.7–4 mm long, conspicuously punctate, the ovules 24 to 30. *Fruits* (immature) globose, 5–7 mm diam., conspicuously punctate and punctate-lineate, inconspicuously costate.

Distribution. *Ardisia aguirreana* is found in Chocó in the area of Baudó and the Parque Nacional Natural de Utria, Colombia, growing from 5 to 100 m in elevation.

Ecology and conservation status. *Ardisia aguirreana* occurs in secondary vegetation on relatively wet, slightly swampy ground. Because of its restricted distribution, it should be considered threatened.

Etymology. This species was named in honor of Jaime Aguirre, ex-director of the Instituto de Ciencias Naturales, Museo de Historia Natural, Universidad Nacional de Colombia.

Common Name. Arrayán (*Fuchs & Zanella 21851*).

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia aguirreana* is closely related to *A. megistophylla*, *A. cogolloi*, *A. crassipes*, and *A. cartagoana* because of its long calyx lobes with thick petioles. *Ardisia aguirreana* is separated from *A. megistophylla* by its shorter calyx lobes to 2.6 mm long, corolla lobes to 4.1 mm long, anthers to 2.6 mm long and styles to 4 mm long. *Ardisia aguirreana* is easily distinguished from the other related taxa by its longer leaf blades to 67 cm long, larger branchlets to 20 mm in diameter, longer peduncles to 6.3 cm long, and narrower corolla lobes to 1.7 mm wide.

Specimens examined. COLOMBIA. **Chocó**: Mpio. de Quibdó, Parque Nacional Natural de Utría, along Quebrada La Aguada, 21 Apr. 1990 (fl), *J. Espina et al. 3751* (CHOCO, MO); Parque Nacional de Utría, SE of the Ensenada de Utría, entering through Charco de las Ballenas, 2 June 1990 (fl), *F. García C. & E. Agualimpia 360* (CHOCO, FTG, MO).

20. Ardisia albisepala (Lundell) Pipoly & Ricketson, Sida 18: 511. 1998. *Auriculardisia albisepala* Lundell, Wrightia 7: 266. 1984. *Ardisia albisepala* (Lundell) Lundell, Phytologia 61: 62. 1986, nom. inval. TYPE: Panama. Veraguas: trail on ridge to summit of Cerro Tute, Cordillera Tute, 1 km past Escuela Agrícola Altos de Piedras, W of Santa Fé, 08°36′N, 081°06′W, 950–1250 m, 15 Dec. 1981 (fl), *S. Knapp & K. Sytsma 2548* (holotype, LL!; isotypes, MO!, NY!). Figure 22.

Trees 6–8 m tall. *Branchlets* slender, terete, 3–5 mm diam., densely cupuliform lepidote. *Leaves* with blades membranous, elliptic, 7.2–10.7 × 2.2–3.9 cm, apically long acuminate, with an acumen 6–14 mm long, basally obtuse, decurrent on the petiole, prominently punctate above and below, glabrous above, furfuraceous-lepidote below except mixed with cupuliform lepidote scales along midrib, the midrib impressed above, prominently raised below, the secondary veins 45 to 51 pairs, prominulous above and below, the margins entire, flat to slightly inrolled; petioles slender, canaliculate, 8–13 mm long, glabrous above, mixed lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, 5.2–13.7 × 4.5–11.7 cm, pyramidal, longer than the leaves, cupuliform lepidote, the branches loosely congested into 3- to 7-flowered corymbs; peduncles obsolete to 1.4–1.7 cm long; inflorescence bracts unknown; inflorescence branch bracts unknown; floral bracts caducous, membranous, lanceolate, 1.2–1.4 × 0.4–0.5 mm, apically acute, prominently punctate, glabrous adaxially, furfuraceous-lepidote, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels stout, obsolete to 1.5 mm long, prominently punctate, furfuraceous-lepidote. *Flowers* 5-merous, light pink; calyx lobes membranous, ovate, 1.2–1.3 × 0.9–1 mm, prominently punctate and punctate-lineate, glabrous adaxially, scattered furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 4.4–4.5 mm long, the tube 1.2–1.5 mm long, the lobes lanceolate, 3–3.2 × 2–2.2 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 3.1–3.2 mm long, the filaments 1.9–2.1 mm long, the staminal tube 0.6–0.7 mm long, the apically free portions 1.3–1.4 mm long, the anthers narrowly ovoid to lanceoloid, 1.7–1.8 × 0.8–0.9 mm, apically apiculate, basally lobate, the connective conspicuously punctate; pistil 4–4.2 mm long, glabrous, ovary oblongoid, 1–1.1 mm long, the style 3.1–3.2 mm long, inconspicuously punctate, the ovules 18 to 20. *Fruits* unknown.

Distribution. *Ardisia albisepala* is endemic to Cerro Tute in Veraguas, Panama, growing from 950 to 1250 m in elevation.

Ecology and conservation status. *Ardisia albisepala* occurs in lower montane rain forests and cloud forests. Because of its restricted distribution, it should be considered threatened.

Etymology. The specific epithet was derived from the Latin "albus" meaning a dull white, and "sepala" referring to the light-colored calyx lobes.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia albisepala* is most closely related to *A. tysonii* because of its short calyx lobes that are as long as or much longer than wide, short pedicels, leaf blades less than 15 cm long and less than 6.5 cm wide, and long petioles. However, *A. albisepala* can easily be separated from *A. tysonii* by its thinner branchlets to 5 mm in diameter, narrower calyx lobes to 1 mm wide, longer and wider corolla lobes to 3.2 × 2.2 mm, shorter anthers to 1.8 mm long, and longer styles to 3.2 mm long.

Specimens examined. PANAMA. **Veraguas:** "Cerro Tute" ridge up from former Escuela Agrícola, Santa Fé, 20 Feb. 1983 (fl), *C. Hamilton & R. Dressler 3109* (LL, MO).

21. Ardisia anchicayana Ricketson & Pipoly, sp. nov. TYPE: Colombia. Valle del Cauca: Alto Yunda, Río Anchicayá, 1000 m, July 1972 (fl), *S. Hilty Jy-28* (holotype, US!; isotype, ARIZ!). Figure 23.

Ob lobulos calycinos parvos et longiores quam latiores, atque foliorum laminas membranaceas pedicellos breviores *A. palmanae* valde arcte affinis, sed ab ea lobulis calycinis longioribus usque ad 1.5 mm longis, lobulis corollinis longioribus usque ad 4.4 mm longis, antheris longioribus usque ad 2.9 mm denique stylis longioribus usque ad 5.4 mm longis perfacile statimque distinguitur.

Trees to 15 m tall. *Branchlets* stout, terete, 5–6 mm diam., bark exfoliating, furfuraceous-lepidote. *Leaves* with blades membranous to chartaceous, elliptic to oblong, 20–36 × 6.9–9.2 cm, apically acute, with an acumen unknown, basally acute, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above, furfuraceous-lepidote, the midrib impressed above, prominently raised below, the secondary veins 75 to 85 pairs, prominulous above and below, the margins entire, inrolled; petioles stout, canaliculate, 3–7 mm long, glabrous above, furfuraceous-lepidote below. *Inflorescences* likely pendent, tripinnately paniculate, 23.5–27.5 × 10–15 cm, pyramidal, shorter than the leaves, densely furfuraceous-lepidote, the branches loosely congested into 5- to 7-flowered corymbs; peduncles obsolete, the lower branch sub-

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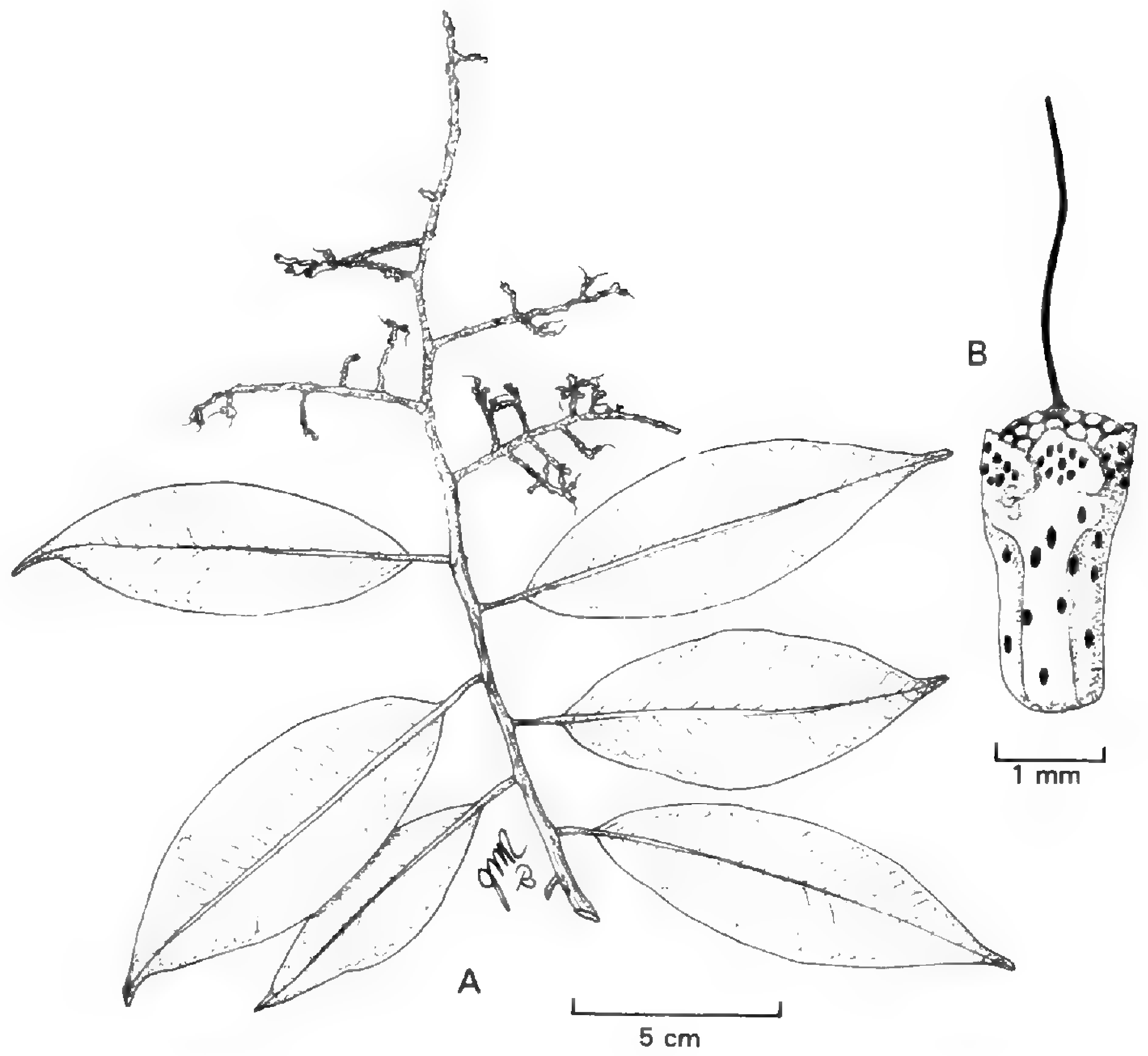

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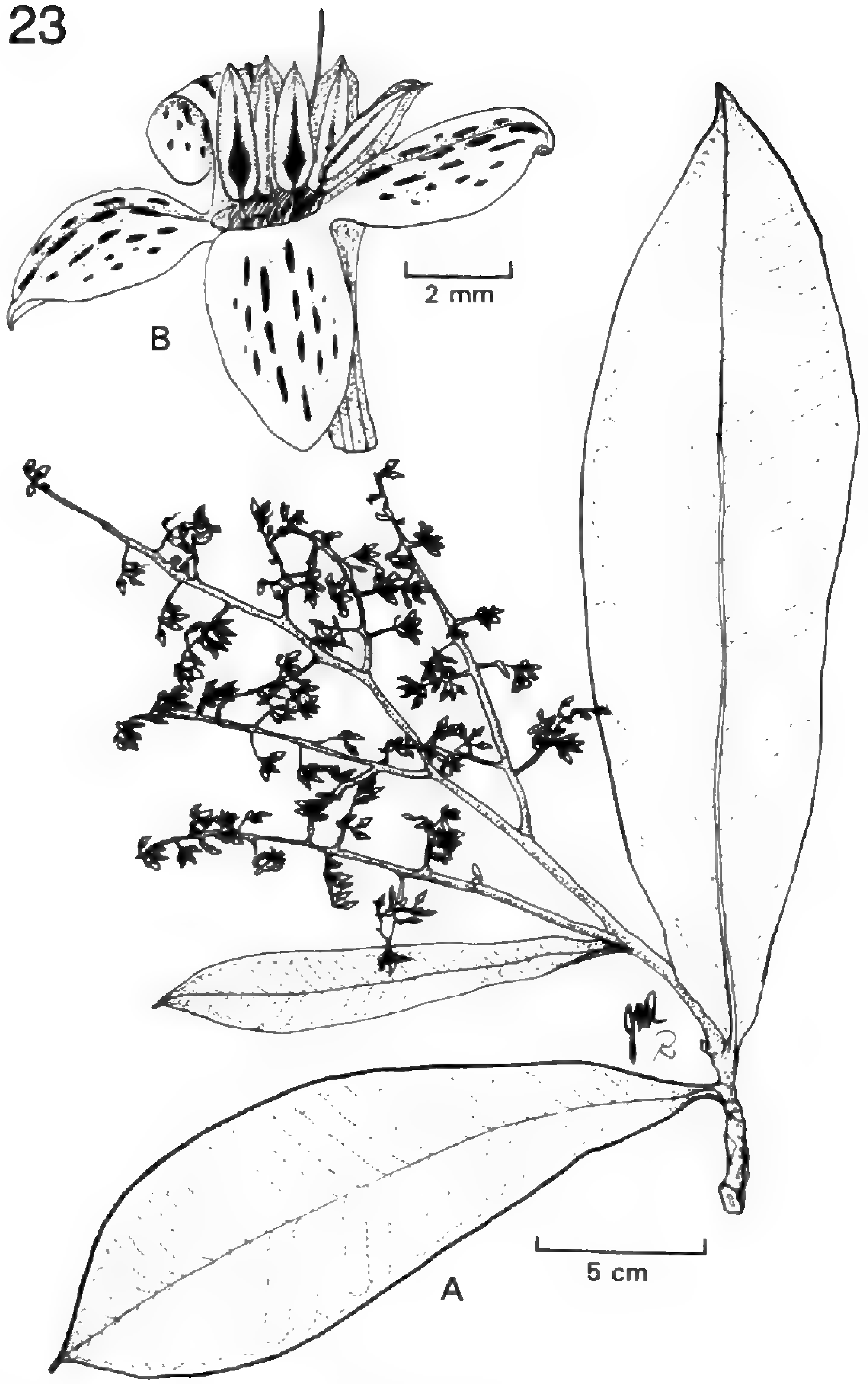

Figure 22 (left). *Ardisia albisepala.* —A. Flowering branch. —B. Fruit. (A, B drawn from isotype, *S. Knapp & K. Sytsma 2548* (MO).)

Figure 23 (right). *Ardisia anchicayana.* —A. Flowering branch. —B. Flower. (A, B drawn from holotype, *S. Hilty Jy-28* (US).)

tended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, ovate to oblong, 1.5–2 × 0.4–0.6 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 1.2–1.7 × 0.4–0.6 mm; pedicels stout, 1–1.5 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, white; calyx lobes membranous, ovate, 1.4–1.5 × 1.8–2 mm, apically acute to rounded, prominently punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 5.4–5.6 mm long, the tube 1.2–1.5 mm long, the lobes narrowly ovate, 4.1–4.4 × 2.4–2.5 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 5.4–5.5 mm long, the filaments 2.6–2.8 mm long, the staminal tube 0.5–0.7 mm long, the apically free portions 1.9–2.3 mm long, the anthers narrowly ovoid, 2.8–2.9 × 1.1–1.2 mm, apically apiculate, basally lobate, the connective conspicuously punctate; pistil 6.4–6.7 mm long, glabrous, the ovary oblongoid, 1.1–1.3 mm long, the style 5.3–5.4 mm long, epunctate, the ovules 18 to 24. *Fruits* unknown.

Distribution. *Ardisia anchicayana* is known only from the type collection from Valle del Cauca, Colombia, growing at 1000 m in elevation.

Ecology and conservation status. *Ardisia anchicayana* occurs in premontane pluvial forest, on the western slopes of the western Andean cordillera. This area of the Chocó Floristic Province is known for annual precipitation of over 8000 mm, and is also known for very large individuals of commercially valuable timber species. Therefore, all the forests of the area are under serious threat.

Etymology. The specific epithet comes from the type collection along the Río Anchicayá in Valle de Cauca, Colombia.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia anchicayana* is most similar to *A. palmana* because of the calyx lobes wider than long, membranous to chartaceous leaf blades, and short pedicels. However, *Ardisia anchicayana* may be separated from *A. palmana* by the longer calyx lobes to 1.5 mm long, longer corolla lobes to 4.4 mm long, longer anthers to 2.9 mm long, and longer styles to 5.4 mm long.

22. Ardisia angucianensis Ricketson & Pipoly, sp. nov. TYPE: Costa Rica. Puntarenas: Cantón de Osa, Fila Costeña, Fila Cruces, headwaters of Río Piedras Blancas, Cerro Angucianа, western slopes, 08°48′56″N, 083°10′37″W, 1400–1600 m, 10 Dec. 1993 (fr), *B. Hammel 19280* (holotype, MO!; isotype, INB not seen). Figure 24.

Propter lobulos calycinos longiores quam latiores ovatos usque ad 2.9 mm longos atque folia ad apices acuminata ad bases acuta *A. nigropunctatae* arcte similis, sed ab ea lobulis calycinis 2.7–2.9 (non 1.7–2.4) mm longis, 2.4–2.7 (nec 1.2–2.0) mm latis, fructibus 4–5 (non 5–9) mm diametro statim separabilis.

Trees to 5 m tall. *Branchlets* slender, terete, 4–5 mm diam., densely and minutely appressed rufous furfuraceous-lepidote, often glabrate with age. *Leaves* with blades membranous to chartaceous, elliptic to narrowly elliptic, 28.8–33.3 × 9.9–11.6 cm, apically acuminate, with an acumen 10–12 mm long, basally acute, decurrent on the petiole, prominently raised below, prominently punctate and punctate-lineate above and below, glabrous above, densely and minutely appressed rufous furfuraceous-lepidote, the midrib impressed above, prominently raised below, the secondary veins 42 to 48 pairs, prominulous above, the margins entire, flat; petioles slender, canaliculate, 11–13 mm long, 2–3 mm diam., glabrous above, sparsely furfuraceous-lepidote below. *Inflorescences* erect, bipinnately paniculate, 29.8–30.5 × 17.5–18.2 cm, pyramidal, longer than the leaves, the rachis, branchlets, and pedicels densely and minutely appressed rufous furfuraceous-lepidote, the branches loosely congested into 5- to 7-flowered corymbs; peduncles 2.7–2.9 cm long; inflorescence bracts and branch bracts unknown; floral bracts unknown; pedicels stout, 2–2.8 mm long, inconspicuously punctate and punctate-lineate. *Flowers* 5-merous, calyx lobes chartaceous to coriaceous, suborbicular to orbicular, 2.7–2.9 × 2.4–2.7 mm, apically acute to rounded, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla, stamens, and pistil unknown. *Fruits* (immature), globose, 4–5 mm diam., prominently punctate and punctate-lineate, glabrous.

Distribution. *Ardisia angucianensis* is known only from the type collection in Puntarenas, Costa Rica, growing from 1400 to 1600 m in elevation.

Ecology and conservation status. *Ardisia angucianensis* occurs in premontane wet forest on limestone. Because it is only known from the type, it should be considered threatened.

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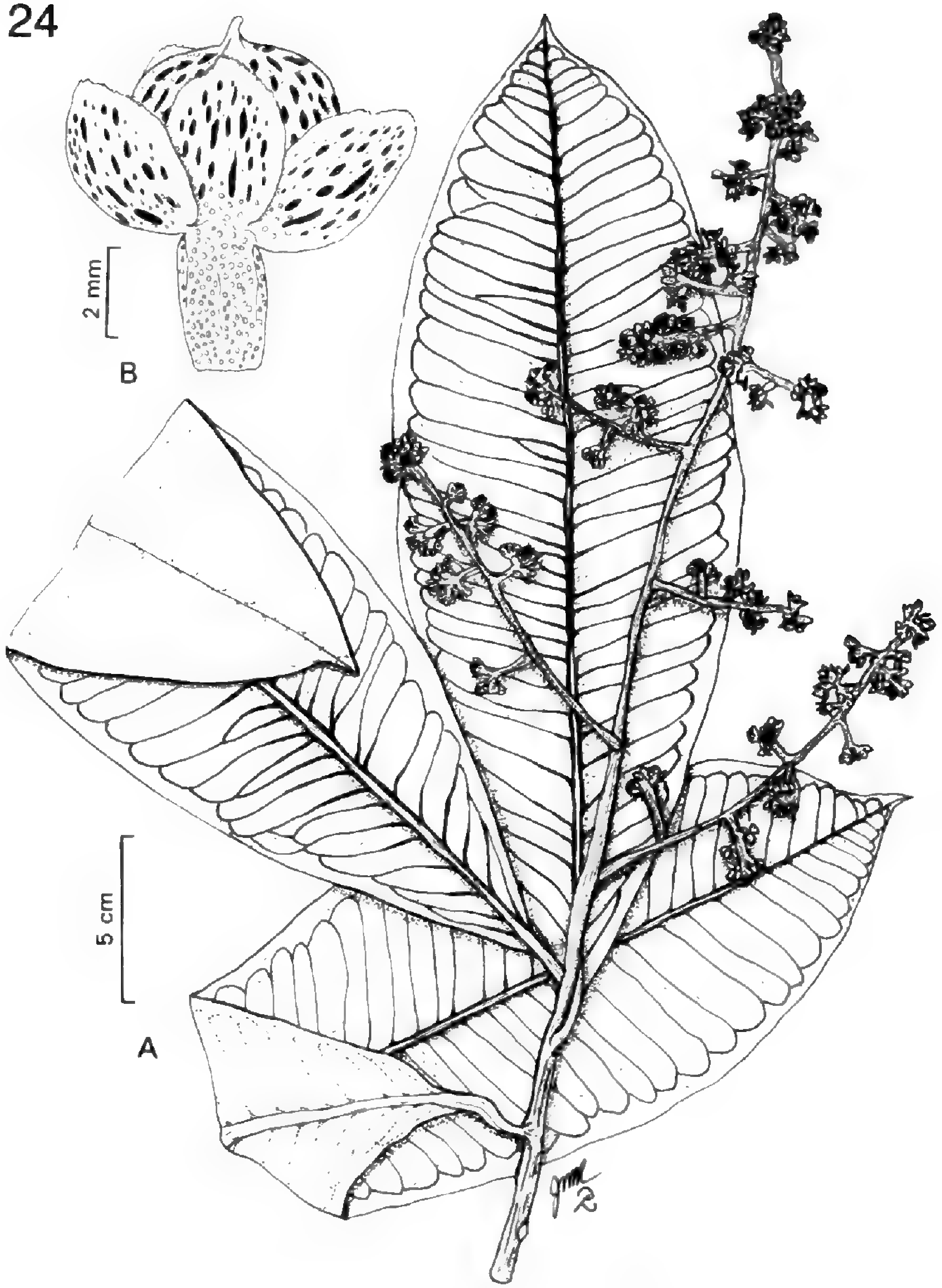

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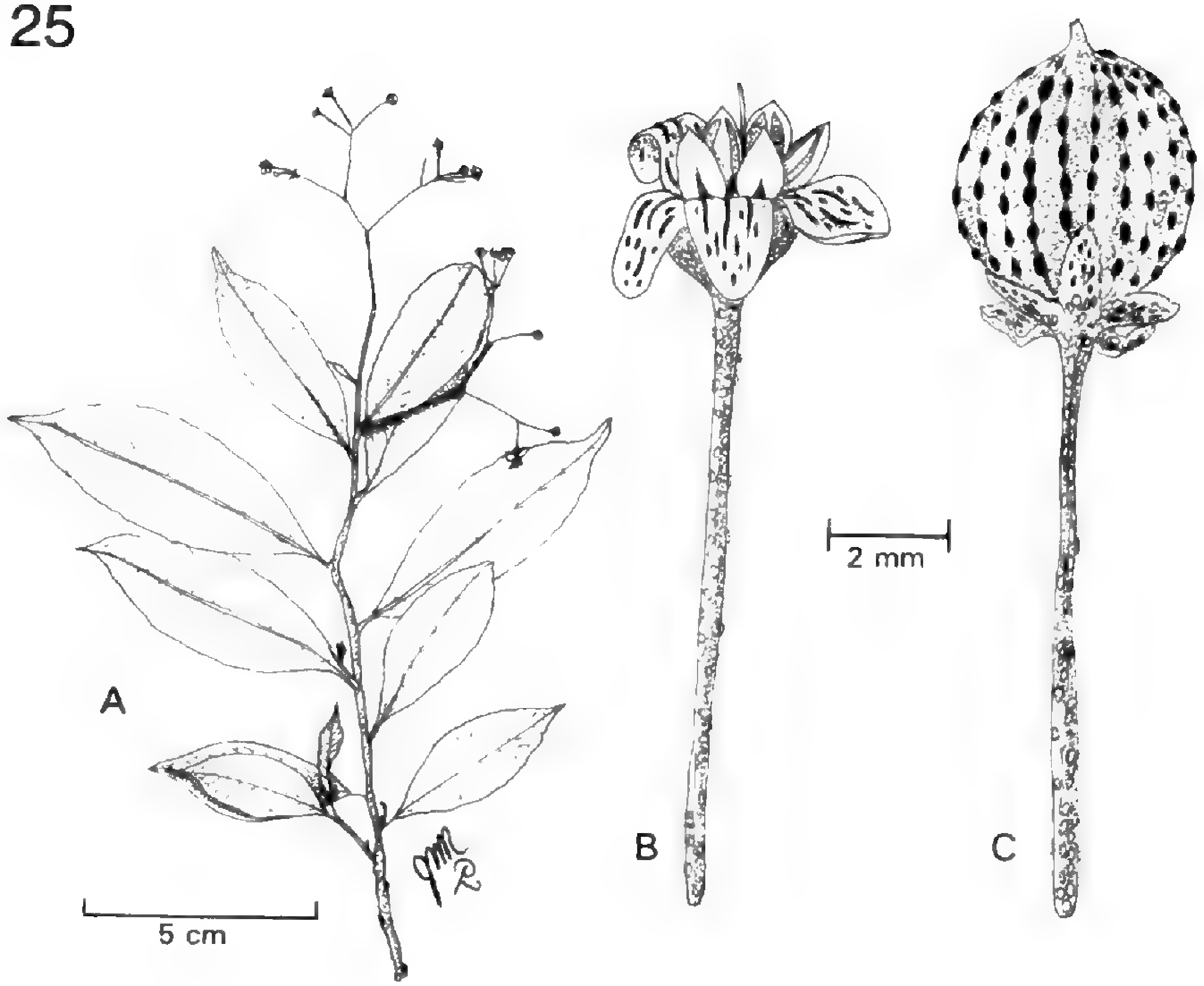

Figure 24 (left). *Ardisia angucianensis.* —A. Flowering branch. —B. Fruit. (A, B drawn from holotype, *B. Hammel 19280* (MO).)

Figure 25 (right). *Ardisia atropurpurea.* —A. Flowering branch. —B. Flower. —C. Fruit. (A, B drawn from isotype, *J. Folsom et al. 4998* (MO); C from *J. Folsom et al. 6617* (MO).)

Etymology. The specific epithet comes from the location where the type was collected on Cerro Anguciana in the Cantón de Osa, Puntarenas, Costa Rica.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia angucianensis* is most similar to *A. nigropunctata* due to its calyx lobes wider than long, to 2.9 mm, acuminate leaf apices, and acute leaf bases. However, *A. angucianensis* can be separated by the longer and wider calyx lobes to 2.9 × 2.7 mm and smaller fruits to 4.5 mm in diameter.

23. Ardisia atropurpurea Lundell, Phytologia 48: 134. 1981. *Auriculardisia atropurpurea* (Lundell) Lundell, Phytologia 49: 342. 1981. TYPE: Panama. Panamá: from Tortí to the Pilota del Toro, the mountain overlooking Tortí Arriba, 400–700 m, 27 Aug. 1977 (fl), *J. Folsom, G. Alonzo de Monte & relatives 4998* (holotype, LL!; isotypes, FTG!, MO!). Figure 25.

Shrubs 1–4 m tall. *Branchlets* slender, terete, 1–2 mm diam., densely furfuraceous-lepidote. *Leaves* with blades membranous, elliptic, 2.8–7.1 × 0.8–2.6 cm, apically acuminate, with an acumen 6–9 mm long, basally acute, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above, densely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 12 to 20 pairs, obscure to prominulous above and below, the margins entire, flat; petioles slender, canaliculate, 4–6 mm long, glabrous above, densely furfuraceous-lepidote below. *Inflorescences* erect, pinnately to bipinnately paniculate, 5–7 × 2–7 cm, pyramidal, longer than the leaves, densely furfuraceous-lepidote, the branches loosely congested into 5- to 7-flowered corymbs; peduncle 1–4 mm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, ovate to oblong, 1.3–2.3 × 0.5–0.8 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, mixed cupuliform and furfuraceous-lepidote, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 1–1.3 × 0.3–0.6 mm; pedicels slender, 7.2–16.3 mm long, prominently punctate and punctate-lineate, mixed furfuraceous- and cupuliform lepidote. *Flowers* 5-merous, deep purple; calyx lobes chartaceous, ovate, 1.5–1.6 × 0.9–1 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 2.5–2.6 mm long, the tube 0.7–0.8 mm long, the lobes lanceolate, 1.7–1.8 × 1.2–1.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins entire, hyaline; stamens 2.3–2.4 mm long, the filaments 0.9–1 mm long, the staminal tube 0.2–0.3 mm long, the apically free portions 0.6–0.8 mm long, the anthers ovoid to narrowly ovoid, 1.8–1.9 × 0.8–0.9 mm, apically apiculate, basally cordate, the connective conspicuously punctate; pistil 2.6–2.7 mm long, glabrous, the ovary ovoid, 0.9–1 mm long, the style 1.6–1.8 mm long, prominently punctate and punctate-lineate, the ovules 12 to 14. *Fruits* globose, 4–7 mm diam., prominently punctate.

Distribution. *Ardisia atropurpurea* is apparently endemic to the area above Tortí Arriba in Panamá, Panama, growing from 400 to 700 m in elevation.

Ecology and conservation status. *Ardisia atropurpurea* occurs in lowland wet forests. Because it is so poorly known, no conservation status evaluation can be made.

Etymology. The specific epithet comes from the Latin "atro" meaning dark and "purpurea" meaning purple, and refers to the dark purple flower color.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia atropurpurea* is most closely related to *A. eucuneata* because of the small calyx lobes, long pedicels, narrow corolla lobes, and short anthers. However, *Ardisia atropurpurea* is separated from *A. eucuneata* by its thinner branchlets to 2 mm in diameter, longer pedicels to 16.3 mm long, shorter and narrower corolla lobes to 1.8 × 1.3 mm, longer and wider anthers to 1.9 × 0.9 mm, and shorter styles to 1.8 mm long.

Specimen examined. PANAMA. **Panamá**: area surrounding Rancho Chorro, mountains above Tortí Arriba, Canazas mountain chain, 3 Dec. 1977 (fl, fr), *J. Folsom et al. 6617* (LL, MO).

24. Ardisia auriculata Donn. Sm., Bot. Gaz. 24: 395. 1897. *Auriculardisia auriculata* (Donn. Sm.) Lundell, Phytologia 54: 285. 1983. TYPE: Costa Rica. Limón: forests of Suerte [Guppies], Llanura de Santa Clara, 900 ft. [274 m], Feb. 1896 (fr), *J. Donnell Smith 6640* (holotype, US!, US neg. 2367!, LL neg. 1971-19!). Figure 26.

Shrubs or small trees 1–8 m tall, 2–7 cm diam. *Branchlets* slender, terete, the bark longitudinally ridged, 3–7.5 mm diam., densely and minutely ferrugineous furfuraceous-lepidote, the scales early caducous. *Leaves* with blades membranous to chartaceous, elliptic or oblong to oblanceolate to ob-

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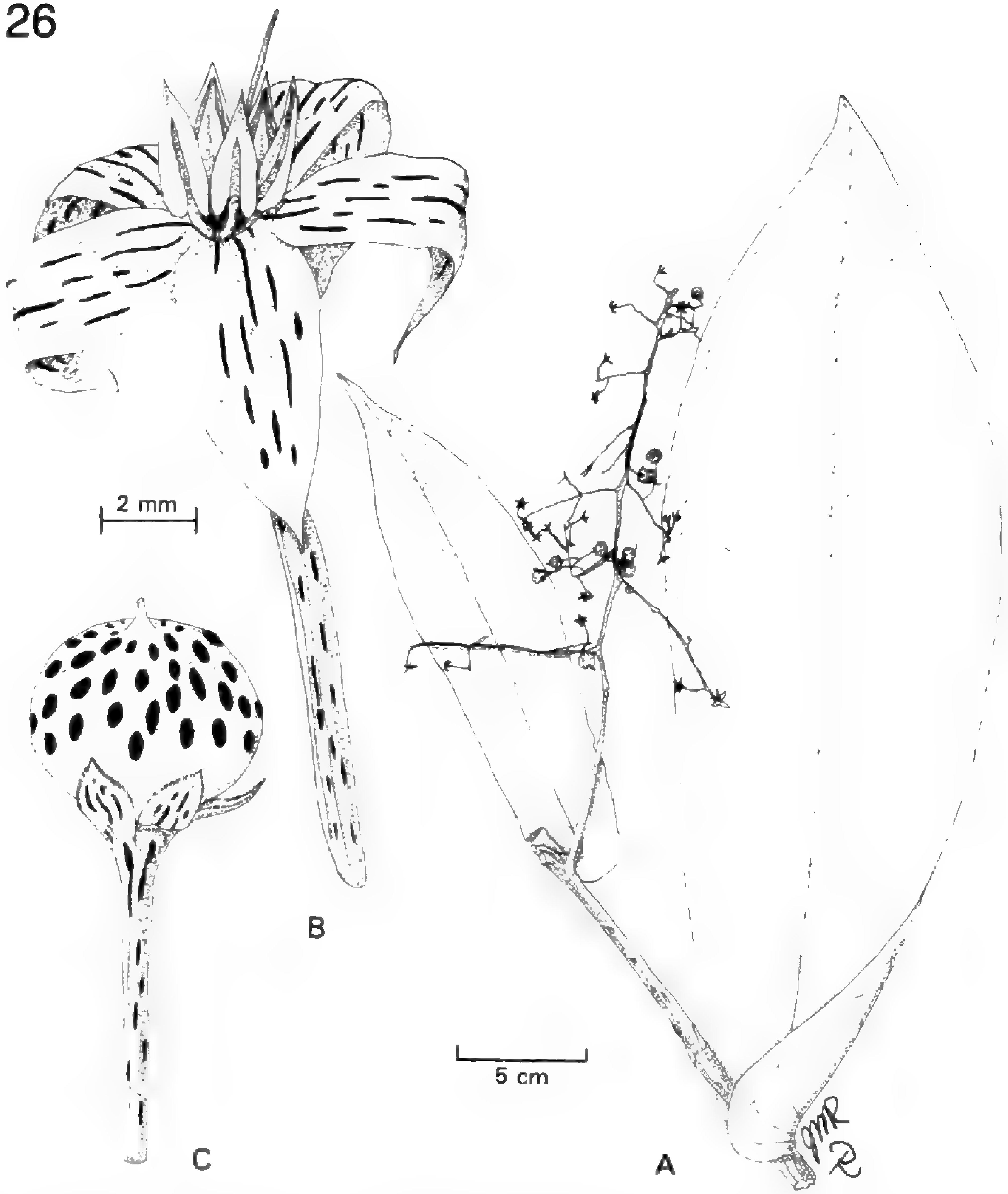


27

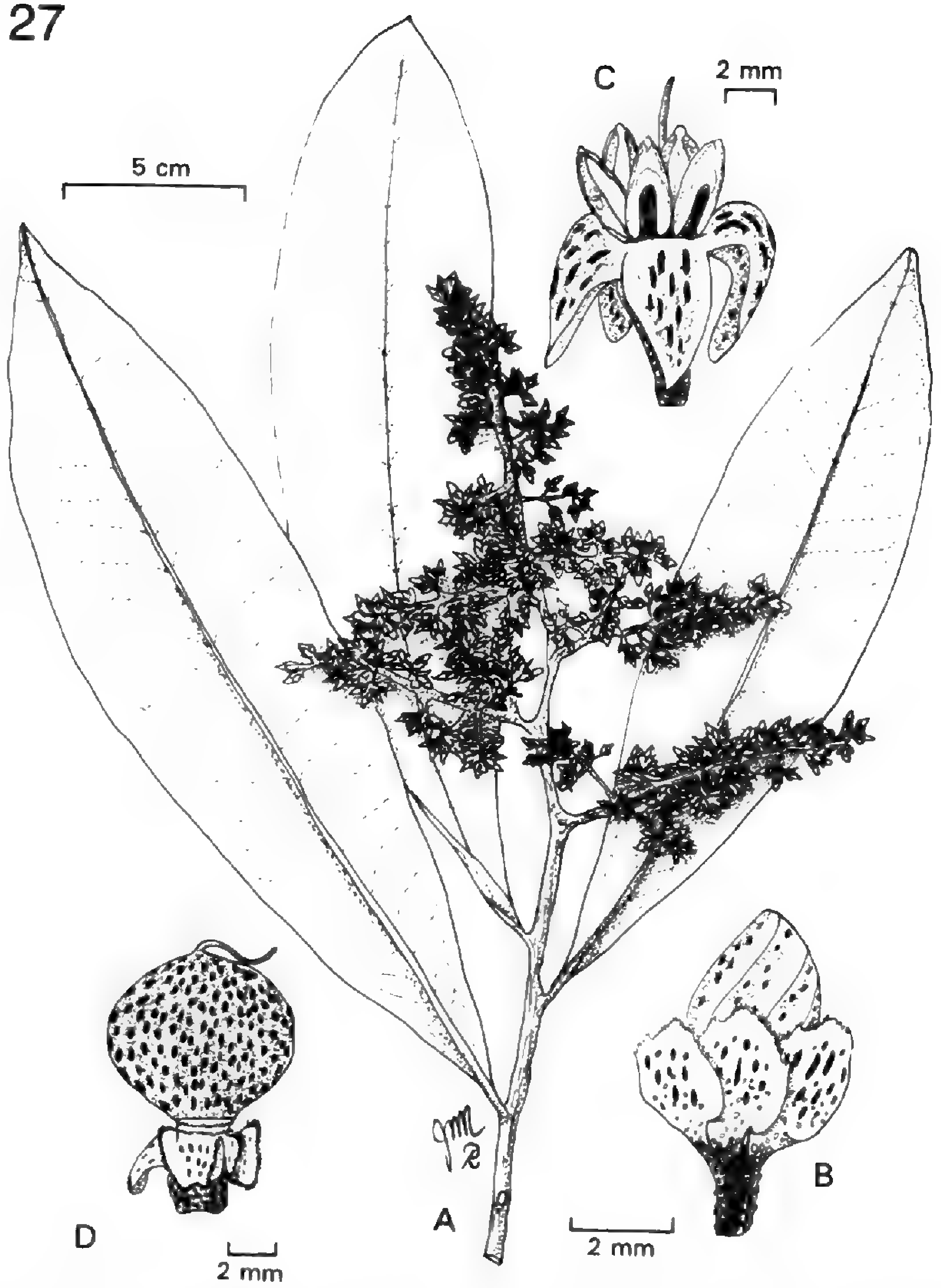


Figure 26 (left). *Ardisia auriculata.* —A. Flowering branch. —B. Flower. —C. Fruit. (A & C drawn from holotype, *J. Donnell Smith 6640* (US); B from *V. Funk et al. 10923* (MO).)

Figure 27 (right). *Ardisia awarum.* —A. Flowering branch. —B. Flower bud. —C. Flower. —D. Fruit. (A–C drawn from holotype, *D. Rubio & C. Quelal 1453* (MO); D from *C. Aulestia et al. 513* (MO).)

ovate, 12.3–46.7 × 3.4–17.7 cm, apically acuminate, with an acumen 2–13 mm long, basally auriculate, prominently punctate and punctate-lineate, glabrous above, scattered minutely ferrugineous furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 32 to 48 pairs, prominulous above, slightly to prominently raised below, the margins entire, flat; petioles stout, marginate, subobsolete to 5 mm long, 2–3 mm diam., glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bipinnate to tripinnately paniculate, 15–40 × 10–30 cm, pyramidal, longer than the leaves, the rachis densely and minutely ferrugineous furfuraceous-lepidote, the branches loosely congested into 3- to 9-flowered corymbs, sparsely furfuraceous-lepidote; peduncle nearly obsolete to 8.6 cm long, densely furfuraceous-lepidote, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, oblong, 10–18 × 2–4.5 mm, apically acute, inconspicuously punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 1.1–1.8 × 0.5–0.8 mm; pedicels slender, 6–10.2 mm long, inconspicuously punctate and punctate-lineate, very sparsely furfuraceous-lepidote, glabrescent. *Flowers* 5-merous, greenish, white, pink, purple; calyx lobes membranous, ovate, 2.3–2.7 × 1.4–1.6 mm, apically acute to acuminate, prominently punctate and punctate-lineate, glabrous throughout, the margins irregular, minutely erose, hyaline sparsely glandular ciliolate; corolla membranous, 5.6–6.2 mm long, the tube 0.4–1.2 mm long, the lobes ovate, 4.8–5.4 × 2.8–3 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 4.7–5.1 mm long, the filaments 2.2–2.5 mm long, the staminal tube 1–1.4 mm long, the apically free portions 0.9–1.4 mm long, the anthers ovoid, 2.5–3.1 × 1.3–1.5 mm, apically apiculate-mucronate, basally cordate, the connective prominently punctate; pistil 6.2–6.4 mm long, glabrous, the ovary oblong, 1.3–1.4 mm long, the style 4.6–4.7 mm long, epunctate, the ovules 19 to 21. *Fruits* globose, 5.5–7 mm diam., prominently punctate and punctate-lineate.

Distribution. *Ardisia auriculata* is found on the Atlantic Slope of Nicaragua in Jinotega, Río San Juan, and Zelaya, throughout Costa Rica (except Cartago and Puntarenas), and Panama in Bocas del Toro, Colón, Coclé, Panamá, San Blas, and Veraguas, growing from sea level to 1200 m in elevation.

Ecology and conservation status. *Ardisia auriculata* occurs as an understory tree in lowland and premontane wet and pluvial forests. It apparently has some tolerance for disturbance and has a broad habitat range. Therefore, we do not believe it is threatened at this time.

Etymology. The specific epithet was derived from the Greek, "auricle," or ear, and refers to the lobed leaf bases.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia auriculata* is closely related to both *A. angucianensis* and *A. nigropunctata* because of its large calyx lobes to 2.9 mm long, which are longer than wide, and slender petioles. *Ardisia auriculata* can easily be distinguished from both *A. angucianensis* and *A. nigropunctata* by its auriculate leaf bases with pedicels nearly obsolete to 5 mm long.

Specimens examined. NICARAGUA. **Jinotega**: Bocaycito, 28 Dec. 1973 (fl), *J. Atwood et al. 6903* (MO). **Río San Juan**: near Caño Chontaleño, 20 km NE of El Castillo, Río Indio watershed, 7–9 Mar. 1978 (fr), *D. Neill 3381* (HNMN, MO); Mpio. Castillo, Reserva Indio-Maíz, Cerro el Diablo, 6 Jan. 1997 (ster.), *R. Rueda et al. 5457* (HULE, MO). **Zelaya**: Atlanta, Caño el Tigrillo, La Picada, 8 Nov. 1982 (fl), *A. Laguna 153* (MO); Río Punta Gorda, Atlanta, "La Richard" 200 m SE, 13 Nov. 1981 (fl), *P. Moreno & J. Sandino 12977* (HNMN, MO); Caño Montecristo, mouth of Caño El Consuelo, 7 Feb. 1982 (fr), *P. Moreno 15054* (MO); E of Nueva Atlanta, 20 Feb. 1994 (fr), *R. Rueda 3291* (HULE, MO); Mpio. de Bonanza, Reserva Bosawás, Cerro Cola Blanca, 2 June 1997 (ster.), *R. Rueda & I. Coronado 6495* (HULE, MO). COSTA RICA. **Alajuela**: San Ramón, 22 Feb. 1931 (fr), *A. Brenes 13459* (F); 3 km NNE of Bijagua, along new road to Upala, 7–8 Nov. 1975 (fl), *W. Burger & R. Baker 9806* (F, NY); Caribbean slope between San Lorenzo and Los Angeles de San Ramón, above the Río San Lorenzo, 20 Sep. 1978 (fl), *W. Burger & T. Antonio 11192* (DUKE, F); Cantón de Guatuso, Cordillera Tilarán, 5 km N of Lago Arenal, near Lago Coter, 14 Oct. 1994 (fl), *A. Cascante et al. 320* (CR, F, K); Arenal Volcano, forest trail SW of volcano, E of road along laguna and N of Río Agua Caliente, 1 Oct. 1991 (fl), *V. Funk et al. 10923* (MO, US); Reserva Biológica Monteverde, Quebrada Cerro Negro, left bank, Río Peñas Blancas, 29 Mar. 1987 (fr), *W. Haber & E. Bello C. 6848* (MO); Cantón de Upala, Dos Ríos, 5 km S of Brasilia, right bank Río Pizote, 28 Oct. 1987 (fr), *G. Herrera 965* (CR, MO); La Fortuna, San Carlos, 2.5 km E Cerro Chato, Catarata Río Fortuna, 7 Nov. 1989 (fr), *Q. Jiménez & L. Elizondo 740* (CR, FTG, INB, MO); Cantón de Agua Zarcas, Hacienda La Marina, Río San Rafael, 8 Feb. 1965 (fr), *L. Williams et al. 29080* (F, MO, NY, US). **Guanacaste**: Parque Nacional Guanacaste, Estación Pitilla, Laguna Path, 2 Jan. 1991 (fr), *C. Moraga 284* (INB, MO). **Heredia**: Parque Nacional Braulio Carrillo, Estación El Ceibo, 29 Oct. 1989 (fl), *R. Aguilar & B. Hammel 26* (CR, FTG, MO); property of Dr. L. Holdridge, ca. 2 km upstream on the Río Puerto Viejo, 5–6 Jan. 1967 (fr), *W. Burger & G. Matta U. 4234* (CR, DUKE, F, G, GH). **Limón**: near Río Toro Amarillo, Guapiles, 10 Feb. 1965 (fr), *R. Godfrey 66352* (MO, LL neg.). **San José**: Parque

Nacional Braulio Carrillo, Botarrama Trail, Quebrada Gonzalez and tributaries, 5 Oct. 1993 (fl), *J. Morales et al. 1855* (CR, FTG, INB, MO). PANAMA. **Bocas del Toro**: along road to Chiriquí Grande, 26 Oct. 1985 (fl), *G. McPherson 7382* (MO). **Coclé**: Coclecito road, elevational transection from 1 mi. beyond the divide to the ridge top, 12 Jan. 1986 (fr), *G. de Nevers et al. 6738* (LL, MO). **Colón**: walking upstream from bridge over Río Guanche, 19 Jan. 1980 (fr), *T. Antonio 3354* (LL, MO); along Río Guanche ca. 3–5 mi. inland, 3 Aug. 1974 (fl), *T. Croat 26189* (LL, MO). **Panamá**: headwaters of Río Chagres, Río Esperanza and Río Piedras, 17 Oct. 1984 (fl), *G. de Nevers et al. 4076* (MO). **San Blas**: Comarca de San Blas, Playón Chico, Río Ukupseni, along Río Ukupseni, from Camp Neba Dummat to the falls, 30 Oct. 1991 (fl), *H. Herrera et al. 1027* (FTG, INB, MO). **Veraguas**: vicinity of Escuela Agricultura Alto Piedra near Santa Fé, 1 hour walk along road beyond school, 1 Dec. 1979 (fl), *T. Antonio 3001* (MO).

25. Ardisia awarum Ricketson & Pipoly, sp. nov. TYPE: Ecuador. Esmeraldas: San Lorenzo de Cantón, Reserva Indígena Awá, Parroquia Ricaurte, comunidad Balsareño, Río Palabí, 01°09′N, 078°31′W, 100 m, 15–29 Apr. 1991 (fl), *D. Rubio & C. Quelal 1453* (holotype, MO!; isotypes, FTG!, QCNE not seen). Figure 27.

Ob lobos calycinos suborbiculares vel orbiculares, atque laminam non coriaceam, *A. dunlapianae* arcte similis sed ab ea laminis foliaribus chartaceis (non membranaceis), calycis coriaceis (non membranaceis) necnon antheris 1.9–2.2 (non 8–13) mm longis praeclare distat.

Trees 8–25 m tall, 10–15 cm diam. *Branchlets* slender, terete, 4.5–6.5 mm diam., densely and minutely appressed rufous furfuraceous-lepidote. *Leaves* with blades chartaceous, oblong elliptic to oblanceolate, 16.2–26.7 × 4.4–6.8 cm, apically acuminate, with an acumen 8–14 mm long, basally acute, decurrent on the petiole, the midrib impressed above, prominently raised below, the secondary veins 32 to 38 pairs, inconspicuously punctate and punctate-lineate above and below, glabrous above, densely and minutely appressed rufous furfuraceous-lepidote, inconspicuously raised above and below, the margins entire, inrolled; petioles slender, marginate, 8–14 mm long, 1.5–2.5 mm diam., glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, tripinnately paniculate, 8–21 × 10–18 cm, pyramidal, usually longer than the leaves, peduncle, the rachis, branchlets, abaxial bract surfaces and pedicels densely cupuliform and furfuraceous-lepidote, the branches loosely congested into 3- to 7-flowered corymbs; peduncle nearly obsolete to 1.7 cm long; inflorescence bracts unknown; inflorescence branch bracts unknown; floral bracts membranous, ovate, 1–1.4 × 1–1.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the veins unknown, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels stout, 1.5–3 mm long, inconspicuously punctate and punctate-lineate, sparsely furfuraceous-lepidote. *Flowers* 5-merous, white; calyx lobes coriaceous, suborbicular, 2–2.5 × 2–2.5 mm, apically acute to rounded, prominently punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially, obsolete flat scales with the margins entire or with small teeth, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla chartaceous, 5–6.2 mm long, the tube 1.4–2 mm long, the lobes lanceolate, 3.9–4.5 × 1.7–2.1 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 3.7–4.2 mm long, the filaments 1.5–2 mm long, the staminal tube 0.5–0.7 mm long, the apically free portions 1–1.3 mm long, the anthers ovoid, 1.9–2.2 × 1.1–1.5 mm, apically apiculate, basally deeply cordate, the connective conspicuously black punctate; pistil 5.2–5.6 mm long, glabrous, the ovary oblong, 1.2–1.4 mm long, the style 4–4.2 mm long, prominently punctate, the ovules 46 to 48. *Fruits* red, then burgundy, then black at maturity, globose, 8–9.2 mm diam., prominently black punctate.

Distribution. *Ardisia awarum* is endemic to the Reserva Indígena Awá in San Lorenzo, Ecuador. We would anticipate that its range extends to the southern portion of Nariño, Colombia, on the western slopes of the Western Cordillera, growing between (80–)200 and 600(–1000) m in elevation.

Ecology and conservation status. *Ardisia awarum* occurs in primary, pluvial premontane forests, apparently along the forest margins. Because the majority of the collections are from protected areas, it does not appear that the species is threatened.

Etymology. The specific epithet is in honor of the Awá, a group of indigenous people found along the western slopes of the western Andean Cordillera, from Esmeraldas, Ecuador, north to central-western Nariño, Colombia.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia awarum* is very similar to *A. dunlapiana* because of its leaf blades coriaceous, calyx coriaceous, corolla chartaceous, the tube glabrous outside, shorter anthers to 2.2 mm long, and shorter styles to 4.2 mm long.

Paratypes. ECUADOR. **Carchi**: Tulcán Cantón, Parroquia Chical, sector Gualpi medio, Reserva Indígena Awá, trail to San Marcos N of the community center, 23–27 May 1992 (fl), *G. Tipaz et al. 1028* (FTG, MO). **Es-**

meraldas: San Lorenzo Cantón, Reserva Étnica Awá, Centro Guadualito, 20–29 July 1992 (fr), *C. Aulestia et al. 70* (FTG, MO, QCNE, US); Reserva Étnica Awá, Parroquia Mataje, Centro Mataje, 21 Sep. 1992 (fr), *C. Aulestia et al. 377* (FTG, MO, QCNE); Reserva Étnica Awá, Parroquia Mataje, Centro Mataje, 21 Sep. 1992 (fr), *C. Aulestia et al. 513* (FTG, MEXU, MO, NY, QCNE); Parroquia Alto Tambo, sector El Cristal, 13 Apr. 1992 (fr), *G. Tipaz et al. 777* (FTG, MO); Reserva Indígena Awá, Ricaurte, 19–24 Oct. 1992 (fr), *G. Tipaz et al. 2044* (FTG, MO, QCNE).

26. Ardisia blepharodes Lundell, Wrightia 4: 55. 1968. *Auriculardisia blepharodes* (Lundell) Lundell, Phytologia 49: 342. 1981. TYPE: Costa Rica. Cartago: El Muñeco on the Río Navarro, 1400–1500 m, 6–7 Mar. 1926 (fr), *P. Standley & R. Torres R. 51266* (holotype, US!, LL neg. 1971-22!; isotype, GH!). Figure 28.

Small trees 3–5 m tall. *Branchlets* slender, terete, 2–5.5 mm diam., densely and minutely appressed rufous furfuraceous-lepidote. *Leaves* with blades membranous to chartaceous, narrowly oblong, narrowly elliptic to oblanceolate, 5.2–12.6 × 1.4–3.2 cm, apically abruptly acuminate, with an acumen 6–12 mm long, basally acute, decurrent on the petiole, prominently punctate and punctate-lineate above and below, glabrous above, densely and minutely appressed rufous furfuraceous-lepidote, the midrib impressed above, prominently raised below, the secondary veins 17 to 29 pairs, prominulous above and below, the margins entire, flat; petioles slender, marginate, 6–11 mm long, 0.5–1.5 mm diam., glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, 9.2–16.7 × 8.1–12.5 cm, pyramidal, longer than the leaves, the rachis, branchlets, abaxial bract surfaces and pedicels furfuraceous-lepidote, the branches loosely congested into 3- to 6-flowered corymbs; peduncle 0.8–2.6 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, ovate, 0.8–2.2 × 0.4–1.2 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 0.5–0.9 × 0.4–1.1 mm; pedicels stout, obsolete to 1.2 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, pink; calyx lobes chartaceous to coriaceous, orbicular to ovate, 2.2–2.8 × 2.4–2.8 mm, apically obtuse to rounded, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla chartaceous, 6.9–7.1 mm long, the tube 2.2–2.4 mm long, the lobes narrowly ovate to lanceolate, 4.5–4.9 × 1.8–2 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins entire, hyaline; stamens 6.5.–6.9 mm long, the filaments 4.5–4.7 mm long, the staminal tube 0.8–0.9 mm long, the apically free portions 3.6–3.9 mm long, the anthers narrowly ovoid, 2.2–2.4 × 0.9–1 mm, apically apiculate, basally deeply cordate, the connective conspicuously punctate; pistil 6.2–6.6 mm long, glabrous, the ovary oblong, 1.1–1.3 mm long, the style 5.1–5.3 mm long, prominently punctate, the ovules 15 to 21. *Fruits* globose, 5–6 mm diam., inconspicuously punctate.

Distribution. *Ardisia blepharodes* is endemic to the Cordillera Talamanca, in Limón and Cartago, Costa Rica, growing from 1200 to 1500 m in elevation.

Ecology and conservation status. *Ardisia blepharodes* occurs in moist premontane forests. Because it is known from so few collections, no further information is available about its conservation status.

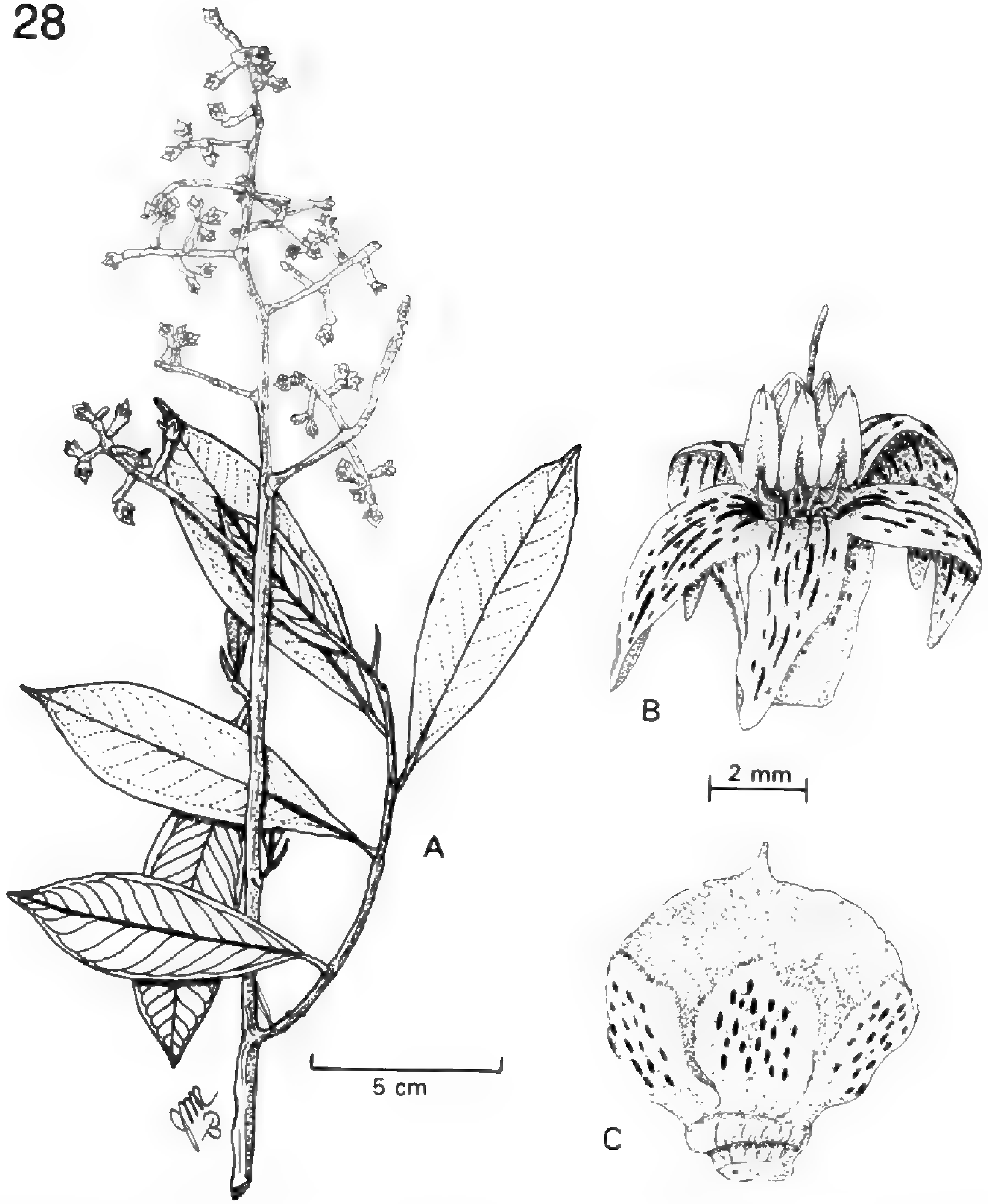
Etymology. The specific epithet was derived from the Greek "Blepha-" meaning relating to eyelashes or eyelids, referring to margins fringed with hairs or ciliated, and "odes" or "oides" meaning like or resembling, specifically referring to the glandular ciliolate calyx lobes.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia blepharodes* is easily distinguished from *A. hagenii* by its smaller leaves to 12.6 cm long, narrower calyx lobes to 2.8 mm wide, shorter corolla lobes to 4.9 mm long, shorter anthers to 2.4 mm long, and shorter styles to 5.3 mm long. *Ardisia blepharodes* is separated from both *A. fimbrillifera* and *A. pseudoracemiflora* by its smaller and narrower leaf blades to 12.6 × 3.2 cm, shorter pedicels obsolete to 1.2 mm long, narrower corolla lobes to 2 mm wide and shorter and narrower anthers to 2.4 × 1 mm.

Specimens examined. COSTA RICA. **Cartago:** knoll W of Quebrada Casa Blanca, Tapantí, 26 Dec. 1984 (fl), *M. Grayum et al. 4648* (FTG, LL, MO), 22 June 1985 (fl), *M. Grayum & R. Warner 5434* (CR, FTG, LL, MEXU, MO). **Limón:** mountain between Cerro Chimú and Cerro Matama, 30 Apr. 1985 (fr), *L. Gómez et al. 23564* (FTG, MO, NY).

27. Ardisia capitellata Lundell, Wrightia 6: 67. 1979. *Auriculardisia capitellata* (Lundell) Lundell, Phytologia 49: 342. 1981. TYPE: Costa Rica. Puntarenas: above coffee fincas along

28



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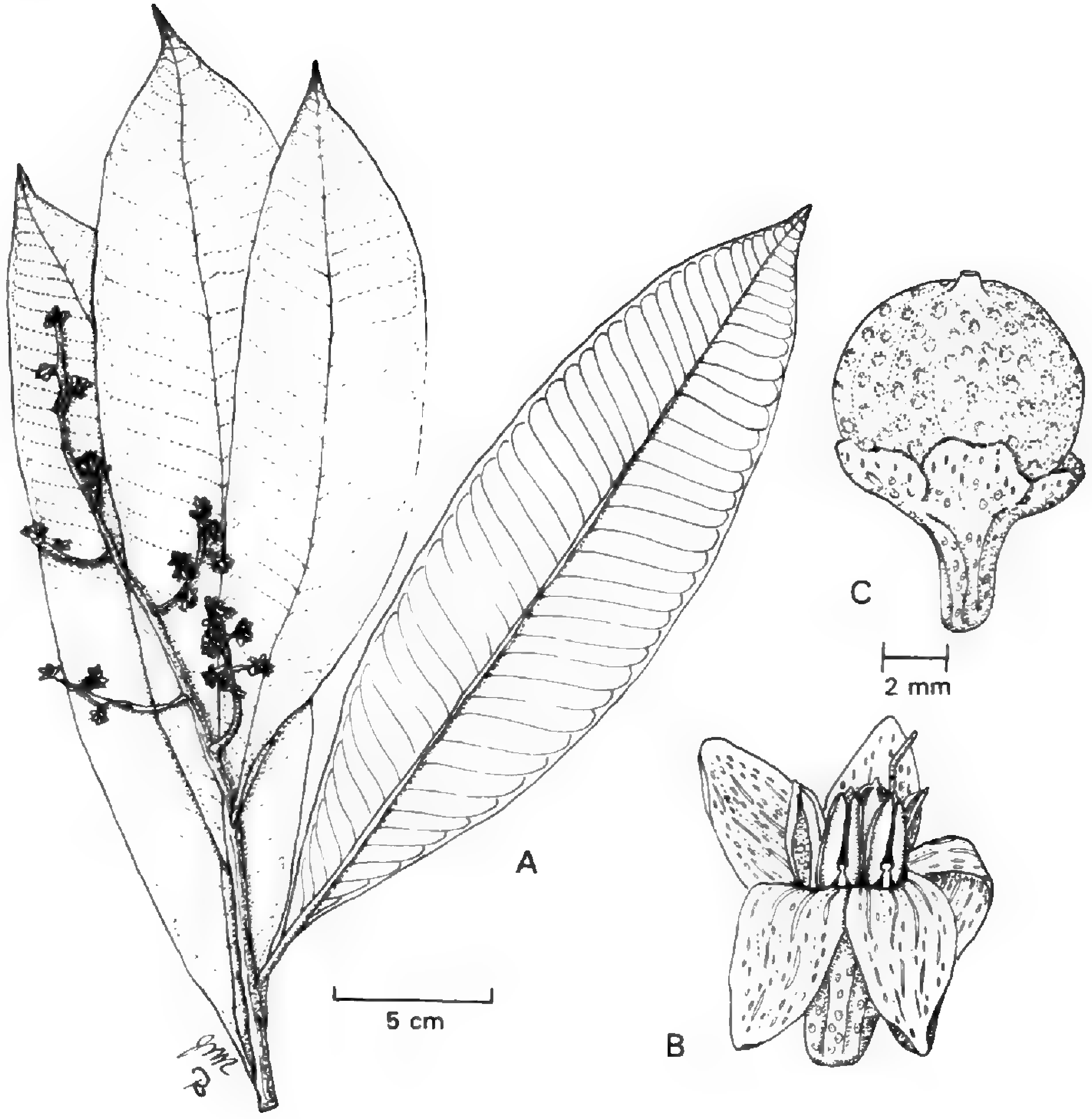

Figure 28 (left). *Ardisia blepharodes.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from holotype, *P. Standley & R. Torres R. 51266* (US); B from *M. Grayum et al. 4648* (MO); C from *M. Grayum & R. Warner 5434* (MO).)

Figure 29 (right). *Ardisia capitellata.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from isotype, *T. Croat 26678* (NY); B from *P. Raven 21653A* (MO isotype of *Auriculardisia latisepala* Lundell); C from *R. Villalobos 6* (MO).)

Río Coto Brus, near Cotán, 23 km N La Unión, on Panama border, 9 Aug. 1974 (fl), *T. Croat 26678* (holotype, LL!, F neg. 55613!; isotypes, MO!, NY!). Figure 29.

Auriculardisia latisepala Lundell, Wrightia 7: 269. 1984. Syn. nov. *Ardisia latisepala* (Lundell) Lundell, Phytologia 61: 65. 1986, nom. inval. *Ardisia latisepala* (Lundell) Pipoly & Ricketson, Sida 18: 513. 1998. TYPE: Costa Rica. Puntarenas: on and around Wilson's finca, 6 km S of San Vito de Java, ca. 4000 ft. [1219 m], 19 Aug. 1967 (fl), *P. Raven 21653A* (holotype, F!, F neg. 68324!; isotype, MO!).

Shrubs or *small trees* to 9.1 m tall, and 10 cm diam. *Branchlets* slender, terete, 3–7.5 mm diam., densely and minutely appressed rufous furfuraceous-lepidote. *Leaves* with blades chartaceous to coriaceous, elliptic to narrowly elliptic, 16.4–32.8 × 4.4–9.8 cm, apically acuminate, with an acumen 0.5–1.7 cm long, basally acute, decurrent on the petiole, inconspicuously punctate and punctate-lineate above and below, mostly glabrous above, densely and minutely appressed rufous furfuraceous-lepidote below, denser along the midrib and secondary veins, the midrib impressed above, prominently raised below, the secondary veins 39 to 57 pairs, prominulous above and below, the margins entire, flat to slightly revolute; petioles slender, 6–18 mm long, 1–3 mm diam., glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, 8.2–32.4 × 4.8–31.5 cm, pyramidal, longer than or as long as the leaves, the peduncle, rachis, branches, and pedicels densely and minutely appressed rufous furfuraceous-lepidote, the branches loosely congested into 4- to 9-flowered corymbs; peduncles 0.6–3.6 cm long, the lower branches subtended by leaves; inflorescence bracts and branch bracts unknown; floral bracts usually persistent, membranous, ovate, 2.5–4.5 × 0.8–3.2 mm, apically rounded to acute, inconspicuously punctate and punctate-lineate, glabrous above and below, the midrib unknown, the secondary veins unknown, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels stout, 0.9–2.5(–4) mm long, inconspicuously punctate and punctate-lineate. *Flowers* 5-merous, rarely 6-merous, white to pink or light purple; calyx lobes chartaceous to coriaceous, orbicular to ovate, 3–3.4 × 2.6–3.2 mm, apically rounded, conspicuously red punctate and punctate-lineate, sparsely furfuraceous-lepidote abaxially, glabrous adaxially, the margins entire, sparsely glandular ciliolate; corolla chartaceous, 7.2–7.6 mm long, the tube 1.4–1.6 mm long, the lobes narrowly ovate to lanceolate, 5.8–6 × 2.8–3.2 mm, apically acute to subulate, inconspicuously red punctate and punctate-lineate, glabrous throughout, the margins entire, opaque; stamens 3.9–4.2 mm long, the filaments 2.6–2.8 mm long, the staminal tube 0.7–0.8 mm long, the apically free portions 1.8–2.1 mm long, the anthers lanceoloid, 3.2–3.5 × 1.3–1.5 mm, apically broadly apiculate, basally deeply cordate, the connective conspicuously punctate; pistil 6–6.2 mm long, glabrous, the ovary ovoid 1–1.1 mm long, styles 5–5.2 mm long, epunctate, the ovules 22 to 24. *Fruits* depressed globose, 7–9 mm diam., inconspicuously punctate and punctate-lineate, inconspicuously costate.

Distribution. *Ardisia capitellata* is endemic to the southwestern portion of the Cordillera Talamanca, Puntarenas, Costa Rica, growing from 1200 to 1800 m in elevation.

Ecology and conservation status. *Ardisia capitellata* occurs in primary and secondary lower montane wet forests, occasionally in disturbed areas. Because it is known from so few specimens, its current conservation status is unknown.

Etymology. The specific epithet refers to the compact, capitulate appearing corymbs of the inflorescence branches.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia capitellata* is very similar to *A. generalensis*, but is distinguished from it by the shorter and narrower leaf blades to 32.8 × 9.8 cm, the smaller inflorescence 32.4 × 31.5 cm, flowers 5- or 6-merous, smaller and narrower calyx lobes to 3.4 × 3.2 mm, shorter and narrower corolla lobes to 6 × 3.2 mm, and shorter and narrower anthers to 3.5 × 1.5 mm.

Populations corresponding to the type of *Auriculardisia latisepala* Lundell match the type of *Ardisia capitellata* Lundell in all respects except for slightly larger flowers.

Specimens examined. COSTA RICA. **Puntarenas**: Cantón de Coto Brus, Parque Indígena La Amistad, Cordillera Talamanca, Estación Pittier, Río Gemelo, 30 Jan. 1995 (fr), *L. Angulo et al. 22* (FTG, INB, MO); foothills of the Cordillera Talamanca, in the area of Sitio Cotón (Cotonsito), along the road to Coto Brus, 3–4 Sep. 1983 (fl), *G. Davidse 24578* (LL, MO); Cordillera Talamanca, area around Río Canasta, 9.5 airline km NW of Agua Caliente, between Cerro Frantzius and Cerro Pittier, 6 Sep. 1984 (fl), *G. Davidse et al. 28363* (LL, MO); Zona Protectora Las Tablas, Estación Biológica Las Alturas, Paralelo Trail, 31 Aug. 1992 (fl), *A. Fernández et al. 331* (CR, FTG, INB, MO); Cantón de Coto Brus, Parque Indígena La Amistad, Cordillera Talamanca, Estación Pittier, Gemelo Trail, 14 May 1995 (fl), *B. Gamboa R. 247* (INB, MO); Cantón de Coto Brus, Cuenca Térraba-Sierpe, Estación Biológica Las Alturas, trail to Cerro Echandí, 28 Oct. 1997 (fl), *B. Gamboa R. 1902* (INB, MO); along trail between Las Cruces Botanical Garden and Río Java, ca. 3.5 km SE of San Vito de Coto Brus, 12 Sep. 1985 (fl), *M. Grayum et al. 5973* (FTG, LL, MO); Las Alturas, 26 Aug. 1974 (fl), *P. Maas & B. Alpin 1492* (F); Cantón de Coto Brus, Parque Indígena La Amistad, Cordillera Talamanca, Estación Pittier, Pittier Trail, 1 Aug. 1995 (fl), *E. Navarro 170* (CR, FTG, INB, MO); Wilson's Farm, 6 km S of San Vito de Java, 16 Aug. 1967 (fl), *P. Raven 21827* (F, MO, NY); Cantón de Coto Brus, Parque Indígena La Amistad, Cordillera Talamanca, trail to Altamira, Río Canasta, 28 Jan. 1995 (fr), *R. Villalobos 6* (FTG, INB, MO); Cantón de Coto Brus, Parque Indígena La Amistad, Cordillera Talamanca, Estación Pittier, 12 June 1995 (fl), *R. Villalobos 205* (FTG, INB, MO).

28. Ardisia cartagoana Lundell, Wrightia 6: 68. 1979. *Auriculardisia cartagoana* (Lundell) Lundell, Phytologia 49: 343. 1981. TYPE: Costa Rica. Cartago: along road between Juan Vinas & Turrialba, 7 km W Turrialba, along ditch, 1 July 1976 (fl), *T. Croat 36841* (holotype, MO!, F neg. 55674!; isotype, LL!). Figure 30.

Shrubs or small trees 1–8 m tall. *Branchlets* stout, terete, 5–10 mm diam., densely rufous furfuraceous-lepidote. *Leaves* with blades membranous, oblanceolate, 15.4–32.9 × 5.1–8.7 cm, apically acuminate, with an acumen 6–10 mm long, basally acute, decurrent on the petiole, inconspicuously and conspicuously punctate and punctate-lineate, glabrous, the midrib impressed above, prominently raised below, the secondary veins 40 to 51 pairs, nitid above, prominulous below, the margins entire, flat to slightly inrolled; petioles stout, marginate, nearly obsolete to 1.5 cm long, 3–4 mm diam., glabrous. *Inflorescences* erect, bi- to tripinnately paniculate, 13.1–28.4 × 9.7–18.8 cm, pyramidal, usually longer than the leaves, mixed minutely cupuliform and furfuraceous-lepidote, the branches congested to loosely congested into 5- to 9-flowered racemes with flowers clustered in a pseudocorymb at apex; peduncles 1.5–3.5 cm long, the lower branches subtended by leaves; inflorescence and branch bracts unknown; floral bracts caducous, membranous, 1.7–2 × 1.4–1.8 mm, apically acute, conspicuously punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline sparsely glandular ciliolate; pedicels stout, obsolete to 2 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, white to pink or violet; calyx lobes chartaceous, orbicular to oblate, 2–2.3 × 2.1–2.4 mm, apically rounded, inconspicuously punctate and punctate-lineate to nearly epunctate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 5.2–5.5 mm long, the tube 1.1–1.3 mm long, the lobes ovate, 4–4.2 × 1.9–2.7 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 4.8–5 mm long, the filaments 2.3–2.4 mm long, the staminal tube 0.6–0.7 mm long, the apically free portions 1.6–1.8 mm long, the anthers lanceoloid, 2.9–3 × 1–1.1 mm, apically apiculate, basally deeply cordate, the connective conspicuously punctate; pistil 6.4–6.5 mm long, glabrous, the ovary oblong, 1.8–1.9 mm long, the style 4.6–4.7 mm long, epunctate, the ovules 16 to 21. *Fruits* (immature) globose, 4.5–5.2 mm long, prominently punctate and punctate-lineate.

Distribution. *Ardisia cartagoana* is endemic to Costa Rica and has been found only in the Cordillera Talamanca near Cerro Turrialba (Cartago) and the Fila de Matamá at the headwaters of the Río Boyei (Limón), growing at 1110 to 1300 m in elevation.

Ecology and conservation status. *Ardisia cartagoana* occurs in premontane wet forest. It has been found in forest remnants near sugar cane fields and thus is very tolerant of disturbance and not considered threatened.

Etymology. The specific epithet referred to the Province of Cartago, Costa Rica, where the type was collected.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia cartagoana* is closely related to *A. megistophylla*, *A. aguirreana*, *A. cogolloi*, and *A. crassipes* because of its long calyx lobes with thick petioles. However, *A. cartagoana* is separated from *A. megistophylla* by its shorter calyx lobes to 2.3 mm long, shorter corolla lobes to 4.2 mm long, shorter anthers to 3 mm long, and shorter styles to 4.7 mm long. *Ardisia cartagoana* is easily distinguished from *A. aguirreana* by its shorter leaf blades to 32.9 cm long, smaller branchlets to 10 mm in diameter, shorter peduncles to 3.5 cm long, and wider corolla lobes to 2.7 mm wide. *Ardisia cartagoana* is separated from *A. cogolloi* by its smaller and wider orbicular, not ovate calyx lobes 2.3 × 2.4 mm, longer and narrower anthers 3 × 1.1 mm, longer styles to 4.7 mm long, and smaller fruits to 5.2 mm in diameter. *Ardisia cartagoana* differs from *A. crassipes* by its membranous not coriaceous leaf blades, which are glabrous above and below, thinner petioles to 4 mm in diameter, narrower calyx lobes to 2.4 mm wide, shorter corolla lobes to 4.2 mm long, and shorter styles 5.2 mm long.

Specimens examined. COSTA RICA. **Cartago**: Cantón de Turrialba, Valle del Reventazón, Grano de Oro, Moravia de Chirripó, 10 Oct. 1992 (fl, fr), *P. Campos 57* (CR, FTG,

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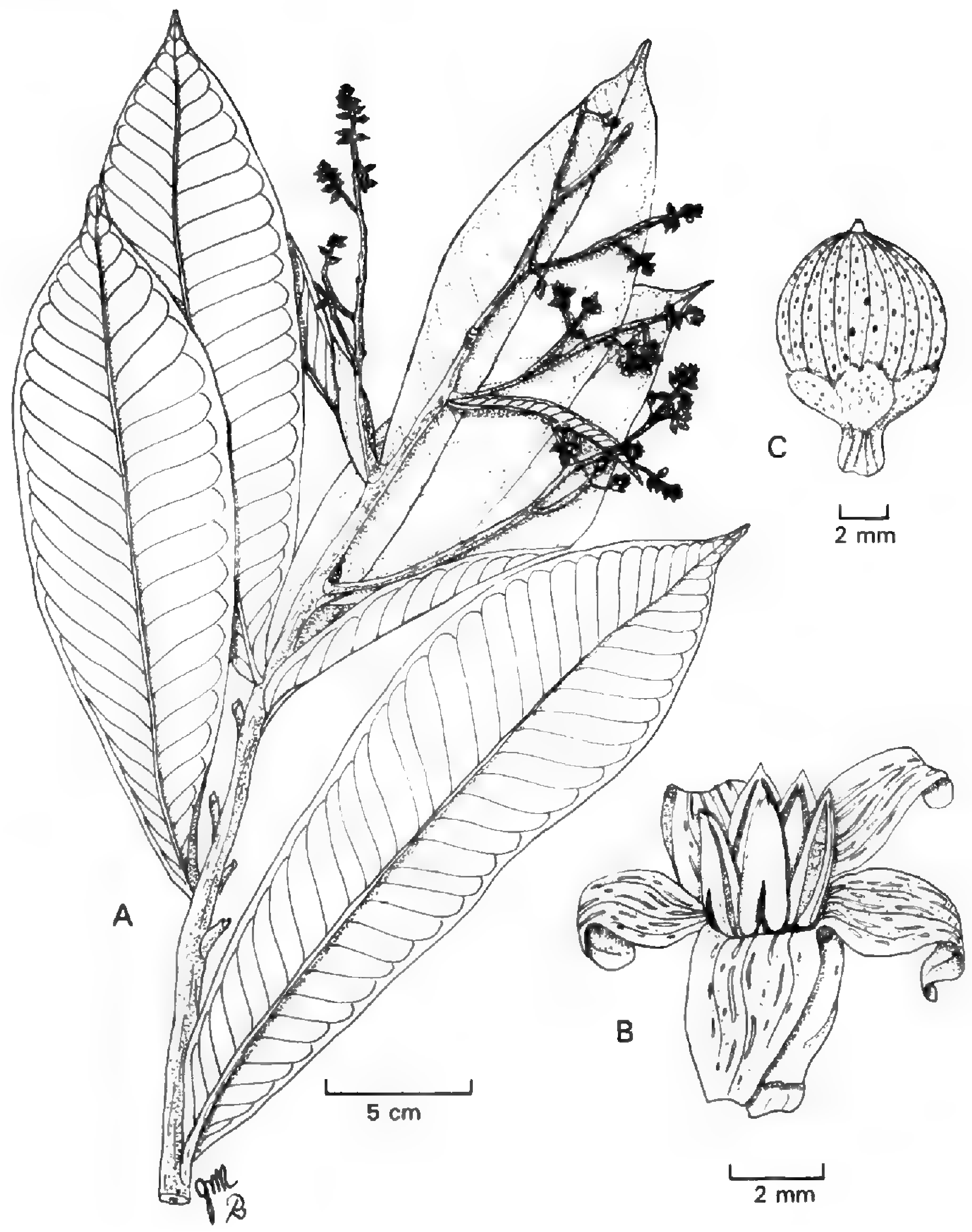

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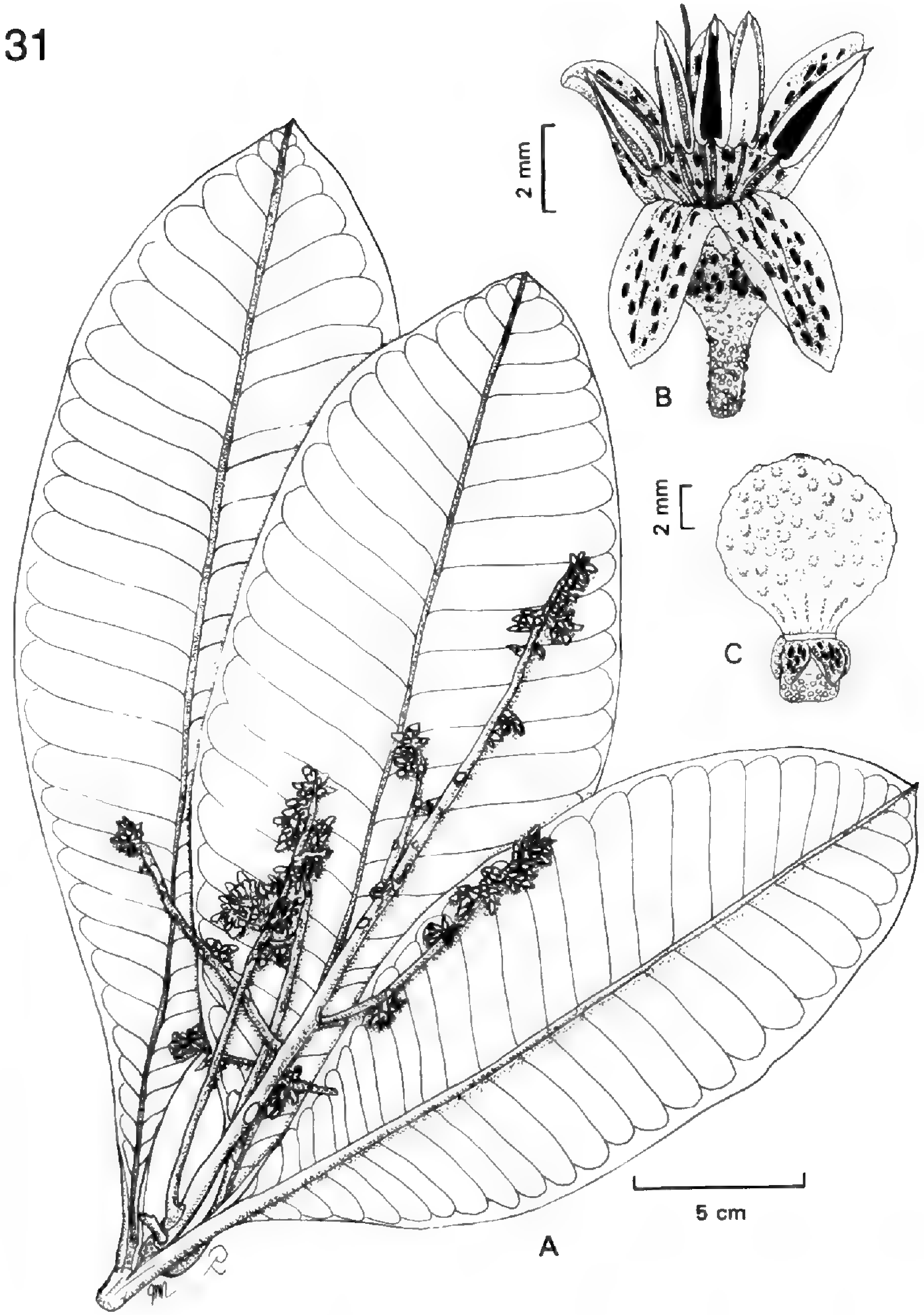

Figure 30 (left). *Ardisia cartagoana.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from holotype, *T. Croat 36841* (MO), B, C from *P. Campos 57* (MO).)

Figure 31 (right). *Ardisia cogolloi.* —A. Flowering branch. —B. Flower. —C. Fruit. (A & B drawn from holotype, *A. Cogollo et al. 3498* (JAUM); C from *J. Pipoly et al. 18307* (MO).)

INB, MO), 29 June 1993 (fl), *P. Campos 76* (FTG, INB, MO). **Limón**: Cantón de Limón, Cordillera Talamanca, N flank of Fila de Matamá at headwaters of Río Boyei, 17 Aug. 1995 (fl), *M. Grayum 11046* (INB, MO).

29. Ardisia cogolloi Pipoly, Caldasia 16: 277. 1991. TYPE: Colombia. Antioquia: Mpio. de Urrao, Parque Nacional Natural "Las Orquídeas," Sector Venados, right bank of upper Río Venados, 06°34′N, 076°19′W, 1150–1300 m, 26 July 1988 (fl), *A. Cogollo, J. Ramírez & O. Alvarez 3498* (holotype, JAUM!; isotypes, COL!, FMB!, HUA!, MO!). Figure 31.

Trees 3–15 m tall, 9.5–26 cm diam. *Branchlets* stout, terete, 6.5–10.5 mm diam., densely rufous furfuraceous-lepidote. *Leaves* with blades chartaceous, elliptic, 14.4–50.2 × 5.9–17.6 cm, apically obtuse with an abrupt acute acumen, acumen 0.6–0.9 cm long, basally cuneate, decurrent on the petiole, prominently and inconspicuously punctate and punctate-lineate above and below, glabrous above, densely rufous furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 38 to 45 pairs, nitid above, raised below, the margins entire, subrevolute petioles stout, canaliculate, 1.5–3.5 cm long, 4–7 mm diam., glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bipinnately paniculate, 15.4–24.6 × 4.5–13.6 cm, pyramidal, shorter than the leaves, the rachis, branchlets, abaxial bract surfaces, and pedicels densely furfuraceous-lepidote, the branches loosely congested into 2- to 7-flowered corymbs; peduncle 0.2–1 cm long; inflorescence bracts and branch bracts unknown; floral bracts caducous, membranous, ovate, 1–1.5 × 0.5–0.8 cm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels stout, obsolete to 0.7 mm long, prominently punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, white; calyx lobes chartaceous, ovate, 2.5–2.6 × 1.8–1.9 mm, apically obtuse, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 6.2–6.5 mm long, the tube 2–2.3 mm long, the lobes narrowly oblong, 4.2–4.5 × 2.4–2.6 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins entire, hyaline; stamens 5.2–5.9 mm long, the filaments 3.6–3.8 mm long, the staminal tube 1–1.1 mm long, the apically free portions 2.5–2.9 mm long, the anthers ovoid, 2.3–2.6 × 1.3–1.5 mm, apically apiculate, basally cordate, the connective conspicuously punctate; pistil 3.7–3.8 mm long, glabrous, the ovary oblong, 1.6–1.7 mm long, the style 2–2.2 mm long, epunctate, the ovules 19 to 27. *Fruits* globose, 8–9.8 mm diam., prominently punctate.

Distribution. *Ardisia cogolloi* is endemic to the Cordillera Occidental of Colombia, growing from 800 to 1750 m in elevation.

Ecology and conservation status. *Ardisia cogolloi* occurs in premontane pluvial forests, where it is ecologically significant, frequently attaining a diameter at breast height over 15 cm. Because the majority of the collections are from protected areas, it does not appear that the species is threatened.

Etymology. This species was named in honor of Biól. Alvaro Cogollo Pacheco, Director of Research at the Fundación Jardín Botánico, "Joaquín Antonio Uribe," in Medellín, Colombia.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia cogolloi* is closely related to *A. megistophylla*, *A. aguirreana*, *A. crassipes*, and *A. cartagoana* because of its long calyx lobes with thick petioles. However, *Ardisia cogolloi* is separated from *A. megistophylla* by its shorter calyx lobes to 2.6 mm long, shorter corolla lobes to 4.5 mm long, shorter anthers to 2.6 mm long, and shorter styles to 2.2 mm long. *Ardisia cogolloi* is easily distinguished from *A. aguirreana* by its shorter leaf blades to 50.2 cm long, smaller branchlets to 10.5 mm in diameter, shorter peduncles to 1 cm long, and wider corolla lobes to 2.6 mm wide. *Ardisia cogolloi* is separated from both *A. crassipes* and *A. cartagoana* by its larger and narrower ovate, not orbicular calyx lobes to 2.6 × 1.9 mm, shorter and wider anthers to 2.6 × 1.5 mm, shorter styles to 2.2 mm long, and larger fruits to 9.8 mm in diameter.

Specimens examined. COLOMBIA. **Antioquia**: Mpio. de Urrao, Parque Nacional Natural "Las Orquídeas," Vereda Calles, right bank of Río Calles, on the range NW of the Cabaña Calles, 13 Nov. 1993 (fl), *A. Cogollo et al. 7312* (FTG, JAUM, MO); Mpio. de Urrao, Parque Nacional Natural "Las Orquídeas," Vereda Calles, Quebrada Honda, on the range NW of Cabaña Calles, 8 Dec. 1992 (ster.), *J. Pipoly et al. 16729* (JAUM, MO), *16782* (JAUM, MO), *16601* (JAUM, MO), *16958* (JAUM, MO); Mpio. de Urrao, Parque Nacional Natural "Las Orquídeas," Vereda Calles, Alto de Palmitas, ca. 1 km from Cabaña Calles, 4 Dec. 1993 (ster.), *J. Pipoly et al. 17648* (FTG, JAUM, MO); Mpio. de Urrao, Parque Nacional Natural "Las Orquídeas," Vereda Calles, right bank of Río Calles, 9 Dec. 1993 (fl), *J. Pipoly et al. 18000* (FTG, JAUM, MO); Mpio. de Frontino, Vereda Venados, Parque Nacional Natural Las Orquídeas, sitio La Miquera, 3 Feb. 1995 (fr), *J. Pipoly et al. 18307* (JAUM, MO).

30. Ardisia coloradoana Lundell, Wrightia 6:

69. 1979. *Auriculardisia coloradoana* (Lundell) Lundell, Phytologia 49: 343. 1981. TYPE: Panama. Chiriquí: Cerro Colorado, 34–35.6 km above Río San Félix, 13–14.6 km above turnoff to Escopeta, 1390–1410 m, 15 July 1976 (fl), *T. Croat 37235* (holotype, MO!, F neg. 55684!). Figure 32.

Treelets or trees 2–6 m tall. *Branchlets* slender, terete, 3–6 mm diam., densely cupuliform and furfuraceous-lepidote. *Leaves* with blades chartaceous to coriaceous, elliptic to oblong, 3.4–10.8 × 1.1–3.6 cm, apically long acuminate, with an acumen 6–12 mm long, basally acute or cuneate, decurrent on the petiole, inconspicuously punctate and punctate-lineate, nearly glabrous above, densely appressed rufous furfuraceous-lepidote, the midrib impressed above, prominently raised below, the secondary veins 23 to 29 pairs, prominulous above and below, the margins entire, flat, at times drying inrolled; petioles slender, canaliculate, 1.1–2.4 cm long, glabrous above, densely appressed furfuraceous-lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, 5–24 × 4.5–14 cm, pyramidal, longer than the leaves, peduncle, the rachis, branches and pedicels densely cupuliform and furfuraceous-lepidote, the branches loosely congested into 3- to 7-flowered corymbs; peduncles nearly obsolete to 3.8 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, oblong, 2.5–2.9 × 1–1.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, appressed furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 2.8–4.1 × 0.6–0.9 mm; pedicels slender, 3.5–5.1 mm long, inconspicuously punctate and punctate-lineate, mixed cupuliform and furfuraceous-lepidote. *Flowers* 5-merous, white or cream; calyx lobes chartaceous, orbicular to oblate, 1.4–1.6 × 1.6–1.9 mm, apically acute to rounded, conspicuously punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous to chartaceous, 3.9–4.1 mm long, the tube 1–1.4 mm long, the lobes lanceolate, 2.7–2.9 × 1.6–1.8 mm, apically acute, inconspicuously punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 2.9–3 mm long, the filaments 1.4–1.6 mm long, the staminal tube 0.6–0.7 mm long, the apically free portions 0.7–1 mm long, the anthers ovoid to narrowly ovoid, 1.5–1.7 × 0.7–0.9 mm, apically apiculate, basally deeply cordate, the connective conspicuously punctate; pistil 3.8–4 mm long, glabrous, the ovary oblong, 1.1–1.5 mm long, the style 2.5–2.7 mm long, nearly epunctate, the ovules 19 to 23. *Fruits* globose, 6.5–7.2 mm diam., inconspicuously punctate and punctate-lineate.

Distribution. *Ardisia coloradoana* is endemic to Cerro Colorado and Cerro Hornito along the Continental Divide, at the junction of Bocas del Toro and Chiriquí, Panama, growing at 1290 to 1950 m in elevation.

Ecology and conservation status. *Ardisia coloradoana* occurs in cloud forests, where it is locally common. Label data indicate that it is common among forest remnants and thus tolerates moderate amounts of disturbance. Therefore, we do not believe it is under threat at this time.

Etymology. The name refers to the type location on Cerro Colorado.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia coloradoana* is most closely related to *A. atropurpurea* because of the small calyx lobes, between 1.4 and 1.7 mm long, long pedicels, narrow corolla lobes, and short anthers. However, *A. coloradoana* is easily distinguished from *A. eucuneata* and *A. atropurpurea* by its thicker branchlets to 6 mm in diameter, shorter petioles to 2.4 cm long, and wider calyx lobes to 1.9 mm wide.

Ardisia coloradoana is most easily confused with *A. pleurobotrya* (sect. *Pleurobotryae*) based on the leaf size and shape. However, it is easily separated by its terminal inflorescence and short pedicels to 4.8 mm long, not lateral inflorescences with long pedicels to 10.5 mm long, as in *A. pleurobotrya.*

Specimens examined. PANAMA. **Bocas del Toro:** 12 mi. beyond Campamento Chamí, 12 + 12 mi. from Río San Félix, 20 June 1986 (fl), *W. D'Arcy 16283* (LL, MO); region of Cerro Colorado, on trails from Continental Divide, 7 mi. from Chamí Camp, 12 Apr. 1986 (fl), *G. McPherson 8802* (LL, MO). **Border of Bocas del Toro and Chiriquí:** Cerro Colorado, road along top, 13 Aug. 1977 (fr), *J. Folsom et al.* 4710 (MO). **Chiriquí:** Fortuna Dam region, along trail to Cerro Hornito, Pate de Macho, on S ridge of watershed, 17 Jan. 1989 (fr), *G. McPherson 13566* (FTG, MO, PMA).

31. Ardisia conglomerata Lundell, Wrightia 6: 71. 1979. *Auriculardisia conglomerata* (Lundell) Lundell, Phytologia 49: 343. 1981. TYPE: Panama. Veraguas: NW of Santa Fé, 2 km from Escuela Agrícola Alto de Piedra, on ridge top below summit Cerro Tute, 28 Mar. 1975 (fr), *S. Mori & J. Kallunki 5275* (holotype, MO!, F neg. 55675!). Figure 33.

Trees 10 m tall. *Branchlets* stout, terete, with

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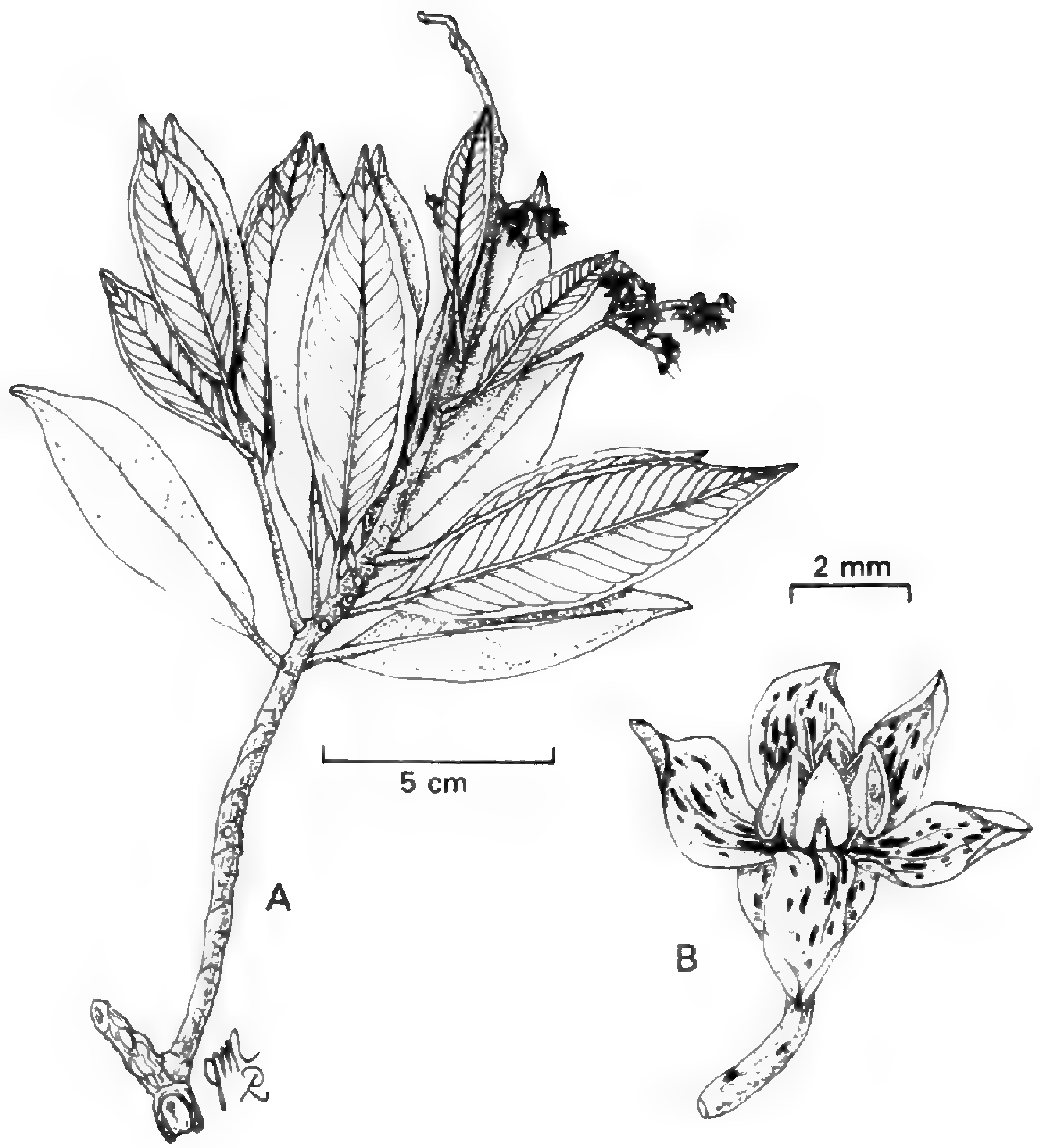

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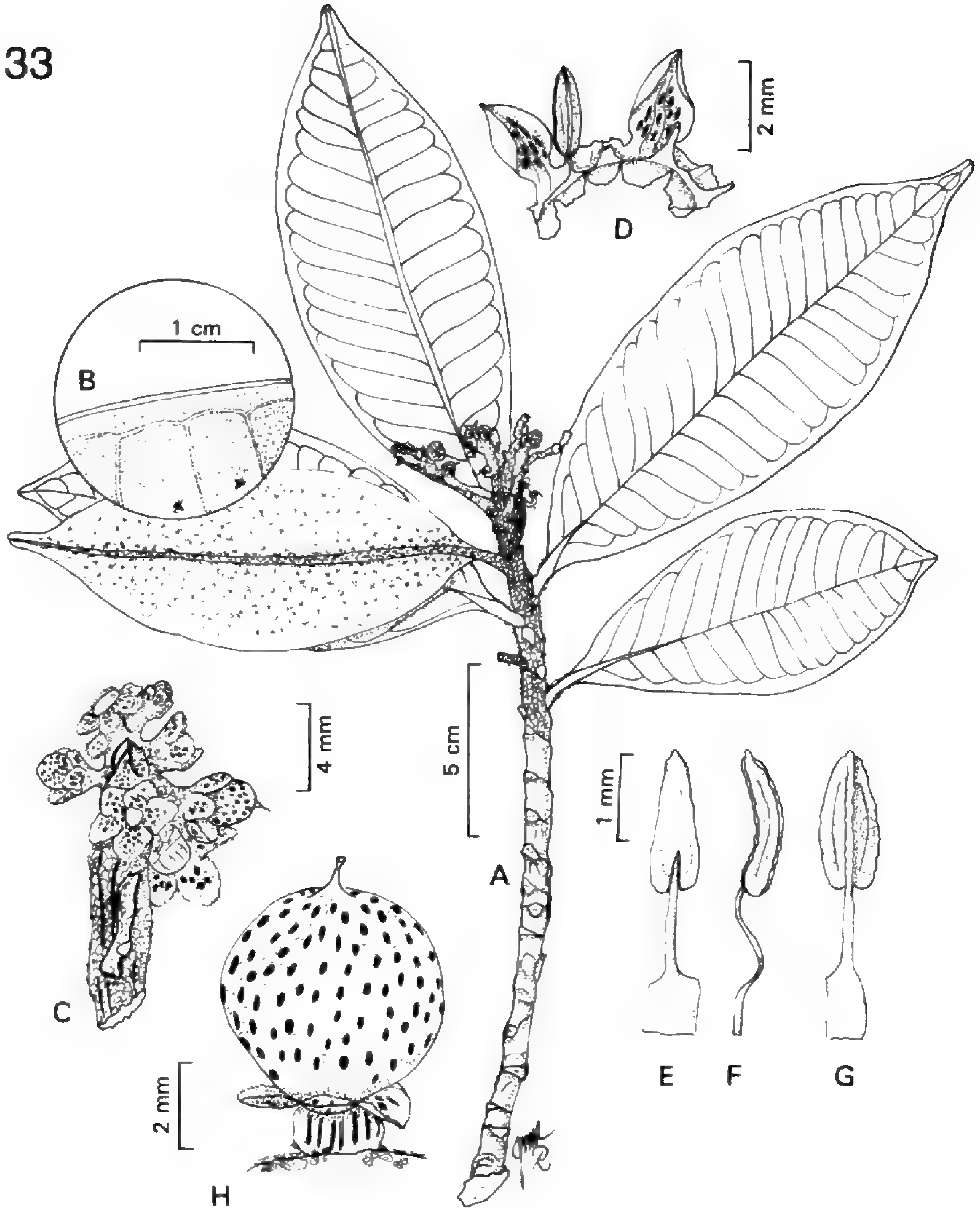

Figure 32 (left). *Ardisia coloradoana.* —A. Flowering branch. —B. Flower. (A, B drawn from, *W. D'Arcy 16283* (MO).)

Figure 33 (right). *Ardisia conglomerata.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Detail of partial flower. —E. Stamen, adaxial surface. —F. Stamen, lateral margin. —G. Stamen, abaxial surface. —H. Fruit. (A–H drawn from holotype, *S. Mori & J. Kallunki 5275* (MO).)

large, swollen leaf scars, 6–9 mm diam., with a mixture of densely cupuliform and furfuraceous-lepidote scales. *Leaves* with blades coriaceous, elliptic, 9.6–16.5 × 3.6–6.8 cm, apically acuminate, with an acumen 0.6–0.9 cm long, basally obtuse, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above at least with age, below with a mixture of densely cupuliform and furfuraceous-lepidote scales, especially so along the midrib, the midrib impressed above, prominently raised below, the secondary veins 22 to 28 pairs, prominulous above and below, the margins entire, revolute; petiole stout, marginate, 0.8–1.2 cm long, glabrous above at least with age, below with a mixture of densely cupuliform and furfuraceous-lepidote scales. *Inflorescences* erect, bipinnately paniculate, 3–3.9 × 4–4.8 cm, obpyramidal, shorter than the leaves, the peduncle, rachis, branchlets, and pedicels with a mixture of densely cupuliform and furfuraceous-lepidote scales, the branches congested into 2- to 8-flowered corymbs; peduncles to 6 mm long; inflorescence bracts persistent, chartaceous, oblong, 1.2–1.4 × 0.6–0.8 cm, apically acute, scattered inconspicuously punctate and punctate-lineate, glabrous above, below with a mixture of scattered cupuliform and furfuraceous-lepidote scales, the midrib inconspicuous, the secondary veins obscure, the margins entire, revolute; inflorescence branch bracts similar to the inflorescence bracts, but 4.5–6.7 × 2.5–5.5 mm; floral bracts persistent, membranous, ovate, 0.6–1.2 × 0.7–0.9 mm, apically acute, scattered inconspicuously punctate and punctate-lineate, glabrous above, sparsely furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels stout, obsolete to 1.2 mm long, inconspicuously punctate, with a mixture of scattered cupuliform and furfuraceous-lepidote scales. *Flowers* [measurements from a single, partial, old flower] 5-merous, color unknown; calyx lobes membranous to chartaceous, orbicular to very widely ovate, 0.9–1.2 × 0.9–1.2 mm, apically obtuse to rounded, prominently punctate and punctate-lineate, glabrous throughout, at least with age, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 2.4–2.6 mm long, the tube 0.5–0.7 mm long, the lobes ovate to narrowly ovate, 1.9–2.1 × 0.8–1 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens ca. 2.8 mm long, the filaments to 1.6 mm long, the staminal tube ca. 0.4 mm long, the apically free portions ca. 1.2 mm long, the anthers lanceoloid, ca. 1.6 × 0.6 mm, apically apiculate, basally subcordate, the connective inconspicuously punctate; pistil 4–4.4 mm long, glabrous, the ovary oblong to globose, 1–1.2 mm diam., the style 3–3.2 mm long, conspicuously punctate, the ovules unknown. *Fruits* globose, 4–5.5 mm diam., prominently punctate.

Distribution. *Ardisia conglomerata* is known only from the type collection on Cerro Tute in Veraguas, Panama, growing at 700 to 800 m in elevation.

Ecology and conservation status. *Ardisia conglomerata* occurs in cloud forests near the summit of Cerro Tute. Because of its restricted distribution, it should be considered threatened.

Etymology. The specific epithet meaning clustered, often spherically so, referred to the small compact corymbs of the inflorescence.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia conglomerata* is one of a number of species that have branchlets covered with a mixture of dense cupuliform and furfuraceous-lepidote scales. *Ardisia conglomerata* can be confused with *A. lundelliana* owing to the coriaceous, elliptic leaves with obtuse to rounded bases and the relatively stout, terete branchlets. However, *Ardisia conglomerata* is easily separated from *A. lundelliana* because of its erect inflorescence with much shorter pedicels obsolete to 1.2 mm long and much shorter anthers to 1.6 mm.

Likewise, within *Ardisia* subg. *Auriculardisia* sect. *Palmanae,* another species that may be confused with *Ardisia conglomerata* is *A. crassiramea,* which also has branchlets covered with a mixture of dense cupuliform and furfuraceous-lepidote scales and straight branchlets. However, *A. conglomerata* differs by the branchlets terete, with large petiole scars, inflorescences bipinnately paniculate and obpyramidal, the pedicels obsolete to 1.2 mm long, the orbicular to widely ovate wider calyx lobes to 1.2 mm wide, the smaller corolla lobes to 2.1 × 1 mm, and the smaller anthers to 1.6 × 0.6 mm.

Ardisia conglomerata is known only from the holotype, which is in young fruit. A fragment of the holotype is located at LL and contains pieces of a single flower consisting of a corolla tube with two attached lobes and two filaments with a single loose anther. The floral measurements in the above description come from this material. It appears that this corolla had failed to completely fall from the expanding ovary.

32. Ardisia crassipedicellata Lundell, Wrightia 6: 73, t. 140. 1979. *Auriculardisia crassipedicellata* (Lundell) Lundell, Phytologia 49: 343. 1981. TYPE: Panama. Veraguas: NW of Santa

Fé, 4.2 km from Escuela Agrícola Alto de Piedra, 25 Feb. 1975 (fr), *S. Mori & J. Kallunki 4830* (holotype, LL!, F neg. 55643!; isotype, MO!). Figure 34.

Auriculardisia roseiflora Lundell, Wrighthia 7: 271. 1984. Syn. nov. Non *Ardisia roseiflora* Pit., Fl. Indo-Chine 3: 866. 1930. *Ardisia dressleri* Lundell, Phytologia 61: 63. 1986, nom. inval. *Ardisia dressleri* Pipoly & Ricketson, Sida 18: 511. 1998. TYPE: Panama. Coclé: trail from Continental Divide near sawmill above El Copé, to Río Blanco del Norte, 08°40′N, 080°36′W, 350–700 m, 20 Feb. 1982 (fl), *S. Knapp, J. Mallet & R. Dressler 3646* (holotype, MO! [unicate]).

Treelets or trees to (4–)12 m tall. *Branchlets* slender, terete, 5–7.5 mm diam., densely furfuraceous-lepidote. *Leaves* with blades coriaceous, elliptic, 14.2–32.4 × 4.7–9.8 cm, apically acuminate, with an acumen 4–13 mm long, basally acute, decurrent on the petiole, inconspicuous, inconspicuously punctate and punctate-lineate, essentially glabrous above, furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 30 to 55 pairs, the margins entire, inrolled; petioles slender, marginate, 12–19 mm long, 2.5–3 mm diam., glabrous above, densely furfuraceous-lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, 6.8–32.4 × 6.2–26.6 cm, pyramidal, usually longer than the leaves, the rachis, branches, and pedicels densely furfuraceous-lepidote, the branches loosely congested into 3- to 7-flowered corymbs; peduncles 0.4–2.8 cm long, the lower branches often subtended by leaves; inflorescence bract unknown; inflorescence branch bracts caducous, chartaceous, oblong, 7–8.2 × 2–2.8 mm, apically acute, prominently punctate and punctate-lineate, essentially glabrous above, furfuraceous-lepidote below, the margins entire, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 0.6–1.3 × 0.6–1.4 mm; pedicels stout, 7–12 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, pink; calyx lobes coriaceous, oblate, 2.4–3 × 4–4.5 mm, apically rounded, inconspicuously punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla coriaceous, 9.6–9.8 mm long, the tube 3.7–3.9 mm long, the lobes lanceolate, 6.1–6.3 × 2.8–3.4 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 7–7.1 mm long, the filaments 4–4.2 mm long, the staminal tube 2–2.1 mm long, the apically free portions 2–2.1 mm long, the anthers narrowly ovoid to lanceoloid, 3.7–3.8 × 1.2–1.4 mm, apically apiculate, basally lobate, the connective conspicuously punctate; pistil 6.9–7.3 mm long, glabrous, the ovary oblong, 1.8–2 mm long, the style 5.1–5.3 mm long, prominently punctate and punctate-lineate, the ovules 37 to 45. *Fruits* globose, 6.8–7.5 mm diam., prominently punctate and punctate-lineate.

Distribution. Ardisia crassipedicellata is endemic to the Cordillera Central near and along the Continental Divide in Bocas Del Toro, Coclé, and Veraguas, Panama, growing at 350 to 900 m in elevation.

Ecology and conservation status. Ardisia crassipedicellata is found in premontane forests. Because it is relatively uncommon, it should be considered threatened.

Etymology. The specific epithet was derived from the Latin "crassi" or thick and "pedicellata" meaning pedicelled, referring to the thick pedicels.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia crassipedicellata* has flowers that are most similar to those of *A. liesneri* because of their large calyx lobes that are as wide as or wider than long, long and slender pedicels, relatively long corolla lobes for the section, and lanceoloid anthers. However, *A. crassipedicellata* is easily separated from *A. liesneri* by its densely furfuraceous-lepidote scales, coriaceous leaf blades, larger oblate calyx lobes to 3 × 4.5 mm, longer corolla lobes to 6.3 mm long, shorter and wider anthers to 3.8 × 1.4 mm, and shorter styles to 5.3 mm long.

The type of *Auriculardisia roseiflora* Lundell is in young bud, and without mature pedicels. While the floral parts are smaller, they match those of *A. crassipedicellata* in all qualitative aspects.

Specimens examined. PANAMA. **Bocas del Toro:** along road above Chiriquí Grande, 25 Oct. 1985 (fr), *G. McPherson 7342* (LL, MO). **Coclé:** Riveras sawmill, El Potroso, 7 km N of El Copé, Alto Calvario, 15 Jan. 1977 (fl), *J. Folsom 1329* (MO); El Copé, El Potroso, first bottom of ridge after 3 small dips but really not so, Atlantic slope of Alto Calvario, 26 Feb. 1977 (fr), *J. Folsom & R. Lantz 1893* (MO, F neg. 55623).

33. Ardisia crassipes Lundell, Wrightia 4: 57. 1968. *Auriculardisia crassipes* (Lundell) Lundell, Phytologia 49: 343. 1981. TYPE: Panama. Bocas del Toro: Robalo Trail, N slopes of Cerro Horqueta, 6000–7000 ft. [1829–2134 m], 5–7 Aug. 1947 (fr), *P. Allen 4991* (holotype, MO!, LL neg. 1971-29!; isotypes, G! [2], GH!, LL!). Figure 35.

Ardisia horquetensis Lundell, Wrightia 4: 181. 1971. Syn. nov. *Auriculardisia horquetensis* (Lundell) Lundell,

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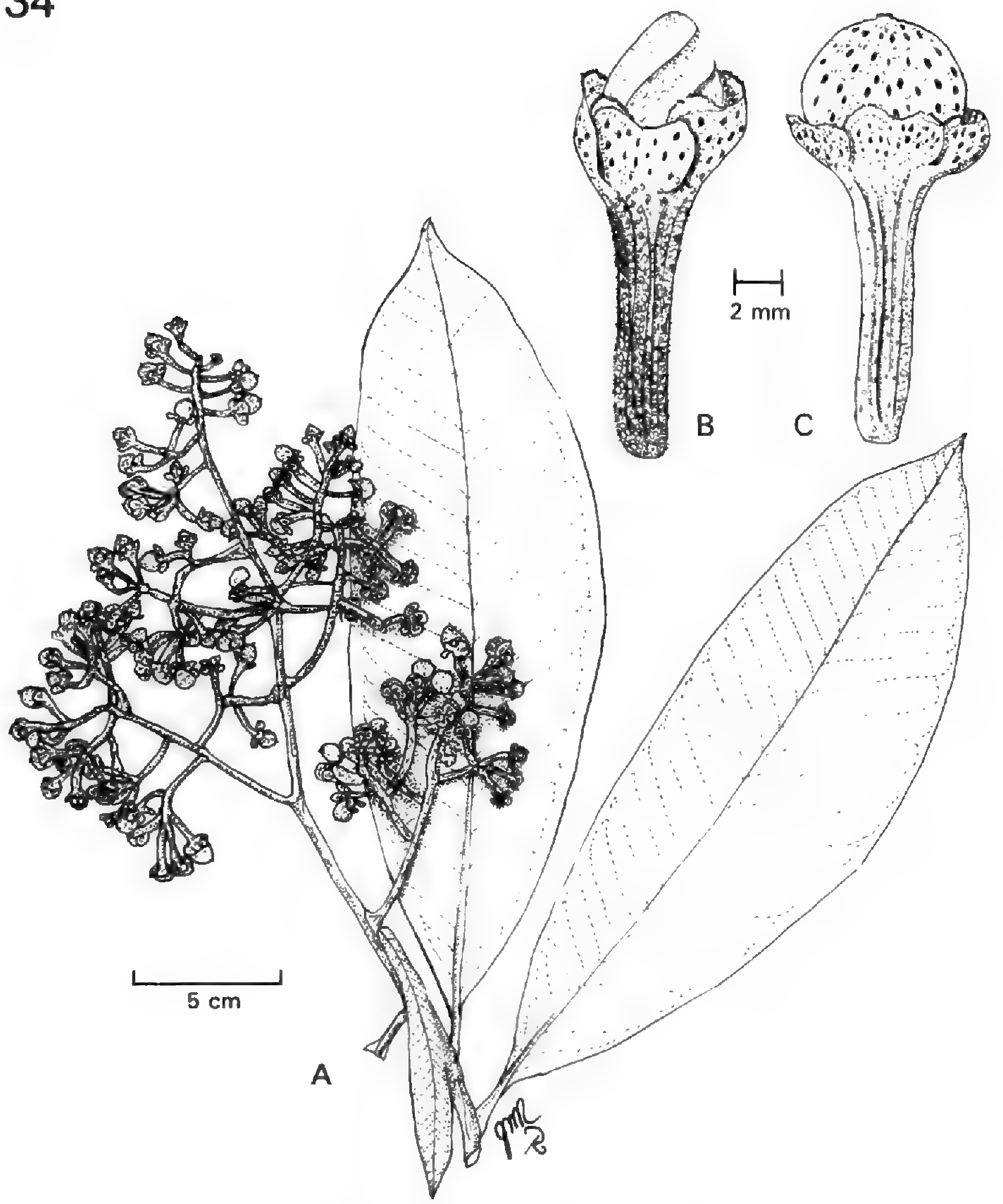

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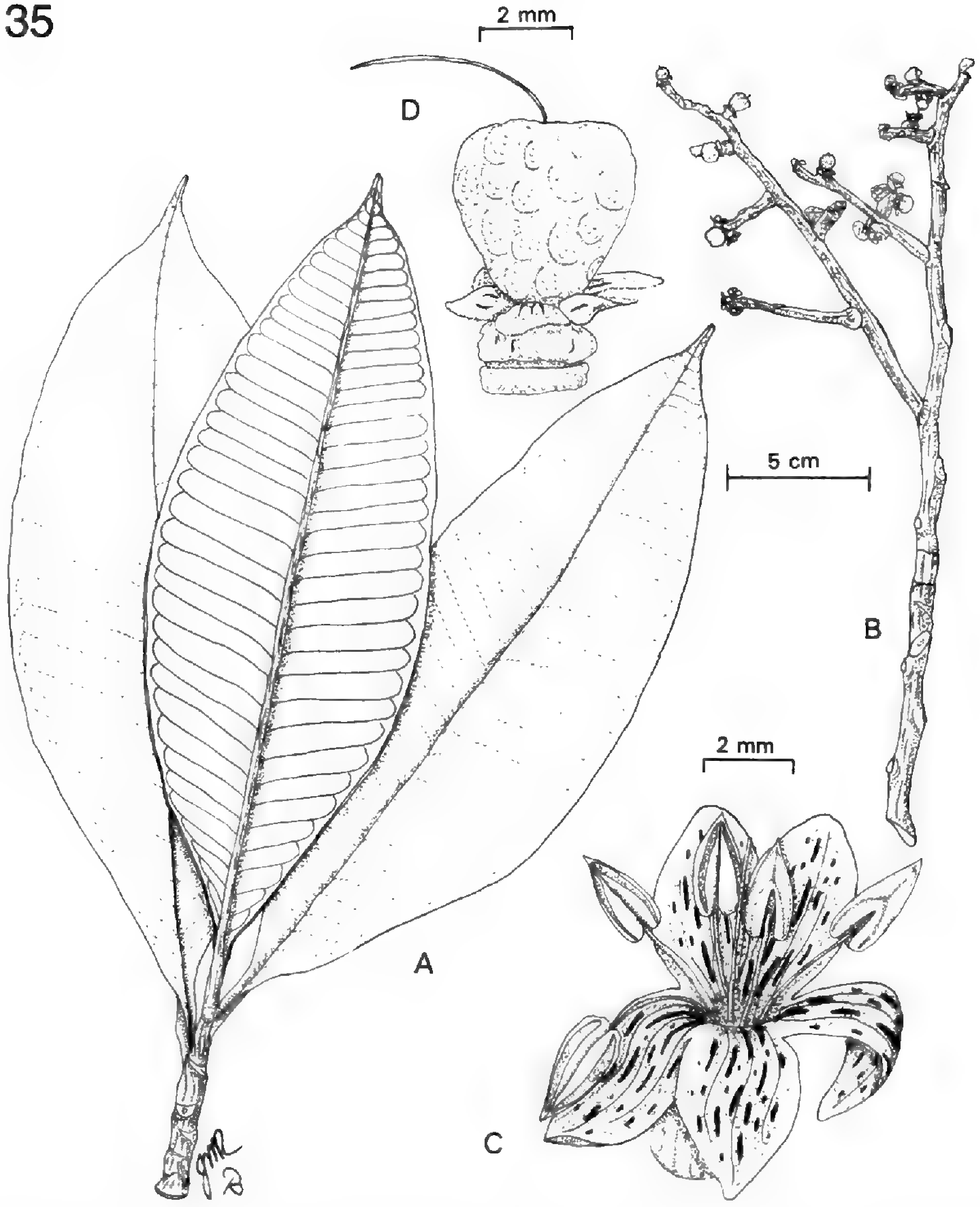

Figure 34 (left). *Ardisia crassipedicellata.* —A. Flowering branch. —B. Flower bud. —C. Fruit. (A & C drawn from isotype, *S. Mori & J. Kallunki 4830* (MO); B from *J. Folsom 1329* (MO).)

Figure 35 (right). *Ardisia crassipes.* —A. Leaf branch apex. —B. Inflorescence. —C. Flower. —D. Fruit. (A, B & D drawn from isotype, *P. Allen 4991* (GH); C from *S. Mori & A. Bolten 7330* (LL), (holotype of *Ardisia florulenta* Lundell).)

Phytologia 49: 344. 1981. TYPE: Panama. Chiriquí: trail to Cerro Horqueta, 6000–6500 ft. [1829–1981 m], 15 May 1971 (fr), *G. Proctor 31925* (holotype, LL!, F neg. 55668!; isotypes, F!, F neg. 61468!, TEX!).

Ardisia florulenta Lundell, Wrightia 6: 75. 1979. Syn. nov. *Auriculardisia florulenta* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Panama. Chiriquí: Cerro Pando, on the Continental Divide and the Panama–Costa Rica border, ca. 16 km NW of El Hato de Volcán, 2000–2482 m, 21 July 1975 (fl), *S. Mori & A. Bolten 7330* (holotype, LL!, F neg. 55664!; isotype, MO!).

Trees 8–20 m tall. *Branchlets* stout, terete, 7–9.5 mm diam., densely rufous furfuraceous-lepidote. *Leaves* with blades coriaceous, elliptic to narrowly elliptic, 12.7–29.8 × 4.7–10.2 cm, apically acuminate, with an acumen 6–16 mm long, basally acute, decurrent on the petiole, inconspicuously punctate and punctate-lineate above and below, sparsely to densely rufous furfuraceous-lepidote above and below, the midrib impressed above, prominently raised below, the secondary veins 45 to 65 pairs, prominulous above and below, the margin entire, flat to inrolled; petioles stout, marginate, 1–1.7 cm long, 4–5 mm diam., furfuraceous-lepidote above and below. *Inflorescences* erect, bi- to tripinnately paniculate, 16.5–29.6 × 11–31.2 cm, pyramidal, longer than the leaves, mixed, densely cupuliform and furfuraceous-lepidote, the branches congested into 5- to 10-flowered pseudospicate corymbs; peduncle obsolete to 2 cm long, the lower branches subtended by leaves; inflorescence bracts and branch bracts unknown; floral bracts caducous, membranous, ovate, 0.9–1.8 × 0.9–1.3 mm, apically acute, inconspicuously punctate and punctate-lineate, glabrous adaxially, mixed lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels, when distinguishable, stout, obsolete to 0.5 mm long, inconspicuously punctate and punctate-lineate, mixed lepidote furfuraceous-lepidote. *Flowers* 5-merous, light pink; calyx lobes chartaceous, orbicular, 2.1–2.3 × 2.8–3.1 mm, apically rounded, prominently punctate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 6–6.1 mm long, the tube 1.5–1.6 mm long, the lobes ovate, 4.4–4.5 × 2.2–2.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 5.6–5.7 mm long, the filaments 4.5–4.6 mm long, the staminal tube 1–1.1 mm long, the apically free portions 3.5–3.6 mm long, the anthers lanceoloid, 2.8–3 × 0.9–1 mm, apically apiculate-subulate, basally cordate, the connective conspicuously punctate; pistil 6.9–7.1 mm long, glabrous, the ovary oblong, 1.9–2 mm long, the style 5–5.1 mm long, epunctate, the ovules 20 to 25. *Fruits* globose, 5–6 mm diam., epunctate.

Distribution. *Ardisia crassipes* is endemic to western Panama, in Bocas del Toro and Chiriquí, growing at 1829 to 2231 m in elevation.

Ecology and conservation status. *Ardisia crassipes* occurs alongside watercourses and footpaths in wet montane and cloud forests. It is locally infrequent, but appears to be able to withstand moderate disturbance. Because of this observed resilience, it should not be considered threatened at this time.

Etymology. The specific epithet means thick, referring to the thick inflorescence rachises.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia crassipes* is closely related to *A. megistophylla*, *A. aguirreana*, *A. cogolloi*, and *A. cartagoana* because of its long calyx lobes with thick petioles. *Ardisia crassipes* is separated from *A. megistophylla* by its shorter calyx lobes to 2.3 mm long, shorter corolla lobes to 4.5 mm long, shorter anthers to 3 mm long, and shorter styles to 5.1 mm long. However, *Ardisia crassipes* is easily distinguished from *A. aguirreana* by its shorter leaf blades to 29.8 cm long, smaller branchlets to 9.5 mm in diameter, shorter peduncles to 2 cm long, and wider corolla lobes to 2.3 mm wide. However, *Ardisia crassipes* is separated from *A. cogolloi* by its smaller and wider orbicular, not ovate calyx lobes 2.1 × 2.3 mm, longer and narrower anthers to 3 × 1 mm, longer styles to 5.1 mm long, and smaller fruits to 6 mm in diameter. *Ardisia crassipes* differs from *A. cartagoana* by its coriaceous not membranous leaf blades, which are tomentose above and not glabrous below, thicker petioles to 5 mm in diameter, wider calyx lobes to 2.3 mm wide, longer corolla lobes to 4.5 mm long, and longer styles to 5.1 mm long.

The type of *Ardisia horquetensis* is in early fruit, with a few flowers remaining, and is unique only for its smaller flowers, but matches *A. crassipes* in all other respects. The type of *A. florulenta* has flowers and is identical to that of *A. crassipes* as well.

Specimens examined. PANAMA. **Chiriquí**: Orilla de la carretera hacia Alto Chiquero, 29 Dec. 1995 (fl), *E. Montenegro 1215* (MO, STRI); Distrito de Boquette, Cerro Horqueta, 28 June 1984 (fr), *J. Pipoly 7064* (NY, PMA); near Cerro Pata de Macho, 7 Jan. 1983 (fl), *R. Schmalzel & D. Roubick 1334* (FTG, LL MO).

34. Ardisia crassiramea Standl., Publ. Field

Mus. Nat. Hist., Bot. Ser. 18: 887. 1938. *Auriculardisia crassiramea* (Standl.) Lundell, Phytologia 49: 343. 1981. TYPE: Costa Rica. Alajuela: Cerros de San Antonio de San Ramón, 1200–1245 m, 26 July 1927 (fl), *A. Brenes 5652 (244)* (holotype, F!, F neg. 68143!, LL neg. 1971-30!). Figure 36.

Ardisia solomonii Lundell, Phytologia 48: 135. 1981. Syn. nov. *Auriculardisia solomonii* (Lundell) Lundell, Wrightia 7: 245. 1983. TYPE: Costa Rica. Puntarenas: Monteverde, cloud forest at edge of Continental Divide and on Pacific side of slope, 10°20′N, 084°48′W, ca. 1300 m, 18 Aug. 1976 (fl), *J. Solomon 5392* (holotype, LL!, NY neg. 11078!, 11078A!; isotype, MO!).

Auriculardisia micrantha Lundell, Wrightia 7: 269. 1984. Syn. nov. Non *Ardisia micrantha* Kunth, Nov. Gen. Sp. 3: 246. 1818 [1819], non *Ardisia micrantha* Donn. Sm., Bot. Gaz. 14: 27. 1889, nom. illeg. *Ardisia dryeri* Lundell, Phytologia 61: 63. 1986, nom. inval. *Ardisia dryeri* Pipoly & Ricketson, Sida 18: 512. 1998. TYPE: Costa Rica. Alajuela, Puntarenas, or Guanacaste: Finca de Monteverde, Cordillera Tilarán, along the Window Path, Continental Divide, 1560–1580 m, 15 Aug. 1976 (fl), *V. Dryer 577* (holotype, MO!; isotype, F!, F neg. 68322!).

Auriculardisia spathulata Lundell, Phytologia 63: 75. 1987. Syn. nov. *Ardisia spathulata* (Lundell) Lundell, Phytologia 63: 463. 1987. TYPE: Costa Rica. Guanacaste: pasture adjoining main road, and Chomogo Trail above Monte Verde, Chomogo Trail near headwaters of Río Guacimal, 8 Jan. 1973 (fr), *D. Stone & A. Welden 3440* (holotype, DUKE!).

Shrubs or trees to 10 m tall, 8–15 cm diam. *Branchlets* straight, stout, angulate, longitudinally ridged, the petiole scars small, inconspicuous, 5–11 mm diam., with a mixture of densely cupuliform and furfuraceous-lepidote scales. *Leaves* with blades chartaceous, elliptic or oblanceolate, rarely obovate, 5.8–25.2 × 1.8–5.8 cm, apically acuminate, with an acumen 0.5–2 cm long, basally acute, decurrent on the petiole, inconspicuously punctate and punctate-lineate, essentially glabrous above, with a mixture of densely cupuliform and furfuraceous-lepidote scales, more densely so along the midrib, the midrib impressed above, prominently raised below, the secondary veins 17 to 23 pairs, prominulous above and below, the margins entire, flat; petiole slender, canaliculate, 0.5–3.5 cm long, essentially glabrous above, below with a mixture of densely cupuliform and furfuraceous-lepidote scales. *Inflorescences* erect, tripinnately paniculate, 9–28.5 × 6–22 cm, pyramidal, usually longer than the leaves, the peduncle, the rachis, secondary branches, and pedicels with a mixture of densely cupuliform and furfuraceous-lepidote scales, the branches loosely congested into 7- to 9-flowered corymbs; peduncles subobsolete to 1.5 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, oblong, 0.5–3.5 × 0.9–3 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 0.6–1.2 × 0.4–0.8 mm; pedicels stout, 2–4 mm long, inconspicuously punctate and punctate-lineate, with a mixture of densely cupuliform and furfuraceous-lepidote scales. *Flowers* 5-merous, white to red or purple after pollination (Pipoly, pers. obs.); calyx lobes membranous to chartaceous, ovate, 1–1.2 × 1.3–1.4 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 4.4–4.7 mm long, the tube 0.9–1 mm long, the lobes elliptic to ovate, 3.5–3.7 × 1.9–2.2 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 3.3–3.5 mm long, the filaments 1.6–1.7 mm long, the staminal tube 0.5–0.8 mm long, the apically free portions 0.9–1.1 mm long, the anthers lanceoloid, 2.1–2.4 × 0.6–0.8 mm, apically apiculate, basally cordate, the connective inconspicuously punctate; pistil 4.2–4.8 mm long, glabrous, the ovary oblong, 1–1.4 mm long, the style 3–3.6 mm long, inconspicuously punctate and punctate-lineate, the ovules 17 to 19. *Fruits* globose, 4.5–5.8 mm diam., prominently punctate and punctate-lineate.

Distribution. *Ardisia crassiramea* is known only from the Cordillera Guanacaste (Volcán Cacao) in Guanacaste, and from the Cordillera Tilarán in the vicinity of the Monteverde Biological Reserve, at the junction of Guanacaste, Alajuela, and Puntarenas, Costa Rica, growing at 1100 to 1700 m in elevation.

Ecology and conservation status. *Ardisia crassiramea* occurs on windy, exposed ridges in elfin and cloud forests, and on ridge tops in montane rain forests. Fieldwork by Pipoly has shown that the species occurs in light gaps and along forest margins. While it is locally common, and the areas in which it occurs are somewhat protected, the species should be considered threatened because of its very restricted distribution.

Etymology. The specific epithet was derived from the Latin, "crassi-" meaning thick and "ramea," for branch, referring to the thick inflorescence rachis.

Within *Ardisia* subg. *Auriculardisia* sect. *Pal-*

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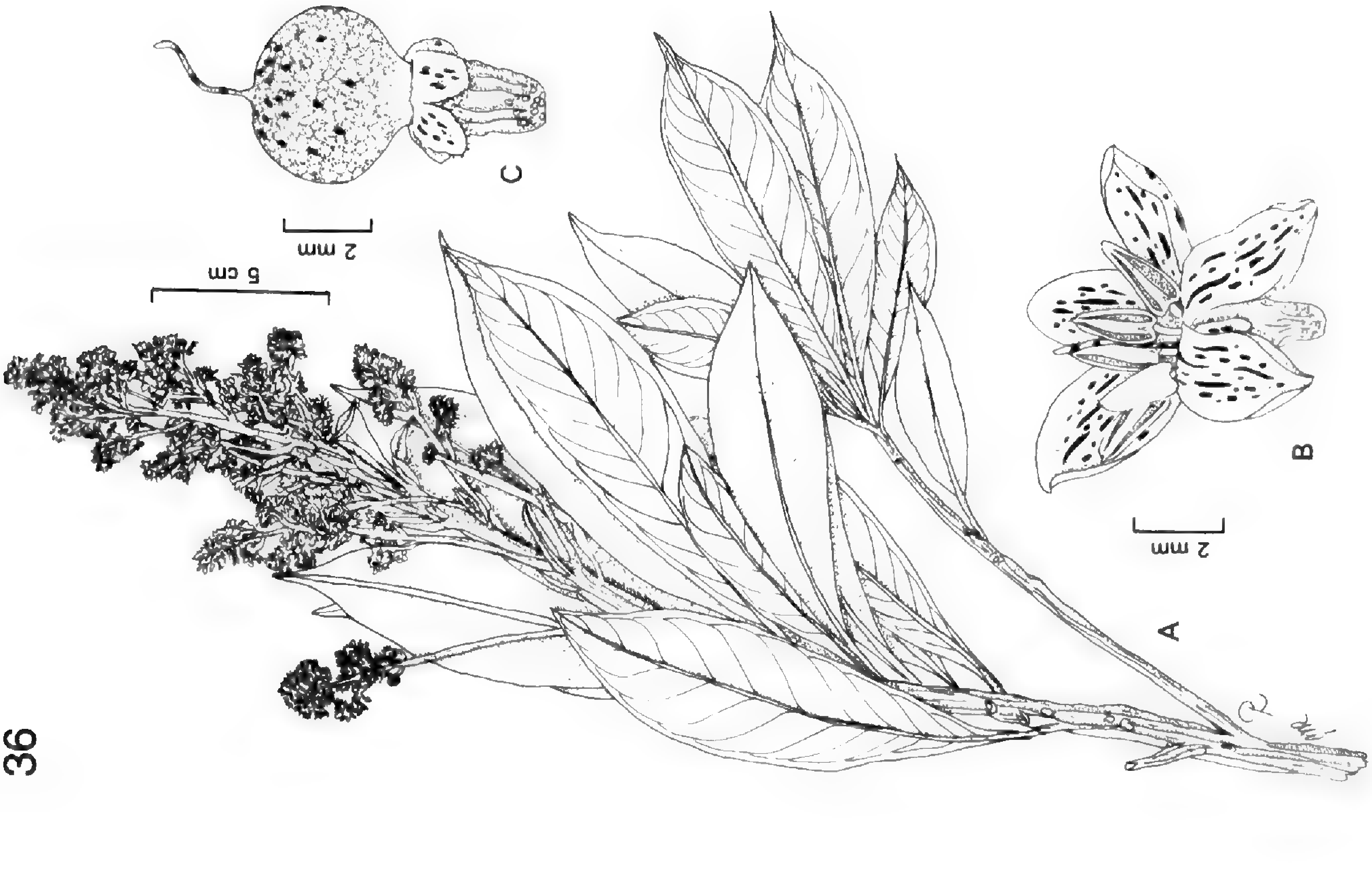

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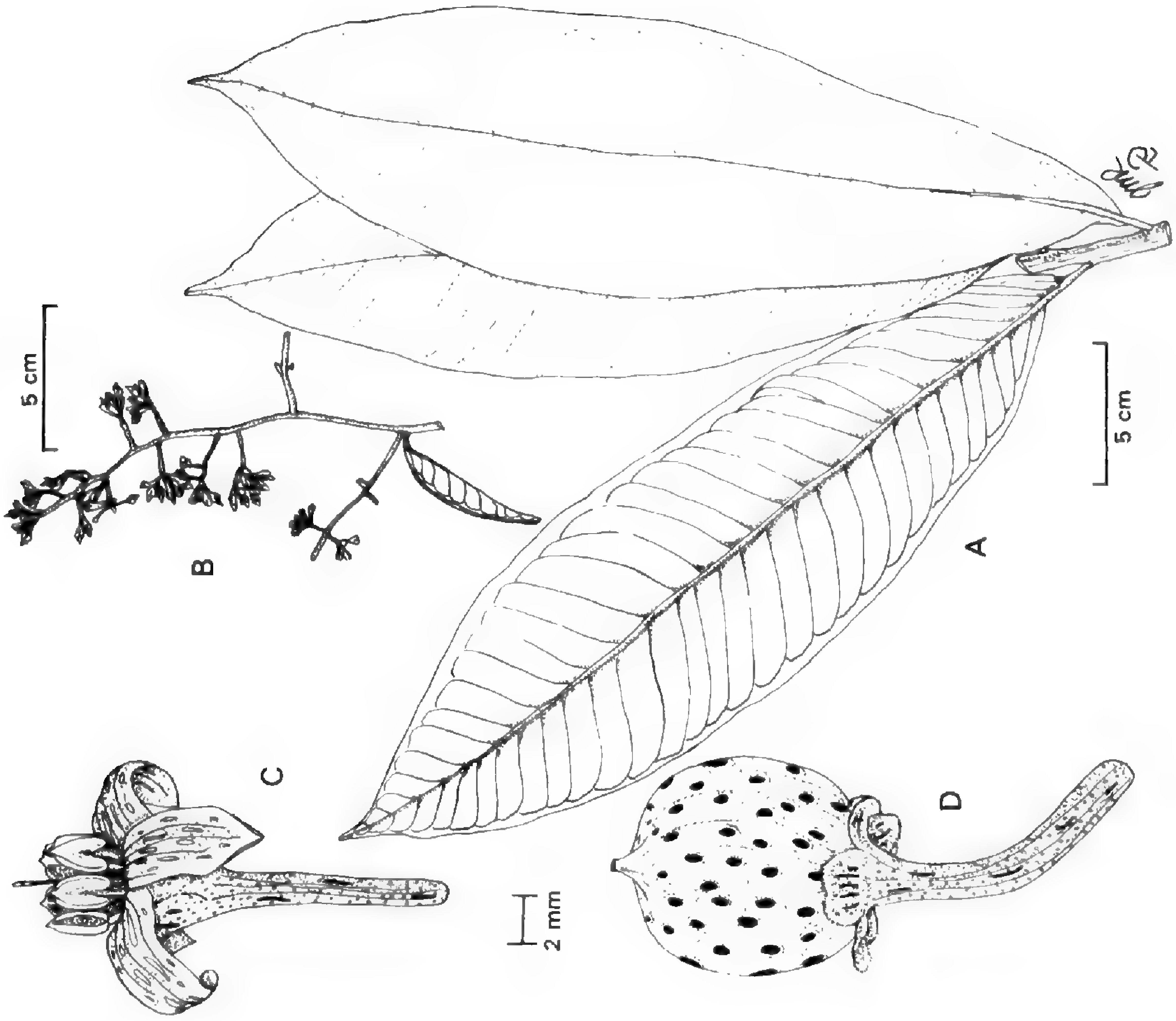

manae, Ardisia crassiramea is one of a number of species that have branchlets covered with a mixture of dense cupuliform and furfuraceous-lepidote scales. *Ardisia crassiramea* may be most easily confused with *A. conglomerata,* with their straight branchlets, elliptic to oblanceolate leaves, narrower calyx lobes to only 1.2 mm wide, and shorter corolla lobes to 3.7 mm long. However, the angulate branchlets with longitudinal ridges, inflorescences tripinnately paniculate and pyramidal, the ovate longer calyx lobes to 1.4 mm wide, the larger corolla lobes to 3.7 × 2.2 mm, and the larger anthers to 2.4 × 0.8 mm distinguish *A. crassiramea* from *A. conglomerata.*

The type of *Ardisia solomonii* was collected in bud, and evidently Lundell (1981a: 136) never compared it to the type of *A. crassiramea,* although he mentioned the "thick branchlets," which are also the basis of *A. crassiramea.* In fact, Lundell's discussion mentioned that *A. solomonii* may be related to the genus *Conomorpha* (= *Cybianthus*). However, the type of *A. solomonii* perfectly matches *A. crassiramea* in all respects.

The type of *Auriculardisia micrantha* is unique only in the more open inflorescences and slightly larger flowers with what Lundell (1984a: 269–270) described as "small dentate, densely punctate foliaceous bracts." However, our studies of the material show that the "dentate" bracts are simply an artifact of the drying process, and the bracts are actually entire. The slightly larger flowers and more open inflorescences in the type of *A. micrantha* occur because of the maturity of the specimen, compared to the inflorescences of the type of *Ardisia crassiramea,* which is congested because the flowers are mostly in bud.

The type of *Auriculardisia spathulata* was separated by the "distinctive spathulate leaves" (Lundell, 1987: 463). However, closer examination shows that the apices of the leaves are all deformed, which gave the appearance of wider apices. The populations represented by the types of *Ardisia crassiramea, A. solomonii, Auriculardisia micrantha,* and *A. spathulata* are all from the same area around the Reserva Biológica Bosque Nuboso Monteverde, and all are similar in appearance and share the same distinctive characters of the abaxial leaf and bract surfaces and inflorescence rachises. Field observations by Pipoly revealed that much of the variation seen among these populations arose from the variable conditions of Monteverde itself, for example, light exposure and shelter from the wind, as well as the relative age of the plants.

Specimens examined. COSTA RICA. **Alajuela**: La Palma de San Ramón, 8 Aug. 1924 (fl), *A. Brenes 4033 (451)* (F, NY); Cordillera Tilarán, Monteverde, Nebuloso and El Brillante Trails, 14 July 1984 (fl), *J. Pipoly 7094* (CR, MO, NY), *7096* (CR, F, NY). **Guanacaste**: Parque Nacional Guanacaste, Estación Cacao, 25 Nov. 1990 (fr), *R. Espinoza 66* (INB, MO); Cantón de Liberia, Parque Nacional Guanacaste, Cordillera Guanacaste, Volcán Cacao, 12 July 1996 (fr), *J. Morales et al. 5480* (FTG, INB, MO). **Puntarenas**: Monteverde, upper San Luís valley on Pacific slope, 20 Oct. 1985 (fl), *E. Bello C. 3083* (FTG, LL, MO); Cantón de Puntarenas, Cordillera Tilarán, San Luís, Cerro Banquete, trail to Surtubal, Monteverde, 22 Mar. 1994 (fl), *Z. Fuentes 701* (CR, FTG, INB, MO); Reserva Monteverde, 26 Aug. 1985 (fl), *W. Haber & E. Bello C. 2428* (MO); Reserva Biológica Monteverde, Brillante Trail, Continental Divide, 13 Mar. 1989 (fr), *W. Haber & W. Zuchowski 9128* (CR, FTG, INB, MO); Reserva Biológica Monteverde Road to divide, swamp on Continental Divide, Pantanoso and Chomogo Trails, 16 July 1990 (fr), *W. Haber & W. Zuchowski 10033* (CR, FTG, INB, MO); along the Chomogo trail, Monteverde Cloud Forest Reserve, 24 Aug. 1975 (fl), *G. Hartshorn 1780* (F, MO); ca. 2 km SE of Monteverde, Pacific watershed, 31 July 1986 (fl), *R. Lawton 1281* (F); Monteverde, 20 Mar. 1959 (fl), *C. Palmer 85* (NY); Monteverde, Chomogo Trail, Reserva Biológica, 8 Aug. 1975 (ster.), *L. Poveda A. 1118* (F, MO). **Border of Alajuela, Guanacaste, and Puntarenas**: Reserva Flora de Monteverde, Continental Divide, Brillante Trail, 14 Dec. 1976 (fr), *V. Dryer 1078* (F, MO). **Border between Alajuela and Puntarenas**: windswept ridge on Continental Divide, 2–5 km E and SE of Monteverde, 17–20 Mar. 1973 (fl), *W. Burger & J. Gentry 8704* (F); Monteverde Reserve, Cordillera Tilarán, Cerro Centinela, 19 Aug. 1984 (fl, fr), *M. Grayum & P. Sleeper 3847* (LL, MO); settlement at Monteverde in NE section of preserve, 5 May 1975 (fl), *J. Utley & K. Utley 2393* (F [2]).

Ardisia croatii Lundell, Wrightia 5: 281. 1976. *Auriculardisia croatii* (Lundell) Lundell, Phytologia 49: 343. 1981. TYPE: Panama. Veraguas: valley of Río Tercero Brazo beyond Escuela Agrícola, Alto Piedra above Santa Fé, along road, 29 Aug. 1974 (fl), *T. Croat 27327* (holotype, LL!; isotypes, MEXU!, MO!).

Shrubs or trees 2–20 m tall, 4.2–16 cm diam.

←

Figure 36 (left). *Ardisia crassiramea.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from holotype, *A. Brenes 5652 (244)* (F); B from *Z. Fuentes 701* (MO); C from *W. Haber & W. Zuchowski 10033* (MO).)

Figure 37 (right). *Ardisia croatii* subsp. *correae.* —A. Vegetative branch. —B. Flowering branch. —C. Flower. —D. Fruit. (A, B drawn from holotype (*A. dodsonii*), *C. Dodson et al. 8677* (MO); C from *W. Palacios et al. 13509* (MO); D from *J. Clark & D. Neill 231* (MO).)

Branchlets slender, terete, 3–6 mm diam., densely and minutely appressed rufous furfuraceous-lepidote. *Leaves* with blades membranous to chartaceous, oblong, elliptic, or rarely narrowly oblanceolate, 4.1–48.5 × 1.4–13.9 cm, apically acuminate, with an acumen 0.4–1.7 cm long, basally asymmetric, acute, decurrent on the petiole, prominently punctate and punctate-lineate, glabrous above, scattered rufous furfuraceous-lepidote below, densely so along the midrib, the midrib impressed above, prominently raised below, the secondary veins 18 to 63 pairs, impressed above, prominulous below, the margins entire, flat; petioles slender, canaliculate, 4–24 mm long, 1–3 mm diam., glabrous above, rufous furfuraceous-lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, 6.2–32.8 × 4.1–21.2 cm, pyramidal, usually longer than the leaves, the rachis, branchlets, abaxial bract surfaces, and petioles densely and minutely appressed rufous furfuraceous-lepidote, the branches loosely congested into 3- to 9-flowered corymbs; peduncles obsolete to 3.7 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, oblong, 5.5–23.5 × 2.5–8.2 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, rufous furfuraceous-lepidote below, the margins entire, flat; floral bracts similar to the inflorescence branch bracts, but 3.2–5.9 × 1.8–2.3 mm; pedicels slender, 8–16 mm long, inconspicuously punctate and punctate-lineate, rufous furfuraceous-lepidote. *Flowers* 5-merous, white, cream, pink to light purple; calyx lobes chartaceous to coriaceous, oblate, 2–2.9 × 2.5–3 mm, apically broadly rounded to truncate, inconspicuously punctate and punctate-lineate, glabrous adaxially, rufous furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla chartaceous, 6.7–8.1 mm long, the tube 1.6–3.1 mm long, the lobes ovate, 4.8–5.2 × 3–3.6 mm, apically acute, inconspicuously punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 4.7–6.5 mm long, the filaments 2.5–4.1 mm long, the staminal tube 0.9–1.2 mm long, the apically free portions 1.3–3 mm long, the anthers narrowly ovoid to lanceoloid, 3–3.4 × 1.4–1.7 mm, apically apiculate, basally deeply cordate, the connective conspicuously punctate; pistil 4.2–8.5 mm long, glabrous, the ovary oblong, 1.7–2 mm long, the style 2.5–7 mm long, inconspicuously punctate and punctate-lineate, the ovules 35 to 49. *Fruits* globose, 7.7–10.8 mm diam., prominently punctate and punctate-lineate.

Etymology. The species was named in honor of Thomas B. Croat, the P. A. Shulze Curator at the Missouri Botanical Garden.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia croatii* can be easily distinguished from *A. glandulosomarginata* by its large, oblate calyx lobes to 2.9 mm, with broadly rounded to truncate apices, tightly appressed rufous furfuraceous-lepidote scales on the branchlets, inflorescence parts, and pedicels, the secondary veins of the leaf blades impressed above and prominently raised below, the larger corollas to 8.1 mm long, and larger anthers to 3.4 × 1.7 mm. *Ardisia croatii* as here circumscribed includes one newly recognized subspecies.

35. Ardisia croatii subsp. **correae** (Lundell) Ricketson & Pipoly, comb. et stat. nov. *Ardisia correae* Lundell, Wrightia 6: 72. 1979. *Auricurdardisia correae* (Lundell) Lundell, Phytologia 49: 343. 1981. TYPE: Panama. Chiriquí: NE of Fortuna Dam camp, Hardwood, trail toward Finca Landau, 08°45′N, 082°15′W, 1000–1200 m, 24 Sep. 1976 (fl), *M. Correa A., R. Dressler, N. Salazar, J. Mediety, C. Garibaldi, F. Barnum & T. Bailees 2690* (holotype, MO!, F neg. 55681!; isotype, PMA!). Figure 37.

Ardisia dodsonii Lundell, Wrightia 6: 102. 1980. Syn. nov. *Auriculardisia dodsonii* (Lundell) Lundell, Phytologia 49: 343. 1981. TYPE: Ecuador. Los Ríos or Pichincha: path following ridge line at El Centinela at crest Montañas de Isla on road from Patricia Pilar to 24 de mayo at km 12, 600 m, 2 Oct. 1979 (fl), *C. Dodson, A. Gentry & G. Shoupp 8677* (holotype, MO!; isotype, SEL!).

Trees 2–20 m tall, 4.2–16 cm diam. *Branchlets* 4–6 mm diam. *Leaves* with blades 17.5–48.5 × 5.1–13.9 cm, with an acumen 0.9–1.7 cm long, the secondary veins 43 to 63 pairs; petioles 15–24 mm long, 2–3 mm diam. *Inflorescences* 19.4–32.8 × 8.3–21.2 cm, 5- to 9-flowered corymbs; pedicels 11–16 mm long. *Flowers* with calyx 2.6–2.8 × 2.7–2.9 mm; corolla 8–8.1 mm long, the tube 2.9–3.1 mm long, the lobes 5–5.2 × 3–3.2 mm; stamens 6.3–6.5 mm long, the filaments 3.9–4.1 mm long, the staminal tube 0.9–1.1 mm long, the apically free portions 2.8–3 mm long, the anthers 3.3–3.4 × 1.4–1.5 mm; pistil 8–8.5 mm long, the ovary 1.5–2.2 mm long, the style 5.8–7 mm long, the ovules 35 to 43. *Fruits* 8.2–10.8 mm diam.

Distribution. *Ardisia croatii* subsp. *correae* is known from three disjunct areas, from near the Fortuna Dam, Bocas del Toro, Panama, and in Ecuador, in Esmeraldas and Pichincha, growing at 400 to 1200 m in elevation.

Ecology and conservation status. *Ardisia croatii* subsp. *correae* is most frequently found in lower cloud forests and upper premontane forests. Because of its restricted distribution, it should be considered threatened.

Etymology. This subspecies was named in honor of Mireya D. Correa, curator of the Panamanian National Herbarium.

Within *Ardisia* subg. *Auricularadisia* sect. *Palmanae, Ardisia croatii* subsp. *correae* is separated from subspecies *croatii* by a series of quantitative characters, including its longer petioles to 24 mm long, longer calyx lobes 2.8 mm long, narrower corolla lobes to 3.2 mm wide, and longer anthers to 3.4 mm long. Despite the similarity between the subspecies in absolute altitudinal range, subspecies *correae* is found more often in cloud and, to a lesser extent, premontane or montane forests, while subspecies *croatii* is found more in elfin and, to a lesser extent, cloud forests.

The type of *Ardisia dodsonii* is unique only for its slightly longer calyx lobes and pedicels; otherwise it matches *Ardisia croatii* subsp. *correae* in all other aspects.

Specimens examined. PANAMA. **Bocas del Toro**: between Buena Vista Coffe Finca and Cerro Pilón, on Chiriquí Trail, 17 Apr. 1968 (fr), *J. Kirkbride & J. Duke 683* (MO, NY); 8.5 road mi. from bridge near Fortuna Dam on road towards Chiriquí Grande, 4.3 mi. N of Continental Divide, 10 Mar. 1985 (fr), *G. McPherson 6752* (FTG, LL, MO, PMA), *6753* (MO); along pipeline road in area of Fortuna Dam, near end of road, ca. 8 Mar. 1986 (fr), *G. McPherson 8706* (FTG, LL, MO, PMA). ECUADOR. **Esmeraldas**: Quinindé Cantón, Bilsa Biological Station, Maché Mountains, 35 km W of Quinindé, 5 km W of Santa Isabel, Dogala trail, 30 Oct. 1994 (fr), *J. Clark & D. Neill 231* (MO, QCNE); Invader trail, 14 Nov. 1994 (fr), *J. Clark et al. 236* (FTG, MO, QCNE), 20 Nov. 1995 (fr), *J. Clark et al. 1677* (FTG, MO, QCNE), (ster.), *J. Clark 2141* (FTG, MO, QCNE); Maché-Chindul Ecological Reserve, Bilsa Biological Station, Maché Mountains, 35 km W of Quinindé, 30 Mar. 1996 (fl), *J. Clark et al. 2375* (F, FTG, MO, NY, QCNE); montañas de Maché Chindúl, 35 km al E de Quinindé, Estáción Biológica Bilsa, Sendero Cueva–Río Cube, 6 June 1997 (fl), *T. Nuñez et al. 522* (MO, QCNE); carretera Herrera–El Páramo, Santa Isabel, Estación Biológica Bilsa, 18 Feb.–5 Mar. 1995 (fl), *W. Palacios et al. 13509* (MO, QCNE); Bilsa Biological Reserve, Montañas, Maché, 35 km W of Quinindé, 5 km W of Santa Isabela, along Dogala trail, 15 Nov. 1994 (fr), *N. Pitman & J. Clark 942* (FTG, MO [2]). **Pichincha**: Tinalandia, property of Hotel Tinalandia, 9.6 km E of Santo Domingo de los Colorados, S of hwy. to Aloag & Quito, above Río Toachi, 3 Apr. 1983 (fl), *T. Croat 55713* (MO).

36. Ardisia croatii subsp. croatii. Figure 38.

Ardisia retusa Lundell, Wrightia 6: 88. 1979. Syn. nov. *Auriculardisia retusa* (Lundell) Lundell, Phytologia 49: 345. 1981. TYPE: Panama. Veraguas: forested mountains W of Alto de Piedras, W of Santa Fé, 3200–5600 ft. [975–1707 m], 8 Sep. 1978 (fl), *B. Hammel 4599* (holotype, MO!, F neg. 55625!; isotype, LL!).

Shrubs or trees 2–12 m tall, to 10 cm diam. *Branchlets* 2–4.5 mm diam. *Leaves* with blades 4.1–25.2 × 1.4–6.7 cm, with an acumen 0.4–1.2 cm long, the secondary veins 18 to 33 pairs; petioles 4–13 mm long, 1–2 mm diam. *Inflorescences* 6.2–20.1 × 4.1–26.3 cm, 3- to 7-flowered corymbs; pedicels 8–14 mm long. *Flowers* with calyx 2–2.5 × 2.5–3 mm; corolla 6.7–6.9 mm long, the tube 1.6–2 mm long, the lobes 4.8–5.1 × 3.4–3.6 mm; stamens 4.7–5 mm long, the filaments 2.5–2.7 mm long, the staminal tube 1–1.2 mm long, the apically free portions 1.3–1.7 mm long, the anthers 3–3.1 × 1.5–1.7 mm; pistil 4.2–6 mm long, the ovary 1.7–1.8 mm long, the style 2.5–4.2 mm long, the ovules 43 to 49. *Fruits* 7.7–9 mm long.

Distribution. *Ardisia croatii* subsp. *croatii* is distributed in central Panama, in Coclé, Veraguas, and San Blas, growing from 400 to 1707 m in elevation.

Ecology and conservation status. *Ardisia croatii* subsp. *croatii* occurs in exposed areas of elfin and, rarely, premontane forests. Locally common in protected areas, we believe it is not threatened at this time.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia croatii* subsp. *croatii* is separated from subspecies *correae* by a series of quantitative characters, including its shorter petioles to 13 mm long, wider calyx lobes 3.6 mm long, shorter corolla lobes to 5.1 mm long, and shorter anthers to 1.7 mm long. See under subspecies *correae* for habitat comparison.

The type of *Ardisia retusa* is unique only for its rounded, somewhat retuse apex of the calyx lobes, and pedicels longer than the median for the species. Otherwise it matches *A. croatii* subsp. *croatii* in all respects.

Specimens examined. PANAMA. **Coclé**: El Potroso, summit of Mountain Mist forest, along mountain ridge, Alto Calvario, 1 Feb. 1977 (fr), *J. Folsom & L. Collins 1538* (MO); forest at base of Cerro Pilón above El Valle, 9 Jan. 1972 (fl), *A. Gentry 3649* (LL, MO, NY); sawmill above El Cope, along stream E of sawmill, Atlantic drainage, 27 July 1978 (fl), *B. Hammel 4142* (MO); near sawmill above El Cope, 25 Nov. 1978 (fl), *B. Hammel 5839* (LL, MO); foothills and summit of Cerro Caracoral, near La Mesa N of El Valle de Anton, 10 Sep. 1981 (LL, MO, NY); near El Valle de Anton, 26 Nov. 1985 (fl), *G. McPherson 7639* (FTG, LL, MEXU, MO, PMA); above El Potroso sawmill at Continental Divide, 24 Oct. 1980 (fl), *K. Sytsma 1774* (MO). **San Blas**: Cerro Obu, 25 June

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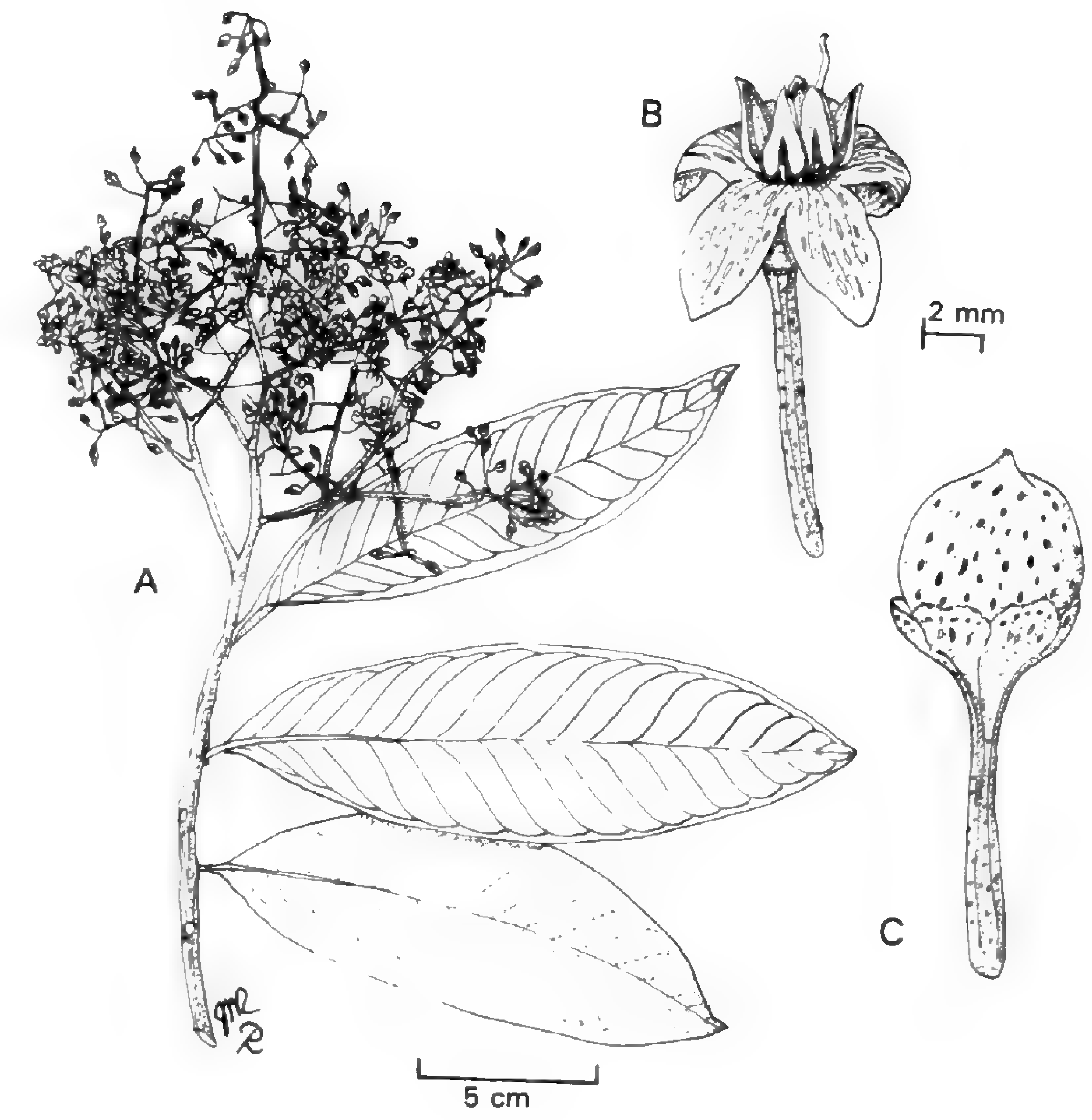

39

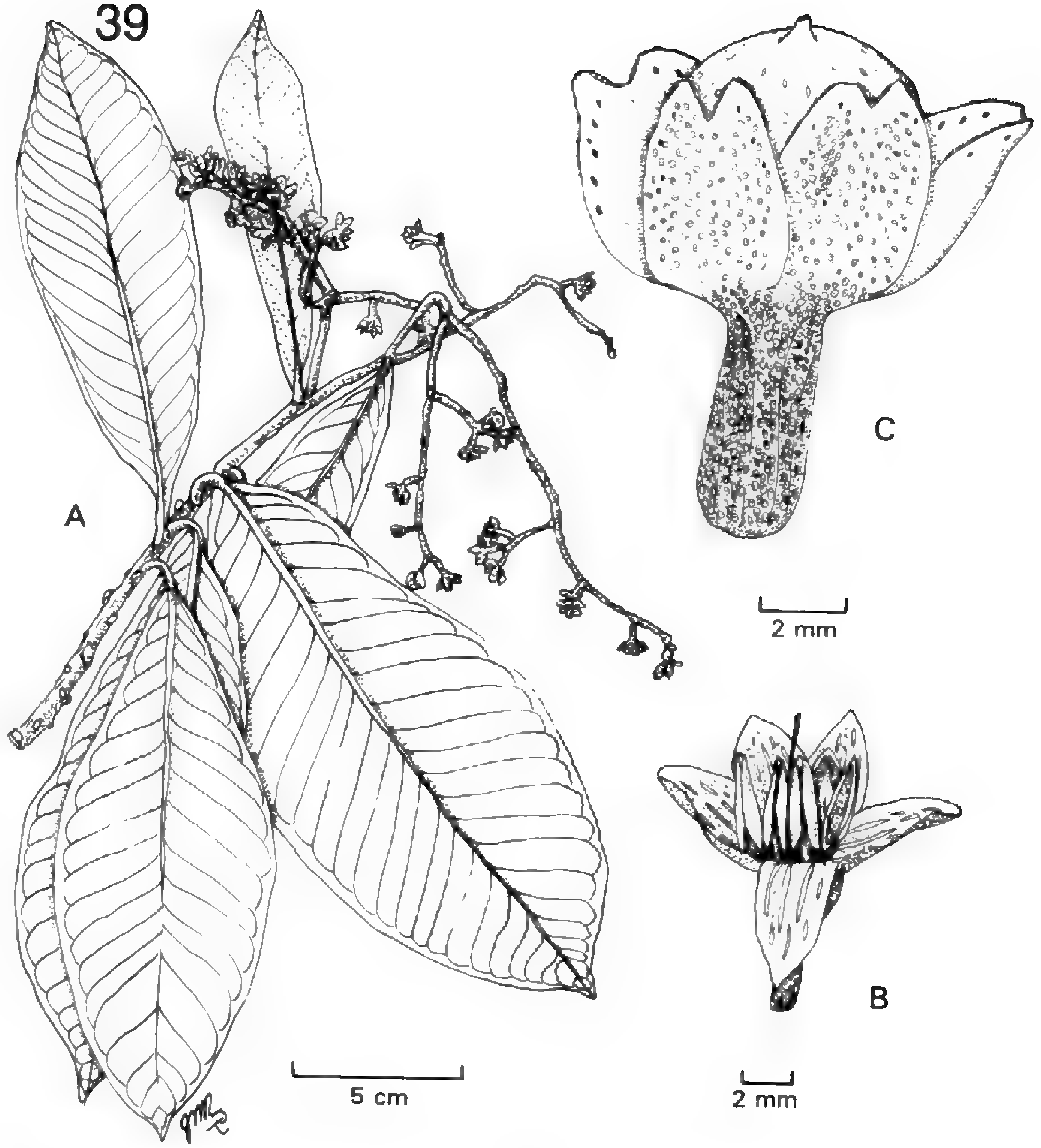

Figure 38 (left). *Ardisia croatii* subsp. *croatii.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from holotype, *T. Croat 27327* (LL); B from *T. Antonio 4025* (MO); C from *S. Knapp & K. Sytsma 2493* (MO).)

Figure 39 (right). *Ardisia darienensis.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from holotype, *M. Terry & R. Terry 1563* (F); B from *G. McPherson 14069* (MO); C from *J. Folsom et al. 6341* (MO).)

1986 (fl), *G. de Nevers et al. 8061* (CAS, LL, MO, US). **Veraguas**: Cerro Tute, trail past agricultural school near Santa Fé, 17 Sep. 1979 (fl), *T. Antonio 1849* (LL, MO, NY); vicinity Agriculture Station at Alto Piedra, near Santa Fé, trail to top of Cerro Tute, 6 Oct. 1979 (fl), *T. Antonio 1999* (LL, MO), 3 Apr. 1980 (fr), *T. Antonio 3985* (LL, MO), (fl), *T. Antonio 4025* (MO); beyond Río Tres Brazos, 9 km from Santa Fé, 24 July 1974 (fl), *T. Croat 25595* (CAS, LL, MO, NY); along road between Escuela Agrícola and Alto Piedra, above Santa Fé, and Río Dos Bocas ca. 5–8 km from Escuela, 26 July 1974 (fl), *T. Croat 25907* (LL (F neg. 55661), MO, NY); along dirt road between Santa Fé and Río San Luís, beyond Escuela Circlo Alto de Piedra, 5.9 mi. N of school, 28 June 1987 (fl), *T. Croat 66938* (FTG, LL, MO, PMA); trail on ridge to summit of Cerro Tute, Cordillera Tute, 1 km past Escuela Agrícola Altos de Piedras, W of Santa Fé, 15 Dec. 1981 (fr), *S. Knapp & K. Sytsma 2493* (LL, MO, NY); along trail to summit to Cerro Tute, ca. 3 km above Escuela Agricultura Alto Piedra near Santa Fé, 4 Jan. 1981 (fl), *K. Sytsma & T. Antonio 3011* (LL, MO), (fr), *K. Sytsma & T. Antonio 3015* (LL, MO).

37. Ardisia darienensis Lundell, Wrightia 4: 58. 1968. *Auriculardisia darienensis* (Lundell) Lundell, Phytologia 49: 343. 1981. TYPE: Panama. Darién: Dtto. de Chepigana, crest, Cana–Cuasi Trail, 5500 ft. [1676 m], 15 Mar. 1940 (fr), *M. Terry & R. Terry 1563* (holotype, F!, F neg. 68145!; isotypes, A!, MO!, LL neg. 1971-41!). Figure 39.

Shrubs or trees to 10 m tall, 14 cm diam. *Branchlets* slender, terete, 3.5–6.5 mm diam., densely and minutely appressed rufous furfuraceous-lepidote. *Leaves* with blades chartaceous, elliptic to obovate, 11.2–28.5 × 3.9–9.8 cm, apically subacuminate to acuminate, with an acumen 4–12 mm long, basally acute, decurrent on the petiole to the stem, inconspicuously punctate and punctate-lineate above and below, furfuraceous-lepidote above and below, the midrib impressed above, prominently raised below, the secondary veins 55 to 70 pairs, prominulous above and below, the margins entire, flat; petioles slender, marginate, 8–28 mm long, 2–3 mm diam., furfuraceous-lepidote above and below. *Inflorescences* erect, bipinnately paniculate, 8–20 × 4–14 cm, pyramidal, usually shorter than the leaves, the peduncle, rachis, branchlets, abaxial bract surfaces, and pedicels densely furfuraceous-lepidote, the branches loosely congested into 4- to 7-flowered corymbs; peduncles nearly obsolete to 2.8 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, ovate, 4.2–6.5 × 3.3–5.2 mm, apically acute, prominently punctate and punctate-lineate, the margins entire, hyaline; floral bracts similar to the inflorescence branch bracts, but 3.9–6.2 × 2.8–4.1 mm; pedicels stout, 4.2–4.8 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, white, cream, or yellow-green; calyx lobes chartaceous to coriaceous, ovate to almost oblong, 4.8–5 × 3.9–4.1 mm, apically acute to rounded, the subapical notch almost medial, so as to make the lobe apex appear emarginate, conspicuously punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla chartaceous and coriaceous, 9.1–9.4 mm long, the tube 3.8–4 mm long, the lobes narrowly ovate, 5.4–5.6 × 2.6–2.9 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 7.3–7.5 mm long, the filaments 4.2–4.4 mm long, the staminal tube 2–2.2 mm long, the apically free portions 2.2–2.4 mm long, the anthers lanceoloid, 3.4–3.6 × 1.2–1.4 mm, apically apiculate, basally lobate, the connective conspicuously punctate; pistil 7.8–8.1 mm long, glabrous, the ovary oblong, 1.5–1.7 mm long, the style 5.9–6.4 mm long, inconspicuously punctate and punctate-lineate, the ovules 15 to 18. *Fruits* globose, 7.2–8.4 mm diam., inconspicuously punctate and punctate-lineate.

Distribution. *Ardisia darienensis* is endemic to Darién and San Blas, Panama, growing from 610 to 1981 m in elevation.

Ecology and conservation status. *Ardisia darienensis* is a common understory tree in cloud and elfin forests, on steep slopes and ridges. Because of its restricted distribution, it should be considered threatened.

Etymology. The specific epithet referred to the locality in the Darién where the type was collected.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia darienensis* is most similar to *A. generalensis* due to its elliptic or obovate leaf blades, bipinnate panicles, and densely corymbose flowers. However, it is easily separated by the longer and thicker marginate petioles to 28 × 3 mm, chartaceous leaves with more numerous secondary veins to 70 pairs, and the apically emarginate calyx lobes.

Specimens examined. PANAMA. **Darién**: Cerro Pirré, 11 Apr. 1967 (fr), *N. Bristan 593* (MO); on Cerro Pirré, 14 Dec. 1962 (fr), *J. Duke 6561* (LL, MO); Cerro Pirré, 9–10 Aug. 1967 (fl), *J. Duke & T. Elias 13750* (GH, LL, MO, US); ridge top area N of Cerro Pirré, between Cerro Pirré and Rancho Plástico, 14 Nov. 1977 (fr), *J. Folsom et al. 6341* (LL, MO); Cana–Altos de Nique, trail on ridge between Río Setegantí and Río Alto Tuira, trail to Paletón, SE of goldmine camp and airstrip, 19 Apr. 1992 (fr), *R. Foster 14148* (MO, PMA); SW ridge leading to Alturas de Nique on the Colombian border, 28 Dec. 1980 (fr), *R.*

Hartman 12337 (LL [2], MO); Cuasi–Cana Trail between Cerro campamento and La Escalera to "páramo," E of Tres Bocas, 30 Apr. 1968 (fr), *J. Kirkbride & J. Duke 1279* (F, FTG, MO, NY); on ridge of Cerro Pirré, 14 Sep. 1989 (fl), *G. McPherson 14069* (FTG, MO); Cana and vicinity, 17 Apr.–8 June 1908 (fr), *R. Williams 833* (NY). **San Blas:** Cerro Obu, 25 June 1986 (fl), *G. de Nevers et al. 8077* (LL, MO).

38. Ardisia dukei Lundell, Wrightia 4: 45. 1968. *Icacorea dukei* (Lundell) Lundell, Phytologia 49: 348. 1981. *Auriculardisia dukei* (Lundell) Lundell, Wrightia 7: 267. 1984. TYPE: Panama. Darién: peak between Río Bales & Río Aretí at their confluence, ca. 300 ft. [91 m], 13 Sep. 1966 (fl), *J. Duke 8741* (holotype, MO!; isotypes, LL!, US!). Figure 40.

Trees with height unknown, 10–10.5 cm diam. *Branchlets* slender, terete, 4–6 mm diam., with densely furfuraceous-lepidote and cupuliform scales. *Leaves* with blades membranous, elliptic to widely obovate, 20.9–31.9 × 8.1–11.4 cm, apically acuminate, with an acumen 7–14 mm long, basally cuneate, decurrent on the petiole, inconspicuously punctate above and below, furfuraceous-lepidote above, with a mixture of furfuraceous-lepidote and cupuliform scales below, the midrib impressed above, prominently raised below, the secondary veins 60 to 68 pairs, prominulous above and below, the margins entire, flat or inrolled; petioles slender, marginate, 9–21 mm long, furfuraceous-lepidote above and below. *Inflorescences* erect, bi- to tripinnately paniculate, 27.8–28.9 × 12–21 cm, pyramidal, longer than the leaves, furfuraceous-lepidote, the branches loosely congested into 5- to 8-flowered corymbs; peduncles obsolete; inflorescence bracts unknown; inflorescence branch bracts unknown; floral bracts usually persistent, membranous, ovate, 0.9–1.1 × 0.7–0.9 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels slender, 0.9–1.5 mm long, inconspicuously punctate and punctate-lineate, indument as in the branchlets. *Flowers* 5-merous, cream; calyx lobes membranous to chartaceous, ovate, 0.9–1.1 × 1.1–1.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla and stamens unknown; pistil in young fruit 3.2–5.0 mm diam., glabrous, the ovary in young fruit globose, 1.2–2 mm long, the styles in young fruit 1–3 mm long, prominently punctate, the ovules (according to Lundell, 1968) 22 to 24. *Fruits* unknown.

Distribution. *Ardisia dukei* is endemic to a small peak in Darién, Panama, and was collected at ca. 91 m in elevation.

Ecology and conservation status. This species is known from one of the most remote but highly exploited areas of the Darién, so its rarity is probably a reality and not a collecting artifact. Therefore, we expect that the species is at least threatened if not in danger of extinction.

Etymology. This species was named in honor of James A. Duke, ethnobotanist and colleague, who has dedicated his life to the understanding of economic and medicinal tropical plants around the world.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia dukei* is most similar to *A. anchicayana* and *A. palmana* because of its short calyx lobes that are wider than long, membranous to chartaceous leaf blades, and short pedicels. However, *Ardisia dukei* may be separated from both *A. anchicayana* and *A. palmana* by the shorter calyx lobes to 1.1 × 1.3 mm, and shorter styles to 3 mm long.

39. Ardisia dunlapiana P. H. Allen, Rain Forests Golfo Dulce 409. 1956. *Auriculardisia dunlapiana* (P. H. Allen) Lundell, Phytologia 49: 343. 1981. TYPE: Costa Rica. Puntarenas: Cantón de Osa, vicinity of Esquinas Experiment Station, sea level, 16 Apr. 1949 (fl), *P. Allen 5274* (holotype, US!, LL neg. 1971-48!; isotypes, F!, F neg. 68148!, MO!, NY!, US!). Figure 41.

Shrubs or trees 2–20 m tall, 8–40 cm diam. *Branchlets* slender, terete, 3–5 mm diam., densely and minutely appressed furfuraceous-lepidote. *Leaves* with blades membranous, elliptic, 7.5–18.6 × 3.1–5.6 cm, apically acuminate, with an acumen 6–21 mm long, basally acute, decurrent on the petiole, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 23 to 31 pairs, prominulous above and below, the margins entire, flat; petiole slender, marginate, 8–13 mm long, 1–2 mm diam., glabrous above, rufous furfuraceous-lepidote below. *Inflorescences* erect, bipinnately paniculate, 7–31 × 3–15 cm, pyramidal, usually longer than the leaves, the rachis, branchlets, abaxial bract surfaces, and pedicels densely and minutely appressed rufous furfuraceous-lepidote, the branches loosely congested into 5- to 12-flowered corymbs; peduncles nearly obsolete to 3.2 cm long, the lower branches subtended by leaves; inflorescence bracts unknown;

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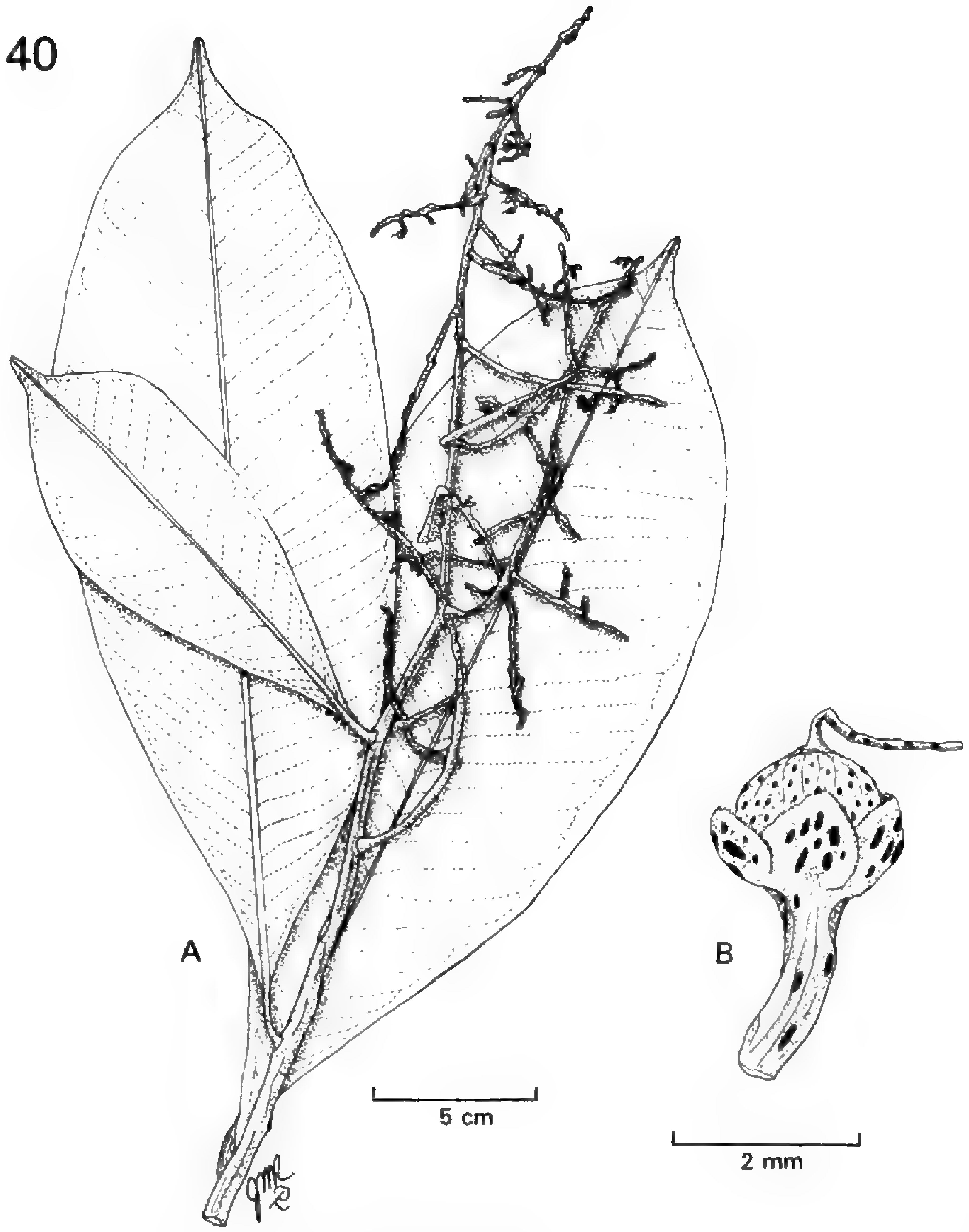

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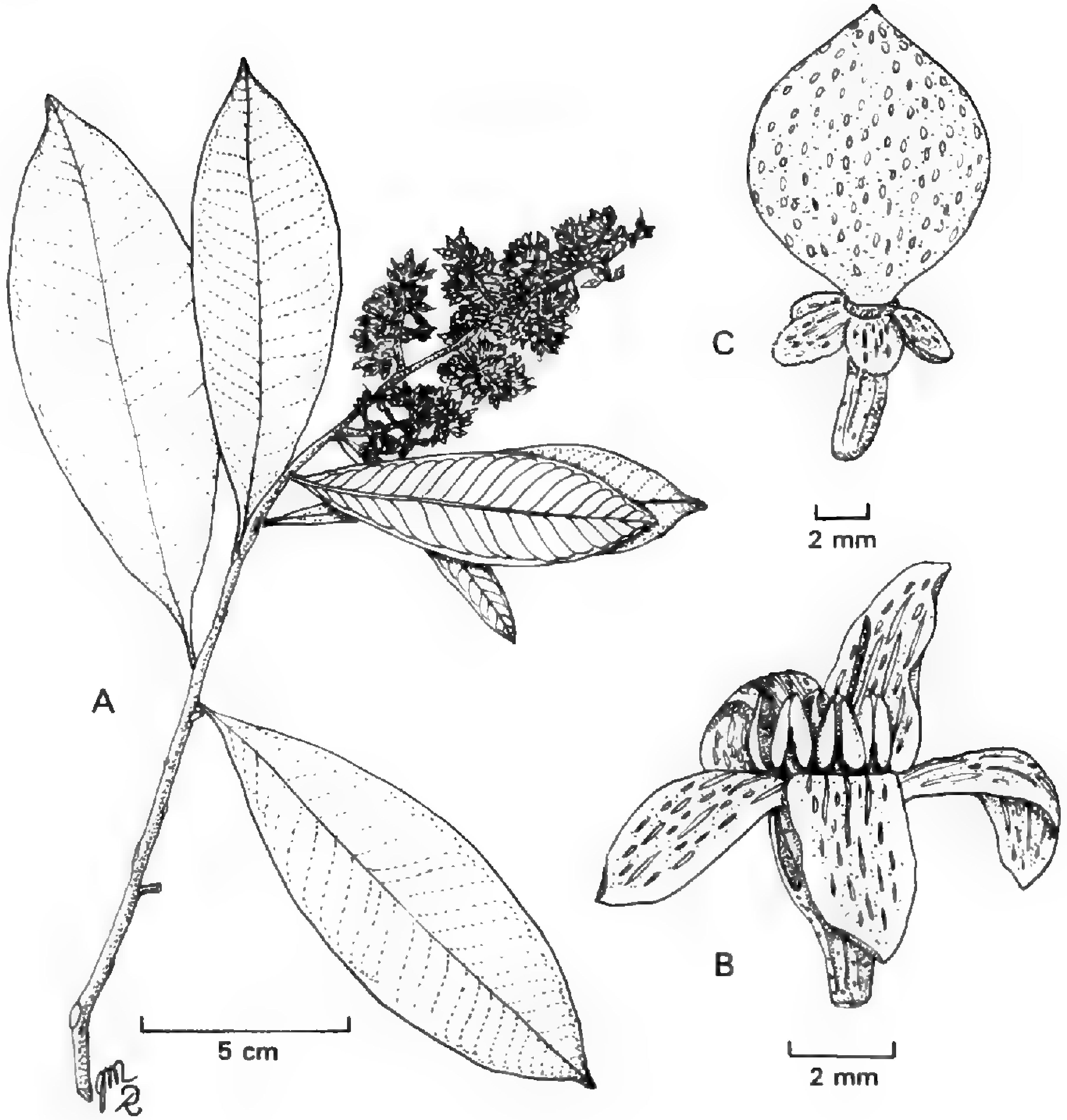

Figure 40 (left). *Ardisia dukei.* —A. Flowering branch. —B. Immature fruit. (A, B drawn from holotype, *J. Duke 8741* (MO).)

Figure 41 (right). *Ardisia dunlapiana.* —A. Flowering branch. —B. Flower. —C. Fruit. (A, B drawn from isotype, *P. Allen 5274* (MO); C from *K. Thomsen 1056* (MO).)

inflorescence branch bracts similar to the leaf blades, but elliptic to oblanceolate, 1.8–5.4 × 0.5–2.4 cm, the secondary veins 13 to 25 pairs; inflorescence branch bract petioles similar to the leaf blade petioles, but nearly obsolete to 12 mm long; floral bracts caducous, membranous, ovate, 1–1.4 × 1–1.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels slender, 1.5–3.5 mm long, inconspicuously punctate and punctate-lineate. *Flowers* 5-merous, white or light pink; calyx lobes chartaceous, orbicular, 2.2–3 × 2.2–3 mm, apically rounded, prominently pellucid to orange punctate and punctate-lineate, scattered furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 5.4–7.1 mm long, the tube 1.5–2.2 mm long, sparsely furfuraceous-lepidote abaxially, glabrous adaxially, the lobes narrowly ovate, 4.2–4.7 × 2–2.5 mm, apically acute, prominently orange punctate and punctate-lineate, completely glabrous, the margins entire, hyaline; stamens 4.2–5 mm long, the filaments 2.5–3.4 mm long, the staminal tube 1–1.2 mm long, the apically free portions 1.5–2.2 mm long, the anthers ovoid to oblongoid, 2.2–2.7 × 1.1–2.1 mm, apically apiculate, basally deeply cordate, the connective conspicuously punctate; pistil 5.2–5.8 mm long, glabrous, the ovary ovoid, 1.1–1.2 mm long, the style 4.4–4.7 mm long, inconspicuously punctate, the ovules 31 to 36. *Fruits* globose, 8–11 mm diam., prominently punctate and punctate-lineate.

Distribution. *Ardisia dunlapiana* is endemic to the Osa Península, Puntarenas, Costa Rica, growing from sea level to 900 m in elevation.

Ecology and conservation status. *Ardisia dunlapiana* occurs along water courses in lowland wet forests. Because it thrives in medium light exposure conditions, it is resilient enough to stand some intervention, and is locally common in some areas. Given that it occurs in several reserve areas, we believe this species is not threatened.

Etymology. This species was named in honor of Albert Atkinson Dunlap, a mycologist.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia dunlapiana* is most closely related to *A. awarum* but differs by its leaf blades membranous, calyx chartaceous, corolla membranous with its tube sparsely furfuraceous-lepidote outside, longer anthers to 2.7 mm long, and longer styles to 4.7 mm long.

Specimens examined. COSTA RICA. **Puntarenas**: Forestal Golfo Dulce, Rancho Quemado, 17 Oct. 1991 (fr), *R. Aguilar 565* (CR, INB, MO); Cantón de Golfito, Coastal Mt. Range, Fila Cruces, headwaters of Río Piedras Blancas, 12 May 1994 (fl), *R. Aguilar & F. Quesada 3265* (CR, FTG, INB, MO); Reserva Forestal Golfo Dulce, Osa Península, Rancho Quemado, ca. 15 km W of Rincón, along Río Riyito, 2 June 1988 (fl), *B. Hammel et al. 16974* (CR, F, FTG, LL, MEXU, MO, NY, US); Cantón de Golfito, Reserva Forestal Golfo Dulce, Osa Península, Playa Campanario or San Josecito, Sierpe, 20 June 1991 (fl), *P. Harmon 242* (INB, MO); Parque Nacional Corcovado, Pavo Forest, 14 July 1988 (fl), *C. Kernan 695* (CR, FTG, MO, US); Parque Nacional Corcovado Sirena, Los Patos Forest, 8 July 1989 (fl), *C. Kernan 1216* (CR, FTG, MO); Cantón de Golfito, Rancho Quemado, forestry station, Eloy Cubero Farm, 8 Aug. 1991 (fr), *J. Marín 107* (CR, MO); near airport area, 4 mi. W of Rincón de Osa, 8 Aug. 1967 (fl), *P. Raven 21643* (G, MO); Parque Nacional Corcovado, S. Esquinas Golfito, Golfo Dulce ca. Río Esquinas, Estación Esquinas, 27 June 1993 (fl), *M. Segura & F. Quesada 93* (FTG, INB, MO); Cantón de Golfito Parque Nacional Corcovado, Valle de Coto Colorado, Estación Esquinas, Sección Esquinas, 25 Aug. 1993 (fl), *M. Segura & F. Quesada 148* (FTG, INB, MO); Cantón de Golfito Parque Nacional Corcovado, Valle de Coto Colorado, near Estación Esquinas, 8 Oct. 1993 (fr), *M. Segura & F. Quesada 189* (INB, MO); Osa Peninsula, Aguabuena, 3.5 km W of Rincón, at trail N of the house of Don Quecho, W of BOSCOSA station, 21 June 1993 (fl), *K. Thomsen 399* (C, FTG), 6 Oct. 1994 (fr), *K. Thomsen 1056* (C, MO).

40. Ardisia dwyeri Lundell, Wrightia 4: 145. 1970. *Auricurlardisia dwyeri* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Panama. Panamá: Cerro Jefe, roadside thicket, 2900 ft. [884 m], 20 Aug. 1967 (fl), *J. Dwyer & S. Hayden 8082* (holotype, LL!, F neg. 55651!, LL neg. 71-167!; isotypes, GH!, MO!, US!). Figure 42.

Ardisia conglobata Lundell, Wrightia 6: 70. 1979. Syn. nov. *Auriculardisia conglobata* (Lundell) Lundell, Phytologia 49: 343. 1981. TYPE: Panama. Panamá: El Llano–Cartí Road, 9.8 km from Inter-American Highway, 1100–1200 ft. [335–366 m], 28 Dec. 1974 (fl), *S. Mori, J. Kallunki & B. Hansen 4172* (holotype, LL!, F neg. 55621!; isotype, MO!).

Shrubs or small trees 1.5–8 m tall, 6–10 cm diam. *Branchlets* slender, terete, 4–5 mm diam., densely furfuraceous-lepidote. *Leaves* with blades coriaceous, elliptic, 4–15.4 × 1.1–5.7 cm, apically acute to acuminate, with an acumen 3–6 mm long, basally cuneate, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above, densely to sparsely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 24 to 32 pairs, indistinct to prominulous above and below, the margins entire, flat; petioles slender, marginate, 5–10 mm long, glabrous above, densely to sparsely furfuraceous-lepidote below. *Inflorescences* erect, pinnately to bipinnately paniculate, 4–9 × 2.5–5

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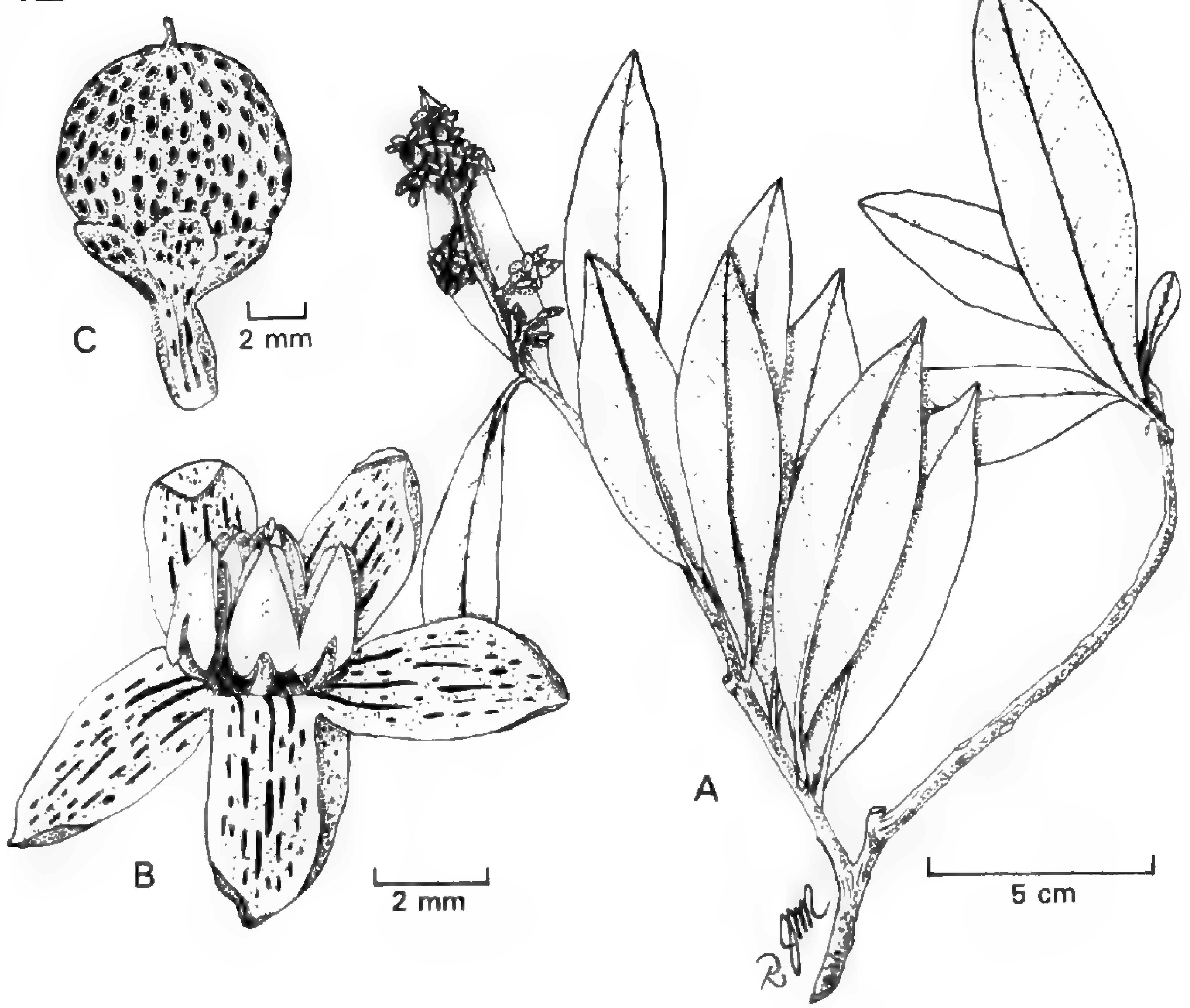

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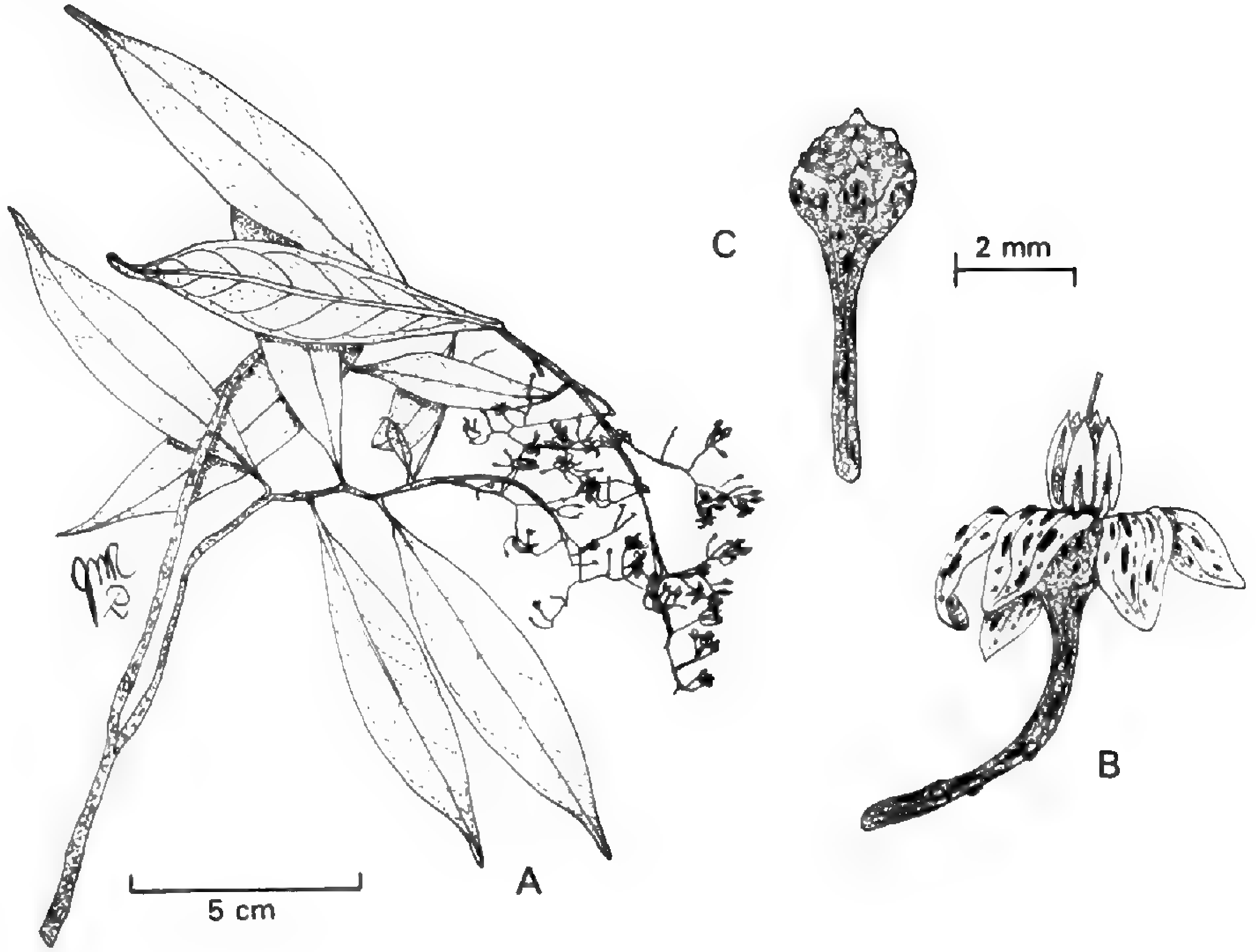

Figure 42 (left). *Ardisia dwyeri.* —A. Flowering branch. —B. Flower. —C. Fruit. (A, B drawn from holotype, *J. Dwyer & S. Hayden 8082* (LL); C from *G. Sullivan 201* (MO).)

Figure 43 (right). *Ardisia eucuneata.* —A. Flowering branch. —B. Flower. —C. Immature fruit. (A–C drawn from isotype, *G. de Nevers & C. de León 3598* (MO).)

cm, pyramidal, usually shorter than or as long as the leaves, densely cupuliform and furfuraceous-lepidote, the branches loosely congested into 5- to 11-flowered corymbs; peduncle 1–1.8 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, often foliaceous, oblong, 1.2–5.7 × 4.9–10.4 mm, apically acute, inconspicuously punctate and punctate-lineate, glabrous above, densely furfuraceous-lepidote below, the midvein inconspicuous or impressed above, prominently raised below, the secondary veins indistinct, the margins entire, flat; floral bracts caducous, membranous, ovate, 2–5.7 × 2.4–3.1 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels stout, 4–5 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, intense white, light pink to purple; calyx lobes coriaceous, oblate, 1.1–1.5 × 2.8–3.2 mm, apically rounded, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla chartaceous, 6.3–7.5 mm long, the tube 1.3–1.5 mm long, the lobes ovate, 5–6 × 2.3–3.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote on the tube and medially abaxially, the margins entire, hyaline; stamens 5–6 mm long, the filaments 2.5–3 mm long, the staminal tube 0.8–1.5 mm long, the apically free portions 1.5–1.8 mm long, the anthers lanceoloid, 3.2–4.2 × 1.2–1.4 mm, apically apiculate-cuspidate, basally cordate, the connective conspicuously punctate; pistil 5.8–6 mm long, glabrous, the ovary globose to oblong, 0.9–1 mm long, prominently punctate, the style 4.9–5 mm long, conspicuously punctate, the ovules 24 to 27. *Fruits* globose, 8–9.8 mm diam., prominently punctate.

Distribution. *Ardisia dwyeri* is most common on Cerro Jefe and along the El-Llano–Cartí Road, in Panamá, but also has a disjunct population along the Santa Rita Ridge in Colón, Panama, growing from 335 to 1007 m in elevation.

Ecology and conservation status. *Ardisia dwyeri* occurs in roadside thickets and premontane and cloud forests. Because of its restricted distribution it should be considered threatened.

Etymology. This species was named in honor of John Dwyer, curator at the Missouri Botanical Garden and author of the Rubiaceae in the *Flora of Panama.*

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia dwyeri* is most closely related to *A. vesca* because of its short calyx lobes, long pedicels, thin branchlets, wide corolla lobes, and long anthers. However, *Ardisia dwyeri* can be separated from *A. vesca* by its coriaceous leaf blades, shorter pedicels to 5 mm long, coriaceous much wider calyx lobes to 3.2 mm wide with rounded apices, chartaceous, longer and wider corolla lobes to 6 × 3.3 mm, longer and wider anthers to 4.2 × 1.4 mm, longer styles to 5 mm long, and larger fruits to 9.8 mm in diameter.

The type of *Ardisia conglobata* is unique only for its small axillary inflorescence of congested flower heads, but because it is in bud, this is not significant. In all other respects it matches the type of *A. dwyeri.*

Specimens examined. PANAMA. **Colón**: Santa Rita Ridge, 8 mi. E of Transisthmus Hwy., 28 July 1968 (fl), *J. Dwyer et al. 8999* (FTG [2], MO, NY). **Panamá**: Cerro Jefe, slopes beyond radio tower, 3 Nov. 1985 (fl, fr), *G. McPherson 7425* (LL, MO); El Llano–Cartí Road, 10 km from InterAmerican Hwy., 4 Oct. 1974 (fl, fr), *S. Mori & J. Kallunki 2245* (LL, MO); Dtto. Panamá, Cerro Jefe, 19 June 1984 (fl), *J. Pipoly & R. Bethancourt 7043* (MO, NY, PMA), 10 July 1976 (fr), *G. Sullivan 201* (MO).

41. Ardisia eucuneata (Lundell) Pipoly & Ricketson, Sida 18: 512. 1998. *Auriculardisia eucuneata* Lundell, Phytologia 57: 449. 1985. *Ardisia eucuneata* (Lundell) Lundell, Phytologia 61: 63. 1987, nom. inval. TYPE: Panama. San Blas: Nusagandi, trail from camp NW to a quebrada, 09°19′N, 078°15′W, 300 m, 31 July 1984 (fl), *G. de Nevers & C. de León 3598* (holotype, LL!; isotype, MO!). Figure 43.

Shrubs 2–2.5 m tall. *Branchlets* slender, terete, 2–3 mm diam., densely rufous furfuraceous-lepidote, glabrescent. *Leaves* with blades membranous, oblong to narrowly oblong to narrowly oblanceolate, 4.1–12.4 × 0.9–3.1 cm, apically long acuminate to caudate, with an acumen 10–18 mm long, basally cuneate, decurrent on the petiole, prominently punctate and punctate-lineate above and below, mostly glabrous above, densely rufous furfuraceous-lepidote, the midrib impressed above, prominently raised below, the secondary veins 15 to 21 pairs, prominulous above and below, the margins entire, flat; petioles slender, canaliculate, 4–7 mm long, glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bipinnately paniculate, 3–9 × 2–6 cm, pyramidal, shorter than the leaves, the peduncle, branches, and pedicels densely furfuraceous-lepidote, the branches loosely congested into 3- to 7-flowered corymbs; peduncle obsolete to 8 mm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, oblong, 1.5–2.4 × 0.4–0.6 mm, apically acute, glabrous adaxially, furfuraceous-lepidote, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 0.4–0.7 × 0.2–0.3 mm; pedicels slender, 3.6–4.8 mm long, prominently punctate and punctate-lineate, mixed cupuliform and furfuraceous-lepidote. *Flowers* 5-merous, light pink or purple; calyx lobes membranous, ovate to narrowly ovate, 1.4–1.6 × 0.8–1 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 3.5–3.6 mm long, the tube 0.5–1 mm long, the lobes narrowly ovate, 2.4–3.1 × 1.7–1.8 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins entire, hyaline; stamens 2.8–2.9 mm long, the filaments 1.3–1.6 mm long, the staminal tube 0.4–0.6 mm long, the apically free portions 0.9–1.2 mm long, the anthers narrowly ovoid, 1.6–1.7 × 0.6–0.7 mm, apically apiculate-cuspidate, basally cordate, the connective conspicuously punctate; pistil 4.2–4.3 mm long, glabrous, the ovary ovoid, 1–1.1 mm long, the style 3.1–3.3 mm long, epunctate, the ovules 7 to 9. *Fruits* unknown.

Distribution. *Ardisia eucuneata* is endemic to the Nusagandi area in San Blas, Panama, growing at 300 to 400 m in elevation.

Ecology and conservation status. *Ardisia eucuneata* occurs in river flood plains. Because of its restricted distribution, it should be considered threatened.

Etymology. The specific epithet was derived from the Greek "eu" meaning well, good, thoroughly, completely, or truly and "-cuneate" referring to the cuneate leaf bases.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia eucuneata* is most easily confused with *A. atropurpurea* (see under that species for similarities). However, *Ardisia eucuneata* is easily distinguished by its branchlets to 3 mm in diameter, pedicels to 4.8 mm long, corolla lobes to 3.1 × 1.8 mm, anthers to 1.7 × 0.7 mm, and the styles to 3.3 mm long.

Specimens examined. PANAMA. **San Blas:** Nusagandi, Wedar Trail, 19 July 1986 (fl), *J. McDonagh et al. 188* (LL, MO).

42. Ardisia fimbrillifera Lundell, Wrightia 4: 180. 1971. *Auriculardisia fimbrillifera* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Costa Rica. Heredia: Tirimbina, 700 ft. [213 m], 2 June 1971 (fl, fr), *G. Proctor 32238* (holotype, LL!, F neg. 55663!; isotypes, F!, LL!). Figure 44.

Trees 3–25 m tall, 4.2–30 cm diam. *Branchlets* slender, terete, 4.5–7.5 mm diam., densely furfuraceous-lepidote. *Leaves* with blades coriaceous, oblong elliptic to oblanceolate, 17.2–34.8 × 4–9.3 cm, apically acuminate, with an acumen 6–21 mm long, basally acute, decurrent on the petiole, inconspicuously punctate and punctate-lineate above, prominently punctate and punctate-lineate below, sparsely furfuraceous-lepidote above, densely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 33 to 45 pairs, inconspicuously raised above and below, the margins entire, inrolled; petioles slender, marginate, 6–15 mm long, 2–3 mm diam., sparsely furfuraceous-lepidote above, densely furfuraceous-lepidote below. *Inflorescences* erect, tripinnately paniculate, 11–37 × 7–27 cm, pyramidal, usually longer than the leaves, the rachis, branchlets, abaxial bract surfaces, and pedicels furfuraceous-lepidote; the branches congested to loosely congested into 5- to 11-flowered corymbs; peduncles 1.6–3.9 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts unknown; floral bracts caducous, membranous, ovate, 0.9–1.4 × 0.9–1.5 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels stout, 2–3.5 mm long, inconspicuously punctate and punctate-lineate, densely furfuraceous-lepidote. *Flowers* 5-merous, white or light yellow; calyx lobes coriaceous, suborbicular, 2–2.8 × 2.2–3 mm, apically rounded, prominently punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla chartaceous, 6.2–6.9 mm long, the tube 1.4–1.9 mm long, the lobes elliptic to lanceolate, 4.5–5.2 × 2.3–3 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 5–5.4 mm long, the filaments 2.6–2.8 mm long, the staminal tube 0.8–1.2 mm long, the apically free portions 1.4–2 mm long, the anthers ovoid, 2.6–2.9 × 1.3–1.5 mm, apically apiculate, basally deeply cordate, the connective conspicuously punctate; pistil 6.4–7.3 mm long, glabrous, prominently punctate and punctate-

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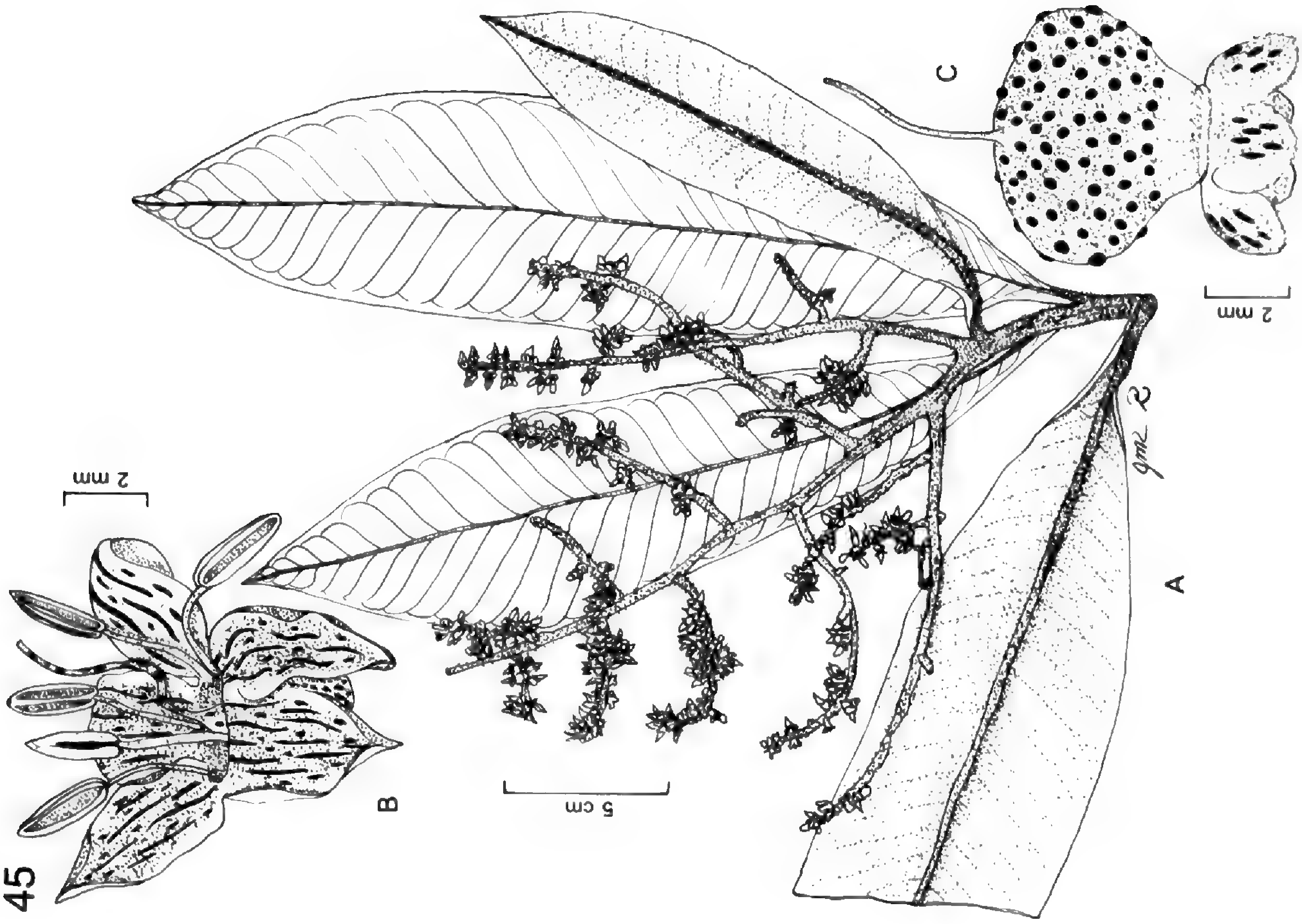

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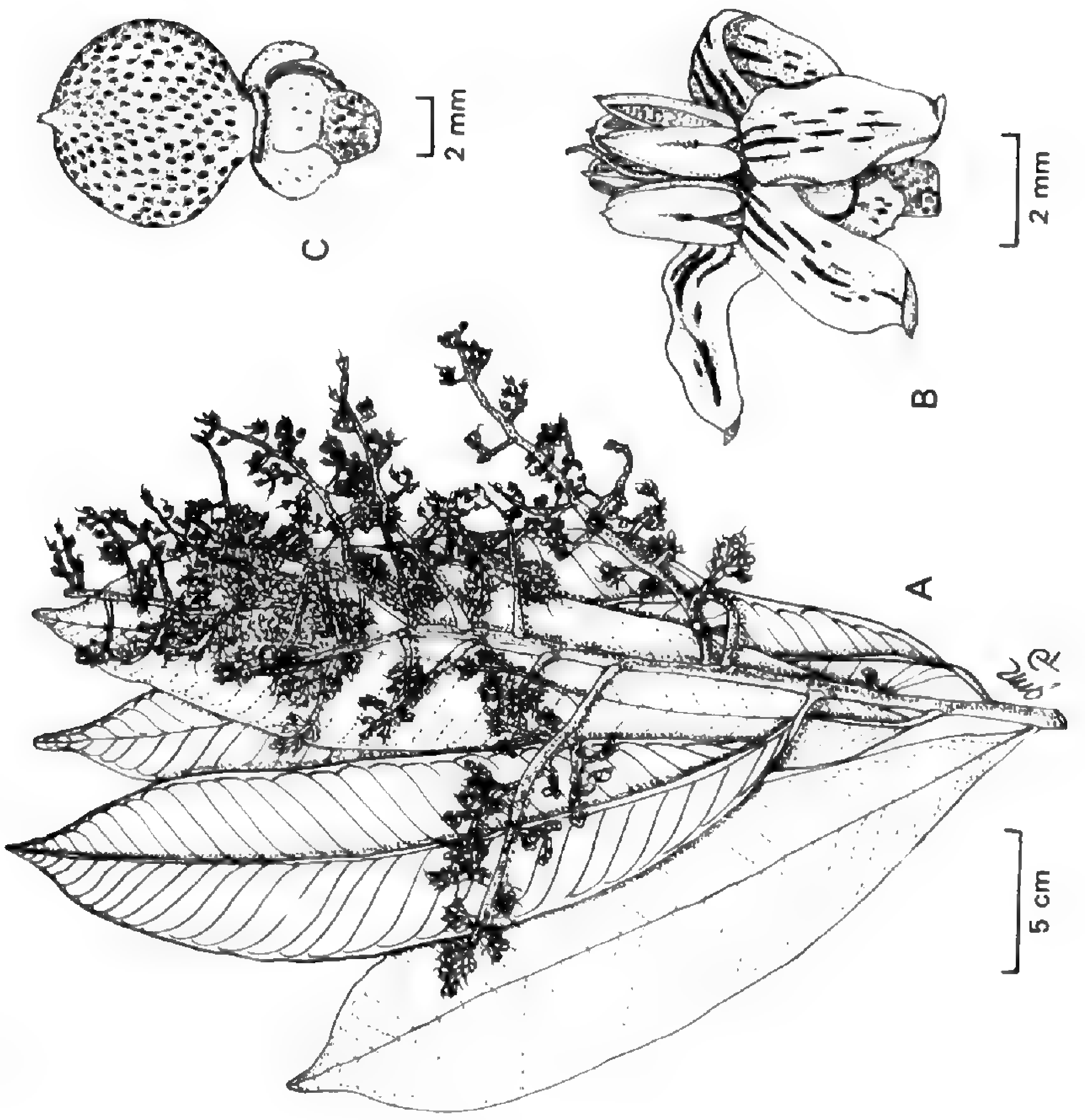

lineate, the ovary oblong, 1.4–1.6 mm long, the style 5–5.7 mm long, prominently punctate and punctate-lineate, the ovules 46 to 51. *Fruits* globose, 7–9.5 mm diam., prominently punctate and punctate-lineate.

Distribution. *Ardisia fimbrillifera* is distributed from Río San Juan in Nicaragua through eastern Costa Rica (Alajuela, Heredia, Limón), and Panama (Panamá, Veraguas, San Blas) to Chocó, Colombia, growing from 10 to 800(–1200) m in elevation.

Ecology and conservation status. *Ardisia fimbrillifera* is locally infrequent in lowland tropical wet forests or, rarely, in premontane forests. It has been collected in locations that are fairly remote and many of them are protected, so we see no immediate threat to this species.

Etymology. The specific epithet was derived from the Latin "fimbri" or "fimbrill" and "ifera" referring to the calyx lobes bearing a fringe of glandular cilia.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia fimbrillifera* is easily distinguished from *A. hagenii* by its narrower calyx lobes to 3 mm wide, shorter corolla lobes to 5.2 mm long, shorter anthers to 2.9 mm long, and shorter styles to 5.7 mm long.

Specimens examined. NICARAGUA. **Río San Juan**: Buena Vista a 1 k W of the Río San Juan delta, 13 Sep. 1983 (fr), *E. Martínez S. & R. Riviere 2100* (MEXU, MO); near Caño Chontaleño 20 km NE of El Castillo, 18–21 Apr. 1978 (fl), *D. Neill & P. Vincelli 3602* (HNMN, LL, MO, NY); Río San Juan, 2 km E of Buena Vista, 14 Sep. 1982 (fr), *R. Riviere 340* (HNMN, MO, NY, US); Mpio. del Castillo, Reserva Indio-Maíz, along Caño el Pavón, 3 km from the mouth of Río Bartola, 31 Dec. 1996 (fr), *R. Rueda et al. 5133* (HULE, MO); Mpio. El Castillo, Reserva Indio-Maíz, 8 km from headwaters of Río Bartola, toward Cerro el Diablo, 3 Jan. 1997 (fr), *R. Rueda et al. 5301* (HULE, MO). COSTA RICA. **Alajuela**: Cantón de San Ramón, Reserva Forestal San Ramón, Cordillera Tilarán, trail to Volcán Muerto, 11 May 1993 (fl), *F. Araya et al. 321* (CR, FTG, INB, MO). **Heredia**: Parque Nacional Braulio Carrillo, Estación Biológica Magsasay, 9 July 1990 (fr), *E. Alcázar et al. 137* (CR, FTG, INB, MO); Finca La Selva, Río Puerto Viejo E of junction with the Río Sarapiquí, Holdridge Trail 3000 m line, 18 Feb. 1981 (fl), *J. Folsom 9025* (CR, DUKE); Horquetas, 1–12 km SW of Horquetas, on road to Finca Plastico, near Finca Plastico and Rara Avis, 21 Apr. 1988 (fl), *B. Hammel & R. Robles 16714* (MO). **Limón**: Cantón de Talamanca, Bratsi, Alto Lari, between Surayo and Dapari 50 m N of Río Dapari mouth, Pare, at Río Lari, 25 Feb. 1992 (fr), *R. Aguilar & H. Schmidt 940* (INB, MO); Refugio Nacional de Fauna Silvestre Barra del Colorado, Llanura de Tortuguero, Puerto Lindo, 24 July 1995 (fr), *F. Araya 792* (CR, F, FTG, INB, MO); Hacienda Tapezco-Hda. La Suerte, 29 air km W of Tortuguero, 10 Mar. 1978 (fl), *C. Davidson et al. 6835* (F, MO); Cantón de Pococi, Parque Nacional Tortuguero, Llanura de Tortuguero, Estación Agua Fría, Sendero Agua Fría hasta entrada Sendero Aguacate, 1 Dec. 1990 (fr), *J. Solano 274* (CR, FTG, INB, MO). PANAMA. **Panamá**: Cerro Jefe, near Río Indio, 17 Feb. 1968 (fl), *J. Duke 15229* (MO); Finca Indio, slopes of Cerro Jefe, 18 Oct. 1971 (fr), *A. Gentry 2150* (MO); on El Llano–Cartí road, near Nusagandi, along Weder Trail, 31 Oct. 1992 (fr), *G. McPherson & M. Richardson 15988* (FTG, MEXU, MO, PMA). **San Blas**: Pemasky, Ina Igar Trail, Dec. 1986 (ster.), *R. Peralta 609* (LL, MO); Nusagandi, Campo de Pemasky, ca. 20 km El Llano–Cartí Road, trails near station, 29 Mar. 1992 (fl), *R. Paredes et al. 665* (MO, PMA). **Veraguas**: N of Santa Fé, ca. 2 km N of Escuela Agrícola Alto de Piedra, 17 Oct. 1974 (fr), *S. Mori & J. Kallunki 2591* (MO); NW of Santa Fé, 1.8 km N of Escuela Agrícola Alto de Piedra, 23 Feb. 1975 (fr), *S. Mori & J. Kallunki 4775* (LL, MO); 7 km W of Santa Fé on new road past agricultural school, 12 Apr. 1974 (fl), *M. Nee 11191* (LL, MO, US). COLOMBIA. **Chocó**: Mpio. de Riosucio, Zona de Urabá, Cerro del Cuchillo, 15 Nov. 1987 (fr), *D. Cárdenas 835* (JAUM, MO); Río San Juan Basin, near Docordó, 29 Mar. 1979 (fr), *E. Forero et al. 4354* (COL, MO).

43. Ardisia furfuracea Standl., J. Wash. Acad. Sci. 17: 525. 1927. *Auriculardisia furfuracea* (Standl.) Lundell, Phytologia 49: 344. 1981. TYPE: Costa Rica. Heredia: Cerro de Las Lajas, N of San Isidro, 2000–2300 m, 7 Mar. 1926 (fl), *P. Standley & J. Valerio 51556* (holotype, US!, LL neg. 1971-34!, US neg. 2372!). Figure 45.

Ardisia duriuscula Lundell, Wrightia 7: 24. 1981. Syn. nov. *Auriculardisia duriuscula* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Costa Rica. Heredia and San José: Cerros de Zurqui, along the Río Para Blanca (Pacific drainage), 10°03′N, 084°01′W, 1600–1800 m, 6–7 Feb. 1977 (fl), *W. Burger, G. Visconti & J. Gentry 10288* (holotype, F!, F neg. 68149!; isotype, MO!).

Auriculardisia trichomata Lundell, Phytologia 63: 75. 1987. Syn. nov. *Ardisia trichomata* (Lundell) Lundell, Phytologia 63: 463. 1987. TYPE: Costa Rica. San José: roadside leading from Alto La Palma to Bajo La Hondura, ca. 10 km NE of San Vincente de Moravia, 1260–1550 m, 24 Feb. 1978 (fl), *R. Wilbur 24906* (holotype, DUKE!).

Small trees 2–6 m tall, to 3.7 cm diam. *Branch-*

←

Figure 44 (left). *Ardisia fimbrillifera.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from holotype, *G. Proctor 32238* (LL); B from *M. Grayum 9761* (MO); C from *R. Riviere 340* (MO).)

Figure 45 (right). *Ardisia furfuracea.* —A. Flowering branch. —B. Flower. —C. Fruit. (A & B drawn from holotype, *P. Standley & J. Valerio 51556* (US); C from *G. Mora et al. 291* (MO).)

lets flexuous, stout, terete, 5–9 mm diam., with a mixture of densely cupuliform and furfuraceous-lepidote scales. *Leaves* with blades coriaceous, oblong to elliptic, 16.2–47.8 × 3.8–13.2 cm, apically acuminate, with an acumen 0.3–1.6 cm long, basally acute to cuneate, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above, below with a mixture of densely cupuliform and furfuraceous-lepidote scales, the midrib impressed above, prominently raised below, the secondary veins 47 to 64 pairs, prominulous above and below, the margins entire, flat; petiole stout, marginate, 0.7–2.2 cm long, glabrous above, below with a mixture of densely cupuliform and furfuraceous-lepidote scales. *Inflorescences* erect, bi- or tripinnately paniculate, 17.4–46.7 × 15.2–29.6 cm, pyramidal, as long as or longer than the leaves, with a mixture of densely cupuliform and furfuraceous-lepidote scales, the branches terminally congested into 5- to 8-flowered corymbs; peduncle nearly sessile to 2.7 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts early caducous, membranous to chartaceous, ovate to oblong, 1.3–1.8 × 0.4–0.5 cm, apically acute to rounded, or nearly so, with scattered prominent punctations and punctate-lineations, glabrous above, below with a mixture of densely cupuliform and furfuraceous-lepidote scales, the midrib inconspicuous, the secondary veins obscure, the margins entire, flat; floral bracts early caducous, membranous, ovate, 0.8–1.3 × 0.8–1.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, scattered furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular-ciliolate; pedicels stout, 0.8–2.1 mm long, inconspicuously punctate-lineate, densely furfuraceous-lepidote. *Flowers* 5- or 6-merous, white; calyx lobes chartaceous, orbicular to oblate, 1.3–1.6 × 1.4–1.7 mm, apically rounded, often prominently and inconspicuously punctate and punctate-lineate, glabrous adaxially, densely furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular-ciliolate; corolla membranous, 5–5.3 mm long, the tube 0.7–1.4 mm long, the lobes ovate, 3.9–4.3 × 2.3–2.5 mm, apically acute, sparsely prominently punctate and punctate-lineate, glabrous throughout, the margin entire, hyaline; stamens 5.8–6 mm long, the filaments 3.9–4.1 mm long, the staminal tube 0.6–0.7 mm long, the apically free portions 3.2–3.5 mm long, the anthers ovoid, 2–2.2 × 0.8–1 mm, apically apiculate, basally cordate, the connective inconspicuously punctate; pistil 5.6–6.5 mm long, glabrous, the ovary oblong, 1.1–1.3 mm long, the style 4.5–5.2 mm long, inconspicuously punctate and punctate-lineate, the ovules 39 to 50. *Fruits* depressed globose, 4.2–5.6 × 5.5–7.2 mm, conspicuously punctate.

Distribution. *Ardisia furfuracea* is endemic to the mountains of central Costa Rica in Cartago, Heredia, and San José, growing at 1260 to 2000 m in elevation.

Ecology and conservation status. *Ardisia furfuracea* occurs in premontane to montane wet forest and often in remnant fragments of forests found in pastures. Although it is found over a wide area, it is known from a relatively small number of collections and should be considered threatened at this time.

Etymology. The specific epithet means scurfy, covered with bran-like scales referring to the vestiture throughout the plant.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia furfuracea* is most closely related to *A. mcphersonii* by virtue of the flexuous branchlets and oblong to narrowly elliptic leaf blades. However, *Ardisia furfuracea* can be distinguished from *A. mcphersonii* by its narrower calyx lobes to 1.7 mm wide and wider corolla lobes to 2.5 mm wide, longer stamens to 6 mm long, smaller anthers to 2.2 × 1 mm, and longer styles to 5.2 mm long.

It appears that Lundell (1981c, 1987) did not note the similarities between *Ardisia furfuracea* and populations represented by the types of *Ardisia duriuscula* and *Auriculardisia trichomata*. The types of *Ardisia duriuscula* and *Auriculardisia trichomata* are identical to that of *Ardisia furfuracea* in all respects.

Specimens examined. COSTA RICA. **Cartago**: Tapantí Reserve, 7 Dec. 1982 (fl), *L. Gómez 19282* (LL [2], MO); Cantón de Paraiso, Parque Nacional Tapantí, Valle del Reventazón, Sector Dos Amigos, Rancho Negro Trail, 20 July 1994 (fr), *G. Mora et al. 291* (INB, MO). **Heredia**: Parque National Braulio Carrillo, Transect Trail, to right of trail, 20 June 1992 (ster.), *B. Boyle & C. Godt 932* (FTG, INB, MO); Parque National Braulio Carrillo, Transect Trail, to left of trail, ca. 50 minute walk below refuge, 2 Sep. 1992 (fr), *B. Boyle & N. Snow 1052* (FTG, INB, MO); along Río San Rafael, Atlantic slope of Volcán Barva, 12 Apr. 1986 (fl), *M. Grayum 7060* (CR, FTG, LL, MO, US). **San José**: along CR 220 between Alto de La Palma and Bajo La Hondura, 5–8 km N of San Jeronimo, 17 Oct. 1974 (fl), *J. Utley & K. Utley 1422* (CR, F).

44. Ardisia generalensis Ricketson & Pipoly, sp. nov. TYPE: Costa Rica. San José: basin of El General, 675–900 m, Mar. 1942 (fl), *A. Skutch 5025* (holotype, US!; isotype, MICH!). Figure 46.

Propter laminam ellipticam vel obovatam, atque inflorescentiam bipinnatipaniculatam, flores dense corymbosos gerentem *A. darienensi* arcte similis, sed ab ea petiolis canaliculatis (non marginatis) 4–8 (nec 8–28) mm longis 0.5–1 (nec 2–3) mm diametro, laminis foliaribus membranaceis (non chartaceis) nervis secundariis 21 ad 25–(nec 55 ad 70–) jugis necnon lobulis calycinis ad apices acutis (nec emarginatis) perfacile recognoscitur.

Trees to 6 m tall. *Branchlets* slender, terete, 3–4 mm diam., densely and minutely appressed rufous furfuraceous-lepidote. *Leaves* with blades membranous, elliptic to narrowly obovate, 4.8–11.5 × 1.7–4.2 cm, apically acute, with an acumen 4–7 mm long, basally acute to cuneate, decurrent on the petiole, inconspicuously punctate and punctate-lineate above and below, glabrous above, densely and minutely appressed rufous furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 21 to 25 pairs, prominulous above and below, the margins entire, flat; petioles slender, canaliculate, 4–8 mm long, 0.5–1 mm diam., glabrous above. *Inflorescences* erect, bipinnately paniculate, 4.8–7.2 × 3–4.5 cm, columnar to narrowly pyramidal, longer than the leaves, the rachis, branchlets, and pedicels densely furfuraceous-lepidote, the branches rarely subtended by leaves, the branches terminating in 3- to 7-flowered corymbs; inflorescence bracts and branch bracts unknown; floral bracts caducous, membranous, ovate, 1.2–1.8 × 0.6–1.1 mm, apically acute, inconspicuously punctate and punctate-lineate, glabrous throughout, the margins irregular, minutely erose, hyaline; pedicels slender, 3.6–5.1 cm long, nearly epunctate. *Flowers* 5-merous, white or pink; calyx lobes coriaceous, ovate, 3.4–3.7 × 3.2–3.4 mm, apically acute, mostly epunctate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins entire, hyaline; corolla chartaceous to coriaceous, 7.9–8.1 mm long, the tube 3.3–3.6 mm long, the lobes narrowly ovate to lanceolate, 4.4–4.7 × 2.2–2.5 mm, apically acute, mostly epunctate, glabrous throughout, the margins entire, hyaline; stamens 6.1–6.2 mm long; the filament 3.3–3.4 mm long, the staminal tube 2.1–2.3 mm long, the apically free portions 1–1.3 mm long, the anthers narrowly ovoid to lanceoloid, 3–3.1 × 1.2–1.3 mm, apically apiculate, basally lobate, the connective inconspicuously punctate; pistil 8–8.3 mm long, glabrous, the ovary oblong, 2.6–2.7 mm long, the style 5.4–5.6 mm long, epunctate, the ovules 25 to 29. *Fruits* unknown.

Distribution. *Ardisia generalensis* is endemic to the basin of El General in San José, Costa Rica, growing from 675 to 900 m in elevation.

Ecology and conservation status. *Ardisia generalensis* occurs in wet forests. The area contains a number of Darién and Chocó floristic elements, such as *Cybianthus pastensis* (Mez) Agostini and *Cybianthus montanus* (Lundell) Agostini. Because it is known only from two old collections, it should be considered threatened.

Etymology. The specific epithet refers to the locality of El General where the type was collected.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia generalensis* is most similar to *A. darienensis* (see under that species for similarities). However, it is easily separated by the shorter and thinner, canaliculate petioles to 8 × 1 mm, membranous leaves with less numerous secondary veins to 25 pairs, and the apically acute calyx lobes.

Paratype. COSTA RICA. **San José**: basin of El General, Aug. 1945 (fr), *A. Skutch 5237* (F, MO, NY, US).

45. Ardisia gigantea Ricketson & Pipoly, sp. nov. TYPE: Panama. Veraguas: NW of Santa Fé, 8.8 km from Escuela Agrícola Alto de Piedra, Pacific slope, 21 Dec. 1974 (fr), *S. Mori, J. Kallunki, T. Cochrane, B. Cochrane, B. Hansen, R. Kowal & M. Nee 4003* (holotype, MO!; isotype, LL!). Figure 47.

Propter folia magna ad apices acuta perdense minute adpresso-furfuraceo-lepidota atque lobulos calycinos chartaceos secus margines erosos cum *A. aguirreana* primo intuitu confunderi potest, sed ab ea laminis foliaribus 45.8–46.6 × 15.7–21.5 (non 51.5–67.0 × 12.0–17.5) cm manifeste (nec inconspicue) punctatis et lineato-punctatis necnon lobulis calycinis oblatis (non ovatis) 1.1–1.6 × 3.3–3.6 (nec 2.1–2.6 × 1.2–1.4) cm ad apices rotundatis (nec acutis) perfacile cognoscitur.

Trees to 8 m tall, to 30 cm diam. *Branchlets* stout, terete, 8–10 mm diam., densely appressed rufous furfuraceous-lepidote. *Leaves* with blades membranous, elliptic, 45.8–46.6 × 15.7–21.5 cm, apically acute, with an acumen 1.8–2.1 cm long, basally acute, decurrent on the petiole, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote, the midrib impressed above, prominently raised below, the secondary veins 48 to 55 pairs, prominently raised above and below, the margins entire, inrolled; petioles slender, marginate, 1.2–1.7 cm long, 4–5 mm diam., glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, to 32 × 25–28 cm, pyramidal, shorter than the leaves, the rachis, branches, and pedicels furfuraceous-lepidote, the branches loosely congested into 3- to 7-flowered corymbs; peduncle obsolete; inflorescence and branch bracts unknown; floral bracts unknown; pedicels slender, 9–13 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, color unknown; calyx lobes chartaceous, oblate, 1.1–1.6 × 3.3–3.6 mm, api-

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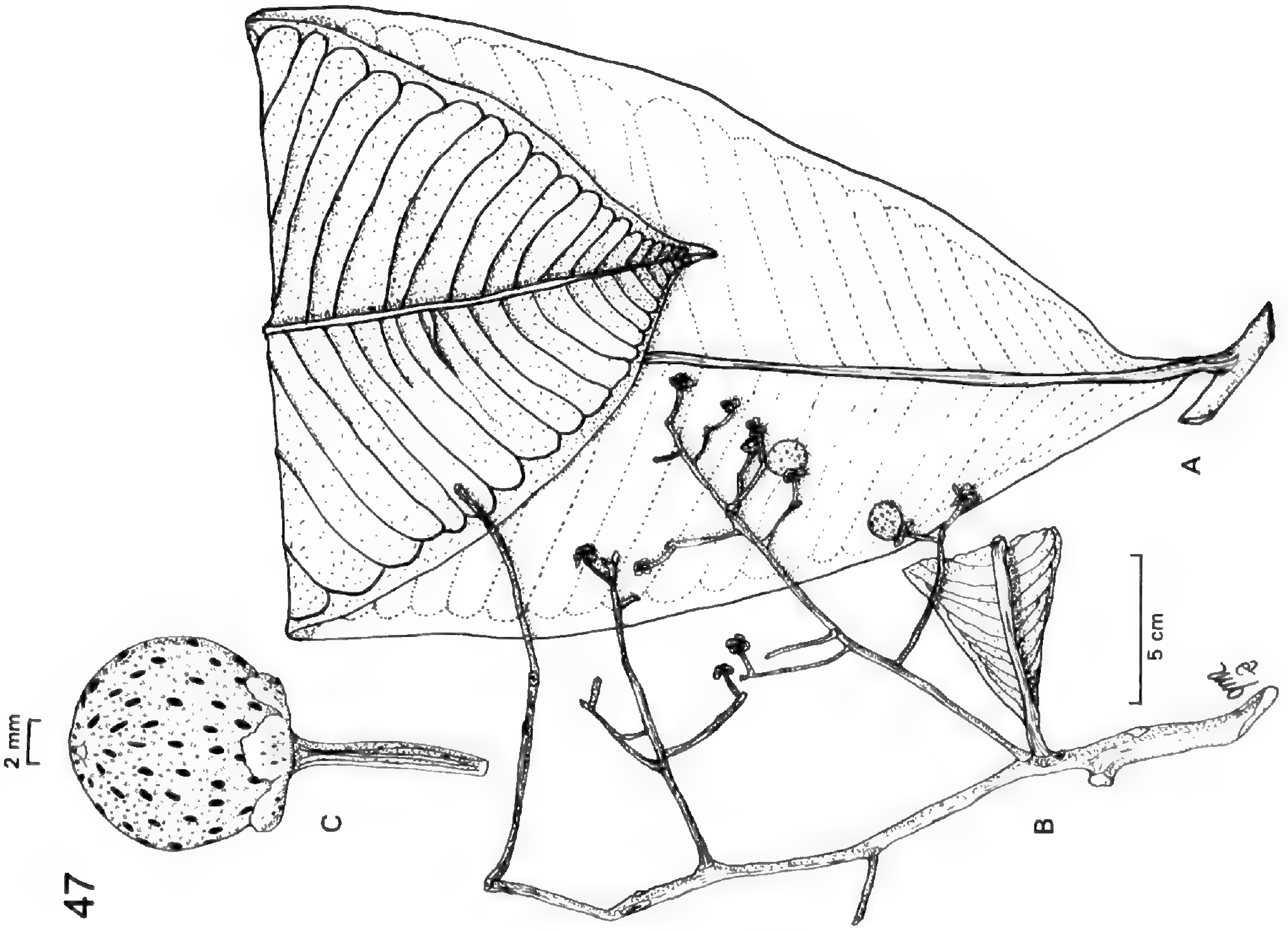

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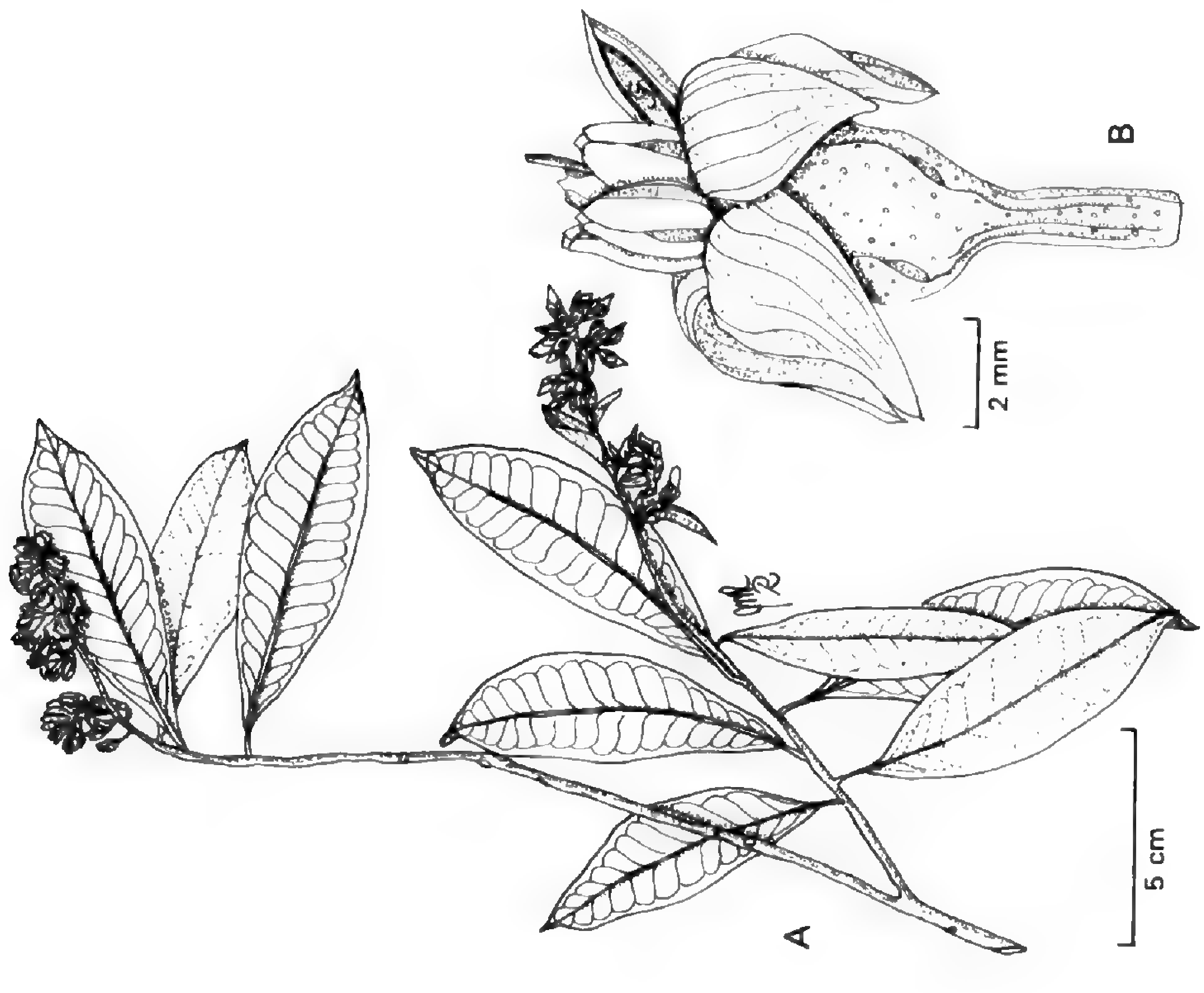

cally rounded, prominently punctate and punctate-lineate, glabrous adaxially, sparsely to densely furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla, stamens, and pistil unknown. *Fruits* globose, 9.5–13.5 cm diam., prominently punctate.

Distribution. *Ardisia gigantea* is known only from the type collection, from near the Escuela Agrícola Alto de Piedra in Veraguas, Panama, growing at 500 to 1000 m in elevation.

Ecology and conservation status. The species occurs in the premontane wet forest zone, but its population biology and consequent conservation status are unknown.

Etymology. The epithet is based on the exceptionally large leaf blades.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia gigantea* is most similar to *A. aguirreana,* but is distinguished by its larger leaves to 46.6 cm long, and distinctive oblate calyx lobes. *Ardisia gigantea* is known only from a fruiting specimen: the holotype is of a single leaf with an attached inflorescence. The LL isotype consists of a single leaf.

46. Ardisia glandulosomarginata Oerst., Vidensk. Meddel. Dansk Naturhist. Føren Kjøbenhavn 1861: 128. 1862. *Auriculardisia glandulosomarginata* (Oerst.) Lundell, Phytologia 54: 285. 1983. TYPE: Costa Rica. Cartago: in monte Irasú, 8000–9000 ft. [2438–2743 m], Jan. 1847 (fl), *A. Oersted 25* (holotype, C!, F neg. 22948!; isotypes, C!, F!, LL!, M!). Figure 48.

Auriculardisia leptopoda Lundell, Phytologia 57: 450. 1985. Syn. nov. *Ardisia leptopoda* (Lundell) Lundell, Phytologia 61: 65. 1986, nom. inval. *Ardisia leptopoda* (Lundell) Pipoly & Ricketson, Sida 18: 513. 1998. TYPE: Panama. Chiriquí: E of Guadeloupe along the Río Chiriquí Viejo, ca. 2 mi. NE of Cerro Punta, ridge of Cerro Respinga, ca. 7000 ft. [2134 m], 13 Jan. 1971 (fl, fr), *R. Wilbur, J. Teeri & R. Foster 13111* (holotype, F!, F neg. 68323!; isotypes, DUKE!, LL!, MO!, US!).

Shrubs or small trees 1.5–12 m tall, 7.6–18 cm diam. *Branchlets* slender, terete, 3–6.5 mm diam., densely appressed ferrugineous furfuraceous-lepidote. *Leaves* with blades membranous to nearly coriaceous, elliptic, 4.2–24.2 × 2.6–8.3 cm, apically acuminate, with an acumen 0.8–2.1 cm long, basally obtuse or acute, decurrent on the petiole, prominently punctate and punctate-lineate, with a few scattered scales above, densely and minutely appressed ferrugineous furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 37 to 42 pairs, prominulous above and below, the quaternary veins prominulous below, the margins nearly entire to deeply crenulate, flat; petioles slender, canaliculate, 11–19 mm long, 1–2 mm diam., essentially glabrous above, densely ferrugineous furfuraceous-lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, 4–20 × 4–22.5 cm, pyramidal, usually longer than the leaves, the rachis, branchlets, abaxial surfaces of all bracts, and pedicels densely ferrugineous furfuraceous-lepidote, the branches loosely congested into 5- to 11-flowered corymbs; peduncle nearly obsolete to 2.1 cm long, the lower branches often subtended by leaves; inflorescence bracts absent; inflorescence branch bracts very early caducous, membranous, ovate, 1.9–3.2 × 0.5–1.5 mm, apically acuminate, prominently punctate and punctate-lineate, glabrous adaxially, ferrugineous furfuraceous-lepidote abaxially, the margins irregular, minutely erose hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 1.2–1.8 × 0.4–0.6 mm; pedicels slender, 7.1–8.7 mm long, prominently punctate and punctate-lineate, ferrugineous furfuraceous-lepidote. *Flowers* 5-merous, light green, white or cream to light pink; calyx lobes membranous to chartaceous, widely ovate to orbicular, 2.3–2.5 × 2.3–2.5 mm, apically acute to obtuse, prominently punctate and punctate-lineate, glabrous adaxially, ferrugineous furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 6.2–6.4 mm long, the tube 1.2–1.5 mm long, the lobes ovate, 4.5–5 × 3.2–3.8 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 4.5–4.7 mm long, the filaments 2.2–2.4 mm long, the staminal tube 0.7–1 mm long, the apically free portions 1.4–1.5 mm long, the anthers narrowly ovoid to lanceoloid, 2.6–2.8 × 1.2–

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Figure 46 (left). *Ardisia generalensis.* —A. Flowering branch. —B. Flower. (A, B drawn from holotype, *A. Skutch 5025* (MICH).)

Figure 47 (right). *Ardisia gigantea.* —A. Leaf. —B. Flowering branch. —C. Fruit. (A & C drawn from holotype, *S. Mori et al. 4003* (MO); B from isotype *S. Mori et al. 4003* (LL).)

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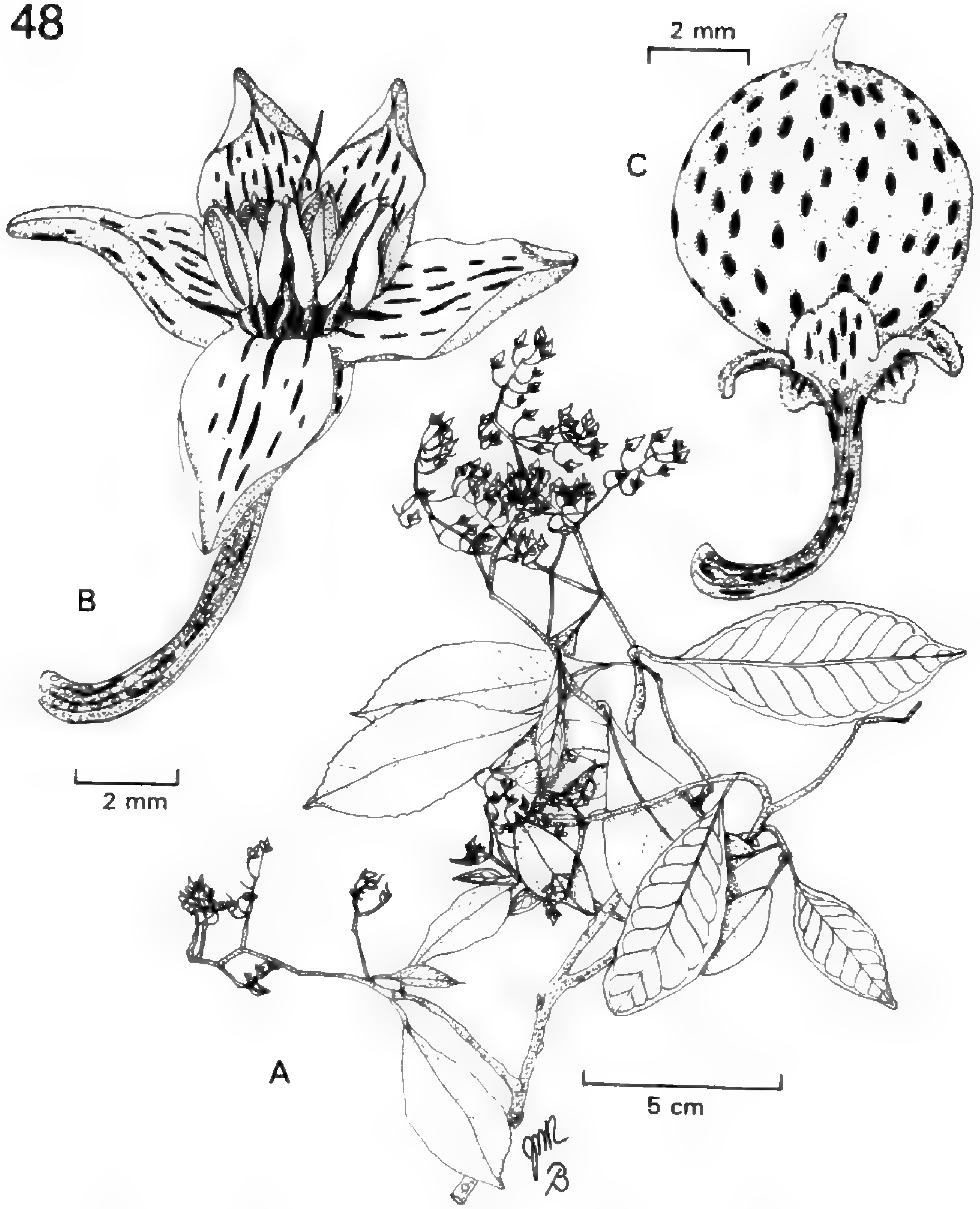

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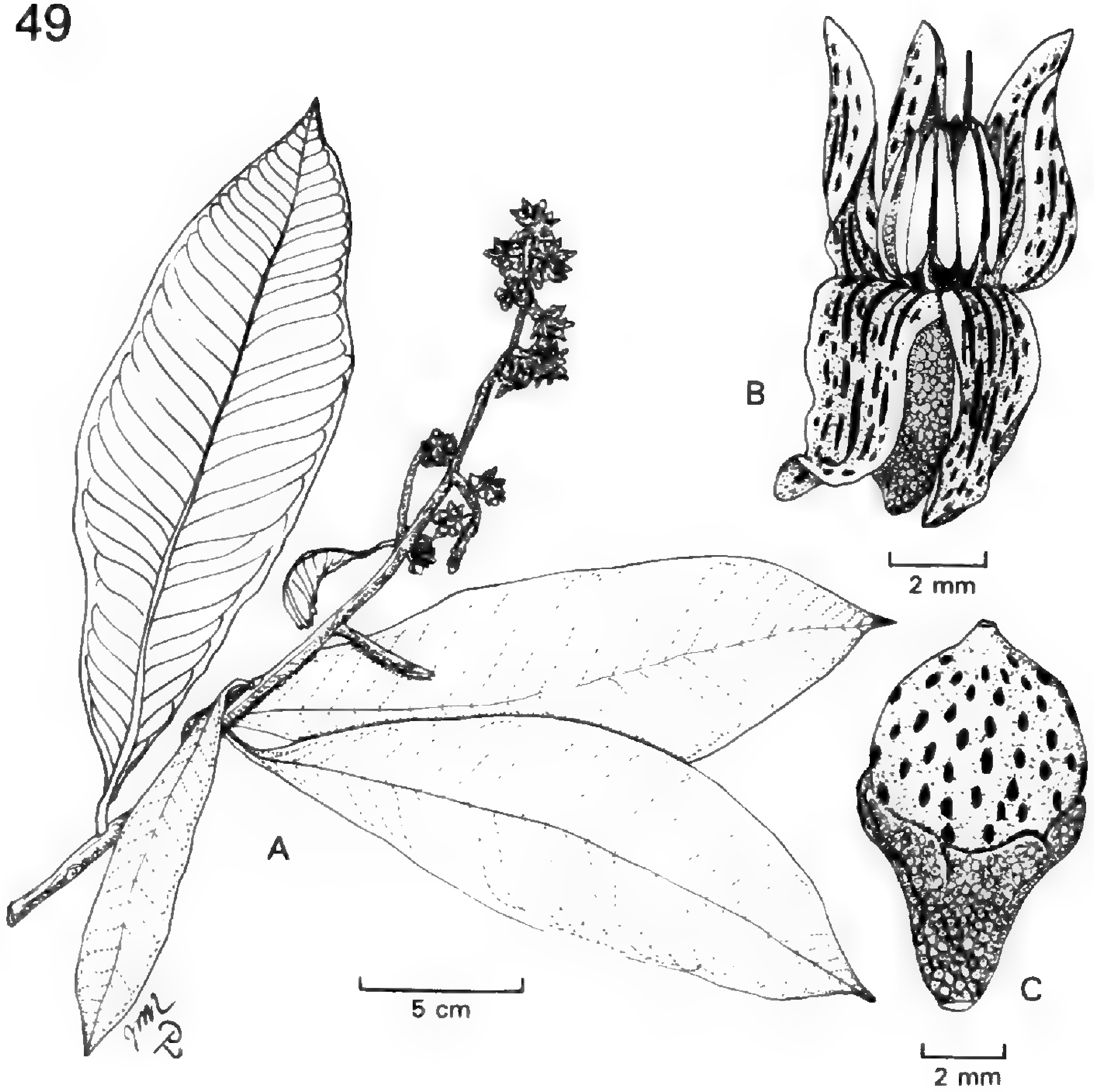


Figure 48 (left). *Ardisia glandulosomarginata.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from holotype, *A. Oersted 25* (C); B from *B. Gamboa R. & A. Picado 1052* (MO); C from *G. Davidse & W. D'Arcy 10184* (MO).)

Figure 49 (right). *Ardisia hagenii.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from holotype, *C. von Hagen & H. von Hagen 2008* (MO); B from *K. Sytsma et al. 4831* (MO); C from *S. Knapp et al. 2086* (MO).)

1.3 mm, apically apiculate-cuspidate, basally deeply cordate, the connective conspicuously punctate; pistil 6.2–6.4 mm long, prominently punctate, glabrous, the ovary oblong, 1.4–1.5 mm long, the style 4.9–5 mm long, prominently punctate and punctate-lineate, the ovules 29 to 33. *Fruits* globose, 6.8–9.2 mm diam., prominently punctate.

Distribution. *Ardisia glandulosomarginata* is found in all provinces of Costa Rica except Guanacaste, and is common from the Costa Rican border to central Panama, growing from 1075 to 3050 m in elevation.

Ecology and conservation status. *Ardisia glandulosomarginata* normally occurs in very wet cloud to elfin forests with occasional populations at the upper limit of premontane and montane forests. It has been collected in areas with remnant forests, and apparently has some tolerance for disturbance. Therefore, we do not believe it is threatened at this time.

Etymology. The specific epithet refers to the prominently raised punctations along the abaxial leaf margin.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia glandulosomarginata* can be separated from *A. croatii* by the ovate calyx lobes to 2.5 mm, with acute to obtuse apices, the early caducous, ferrugineous furfuraceous-lepidote scales, and the secondary veins prominulous above and below.

The type of *Auriculardisia leptopoda* is in bud and notable only for its petioles that are slightly longer than the median for the species.

Specimens examined. COSTA RICA. **Alajuela**: Colinas de San Pedro de San Ramón, 25 Oct. 1925 (fl), *A. Brenes 4495* (F, NY); Volcán Poás, S slope of crater, 26 Apr. 1930 (fl), *G. Cufodonti 539* (G, W); Cantón de Alfaro Ruíz, Zarcero, 17 Jan. 1938 (fl), *A. Smith H-145* (F). **Cartago**: along stream valleys on the SW slope of Volcán Irazú, W of Sabanilla, 7 Mar. 1987 (fl), *W. Burger et al. 12058* (F, NY, TEX). **Heredia**: Río Vueltas, upper Río Patria, E slope of Volcán Barba near the Continental Divide, 2 July 1983 (fr), *K. Barringer & E. Christenson 3385A* (F); Rancho Flores, 22 Feb. 1890 (fl), *A. Tonduz 2143* (BR); Finca La Selva, the OTS Field Station on the Río Puerto Viejo just E of its junction with the Río Sarapiquí, Sendero Tres Rios at 2500 m line, 7 Jan. 1995 (fl), *R. Wilbur 63199* (DUKE, MO). **Limón**: Cordillera Talamanca, headwaters of the unnamed W branch of the Río Teribe, between the Río Sini and the Continental Divide at Cerro Bekom, along river, 21–27 Mar. 1984 (fl), *G. Davidse et al. 25719* (LL, MO); Refugio Barra del Colorado Forests and pastures between Río Chirripocito and Río Sardina, 10°38′N, 083°45′W, 19 Apr. 1990 (fl), *M. Grayum 9761* (CR, FTG, MO). **Puntarenas**: Cantón de Perez Zeledón, Parque Indígena La Amistad, Cordillera Talamanca, between headwaters of Río Barranca y Río Blanco, Finca San Carlos, 5 Apr. 1995 (fl), *R. Aguilar & O. Garrote 3834* (CR, FTG, INB, MO); Cantón de Coto Brus, Zona Protectora Las Tablas, Cuenca Térraba-Sierpe, 8 km NE of Progreso, 19 Feb. 1997 (fl), *B. Gamboa & A. Picado 1052* (INB, MO). **San José**: Cantón de Pérez Zeledón, Parque Nacional Chirripó, Cuenca Térraba-Sierpe, Llano Bonito, 5 May 1997 (fl), *R. Aguilar 5063* (INB, MO); Copey, June 1898 (fl), *A. Tonduz 11824* (US). PANAMA. **Bocas del Toro**: border of Bocas del Toro–Chiriquí, trail along Continental Divide NE of Boquete, above Palo Alto, down slope on Bocas del Toro side of trail, 23 May 1979 (fr), *B. Hammel 7363* (MO). **Chiriquí**: E slope of Volcán de Chiriquí (Barú), WNW of Boquete, 19 Nov. 1975 (fl, fr), *G. Davidse & W. D'Arcy 10184* (LL, MO); vicinity of Boquete, Finca Collins, 15 Mar. 1963 (fl), *W. Stern et al. 2053* (MICH, MO); ca. 3.7 km E of bridge NE of Cerro Punta on road through Bajo Grande, 9 Nov. 1980 (fl, fr), *W. Stevens 18242* (MO). **Panamá**: Cerro Jefe, 10–13 mi. beyond Goofy Lake, 12 Feb. 1966 (fl, fr), *J. Duke 8028* (MO).

47. **Ardisia hagenii** Lundell, Wrightia 4: 59. 1968. *Auriculardisia hagenii* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Panama. Chiriquí: Boquete region, Horqueta, [6500 ft.] 1981 m, 17 Apr. 1940 (fl), *C. von Hagen & W. von Hagen 2008* (holotype, MO!, LL neg. 71-166!; isotype, NY!). Figure 49.

Auriculardisia chiriquiana Lundell, Wrightia 7: 267. 1984. Syn. nov. *Ardisia chiriquiana* (Lundell) Lundell, Phytologia 61: 62. 1986, nom. inval. *Ardisia chiriquiana* (Lundell) Pipoly & Ricketson, Sida 18: 511. 1998. TYPE: Panama. Chiriquí: trail up Cerro Pate Macho, 08°50′N, 082°25′W, 1500–1900 m, 7 Jan. 1983 (fl), *B. Stein, B. Schmalzel & D. Roubik 1223* (holotype, LL!; isotype, MO!).

Auriculardisia toroana Lundell, Wrightia 7: 273. 1984. Syn. nov. *Ardisia toroana* (Lundell) Lundell, Phytologia 61: 67. 1986, nom. inval. *Ardisia toroana* (Lundell) Pipoly & Ricketson, Sida 18: 514. 1998. TYPE: Panama. Bocas del Toro: 15 km up the Changuinola river to I.R.H.E. dam site no. 1, near campsite on trail to ridge NE of campsite, 800–900 ft. [244–274 m], 12 Dec. 1979 (fl), *T. Antonio 3079* (holotype, LL!; isotype, MO!).

Shrubs or small trees to 11 m tall, to 12.5 cm diam. *Branchlets* stout, terete, 3.5–5.5 mm diam., densely and minutely appressed rufous furfuraceous-lepidote. *Leaves* with blades chartaceous to coriaceous, elliptic to narrowly elliptic, 13.5–24.6 × 3.6–7.7 cm, apically acuminate, with an acumen 0.6–1.6 cm long, basally acute, decurrent on the petiole, inconspicuously punctate and punctate-lineate above and below, mostly glabrous above, densely and minutely appressed rufous furfuraceous-lepidote below, more so along the midrib and secondary veins, the midrib impressed above, prominently raised below, the secondary veins 42 to 49 pairs, slightly impressed above, prominently raised below, margins entire, flat; petioles slender, 7–28 mm long, 1–3 mm diam., glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, 9.1–20.5 × 4.2–20.5 cm, pyramidal, longer than the leaves, the rachis, branchlets, abaxial bract surfaces, and pedicels densely furfuraceous-lepidote, the branches loosely congested into 4- to 9-flowered corymbs; peduncles 0.8–3.2 mm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts usually persistent, chartaceous, ovate, 2.5–4.5 × 1.5–2.2 mm, apically acute, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote abaxially, glabrous adaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts but membranous to chartaceous, 1.4–2.3 × 1.6–2.8 mm; pedicels stout, 1–2.2 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, pink to red-violet; calyx lobes coriaceous, orbicular, 2.6–2.8 × 3.5–3.7 mm, apically rounded, conspicuously black punctate and punctate-lineate, furfuraceous-lepidote abaxially, glabrous adaxially, the margin entire, erose, hyaline, sparsely glandular ciliolate; corolla chartaceous, 8.6–8.9 mm long, the tube 1.2–1.3 mm long, the lobes ovate, 5.3–5.6 × 2.6–2.8 mm, apically acute, conspicuously black punctate and punctate-lineate, glabrous throughout, the margins entire, slightly hyaline; stamens 7.2–7.3 mm long, the filaments 4.3–4.4 mm long, the staminal tube 1.2–1.3 mm long, the apically free portions 3.0–3.2 mm long, the anthers lanceoloid, 3.6–3.8 × 1.1–1.4 mm, apically apiculate, basally lobate, the connective conspicuously punctate; pistils 8.6–8.9 mm long, glabrous, the ovary oblong, 1.8–2 mm long, the style 6.9–7.1 mm long, conspicuously punctate, the ovules 50 to 55. *Fruits* globose, 5.2–6.7 mm diam., inconspicuously punctate and punctate-lineate, inconspicuously costate.

Distribution. *Ardisia hagenii* is endemic to western Panama, in Bocas del Toro and Chiriquí, growing from 1000 to 2100 m in elevation.

Ecology and conservation status. *Ardisia hagenii* occurs in montane wet, cloud, and elfin forests. While it is certainly not common, at this time there are no data to suggest the species is threatened.

Etymology. This species was named in honor of Christine and Wolfgang von Hagen, collectors of the type specimen.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia hagenii* may be most easily confused with *A. pseudoracemiflora* because of its elliptic to narrowly elliptic leaves and inflorescence much longer than wide. However, *Ardisia hagenii* is easily separated from *A. pseudoracemiflora* by its wider, coriaceous, orbicular calyx lobes to 3.7 mm wide, longer corolla lobes to 5.6 mm long, longer anthers to 3.8 mm long, longer styles to 7.1 mm long, fewer secondary veins of the leaf blades, and thicker branchlets.

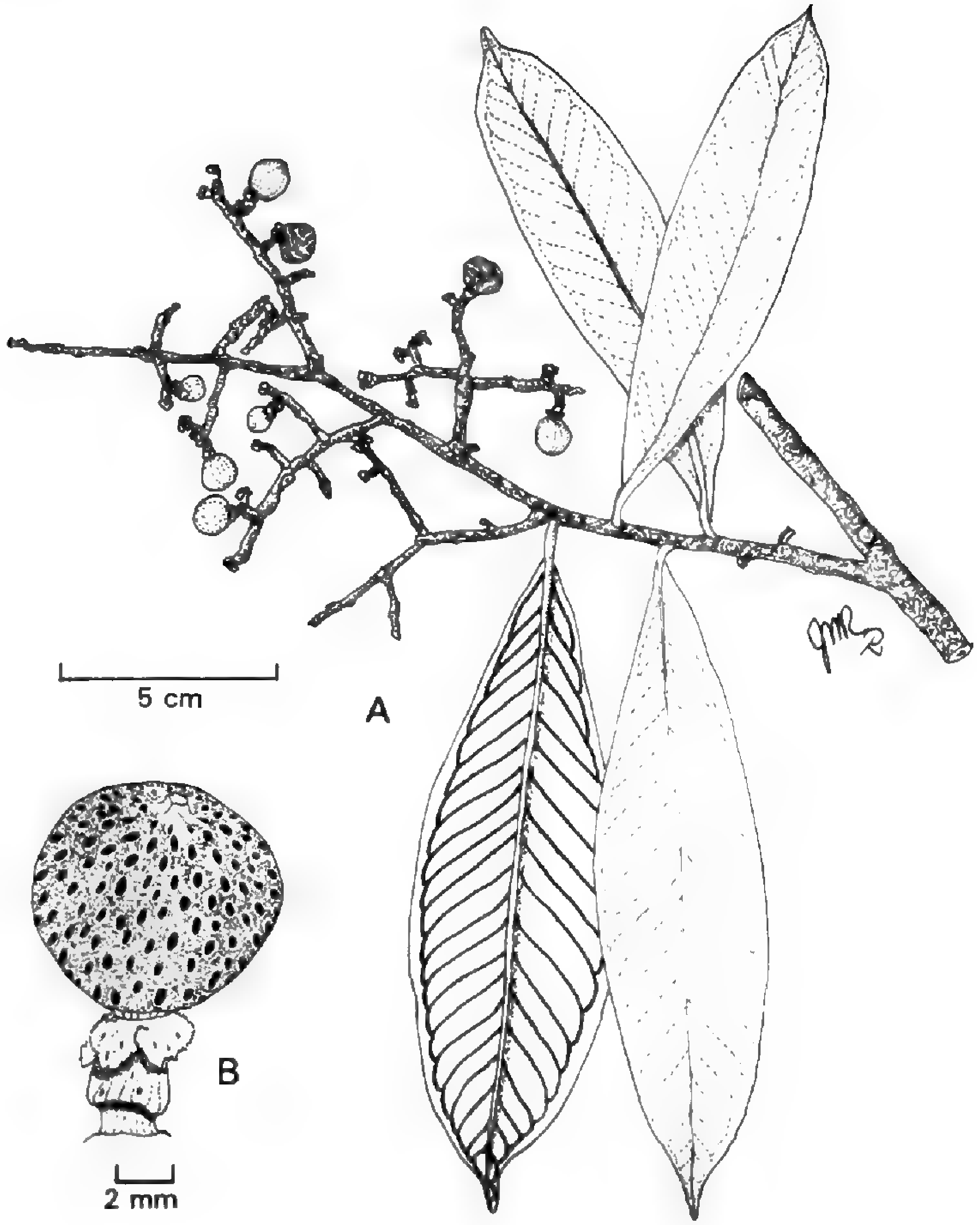
The von Hagen collections are atypical of the species. The inflorescence branches appear fasciated, causing some branches to be swollen and reduced, giving the inflorescence a "columnar" appearance as noted by Lundell (1968). Unfortunately, Lundell failed to understand the atypical nature of his type and never annotated any other specimens as *Ardisia hagenii*. Instead, Lundell described *Auriculardisia chiriquiana* Lundell, which has normal branches and an inflorescence in young bud. The type of *Auriculardisia toroana* is in flower and unique only because of the hyaline margin of its calyx lobes. However, the types corresponding to both *Auriculardisia chiriquiana* and *A. toroana* match *Ardisia hagenii* in all other respects.

Specimens examined. PANAMA. **Bocas del Toro**: Campamento Changuinola, 1 km from Corriente Grande, Cerro Bracha, 18 Jan. 1980 (fl), *M. Correa et al. 3180* (MO, PMA); SE and NE of Changuinola 1 km from IRHE, 19 Jan. 1980 (fl), *M. Correa et al. 3323* (MO, PMA); along Changuinola and near the Corriente Grande School, 25 Feb. 1980 (fr), *M. Correa 3985* (MO, PMA); Fortuna Dam region, along pipeline service road, 7 Dec. 1985 (fr), *G. McPherson 7827* (F, FTG, LL, MO, PMA). **Chiriquí**: along road between Fortuna Lake and Chiriquí Grande, 4.5–5 km N of dam over Fortuna Lake, 8 Mar. 1985 (fl), *T. Croat & M. Grayum 60032* (LL, MO); 3.5 mi. NE of Boquete, end of road along Río Palo Alto, 19 Nov. 1978 (fl), *B. Hammel 5736* (MO); S slopes of Cerro Pate Macho along Río Palo Alto, 11 Nov. 1981 (fr), *S. Knapp et al. 2086* (LL, MO, NY); near Fortuna Dam, along Quebrada de Arena, S of Continental Divide, 5 Dec. 1985 (fl), *G. McPherson 7782* (FTG, LL, MO); along trail to Cerro Pate Macho, 6 Feb. 1986 (fl), *G. McPherson & M. Merello 8296* (FTG, LL, MO); Fortuna Dam region, above N edge of lake, 27 Apr. 1986 (fl) *G. McPherson 9083* (F, FTG, MEXU, MO, NY, PMA); SE slopes and summit of Cerro Pate Macho, trails from Río Palo Alto, 4 km NE of Boquete, 26 May 1981 (fl), *K. Sytsma et al. 4831* (LL, MO); Fortuna Dam region, along Quebrada Arena, S of Continental Divide, 15 Jan. 1989 (fl), *G. McPherson 13541A* (FTG, MEXU, MO, PMA).

48. Ardisia hugonensis (Lundell) Pipoly & Ricketson, Sida 18: 513. 1998. *Auriculardisia hugonensis* Lundell, Wrightia 7: 268. 1984. *Ardisia hugonensis* (Lundell) Lundell, Phytologia 61: 64. 1986, nom. inval. TYPE: Colombia. Chocó: Mpio. de Quibdó, Corregimiento de Guayabal, Río Hugón, ca. 80 m, 12 Sep. 1976 (fr), *E. Forero & R. Jaramillo 2812* (holotype, NY!; isotype, MO!). Figure 50.

Trees 10 m tall. *Branchlets* 4.5–6 mm diam., smooth, densely appressed rufous furfuraceous-lep-

50



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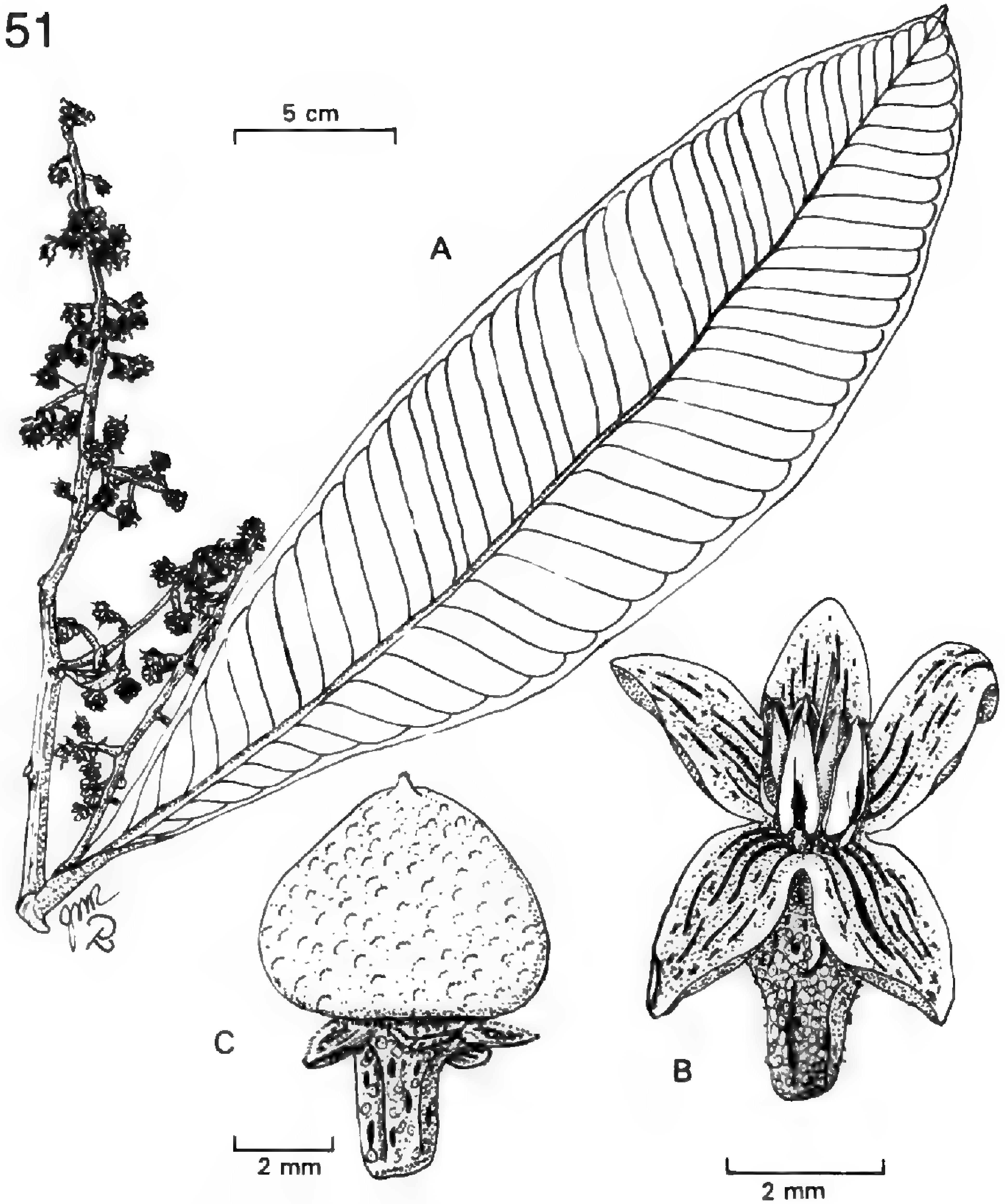


Figure 50 (left). *Ardisia hugonensis.* —A. Flowering branch. —B. Fruit. (A, B drawn from holotype, *E. Forero & R. Jaramillo 2812* (NY).)

Figure 51 (right). *Ardisia knappii.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from isotype, *S. Knapp 1843* (MO); B from *S. Knapp & M. Huft 4423* (MO); C from *S. Mori & J. Kallunki 2919* (MO).)

idote. *Leaves* with blades coriaceous, elliptic, 11.3–14.9 × 2.9–4.4 cm, apically acuminate, with an acumen 4–9 mm long, basally acute, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 25 to 33 pairs, prominulous above and below, the margins entire, inrolled; petioles slender, canaliculate, 3–6 mm long, glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, tripinnately paniculate, 11.8–13.1 × 9.5–10.5 cm, pyramidal, mostly longer than the leaves, densely cupuliform and furfuraceous-lepidote, the branches loosely congested into 3- to 7-flowered corymbs; peduncles obsolete to 5 mm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts unknown; floral bracts unknown; pedicels stout, terete, 1–1.8 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, color unknown; calyx lobes chartaceous, ovate, 1.3–1.6 × 1.3–1.8 mm, apically acute to rounded, prominently punctate and punctate-lineate, glabrous adaxially, glabrous to sparsely furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla, stamens, and pistil unknown. *Fruits* globose, 6.8–10.4 mm diam., prominently punctate and punctate-lineate, glabrous.

Distribution. *Ardisia hugonensis* is known only from the type and is endemic along the Río Hugón in Chocó, Colombia, growing at about 80 m in elevation.

Ecology and conservation status. *Ardisia hugonensis* occurs in the wettest of Neotropical forests, a true pluvial forest that may receive up to 11 m of rain per year. With increasing expansion of human populations in the area, the species should be considered threatened.

Etymology. The specific epithet refers to the Río Hugón from where the type was collected.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia hugonensis* is most closely related to *A. smurfitana* because of its short calyx lobes that are as long as or much longer than wide, short pedicels, and very long and wide coriaceous leaf blades. However, *A. hugonensis* differs from *A. smurfitana* by its smooth branchlets, smaller leaf blades to 14.9 × 4.4 cm, slender, canaliculate, shorter petioles to 6 mm long, and chartaceous, ovate, larger calyx lobes to 1.6 × 1.8 mm.

49. Ardisia knappii (Lundell) Pipoly & Ricketson, Sida 18: 513. 1998. *Auriculardisia knappii* Lundell, Phytologia 55: 235. 1984. *Ardisia knappii* (Lundell) Lundell, Phytologia 61: 65. 1986, nom. inval. TYPE: Panama. San Blas: 23–29 km from Pan-American Highway on El Llano–Cartí Road, 09°22′N, 078°69′W, 300–400 m, 28 Oct. 1981 (fl), *S. Knapp 1843* (holotype, LL!; isotype, MO!). Figure 51.

Shrubs or treelets 2.5–5 m tall. *Branchlets* stout, terete, 8–14 mm diam., densely and minutely appressed rufous furfuraceous-lepidote, glabrescent. *Leaves* with blades membranous and chartaceous, elliptic or oblong, 24.5–51 × 9.2–15.4 cm, apically acuminate, with an acumen 5–18 mm long, basally cuneate, decurrent on the petiole, prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote above, densely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 60 to 70 pairs, prominulous above, prominently raised below, the margins entire, inrolled; petioles stout, marginate, 3–8 cm long, sparsely furfuraceous-lepidote above, densely furfuraceous-lepidote below. *Inflorescences* erect, tripinnately paniculate, 9–29.5 × 5.5–17 cm, pyramidal, shorter than the leaves, densely mixed cupuliform and furfuraceous-lepidote, the branches congested, nearly glomerulate, into 15- to 25-flowered corymbs; peduncles obsolete to 1 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, ovate to oblong, 1.4–2.9 × 1.4–1.9 mm, apically acute, the veins unknown, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but ovate, 1.2–1.5 × 0.7–1 mm; pedicels slender, 1–1.7 mm, prominently punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, purple to magenta; calyx lobes membranous, ovate, 1.4–1.6 × 1.3–1.5 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 5.1–5.2 mm long, the tube 1.2–1.3 mm long, the lobes ovate, 3.8–4 × 1.8–2 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, mixed lepidote abaxially, the margins entire, hyaline; stamens 3.9–4.1 mm long, the filaments 1.8–1.9 mm long, the staminal tube 0.8–0.9 mm long, the apically free portions 0.9–1.1 mm long, the anthers narrowly ovoid, 2.3–2.4 × 1–1.1 mm, apically apiculate, basally subcordate, the connective conspicuously punctate;

pistil 4.7–4.8 mm long, glabrous, the ovary oblongoid, 0.9–1 mm long, the style 3.7–3.9 mm long, prominently punctate, the ovules 12 to 15. *Fruits* globose, 6–7.3 mm diam., prominently punctate.

Distribution. *Ardisia knappii* is found on Cerro Canta Gallo in the Indio–Maíz, in Río San Juan, Nicaragua, and along the El Llano–Cartí Road in Panamá, Veraguas, and San Blas in Panama. It is not currently known from Costa Rica. It grows from 0 to 450 m in elevation.

Ecology and conservation status. *Ardisia knappii* occurs in tropical wet forests along ridges and steep slopes. Not enough is known of its population biology to accurately determine its conservation status.

Etymology. This species was named in honor of Sandra Knapp (BM), preeminent authority on the systematics of Neotropical *Solanum.*

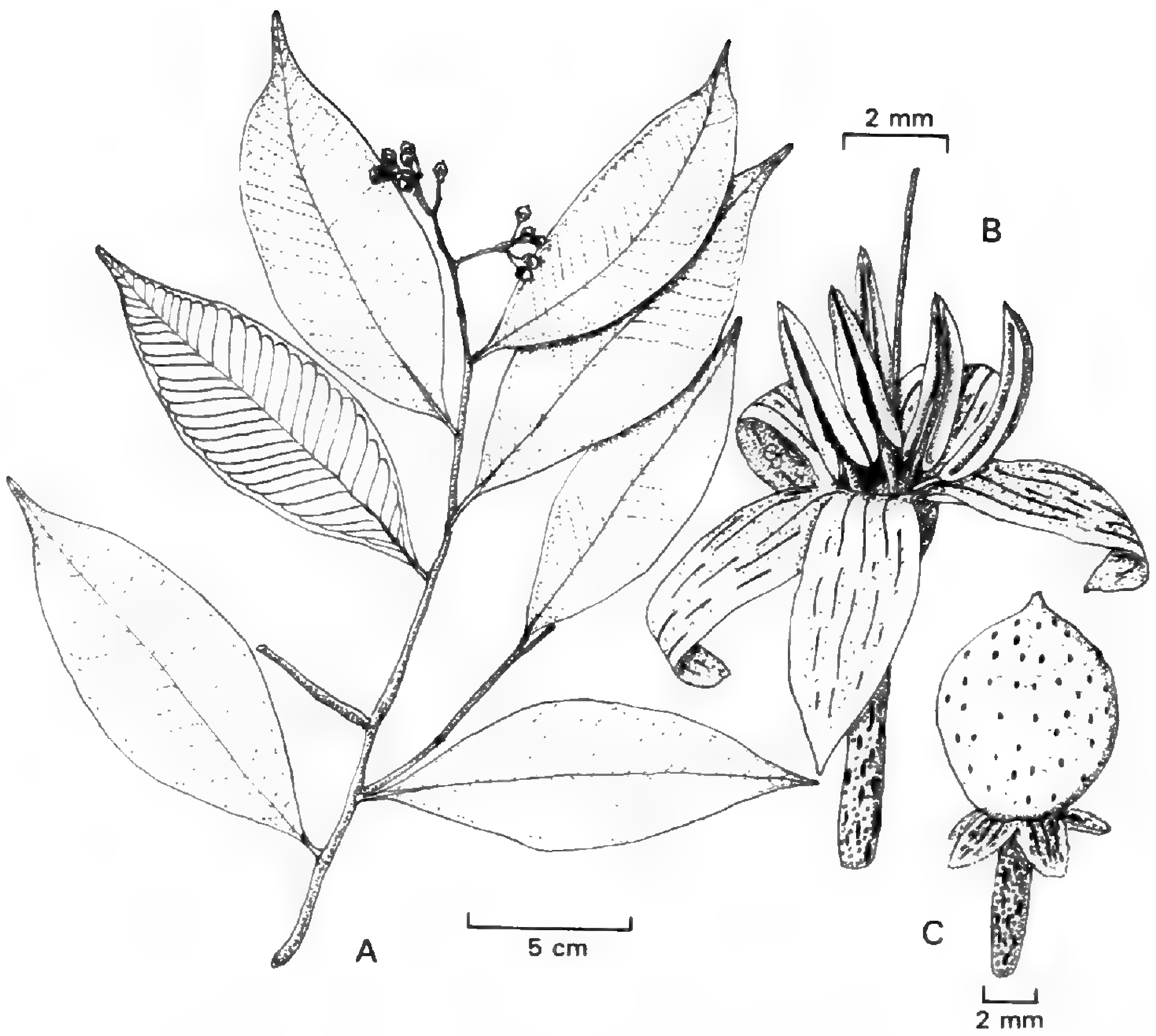
Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia knappii* is most closely related to *A. pulverulenta* because of its short calyx lobes that are as long as or longer than wide, short pedicels, and large leaf blades. However, *Ardisia knappii* differs from *A. pulverulenta* by its thicker branchlets to 14 mm in diameter, longer and wider leaf blades to 51 × 15.4 cm, wider inflorescence to 17 cm wide, longer and wider calyx lobes to 1.6 × 1.5 mm, longer and wider corolla lobes to 4 × 2 mm, wider anthers to 1.1 mm wide, and longer styles to 3.9 mm long.

Specimens examined. NICARAGUA. **Río San Juan**: Mpio. de San Juan del Norte, Reserve Indio-Maiz, Río Indio, Cerro Canta Gallo, 14 Sep. 1998 (fl), *R. Rueda et al. 8551* (HULE), 15 Sep. 1998 (fl), *R. Rueda et al. 8611* (HULE, MO), 16 Sep. 1998 (fl), *R. Rueda et al. 8656* (HULE, MO). PANAMA. **Bocas del Toro**: Escudo de Veraguas, SE side of island, 30 Mar. 1990 (fl), *P. M. Peterson 8522* (MO, US). **Panamá**: 8.2 mi. (on new road, 8.6 mi. on old road), from Pan-American Highway on the El Llano–Cartí Road, 24 Mar. 1982 (fl), *S. Knapp & M. Huft 4423* (LL, MO); 10 mi. from the Pan-American Highway on the El Llano–Cartí Road, 21 Apr. 1982 (fl), *S. Knapp et al. 4738* (LL, MO); El Llano–Cartí Road, 10–12 km from junction with Inter-American Highway, 31 Oct. 1974 (fl, fr), *S. Mori & J. Kallunki 2919* (MO); on El Llano–Cartí road, near Nusagandi, along trail to waterfall, 1 Nov. 1992 (fr), *G. McPherson & M. Richardson 16002* (FTG, MO, PMA). **San Blas**: trail along Continental Divide, 25 July 1986 (fl), *J. McDonagh et al. 394* (BM, MO); Nusagandi, ca. 20 km on El Llano–Cartí Road, trails near station, 1 May 1992 (fl), *R. Paredes et al. 908* (MO, PMA).

50. Ardisia liesneri Lundell, Wrightia 6: 106. 1980. *Auriculardisia liesneri* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Costa Rica. Puntarenas: Osa Peninsula, Corcovado National Park, slopes above Llorona, 08°36′N, 083°42′W, 0–200 m, 13 July 1977 (fr), *R. Liesner 3266* (holotype, MO!; isotype, CR!). Figure 52.

Trees 2.5–8 m tall, 4–10 cm diam. *Branchlets* slender, terete, 2–7 mm diam., densely cupuliform lepidote and stipitate stellate-tomentellous. *Leaves* with blades chartaceous, elliptic, 6.6–17.4 × 2.6–5.8 cm, apically acuminate, with an acumen 7–17 mm long, basally acute, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above, cupuliform lepidote below, with additional stipitate-stellate trichomes along the midrib, the midrib impressed above, prominently raised below, the secondary veins 21 to 41 pairs, prominulous above and below, the margins entire, flat; petioles slender, canaliculate, 8–13 mm long, 1–3 mm diam., glabrous above, vestiture below as in branchlets. *Inflorescences* erect, bipinnately paniculate, 4–8 × 3–7 cm, pyramidal, usually shorter than the leaves, cupuliform lepidote and stipitate-stellate tomentose, the branches loosely congested into 5- to 12-flowered corymbs; peduncles 0.5–1.2 cm long; inflorescence bracts unknown; inflorescence branch bracts membranous, oblong, 6–18 × 3.2–4.2 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, vestiture as in branchlets below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but spathulate, enclosing the bud (similar to *Geissanthus*), 2.5–4.2 × 1.5–2.5 mm; pedicels slender, 4.5–6.2 mm long, inconspicuously punctate and punctate-lineate, sparsely furfuraceous-lepidote and stipitate-stellate. *Flowers* 5-merous, pale orange to light pink or pink-tan; calyx lobes chartaceous, orbicular, 1.7–1.9 × 1.7–1.9 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 8.5–8.7 mm long, the tube 2.1–2.3 mm long, the lobes lanceolate, 6.2–6.4 × 2.5–2.7 mm, apically acute, conspicuously punctate and punctate-lineate, glabrous or rarely with a few furfuraceous-lepidote scales, the margins entire, hyaline; stamens 6.6–6.8 mm long, the filaments 2.8–3 mm long, the staminal tube 1.2–1.4 mm long, the apically free portions 1.4–1.8 mm long, the anthers linear-lanceoloid, 4.2–4.3 × 1–1.1 mm, apically apiculate, basally sagittate, the connective conspicuously punctate; pistil 7.1–7.3 mm long, glabrous, the ovary oblong, 1.2–1.4 mm long, the style 5.7–5.9 mm long, mostly epunctate, the ovules 33 to

52



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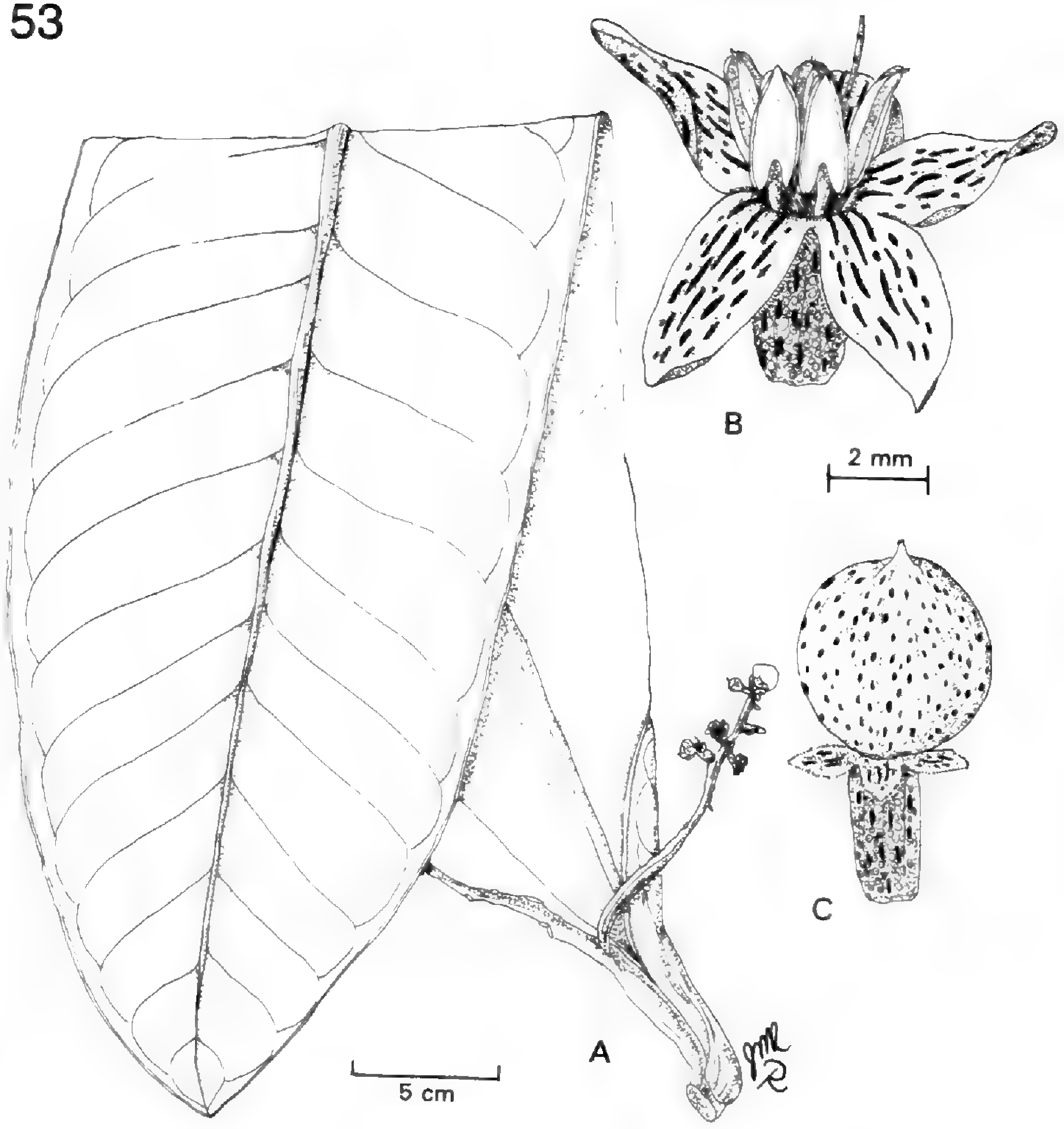

Figure 52 (left). *Ardisia liesneri.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from holotype, *R. Liesner 3266* (MO); B from *B. Hammel et al. 16899* (MO); C from *J. Marín 134* (MO).)

Figure 53 (right). *Ardisia megistophylla.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from holotype, *A. Fernández 251* (US); B from *B. Hammel 3952* (MO); C from *M. Correa A. 598* (MO).)

38. *Fruits* globose, 6.5–9.3 mm diam., inconspicuously punctate and punctate-lineate.

Distribution. *Ardisia liesneri* is endemic to the Osa Peninsula of Puntarenas, Costa Rica, growing from sea level to 400 m in elevation.

Ecology and conservation status. *Ardisia liesneri* occurs as an understory element in primary lowland wet forest. Its extremely limited distribution makes it vulnerable to threat, even though most of its known range occurs in protected lands.

Etymology. This species was named in honor of Ronald L. Liesner, senior curatorial assistant at the Missouri Botanical Garden.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia liesneri* has flowers that are most similar to those of *A. crassipedicellata* (see under that species for similarities). However, *A. liesneri* is easily separated from *A. crassipedicellata* by the mixture of cupuliform lepidote and glandular-stellate tomentum, chartaceous leaf blades, the smaller orbicular calyx lobes 1.9 × 1.9 mm, smaller corolla lobes 6.4 mm long, longer and narrower anthers to 4.3 × 1.1 mm long, and longer styles to 5.9 mm long.

Specimens examined. COSTA RICA. **Puntarenas**: Reserva Forestal Golfo Dulce, two ranges of Cerro de Oro, confluence of Río Pavón and Río Rincón, 8 Aug. 1991 (fl), *R. Aguilar 220* (CR, FTG, INB, MO); Cantón de Osa, Reserva Forestal Golfo Dulce, Península de Osa, Los Mogos, Bahía Chal, 30 July 1993 (fr), *R. Aguilar & M. Segura 2064* (CR, FTG, INB, MO); Corcovado National Park, along Llorona trail to San Pedrillo, 21 July 1977 (fr), *G. Hartshorn 1882* (F, FTG, MO); Reserva Forestal Golfo Dulce, Osa Península, trocha de La Tarde road, 10 km SW of La Palma, S of Rincón de Osa, along ridge E of the Río Rincón valley, 28 Apr. 1988 (fl), *B. Hammel & R. Robles 16737* (CR, INB, MO); Reserva Forestal Golfo Dulce, Osa Península, Rancho Quemado, ca. 15 km W of Rincón on ridge at NW end of valley, near Fila Ganado, 30 May 1988 (fl), *B. Hammel et al. 16899* (CR, FTG, LL, MEXU, MO, NY); Cantón de Osa, Reserva Forestal Golfo Dulce, Rancho Quemado Valley, ca. 15 km W of Rincón, S side of valley along Quebrada Quebradóna and Río Riyito, 11 Sep. 1990 (fr), *B. Hammel et al. 17838* (INB, MO); Cantón de Osa, Reserva Forestal Golfo Dulce, Rancho Quemado, ca. 15 km W of Rincón, in range before Rancho Quemado Valley, 1 Nov. 1992 (fr), *B. Hammel & R. Aguilar 18572* (FTG, INB, MO); Parque Nacional Corcovado, Sirena, Los Patos Forest, 26 May 1989 (fl), *C. Kernan & P. Phillips 1126* (CR, FTG, MO); Cantón de Osa, Reserva Forestal Golfo Dulce, Península de Osa, Rancho Quemado range, 21 Sep. 1993 (fr), *A. Marín & H. Gutiérrez 66* (INB, MO); Cantón de Osa, Cerro Rancho Quemado, Rincón, 20 Aug. 1991 (fr), *J. Marín 134* (CR, INB, MO); Aguabuena, 3.5 km W of Rincón, permanent plot 1 km of BOSCOSA station, 9 Sep. 1992 (fr), *K. Thomsen 95* (FTG).

51. Ardisia lundelliana Pipoly, Ann. Missouri Bot. Gard. 78: 524. 1991. TYPE: Panama. Chiriquí: vicinity Fortuna Dam, forested slopes along ridge at S boundary of watershed, 08°45′N, 082°15′W, 1250 m, 28 Apr. 1986 (fl, fr), *G. McPherson 9107* (holotype, MO! [unicate]).

For illustration, see Pipoly (1991b: 524, fig. 1).

Tree to 4 m tall. *Branchlets* stout, with fine longitudinal ridges, 5–7 mm diam., with a dense mixture of cupuliform and furfuraceous-lepidote scales. *Leaves* with blades coriaceous, elliptic, 7–18 × 4–7.7 cm, apically acute to short-acuminate, with an acumen 3–6 mm long, basally obtuse to rounded, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above, with a dense mixture of cupuliform and furfuraceous-lepidote scales below, the midrib impressed above, prominently raised below, the secondary veins 39 to 48 pairs, prominulous above and below, the margins entire, revolute; petioles slender, marginate, 1.1–2 cm long, glabrous or sparsely furfuraceous-lepidote above, with a dense mixture of cupuliform and furfuraceous-lepidote scales below. *Inflorescences* pendent, pinnate to bipinnate paniculate, 8–15 × 8–9 cm, globose, shorter than the leaves, vestiture of the rachis, abaxial bract surfaces, branchlets and pedicels similar to the branchlets, the branches loosely congested into 4- to 9-flowered corymbs; peduncles 2.3–2.7 mm long; inflorescence bracts unknown; inflorescence branch bracts membranous, lanceolate, 1.5–3.5 × 0.6–1.6 mm, apically acute, the veins inconspicuous; floral bracts similar to the inflorescence branch bracts except acute, 1.8–2 × 0.8–1 mm; pedicels slender, recurved, 6–14 mm long, inconspicuously punctate and punctate-lineate. *Flowers* 5-merous, pale pink; calyx lobes coriaceous, widely ovate, 5.2–6 × 3.6–4 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, with a dense mixture of cupuliform and furfuraceous-lepidote scales abaxially, margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous to chartaceous, 9.9–10.1 mm long, the tube 2.7–2.9 mm long, the lobes narrowly ovate, 7–7.8 × 3.4–3.6 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout except the tube sparsely furfuraceous-lepidote basally abaxially, the margin entire, hyaline; stamens 6.9–7.1 mm long, the filaments 3.5–3.6 mm long, the staminal tube 1–1.2 mm long, the apically free portions 2.4–2.5 mm long, the anthers lanceoloid, 4–4.1 × 1.2–1.3 mm, apically apiculate, basally lobate, the connective conspicuously punctate; pistil 14.4–15.1 mm long, glabrous, the ovary ovoid, 5.3–5.7 mm long, the style 9.1–9.4 mm long, prominently punctate and punctate-lineate, the ovules 19 to 24. *Fruits* (immature) globose, 5–7 mm diam., inconspicuously punctate.

Distribution. *Ardisia lundelliana* is known only from the holotype collection, growing around the Fortuna Dam in Chiriquí, Panama, at around 1250 m in elevation.

Ecology and conservation status. *Ardisia lundelliana* is a ridge-top species in montane forests. Because of its restricted distribution, it should be considered threatened.

Etymology. This species was named in honor of the late Cyrus Longworth Lundell, specialist in Myrsinaceae for over 60 years.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia lundelliana* is one of a number of species that have branchlets covered with a mixture of dense cupuliform and furfuraceous-lepidote scales. In sterile condition, *Ardisia lundelliana* may be most easily confused with *A. conglomerata* (see under that species for similarities). However, *Ardisia lundelliana* is easily separated from *A. conglomerata* because of its pendent inflorescence with much longer, recurved pedicels to 14 mm long and much larger anthers to 4.1 mm.

52. Ardisia mcphersonii Pipoly, Novon 4: 38. 1994. TYPE: Colombia. Antioquia: Mpio. Frontino, area called Murrí, in W-Central part of Antioquia, ca. 15 km from Nutibarra, 06°40′N, 076°20′W, 1875 m, 3 Nov. 1988 (fl buds), *G. McPherson, J. Zarucchi, F. Roldán & O. Escobar 12954* (holotype, HUA!; isotypes, MO!, US!).

For illustration, see Pipoly (1994: 38, fig. 1).

Trees 4–6 m tall, to 7 cm diam. *Branchlets* flexuous, slender to stout, subterete, 5–7 mm diam., with a mixture of densely cupuliform and furfuraceous-lepidote scales. *Leaves* with blades chartaceous, oblong to narrowly elliptic, 18–33 × 5.8–8.5 cm, apically abruptly acuminate, with an acumen 1.2–1.5 cm long, basally acute, decurrent on the petiole, prominently punctate above and below, essentially glabrous above, with a mixture of densely cupuliform and furfuraceous-lepidote scales, more densely so along the midrib, the midrib impressed above, prominently raised below, the secondary veins 30 to 38 pairs, prominulous above and below, the margins entire, revolute; petioles stout, canaliculate, 1.2–1.5 cm long, essentially glabrous above, below with a mixture of densely cupuliform and furfuraceous-lepidote scales. *Inflorescences* erect, tri- to quatripinnately paniculate, 21–30 × 20–30 cm, pyramidal, nearly as long as the leaves, the peduncle, rachis, secondary branches, and pedicels with a mixture of densely cupuliform and furfuraceous-lepidote scales, the branches loosely congested into 5- to 8-flowered corymbs; peduncle 2.6–3.1 cm long, the lower branches subtended by leaves; inflorescence bracts and branch bracts unknown; floral bracts early caducous, chartaceous, lanceolate, 1–1.4 × 0.3–0.4 mm, apically attenuate, prominently punctate and punctate-lineate, glabrous above, below with a mixture of densely cupuliform and furfuraceous-lepidote scales, the margins entire, densely lepidote; pedicels slender, 1.2–1.8 mm long, inconspicuously punctate and punctate-lineate, with a mixture of densely cupuliform and furfuraceous-lepidote scales. *Flowers* 5-merous, cream; calyx lobes chartaceous, suborbicular to oblate, 1.4–1.8 × 1.7–1.9 mm, apically rounded to obtuse, densely and prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular-ciliolate; corolla coriaceous, 4.2–4.4 mm long, the tube 0.3–0.5 mm long, the lobes oblong, 3.7–4.1 × 1–1.2 mm, apically acuminate, prominently punctate and punctate-lineate, glabrous throughout, the margin entire, erose, hyaline; stamens 3.2–3.6 mm long, the filaments 1–1.2 mm long, the staminal tube 0.3–0.5 mm long, the apically free portions 0.5–0.9 mm long, the anthers narrowly ovoid to lanceoloid, 2.4–2.6 × 1–1.2 mm, apically apiculate, basally sagittate, the connective epunctate; pistil 3.5–3.9 mm long, glabrous, the ovary ovoid, costate, 5-angled, 1.4–1.6 mm long, 1–1.2 mm diam., the style 2.1–2.3 mm long, epunctate, the ovules 24 to 35. *Fruits* unknown.

Distribution. *Ardisia mcphersonii* is known only from the Murrí area of Mpio. de Frontino in Antioquia, Colombia, growing from 1700 to 1990 m in elevation.

Ecology and conservation status. *Ardisia mcphersonii* occurs in montane and cloud forests. Because of its restricted distribution, it should be considered threatened.

Etymology. This species was dedicated to Gordon McPherson of the Missouri Botanical Garden, colleague and specialist in Madagascan Euphorbiaceae.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia mcphersonii* is most closely related to *A. furfuracea* (see under that species for similarities). However, *Ardisia mcphersonii* can be distinguished from *A. furfuracea* by its wider calyx lobes to 1.9 mm wide and narrower corolla lobes to 1.2 mm wide, shorter stamens to 3.6 mm long, larger anthers to 2.6 × 1.2 mm, and shorter styles to 2.3 mm long.

Specimens examined. COLOMBIA. **Antioquia**: Mpio. de Frontino, Alto de Cuevas, 10 km W of Blanquita, 12 km W of Nutibara, 3 Mar. 1992 (ster.), *A. Gentry et al. 76104* (MO); Mpio. de Frontino, km 13 of road Nutibara–La Blanquita, region of Murrí, Alto de Cuevas, 6 Nov. 1988 (fl bud), *J. Zarucchi et al. 7232* (MO).

53. Ardisia megistophylla Lundell, Wrightia 4: 147. 1970. *Auriculardisia megistophylla* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Colombia. Chocó: Costa del Pacifico, ensenada de Utria, 5 June 1950 (fr), *A. Fernández 251* (holotype, US!, LL neg. 1971-69!). Figure 53.

Ardisia atrata Lundell, Wrightia 6: 60. 1979. Syn. nov. *Auriculardisia atrata* (Lundell) Lundell, Phytologia 49: 342. 1981. TYPE: Panama. Colón: Río Gaunche in forest along Río Gaunche, 3–7 km above bridge on forested slope above river, 300–700 ft. [91–213 m], 1 Oct. 1978 (fl), *B. Hammel, R. Foster & L. McDade 4902* (holotype, MO!, F neg. 55670!, LL neg. 1979-33!; isotype, LL!).

Ardisia macrostachya Lundell, Wrightia 6: 81. 1979. Syn. nov. *Auriculardisia macrostachya* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Panama. Panamá: Gorgas Memorial Labs yellow fever research camp, "Campamento Quatro," 5–10 km NE Altos de Pacora, on ridge top, ca. 600 m, 21–24 Nov. 1974 (fl), *S. Mori & J. Kallunki 3417* (holotype, MO!, F neg. 55666!).

Trees 2–8 m tall. *Branchlets* stout, terete, 9–15 mm diam., densely rufous furfuraceous-lepidote. *Leaves* with blades chartaceous, elliptic to oblong or narrowly oblong, 23.2–61.4 × 7.1–21.3 cm, apically acute, with an acumen 6–17 mm long, basally acute, decurrent on the petiole, prominently punctate and punctate-lineate above and below, nearly glabrous above, furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 70 to 85 pairs, prominently raised above and below, the margins entire, inrolled; petiole stout, marginate, 1.4–5.5 cm long, 4–12 mm diam., nearly glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, 12–37 × 9–19 cm, pyramidal, shorter than the leaves, the branches congested into 9- to 13-flowered corymbs; peduncles obsolete to 2 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, ovate to oblong, 3.2–8.3 × 1.2–4.8 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below of dense, obsolete flat scales with the margins entire or with small teeth, the midrib impressed above, prominulous below, the secondary veins inconspicuously raised, the margins entire, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 0.6–1.1 × 0.5–0.8 mm; pedicels stout, 0.5–3 mm long, prominently punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5- or 6-merous, white, light pink, pink-blue, or red; calyx lobes chartaceous, ovate, 2.6–2.8 × 1.8–2 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 7–7.2 mm long, the tube 1.5–1.8 mm long, the lobes ovate to narrowly ovate, 5.4–5.5 × 2.2–2.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 5.5–5.7 mm long, the filaments 2.7–2.8 mm long, the staminal tube 1–1.1 mm long, the apically free portions 1.6–1.8 mm long, the anthers lanceoloid, 3.1–3.3 × 0.9–1 mm, apically apiculate, basally cordate, the connective conspicuously punctate; pistil 6.4–6.8 mm long, glabrous, the ovary ovoid to oblong, 1–1.2 mm long, the style 5.4–5.6 mm long, epunctate, the ovules 11 to 13. *Fruits* globose, 6–9 mm diam., prominently punctate.

Distribution. *Ardisia megistophylla* ranges from central Panama to Chocó, Colombia, growing from 91 to 1000 m in elevation.

Ecology and conservation status. *Ardisia megistophylla* occurs in lowland pluvial riverine forests. Apparently, it is a fairly rare species and should be considered threatened.

Etymology. The specific epithet was derived from the Greek "megisto," very big or very large, and "phyla," leaves.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia megistophylla* is most closely related to *A. aguirreana*, *A. cogolloi*, *A. crassipes*, and *A. cartagoana* because of its long calyx lobes and thick petioles. *Ardisia megistophylla* can easily be separated from all these by its longer calyx lobes to 2.8 mm long, longer corolla lobes to 5.5 mm long, longer anthers to 3.3 mm long, and longer styles to 5.6 mm long.

The type of *Ardisia atrata* is unique only for its slightly longer pedicels and slightly larger calyx lobes. The type of *A. macrostachya* is unique only for its slightly subsessile petioles and slightly larger calyx lobes.

Specimens examined. PANAMA. **Coclé**: along river leading up mountain to Alto Calvario and trout stream from La Junta near Limón, 12 Oct. 1977 (fl, fr), *J. Folsom 5898* (MO). **Colón**: E Santa Rita Ridge, lumber road, 11

Jan. 1968 (fr), *M. Correa A. 598* (MO); vicinity of San Miguel de la Borda, 21 Apr. 1970 (fl, fr), *T. Croat 9859* (MO); swampy area behind beach, 21 Apr. 1970 (fr), *T. Croat 9868A* (MO); swampy area between beach and forest, 25 Apr. 1970 (fl), *T. Croat 10071A* (MO); Santa Rita Ridge, 1 Mar. 1971 (fr), *T. Croat 13839* (MO); head waters of Río Boqueron near fork with Río Nombre de Diosito, near area where abandoned trail road crosses the ridge, 21 July 1978 (fl), *B. Hammel 3952* (MO); Santa Rita Ridge Rd., 20–22 km from Transisthmus Hwy., 25 Sep. 1980 (fl), *K. Sytsma 1326* (LL, MO). **San Blas:** Cerro Brewster, 16 Oct. 1984 (fr), *G. de Nevers et al. 4046* (MO). **Veraguas:** mouth of Río Concepción, 4 Dec. 1967 (fr), *W. Lewis et al. 2808* (LL, MO, MOCZ). COLOMBIA. **Chocó:** N ridge of Alto de Buey, above Dos Bocas del Río Mutatá, tributary of Río El Valle, ESE of El Valle, 8 Aug. 1976 (fl), *A. Gentry & M. Fallen 17418* (LL, MO).

54. Ardisia nigropunctata Oerst., Vidensk. Meddel. Dansk Naturhist. Føren Kjøbenhavn 1861: 127. 1862. *Auriculardisia nigropunctata* (Oerst.) Lundell, Phytologia 54: 285. 1983. TYPE: Costa Rica. Cartago: Monte Irasú [Irazú], 8000–9000 ft. [2438–2743 m], Jan. 1847 (fr), *A. Oersted 28D* (lectotype, designated here, C!, F neg. 22953!). Figure 54.

Ardisia chontalensis Mez, in Engl., Pflanzenr. IV. 236 (Heft 9): 90. 1902. Syn. nov. *Auriculardisia chontalensis* (Mez) Lundell, Phytologia 54: 285. 1983. TYPE: Panama. Bocas del Toro: Laguna de Chiriquí and its neighborhood, Nov.–Dec. 1885 (fl), *J. Hart 136* (lectotype, designated here, K!, LL neg. 71-147!; isolectotype, US!).

Ardisia mammosa Lundell, Wrightia 4: 60. 1968. Syn. nov. *Auriculardisia mammosa* (Lundell) Lundell, Phytologia 54: 285. 1983. TYPE: Nicaragua. Granada: summit of Mt. Mombacho, near Granada, 1160 m, 24 Dec. 1940 (fl), *V. Grant 869* (holotype, A!, LL neg. 1971-65!).

Auriculardisia quadrata Lundell, Phytologia 56: 413. 1984. Syn. nov. *Ardisia quadrata* (Lundell) Lundell, Phytologia 61: 66. 1986, nom. inval. *Ardisia quadrata* (Lundell) J. F. Morales, Phytologia 83: 111. 1997. TYPE: Costa Rica. Puntarenas: foothills of the Cordillera Talamanca, around Tres Colinas, 1800–1850 m 20 Mar. 1984 (fl, fr), *G. Davidse, G. Herrera Ch. & R. Warner 25645* (holotype, LL!; isotypes, INB not seen, MO!).

Auriculardisia moraviana Lundell, Phytologia 63: 74. 1987. Syn. nov. *Ardisia moraviana* (Lundell) Lundell, Phytologia 63: 463. 1987. TYPE: Costa Rica. San José: roadside leading from Alto La Palma to Bajo La Hondura, ca. 10 km NE of San Vicente de Moravia, 1260–1550 m, 24 Feb. 1978 (fr), *R. Wilbur 24919* (holotype, DUKE!).

Trees 1.5–10 m tall, 2.6–25 cm diam. *Branchlets* slender, terete, 2–7 mm diam., densely and minutely appressed ferrugineous furfuraceous-lepidote. *Leaves* with blades membranous to coriaceous, oblong or elliptic to oblanceolate, 6–45 × 2–16 cm, apically acute to acuminate or rounded, with an acumen 5–25 mm long, basally obtuse to acute or cuneate, decurrent on the petiole, prominently punctate and punctate-lineate, mostly glabrous above, densely and minutely appressed rufous furfuraceous-lepidote, the midrib impressed above, prominently raised below, the secondary veins 30 to 50 pairs, bullate above, prominently raised below, the margins entire to dentate or serrate, flat; petioles slender, marginate, 4–18 mm long, 1–3 mm diam., glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, 7–52 × 5–28 cm, pyramidal, usually longer than the leaves, the rachis straight to geniculate, the peduncle, rachis, branches, and pedicels furfuraceous-lepidote, the branches loosely congested into 3- to 9-flowered corymbs; peduncle nearly obsolete to 4.2 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, lanceolate to oblong, 1.3–4.3 × 0.5–1.2 cm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 0.5–2.1 × 0.2–0.5 mm; pedicels slender, furfuraceous-lepidote. *Flowers* 5- or 6-merous, white to pink or light purple; calyx lobes membranous to chartaceous, ovate, 1.7–2.4 × 1.2–2 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote, the margins erose, hyaline, sparsely glandular ciliolate; corolla membranous, 4.9–5.8 mm long, the tube 0.8–1.1 mm long, the lobes narrowly ovate to lanceolate, 3.9–5 × 1.5–2.5 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins entire, hyaline; stamens 3.3–4.5 mm long, the filaments 1.9–3.6 mm long, the staminal tube 0.5–0.8 mm long, the apically free portions 1.4–2.8 mm long, the anthers narrowly ovoid, 1.9–2.8 × 0.8–1.4 mm,

→

Figure 54 (left). *Ardisia nigropunctata.* —A. Flowering branch. —B. Flower. —C. Fruit. (A & C drawn from lectotype, *A. Oersted 28D* (C); B from *R. Wilbur 63199* (MO).)

Figure 55 (right). *Ardisia palmana.* —A. Flowering branch. —B. Flower. —C. Fruit. (A, B drawn from isotype, *A. Tonduz 12632* (*7406*) (K); C from *D. Acevedo 78* (MO).)

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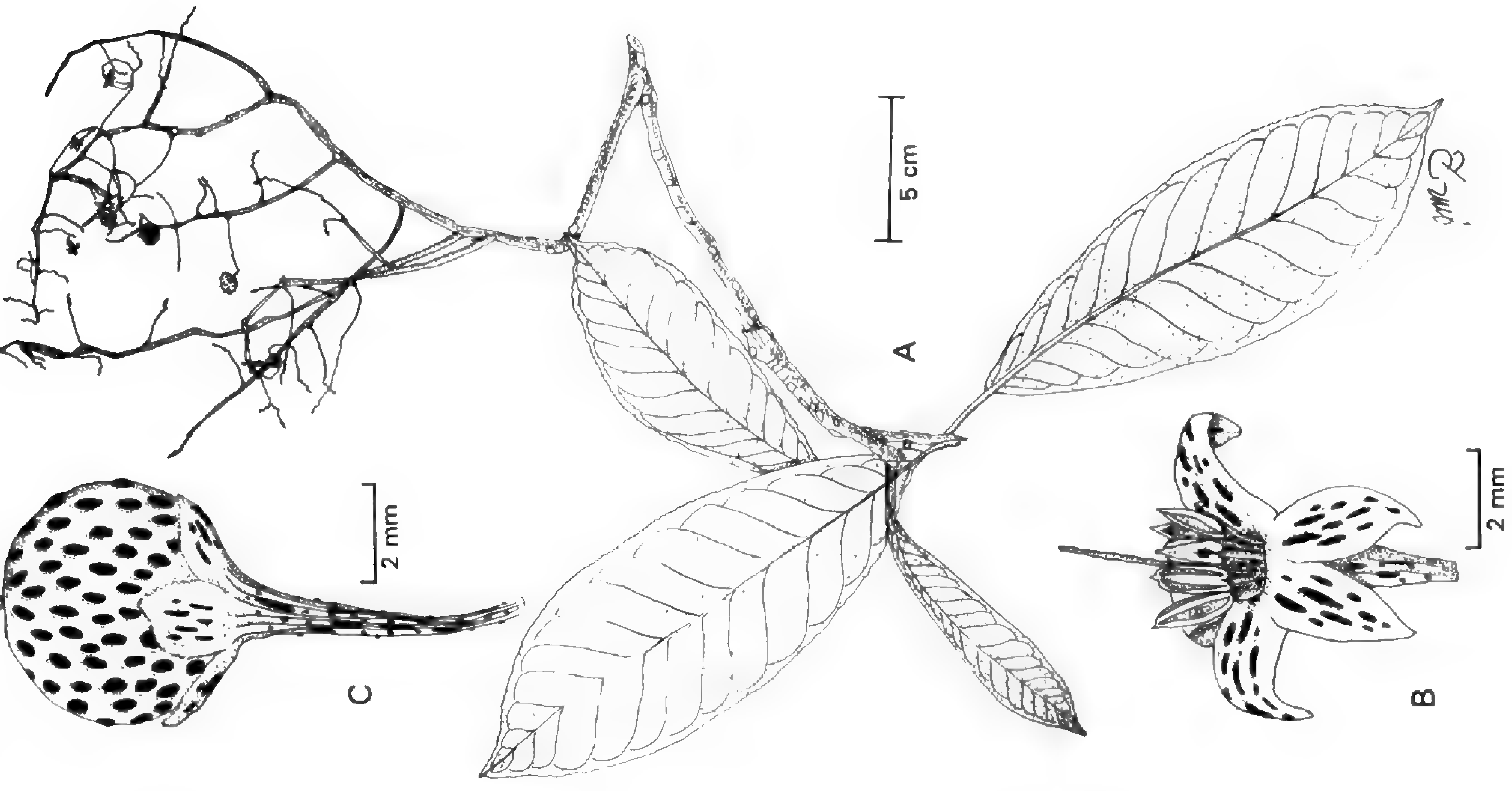

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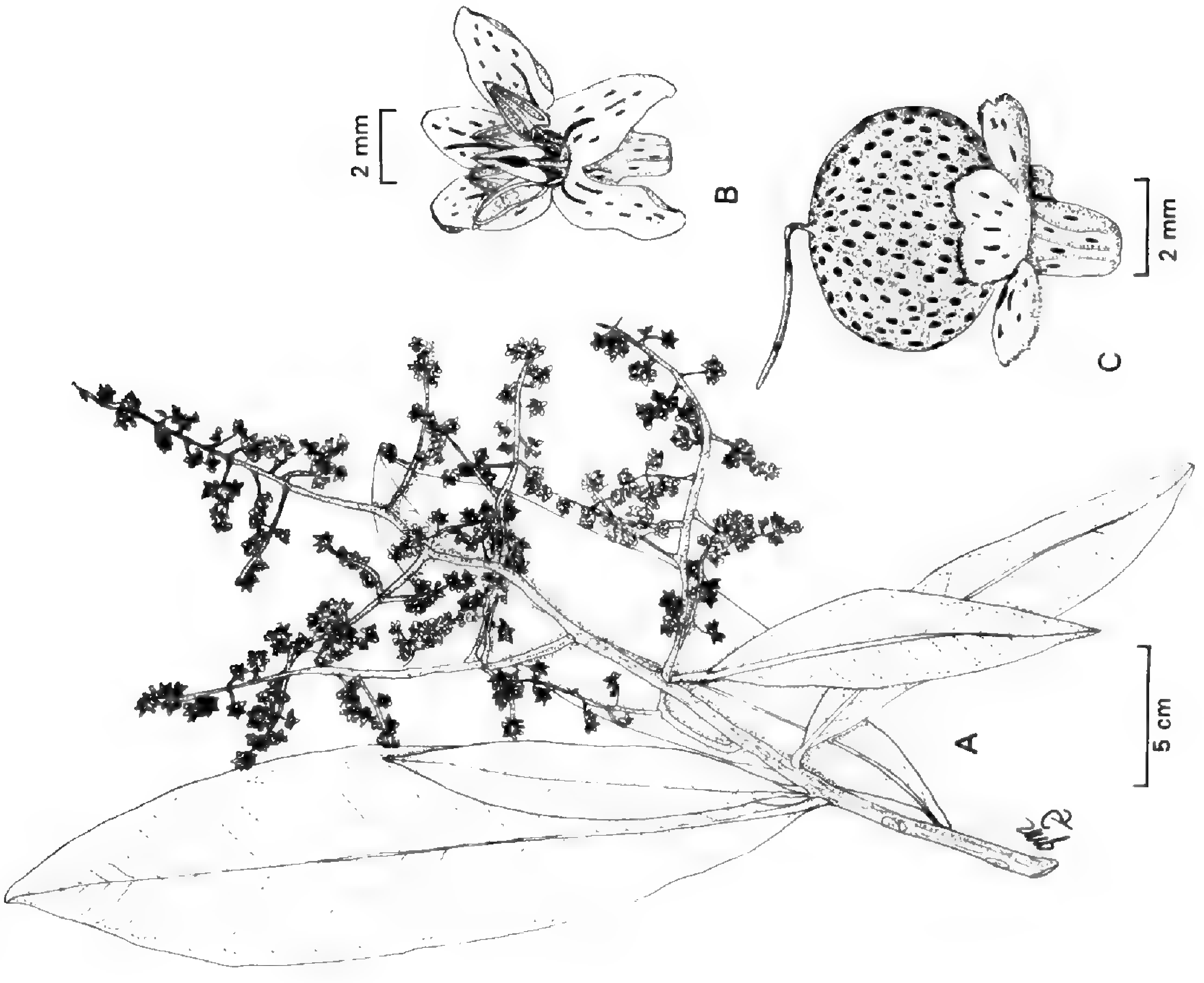

apically apiculate-mucronate, basally deeply cordate, the connective conspicuously punctate; pistil 8.5–9.3 mm long, glabrous, prominently punctate, the ovary oblong, 1–1.1 mm long, the style 7.5–8.3 mm long, prominently punctate and punctate-lineate, the ovules 12 to 20. *Fruits* globose, 5–9 mm diam., prominently punctate.

Distribution. *Ardisia nigropunctata* is widely distributed from Belize to Panama, growing at 5 to 3200 m in elevation.

Ecology and conservation status. *Ardisia nigropunctata* occurs in moist forests, from premontane to cloud forests, and is always found along the forest margins. Its tolerance to disturbance and broad habitat range combine to give the species great resiliency, and it is not considered threatened.

Etymology. The specific epithet refers to the black punctations throughout the plant.

Common Names. "High Ridge Blossom Berry" (*P. Gentle 3982*); "Blossom berry" (*P. Gentle 6406*); "Asib" (*P. Gentle 7187*); "Blossom berry grape" (*P. Gentle 3294*); "Manchador" (*S. Record 25*); "Uva Montañera" (*R. Rueda et al. 2674*).

Pipoly (unpublished data) has observed that this species is the favorite for adorning altars in religious services throughout northeastern Nicaragua.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia nigropunctata* is most similar to *A. angucianensis* (see under that species for similarities). However, *A. nigropunctata* can be separated by its shorter and narrower calyx lobes to 2.4 × 2 mm and larger fruits to 9 mm in diameter.

In the description by Oersted (1862: 127) two collections were listed, one flowering in May 1847 from "monte Barba," and the other in fruit collected in January 1847 from "monte Irasu," both present at C. The collection from Barba is labeled as *A. Oersted 28C,* and the Irasu collection is labeled as *A. Oersted 28D.* We hereby designate the *A. Oersted 28D* collection at C as the lectotype because it is by far the more complete collection.

In his original description, Mez (1902) listed three collections for *Ardisia chontalensis, R. Tate 228* from Nicaragua (in young fruit), *B. Seemann 59* from Chontales, Nicaragua (in bud), and *J. Hart 136* from Chiriquí, Panama (in flower), all from K. All three sheets are fragmented with no attached leaves. We here select the original K specimen of *J. Hart 136* as the lectotype because it is in flower.

Ardisia nigropunctata, as with many species of *Ardisia,* exhibits continuous quantitative variation over a broad range of leaf and floral part sizes, and this has caused much over-description. Material corresponding to the type of *A. chontalensis* is unique only for its less geniculate inflorescence, but matches *A. nigropunctata* in all other respects. The type of *A. mammosa* is unique only for its buds with strongly contorted and constricted corolla, which Lundell (1968) characterized as "mammose" or nipple-shaped. The type of *Auriculardisia quadrata* is unique for its slightly larger and more glabrous leaf blades with conspicuously punctate and punctate-lineations; however, these fall into the variation of *A. nigropunctata* as circumscribed by us. The type of *Auriculardisia moraviana* is in fruit and unique only for its large, glabrous leaf blades, which are similar to those of *A. quadrata*; however, the fruits match those of *Ardisia nigropunctata* exactly.

Specimens examined. BELIZE. **Cayo**: Chiquibul, Raspaculo Camp, 28 Mar. 1996 (fr), *A. Monro 1347* (BM, MO). **Stann Creek**: Stann Creek Valley, 17 mi., 7 Feb. 1940 (fl), *P. Gentle 3205* (A, K, LL [2], MICH, NY, US); Stann Creek Valley, Mountain Cow Ridge, 30 Mar. 1940 (fr), *P. Gentle 3294* (A, LL, MICH, MO, NY). **Toledo**: southern Maya Mountains, Bladen Nature Reserve, riverside vegetation between AC Camp and AC Camp helicopter landing site, upper Bladen Branch, 8 May 1996 (fr), *G. Davidse & M. Meadows 35751* (BRH, FTG, MO, SEL); southern Maya Mountains, Bladen Nature Reserve, West Snake Creek, 28 May 1997 (fl), *D. Holland & B. Kid 105* (BRH, MO, SEL). GUATEMALA. **Alta Verapaz**: between Cubilgüitz and Yakapur, 10 Mar. 1942 (fr), *J. Steyermark 44888* (F). **Izabal**: Los Andes to Entre Ríos, 1 Mar. 1926 (fr), *S. Record 25* (MAD-Y, US); along Río Bonita, 21 Dec. 1941 (fl), *J. Steyermark 41701* (F). **Petén**: on Sebol Road, 18 km from San Luís, 20 Nov. 1966 (fl), *E. Contreras 6619* (LL [2]). HONDURAS. **Cortes**: Cienaga tract near Agua Azul, Lake Yojoa, 31 Dec. 1952 (fl), *L. Williams & R. Williams 18793* (US). **Gracias a Dios**: Camp Tiro, 2 mi. NW of Bulebar on third N branch of Quebrada Tiro, tributary of Río Platano, between Río Platano and camp, 30 Mar. 1981 (fl), *J. Saunders 1161* (LL, NY). **Olancho**: Quebrada Catacamas cerca de la Oresa del agua potable en Montaña Peña Blanca, Catacamas, 28 Apr. 1957 (fr), *A. Molina R. 8338* (F, NY). **Santa Barbara**: Cienaga tract, area E of Lake Yojoa, 9 Feb. 1952 (fl), *P. Allen 6445* (F). **Yoro**: Cerro between Río Guán Guán and Río Texíguat, E of Cerro Guán Guán, S of San José in the Río Leán Valley, W end of the Cordillera Nombre de Dios, 6 Nov. 1988 (fl), *J. MacDougal et al. 3231* (LL, MO). NICARAGUA. **Chontales**: Cerro Oluma, ca. 3 km SW of Cuapa, 3 Jan. 1984 (fr), *A. Grijalva et al. 3380A* (MO). **Granada**: Volcán Mombacho, hacienda Las Delicias, ca. 10 km al SE, ciudad Granada, 21 Mar. 1984 (fr), *A. Grijalva et al. 3675* (HNMN, MO). **Jinotega**: Mpio. de Wiwilí, buffer zone to Bosawás, Macizos del Cerro Kilambé, 9 Apr. 1998 (fr), *R. Rueda & I. Coronado 8114* (HULE, MO). **Matagalpa**: Macizos de Peñas Blancas, SE side drainage of Quebrada El Quebradón, slopes N & W of Hda. San Martín, on border with Dept. Jinotega, 18–20 Jan. 1982 (fr), *W. Stevens et al. 20996* (DUKE, HNMN, MO, NY). **Nueva Segovia**: along Quebrada Tastaslí, branch of Río Solonlí, 3 km S of Jalapa, 6 Apr. 1977 (fr), *D. Neill 1659* (MO). **Río San Juan**: valley of Río Indio, 6 km upstream from the junction with Caña La Pimienta, 24 Feb. 1977 (fr), *D. Neill 1503* (HNMN, MO); Mpio. San

Juan del Norte, delta 1 km E and 2 km N, 8 July 1995 (fr), *R. Rueda et al. 2674* (FTG, HULE, MO). **Rivas**: Isla de Ometepe, slopes of Volcán Maderas S of Hacienda Magdalena, 28 Nov. 1982 (fl), *P. Moreno 18873* (MO); Isla Ometepe, Volcán Concepción, N slope, 21 Jan. 1983 (fr), *P. Moreno 19789* (MO, NY). **Zelaya**: NE Nicaragua, region of Braggman's Bluff, near Station 451, 16 Dec. 1927 (fl), *F. Englesing 79* (F, K); Monkey Point, Caño El Pato, 1.5 km from canyon, 25 Oct. 1981 (fr), *P. Moreno 12377* (MO, NY); near Bil Tingnia, 6 km NW of Bonanza, 13 May 1978 (fl), *D. Neill 3974* (HNMN, MO); Bonanza, on grounds of Neptune Mining Co., 26 Feb. 1979 (fr), *J. Pipoly 3522* (HNMN, MO, NY); Estación Experimental El Recreo, 7 Feb. 1985 (fr), *D. Ríos 305* (MO, NY). **Without locality**: s.d. (fl, fr), *E. Friedrichsthal 6* (K), 1867–1868 (fl), *R. Tate 228* (K). COSTA RICA. **Alajuela**: E slopes of Volcán Miravalles, W of Bijagua, near the Río Zapote, 11–12 Feb. 1982 (fl), *W. Burger et al. 11676* (CR, F, LL, NY); Reserve Forestal, San Ramón, 18 Feb. 1983 (fr), *A. Carvaljal 355* (LL MO, NY). **Cartago**: near bridge over Río Grande de Orosi at Tapanti, 2 Dec. 1978 (fl, fr), *T. Antonio 872* (F, LL); Turrialba, Tayutis, between Hacienda Moravia and Calaveras, 3 Aug. 1995 (fl), *G. Herrera 8273* (CR, F). **Guanacaste**: Cantón de Tilarán, San Gerardo Abajo, Río Caño Negro, Fincas Quesada and Arce, 5 Dec. 1991 (fl), *E. Bello C. & E. Cruz 4298* (FTG, INB, MO). **Heredia**: Cantón de Sarapiquí, Parque Nacional Braulio Carrillo, Puesto El Ceibo, on ridge crest 250 m E of Transect trail, 5 Mar. 1994 (ster.), *B. Boyle et al. 2920* (FTG, INB, MO); Monte Barba [Barva], May 1847 (fl), *A. Oersted 28C* (C). **Limón**: Braulio Carrillo National Park, trail S of Quebrada Gonzales, 11 Aug. 1992 (ster.), *M. Böhlke 106* (F); Limon River, Nov. 1904 (fl), *H. Pittier s.n.* (NY, US). **Puntarenas**: Cantón de Osa, Fila Costeña, Fila Cruces, headwaters of Río Piedras Blancas, Cerro Anguciana, W slope, 9 Dec. 1993 (fr), *B. Hammel et al. 19258* (CR, FTG, INB, MO). **San José**: Cantón de Pérez Zeledón, Cuenca Térraba Sierpe, Estación Santa Elena, 13 Sep. 1997 (ster.), *E. Alfaro & M. Segura 1387* (INB, MO); Cantón de Pérez Zeledón, Chirripó, Cordillera Talamanca, Camino a Cerro Chirripó, 31 July 1996 (ster.), *B. Gamboa & A. Rojas 538* (INB, MO). PANAMA. **Bocas del Toro**: 1.5 mi. W of Almirante, 15 Oct. 1965 (fl), *K. Blum 1378* (MO); near headwaters of Río Culebra ca. 5 km ENE of Cerro Pate Macho, 11 Feb. 1979 (fr), *B. Hammel 6119* (MO); vicinity of Chiriquí Lagoon, Water Valley, 4 Dec. 1940 (fl), *H. von Wedel 1823* (F). **Chiriquí**: Fortuna Dam area, N fork of the Quebrada de Arena, along river, 6 Feb. 1984 (fr), *H. Churchill et al. 4670* (LL, MO). **Panamá**: Canal Zone, Río Providencia 3 km SE of Achiote near W border of Canal Zone, 5 Dec. 1973 (fl, fr), *A. Gentry & M. Nee 8691* (LL, MO). **Veraguas**: road from Santa Fé, past Ag School to base of Cerro Tuti, along first stream, flows from Cerro Tuti, 4 Feb. 1977 (ster.), *J. Folsom 1593* (MO); Islotes de Cativo, 1841 (fr), *E. Friedrichsthal 613* (W [2], F neg. 31990).

55. Ardisia palmana Donn. Sm., Bot. Gaz. 27: 434. 1899. *Auriculardisia palmana* (Donn. Sm.) Lundell, Phytologia 49: 345. 1981. TYPE: Costa Rica. San José: in sylvis prope La Palma, 1460 m, Sep. 1898 (fl), *A. Tonduz 12632 (7460)* (holotype, US! [2]; isotypes, BM!, CR not seen, F!, F neg. 68244!, G! [3], GH!, K!, LL!, LL neg. 71-125!, M!, NY! [2]). Figure 55.

Ardisia rufa Lundell, Wrightia 4: 182. 1971. Syn. nov. *Auriculardisia rufa* (Lundell) Lundell, Phytologia 49: 345. 1981. TYPE: Panama. Chiriquí: mountain slopes SE of Cerro Punta, 6500–7000 ft. [1981–2134 m], 22 May 1971 (fr), *G. Proctor 32020* (holotype, LL!, F neg. 55644!; isotypes, F!, F neg. 68248!, K!, LL!, MICH!).

Ardisia boquetensis Lundell, Wrightia 6: 64. 1979. Syn. nov. *Auriculardisia boquetensis* (Lundell) Lundell, Phytologia 49: 342. 1981. TYPE: Panama. Chiriquí: on Boquete Trail, 4 km from Cerro Punta, near Pas de Respingo, ca. 2300 m, 22 Apr. 1975 (fr), *S. Mori & J. Kallunki 5733* (holotype, LL!; isotype, MO!).

Ardisia gentryi Lundell, Wrightia 6: 77. 1979. Syn. nov. *Auriculardisia gentryi* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Colombia. Chocó: N ridge of Alto de Buey, ESW of El Valle, 500–1150 m, 8 Aug. 1976 (fl), *A. Gentry & M. Fallen 17348* (holotype, LL!, F neg. 55656!; isotypes, LL!, MO!, NY!).

Ardisia ometepensis Lundell, Wrightia 6: 85. 1979. Syn. nov. *Auriculardisia ometepensis* (Lundell) Lundell, Phytologia 49: 345. 1981. TYPE: Nicaragua. Rivas: Isla Ometepe, Lago de Nicaragua, Volcán Maderas, N slope on wind beaten ridge near summit, 1200 m, 24 Feb. 1978 (fr), *D. Neill & P. Vincelli 3298* (holotype, MO!).

Auriculardisia eurubiginosa Lundell, Phytologia 56: 413. 1984. Syn. nov. *Ardisia eurubiginosa* (Lundell) Lundell, Phytologia 61: 63. 1986, nom. inval. *Ardisia eurubiginosa* (Lundell) J. F. Morales, Phytologia 83: 111. 1997. TYPE: Panama. Bocas de Toro: Cordillera Talamanca, 2–5 airline km NW of the peak of Cerro Echandi on the Costa Rican–Panamanian international border, 09°03–04′N, 082°50–51′W, 2600–2850 m, 1 & 9 Mar. 1984 (fr), *G. Davidse, L. Gómez, G. Herrera, C. Chacón & I. Chacón 25486* (holotype, LL!; isotypes, MO!, NY!).

Auriculardisia microcalyx Lundell, Wrightia 7: 270. 1984. Syn. nov. Non *Ardisia microcalyx* Lundell, Wrightia 4: 46. 1968. *Ardisia azaharensis* Lundell, Phytologia 61: 62. 1986, nom. inval. *Ardisia azaharensis* Pipoly & Ricketson, Sida 18: 511. 1998. TYPE: Costa Rica. Alajuela: 15 km NW of San Ramón by air, Cerro Azahar, headwaters of Río San Pedro, by road, 9 km NW of San Ramón to Piedades Norte, then 3 more km NW to La Paz, 1.7 km to cluster of houses, then left again on jeep road 45 km to top of ridge, 10°09′30″N, 084°34–35′W, 1400–1500 m, 14 May 1983 (fr), *R. Liesner, E. Judziewicz, J. Gómez-Laurito, B. Pérez G. & A. Carvajal 15575* (holotype, LL!; isotypes, F!, MO!).

Small to large trees 2–22 m tall, 10–35 cm diam. *Branchlets* slender, terete, 3–10 mm diam., densely furfuraceous-lepidote. *Leaves* with blades membranous or chartaceous, elliptic or oblong, 8.3–32.7 × 3.1–8.8 cm, apically acuminate, with an acumen 2–19 mm long, basally acute, decurrent on the petiole, the midrib impressed above, prominently raised below, the secondary veins 52 to 65 pairs, prominulous above and below, prominently punctate and punctate-lineate, densely furfuraceous-lepidote, mostly glabrescent with age above, the margins entire, flat to inrolled; petioles slender, canaliculate, 5–12 mm long, sparsely to densely furfuraceous-lepidote. *Inflorescences* erect, tripinnately paniculate, 14–27.5 × 14–38 cm, pyramidal, longer than the leaves, mixed cupuliform and furfuraceous-lepidote, the branches loosely congested into 3- to 12-flowered corymbs; peduncles obsolete to 18 mm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts unknown; floral bracts caducous, membranous, ovate, 1.6–1.9 × 1–1.2 mm, apically acute, glabrous adaxially, furfuraceous-lepidote abaxially, the margin minutely erose, hyaline, sparsely glandular ciliolate; pedicels stout, 1–2.5 mm long, inconspicuously punctate and punctate-lineate, cupuliform lepidote. *Flowers* 5-merous, white to light pink; calyx lobes chartaceous to coriaceous, orbicular to oblate, 1.1–1.4 × 1.4–1.9 mm, apically acute to rounded, prominently punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 4–4.8 mm long, the tube 1.1–1.4 mm long, the lobes narrowly ovate to ovate, 2.7–3.7 × 2.2–2.5 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 4.1–4.4 mm long, the filaments 2.3–2.5 mm long, the staminal tube 0.6–0.8 mm long, the apically free portions 1.6–1.9 mm long, the anthers narrowly ovoid to lanceoloid, 1.9–2.5 × 0.8–1.2 mm, apically apiculate, basally subcordate, the connective conspicuously punctate; pistil 4.9–5 mm long, glabrous, the ovary oblongoid, 1.3–1.4 mm long, the style 3.5–3.6 mm long, epunctate to inconspicuously punctate, the ovules 30 to 33. *Fruits* globose, 5–9 mm diam., prominently punctate and punctate-lineate.

Distribution. *Ardisia palmana* is distributed from Rivas, Nicaragua, throughout Costa Rica to Bocas del Toro and Chiriquí, Panama, growing from 600 to 2850 m in elevation.

Ecology and conservation status. *Ardisia palmana* occurs in primary and secondary forests and forest edges from lower premontane, montane, evergreen cloud forests, cloud forests, and elfin forests. This species should not be considered threatened.

Etymology. The specific epithet was derived from the name of the type locality, La Palma, San José, Costa Rica.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia palmana* is most similar to *A. anchicayana* (see under that species for similarities). However, *Ardisia palmana* may be separated from *A. anchicayana* by the shorter calyx lobes to 1.4 mm long, shorter corolla lobes to 3.7 mm long, shorter anthers to 2.5 mm long, and shorter styles to 3.6 mm long.

The original handwritten collection labels state, "Forêts de La Palma, 1459 m, 25 IX 1898, *Ad. Tonduz 12632*." However, two different handwritten labels can be found, one from the Herb. Instit. Physico-Geogr. Nat. Costaricensis, the other from the Herbier Boissier. In John Donnell Smith's original description he Latinized the type collection stating, "In sylvis propre La Palma, alt. 1460 m, Sept. 1898, *Tonduz n. 12632* herb. nat. Cost." John Donnell Smith made mass distributions of this collection with labels titled "Ex Plantis Guatemalensibus Necnon Salvadorensibus, Hondurensibus, Nicaraguensibus, Costaricensibus, Quas Edidit John Donnell Smith." The remaining label for this species states, "7460. Ardisia Palmana, Donn. Sm. in Bot. Gaz. xxvii. 434. La Palma, Prov. San José, Costa Rica, alt. 1460 m. M.[month] Sept. 1898. Leg. [collector] *Tonduz*, (n. *12,632* herb. nat. Cost.)." Thus the number *7460* has often been associated with this collection, which is the Donnell Smith Herbarium number rather than Tonduz's collection number. It is important to note that the holotype at US consists of two sheets comprising a single gathering, one with the inflorescence and the other with the branchlet apex. Therefore, no lectotypification is necessary.

Ardisia palmana, as with many species of *Ardisia*, exhibits continuous quantitative variation over a broad range of vegetative and floral parts, and this has caused much over-description. Material corresponding to the type of *Ardisia rufa* is unique only for its slightly more rufous indument. The type of *A. boquetensis* is unique only for its thinner leaves and apparently few flowers; however, it is in fruit and appears to have lost most of its flowers. The type of *A. gentryi* is unique for its smaller flowers, which are primarily in bud. The type of *A. ometepensis* is in young fruit and only unique for slightly larger and more numerous ovules and slightly thicker pedicels. The type of *Auriculardisia eurubiginosa* is unique for its slightly narrower leaf blades and thicker calyx lobes. The type of *A. microcalyx* is in fruit and unique for its slightly smaller calyx and thicker, shorter pedicels. However, all these specimens fall into the variation of *A. palmana* as circumscribed by us.

Specimens examined. NICARAGUA. **Rivas:** near summit and upper slopes of Volcán Maderas above Balgüe, Isla Ometepe, 14 Sep. 1983 (fl), *M. Nee & W. Robleto*

T. 28089 (MO). COSTA RICA. **Alajuela**: vicinity of Bajos del Toro, road along Río Gorrión, ca. 10 (by air) ENE of Zarcero, 5 Dec. 1982 (fr), *W. Alverson 2004* (MO, WIS); Cantón de San Ramón, Cordillera Tilarán, Monteverde, San Gerardo Biological Station, 31 Mar. 1995 (fl), *D. Penneys 288* (CR, FTG, INB, MEXU, MO); Reserva Forestal San Ramón, ca. Colonia Palmareña, 20 July 1984 (fl), *J. Pipoly 7123* (MO, NY, TEX); Palmira, Región of Zarcero, 12 Oct. 1937 (fl), *A. Smith 501* (F, MICH, MO). **Cartago**: Volcán Turrialba, 17 Sep. 1965 (fl), *L. Bernardi 10602* (G); vicinity of Quebrada Casa Blanca, Tapantí, 29 Sep. 1984 (fl), *M. Grayum 3941* (LL, MO); Panamerican Highway S of Cartago, between Tejar and Empalme, La Trinidad, about 36–41 km from San José, 11 Sep. 1964 (fl), *K. Lems 5156* (F, NY, US); vicinity of La Cangreja about 10 km S of El Tejar, Cordillera Talamanca, 1 Feb. 1963 (fr), *L. Williams et al. 24118* (F, GH). **Guanacaste**: Cantón de Liberia, Parque Nacional Guanacaste, Estación Cacao, 17 Dec. 1990 (fr), *C. Chávez 486* (FTG, INB, MO); Zona Prot. Tenorio, Tilarán, Cordillera Tilarán, Tierras Morenas, Río San Lorenzo, 29 Aug. 1993 (fl), *G. Rodríguez 226* (INB, MO). **Heredia**: Cantón de Sarapiquí, Parque Nacional Braulio Carrilo, Estación Magsasay, 23 June 1990 (fr), *D. Acevedo 78* (CR, K [2], MO); Cantón de Barva, Montaña La Isla, 3 km al N de Porrosatí, 21 Apr. 1990 (fr), *G. Rivera 231* (FTG, INB, MO); Vara Blanca de Sarapiquí. N slope of Central Cordillera. July–Sep. 1937 (fl), *A. Skutch 3296* (A, MO, NY, US); Cerro Zurquí, NE of San Isidro, 3 Mar. 1926 (fr), *P. Standley & J. Valerio 50843* (US). **Heredia & San José**: Calle Yerbabuena, road toward Cerro Hondura, 3 Apr. 1976 (fl), *J. Utley & K. Utley 4463* (DUKE, F); Los Cartagos, 24 Feb. 1937 (fr), *M. Valerio 1579* (F); Cantón de San Rafael, Cerro Chompipe, 16 Dec. 1993 (fr), *G. Vargas et al. 1628* (CR, K). **Limón**: Cantón de Talamanca, Parque Nacional Cordillera Talamanca. Cordillera Talamanca, Queb. Kuisa, Ujarrás Trail to San José Cabécar, 25 Mar. 1993 (fr), *A. Fernández 836* (FTG, INB, MO). **Puntarenas**: Monteverde, upper San Luís valley on Pacific slope, 20 Oct. 1985 (fl), *E. Bello C. 3097* (CR, F, FTG, LL, MO, NY, US). **Puntarenas & Alajuela**: on or near the Continental Divide 2–5 km ESE of Monteverde, 17–20 Mar. 1973 (fr), *W. Burger & J. Gentry 8593* (F); Monteverde, upper community, 24 Feb. 1985 (fr), *W. Haber 1347* (LL, MO). **San José**: La Palma area, S of the escarpment and Continental Divide, NE of San Jerónimo, 16–17 Nov. 1969 (fl, fr), *W. Burger & R. Liesner 6202* (DUKE, F, MO, NY); Zona Prot. Cerro de Escazú, N slope of Cerro Rabo de Mico., Río Poás Basin, 9 Oct. 1991 (fl), *J. Morales 152* (CR, INB, MO); mountains E of San José, 28 Oct. 1960 (fl), *C. Palmer s.n.* (NY); forêts de Rancho Flores, 22 Feb. 1890 (fr), *A. Tonduz 2131* (BR); Tablazo, 23 Jan. 1935 (fr), *M. Valerio 1194* (F). PANAMA. **Bocas del Toro**: Cordillera Talamanca, headwaters of the Río Culubre, 6 airline km NW of the peak of Cerro Echandí on the Costa Rican–Panamanian international border, 2–3 Mar. 1984 (fl), *G. Davidse et al. 25252* (LL, MO). **Chiriquí**: Monte Azul, 1.4 mi. N of Entre Ríos on E slopes of Cerro Punta, 3 mi. by road from town of Cerro Punta, 2250 m, 22 Nov. 1979 (fr), *T. Antonio 2707* (LL, MO); Las Cumbres, hogback ridge N of Quebrada Iglesia, near town of Cerro Punta, 22 July 1971 (fl, fr), *T. Croat & D. Porter 16093* (LL, MO, US).

56. Ardisia panamensis Lundell, Wrightia 3: 198. 1966. *Ardisia pallidiflora* Standl., J. Wash. Acad. Sci. 17: 523. 1927, nom. superfl., non *Ardisia pallidiflora* Ridl., J. Straits Branch Roy. Asiat. Soc. 61: 27. 1912. *Auriculardisia panamensis* (Lundell) Lundell, Phytologia 49: 345. 1981. TYPE: Panama. Chiriquí: between Alto de las Palmas and top of Cerro de la Horqueta, 2100–2268 m, 18 Mar. 1911 (fl), *H. Pittier 3255* (holotype, US!, LL neg. 1971-79!, US neg. 2380!). Figure 56.

Shrubs 1–2 m tall, to 3 cm diam. *Branchlets* slender, terete, 1–3.5 mm diam., sparsely to densely and minutely rufous furfuraceous-lepidote. *Leaves* with blades membranous, elliptic, 2–8.4 × 0.8–3.2 cm, apically acuminate, with an acumen 0.3–1.7 mm long, basally acute, decurrent on the petiole, prominently punctate and punctate-lineate above and below, glabrous above, sparsely and minutely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 28 to 36 pairs, prominulous above and below, the margins entire, flat; petioles slender, canaliculate, 5–16 mm long, glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, pinnately, rarely bipinnately, paniculate, 3–6.5 × 2.5–8 cm, pyramidal, usually as long as the leaves, sometimes shorter or longer than the leaves, densely to sparsely furfuraceous-lepidote, the branches loosely congested into 6- to 14-flowered corymbs; peduncles 0.9–1.8 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, oblong, 3.1–4.2 × 0.8–1.4 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 1.4–2.6 × 0.5–0.9 mm; pedicels slender, 12–15 mm long, epunctate to inconspicuously punctate and punctate-lineate, usually glabrous, rarely with a few scattered furfuraceous-lepidote scales. *Flowers* 5- or 6-merous, white, pale pink or light purple; calyx lobes membranous, orbicular to ovate, 0.9–1.2 × 1–1.2 mm, apically acute to rounded, with few prominently punctate and punctate-lineate, glabrous throughout, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 4.3–4.5 mm long, the tube 1.1–1.5 mm long, the lobes ovate, 3–3.2 × 2.2–2.4 mm, apically acute, with few prominently punctate and punctate-lineate, glabrous throughout except sparsely furfuraceous-lepidote on tube abaxially, the margins entire, hyaline; stamens 3.1–3.2 mm long, the filaments 1–1.1 mm long, the staminal tube 0.5–0.6 mm long, the apically free portions 0.5–0.6 mm long, the anthers

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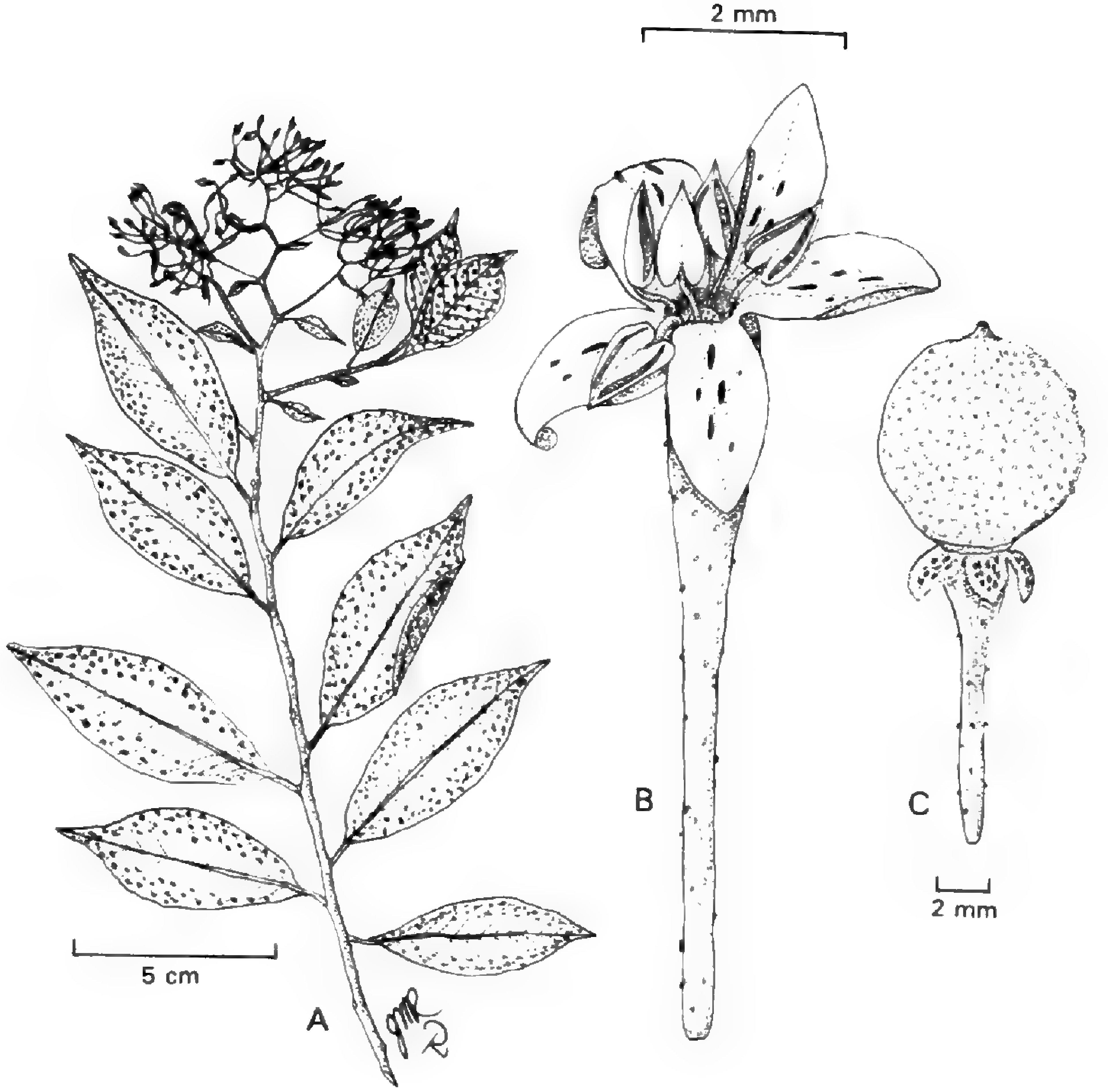


57

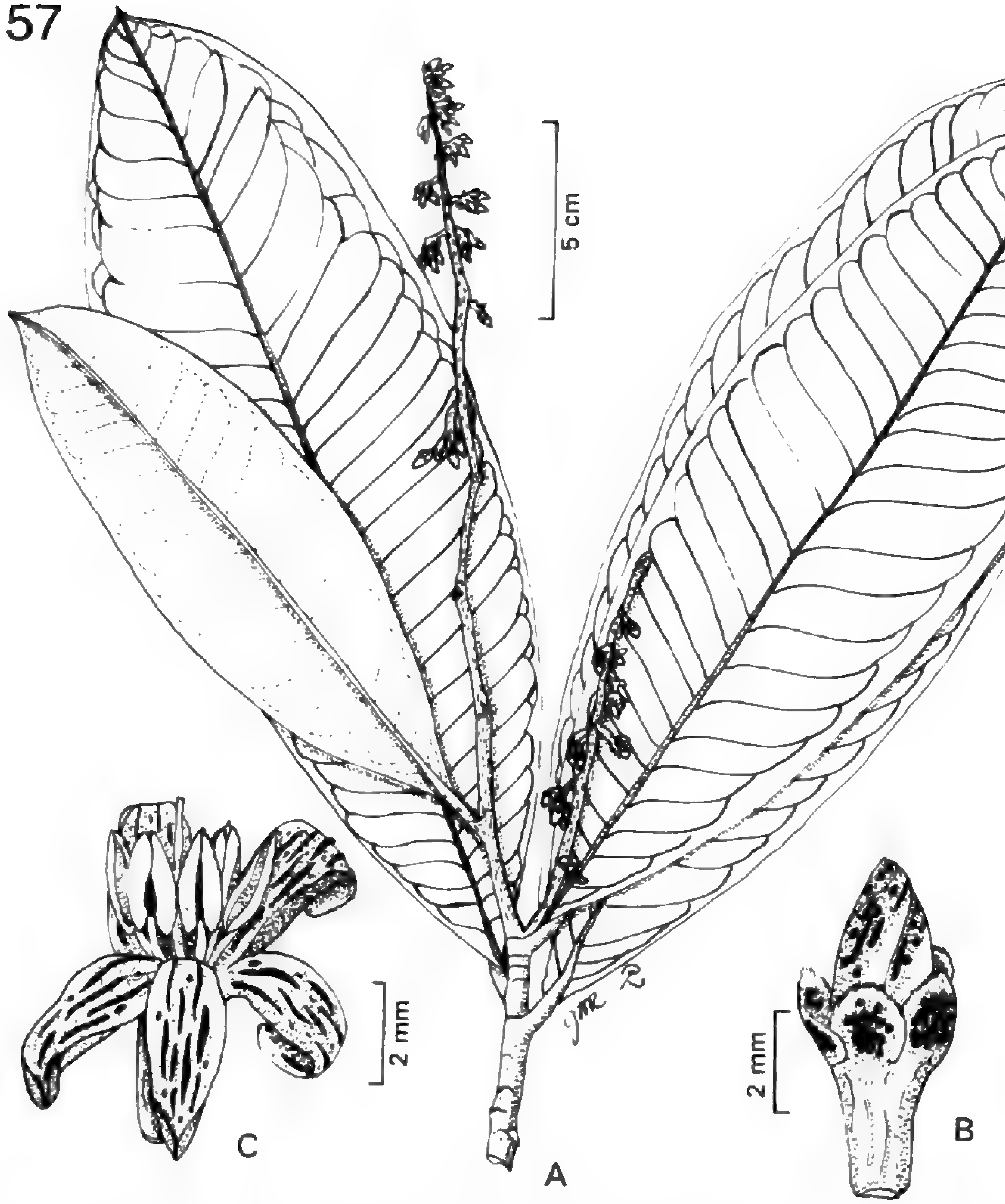


Figure 56 (left). *Ardisia panamensis.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from holotype, *H. Pittier 3255* (US); B from *J. Pipoly 7065* (MO); C from *T. Cochrane et al. 6277* (MO).)

Figure 57 (right). *Ardisia pseudoracemiflora.* —A. Flowering branch. —B. Detail of bud. —C. Flower. (A–C drawn from holotype, *L. E. Mora 2292* (JAUM).)

lanceoloid, 2.2–2.3 × 0.6–0.8 mm, apically subulate-apiculate, basally deeply cordate, the connective conspicuously punctate; pistil 4–4.1 mm long, glabrous, the ovary oblong, 1.2–1.3 mm long, apically prominently punctate, the style 3.2–3.4 mm long, epunctate, the ovules 16 to 18. *Fruits* globose, 6–10 mm diam., prominently punctate.

Distribution. *Ardisia panamensis* is endemic to Cerro Horqueta in Chiriquí, Panama, growing at 1750 to 2268 m in elevation.

Ecology and conservation status. Fieldwork by Pipoly has revealed that *Ardisia panamensis* occurs along the forest edge at the junction of the montane and cloud forests. It is locally common, but should be considered threatened because it borders the life zone preferred for coffee plantations.

Etymology. The specific epithet was derived from the type location.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia panamensis* belongs to a group of species including *A. dwyeri* and *A. vesca* because of its short calyx lobes, long pedicels, thin branchlets, wide corolla lobes, and long anthers. However, *Ardisia panamensis* is easily separated from the other species by its extremely long pedicels to 15 mm long, and on most specimens the highly geniculate branches of the inflorescence and persistent secondary branch bracts are highly distinctive.

Specimens examined. PANAMA. **Chiriquí**: Cordillera de Talamanca above Boquete, W-facing slopes of S flank of Cerro Horqueta along high trail to summit, 2 Jan. 1975 (fr), *T. Cochrane et al. 6277* (F, MO); Cerro Horqueta, 8 km NW of Boquete, at top, 20 Oct. 1980 (fr), *P. Maas & R. Dressler 4952* (NY, U); Dtto. Boquete, Cerro Horqueta, 28 June 1984 (fl), *J. Pipoly 7065* (DUKE, FTG, MO, NY, TEX, UC); trail to Cerro Horqueta, 15 May 1971 (fl, fr), *G. Proctor 31907* (LL [2]); S slopes of Cerro Horqueta, N of Boquete, 21 Jan. 1971 (fl, fr), *R. Wilbur et al. 13453* (DUKE).

57. **Ardisia pseudoracemiflora** Pipoly, Caldasia 16(78): 279. 1991. TYPE: Colombia. Nariño: Mpio. de Barbacoas, on the road from Barbacoas to Junín, 1050 m, 7 Aug. 1962 (fl), *L. Mora 2292* (holotype, COL!; isotypes, PSO!, US!). Figure 57.

Trees 30–40 m tall. *Branchlets* stout, terete, 6–7 mm diam., densely and minutely rufous furfuraceous-lepidote. *Leaves* with blades chartaceous, elliptic, 12.6–29.6 × 5.1–9.7 cm, apically acute, with an acumen 2–7 mm long, basally obtuse, decurrent on the petiole, prominently punctate and punctate-lineate, densely furfuraceous-lepidote, often glabrescent above, the midrib impressed above, prominently raised below, the secondary veins 55 to 64 pairs, prominulous above and below, the margins entire, inrolled; petioles slender, canaliculate, 5–11 mm long, 2–3 mm diam., furfuraceous-lepidote above and below at first, then glabrescent above. *Inflorescences* a pseudoracemose pinnate panicle, 17–22.5 × 3–8 cm, usually shorter than the leaves, the rachis, branches, abaxial floral bract surfaces, and pedicels furfuraceous-lepidote, the branches loosely congested into 3- to 5-flowered corymbs, the lower branches often subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, oblong, 2.9–4.1 × 1–1.5 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 1.6–2.5 × 0.5–0.9 mm; pedicels stout, 1.8–3.3 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, white to light pink; calyx lobes chartaceous, ovate, 2.6–2.8 × 1.8–2 mm, apically rounded, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margin entire, minutely erose, hyaline, sparsely glandular ciliolate; corolla chartaceous, 6.4–6.6 mm long, the tube 1.2–1.3 mm long, the lobes ovate, 4.7–4.8 × 2.4–2.5 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margin entire, hyaline; stamens 6–6.2 mm long, the filaments 2.9–3 mm long, the staminal tube 1–1.1 mm long, the apically free portions 1.8–2 mm long, the anthers lanceoloid, 3.1–3.2 × 1.1–1.2 mm, apically cuspidate-apiculate, basally cordate, the connective conspicuously punctate; pistil 7.6–7.8 mm long, glabrous, the ovary globose, 2.3–2.5 mm long, the style 5.1–5.5 mm long, slender, erect, inconspicuously punctate, the ovules 28 to 35. *Fruits* unknown.

Distribution. *Ardisia pseudoracemiflora* is known only from western slopes of the western Andean cordillera, near Barbacoas, in Nariño, Colombia, growing at 1050 m in elevation.

Ecology and conservation status. *Ardisia pseudoracemiflora* occurs in one of the floristically richest areas of the Cordillera Occidental of Colombia. It occurs in montane pluvial forest, which receives well over 8000 mm of rain per year. The area is also known to house many endemics, including *Clusia garciabarrigae, C. niambiensis, C. tetragona, Ardisia niambiensis,* four more undescribed Myrsinaceae, and many new species from other families, especially Araceae and Gesneriaceae. The area is undergoing rapid development, and while there are several nature reserves, many forests have been threatened by new roads, communication towers, and rural electrification projects. For these reasons, the species should be considered threatened.

Etymology. The specific epithet refers to the overall shape of the inflorescence, resembling a raceme.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia pseudoracemiflora* may be most easily confused with *A. hagenii* because of its elliptic leaves and pseudoracemose inflorescence. However, *A. pseudoracemiflora* is easily separated from *A. hagenii* by its narrower, chartaceous calyx lobes to 2 mm wide, shorter corolla lobes to 6.6 mm long, shorter anthers to 3.2 mm long, shorter styles to 5.5 mm long, larger number of secondary veins of the leaf blades, and thinner branchlets.

58. Ardisia pulverulenta Mez, in Engl., Pflanzenr. IV. 236 (Heft 9): 88. 1902. *Auriculardisia pulverulenta* (Mez) Lundell, Phytologia 54: 285. 1983. TYPE: Panama. Veraguas: Cap Corrientes, Feb. 1848 (fl), *B. Seemann 1093* (lectotype, designated by Lundell (1968), K!, LL neg. 1971-88!; isolectotype, BM!). Figure 58.

Shrubs or trees. Branchlets slender, terete, exfoliating, 3–3.5 mm diam., furfuraceous-lepidote. *Leaves* with blades membranous, elliptic, 18.5–20 × 6.7–7.9 cm, apically acute, with an acumen 5–7 mm long, basally obtuse, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 36 to 42 pairs, prominulous above and below, the margins minutely crenulate, revolute; petioles slender, marginate, 3–5 mm long, glabrous above, densely furfuraceous-lepidote below. *Inflorescences* erect, pinnate or bipinnately paniculate, 11–13.5 × 2.5–4.2 cm, pyramidal, shorter than the leaves, furfuraceous-lepidote, the branches loosely congested into 5- to 7-flowered corymbs; peduncles obsolete; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, ovate, 1.5–2.2 × 1.2–1.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 1–1.3 × 0.5–0.7 mm; pedicels slender, 1.5–2.5 mm long, prominently punctate and punctate-lineate, furfuraceous-lepidote. *Flowers* 5-merous, appearing light pink or red; calyx lobes membranous, ovate, 1.2–1.3 × 0.7–0.8 mm, apically acute, prominently punctate and punctate-lineate, furfuraceous-lepidote, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 2.4–2.6 mm long, the tube 0.6–0.9 mm long, the lobes narrowly ovate, 1.7–1.8 × 1–1.2 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 1.7–1.8 mm long, the filaments 0.7–0.8 mm long, the staminal tube 0.3–0.4 mm long, the apically free portions 0.3–0.5 mm long, the anthers ovoid, 1.1–1.2 × 0.6–0.7 mm, apically apiculate, basally lobate, the connective conspicuously punctate; pistil 1.5–1.6 mm long, glabrous, the ovary globose, 0.2–0.3 mm long, the style 1.2–1.4 mm long, prominently punctate, the ovules 12 to 16. *Fruits* unknown.

Distribution. Ardisia pulverulenta is known only from the type collection, with a vague description of location, and no elevation.

Ecology and conservation status. Because of the vague description the ecology of *Ardisia pulverulenta* is unknown. However, because it is known only from the type, it should be considered threatened.

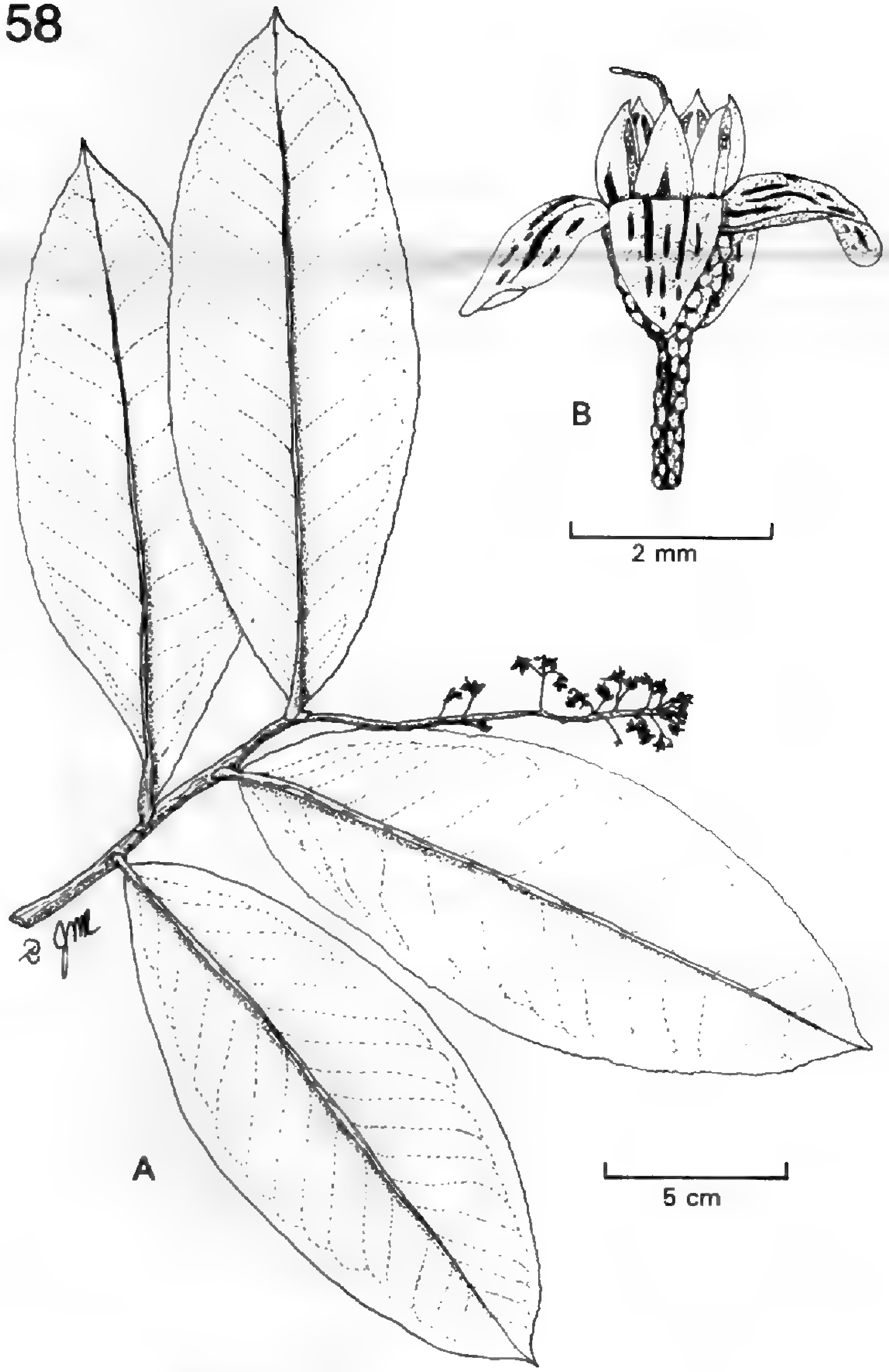
Etymology. The specific epithet comes from Mez's description of the "flores pulverulento-lepidoti" meaning the lepidote scales of the flowers covered with a fine bloom or powdery matter.

Ardisia pulverulenta is most closely related to *A. knappii* (see under that species for similarities). However, *A. pulverulenta* differs from *A. knappii* by its thinner branchlets to 3.5 mm in diameter, shorter and narrower leaf blades to 20 × 7.9 cm, narrower inflorescence to 4.2 cm wide, shorter and narrower calyx lobes to 1.3 × 0.8 mm, shorter and narrower corolla lobes to 1.8 × 1.2 mm, narrower anthers to 0.7 mm wide, and shorter styles to 1.4 mm long.

59. Ardisia ruedae Ricketson & Pipoly, sp. nov. TYPE: Nicaragua. Río San Juan: Mpio. de San Juan del Norte, Reserva Indio-Maíz, down river 10 km from Cerro Canta Gallo, La Chiripa hunting trail, 11°07′N, 083°54′W, 100 m, 18 Sep. 1998 (fl), *R. Rueda, I. Coronado, W. Velásquez & Y. Rubi 8765* (holotype, MO!; isotype, HULE not seen). Figure 59.

Propter laminam foliarem ellipticam, pedicellos usque ad 4.5 mm longos atque stylos usque ad 3.5 mm longos *A. dunlapianae* similis, sed ab ea ramulis semiteretibus (non teretibus), laminis foliaribus coriaceis (non membranaceis) nerviis secundariis 38 ad 53 (nec 23 ad 31)-jugis, lobulis calycinis ovatis (non orbicularibus) denique antheris 0.8–1.0 (non 1.1–2.1) mm latis statim cognoscitur.

58



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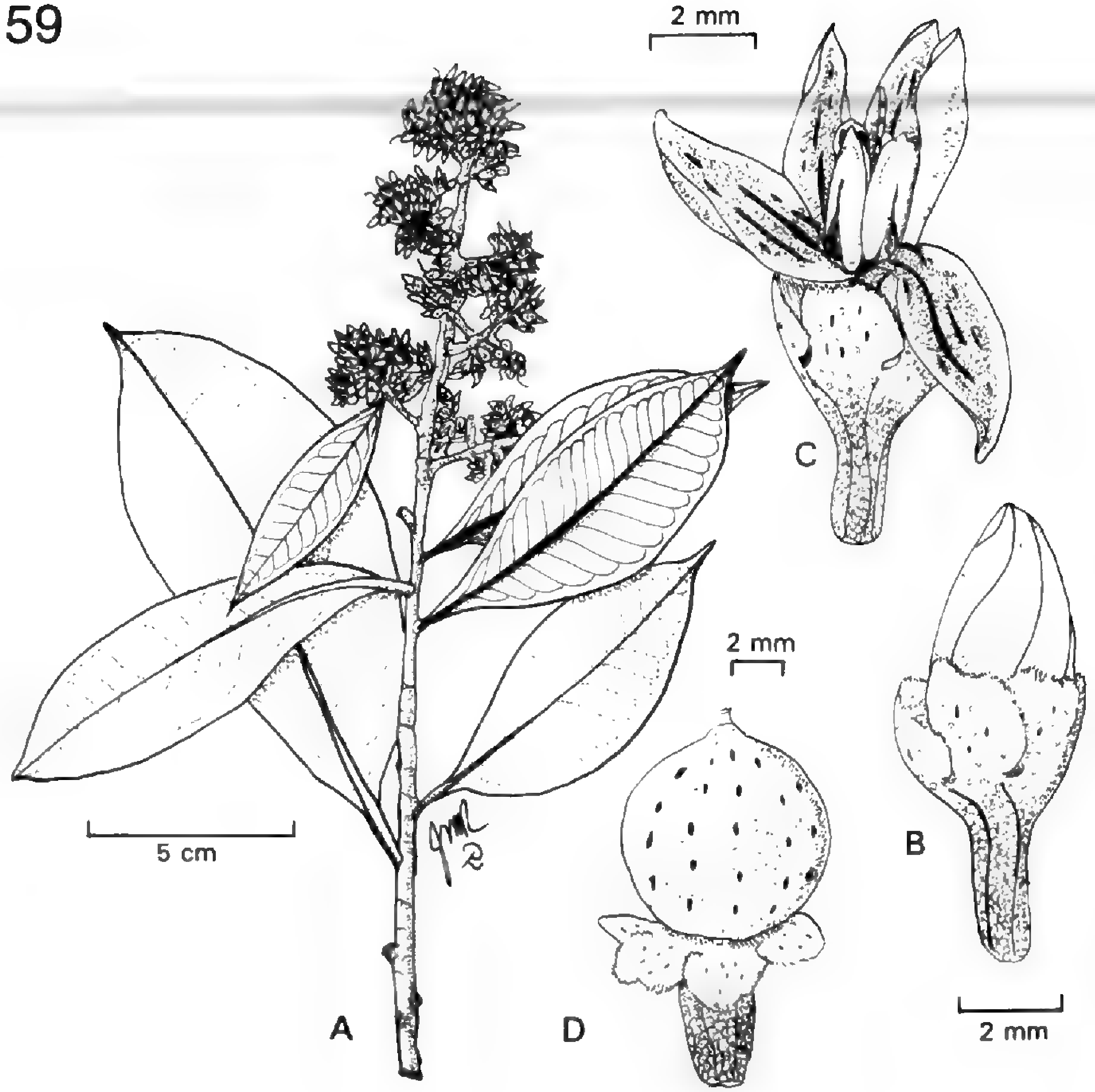

Figure 58 (left). *Ardisia pulverulenta.* —A. Flowering branch. —B. Flower. (A, B drawn from *B. Seemann 1093* (BM).)

Figure 59 (right). *Ardisia ruedae.* —A. Flowering branch. —B. Flower bud. —C. Flower. —D. Fruit. (A–C drawn from holotype, *R. Rueda et al. 8765* (MO); D from *R. Rueda et al. 10022* (MO).)

Trees 5–20 m tall. *Branchlets* slender, semi-terete, 3.5–5.5 mm diam., densely and minutely appressed rufous furfuraceous-lepidote. *Leaves* with blades coriaceous, elliptic, 5.5–15.6 × 2.7–7.1 cm, apically acuminate, with an acumen 5–13 mm long, basally acute, decurrent on the petiole, prominently punctate and punctate-lineate above and below, glabrous above, densely and minutely appressed furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 38 to 53 pairs, inconspicuously raised above and below, the margins entire, flat; petioles slender, marginate, 6–14 mm long, 2–3 mm diam., glabrous above, densely and minutely appressed rufous furfuraceous-lepidote below. *Inflorescences* erect, bipinnately paniculate, 4.8–10.5 × 4–7.5 cm, pyramidal, usually shorter to slightly longer than the leaves, the rachis, branchlets, abaxial bract surfaces, and pedicels densely and minutely rufous furfuraceous-lepidote, the branches congested into 5- to 9-flowered corymbs; peduncles 1.1–2.8 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts unknown; floral bracts caducous, membranous, ovate, 0.8–1.2 × 0.8–1.2 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, densely and minutely appressed rufous furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels stout, 1.8–4.5 mm long, inconspicuously punctate and punctate-lineate, densely and minutely appressed rufous furfuraceous-lepidote. *Flowers* 5-merous, yellow to purple; calyx lobes coriaceous, ovate, 2.4–2.6 × 2.5–3 mm, apically rounded, prominently punctate and punctate-lineate, glabrous adaxially, densely furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla coriaceous, 6.4–6.7 mm long, the tube 2–2.1 mm long, the lobes lanceolate, 4.4–4.6 × 1.8–2 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire; stamens 5–5.5 mm long, the filaments 1.8–2.2 mm long, the staminal tube 0.8–1 mm long, the apically free portions 2.8–3 mm long, the anther ovate, 2.6–2.9 × 0.8–1 mm, apically apiculate, basally deeply cordate, the connective conspicuously punctate; pistil 4.5–5.1 mm long, glabrous, the ovary oblong, 1–1.6 mm long, the style 3–3.5 mm long, prominently punctate and punctate-lineate, the ovules 38 to 44. *Fruits* globose, 7.5–8.2 mm diam., inconspicuously punctate.

Distribution. *Ardisia ruedae* is endemic to the Atlantic Slope of Nicaragua, in Río San Juan and Zelaya, growing at 50 to 412 m in elevation.

Ecology and conservation status. *Ardisia ruedae* occurs in tall, pluvial forests on lateritic soils, and label data indicate that it is locally common. Rainfall in this area of Central America is comparable only to the wettest area of the Chocó Floristic Province of Colombia. Because of the remoteness of the populations, and the fact that the land it occurs on is protected, it is probable that this species does not face immediate threat.

Etymology. It is our pleasure to name this species in honor of Ricardo Rueda, dean of arts and sciences at the Universidad Nacional Autónoma de Nicaragua–León, who is a specialist in Verbenaceae.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia ruedae* is similar to *A. dunlapiana* because of its elliptic leaves, pedicels up to 4.5 mm long, and styles up to 3.5 mm long, but may be separated from it by the semiterete branchlets, coriaceous leaf blades with more secondary veins, ovate calyx lobes, and shorter anthers to 2.9 mm long.

Paratypes. NICARAGUA. **Río San Juan**: Mpio. de San Juan del Norte, Reserva Indio-Maíz, Cerro El Gigante, 24 July 1996 (ster.), *R. Rueda et al. 4458* (HULE, MO), 25 July 1996 (fl), *R. Rueda et al. 4528* (HULE, MO), 26 Sep. 1998 (ster.), *R. Rueda et al. 9005* (HULE, MO). **Zelaya**: Mpio. de Nueva Guinea, Reserva Indio-Maíz, Río Pijibaye entre el caño Bijagua y El Cerro Chiripa, 13 Jan. 1999 (fr), *R. Rueda et al. 10022* (HULE, MO), (fl), *R. Rueda et al. 10027* (HULE, MO), 15 Jan. 1999 (fr), *R. Rueda et al. 10131* (HULE, MO).

60. Ardisia smurfitana Ricketson & Pipoly, sp. nov. TYPE: Colombia. Valle del Cauca: Bajo Calima, Concesión Pulpapel-Buenaventura, carretera Nacional km 28, ca. 100 m, 03°55′N, 077°W, 26 July 1989 (fl, fr), *M. Monsalve B. 3111* (holotype, CUVC!; isotypes, FTG!, MO!). Figure 60.

Propter lobulos calycinos 0.9–1.3 × 0.7–1.1 mm, atque laminam foliarem ellipticam vel oblongam *A. pulverulentae* similis sed ab ea laminis foliaribus coriaceis (non membranaceis), inflorescentiis 25–32 (non 2.5–4.2) cm latis atque lobulis calycinis 0.8–1.0 × 0.6–1.1 (non 1.2–1.3 × 0.7–0.8) mm praeclare distat.

Unknown habit or height. *Branchlets* stout, terete, horizontally checking and exfoliating, 8–11 mm diam., densely furfuraceous-lepidote. *Leaves* with blades coriaceous, elliptic to oblong, 23–23.5 × 5–5.6 cm, apically acute, with an acumen 5–7 mm long, basally acute to cuneate, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below,

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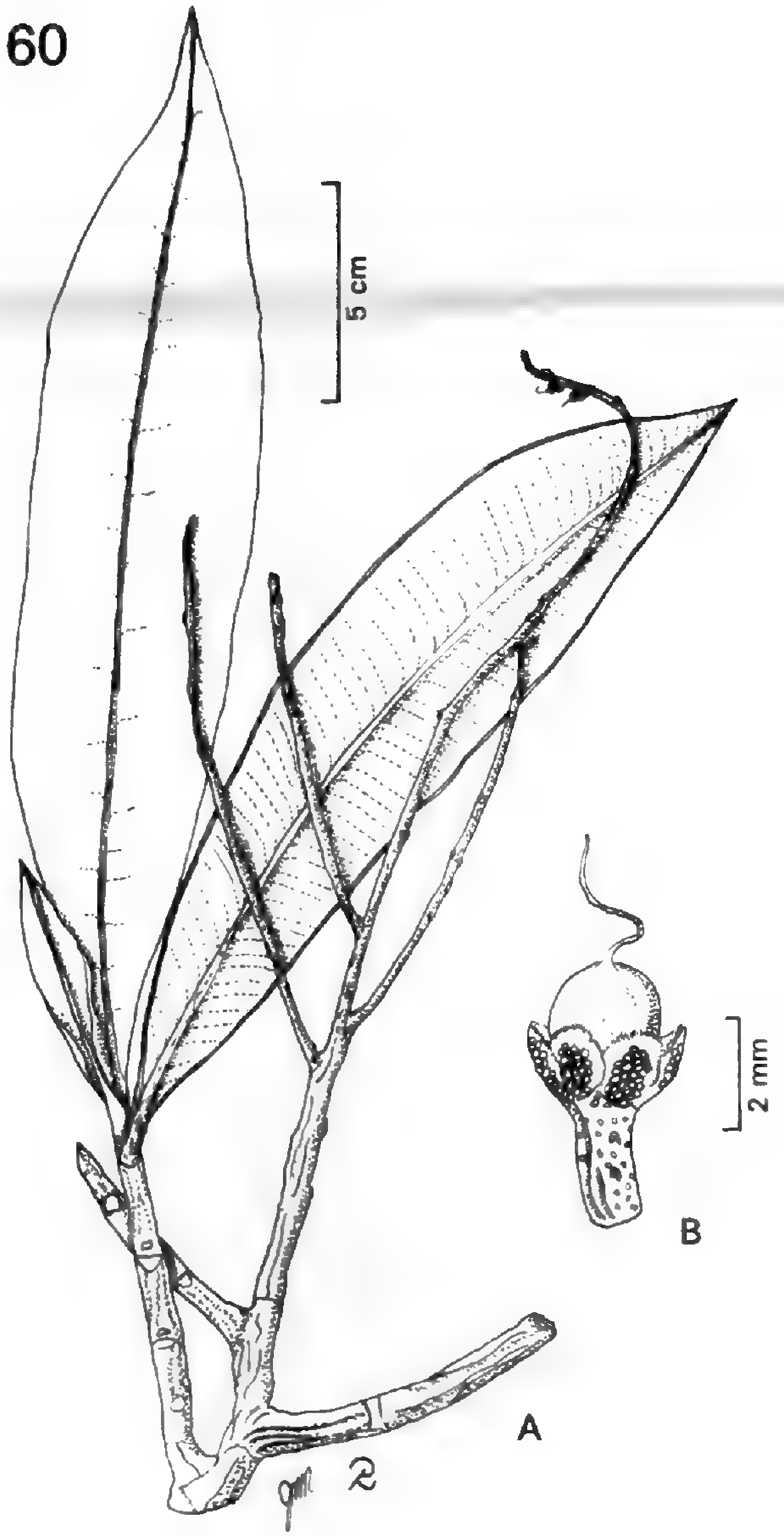

61

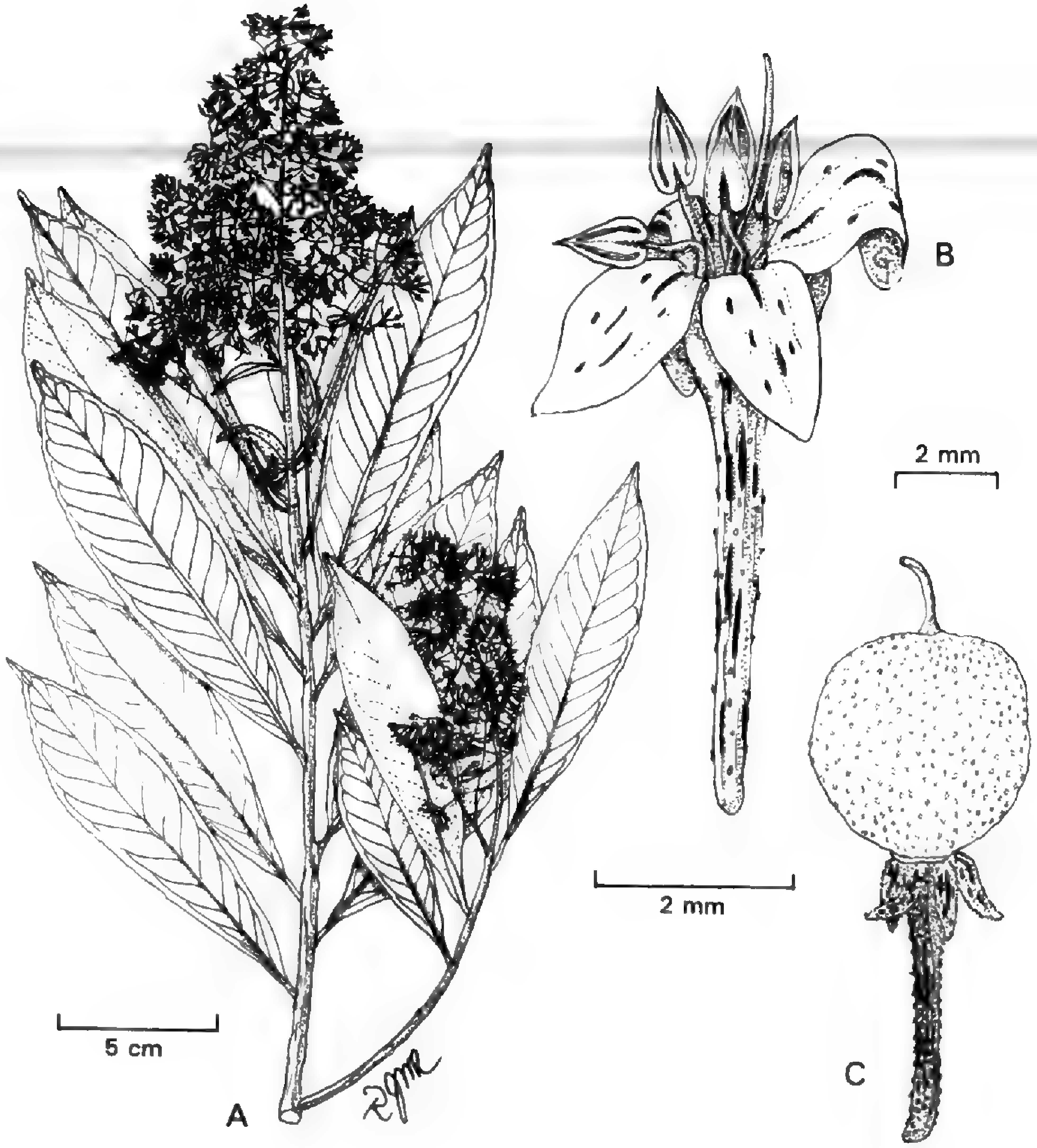

Figure 60 (left). *Ardisia smurfitana.* —A. Flowering branch. —B. Fruit. (A, B drawn from holotype, *M. Monsalve B. 3111* (MO).)

Figure 61 (right). *Ardisia tarariae.* —A. Flowering branch. —B. Flower. —C. Fruit. (A, B drawn from isotype, *G. Davidse et al. 28882* (MO); C from *G. Davidse et al. 29065* (MO).)

the midrib impressed above, prominently raised below, the secondary veins inconspicuous, 68 to 79 pairs, the margins entire, revolute; petiole stout, marginate, 1–1.3 mm long, glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bipinnate to tripinnately paniculate, 24–25 × 28–32 cm, pyramidal, usually longer than the leaves, furfuraceous-lepidote, the branches loosely congested into 5- to 11-flowered corymbs; peduncles 8–10 mm long, densely furfuraceous-lepidote; inflorescence and branch bracts unknown; floral bracts unknown; pedicels slender, 1–1.3 mm long, inconspicuously punctate and punctate-lineate, densely to sparsely furfuraceous-lepidote. *Flowers* 5-merous; calyx lobes membranous, orbicular to oblate, 0.8–1 × 0.6–1.1 mm, apically acute to rounded, prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 3.9–4.1 mm long, the tube 0.9–1.2 mm long, the lobes narrowly lanceolate, 2.6–2.9 × 1.4–1.6 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 2.8–3.7 mm long, the filaments 1.9–2.1 mm long, the staminal tube 0.2–0.4 mm long, the apically free portions 1.5–1.7 mm long, the anthers ovoid, 1.6–1.7 × 1.6–1.7 mm, apically apiculate, basally lobate, the connective conspicuously punctate; pistil unknown. *Fruits* globose, 1.4–1.6 mm diam., conspicuously punctate and punctate-lineate.

Distribution. *Ardisia smurfitana* is known only from the type collection in Bajo Calima in Valle del Cauca, Colombia, growing at about 100 m in elevation.

Ecology and conservation status. *Ardisia smurfitana* occurs in lowland pluvial forest. Because it is apparently endemic in the most valuable timber stand on the continent, it should be considered threatened.

Etymology. The specific epithet does not refer to blue, elf-like creatures, but rather, is named for the Smurfit Carton Colombia Company, whose generous subsidies provided a group of investigators with opportunities to better study and understand the flora of Bajo Calima.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia smurfitana* is most closely related to *A. hugonensis* (see under that species for similarities). However, *A. smurfitana* differs from *A. hugonensis* by its branchlets horizontally checking and exfoliating; larger leaf blades to 23.5 × 5.6 cm; shorter, stouter, marginate, petioles to 1.3 mm long; and membranous, orbicular to oblate, smaller calyx lobes to 1 × 1 mm.

61. Ardisia tarariae Lundell, Phytologia 61: 67. 1986. *Auriculardisia tarariae* (Lundell) Lundell, Phytologia 63: 75. 1987. TYPE: Costa Rica. Limón: Cordillera Talamanca, Atlantic slope, Cerro Tararia, locally known as Tres Picos, 09°09′N, 082°58′W, 2400–2600 m, 10 Sep. 1984 (fl), *G. Davidse, G. Herrera Ch. & M. Grayum 28882* (holotype, LL!; isotype, MO!). Figure 61.

Treelets to 4 m tall. *Branchlets* slender, the interpetiolar ridges forming up to 5 angles, 3–5 mm diam., densely furfuraceous-lepidote. *Leaves* with blades membranous to chartaceous, elliptic to oblanceolate; 2.2–16.6 × 1–5.2 cm, apically acuminate, with an acumen 4–14 mm long, basally cuneate, decurrent on the petiole to the stem, prominently punctate and punctate-lineate above and below, glabrous above, densely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 23 to 29 pairs, prominulous above and below, the margins entire to shallowly crenate, flat; petioles slender, marginate, 6–19 mm long, glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bipinnately paniculate, 9–22 × 4–19 cm, pyramidal, longer than the leaves, the rachis and branches minutely rufous cupuliform lepidote, the branches loosely congested into 5- to 11-flowered corymbs; peduncle obsolete to 0.5 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, oblong, 2.3–3.2 × 0.4–0.8 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 0.9–2 × 0.3–0.4 mm; pedicels slender, 4.5–6 mm long, recurved upward, inconspicuously punctate and punctate-lineate, sparsely furfuraceous-lepidote. *Flowers* 5-merous, light pink; calyx lobes membranous, suborbicular, 1.2–1.4 × 1–1.2 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 3.6–3.8 mm long, the tube 0.6–0.8 mm long, the lobes ovate to narrowly ovate, 2.8–3 × 1.6–1.7 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 3.8–4 mm long, the filaments 2.5–2.6 mm long, the staminal tube

0.5–0.6 mm long, the apically free portions 2–2.1 mm long, the anthers ovoid, 1.5–1.7 × 0.7–0.9 mm, apically subulate-apiculate, basally deeply cordate, the connective conspicuously punctate; pistil 3.7–3.9 mm long, glabrous, the ovary globose, 0.7–0.8 mm diam., the style 3–3.1 mm long, epunctate, the ovules 18 to 19. *Fruits* globose, 3–5 mm diam., prominently punctate.

Distribution. *Ardisia tarariae* is known from the Cordillera Talamanca near the Costa Rica–Panama border in Limón and Puntarenas, Costa Rica, growing at 2100 to 2750 m in elevation.

Ecology and conservation status. *Ardisia tarariae* occurs at the interface of upper cloud and elfin forest. In this geographic area, the forests are dominated by oaks, but also have sizeable *Podocarpus* populations as well. Because it is known from so few specimens, its current conservation status is unknown.

Etymology. The specific epithet was derived from the type locality on Cerro Tararia.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia tarariae* is most closely related to *A. tenuicaulis* and *A. tenuis* because of its very small calyx lobes, less than 1.4 mm long, long pedicels, narrow corolla lobes, and short anthers. *Ardisia tarariae* can easily be distinguished from both related taxa by its larger calyx lobes to 1.4 × 1.2 mm, longer and wider corolla lobes to 3 × 1.7 mm, wider anthers to 0.9 mm wide, longer styles to 3.1 mm long, and smaller fruits to 5 mm in diameter.

Specimens examined. COSTA RICA. **Limón**: Cordillera Talamanca, Atlantic slope, Valle de Silencio, area N of Cerro Hoffman, along Quebrada, 4.5 airline km W of the Costa Rica–Panama border, 8 Sep. 1984 (fl), *G. Davidse et al. 28656* (LL, MO), *28703* (MO); Cordillera Talamanca, Atlantic slope, unnamed cordillera between the Río Terbi and the Río Siní, 13 Sep. 1984 (fr), *G. Davidse et al. 29065* (LL, MO). **Puntarenas**: Cantón de Coto Brus, Parque Indígena La Amistad, Cordillera Talamanca, Estación Altamira, path from the Casa de Coca to the Valle del Silencio, 17 Apr. 1995 (fr), *L. Angulo 199* (INB, MO).

62. Ardisia tenuicaulis Lundell, Wrightia 6: 110. 1980. *Icacorea tenuicaulis* (Lundell) Lundell, Phytologia 49: 352. 1981. TYPE: Panama. Chiriquí: Fortuna Dam site, 1400–1600 m, 15 Sep. 1977 (fr), *J. Folsom, R. Dressler & K. Dressler 5561* (holotype, MO!). Figure 62.

Shrubs to 1 m tall. *Branchlets* slender, angled, 1.5–3 mm diam., sparsely and minutely ferruginous furfuraceous-lepidote. *Leaves* with blades membranous, elliptic, 3.7–8.8 × 1.6–3.9 cm, apically acuminate to caudate, with an acumen 5–12 mm long, basally acute to obtuse, decurrent on the petiole, prominently punctate and punctate-lineate, glabrous above, sparsely and minutely furfuraceous-lepidote, the midrib impressed above, prominently raised below, the secondary veins 20 to 25 pairs, prominulous above and below, the tertiary veins above and below, the margins entire, flat; petioles slender, canaliculate, 5–7 mm long, glabrous above, sparsely furfuraceous-lepidote below, the margins entire or with small teeth. *Inflorescences* terminal pendent, bipinnately paniculate, 4–8 × 4–7 cm, pyramidal, longer than the leaves, sparsely furfuraceous-lepidote, the branches loosely congested into 5- to 7-flowered corymbs; peduncles 4–6 mm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, lorate, 1.9–3.7 × 0.5–0.9 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, usually glabrous abaxially or with a few scattered scales, the margins irregular, minutely erose, hyaline, rarely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 0.8–1.1 × 0.2–0.3 mm; pedicels slender, recurved, 4–5.2 mm long, epunctate to inconspicuously punctate and punctate-lineate, nearly glabrous or sparsely furfuraceous-lepidote. *Flowers* 5-merous, light pink; [measurements from buds] calyx lobes membranous, orbicular to oblate, 1–1.2 × 1–1.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout or sparsely furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 2.7–3 mm long, the tube 0.3–0.4 mm long, the lobes ovate to narrowly ovate, 2.4–2.6 × 1.2–1.4 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 2–2.2 mm long, the filaments 0.2–0.4 mm long, the staminal tube 0.1–0.2 mm long, the apically free portions 0.1–0.3 mm long, the anthers ovoid to narrowly ovoid, 1.8–1.9 × 0.5–0.7 mm, apically apiculate, basally lobate, the connective conspicuously punctate; pistil 2.2–2.4 mm long, glabrous, the ovary ovoid, 0.8–0.9 mm long, the style 1.3–1.5 mm long, epunctate, the ovules 5 to 7. *Fruits* globose, 7–8 mm diam., inconspicuously punctate.

Distribution. *Ardisia tenuicaulis* is known only from the Fortuna Dam area of Chiriquí, Panama, growing from 1200 to 1600 m in elevation.

Ecology and conservation status. *Ardisia tenuicaulis* occurs in premontane wet forests. It is known only from one locality, and given the intensity with which the area has been surveyed, we should assume the species is rare and thus threatened.

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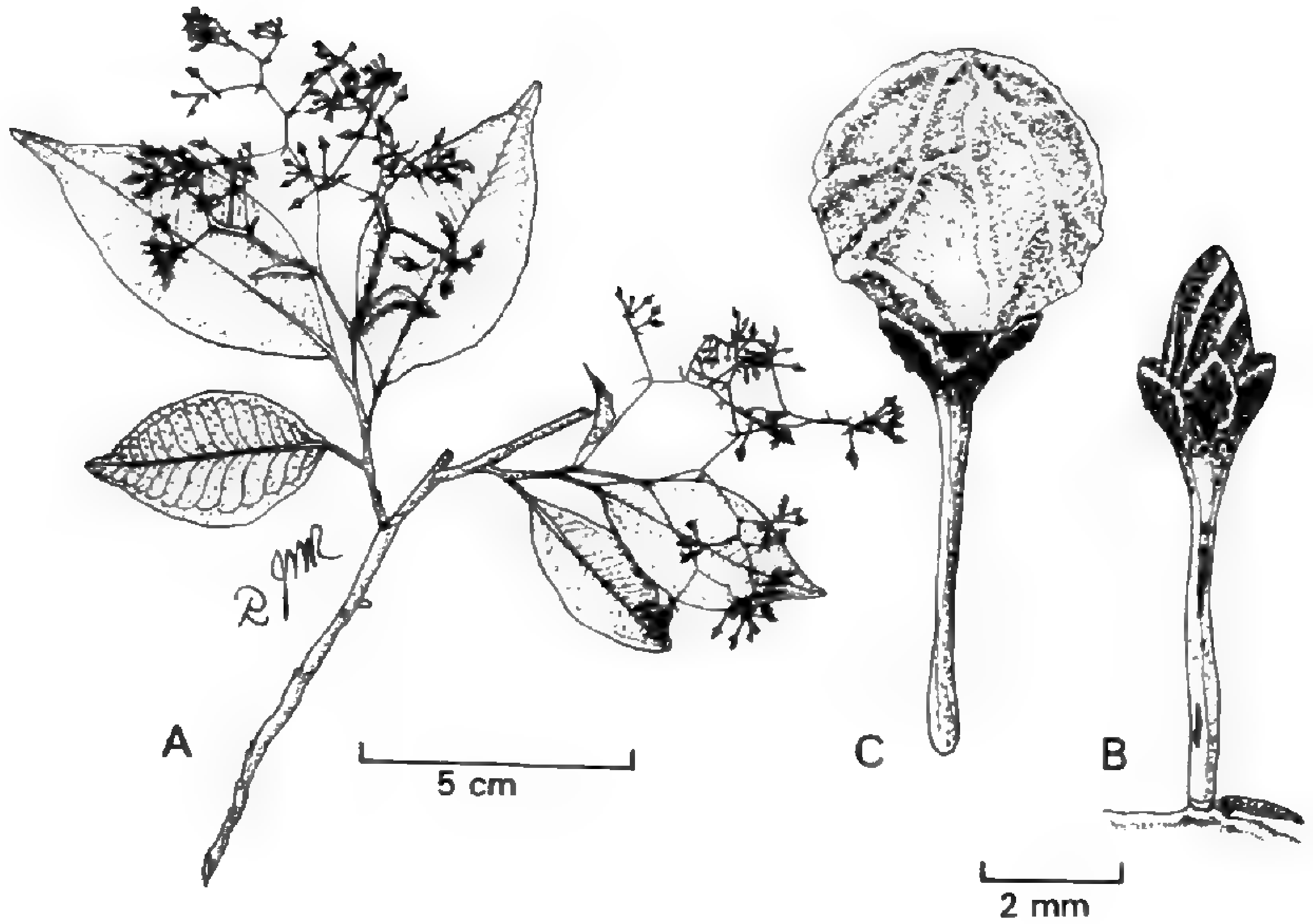

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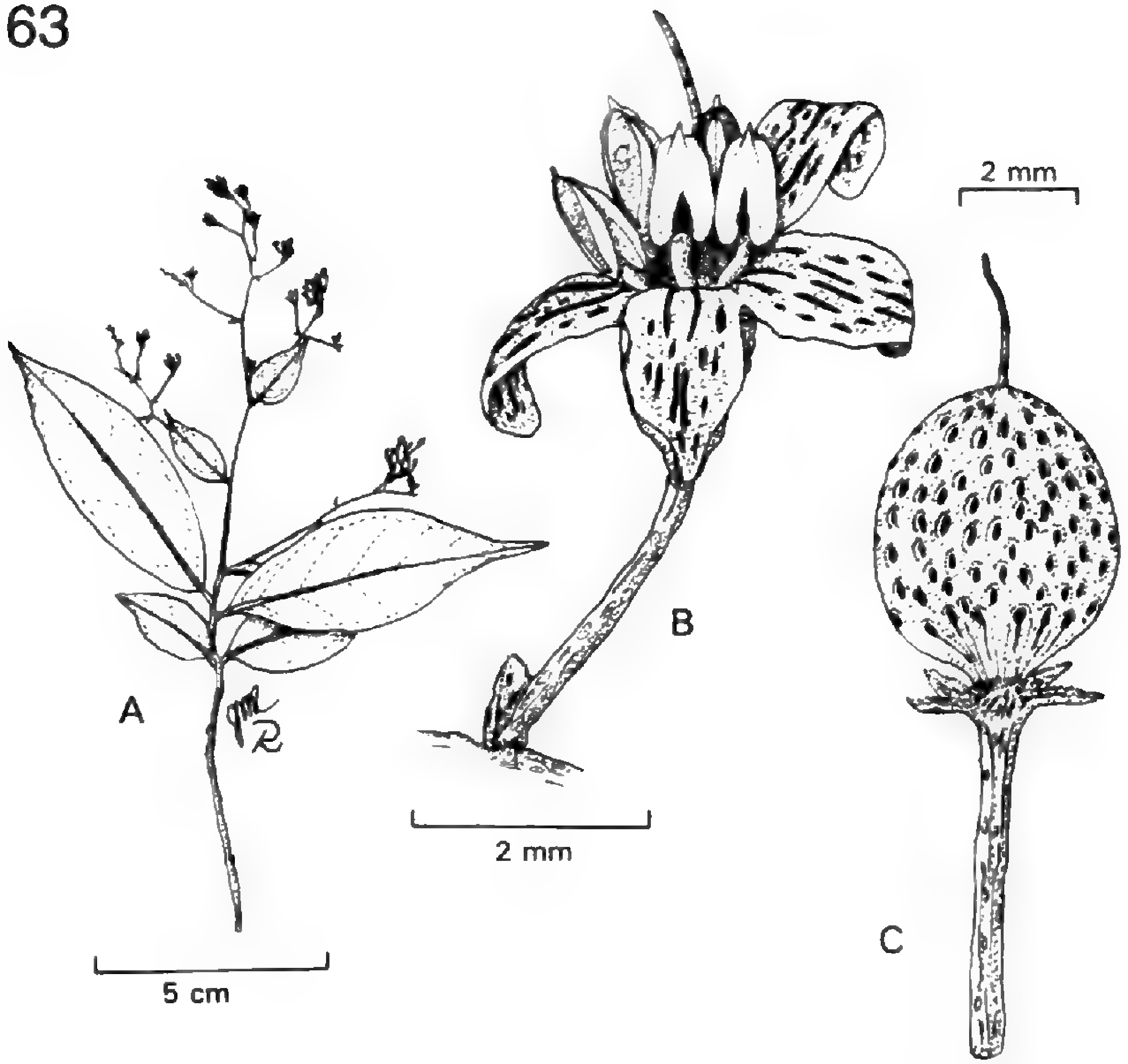

Figure 62 (left). *Ardisia tenuicaulis.* —A. Flowering branch. —B. Flower bud. —C. Fruit. (A, B drawn from *G. McPherson & J. Aranda 10114* (MO); C from holotype, *J. Folsom et al. 5561* (MO).)

Figure 63 (right). *Ardisia tenuis.* —A. Flowering branch. —B. Flower. —C. Fruit. (A drawn from isotype, *J. Duke & T. Elias 13762* (US); B from *A. Gentry & A. Clewell 7049* (MO); C from *J. Folsom et al. 6297* (MO).)

Etymology. The specific epithet was derived from the Latin "tenui" meaning slender or thin and "-caulis" meaning stem.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia tenuicaulis* has been confused with *A. panamensis,* and is vegetatively very similar. However, the extremely small calyx lobes align it more closely with *A. tenuis,* from which it is separated by the longer calyx to 1.2 mm long, longer corolla lobes to 2.6 mm long, longer anthers to 1.9 mm long, shorter style to 1.5 mm long, and much larger fruits to 8 mm in diameter. *Ardisia tenuicaulis* is most closely related to *A. tarariae* and *A. tenuis* because of its very small calyx lobes to 1.2 × 1.3 mm, longer pedicels 5.2 mm long, narrower corolla lobes to 1.4 mm wide, and shorter anthers to 1.9 mm long.

Specimen examined. PANAMA. **Chiriquí:** vicinity of Fortuna Dam, in valley S of lake, 25 Dec. 1986 (fl), *G. McPherson & J. Aranda 10114* (MO).

63. Ardisia tenuis Lundell, Wrightia 4: 149. 1970. *Icacorea tenuis* (Lundell) Lundell, Phytologia 49: 352. 1981. *Auriculardisia tenuis* (Lundell) Lundell, Wrightia 7: 273. 1984. TYPE: Panama. Darién: Cerro Pirré, 2500–4500 ft. [762–1372 m], 9–10 Aug. 1967 (fl), *J. Duke & T. Elias 13762* (holotype, LL!, LL neg. 1979-4!; isotypes, GH!, MO!, US!). Figure 63.

Ardisia pirreana Lundell, Phytologia 48: 134. 1981. Syn. nov. *Auriculardisia pirreana* (Lundell) Lundell, Phytologia 49: 345. 1981. TYPE: Panama. Darién: Cerro Pirré, ridge top near Rancho Plastico, 1200 m, 10–20 July 1977 (fl), *J. Folsom, R. Hartman & R. Dressler 4251* (holotype, LL!; isotypes, MEXU!, MO!).

Shrubs 3 m tall. *Branchlets* slender, terete, 1–3.5 mm diam., densely cupuliform and furfuraceous-lepidote. *Leaves* with blades membranous, elliptic to narrowly ovate, 2.1–11 × 0.6–3.7 cm, apically caudate-acuminate, with an acumen 6–19 mm long, basally obtuse to rounded, decurrent on the petiole, prominently punctate and punctate-lineate, glabrous above, sparsely furfuraceous-lepidote below across the blade, more densely mixed cupuliform and furfuraceous-lepidote along the midrib, the midrib impressed above, prominently raised below, the secondary veins 25 to 34 pairs, prominulous above and below, the margins entire to minutely crenulate, flat; petioles slender, marginate, 4–9 mm long, glabrous above, densely cupuliform and furfuraceous-lepidote below. *Inflorescences* erect, bipinnate to tripinnately paniculate, 5–16 × 5–11 cm, pyramidal, longer than the leaves, indument of dense scales, obsolete or short stalked, flat or cupulate with the margins entire or deeply toothed, the branches loosely congested into 5- to 9-flowered corymbs; peduncle nearly obsolete to 0.9 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, oblong or ovate, 1.3–6.2 × 0.3–2.5 mm, apically acute, or short petiolate, the midrib impressed above, prominently raised below, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote as in leaves below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 0.4–0.7 × 0.1–0.2 mm; pedicels slender, 4.5–6.2 mm long, inconspicuously punctate and punctate-lineate, densely cupuliform and furfuraceous-lepidote. *Flowers* 5-merous, cream or white; calyx lobes chartaceous, ovate, 0.9–1.2 × 0.7–0.8 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, mixed lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 2.9–3 mm long, the tube 0.5–0.6 mm long, the lobes ovate to narrowly ovate, 2.3–2.4 × 1.4–1.5 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 2.1–2.3 mm long, the filaments 1.1–1.3 mm long, the staminal tube 0.3–0.4 mm long, the apically free portions 0.7–1 mm long, the anthers ovoid, 1–1.1 × 0.6–0.7 mm, apically cuspidate-apiculate, basally subcordate, the connective conspicuously punctate; pistil 3.1–3.6 mm long, glabrous, the ovary ovoid, 0.5–0.7 mm long, the style 2.6–2.9 mm long, prominently punctate and punctate-lineate, the ovules 4 to 6. *Fruits* globose, 4.3–4.7 mm diam., prominently punctate.

Distribution. *Ardisia tenuis* is known from Cerro Pirré in Darién, Panama, and on Alturas de Nique in Chocó, Colombia, on the Panama–Colombia border. The collection bearing the label *Lawrance 114* is probably mislabeled, because the flora of Cerro Chapón in Boyacá is totally unrelated to that of the Chocó, and we know of no non-weedy species of angiosperms that are shared between the two. It has been collected at 750 to 1500 m in elevation.

Ecology and conservation status. *Ardisia tenuis* occurs in pluvial montane, cloud, and elfin forest. Although locally abundant, because of its restricted distribution it should be considered threatened.

Etymology. The specific epithet was derived from the Latin meaning thin, fine or slender, and refers to the very thin branchlets and inflorescence rachis.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, *Ardisia tenuis* is most closely related to *A. tarariae* and *A. tenuicaulis* because of its very small calyx lobes, less than 1.4 mm long with long pedicels, narrow corolla lobes, and short anthers. *Ardisa tenuis* can easily be distinguished from *A. tarariae* by its smaller calyx lobes to 1.2 × 0.8 mm, shorter and narrower corolla lobes to 2.4 × 1.5 mm, narrower anthers to 0.7 mm wide, shorter styles to 2.9 mm long, and larger fruits to 4.7 mm in diameter. *Ardisia tenuis* can be separated from *A. tenuicaulis* by its narrower calyx lobes to 0.8 mm wide, shorter but wider corolla lobes to 2.4 × 1.5 mm, shorter anthers to 1.1 mm long, longer styles to 2.9 mm long, and smaller fruits to 4.7 mm in diameter.

The type of *Ardisia pirreana* is unique only for its slightly larger inflorescence and leaf blades; however, these fall well within the range of *A. tenuis*.

Specimens examined. PANAMA. **Darién:** Cerro Pirré, 11 Apr. 1967 (fl, fr), *N. Bristan 468* (MO); Serranía de Pirré, along ascent of Serranía de Pirré above Cana Gold Mine between Río Cana and Río Escucha Ruido, 27 July 1976 (fl), *T. Croat 37800* (MO); Parque Nacional del Darién, slopes of Cerro Mali, headwaters of S branch of Río Pucuro, ca. 22 km E of Pucuro, 21 Oct. 1987 (fl), *H. Cuadros et al. 3939* (MO); ridgetop area N of Cerro Pirré, between Cerro Pirré top and Rancho Plastico, 14 Nov. 1977 (fl, fr), *J. Folsom et al. 6297* (MO); summit of Cerro Pirré, 29 Dec. 1972 (fl), *A. Gentry & A. Clewell 7049* (F, MO); Parque Nacional del Darién, Panama–Colombia border, near gold mine at headwaters of N branch of Río Pucuro slopes of Cerro Tacarcuna, ca. 6 km N of Cerro Mali, 27 Oct. 1987 (fr), *G. de Nevers et al. 8523* (LL, MO); Chepigana District, crest of Cana–Cuasi trail, 15 Mar. 1940 (fr), *M. Terry & R. Terry 1568* (F). COLOMBIA. [Doubtful, probably represents a label mix-up—**Boyacá:** Chapón region, 100 mi. NW of Bogotá, 25 May 1932 (fr), *A. Lawrance 114* (GH, MO)]. **Chocó:** SW ridge leading to Alturas de Nique on border with Panama, 29 Dec. 1980 (fl, fr), *R. Hartman 12376* (LL, MO); Alturas de Nique and ridge to SW, 31 Dec. 1980 (fl, fr), *R. Hartman 12473* (LL, MO).

64. Ardisia tysonii Lundell, Wrightia 4: 165. 1971. *Auriculardisia tysonii* (Lundell) Lundell, Phytologia 49: 345. 1981. TYPE: Panama. Panamá: Cerro Jefe, in *Clusia* forest, 2700–3000 ft. [823–914 m], 27 Jan. 1966 (fr), *E. Tyson, J. Dwyer & K. Blum 3279* (holotype, MO!, LL neg. 71-117!; isotypes, LL!, F neg. 55646!, MO!). Figure 64.

Ardisia pilonensis Lundell, Wrightia 6: 86. 1979. Syn. nov. *Auriculardisia pilonensis* (Lundell) Lundell, Phytologia 49: 345. 1981. TYPE: Panama. Coclé: La Mesa above El Valle de Anton, ca. 2 km W of Cerro Pilón, on slopes of steep knife-like ridge, 900–930 m, 22 July 1976 (fr), *T. Croat 37431* (holotype, MO!, LL neg. 1979-3!; isotype, LL!).

Shrubs or trees 3–7 m tall, 4–12 cm diam. *Branchlets* stout, terete, 5–8 mm diam., densely furfuraceous-lepidote. *Leaves* with blades coriaceous, elliptic, 3.7–12.2 × 2.1–6.2 mm, apically acute, with an acumen 3–8 mm long, basally acute, decurrent on the petiole, inconspicuously punctate and punctate-lineate above and below, glabrous above, densely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 27 to 38 pairs, prominulous above and below, the margins entire, flat; petioles slender, marginate, 8–17 mm long, glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bipinnately paniculate, 6–14 × 4–12 cm, pyramidal, usually longer than the leaves, sparsely furfuraceous-lepidote, the branches loosely congested into 5- to 7-flowered corymbs; peduncles nearly obsolete to 2 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, ovate to oblong, 0.8–4.5 × 1.2–1.8 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 1–1.4 × 0.5–0.8 mm; pedicels stout, 0.7–1.8 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote to glabrescent. *Flowers* 5-merous, white to light pink; calyx lobes membranous to chartaceous, orbicular to ovate, 1.2–1.6 × 1.4–1.6 mm, apically acute to rounded, prominently punctate and punctate-lineate, densely furfuraceous-lepidote, glabrescent, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 4.1–4.2 mm long, the tube 1.2–1.3 mm long, the lobes narrowly ovate, 2.9–3 × 1.6–1.9 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 3.2–3.3 mm long, the filaments 1.3–1.4 mm long, the staminal tube 0.3–0.4 mm long, the apically free portions 1–1.1 mm long, the anthers ovoid, 2.2–2.4 × 0.7–0.9 mm, apically apiculate, basally lobate, the connective conspicuously punctate; pistil 3–3.2 mm long, glabrous, the ovary oblongoid, 1.2–1.3 mm long, the style 1.9–2 mm long, prominently punctate, the ovules 23 to 25. *Fruits* globose, 5.5–7 mm diam., prominently punctate.

Distribution. *Ardisia tysonii* is known from the area around Cerro Jefe and Cerro Azul in Panamá, the area around Cerro Tute in Veraguas, and the

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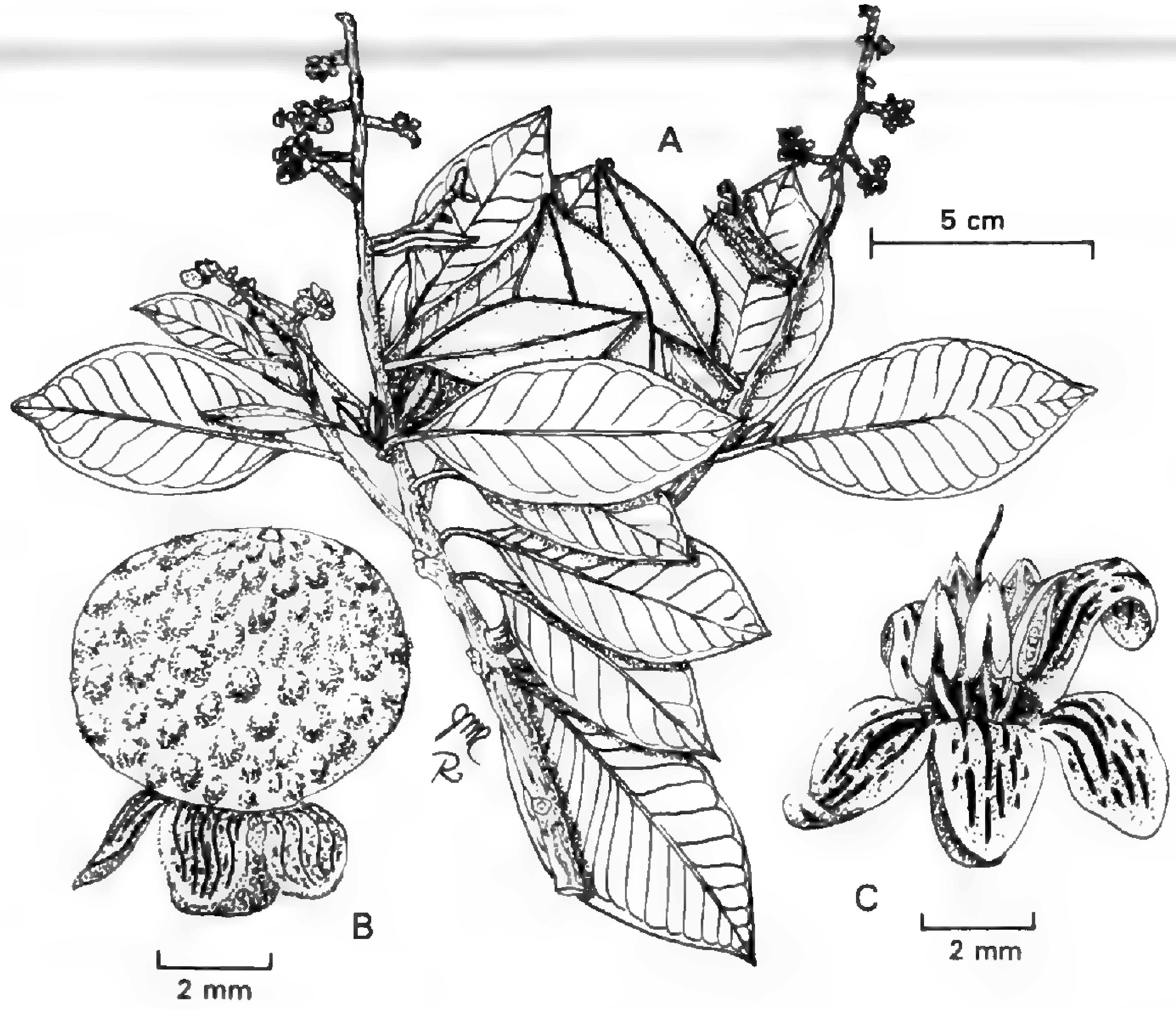

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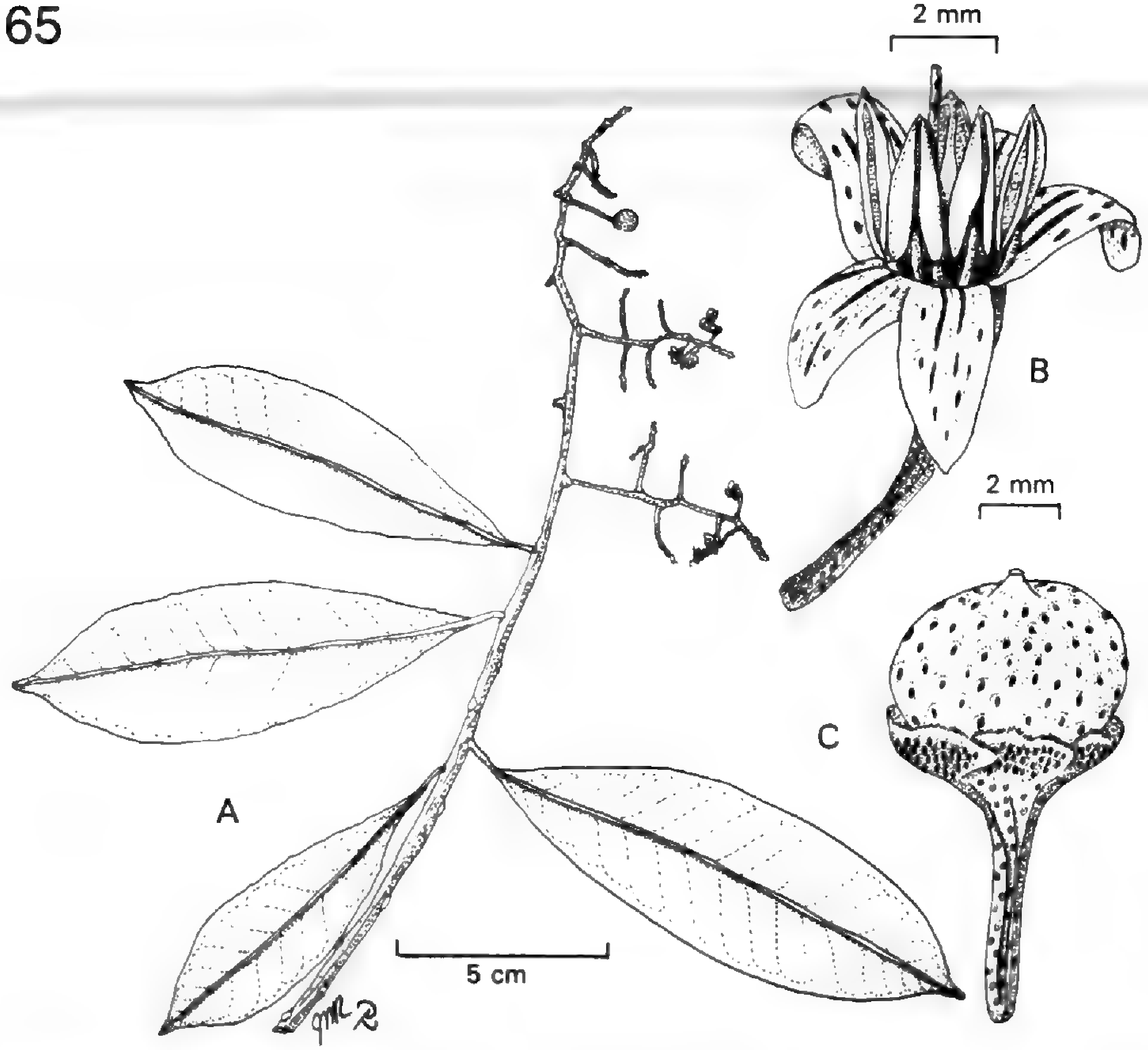


Figure 64 (left). *Ardisia tysonii.* —A. Flowering branch. —B. Fruit. —C. Flower. (A drawn from holotype, *E. Tyson 3279* (MO); B from *B. Hammel 4844* (MO); C from *I. Valdespino & J. Aranda 334* (MO).)

Figure 65 (right). *Ardisia unguiensis.* —A. Flowering branch. —B. Flower. —C. Fruit. (A, B drawn from holotype, *A. Gentry et al. 17032* (LL); C from *M. Nee 9287* (MO).)

area around La Mesa near Cerro Pilón in Coclé, Panama, growing from 823 to 1219 m in elevation.

Ecology and conservation status. *Ardisia tysonii* occurs in very wet cloud and elfin forests and is relatively common. For this reason, it is not endangered at the moment.

Etymology. This species was named in honor of Edwin L. Tyson, the collector of the type.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia tysonii* is most closely related to *A. albisepala* (see under that species for similarities). However, *A. tysonii* can easily be separated from *A. albisepala* by its thicker branchlets to 8 mm in diameter, wider calyx lobes to 1.6 mm in diameter, shorter and narrower corolla lobes to 3 × 1.9 mm, longer anthers to 2.4 mm long, and shorter styles to 2 mm long.

Lundell (1979) failed to compare the type of *Ardisia pilonensis,* which is in fruit, with that of *A. tysonii.* Examination of both revealed that they are identical.

Specimens examined. PANAMA. **Panamá**: summit of Cerro Jefe, on road below tower, 20 Jan. 1984 (fl), *H. Churchill 4286* (LL, MO, PMA); Cerro Jefe, along trail in forest at end of road, right hand fork, W past radio tower, 30 Sep. 1978 (fl, fr), *B. Hammel 4844* (MO); Dtto. Panamá, Cerro Jefe, below antenna, 18 June 1984 (ster.), *J. Pipoly 7026* (MO, NY); along road from Cerro Azul to Cerro Jefe, 19 Jan. 1969 (fr), *E. Tyson 5309* (MO); Cerro Jefe about 10 km beyond Cerro Azul in the mountains above Tocumen Airport, 8 Jan. 1975 (fr), *R. Wilbur & J. Luteyn 19465* (DUKE); Cerro Jefe, at tower, 24 Jan. 1987 (fr), *I. Valdespino & J. Aranda 334* (MO, NY, PMA). **Veraguas**: NW of Santa Fé, 2 km from Escuela Agrícola Alto de Piedra, ridge top below summit of Cerro Tute, 28 Mar. 1975 (fr), *S. Mori & J. Kallunki 5258* (LL, MO); Cerro Tute, ca. 10 km NW of Santa Fé, on ridge top, 19 May 1975 (fr), *S. Mori 6278* (LL, MO).

65. Ardisia unguiensis Lundell, Wrightia 6: 112. 1980. *Auriculardisia unguiensis* (Lundell) Lundell, Phytologia 49: 345. 1981. TYPE: Colombia. Chocó: Serranía del Darién, W of Unguía near Panama border, 550–1000 m, 25 July 1976 (fl), *A. Gentry, H. León & L. Forero 17032* (holotype, LL!; isotypes, FTG!, MO!). Figure 65.

Auriculardisia nebulosa Lundell, Wrightia 7: 270. 1984. Syn. nov. *Ardisia nebulosa* (Lundell) Lundell, Phytologia 61: 65. 1986, nom. inval. *Ardisia nebulosa* (Lundell) Pipoly & Ricketson, Sida 18: 513. 1998. TYPE: Panama. Panamá: Cerro Jefe, 850–900 m, 29 Oct. 1980 (fr), *K. Sytsma 1980* (holotype, LL!; isotypes, BM!, MO!).

Auriculardisia parviflora Lundell, Wrightia 7: 271. 1984. Syn. nov. Non *Ardisia parviflora* Talbot, Syst. List Trees Bombay (ed. 2), 204. 1902. *Ardisia bristanii* Lundell, Phytologia 61: 62. 1986, nom. inval. *Ardisia bristanii* Pipoly & Ricketson, Sida 18: 511. 1998. TYPE: Panama. Darién: Cerro Pirré, 4 Aug. 1967 (fl), *N. Bristan 1236* (holotype, US!; isotypes, LL!, MO!, PMA!).

Small shrubs or trees 4–25 m tall, to 20 cm diam. *Branchlets* slender, terete, 3–5 mm diam., densely and minutely rufous furfuraceous-lepidote, often glabrescent. *Leaves* with blades coriaceous, elliptic, 7.8–17.1 × 2.9–6.6 cm, apically acuminate, with an acumen 4–9 mm long, basally acute, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrescent above, densely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 24 to 29 pairs, inconspicuous above and below, the margins entire, flat; petiole slender, canaliculate, 7–19 mm long, 1–2 mm diam., glabrous above, furfuraceous-lepidote below. *Inflorescences* erect, bi- to tripinnately paniculate, 6.7–11.9 × 8.1–12.6 cm, pyramidal, longer or shorter than the leaves, the rachis, branchlets, abaxial bract surfaces, and pedicels densely furfuraceous-lepidote, the branches loosely congested into 3- to 7-flowered corymbs; peduncles 0.5–2.3 cm long, the lower branches subtended by leaves; inflorescence bracts absent; inflorescence branch bracts unknown; floral bracts caducous, membranous, ovate, 0.9–1.1 × 0.5–0.7 mm, apically acute, prominently punctate and punctate-lineate, glabrous above, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; pedicels slender, 5–7.8 mm long, inconspicuously punctate and punctate-lineate, indument as in the branchlets. *Flowers* 5-merous, lavender, calyx lobes chartaceous to coriaceous, oblate, 1.7–2 × 2.5–3.1 mm, apically broadly rounded to truncate, prominently punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla coriaceous, 4.8–5.1 mm long, the tube 1–1.8 mm long, the lobes ovate to lanceolate, 3.1–4.1 × 1.6–2.2 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire; stamens 2.6–3.4 mm long, the filaments 1.5–1.8 mm long, the staminal tube 0.7–0.9 mm long, the apically free portions 0.6–1.1 mm long, the anthers ovoid to lanceoloid, 1.8–3 × 1–1.4 mm, apically apiculate, basally lobate, the connective conspicuously punctate; pistil 4.7–5.4 mm long, glabrous, the ovary ovoid to oblong, 1.2–1.4 mm long, the style 3.5–4 mm long, prominently punctate and punctate-lineate, the ovules 45 to 48. *Fruits* globose, 6.5–8 mm diam., inconspicuously punctate and punctate-lineate.

Distribution. *Ardisia unguiensis* is distributed from Cerro Azul and Cerro Jefe in Panamá to Cerro Pirré in Darién, Panama, growing at 550 to 1372 m in elevation.

Ecology and conservation status. *Ardisia unguiensis* occurs in premontane wet forests, cloud forests, and elfin forests. It has been found in areas where only remnant forest occurs and appears to be fairly resilient, doing well in full-light situations. Because of its ability to live in full sunlight, we do not believe it is threatened at this time.

Etymology. Named for the town of Unguía, Chocó, Colombia, where the type was collected.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia unguiensis* may be separated from both *A. glandulosomarginata* and *A. croatii* by its inconspicuous abaxial leaf punctations, flat quaternary venation, smaller calyx lobes to 2 × 3.1 mm, dense long glandular-ciliolate along the entire margin, and smaller corolla lobes to 4.1 × 2.2 mm.

The type of *Ardisia unguiensis* is in very young fruit, while the type of *Auriculardisia nebulosa* is in mature fruit, and the type of *A. parviflora* is in bud. The types of both *A. nebulosa* and *A. parviflora* are notable only for the more densely black punctations of the floral parts, with no other significant feature to separate them.

Specimens examined. PANAMA. **Darién:** Cerro Pirré, 9–10 Aug. 1967 (fl bud), *J. Duke & T. Elias E13662* (LL, MO, MOCZ); forest trail N from Ensenada del Guayabo, 18 km SE Jaqué, 13 Jan. 1983 (fr), *N. Garwood et al. 246* (BM, MO); Parque Nacional del Darién, W slope of Cerro Mali, on ridge between N & S branches of Río Pucuro, ca. 18 km E of Pucuro, 22 Oct. 1987 (fr), *B. Hammel et al. 16432* (CAS, F, FTG, LL, MEXU, MO, PMA); S of El Real, region called Alturas del Nique, near Cana mine, along old Camino Real toward Colombia, 22 Aug. 1987 (fr), *G. McPherson 11533* (FTG, LL, MO). **Panamá:** 6.5 km by road N of Lago Cerro Azul, 13 Jan. 1974 (fr), *M. Nee 9287* (LL, MO, NY); Cerro Jefe, 4.7 mi. above Goofy Lake, 27 Dec. 1980 (fr), *K. Sytsma et al. 2828* (LL, MO).

66. Ardisia vesca Lundell, Wrightia 6: 93. 1979. *Auriculardisia vesca* (Lundell) Lundell, Phytologia 49: 345. 1981. TYPE: Panama. Coclé: near Continental Divide along lumbering road 8.4 km above El Copé, 1 km beyond sawmill, 900 m, 19 Jan. 1978 (fl, fr), *B. Hammel 952* (holotype, MO!, F neg. 55676!). Figure 66.

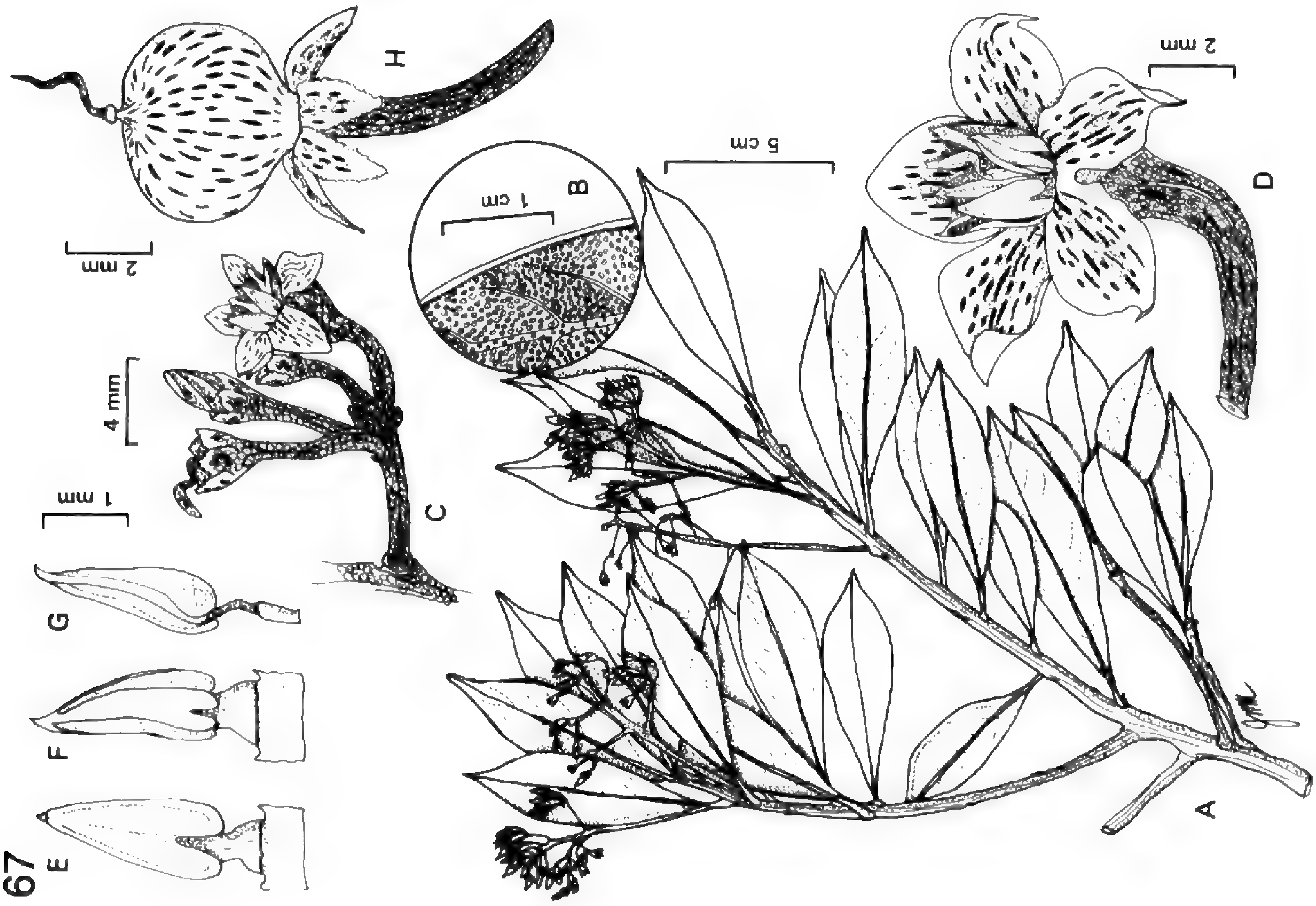
Ardisia minima Lundell, Wrightia 6: 83. 1979. *Icacorea minima* (Lundell) Lundell, Phytologia 49: 350. 1981. TYPE: Panama. Coclé: La Mesa, above El Valle de Anton, ca. 2 km W of Cerro Pilon on slopes of steep knife-like ridge, 900–930 m, 22 July 1976 (fl bud), *T. Croat 37461* (holotype, MO!, F neg. 55601!; isotype, LL!).

Shrubs or trees to 4 m tall. *Branchlets* slender, terete, longitudinally ridged, exfoliating, 2–4.5 mm diam., densely appressed rufous furfuraceous-lepidote, glabrescent. *Leaves* with blades membranous, elliptic, 3.4–9.6 × 0.8–3.1 cm, apically acuminate, with an acumen 5–12 mm long, basally obtuse to rounded, decurrent on the petiole, prominently punctate and punctate-lineate above and below, tertiary venation prominulous above and below, glabrous above, sparsely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 27 to 36 pairs, prominulous above and below, the margins entire, flat; petioles slender, canaliculate, 5–7 mm long, glabrous above, sparsely furfuraceous-lepidote below. *Inflorescences* erect, pinnate to bipinnately paniculate, 5–7 × 3–4.5 cm, pyramidal, shorter than the leaves, appressed furfuraceous-lepidote, the branches loosely congested into 5- to 7-flowered corymbs; peduncles nearly obsolete to 0.8 cm long, the lower branches subtended by leaves; inflorescence bracts unknown; inflorescence branch bracts caducous, membranous, oblong, 2.7–3.8 × 0.8–1.3 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; floral bracts similar to the inflorescence branch bracts, but 1–1.6 × 0.5–0.7 mm; pedicels slender, 6–9 mm long, inconspicuously punctate and punctate-lineate, furfuraceous-lepidote or often glabrous. *Flowers* 5- or 6-merous, deep pink to pale purple; calyx lobes membranous to chartaceous, ovate, 1.4–1.5 × 1.1–1.2 mm, apically acute, prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote, the margins irregular, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 4.5–4.7 mm long, the tube 1.2–1.3 mm long, the lobes ovate, 3.3–3.4 × 1.9–2 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout except sparsely furfuraceous-lepidote abaxially, the margins entire, hyaline; stamens 4–4.2 mm long, the filaments 1.9–2 mm long, the staminal tube 0.8–0.9 mm long, the apically free portions 1–1.2 mm long, the anthers lanceoloid, 2.3–2.4 × 0.8–0.9 mm, apically apiculate, basally cordate, the connective conspicuously punctate; pistil 4.4–4.5 mm long, glabrous, the ovary ovoid, 1–1.1 mm long, epunctate, the style 3.4–3.5 mm long, epunctate, the ovules 9 to 11. *Fruits* globose, 4–5 mm diam., prominently punctate and punctate-lineate.

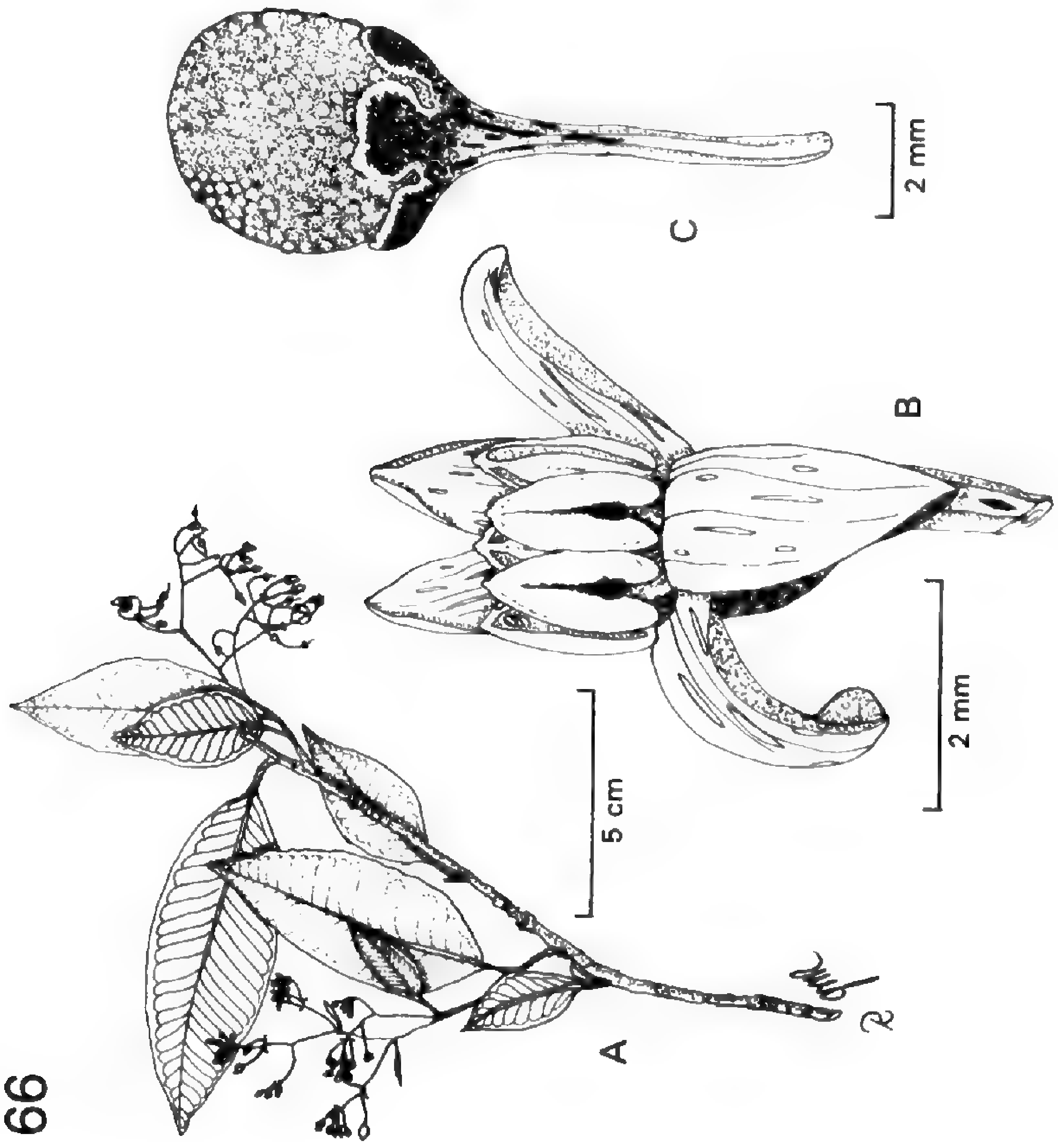
Distribution. *Ardisia vesca* is known from only a few locations in Coclé, Panama, growing at 850 to 930 m in elevation.

Ecology and conservation status. *Ardisia vesca* occurs in cloud forests along the Continental Di-

67



66



vide. It is apparently rare and should thus be considered threatened.

Etymology. The specific epithet refers to the bladder-like shape of the flower buds.

Within *Ardisia* subg. *Auriculardisia* sect. *Palmanae, Ardisia vesca* is most closely related to *A. dwyeri* (see under that species for similarities). However, *A. vesca* differs from *A. dwyeri* by its membranous leaf blades, longer pedicels to 9 mm long, membranous or chartaceous much narrower calyx lobes to 1.2 mm wide with acute apices, shorter and narrower membranous corolla lobes to 3.4 × 2 mm, shorter and narrower anthers to 2.4 × 0.9 mm, shorter styles to 3.5 mm long, and smaller fruits to 5 mm in diameter.

The type of *Ardisia minima* is in very young bud and is notable only for its slightly larger leaves, and although both the types of *A. vesca* and *A. minima* were described at the same time, *A. vesca* is selected over *A. minima* because it has a few flowers in anthesis.

Specimen examined. PANAMA. **Coclé**: vicinity of La Mesa, beyond El Valle, on N slope of Cerro Gaital, 12 July 1987 (fl), *G. McPherson 11230* (LL, MO).

TAXONOMIC TREATMENT OF *ARDISIA* SUBG. *AURICULARDISIA* SECT. *PLEUROBOTRYAE*

Ardisia subg. **Auriculardisia** sect. **Pleurobotryae** Ricketson & Pipoly, sect. nov. TYPE here designated: *Ardisia pleurobotrya* Donn. Sm.

Quoad sepala asymmetrica ad bases auriculata atque ramulos furfuraceo-lepidotosque ad *Ardisiam* subg. *Auriculardisiam* pertinet, sed species unica hujus sectionis ab aliis sectionibus subgeneris inflorescentiis manifeste lateralibus, pedunculis usque ad 6.2 cm longis, tota planta squamis lepidotis dense manifeste superpositis brunneisque induta atque floribus pedicellis sigmoideis insidentibus perfacile cognoscitur.

Within *Ardisia* subg. *Auriculardisia,* section *Pleurobotryae* is monotypic and is defined by its strictly lateral inflorescences, long naked peduncles, to 6.2 cm long, dense furfuraceous-lepidote scales on most plant parts, and pendent flowers on long, usually sigmoid pedicels.

67. Ardisia pleurobotrya Donn. Sm., Bot. Gaz. 25: 148. 1898. *Auriculardisia pleurobotrya* (Donn. Sm.) Lundell, Phytologia 49: 345. 1981. TYPE: Costa Rica. Alajuela: Potrero del Alto, Volcán Poás, 2450 m, 20 July 1888 (fl), *H. Pittier 389* (lectotype, designated here, US!, US neg. 2382!, LL neg. 1971-85!; isolectotypes, B!, BR!, CR!, G! [2], W!). Figure 67.

Auriculardisia pleurobotrya var. *parva* Lundell, Phytologia 55: 236. 1984. Syn. nov. TYPE: Panama. Bocas del Toro: Upper Río Colubre, 2500–3000 m, Aug. 1983 (fl, fr), *L. Gómez, R. Chacón, I. Chacón & G. Herrera 21919* (holotype, LL!; isotypes, MO!, PMA!).

Shrubs or trees to 20 m tall, 35 cm diam. *Branchlets* stout, terete, 4–6 mm diam., densely furfuraceous-lepidote, the scales sessile, flat. *Leaves* monomorphic; blades coriaceous, elliptic to oblanceolate, 2.4–11.4 × 0.9–3.7 cm, apically acuminate, with an acumen 0.4–1.2 mm long, basally acute to acuminate, decurrent on the petiole, inconspicuously pellucid punctate and punctate-lineate, glabrous above, densely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 6 to 15 pairs, obscure above and below, the margins entire, revolute; petioles slender, canaliculate, 0.4–1.5 mm long, glabrous above, furfuraceous-lepidote below. *Inflorescences* lateral, erect, pinnately or bipinnately paniculate, 3.4–13.6 × 2.4–8.2 cm, pyramidal, longer than the leaves, the rachis inconspicuously punctate and punctate-lineate, furfuraceous-lepidote like the branchlets, the branches terminating in 3- to 8-flowered corymbs; peduncle 2.4–6.2 cm long; inflorescence bracts early caducous, unknown; inflorescence branch bracts caducous, membranous, oblong, 2.4–7.1 × 0.5–2.1 mm, apically acute to rounded, prominently punctate and punctate-lineate, glabrous above, furfuraceous-lepidote below like the branchlets, the margins erose, hyaline; floral bracts similar to inflorescence branch bracts, but 2.4–3.9 × 0.5–1.5 mm; pedicels slender, terete, 6.2–10.5 mm long, usually sigmoid at anthesis, inconspicuously punctate and punctate-lineate, densely appressed furfuraceous-lepidote. *Flowers* 5-merous, white to light pink or yellow; calyx lobes chartaceous, suborbicular to ovate, 1.4–2.8 × 1.3–1.8 mm, apically

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Figure 66 (left). *Ardisia vesca.* —A. Flowering branch. —B. Flower. —C. Fruit. (A–C drawn from holotype, *B. Hammel 952* (MO).)

Figure 67 (right). *Ardisia pleurobotrya.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, adaxial surface. —G. Stamen, lateral margin. —H. Fruit. (A, B drawn from *J. Pipoly 7124* (MO); C–G from *A. Jiménez M. 3949* (F); H from *R. Lent 679* (MO).)

acute, densely and conspicuously punctate and punctate-lineate, densely furfuraceous-lepidote medially, the margins irregular, erose-fimbriate, the fimbriae composed of simple or stellate trichomes; corolla membranous, 4.1–5.5 mm long, the tube 1.3–1.8 mm long, the lobes ovate, 3.9–4.9 × 2.8–3.1 mm, apically acute, prominently punctate and punctate-lineate, glabrous, the margins entire; stamens 3.8–4.1 mm long, the filaments 1.4–1.6 mm long, the staminal tube 0.7–0.9 mm long, inconspicuously punctate and punctate-lineate, the apically free portions 0.5–0.9 mm long, the anthers narrowly ovoid, 2.4–2.6 × 0.7–1.1 mm, apically subulate, basally sagittate, dehiscent by subapical pores, the connective punctate dorsally; pistil 3.3–4.5 mm long, the ovary obturbinate, 0.9–1.1 mm long, the style 2.3–3.5 mm long, conspicuously punctate and punctate-lineate, the ovules 14 to 16. *Fruit* globose, 7.7–9.1 mm diam., prominently punctate and punctate-lineate, glabrous.

Distribution. *Ardisia pleurobotrya* is found throughout the high mountains of Costa Rica and in Bocas del Toro and Chiriquí, Panama, from 1100 to 3300 m in elevation.

Ecology and conservation status. Primary and disturbed or remnant, oak, montane, cloud, and elfin forests. It appears to be quite common in protected areas on mountaintops, and Pipoly has observed it thriving in public, open areas on Volcán Poás, so we believe it is not threatened at this time.

Etymology. The specific epithet was derived from the Greek, "pleuro," meaning lateral, in a sideways position, and "botrya," meaning bunch, which refers to the elongate lateral inflorescence branches with clustered corymbs.

Common Name. "Tucuico" (*Standley 35090*).

Ardisia pleurobotrya has asymmetric calyx lobes with auriculate bases and furfuraceous-lepidote indument, which clearly place it in subgenus *Auriculardisia*. However, the strictly lateral inflorescences with long naked peduncles with pendent flowers on long pedicels clearly mark this species. No other taxa within subgenus *Auriculardisia* have strictly lateral inflorescences.

Although Donnell Smith's types are generally assumed to be at US, his original description of *Ardisia pleurobotrya* listed four different collections without designating a type, necessitating the need to select a lectotype. We hereby designate the *H. Pittier 389* collection at US as the lectotype. This collection has generally been regarded as the type and has been photographed by both LL (neg. 1971-85) and US (neg. 2382). Lundell annotated this sheet as a type but failed to officially designate it as a lectotype.

Lundell's concept of *Auriculardisia pleurobotrya* var. *parva* came solely from his holotype, now at LL, which has eight inflorescences in very young bud and one inflorescence slightly older, with smaller leaves. However, the isotype at MO has two branches, one similar to the holotype, but with larger leaves more typical of *Ardisia pleurobotrya.* The other branch is in fruit with mature calyx and matches the species in all respects. Lundell (1984b: 236) stated that variety *parva* "appears to be a diminutive form of *Auriculardisia pleurobotrya* (Donn. Sm.) Lundell, and all parts of the variety are smaller than the species," which was true given the nature of the material he had to work with.

Specimens examined. COSTA RICA. **Alajuela**: Volcán Poás, near crater, s.d. (fl), *A. Endres s.n.* (W); near Volcán Poás, 5 May 1966 (fl, fr), *A. Jiménez M. 3949* (F); Parque Nacional Volcán Poás, 19 July 1984 (fl), *J. Pipoly 7124* (DUKE, F, G, K, MO, NY, TEX, US); slopes of Volcán Poás from rim of crater to a distance 2 mi. down road toward Varablanca, 28 Jan. 1971 (fl, fr), *R. Wilbur & J. Teeri 13677* (DUKE, LL). **Cartago**: terminus of road to Volcán Turrialba, vicinity of Finca Quemados, 2 May 1971 (fl, fr), *F. Almeda 570* (DUKE); Volcán Irazú, pasture along CR route 40 from Cartago to the crater, 21 June 1983 (fl, fr), *K. Barringer et al. 3242* (CAS, F, NY, TEX); pasture below crater of Turrialba Volcano, 26 July 1965 (fl, fr), *R. Lent 679* (F, LL, MO); vicinity of La Picada and Finca Retiro on the E slope of Volcán Turrialba, 21 Feb. 1978 (fl, fr), *R. Wilbur 24671* (DUKE). **Cartago–San José**: about 22 km SE of El Empalme, along the Interamerican Hwy., 27 Nov. 1969 (fl), *W. Burger & R. Liesner 6481* (F, G, GH). **Guanacaste**: Parque Nacional Rincón de la Vieja, trail to Volcán Santa María, 15 Mar. 1989 (fl), *N. Zamora et al. 1540* (CR, INB, K, MO). **Heredia**: Parque Nacional Braulio Carrillo, Estación Barva, 20 June 1990 (fl, fr), *B. Apú 96* (CR, FTG, INB, MO); near Porrosati on the S slope of Volcán Barva, 22 June 1968 (fl, fr), *W. Burger & R. Stolze 6082* (F, MO, NY); Potero del Alto, SW slope of Volcán de Poás, Jan. 1889 (fl), *H. Pittier s.n.* (BR); Laguna de Barva, 6 Feb. 1890 (fl), *A. Tonduz 1949* (BR [2], US); between Sacramento and Laguna de Barva at summit of Volcán Barva, 12 Apr. 1975 (fl), *J. Utley & K. Utley 2035* (F, NY). **Limón**: Cordillera de Talamanca, Atlantic slope, unnamed cordillera between Río Terbi and Río Siní, 13 Sep. 1984 (fr), *G. Davidse et al. 29021* (CR, LL, MO); Cantón de Talamanca, Parque Nacional Cordillera de Talamanca, SE slopes, Cerro Biricuacua, Río Dapari, between Ujarrás and San José Cabécar, 5 Apr. 1993 (fl), *G. Herrera & W. Gamboa 6248* (FTG, INB, MO). **Puntarenas**: Cantón de Coto Brus, Zona Protectora Las Tablas, Cuenca Térraba-Sierpe, Sabana de Cerro Echandi, 13 Aug. 1997 (fl), *E. Alfaro 1344* (CR, INB, MO); Cordillera de Talamanca, upper slopes of Cerro Echandi, 23 Aug. 1983 (fl), *G. Davidse et al. 23883* (LL, MO, NY); Cantón de Buenos Aires, Ujarraz, slopes of Cerro Betsú, to the Continental Divide, Pacific slope, 6 Oct. 1989 (fl), *G. Herrera 3626* (CR, F, FTG, MO, USJ). **San José**: area N of Cerro de la Muerte, Cordillera de Talamanca, 1 Feb. 1963 (fl, fr), *L. Williams et al. 24150* (F, G). PANAMA. **Bocas del Toro**: Cordillera de Talamanca, 2–5 airline km NW of the peak of Cerro Echandi on the Costa Rican–Panamanian international border, 1 & 9 Mar. 1984 (fl), *G. Davidse et al. 25124* (CR, LL, MO). **Chiriquí**: ridge N of Potrero Muleto, 15 Mar. 1979 (fl, fr), *W. D'Arcy & B. Hammel 12513* (F, FTG, MO, PMA); Volcán Bar, along road E of Potrero Muleto, 17 Nov. 1978 (fl, fr), *B. Hammel 5655* (MO); Cerro Pando, valley of the upper Río Chiriquí, 13 Mar. 1938 (fr), *P. White 14* (MO).

TAXONOMIC TREATMENT OF *ARDISIA* SUBG. *AURICULARDISIA* SECT. *WEDELIA*

Ardisia subg. **Auriculardisia** sect. **Wedelia** Ricketson & Pipoly, sect. nov. TYPE here designated: *Ardisia wedelii* Lundell.

Quoad lobulos calycinos fere liberos asymmetricos sub apicibus incises ad bases auriculatos ad *Ardisiam* subg. *Auriculardisiam* pertinet. Sectio haec ab aliis sectionibus subgeneris foliis monomorphis atque inflorescentiis longepedunculatis columnaribus vel subcolumnaribus perfacile cognoscitur.

Few-branched subshrubs, shrubs, or small trees, to 4 m tall. *Branchlets* stout, terete, vestiture of usually dense furfuraceous-lepidote scales or a mixture of furfuraceous-lepidote scales and cupuliform scales or a mixture of dense cupuliform scales and dense, stellate trichomes or erect, stipitate-stellate trichomes on long multicellular stalks, 0.7–0.9 mm long with long multiple uniseriate arms. *Leaves* monomorphic; the blades membranous to chartaceous, inconspicuously to conspicuously and often prominently punctate and punctate-lineate; petioles slender to stout, marginate, sessile to 1.6 cm long. *Inflorescences* terminal, erect, pinnately to tripinnately paniculate, columnar to sub-columnar, usually shorter than the leaves, usually loosely congested corymbs; inflorescence bracts usually persistent, foliaceous; inflorescence branch bracts and floral bracts caducous; pedicels stout, terete. *Flowers* 5-merous, white, light pink, light purple, red, or light orange; calyx lobes essentially free, membranous to coriaceous, lanceolate or ovate to suborbicular, basally auriculate; corolla membranous to chartaceous, the lobes ovate to lanceolate, inconspicuously to conspicuously and usually prominently punctate and punctate-lineate; stamens connate, the filaments apically free, connate basally into an elobate tube, free from the corolla tube, epunctate, the anthers ovoid or narrowly ovoid to lanceoloid, dehiscent by subapical pores, opening into longitudinal slits, the connective punctate; pistil glabrous, the ovary oblong, the style slender, erect, inconspicuously or conspicuously, rarely prominently punctate, the ovules pluriseriate. *Fruits* globose, inconspicuously or conspicuously, often prominently punctate and punctate-lineate, smooth to costate.

Distribution. Members of *Ardisia* subg. *Auriculardisia* sect. *Wedelia* occur from Jinotega and Zeyala in Nicaragua to Darién, Panama, where they grow between sea level and 1400 m in elevation.

Ecology and conservation status. Species in *Ardisia* subg. *Auriculardisia* sect. *Wedelia* occur in primary, secondary, disturbed, or remnant forests, swamp forests, evergreen forests, premontane or montane wet forests, and cloud forests. Members of this section should be considered threatened or endangered.

Ardisia subg. *Auriculardisia* sect. *Wedelia* is defined by its subshrubby to small arborescent habit, terminal, columnar to sub-columnar inflorescences on peduncles at least ⅓ the length of the inflorescence, and subtended by large, foliaceous bracts.

KEY TO THE TAXA OF *ARDISIA* SUBG. *AURICULARDISIA* SECT. *WEDELIA*

1a. Indument of branchlets, petioles, and inflorescence branches mixed, of two types: open cupuliform lepidote, the other dense, erect, stipitate-stellate hairs on long multicellular trichomes, the stalks 0.7–0.9 mm long with multiple uniseriate arms .... 71. *Ardisia heterotricha*
1b. Indument of branchlets, petioles, and inflorescence branches densely furfuraceous-lepidote and/or cupuliform scales.
    2a. Anthers 2.5–2.8 × 1–1.3 mm; the filaments fused well above the tube throat.
        3a. Indument of the branchlets and inflorescences of scattered furfuraceous-lepidote scales; leaves obovate to widely obovate, 24.5–42.4 cm long; calyx lobes 2.2–2.5 mm long; corolla lobes 2.3–2.5 mm wide; anthers ovoid, 2.6–2.8 × 1.1–1.3 mm; pistils 5.3–5.7 mm long; styles 4.4–4.6 mm long .... 69. *Ardisia folsomii*
        3b. Indument of the branchlets and inflorescences of densely furfuraceous-lepidote scales, leaves oblanceolate, 42.2–45.4 cm long; calyx lobes 1.8–2 mm long; corolla lobes 1.9–2 mm wide; anthers oblong, 2.5–2.6 × 1–1.1 mm; pistils 3.8–4 mm long; styles 2.8–3 mm long .... 70. *Ardisia hammelii*
    2b. Anthers 1.2–2.4 × 0.6–1 mm; the filaments separate, at least above the tube throat.
        4a. Leaves apically obtuse, with an acumen 0.2–0.6 cm long; calyx lobes 0.8–1.3 × 0.7–1 mm; corolla lobes 2–2.4 mm long .... 72. *Ardisia kennedyae*
        4b. Leaves apically acute to acuminate, with an acumen 0.6–2.9 cm long; calyx lobes 1.6–2.5 × 1–2.4 mm; corolla lobes 3–4.4 mm long.
            5a. Anthers 2.1–2.4 × 0.8–1 mm.
                6a. Calyx lobes 2.2–2.4 mm wide; corolla lobes ovate, 3–3.5 mm long; stamens 3.6–4 mm long; anthers ovoid, 2.1–2.3 mm long .... 68. *Ardisia conoidea*

6b. Calyx lobes 1.1–1.3 mm wide; corolla lobes lanceolate, 3.8–4.2 mm long; stamens 2.9–3.1 mm long; anthers oblong, 2.3–2.4 mm long .... 74. *Ardisia talamancensis*

5b. Anthers 1.2–2.1 × 0.5–0.8 mm.

7a. Corolla lobes 0.9–1.2 mm wide; stamens 4.2–4.9 mm long; filaments 2.7–2.9 mm long, the apically free portion of the filaments 2.2–2.4 mm long, the tube 0.5–1.6 mm long; pistil 4.8–5.2 mm long; style 4–4.6 mm long .... 75. *Ardisia wedelii*

7b. Corolla lobes 2–2.2 mm wide; stamens 2.4–2.5 mm long; filaments 1.1–1.2 mm long, the apically free portion of the filaments 0.7–0.8 mm long, the tube 0.3–0.5 mm long; pistil 3.7–4.1 mm long; style 2.5–2.8 mm long 73. *Ardisia mameyensis*

68. Ardisia conoidea Lundell, Wrightia 4: 56. 1968. *Auriculardisia conoidea* (Lundell) Lundell, Phytologia 54: 285. 1983. TYPE: Costa Rica. Cartago: Tapanti, 1300 m, 15 July 1937 (fl), *M. Valerio 1624* (holotype, F!, F neg. 68140!, LL neg. 1971-25!). Figure 68.

Auriculardisia sessilifolia Lundell, Wrightia 7: 272. 1984. Syn. nov. Non *Ardisia sessilifolia* Mez in Engl., Pflanzenr. IV. 236 (Heft 9): 125. 1902. *Ardisia zarceroana* Lundell, Phytologia 61: 68. 1986, nom. inval. *Ardisia apodophylla* J. F. Morales, Phytologia 83: 111. 1997. TYPE: Costa Rica. Alajuela: Cordillera Central near San Juan de Laja about 15 km N of Zarcero, ca. 1350 m, 7 Feb. 1965 (fl, fr), *L. Williams, A. Molina R., T. Williams & D. Gibson 28998* (holotype, F!, F neg. 68321!, LL! [fragment]).

Subshrubs to 2 m tall. *Branchlets* 5–9 mm diam., with densely furfuraceous-lepidote scales. *Leaves* with blades chartaceous, oblanceolate, 24.4–39.6 × 5.1–12.9 cm, apically acuminate, with an acumen 1.4–2.1 cm long, gradually tapering to an auriculate base, prominently punctate above and below, nearly glabrous above, densely furfuraceous-lepidote scales below, even more dense along the midrib, the midrib impressed above, prominently raised below, the secondary veins 39 to 53 pairs, prominulous above, prominent below, the margins entire, revolute; petioles subobsolete to 0.5 cm long, densely furfuraceous-lepidote below. *Inflorescences* bipinnately or tripinnately paniculate, columnar, 15.2–33.6 × 5.1–13.4 cm, rachis and branches densely furfuraceous-lepidote, the branches terminating in 6- to 11-flowered corymbs; peduncles (1.5–2.7)4.7–11.8 cm long; inflorescence bracts caducous, oblate, 2.5–3.2 × 5.4–6.9 mm, apically acute, prominently punctate and punctate-lineate, densely furfuraceous-lepidote, midvein and secondary veins obscure, the margins entire, flat; inflorescence branch bracts similar to the inflorescence bracts but lanceolate, 4.2–5.6 × 0.9–1.4 mm; floral bracts similar to the inflorescence branch bracts, but 1.2–2.1 × 0.6–1.2 mm, the margins minutely erose, hyaline; pedicels 3.9–5.6 mm long, enlarged apically in fruit, conspicuously punctate and punctate-lineate, densely furfuraceous-lepidote. *Flowers* white or pale red to dark purple; calyx lobes chartaceous, suborbicular to ovate, 1.8–2.2 × 2.2–2.4 mm, apically acute or rounded, scattered conspicuously punctate, sparsely furfuraceous-lepidote abaxially, the margins minutely erose, hyaline, sparsely glandular-ciliolate; corolla membranous, 3.6–3.9 mm long, the tube 0.4–0.6 mm long, the lobes ovate, 3–3.5 × 1.4–1.6 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire; stamens 3.6–4 mm long, the filaments 1.9–2.1 mm long, the staminal tube 0.5–0.7 mm long, the apically free portions 1.4–1.6 mm long, epunctate, the anthers ovoid to lanceoloid, 2.1–2.3 × 0.8–1 mm wide, apically subulate-apiculate, basally deeply cordate, the connective punctate; pistil 5.1–5.4 mm long, glabrous, the ovary 0.6–0.9 mm long, the style 4.4–4.5 mm long, prominently punctate and punctate-lineate, the ovules 9 to 12. *Fruits* globose, 6.4–8.2 mm diam., prominently punctate and punctate-lineate, slightly costate.

Distribution. Ardisia conoidea is endemic to Alajuela and Cartago, Costa Rica, growing from 700 to 1350 m in elevation.

Ecology and conservation status. Ardisia conoidea occurs in disturbed and remnant montane, evergreen, and cloud forests. Because of its restricted distribution, it should be considered threatened.

Etymology. The specific epithet referred to the pedicels, which are enlarged apically, and cone-shaped in fruit.

Ardisia conoidea may be distinguished from the other species of *Ardisia* subg. *Auriculardisia* sect. *Wedelia* by its larger anthers to 2.3 × 1 mm, larger calyx lobes to 2.2 × 2.4 mm, smaller corolla lobes to 3.5 × 1.6 mm, and larger stamens to 4 mm long with broad filaments.

The only type material of *Ardisia conoidea* is from the holotype at F, which is in very poor condition. The specimen is in young bud and the inflorescence has not yet expanded, a condition that would at first glance exclude this species from section *Wedelia*. The leaf blades are also smaller and shriveled. However, the type material corresponding to *Auriculardisia sessilifolia* is in much better shape with a mature inflorescence and leaves and clearly shows that it belongs to this species.

Specimens examined. COSTA RICA. **Alajuela**: along road from San Ramón northward through Balsa, ca. 13.8 km N of bridge over Quebrada Volio and ca. 4.6 km N of bridge over (apparently) Río Balsa, at small stream (Río San Luis?), 29 Aug. 1979 (fl), *W. Stevens 13784* (MO); along road from San Ramón northward through Balsa, ca. 16.7 km N of bridge over Quebrada Volio and ca. 7.5 km N of bridge over (apparently) Río Balsa, at bridge over stream Río Cataratas, 29 Aug. 1979 (fl), *W. Stevens 13863* (MO). **Cartago**: just W of Quebrada Casa Blanca, Tapantí, 26 Dec. 1984 (fr), *M. Grayum et al. 4649* (LL, MO).

69. Ardisia folsomii Lundell, Wrightia 6: 76. 1979. *Auriculardisia folsomii* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Panama. Coclé: Atlantic slope NW El Copé along Río San Juan near fork with Río Tife, 5–6 hour walk on trail to El Copé sawmill, ca. 1200 ft. [366 m], 9 June 1978 (fl), *B. Hammel 3316* (holotype, LL!, LL neg. 1979-2!; isotype, MO!). Figure 69.

Subshrubs 0.3–3 m tall. *Branchlets* 6–9 mm diam., indument a mixture of densely furfuraceous-lepidote scales and chocolate brown cupuliform scales with irregular arms (not as pronounced as in *A. brenesii*). *Leaves* with blades chartaceous, obovate to widely obovate, 24.5–42.4 × 12.5–23.1 cm, apically abruptly acuminate, with an acumen 0.5–0.9(–1.2) cm long, basally auriculate, prominently punctate above and below, scattered furfuraceous-lepidote below, but denser along the midrib below, the midrib impressed above, prominently raised below, the secondary veins 21 to 49 pairs, prominulous above, prominent below, the margins entire, revolute; petioles sessile to 0.5 cm long, densely furfuraceous-lepidote below. *Inflorescences* bipinnately or tripinnately paniculate, columnar, 8.6–26.4 × 3.2–15.4 cm, the rachis and branches as in branchlets, the branches terminating in 8- to 14-flowered corymbs; peduncles 5.8–12.7 cm long; inflorescence bracts caducous, ovate, 2.9–3.8 × 10.9–11.4 mm, apically acute, basally sessile or nearly so, prominently punctate and punctate-lineate, vestiture as in the branchlets, midvein and secondary veins obscure, the margins entire, flat; inflorescence branch bracts caducous, ovate, 0.18–2.8 × 0.12–1.2 cm, progressively smaller, apically acute, sessile, prominently punctate and punctate-lineate, densely furfuraceous-lepidote, midvein and secondary veins obscure, the margins entire, flat; floral bracts similar to the inflorescence branch bracts, but 1.6–2.8 × 0.9–1.4 mm, margins minutely erose, hyaline; pedicels 5.2–6.7 mm long, inconspicuously punctate-lineate, vestiture as in the branchlets. *Flowers* pale red to dark purple; calyx lobes chartaceous, suborbicular to ovate, 2.2–2.5 × 2–2.2 mm, apically acute or rounded, prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote abaxially, the margins minutely erose, hyaline, sparsely glandular-ciliolate; corolla membranous, 5.5–5.9 mm long, the tube 1.2–1.5 mm long, the lobes lanceolate, 4–4.7 × 2.3–2.5 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially, the margins entire; stamens 4–4.3 mm long, the filaments 2.1–2.3 mm long, the staminal tube 1.7–2 mm long, the apical free portion 0.3–0.5 mm long, epunctate, the anthers ovoid, 2.6–2.8 × 1.1–1.3 mm, apically cuspidate-apiculate, basally sagittate, the connective punctate; pistil 5.3–5.7 mm long, the ovary 0.9–1.1 mm long, the style 4.4–4.6 mm long, conspicuously punctate and punctate-lineate, the ovules 9 to 12. *Fruits* globose, 5.8–6.8 mm diam., prominently and conspicuously punctate, slightly costate.

Distribution. Ardisia folsomii is endemic to the area around the El Potroso sawmill at Alto Calvario near the Continental Divide, above El Copé, Coclé, Panama, growing at 700 to 1300 m in elevation.

Ecology and conservation status. Ardisia folsomii occurs in cloud forests. Because of its location near the lumber camps and sawmills in the area, it should be considered threatened.

Etymology. This species was named in honor of James P. Folsom, indefatigable plant collector, taxonomic specialist in *Dichaea* (Orchidaceae), and director of the Huntington Botanical Gardens.

Within *Ardisia* subg. *Auriculardisia* sect. *Wedelia*, *Ardisia folsomii* is most closely related to *A. hammelii* by its small anthers to only 2.8 × 1.3 mm, the filaments fused well above the tube throat. However, *Ardisia folsomii* can easily be separated by its indument of the branchlets and inflorescences densely furfuraceous-lepidote, the shorter leaves obovate to widely obovate to 42.4 cm long, the longer calyx lobes to 2.5 mm long, the longer corolla lobes to 2.5 mm wide, the longer anthers ovoid to 2.8 × 1.3 mm, the longer pistils to 5.5 mm long, and the longer styles to 4.6 mm long.

Specimens examined. PANAMA. **Coclé**: El Copé on Pacific side 2 hour walk from sawmill, 16 Oct. 1979 (fr), *T. Antonio 2111* (MO); Alto Calvario, forest above sawmill, on Continental Divide, 5.2 mi. above El Copé, 6 Dec. 1979 (fr), *T. Croat 49215* (MO); Continental Divide, about 10 km from La Pintada, on road from La Pintada to Coclecito, 16 Aug. 1980 (fr), *R. Dressler s.n.* (FLAS, LL); near Cascajal, ca. 10 km from La Pintada, 31 Aug. 1980 (fr), *R. Dressler 5918* (FLAS [2]); lumber camp at Alto

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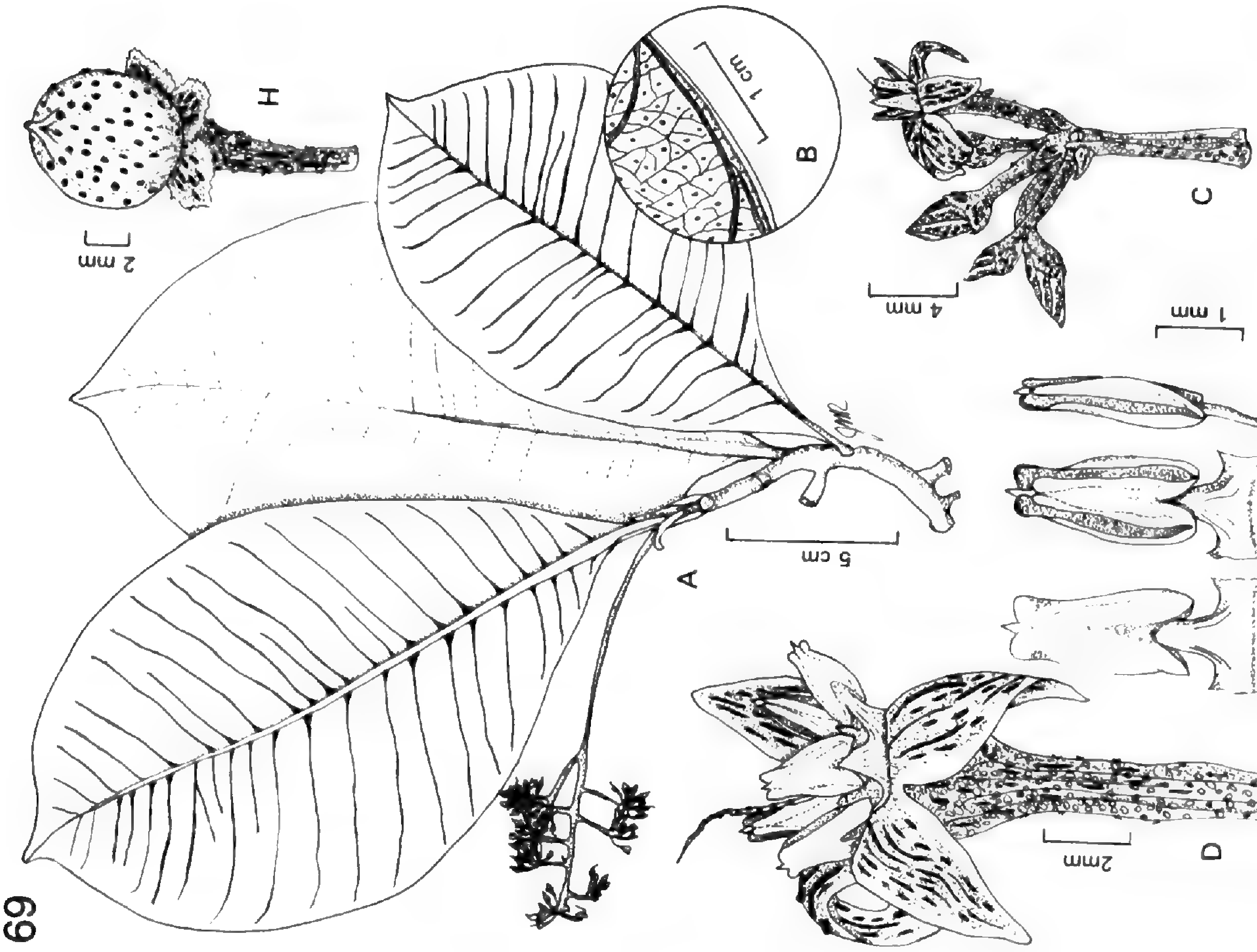
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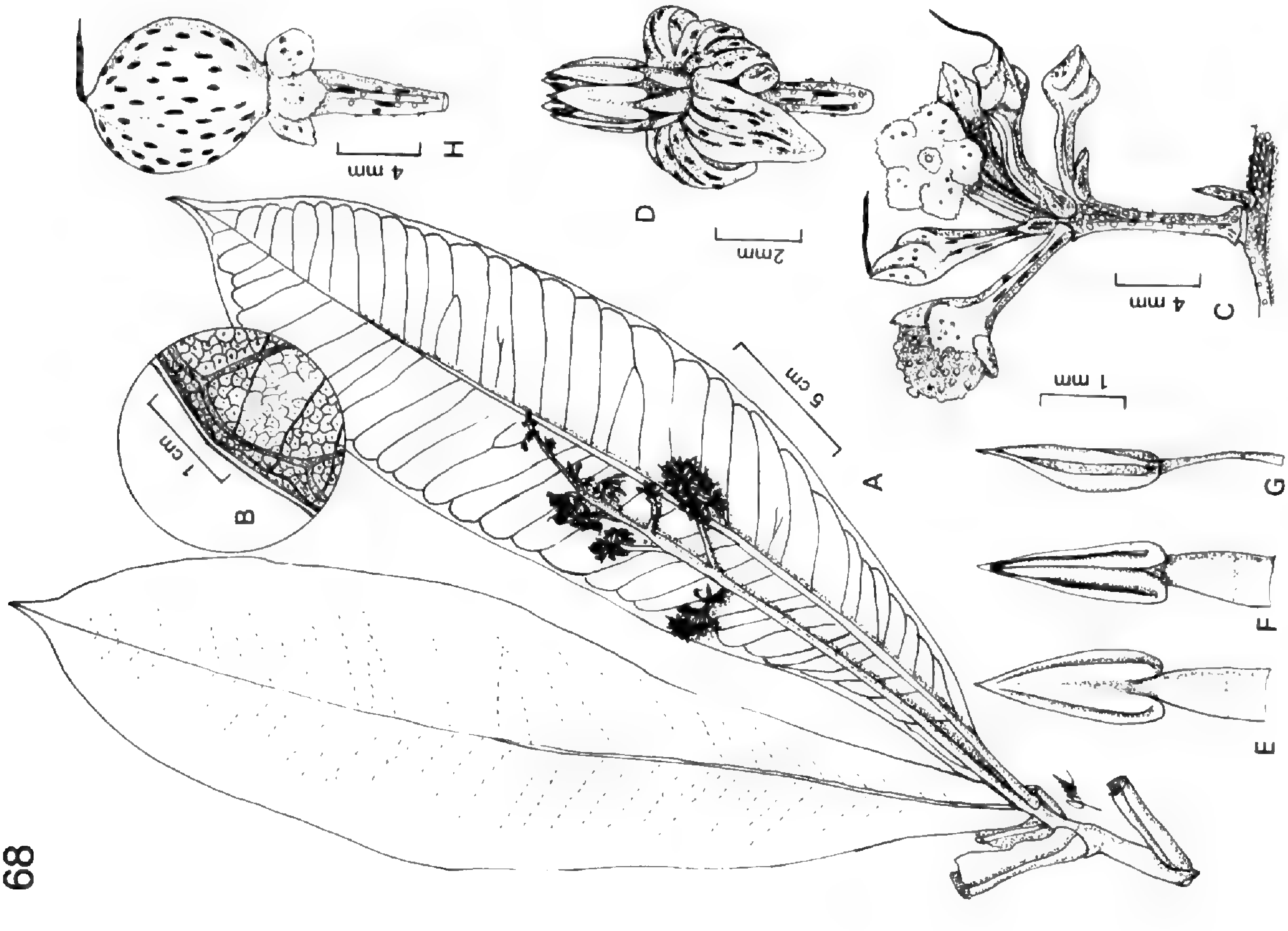
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Calvario, 7 km N of El Copé, 14 Jan. 1977 (fr), *J. Folsom 1308* (MO); Alto Calvario, 20 Apr. 1977 (fl), *J. Folsom & A. Jaslon 2686* (MO); Continental Divide area N of El Copé, an active lumber camp at a site known as Alto Calvario, just above El Potroso, 28 May 1980 (fl), *J. Folsom & J. Mauseth 7853* (TEX); along road from La Pindeda to El Copé by way of Piedras Gordas, sawmill above El Copé, 20 Apr. 1978 (fl), *B. Hammel 2629* (MO, F neg. 55624); El Copé sawmill, on peak right of road just before, S of, sawmill, 28 July 1978 (fl), *B. Hammel 4148* (MO); above El Copé, 27 Nov. 1985 (fr), *G. McPherson 7691* (MO); between Caño Sucio and waterfall at base of Cerro Tife, ca. 4 hr. hike, Caño Sucio is 1 hr. W of the Río Blanco, which is a 5 hr. hike N of the Continental Divide above El Copé and El Potroso sawmill, 13 Dec. 1980 (fr), *K. Sytsma et al. 2515* (MO); above El Potroso sawmill at Continental Divide, N of El Copé, 13 May 1981 (fl), *K. Sytsma & L. Andersson 4527* (MO).

70. Ardisia hammelii Lundell, Wrightia 6: 78. 1979. *Auriculardisia hammelii* (Lundell) Lundell, Phytologia 49: 344. 1981. TYPE: Panama. Colón: S approach of Cerro Bruja from Río Escandaloso, 2600 ft. [792 m], 18 May 1978 (fl), *B. Hammel 3141* (holotype, MO!, F neg. 55667!; isotype, PMA!). Figure 70.

Shrubs to 3 m tall. *Branchlets* ca. 9 mm diam., densely furfuraceous-lepidote, the scales overlapping. *Leaves* with blades chartaceous, oblanceolate, 42.2–45.4 × 13.9–15.4 cm, apically acute to acuminate, with an acumen 1–1.4 cm long, basally tapering to a somewhat auriculate base, inconspicuously punctate above and below, nearly glabrous above, densely furfuraceous-lepidote below, especially denser along the midrib, the midrib impressed above, prominently raised below, the secondary veins raised above and below, the margins entire, flat; petioles subobsolete to 0.5 cm long, densely furfuraceous-lepidote below. *Inflorescences* bipinnately paniculate, sub-columnar, ca. 25.3 × 10.8 cm, the rachis, branches, abaxial bract surfaces, and pedicels densely furfuraceous-lepidote, the branches terminating in 9- to 11-flowered corymbs; peduncles ca. 12.3 cm long; inflorescence bracts caducous, ovate, 2.9–5.8 × 1.4–1.6 cm, apically acute, basally sessile, midvein and secondary veins obscure, inconspicuously punctate and punctate-lineate, densely furfuraceous-lepidote, the margins entire, flat; inflorescence branch bracts similar to the inflorescence bracts, but 0.3–1.8 × 0.1–0.9 cm; floral bracts similar to the inflorescence branch bracts, but 0.9–1.6 × 0.3–0.6 mm, the margins minutely erose, hyaline; pedicels 4.2–6.3 mm long, inconspicuously punctate-lineate, densely furfuraceous-lepidote. *Flowers* pale purple; calyx lobes chartaceous, suborbicular to ovate, 1.8–2 × 1.9–2.4 mm, apically acute or rounded, conspicuously punctate, densely furfuraceous-lepidote, the margins minutely erose, hyaline, sparsely glandular-ciliolate; corolla chartaceous, 5.9–6.1 mm long, the tube 1.6–1.8 mm long, the lobes lanceolate, 4.2–4.4 × 1.9–2 mm, apically acute, inconspicuously punctate and punctate-lineate, glabrous throughout, the margins entire; stamens 3.9–4.1 mm long, the filaments 1.8–2.1 mm long, the staminal tube 0.8–0.9 mm long, the apically free portions 1–1.1 mm, the anthers oblong, 2.5–2.6 × 1–1.1 mm, apically apiculate, basally sagittate, the connective punctate; pistil 3.8–4 mm long, the ovary 0.9–1 mm long, the style 2.8–3 mm long, prominently punctate and punctate-lineate, the ovules 14 to 17. *Fruits* unknown.

Distribution. *Ardisia hammelii* is known only from the type collection from Cerro Bruja, Colón, Panama, growing at 792 m in elevation.

Ecology and conservation status. *Ardisia hammelii* occurs in cloud forest. Because it is only known from the type collection, it should be considered threatened.

Etymology. This species was named in honor of Barry Hammel, Curator at the Missouri Botanical Garden, taxonomic authority in the Cyclanthaceae and Clusiaceae, prodigious field botanist, and co-editor of the *Manual de Plantas de Costa Rica* project.

Within *Ardisia* subg. *Auriculardisia* sect. *Wedelia*, *Ardisia hammelii* is most closely related to *A. folsomii* (see under that species for the similarities). However, *Ardisia hammelii* can easily be separated by its indument of the branchlets and inflorescenc-

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Figure 68 (left). *Ardisia conoidea.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, adaxial surface. —G. Stamen, lateral margin. —H. Fruit. (A, B drawn from *M. Grayum et al. 4649* (LL); C–G from *L. Williams et al. 28998* (F holotype of *Auriculardisia sessilifolia* Lundell); H from *M. Grayum 4649* (MO).)

Figure 69 (right). *Ardisia folsomii.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, adaxial surface. —G. Stamen, lateral margin. —H. Fruit. (A–C drawn from holotype, *B. Hammel 3316*; D–G drawn from *B. Hammel 4148* (MO);. H drawn from *T. Antonio 2111* (MO).)

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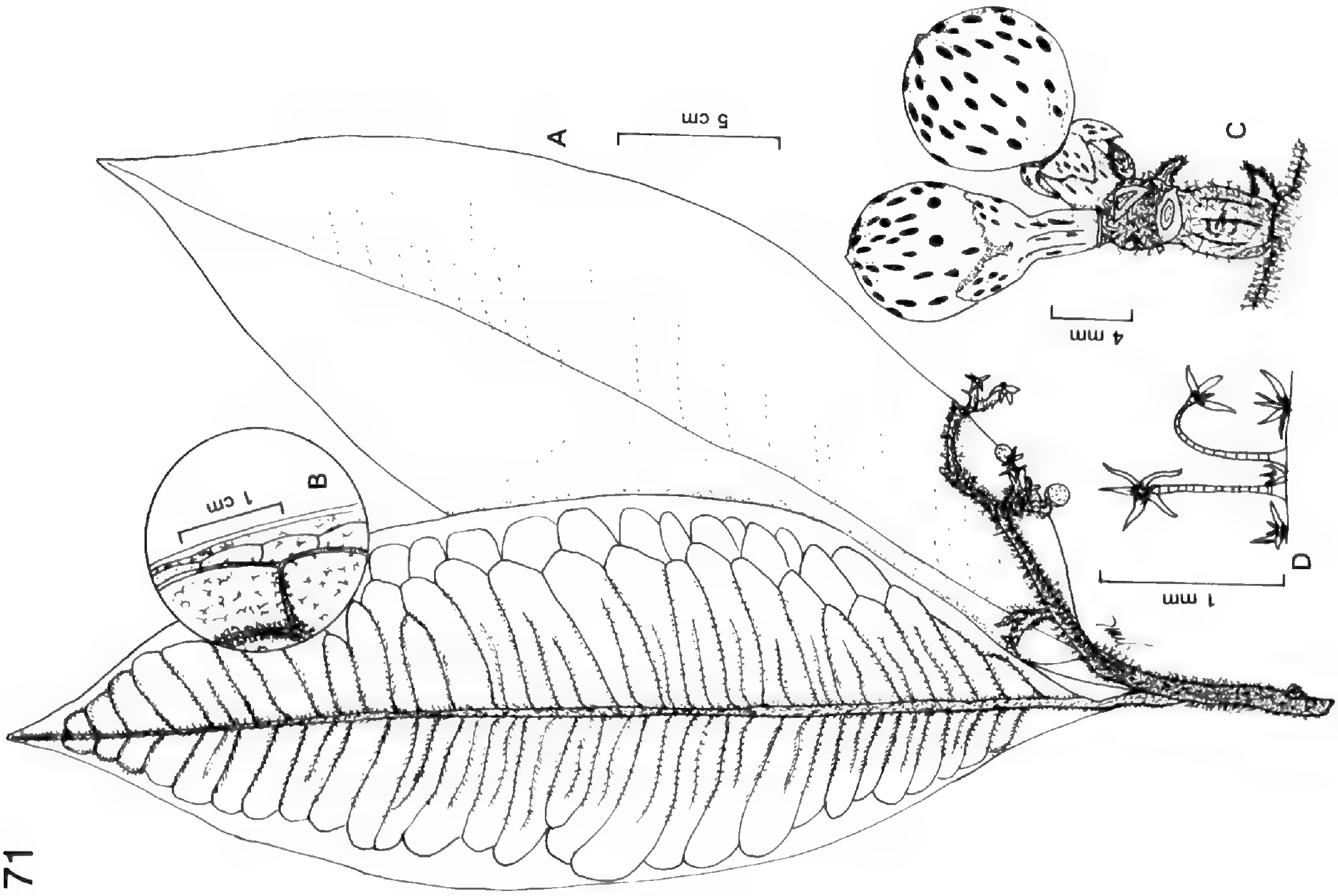

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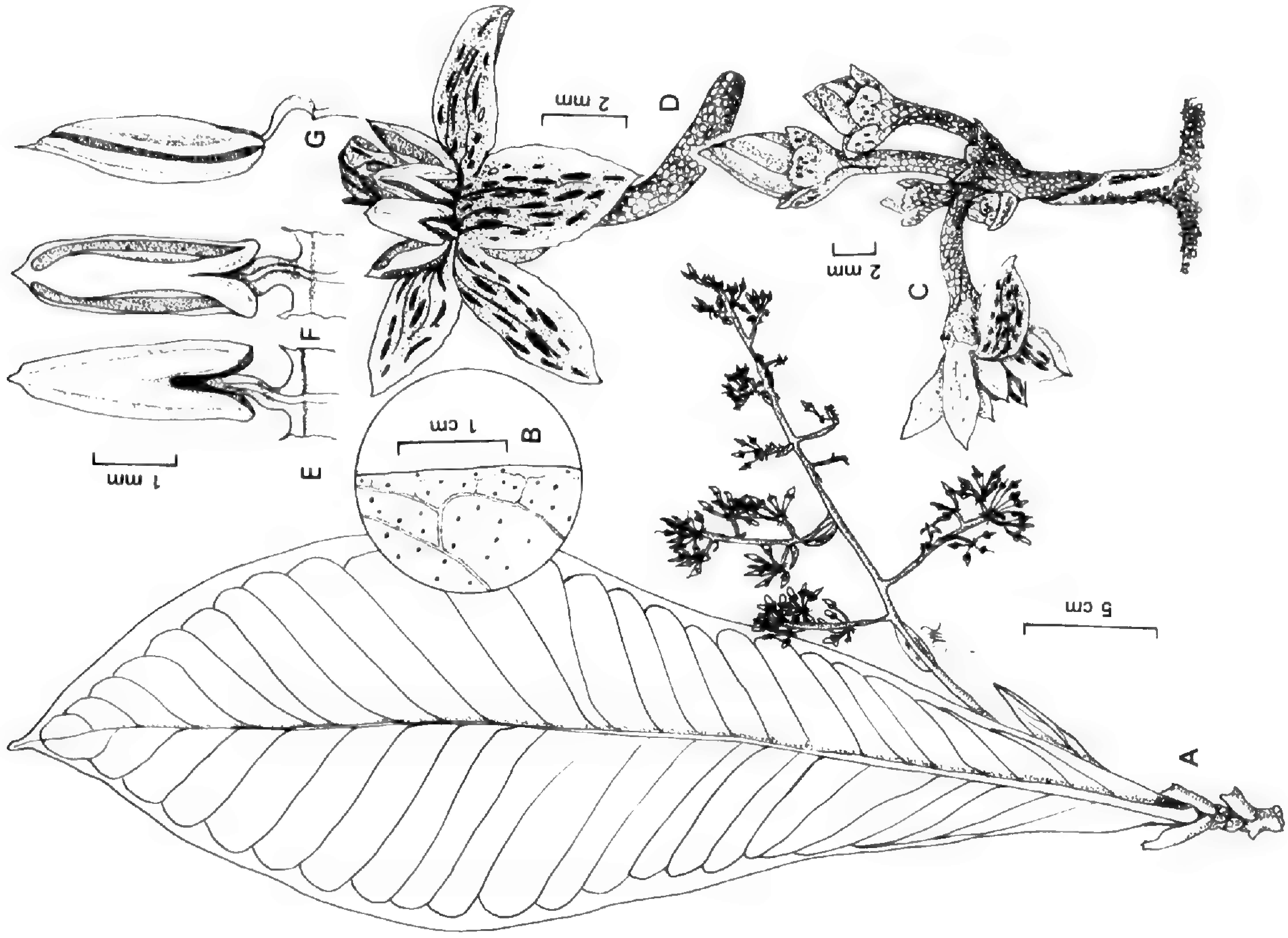

es of densely furfuraceous-lepidote scales, leaves oblanceolate, longer, to 45.4 cm long, the shorter calyx lobes to only 2 mm long, the thinner corolla lobes to only 2 mm wide, the smaller anthers oblong to only 2.6 × 1.1 mm, the smaller pistils to only 4 mm long, and the shorter styles to 3 mm long.

71. Ardisia heterotricha (Lundell) Pipoly & Ricketson, Sida 18: 512. 1998. *Auriculardisia heterotricha* Lundell, Wrightia 7: 268. 1984. *Ardisia heterotricha* (Lundell) Lundell, Phytologia 61: 64. 1986, nom. inval. TYPE: Panama. Panamá: on road near slopes of Cerro Jefe, 2400 ft. [732 m], 20 Jan. 1980 (fr), *T. Antonio, H. Moore & F. Putz 3417* (holotype, MO!). Figure 71.

Shrubs or small trees to 1.2 m tall. *Branchlets* 4–5.5 mm diam., vestiture a mixture of two types: sessile cupuliform scales with varying numbers of arms, the other uniseriate, multicellular stipitate-stellate trichomes, the stalks 0.7–0.9 mm long with multiple uniseriate arms, the stellate portion at times breaking off and the remaining hair appearing villous. *Leaves* with blades membranous to chartaceous, oblong to narrowly oblong, 33.3–35 × 12–12.4 cm, apically acuminate, with an acumen 2.5–2.8 cm long, basally acute, decurrent on the petiole, prominently punctate above and below, glabrous above, vestiture below mixed, scattered on the blade and denser on the midrib and secondary veins, like that of the branchlets, the midrib impressed above, prominently raised below, the secondary veins 24 to 40 pairs, prominulous above, prominent below, the margins entire, revolute; petioles 0.8–1.6 cm long, vestiture like that of the branchlets. *Inflorescences* bipinnately or tripinnately paniculate, 8–8.4 × 4–5.5 cm, sub-columnar, the rachis and branches with vestiture like that of branchlets, the branches terminating in 6- to 9-flowered corymbs; peduncles 2.3–2.7 cm long; inflorescence bracts unknown; inflorescence branch bracts early caducous, oblong, 2.8–3.4 × 0.7–0.9 mm, apically acute or rounded, basally sessile or nearly so, prominently punctate and punctate-lineate, glabrous above, vestiture below like that of branchlets, midvein and secondary veins obscure, the margins entire; floral bracts similar to the inflorescence branch bracts, but 0.8–1.4 × 0.7–1 mm; pedicels 3.1–5.7 mm long, 1.3–2.1 mm diam., conspicuously punctate, nearly glabrous, but with scattered furfuraceous-lepidote scales. *Flower* color unknown; calyx lobes chartaceous, ovate to suborbicular, 2.2–2.5 × 2.5–2.8 mm, apically acute, prominently punctate and punctate-lineate, vestiture abaxially like that of the branchlets, the margins minutely erose, hyaline, sparsely glandular-ciliolate; corolla unknown; stamens unknown; pistil unknown. *Fruits* globose, 7.2–8.6 mm diam., prominently and conspicuously punctate, non-costate.

Distribution. *Ardisia heterotricha* is known only from the type collection from Cerro Jefe, Panamá, Panama, growing at 732 m in elevation.

Ecology and conservation status. The summit of Cerro Jefe is a cloud forest with an unusual open canopy, dominated by *Colpothrinax aphonopetala* R. Evans (Arecaceae) and containing numerous endemic species. Many taxa otherwise known from much higher altitudes are present on Cerro Jefe. There were no details regarding the ecology of this species on the label, and given that a long history of collection at this locality has generated only the type collection, the species should be considered rare.

Etymology. The specific epithet was derived from the Greek, "hetero," meaning different, and "tricho," meaning hairs, referring to the two types of trichomes present on most plant parts.

Ardisia heterotricha is unique within *Ardisia* subg. *Auriculardisia* sect. *Wedelia* because of its vestiture of a mixture of two types: sessile cupuliform scales with varying numbers of arms, the other uniseriate, multicellular stipitate-stellate trichomes, the stalks 0.7–0.9 mm long with multiple uniseriate arms, the stellate portion at times breaking off and the remaining hair appearing villous.

72. Ardisia kennedyae Ricketson & Pipoly, sp. nov. TYPE: Panama. Bocas del Toro: Chan-

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Figure 70 (left). *Ardisia hammelii.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, adaxial surface. —G. Stamen, lateral margin. (A–G drawn from holotype, *B. Hammel 3141* (MO).)

Figure 71 (right). *Ardisia heterotricha.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence with mature fruits. —D. Detail of vestiture consisting of a mixture of two types, one of dense, sessile, flat scales, usually with multiple arms, and the other of stipitate-stellate hairs on long multicellular stalks with multiple uniseriate arms. (A–D drawn from holotype, *T. Antonio et al. 3417* (MO).)

guinola, swamp forest near Luzon, 20 June 1973 (fl, fr), *H. Kennedy 3258* (holotype, MO!). Figure 72.

Quoad folia obovata ad bases acutas ad apices acuminatas atque pedicellos graciles *A. folsomii* valde arcte affinis, sed ab ea lobulis calycinis 0.8–1.3 (non 2.2–2.5) mm longis 0.7–1.0 (nec 2.0–2.2) mm latis ad apices acutis (nec obtusis vel rotundatis), lobulis corollinis 2.0–2.4 (non 4.0–4.7) mm longis 1.0–1.4 (nec 2.3–2.5) mm latis, denique antheris 1.2–1.7 (non 2.6–2.7) mm longis statim distinguitur.

Subshrubs to 1 m tall. *Branchlets* 5–6 mm diam., with densely furfuraceous-lepidote scales. *Leaves* with blades membranous, obovate to oblanceolate, 17.3–25.2 × 7.8–11.2 cm, apically obtuse, with an acumen 0.2–0.6 cm long, basally acute, decurrent on the petiole, punctations obscure, glabrous above or sparsely furfuraceous-lepidote, densely furfuraceous-lepidote below, denser along midrib, the midrib impressed above, prominently raised below, the secondary veins 23 to 31 pairs, prominulous above, prominently raised below, the margins entire, revolute; petioles 0.3–1 cm long, glabrous above, densely furfuraceous-lepidote below. *Inflorescences* pinnately paniculate, columnar, 10.5–11 × 2–2.5 cm, peduncle, rachis, and branches densely furfuraceous-lepidote, the branches terminating in 8- to 12-flowered corymbs; peduncle 7–7.4 cm long; inflorescence bracts persistent, oblong, 1.4–2.3 × 0.3–0.7 cm, apically acute, prominently punctate and punctate-lineate, densely furfuraceous-lepidote, midvein and secondary veins obscure, the margins entire, flat; inflorescence branch bracts persistent, oblong, 1.7–2.3 × 0.6–0.8 mm, progressively smaller, apically acute, sessile, prominently punctate and punctate-lineate, glabrous above, densely furfuraceous-lepidote below, midvein and secondary veins obscure, the margins entire; floral bracts similar to the inflorescence branch bracts, but 1–1.7 × 0.2–0.8 mm; pedicels 4.5–5.4 mm long, inconspicuously punctate and punctate-lineate, densely furfuraceous-lepidote. *Flowers* pale pink to purple; calyx lobes membranous to slightly chartaceous, ovate to suborbicular, 0.8–1.3 × 0.7–1 mm, apically acute, prominently punctate and punctate-lineate, scattered furfuraceous-lepidote abaxially, the margins minutely erose, hyaline, sparsely glandular-ciliolate; corolla membranous, 2.8–3.2 mm long, the tube 0.6–0.7 mm long, the lobes ovate, 2–2.4 × 1–1.4 mm, apically acute, prominently black punctate and punctate-lineate, glabrous adaxially, glabrous to sparsely furfuraceous-lepidote abaxially, the margins entire; stamens 2.2–2.7 mm long, the filaments 1.1–1.3 mm long, the staminal tube 0.6–0.7 mm long, the apically free portions 0.4–0.7 mm long, epunctate, the anthers ovoid, 1.2–1.7 × 0.7–0.8 mm, apically obtuse with a minute apiculum, basally cordate; pistil 1.7–1.9 mm long, the ovary 0.4–0.5 mm long, the style 1.2–1.4 mm long, epunctate, the ovules 7 to 11. *Fruits* (immature) globose, 2.5–3 mm diam., prominently punctate, slightly costate.

Distribution. *Ardisia kennedyae* is known only from the type collection in Bocas del Toro, Panama, at or near sea level.

Ecology and conservation status. *Ardisia kennedyae* occurs in swamp forests and secondary vegetation on terra firme. Because it is only known from the type, it should be considered threatened.

Etymology. It is a pleasure to dedicate this species to Helen Kennedy, prodigious plant collector and preeminent authority on the systematics of Neotropical Marantaceae.

Ardisia kennedyae is unique within *Ardisia* subg. *Auriculardisia* sect. *Wedelia* because its leaves have obtuse apices to only 0.6 cm long and the smallest flowers have calyx lobes to only 1.3 × 1 mm and corolla lobes to only 2.4 mm long.

73. Ardisia mameyensis Ricketson & Pipoly, sp. nov. TYPE: Panama. Darién: Mamey, beside river, 8 Mar. 1982 (fl, fr), *C. Whitefoord & A. Eddy 430* (holotype, MO!; isotypes, BM! [2]). Figure 73.

Propter inflorescentiam longipedunculatam bracteam foliaceam subtentam ad sectionem *Wedeliam* pertinet. Species haec ab aliis speciebus sectionis staminum filamentis minutis 1.1–1.2 mm longis atque antheris ovoideis apiculatis ad bases subcordatis perfacile separabilis.

Shrubs to 2.4 m tall. *Branchlets* 3.5–5 mm diam., densely furfuraceous-lepidote, the scale margins overlapping among them. *Leaves* with blades membranous and chartaceous, elliptic, 11.5–23.6 × 5.2–7.1 cm, apically long acuminate, with an acumen 0.6–2.4 cm long, basally obtuse, decurrent on the petiole, inconspicuously punctate and punctate-lineate, glabrous above, densely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 25 to 31 pairs, prominulous above and below, the margins inrolled; petioles subobsolete to 0.6 cm long, glabrous above, furfuraceous-lepidote below. *Inflorescences* pinnately to bipinnately paniculate, columnar, 7.5–12.9 × 1.8–3.8 cm, rachis and branches densely furfuraceous-lepidote, the branches terminating in 5- to 9-flowered corymbs; peduncles 3.8–8.1 cm long; inflorescence bracts persistent, membranous, ovate to lanceolate, 1.6–5.1 × 0.3–1.1 cm, apically acute, basally auriculate, prominently punctate and punctate-lineate, glabrous above, densely furfuraceous-lepidote below, the midrib impressed above, prominently raised below, the secondary veins 25 to 31 pairs, prominulous above, obscure below, the margins entire, inrolled; inflorescence branch bracts caducous, membranous, ovate, 2–4.6 × 0.2–0.6 mm, apically acuminate, the veins obscure, prominently punctate and punctate-lineate, glabrous above, densely furfuraceous-lepidote below, the margins minutely erose, hyaline; floral bracts similar to the inflorescence branch bracts, but 0.8–1.8 × 0.7–1 mm; pedicels 2.5–5 mm long, inconspicuously punctate and punctate-lineate, densely furfuraceous-lepidote. *Flowers* pink; calyx lobes membranous, ovate, 1.7–2 × 1–1.2 mm, apically acute, inconspicuously punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially, the margins entire, minutely erose, hyaline, sparsely glandular ciliolate; corolla membranous, 4–4.2 mm long, the tube 0.6–0.8 mm long, the lobes narrowly lanceolate, 3.2–3.4 × 2–2.2 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, the margins entire, hyaline; stamens 2.4–2.5 mm long, the filaments 1.1–1.2 mm long, the staminal tube 0.3–0.5 mm long, the apically free portions 0.7–0.8 mm, epunctate, the anthers ovoid, 1.6–1.8 × 0.7–0.8 mm, apically apiculate, basally subcordate, the connective conspicuously punctate; pistil 3.7–4.1 mm long, the ovary 1–1.4 mm long, the style 2.5–2.8 mm long, epunctate to inconspicuously punctate, the ovules 10 to 17. *Fruits* (immature) globose, 4–4.7 mm diam., prominently punctate, style base persistent.

Distribution. *Ardisia mameyensis* is known only from the type, collected near Mamey in Darién, Panama, below 100 m in elevation.

Ecology and conservation status. *Ardisia mameyensis* occurs along riverbanks in wet forests. Because it is known only from the type it should be considered threatened.

Etymology. The specific epithet refers to the locality where it was discovered.

Ardisia mameyensis is distinguished within *Ardisia* subg. *Auriculardisia* sect. *Wedelia* by its anthers to 1.8 × 0.8 mm, larger corolla lobes to 2.2 mm wide, shorter stamens to 2.5 mm long, the filaments to 1.2 mm long, the apically free portion of the filaments to 0.8 mm long, the tube to 0.5 mm long, the shorter pistil to 4.1 mm long, and shorter style to 2.8 mm long.

74. Ardisia talamancensis Ricketson & Pipoly, sp. nov. TYPE: Costa Rica. Limón: Cantón de Talamanca, Sukut, de las juntas de Río Urén y Río Sukut, 1.5 km aguas arriba sobre éste, margen derecha, 09°24′30″N, 082°58′10″W, 350 m, 7 July 1989 (fl), *G. Herrera 3172* (holotype, MO!; isotypes, CR not seen, FTG!, INB not seen). Figure 74.

Propter inflorescentiam longipedunculatam bracteam foliaceam subtentam ad sectionem *Wedeliam* pertinet. Species haec inter alias *A. conoideae* similis, sed ab ea antheris oblongoideis (non anguste ovoideis) 2.3–2.4 (nec 2.1–2.3) mm longis ad apices rotundato-(nec subulato-) apiculatis statim separabilis.

Subshrubs 0.5–0.7 m tall. *Branchlets* 7–8 mm diam., densely furfuraceous-lepidote, the scales nearly overlapping. *Leaves* with blades membranous to chartaceous, oblanceolate, 28.8–30.7 × 7.4–8.6 cm, apically acute to acuminate, with an acumen 1.1–2.9 cm long, gradually tapering to an acute base, inconspicuously punctate, glabrate above, densely furfuraceous-lepidote below, denser along the midrib, the midrib impressed above, prominently raised below, the secondary veins 43 to 56 pairs, prominulous above, prominently raised below, the margins entire, flat; petioles subobsolete to 0.5 cm long, densely furfuraceous-lepidote below. *Inflorescences* bipinnately paniculate, columnar, 16.9–20.5 × 4.8–5.6 cm, rachis and branches densely furfuraceous-lepidote, the branches terminating in 7- to 11-flowered corymbs; peduncle 7.5–11.2 cm long; inflorescence bract persistent, linear oblong, 5.3–7.8 × 0.6–1 cm, apically acute, inconspicuously punctate, glabrous above, densely furfuraceous-lepidote below, denser along the midrib, midvein and secondary veins obscure, the margins entire, flat; inflorescence branch bracts early caducous, unknown; floral bracts persistent, lanceolate, 1.4–2.8 × 0.9–1.2 mm, apically acute, sessile, prominently punctate and punctate-lineate, glabrous above, densely furfuraceous-lepidote below, midvein obscure, the margins entire, minutely erose, hyaline; pedicels 2.5–6.2 mm long, inconspicuously punctate, densely furfuracous-lepidote. *Flowers* rose; calyx lobes chartaceous, ovate, 1.6–1.9 × 1.1–1.3 mm, apically acute, scattered prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote, the margins minutely erose, hyaline, sparsely glandular-ciliolate; corolla membranous, 5.2–5.4 mm long, the tube 1–1.2 mm long, the lobes lanceolate, 3.8–4.2 × 1.3–1.5 mm, apically acute, prominently punctate and punctate-lineate, glabrous throughout, margins entire; stamens 2.9–3.1 mm long, the filaments 1.7–1.8 mm long, the staminal tube 0.9–1 mm long, the apical free portions 0.8–1 mm long, the anthers ovoid to lanceoloid, 2.3–2.4 × 0.8–1 mm, apically rounded-apiculate, basally cordate, the connective punctate; pistil 5.2–5.3 mm long, the ovary 0.7–0.8 mm long, the style 4.4–4.5 mm long, inconspicuously punctate, the ovules 9 to 11. Fruits unknown.

Distribution. *Ardisia talamancensis* is known only from the type collection in Limón, Costa Rica, growing at 350 m in elevation.

Ecology and conservation status. *Ardisia talamancensis* occurs in premontane rain forests. Because it is known only from the type collection, it should be considered threatened.

Etymology. The specific epithet refers to the region in which it was found, the Cantón de Talamanca of Limón, Costa Rica.

Ardisia talamancensis may be distinguished from the other species of *Ardisia* subg. *Auriculardisia* sect. *Wedelia* by its larger anthers to 2.4 × 1 mm, smaller calyx lobes to 1.9 × 1.3 mm, larger corolla lobes to 4.2 × 1.5 mm, and smaller stamens to 3.1 mm long.

75. Ardisia wedelii Lundell, Amer. Midl. Naturalist 29: 486. 1943. *Auriculardisia wedelii* (Lundell) Lundell, Phytologia 54: 285. 1983. TYPE: Panama. Bocas del Toro: 1 Aug. 1940 (fl), *H. von Wedel 299* (holotype, MO!, LL neg. 71-121!). Figure 75.

Ardisia boltenii Lundell, Wrightia 6: 63. 1979. Syn. nov. *Auriculardisia boltenii* (Lundell) Lundell, Phytologia 49: 342. 1981. TYPE: Panama. Veraguas: valley of Río Dos Bocas along road between Escuela Agrícola Alto Piedra and Calovebora, 15.6 km NW of Santa Fé, along Santa Fé trail, steep forested hill E of river, 450–550 m, 31 Aug. 1974 (fr), *T. Croat 27652* (holotype, MO!, F neg. 55671!).

Shrubs or small trees 0.2–4 m tall. *Branchlets* 5.1–9.5 mm diam., densely furfuraceous-lepidote, the scales appressed and touching. *Leaves* with blades chartaceous, oblong or elliptic to narrowly elliptic or oblanceolate, 18.7–41.2 × 6.8–15.2 cm, apically acuminate, with an acumen 1.6–2.9 cm long, basally auriculate, prominently punctate above and below, sparsely furfuraceous-lepidote above, more densely so below, the midrib impressed above, prominently raised below, the secondary veins 29 to 48 pairs, prominulous above, prominent below, the margins entire, revolute; petioles 0.3–0.6 cm long, densely furfuraceous-lepidote. *Inflorescences* pinnately or bipinnately paniculate, columnar, 8.5–25.2 × 1.2–7.1 cm, rachis and branchlets densely furfuraceous-lepidote, the branches terminating in 12- to 27-flowered corymbs; peduncles 3.5–9.2 cm long; inflorescence bract 0.8–11.2 × 0.3–3.3 cm; inflorescence branch bracts early caducous, oblong, 3.5–13.6 × 2.5–5.3 mm, apically acute or rounded, prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote above, densely so below, midvein and secondary veins obscure, the margin entire; floral bracts similar to the inflorescence branch bracts, but 1.3–2.2 × 0.6–1.2 mm; pedicels 5.1–8.7 mm long, inconspicuously punctate, densely furfuraceous-lepidote. *Flowers* orange-white, pink to red to purple; calyx lobes coriaceous, thick medially, ovate, 1.8–2.5 × 1.3–1.5 mm, apically acute, prominently punctate and punctate-lineate, sparsely furfuraceous-lepidote, the margins minutely erose, hyaline, sparsely glandular-ciliolate; corolla membranous, 4.3–5.1 mm long, the tube 0.7–0.9 mm long, the lobes lanceolate, 3.2–4.4 × 0.9–1.2 mm, apically acute, prominently punctate and punctate-lineate, glabrous adaxially, sparsely furfuraceous-lepidote abaxially, the margins entire; stamens 4.2–4.9 mm long, the filaments 2.7–2.9 mm long, the staminal tube 0.5–1.6 mm long, the apically free portions 2.2–2.4 mm long, epunctate, the anthers ovoid to lanceoloid, 1.5–2.1 × 0.5–0.8 mm, apically subulate-apiculate, basally deeply cordate, the connective punctate; pistil 4.8–5.2 mm long, the ovary 0.6–1 mm long, the style 4–4.6 mm long, epunctate, the ovules 10 to 12. *Fruits* globose, 4.8–5.7 mm diam., prominently and conspicuously punctate, slightly costate.

Distribution. Along the Caribbean coast of Mesoamerica from Nicaragua to Panama, growing from sea level to 1400 m in elevation.

Ecology and conservation status. *Ardisia wede-*

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Figure 72 (left). *Ardisia kennedyae.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Detail of calyx, showing asymmetric, auriculate ovate calyx lobes. —E. Flower. —F. Stamen, abaxial surface. —G. Stamen, adaxial surface. —H. Stamen, lateral margin. —I. Fruit. (A–I drawn from holotype, *H. Kennedy 3258* (MO).)

Figure 73 (right). *Ardisia mameyensis.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, lateral margin. —G. Stamen, adaxial surface. —H. Fruit. (A, B drawn from isotype, *C. Whitefoord & A. Eddy 430* (BM); C–H from holotype, *C. Whitefoord & A. Eddy 430* (MO).)

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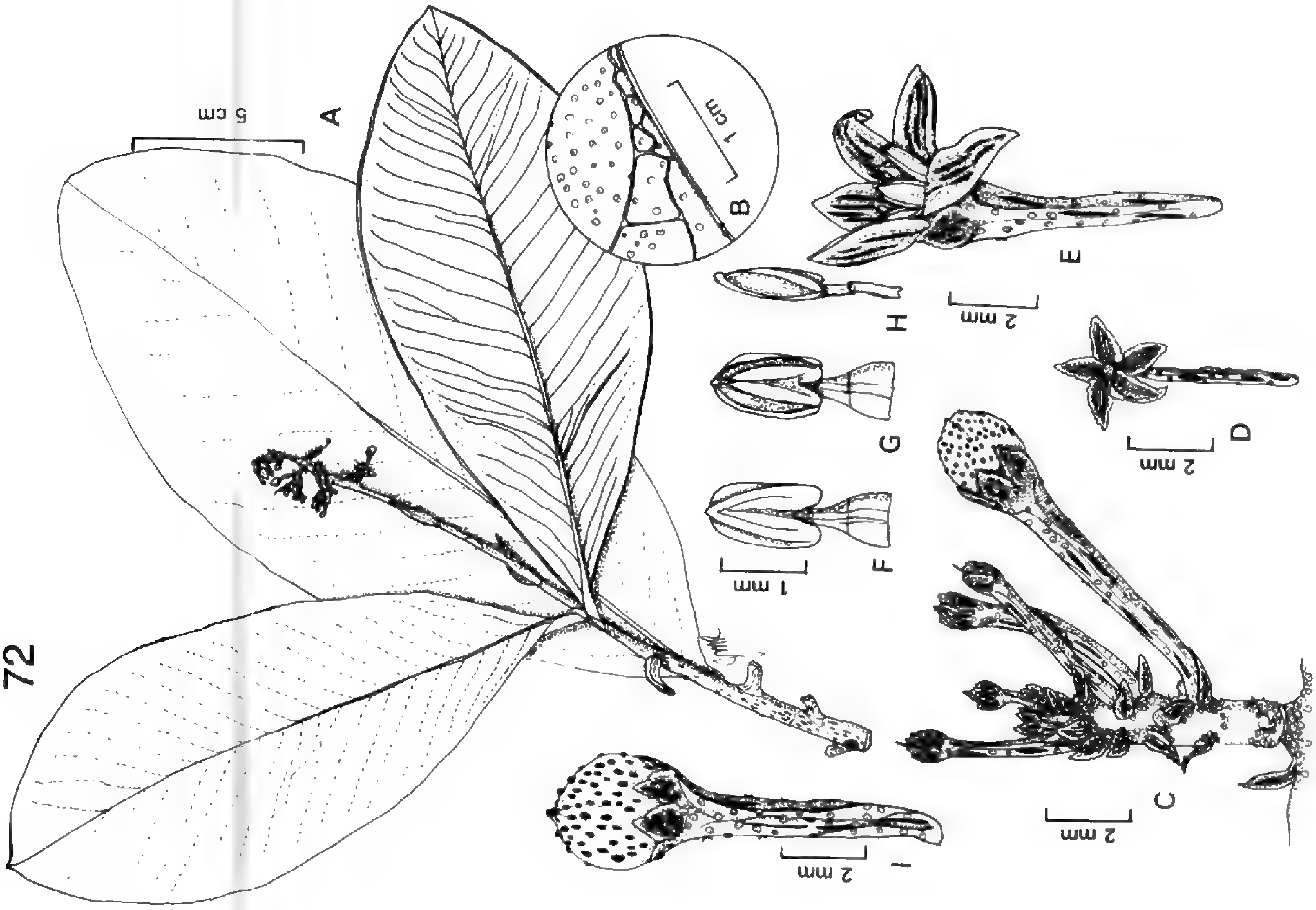
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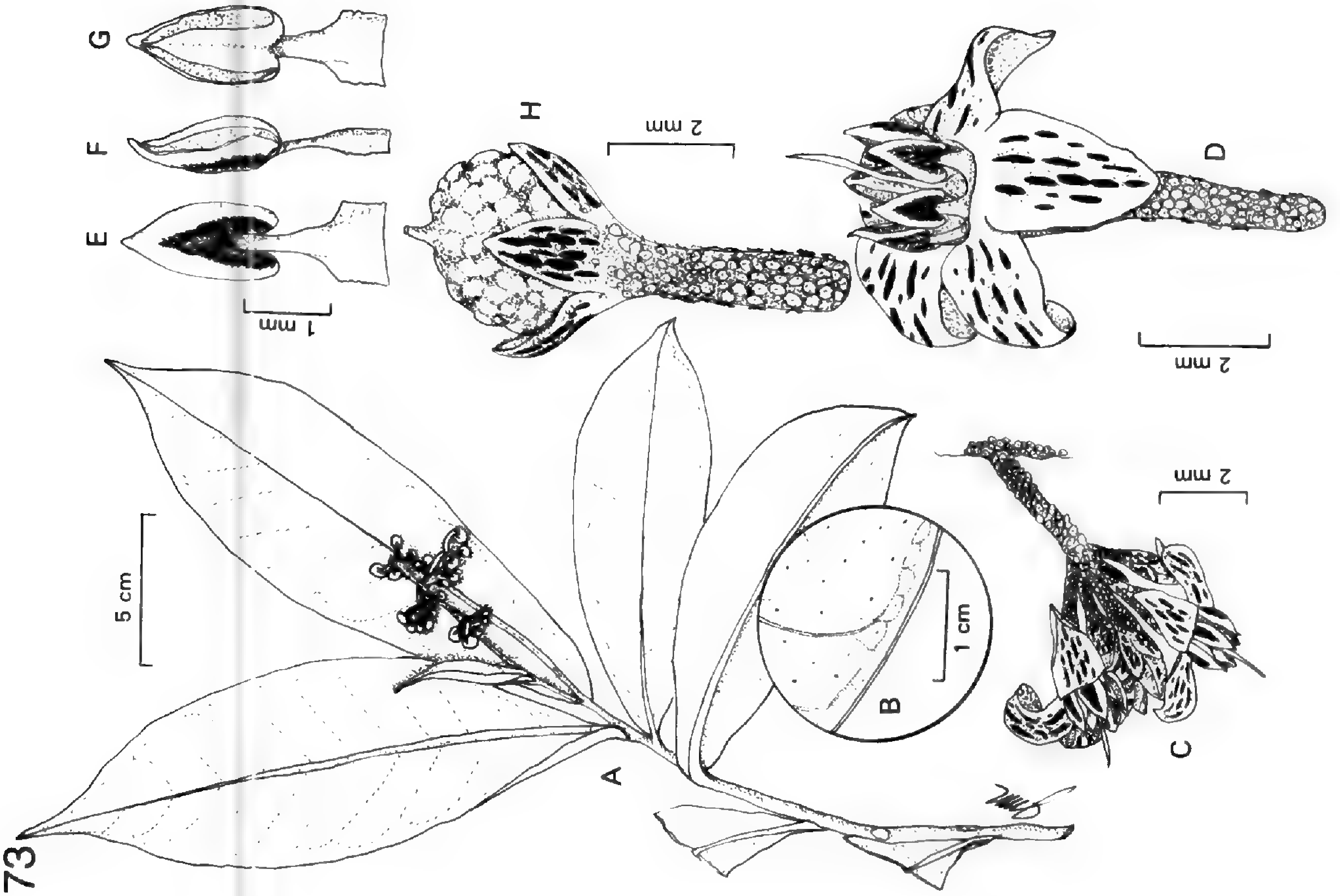
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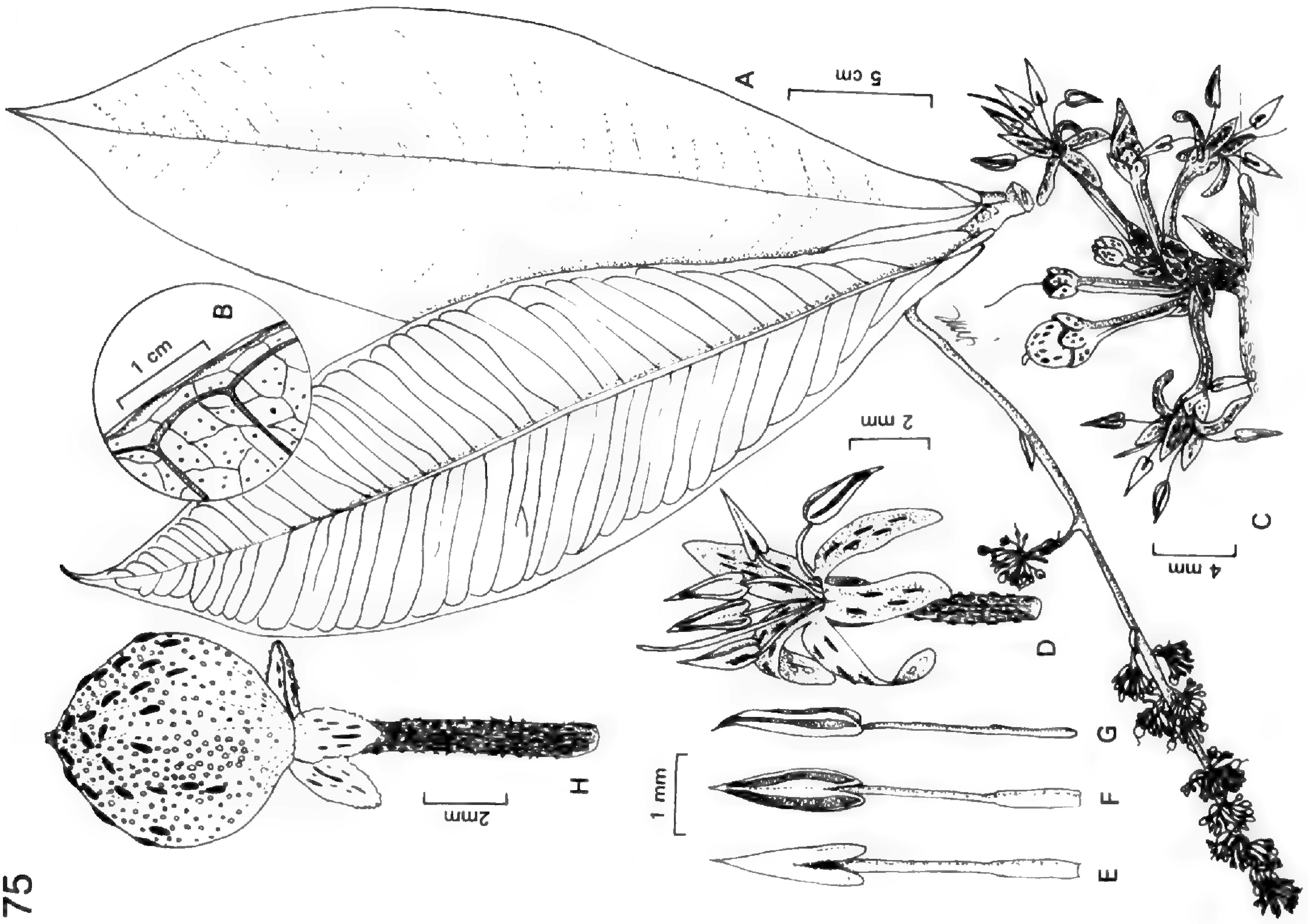

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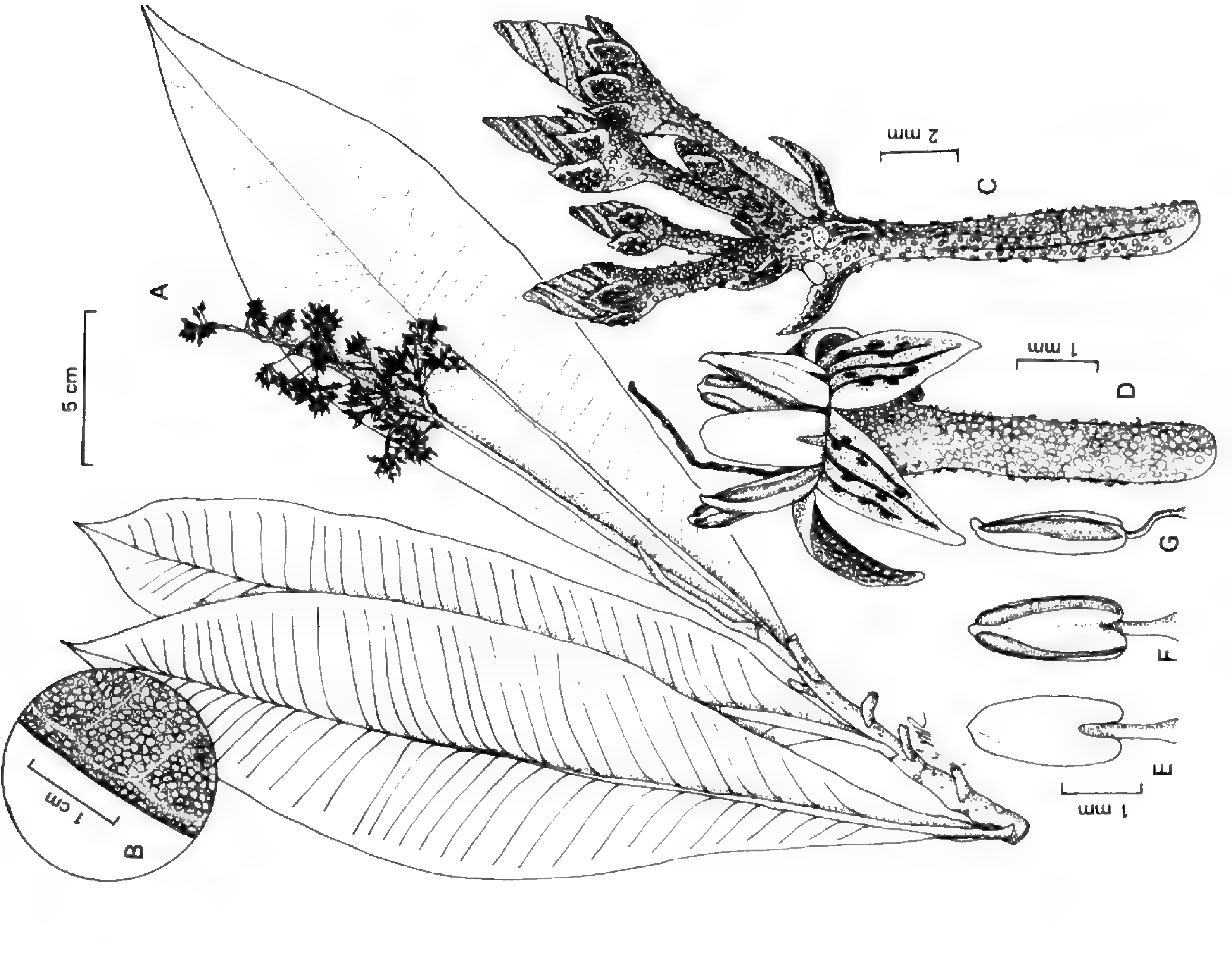

lii inhabits primary and remnant evergreen forests and secondary growth in the tropical-premontane wet forest transition zone, or rarely, in cloud forests. At this time, it does not appear to be threatened.

Etymology. This species was named in honor of H. von Wedel, who collected a large number of specimens from Panama.

Ardisia wedelii is distinguished within *Ardisia* subg. *Auriculardisia* sect. *Wedelia* by its anthers to 2.1 × 0.8 mm, with smaller corolla lobes to 1.2 mm wide, larger stamens to 4.9 mm long, the longer filaments to 2.9 mm long, the apically free portion of the filaments to 2.4 mm long, the tube to 1.6 mm long, the larger pistil to 5.2 mm long, and longer style to 4.6 mm long.

The type of *Ardisia wedelii* is in poor condition, with its inflorescence very young and the peduncle not fully expanded, although similar specimens clearly show the long peduncle. When Lundell (1979) described *Ardisia boltenii* he failed to compare it with *A. wedelii.* However, upon close examination of all additional material, the type of *Ardisia boltenii* clearly matches *A. wedelii* in all aspects, and the species is synonymized herein.

Specimens examined. NICARAGUA. **Jinotega**: Kilambé, "Cerro San Pedro," 25 Mar. 1981 (fr), *P. Moreno 7511* (MO). **Río San Juan**: Mpio. El Castillo, Sábalos, comarca Las Maravillas, 15 Jan. 1995 (fl), *R. Rueda et al. 2870* (HULE, MO); NW of Nueva Atlanta village, 17 Feb. 1994 (fr), *R. Rueda et al. 3178* (HULE, MO); Mpio. Castillo, Reserva Indio-Maíz, Cerro el Diablo, 9 Jan. 1997 (fl, fr), *R. Rueda et al. 5610* (HULE, MO). **Zeyala**: 2 km NW of Rosita, 4 Jan. 1974 (fl), *J. Atwood et al. 6975* (MO); El Escobillo, 2 km from Colonia Serrano, trail to Yolania, 29 July 1982 (fl), *J. Sandino 3341* (MO); Esquipulas and Alemán, Río Alemán Basin, 27–29 Nov. 1951 (fr), *P. Shank & A. Molina R. 4891* (GH); ca. 6.3 km S of bridge at Colonia Yolania and ca. 0.8 km S of ridge of Serranias de Yolania on road to Colonia Manantiales (Colonia Somoza), 29–31 Oct. 1977 (fr), *W. Stevens 4799* (MO); Caño Costa Riquita, ca. 1.8 km SW of Colonia Naciones Unidas, above (S of) road between Colonia Nueva León and Colonia Naciones Unidas, 6–7 Nov. 1977 (fr), *W. Stevens 5061* (MO). COSTA RICA. **Alajuela**: ca. 13 km NNE of Bijagua along new road to Upala, 7–8 Nov. 1975 (fr), *W. Burger & R. Baker 9810* (DUKE, F [2]); Cantón de Upala, Dos Ríos, 1 km before Río Pizote along the road from Dos Ríos to Brasilia, 2 Nov. 1987 (fr), *G. Herrera 1093* (CR, MO, US); N slope of Volcán Arenal, in lava flows above Río Guillermina, 24 Feb. 1989 (fr), *G. Russell et al. 942* (US); ca. 9 km N of Río Naranjo along road to Upala, 8 July 1976 (fl), *J. Utley & K. Utley 5349* (DUKE). **Guanacaste**: between Guachipelín and Volcán La Vieja, 26 May 1932 (ster.), *A. Brenes 15551* (F); edge of road 30 km E of PanAm Hwy., on road to Upala, 25 Aug. 1980 (fr), *J. Kress et al. 9593* (DUKE). **Heredia**: Finca La Selva, the OTS Field Station on the Puerto Viejo just E of its junction with the Río Sarapiquí, far side of research trail 400 m S in small gap at edge of trail, 5 July 1981 (fl), *B. Hammel 10959* (DUKE). **Limón**: Cantón de Limón, Cordillera de Talamanca, along divide between Río Xikiari and Río Boyei above Cabécar village of Almirante (not on current maps), 13 Aug. 1995 (fr), *M. Grayum 10928* (FTG, INB, MO); Parque Tortuguero, Estación Agua Fría, 8 km SE of park HQ along Los Raudales Trail, 27 Oct. 1987 (fr), *R. Robles 1160* (CR, MO). **San José**: W part of Montañas Jamaica, ca. 3 km NE of Bijagual de Turrubares, Carara Reserve, 7 Aug. 1985 (fl), *M. Grayum et al. 5866* (CR, MO); El General, San Isidro, Jan. 1891 (fr), *H. Pittier 3504* (BR). PANAMA. **Bocas del Toro**: road from Fortuna Dam to Chiriquí Grande, 10 mi. from Continental Divide, 2 Aug. 1984 (fl), *H. Churchill 5929* (MO); Fish Creek lowlands, vicinity of Chiriquí Lagoon, 7 May 1941 (fl), *H. von Wedel 2393* (MO). **Chiriquí**: Fortuna Dam area, unnamed creek to E of road flowing into Río Hornito near Quebrada Moro, 16 June 1984 (fl), *H. Churchill 5497* (LL, MO). **Veraguas**: along Río Dos Bocas, ca. 12 km beyond Santa Fé, 25 July 1974 (fl), *T. Croat 25791* (MO); Cerro Tute, W of Santa Fé, beyond Alto de Piedra, 17 Oct. 1985 (fr), *G. McPherson 7158* (MO); 8.8 km from Escuela Agrícola Alto de Piedra, 16 Nov. 1974 (fr), *S. Mori & J. Kallunki 3211* (MO, F neg. 55683); 14 km NW of Santa Fé, on road to Calovebora, Panama Hwy. 35, 4 Aug. 1975 (fl), *S. Mori & A. Bolton 7650* (MO, F neg. 55682).

EXCLUDED NAMES

Ardisia angustialata Lundell, Wrightia 3: 25. 1962. *Amatlania angustialata* (Lundell) Lundell, Wrightia 7: 40. 1982. TYPE: Mexico. Chiapas: Pinabeto, near Motozintla, 2585 m, 9 July 1945 (fr), *E. Matuda 5462* (holotype, LL!, F neg. 55688!; isotypes, LL! [2]).

This species is a synonym of *Gentlea micranthera* (Donn. Sm.) Lundell. In fruit, members of *Ardisia* subg. *Auriculardisia* sect. *Amatlania* can be difficult to distinguish from species of *Gentlea* because of the dense to scattered papillae on the inflorescence branches. However, the calyx lobes in *Gentlea* are symmetric and lack auriculate bases. Also the inflorescences in *Gentlea* are usually smaller

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Figure 74 (left). *Ardisia talamancensis.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, adaxial surface. —G. Stamen, lateral margin. (A–G drawn from holotype. *G. Herrera 3172* (MO).)

Figure 75 (right). *Ardisia wedelii.* —A. Flowering branch. —B. Detail of abaxial leaf surface. —C. Detail of inflorescence. —D. Flower. —E. Stamen, abaxial surface. —F. Stamen, adaxial surface. —G. Stamen, lateral margin. —H. Fruit. (A, B drawn from *T. Croat 27652* (MO holotype of *Ardisia boltenii* Lundell); C–G from *W. Burger & R. Baker 9810* (F); H from *G. Herrera 1093* (MO).)

and shorter than the leaves. Careful examination of the type material showed that its inflorescence is small and shorter than the leaves, the calyx lobes are symmetric and without auriculate bases, and the leaf margins are slightly crenate. These are characters typical of *Gentlea micranthera* and leave no doubt about the true identity of this taxon.

Geissanthus carchianus (Lundell) Ricketson & Pipoly, comb. nov. Basionym: *Ardisia carchiana* Lundell, Wrightia 7: 23. 1981. *Auriculardisia carchiana* (Lundell) Lundell, Phytologia 49: 342. 1981. TYPE: Ecuador. Carchi: Peñas Blancas, 20 km below Maldonado on the Río San Juan, 900–1000 m, 27 May 1978 (fr), *M. Madison, T. Plowman, H. Kennedy & L. Besse 4625* (holotype, F!; isotype, SEL!).

This taxon is actually a species of *Geissanthus*, and the new combination is made here. Lundell (1981b) transferred this taxon to his segregate genus *Auriculardisia* based on its supposed affinity to *Ardisia megistophylla* Lundell (large leaves?), a member of *Ardisia* subg. *Auriculardisia* sect. *Palmanae*, and noted that "the calyx is atypical." The type has a few fruits, the calyx clearly shows characteristics consistent with *Geissanthus*, and the calyx tube splits below the basal calyx lobe and forms a callus with uneven sinuses between the calyx lobes. The calyx lobes clearly are not auriculate basally, thus eliminating the possibility that this taxon belongs to *Ardisia* subg. *Auriculardisia*. Instead, *Geissanthus carchianus* has affinities to *G. longistamineus* (A. C. Sm.) Pipoly.

Geissanthus zakii (Pipoly) Ricketson & Pipoly, comb. nov. Basionym: *Ardisia zakii* Pipoly, Sida 17: 449. 1996. TYPE: Ecuador. Pichincha: Carretera Quito–San Juan Chiriboga–Empalme, Km 59, 16 km NW of road, 1700–2000 m, 23 Sep. 1986 (fl, fr), *V. Zak 1298* (holotype, MO!; isotypes, FTG!, QCNE not seen).

This taxon also turns out to be a species of *Geissanthus*, and the new combination is made here. The type is in fruit but none is attached to the rachis. The calyx clearly has characteristics consistent with *Geissanthus* in that the calyx tube splits below the basal calyx lobe and forms a callus with uneven sinuses between the calyx lobes, and the calyx lobes clearly are not auriculate basally. This definitively eliminates the possibility that this taxon belongs to *Ardisia* subg. *Auriculardisia*.

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APPENDIX 1

LIST OF SPECIES AND SUBSPECIES

Ardisia subg. **Auriculardisia** sect. **Amatlania**

1. *A. liebmannii* Oerst. subsp. *jalapensis* (Lundell) Ricketson & Pipoly
2. *A. liebmannii* subsp. *liebmannii*
3. *A. pellucida* Oerst. subsp. *lancetillensis* Ricketson & Pipoly
4. *A. pellucida* subsp. *pectinata* (Donn. Sm.) Ricketson & Pipoly
5. *A. pellucida* subsp. *pellucida*
6. *A. pellucida* subsp. *thomascroatii* Ricketson & Pipoly
7. *A. schippii* Standl.

Ardisia subg. **Auriculardisia** sect. **Auriculardisia**

8. *Ardisia dodgei* Standl.
9. *Ardisia glomerata* Lundell
10. *Ardisia nervosissima* Lundell
11. *Ardisia ursina* Lundell

Ardisia subg. **Auriculardisia** sect. **Fagerlindia**

12. *Ardisia apoda* Standl. & Steyerm.
13. *Ardisia bastonalensis* Ricketson & Pipoly
14. *Ardisia brenesii* Standl.
15. *Ardisia gordonii* Ricketson & Pipoly
16. *Ardisia nevermannii* Standl.
17. *Ardisia tilaranensis* Standl.
18. *Ardisia tortuguerensis* Ricketson & Pipoly

Ardisia subg. **Auriculardisia** sect. **Palmanae**

19. *Ardisia aguirreana* Pipoly
20. *Ardisia albisepala* (Lundell) Pipoly & Ricketson
21. *Ardisia anchicayana* Ricketson & Pipoly
22. *Ardisia angucianensis* Ricketson & Pipoly
23. *Ardisia atropurpurea* Lundell
24. *Ardisia auriculata* Donn. Sm.
25. *Ardisia awarum* Ricketson & Pipoly
26. *Ardisia blepharodes* Lundell
27. *Ardisia capitellata* Lundell
28. *Ardisia cartagoana* Lundell
29. *Ardisia cogolloi* Pipoly
30. *Ardisia coloradoana* Lundell
31. *Ardisia conglomerata* Lundell
32. *Ardisia crassipedicellata* Lundell
33. *Ardisia crassipes* Lundell
34. *Ardisia crassiramea* Standl.
35. *Ardisia croatii* Lundell subsp. *correae* (Lundell) Ricketson & Pipoly
36. *Ardisia croatii* subsp. *croatii*
37. *Ardisia darienensis* Lundell
38. *Ardisia dukei* Lundell
39. *Ardisia dunlapiana* P. H. Allen
40. *Ardisia dwyeri* Lundell
41. *Ardisia eucuneata* (Lundell) Pipoly & Ricketson
42. *Ardisia fimbrillifera* Lundell
43. *Ardisia furfuracea* Standl.

44. *Ardisia generalensis* Ricketson & Pipoly
45. *Ardisia gigantea* Ricketson & Pipoly
46. *Ardisia glandulosomarginata* Oerst.
47. *Ardisia hagenii* Lundell
48. *Ardisia hugonensis* (Lundell) Pipoly & Ricketson
49. *Ardisia knappii* (Lundell) Pipoly & Ricketson
50. *Ardisia liesneri* Lundell
51. *Ardisia lundelliana* Pipoly
52. *Ardisia mcphersonii* Pipoly
53. *Ardisia megistophylla* Lundell
54. *Ardisia nigropunctata* Oerst.
55. *Ardisia palmana* Donn. Sm.
56. *Ardisia panamensis* Lundell
57. *Ardisia pseudoracemiflora* Pipoly
58. *Ardisia pulverulenta* Mez
59. *Ardisia ruedae* Ricketson & Pipoly
60. *Ardisia smurfitana* Ricketson & Pipoly
61. *Ardisia tarariae* Lundell
62. *Ardisia tenuicaulis* Lundell
63. *Ardisia tenuis* Lundell
64. *Ardisia tysonii* Lundell
65. *Ardisia unguiensis* Lundell
66. *Ardisia vesca* Lundell

Ardisia subg. **Auriculardisia** sect. **Pleurobotryae**
67. *Ardisia pleurobotrya* Donn. Sm.

Ardisia subg. **Auriculardisia** sect. **Wedelia**
68. *Ardisia conoidea* Lundell
69. *Ardisia folsomii* Lundell
70. *Ardisia hammelii* Lundell
71. *Ardisia heterotricha* (Lundell) Pipoly & Ricketson
72. *Ardisia kennedyae* Ricketson & Pipoly
73. *Ardisia mameyensis* Ricketson & Pipoly
74. *Ardisia talamancensis* Ricketson & Pipoly
75. *Ardisia wedelii* Lundell

APPENDIX 2

INDEX TO EXSICCATAE

The figures in parentheses refer to the numbers from the list of species and subspecies. Collection numbers in **boldface type** indicate type specimens.

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SYSTEMATICS OF EURASIAN AND NORTH AFRICAN *DORONICUM* (ASTERACEAE: SENECIONEAE)[1]

Inés Álvarez Fernández[2]

ABSTRACT

The genus *Doronicum* (Asteraceae: Senecioneae) comprises perennial herbs distributed in Europe, North Africa, and Asia. A worldwide revision of the genus recognizing 26 species and 4 subspecies is presented. In the present taxonomic treatment no infrageneric groups are recognized. Seven names are newly lectotypified herein: *Arnica doronicum* Jacq., *Doronicum caucasicum* M. Bieb., *Doronicum portae* Chabert, *Doronicum scorpioides* Lam., *Doronicum souliei* Cavill., *Doronicum thibetanum* Cavill., and *Doronicum turkestanicum* Cavill. A new chromosome count is provided for *D. carpetanum* subsp. *diazii*.

Key words: Asia, Asteraceae, *Doronicum*, Europe, North Africa, Senecioneae.

The genus *Doronicum* L. (Asteraceae: Senecioneae) includes rhizomatous herbs with yellow or green-tinted radiate capitula. All phyllaries are similar, generally herbaceous and arranged in two or three rows. Cypselae are cylindric to obovate-cylindric with 10 longitudinal ribs and bear a pappus of white-tinted minutely scabrous capillary bristles. The pappus can be absent in ray flowers of some heterocarpic species.

This genus belongs in the Senecioneae, one of the largest and most complex tribes in the Asteraceae with 123 genera and around 3200 species (Cassini, 1819; Bentham & Hooker, 1873b; Hoffmann, 1892; Nordenstam, 1977; Bremer, 1994). Its 26 species constitute a presumably natural group (Bremer, 1994; involucre without shorter supplementary bracts, phyllaries herbaceous arranged in two or three rows, and cypselae cylindric to ob-

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ovate-cylindric with 10 longitudinal ribs). Its geographical area extends from Europe and North Africa to Asia, growing in mesic woods and open rocky places with moist soil, and near watercourses, from sea level to 5000 m of elevation.

Although there are several regional studies of the genus (Turkey, Edmondson, 1973, 1975, 1978; Armenia, Avetisyan, 1980; Iberian peninsula, Chacón, 1987; Belgium, Duvigneaud, 1992), there is only one previous worldwide revision of *Doronicum* (Cavillier, 1907, 1911). Fifteen new species (Diels, 1922; Widder, 1925; Sergievskaja, 1949; Widder & Rechinger, 1950; Edmondson, 1973, 1978; Chacón, 1987; Pérez & Penas, 1990; Pérez et al., 1994; Chen, 1998) and six hybrids (Bornmüller & Koch, 1930; Widder, 1934, 1948; Stace, 1991) were subsequently described. Two species included in Cavillier's monograph have since been transferred to other genera (i.e., *D. hookeri* C. B. Clarke ex Hook. to *Nannoglottis* (Kitamura, 1980), and *D. thibetanum* Cavill. to *Aster* (Álvarez Fernández & Nieto Feliner, 2000)). Cavillier (1907, 1911) studied the morphology of the genus in great detail, especially the indumentum, but his proposed infrageneric classification is of rather limited value since these groups are obscurely defined based mainly on nonexclusive characters. As a result, classifying newly described taxa in any infrageneric framework is problematic.

The need to evaluate the newly described species and to assess the infrageneric taxonomy provides justification for this work. The objectives were to study as many morphological characters (qualitative and quantitative) as possible so that (1) only entities that could be consistently diagnosed were recognized in the taxonomic treatment, and (2) species were classified as groups on the basis of shared synapomorphies (secondary homologies, De Pinna, 1991).

MATERIAL AND METHODS

More than 50 qualitative and quantitative morphological characters were studied in ca. 4300 dried specimens from the following herbaria: B, BC, BCF, BM, BR, BRNM, COI-WILLK, E, FI, G, GAZI, GH, GZU, HVR, IRAN, JACA, JE, K, LAU, LE, LINN, LY, MA, MACB, MAF, MO, NY, RO, S, SANT, UPS, W, WU, ZA, and the Sánchez-Pedraja personal herbarium. From other institutions, only photographs and photocopies of specimens, or additional information, were available: AV, B-W, BOLO, BP, C, CL, G-BOIS, G-DC, GE, GRM, LD, NAP, P-HA, P-LA, LEB, PAL, and SZB. A list of species and subspecies and an index to exsiccatae are presented in Appendices 1 and 2, respectively.

Observations were made directly or with the aid of binocular lenses. Microcharacters of indumentum and cypselae were studied by SEM. Quantitative characters were recorded using a Brown & Shape Plus digital caliper (model 599-571-3). Measurements were made on herbarium specimens, after flattening and drying.

Distribution maps for each taxon are based on the specimens studied. Note that geographical areas and countries follow Hollis and Brummitt (1992), and major political divisions for countries were included when that information was available.

TAXONOMIC HISTORY

The name *Doronicum* is apparently derived from the Arabic word "darawnay," used for at least two different plants (Dozy, 1877). The pre-Linnaean botanists (Dioscorides, 1554, 1557; Dodoens, 1574) and other Greek authors referred to species of *Doronicum* as *Aconitum pardalianches*, and the plant was probably introduced in Western culture by Avicenna (Dodoens, 1574; Dalenchamps, 1587).

The genus *Doronicum* was described by Linnaeus (1753) to include four species, only two of which are currently accepted in the genus: *D. pardalianches* and *D. plantagineum*. The remaining species correspond to *Senecio* and *Aster*, respectively. Further, one species of *Arnica* described by Linnaeus (1753), *A. scorpioides* L., also belongs in *Doronicum* as recognized by Lamarck (1786). Several pre-Linnaean authors also confused species of *Senecio*, *Aster*, and *Arnica* with *Doronicum* (Dalenchamps, 1587; Clusius, 1601; Bauhin, 1623; Tournefort, 1700). In particular, the overall morphological similarity between *Arnica* and *Doronicum* suggested their close affiliation until the 1970s. However, Nordenstam's (1977) micromorphological study of style, anthers, and pollen definitively has excluded *Arnica* from the Senecioneae.

The cypsela dimorphism that occurs in some species has been a relevant feature in the taxonomic history of the genus. Lamarck (1786) referred to the heterocarpic and homocarpic species as "arniques" and "doronics," respectively. Necker (1790) even proposed the different genus *Aronicum* for the homocarpic species, and his classification had wide acceptance in the 19th century (de Candolle, 1838; Koch, 1843; Hausmann, 1851; Reichenbach, 1854; Schur, 1866; Ardoino, 1867; Simonkai, 1886), although some authors only recognized *Aronicum* as a section of *Doronicum*

(Ambrosi, 1854; Willkomm & Lange, 1870; Nyman, 1879; Hoffmann, 1892; Beck, 1893). This classification persisted until Bentham and Hooker (1873a) placed *Aronicum* as a synonym of *Doronicum.* Tausch (1828) also recognized these two groups but referred the heterocarpic species to *Pardalianches,* not *Aronicum.*

Cassini (1817) established the genus *Grammarthron* with two species, *G. biligulatum* and *G. scorpioides,* now subsumed within *Doronicum* (Jacquin, 1773; Lamarck, 1786); de Candolle (1836) described the monotypic genus *Fullartonia* (*F. kamaonensis*), now *D. kamaonense* (DC.) Álv. Fern. (Álvarez Fernández, 2001). In 1838, de Candolle proposed two sections within *Doronicum*: section *Eudoronicum,* including some species of *Senecio,* and the monotypic section *Chromochaeta,* with *Doronicum linifolium* (Wall.) DC., now also in *Senecio* (Maguire, 1943).

Webb in Webb and Berthelot (1846) treated the genus *Pericallis* D. Don (in Sweet, 1833–1835: tab. 228) including five species as a section of *Doronicum* (*D. cruentum, D. echinatum, D. papyraceum, D. tussilaginis,* and *D. webbii*), but it is now treated at its original rank (Nordenstam, 1978).

Cavillier (1907, 1911) divided his study of the genus *Doronicum,* the first devoted to the study of the homocarpic species (1907), and the second to the heterocarpic ones (1911). However, he later concluded (1911) that this character was not useful to delimit natural groups. Cavillier proposed a new classification (1911) that included 3 sections, 7 subsections, and 34 species within *Doronicum*: section *Doronicastrum* (subsect. *Corsica,* subsect. *Austriaca,* subsect. *Cardiophylla,* subsect. *Macrophylla,* subsect. *Pardalianchia,* subsect. *Plantaginea,* and subsect. *Grandiflora*), section *Soulieastrum* (*D. stenoglossum* Maxim.), and section *Hookerastrum* (*D. hookeri* C. B. Clarke ex Hook.). However, this sectional treatment is not satisfactory, since section *Hookerastrum* was described on the basis of a species from another tribe (*Nannoglottis hookeri,* Astereae) and the phylogenetic position (Álvarez Fernández et al., 2001) of section *Soulieastrum*'s only taxon precludes recognition at the sectional level without artificially splitting the bulk of the genus. The subsections in *Doronicum* were defined (Cavillier, 1911) mainly from the shape of basal leaves, the size of leaves, and the presence of cypselae dimorphism. Phylogenetic study of the genus (Álvarez Fernández et al., 2001) concluded that these are not synapomorphic characters, and therefore Cavillier's classification does not recognize natural groups.

Even after Cavillier's work the relevance of heterocarpy was claimed again (Gorschkova, 1961). In the *Flora of the U.S.S.R.,* the classification proposed by Willkomm and Lange (1870) was merged with that of Cavillier (1911) to distinguish two sections in *Doronicum* (Gorschkova, 1961): section *Aronicum* (ser. *Altaica,* ser. *Carpatica*), and section *Pardalianches* (ser. *Austriaca,* ser. *Cardiophylla,* ser. *Macrophylla,* ser. *Pardalianches,* and ser. *Plantaginea*). More recently, Edmondson (1978) followed Cavillier's classification (1911) instead of Gorschkova's (1961), but described the monotypic subsection *Isaurica* (*D. cacaliifolium* Boiss. & Heldr.) within section *Doronicum,* which corresponded to Cavillier's section *Doronicastrum* (1911).

The phylogenetic analysis herein confirms what a preliminary morphological study suggested: the morphological characters used are too labile to provide a sound classification at the infrageneric level (Álvarez Fernández et al., 2001). The molecular data from nuclear ribosomal and chloroplast DNA suggest some groups but without enough support to recommend formal taxonomic groupings. One exception is a Mediterranean group of species (*D. plantagineum* group), which receives good support from both molecular and morphological data. To avoid adding to the already complex taxonomic history of the genus, a formal infrageneric treatment is not proposed here, but is deferred against new evidence.

As already mentioned in the introduction, after Cavillier's revision and until the present work, a large number of taxonomic actions were taken within *Doronicum.* These include the description of new species (Sergievskaja, 1949; Edmondson, 1973, 1978; Chen, 1998, among others) and one subsection (Edmondson, 1978), and a few lectotypifications (Chacón, 1987; Pérez et al., 1997; Jarvis & Turland, 1998). Despite all of these actions the genus was still lacking nomenclatural stability. Thus, during this study and immediately preceding this work, several nomenclatural and taxonomic clarifications were done (Álvarez Fernández & Nieto Feliner, 1997, 1999, 2000; Álvarez Fernández, 2001). The lectotypification of 16 names of *Doronicum* in current use (Álvarez Fernández & Nieto Feliner, 1999) gave the genus nomenclatural stability leading up to this revision. In this work, additional lectotypification of seven names belonging in *Doronicum,* although not in current use, is also presented to consolidate and clarify as far as possible the nomenclature of the genus. Despite the efforts made to locate type material for all the names in current use, 4 out of 30 names (i.e., *D. carpaticum, D. clusii, D. corsicum,* and *D. orientale*) still required further investigations for lectotype designation. Because at present these names clearly represent different recognized taxonomic entities, they are cited herein as names in current use, although their formal identity is not conclusive until lectotypes are designated.

GEOGRAPHICAL DISTRIBUTION

Half of the 26 recognized species of *Doronicum* are distributed in Europe and North Africa. Seven of the remainder are from southwestern Asia (Iran, Iraq, Caucasus, and Turkey), and 6 species are distributed in central Asia (Turkistan, Altay, Tibet, Yunnan, and the Himalayas).

With the exception of *Doronicum orientale*, each species is restricted to one of the three well-delimited areas: Europe, southwestern Asia, central Asia. *Doronicum orientale* is distributed in Europe and southwestern Asia, abundantly in the eastern Mediterranean (Greece, western Turkey, southern Italy, and Lebanon–Syria), and scattered in central Europe, where its proximity to inhabited places suggests possibly having escaped from gardens. Delimiting the natural areas of distribution is also difficult in the case of two other European species: *D. plantagineum* and *D. pardalianches*. Both were used as ornamental plants in previous centuries (Pena, 1571; Miller, 1787) and now are considered alien plants in the United Kingdom (Harron, 1986; Clement & Foster, 1994).

The species discussed above (*D. orientale, D. plantagineum*, and *D. pardalianches*) occur in similar mesic habitats from sea level up to subalpine regions, but not in high mountain habitats (the upper tree-line). *Doronicum hungaricum*, occupying similar habitats in Eastern Europe, can be considered vicariant with *D. plantagineum* in this region. *Doronicum austriacum* is widely distributed in Europe, most abundantly in the Austrian Alps, Macedonia, and Ukraine, always in subalpine regions, and in the Iberian peninsula it occurs only in a few localities in the eastern Pyrenees.

The strictly alpine species of the genus in Europe are represented by *Doronicum grandiflorum, D. clusii*, and *D. glaciale*. The first of these species is the most widely distributed of them. It is abundant in the Alps, the Pyrenees, and in the Cantabrian range (northern Spain). In addition, there are two specimens from Corsica dated 1878 and 1917, suggesting its extinction on this Mediterranean island, which has well known floristic affinities with the Alps (Briquet, 1901). *Doronicum clusii* is present in the Alps and Carpathians, while *D. glaciale* is restricted to the Alps (mainly the Austrian Alps), where it can coexist with *D. clusii*. The alpine and subalpine habitats of the central and northern half of the Iberian peninsula (except the Pyrenees) are occupied by *D. carpetanum*, under which four subspecies are recognized.

Other alpine to subalpine species in central and eastern Europe are *Doronicum columnae* and *D. carpaticum*. The first is widely distributed from Italy to Romania, and *D. carpaticum* is restricted to the Carpathians.

The remaining two European species are endemics, *D. cataractarum* in the Austrian Alps and *D. corsicum* in Corsica, and both occur in subalpine habitats.

The genus *Doronicum* in southwestern Asia is represented by seven species. Only one, *D. oblongifolium* (from the Caucasus), is morphologically quite different from the others. Three of them are widely distributed: *D. macrophyllum* (Caucasus and northern Turkey), *D. dolichotrichum* (Caucasus and south of the Caspian Sea), and *D. maximum* (eastern Turkey, and south of the Caspian Sea). Of the three remaining species a limited number of specimens are known, and this results in a scattered distribution.

All of the central Asian species (*D. altaicum, D. briquetii, D. falconeri, D. gansuense, D. kamaonense, D. stenoglossum*) overlap at least in one point of their distributions.

MORPHOLOGY

RHIZOMES

All representatives of *Doronicum* are perennial rhizomatous herbs. The shape and structure of the rhizome are constant within each species, but are not exclusive to any one. These characters are useful, sometimes indispensable, to discriminate between species. There are fleshy or woody (or somewhat woody) rhizomes in *Doronicum*. This character was described by Cavillier (1911: 199), who provided histological diagrams, as "tubéreux" and "non tubéreux," respectively. To distinguish between these, observations on fresh material are required, although when pressed, fleshy rhizomes flatten easily while the woody ones retain their original more or less terete shape. When fresh, fleshy rhizomes are succulent and brittle, while woody ones are fibrous and tough. Fleshy rhizomes are easily recognized in some European species (e.g., *D. plantagineum, D. pardalianches, D. hungaricum*), while woody rhizomes are well represented in Asian species (e.g., *D. macrophyllum, D. maximum, D. stenoglossum*). In a few cases, rhizomes are fleshy to somewhat woody and cannot be assigned to either type (e.g., *D. grandiflorum*, *D. cataractarum*).

Within a species, rhizome internodes may have roughly constant length and width (e.g., *D. altaicum*, Fig. 1G), or may vary in length and width, resulting in stolon-like structures. Most species have the former condition, and only *D. orientale* (Fig. 1A), *D. plantagineum*, *D. pardalianches*, and sometimes *D. hungaricum* have clearly irregular internodes.

Sometimes rhizome nodes have brown-tinted scales remaining from the sheath of basal leaves from previous years (e.g., *D. carpetanum*, Fig. 1F).

The persistent remains of basal fibers from old petioles occur, for example, in *Doronicum oblongifolium*, but they are frequently absent (e.g., *D. austriacum*, Fig. 1C).

Hyaline, shiny, and smooth trichomes are sometimes present on the younger nodes of rhizomes and also in the axils of basal leaves. Sometimes these trichomes are long, abundant, entangled, and white to yellow, and they can cover a large part of the rhizome (e.g., *D. orientale*). Such rhizomes were referred to as "ériopode" by Cavillier (1911: 199) in contrast to "gymnopode" rhizomes, which lack this indumentum (e.g., *D. columnae*). In many cases it is difficult to see trichomes on rhizomes, because they are short and scarce and can be covered with leaf remains (e.g., *D. carpetanum*, *D. clusii*, *D. glaciale*, and *D. grandiflorum*).

Buds are evident on some fleshy rhizomes (e.g., *D. hungaricum*, Fig. 1B). These stem buds can be seen in plants two years or older, but these must be collected carefully. Sometimes the scales that cover young buds can also be observed.

Two species each have unique rhizomes. *Doronicum cacaliifolium* has moniliform rhizomes with uniform, spherical, swollen internodes, alternating with nodal constrictions, sometimes covered by a fibrous net. In the second type, seen in most *D. stenoglossum*, the main stem is inserted on a convex swollen woody surface. Sometimes, pieces of a woody organ perpendicular to the stem were also collected. Although the whole structure has not been seen, it is presumed to be a kind of distinct woody rhizome, but further study of the subterranean organ is needed.

Adventitious roots are present in *Doronicum stenoglossum* and sometimes in *D. kamaonense* a few centimeters above the subterranean woody organ, suggesting that the lowest vertical part of the stem was buried.

STEMS

The stems in *Doronicum* are always erect, fistulose, cylindric, and slightly ribbed, green when fresh, and pale yellow to brown when dry. Generally stems are straight, but zigzag stems occur in some species (e.g., *D. austriacum*). The stems are often simple and end in a single capitulum. When bearing several capitula, the stem is branched only in the upper part. Exceptions are seen in *D. stenoglossum* and *D. kamaonense*, which sometimes have branches on the lower part of the stem.

The main stem terminates in a capitulum, which matures first. Further capitula, if any, are on terminal lateral branches, which for the most part overtop the main head. Each species generally has a characteristic number of capitula, e.g., one in *D. falconeri*, up to 5 in *D. pardalianches*, and more than 5 (up to 20) in *D. corsicum*.

LEAVES

Leaves are simple and alternate. Leaf characters have been traditionally used in the taxonomy of the genus (Cavillier, 1911), but their usefulness is limited to the specific level. The shape and size of leaves are variable even within a single specimen for some species. For this reason, basal leaves (those inserted on the rhizome nodes) and cauline leaves are necessary for descriptive purposes. Similarly, cauline leaves are distinguished by position as lower, middle, and upper, i.e., inserted in the basal, middle, and upper third of the stem, respectively. In some species, basal and lower cauline leaves are usually absent at flowering time.

Basal leaves are petiolate, the petiole being short and wide (e.g., *D. briquetii*), or much longer than the leaf blade (e.g., *D. columnae*). In species with large basal leaves, sheaths are conspicuous (e.g., *D. macrophyllum*, *D. maximum*, and *D. dolichotrichum*). Acropetally, along the stem, the petiole gradually shortens, often leading to fiddle-shaped leaves. The upper cauline leaves are reduced, sessile, and ovate to bract-like. This leaf transition is marked in *D. austriacum*, *D. carpetanum*, *D. macrophyllum*, and *D. pardalianches*.

Leaves may be orbicular, ovate, elliptic, and obovate, as well as fiddle-shaped or bract-like. The base of leaves can be cordate (Fig. 2A), subcordate, truncate, or attenuate (Fig. 3A, C, F, I). Leaf margins are generally entire to subentire, sometimes markedly dentate (e.g., *D. cacaliifolium*, *D. columnae*, *D. corsicum*, and *D. grandiflorum*).

Number and arrangement of cauline leaves determine to a large extent the architecture of the plant. In some species the number of cauline leaves is low (2 to 4, e.g., *D. orientale*) and they are confined to the basal third of the stem. In other leafy species (*D. austriacum*, *D. corsicum*, or *D. altai-*

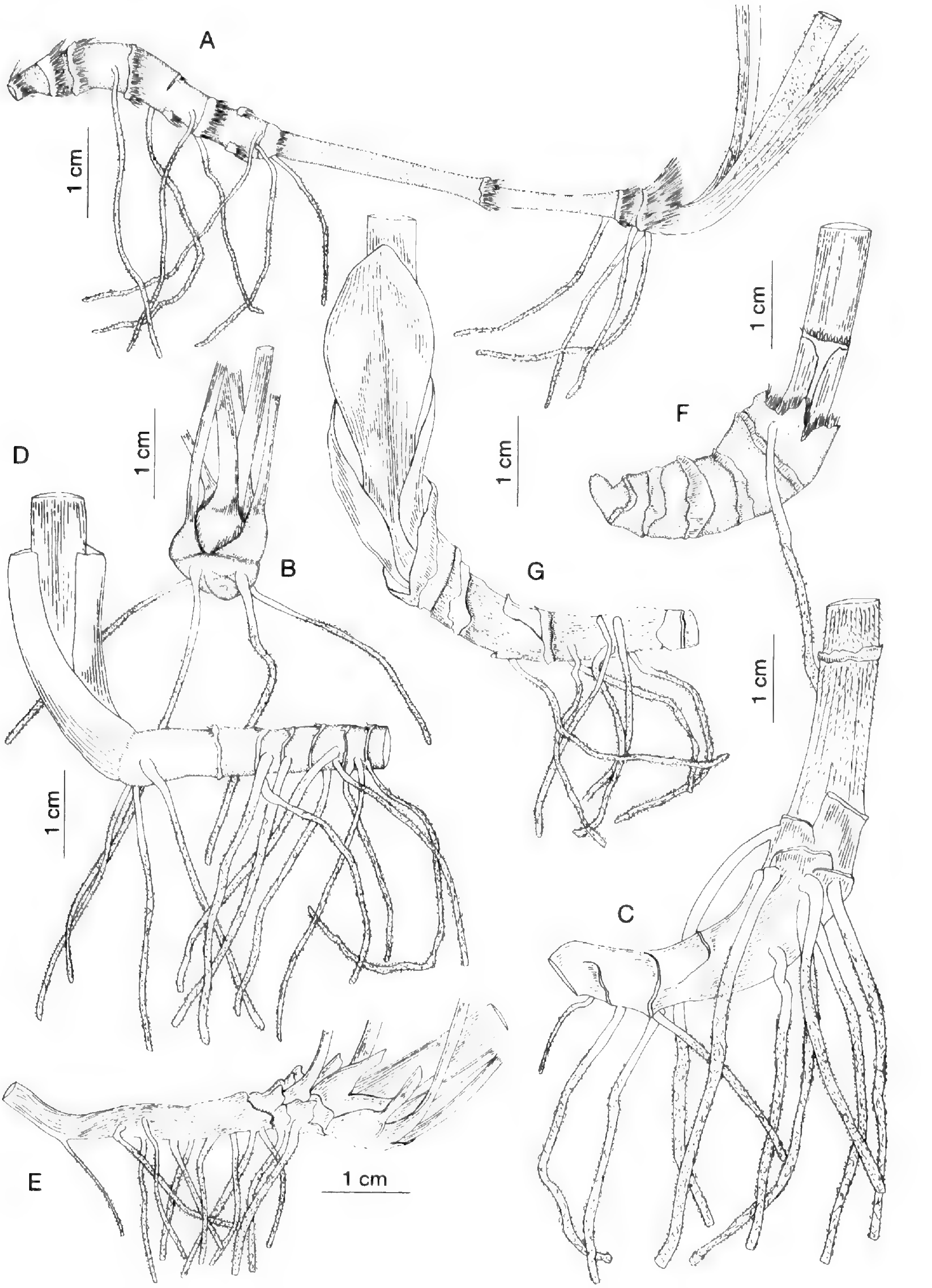

Figure 1. Rhizomes in *Doronicum*. —A. *Doronicum orientale* (drawn from *Willing 3515*, B). —B. *Doronicum hungaricum* (drawn from *Grundl s.n.*, G, as *D. longifolium*). —C. *Doronicum austriacum* (drawn from *Strid et al. 18585*, B). —D. *Doronicum cataractarum* (drawn from *Höpflinger s.n.*, BM). —E. *Doronicum columnae* (drawn from *Sladen 9/4/452*, BM). —F. *Doronicum carpetanum* subsp. *carpetanum* (drawn from *Luceño & Vargas 208*, MA). —G. *Doronicum altaicum* (drawn from *Krasnoborov et al. 959*, K).

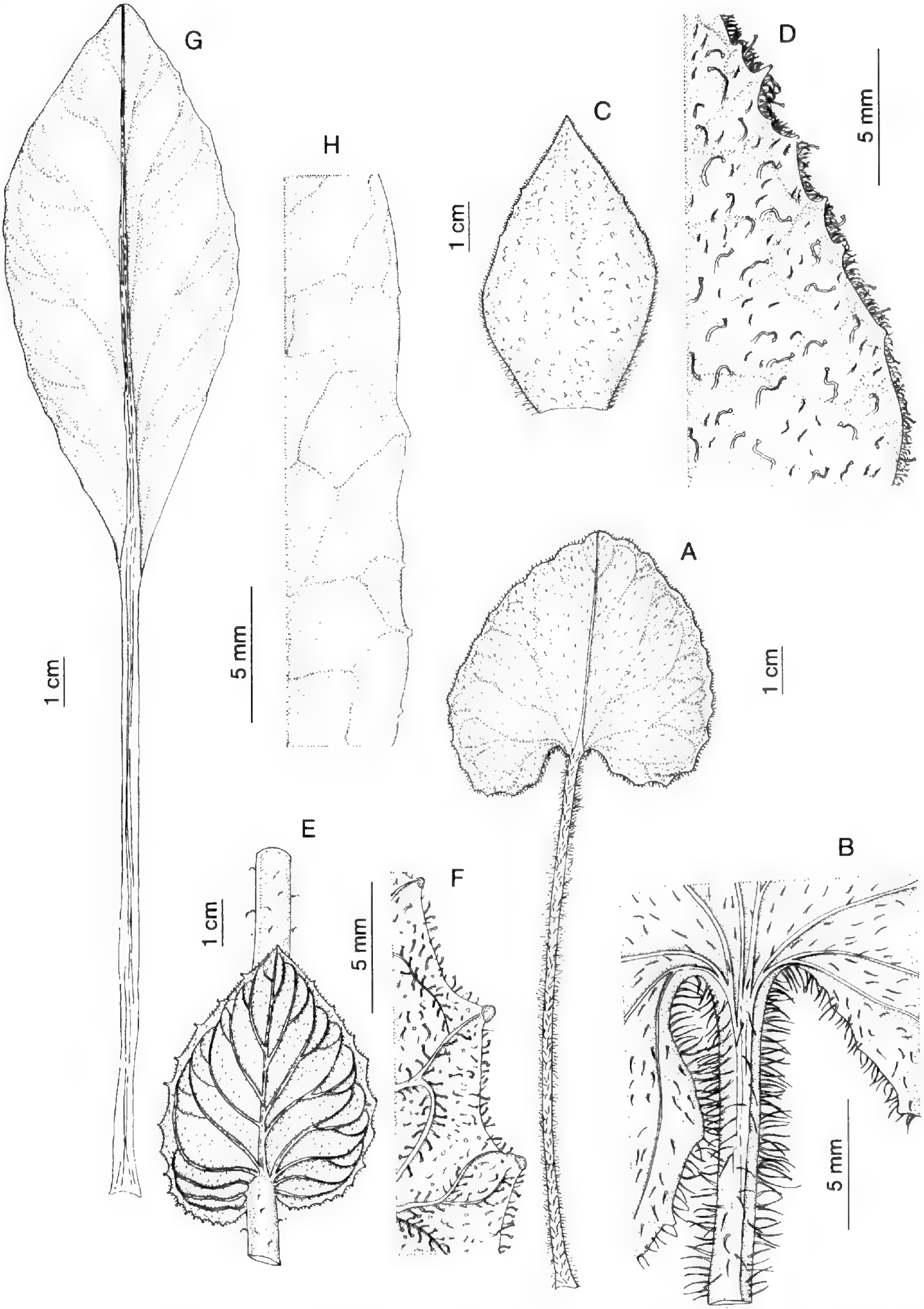

Figure 2. A, B. *Doronicum pardalianches* (drawn from *Rivas-Goday s.n.*, MA). —A. Basal leaf. —B. Indumentum of basal leaf. C, D. *Doronicum dolichotrichum* (drawn from *Davis & Hedge 29493*, K). —C. Upper cauline leaf. —D. Indumentum of upper cauline leaf. E, F. *Doronicum briquetii* (drawn from *Rock 22380*, E). —E. Upper cauline leaf. —F. Indumentum of upper cauline leaf. G, H. *Doronicum altaicum* (drawn from *Krasnoborov et al. 959*, K). —G. Basal leaf. —H. Margin of basal leaf.

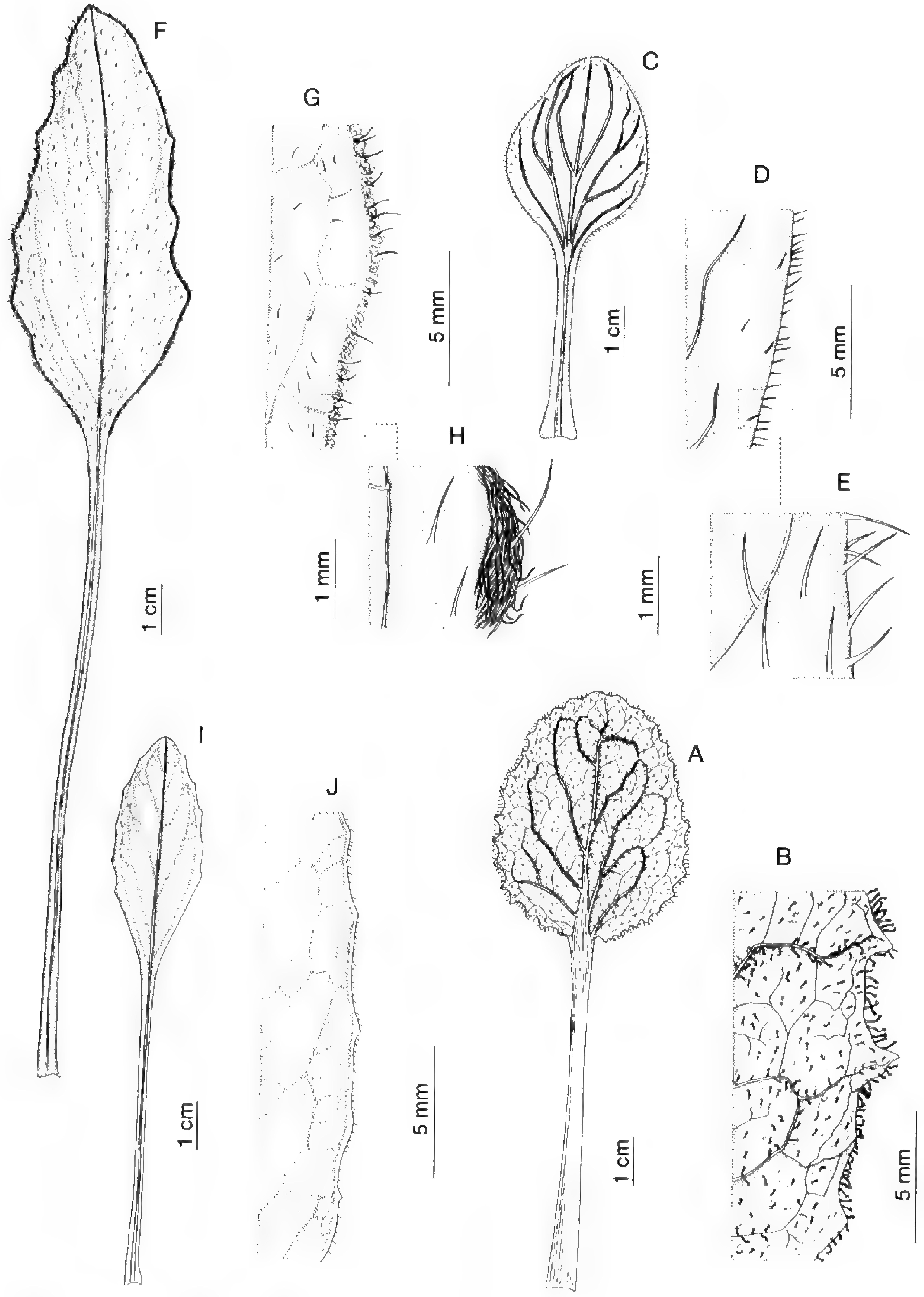

Figure 3. A, B. *Doronicum grandiflorum* (drawn from *Maquet 83/56*, MA). —A. Basal leaf. —B. Indumentum of basal leaf. C–E. *Doronicum glaciale* (drawn from *Steininger s.n.*, B). —C. Basal leaf. —D, E. Indumentum of basal leaf. F–H. *Doronicum clusii* (drawn from *Castroviejo et al. 11615*, MA). —F. Basal leaf. —G, H. Indumentum of basal leaf. I, J. *Doronicum oblongifolium* (drawn from *Albury et al. 3176*, K). —I. Basal leaf. —J. Margin of basal leaf.

cum) leaves are arranged along the stem. The largest leaves are usually seen at the middle or basal parts of stems.

Leaf venation is a good taxonomic character, easily observed in dry specimens and preferably from basal leaves. For its description and categorization the terms proposed by the Leaf Architecture Working Group (1999) are used. Most species have an actinodromous venation for first vein category (e.g., *D. grandiflorum, D. carpetanum, D. reticulatum*) in which all secondary and tertiary veins are more or less equally evident. Pinnate venation for the first vein category occurs in central Asian species. In this type, the tertiary veins are not well marked, and both the secondary veins and the main vein are equally prominent and thick (e.g., *D. altaicum, D. gansuense, D. kamaonense, D. stenoglossum*). The acrodromous type of venation for the first vein category is restricted to a European group of species (*D. hungaricum, D. orientale, D. plantagineum,* and *D. columnae*). Intermediate cases between the latter and the actinodromous type occur in *D. columnae, D. carpaticum,* and *D. pardalianches,* and between pinnate and actinodromous venation in *D. clusii* and *D. glaciale.*

HABIT

Four main habit classes can be distinguished:
(1) An "*orientale*" type: solitary capitulum with a scapose stem, sometimes bearing bract-like leaves; a few cauline leaves (2 to 4) inserted in the basal third of the stem. It is displayed by some European species (e.g., *D. orientale, D. columnae, D. plantagineum*).
(2) An "*altaicum*" type: generally a single capitulum; a mostly leafy stem and a variable number of uniform leaves (4+) along the stem length, or at least in its lower half. This is present in some central Asian as well as European species (e.g., *D. altaicum, D. falconeri, D. grandiflorum*).
(3) A "*macrophyllum*" type: several capitula; stem branched in the upper third; large cauline leaves (3 to 5) mainly in the lower half of the stem, and bract-like leaves on the upper stem. This is restricted to the southwestern Asian species.
(4) A "*corsicum*" type: several capitula; a variable number of ± uniform leaves (5+) ± evenly inserted along the stem. This is characteristic of *D. corsicum* and *D. austriacum.*

In some species the habit does not correspond to these patterns (e.g., *D. kamaonense* and *D. stenoglossum,* which are sometimes branched from the base), and sometimes intermediate patterns occur (e.g., *D. pardalianches, D. cacaliifolium*).

CAPITULA

All *Doronicum* species have radiate, hemispheric to widely campanulate, homochromous capitula (Fig. 5A, E) with yellow or green-yellow corollas. Capitulum diameter ranges from 8 to 15 mm (e.g., *D. cacaliifolium* and *D. kamaonense*) and 7 to 8 cm (e.g., *D. falconeri* and *D. cataractarum*). The receptacle is convex to hemispheric, glabrous or pubescent. In fruit, the base of the capitulum is sometimes widely turbinate.

Ray flowers are female with strap-like or narrowly elliptic to slightly obovate rays, generally ending in three or two teeth, sometimes entire (e.g., *D. altaicum*). Disk flowers are hermaphrodite, actinomorphic, and narrowly funnel-shaped.

Phyllaries are herbaceous to slightly papery at the base in some species (e.g., *D. austriacum*) and arranged in 2 or 3 rows, the outer being wider than the inner. In most species the phyllaries are clearly shorter than the ray flowers, but they can be almost equal or even longer than them (e.g., *D. stenoglossum, D. pardalianches*). Phyllaries are ovate-triangular, ovate-elliptic, or ovate-lanceolate to linear. The phyllary apex is usually acute, except in *D. gansuense* where it bears a sessile gland (Fig. 4A–C). Phyllary margins are entire, except in *D. hausknechtii* where they are slightly fimbriate. A group of species (*D. orientale, D. plantagineum, D. hungaricum, D. carpaticum,* and *D. columnae*) have phyllaries with ciliate margins, bearing thin, stiff, acute, and equidistant trichomes (0.2–1.5 mm) (Fig. 5E–G).

FRUITS

Some species of the genus have dimorphic cypselae (heterocarpy), evident primarily by the absence of a pappus in ray flowers. Cypselae without pappuses are also generally larger than those with a pappus in the same specimen (Fig. 6A, B). Heterocarpy occurs in other genera of Asteraceae such as *Senecio, Crepis, Erigeron, Leontodon,* and *Heterotheca,* as well as in other families, Caryophyllaceae, Apiaceae, Poaceae (Zohary, 1950). These morphologic differences serve different functions. In *Heterotheca latifolia,* in which the type of dimorphism is similar to *Doronicum,* Venable and Levin (1985) suggested that the pappose cypselae are dispersed away by wind, while epappose cypselae fall near the mother plant. This double dispersal strategy implies the potential to colonize different habitats (Venable & Levin, 1985; Tanowitz et al., 1987; Imbert et al., 1996). Although plants with incompletely developed pappuses on ray florets are found in some species (e.g., *D. carpaticum,*

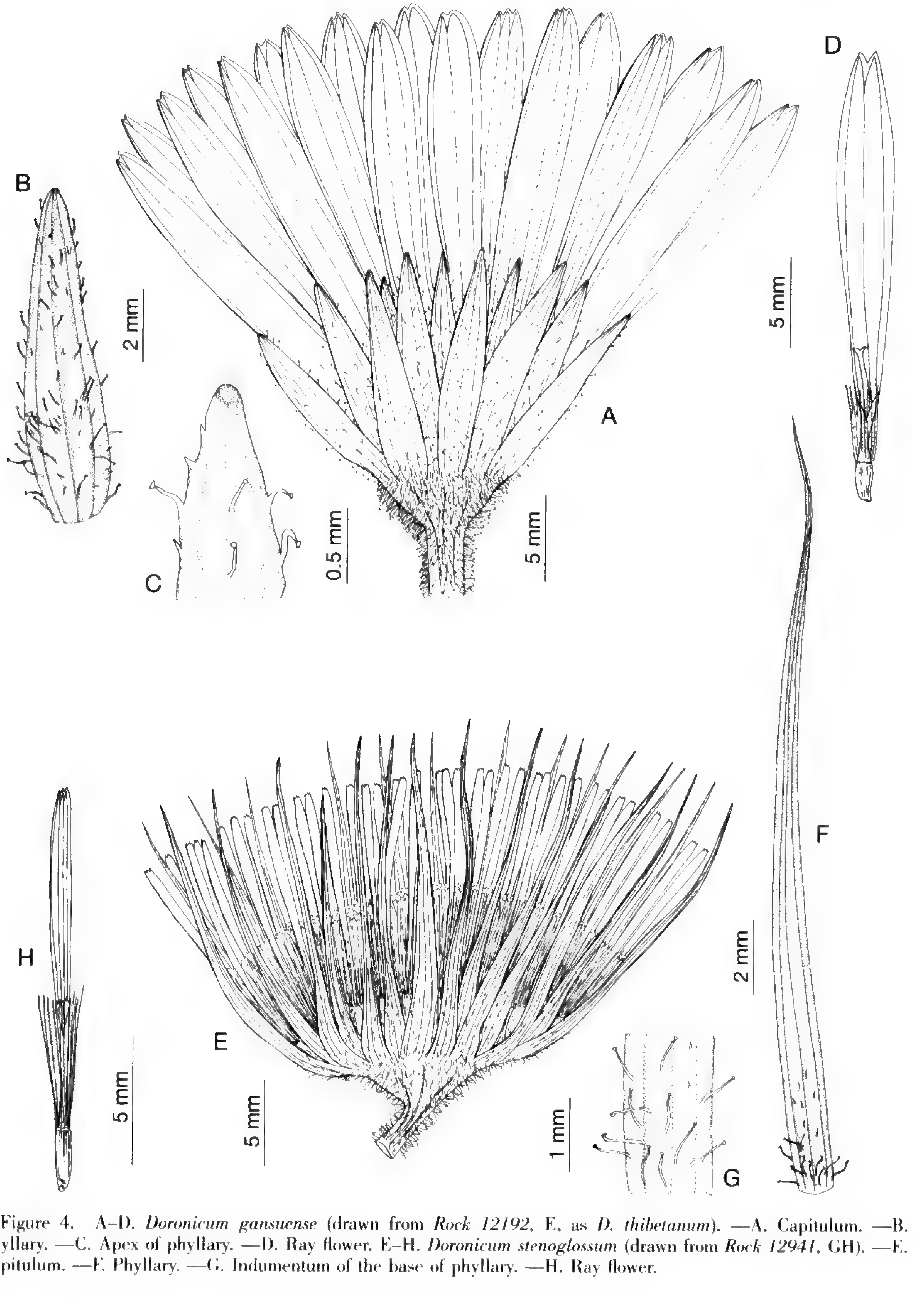

Figure 4. A–D. *Doronicum gansuense* (drawn from *Rock 12192*, E, as *D. thibetanum*). —A. Capitulum. —B. Phyllary. —C. Apex of phyllary. —D. Ray flower. E–H. *Doronicum stenoglossum* (drawn from *Rock 12941*, GH). —E. Capitulum. —F. Phyllary. —G. Indumentum of the base of phyllary. —H. Ray flower.

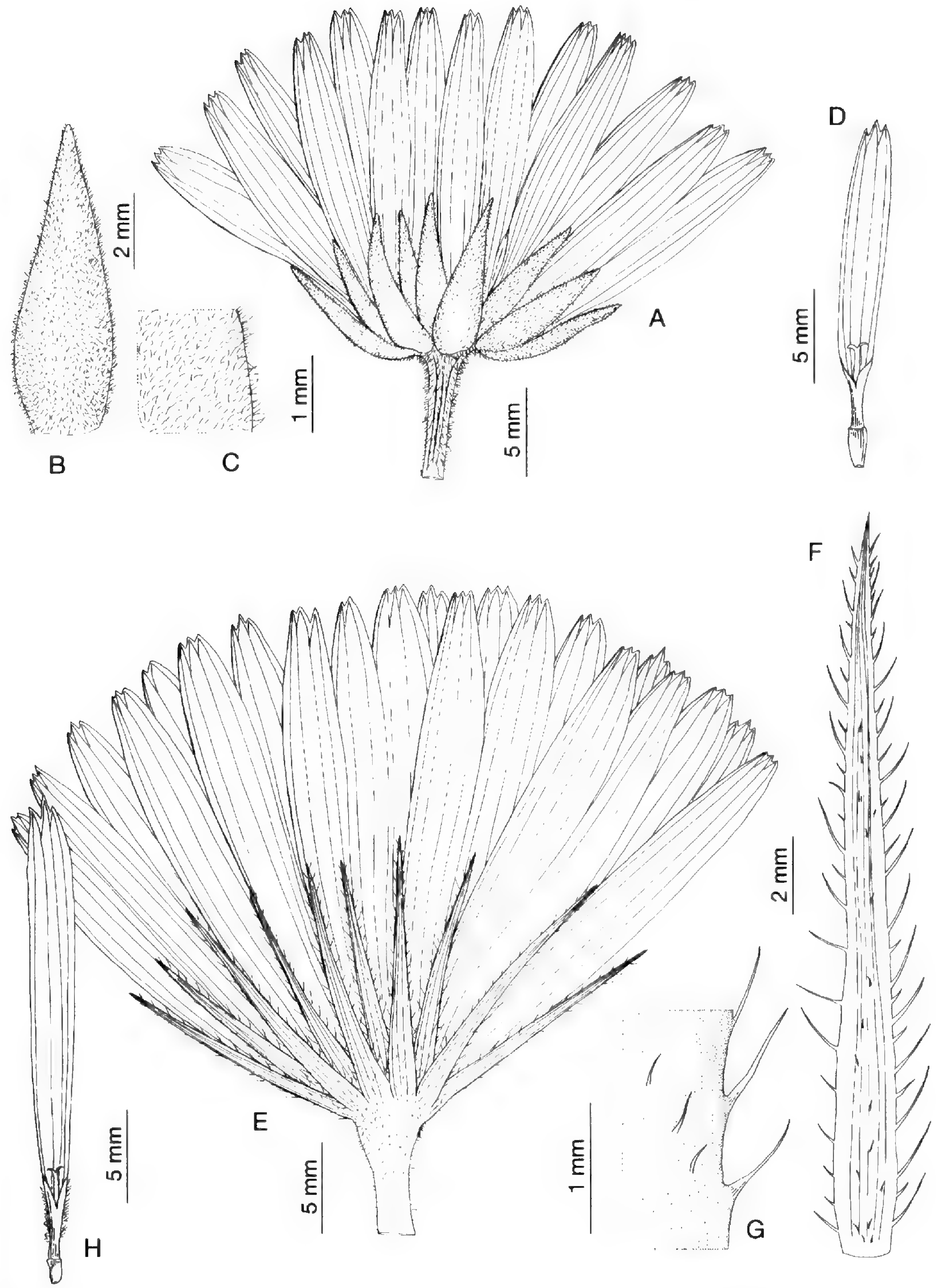

Figure 5. A–D. ***Doronicum cacaliifolium*** (drawn from *Davis 14381*, K). —A. Capitulum. —B. Phyllary. —C. Indumentum of phyllary. —D. Ray flower. E–H. *Doronicum orientale* (drawn from ***Willing 14441***, B). —E. Capitulum. —F. Phyllary. —G. Indumentum of phyllary. —H. Ray flower.

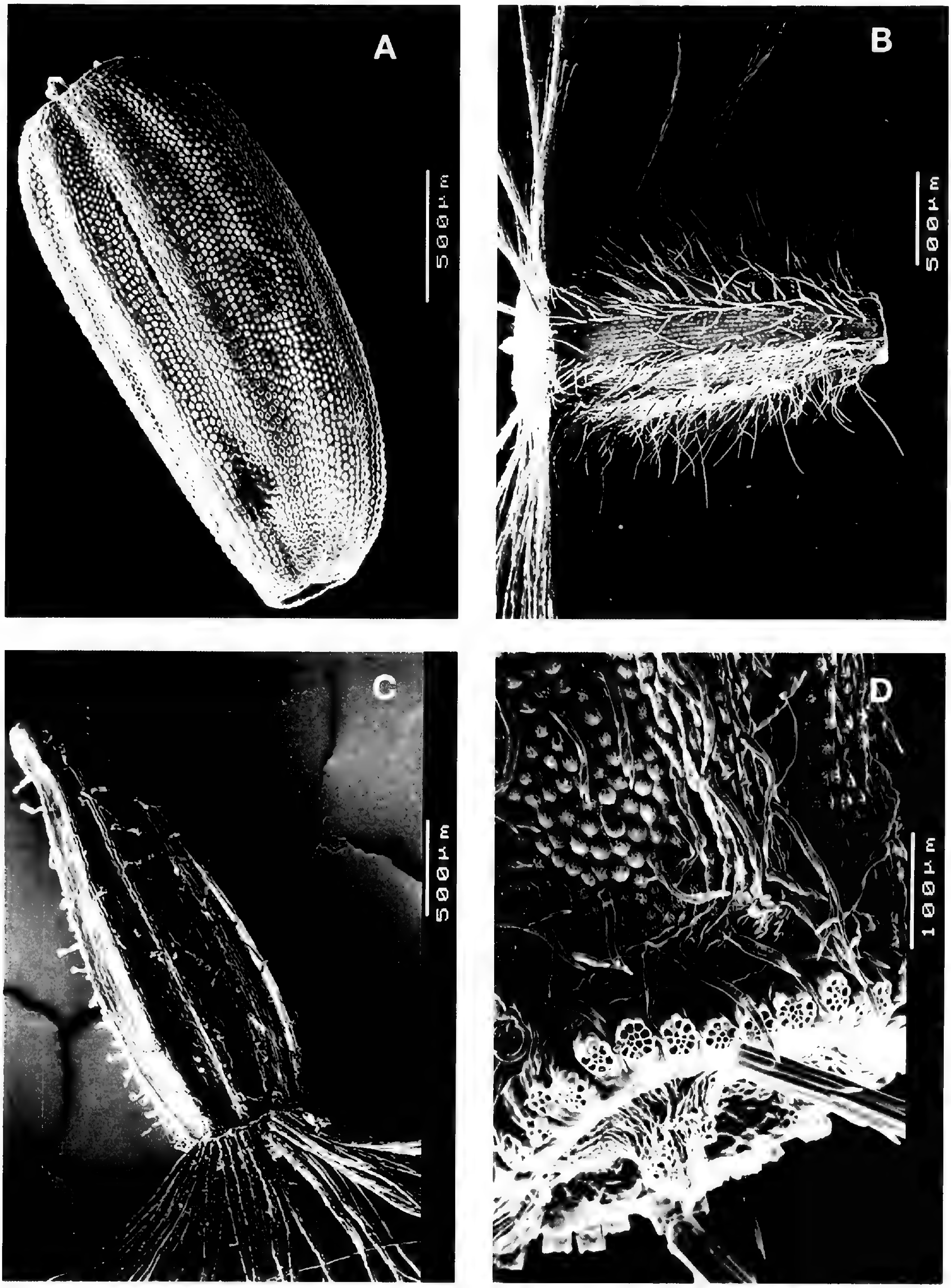

Figure 6. A, B. *Doronicum plantagineum* (from *Álvarez et al. 954*, MA). —A. Cypsela from a ray flower. —B. Cypsela from a disk flower. —C. Cypsela of *Doronicum carpetanum* subsp. *diazii* (from *Álvarez et al. 924*, MA). —D. Base of caducous pappus in *Doronicum stenoglossum* (from *Bartholomew & Gilbert 1205*, E).

D. carpetanum), dimorphism is generally either present or not in *Doronicum*. Such intermediate situations were considered hybrids by Cavillier (1911). In the present taxonomic treatment, since hybrids were not confirmed, intermediates are included with the closest species.

Cypselae are cylindric to obovate, have 10 longitudinal ribs, and are black, brown, brown-red, or olive-green. When an indumentum is present, this occurs mainly on the ribs, except for *D. stenoglossum*, where trichomes are spread across the cypsela surface. In most species, the pappus consists of 2 or 3 rows of minutely scabrous, white or yellow-tinged capillary bristles. A single row of bristles is present in some southwestern Asian species (e.g., *D. macrophyllum*, *D. maximum*) as well as in *D. stenoglossum*. This latter species is functionally heterocarpic since the pappus in ray flowers is caducous. A thick base, or "crown," remains when the pappus falls (Fig. 6D).

Surfaces of cypselae are warty to slightly warty (Fig. 7A), reticulate-grooved (Fig. 7B), grooved to slightly grooved (Fig. 7C), or smooth (Fig. 7D).

INDUMENTUM

This was the most relevant taxonomic character for Cavillier (1907, 1911) at the specific level. Other authors also considered the type and arrangement of indumentum very important (Pérez et al., 1994). While the indumentum pattern identifies certain species (e.g., *D. clusii*, *D. glaciale*, *D. haussknechtii*, *D. hungaricum*, *D. dolichotrichum*), any quantitative variation within the same indumentum type is not useful in distinguishing species. The latter quantitative criterion led to the erroneous characterization of the species *D. austriacum* (Pérez et al., 1997). When indumentum is scarce, it may be most dense on the upper third of the stem, on veins, margins and abaxial surfaces of leaves, as well as in the basal part of outer phyllaries (abaxial surfaces). In *Doronicum*, the adaxial surfaces of the phyllaries are always glabrous. The following types of trichomes have been recognized in *Doronicum*:

Eglandular trichomes

(1) Multiseriate trichomes with blunt apices that are formed at least by two rows of rectangular cells, these trichomes are usually 0.3–0.5 mm long, but sometimes up to 1.5 mm (in *D. plantagineum*) or even up to 4.5 mm (in *D. hungaricum*). They occur on stems, leaves, and phyllaries, more frequently in European species but are almost absent in central Asian species.

(2) Uniseriate trichomes with blunt apices that are formed by a single row of rectangular or square cells, these trichomes are 0.1–0.4 mm long. This is the most common pubescence, occurring on stems, leaves, and phyllaries in almost all species. In *D. cacaliifolium* (Fig. 5A–C) they cover the abaxial phyllary surface and differ from others by their enlarged basal part and curved apex (Fig. 8B). This type of trichome also occurs in *D. clusii*, in which the cells are clearly rectangular, but the trichome length is up to 5 mm, and they may form an entangled covering on the leaf margins.

(3) Multiseriate trichomes with acute apices. These consist of at least two rows of fusiform cells ending in one or two cells with an acute apex. Four subtypes occur:

(3a) Stiff trichomes (0.5–2.5 mm long), consisting generally of more than two rows of cells, characteristic of leaves and phyllaries in *D. glaciale* and *D. clusii* (Fig. 3C–H).

(3b) Somewhat stiff trichomes (0.2–1.5 mm long), sometimes crooked (cilia). They are only present on the margins of phyllaries of *D. orientale* (Fig. 5E–G), *D. plantagineum*, *D. hungaricum*, *D. carpaticum*, and *D. columnae*.

(3c) Trichomes (ca. 0.3 mm long), formed by two or three cells. They occur on the cypselae of almost all *Doronicum* species (Fig. 8A).

(3d) Trichomes (0.5–5 mm long) that end in two acute cells, and are present only on leaves and petioles of *D. pardalianches*.

Glandular trichomes

The following types of glandular trichomes are recognized in this work:

(1) Short-stalked glandular trichomes. These consist of 4 to 8 cells, 0.05–0.3 mm long, and are present on the stems, leaves, phyllaries, cypselae, and flowers of all the species. Two subtypes are distinguished:

(1a) Trichomes with apices (of 2 cells) of the same diameter as the cells of the trichome stalk (Fig. 8C).

(1b) Trichomes with capitate apices (of 3 or 4 cells) and wider than the stalk.

(2) Long-stalked glandular trichomes. These consist of more than 6 cells, 0.3–5 mm long, and are present on the stems, leaves, and phyllaries in many *Doronicum* species. Two subtypes are distinguished:

(2a) Trichomes with apices of 3 or 4 cells of the same diameter as stalk cells.

(2b) Trichomes with apices (of more than 4 cells) exceeding stalk cells (Fig. 8D). This latter type is present in a few species (*D. macrophyllum*, *D. hun-*

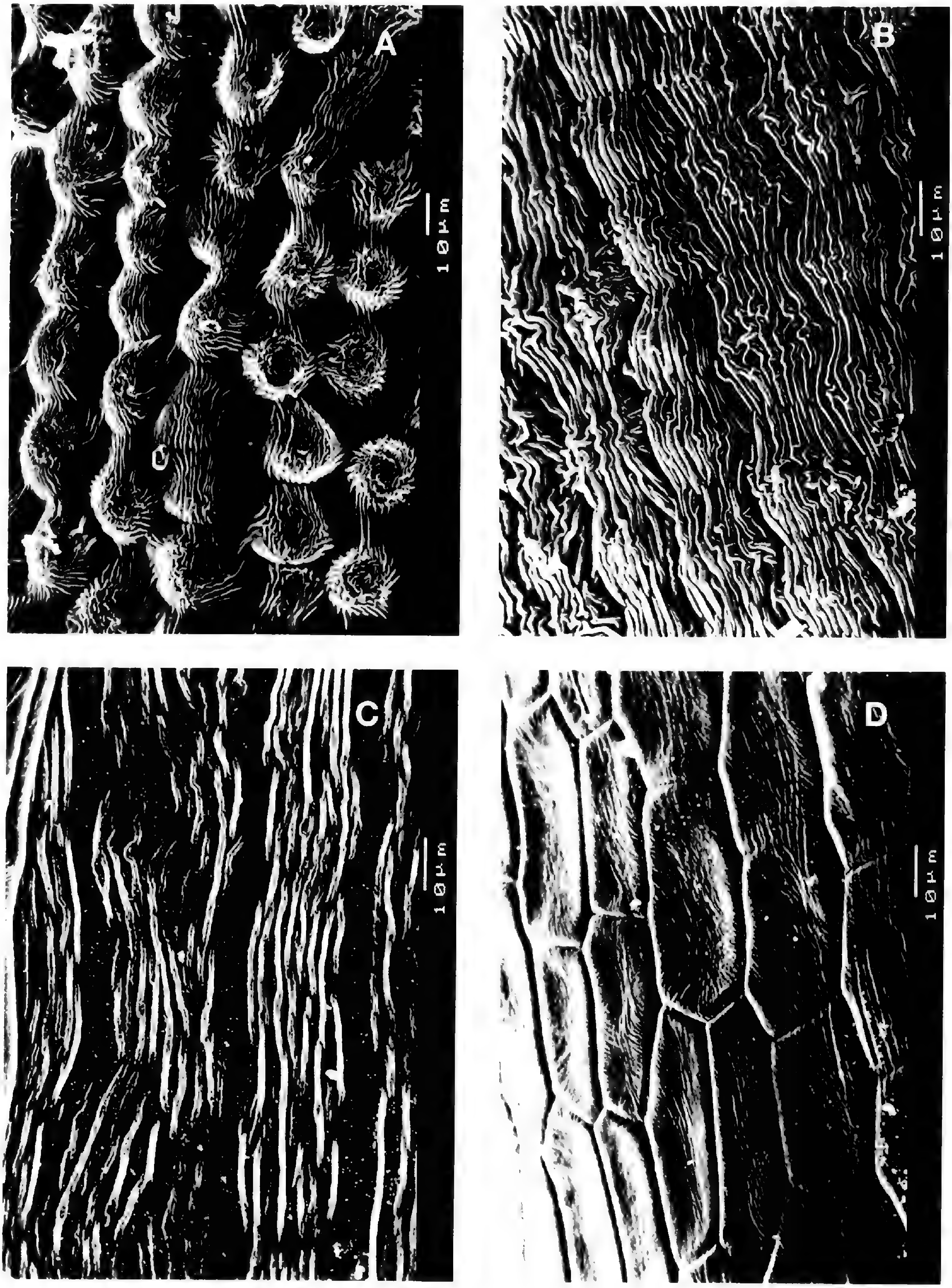

Figure 7. Cypselae surfaces in *Doronicum*. —A. *Doronicum pardalianches* (from *Almaraz et al. 1015*, MA). —B. *Doronicum reticulatum* (from *Baytop & Baytop 20972*, E, as *D. bithynicum*). —C. *Doronicum cacaliifolium* (from *Davis 14551*, K). —D. *Doronicum dolichotrichum* (from *Davis & Polunin 24383*, E).

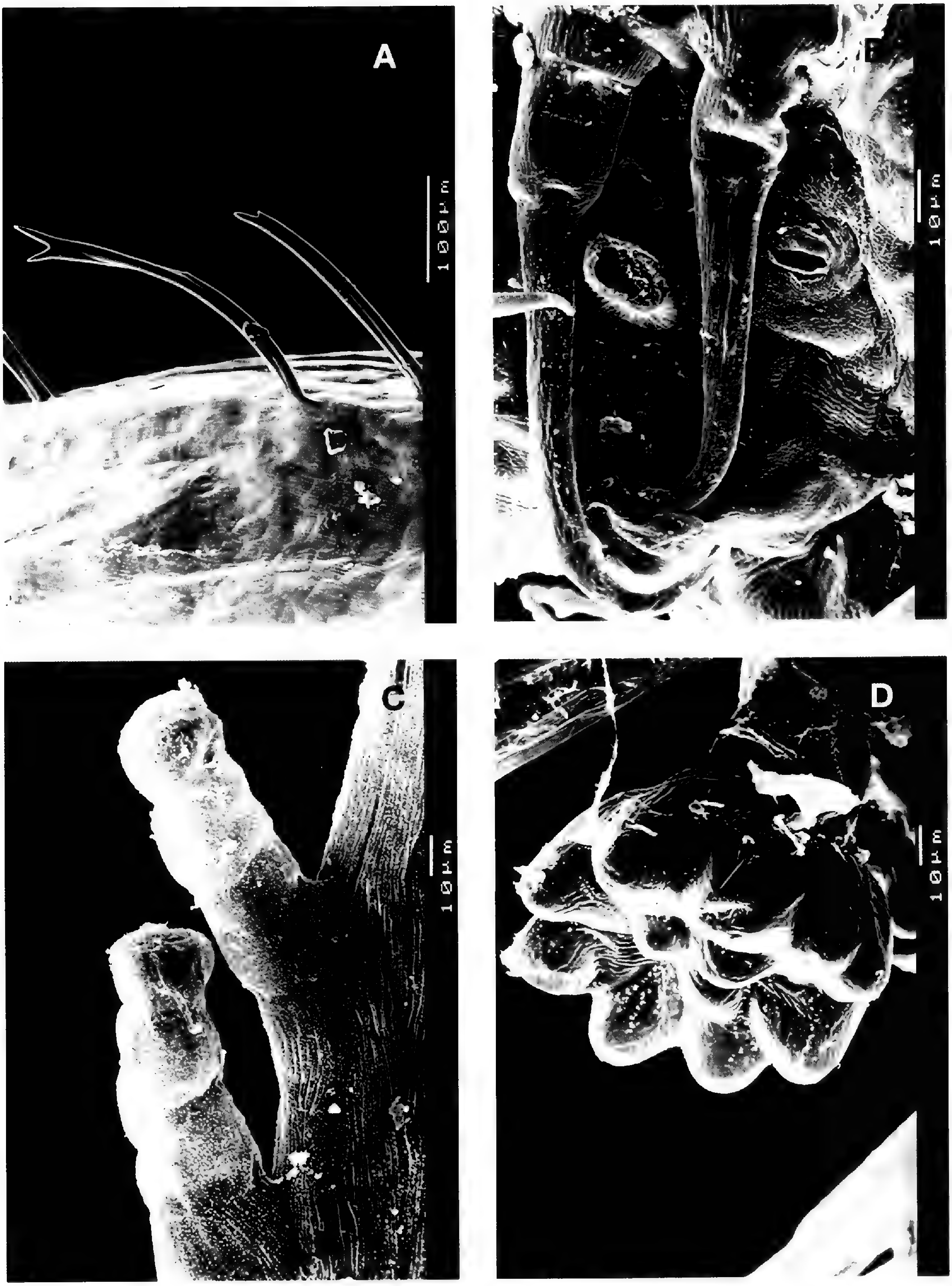

Figure 8. —A. Uniseriate eglandular trichomes with acute apices on a cypsela of *Doronicum maximum* (from *Davis & Polunin 24113*, E). —B. Uniseriate eglandular trichomes with blunt apices on a phyllary of *Doronicum cacaliifolium* (from *Davis 14551*, K). —C. Uniseriate glandular trichomes on the margins of a phyllary of *Doronicum cataractarum* (from *Fest 571*, B). —D. Apex of a multiseriate glandular trichome from the base of the capitulum in *Doronicum kamaonense* (from *Polunin et al. 401*, G, as *D. roylei*).

garicum, and *D. kamaonense*). Only in this last species is the apex markedly obconical and can be observed near the capitula without a magnifying glass.

CHEMISTRY

Several chemical analyses on *Doronicum macrophyllum* (Bohlmann & Grenz, 1979), *D. pardalianches* (Bohlmann & Abraham, 1979), *D. hungaricum* (Bohlmann et al., 1980), and *D. grandiflorum* (Reynaud & Raynaud, 1984, 1986; Reynaud et al., 1985) have resulted in the isolation of 52 different compounds. Two of them are pyrrolizidine alkaloids, a few are aromatic compounds: 10 benzofurane-derivatives, 4 phenols, and 2 flavonoids. Twenty-one monoterpenes, mainly thymol-derivatives, were also isolated. The remaining compounds are 5 diterpenes with kaurane structure, 2 triterpenes (one of them a lupane-derivative and other oleanane-derivative), and 6 sesquiterpenes, most of these germacradiene-derivative.

Since only four species were analyzed, the taxonomic usefulness of these chemical characters at the specific level cannot be assessed. However, the presence of alkaloids of the pyrrolizidine group (Bohlmann & Grenz, 1979) is consistent with the inclusion of the genus within the tribe Senecioneae, which is characterized by these alkaloids (Robins, 1977).

CHROMOSOME NUMBERS

Chromosome numbers in *Doronicum* are rather constant. Most reports included herein were obtained from the literature (Lindqvist, 1950; Skalinska, 1950; Baksay, 1956; Contandriopoulos, 1957; Favarger & Huynh, 1964; Polatschek, 1966; Favarger & Küpfer, 1968; Lovka et al., 1972; Kuzmanov & Ancev, 1973; Löve & Kjellqvist, 1974; Garbari et al., 1980; Van Loon, 1980; Belaeva & Siplivinsky, 1981; Van Loon & Oudemans, 1982; Kuzmanov & Georgieva, 1983; Strid & Franzén, 1983; Davlianidze, 1985; Strid & Anderson, 1985; Chacón, 1987; Lippert & Heubl, 1988; Tasenkevitch et al., 1989; Vir Jee & Kachroo, 1989; Baltisberger, 1991; Ruiz de Clavijo, 1993). Only when no original sources were available (i.e., *D. cataractarum, D. macrophyllum,* among other counts), data from indexes of plant chromosome numbers (Fedorov, 1969; Moore, 1982; Goldblatt, 1985, 1988; Goldblatt & Johnson, 1994, 1996, 1998) were cited, and they are indicated by an asterisk after the number. However, chromosome counts were made here for *D. carpetanum* subsp. *diazii* ($2n = 60$) and *D. carpetanum* subsp. *kuepferi* ($2n = 60$). Material was cultivated from fresh rhizomes or seeds. Apices of secondary roots as well as immature disk flowers were used for counting. Both were fixed in 3:1 ethanol: acetic acid for 48 hours and then kept in 70% ethanol at −20°C. Chromosomes were stained with acetic orcein.

The basic chromosome number $x = 30$, characteristic of the "cacalioid" group in Senecioneae, is also considered to be the basic number in *Doronicum* (Bremer, 1994), although previous authors suggested $x = 10$ (Fernandes & Queirós, 1971; Májovský & Murín, 1987). Chromosome numbers, known for 19 taxa, are consistent with both hypotheses, although the fact that most of them are multiples of 30 ($2n = 60$) may support the basic number $x = 30$. Only *D. carpetanum* subsp. *carpetanum, D. carpetanum* subsp. *pubescens, D. plantagineum,* and several populations of *D. clusii* and *D. pardalianches* had higher counts, at $2n = 120$. Other species show both ploidy levels (e.g., *D. altaicum* $2n = 30$*, 60; *D. macrophyllum,* $n = 30$*, 60; and *D. oblongifolium,* $2n = 60, 40$), suggesting that polyploidy is common in the genus. *Doronicum oblongifolium* ($2n = 40$) is the only count that is inconsistent with $x = 30$, and it should be recounted.

PHYLOGENY

The first phylogenetic hypothesis for *Doronicum* sect. *Doronicastrum* (i.e., *D. altaicum, D. austriacum, D. balansae, D. briquetii, D. cacaliifolium, D. carpaticum, D. carpetanum, D. clusii, D. cordatum, D. corsicum, D. dolichotrichum, D. falconeri, D. glaciale, D. grandiflorum, D. haussknechtii, D. longifolium, D. macrolepis, D. macrophyllum, D. maximum, D. oblongifolium, D. orientale, D. pardalianches, D. plantagineum, D. portae, D. reticulatum, D. thibetanum, D. thirkei, D. turkestanicum,* and *D. viscosum*) was presented by Cavillier (1911).

Cavillier (1911) mentioned that his three sections (sect. *Doronicastrum,* sect. *Soulieastrum,* and sect. *Hookerastrum*) were not closely related, and thus the genus so circumscribed is polyphyletic.

Cavillier considered the *Doronicum* subsections included in section *Doronicastrum* to be natural groups, and his classification was developed accordingly. He thought that subsection *Plantaginea* (*D. plantagineum, D. longifolium* (= *D. hungaricum* herein), *D. oblongifolium,* and *D. falconeri*) was monophyletic and the most ancient group in the genus. *Doronicum* subsect. *Pardalianchia* (*D. pardalianches, D. roylei* (= *D. kamaonense* herein), *D. reticulatum,* and *D. atlanticum* (= *D. plantagineum* herein)) was a grouping derived from subsection *Plantaginea. Doronicum* subsects. *Cardiophylla* (*D. carpetanum, D. orientale, D. carpaticum,* and *D. cordatum* (= *D. columnae* herein)) and *Macrophylla* (*D. macrophyllum, D. dolichotrichum, D. haussknechtii, D. maximum,* and *D. cacaliifolium*) were derived from subsection *Pardalianchia,* and were also natural groups. In contrast, Cavillier placed the probable origin of subsection *Grandiflora* (*D. altaicum, D. briquetii, D. grandiflorum, D. glaciale,* and *D. clusii*) among several members of subsection *Plantaginea.* The monotypic subsections *Corsica* and *Austriaca* would be derived from different members of subsection *Pardalianchia.* Morphologically, Cavillier (1911) noted a trend from ancient plants bearing one capitulum and basal leaves with a truncate or attenuate base to evolved plants with several capitula and basal leaves with cordate bases. Biogeographically this is not easy to reconcile since these groups include members from different continents.

The phylogenetic analysis of Álvarez Fernández et al. (2001) was based on morphological evidence as well as molecular data (nuclear ribosomal ITS and chloroplast *trn*L-F sequences).

When morphological characters were mapped onto the most parsimonious topologies, only three were free from homoplasy (scapiform habit, acrodromous basal leaf venation, and ciliate involucral bracts). All of these characters are synapomorphic for the *D. plantagineum* clade, and the strict consensus can be seen in Figure 9.

There are only two clades with bootstrap support above 90%, both basal. The *Doronicum* clade had 100% bootstrap support in all analyses, using *Ligularia* and *Tussilago* as outgroups. Although the use of only two outgroups does not provide stringent conditions for testing the monophyly of the ingroup, other evidence also indicates the monophyly of *Doronicum.* In particular, sequences aligned well within *Doronicum* but were difficult to align with any other genera suggesting that *Doronicum,* as circumscribed in this work, is monophyletic. The other clade with strong bootstrap support (97%) includes all the species of *Doronicum* except *D. corsicum,* which is sister to it (Fig. 9). This noteworthy result has strong biogeographic implications. The next taxon that is a derivative of this Corsican endemic is *D. pardalianches,* followed by the *D. plantagineum* group, which has 85% of bootstrap support. All these species are European, mostly Mediterranean, suggesting that early diversification took place on the European continent, specifically within the Mediterranean Basin.

Taxonomy

Doronicum L., Sp. Pl. 885. 1753. *Pardalianches* Tausch, Flora 11: 182. 1828. *Doronicum* sect. *Doronicastrum* Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 337. 1911. *Doronicum* subsect. *Pardalianches* [*Pardalianchia*] Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 338. 1911. *Doronicum* sect. *Pardalianches* (Tausch) Gorschk., in Schischk. & Bobrov, Fl. URSS 26: 773. 1961. *Doronicum* ser. *Pardalianches* (Tausch) Gorschk., in Schischk. & Bobrov, Fl. URSS 26: 778. 1961. TYPE: Herb. Clifford, 411.1 [sine collector] (lectotype, designated by Llamas et al. in Jarvis & Turland (1998: 360), BM!).

Aronicum Neck., Elem. Bot. 1: 27. 1790, nom. inval. (ICBN, App. V, Greuter et al., 2000).

Grammarthron Cass., Bull. Soc. Philom. Paris: 32. 1817. TYPE: "Doronicum radice scorpii brachiata," Herb. Burser X: 16 [sine collector] (lectotype, designated by Álvarez in Jarvis & Turland (1998: 353), UPS!, photograph). [= *Doronicum pardalianches* L.]

Fullartonia DC., Prodr. 5: 281. 1836. TYPE: "Comp. angl. des Indes 1830" [sine collector], ex herb. de Candolle (lectotype, designated by Álvarez Fernández (2001: 294), G-DC!, photograph). [≡ *Doronicum kamaonense* (DC.) Álv. Fern.]

Doronicum subsect. *Corsica* Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 337. 1911. TYPE: not located; protologue citation: "in Corsica, ad rupes aquis fluentibus irriguas (D. Richard. Herb.)."

Doronicum subsect. *Austriaca* Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 338. 1911. *Doronicum* ser. *Austriaca* (Cavill.) Gorschk., in Schischk. & Bobrov, Fl. URSS 26: 774. 1961. TYPE: [sine collector] ex herb. Linnaeus (LINN n.° 1002.4!) (lectotype, designated by Pérez et al. (1997: 3)).

Doronicum subsect. *Cardiophylla* Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 338. 1911. *Doronicum* ser. *Cardiophylla* (Cavill.) Gorschk., in Schischk. & Bobrov, Fl. URSS 26: 775. 1961. TYPE: not designated; although this subsection was originally published without a type species, its name is valid (ICBN, Art. 37.1, Greuter et al., 2000).

Doronicum subsect. *Macrophylla* Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 338. 1911. *Doronicum* ser. *Macrophylla* (Cavill.) Gorschk., in Schischk. & Bobrov, Fl. URSS 26: 776. 1961. TYPE: North Caucasus. Beschtau, [*F. A. F. Marschall von Bieberstein s.n.*], ex herb. Marschall von Bieberstein (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 804), LE!).

Doronicum subsect. *Plantaginea* Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 338. 1911. *Doronicum* ser. *Plantaginea* (Cavill.) Gorschk., in Schischk. & Bobrov, Fl. URSS 26: 779. 1961. TYPE: Herb. Clifford, 411.2 [sine collector] (lectotype, designated by Llamas et al., in Jarvis & Turland (1998: 360), BM!).

Doronicum subsect. *Grandiflora* Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 338. 1911. TYPE: "Arnica altaic. pall., tige simple unifl. haute de 4 ou

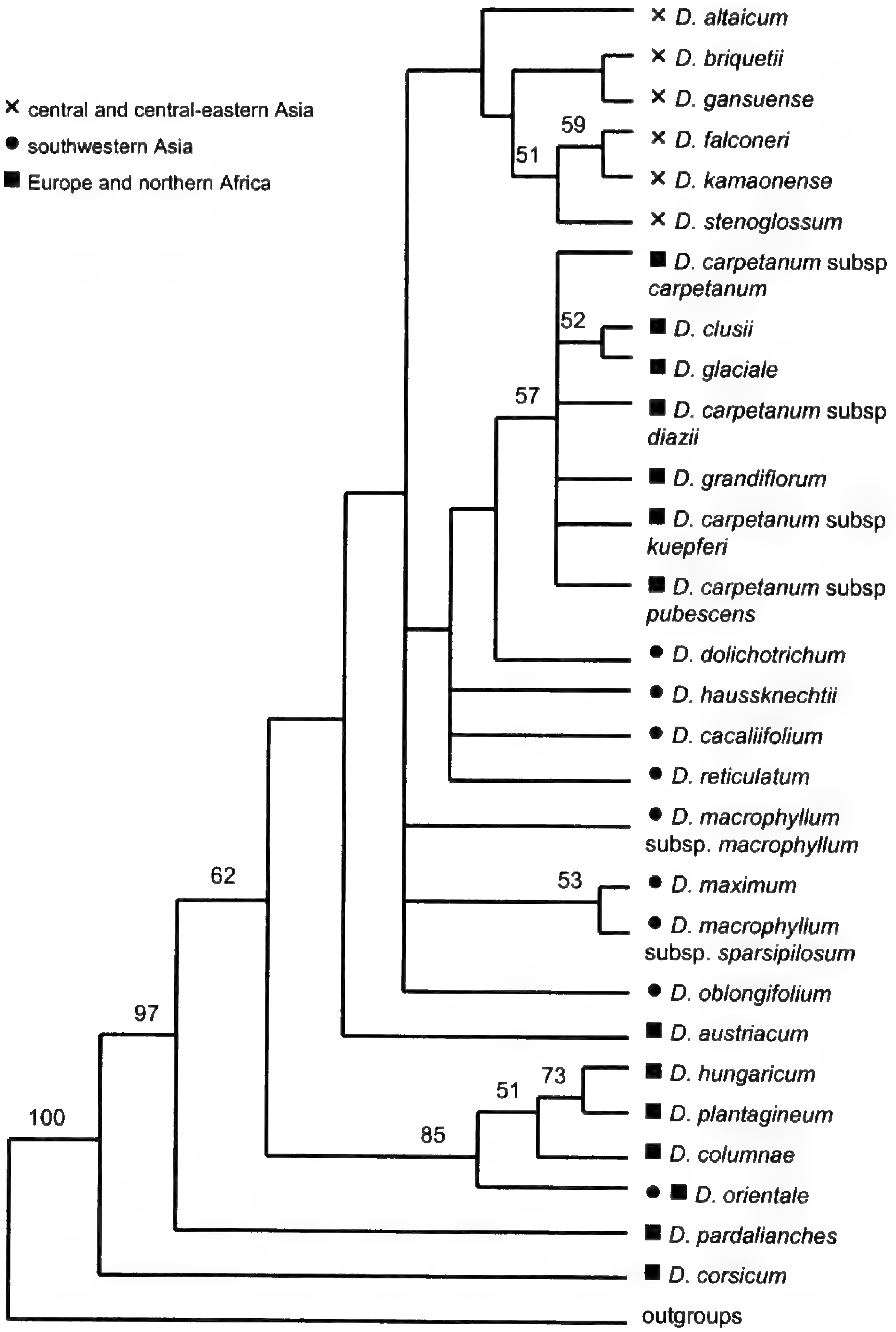

Figure 9. Strict consensus from 228 most parsimonious trees resulting from the combined analysis of three data sets in *Doronicum* (morphology, nrITS, cpDNA *trn*L-F sequence data, see Álvarez Fernández et al., 2001). Bootstrap values above 50% are shown above the branches. Outgroups: *Tussilago farfara* L. and *Ligularia sibirica* (L.) Cass. Geographical distribution of taxa: central and central-eastern Asia (crosses), southwestern Asia (circles), and Europe and northern Africa (squares).

7 pouces, fl. tres grande, fleurit au com. + de mai" [sine collector], ex herb. Lamarck (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 803), P-LA!, photograph).

Doronicum sect. *Soulieastrum* Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 338. 1911. TYPE: China. Tibet: Kiala, Tongolo, *J. A. Soulié 335* (lectotype, designated here, G!; isotype, K!), [= *Doronicum stenoglossum* Maxim.]

Doronicum ser. *Altaica* Gorschk., in Schischk. & Bobrov, Fl. URSS 26: 768. 1961. TYPE: [Asia] "E Sumis montium altaicorum" [sine collector], ex herb. Pallas (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 801), BM!).

Doronicum ser. *Carpatica* Gorschk., in Schischk. & Bobrov, Fl. URSS 26: 771. 1961. TYPE: not located; protologue citation: "Siebenbürgen: in der alpinen Region der südlichen Karpaten, z. B. am Szurul (Fuss), nach Schur bis 7000' austeigend."

Doronicum subsect. *Isaurica* J. R. Edm., Notes Roy. Bot. Gard. Edinburgh 37(1): 72. 1978. TYPE: Turkey. Taurus, Mt. Gheï-Dagh, [*T. Heldreich*] *1043* (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 802), G-BOIS!; isotype, BM!).

Perennial herbs, 10–150(+) cm tall. *Rhizomes* fleshy or woody, glabrous to pubescent, sometimes with buds. *Stems* terete, fistulous, slightly ribbed, erect, branched or not, scape-like to leafy, sometimes with persistent leaf remains forming dark scales or fibers at the base, yellow to brown-tinged when dry. Indumentum variable, eglandular or glandular, abundant near the capitulum to very scarce at the base of the plant, sometimes absent. *Leaves* alternate, simple, entire to dentate, pubescent or glabrous, with actinodromous or pinnate-actinodromous venation, sometimes somewhat acrodromous. Basal leaves sometimes reduced to cataphylls or absent at flowering time, petiolate, with orbicular, ovate, elliptic or obovate blades, generally with a blunt apex; base of blade truncate, attenuate or cordate; petiole generally as long as the blade or longer, sometimes shorter. Lower cauline leaves similar to basal leaves, sometimes sessile. Middle cauline leaves sessile, ovate, elliptic, obovate, or fiddle-shaped, semi-amplexicaul, with blunt or acute apex. Upper cauline leaves similar, sometimes bract-like. *Capitula* 1 to 20(+), heterogamous, arranged in cymose synflorescences, terminal when solitary, radiate, 0.8–8 cm diam. including rays. Involucre much shorter than rays or rarely exceeding them. *Phyllaries* arranged in 2 to 3 rows, similar, herbaceous to somewhat papery at base and margins, ovate-elliptic to obovate-elliptic, or linear, generally with acute to tapering apex; margins entire, sometimes ciliate or minutely fimbriate; pubescent on the abaxial surface, rarely glabrous, indumentum absent on the adaxial surface. *Receptacles* convex, glabrous to pubescent. *Flowers* with yellow or green-yellow shaded corollas, uniform in color. Style branches short and blunt, adaxial papillate. Anthers without appendages. Ray flowers female, arranged in 1 row. Rays oblong-elliptic to linear; apex with 2 or 3 teeth or acute; sometimes pubescent at the base. Disk flowers, tubular, bisexual. *Cypselae* homomorphic (all cypselae with pappus) or dimorphic (ray flower cypselae without pappus), cylindrical, elliptic-obovate, with 10 ribs, light brown to brown, brown-red, olive green, or black. Surface smooth, grooved or warty, glabrous, or pubescent. Pappus arranged in 1 to 3 rows, with minutely scabrous capillary bristles, white to yellow tints. Base chromosome number $x = 30$.

Distribution. *Doronicum* is found mostly between 25º and 55° longitude in Asia, Europe, and North Africa (Morocco and northeastern Algeria), growing in forests, open rocky places with moist soil, meadows, and near watercourses, from sea level up to 5000 m in elevation.

KEY TO SPECIES OF *DORONICUM*

1. Ray flowers without pappus (heterocarpic plant) 2

1′. Ray flowers with pappus, although sometimes poorly developed (homocarpic plant) 20

2(1). Base of blade of basal leaves truncate or attenuate; plants usually bearing a single capitulum 3

2′. Base of blade of basal leaves cordate or subcordate; plants bearing one to several capitula 6

3(2). Basal leaves with acrodromous venation 4

3′. Basal leaves with pinnate-actinodromous, or actinodromous venation 5

4(3). Basal leaves oblong-elliptic; indumentum of the adaxial surface of basal leaves generally consisting of eglandular trichomes (2–5 mm long), sometimes sparse .... 17. *D. hungaricum*

4′. Basal leaves ovate to ovate-elliptic; indumentum of the adaxial surface of basal leaves mainly glandular, sometimes with eglandular trichomes (up to 2 mm) .... 24. *D. plantagineum*

5(3). Outer phyllaries 2.5–5 mm wide; petiole of basal leaves with well-marked veins, and sometimes persisting fibers at the base of the stem; margins of leaf blades slightly swollen, sometimes with white-tinted eglandular trichomes (up to 1 mm) .... 21. *D. oblongifolium*

5′. Outer phyllaries 1–3.5 mm wide; petiole of basal leaves without well-marked veins; margins of leaf blades flat, glabrous, glabrate or glandular .... 12. *D. falconeri*

6(2). At least ray cypselae black, with warty surface; plant branched in the upper part, usually with more than 2 capitula; basal leaves eglandular pubescent, with base of blade clearly cordate and margins entire to subentire .... 23. *D. pardalianches*

6′. All cypselae brown, red-brown, or olive-green; plants branched or not; basal leaves eglandular or glandular pubescent or glabrous, with base of blade cordate, subcordate, or truncate and margins entire or dentate 7

7(6). Outer phyllaries ciliate (cilia not glandular) 8

7′. Outer phyllaries not ciliate 10

8(7). Rhizome woody to somewhat woody, glabrous ..... 9. *D. columnae*

8′. Rhizome fleshy, with pubescent nodes 9

9(8). Basal leaves with ovate blades, subcordate to truncate at base ..... 24. *D. plantagineum*

9′. Basal leaves with reniform to widely ovate blades, cordate to subcordate at base ..... 22. *D. orientale*

10(7). Rhizome fleshy with short trichomes on nodes, sometimes scarce and absent on the oldest nodes 11

10′. Rhizome woody to somewhat woody, glabrous 12

11(10). Upper part of stem and phyllaries glabrous or with short-stalked glandular trichomes (up to 0.3 mm), sometimes also with scattered eglandular trichomes (up to 0.4 mm); plants bearing more than 2 capitula; receptacle glabrous ..... 7. *D. cataractarum*

11′. Upper part of stem with long-stalked glandular trichomes (up to 5 mm), sometimes also with eglandular trichomes and short-stalked glandular trichomes; plants bearing 1 to 6 capitula; receptacle glabrous or pubescent ..... 6. *D. carpetanum*

12(10). Leaves with pinnate-actinodromous venation; upper part of stem and base of phyllaries generally with long-stalked glandular trichomes, the gland markedly obconical; sometimes with adventitious roots and sometimes branched near the base ..... 18. *D. kamaonense*

12′. Leaves with actinodromous venation; upper part of stem and phyllaries glabrous, with eglandular or glandular trichomes, but if glandular, the gland not obconical; plants without adventitious roots and branched in the upper part of stem 13

13(12). Stem leafy (more than 6 cauline leaves); middle and upper cauline leaves generally longer than the adjacent internodes; basal leaves and lower cauline leaves generally absent at flowering time; receptacle generally pubescent ..... 2. *D. austriacum*

13′. Stem not leafy (less than 6 cauline leaves); middle and upper cauline leaves generally shorter than the adjacent internodes; basal leaves and lower cauline leaves sometimes present at flowering time; receptacle glabrous to glabrate 14

14(13). Plants with a single capitulum (exceptionally 2 to 3); basal leaves dentate; petiole of basal leaves 0.5–2 mm wide ..... 9. *D. columnae*

14′. Plants with two to several capitula; basal leaves dentate to entire; petiole of basal leaves more than 2 mm wide, sometimes with a sheath more than 3 cm long 15

15(14). Basal leaves with a reniform blade and dentate margins; phyllaries covered with sericeous uniseriate eglandular trichomes (0.2–0.4 mm); rhizome moniliform, covered with scarious remains or fibers ..... 4. *D. cacaliifolium*

15′. Basal leaves ovate to widely ovate with cordate to subcordate base or reniform, margins dentate to entire; phyllaries glabrous, pubescent (eglandular or glandular), but not sericeous; rhizome not moniliform 16

16(15). Upper part of stem with long-stalked glandular trichomes or pubescent 17

16′. Upper part of stem glabrous to glabrate or with very short white eglandular trichomes restricted to the base of capitula 19

17(16). Phyllaries with subulate apex and dark-colored longitudinal veins ..... 25. *D. reticulatum*

17′. Phyllaries with acute but not subulate apex, veins not dark-colored 18

18(17). Upper part of stem and upper cauline leaves with white multiseriate glandular and/or eglandular trichomes (0.5–3 mm), sometimes scattered, sometimes also glandular ..... 11. *D. dolichotrichum*

18′. Upper part of stem generally glandular and without white multiseriate eglandular trichomes ..... 19. *D. macrophyllum*

19(16). Base of capitula with short white eglandular trichomes (ca. 0.2 mm); margins of phyllaries sometimes slightly fimbriate or glandular ..... 16. *D. haussknechtii*

19′. Base of capitula glabrous; margins of phyllaries entire ..... 20. *D. maximum*

20(1). Corollas with pale yellow to green tints; rays linear (0.5–1.8 mm wide); phyllaries erect, triangular-subulate, generally longer than rays; pappus consisting of one row of thin capillary bristles, caducous (at least in ray flowers); lower stems sometimes with adventitious roots ..... 26. *D. stenoglossum*

20′. Corollas yellow; rays elliptic to obovate-elliptic (1.2–4.5 mm wide); phyllaries erect to patent or patent, generally shorter than rays; pappus with more than one row of trichomes, not caducous (sometimes poorly developed in ray flowers); lower stems without adventitious roots 21

21(20). All cauline leaves sessile; plants bearing several capitula ..... 10. *D. corsicum*

21′. At least lower cauline leaves petiolate; plants bearing one to several capitula 22

22(21). Rhizomes with very short trichomes on nodes, generally covered by scarious remains of basal leaves, these sometimes scarce 23

22′. Rhizomes glabrous 27

23(22). Stems generally more than 50 cm; basal leaves with cordate to subcordate base; plants bearing several capitula; base of capitula glabrous or with short-stalked glands, generally scattered ..... 7. *D. cataractarum*

23′. Stems generally less than 50 cm; basal leaves with subcordate, truncate or attenuate base; plants bearing one to several capitula; base of capitula with eglandular or long-stalked glandular trichomes 24

24(23). Leaf margins mainly glandular, sometimes also with scattered eglandular trichomes 25

24′. Leaf margins with eglandular trichomes, these sometimes scarce 26
25(24). Pappus of ray flowers well developed, similar to pappus of disk flowers; cypselae of disk flowers pubescent, sometimes with glands .... 15. *D. grandiflorum*
25′. Pappus of ray flowers poorly developed; cypselae of disk flowers mainly glandular .... 6. *D. carpetanum*
26(24). Leaf margins scarcely hirsute (acute, stiff, multiseriate eglandular trichomes 0.5–2.5 mm), sometimes also with short-stalked glands, scattered (Fig. 3C–E) 14. *D. glaciale*
26′. Leaf margins pubescent (tangled, hyaline, uniseriate eglandular trichomes longer than 1 mm), sometimes also with hirsute scattered eglandular trichomes and short-stalked glands (Fig. 3F–H) .... 8. *D. clusii*
27(22). Basal leaves with cordate base .... 5. *D. carpaticum*
27′. Basal leaves with truncate, attenuate, or subcordate base 28
28(27). Phyllaries with blunt apex that bears a sessile gland .... 13. *D. gansuense*
28′. Phyllaries with acute apex, without a sessile gland 29
29(28). Base of capitula with long-stalked glandular trichomes (1–5 mm); plants bearing one capitulum .... 3. *D. briquetii*
29′. Base of capitula glabrous or with short-stalked glandular trichomes (up to 1.5 mm), scattered; plants bearing 1 to 4 capitula .... 1. *D. altaicum*

1. **Doronicum altaicum** Pall., Acta Acad. Sci. Imp. Petrop. 2: 271, tab. 16. 1779. *Aronicum altaicum* (Pall.) DC., Prodr. 6: 320. 1838. *Arnica altaica* (Pall.) Turcz., Bull. Soc. Imp. Naturalistes Moscou 1: 95. 1838. TYPE: [Asia] "E Sumis montium altaicorum" [sine collector], ex herb. Pallas (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 801), BM!).

Plant up to 80 cm tall. *Rhizomes* somewhat woody, glabrous, generally with scaly leaf remains. *Stems* simple, sometimes branched at the upper part, leafy, with leaves all along the stem, internodes generally shorter than adjacent leaves. Indumentum of short-stalked glandular trichomes and eglandular trichomes (up to 1 mm), more abundant near the capitula, sometimes glabrate to glabrous. *Leaves* entire to slightly dentate. Basal leaves generally absent at flowering time; blade 5–8(10) × 2.5–3 cm, ovate, elliptic or obovate, with attenuate base, and blunt or subacute apex, with actinodromous to pinnate-actinodromous venation; petiole (2)7–10(27) cm long, 3–4(7) mm wide. Lower and middle cauline leaves (2.5)3–8(11.2) × (1)3–5(6) cm, similar to basal leaves or sessile, elliptic to obovate, sometimes widely ovate to suborbiculate, semi-amplexicaul, with blunt apex. Upper cauline leaves 2.5–7(8.5) × (0.5)0.2–4(5.5) cm, similar to middle cauline leaves or ovate-lanceolate and with subacute apex. Indumentum similar to the adjacent part of stem, sometimes glabrous. *Capitula* 1 to 4; (2.5)4–5 cm diam. including rays; involucre shorter than rays, (3)3.5–4.5 cm diam. *Phyllaries* herbaceous, (0.7)1–1.2(1.7) cm long, 1.2–2 mm wide, ovate-lanceolate to subulate. Indumentum similar to the upper part of stem, sometimes glabrate. *Receptacles* glabrous. *Flowers* with yellow corollas. Ray flower corollas 1.2–2.1 cm long, (1.5)2–3.5 mm wide, obovate-elliptic, apex with 2 or 3 teeth, sometimes toothless, acute or blunt. Disk flower corollas 4–5.5 × 2–2.5 mm. *Cypselae* dark brown, with smooth or slightly grooved surface, homomorphic, ca. 2.8 × 1 mm, generally glabrous, sometimes with scattered eglandular trichomes or glands. Pappus up to 5 mm, white to brown yellow-tinted. Chromosome number, $2n = 30^*$, 60 (Belaeva & Splivinsky, 1981, as *D. bargusiense* Serg.; *Goldblatt & Johnson, 1998, see comments below).

Illustrations. Pallas (1779: tab. 16); Figures 1G, 2G, H, 10A, B.

Distribution. Central Asia (Turkistan and Altai region to lake Baikal). Woods, meadows, and near watercourses, altitude 1300–3400 m (Fig. 11).

In central Asia there are some species morphologically similar to *Doronicum altaicum* (i.e., *D. briquetii*, *D. falconeri*, and *D. gansuense*). All of them have the same habit (solitary capitulum and mostly leafy stems with uniform leaves), but only one of these, *D. falconeri*, overlaps its area of distribution with *D. altaicum*. The character used to distinguish between these two species is the presence of a pappus in the ray flowers of *D. altaicum* versus its absence in *D. falconeri*. The remaining similar species are differentiated based on the indumentum (long trichomes on the base of capitulum in *D. briquetii* vs. short trichomes in *D. altaicum* (Fig. 10)), and on the apex shape of phyllaries, which is blunt (due to a sessile gland) in *D. gansuense* (Fig. 4B, C) and acute (lacking the sessile gland) in *D. altaicum*.

The citation of the chromosome number $2n = 30$ for *Doronicum altaicum* was found in Goldblatt and Johnson's (1998) index, but the original source for this data was not seen.

Selected specimens examined. KAZAKHSTAN. Lepsoi i Tentekom, 11 Sep. 1931, *Enden s.n.* (LE); Belogore, Tukschinskoe, 15 Aug. 1949, *Fedorov et al. s.n.* (LE); Alatau, *Richter 2772* (GH). RUSSIA. **Altay:** montes del Altai, Ayu-Kel, río Baijs, *Castroviejo & Valdés Bermejo 14032* (MA); Tigeretzkyi, 31 July 1891, *Krylov s.n.* (S); Tomskaya,

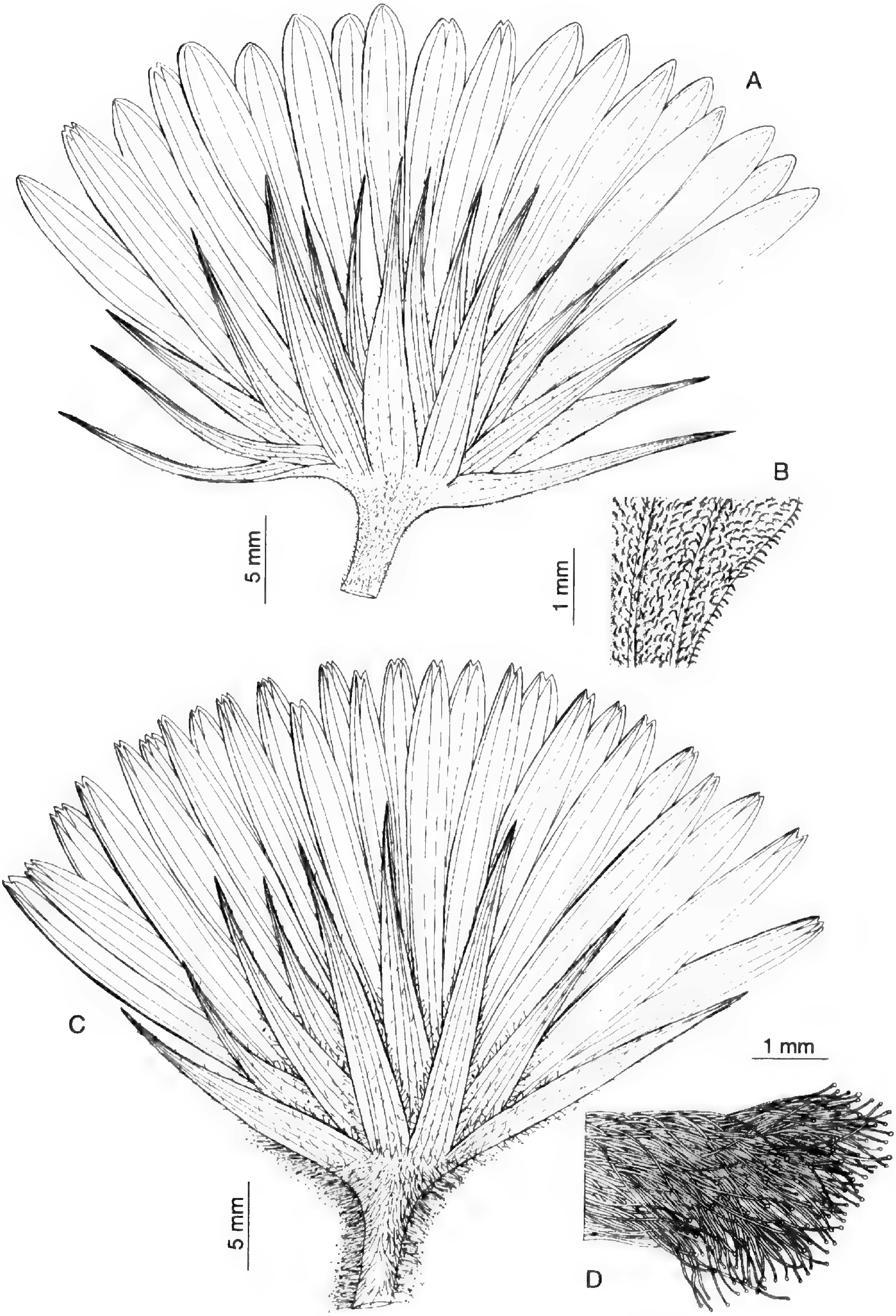

Figure 10. A, B. *Doronicum altaicum* (drawn from *Krasnoborov et al. 959*, K). —A. Capitulum. —B. Indumentum of the base of capitulum. C, D. *Doronicum briquetii* (drawn from *Rock 22380*, E). —C. Capitulum. —D. Indumentum of the base of capitulum.

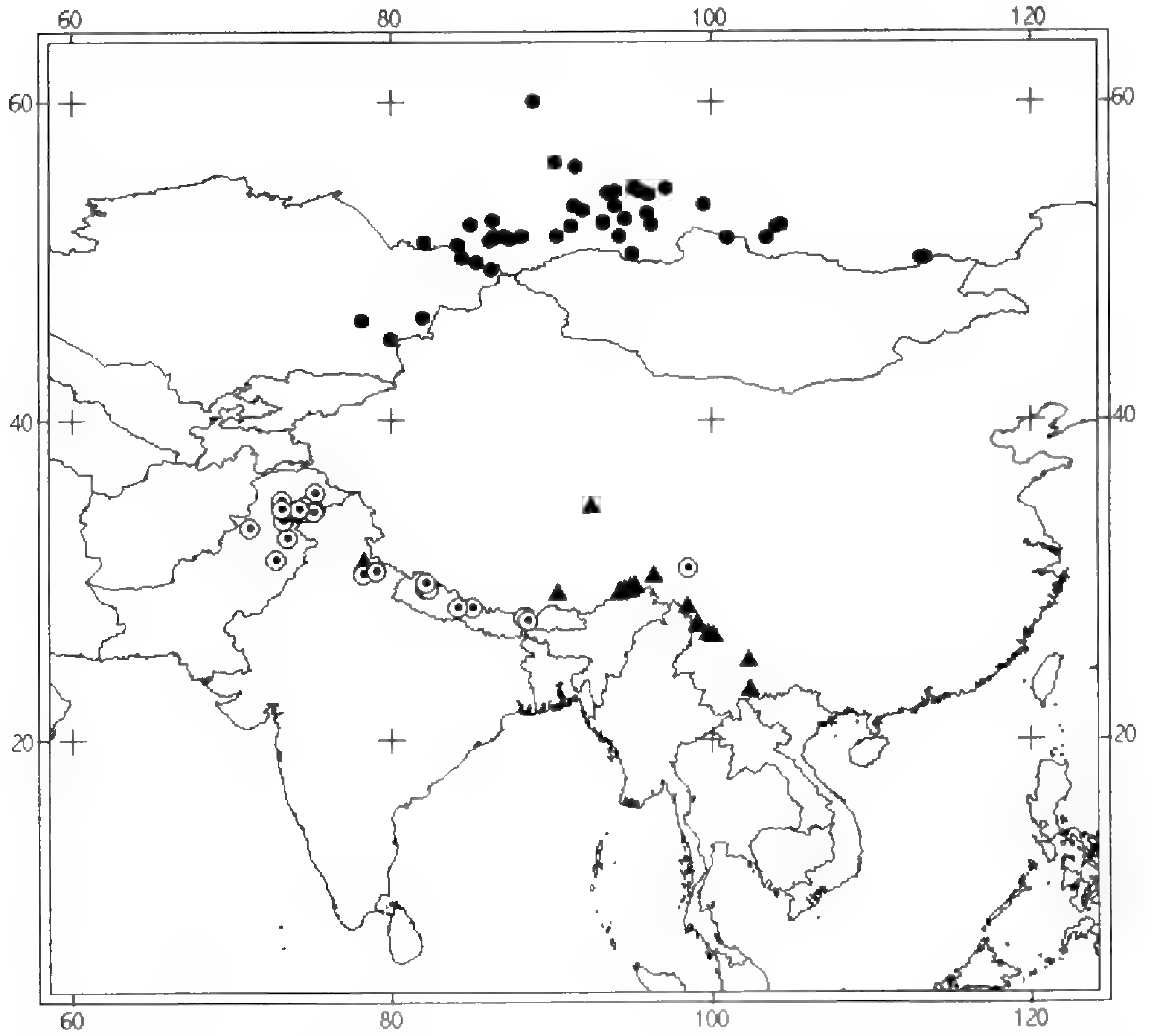

Figure 11. Distribution map for: *Doronicum altaicum* (●); *Doronicum briquetii* (▲); *Doronicum kamaonense* (⊙).

Bijskij, Inskoj, 16 July 1913, *Kuznetsov s.n.* (LE); Elekmonarskij, Chemal, Katuni, 12 July 1947, *Matveeva & Tkatchenko s.n.* (LE); Sumultinskije, 14 Aug. 1923, *Saposhnikov s.n.* (W); Gorno-Altaiskaya, Mt. Eshumo, lake Teletskoye, *Turesson 848* (UPS). **Buryatiya:** Sibiria, gubernium Ircutense, montes Sajan ad decursum superiorem fluviorum Ircut et Oka, 30 July 1902, *Komarov s.n.* (K, LE). **Chita:** Zabajkalskaya, Akshinskij, *Smirnov 314* (LE). **Irkutsk:** Verkhove, Belki, Agulskie, 7 Aug. 1949, *Fedorov et al. s.n.* (LE); Inzhneud, *Golovnin 158* (LE); Baikal, Kultuk Khamar-Dazang, *Poplavskaja, Tzinzerling & Sukačev 2069* (LE); Enisejskaya, Kanskij, Dor Gutara, 14 June 1912, *Troickij s.n.* (LE). **Krasnoyarsk:** Shushenskij, Stanitsya Olenya, 12 July 1963, *Cherepnin & Laletina s.n.* (LE); Yangi, Belogore, Tukshinskoe, *Fedorov et al. 219* (LE); Sayan, Aradanki, 20 July 1967, *Gudoshnikov & Dirin s.n.* (LE); Kuraginskij, Mt. Moskva, 22 Aug. 1962, *Krasnoborov & Ershova s.n.* (LE); Sayan, Alan, Taskalik, Dzhoya i Klaya, *Krasnoborov 8179* (LE); Severnaya, Aradanskago, 8 June 1892, *Krylov s.n.* (LE); Enisejskaya gub., Kanskij, *Kuznetsov 927* (LE); Sidi, Sisima i Mani, Eniseya, *Volkov 185* (LE). **Tuva:** Sayan, Sayanskij, Aldi-Ishkina, *Krasnoborov 8172* (LE); Baj-Tajhinskij, Sajan, Kara-Chol', Jerjitajha, *Krasnoborov, Hrubov & Jakovleva 959* (K); Pij-Khemskij, Sayan, Uyukskij Azyut, Chakpak, *Lomonosova & Shaulo 732* (LE); Todzhinskij, Ak-Attig-Khol, Ulug-Taiga, 3 July 1971, *Vidrina s.n.* (LE). **West Siberia:** Tomskaya, Zmeinogorsk, 15 June 1909, *Iljin s.n.* (LE).

2. Doronicum austriacum Jacq., Fl. Austriac. 2: 18, tab. 130. 1774. *Arnica austriaca* (Jacq.) Hoppe, in Sturm, Deutschl. Fl. 10: 16. 1814. TYPE: [sine collector] ex herb. Linnaeus (LINN n.º 1002.4!) (lectotype, designated by Pérez et al. (1997: 3)).

Plant up to 150(+) cm tall. *Rhizomes* woody to somewhat woody, glabrous, and generally without scaly or fibrous leaf remains. *Stems* generally branched in the upper part, leafy, internodes generally shorter than the adjacent leaves. Indumentum of glandular trichomes, uniseriate and multiseriate eglandular trichomes (up to 2 mm), sometimes only eglandular trichomes, sometimes glabrate, more abundant near the capitula. *Leaves* entire to slightly dentate. Basal leaves absent at flowering time, petiolate, ovate to orbicular, with cordate to subcordate base and blunt apex, with actinodromous venation. Lower and middle cauline leaves 6.5–19 × 4.5–12.5 cm, similar to basal leaves or sessile, fiddle-shaped, semi-amplexicaul. Upper cauline leaves 2.5–13 × 0.7–5 cm, ovate-lanceolate, generally with acute apex. Indumentum similar to the adjacent part of the stem. *Capitula* (1)2 to 16; 3–7 cm diam. including rays; involucre generally shorter than rays, 1.5–3.5 cm diam.; peduncles 1.5–16 cm long, 0.5–2 mm diam. *Phyllaries* herbaceous, sometimes slightly papery at the base or at the margins, ovate-subulate, generally with acute apex; the outer 0.5–1.8 cm long, 1.2–4 mm wide; the inner 0.6–1.4 cm long, 0.7–3 mm wide. Indumentum of glandular and eglandular trichomes, sometimes glabrous. *Receptacles* pubescent, rarely glabrate. *Flowers* with yellow corollas. Ray flower corollas (1.2)1.5–3.5 cm long, (1)2–4 mm wide, oblong-elliptic to obovate-elliptic; apex generally with 3 teeth. Disk flower corollas 4.5–5.5 × 1–1.5 mm. *Cypselae* brown-tinted to olive-green, with grooved-reticulate surface, dimorphic. Cypselae of ray flowers 2–3.5 × 0.7–1.3 mm, glabrous or glabrate, without pappus. Cypselae of disk flowers 1.5–3 × 0.7–1 mm, pubescent, with white pappus 3–6 mm. Chromosome number $2n = 60$ (Skalinska, 1950; Baksay, 1956; Kuzmanov & Ancev, 1973; Strid & Franzén, 1983).

Illustrations. Jacquin (1774: tab. 130); Hegi (1928: 713, fig. 421); Săvulescu (1964: pl. 189, fig. 2); Bolòs & Vigo (1995: 839); Figures 1C, 12A–D.

Distribution. Europe (Carpathians, Balkans, Alps, Apennines, and eastern Pyrenees). Cultivated and naturalized at least in Great Britain. Growing in forest, meadows, near watercourses, and in moist rocky places, altitude 300–2200 m (Fig. 13).

Doronicum austriacum is a variable species with regard to phyllary shape, number of capitula and, in particular, type and abundance of indumentum. Based on the protologue, where there is no mention of the presence of glandular trichomes, Pérez et al. (1997) characterized it as a non-glandulose species, and accordingly, they chose a lectotype with no glandular trichomes. Although their lectotypification is technically correct, the distinguishing characters given for this species are erroneous since many populations from Greece are glandular. According to Pérez et al. (1997), these glandular populations might be included in *Doronicum carpetanum,* a different species as recognized here. Although both *D. austriacum* and *D. carpetanum* are similar, they basically differ in type of rhizome (fleshy and scarcely pubescent in *D. carpetanum* vs. woody to somewhat woody and glabrous in *D. austriacum*), but not in type of indumentum, which can be glandular in both species. These two species do not overlap their areas of distribution.

In addition, there are two other species morphologically similar to *Doronicum austriacum* (i.e., *D. cataractarum* and *D. pardalianches*) that may overlap their distributions with *D. austriacum.* The characters to distinguish between those species and *D. austriacum* are the type of rhizome (fleshy rhizomes in *D. pardalianches* vs. woody to somewhat woody in *D. austriacum*), the fruit color at maturity (black cypselae in *D. pardalianches* vs. brown-tinted to olive-green in *D. austriacum*), the indumentum on the base of capitulum (scarce and short (up to 0.4 mm long) to glabrate in *D. cataractarum* vs. pubescent (glandular or not) in *D. austriacum* (Fig. 12A, E, F)), and the heterocarpy in *D. austriacum* versus homocarpy (sometimes pappus poorly developed) in *D. cataractarum.*

Selected specimens examined. ALBANIA. **Korçë:** Ostrovicë, Moskopolë, *Alston & Sandwith 2119* (BM, K). ANDORRA. Pla de Sorteny, 7 Aug. 1948, *Losa & Montserrat s.n.* (BCF). AUSTRIA. **Kärnten:** Plöcken pass, 4 Aug. 1972, *Lousley s.n.* (BM). **Niederösterreich:** Lackenhof, 19 July 1933, *Cufodontis s.n.* (W). **Oberösterreich:** Oberar Gosausee, Vachsteingebiet, *Baschant H531* (B). **Salzburg:** Boden der Alpen Lofers, *Spitzel 972* (B, NY). **Steiermark:** valle Schaftal prope urbem Graz, July 1907, *Fritsch s.n.* (BM, E). **Tirol:** Zillertaler Alps, Gerlostal-Zillertal, *Kramer 1366* (NY). BULGARIA. **Blagoevgrad:** Mt. Pirin, lago Okomo, 27 July 1993, *Carrasco, Burgaz & Martín-Blanco s.n.* (MACB). **Kyustendil:** Rila planina, in valle Bistritza, *Schneider & Bergmann 881* (B, BM, K, MO). **Smolyan:** Pamprovo, Smolyan, *Jury & Thornton-Wood 9876* (BM). **Veliko Tŭrnovo:** Béla Cherkva, July 1909, *Stříbrný s.n.* (K). CZECHOSLOVAKIA. Tatra Magna, Velká Studená, 14 July 1925, *Suza s.n.* (K, MO). FRANCE. **Cantal:** L'Ombrière, commune de Raulhac, *Puyfol 4925* (BM, NY). **Loire:** Pilat, route de Pélussin au Crêt de l'Oeillon, *Barbezat 1834* (K). **Pyrénées-Orientales:** Cerdagne, massif du Carlite à Matanègre, *Sennen 3968* (BC, MA). GERMANY. **Oschatz:** Hirschkamm, Gusenke, Wermsdorf, 12 Aug. 1878, *Oborny s.n.* (K). GREECE. **Makedhonía:** Pisoderion, *Alston & Sandwith 441* (BM, K); Kastoria, *Polunin 8268* (E); Kozani, Mt. Pieria, supra Kataphygion, *Rechinger 17881* (B, G, K, W). HUNGARY. Szepes, Zips, Hohern-Tatra, Kleineskohlbachtal, 28 Aug. 1911, *Nyárády s.n.* (MA). ITALY. **Toscana:** Etruria, Firenze, Boscolungo, 25 Aug. 1917, *Fiori s.n.* (B, BM, K). POLAND. **Olkusz:** Klucze, Biala, 31 May 1971, *Frey & Sztyler s.n.* (LE, NY). ROMANIA. **Gorj:** Oltenia, valle Gilort, Rînca, 28 June 1972, *D. & M. Cîrtu s.n.* (B, BM, MA, NY). UKRAINE. **Ivano-Frankovskaja:** Verkhovinskij, Chernij Cheremosh, Popadinets, *Geltman et al. 1650* (LE). **Zakarpatskaja:** Veritskij, 19 June 1950, *Igoshina s.n.* (LE). YUGOSLAVIA. **Crna Gora:** between Ramna and Banasnica, *Edmonson 328* (BM, E). **Hrvatska:** Gerovo, *M. F. & S. G. Gardner 2586* (BM); Žumberačka gora circa Sošice, 17 May 1874, *Vukotinović s.n.* (ZA). **Makedonija:** Gebiet der Mala Rupa, *Biesalski 469* (B); Golešnica-planina, Begova, *Bornmüller 4269* (B). **Slovenija:** Pekel-Schluchbi Ohonica südlich Borovnica, südwestlich von Lubljana, 28 May 1966, *Lippert s.n.* (LE).

3. **Doronicum briquetii** Cavill., Annuaire Conserv. Jard. Bot. Genève 10: 197. 1907. TYPE: India. Kumaun, near the Kalam glacier, *J. F. Duthie 3066* (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 802), G!).

Plant up to 80 cm tall. *Rhizomes* somewhat woody, glabrous, generally with scaly leaf remains. *Stems* not branched, leafy completely up entire stem, internodes generally shorter than adjacent leaves. Indumentum of short- and long-stalked glandular trichomes (1–5 mm), more abundant near the capitula, rarely only eglandular trichomes. *Leaves* entire to slightly dentate. Basal leaves generally absent at flowering time; blade (1.2)2–4 × (0.9)1–2(3) cm wide, ovate, elliptic or obovate, with

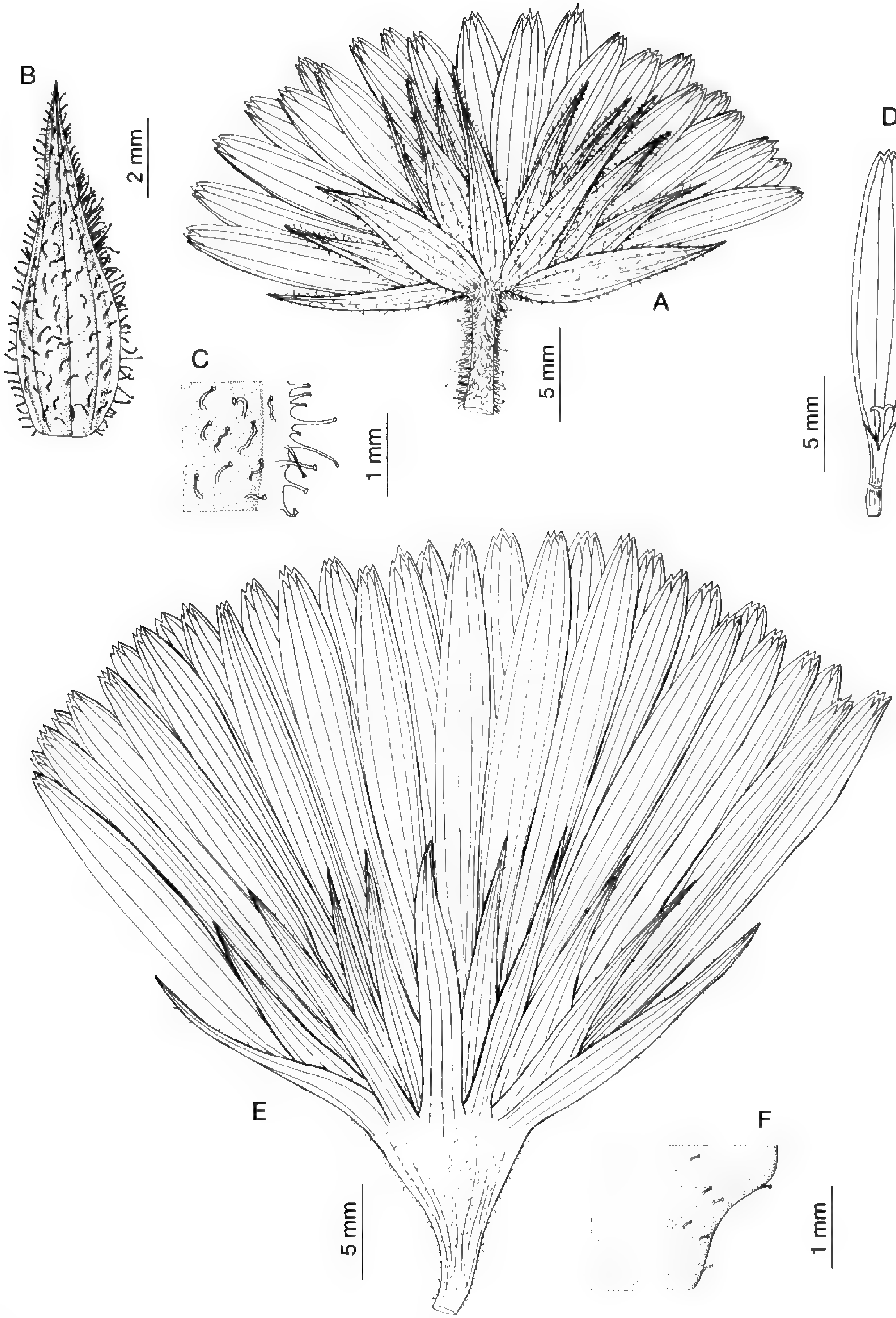

Figure 12. A–D. *Doronicum austriacum* (drawn from *Strid et al. 18585*, B). —A. Capitulum. —B. Phyllary. —C. Indumentum of a phyllary. —D. Ray flower. E, F. *Doronicum cataractarum* (drawn from *Höpflinger s.n.*, BM). —E. Capitulum. —F. Base of the capitulum.

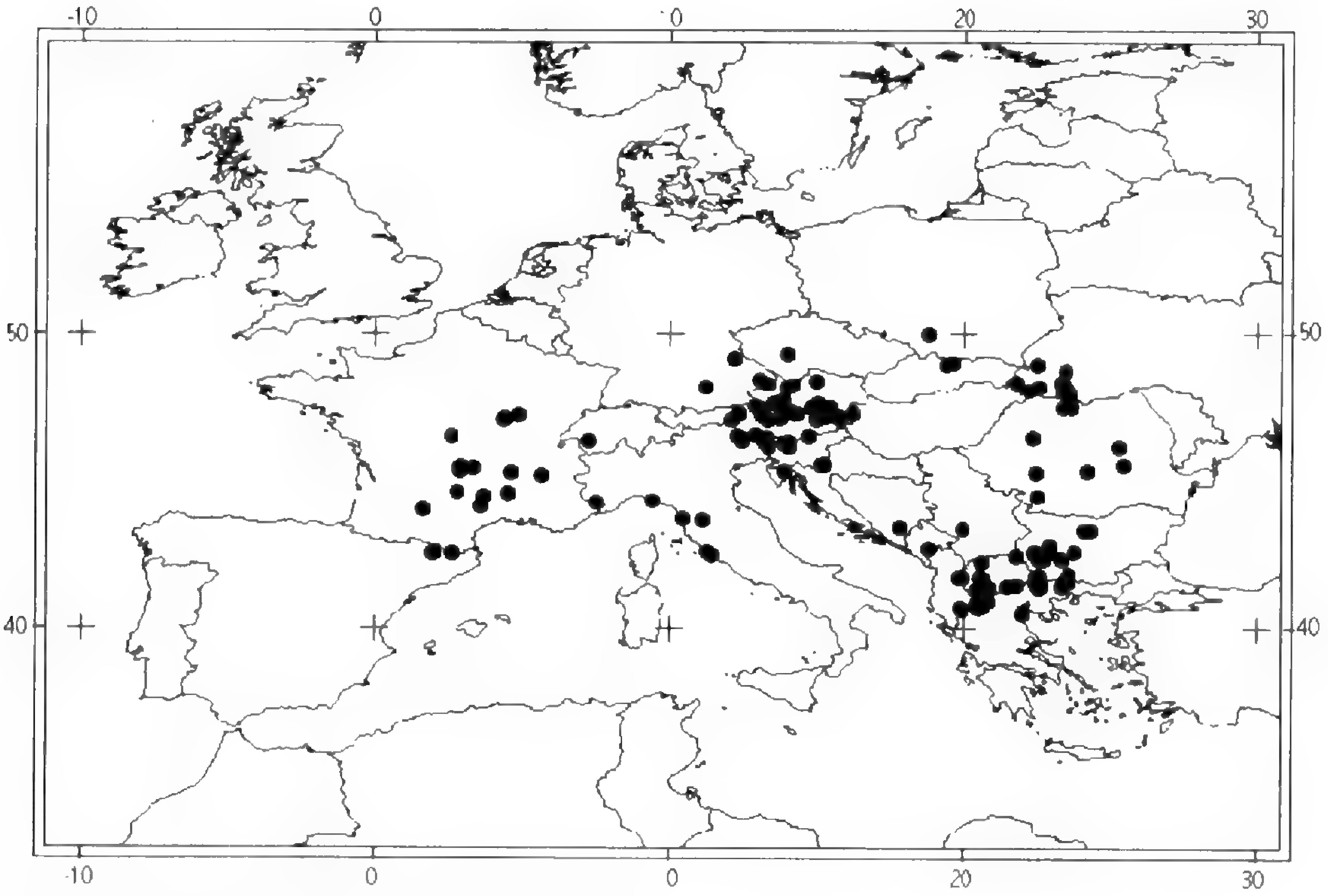

Figure 13. Distribution map for *Doronicum austriacum.*

attenuate base, and blunt or subacute apex, with actinodromous to pinnate-actinodromous venation; petiole (0.9)1.5–3(5) cm long, (1)2–3(5) mm wide. Lower and middle cauline leaves (3)4–9(12.3) × (0.5)1.5–3.5(6.2) cm, sessile, ovate-elliptic to obovate-elliptic, semi-amplexicaul. Upper cauline leaves 2–4(5.5) × (0.3)1–2(3) cm, similar to middle cauline leaves or ovate. Indumentum similar to the adjacent part of stem, sometimes with glandular margins. *Capitula* solitary, (4)5–7(8) cm diam. including rays; involucre shorter than rays, rarely equaling them, (3)3.5–4.5(5) cm diam. *Phyllaries* herbaceous; the outer (1)1.5–2(2.5) cm long, 1.5–2.5(3) mm wide; the inner 1–2 cm long, 1–2(3.5) mm wide, ovate-lanceolate to subulate. Indumentum similar to the upper part of stem, more abundant at the base. *Receptacles* glabrous, rarely with scattered short-stalked glandular trichomes. *Flowers* with yellow corollas. Ray flower corollas (1.8)2–3 cm long, 2–3(3.5) mm wide, obovate-elliptic, apex generally with 2 or 3 teeth. Disk flower corollas 3.5–5 × 1.5–2 mm. *Cypselae* dark brown, homomorphic, 1.5–3 × 1 mm, glabrous, sometimes with scattered eglandular trichomes or glands. Pappus up to 6 mm, white to yellow-tinted. Chromosome number unknown.

Illustrations. Figures 2E, F, 10C, D.

Distribution. Central and southern China (provinces of Sichuan, Tibet-Qinghai, and Yunnan), and the Himalayas. Open moist rocky places and woods, altitude 3000–5000 m (Fig. 11).

As already discussed (see comments for *D. altaicum*), there is a group of central Asian species morphologically very similar to each other. *Doronicum briquetii* is included in this group, but its distribution may only overlap that of *D. falconeri.* The character used to distinguish between them is the heterocarpy in *D. falconeri* versus the homocarpy in *D. briquetii.* There are other species outside this morphological group, *D. kamaonense* and *D. stenoglossum,* that also overlap part of their area of distribution with *D. briquetii.* But *D. stenoglossum* is quite different from *D. briquetii* in noticeable characters (i.e., numer of capitula, color, shape and size of ray flowers, and shape and size of phyllaries) as well as *D. kamaonense* (i.e., number and size of capitula and type of indumentum). (See also comments under *D. gansuense.*)

Selected specimens examined. CHINA. **Sichuan:** Mt. Konka, Risonquemba, Konkaling, *Rock 16834* (E, K, GH, MO, NY, W); Dongrergo, *Smith 3270* (S, UPS); Sikang, Kangting, Tachienlu, Tapaoshan, *Smith 11473* (S, UPS). **Tibet-Qinghai:** Mekong–Salween divide behind Tzekon, *Forrest 666* (E); Bei-lua Shan, Mekong–Yangtze divide, *Forrest 13164* (E); Oika-gur-pu, Mekong–Salween divide, Sarong, *Forrest 14526* (BM, E, K, W); Dü Chu valley, Pashö, Kham, *Hanbury-Tracy 22* (BM); Doshong La, *Kingdon Ward 5866* (E); Sobbé La, *Kingdon Ward 12125* (BM); Tha Chu valley, *Kingdon Ward 19592* (BM, E, UPS); Kongbo, Tsangpo valley, Lusha Chu, *Ludlow et al. 4752* (BM, E, UPS); Kongbo, Tsangpo valley, Pero La, *Ludlow et al. 5205* (BM, E, UPS); Kongbo, Tsangpo valley, Doshong La, *Ludlow et al. 5258* (BM, E, UPS); Tsanang La, near Paka, *Ludlow et al. 5870* (BM, E, UPS); above Showa Dzong, Pome, *Ludlow et al. 13148* (BM, E, UPS); Ba La, Pasum Chu, Kongbo, *Ludlow et al. 13955* (BM, E, G, UPS); Budi Tsepo La, Kongbo, *Ludlow et al. 15261* (BM, E, UPS); Kongbo, Nyoto Sama, *Ludlow et al. 15604* (BM,

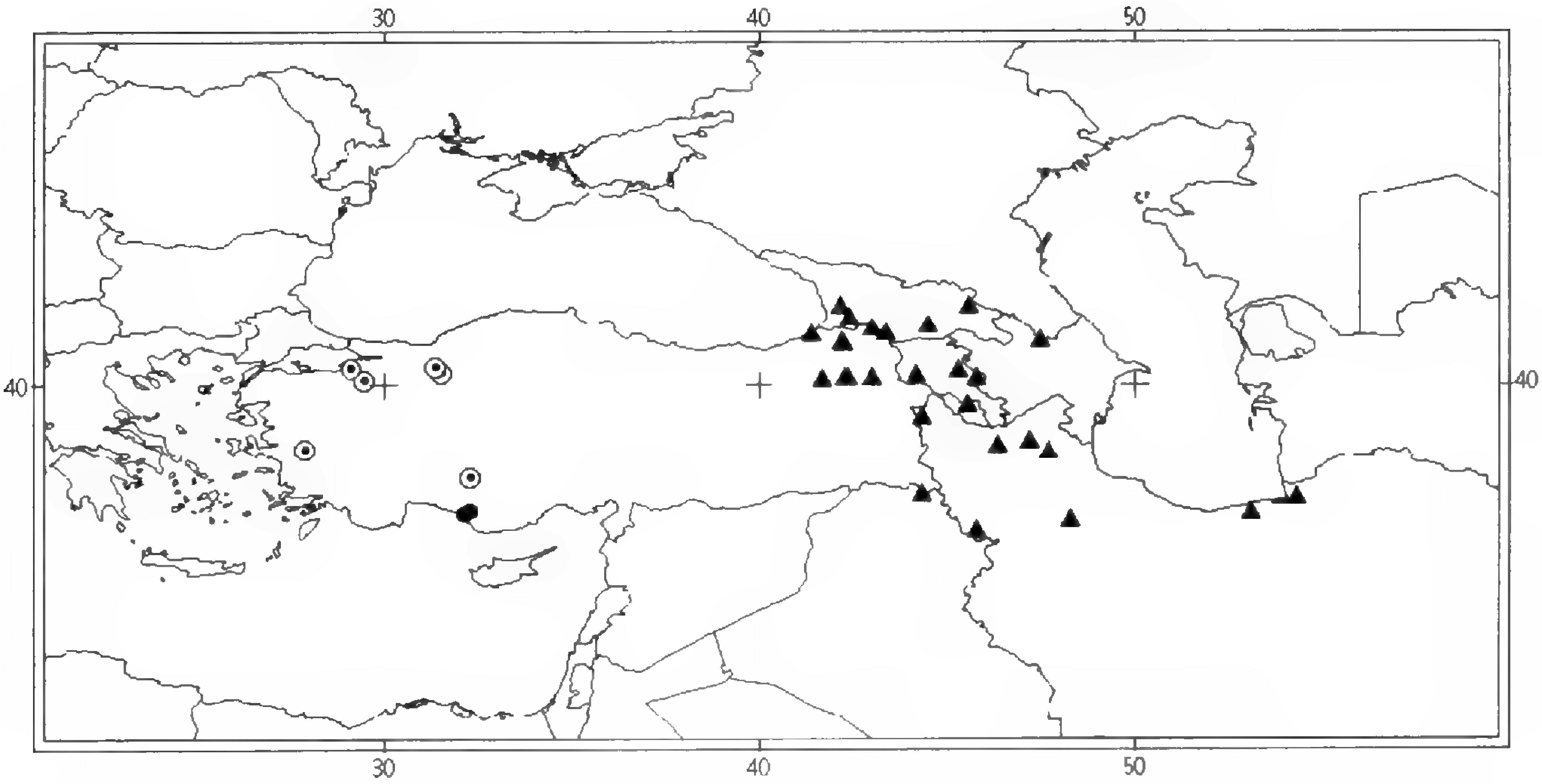

Figure 14. Distribution map for: *Doronicum cacaliifolium* (●); *Doronicum dolichotrichum* (▲); *Doronicum reticulatum* (⊙).

E); Tsarung, Wuli-la, *Rock 22380* (GH, NY); Bálti, Thále La to Bagmaharál, *Schlagintweit 5962* (GH). **Yunnan:** Chien Chuan & Hsi valleys, *Forrest 7662* (E); Chungtian plateau mountains, *Forrest 13009* (E); Mekong–Salween divide, *Forrest 14413* (E, K); Mekong–Yangtze divide, A-wa, *Forrest 25695* (E, G, K); Wei-Hsi area, *Forrest 30434* (BM, E); inter fluvios Lu-djiang Salween et Djiou-djiang, in jugi Tschiangschel, *Handel-Mazzetti 1765* (W); A-tun-tse, 3660 m, *Kingdon Ward* (E); Lichiang, *McLaren 167D* (BM); Mt. Habashan, Ndaku, Likiang range, Yangtze drainage basin, *Rock 9681* (E, GH, K); mountains of Hung-po, Tung-chu-ling, *Rock 22891* (BM, E, GH, K, MO, NY); Dokerla, A-tun-tze, *Wang 64905* (GH); Mekong–Salween divide, Sila, *Yü 22268* (E, GH). INDIA. **Uttar Pradesh:** Tilvie-Garheval, Chimpul opposite Bandarpunch, *Duthie 849* (G, K).

4. Doronicum cacaliifolium Boiss. & Heldr., Diagn. Pl. Orient. ser. 1, 11: 31. 1849. TYPE: Turkey. Taurus, Mt. Gheï-Dagh, [*T. Heldreich*] *1043* (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 802), G-BOIS!; isotype, BM!).

Plant up to 50(+) cm tall. *Rhizomes* woody to somewhat woody, glabrous, moniliform, sometimes with fibrous leaf remains. *Stems* branched in the upper part, leaves mainly distributed in the lower middle, upper internodes generally longer than the adjacent leaves. Indumentum of uniseriate eglandular trichomes (0.2–0.4 mm), sometimes with short-stalked glandular trichomes and a few multiseriate eglandular trichomes, more abundant near the capitula and sometimes glabrous at the base. *Leaves* dentate. Basal leaves generally present at flowering time; blade 5.5–8 × 5–9 cm, orbicular to suborbicular, with cordate base and blunt apex, with actinodromous venation; petiole 8–19.5 cm long, 2–2.3 mm wide. Lower cauline leaves with blade ca. 6 × 8 cm; petiole ca. 6.5 cm long, 1.5 mm wide, similar to basal leaves. Middle and upper cauline leaves 3–4 × 1.2–5.5 cm, sessile, fiddle-shaped, semi-amplexicaul, the upper leaves ovate to bract-like. Indumentum similar to the adjacent part of the stem or glabrate. *Capitula* 2 to 13; ca. 3.5 cm diam. including rays; involucre shorter than rays, 1–2 cm diam. *Phyllaries* herbaceous, 6–7 × 2.5 mm, ovate-elliptic to ovate-subulate, generally with acute apex. Indumentum of uniseriate eglandular trichomes (0.2–0.4 mm), sericeous, abundant. *Receptacles* glabrous or glabrate. *Flowers* with yellow corollas. Ray flower corollas ca. 1.7 cm long, 2 mm wide, oblong-elliptic, apex generally with 3 teeth. Disk flower corollas ca. 5 mm long. *Cypselae* brown-tinted, with slightly reticulate surface, dimorphic. Cypselae from ray flowers 2–3 × 0.9–1.2 mm, glabrous or glabrate, without pappus. Cypselae from disk flowers 2–2.7 × 0.9–1 mm, pubescent (eglandular trichomes), with pappus white-tinted, 3–4 mm. Chromosome number unknown.

Illustrations. Figures 5A–D, 7C, 8B.

Distribution. Southern Turkey (Antalya and Konya provinces). Growing in shady rocky places, elevation 1800–2300 m (Fig. 14).

Most of the *Doronicum* species from Turkey are similar morphologically (rhizomes woody to somewhat woody and glabrous, several heterocarpic capitula, and a few but very large leaves). These species have a few diagnostic characters; sometimes only one of these is consistent, making species identification difficult. *Doronicum cacaliifolium* is one of the best delimited species within this morphological group, and is also the one that has the most restricted area of distribution. The distinctive characters are its exclusive type of rhizome (moniliform) and the shape, size, and type of indumentum of phyllaries (Figs. 5A–C, 8B). Geographically, the closest species within its morphological group is *D. reticulatum* from western Turkey (Figs. 14, 26), but this one has different shape, size, type of indumentum, and color of phyllaries (Fig. 26E–G). Outside this morphological group, only *D. orientale* may overlap its area of distribution with *D. cacaliifolium* (Figs. 14, 27), but there are noticeable characters to distinguish between them. In addition to the difference in their phyllary characters (Fig. 5A–C, E–G), rhizomes from both species are quite different (fleshy and pubescent in *D. orientale* vs. woody to somewhat woody, glabrous, and moniliform in *D. cacaliifolium*).

Selected specimens examined. TURKEY. **Antalya:** Ak dag, *Davis 14381* (E, G, K, MO, W); Ak dag, *Davis 14551* (K). **Konya:** Hadim-Alanya, *Duman 5581* (GAZI).

5. Doronicum carpaticum (Griseb. & A. Schenk) Nyman, Syll. Fl. Eur. Suppl.: 1. 1865. *Aronicum scorpioides* var. *carpaticum* Griseb. & A. Schenk, Arch. Naturgesch. 18: 342. 1852. *Aronicum carpaticum* (Griseb. & A. Schenk) Schur, Verh. Mitth. Siebenbürg. Vereins Naturwiss. Hermannstadt 10: 137. 1859, as "*carpathicum.*" *Doronicum grandiflorum* subsp. *carpaticum* (Griseb. & A. Schenk) Rouy, Rev. Bot. Syst. Géogr. Bot. 1: 53. 1903. TYPE: not located; protologue citation: "Siebenbürgen: in der alpinen Region der südlichen Karpaten, z. B. am Szurul (Fuss), nach Schur bis 7000′ austeigend."

Plant up to 50 cm tall. *Rhizomes* woody to somewhat woody, glabrous, sometimes with leaf remains forming dark scales on nodes. *Stems* not branched, generally scape-like. Indumentum of uniseriate, multiseriate, and glandular trichomes, scattered, glabrous in the lower part. *Leaves* dentate to slightly dentate. Basal leaves generally present at flowering time; blade 2–4 × 2–4 cm, orbicular to broadly ovate with cordate base and with blunt or subacute apex, with an actinodromous venation that sometimes tends to be acrodromous; petiole 4–11 cm long, 0.5–1 mm wide. Lower and middle cauline leaves 3–6 × 1.4–3 mm, similar to basal leaves or sessile, fiddle-shaped, semi-amplexicaul. Upper cauline leaves 1.5–3 × 0.9–2.5 cm, ovate-elliptic to ovate-lanceolate, sometimes bract-like. Indumentum of white-tinted scattered multiseriate eglandular trichomes (up to 1.5 mm), uniseriate eglandular trichomes mainly on the edge of the blade, and scarce short-stalked glandular trichomes. *Capitula* solitary, 3.5–5 cm diam. including rays; involucre shorter than rays, 2.5–3 cm diam. *Phyllaries* herbaceous, 0.9–1.2 cm long, 1.5–4 mm wide, ovate-subulate; margins sometimes ciliate, with acute, stiff and equidistant multiseriate eglandular trichomes (up to 0.6 mm long). Indumentum mainly glandular, and sometimes with uniseriate eglandular trichomes. *Receptacles* glabrous or almost glabrous. *Flowers* with yellow corollas. Ray flower corollas 1.4–2.2 cm long, 2–2.8 mm wide, oblong-elliptic, apex generally with 3 teeth. Disk flower corollas up to 4 mm long. *Cypselae* (not seen at maturity), brown-tinted, homomorphic, 1.5 × 0.8 mm, scarcely pubescent (eglandular trichomes) to glabrate. Cypselae from ray flowers sometimes with a poorly developed pappus. Pappus up to 3.5 mm, white-tinted. Chromosome number $2n = 60$ (Tasenkevitch et al., 1989).

Illustrations. Săvulescu (1964: pl. 98, fig. 3).

Distribution. Europe (Carpathians). Meadows, shady rocky places, and near watercourses, altitude 1200–2200 m (Fig. 15).

The type material of *Aronicum scorpioides* DC. var. *carpaticum* Griseb. & A. Schenk could not be found, and although the protologue matches the diagnostic features of this taxa, its identity here is tentative and the formal synonymy needs to wait until clarification.

Doronicum carpaticum and *D. columnae* are closely related species, which differ only by their heteromorphic versus homomorphic fruits, respectively. Simonkai (1886) described a new species, including specimens without well-developed pappus: *Aronicum barcense.* Later, this name was considered by Cavillier (1911) to be a hybrid species (*D. carpaticum* × *D. columnae*). I cannot confirm the hybrid origin for this taxon and therefore include it as a synonym of *D. carpaticum* due to the presence of pappus, although poorly developed.

Selected specimens examined. BULGARIA. **Plovdiv:** Kalofer, *Wagner 77* (G). HUNGARY. **Beszteroze–Naszód:** monte Clisia ad Rodnam, 25 Aug. 1902, *Degen s.n.* (LE). ROMANIA. **Maramureş:** montis Hagy Pietrosz, 5 July 1907, *Filarszky & Jávorka s.n.* (LE). **Neamţ:** Mt. Ceahlau, 1900 m, 11 July 1922, *Grintescu s.n.* (BM, G, K, MO, S). **Fogaras:** Bîlea Cascada, 17 Aug. 1960, *Liebenow s.n.* (B); Transsilvaniae alpes Arpasenses, Vurtop, 9 Aug. 1883, *Simkovics s.n.* (B); Vertop et Vertopul, *Simonkai 1816* (B, BM, G, K, S); circa lacum Bîlea, supra pag. Arpás, 23 July 1914, *Tuzson s.n.* (B). UKRAINE. **Ivano–Frankovskaja:** Verkhovinskij r-n, r. Chernij Cheremosh,

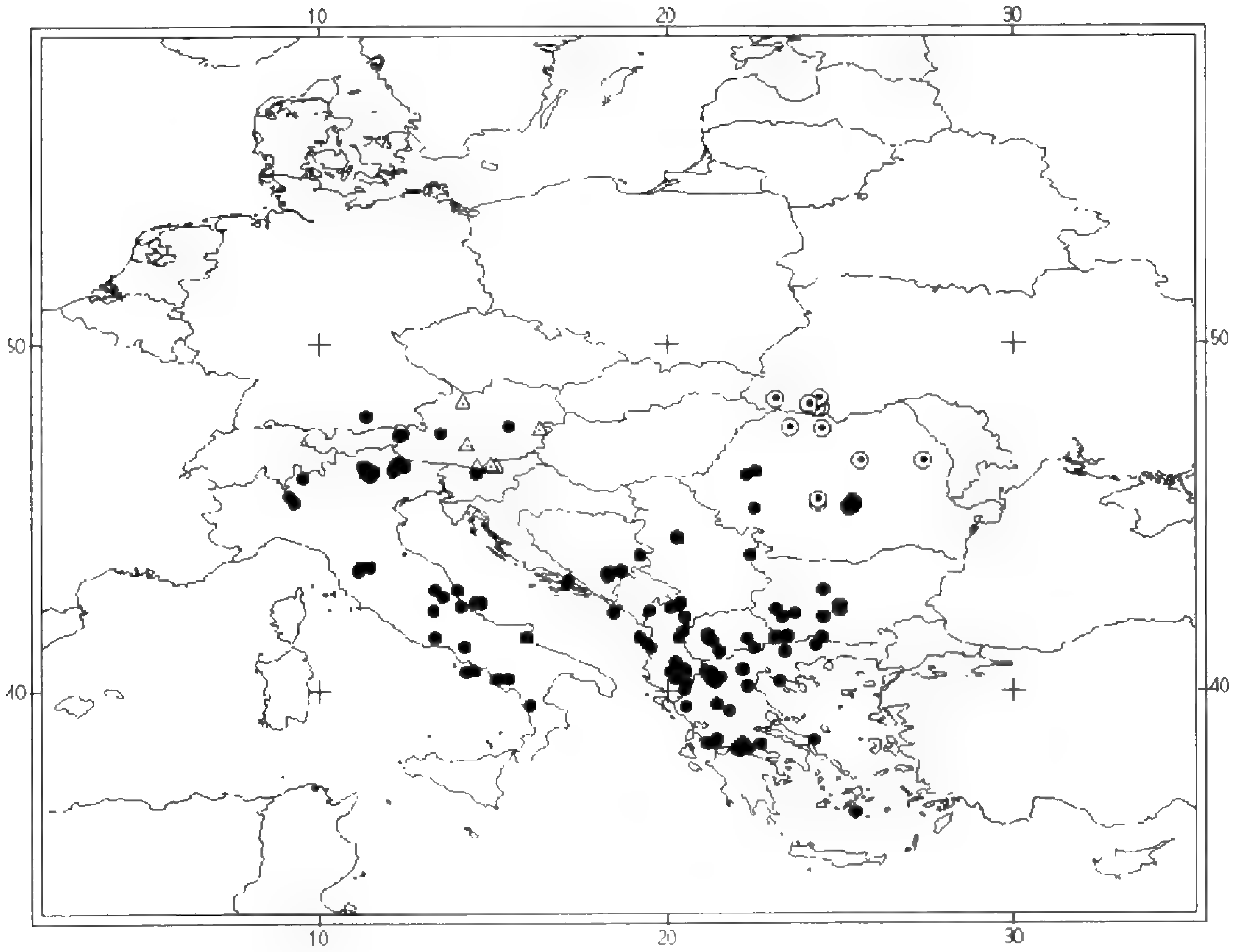

Figure 15. Distribution map for: *Doronicum carpaticum* (⊙); *Doronicum cataractarum* (△); *Doronicum columnae* (●).

ur. Popadinets, *Geltman et al. 1636* (LE); Verkhovinskij r-n, 30–33 km k Yuyuz ot Verkhovini g. Chivchin, *Geltman et al. 1880* (LE); Karpati khr. Chernogora, 7 July 1964, *Ivanina s.n.* (LE). **Stanislavskaja:** Mt. Goberla, Rakhovskij r-n, 13 July 1958, *Fodor s.n.* (LE). **Zakarpatskaja:** Rakhovskij r-n, 27 July 1976, *Borodina et al. s.n.* (LE). YUGOSLAVIA. **Srbija:** Mt. Gnila greda supra vallem Dobrido dispersum, propе Trebinje, Aug. 1891, *Vandas s.n.* (K).

6. **Doronicum carpetanum** Boiss. & Reut. ex Willk. & Lange, Prodr. Fl. Hispan. 2: 108. 1870. *Doronicum plantagineum* subsp. *carpetanum* (Boiss. & Reut. ex Willk.) Rouy, Rev. Bot. Syst. Géogr. Bot. 1: 34. 1903. TYPE: Spain. Madrid, sierra de Guadarrama, Peña Lara, July 1858 [*P. E. Boissier s.n.*] (lectotype, designated by Chacón (1987: 267), COI-WILLK!).

Plant up to 120 cm tall. *Rhizomes* fleshy, with shining white-tinted short trichomes on nodes, sometimes with buds, and generally with leaf remains. *Stems* branched in the upper part or simple. Indumentum of multiseriate eglandular trichomes (up to 1.5 mm) and short-stalked glandular trichomes at the middle part of stem, and also long-stalked glandular trichomes (up to 5 mm) at the upper part of the stem, sometimes glabrous at the base, sometimes mainly glandular, more abundant near the capitula. *Leaves* entire to slightly dentate. Basal leaves generally absent at flowering time; blade 2.5–9 × 2–7 cm, ovate to orbicular, with subcordate to truncate base and blunt or subacute apex, with actinodromous venation; petiole (1.5)3.5–13.5 cm long, (0.5)1–3 mm wide. Lower and middle cauline leaves 3–11(15) × 1.5–7.5(10) cm, similar to basal leaves or sessile, fiddle-shaped, sometimes ovate, semi-amplexicaul. Upper cauline leaves 1–7.5(9) × 0.2–4 cm, ovate-lanceolate, sometimes bract-like. Indumentum similar to the adjacent part of the stem. *Capitula* 1 to 6, 2.5–6(7) cm diam. including rays; involucre shorter than rays, 1.5–4 cm diam.; peduncles (0.7)1–16(21) cm long, 0.5–2.5 mm wide. *Phyllaries* herbaceous, ovate-subulate to narrowly elliptic; the outer 0.8–2.2 cm long, 1–3(3.5) mm wide; the inner 0.7–2.1 cm long, 0.5–2.5 mm wide. Indumentum of long-stalked glandular trichomes and sometimes also with eglandular trichomes. *Receptacles* pubescent or glabrous. *Flowers* with yellow corollas. Ray flower corollas (1.2)1.5–3 cm long, 1.7–5 mm wide, obovate-elliptic, apex generally with 3 teeth. Disk flower corollas 4–7(8) × 1–2.5 mm. *Cypselae* brown-tinted to olive-green, with grooved-reticulate to somewhat warty surface, dimorphic or homomorphic. Cypselae from ray flowers (1.5)3–4.3 × 0.7–1.5 mm, glabrous or glabrate, with or without pappus. Cypselae from disk flowers (1.5)2–4 × 0.2–

1.3 mm, with eglandular or glandular trichomes, with pappus. Pappus (2.5)4–5.5 mm, white. Chromosome number $2n = 60$, 120 (Fernandes & Queirós, 1971, as *D. pardalianches*).

Illustrations. Figures 1F, 6C, 16.

Distribution. North of the Iberian peninsula and mountains in central Spain and eastern Portugal. Open moist rocky places, cliffs, screes, woods, and near watercourses, from sea level to 2500 m elevation (Figs. 17, 18).

This taxon can be confused with *Doronicum austriacum* due to their similarities (e.g., habit, leaves, capitula, habitat; see comments under this species), but the presence of this latter species in the Iberian peninsula is only based on a few gatherings more than 50 years old from Andorra and Cerdagne in the Pyrenees. This species must be searched for in these areas in the Pyrenees.

Doronicum carpetanum is variable with regard to quantity of indumentum, size, ploidy level, and presence of pappus in the ray flowers. Variation in these characters follows geographical patterns, and in most cases these populations can be distinguished morphologically. Hybridization events both contemporary and in the origin of one of the subspecies here recognized (subsp. *diazii*) cannot be discarded in this group. However, further investigation is needed, and at present, taxonomic recognition at the subspecific level is preferred to handle the intraspecific variability (see also comments for *D. grandiflorum*). In the present taxonomic treatment the following subspecies are recognized:

KEY TO SUBSPECIES OF *DORONICUM CARPETANUM*

1. Receptacle glabrous or glabrate; plants generally bearing one capitulum 2
1′. Receptacle pubescent; plants bearing one to several capitula 3
2(1). Cypselae of disk flowers with mostly glandular trichomes .... 6b. *D. carpetanum* subsp. *diazii*
2′. Cypselae of disk flowers with mostly eglandular trichomes .... 6c. *D. carpetanum* subsp. *kuepferi*
3(1). Lower and middle cauline leaves with eglandular trichomes, sometimes also with glandular trichomes ..... 6d. *D. carpetanum* subsp. *pubescens*
3′. Lower and middle cauline leaves glabrous or with mainly glandular trichomes .... 6a. *D. carpetanum* subsp. *carpetanum*

6a. **Doronicum carpetanum** subsp. **carpetanum**

Plants glabrous or glabrate, generally glandular in the upper part, sometimes also with scattered eglandular trichomes. *Receptacle* pubescent. *Cypselae* dimorphic, the inner with eglandular trichomes. Chromosome number $2n = 120$ (Chacón, 1987).

Illustrations. Figures 1F, 16A–D.

Distribution. Massifs in the center of the Iberian peninsula in Spain, plus some scattered populations in the north. Open moist rocky places and near watercourses, altitude 900–2300 m (Fig. 17).

Selected specimens examined. SPAIN. **Castilla–La Mancha:** Guadalajara, Cantalojas, Tejera Negra, 20 June 1985, *Burgos & Cardiel, s.n.* (MACB). **Castilla y León:** Ávila, Solana de Ávila, laguna del Duque, arroyo Malillo, *Álvarez & Yagüe 931* (MA); Salamanca, Candelario, sierra de Béjar, 28 June 1979, *Amich et al. s.n.* (MA); Burgos, Pineda de la Sierra, pico Mancillas, 14 July 1984, *Benedí et al. s.n.* (MA, MAF); Ávila, sierra de Majarreina au dessus de Tornavacas près Plasencia, *Bourgeau 2508* (COI-WILLK, K, MA, NY); Ávila, El Calvitero, 16 July 1979, *Carrasco et al. s.n.* (MACB); Zamora, Puebla de Sanabria, sierra Calva de Porto, 19 July 1973, *Casaseca s.n.* (MA); Burgos, pico Trigaza, *Castroviejo & Fernández Quirós 5868* (MA); Ávila, El Barco de Ávila, sierra del Barco, *Castroviejo et al. 7133* (MA); Segovia, Cerezo de Arriba, pico del Lobo, *Castroviejo et al. 10709* (MA); Burgos, valle de Valdelaguna, sierra de Neila, Mt. Haedillo, *Gil Zúñiga & Alejandre 225–88* (MA); Ávila, Hoyos del Espino, Las Chorreras, *Luceño & Vargas 208* (MA); Soria, sierra Cebollera, rio Racioncillo, 5 July 1979, *Mendiola s.n.* (MACB); Soria, sierra Carbonera, 6 July 1979, *Mendiola s.n.* (MACB); Soria, El Bercolar, sierra Cebollera, 17 July 1980, *Mendiola s.n.* (MACB); Soria, Laguna Negra de Urbión, 15 July 1985, *Navarro s.n.* (MAF); Ávila, Cepeda de la Mora, La Serrota, El Nevero, 5 July 1982, *Rivas Martínez et al. s.n.* (MAF); Zamora, San Martín de Castañeda, El Cabezo, 22 June 1987, *Roa s.n.* (MA); Ávila, sierra de Gredos oriental, puerto de Mijares, July 1984, *Sánchez-Mata s.n.* (MAF); Ávila, Navalguijo, garganta de los Caballeros, 3 June 1990, *Sardinero s.n.* (MAF); Soria, Santa Inés, Majadarrubia, *Segura Zubizarreta 12525* (MA); Ávila, San Martín del Pimpollar, *Segura Zubizarreta 22654* (MA). **Comunidad de Madrid:** Sierra de Guadarrama, laguna de Peñalara, *Almaraz et al. 802* (MA). **La Rioja:** Ezcaray, cerro de San Lorenzo, *Almaraz et al. 805* (MA); puerto de Piqueras, *Sandwith 5684* (K); Zaldierna, sierra de la Demanda, pico Torocuervo, 14 July 1992, *Urrutia s.n.* (MA). **País Vasco:** Álava, La Leze, sierra de Alzarria, 1 July 1985, *Uribe-Echebarría s.n.* (MA). **Principado de Asturias:** lagos de Saliencia, *Luceño & Vargas 2569′* (MA).

6b. **Doronicum carpetanum** subsp. **diazii** (Pérez Morales & Penas) Álv. Fern., Novon 11: 294. 2001. *Doronicum diazii* Pérez Morales & Penas, Lagascalia 15: 155, fig. 2. 1990. TYPE: Spain. León, Abelgas, Puerto Bermejo, July 1974, *C. Romero s.n.* (holotype, LEB 4290 not seen).

Plant up to 70 cm tall, glabrous or glabrate in the lower part, glandular at the middle and upper part, sometimes also with scarce eglandular trichomes. *Stems* generally simple. Basal leaves

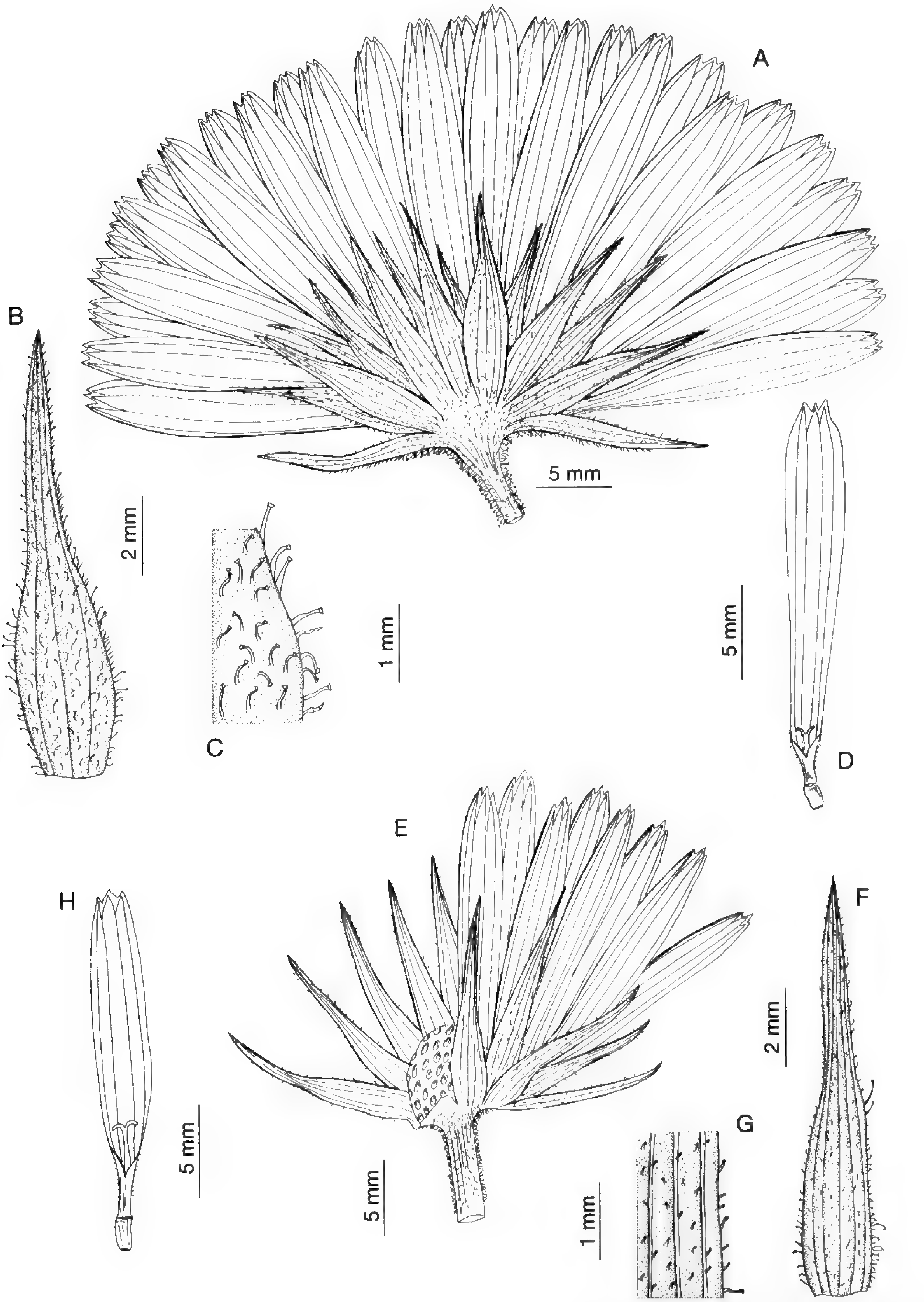

Figure 16. A–D. *Doronicum carpetanum* subsp. *carpetanum* (drawn from *Luceño & Vargas 208,* MA). —A. Capitulum. —B. Phyllary. —C. Indumentum of a phyllary. —D. Ray flower. E–H. *Doronicum carpetanum* subsp. *kuepferi* (drawn from *Navarro & Valle s.n.,* MA). —E. Capitulum. —F. Phyllary. —G. Indumentum of a phyllary. —H. Ray flower.

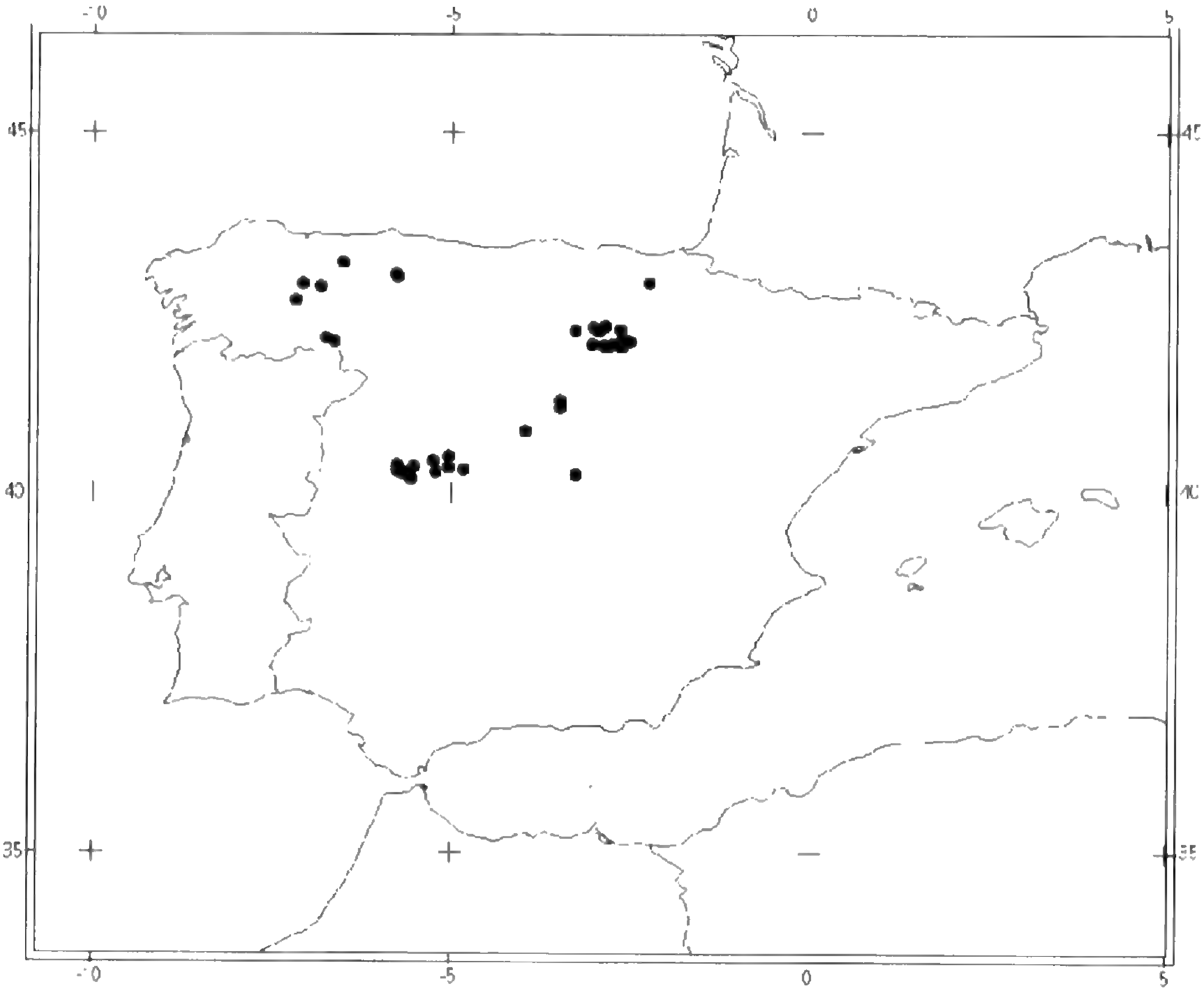

Figure 17. Distribution map for *Doronicum carpetanum* subsp. *carpetanum*.

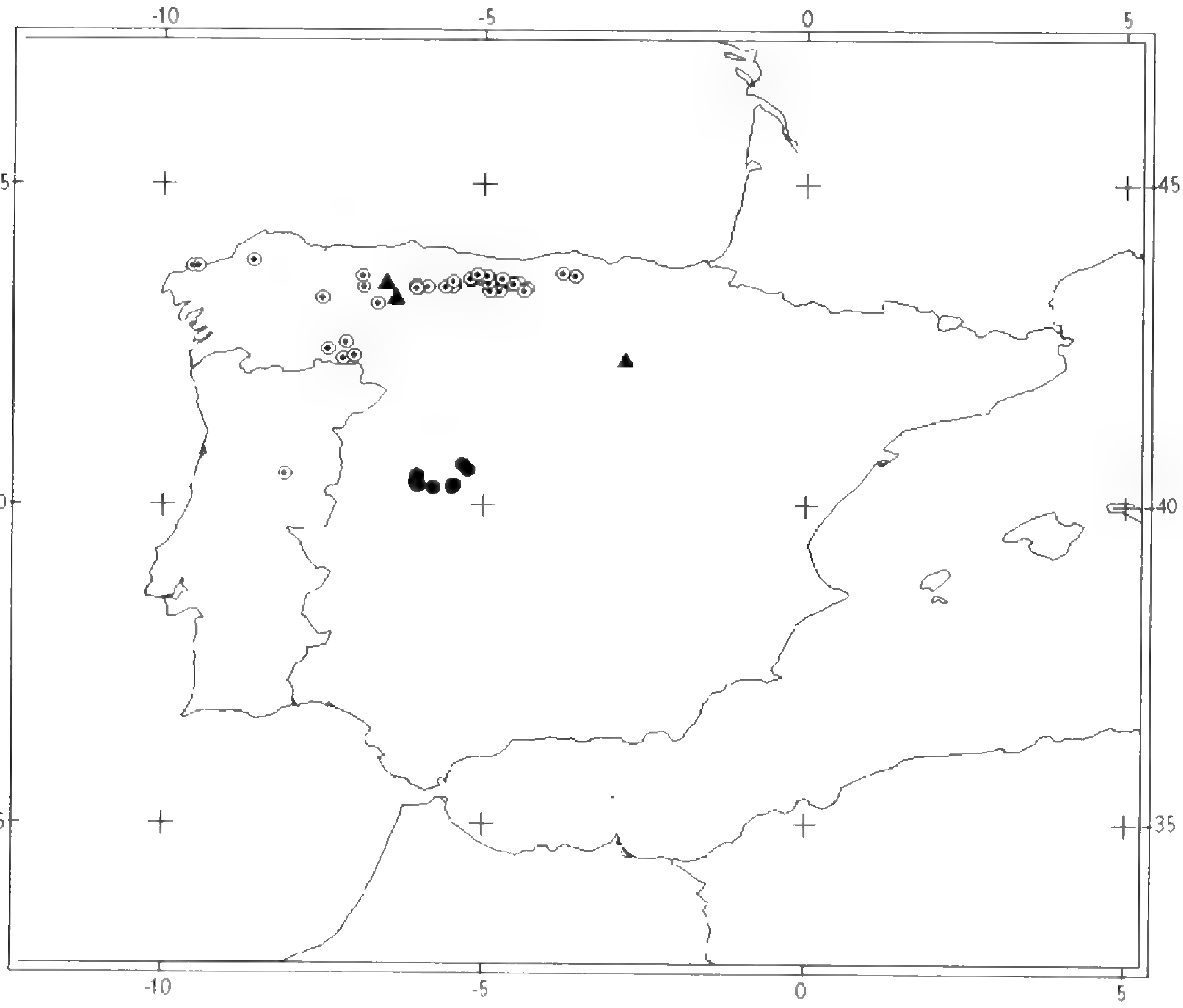

Figure 18. Distribution map for: *Doronicum carpetanum* subsp. *diazii* (▲); *Doronicum carpetanum* subsp. *kuepferi* (●); *Doronicum carpetanum* subsp. *pubescens* (⊙).

sometimes present at flowering time; blade 4–6 × 3–4 cm; petiole 6.5–10 cm long, 1–2 mm wide. Lower and middle cauline leaves 3.5–8.5 × 2–6 cm. Upper cauline leaves 1.2–5.5 × 0.5–2 cm. *Capitula* 1 to 2(4), 3–4 cm diam. including rays; involucre 2–2.5 cm diam. *Phyllaries* 0.9–1.4 cm long, 1.5–3 mm wide. *Receptacles* glabrous to glabrate. Ray flower corollas 1.3–1.9 cm long, 3–3.5 mm wide. *Cypselae* generally dimorphic, ray flowers sometimes with pappus poorly developed. The inner cypselae mainly glandular. Chromosome number $2n = 60$ (new count reported here: Spain. León, Riolago, *Álvarez et al. 924* (MA 611192)).

Illustrations. Pérez & Penas (1990: 156, fig. 2); Figure 6C.

Distribution. Northern Iberian peninsula (Cantabrian range) and central-eastern ranges (Picos de Urbión) in Spain. Open moist rocky places and screes, altitude 1700–2100 m (Fig. 18).

Although type material was not available, plants collected at the type locality and also several specimens identified by Pérez (one of the authors) as *Doronicum diazii* were studied.

Selected specimens examined. SPAIN. **Castilla y León:** León, San Emiliano, Riolago, pico Penouta, *Álvarez et al. 924* (MA); Soria, Sierra de Urbión, *Ceballos & Vicioso 1136* (MA); Soria, Covaleda, macizo de Urbión, laguna Larga, *Gil Zúñiga & Alejandre 320/93* (MA); Soria, sierra de Urbión, Laguna Negra, *Harrold & McBeath 240* (E); Soria, del pico de Urbión al pico Tres Cruces, 26 July 1982, *Navarro s.n.* (MAF); León, peña Penouta, Abelgas, 27 July 1988, *Puente & Pérez Morales s.n.* (MA, MAF); Soria, sierra de Urbión, *Sandwith 5340* (K). **Principado de Asturias:** Somiedo, braña de Murias Longas, 25 Aug. 1985, *Aedo s.n.* (MA).

6c. Doronicum carpetanum subsp. **kuepferi** (R. Chacón) Álv. Fern., Novon 11: 294. 2001. *Doronicum kuepferi* R. Chacón, Anales Jard. Bot. Madrid 43: 269. 1987. TYPE: Spain. Cáceres, sierra de Majarreina, cerca del pico del Telégrafo, 7 Aug. 1946, *S. Rivas Goday s.n.* (holotype, MA 155587!; isotypes, MA 348763!, MAF 11944!).

Plants up to 70 cm tall, glabrous or glabrate in the lower part, glandular at the middle and upper part, sometimes also with scarce eglandular trichomes. *Stems* generally simple. Blade of basal leaves 2.5–5 × 2–6 cm; petiole 4.5–14 cm long, 1–2 mm wide. Lower and middle cauline leaves 3–6 × 1.5–4 cm. Upper cauline leaves 1–3 × 0.2–1.5 cm. *Capitula* 1 to 2(4), 2.5–5.5 cm diam. including rays; involucre 2–3.5 cm diam. Phyllaries 0.9–1.7 cm long, 0.5–2.5 mm wide. *Receptacles* glabrous to glabrate. Ray flower corollas 1.4–1.7 cm long, 1.7–4 mm wide. *Cypselae* dimorphic, ray flowers sometimes with pappus poorly developed. The inner cypselae mainly with eglandular trichomes. Chromosome number $2n = 60$ (Chacón, 1987; recounted and confirmed here: Spain. Ávila, Portilla de Talamanca, *Álvarez & Yagüe 933* (MA 611198)).

Illustrations. Figure 16E–H.

Distribution. Central-western of the Iberian peninsula (Sierra de Gredos). Open moist rocky places, screes, and near watercourses, altitude 1800–2500 m (Fig. 18).

Selected specimens examined. SPAIN. **Castilla y León:** Ávila, Solana de Ávila, Portilla de Talamanca, *Álvarez & Yagüe 933* (MA); Ávila, El Calvitero, 16 July 1979, *Carrasco et al. s.n.* (MA); Salamanca, sierra de Béjar, El Trampal, 4 Aug. 1977, *Casaseca et al. s.n.* (MA); Ávila, laguna de Gredos, sierra de Gredos, *Dresser 846* (E); Salamanca, sierra de Béjar, El Trampal, *Nieto Feliner et al. 2736* (MA); Ávila, Villatoro, La Serrota, 5 July 1997, *Palacio et al. s.n.* (MA); Salamanca, Trampal, 27 July 1900, *Pau s.n.* (LY); Salamanca, sierra de Béjar, Hoyamoro, 22 Aug. 1983, *Rico s.n.* (MACB); Ávila, Sierra de Gredos, El Morezón, 26 July 1958, *Rivas Goday s.n.* (MAF); Ávila, sierra de Béjar, La Ceja, 26 July 1989, *Rivas Martínez et al. s.n.* (MAF); Ávila, puerto de Villatoro-Villanueva del Campillo, 20 May 1982, *Sánchez-Mata et al. s.n.* (MAF); Salamanca, sierra de Béjar, La Hoya, circo de la Peña Negra, 14 July 1990, *Sardinero s.n.* (MAF); Ávila, sierra de Tormantos, Puerto Castilla, circo de El Barco, 23 Aug. 1990, *Sardinero s.n.* (MAF); Salamanca, Candelario, Calvitero, *Valdés Bermejo et al. 5812* (MA). **Extremadura:** Cáceres, sierra Majarreina, cerca del Pico del Telégrafo, 7 Aug. 1946, *Rivas Goday s.n.* (MA, MAF).

6d. Doronicum carpetanum subsp. **pubescens** (C. Pérez Morales, A. Penas, F. Llamas & C. Acedo) Aizpuru, in Aizpuru et al., Munibe 50: 11. 1998. *Doronicum pubescens* C. Pérez Morales, A. Penas, F. Llamas & C. Acedo, Lazaroa 14: 7. 1994. TYPE: Spain. León: puerto del Pontón, 12 June 1992, *A. Penas & M. E. García s.n.* (holotype, LEB 47120 not seen).

Plants mainly with eglandular trichomes at least in the middle part, also glandular in the upper part. Blade of basal leaves 4–6.5 × 3.5–5.5 cm; petiole 7–9 cm long. *Capitula* 4.5–5(7) cm diam. including rays. *Receptacles* pubescent. *Cypselae* dimorphic, the inner with eglandular trichomes. Chromosome number $2n = 120$ (Chacón, 1987, as *D. carpetanum*).

Distribution. Northern Iberian peninsula in Spain and central Portugal (Serra da Estrela). Open moist rocky places, cliffs, woods, and near watercourses, altitude 50–2200 m (Fig. 18).

Although type material of *Doronicum pubescens* was not seen, plants collected at the type locality as well as several specimens identified by Pérez (one of the original authors) as *Doronicum pubescens*, were studied.

Selected specimens examined. PORTUGAL. **Beira Alta:** Manteigas, Serra da Estrela, Mondeguinho, *Álvarez et al. 1296* (MA). SPAIN. **Cantabria:** pico Tresmares, 25 July 1982, *Aedo s.n.* (MA); Mt. Gulatrapa, Mazandrero, 2 July 1983, *Aedo s.n.* (MA); puerto de Piedrasluengas, *Álvarez 923* (MA); Vega de Liébana, Ledantes, puertos de Pineda, *Álvarez & Yagüe 941* (MA); Fuente Dé, *Harrold & McBeath 158* (E); Vega de Pas, puerto de Estacas de Trueba, *Pardo de Santayana & Morales 1690* (MA); Soba, puerto de La Sía, 27 May 1990, *Patino et al. s.n.* (MA); El Henar, 13 July 1977, *Rivas Martínez et al. s.n.* (MAF); Curavacas, *Valdés Bermejo et al. 4233* (MA). **Castilla y León:** Palencia, Cardaño de Arriba, *Aedo et al. 3631b* (MA); León, Encinedo, laguna de La Baña, *Álvarez 927* (MA); León, Oseja de Sajambre, puerto del Pontón, *Álvarez & Yagüe 936* (MA); León, Boca de Huérgano, Coriscao, arroyo Luriana, *Álvarez & Yagüe 937* (MA); León, Puebla de Lillo, 18 July 1974, *Andrés s.n.* (MAF); León, Nocedo, Cueto Ancino, 18 July 1951, *Borja s.n.* (MAF); León, circo Cebollero, puerto de San Isidro, 16 July 1974, *Casaseca & Fernández Díaz s.n.* (MA); León, puerto de las Señales, 27 July 1979, *Casaseca et al. s.n.* (MA); León, entre le col de Panderruedas et Posada de Valdeón, *Charpin 15017* (B); León, Palacios del Sil, pico Catoute, 15 Aug. 1997, *Martín Blanco s.n.* (MACB); León, puerto de Pandetrave, 16 June 1981, *Rivas Martínez et al. s.n.* (MAF); Zamora, Portilla del Padornelo, 24 July 1972, *Valdés Bermejo s.n.* (MA). **Galicia:** Lugo, Cervantes, monte Camporredondo, Degrada, pico Tres Obispos, *Álvarez et al. 926* (MA); La Coruña, Caaveiro, 25 Apr. 1981, *Amich et al. s.n.* (MA); La Coruña, Puente Carreira, 29 May 1953, *Bellot s.n.* (MA, MACB, MAF); Orense, sierra do Invernadeiro, Cabeza de Val do Cabreiro, 10 July 1973, *Castroviejo s.n.* (MA); Orense, Viana del Bollo, montaña de Ramilo, *Merino 18* (MA); La Coruña, Malpica, As Portelas, 19 June 1994, *Soñora s.n.* (SANT). **Principado de Asturias:** supra Pajares, 14 July 1892, *Lomax s.n.* (MA); Cangas de Narcea, vega de Renfos, Muniellos, *Silva Pando et al. 1394* (MA, MACB, MAF).

7. **Doronicum cataractarum** Widder, Feddes Repert. 22: 115, Taf. 25–27. 1925. TYPE: Kärnten, Koralpe, Im obersten Weiβwassergraben, nahe der Waldgrenze bei etwa 1630 m, zwischen den Felsblöcken des Baches, 20 Aug. 1923, *F. J. Widder s.n.* (holotype, GZU!; isotypes, GZU!).

Plant up to 100(+) cm tall. *Rhizomes* woody to somewhat woody, scarcely pubescent to pubescent, and generally with leaf remains forming dark scales on nodes. *Stem* branched in the upper part, leafy, internodes generally shorter than the adjacent leaves. Indumentum of uniseriate eglandular trichomes (up to 0.4 mm), also with short-stalked or subsessile glandular trichomes near the capitula, sometimes glabrate. *Leaves* slightly dentate to dentate. Basal leaves sometimes present at flowering; blade 8–20 × 8.5–19.5 cm, ovate to orbicular, with cordate to subcordate base and generally blunt apex, with actinodromous venation; petiole 21–26 cm long, 2.5–4.5 mm wide. Lower and middle cauline leaves 7–19 × 6–15 cm, similar to basal leaves or sessile, fiddle-shaped, semi-amplexicaul. Upper cauline leaves 2.5–4.5 × 0.8–2 cm, ovate to ovate-lanceolate, sometimes bract-like. Indumentum similar to the adjacent part of the stem, sometimes with uniseriate and multiseriate eglandular trichomes (up to 2 mm). *Capitula* 2 to 14, 4–8 cm diam. including rays; involucre shorter than rays, 2.5–5 mm diam.; peduncles 3–16 cm long, 0.7–1.5 mm wide, sometimes with turbinate base during fruit (up to 12 mm width). *Phyllaries* herbaceous, 1.2–1.8 cm long, 1.5–3.5 mm wide, ovate-lanceolate to elliptic, generally with acute apex. Indumentum of short-stalked glandular trichomes and uniseriate eglandular trichomes, sometimes glabrate. *Receptacles* glabrous. *Flowers* with yellow corollas. Ray flower corollas 2.5–3.5 cm long, 1.7–3 mm wide, oblong-elliptic to obovate-elliptic, apex generally with 3 teeth. Disk flower corollas 4–5 × 2–3 mm. *Cypselae* brown-tinted, with grooved-reticulate surface, dimorphic. Cypselae from ray flowers ca. 3.5 × 1 mm, glabrous or glabrate, without pappus or sometimes with a poorly developed pappus. Cypselae from disk flowers 2.5–3 × 0.6–0.8 mm; pappus 4–5.5 mm, white. Chromosome number $2n = 60$ (data obtained from several indexes of plant chromosome numbers: Fedorov, 1969; Goldblatt, 1985; Goldblatt & Johnson, 1994, 1996; original sources not seen).

Illustrations. Widder (1925: Taf. 25–27); Hegi (1928: 716, fig. 424); Figures 1D, 8C, 12E, 12F.

Distribution. Europe (Austrian Alps). In gullies and rocky places near watercourses, altitude 1600–1900 m (Fig. 15).

Morphologically, the closest species to *Doronicum cataractarum* is *D. austriacum* (see comments above), and there are only slight and few differences between them. *Doronicum cataractarum* is an endemic from the Austrian Alps, which is included within the area of distribution of *D. austriacum*. The characters used to distinguish them are the scarcely pubescent to pubescent rhizomes of *D. cataractarum* versus glabrous rhizomes of *D. austriacum*; base of capitula glabrous to glabrate with short-stalked or subsessile gladular trichomes in *D. cataractarum* versus base of capitula glabrate to pubescent or with long-stalked glandular trichomes in *D. austriacum*. In addition, although these two species have dimorphic cypselae (ray flowers without pappus and disk flowers with pappus), this is not a very stable character in *D. cataractarum* and sometimes the ray flowers in this species have a poorly developed pappus, which is never present in *D. austriacum.*

Selected specimens examined. AUSTRIA. **Kärnten:** Koralpe, am Bache im Himmelreich, 22 Aug. 1934, *Drobny s.n.* (B); Koralpe bei Deutschlandberg, *Fest 571* (B); Koralpe, Bachufer unterhalb der Grillitschhütte, 30 July 1950, *Höpflinger s.n.* (BM, G); Koralpe, Grosses Kaar, Sep. 1953, *Patzak s.n.* (K); Weißwassergraben, Waldgrenze, 20 Aug. 1923, *Widder s.n.* (GZU); Weißwassergraben, Grillitschhütte, Sturzbach, 19 Aug. 1928, *Widder s.n.* (MAF). **Steiermark:** Ronde des Seebaches, Seekar der Koralpe, 24 Aug. 1936, *Widder s.n.* (G); Seebach der Koralpe, Seekar, 28 Aug. 1939, *Widder s.n.* (B).

8. Doronicum clusii (All.) Tausch, Flora 11: 178. 1828. *Arnica clusii* All., Auct. Syn. Stirp. Taurin.: [18]. 1773. *Aronicum clusii* (All.) W. D. J. Koch, Syn. Fl. Germ. Helv.: 382. 1837. TYPE: not located; protologue citation: "in Albula Rhaetica & aliis Rhaetorum alpibus."

Plant up to 40 cm tall. *Rhizomes* fleshy to somewhat woody, with shining white-tinted short trichomes on nodes, generally with leaf remains. *Stems* generally not branched, with leaves mainly at the base or in the middle basal part of stem. Indumentum of eglandular and glandular trichomes, more abundant near the capitula. *Leaves* entire to dentate. Basal leaves generally present at flowering time; blade 7(8.5)–(1.5)2 × 1–2.5(3.5) cm, elliptic to ovate-elliptic, truncate or attenuate base, blunt to acute apex, with actinodromous to pinnate-actinodromous venation; petiole (0.8)2–10 cm long, 1–3(4) mm wide. Lower and middle cauline leaves 2.5–10 × 0.7–2.5(3.5) cm, similar to basal leaves or sessile, ovate-elliptic to narrowly elliptic, semi-amplexicaul. Upper cauline leaves 1.5–5.5 × 0.5–3 cm, similar to middle cauline leaves, or ovate-lanceolate. Indumentum of stiff, acute, and shiny multiseriate eglandular trichomes (up to 2.5 mm), and thin, tangled uniseriate eglandular trichomes (up to 2 mm), mainly on leaf margins, also short-stalked glandular trichomes on leaf blade. *Capitula* 1(to 4), 4–7.5 cm diam. including rays; involucre shorter than rays, 2.5–5 cm diam. *Phyllaries* herbaceous; the outer 1.2–2 cm long, 1.5–3.3 mm wide; the inner 1–2 cm long, 1–2.3 mm wide, ovate-lanceolate to widely subulate. Indumentum similar to the upper part of stem. *Receptacles* glabrous. *Flowers* with yellow corollas. Ray flower corollas 1.8–2.5 cm long, 2.5–4.5 mm wide, obovate-elliptic, apex generally with 3 teeth. Disk flower corollas 4–5 × 1.5–2 mm long. *Cypselae* brown, with grooved-reticulate surface, homomorphic, 1.5–2.5 × 0.7–1 mm, with eglandular trichomes or glabrate. Pappus up to 5.5 mm, white. Chromosome number $2n = 60^*$, 120 (Skalinska, 1950, as *Aronicum clusii*; Tasenkevitch et al., 1989; *Goldblatt & Johnson, 1996, see comments below).

Illustrations. Reichenbach (1854: tab. 63, fig. 2); Hegi (1928: fig. 432); Săvulescu (1964: pl. 99, fig. 1), Resmeriță & Moravetz (1956: fig. 1); Figure 3F–H.

Distribution. Europe (Alps and Carpathians). Open moist rocky places and screes, altitude 1500–3000 m (Fig. 19).

The type material of *Arnica clusii* could not be found, and although the protologue matches the diagnostic features of this taxon, its identity here is tentative and the formal synonymies need to wait until clarification.

There are three European species, *Doronicum clusii, D. glaciale,* and *D. grandiflorum,* that are morphologically similar, and whose areas of distribution overlap in some places in the Alps occupying the same habitats. All of them have homomorphic fruits (all cypselae with pappus), ovate to elliptic basal leaves with truncate or attenuate bases, and rhizomes fleshy to somewhat woody with short trichomes on nodes, generally with a single capitulum or sometimes a few (2 to 4). All of them grow in open moist rocky places in the mountains, preferably the upper tree line to 3000 m in elevation. Although they only differ in the type of indumentum, it is a very constant character (more noticeable on the leaf margins). In *D. clusii* and *D. glaciale,* stalked glandular trichomes are absent or scarce, while they are common in *D. grandiflorum* (Fig. 3B). In contrast, long (up to 2.5 mm) nonglandular trichomes are present in both *D. clusii* and *D. glaciale* (Fig. 3E, H). Differences between *D. clusii* and *D. glaciale* are slight, and it is difficult to delimit them. Typical individuals from *D. clusii* and from *D. glaciale* present the indumentum as it is represented (Fig. 3H and E, respectively), but some individuals have a very few scattered thin and tangled uniseriate trichomes, which are abundant in typical *D. clusii* and absent in typical *D. glaciale.* Because of this, the present taxonomic treatment includes those exceptional individuals within *D. clusii,* although the existence of hybrids between these two species is not rejected.

The citation of the chromosome number $2n = 60$ for *D. clusii* was found in Goldblatt and Johnson's (1996) index, but the original source for this data was not seen.

Selected specimens examined. AUSTRIA. **Steiermark:** Grafenalpe, Krakaudorf, July 1902, *Fest s.n.* (B); Rottenmanner Tauern, Haute Styrie, 21 July 1868, *Ober-*

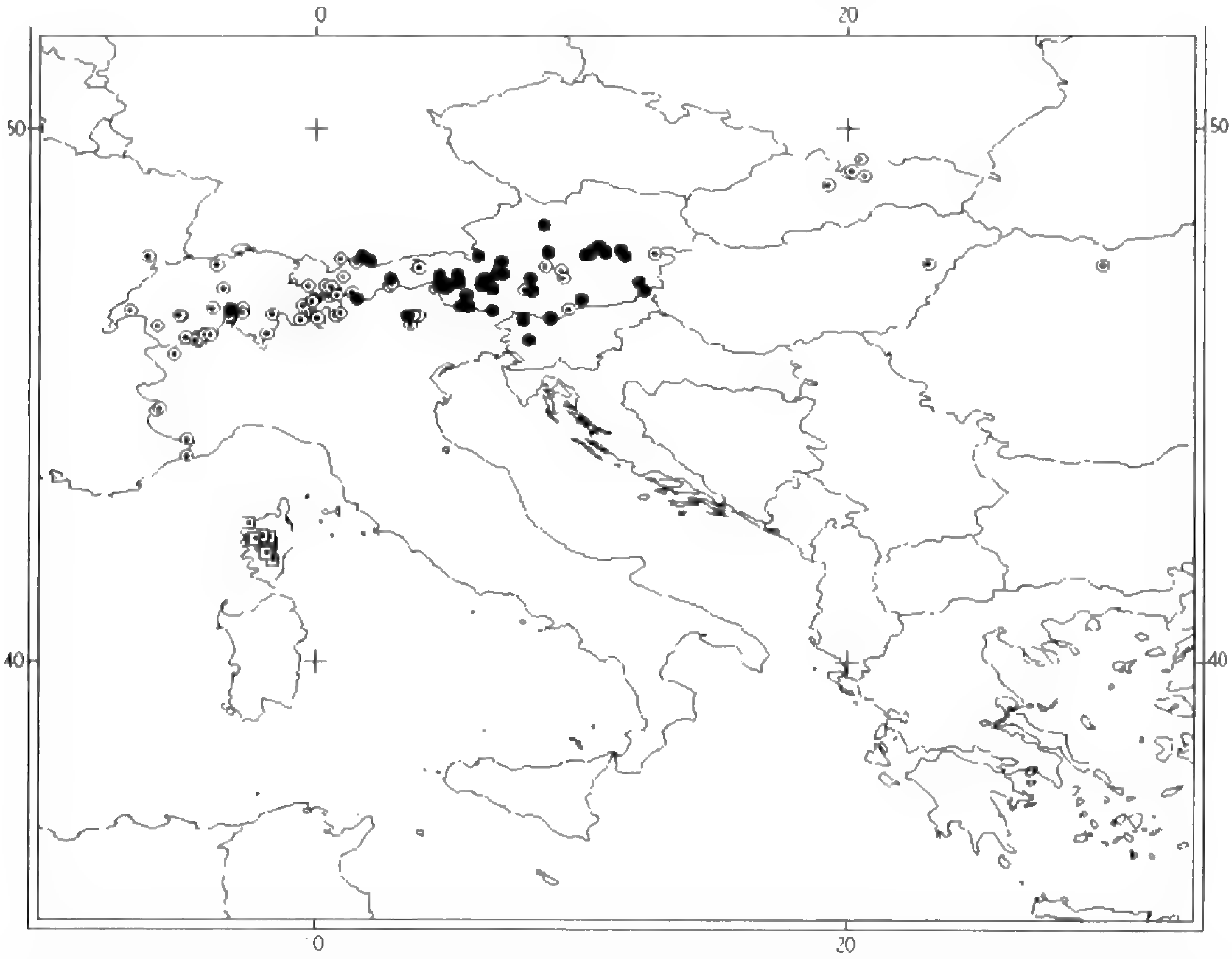

Figure 19. Distribution map for: *Doronicum clusii* (⊙); *Doronicum corsicum* (⊡); *Doronicum glaciale* (●).

leitner s.n. (B, LE). **Tirol:** Paznaun, Fladner Massio, 2 Aug. 1932, *Bornmüller s.n.* (B); Ferwallgruppe, Fasultal, 2 Aug. 1942, *Freiberg s.n.* (MA); Ötzthaler Alpen, Oberimtal, Glocktürmgebrit Felsblock in der Radurschelalm, 25 Aug. 1939, *Günther s.n.* (B); Alpbach bei Brixlegg am Galtenberg, Schiefer, 10 Aug. 1933, *Reiter s.n.* (B); Gsehnitz, Mt. Muttenjoch, 16 Aug. 1890, *Schafferer s.n.* (B). **Vorarlberg:** Schruns, Sulzfluh, 27 July 1895, *Bornmüller s.n.* (B). CZECHOSLOVAKIA. Vysoké Tatry in valle montana Mlynica, 6 Aug. 1933, *Dostál s.n.* (BM, MA, NY); Felka pod Gerlachovský Štít, July 1895, *Fitko s.n.* (B); Magas Tátra, lacum Késmárki Zöld-tó, *Kümmerle & Timkó 790* (B, E, MO); Brezno, Mt. Dumbier, 3 Aug. 1898, *Kupčok s.n.* (E). FRANCE. **Alpes-Maritimes:** Mt. Bissa, col de Tende, *Bourgeau 139* (COI-WILLK, G, K). ITALY. **Lombardia:** Bormio, passo dello Stelvio, *Álvarez et al. 1355* (MA); Sondrio, Bormio, Mt. Leverone, 31 July 1911, *Longa s.n.* (BM). **Piemonte:** passo del Domignone, Alpes Bergamasques, 31 July 1910, *Chenevard s.n.* (G). **Trentino-Alto Adige:** Trento, Canazei, col del Cuc, *Álvarez et al. 1353* (MA). **Valle d'Aosta:** Aufstieg zum Colle Pinter, am Bergbach, in Felsen, 1982, *Royl & Schiers s.n.* (B). POLAND. Zakopane, Beskid, o-alpin, Karpaten, *Hempel 2786* (B); Rysy, lacum Czarny Staw, Tatry Wysokie, Tatri Alti, 3 Sep. 1938, *Madalski s.n.* (B). SWITZERLAND. **Graubünden:** Alp d'Ischolàs, Engadine, *Binz 405* (MO); Pontresina, Morteratsch, paso del Bernina, Lejner, *Castroviejo et al. 11615* (MA). **Tessin:** San Bernardino, 28 July 1920, *Valentine s.n.* (NY). **Valais:** près Zermatt, 14 Aug. 1888, *Bernouilli s.n.* (MA); Ferpècle-Barcolla, *Bonnier 163* (MO); Weismieshütte, Quellflur, *Damboldt 679/70* (B); Saas-Tal, Grashang bei Spielbodenalm, Saas-Fee, *Damboldt 714/70* (B); près des alpes de Taesch, 5 June 1908, *Palibin s.n.* (LE). YUGOSLAVIA. Visoki Verch, Liptau, July 1894, *Ullepitsch s.n.* (B).

9. Doronicum columnae Ten., Fl. Napol.1, Prodr.: 49. 1811. TYPE: Italy. "Majella" [*M. Tenore s.n.*] (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 802), NAP!).

Plant up to 70 cm tall. *Rhizomes* woody to somewhat woody, glabrous, generally with leaf remains forming dark fibers or scales on nodes. *Stems* not branched, generally scape-like. Indumentum of uniseriate, multiseriate eglandular trichomes, short-stalked and long-stalked glandular trichomes, scarce at the base, more abundant near the capitula. *Leaves* dentate to slightly dentate. Basal leaves generally present at flowering time; blade 1.5–7 × 2–6.5 cm, orbicular to broadly ovate with cordate to subcordate base, with blunt or subacute apex, with actinodromous venation that sometimes tends to be acrodromous; petiole thin and stiff, 4–15(24) cm long, 0.5(–2) mm wide. Lower and middle cauline leaves 1.9–8(10.4) × 1.2–6(7) cm, similar to basal leaves or sessile, fiddle-shaped, semi-amplexicaul. Upper cauline leaves 1.5–4.5(7.1) × 0.8–3 cm, ovate-elliptic to ovate-lanceolate, sometimes bract-like. Indumentum of uniseriate eglandular trichomes (up to 0.5 mm), conspicuously on the blade edge. *Capitula* 1(2 to 3), 2.8–7 cm diam. including rays; involucre shorter than rays, rarely equaling them, 1.8–4 cm diam. *Phyllaries* herbaceous, ovate-subulate, generally with acute apex; the outer 0.7–1.8 cm long, 0.7–2.8 mm wide, the inner 0.7–1.6 cm long, 0.5–1.8 mm wide; margins sometimes ciliate, with acute, stiff and equidistant multiseriate eglandular trichomes (up to 0.6 mm). Indumentum mainly glandular, but also with uniseriate eglandular trichomes. *Receptacles* glabrous or pubescent. *Flowers* with yellow corollas. Ray flower corollas 1–3 cm long, 1.5–3.8 mm wide, oblong-elliptic, apex generally with 3 teeth. Disk flower corollas 3.5–4.5 × 1.8–2 mm. *Cypselae* brown, with grooved-reticulate surface, dimorphic. Cypselae from ray flowers 2–2.5 × 0.7–1 mm, glabrous to glabrate, without pappus. Cypselae from disk flowers 1–2.3 × 0.4–0.8 mm, with eglandular trichomes; pappus 3–4 mm, white. Chromosome number $2n = 60$ (Garbari et al., 1980; Van Loon, 1980; Strid & Franzén, 1983; Lippert & Heubl, 1988; Baltisberger, 1991).

Illustrations. Reichenbach (1854: tab. 64, fig. 1); Hegi (1928: 715, fig. 423); Săvulescu (1964: pl. 98, fig. 2); Figure 1E.

Distribution. Europe (Balkans extending to central Greece, Carpathians, Alps, and Appenines). Meadows, shady rocky places and gullies, from sea level up to 2700 m in elevation (Fig. 15).

Doronicum columnae is a polymorphic species morphologically similar to *D. carpaticum* and *D. orientale.* These species share the habit (scape-like stem with a few caulinar leaves bearing a single capitulum), the shape of basal leaves (orbicular to ovate with cordate to subcordate base), and the ciliate margins of phyllaries (Fig. 5E, F), although this latter character is not constant in *D. columnae* and *D. carpaticum.* The most distinctive character between *D. orientale* and both *D. columnae* and *D. carpaticum* is the type of rhizome, which is fleshy with pubescent nodes in *D. orientale* versus woody to somewhat woody and glabrous in *D. columnae* and *D. carpaticum.* There is only one character to distinguish *D. columnae* and *D. carpaticum*: the dimorphic cypselae (ray flowers without pappus) in *D. columnae* versus the homomorphic cypselae (all flowers with pappus) in *D. carpaticum.* Some specimens that have poorly developed pappus in the ray flowers are included in *D. carpaticum,* although the hybrid nature of them is not rejected. In addition, there are some exceptional specimens of *D. columnae* that have a few capitula instead of a single one and that can be confused with another sympatric species, *D. pardalianches.* It is easy to distinguish between them by comparing their rhizomes, which are woody and glabrous in *D. columnae* while fleshy with pubescent nodes in *D. pardalianches.* Besides, cypselae in *D. pardalianches* turn black at maturity, which is a unique character in the genus.

The type designation for *Doronicum columnae* was difficult (Álvarez Fernández & Nieto Feliner, 1999). Since there is no collection date, doubt remains concerning this issue. Based on historical records, Tenore visited the type locality himself describing several new species in his *Prodromus* in 1811. Taking into account this fact, and without other suitable type material, this was the best choice as lectotype.

Selected specimens examined. ALBANIA. **Gjirokastër:** Mali Gjer, *Alston & Sandwith 1528* (BM, K). **Korçë:** Ostrovicë, Moskopolë, Korcë, *Alston & Sandwith 2065* (BM, K). **Shkodër:** Nikči, Klementi, *Baldacci 457* (BM). **Tiranë:** Dajti, *Pennington 41* (K). AUSTRIA. **Tirol:** Schlern, auf Felsgeroll in der Klamm, 14 July 1903, *Behrendsen s.n.* (G). BULGARIA. **Grad Sofiya:** Vitoša, ref. Salzica, 16 June 1974, *Markova, Cerneva & Gerginov s.n.* (BM, E, G, MA). **Plovdiv:** Kalofer, *Wagner 77* (BM). **Sofiya:** Borovez, Musala, 11 Aug. 1976, *Beck s.n.* (B). GERMANY. **Bayern:** Hocheis-spitz-Gruppe, Hirschbichl Bind-Alm Mittereis-Alm Hocheis-Alm Hintereis, *Lippert & Podlech 25818* (NY). GREECE. **Ípiros:** Mt. Smolika, *Atchley 945* (K); Papignon, Mt. Gamila, *Lancaster 120* (BM). **Makedhonía:** Chaliki, Mt. Peristeri, *Sintenis 733* (B, E, G, K). **Nísoi Ayaíou:** Mt. Korax Aetoliae adjectae, 23 July 1879, *Heldreich s.n.* (K, LE). **Stereá Ellás–Evvoia:** Trapeza, Katafigon, Oeta, *Balls & Gourlay B3231* (BM, E, K). **Thessalía:** Mt. Olympus, *Archibald 326* (E). HUNGARY. **Nógrad:** Orsova, in valle Kazár, *Schneider 11* (B, BM, K, MO). **Veszprém:** Bihania, in valle Izvor, Remecse, 22 May 1906, *Gulyás s.n.* (G). ITALY. **Abruzzi:** La Majella, *Bornmüller 127* (B). **Campània:** Montevergine, Avellino, 10 May 1913, *Pellanda s.n.* (G). **Emilia-Romagna:** Corniolo, Forli, Foresta di Campigna, *Chiapella & Poldini 8743* (G, MA, MAF). **Lombardia:** Como, Mt. Barbisino, Val Massino, 17 July 1850, *Daenen s.n.* (LE). **Puglia:** Gargano, Mt. S. Angelo, 29 May 1895, *Porta & Rigo s.n.* (LE). **Toscana:** Mt. Senario prope Florentiam, 20 Apr. 1856, *Caruel s.n.* (LE). **Trentino-Alto Adige:** Trento, passo Gardena, Sella Gruppe, *Álvarez et al. 1354* (MA). ROMANIA. **Alba:** Piatra Strutu prope pag. Avram lancu, 24 May 1973, *Gergely & Toader s.n.* (B, BM, G, K, MA). **Braşov:** Mt. Bucegi, m. Predeal, S of Braşov, Ploiesti, *Sidebotham 15* (BM). **Hunedoara:** Mt. Retezat, lacum Zanoaga, 9 Aug. 1933, *Borza & Nyárády s.n.* (BM, G, K, MO). **Prahova:** Mt. Baiului, Muntele Cumpatu, 17 June 1983, *Zamfir s.n.* (B). YUGOSLAVIA. **Bosna i Hercegovina:** Mt. Frebovic, Sarajevo, *Beck & Fiala 232* (G, K, LE). **Crna Gora:** Mt. Durmitor, *Leaver 174* (BM). **Makedonija:** Usküb, ad fluvium Treska, *Bornmüller 4263* (NY). **Srbija:** Belgrad, Ripanj, 8 May 1887, *Bornmüller s.n.* (B).

10. Doronicum corsicum (Loisel.) Poir., in Lam., Encycl. Suppl. 2: 517. 1811. *Arnica corsica* Loisel., Fl. Gall. 2: 576, tab. 20. 1807. *Aronicum corsicum* (Loisel.) DC., Prodr. 6: 319. 1838. TYPE: not located; protologue citation: "in Corsica, ad rupes aquis fluentibus irriguas (D. Richard. Herb.)."

Plant up to 100(+) cm tall. *Rhizomes* woody to somewhat woody, glabrous. *Stems* branched in the upper part, leafy, internodes generally shorter than the adjacent leaves. Indumentum glandular and also with uniseriate and multiseriate eglandular trichomes, abundant near the capitulum, sometimes glabrous in the lower part. *Leaves* dentate to slightly dentate. Basal leaves absent at flowering time, similar to cauline leaves. Cauline leaves oblong-elliptic, sessile, slightly auriculate, semi-amplexicaul, acute apex, pinnate-actinodromous venation. Middle cauline leaves 7–16 × 2–5.5 cm. Upper cauline leaves 3.5–10 × 1–2.5 cm. Indumentum scarce, with uniseriate and multiseriate eglandular trichomes, and short-stalked glands. *Capitula* several, 5(+), ca. 5 cm diam. including rays; involucre much shorter than rays, 2–2.5 cm diam.; peduncles 3.5–7 cm long, 1 mm wide. *Phyllaries* herbaceous, ovate to ovate-lanceolate, generally with acute apex, sometimes slightly papery at the base or at the margins; the outer 0.6–0.8 cm long, 1.7–2.5 mm wide; the inner 0.7–1 cm long, 0.7–1.6 mm wide. Indumentum mainly of uniseriate eglandular trichomes, sometimes also with multiseriate eglandular trichomes and glandular trichomes. *Receptacles* glabrous or pubescent. *Flowers* with yellow corollas. Ray flower corollas ca. 2.5 × 0.4 cm, oblong-elliptic to obovate-elliptic, apex generally with 3 teeth. Disk flower corollas up to 0.7 cm long. *Cypselae* brown and with a smooth to grooved surface, homomorphic, ca. 3 × 1 mm, glabrous or glabrate; pappus ca. 5.5 mm, white. Chromosome number $2n = 60$ (Contandriopoulos, 1957).

Illustrations. Loiseleur-Deslongchamps (1807: tab. 20).

Distribution. Corsica. In forests and gullies and on rocky slopes that are sometimes inundated, altitude 700–1750 m (Fig. 19).

The type material cited in the protologue of *Arnica corsica* refers to one sheet from the D. Richard herbarium. This collection should be in P, but no material was found there. Unfortunately, the protologue includes only a crude and incomplete illustration that is not appropriate as a lectotype. Although the protologue and the illustration included both match the diagnostic features of this taxon, its formal identity needs further investigation in the search of an appropriate lectotype or a neotype.

Currently, this is the only species of *Doronicum* growing in Corsica (see comments under *D. grandiflorum*). Although *D. corsicum* is morphologically similar to *D. austriacum*, they differ basically in the homomorphic cypselae in *D. corsicum* versus dimorphic in *D. austriacum*. In addition, *D. corsicum* has uniform, elliptic, sessile caulinar leaves with dentate margins, while *D. austriacum* presents different types of caulinar leaves in the same specimen (acropetally, petiolate to fiddle-shaped and ovate), with entire to slightly dentate margins.

Selected specimens examined. FRANCE. **Corse:** forêt d'Aïtone bei Evisa, 20 July 1932, *Aellen s.n.* (MA); Calacuccia, Golo, Sidossi, July 1912, *Cousturier s.n.* (NY); Mt. d'Oro, 12 July 1916, *Forsyth-Major s.n.* (K); valleé de Mangamullo, près Vriario, 18 July 1906, *Gysperger s.n.* (B); Calvi, Mt. Sollier, 1822, *Jacquemont s.n.* (NY); Tavignano, Corte, *Kralik 538* (E, K); Fiumorbo, Pazzi du Mt. Renoso, *Kralik 638a* (E, K); l'Incudine, *Lambinon 86/Co/264* (MA); Lit de la Restonica, près de Corte, *Mabille 142* (BM, K); Mt. Niolo, *Requien 250* (BM, K); Bastelica, 18 July 1878, *Reverchon s.n.* (COI-WILLK, E, K, NY); forêt d'Aïtone, 1885, *Reverchon s.n.* (B, E, NY).

11. Doronicum dolichotrichum Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 252. 1911. TYPE: Transcaucasus. Gourie, descente du mont Khino au défilé Goghieti, 18 July 1893, *N. M. Alboff s.n.* (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 802), G!).

Doronicum hyrcanum Widder & Rech. f., Oesterr. Bot. Z. 97: 235. 1950. Syn. nov. TYPE: Transcaucasus. Azerbaidjan, Sari Chaman, *Mirdamadi K2381* (holotype, W!).

Doronicum hakkiaricum J. R. Edm., Notes Roy. Bot. Gard. Edinburgh 32(2): 255. 1973. Syn. nov. TYPE: Turkey. Hakkâri, Kara Da, *P. H. Davis & O. Polunin D24383* (holotype, E!; isotypes, BM!, K!).

Doronicum bracteatum J. R. Edm., Notes Roy. Bot. Gard. Edinburgh 32(2): 257. 1973. Syn. nov. TYPE: Iraq. Arl Gird Dagh, near Rust, *E. R. Guest & E. R. Ludlow-Hewitt 2928* (holotype, K!).

Plant up to 100(+?) cm tall. *Rhizomes* woody, glabrous, generally without leaf remains. *Stems* branched in the upper part, leaves distributed along the stem, upper internodes generally longer than the adjacent leaves. Indumentum of triangular, white-tinted, multiseriate eglandular trichomes (1–3 mm), sometimes scattered, long-stalked glandular trichomes (0.5–3 mm), sometimes abundant near the capitula, and occasionally uniseriate eglandular trichomes and short-stalked glandular trichomes, sometimes glabrous at the base. *Leaves* entire to dentate. Basal leaves sometimes present at flowering time; blade 6–15 × 8.5–18.5 cm, orbicular or ovate, with cordate base and blunt or acute apex, with actinodromous venation; petiole 4.7–23 cm long, 3–3.5(6) mm wide, with sheathing base, sheath ca. 5 cm long. Lower and middle cauline leaves with blade 10–26 × 5–21.5 cm, similar to basal leaves or sessile, fiddle-shaped, semi-amplexicaul; petiole 12–20 cm long, 3.5–5.5 mm wide. Upper cauline leaves 4–9 × 1.6–7.5 cm, sessile, ovate to obovate, or bract-like. Indumentum similar to the adjacent part of the stem, sometimes also with uniseriate eglandular trichomes on margins and on veins in the abaxial surface of leaves. *Capitula* 2 to 8, 4–5.5 cm diam. including rays; involucre shorter than rays, 2.5–3.5 cm diam.; peduncles 2–9 cm long, 1.5–2.3 mm wide, sometimes turbinate at the base of capitula (4–7 mm wide) in fruit. *Phyllaries* herbaceous, ovate-lanceolate to obovate-lanceolate with acute apex; the outer 1.1–1.7 cm long, 2–5.5 mm wide; the inner 1.2–1.5 cm long, 1.5–2.3 mm wide. Indumentum similar to the upper part of stem. *Receptacles* glabrous. *Flowers* with yellow corollas. Ray flower corollas 1.5–2.5 cm long, 2–3.8 mm wide, obovate-elliptic to oblong-elliptic, apex generally with 3 teeth. Disk flower corollas 4–5 mm long. *Cypselae* brown, with smooth or slightly reticulate surface, dimorphic. Cypselae from ray flowers 2.8–4.3 × 1–1.5 mm, glabrous or glabrate, without pappus. Cypselae from disk flowers 2–2.5 × 1–1.5 mm, sometimes with eglandular trichomes; pappus ca. 4.5 mm, white. (Only immature cypselae seen.) Chromosome number unknown.

Illustrations. Figures 2C, D, 7D, 20A–D.

Distribution. Northeastern Turkey, Caucasus, and south of the Caspian Sea. Growing in woods, open moist rocky places, meadows, gullies, and near watercourses, altitude 800–3300 m (Fig. 14).

The type of indumentum is critical for distinguishing among species of *Doronicum* in southwestern Asia. The variability of this character both in type and abundance in *D. dolichotrichum* (Fig. 2C, D) sometimes makes it difficult to identify material conclusively. Plants with intermediate characters between *D. maximum* (Fig. 23B, C) and *D. macrophyllum* (Fig. 26B, C) have been found.

The diagnostic characters used to separate *Doronicum bracteatum* (Edmondson, 1973), *D. hakkiaricum* (Edmondson, 1973), and *D. hyrcanum* (Widder & Rechinger, 1950) overlap substantially with those of *D. dolichotrichum.* The patterns of indumentum variability also match those of *D. dolichotrichum.* Accordingly, these names are considered synonyms.

Selected specimens examined. CAUCASUS. **North Caucasus:** Daghistan, Schalbur dagh, *Backir 183* (LE). **Transcaucasus:** Carthalinia, Tabiszchuri, *A. H. & V. F. Brotherus 500b* (BM, G); Kachetia, Mt. Choczal-dagh, 12 July 1898, *Fomin s.n.* (LE); Armenia, Migri Gjunej, inter m. Gjeljedzhik et m. Ketshmas, 20 Aug. 1932, *Karjagin & Grossheim s.n.* (K); Tiflisskaja, Gorijskij, Gora Tschra-Tscharò, 7 July 1916, *Krylov & Schteinberg s.n.* (LE); Batumskaja, Artvinskij, Arsiyanskij, 16 June 1910, *Nesterov s.n.* (LE); Nachitschevan, Mt. Ketshal-dagh, 4 Aug. 1934, *Prilipko & Isaev s.n.* (K); Nor-Bajazet, Gri-zör, 16 Aug. 1928, *Schelkovnikov & Kara-Murza s.n.* (LE); Mt. Alagëz, Kaznafar, 31 July 1931, *Tamemshian & Maleer s.n.* (E); Chokhatauri, Bakhmaro, Meskhetski, Mt. Grdzeli-vake, 22 July 1979, *Vašák & Esvandzhia s.n.* (G, W). IRAN. Azerbaidjan, Maku to Khoy, Kelisakandi, *Assadi & Mozaffarian 30306* (E); Zanjan, Vansar mountains, 20 June 1983, *Moussavi et al. s.n.* (IRAN); Ostan 2, Dimelo, *Schmid 5989* (G, W); Gorgan, Ketul, *Sharif 224* (W); Azerbaidjan, Ahar, Hassano, 8 Aug. 1968, *Termeh s.n.* (IRAN); Azerbaidjan, Kalibar, Nabidjan, Kouhha-ye Doghroun, 26 June 1978, *Termeh et al. s.n.* (IRAN). IRAQ. Helgord range, *Rawi & Serhang 24553* (K); Qandil mountain, Qala Diza, *Thesiger 1154* (BM). TURKEY. **Artvin:** Yalniczam Silsilesi, Savsat, *Albury et al. 3159* (K); Ardanuç, Kordevan dag, Yalnizcam Daglari, at Kütül yayla, *Davis & Hedge 30342* (BM, E, K, W); Yalnizcam-Gebirge bei Karaköy, Savsat, *Raus 4864* (B). **Erzurum:** Bingöze Köyü yaylas, Yildiz Dagi, *Tatli 5171* (E). **Hakkari:** Kara dag, *Davis & Polunin 24383* (BM, E, K). **Kars:** Yagmurlu dag between Sarikamis and Karuargan, *Davis & Hedge 30819* (E, K); Arpogay, Kaya Diplei, *Ocakverdi 2340* (GAZI).

12. **Doronicum falconeri** C. B. Clarke, Fl. Brit. Ind. 3: 333. 1881. TYPE: Karakorum, *C. B. Clarke 30258 A* (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 803), K!).

Doronicum turkestanicum Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 301. 1911. Syn. nov. TYPE: Russia. Siberia: "Mont. sent. milit.," *M. J. Chaffanjon 385* (lectotype, designated here, G!).

Plant up to 90 cm tall. *Rhizomes* woody to somewhat woody, glabrous, generally with leaf remains forming dark scales. *Stems* not branched, leaves generally arranged all along the stem, internodes generally shorter than adjacent leaves. Indumentum of glandular trichomes (up to 2 mm), more abundant near the capitula, sometimes only very scarce eglandular trichomes or glabrate. *Leaves* entire. Basal leaves sometimes absent at flowering time; blade 2–7(9) × (0.2)1–2.5(3.2) cm, elliptic to obovate, with attenuate base and generally blunt apex, with actinodromous to pinnate-actinodromous venation; petiole 1–4.5 cm long, 2–5 mm wide. Lower and middle cauline leaves (3)5–12.5 × (0.3)1.5–4(5.5) cm, similar to basal leaves or sessile, obovate, ovate, elliptic, or almost fiddle-shaped, semi-amplexicaul, with blunt apex. Upper cauline leaves 2.5–6(7.5) × (0.4)0.5–1.5(3.6) cm, similar to middle cauline leaves or ovate-lanceolate. Indumentum similar to the adjacent part of stem, sometimes also with uniseriate eglandular trichomes and glands on margins. *Capitula* solitary, (4)5–7.5 cm diam. including rays; involucre shorter than rays, rarely equaling them, 3–5 cm diam. *Phyllaries* herbaceous, ovate-lanceolate to subulate; the outer 1.2–2(3) cm long, (1)1.5–2.5(3.5) mm

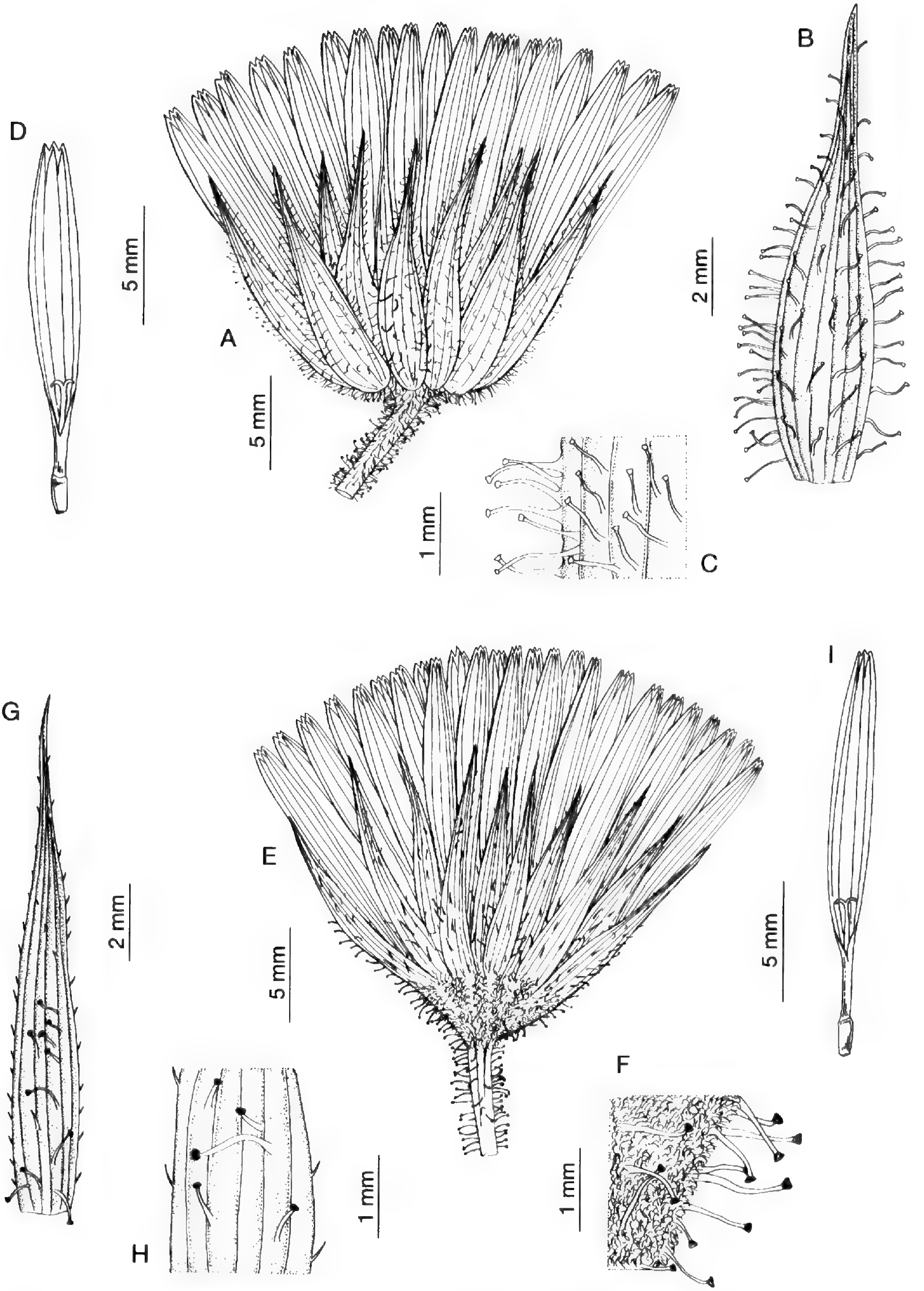

Figure 20. A–D. *Doronicum dolichotrichum* (drawn from *Davis & Hedge 29493*, K). —A. Capitulum. —B. Phyllary. —C. Indumentum of a phyllary. —D. Ray flower. E–I. *Doronicum kamaonense* (drawn from *Polunin 56/170* E, as *D. roylei*). —E. Capitulum. —F. Indumentum of the base of capitulum. —G. Phyllary. —H. Indumentum of a phyllary. —I. Ray flower.

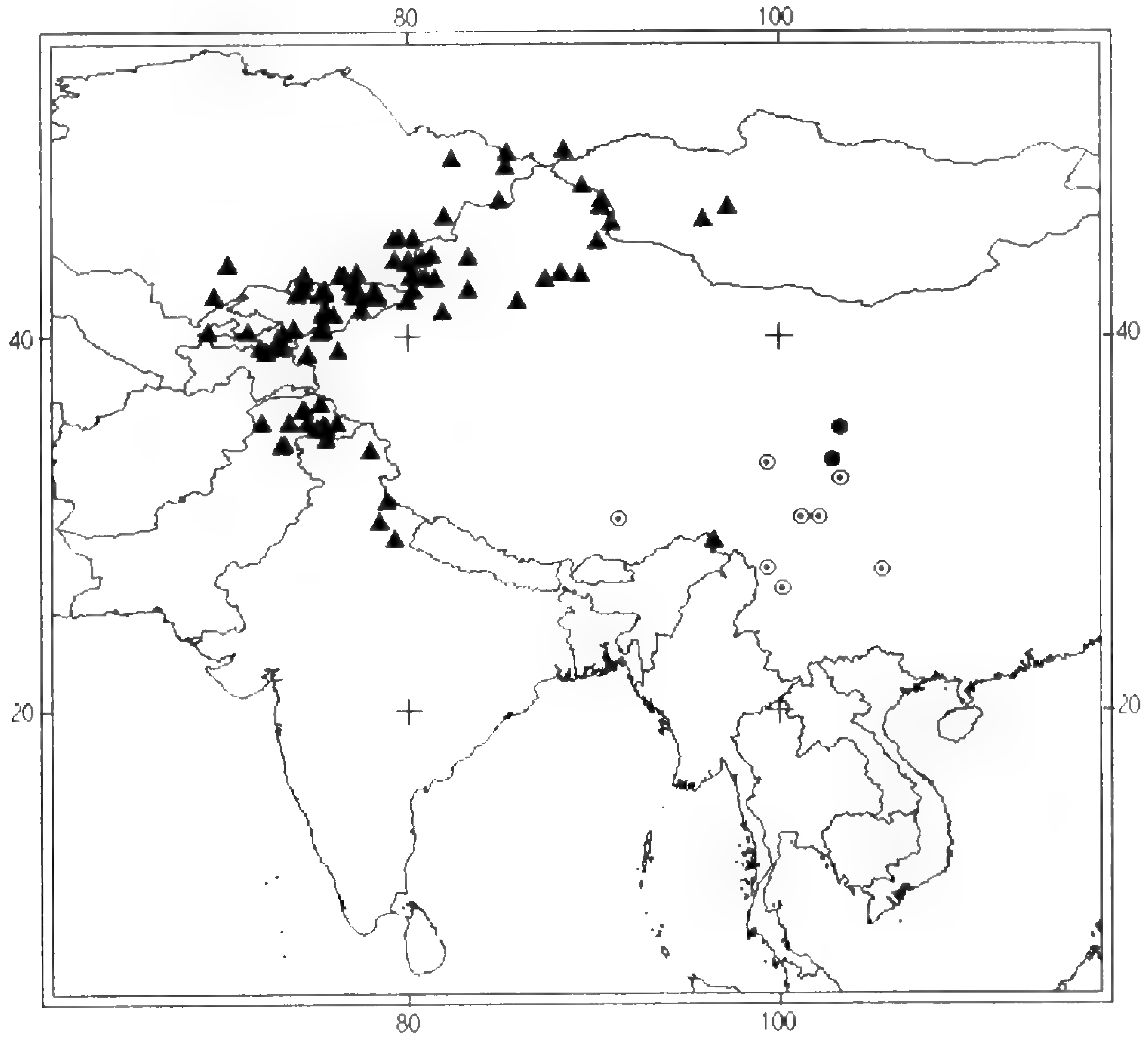

Figure 21. Distribution map for: *Doronicum gansuense* (●); *Doronicum falconeri* (▲); *Doronicum stenoglossum* (⊙).

wide; the inner 1–2 cm long, 0.7–2 mm wide. Indumentum similar to the upper part of stem, very scarce at the apex. *Receptacles* glabrous. *Flowers* with yellow corollas. Ray flower corollas 2–3 cm long, 1–2.5(3) mm wide, obovate-elliptic, apex with 2 or 3 teeth, sometimes without teeth, acute. Disk flower corollas 4.3–5.3 × 1.3 mm. *Cypselae* brown, with smooth surface, dimorphic, generally glabrous, sometimes with scattered eglandular or glandular trichomes. Cypselae from ray flowers without pappus. Pappus up to 5 mm, white. (Mature cypselae not seen.) Chromosome number unknown.

Distribution. Central-western China (provinces of Tibet-Qinghai and Xinjiang), Mongolia, Turkistan, Pamir, and Himalayas. Woods, open rocky places, gullies, and near watercourses, altitude 1800–5000 m (Fig. 21).

Cavillier (1911) recognized two sympatric species, *Doronicum falconeri* and *D. turkestanicum.* The character claimed to distinguish them (shape of leaves) is vague and quite polymorphic, and based on it the differentiation into two groups of species is not easy to make. Some specimens determined by Cavillier as *D. falconeri* and *D. turkestanicum* were included in a multivariate morphometric study (Álvarez Fernández & Nieto Feliner, 2001) resulting in no discrimination at all. Because of the lack of consistency in the delimitation between these two species, *D. turkestanicum,* which was described later, is here treated as synonym of *D. falconeri.*

Despite the recognition of Cavillier's species *Doronicum turkestanicum* in a local floristic study (Gorschkova, 1961), this name was still lacking a type designation. Thus, in this work the best preserved specimen chosen among Cavillier's citations as *D. turkestanicum* is designated as its lectotype (see synonym above).

The morphological similarities of *Doronicum falconeri* with other central Asian species is discussed above (see comments for *D. altaicum* and *D. briquetii*).

Selected specimens examined. CHINA. **Tibet-Qinghai:** Ata Kang La, Nagong, *Kingdon Ward 10876* (BM, E). **Xinjiang:** Thianschan, Rigil-tasch, l'Ak-son, *Brocherel 39* (G); Sairam, 18 July 1878, *Fetissow s.n.* (LE, S); Tien Shan, Urumqi river, *Liston 818-1* (MO); Mts. Bogdo-ola et Urumtschi, *Merzbacher 1275* (LE, W); Pamir, Kashgar, Bostan Terek, 5 Aug. 1934, *Persson s.n.* (S); Tian-Shan, Karagajte, Sari-dzhasa, 30 June 1902, *Saposhnikov s.n.* (LE). INDIA. **Uttar Pradesh:** Bhowáni, *Duthie 4127* (LE). **Punjab:** Rotang, Kulu Lahaul, *Drummond 22598* (K); Rupin pass, Dhaola Dhar, Simla Hill, *Sherriff 7405* (BM, E). JAMMU-KASHMIR. Kagan valley between Balakot and Babusar pass, *Abel 94* (BM); Astor, Alampi Lá, *Duthie 12164* (BM, E, K); Burzil, *Koelz 9429* (GH, NY); Srinagar, Vishensar, *Lancaster 160* (BM); Haramukh, *Ludlow & Sherriff 7850* (BM, E, UPS); Karakoram, Gharesa glacier, Nagar, *Polunin 6238* (B, BM, E); Karakoram, Hispar glacier, Turmun-Makerum, *Russell 1235* (BM); Nafran, Lidder, *Stewart 12638* (NY). KAZAKHSTAN. Talgarskoe, 14 June 1909, *Bogolubow s.n.* (LE); Alma-Atinskij, Alma-Atinskoe, 16 July 1927, *Dubiansky & Basilevskaja s.n.* (LE); Sarkana, Basken-Sarkan, 25 Aug. 1930, *Matveeva s.n.* (LE); Ketmen pass, 19 June 1878, *Regel s.n.* (LE); Narymense, Katon-Karagaj, 10 Aug. 1930, *Smirnow s.n.* (E, W). KIRGIZISTAN. Fergana, Ak-basoga, 31 June 1901, *Alexcenko s.n.* (LE); Sir-Darinsk, Tian-shan, Alamed, 6 July 1910, *Golbek s.n.* (LE); Boamskoe, Issik-Kulskaya, Terskej-Alatau, Turgen-Aksu, Kujliu, Inilchek, 23 July 1965, *Grudzinskaja s.n.* (LE); Zailyijskij Alatau, Semirechenskaya, Vernenskij, *Lipsky 1179* (LE); Terskej Alatau, Tekes, 26 May 1950, *Medvedeva et al. s.n.* (LE); Semirechenskaja, Pishpekskij, Aleksandrovskago, Ala-archi, *Sovetkina 428* (LE). MONGOLIA. Changai, *Kondratieva 68* (LE); Khara-Chzarga, Khairkhan-Duru, *Pobedimova 339* (LE); Mt. Alaschan, *Przevalski 101* (LE); Kobdosekij, Bulugun, *Yunatov 13101* (LE). RUSSIA. **Altay:** Ojrotiya, Koshagachskij, Chujskij, Chegan-uzuna, 17 Aug. 1937, *Shatakelberg & Knorring s.n.* (LE). TADZHIKISTAN. Zaalajskij, Gordaba, 2 July 1901, *O. A. & B. A. Fedchenko s.n.* (LE). UZBEKISTAN. Fergana, Osch., in Frag. Schart jugi Alaici, 12 July 1900, *Tranzschel s.n.* (LE).

13. Doronicum gansuense Y. L. Chen, Acta Phytotax. Sin. 36: 73. 1998. TYPE: China. Gansu: Tebbu Yian, *J. F. Rock 12102* (holotype, PE not seen).

Doronicum cavillieri Álv. Fern. & Nieto Fel., Ann. Bot. Fenn. 37: 250. 2000. Syn. nov. TYPE: China. Gansu: T'ao river basin, Minshan range, Kuang ke, *J. F. Rock 12389* (holotype, NY!; isotypes, BM!, GH!, LE!).

Plant up to 30 cm tall. *Rhizomes* somewhat woody, glabrous, generally with leaf remains. *Stems* not branched, with leaves all along the stem, internodes generally shorter than adjacent leaves. Indumentum of glandular trichomes (up to 2 mm), more abundant near the capitula, sometimes glabrous at the base. *Leaves* entire. Basal leaves sometimes absent at flowering time; blade 1.4–3.5 × 1.5–3 cm, orbicular, suborbicular, or elliptic, with truncate or attenuate base and blunt apex, with actinodromous to pinnate-actinodromous venation; petiole 3–8.5 cm long, 0.8–1.5 mm wide. Lower and middle cauline leaves 3–5 × 1–3 cm, sessile, ovate-elliptic to widely elliptic, semi-amplexicaul. Upper cauline leaves 1.5–4 × 0.7–2 cm, similar to middle cauline leaves. Indumentum of uniseriate eglandular trichomes (up to 0.5 mm), short-stalked glandular trichomes, and sometimes also long-stalked glandular trichomes, mainly on leaf margins, scarce, sometimes glabrous. *Capitula* solitary, 3–5.5 cm diam. including rays; involucre shorter than rays, 2–3 cm diam. *Phyllaries* herbaceous, 1.2–1.4 cm long, 1.5–2.5 mm wide, ovate-lanceolate to widely subulate, with blunt apex (bearing a sessile gland). Indumentum similar to the upper part of stem, more abundant at the base. *Receptacles* glabrous. *Flowers* with yellow corollas. Ray flower corollas 2–2.5 cm long, 2–3 mm wide, obovate-elliptic, apex generally with 2 or 3 teeth. Disk flower corollas ca. 5 × 2 mm. *Cypselae* brown, homomorphic, ca. 3 × 1 mm, with eglandular trichomes or glabrate, sometimes glandular. Pappus up to 4 mm, white. (Mature cypselae not seen.) Chromosome number unknown.

Illustrations. Chen (1998: 36, fig. 1); Álvarez Fernández & Nieto Feliner (2000: 251, fig. 1); Figure 4A–D.

Distribution. Central China (provinces of Gansu and Sichuan). Woods, rocky places, and grassy slopes, altitude 3000–3700 m (Fig. 21).

After the name *Doronicum cavillieri* (Álvarez Fernández & Nieto Feliner, 2000) was published, the authors realized that a previously published name of which they were not aware corresponded to the same species. Although the type material of *Doronicum gansuense* was not available for the present study, plants from the type locality, as well as from other localities cited in protologue were examined. Morphological relationships of *D. gansuense* with other central Asian species is discussed above (see comments for *D. altaicum* and *D. briquetii*).

Selected specimens examined. CHINA. **Gansu:** T'ao river, Merku valley, *Rock 12192* (E, K, NY, S, W); T'ao river, Minshan range, Mt. Kuang ke, *Rock 12389* (BM, GH, LE, NY); Tebbu, Shimen, *Rock 13020* (E, GH, K, LE, NY, S, W); Lianhuashan, Kangle Xian, *Wang 91161* (MO). **Sichuan:** Hongyuan plain, road to Songpan, 1989, *Chamberlain et al. s.n.* (E).

14. Doronicum glaciale (Wulfen) Nyman, Syll. Fl. Eur.: 1. 1855. *Arnica glacialis* Wulfen, in Jacq., Collectanea 1: 230. 1786. *Aronicum glaciale* (Wulfen) Rchb., Fl. Germ. Excurs. 1: 234. 1831–1832. *Doronicum hirsutum* subsp. *glaciale* (Wulfen) Rouy, Rev. Bot. Syst. Géogr. Bot. 1: 55. 1903. TYPE: Austria. Malnizer Tauern [sine collector], ex herb. Wulfen (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 803), W!).

Arnica doronicum Jacq., Fl. Austriac. 1: 57, tab. 92. 1773. *Grammarthron biligulatum* Cass., in Cuvier, Dict. Sci. Nat. 19: 295. 1821. *Aronicum doronicum* (Jacq.) Rchb., Fl. Germ. Excurs. 1: 233. 1831–1832. TYPE: "Arnica doronicum" [sine collector], ex herb. Linnaeus (lectotype, designated here, LINN nº 1001.4!).

Plant up to 30 cm tall. *Rhizomes* fleshy to somewhat woody, with shining white-tinted short trichomes on nodes, generally with leaf remains. *Stems* not branched, with leaves mainly at the base or on the middle lower part of stem. Indumentum of short-stalked glandular trichomes, also with eglandular trichomes more abundant near the capitula. *Leaves* entire to slightly dentate. Basal leaves generally present at flowering time; blade 1.5–4.5 × 1–2 cm, elliptic to ovate-elliptic, with truncate or attenuate base, blunt to subacute apex, with actinodromous to pinnate-actinodromous venation; petiole 2–6 cm long, 1–2.5 mm wide. Lower and middle cauline leaves 3–7.5 × 1–4 cm, similar to basal leaves or sessile, ovate-elliptic to narrowly elliptic, semi-amplexicaul. Upper cauline leaves 1.5–3.5 × 0.3–2 cm, similar to middle cauline leaves, or ovate-lanceolate. Indumentum of stiff, acute, and shiny eglandular trichomes (up to 2.5 mm), mainly on leaf margins, and also short-stalked glandular trichomes. *Capitula* solitary, 4–5.5 cm diam. including rays; involucre shorter than rays, 1.5–3.5 cm diam. *Phyllaries* herbaceous, ovate-lanceolate to widely subulate; the outer 1.2–1.5 cm long, 1.5–3.3 mm wide; the inner 1–1.4 cm long, 1–1.3 mm wide. Indumentum similar to the upper part of stem. *Receptacles* glabrous to glabrate. *Flowers* with yellow corollas. Ray flower corollas 2–2.2 cm long, 2.5–3 mm wide, obovate-elliptic, apex generally with 3 teeth. Disk flower corollas up to 4 mm long. *Cypselae* brown, with grooved-reticulate surface, homomorphic, up to 2 mm long, with eglandular trichomes or glabrate. Pappus up to 4 mm, white. Chromosome number $2n = 60$ (Polatschek, 1966, as *D. calcareum*; Lovka et al., 1972).

Illustrations. Jacquin (1773: tab. 92, 1789: tab. 586); Sturm (1814: tab 19.2); Reichenbach (1854: tab. 62, tab. 63 figs. 1, 3); Hegi (1928: fig. 431); Figure 3C–E.

Distribution. Europe (central-eastern Alps). Open moist rocky places and screes, altitude 1000–2800 m (Fig. 19).

In 1773 Jacquin described *Arnica doronicum*. This species corresponds to *Doronicum* and although Jacquin named it first, the ICBN (Greuter et al., 2000) does not allow the use of the same epithet for both genus and species; thus the correct epithet is "*glaciale*" given by Wulfen in Jacquin (1786). Part of Jacquin's collection is kept at LINN. When this herbarium was studied, one sheet of Jacquin's material labeled as "*Arnica doronicum*" was found. To clarify as far as possible the identity of Jacquin's name, its lectotype is designated here (see *D. glaciale* synonyms).

Doronicum glaciale is a species very similar to *D. clusii* and to a lesser extent to *D. grandiflorum*. Similarities and differences among these species are discussed above (see comments for *D. clusii*).

Selected specimens examined. AUSTRIA. **Kärnten:** Gartnerkofel zur Kühnveger Alp., 15 July 1928, *Bothe s.n.* (B); Wolayer-Alpe, Bierbaum, Lesachthal, 25 July 1907, *Engelhardt s.n.* (B); Stonhütte, Bärental, Karawanken, *Hodgkin 168* (K); Wolayer See, Qailtal, *Hodgkin 220* (K); Gloknerhauses am Steige zur Pasterze, 27 July 1899, *Schulz s.n.* (B). **Salzburg:** Radstädter Tauern, Plu Menspitze, *Jacquemoud 3888* (G); Auf den Thanern bei Wildbad Sastein, July 1892, *Pichler s.n.* (G); Pinzgau, *Sauter 971* (B, K); Gamskaar Kogel, *Wyatt 28* (K); Sulzkar, Ennothaler Alps, *Wyatt 89* (K). **Steiermark:** Grafenalpe prope Krakaudorf, July 1902, *Fest s.n.* (K); Mt. Hochschwab, Aug. 1887, *Steininger s.n.* (G, LY). **Tirol:** Virgen in valle Isolae, 10 Aug. 1873, *Ausserdorfer s.n.* (E, K); Kleiner Ispeltal, Johannishütte, July 1929, *Beger s.n.* (B); Gröden, Dolomiten, Hochjoch, Geislen gruppe, 27 July 1907, *Bornmüller s.n.* (B); montem Weisspitz pr. Herzing, Aug. 1888, *Huter s.n.* (K); Pfumpenseetauern, Bavaria, 25 July 1955, *Launert s.n.* (BM); Lienz, auf der Zoche, Herschbaummer Alpe, 31 July 1899, *Schulz s.n.* (B); Steinhaus, June 1878, *Treffer s.n.* (B); Tristen in Weissenbach, 24 July 1890, *Treffer s.n.* (G); Bendelstein, Wippthal, *Wyatt 56* (K). GERMANY. **Bayern:** Steinige zehatteze Triften in Hasenthal Prettan, Aug. 1882, *Treffer s.n.* (B). ITALY. **Trentino-Alto Adige:** Trento, Campitello di Fassa, col Rodella, *Álvarez et al. 1350* (MA). SWITZERLAND. Furka pass, Rhônegletscher, 24 July 1886, *Bornmüller s.n.* (B).

15. Doronicum grandiflorum Lam., Encycl. 2: 313. 1786. TYPE: "Arnica altaic. pall., tige simple unifl. haute de 4 ou 7 pouces, fl. tres grande, fleurit au com. + de mai" [sine collector], ex herb. Lamarck (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 803), P-LA!, photograph).

Doronicum scorpioides Lam., Encycl. 2: 313. 1786. TYPE: "A Arnica scorpioides L." [sine collector], ex herb. Lamarck (lectotype, designated here, P-LA!, photograph).

Doronicum portae Chabert, Bull. Soc. Bot. France 53: 547. 1906. Syn. nov. TYPE: Austria. Valbona, Aug. 1893, *P. Porta s.n.* (lectotype, designated here, FI!).

Plant up to ca. 70 cm tall. *Rhizomes* fleshy to somewhat woody, with shining white-tinted short trichomes on nodes, generally with leaf remains. *Stems* generally simple. Indumentum of short- and long-stalked glandular trichomes, also with multiseriate eglandular trichomes more abundant near the capitula. *Leaves* slightly dentate to dentate. Basal leaves sometimes present at flowering time; blade 3–6(7) × (1)2–5 cm, ovate-elliptic, ovate or suborbicular, with subcordate, truncate or attenuate base, blunt apex, actinodromous venation; petiole 10(20)–(1.5)4 cm long, 1–4(6) mm wide. Lower and middle cauline leaves (1)4–9(13.2) × (1)1.5–6(7) cm, similar to basal leaves or sessile, ovate-elliptic, sometimes almost fiddle-shaped, semi-amplexicaul. Upper cauline leaves 1.2–5.5 × 0.5–2 cm, similar to middle cauline leaves, ovate to ovate-lanceolate.

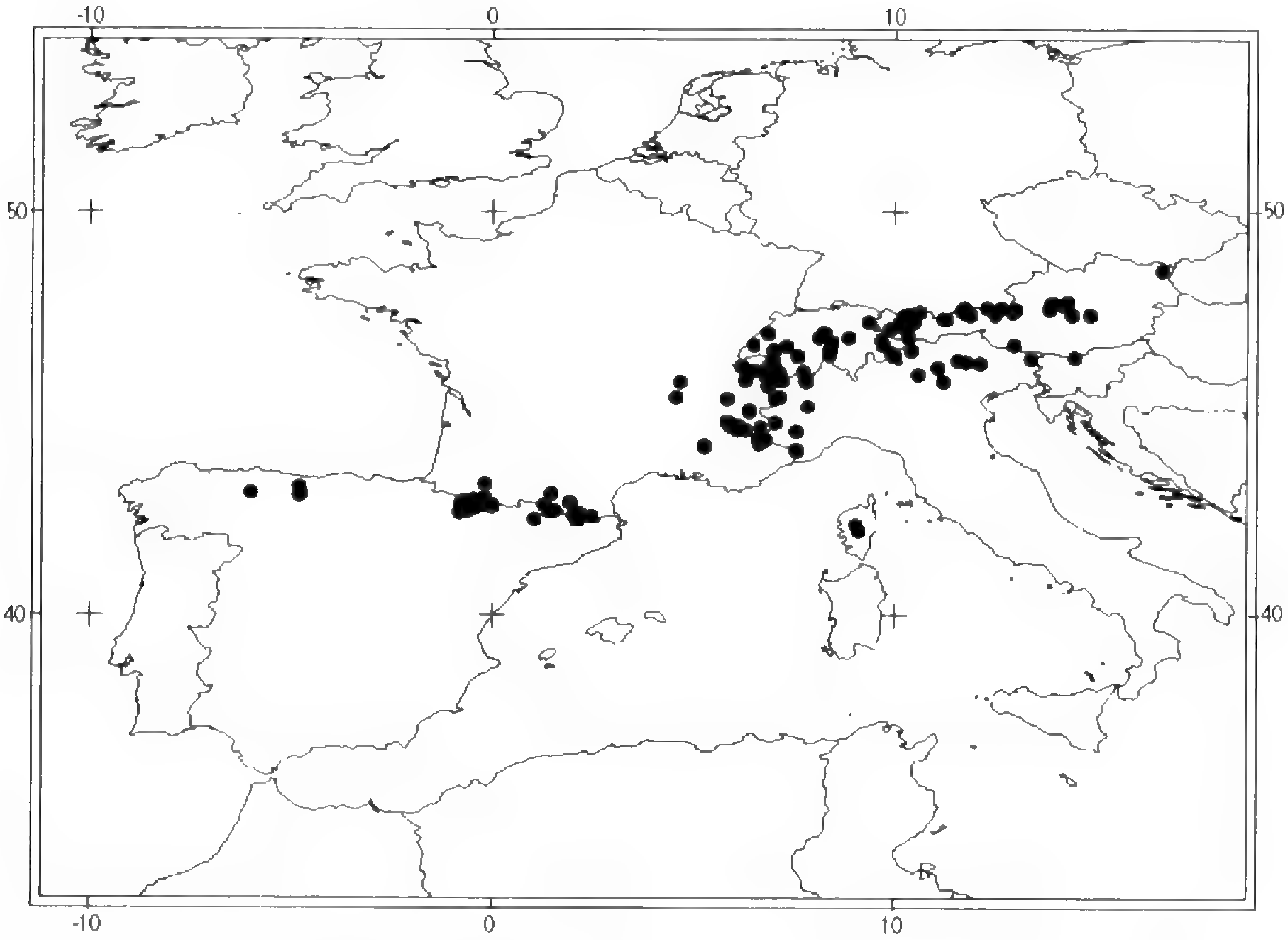

Figure 22. Distribution map for *Doronicum grandiflorum.*

Indumentum mainly of glandular trichomes, sometimes also with eglandular trichomes. *Capitula* 1(to 4), 3.5–5.5 cm diam. including rays; involucre shorter than rays, 2–4 cm diam. *Phyllaries* herbaceous, ovate-lanceolate to widely subulate; the outer 1–2(2.5) cm long, 1.5–4 mm wide; the inner 1–2 cm long, 1–2.8 mm wide. Indumentum of glandular trichomes, sometimes also with eglandular trichomes. *Receptacles* glabrous to glabrate. *Flowers* with yellow corollas. Ray flower corollas 1.3–2.6 cm long, 2–4.5 mm wide, obovate-elliptic, apex generally with 3 teeth. Disk flower corollas 3.5–5 × 1–2.5 mm. *Cypselae* brown, with grooved-reticulate surface, homomorphic, 2.5–4.5 × 0.5–1.5 mm, with eglandular trichomes or glabrate, sometimes with glandular trichomes. Pappus up to 5.5 mm, white. Chromosome number $2n = 60$ (Favarger & Huynh, 1964; Favarger & Küpfer, 1968).

Illustrations. Jacquin (1776: tab. 349); Sturm (1814: tab 19.2); Reichenbach (1854: tab. 62); Săvulescu (1964: pl. 188 fig. 1); Bolòs & Vigo (1995: 837); Figure 3A, B.

Distribution. Central-western Europe. Open moist rocky places, screes, and near watercourses, altitude 900–3000 m (Fig. 22).

Variable in size and shape of basal leaves and type of indumentum. Based on the latter, two species were recognized in the previous revision of the genus (Cavillier, 1907), *Doronicum viscosum* and *D. portae*, which are separated virtually solely by glandular versus mainly eglandular indumentum, respectively. Although type material of *D. viscosum* was not seen, several populations from the type locality were studied. The type material of *D. portae* was found at FI, and its lectotype is designated above. Abundant intermediates preclude recognition of these two species, which are here placed as synonyms of *D. grandiflorum.*

To clarify as far as possible the confusion around the epithet "*scorpioides*" the lectotype for *Doronicum scorpioides* is designated above. In the protologue, Lamarck mentioned "A *Arnica scorpioides* L.," refering to Jacquin's plate *Arnica scorpioides* L. (Jacquin, 1776: tab. 349). Although the type of Linnaeus's name corresponds to *D. pardalianches* L., Jacquin's plate represents a specimen of *D. grandiflorum*, as well as the only sheet kept at P-LA with the handwritten "A *Arnica scorpioides* L." (see comments below about *D. pardalianches*).

Although similar in their morphology, the differences in the type of indumentum among *Doronicum grandiflorum, D. clusii,* and *D. glaciale* are quite clear. In *D. grandiflorum* the trichomes are never entangled and always have a blunt apex (generally ending in two cells), and the stalked glands are similar to these trichomes (Fig. 3B) but with a glandular apex (generally two or more cells containing a brown substance). In *D. glaciale* the trichomes are stiff with an acute apex, and in *D. clusii*, which also has this latter type of indumentum, trichomes are very thin, long, and entangled (see comments under *D. clusii*).

Some populations of *Doronicum grandiflorum* from the Cantabrian range in northern Spain have broadly ovate to suborbicular, scarcely dentate to subentire basal leaves, and are difficult to distinguish from *D. carpetanum* subsp. *diazii.* These two taxa are similar but the nature of their relationship is not clear. A likely hypothesis, which should be investigated, is that *D. carpetanum* subsp. *diazii* is of hybrid origin, its putative progenitors being *D. grandiflorum* and *D. carpetanum* subsp. *carpetanum.*

Although widely distributed in the European mountains, the most recent collection of *Doronicum grandiflorum* from Corsica was in 1917, suggesting that it is now extinct there.

Selected specimens examined. ANDORRA. Mt. Canillo, 27 June 1847, *Bourgeau s.n.* (G, LY). AUSTRIA. **Kärnten:** Dobratsch, 20 July 1928, *Widder s.n.* (MAF). **Oberösterreich:** Windischgarsten, *Oberleitner 73* (B). **Steiermark:** Totes Gebirge, Feuertal, *Rechinger 2377* (BM, E, K). **Tirol:** Paznauntal, Ischgl, *Townsend 93/574* (K). **Vorarlberg:** Schruns, 27 July 1895, *Bornmüller s.n.* (B). FRANCE. **Alpes-Maritimes:** col de Tende, *Bourgeau 140* (COI-WILLK). **Ariège:** Artigues, étang du Laurenti, *Charpin & Dittrich 17387* (G). **Basses-Alpes:** Le Lautaret Dauphiny, July 1906, *Brown s.n.* (E). **Corse:** Mt. Rotondo, *Forsyth-Major 292–23* (K). **Isère:** Mt. Obiou, 7 Aug. 1864, *Borel s.n.* (K). **Haute-Savoie:** Mt. Vergy, *Timothée 4264* (BR). **Hautes-Alpes:** Vars, Saint-André d'Embrun, *Sieber 85* (G, K). **Hautes-Pyrénées:** Vignemale, 24 July 1850, *Hennecart s.n.* (NY). **Loire:** Pilatus, 10 Sep. 1884, *Hamilton s.n.* (E). GERMANY. **Bayern:** Bavaria, Mts. Krotten-kopf, 15 July 1894, *Bornmüller s.n.* (B). ITALY. **Friuli-Venezia Giulia:** Mts. Baldi, 8 July 1870, *Rigo s.n.* (E). **Liguria:** Carro, lago della Seala, 3 Aug. 1912, *Beger s.n.* (B). **Lombardia:** Sondrio, Bormio, Valpisello, Aug. 1920, *Longa s.n.* (BM). **Piemonte:** Cúneo, Colla dell Pizzo, Alpes d'Ormea, *Charpin & Salaman 17480* (G). **Trentino-Alto Adige:** Avisio, inter Peniam et jugum Fedaja, 18 July 1906, *Handel-Mazzetti s.n.* (G). **Valle d'Aosta:** Grand St. Bernard pass, *Brummitt 5494a* (K). **Veneto:** Belluno, Forcella Beccher, 11 July 1970, *Dusa & Mortin s.n.* (MA). SPAIN. **Aragón:** Huesca, San Juan de Plan, Posets, *Almaraz & Cano 288* (MA); Huesca, Jaca, Canfranc, ibón de Ip, *Vogt 3960* (B). **Cantabria:** Vega de Liébana, laguna de Peña Prieta, *Álvarez et al. 943* (MA); Picos de Europa, inter lacus Los Pozos et La Canalona, *Rechinger 1701* (W). **Castilla y León:** León, San Emiliano, Peña Ubiña, 8 July 1990, *Aedo s.n.* (MA). **Cataluña:** Lérida, val de Arán, torrent de Barrongueta, *Vogt & Prem 7327* (B). SWITZERLAND. **Graubünden:** Piz Padella, *Lorenz 27532* (B). **Valais:** val d'Entremont, Bec Rond, 4 Aug. 1927, *Cuatrecasas s.n.* (MAF). **Vaud:** Ormond-Dessous, pic Chaussy, col des Mosses, *Kramer 8672* (MA). YUGOSLAVIA. **Slovenija:** Julijske Alpe, Vrh Krnic, lacum Bohinjsko, *Wraber 9748/4* (B, BM).

16. Doronicum haussknechtii Cavill., Annuaire Conserv. Jard. Bot. Genève 13–14: 255. 1911. TYPE: Turkey. Beryt dagh, *H. K. Haussknecht 1029* (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 804)).

Doronicum tobeyi J. R. Edm., Notes Roy. Bot. Gard. Edinburgh 32(2): 256. 1973. Syn. nov. TYPE: Turkey. Giresun, Karagöl, *C. Tobey 1484* (holotype, E!).

Plant up to 100(+) cm tall. *Rhizomes* woody, glabrous, with or without leaf remains. *Stems* branched in the upper part, leaves distributed along the stem, upper internodes generally longer than the adjacent leaves. Indumentum of multiseriate and uniseriate white eglandular trichomes (ca. 0.2 mm), abundant near the capitula, sometimes glabrate. *Leaves* entire to dentate. Basal leaves sometimes present at flowering time; blade ca. 11 × 12–12.5 cm, orbicular or ovate, with cordate base and generally blunt apex, with actinodromous venation; petiole 12–20 cm long, with sheathing base, sheath ca. 6–8 cm long. Lower cauline leaves with blade ca. 23 × 18 cm; petiole (0.7–)37.5 cm long, similar to basal leaves. Middle cauline leaves ca. 16 × 9 cm, sessile, fiddle-shaped, semi-amplexicaul. Upper cauline leaves ca. 5 × 2.5 cm, similar to middle cauline leaves or ovate to obovate, sometimes bract-like. Indumentum similar to the adjacent part of the stem and with short-stalked glandular trichomes, generally scarce, more abundant on margins of leaves. *Capitula* up to 17(+), ca. 4 cm diam. including rays; involucre shorter than rays, ca. 2 cm diam.; sometimes turbinate at the base of capitula in fruit. *Phyllaries* herbaceous, ca. 1.3 cm long, 2 mm wide, ovate-lanceolate to obovate-lanceolate and acute. Margins scarcely and slightly fimbriate. Indumentum similar to the upper part of stem, sometimes with scarce multiseriate eglandular trichomes. *Receptacles* glabrous or glabrate. *Flowers* with yellow corollas. Ray flower corollas 1.3–1.6 cm long, 2–4 mm wide, obovate-elliptic to oblong-elliptic, apex generally with 3 teeth. Disk flower corollas 4–4.5 × 1.5 mm. *Cypselae* brown, with smooth to slightly grooved surface, dimorphic. Cypselae from ray flowers 4–6 × 1.5–2 mm, glabrous or glabrate, without pappus. Cypselae from disk flowers 3.5–4 × 1.2–1.7 mm, sometimes with eglandular trichomes; pappus 3.5–4.5 mm, white. Chromosome number unknown.

Illustrations. Figure 23F–J.

Distribution. Northern and central Turkey (provinces of Giresun, Kayseri, and Maraş). Meadows and near watercourses, altitude 2100–2600 m (Fig. 24).

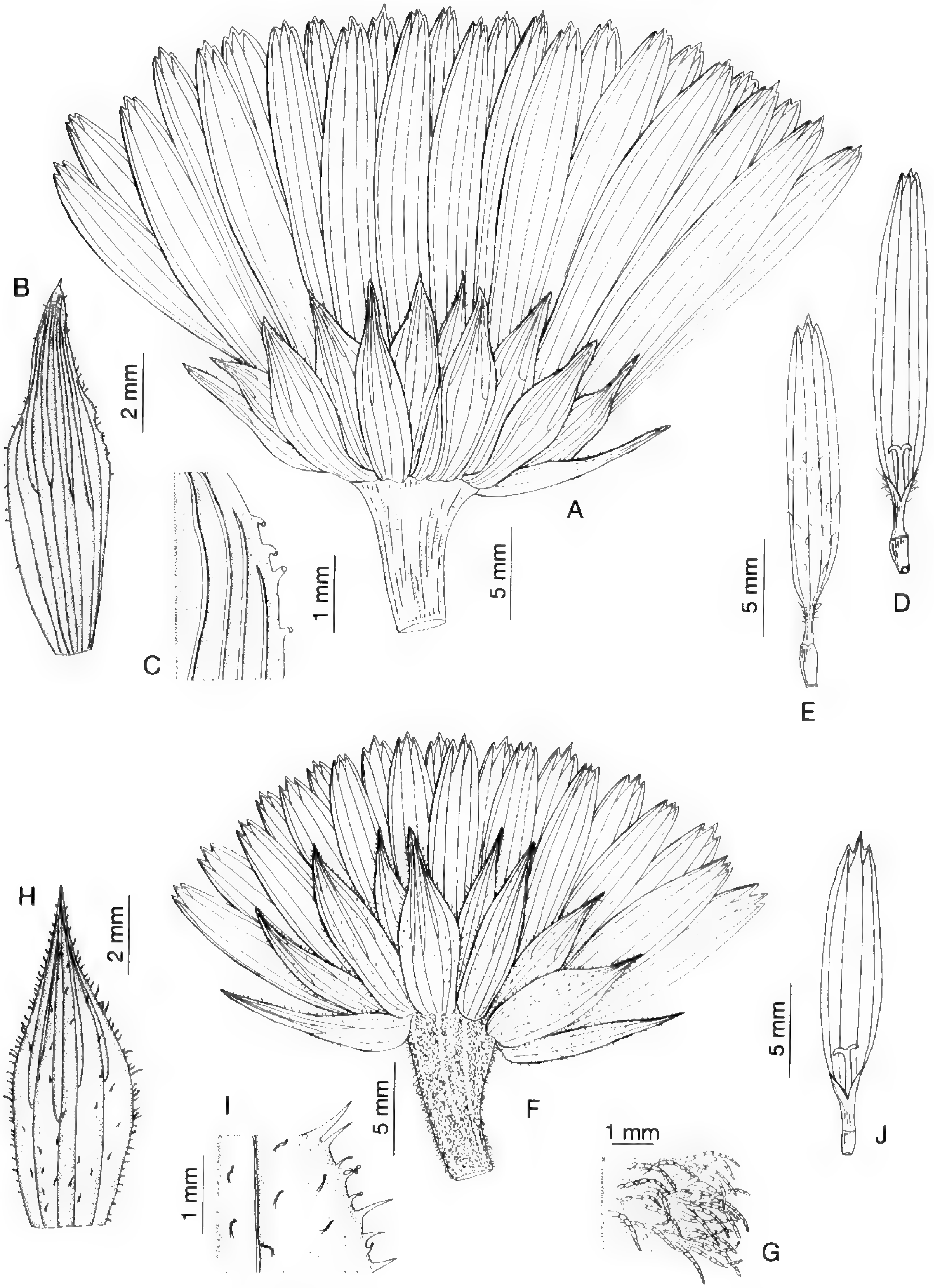

Figure 23. A–E. *Doronicum maximum* (drawn from *Davis et al. 20588,* E). —A. Capitulum. —B. Phyllary. —C. Indumentum of a phyllary. —D–E. Ray flower. F–J. *Doronicum haussknechtii* (drawn from *Davis et al. 20010,* E). —F. Capitulum. —G. Indumentum of the base of the capitulum. —H. Phyllary. —I. Indumentum of a phyllary. —J. Ray flower.

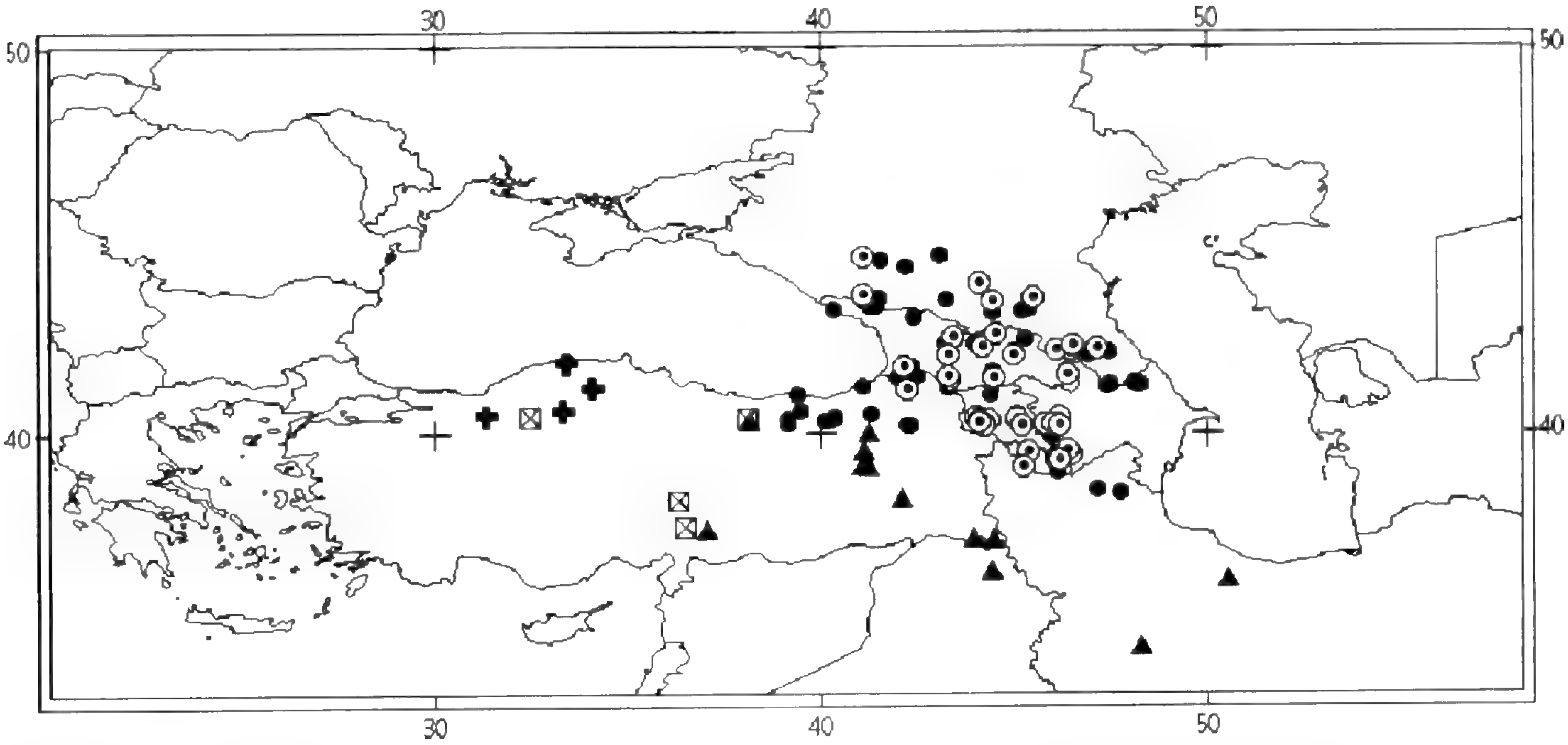

Figure 24. Distribution map for: *Doronicum haussknechtii* (☒); *Doronicum macrophyllum* subsp. *macrophyllum* (●); *Doronicum macrophyllum* subsp. *sparsipilosum* (+); *Doronicum maximum* (▲); *Doronicum oblongifolium* (⊙).

There are several Turkish species included in the same morphological group (see comments for *D. cacaliifolium* and *D. dolichotrichum* above) that are distinguished from each other only based on the type of indumentum. *Doronicum haussknechtii* is included in this group, and morphologically the most similar species is *D. maximum,* which also overlaps part of its area of distribution with *D. haussknechtii* (Fig. 24). In both *D. haussknechtii* and *D. maximum,* the indumentum on the phyllaries is very scarce or even absent (Fig. 23B, C, H, I), while the rest of the Turkish species have pubescent or glandular phyllaries. The characters to distinguish between these two species are the white pubescence at the top of the peduncle (base of the capitulum) in *D. haussknechtii* (Fig. 23F, G), which is glabrous in *D. maximum* (Fig. 23A), and the scarcely fimbriate margins of phyllaries in *D. haussknechtii* (Fig. 23H, I), which are entire, sometimes with glands in *D. maximum* (Fig. 23B, C).

The diagnostic characters used to separate *Doronicum tobeyi* (Edmondson, 1973) overlap substantially with those of *D. haussknechtii,* and its patterns of indumentum match those of *D. haussknechtii.* Accordingly, this name is considered a synonym.

Selected specimens examined. TURKEY. **Kayseri:** Isikdagi, Karlidere, *Duman. & Aytaç 5413* (GAZI). **Maraş:** Goksun, Binboga dag, Isik dag, *Davis et al. 20010* (BM, E, K).

17. Doronicum hungaricum Rchb. fil., Icon. Fl. Germ. Helv. 16: 34, tab. 65, fig. 1. 1854. TYPE: icon in Reichenbach (1854: tab. 65, fig. 966 I 1–8) (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 804)).

Plant up to 80 cm tall. *Rhizomes* fleshy, glabrate to scarcely pubescent, with inconspicuous shining white-tinted trichomes on nodes, thick and short, sometimes stoloniform, with buds. *Stems* generally unbranched, scape-like. Indumentum mainly glandular, with short-stalked and long-stalked glandular trichomes, sometimes also uniseriate and multiseriate eglandular trichomes, more abundant near the capitula. *Leaves* entire, rarely subdentate. Basal leaves generally present at flowering time; blade 4–9 × 1–3 cm, oblong-elliptic with truncate or attenuate base, blunt apex, with acrodromous venation; petiole 4–8 cm long, 1–2 mm wide. Lower cauline leaves 3–11 × (0.5)1–2.6 cm, similar to basal leaves or sessile, elliptic to fiddle-shaped, sometimes semi-amplexicaul. Upper cauline leaves 2–5 × 0.4–1.3 cm, ovate-lanceolate, sometimes bract-like. Indumentum with uniseriate eglandular trichomes and short-stalked glands, scarce. Generally also with long multiseriate eglandular trichomes (up to 5 mm), mainly on the adaxial surface of middle vein. *Capitula* 1(2 to 3), 3–6 mm diam. including rays; involucre a little shorter than rays or equaling them, 2.5–4.5 cm diam. *Phyllaries* herbaceous, ovate-subulate, generally with acute apex; the outer 1–1.5 cm long, 1–1.5 mm wide; the inner 1.1–1.8 cm long, 0.7–1 mm wide. Margins sometimes ciliate, with acute, stiff and equidistant multiseriate eglandular trichomes (up to 1 mm). Indumentum mainly glandular. *Receptacles* glabrous or scarcely pubescent. *Flowers* with yellow corollas. Ray flower corollas 1.4–2.5 cm long, 1–2(3) mm wide, oblong-elliptic, apex generally with 3 teeth. Disk flower corollas up to 4 mm long. *Cypselae* brown, with

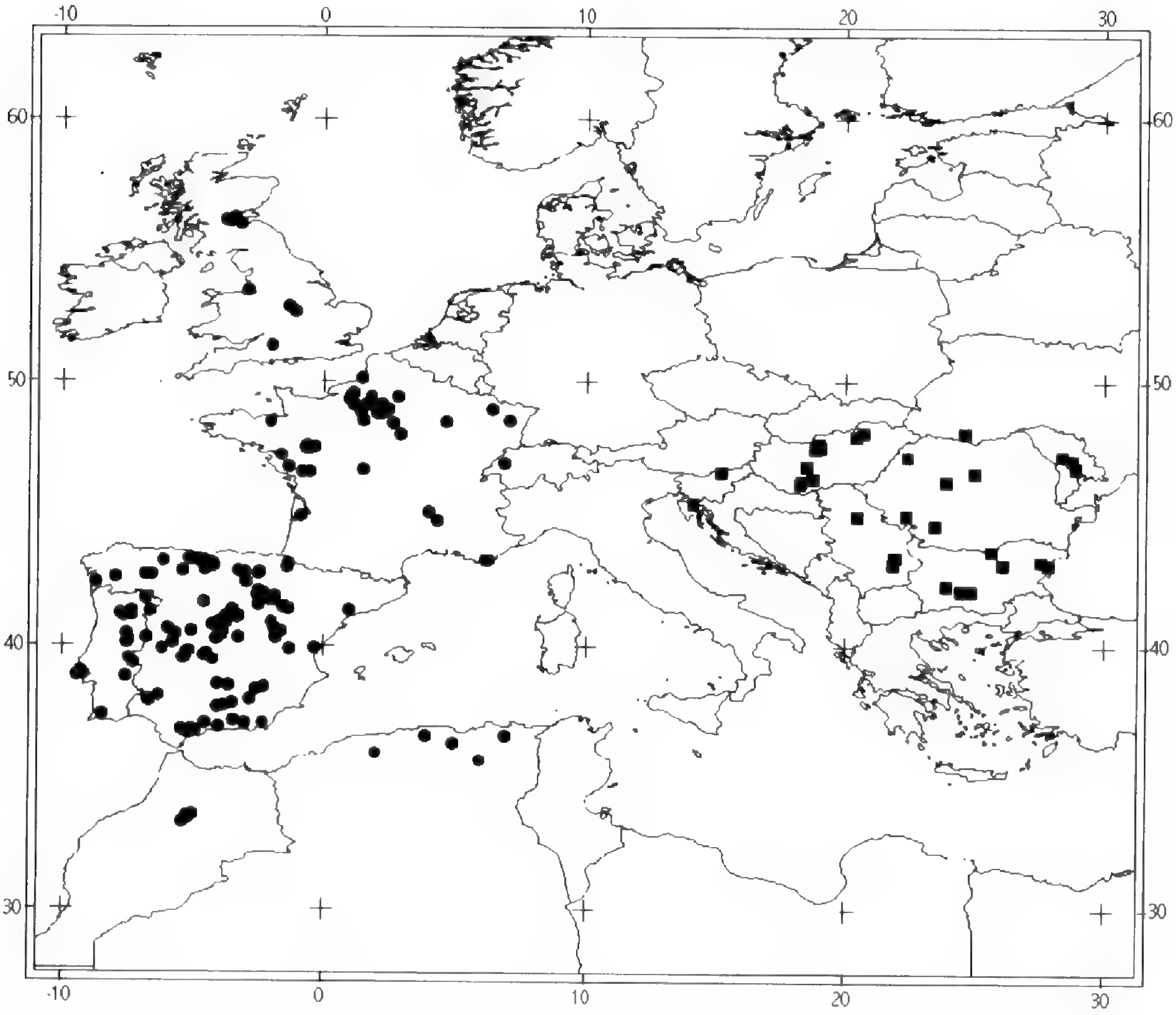

Figure 25. Distribution map for: *Doronicum hungaricum* (■); *Doronicum plantagineum* (●).

rugose-reticulate surface, dimorphic. Cypselae from ray flowers 2–2.3 × 0.6–1 mm, generally glabrous, without pappus. Cypselae from disk flowers 1.7–2 × 0.7–1 mm, with eglandular trichomes; pappus up to 3.5 mm, white. Chromosome number $2n = 60$ (Baksay, 1956).

Illustrations. Reichenbach (1854: tab. 65, fig. 966 I 1–8); Săvulescu (1964: pl. 98, fig. 1); Figure 1B.

Distribution. Eastern Europe (Balkans, Carpathians, and Ukraine). Forests and meadows, altitude 160–1900 m. Cultivated and sometimes naturalized (Fig. 25).

The name *Doronicum plantagineum* var. *hungaricum* Sadler (1840) was published before the accepted name for this species, *Doronicum hungaricum* Rchb. fil. (1854). Plants collected by Sadler are included in the protologue of Reichenbach's specific name. However, in the protologue Reichenbach did not mention the earlier name, and so his name is not based on Sadler's.

The name *Doronicum longifolium* Rchb. (1831–1832) is clearly a synonym of *Doronicum clusii* (All.) Tausch. However, when Grisebach (1846) combined it as *Doronicum plantagineum* var. *longifolium* (Rchb.) Griseb., his description and geographical distribution were those of *D. hungaricum*, not *D. clusii*. Later, the same author (Grisebach & Schenk, 1852) explicitly treated Reichenbach's name as a synonym of *D. plantagineum* var. *hungaricum* Sadler. Thus, the names *D. longifolium* auct., non Rchb., and *D. plantagineum* var. *longifolium* (Rchb.) sensu Griseb. are synonyms of *D. hungaricum* Rchb. fil.

Doronicum hungaricum could be confused with *D. clusii*, *D. glaciale*, and the Caucasian *D. oblongifolium* because of the elliptic entire basal leaves and similar habit in some specimens of those species, but in the case of *D. hungaricum* the rhizome is fleshy with pubescent nodes, the basal leaf venation has an acrodromous pattern, and the phyllary margins are ciliate to somewhat ciliate. All these characters together lead to the inclusion of this species in the morphologic and phylogenetic "*plantagineum*" group (see Phylogeny above and Fig. 9). Within this group the most closely related species is *D. plantagineum*, which differs mostly in the shape of basal leaves (ovate in *D. plantagineum* vs. elliptic in *D. hungaricum*) and in the type of indumentum. *Doronicum hungaricum* is considered the vicariant species of *D. plantagineum* in eastern Europe, although it has a more restricted area than *D. plantagineum* has in western Europe and northern Africa (Fig. 25).

Selected specimens examined. BULGARIA. **Pazardzhik:** Belovo, May 1894, *Stříbrný s.n.* (E, K); Sestrimo, May 1907, *Stříbrný s.n.* (E). **Plovdiv:** Krichim, May 1901, *Stříbrný s.n.* (E). **Ruse:** Mt. Rhodope ad Čaušovo, 26 May 1900, *Stříbrný s.n.* (W); Rhodope ad Stanimaka, May 1900, *Stříbrný s.n.* (G). **Varna:** Varna, *Gilliat-Smith 554* (K); Kamcyr, *Schneider 300* (B, BM, MO). HUNGARY. **Baranya:** Mecsek prope Pécs, 25 May 1922, *Boros s.n.* (BM). **Heves:** Agria, Mt. Mészhegy, 10 May 1870, *Vrabélyi s.n.* (B). **Pest:** Kameraerdo, 18 May 1885, *Degen s.n.* (W); Mt. Hárshegy prope Budapest, May 1886, *Degen s.n.* (B); Mt. Kamen prope Pomáz, 16 May 1904, *Degen s.n.* (LE); vallis Farkasvölgy prope Budam, *Filarszky & Schilberszky s.n.* (B, BM, E, G, K, MO, NY); Leopoldifeld bei Ofen, 1873, *Freyn s.n.* (W); Budapest, Crilleberc bei Budakeszi, 24 May 1933, *Korb s.n.* (W); Mt. Kopaszhegy, Nagykovácsi supra Budapest, 28 Apr. 1912, *Kümmerle Szurák & Timkó s.n.* (B, BM, E, G, K, MO, NY, W); Kammerwald, prope Budam, *Richter 520* (B, BM, G, W). **Tolna:** Mt. Csòkás, Simontornya, 27 May 1875, *Tauscher s.n.* (G, LE). ROMANIA. **Alba:** Blaj, Apr. 1923, *Pop s.n.* (E, G, K, MO, W). UKRAINE. Strashenskij, 28 May 1955, *Ananiva s.n.* (LE); Chernaya, 22 Apr. 1961, *Fodor s.n.* (LE); Zlotij, Bendery, 23 Apr. 1909, *Paczoski s.n.* (LE); Stramenskogo, 6 May 1948, *Shirokova s.n.* (LE). YUGOSLAVIA. **Srbija:** Belgrad, Tapeider, 1888, *Bornmüller s.n.* (B); Gabrovac prope Nisch, *Petrovič 2200* (BM, G, K, W).

18. Doronicum kamaonense (DC.) Álv. Fern., Novon 11: 294. 2001. *Fullartonia kamaonensis* DC., Prod. 5: 281. 1836. TYPE: "Comp. angl. des Indes 1830" [sine collector], ex herb. de Candolle (lectotype, designated by Álvarez Fernández (2001: 294), G-DC!, photograph).

Doronicum roylei DC., Prodr. 6: 321. 1838. TYPE: Cachemire, *J. F. Royle 232* (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 805), G-DC!, photograph).

Plant up to 130 cm tall. *Rhizomes* woody to somewhat woody, glabrous. *Stems* branched in the upper part or sometimes from the base, internodes generally longer than the adjacent leaves. Indumentum in the lower part of stem made up of multiseriate, retrorse and white-tinted eglandular trichomes (up to 4 mm), sometimes absent, upper part of stem generally glandular, with long-stalked glandular trichomes (up to 4 mm), sometimes also with uniseriate or multiseriate eglandular trichomes, rarely without glands; apex of glandular trichomes capitate, with more than 6 cells, peduncle capillary. *Leaves* entire to slightly dentate. Basal leaves generally absent at flowering time; blade 3.5–6.5 × 3.5–7 cm, ovate to ovate-elliptic, with attenuate, truncate, or subcordate base and generally blunt apex, with pinnate-actinodromous venation; petiole 5–16 cm long, 1.5–2 mm wide. Lower cauline leaves 3–11 × (0.8)2.5–9 cm; petiole 3–13 cm long, 1.5–4 mm wide, similar to basal leaves. Middle cauline leaves 7–15.5 × 3–10 cm, sessile, fiddle-shaped, semi-amplexicaul. Upper cauline leaves (0.8)1.5–7.5(11.6) × (0.1)0.8–4.5(6.2) cm, ovate-lanceolate, sometimes bract-like. Indumentum similar to the adjacent part of the stem. *Capitula* 2 to 18, 1.5–4 cm diam. including rays; involucre shorter than rays, 0.8–3 cm diam.; peduncles 1–10(18.5) cm long, 0.5–1.5(2) mm wide. *Phyllaries* herbaceous, ovate-subulate, generally with acute apex; the outer 0.6–1.2 cm long, 1–3 mm wide; the inner 0.6–1.2 cm long, 0.5–1.5 mm wide. Indumentum similar to the upper part of stem. *Receptacles* glabrous. *Flowers* with yellow corollas. Ray flower corollas 0.8–1.5 cm long, 1.2–2 mm wide, oblong-elliptic, apex generally with 3 teeth. Disk flower corollas 2.5–4 × 1–2.5 mm. *Cypselae* brown to brown-red with grooved-reticulate surface, dimorphic. Cypselae from ray flowers 2–3.6 × 1–1.5 mm, glabrous or glabrate, without pappus. Cypselae from disk flowers 2–3 × 1–1.5 mm, with eglandular trichomes; pappus (1.7)2–4 mm, white to yellow. Chromosome number $2n = 60$ (Vir Jee & Kachroo, 1989, as *D. roylei*).

Illustrations. Figures 8D, 20E–I.

Distribution. Central-southern Asia (Jammu-Kashmir to Nepal, Bhutan, and Tibet). Forests and meadows, elevation 1900–5000 m (Fig. 11).

There is only one species in central-southern Asia, *Doronicum stenoglossum,* which could become confused with *D. kamaonense* because of their similarities in habit. The differences between them are remarkable, since both have unique characters within the genus. *Doronicum stenoglossum* has corollas pale yellow to green shaded, linear ray flower corollas, and linear phyllaries (Fig. 4E, F). In *D. kamaonense* the type of indumentum at the base of the capitulum (glandular trichomes with a capillar peduncle and capitate apex bearing 6 or more cells; Figs. 8D, 20E, F) is a character to distinguish it from other species. Although the area of distribution of *D. kamaonense* overlaps in part with *D. briquetii* and *D. falconeri* (see comments for these species and Figs. 11, 21), there are no noticeable morphological similarities between those and *D. kamaonense.*

The name *Doronicum roylei* DC. was in use until the recent realization that the name *Fullartonia ka-*

maonensis DC. represents the same species and that it has priority (Álvarez Fernández, 2001).

Selected specimens examined. BHUTAN-SIKKIM. Sikkim, Gharu napo, *Cooper 867* (E). CHINA. **Sichuan:** Shingbe, Me La, *Ludlow et al. 20406* (E). **Tibet-Qinghai:** Chumbi, *Cooper 230* (E). INDIA. **Uttar Pradesh:** Chitona, Tehri, *Koelz 22052* (NY); Garhvál, Gaurikúnd via Tríjugi Naráin and Máser Tal to Bílung, 1855, *Schlagintweit s.n.* (GH). JAMMU-KASHMIR. Grorai, *Clarke 29287D* (BM, LE); Sonamurg, *Clarke 30842* (BM, K); Liddar Valley, *Drummond 14024* (E, K); Satrundi, Chamba, 13 Aug. 1897, *Lace s.n.* (E); Srinagar, Gulmarg, Khillanmarg plateau, *Lancaster 206* (BM); Sinthan pass, *Ludlow & Sherriff 9292* (BM, E); Karauli forest, near Rampur, Jhelun valley, *Ludlow & Sherriff 7719* (BM); Kishenganga valley, *Osmaston 28* (K); Khelanmarg, *Polunin 56/170* (B, BM, E); Sind valley, *Stainton 7894* (E); Shanda-Kel, Kishenganga valley, road to Nanga Parbat, *R. R. & I. D. Stewart 17786* (NY); Harwart, *Timins 174* (BM, E); Hazara, Mokspuri, Murree hills, *Webster & Sack 5715* (G, GH, K, S, W). NEPAL. Lamrak, *Dhwoj 196* (BM); Ghurchi Lagua, *Polunin et al. 4364* (BM, E, G, UPS); Barbaria Lekh, *Polunin et al. 89* (E, UPS); Balangra pass, *Polunin et al. 2622* (BM, E, UPS); Ratamata, Chakure Lekh, *Polunin et al. 401* (BM, E, G, UPS); Mailung Khola, *Stainton 7400* (BM); Chalike Pahar, *Stainton et al. 3145* (BM, E, UPS); Rambrong, Lamjung Himal, *Stainton et al. 6051* (E, UPS); Kapthad, Doti, *Tabata et al. 1072* (GH); Rara, Mugu, *Tabata et al. 12900* (BM, GH); Kali Lagna, Jumla, *Tabata et al. 19355* (GH); between Chautra and Maure lekh, Jumla district, *Tabata et al. 3309* (GH); Merghang, *Wigram 45* (E, K).

19. Doronicum macrophyllum Fisch., Cat. Jard. Gorenki ed. 2: 40. 1812. TYPE: North Caucasus. Beschtau [*F. A. F. Marschall von Bieberstein s.n.*], ex herb. Marschall von Bieberstein (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 804), LE!).

Plant up to 120(+) cm tall. *Rhizomes* woody to somewhat fleshy, glabrous, with or without leaf remains. *Stems* branched in the upper part, leaves distributed along the stem or mainly on the basal part of stem, upper internodes generally longer than the adjacent leaves. Indumentum of uniseriate (ca. 0.2 mm), multiseriate (up to 1 mm) eglandular trichomes, and glandular trichomes (0.5–2 mm) generally abundant near the capitula, sometimes glabrate at the base. *Leaves* entire to dentate. Basal leaves sometimes present at flowering time; blade (8)19–26(30) × (7)17–23 cm, orbicular or ovate, with cordate base and blunt or acute apex, with actinodromous venation; petiole 7–18 cm long, with sheathing base, sheath 3–8(10.7) cm long. Lower cauline leaves with blade 6–24 × 5–19.5 cm; petiole 9–33 cm long, 1–5 mm wide, similar to basal leaves. Middle cauline leaves 5–21.5 × 2–16.5 cm, sessile, fiddle-shaped, semi-amplexicaul. Upper cauline leaves 3–17 × 0.9–14(15) cm, similar to middle cauline leaves or ovate to obovate, sometimes bract-like. Indumentum similar to the adjacent part of the stem, more abundant on margins and on veins on the abaxial surface of leaves. *Capitula* 2 to 13, 3–5.5(7) cm diam. including rays; involucre shorter than rays, 1.5–3.5(4.5) cm diam.; peduncles (1.5)3–10.5(16) cm long, 1–1.6 mm wide, sometimes turbinate at the base of capitula (1.3 cm wide) in fruit. *Phyllaries* herbaceous or sometimes slightly papery at the base or at the margins, 0.6–1.5(2) cm long, 0.8–3(4) mm wide, ovate-lanceolate to obovate-lanceolate or subulate. Indumentum similar to the upper part of stem. *Receptacles* glabrous or glabrate. *Flowers* yellow. Ray flower corollas 1.5(1.9)–3(3.5) cm long, (1.7)2.3–3.3(5) mm wide, obovate-elliptic to oblong-elliptic, apex generally with 3 teeth. Disk flower corollas (3.5)4–6 × 1.5–2.5 mm. *Cypselae* brown, with smooth to grooved surface, dimorphic. Cypselae from ray flowers 3–4.5 × 1–1.3 mm, glabrous or glabrate, without pappus. Cypselae from disk flowers (2)2.3–4.5 × 0.5–1(1.5) mm, sometimes with eglandular trichomes; pappus (1.5)3–5 mm, white. Chromosome number $2n = 30, 60$ (data obtained from two indexes of plant chromosome numbers: Fedorov, 1969; Goldblatt, 1988; original sources not seen).

Illustrations. Figures 24, 26A–D.

Distribution. Northern Turkey and Caucasus. Growing in woods, open moist rocky places, meadows, and near watercourses, altitude 1500–3700 m.

The characters distinguishing this species from others in southwestern Asia are mainly based on the type of indumentum (see comments on *D. dolichotrichum*). *Doronicum macrophyllum* is a polymorphic species, and within it, two subspecies can be distinguished:

KEY TO THE SUBSPECIES OF *DORONICUM MACROPHYLLUM*

1. Plants generally with more than 3 capitula and more than 3 cauline leaves (including bract-like leaves) .... 19a. *D. macrophyllum* subsp. *macrophyllum*
1′. Plants bearing 1 to 3 capitula and 2 or 3 cauline leaves (including bract-like leaves) .... 19b. *D. macrophyllum* subsp. *sparsipilosum*

19a. Doronicum macrophyllum subsp. **macrophyllum**

Doronicum macrolepis Freyn & Sint., in Freyn, Bull. Herb. Boissier 3: 351. 1895. Syn. nov. TYPE: Turkey. Gümüschkane, in valle Böjükdere tractu Karagölldagh supra Artabir, *P. Sintenis 7173* (lectotype, designated by Edmondson (1975: 142), G!; isotypes, B!, BM!,

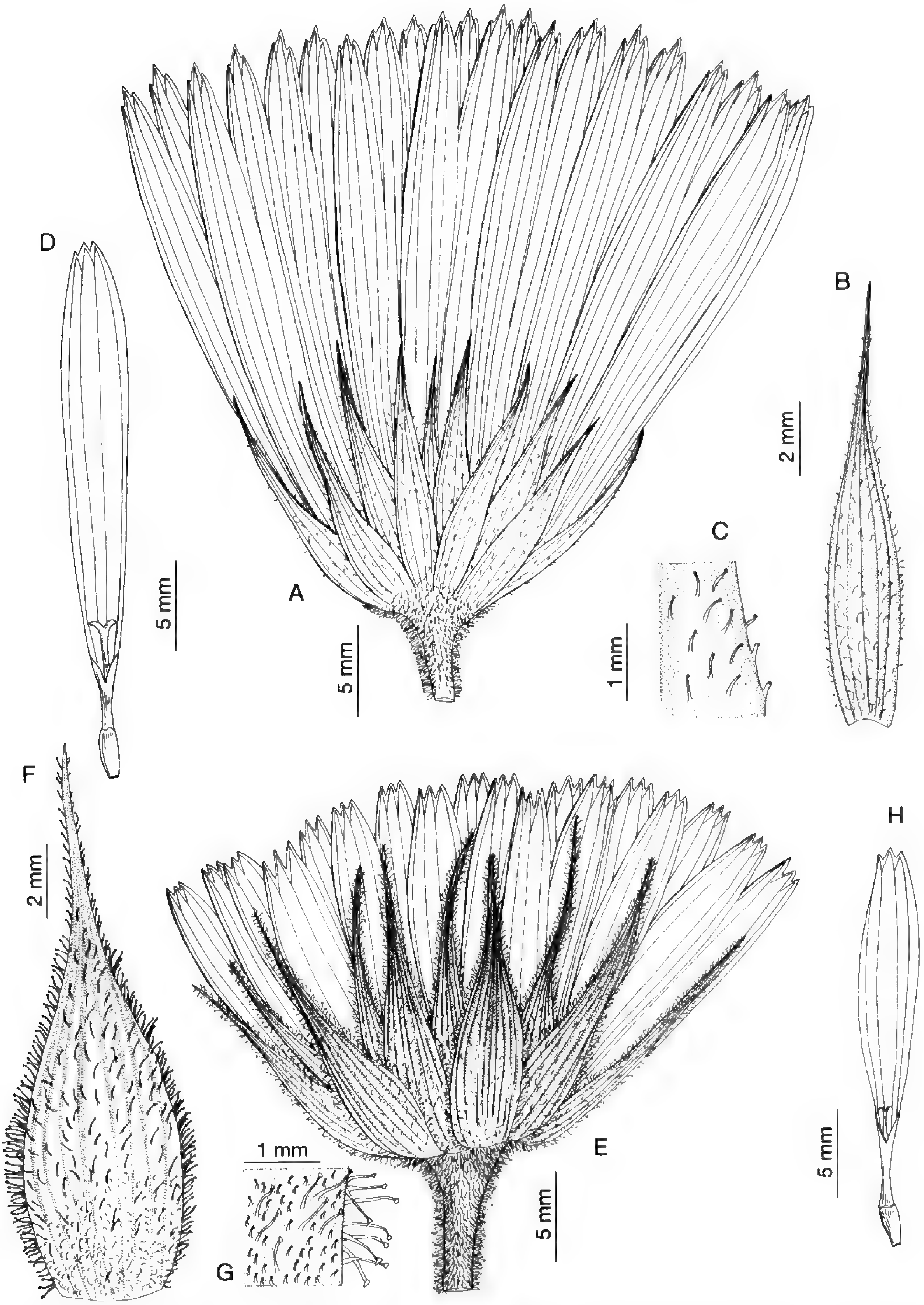

Figure 26. A–D. *Doronicum macrophyllum* subsp. *macrophyllum* (drawn from *Hohenacker s.n.*, K). —A. Capitulum. —B. Phyllary. —C. Indumentum of a phyllary. —D. Ray flower. E–H. *Doronicum reticulatum* (drawn from *Bornmüller 9620*, B). —E. Capitulum. —F. Phyllary. —G. Indumentum of a phyllary. —H. Ray flower.

BRNM!, E not seen, K!, LD! photograph, P not seen, S!, W!).

Doronicum balansae Cavill., Annuaire Conserv. Jard. Bot. Genève 14: 260. 1911. Syn. nov. TYPE: Turkey. Lazistan, près de Djimil, 1866, *B. Balansa s.n.* (lectotype, designated by Edmondson (1975: 140), G!; isotype, W!).

Rhizome woody. Stem with more than 3 cauline leaves. Plants generally bearing more than 3 capitula, which are sometimes turbinate at the base (1.3 cm wide) in fruit. Chromosome number unknown.

Illustrations. Avetisyan & Oganesyan (1995: tab. 174); Figure 26A–D.

Distribution. Northern Turkey and Caucasus. Growing in woods, open moist rocky places, meadows, and near watercourses, altitude 1500–3700 m (Fig. 24).

All the specimens from the only collection of *Doronicum macrolepis* differ from *D. macrophyllum* subsp. *macrophyllum* in size of capitula. Although the population is somewhat anomalous, the name is treated as a synonym of *D. macrophyllum* subsp. *macrophyllum.* The diagnostic characters used to separate *D. balansae* (Cavillier, 1911) overlap substantially with those of *D. macrophyllum* subsp. *macrophyllum.* Besides, the patterns of indumentum variability match those of *D. macrophyllum* subsp. *macrophyllum.* Accordingly, this name is considered a synonym.

Selected specimens examined. CAUCASUS. **North Caucasus:** Dagestan, Dargi, Maara, Akuscha, *Alexcenko 12861* (LE); Sharoj, Sharoargun, Serchikhi, *Averianov et al. 2837* (LE); Schelbur dagh, Daghestania, *Becker 132* (LE); Digoriya, Tators, Digor-Tors, 12 Aug. 1927, *E. & N. Busch s.n.* (LE); Stavropolskij, Karachaevo-Cherkesskaya, Pastvishnogo, *Geltman et al. 1179* (LE); Checheno-Ingushskaya, Argun, Itum-kale, *Geltman et al. 2358* (LE); Beschtau, June 1842, *Hohenacker s.n.* (G, GH, K, W); Kuba, Kardtokiurt, 5 July 1890, *Lipsky s.n.* (LE); Kavardino-Balkariya, Baksanskij, Bilim, Aktoprak, 18 July 1990, *Menitskij et al. s.n.* (LE); Dagestan, Lakskij, 9 Sep. 1927, *Poretsky & Schultz s.n.* (LE). **Transcaucasus:** Ossetia, Brutsabseli, Didi Liachva, *A. H. & V. F. Brotherus 500 a* (S); Tersk, Adai-su, *E. & N. Busch 47* (S); Teberda, 18 June 1968, *Ehwald & Wendt s.n.* (B); Cartalinia, Mts. Tzkura-Tzkharo, 9 July 1923, *Juzepczuk s.n.* (LE); Azerbajdzhan, Kuba, Leze, Schach-dagh, 8 July 1935, *Karjagin s.n.* (NY); Azerbayan, Baku, Gandzha, Rashnar-dagh, 30 June 1929, *Kasumova s.n.* (LE); Azerbayan, Karabach, Lyzagorsk, 30 June 1929, *Kolakovsky s.n.* (LE); Armenia, Daratschitschach, *Radle 400* (LE); Tiflis, Mt. Saghuramo, 6 July 1919, *Schischkin s.n.* (BM); Svanetia, Latpari inter flumina Hippum et Ingur, *Sommier & Levier 709* (G); Gruzniskaya, Bogdanovskij, Bogdanovka, *Tsvelev & Cherepanov 1032* (LE); Goris, Mts. Karabakhskoie, Brun, 27 July 1975, *Vašák s.n.* (B); Tiflis, *Wittmann 294* (LE). IRAN. Azerbaijan, Qareh Dagh, Aliabad, *Lamond & Termeh 4876* (E, G, IRAN, K, W). TURKEY. **Artvin:** Yusufeli, Altiparmak, Kaçkar Daglari, *Aytaç 2933* (GAZI). **Kars:** Ardahan, *Sorger & Buchner 82-94-38* (W). **Rize:** Ikizdere, Balliköy, Anzer, Çevresi, Sulak, *Güner & Vural 5974* (GAZI); Çamlihemsin, Yukari Amlakit, Çayirlik, Çokyillik, *Güner & Vural 6115* (GAZI); Ikizdere, Gölyayla-Cihantepe, *Güner & Vural 6643* (GAZI). **Trabzon:** Soganli Daglari, Bayburt, *Edmondson 851* (E); Zigana Passhöhe, *Sorger & Buchner 82-89-3* (W).

19b. Doronicum macrophyllum subsp. **sparsipilosum** (J. R. Edm.) Álv. Fern., Novon 11: 295. 2001. *Doronicum bithynicum* subsp. *sparsipilosum* J. R. Edm., Notes Roy. Bot. Gard. Edinburgh 32: 258. 1973. TYPE: Turkey. "Ilgaz Daglari, 35 km S of Kastamonu, roadside on N side of pass top," 27 July 1971, *J. R. Edmondson 463* (holotype, E!; isotypes, G!, ISTF not seen, K!, W!).

Plant up to 90 cm tall. *Rhizomes* woody to somewhat fleshy. *Stems* with 2 or 3 cauline leaves. Blade of basal leaves 6.5–13.5 × 7–11 cm. Blade of lower cauline leaves 7.5–9.6 × 9.3–12 cm. Middle and upper cauline leaves 4.5–11 × 3–6 cm. *Capitula* 2 or 3, ca. 6.5 cm diam. including rays; involucre ca. 3.5 cm diam.; peduncles up to 16 cm long. *Receptacles* glabrous. Ray flower corollas 1.9–3.5 cm long, 1.7–4 mm wide. Disk flower corollas 3.5–4.5 mm long. Pappus 1.5–3.5 mm (on immature ovaries). Chromosome number unknown.

Distribution. Northern Turkey (provinces of Bolu and Kastamonu). Growing in woods and open moist rocky places, altitude 1700–2200 m (Fig. 24).

Selected specimens examined. TURKEY. **Bolu:** Ala dag, Kartal Kaya, *Davis & Coode 37370* (E, K). **Kastamonu:** Ilgaz Dag, *Davis et al. 38312* (E, K); Ilgaz, Karakol, Çankiri, *Nydegger 19037* (G).

This subspecies combines characters from two species of *Doronicum.* Rhizome, phyllary shape, and indumentum are similar to *D. macrophyllum* subsp. *macrophyllum,* while size and leaf arrangement are similar to *D. orientale.* It was described as a subspecies of *D. bithynicum* J. R. Edm., which is considered a synonym of *D. reticulatum* Boiss., but the diagnostic character for this species (ovate phyllaries with a dark-colored major venation and a long tapered-acute apex) does not occur in subspecies *sparsipilosum.* The subspecies has the phyllary type and other characters of *D. macrophyllum* subsp. *macrophyllum,* from which it differs mainly in having fewer capitula and in leaf arrangement, and there are intermediate specimens.

20. Doronicum maximum Boiss. & A. Huet, in Boiss., Diagn. Pl. Orient. ser. 2, 3: 31. 1856. TYPE: Turkey. Tech-Dagh, *A. Huet du Pavillon s.n.* (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 805), G-BOIS!, photograph; isotypes, BM!, G!, K!).

Plant up to 100(+) cm tall. *Rhizomes* woody, glabrous, with or without leaf remains. *Stems* branched in the upper part, leaves distributed along the stem, upper internodes generally longer than the adjacent leaves. Indumentum of multiseriate and uniseriate eglandular trichomes (ca. 0.2 mm) and glandular trichomes (up to 1.7 mm), scattered, sometimes glabrous. *Leaves* entire to dentate. Basal leaves sometimes present at flowering time; blade 11–20 × 10–21.5 cm, orbicular or ovate, with cordate base and generally blunt apex, with actinodromous venation; petiole 8–36 cm long, with sheathing base, sheath ca. 3 cm long. Lower cauline leaves with blade 4.5–17 × 5.5–24 cm; petiole 6.5–40 cm long, 2–3.5 mm wide, similar to basal leaves. Middle cauline leaves 3–13 × 2–14 cm, sessile, fiddle-shaped, semi-amplexicaul. Upper cauline leaves 1.2–5.5 × 1–3.5 cm, similar to middle cauline leaves or ovate to obovate, sometimes bract-like. Indumentum similar to the adjacent part of the stem, generally scarce, more abundant on margins of leaves. *Capitula* 3 to 18(+), 2–4 cm diam. including rays; involucre shorter than rays, 1.5–2 cm diam., sometimes turbinate at the base of capitula (ca. 5 mm wide) in fruit. *Phyllaries* herbaceous, ovate-lanceolate to obovate-lanceolate and acute, glabrous or glabrate; the outer 0.7–1.2 cm long, 2–2.3 mm wide; the inner 0.9–1.2 cm long, 1.5–2.3 mm wide. *Receptacles* glabrous. *Flowers* with yellow corollas. Ray flower corollas 1.2–2 cm long, 1.5–3 mm wide, obovate-elliptic to oblong-elliptic, apex generally with 3 teeth. Disk flower corollas 4–5 × 1.5 mm. *Cypselae* brown, with smooth to slightly grooved surface, dimorphic. Cypselae from ray flowers 2.2–3.3 × 1–1.3 mm, glabrous or glabrate, without pappus. Cypselae from disk flowers 1.5–2.3 × 0.5–1 mm, sometimes with eglandular trichomes; pappus 3–5 mm, white. Chromosome number unknown.

Illustrations. Figures 8A, 23A–E.

Distribution. Eastern Turkey, south of Caucasus and south of the Caspian Sea. Moist rocky places and near watercourses, altitude 1700–3300 m (Fig. 24).

Doronicum maximum is morphologically close to those southwestern Asian species with a "*macrophyllum*" type of habit, and the type of indumentum is the only character to distinguish among them. Within this "*macrophyllum*" group it is more similar to *D. haussknechtii* than to any other (see comments on *D. haussknechtii*), but the almost absolute absence of indumentum at the base of the capitula in *D. maximum* makes it different (Fig. 23A–F).

Selected specimens examined. IRAN. Mt. Elvend, *Pabot 1717* (G); Azerbaijan, Chalil Kuh, Selvana, *Renz 48989* (E, G, W); Kurdistania, Mt. Takht-i-Soleiman, June 1898, *Strauss s.n.* (B); Azerbaidjan, Rezaich, Silvaneh, 24 June 1970, *Termeh s.n.* (W). IRAQ. Arl Gird Dagh, Algurd Dagh, Rawandiz, *Guest & Ludlow-Hewitt 2928* (K). TURKEY. **Bitlis:** Tatvan, *Sorger 84-41-5* (W). **Erzurum:** Mt. Tech-Dagh, July 1853, *Huet du Pavillon s.n.* (BM, G, K); Bachrunse, Karliova-Çat, Karliova, *Nydegger 17340* (G). **Giresun:** Balabandaglari, Kilinc Tepe, Tamdere, *Davis et al. 20588* (BM, E, K). **Hakkari:** Cilo Tepe, Cilo yayla, *Davis & Polunin 24113* (BM, E). **Maraş:** Çaglayancerit, Engizek Dagi, *Duman 4068* (GAZI). **Muş:** vallis Merga Sauk, Bimgoell, Gumgum, Warto, *Kotschy 363* (B, G, K, S, UPS, W).

21. Doronicum oblongifolium DC., Prodr. 6: 321. 1838. TYPE: "Doronicum plantagineum, En. pl. cauc. nº 674," 1832, *C. A. Meyer* (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 805), G-DC!, photograph).

Plant up to 50 cm tall. *Rhizomes* woody to somewhat woody, glabrous, generally with leaf remains forming fibers or dark scales. *Stems* not branched, leaves mainly in the lower middle of the stem. Indumentum of white eglandular trichomes (up to 2.5 mm), more abundant near the capitula, also with scarce glandular trichomes, sometimes glabrous at the base. *Leaves* entire to slightly dentate. Basal leaves generally present at flowering time; blade (1.8)2–6 × (0.9)1.5–3 cm, elliptic, with attenuate base, and generally blunt apex, with actinodromous to pinnate-actinodromous venation; petiole 3–10 cm long, 1–3 mm wide. Lower and middle cauline leaves 3.5–8(9.5) × 1.4–2.5 cm, similar to basal leaves or sessile, elliptic to ovate-elliptic, sometimes widely ovate to suborbiculate, semi-amplexicaul, with blunt apex. Upper cauline leaves (1.6)3–6 × (0.2)1–2 cm, similar to middle cauline leaves or ovate-lanceolate, sometimes bract-like. Indumentum similar to the adjacent part of stem, sometimes with white, tangled, uniseriate eglandular trichomes (up to 1 mm), more abundant on leaf margins. *Capitula* solitary, 4.5–7.5 cm diam. including rays; involucre shorter than rays, 2–5 cm diam. *Phyllaries* herbaceous, 1–1.5(2) cm long, 2.5–5 mm wide, ovate-lanceolate to elliptic. Indumentum similar to the upper part of stem, sometimes abundant. *Receptacles* glabrous. *Flowers* with yellow corollas. Ray flower corollas 2–3.5 cm long, 2.5–5.5 mm wide, obovate-elliptic, apex with 2 or 3 teeth. Disk flower corollas 4–5 mm long. *Cypselae* brown, with striate-reticulate to warty surface, dimorphic, ca. 4 × 1 mm, generally glabrous, sometimes with eglandular trichomes or glabrate. Cypselae from ray flowers without pappus. Pappus up to 4.5 mm, white. Chromosome number $2n = 40$, 60* (Davlianidze, 1985; *Fedorov, 1969).

Illustrations. Avetisyan & Oganesyan (1995: tab. 175); Figure 3I, J.

Distribution. Caucasus. Open moist rocky places, and along watercourses, altitude 1400–3900 m (Fig. 24).

Doronicum oblongifolium is distinctive among the species from Caucasus. While the rest of the species in this area (except *D. orientale*) have the "*macrophyllum*" type of habit, *D. oblongifolium* bears only one capitulum and has elliptic basal leaves making it similar in habit to other European or central Asian species (e.g., *D. clusii, D. hungaricum, D. falconeri,* among others). Besides, the type of rhizome (woody, glabrous, and with fibrous leaf remains) is quite different from that of *D. orientale* (fleshy and with pubescent nodes). In addition, *D. oblongifolium* has a special type of indumentum on margins of basal leaves (Fig. 3I, J).

The citation of the chromosome number $2n = 60$ for *Doronicum oblongifolium* was found in Fedorov's index (1969), but the original source for this data was not seen.

Selected specimens examined. CAUCASUS. **North Caucasus:** Dagestan, Kaitag, Tabassaran, Urgah, Dshufu dag, *Alexcenko & Woronow 13586* (LE); Checheno-Ingushskaya, Argun, Itum-kale, *Averianov et al. 2421* (LE); Balkariya, Sukan, 1 July 1927, *E. A. & N. A. Busch s.n.* (LE); Kaepes-Dagh, Karabach, June 1844, *Kolenati s.n.* (LE); Digoria, Ossetia, Alagir, *Ruprecht 156* (LE); Tindal, Mts. Bogos, Aatschabala, 10 June 1861, *Ruprecht s.n.* (LE). **Transcaucasus:** Azerbajdzhan, Mt. Mechtukjan, 15 Aug. 1929, *Achverdov & Doluchanow s.n.* (LE); Carthalinia, Zhra Zhraras, *A. H. & V. F. Brotherus 501* (BM, G, S); Armenia, Alägez, 20 July 1932, *E. & N. Busch s.n.* (LE); Azerbajdzhan, Gandzha, Koshkar-dagh, 22 July 1928, *Doluchanow s.n.* (LE); Aragac, lacum Kari, *Gabrielian 12787* (E, G); Azerbayan, Nachitshevan, Zangezur, inter Dashurry-Dagh et Kjavin-Kaja, 1 July 1928, *Gavrilov s.n.* (LE); Mt. Sarial, May 1838, *Hohenacker s.n.* (B, E, G, K, W); Armenia, Daralogez, Alogez, 25 July 1931, *Karjagin & Saflev s.n.* (LE, S); Azerbayan, Nagornogo Karabacha, Gadrutskij, Znarat, 27 May 1948, *Kirpichnikov s.n.* (LE); Azerbajdzhan, Karabach, inter Lysagorse et Mt. Kyus, 17 June 1929, *Kolakovsky s.n.* (LE); Tiflis, Bokhriani, Mt. Sanislo, 7 Aug. 1928, *Kozlovsky s.n.* (LE); Georgia, Borzhom, Bakuriani, 24 May 1936, *Kozlovsky s.n.* (LE); Gruzinkaya, Chevsuretiya, Tsuvrovani, Choki, 6 Aug. 1982, *Menitskij s.n.* (LE); Azerbayan, Nachitschevan, Mt. Agdaban, 17 July 1934, *Prilipko & Isaev s.n.* (LE); Armenia, Mt. Alajos, *Radle 142* (LE); Murov-dag, Giamish, Elisabetholsk, 15 July 1909, *Schelkovnikov s.n.* (LE); Mts. Areguni, ad lacum Sevan, Krasnoselsk, Shorsha, 8 Oct. 1974, *Vašák s.n.* (B, G); Ashtarak, Mt. Aragac, 13 July 1975, *Vašák s.n.* (G, W); Armenia, Razdan, Mt. Alibeg, Cakhkdzor, 4 July 1982, *Vašák s.n.* (W). TURKEY. **Artvin:** Yalnizçam Silsilesi, Savsat, *Albury et al. 3176* (K); Çoruh, Ardanuç, Kordevan dag, Yalnizcam Daglari, *Davis & Hedge 30365* (E, K, W). **Erzurum:** Dumluda, *Sorger & Buchner 82-123-9* (W).

22. Doronicum orientale Hoffm., Com. Soc. Phys. Med. Moscou 1: 8. 1808. TYPE: not located; protologue citation: "Habitat passim circa Zehet in Iberia."

Doronicum caucasicum M. Bieb., Fl. Taur.-Caucas. 2: 321. 1808. TYPE: "ex Caucaso iberico. Adam. 1805" [*Adam.? s.n.*], ex herb. Marschall von Bieberstein (lectotype, designated here, LE!).

Plant up to 140 cm tall. *Rhizomes* fleshy, pubescent to very pubescent, with shining white-tinted trichomes on nodes, stoloniform, sometimes with buds. *Stems* unbranched, scape-like. Indumentum of uniseriate and multiseriate eglandular trichomes and short-stalked glandular trichomes. *Leaves* entire to slightly dentate. Basal leaves sometimes present at flowering time; blade (2)4–7(8.5) × 2(3)–6(7.5) cm, reniform to widely ovate with cordate base and generally blunt apex, with acrodromous venation; petiole (1.8)4–10(20) cm long, (0.5)1–2(3.5) mm wide. Lower cauline leaves (3.2)5–7.5(9) × (1.8)3–5(7.7) cm, similar to basal leaves or sessile, fiddle-shaped, semi-amplexicaul. Upper cauline leaves (1.5)4–7(10.5) × (0.4)3–6(7.6) cm, ovate-elliptic to ovate-lanceolate, sometimes bract-like. Indumentum mainly of short-stalked glandular trichomes, also with uniseriate and multiseriate eglandular trichomes. *Capitula* 1(2 or 3), 3(4)–(6)7 cm diam. including rays; involucre shorter than rays or equaling them, (2.3)3–5(5.5) mm diam. *Phyllaries* herbaceous, ovate-subulate, generally with acute apex; the outer (1)1.5–2(2.5) cm long, (1)1.5–2 (3) mm wide; the inner 1–1.5(2) cm long, 0.5–1.5(2) mm wide. Margins ciliate, with acute, stiff and equidistant multiseriate eglandular trichomes (up to 1.5 mm). Indumentum mainly glandular, but also with eglandular trichomes. *Receptacles* generally pubescent, sometimes glabrous. *Flowers* with yellow corollas. Ray flower corollas (1.4)2–2.5(3) cm long, 2–2.5(3.8) mm wide, oblong-elliptic, apex generally with 3 teeth. Disk flower corollas 3.5–4(5) × 1.2–1.5 mm. *Cypselae* olive-green or brown, with warty or rugose-reticulate surface, dimorphic. Cypselae from ray flowers (1)1.5–2(2.3) × (0.2)0.5–0.8(1.7) mm, glabrous, without pappus. Cypselae from disk flowers (1)1.3–1.5(1.8) × 0.5–0.7(1) mm, with eglandular trichomes; pap-

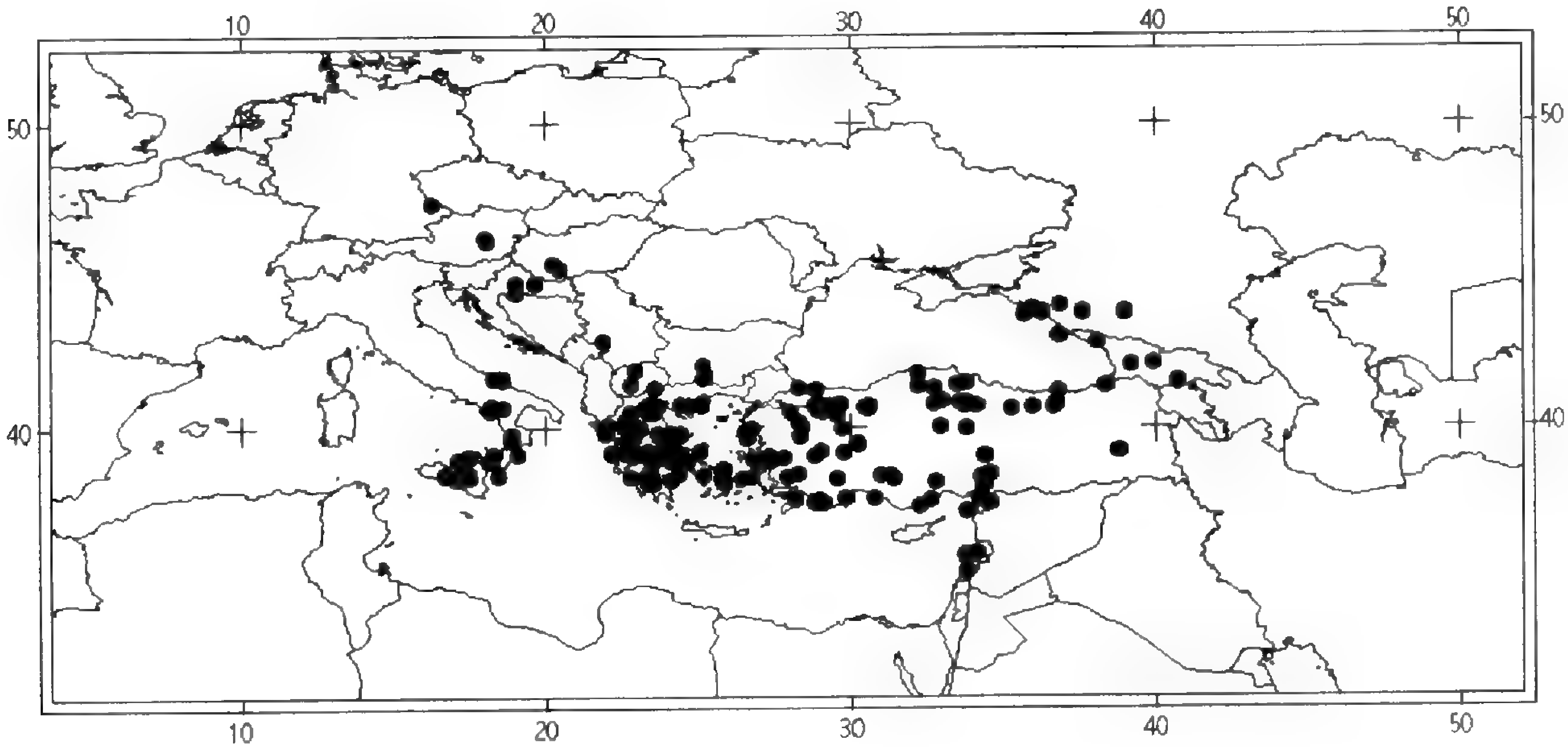

Figure 27. Distribution map for *Doronicum orientale*.

pus (2.5)3–5 mm, white. Chromosome number $2n = 60$ (Lindqvist, 1950, as *D. cordatum*; Baksay, 1956; Strid & Anderson, 1985).

Illustrations. Sadler in Nendtvich (1836: tab. 2): Săvulescu (1964: pl. 99, fig. 2); Figures 1A, 5E–H.

Distribution. Eastern Mediterranean region, from Syria to Sicily, and Caucasus (absent in northern Africa?). Cultivated and naturalized in central Europe. Forests, meadows, rocky places, and shady gullies, from sea level up to 2000 m in elevation (Fig. 27).

Both *Doronicum orientale* Hoffm. and *D. caucasicum* M. Bieb. were described in 1808 with the month of publication unknown. One year later the former name was choosen by Willdenow (1809) as the valid name, and, hence, it is the correct name (ICBN, Art. 11.5, Greuter et al., 2000). The type material of *D. orientale* has so far not been located, and although its description in the protologue matches the taxonomic identity recognized as *D. orientale* by Willdenow (1809), its formal identity needs to wait until a lectotype is designated. Since both names were alternately used by different authors in floristic studies, the lectotype for *D. caucasicum* M. Bieb. is designated above. The only sheet found in Marschall von Bieberstein's herbarium that matches the protologue was selected as the lectotype.

The possible occurrence of *Doronicum orientale* in North Africa requires further work (see comments for *D. pardalianches* and *D. plantagineum*).

Selected specimens examined. LEBANON–SYRIA. Beikos agri Byzantini, *J. & F. Bornmüller 11965* (B); Faraya, *Polunin 5332* (B, E, K). CAUCASUS. **Northcaucasus:** Kuban, *Busch & Klopotov 668* (LE, NY); Krasnodarskii, Gelendzhikskii, Pschadi, Pschala, *Dolmatova et al. 2360* (LE). **Transcaucasus:** Tiflis, ad rivulum Kura, 22 Mar. 1861, *Ruprecht s.n.* (LE). TURKEY. **Adana:** Bahçe, Dildil dag, Haruniye, *Davis & Polunin 26107 D* (BM, E, K). **Afyon:** Darkiri, Hisaralan, *Aytaç 1167* (GAZI). **Amasya:** Direkli, Üçoluk, *Peker 1178* (GAZI). **Antalya:** Termessos, *C. & M. North 42* (E). **Aydin:** Karacasu, Baba Dag, Seki, *Davis 41627* (E, K). **Balikesir:** Kaz Dag, Sarakoy, *Dudley 34813* (E, K, MO). **Bolu:** Abant, *Prieè 492* (K). **Bursa:** Ulu Dag, *Wilde 4026* (E). **Çorum:** Iskilip, Kebabdere, Karmis, *Coode & Jones 1754* (E, GH). **Hatay:** Belen, Amanus, Karlik, Soguk Oluk, *Davis & Hedge 27089* (BM, E, K). **Izmir:** Kusadasi, *Kayacik & Yaltirik 3368* (E). **Kastamonu:** Paphlagonia, Tossia, Bepik-Ilkazdagh, *Sintenis 3995* (B, BM, BRNM, K). **Kütahya:** Simav, Kiçir to Akdag, *Coode & Jones 2733* (E, K). **Muğla:** Inçealiler, *H. & E. Walter 342* (B). **Trabzon:** Trabzon, *Stainton 8113* (E, K). **Yozgat:** Akdagmadeni, Aktas, *Curtis 144* (E). AUSTRIA. **Niederösterreich:** Theresienthal bei Gratzen, 19 May 1899, *Jahn s.n.* (B, S). BULGARIA. **Plovdiv:** Stanimaka, 10 June 1889, *Stříbrný s.n.* (G). GREECE. **Ípiros:** Arta, Skoulikaria, *Willing 33327* (B). **Makedhonía:** Naussa, Mt. Vermion, *K. H. & F. Rechinger 8758* (BM). **Nísoi Aiyaíou:** Samos, Mt. Kerkis, Agia, *Davis 1654 K* (E, K); Nenedes, insula Samos, *K. H. & F. Rechinger 3794* (BM, K, G). **Pelopónnisos:** Lirkio, Kefalovrison, *García 953* (MA). **Stereá Ellás-Évvoia:** Katafigon, Oeta, *Balls & Gourlay B3264* (BM, E, K); Mt. Hymetti, *Orphanides 196* (COI-WILLK, E). **Thessalía:** Pelion, Kissos, *Beauverd 272* (G). HUNGARY. **Baranya:** Pécs, Mecsek, 25 Apr. 1946, *Papp s.n.* (S). **Tolna:** silva Gurovica prope Szekszárd, 13 May 1914, *Hollós s.n.* (S). ITALY. **Basilicata:** Potenza, in silva Pallareta, 20 Apr. 1924, *Gavioli s.n.* (MA). **Calabria:** Pizzo, 20 Apr. 1938, *Lenander s.n.* (S). **Sicilia:** Parco delle Madonie, Piano Sempria, *Nieto 3888* (MA). YUGOSLAVIA. **Makedonija:** Doiran, Marianska planina, Hudowa, *Bornmüller 4265* (B, NY). **Srbija:** Rakovika, prope Belgradum, *Petrovič 2340* (G, K, MA).

23. Doronicum pardalianches L., Sp. Pl.: 885. 1753. TYPE: Herb. Clifford, 411.1 [sine collector] (lectotype, designated by Llamas et al. in Jarvis & Turland (1998: 360), BM!).

Arnica scorpioides L., Sp. Pl.: 884. 1753. *Aster scorpioides* (L.) Scop., Fl. Carniol. ed. 2, 2: 169. 1771. *Grammarthron scorpioides* (L.) Cass., in Cuvier, Dict. Sci. Nat. 19: 294. 1821. *Aronicum scorpioides* (L.) Rchb., Fl. Germ. Excurs. 1: 233. 1831–1832. TYPE: "Doronicum radice scorpii brachiata," Herb. Burser X: 16 [sine collector] (lectotype, designated by Álvarez in Jarvis & Turland (1998: 353), UPS!, photograph).

Plant up to 150(+) cm tall. *Rhizomes* fleshy, pubescent to scarcely pubescent or glabrate with shining white-tinted trichomes on nodes, stoloniform, sometimes with buds. *Stems* scarcely branched in the upper part, with few leaves mainly distributed along the basal ⅔ of the stem, internodes generally longer than the adjacent leaves. Indumentum of thin and acute multiseriate eglandular trichomes (up to 5 mm) in the lower part, uniseriate eglandular trichomes and glandular trichomes in the middle and upper part, abundant near the capitula. *Leaves* entire to slightly dentate. Basal leaves sometimes present at flowering time; blade 3.6–16.5 × 3.3–14 cm, ovate with cordate base and blunt apex, with acrodromous to actinodromous venation; petiole 4.5–27 cm long, 1–4.5 mm wide. Lower cauline leaves 3.3–22 × 2.3–11 cm; petiole (3.4)6–10(27) cm long, 1–1.5 mm wide, similar to basal leaves. Middle cauline leaves (2.7)5–9(15.3) × (1.6)3–6(10) cm, sessile, fiddle-shaped, semi-amplexicaul. Upper cauline leaves (1)2–6(10) × (0.2)1–2(5.5) cm, ovate-elliptic to ovate-lanceolate, sometimes bract-like. Indumentum similar to the adjacent part of the stem. *Capitula* (1)2–7, 2–5.1 cm diam. including rays; involucre almost equaling rays, sometimes exceeding them, 1–3.3 cm diam.; peduncles (0.5)5–7(20) cm long, (0.5)0.8–1(2) mm wide. *Phyllaries* herbaceous, (1)1.2–1.4(1.7) cm long, (0.7)1–1.5(2.7) mm wide, ovate-subulate, generally with acute apex. Margins sometimes ciliate, with acute, stiff and equidistant multiseriate eglandular trichomes. Indumentum of glandular and eglandular trichomes. *Receptacles* pubescent or glabrate. *Flowers* with yellow corollas. Ray flower corollas 1.1–2.5 cm long, 2–3.5 mm wide, oblong-elliptic, apex generally with 3 teeth. Disk flower corollas 4–6 × 1–2.5 mm. *Cypselae* black and with warty surface in maturity, dimorphic. Cypselae from ray flowers 1.7–3.5 × 0.7–1.3 mm, glabrous, without pappus. Cypselae from disk flowers 1.2–1.8 × 0.7–1 mm, with eglandular trichomes; pappus (2.5)3–4 mm, white. Chromosome number $2n = 60, 120^*$ (Lindqvist, 1950; *Moore, 1982, see comments below).

Illustrations. Jacquin (1776: t. 350); Reichenbach (1854: t. 64, fig. 2); Săvulescu (1964: pl. 97, fig. 2; pl. 189, fig. 1); Bolòs & Vigo (1995: 839); Figures 2A, B, 7A.

Distribution. Northeastern Iberian peninsula and central Europe. Cultivated and naturalized at least in Great Britain and Northern Europe, so that the limits of the natural distribution are uncertain. Forests, meadows, hedges, and near watercourses, from sea level up to 1800 m in elevation (Fig. 28).

As indicated above, in the protologue of *Arnica scorpioides* L., several pre-Linnaean synonyms are included. This name has been treated as a synonym of *Doronicum grandiflorum* Lam. by all the authors that combined it, probably because Jacquin (1776: 26, t. 349) illustrated it with a plant of *D. grandiflorum* Lam. However, the lectotype designated by Álvarez in Jarvis and Turland (1998) represents *Doronicum pardalianches* L., since all of the original elements of *A. scorpioides* belong to *D. pardalianches* L. Formally, all the combinations based on *Arnica scorpioides* L. are homotypic synonyms of *Arnica scorpioides* L. and thus synonyms of *D. pardalianches* L., even though the descriptions and references in protologues correspond mainly to *Doronicum grandiflorum* Lam. (see also comments above on *D. scorpioides* Lam. under *D. grandiflorum* Lam.).

Desfontaines (1798) cited *Doronicum pardalianches* in North Africa: "in cacumis Atlantis prope Belide," but all the specimens from North Africa represent *D. plantagineum.* A few populations have broadly ovate basal leaves with subcordate bases that are similar to *D. orientale,* so their identity is uncertain. *Doronicum pardalianches* has similar basal leaves, but is quite different from both *D. orientale* and *D. plantagineum* in habit, number of capitula, number of cauline leaves, and color of cypselae. Although no sheet from Desfontaines's locality was seen, the presence of *D. pardalianches* in North Africa is unlikely. Desfontaines's description matches *D. plantagineum,* or even *D. orientale* (whose presence in North Africa is questionable). Hybridization between *D. plantagineum* and *D. orientale* in this area is a possibility. (See comments for *D. orientale* and *D. plantagineum.*)

Determining the native distribution of *Doronicum pardalianches* is difficult. Records are scattered in central Europe, but absent in the Iberian peninsula, except for northeastern Spain, where it is notably abundant, exactly in the gap presented by *D. plantagineum* (Figs. 25, 28). This suggests these species do not overlap in their presumably natural areas of distribution, and that the native area of *D. pardalianches* reaches southwestern Europe in northeastern Spain.

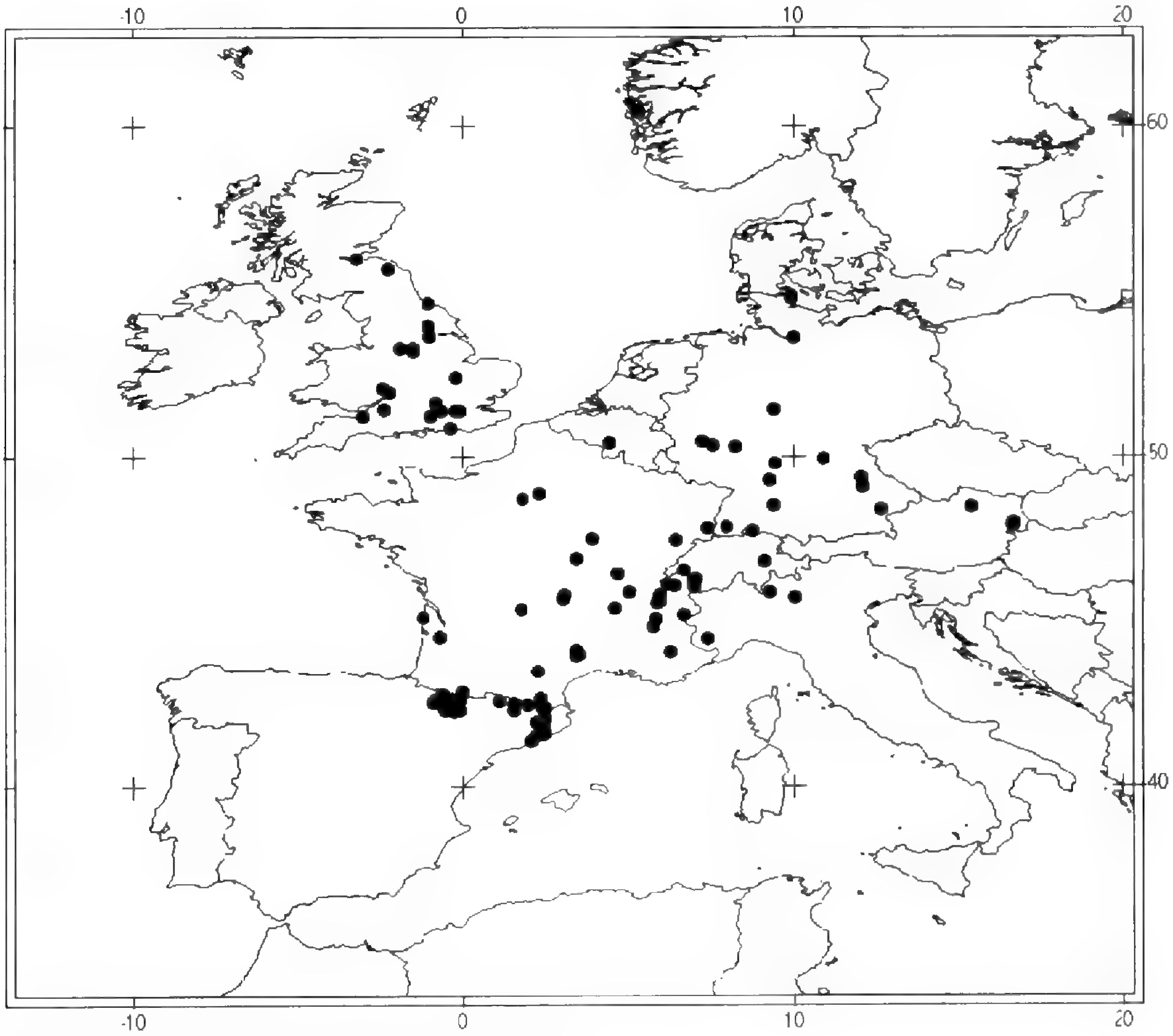

Figure 28. Distribution map for *Doronicum pardalianches.*

The citation of the chromosome number $2n = 120$ for *Doronicum pardalianches* was found in Moore's (1982) index, but the original source for this data was not seen.

Selected specimens examined. ANDORRA. Sant Miquel d'Engolasters, Les Escaldes, *Almaraz et al. 1015* (MA). AUSTRIA. **Niederösterreich:** Sachsen, Schlopberg Hartenstein, May 1904, *Lehmann s.n.* (B). BELGIUM. **Hainaut:** Marchienne-au-Pont, *Duvigneaud 76 B 325* (MA). FRANCE. **Basses-Alpes:** Mt. des Dourbes, près de Digne, 2 June 1868, *Borel s.n.* (K). **Cote d'Or:** bois de Saulon, 19 June 1873, *Bonnet s.n.* (K). **Doubs:** bois de Châtay à Uzelle, *Paillot 2279'* (B, G, NY). **Haute-Savoie:** St. Pierre-de-Rumilly à St. Laurent, *Jacquemoud 3459* (G). **Hautes-Alpes:** Séuse, 23 July 1885, *Girod s.n.* (G). **Hautes-Pyrénées:** bois de Sia près Luz, July 1872, *Borderè s.n.* (K). **Iserè:** Grenoble, 2 June 1850, *Chabert s.n.* (G). **Loire:** Mt. Pilat, *Mutel 120* (MA). **Pyrénées-Orientales:** Vernet, Aug. 1843, *Handris s.n.* (G). **Saône-et-Loire:** Cluny, 31 May 1892, *Grandmaison s.n.* (G). **Seine-et-Oise:** Paris, *Duby 263* (MA). GERMANY. **Bayern:** Steiniger Wald, Baumberg, 20 June 1908, *Harz s.n.* (NY, W). **Berlin:** prope Berolinum, Borussia, 10 July 1887, *Scheppig s.n.* (G). **Halle:** Winningen, 1 June 1857, *Wirtgen s.n.* (B, G). **Hessen:** Taunus, *Andres 695* (B). **Rheinland-Pfalz:** Binningen, Birtgen, *Lechler 48* (B, E). GREAT BRITAIN. **England:** Ledbury, *Bickham 876* (K); Woodchester Park, West Gloucester, *Lousley 954* (K); Bucks, between Marlow and Medneuham, *Sandwith 3737'* (K). **Scotland:** Inverness, Edinburgh, *Syme 653* (K). ITALY. **Lombardia:** Mt. Bronzone sur Tavernola, 16 May 1910, *Wilczek s.n.* (G). **Piemonte:** Turin, Val Salice, 5 May 1870, *Joad s.n.* (E). NORWAY. Bergen, *Fredholm 1189* (NY). SPAIN. **Aragón:** Huesca, sierra de Guara, Nocito, barranco Fuente Espátula, *Álvarez et al. 801* (MA); Huesca, Las Paúles, 2 Aug. 1988, *Aseginolaza & Gómez s.n.* (JACA). **Cataluña:** Lérida, Cava, sierra del Cadí, arroyo de la Vena, collado de Basses, *Almaraz et al. 1008* (MA); Lérida, Alta Ribagorza, bosque de Besiberri, 10 Aug. 1987, *Arán & Tohá s.n.* (MA); Barcelona, Olzinelles, *Fernández Casas 605* (MA); Gerona, San Feliu de Pallarols à la Salut, 9 June 1927, *Gonzalo s.n.* (G, MA). SWEDEN. Insula Haito prope Carlskra Majest, June 1880, *Lübeck s.n.* (G). SWITZERLAND. **Valais:** pres Allesse, 1869, *Thomas s.n.* (K). **Vaud:** Graugette prope Pandex, 28 May 1870, *Faurat s.n.* (BM).

24. **Doronicum plantagineum** L., Sp. Pl.: 885. 1753. TYPE: Herb. Clifford, 411.2 [sine collector] (lectotype, designated by Llamas et al. in Jarvis & Turland (1998: 360), BM!).

Plant up to 150 cm tall. *Rhizomes* fleshy, pubescent to very pubescent, with shining white-tinted trichomes on nodes, stoloniform, sometimes with buds. *Stems* generally unbranched, scape-like. Indumentum mainly glandular, with short-stalked and long-stalked glandular trichomes (up to 0.7 mm), sometimes also uniseriate and multiseriate eglandular trichomes, more abundant near the capitula. *Leaves* entire to slightly dentate. Basal leaves sometimes present at flowering time; blade (2.5)4–8(12) × (1.5)2.5–6(9.5) cm, ovate with truncate, attenuate or subcordate base, blunt or somewhat acute apex, with acrodromous venation; petiole (2)4–8(19) cm long, (0.5)1.5–3(7) mm wide. Lower cauline leaves (1.5)3–7(19) × (1)2–5(8.5) cm, similar to basal leaves or sessile, fiddle-shaped to ovate-elliptic, semi-amplexicaul. Upper cauline leaves (1)2–4(9.5) × (0.1)0.7–2(5.5) cm, ovate-elliptic to ovate-lanceolate, sometimes bract-like. Indumentum mainly glandular, with short-stalked and long-stalked glandular trichomes, also with uniseriate (0.2 mm), and multiseriate (up to 2 mm) eglandular trichomes. *Capitula* 1(2 or 3), 3–4(6.5) cm diam. including rays; involucre almost equaling rays, sometimes exceeding them, 3–4(5.5) cm diam. *Phyllaries* herbaceous, ovate-subulate, generally with acute apex; the outer (1)1.5–2.5(3) cm long, (1)1.3–2(3) mm wide; the inner (1)1.5–2(2.5) cm long, 0.5–0.7(2) mm wide. Margins ciliate, with acute, stiff and equidistant multiseriate eglandular trichomes (up to 1.5 mm). Indumentum mainly glandular. *Receptacles* glabrous or scarcely pubescent. *Flowers* with yellow corollas. Ray flower corollas (1.1)1.5–2.5(3) cm long, (1.5)–2(3) mm wide, oblong-elliptic, apex generally with 3 teeth. Disk flower corollas 4(4.3)–4.5(5.5) × (1)1.3–1.5(2) mm. *Cypselae* olive-green or brown, with warty surface, dimorphic. Cypselae from ray flowers 2–2.8(4) × (0.7)1–1.3 mm, generally glabrous, without pappus. Cypselae from disk flowers (1.5)2–2.7(3) × (0.7)1–1.3 mm, with eglandular trichomes; pappus (3)3.5–4.5(5) mm, white. Chromosome number $2n = 120$ (Lindqvist, 1950; Fernandes & Queirós, 1971; Löve & Kjellqvist, 1974; Ruiz de Clavijo, 1993).

Illustrations. Reichenbach (1854: tab. 65, fig. 2); Hegi (1928: 711, fig. 420); Valdés et al. (1987: 77); Bolòs & Vigo (1995: 838); Figure 6A, B.

Distribution. Southwestern Europe (Portugal and Spain) and northern Africa (Morocco and Algeria). Cultivated and naturalized in Great Britain and central Europe. Limits of its native range uncertain. Forests, meadows, hedges, and on shady moist rocky places, altitude 400–2200 m (Fig. 25).

Doronicum plantagineum is variable for some characters (e.g., size and robustness of the plants, size and shape of basal leaves, number of leaves and capitula, type and abundance of indumentum). Cultivated, naturalized plants, and a few natural populations tend to have basal leaves broadly ovate-elliptic to elliptic, with slightly dentate margins, attenuate bases and somewhat acute apices. Some authors (Rouy, 1893, 1903a, 1903b; Legrand, 1894; Coutinho, 1939; Fournier, 1939) have given taxonomic recognition to these trends.

The North African populations are the most distinctive, generally being more robust and pubescent than the European, and having broadly ovate basal leaves with subcordate bases. The shape of the basal leaves in these plants does not allow a clear distinction between *Doronicum plantagineum* and *D. orientale.* These North African populations have been treated as subspecies or varieties of *D. pardalianches* or *D. plantagineum* (Chabert, 1892; Barratte, 1893), or as a separate species, *D. atlanticum* (Chabert, 1891; Rouy, 1893), as in Cavillier's monograph (1907, 1911). A multivariate morphometric analysis (PCA and DA) of *Doronicum* (Álvarez Fernández & Nieto Feliner, 2001) reveals no morphometric support for the segregation of these populations as a species from the European populations of *D. plantagineum.* On the other hand, a phylogenetic analysis based on morphological, nuclear ribosomal (ITS), and chloroplast (*trn*L-F) data (Álvarez Fernández et al., 2001) showed differences in ITS sequences between these populations that somewhat support separate species status despite the poor morphological differentiation. Introgression from *D. orientale* into populations of *D. plantagineum* is not ruled out as the cause of sequence differences. Until further work is done, these populations are provisionally included in *D. plantagineum.*

The bulk of the records of *Doronicum plantagineum* are from the Iberian peninsula; a gap occurs in northeastern Spain and southern France, and most of the French records are from near Paris. This is the only representative of the genus in North Africa (northern Algeria and Atlas) and thus seems to be native to the Iberian peninsula and North Africa, its current area of distribution being expanded by human action.

Selected specimens examined. ALGERIA. Teniet el Had, pic des Cêdres, *Alston & Simpson 37736* (BM); Djurdjura, Tala Guilef, Boghni, *Davis 59243* (BM, E); Kabylie, Mt. Magris, *Reverchon 391* (BM, G). MOROCCO. **Meknès:** Ifrane, Azrou, *Bocquet 10476* (BM); Aïn Leuh, *Jahandiez 386* (B, MA). FRANCE. **Haute-Marne:** Louze, Brienne-le Château, *Retz 89985* (G, MA, MACB, MAF). **Seine-et-Marne:** Fontainebleau, *Feuilleaubois 2872* (BR, MA). **Seine-et-Oise:** Port-Villez, 11 May 1873, *Delacour s.n.* (K); forêt de Bondy, Paris, 15 May 1846, *Kralik s.n.* (K); Yvelines, Véthenil, bois du Coudray, *Lawalrée 15798* (BR); Verrières-le-Buisson, Essone, forêt de Verrières, *Retz 67398* (BR, G, MA, MAF). **Somme:** bois de Lize près Ault, May 1862, *Brutelette s.n.* (G). **Var:** bois del Mauret, 28 May 1884, *Leresche s.n.* (B). GREAT BRITAIN. **England:** Great Saling, Essex, *Fox 780* (B, W); Belton, Grantham, 14 June 1887, *Woodward s.n.* (K). **Scotland:** Blair, Culross, 18 Apr. 1872, *Drummond s.n.* (K); Amiston

Wood, Edinburgh, *Syme 654* (G). PORTUGAL. **Algarve:** entre Monchique e Alferce, *Malato-Beliz et al. 3120* (MA). **Alto Alentejo:** Castelo de Vide, Amieira, *Malato-Beliz 196* (MA). **Beira Alta:** serra da Estrela inter Caldas de Manteigas et Poço do Inferno, *Lawrence et al. 4844* (MA). **Beira Baixa:** Fundao, 25 Mar. 1926, *Carrisso & Mendoça s.n.* (BR). **Estremadura:** Malveira, Mt. Leite, *Rainha 1047* (G, MA). **Tras-os-Montes:** Tabuaço, foz do Távora, *G. B., F. G. & J. Vasconcellos 7877* (HVR). SPAIN. **Andalucía:** Jaén, sierra Morena, Despeñaperros, collado de los Jardines, *Cuatrecasas 3526* (MAF); Cádiz, Grazalema, sierra del Pinar, *López & Morales 3008 GF* (MA). **Aragón:** Zaragoza, entre Cosuenda et Tobed, sierra de Algairén, *Gómez et al. 63591* (G, MAF). **Cantabria:** Vega de Liébana, entre Dobres y Bárago, *Álvarez et al. 966* (MA). **Castilla-La Mancha:** Guadalajara, Retiendas, hoz del río Jarama, *Álvarez et al. 954* (MA). **Castilla y León:** Burgos, Frías, entre Tobera y Valderrama, *Almaraz & Álvarez 977* (MA). **Comunidad de Madrid:** Lozoya, puerto de Navafría, *Susanna 776* (MA, MO, NY); **Comunidad foral de Navarra:** Foz de Arbayún, 11 May 1971, *Villar s.n.* (JACA). **Extremadura:** Cáceres, Guadalupe, 18 May 1991, *Rubio s.n.* (MAF). **Galicia:** Orense, Cobas, *García Martínez et al.* (MA); **Principado de Asturias:** Ponga, Beleño, 10 Apr. 1998, *Medina s.n.* (MA). **Región de Murcia:** Moratalla, sierra de La Muela, *Álvarez et al. 1103* (MA).

25. Doronicum reticulatum Boiss., Diagn. Pl. Orient. ser. 1, 4: 12. 1844. TYPE: Turkey. Tmolus Bogdagh, Lydia, [*P. E. Boissier*] *3969* (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 805), G-BOIS!).

Doronicum bithynicum J. R. Edm., Notes Roy. Bot. Gard. Edinburgh 32(2): 257. 1973. Syn. nov. TYPE: Turkey. Bursa, Olympi Bithyni, *P. M. R. Aucher-Eloy 3269* (holotype, G!; isotypes, BM!, E!, K!).

Plant up to 80(+) cm tall. *Rhizomes* woody to somewhat woody, glabrous, sometimes with leaf remains forming scales on nodes. *Stems* branched in the upper part, leaves mainly distributed in the lower middle portion, upper internodes generally longer than the adjacent leaves. Indumentum of uniseriate eglandular trichomes, rarely with a few multiseriate eglandular trichomes, sometimes with glandular trichomes, more abundant near the capitula and sometimes glabrous at the base. *Leaves* entire or subentire. Basal leaves sometimes present at flowering time; blade 7.5–16.5 × 7–15 cm, orbicular or ovate, with cordate base and blunt apex, with actinodromous venation; petiole 10–17.5 cm long, with sheathing base, sheath (1)3–5 cm long. Lower cauline leaves with blade 8–9.5 × 7–8 cm; petiole 10–13 cm long, 1.5–2.5 mm wide, similar to basal leaves. Middle cauline leaves 6.3–10 × 2.6–7 cm, sessile, fiddle-shaped to obovate, semiamplexicaul. Upper cauline leaves 2.8–4.5 × 1–1.6 cm, sessile, ovate to obovate, or bract-like. Indumentum similar to the adjacent part of the stem, sometimes abundant on veins on the abaxial surface of leaves. *Capitula* 3 to 5, 4–6.5 cm diam. including rays; involucre shorter than rays or equaling them, 3.5–4 cm diam.; peduncles up to 11 cm. *Phyllaries* herbaceous, sometimes slightly papery, ovate-lanceolate with very tapering acute apex, generally with 8 to 12 longitudinal veins dark-colored; the outer 1.5–2 cm long, 2.2–5.5 mm wide; the inner 1.4–1.6 cm long, 1.2–3 mm wide. Indumentum of glandular trichomes. *Receptacles* glabrous. *Flowers* with yellow corollas. Ray flower corollas 1.7–3 cm long, 4–6 mm wide, obovate-elliptic to oblong-elliptic, apex generally with 3 teeth. Disk flower corollas 5–6 × 1–3 mm. *Cypselae* brown, with slightly grooved-reticulate surface, dimorphic. Cypselae from ray flowers 3.5 × 0.8 mm, glabrous or glabrate, without pappus. Cypselae from disk flowers 3 × 1 mm, sometimes with eglandular trichomes; pappus ca. 4 mm, white. (Completely mature cypselae not seen.) Chromosome number unknown.

Illustrations. Figures 7B, 26E–H.

Distribution. Western Turkey (Bolu, Bursa, and Konya provinces). Growing in woods and open moist rocky places, altitude 1800–2200 m (Fig. 14).

Doronicum reticulatum is morphologically similar to those species with a "*macrophyllum*" habit in southwestern Asia, but it is quite distinctive because of its unique type of phyllaries (Fig. 26E, F), which are ovate-lanceolate ending in a long tapering apex, and with 8 to 12 longitudinal veins dark-colored. *Doronicum reticulatum* grows only in western Turkey where there is no overlap with any other species of the "*macrophyllum*" group, although it is geographically close to *D. cacaliifolium.* The only species that overlaps its area is *D. orientale,* which is morphologically quite different (i.e., habit, type of phyllaries, type of rhizome; Figs. 5E, F, 26E, F). See also comments on *D. cacaliifolium* and *D. macrophyllum* subsp. *sparsipilosum.*

The name *Doronicum bithynicum* J. R. Edm. was given by Edmondson (1973) for a *pro parte* of the illegitimate name *D. thirkei* Schultz Bip. ex Boiss. (Boissier, 1875: 379). Boissier's name includes his *D. reticulatum* Boiss. (1844), which was collected in Tmolus Bogdagh, and also plants from Mt. Olympus in Bithynia. Edmondson (1973) considered these to be two different species, and he gave the name *D. bithynicum* for those plants from Mt. Olympus, reserving the name *D. reticulatum* for those from Tmolus Bogdagh. In this study, however, no diagnostic characters to separate *D. bithynicum* (Edmondson, 1973) and *D. reticulatum* were found.

Accordingly, these names are here considered synonyms.

Selected specimens examined. TURKEY. **Bolu:** Ala dag Kartalkoy, *Alpay 2642* (E); Köroglu, *Buchner 83-70-13* (W); Ala dag, Kartal Kaya, *Davis & Coode 37372* (E, K). **Bursa:** Uludag, *Aytaç & Ekici 6229* (GAZI); Uludag, *A. & T. Baytop 20972* (E); Uludag, Bithyniae, *Bernardi 18013* (G); Mt. Olymp., July 1873, *Pichler s.n.* (K); Belvedere above Bursa, *Polunin 15054* (E); Uludag, 1968, *Sorger 68-53a-6* (W); Uludag bei Bursa, *H. & E. Walter 641* (B). **Konya:** Phrygia, Akscheher, Mt. Sultandagh, *Bornmüller 9620* (B).

26. Doronicum stenoglossum Maxim., Bull. Acad. Imp. Sci. Saint-Petersbourg 27: 483. 1881. TYPE: "China occidentalis, Regio Tangut (prov. Kansu)," 1880, *N. M. Przevalski s.n.* (lectotype, designated by Álvarez Fernández & Nieto Feliner (1999: 805), K!).

Doronicum souliei Cavill., Annuaire Conserv. Jard. Bot. Genève 10: 235. 1907. Syn. nov. TYPE: China. Tibet, Kiala, Tongolo, *J. A. Soulié 335* (lectotype, designated here, G!; isotype, K!).

Plant up to 120 cm tall. *Rhizomes* woody, glabrous, without leaf remains, sometimes with adventitious roots at the base of stem. *Stems* simple or branched, sometimes branched from the base, with leaves all along the stem. Indumentum of long-stalked glandular trichomes (0.5–1 mm), and sometimes also eglandular blunt trichomes (ca. 1 mm), more abundant near the capitula, sometimes glabrous to glabrate at the base. *Leaves* entire to very slightly dentate. Basal leaves absent at flowering time; blade ca. 6 × 3 cm, oblong elliptic, with attenuate base and blunt to subacute apex, with actinodromous to pinnate-actinodromous venation; petiole ca. 13 cm long, 2 mm wide. Lower and middle cauline leaves 3.5–15 × 1.1–6 cm, similar to basal leaves or sessile, almost fiddle-shaped to ovate-elliptic, semi-amplexicaul. Upper cauline leaves 2–6 × 0.5–2.5 cm, similar to middle cauline leaves, or ovate-lanceolate, sometimes bract-like. Indumentum scarce, mainly glandular, sometimes also eglandular blunt trichomes, more abundant on margins of upper leaves. *Capitula* 2 to 11, 1.5–3 cm diam. including rays and phyllaries; involucre longer than rays or equaling them. *Phyllaries* herbaceous, very narrowly triangular-subulate, almost linear, erect, acute; the outer 1.3–2.1 cm long, 1–2 mm wide; the inner 1.3–1.8 cm long, 0.7–1.5 mm wide. Indumentum only present in the lower half, similar to the upper part of stem, absolutely glabrous in the upper half. *Receptacles* glabrous. *Flowers* with pale yellow to green corollas. Ray flower corollas 1–1.3 cm long, 0.5–1.8 mm wide, linear, apex generally with 3 teeth. Disk flower corollas 3.5–4.3 × 0.5–0.8 mm, narrowly obconical. *Cypselae* brown to brown-red, with warty surface, homomorphic, 2–3 × 0.7–1.8 mm, glabrous to glabrate, with scattered short eglandular trichomes (ca. 0.1 mm). Pappus 4–6 mm, consisting of one row of white to white-yellow capillary bristles; pappus from ray flowers caducous as a whole crown. Chromosome number unknown.

Illustrations. Figures 4E–H, 6D.

Distribution. South-central China (provinces of Gansu, Sichuan, Tibet-Qinghai, and Yunnan). Open moist rocky places, woods, meadows, and near watercourses, altitude 3000–5000 m (Fig. 21).

Doronicum stenoglossum is the most distinctive species within the genus. In fact, historically it was treated as a different section (*Soulieastrum*), under *D. souliei* Cavill. by Cavillier (1911). Together, the large amount of autapomorphies makes its appearance quite different, specially regarding the capitula. The shape, size, and color of flowers and shape and size of phyllaries are unique within the genus (Fig. 4E, F). In a phylogenetic analysis based on molecular data (Álvarez Fernández et al., 2001) it is deeply nested within a group of central Asian species that share no morphological synapomorphies at all, indicating that its distinctive characters are autapomorphies and that the subgeneric treatment in this case is not appropriate. (See also comments under *D. briquetii* and *D. kamaonense.*)

Cavillier (1911: 360) included *Doronicum stenoglossum* in his section *Soulieastrum*, but because he could not see the type material, he concluded that the treatment was tentative. He mentioned that based on its protologue, the most similar species is *D. souliei* Cavill. When type material of both names was studied, the same identity was determined in both cases. Thus, the name *D. souliei* is treated as a synonym of *D. stenoglossum*, which has priority. To clarify the identity of *D. souliei*, a lectotype was designated above based on Cavillier's citation in the protologue. Two sheets that match his citation were found at G and K, respectively, and the one best preserved was selected as lectotype.

Selected specimens examined. CHINA. **Gansu:** Hai Tchoang ze, *Licent 4730* (BM, K); T'ao river, Merku valley, *Rock 12941* (GH); Tebbu, Drakana, Wapaku, *Rock 14599* (E, K, NY). **Sichuan:** Sungpan-hsien, *Fang 4129* (E, K, NY); Mts. Hu-li, *Forrest 16825* (E, K); Mt. Kungala, 25 July 1885, *Potanin s.n.* (LE); Guma-Kika, 6 Aug. 1885, *Potanin s.n.* (LE); Mt. Mitzuga, Muli Gomba, *Rock 16566* (E); Sikang, Kangting, Tachienlu, Chungo Valley, Hsintientzü, *Smith 11378* (BM, GH, MO, UPS, W); Dongrergo, *Smith 3587* (E, UPS); Hsioeh-shan, 19 July 1922, *Smith 3880* (UPS); Tachienlu, Hadjaha, *Stevens 392* (W); Sungpan, 1914, *Weigold s.n.* (W). **Tibet-Qinghai:** Dari Darlag Xian, Sainaniuda, Jimai Güymai Xiang, Huang He, *Bartholomew & Gilbert 1205* (E, MO); Reting, *Ludlow & Sherriff 8931* (BM, E). **Yunnan:** Lai-cha-tse-ka, Hsia-Chungtien, *Feng 1893* (GH); Lichiang, *Forrest 2663* (BM, E); Chungtien plateau, *Forrest 10586* (BM, E, K, W); Muli, Dschungdien, Tschako, *Handel-Mazzetti 1343* (W); between Likiang, Tungshan, Tuinaoko and Tsilikiang, *Rock 9747* (E, GH, NY); Muli, Wachin, Jin-chang, *Yü 14593* (BM, E, GH).

TAXA EXCLUDED FROM *DORONICUM*

Doronicum thibetanum Cavill., Annuaire Conserv. Jard. Bot. Genève 10: 225. 1907. TYPE: "Thibet" 1882, *J. Murr s.n.* (lectotype, designated here, G-BOIS!).

This taxon belongs in the genus *Aster* sect. *Alpigeni* subsect. *Homochaeta* (cf. Álvarez Fernández & Nieto Feliner, 2000). To clarify the identity of this name that was in current use until a recent study (Álvarez Fernández & Nieto Feliner, 2000), its lectotype was designated above.

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APPENDIX 1

LIST OF SPECIES AND SUBSPECIES

1. *Doronicum altaicum* Pall. [LT (lectotype) by Álvarez Fernández & Nieto Feliner, 1999]

2. *Doronicum austriacum* Jacq. [LT by Pérez, Llamas, Acedo & Penas, 1997]

3. *Doronicum briquetii* Cavill. [LT by Álvarez Fernández & Nieto Feliner, 1999]

4. *Doronicum cacaliifolium* Boiss. & Heldr. [LT by Álvarez Fernández & Nieto Feliner, 1999]

5. *Doronicum carpaticum* (Griseb. & A. Schenk) Nyman

6. *Doronicum carpetanum* Boiss. & Reut. ex Willk. [LT by Chacón, 1987]

6a. *Doronicum carpetanum* Boiss. & Reut. ex Willk. subsp. *carpetanum*

6b. *Doronicum carpetanum* Boiss. & Reut. ex Willk. subsp. *diazii* (C. Pérez Morales & A. Penas) Álv. Fern.

6c. *Doronicum carpetanum* Boiss. & Reut. ex Willk. subsp. *kuepferi* (R. Chacón) Álv. Fern.

6d. *Doronicum carpetanum* Boiss. & Reut. ex Willk.

subsp. *pubescens* (C. Pérez Morales, A. Penas, F. Llamas & C. Acedo) Aizpuru

7. *Doronicum cataractarum* Widder

8. *Doronicum clusii* (All.) Tausch

9. *Doronicum columnae* Ten. [LT by Álvarez Fernández & Nieto Feliner, 1999]

10. *Doronicum corsicum* (Loisel.) Poir.

11. *Doronicum dolichotrichum* Cavill. [LT by Álvarez Fernández & Nieto Feliner, 1999]

12. *Doronicum falconeri* C. B. Clarke [LT by Álvarez Fernández & Nieto Feliner, 1999] = *Doronicum turkestanicum* Cavill. [LT here]

13. *Doronicum gansuense* Y. L. Chen

14. *Doronicum glaciale* (Wulfen) Nyman [LT by Álvarez Fernández & Nieto Feliner, 1999]

= *Arnica doronicum* Jacq. [LT here]

15. *Doronicum grandiflorum* Lam. [LT by Álvarez Fernández & Nieto Feliner, 1999]

= *Doronicum portae* Chabert [LT here]

= *Doronicum scorpioides* Lam. [LT here]

16. *Doronicum haussknechtii* Cavill. [LT by Álvarez Fernández & Nieto Feliner, 1999]

17. *Doronicum hungaricum* Rchb. fil. [LT by Álvarez Fernández & Nieto Feliner, 1999]

18. *Doronicum kamaonense* (DC.) Álv. Fern. [LT by Álvarez Fernández, 2001]

19. *Doronicum macrophyllum* Fisch. [LT by Álvarez Fernández & Nieto Feliner, 1999]

19a. *Doronicum macrophyllum* Fisch. subsp. *macrophyllum*

19b. *Doronicum macrophyllum* Fisch. subsp. *sparsipilosum* (J. R. Edm.) Álv. Fern.

20. *Doronicum maximum* Boiss. & A. Huet [LT by Álvarez Fernández & Nieto Feliner, 1999]

21. *Doronicum oblongifolium* DC. [LT by Álvarez Fernández & Nieto Feliner, 1999]

22. *Doronicum orientale* Hoffm.

= *Doronicum caucasicum* M. Bieb. [LT here]

23. *Doronicum pardalianches* L. [LT by Llamas, Pérez, Acedo & Penas in Jarvis & Turland, 1998]

24. *Doronicum plantagineum* L. [LT by Llamas, Pérez, Acedo & Penas in Jarvis & Turland, 1998]

25. *Doronicum reticulatum* Boiss. [LT by Álvarez Fernández & Nieto Feliner, 1999]

26. *Doronicum stenoglossum* Maxim. [LT by Álvarez Fernández & Nieto Feliner, 1999]

= *Doronicum souliei* Cavill. [LT here]

APPENDIX 2

INDEX TO EXSICCATAE

Specimens are listed alphabetically by collector, followed by collection number or date, only when collector number is unavailable. The number in parentheses corresponds to the number in the List of Species and Subspecies above.

J. Abel, 94 (12); A. Achverdov & A. Doluchanow, 15 Aug. 1929 (21), 17 Aug. 1929 (21); Adamovic, May 1896 (17), June 190? (22), July 1900 (9), July 1905 (9), July 1917 (5); C. Aedo, 25 July 1982 (6d), 2 July 1983 (6d), 25 Aug. 1985 (6b), 16 May 1987 (24), 2 Aug. 1987 (15), 8 July 1990 (15); C. Aedo et al., 2888 (23), 3631b (6d); P. Aellen, 20 July 1932 (10); R. Ajdarova, 21 May 1983 (12); J. R. Akeroyd, 53 (9); I. Akinfiew, 29 July 1893 (21); Al. Buia, 2 May 1963 (17); Albury, Cheese & Watson, 705 (22), 1751 (22), 3159 (11), 3176 (21); J. A. Alejandre, 333-86 (24); J. A. Alejandre et al., 1460 (6d); R. C. Alexander, 1842 (2) (14); Alexcenko, 12861 (19a), 8 July 1897 (19a), 31 June 1901 (12); Alexcenko & Woronow, 13586 (21); Ch. S. Ali & Metz, 157 (12); T. Almaraz, 26 July 1997 (15); T. Almaraz & I. Álvarez, 977 (24), 979 (24); T. Almaraz, I. Álvarez, & M. A. García, 1008 (23), 1009 (23), 1015 (23); T. Almaraz, I. Álvarez, M. A. García & R. Duno, 984 (24); T. Almaraz, I. Álvarez, M. A. García & L. Medina, 802 (6a); T. Almaraz, I. Álvarez, M. A. García & E. Monasterio-Huelín, 804 (6a), 805 (6a); T. Almaraz & A. Cano, 275 (15), 288 (15); Alpay, 2641 (22), 2642 (25); A. H. G. Alston & N. Y. Sandwith, 45 (9), 441 (2), 691 (9), 2119 (2), 2065 (9), 1528 (9); A. H. G. Alston & N. D. Simpson, 37736 (24); I. Álvarez, 923 (6d), 927 (6d); I. Álvarez, M. A. García, Jansen, L. Medina & M. Sequeira, 1296 (6d); I. Álvarez, M. A. García & E. Monasterio-Huelín, 924 (6b), 926 (6d); I. Álvarez & N. Yagüe, 929 (6a), 931 (6a), 932 (6a), 933 (6c), 935 (6c), 936 (6d), 937 (6d), 941 (6d), 942 (6d), 944 (15); I. Álvarez et al., 800 (23), 801 (23), 943 (15), 954 (24), 966 (24), 1038 (6c); I. Álvarez, A. Herrero & N. Yagüe, 1350 (14), 1353 (8), 1354 (9), 1355 (8); F. Amich, 22 Apr. 1978 (24), 12 May 1978 (24); F. Amich. & F. Herrero, 17 May 1983 (24); F. Amich, E. Rico & J. Sánchez, 26 July 1977 (15), 28 June 1979 (6a); F. Amich, E. Rico, J. Sánchez & X. Giráldez, 25 Apr. 1981 (6d); Ananiva, 28 May 1955 (17); H. Andres, 695 (23); R. M. Andrés, 18 July 1974 (6d); R. Ansin, 392 (22); A. Aparicio, P. Murillo & S. Silvestre, 28 June 1984 (24); J. M. Aparicio & P. M. Uribe-Echevarría, 27 July 1993 (15); H. Appleton, 749 (12), 902 (12); V. J. Arán & M. J. Tohá, 10 Aug. 1987 (23), 13 May 1995 (24); M. Arbella, 16 June 1981 (15); J. C. Archibald, 326 (9), 585 (2); Ar-Leybuev, 532 (9); E. Armstrong, 19 May 1949 (23); A. Arvat, 7 May 1934 (17); Arvet-Touvet, Chaboisseau & Fauré, 1687 (8); C. Aseginolaza & D. Gómez, 21 July 1988 (23), 2 Aug. 1988 (23); Assadi & Mozaffarian, 30306 (11); S. C. Atchley, 945 (9), 2250 (9); L. Aterido, Aug. 1918 (15); Aucher-Eloy, 3268 (22), 3269 (25), 3848 (22), 4751 (22), 2 Apr. 1865 (22); Audibert, 1828 (24); Ausserdorfer, July 1863–65 (9), 6 July 1865 (9), 13 July 1865 (9), 10 Aug. 1873 (14); Averianov et al., 2421 (21), 2461 (21), 2837 (19a), 3200 (19a); Z. Aytaç, 1167 (22), 2933 (19a); Z. Aytaç & M. Ekici, 6229 (25); G. V. Aznavour, 27 Mar. 1892 (22), 10 May 1896 (22), 7 Apr. 1889 (22), 12 Apr. 1904 (22).

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Benito & D. Goñi, 14 July 1996 (15); Berg, 12 Oct. 1924 (14); E. Berger, 30 May 1946 (23); Bernard, 20 July 1901 (15), Aug. 1902 (15); Bernardi, 18013 (25); J. Bernátsky, 20 May 1898 (9); W. Bernouilli, 14 Aug. 1888 (8); S. Besalet, 163 (22); S. H. Bickham, 876 (23); Bierbach, May 1903 (9), June 1903 (2), July 1903 (9); E. Biesalski, 469 (2); C. Billot, 26 June 1846 (2); Binder, Hagemann, Hempel & Raus, 297 (9); Binz, 405 (8) (15); E. Blanco, 1348 (24); G. Bocquet, 10476 (24); M. O. Boggiani, 22 Aug. 1912 (8), 28 Aug. 1912 (15); S. N. Bogolubow, 6 June 1909 (12), 14 June 1909 (12); Boissier, 1842 (22); Boissier & Reuter, July 1858 (6a); Bonnet, 19 June 1873 (23), 26 May 1873 (23), 6 May 1877 (24); Bonnier, 163 (8); N. L. Bor, 11948 (12); Bordère, July 1866 (23), July 1872 (23), July 1873 (23); A. Boreau, 27 Apr. 1846 (24); J. M. Borel, June 1850 (23), 13 July 1862 (15), 7 Aug. 1864 (15), 5 Aug. 1866 (15), 2 June 1868 (23); J. Borja & S. Rivas Martínez, 1962–63 (15); Borja, 18 July 1951 (6d); J. Bornmüller, 76 (17) (22), 127 (9), 176 (22), 688 (22), 1165 (2), 1166 (2), 2624 (22), 2371 (9), 4263 (9), 4264 (22), 4265 (22), 4266 (22), 4267 (22), 4268 (9), 4269 (2) (9), 4621 (22), 4622 (22), 4623 (22), 9607 (22), 9620 (25), 9666 (22), 14245 (22), Apr. 1884 (9), 24 July 1886 (14), 8 May 1887 (9), 22 July 1887 (2), Apr. 1888 (22), 4 May 1888 (9), 24 July 1888 (8), 1 June 1894 (23), 15 July 1894 (15), 9 Aug. 1894 (15), 1 July 1895 (8), 10 Aug. 1895 (15), 13 Aug. 1895 (15), 7 June 1887 (9), 9 July 1895 (8), 1 June 1896 (2), 3 Sep. 1896 (14), 27 June 1906 (14), 18 July 1907 (9), 27 July 1907 (14), 30 July 1907 (14), 10 June 1908 (2), July 1911 (23), 28 June 1912 (9), 7 July 1912 (9), 9 July 1912 (9), 19 July 1912 (8), 24 July 1912 (8), 25 July 1912 (8), 7 Aug. 1912 (2), July 1916 (2), 28 Aug. 1922 (15), 8 July 1925 (8), 21 July 1925 (15), 28 July 1925 (15), 4 June 1931 (9), 26 July 1932 (8), 2 Aug. 1932 (8); J. & F. Bornmüller, 11965 (22); Bornmüller & Schuller, 1918 (9); A. B. Borodina et al., 27 July 1976 (5); A. Boros, 25 May 1922 (17); A. Borza & E. I. Nyárády, 9 Aug. 1933 (9); Bothe, May 1907 (23), 15 July 1928 (14); Bouchard, 3 Aug. 1906 (15), 7 Sep. 1909 (15); H. Bourdot, July 1889 (23); E. Bourgeau, 19 (15), 139 (8), 140 (15), 2508 (6a), 2671 (6a), 21 June 1849 (24), 20 Apr. 1860 (22), July 1862 (15); Bracht, 1842 (15); E. Brandis, Apr. 1898 (9); J. Briquet, 3585 (23), 7354 (23); C. E. Britton, 27 May 1905 (23); J. Brocherel, 39 (12), 69 (12); A. H. & V. F. Brotherus, 500a (19a), 500b (11) 500c (11), 501 (21), 501a (21); V. F. Brotherus, 477 (12); G. C. Brown, 381/1 (23); R. Brumm, Aug. 1900 (14), July 1903 (8), Aug. 1904 (8) (15), July 1906 (15), Aug. 1907 (15); R. K. Brummitt, 5494a (15), 6554 (22); R. K. Brummitt & A. O. Chater, 135 (24); Brunner, July 1852 (23); Brutelette, May 1862 (24); Buades, Mazimpaka, Pajarón & Ron, 20 May 1976 (24); J. Bubela, 24 July 1883 (2); J. Bucek, June 1931 (17); P. Buchner, 83-70-13 (25); Bührer, 2 Aug. 1942 (15); Burgos & Cardiel, 3472 (24), 20 June 1985 (6a); E. Burnat, 9 June 1889 (22); J. Burtt-Davy, 121/27 (2); E. & N. A. Busch, 23 (19a), 47 (19a), 8 July 1913 (21), 10 July 1913 (21), 14 June 1925 (19a), 4 July 1925 (21), 13 July 1925 (19a), 28 June 1927 (21), 1 July 1927 (21), 3 July 1927 (19a), 12 Aug. 1927 (19a), 9 July 1928 (19a), 21 July 1928 (19a), 28 July 1928 (19a), 12 Aug. 1928 (19a), 19 July 1929 (19a), 1 Aug. 1929 (11), 5 Aug. 1929 (19a), 8 Aug. 1929 (19a), 18 Aug. 1929 (19a), 12 July 1930 (19a), 19 July 1931 (19a), 25 July 1931 (19a), 7 Aug. 1931 (19a), 31 Aug. 1931 (21), 17 July 1932 (21), 20 July 1932 (21), 4 Aug. 1932 (21), 18 July 1933 (19a), 20 July 1933 (19a), 1 Aug. 1933 (21), 23 Aug. 1933 (19a), 6 Sep. 1935 (19a); N. A. Busch, 2 July 1903 (19a), 14 July 1903 (21), 18 July 1904 (19a); N. A. Busch & B. Klopotow, 668 (22), 16 Apr. 1907 (22).

A. Caballero, 20 May 1949 (24); Callier, Hirte & Scholz, 21 Aug. 1893 (2); C. Calvo, 25 July 1984 (15); F. Cámara, 17 July 1935 (6a); Cardiel & Burgos, 20 June 1985 (24); Carrasco, Burgaz & Martín-Blanco, 27 July 1993 (2); Carrasco, Casaseca, Fernández Díez & Velayos, 16 July 1979 (6a); Carrasco & Velayos, 13 Apr. 1987 (24); Carrisso & Mendoça, 25 Mar. 1926 (24); Caruel, 20 Apr. 1856 (9); B. Casaseca, 17 May 1968 (24), 30 Mar. 1973 (24), 19 July 1973 (6d); B. Casaseca, & F. J. Fernández Díez, 16 July 1974 (6d); B. Casaseca, Fernández Díez & E. Rico, 8 Mar. 1977 (24), 4 Aug. 1977 (6c); Casaseca et al., 27 July 1979 (6d); J. L. Castillo & R. Cordero, 26 May 1981 (24), 1 May 1990 (24); S. Castroviejo, 10 July 1973 (6d); S. Castroviejo, B. Casaseca & E. Rico, 10835 (6a); S. Castroviejo & Fernández Quirós, 5868 (6a); S. Castroviejo, C. Fraile & T. Romero, 10709 (6a); S. Castroviejo & E. Valdés Bermejo, 917 (15), 14032 (1); S. Castroviejo et al., 7133 (6a), 11432 (8), 11615 (8), 10 July 1989 (6c); Cavanilles, May 1784 (24); L. Ceballos, 15 May 1933 (24), 1 June 1933 (24), 28 May 1934 (24); L. Ceballos & C. Vicioso, 1136 (6b); Celakovsky, May 1885 (22); Chabert, 2 June 1850 (23), 22 Aug. 1878 (23), 8 June 1892 (23); M. J. Chaffanjon, 385 (12); D. Chamberlain, P. Cox & P. Hutchison, 1989 (13); Chamberlain, Jwand & Kupicha, 286 (24); F. S. Chapman, 449 (12); A. Charpin, 15017 (6d), 15845 (9), 21087 (24), 24244 (23), 3 July 1959 (23), 10 May 1961 (23); A. Charpin & C. Defferrard, 16853 (24); A. Charpin & M. Dittrich, 17387 (15); A. Charpin, Dittrich, Greuter & Von Auw, 11014 (9), 11314 (9); A. Charpin, Jaquemoud & Jeanmonod, 808 (24); A. Charpin & R. Salaman, 17480 (15); A. Charpin et al., 22 Sep. 1969 (15); Charrier, 230 (24); A. O. Chater, 310 (9), 515 (9), 562 (9); J. L. Chaworth-Musters, 3 May 1931 (22); Cheese, Mitchell & Watson, 2642 (22); P. Chenevard, 31 July 1910 (8), 11 Aug. 1911 (9), 5 Aug. 1912 (15); V. L. Cherepnin & M. T. Laletina, 12 July 1963 (1); L. F. Chiapella & L. Poldini, 28 May 1976 (9); H. G. Chick, 22A (9); Chick, Hill, Sandwith & Turrill, 2624 (22); Chinese collectors, D167 (3); J. R. Chodat, 28. Mar. (24); J. R. Churchill, 9 Sep. 1907 (15), 12 Sep. 1907 (8), 5 July 1913 (9); S. Cimarolli, 8 July 1899 (15); D. & M. Cîrtu, 28 June 1972 (2); C. B. Clarke, 29287D (18), 30258 (12), 30842 (18), 48753 (15); Clemente, 1803 (24); P. Conrath, 1888 (21); A. Contardo, 3 July 1966 (2); E. Contré, 12 June 1955 (23); W. M. Conway, 211 (12), 267 (12); M. J. E. Coode & B. M. G. Jones, 408 (22), 1199 (22), 1754 (22), 2031 (22), 2077 (22), 2733 (22); Cook, Grubb, Newman & Whitmore, 145 (9); R. E. Cooper, 230 (18), 867 (18), 5132 (3); E. Cornaz, 14 Aug. 1881 (8); E. Cosson, 1839 (24); E. Cosson & C. Duval, 6 May 1888 (24); Vid. H. Coste Perrault, 10 June 1915 (2); P. Cousturier, July 1912 (10); P. Cousturier & M. Gandoger, Aug. 1913 (15); A. Craig-Christie, 31 May 1873 (24); F. C.

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E. Hackel, 26 May 1876 (24); J. Hafellner & S. Titze, 222 (9); I. Hagemann, H. Scholz & W. Schwarz, 85 (22), 187 (9), 332 (9), 553 (9); H. Hal, 13 Apr. 1869 (9); Halácsy, July 1878 (2); Hamilton, 10 Sep. 1884 (15), 21 July 1859 (15), Aug. 1892 (8); Hanbury-Tracy, 22 (3); Handel-Mazzetti, 763 (19a), 1343 (26), 1765 (3), 18 July 1906 (15), 17 July 1927 (9); A. Hansen & H. Nielsen, 1440 (22); A. Hardy, July 1881 (15); P. Hariot, 23 May 1873 (24); R. M. Harley, 17721 (2); R. M. Harley & D. Peev, 11907 (2); G. W. Harris, 259 (22), 433 (22); T. D. Harrison, 18 May 1978 (24); P. Harrold & R. J. D. McBeath, 158 (6d), 240 (6b), 252 (6b), 346 (15); Harz, 20 June 1908 (23); E. Hausser, 27 Apr. 1885 (9); Haussknecht, 5 Aug. 1865 (16); A. & F. v. Hayek, July 1907 (8); Hayek, 16 July 1913 (5); Hayes, 1839 (9); M. Heard, Aug. 1926 (15); Heiland, May 1867 (22), July 1878 (23), 23 Apr. 1879 (9); T. Heldreich, 122 (22), 1249 (22), 25 Apr. 1828 (22), Apr. 1843 (22), May 1844 (22), June 1844 (22), 1845 (4) (22), 1 May 1848 (22), 27 Apr. 1875 (22), 23 July 1879 (9); T. Heldreich & T. Holzmann, May 1883 (22); Heltman, 28 June 1958 (2); W. Hempel, 2786 (8), 16 June 1964 (2), 17 June 1964 (9); J. Hennecart, 24 July 1850 (15); E. Hennipman et al., 475 (22), 741 (22), 1272 (22); F. N. Hepper, 4739 (23); F. Heras & J. A. Alejandre, 1192-85 (6a), 1982–85 (6a); J. Herranz et al., 1 June 1990 (24); A. Herrero, 2 Aug. 1996 (15), 23 Aug. 1996 (15); L. Herrero, 2 May 1987 (24); Heuffel, 44 (9), 45 (9); P. Hiepko, 145 (9); A. W. Hill, 1896 (15); T. N. Ho, B. Bartholomew & M. Gilbert, 1205 (26); E. Hodgkin, 168 (14), 220 (14); H. Hofmann, 29 July 1901 (2); R. F. Hohenacker, June 1834 (19a), May 1838 (21), 1838 (19a) (22), June 1842 (19a); L. Hollós, 13 May 1914 (22); L. B. Holm-Nielsen, 10 June 1966 (23); D. Höner & S. Potthoff, 1673 (22), 1718 (9); J. D. Hooker, 1862 (15); F. Höpflinger, 30 July 1950 (7), 1 Aug. 1961 (8); J. F. Horcajo, 6 May 1984 (24); J. Houska, 11 May 1939 (9); A. Huber, 17 Aug. 1930 (15); Huet du Pavillon, July 1853 (20), July 1854 (2); E. & A. Huet du Pavillon, 362 (9), 12 June 1855 (22), 19 Mar. 1856 (22); J. Hulják, 26 Apr. 1913 (17), 26 May 1913 (17); L. H. Hurst, 71 (9); J. Hutchinson, 29 May 1958 (23); Hutchinson, Matthews & Riley, 60 (15), 156 (15); R. Huter, 1126 (9), 1814 (9), 17 July 1871 (2), 17 July 1878 (2), 20 July 1878 (9), July 1880 (8), Aug. 1888 (14), 18 July 1907 (9); Huter, Porta & Rigo, 67 (22); F. Ch. Hy, Apr. 1903 (24).

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Jabornegg, Aug. 1875 (15), 1886 (8); A. B. Jackson, 565 (24), 11 Apr. 1927 (24); Jacquemont, July 1821 (2), 1822 (10) (15); F. Jacquemoud, 3459 (23), 3888 (14); E. Jahandiez, 386 (24), 436 (24), 10 May 1907 (24); J. Jahn, 7 July 1886 (15), June 1890 (2), 19 May 1899 (22); D. Jakovlev, 22 July 1914 (12); Janka, 18 May 1884 (17), Apr. 1885 (17); Jaquet, 12 Aug. 1904 (15); U. Jath, 11 Apr. 1990 (22); S. Jávorka, Apr. 1913 (9), 27 Apr. 1930 (22); Jeanpert, 7 June 1891 (24), 20 May 1894 (23), 25 May 1894 (23), 27 May 1897 (24), 6 May 1900 (24); Jermy, 1868 (2); A. J. Jhorp, 13 July 1886 (15); G. Jlié, 1887 (17), 1889 (9); G. C. Joad, 18 July 1867 (15), 29 July 1867 (15), 12 July 1868 (15), 5 May 1870 (23), 22 July 1876 (15); S. L. Jury & S. P. Thornton-Wood, 9876 (2); Jury, Watson, Webb & Wyse Jackson 6638 (9); S. Juzepczuk, 593 (12), 9 July 1923 (19a).

G. Karelin & Kirilov, 463 (12), 1621 (12); I. Karjagin, 20 Aug. 1932 (19a), 8 July 1935 (19a); I. Karjagin & A. Grossheim, 20 Aug. 1932 (11) (19a); I. Karjagin & B. Saflev, 25 July 1931 (21); I. Karjagin & J. Tsaev, 25 Aug. 1933 (11); M. Kasumova, 30 June 1929 (19a), 15 July 1930 (19a); Kayacik & Yaltirik, 3368 (22); C. Keck & T. Pichler, May 1890 (9), Aug. 1890 (2); L. Keller, 22 June 1879 (14), 17 July 1889 (2); R. Keller, July 1886 (8); Kerck, 40/8 (11); A. Kerner, 875 (8); Ketelhut & Schiers, 17 Sep. 1981 (15); E. J. Khek, 27 May 1886 (22), 10 June 1895 (22); Kiener, 6 May 1860 (24); E. I. Kikodse, July 1914 (11); F. Kingdon Ward, 4711 (26), 5866 (1) (3), 10876 (12), 12125 (3), 19592 (3), 1913 (3); Z. Kiogkova, 127 (19a); Kirpichnikov, 27 May 1948 (21); Klemenc, 1894 (12); B. Klopotov, 28 June 1909 (1); J. Knoph & R. Vogt, 2407 (23); O. Knorring, 12 July 1913 (12), 31 July 1913 (12); O. Knorring & Z. Minkwitz, 20 Aug. 1911 (12); Koch, 123 (14) (15); W. Koelz, 20964 (18), 22052 (18), 9429 (12), 9716 (12); St. Kogeoucharov, 50 (9); E. Köhler & C. Beck, 13 July 1964 (19a); A. Kolakovsky, 10 June 1927 (21), 17 June 1929 (21), 30 June 1929 (19a); Kolenati, 1663 (19a), June 1844 (21); P. A. Kolovski, 1913 (1); V. I. Komarov, 30 July 1902 (1); M. Kondratieva, 68 (12); A. Konnov et al., 742 (12); E. Korb, 8 July 1908 (2), 24 May 1933 (17), 19 July 1936 (23); E. Korotkova & Z. Klimovskaya, 112 (12); S. Korshinsky, 1504 (12); Košanin, 14 June 1924 (9); T. Kotschy, 147 (22), 363 (20); W. Kotte, 18 Apr. 1932 (22); Kováts, 100 (17), July 1843 (17); G. Kozij, 16 July 1938 (5); E. Koziol, 28 July 1975 (2); V. Kozlovsky, 7 Aug. 1928 (21), 24 May 1936 (21); Kralik, 538 (10), 538a (10), 638a (10), 16 May 1844 (24), 18 May 1845 (24), 15 May 1846 (24); K. U. Kramer, 1366 (2), 8672 (15); I. Krasnoborov, 8172 (1), 8179 (1); I. Krasnoborov & Chanmicun, 240 (1); I. Krasnoborov & Ershova, 22 Aug. 1962 (1); I. Krasnoborov, Hrubov & Jakovleva, 959 (1); I. Krasnoborov & Merzliakova, 8181 (1); I.

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C. Naegeli, 3 Aug. 1837 (8); Naumann, 1818 (8); F. Navarro & C. J. Valle, 28 July 1982 (6c); G. Navarro, 26 July 1982 (6b), 25 May 1984 (24), 15 July 1985 (6a); L. Neé, June 1786 (24); V. Nekrasova, 2 July 1911 (1); V. Nekrasova & L. Aleksandrov, 43 (22); W. E. Nelmes, 1 (23); Nendtvich, May 1866 (22); P. V. Nesterov, 23 June 1907 (1), 16 June 1910 (11); A. Neumann, 2 May 1959 (23); F. Niedereder, 9 July 1904 (2), 16 June 1905 (2); G. B. Nielson, 503 (2); G. Nieto Feliner, 3888 (22); G. Nieto Feliner & J. Pedrol, 1543 (6a); G. Nieto Feliner et al., 2736 (6c), 30 May 1986 (23); Nordmann, 647 (11); Norris, May 1945 (22); C. & M. North, 42 (22); Nüsser, 82 (12); E. I. Nyárády, 28 Aug. 1911 (2), 29 July 1929 (2); M. Nydegger, 17340 (20), 19037 (25), 40085 (22), 40323 (22), 40766 (22), 16 Apr. 1976 (22); F. Nyman, Apr. 1844 (22).

F. Oberleitner, 73 (15), 8 July 1864 (2), 30 July 1865 (14), 19 July 1867 (8), 21 July 1868 (8), 30 June 1869 (2), 2 Aug. 1872 (8), 28 July 1874 (14); L. Oberneder, 5817 (15), 5935 (2); R. & L. Oberneder, 6497 (8); A. Oborny, 12 Aug. 1878 (2); H. Ocakverdi, 2340 (11); V.

M. & B. M. Ogievskie, 25 June 1913 (1); T. G. Orphanides, 196 (22), 340 (9), July 1854 (9), July 1854 (9), 5 May 1857 (22); B. B. Osmaston, 28 (18); B. Ovchinnikov & M. Usov, 301 (12); Owerin, 26 June 1861 (19a); Ch. Ozanon, 3 Aug. 1858 (15).

H. Pabot, 1717 (20); J. Paczoski, 6 May 1901 (17), 23 Apr. 1909 (17); J. Paillot, 2279′, 24 May 1859 (23); Pajarón, 683 (24); Palacio, Carrillo & Ferrero, 5 July 1997 (6c); P. Palézieux, 1 Aug. 1898 (9); I. V. Palibin, 5 June 1908 (8), 7 Aug. 1908 (15); A. Pallarés, 15 Apr. 1990 (24), July 1994 (15), May 1996 (24); W. Panknin, 24 May 1936 (23); J. Pantocsek, May 1868 (17), 8 Apr. 1906 (17); J. Papp, 25 Apr. 1946 (22); D. Parascan, 7 June 1960 (5); D. Parascan, E. Lungescu & D. Radu, 30 June 1960 (9); M. Pardo de Santayana & R. Morales, 1690 (6d); Parlatore, 18 Apr. 1856 (9), 1863 (22), 1866 (2); Parseval-Grandmaison, 31 May 18?2 (23); N. L. Pastushov, 20 Apr. 1925 (22); S. Patino, Uribe-Echevarría & Valencia, 27 May 1990 (6d); Patrin, 1780 (1); Patzak, Sep. 1953 (2) (7); C. Pau, 2386 (24), 27 July 1900 (6c); A. Pávai, 1875 (17), 187? (9); N. V. Pavlov, 601 (12); V. Payot, 1855 (15); S. Peker, 1178 (22); G. Pellanda, 10 May 1913 (9); A. Penas & M. E. García, 31 Mar. 1983 (24); A. Penas, M. E. García & L. Herrero, 3 May 1987 (24); E. Penkovskaya & I. Krasnoborov, 1 July 1964 (1); R. V. Pennington, 22 (9), 25 (9), 30 (9), 41 (9); J. L. Pérez Chiscano, 1 June 1974 (24); Tx. Pérez, A. Salazar & P. Urrutia, 20 July 1991 (6a); C. Pérez Morales, 27 July 1988 (6b); Pérez Morales et al., 11 July 1992 (6d); E. Perrier, 1849 (23); C. Persson, 5 Aug. 1934 (12); H. Pesmen, 727 (22); H. Pesmen & A. Güner, 2213 (22); S. Petrovič, 2200 (17), 2340 (22), Apr. 1882 (22), Apr. 1885 (17), Apr. 1887 (22), June 1887 (2); F. Petzi, 193 (2); V. V. Peznichenko, 108 (12); T. Pichler, 81 (22), 21 Aug. 1864 (15), Aug. 1864 (9), June 1872 (9), July 1873 (25), June 1874 (22), July 1874 (25), Apr. 1876 (22), 1878 (14), May 1890 (9), July 1892 (14); C. Pinard, 1843 (22); Pirker, Royl & Fleischer, 315 (2); C. J. Pitard, July 1906 (15); E. Pobedimova, 45 (12), 339 (12); D. Podlech, 37607 (9); Poisson, May 1879 (24); A. Polatschek, July 1969 (2), 9 May 1981 (23); A. V. Polo hij, 18 July 1947 (1); O. Polunin, 56/170 (18), 5332 (22), 6238 (12), 8268 (2), 14033 (22), 15054 (25), 15940 (22), 18 Apr. 1956 (22); O. Polunin, W. R. Sykes & L. Williams, 89 (18), 401 (18), 2622 (18), 4364 (18); E. Pop, Apr. 1923 (17); Poplavskaja, Tzinzerling & Sukačev, 2069 (1); M. G. Popov, 311 (12); T. Popova et al., 325 (11); Popovic, 8 July 1954 (8); A. Poretsky, 23 July 1928 (19a); A. Poretsky & G. Schultz, 9 Sep. 1927 (19a); P. Porta, July 1911 (15), Aug. 1858 (15), 27 June 1867 (15), July 1889 (9), Aug. 1893 (15); P. Porta & G. Rigo, 160 (24), 257 (24), 319 (9), 29 May 1895 (9); Post, 12 Aug. 1893 (22); G. N. Potanin, 1884–85 (3), 25 July 1885 (26), 6 Aug. 1885 (26), 24 June 1893 (3); Pojarkova, Rozhetits & Shishkin, 21 July 1940 (2); A. E. Pratt, 570 (26); Preissmann, 31 May 1886 (2); C. Prem & R. Vogt 5026 (2); F. Prenn, 13 Aug. 1945 (15); Prescott, 1830 (1) (22); Prescott-Decie, 1915 (18); M. P. Price, 1910 (1); W. R. Prieè, 492 (22); L. Prilipko, 19 June 1932 (21); L. Prilipko & J. Isaev, 17 July 1934 (21), 4 Aug. 1934 (11); E. Pritzel, July 1927 (8); N. M. Przevalski, 101 (12), 333 (26), 7 July 1877 (12); M. I. Ptaschizky, 16 July 1908 (12); E. Puente & C. Pérez Morales, 27 July 1988 (6b); J. Puyfol, 4925 (2).

H. Raap, 25 May 1895 (9); E. I. Rachkovskaja & V. I. Grubov, 4 Sep. 1949 (2); G. Radle, 40 (19a), 142 (21), 149 (21), 400 (19a); B. Rainha, 1047 (24); J. Ramsbottom, 1918 (22); V. Rastetter, 16 May 1993 (23); Raus, 4864 (11); Raus & Royl, 5057a (9); A. Rawi & I. Serhang, 24553 (11); K. H. Rechinger, 1701 (15), 3224 (15), 17881 (2), 20984 (9), 22674 (22), 23159 (22), 38768 (9), 54337 (22); K. H. & F. Rechinger, 851 (22), 661 (22), 3128 (2), 3794 (22), 3927 (22), 8758 (22), 10735 (2), 25 July 1928 (8); K. H. Rechinger & Scheffer, 711 (9), 1367 (9); L. Rechinger, 2377 (15); A. Regel, 686 (12), 19 July 1877 (12), 26 Aug. 1877 (12), 11 Sep. 1877 (12), 19 June 1878 (12), 20 June 1878 (12), 22 June 1878 (12), 24 July 1878 (12), 4 June 1879 (12), 14 June 1879 (12), 15 June 1879 (12), 16 June 1879 (12); C. Regel, 1 June 1964 (22), 10 June 1964 (22); J. R. Reid, 9 Sep. 1885 (18); Reiter, 10 Aug. 1933 (8); J. Renz, 48989 (20); Renz et al., 11 July 1974 (11); Requien, 250 (10); F. Ressman, 1878 (14); B. Retz, 46062 (24), 67398 (24), 89985 (24), 17 July 1856 (12); E. Reverchon, 16 Aug. 1872 (15), 18 July 1878 (10), 25 July 1878 (15), 28 Aug. 1878 (10), 21 July 1885 (10), 22 June 1886 (23), June 1898 (24); V. V. Reverdatto, 26 July 1942 (1); M. Reymond, 27 July 1931 (12); H. H. Rich, 1165 (18); A. Richter, 520 (17), 2772 (1), May 1872 (17), 13 May 1900 (17), 25 June 1900 (2), 12 May 1902 (9), 15 May 1907 (17), 31 July 1908 (9), 11 July 1909 (9); K. Richter, 17 July 1887 (2); E. Rico, 27 May 1983 (6a), 22 Aug. 1983 (6c); E. Rico, X. Giráldez & T. Romero, 17 July 1985 (6a); G. Rigo, 24 (22), 70 (9), 430 (9), 8 July 1870 (15), May 1873 (17), 12 July 1886 (9); S. Rivas Goday, 15 May 1924 (24), 18 May 1941 (24), 30 Apr. 1944 (23), 22 Apr. 1945 (24), 7 Aug. 1946 (6c), 18 Apr. 1957 (24), 26 July 1958 (6c), 20 May 1959 (24), 1 June 1966 (24); S. Rivas Goday & F. Bellot, 30 Mar. 1940 (24); S. Rivas Goday & M. Ladero, 3 Apr. 1969 (24); S. Rivas Goday, M. Ladero & Valdés, 12 July 1974 (6a); S. Rivas Goday & Monasterio, 10 Aug. 1947 (6a); S. Rivas Goday, S. Rivas Martínez & M. Ladero, 28 June 1970 (6a), 30 June 1973 (6a); S. Rivas Goday & E. Valdés Bermejo, 11 July 1974 (6d); S. Rivas Martínez, 25 Aug. 1957 (6a), 25 July 1958 (6c), 13 July 1965 (15), 1 June 1975 (24), 24 Aug. 1978 (6a); Rivas Martínez, M. Costa & J. Izco, 11 July 1973 (6a); S. Rivas Martínez & J. Izco, 25 Aug. 1967 (6c); S. Rivas Martínez, M. Ladero & M. Mayor, 1 June 1966 (24); S. Rivas Martínez & E. Valdés Bermejo, 7312 (6d); S. Rivas Martínez et al., 13 July 1965 (15), 13 July 1977 (6d), 16 June 1981 (6d), 5 July 1982 (6a) (24), 26 July 1989 (6c); J. Rivera, 25 Apr. 1978 (24); A. Roa, 22 June 1987 (6a); V. I. Roborowski, 205 (12); J. F. Rock, 9681 (3), 9747 (26), 9989 (3), 12192 (13), 12389 (13), 12941 (26), 13020 (13), 14599 (26), 16566 (26), 16834 (3), 22380 (3), 22891 (3), 23067 (1); L. Rodin, 1231 (12); J. Rodríguez-Oubiña & I. Cruces, 20 June 1997 (6d); Rogers, 234 (23), 717 (22); J. Rohlena, Aug. 1912 (9), June 1922 (9), July 1933 (9); I. Roldugin, 4871 (12); Römer, 30 May 1886 (9), June 1892 (9); C. Romero, July 1976 (15); K. Ronniger, 29 July 1883 (2), 29 July 1892 (2), 8 July 1918 (8), 20 May 1924 (9), 21 July 1930 (2), 24 July 1930 (2); R. J. Roshevitz, 11 June 1908 (12), 27 June 1908 (12), 7 July 1908 (12), 9 July 1908 (12), 1 Aug. 1908 (12), 3 July 1909 (12); H. Ross, July 1888 (22), May 1901 (22), June 1901 (22); S. Rossi & A. Malladra, Aug. 1890 (8) (15); W. Rössler, 8 (2); E. Rostan, 1850 (8), July 1860 (15); J. Röthlisberger, 29 July 1978 (9), 17 Apr. 1979 (22); W. Rothmaler, 8 Aug. 1933 (6d); W. Rothmaler & A. P. Silva, 15813 (24); Rotky, July 1885 (15); Rottenbach, 23 May 1894 (23); N. Roux & Blanc, 28 July 1899 (15); G. Rouy, 24 July 1874 (2), 14 May 1876 (24), 7 May 1879 (24); C. Royer, July 1874 (2); Royl & Hempel, 22 Sep. 1986 (8); Royl, Hempel & Richter, 19 Sep. 1986 (8); Royl & Ketelhut, 4 Sep. 1987 (15); Royl & Schiers, 1982

(8); A. Rozeira, 19 May 1946 (24); A. Rubio, 18 May 1991 (24); N. I. Rudstov, 13 July 1934 (12); Ruprecht, 154 (21), 156 (21), 1354 (19a), 22 Mar. 1861 (22), 10 June 1861 (21), 5 July 1861 (21), 8 July 1861 (21), 15 July 1861 (21), 26 July 1861 (21), 9 Aug. 1861 (19a), 7 Sep. 1861 (19a); Russell, 1235 (12), 1291 (12), 1424 (12).

J. Šafer, 15 June 1895 (2); Saint-Lager, 3 July 1896 (22), 7 June 1919 (23); G. Samuelsson, 21 May 1933 (22), 26 Apr. 1933 (22); G. Samuelsson & A. Zander, 22 Apr. 1931 (22); D. Sánchez-Mata, 9 June 1984 (24), July 1984 (6a), 9 July 1986 (6a); D. Sánchez-Mata, S. Laorge & D. Belmonte, 20 May 1982 (6c); Sánchez Pedraja, 21 Apr. 1992 (24); Sánchez Pedraja & Tapia Bon, 226/96 (24), 598b/96 (6d); N. Y. Sandwith, 3737B (23), 5340 (6b), 5684 (6a), 18 May 1935 (24), 30 June 1935 (23); V. Saposhnikov, 16 June 1902 (12), 30 June 1902 (12), 6 July 1912 (12), 22 June 1913 (12), 13 July 1913 (12), 14 Aug. 1923 (1); V. Saposhnikov & Shishkin, 15 July 1912 (12); V. Saposhnikov & T. Tripolitova, 7 July 1915 (12); F. Sappa & E. F. Galiano, 9 Aug. 1952 (15); S. Sardinero, 3 June 1990 (6a), 12 July 1990 (6a), 14 July 1990 (6c), 3 Aug. 1990 (6c), 23 Aug. 1990 (6c), 21 June 1991 (6a), 12 July 1991 (6c), 19 July 1991 (6a), 25 July 1990 (6c), 29 July 1991 (6a); E. M. Saunders, June 1915 (18); D. Sauter, 971 (14); D. Sauter & A. Traunsteiner, May 1836 (14); Schafferer, 16 Aug. 1890 (8); K. Scheer, 5 May 1918 (22); A. B. Schelkovnikov, 29 June 1909 (21), 15 July 1909 (21), 2 July 1911 (19a); A. B. Schelkovnikov & E. Kara-Murza, 13 July 1927 (19a), 9 Aug. 1928 (21), 16 Aug. 1928 (11) (19a); C. Scheppig, 30 June 1885 (23), 10 July 1887 (23); A. Scherfel, July 1880 (8), 28 July 1893 (8); N. Schestunov, 1137 (22); B. Schischkin, 26 May 1912 (12), 7 June 1912 (12), 2 Apr. 1917 (22), 6 July 1919 (19a), 4 July 1920 (11); B. Shishkin & G. Sumnevicz, 24 June 1931 (1); Schlagintweit, 5962 (3), 1855 (18); F. Schmid, 438 (12), 5989 (11); C. K. Schneider, 11 (9), 300 (17); C. K. Schneider, & Bergmann, 881 (2); J. Schneider, 22 May 1929 (17); Schneller, 23 June 1859 (17); H. Scholz & P. Hiepko, 988 (24); M. Schreiber, 10 Aug. 1911 (8); H. Schrenk, 8 Aug. 1925 (15); F. Schuhwerk, 85/32 (23); O. & R. Schulz, 20 July 1894 (2), 21 July 1894 (2); R. Schulz, 6 May 1894 (23), 19 July 1894 (2), 27 July 1899 (14), 31 July 1899 (14), 1 Aug. 1899 (9), 6 July 1902 (23); R. & O. Schulz, 18 May 1895 (9), 7 July 1896 (9); A. Schumacher, 1 June 1933 (23), 4 June 1968 (23); Schur, July 1839 (2), 27 July 1850 (5); O. Schwarz, 642 (22); Schwarzer, 28 Apr. 1848 (9); Schwerdtfeger, 17789 (6a); A. Segura Zubizarreta, 12525 (6a), 12526 (6a), 12527 (6a), 22654 (6a), 16 May 1970 (24), 10 June 1960 (24), 10 Apr. 1961 (24), 8 June 1967 (24), 23 Apr. 1970 (24); Seidl, 90 (21); Seidlitz, 33 (19a); R. Seligman, 53 (9), 103 (9); Sendtner, 301 (9), 302 (2); F. Sennen, 1973 (15), 3968 (2), 4433 (15), 3 Aug. 191? (15), May 1910 (23), 4 Aug. 1916 (15), 10 Aug. 1916 (15), 27 July 1931 (15); F. Sennen & Elías, 1906 (24); M. Serim, 17 S (22); J. A. Sesé, 7 July 1992 (23); J. A. Sesé et al., 18 July 1987 (15); Sharif, 224 (11); B. A. Shatakelberg & I. G. Knorring, 17 Aug. 1937 (12); G. Sherriff, 7405 (12); Shirokova, 6 May 1948 (17); H. Sholz, 19 May 1974 (23); T. B. Shrestha, 5165 (18), 5180 (18); Siami, 3809 (11); Sidebotham, 15 (9); F. G. Sieber, 85 (15); W. Siehe, 118 (22), 1895 (22); F. J. Silva Pando et al., 1394 (6d); L. Simkovics, 20 Apr. 1873 (22), 9 Aug. 1883 (5); Simonkai, 1816 (5); P. Sintenis, 80 (22), 196 (22), 244 (22), 414 (2), 731 (2), 733 (9), 882 (22), 3844 (22), 3902 (22), 3995 (22), 5529 (22), 7173 (19a); P. Sintenis & J. Bornmüller, 17 May 1891 (22); W. Sladen, 9/4/451 (2), 9/4/452 (9); J. Šmarda, Aug. 1934 (8); P. Smirnov, 10 Aug. 1930 (1); V. I. Smirnow, 314 (1), 2968 (1), 17 June 1910 (1), 4 Aug. 1936 (1); A. M. Smith, 17 July 1872 (9); H. Smith, 3270 (3), 3477 (3), 3587 (26), 3880 (26), 11378 (26), 11473 (3); Soc. Rochelaise, 1881 (24); N. D. Socalsky, 76, (12), 141 (12); Soleirol, 2303 (10); Sommier & Levier, 709 (19a); F. X. Soñora, 19 June 1994 (6d); F. Sorger, 84-41-5 (20), 68-53a-6 (25), May 1960 (22), July 1960 (9); F. Sorger & Buchner, 82-89-3 (19a), 82-94-38 (19a), 82-119-16 (19a), 82-123-9 (21); J. A. Soulié, 335 (26); M. Sovetkina, 187 (12), 319 (12), 428 (12); M. Sovetkina & S. Chausova, 1963 (12); V. Spitzel, 1150 (15), 972 (2), May 1836 (2); Sredinski, 1873 (19a); J. D. A. Stainton, 8113 (22), 7381 (9), 7400 (18), 7894 (18), 7961 (9), 8011 (2); J. D. A. Stainton & Henderson, 6197 (19a); J. D. A. Stainton, Sykes & Williams, 3145 (18), 6051 (18); Steane, 62 (18); H. Steininger, July 1881 (2), July 1883 (2), 5 Aug. 1887 (14), 6 Aug. 1887 (2); W. Steinitz, 24 May 1879 (17), 10 May 1881 (17), 20 Apr. 1882 (17), 10 May 1889 (17); W. Steiniz & J. Briquet, 2 May 1880 (17); H. Sterking et al., 28 Apr. 1885 (9); Sterneck, July 1904 (15), July 1908 (9); C. Steurer, 17 Aug. 1886 (15); H. Stevens, 392 (26); J. L. Stewart, 1733 (18); R. R. Stewart, 350a (18), 5367 (18), 6854 (18), 10370 (18), 12638 (12), 20301 (12), 20755 (12), 21539a (18), 21839 (12), 23132 (18); R. R. & I. D. Stewart, 17786 (18); Stewart, 627/K (18); A. Stork, 7025–6 (22), 17 May 1987 (22); I. F. Stranskij, 25 July 1911 (2); T. Strauss, June 1898 (20); V. Stříbrný, 10 June 1889 (22), 17 Apr. 1893 (9), 13 May 1893 (9), May 1894 (17), 19 May 1895 (22), 9 May 1896 (17), Aug. 1896 (2), 11 May 1898 (22), 14 May 1899 (22), 5 Aug. 1899 (2), 10 Aug. 1899 (2), 12 Aug. 1899 (2), 26 May 1900 (17), May 1901 (17), Aug. 1903 (2), July 1909 (2), May 1910 (17) (22); Strid, Christiansen & Laulund, 26639 (22); Strid, Christiansen, Moller, 26147 (22); Strid & Papanicolau, 16449 (2); Strid et al., 18182 (9), 18205 (9), 18862 (2), 19540 (2); I. Strupinsij, 25 June 1913 (1); Stubbendorf, 1848 (1); E. Stuckenberg, 29 June 1912 (19a); Stud. biol. Rheno-Trai., 327 (15), 68–1979 (2); Sukačev, Rassadina & Brizshev, 1606 (1); V. S. Summerhayes, 2035 (23), 3548 (2); V. S. Summerhayes & P. F. Hunt, 3767 (23); A. Susanna, 776 (24); J. Suza, 14 July 1925 (2); J. T. Syme, 653 (23), 654 (24); Szépligeti, 6 May 1885 (17), 1890 (17); A. Sztehlo, Aug. 1876 (2).

H. Tabata, Rajbhandari & Tsuchiya, 1072 (18), 3309 (18); H. Tabata et al., 12900 (18), 19355 (18); K. Tamanjan, 4 June 1988 (21); J. Tamemshian & W. Maleer, 31 July 1931 (12); Targioni, 12 July 1857 (2); A. Tatli, 5171 (11); Tausch, Apr. 1865 (17); J. A. Tauscher, 27 May 1875 (17); C. F. Tebbutt, 15 May 1957 (23); H. G. Tedd, 1648 (22); N. I. Temnoev, 123 (1); T. A. Tengwall, 278 (22); Termeh, 8 Aug. 1968 (11), 24 June 1970 (20), 20 July 1971 (19a); Termeh, Moussavi & Habibi, 26 June 1978 (11); Terracciano, July 1871 (9); C. G. H. Thedenius, Aug. 1903 (23); W. Thesiger, 1154 (11); Thomas, 1869 (23); H. P. & H. P. Thompson, 199 (9); Rev. & H. P. Thompson, 77 (9), 123 (9), 176 (9), 523 (9); Thompson, July 1922 (23); Thuillier, 1812 (24); M. K. Timins, 174 (18); Timothée, 4264 (15); V. S. Titov, 15 June 1910 (1), 22 June 1910 (1), 1 July 1914 (12); V. I. Tkatchenko, 182 (12); C. Tobey, 1 (22), 570 (22), 570A (22), 1484 (16), 2563–3 (22); Todaro, 537 (22); A. I. Tolmačev, 10 July 1964 (2); M. Toma, 7 June 1967 (17); E. Topa, 3482b (9); S. Topali, 23 Aug. 1937 (9), 8 July 1938 (9); A. Topitz, 8 July 1885 (2), 20 June 1887 (22); A. Topitz & Jahn, 20 June 1887 (22), July 1889 (22); Torges, 21 May 1894 (23); Touton, July 1887 (15), 6 Aug. 1887 (15), 20 Apr. 1902 (23), 1

June 1902 (23), 21 July 1902 (9), 30 July 1902 (15), 22 July 1903 (15), 13 Aug. 1905 (15), 30 July 1907 (15), 15 July 1912 (15); C. C. Townsend, 84/55 (15), 90/247 (2), 93/574 (15), 94/32 (2), 4 June 1952 (23), 25 May 1953 (23), 18 June 1957 (23); W. Tranzschel, 12 July 1900 (12); G. Treffer, June 1878 (14), 13 July 1878 (8), Aug. 1882 (14), 3 July 1888 (14), 24 July 1890 (14), 13 July 1896 (14), 30 June 1900 (14); A. W. Trethewy, May 1932 (23), May 1937 (23); W. C. Trevelyan, 4 May 1846 (24); L. C. Treviranus, 1825 (14); W. P. Troickij, 14 June 1912 (1), 23 June 1912 (1); N. Tsvelev & S. Cherepanov, 1032 (19a); A. I. Tugarinov, 17 June 1912 (1); Tuhrman, 46 (1); Turczaninov, 1828 (1), 1836 (1); G. Turesson, 848U (1); Turland, 314 (22); J. Tuzson, 23 July 1914 (5); Y. Tzinzerling, 2015 (1).

J. Ullepitsch, 88 (8), July 1894 (8); P. M. Uribe-Echebarría, 228 (24), 1 July 1985 (6a), 30 June 1987 (23); P. Urrutia, 14 July 1992 (6a).

Valdés, Demetrio & Pavón, 14 May 1969 (24); E. Valdés Bermejo et al., 4233 (6d); E. Valdés Bermejo et al., 5812 (6c); V. Valdés Bermejo, 24 July 1972 (6d); O. Valentine, 28 July 1920 (8); Vallin, 20 May 1911 (23); E. Valon, 3 (15); K. Vandas, Aug. 1891 (5), Sep. 1891 (15); C. Vanden Berghen, 18 Aug. 1975 (15); P. Vargas, 2151 (24); V. Vašák, 26 May 1973 (22), 8 Oct. 1974 (21), 9 Oct. 1974 (21), 13 July 1975 (21), 27 July 1975 (19a), 4 July 1982 (21); V. Vašák & G. Esvandzhia, 22 July 1979 (11), 24 July 1979 (11); V. Vašák & A. Zlatník, 28 May 1974 (12); G. B., F. G. & J. Vasconcellos, 7877 (24); Y. Y. Vasiliev, 15 May 1930 (22); S. Vautier, 23 May 1954 (23); Veitch, July 1912 (14); A. Velasco, 6 Apr. 1977 (24), May 1980 (24); M. Velayos et al., 7574 (6d); B. Verlot, 27 Aug. 1879 (15); Veselský, 1862 (17); J. Vetter, 30 June 1916 (2), 11 June 1931 (2), 9 June 1932 (2); E. Vetterhall, 18 June 1898 (9); C. Vicioso, 22 Apr. 1908 (24), May 1912 (24), Aug. 1912 (6a), June 1916 (24), 5 May 1918 (24), 18 June 1918 (24), 5 June 1934 (24); C. Vicioso & F. Beltrán, Aug. 1912 (6a); S. N. Vidrina, 3 July 1971 (1); J. Vigo & L. Villar, 5 Aug. 1974 (2); L. Villar, 11 May 1971 (24), 23 July 1975 (15), 6 June 1986 (23); L. Villar & D. Gómez, 17 Aug. 1984 (15); E. Violleau, 23 Apr. 1897 (24); J. Vivant, 14 May 1970 (24); R. Vogt, 3299 (24), 3321 (24), 3502 (6c), 3960 (15); R. Vogt & C. Oberprieler, 13937 (22), 13942 (22), 14039 (9); R. Vogt & C. Prem, 7069 (15), 7315 (15), 7327 (15); Volkov, 185 (1); E. V. Volkova & L. I. Ivanina, 5 July 1964 (2), 10 July 1964 (2); E. V. Volkova, Ivanina, Egorova & Matsenko, 7 July 1964 (5); E. A. Volkova et al., 7279 (12); V. J. Vorobiev & B. N. Klopotov, 1906 (21); Vrabélyi, 11 May 1867 (17), 10 May 1870 (17); Vukotinović, 17 May 1874 (2), 20 May 1880 (2), 29 May 1880 (2), 23 June 1880 (2), June 1897 (2); Vulpius, 26 July 1849 (8).

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T. I. Zaikonnikova, 18 July 1974 (19a), 12 Aug. 1977 (2); M. Zamfir, 17 June 1983 (9); O. Zedelmejer, 10 May 1925 (22); O. Zedelmejer et al., 9 Aug. 1928 (19a); Zehzad, 1305 (11); Zeller, 15 May 1904 (23); H. Zerny, 19 June 1919 (2), 21 July 1930 (2); W. Zovits, 1829 (21), 7 May 1830 (22).

A SYNOPTIC REVIEW OF THE AFRICAN GENUS *HESPERANTHA* (IRIDACEAE: CROCOIDEAE)[1]

Peter Goldblatt[2]

Abstract

Although revised in the past 20 years for the two major centers of its range, the southern African winter-rainfall zone and the eastern southern African Drakensberg, the sub-Saharan African genus *Hesperantha* remains inadequately understood. Continuing botanical exploration in southern Africa has resulted in the discovery of several new species and of populations of species known only from the type or very few collections. Species are listed here in a revised taxonomic order together with keys for the genus in the southern African winter-rainfall zone and in eastern southern Africa and tropical Africa that have a summer-rainfall climate. Included here are 11 new species, a shift in the application of the name *H. candida* to plants called *H. vernalis*, recognition of *H. leucantha* for plants previously called *H. candida*, and a series of novel observations relating to species delimitation, biology, geography, and taxonomy. Important range extensions are also noted for poorly known species, among them *H. ciliolata*, *H. flava*, *H. quadrangula*, and *H. teretifolia*. Including the novelties described in this account, 79 species of *Hesperantha* are now recognized, 4 in tropical Africa, 37 in summer-rainfall southern Africa, mostly of the Drakensberg, and 42 in winter-rainfall southern Africa. *Hesperantha longicollis* and *H. coccinea* are shared between tropical and eastern southern Africa, and *H. radiata* and *H. bachmannii* between the winter- and summer-rainfall zones of southern Africa. The new species from the southern African winter-rainfall zone are: *H. decipiens*, from Namaqualand, allied to *H. radiata*; *H. glabrescens*, from the Roggeveld Escarpment, closely related to *H. pilosa*; *H. malvina*, also related to *H. pilosa*, from cliffs on the Anysberg in the Little Karoo; *H. rupicola*, a lithophyte from western Bushmanland, possibly most closely related to *H. acuta*; and *H. sufflava*, a member of section *Hesperantha* from Malmesbury in Western Cape Province. New species from the southern African summer-rainfall zone are: *H. altimontana*, a spring-blooming, white-flowered species of the high Drakensberg of Lesotho and KwaZulu-Natal; *H. brevistyla*, a dwarf plant from Free State and adjacent KwaZulu-Natal; *H. debilis*, evidently allied to the widespread *H. bachmannii*, from the Albany District of Eastern Cape Province; *H. exiliflora*, from Lesotho, which has small, purple flowers; *H. saxicola*, of rocky outcrops in Mpumalanga, South Africa, which has large white flowers with short anthers; and *H. stenosiphon*, a long-tubed, pink-flowered species with blackish anthers from Eastern Cape, South Africa.

Key words: Africa, biogeography, Crocoideae, *Hesperantha*, Iridaceae, systematics.

Despite the publication in the past 20 years of revisions and floristic accounts of *Hesperantha* Ker Gawl. covering most of its range across southern and tropical Africa (Goldblatt, 1984; Hilliard & Burtt, 1986; Goldblatt, 1986, 1987, 1993; Goldblatt & Manning, 1996) and extensive fieldwork by many botanists, this sub-Saharan African and largely southern African genus of Iridaceae subfamily Crocoideae G. T. Burnett (1835) (syn. Ixioideae Klatt, 1866, as subordo Ixieae) continues to yield novelties, significant range extensions, and new collections that contribute to our understanding of known species. In the southern African winter-rainfall zone, several major range extensions have been recorded in the past 10 years and new collections have been made of plants that are here recognized as the new species *H. decipiens*, *H. glabrescens*, *H. malvina*, *H. rupicola*, and *H. sufflava*. Important range extensions or additional populations in the winter-rainfall zone include those for *H. ciliolata*, *H. flava*, *H. quadrangula*, and *H. teretifolia*, while the rare *H. minima*, a species first collected in 1830, was rediscovered in Namaqualand in 1991.

Collecting in the summer-rainfall region of eastern southern Africa over the past 15 years has yielded three new species, *Hesperantha exiliflora* from subalpine elevations in Lesotho, *H. brevistyla*

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from the northern high Drakensberg of Free State and KwaZulu-Natal in South Africa, and *H. stenosiphon* from Eastern Cape Province, South Africa. Additional records suggest that white-flowered *H. hygrophila,* as defined by Hilliard and Burtt, includes three species. *Hesperantha hygrophila* has distinctive leaves with raised and winged margins and midrib, features that define the species (Hilliard & Burtt, 1986). A second species has nearly plane, somewhat leathery leaves and a robust habit with an erect, many-flowered spike, while the third, confined to cliffs in the Long Tom Pass area of Mpumalanga, has trailing stems and leaves, and a few-flowered spike. The earliest name for the former is *Gladiolus inconspicuus,* here transferred to *Hesperantha,* and the second is a new species, *H. saxicola.* Late winter- and spring-flowering plants included in *H. baurii* (which flowers in mid to late summer) by Hilliard and Burtt and corresponding to *H. modesta* Baker are recognized as a distinct species. In addition, spring-flowering plants with large, white flowers from the northern Drakensberg allied to *H. schelpeana* are recognized as a new species, *H. altimontana.* First discussed by Hilliard and Burtt (1986) as differing from *H. schelpeana* in having a white flower with a longer perianth tube, *H. altimontana* has plane, falcate leaves whereas *H. schelpeana* has slender, terete leaves. The enigmatic high-altitude Drakensberg endemic, *H. pubinervia,* originally known from fragmentary material, has been rediscovered, and the range of *H. grandiflora* extended northward to The Sentinel in Free State, South Africa. Study of living plants in the southern Drakensberg has shown that a second species was included in *H. grandiflora* by Hilliard and Burtt (1986). These plants match the type of *H. galpinii* (Foster, 1948), currently a synonym of *H. grandiflora,* and indicate the need for an expanded definition of *H. woodii,* of which *H. galpinii* must be a synonym. Lastly, reexamination of the type collection of *H. candida* makes this species an earlier name for *H. vernalis* Hilliard & Burtt. The species called *H. candida* by Hilliard and Burt assumes its earlier name, *H. leucantha.*

Additional species described for the southern African winter-rainfall zone (Goldblatt, 1987) and here render my 1984 account of *Hesperantha* out of date and the keys valueless. Likewise, for eastern southern Africa the only post-*Flora Capensis* (Baker, 1896) treatment of the genus by Hilliard and Burtt (1986) dealt only with the species of the KwaZulu-Natal–Lesotho region and now requires expansion even there. Keys for the entire genus are provided here, one for the southern African winter-rainfall zone, and the other for tropical and eastern southern Africa combined. This account includes expanded descriptions and geographic information for *H. pubinervia, H. woodii,* and the incompletely understood species of Limpopo and Mpumalanga Provinces, *H. schlechteri* and *H. brevicaulis.* This last species is the only long-tubed *Hesperantha* with pink flowers from the northern provinces of South Africa.

The difficulty in distinguishing herbarium specimens of several closely allied species, including, for example, *Hesperantha grandiflora* from *H. woodii, H. hygrophila* from *H. inconspicua,* and *H. glareosa* from *H. schlechteri,* emphasizes the importance of fieldwork and knowledge of living plants, particularly for a genus like *Hesperantha* in which the basic floral morphology is highly conserved and useful taxonomic characters include the timing of anthesis, perianth and anther color, and the orientation of floral parts. It is likely, too, that critical characters for some species lie in the capsules and seeds, or in the corms. These are, however, seldom collected: fruiting material because it is absent at flowering time, and corms because they are often difficult to dig up (and because collectors are often reluctant to destroy plants). For *Hesperantha,* collectors should try to record time of opening and closing of the flower, presence or absence of scent (and scent characteristics), flower color, presence of nectar, and any other feature not evident when the plant is pressed.

MORPHOLOGY AND DIAGNOSTIC CHARACTERS OF *HESPERANTHA*

Species of *Hesperantha* are small to medium-sized, deciduous geophytes, and with the exception of the rhizomatous *H. coccinea,* have a cormous rootstock (Fig. 1). Although I formerly subdivided the genus into four sections (Goldlbatt, 1982, 1984), I now recognize only three sections, section *Concentrica* (62 species), section *Hesperantha* (8 species), and section *Radiata* (9 species), based largely on corm characters. The corm body is asymmetric with a lateral ridge produced from the base from which the roots emerge. The woody corm tunics usually reflect the internal asymmetry in section *Concentrica,* but in sections *Hesperantha* and *Radiata* the corms are more or less symmetric and bell-shaped (but the flat base is often oblique) (Fig. 1C–E). Section *Radiata* is additionally distinguished by a bract character, the outer bracts united in the lower half around the spike axis, and flowers with a curved perianth tube. Species of section *Hesperantha* also appear to comprise a close-knit assemblage based on their distinctive corm,

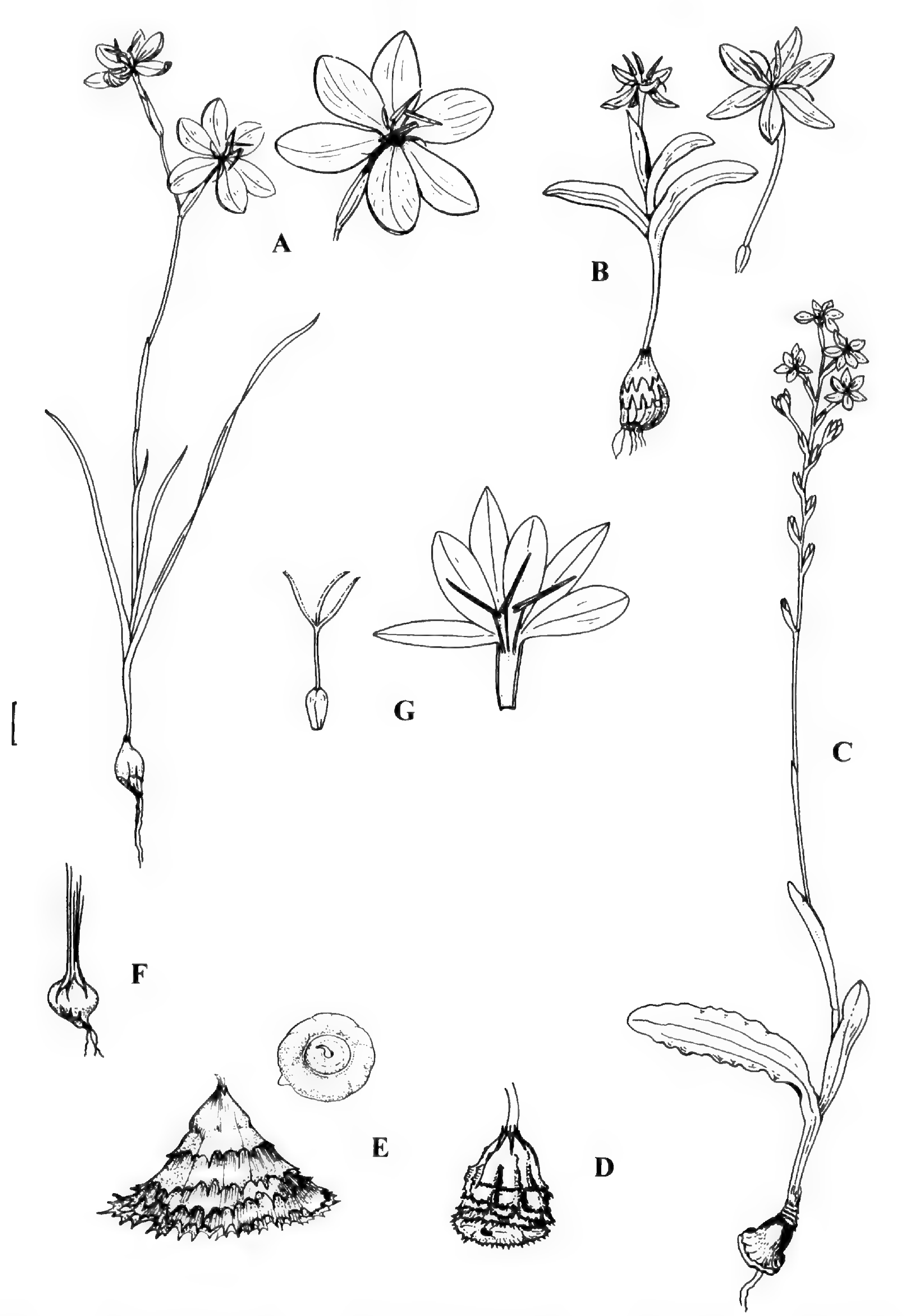

Figure 1. Morphology of *Hesperantha*. —A. *H. acuta* (*Goldblatt 6373,* MO), with small corm with concentric tunics. —B. *H. humilis* (*van Zyl s.n.,* MO), acaulescent habit with imbricate corm tunics. —C. *H. spicata* (*Goldblatt 5774,* MO, NBG), with large, flat-based corm. D–F. Corm detail. —D. *H. radiata* (*Goldblatt 5179A,* MO), corm with tunics. —E. *H. falcata* (*Goldblatt s.n.,* no voucher), intact corm and with the woody tunics removed to show the lateral projection from which roots are produced. —F. *H. fibrosa* (*Goldblatt 6101,* MO), corm with tunics. —G. Flower of *H. pilosa* (*Goldblatt 5810,* MO) with tube opened vertically to show filament insertion and separated gynoecium with inferior ovary, slender style as long as the perianth tube and long style branches. Drawn by Margo Branch from live plants. Scale bar 1 cm; corms D and E much enlarged.

and I continue to recognize this section, restricted to the southern African winter-rainfall zone.

Comparison with the related genera *Romulea* Maratti and *Geissorhiza* Ker Gawl. (which also have asymmetric corms with woody tunics) suggests that the asymmetric corm with concentric tunics (Fig. 1A, F) that fragment into vertical segments, characteristic for *Hesperantha* sect. *Concentrica,* is ancestral. In modification of this type of corm, the tunics split mainly from the base and as a result the older tunics partly overlap the newer ones (Fig. 1B). This corm defined a second section *Imbricata* (Goldblatt, 1982). Sections *Hesperantha* and *Radiata* both have bell-shaped corms with an oblique to horizontal base (Fig. 1C–E). In section *Radiata* the tunics mostly have concave, somewhat scalloped segments. The classification has not proved entirely workable, particularly for the summer-rainfall zone, where corm tunics seldom accumulate over several seasons. Most species there have corm tunics of the concentric type that taper above into prominent, fairly stiff points, but sometimes the accumulated tunics take on the appearance of the imbricate type. Most of the species of the summer-rainfall zone are so morphologically similar to one another in other ways that sectional separation on the basis of minor corm differences does not seem warranted. The distinction between sections *Concentrica* and *Imbricata* thus no longer seems useful, and they have been united under the first name. No infrasectional groups are recognized in this large section of 62 species.

Leaves of *Hesperantha* species are generally plane (Fig. 1A–C) and reflect few taxonomically significant specializations. The leaves of *H. spicata* often have undulate or crisped margins (Fig. 1C). The midribs are usually slightly thickened, and the margins are frequently also slightly raised. *Hesperantha juncifolia* and *H. teretifolia* have centric leaves, round in transverse section, and in the latter the surface is vertically ribbed with the rib edges microscopically ciliate. A few species have pilose (*H. pilosa, H. pseudopilosa, H. pubinervia, H. glabrescens*) or minutely ciliate leaves (*H. ciliolata, H. teretifolia*). Leaf number is often constant in a species and is a useful defining character. Leaf number ranges from several and indeterminate in number in a species to consistently four, or three, often with the lower three or two basal and the remaining one cauline and largely sheathing. A minute scale-like leaf, borne on the stem shortly below the spike, characterizes several species allied to *H. pilosa.*

Flowers are borne on aerial or largely subterranean flowering stems that are usually unbranched, and as in most Crocoideae, are arranged in spikes (Figs. 1A–C, 2, 4, 5). Flowering phenology is constant in a species and, except for minor shifts due to seasonal variation in temperature, timing of critical rainfall, or elevation, flowering occurs at the same time each year. The bracts are green and similar in texture to the leaves, or tend to become dry above. The inner bracts have two main veins, a bifid apex, and often have membranous margins. The perianth always has a well-developed perianth tube, typically ranging in length from about half as long as the tepals to elongate and up to three times as long. In *Hesperantha quadrangula,* however, the perianth tube is ca. 3 mm long, and about one-third to one-quarter as long as the tepals. The perianth tube is straight in most species of sections *Concentrica* and *Hesperantha* except in *H. bachmannii, H. bulbifera,* and *H. grandiflora* where the tube is curved outward near the apex as it is in section *Radiata.*

The tepals typically spread at right angles to the tube, the flower thus being rotate to hypocrateriform (Fig. 1A–C). The tube is narrow with a short, expanded upper portion at the base of which the filaments are inserted (Fig. 1G). The filaments are filiform and erect, and bear linear, longitudinally dehiscent anthers that are twisted at the top of the filaments and face inward. In several species the anthers are articulated on the filaments and lie horizontally. Characteristic of the genus is the style, which divides shortly below the top of the perianth tube into three long, diverging to laxly spreading branches (Fig. 1A, B, G), stigmatic in the upper half or for almost their entire length. Three species of Western Cape Province, South Africa, *Hesperantha cedarmontana, H. elsiae,* and *H. saldanhae,* are unusual in having the style branches and, except in *H. saldanhae,* the stamens included in the perianth tube. The eastern southern African *H. grandiflora* has a zygomorphic flower with the tube curved at the apex, the tepals oriented vertically, and the stamens and style branches unilateral and declinate. In other species with a curved tube, the stamens lie in a drooping, more or less pendent cluster.

Flower color is fairly conservative, and many species of the southern African winter-rainfall zone have white or cream flowers while most eastern southern African species have pink flowers. A few predominantly white-flowered species have populations with a yellow perianth (*Hesperantha acuta, H. falcata*), and some populations of *H. pilosa* have white, blue, or magenta flowers. Flower color is often associated with times of opening and closing of the perianth. In general, colored flowers open during the day (usually only in the morning or afternoon) and white flowers open in the afternoon or evening and close during the night. White perianths that open in the evening appear derived (Reeves et al., 2001a, 2001b). If this is correct, the eastern southern African species, most of which have pink to mauve flowers open during the day, constitute the ancestral type. White, crepuscular to nocturnal flowers would then be derived and the few winter-rainfall zone species with pink or yellow flowers then represent a reversal to an ancestral condition.

Scent is a common feature of white-flowered species of the winter-rainfall zone of southern Africa and is otherwise rare, although some populations of the mauve-flowered *Hesperantha ciliolata* of the winter-rainfall zone have scented flowers, as do the white- or cream-flowered *H. longicollis* and *H. radiata* (and perhaps *H. ballii*) of summer-rainfall southern Africa. Scent is variable and to the human nose either pleasant and sweet to sweet-spicy, or acrid-musty, or bitter. Scent can be inconsistent within species, and may sometimes be absent in some populations of otherwise scented species, while in widespread species like *H. falcata* scent is variable, ranging from narcissus to frangipani, somewhat musty, or evidently absent. Scent is often weakly developed at anthesis and the intensity reaches a peak only an hour after flowers open in some species; it falls in intensity again before the flower begins to close. Scent is an unreliable character because it varies so much among populations, sometimes even changing under different conditions and times of sampling.

Capsules, and in particular seeds, vary across the genus, although they are seldom recorded. Capsules are usually globose to oblong, but may be cylindric in section *Radiata*. Seeds are primitively globose (sometimes weakly faceted by pressure in the capsule) and have a flattened chalazal end (Goldblatt & Wagner, 1984). Notable variants include *Hesperantha spicata*, which has seeds with a loose, white spongy coat, and *H. pseudopilosa*, which is distinguished from *H. pilosa* partly by its large seeds with a spongy coat (Goldblatt, 1987). Seeds of *H. coccinea*, described in more detail under that species in the systematic account, have a loose coat that contains a much smaller globose seed body, and I assume they are both aerodynamic and dispersed by water, as they are unusually buoyant. In eastern southern Africa several long-tubed species, including *H. grandiflora* and *H. huttonii*, have winged seeds (Hilliard & Burtt, 1986), which provides support for the monophyly of the long-tubed species with this character. Seeds of *H. scopulosa*, which also has long-tubed flowers, are narrowly ovoid-oblong, have a very long persistent, twisted funicle, and have no wing at all.

Seeds of *Hesperantha* species, especially of eastern southern Africa, are not well known, and every effort should be made by collectors to obtain ripe seeds as well as flowering material. Because capsules mature several weeks after flowering in most species, seed collection is seldom possible unless a later visit to the site can be made.

Chromosome number is conservative. Nearly all 30 species counted are diploid with an ancestral base number of $x = 13$ (Goldblatt, 1984, 1987; Goldblatt & Takei, 1997). The tropical African *Hesperantha petitiana* is polyploid, with tetraploid or hexaploid populations (Goldblatt, 1986), and it may have a derived base number of $x = 12$. The only count for *H. baurii* (Goldblatt & Takei, 1997) is also $2n = 24$. Examination of vouchers for earlier counts (Goldblatt, 1971) shows that the reports of $2n = 26$ for *H. baurii* and *H. longituba* are both for *H. brevicaulis*. The basic number of $x = 13$ is uncommon in the Iridaceae but is shared with the largely Cape genus *Geissorhiza*. The base of $x = 12$ is probably secondary in the genus, and an example of dysploid reduction.

Both morphology (Goldblatt, 1985, 1990) and molecular data (Reeves et al., 2001a, 2001b) confirm the close relationship of these two genera. Reeves's analysis of generic relationships using sequences from four plastid DNA regions of the chloroplast genome yields a bootstrap value (BS) of 99% for the clade including the one species of *Geissorhiza* and two of *Hesperantha*. One of the two species of *Hesperantha* in that study was *H. coccinea*, only species of the rhizome-bearing *Schizostylis* Back. & Harv., which was reduced to synonymy in *Hesperantha* by Goldblatt and Manning (1996). A second molecular study using the plastid DNA exon *mat*K confirms the close relationship between *Hesperantha* and *Geissorhiza* (BS 100%) (Goldblatt et al., 2003). Neither the *mat*K, nor the Reeves et al. study have provided any well supported indication of the relationship within Crocoideae of the *Hesperantha–Geissorhiza* clade, which is unresolved.

The basic floral morphology is so constant in *Hesperantha* that species identification often rests on vegetative characters, especially the nature of the corm tunics in the southern African winter-rainfall zone, or on leaf number and color and the relative lengths of the floral parts, especially the perianth tube and the stamens. Flowering time is also constant within a species so that this can safely be used as an aid to identification.

THE SHORT-TUBED SPECIES OF EASTERN SOUTHERN AFRICA

The short-tubed species of *Hesperantha* from eastern southern Africa, most of which have pink flowers, are difficult taxonomically and need further study. Hilliard and Burtt's (1986) account of the genus for KwaZulu-Natal and adjacent areas constituted a major advance in the understanding of these species. Using this treatment, I have identified three species that appear to be new and describe them below. Hilliard and Burtt did not deal in detail with all the species that occur north of the KwaZulu-Natal area, that is, in Swaziland and what are now Mpumalanga and Limpopo Provinces of South Africa. This left *H. brevicaulis* (Baker) G. J. Lewis, *H. rupestris* N. E. Br. ex R. C. Foster, *H. schlechteri* (Baker) R. C. Foster, *H. similis* N. E. Br. ex R. C. Foster, and *Gladiolus inconspicuus* Schlechter not, or incompletely, accounted for and evidently endemic there. All except *H. brevicaulis* appear to be closely allied to the widespread and common *H. baurii.* The fairly robust *H. rupestris* is distinguished by its white flowers with red on the reverse of the outer tepals, tall stature, and four leaves (Hilliard & Burtt, 1986). *Hesperantha schlechteri,* based on one ample collection from Limpopo Province, and *H. similis* appear to represent the same species, which often has branched stems and five leaves. The latter, based on *Wilms 1443* from Devil's Knuckles (Long Tom Pass in Mpumalanga), is readily matched by several collections from this area between Sabie and Lydenburg that usually have five leaves, the lower four basal and with firm, narrow blades 1.5–3 mm wide, a flexuose stem usually looped above the sheath of the uppermost leaf, and large pink flowers, the outer tepals coppery on the outside. *Hesperantha baurii* and *H. glareosa* have four (or three) leaves, only two basal. In *H. baurii* they are often longer and wider than the leaves of *H. schlechteri,* while *H. glareosa* has even narrower leaves. Leaf number and potential for branching are remarkably consistent in most species of *Hesperantha* and may be relied upon as useful taxonomic characters, and thus *H. schlechteri* can usually be distinguished by its unusual leaf number and frequent branching.

The only other species of *Hesperantha* from eastern southern Africa with short-tubed, pink flowers that occasionally have five leaves are *H. brevistyla* and *H. leucantha* (*H. candida* sensu Hilliard & Burtt), both somewhat different plants with pale pink flowers (I have seen no white-flowered plants in the field or herbarium, although Hilliard and Burtt described the latter as sometimes having white flowers). *Hesperantha brevistyla* has small flowers, the tepals ca. 7 mm long, and short style branches reaching only to the lower third of the short white anthers, while *H. leucantha* normally has a relatively long perianth tube, mostly 12–15 mm long. Tepals in this species are 10–17 mm long, and living plants that I have examined have whitish anthers and pollen, the anthers are 5–7 mm long, and the style branches appear exceptionally long, sometimes exceeding the anthers by 2–3 mm.

In contrast, the more common *Hesperantha baurii* has bright yellow anthers and pollen, deep pink to almost magenta tepals, and style branches just barely exceeding the anther apices. *Hesperantha leucantha,* as understood by Hilliard and Burtt, seems to me too loosely delimited and I have redefined it, referring plants with particularly small flowers with a tube 3.5–7 mm long and tepals 6–8 mm long from interior Lesotho to the new *H. exiliflora.* Plants with an erect stem and large, white flowers often fading pink, from Mpumalanga and interior lowland and coastal KwaZulu-Natal are referred to *H. inconspicua,* which may distinguished from *H. hygrophila* by their more or less plane leaves. *Hesperantha hygrophila* in contrast has leaves with the midrib and margins raised and the edges winged, thus arching over the laminar surface, and a prominent pair of secondary veins. These features are difficult to see in dry specimens, especially in *H. inconspicua* in which the leathery leaf blade dries to leave the midrib prominent and the non-vascular part of the leaf partly collapsed. Populations of another white-flowered species from the Long Tom Pass area of Mpumalanga that grow on damp cliffs, have trailing leaves and stems, linear leaf blades, and short anthers represent another new species, *H. saxicola,* a collection of which was included in *H. leucantha* by Hilliard and Burtt.

Among the remaining short-tubed specimens I have examined, spring-flowering plants with pink flowers from the sandstone belt of coastal KwaZulu-Natal and adjacent Transkei correspond closely with *Hesperantha modesta,* described by J. G. Baker in 1892, and tentatively included in *H. baurii* by Hilliard and Burtt. Apart from the difference in flowering time, plants can readily be distinguished from summer-flowering *H. baurii* by having spikes of only two or three (rarely more) flowers and usually three or sometimes four leaves, the lower two basal and with long blades and the remaining one or two largely to entirely sheathing.

BIOGEOGRAPHIC NOTE

Including the novelties described in this account, and *Hesperantha coccinea,* which has been transferred to the genus from *Schizostylis* (Goldblatt & Manning, 1996), *Hesperantha* now includes 79 species, 4 in tropical Africa, 37 in summer-rainfall southern Africa, mostly of the Drakensberg, and 42 in winter-rainfall southern Africa. Most species are fairly narrow endemics, but *H. petitiana* extends from eastern Zimbabwe to Ethiopia, *H. longicollis* from the Vaal River, in Gauteng Province, South Africa, to Malawi, and *H. radiata* (including *H. tysonii,* which was recognized as a separate species by Hilliard & Burtt, 1986) from Namaqualand in the west across the Western and Eastern Cape as far east as Swaziland. The southwestern and southern Cape (from the Bokkeveld Mountains to Port Elizabeth) remains the most species-rich area with 30 species, 18 endemic; the Drakensberg of Eastern Cape, KwaZulu-Natal, and Lesotho has 22 species, 15 endemic; the western (winter-rainfall) Karoo has 20 species, 8 endemic; and Namaqualand–Bushmanland has 10 species, 6 endemic. Diversity decreases northward: southern Africa north of the Vaal River axis has 12 species, 5 endemic, while tropical Africa has 4 species, 2 of which, *H. ballii* and *H. petitiana,* are endemic.

FLORAL BIOLOGY

For a genus of only modest floral variation, *Hesperantha* species show considerable diversity in their pollination systems (Manning & Goldblatt, 1996; Goldblatt & Manning, 2000; Goldblatt et al., in press). In general, the short-tubed pink-, lilac-, or blue-flowered species are pollinated by a range of apid bees, mostly *Apis mellifera* and species of *Anthophora* (in the southern African winter-rainfall zone) or *Amegilla* (in the summer-rainfall zone), sometimes in combination with hopliine beetles, e.g., *H. baurii, H. pauciflora.* White-flowered diurnal flowers are pollinated by the same suite of bees as well as Halictidae, but the white flowers that are crepuscular are pollinated by small night-flying moths, mostly species of Noctuidae and Drepanogynidae that settle on open flowers, and if the flowers open before sunset, also by apid bees. Several long-tubed pink- or purple-flowered species are known to be pollinated by long-proboscid flies. These include the nemestrinids *Prosoeca ganglbaueri* (*H. grandiflora, H. scopulosa, H. woodii*) and *Stenobasipteron wiedmannii* (*H. brevicaulis*) in eastern southern Africa, and *P. peringueyi* and *P.* sp. (*H. latifolia, H. oligantha*) in the winter-rainfall zone (Goldblatt & Manning, 2000; Goldblatt et al., in press). Other species with similar flowers must be assumed to have the same reproductive biology. Most likely, some cream- to yellow-flowered, long-tubed species of the winter-rainfall zone (e.g., *H. muirii, H. pallescens*) will prove to be pollinated by horseflies (Tabanidae) of the genus *Philoliche.* The common red-flowered form of the long-tubed *H. coccinea* is pollinated by a guild of large butterflies of the families Papilionidae (*Papilio* spp.) and Satyridae (*Aeropetes tulbaghia*). The less common pink-flowered form is presumably also pollinated by the long-proboscid fly, *Prosoeca ganglbaurii.* Lastly, the yellow-flowered *H. vaginata* is pollinated by hopliine scarab beetles, and yellow-flowered populations of *H. falcata* and *H. pauciflora* are pollinated by these beetles in combination with apid bees.

Hesperantha Ker Gawl., Ann. Bot. (König & Sims) 1: 225. 1804. TYPE: *Hesperantha falcata* (L. f.) Ker Gawl.

Most recent revisionary accounts: Goldblatt, J. S. African Bot. 50: 123. 1984; Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 436. 1986.

Schizostylis Backh. & Harv., Curtis's Bot. Mag. 90: pl. 5422. 1864. TYPE: *Schizostylis coccinea* Backh. & Harv.

In the account of the species that follows the keys, treatment of species is deliberately inconsistent. As this is a synoptic review, when no new information about species has come to hand I have provided only its name, primary nomenclature, and a reference to the most recent revisionary account, Goldblatt (1984, 1987) for species of the southern African winter rainfall zone, Hilliard and Burtt (1986) for species of KwaZulu-Natal and adjacent areas. When new biological, geographic, or taxonomic information is available, this is presented in narrative form. Only significant range extensions are listed in full at the end of the species entry; new collections made since the appropriate revision was published are only listed if they expand the range of the species. Full descriptions are provided for new species and for those that were incompletely known in the past or are resurrected from synonymy.

Exsiccatae are cited below following the quarter-degree square system in use in southern Africa as outlined by Edwards and Leistner (1971). All of these specimens have been examined unless stated to the contrary.

It serves no useful purpose to provide a single key to the entire genus; thus two keys are provided, one for the winter-rainfall zone and one for tropical and eastern southern Africa. The species are listed in the account that follows in taxonomic order within sections in a sequence that reflects as far as possible my current understanding of their relationships. Appendix 1 provides a list of the species in alphabetical order, together with their corresponding number in this article.

KEYS TO THE SPECIES OF *HESPERANTHA*

Note: For leaf number include the entirely sheathing leaves on the upper part of the stem and examine more than one plant since the character is, to a limited extent, variable. Measure leaf width near the middle of one of the lower leaves.

KEY 1. SPECIES OF THE SOUTHERN AFRICAN WINTER-RAINFALL ZONE (NAMAQUALAND, THE WESTERN KAROO, AND THE SOUTHWESTERN AND SOUTHERN CAPE AS FAR EAST AS PORT ELIZABETH)

1a. Flowers with the perianth tube curved at the apex and thus facing to the side or nodding; outer floral bracts with the margins united around the axis in the lower part (sometimes only near the base); corm bell-shaped with a flat or oblique base, the tunics often forming scalloped, concave segments (sect. *Radiata*).

  2a. Flowers deep pink; stamens and style branches included in the perianth tube .... 78. *H. elsiae*

  2b. Flowers white to cream or pale pink; stamens and style branches exserted.

    3a. Bract margins united only basally; perianth tube 6–8 mm long .... 71. *H. brevifolia*

    3b. Bract margins united for at least 2 mm.

      4a. Flowers large with tepals 16–25 mm long and tube 15–25 mm long; perianth pale pink with darker veins .... 79. *H. muirii*

      4b. Flowers smaller with tepals 10–17 mm long and tube 5–12 mm long; perianth white or cream.

        5a. Leaves terete .... 72. *H. juncifolia*

        5b. Leaves ± plane, often somewhat thicker in the middle and occasionally weakly cross-shaped.

          7a. Bracts usually united around stem for 6–10 mm, i.e., about half their length; spike straight with the bracts parallel to the axis; plants mostly 20–60 cm high with (1–)5 to 15 flowers per spike .... 75. *H. radiata*

          7b. Bracts usually united around stem for about one third their length; spike flexuose with the bracts diverging from the axis; plants short, mostly 5–10 cm high, with 1 to 5 flowers per spike.

            8a. Corm base with prominent horizontal spines; bracts united around the axis for up to 3 mm .... 73. *H. marlothii*

            8b. Corm base without spines; bracts united around the axis for 3–5 mm .... 74. *H. decipiens*

1b. Flowers with the perianth tube straight, rarely curved at the apex and secund or half nodding; outer floral bracts with the margins free to the base, corm tunics asymmetric or symmetric and with a round or flat base, but never with the tunic layers forming scalloped sections (sects. *Concentrica* and *Hesperantha*).

  9a. Plants acaulescent or stem extending barely above the ground but sheathed by the leaf bases.

    10a. Flowers small, tepals 8–10(–12) mm long .... 23. *H. hantamensis*

    10b. Flowers larger, tepals 13–25 mm long.

      11a. Perianth tube elongate, 30–45 mm long; tepals with dark blotches toward the base .... 68. *H. luticola*

      11b. Perianth tube less than 30 mm long (mostly 18–28 mm); tepals uniformly colored within.

        12a. Flowers yellow, closed during the day and opening at sunset .... 25. *H. flava*

        12b. Flowers pink to red-purple, open during the day, closing at night.

          13a. Corm with a rounded base; leaves falcate, obtuse or subobtuse, leathery and with slightly thickened margins .... 24. *H. humilis*

          13b. Corm with a flat base; leaves sword-shaped, acute, fairly soft-textured with the margins not or barely thickened .... 67. *H. latifolia*

  9b. Plants with an aerial stem.

    14a. Leaves pilose to scabrid ciliate, sometimes visible only microscopically.

      15a. Leaves hollow or ± solid and with narrow longitudinal grooves; finely scabrid ciliate along the groove edges.

        16a. Leaves ± round in cross section; flowers white to cream, nocturnal, opening in the late afternoon and closing during the night .... 13. *H. teretifolia*

        16b. Leaves oval in cross section; flowers pink, mauve, or purple, open in the day and closing in the early afternoon .... 12. *H. ciliolata*

      15b. Leaf blade flat or the margins and midrib somewhat raised; pilose along the sheath and blade margins and veins.

        17a. Leaves sword-shaped to oblong; scale-like leaf below the spike mostly 12–20 mm long, often pilose .... 10. *H. pseudopilosa*

        17b. Leaves linear to narrowly sword-shaped; scale-like leaf below the spike 3–5(–10) mm long, usually glabrous.

18a. Plants dwarf, to 5 cm high with spikes 1-flowered; flowers magenta; leaves sparsely hairy (rarely evidently glabrous) .... 11. *H. glabrescens*

18b. Plants mostly at least 10 cm high, with spikes rarely with less than 2 flowers; flowers white, blue, magenta, or mauve; leaf blades and sheath of the third leaf sparsely to densely hairy.

19a. Leaf blades usually conspicuously hairy; leaf tips usually acute (plants of open sandy slopes and flats) .... 9. *H. pilosa*

19b. Leaf blades sparsely hairy (often visible only under the microscope); leaf tips obtuse (plants of rocky cliffs) .... 8. *H. malvina*

14b. Leaves and stems smooth.

20a. Perianth tube curved outward near the top, flowers half nodding .... 32. *H. bachmannii*

20b. Perianth tube straight throughout, flowers facing upward.

21a. Corms triangular to bell-shaped in outline, with a horizontal or oblique flat base.

22a. Corm base usually with prominent radiating spines or the margins toothed; flowers mostly pink to reddish purple, rarely yellow.

23a. Perianth tube 6–11 mm long .... 66. *H. pauciflora*

23b. Perianth tube 15–25 mm long .... 67. *H. latifolia*

22b. Corm base with small teeth or scarcely serrated, but without prominent spines; flowers white, cream, or yellow.

24a. Style dividing at or below the middle of the perianth tube; style branches and sometimes the anthers partly or completely included in the perianth tube.

25a. Flowers 20–25 mm diam. with tepals 10–12 mm long; stamens and style branches fully included in the perianth tube .... 65. *H. cedarmontana*

25b. Flowers ca. 18 mm diam. with tepals 9–10 mm long; anthers exserted but style branches reaching only to the mouth of the tube .... 70. *H. saldanhae*

24b. Style dividing just below the mouth of the perianth tube; anthers and style branches fully exserted and filaments usually at least partly exserted from the perianth tube.

26a. Flowers small, and secund on a straight spike; perianth tube slightly curved, 4–6 mm long; tepals 4–7 mm long; leaves either plane and sometimes with crisped margins, or terete to ovoid in cross section and hollow; seeds with sharp angles (minute wings) and seed coat with whitish spongy cells .... 69. *H. spicata*

26b. Flowers medium to large, not obviously secund, on a straight or flexuose spike; perianth tube straight, (5–)7–14 mm long; tepals 6–18 mm long; leaves plane with straight margins; seeds globose or the sides slightly flattened by pressure, seed coat dark brown.

27a. Plants with 3 basal leaves only; perianth tube 12–16 mm long; tepals 7–9(–10) mm long, always shorter than the tube; flowers pale yellow .... 64. *H. sufflava*

27b. Plants with 2 or more basal leaves and usually 1 subbasal or cauline and largely sheathing; perianth tube 5–9 mm long; tepals (9–)12–18 mm long, usually longer than the tube; flowers white, cream, or yellow.

28a. Bracts green, rounded to truncate and often with a reddish margin; leaves usually at least four; flowers usually remote from the leaves, borne on the upper third of the stem .... 63. *H. falcata*: typical form

28b. Bracts green or becoming membranous and dry above, and then ± acute; leaves often only 3; flowers usually borne close to the leaves and from about the middle of the stem .... 63. *H. falcata*: *pentheri* and *trifolia* forms

21b. Corms rounded, often ± asymmetric, often with one side somewhat flattened.

29a. Flowers shades of pink, mauve, or purple.

30a. Perianth tube elongate, 20–35 mm long, exceeding the tepals.

31a. Leaves linear, 2–3 mm wide; tube 25–30 mm long and filaments ca. 8–10 mm long .... 5. *H. oligantha*

31b. Leaves sword-shaped, 7–10 mm wide; tube ca. 20 mm long and filaments ca. 2 mm long .... 20. *H. purpurea*

30b. Perianth tube 7–12 mm long, usually shorter than to about as long as the tepals.

32a. Basal leaves sword-shaped to linear, 40–100 × 2–4 mm; leaf margins and often the midrib much thickened; stem lacking a scale-like leaf in the upper part of the stem .... 17. *H. fibrosa*

32b. Basal leaves ovate, 12–20 × 4–8 mm, margins and midrib hardly thickened; stem with a short, scale-like leaf in the upper part of the stem .... 19. *H. truncatula*

29b. Flowers white, cream, or yellow.

33a. Perianth tube mostly 16–20 mm long, as long as to slightly longer than the tepals .... 34. *H. pallescens*

33b. Perianth tube 3–12(–17) mm long, shorter than to rarely about as long as the tepals.

34a. Plants consistently with two basal leaves and a third entirely sheathing leaf enclosing the lower half of the stem.

35a. Plants tiny, mostly 4–5 cm high; tepals 5–10 mm long; leaves linear, 1–2 mm wide.

36a. Tepals 5–6 mm long; leaves linear-filiform, less than 1 mm wide .... 16. *H. minima*

36b. Tepals ca. 10 mm long; leaves linear, 1.4–3.5 mm wide .... 4. *H. rupicola*

35b. Plants moderate in size, usually at least 10–20 cm high; tepals 8–13 mm long; leaves linear to lanceolate and 1–7 mm wide.

37a. Sheathing leaf inflated and quadrangular in cross section; perianth tube 2–3 mm long; anthers 3–4 mm long .... 14. *H. quadrangula*

37b. Sheathing leaf not inflated or noticeably quadrangular in cross section; perianth tube 5–10 mm long; anthers 4.5–6 mm long .... 15. *H. flexuosa*

34b. Plants mostly with four leaves, sometimes the uppermost ± scale-like.

38a. Flowers bright yellow.

39a. Tepals 10–17 mm long; anthers ca. 7 mm long 3. *H. acuta*

39b. Tepals 20–35 mm long; anthers 9–15 mm long.

40a. Plants up to 6 cm tall, almost acaulescent; flowers moderate in size, the tepals ca. 20 mm long, uniformly yellow .... 22. *H. karooica*

40b. Plants 12–18 cm tall, with a well developed aerial stem; flowers large with tepals 25–35 cm long, usually but not invariably marked with dark chocolate brown .... 21. *H. vaginata*

38b. Flowers white, rarely cream.

41a. Leaves elliptic in cross section and hollow, without a thickened midrib .... 7. *H. rivulicola*

41b. Leaves ± parallel-sided in cross section, not hollow, and with midrib slightly thickened.

42a. Corm tunics ± imbricate or concentric but corms relatively large, mostly 10–14 mm diam.

43a. Perianth tube 6–9 mm long .... 18. *H. cucullata*

43b. Perianth tube 13–17 mm long .... 2. *H. namaquana*

42b. Corm tunics concentric and corms fairly small, mostly 3–8 mm diam.

44a. Stem with a short, sheathing leaf in the upper half .... 3. *H. acuta*

44b. Stem without a short, sheathing leaf in the upper half.

45a. Leaves (3–)4 to 5, the lower 3 basal, linear to sword-shaped and acute, always erect; perianth tube 8–10 mm long; flowers cream, occasionally white (plants of the Cape West Coast, mostly on granite rocks) .... 1. *H. erecta*

45b. Leaves (3–)4, the lower 2 basal, oblong and obtuse, normally prostrate; perianth tube ca. 12 mm long; flowers white (plants of mountain habitats growing in rocky sandstone soil) .... 6. *H. montigena*

KEY 2. SPECIES OF TROPICAL AND EASTERN SOUTHERN AFRICA (THE SUMMER-RAINFALL PART OF THE SUBCONTINENT WITH A PROLONGED DRY SEASON IN THE WINTER AND SPRING MONTHS—EXTENDING FROM THE EASTERN CAPE PROVINCE, SOUTH AFRICA, EAST OF PORT ELIZABETH TO ETHIOPIA AND CAMEROON)

1a. Flowers white to cream, the outer tepals usually brown on the outside; perianth tube curved just below the apex and flowers nodding.
  2a. Bract margins free to the base .... 33. *H. bulbifera*
  2b. Bract margins united around the spike axis for up to half their length.
    3a. Perianth tube 18–30 mm long; plants flowering in spring (plants of Free State, northern provinces of South Africa, Zimbabwe, Zambia, and Malawi) .... 77. *H. longicollis*
    3b. Perianth tube 8–15 mm long; plants flowering in the early to mid summer, November to January.
      4a. Spike with 1 or 2 flowers; bract margins united for ca. 3 mm (plants of eastern Zimbabwe) .... 76. *H. ballii*
      4b. Spike mostly with 5 to 10 flowers; bract margins united around the axis in the lower half (plants of South Africa, Lesotho, and Swaziland) .... 75. *H. radiata*

1b. Flowers variously pink to mauve, red, or white to creamy yellow, sometimes the outer tepals darker on the outside; perianth tube mostly straight, weakly curved in two species but flowers not nodding.
  5a. Flowers produced in the spring (dry season) when foliage leaves are absent or partly emergent; leaves one or two, fully developed after flowering and produced on separate shoots (occasionally old, partly to completely dry foliage leaves still attached to the flowering stem at flowering time).
    6a. Flowers borne close to ground level, raised above ground by the perianth tube 9–14 mm long; tepals short, 6–7 mm long .... 31. *H. crocopsis*
    6b. Flowers borne above ground on a short flowering stem, the perianth tube short or long; tepals fairly long, 14–22 mm long.
      7a. Perianth tube 6–10 mm long; tepals white or pale pink inside, the outer tepals slightly to strongly marked purple to brownish on the outside; leaves two or more, ± terete .... 29. *H. schelpeana*
      7b. Perianth tube 20–27 mm long; tepals uniformly whitish cream; leaf solitary, falcate, plane .... 30. *H. altimontana*
  5b. Flowers produced in the spring, summer, or autumn (dry or rainy season) but always bearing fully developed foliage leaves on the flowering stem.
    8a. Perianth tube (14–)18–60 mm long, perianth tube sometimes curved near the apex; seeds (where known) often with a prominent wing or threadlike appendage at one or both ends.
      9a. Perianth tube strongly curved near the apex and tepals vertically oriented; stamens and style branches unilateral and declinate; anthers 8–13 mm long, dark brown .... 57. *H. grandiflora*
      9b. Perianth tube straight or weakly curved above, the tepals spreading horizontally or weakly ascending; stamens ascending to erect, and style branches spreading but not unilateral; anthers 3–9 mm long, yellow to whitish, or dark brown to black in two species.
        10a. Leaves and often the stem weak and trailing; plants of cliffs and rock outcrops.
          11a. Plants with cormlets in the lower leaf axils (sometimes lost when handled); leaves 4 to 6 (plants of the Eastern Cape) .... 58. *H. huttonii*
          11b. Plants not bearing cormlets in the lower leaf axils; leaves 4 or sometimes 3.
            12a. Flowers mauve pink; perianth tube mostly 18–30 mm long; anthers 6–10 mm long (plants of Mpumalanga and Limpopo Province) .... 60. *H. brevicaulis*
            12b. Flowers deep pinkish purple; perianth tube 18–42 mm long; anthers 3–6 mm long (plants of KwaZulu-Natal and nearby).
              13a. Perianth tube 18–25 mm long; anthers 3–4 mm long .... 61. *H. curvula*
              13b. Perianth tube mostly 30–42 mm long; anthers mostly 5–6 mm long .... 62. *H. scopulosa*
        10b. Stem erect and leaves usually firm and upright; plants of grassland, open slopes, or streams and marshes.
          14a. Filaments 6–12 mm long.
            15a. Plants of streams, growing in water; rootstock a rhizome or vestigial, but reproducing from slender underground rhizomes and sometimes from axillary cormlets produced in the aerial nodes; flowers pink or red, tepals spreading horizontally .... 56. *H. coccinea*
            15b. Plants of grassland, rocky slopes, or grassy marshes; rootstock a corm with woody tunics and stems lacking axillary cormlets; flowers shades of pink to mauve-pink .... 54. *H. woodii*
          14b. Filaments 3–6 mm long.
            16a. Leaves scabrid-pubescent; stamens erect and style branches evidently remaining suberect and noticeably shorter than the anthers .... 52. *H. pubinervia*
            16b. Leaves glabrous; stamens and style branches ascending to spreading, the style branches as long as or longer than the stamens.
              17a. Plants flowering in the spring, August to October; flowers white .... 28. *H. longituba*

17b. Plants flowering in the summer and autumn, December to April; flowers pink.

18a. Perianth tube mostly 45–60 mm long; anthers blackish .... 55. *H. stenosiphon*

18b. Perianth tube mostly 14–21 mm long; anthers yellow.

19a. Spike with 5 to 11 flowers; leaves 3–5.5 mm wide; perianth tube 14–20 mm long .... 53. *H. pulchra*

19b. Spike with 1 to 3 flowers; leaves 1.5–2 mm wide; perianth tube 16–23 mm long .... 59. *H. hutchingsiae*

8b. Perianth tube 3–15(–22) mm long, always straight; seeds (where known) globose or slightly angled, sometimes ridged on the angles but never winged.

20a. Plants of southern Africa, flowering in the spring, August–October, before the main rainy season; flowers pale pink or white.

21a. Perianth tube mostly 14–22 mm long; flowers white, opening in the later afternoon and closing after dark .... 28. *H. longituba*

21b. Perianth tube mostly 4–12 mm long; flowers white or pink to mauve-pink, the outer tepals often flushed or feathered pink to mauve outside, open during the day, closing in the later afternoon.

22a. Leaves usually 3 (rarely 4), the lower 2 basal and with long, linear blades 2–3 mm wide, the upper 1(or 2) largely or entirely sheathing; spike usually 2–3-flowered (plants of coastal KwaZulu-Natal and Transkei) .... 49. *H. modesta*

22b. Leaves usually 4, 2 basal, 1 subbasal and partly sheathing and a short, sheathing leaf in the upper part of the stem, the basal leaves linear to oblong-lanceolate, 1–6 mm wide; spike mostly 1–6-flowered; perianth tube (7–)9–12 mm long (plants of interior southern Africa, from southern Mpumalanga to Grahamstown in the south).

23a. Leaves oblong-lanceolate, 2–6 mm wide; spike mostly 2–6-flowered; perianth tube (7–)9–12 mm long .... 26. *H. candida*

23b. Leaves linear, 1–2 mm wide; spike 1–2-flowered; perianth tube 4–6 mm long .... 27. *H. debilis*

20b. Plants of southern or tropical Africa, flowering in the wet season, summer and autumn (in southern Africa mainly December to April, rarely in November); flowers mostly pink to mauve or white to cream.

24a. Plants growing in rock outcrops, often on cliffs, stem weak and drooping; leaves ± linear.

25a. Flowers pink, mauve, or white; perianth tube 6–8 mm long; anthers 6–7.5 mm long (plants of KwaZulu-Natal) .... 51. *H. gracilis*

25b. Flowers white, sometimes flushed pale pink on fading; perianth tube 7–11 mm long; anthers ca. 4 mm long (plants of Mpumalanga) .... 46. *H. saxicola*

24b. Plants not hanging from cliffs, stem erect.

26a. Leaf blades with thickened margins, secondary veins, and midrib, the marginal and midrib thickenings flattened rather than rounded and arching over the blade surface .... 47. *H. hygrophila*

26b. Leaf blades with or without thickened margins and midrib, but secondary veins not or hardly thickened and midrib and marginal thickenings rounded, not obviously flattened in outline nor arching over the blade surface.

27a. Flowers white to cream or palest yellow entirely or pink or red only on the reverse of the outer tepals.

28a. Outer tepals speckled or uniformly bright red on the reverse.

29a. Stem usually 7–12 cm high (taller in cultivated plants); tepals 9.5–15 mm long; anthers 3–4 mm long (plants of KwaZulu-Natal) .... 41. *H. alborosea*

29b. Stem usually 30–45 cm high; tepals 12–15 mm long; anthers 6–7 mm long (plants of Mpumalanga) .... 48. *H. rupestris*

28b. Tepals uniformly white to cream, or sometimes faintly pink on the reverse of the outer tepals, especially on fading.

30a. Flowers tiny, the tepals ca. 5–6 mm long, perianth tube ca. 4–5 mm long, and anthers ca. 2–3 mm long; leaves soft-textured .... 50. *H. umbricola*

30b. Flowers medium to large, the tepals 12–20(–23) mm long, perianth tube (5–)6–8.5 mm long, and anthers 5–8 mm long, leaves firm, with thickened margins and midrib.

31b. Tepals uniformly cream to pale yellow, remaining cream on fading, 14–20(–23) mm long; filaments 3–4 mm long;

anthers mostly golden-brown, dark when dry, 5–7(–8) mm long .... 44. *H. lactea*

31b. Tepals uniformly white to cream or faintly flushed pink on the reverse of the outer tepals especially on fading, 12–16 mm long; filaments 2.5–3 mm long; anthers cream, not darker on fading, mostly 6.5–8 mm long .... 45. *H. inconspicua*

27b. Flowers pink to mauve entirely.

32a. Perianth tube 3–6 mm long.

33a. Leaves 5.5–7 mm wide, falcate; spike with 1 or 2 flowers; tepals 10–12 mm long .... 43. *H. ingeliensis*

33b. Leaves mostly 0.7–2 mm wide, linear.

34a. Stem slender and evidently soft, with 1 to 3 flowers widely spaced; tepals 6–8 mm long .... 40. *H. exiliflora*

34b. Stem slender but firm and wiry, mostly with 3 to 8 flowers; tepals 10–14 mm long.

35a. Leaves usually 5 (unless plants depauperate), mostly 2–4 mm wide; tepals 13–16 mm long; anthers 4–4.5 mm long .... 38. *H. schlechteri*

35b. Leaves usually 4, mostly 1–2 mm wide; tepals 10–12 mm long; anthers 4.5–5 mm long .... 37. *H. glareosa*

32b. Perianth tube mostly 6–13(–15) mm long.

36a. Leaves 4 or 5, the lower 3 basal, often about as long as the stem or slightly longer; anthers 2.3–5.5 mm long, pollen white; perianth tube 7–12(–15) mm long.

37a. Tepals 7–8 mm long; perianth tube 7–9 mm long; anthers 2.5–4 mm long; style branches unusually short, suberect, reaching to between the base and the middle of the anthers; reverse of the outer tepals pale greenish toward the base and with darker green longitudinal veins .... 42. *H. brevistyla*

37b. Tepals 12–16 mm long; perianth tube 5–14 mm long; anthers 4–6 mm long; style branches 10–12 mm long, exceeding the anthers in the closed flower; reverse of the outer tepals not pale green with dark veins, ± uniformly colored outside.

38a. Perianth tube 12–14(–15) mm long; anthers 4.5–5.5 mm long; perianth pale pink; stem and leaves weak and trailing .... 39. *H. leucantha*

38b. Perianth tube to 10 mm long; anthers 4–6 mm long; perianth middle to deep pink; stem and leaves ± erect .... 38. *H. schlechteri*

36b. Leaves normally 4, sometimes 3, with the lower 2 basal, usually about half to two-thirds as long as the stem; anthers mostly 3–7 mm long, pollen yellow or white; perianth tube (4.5–)6–12 mm long.

39a. Flowers mauve-pink or almost white; anthers 3–4.8 mm long; capsules usually 8–14 mm long, often exceeding the bracts; seeds usually angular, 1.0–1.2 mm diam. (plants of tropical Africa: Zimbabwe to Ethiopia and Cameroon) .... 36. *H. petitiana*

39b. Flowers mostly bright pink; anthers 5–9 mm long, pollen yellow; capsules usually 6–9 mm long and enclosed by the bracts; seeds usually uniformly globose, 0.9–1.0 mm diam. (plants of eastern southern Africa).

40a. Outer tepals darker pink to reddish on the outside, ca. 16 × 9 mm; leaves often 3, the lower 2 basal, leathery, the midrib and margins not raised above the fleshy surface (when alive); spike mostly with 2 to 4 flowers .... 35. *H. baurii* subsp. *formosa*

40b. Outer tepals not or barely darker than the outside, ca. 12–15 × 5–6.5 mm; leaves 4, the lower 3 basal or subbasal; firm to leathery, the midrib and margins often slightly thickened and raised above the surface; spike mostly with 5 to 12 flowers .... 35. *H. baurii* subsp. *baurii*

I. Hesperantha sect. **Concentrica** Goldblatt, Ann. Missouri Bot. Gard. 69: 375. 1982. TYPE: *Hesperantha pilosa* (L. f.) Ker Gawl.

Hesperantha sect. *Imbricata* Goldblatt, Ann. Missouri Bot. Gard. 69: 376. 1982. Syn. nov. TYPE: *Hesperantha humilis* Baker.

Plants with small to large asymmetrical corms, ± rounded at the base, usually with a flattened lateral ridge; older corm tunics splitting from the base into vertical segments. Spike with floral outer bract margins free to the base. Flowers variously colored, usually with a straight perianth tube (curved near the apex in *H. bachmannii*, *H. bulbifera*, and *H. grandiflora*).

Species 1–62. Occurring across the entire range of the species from Western Cape Province, South Africa, to Ethiopia.

1. Hesperantha erecta (Baker) Benth. ex Baker, Handbk. Irideae 150. 1892. *Geissorhiza erecta* Baker, J. Bot. 14: 238. 1876. TYPE: South Africa. Western Cape: Olifants River, July–Aug. 1830, *J. F. Drège 8468* (lectotype, designated by Foster (1948: 11), K!; isotypes, K!, L!, P!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 45. 1984.

2. Hesperantha namaquana Goldblatt, J. S. African Bot. 50: 47. 1984. TYPE: South Africa. Northern Cape: Bitterfontein, Kareebergen, 24 July 1896, *R. Schlechter 8304/5* (holotype, K!; isotypes, B!, BOL!, PRE!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 47. 1984.

Restricted to southern Namaqualand in Western Cape Province, South Africa, *Hesperantha namaquana* was re-collected in 1999, along the banks of a seasonal stream northeast of Bitterfontein. This seems to be the habitat for the species, and until now has not been reported. This specialized habitat, in a largely arid landscape, may explain why it is so seldom seen.

Additional specimens. SOUTH AFRICA. **Western Cape:** 30.18 (Kamiesberg) NE of Bitterfontein on road to Kliprand, along seasonal stream (CD), 7 Aug. 1999, *Goldblatt & Manning 11681* (MO, NBG).

3. Hesperantha acuta (Licht. ex Roem. & Schult.) Ker Gawl., Gen. Irid. 91. 1827. *Ixia acuta* Licht. ex Roem. & Schult., Syst. Veg. 1: 383. 1817. TYPE: South Africa. Northern Cape: foot of the Roggeveld Mts., Aug. 1805, *M. H. C. Lichtenstein s.n.* (holotype, B!). Figure 1A.

Last revisionary account: Goldblatt, J. S. African Bot. 50: 48. 1984.

As circumscribed by Goldblatt (1984), *Hesperantha acuta* included both white- and yellow-flowered populations, the latter referred to *H. tugwelliae* by R. C. Foster. No information has become available to suggest this treatment was incorrect. Both *H. acuta* and *H. falcata* have populations of plants with either white or yellow flowers. In *H. falcata* the unscented yellow-flowered plants open during the day and close at night, the opposite phenology to the sweetly fragrant white-flowered plants. This is not the case in yellow-flowered populations of *H. acuta* from the Swartberg Mountains and Prince Albert (*Goldblatt & Porter 11859*, 9 Sep. 2001, MO, NBG; *Goldblatt & Porter 12191*, 10 Sep. 2002, MO, NBG). Flowers of these plants opened at sunset when they produced a sweet scent, and closed again at sunrise, the same pattern as in white-flowered plants. Corms of *H. acuta* seem unusually varied and in some populations conform closely to the section *Concentrica* type with a rounded base and oblique lateral ridge, while others have an oblique but flat base, approaching the corms of section *Hesperantha*, which are bell-shaped with a broad flat base. Too few collections of the species have corms for me to detect a pattern associated with either geography or some other factor. This calls for future investigation.

4. Hesperantha rupicola Goldblatt, sp. nov. TYPE: South Africa. Northern Cape: Bushmanland, Farm Naab, E of Springbok, S-facing quartzite rocks, 14 Aug. 2000, *P. Desmet 3009* (holotype, NBG!).

Plantae 3–5 cm altae eramosae, cormo globoso, foliis 3 omnibus basalibus, laminis plus minusve linearibus 1.4–3.5 mm latis marginibus costaque vix incrassatis, spica 1-(vel 2–3-)flora, floribus albis tepalis exterioribus extus leviter malvinotinctis, tubo perianthii ca. 10 mm longo, tepalis ca. 10 × 3–4 mm, filamentis ca. 4 mm longis, antheris ca. 5 mm longis, styli ramis ca. 3.5 mm longis.

Plants 3–5 cm high, unbranched. *Corm* globose with an obliquely flattened side, 9–11 mm diam., tunics dark brown, the layers ± imbricate. *Leaves* 3, all basal, spreading or drooping, as long to twice as long as the stem and up to 9 cm long, the blades ± linear to falcate, 1.4–3.5 mm wide, soft-textured, the midrib and margins barely thickened. *Stem* erect, unbranched. *Spike* 1-, occasionally 2- or 3-flowered; bracts 9–10 mm long, soft-textured, pale green or becoming membranous above, the inner slightly shorter than the outer, membranous with 2 green keels. *Flowers* white, the outer tepals slightly flushed mauve on the outside; *perianth tube* funnel-shaped, ca. 10 mm long; *tepals* spreading, ovate, ca. 10 × 3–4 mm, obtuse. *Filaments* ascending, ca. 4 mm long, inserted at the mouth of the tube; *anthers* ca. 5 mm long, shortly tailed, pale yellow, pollen whitish. *Ovary* ovoid, ca. 3 mm long; *style* dividing near the mouth of the tube, the branches spreading over the tepals, reaching nearly to the anther tips in the closed flower. *Capsules* and *seeds* unknown.

Flowering. August.

Distribution. South Africa, Northern Cape, in shade on south-facing slopes on cliffs and among boulders, in quartzite or granite rocks, interior Namaqualand and western Bushmanland.

Hesperantha rupicola was evidently first collected in 1977, by E. G. H. Oliver, H. Tölken, and F. Venter, on Aggenys Mountain near Soutkloof, in Bushmanland in central Northern Cape Province. It was subsequently brought to my attention in 1999 by Philip Desmet and members of the University of Cape Town's Institute for Plant Conservation Expedition to Namaqualand. Only a few plants have ever been found in flower, and corms can only be extracted with difficulty from the rock crevices in which they usually grow. Philip Desmet reports that the species occurs on several more hills in Bushmanland. In 2001 a small population was discovered southeast of Kliprand, extending the range of the species some 150 km to the south. Rather than wait until more adequate material can be obtained, I have decided to describe the species here, hoping that by publishing the incomplete description others may be encouraged to seek additional plants, including capsules and seeds.

The material available suggests that *Hesperantha rupicola* may be distinguished by the short stature, 1- to 3-flowered spike, moderate-sized white flowers, and soft-textured, spreading to drooping leaves. The corms are relatively large, have an oblique flat side, and more or less concentric tunics. Similar corms are found in *H. acuta*, and this suggests a relationship with this interior southern Cape and Karoo species. The similarity in the size of the flowers to those of the Namaqualand species, *H. flexuosa*, may be convergent for the latter species has small corms with a rounded base and spikes of several flowers.

Paratypes. SOUTH AFRICA. **Northern Cape:** 29.18 (Aggenys) Aggenys Mountain, Soutkloof WSW of Aggenys farm, shady rock crevices (BB), 24 Aug. 1977, *Oliver, Tölken & Venter 54* (PRE); Aggenys, Rosynebos, S-facing cliffs on Witberg, Aug. 1999, *Desmet et al.* in IPC Expedition *364* (NBG). 3018 (Kamieskroon) 13 km toward Loeriesfontein from Kliprand–Vanrhynsdorp road, low granite hill (DB), 7 Aug. 2001, *Goldblatt & Manning 11690* (MO, NBG).

Figure 2. Morphology of *H. oligantha.* Scale bar 1 cm. Single flower much enlarged. Drawn by Margo Branch from live plants (*Thomas & van Jaarsveld 8967,* NBG).

5. **Hesperantha oligantha** (Diels) Goldblatt, J. S. African Bot. 50: 87. 1984. *Lapeirousia oligantha* Diels, Bot. Jahrb. Syst. 44: 117. 1910. TYPE: South Africa. Northern Cape: Hantam Mts., Oct. 1900, *F. L. E. Diels 725* (holotype, B!; isotype, MO!). Figure 2.

Last revisionary account: Goldblatt, J. S. African Bot. 50: 87. 1984.

Known only from the type collection when the genus was revised for the southern African winter-rainfall zone (Goldblatt, 1984), *Hesperantha oligantha* was rediscovered in 1986 on the summit plateau of the Hantamsberg above Calvinia in the western Karoo (*Thomas & van Jaarsveld 8967,* NBG), and was then re-collected in 1994 (*Goldblatt & Manning 10043,* MO) in the course of research on the pollination biology of long-tubed, purple-flowered Iridaceae pollinated by long-proboscid flies (Goldblatt et al., 1995; Manning & Goldblatt, 1996). These new collections confirm the narrow range and unusual morphology of *H. oligantha* (Fig. 2) and show that it is a species of seasonal streams, seeps, and shallow pools. The corms of the new collections cast doubt on the relationships of *H. oligantha* for they appear to have concentric rather than imbricate tunics (Goldblatt, 1984), although this is by no means certain owing to the limited material available. *Hesperantha oligantha* is, however, now placed among species with similar concentric corm tunics in the taxonomic sequence.

6. Hesperantha montigena Goldblatt, J. S. African Bot. 50: 51. 1984. TYPE: South Africa. Western Cape: Hex River Mts., 11 Oct. 1980, *E. E. Esterhuysen 35528* (holotype, BOL!; isotypes, K!, MO!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 51. 1984.

7. Hesperantha rivulicola Goldblatt, J. S. African Bot. 50: 60. 1984. TYPE: South Africa. Northern Cape: Calvinia district, stream beds below the Hantamsberg, 16 Sep. 1980, *P. Goldblatt 5807* (holotype, MO!; isotypes, B!, BOL!, E!, K!, NBG!, PRE!, S!, US!, WAG!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 60. 1984.

When described by me in 1984, *Hesperantha rivulicola* was known from two records, one from the slopes of the Hantamsberg at Calvinia and the other from "van Wyk's farm" near Nieuwoudtville, an uncertain locality, there being several farms in the area with owners of that name. *Hesperantha rivulicola* has since been found in streams on the farms Oorlogskloof and Matjiesfontein (*Goldblatt & Manning 9466*), both located south of Nieuwoudtville, the latter owned by the van Wyk family. The flowers are pollinated by large anthophorine bees when they open after 16:00H and after dark by a range of moths that settle on the flowers (Goldblatt et al., in press).

8. Hesperantha malvina Goldblatt, sp. nov. TYPE: South Africa. Western Cape: Anysberg, farm Tapfontein, W of Matjiesgoedkop, ledges on cliff face, 3 Sep. 1987, *J. W. Lloyd 1120* (holotype, NBG!).

Plantae 10–27 cm altae eramosae, cormo ovoideo ca. 6 mm diam., tunicis lignosis concentricis, foliis 4 sparse villosis vel glabrescentibus, inferioribus duobus basalibus, linearibus ca. 2 mm latis, summo omnino vaginante marginibus leviter incrassatis, spica 1- ad 3-flora, floribus malvinis, tubo perianthii 8–9 mm longo, tepalis 13–14 × 4–5 mm, filamentis ca. 3 mm longis, antheris 5.5–6.0 mm longis, styli ramis ca. 7 mm longis.

Plants 10–27 cm high, stem unbranched. *Corm* ovoid, ca. 6 mm diam., tunics woody, concentric. *Leaves* 4, the lower 2 basal, linear-oblong, the third largely sheathing and with a short free apex, the uppermost entirely sheathing, partly membranous, 8–22 mm long, inserted a short distance below the spike, blades ca. 2 mm wide, the margins and midrib slightly thickened and sparsely long-hairy in the lower half. *Spike* 1- to 3-flowered; *bracts* ca. 10–14 mm long, green or flushed purplish, the margins and apex membranous. *Flowers* mauve, open during the day; *perianth tube* cylindric below, expanded near the apex, 8–9 mm long; *tepals* subequal, elliptic, 13–14 × 4–5 mm, spreading at right angles to the tube. *Filaments* ca. 3 mm long; *anthers* 5.5–6 mm long, yellow, pollen yellow. *Ovary* ovoid, ca. 3 mm long; *style branches* ca. 7 mm long, reaching the upper third of the anthers in bud, spreading when mature. *Capsules* and *seeds* unknown.

Flowering. Late September to early October.

Distribution. South Africa, Western Cape, Little Karoo, Anysberg, on damp, south-facing sandstone cliffs and rocks.

Assigned to *Hesperantha pilosa* when first named in the herbarium, owing to the sparsely hairy leaves, *H. malvina* actually bears little further resemblance to that species. The flowers are in general larger, with the broadly elliptic tepals up to 14 mm long and 4–5 mm wide, while the leaves are linear-oblong and somewhat obtuse at the tips. In *H. pilosa* the tepals are seldom as long as 14 mm, are rarely more than 3 mm wide, and the leaves are usually linear or linear-lanceolate and acute. The habitat, rocky sandstone cliffs, is quite different from that of *H. pilosa,* which grows on granitic or sandy flats or lower slopes. *Hesperantha malvina* is evidently restricted to the Anysberg in the western Little Karoo of Western Cape Province. To date it is known only from the holotype, and must be assumed to be rare and very local in distribution.

9. Hesperantha pilosa (L. f.) Ker Gawl., Ann. Bot. (König & Sims) 1: 225. 1804. *Ixia pilosa* L. f., Suppl. Pl. 92. 1782. TYPE: South Africa. Western Cape: hills around Cape Town, Sep., *C. P. Thunberg s.n.* (lectotype, designated by Goldblatt (1984: 54), Herb. Thunberg 979, UPS!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 54. 1984.

Since the treatment of *Hesperantha pilosa* in my 1984 account of the genus, subspecies *latifolia* has been raised to species rank as *H. pseudopilosa* (Goldblatt, 1987). Nevertheless, this relatively common Western Cape and western Karoo species remains a fairly variable series of populations in both vegetative and floral morphology. Plants have small corms with concentric tunics, three basal leaves, the uppermost largely sheathing and enveloping the stem for over half its length. The stem may be smooth or sparsely villous and always bears a bract-like scale a short distance below the spike. The leaf blades are linear or narrowly sword-shaped with slightly thickened margins and midrib, and the margins, midrib, and a pair of secondary veins bear long, usually spreading hairs. The spike is straight to slightly flexuose, and mature, healthy plants bear several flowers, either in a loose spiral or in secund arrangement.

The flowers are unremarkable in the genus and are usually white, occasionally blue, mauve, or purple, with the outer tepals flushed dull red to brown on the outside, but white-flowered plants have the anthers held more or less horizontally and parallel to the spreading tepals and short style branches, seldom reaching to the middle of the anthers in the closed flower (when the stamens and style branches are aligned). Most populations in the Bokkeveld Mountains and in the Roggeveld have blue to mauve flowers, but otherwise seem identical except that the anthers are ascending to suberect and the style branches are sometimes longer, often reaching to the anther apices in bud. White flowers typically open shortly before sunset and close again during the night, whereas blue or mauve flowers open in the morning and close in the early afternoon. It would be preferable to recognize the populations of plants with colored flowers as a separate species (for which the name *H. puberula* is available). However, there is doubt as to whether the populations with colored flowers represent a single clade or multiple origins of a colored perianth. Moreover, there is little apart from perianth color to reliably distinguish these plants.

A remarkable collection of what appears to be *Hesperantha pilosa* from the Hex River Mountains (*Esterhuysen 36196A*, BOL), flowering in December, consists of plants with only two foliage leaves. The lower leaf is linear-lorate and 4 mm wide, with an obtuse apex, and the second leaf sheaths the lower two-thirds of the stem. The margins, midrib, and secondary veins all bear the long hairs that are diagnostic for *H. pilosa*, but these seem unusual in being slightly reflexed. The plants are taller than usual for *H. pilosa*, and the spikes bear only one or two flowers. The style branches appear longer than those of any other white-flowered *H. pilosa* and in the closed flower reach the top of the anthers. The habitat, cool shaded slopes below a waterfall, is unusual for *H. pilosa*, which normally grows in light bush on exposed slopes and flowers in September and October. It seems unlikely that the habitat is responsible for the unusual morphology and late flowering time of the Esterhuysen collection. These plants more likely represent a distinct species. Additional material is needed before an informed decision can be made about these plants.

10. Hesperantha pseudopilosa Goldblatt, S. African J. Bot. 53: 461. 1987. Replaced name: *Hesperantha pilosa* subsp. *latifolia* Goldblatt, J. S. African Bot. 50: 56. 1984. Non *Hesperantha latifolia* (Klatt) de Vos. 1974. TYPE: South Africa. Northern Cape: Roggeveld, slopes of Sneeukrans, 22 Sep. 1981, *P. Goldblatt 6339* (holotype, MO!; isotypes, K!, NBG!).

When first raised from subspecies rank as subspecies *latifolia* of *Hesperantha pilosa* in 1987, *H. pseudopilosa* was known from isolated sites on the Bokkeveld Plateau (west of Nieuwoudtville), Sneeukrans on the Roggeveld Escarpment, and the northern foothills of the Kleinswartberg (Goldblatt, 1987). Additional populations (see specimens listed below) have since been found at several more sites on the Bokkeveld Plateau and along the Roggeveld Escarpment, as well as north of Matjiesfontein in the southern Karoo, which substantially fills in what seemed to be an erratic distribution pattern. The species now appears to have a nearly continuous range along the interior edge of the southern African winter-rainfall zone from the Bokkeveld Escarpment in the north to the northern slopes of the Klein Swartberg.

The white flowers open relatively late in the day, mostly after 18:00H, and then produce a strong sweet scent. They are visited by a range of settling moths, mostly of the family Noctuidae (Goldblatt et al., in press).

Additional specimens. SOUTH AFRICA. **Northern Cape:** 31.19 (Calvinia) Nieuwoudtville trekpath (AC), 27 Aug. 1999, *Goldblatt 11108* (MO); Nieuwoudtville Wildflower Reserve, 25 July 1983, *Perry & Snijman 2155* (NBG). 3120 (Williston) farm Knechtsbank W of Middelpos (CC), *Oliver 8917* (NBG). 32.20 (Sutherland) S of Sutherland, farm Verlatekloof (DA), 26 Aug. 1986, *Cloete & Haselau 47* (NBG); 2 km N of the top of Komsberg Pass (DB), 31 Aug. 1993, *Goldblatt & Manning 9677* (MO, NBG). **Western Cape:** 33.20 (Sutherland) hills between Verlatekloof and Matjesfontein (DC), 3 Aug. 1998, *Goldblatt & Manning 10951* (MO). 33.20 (Montagu) hill ca. 2 km W of Tweedside Station, 1200 m (AB), 12 Aug. 1988, *Vlok 1988* (MO).

11. Hesperantha glabrescens Goldblatt, sp. nov. TYPE: South Africa. Northern Cape: farm Hottentotskloof, ca. 15 km SW of Sutherland on Bo–Visrivier road, 2 Oct. 1999, *P. Goldblatt & I. Nänni 11190* (holotype, NBG!; isotypes, K!, MO!).

Plantae 3–5 cm altae eramosae, cormo ovoideo 4–6 mm diam., tunicis lignosis concentricis, foliis 3, inferioribus duobus falcatis summo vaginante laminis 1.0–1.3 mm latis marginibus incrassatis sparse villosis, spica uniflora (vel biflora), flore magenteo, tubo perianthii ca. 3.5 mm longo, tepalis ca. 8 × 2 mm, filamentis ca. 2 mm longis, antheris ca. 3 mm longis, styli ramis ca. 3.5 mm longis, purpureis.

Plants 3–5 cm high, stem unbranched, bearing a bract-like scale a short distance below the spike. *Corm* ovoid, 4–6 mm diam., tunics woody, concentric. *Leaves* 3, the lower 2 falcate, the upper suberect, largely sheathing, the blades 1–1.3 mm wide, the margins and midrib slightly thickened, the margins and veins sparsely hairy. *Spike* 1(or 2)-flowered; *bracts* ca. 6 mm long, purplish, becoming dry and brown above. *Flowers* magenta, open in the morning and closing in early afternoon; *perianth tube* cylindric, expanded near the apex, ca. 3.5 mm long; *tepals* subequal, elliptic, 8 × 2 mm, spreading at right angles to the tube. *Filaments* ca. 2 mm long; *anthers* 3 mm long, yellow, pollen yellow. *Ovary* ovoid, ca. 2 mm long; *style branches* ca. 3.5 mm long, purple, spreading. *Capsules* and *seeds* unknown.

Flowering. Late September and early October.

Distribution. South Africa, Northern Cape, Roggeveld Escarpment southwest of Sutherland, on moist clay flats along watercourses.

Closely related to, and initially appearing to be a depauperate form of, the widespread Western Cape *Hesperantha pilosa, H. glabrescens* was first collected in 1998 by the Cape Town botanist Nick Helme. It can be distinguished from its ally in several features. The leaves are sparsely hairy, unlike the fairly densely hairy or even downy leaves of *H. pilosa,* and the spikes are mostly 1-, or rarely 2-flowered, whereas *H. pilosa* typically has several, sometimes up to 10 flowers per spike. More unusual is the small size of the plants, only 3–5 cm high, shorter than any *H. pilosa.* The flowers are magenta in color, and quite small, with a perianth tube ca. 3.5 mm long and tepals about 8 mm long. Flowers of *H. pilosa* are often larger, usually white, although sometimes blue or magenta, have a perianth tube 6–10 mm long, and tepals (8–)12–15 mm long. The decision to recognize *H. glabrescens* was made in part because of the consistent morphology and because plants of what I consider true *H. pilosa* grew nearby (*Goldblatt & Nänni 11191*), always in the shade of shrubs, and always taller with the spikes up to 12 cm high, and with 2 to 4 flowers. These plants had plane, densely pilose leaf blades, a stark contrast to those of *H. glabrescens.* The flowers of the two species were virtually identical in size and pigmentation at the type locality.

Paratypes. SOUTH AFRICA. **Northern Cape:** 32.20 (Sutherland) 15 km SW of Sutherland on Bo–Visrivier road (BC), 25 Sep. 1998, *N. Helme 1554A* (NBG).

12. Hesperantha ciliolata Goldblatt, J. S. African Bot. 50: 59. 1984. TYPE: South Africa. Northern Cape: Roggeveld Escarpment, farm Geelhoek, 21 Sep. 1953, *J. P. H. Acocks 17176* (holotype, PRE!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 59. 1984.

Described in 1984 from a single collection from the farm Geelhoek in the center of the Roggeveld Escarpment, *Hesperantha ciliolata* is distinguished mainly by its straight, ribbed leaves, oval to terete in transverse section, with fine scabrid cilia on the rib edges. The type population had violet flowers according to the collection information. A second population was found in about 1995, some 50 km to the north, on the farm Botuin, west of Middelpos, and these plants, which flowered in cultivation in 1998, have mauve-pink flowers that are open in the morning and close in the early afternoon. The flowers of the Botuin collection have an unusual acrid-sweet odor, characteristic of the orchid genera *Corycium* Sw. and *Pterygodium* Sw. The scent is so unusual and distinctive that I wonder whether it may attract the same bees that pollinate those orchids, species of *Rediviva* (Melittidae), females of which visit the orchids to collect floral oils for nest provisioning (Steiner, 1989). A third collection from south of Sutherland (*Goldblatt & Nänni 11189*) consists of plants with pale blue-mauve to light purple flowers, also opening in the morning and closing at ca. 14:00H. The flowers of this population are evidently unscented.

Plants from the Voetpadsberg east of Touwsrivier (*Goldblatt & Nänni 11200,* in fruit; *Goldblatt & Porter 11877,* in flower) have the same overall appearance as *Hesperantha ciliolata* except that the leaves mostly have only two grooves, or sometimes a pair of secondary ones strongly raised, but the edges of the raised parts are ciliate-scabrid, as are the edges of the ribs of the sheathing, upper leaf. The flowers closely resemble those of *Goldblatt & Nänni 11189* in their bluish color but have a light, musky acrid scent. These plants must be regarded as a minor variant of this otherwise Roggeveld Escarpment species and represent a new record for the Cape Floral Region. The seeds of the Voetpadsberg plants are wedge-shaped, thus strongly angular with flat faces, the edges of which are slightly winged. The seeds of Roggeveld populations of *H. ciliolata* are unknown.

Additional specimens. SOUTH AFRICA. **Northern Cape:** 32.20 (Sutherland) S of Sutherland (AC), 2 Oct. 1999, *Goldblatt & Nänni 11189* (MO, NBG). **Western Cape:** 33.20 (Montagu) foot of the Voetpadsberg, 21.5 km E of Touwsrivier, foot of sandstone slope (AC), 3 Oct. 1999 (fr), *Goldblatt & Nänni 11200* (K, MO, NBG, PRE), 11 Sep. 2001, *Goldblatt & Porter 11877* (K, MO, NBG, PRE, WAG).

13. Hesperantha teretifolia Goldblatt, S. African J. Bot. 53: 460. 1987. TYPE: South Africa. Northern Cape: Roggeveld Escarpment between Middelpos and Calvinia, 13 Oct. 1983, *P. Goldblatt 7090* (holotype, NBG!; isotypes, K!, MO!, PRE!, S!, STE!, WAG!).

Described in 1987 from plants from the Roggeveld Escarpment near the farm Botuin west of Middelpos, *Hesperantha teretifolia* is unusual in having centric, more or less terete, minutely grooved, hollow leaves. A feature not noted in the protologue is that the leaf surface between the grooves is densely covered by minute papillae (or extremely short, cilia-like hairs) visible only under the microscope at 10× magnification. Specimens collected 10 years later, in September 1997, close to the type locality, growing in rocky sites among low bushes, clearly show this unusual epidermal feature, which is rare in the genus. A third population was discovered in 1998 at Uitkyk Farm, some 60 km south of the type locality, by N. A. Helme. Like the northern population, these plants have white flowers that open late in the afternoon, mostly after 16:30H, and are then sweetly scented. The leaves differ slightly in having the papillate hairs mostly confined to edges of the grooves, and the ridged areas between the grooves in the upper part of the leaf sometimes have a transparent center. *Hesperantha teretifolia* may be less rare than available records indicate, and exploration of the more rugged and remote parts of the Roggeveld Escarpment will likely yield additional populations.

Additional specimens. SOUTH AFRICA. **Northern Cape:** 31.19 (Calvinia) between Calvinia and Middelpos, Farm Botuin, 16 Sep. 1997, *Goldblatt & Manning 10747* (MO, NBG); 32.20 (Sutherland) SW of Sutherland on the road to Calvinia, Farm Uitkyk (AA), 26 Sep. 1998, *Helme 1556* (NBG).

14. Hesperantha quadrangula Goldblatt, J. S. African Bot. 50: 62. 1984. TYPE: South Africa. Northern Cape: Hantamsberg, slopes below the summit cliffs, 16 Sep. 1980, *P. Goldblatt 5795* (holotype, MO!; isotype, NBG!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 62. 1984.

Known from only two collections from the Hantamsberg at Calvinia in Northern Cape Province when described, *Hesperantha quadrangula* was found on the Roggeveld Escarpment west of Middelpos in 1999 (*Goldblatt & Nänni 11157*), a range extension of some 60 km. The stony habitat of the Roggeveld population is similar to that on the Hantamsberg, although the ground is only slightly sloping, unlike the steep flanks of the Hantamsberg where the earlier collections were made. The white flowers open at 16:00–16:30H and then produce a sweet, rose-like fragrance. Surprisingly for a white-flowered species, the tepals close again at nightfall, and the flowers are completely closed by 19:30H. The flowers are visited by a range of bees including *Anthophora diversipes* and *Apis mellifera* and by the occasional hopliine scarab beetle (Goldblatt et al., in press). The species is remarkable for the particularly short perianth tube, ca. 3 mm long, and may reliably be identified by this feature alone or in combination with the brown cataphyll, two basal foliage leaves, and sheathing upper leaf, which is quadrangular in cross section.

Additional specimens. SOUTH AFRICA. **Northern Cape:** 31.20 (Williston) road to Middelpos 55 km SE of Calvinia, farm Knechtsbank (CC), 19 Sep. 1999, *Goldblatt & Nänni 11157* (MO, NBG, PRE).

15. Hesperantha flexuosa Klatt, Abh. Nat. Ges. Halle 15: 394. 1882. TYPE: South Africa. Northern Cape: Namaqualand, Kamiesberg, Elboogfontein, Aug.–Sep. 1830, *J. F. Drège 2639* (holotype, B ["Herb. Lubeck"]!; isotypes, G!, P!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 63. 1984.

16. Hesperantha minima (Baker) R. C. Foster, Contr. Gray Herb. 135: 77. 1941. *Geissorhiza minima* Baker, J. Bot. (London) 5: 239. 1876. TYPE: South Africa. Northern Cape: Namaqualand, Kamiesberg "Modderfonteinsberg," Oct. 1830, *J. F. Drège 2632* (lectotype, designated by Foster (1941: 77), K!; isotypes, B!, G!, K!, L!, MO!, P!, S!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 65. 1984.

The diminutive *Hesperantha minima* was described by J. G. Baker for a dwarf species from Namaqualand collected in about 1830 by the notable collector J. F. Drège, and then referred to the related genus *Geissorhiza.* R. C. Foster correctly transferred the species to *Hesperantha* in 1941. When the genus was revised in 1984, the plant was still known from this single collection, one so well represented in the world's herbaria that there was no doubt that it represented a good species. The locality was also quite clear. Drège's collection is from "Modderfonteinsberg," i.e., the mountain on the farm Modderfontein, where he also collected the plants later to be described as *Xenoscapa uliginosa* Goldblatt & J. C. Manning (Goldblatt & Manning, 1995). That species was rediscovered in 1990 by John Rourke and E. C. Nelson while exploring Sneeuberg, the second highest mountain in Namaqualand, reaching 1591 m, and located partly on the farm Modderfontein. When I visited the site in 1991 to collect more material of the *Xenoscapa*, plants resembling *H. minima* were seen in leaf, growing in moss on thin soil on wet granite domes. Subsequently, flowering plants were located and their identity confirmed as *H. minima* (*Goldblatt 9246*, MO). Both *H. minima* and *X. uliginosa* are known from only this one locality, presumably the very site discovered by Drège over 170 years ago.

17. Hesperantha fibrosa Baker, Handbk. Irideae 149. 1892. TYPE: South Africa. Western Cape: Kleinrivier Mts., Aug., *C. L. Zeyher 3960* (lectotype, designated by Goldblatt (1984: 66), K!; isotypes, B!, G!, K!, S!, SAM!, W!, Z!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 66. 1984.

Collections of *Hesperantha fibrosa* from "Elandskloof" (*Esterhuysen 3160*, BOL) suggested that the species occurs in the Cold Bokkeveld as well as to the south in the Caledon and Bredasdorp Districts of Western Cape Province where it was once common (Goldblatt, 1984). More likely the Elandskloof of the Esterhuysen plants is the less well known place of that name in the Bredasdorp Mountains near Napier, which lies within the expected range of the species. Unless the species is re-collected at Elandskloof in the Cold Bokkeveld, it must be assumed that *H. fibrosa* does not occur there and that it has a coherent distribution range in the southern Cape.

18. Hesperantha cucullata Klatt, Abh. Naturf. Ges. Halle 15: 393. 1882. TYPE: South Africa. Northern Cape: Hantam Mts., Aug., *H. Meyer 9* (lectotype, designated by Goldblatt (1984: 72), B!; possible isotypes, S!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 72. 1984.

19. Hesperantha truncatula Goldblatt, S. African J. Bot. 53: 461. 1987. TYPE: South Africa. Western Cape: northern foothills of the Kleinswartberg, farm Vleiland, 10 Sep. 1983, *J. H. J. Vlok 662* (holotype, NBG!; isotypes, MO!, PRE!).

20. Hesperantha purpurea Goldblatt, J. S. African Bot. 50: 85. 1984. TYPE: South Africa. Northern Cape: farm Perdekraal, NW of Calvinia, 12 Sep. 1981, *P. Goldblatt 6246* (holotype, MO!; isotypes, K!, NBG!, PRE!, S!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 85. 1984.

21. Hesperantha vaginata (Sweet) Goldblatt, J. S. African Bot. 36: 298. 1970. *Geissorhiza vaginata* Sweet, British Fl. Gard. 2: pl. 138. 1836. TYPE: South Africa. Without precise locality, British Fl. Gard. 2: pl. 138. 1836.

Last revisionary account: Goldblatt, J. S. African Bot. 50: 72. 1984.

Hesperantha vaginata is the only species of the genus known to be pollinated exclusively by hopliine scarab beetles, Scarabaeidae: Hopliini (Goldblatt et al., in press). The unscented, yellow flowers, in most populations conspicuously patterned with chocolate-brown, are visited by numerous *Clania glenyonensis* individuals on warm days after the tepals unfold after 14:30H. The beetles use the flowers as sites for assembly, mate selection, and copulation, but they also consume pollen, which appears not to affect the fitness of the species, which reproduces well (Goldblatt et al., in press).

22. Hesperantha karooica Goldblatt, J. S. African Bot. 50: 79. 1984. TYPE: South Africa. Northern Cape: Calvinia, foot of the Hantamsberg, 25 Aug. 1968, *F. J. Stayner s.n.* (holotype, NBG 87606!; isotype, STE!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 79. 1984.

Although so closely resembling *Hesperantha vaginata* that there remains doubt about the status of *H. karooica*, no plants resembling either species have been re-collected at Calvinia, the type locality, or elsewhere that match the small flowers and diminutive size of the type plants. In the absence of intermediates the species must continue to be recognized.

23. Hesperantha hantamensis Schltr. ex R. C. Foster, Contr. Gray Herb. 166: 15. 1948. TYPE: South Africa. Northern Cape: Calvinia, dolerite hills, Aug. 1921, *R. Marloth 10262* (holotype, B!; isotypes, PRE!, STE!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 84. 1984.

24. Hesperantha humilis Baker, J. Bot. 14: 239. 1876. TYPE: South Africa. Northern Cape: Roggeveld near Jakkalsfontein, 7 Aug. 1811, *W. J. Burchell 1320* (holotype, K!). Figure 1B.

Last revisionary account: Goldblatt, J. S. African Bot. 50: 84. 1984.

Hesperantha humilis is readily recognized by the more or less acaulescent habit and 1- to 3-flowered spike of deep pink flowers with an elongate perianth tube. As in other species of the genus with a similarly colored perianth, the flowers open during the day and close in the mid afternoon. The perianth tube, 17–24 mm long, seems to indicate that the flowers are pollinated by a long-tongued insect. However, the tube is narrow and the walls tightly envelop the style, leaving no room for an insect's tongue. The little nectar produced is forced into the top of the tube and is accessible to insects with mouth parts no more than 5 mm long.

25. Hesperantha flava G. J. Lewis, S. African Gard. 23: 255. 1933. TYPE: South Africa. Western Cape: Whitehill, 31 July 1937, *R. H. Compton 4276* (lectotype, designated by Goldblatt (1984: 82), BOL!; isotype, K!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 82. 1984.

When described in 1933, the acaulescent, yellow-flowered *Hesperantha flava* was known from a single population near Whitehill in the southwestern Karoo of Western Cape Province. Even in 1984 when the genus was revised for the winter-rainfall zone (Goldblatt, 1984), it was known to me from only two more populations, one near Steinkopf in northern Namaqualand in Northern Cape Province, and the other from Matjesfontein, near Whitehill, a disjunction of some 500 km. Such disjunctions are not common in the southern African flora and were thus suspect. Two more populations are now known from the area between these two stations, one from near Kliprand in southwestern Namaqualand (*Oliver 9846A*, NBG), and the other between Middelpos and Calvinia (*Manning s.n.*, NBG) in the western Karoo. The range now forms a coherent pattern, and *H. flava* may be assumed to extend more or less continuously in suitable habitats along the interior edge of the winter-rainfall zone from Steinkopf in northern Namaqualand to Matjesfontein and Whitehill. Its flowering time, early winter, often in May or June, largely explains why it is so poorly known, for little collecting is done at this time of the year.

26. Hesperantha candida Baker, Handbk. Irideae 151. 1892. TYPE: South Africa. Free State, 1861, *K. H. Cooper 746* (holotype, K!; isotypes, E!, NH!, PRE!).

Hesperantha vernalis Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 423. 1986. Syn. nov. TYPE: South Africa. KwaZulu-Natal: Estcourt, S side of Kamberg, 9 Sep. 1973, *F. B. Wright 1530* (holotype, E not seen; isotypes, MO!, NU!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 423. 1986, as *Hesperantha vernalis.*

Although I believed *Hesperantha candida* to be conspecific with *H. longituba* (Goldblatt, 1984), Hilliard and Burtt (1986) argued convincingly that these were two separate species, *H. candida* called by them *H. vernalis.* The two differ mainly in floral features, especially the length of the perianth tube, timing of flower opening, and sometimes perianth color. One of just a few eastern southern African species of the genus that flower in the spring, *H. candida* may be recognized by the moderate-sized to fairly large flowers, the tepals mostly 15–20 mm long, usually pink to mauve-pink but occasionally white, with a perianth tube (5–)7–12(–14) mm long, and anthers 5–7.5 mm long. Plants bear leaves when in flower, although the leaf tips may be dry, or in exceptional cases are lacking, having been grazed or burnt off before the flowering stem has emerged. Vegetatively similar, even apparently identical, *H. longituba* consistently has white flowers with a longer perianth tube, usually at least 14 mm and up to 22 mm long. I admit to sometimes finding it difficult to distinguish herbarium specimens of *H. candida* from *H. longituba,* for the range in the length of the perianth tube in the two species overlaps and the perianth of *H. candida* is also sometimes white, although then usually the outer tepals are flushed or feathered with pink, whereas flowers of *H. longituba* are, as far as I know, uniformly white.

Leaves of *Hesperantha candida* are typically sword-shaped or nearly linear with a raised midrib and margins and an otherwise plane surface. A few collections from the Eastern Cape (e.g., *Bester 850* and *866,* PRU) consist of plants with oblong to nearly ovate leaves that appear to lack thickened margins. Other collections, among these *Bester 830*

(PRU), are intermediate, having the lowermost leaf sword-shaped and the other basal leaves oblong, leaving no doubt that the broader-leaved plants belong to the same species, *H. candida.* Whatever the shape of the leaves, the leaf surface between the margins and midrib is always plane and smooth, with secondary veins not thickened and seldom visible.

Hesperantha candida was called *H. vernalis* by Hilliard and Burtt (1986) because they associated the type (*Cooper 746*) with what I consider a second species, *H. leucantha.* This is a fairly slender, pale pink- to mauve-flowered species of the Drakensberg and nearby that flowers from December to February. Like *H. candida* the flowers open during the day but they seem generally smaller, with tepals 12–15 × 3–5 mm long and anthers 4.5–5.5 mm long, whereas those of *H. candida* have tepals mostly 15–20 × 6–9 mm, and anthers 5–7.5 mm long. Leaves of the two species also differ, for those of *H. candida* usually have a prominently thickened midrib and margins, are usually fairly broad (2–5 mm wide in the type, but on most other collections 3–6 mm wide), and the leaf tips are often dry and sometimes broken at anthesis. In contrast, the leaves of *H. leucantha* are usually quite slender, mostly 1.5–2.5 mm wide, have only slightly thickened midribs and margins, and are rarely dry at the tips. Flowering time, which would be useful additional information for the interpretation of *H. candida,* is unknown. Cooper made the type collection in 1861, and according to records (Gunn & Codd, 1981) he crossed the Lesotho frontier at Ficksburg, reaching Harrismith on 25 September where he remained until 10 October. He may well have collected the type of *H. candida* at this time. Unfortunately, the details of his subsequent travels are incomplete. Records indicate that he was in Pietermaritzburg in July of the following year, having reached there via Ladysmith. Whether he was still in the Free State that summer is evidently unknown so that the month of his collection of *H. candida* cannot be determined with any confidence. After re-examining the lectotype (which is duplicated at E, G, PRE, and Z), I remain convinced that *H. candida* is the spring-flowering species allied to *H. longituba.*

Hesperantha candida has a fairly wide distribution, plants extending not only from the Witteberg in the Eastern Cape to Harrismith in the Free State, but farther north into southern Mpumalanga, if I have correctly placed *Rogers 21282* (BOL, K, PRE), from Carolina. Plants of this gathering have flowers with a tube 11–14 mm long, tepals ca. 18 mm long, and anthers ca. 6 mm long. Collections provisionally assigned here also extend the range southward as far as the Hogsback in the Amatola Mountains (*Giffen s.n.,* GRA, PRE), Grahamstown (*Britten 2800,* GRA; *Jacot Guillarmod 8575,* GRA; *Schönland 775,* PRE; *Snijman 464,* NBG), and Alexandria (*Archibald 5977,* PRE). The plants from Grahamstown, at the southwestern extremity of the range, have the smallest flowers, the tepals ca. 12 × 6 mm, found in the species. Some specimens also have more flowers per spike than has been recorded elsewhere. They have 4 to 6 flowers per spike versus the more usual 1 to 3 in populations further north. These plants are puzzling, but it is more likely that they represent a southern and lower elevational form of *H. candida* than an undescribed species. Sometimes identified as *H. falcata,* they do not have the bell-shaped corm of this southern and western Cape species.

27. Hesperantha debilis Goldblatt, sp. nov. TYPE: South Africa. Eastern Cape: Grahamstown Nature Reserve, W of Dassie Krantz, Oct. 1951, *A. R. H. Martin s.n.* (holotype, RUH 9554!).

Plantae 10–15 cm altae plerumque pauciramosae, cormo ovoideo 4–5 mm diam., tunicis lignosis concentricis, foliis 4, inferioribus duobus basalibus, linearibus 1–2 mm latis summo vaginante marginibus costaque leviter incrassatis, spica 1- vel 2-flora, floribus albis, tubo perianthii 4–6 mm longo, tepalis 12–14 × ca. 5 mm, filamentis 2.5–3.0 mm longis, antheris ca. 5 mm longis, styli ramis ca. 10 mm longis antheras excedentibus.

Plants 10–15 cm high, stem usually branched. *Corm* ovoid, 4–5 mm diam., tunics woody, concentric. *Leaves* 4, the lower 2 basal, linear, the third partly sheathing, free in the upper half, the uppermost largely sheathing, 15–20 mm long, inserted in the upper third of the stem, blades 1–2 mm wide, the margins and midrib slightly thickened. *Stem* erect, slender, usually branched at the uppermost node and sometimes at the second node. *Spike* 1- or 2-flowered; *bracts* 8–11 mm long, green or flushed purplish, the margins and apex membranous. *Flowers* white, the outer tepals flushed red on the outside; *perianth tube* cylindric below, expanded near the apex, 4–6 mm long; *tepals* subequal, elliptic, 12–14 × ca. 5 mm, spreading. *Filaments* 2.5–3 mm long; *anthers* ca. 5 mm long, ?yellow, pollen ?yellow. *Ovary* ovoid, ca. 3 mm long; *style branches* ca. 10 mm long, overtopping the anthers by up to 2 mm in the closed flower, spreading in the open flower. *Capsules* globose, ca. 3 mm long; *seeds* unknown.

Flowering. October.

Distribution. South Africa, Eastern Cape, near Grahamstown and the Suurberg, on sandy slopes.

Plants first collected in the 19th century in the Grahamstown district of Eastern Cape Province and still poorly known, match no known species of *Hesperantha* although they are not particularly distinctive. Described here as *H. debilis* the species may be recognized partly by the small corms 4–5 mm in diameter, lax, linear leaves 1–2 mm wide, and a slender, branched stem bearing one or two flowers on each branch. It may be most closely allied to the eastern southern African *H. candida*, a more robust plant, the stems of which are rarely branched. The bracts of *H. debilis* are soft in texture and have broad membranous margins.

Paratypes. SOUTH AFRICA. **Eastern Cape:** 33.26 (Grahamstown) New Years River, Albany (AC–AD), without date, *Barber 255* (K); near Grahamstown (BC), without date, *Bolton s.n.* (K).

28. Hesperantha longituba (Klatt) Baker, Gard. Chron. 7: 652. 1877. *Geissorhiza longituba* Klatt, Linnaea 35: 383. 1867–1868. TYPE: South Africa. Eastern Cape: Somerset East, date unknown, *J. H. Bowker s.n.* (lectotype, designated by Goldblatt (1984: 69), K!; isotypes, K!, S!).

Hesperantha candida var. *bicolor* Baker, Fl. Cap. 6: 63. 1896. *Hesperantha bicolor* (Baker) R. C. Foster, Contr. Gray Herb. 166: 5. 1948. TYPE: South Africa. Somerset East, Boschberg, *P. MacOwan s.n.* (lectotype, designated by Foster (1948: 5), K!; isotypes, BOL!, G!, GRA!, M!, WU!, Z!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 69. 1984.

Largely a species of the southern Karoo and adjacent dry mountains of the Eastern Cape, *Hesperantha longituba* flowers in the spring when the veld is usually dry. The white flowers open in the late afternoon, according to Hilliard and Burtt (1986), and close after dark. The species may be recognized by the relatively large flowers with tepals 15–22 mm long and a perianth tube usually 16–22 mm long, and by the broad, leathery leaves with prominent margins and midrib. Unlike most species of eastern southern Africa, the corms are large and have overlapping tunic layers notched into segments below, like those of several western Karoo species, e.g., *H. cucullata*, *H. vaginata*, included in section *Imbricata* (now sect. *Concentrica*) by Goldblatt (1984). Most other eastern southern African species have corms with concentric tunics that fragment along vertical fracture lines into discrete segments and appear to be a fundamentally different type. The relationships of *H. longituba* presumably lie with this predominantly winter-rainfall group of species.

Among the spring-flowering species of the eastern southern African summer-flowering zone, *Hesperantha candida* is the only one that may be confused with *H. longituba.* That species (called *H. vernalis* by Hilliard & Burtt, 1986) differs mainly in the length of the perianth tube, mostly 14–22 mm long (and associated bracts), and its flowering phenology. The latter feature cannot be determined from most herbarium specimens, but Hilliard and Burtt have determined that flowers of the shorter-tubed species (tube mostly 7–12 mm long) are diurnal (confirmed by notes on some herbarium collections) and those of the longer-tubed species are crepuscular. This provides additional evidence for regarding them as separate species. Plants from the Aliwal North and Stutterheim areas are intermediate in tube length and make the distinction between the two sometimes seem arbitrary. Collections from further west, at Cradock (*Marloth 2152,* PRE), Somerset East (*van der Walt 186,* PRE), and Graaf Reinett (*Linger 2106,* PRE), always have a longer perianth tube, sometimes up to or even exceeding 22 mm. As indicated in the key, *H. longituba* may be distinguished by having a perianth tube mostly 16–22 mm long and white flowers that open in the later afternoon and remain open at night. In contrast, *H. candida* has a perianth tube mostly 7–12 mm long and white or pale pink flowers that are open during the day and closed at night. *Hesperantha candida* was included in *H. longituba* by Goldblatt (1984), but Hilliard and Burtt (1986) argued convincingly that they are separate, albeit allied, species.

29. Hesperantha schelpeana Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 37: 302. 1979. TYPE: Lesotho. Black Mts. between Sani and Mokhotlong, 5 Nov. 1973, *O. M. Hilliard & B. L. Burtt 7075* (holotype, E not seen; isotype, NU!). Figure 3A.

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 434. 1986.

Collections made since *Hesperantha schelpeana* was described in 1979 make it necessary to amplify the circumscription of the species. Plants may have one or two flowers (*Bester 3098, Strever 433,* PRU), or even three (*Bester 2961,* PRU) or more (*Hilliard & Burtt 13117,* NU), and although described as leafless when in flower, plants usually bear two sheathing leaves (the cataphylls of Hilliard & Burtt's description) as well as a basal cataphyll that

Figure 3. Morphology of *H. schelpeana* (A) and *H. altimontana* (B), full size. Drawn by John Manning from pressed plants and accompanying photographs (*H. schelpeana: Cubitt s.n*, NBG; *H. altimontana: Cubitt s.n.*, NBG (flowering plant), and *Goldblatt 11239*, NBG (leaf)). Scale bar 1 cm.

is colorless, and occasionally the sheathing leaves overlap and may even have a short, unifacial tip. Collections from Naude's Nek (*Strever 433*, PRU), Lapa Munnik Pass (*Bester 3098*, PRU), and Saalboom Nek (*Hilliard & Burtt 13117*, NU) show that plants occasionally bear one long basal leaf and sometimes a second shorter one at flowering. These longer leaves are often dry or dying back at flowering time, but are evidently occasionally still at least partly green. The leaves are about 2 mm wide, and it appears from the way they dry that they are oval in section when alive. As they dry the soft internal tissue shrinks, leaving each surface with two or more narrow but irregular, longitudinal grooves, making it appear as if the living leaf had thickened veins and thinner intercostal areas. Evidently new leaves are normally produced on a separate shoot after flowering, but sometimes the fully developed leaves of the past season persist until next flowering.

The occasional presence of leaves at flowering time makes it possible to confuse *Hesperantha schelpeana* with *H. candida,* which flowers at the same time of year and normally has leaves present on the flowering stem (unless destroyed by fire or grazing). Properly developed plants of *H. candida* have four leaves, two basal, a third subbasal and partly sheathing, and a short, sheathing leaf in the upper part of the stem. *Hesperantha schelpeana,* however, never has more than three leaves, the lowermost slender and exceeding the stem (when still present at flowering), the second much shorter, often largely sheathing, and a third, short, sheathing leaf usually present on the upper part of the stem. The leaf blades also differ, and *H. candida* can be distinguished by the fairly broad leaves with clearly thickened and raised margins and midrib and the surface plane and smooth elsewhere. Several specimens assigned in herbaria to *H. candida* (or its synonym *H. vernalis*) seem to me to be *H. schelpeana* in which the foliage leaves have persisted later in the year than usual, and then the two species can only be separated by examination of leaf number, size, and shape of the blade.

The flowers of *Hesperantha schelpeana* were described by Hilliard and Burtt as whitish or pale pink with the outer tepals feathered red-purple outside. Plants from The Sentinel on the Free State–KwaZulu-Natal border in the Drakensberg Mts., at the northern limit of the species (*Cubitt s.n.*, NBG), have pink flowers, shading darker at the tips of the tepals, with the throat dark brown, providing a stark contrast to the deep yellow anthers and pollen. The reverse of the outer tepals is so strongly feathered with brown as to appear nearly uniformly pigmented. Some plants from the southern end of its range (e.g., *Bester 2961, 3018,* PRU) have white flowers with the outer tepals barely tinged with mauve near the tips.

30. Hesperantha altimontana Goldblatt, sp. nov. TYPE: South Africa. Free State: Drakensberg Mts., The Sentinel, ca. 2500 m, 10 Oct. 1979, *G. Cubitt s.n.* (holotype, NBG!). Figure 3B.

Plantae 10–12 cm altae eramosae, cormo ovoideo, 8–12 mm diam., foliis caulis florentis 2 omnino vaginantibus 2.5–3.5 cm longis, foliis post anthesis productis solitariis falcatis 6–8 cm × 3–4 mm, spica 1-flora, flore cremeoalbo, tubo perianthii 20–27 mm longo, tepalis 20–23 × 9–10 mm, filamentis ca. 3 mm longis, antheris ca. 10 mm longis, styli ramis ca. 10 mm longis.

Plants 10–12 cm high, erect, unbranched, flowering without the leaves. *Corm* ovoid, 8–12 mm diam., with relatively soft, imbricate tunics. *Leaves* (of the flowering stem) 2, entirely sheathing, 2.5–3.5 cm long; foliage leaves produced later in the season, solitary, falcate, to 6–8 cm long, 3–4 mm wide, leathery, the midrib hyaline but not raised when alive. *Spike* 1-flowered; *bracts* ca. 20 mm long, green, flushed with purple, the inner slightly shorter than the outer. *Flowers* uniformly creamy white, shading to pale yellow both inside and outside the tube; *perianth tube* 20–27 mm long, cylindrical, expanded near the mouth; *tepals* spreading, elliptic-ovate, 20–23 × 9–10 mm, subacute. *Filaments* erect, ca. 3 mm long, inserted in the mouth of the tube; *anthers* diverging, ca. 10 mm long, yellow, pollen yellow. *Ovary* oblong, ca. 5 mm long; *style* dividing in the mouth of the tube, the branches reaching to the upper third of the anthers in bud, ca. 10 mm long, laxly spreading above. *Capsules* and *seeds* unknown.

Flowering. October.

Distribution. Lesotho and South Africa in Free State and KwaZulu-Natal Provinces, stony, open ground in the high Drakensberg.

Hesperantha altimontana is presumably allied to the two other southern African Drakensberg species that flower early in the season and without their foliage leaves, *H. crocopsis* and *H. schelpeana.* Of the two, it is most like *H. schelpeana* in its fairly large flowers, but it differs in having a perianth tube 20–27 mm long and uniformly creamy white perianth, whereas *H. schelpeana,* with a perianth tube 5–10 mm long, has whitish or pale pink flowers with the outer tepals flushed with darker pink to purple on the outside (Fig. 3A). *Hesperantha crocopsis* has much smaller flowers than *H. altimon-*

tana, the tepals only 6–7 mm long, but a perianth tube 9–14 mm long, and like *H. schelpeana* the outer tepals are red to purple on the outside. Illustrations of *H. schelpeana* (Hilliard & Burtt, 1979) and *H. altimontana* (Trauseld, 1969: 41, number 670, as *Hesperantha* species) show the difference between the flowers of the two species.

This plant was known to Hilliard and Burtt who discussed the few available specimens under *Hesperantha schelpeana,* concluding that they probably represented a new species. *Hesperantha altimontana* is thus the third species of the genus, all of the high Drakensberg, in which the foliage leaves are produced after flowering on new shoots on the corm near the base of the flowering stem. Foliage leaves are lacking on flowering specimens, but plants from ridges west of Thaba Ntlenyana in Lesotho (*Goldblatt 11239,* NBG) that appear to be *H. altimontana* have a distinctive, falcate leaf with a plane blade like no other known member of the genus. This collection is assumed to be vegetative *H. altimontana.* The illustration of *H. altimontana* (Fig. 3B) is based on the collection and photographs made by the photographer Gerald Cubitt and vegetative specimens from Thaba Ntlenyana.

Paratypes. LESOTHO. 29.29 (Underberg) top of Black Mountain Pass on slopes W of Thaba Ntlenyana, 3200 m (CA), 5 Feb. 2000 (fr), *Goldblatt 11239* (NBG). SOUTH AFRICA. **KwaZulu-Natal:** 29.29 (Underberg) Giants Castle Game Reserve, The Gable (BC), 25 Oct. 1966, *Trauseld 670* (NU, PRE), date unknown, *Trauseld 1104* (PRE not seen).

31. Hesperantha crocopsis Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 37: 302. 1979. TYPE: Lesotho. Mokhotlong District, above Mashai Pass, 7 Nov. 1977, *O. M. Hilliard & B. L. Burtt 10489* (holotype, E not seen; isotype, NU!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 435. 1986.

32. Hesperantha bachmannii Baker, Bull. Herb. Boissier ser. 2, 1: 863. 1901. TYPE: South Africa. Western Cape: near Hopefield, date unknown, *F. E. Bachmann 1177* (lectotype, designated by Foster (1948: 4), G!; isotypes, B!, Z!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 90. 1984.

33. Hesperantha bulbifera Baker, J. Bot. 14: 183. 1876. TYPE: South Africa. Eastern Cape: Somerset East, Boschberg, Nov. 1876, *P. MacOwan 2215* (lectotype, designated by Goldblatt (1984: 95), K!; isotypes, BOL!, G!, K!, PRE!, WU!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 95. 1984.

Hesperantha bulbifera remains a puzzling species, for although readily recognized by the white flower with a curved perianth tube and soft-textured leaves, it has an unusually scattered distribution across the southern African summer-rainfall zone. Populations extend from Somerset East in Eastern Cape Province in the south to Limpopo Province and Sabie in Mpumalanga in the east, always in wet habitats such as wet cliffs and within the spray of waterfalls. It is poorly distinguished from the related *H. bachmannii* by larger size, a characteristic cormlet in the lower leaf axils, and sometimes a longer perianth tube, but for the present it seems advisable to continue to recognize the species. Although mostly flowering in the summer months, the type collection, from Somerset East, was in bloom when collected in September. The collection from the Soutpansberg, *Venter 6205* (PRE, July, 1981) and another from Iron Crown in the Wolkberg (*Venter s.n.,* PRE, 15 Oct. 1985), extends the range of the species substantially to the north of its next nearest sites at Thabazimbi (*Venter 1936,* PRE) and Sabie (*Cunliffe sub Moss 4311,* K, Z) (Goldblatt, 1984).

34. Hesperantha pallescens Goldblatt, J. S. African Bot. 50: 88. 1984. TYPE: South Africa. Western Cape: below Piekenierskloof Pass, 3 Sep. 1980, *P. Goldblatt 5645* (holotype, MO!; isotypes, B!, BOL!, C!, K!, M!, NBG!, P!, PRE!, S!, US!, WAG!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 88. 1984.

My field studies at the only known site for the species indicate that this narrow endemic is seriously threatened. Plants grow at the edges of cultivated fields at the foot of Piekenierskloof Pass, north of Piketberg. The long-tubed, pale yellow flowers open in the morning and close at sunset and are unscented. Perianth tube length, 18–22 mm, and self-compatibility (Goldblatt, 1984) suggest the species may have a specialized pollinator, probably a long-proboscid fly (Goldblatt et al., in press).

35. Hesperantha baurii Baker, J. Bot. 14: 182. 1876. TYPE: South Africa. Eastern Cape: Transkei, Baziya Mountain, Mar., *L. R. Baur 628* (holotype, K!; isotype, BOL!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 426. 1986.

35a. Hesperantha baurii subsp. **baurii**

See Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 426. 1986.

35b. Hesperantha baurii subsp. **formosa** Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 430. 1986. TYPE: Lesotho. Sani top, W of border post, 9500 ft., 16 Jan. 1976, *O. M. Hilliard & B. L. Burtt 8829* (holotype, NU!; isotypes, E not seen, MO!).

By far the most common species of *Hesperantha* in eastern southern Africa, *H. baurii* extends from Satana's Nek near Engcobo in the Eastern Cape in the south through KwaZulu-Natal, Lesotho, the eastern Free State to Mpumalanga Province. Frequent in grassland from 500 to 2000 m, it favors relatively well-watered grassy slopes and may occasionally even be found in seasonal seeps or rocky pavement, where it flowers from mid to late summer, December to March. Flowers are bright pink with large deep yellow anthers and pollen and when open from mid morning to about 16:00H they can make a striking display. In combination with these features, *H. baurii* can be recognized by the relatively short perianth tube, mostly 7–10 mm long, tepals 12–18 mm long, and a remarkably consistent vegetative morphology, with four leaves, the lower two largest and basal, the third leaf sheathing in the lower half, and the uppermost leaf usually short, inserted in the middle of the stem and entirely sheathing. Plants are erect, and only the most robust individuals may have a single branch. The spike ranges from weakly to markedly flexuose and bears up to 12 flowers, occasionally more, and spikes with as many as 18 flowers have been reported (Hilliard & Burtt, 1986). My circumscription of *H. baurii* largely agrees with that of Hilliard and Burtt except that I regard the late winter- to spring-flowering plants from coastal Transkei and KwaZulu-Natal included by them in the species as the separate *H. modesta*, which with its presumed synonym *H. subexserta* are here removed from *H. baurii*. Apart from the spring flowering time, *H. modesta* may be recognized by the fewer-flowered spikes, mostly bearing 2 or 3 flowers, and the presence of only 3, or occasionally 4 leaves, of unusually soft texture.

Subspecies *formosa* of *Hesperantha baurii*, described by Hilliard and Burtt (1986) for plants with few-flowered spikes (usually with 2–4(–6) flowers), normally only 2 basal and 1 sheathing, cauline leaf, and somewhat larger flowers, with tepals 15–21 mm long versus 12–16(–18) mm in subspecies *baurii*, from the higher parts of the KwaZulu-Natal Drakensberg and adjacent Lesotho, remains somewhat puzzling. It is usually easy to distinguish this subspecies from more typical *H. baurii*, but plants from slightly lower altitudes appear to be intermediate between the two taxa. I have not seen enough plants in the field to make any change to Hilliard and Burtt's taxonomy. Their record of the co-occurrence at Sani Pass of subspecies *formosa* in fruit when subspecies *baurii* was in flower suggests that this plant deserves at least subspecies rank (or should even be recognized as a separate species). In the key to the genus (p. 402), I have included both subspecies, but care should be taken in identifying intermediate plants, which may not be accommodated in the key.

A collection from damp sites in the Ngeli Forest (*Balkwill & Cadman 2886*, NU), flowering in late January, must be mentioned here. Plants bear 4 leaves, the lower 3 basal and the uppermost inserted in the middle part of the stem. All the leaves have long blades, reaching almost to the base of the spike and 1 mm wide or less, narrower than any recorded in *Hesperantha baurii*. Despite the narrow blade, the midrib appears in the dry state to be strongly thickened and perhaps winged, with the wings reaching over the blade surface. The slender stem bears only 4 flowers, themselves relatively small: the tube 5–6 mm long, the tepals 9–10 × ca. 3 mm, and the anthers ca. 4 mm long. These dimensions are all smaller than any encountered in plants that can be confidently placed in *H. baurii*. From the scanty material available it is impossible to say if this plant represents a new species or a depauperate form of *H. baurii* growing in shady conditions.

36. Hesperantha petitiana (A. Rich.) Baker, J. Linn. Soc. 16: 96. 1877. *Ixia petitiana* A. Rich., Tent. Fl. Abyssinia 2: 309. 1850. TYPE: Ethiopia. Tigre, near Mai Gouagoua, *L. R. Quartin-Dillon & A. Petit s.n.* (lectotype, designated by Goldblatt (1986: 138), P!).

Last revisionary account: Goldblatt, Ann. Missouri Bot. Gard. 73: 138. 1986.

Unspecialized in general aspect, pale pink- or white-flowered *Hesperantha petitiana* seems hardly to differ from the common southern African *H. bau-*

rii (Goldblatt, 1986). Although Hilliard and Burtt (1986) suggested that *H. petitiana* could readily be distinguished from *H. baurii* by the smaller anthers, 4–4.8 mm long versus 5–9 mm in *H. baurii*, material I have examined of *H. petitiana* has anthers 3–5 mm long. This tropical African species may also be distinguished in fruit from similar, short-tubed eastern southern African species by the larger capsules, (7–)10–15 mm long and often slightly exceeding the bracts. In *H. baurii* the capsules are mostly 6–9 mm long, thus shorter than the bracts that subtend them (Goldblatt, 1993). The two species also appear to have different seeds, those of *H. petitiana* often being angular and slightly larger, 1.0–1.2 mm diam., compared with those of *H. baurii* and its immediate allies, which typically have more or less uniformly rounded and small seeds, 0.8–1.0 mm in diameter. Spikes of *H. petitiana* often bear only 2 to 4 flowers on nearly straight spikes, but sometimes up to 10 flowers, whereas flexuose spikes of 8 to 12 flowers or more are more common in *H. baurii*.

37. Hesperantha glareosa Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 424. 1986. TYPE: South Africa. KwaZulu-Natal: Underberg, headwaters of Mlahlangubo River, 23 Jan. 1982, *O. M. Hilliard & B. L. Burtt 15367* (holotype, NU!; isotype, E not seen).

Last revisionary account: Hilliard & Burtt, Notes. Roy. Bot. Gard. Edinburgh 43: 424. 1986.

Although *Hesperantha glareosa* is largely a species of the Drakensberg Mountains of KwaZulu-Natal, specimens cited by Hilliard and Burtt (1986) from Mpumalanga (then the Transvaal) are similar to some depauperate specimens of *H. glareosa* and may be this species. It is impossible to say if these slender, one- or two-flowered plants (e.g., *Galpin 14329*, BOL, PRE; *Jacobsen 4780*, PRE) are depauperate, four-leaved *H. schlechteri*, or truly *H. glareosa* as Hilliard and Burtt (1986) believed. The flowers are moderate in size, the tepals 10–14.5 mm long, but the perianth tube length given by Hilliard and Burtt for the species, (3–)5–15 mm, must be a typographic error, for all plants I have seen, including most of those examined by Hilliard and Burtt, have a perianth tube 5–7 mm long. Their key is correct in placing *H. glareosa* under those species with anthers 3–5.5 mm long, but specimens I have examined have anthers mostly 4.5–5.5 mm long. Depauperate and/or poorly pressed, and apparently small-flowered plants from Lesotho cited under *H. glareosa* by Hilliard and Burtt are probably *H. exiliflora* of which they had no adequate material in 1986. *Dieterlen 1095* (PRE, SAM) and *Werger 1662* (PRE), which they cited, are probably that species. Differences between *H. glareosa* and *H. exiliflora* are discussed under *H. exiliflora*, species number 40 below.

38. Hesperantha schlechteri (Baker) R. C. Foster, Contr. Gray Herb. 114: 64. 1936. *Geissorhiza schlechteri* Baker, Bull. Herb. Boissier, ser. 2, 1: 863. 1901. TYPE: South Africa. Limpopo Province: Woodbush, 27 Mar. 1894, *R. Schlechter 4701* (syntypes, BOL!, G!, K!, P!).

Hesperantha similis N. E. Br. ex R. C. Foster, Contr. Gray Herb. 166: 24. 1948. Syn. nov. TYPE: South Africa. Mpumalanga: Sabie District, Devil's Knuckles, Apr. 1887, *F. Wilms 1446* (holotype, K!; isotypes, B!, Z!).

Because of the confusion over the identity of *Hesperantha schlechteri* and *H. similis*, both based only on their respective types (Foster, 1941), I include an extended description of the species as circumscribed here. Neither species was treated in the revision of the genus for part of eastern southern Africa (Hilliard & Burtt, 1986), and thus no modern account of the species exists. Likewise, I cite all specimens that I have seen in support of my circumscription of *H. schlechteri*.

Plants 18–30 cm high, stem usually unbranched, flexuose and often looped above the sheaths of the upper leaves. *Corm* ovoid, 8–12 mm diam., tunics woody, concentric. *Leaves* mostly 5, occasionally 4, usually the lower 4 (or 3) basal or subbasal and largest, the uppermost one or two inserted in the middle of the stem and sometimes entirely sheathing or with short free unifacial tip, linear, 2–4 mm wide, the margins and midrib not, or barely thickened when alive. *Spike* mostly 4- to 8-flowered, flexuose; *bracts* mostly 9–12 mm long, green, the inner about two thirds as long as the outer. *Flowers* pale to deep pink, the outer tepals with a coppery brown flush; *perianth tube* slender below, widening near the top, 5–7(–10) mm long; *tepals* subequal, lanceolate-ovate, 13–16 × 5–6.5 mm, spreading ± at right angles to the tube when fully open in the morning. *Filaments* 2–3 mm long; *anthers* 4–4.5 (–6) mm long. *Ovary* ovoid, ca. 2.5 mm long; *style* branches 10–12 mm long, laxly spreading, exceeding the anthers by ca. 2 mm in the closed flower. *Capsules* oblong-obovoid, 7–9 × ca. 3 mm; *seeds* subglobose or the sides flattened by pressure, ca. 0.6 mm long.

Flowering. January to mid March.

Distribution. South Africa, Limpopo Province and Mpumalanga, along the Drakensberg escarpment from Woodbush in the north to Long Tom Pass in the south, on rocks and thin soil on sandstone pavement.

Although first collected in 1887 near Lydenburg in Mpumalanga Province, South Africa, by the German apothecary Friedrich Wilms, *Hesperantha schlechteri* was described in 1901 by J. G. Baker from a later gathering made by Rudolf Schlechter in 1894 in what is now Limpopo Province of South Africa. Baker referred the species to the related genus, *Geissorhiza,* and it was only in 1936 that *G. schlechteri* was transferred to *Hesperantha* by the American botanist R. C. Foster. The Wilms collection formed the basis for a second species, *H. similis,* described by Foster in 1948. Then known from relatively few collections, the two species remained poorly understood, and some specimens from Mpumalanga that closely match the type of *H. similis* fairly closely were referred to "*H. sp.* (= *Codd 9481,* PRE)" by Hilliard and Burtt (1986: 429), who also identified a few specimens in herbaria as *H. glareosa,* a species otherwise largely restricted to Lesotho and the KwaZulu-Natal Drakensberg. I here include *H. similis* in *H. schlechteri,* which is easily distinguished from all the similar short-tubed, pink-flowered species of *Hesperantha* in eastern southern Africa, including *H. glareosa,* by normally having 5 narrow leaves with blades 2–4 mm wide and a flexuose stem, often with a pronounced loop above the sheaths of the uppermost leaves. The pink flowers have a relatively short perianth tube, 5–7(–10) mm long, and anthers are mostly 4–4.5 mm long. *Hesperantha glareosa* has flowers with a perianth tube of similar length, anthers 4.5–5.5 mm long, and consistently only 4 leaves, the blades mostly 1–2 mm wide.

Hesperantha schlechteri appears to have a fairly narrow distribution, occurring in the Woodbush and Wolkberg of Limpopo Province and the higher parts of the Mpumalanga Escarpment, which extends a short distance to the north and south of Long Tom Pass. Plants cited below from Mariepskop have four or five leaves, the blades only about 1 mm wide, and may not be correctly placed in *H. schlechteri.*

The collection *Codd 9481* (PRE), mentioned above, from near MacMac Falls, is puzzling, for the plants have five leaves, the blades of the lower ones 4–6 mm wide, unusually broad for any species of *Hesperantha* in Mpumalanga. The flowers are quite small, with tepals ca. 7 mm long and a tube ca. 5 mm long, and the anthers 4 mm long. It may be an unusual form of *H. schlechteri* or an undescribed species. I have visited the MacMac Falls area in Mpumalanga several times and failed to locate any *Hesperantha* there. A few more collections, including *Goldblatt & Manning 9814* (MO, NBG) from Dullstroom, also represent this form.

Additional specimens. SOUTH AFRICA. **Limpopo:** 23.30 (Tzaneen) Wolkberg, rocky grassland on approach to Serala Peak (CC), 23 Feb. 2002, *Goldblatt & Porter 11954* (MO, NBG). **Mpumalanga:** 24.30 (Pilgrims Rest) summit of Black Hill, Pilgrims Rest (DC), 1 Mar. 1937, *Galpin 14329* (BOL, K); Mariepskop (DB), 10 Apr. 1958, *van der Schijff 4382* (K, PRE). 25.30 (Lydenburg) Dullstroom, farm Verlorenvalei (AC), 27 Mar. 1985, *Krynauw 265* (LYD, PRE); Mauchsberg (BA), 22 Dec. 1932, *Smuts & Gillett 2286* (PRE); summit of Mt. Anderson, Mar. 1933, *Galpin 22486* (BOL); summit plateau, Mt. Anderson, Mar. 1933, *Galpin 21485* (BOL), *Galpin 13779* (PRE); top of Long Tom Pass, Feb. 1972, *Goldblatt 611* (BOL), 6 Feb. 1994 (fr), *Goldblatt & Manning 9835* (MO, NBG), 6 Feb. 1994, *Goldblatt & Manning 9836* (MO, NBG), 12 Mar. 1996, *Goldblatt & Manning 10480* (MO, NBG); Long Tom Pass, Whisky Spruit, 11 Feb. 1986, *Krynauw 1032* (LYD); Mokobu Nature Reserve, 20 Jan. 1953, *Marais 43* (PRE).

39. Hesperantha leucantha Baker, Handbk. Irideae 150. 1892. TYPE: South Africa. KwaZulu-Natal, Oliviershoek Pass, 14 Jan. 1886, *J. M. Wood 3437* (holotype, K!).

Geissorhiza macra Baker, Bull. Herb. Boissier ser. 2, 4, 1005. 1904. TYPE: Lesotho. Mt. Machache, without date, *H. Jacottet 1937* (holotype, G!).

As outlined above under *Hesperantha longituba,* I regard *H. leucantha* as the correct name for the species called *H. candida* by Hilliard and Burtt (1986). The type of *H. candida,* described by J. G. Baker in 1892, is the spring-flowering species that Hilliard and Burtt called *H. vernalis. Hesperantha leucantha* can be recognized by the fairly straight stem, few-flowered spike, and pale pink to pale lilac flowers with a relatively long perianth tube compared to the narrow tepals. In the plants I have seen from the Witzieshoek area of Free State, not far from the type locality of *H. leucantha,* the anthers and pollen are always white and the horizontally spreading style branches are unusually long in relation to the tepals, ca. 15 mm long. Although Hilliard and Burtt described the flowers as white or pale pink to lilac-mauve, white-flowered plants are unusual, and probably not part of the normal pattern of variation. Among the ample material at K, MO, NBG, and PRE there are no white-flowered plants that appear to match the distinctive appearance of *H. leucantha.* The specific epithet *leucantha* (white flower) is therefore misleading, but I suspect that Baker assumed that the flowers were white. The species is distinctive in having very pale pink flowers, white anthers and pollen, and particularly long, spreading style branches, which in the closed flower usually exceed the anthers by 3–4 mm. The weak, often inclined to drooping stem, and drooping leaves are also a notable feature of *H. leucantha.*

Hesperantha leucantha is sometimes confused with *H. glareosa,* a species with deep pink flowers with a much shorter perianth tube, mostly 4–6 mm long, while the tepals are 10–14.5 mm long. *Hesperantha glareosa* also has four leaves, the lower three basal and with firm, narrow blades, mostly 1–2 mm wide. In *H. leucantha* the perianth tube is usually 12–15 mm long, and exserted from the bracts unless these are unusually long, and the tepals are 9–12(–15) mm long across its main range in interior Lesotho, eastern Free State, and northern KwaZulu-Natal. The erect stem and flexuose spike of *H. glareosa* also help prevent confusion between these two species, for *H. leucantha* typically has a more or less inclined to drooping stem and straight spike, and fairly soft-textured leaves, weakly trailing over rocks.

Plants from north of the Vaal River, in Gauteng and Northwest Province, included (as *Hesperantha candida*) in *H. leucantha* by Hilliard and Burtt, are somewhat atypical in their greater height and slender habit, but for the present it seems best to include them here. Sheets at K and PRE of a collection from Milner Park, Johannesburg (*Moss 18285*) are annotated *H. mossii* by N. E. Brown. The specimens referred to *H. leucantha* from Mt. Anderson (*Galpin 13781,* BOL, PRE), in what is now Mpumalanga, are here assigned to the new species *H. saxicola,* as they have relatively large white flowers, exceptional for *H. leucantha* in both size (tepals 15 × 7 mm and small anthers only ca. 4 mm long) and the white perianth, and they occur in what would otherwise be outside its recorded range.

Geissorhiza macra from Mt. Machache, and thought to come from the Transvaal by J. G. Baker, who described the species in 1904, matches closely collections of *Hesperantha leucantha* from northern Lesotho and southern Free State. The two plants of its type collection have spikes of one or two pink flowers, soft-textured leaves about 2 mm wide, and the perianth tube ca. 13 mm long. Until now the type has not been matched with any *Hesperantha* species, although it was known to belong to the genus by Foster (1948). Mt. Machache is actually in eastern Lesotho some 32 km from Maseru where Jacottet collected (Gunn & Codd, 1981), thus well within the expected range of *H. leucantha.*

40. Hesperantha exiliflora Goldblatt, sp. nov. TYPE: Lesotho. 3 km from New Oxbow Inn on road to Moteng Pass, subalpine grassland, 2550 m, 3 Feb. 1987, *D. J. B. Killick 4477* (holotype, PRE!; isotype, MO!).

Plantae 12–25(–30) cm altae eramosae, cormo conico prope basem ca. 8 mm diam., tunicis lignosis, foliis usitate 4, 3 inferioribus falcatis summo pro maxima parte vaginante, laminis inferioribus 1.2–2.3 mm latis marginibus costaque leviter incrassatis, spica plerumque 1- ad 3-flora, floribus roseis in ore tubi flavis, tubo perianthii 3.5–5.0 mm longo, tepalis 6–8 × ca. 2.5 mm, filamentis ca. 2.5 mm longis, antheris 2.5–3.3 mm longis, styli ramis 3.0–3.5 mm longis.

Plants mainly 12–25(–30) cm high. *Corm* conic, ca. 8 mm diam. near the base, with woody tunics soon breaking into elliptic segments tapering above into short points. *Leaves* normally 4, the lower 2 basal and longest, reaching to between the upper third of the stem and the top of the spike, the third leaf inserted shortly above the ground and largely sheathing, the uppermost leaf entirely sheathing and bract-like, 12–32 mm long, inserted in the middle to upper third of the stem, the blades of the lower leaves ± linear, 1.2–2.3 mm wide, firm and erect, the midrib and margins slightly raised, hyaline at least when dry. *Stem* erect, unbranched. *Spike* mostly 1- to 3-flowered, lax and ± straight; *bracts* 6–8(–9.5) mm long, green, the upper margin transparent, the inner bract slightly shorter than the outer, ± membranous with 2 green keels, 2-lobed at the tip. *Flowers* pink, pale yellow in the mouth of the tube; *perianth tube* funnel-shaped, 3.5–5 mm long; *tepals* spreading, elliptic, 6–8 × ca. 2.5 mm, acute. *Filaments* ascending, ca. 2.5 mm long; *anthers* ascending, 2.5–3.3 mm long, shortly tailed, yellow, pollen yellow. *Ovary* oblong, 3–4 mm long; *style* dividing below the mouth of the tube, the branches 3–3.5 mm long, diverging above, reaching to between the middle of the anthers to just beyond the apices in the closed flower. *Capsules* and *seeds* unknown.

Flowering. January and February.

Distribution. Lesotho, Drakensberg plateau in subalpine grassland, often in damp sites.

Although collections of *Hesperantha exiliflora* were at first associated with the Drakensberg Mountain species *H. glareosa* in both herbaria and the literature, I can see no particular reason to consider them closely related, beyond their common occurrence. Plants of the few known populations of *H. exiliflora* have remarkably small flowers, the perianth tube 3.5–5 mm long and the tepals 6–8 mm long. The only other species of pink-flowered *Hesperantha* from eastern southern Africa with comparably small flowers, *H. ingeliensis* is rather different for it has tepals 10–12 mm long and broader, falcate leaves, 5.5–7 mm wide. This is quite unlike the straight, slender leaves of *H. exiliflora,* which are only up to 2.3 mm wide and appear to have a fairly soft texture. The straight stem and seemingly consistently few-flowered spikes of *H. exiliflora* are unlike the rather wiry, flexuose spikes of *H. glareosa*, which has larger flowers with a tube 5–6 mm long and tepals 10–12 mm long.

Hesperantha exiliflora seems most closely allied to a second new species, *H. brevistyla*, of the northern high Drakensberg, which has pale pink flowers with a tube 7–9 mm long, tepals ca. 7 × 3.5 mm, short white anthers 2.5–3.5 mm long, and short style branches, ca. 6 mm long, that reach to about the lower third of the anthers at most. The flowers of *H. exiliflora* dry a dark purple color, while those of *H. brevistyla* dry pale pink. In contrast, the anthers of *H. exiliflora* are yellow and the style branches are 3–3.5 mm long, reaching to between the middle of the anthers to just beyond their tips in the closed flower.

Paratypes. LESOTHO. 29.28 (Marakabei) 1 km E of Tiping village, above the dip tank, ca. 5 km E of Ha Lejone (AA/AB), 3 Feb. 2000, *Trinder-Smith 195* (BOL); Mountain Road, 32.5 km E of Thaba Putsoa, 1500 m (AC), 20 Mar. 1983, *Halliwell 5060* (PRE). 29.29 (Underberg) top of Sani Pass, marshy turf (BA), 20 Feb. 1985, *Manning 550* (NU).

41. Hesperantha alborosea Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 421. 1986. TYPE: South Africa. KwaZulu-Natal: Underberg, Cobham, Upper Polela Cave area, 13 Feb. 1979, *O. M. Hilliard & B. L. Burtt 15367* (holotype, E not seen; isotype, NU!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 421. 1986.

42. Hesperantha brevistyla Goldblatt, sp. nov. TYPE: South Africa: Free State, Sentinel trail, rocky pavement below sheer basalt cliffs on trail to the chain ladders, 5 Mar. 2002, *P. Goldblatt & L. J. Porter 11989* (holotype, NBG!; isotypes, MO!, PRE!). Figure 4.

Plantae 4–10(–16) cm altae eramosae, cormo conico prope basem ca. 3 mm diam., tunicis lignosis, foliis 4 vel 5, 3 vel 4 inferioribus falcatis summo pro maxima parte vaginante, laminis inferioribus 2–4(–5) mm latis marginibus costaque leviter incrassatis, spica 1–4(–5)-flora, floribus pallide roseis in ore tubi cremeis, tubo perianthii 7–9 mm longo, tepalis 7–8 × ca. 3.5 mm, filamentis 1.8–2 mm longis, antheris 2.5–4 mm longis, styli ramis ca. 6 mm longis.

Plants 4–10(–16) cm high. *Corm* conic, ca. 3 mm diam. near the base, with woody tunics soon breaking into elliptic segments tapering above into short points. *Leaves* 4 or 5, the lower 3 or 4 basal and longest, about as long as the spike, uppermost leaf inserted between ground level and the middle of the stem, and partly or rarely entirely sheathing, the blades of the basal leaves falcate to suberect, firm textured, 2–4(–5) mm wide, the midrib and margins slightly raised, hyaline when dry. *Stem* erect, unbranched. *Spike* 1–4(–5)-flowered, ± straight; *bracts* 9–13 mm long, green, the inner bract slightly shorter than the outer, 2-lobed at the tip. *Flowers* pale pink, cream in the mouth of the tube, outer tepals pale greenish with darker green veins; *perianth tube* funnel-shaped, 7–9 mm long, expanded in the upper 2 mm; *tepals* spreading horizontally, elliptic, 7–8 × ca. 3.5 mm, acute. *Filaments* ascending, 1.8–2 mm long; *anthers* ascending, 2.5–4 mm long, white, pollen white. *Ovary* oblong, ca. 3 mm long, enlarging rapidly after pollination; *style* dividing at the base of the upper part of the tube, the branches suberect, reaching to between the base and middle of the anthers, ca. 6 mm long. *Capsules* oblong, 8–12 mm long; *seeds* angular, ± prismatic, reddish brown, ca. 1.3 × 1 mm, the edges forming membranous ridges.

Flowering. February to mid March.

Distribution. South Africa, in the northern Drakensberg of Free State and KwaZulu-Natal, and probably also in Lesotho, on basalt slopes and rocky pavement in shallow damp soil.

The earliest collection of *Hesperantha brevistyla* appears to have been made by Hilliard and Burtt in 1984 on the trail from Royal Natal National Park to The Sentinel at Basuto Gate. The collection was referred by them to *H. leucantha* (as *H. candida*) without comment (Hilliard & Burtt, 1986). Plants collected nearby on the trail to The Sentinel in 1999 (*Goldblatt & Manning 11053*, MO, NBG) represent the same species, which I reluctantly identified as *H. leucantha* following Hilliard and Burtt. The following year, 2000, I found growing nearby, however, but at lower elevation on Cave Sandstone slopes, quite typical *H. leucantha* (e.g., *Goldblatt & Nänni 11232*, MO, NBG; *Goldblatt & Porter 11991*, MO, NBG), which has larger flowers with longer anthers and particularly long, spreading style branches. This population made it clear that the smaller plants growing on basalt are not this species, but represent a separate taxon that is readily characterized by small, pale pink flowers with the outer tepals pale greenish pink on the outside and veined dark green, and unusually small white anthers, 2.2–4 mm long. Perhaps the most distinctive feature of the species, which I am calling *H. brevistyla*, are the remarkably short, suberect style branches that reach to the base or lower third of the anthers. In most other species of the genus, the

Figure 4. Morphology and floral details of *Hesperantha brevistyla*. Scale bar 1 cm; single flower and seed much enlarged. Drawn by John Manning from photographs and pressed plants (*Goldblatt & Porter 11989*, MO, NBG, PRE).

laxly spreading style branches reach at least to the anther apices in the closed flower and in *H. leucantha* usually exceed the anthers by 3–4 mm.

Comparison of *Hesperantha brevistyla* with *H. leucantha* now seems inappropriate for there is no reason to regard the two species as particularly closely allied, despite the shared pale pink color of the flowers and the whitish anthers. *Hesperantha brevistyla* may, instead, be most closely allied to a second small-flowered Drakensberg species, *H. exiliflora*, which has pink flowers with a tube 3.5–5 mm long, tepals 6–8 × ca. 2.5 mm, yellow anthers 2.5–3.3 mm long, and style branches 3–3.5 mm long, reaching to between the middle of the anthers to just beyond their tips in the closed flower. This contrasts with *H. brevistyla*, which has a tube 7–9 mm long, tepals ca. 7 × 3.5 mm, white anthers 2.5–4 mm long, and style branches ca. 6 mm long, reaching to the lower third of the anthers at most.

Paratypes. SOUTH AFRICA. **Free State:** 28.28 (Bethlehem) Drakensberg Mountains, trail to The Sentinel, among rocks in wet ground (DB), 15 Feb. 1999, *Goldblatt & Manning 11053* (MO, NBG); Sentinel trail, slopes of The Pudding, in shallow wet ground, 6 Mar. 2002, *Goldblatt & Porter 11989* (MO, NBG). **KwaZulu-Natal:** 28.28 (Bethlehem) Royal Natal National Park, near Basuto Gate, ca. 7200 ft. (DB), 18 Feb. 1984, *Hilliard & Burtt 17689* (E, MO, NU); Drakensberg plateau near Mont-aux-Sources, damp flats along trail from the chain ladders to Tugela Falls, 5 Mar. 2002 (in fruit), *Goldblatt & Porter 11977* (MO, NBG, PRE).

43. Hesperantha ingeliensis Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 424. 1986. TYPE: South Africa. KwaZulu-Natal: Alfred District, Ngeli Mountain, 4 Jan. 1969, *O. M. Hilliard & B. L. Burtt 5838* (holotype, NU!; isotype, E not seen).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 421. 1986.

44. Hesperantha lactea Baker, Handbk. Irideae 151. 1892. TYPE: South Africa. KwaZulu-Natal: Verulam, Nov., *J. M. Wood 1118* (lectotype, designated by Hilliard & Burtt (1986: 431), K!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 431. 1986.

Readily identified by its creamy, sometimes palest yellow flowers with a tube 6–8.5 mm long, spreading tepals 14–20(–23) mm long, and prominent anthers up to 8 mm long, *Hesperantha lactea* is well known from coastal and near interior KwaZulu-Natal, but is actually recorded from as far south as the Transkei and from Hlobane in the Vryheid District in northern KwaZulu-Natal (Hilliard & Burtt, 1986). Like other white- or cream-flowered *Hesperantha* species of eastern southern Africa the flowers are open during the day (opening 11:45–12:30H and closing 4:40–5:15H at Inchanga, near Durban). This contrasts sharply with most white-flowered species of the genus from the southern African winter-rainfall zone, the flowers of which open in the mid to late afternoon and close long after dark, and sometimes only after midnight (Goldblatt, 1984; Goldblatt et al., in press).

45. Hesperantha inconspicua (Baker) Goldblatt, comb. nov. Basionym: *Gladiolus inconspicuus* Baker, Bull. Herb. Boissier ser. 2, 4: 1005. 1904. TYPE: South Africa, as "Transvaal, Donkerhoek, 4 Jan. 1894," but both locality and collection number, and perhaps date, are incorrect, *R. Schlechter 4188* (holotype, G!).

Plants 25–45 cm high. *Leaves* mostly 4, the lower 3 basal or subbasal, the uppermost inserted in the middle of the stem, partly to entirely sheathing, blade reaching to about the base of the spike, leathery, narrowly sword-shaped-linear, mostly 3–4.5 mm wide, the midrib and margins slightly thickened, the midrib rounded. *Stem* ± erect, often branched from the axil of the third leaf. *Spike* mostly 6–12-flowered; *bracts* green or purplish at the tips, 10–15 mm long, the inner slightly smaller than the outer. *Flowers* white, sometimes faintly flushed pink on the reverse of the outer tepals, often only on fading, unscented; *perianth tube* slender, expanded near the tip, 7–8.5 mm long; *tepals* subequal, spreading at right angles to the tube, 12–16(–18) × 6–8 mm. *Filaments* 2.5–3 mm long; *anthers* 6.5–8 mm long, cream, pollen yellow. Ovary ovoid, 2–3 mm long, style branches reaching to apex of the anthers in the closed flower. *Capsules* subglobose, 4–7 mm long; *seeds* angular-prismatic to ± ovoid, 1.5–1.8 × 1.2 mm.

Flowering. December to mid March.

Distribution. South Africa, from the Blyde River hills and Lydenburg in Mpumalanga to the Umtamvuna Gorge in southern KwaZulu-Natal.

Although known since the 1890s when it was first collected in the Transvaal by Rudolf Schlechter, *Hesperantha inconspicua* has largely been overlooked. The species was described by J. G. Baker in 1904 who referred it to *Gladiolus*. The locality and collector's number on the type are confusing, for Schlechter was not at the purported type locality, Donkerhoek, east of Pretoria, at that date but at Hammanskraal to the north. A collection bearing the same number as the type of *Gladiolus inconspicuus* is *Dicoma gerrardii* Harv. ex F. C. Wilson. Since *H. inconspicua* is not known from the vicinity of Donkerhoek or Hammanskraal and the collection number is evidently incorrect, Schlechter may be assumed to have collected the type in December 1893, when he was in the Dullstroom–Lydenburg area of Mpumalanga Province, or less likely in March 1894, when he traveled in the mountains of Limpopo Province (where the species has not been recorded). Subsequently the collection must have been mislabeled.

A later collection made by Ernest Galpin in the 1930s in the Little Berg in KwaZulu-Natal was immediately recognized as being a species of *Hesperantha* but it was not associated with Schlechter's plants. The Galpin collection from the Little Berg and a few more specimens of the species were included in *H. hygrophila* by Hilliard and Burtt (1986). *Hesperantha hygrophila* is largely a species of the KwaZulu-Natal Drakensberg, where plants grow on wet rocks or in marshes. Its leaves are distinctive among the eastern southern African species, being pale green, without the common gray bloom of most *Hesperantha* species, and the blades have thickened margins, prominent secondary veins and a raised midrib, which is flattened rather than rounded in outline and the edges of the thickened part form wings that extend outward over the laminar surface.

The vegetative aspect and flowers of *Hesperantha inconspicua* are unexceptional among the eastern southern African species of the genus except that the perianth is white, sometimes faintly flushed pink on the reverse of the outer tepals, especially on fading. That the type has not until now been associated with any species of *Hesperantha* is not surprising. Only the holotype is known, at the Geneva Herbarium, and consists of a plant mostly in bud. The single mature flower was boiled up by G. J. Lewis who at once realized it belonged in *Hesperantha*. She annotated the sheet as *H. baurii* but did not publish her conclusion. Hilliard and Burtt thought the plant might be *H. rupestris*, which has somewhat smaller white flowers, with the outer tepals usually red on the outside. Among the few other white or cream-flowered species of eastern southern Africa, *H. inconspicua* may also be confused with the coastal KwaZulu-Natal species, *H. lactea*, which has creamy-yellow flowers and dull yellow to brownish anthers and pollen. The leaves of the two species are virtually identical, both having thickened margins, a slightly raised, rounded midrib, and the other veins obscure and not visible when alive. Plants are typically fairly tall, mostly 40–60 cm high, but collections from southern KwaZulu-Natal are often smaller, sometimes no more than 15 cm high. They may be a separate taxon. One collection from Icwaka River Gorge near Port Shepstone (*van Wyk 7197*, PRU) has particularly small flowers and soft-textured leaves, and these plants are reminiscent of the Swaziland endemic *H. umbricola*, which has the tepals ca. 5 mm long, a perianth tube ca. 4 mm long, and anthers ca. 2 mm. The resemblance is probably due to convergence.

The related *Hesperantha saxicola*, which also has white flowers, often fading pink, stands out both in its shorter stature and unusual habitat, rocky outcrops and cliffs. These plants have drooping leaves and stems that are 10–18 cm long and have flexuose spikes of up to five large flowers with tepals mostly 15–16 × 7 mm and anthers ca. 4 mm long. *Hesperantha inconspicua* often has smaller flowers with tepals 12–15 mm long, but longer anthers, 6.5–8 mm long, and more flowers per spike.

Additional specimens. SOUTH AFRICA. **Mpumalanga:** 24.30 (Pilgrims Rest) 2 km from Graskop on road to Blyde River Canyon (DD), 14 Mar. 1981, *Hilliard & Burtt 14334* (NU). 25.30 (Lydenburg) marshy grassland S of Dullstroom (AC), 8 Feb. 1997, *Goldblatt 10867* (MO, NGB, PRE); vlei on farm Wanhoop, 20 Feb. 1985, *Carser s.n.* (LYD). 26.30 (Carolina) Ermelo, ½ mi. W of Vossman's Beacon (BA), 20 Feb. 1951, *Codd 6384* (PRE). **KwaZulu-Natal:** 27.30 (Vryheid) near Vryheid (DD), Jan. 1936, *Pole-Evans 3897* (PRE). 29.29 (Underberg) Cathkin Park, top of the Little Berg, under rocks (AB), 7 Mar. 1932, *Galpin 11884* (PRE); Highmoor Forest Station, in vlei (BB), *Killick & Vahrmeijer 3582* (PRE); Coleford, S of Nature reserve above Endewana River, 25 12 1976, *Hilliard & Burtt 9565* (NU). 29.30 (Pietermaritzburg) Karkloof, Mbona mountain, rocky seep (AC), Feb. 2000, *Goldblatt & Nänni 11245* (MO, NBG), 30 Dec. 2000, *Nänni 153* (NBG); 8 mi. N of Pietermaritzburg, marshy ground (CB), Nov. 1939, *Thomas 9* (NBG). 30.30 (Port Shepstone) Umtamvuna Nature Reserve, NE face of Iron Crown, damp rocks (CC), 23 Dec. 1983, *Abbott 1583* (PRU); Icwaka River Gorge, seep in shallow soil, 24 Jan. 1986, *van Wyk 7179* (PRU). 31.30 (Port Edward) Umtamvuna Waterfall (AA), 25 Oct. 1962, *Strey 4468* (PRE).

46. **Hesperantha saxicola** Goldblatt, sp. nov. TYPE: South Africa. Mpumalanga: rocks at the top of Mt. Anderson, Mar. 1933, *E. E. Galpin 13781* (holotype, PRE!; isotypes, BOL!, K!).

Plantae 10–25 cm altae ex scopulis trahentes, foliis usitate 4 plus minusve linearibus 1.5–2.2 mm latis, caule eramoso, spica 2- ad 4-flora, bracteis 10–15 mm longis, floribus albis, tubo perianthii (7–)11 mm longis, tepalis subaequalibus patentibus (11–)15–16 × 5.5–7.0 mm, filamentis 2.5–3.0 mm longis, antheris ca. 4 mm longis, ramis styli antheras excedentibus.

Plants 10–25 cm high, trailing from cliffs, simple or branched, corm with the tunics extended above as a neck of fibers. *Leaves* mostly 4, the lower 3 basal or subbasal, the uppermost inserted in the middle of the stem and partly to entirely sheathing, shorter than the basal, blades of the basal leaves reaching to about the base of the spike, soft-textured, ± linear, mostly 1.5–2.2 mm wide, the midrib and margins hardly thickened. *Stem* weak and arching toward the ground, unbranched. *Spike* 2- to 4-flowered; *bracts* green, often drying at the tips, 10–15 mm long, the inner two-thirds as long to about as long as the outer. *Flowers* white, probably unscented; *perianth tube* funnel-shaped, expanded in the upper half, (7–)11 mm long; *tepals* subequal, spreading at right angles to the tube, (11–)15–16 × 5.5–7 mm. *Filaments* 2.5–3 mm long; *anthers* ca. 4 mm long, cream, pollen yellow. Ovary ovoid, 1.5–2 mm long, *style branches* exceeding the anthers by ca. 1.8 mm in the closed flower. *Capsules* and *seeds* unknown.

Flowering. March–April.

Distribution. South Africa, in Mpumalanga, and possibly Limpopo Provinces, on wet cliffs and rock seeps.

Known to Hilliard and Burtt (1986) from a single collection (*Galpin 13781*) made in 1933, on Mt. Anderson in Mpumalanga, the species was referred by them to *Hesperantha leucantha* (which they called *H. candida*) in their study of the genus in KwaZulu-Natal and surrounding areas. That species, centered in the KwaZulu-Natal and Lesotho highlands, is generally less robust and has smaller, pale pink flowers, and except for the Mpumalanga collection they cited, does not occur along the Mpumalanga escarpment. *Hesperantha saxicola* is confined to cliffs and damp rocks and grows in rock crevices, often associated with moss. Plants have trailing stems 10–25 cm long, long linear leaves up to 2.2 mm wide, and spikes of 2 to 5 fairly large flowers. The tepals are 11–16 mm long and either uniformly white or faintly flushed with pink or mauve on the outside, while the anthers stand out in their relatively small size, ca. 4 mm long. Two more recent collections from nearby, close to the top of Long Tom Pass, *Krynauw 335* (LYD) and *Linder 3203* (PRE), closely match the Galpin plants. A collection from Mt. Sheba, a short distance to the north of Long Tom Pass, appears to belong here, but the flowers have tepals slightly flushed with purple on the outside, leaves less than 1 mm wide, and flowers with a perianth tube ca. 7 mm long and tepals ca. 11 mm long, somewhat smaller than in the populations to the south. Similar small-flowered plants with a white perianth from God's Window (*Lötter 324*, NBG) may also be this species.

A recent collection made in mid February on Formosa Mt. east of Lydenburg (*Burrows 7296*) is included here with reservation. The plants appear to have white flowers (possibly fading pale mauve) but the collection notes describe the flowers as pink-mauve. Two of the three plants of the collection have branched stems and the spikes have up to five flowers, whereas other specimens of *Hesperantha saxicola* that I have seen have unbranched stems and spikes with at most four flowers. The flowers do, however, have the distinctive short stamens with anthers only about 4 mm long. A feature not noted in other collections of *H. saxicola* is the corm, which has the tunics extended upward as a neck of fibers.

Specimens examined. SOUTH AFRICA. **Mpumalanga:** 24.30 (Pilgrims Rest) Mt. Sheba Nature Reserve (DC), Apr. 1972, *Goodman s.n.* (J). 25.30 (Lydenburg) rocks at the top of Mt. Anderson (BA), Mar. 1933, *Galpin 13781* (BOL, K, PRE); Long Tom Pass, farm De Kuilen, on low cliffs, 13 Mar. 1985, *Krynauw 335* (LYD); between the summit of Long Tom Pass and Mt. Anderson, shady cliffs, 20 Mar. 1982, *Linder 3203* (PRE); Formosa Mt., SE of look-out tower, cool SE-facing slopes in rock cracks at 2100 m, 18 Feb. 2001, *Burrows 7296* (BKH, NBG).

47. **Hesperantha hygrophila** Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 40: 278. 1982; 43: 433. 1986. TYPE: South Africa. KwaZulu-Natal: Alfred District, Ngeli Mountain, 2 Jan. 1969, *O. M. Hilliard & B. L. Burtt 5762* (holotype, E not seen; isotypes, NH!, NU!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 433. 1986.

As described by Hilliard and Burtt (1986), *Hesperantha hygrophila* has unremarkable white flowers fading pink with age and distinctive leaves, pale green in color, with the midrib, margins, and a secondary pair of veins quite clearly thickened. The midrib is flattened and the edges of the flattened ridge arch slightly over the laminar surface. Plants with this leaf type are restricted to the KwaZulu-Natal–Lesotho Drakensberg and the Ngeli range to the south. White-flowered plants from the KwaZulu-Natal Midlands and Little Berg (e.g., *Galpin 11884*, PRE, referred to *H. hygrophila*) have leaves quite typical of most other eastern southern African *Hesperantha* in their slightly raised midrib, rounded in outline, and slightly thickened margins. These plants represent another species, the earliest name for which is *Gladiolus inconspicuus*, now transferred to *Hesperantha*, the identity of which has long been uncertain. G. J. Lewis examined the type in preparation for her revision of *Gladiolus* in South Africa and referred the specimen to *H. baurii*. Apart from the leaf differences, *H. inconspicua* is generally more robust than *H. hygrophila*, has many flowers per spike (up to 16 in plants from *Goldblatt & Nänni 11245*, MO, NBG), and sometimes has the stem branched in the axil of the third leaf.

This narrower definition of *Hesperantha hygrophila* leaves the species fairly uniform as regards vegetative morphology. The flowers are usually white, but specimens collected at Highmoor (*Goldblatt & Nänni 11248*) have pale pink flowers, otherwise identical to typical *H. hygrophila* both vegetatively and florally. The flowers of this population open between 8:30 and 9:00H and close again by 12:30H.

Hesperantha hygrophila may also be confused with the cream(or pale yellow)-flowered *H. lactea*, which grows in drier, well-drained grassland at altitudes of up to 800 m, rather than on wet rocks and scree in mountains mostly above 2000 m (Hilliard & Burtt, 1986). In *H. lactea* the anthers are deep yellow to light brown and tend to dry a brownish color, a feature that conveniently separates it from *H. hygrophila* in which the pale cream anthers remain pale when dry. The differences in leaf venation also separate the two, but this feature is not always easy to see in dried specimens.

48. Hesperantha rupestris N. E. Br. ex R. C. Foster, Contr. Gray Herb. 166: 23. 1948. TYPE: South Africa. Mpumalanga: Waterval Boven, among rocks, 29 Mar. 1929, *C. E. Moss 17314* (syntypes, K!, PRE!).

A fairly robust species, plants sometimes standing 45–50 cm high, *Hesperantha rupestris* is distinguished from the closely allied *H. baurii* in having white flowers, the outer tepals flushed dark pink to red on the outside, as well as in the height of the stem. It is restricted to rocky habitats in the central Mpumalanga highlands. As in most other eastern southern African *Hesperantha* species in which the timing of flower opening is known, the flowers of *H. rupestris* are diurnal, being open in the morning, according to information on some herbarium sheets.

49. Hesperantha modesta Baker, Handbk. Irideae 150. 1892. TYPE: South Africa. KwaZulu-Natal: Umlaas Location [or Bevaan River on the type at K, evidently in error], 17 July 1885, *J. M. Wood 3201* (holotype, K!; isotype, NH not seen).

Plants mainly 15–25 cm high, erect, unbranched. *Corm* conic, 7–9 mm diam. near the base, with woody tunics soon breaking into elliptic segments tapering above into short points. *Leaves* 3, occasionally 4, the lower 2 basal and longest, reaching to about the middle of the stem, the upper one (or two) leaves smaller, 4.5–6 mm long, inserted in the lower third to middle of the stem, sheathing for most of their length, with a short free tip, the blades ± linear, 2–3 mm wide, firm and erect, the midrib and margins slightly raised. *Spike* lax, mostly 2–3-flowered; *bracts* 12–15 mm long, green, the inner bracts about two-thirds as long as the outer, translucent with 2 green keels, shortly forked at the tip. *Flowers* bright mauve-pink, pale yellow in the mouth of the tube; *perianth tube* 6–9 mm long, cylindrical, expanded near the mouth; *tepals* spreading, elliptic, 10–15 × 3.5–5 mm, acute. *Filaments* erect, ca. 3 mm, inserted on the tepals above the mouth of the tube, decurrent; *anthers* diverging, ca. 5 mm long, shortly tailed, yellow, pollen yellow. *Ovary* oblong, ca. 2.5 mm long; *style* branches reaching to the anther apices in bud, ca. 10 mm long, laxly spreading in the open flower. *Capsules* and *seeds* unknown.

Flowering. August to October.

Distribution. South Africa, KwaZulu-Natal and coastal Transkei in the sandstone belt from Durban to Port St. Johns, possibly also in Zululand near Eshowe, in marshy grassland, vlei edges, and stream banks.

A full description of *Hesperantha modesta* is presented here because it was included in *H. baurii* by Hilliard and Burtt (1986) and no complete description is available. It is difficult to assess the immediate relationships of this spring-flowering species for its unremarkable morphology suggests no particular affinity, except a general one to the *H. baurii* complex of eastern southern African grassland species. It can, however, readily be recognized by the presence of just three or sometimes four leaves, the lower two basal and with long blades, and the upper one or two inserted on the stem and short and largely sheathing. The leaf blades have a fairly soft texture and slightly thickened margins and midrib. Plants flower in late winter and spring. Other species in the *H. baurii* alliance flower in the summer and typically have four, or sometimes five leaves, usually three of them basal or subbasal. An exception, *H. baurii* subsp. *formosa*, has either three or four leaves, but this is a high Drakensberg plant that flowers in January and February and has a large, deep pink perianth. The flowers of *H. modesta* are relatively large, in the middle of the range found in *H. baurii*, but judging from the available specimens it appears unusual in having only two to four flowers per spike. So few flowers per spike, even when associated with a relatively robust plant body, the unusual leaf number, and late winter to spring flowering make it clear that these plants should be recognized as a separate species, when the criteria for distinguishing species in *Hesperantha* are followed.

There is confusion about the type locality of *Hesperantha modesta* for the isotype at the KwaZulu-Natal Herbarium has the locality, Umlaas location, whereas the sheet at K with the same number and date is purportedly from the Bevaan river. The latter, in the interior in the Vryheid District, seems unlikely for any spring-flowering *Hesperantha* bearing foliage leaves at flowering time. The discrepancy was noted by Hilliard and Burtt, who were not able to resolve this conflict after examining Wood's collecting registers. *Hesperantha modesta* was provisionally included in *H. baurii* by Hilliard and Burtt, although they discussed it and a few collections of like plants separately.

I concur with Hilliard and Burtt's observation that *Hesperantha subexserta* (Baker, 1896), based on a Medley Wood collection from Botha's Hill in the sandstone hills between Pietermaritzburg and Durban, flowering in October, may also belong here. These plants have two basal leaves, and one or two cauline, sheathing leaves of the soft texture typical of *H. modesta*, but the spike of one of the plants of the type collection has up to eight flowers and a short lateral branch. Other specimens of *H. modesta* have two or three, or at most four flowers per spike. Plants resembling *H. subexserta* should be sought again at the type locality, no great distance from Umlaas Location where the type collection of *H. modesta* was most likely made.

A collection from Eshowe, Zululand (*Lawn 1179*, NH), well to the north of the recorded range of *Hesperantha modesta*, is provisionally included here. The rather poor condition and crowded mounting of the specimens makes them difficult to identify for certain, but the flowering time, October, and marshy habitat, suggest this species.

Additional specimens. SOUTH AFRICA. **KwaZulu-Natal:** 28.31 (Nkandhla) Reservoir Marsh, Eshowe (CD), 3 Oct. 1949, *Lawn 1179* (NH). 31.30 (Port Edward) Mtamvuna Nature Reserve, marsh at Etheldale (AA), 11 Oct. 1986, *Goldblatt 7897* (E, MO). **Eastern Cape**: 31.29 (Port St. Johns) Ntsubane Forest Station, near Fraser falls, seepage area in peaty sand (AC), 22 Aug. 1976, *Venter & Vorster 39* (K, PRE); near Magwa, junction of Magwa Falls–Mbotyi roads (BC), 23 Aug. 1984, *Balkwill, Manning & Gettliffe Norris 1914* (NU); 3 mi. inland from Port Grosvenor, in a bog (BD), 23 Aug. 1969, *Strey 8894* (PRE).

50. Hesperantha umbricola Goldblatt, S. African J. Bot. 53: 459. 1987. TYPE: Swaziland. Near Mbabane, among rocks, 21 Feb. 1982, *P. Goldblatt 6610* (holotype, MO!; isotypes, E!, K!, NBG!, NU!, PRE!, S!).

The tiny white flowers of *Hesperantha umbricola*, only ca. 11 mm long, with a perianth tube ca. 4–5 mm long, tepals 5–6 mm long, and anthers 2–3 mm long, make the species unmistakable in the genus. Like other white-flowered species of *Hesperantha* in eastern southern Africa, flowering is diurnal. There appear to be no records of the species other than the type collection. I suspect that *H. umbricola* is allied to the white-flowered *H. inconspicua*, but its much smaller flowers that do not fade pink, and narrow, soft-textured leaves seem to confirm that it is indeed a separate species.

51. Hesperantha gracilis Baker, Handbk. Irideae 149. 1892. TYPE: South Africa. KwaZulu-Natal: base of perpendicular rocks at Isangwaan, Apr., *J. M. Wood 923* (holotype, K!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 422. 1986.

52. Hesperantha pubinervia Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 419. 1986. TYPE: South Africa: KwaZulu-Natal, Royal Natal National Park, Mont-aux-Sources, Feb. 1927, *Prescott-Decie s.n.* (holotype, BOL!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 419. 1986.

Plants 12–30 cm high, erect, unbranched. *Corm* conic, 7–9 mm diam. near the base, with woody tunics soon breaking into elliptic segments tapering above into short points. *Leaves* 4, the lower 2 basal, the upper smaller and partly to entirely sheathing, the blade ± linear, 2.5–3.5 mm wide, ± erect, with scabrid hairs on the margins, midrib, and secondary veins, the midrib prominently thickened, the margins less so. *Spike* 1–3(–4)-flowered; *bracts* 20–24 mm long, green. *Flowers* dull salmon pink, pale yellow-green in the mouth of the tube edged in darker salmon; *perianth tube* 20–25 mm long, unusually slender, the hollow interior filled by the style and without nectar; *tepals* spreading at right angles to the tube, 14–18 × 3.5 mm, subacute. *Filaments* erect, ca. 5 mm long; *anthers* erect and ± contiguous, ca. 4.5 mm long, pollen yellow. *Ovary* narrowly ovoid, ca. 4 mm long; *style branches* remaining suberect in the open flower, ca. 6 mm long, reaching to about the upper third of the anthers and emerging between them. *Capsules* oblong, (10–)12–14 mm long; *seeds* angular-prismatic, ca. 1.2 × 1.0, the edges forming membranous ridges.

Flowering. February and March.

Distribution. South Africa and probably Lesotho, in the high northern Drakensberg on the slopes below The Sentinel and on the Mont-aux-Sources plateau, in rocky grassland.

Growing along a well-used path to The Sentinel and Mont-aux-Sources in eastern Free State and adjacent KwaZulu-Natal, *Hesperantha pubinervia* nevertheless seems to have been overlooked there, which makes it appear that this area of the Drakensberg is poorly collected. My observations in general confirm the original description made from just one gathering. However, one feature, the length of the style branches, is not consistent with the protologue, for plants on the slopes of The Sentinel have ascending style branches shorter than the stamens and about 6 mm long, less than the 11 mm length recorded by Hilliard and Burtt. The style branches reach to the upper third of the anthers and in one flower, perhaps not fully developed, only to the anther bases. The tepals are an unusual salmon pink, unique in the genus. The color contrasts markedly with the deep pink to magenta flowers of sympatric and co-blooming *H. baurii* and *H. scopulosa,* and with the pale pink flowers of *H. brevistyla.*

The capsules, not previously described, are oblong and about as long as the bracts, mostly 12–14 mm long. The numerous seeds are angular (prismatic) and about 1 mm long. The specimens on which the amplified description are based are cited below.

Additional specimens. SOUTH AFRICA. **Free State:** 28.28 (Bethlehem) Drakensberg, slopes of The Sentinel (DB), 15 Feb. 1999, *Goldblatt & Manning 11052* (MO, NBG, PRE), 29 Jan. 2000, *Goldblatt & Nänni 11227A* (NBG). **KwaZulu-Natal:** rocky slopes on plateau along trail from the chain ladders to Tugela Falls, 5 Mar. 2002 (fr), *Goldblatt & Porter 11977* (MO, NBG, PRE).

53. Hesperantha pulchra Baker, Handbk. Irideae 150. 1892. TYPE: South Africa. Eastern Cape: Transkei, Baziya Mountain, Apr., *L. R. Baur 159* (holotype, K!; isotype, B!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 413. 1986.

Extending from the Amatola Mountains of the Eastern Cape north through the Transkei to Naude's Nek, the late-flowering *Hesperantha pulchra* has until now seemed fairly well understood. It is readily recognized by the bright pink flowers, relatively short filaments, 3–6 mm long, and perianth tube of intermediate length, 15–20 mm long (14–28 mm, according to Hilliard & Burtt, 1986). Plants from KwaZulu-Natal, north of the Tugela River, which Hilliard and Burtt mentioned as like *H. pulchra* but with a tube ca. 15 mm long (*Gerstner 6713,* PRE) and ca. 12 mm (*Fakude 3,* NH), fit uncomfortably in this otherwise Eastern Cape species. We need to know more about the Zululand plants, which could perhaps be accommodated in *H. baurii* equally well except for the late flowering, in April and May. I hesitate to treat these populations as representing an undescribed taxon given our current knowledge about *H. pulchra.*

An interesting collection from Mt. Thomas, near Stutterheim in the Amatola Mountains (*McMaster s.n.,* NBG), collected in later flower on 11 February, with ripe capsules at the base of the spike, resembles *Hesperantha pulchra* except for the early flowering. Plants have narrowly elliptic capsules 25 mm long that contain large seeds, up to 4 mm long with the wings at either end ca. 1 mm long and the seed body ca. 2 mm long. Capsules of *H. pulchra* are described by Hilliard and Burtt as 10–17 mm long with seeds ca. 1.25 mm in diameter, with weakly or strongly developed wings. The Mt. Thomas plants may represent a novelty.

Echoing Hilliard and Burtt's remark regarding *Hesperantha pulchra,* we need to know more about both the Zululand and Mt. Thomas plants. Additional collections, especially in fruit, will be helpful in understanding the range of variation in this species.

54. Hesperantha woodii Baker, Handbk. Irideae 150. 1892. TYPE: South Africa. KwaZulu-Natal: Richmond district, Peak of Byrne, Apr. or May 1883, *J. M. Wood 1868* (isotypes, K!, NH!). Figure 5A.

Hesperantha galpinii R. C. Foster, Contr. Gray Herb. 166: 13. 1948. Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 426. 1986, pro syn. *H. grandiflora.* TYPE: South Africa. Lesotho, valley above Buffalo River falls, 14 Mar. 1904, *E. E. Galpin 6856* (lectotype, designated here, BOL!; isotypes, B!, GRA not seen, K!, NH not seen, PRE!, SAM!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 413. 1986.

Plants 20–45 cm high, erect, unbranched. *Corm* conic, 8–10 mm diam. near the base, with woody tunics soon breaking into triangular segments tapering above into short points. *Leaves* usually 4, the lower 2 basal, longest, reaching to between the middle of the stem and the apex of the spike, the upper smaller and partly to entirely sheathing, the

Figure 5. —A. Flowers of *Hesperantha woodii* (*Goldblatt & Manning 11054*, MO, NBG, from Naude's Nek). —B. Flowers of *H. grandiflora* (*Goldblatt & Porter 11976*, MO, NBG, from The Sentinel). Compare suberect flowers with barely curved perianth tube and large, pale-colored anthers of *H. woodii* with the secund flower with strongly curved perianth tube and darkly colored anthers of *H. grandiflora*.

blades ± linear, 2–3 mm wide, firm and erect, the midrib prominently raised, the margins slightly thickened. *Spike* mostly 2–4-flowered; bracts 22–30 mm long, green, becoming dry and brownish above. *Flowers* bright mauve-pink, pale yellow in the mouth of the tube; *perianth tube* (18–)22–38 mm long, cylindrical, slightly curving toward the apex, expanded near the mouth, with nectar in the base; *tepals* weakly ascending, elliptic, 23–27 × 6–7.5 mm, acute. *Filaments* ascending, 6–8 mm long; *anthers* diverging, 9–10 mm long, tailed in the lower 2 mm, yellow, pollen yellow. *Ovary* ellipsoid, 6–8 mm long; *style branches* 18–20 mm long, longer than the stamens, laxly spreading. *Capsules* oblong, 16–18 mm long; *seeds* unknown.

Flowering. February and March.

Distribution. Southern Lesotho and South Africa in KwaZulu-Natal and the Eastern Cape, on stony slopes and rocks often near streams and in montane habitats.

Living plants of a long-tubed *Hesperantha* (Fig. 5A) in the southern Drakensberg near Naude's Nek in Eastern Cape Province proved difficult to identify using Hilliard and Burtt's (1986) key, which led me first to *H. grandiflora*, a species with a curved, elongate perianth tube (26–)33–55 mm long, and zygomorphic flowers with unilateral stamens and style branches. The Naude's Nek plants, however, had actinomorphic flowers with symmetrically disposed stamens and style branches, but a weakly curved perianth tube. They seemed to closely match *H. galpinii*, a species regarded as a synonym of *H. grandiflora* by Hilliard and Burtt, and careful examination of the type material shows that *H. galpinii* probably does not have a zygomorphic flower and nor do a few similar specimens cited under *H. grandiflora*. The type locality of *H. galpinii* cannot easily be revisited to examine plants there, and the question of stamen and style branch orientation cannot be readily resolved.

Subsequent comparison of several collections matching *Hesperantha galpinii* led me to *H. woodii*. It became clear that specimens such as *McClean 763* (PRE), which have flowers with a perianth tube 26–32 mm long, assigned by Hilliard and Burtt to

H. woodii, closely match *H. galpinii* and that this species should be regarded as a synonym of *H. woodii* rather than *H. grandiflora* to which it was referred by Hilliard and Burtt. Although the dimensions of the perianth tube in *H. woodii* are 14–28 mm according to Hilliard and Burtt's circumscription of the species, the majority of specimens they cited have a tube exceeding 20 mm and I have seen none with a tube less than 18 mm long. Perianth tube length in the type collection is ca. 20 mm. The addition of *H. galpinii* and some longer-tubed plants from Naude's Nek to *H. woodii* thus leaves the definition of that species little changed, although the upper extreme of the perianth tube becomes 38 mm. *Hesperantha woodii* can be distinguished from *H. grandiflora* by tepal, stamen, and style branch orientation, rather than by perianth tube length, which overlaps too much to be useful in comparing the two species (Fig. 5). *Hesperantha grandiflora* has a perianth tube (26–)33–55 mm long, strongly curved at the apex, vertically oriented tepals, and unilateral, declinate stamens and style branches.

The geographic range of *Hesperantha grandiflora* extends from The Sentinel in the north through the Drakensberg to Mt. Currie (the type locality) in the south, and to Naude's Nek and Barkly Pass in the west. Thus both *H. grandiflora* and *H. woodii* occur in the Naude's Nek area and in the mountains above Kokstad. The transfer of specimens matching *H. galpinii* to *H. woodii* extends the geographical range of the species very little, for *H. woodii* has already been recorded at Mhlahlane, near Umtata in the Eastern Cape, although not from southern Lesotho.

Examination of collections at the herbaria at Kew and Zurich has revealed an interesting historical record for *Hesperantha woodii, Drège 4540,* which must have been gathered in 1832 when J. F. Drège traveled overland from Grahamstown to Port Natal (Gunn & Codd, 1981). Thus, Drège may be credited with the discovery of the species, although Wood's specimens, gathered in 1883, are the type and he is commemorated in the name of the species.

Additional specimens. LESOTHO. 28.30 (Matatiele) summit slopes of Maquaba peak, near Quacha's Nek (BA),13 Mar. 1936, *Galpin 14247* (K). SOUTH AFRICA. **KwaZulu-Natal:** 29.29 (Underberg) Cobham Forest Station, Sipongweni Caves (CC), 13 Apr. 1972, *Hilliard 5509* (K, NU); river banks, Underberg, Mar. 1938, *McClean 753* (K, PRE); Polela, Glengarif, Marwaqa, 26 Mar. 1977, *Rennie 815* (NU); Sunset Farm, Polela District, 17 Feb. 1979, *Rennie 1006* (NU). **Eastern Cape:** 30.28 (Matatiele) 1–2 km W of Naude's Nek, Feb. 1999, *Goldblatt & Manning 11054* (K, MO, NBG, PRE).

55. Hesperantha stenosiphon Goldblatt, sp. nov. TYPE: South Africa. Eastern Cape: Stutterheim district, Moonstone farm, steep grassy slope, 1120 m, 20 Mar. 2001, *C. McMaster s.n.* (holotype, NBG!; isotypes, MO!, PRE!). Figure 6.

Plantae 25–50 cm altae eramosae, cormo globoso ca. 12 mm diam., foliis 4 inferioribus duabus basalibus, ensiformibus 2–3 mm latis, spica (2–)4–8(–12)-flora, bracteis 18–24 mm longis, floribus roseis albescentibus prope orem tubi, perianthii tubo 45–60 mm longo recto, tepalis 18–21 × 7–8 mm, filamentis ca. 3 mm longis, antheris 9–10 mm longis, ramis styli ca. 8.5 mm longis.

Plants 25–50 cm high, erect, unbranched. *Corm* globose, ca. 12 mm diam., with woody tunics soon breaking into segments tapering above into short points. *Leaves* usually 4, the lower 2 basal, longest, reaching to between the middle of the stem and the apex of the spike, the upper smaller and partly to entirely sheathing, the blades ± linear, 2–3 mm wide, firm and erect, the midrib and margins slightly thickened. *Spike* (2–)4–8(–12)-flowered; bracts 18–24 mm long, green, becoming dry and brownish near the tips. *Flowers* bright pink, whitish in the mouth of the tube; *perianth tube* 45–60 mm long, cylindrical, slightly curved or straight, barely expanded near the mouth; *tepals* ascending, elliptic, 18–21 × 7–8 mm, subacute. *Filaments* suberect, ca. 3 mm long; *anthers* diverging, 9–10 mm long, dark brown to blackish, pollen yellow. *Ovary* ovoid, ca. 3.5 mm long; *style branches* ca. 8.5 mm long, in the closed flower reaching to just below the anther apices. *Capsules* and *seeds* unknown.

Flowering. March and April.

Distribution. Eastern Cape, Cathcart district, among rocks partly shaded by bush and small trees or in rocky grassland on hill tops.

Evidently unknown until 2000, the striking, long-tubed *Hesperantha stenosiphon* was discovered by the naturalist, Cameron McMaster, in the Cathcart area of Eastern Cape Province, South Africa. The plant is probably most closely allied to the long-tubed *H. grandiflora* and *H. woodii* and shares with them the linear leaves with slightly to moderately thickened margins and midribs as well as the pink perianth with an elongate tube, usually more than 20 mm long. *Hesperantha stenosiphon* is readily recognized by the symmetrically arranged stamens with unusually short filaments, only about 3 mm long, long blackish anthers, and spike of (2 to)4 to 9 flowers. *Hesperantha grandiflora* has flowers that face to the side with vertically oriented tepals and unilateral, downcurving stamens and style branches, filaments 8–14 mm long, and brown anthers and pollen, while *H. woodii* has similarly

Figure 6. Morphology and floral details of *Hesperantha stenosiphon*. Scale bar 1 cm. Drawn by John Manning from photographs and pressed plants (*Goldblatt & Porter 12005* (K, NBG, MO, PRE).

large, but nearly upright flowers, symmetrically disposed stamens with filaments 6–8 mm long, and yellow anthers and pollen. The two latter species have flowers with a perianth tube (18–)22–55 mm long, whereas *H. stenosiphon* has a tube 45–60 mm long. The elongate perianth tube suggests that the flowers are pollinated by the long-proboscid fly, *Prosoeca ganglbaurii*, which also pollinates *H. grandiflora* and *H. woodii* (Goldblatt & Manning, 2000; Goldblatt et al., in press). At the Bombazi locality where plants were common and in full bloom, however, I found no long-proboscid flies, but flowers were instead visited by honey bees, which collected pollen after failing to reach the nectar contained in the lower part of the perianth tube, well beyond the reach of their tongues.

Common at the two sites where it is recorded, *Hesperantha stenosiphon* is nevertheless rare, and appears to be restricted to the hills east of the main Amatola range that extend toward the valley of the Great Kei river. Plants are mostly confined to dolerite outcrops on the upper slopes and summits of these hills where they seem to prefer partly shaded situations close to shrubs and small trees.

Paratypes. SOUTH AFRICA. **Eastern Cape:** 33.26 (Stutterheim) Cathcart district, ca. 50 km NE of Stutterheim, Bombazi farm, Mar. 2001, *McMaster s.n.* (NBG), 8 Mar. 2002, *Goldblatt & Porter 12005* (K, NBG, MO, PRE); Bolo district, Moonstone farm, on steep grassy slopes, 1076 m, 27 Feb. 2002, *McMaster s.n.* (MO).

56. Hesperantha coccinea (Backh. & Harv.) Goldblatt & J. C. Manning, Novon 6: 263. 1996. *Schizostylis coccinea* Backh. & Harv., Curtis's Bot. Mag. 90: pl. 5422. 1864. TYPE: South Africa. Eastern Cape: without precise locality, Curtis's Bot. Mag. 90: pl. 5422. 1864.

With a flower structure exactly like that of any *Hesperantha* species, and virtually identical, except in the red color, to that of long-tubed species like *H. woodii*, *H. coccinea* seems well placed in the genus to which it was transferred in 1996 (Goldblatt & Manning, 1996). *Hesperantha coccinea* was long regarded as the sole species of a separate genus, *Schizostylis*, distinguished in subfamily Crocoideae by its rhizomatous rootstock. A plant of stream banks and marshes, *H. coccinea* is believed to have lost its corm because this xeromorphic feature is not adaptive in such mesic conditions. Curiously, the aerial leaf axils of some populations produce a small corm of the asymmetrical shape typical of *Hesperantha*. There are two color morphs of *H. coccinea*, the typical, and more widespread red form, which extends from the Amatola Mountains in Eastern Cape Province, South Africa, to Zimbabwe, and a pink form local in the northern Drakensberg and Witwatersrand in Gauteng Province. The name *Schizostylis pauciflora* has been applied to plants from Witpoortjie in the western Witwatersrand that are depauperate and have spikes of few flowers. Unusual for *Hesperantha*, the common red-flowered form of *H. coccinea* is pollinated by a guild of large butterflies of the families Papilionidae (*Papilio* spp.) and Satyridae (*Aeropetes tulbaghia*) (Goldblatt et al., in press).

Seeds of *Hesperantha coccinea*, not previously described, are unusual in the genus. Approximately 2 × 1.2 mm, the more or less prismatic (segmental) seeds have a loose, translucent, light brown seed coat with a smooth outline, but with slightly developed ridges on the angles of the segments. Within the translucent coat a small, more or less spherical seed body, ca. 1 mm in diameter, is evident. The surface cells of the seed coat are aligned in straight files and have a domed (colliculate) outer wall and appear empty. This seed is somewhat aerodynamic and will float for some time before becoming waterlogged. The seed is evidently adapted for dispersal by water, a not unexpected adaptation in this semi-aquatic plant. Other species of *Hesperantha* have a seed coat that closely envelops the seed body, but other features conform to the pattern described for the genus (Goldblatt & Wagner, 1984).

57. Hesperantha grandiflora G. J. Lewis, J. S. African Bot. 7: 30. 1941. *Acidanthera tysonii* Baker, Handbk. Irideae 187. 1892, non *H. tysonii* Baker (1892), = *H. radiata* (Jacq.) Ker Gawl. TYPE: South Africa. KwaZulu-Natal: waterfall near Mt. Currie, Apr. 1883, *W. Tyson 1151* (= Herb. Norm. Austro-Afr. 895) (holotype, K!; isotypes, BOL!, NBG!, PRE!). Figure 5B.

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 410. 1986.

One of the most distinctive of the species of pink-(or red-)flowered *Hesperantha* of eastern southern Africa that have flowers with an elongate perianth tube at least 15 mm long, the high Drakensberg *H. grandiflora* is easily recognized by its flowers with a perianth tube (26–)33–55 mm long, curved outward near the apex and tepals held more or less vertically (Fig. 5B). It also has unilateral stamens and style branches that are declinate, thus arching downward above the lower (abaxial or anterior) tepal. A feature of *H. grandiflora* not recorded in the literature is that it has reddish brown anthers and pollen, whereas most other species have yellow or cream to whitish pollen. The darkly colored pollen is still evident in the type collection after more than 100 years, and I have confirmed this feature in living plants seen at Sani Pass, Giants Castle Pass, on The Sentinel trail on the Free State–KwaZulu-Natal border, and at Barkly Pass in Eastern Cape Province (Fig. 5B). Plants from the latter two localities constitute range extensions to the north and west of the range of *H. grandiflora* and represent the first record of the species from the Free State. Seeds of this population conform to the description given by Hilliard and Burtt (1986): they are 1.5–2 mm long and have a small wing at opposite ends of the globose seed body ca. 0.8 mm long (the seed is described as 1–1.5 mm diam. by Hilliard & Burtt).

Examination of living plants collected in the southern Drakensberg near Naude's Nek Pass has shown that *Hesperantha grandiflora* as circumscribed by Hilliard and Burtt included plants with more or less upright flowers, a weakly curved tube and symmetrically disposed, ascending stamens, quite different from *H. grandiflora.* As explained above, these plants are better referred to *H. woodii* as is *H. galpinii,* which was treated as a synonym of *H. grandiflora* by Hilliard and Burtt.

A collection at the Kew Herbarium made by J. F. Drège in 1832 is almost certainly this species, and represents the earliest record of *Hesperantha grandiflora.* The specimen is identified as "*Gladiolus spilanthus,*" a later synonym for the Western Cape *G. gracilis,* but has no specific locality information and it does not appear to be listed in the report of Drège's travels (Meyer, 1843).

Additional specimens. SOUTH AFRICA: **Free State–KwaZulu-Natal:** 28.28 (Bethlehem) grassy slope on road to The Sentinel trail along Free State–KwaZulu-Natal border (DB), 4 Mar. 2002, *Goldblatt & Porter 11976* (MO, NBG). **Eastern Cape:** 31.27 (Lady Frere) Barkly Pass, moist gully on Cave Sandstone slope near top of pass (BB), 6 Mar. 2002, *Goldblatt & Porter 11995B* (MO, NBG).

58. Hesperantha huttonii (Baker) Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 40: 278. 1982. *Acidanthera huttonii* Baker, J. Bot. 14: 339. 1876. TYPE: South Africa. Eastern Cape: Stockenstrom Division, Katberg, date unknown, *H. Hutton s.n.* (holotype, K!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 415. 1986.

A species of shady rock outcrops and forest margins, *Hesperantha huttonii* has long been thought to be restricted to the Amatola Mountains between Stutterheim and Adelaide in Eastern Cape Province, South Africa. Apart from the long-tubed, pale pink flowers with large yellow anthers, 7–10 mm long, it can be recognized by the fairly broad, flaccid, drooping leaves, suberect to drooping stem, and the presence of a cormlet in the axils of the lower leaves (Hilliard & Burtt, 1986). Plants from coastal Transkei (*Flanagan 2514,* PRE; *Cloete 1661,* NH), some 250 km to the east, best match the species. However, the Flanagan collection appears to lack axillary cormlets and has a perianth tube ca. 23 mm long, while the Cloete collection has flowers with a tube 15–17 mm long. *Hesperantha huttonii* typically has a tube 30–39 mm long with a lower limit 21 mm. Provisionally, the Transkei plants must be included in *H. huttonii* until more information becomes available.

The seeds of this species are distinctive. Borne in capsules 12–20 mm long, they are approximately 2.5–3.5 mm long and ca. 1.25 mm wide, and have a membranous wing at either end, the wings each about half as long as the seed body, which is about 1.2–1.5 × 1 mm (*Goldblatt & Porter 12011,* MO, NBG, from the Kologha Forest, near Stutterheim). Slightly smaller seed dimensions, ca. 1.5 × 1.25 mm, provided by Hilliard and Burtt (1986), probably indicate variation in seed size across populations of the species. The seeds recall those of *Gladiolus,* which have a broad circumferential wing (Goldblatt & Manning, 1998).

The long-tubed flowers of *Hesperantha huttonii* are pollinated by the long-proboscid nemestrinid fly, *Stenobasipteron wiedmannii,* which has been recorded visiting the species in the Kologha Forest (Goldblatt et al., in press). This fly has a proboscis 19–23 mm long, thus well suited to acquire pollen loads on its thorax as it probes the perianth tubes of *H. huttonii,* which are 23–35 mm long at this site and contain nectar at the base. Indirect evidence for the pollination of *H. huttonii* by the same fly has been recorded by Potgieter and Edwards (pers. comm.) who found pollen of *H. huttonii* on a fly caught visiting *Plectranthus ciliatus* E. Mey. ex Benth. as well as *Plectranthus* pollen on *Hesperantha* anthers, presumably carried there by *Stenobasipteron,* an important pollinator of *Plectranthus* species.

Additional specimens. SOUTH AFRICA. **Eastern Cape:** 31.29 (Port St. Johns) Lusikisiki, Lupatana, sandstone cliff face above the river, ca. 15 m, in mats of moss (BD), 20 Dec. 1991, *Cloete 1661* (NH); Port St. Johns, *Flanagan 2514* (PRE).

59. Hesperantha hutchingsiae Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 414. 1986. TYPE: South Africa. Eastern Cape: Transkei, Mhlahlane Forest Station, Mjika, 21 Mar. 1985, *A. Hutchings & Plumstead 1621* (holotype, E not seen).

When first described by Hilliard and Burtt (1986), *Hesperantha hutchingsiae* was known only from the type collection from a marsh at Mhlahlane near Umtata. A second collection has come to hand from near Naude's Nek some distance to the east. This collection, *Strever 755,* has three flowers per spike, and the flowers have a perianth tube 23 mm long. In the type collection the spike has only two flowers and the perianth tube is 21 mm long. The new record slightly expands the range of variation in the species. Notes on the Strever collection indicate that the anthers are dark purple, an unusual character in the genus, but recorded in *H. grandiflora* and *H. stenosiphon,* both of which have large flowers with a substantially longer perianth tube, (26–)33–55 mm long in *H. grandiflora* and 45–60 mm long in *H. stenosiphon.*

Additional specimens. SOUTH AFRICA. **Eastern Cape:** 30.28 (Matatiele) valley of Lehana's Pass, Naude's Nek, moist area on S slope below dolerite rocks (CA), 17 Mar. 1988, *Strever 755* (NU).

60. Hesperantha brevicaulis (Baker) G. J. Lewis, J. S. African Bot. 6: 30. 1941. *Acidanthera brevicaulis* Baker, Fl. Capensis 6: 132. 1896. TYPE: South Africa. Barberton, Devil's Bridge, Makwonga Range, Mar. 1891, *E. E. Galpin 1252* (holotype, K!).

Plants 10–25 cm high, the stem drooping, unbranched. *Corm* conic, 7–9 mm diam. near the base, tunics unknown. *Leaves* 4, occasionally 5, ± linear, 2–4 mm wide, the lower with fairly soft-textured blades trailing distally, the midrib slightly raised, the uppermost leaf largely to entirely sheathing. *Spike* mostly 2–3(–4)-flowered; *bracts* green, soft-textured, the outer 20–28 mm long. *Flowers* dull mauve-pink, pale yellow in the mouth of the tube; *perianth tube* (18–)22–35 mm long, cylindrical, slightly curving toward the apex and expanded near the mouth, with nectar in the base; *tepals* spreading ± at right angles to the tube, 20–25 × 7–8 mm, subobtuse. *Filaments* ascending, 5–8 mm long; *anthers* diverging, 6–10 mm long, pollen yellow. *Ovary* 4–5 mm long; *style branches* laxly spreading, 12–15(–20) mm long, alternating with the stamens and exceeding them in the closed flower. *Capsules* narrowly ovoid, 15–20 mm long; *seeds* unknown.

Flowering. March to May, sometimes in February.

Distribution. South Africa, Mpumalanga and Limpopo Provinces, along the eastern escarpment on steep rocks and cliffs, the corms growing in damp moss and in rock crevices.

Although the type collection of *Hesperantha brevicaulis* is from the mountains near Barberton in Mpumalanga Province, and has somewhat longer stamens than more recent collections from the Sabie–Graskop part of the Escarpment some 90 km to the north, there seems no difficulty in regarding all these collections as a single species, the only long-tubed, pink-flowered member of the genus from the northern provinces of South Africa. Hilliard and Burtt (1986) concluded that it differed from all of the long-tubed species treated in their account of the KwaZulu-Natal, Lesotho, and Eastern Cape species of the genus, but Retief and Herman (1997) did not include *H. brevicaulis* in their flora of the northern provinces of South Africa. *Hesperantha brevicaulis* flowers relatively late in the season and is seldom seen before the last week of March. Like other species of the genus with similar, long-tubed flowers, it appears to be adapted for pollination by long-proboscid flies. The nemestrinid fly *Stenobasipteron wiedmannii* has been recorded visiting the species at God's Window near Graskop (Goldblatt & Manning, 2000).

Plants from the Wolkberg in Limpopo Province (*Davidson 3153,* J; *Goldblatt & Porter 11953,* MO, NBG) seem at first to represent this species, but they flower earlier in the season, beginning to bloom as early as the middle of February. They also have flowers with a somewhat shorter perianth tube, 13–16 mm, compared with (18–)22–28 mm for the Sabie–Graskop populations and ca. 35 mm in the type, from Barberton. Provisionally I include the Wolkberg populations in *Hesperantha brevicaulis.* Plants from Serala have the following features that seem to differ significantly from populations to the south: bracts (11–)15–18 mm long, the inner about two thirds as long; flowers with a perianth tube 13–16 mm long; tepals 20–22 × 7–9 mm; filaments (4–)5–6 mm; anthers 5–6.5 mm long; ovary ca. 3 mm long; style branches 15–18 mm long. The shorter perianth tube (and associated shorter bracts) suggests a less specialized pollination system, perhaps including bees and nemestrinid flies with somewhat shorter probosces than *Stenobasipteron wiedmannii,* the proboscis of which is up to 25 mm long.

Equally puzzling is a recent collection from Mt. Prospect, near Lydenburg (*Burrows 7309,* BKH), collected in early flower in mid February. This plant has long-tubed mauve flowers with a tube 30–32 mm long, tepals ca. 18 mm long, short filaments ca. 3 mm long, and anthers ca. 6 mm long. The four leaves have well developed blades and there is no sign of a largely sheathing upper leaf. The blades have a firm texture, an apparently dropping flowering stem, and a spike of five flowers. The plant thus fits poorly in *Hesperantha brevicaulis* because of the firm leaves, absence of a sheathing upper leaf, spike with more than four flowers, short filaments, and relatively short anthers. Additional material is needed before a decision can be made on its status.

Additional specimens. SOUTH AFRICA. **Limpopo:** 23.30 (Tzaneen) Wolkberg Mountain, below cliffs (CC), 9 Apr., *Davidson 3154* (J); Wolkberg, damp cliffs below Serala Peak, 23 Feb. 2002, *Goldblatt & Porter 11953* (K, MO, NBG, PRE). **Mpumalanga:** 24.30 (Pilgrim's Rest) MacMac Falls, in grass on sheer cliffs (DD), 14 Mar. 1959, *Germishuizen 116/50* (PRE); God's Window and The Pinnacle, 20 Apr. 1969, *MacNeil s.n.* (PRE); rock outcrops near God's Window, 25 Apr. 1966, *Goldblatt 72* (J), 27 Apr. 1967, *Goldblatt 73* (J), *Kluge 2505* (NBG, PRE), *Venter 7783* (MPU, PRE). 25.30 (Lydenburg) Mt. Prospect, rocky shale slopes above stream, 2010 m, 18 Feb. 2001, *Burrows 7309* (BKH); Buffelskloof Nature Reserve, crevices in cliffs (BC), 2 May 1988, *Burrows 4070* (BKH, J).

61. Hesperantha curvula Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 416. 1986. TYPE: South Africa. KwaZulu-Natal: Underberg, Bushman's Nek, Thamathu Pass, 5 Feb. 1976, *O. M. Hilliard & B. L. Burtt 8981* (holotype, NU!; isotypes, E not seen, MO!).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 416. 1986.

62. Hesperantha scopulosa Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 417. 1986. TYPE: South Africa. KwaZulu-Natal: Underberg, Bamboo Mountain, 8 Mar. 1977, *O. M. Hilliard & B. L. Burtt 10074* (holotype, NU!; isotype, E not seen).

Last revisionary account: Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 417. 1986.

Fairly common on wet basalt cliffs and rocks along the approach to The Sentinel in Free State Province, and known from several localities on basalt and sandstone in KwaZulu-Natal, *Hesperantha scopulosa* belongs to a guild of plant species with long-tubed pink flowers that are pollinated by the long-proboscid fly, *Prosoeca ganglbaurii* (Goldblatt & Manning, 1999, 2000). Interestingly, although flowers with a long perianth tube usually secrete ample amounts of nectar, which is retained in the tube, *H. scopulosa* seems to be deceptive. The tube is very narrow, and I have not been able to detect any nectar in the tube in two populations I examined. Successful pollination of these flowers must depend on their similarity to those of nectar-producing species growing nearby, among them *Gladiolus microcarpus* G. J. Lewis, *Hesperantha grandiflora*, and *Zaluzianskya microsiphon* (Kuntze) K. Schum. (Scrophulariaceae).

Seeds of *Hesperantha scopulosa*, collected on The Pudding below The Sentinel (*Goldblatt & Manning 9856*, NBG), are narrowly ovoid-oblong, ca. 1.3 × 0.4 mm, and have a long, irregularly twisted persistent funicle several times longer than the seed body. The chalazal end is flattened and has a small membranous flap of tissue, perhaps a vestigial wing. These seeds conform to the description of Hilliard and Burtt (1986) who called them oblong-elliptic in shape, 1.25 × 0.5 mm, with a narrow wing on one end, and with a long pale funicle. The only other comparable seeds in the genus may be those of *H. gracilis*, which Hilliard and Burtt described as narrowly obovoid and with a long slender funicle.

II. **Hesperantha** sect. **Hesperantha**

Plants with relatively large symmetrical, bell-shaped corms with a flat, horizontal or oblique base; older corm tunics remaining entire, not splitting from the base. Spike with floral outer bract margins free to the base. Flowers variously colored, with a straight perianth tube.

Species 63–70. Restricted to the southern African winter-rainfall zone.

63. Hesperantha falcata (L. f.) Ker Gawl., Ann. Bot. (König & Sims) 1: 225. 1804. *Ixia falcata* L. f., Suppl. pl. 92. 1782. TYPE: South Africa. Western Cape: hills around Cape Town, without date, *C. P. Thunberg s.n.* (holotype, Herb. Thunberg 9052B, UPS!).

Hesperantha pentheri Baker, Kew Bull. 1906: 26. 1906. TYPE: South Africa. Western Cape: Olifants River valley, Clanwilliam, Sep. 1894, *A. Penther 686* (lectotype, designated by Foster (1948: 21), K!).
Hesperantha trifolia R. C. Foster, Contr. Gray Herb. 166: 26. 1948. TYPE: South Africa. Western Cape: Bulshoek, 2 Aug. 1896, *R. Schlechter 8378* (holotype, B!; isotypes, BOL!, G!, K!, MO!, P!, PH!, PRE!, US!, Z!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 97. 1984.

Although both *H. pentheri* and *H. trifolia* were recognized by R. C. Foster (1948) in his preliminary account of *Hesperantha*, they were included in *H. falcata* in the 1984 revision of the genus for the winter-rainfall zone (Goldblatt, 1984). They undoubtedly represent distinct geographical races and an argument can be made for their recognition as separate species or subspecies; they are treated as separate entities in my key to the winter-rainfall species. Plants matching *H. trifolia* almost always have only three leaves, and whether dwarfed by poor growing conditions or robust, they have relatively large white flowers, often only two or three per spike, always evenly spaced along the stem, and a pink to light reddish pigmentation on the reverse of the outer tepals, rather different from *H. falcata*, in which the flowers are somewhat crowded at the tip of the spike. The bracts of *H. pentheri* and *H. trifolia* are soft-textured or even membranous, thus unlike the firm green bracts of typical *H. falcata*, which have prominent veins, a reddish margin, and obtuse apex. Plants matching *H. pentheri* have deep cream to light yellow flowers, the outer tepals often flushed dull red to purple on the outside. Both flower relatively early, mostly in August (typical *H. falcata* flowers in September or October), and are confined to the northwest Cape, in the Olifants River valley and surrounding mountains where typical *H. falcata* does not occur. The most northerly record of plants matching *H. pentheri* is from the Kobee Valley, northeast of Vanrhynsdorp (*Goldblatt & Porter 11794*, MO, NBG), not far from the southernmost populations of *H. pauciflora*, which also have pale yellow flowers. The two can readily be distinguished by their different corms, those of *H. pauciflora* having spines radiating from the base.

64. Hesperantha sufflava Goldblatt, sp. nov. TYPE: South Africa. Western Cape: Malmesbury, sandy gravel slopes in renosterveld, 14 Aug. 1999, *P. Goldblatt & I. Nänni 11087* (holotype, NBG!; isotypes, K!, MO!, PRE!, WAG!). Figure 7.

Plantae 8–15 cm altae prope basem saepe ramosae, cormo campanulato basi plano tunicis lignosis marginibus leviter denticulatis 10–18 mm diam., foliis 3 omnibus basalibus vel summo subbasali, lanceolatis vel falcatis 2–7 mm latis, spica (2-vel)3-ad 7-flora flexuosa, floribus pallide flavis tepalis externis abaxialiter pallide brunneis, tubo perianthii 12–14(–16) mm longo recto, tepalis 7–9 (–10) × 4–5 mm, filamentis ca. 2 mm longis, antheris ca. 4 mm longis, ramis styli ca. 12 mm longis, in medio tubi perianthii divisis, apices antherarum non attingentibus.

Plants mostly 8–15 cm high, often branching from near the base in the axil of the uppermost leaf. *Corm* bell-shaped with a flat base, 10–18 mm diam., tunics woody, the margins denticulate. *Leaves* 3, all basal or the uppermost subbasal, lanceolate to falcate, the upper leaf partly sheathing, with a short free unifacial tip, 2–7 mm wide, slightly fleshy, the midrib not visibly thickened. *Spike* slightly flexuose, (2–)3–7-flowered; *bracts* 10–14 mm long, green, often red along the upper margins, diverging from the stem, the outer about as long as or slightly shorter than the stem. *Flowers* pale yellow, the outer tepals flushed light brown on the outside; *perianth tube* slender, straight, 12–14(–16) mm long; *tepals* subequal, ovate, slightly spooned, 7–9(–10) × 4–5 mm, spreading ± at right angles to the tube when fully open after 15:00H. *Filaments* ca. 2 mm long, inserted at the base of the tepals; *anthers* ca. 4 mm long, erect, yellow. *Ovary* oblong, ca. 2.5 mm long; *style* branches ca. 12 mm long, dividing in the middle of the tube, exserted for ca. 7 mm and then weakly diverging, reaching to about the upper third of the anthers in bud. *Capsules* oblong, (6–)7–9 × ca. 4 mm; *seeds* ± globose or weakly angled by pressure, ca. 1.3 mm long.

Flowering. Late July and August.

Distribution. South Africa, Western Cape, local in the Malmesbury District in renosterveld on sandy gravel.

A member of section *Hesperantha*, *H. sufflava* at first appears to be intermediate between the common, usually white-flowered *H. falcata* and the much rarer *H. spicata*. At the type locality *H. spicata* grows together with *H. sufflava* and is obviously quite different in its secund spike of small, pure white flowers, distinctive in the slightly curved perianth tube 4–6 mm long and tiny tepals 4–7 mm long. Moreover, flowers of *H. spicata* open at about 18:30H when they release a strong, sweet, narcissus-like scent with a strong clove component. Flowers of *H. sufflava* are pale yellow and open at about 15:00H, and they have a quite different, slightly acrid, pyrethrum-like odor. Particularly unusual are the style branches, which divide in the middle of the perianth tube, and only the upper 7 mm are exserted. In nearly all *Hesperantha* species the style divides at the throat of the perianth tube and not within the narrow part of the tube.

Superficially *Hesperantha sufflava* is not much like *H. falcata* for the flowers seem much smaller. The tepals, 7–10 mm long, are smaller than in most populations of *H. falcata*, but the perianth tube is substantially longer, usually 12–16 mm long, and is always longer than the tepals (Fig. 5). In *H. falcata* the tepals are usually 12–18 mm long, exceptionally only 9–11 mm in southern Cape coastal populations, and the perianth tube is 4–9 mm long, thus usually shorter than the tepals. Apart from the flowers, *H. sufflava* is distinctive in always having only three leaves, all basal or the uppermost one subbasal, and the stem often has a branch produced from the axil of the upper leaf. Most populations of both *H. spicata* and *H. falcata* have three (or more) basal leaves and one, largely or entirely sheathing cauline leaf.

Paratypes. SOUTH AFRICA. **Western Cape:** 33.18 (Cape Town) Malmesbury, sandy gravel slopes in renosterveld 1.7 km from town center on road to Tulbagh (DB), 12 Aug. 2000, *Goldblatt & Nänni 11383* (K, MO, NBG, PRE, WAG).

65. Hesperantha cedarmontana Goldblatt, J. S. African Bot. 50: 106. 1984. TYPE: South Africa. Western Cape: Pakhuis Mts. W of Leipoldt's Grave, 27 Sep. 1981, *P. Goldblatt 6403* (holotype, MO!; isotypes, K!, NBG!, PRE!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 106. 1984.

66. Hesperantha pauciflora (Baker) G. J. Lewis, Fl. Pl. Africa 18: pl. 682. 1938. *Tritonia pauciflora* Baker, Handbk. Irideae 193. 1892. TYPE: South Africa. Northern Cape: Namaqualand, near Naries, Sep. 1883, *H. Bolus 6622* (lectotype, designated by Goldblatt (1984: 108), BOL!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 108. 1984.

The typically pink- to purple-flowered *Hesperantha pauciflora* extends from northern Namaqualand to the Bokkeveld Escarpment at the northern edge of the Cape Floristic Region of South Africa and is locally common at the southern end of its geographic range. Plants with pale yellow flowers from the extreme south of its range at Papkuilsfontein, south of Nieuwoudtville (e.g., *Goldblatt 11102*, MO), are included here, expanding the range of variation in *H. pauciflora*. They appear to differ in no other significant way from the pink-flowered populations and have identical bell-shaped corms with prominent radiating spines, spikes of only 2 to 4 flowers, and submembranous bracts, dry near the tips. The flowers also have the same daily opening and closing pattern. On warm days the tepals unfold after 13:00H and close again after 17:00H (Goldblatt et al., in press). The flowers are visited by a variety of bees and by hopliine beetles, both of which appear to be legitimate pollinators of the species.

There are also significant differences between the Namaqualand and Bokkeveld Escarpment populations. Plants from Namaqualand have dark pink to purplish flowers with a white throat (Goldblatt, 1984: fig. 4), stamens with relatively long filaments, 4–8 mm long, anthers 6.5–9 mm long, and the style branches reach the anther apices or exceed them by up to 2 mm. On the Bokkeveld Escarpment, about 100 km south of the nearest Namaqualand populations, the flowers are either uniformly pale to deep pink, or often have darker pigmentation at the base of the tepals and in the throat (or they are uniformly pale yellow). The stamens in these populations have filaments only 2–3 mm long while the anthers are 7–9 mm long, and the style branches barely reach the anther tips or up to 2 mm below them. These differences appear to reflect population divergence due to isolation, and perhaps signify a pollinator shift, which remains to be studied.

67. Hesperantha latifolia (Klatt) M. P. de Vos, J. S. African Bot. 40: 252. 1974. *Syringodea latifolia* Klatt, Abh. Naturf. Ges. Halle 15: 403. 1882. TYPE: South Africa. Northern Cape: Kamiesberg, Ellenboogsfontein, Sep. 1830, *J. F. Drège 2633* (lectotype, designated by de Vos (1974: 252), B!; isotypes, P!, S!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 111. 1984.

Restricted to higher elevations in the Kamiesberg Mountains of central Namaqualand, this winter-rainfall zone species is relatively common in shallow soils overlying granite pavement. Plants are typically short, usually less than 5 cm high, but robust plants growing in rock crevices or through low bushes may reach 15 cm. The dark red-purple flowers with a perianth tube 15–25 mm long are now known to be pollinated by the long-proboscid fly, *Prosoeca peringueyi*, which also pollinated several other long-tubed species with similarly colored flowers in Namaqualand, among them *Babiana dregei* Bak., *Lapeirousia silenoides* (Jacq.) Ker Gawl. (Iridaceae), and *Pelargonium incrassatum* (Andr.) Sims (Geraniaceae) (Goldblatt et al., 1995; Goldblatt & Manning, 2000).

68. Hesperantha luticola Goldblatt, J. S. African Bot. 50: 113. 1984. TYPE: South Africa. Northern Cape: between Midddelpos and Calvinia, Farm Knechtsbank, 21 Aug. 1974, *M. F. Thompson 2529* (holotype, STE!; isotype, PRE!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 113. 1984.

An aspect of the acaulescent *Hesperantha luticola* not known when the species was described is the fact that the perianth tube is virtually closed. The tube, 30–45 mm long, might be expected to be hollow and to contain nectar as it does in many other long-tubed species of the genus. The walls of the tube are, however, thick, and they closely envelop the style leaving no internal cavity. The small amount of nectar produced by the flowers is forced into the upper, slightly wider part of the tube where it is accessible to insects with relatively short probosces. The perianth tube thus appears to serve as

Figure 7. Morphology and floral and capsule and seed details of *H. sufflava*. Drawn by John Manning from live plants (*Goldblatt & Nänni 11087*, MO, NBG). Scale bar 1 cm; single flowers and seed much enlarged.

a pseudopedicel, raising the tepals, stamens, and style branches above the basal cluster of leaves. The ovary remains close to or below ground level, and is thus protected from damage during its maturation. The ripe capsules are borne a short distance above the ground.

69. Hesperantha spicata (Burm. f.) N. E. Br., Kew Bull. 1929: 136. 1929. *Ixia spicata* Burm. f., Prod. Pl. Cap. 1. 1768. TYPE: South Africa. Without precise locality or date, probably cultivated in Holland, *N. L. Burman s.n.* (holotype, herb. Burman, G!). Figure 1C.

Last revisionary account: Goldblatt, J. S. African Bot. 50: 114. 1984.

In my 1984 account of *Hesperantha* in the southern African winter-rainfall zone I treated *Hesperantha spicata* as comprising three subspecies: subsp. *spicata,* with falcate basal leaves with crisped margins, subsp. *graminifolia* (Sweet) Goldblatt, with narrow, erect leaves with plane margins, and subsp. *fistulosa* (Baker) Goldblatt, with terete leaves. While the two former subspecies seem satisfactorily defined, a new record of subspecies *fistulosa* from the farm Joostenbergkloof, west of Paarl, expands our understanding of this plant, previously reported only from wet flats in the Porterville district, well to the north of Paarl. Plants at the Joostenbergkloof site grew in a wet seep and were in full flower (though closed during the day time) in mid September while nearby in well drained, stony sand, plants of subspecies *spicata* were in fruit. Despite the similarity of the flowers of subspecies *spicata* and subspecies *fistulosa,* the two subspecies seem well separated from one another not only in leaf morphology and habitat, but in flowering time. Alternative treatment of the latter as a separate species for subspecies *fistulosa* seems equally acceptable.

70. Hesperantha saldanhae Goldblatt, J. S. African Bot. 50: 119. 1984. TYPE: South Africa. Western Cape: granite rocks at Vredenburg, 8 Aug. 1962, *G. J. Lewis 5977* (holotype, NBG!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 119. 1984.

Hesperantha saldanhae remains known only from the type collection made by G. J. Lewis in August 1964. Plants were collected on granite rocks at Vredenburg. Repeated visits to the presumed type locality, a prominent cluster of exposed granite rocks at the edge of the town, have failed to reveal any sign of the species. Only moderate disturbance at the site makes it seem unlikely that the species is extinct due to human activity. Nevertheless, *H. saldanhae* must be considered seriously endangered, and possibly extinct.

III. Hesperantha sect. Radiata Goldblatt, Ann. Missouri Bot. Gard. 69: 377. 1982. TYPE: *Hesperantha radiata* (Jacq.) Ker Gawl.

Plants with relatively large symmetrical, bell-shaped corms with a flat, horizontal or oblique base; tunics often scalloped below and fringed at the lower margins, older corm tunics not splitting from the base into segments but often the tunics forming scalloped, concave segments. Spike with floral outer bract margins united around the spike axis for up to half their length. Flowers variously colored, most species with a strongly curved perianth tube, nearly straight in *H. juncifolia* and *H. elsiae.*

Species 71–79. Mainly in the southern African winter-rainfall zone, but *H. radiata* extends from Namaqualand, South Africa, in the west to Swaziland in the east, *H. longicollis* is eastern southern African, and *H. ballii* is endemic to Zimbabwe in tropical Africa.

71. Hesperantha brevifolia Goldblatt, J. S. African Bot. 50: 121. 1984. TYPE: South Africa. Western Cape: Piketberg, Zebrakop, 16 Dec. 1971, *E. E. Esterhuysen 35320* (holotype, MO!; isotypes, B!, BOL!, BR!, C!, E!, K!, M!, NBG!, P!, PRE!, S!, US!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 121. 1984.

Known since 1800 when plants were collected by British botanist John Roxburgh near Tulbagh in Western Cape Province (*Roxburgh s.n.,* G), this species of section *Radiata* is rare and has not often been recorded. It was only described in 1984, by which time populations were known from Piketberg, the Cold Bokkeveld, and the mountains north of Bainskloof (Goldblatt, 1984) as well as Tulbagh. It has only become evident recently that *Hesperantha brevifolia* extends to the north as far as the slopes of the Nardouwsberg between Clanwilliam and Klawer, some 80 km from the next closest station (*Goldblatt & Manning 10720B,* MO, NBG; *Maguire 1032,* NBG). The flexuose stem, bract margins united around the axis only at the base, and short leaf blades make it relatively easy to recognize *H. brevifolia* within section *Radiata.*

72. Hesperantha juncifolia Goldblatt, J. S. African Bot. 50: 135. 1984. TYPE: South Africa. Western Cape: Bredasdorp, Ratelrivier, limestone flats, 29 Sep. 1970, *P. Goldblatt 403* (holotype, BOL!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 135. 1984.

Known only from the type collection when first described, *Hesperantha juncifolia* has since been re-collected twice (*Esterhuysen 36425,* BOL, MO, *Esterhuysen 36371,* BOL, MO) at Brandfontein along the west coast of Cape Agulhas, a short distance from the type locality (Goldblatt, 1987). The new collections confirm that the species is a local endemic of wet depressions on coastal limestone flats and distinguished from the related *H. radiata* by the terete leaf blades, outer bract sheathing the stem only in the lower third, and the straight perianth tube 5–6 mm long. Flat-leaved *H. radiata* has flowers with a curved perianth tube mostly 7–15 mm long, and the outer bract sheathing the stem for about half its length. Additional biological notes were recorded by Goldblatt (1987), including the fact that the white flowers open early in the morning and close at about 16:00H, unusual for white-flowered species of section *Radiata*.

73. Hesperantha marlothii R. C. Foster, Contr. Gray Herb. 166: 20. 1948. TYPE: South Africa. Northern Cape: Sutherland District, near Waterkloof, Sep. 1921, *Marloth 10412* (holotype, B!; isotypes, PRE!, STE!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 130. 1984.

74. Hesperantha decipiens Goldblatt, sp. nov. TYPE: South Africa. Northern Cape: Kamiesberg, northern slopes of Rooiberg, 19 Sep. 1991, *P. Goldblatt 9258* (holotype, NBC!; isotypes, K!, MO!, PRE!). Figure 8.

Plantae 10–15 cm altae plerumque eramosae, cormo campanulato basi obliqua plana 8–12 mm diam., tunicis lignosis concentricis, foliis 4 linearibus vel falcatis 1.2–2.0 mm latis, in medio incrassatis, spica plerumque 3- ad 6-flora flexuosa, floribus albis vel cremeis odoratis tepalis externis abaxialiter ex rufis brunneis, tubo perianthii 10–13 mm longo ad apicem curvato, tepalis 12–14 × 2.5–3.5 mm, filamentis ca. 4 mm longis, antheris ca. 5 mm longis, ramis styli antheras parum excedentibus.

Plants 10–15 cm high, stem usually unbranched. *Corm* ovoid with an oblique flat base, 8–12 mm diam., tunics woody, concentric, somewhat scalloped into concave segments with fringed edges. *Leaves* 4, the lower 3 basal and largest, the uppermost inserted in the middle of the stems and sometimes entirely sheathing or with a short free unifacial tip, linear, 1.2–2 mm wide, slightly fleshy, slightly thickened in the midline. *Spike* mostly 3–6-flowered, flexuose; *bracts* 10–15 mm long, green, becoming dry above, the outer with margins united around the stem for 3–5 mm, the inner about as long as the outer. *Flowers* white to cream, the outer tepals pale pink to reddish or brown on the outside, strongly scented of stocks when open after dark; *perianth tube* slender, recurving above, 10–13 mm long; *tepals* subequal, lanceolate, 12–14 × 2.5–3.5 mm, spreading ± at right angles to the tube when fully open in the later afternoon. *Filaments* ca. 4 mm long; *anthers* 5–7 mm long. *Ovary* oblong, ca. 3 mm long; *style* branches ca. 12 mm long, weakly spreading, slightly shorter or slightly longer than the anthers. *Capsules* oblong-obovoid, 6–8 × ca. 3.5 mm; *seeds* angular, the edges ± winged, ca. 1 mm long.

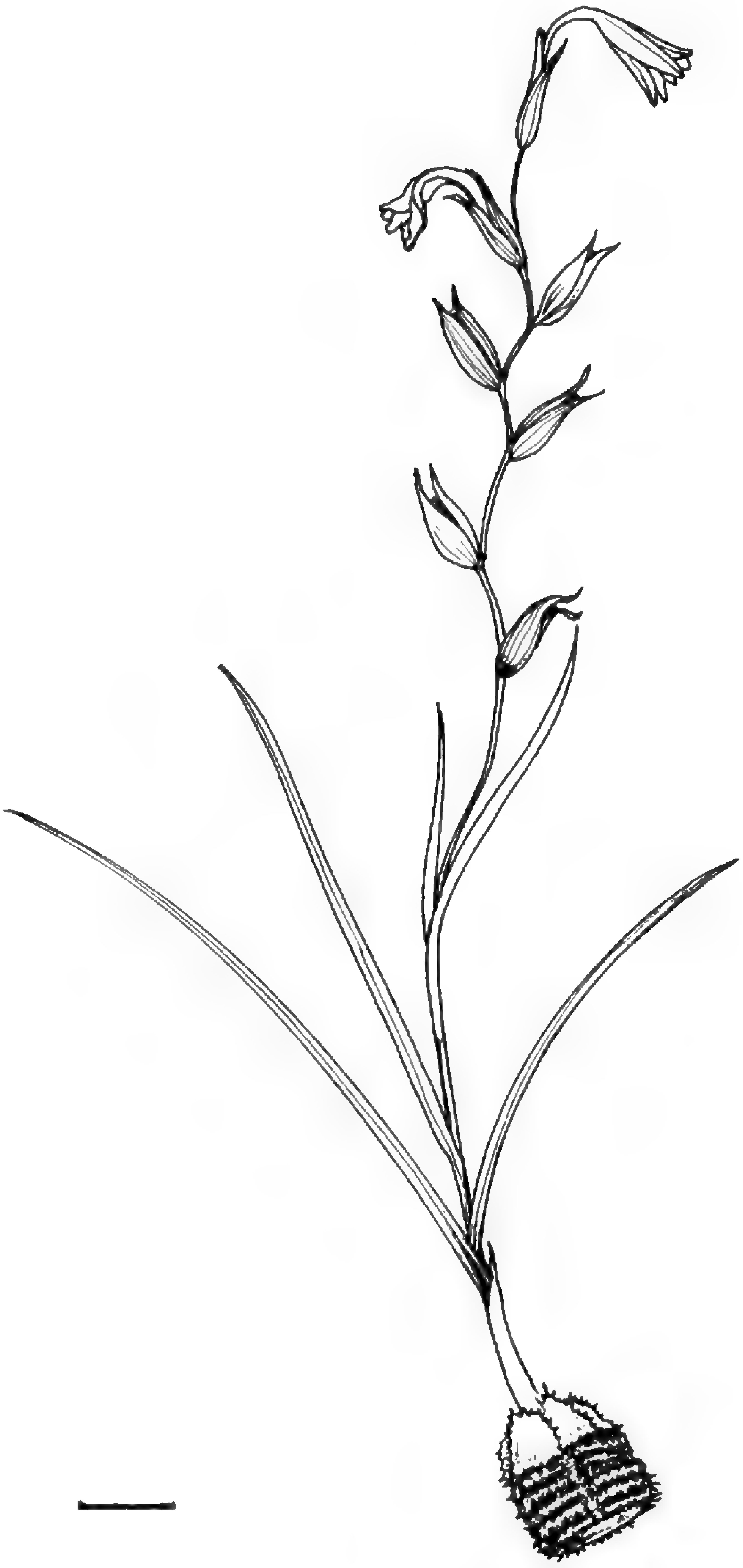

Figure 8. Morphology of *H. decipiens*, full size. Drawn by Yevonn Wilson-Ramsay from pressed specimens (*Goldblatt 9258*, K, MO, NBG). Scale bar 1 cm.

Flowering. August and September.

Distribution. South Africa, Northern Cape, extending from near Springbok in the north through the Kamiesberg to the northern Knersvlakte, on thin, sandy gravel on granite pavement.

Evidently first collected in 1897 by Rudolf Schlechter and only occasionally since then, *Hesperantha decipiens* is still relatively poorly recorded. Confused with either the widespread *H. radiata* or its relative from the Roggeveld and Bokkeveld Mountains, *H. marlothii, H. decipiens* has the outer bract margins united around the spike axis and flat-based corms that define section *Radiata*. Superficially it seems to merely represent a northern series of populations of *H. marlothii*. That species is, however, defined by a few-flowered, flexuose spike, outer bract margins united only near the base, and corms with prominent lateral spines. *Hesperantha decipiens* has the flexuose, few(or several)-flowered spike of *H. marlothii*, but the outer bract margins are united for up to 5 mm, about a third of their length, and more significantly, the corms lack lateral spines. Instead the corms closely resemble those of *H. radiata* in their scalloped, slightly fringed lobes. Close examination of the flowers shows that the style branches of *H. decipiens* usually exceed the anthers by 1–2 mm and the anthers are 5–7 mm long. Robust specimens of *H. marlothii* have anthers 6–8 mm long and the style branches reach only to about the middle of the anthers. Less robust specimens have anthers 4.5–6 mm long, but the style branches are still slightly short of the anther apices. *Hesperantha decipiens* can be distinguished from *H. radiata* because that species has the outer bract margins united for at least half their length and a straight spike typically bearing more than 8 flowers. The capsules of *H. decipiens* are slightly shorter than the bracts and 6–8 mm long, whereas those of *H. radiata* are usually slightly longer than the bracts and 8–10 mm long. Mature capsules are seldom collected so that it is uncertain that this distinction holds for all populations of both species.

Paratypes. SOUTH AFRICA. **Northern Cape:** 29.17 (Springbok) near Wildepaardehoek Pass, damp sand on granite (DC), 9 Sep. 1980, *Goldblatt 5751* (MO). 30.17 (Hondeklipbaai) hills at Rietkloof (BD), 11 Sep. 1897, *Schlechter 11202* (B, GRA, K, Z). 3018 (Kamiesberg) Kamiesberg 2 km S of Leliefontein, 17 Sep. 2002, *Goldblatt & Porter 12226* (MO, NBG); farm Welkom, lower eastern slopes of Rooiberg (AC), 9 Sep. 1980, *Goldblatt 5768* (M, MO, PRE); Damsland Kloof, northern approach to Rooiberg peak, 19 Sep. 1991, *Goldblatt 9258* (MO, NBG, PRE); N of FM tower at Leliefontein, 20 Sep. 1991, *Goldblatt & Manning 10008* (MO, NBG). **Western Cape:** 3118 (Vanrhynsdorp) Knersvlakte, near gypsum mine N of the Sishen rail-line (BC), 21 Aug. 1983, *Bean 1272* (BOL).

75. Hesperantha radiata (Jacq.) Ker Gawl., Ann. Bot. (König & Sims) 1: 225. 1804. *Ixia radiata* Jacq., Icones Pl. Rar. 2: pl. 280. 1782. TYPE: South Africa. Without precise locality, Jacq., Icones Pl. Rar. 2: pl. 280. 1782.

Hesperantha tysonii Baker, Handbk. Irideae 151. 1892. TYPE: South Africa. KwaZulu-Natal: streambanks near Kokstad, Oct. 1883, *W. Tyson* 1585 (holotype, K!; isotypes, B not seen, GRA not seen, NH!, SAM!).

Hesperantha radiata var. γ *caricina* Ker Gawl., Curtis's Bot. Mag. 21: pl. 790. 1804. TYPE: South Africa. Without precise locality, Curtis's Bot. Mag. 21: pl. 790. 1804.

Hesperantha tenuifolia Salisb., Trans. Hort. Soc. 1: 321. 1812, as a new name for *H. radiata* var. γ *caricina* Ker Gawl., Curtis's Bot. Mag. 21: pl. 790. 1804. *Hesperantha caricina* (Ker Gawl.) Klatt, Abh. Naturf. Ges. Halle 15: 395 (Erganz. 61). 1882, nom. illeg. superfl. pro *H. tenuifolia* (based on the same type).

Last revisionary accounts: Goldblatt, J. S. African Bot. 50: 123. 1984. Hilliard & Burtt, Notes Roy. Bot. Gard. Edinburgh 43: 436. 1986 (as *H. tysonii*).

The circumscription of *Hesperantha radiata* has been unsettled since Hilliard and Burtt (1986) maintained that the eastern southern African plants included in *H. radiata* by Goldblatt (1984) represent a separate species, *H. tysonii*. Clearly populations in eastern southern Africa are more uniform than in the winter-rainfall zone, favor moist habitats, and flower mostly in November or December (although the type collection of *H. tysonii* was made in October). These authors do not, however, list any morphological features in which the eastern plants differ from the western apart from having less woody corm tunics (in the few specimens available that have corms). If these are separate species I fail to see how to distinguish them or to determine what the populations from the area between KwaZulu-Natal–Lesotho and the southwestern Cape (the eastern Cape and Karoo mountains) should be called since they cannot be distinguished from many collections from either the summer- or winter-rainfall zone. As a matter of practicality, if nothing more, *H. tysonii* must be regarded as conspecific with *H. radiata*. The two can only be keyed out if distribution and flowering time are invoked.

In an effort to distinguish eastern populations from those in the winter-rainfall zone I have reexamined a selection of specimens of *Hesperantha radiata* from its entire range. Plants from the winter-rainfall zone differ slightly in having anthers (4–)5.5–7 mm long and a perianth tube (6–)8–12 mm long, and thus mostly slightly smaller flowers than eastern populations in which anthers are 7–8 mm long and the perianth tube is 9–14 mm long (Hilliard & Burtt provided dimensions of 5.5–9 mm long for anthers and 7–13 mm for the perianth tube based on plants they examined from eastern southern Africa). These overlapping dimensions reflect a surprising consistency in flower size from Namaqualand and the western Karoo in the winter-rainfall zone west to the northeasternmost populations in Swaziland and Dullstroom in Mpumalanga in the summer-rainfall part of the subcontinent. The Dullstroom population is a particularly distinctive form (*Drews 188,* NBG) in which the flowers are uniformly cream and the tepals large, ca. 17 × 5 mm, the anthers 8.5 mm long, but the perianth tube, ca. 10 mm long, is well within the expected range. All that remains is a possibly weak distinction in the corm tunics. Paucity of material with corms makes comparison difficult, but corms of a collection from Lesotho (*Dieterlen s.n.,* SAM 2408) differ not at all from some specimens from the Western Cape (e.g., *Lewis 5988,* NBG). I suggest that *H. radiata* must be considered one of a relatively small number of species that occur across southern Africa bridging the opposed climate regimes of the subcontinent.

More puzzling to me are collections of small-flowered plants of *Hesperantha radiata* from the Cape Peninsula and hills around Stellenbosch and Somerset West in the extreme southwest of the southern African winter-rainfall zone. These plants have many-flowered, unusually crowded spikes in which the bracts slightly overlap one another and the uppermost leaf is always entirely sheathing and reaches almost to the base of the spike. The flowers have tepals 7–9.5 mm long, a tube 6–7 mm long, and anthers 4–5 mm long. The stems also have a weakly developed neck of fine fibers around the base. Including these plants in *H. radiata* makes winter-rainfall *H. radiata* appear even more variable than do the dimensions mentioned above. Particularly notable is the fact that the small-flowered plants bloom later than the typical ones, and they may be sympatric, as for example, *Oliver 4332,* NBG (21 August), and *4756,* NBG (17 October), both collected in 1973 in the hills at Langverwacht near Stellenbosch. The August-flowering plants are typical *H. radiata* and the October-flowering ones the small-flowered form with crowded spikes. Specimens of the latter, collected by C. F. Ecklon and C. L. Zeyher in the early 19th century, are annotated *H. setacea* Eckl. (e.g., *Ecklon & Zeyher Irid. 233*—89.9) (Ecklon, 1827), while some sheets at the Kew Herbarium are annotated *H. tenuifolia.* This is R. A. Salisbury's (1812) name for *H. radiata* var. γ *caricina* of Curtis's Bot. Mag. pl. 790 (Ker-Gawler, 1804). The epithet alludes to the characteristic narrow leaves, also, however, found in some populations of larger-flowered plants that correspond to the type of *H. radiata.*

76. Hesperantha ballii Wild, Kirkia 4: 136. 1963. TYPE: Zimbabwe. Chimanimani Mts., Point 71, July 1961, *Ball 948* (holotype, SRGH!).

Last revisionary account: Goldblatt, Ann. Missouri Bot. Gard. 73: 135. 1986.

77. Hesperantha longicollis Baker, Bull. Herb. Boissier ser. 2, 4: 1004. 1904. TYPE: South Africa. Gauteng (as Transvaal), Modderfontein, 11 Sep. 1898, *P. Conrath 600* (syntype, K!).

Last revisionary account: Obermeyer, Fl. Pl. Africa 46: pl. 1810. 1980.

78. Hesperantha elsiae Goldblatt, J. S. African Bot. 50: 136. 1984. TYPE: South Africa. Western Cape: Cedarberg, Krom River Kloof, above Disa Pool, 11 Nov. 1979, *P. Goldblatt 5331* (holotype, MO!; isotypes, K!, NBG!, PRE!, S!, US!, WAG!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 136. 1984.

79. Hesperantha muirii (L. Bolus) G. J. Lewis, J. S. African Bot. 7: 32. 1941. *Acidanthera muirii* L. Bolus, Ann. Bolus Herb. 1: 195. 1915. TYPE: South Africa. Western Cape: Riversdale District, Farm Plattekop, Oct. 1931, *J. Muir 1087* (holotype, BOL!).

Last revisionary account: Goldblatt, J. S. African Bot. 50: 133. 1984.

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APPENDIX 1

LIST OF SPECIES WITH NUMBERING AS PRESENTED WITHIN THE ARTICLE

Geissorhiza macra see *H. leucantha*	
Hesperantha acuta	3
H. alborosea	41
H. altimontana	30
H. bachmannii	32
H. ballii	76
H. baurii	35
H. brevicaulis	60
H. brevifolia	71
H. brevistyla	42
H. bulbifera	33
H. candida	26
H. candida var. *bicolor* see *H. longituba*	
H. cedarmontana	65
H. ciliolata	12
H. coccinea	56
H. crocopsis	31
H. cucullata	18
H. curvula	61
H. debilis	27
H. decipiens	74
H. elsiae	78
H. erecta	1
H. exiliflora	40
H. falcata	63
H. fibrosa	17
H. flava	25
H. flexuosa	15
H. galpinii, see *H. woodii*	
H. glabrescens	11
H. glareosa	37
H. gracilis	51
H. grandiflora	57
H. hantamensis	23
H. humilis	24
H. hutchingsiae	59
H. huttonii	58
H. hygrophila	47
H. inconspicua	45
H. ingeliensis	43
H. juncifolia	72

BIOGEOGRAPHY AND FLORISTIC AFFINITIES OF THE LIMESTONE FLORA IN SOUTHERN YUNNAN, CHINA[1]

H. Zhu,[2] H. Wang,[2] B. Li,[2] and P. Sirirugsa[3]

ABSTRACT

The forests on limestone in southern Yunnan, in tropical southwest China, were inventoried, and their floristic composition and biogeographical affinities are discussed. These limestone forests were characterized by phanerophytes making up ca. 78% of the total species and those with mesophyllous leaves comprising 75%. Ecological species groups based on their habitat preferences were discerned from field observations: the species exclusive to the limestone habitats make up 10% and the preferents make up ca. 12% of the total limestone flora. From these limestone forests, 1394 vascular plant species belonging to 640 genera and 153 families were recorded. Based on their distributions, 12 biogeographic elements at the generic level and nine at the specific level were recognized. About 90% of the seed plant genera (over 90% of the species) were tropical; furthermore, 35% of the seed plant genera (65% of the species) have tropical Asian affinities. In a comparison with other regional floras from southern China and tropical Asia, the limestone flora of southern Yunnan revealed closer affinity to tropical floras than to temperate elements of eastern Asian floras. This limestone flora is thus tropical and part of the tropical Asian flora at its northern margin.

Key words: biogeography, China, limestone forest, southern Yunnan.

Limestone in tropical China occurs mainly in Yunnan and Guangxi Provinces of southern and central China. Because of the great diversity of edaphic conditions and topography, vegetation types on limestone are extremely diverse and rich in endemic taxa. Limestone vegetation in southern China has been destroyed as much as other vegetation types even though these limestone areas are more difficult to access and to farm. Limestone vegetation is also more vulnerable because it recovers much more slowly on usually thin soils. Our research was conducted mainly in the area of Xishuangbanna, in the southern part of Yunnan, where about 19% (3600 km^2) of the total area is limestone (Liu et al., 1990). Most of this limestone area is still forested and is receiving increasing attention for its biodiversity and its urgent need of conservation. Primary floristic works in southern Yunnan have been written (Zhu et al., 1996, 1997, 1998a, 1998b; Wang et al., 1997). This paper represents a synthesis of its floristics, physiognomy, and biogeographical affinities.

GENERAL GEOGRAPHY

Xishuangbanna, the southern part of Yunnan, which borders Burma and Laos, is a mountainous area at the northern margin of tropical Southeast Asia (Fig. 1). Basically, the study area has a mountainous topography with the mountains running north-south and decreasing in elevation southward. Altitude varies from 480 m in the lowest valley in the south to 2400 m at the top of the highest mountain in the north. The limestone strata occur mainly in southeastern Xishuangbanna and range in altitude from 600 to 1600 m.

The region of Xishuangbanna has a typical tropical monsoon climate with an annual mean temperature of 22ºC, annual temperature accumulation (the sum of daily temperature means where they are > 10°C) of 8000°C, and annual precipitation varying from 1200 to 1556 mm, of which more than 80% falls during the rainy season between May and the end of October (Xu et al., 1987).

The rock substrate is hard limestone of Permian origin with a rugged topography. The soil is mainly

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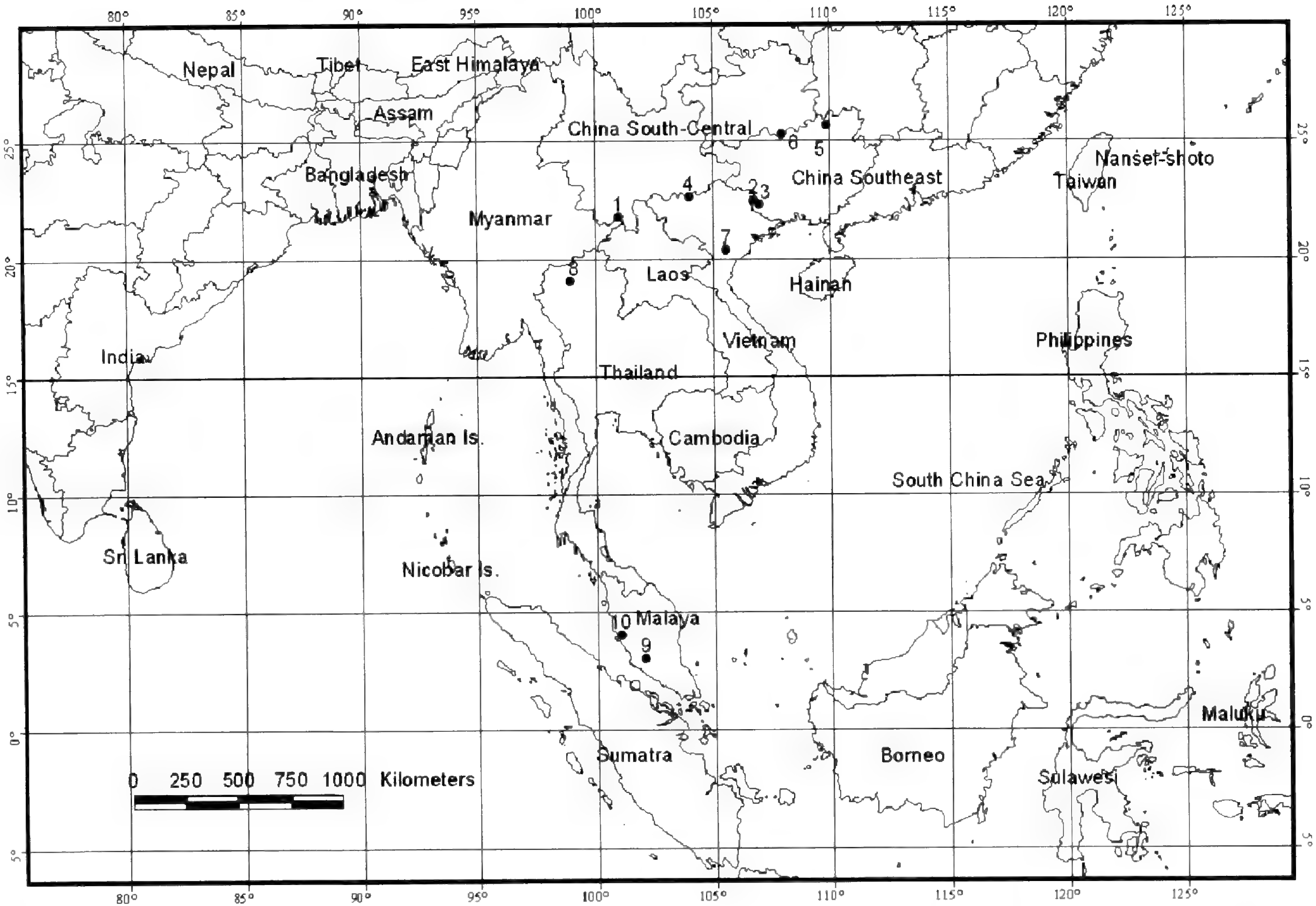

Figure 1. Locations of the research area in Xishuangbanna, southern Yunnan, China, and compared regional floras (see Table 6). —1. Our research area. —2. Longgan, SW China. —3. Daqinshan Mountains, SW China. —4. Gulinqing, SW China. —5. Huapin, China. —6. Dongyang Mountains, China. —7. Cucphuong, N Vietnam. —8. Chiengdao, N Thailand. —9. The Malay Peninsula limestone. —10. Taiping, Malay Peninsula.

brown, coarse in texture, and composed of loamy limestone with a pH of ca. 6.75 and ca. 3.56% organic matter (Liu et al., 1990).

METHODS

A complete floristic inventory was made based on the identification of more than 5000 plant specimens collected from the limestone habitat in southern Yunnan during 1985–1995 and deposited mainly at HITBC and SYS. The flora of the vegetation on the limestone consisted of 153 families of vascular plants, including 640 genera and 1394 species. An initial floristic analysis was made based on the inventory (Zhu et al., 1996). Three main vegetation types occur on the limestone—tropical seasonal rain forest, tropical seasonal moist forest, and tropical montane dwarf forest—which were selected for establishing plots. For the tropical seasonal rain forest, seven separate plots ranging in size from 2000 to 2500 m² were established. For the tropical seasonal moist forest seven separate plots ranging in size from 500 to 2000 m² were laid out. For the tropical montane dwarf forest, only two plots of 10 by 10 m were made due to its restriction to limestone summits. These different plot sizes were used because of the differential coverage of forest type and site restrictions. The structure and species composition of the vegetation on the limestone were analyzed based on plot data already published (Zhu et al., 1998a). In the present paper, plant inventory lists of the two main forest types (excluding montane dwarf forest) were compiled from sample plots separately for the physiognomic (life form and leaf size) analysis. The criteria for life form and leaf size classes suggested by Raunkiaer (1934) and the importance value index (IVI) suggested by Curtis and McIntosh (1951) were used in the physiognomic or ecological analysis. Ecological species groups were discriminated from field observation and correspond to groups used in Shimizu (1964) and Chin (1977). Species-level biogeographical affinities were assessed for the total flora of the limestone vegetation. The floristic similarities between the limestone flora of southern Yunnan and the floras on limestone and non-limestone habitats from southwest China, northern Vietnam, northern Thailand, and the Malay Peninsula were also discussed.

CLASSIFICATION OF LIMESTONE VEGETATION

Based on plant physiognomy, forest profile, floristic composition, and habitat, the primary limestone vegetation can be classified into three vegetation types, i.e., tropical seasonal rain forest, tropical seasonal moist forest, and tropical montane dwarf forest (Zhu et al., 1998a). Within these, six formations, including nine communities, were recognized:

(1) Ravine seasonal rain forest (including the *Pometia tomentosa–Alphonsea monogyna* community and *Pometia tomentosa–Celtis philippensis* var. *wightii* community);
(2) Lower hill seasonal rain forest (including only the *Celtis philippensis* var. *wightii–Lasiococca comberi* var. *pseudoverticillata* community);
(3) Evergreen moist forest (including the *Osmanthus polyneurus–Dracaena cochinchinensis* community and *Lasiococca comberi* var. *pseudoverticillata–Cleistanthus sumatranus* community);
(4) Semi-evergreen moist forest (including the *Bombax insignis–Colona floribunda* community and *Bombax insignis–Garcinia bracteata* community);
(5) Evergreen dwarf forest (including only the *Photinia angusta–Pistacia weinmannifolia* community);
(6) Semi-evergreen dwarf forest (including only the *Ficus neriifolia–Dracaena cochinchinensis* community).

Detailed descriptions and ecological analyses of the communities have been reported earlier (Zhu et al., 1998a). Here the classification of the limestone vegetation is concisely enumerated so that the biogeographical components of the limestone vegetation can be better understood.

TROPICAL SEASONAL RAIN FOREST

Tropical seasonal rain forest on limestone, just as the regional tropical seasonal rain forest off limestone, shares characteristics with the equatorial lowland rain forest. These forests are mainly evergreen, but there are some deciduous trees in the emergent layer. This is equivalent to the tropical semi-evergreen rain forest of Southeast Asia (Whitmore, 1984), or the tropical semi-evergreen forest of India–Burma (Champion, 1936), as well as the evergreen seasonal forest of tropical America (Beard, 1944, 1955). In southern Yunnan, these limestone forests occur in wet valleys and on lower slopes of hills or mountains below 1000 m altitude. This same forest type also occurs in northern Thailand (Smitinand, 1966) and North Vietnam (Thin, 1997), although different names were used. The tropical seasonal rain forest represents Southeast Asian tropical rain forest at its latitudinal and altitudinal limits. The ecological structure of the tropical seasonal rain forest on limestone is almost exactly the same as the seasonal rain forest off limestone in the Xishuangbanna region (Zhu, 1992,

Table 1. Life forms of the limestone forest in southern Yunnan.

Life form*	Para	Epiph	Liana		Phanerophytes						Cham	Geoph	Thero-phytes
			Woody	Herb	Megaph	Mesoph	Microph	Nanoph	Hph	All			
Limestone seasonal rain forest	1	7	48	3	9	84	34	17	12	156	31	3	—
(14800 m² of 7 plots, total 249 species)	0.4%	2.8%	19.3%	1.2%	3.6%	33.7%	13.7%	6.8%	4.8%	62.7%	12.4%	1.2%	—
Limestone seasonal moist forest	—	18	27	5	2	62	36	21	3	124	28	7	2
(9650 m² of 7 plots, total 211 species)	—	8.5%	12.8%	2.3%	0.9%	29%	17%	9.9%	1.4%	58.8%	13%	3.3%	0.9%

* Life form (Raunkiaer, 1934); Megaph = Megaphanerophyte (perennials over 30 m high); Mesoph = Mesophanerophyte (perennials 8 to 30 m high); Microph = Microphanerophyte (perennials 2 to 8 m high); Nanoph = Nanophanerophyte (perennials 0.25 to 2 m high); Hph = Herbaceous phanerophyte (herbaceous perennials over 0.25 m high); Cham = Chamaephytes (perennials less than 0.25 m high above ground); Geoph = Geophyte (perennials, dying back above ground); Para = Parasitic; Epiph = Epiphytes; Therophytes (annuals).

1997). Most species in the seasonal rain forest on limestone are also found in the adjacent non-limestone seasonal rain forest, but the latter is more diverse with additional species, which are not found on the limestone.

TROPICAL SEASONAL MOIST FOREST

Tropical seasonal moist forest occurs on the middle and upper limestone slopes ranging from 650 to 1300 m altitude. This vegetation type abuts the seasonal rain forest and was called monsoon forest by some Chinese authors (Liu, 1987; Wu, 1980). The term seasonal moist forest is preferred here because the forest is not equivalent to Schimper's monsoon forest (Schimper, 1903), in spite of the fact that it is affected by seasonal dryness and contains a variable percentage of deciduous trees. The seasonal dryness in the region is compensated to some extent by dense fog accompanied by low temperatures in the same months (November to April) (Whitmore, 1984). Some deciduous trees, such as *Gmelina arborea* Roxb., *Anthocephalus chinensis* (Lam.) Rich. ex Walp., and *Homalium laoticum* Gagn. var. *glabretum* C. Y. Wu, shed leaves toward the end of the dry season, while others, such as *Cratoxylon cochinchinensis* (Lour.) Bl., *Ficus religiosa* L., and *Elaeocarpus varunua* Buch.-Ham. ex Mast., shed their old leaves as new ones develop. This suggests that deciduousness in the region is more frequently associated with locally dry habitats than the seasonal dryness of climate. Therefore, using the term monsoon forest for the evergreen or semi-evergreen forest on limestone is confusing because Schimper's monsoon forest is more or less completely leafless during the dry season.

MONTANE DWARF FOREST

Montane dwarf forest occurs only on the tops of hills and summits of mountains at altitudes above 900 m. There is only one dwarf tree layer with a canopy height of 7–15 m. Epiphytic orchids, such as *Eria hainanensis* Rolfe and *Bulbophyllum nigrescens* Rolfe, and non-vascular epiphytes (bryophytes and lichens) are abundant. In some sites small woody climbers, such as *Derris caudatilimba* How (Papilionaceae) and *Pristimera arborea* (Roxb.) A. C. Smith (Hippocrateaceae), are also frequent.

PLANT PHYSIOGNOMY OR ATTRIBUTES

From plot data, life form spectra (Raunkiaer, 1934) of the two main forest types (seasonal rain forest and seasonal moist forest) are compiled in

Table 2. Physiognomic characteristics of the limestone forest in southern Yunnan.

		Leaf form		Leaf texture		Leaf size			
	Forest type	S	C	P	L	Na	Mi	Me	Ma
Limestone seasonal rain forest[1]	Percentage of species	72.3	27.7	47.9	52.1	0	13.8	76.6	9.6
	Percentage of Importance Value Index (IVI)[3]	76.3	23.7	52.8	47.2	0	3.8	91	5.3
Limestone seasonal moist forest[2]	Percentage of species	68	32	51.5	48.5	1	21.5	74.2	3.1
	Percentage of Importance Value Index (IVI)	74.8	25.2	41.7	58.3	0.4	23.3	66.5	9.7

[1] From 14800 m² of 7 plots, total of 94 tree species > 5 cm DBH.

[2] From 9650 m² of 7 plots, total of 97 tree species > 5 cm DBH.

[3] IVI = Relative dominant density + Relative frequency + Relative dominant breast area (Curtis & McIntosh, 1951).

S: Simple leaves; C: Compound leaves; P: Papery leaves; L: Leathery leaves; Ma: Macrophyll (large to 164,025 mm²); Me: Mesophyll (to 18,222 mm²); Mi: Microphyll (to 2025 mm²); Na: Nanophyll (to 225 mm²) (Raunkiaer, 1934).

Table 1. Leaf size spectra, leaf form, and leaf texture are shown in Table 2. Both forest types were dominated by phanerophytes. Including lianas, these perennial phanerophytes make up 73.9–83.2% of the total species, while annual chamaephytes account for only 12.4–13%. However, the seasonal moist forest shows lower percentages of woody lianas as well as megaphanerophytes and mesophanerophytes, but higher percentages of epiphytes as well as microphanerophytes and nanophanerophytes than the seasonal rain forest.

Both forest types have species with mesophyllous leaves making up ca. 75% of the total tree species, but the forests show clear differences if the species are weighted by importance value index (IVI). This increases the percentage of mesophyllous perennials and decreases the percentage of micro- and macrophyllous trees in seasonal rain forest, while the opposite trend is seen in seasonal moist forest. Seasonal moist forest occupies much more rugged habitats with thinner and drier soils, and has more microphyllous species. In weighting by IVI, the increase in percentage of macrophyllous trees in seasonal moist forest is mainly due to the dominant evergreen species *Dracaena cochinchinensis* (Lour.) S. C. Chen (Agavaceae), with its long leathery lanceolate leaves, and the dominant deciduous tree species *Colona floribunda* (Wall. ex Voigt) Craib (Tiliaceae) also with large leaves to 30 cm long. In weighting the species by IVI, the percentage of leathery leaves decreases in seasonal rain forest but increases in seasonal moist forest due to the presence of some species with these leathery leaves such as *Cleistanthus sumatranus* (Miq.) Muell.-Arg. (Euphorbiaceae) and *Dracaena cochinchinensis.*

ECOLOGICAL SPECIES GROUP

Based on the study of the limestone floras of Japan and Taiwan, Shimizu (1964) divided limestone plants into five ecological groups:

(1) plants exclusive to limestone habitat;
(2) plants selective for and found mainly in limestone;
(3) plants preferring and dominant on limestone;
(4) taxa indifferent, with no special association with limestone;
(5) plants found only occasionally on limestone or strangers to limestone.

To Shimizu, these first three groups were characteristic species for the limestone habitats and in particular his exclusive and selective taxa were calcicoles. Chin (1977) accepted this classification and similarly categorized plants on limestone in the Malay Peninsula into four groups, combining selective and preferent plants. Similar ecological species groups have been later recognized by Chinese botanists (Liang et al., 1985; Liu et al., 1994).

Table 3. The ecological species groups of the limestone flora of southern Yunnan.

Ecological species groups (see Shimizu, 1964; Chin, 1977)	Number of species	%
Plants found only on limestone: endemic to southern Yunnan	24	1.7
not endemic to southern Yunnan	117	8.4
Plants dominant on limestone	170	12.2
Plants no restriction on limestone	858	61.6
Plants found occasionally on limestone	225	16.1
Total	1394	100

Table 4. Predominant families found in limestone forests of southern Yunnan.

	No. of genera	No. of species	%*		No. of genera	No. of species	%
Orchidaceae	35	86	26.9	Verbenaceae	6	20	43.5
Rubiaceae	34	58	64.1	Labiatae	13	20	30.1
Euphorbiaceae	27	58	60.4	Gesneriaceae	13	19	63.3
Papilionaceae	22	55	43.4	Sterculiaceae	7	18	46.8
Moraceae	7	48	73.8	Dioscoriaceae	1	18	64.3
Vitaceae	7	38	79.5	Menispermaceae	10	17	60.7
Acanthaceae	26	36	65.4	Liliaceae	10	16	64.0
Rutaceae	11	35	71.4	Araceae	10	15	44.1
Asclepiadaceae	16	35	53.0	Compositae	8	15	14.6
Urticaceae	12	35	53.0	Myrsinaceae	4	14	38.2
Lauraceae	10	35	45.0	Commelinaceae	7	14	60.9
Apocynaceae	19	33	58.9	Zingiberaceae	6	14	42.4
Meliaceae	12	30	83.0	Myrtaceae	1	13	45.8
Annonaceae	12	30	50.9	Tiliaceae	3	12	57.1
Cucurbitaceae	9	24	52.3	Mimosaceae	6	12	66.6
Rhamnaceae	19	21	70.4	Anacardiaceae	7	11	64.7
Piperaceae	3	20	54.8	Convolvulaceae	4	11	37.4
				Ulmaceae	5	11	100

$$* \% = \frac{\text{the no. of species on limestone}}{\text{the total no. of species in southern Yunnan}} \times 100$$

Following Shimizu and Chin's classifications, we divided the limestone flora of southern Yunnan into these four ecological species groups (Table 3). In our study, 141 vascular plant species are restricted to limestone habitats and thus are exclusively found here. These include the following common species *Celtis philippensis* var. *wightii, Amoora calcicola, Murraya tetramera, Pistacia weinmannifolia,* as well as species in *Agapetes, Sageretia, Tupistra,* and *Pristimera.* Of these, 24 species are endemic to southern Yunnan. Taxa exclusive to limestone make up about 10% of the total limestone flora, which agrees with the results from Longgan limestone (exclusive taxa, 13%) (Liang et al., 1985) and Longhua limestone (exclusive taxa, 10%) (Liu et al., 1994) from Guangxi Province in China. Both the exclusive and preferent taxa make up 22.3% of the total sum. They could be termed as characteristic species for limestone habitats (see Appendix 1). This is similar to the results from Longgan in Guangxi (with these characteristic species making up 20% of the total sum) (Liang et al., 1985) and from the Malay Peninsula (27.5%) (Chin, 1977).

THE FLORA AND ITS BIOGEOGRAPHY

In the limestone forests of southern Yunnan, China, 153 families of vascular plants including 640 genera and 1394 species and varieties, were recorded, of which seed plants compose 129 families, 558 genera, and 1269 species (see Appendix 1). More than 80% of the species also occur in the non-limestone habitats of the Xishuangbanna region.

The limestone flora makes up about one quarter of the total species of the regional flora. (The flora of the Xishuangbanna region was primarily documented with 3336 native species of 1218 genera and 207 families of seed plants; see Li, 1996.) Some families show relative preference for limestone habitats (with more than 60% of the total number of species in the region on limestone), for example, Acanthaceae, Euphorbiaceae, Gesneriaceae, Meliaceae, Menispermaceae, Moraceae, Rhamnaceae, Rubiaceae, Rutaceae, Vitaceae, and Ulmaceae (Table 4). Other families, such as Hippocrateaceae, Icacinaceae, and Vacciniaceae, show an even stronger preference for limestone (found almost exclusively in limestone habitats in southern Yunnan), although they are not among the predominant families in species richness.

The distribution types of Chinese seed plants at the generic level were documented by Wu (1991). Based on Wu's document, 544 of the 558 genera of seed plants from the limestone forest of southern Yunnan can be divided into 12 distribution types or geographic elements (14 genera, which are cosmopolitan in distribution, are not included in the geographic statistics). One thousand two hundred forty-four of the 1269 species of seed plants from the limestone forest can be recognized in nine dis-

Table 5. Geographic affinities of the limestone forests of southern Yunnan.

Geographic element at the generic level (see Wu, 1991)	Percentage of genera	Geographic elements at the specific level	Percentage of species
1. Pantropic	21.1%	1. Pantropic	0.6%
2. Tropical Asia–Tropical America disjunct	2.9%	2. Tropical Asia–Tropical America disjunct	0.2%
3. Old World Tropics	13.8%	3. Old World Tropics	0.4%
4. Tropical Asia to Tropical Australia	9.0%	4. Tropical Asia to Tropical Australia	3.2%
5. Tropical Asia to Tropical Africa	7.9%	5. Tropical Asia to Tropical Africa	1.3%
6. Tropical Asia	35.3%	6. Tropical Asia	(64.5%)
7. Northern Temperate	2.8%	6a. India-Malaysia	17.0%
8. Temperate Eastern Asia and Northern America disjunct	2.8%	6b. Mainland Southeastern Asia to Malaysia	7.3%
9. Old World Temperate	0.9%	6c. Southern Asia to Mainland Southeastern Asia	19.9%
10. Temperate Mediterranean, Western Asia to Central Asia	0.2%	6d. Mainland Southeastern Asia to Southern China	20.3%
11. Eastern Asia	2.9%	7. Eastern Asia	0.5%
12. Endemic to China	0.4%	8. Southern China	10.6%
		9. Endemic to Yunnan	18.6%
Total of 544 genera	100%	Total of 1244 species	100%

tribution types based on their geographic distribution (25 species of seed plants are not included due to insufficient distribution references) (Table 5). At the generic level, the geographic elements of tropical distribution (1–6, Table 5) compose 90% of the total genera; the geographic elements of temperate distribution (7–10, Table 5) make up only 6.7%. At the specific level, the species that are of typical tropical distribution (1–6, Table 5) account for 70.2% of the total species. Among these, the geographic types that are considered to be from tropical Asia make up 64.5% of the total species from limestone forests in Xishuangbanna. If the species from the tropical areas adjacent to Xishuangbanna from southern China and Yunnan are included, these tropical species compose more than 90%. This indicates that the limestone flora at Xishuangbanna is principally tropical in nature and represents the tropical Asian flora at its northern tropical margin.

In a floristic comparison with nine similar floras, both limestone and non-limestone, from southwest China, northern Vietnam (Thin, 1997), northern Thailand (Smitinand, 1966), and the Malay Peninsula (Chin, 1977, 1979; Burkill & Henderson, 1925) (Table 6), the limestone flora of southern Yunnan displays explicit taxonomic affinities to the tropical floras and shows a closer affinity to the floras from the Malay Peninsula than to other floras from subtropical China (the floras of Huapin and Dongyang, see Li et al., 1986; Xu, 1984), even though these Malaysian floras lie farther away geographically from southern Yunnan. Our limestone flora in southern Yunnan shares the most genera with the limestone flora of northern Vietnam (Cucphuong, see Thin, 1997) among those floras compared in this study. The similarity at the generic level between our limestone flora and the limestone flora of northern Thailand (Doi Chiengdao) (Smitinand, 1966) is less than would be expected from its geographic proximity. This lack of correspondence could be because the plant list for Doi Chiengdao used here for comparison is an incomplete one consisting of only 512 species, less than half reported for most other sites in Table 6. The limestone flora of Xishuangbanna did not show a higher floristic similarity to other regional limestone floras than to non-limestone floras in our comparison. It appears that limestone floras develop from local or regional floras, supported also by the fact that only about 10% of the total species of limestone floras (the exclusive group) are restricted to limestone habitats in our study.

The floristic relationships between our limestone flora in southern Yunnan and neighboring floras of

Table 6. Comparison of floristic similarities between the limestone habitats of Xishuangbanna, southern Yunnan, and the limestone and non-limestone habitats from southwestern China and southeastern Asia.

Location	Habitat	Size of flora (Seed plants)	Shared taxa by both floras	Similarity coefficients
2. Longgan, SW China	limestone	149 families	118	91.2
22°14–33′N, 106°46′E		669 genera	371	66.5
		1363 species		
3. Daqinshan Mountains, SW China	non-limestone	182 fam.	126	97.4
22°14′N, 107°E		871 gen.	389	69.8
		1813 spp.		
4. Gulinqing, SW China	limestone	143 fam.	116	89.9
22°36′N, 104°E		496 gen.	261	52.6
		1095 spp.		
5. Huapin, SW China	non-limestone	151 fam.	83	72.8
25°31–39′N, 109°50′E		475 gen.	150	33.2
		1051 spp.		
6. Dongyang Mountains, SW China	limestone	116 fam.	86	73.7
25°14′N, 107°56′E		367 gen.	153	41.6
		736 spp.		
7. Cucphuong, N Vietnam	limestone	167 fam.	120	93
20°14–24′N, 105°24–44 ′E		860 gen.	428	76.7
		1661 spp.		
8. Chiendae, N Thailand	limestone	101 fam.	93	92.1
19°2′N, 98°54′E		342 gen.	181	52.9
		512 spp.		
9. Malay peninsula limestone	limestone	117 fam.	93	81.6
1–6°N, 100–104°E		535 gen.	244	51.6
		1112 spp.		
10. Taiping, Malay peninsula	non-limestone	115 fam.	94	82.5
4°N, 101°E		682 gen.	243	51.6
		1939 spp.		

Notes: The direct comparison of species composition between the different floras is not very significant before the local floras are updated and the taxa revised; therefore, the comparison of floristic similarities between the different floras at the specific level is not made.

References: location 2 (Chen, 1985); 3 (Daqinshan Forest station of Guanxi Forestry Bureau, 1980); 4 (Li, 1987); 5 (Li et al., 1986); 6 (Xu, 1984); 7 (Thin, 1997); 8 (Smitinand, 1966); 9 (Chin, 1977, 1979); 10 (Burkill & Henderson, 1925).

tropical Asia and southern China were discussed by Zhu (1997). This limestone flora shares all families and 88% of its genera with the flora of Indochina (Lecomte, 1907–1951; Aubréville et al., 1960–1996), 96% of its families and 68% of its genera with the flora of the Malay Peninsula (Ridley, 1967; Keng, 1978), 73% of its woody plant genera with Burma (Kurz, 1877), and more than 97% of its families and more than 80% of its genera with other tropical floras of south China (including Hainan Island; see Wu, 1994). The limestone flora of Xishuangbanna demonstrates strong affinity to other tropical Asian floras.

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Appendix 1. Ecological species groups of the limestone vegetation in southern Yunnan. *Flora Reipublicae Popularis Sinicae* is the authoritative source for specific and infraspecific names except for ones recently revised and in IPNI (www.ipni.org) and TROPICOS (http://mobot.mobot.org/W3T/Search/vast.html). The family names of angiosperms are according to the Angiosperm Phylogeny Website (http://www.mobot.org/MOBOT/research/APweb/).

Seed Plant Taxa exclusive to limestone habitats and endemic to southern Yunnan	
ACANTHACEAE	
Baphicacanthus multibracteolata H. T. Chang & H. Chu	*Chu Hua 1192* (holotype, SYS)
AGAVACEAE	
Dracaena menglaensis G. Z. Ye	*Ye Guang-zheng 9035* (holotype, YCE; isotype, KUN)
ALANGIACEAE	
Alangium kurzii var. *pachyphyllum* W. P. Fang & H. Y. Su	*Zhang Shun-cheng 24027* (HITBC); *Li Yan-hui 1255* (holotype, KUN)
DIOSCOREACEAE	
Dioscorea menglaensis H. Li	*Pei Sheng-ji 10347* (holotype, KUN)
EBENACEAE	
Diospyros atrotricha H. W. Li	*Li Yan-hui 4215* (holotype, KUN; isotype, HITBC)
EUPHORBIACEAE	
Croton yanhuii Y. T. Chang	*Ch1050* (SYS); *Li Yan-hui 03587* (holotype, KUN; isotype, HITBC)
Trigonostemon lii Y. T. Chang	*Li Yan-hui 4576* (holotype, KUN)
FAGACEAE	
Quercus yiwuensis Huang	*Pei Sheng-ji 59-10040* (holotype, KUN)
GESNERIACEAE	
Ornithoboea calcicola C. Y. Wu ex H. W. Li	*Pei Sheng-ji 59-10072* (isotype, HITBC)
LAURACEAE	
Lindera nacusua var. *monglunensis* H. P. Tsui	*Li Yan-hui 4231* (HITBC), *386* (holotype, KUN)
Neolitsea menglaensis Y. C. Yang & P. H. Huang	*Li Yan-hui 20078* (holotype, KUN; isotype, HITBC)
MALVACEAE	
Pterospermum menglunensis H. H. Hsue	*Ch378* (SYS); *Li Yan-hui 4634* (holotype, KUN; isotype, HITBC)
Pterospermum yunnanensis H. H. Hsue	*Li Yan-hui 33830* (HITBC), *3717* (holotype, KUN); *Tao Guo-da 13655* (HITBC)
MELIACEAE	
Amoora calcicola C. Y. Wu & H. Li	*Li Yan-hui 3712* (HITBC), *3814* (HITBC), *2804* (HITBC); *Pei Sheng-ji 59-10292* (holotype, KUN)
PIPERACEAE	
Piper mischocarpum Y. C. Tseng	*Cai C.T. 59-10784* (holotype, KUN); *Li Yan-hui 3771* (HITBC); *Tao Guo-da 4177* (HITBC), *7152* (HITBC)
Sageretia thea var. *cordiformis* Y. L. Chen & P. K. Chou	*W. T. Wang 10496* (holotype, KUN)

Appendix 1. Continued.

THEACEAE	
Pyrenaria menglaensis G. D. Tao	*Tao Guo-da 15933* (holotype, KUN; isotype, HITBC)
Seed Plant Taxa exclusive to limestone habitats but not endemic to southern Yunnan	
ACANTHACEAE	
Andrographis laxiflora var. *glomeruliflora* (Bremek.) H. Chu	*Ch1193* (SYS), *Ch1219* (SYS)
Daedalacanthus tetragonus T. Anders.	*Ch255* (SYS), *Ch1175* (SYS), *Ch1217* (SYS); *Tao-Guo-da 3797* (HITBC)
Pteracanthus alatus (Wall. ex Nees) Bremek.	*Li Yan-hui 20047* (HITBC)
Strobilanthes psiostachys C. B. Clarke ex W. W. Smith	*Li Yan-hui 4605* (HITBC)
Thunbergia coccinea Wall.	*Ch454* (SYS), *Ch1186* (SYS); *Li Yan-hui 5190* (HITBC), *2911* (HITBC)
AGAVACEAE	
Dracaena cambodiana Pierre ex Gagnep.	*Wang Hong 3159* (HITBC), *3160* (HITBC)
Dracaena terniflora Roxb.	*Yang Zheng-hong 12178* (HITBC); *Expedition 32120* (HITBC), *34923* (HITBC)
ANACARDIACEAE	
Pistacia weinmannifolia Poiss. ex Franch.	*Expedition 32613* (HITBC); *Pei Sheng-ji 10045* (HITBC); *Tao Guo-da 1212* (HITBC)
Spondias lakonensis var. *hirsutus* C. Y. Wu & T. L. Ming	*Wang Hong 1792* (HITBC)
Toxicodendron fulvum (Craib) C. Y. Wu & T. L. Ming	*Pei Shengji 10034* (HITBC); *Tao Guo-da 13650* (HITBC)
ANNONACEAE	
Alphonsea boniana Finet & Gagnep.	*Ch56* (SYS)
Alphonsea mollis Dunn	*Li Yan-hui 1043* (HITBC), *4610* (HITBC)
Alphonsea squamosa Finet & Gagnep.	*Ch815* (SYS)
Miliusa velutina Hook. f. & Thoms.	*Ch386* (SYS), *Ch814* (SYS), *Ch985* (SYS); *Zhu Hua & Wang Hong 2416* (HITBC)
Mitrephora calcarea Diels ex Ast	*Ch545* (SYS)
Polyalthia petelotii Merr.	*Ch909* (SYS)
APOCYNACEAE	
Aganosma acuminata (Roxb.) G. Don	*Ch584* (SYS)
Anodendron affine var. *pingpienense* Tsiang & P. T. Li	*Ch802* (SYS), *Ch715* (SYS)
Cosmostigma hainanense Tsiang	*Ch870* (SYS)
ARACEAE	
Amorphophallus yunnanensis Engl.	*Li Yan-hui 4225* (HITBC)
Gonatanthus pumilus Engl. & K. Krause	*Tao Guo-da et al. 16166* (HITBC)
Remusatia vivipara Schott	*Expedition 10201* (HITBC)
BOMBACACEAE	
Bombax insigne Wall.	*Tao Guo-da 9007* (HITBC), *9008* (HITBC)
BORAGINACEAE	
Ehretia dunniana Lév.	*Ch29* (SYS), *Ch373* (SYS); *Li Yan-hui 3300* (HITBC), *3726* (HITBC)

Appendix 1. Continued.

BUXACEAE	
Sarcococca vagans Stapf	*Tao Guo-da 15739* (HITBC), *13691* (HITBC)
CAPPARIDACEAE	
Capparis bodinieri Lév.	*Ch321* (SYS)
CELASTRACEAE	
Loeseneriella merrilliana A. C. Smith	*Li Yan-hui 455* (HITBC); *Tao Guo-da 13672* (HITBC)
Loeseneriella yunnanensis (Hu) A. C. Smith	*Ch1015* (SYS), *Ch1063* (SYS); *Li Yan-hui 2736* (HITBC); *Wang Hong 1573* (HITBC)
Pristimera cambodiana (Pierre) A. C. Smith	*Ch24* (SYS); *Wang Hong 1575* (HITBC)
Pristimera setulosa A. C. Smith	*Li Yan-hui 3141* (HITBC)
COMBRETACEAE	
Anogeissus acuminata Wall.	*Tong Shao-quan 24960* (HITBG)
COMPOSITAE	
Pterocypsela indica (L.) C. Shih	*YB004125* (HITBC)
Vernonia curtisii Craib & Hutchison	*Li Yan-hui 3780* (HITBC); *Tao Guo-da 13664* (HITBC)
CONVOLVULACEAE	
Porana paniculata Roxb.	*Ch1170* (SYS); *Wang Hong 2655* (HITBC)
Porana racemosa Roxb.	*Ch469* (SYS); *Zhu Pei-zhi 10527* (HITBC)
Tridynamia sinensis (Hemsl.) G. W. Staples	*Ch1232* (SYS)
Tridynamia sinensis var. *delavayi* (Gagnep. & Courchet) G. W. Staples	*Ch513* (SYS)
CRUCIFERAE	
Cardamine calcicola W. W. Smith	*Li Yan-hui 4217* (HITBC)
DIOSCOREACEAE	
Dioscorea arachidna Prain & Burkill	*Ch845* (SYS)
Dioscorea aspersa Prain & Burkill	*Ch921* (SYS)
Dioscorea chingii Prain & Burkill	*Ch473* (SYS); *Li Yan-hui 2036* (HITBC)
Dioscorea pulverea Prain & Burkill	*Ch791* (SYS); *Wang Hong 3147* (HITBC)
Dioscorea tentaculigera Prain & Burkill	*Pei Sheng-ji 9985* (HITBC)
ERICACEAE	
Agapetes burmanica W. E. Evans	*Li Yan-hui 3718* (HITBC), *2739* (HITBC)
Agapetes lobbii C. B. Clarke	*Li Yan-hui 3719* (HITBC)
Agapetes mannii Hemsl.	*Li Yan-hui 3629* (HITBC)
EUPHORBIACEAE	
Cleistanthus sumatranus (Miq.) Muell.-Arg.	*Li Yan-hui 3095* (HITBC), *2529* (HITBC)
Croton argyratus Blume	*Ch179* (SYS)
Phyllanthus clarkei Hook. f.	*Ch563* (SYS), *Ch812* (SYS)
Trigonostemon bonianus Gagnep.	*Ch367* (SYS), *Ch39* (SYS), *Ch353* (SYS)

Appendix 1. Continued.

FABACEAE	
Albizia odoratissima (L.) Benth.	*Li Yan-hui 1411* (HITBC)
Bauhinia carcinophylla Merr.	*Ch1097* (SYS)
Caesalpinia tsoongii Merr.	*Ch118* (SYS)
Callerya eurybotrya (Drake) A. M. Schot	*Li Yan-hui 4200* (HITBC)
Derris caudatilimba How	*Ch398* (SYS), *Ch504* (SYS)
Milettia tetraptera Kurz	*Li Yan-hui 4100* (HITBC)
Sophora prazeri Prain	*Ch394* (SYS), *Ch559* (SYS); *Li Yan-hui 2802* (HITBC), *4277* (HITBC)
Sophora tonkinensis Gagnep.	*Ch619* (SYS)
FUMARIACEAE	
Corydalis taliensis var. *siamensis* (Craib) X. Zhang	*Li Yan-hui 20062* (HITBC), *3727* (HITBC)
GESNERIACEAE	
Raphiocarpus begoniifolius (H. Lév.) B. L. Burtt	*Ch947* (SYS); *Pei Sheng-ji 9892* (HITBC); *Tao Guo-da 15902* (HITBC)
Didymocarpus margaritae W. W. Sm.	*Pei Sheng-ji 1054* (HITBC)
Lysionotus serratus D. Don	*Ch624* (SYS), *Ch806* (SYS); *Pei Sheng-ji 59-9937* (HITBC); *Tao Guo-da 15750* (HITBC)
Ornithoboea henryi Craib	*Expedition 32625* (HITBC); *Pei Sheng-ji 59-10069* (HITBC)
GUTTIFERAE	
Garcinia bracteata C. Y. Wu ex Y. H. Li	*Li Yan-hui 4103* (HITBC), *3813* (HITBC)
ICACINACEAE	
Gomphandra tetrandra (Wall.) Sleum.	*Tao Guo-da 11182* (HITBC)
LABIATAE	
Coleus xanthanthus C. Y. Wu & Y. C. Huang	*Pei Sheng-ji 10138* (HITBC)
Gomphostemma parviflorum Wall.	*Cui Jing-yun 14659* (HITBC); *Tao Guo-da 15798* (HITBC)
Rabdosia eriocalyx var. *laxiflora* C. Y. Wu & H. W. Li	*Li Bao-gui 9911209* (HITBC); *Li Yan-hui 3759* (HITBC); *Wang Zhong-yu s.n.* (HITBC)
LAMIACEAE	
Symphorema involucratum Roxb.	*Li Yan-hui 2988* (HITBC), *4852* (HITBC)
LAURACEAE	
Cryptocarya acutifolia H. W. Li	*Li Yan-hui 1029* (HITBC), *3052* (HITBC)
LINACEAE	
Reinwardtia indica Dum.	*Expedition 34310* (HITBC)
MALVACEAE	
Pterospermum chingtungense C. Y. Wu & Hsue	*Expedition 34533* (HITBC)
Pterospermum proteus Burkill	*Li Yan-hui 3586* (HITBC); *Wang Hong 831* (HITBC), *842* (HITBC)

Appendix 1. Continued.

MELIACEAE	
Aglaia testicularis C. Y. Wu	*Ch339* (SYS)
Amoora tetrapetala (Pierre) C. Y. Wu	*Ch529* (SYS); *Wang Hong 1710* (HITBC), *1715* (HITBC)
Munronia henryi Harms	*Ch351* (SYS), *Ch192* (SYS); *Li Yan-hui 3327* (HITBC)
MENISPERMACEAE	
Cyclea sutchuenensis Gagnep.	*Ch901* (SYS)
Stephania chingtungensis H. S. Lo	*Tao Guo-da 43898* (HITBC)
Stephania epigaea H. S. Lo	*Tao Guo-da 15672* (HITBC)
MYRSINACEAE	
Myrsine semiserrata Wall.	*Li Yan-hui 20032* (HITBC); *Tao-Guo-da 15729* (HITBC); *Wang Hong 1960* (HITBC)
OLACACEAE	
Natsiatopsis thunbergiaefolia Kurz	*Tao Guo-da 42370* (HITBC)
OLEACEAE	
Ligustrum sinense var. *coryanum* (W. W. Smith) Hand.-Mazz.	*Li Yan-hui 429* (HITBC); *Tao Guo-da 16440* (HITBC); *Wang Hong 2101* (HITBC), *2091* (HITBC)
ORCHIDACEAE	
Bulbophyllum ambrosia (Hance) Schltr.	*Ch679* (SYS)
Bulbophyllum kwangtungense Schltr.	*Ch22* (SYS)
Bulbophyllum nigrescens Rolfe	*Zhu Pei-zhi 8683* (HITBC)
Dendrobium salaccense Lindl.	*Ch158* (SYS)
Eulophia bracteosa Lindl.	*Li Yan-hui 4150* (HITBC)
Pholidota chinensis Lindl.	*Tao Guo-da 44107* (HITBC)
PALMAE	
Caryota urens L.	*Chen San-yang 18959* (HITBC)
PIPERACEAE	
Peperomia leptostachya var. *cambodiana* (C. DC.) Merr.	*Ch950* (SYS)
PRIMULACEAE	
Lysimachia garrettii Fletcher	*Li Yan-hui 3302* (HITBC)
RHAMNACEAE	
Gouania javanica Miq.	*Ch798* (SYS), *Ch850* (SYS); *Li Yan-hui 3714* (HITBC)
Hovenia acerda var. *kiukiangensis* (Hu & Cheng) C. Y. Wu ex Y. L. Chen	*Tao Guo-da 39915* (HITBC)
Sageretia laxiflora Hand.-Mazz.	*Ch399* (SYS); *Zhu Pei-zhi 10478* (HITBC), *10479* (HITBC)
Ventilago calyculata var. *trichoclada* Y. L. Chen & P. K. Chou	*Ch550* (SYS); *Li Yan-hui 5230* (HITBC)

Appendix 1. Continued.

RUBIACEAE	
Damnacanthus indicus Gaertn. f.	*Ch361* (SYS), *Ch816* (SYS)
Hymenopogon parasiticus var. *longiflorus* How ex W. C. Chen	*Tao Guo-da 13651* (HITBC)
Pavetta polyantha R. Br.	*Ch368* (SYS), *Ch270* (SYS); *Li Yan-hui 1773* (HITBC), *4111* (HITBC)
Pavetta scabrifolia Bremek.	*Li Yan-hui 4240* (HITBC), *3871* (HITBC)
RUTACEAE	
Murraya euchrestifolia Hayata	*Li Yan-hui 3716* (HITBC), *3309* (HITBC); *Tao Guo-da 15722* (HITBC); *Expedition 32673* (HITBC)
Murraya tetramera Huang	*Li Yan-hui 3815* (HITBC), *4269* (HITBC)
SCROPHULARIACEAE	
Lindenbergia philippinensis (Cham. & Schltdl.) Benth.	*Ch96* (SYS); *Li Yan-hui 363* (HITBC), *3952* (HITBC)
SIMARUBACEAE	
Brucea mollis Wall.	*Li Yan-hui 4203* (HITBC)
STAPHYLEACEAE	
Turpinia robusta Craib	*Li Yan-hui 393* (HITBC); *Zhang Jian-hou 13707* (HITBC)
ULMACEAE	
Celtis wightii var. *philippensis* (Planch.) E. Soepadmo	*Ch32* (SYS), *Ch371* (SYS), *Ch1089* (SYS); *Li Yan-hui 391* (HITBC), *4211* (HITBC)
URTICACEAE	
Elatostema herbaceifolium Hayata	*Ch877* (SYS)
Elatostema salvinioides W. T. Wang	*Ch879* (SYS); *Li Yan-hui 4105* (HITBC); *Zhu Pei-zhi 8649* (HITBC)
Laportea urentissima Gagnep.	*Li Yan-hui 396* (HITBC)
Pellionia scabra Benth.	*Ch917* (SYS)
Pilea cadierei Gagnep. & Guillaumin	*Ch572* (SYS), *Ch719* (SYS)
Procris crenata C. B. Rob.	*Ch514* (SYS), *Ch632* (SYS); *Li Yan-hui 3751* (HITBC)
VERBENACEAE	
Garrettia siamensis Fletcher	*Ch358* (SYS), *Ch710* (SYS), *Ch941* (SYS)
VITACEAE	
Tetrastigma cambodianum Pierre ex Gagnep.	*Ch91* (SYS), *Ch925* (SYS); *Zhang Jian-hou 13602* (HITBC)
Tetrastigma dubium (Lawson) Planch.	*Li Yan-hui 3700* (HITBC), *2737* (HITBC)
Tetrastigma rupestre Planch.	*Ch139* (SYS)
ZINGIBERACEAE	
Pommereschea lackneri Wittm.	*Pei Sheng-ji 10073* (HITBC); *Tao Guo-da 44091* (HITBC)

Seed Plant Taxa preferent to limestone habitats

Appendix 1. Continued.

ACANTHACEAE	
Andrographis laxiflora (Blume) Lindau	*Ch376* (SYS), *Ch808* (SYS), *Ch974* (SYS); *Li Yan-hui 3721* (HITBC)
Eranthemum pulchellum Andr.	*Li Yan-hui 2898* (HITBC)
Goldfussia glomerata Nees	*Ch1191* (SYS); *Tao Guo-da 3775* (HITBC)
Pseuderanthemum palatiferum Radlk.	*Ch137* (SYS); *Ch172* (SYS), *Ch180* (SYS), *Ch310* (SYS)
Pseuderanthemum polyanthum (C. B. Clarke) Merr.	*Ch91* (SYS); *Li Yan-hui 1011* (HITBC)
Rhapidospora vagabunda (R. Ben) C. Y. Wu	*Ch36* (SYS), *Ch247* (SYS); *Li Yan-hui 2829* (HITBC)
Semnostachya longispicata (Hayata) C. F. Hsieh & T. C. Huang	*Ch1182* (SYS)
ANNONACEAE	
Miliusa chunii W. T. Wang	*Ch499* (SYS), *Ch1211* (SYS); *Unknown coll. 74317* (HITBC), *74318* (HITBC)
Mitrephora maingayi Hook. f. & Thoms.	*Li Yan-hui 3139* (HITBC)
Mitrephora thorelii Pierre	*Ch673* (SYS), *Ch420* (SYS); *Li Yan-hui 67493* (HITBC)
APOCYNACEAE	
Antiostelma lantsangensis (Tsiang & P. T. Li) P. T. Li	*Ch658* (SYS)
Bidaria yunnanense (Tsiang) P. T. Li	*Ch242* (SYS), *Ch764* (SYS)
Dischidia esquirolii (Lév.) Tsiang	*Ch23* (SYS)
Dischidia minor (Vahl) Merr.	*Ch729* (SYS)
Gymnema sylvestre (Retz.) Schult.	*Expedition 34523* (HITBC)
Gymnema latifolium Wall. ex Wight	*Ch586* (SYS), *Ch633* (SYS), *Ch716* (SYS); *Yang Zheng-hong 10976* (HITBC)
Hoya carnosa (L. f.) R. Br.	*Ch651* (SYS)
Hoya lyi Lév.	*Tao Guo-da 35474* (HITBC)
Hoya nervosa Tsiang & P. T. Li	*Zhang Jian-hou 18562* (HITBC)
Hoya villosa Costanin.	*Ch960* (SYS); *Li Yan-hui 2574* (HITBC)
Jasminanthes saxatilis (Tsiang & P. T. Li) W. D. Stevens & P. T. Li	*Tao Guo-da 44195* (HITBC)
Marsdenia tenacissima (Roxb.) Moon	*Ch438* (SYS); *Expedition 32621* (HITBC)
Toxocarpus villosus (Blume) Decne.	*Ch544* (SYS), *Ch587* (SYS), *Ch646* (SYS)
ARACEAE	
Aglaonema pierreanum Engl.	*Ch233* (SYS); *Ch240* (SYS); *Pei Sheng-ji 10274* (HITBC)
Colocasia gigantea Hook. f.	*Ch1169* (SYS); *Tao Guo-da 9123* (HITBC)
Rhaphidophora decursiva (Roxb.) Schott	*Ch1160* (SYS); *Li Jie 722* (HITBC)
Rhaphidophora hongkongensis Schott	*Ch706* (SYS), *Ch1179* (SYS)
BEGONIACEAE	
Begonia augastinei Hemsl.	*Ch265* (SYS); *Tao Guo-da 15926* (HITBC)
Begonia dryadis Irmsch.	*Zhu Pei-zhi 10364* (HITBC)
Begonia prostata Irmsch.	*Ch976* (SYS)
BOMBACACEAE	
Bombax ceiba L.	*Li Yan-hui 2946* (HITBC)

Appendix 1. Continued.

BORAGINACEAE	
Ehretia tsangii I. M. Johnst.	*Li Yan-hui 3360* (HITBC), *3726* (HITBC)
CAPPARIDACEAE	
Capparis membranifolia Kurz	*Ch612* (SYS); *Zhao Shi-wang 22582* (HITBC)
Capparis urophylla F. Chun	*Ch853* (SYS), *Ch136* (SYS), *Ch153* (SYS), *Ch195* (SYS); *Li Yan-hui 2112* (HITBC)
CAPRIFOLIACEAE	
Viburnum tsangii Rehder	*Li Yan-hui 4235* (HITBC); *Zhu Pei-zhi 10470* (HITBC)
CARDIOPTERIDACEAE	
Peripterygium quinquelobum Hassk.	*Expedition 34761* (HITBC)
COMMELINACEAE	
Porandra scendens D. Y. Hong	*Ch902* (SYS); *Pei Sheng-ji 9947* (HITBC); *Unknown coll. 262* (HITBC)
COMPOSITAE	
Youngia japonica (L.) DC.	*Ch1201* (SYS), *Ch326* (SYS); *Tao Guo-da 1742* (HITBC)
EBENACEAE	
Diospyros yunnanensis Rehder & Wils.	*Ch516* (SYS), *Ch1214* (SYS); *Cui Jing-yun 14656* (HITBC); *Pei Sheng-ji 10300* (HITBC)
EUPHORBIACEAE	
Adenochlaena silhetensis Benth.	*Ch807* (SYS); *Zou Shuang-yun 356* (HITBC)
Antidesma montanum var. *microphyllum* (Hemsl.) P. Hoffmann	*Li Yan-hui 3575* (HITBC)
Cleidion bracteosum Gagnep.	*Li Yan-hui 4250* (HITBC)
Cleidion brevipetiolatum Pax & K. Hoffm.	*Ch922* (SYS); *Li Yan-hui 399* (HITBC)
Lasiococca comberi var. *pseudoverticellata* (Merr.) H. S. Ku	*Ch309* (SYS), *Ch226* (SYS), *Ch38* (SYS); *Li Yan-hui 1694* (HITBC)
Sumbaviopsis albicans (Blume) J. J. Smith	*Ch131* (SYS); *Li Yan-hui 2423* (HITBC)
FABACEAE	
Bauhinia genuflexa Craib	*Ch25* (SYS), *Ch97* (SYS); *Li Yan-hui 1500* (HITBC)
Millettia yunnanensis Pampan.	*Tao Guo-da 13668* (HITBC)
Whitfordiodendron filipes (Dunn) Dunn	*Zhao Shi-wang 22492* (HITBC)
FLACOURTIACEAE	
Flacourtia rukam Zoll. & Mor.	*Ch784* (SYS)
GESNERIACEAE	
Chirita dimidiata R. Br.	*Ch948* (SYS)
Paraboea rufescens (Franch.) B. L. Burtt	*Ch379* (SYS); *Wang Hong 2724* (HITBC)
Paraboea dictyoneura (Hance) B. L. Burtt	*Ch842* (SYS); *Wang Hong 2707* (HITBC)
Paraboea sinensis f. *macrophylla* (Stapf) C. Y. Wu	*Ch272* (SYS); *Expedition 34359* (HITBC); *Tao Guo-da 16748* (HITBC), *3792* (HITBC)

Appendix 1. Continued.

GRAMINEAE	
Dendrocalamus strictus (Roxb.) Nees	*Ch1058* (SYS); *Sun Ji-liang 18151* (HITBC)
ICACINACEAE	
Apodytes dimidiata E. Meyer ex Arn.	*Tao Guo-da 16690* (HITBC)
LABIATAE	
Colebrookea oppositifolia Sm.	*Ch51* (SYS); *Li Yan-hui 252* (HITBC), *Sun Ji-liang 18005* (HITBC)
Elsholtzia stachyodes (Link) C. Y. Wu	*Tao Guo-da 3798* (HITBC)
LAMIACEAE	
Clerodendron henryi Pei	*Wang Hong 2921* (HITBC), *2922* (HITBC), *2940* (HITBC)
Garrettia siamensis Fletcher	*Expedition 32276* (HITBC); *Unknown coll. 2434* (HITBC), *456* (HITBC); *Wang Hong 2727* (HITBC)
Premna hamiltonii J. L. Ellis	*Ch177* (SYS), *Ch278* (SYS); *Expedition 32617* (HITBC)
Sphenodesme mollis Craib	*Ch864* (SYS)
LAURACEAE	
Litsea dilleniifolia P. Y. Bai & P. H. Huang	*Li Yan-hui 3053* (HITBC)
Litsea elongata (Wall. ex Nees) Benth. & Hook. f.	*Ch269* (SYS), *Ch119* (SYS)
Phoebe lanceolata (Wall. ex Nees) Nees	*Ch161* (SYS), *Ch61* (SYS), *Ch324* (SYS); *Li Yan-hui 754* (HITBC)
LILIACEAE	
Polygonatum punctatum Royle ex Kunth	*Ch711* (SYS)
Tupistra wattii Hook. f.	*Expedition 34321* (HITBC); *Yang Zhen-hong 6971* (HITBC); *Wang Hong 3102* (HITBC)
MALPIGHIACEAE	
Hiptage benghalensis var. *tonkinensis* (Dop) S. K. Chen	*Ch45* (SYS); *Li Yan-hui 1051* (HITBC)
MALVACEAE	
Sterculia villosa Roxb.	*Zou Shuang-yun 324* (HITBC)
MELIACEAE	
Chukrasia tabularia var. *velutina* King	*L. Yan-hui 385* (HITBC)
Dysoxylum lenticellatum C. Y. Wu & H. Li	*Ch508* (SYS); *Cui Jing-yun 22658* (HITBC)
Dysoxylum spicatum H. L. Li	*Unknown coll. 250* (SYS)
Toona ciliata var. *pubescens* (Franch.) Hand.-Mazz.	*Ch680* (SYS), *Ch566* (SYS), *Ch581* (SYS)
MORACEAE	
Cudrania jinghongensis S. S. Chang	*Li Yan-hui 3135* (KUN)
Ficus orthoneura Lév. & Vaniot	*Ch41* (SYS); *Li Yan-hui 3802* (HITBC)
Ficus prostata Wall. ex Miq.	*Zhu Hua & Wang Hong 88-11* (HITBC)
Ficus pubigera var. *maliformis* (King) Corner	*Li Yan-hui 3223* (HITBC)
MYRSINACEAE	
Ardisia garrettii Fletcher	*Ch130* (SYS), *Ch170* (SYS), *Ch47* (SYS); *Li Yan-hui 3867* (HITBC)

Appendix 1. Continued.

MYRTACEAE	
Syzygium claviflorum (Roxb.) Wall ex A. M. & J. M. Cowan	*Ch501* (SYS), *Ch492* (SYS)
ORCHIDACEAE	
Gastrochilus obliquus (Lindl.) Kuntze	*Li Yan-hui 2734* (HITBC)
Nervilia plicata (Andr.) Schltr.	*Ch713* (SYS); *Li Yan-hui 3138* (HITBC)
Tropidia angulosa (Lindl.) Blume	*Li Yan-hui 392* (HITBC); *Wang Pei-qun 11115* (HITBC)
OROBANCHACEAE	
Aeginetia indica L.	*Zhao Shi-xiang 165* (HITBC)
OXALIDACEAE	
Averrhoa carambola L.	*Li Yan-hui 3129* (HITBC)
Biophytum esquirolii Lév.	*Li Yan-hui 4004* (HITBC)
PALMAE	
Caryota ochlandra Hance	*Chen Yu 62079* (HITBC)
PIPERACEAE	
Peperomia heyneana Miq.	*Ch804* (SYS); *Li Yan-hui 2738* (HITBC)
Piper arboricola C. DC.	*Ch585* (SYS), *Ch924* (SYS), *Ch1216* (SYS); *Unknown coll. 865* (HITBC)
Piper curtipedunculatum C. DC.	*Cui jing-yun 22811* (HITBC)
RHAMNACEAE	
Ventilago leiocarpa var. *pubescens* Y. L. Chen & P. K. Chou	*Ch1088* (SYS), *Ch645* (SYS)
Zizyphus attopensis Pierre	*Li Yan-hui 1289* (HITBC), *Ch251* (SYS)
RUBIACEAE	
Ixora cephalophora Merr.	*Ch1218* (SYS), *Ch1229* (SYS)
Pavetta arenosa Lour.	*Li Yan-hui 246* (HITBC), *2814* (HITBC)
Pavetta hongkongensis Bremek.	*Ch355* (SYS); *Zhu Hua & Wang Hong 3004* (HITBC)
Psychotria pilifera Hutch.	*Ch712* (SYS), *Ch165* (SYS); *Li Yan-hui 1498* (HITBC)
Psychotria siamica (Craib) Hutch.	*Ch836* (SYS); *Li Yan-hui 2473* (HITBC), *258* (HITBC)
Spiradiclis caespitosa f. *subimmersa* Lo	*Li Yan-hui 12675* (HITBC)
RUTACEAE	
Glycosmis citrifolia (Willd.) Lindl.	*Ch222* (SYS), *Ch146* (SYS); *Zou Shuang-yun 333* (HITBC)
Murraya koenigii (L.) Spreng.	*Ch176* (SYS), *Ch330* (SYS), *Ch352* (SYS), *Ch313* (SYS); *Li Yan-hui 1859* (HITBC)
Murraya microphylla (Merr. & Chun) Swingle	*Expedition 34267* (HITBC); *Tao Guo-da 44056* (HITBC)
Murraya paniculata (L.) Jack.	*Li Yan-hui 3315* (HITBC)
Zanthoxylum armatum var. *ferrugineum* (Rehder & E. H. Wilson) C. C. Huang	*Ch887* (SYS); *Unknown coll. 1010* (HITBC)
Zanthoxylum laetum Drake	*Ch475* (SYS), *Ch578* (SYS)
Zanthoxylum utile C. C. Huang	*Ch636* (SYS), *Ch777* (SYS)

Appendix 1. Continued.

STAPHYLEACEAE	
Tapiscia yunnanensis W. C. Cheng & S. D. Chu	*Zhu Hua 93011* (HITBC)
TETRAMELACEAE	
Tetrameles nudiflora R. Br.	*Li Yan-hui 8541* (HITBC)
TILIACEAE	
Colona floribunda (Wall.) Craib	*Ch700* (SYS), *Ch932* (SYS); *Pei Sheng-ji 10084* (HITBC)
Colona thorelii (Gagnep.) Burret	*Li Yan-hui 1696* (HITBC)
URTICACEAE	
Boehmeria zollingeriana Wedd.	*Ch1064* (SYS); *Cui Jing-yun 19416* (HITBC)
Debregeasia edulis (Siebold & Zucc.) Wedd.	*Ch311* (SYS); *Tao Guo-da 41641* (HITBC)
Elatostema rupestre (Buch.-Ham.) Wedd.	*Ch168* (SYS), *Ch388* (SYS), *Ch359* (SYS); *Wang Hong 1494* (HITBC)
Pilea monilifera Hand.-Mazz.	*Ch984* (SYS); *Wang Hong 1484* (HITBC)
Pilea plataniflora C. H. Wright	*Ch381* (SYS); *Ch657* (SYS); *Li Yan-hui 4210* (HITBC); *Tao Guo-da 16090* (HITBC)
Pouzolzia sanguinea (Blume) Merr.	*Cui Jing-yun 22793* (HITBC)
VITACEAE	
Leea aequata L.	*Ch468* (SYS), *Ch714* (SYS); *Pei Sheng-ji 9359* (HITBC)
Yua austro-orientalis (Metcalf) C. L. Li	*Ch844* (SYS)
Tetrastigma cauliflorum Merr.	*Ch268* (SYS); *Li Yan-hui 11915* (HITBC)
Tetrastigma delavayi Gagnep.	*Ch507* (SYS); *Ch811* (SYS)
Tetrastigma erubescens var. *monospermum* Gagnep.	*Ch463* (SYS), *Ch1054* (SYS); *Tao Guo-da 9189* (HITBC)
Tetrastigma pubinerve Merr. & Chun	*Ch653* (SYS), *Ch616* (SYS)
Vitis balansaeana Planch.	*Ch668* (SYS), *Tao Guo-da 16447* (HITBC)
Vitis betulifolia Diels & Gilg	*Ch654* (SYS), *Ch408* (SYS)
ZINGIBERACEAE	
Hedychium sino-aureum Stapf	*Ch1240* (SYS); *Wang Hong 3066* (HITBC); *Tao Guo-da 16049* (HITBC)
Hedychium villosum var. *tenuiflorum* Wall. ex Baker	*Li Yan-hui 4866* (HITBC)
Pommereschea spectabilis (King & Prain) K. Schum.	*Tao Guo-da 13661* (HITBC); *Zhu Pei-zhi 8642* (HITBC)
Pterydophyta preferent to limestone habitats	
ADIANTACEAE	
Adiantum capillus-veneris L.	*Expedition 34430* (HITBC)
Adiantum caudatum L.	*Li Yan-hui 2554* (HITBC)
Adiantum caudatum var. *edgeworthii* (Hook.) Bedd.	*Li Bao-gui 734* (HITBC)
Adiantum malesianum J. Ghatak	*Zhu Pei-zhi 8668* (HITBC)
ANTROPHYACEAE	
Antrophyum callifolium Blume	*Li Bao-gui 803* (HITBC)

Appendix 1. Continued.

ASPLENIACEAE	
Asplenium austrochinense Ching	*Li Yan-hui 3810* (HITBC)
Asplenium excisum C. Presl	*Li Bao-gui 737* (HITBC); *Unknown coll. 9498* (HITBC)
Asplenium interjectum H. Christ	*Li Bao-gui 880* (HITBC)
Asplenium prolongatum Hook.	*Li Yan-hui 3739* (HITBC)
Asplenium saxicola Rosenst.	*Li Yan-hui 2749* (HITBC)
Asplenium varians Wall. ex Hook. & Grev.	*Tao Guo-da 43453* (HITBC)
Hymenasplenium cheilosorum (Kunze ex Mett.) Tagawa	*Li Qing-jun 42749* (HITBC)
Neottopteris antrophyoides (H. Christ) Ching	*Zhu Pei-zhi 10487* (HITBC)
ATHYRIACEAE	
Allantodia alata (Christ) Ching	*Li Bao-gui 674* (HITBC)
Allantodia pinnatifido-pinnata (Hook.) Ching	*Tao Guo-da 43571* (HITBC)
Kuniwatsukia cuspidata (Bedd). Pic. Serm.	*Tao Guo-da 17161* (HITBC)
BOLBITIDACEAE	
Egenolfia tonkinensis C. Chr. ex Ching	*Li Bao-gui 756* (HITBC)
DRYNARIACEAE	
Drynaria bonii H. Christ	*Li Yan-hui 2735* (HITBC)
Drynaria fortunei (Kunze ex Mett.) J. Sm.	*Tao Guo-da 38772* (HITBC)
Drynaria rigidula (Sw.) Bedd.	*Expedition 34292* (HITBC)
DRYOPTERIDACEAE	
Dryopteris cochlaeta (D. Don) C. Chr.	*Li Bao-gui 98085* (HITBC)
Polystichum deltodon (Baker) Diels	*Tao Guo-da 15730* (HITBC)
HEMONITIDACEAE	
Pityrogramma calomelanos (L.) Link	*Li Bao-gui 45749* (HITBC)
NEPHROLEPIDACEAE	
Nephrolepis auriculata (L.) Trimen	*Tao Guo-da 16010* (HITBC)
POLYPODIACEAE	
Lepisorus bicolor (Takeda) Ching	*Tao Guo-da 39738* (HITBC)
Lepidogrammitis rostrata (Bedd.) Ching	*Li Bao-gui 774* (HITBC)
Lemmaphyllum microphyllum C. Presl	*Li Bao-gui 600* (HITBC)
Lemmaphyllum carnosum (Wall.) C. Presl	*Li Bao-gui 604* (HITBC)
Phymatodes cuspidata (D. Don) J. Sm.	*Li Yan-hui 3808* (HITBC)
Pyrrosia assimilis (Baker) Ching	*Expedition 34719* (HITBC)
Pyrrosia mollis (Kunze) Ching	*Tao Guo-da 38843* (HITBC)
Pyrrosia nuda (Giesenh.) Ching	*Tao Guo-da 38875* (HITBC)
Pyrrosia nummularifolia (Sw.) Ching	*Li Qing-jun 42624* (HITBC)
Pyrrosia subfurfuracae (Hook.) Ching	*Li Bao-gui 9904152* (HITBC)
Pyrrosia tonkinensis (Giesenh.) Ching	*Pei Sheng-ji 9933* (HITBC)

Appendix 1. Continued.

PTERIDACEAE	
Pteris actiniopteroides H. Christ	*Li Bao-gui 921* (HITBC)
SELAGINELLACEAE	
Selaginella involvens (Sw.) Spring	*Li Bao-gui 960463* (HITBC)
Selaginella pulvinata (Hook. & Grev.) Maxim.	*Li Bao-gui 45178* (HITBC)
SINOPTERIDACEAE	
Aleuritopteris pseudofarinosa Ching & S. K. Wu	*Mengliandui 10242* (HITBC)
Cheilosoria tenuifolia (Burn. f.) Trev.	*Mengliandui 10140* (HITBC)
TECTARIACEAE	
Ctenitopsis devexa (Kunze) Ching & C. H. Wang	*Li Qing-jun 42687* (HITBC)
Tectaria decurrens (C. Presl) Copel.	*Pei Sheng-ji 9277* (HITBC)
Tectaria simaoensis (Bedd.) Ching & C. H. Wang	*Sun Ji-liang 18185* (HITBC)
THELYPTERIDACEAE	
Cyclosorus papilio (Hope) Ching	*Li Bao-gui 98086* (HITBC)
Cyclosorus parasitica (L.) Tardieu	*Li Yan-hui 1326* (HITBC)

THE POPULATION STRUCTURE AND FLORAL BIOLOGY OF *AMBORELLA TRICHOPODA* (AMBORELLACEAE)[1]

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ABSTRACT

The shrubs and small trees of *Amborella trichopoda* are functionally unisexual and the populations are dioecious, male biased, and occur primarily in clumps. Floral size dimorphism reported for this species was confirmed by differences in floral biomass. At the level of the inflorescence, there were significantly greater numbers of male versus female flowers/inflorescence. No differences were observed between male and female plants in height, stem number, and diameter at the ground level. Male flowers bear 6 to 21 stamens and female flowers 3 to 6 spirally arranged carpels and staminodes that mimic the fertile androecia in male flowers. Flowering within a population was synchronous, and flowers of *Amborella trichopoda* are both insect- and wind-pollinated. A wide variety of insects ranging in size from ca. 1 mm to 7 cm in length pollinate the flowers, indicating a generalist pollination system. Beetles involved in pollination dwell in the forest litter but also spend hours on the leaves, flowers, and branches feeding on pollen. Pollen is the reward for insects as there is an absence of detectable floral volatiles and nectars, and anthers lack secretions or food bodies. A free-flowing stigma secretion was occasionally present, but it was not consumed by pollinators. Structural studies indicate that the stigma is of the dry-type, and the pollinators probably visit female flowers because of the mimetic role of the staminodes. The combination of wind and insect pollination exhibited in *A. trichopoda* is rare in basal angiosperms. Gall midges, parasitoid wasps, and thrips utilize floral tissue as a breeding site, impeding reproduction. Two species of gall-inducing midges (Cecidomyiidae) insert egg(s) into the gynoecia of developing flower buds, converting one or more ovaries into galls. Parasitoid wasps (Chalcidae) lay eggs in the galls that develop into larvae that prey upon the midge maggots. The Cecidomyiidae expanded with the angiosperms, but the earliest fossils of gall-inducing gall midges occur in the Miocene. Deceptive mechanisms involving numerous floral traits in small bisexual and unisexual flowers are common in the ANITA group and other basal angiosperms.

Key words: *Amborella trichopoda*, Amborellaceae, ANITA group, beetles, dioecy, gall midges, insect/wind pollination, New Caledonia.

The woody evergreen plant *Amborella trichopoda* Baill. (Figs. 1a, 2a, b, 3b), the only species of Amborellaceae, is endemic to New Caledonia in the South Pacific (Jérémie, 1982). This species has attracted worldwide attention, as molecular phylogenies constructed with a variety of genes place it as the sister group of the rest of the flowering plants (Mathews & Donoghue, 1999; Qiu et al., 1999; Soltis et al., 1999). It is a member of the paraphyletic ANITA group, a grade comprising the first three

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branches of angiosperm phylogeny [Amborellaceae, Nymphaeaceae and Austrobaileyales (Austrobaileyaceae, Illiciaceae, Schisandraceae, and Trimeniaceae); APG II, 2003]. There is some controversy over the precise branching order at the base of the flowering plant tree (Parkinson et al., 1999; Barkman et al., 2000; Graham & Olmstead, 2000; Graham et al., 2000; Qiu et al., 2000, 2001; Zanis et al., 2002), but *Amborella* is clearly the sole living representative of a lineage that emerged at (or at least very close to) the base of the crown (extant) flowering plants.

Recent discoveries of many small fossils of bisexual and unisexual flowers in the mesofossil floras of the Early Cretaceous (Barremian–Aptian) can be attributed to relictual extant lineages (Illiciaceae, etc.), further supporting the ANITA grade as a set of ancient lineages (Friis et al., 2000). The discovery of complete flowering branches of the extinct, basal family (Archaefructaceae, with two species) from the Lower Cretaceous (124.6 mya; Yixian Formation) in western China (Sun et al., 2002) also supports the basal phylogenetic position of ANITA taxa. In a cladogram constructed with molecular characters and morphological characters relevant only to fossils, Archaefructaceae are the sister group to all flowering plants and Amborellaceae are basal to all extant angiosperms (Sun et al., 2002). *Archaefructus* was monoecious with male and female "flowers" borne on different parts of the same stem.

Amborella trichopoda is dioecious with flowers of both sexes (Figs. 1, 3b) arranged in botryoids or poorly ramified panicles (Bailey & Swamy, 1948; Jérémie, 1982; Endress & Igersheim, 2000). Flowers of both sexes are small, dull white or cream in color (Bailey & Swamy, 1948; Endress & Igersheim, 2000). Male flowers, which are larger than the female, develop a terminal abortive organ that has been described as a potential reduced gynoecium, and female flowers develop abortive stamens (staminodes, Bailey & Swamy, 1948; Endress & Igersheim, 2000). Male and female flowers reportedly develop secretory tissue on the anthers and stigmas, respectively (Endress & Igersheim, 2000). The fruit of *A. trichopoda* is an ovoid red drupelet containing a similarly ovoid seed; gall-like fruits have also been reported (Endress & Igersheim, 2000).

In spite of the abundant information on the reproductive development and anatomy of *Amborella trichopoda*, virtually nothing is known about its pollination biology and breeding system(s) under natural conditions. It has been suggested that *A. trichopoda* may be insect-pollinated with secretions on anthers and stigmas serving as insect rewards (Endress & Igersheim, 2000), and moths, potentially attracted by a nocturnal floral scent, have been observed visiting greenhouse-grown plants in the evening (Collett, 1999). Moreover, Sampson (1992) noted that staminodes of female flowers may in some instances develop abnormal pollen, thereby providing a deceit reward for pollinators. Endress (2001), however, noted that *A. trichopoda* may be wind-pollinated. Fossil evidence indicates that insects have been important as selective forces in the evolution of seed plants (Baker & Hurd, 1968; Regal, 1977; Crepet & Friis, 1987; Grimaldi, 1999), and Labandeira (1998) noted that pollen consumption by an extinct lineage of insects occurred before the end of the Carboniferous based on the contents of insect coprolites. There is insect pollination in some extant gymnosperms (Norstog, 1987). However, whether there are floral scents and anther and stigmatic secretions in *A. trichopoda* requires investigation. In general, basal angiosperms show insect pollination systems emphasizing beetles (Coleoptera) and flies (Diptera), while thrips (Thysanoptera) and bees (Hymenoptera) are more likely to play secondary roles, and wind pollination is noted as uncommon to rare (Endress, 1990, 2001; Thien et al., 2000).

It has been documented that male flowers are larger than female flowers of *Amborella trichopoda*, but it is not apparent if dimorphisms exist in other reproductive or vegetative traits. Dimorphisms in vegetative and reproductive features are common in dioecious species and are often correlated with specific modes of pollination (Feil & Renner, 1991; Feil, 1992; Renner & Feil, 1993).

The purpose of the present study was to address some of the unexplored issues regarding the reproductive biology of *Amborella trichopoda*. The specific questions addressed by studying the species in its naturally occurring environment were: (1) Is *A. trichopoda* insect- and/or wind-pollinated? (2) Do flowers produce floral volatiles and floral rewards such as secretions on anthers and stigmas and, if so, what is their chemical composition? (3) What is the population structure (distribution pattern) of male and female plants? Three locations in New Caledonia, Mèè, Plateau de Dogny, and Col d'Amieu, were utilized to focus on these issues in 2001 and 2002.

MATERIALS AND METHODS

ECOLOGICAL, EDAPHIC, AND FLORISTIC CHARACTERS OF *AMBORELLA TRICHOPODA*

New Caledonia, located in the Southwest Pacific approximately 1200 km east of subtropical Queens-

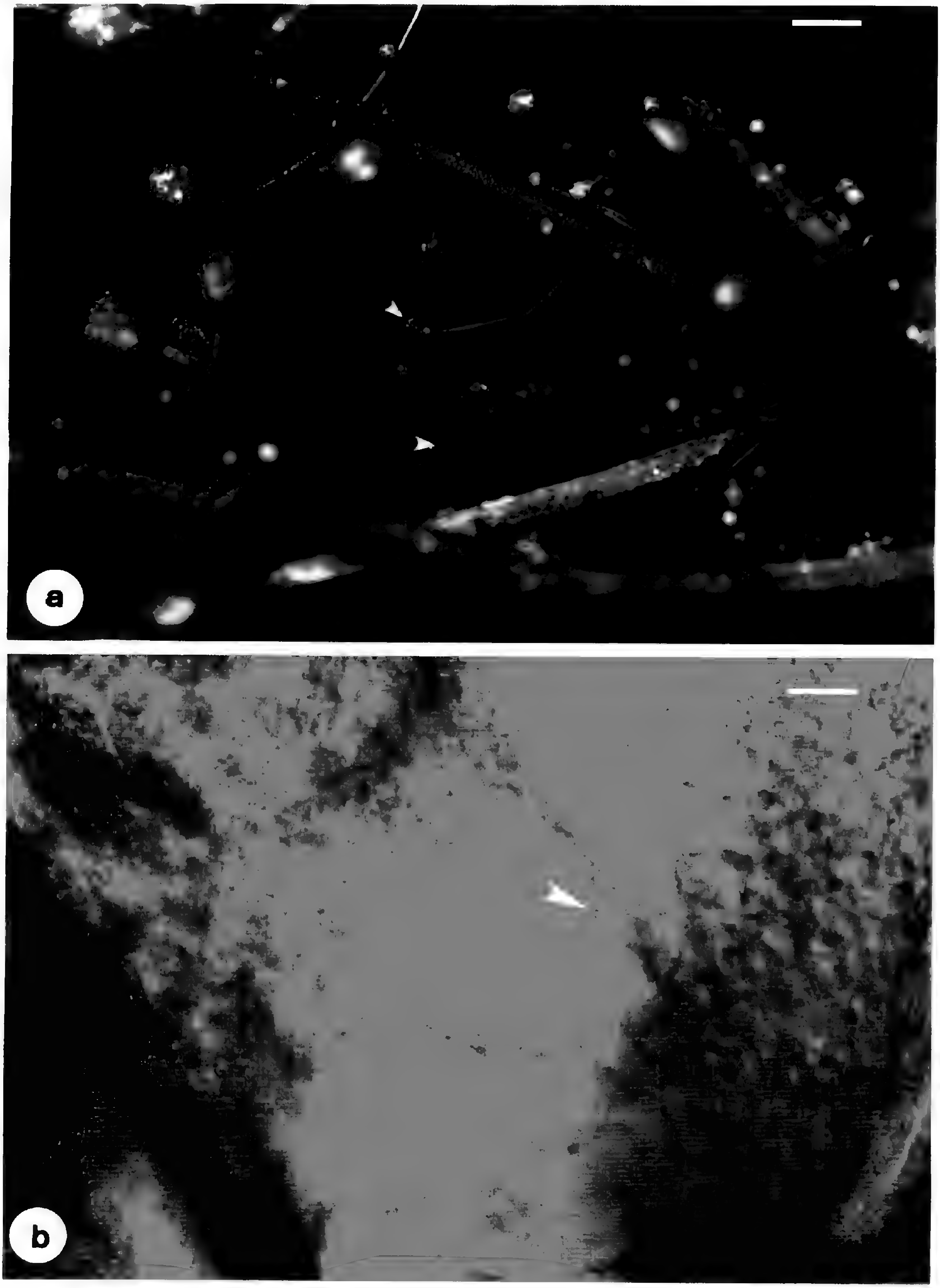

Figure 1. Features of fruit, gall, and oviposited floral buds in *Amborella trichopoda*. —a. Red fruits are distinguished from larger green galls. Floral buds marked with arrowheads are slightly black indicating the presence of fungus. Bar 5 mm. —b. Arrowhead denotes cecid larva within a recently opened female flower. Bar 13 μm.

land, Australia, is rich in gymnosperms and relictual representatives of the Cretaceous–early Tertiary Gondwana floras of Australasia (Lowry, 1998; Morat et al., 1984; Jaffré et al., 2001) including basal angiosperms. *Amborella trichopoda* occurs in rain forests with acid soils along a chain of high mountains from Plateau de Dogny to the high valley of the Tipindjé River (Jérémie, 1982; see soil map, Pintaud et al., 2001). In the rain forests, *A. trichopoda* occurs within the 1500 mm (and above) rainfall isohyet determined by Pintaud et al. (2001).

The restricted distribution of *Amborella trichopoda* on the island can be correlated with some wet conifer and palm sites (Jaffré, 1994; Pintaud et al., 2001). Nearly all palm populations occur within the 1500 mm isohyet, with maximum species diversity in four areas receiving > 3000 mm of rainfall per year (Pintaud et al., 2001). The four areas are designated Pleistocene rain forest refugia by Pintaud et al. (2001). In the dry periods of the Pleistocene these refuge areas may have remained within the 1500 mm isohyet (Pintaud et al., 2001; Jaffré, 1994). Some populations of *A. trichopoda* currently occur in the Massif des Levrès Pleistocene refuge (number 2) of Pintaud et al. (2001).

Herbarium specimens (IRD, Noumea, New Caledonia) indicate two flowering periods, one from early March to the end of May and the other in August (Jérémie, 1982); however, in August 2001 no plants flowered at Mèè and Plateau de Dogny. The primary flowering time of *Amborella trichopoda* is during the warm season (mid November to mid April), in which rainfall is high with frequent tropical depressions and cyclones (Lowry, 1998).

Jaffré (unpublished data) suggests *Amborella trichopoda* occurs on acid soils rich in Al, in habitats with high precipitation, but is not found on ultramafic soils (peridotites and serpentines). The soils at Plateau de Dogny have a pH of 4.2 and contain 10.6% Al, and at Col d'Amieu soils contain 14.03% Al with a pH of 4.14 (Jaffré, unpublished data). The accumulated Al content of some plants at Plateau de Dogny are as follows: *Rapanea* Aubl. sp.—30 ppm; *Phelline* Labill. sp.—40 ppm; *A. trichopoda*—75 ppm; *Ixora montana* Schltr.—75 ppm; *Psychotria balansae* (Baill.) Guillaumin—163 ppm; *Hedycarya baudouini* Baill.—375 ppm; *Psychotria* L. sp.—6875 ppm; *Zygogynum crassifolium* (Baill.) Vink—9250 ppm; *Knightia stobilina* (Labill.) R. Br.—10,625 ppm; and *Melastoma denticulata* Labill.—11,375 ppm. Mabberley (1993) recorded *A. trichopoda* as accumulating Al; however, the tissue values provided by Jaffré suggest Al accumulation is negligible.

Site description. Natural populations of *Amborella trichopoda* used in the present study are located at three sites: (1) Col d'Amieu 500–800 m near Sarraméa, Province Sud; (2) Plateau de Dogny 500–800 m, near Sarraméa, Province Sud; and (3) Mèè, located on the eastern side of the island (570 m). The Col d'Amieu site was the most accessible and hence was the primary study area visited in August 2001 and March 2002. Plateau de Dogny was the secondary study area visited in March–April 2001 and August 2001. The Mèè site was visited in August of 2001 and was used to determine the production of galls and observe insect/plant interactions. During all site visits conducted in August, flowering was examined to evaluate whether it corresponded to the information from herbarium sheets (IRD, Noumea, New Caledonia).

The forest floor of the Col d'Amieu site (Fig. 2), a mature rain forest on the eastern slope of the mountain range, is dominated by ferns, especially *Marattia attenuata* Labill. and *Orthiopteris firma* (Kuhn) Brownlie (1 m in height). The arborescent fern *Cyathea vieillardii* Mett. and the palm *Burretiokentia vieillardii* (Brongn. & Gris) Pichi-Serm. are common in the forest. An unidentified species of *Freycinetia* Gaudich. is also abundant. Other understory plants include *Amborella trichopoda, Psychotria baillonii* Schltr., *Hedycarya cupulata* Baill., *Phelline brachyphylla* Baill., *Zieridium pseudobtusifolium* Guillaumin, *Tapeinosperma acutangulum* Mez, and *Casearia silvana* Schltr. Trees in the understory include *Cryptocarya macrocarpa* Guillaumin, *Calophyllum caledonicum* Vieill., *Garcinia* L. sp., *Hernandia moerenhoutiana* Guillem., *Syzygium* Gaertn. sp., *Harpullia austrocaledonica* Baill., *Schefflera* Foster & Foster f. sp., *Niemeyera balansae* (Baill.) Aubrév., and *Ficus* L. spp. The forest differs from the nearby "forêt Persan" on the Col d'Amieu massif (Jaffré & Veillon, 1995) in its steeper slopes (with a slope aspect of 50–65% vs. 30–50%, respectively), at slightly higher elevation (540 m vs. 500 m) with greater precipitation (> 2000 mm vs. ca. 1800 mm).

DIMORPHISM IN SELECT VEGETATIVE AND FLORAL FEATURES

In dioecious breeding systems it is necessary to determine the various factors that affect reproductive success, i.e., number of male versus female plants, number of flowers produced by each sex, pollen to ovule ratios, etc. (for techniques see: Kearns & Inouyne, 1993; Real, 1983; Dafni, 1992). An initial assessment of dimorphism in secondary sex characters in *Amborella trichopoda* was con-

Figure 2. Growth form and habitat of *Amborella trichopoda* at Col d'Amieu. —a. Arrowhead shows point where trunk has been broken. Arrow indicates leaf herbivory. Note detritus on forest floor. —b. Forest habitat.

ducted by establishing six 10 × 30 m plots laid out at random along the eastern slope of Col d'Amieu (Fig. 4). Within each plot, the spatial distribution of male and female plants of *A. trichopoda* was mapped. Plant height, number of stems at ground level, and stem diameter were determined for all individuals within each plot (voucher specimens deposited at RYD and MO; Table 1). The gender of each plant was determined by inspecting all accessible open or opening flowers in the lower canopy and inspecting plants for the presence of fruit. As well, branches (N = 4 to 6 per plant; N = 75) with flowers and floral buds were randomly selected and removed from the higher canopy (ca. 2.5 m), 3 females and 3 males from each of 3 plots. They were immediately placed in water and taken to the laboratory for observations. It was noted that these unattached branches continued to develop flowers for up to two weeks. All male flowers and floral buds from these branches were inspected in the laboratory with a dissecting microscope to determine if a functional carpel was present. Anthers and staminodes were squashed with Alexander's Triple stain (Alexander, 1969) to assess the number of aborted and non-aborted pollen grains per anther. The sampled branches were also used to determine the number of flowers/inflorescence, and the dry weight of male and female flowers at anthesis.

A transect from 625 to 730 m at Plateau de Dogny was laid out to determine the gender of individual plants. Five branches each from 5 males and 3 females were removed and floral buds were examined for the development of functional carpels and pollen, and to quantify flowers/inflorescence and inflorescence/cm. Plots were not established at Plateau de Dogny due to the steep slopes (55–70°), unpredictability of weather, and difficulty of access.

To determine floral longevity, 3 male and 3 female plants from the Col d'Amieu population were marked with colored plastic wire, and the phenology of flowers was examined for each of 8 consecutive days. Flowers were observed with a 10× hand lens and the following traits recorded: tepal movements, presence or absence of stamen and stigmatic secretions, period(s) of secretion, stamen dehiscence, duration of pollen retention in anthers, and onset of necrosis. Floral longevity was also determined on flowers opening on materials brought into the laboratory from Plateau de Dogny and Col d'Amieu.

All statistical analysis of morphological traits was conducted using one-way ANOVA or the Mann-Whitney Rank Sum test (SigmaStat 2.03). Mann-Whitney Rank Sum tests comparing data collected from Col d'Amieu and Plateau de Dogny showed no significant differences; therefore all data from these two sites were pooled.

WIND DISPERSAL OF POLLEN

Experiments to assess the possibility of wind pollination were conducted at Col d'Amieu in March

Table 1. Vegetative and reproductive parameters of male and female *Amborella trichopoda* plants in six, 10 × 30 plots at Col d'Amieu, New Caledonia. Voucher specimens are deposited at RYD and MO. Stem diameters in cm.

Plot	Number of plants*	Male : female	Male height (m), range/(avg ± SD)	Female height (m), range/(avg ± SD)	Number of male stems at ground level range/(avg ± SD)	Number of female stems at ground level range/(avg ± SD)	Male stem diameter at ground level range/(avg ± SD)	Female stem diameter at ground level range/(avg ± SD)
A	18 (1)	2.4:1.0	2–7/(4.1 ± 1.8)	2–9/(5.1 ± 2.7)	1–2/(1.18 ± 0.40)	1–2/(1.4 ± 0.54)	2.5–25.4/(9.9 ± 8.3)	7.6–25.4/(12.7 ± 6.4)
B	14 (1)	3.0:1.0	2–7/(3.8 ± 1.7)	4/(4 ± 0.0)	1–4/(1.4 ± 1.1)	1/(1 ± 0.0)	2.5–22.9/(9.4 ± 6.1)	10.2/(10.2 ± 0.0)
C	6 (1)	4.0:1.0	1–3/(1.8 ± 0.0)	3/(3 ± 0.0)	1–2/(1.2 ± 0.45)	1/(1 ± 0.0)	1.27–12.7/(4.7 ± 4.5)	12.5/(12.5 ± 0.0)
D	11	2.7:1.0	3–6/(4.5 ± 0.9)	4–6/(5.0 ± 1.0)	1–2/(1.1 ± 1.3)	1–4/(2.0 ± 1.7)	7.6–20.3/(12.7 ± 5.1)	2.5–25.4/(10.9 ± 7.6)
E	19	2.2:1.0	2–6/(3.6 ± 1.4)	2–6/(3.0 ± 1.5)	1/(1 ± 0.0)	1–2/(1.8 ± 0.4)	2.5–20.3/(9.7 ± 4.3)	5.1–10.2/(5.6 ± 1.6)
F	7	2.5:1.0	1–6/(4.2 ± 1.9)	3/(3.0 ± 0.0)	1–3/(1.4 ± 0.89)	1–2/(1.0 ± 1.0)	2.5–11.3/(8.1 ± 4.1)	7.6–25.4/(16.5 ± 12.4)

* Values in parentheses indicate the number of individuals not in flower, e.g., A, 19 total plants.

2002. Pollen traps consisting of petroleum jelly-covered slides were placed within the canopy at distances of approximately 5 to 30 m from male and female plants at 1 to 5 m above the ground. The traps were removed after four days, placed in a microscope slide box that was then sealed with tape, and transported to the University of Toronto. Slides were then observed with differential interference optics to quantify the number of *Amborella trichopoda* grains present (Fig. 5).

INSECT POLLINATION

Insect activity on floral organs of *Amborella trichopoda* was documented for 2 to 3 hours over 11 days at Col d'Amieu in March 2002. Male and female plants were also observed at the site on a clear night beginning at sunset and continuing for 3 hours. It was noted that parasitoids associated with the cecid gall ecosystem and other insects (not captured on flowers) lay eggs in the galls and in the male and female buds of *A. trichopoda.* This paper, however, emphasizes pollinating insects (captured on flowers) and insect interactions in the galls. A sample of insects visiting plants was collected and examined for pollen loads as described by Bernhardt (1990). Insect specimens were sent to the Smithsonian Institution for identification and deposition.

NATURAL RATES OF OPEN POLLINATION

Natural rates of pollination in *Amborella trichopoda* were determined by recording the number and length of pollen tubes found in carpels in each flower. Approximately 200 female flowers with fresh, receptive stigmas were picked from 11 plants along a transect from 625 to 730 m at Plateau de Dogny and fixed overnight in a 3:1, 95% ethanol:glacial acetic acid mixture. The material was stored in 70% ethanol. The carpels were excised and softened in a 10% solution of sodium sulphite and water at room temperature for 24 hours, then prepared for softening and epifluorescence microscopy following Goldblatt and Bernhardt (1990), except that all carpels within the same gynoecium were squashed under a single cover slip (no material remaining). Flowers showing early signs of galling were discarded.

HISTOCHEMICAL AND STRUCTURAL CHARACTERIZATION OF ANTHERS AND STIGMAS

To determine whether secretions were present on anthers, stigmas, or other floral tissue, flowers from Plateau de Dogny (April 2001) and Col d'Amieu

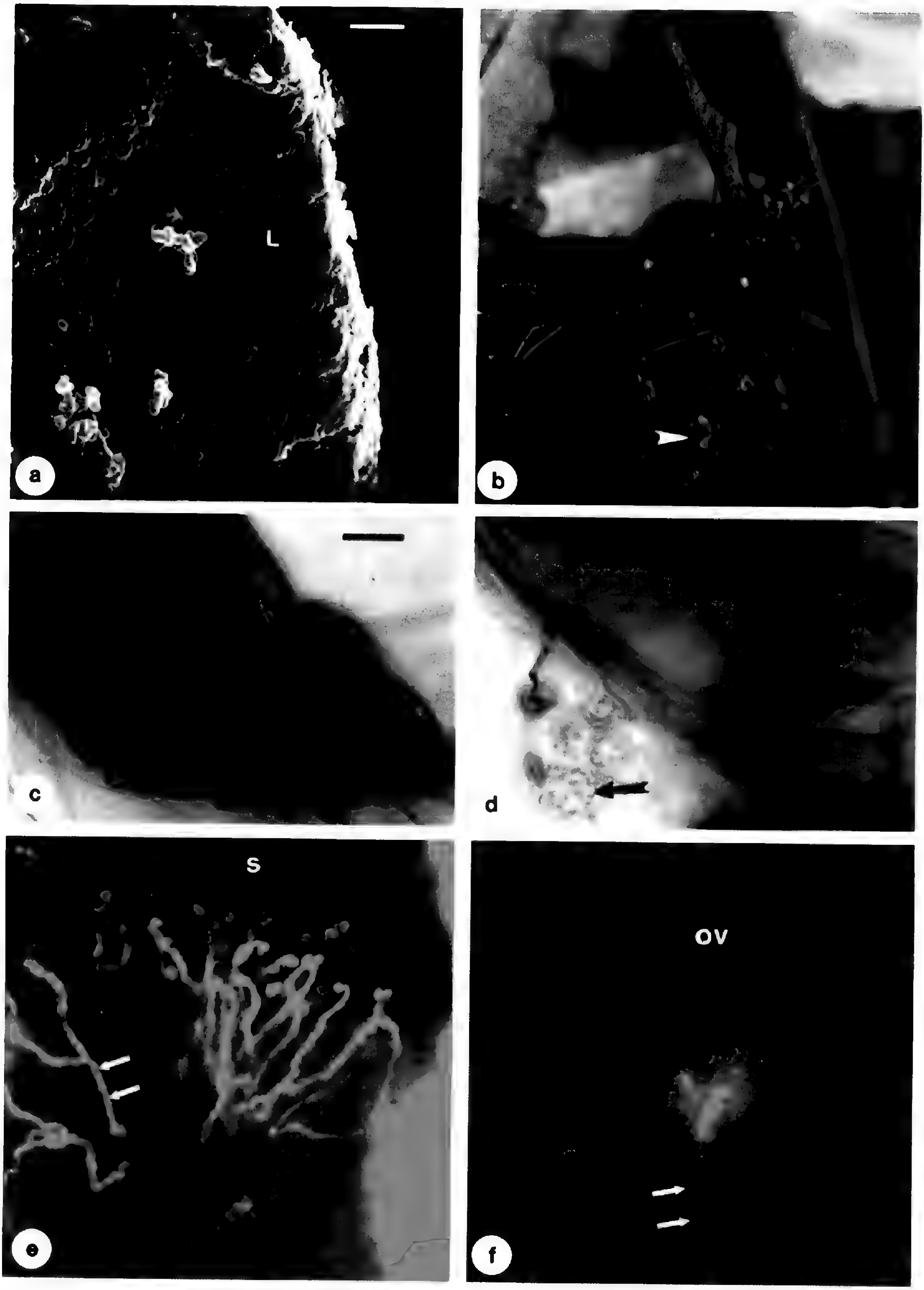

Figure 3. Features of the pollination biology of *Amborella trichopoda*. —a. Scanning electron micrograph illustrating lipid pollen coat on pollen grain. Tissue prepared with cryofixation. Bar = 1.3 μm. —b. The beetle *Neoadelium faureli* (Azszab) on female inflorescence. Large white arrowhead denotes positive ruthenium red staining of stigma indicating pectin. Small black arrowhead marks *in situ* positive aniline blue black staining of stigma indicating protein.

(March 2002) were examined in the natural populations or on cut branches in the laboratory. To assess the presence of various chemical constituents drops of the following stains were applied to flowers from both populations: 1% alcian blue in 3% acetic acid for acidic polysaccharides, pectins, and mucilages (Jensen, 1962; Benes, 1968); 0.05% ruthenium red for pectic substances (Gurr, 1965); 1% aniline blue-black in 7% acetic acid for proteins (Fisher, 1968); and Sudan black B in 70% ethanol for lipids (O'Brien & McCully, 1981). Nonspecific esterase activity was detected on flowers immediately removed from branches, described by Dejong et al. (1967). Controls were run by omitting the substrate.

Male and female flowers were also sampled at anthesis and from 1 to 3 days post-anthesis and were prepared for cryofixation and freeze-substitution at IRD (Institut de recherche pour le développement). Freeze-substituted flowers were then prepared for light, scanning, and transmission electron microscopy after warming to room temperature as described by Koehl (2002). To determine the presence of pectins and arabinogalactan proteins (AGPs) in the extracellular matrix (ECM), immunolocalization at the level of the TEM was conducted using monoclonal antibodies JIM5 and JIM13 specific to highly esterified homogalacturonans and AGPs, respectively, as described by Koehl (2002).

FLORAL AND LEAF ODORS

Volatile compounds were sampled by head space methods and analyzed using GC-MS as described by Azuma et al. (1997, 2001). A mini-pump (model MP-2N, Shibata Scientific Instrument, Tokyo) was used to extract air from the enclosed flowers, buds, and leaves of male and female plants. Glass cartridges (7 mm × 5 cm) containing adsorbent (30 mg Tenax GR, Mesh 60/80, GL Sciences, Tokyo) were inserted into the flow line (silicon tubing) to capture the chemicals. A total of 12 samples (including controls) were taken for various lengths of time during day and night periods to span a complete day. The pumps were driven at approximately 150 ml/min for 2 to 6 hours (plus control). The glass cartridges were subsequently sealed in aluminum foil and stored in a freezer (−20°C).

CHARACTERIZATION OF FUNGI IN FLORAL GALLS

Male and female plants were inspected in the field for the presence or absence of fruit-like galls. Inspection indicated that female plants only produced fruit-like galls. However, holes indicating the emergence of insects were regularly observed in 2 mm male floral buds. Similar observations were made on female floral buds in addition to the fruit-like galls. The fruit-like floral galls of *Amborella trichopoda* were collected from plants growing in the Col d'Amieu (2001 and 2002) and Plateau de Dogny (2001) and placed in closed sterile vials where insects were allowed to emerge. Branches used to determine flower number/node (see above) were also used to quantify the number of fruit-like galls/node as well as fruits/node. Insects from the floral buds and fruit-like galls were stored in 70% ETOH and sent to the Smithsonian Institution for identification and deposition.

Dissection of both parasitized floral buds and floral galls indicated the presence of fungal growth therein. To identify the fungi, intact flowers and galls were placed in sealed sterile vials and transported to the University of Toronto. Within 5 days, the galls were split into halves using a flame-sterilized razor blade and then pulled apart. This allowed the larval chamber to be exposed without introducing contamination material. All galls examined contained insect larvae or pupae and/or evidence of insect activity (with insect exit holes).

Using a dissecting microscope, small pieces (4–5 per gall) of the chamber wall or frass of 10 galls were aseptically transferred to petri dishes to isolate (grow) fungi that were living in the plant tissue. The culture medium contained Modified Leonian's Agar (Malloch, 1981) supplemented with chlortetracycline and incubated at 21°C for several days. Modified Leonian's Agar was chosen because it is an all-purpose medium that generally allows good growth for most fungi. The resulting colonies were then subcultured on Modified Leonian Agar.

←

—c. Tissue on ovipositor (arrow) of cecid captured on petroleum jelly-covered slide placed on female plant. Bar = 25 μm. —d. Pollen tetrad possibly of *A. trichopoda* (arrow) adjacent to mouth part of the same cecid illustrated in Figure 3c. Bar = 13 μm. —e. Pollen tubes (arrows) growing on stigma of *A. trichopoda* (open pollinated). Bar = 25 μm. —f. Pollen tube (arrows) entering micropyle and embryo sac of ovule of *A. trichopoda* (open pollinated). Bar = 25 μm. Figure abbreviations: L, lipid pollen coat; S, stigma; OV, ovule.

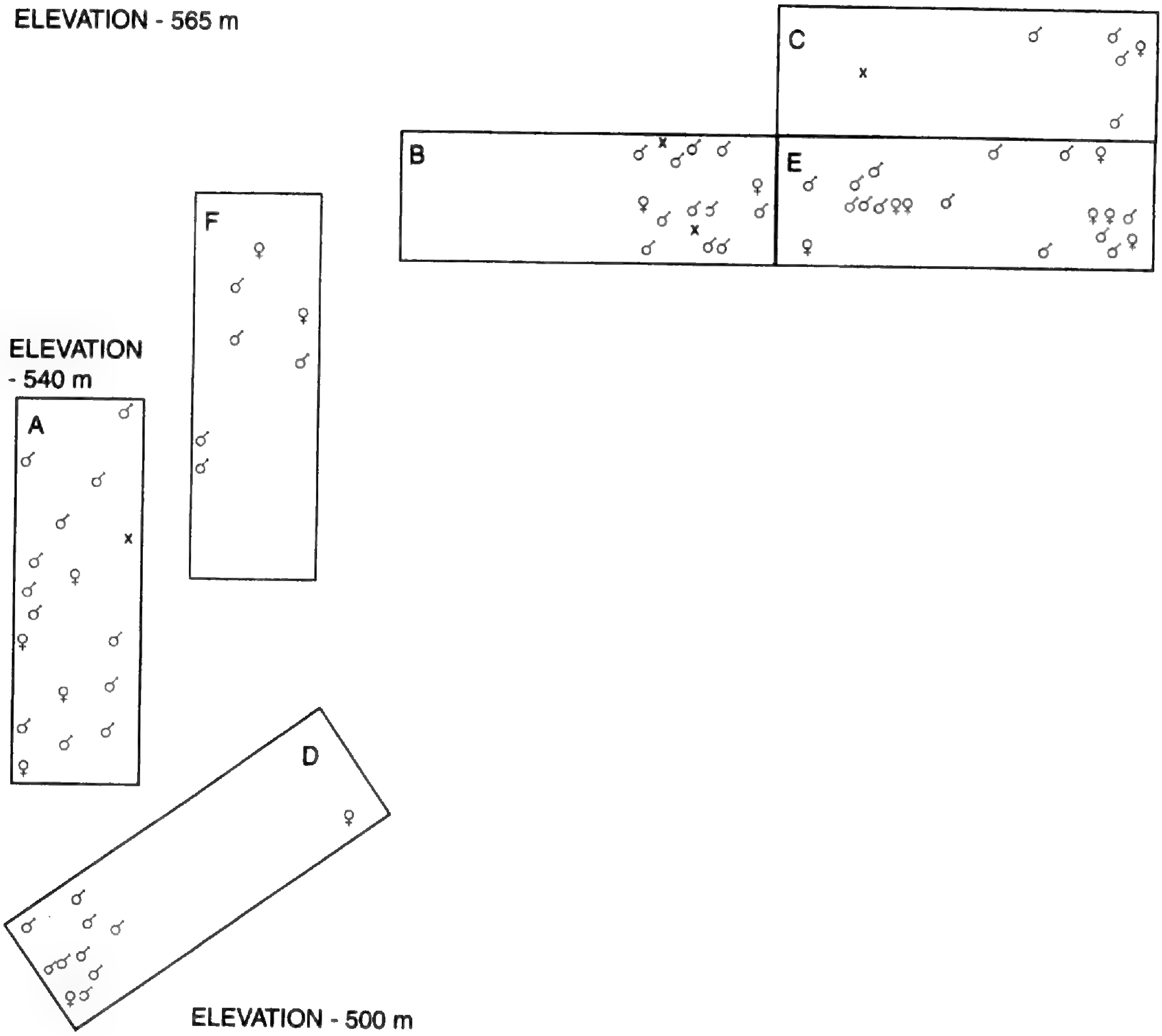

Figure 4. Map of 10 × 30 m plots at Col d'Amieu showing distribution of male and female plants of *Amborella trichopoda*.

RESULTS

DIMORPHISM IN SELECT VEGETATIVE AND REPRODUCTIVE FEATURES

No significant differences were observed at Col d'Amieu between male and female individuals with respect to height, number of stems at ground level, and stem diameter (Table 1). In general, *Amborella trichopoda* is an evergreen shrub (Fig. 2) with a slightly scandent habit (Bailey & Swamy, 1948), or it forms a small tree 7–8 m tall (Posluszny & Tomlinson, 2003). The main shoot (trunk) of *A. trichopoda* tends to branch at or near the soil surface (Fig. 2). Adventitious roots occur on the trunks of some plants. Trees of *A. trichopoda* with tall and large diameter trunks are rare, although four individuals were recorded with trunk heights ranging from 1 to 5 meters (3.04, 5.0, 1.3, and 1.0 m); the trunks of these individuals tended to be broken and/or hollow and rotten (Figs. 1, 2). Signs of herbivory and necrosis are common on leaves as is the growth of lichens.

All plants examined at Plateau de Dogny and Col d'Amieu were strictly male or female. No female flowers, fruits, or fruit-like galls were identified on any male plants and no functional carpels were identified on male flowers, thereby confirming previous reports that the plants are functionally unisexual and the populations are dioecious (Bailey & Swamy, 1948; Endress, 2001). Male flowers produced 9552 ± 996 pollen grains/flower (N = 12 flowers/4 plants) with a pollen abortion rate of 7.9% ± 4.9% (N = 12 flowers/4 plants), whereas staminodes on females produced no pollen grains, aborted or otherwise. The plots from the Col d'Amieu population of *Amborella trichopoda* were all male biased (Table 1). The male and female plants at Plateau de Dogny were not mapped, although the male to female ratio was 1.8 to 1, N = 118 plants in a transect from 625 to 730 m. Although female

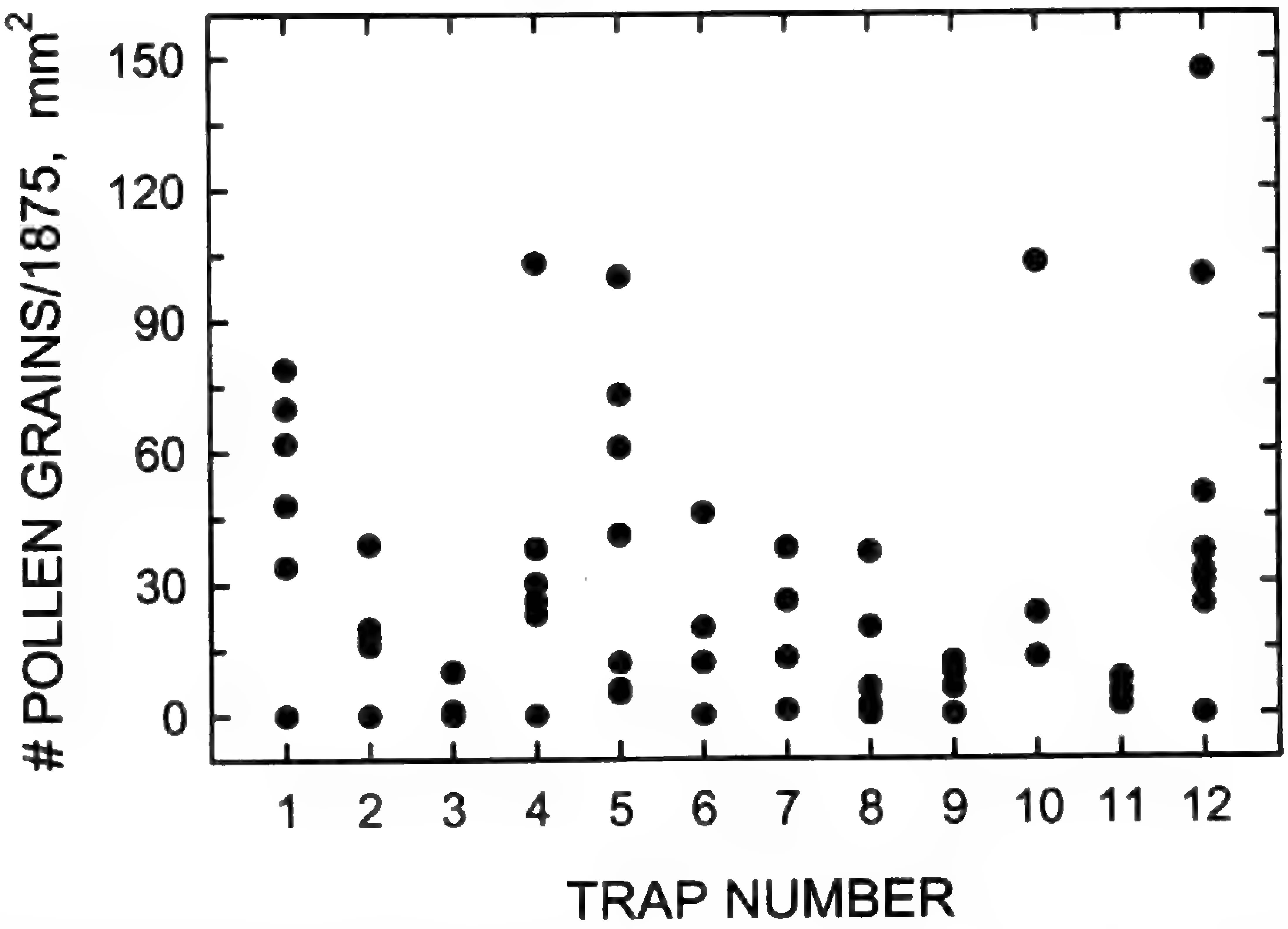

Figure 5. Number of pollen grains captured on petroleum jelly-covered slides placed within the canopy of female (traps 1–3) and male (traps 4–6) plants of *Amborella trichopoda*, respectively, and within 3 m (traps 7–9) and 10 m (traps 10–12) of the co-occurring males and females, from three separate locations for four days.

and male plants did occur singly, more commonly they were clustered, but preliminary AFLP analyses of their DNA indicate the plants do not form clones (Graham et al., in prep.). Flowering and nonflowering branches from adjacent male and female plants were often intertwined.

THE MORPHOLOGY AND PHENOLOGY OF REPRODUCTIVE ORGANS

The male and female flowers of *Amborella trichopoda* are small, flat structures with organs arranged on a floral platform that rips as the flower expands (Endress & Igersheim, 2000; Posluszny & Tomlinson, 2003). The tepals of flowers of both sexes are cream-colored (the ovary is green in female flowers), and flower size ranges from 3 to 5 mm across (male flowers are slightly larger; Bailey & Swamy, 1948; Endress & Igersheim, 2000). The flowers are produced on short (4 cm) paniculate inflorescences in the axils of leaves (Money et al., 1950; Endress & Igersheim, 2000) and are also cauliflorous on stout branches and trunks. The male flowers bear 6 to 21 short stamens with strap-like filaments and triangular anthers (Baillon, 1869; Bailey & Swamy, 1948; Endress & Igersheim, 2000). Each female flower usually contains 0 to 4 staminodes and 3 to 9 spirally arranged carpels. The number of floral organs in both female and male flowers is highly variable, a pattern common to the ANITA grade and other families of basal angiosperms (e.g., Magnoliidae sensu Endress, 1990).

Flowering of male and female plants was synchronous at Plateau de Dogny and Col d'Amieu. Significant differences were observed between the number of female and male flowers per inflorescence (number of female flowers/inflorescence = 4.2 ± 1.3, N, 106 inflorescences; number of male flowers/inflorescence = 4.6 ± 1.6, N, 98 inflorescences; $P = 0.05$). Significant differences were observed in dry weight of female versus male flowers at anthesis (female = .011 g ± .006 g/, N, 10 flowers/9 plants; male = 0.0226 g ± .006 g/, N, 10 flowers/9 plants; $P = .05$).

Observations of 127 buds and flowers (at 14 nodes) over 8 days on 3 male plants (7 branches) at Col d'Amieu indicate the buds open throughout the day and night. This begins as the tepals form a small, circular aperture during expansion at the perianth apex. Approximately 18 to 45 hours are required for the process to reach completion with the dehiscence of the outermost stamens. Pollen is dispersed for 36 to 96 hours. Inspection of fresh, unfixed anthers indicated that no exudates were present on the anthers. The average life span of a "typical" male flower from bud opening to complete anther dehiscence of pollen ranges from 4 to 5 days. As the perianth expands the rim of the floral platform gradually curls downward, spreading the stamens. Once the anther sacs are empty of pollen the center of the flower becomes concave, the floral platform curls further and the greenish white stamens turn brown, and the entire flower abscises, usually within one day.

Observations of 29 buds and 15 flowers at 4 nodes over 9 days on one female plant (2 branches) at Col d'Amieu, showed the flower bud opening process was similar to that of male plants. The time from bud opening to open flowers with receptive stigmas (visual inspection), varied from 18.5 to 24 hours, with stigmas appearing receptive for up to 24–30 hours. When the perianth first opens the staminodes and stigmas are held upright but gradually reflex as the flower progressively ages. The staminodes lie perpendicular to the carpels when the flower is fully open. As the flower ages the green-white stigmas and tepals gradually turn brown or faint red to yellow and abscise after 1 to 2.8 days.

HISTOCHEMICAL AND STRUCTURAL ANALYSIS OF THE ANTHERS AND STIGMAS

Inspection of fresh, unfixed anthers combined with histochemical and structural analysis indicated that no exudates were present on the anthers. As well, no exudates were observed to be present on the anther when cryofixation was used prior to preparation for SEM. The irregularly shaped cuticle was thick and blistered with an underlying pectin-rich layer (Fig. 6a, b). The cuticle was uniform throughout except for a reduced number of blistered regions at the connective tip.

Stigmas varied as to whether an apparent free-flowing secretion was present or not. An apparent free-flowing stigmatic secretion was observed only on 3 of more than 1200 female flowers under natural and laboratory conditions from plants at Plateau de Dogny and only 30 of approximately 1000 flowers at Col d'Amieu. The apparent free-flowing secretions were only present at Col d'Amieu during the second week of observations after a day of rain. The following observations apply whether the free-flowing stigmatic secretion was apparent or not. Stigmas were histochemically positive for pectins and proteins (Fig. 3b). A thin cuticle with positive esterase activity covered the multiseriate stigmatic papillae, which was subtended by a heterogeneous extra cellular matrix (ECM) containing low-esterified pectins, and moderate amounts of AGP (Fig. 6d, e). This ECM extended between all files of cells comprising the stigma and into the region of angiospermy (Fig. 6f).

FRUITS AND GALLS

The small (5 × 7 mm) drupaceous fruit of *Amborella trichopoda* (Bailey & Swamy, 1948; Endress & Igersheim, 2000) has slightly compressed sides, a fleshy mesocarp with red juice (Fig. 1a), and a stony endocarp (Bailey & Swamy, 1948; Endress & Igersheim, 2000). Both fruits and galls (Fig. 1a) were observed at all three locations during August and March. Observations of mature fruits and galls at Col d'Amieu and Plateau de Dogny suggest both remain attached to the plant through overlapping flowering seasons. The mean number of fruit/node was not significantly different from that of galls/node (fruit/node = 1.7 ± 2.3, N, 259 nodes; galls/node = 1.7 ± 1.3, N, 183 nodes; P = 0.231). There was an expected significant difference in dry weight between fruits and galls (fruit dry weight/5 fruit = 0.21 g ± 0.02; gall dry weight = 0.17 g ± 0.03; t = 3.508, df = 18, P = 0.003). Only 5 out of 550 galls dissected appeared to contain a seed. The number of fruits and galls developing per flower ranged from none to 5. Both fruits and galls developed in the same flower(s).

DEVELOPMENT AND ASSOCIATED ENTOMOLOGY OF CARPEL GALLS

Insects oviposited either within the whorls of initiating organs of both male and female flowers or within the ovary locule of *Amborella trichopoda* (Fig. 1b). Insects developing following ovipositing within the whorls of organs were easily identified as the floral buds were swollen and frequently dark in appearance due to the presence of a dark fungus (Fig. 1a). Ovipositing within the ovary locule only resulted in the production of galls. Insects isolated from the floral buds where ovipositing did not induce gall development included *Rileya, Megastigmus,* and *Thysanoptera.* Pollen placed on the stigma of an oviposited ovary failed to germinate.

The breeding system of *Amborella trichopoda* is impacted by two species of gall-inducing gall midges (Cecidomyiidae; Roskam, 1985; Hawkins & Gagné, 1989; Gagné, 1989). The most common gall midge (maggot) in the galls of *A. trichopoda* is a new species in the genus *Asphondylia,* probably endemic to New Caledonia. It is known that many species of *Asphondylia* have a needle-like chitinized ovipositor to place eggs into plant tissue (like buds). Pupal development of *Asphondylia* takes place in the galls of *A. trichopoda.* In other seed plants, emergence of adults is usually correlated with specific plant tissue formation of the host. Typically males emerge first and after mating females search for the host plant (Harris, 1994). The insect's adult life tends to be brief (usually hours or days, but some live longer) and eggs hatch within days or weeks, followed by development of the larvae (Harris, 1994). The development time of the larvae feeding in the galls of *A. trichopoda* is unknown. As noted, the primary flowering season of *A. trichopoda* extends from March to May, allowing adequate tissue for repeated infection of the female flower buds. The insects insert an egg(s) into the carpels of developing flowers (in 2 mm buds) on female plants (Fig. 1a). Subsequently, with emergence and feeding of the larva (Fig. 1b), the carpel develops into a hollow gall (ca. 8 × 9 mm), nourished by vascular traces from the plant. In the mature gall, fungi line the cavity of the gall and are perhaps eaten by the developing maggot (Roskam, 1992; for galls in general see Dreger-Jauffret & Shorthouse, 1992, and Mani, 1964).

In a sample of 10 galls, each larval chamber contained fungi, but the surrounding gall tissues did not. The fungal material clearly differed from gall to gall in color (white, black, or brown) and texture. Seven of the 10 galls yielded only 1 fungal species, while 3 contained 2 species of fungi. Sporulating black or brown colonies have been identified as *Phoma* and *Cornucopiella.* All fungi were mitosporic (Fungi Imperfecti). Four of the 17 isolates (from the 10 galls) produced white colonies: 2 have tentatively been placed in the genera *Acremonium* and *Gliocladium,* but 2 of the isolates remain sterile and unidentified.

Isolates of two floral buds and one pupa (cadaver) from inside one of the galls also yielded fungi. The buds yielded isolates of *Fusarium* spp., and the cadaver was infected with vigorously sporulating species that produced apothecium-like conidiomata of *Cornucopiella.* Floral buds with *Fusarium* did not develop mature anthers or carpels.

Non-sporulating fungi were common in the isolates, as has been found in other insect-associated fungi, e.g., fungi cultivated with attine ants (Muchovej et al., 1991), and in ambrosia fungi (Cassar & Blackwell, 1996), in which the fungus exists in an asexual yeast-like form.

Several fungi have previously been reported from galls produced by *Asphondylia* species (insects). Many of the fungi appear to be common plant endophytes, but their relationship to the insects is not clear (Wilson, 1995). *Macrophomopsis coronillae* (Desm.) Petrak has been repeatedly isolated from galls produced by *Asphondylia* species in north temperate regions since the early 20th century (Kehr, 1999) and has been thought to be used by the larvae as food, since Neger (1909, 1910) first identified it and labeled it as "Ambrosiapilz." None of the isolates from galls of *A. trichopoda* could be identified as species of *Macrophomopsis.* The non-sporulating strains, however, require further study before they can be identified.

GALL INSECT ASSOCIATES

Each gall is essentially a small ecosystem with its own species composition of parasitoids (Zwölfer, 1979; Hawkins & Goeden, 1984; Hawkins & Gagné, 1989). The galls produced by *Asphondylia* sp. nov. on *Amborella trichopoda* also have a guild of associated insect taxa, mostly parasitic wasps (Hymenoptera). Although the exact relationships have not been elucidated in this particular system, it seems most likely that these wasps are primary or secondary parasitoids in the gall system, consuming the larvae of gall-forming flies. The most common chalcidoid is a new species of *Rileya* (Chalcidoidea: Eurytomidae), which resembles three other species, *R. insularis* and *R. cecidomyiae* from the New World, and an undescribed Australian species. *Rileya* species to date are associated exclusively with galls made by the Cecidomyiidae, and several *Rileya* species have been documented from non-economically important cecidomyiids in the United States (Plakidas, 1982; Plakidas & Weis, 1994; Waring & Price, 1989; Hawkins & Goeden, 1984). However, *Rileya cecidomyiae* Ashmead (cited as *R. tegularis* Gahan by Hawkins & Goeden, 1984) can switch from entomophagy to phytophagy during its larval existence. This mixed feeding habit is apparently an important component in parasitoid success (Hawkins & Goeden, 1984). One unidentified braconid wasp (Ichneumonoidea: Braconidae) also emerged from galled *A. trichopoda* fruit. It is likely parasitic and may attack the gall formers or its parasitoids.

The genus *Systasis* (Chalcidoidea: Pteromalidae) was collected on and near flowering plants of *Amborella trichopoda.* This genus is cosmopolitan, with over 30 species worldwide and 21 from Australasia (Boucek, 1988). The various species are seed feeders or parasites of Cecidomyiidae, and some host associations may be mixed phytophagous and entomophagous (Boucek, 1988).

Two larvae of *Megastigmus* were found in galls of *Amborella trichopoda.* The genus *Megastigmus* Dalman (Chalcidoidea: Torymidae) comprises about 125 described species, most of which are believed to be seed-eaters. A few species, however, parasitize gall-formers, their parasitoids, and in some cases they also consume plant tissue. The most common host insects are Cynipidae, but gall-forming Eurytomidae and Pteromalidae also serve as rare hosts, as well as two species of parasitic Torymidae. One species is known to parasitize Cecidomyiidae in flowers of *Eucalyptus* spp., and two attack gall-forming Eriococcidae (Grissell, 1999). Many hosts remain to be discovered.

FOLIAGE AND FLORAL FORAGERS AS PROSPECTIVE POLLINATORS

A wide variety of insects visit floral and foliage organs of *Amborella trichopoda.* Most notably, the

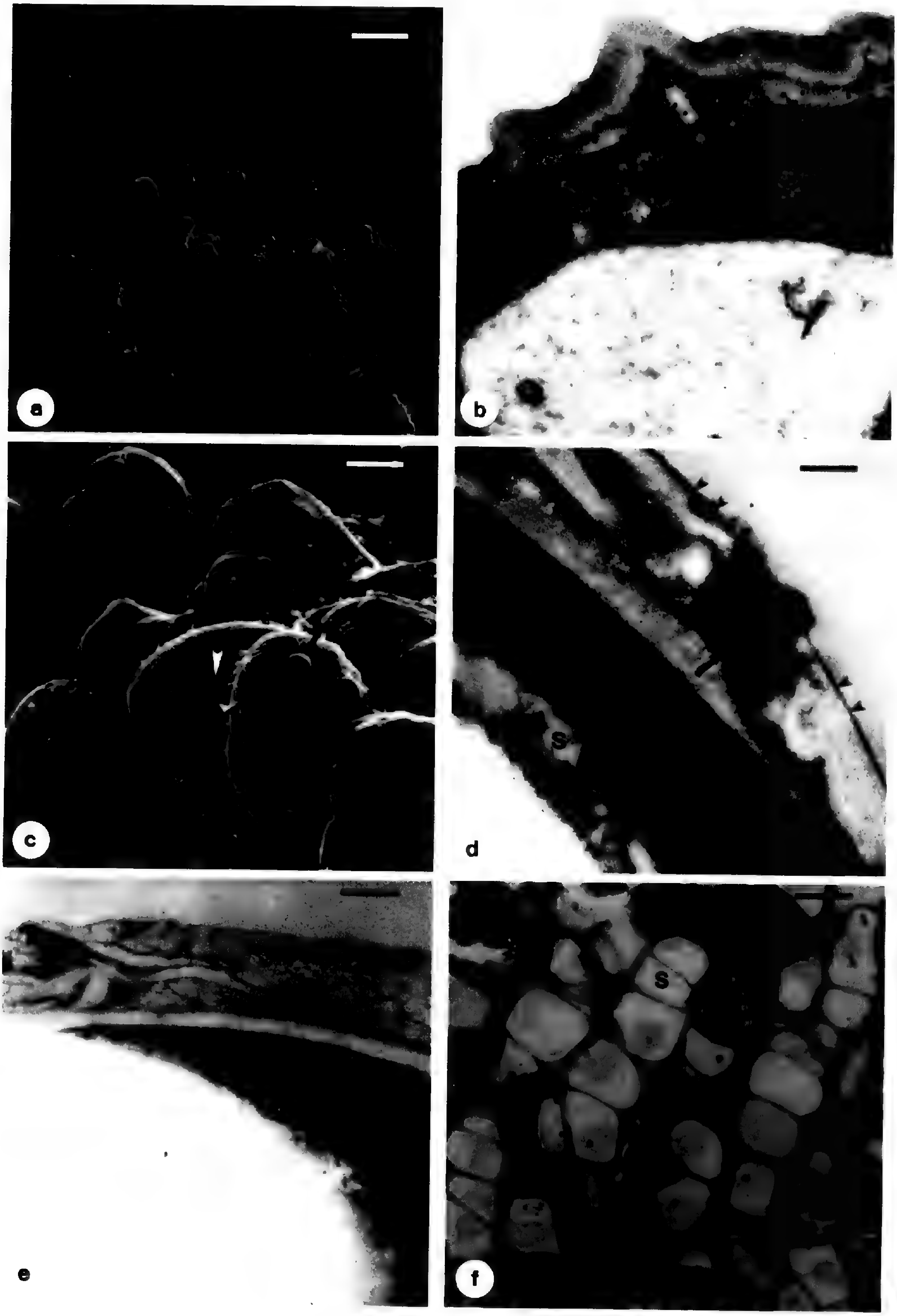

Figure 6. Micrographs of anther and stigma of *Amborella trichopoda.* All tissues prepared by cryofixation. —a. Epidermal cells of terminal region of the anthers. Note absence of secretions. Arrow shows blistered appearance of cuticle. Bar = 3 μm. —b. Transmission electron micrograph of anther epidermal cell showing immunolocalization of pectin (arrowhead) below thick cuticle. Bar = 0.2 μm. —c. Scanning electron micrograph of stigmatic cells showing ruptured thin cuticle (arrowhead) and localized uplifts of pectin (arrow). Bar = 6 μm. —d. Transmission electron

majority of these insects also occur in the litter of the forest. Insects collected and observed on both flowers and vegetative parts of *Amborella trichopoda* at Col d'Amieu are listed by identification number in Table 2. Two species of Curculionidae (Cryptorhynchinae) are common pollinators of *A. trichopoda* at Col d'Amieu (Table 2). One species, a small black cryptorhynchine ca. 4–5 mm in length was collected and observed at all study sites. In the flowering season this insect was observed on male and female flowers and leaves of *A. trichopoda*. However, in August 2001 (*A. trichopoda* was not in flower) it was again recorded on the leaves of *A. trichopoda* but not observed on other plant species in the populations. The larger cryptorhynchine (2–3 cm in length) spends hours walking on the branches, leaves, and flowers of *A. trichopoda,* and pollen of *A. trichopoda* was removed and identified from the ventral surface of one individual (Table 2). When the rostrum (beak or snout) of the insect is folded, this weevil becomes difficult to detect due to its cryptic coloration, as its body then resembles a seed or a fungus.

Neoadelium fauveli (Zaszab) (Coleoptera: Tenebrionidae: Adelinae) belongs to what is considered to be the most primitive tribe of the family (Fig. 3b; Doyen et al., 1989; Hawkeswood, 1987). The genus *Neoadelium* is endemic to New Caledonia and contains five known species (Kaszab, 1982; Matthews, 1998). The insects were observed scooping pollen out of the anthers, and their mouth parts were covered with pollen. Microscopic examination of the hind gut contents of two male specimens and the foregut of another (collections 3, 17) revealed abundant wood bits and other plant tissue, but no pollen. Pollen feeding has been observed in some unrelated tenebrionids (Steiner, 1988) and by P. Bernhardt and P. Weston (in prep.) on *Eidothea hardeniana* P. H. Weston & Kooyman, a Proteaceae (Weston & Kooyman, 2002). Members of Adelinae are not known to feed on pollen but "on leaf litter and other accumulations of dead plant matter—some in rotten wood" (Matthews, 1998). Otherwise, members of tenebrionid groups are regarded as uncommon flower and pollen foragers, and have been unrecorded previously as prospective pollinators (Bernhardt, 2000). However, *Neoadelium fauveli* is flightless, as its hind wings are very reduced and presumably would not be as efficient a pollinator as winged beetles.

Long-horn beetles (Coleoptera: Cerambycidae: Lamiinae) were observed at night on female plants of *Amborella trichopoda* walking on leaves and flowers. This species is flightless and rare. The larvae of Cerambycidae are generally xylophagous (Hawkeswood, 1987), while adults often feed on flowers or fruits (Bernhardt, 2000). This particular species may be associated with fungus or lichens as an adult (Lingafelter, pers. comm.). Lamiinae are well developed in Australia, and several endemic species occur in New Caledonia (Gressitt, 1982).

Other taxa collected on *Amborella trichopoda* are listed in Table 2 (Nos. 1, 2, 5, 7, 8, 11, and 14), and general comments are offered below on what is known about their habits. The aderid and the corylophid (Nos. 1 and 2) are usually found on vegetation and are most likely detritivores. The mirid insect (No. 5) is probably phytophagous, although predatory species do occur. The aphrophorid insect (No. 8) and the cicadellid (No. 7) are phytophagous, the latter being endemic to New Caledonia. The unidentified coccinellid insect (No. 20) is likely predaceous both as a larva and an adult on various sessile insects (scales, aphids, etc.). The braconid insect (No. 11), collected from a leaf, was likely searching for a host plant to parasitize. The unidentified Microlepidoptera insect (No. 14) may be an important pollinator, as Collett (1999) reported nocturnal moths visiting and pollinating flowers of *A. trichopoda* in greenhouses at the Santa Cruz Arboretum, California. Some Microlepidoptera retain pollen-scraping mouth parts, e.g., *Sabatinca* sp. that pollinate *Zygogynum* in New Caledonia (Thien et al., 1985).

Insects attracted to the small flowers of *Amborella trichopoda* range in size from approximately 1.0 mm to over 7 cm in length. The larger insects walk on the branches and crawl through the inflorescences feeding on pollen, and in the process their ventral surface is coated with pollen. The flat platform morphology of male and female flowers and the adhesion of the pollen grains aid in pollen transfer as the ventral surface of the insect scrapes over the flower. Pollen is also deposited on an in-

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micrograph of stigmatic cells showing thin cuticle (arrowheads) and immunolocalization of pectins (JIM5—arrow). Bar = 0.4 μm. —e. Transmission electron micrograph of stigmatic epidermal cells showing immunolocalization of arabinogalactans (JIM13—arrowhead) in the extracellular matrix. Bar = 0.4 μm. —f. Light micrograph showing exudate among stigmatic epidermal cells. Bar = 25 μm. Figure abbreviations: C, cuticle; E, extracellular matrix; S, single cell of multicellular stigmatic trichome.

Table 2. Insects captured and observed on male and female plants of *Amborella trichopoda* at Col d'Amieu, New Caledonia (approximately 25 hours of observation over 11 days). N = collection number; Fl = flowers; L = leaves; ( ) = number of pollen grains on captured insects; yes = captured and also observed on leaf and flower. Voucher specimens are deposited at the Smithsonian Institution.

		Captured				Observed			
		Male		Female		Male		Female	
Taxon	N	L	Fl	L	Fl	L	Fl	L	Fl
Coleoptera									
Corylophidae (minute fungus beetles)	1	1 (71)						3	
Aderidae (ant-like leaf beetles)	2	1 (7)							
Tenebrionidae: Adelinae (darkling beetles), *Neoadelium fauveli*	3, 15, 17	1 (3)		2 (48, 0)		3	1	5	
Curculionidae (Cryptorhynichinae)									
large snout insect, 2–3 cm	4, 16	1 (many grains)		1 (13)		5		1	
snout insect (small, 4–5 mm)	6, 18	1 (0)		1 (0)		8		2	
Coccinellidae (ladybird beetles)	20			1 (0)					
Cerambycidae: Lamiinae (long-horned beetles); 7–8 cm	19							2	yes
Homoptera									
Aphrophoridae	8	1 (12)	yes						
Cicadellidae: *Thara picta*	7	1 (1)							
Hemiptera									
Miridae (leaf bugs)	5	1 (10)							
Microlepidoptera	14	1 (0)	yes						1
Hymenoptera									
Chalcidoidea: Eurytomidae *Rileya* sp. nov.	9, 12		1 (0; bud)		1 (0)				
Chalcidoidea: Pteromalidae, *Systasis*	10				1 (0; bud)				
Braconidae	11				1 (0)				
Diptera									
Cecidomyiidae (gall midges)	13		1 (20)						1 (bud)

Table 3. Number of pollen tubes in stigmas (carpels) of *Amborella trichopoda.* Data recorded from 208 flowers collected in 1 day from 11 plants along a transect at Plateau de Dogny.

Plant number	Altitude meters	Number of flowers	Number of carpels	Carpels with tubes	Flowers with no tubes	Flowers with tubes
1	625	14	58	26	3	11
2	640	26	119	38	6	20
3	640	7	31	12	1	6
4	660	6	25	7	3	3
5	660	17	80	11	13	4
6	690	27	133	22	13	14
7	700	17	74	4	14	3
8	710	15	70	12	7	8
9	725	26	121	18	14	12
10	730	27	134	19	15	12
11	730	26	98	9	20	6
						99
Totals		208	943	178	109	99
				18.8%	52.4%	47.5%
					Unpollinated	Pollinated

sect's body by other flowers in the same inflorescence as it crawls over individual flowers to feed on pollen. The male flowers of *Amborella trichopoda* produce large quantities of pollen, as indicated by its high pollen to ovule ratio (9552 to 6), which suggests both that wind pollination takes place and that ample pollen is available as food and for deposition and transport on the bodies of insects. In addition, the floral phenology of the paniculate inflorescences maintains several functional flowers per inflorescence throughout the flowering season, potentially increasing the rate of pollination.

The parasitic Hymenoptera occur in large numbers on the flowers of *Amborella trichopoda* (Table 2), although the precise number of observations was not recorded because it was not possible to identify the various species in the low light conditions in the forest. The role of parasitic Hymenoptera as potential pollinators of *A. trichopoda* is unknown. We are aware of only a few documented examples of pollination of a plant by a parasitoid (Ferguson & Donham, 1999; Nilsson, 1979; Dixon et al., 1990; Feil, 1992; Feil & Renner, 1991).

The Cecidomyiidae (No. 13) collected from male and female flowers of *Amborella trichopoda* appear to be the same species reared from a gall. An insect captured from the male flower carried pollen on its legs, but more of these small insects must be captured and examined for pollen to determine what role they play in pollination.

WIND POLLINATION

Pollen of *Amborella trichopoda* was dispersed onto the petroleum jelly-covered microscope slides placed within the crown of male and female plants up to 30 m from the nearest male (Fig. 5). It should be noted that all pollen traps were continuously hung for four days, whereas the average life span of a female flower is one day. Significantly, although the number of grains captured per slide was quite variable, grains were dispersed onto slides in clumps of 7 to 12 suggesting the presence of a lipid pollen coat, an interpretation subsequently confirmed by SEM of cryofixed anthers (Fig. 3a). Eight of the 58 slides also captured at least one insect species each of Cecidomyiidae and Thysanoptera. One cecid had both plant material associated with its ovipositor and microspores associated with its mouthparts (Fig. 3c, 3d).

ANALYSES OF OPEN-POLLINATED FLOWERS

Pollen germination in pollinated flowers resulted in numerous pollen tubes reaching the base of the stigma (Fig. 3e), but only one to three tubes were observed to enter the ovary locule and one to enter the ovule (Fig. 3f).

Flowers of *Amborella trichopoda* collected along a transect at Plateau de Dogny (a one-day sampling period) were examined for the presence and number of pollen grains on stigmatic surfaces and pollen tubes penetrating gynoecium tissues (Table 3). In a sample of 208 flowers collected from 11 plants along a transect from 625 to 730 m elevation, 52.4% contained gynoecia in which all the carpels lacked adherent grains and pollen tubes (not pollinated; Table 3). The data also show that the 208 flowers bore 943 carpels, but only 178 (18.8%) carpels had pollen grains adhering to their stigmas and/or penetrating pollen tubes (Table 3). The maximum number of germinating-penetrating pollen tubes in a carpel was 13 taken from a flower collected at 625 m. All other pollinated carpels analyzed contained one to five pollen tubes. Only five flowers (2.4%), collected on five separate trees, contained gynoecia in which all of the carpels on the receptacle contained at least one germinating grain. These fully pollinated gynoecia were taken from plants 1, 2, 3, 5, and 11 (Table 3) representing a total of 19 pollinated carpels. Although this is only a single sample over a long flowering season, we noted that the stigmas of female flowers remained receptive for 1 to 2.8 days, and this may be indicative of the actual rate of natural (open) pollinations.

In another sample in which 127 buds and flowers were observed over 8 days (April 2001) at Col d'Amieu, none of the flowers set fruit.

FLORAL ODORS

Labels on herbarium sheets (IRD, Noumea, New Caledonia) indicate the flowers of *Amborella trichopoda* produce a sharp odor. Observations of flowering plants in the greenhouses of *A. trichopoda* indicate that the plants produce an odor late in the evening (Collett, 1999, and pers. comm.). One author (LBT) detected an odor from flowers on cut branches of *A. trichopoda.* While carrying the specimens from the field to the laboratory, a faint odor was detected that smelled like licorice, scented hay, and also at times like feces. Other efforts to detect any odor from the flowers at all hours of the day failed. No specific signals for odor were detected from the samples. More sensitive techniques are currently being devised to attempt capture of odors from the buds and flowers. It has been well demonstrated that odors are involved in parasitoid search for host plants (Godfray, 1994), and it therefore seems likely that they are produced by *Amborella trichopoda.*

DISCUSSION

INSECT VERSUS WIND POLLINATION

Field observations, insect collections, and pollen-load analyses of floral foragers as well as wind traps strongly suggest *Amborella trichopoda* is pollinated by representatives of families placed in the insect order Coleoptera and other taxa of insects, as well as by air currents, reflecting a generalist mode of pollen deposition (sensu Faegri & van der Pijl, 1979). *Amborella trichopoda* shares a suite of characters common to many tropical, woody dioecious species that occupy the understory with a generalist mode of pollination. In these instances, the dioecious species produce numerous small flowers with few floral attractants ranging in color from white to yellow to pale green with pollination conferred by unspecialized pollinators that typify such understory habitats (Bawa & Opler, 1975; Mayer & Charlesworth, 1991; Sakai et al., 1995). Insects effecting pollination in many dioecious tropical species are generally small. In contrast, both small and large insects appear to disperse pollen in *A. trichopoda.*

The pollination of *Amborella trichopoda* by Cerambycidae, and the large-bodied Curculionidae, and Tenebrionidae (of which the latter two spend long periods of time walking on the intertwined flowering/vegetative branches of male and female plants) is a distinct mode of beetle pollination (see Bernhardt, 2000). If the flowers of *A. trichopoda* were bisexual, these large insects would undoubtedly effect geitonogamy in the absence of any self-incompatibility mechanism. Although pollen feeding has been observed in some unrelated tenebrionids (Steiner, 1988; Bernhardt, Kooyman & Weston, in prep.), the role of the Adeliini, to which *N. fauveli* belongs, as a primary pollinator represents an entirely novel relationship between plants and insects.

While both wind and insect pollination occur in *Amborella trichopoda* the question remains as to which mode of pollination provides the primary and most dependable mode of pollen transport to receptive stigmas. Our current data suggest that wind pollination is a "failsafe mechanism" for insect pollination and vice versa. The relative importance of insects versus air currents probably fluctuates with seasonal (climatic) pressures as in some *Salix* spp. (Vroege & Stelleman, 1990). While flowering far below the canopy layer of a wet, broad-leafed, evergreen, tropical forest is not associated typically with wind-pollinated angiosperms (Faegri & van der Pijl, 1979) neither is a pollinator spectrum dominated currently by flightless beetles. Whether or not the winged insects associated with the ecology of the galls on *A. trichopoda* act as pollinators remains to be determined. This feature will be valuable to address since cecids and parasitoid wasps that have been demonstrated to use floral tissue as a breeding site in other angiosperms also effect pollination (Monimiaceae; Feil, 1992: Orchidaceae; Nilsson, 1979; Dixon et al., 1990; Ferguson & Donham, 1999).

Insect and wind pollination in *Amborella trichopoda* most probably share similar modes of pollen dispersal for one important reason. The range of pollen vectors, the dispersal of pollen in sticky-adherent clusters, and the population structure of *A. trichopoda* at Col d'Amieu indicate that clumped (leptokurtic) pollination has a greater chance of success than either linear (sensu Richards, 1986) or long-distance pollination. This is particularly important as male bushes surround and overlap solitary females. In this respect, the combination of insect and short-distance wind pollination in *A. trichopoda* shows some similarities with insect and "gravitational" pollination (sensu Meeuse et al., 1990) in *Ephedra* spp.

Given the phylogenetic position of *Amborella trichopoda,* our results on the pollination biology of the species are consistent with the hypothesis that the first flowering plants had a generalist pollination mechanism (Bernhardt & Thien, 1987). Fossil evidence indicates that the earliest pollen vectors lacked both elongated nectar-collecting probosces and specialized behaviors to shake, vibrate, or manipulate anthers to remove pollen/or other edible rewards (see Grimaldi, 1999; Labandeira, 1997, 1998; Bernhardt & Thien, 1987). It has been posited that these early pollinators included beetles with chewing mouth parts, "short-tongued" but mandibulate moths, sphecid wasps, and early flies now placed within suborder Brachycera (Grimaldi, 1999; Kato & Inouye, 1994; Labandeira, 1998).

Do any members of the generalist system represent a long-term association with *Amborella trichopoda*? Wind and weevils (Curculionidae) appear to be the most likely candidates. Although wind pollination is rare among basal angiosperms (Thien et al., 2000), it also occurs within the ANITA grade, i.e., in *Brasenia schreberi* J. F. Gmel. (Nymphaeaceae; Osborn & Schneider, 1988) and in *Trimenia moorei* (Oliv.) W. R. Philipson (Trimeniaceae; Bernhardt et al., 2003). Wind pollination is also an option for *Saururus cernuus* L., a eumagnoliid species within the Saururaceae (Piperales; Thien et al., 1999; Pontieri & Sage, 1999), which, along with *Trimenia moorei,* is also pollinated by a wide variety of insects (Bernhardt et al., 2003). The association between curculionids and seed plants is an ancient one (Farrell, 1998), and weevils remain important generalist and specialist pollinators of a wide variety of cycads (Norstog, 1987) as well as basal angiosperms and eumagnoliid species (Bernhardt, 2000). For example, members of the genus *Elloschodes* are the only known pollinators of the relictual Australian eumagnoliid genus *Eupomatia* (Eupomatiaceae; Bernhardt & Thien, 1987).

The mesofossil floras of the Early Cretaceous (Barremian–Aptian) contain many small flowers (Friis et al., 2000). Indeed, the stamens of some of these fossil flowers are similar to those of *Amborella trichopoda* and members of other basal angiosperm families, including members of the ANITA group (Friis et al., 2000). Although the insects associated with *A. trichopoda* show more morphological similarities corresponding to taxa of the mid-Tertiary taxa, the insect-flower interactions seen in modern *A. trichopoda* may reveal novel interactions. Notably, the Cucurlionidae and the Tenebrionidae are actually part of a detritus fauna (e.g., insects crawling from litter to flowers) as reported for fly pollinators of another ANITA species, *Illicium floridanum* Ellis (Illiciaceae: Thien et al., 1983). This feature is significant, as it may give insight into the evolution of floral presentation in the early flowers of the late Jurassic–early Cretaceous (see Mitter & Farrell, 1991, for discussion of insect-plant phylogenetic relationships).

Based on these observations and analyses of pollen grains attached to insects, it is tempting to suggest that non-volant insects (such as wingless beetles), maturing within the forest litter, played a unique role in the pollination of the earliest angiosperms growing under a gymnosperm forest canopy. Along these lines, Feild et al. (2001), using *Amborella trichopoda* as a guide to extrapolate physiological characteristics of early angiosperms, noted cautiously that success in shady, wet forest understory habitats may account for the initial ecological success gained by angiosperms in Cretaceous landscapes. However, it is also possible that the relationship between non-flying beetles and dioecious *A. trichopoda* may be merely the consequence of a relictual angiosperm restricted to an island refugium in the southern Pacific basin. Carlquist (1974) noted that both wingless insects derived from winged ancestors and plants with unisexual flowers derived from ancestors with bisexual flowers are recurrent evolutionary "trends" on tropical Pacific islands.

FLORAL REWARDS VERSUS POLLINATION-BY-DECEIT

Insect pollination in angiosperms as well as other seed plants is closely tied to the evolution of attractants and rewards produced by the plant for the insect (Thien et al., 2000). Within the basal angiosperms, attractants include flower color and odors (pollen vs. floral epidermis) and rewards often combining physical warmth, breeding sites (copulation vs. brood chambers), pollen, nectar, food bodies, and other secreted metabolites (Thien et al., 2000). Heat and the production of volatile substances are regarded as ancient mechanisms for enlisting insect pollinators that may have evolved before floral pigmentation patterns. The first floral odors are posited to have been associated with a lipid-rich pollen coat (van der Pijl, 1960; Porsch, 1950, 1954; Thien et al., 2000). In addition, "protonectar" produced by wet stigmas is believed to be a relictual reward that evolved before the first interfloral (nuptial) nectar gland (Endress & Igersheim, 2000).

In the absence of detectable leaf or floral volatiles, starchy food bodies, free-flowing anther secretions, or an edible liquid associated consistently with the stigmatic surfaces, the primary attractant and reward for insects visiting male flowers of *Amborella trichopoda* is pollen. Pollen was the only floral component documented to be actively collected, in particular by the wingless tenebrionid, *N. fauveli.* Notably, a lipid-rich pollen coat was detected on the pollen grains of *A. trichopoda.* The pollen coat of *A. trichopoda* aids in the dispersal of pollen from anthers in clumps (even during wind dispersal). Although the pollen coat has been noted to function in increased pollen removal from anthers by pollen vectors (Endress, 1994), this feature represents a novel observation for a member of the ANITA group. It is tempting to speculate that the lipid coat may function as a pollinator reward. As well, the pollen of *A. trichopoda* may have an odor as observed in other species (Dobson & Bergström, 2000), which must be detected with alternative techniques, but the precise role of the pollen coat in the pollination biology of *A. trichopoda* remains to be determined.

In contrast to the pollen coat operating as a potential attractant and reward, a free-flowing stigmatic secretion was rarely observed in female flowers. Structural and histochemical observations of the stigma of *Amborella trichopoda* provide evidence that it is of the dry-type. The receptive surface in dry stigmas consists of a thin protein layer associated with non-specific esterase activity that is secreted onto the surface of the cuticle. The cuticle of dry stigmas remains intact and is only partially disrupted at anthesis. Although wet stigmas may possess an overlying pellicle layer, the receptive surface is composed of free-flowing exudates associated with a ruptured cuticle. In *A. trichopoda,* free-flowing liquid is not always present at the stigmatic surface and when present, the structural nature of the thin cuticle remains unchanged. The presence of a random stigmatic secretion in *A. trichopoda* parallels observations from a recent field study on the pollination biology of *Sarcandra glabra* (Thunb.) Nakai (Chloranthaceae). Droplets are also secreted occasionally by carpels of *S. glabra* (Tosaki et al., 2001). However, when these droplets are present they are consumed by insects associated with pollination of *S. glabra.* In contrast, no insect was ever found to consume the infrequent, stigmatic secretions of *A. trichopoda,* suggesting that this fluid is not a significant source of protonectar for prospective pollinators.

In fact, previous descriptions of wet stigmas in some members of the ANITA group require reinterpretation. Wet-type stigmas described in *Illicium floridanum* (Illiciaceae) and *Trimenia moorei* (Trimeniaceae) have been shown recently to be dry-types (Koehl, 2002; Bernhardt et al., 2003). The presence of a dry-type stigma in these basal groups calls into question views that a wet stigma was the plesiomorphic condition functioning in pollinator attraction or pollen capture, recognition, retention, and germination (Endress & Igersheim, 2000; Pontieri & Sage, 1999). Based on the flowers of extant taxa, it is more likely that a protonectar based on stigmatic secretions evolved independently and along early diverging lineages.

Why would insects collecting pollen of *Amborella trichopoda* ever visit a female plant, as these female flowers contain none of the edible rewards associated with basal angiosperms such as protonectar, pollen, or starch food bodies normally consumed by beetles (Bernhardt, 2000)? We suspect the pollination mechanism of *A. trichopoda* incorporates a form of cryptic dioecy (sensu Mayer & Charlesworth, 1991) in which the comparatively large and succulent staminodes in female flowers mimic the fertile androecia in male flowers (Mayer & Charlesworth, 1991). In cryptic dioecy (sensu Mayer & Charlesworth, 1991), one or both of the functionally unisexual morphs appear to have perfect, hermaphroditic flowers, making the dioecious condition difficult for both insects (and botanists) to detect. This mode of floral presentation has not been described in many taxa but has evolved independently in some unrelated families including the Myrtaceae, Araliaceae, and Trochodendronaceae (Mayer & Charlesworth, 1991).

Within the ANITA group (e.g., Nymphaeaceae and other basal angiosperms), floral deception mechanisms in both bisexual and small unisexual flowers attract insects to increase pollination (see reviews in Bernhardt & Thien, 1987; Bernhardt, 2000). *Amborella trichopoda* utilizes staminodes with no functional pollen and a dry stigma that produces little or no secretions (dry-type stigma). Pollen is the sole source of food for the visiting insects. Mayer and Charlesworth (1991) noted that in apparent androdioecy, nectar is absent or scarce, which fits the pollinator-attraction hypothesis.

In another member of the ANITA group, *Trimenia moorei,* the stigma of the small bisexual flower is also of the dry-type and produces no nectar yet appears to be wet (producing nectar) due to the high pectin content of the cell wall (Bernhardt et al., 2003). In addition, the flowers produce floral odors and one chemical, 2-phenylethanol, is known to attract insects and elicit a reflex extension of the proboscis (Bernhardt et al., 2003). Indeed, flies visiting the flowers of *T. moorei* were observed and filmed extending their probosces to touch the shiny stigma even though no nectar was ever present (Bernhardt et al., 2003).

The presence of deceptive mechanisms involving numerous floral traits in small unisexual and bisexual flowers of extant members of the ANITA group and other basal angiosperms suggests floral deception played an important role in the evolution of the early angiosperms. These mechanisms (Dufaÿ & Anstett, 2003) provided adaptations whereby small flowers could attract insects to increase rates of pollination at a relatively low cost in resources.

POLLINATION AND LIMITS TO SEED SET

While it is obvious that many potential seeds are lost to gall maggots in this species, our observations of fruits set at Col d'Amieu and analyses of open-pollinated carpels at Plateau de Dogny suggest strongly that a sheer lack of pollination may also limit seed set in *Amborella trichopoda.* At certain times in the flowering season and in certain populations of *A. trichopoda* pollen fails to reach the receptive stigmas on the majority of carpels regardless of whether the major pollinators are air currents, moths, or wingless, leaf-gleaning insects. This limit to fecundity occurs throughout the angiosperms when species have discontinuous populations and relatively long flowering seasons but are incapable of mechanical modes of self-pollination (see Lipow et al., 2002).

As *Amborella trichopoda* is a mass-flowering plant, a low conversion rate of tiny flowers into large fruits may be expected provided it is understood that the comparative rate of fruit set between mass-flowering species is extremely variable. Under certain circumstances, for example, almost half of the female flowers of *A. trichopoda* are likely to be pollinated by single or clumped pollen grains, while only a third of the stigmas of the bisexual florets of *Acacia retinodes* J. M. Black receive polyads (Bernhardt et al., 1984). The gynoecium of *Acacia* is a single carpel containing several ovules, while the gynoecium of *A. trichopoda* is limited to a variable number of free carpels and each carpel contains a solitary ovule (Bernhardt, 1989). Pollination in *A. trichopoda* must occur several times if *all* carpels are to mature into fruits; the sample in this study indicates that this event occurred in less than 3% of the standing crop of open and receptive flowers.

CECIDOMYIIDAE

Is the relationship with the Cecidomyiidae and *Amborella trichopoda* indicative of a long-term association between angiosperms? Gall midges were derived from the Fungivoridea, a Mesozoic representative (Rohdendorf, 1974). The oldest fossil members are found in the Cretaceous; none of these, however, were phytophagous (Gagné, 1977). Fossil Cecidomyiidae found in the Upper Oligocene–Lower Miocene are representative of present-day taxa (Rohdendorf, 1974; Gagné, 1977). The larvae of all species of extant Cecidomyiidae are detritus eaters (decaying plants, fungi, and live mycelia) except for tribes Cecidomyii, Asphondyliini, Lasiopterini, and Oligotrophini, which can form galls (Roskam, 1992). Asphondyliini and a few Lasiopterini form galls in which a layer of fungal hyphae may serve as food for larvae (Roskam, 1992).

It is hypothesized that the radiation of the gall midges coincided with the rise of the angiosperms (Roskam, 1985, 1992; Harris, 1994), which offered new adaptive feeding sites for the insects in the cambium of damaged stems and flowers and in vascular systems with large sap flows. Roskam (1992) suggested the diversification of the Cecidomyiidae might also be due to the development of flowers (nutrient-rich sites). Their transition from mycetophagy to phytophagy completed by the end of the Cretaceous (Mamaev, 1975) may have been facilitated by fungal infections in damaged flowers (many phytophagous gall midges feed on flowers), and once begun, other plant organs were exploited as food (Roskam, 1992; Mamaev, 1975). Roskam (1992) further suggested that galls evolved as a reaction of the host plant to the irritation of the larvae (excreted juices, etc.; Roskam, 1992). Most gall-inducing gall midges display a narrow host range (Roskam, 1985).

In extant Magnoliidae s.l., no galls were recorded on plants infected by gall midges, gall wasps, or gall-making sawflies (Roskam, 1992). However, Feil (1992) and Feil and Renner (1991) found that gall midges pollinated members of the Siparunaceae s. str., in which eggs are laid in the flowers but gall induction is not involved. In contrast, 25.5% of species in the Rosidae are infected by gall midges, 11.5% by gall wasps, and 19.2% by gall-making sawflies. In the Hamamelidae 8.3% of the species were infected by gall-inducing midges, 69.1% by gall wasps, and 13.7% by gall-making sawflies (Roskam, 1992). The numbers of fern and gymnosperm species infected with galls were 1.6% by gall midges, 0% by gall wasps, and 4.1% by gall-forming sawflies (Roskam, 1992). The gymnosperms are thought to have been colonized by gall-inducing Cecidomyiidae later than the angiosperms (Roskam, 1992).

Amborella trichopoda, the sister species of all extant angiosperms, is the first member of the ANITA group to be infected by a gall-inducing Cecidomyiidae. The Cecidomyiidae diversified with the angiosperms, but the earliest fossils of gall-inducing gall midges occur in the Miocene (Roskam, 1992; Zwölfer, 1978). Phytophagy and gall induction are derived trophic types in the Cecidomyiidae (Roskam, 1992). Thus the gall-inducing gall midges are unlikely to have played a role in the early evolution of the angiosperms (instead they were probably a late invasion similar to the colonization of the gymnosperms). Present-day interactions between *A. trichopoda* and the gall-inducing gall midges (not to be confused with other interactions of phytophagous Cecidomyiidae in basal angiosperms; see Feil, 1992; Feil & Renner, 1991) are consistent with aspects of the sequential model of co-evolution or interaction, i.e., no correlation between the evolutionary age of the plant and the insect species (Jermy, 1984).

Furthermore, Hickey and Doyle (1977) described a fossil gall on *Sassafras potomacensis* Berry (Upper Cretaceous, 115 mya, Maryland) that resembles a cynipid spangle gall wasp on extant oaks (Larew, 1992), but extant *Sassafras* (Lauraceae) do not bear such galls (Larew, 1992). Apparently the identification of the leaf bearing the gall is uncertain, which limits analysis of the gall with regard to a specific lineage (Larew, 1992). Recent fossil finds of gall wasps indicate that their history extends back to the Upper Cretaceous, and the host plants of cynipids then were species of Papaveraceae (Ronquist & Liljeblad, 2001).

AMBORELLA AND THE EVOLUTIONARY ECOLOGY OF DIOECY

Using multivariate analysis, Renner and Ricklefs (1995) correlated the occurrence of dioecy (at the family level) with several attributes, including monoecy, climbing growth, biotic dispersal of diaspores, abiotic pollination (wind, water), a shrub habit, and presence in tropical habitats. Only 5% of the extant angiosperm taxa are dioecious, but this arrangement of sexual functions is widely distributed in basal as well as advanced taxa (Renner & Ricklefs, 1995). In the ANITA group, dioecy is restricted to the Amborellaceae and some species in the Schisandraceae (Thien et al., 2000). However, a diverse group of unisexual and bisexual flowers occur in the mesofossil floras (Early Cretaceous) of Portugal (Friis et al., 2000) indicating that dioecy may have evolved early in the flowering plants.

Despite putatively severe effects of dioecy on female fitness and strict evolutionary requirements, etc., some lineages of dioecious seed plants show long-term evolutionary stability (Heilbuth, 2000; Heilbuth et al., 2001). More important, the fossil record indicates that some are obviously ancient (e.g., Chloranthaceae, Schisandraceae, cycadophytes, Gnetophyta, etc.) and often show a distribution that is highly disjunctive yet very broad and often intercontinental surviving in an equally broad range of tropical and subtropical ecosystems. As mentioned above, dioecious plants are relatively diverse and dense on oceanic islands including New Caledonia (Carlquist, 1974; Baker, 1955, 1959; Godley, 1979; Sakai et al., 1995; Bawa, 1980, 1981). It is hypothesized that on oceanic islands seed dispersal by birds and bats as well as other ecological factors may have played a large role in the evolutionary success of dioecy (Carlquist, 1974; Cox, 1982, and pers. comm.).

As noted above, the male and female plants in the study population Col d'Amieu of *Amborella trichopoda* are clumped with female plants tending to be surrounded by male individuals. The reduction in potential seed production on female plants as a result of the gall-inducing Cecidomyiidae, the loss of pollen in males to endophytic parasitoids, and the apparent low dispersal ability, probably combine to affect the spatial distribution and fitness of the plants.

Any factor that alters gain curves toward linearity (even if the evolutionary stable strategy for sex allocation is bisexual) can cause dioecy (Charlesworth, 1984). Did floral parasitism (brood parasitism) induce dioecy in *Amborella trichopoda* by altering male and/or female gain curves? Weevils do not pollinate flowers of *Sagittaria latifolia* Willd., but their clear preference for laying eggs on inflorescences with male flowers favors higher seed set in all female inflorescences (Muenchow & Delesalle, 1992). Female wasps actively pollinate the female flowers of figs, but the larvae they leave as eggs ultimately consume some of the ovules (Dufaÿ & Anstett, 2003). Large bats pollinate *Freycinetia* but they eat the stamens and in the process damage ovules resulting in division of the sexes (dioecy; Cox, 1982; Feil, 1992). It is presumed that *Amborella trichopoda* once possessed bisexual flowers, but the mechanism(s) inducing dioecy and pathway are unknown.

SUMMARY

1. The male and female plants of *Amborella trichopoda* are clumped but not clonal in a population. Male and female flowers are small flat structures; male flowers are functional for 4 to 5 days and female flowers 1 to 2.8 days. A lipid coat is present on the pollen and the stigma is of the dry-type.
2. *Amborella trichopoda* exhibits a wind and insect pollination breeding system; staminodes of female flowers mimic fertile male stamens. The insect visitors and pollinators vary greatly in size, and many live in the forest litter and forage on the flowers of *A. trichopoda* for pollen.
3. Two species of Cecidomyiidae parasitize the carpels of *Amborella trichopoda*; this turns the carpels into galls and reduces seed set. Several species of parasitoid insects in turn prey upon the cecid insect larvae in the galls.
4. While dioecy is common in the ANITA group, the combined wind and insect pollination breeding system of *Amborella trichopoda* utilizing staminodes that mimic fertile anthers in female flowers *is* rare in dioecious angiosperms in general.
5. Deceptive floral mechanisms are common in the ANITA group and other basal angiosperms and may have played a role in the early evolution of flowering plants.

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A REVISION OF THE IMBRICATE GROUP OF *STYRAX* SERIES *CYRTA* (STYRACACEAE) IN ASIA[1]

Yelin Huang,[2] *Peter W. Fritsch,*[3] *and Suhua Shi*[2]

Abstract

Several taxonomic treatments of *Styrax* (Styracaceae) exist in regional floras of Asia, but the Asian species of the genus have not been comprehensively revised since 1907. To help rectify this, we conducted a taxonomic revision of the Asian species of *Styrax* series *Cyrta* with imbricate corolla aestivation. Our revision comprises 17 species with a combined distribution from Japan south to Sumatra and west to Nepal. The circumscriptions of the heretofore poorly defined species *S. hookeri* and *S. serrulatus* are clarified. *Styrax agrestis* var. *curvirostratus* is elevated to the species level, and lectotypes are selected for *S. duclouxii*, *S. floribundus*, *S. hemsleyanus*, *S. hookeri*, *S. hookeri* var. *yunnanensis*, *S. hypoglaucus*, *S. japonicus*, *S. limprichtii*, *S. macranthus*, *S. obassia*, *S. perkinsiae*, *S. serrulatus* var. *latifolius*, *S. shiraianus*, *S. supaii*, and *S. wilsonii*. Keys, descriptions, and distribution maps are provided for all species.

Key words: eastern Asia, Styracaceae, *Styrax*, *Styrax* series *Cyrta*.

Styrax L. comprises about 130 species of trees and shrubs distributed in eastern and southeastern Asia, the New World, and the Mediterranean region (Fritsch, 1999). The range of this genus is typical of many plant groups distributed among the refugia of Tertiary mixed-mesophytic forests in the Northern Hemisphere, except that it also includes a large Neotropical component that extends south to northern Argentina and Uruguay (Fritsch, 1999, 2001). *Styrax* is by far the largest and most widespread of the 11 genera in the Styracaceae sensu Fritsch et al. (2001) and Fritsch (in press a). Characters unique to *Styrax* in relation to the family include a stamen tube attached high (vs. low) on the corolla, the presence (vs. absence) of placental obturators, bitegmic (vs. unitegmic) ovules, and an indu-

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rate (vs. thin) seed coat; these have been identified as putative synapomorphies for the genus (Fritsch, 1999; Fritsch et al., 2001). The combination of the following characters also serves to delimit *Styrax* from other genera of Styracaceae: absence of bud scales, presence of pseudoterminal fertile shoots (except in *S. macrocarpus* W. C. Cheng; presumably a reversal), a short hypanthium, unarticulated pedicels, glossy stamen filament trichomes that are circular in cross section, a 3-carpellate ovary, the presence of mesocarp, and a seed-to-carpel ratio ≤ 1 (Fritsch et al., 2001; Fritsch, in press a). Like other Styracaceae, *Styrax* has a vestiture of stellate trichomes (in some cases modified to peltate scales or rarely simple trichomes), generally twice the number of stamens as petals, and introrsely dehiscent anthers with a large, linear connective (Fritsch et al., 2001; Fritsch, in press a).

TAXONOMIC HISTORY AND PRESENT OBJECTIVES

In the most recent worldwide monograph of the genus (Perkins, 1907), *Styrax* was divided into section *Styrax*, with 16- to 24-ovulate gynoecia (most of the genus) and section *Foveolaria* (Ruiz & Pav.) Perkins, with 3- to 5-ovulate gynoecia (2 Neotropical species). Section *Styrax* was in turn divided into series *Styrax* (= series *Imbricatae* Perkins, invalid name) and series *Valvatae* (Gürke) Perkins, each defined, as the names suggest, on the basis of corolla aestivation. Despite the use of aestivation type for infrageneric delimitation, Perkins (1907) acknowledged that some species of *Styrax* placed in series *Valvatae* are occasionally slightly imbricate (= "subvalvate"), whereby the edges of the corolla lobes are contiguous but oblique in cross section, with a mixed condition of valvate and subvalvate aestivation sometimes occurring within one and the same flower. On this basis, Steenis (1932), in a revision of the Malesian species of *Styrax*, did not recognize either series of Perkins and placed several imbricate-flowered species of series *Styrax* (*S. subpaniculatus* Jungh. & de Vriese, *S. porterianus* G. Don, and *S. subdenticulatus* Miq.) under *S. serrulatus* Roxb., a species with otherwise valvate to subvalvate aestivation.

Fritsch (1999) conducted a morphological phylogenetic analysis of *Styrax* and revised the infrageneric classification of the genus based on the results. In addition to corolla aestivation type, several other characters diagnosed the deep divergences of the *Styrax* topology, whereas clades diagnosed by a reduced number of ovules per gynoecium were highly nested. In the recircumscribed sectional and series classification, the clade corresponding to the deciduous section *Styrax* (about 33 species) was supported by the presence of young shoots with scattered stalked stellate trichomes distinct from the rest of the vestiture patterns (vs. without stalked trichomes unless accompanied by a dense tomentum consisting of trichomes of the same general type) and membranaceous (vs. subcoriaceous) corolla lobes, whereas the clade corresponding to section *Valvatae* Gürke (about 97 species) was supported by valvate (vs. imbricate or subvalvate) corolla aestivation, the evergreen (vs. deciduous) condition, sides of the corolla straight (vs. convex) in bud, and concave (vs. planar) stamen filaments. The delimitation of these two species groups corresponds roughly to a geographic distribution in warm-temperate versus humid-tropical regions, respectively. Within section *Styrax*, the clade corresponding to series *Styrax* (3 species, western North America, Mediterranean region) was supported by strictly pseudoterminal (vs. pseudoterminal and lateral) inflorescences, whereas that corresponding to series *Cyrta* (Lour.) P. W. Fritsch (about 30 species, eastern and southeastern Asia, southern North America) was supported by glandular-serrate (vs. entire) leaf margins.

The character states of corolla aestivation delimited in the morphological analysis reflected the distinction made previously (Perkins, 1907; Steenis, 1932) between a truly valvate type of corolla aestivation and the subvalvate type. The results of Fritsch (1999) demonstrated that valvate aestivation as defined by Perkins has evolved at least twice in *Styrax*, once in the most recent common ancestor of the evergreen species and once (as the subvalvate condition) in the deciduous species. Therefore, according to Fritsch's revision, valvate aestivation is possessed by all members of section *Valvatae*, imbricate aestivation is possessed by all members of series *Styrax* and some members of series *Cyrta*, and the remaining members of series *Cyrta* possess the subvalvate type. The morphological analysis of Fritsch (1999) supported the idea of Hwang (1999) that imbricate aestivation is the primitive state in *Styrax*.

A molecular phylogenetic analysis of *Styrax* based on DNA sequences from the internal transcribed spacer (ITS) region of nuclear ribosomal DNA, both separately and in combination with morphology, provided strong support for the series classification of Fritsch (1999, 2001). The ITS phylogeny was ambiguous as to the sectional classification, although a combined analysis recovered a topology consistent with it. A family-wide phylogenetic analysis based on DNA sequences of the chloroplast genes *rbc*L and *trn*L-F in combination with ITS sequences and morphology (Fritsch et al., 2001) provided some support for section *Styrax*, but support for section *Valvatae* was ambiguous. The placement of *Huodendron* Rehder as sister to *Styrax* with strong support rendered the original state for corolla aestivation in the genus ambiguous because both genera are polymorphic for this character. The monophyly of the subvalvate members of series *Cyrta* as predicted from morphology was not supported by the ITS results (Fritsch, 2001) because several major clades contained both subvalvate and imbricate species. For example, *S. japonicus* Siebold & Zucc., a species with imbricate aestivation, grouped strongly with *S. formosanus* Matsum., a species with subvalvate aestivation. Fritsch (2001) concluded that reticulate evolution may at least partly explain the discordance between morphological and molecular data in series *Cyrta* but cautioned that the absence of chromosome counts for most species hinders further progress on this issue.

During the course of our study it became clear that, despite the discordance between morphological and molecular data and the conclusions of Perkins (1907) and Steenis (1932), corolla aestivation is species-specific without exception in series *Cyrta* and apparently is one of the few discontinuous and potentially phylogenetically informative characters in the series. This indicated to us that the treatment of *S. serrulatus* by Steenis (1932), in which a mixture of distinctly imbricate and subvalvate types of aestivation was postulated, would require careful re-evaluation. Furthermore, our study of regional floristic treatments of the genus for Asia (Steenis, 1932, 1949; Hwang, 1987; Svengsuksa & Vidal, 1992; Yamazaki, 1993; Hwang & Grimes, 1996; Y. N. Lee, 1996; Long, 1999) suggested that the species of series *Cyrta* are often poorly understood taxonomically across political boundaries, likely through the lack of comprehensive examination of Asian types and other collections.

Here we provide a taxonomic revision of the members of *Styrax* series *Cyrta* in Asia with imbricate corolla aestivation (17 species). Restricting our revision to the species with imbricate aestivation provides a practical limit to the scope of the study and is not meant to suggest that the group is necessarily monophyletic. A revision of the remaining species of series *Cyrta* (i.e., those with subvalvate corolla aestivation) is anticipated as part of a comprehensive revision of *Styrax*. The four North American species of the series (*S. americanus* Lam., *S. glabrescens* Benth., *S. grandifolius* Ait., and *S. jaliscanus* S. Wats., all with imbricate aestivation) are treated in more taxonomic detail elsewhere (Gonsoulin, 1974; Fritsch, 1997; Fritsch, in prep.), but are included in the key to species and various discussion sections to provide complete coverage and facilitate identification of cultivated material.

GEOGRAPHIC DISTRIBUTION AND ENDEMISM

The 30 or so species of *Styrax* series *Cyrta* occur in temperate lowland to tropical montane forests of eastern and southeastern Asia and North America with 80–300 cm mean annual precipitation and without a prolonged dry season (Fritsch, 2001). This intercontinentally disjunct distribution is common in many plant and animal groups, and is best explained by periods of relatively warm climate in the Tertiary that allowed widespread Northern Hemisphere distributions and transcontinental migration of lineages across the Bering and North Atlantic land bridges. Cooling and drying trends over the course of the Tertiary eventually restricted these lineages to "Tertiary refugia" today (Wolfe, 1975; Tiffney 1985a, b, 2000; Tiffney & Manchester, 2001). Most of the species in the series (ca. 26) occur in eastern and southeastern Asia, consistent with the general pattern of higher species richness in eastern Asia versus eastern North America in plant genera disjunct between these two regions (Wen, 1999). The remaining 4 species occur in the eastern United States (*S. americanus*, *S. grandifolius*), southwestern Mexico (Jalisco and Nayarit; *S. jaliscanus*), and eastern and southern Mexico to Costa Rica (*S. glabrescens*).

In Asia, the imbricate members of *Styrax* series *Cyrta* exhibit a combined distribution from Hokkaido, Japan, south to Sumatra, Indonesia, and west to Mechi, eastern Nepal. The 17 Asian species here recognized are all endemic to the region of interest. Most species possess a range that overlaps that of at least one other species in the group, except the southernmost species *S. curvirostratus* (B. Svengsuksa) Y. L. Huang & P. W. Fritsch, *S. porterianus*, and *S. subpaniculatus*. *Styrax japonicus* and *S. obassia* Siebold & Zucc. both exhibit a disjunct distribution among China, Korea, and Japan. *Styrax japonicus* extends along the Ryukyu Islands south to the northernmost islands of the Philippines, bypassing Taiwan. The most common and widespread species in more or less relative order are *S. japonicus*, *S. obassia*, *S. odoratissimus* Champ. ex Benth., *S. hookeri* C. B. Clarke, and *S. tonkinensis* (Pierre) Craib ex Hartwich. Species that can be considered narrow endemics are *S. buchananii* W. W. Sm., *S. chrysocarpus* H. L. Li, *S. curvirostratus*, *S. macrocarpus*, *S. porterianus*, *S. shiraianus* Makino, *S. sub-*

paniculatus, S. supaii Chun & F. Chun, and *S. wilsonii* Rehder, i.e., 53% of the Asian species of the group (Table 1).

Two other series of *Styrax* have representatives in Asia. *Styrax officinalis* L. of series *Styrax* occurs in the eastern Mediterranean region and extends into southwest Asia in Cyprus, Israel, Jordan, Lebanon, Syria, and Turkey. All ten or so species of series *Benzoin* P. W. Fritsch are endemic to eastern and southeastern Asia. The species of series *Benzoin* are easily distinguished from those of series *Cyrta* by the following characters: plants evergreen (vs. usually deciduous), bases of young shoots without stalked ferrugineous or fulvous stellate trichomes unless these accompanied by a dense tomentum consisting of trichomes of the same general color and type (vs. ferrugineous or fulvous stalked trichomes present, distinct from the rest of the vestiture), sides of the corolla straight or nearly so (vs. convex) in bud, corolla lobes subcoriaceous (vs. membranaceous or chartaceous), seeds depressed-globose (vs. generally ellipsoid, resting on the hilum on a flat surface instead of the sides between the hilum and apex), and seed coat crackled (i.e., coarsely reticulate-sutured; vs. generally smooth or with other types of patterns; see Fritsch, 1999). Although the geographic ranges of series *Cyrta* and series *Benzoin* overlap nearly completely, the species of series *Cyrta* tend to occur in warm-temperate regions, whereas those of series *Benzoin* tend to occur in subtropical to tropical regions.

Morphological and Taxonomic Characters

Here we discuss the principal diagnostic characters used in the systematics of the imbricate group of *Styrax* series *Cyrta* in Asia.

HABIT

All species herein are deciduous shrubs or trees except perhaps *Styrax curvirostratus* and *S. subpaniculatus*, which may be at least semi-evergreen. The tree species are typically less than 20 m tall but occasionally attain a height of greater than 30 m. Two species are known only as shrubs (*Styrax limprichtii* Lingelsh. & Borza and *S. wilsonii*). *Styrax rugosus* Kurz is typically a shrub but can occur as a small tree to 6 m, whereas *S. macrocarpus, S. obassia,* and *S. supaii* are typically small trees or rarely shrubs. *Styrax grandifolius* from the southeastern United States often forms colonies through root-suckering, but this habit is not known in any Asian species of *Styrax*.

LEAVES

Leaves are generally alternate but display two general patterns of phyllotaxis, one with more or less regularly spaced alternate leaves (*Styrax buchananii, S. chrysocarpus, S. curvirostratus, S. odoratissimus, S. porterianus, S. subpaniculatus,* and *S. tonkinensis*), the other with the two most basal leaves opposite or subopposite (sometimes one or both of these are replaced by scales). The latter condition, occurring on each new shoot, is nearly constant in *S. hemsleyanus* Diels, *S. macrocarpus, S. obassia,* and *S. supaii*, but less so in the remaining species, especially *S. limprichtii* and *S. rugosus*. The petioles of larger leaves are dilated at the base and completely cover the bud in two northern species (*S. obassia* and *S. shiraianus*); this feature is unique to these two species within *Styrax*. Petiole length differs greatly within and among species and is of diagnostic value in some instances (e.g., *S. macrocarpus*). The margins of the laminae are nearly always serrate or dentate, with each tooth tipped by a gland. Occasionally (e.g., *S. japonicus, S. porterianus, S. subpaniculatus*), some leaves are entire except for the tooth-like gland.

The size and shape of the leaves are variable within many species. The leaves of *Styrax hookeri, S. japonicus,* and *S. odoratissimus*, all relatively common and widespread species, are especially variable. The tertiary veins are more or less subparallel and perpendicular to the secondary veins in most species, but in *S. chrysocarpus, S. curvirostratus, S. japonicus, S. limprichtii,* and *S. supaii* they are more or less reticulate. Typically the leaves of sterile shoots are larger than those of fertile shoots.

VESTITURE

Although trichome types and the density of pubescence on various parts of the plants are useful characters for identifying some *Styrax* species, high infraspecific variation is common in the genus (Fritsch, 1996, 1997, in prep.). Many species in our revision exhibit such variation (*S. buchananii, S. hemsleyanus, S. hookeri, S. japonicus, S. limprichtii, S. odoratissimus,* and *S. subpaniculatus*). The lower laminar surface in these species can be essentially glabrous or sparsely to densely pubescent, the pubescence (if present) consisting of short or long stellate trichomes, or a mixture of both. In diagnostic terms, these differences are a matter of degree rather than kind and exhibit no correlated gaps with other characters, elevation, or geography (see discussions under each species in the Taxonomic Treatment section). The pubescence on reproductive parts of *Styrax* in our treatment can be

Table 1. Species distribution, richness, and endemism, by country. *, endemic.

Country	No. species/ No. endemics	Species
Bhutan	1/0	*S. hookeri*
China	12/7	**S. chrysocarpus*, **S. hemsleyanus*, *S. hookeri*, *S. japonicus*, **S. limprichtii*, **S. macrocarpus*, *S. obassia*, **S. odoratissimus*, *S. rugosus*, **S. supaii*, *S. tonkinensis*, **S. wilsonii*
India	1 [or 2]/0	*S. hookeri*, ? *S. japonicus*
Indonesia	1/1	**S. subpaniculatus*
Japan	3/1	*S. japonicus*, *S. obassia*, **S. shiraianus*
Laos	2/0	*S. japonicus*, *S. tonkinensis*
Malaysia	1/0	*S. porterianus*
Myanmar	5/1	**S. buchananii*, *S. hookeri*, *S. japonicus*, *S. porterianus*, *S. rugosus*
Nepal	1/0	*S. hookeri*
North Korea	2/0	*S. japonicus*, *S. obassia*
Philippines	1/0	*S. japonicus*
South Korea	2/0	*S. japonicus*, *S. obassia*
Thailand	2/0	*S. porterianus*, *S. rugosus*
Vietnam	3/1	**S. curvirostratus*, *S. japonicus*, *S. tonkinensis*

used to identify species such as *S. chrysocarpus* (with trichome color), *S. buchananii* (with trichome length), and *S. supaii* (with trichome type). Nonetheless, in some species pubescence presence and amount on reproductive parts varies continuously or sporadically, e.g., on the inner surface of the corolla lobes and style (*S. hookeri*), the pedicel and calyx (*S. japonicus*), or on the surface of seeds (*S. odoratissimus* and *S. tonkinensis*). In *S. japonicus*, the amount and density of pubescence is strongly associated with geography, whereby the most pubescent plants occur in the southernmost portion of the range and least pubescent and glabrous plants in the northernmost portion.

INFLORESCENCES

All inflorescences in members of series *Cyrta* are produced on the shoots of the current growing season except those of *Styrax macrocarpus*, which consist of single flowers produced on shoots of the previous growing season. The inflorescences of *S. macrocarpus* are unique within the genus in this respect, although several other genera of Styracaceae show the same pattern (Fritsch et al., 2001). This feature has presumably been derived independently in the ancestor of these genera and in *S. macrocarpus* because *Huodendron*, the sister group of *Styrax*, possesses the common state in *Styrax*. In species other than *S. macrocarpus*, inflorescences are both pseudoterminal and lateral; occasionally only pseudoterminal inflorescences are produced on some shoots of some species, but lateral inflorescences can always be found. Pseudoterminal inflorescences are always racemose or paniculate, sometimes two or more arising from the same node (e.g., *S. buchananii*, *S. hemsleyanus*, *S. obassia*, *S. odoratissimus*, *S. subpaniculatus*, and *S. tonkinensis*). Lateral inflorescences are 1- to 2-flowered or racemose; they are shorter than the pseudoterminal inflorescence and occur in the leaf axils immediately below it. We agree with Perkins (1902, 1907) that inflorescence length and flower number per inflorescence are relatively constant within most species of our revision, and have used these as fundamental key characters. Only *S. odoratissimus*, *S. tonkinensis*, and two North American species (*S. glabrescens* and *S. grandifolius*) exhibit significant variation in this respect (hence each must fall out twice in the key).

FLOWERS

Flowers are bisexual and actinomorphic with a short hypanthium (see Dickison, 1993) adnate to the basal third or less of the ovary wall. Flower length ranges from 0.7 to 3.2 cm. Some species (e.g., *Styrax curvirostratus*, *S. hemsleyanus*, *S. hookeri*, *S. japonicus*, *S. macrocarpus*, *S. obassia*, and *S. shiraianus*) have generally larger flowers than others, especially those whose flowers are consistently less than 1.5 cm long (e.g., *S. odoratissimus*, *S. porterianus*, *S. subpaniculatus*, and *S. wilsonii*).

The long pedicels (15–50 mm) of *Styrax japonicus* distinguish this species from all others in our revision. Except for most specimens of *S. japonicus*, the abaxial surface of the gamosepalous calyx in *Styrax* is always covered with stellate trichomes. Abaxial calyx pubescence can be used in species identification, e.g., the presence (vs. absence) of various amounts of scattered dark yellow, orange, or brown stiff stellate trichomes in addition to the base tomentum (*S. hemsleyanus, S. hookeri, S. limprichtii, S. obassia, S. rugosus, S. shiraianus,* and *S. wilsonii*), and a more sparsely pubescent to glabrous region than the rest of the calyx within 1 mm of the margin (*S. buchananii, S. curvirostratus, S. hookeri, S. japonicus, S. macrocarpus, S. odoratissimus, S. porterianus,* and *S. shiraianus*) versus a calyx that is evenly pubescent throughout. The calyx margin can be truncate, undulate, irregularly lobed, or distinctly dentate. If the margin is dentate, then the teeth are usually contiguous or separated by a shallow concave portion. *Styrax supaii* is distinguished from all other species by the long, simple or 2-armed trichomes covering the abaxial surface of the calyx, and long calyx teeth (4–5 mm long).

The gamopetalous corolla is completely white or rarely flushed with pink, and it is nearly always sparsely to densely stellate-pubescent on both sides. Some specimens of *Styrax hookeri* are glabrous adaxially. The corolla tube is almost always shorter than the lobes, usually ranging from 2 to 5 mm long. Only *S. shiraianus* possesses a corolla tube (10–12 mm long) longer than the lobes. In our species, the 5 (to 7) lobes range from 5 to 26 mm long and from 2.5 to 11 mm wide.

The stamens are adnate to the corolla tube proximally, free distally, and are twice the number of corolla lobes. The corolla lobes and stamen filaments become both free and distinct at approximately the same point along the floral axis in all species. Filaments range from 1.5 to 10 mm long and are usually equal or slightly unequal within a flower, but sometimes are distinctly alternately unequal in length, especially in *Styrax supaii.* The filaments are flexuous at mid-length in some species (*S. buchananii, S. curvirostratus, S. odoratissimus, S. subpaniculatus,* and sometimes *S. porterianus*). The filaments are of equal width throughout in *S. curvirostratus, S. hemsleyanus, S. obassia, S. rugosus, S. shiraianus,* and *S. tonkinensis,* and distally attenuate in the rest. Filament pubescence varies from absent (e.g., *S. obassia*) to proximally pubescent (e.g., *S. hemsleyanus*) or densely pubescent throughout (e.g., *S. buchananii, S. curvirostratus, S. odoratissimus, S. subpaniculatus*). The amount of filament pubescence is variable in *S. hookeri* and *S. tonkinensis.* Anthers are wider than the distal portion of the filament except in *S. curvirostratus, S. obassia, S. subpaniculatus,* and *S. tonkinensis,* where they are more or less the same width as the adjacent filament apex. The connectives are glabrous to stellate-pubescent. The length of the anthers, ranging from 2 to 7 (to 10) mm, is useful for species identification.

The ovary is always apically pubescent; it appears to hold little taxonomic value in the group under revision. The style is filiform and varies from glabrous (e.g., *Styrax hemsleyanus*) to densely hirsute (e.g., *S. buchananii, S. curvirostratus*). The amount of style pubescence varies substantially within some species, thus limiting its usefulness in species identification. The number of ovules per carpel in the group under study is often difficult to ascertain due to the small size of the placental region. The few samples that we have examined indicate that the number is variable, but is rarely less than 5 or more than 8 per carpel.

FRUIT

The fruit is usually globose, ovoid, or ellipsoid. *Styrax curvirostratus* has a cylindrical fruit, and that of *S. macrocarpus* is occasionally pyriform. The apex may be rounded (e.g., *S. subpaniculatus*), apiculate through persistence of the style base (e.g., *S. japonicus*), or rostrate (*S. curvirostratus* and *S. odoratissimus*). Fruit size ranges from 0.5 to 3 cm long and from 0.4 to 2.5 cm wide. The outer surface of the pericarp is white-gray to gray-yellow stellate-tomentose or -pubescent, except in *S. chrysocarpus,* in which it is golden yellow stellate-tomentose. The inner surface of the pericarp is typically glabrous or sparsely pubescent; only in *S. chrysocarpus* and *S. macrocarpus* is the pericarp densely pubescent inside. In both of these species the fruit is apparently indehiscent, although the limited material available for study leaves the constancy of this character in doubt. The fruit is unquestionably indehiscent in *S. porterianus* and *S. subpaniculatus*; the fruit is dehiscent by two or three valves in the other species. *Styrax porterianus* and *S. subpaniculatus* are similar in fruit dehiscence to the North American species *S. glabrescens* and *S. grandifolius,* which nearly always possess an indehiscent fruit. *Styrax porterianus* is the only species in our treatment with a fleshy pericarp (ca. 2 mm thick). The pericarp of all other species is dry. The thickness of the pericarp is variable within the dry-fruited species, but *S. macrocarpus* always has a pericarp greater than 1 mm thick, distinguishing this species from all other dry-fruited species in our revision.

SEEDS

The seeds of the imbricate group of series *Cyrta* are globose, ovoid, or ellipsoid, from beige to brown and smooth to finely reticulate-fissured or irregularly rugose (i.e., with a wrinkled appearance). Seed coat pubescence occurs in *Styrax curvirostratus, S.*

macrocarpus, *S. odoratissimus*, and *S. tonkinensis*. This pubescence is absent, however, in some individuals of each of these species. The seed coat is usually tuberculate in *S. tonkinensis*. These tubercles are sometimes arranged in a stellate pattern, in which case they often resemble stalked stellate trichomes.

CHROMOSOME NUMBERS

Only three species in our revision have been counted: *Styrax hookeri* ($n = 8$, Arora, 1961; Mehra & Bawa, 1969; Mehra, 1976), *S. japonicus* ($n > 20$, Manshard, 1936; $n = 8$, Yamazaki, 1993), and *S. obassia* ($n = 8$, Manshard, 1936; Yamazaki, 1993). Chromosome numbers of two North American species of series *Cyrta* have also been reported (*S. americanus*, $n = 8$; *S. grandifolius*, $n = 16$; Gonsoulin, 1974). From these numbers and reports for species in the other series, the base number of *Styrax* is inferred to be $x = 8$ (Fritsch, 2001). Polyploidy is thus far known with relative certainty only in series *Cyrta* (*S. grandifolius*; the old number for *S. japonicus* of $n > 20$ must be questioned in light of the more recent number of $n = 8$).

ECOLOGY AND ECONOMIC IMPORTANCE

According to herbarium specimen labels, species of the imbricate group of series *Cyrta* are found most often from 500 to 2700 m elevation in Asia. Several species (*Styrax japonicus*, *S. obassia*, *S. odoratissimus*, *S. porterianus*, *S. subpaniculatus*, *S. supaii*, and *S. tonkinensis*) occur additionally or exclusively at elevations less than 500 m; only *S. hookeri* extends to 3000 m or higher. Some species (*S. hemsleyanus*, *S. hookeri*, *S. japonicus*, *S. odoratissimus*, and *S. tonkinensis*) have a wide elevation range (2000 m or more in extent). Many of these species are found in a variety of habitats, such as open woodlands, pastures, mountain slopes, roadsides, high-elevation forests, and successional areas. Many species show a distinct preference for mesic microhabitats, such as canyons, draws, and other riparian situations.

Styrax species are most frequently pollinated by bumble bees and honey bees (Gonsoulin, 1974; Sugden, 1986; Kato & Hiura, 1999). Other pollinators reported for *Styrax* species are papilionoid butterflies, syrphid flies, sphingid moths, wasps, and other groups of bees (e.g., carpenter bees, halictids, anthophorids; Copeland, 1938; Gonsoulin, 1974; Sugden, 1986; Saraiva et al., 1988; Tamura & Hiura, 1998). Both nectar and pollen serve as floral rewards for pollinators, although there are no specialized structures recognizable as nectaries. The stellate trichomes present on the exterior surface of the corolla in most species of Styracaceae have been suggested as an adaptation for supporting large pollinators, which use them as "toe holds" to gather nectar and pollen (Sugden, 1986). The flowers of *Styrax* are sweetly fragrant (Perkins, 1907; Copeland, 1938; Fritsch, pers. obs.).

Nearly all species have exclusively hermaphroditic flowers. Partial self-incompatibility has been suggested for *Styrax obassia* (Tamura & Hiura, 1998), the only member of series *Cyrta* examined for breeding system. Obligate xenogamy is documented for several species of *Styrax* from other series (Sugden, 1986; Saraiva et al., 1988). Morphological gynodioecy is reported for ten species in series *Valvatae* (Wallnöfer, 1997; Fritsch, 1999, in press b), but experiments to confirm functional gynodioecy in these species have not been conducted.

Little data exist on the dispersal mechanisms of *Styrax*. Fruits of *S. obassia* are dispersed by ground mice and food-hoarding birds (Kato & Hiura, 1999). After the fruit wall has become detached, the seeds of the riparian species *S. faberi* Perkins, a valvate-flowered member of series *Cyrta*, remain attached to the receptacle by the hilum. The seeds, which would otherwise sink, can thus be transported in water by the floating infructescence (P. Fritsch, pers. obs.). The seeds of *S. japonicus*, an imbricate-flowered species of series *Cyrta* that exhibits the same type of seed attachment, may also be dispersed in this way. The seeds of *S. americanus* reportedly have been found attached to the feet of waterfowl (Ridley, 1930), but this is probably not a primary means of dispersal of *Styrax* species because the surface of the seeds is generally smooth and curved, and therefore not obviously adapted for attachment.

The benzofuran egonol and its glycosides occur in the seed oil of several species of *Styrax*. The fruit of *Styrax* contains significant amounts of jegosaponin, a potent defense chemical. Various species of *Styrax* also contain styracitol, β-phenyl ethyl alcohol, and coniferin (Hegnauer, 1962; Gibbs, 1974).

In many species of *Styrax*, a balsamic resin (benzoin, gum benjamin) exudes from the bark and wood tissues following injury to the cambium. This resin consists chiefly of coniferyl cinnamate, cinnamyl cinnamate (styracin), and coniferyl benzoate associated with cinnamic and benzoic acids; minor components are fragrant benzaldehyde, vanillin, and styrene (Hegnauer, 1962; Langenheim, 2003). It is used medicinally as an antiseptic and expectorant, and in the flavor and fragrance industries (Pratt & Youngken, 1951; Duke, 1985; Langenheim, 2003). The best known source of benzoin is *S. benzoin* Dryand., a species of series *Benzoin*. Within series *Cyrta*, three species have been reported as sources of benzoin (Burkill, 1966): *S. serrulatus*, *S. subpaniculatus*, and *S. tonkinensis*, the latter two of which are included in our revision. The benzoin from *S. tonkinensis* is called "Siam benzoin" because of its source in "the western parts of Indochina and eastern parts of Siam" (Burkill, 1966: 2146). We have not seen any specimens of *S. tonkinensis* from Thailand to confirm its occurrence there.

The oil extracted from the seeds of some species in our revision can be used to make soap or lubricating oil (e.g., *Styrax hemsleyanus*, *S. japonicus*, *S. obassia*, and *S. odoratissimus*; Tai & Pan, 1981; Hwang, 1987), or medicinally as an antiseptic to treat scabies (*S. tonkinensis*; Hwang, 1987). The young leaf of *S. japonicus* is used as tea in certain regions of China (*K. M. Feng 11082*, Yunnan), and the fruit of this species can be used as a source of sugar extract to brew wines (*P. C. Tam 63659*, Hunan). The flowers, leaves, fruits, and galls of some species are used as Chinese herbal medicines (e.g., *S. hemsleyanus* and *S. japonicus*; Tai & Pan, 1981). Several *Styrax* species of series *Cyrta* native to Asia are cultivated for ornament (Raulston, 1992). *Styrax japonicus* and *S. obassia* are most commonly cultivated, but also occasionally planted are *S. hemsleyanus*, *S. limprichtii*, *S. odoratissimus*, *S. shiraianus*, *S. tonkinensis*, and *S. wilsonii*. Many cultivars of *S. japonicus* have been developed (Raulston, 1992).

Most species of *Styrax* series *Cyrta* serve as the primary host for aphids of the family Hormaphididae (tribe Cerataphidini). These aphids produce conspicuous galls of various shapes on the vegetative and reproductive shoots of *Styrax*. Most individual cerataphidine aphid species use a single species of *Styrax* as primary host, although it is common for several species of aphid to parasitize the same species (Stern et al., 1997). Often the shapes of the galls produced by aphid species are characteristic of particular species of *Styrax*, e.g., spiral galls on *S. paralleloneurus* Perkins and coralline galls on *S. subpaniculatus*. The aphids produce a sterile soldier caste that defends the rest of the colony from predators. The morphology of these aphids and their galls, aphid behavior, and soldier production have been studied extensively (e.g., Docters van Leeuwen, 1922; Aoki, 1982; Kurosu & Aoki, 1990, 1991, 1997; Aoki & Kurosu, 1993; Aoki et al., 1998; Kurosu et al., 1998), and the evolution of soldier production has been investigated in ecological and phylogenetic contexts (Stern, 1994, 1998; Stern & Foster, 1996). Evidence for co-evolutionary patterns of host-switching comes from phylogenetic analyses of both the aphids (Stern, 1995) and *Styrax* (Fritsch, 1999). The four North American species of series *Cyrta* and *S. shiraianus* from Japan are apparently not parasitized by these aphids (P. Fritsch, pers. obs.; S. Aoki, pers. comm.); neither are any species of series *Styrax* or series *Valvatae* (P. Fritsch, pers. obs.). Thus, this interaction is apparently restricted to eastern and southeastern Asia and associated islands.

MATERIALS AND METHODS

Nearly 5000 herbarium specimens from 22 herbaria (A, AAU, BM, BO, BR, C, CAS, DS, E, GH, IBK, IBSC, K, KUN, KYO, L, MO, P, PE, TAI, TI, and UC) were examined for this study. All descriptions were derived from examination of herbarium specimens. Flowering and fruiting times, elevation ranges, habitats, distributions, common names, and uses were derived from label information. Descriptions of leaves generally refer to those of the fertile branches; leaves of sterile branches are consistently larger and often possess more variation in trichome quantity and quality than those of fertile branches and thus are less useful for species identification. Leaf and petiole measurements were taken from the larger examples on each herbarium sheet. At the proximal ends of the twigs many deciduous species of *Styrax* have small leaves of roughly equivalent size among species, and the incorporation of these into descriptions would make species identification more difficult. Flowers are described at the stage of anthesis except where noted. Calyx dimensions are presented as height (from the end of the pedicel to the distal margin) times width at the apex, and thus include the short hypanthium. Fruit length was measured from the base of the fruiting calyx to the tip of the fruit (the calyx is persistent). Fruiting measurements were taken from mature fruits where possible. Often immature fruits are the only types available for examination on a herbarium sheet, in which case the larger fruits on the sheet were measured. Most observations were made by eye or with the aid of a dissecting microscope (maximum magnification = 64×).

Because our study is based primarily on herbarium specimens, we employ the morphological species concept, as discussed in Stuessy (1990), for species recognition. We base our species on the existence of correlated gaps in states among morphological characters, and treat clinal patterns as infraspecific variation that requires no formal taxonomic recognition. We explain our decisions on circumscription under each species, often in the context of the relevant taxonomic work of previous authors. We assume that the morphological differences among the species we recognize have a genetic basis, as can be inferred from examination of several species in a common garden setting (e.g., *Styrax japonicus, S. obassia,* and *S. odoratissimus* at the University of California Botanical Garden, Berkeley, California, U.S.A.), and regard the species we have recognized as hypotheses to be tested as new morphological data become available. Appendix 3 provides an alphabetic listing of species in the Taxonomic Treatment, including synonyms and excluded names.

The dots in the distribution maps are based on the specimens cited in this revision (see Taxonomic Treatment and Appendices 1 and 2). For collections in which geographic coordinates were not indicated on specimen labels (most collections), we estimated coordinates based on descriptive label information about the location of the collection. Our estimate was aided with a variety of published maps, atlases, and gazetteers, particularly the (United States) National Imagery and Mapping Agency (NIMA) database of foreign geographic feature names, with access provided by the GEOnet Names Server (GNS) at <http://www.nima.mil/gns/html/>. Mapped localities in China are resolved to the level of county (xian) or occasionally minutes; in all other countries, resolution is to the level of minutes unless more precise information was provided on labels. Geographic information provided on labels was often inadequate for estimation of locality, in which case the collection was not mapped. Some of these are listed at the beginning of collection citations in the Additional Specimens Examined sections, under the lowest-ranking political subdivision for which locality is known; otherwise they are listed under "Locality unknown." A database of all collection information used for this revision, including geographic coordinates linked to geographic information system software (ArcView, ESRI, Inc.), is available from the authors upon request.

TAXONOMIC TREATMENT

Styrax L., Sp. Pl. 444. 1753. TYPE: *Styrax officinalis* L. [as *S. "officinale"*].

Strigilia Cav., Diss. 7: 358, t. 201. 1789. TYPE: *Strigilia racemosa* Cav. [= *Styrax racemosus* (Cav.) A. DC.].

Foveolaria Ruiz & Pav., Fl. peruv. prodr. 57, t. 9. 1974. *Tremanthus* Pers., Syn. Pl. 1: 467. 1805. TYPE: *Foveolaria ferruginea* Ruiz & Pav., lectotype, designated by Fritsch (1999) [= *Styrax foveolaria* Perkins].

Epigenia Vell., Fl. flumin. 183. 1829. TYPE: *Epigenia integerrima* Vell., lectotype, designated by Fritsch (1999) [= *Styrax glabratus* Schott].

Pamphilia Mart. ex A. DC., in DC., Prodr. 8: 271. 1844. TYPE: *Pamphilia aurea* Mart. ex A. DC., lectotype, designated by Hutchinson (1967) [= *Styrax maninul* B. Walln.].

Darlingtonia Torr., Proc. Amer. Assoc. Advancem. Sci. 4: 191. 1851, nom. rej. TYPE: *Darlingtonia rediviva* Torr. [= *Styrax redivivus* (Torr.) L. C. Wheeler].

Evergreen or deciduous trees or shrubs; bark smooth or longitudinally fissured, gray to dark brown; twigs terete or subterete, outer layer of older twigs fibrous, dull brown or more often gray; inner layer yellow to dull maroon; buds superposed, stellate-pubescent or occasionally lepidote, naked (i.e., with a single outer scale that develops into the first leaf on new shoots). Vestiture consisting of stalked or unstalked, free or appressed stellate trichomes or less commonly scales, rarely also with simple trichomes. Leaves simple, pinnately nerved, estipulate, petiolate, generally alternate but sometimes basal leaves of the current year's growth opposite or subopposite, the margins glandular-serrate, glandular-dentate, or entire (but still glandular), rarely coarsely lobed. Inflorescences of bracteolate lateral and pseudoterminal (occasionally strictly pseudoterminal, rarely strictly lateral) racemes or panicles, essentially cymose but often appearing racemose, sometimes two or more arising from the same node, lateral inflorescences usually 1- to several-flowered; bracteoles small, positioned at various places along the pedicel or near the calyx base. Flowers actinomorphic, hermaphroditic, or (in gynodioecious species) female, fragrant, with a short hypanthium adnate to the basal third or less of the ovary wall; pedicel not articulated; calyx gamosepalous, campanulate, cupuliform or funnelform, teeth generally (4)5(6) or absent; corolla gamopetalous for ca. 2 mm or more, the petals distinct distally, the lobes (4)5(to 10), usually longer than the tube, imbricate, subvalvate, or valvate in bud, white, pink, or rarely yellow, pubescent, at least abaxially; stamens adnate to the corolla tube, free distally, (8 to)10(to 14), usually twice the number of the corolla lobes, uniseriate but often appearing biseriate in bud, the 5 inner, sepalad stamens often exceeding the 5 outer, petalad stamens, if 5 then all stamens petalad; filaments often connate proximally and distinct distally, sometimes completely distinct, flattened (but often auriculate ventrally), glabrous to stellate-pubescent or lepidote, the branches of the trichomes cylindrical in cross section, generally glossy; staminodia replacing the stamens in female plants; anthers linear, basifixed, 2-locular, introrse, longitudinally dehiscent, the anther sacs glabrous to moderately stellate-pubescent along the margins, the connective broad, tangentially thickened throughout the length, white, glabrous or stellate-pubescent; pollen light or golden yellow; ovary semi-inferior, 3-carpellate, 3-septate at the base but 1-locular through the distal attenuation of the septa, with essentially axile or near-basal placentation; style filiform, hollow; stigma terminal, obscure, capitate, punctiform or faintly 3-lobed; placental obturators usually present; ovules 1 to ca. 8 per carpel, anatropous, apotropous, bitegmic, tenuinucellate. Fruit a drupe, a capsule dehiscent by (2)3 valves, or nut-like (dry and indehiscent), globose, depressed-globose, ovoid, or ellipsoid, 1(to 3)-seeded, with persistent calyx; exocarp and endocarp thin, mesocarp dry, mealy, or juicy. Seeds ± globose, ovoid, or ellipsoid, beige to brown, completely filling the fruit cavity, with a broad hilum; seed coat 5 to 50 cells thick, usually smooth except for 3(to 6) longitudinal grooves, sometimes also finely reticulate-fissured to irregularly rugose, sometimes pubescent, rarely tuberculate; endosperm copious; embryo straight; cotyledons flattened. About 130 species. U.S.A to Argentina, eastern Mediterranean, eastern and southeastern Asia.

Styrax series **Cyrta** (Lour.) P. W. Fritsch, Syst. Bot. 24: 373. 1999. *Cyrta* Lour., Fl. cochinch. Ed. 1: 278. 1790. TYPE: *Cyrta agrestis* Lour. [= *Styrax agrestis* (Lour.) G. Don].

Adnaria Raf., Fl. ludov. 56. 1817. TYPE: *Adnaria odorata* Raf. [= *Styrax americanus* Lam.].

Anthostyrax Pierre, Fl. forest. cochinch. sub t. 260. 1892. TYPE: *Anthostyrax tonkinense* Pierre [= *Styrax tonkinensis* (Pierre) Craib ex Hartwich].

Deciduous (possibly at least semi-evergreen in *S. curvirostratus* and *S. subpaniculatus*) trees or shrubs; bases of young shoots with scattered stalked ferruginous or rarely fulvous stellate trichomes distinct from the rest of the vestiture. Vestiture consisting of stalked or unstalked, erect to appressed stellate trichomes, rarely also with simple trichomes. Leaf margins of at least some leaves on sterile shoots (and often of fertile shoots) glandular-denticulate to glandular-serrate, rarely also lobed; occasionally margins of some leaves entire (but still glandular). Inflorescences produced laterally and pseudoterminally on at least some shoots (strictly laterally in *S. macrocarpus*), the lateral inflorescences often reduced to 1 to 3 flowers, the subtending leaves often reduced. Flowers hermaphroditic; corolla white or rarely white flushed with pink, the sides generally convex in bud; corolla lobes imbricate or subvalvate in bud, membranaceous to chartaceous; stamen filaments planar ventrally, straight or occasionally flexuous, glabrous or stellate-pubescent; placentation essentially axile, placental obturators present; ovules ca. 5 to 8 per carpel. Fruit a capsule dehiscent by (2)3 valves, or nut-like (dry and indehiscent), rarely (*S. porterianus*) a drupe; outer surface of pericarp smooth to irregularly rugose; endocarp at maturity adherent to the mesocarp, not the seed. Seeds ovoid, ellipsoid, subglobose to globose, resting on the side between the hilum and the apex when placed on a flat surface; seed coat usually smooth, sometimes finely reticulate-fissured to irregularly rugose, sometimes pubescent, rarely tuberculate (*S. tonkinensis*). About 30 species, eastern Asia (about 26 species, Japan to Indonesia and several island chains of the western Pacific, west to eastern Nepal) and North America (4 species, southeastern United States, Mexico, Central America).

KEY TO SPECIES OF THE IMBRICATE GROUP OF *STYRAX* SERIES *CYRTA*
(* indicates species that fall out twice in the key)

1a. Outer surface of the pericarp golden yellow stellate-tomentose; inner surface of pericarp densely pale yellow appressed-pubescent ..... 2. *S. chrysocarpus*

1b. Outer surface of the pericarp not golden yellow-stellate-tomentose; inner surface of pericarp glabrous or sparsely to densely white-pubescent.

- 2a. Pseudoterminal inflorescences ≥ 7 cm long, often 8- to 20(to 23)-flowered.
  - 3a. Two most proximal leaves on each shoot of the current year subopposite to opposite.
    - 4a. Petiole of larger leaves dilated at base and covering the bud; rachis glabrous or nearly so; inner surface of calyx glabrous; pericarp coarsely and irregularly rugose ..... 9. *S. obassia*
    - 4b. Petiole not dilated at base, not covering the bud; rachis stellate-tomentose; inner surface of calyx appressed-pubescent; pericarp smooth or slightly longitudinally rugose.
      - 5a. Vegetative end buds ≤ 3 mm long; calyx campanulate or broadly cupuliform; fruit globose, indehiscent or rarely dehiscent, not longitudinally rugose; North America.
        - 6a. Tree to 30 m, not suckering from roots; leaves membranaceous; corolla lobes 11–23 × 6–10 mm; fruit 10–17 × 9–19 mm; Mexico and Mesoamerica ..... *S. glabrescens Benth.
        - 6b. Tree to 6 m, often suckering extensively from roots; leaves chartaceous; corolla lobes 8–16 × 3–7 mm; fruit 8–12 × 6–8 mm; southeastern United States ..... *S. grandifolius Ait.

5b. Vegetative end buds 4–6 mm long; calyx narrow-cupuliform; fruit globose to ovoid, dehiscent, slightly longitudinally rugose; Asia .... 4. *S. hemsleyanus*

3b. Two most proximal leaves on each shoot of the current year alternate.

7a. Abaxial surface of the lamina completely concealed by the tomentum; calyx distinctly dentate, the teeth usually contiguous or separated by a shallow concave margin; filaments of equal width throughout, straight; seeds densely tuberculate, sometimes the tubercles arranged in stellate formations .... *16. *S. tonkinensis*

7b. Abaxial surface of the lamina visible through the pubescence, if present (rarely nearly concealed by the tomentum in *S. subpaniculatus*); calyx truncate, undulate, or irregularly lobed, the teeth not contiguous if present; filaments narrowing distally, flexuous at middle (occasionally straight in *S. subpaniculatus*); seeds smooth, glabrous, appressed-stellate-pubescent, or lepidote (seeds unknown in *S. buchananii*).

8a. Corolla lobes 1.7–2.2 times as long as wide; pseudoterminal inflorescences usually racemose, rarely paniculate; fruit apex rostrate, rarely merely apiculate; seeds usually appressed-stellate-pubescent or lepidote .... *10. *S. odoratissimus*

8b. Corolla lobes 2.3–3.0 times as long as wide; pseudoterminal inflorescences usually paniculate; fruit apex rounded or subacute, rarely also apiculate (fruit unknown in *S. buchananii*); seeds glabrous.

9a. Connectives (at least proximally) and style densely stellate-hirsute; anthers 5–7 mm long; flowers 1.3–1.6 cm long; calyx stellate-hirsute, arms of trichomes averaging ca. 1 mm long .... 1. *S. buchananii*

9b. Connectives and style glabrous; anthers 3–4 mm long; flowers 0.9–1.2 cm long; calyx tomentose, arms of trichomes < 0.2 mm long .... 14. *S. subpaniculatus*

2b. Pseudoterminal inflorescences < 7 cm long, ≤ 7-flowered (3- to 11-flowered in *S. shiraianus*).

10a. Petiole of larger leaves dilated at base, covering the bud; inflorescences distally congested; pedicel < 1 mm long; corolla tube 10–12 mm long .... 13. *S. shiraianus*

10b. Petiole not dilated at base, not covering the bud; inflorescences not distally congested; pedicel ≥ 2 mm long; corolla tube 2–5 mm long.

11a. Calyx teeth 4–5 mm long; calyx abaxially with simple or 2-armed trichomes ca. 1–1.5 mm long .... 15. *S. supaii*

11b. Calyx truncate or teeth < 3 mm long; calyx abaxially with stellate trichomes averaging $<$ 1 mm long or glabrous.

12a. Distalmost leaves on sterile shoots usually > 7 cm wide; fruit indehiscent (rarely dehiscent by 3 valves), with corolla 10–28 mm long; North America.

13a. Tree to 30 m, not suckering from roots; leaves membranaceous; corolla lobes 11–23 × 6–10 mm; fruit 10–17 × 9–19 mm; Mexico and Mesoamerica .... **S. glabrescens* Benth.

13b. Tree to 6 m, often suckering extensively from roots; leaves chartaceous; corolla lobes 8–16 × 3–7 mm; fruit 8–12 × 6–8 mm; southeastern United States .... **S. grandifolius* Ait.

12b. Distalmost leaves usually < 7 cm wide (occasionally > 7 cm wide in *S. jaliscanus*, *S. odoratissimus*, *S. subpaniculatus*, and *S. tonkinensis*); fruit dehiscent or if indehiscent, then corolla 5–9 mm long; Asia.

14a. Calyx truncate, undulate, irregularly lobed or toothed, if toothed then the teeth not contiguous; calyx abaxially glabrous, or if stellate trichomes present, within 1 mm of the margin more sparsely pubescent than the rest of the calyx or subglabrous to glabrous, somewhat scarious, brown when dry.

15a. Longer pedicels on each twig 15–50 mm long, usually equal to or longer than subtended flower .... 6. *S. japonicus*

15b. Longer pedicels on each twig 2–10(–13) mm long, usually shorter than subtended flower.

16a. All flowers solitary, arising from shoots of the previous growing season; petioles $< 1(-2.5)$ mm long; pericarp dry, (1–)1.5–3 mm thick; inner surface of pericarp densely appressed-pubescent .... 8. *S. macrocarpus*

16b. At least some flowers paired or in racemes arising from shoots of the current growing season; petioles > 2.5 mm long; pericarp < 1 mm thick or fleshy; inner surface of pericarp glabrous or sparsely pubescent.

17a. Stems of young fertile shoots generally < 0.6 mm wide at the narrowest points proximally; pedicels slender, 0.2–0.6 mm wide proximally; calyx toothed, the teeth linear-subulate at least at apex but often wider proximally, 0.5–1.2 mm long; corolla lobes 1–5 mm wide, apex acute; North America (eastern United States) .... *S. americanus* Lam.

17b. Stems of young fertile shoots generally ≥ 1 mm wide proximally (often narrower distally); pedicels stouter, (0.4–)0.6–1 mm wide proximally; calyx truncate, undulate, irregularly lobed, or toothed, if toothed the teeth deltoid to linear-deltoid; corolla lobes 3–13 mm wide, apex obtuse or acute-acuminate; Asia.

18a. Flowers (1.3–)1.5–2.5 cm long; corolla lobes (11–)12–18 mm long; calyx (3.5–)5–7(–9) × 4–7(–11) mm; filaments 4–7 mm long; pericarp at least faintly longitudinally striate.

19a. Tertiary and quaternary veins of lamina plane adaxially, the tertiaries subparallel; calyx often abaxially with various amounts of stiff stellate trichomes, especially proximally, scattered among the base tomentum; filaments 5–7 mm long, distally attenuate; anthers 3–5 mm long, wider than distal portion of filament; fruit subglobose or ovoid, (1.0–)1.5–2 cm long; apex acute, occasionally short-rostrate .... 5. *S. hookeri*

19b. Tertiary and quaternary veins of lamina conspicuously raised adaxially (as well as abaxially), the tertiaries irregularly reticulate; calyx abaxially without scattered stiff stellate trichomes; filaments 4–5 mm long, of equal width throughout; anthers 5–6 mm long, as wide as or narrower than distal portion of filament; fruit cylindrical to obliquely ovoid, 2–2.5 cm long; apex usually rostrate, rostrum up to 2 cm long. .... 3. *S. curvirostratus*

18b. Flowers < 1.5 cm long; corolla lobes 9–11 mm long; calyx 3–4(–5) × 3–4 mm; filaments 1.5–4 mm long; pericarp not longitudinally striate.

20a. Connectives (at least proximally) and style densely stellate-pubescent; pericarp dry, 0.5–1 mm thick, smooth or slightly rugose; seeds usually appressed-stellate-pubescent or lepidote, rarely glabrous; mature leaves light green to yellow-green when dry, chartaceous or thick-chartaceous .... *10. *S. odoratissimus*

20b. Connectives and style glabrous; pericarp fleshy, ca. 2 mm thick, deeply rugose when dried; seeds glabrous; mature leaves green to dark green when dry, membranaceous or thin-chartaceous .... 11. *S. porterianus*

14b. Calyx distinctly dentate, the teeth usually contiguous or separated by a shallow concave portion; calyx abaxially within 1 mm of the margin evenly pubescent, the color and texture ± similar to the rest of the calyx.

21a. Trees to 30 m tall; petiole 8–12(–15) mm long; pericarp not longitudinally striate, apex rostrate; seeds densely tuberculate, sometimes the tubercles arranged in stellate formations .... *16. *S. tonkinensis*

21b. Shrubs to 2.5 m tall (sometimes a tree to 6 m in *S. rugosus*); petiole ≤ 5 mm long; pericarp longitudinally striate, apex rounded or apiculate; seeds smooth or finely reticulate-fissured, glabrous.

22a. Lamina 1–2.5(–4) × 0.7–2(–2.5) cm; fruit 0.4–0.6 cm wide .... 17. *S. wilsonii*

22b. Lamina 3–13 × 2–8 cm; fruit ≥ 0.7 cm wide.

23a. Secondary veins of lamina 7–10 on each side of midvein; inflorescence rachis gray-green tomentose; calyx gray-green lanate throughout; North America (western Mexico) .... *S. jaliscanus* S. Wats.

23b. Secondary veins of lamina 4–7 on each side of midvein; inflorescence rachis yellow or orange tomentose; calyx yellow, yellow-brown, or orange tomentose, often also with various amounts of larger scattered dark yellow, orange, or brown stiff stellate trichomes, especially proximally; Asia.

24a. Quaternary as well as the tertiary veins of lamina abaxially prominent and raised in young leaves; rachis with stalked trichomes; fruit 0.8–0.9 cm wide .... 12. *S. rugosus*

24b. Only the tertiary veins of lamina abaxially prominent and raised in young leaves; rachis without stalked trichomes; fruit 1.0–1.5 cm wide .... 7. *S. limprichtii*

1. Styrax buchananii W. W. Sm., Notes Roy. Bot. Gard. Edinburgh 12: 234. 1920 [as *S. "Buchananii"*]. TYPE: Myanmar. Kachin State: Myitkyina in Mara Nantan forest, Kaukkwe Valley, 606 m, Mar. 1912, *E. M. Buchanan 51* (holotype, E!; isotype, E!). Figure 1.

Styrax serrulatus var. *latifolius* Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 37. 1907. TYPE: Myanmar. Mandalay Division: *W. Griffith 3670* (lectotype, designated here, K [loan accession no. H2000/01016-29]!; isotypes, GH!, K [loan accession no. H2000/01016-30]!).

Small trees. Young twigs densely yellow-brown stellate-pubescent; older twigs becoming gray, subglabrous. Petiole 3–4 mm long. Two most proximal leaves on each shoot alternate. Lamina of fertile shoots 6–11 × 4–6 cm, those of sterile shoots to 16 × 11 cm, chartaceous, ovate-oblong; apex slightly acuminate to obtuse, base rounded or broadly cuneate, rarely truncate; adaxially sparsely yellow-gray pubescent with 2- or 3-armed or stellate trichomes; abaxially sparsely to densely yellow-gray stellate-hirsute, the surface visible through the pubescence, the pubescence especially prevalent on veins; margin remotely irregularly serrulate apically; secondary veins 5 or 6 on each side of midvein, adaxially faintly prominent, abaxially prominent; tertiary veins parallel and perpendicular to the secondaries, plane or slightly sunken adaxially, abaxially prominent. Fertile shoots 19–30 cm long, 3- or 4-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences racemose, 2–5 cm long, 3- to 5-flowered, often with 1 or 2(to 4) flowers occurring in the same leaf axil; pseudoterminal inflorescences usually paniculate, sometimes racemose, 9–13 cm long, 10- to 22-flowered, lateral branches 2 to 5, sometimes with 2 or 3 short lateral racemes from the base of inflorescence, rachis and branches densely yellow stellate-pubescent. Pedicel (1–)3–5 mm long, densely yellow stellate-hirsute; bracteoles ca. 3 mm long, linear, usually positioned at the base of pedicels. Flowers 1.3–1.6 cm long. Calyx 4–5.5 × 4–5 mm, cupuliform; adaxially white appressed-pubescent with 2- or 3-armed or stellate trichomes; abaxially densely yellow stellate-hirsute, arms of trichomes averaging ca. 1 mm long, within 1 mm from the margin more sparsely pubescent, somewhat scarious, brown when dry; margin truncate, undulate, or irregularly lobed, the teeth minute and not contiguous if present. Corolla 0.8–1.1 cm long, white, tube ca. 3 mm long, glabrous, lobes 5, 9–13 × 3–4.5 mm, 2.4–3.0 × as long as wide, lanceolate or ovate-lanceolate, stellate-tomentose on both sides. Stamens 10; filaments 3–4 mm long, slightly flexuous at middle, distally attenuate, densely white to yellow stellate-hirsute throughout, arms of the trichomes predominantly pointing upward; anthers 5–7 mm long, wider than distal portion of filament; connectives (at least proximally) densely stellate-hirsute. Style densely white stellate-hirsute nearly throughout, thinning distally; stigma 0.4–0.7 mm wide, punctiform. Fruit unknown.

Illustrations. None previously published.

Phenology. Flowering: February–April. Fruiting: unknown.

Distribution. Myanmar (Kachin State, Mandalay Division, and Sagaing Division); Figure 2.

Habitat. In valley forests; 600–1500 m.

Styrax buchananii is geographically isolated in Myanmar from all other *Styrax* species except *S. hookeri* and *S. japonicus*, from which it can easily be distinguished by its longer inflorescences and more numerous flowers. It has been only rarely collected throughout its range and is only known from flowering collections.

This species was first described by Perkins (1907) as a variety of *Styrax serrulatus*. Perkins suggested that it likely represented a new species, but the available material at the time of description (*Griffith 3670* from the Ruby Mines District (Smith, 1920) of Mandalay Division, Myanmar) was inadequate for a proper assessment of species status. Similarly, Smith (1920), in describing *S. buchananii* based solely on *Buchanan 51*, was uncertain whether *S. serrulatus* var. *latifolius* Perkins should be listed as a synonym. With the benefit of additional material available to us, we affirm that *Griffith 3670* and *Buchanan 51* represent one and the same species, based on the combination of imbricate corolla aestivation, pubescent style, many-flowered inflorescences, and other key characters present in these collections. Furthermore, the general locality of *Griffith 3670* lies in the vicinity of all other collections of *S. buchananii*. Smith (1920) described *S. buchananii* with valvate corolla aestivation, but our observations confirm that all specimens cited in the protologue of *S. buchananii* have distinctly imbricate aestivation.

Several shared characteristics, e.g., the two most proximal leaves on each shoot of the current year subopposite to opposite and stellate pubescence covering nearly the whole length of the filaments and styles, suggest that *Styrax buchananii* is a close relative of *S. odoratissimus*. *Styrax buchananii* can be distinguished from *S. odoratissimus* by the shorter petioles (3–4 vs. 5–12 mm), the typically paniculate (vs. typically racemose) inflorescences, corol-

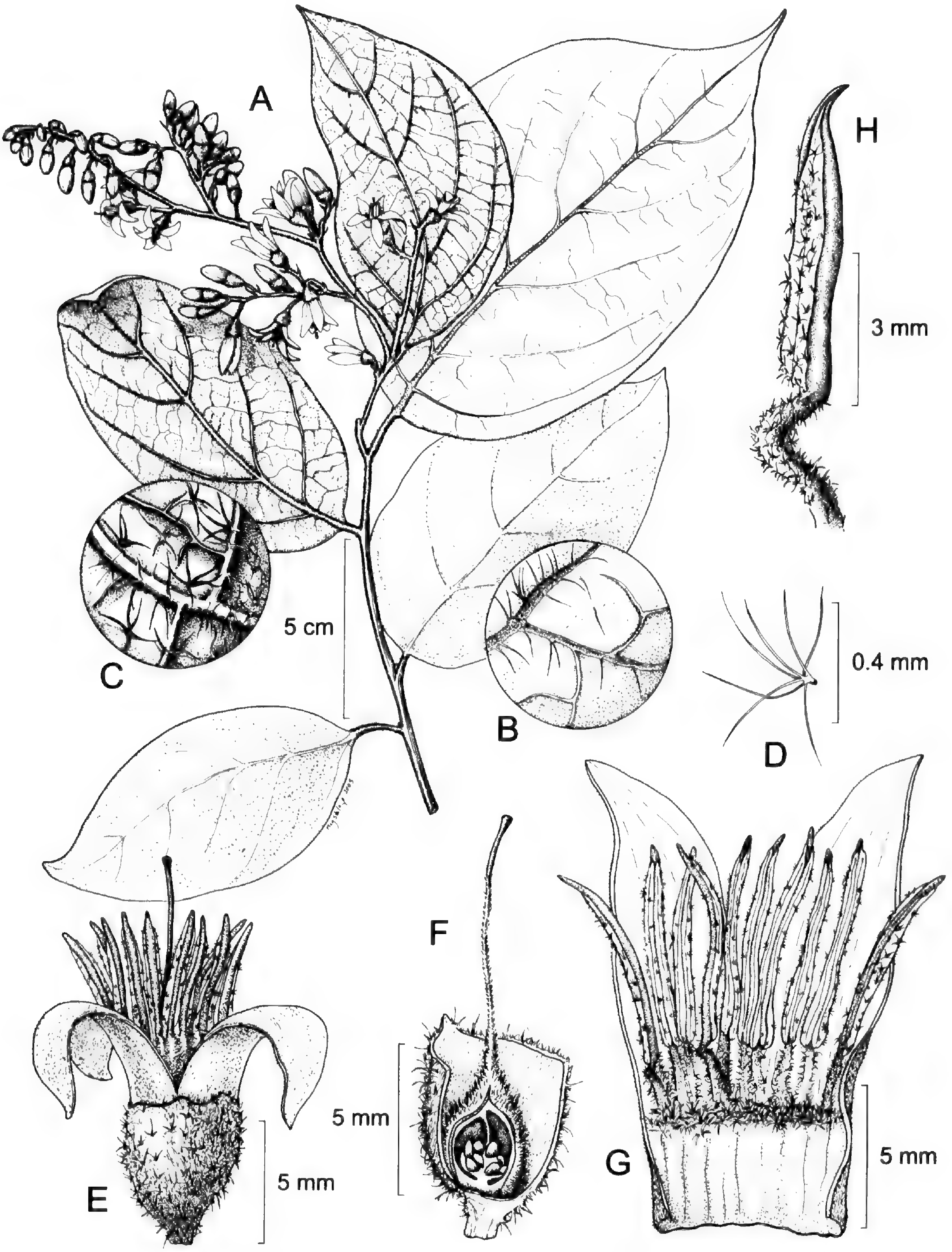

Figure 1. *Styrax buchananii.* —A. Flowering branch. —B. Leaf surface, adaxial view. —C. Leaf surface, abaxial view. —D. Stellate trichome from the abaxial side of the leaf. —E. Flower. —F. Calyx + gynoecium, median long-section. —G. Part of corolla + androecium, opened. —H. Stamen, lateral view. Based on *Kingdon-Ward 20550.*

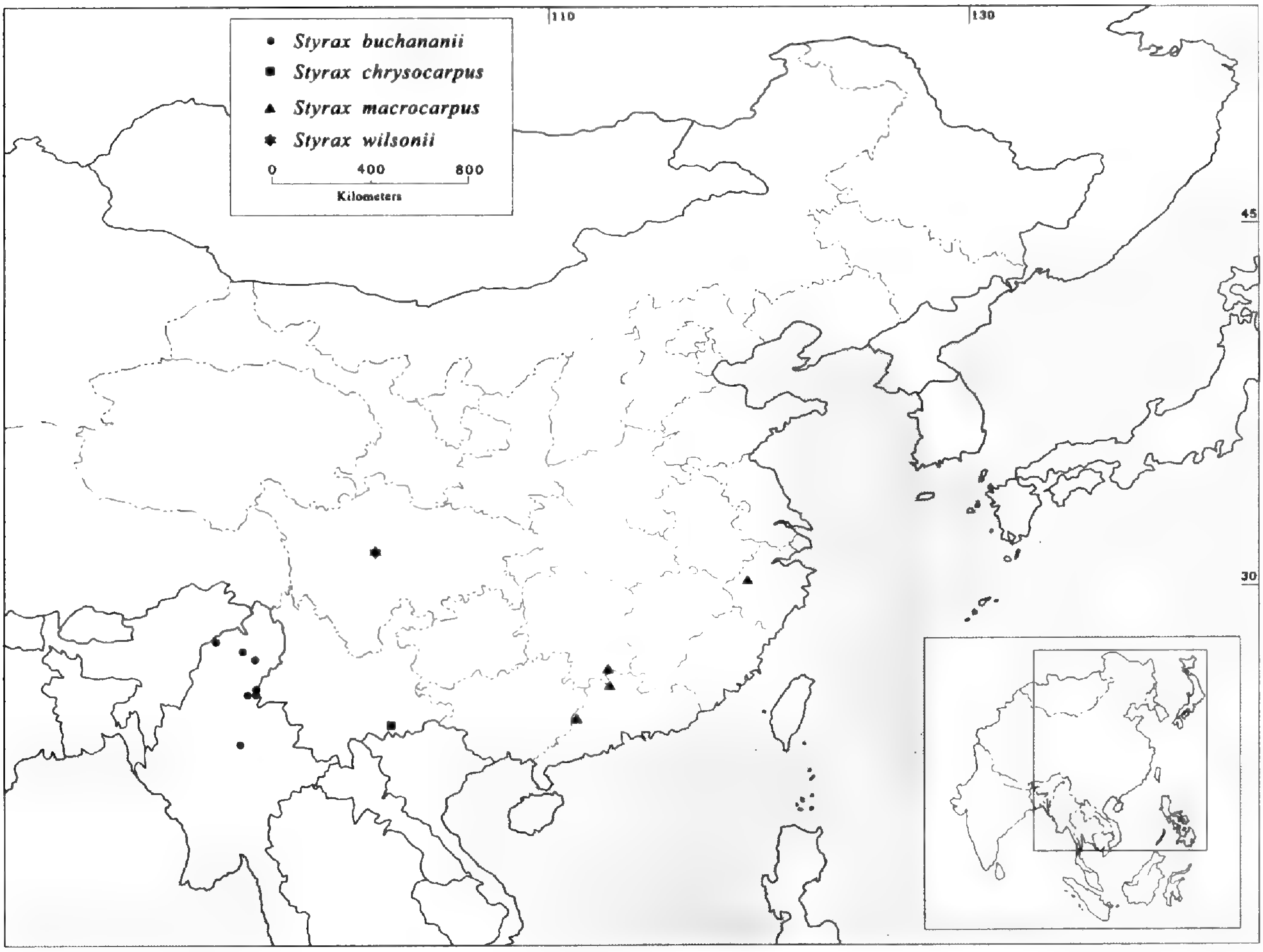

Figure 2. Geographic distribution of *Styrax buchananii, S. chrysocarpus, S. macrocarpus,* and *S. wilsonii.*

la lobes 2.4–3 (vs. 1.7–2.2) times as long as wide, and a distribution (northern Myanmar) that is outside the known range of *S. odoratissimus* (China).

Another probable close relative of *Styrax buchananii* is *S. chrysocarpus,* a species whose range in Yunnan Province is located between those of *S. buchananii* and *S. odoratissimus. Styrax chrysocarpus* has a leaf texture and average petiole length (5–8 mm) similar to the other two species, and in all three the two most proximal leaves are alternate. The differences between *S. buchananii* and *S. chrysocarpus* are not entirely clear in the absence of data from flowers (*S. chrysocarpus*) and fruits (*S. buchananii*).

The protologue of *Styrax serrulatus* var. *latifolius* cites both B and K specimens of *Griffith 3670.* The B specimen has presumably been destroyed, and thus we have chosen one of the two K specimens that we have seen as a lectotype. Neither sheet harbors Perkins's annotation, but that with loan accession number H2000/01016–29 has better flowering material. Thus, we have chosen this sheet as the lectotype.

Additional specimens examined. MYANMAR. **Kachin State:** Myitkyina at Lamaing, *E. M. Buchanan 21* (E); Japing Valley, *G. Forrest 21083* (E); Myitkyina Dist., Sumprabum Subdivision, Hlingnan, *Y. Hla & C. Koko 3746* (K); Bhamo Dist., road to Sinlumkaba, *J. H. Lace 5737* (E); Bhamo Dist., *J. H. Lace 5774* (E, K); Sumpra Bum, *F. F. K. Ward 20550* (A, BM). **Sagaing Division:** Patkoi Range, border betw. Burma [Myanmar] & India, *R. S. Hole 17* (K).

2. Styrax chrysocarpus H. L. Li, J. Arnold Arbor. 25: 312. 1944. TYPE: China. Yunnan: Pingbian Miaozu Zizhixian, 1400 m, 9 July 1934, *H. T. Tsai 62505* (holotype, A!; isotypes, IBSC!, KUN!, PE!).

Trees 7–20 m tall. Young twigs yellow-brown stellate-tomentose; older twigs dark brown, subglabrous. Petiole 5–8 mm long. Two most proximal leaves on each shoot alternate. Lamina 10–20 × 5.5–11 cm, chartaceous, oblong-ovate to oblong; apex acute to slightly acuminate; base rounded or broadly cuneate; adaxially sparsely yellow-gray stellate-pubescent, arms of the trichomes up to 0.2–0.3 mm long, the pubescence especially prevalent on veins; abaxially densely yellow-gray stellate-hirsute, arms of the trichomes up to 0.5–0.6 mm long, the surface remaining visible through the pubescence; margin subentire or remotely irregular serrulate apically; secondary veins 5 to 10 on each side of midvein, adaxially plane or slightly sunken, abaxially prominent; tertiary veins reticulate, abaxially prominent. Flowers unknown. Infructescences arising from shoots of the current growing season, apparently racemose, 1- to 5-fruited, yellow stellate-tomentose. Fruiting pedicel 4–5 mm long. Fruiting calyx 5–6 × 10–15 mm, cupuliform, red-brown, the margin not appressed to the fruit, glabrous adaxially, densely stellate-pubescent abaxially; margin irregularly 5- or 6-crenately lobed, lobes ca. 4 × 10 mm. Fruit 1.6–1.8 × 1.0–1.2 cm, ovoid, apex shortly pointed, apparently indehiscent; pericarp dry, 0.3–0.5 mm thick, outside golden yellow stellate-tomentose, inside densely pale yellow appressed-pubescent. Seeds dull dark-brown, ovoid, smooth, glabrous.

Illustrations. C. Y. Wu, Fl. Yunnan. 3: 430, pl. 123 (1–3). 1983.

Phenology. Flowering: unknown. Fruiting: July.

Distribution. China (Yunnan); Figure 2.

Habitat. In ravine forests; 1400–1500 m.

Vernacular names. Huang-guo-an-xi-xiang (Hwang & Qi, 1985), Mao-guo-an-xi-xiang (Wu, 1983).

Styrax chrysocarpus is known with certainty only from Pingbian Miaozu Zizhixian, southeastern Yunnan Province. This species is easily distinguished from other members of *Styrax* by its golden yellow fruit and densely pale yellow pubescent inner surface of the pericarp. A sterile specimen with aphid galls collected between 1550 and 1650 m elevation in Yongshan Xian, extreme northeastern Yunnan Province (*H. T. Tsai 51156*), might be this species. Its leaves, however, are glabrous, unlike the densely hirsute upper and lower surfaces of those in the type. More fertile material from the vicinity of Tsai's localities is highly desirable to better understand the taxonomy of this species.

Although only fruits are available for comparison, careful analysis of vegetative and fruit morphology suggests that *Styrax chrysocarpus* is most likely allied to other deciduous species with imbricate aestivation. Sterile specimens of *S. chrysocarpus* are similar to some specimens of *S. buchananii* and *S. odoratissimus* in the relatively large leaves, the lower laminar surface somewhat rough to the touch, and the strictly alternate leaves. *Styrax chrysocarpus* consistently differs from *S. odoratissimus,* however, in its shorter infructescences and larger yellow stellate-hirsute fruit, and differs from most specimens of *S. odoratissimus* in its glabrous seeds (differences between *S. chrysocarpus* and *S. buchananii* are addressed in the discussion under *S. buchananii*). Furthermore, none of the distributional ranges of these three species overlap: *S. buchananii* is restricted to Myanmar, *S. odoratissimus* to southeastern China, and *S. chrysocarpus* to eastern Yunnan Province, China.

Additional specimens examined. CHINA. **Yunnan:** Pingbian Miaozu Zizhixian, *H. T. Tsai 62522* (A, KUN, PE), *62766* (A, IBSC, KUN, PE); Yongshan Xian, *H. T. Tsai 51156* (A, BO).

3. Styrax curvirostratus (B. Svengsuksa) Y. L. Huang & P. W. Fritsch, stat. nov. Basionym: *Styrax agrestis* var. *curvirostratus* B. Svengsuksa, Flore du Cambodge du Laos et du Viêtnam 26: 176. 1992. TYPE: Vietnam. Lam Dong: Massif du Lang Bian, between Dankia and Dangle, 1000–1200 m, 25 Oct. 1930, *E. Poilane 18626* (holotype, P not seen; isotype, P!). Figure 3.

Trees to 15(–20) m tall. Young twigs dark gray or brown, sparsely gray-white stellate-pubescent; older twigs dark brown or nigrescent, glabrescent. Petiole 7–10 mm long. Two most proximal leaves on each shoot alternate. Lamina 6–11 × 3–4.5 cm, thick-chartaceous, elliptic to oblong; apex short-acuminate to acuminate; base rounded to broadly cuneate; glabrous, rarely abaxially sparsely short-stellate-pubescent on the veins and vein axils, both surfaces glossy, bright green when dry; margin entire or slightly undulate, rarely irregularly denticulate; secondary veins 5 or 6 on each side of midvein; tertiary and quaternary veins irregularly reticulate and conspicuously raised on both sides. Fertile shoots 8–15 cm long, 3- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1(2)-flowered; pseudoterminal inflorescences 1- or 2-flowered or racemose, 1–3 cm long, (1- to)3- to 5-flowered, rachis yellow stellate-tomentose. Pedicel 8–9 mm long, yellow stellate-tomentose; bracteoles 1–2 mm long, linear, positioned at various places along the pedicel but mostly near the base. Flowers 1.6–1.8 cm long. Calyx 6–7 × 6.5–7 mm, cupuliform; adaxially densely white appressed-stellate-pubescent, proximally becoming sparsely pubescent with white 2- or 3-armed trichomes; abaxially densely yellow stellate-pubescent, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry; margin truncate, undulate, or irregularly lobed, the teeth minute, not contiguous if present. Corolla 0.9–1.2 cm long, white, tube ca. 4 mm long, slightly pubescent, glabrous

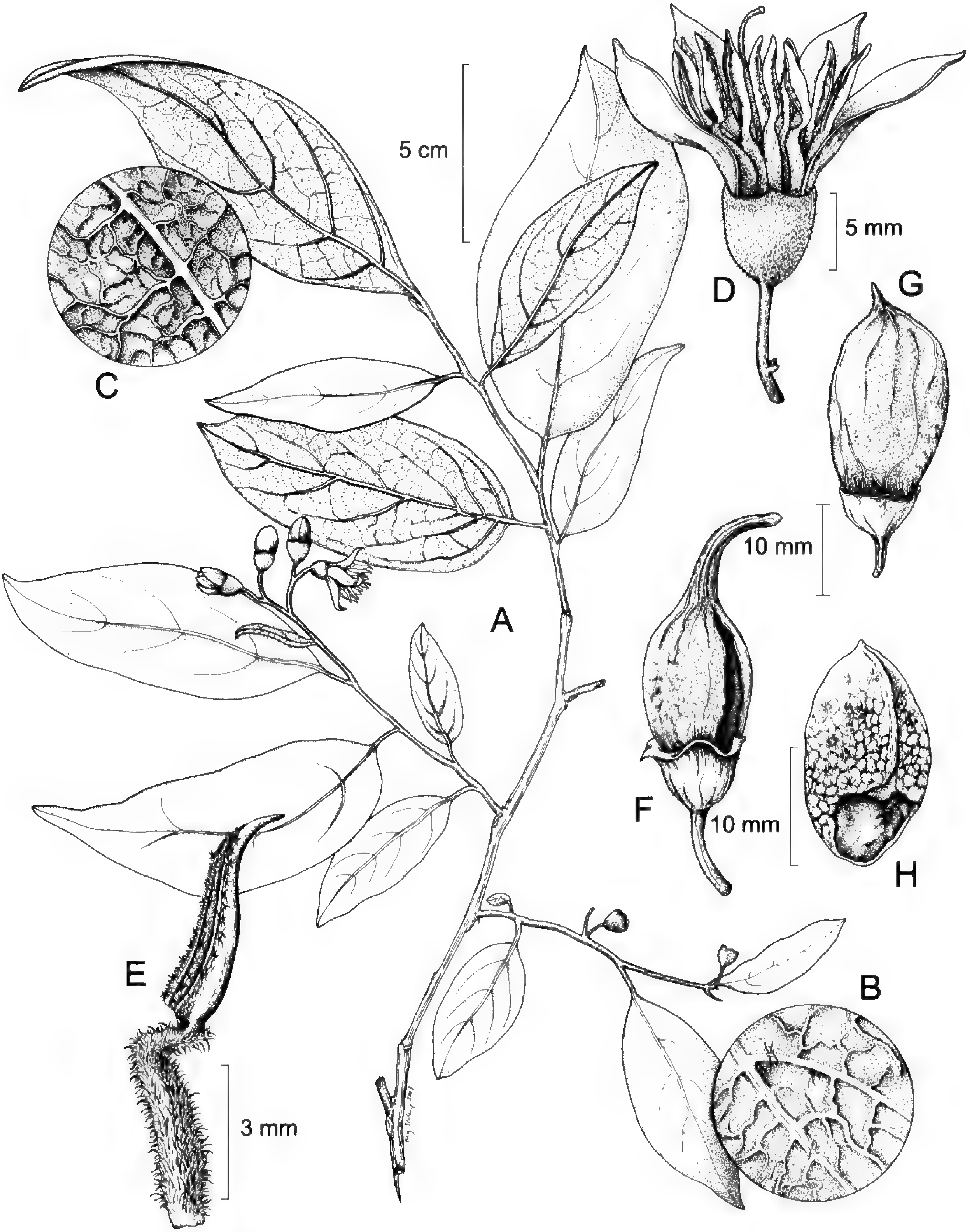

Figure 3. *Styrax curvirostratus.* —A. Flowering branch. —B. Leaf surface, adaxial view. —C. Leaf surface, abaxial view. —D. Flower. —E. Stamen, lateral view. —F, G. Fruit. —H. Seed. A–E based on *Averyanov et al. VH 4544*; F based on *Poilane 18626*; G, H based on *Chevalier 38674.*

proximally, lobes 5, 12–13 × 5–6 mm, obovate to obovate-elliptic, apex acute, densely pale yellow stellate-hirsute on both sides. Stamens 10; filaments 4–5 mm long, strongly flexuous at middle, of equal width throughout, densely white stellate-villous throughout, arms pointing upward; anthers 5–6 mm long, as wide as or narrower than distal portion of filament; connectives glabrous. Style densely

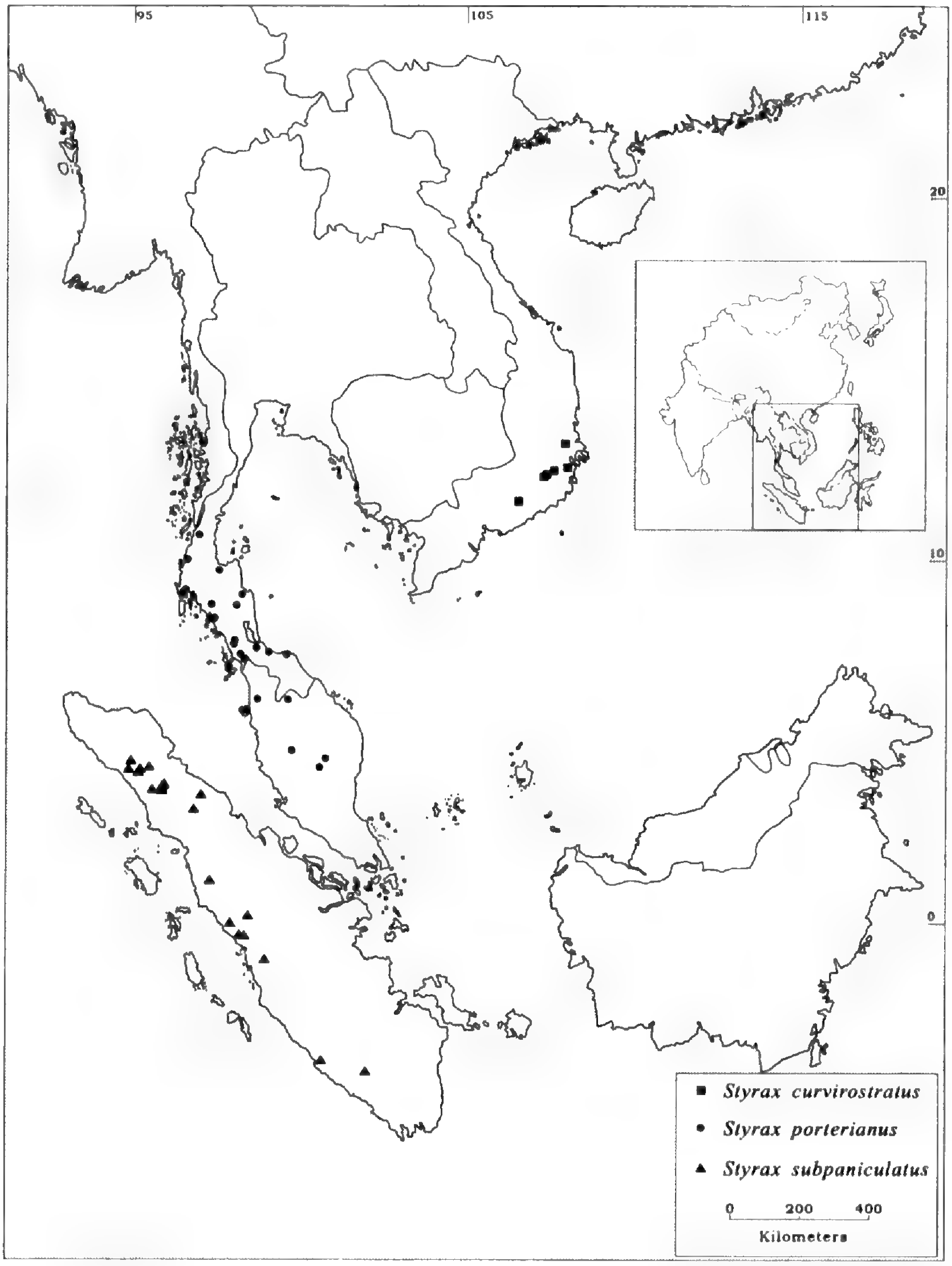

Figure 4. Geographic distribution of *Styrax curvirostratus*, *S. porterianus*, and *S. subpaniculatus*.

white stellate-pubescent throughout, conspicuously 3-angular and 3-furrowed, stigma ca. 0.2 mm wide, capitate. Fruit 2.0–2.5 × 1.1–1.5 cm, cylindrical to oblique-ovoid, apex usually rostrate, rostrum up to 2 cm long, dehiscent; pericarp dry, 0.3–0.4 mm thick, outside irregularly longitudinally striate, gray stellate-tomentose, inside minutely downy-pubescent. Seeds brown, ellipsoid, smooth to finely reticulate-fissured, glabrous or occasionally appressed-stellate-pubescent.

Illustrations. B. Svengsuksa & J. E. Vidal, *Flore du Cambodge du Laos et du Viêtnam* 26: 173, pl. 31 (10–11). 1992 (as *S. agrestis* var. *curvirostratus*).

Phenology. Flowering: April, May. Fruiting: January, September, October.

Distribution. Vietnam (Binh Thuan, Dac Lac, Khanh Hoa, and Lam Dong); Figure 4.

Habitat. In primary, closed, evergreen broad-leaved mountain forests; 1000–1700 m.

Styrax curvirostratus is the only imbricate species of *Styrax* documented in southern Vietnam; it is thus easily distinguishable from the several sympatric members of the genus with valvate aestivation. This species is distinguished from most other imbricate species by its long-rostrate, cylindrical to oblique-ovoid fruit 2–2.5 × 1.1–1.5 cm. The other species in this group with at least some rostrate-fruited individuals are *S. hookeri*, *S. odoratissimus*, and *S. tonkinensis.* These species possess smaller (less than 2 cm long) fruit with a shorter rostrum (typically less than 2 mm long) than *S. curvirostratus.* Features of *S. curvirostratus* shared with *S. odoratissimus* and *S. buchananii* are the (1) densely white stellate-villous filaments and style, (2) truncate, undulate, or irregularly lobed calyx with noncontiguous teeth if present, and (3) sparsely pubescent or subglabrous calyx within 1 mm of the margin, without larger stiff stellate trichomes. In addition, *S. curvirostratus* and *S. buchananii* have longer anthers (5–6 mm long) than the other imbricate species of series *Cyrta. Styrax curvirostratus* occasionally possesses appressed-stellate-pubescent seeds, as in most individuals of *S. odoratissimus. Styrax curvirostratus* can be distinguished from both *S. buchananii* and *S. odoratissimus* by its larger calyx (6–7 × 6.5–7 mm), longer flowers (1.6–1.8 cm long), and longer, wider, straight (vs. flexuous) filaments of equal width throughout (vs. narrowing distally). Moreover, *S. curvirostratus* is easily separable from *S. buchananii* by its shorter inflorescences (1–3 cm vs. 9–13 cm long) with fewer (1 to 5 vs. 10 to 22) flowers. *Styrax curvirostratus* can be recognized when sterile by the reticulate and distinctly raised quaternary veins on both surfaces of the lamina.

This species was first collected in Lam Dong in 1930 (*Poilane 18626*), but was left undescribed until Svengsuksa and Vidal (1992) assigned this specimen and several others to *Styrax agrestis* (Lour.) G. Don, a species with valvate corolla aestivation, as a new variety. The variety was based on fruiting specimens only, as no flowering material was available. *Styrax curvirostratus* typically shares with *S. agrestis* a rostrate fruit, which separates these two species from most others in Southeast Asia, and the ranges of the two taxa overlap, with that of *S. agrestis* the larger. It was thus not unreasonable for Svengsuksa and Vidal to place *S. curvirostratus* as a variety of *S. agrestis,* distinguishable in fruit from the typical variety by its shorter petioles and pedicels, usually glabrous seeds, and more conspicuous rostrum. Recently, however, a flowering specimen (*Averyanov et al. VH4544*) was collected at a locality within the range of *S. curvirostratus* that matches the vegetative morphology of this taxon in every respect, yet has distinctly imbricate, rather than valvate, corolla aestivation and fewer flowers per inflorescence than *S. agrestis* (1 to 5 vs. 5 to 10). These features clearly distinguish *S. curvirostratus* from *S. agrestis.* Furthermore, the conspicuously reticulate quaternaries on both surfaces, long anthers, and other features listed above distinguish this taxon from all other species of *Styrax,* thus warranting its recognition at the species level.

Additional specimens examined. VIETNAM. **Dac Lac:** N de Ninh-Hoa, Massif de la Mère et l'Enfant, *E. Poilane 6578* (P). **Khanh Hoa:** Phu Khanh, Massif du Hon Ba, *A. J. B. Chevalier 38674* (P). **Lam Dong:** Lac Duong, Mun. Da Chay, 35 km NE from Dalat City, *L. Averyanov et al. VH4544* (AAU, CAS); Massif du Haut Donai, betw. Dankia & Dangle, *E. Poilane 23457* (P), *23569* (P).

4. **Styrax hemsleyanus** Diels, Bot. Jahrb. Syst. 29: 530. 1900 [as *S. "Hemsleyana"*]. TYPE: China. Sichuan: Wushan Xian, 1885–1888, *A. Henry 5676* (lectotype, designated here, A!; isotypes, BM!, GH!, IBSC[2]!).

Styrax hemsleyanus var. *griseus* Rehder, in Sarg., Pl. Wilson. 1: 291. 1912. TYPE: China. Hubei: Changyang Tujiazu Zizhixian, 1212–1818 m [1300–2000 m, protologue], June 1907, *E. H. Wilson 2574a* (holotype, A!; isotypes, BM!, E!, K!).

Styrax huanus Rehder, J. Arnold Arbor. 11: 167. 1930 [as *S. "Huanus"*]. TYPE: China. Sichuan: Nanchuan Shi, 2273–2576 m [1200–2700 m, protologue], 3 June 1928, *W. P. Fang 1376* (holotype, A!; isotypes, BM!, DS!, E!, IBSC!, K!, PE[4]!).

Trees to 12 m tall. Young twigs densely gray-brown stellate-pubescent; older twigs dark brown, glabrescent. Petioles 10–24 mm long, neither dilated nor covering the bud. Two most proximal leaves on each shoot subopposite to opposite. Lamina 7–15 × 4–9 mm, chartaceous, elliptic or ovate-elliptic, rarely broadly elliptic, gray-green to dark green when dry; apex acute to short-acuminate; base oblique and subrounded to broadly cuneate, often shortly decurrent into petiole; adaxially sparsely gray-white pubescent with 2- or 3-armed or stellate trichomes; abaxially glabrous or sparsely to densely gray-white stellate-pubescent or -tomentose; margin subentire or serrate apically; secondary veins 7 to 10 on each side of midvein, tertiary veins subparallel, abaxially prominent. Fertile shoots (12–)15–20 cm long, 2- to 4-leaved. Inflorescences arising from shoots of the current growing season, racemose; lateral racemes 4- to 9(to 13)-flowered, often with solitary flowers occurring in the same leaf axil; pseudoterminal racemes 1(to 3), 8–15 cm long, 8- to 15(to 20)-flowered, rachis yellow-brown stellate-tomentose. Pedicel 2–4 mm long, yellow-brown stellate-tomentose; bracteoles 2–3 mm long, subulate or linear, positioned at the base or middle part of pedicel, sometimes those toward the base of the inflorescence leaf-like. Flowers 1.5–2.5 cm long. Calyx 4–8 × 3–6 mm, narrow-cupuliform; adaxially densely appressed-pubescent, proximally becoming sparsely pubescent with white

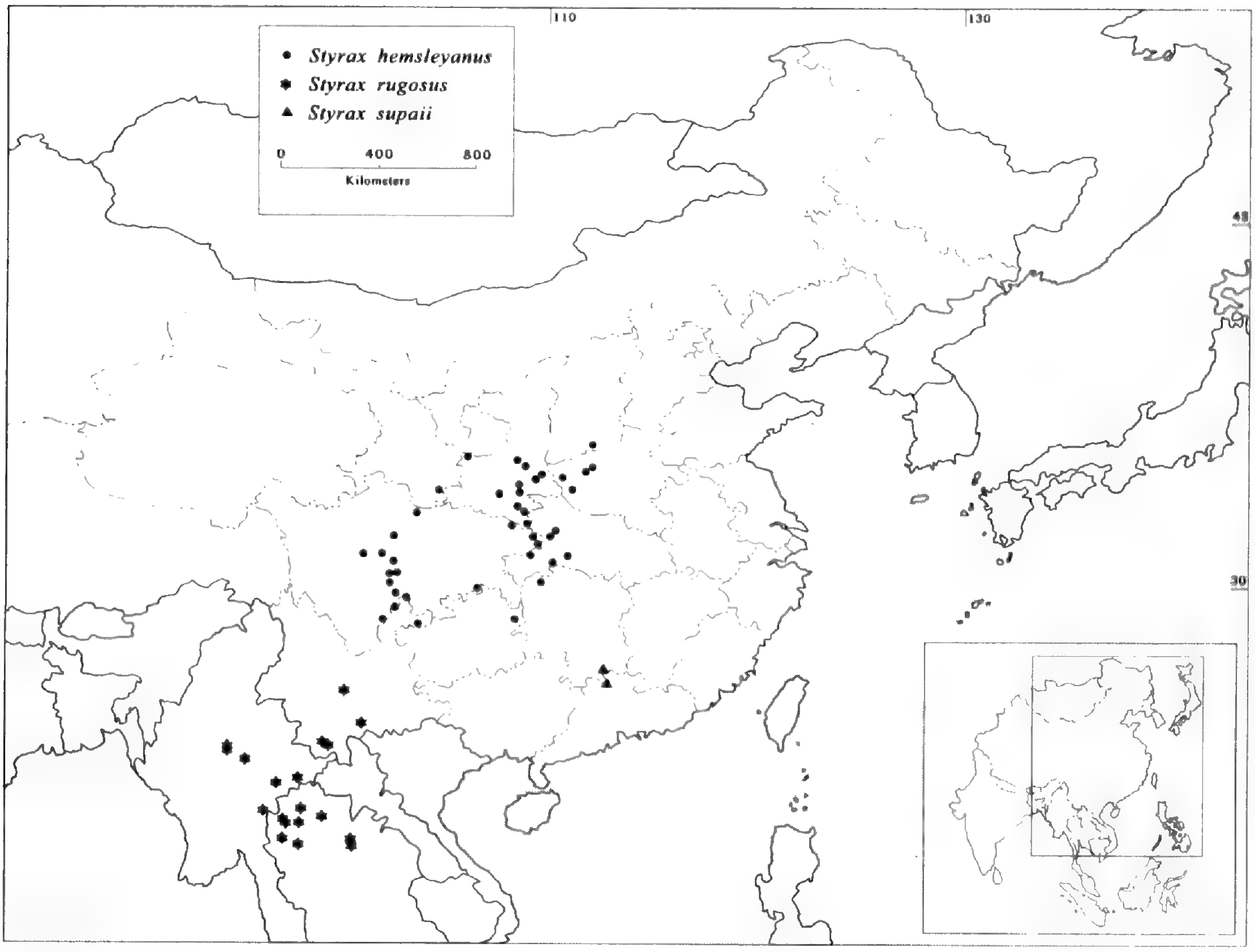

Figure 5. Geographic distribution of *Styrax hemsleyanus*, *S. rugosus*, and *S. supaii.*

2- or 3-armed trichomes; abaxially yellow-brown stellate-tomentose throughout, often also with various amounts of larger dark brown stiff stellate trichomes especially proximally; margin with 5 unevenly distributed teeth 2–3 mm long, unequal, subulate or deltoid, contiguous, densely pubescent on both sides. Corolla 1.1–1.7 cm long, white, tube 4–5 mm long, glabrous, lobes 5 or 6, 12–15 × 4.5–5 mm, elliptic to elliptic-obovate, apex acute, adaxially subglabrous except distally, abaxially pale yellow stellate-tomentose. Stamens 10 to 12; filaments 6–7 mm long, straight, relatively broad, of equal width throughout, ventrally ± pubescent proximally, glabrous distally; anthers 3.5–4.5 mm long, wider than distal portion of filament; connective subglabrous. Style glabrous; stigma 0.4–0.5 mm wide, capitate. Fruit 0.8–1.3(–1.6) × 1–1.5 cm, globose to ovoid, apex apiculate, dehiscent; pericarp dry, 0.1–0.4 mm thick, outside slightly longitudinally rugose, yellow-brown to gray-yellow stellate-tomentose, inside sparsely appressed-stellate-pubescent or glabrous. Seeds brown, ovoid, nearly smooth, sometimes irregularly rugose or finely reticulate-fissured, glabrous.

Illustrations. Prain, Bot. Mag. 136: t. 8339. 1910; W. P. Fang, Ic. Pl. Omei. 1(1): t. 47. 1942; Anonymous, Ic. Cormophyt. Sin. 3: 337, fig. 4628. 1974; F. T. Tai & T. C. Pan in W. P. Fang, Fl. Sichuan. 1: 418, fig. 161. 1981 (as *S. huanus*); ibid.: 426, pl. 165. 1981; C. Y. Wu, Fl. Yunnan. 3: 430, pl. 123 (4–7). 1983; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1602, fig. 797. 1985 (as *S. huanus*); ibid.: 1619, fig. 812. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 85, pl. 28 (6–7). 1987 (as *S. huanus*); ibid.: 96, pl. 32 (8–14). 1987; W. Q. Yin in Y. C. Xu, Ic. Arbor. Yunnan. 2: 896, pl. 472 (1–6). 1990; S. Y. Wang in B. Z. Ding, Fl. Henan 3: 230, fig. 1775 (5–8). 1997; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 197, fig. 197 (6–7). 2000 (as *S. huanus*); ibid.: 201, fig. 201 (8–14). 2000.

Phenology. Flowering: March, May, June. Fruiting: February, May–September.

Distribution. China (Gansu, Guizhou, Henan, Hubei, Hunan, Shaanxi, Shanxi, Sichuan, and Yunnan); Figure 5.

Habitat. In relatively mesic, semi-open mixed forests on mountain slopes and in ravines; 700–2700 m.

Vernacular names. He-si-li-ye-mo-li (China, Sichuan; Fang, 1942), Hui-mao-lao-gua-ling (China, Yunnan; Wu, 1983), Jin-shan-an-xi-xiang (China, Sichuan; Tai & Pan, 1981), Lao-gua-ling (China, Henan; Anonymous, 1974), Ma-lin-guang (China, Shaanxi; *J. Q. Xiang 6053*), Mai-pao (China, Sichuan; *J. H. Xiong et al. 91179*), Mo-pao (China, Henan; Anonymous, 1974), Nan-chuan-an-xi-xiang (China, Sichuan; Tai & Pan, 1981).

Styrax hemsleyanus is a relatively common species, occurring mainly in the mountains at middle elevations surrounding the Sichuan basin. It can be distinguished from sympatric imbricate-flowered species by the combination of the subopposite to opposite two most proximal leaves on each shoot, long, multi-flowered pseudoterminal racemes, and prominent calyx teeth. *Styrax hemsleyanus* is similar in these respects only to *S. obassia*, a species ranging farther to the east, but these two species are easily distinguished even when sterile by the petiole base of the larger leaves, which covers the bud in *S. obassia* but not in *S. hemsleyanus*. Furthermore, the rachis of the raceme is pubescent in *S. hemsleyanus* and glabrous or nearly so in *S. obassia*.

Rehder (1930) described *Styrax huanus* from Nanchuan Shi in southeastern Sichuan, considering the white-stellate tomentum on the lower laminar surface and the longer and glabrous stamen filaments as distinguishing it from *S. hemsleyanus*. Rehder (1912) also differentiated *S. hemsleyanus* var. *griseus* from the typical variety by the presence and quantity of pubescence on the lower laminar surface. Hwang (1987) treated this variety as a synonym of *S. hemsleyanus*, but agreed with Rehder on the status of *S. huanus*, citing the leaf pubescence difference and the type of trichomes as justification for recognizing two species.

Contrarily, we have found no basis for recognizing any taxon other than a single species among these entities. Filament length and pubescence quantity exhibit a complete range of variation among individuals of *Styrax hemsleyanus* and *S. huanus*. Pubescent-leaved individuals of *S. hemsleyanus* have a combined distribution largely overlapping that of glabrous-leaved individuals, occurring from Yangcheng Xian, Shanxi Province (e.g., *T. W. Liu & Z. F. Zeng 226, 245, 1285,* and *1393*), at the extreme northern edge of the species' range, south to Zhenxiong Xian, Yunnan Province (*Exp. NE Yunnan 1161*), whereas glabrous-leaved individuals occur throughout the range of the group. The pubescent-leaved individuals also exhibit no obvious elevation or habit distinctions, and seem to occur sporadically, often near collection localities of glabrous-leaved individuals. Furthermore, several collections show an intermediate amount of pubescence between the types of *S. hemsleyanus* and *S. huanus*, even among collections from the vicinity of the type locality of *S. huanus*.

In addition to the density of pubescence on the abaxial leaf surface, Hwang (1980) considered *Styrax huanus* distinguishable from *S. hemsleyanus* based on leaf trichome types. We consider this difference to reflect merely the length of the stellate trichomes. The arms of the trichomes on the abaxial surface of the leaves are small (averaging ca. 0.15 mm long) in *S. huanus* versus some specimens of *S. hemsleyanus* (averaging ca. 0.5 mm long), but careful inspection of all collections of this group available to us indicates that arm length varies continuously.

In the protologue of *Styrax hemsleyanus*, three collections (syntypes) are cited by Diels: *A. Henry 5676*, *A. Henry 6895*, and *B. von Rosthorn 2078*. Because Diels's herbarium was B, we assume that the material on which the description of *S. hemsleyanus* was based has been destroyed. We therefore have designated the A specimen of *A. Henry 5676* as the lectotype because duplicates are apparently more widely distributed than those of the other two syntypes (in particular, *A. Henry 5676* is represented by two duplicates in a Chinese herbarium (IBSC), unlike either of the other syntypes), and only the *A. Henry 5676* specimen from A possesses collection locality data. There is no evidence of Diels's handwriting on the type material that we have examined.

Selected specimens examined. CHINA. **Gansu:** Kang Xian, Yang-ba-xiang, *Z. Y. Zhang 16612* (PE). **Guizhou:** Jiangkou Xian, Niu-wei-he, *Exp. Fan-jin-shan & Feng-huang-shan 402110* (IBSC, PE). **Henan:** Lushi Xian, Lao-chun-shan, *K. M. Liou 4421* (K, PE); Song Xian, Sang-shi, Long-di-man, *Henan Forestry Dept. 1074* (PE); Xixia Xian, *T. L. Dai 1296* (PE); Yichuan Xian, *Pu-cha-biao-ben 20304* (PE). **Hubei:** Changyang Tujiazu Zizhixian, *T. P. Wang 11480* (KUN); Jianshi Xian, Hua-guo-ping, *W. B. Lin 91* (PE); Shennongjia Linqu, Shen-nong-jia Forest Dist., *Sino-Amer. Bot. Exp. (1980) 1133* (A, E, KUN, UC); Wufeng Tujiazu Zizhixian, *H. J. Li 5861* (IBSC, PE). **Hunan:** Sangzhi Xian, Ba-mao-xi-xiang, Tian-ping-shan, *B. G. Li 750286* (PE). **Shaanxi:** Ankang Xian, Tao-he-gong-she, *P. Y. Li 7778* (KUN); Fuping Xian, He-tao-ping, *K. T. Fu 4849* (PE); Long Xian, Shen-si, Lung-chow, Kuan-shan, *collector unknown 2346* (A); Luonan Xian, *P. C. Kuo 342* (KUN); Ningshan Xian, Jiang-kou-xiang, *J. Q. Xing 6053* (IBK); Pingli Xian, Da-dang-fu-shan, *P. Y. Li 1380* (KUN); Shangzhou Shi, Long-ju-xiang, *Z. C. Zhu et al. 34* (IBSC); Weinan Shi, Qing-gang-ping, Zhu-zi-gou, *Z. B. Wang 15652* (IBSC, KUN, PE); Zhashui Xian, Qing-ling-shan., *collector unknown 66*

(PE); Zhen'an Xian, *X. X. Hou et al. 601* (IBSC); Zhenping Xian, Zhong-hong-xiang, *P. Y. Li 2209* (KUN). **Shanxi:** Yangcheng Xian, Sang-lin, Shu-pi-gou, Gan-qi-tong, *T. W. Liu & Z. B. Zeng 1285* (CAS). **Sichuan:** Chengkou Xian, Hou-ping-xiang, *T. L. Dai 105634* (KUN, PE); Ebian Yizu Zizhixian, Wa-shan, *E. H. Wilson 2578* (A, BM, E); Emeishan Shi, E-mei-shan, *W. P. Fang 14826* (A, KUN); Dujiangyan Shi, *W. P. Fang 2225* (A, E, IBSC, K); Jinyang Xian, *Sichuan Economic Pl. Exp. 2483* (PE); Kangding Xian, near Ta-chien-lu, *A. E. Pratt 406* (BM, K); Leibo Xian, *Z. T. Guan 411* (IBSC); Mabian Yizu Zizhixian, *F. T. Wang 23029* (A, KUN, PE); Nanchuan Shi, *W. P. Fang 1401* (A, E, IBSC, K, PE); Pingshan Xian, *Sichuan Economic Pl. Exp. 1206* (PE); Pingwu Xian, *H. L. Tsiang 19* (IBSC); Tianquan Xian, *F. C. Tai & C. M. Teng 4215* (KUN); Wushan Xian, *A. Henry 5676A* (IBSC); Wuxi Xian, Hong-chi-ba, *G. H. Yang 59375* (IBSC, KUN, PE). **Yunnan:** Zhenxiong Xian, Hua-shan, *Exp. NE Yunnan 1161* (KUN).

5. Styrax hookeri C. B. Clarke, in Hook. f., Fl. Brit. India 3: 589. 1882 [as *S.* "*Hookeri*"]. TYPE: India. Sikkim: 1828–2121 m, *J. D. Hooker s.n.* (lectotype, designated here, K! [loan accession no. H2000/01016, fl branch]; isotypes, BM!, BR!, C!, K!, L[2]!).

Styrax macranthus Perkins, Bot. Jahrb. Syst. 31: 487. 1902. TYPE: China. Yunnan: Lüchun Xian, region of Feng Chun Ling, 2121 m [2000 m, protologue], S of the Red River, *A. Henry 10644* (lectotype, designated here, K!; isotypes, A!, BM!, E[2]!, IBSC[2]!, MO!, PE!).

Styrax caudatus Perkins, in Engl., Pflanzenr. IV. 241 (Heft 30): 74. 1907. TYPE: India. Assam: Mt. Sillet (Perkins, 1907), *Wallich 4400B* (holotype, B destroyed; isotype, K not seen; digital image of K specimen!).

Styrax hookeri var. *yunnanensis* Perkins, Repert. Spec. Nov. Regni Veg. 8: 84. 1910. TYPE: China. Yunnan: Zhaotong Shi, Hay Tse Pa, 6 July 1906, *F. Ducloux 4626* (lectotype, designated here, P!).

Styrax roseus Dunn, Bull. Misc. Inform. Kew 1911: 273. 1911. TYPE: China. Sichuan: Ebian Yizu Zizhixian, Mt. Wu [from protologue], Wa-shan (Rehder, 1912), 2424 m [2600 m, protologue], July 1903, *E. H. Wilson 4065* (holotype, K!; isotypes, A[2]!, BM!, IBSC!).

Styrax perkinsiae Rehder, in Sarg., Pl. Wilson. 1: 292. 1912 [as *S.* "*Perkinsiae*"]. TYPE: China. Sichuan: Ebian Yizu Zizhixian, Wa-shan, 1828–2121 m [2000 m, protologue], 1908, *E. H. Wilson 2576* (lectotype, designated here, A [July 1908]!; isotypes, BM!, E!).

Styrax shweliensis W. W. Sm., Notes Roy. Bot. Gard. Edinburgh 12: 236. 1920. TYPE: China. Yunnan: Tengchong Xian, Tengyueh-Shweli divide; 25°N, 2121 m, May 1913, *G. Forrest 9869* (holotype, E!; isotypes, A!, K!).

Shrubs or trees to 10 m tall. Young twigs gray-brown stellate-puberulent; older twigs purplish brown, glabrescent. Petiole (2.5–)4–6(–10) mm long. Two most proximal leaves on each shoot subopposite to opposite. Lamina 6–8(–12) × 3–4(–6) cm but sometimes distalmost lamina smaller, chartaceous to thick-chartaceous, oblong, lance-ovate, or narrowly elliptic, often dark green when dry; apex acuminate to caudate, rarely acute, slightly oblique; base often slightly oblique, rounded to broadly cuneate, rarely shallowly cordate or narrowly cuneate; adaxially sparsely gray-white (rarely yellow-brown) pubescent with simple or 2- or 3-armed to stellate trichomes, glabrescent; abaxially glabrous or sparsely to gray-white stellate-pubescent to -tomentose, pubescence especially prevalent on the veins and especially longer on the axils of the midvein and secondary veins; margin glandular-serrulate and slightly revolute; secondary veins 5 to 7 on each side of midvein, tertiary veins subparallel and perpendicular to the secondary nerves, together with the quaternaries adaxially plane and abaxially prominent. Fertile shoots 4–12 cm long, 3- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- to 3-flowered; pseudoterminal inflorescences 1- or 2-flowered or racemose, 2–4 cm long, (1)2- or 3(to 6)-flowered, rachis yellow stellate-tomentose. Pedicel (2–)5–8(–13) mm long, yellow-brown stellate-tomentose; bracteoles 3–4 mm long, subulate or linear, positioned at various places along the pedicel but mostly near the middle, more rarely near the base, sometimes those toward the base of the inflorescence leaf-like. Flowers (1.3–)1.5–2.5 cm long. Calyx (3.5–)5–7(–9) × 4–6(–11) mm, cupuliform; adaxially covered with 2- or 3-armed to stellate appressed trichomes, becoming glabrous proximally; abaxially yellow stellate-tomentose, often also with various amounts of larger scattered gray, tawny, orange, or brown stiff stellate trichomes especially proximally, within 1 mm from the margin more sparsely pubescent, somewhat scarious, brown when dry; margin truncate, undulate, irregularly 2- or 3-lobed, or toothed, the teeth if present minute to 1 mm, deltoid to linear-deltoid, not contiguous. Corolla (0.8–)1.2–1.9 cm long, white or pink, tube 3–4 mm long, glabrous, lobes 4(5), (11–)12–18 × (4–)5–10 mm, obovate to obovate-elliptic, adaxially appressed-stellate-pubescent or nearly glabrous, abaxially densely pale yellow stellate-pubescent. Stamens 8 to 10; filaments 5–7 mm long, straight, distally attenuate, densely pubescent proximally, glabrous or sparsely stellate-pubescent distally, pubescence especially prevalent along the margin; anthers 3–5 mm long, wider than distal portion of filament; connectives glabrous. Style usually ± white stellate-pubescent throughout, occasionally subglabrous; stigma 0.2–0.5 mm wide, capitate. Fruit (1.0–)1.5–2 × (0.7–)1–1.5 cm, subglobose or ovoid, apex acute, occasionally short-rostrate, dehiscent; pericarp dry, 0.1–0.3(–0.6) mm thick, rarely up to 0.9 mm thick, outside at least

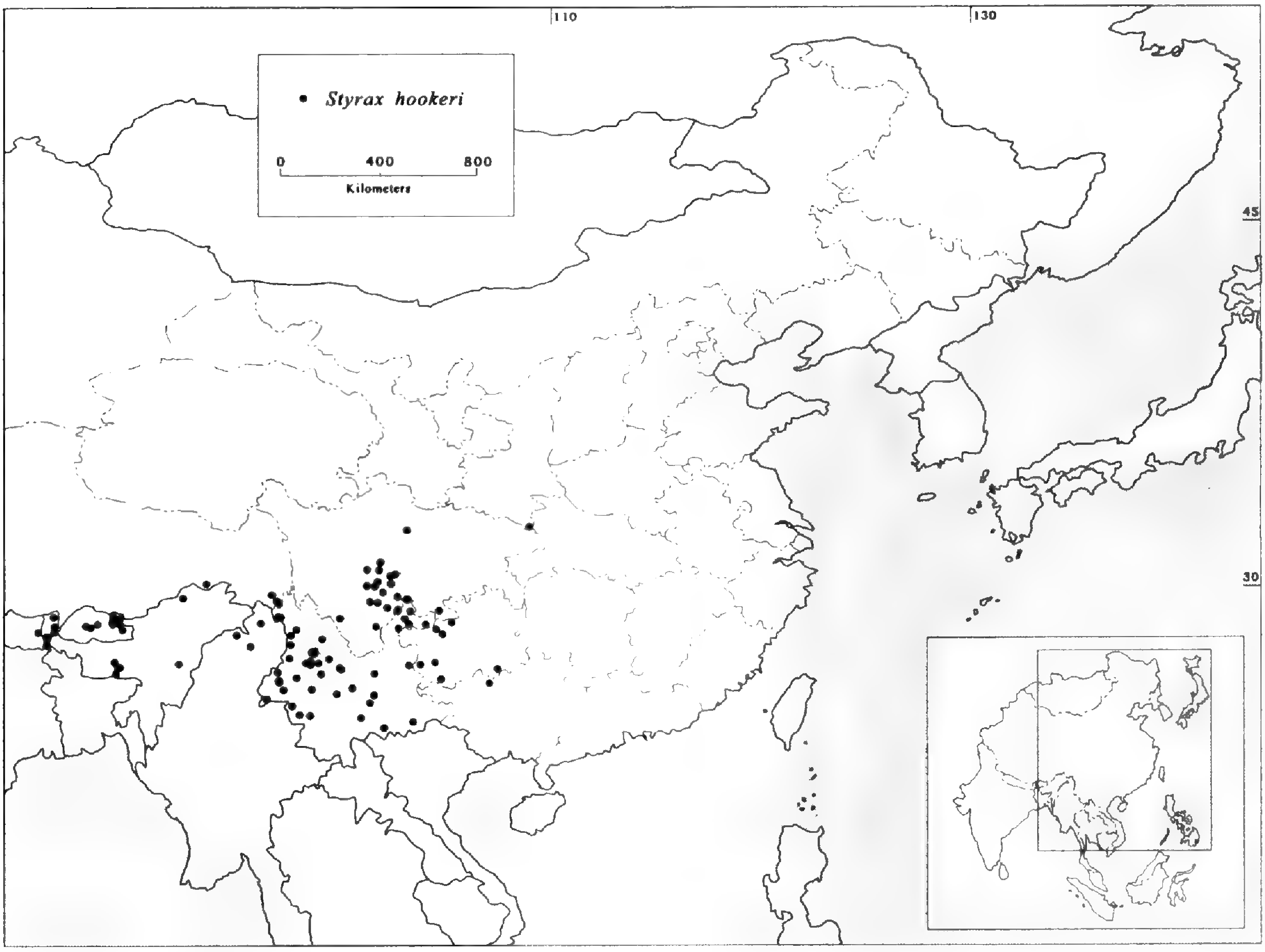

Figure 6. Geographic distribution of *Styrax hookeri*.

faintly longitudinally striate and ± rugose when dry, gray-yellow stellate-tomentose, inside glabrous. Seeds beige or brown, subglobose or ovoid, smooth, glabrous.

Illustrations. Anonymous, Ic. Cormophyt. Sin. 3: 337, fig. 4627 (as *S. roseus*). 1974; F. T. Tai & T. C. Pan in W. P. Fang, Fl. Sichuan. 1: 428, fig. 166. 1981 (as *S. roseus*); C. Y. Wu, Fl. Yunnan. 3: 424, pl. 120 (7–10). 1983 (as *S. perkinsiae*); ibid.: 433, pl. 124. 1983 (as *S. roseus* and *S. macranthus*); S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1607, fig. 802. 1985 (as *S. perkinsiae*); ibid.: 1621, fig. 814. 1985 (as *S. macranthus*); ibid.: 1622, fig. 815. 1985 (as *S. roseus*); T. L. Ming in C. Y. Wu, Fl. Xizang. 3: 869, fig. 335 (1–3). 1986; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 90, pl. 30 (6–9). 1987 (as *S. perkinsiae*); ibid.: 101, pl. 34 (6–10). 1987 (as *S. macranthus*); ibid.: 103, pl. 35 (1–6). 1987 (as *S. roseus*); W. Q. Yin in Y. C. Xu, Ic. Arbor. Yunnan. 2: 894, pl. 471 (7–12). 1990 (as *S. roseus*); D. G. Long in Grierson & D. G. Long, Fl. Bhutan 2(2): 577, fig. 58(e–g). 1999 (as *S. grandiflorus*); Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 199, fig. 199 (6–9). 2000 (as *S. perkinsiae*); ibid.: 203, fig. 203 (7–12). 2000 (as *S. macranthus*); ibid.: 204, pl. 204 (1–7). 2000 (as *S. roseus*).

Phenology. Flowering: March–September. Fruiting: April–November, January.

Distribution. Bhutan (Lhun Tshi, Tashigang, Tongsa, and Wangdi Phodrang), China (Guangxi, Guizhou, Sichuan, Xizang, and Yunnan), India (Arunachal Pradesh, Assam, Meghalaya, Nagaland, Sikkim, and West Bengal), Myanmar (Kachin State), and Nepal (Mechi); Figure 6.

Habitat. In a variety of open or semi-open wooded habitats and forest edges on mountain slopes; 730–3352 m.

Vernacular names. Da-rui-ye-mo-li (China, Sichuan; *Exp. E-shan 155*), Fen-hua-an-xi-xiang (Hwang, 1980), Fen-hua-ye-mo-li (SW China; Anonymous, 1974), Feng-chun-an-xi-xiang (Hwang, 1980), Lü-chun-an-xi-xiang (Hwang, 1987), Mai-mu (China, Sichuan; *Z. T. Guan 8448*), Mao-zhu-ye-mo-li (China, Yunnan; Wu, 1983), Qing-ye-dong-gua-shu (China, Guangxi; *S. Q. Chen 14376*), Rui-li-an-xi-xiang (Hwang, 1980), Rui-li-ye-mo-li (China, Yunnan; Anonymous, 1974), Shui-liang-zi (China, Sichuan; *Sichuan Economic Pl.*

Exp. 169), Trali Shing (Bhutan; *F. Ludlow et al. 18802*), Wa-shan-an-xi-xiang (Tai & Pan, 1981), Xi-shu-mai-mu (China, Sichuan; *Z. T. Guan 8197*), Yun-nan-ye-mol-li (China, Yunnan; Wu, 1983).

Styrax hookeri is a common and widespread species, occurring at relatively high elevations from eastern Nepal along the Himalayas through Assam, India, and extending into southwestern China. It is apparently most common in Yunnan Province.

Our treatment of *Styrax hookeri* differs from those of Perkins (1907) and Hwang (1987). We agree with Perkins (1907) that this species is not an extreme variant of *S. serrulatus*, as suggested by Clarke (1882). Perkins (1907) treated *S. hookeri* narrowly by simultaneously recognizing *S. caudatus* Perkins (Assam, India) and *S. macranthus* Perkins (southern and eastern Yunnan Province). Later, Perkins (1910) distinguished *S. hookeri* var. *yunnanensis* Perkins from the typical variety by its smaller and narrower leaves. This collection is geographically isolated (northeastern Yunnan Province) from variety *hookeri* sensu Perkins (Himalayas). Three new species of *Styrax* from the provinces of Yunnan and Sichuan (*S. perkinsiae* Rehder, *S. roseus* Dunn, and *S. shweliensis* W. W. Sm.) were subsequently described by various authors. Their types, along with that of *S. macranthus*, are centrally located between the apparently disjunct localities of *S. hookeri* sensu Perkins (i.e., its known range as of 1910). These species were delimited primarily by poorly defended features of the leaves, inflorescence, and calyx. Hwang (1987) considered *S. macranthus*, *S. perkinsiae*, and *S. roseus* to be separate species, and treated *S. shweliensis* as a synonym of *S. perkinsiae*. Because Hwang's treatment was in a regional flora of China, Hwang apparently did not examine collections of *S. hookeri* sensu Perkins from outside China. She may also not have had access to the type of *S. hookeri* var. *yunnanensis*, which she cited as a synonym of *S. grandiflorus* Griff. (= *S. japonicus*). *Styrax hookeri* var. *yunnanensis* has a shorter pedicel and a calyx with scattered orange stiff trichomes, among other features, that clearly distinguish it from *S. japonicus* and establish its placement within our concept of *S. hookeri*.

Access to many more collections than were available to either Perkins or Hwang has allowed us to reassess these high-elevation taxa. We interpret the highly overlapping range of morphological variation exhibited by this group as warranting only a single widely distributed species. Although trichome type and the amount of pubescence on various parts of the plants are diagnostic characters in the delimitation of some *Styrax* species, these features are highly variable in *S. hookeri*. The vestiture on the inner surface of the corolla lobes and the lower laminar surface consists of either long or short stellate trichomes, or else is lacking; that on the lower laminar surface can be sparse to dense. The styles are usually densely stellate-pubescent nearly throughout, at least proximally, but in some specimens from northeastern Yunnan Province and the Khasi Hills in Meghalaya, India, they are glabrous. Several other characters are also variable across the range of *S. hookeri* (e.g., leaf shape and size, flower and fruit size, petiole and pedicel length). We detect no gaps in character state variation, either associated with gaps in other characters or with geographic or ecophysiographic variables, for use in recognizing any of the synonyms of *S. hookeri*.

Although recognizing species segregates of *Styrax hookeri* is not warranted, there has clearly been some regional isolation among populations of this species resulting in geographically correlated (although not discontinuous) morphological trends. For example, individuals with the most densely pubescent abaxial leaf surfaces occur in western and central Yunnan Province, with consistently glabrous or sparsely pubescent populations to the west in the Himalayas. Some collections from the edge of the species' range exhibit slightly atypical features. The collections from the Khasi Hills (e.g., *C. B. Clarke 43631A*) have leaf margins with more numerous and prominent serrations than are typical in the species. This variation, however, also appears in other areas scattered throughout the species' range. Perhaps the most distinctive morphological variants within *S. hookeri* come from the provinces of Guangxi and Guizhou (e.g., *X. H. Song 272* and *907*, *C. Wang 41180*, *S. Q. Chen 14376*, and *Exp. Guizhou 6836*). These specimens have narrowly lance-elliptic, subcoriaceous leaves and/or relatively small fruits ca. 7 mm wide. We have opted against the formal recognition of these populations of *S. hookeri* at an infraspecific level because many specimens collected from areas scattered throughout the range of the species exhibit intermediacy in these characters.

Differences between *Styrax hookeri* and all sympatric imbricate-flowered species of *Styrax* are addressed in the discussions under *S. buchananii*, *S. hemsleyanus*, *S. limprichtii*, *S. odoratissimus*, and *S. rugosus*. Flowering individuals of *S. hookeri* with a pedicel length approaching that of *S. japonicus* can usually be distinguished by the presence of scattered orange or brown stiff long-stellate trichomes on the calyx. Fruiting individuals are more easily distinguished, because the pericarp of *S. hookeri* is usually thinner and at least faintly longitudinally striate (vs. irregularly rugose), and the seeds are smooth (vs. usually finely reticulate-fissured or irregularly rugose). Sterile specimens of *S. hookeri* can be distinguished from those of *S. japonicus* by a tendency toward elliptical leaves with acuminate to caudate apices and subparallel tertiary veins that are conspicuously raised only abaxially, versus a tendency toward subrhombic leaves with acute to slightly acuminate apices and narrowly reticulate tertiary veins that are conspicuously raised on both surfaces. These characters, however, exhibit some degree of overlap.

The closest putative relatives of *Styrax hookeri* (i.e., *S. limprichtii*, *S. rugosus*, and *S. wilsonii*) occur at relatively high elevations scattered throughout southwestern China and northern Myanmar. These species share with *S. hookeri* a typically subglobose or ovoid fruit rounded or apiculate at the apex and with usually at least a faintly longitudinally striate pericarp, seed surfaces that are smooth or irregularly rugose, and a calyx with usually various scattered orange or brown stiff stellate trichomes larger than those of the base tomentum. *Styrax hookeri* is easily distinguished from them, however, by the characters in couplet 14 of the key. The presence of abaxially glabrous or sparsely pubescent leaves and a densely pubescent style can often be used to distinguish *S. hookeri* from these species as well but are not as reliable.

According to the protologue, the type locality of *Styrax roseus* is Mt. Wu ("Wushan" in Pinyin) in Sichuan Province. Hwang (1987) interpreted this as Wushan Xian in eastern Sichuan, but the label on the type indicates that the locality is in western Sichuan. Rehder (1912) confirmed that the western Sichuan locality is correct by citing the type locality as Mt. Wa (a variant of Mt. Wu) in western Sichuan, also the type locality of *S. perkinsiae*.

The type material of *Styrax hookeri* at K consists of two sheets of *J. D. Hooker s.n.* from Sikkim, both of which possess flowering and fruiting branches. Individuals of *S. hookeri* flower and fruit at different times of the year within the same geographic region, indicating that these branches were collected on different dates. Thus, we interpret the material as consisting of four syntypes. This conclusion is supported by the writing "2 Styrax Sikkim" followed by Hooker's initials in his handwriting on each of the sheets, implying that there are two *Styrax* specimens on each sheet. There appears to be no basis for a decision regarding selection of the most appropriate specimen as the lectotype other than the condition of the material and the fact that one of the sheets possesses what is likely to be a field label in Hooker's handwriting. Thus, we have lectotypified on the largest branch with the most reproductive material on this sheet. In further support of our selection, this branch is also the largest and most floriferous of those on either sheet.

The holotype of *Styrax macranthus* at B is presumably destroyed. It is possible that Perkins only saw the specimen at B; none of the other sheets of *A. Henry 10644* that we have examined possess Perkins's annotation label, and no herbarium other than B is mentioned in either Perkins (1902) or Perkins (1907) to confirm Perkins's examination of additional material. On this basis, we have chosen the K specimen of *A. Henry 10644* as the lectotype, because Kew was the location of Henry's headquarters.

The holotype of *Styrax hookeri* var. *yunnanensis* at B is presumably destroyed. We have designated the specimen at P as the lectotype because it is the only duplicate specimen that we have seen, and it possesses Perkins's annotation.

The protologue of *Styrax perkinsiae* cites *E. H. Wilson 2576* as the type. There are two sheets of this number at A, but each has a different date. The word "holotype" is written on one of the sheets, but this is apparently not in Rehder's handwriting and it is not clear who wrote it. As such, these sheets must be considered syntypes. We have chosen the specimen that was collected in July 1908 as the lectotype because the material has more flowers for examination than the 17 September 1908 collection. Also, because the word "holotype" is written on this sheet, designating this sheet as the lectotype will avoid the risk of undue confusion.

Selected specimens examined. BHUTAN. **Lhun Tshi:** Dengchung, Khoma Chu, *F. Ludlow et al. 18802* (A, BM). **Tashigang:** Yonpu La, near Tashigong Dzong, *F. Ludlow et al. 12593* (BM, E). **Tongsa:** 1 km S of Tongsa, *A. J. C. Grierson & D. G. Long 1107* (E, K). **Wangdi Phodrang:** Mara Chu Valley, *F. Ludlow & G. Sherriff 3133* (BM, E). CHINA. **Guangxi:** Nandan Xian, *C. Wang 41180* (A, CAS, IBSC); Rongshui Miaozu Zizhixian, San-fang-xiang, Jiu-wan-da-shan, *S. Q. Chen 14376* (IBK, IBSC, KUN, PE). **Guizhou:** Anlong Xian, Long-shan-xiang, *Exp. Guizhou 4737* (KUN); Bijie Shi, Sheng-ji-xiang, *P. H. Yu 240* (KUN); Dafang Xian, Bai-na-qu, Jiu-long-shan, *Exp. Bi-jie 847* (PE); Libo Xian, Dong-ting, *X. H. Song 272* (K, MO); Panxian Tequ, Ba-da-shan, *Exp. An-shun 890* (KUN); Qinglong Xian, *Exp. S Guizhou 205* (KUN); Xingyi Shi, Ding-xiao-xiang, *Exp. Guizhou 6836* (IBSC, PE). **Sichuan:** Baoxing Xian, Er-lang-shan, Tuan-niu-ping, *Nan-shui-bei-diao-dui 1871* (PE); Ebian Yizu Zizhixian, *T. T. Yü 853* (A, IBSC, PE); Emeishan Shi, E-mei-shan, *G. H. Yang 55400* (IBSC, KUN, PE); Ganluo Xian, Hai-tang, *Sichuan Economic Pl. Exp. 4086* (KUN, PE); Hanyuan Xian, *Y. X. Zhao 511* (PE); Leibo Xian, Ma-hu-xiang, Tang-jia-shan, *Sichuan Economic Pl. Exp. 315* (KUN, PE); Mabian Yizu Zizhixian, Da-zhu-bao, Shan-mu-gang, *T. H. Tu 5494* (PE); Mao Xian, *S. K. Wu 840104* (KUN); Meigu Xian, Shu-dang-xiang, *Sichuan Economic*

Pl. Exp. 13556 (PE); Mianning Xian, from Guanling Xian to Muli Xian, *S. K. Wu 2204* (KUN); Muli Zangzu Zizhixian, from Guanling Xian to Muli Xian, *S. K. Wu 2203* (KUN, PE); Pingshan Xian, Wu-zhi-shan, *Q. S. Zhao 504* (PE); Puge Xian, You-jia-ping, *Z. T. Guan 8059* (PE); Shimian Xian, *C. C. Hsieh 39893* (IBSC, PE); Tianquan Xian, Er-lang-shan, *H. L. Tsiang 35129* (IBSC, PE); Xuyong Xian, Yi-shui-qu, *Sichuan Economic Pl. Exp. 351* (KUN); Yanyuan Xian, Ni-ba-shan, *Q. S. Zhao 309* (PE); Yuexi Xian, Bao-an, Da-long-tang, *Sichuan Economic Pl. Exp. 3813* (PE). **Xizang (Tibet):** Motuo Xian, Han-mi, Duo-xiong, Qu-lan, *B. S. Li & S. Z. Cheng 5062* (PE). **Yunnan:** Baoshan Shi, San-dao-qiao, *China-USSR team 6268* (IBSC, PE); Binchuan Xian, Ji-zhu-shan, *S. Y. Bao 4* (KUN); Daguan Xian, Lian-he, Tang-jia-shan, *B. S. Sun 676* (IBSC, KUN, PE); Dali Shi, He-yang, Cang-shan, *R. C. Ching 22673* (KUN, PE[2]); Eryuan Xian, N end of Cang-shan, *Sino-British Exp. Cang-shan 850* (A, E, K, KUN); Eshan Yizu Zizhixian, Huang-cao-ling, *Exp. E-shan 88155* (KUN); Fengqing Xian, Shun-ning, Wu-mu-lung, *T. T. Yü 16624* (A, E, KUN, PE); Fugong Xian, Fen-quan, *Exp. Qinghai & Xizang 7245* (KUN); Fumin Xian, Djiunienping, *H. F. Handel-Mazzetti 6119* (A, E); Fuyuan Xian, Shi-ba-lian-shan, Xiao-nao-chang, *Exp. Hong-shui-he 2356* (KUN); Gengma Daizu Wazu Zizhixian, Xi-shan, *China-USSR team 5570* (IBSC, PE); Gongshan Dulongzu Nuzu Zizhixian, from Gong-shan to Du-long, Da-ba-di, Gao-li-gong-shan, *P. Y. Mao 427* (KUN, PE); Jingdong Yizu Zizhixian, Feng-kua-shan, *M. K. Li 3493* (IBSC, KUN); Lanping Baizu Pumizu Zizhixian, Bing-zhong, Luo-he, *X. F. Deng 791361* (KUN); Lijiang Naxizu Zizhixian, Lichiang Range, *H. D. McLaren L100A* (BM); Longling Xian, Salwin-Kiukiang divide, *T. T. Yü 20294* (A, E, PE); Lüchun Xian, Feng-chun-ling, S of Red River, *A. Henry 10644* (A, BM, E[2], IBSC[2], K, MO, PE); Lushui Xian, from Ya-kou to Pian-ma, *S. K. Wu 8478* (KUN); Ruili Shi, Luckoag-Salween divide, *G. Forrest 18249* (A, E, K); Shuangbai Xian, Shuang-bai-si-qu, Bai-zhu-shan, *W. C. Yin 490* (IBSC, KUN[2], PE); Shuangjiang Lahuzu Wazu Bulangzu Daizu Zizhixian, Tai-ping-xiang, *J. S. Xing 832* (IBSC, KUN, PE); Suijiang Xian, Luo-han-ping, *B. S. Sun 359* (IBSC, PE); Tengchong Xian, Lang-ya-shan, *D. Y. Xia BG58* (KUN); Weishan Yizu Huizu Zizhixian, Wu-liang-shan, Menghwa, *Y. Tsiang 12204* (IBSC); Weixi Lisuzu Zizhixian, Wei-deng-xiang, *Exp. Qinghai & Xizang 6603* (KUN); Wenshan Xian, Lao-jun-shan, *K. M. Feng 22401* (IBSC, KUN); Yangbi Yizu Zizhixian, Shi-zhong-xiang, Shang-chang, *Sino-British Exp. Cang-shan 269* (A, E, K, KUN); Yanjin Xian, Cheng-feng-shan, *Exp. NE Yunnan (1970s) 1163* (KUN); Yao'an Xian, Tai-ping-xiang, *Y. Chen & B. Bai 562* (KUN); Yiliang Xian, Cao-tian-ma, *Exp. NE Yunnan (1970s) 568* (KUN, PE); Yongping Xian, betw. Sha-yang & Chu-tong, *G. Forrest 21112* (A, BM, E, K, PE[2], UC); Yongshan Xian, *H. T. Tsai 50936* (A, IBSC[2], KUN, PE); Yuanjiang Hanizu Yizu Daizu Zizhixian, Hou-shan, *Qin Lin 770497* (KUN); Yuxi Shi, Gao-lu-shan, *S. K. Wu 57* (KUN); Zhaotong Shi, Tang-lang-pa, *F. Ducloux 4951* (P); Zhenkang Xian, Snow Range, *T. T. Yü 17074* (A, E, KUN, PE); Zhenxiong Xian, Mo-dong, *X. W. Li 173* (IBSC). INDIA. **Arunachal Pradesh:** Pachakshiri Dist., Lalung, *F. Ludlow et al. 3713* (BM, E). **Assam:** *Dr. King's collector s.n.* (BM, L). **Meghalaya:** Khasi Hills, *J. D. Hooker & J. J. Hooker s.n.* (BM, C, E, K, L). **Nagaland:** Naga Hills, Kohima, *W. N. Koelz 25269* (L, UC). **Sikkim:** *J. D. Hooker s.n.* (BM, BR, C, K, L[2]). **West Bengal:** Takdah, Darjeeling, *H. Hara & M. Togashi 2141* (BM, K, KYO). MYANMAR. **Kachin State:** N Triangle (Camp III Tama Bum), *F. F. K. Ward 20990* (A, BM, E). NEPAL. **Mechi:** Salpa Dara, *J. D. A. Stainton 8332* (BM).

6. Styrax japonicus Siebold & Zucc., Fl. Jap. 1: 53. 1837–1838 [as *S. "japonicum"*]. *Cyrta japonica* (Siebold & Zucc.) Miers, Ann. Mag. Nat. Hist., ser. 3, 3: 279. 1859. TYPE: Japan. Kyushu: Kumamoto Pref., Simabara, *I. Keiske s.n.* (lectotype, designated here, L [accession no. 908240–682] not seen; digital image of lectotype!).

Styrax grandiflorus Griff., Not. Pl. Asiat. 4: 287. 1854 [as *S. "grandiflora"*]. TYPE: Myanmar [Sagaing Division] or India [Assam]: Naga Hills, Namtuzceh [Mar. 1837, protologue] and Nempea [19 Mar. 1837, protologue], *W. Griffith 3671* (Perkins, 1907) (holotype, K!; isotype, GH!).

Styrax japonicus var. *calycothrix* Gilg, Bot. Jahrb. Syst. 34 (Beibl. 75): 58. 1904. TYPE: China. Shandong: Qingdao Shi, Lao-shan, Aug. 1907, *O. Nebel s.n.* (holotype, B destroyed).

Styrax cavaleriei H. Lév., Repert. Spec. Nov. Regni Veg. 4: 331. 1907 [as *S. "Cavaleriei"*]. TYPE: China. Guizhou: Longli Xian, 7 May 1903, *J. Cavalerie 997* (holotype, E!; isotype, A!).

Styrax bodinieri H. Lév., Repert. Spec. Nov. Regni Veg. 4: 332. 1907 [as *S. "Bodinieri"*]. TYPE: China. Guizhou: Guiyang Shi, vicinity of Guiyang, Collège Mt., Apr. 1898, *E. Bodinier 2221* (holotype, E!; photo of holotype, A!).

Styrax duclouxii Perkins, Repert. Spec. Nov. Regni Veg. 8: 83. 1910 [as *S. "Duclouxii"*]. TYPE: China. Yunnan: Nanjian Yizu Zizhixian, near Lanngy Tsin, 20 Apr. 1904, *F. Ducloux 2716* (lectotype, designated here, P!).

Styrax touchanensis H. Lév., Repert. Spec. Nov. Regni Veg. 11: 64. 1912. TYPE: China. Guizhou: Dushan Xian, Apr. 1902, *E. Bodinier s.n.* (holotype, E!; isotypes, A!, E!).

Styrax kotoensis Hayata, Icon. Pl. Formos. 5: 121. 1915. *Styrax japonicus* var. *kotoensis* (Hayata) Masam. & Suzuki, Annual Rep. Taihoku Bot. Gard. 3: 65. 1933. TYPE: China. Taiwan: Taitung Xian, Kotosho [Lanyu Island], July 1912, *Y. Tashiro, T. Kawakami & S. Sasaki 44* [collection number not indicated in protologue] (holotype, TI!; isotype, IBSC!).

Styrax jippei-kawamurai Yanagita, J. Soc. Forest. 15: 693. 1933 [as *S. "Jippei-Kawamurai"*]. *Styrax japonicus* var. *jippei-kawamurai* (Yanagita) H. Hara, Enum. Sperm. Jap. 1: 111. 1948 [as *S. "japonicus* var. *Jippei-Kawamurai"*]. *Styrax japonicus* f. *jippei-kawamurai* (Yanagita) T. Yamazaki, Fl. Japan 3a: 104. 1993 [as *S. "japonicus* f. *jippei-kawakamii"*]. TYPE: Japan. Honshu: Shizuoka Pref., O Shima Island, Jan. 1930, *J. Kawamura s.n.* (type material missing).

Styrax japonicus var. *iriomotensis* Masam., Trans. Nat. Hist. Soc. Taiwan 25: 250. 1935. TYPE: Japan. Ryukyu Islands: Okinawa Pref., Iriomote, Oct. 1923, *Ipse s.n.* (holotype, TAI not seen).

Styrax philippinensis Merr. & Quisumb., Philipp. J. Sci. 56: 313. 1935. TYPE: Philippines. Babuyan: Camiguin Island, Mt. Malabsing, 9 Mar. 1930, *G. E. Edaño 79248* (holotype, NY not seen; isotype, L!).

Styrax japonicus var. *zigzag* Koidz., Acta Phytotax. Geobot. 6: 212. 1937. TYPE: Japan. Honshu: Iwate Pref., Rikuchiu, Higashiiwaigun, Ohtsuhomura, *G. Toba s.n.* (holotype, KYO not seen).

Styrax japonicus f. *parviflorus* Y. Kimura, J. Jap. Bot. 16: 59. 1940 [as *S. "japonica* f. *parviflora"*]. TYPE: Japan. Kyushu: Fukuoka Pref., Buzen, Tikuzyô-gun, Iwaya-mura, 30 May 1937, *S. Yosioka 23* (holotype, TI!).

Styrax japonicus var. *angustifolius* Koidz., Acta Phytotax. Geobot. 10: 55. 1941 [as *S. "japonicum* var. *angustifolia"*]. TYPE: Japan. Honshu: Wakayama Pref., Kii, Koyasan, 1 June 1940, *G. Koidzumi s.n.* (holotype, KYO!; isotype, KYO!).

Styrax japonicus var. *tomentosus* Hatus., J. Jap. Bot. 29: 230. 1954 [as *S. "japonicum* var. *tomentosum"*]. *Styrax japonicus* f. *tomentosus* (Hatusima) T. Yamazaki, Fl. Japan 3a: 104. 1993. TYPE: Japan. Ryukyu Islands: Kagoshima Pref., Tokara Islands Group, Nakanoshima Island, Apr. 1936 and 18 Aug. 1933 [1934 from protologue], *T. Naito s.n.* (holotype, FU not seen; photo of holotype, TI!).

Styrax japonicus f. *rubicalyx* Satomi, J. Geobot. 6: 110. 1957. TYPE: Japan. Honshu: Ishikawa Pref., Kaga, Yokotani-pass, Asakawa-mura, Kahoku-gun, 20 July 1952, *N. Satomi s.n.* (holotype, KANA not seen).

Styrax japonicus var. *longipedunculatus* Z. Y. Zhang, Fl. Tsinlingensis 1(4): 395. 1983 [as *S. "japonica* var. *longipedunculata"*]. TYPE: China. Gansu: Wen Xian, Bi-kou-zhen, Bi-shan-gou, Quai-miao, 750 m, 31 Aug. 1967, *C. L. Tang 1739* (holotype, HW not seen).

Styrax japonicus var. *nervillosus* Z. Y. Zhang, Fl. Tsinlingensis 1(4): 395. 1983 [as *S. "japonica* var. *nervillosa"*]. TYPE: China. Shaanxi: Shiquan Xian, Gangtie-gong-she, Lu-jia-gou, 1010 m, 21 June 1959, *J. Q. Xing 9028* (holotype, HW not seen; isotype, IBK!).

Styrax japonicus f. *pendulus* T. Yamazaki, Fl. Japan 3a: 104. 1993. TYPE: Japan. Honshu: Tokyo Pref., Tokyo, cultivated, 18 Sep. 1991, *T. Yamazaki s.n.* (holotype, TI not seen).

Shrubs or trees to 8(–10) m tall. Young twigs brown, sparsely gray-yellow or pale yellow stellate-pubescent; older twigs gray or nigrescent, glabrescent. Petiole (2–)4–7(–10) mm long. Two most proximal leaves on each shoot (when both present) subopposite to opposite. Lamina 3–11 × 2–5(–7) cm, chartaceous to thick-chartaceous, oblong-elliptic, ovate-elliptic, ovate to ovate-lanceolate, or subrhombic; apex acute to slightly acuminate; base cuneate to broadly cuneate or subrounded, often decurrent into petiole; adaxially sparsely stellate-pubescent when young, especially prevalent on veins, glabrescent; abaxially glabrous except along the vein and the axils of the secondary veins; margin entire to apically remotely serrate; secondary veins 5 to 8 on each side of the midvein, tertiary veins reticulate, conspicuously raised on both surfaces. Fertile shoots 2–9 cm long, 1- to 4-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- or 2-flowered; pseudoterminal inflorescences 2-flowered or racemose, 1–4 cm long, 2- to 5-flowered; rachis glabrous or pubescent. Pedicels (10–)15–50 mm long, the longer pedicels on each twig $\geq$ 15 mm long, usually equal to or longer than subtended flower, slender, glabrous or stellate-pubescent; bracteoles 3–5 mm long, linear or subulate, usually positioned at the base of pedicels, sometimes those toward the base of the inflorescence leaf-like. Flowers (1.2–)1.5–2.5(–3) cm long. Calyx 4–7 × 3–5 mm, cupuliform to funnelform; adaxially glabrous; abaxially glabrous or sparsely to densely white or gray-yellow stellate-pubescent, if stellate trichomes present, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry; margin with 5 irregularly spaced triangular-ovate teeth 0.5–1 mm long or sometimes less, not contiguous. Corolla (0.8–)1.0–1.6(–2.3) cm long, white, occasionally pink, tube 3–5 mm long, glabrous, lobes 5 or 6, 11–20 × (3–)5–7(–9) mm, ovate, oblong-ovate, obovate, or ovate-lanceolate, apex obtuse, densely appressed-stellate-pubescent on both sides, sometimes sparsely pubescent adaxially. Stamens 10 to 12; filaments 5–6 mm long, straight, slightly broadened proximally and white-villous, distally attenuate and glabrous; anthers 4–5(–10) mm long, wider than distal portion of filament; connective glabrous. Style proximally white stellate-pubescent, distally glabrous; stigma 0.2–0.4 mm wide, punctiform. Fruit 0.8–1.5 × 0.8–1 cm, ovoid or ellipsoid, apex apiculate, usually dehiscent by 3 valves from the base; pericarp dry, 0.4–1.0 mm thick, dry, outside coarsely and irregularly rugose when dry, gray or gray-yellow stellate-tomentose, inside glabrous. Seeds brown, ellipsoid, smooth or finely reticulate-fissured to irregularly rugose, glabrous.

Selected illustrations. Siebold & Zucc., Fl. Jap. 1: t. 23. 1835; Griff., Ic. Pl. Asiat. 4: t. 423. 1854 (as *S. grandiflorus*); Regel, Gartenfl. 17: t. 583. 1868; Hook. f., Bot. Mag. 98: t. 5950. 1872 (as *S. serrulatus* Roxb.); Gard. Chron. ser. 2, 24: fig. 166. 1885; Gartenflora 36: fig. 89. 1887; Dippel, Handb. Laubholzkunde 1: fig. 207. 1889; Gard. Chron. ser. 3, 65: 279, fig. 140. 1919; Addisonia 7: t. 231. 1922; Merr. & Quisumb., Philipp. J. Sci. 56: 316, pl. 1. 1935 (as *S. philippinensis*); W. P. Fang, Ic. Pl. Omei. 1(1): t. 48. 1942; Anonymous, Ic. Cormophyt. Sin. 3: 336, fig. 4625. 1974; F. T. Tai & T. C. Pan in W. P. Fang, Fl. Sichuan. 1: 424, fig. 164. 1981; C. Y. Wu, Fl. Yunnan. 3: 428, pl. 122 (1–10). 1983 (7–10 as *S. grandiflorus*); L. Yang in Y. K. Li, Fl. Guizhou. 2: 541, fig. 231. 1984 (including *S. japonicus* var. *calycothrix*); S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1614, fig. 808.

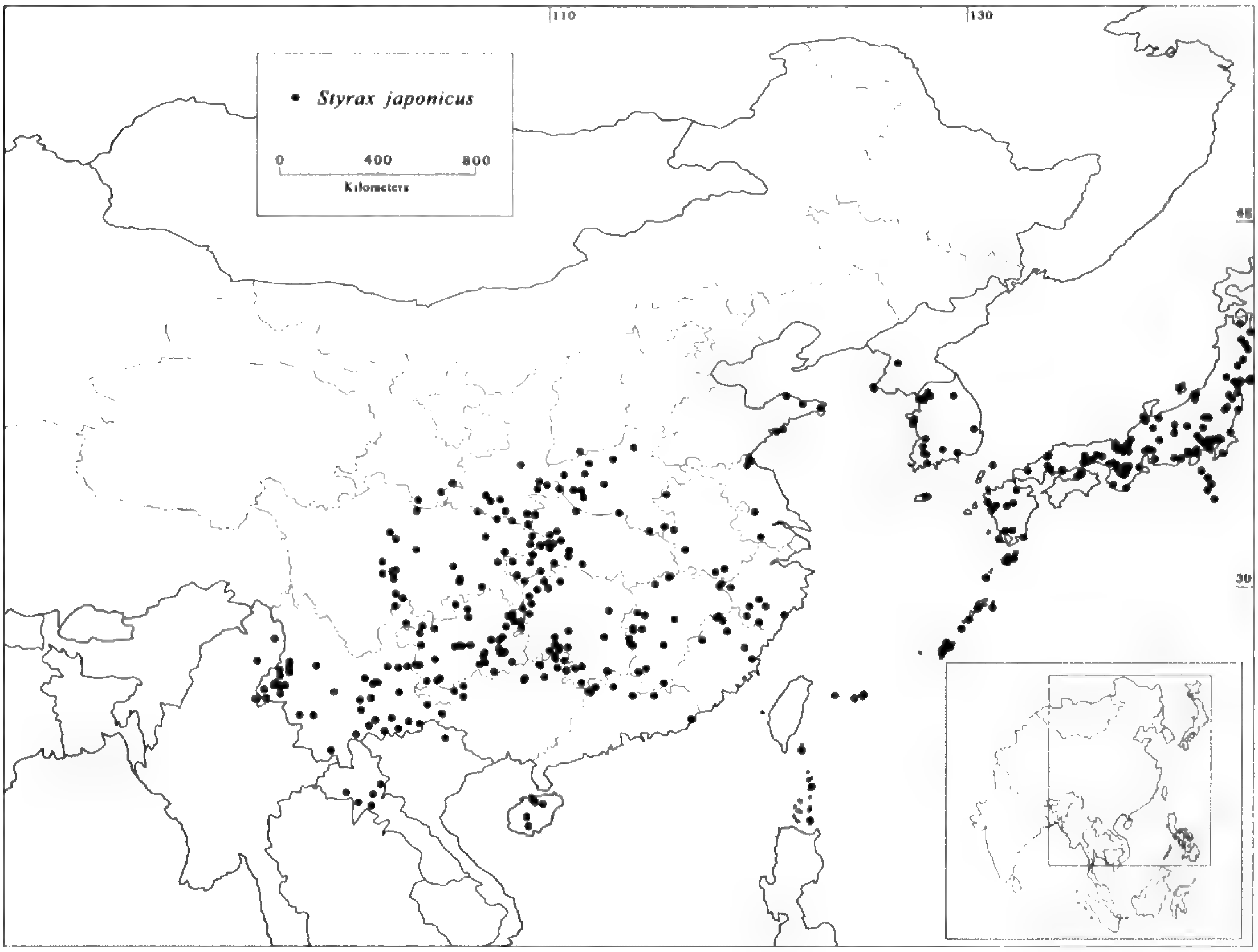

Figure 7. Geographic distribution of *Styrax japonicus.*

1985; ibid.: 1616, fig. 809. 1985 (as *S. grandiflorus*); S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 93, pl. 31. 1987 (1–11; 8–11 as *S. grandiflorus*); S. M. Hwang in F. H. Chen, Fl. Guangdong 1: 387, fig. 419. 1987; ibid.: 387, fig. 420. 1987 (as *S. grandiflorus*); J. Q. Liu in L. G. Lin, Fl. Fujian. 4: 351, fig. 284. 1989; X. M. Liu in X. H. Qian, Fl. Anhui 4: 65, fig. 1769. 1991; S. Y. Wang in B. Z. Ding, Fl. Henan 3: 230, fig. 1775 (1–4). 1997; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 200, fig. 200 (1–11). 2000 (8–11 as *S. grandiflorus*).

Phenology. Flowering: January–October, December. Fruiting: February–November.

Distribution. China (Anhui, Fujian, Gansu, Guangdong, Guangxi, Guizhou, Hainan, Henan, Hubei, Hunan, Jiangsu, Jiangxi, Shaanxi, Shandong, Shanxi, Sichuan, Taiwan, Yunnan, and Zhejiang), Japan (Honshu, Kyushu, Ryukyu Islands, and Shikoku), Laos (Houaphan and Xiangkhoang), Myanmar (Kachin State), North Korea (Pyongyang City), Philippines (Babuyan Islands and Batan Islands), South Korea (Cheju, Inchon City, Kangwon, Kyonggi, North Cholla, North Kyongsang, Seoul City, South Cholla, South Chungchong, and South Kyongsang), and Vietnam (Cao Bang); Figure 7.

Habitat. In a variety of open wooded habitats, in woodlands and forest edges, successional habitats, rarely in dense shade, mostly in mesic microhabitats, such as canyons, draws, ravines, and other riparian situations; 3–2700 m.

Vernacular names. Benigaku-egonoki (Japan; Satomi, 1957), Chun-shu (China, Sichuan; *Sichuan Economic Pl. Exp. 12*), Da-hua-an-xi-xiang (Hwang, 1980), Da-hua-ye-mo-li (Anonymous, 1974), Diao-gong-zai (China, Guangxi; *Z. F. Hunag 15*), Egonoki (Japan; *Shigetaka Suzuki AA1108*), Er-wan-tao (China, Guangdong; *X. Q. Liu 24221*), Ganboku-egonoki (Japan; Koidzumi, 1937), Gou-bi-zi-shu (China, Hunan; *L. H. Liu 1877*), Gou-luan-zi (China, Zhejiang; *Zhejiang Bot. Res. Team 26071*), Hei-Cha-hua (China, Sichuan; Tai & Pan, 1981), Hime-egonoki (Japan; Anonymous, 1940), Hosoba-yegonoki (Japan; Koidzumi, 1941), Hou-feng-teng (Hwang & Qi, 1985), Hui-lu-tui (China, Henan; *collector unknown 334*), Jun-qian-zi (China, Shaanxi; *P. C. Kuo 2180*), Kôtô-egonoki (Japan; Masamune & Suzuki, 1933), Lai-xiang-mei (China, Hunan; *P. C. Tam 63659*), Lan-yu-an-xi-xiang (Li, 1978), Lan-yu-ye-mo-li (Li, 1978), Li-jia (China, Hunan; *P. C. Tam 62899*), Ling-dang-hua (China, Guizhou; *R. B. Jiang 521*), Mao-e-ye-mo-li (Anonymous, 1974), Mo-li-bao (China, Guizhou; *P. C. Tsoong 1032*), Mu-jie-zi (China, Hubei; Hwang & Qi, 1985), Mu-xin-zi (China, Sichuan; *Z. R. Zhang 25145*), Ni-chi-yang (China, Jiangxi; *Jiangxi Normal Univ. 1243*), Padong mao (Laos; *A. F. G. Kerr 20941*), Ru-xiang-shu (China, Yunnan; *Y. Y. Hu 580582*), Sa-ye-shu (China, Hunan; *P. C. Tam 61328*), Sei-ton-kwa (Japan; Siebold, 1835–1841), Shui-dong-gua (China, Guangxi; *Q. H. Lu 2441*), Tsisjano-ki (Japan; Siebold, 1835–1841), Ttaejuk namu (South Korea; *B. R. Yinger et al. 2525*), Yang-huai-zi (China, Yunnan; *L. S. Xie & M. Cai 440*), Yang-jiao-shu (China, Sichuan; *H. F. Zhou 11150*), Yao-bai-he (China, Shaanxi; *J. Q. Xing 9018*), Ye-hua-bei (Hwang, 1987), Ye-mo-li (China, Guizhou; *K. M. Lan 351*), Ye-ping-guo (China, Hubei; *K. R. Liu 142*), Ye-wu-wei-zi-shu (China, Guangxi; *Z. F. Hunag 19*), Ye-xun-zi (China, Henan; *P. C. Kuo 3945*), Zhuang-shu (China, Sichuan; Tai & Pan, 1981).

Probably the most common species of *Styrax* in Asia, *S. japonicus* occurs from Japan to Myanmar south to Vietnam and Laos, with a few outliers in the far northern Philippines and the islands of Lanyu and Hainan, China.

Styrax japonicus is distinguished from all other species of *Styrax* by pedicels that are usually greater than 1.5 cm long (vs. ≤ 1.3 cm long) and equal to or longer (vs. shorter) than the subtended flower. Populations on Hainan Island and in several localities in Yunnan Province, China, have the shortest pedicels (as short as 10 mm, although pedicels on specimens from these areas can be found that are at least 15 mm). Also, some specimens of *S. hookeri* in Yunnan Province have unusually long pedicels that approach the length of the shortest pedicels of *S. japonicus*.

This species is highly variable across its range. The pubescence on the calyx consists of a sparse to dense layer of stellate trichomes, or is absent. Like other widespread species of *Styrax* on other continents (e.g., *S. americanus*, *S. glabrescens*, *S. sieberi* Perkins), *S. japonicus* exhibits variation in the size and shape of the flowers, fruits, and especially leaves. Consequently, many varieties and forms of this species have been recognized. Our study, however, does not reveal consistent combinations of characters for use in delimiting infraspecific taxa in *S. japonicus*. For example, the type of *S. japonicus* f. *parviflorus* Y. Kimura has extremely small flowers and leaves, but collections with one or both of these features have also been collected in Yunnan Province (e.g., *H. T. Tsai 55793*). Such a pattern suggests that this extreme represents a sporadic variant rather than a taxonomically significant geographic entity. Other populations in the Ryukyu Islands and Honshu Island, Japan, and Lanyu Island, China, have flowers and leaves that are larger than is typical for the species. These populations have been recognized in some works as varieties *kotoensis* (Hayata) Masam. & Suzuki, *jippei-kawamurai* (Yanagita) H. Hara, and *iriomotensis* Masam. Although the presence of a relatively high percentage of individuals with these features in insular East Asia might prompt the question of why such a pattern exists, the individuals themselves merely possess extremes of completely continuous characters that can be found in other parts of Asia. We therefore do not formally recognize such plants.

Perkins (1907) and Hwang (1987) maintained *Styrax grandiflorus* as a species distinct from *S. japonicus* by its densely pubescent pedicel and calyx and apparently its general range, extending farther south than *S. japonicus*. The leaves of *S. grandiflorus* also tend to be elliptic (vs. subrhombic) with an acute (vs. slightly acuminate) apex, but these features are apparently only weakly correlated with pedicel and calyx pubescence from south to north. Several specimens from Japan, Korea, and Shandong Province, China, possess a densely pubescent calyx, whereas specimens with glabrous pedicels occur sporadically throughout southern China (e.g., Yunnan Province and Hainan Island). Furthermore, many collections exhibit an intermediate amount of pubescence. The pubescent phase also exhibits no obvious elevation or habit distinctions and seems to occur sporadically, often near collection localities of the glabrous phase. A similar pattern of variation in pubescence density unaccompanied by geographic or ecological separation occurs in *S. hemsleyanus* and *S. hookeri*, and those species have not been subdivided in this revision. For the same reason, we have subsumed *S. grandiflorus* under *S. japonicus*.

The distribution of *Styrax japonicus* exhibits some notable patterns. No specimens from mainland China have been collected south of the Nanling Mountains, which extend along the northern border of Guangxi and Guangdong Provinces, but the species has been collected south of the mainland on Hainan Island. Long-distance dispersal is not likely as an explanation for this distribution because the fruit of *S. japonicus* appears not to possess high vagility (Fritsch, 1999). A more likely explanation is that intervening populations have gone extinct due to habitat changes (vicariance).

Hainan was connected with mainland China until the early Quaternary (Chang, 1962), and insofar as Hainan Island is considered part of the Guangdong floristic region (Chang, 1962), the appearance of the Qiongzhou Strait separating Hainan Island from the mainland seems not to have had a major influence on the flora of Hainan. It is also possible that populations have become extirpated through human disturbance.

The disjunct distribution of *Styrax japonicus* between Lanyu Island (Taiwan) and the Philippines is paralleled in about 110 other flowering plant species, suggesting that land connections between the two islands are likely to have existed previously (Chang, 1994). The flora of Lanyu Island appears to have greater similarity to the flora of the Philippines than to Taiwan in that 46 genera not appearing on Taiwan are shared by Lanyu and the Philippines (Chang, 1994). The Taiwan Strait may have first appeared in the late Mesozoic, after which Taiwan contacted Mainland China several times (Chang, 1994). Although the floras of Taiwan and the mainland share many species, Taiwan does possess some distinctive floristic characteristics. The absence of *S. japonicus* from Taiwan suggests that the evolution of *Styrax* has proceeded in isolation on this island. *Styrax japonicus* is very similar to the Taiwanese endemic species *S. formosanus*, differing mainly by imbricate (vs. valvate) corolla aestivation and a slightly longer pedicel. Phylogenetic analysis of DNA sequences of the ITS region (Fritsch, 2001) strongly suggests that *S. japonicus* and *S. formosanus* are sister species. Thus, it appears that *S. formosanus* on Taiwan has speciated from *S. japonicus* ancestral stock and that the imbricate-flowered species of *Styrax* do not constitute a clade (see Taxonomic History and Present Objectives).

The locality of *W. Griffith 3671* (the type of *Styrax grandiflorus*) is in the Naga Hills, either in the Sagaing Division of Myanmar or Nagaland, India. We could not determine the geographic coordinates of the specific localities mentioned in the protologue of this species ("Nempea" and "Namtuzceh") with sufficient precision to map them. The collection appears to represent the westernmost locality of *S. japonicus* known.

No specimens were cited in the protologue of *Styrax japonicus*. New species in volume 1 of *Flora Japonica* were described by J. G. Zuccarini based on data supplied by von Siebold. The only material that we have seen from the von Siebold herbarium consists of on-line images of two L collections from a database of the von Siebold collections maintained by the National Herbarium Nederland (<http://www.nationaalherbarium.nl>). We chose *I. Keiske s.n.*, accession number 908240-682, as the lectotype because it has better flowering material than *I. Keiske 64* (accession number 908240-688). Furthermore, the *I. Keiske s.n.* collection bears insect galls of the same general type as those that appear on the illustration accompanying the protologue, whereas *I. Keiske 64* does not possess galls.

The type material of *Styrax jippei-kawamurai* Yanagita (*J. Kawamura s.n.*) is missing. Yanagita worked at the National Forestry Agency in Tokyo, the herbarium of which is now part of the herbarium of the Tama Forest Museum, Tokyo. None of Yanagita's specimens can be found in this herbarium or are known elsewhere (H. Ohba, TI, pers. comm.).

Selected specimens examined. CHINA. **Anhui:** Huangshan Shi, Huang-shan-qu, Huang-shan, *M. P. Deng & K. Yao 79022* (A); Jinzhai Xian, Bai-ma-zhai, Guan-cai-gou, *K. Yao 8965* (A, CAS, K, MO); Qimen Xian, Mao-peng-dian, *Z. W. Xue 830187* (IBSC); Yuexi Xian, Yao-luo-ping, *Z. W. Xie & L. Zheng 97133* (CAS). **Fujian:** Chong'an Xian, Xin-chun-xiang, *Exp. Wu-yi-shan 912* (PE); Fuzhou Shi, Gu-shan, Bai-yun-dong, *L. G. Lin 48* (CAS); Gutian Xian, *L. G. Lin 1406* (PE); Taining Xian, Xin-qiao-xiang, *G. L. Cai 464* (IBSC, KUN). **Gansu:** Hui Xian, Fan-ba, *Z. B. Wang 19392* (KUN); Kang Xian, Yang-ba-xiang, from Nao-hui-ba to Yang-ba, *Z. Y. Zhang 16760* (PE); Wen Xian, Xiao-wan-li, Bi-feng-gou, Bi-kou, *X. Wang 98* (MO). **Guangdong:** Heping Xian, *G. C. Zhang 35* (IBSC); Liannan Yaozu Zizhixian, Jin-keng-xiang, *P. C. Tam 59492* (IBSC, KUN, PE); Lianshan Zhuangzu Yaozu Zizhixian, *P. C. Tam 58283* (KUN); Ruyuan Yaozu Zizhixian, Xi-shan-xiang, Ba-bao-shan, *C. Wang 44043* (IBSC, KUN, MO, PE); Shantou Shi, Wu-king-fu, 1906, *J. M. Dalziel s.n.* (E); Wengyuan Xian, Long-xian, *X. Q. Liu 24221* (IBSC). **Guangxi:** Guanyang Xian, Dou-yan-lin, *Z. Z. Chen 52458* (IBK, IBSC, KUN); Leye Xian, Niu-wei, Ba-wang-shan, *Exp. Hong-shui-he 89–1109* (KUN); Lingui Xian, Huang-sha-xiang, *Z. Z. Chen 50983* (IBK, IBSC, KUN[2]); Lingyun Xian, Loe-hoh-tsuen, *A. N. Steward & H. C. Cheo 415* (A, BM); Longsheng Gezu Zizhixian, San-men-xiang, *D. A. Huang 60211* (IBK, IBSC); Rongshui Miaozu Zizhixian, Luo-dong-xiang, Jiu-wan-da-shan, *S. Q. Chen 14442* (IBK, IBSC, KUN, PE); Xing'an Xian, Liang-jin-kuang-xiang, Mao-er-shan, *Z. Z. Chen 51257* (IBK, IBSC, KUN); Ziyuan Xian, Shuen-yuen, *T. S. Tsoong 81668* (A). **Guizhou:** Anlong Xian, Long-shan-xiang, *Exp. Guizhou 4481* (KUN, PE); Bijie Shi, Bao-he-xiang, *P. H. Yu 331* (KUN, PE); Dushan Xian, Shui-li-guang-li-qu, *Exp. Li-bo 1115* (KUN); Duyun Shi, Yun-fou-shan, Tuyun, *Y. Tsiang 5930* (IBSC[3], PE); Guiyang Shi, Qian-ling-shan, *Z. Y. Cao 191* (PE); Hezhang Xian, Shui-kuang forest farm, *R. B. Jiang 521* (IBSC); Huangping Xian, Wu-xi, *Exp. S Guizhou 2745* (KUN); Jiangkou Xian, Tai-ping River above confluence with Hei-wan River, SE side of Fan-jing-shan, *Sino-Amer. Guizhou Bot. Exp. 274* (A, BR, CAS, PE); Kaili Shi, Xi-jiang-xiang, Lei-gong-ping, *Exp. S Guizhou 2102* (KUN, PE); Leishan Xian, *Z. P. Jian 51245* (KUN); Libo Xian, Jie-na, *X. H. Song 558* (K, MO); Longli Xian, *J. Cavalerie 997* (A[2], E); Nayong Xian, Ju-ren-qu, *Exp. Bi-jie 358* (KUN, PE); Panxian Tequ, *P. C. Tsoong 1740* (PE); Ping-tang Xian, *Exp. S Guizhou 2745* (PE); Pu'an Xian, Qingshan-xiang, *Exp. An-shun 1353* (KUN, PE); Qingzhen Shi, Yun-gui-shan, Zhu-sha-dong, *Exp. Sichuan & Guizhou 1860* (PE); Rongjiang Xian, Yue-liang-shan, *Exp. S Guizhou 2902* (PE); Shibing Xian, Ma-xi, Zhu-ye-cun, *Exp. Wu-ling-shan 2598* (KUN); Shiqian Xian, Fu-yan, Mai-zi-cao, *Exp. Wu-ling-shan 1989* (KUN); Shuicheng Xian, *P. C. Tsoong 1786* (PE); Songtao Miaozu Zizhixian, Gao-diao-xiang, Huang-tang-ping, *Exp. Wu-ling-shan 616* (KUN); Tongren Shi, Ta-ho-yen, Fan-jing-shan, *A. N. Steward et al. 352* (A, BM, E, K, PE[2]); Tongzi Xian, Tien-chu-tze, Tungtze, *Y. Tsiang 5004* (PE); Weng'an Xian, Yong-he-xiang, *Exp. Li-bo 2240* (KUN); Xingyi Shi, Ba-ling-xiang, *Exp. Guizhou 7361* (IBK, PE); Xishui Xian, Guan-du-qu, *Exp. Bi-jie 1491* (PE); Yinjiang Tujiazu Miaozu Zizhixian, Su-jia-po, Xiao-jia-he, *Z. P. Jian 31437* (PE); Zhenning Buyizu Miaozu Zizhixian, Tschenning-Huang-tsauba-Yunnan, *H. F. Handel-Mazzetti 10310* (A, C, E); Zunyi Shi, Liang Feng Yah, *A. N. Steward et al. 137* (A, BM, E, L, PE). **Hainan:** Baisha Lizu Zizhixian, Yuan-men, *Exp. Hainan 711* (IBSC[2]); Chengmai Xian, Bai-shi-ling, Gu-dong-cun, *C. I. Lei 376* (A, IBSC[2], PE[2], UC); Qiongzhong Lizu Miaozu Zizhixian, Hong-mao-shan, *W. T. Tsang & H. Fung 491* (BM, IBSC, PE). **Henan:** Baofeng Xian, *Pu-cha-biao-ben 18727* (PE); Lushi Xian, from Da-quai-di to Qi-he, *J. Q. Fu 2210* (KUN); Neixiang Xian, Bao-tian-man Nature Reserve, Da-hong-si River, *D. E. Boufford et al. 26287* (AAU, E); Shangcheng Xian, *Pu-cha-biao-ben 10363* (PE); Song Xian, Hong-luo-he, *K. J. Guan et al. 1905* (PE[2]); Tongbai Xian, Fu-niu-shan, *Henan Forestry Dept. 59* (PE); Weihui Shi, Long-chi, *Pu-cha-biao-ben 34393* (PE); Xin Xian, Wu-ma, *Pu-cha-biao-ben 8269* (PE); Xingyang Shi, Ji-gong-shan, *China-USSR team 346* (PE); Xixia Xian, Tai-ping-zhen, *K. J. Guan et al. 1405* (PE[2]); Yiyang Xian, *Pu-cha-biao-ben 6239* (PE). **Hubei:** Badong Xian, *A. Henry 1430* (K); Baokang Xian, *E. H. Wilson 2134* (K); Changyang Tujiazu Zizhixian, Huo-jia-ping, *T. P. Wang 11375* (PE); Enshi Shi, He-wan-chang, *L. Y. Dai & C. H. Qian 616* (PE); Hefeng Xian, *H. J. Li 5516* (KUN); Jianshi Xian, Hua-guo-ping, *W. B. Lin 70* (PE); Lichuan Shi, Shui-shan-ba, Yang-he-xiang, *W. C. Cheng & C. T. Hwa 559* (A, PE, UC); Shennongjia Linqu, Shen-nong-jia Forest Dist., NE of Guan-men-shan along the S side of the Shi-cao River, *Sino-Amer. Bot. Exp. (1980) 763* (A, E, KUN, UC); Songzi Xian, Mo-pan-zhou, *Père C. Silvestri 17704* (A); Wufeng Tujiazu Zizhixian, *H. J. Li 6802* (KUN, PE); Xianfeng Xian, Qing-shui-kuang-qu, *W. B. Lin 575* (PE); Xingshan Xian, Yan-tang-ping, Hing-shan, *H. J. Li 1064* (PE); Yichang Shi, Nan-T'O, *A. Henry 3926* (K); Yun Xian, Wu-dang-shan, *K. R. Liu 142* (PE); Zhuxi Xian, *K. M. Liou 8776* (PE); Zigui Xian, *H. J. Li 318* (PE). **Hunan:** Baojing Xian, *X. L. Yu 91440* (KUN); Changsha Shi, *collector unknown 27495* (PE); Chengbu Miaozu Zizhixian, Jin-tong-shan, *Q. Z. Lin 11145* (IBSC); Cili Xian, Suo-xi-luo Nature Reserve, *Exp. W Hunan 1087* (PE); Dao Xian, Lan-zhu-ping, *P. C. Tam 61328* (IBK, IBSC); Dayong Xian, Zhang-jia-ba, *Z. H. Shen 1577* (IBSC); Dongkou Xian, *X. D. Yun 104* (IBSC); Fenghuang Xian, Yong-shui, *Exp. Hunan 614* (PE); Hengshan Xian, Guang-ji-shi, *P. C. Tam 63944* (IBK, IBSC); Jianghua Yaozu Zizhixian, He-luo-kou-xiang, *B. G. Li 5149* (PE); Longshan Xian, Wu-ya-xiang, *L. H. Liu 1877* (KUN); Ningyuan Xian, Jiu-wan-shan, *P. C. Tam 61690* (IBK); Sangzhi Xian, Ba-mao-xi-xiang, Tian-ping-shan, *B. G. Li 750013* (PE); Shaoyang Shi, *P. C. Tam 64023* (IBK); Wugang Shi, Yun-shan, *P. C. Tsoong 1241* (PE); Xinhuang Dongzu Zizhixian, Li-wan, *Exp. Hunan 281* (PE); Xinning Xian, Shun-huang-shan, *Q. Z. Lin 10035* (IBSC); Yizhang Xian, Mang-shan, Jin-quan-xiang, *P. H. Liang 83552* (IBK, MO); Yongshun Xian, Xiao-xi-xiang, *X. L. Yu 91655* (KUN); Zhijiang Dongzu Zizhixian, Nan-mu-ping, *collector unknown 490* (KUN). **Jiangsu:** Ganyu Xian, Liu-lin-shan, near Hai-chow, *J. Hers H636* (A); Lianyungang Shi, Yun-tai-shan, *K. Yao 8497* (MO); Yixing Shi, *R. C. Ching 4825* (K). **Jiangxi:** Anfu Xian, Wu-gong-shan, *J. S. Yue 3551* (IBSC, KUN, PE); Dayu Xian, Zuo-bo-xiang, *M. Q. Nie et al. 9644* (IBK[2], IBSC, KUN); Jinggangshan Shi, Da-jing-shan, *J. Xiong 2349* (PE); Jiujiang Shi, Lu-shan, *F. C. Liang 137* (IBSC); Lianhua Xian, Wu-gong-shan, Cai-jia-xiang, *Exp. Jiangxi 377* (PE); Linchuan Shi, Da-fen-qu, *J. S. Yue 4669* (PE); Nankang Xian, Fu-shi-xiang, *M. Q. Nie et al. 9797* (KUN); Ninggang Xian, Da-long-xiang, *S. S. Lai 5182* (IBSC, KUN); Taihe Xian, *S. S. Lai 558* (PE); Tonggu Xian, Long-men, *S. S. Lai 900* (PE); Wuning Xian, Luo-ping-xiang, *S. S. Lai 2695* (KUN, PE); Wuyuan Xian, *R. C. Ching 3273* (A, E, K, UC); Xunwu Xian, Jian-xi-xiang, Bi-jia-shan, *J. S. Yue 1810* (IBSC, KUN, PE); Yifeng Xian, Huang-gang-xiang, *S. S. Lai 287* (PE). **Shaanxi:** Danfeng Xian, *P. C. Kuo 3713* (IBK, KUN); Fuping Xian, Yue-ba-xiang, Ma-jia-gou, *J. S. Ying et al. 436* (MO); Pingli Xian, Shi-chi-he, *Xi-da-an-kang Coll. Team 18* (KUN); Shangnan Xian, Cao-yin, *S. B. He 614* (KUN); Shangzhou Shi, Si-ji-he, *P. Y. Li 8461* (KUN); Shanyang Xian, Xiao-he-kou-xiang, Hei-gou-da-dui, *Z. Y. Zhang 15926* (PE); Shiquan Xian, Liang-he-xiang, *J. Q. Xing 8048* (IBK); Xixiang Xian, Xia-guan-kou, Lao-cheng, *J. Q. Xing 1843* (PE); Yang Xian, Hua-yang, *K. T. Fu 5240* (IBK, PE); Zhenping Xian, *P. Y. Li 2692* (KUN, PE); Ziyang Xian, Feng-duo-dian, *P. C. Kuo 2180* (PE). **Shandong:** Penglai Shi, Tsing Lai, Kap Yatau, *R. Zimmermann 422* (A, BR, K); Qingdao Shi, Lao-shan, Pai-ying-tung, *C. Y. Chiao 2800* (A, C, E, K, PE, UC); Rongcheng Shi, *T. Y. Zhou 2297* (PE); Yantai Shi, Kun-yu-shan, *T. N. Liou et al. 1516* (PE). **Shanxi:** Yuanqu Xian, Shi-ban-po, Shang-guo-dui, *T. W. Liu & Z. F. Zeng 110* (MO). **Sichuan:** Chengkou Xian, Tien-pa-ho, *W. P. Fang 10307* (A, DS, E, IBSC, PE[2]); Chongqing Shi, Bei-pei-qu, Jin-yun-shan, *Exp. Sichuan & Guizhou 192* (PE); Da Xian, Sui-ting-fu, *W. P. Fang 10249* (BM, IBSC, PE); Dujiangyan Shi, betw. Nan-yue & Lu-zi-tang, *D. E. Boufford & B. Bartholomew 24853* (A, AAU, CAS, L, MO); Ebian Yizu Zizhixian, Sha-ping, *Z. S. Zheng 230* (KUN); Emeishan Shi, E-mei-shan, *G. H. Yang 55688* (IBSC, PE); Fengjie Xian, Zhu-yuan-xiang, *Z. R. Zhang 25586* (IBSC, KUN, PE); Hanyuan Xian, *Sichuan Economic Pl. Exp. 1013* (KUN); Hechuan Shi, *X. L. Sun 5597* (PE); Jianyang Shi, Hong-jia-yan-he, *Sichuan Economic Pl. Exp. 2226* (KUN); Leibo Xian, Xi-ning-xiang, *Q. S. Zhao 428* (PE); Li Xian, Suo-luo-gou, *R. Li 46764* (IBSC); Mabian Yizu Zizhixian, *F. T. Wang 22866* (IBSC[2], KUN, PE[3]); Nanchuan Shi, Jin-fo-shan, *G. F. Li 61931* (IBSC, KUN, PE); Nanjiang Xian, Pei-pah, *Y. W. Law 508* (K); Pingwu Xian, Tu-cheng-xiang, *H. F. Zhou 11150* (IBSC); Tianquan Xian, Yong-xing-qu, *D. Y. Peng 45496* (IBSC); Wanxian Shi, Mou-tao-chi, Ma-hwang-au, *C. T. Hwa 16* (PE); Wanyuan Shi, *K. L. Chu 2179* (PE); Wushan Xian, Dang-yang-xiang, *G. H. Yang 59092* (IBSC, KUN, PE); Wuxi Xian, Ban-xi-xiang, *G. H. Yang 65343* (PE); Zhong Xian, Shuang-he-xiang, *Sichuan Economic Pl. Exp. 1270* (KUN). **Taiwan:** Taitung Xian, Lanyu Island, W slope of Hung T'ou-shan, *W. L. Wagner 6721* (CAS, MO). **Yunnan:** Dali Shi, *T. N. Liou 16474* (IBSC[2], KUN); Eshan Yizu Zizhixian, *Exp. E-shan 88441* (KUN); Funing Xian, Jar-gei, *C. W. Wang 89592* (IBSC, KUN, PE); Fuyuan Xian, Huang-ni-he, *Exp. Hong-shui-he 2943* (KUN); Gengma Daizu Wazu Zizhixian, *C. W. Wang 72938* (A, IBSC, KUN, PE[2]); Guangnan Xian, Mao-yi-xiang, *Q. A. Wu 9740* (KUN); Jiangcheng Hanizu Yizu Zizhixian, *Y. H. Li 5408* (KUN); Jingdong Yizu Zizhixian, Meng-soong, Dah-meng-lung, *C. W. Wang 78470* (A, IBSC, KUN, PE); Jinghong Shi, Meng-soong, Dah-meng-lung, *C. W. Wang 78470* (A, IBSC, KUN, PE[2]); Jinping Miaozu Yaozu Daizu Zizhixian, Fen-shui-ling-lin-qu, *B. Y. Qiu 57007* (KUN); Kunming Shi, Xi-shan, *K. M. Feng 10406* (KUN, PE); Longchuan Xian, Hu-sa, *J. S. Yang 8311* (KUN); Longling Xian, *H. T. Tsai 55793* (A, B, IBSC, KUN, PE); Lüchun Xian, Fen-shui-ling, Lei-bo Valley, *D. D. Tao 238* (IBSC, KUN[2]); Lufeng Xian, W of Lufeng City, *Sino-Amer. Bot. Exp. (1984) 1307* (A, CAS, KUN); Luxi Xian, Lo-shiueh-shan, *H. D. McLaren U219* (C, E); Malipo Xian, Chung-dzai, *K. M. Feng 12740* (A, KUN, PE[2]); Mengzi Xian, Yang-cao-tang-xiang, *Y. Y. Hu 580574* (KUN); Nanjian Yizu Zizhixian, *F. Ducloux 2716* (P); Pingbian Miaozu Zizhixian, Liang-zi-xiang, Yao-shan-qu, *P. Y. Mao 4154* (IBSC[3], KUN, PE); Qujing Shi, Ma-xiong-shan, *Exp. Hong-shui-he 2065* (KUN); Shuangjiang Lahuzu Wazu Bulangzu Daizu Zizhixian, from Shuang-jiang to Tai-ping-xiang, *J. S. Xing 763* (IBSC, KUN[2]); Suijiang Xian, Mo-dao-xi, *B. S. Sun 141* (IBSC, KUN); Tengchong Xian, Dong-shan-xiang, Qing-cai-tang, *H. Li 11357* (CAS); Wenshan Xian, Lao-jun-shan, *K. M. Feng 11082* (A, KUN, PE); Xinping Yizu Daizu Zizhixian, Mao-er-shan, *Exp. Yuxi 2992* (KUN); Xundian Huizu Yizu Zizhixian, Hay tien, *F. Ducloux 2717* (P); Yiliang Xian, from Cao-tian-ma to Niu-jie, *Exp. NE Yunnan 905* (KUN); Yingjiang Xian, *G. D. Tao 13063* (KUN); Yuanjiang Hanizu Yizu Daizu Zizhixian, Er-qu, He-ping-shui-ku, *Y. H. Li 5739* (KUN); Yuanyang Xian, *S. C. Ho 85196* (IBSC); Zhanyi Xian, Xiao-ma-la, *Y. H. Li 148* (KUN, PE); Zhenxiong Xian, Shi-jia-wan, *P. H. Yu 1096* (IBSC, KUN, PE). **Zhejiang:** Jinyun Xian, Yan-ling-keng, Wen-yang, *S. Y. Chang 1740* (MO); Kaihua Xian, Gu-tian-miao, *J. X. Wang 2123* (PE); Longquan Shi, Feng-yang-shan, *S. Y. Chang 3319* (MO); Rui'an Shi, Shi-yang, *S. Y. Zhang 6613* (MO, PE); Suichang Xian, Shui-chang, *Zhejiang Bot. Res. Team 25807* (MO, PE); Taishun Xian, Wu-ling-yan, *S. Y. Zhang 5667* (KUN, PE); Wuyi Xian, Xi-lian-xiang, *Z. W. Zhang J8311260* (IBSC). JAPAN. **Honshu:** Aichi Pref., Seto-shi, *M. Ito 675* (KYO); Aomori Pref., Hachinohe, *Père U. J. Faurie 13031* (K, MO); Chiba Pref., Matsudo-shi, Takatsuka, *Y. Tateishi 816* (TI); Fukuoka Pref., Buzen, Tikuzyô-gun, Iwaya-mura, *S. Yosioka 23* (TI); Fukushima Pref., Ishikawa-gun, Ishikawa-cho, *H. Iketani 1117* (MO); Gifu Pref., Mizunami-shi, Matsuno-ko, *S. Tsugaru et al. 23572* (KYO); Gumma Pref., Usui-gun, Matsuida-machi, Usui-tooge, *J. Murata & T. T. Chen 7672* (TI); Hiroshima Pref., Saeki-gun, Yuki-cho, Hontada-gawa, 1979, *T. Nakano s.n.* (AAU); Hyogo Pref., Mt. Rokko, *H. Muroi 3092* (A); Ishikawa Pref., Enuma-gun, Natani, *H. Muroi 2243* (A); Iwate Pref., Morioka, Mt. Iwayama, *H. Muroi 5010* (A); Kanagawa Pref., Musashi, Yokohama, Totsuka, *S. Kobayashi 16251* (BR); Kyoto Pref., Funai-gun, Wachi-cho, Mt. Choro-ga-dake, *S. Tsugaru et al. 18431* (MO); Mie Pref., Itsushi-gun, *M. Hiroe 16424* (UC); Miyagi Pref., Matsushima-cho. W side of Mt. Otakamori, *E. W. Wood & D. E. Boufford 3967* (A, CAS); Nagano Pref., Nishichi-kumagun, Okuwa-mura, betw. Noziri & Mt. Aterayama, along the River Ayera-gawa, *G. Murata & H. Nishimura 122* (AAU, KYO); Nagasaki Pref., Tsushima Island, Shimoagata-gun, Mitsushima-cho, Sumo, *K. Mimoro 1840* (MO); Nara Pref., Nara-shi, Ninnikusen-cho, *H. Iketani 2256* (MO); Nigata Pref., Morimachi, Minami-Kambara, *Y. Ikegami 17502* (A); Okayama Pref., Maniwa-gun, *M. Hiroe 16409* (UC); Osaka Pref., Kawachinagano City *N. Fukuoka 5852* (AAU, C, E, K, L, UC); Saitama Pref., Kitaadachi-gun, Niiza-machi, Heirinzi, 1966, *H. Ohashi s.n.* (TI); Shiga Pref., Takashima-gun, Makino-machi, Minamimakino, *H. Ohashi et al. 8653* (A); Shimane Pref., Yatsuka-gun, Shimane-cho, Kukedo-bana, *K. Deguchi & S. Tsugaru 3819* (MO); Shizuoka Pref., Izu Peninsula, Ito-shi, *K. Nakayama & F. Konta 1433* (KUN); Tochigi Pref., *P. A. Savatier 810* (P); Tokyo Pref., Hachioji-shi, *H. T. Im & T. Karahara 9714* (A, AAU, C, E, K, KUN, MO, PE); Toyama Pref., Mt. Tonami in town of Isurugi, *S. Kirino 360* (MO); Wakayama Pref., Kii, Koyasan, *G. Koidzumi s.n.* (KYO[2]); Yamagata Pref., Higashine-shi, Inosawa, *H. Ohashi et al. 10779* (A); Yamaguchi Pref., Mukaidoi, Tukuyama, 1954, *H. Migo s.n.* (A). **Kyushu:** Kagoshima Pref., Phsumi, Yaku-shima Island, Mt. Motchomu Hara Yaku-choo, *F. Miyoshi 10778* (K); Kumamato Pref., Aso-gun, Aso-machi, Futae Pass, 1983, *Y. Endo s.n.* (MO); Miyazaki Pref., Cape Toi, *K. Kondo 2228* (TI). **Ryukyu Islands:** Okinawa Pref., Okinawa Island, Kunigami, Nago-dake, *E. H. Walker et al. 6157* (E, GH, K, L, UC). **Shikoku:** Kagawa Pref., Mitoyo-gun, Toyono-mura, *M. Takahashi 1197* (A, KUN, PE). LAOS. **Houaphan:** Muang awin, Clueng Kwang, *A. F. G. Kerr 20941* (BM, K, L). **Xiangkhoang:** betw. Muong Hom & Ta Thom, *J. Vidal 880B* (P). MYANMAR. **Kachin State:** N Triangle (Hkunlum), *F. F. K. Ward 20632* (A, BM, E). NORTH KOREA. **Pyongyang City:** Chonbuk, Chonju, Wansan Chilbong, 1988, *B. Y. Sun s.n.* (A). PHILIPPINES. **Babuyan Islands:** Camiguin Island, Mt. Malabsing, *G. E. Edaño 79248* (L). **Batan Islands:** Batan Island, Mt. Matarem, *M. Ramos 80424* (BO, L). SOUTH KOREA. **Cheju:** Nam-cheju-gun, Shinye-ri, *D. E. Boufford et al. 25729* (CAS, E). **Kangwon:** Kogen, *E. H. Wilson 9328* (A). **Kyonggi:** Keiki, Kosyo *E. H. Wilson 8754* (A, K). **North Cholla:** Wanju-gun, Moak san, *D. E. Boufford et al. 25808* (CAS, E, KUN). **North Kyongsang:** Daegwannim, 1987, *Y. S. Kim s.n.* (A, MO). **Seoul City:** Sammaksa Temple, *R. Moran 4327* (BM, BR, E, GH, MO, UC). **South Cholla:** Mt. Moodung, 1984, *Y. S. Kim s.n.* (A). **South Chungchong:** Sosan Gun, Anmyon Island, *B. R. Yinger et al. 2525* (A). **South Kyongsang:** Chilean Keisyonando Chosen Nippon, *K. Uno 23243* (A). VIETNAM. **Cao Bang:** Mt. Pia Oac, 1997, *U. Kurosu s.n.* (CAS).

7. Styrax limprichtii Lingelsh. & Borza, Repert. Spec. Nov. Regni Veg. 13: 386. June 1914 [as *S.* "*Limprichtii*"]. TYPE: China. Yunnan: Chuxiong Shi, Tschu-hsiung-fu, 2000 m, 24 Aug. 1913, *K. G. Limpricht 920* (lectotype, designated here, WRSL not seen; photo of lectotype, A!, PE!; isotype, A!).

Styrax langkongensis W. W. Sm., Notes Roy. Bot. Gard. Edinburgh 8: 208. September 1914. TYPE: China. Yunnan: xian unknown, hills at the S end of the Lang-kong Valley, 26°10′N, 2121–2727 m, May 1910, *G. Forrest 5585* (holotype, E!; isotypes, BM[2]!, IBSC!, K[2]!, PE!, UC!).

Shrubs to 2.5 m tall. Young twigs gray-yellow or yellow-brown stellate-tomentose; older twigs dark purple, glabrescent. Petiole 1–3 mm long. Two most proximal leaves on each shoot alternate or more often subopposite to opposite. Lamina 3.5–7(–9.5) × 2–4.5 cm, chartaceous, elliptic to obovate; apex obtuse to slightly acuminate; base rounded to broadly cuneate; adaxially densely stellate-pubescent when young, becoming sparsely pubescent; abaxially white stellate-tomentose, rarely subglabrous, often with additional scattered orange or dark brown stellate pubescence especially prevalent on veins and the two most proximal leaves on each shoot; margin serrate or nearly entire (but still glandular), often irregularly dentate apically; secondary veins 5 or 6 on each side of midvein, tertiary veins reticulate, plane or slightly sunken, abaxial surface of the secondary and tertiary veins obscured by the tomentum, only the tertiaries abaxially prominent and raised in young leaves. Fertile shoots 1–7 cm long, 3- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1(2)-flowered; pseudoterminal inflorescences 2-flowered or racemose, 1–2 cm long, 2- or 3(4)-flowered, rachis yellow or orange stellate-tomentose, stalked trichomes absent. Pedicel 3–4 mm long, densely pubescent; bracteoles 3–5 mm long, subulate, positioned at various places along the pedicel but mostly near the middle, more rarely near the base, sometimes those toward the base of the inflorescence leaf-like. Flowers 1.5–2.0 cm long. Calyx 5–6 × 5–6 mm, cupuliform; adaxially sparsely appressed-pubescent with white 2- or 3-armed or stellate trichomes, becoming glabrous proximally; abaxially yellow-brown or orange stellate-tomentose throughout, often also with various amounts of larger scattered orange or brown stiff stellate trichomes, especially proximally; margin distinctly dentate, the teeth (0.6–)1–1.5(–2) mm long, subulate to deltoid, unequal, usually contiguous or separated by a shallow concave portion. Corolla 1.0–1.4 cm long, white, tube ca. 4 mm long, glabrous, lobes 5, 9–11 × 4–6 mm, elliptic to ovate-elliptic, short-stellate-pubescent on both sides. Stamens 10; filaments 5–6 mm long, straight, proximally broadened, densely white stellate-pubescent, trichomes up to 0.5 mm long, distally subulate-attenuate and glabrous; anthers 4–5 mm long, wider than distal portion of filament; connectives glabrous. Style proximally stellate-pubescent and distally glabrous, sometimes sparsely stellate-pubescent or glabrous throughout; stigma 0.2–0.4 mm wide, capitate. Fruit 1.4–1.6 × 1–1.5 cm, globose, apex rounded or apiculate, dehiscent by 3 valves from apex; pericarp dry, 0.3–0.6 mm thick, outside regularly longitudinally striate throughout, rugose, gray stellate-tomentose, inside glabrous or minutely downy-pubescent. Seeds brown, ovoid, finely reticulate-fissured, glabrous.

Illustrations. Anonymous, Ic. Cormophyt. Sin. 3: 339, fig. 4631. 1974; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1606, fig. 801. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 90, pl. 30 (1–5). 1987; W. Q. Yin in Y. C. Xu, Ic. Arbor. Yunnan. 2: 892, pl. 470 (7–10). 1990; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 199, fig. 199 (1–5). 2000.

Phenology. Flowering: February–October. Fruiting: April, June–November.

Distribution. China (Sichuan and Yunnan); Figure 8.

Habitat. In relatively sunny, dry stony pastures, more often in forests on open rocky slopes; 1400–2750 m.

Vernacular names. Chu-xiong-an-xi-xiang (Hwang, 1980), Chu-xiong-ye-mo-li (Anonymous, 1974).

Styrax limprichtii, a much-branched shrub that rarely exceeds 2.5 m, occurs only in northeastern Yunnan Province and adjacent southwestern Sichuan Province.

The ranges of *Styrax limprichtii* and *S. rugosus* are contiguous. These two species are morphologically similar in many respects, as demonstrated by their adjacency in the key, and are probably sister taxa. They nonetheless exhibit enough differences throughout their ranges to justify the recognition of these two entities as species (see couplet 24 of the key). Furthermore, *S. rugosus* usually occurs at lower elevations (700–1650 m) than *S. limprichtii* (1400–2750 m). Besides these differences, *S. limprichtii* differs from *S. rugosus* by a tendency toward shorter calyx teeth, shorter bracteoles, shorter shoots, and less rugose leaves. These characters, however, exhibit some degree of overlap. Also similar to *S. limprichtii* is *S. wilsonii* (see comparisons under that species).

Styrax limprichtii, S. rugosus, S. wilsonii, and the western Mexican endemic *S. jaliscanus* are all similar morphologically, sharing a shrubby habit, a calyx that is densely pubescent throughout abaxially and distinctly dentate with the teeth contiguous or nearly so, a petiole ≤ 5 mm long, and an evenly longitudinal-striate pericarp. The striate pericarp appears to be restricted to these species within *Styrax.* Phylogenetic analysis of DNA sequences of the ITS region, however, places *S. limprichtii* at the base of series *Cyrta,* and *S. jaliscanus* groups with the rest of the North American species of series *Cyrta* (Fritsch, 2001). Nonetheless, support for these positions is weak, and this group is in need

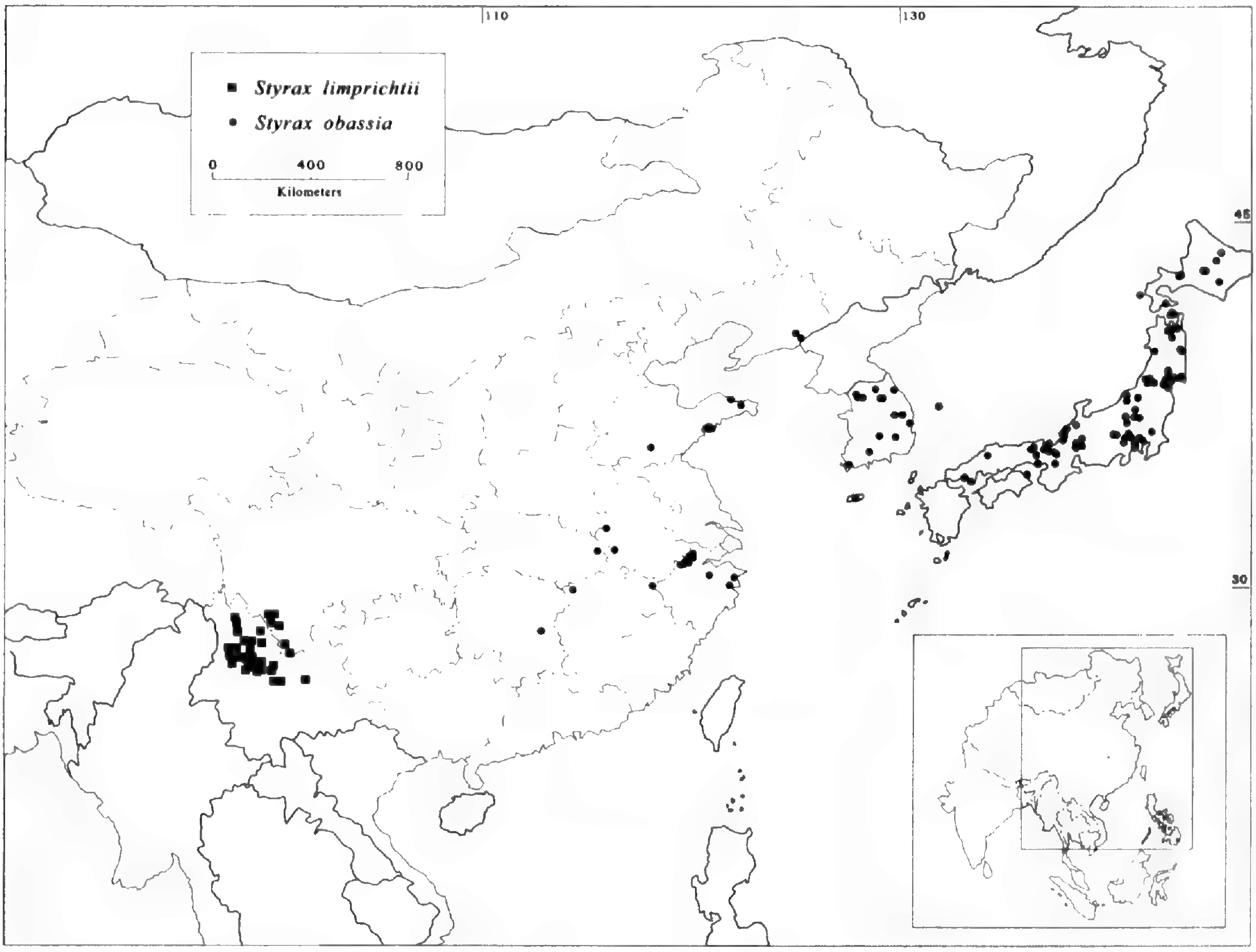

Figure 8. Geographic distribution of *Styrax limprichtii* and *S. obassia.*

of more detailed study to resolve the apparent discrepancy between molecular and morphological data.

Only two imbricate-flowered species of *Styrax* are sympatric with *S. limprichtii. Styrax hookeri* is normally easily distinguished from *S. limprichtii* by its tree (vs. shrub) habit. *Styrax limprichtii* can be further distinguished from small individuals of *S. hookeri* by its distinctly dentate (vs. usually truncate or undulate) calyx, which is ± pubescent throughout (vs. more sparsely pubescent within 1 mm of the margin). *Styrax limprichtii* also tends toward leaves with acute to blunt (vs. acuminate to caudate) apices, coarsely serrate margins, especially distally (vs. more finely serrate), and a rugose (vs. smooth) surface abaxially. Moreover, *S. limprichtii* also usually has densely pubescent laminae abaxially, and anthesis often occurs before the full expansion of the leaves, whereas the leaves of *S. hookeri* can be densely pubescent to glabrous abaxially and anthesis occurs at the same time as or after full leaf expansion. The only other species of imbricate-flowered *Styrax* sympatric with *S. limprichtii* is *S. japonicus,* occurring near Dali Shi and Kunming Shi, Yunnan Province. This species is readily distinguished from *S. limprichtii* by its longer pedicels and nonstriate (vs. longitudinally striate) pericarp.

The collections of K. G. Limpricht numbers 896, 920, and 973 are all cited in the protologue of *S. limprichtii* without a clear indication of type, and thus are all syntypes of this name. We have chosen the *K. G. Limpricht 920* specimen at WRSL as the lectotype because it is apparently the most widely distributed of the three collections.

Selected specimens examined. CHINA. **Sichuan:** Muli Zangzu Zizhixian, *G. Forrest 22394* (A, E, K); Luo-boxiang, *Nan-shui-bei-diao-dui 5709* (KUN, PE); Mu-li Valley, mtns. betw. Mu-li & Ku-lu, *J. F. Rock 24150* (A, E, UC); from Ke-tze to Ku-ba-dian, *T. T. Yü 7216* (A, KUN, PE); from Tuo-li-gou to Ke-tze, *T. T. Yü 14198* (A, KUN, PE); Panzhihua Shi, Da-bao-ding, *Exp. Qinghai & Xizang 11362* (KUN); Yanyuan Xian, *H. F. Handel-Mazzetti 2068* (A, E), *Nan-shui-bei-diao-dui 5584* (PE); Wei-luo-he, Mao-niu-shan, *Nan-shui-bei-diao-dui 5967* (KUN, PE). **Yunnan:** Binchuan Xian, Hi-zu-shan, *S. Y. Bao 1* (KUN); Sin-tien, Pin-tchouan, *F. Ducloux 4627* (P); Ji-zhu-shan, *H. Li 503* (KUN); Gan-dian, *Y. Q. Lin 11* (KUN); from Xia-yang to Wa-xi, *T. N. Liou 21495* (IBSC, PE); Niu-jing, *T. N. Liou 21688* (IBSC, PE); Simeon Yen, *S. Ten 351* (E, UC); Ji-shan, *H. C. Wang 1988* (KUN, IBSC, PE); Chuxiong Shi, Guang-ba-he Reservoir, *S. C. Huang 20* (KUN);

Long-tang, *Sino-Amer. Bot. Exp. (1984) 1256* (A, CAS, KUN, MO); Dali Shi, Kong-ti, *J. M. Delavay 2782* (A, P); Pu-peng, *Exp. NW Yunnan 4010* (KUN, PE), *Exp. Qinghai & Xizang 20* (KUN); W slopes of the Sung-kuiei Range, *G. Forrest 23057* (A, E, K); Xiao-tuan-shan, Erhai Park, *Sino-British Exp. Cang-shan 1* (A, E, K, KUN), *Y. Tsiang 11337* (IBSC, KUN); Wu-tai-feng, Shi-tou-cun, *H. C. Wang 1740* (IBSC[2], KUN[2]); Yang-tze divide, E of Dali lake, *J. K. Ward 3831* (E); Dayao Xian, Shi-yang-qu, *Coll. Team for Oil Pl. (1965) 650302* (KUN); Kang-jia-shan, *P. Di 60022* (KUN); Eryuan Xian, San-ying-qu, Jiao-shi-he, *Exp. NW Yunnan 6389* (KUN, PE); Heqing Xian, Bai-yan, *R. C. Ching 24523* (KUN, PE); from Sarchatze to Chiang-Ing near Sung-kuei, *K. M. Feng* 801 (A, IBSC, KUN); Dsolin-ho, *H. F. Handel-Mazzetti 6224* (A, E); Li-chiang Range, *H. D. McLaren S114* (BM); Jsu-yung, *H. D. McLaren 114F(AA)* (C, E); Pai-ching, *H. D. McLaren F199* (AAU, E); Sung-kuei, *H. D. McLaren e233* (E); He-chuan-xiang, *W. C. Wang 390* (KUN); Kunming Shi, Yi-ping-lang, *T. N. Liou 16614* (IBSC[2], PE); Lanping Baizu Pumizu Zizhixian, in the Lang-kong Valley, *G. Forrest 9954* (BM, E, K, PE, UC); Lijiang Naxizu Zizhixian, Tze-li on Yang-tze River, *R. C. Ching 20264* (A, KUN, PE); Tai-ngo-koo, *R. C. Ching 21670* (KUN); Tze-li on Yang-tze, *R. C. Ching 22139* (A); Shu-di-du-kou, *Exp. Qinghai & Xizang 638* (KUN[2]); near Jin-sha-jiang, *Exp. SW China (Guizhou, Sichuan & Yunnan) 200* (PE); Jia-zi-xiang, Bai-shui-he, *K. M. Feng 21567* (KUN, PE); Li-chiang Range, *H. D. McLaren 46No.2* (BM); high plateau betw. Ta-li-fu & Li-kiang, *J. F. Rock 3198* (A, E, UC); betw. Li-kiang & Ta-li-fu, *J. F. Rock 6397* (A, UC); S Li-kiang-shan, Sung-kwe-ho-chin Range, *J. F. Rock 8268* (A, UC); betw. Li-kiang, Tung-shan, Tui-nao-ko, & Tsi-li-kiang, *J. F. Rock 8520* (A, UC); Yulung-shan, *C. K. Schneider 3965* (IBSC); Da-dong-qu, *H. Sun 771038* (KUN); *C. Y. Zhao 21670* (KUN, PE); Shi-er-lan-gan-ban-shan, *Y. X. Zhao 22139* (KUN); Ninglang Yizu Zizhixian, from Ku-ba-dian to Tuo-li-gou, *T. T. Yü 7309* (A, KUN, PE); Yangbi Yizu Zizhixian, betw. Li-kiang, Young-ning & Young-pei, *J. F. Rock 5058* (A, UC); Yao'an Xian, Da-jian-shan, 1965, *Exp. SW China (Guizhou, Sichuan & Yunnan) s.n.* (PE); Yao-chou, *H. D. McLaren 205F* (C); Yongsheng Xian, Song-ping-xiang, *Exp. Qinghai & Xizang 692* (KUN); Jong-shan, *G. Forrest 16929* (E); Xin-liang-gong-she, *C. X. Lü 62168* (KUN); Yunlong Xian, Jin-yue-liang, *Xiang-liao-dui (Coll. Team for Perfume Pl.) 156* (KUN); Zhongdian Xian, mtns. NE of Yang-tze Bend, *G. Forrest 10696* (A, BM, PE, UC); Chung-tien plateau, *G. Forrest 12653* (AAU, BM, E, PE).

8. Styrax macrocarpus W. C. Cheng, Contr. Biol. Lab. Chin. Assoc. Advancem. Sci., Sect. Bot. 10: 242. 1938 [as *S.* "*macrocarpa*"]. TYPE: China. Hunan: Yizhang Xian, Mang-shan, 800 m, 21 Aug. 1937, *W. C. Cheng 7000* [from protologue] (holotype, PE!; isotype, PE! [no collection number indicated on either sheet]).

Styrax zhejiangensis S. M. Hwang & L. L. Yu, Acta Bot. Austro Sin. 1: 75. 1983. TYPE: China. Zhejiang: Jiande Xian, 27 June 1958, *Y. Y. Ho 29344* (holotype, IBSC!; isotype, IBSC!).

Shrubs to 2 m tall or trees to 9 m tall. Young twigs densely gray-brown stellate-pubescent, older twigs becoming gray, glabrescent. Petiole < 1(–2.5) mm long. Two most proximal leaves on each shoot subopposite to opposite. Lamina 2.5–17 × 2–7.5 cm, chartaceous, elliptic to obovate-elliptic; apex acute; base cuneate, broadly cuneate or rounded; sparsely stellate-pubescent on veins when young, otherwise glabrous; margin subentire or apically slightly serrate, secondary veins 6 to 10 on each side of midvein; tertiary veins subparallel, adaxially plane or slightly sunken, abaxially raised. Pedicel 7–12 mm long, white stellate-tomentose; bracteoles 3–5 mm long, ovate-lanceolate, positioned at the base or middle part of pedicel. Flowers 2.3–3.2 cm long, solitary, arising only laterally from shoots of the previous growing season, opening before the leaves. Calyx 5–7 × 7–9 mm, cupuliform; adaxially glabrous; abaxially gray stellate-tomentose, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry; margin with 4 to 6 broadly deltoid teeth, subglabrous on both sides. Corolla 1.6–2.6 cm long, white, tube 3–4 mm long, glabrous, lobes 5–7, 1.6–2.3 × 0.8–1.1 cm, elliptic or narrowly elliptic, apex obtuse to acute, sparsely white stellate-pubescent on both sides. Stamens 10 to 12; filaments 8–10 mm long, straight, proximally broadened and ventrally densely white stellate-villous, distally attenuate and glabrous; anthers 5–6 mm long, wider than distal portion of filament; connectives glabrous. Style proximally sparsely white stellate-pubescent proximally, distally glabrous; stigma 0.2–0.4 mm wide, punctiform. Fruit 1.8–3 × 1.0–2.5 cm, ovoid to pyriform, apex rounded or apiculate, apparently indehiscent; pericarp dry, (1–)1.5–3 mm thick, outside smooth, gray or pale brown stellate-tomentose, inside densely appressed-pubescent with long simple, 2-armed, or stellate white trichomes. Seeds brown or dark brown, ellipsoid to ovoid-ellipsoid, irregularly rugose, glabrous, sometimes sparsely white stellate-villous.

Illustrations. W. C. Cheng, Contr. Biol. Lab. Chin. Assoc. Advancem. Sci., Sect. Bot. 10: 243, fig. 25. 1938; S. M. Hwang, Acta Bot. Austro Sin. 1: 76, fig. 1. 1983 (as *S. zhejiangensis*); S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1618, fig. 811. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 98, pl. 33 (1–2). 1987; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 98, pl. 33 (3–5). 1987 (as *S. zhejiangensis*); Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 202, fig. 202 (1–5). 2000 (3–5 as *S. zhejiangensis*).

Phenology. Flowering: April, May. Fruiting: June, July, September, October.

Distribution. China (Guangdong, Hunan, and Zhejiang); Figure 2.

Habitat. In shady mountain forests, and along the margins of mixed forests in ravines; 570–950 m.

Vernacular names. Da-guo-an-xi-xiang (Hwang, 1980), Zhe-jiang-an-xi-xiang (Hwang, 1983).

Styrax macrocarpus, occurring in mountainous regions between 570 and 950 m elevation, has been collected only rarely. This species is easily distinguished from sympatric species of *Styrax* by its much shorter petioles (less than 1(–2.5) mm long); solitary, lateral, and larger (2.3–3.2 cm long) flowers that open before the leaves on shoots of the previous year; and a larger (1.0–2.5 cm wide) fruit, with a pericarp (1–)1.5–3 mm thick that is densely appressed-pubescent inside with long simple or 2-armed white trichomes.

Hwang (1983) described *Styrax zhejiangensis* from a single fruiting specimen collected in Jiande Xian, Zhejiang Province. Although she considered a possible relationship of *S. zhejiangensis* with *S. macrocarpus* based on their common solitary, laterally produced flowers, Hwang (1983) felt that the combination of a smaller, pyriform (vs. ovoid) fruit, broadly elliptic to ovate-oblong (vs. elliptic to obovate-elliptic) leaves, and sparsely stellate-pubescent (vs. glabrous) seeds was sufficient justification for the recognition of a new species. There is, however, ample evidence for a close affinity between the two taxa, so much so that we regard the two as conspecific. In addition to their solitary, laterally produced flowers, *S. macrocarpus* and *S. zhejiangensis* share many other features such as the two most proximal leaves on each shoot subopposite to opposite; the petiole very short or absent; the leaves with a similar number of secondary veins and an entire or indistinctly toothed margin; the calyx adaxially glabrous, abaxially gray stellate-tomentose, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry, margins with 4 to 6 broadly deltoid teeth, subglabrous on both sides; the fruiting calyx patelliform, not appressed to the fruit; the fruit ovoid to pyriform with the apex rounded or apiculate, a smooth gray to brown stellate-tomentose surface, and an inner fruit wall densely appressed-pubescent with long simple or 2-armed white trichomes; and seeds ellipsoid to ovoid-ellipsoid, with an irregularly rugose testa.

Furthermore, characters that reportedly distinguish *Styrax zhejiangensis* from *S. macrocarpus* are unreliable or do not otherwise serve to delimit the two taxa. According to the protologues of the species, *S. zhejiangensis* tends to have wider leaves with reticulate tertiary veins and a smaller, pyriform fruit, whereas *S. macrocarpus* tends to have narrower leaves with subparallel tertiary veins and a larger, ovoid fruit. We regard the tertiary veins of *S. zhejiangensis* as subparallel rather than reticulate and the fruit shape of *S. macrocarpus* (i.e., specimens outside of Zhejiang Province) as encompassing both ovoid and pyriform variants, as was also observed by Hwang (1987). Hwang (1987) described *S. macrocarpus* as a tree (6–9 m tall) with glabrous seeds, and *S. zhejiangensis* as a shrub (less than 2 m tall) with pubescent seeds. Our examination of more collections than were available to Hwang (1983, 1987), however, has revealed several specimens of *S. macrocarpus* that exhibit a shrub habit with intermediate height (ca. 4 m; e.g., *X. Q. Liu 28884* and *G. L. Shi 14815*). The number of stellate trichomes distributed on the surface of the seeds of *S. zhejiangensis* varies from several to dozens, even on those from the same plant. High infraspecific seed pubescence variation is present in two other species in this revision (*S. odoratissimus* and *S. tonkinensis*), so this character by itself cannot be used to justify the recognition of *S. zhejiangensis.*

Most collections of *Styrax macrocarpus* are from Mang-shan, Yizhang Xian, southern Hunan Province, where the type collection was made. All other collections were made far from the type locality except one specimen from adjacent Ruyuan Xian, northern Guangdong Province (*Z. L. Chen 30610*). This species exhibits a discontinuous distribution between Fengkai Xian, western Guangdong Province (*G. L. Shi 14815* and *Exp. Guangdong 5185*), Jiande Xian, Zhejiang Province (*Y. Y. Ho 29344*), and the region of the type locality. This discontinuity may be an artifact of human-induced extirpation between the known localities, rather than the species' original distribution, because the original vegetation of the whole region encompassing the range of *S. macrocarpus* has been heavily modified by human disturbance.

Additional specimens examined. CHINA. **Guangdong:** Fengkai Xian, Qi-xing-xiang, *Exp. Guangdong 5185* (IBSC); Hei-shi-ding, *G. L. Shi 14815* (IBSC); Ruyuan Yaozu Zizhixian, Tian-men-zhang, *Z. L. Chen 30610* (IBSC). **Hunan:** Yizhang Xian, Mang-shan, *collector unknown* (PE); Mang-shan, Shui-kou-miao, *S. Q. Chen 2889* (AAU, BR, IBK, IBSC, KUN, PE); Mang-shan, *S. Q. Chen 5408* (IBSC), *M. X. Huang 112743* (IBSC); Mang-shan, Yang-gong-dong, *P. H. Liang 85107* (IBK, IBSC); Mang-shan, *X. Q. Liu 28884* (IBK, IBSC, PE), *Zhong-nan-lin-shi-xi-dui 137* (IBSC).

9. Styrax obassia Siebold & Zucc., Fl. Jap. 1: 93. 1839. TYPE: Japan. *I. Keiske 287* (lectotype, designated here, L [accession no. 908241–452] not seen; digital image of lectotype!).

Shrubs or trees to 15 m tall. Young twigs brown stellate-pubescent; older twigs dark purple, glabrescent. Petiole of larger leaves 10–15(–20) mm long, dilated at base and covering the bud. Two most proximal leaves on each shoot subopposite to opposite, smaller than distal leaves, with petioles not dilated at base or covering the bud. Lamina 5–17 × 4–15 cm, chartaceous, broadly elliptic, broadly obovate, or suborbicular; apex abruptly caudate-acuminate; base subrounded to broadly cuneate; adaxially glabrous except for sparse gray pubescence on major veins, abaxially gray-white stellate-tomentose; margin subentire or remotely apiculate-dentate; secondary veins 5 to 8(to 10) on each side of midvein, tertiary veins ± parallel and perpendicular to the secondary nerves, abaxially prominent. Fertile shoots 14–26 cm long, 1- to 3-leaved. Inflorescences arising from shoots of the current growing season, usually pseudoterminal, occasionally also lateral; lateral inflorescences usually consisting of a single flower; pseudoterminal racemes 10–18 cm long, 10- to 18(to 23)-flowered, rachis glabrous or nearly so. Pedicel 4–6(–10) mm long, white stellate-tomentose, sometimes with larger scattered brownish stellate trichomes; bracteoles 3–5 mm long, linear, positioned at the base or middle part of pedicel, sometimes those toward the base of the inflorescence leaf-like. Flowers 1.2–2 cm long. Calyx 5–6 × 4–5 mm, campanulate; adaxially glabrous; abaxially white stellate-tomentose throughout, often also with various amounts of larger yellow or brownish stiff stellate trichomes especially proximally; margin with 5 or 6 lanceolate to narrowly deltoid, irregularly distributed teeth, contiguous. Corolla 1.0–1.5 cm long, white or rarely pink, tube 4–5 mm long, glabrous, lobes 5(6), 13–16 × 4–6 mm, elliptic, apex acute, white stellate-tomentose on both sides. Stamens 10(12); filaments 6–8 mm long, straight, of equal width throughout, subglabrous or glabrous; anthers 4–5 mm long, equal to filament in width or narrower; connective glabrous. Style proximally stellate-pubescent, otherwise glabrous; stigma 0.1–0.3 mm wide, punctiform. Fruit 1.4–2.0 × 0.7–1.2 cm, ovoid to subovoid, apex rounded or apiculate, dehiscent by 2 valves; pericarp dry, 0.2–0.5 mm thick, outside coarsely and irregularly rugose, white or yellow-brown stellate-tomentose, inside glabrous. Seeds dark brown, ellipsoid, smooth, glabrous.

Illustrations. Siebold & Zucc., Fl. Jap. 1: t. 46. 1835; Gard. Chron. ser. 3, 16: 513. 1888, 34: 507. 1897; Hook. f., Bot. Mag. 115: t. 7039. 1889; Dippel, Handb. Laubholzkunde 1: fig. 205. 1889; Nakai, Sylv. Korea 13: t. 13. 1923; Nakai, Trees Shrubs Japan ed. 2: fig. 157. 1927; Anonymous, Ic. Cormophyt. Sin. 3: 338, fig. 4629. 1974; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1601, fig. 796. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 85, pl. 28 (1–5). 1987; X. M. Liu in X. H. Qian, Fl. Anhui 4: 64, fig. 1766. 1991; S. Y. Wang in B. Z. Ding, Fl. Henan 3: 229, fig. 1774. 1997; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 197, fig. 197 (1–5). 2000.

Phenology. Flowering: May–July. Fruiting: June–November.

Distribution. China (Anhui, Hubei, Hunan, Jiangsu, Jiangxi, Liaoning, Shandong, and Zhejiang), Japan (Hokkaido and Honshu), North Korea, and South Korea (Cheju, Kangwon, Kyonggi, North Chungchong, North Kyongsang, Seoul City, and South Kyongsang); Figure 8.

Habitat. In mesic, open mixed forests on mountain slopes, and in deciduous forests in ravines; 9–1400 m.

Vernacular names. Lao-dan-pi (China, Shandong; *Shandong Wild Pl. Exp. [1959] 89*), Lao-kai-pi (Anonymous, 1974), Oho-ba zisja (Japan; Siebold, 1835–1841), Sei ton kwa (Japan; Siebold, 1835–1841), Shan-zhen-zi (China, Shandong; Hwang & Qi, 1985), Shu-ling-hua (China, Anhui; *Exp. Anhui 219*), Yu-ling-hua (Hwang, 1987; Anonymous, 1974), Yun-jin-du-juan (China, Zhejiang; *Y. Y. Ho 23309*).

Styrax obassia occurs at the extreme northern edge of the range of *Styrax* in Asia, extending from the island of Hokkaido (northern Japan) through North and South Korea to southeastern China. *Styrax obassia* is the only species of *Styrax* that occurs as far north as Hokkaido and Liaoning Province, northeastern China. It appears to be a relatively common component of wet temperate forests in Japan. The dilated petiole base covering the bud separates *S. obassia* from most other species of *Styrax* except *S. shiraianus*, which is distinguished from *S. obassia* by its shorter shoots (4–8 cm) and inflorescences (2–3 cm), much shorter pedicels (less than 1 mm), and generally narrower leaves (to 9.5 cm) with more robust teeth. These species range farther north than any other species of *Styrax* in Asia except *S. japonicus*, suggesting that the dilated petiole base is an adaptation to temperate conditions in lieu of bud scales. Besides the dilated petiole base, *S. obassia* differs from other sympatric species by its larger flowers with glabrous filaments and styles (cf. *S. odoratissimus*) and shorter pedicels and longer inflorescences (cf. *S. japonicus*). See also *S. hemsleyanus* for additional comments.

This wide-ranging species is not extremely variable morphologically, and no unusual specimens were encountered in this revision. This could explain the highly constant treatment regarding this species since its description in 1839.

No specimens were cited in the protologue of *Styrax obassia.* New species in volume 1 of *Flora Japonica* were described by J. G. Zuccarini based on data supplied by von Siebold. The only material that we have seen from the von Siebold herbarium consists of on-line images of two L collections from a database of the von Siebold collections maintained by the National Herbarium Nederland (<http://www.nationaalherbarium.nl>). One of these collections (L accession number 950161–812) bears the stamp "Herbarium Ch. D'Alleizette" and a typeset (not handwritten) label that contains a reference to K. I. Maximovicz, who collected in Japan between about 1860 and 1866, long after von Siebold was there (from 1823 to 1830). The label also bears an indication that this specimen was designated for exchange. D'Alleizette was a plant collector residing in Bordeaux, France, and apparently never collected in Japan. Based on these data, we conclude that this specimen was not part of von Siebold and Zuccarini's original material. The other collection (*I. Keiske 287,* L accession number 908241-452) bears labels that are consistent in handwriting and format with most others in von Siebold's herbarium. Keiske was one of von Siebold's collaborators while von Siebold was in Japan. Although only a single leaf constitutes this specimen, it is clearly recognizable as that of *S. obassia* on the basis of, among other features, the overall obovate-orbicular shape and a coarsely dentate margin with the teeth most prominent apically. On this basis, we have lectotypified the name *S. obassia* on the L specimen of *I. Keiske 287.*

The specific epithet "*obassia*" is derived from the common name for the species in Japanese. Because the epithet is a noun in apposition, it should not be modified to "*obassis*" (see Greuter et al., 2000: Article 23.5), as was done by Hwang and Grimes (1996).

Selected specimens examined. CHINA. **Anhui:** Jinzhai Xian, Bai-ma-zhai, Xi-da-wa, *K. Yao 8928* (A, CAS, K, MO); Yuexi Xian, *E China Work Station 7007* (IBSC). **Hubei:** Luotian Xian, *G. Hei 1251* (PE). **Hunan:** Hengshan Xian, Heng-shan, *S. Q. Chen 3431* (IBSC). **Jiangsu:** *collector unknown 2337* (BR). **Jiangxi:** Wuyuan Xian, *R. C. Ching 3253* (A, E, IBSC, K, PE, UC); Xiushui Xian, Mo-fu-shan, Tian-yu-tang, *Y. K. Hsiung 5891* (PE[2]). **Liaoning:** Dandong Shi, An-dong, Zhen-jiang-shan, *G. Sato 5250* (PE); Fengcheng Shi, Feng-huang-shan, *Z. Wang 1611* (PE). **Shandong:** Pingyi Xian, Meng-shan, *T. Y. Zhou 6389* (PE); Qingdao Shi, Lao-shan, *F. N. Meyer 275* (A, DS, UC); Yantai Shi, Kun-yu-shan, *Shandong Wild Pl. Exp. 89* (PE). **Zhejiang:** Anji Xian, Tian-mu-shan, *Y. Y. Ho 22113* (IBSC, PE); Lin'an Shi, Da-ming-shan, *Y. Y. Ho 23309* (IBSC, MO, PE); Tiantai Xian, *G. R. Chen 2442* (KUN, PE); Zhuji Shi, *Y. Y. Ho 24026* (IBSC, MO). JAPAN. **Hokkaido:** Haku-unloke, *collector unknown* (K), in 1887 (A); Sapporo, Yezo, 1903, *S. Arimoto s.n.* (GH, MO); Hakodate, 1861, *K. I. Maximovicz s.n.* (BM); Shirileshi, Okushiri, 1890, *K. Miyabe & E. Tokubuchi s.n.* (GH); Furano City, Yamabe, *K. Sohma & M. Takahashi 535* (A, MO). **Honshu:** Aomori Pref., Shimokita-gun, Kawauchi-cho, *K. Deguchi 5737* (MO); Fukui Pref., Nanjo-gun, Imajo-cho, N slope of Yashaga-ike, *G. Murata & H. Nishimura 5663* (A, AAU, KYO, L, PE, TI); Gifu Pref., Ohno-gun, Takane-mura, Dohgo-gawa, *H. Kanai & H. Ohashi 731182* (BM, BR, E, K, L, UC); Gumma Pref., Tano-gun, Uenomura, Narahara, betw. Akegasawa & Shionosawa, *J. Murata 1769* (A); Hyogo Pref., Tabu-gun, Oya-cho, Ikada, Tentaki, *G. Murata 1030* (A, AAU, C, E, L, MO, UC); Ishikawa Pref., Shiramine-mura, Akatani, Akatani-rindo, *S. Tsugaru et al. 22237* (KYO); Iwate Pref., Morioka, Mt. Iwayama, *H. Muroi 5028* (A); Kyoto Pref., Kitakuwata-gun, Miyama-cho, Ashiu, from Sugou to Kadzura-goya, *M. Ito et al. 1293* (TI); Miyagi Pref., Mono-gun, Kitakami-machi, Yoogai, S side of Okinakura-yama, *D. E. Boufford & E. W. Wood 25412* (A, CAS, E, MO); Nagano Pref., Suwa-gun, Fujimi-cho, Hanaba, Shiraya-zawa, *T. Shimizu 22540* (AAU); Nara Pref., Mt. Kurokami-yama, *H. Muroi 6962* (A); Niigata Pref., Minami-uwonuma, Mikuni, *Y. Ikegami 2628* (A); Saitama Pref., Chichibu-gun, Kamiizumi-mura, Inamura, *J. Murata et al. 1790* (AAU[2], PE); Shiga Pref., Ika-gun, Kinomoto-cho, Harikawa, *G. Murata & S. Kitamura 3362* (AAU, C, E, K, L, UC); Shimane Pref., Lishi-gun, Tonbara-cho, Mt. Oyorogi, *K. Mimoro & S. Thugaru 3195* (A, MO); Tochigi Pref., Nikko, 1864, *S. Tschonoski s.n.* (A, BM, C, K); Tokyo Pref., Nishitama-gun, Mt. Mitake-Nanayo Fall, *S. Kobayashi 1055* (CAS); Yamagata Pref., Nishi-murayama-gun, Nishikawa-machi, upper Mazawa River, *S. Tsugaru & T. Takahashi 6607* (MO). NORTH KOREA. **Locality unknown:** 1963, *collector unknown* (IBSC); Wolgoic Jongsan, 1914, *R. G. Mills s.n.* (PE). SOUTH KOREA. **Cheju:** Halla-san, *T. Taquet 3036* (A, C, E). **Kangwon:** Kongo-san, *E. H. Wilson 10422* (BM, K). **Kyonggi:** near Duigen, *E. H. Wilson 8467* (A). **North Chungchong:** Hwanghak-san, 33 mi. SE of Taejon, *Chung In Cho 8276* (E). **North Kyongsang:** Port Chusan, *C. Wilford 934* (A, K). **Seoul City:** Tobong-san, *R. Moran 5209* (BM, BR, E, GH, L, MO, UC). **South Kyongsang:** S'onch'ong Dist., slopes of Chiri-san, Chirisan Natl. Park, *F. Kirkham & Boyce KFBX86* (K).

10. Styrax odoratissimus Champ. ex Benth., Hooker's J. Bot. Kew. Gard. Misc. 4: 304. 1852 [as *S.* "*odoratissimum*"]. TYPE: China. Hong Kong: ravines of Mt. Victoria, *J. G. Champion 138* (holotype, K!; isotypes, E!, K[3]!).

Styrax prunifolius Perkins, Bot. Jahrb. Syst. 31: 486. 1902. TYPE: China. Province unknown: Pokfolanz [from Perkins, 1907], *Hillebrand s.n.* (holotype, B destroyed).

Styrax veitchiorum Hemsl. & E. H. Wilson, Bull. Misc. Inform. Kew 1906: 161. 1906 [as *S.* "*Veitchiorum*"]. TYPE: China. Hubei: Fang Xian, 2100–2400 m [protologue], June 1907, *E. H. Wilson 2015* (holotype, K not seen; isotypes, A[2]!, IBSC!).

Trees to 10 m tall. Young twigs sparsely short-yellow-brown stellate-pubescent; older twigs purplish or dark brown, glabrescent. Petiole 5–12 mm long. Two most proximal leaves on each shoot alternate. Lamina 4–15 × 2–8 cm, chartaceous to thick-chartaceous, ovate, ovate-elliptic, or elliptic, dull light green to yellow-green at maturity when dry; apex acute to short-acuminate; base broadly cuneate to rounded; adaxially usually glabrous except midvein, abaxially usually glabrous except midvein and axils of secondary veins, sometimes yellow-brown stellate-tomentose or -hirsute but surface remaining visible through the pubescence; margin entire or remotely serrulate apically, secondary veins 6 to 9 on each side of midvein; tertiary veins subparallel, densely, adaxially plane or slightly sunken, abaxially prominent. Fertile shoots 7–15 cm long, 3- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- to 2-flowered or racemose, 3–5 cm long, (3- to)5- to 7-flowered; pseudoterminal inflorescences usually racemose or rarely paniculate, 3–8 cm long, 5- to 7(to 11)-flowered, rarely 1-flowered, rachis and branches yellow stellate-tomentose. Pedicel 4–9 mm long, yellow stellate-tomentose; bracteoles 2–4 mm long, subulate, positioned at various places along the pedicel but mostly near the base, more rarely near the middle. Flowers 1–1.5 cm long. Calyx 3–4(–5) × 3–4 mm, cupuliform; adaxially glabrous; abaxially yellow stellate-tomentose, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry; margin truncate, undulate, or irregularly lobed, the teeth minute, not contiguous if present. Corolla 0.6–1.0 cm long, white, tube 3–4 mm long, glabrous, lobes 5(6), 9–11 × 4–6 mm, 1.7–2.2 × as long as wide, elliptic to obovate-elliptic. Stamens 10(12); filaments 1.5–3 mm long, slightly flexuous at middle, proximally broadened, distally attenuate, densely white stellate-pubescent throughout; anthers 4–5 mm long, wider than distal portion of filament; connectives (at least proximally) densely appressed-stellate-pubescent. Style densely white stellate-pubescent nearly throughout, distally thinning; stigma 0.2–0.5 mm wide, punctiform. Fruit 0.8–1.0 × 0.6–0.8 cm, usually subglobose, occasionally ovoid, apex rostrate, rarely merely apiculate, dehiscent; pericarp dry, (0.3–)0.5–1.0 mm thick, outside smooth or slightly rugose, gray-yellow stellate-tomentose, inside sparsely appressed-stellate-pubescent. Seeds brown, ovoid, slightly rugose, usually appressed-stellate-pubescent or lepidote, rarely glabrous.

Illustrations. Miers, Contr. Bot. I: t. 29. 1851–1861; Hu, Bull. Fan Mem. Inst. Biol. 3: pl. 16. 1932; Anonymous, Ic. Cormophyt. Sin. 3: 336, fig. 4626. 1974; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1620, fig. 813. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 101, pl. 34 (1–5). 1987; J. Q. Liu in L. G. Lin, Fl. Fujian. 4: 352, fig. 285. 1989; X. M. Liu in X. H. Qian, Fl. Anhui 4: 67, fig. 1771. 1991; S. Y. Wang in B. Z. Ding, Fl. Henan 3: 231, fig. 1776 (1–2). 1997; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 203, fig. 203 (1–6). 2000.

Phenology. Flowering: March–July, September. Fruiting: March–November.

Distribution. China (Anhui, Fujian, Guangdong, Guangxi, Guizhou, Hong Kong, Hubei, Hunan, Jiangsu, Jiangxi, Shanxi, Sichuan, Yunnan, and Zhejiang); Figure 9.

Habitat. In relatively mesic, semi-open, broad-leaved forests on mountain slopes, along streams in ravines; 30–2100 m.

Vernacular names. Bai-mu (China, Guangxi; *G. X. Li 54*), Er-huan-dong-gua (China, Hunan; *P. C. Tam 61731*), Fen-fang-an-xi-xiang (Hwang, 1980), Gou-len-cai (China, Guangdong; *K. P. To et al. 12645*), Guang-ye-mo-li-bao (China, Guizhou; *P. C. Tsoong 681*), Hong-la-jiu-shu (China, Guangdong; *W. T. Tsang 20435*), Huang-ye-shu (China, Anhui; *Exp. Anhui 2376*), Ji-gu-duan (China, Jiangxi; *J. Xiong 1860*), Mao-ye-mo-li (China, Zhejiang; *Y. Y. Ho 24610*), Mao-ye-shui-dong-gua (China, Guangxi; *S. Q. Chen 14692*), Niu-zi-shu (China, Jiangxi; *C. M. Hu 5271*), Ru-bai-ye-mo-li (Hwang & Qi, 1985), Shan-long-yan (China, Guangdong; *W. T. Tsang 21712*), Shuang-chi-shan-mo-li (China, Hunan; *Z. H. Shen 1235*), Ye-jin-gu (China, Zhejiang; *Zhejiang Bot. Res. Team 25888*), Ye-ling-li (China, Zhejiang; *Y. Y. Ho 26445*), Yu-xiang-ye-mo-li (China, Shanxi; *T. W. Liu & Z. B. Zeng 1372*), Xiang-ye-ye-mo-li (China, Zhejiang; ***Zhejiang Bot. Res. Team** 28350*), Yu-xiang-ye-mo-li (Anonymous, 1974).

The Chinese endemic species *Styrax odoratissimus* is one of the most common and widespread species treated in this revision. This species is most abundant in eastern and southeastern China, gradually decreasing in abundance northward and westward.

Styrax odoratissimus exhibits much morphological variation across its range. The lower laminar surface is mostly glabrous, but is sometimes stellate-tomentose or -hirsute, although the surface always remains visible through any pubescence present. In addition, leaf size, inflorescence length, and flower number vary significantly throughout the range of the species. It nonetheless can easily be distinguished from other sympatric species with imbricate corolla aestivation (i.e., *S. hemsleyanus*, *S. hookeri*, *S. japonicus*, *S. macrocarpus*, *S. supaii*, and

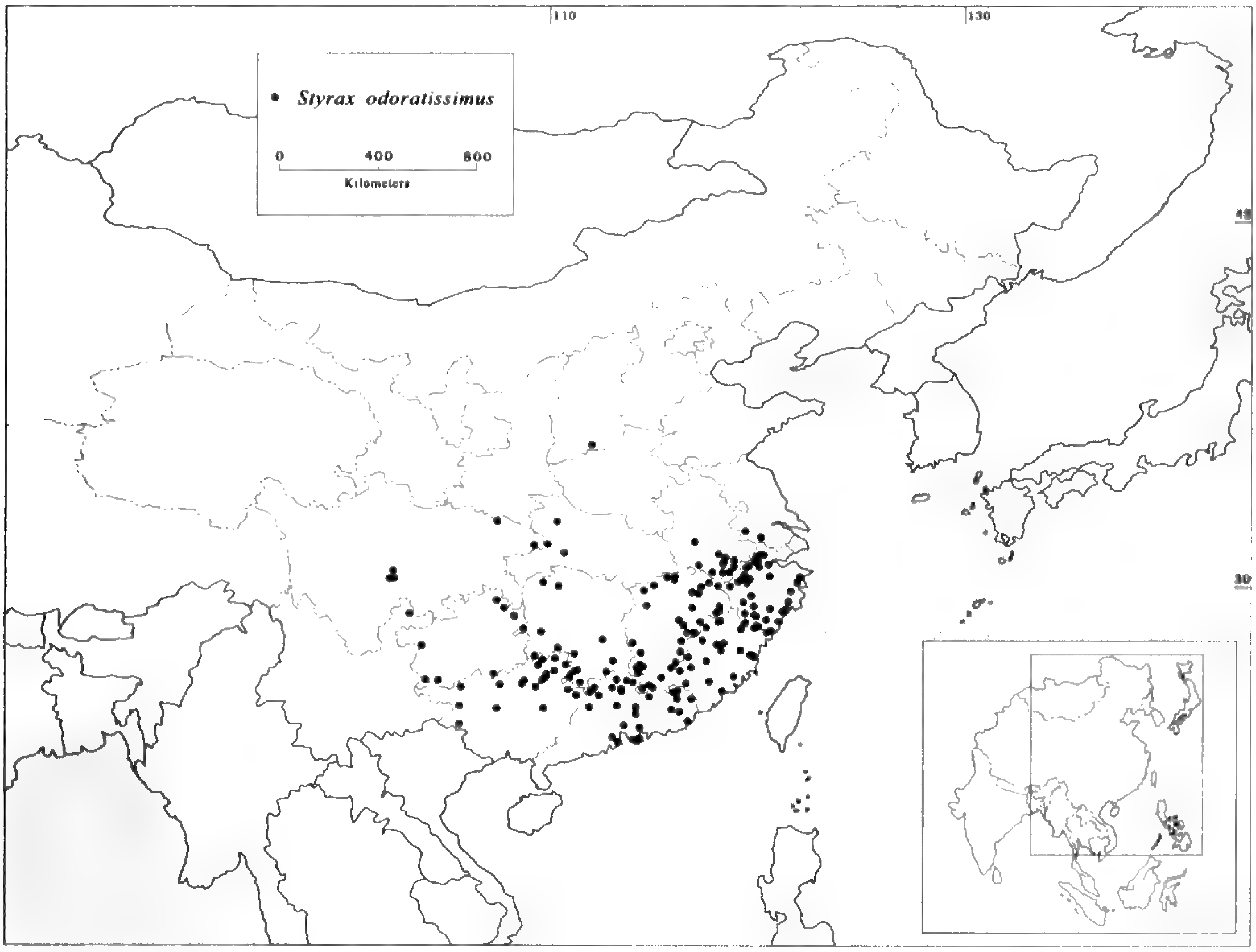

Figure 9. Geographic distribution of *Styrax odoratissimus*.

S. tonkinensis) by the combination of its distinctively flexuous filaments and densely pubescent stamens and styles. Furthermore, the appressed-stellate-pubescent or lepidote seeds often served to distinguish it from other species of *Styrax*, although some glabrous individuals exist. Sterile herbarium specimens can usually be distinguished from other sympatric species by leaves that are yellow-green in the dried state and often slightly scabrous adaxially. Moreover, the petiole and proximal portion of the midvein are both usually red-tinged in the living state. It is unknown whether this feature is restricted to this species within the genus, but it seems at least to distinguish *S. odoratissimus* from sympatric species.

Perkins (1907) considered differences in inflorescence length and the leaf margin sufficient to separate *Styrax veitchiorum* Hemsl. & E. H. Wilson, a species described from flowering material collected in Fang Xian, Hubei Province, China, from *S. odoratissimus*. Subsequently, Rehder (1912) identified fruiting material from the same county (*Wilson 308*) as *S. veitchiorum*. We consider the characters used by Perkins (1907) to separate these two taxa to vary continuously. The fruit of *S. veitchiorum* differs from that of most other fruiting collections of *S. odoratissimus* in its glabrous (vs. pubescent or lepidote) seeds. Glabrous seeds, however, appear sporadically in other individuals of *S. odoratissimus*. Because no other characters are apparent for use in delimiting the two entities, our treatment follows that of Hwang (1987) in placing *S. veitchiorum* as a synonym of *S. odoratissimus*.

Perkins (1902) described *Styrax prunifolius* Perkins based on a specimen from China (*Hillebrand s.n.*) but later (1907) treated this species as a synonym of *S. odoratissimus*. We assume that the holotype of *S. prunifolius* was at B because that is where Perkins conducted her work on *Styrax*, and that this has been destroyed. Having seen no duplicate material of *Hillebrand s.n.*, we here place *S. prunifolius* under *S. odoratissimus* following the precedent set by Perkins (1907), and in considering its similarity to *S. odoratissimus* as inferred from the original description.

Some specimens of *Styrax odoratissimus* collected at the northwestern edge of the species' range, especially on and near Mt. Emei (E-mei-shan in Pinyin) in Sichuan Province, exhibit atypical features (i.e., a more cylindrical fruit, larger leaves, and glabrous seeds; e.g., *China-USSR team 1853*; *Ching & Shun 80*; *H.-C. Chow 7547* and *8016*; *Rev. E. Faber 195*; *W. P. Fang 2462, 7560, 12624,* and *16790*; *X. Y. Huo 5654*; *C. B. Peng 6070*; *S. L. Sun 540*; *T. H. Tu 347* and *407*; *G. H. Yang 55029*). Several of these have been identified as *S. hemsleyanus*, but are easily distinguished from that species by the alternate (vs. subopposite to opposite) arrangement of the two most proximal leaves on each shoot. Furthermore, the fruits available for study from these specimens are rostrate, as in *S. odoratissimus*, and the flower buds (no open flowers are available for study) do not deviate from the range of variation within *S. odoratissimus* as defined here (e.g., the filaments and styles are densely pubescent throughout, the connectives are slightly pubescent, and the filaments are flexuous). The atypical fruits and seeds observed in these specimens are distributed sporadically across the range of *S. odoratissimus*, i.e., in the provinces of Anhui (*C. S. Fan & Y. Y. Li 221*), Guangdong (*H. G. Liu 490* and *P. C. Tam 58332*), Guangxi (*L. X. Chen 500159*), Hunan (*P. H. Liang 83722*), and Yunnan (*B. X. Sun et al. 254*) in addition to Sichuan and Hubei mentioned above, and thus have no apparent taxonomic significance. Thus, we place the Emei specimens under this species, with the caveat that specimens collected at anthesis would be highly desirable for corroboration.

The closest relatives of *Styrax odoratissimus* appear to be several species from the southern part of the range of *Styrax* in Asia. These include *S. buchananii*, *S. chrysocarpus*, *S. curvirostratus*, *S. porterianus*, and *S. subpaniculatus*. The relationships among these species are not well understood, but each shares with *S. odoratissimus* the alternate arrangement of the two most proximal leaves on each shoot; a lower laminar surface that is visible through any pubescence that may be present (vs. a tomentum that obscures the surface); a calyx that is truncate, undulate, or irregularly lobed, the teeth not contiguous if present, and the outer surface within 1 mm of the margin more sparsely pubescent than the rest of the calyx or subglabrous to glabrous, somewhat scarious, and brown when dry, but without scattered orange or brown stiff long stellate pubescence. Differences between *S. odoratissimus* and these species are addressed in respective discussion sections of each species.

Selected specimens examined. CHINA. **Anhui:** Dongzhi Xian, Xiang-ling, *C. M. Tan 971113* (PE); Huangshan Shi, Huang-shan-qu, Huang-shan, *M. J. Wang 3780* (IBSC, PE); Jingde Xian, Ou-yuen, *P. Courtois 25676* (P); Jixi Xian, *Exp. Anhui 1059* (PE); Qimen Xian, Li-xi, Ku-liu-feng, *Y. F. Xiao & W. Z. Xie 152* (IBSC); Qingyang Xian, Jiu-hua-shan, *S. C. Sun 1204* (A); She Xian, Huang-shan, *M. Chen 1061* (IBSC, PE); Shucheng Xian, Wan-fu-shan, *M. P. Deng 11153* (PE); Xiuning Xian, Wu-cheng, *Exp. Anhui 2344* (PE). **Fujian:** Changting Xian, Gui-long-shan, *C. M. Hu 3737* (IBSC, KUN, PE); Chong'an Xian, Xin-chun-xiang, *Exp. Wu-yi-shan 11* (IBSC, PE); Fuding Xian, Tong-mu-xiang, Tong-shan, *P. X. Qiu 1487* (PE[2]); Fuzhou Shi, hillside near University Foo-chow, *T. S. Ging 7524* (A); Guangze Xian, Chu-fu-xiang, Xia-yang-da-dui, *Y. T. Zhang 79025* (IBSC); Gutian Xian, *Y. G. Yan 6215* (KUN); Hua'an Xian, Xin-kou, *P. C. Tsoong 648* (IBSC[2], PE); Liancheng Xian, Zhang-di-jing, 1932, *Y. Ling s.n.* (PE); Minhou Xian, *H. H. Chung 2742* (A, UC); Nanping Shi, Yan-dang-shan, *G. S. He 4256* (MO); Ninghua Xian, Hui-hua, Shui-kou-xiang, *K. M. Wu 60225* (IBSC); Shanghang Xian, Bu-yun, *Exp. Wu-yi-shan 6839* (PE); Sha Xian, Xi-qing, *Pl. Res. Exp. in Fujian 52459* (IBSC); Shouning Xian, *R. C. Ching 2241* (A[2], IBSC, UC); Shunchang Xian, Tian-ping, Hou-shan, *M. S. Li & Z. Y. Li 4584* (PE); Taining Xian, Long-an, Chen-keng, Wu-niu-wan-shan, *M. S. Li & Z. Y. Li 252* (IBSC); Xiamen Shi, Ban-tou Reservoir, *G. L. Cai 38* (IBSC); Yong'an Xian, *D. S. Wang 453* (PE); Yongchun Xian, Fang-guang, *collector unknown 273* (PE); Zhenghe Xian, *H. H. Chung 2615* (A, IBSC, PE, UC). **Guangdong:** Dabu Xian, Tong-gu-shan, *W. T. Tsang 21712* (A[3], BM, IBSC, K, PE[2], UC); Fengshun Xian, Da-tian-xiang, Bei-xi, *X. G. Li 200955* (IBSC, PE); Heping Xian, Li-ming-shan, *G. C. Zhang 256* (IBSC); Huaiji Xian, Hei-chong, Yuan-shan-lin-chang, *Z. Y. Li 1681* (MO); Huiyang Shi, Luo-fu-shan, Hua-sou-tai, *N. K. Chun 41677* (IBK, IBSC, KUN, PE); Jiaoling Xian, Si-hu-xiang, *L. Tang 4630* (IBSC, PE); Lechang Shi, Heo-tse-ling, Da-lang, *Y. Tsiang 1386* (A, IBSC, UC); Liannan Yaozu Zizhixian, Jin-keng-xiang, *P. C. Tam 59535* (PE); Lianshan Zhuangzu Yaozu Zizhixian, He-gang-xiang, Huang-niu-shan, *P. C. Tam 58332* (IBK, IBSC, PE); Lianzhou Shi, Xin-jiu-xiang, *Exp. Nan-ling 272* (IBSC); Longmen Xian, San-jiao-shan, Cong-hua, *W. T. Tsang 20435* (PE); Meizhou Shi, Mei-song-dong, *X. G. Li 202464* (IBK, IBSC, PE); Nanhai Shi, Shih-pi-keng, Hao-shan, *S. S. Sin 9444* (A); Pingyuan Xian, Cha-gan-xiang, Huang-zhu-ping, *L. Tang 4380* (IBSC, PE); Qujiang Xian, Long-tou-shan, *S. P. Ko 50337* (IBK, IBSC, MO, PE); Renhua Xian, Jen-hwa Dist., Shi-bi-xia-cun, Wan-chi-shan, *W. T. Tsang 26345* (A, E, IBSC); Ruyuan Yaozu Zizhixian, Qing-xi-dong, *S. P. Ko 52889* (A, IBK, IBSC); Shantou Shi, Wu-king-fu, 60 mi. W of Swa-tow, *J. M. Gilchrist 79* (IBSC); Shaoguan Shi, *Exp. Guangdong 1244* (IBSC); Shixing Xian, Chang-keng, Che-ba-ling, *C. L. Zhang 56031* (MO); Wuhua Xian, Chang-bu-xiang, Qi-mu-shan, *X. G. Li 201687* (IBK, IBSC, PE); Xinfeng Xian, Ah-p'o-kai-shan, Cha-ping-cun, *Y. W. Taam 721* (A, CAS, K, KYO); Yangshan Xian, Wu-yuan-xiang, *L. Tang 1069* (IBSC, KUN); Yingde Shi, Sha-kou-xiang, Hua-shui-shan, *C. Huang 163471* (IBSC); Zengcheng Shi, Nan-kun-shan, *W. T. Tsang 20301* (PE). **Guangxi:** Bose Shi, Wu-lao-shan, *Exp. S China 2658* (IBSC); Du'an Yaozu Zizhixian, He-jing-xiang, Mao-er-shan, *Exp. Guangxi 455* (IBSC, KUN, PE); Fuchuan Yaozu Zizhixian, Ku-cun, *S. S. Sin 21326* (IBSC); Guilin Shi, Da-jiang-yuan-cun, Jin-gang-shan, *W. T. Tsang 28311* (A, IBSC); Hezhou Shi, Xi-shan-xiang, *H. C. Chen et al. 500072* (IBK, IBSC); Huanjiang Maonanzu Zizhixian, Wu-hua-shan, Jiu-ren, *H. N. Qin 895180* (K); Jingxi Xian, Biao-lin-xiang, Long-yang-shan, *S. P. Ko 55648* (A, IBSC); Jinxiu Yaozu Zizhixian, Niu-xiang-xiang, Da-ling, *D. H. Qin et al. 65266* (PE); Leye Xian, Niu-wei, Ba-wang-shan, *Exp. Hong-shui-he 1085* (KUN);

Lingchuan Xian, Qi-fen-shan, *Z. Z. Chen 53822* (KUN); Lingui Xian, Huang-sha-xiang, *Z. Z. Chen 51016* (IBK, IBSC, KUN, PE); Longsheng Gezu Zizhixian, Da-di-xiang, *Guang-fu Coll. Team 707* (IBK, IBSC, KUN, PE); Quanzhou Xian, Shan-chuan-xiang, Bao-ding-shan, *C. H. Tsoong 83331* (IBK, IBSC, PE); Xing'an Xian, Wu-tong-shan, *T. M. Tsui 250* (A, IBSC, K, PE); Yongfu Xian, He-shun-xiang, *G. X. Li 54* (IBK, IBSC); Ziyuan Xian, Chuen yuen, *T. S. Tsoong 82058* (A, IBK). **Guizhou:** Anlong Xian, Shi-pan-xiang, Shi-hui-dui, *Exp. Guizhou 2924* (PE); Jiangkou Xian, Fan-jing-shan, *Exp. Hunan & Guizhou (1983) 2626* (KUN); Libo Xian, Wei-zi, *X. H. Song 185* (MO); Shuicheng Xian, *P. C. Tsoong 437* (KUN); Wuchuan Xian, Lian-tai-shan, *P. C. Tsoong 681* (KUN, PE[2]); Yinjiang Xian, Qing-du-he, Fan-jing-shan, *Z. S. Zhang et al. 402501* (IBSC). **Hongkong:** N of Shou-son Hill, Hong Kong Island, *B. Bartholomew 1916* (CAS). **Hubei:** Badong Xian, Ge-zi-he, *Z. Y. Wang 618* (PE); Fang Xian, *E. H. Wilson 308* (A, BM, E, K); Yichang Shi, 1888, *A. Henry s.n.* (K). **Hunan:** Cili Xian, Suo-xi-yu Nature Reserve region, *X. Y. Xi et al. 443* (PE); Dao Xian, Niu-tou-jiang, *P. C. Tam 61731* (IBK, IBSC); Hengyang Shi, Li-mu-you, *P. C. Tam 62348* (IBK, IBSC); Jianghua Yaozu Zizhixian, He-luo-kou-xiang, *B. G. Li 5149* (IBSC); Lingling Xian, Yang-ming-shan, Huang-jiang-yuan, *S. Q. Chen 674* (IBK, IBSC); Qianyang Xian, Huai-hua, *X. G. Li 203380* (IBSC); Sangzhi Xian, Bao-mao-xi, *T. R. Cao 90621* (KUN); Tongdao Dongzu Zizhixian, *T. C. Chen 1028* (IBSC); Xinhuang Dongzu Zizhixian, Tian-lei forest farm, *Zhong-nan-lin-shi-xi-dui 163* (IBSC); Xinning Xian, Jin-shi-zhen, Dong-tou-cun, *L. B. Luo 93* (BM, BR, CAS, IBSC, PE); Yizhang Xian, Mang-shan, Jin-quan-xiang, *P. H. Liang 83707* (IBK, IBSC, MO); Zixing Shi, Ping-jiang-xiang, Luo-jia-qiao, *P. H. Liang 86298* (IBSC, MO). **Jiangsu:** Yixing Shi, Long-chi-shan, *S. H. Mao et al. 44* (IBK, KUN, MO, PE). **Jiangxi:** Anyuan Xian, Du-jiang-xiang, *C. M. Hu 2758* (IBK, IBSC, KUN, PE); Boyang Xian, Li-ming-shan, *Q. H. Li & C. Chen 1146* (PE); Chongren Xian, Kou-ling, Tsoong-jen, *Y. Tsiang 10140* (IBSC, UC); Chongyi Xian, Mi-xi, Ji-gong-zui, *M. Q. Nie et al. 8625* (IBK, IBSC, KUN); Dayu Xian, Huang-long, *M. Q. Nie et al. 6700* (IBSC); Dingnan Xian, Da-cha, *J. Xiong 1860* (PE); Dongxiang Xian, *Q. H. Li & C. Chen 1470* (PE); Guangchang Xian, Ping-fang-xiang, *C. M. Hu 5271* (IBSC, PE); Huichang Xian, Fu-cheng-xiang, *C. M. Hu 3342* (IBK[2], IBSC, KUN, PE); Jingdezhen Shi, Fu-liang, Xi-hu-xiang, *Q. H. Li & C. Chen 834* (PE); Jinggangshan Shi, *S. K. Lai et al. 5008* (IBSC); Jiujiang Shi, Lu-shan, Sai-yin, *M. X. Nie 7265* (KUN); Leping Shi, Li-jun-shan, Da-he-shan, *Q. H. Li & C. Chen 1335* (PE); Lichuan Xian, Yan-chuan-qu, Wu-yi-shan, *M. X. Nie & S. S. Lai 2881* (IBSC, KUN[2]); Longnan Xian, Wu-zhi-shan, near Lin-wu-dong-cun, *S. K. Lau 4432* (A, BM); Nanfeng Xian, San-xi-xiang, *X. X. Yang 650492* (IBSC, PE); Nankang Xian, *X. X. Yang 650367* (IBSC); Quannan Xian, Zhu-shan-xiang, Yao-shan, *J. Xiong 723* (PE); Ruijin Shi, Qing-xi-xiang, Lian-tang, *C. M. Hu 4252* (IBSC, KUN[2], PE); Shangrao Shi, Wu-yi-shan, *M. X. Nie & S. S. Lai 4331* (IBSC, KUN); Shangyou Xian, Guang-gu-shan, *M. Q. Nie et al. 8342* (IBK, KUN); Shicheng Xian, Jing-kou-xiang, *C. M. Hu 4585* (KUN, PE); Suichuan Xian, Qi-ling-xiang, *S. K. Lai et al. 235* (PE); Wuning Xian, Yi-shan-gong-she, *S. S. Lai 2464* (KUN, PE); Xiushui Xian, Huang-sha-gang, Xiang-jia-ping, *S. S. Lai 3458* (KUN); Yifeng Xian, Guan-shan, Xi-keng, *S. K. Lai et al. 433* (PE); Yihuang Xian, Bai-zhu-xiang, *X. X. Yang 16820* (IBSC); Zixi Xian, Ma-tou-shan-xiang, Wu-yi-shan, *M. X. Nie & S. S. Lai 3530* (IBSC, KUN). **Shanxi:** Yangcheng Xian, Gan-qi-tong, Shu-pi-gou, *T. W. Liu & Z. F. Zeng 235* (MO). **Sichuan:** Emeishan Shi, E-mei-shan, *W. P. Fang 2462* (A, IBSC, K, PE); Fengjie Xian, Xin-he-xiang, *H. F. Zhou 26228* (KUN); Hongya Xian, Chang-tsun, *T. H. Tu 347* (PE); Wanyuan Shi, *K. L. Chu 1266* (IBSC). **Yunnan:** Yanjin Xian, Cheng-feng-shan, *Exp. NE Yunnan 1163* (KUN). **Zhejiang:** Anji Xian, Long-wang-shan, *W. C. Wang L8532018* (IBSC); Chun'an Xian, Lin-qi-xiang, Xia-keng, *Zhejiang Bot. Res. Team 27581* (MO, PE); Hangzhou Shi, Bei-gao-feng, Ning-ying-shi, *S. Y. Chang 1512* (MO); Jiande Xian, from Jian-de to Shuang-xi-kou, *Y. Y. Ho 29245* (MO); Kaihua Xian, Gu-tian-miao, *J. X. Wang 2099* (PE); Lin'an Shi, Shun-xi, *G. B. Li J8112140* (PE); Lishui Shi, Da-gang-tou, Xiao-jing, *S. Y. Zhang 6054* (KUN, PE); Longquan Shi, Feng-yang-shan, *H. Y. Zou 123* (A); Pingyang Xian, Suan-ke, S of Ping-yung, *R. C. Ching 2080* (A, IBSC, K, UC); Qingtian Xian, Tsimp-tien, *Y. L. Keng 211* (A, PE); Qingyuan Xian, Long-gong, *S. Y. Zhang 3450* (PE); Suichang Xian, Qiu-jia-ping, *R. C. Ching 1622* (A, UC); Taishun Xian, Jin-fen, Liao-yan, *S. Y. Chang 8514* (MO); Tiantai Xian, Tian-tai-shan, *R. C. Ching 1434* (A, IBSC); Wencheng Xian, Da-jun, Jing-ning, *S. Y. Chang 5178* (MO); Wuyi Xian, Xi-lian-xiang, *R. J. Jin et al. J8311012* (IBSC); Xianju Xian, *S. Y. Chang 7772* (MO); Yunhe Xian, Chen-chiong, 40 mi. S of Sia-chu, *R. C. Ching 1809* (A, E, IBSC, UC); Zhuji Shi, Wu-qian, *X. B. Li et al. J8212029* (PE).

11. Styrax porterianus G. Don, Gen. Hist. 4: 5. 1838 [as *S.* "*Porterianum*"]. *Styrax serrulatus* var. *rugosus* Steenis, Bull. Jard. Bot. Buitenzorg, sér. 3, 12: 249. 1932. TYPE: Malaysia. Pulau Pinang: Pinang, *Wall. Cat. No. 4401* (*G. Porter s.n.*) (holotype, BM!; isotypes, K[3]!).

Styrax floribundus Griff., Not. Pl. Asiat. 4: 287. 1854 [as *S.* "*floribunda*"]. TYPE: Myanmar. Tenasserim: between Kulweng and Mergue, Apr. 1835, *W. Griffith s.n.* (lectotype, designated here, K [loan accession no. H2000/01016-380]!; isotypes, K [loan accession no. H2000/01016-39]!, E!).

Styrax betongensis H. R. Fletcher, Bull. Misc. Inform. Kew 1937: 509. 1938. TYPE: Thailand. Pattani: Betong, 200 m, 6 Aug. 1923, *A. F. G. Kerr 7494* (holotype, K!; isotypes, BM!, E!, K!).

Trees to 20 m tall. Young twigs dull red or gray tomentose; older twigs gray, glabrescent. Petiole 3–7 mm long. Two most proximal leaves on each shoot alternate. Lamina 5–11 × 3–5 cm, membranaceous or thin-chartaceous, ovate- to elliptic-oblong, green to dark green at maturity when dry; apex slightly acuminate; base usually oblique-rounded, rarely oblique-cuneate, short-attenuate; adaxially glabrous except along the major veins; abaxially glabrous or sparsely to densely white stellate-pubescent, pubescence especially prevalent on veins and the most proximal two leaves on each shoot, surface remaining visible through the pubescence; margin entire or usually remotely serrulate; secondary nerves 5 or 6 on each side of midvein; tertiary veins ± parallel and perpendicular to the secondaries, faintly prominent on both sides. Fertile shoots 5–12 cm long, 2- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- to 2-flowered or racemose, 2–3 cm long, 1(to 5)-flowered; pseudoterminal inflorescences racemose, 2–4 cm long, 3- to 5(7)-flowered, rachis red-gray stellate-tomentose. Pedicel 3–10 mm long, densely stellate-pubescent; bracteoles 0.5–2 mm long, linear, positioned at various places along the pedicel but mostly near the base, more rarely near the middle, sometimes those toward the base of the inflorescence leaf-like. Flowers 0.7–1.3 cm long. Calyx 3–4 × 3–4 mm, campanulate; adaxially glabrous or sparsely short-appressed-stellate-pubescent; abaxially gray stellate-tomentose, within 1 mm from the margin more sparsely pubescent, somewhat scarious, brown when dry; margin truncate, undulate, or slightly 5-lobed, the teeth minute and not contiguous. Corolla 0.5–0.9 cm long, white, tube 2–3 mm long, glabrous proximally, lobes 5, 10–11 × 3–4 mm, linear-lanceolate, apex acute-acuminate, adaxially sparsely stellate-pubescent, abaxially densely so. Stamens 10; filaments 3–4 mm long, straight or flexuous at middle, distally attenuate, moderately to densely white stellate-pubescent on both sides, thinning to glabrous distally; anthers 3–4.5 mm long, wider than distal portion of filament; connective glabrous. Style glabrous; stigma 0.4–0.5 mm wide, subcapitate. Fruit 0.9–1.5 × 0.8–1.2 cm, subglobose to globose, apex rounded or short-apiculate, indehiscent; pericarp fleshy, ca. 2 mm thick, outside deeply rugose when dried, gray stellate-tomentose, inside glabrous. Seed brown, ellipsoid to ovoid-ellipsoid, nearly smooth, glabrous.

Illustrations. Miers, Contr. Bot. I: t. 29. 1851–1861; Steenis, Bull. Jard. Bot. Buitenzorg, sér. 3, 12: 222, fig. 3 (5). 1932 (as *S. serrulatus* var. *rugosus*). F. E. Putz & F. S. P. Ng, Tree Flora of Malaya 3: 265, fig. 1. 1978 (as *S. serrulatus* var. *rugosus*).

Phenology. Flowering: March–May, July. Fruiting: March–May, July, August, November.

Distribution. Malaysia (Kedah, Pahang, Perlis, and Pulau Pinang), Myanmar (Tenasserim), and Thailand (Chumphon, Krabi, Nakhon Si Thammarat, Pattani, Phangnga, Phuket, Satun, Songkhla, Surat Thani, and Trang); Figure 4.

Habitat. In mesic, mixed primary forests; 50–400 m.

Vernacular names. Fa La Mi Bai Leg (Thailand; *S. Phusomsaeng 241*), Kam Yan (Thailand; *A. F. G. Kerr 7494*), Lang Ka Re (Thailand; *A. F. G. Kerr 15300*), Pang Ka Re (Thailand; *A. F. G. Kerr 18505*).

Styrax porterianus is the only species of *Styrax* with imbricate corolla aestivation known from the Malay Peninsula, where it is endemic. *Styrax porterianus* appears to be most closely related to *S. odoratissimus* and *S. subpaniculatus.* All three species share relatively small flowers, a truncate, undulate, or irregularly lobed calyx margin, and an abaxial laminar surface usually visible through any pubescence present. Furthermore, they all occur at relatively low elevations. *Styrax porterianus* is easily distinguished from *S. subpaniculatus* by its shorter raceme and thinner, dry and rigid pericarp, and from *Styrax odoratissimus* by the characters in couplet 20 of the key.

Despite the placement of *Styrax porterianus* into series *Imbricatae* by Perkins (1907), Steenis (1932) considered this species to be a variety of *S. serrulatus* (var. *rugosus* Steenis). Perkins (1907) placed *Styrax serrulatus* in series *Valvatae* based on its valvate corolla aestivation. Steenis's concept of *S. serrulatus,* however, contained both imbricate and valvate types of aestivation based on Perkins's (1907) assertion that this and several other species in series *Valvatae* include individuals that exhibit a mixture of these types, even within the same flower. In contrast, we consider aestivation type to be a reliable taxonomic character with which to distinguish *S. porterianus* from *S. serrulatus.* In several species of series *Cyrta* (those listed by Perkins under series *Valvatae* and several other more recently described species), a subvalvate condition occurs whereby the edges of the corolla lobes are contiguous but oblique in cross section (see Steenis, 1932: fig. 10c). This is qualitatively different, however, from the strictly imbricate corolla aestivation observed in all specimens of *S. porterianus* (see Steenis, 1932: fig. 10d).

Styrax porterianus differs from *S. serrulatus* s. str. in other aspects of both the foliage and fruit, as Steenis recognized. In *S. porterianus,* the margin of the lamina is entire or at most remotely denticulate, whereas that of *S. serrulatus* is distinctly toothed. The fruit of *S. porterianus* has a fleshy pericarp at maturity (Putz & Ng, 1978; unique among species of section *Styrax*) that is rugose and ca. 2 mm thick in the dried state. In contrast, the pericarp of *S. serrulatus* is dry and rigid at maturity, nearly smooth, and less than 1 mm thick. Furthermore, the ranges of these two entities are geographically distinct, with *S. serrulatus* in the Himalayan region and not extending as far south as the Malay Peninsula (P. Fritsch, unpublished data). The sum of these differences warrants the recognition of *S. por-*

terianus at the species level. Fletcher (1938) appears to have understood the significance of these differences as well in describing *S. betongensis* H. R. Fletcher from Thailand, apparently unaware of the earlier name.

We have seen two sheets of W. Griffith's collection of *Styrax floribundus* from K and one from E. None of these display any indication of holotype status. Because Griffith's herbarium was transferred to K, we have chosen a lectotype from among the two K specimens. The two sheets offer little evidence for a decision on proper lectotypification, and we could not locate a literature source with a sample of Griffith's handwriting. On one of the K sheets, however, the locality is spelled as in the protologue ("Mergue"), whereas on the other it is spelled differently ("Mergui"), suggesting that the locality information on the latter was transcribed incorrectly some time after the original collection was made. On this basis, we have designated the sheet with the protologue spelling of the locality as the lectotype.

Additional specimens examined. MALAYSIA. **Kedah:** Jeniang, Kedah, bin Kiah, *Sidek S345* (C, L). **Pahang:** Tembeling, Ulu Sg., NW Tanjong Bungkal, *M. Shah Bin Haji Mohamad Nur & M. Noor MS2027* (C, L). **Perlis:** Kaki bukit, *M. S. Kiah bin Hadji 35302* (BM, K, L). **Pulau Pinang:** Pinang, *collector unknown* (BM), 1890, *collector unknown* (E), *C. Curtis 1538* (BM, L), *M. R. Henderson 18* (L); Pinang Island, 1824, *J. Phillips s.n.* (K); Peuara Bakir, 1896, *collector unknown* (BM); Polo Boelong, *collector unknown 1189* (K). THAILAND. **Chumphon:** Kao Po Ta luang Kaew, Ranong, *C. Niyomdham 339* (L). **Krabi:** Pen, Nong Khon, *B. Sangkhachand 1014* (C, K, L). **Nakhon Si Thammarat:** Tung Song, *N. Rabil Bunnag 92* (BM, K, L); Ban Kram, Nakawn Sritamarat, *A. F. G. Kerr 15300* (E[2], K); Ban Kram, Palatung, *A. F. G. Kerr 15302* (BM). **Phangnga:** Khao Phra Mi, *Flora of Thailand Project 4th Exp. (1972) 30878* (L); Nai chong, *R. Geesink & T. Santisuk 5275* (AAU, C, E, K, L). **Phuket:** Satul, Tung nui, *A. F. G. Kerr 14659* (BM, E, K); Kaokatawam, *A. F. G. Kerr 18505* (BM, E, K); Lanta, *A. F. G. Kerr 18988* (BM, E, K). **Satun:** Tarutao Natl. Park, from Talo Wao to Talo Oo Dang, *G. Congdon 507* (AAU). **Songkhla:** Dist. Haad Yai, Ko Hong Hill, *J. F. Maxwell 85346* (AAU, BM, E, L), *85535* (AAU, E, L); Lansagah Dist., Khao Luang Natl. Park, Gahrome Galls, Nakorns Itammarat, *J. F. Maxwell 85669* (L). **Surat Thani:** Klaung Jan, *A. F. G. Kerr 12519* (BM, E, K). **Trang:** Pen, Khao Chong, *S. Phusomsaeng 241* (AAU, C, E, L[2]).

12. Styrax rugosus Kurz, J. Asiat. Soc. Bengal, Pt. 2, Nat. Hist. 40(2): 61. 1871 [as *S.* "*rugosum*"]. TYPE: Myanmar. Pegu: hills between Sittang & Salween, 1212 m, *Brandis s.n.* (as *Brandis 936,* Perkins, 1907) (holotype, CAL not seen).

Shrubs or trees to 6 m tall. Young twigs yellow-brown stellate-tomentose; older twigs purplish and glabrescent. Petiole 2–3 mm long. Two most proximal leaves on each shoot alternate, or more often subopposite to opposite. Lamina 3–7 × 2–3 cm on fertile branches, those on sterile branches usually larger, to 9 × 4.5 cm, chartaceous, ovate-oblong, ovate, or elliptic; apex acute or more often acuminate; base rounded to broadly cuneate, often slightly oblique; adaxially rugose and densely covered with simple and 2- or 3-armed to stellate trichomes when young, becoming sparsely pubescent or rarely glabrous; abaxially gray-yellow stellate-tomentose; margin serrate or apically dentate, secondary veins 4 to 7 on each side of midvein, tertiary veins parallel, quaternaries as well as the tertiaries abaxially prominent and raised in young leaves. Fertile shoots (4–)6–10(–12) cm long, 3- to 5-flowered. Inflorescences arising from shoots of the current growing season; lateral inflorescences usually 1- or 2-flowered; pseudoterminal inflorescences racemose, 2–4(–6) cm long, 3- to 6-flowered, rachis yellow stellate-tomentose, also intermixed with stalked trichomes; bracteoles 4–12 mm long, linear, positioned at various places along the pedicel or at the base of the calyx, sometimes those toward the base of the inflorescence leaf-like, margin conspicuously serrate. Pedicel 3–4 mm long, stellate-tomentose. Flowers 1.4–1.6 cm long. Calyx 4.5–5 × 3.5–5 mm, cupuliform; adaxially sparsely appressed-pubescent with short white 2- or 3-armed or stellate trichomes; abaxially yellow stellate-tomentose throughout, often also with various amounts of larger scattered dark yellow or orange stiff stellate trichomes, especially proximally; margin distinctly dentate, the teeth usually contiguous or separated by a shallow concave portion; teeth 2–3 mm long, lanceolate to subulate, apex acuminate, densely stellate-pubescent on both sides. Corolla 1.0–1.2 cm long, white, tube 4–5 mm long, glabrous proximally, lobes 5, 5–10 × 4–5 mm, elliptic to obovate, adaxially subglabrous, abaxially densely pale yellow stellate-pubescent. Stamens 10; filaments 7–8 mm long, straight, of equal width throughout, densely white stellate-villous proximally, trichomes up to 0.5 mm long, becoming glabrous distally; anthers ca. 5 mm long, wider than distal portion of filament; connectives glabrous. Style glabrous or sparsely white stellate-villous; stigma 0.2–0.4 mm wide, punctiform. Fruit 0.7–0.9 × 0.5–0.6 cm, ovoid, apex rounded or apiculate, dehiscent; pericarp dry, 0.2–0.3 mm thick, outside irregularly longitudinally striate throughout, yellow-brown stellate-tomentose, inside glabrous or sparsely downy-pubescent. Seeds brown, ovoid, smooth, glabrous.

Illustrations. C. Y. Wu, Fl. Yunnan. 3: 426, pl. 121 (1–5). 1983; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1605, fig. 800. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 85, pl. 28 (7–12). 1987; W. Q. Yin in Y. C. Xu, Ic. Arbor. Yunnan. 2: 894, pl. 471 (1–6). 1990; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 198, fig. 198 (8–14). 2000.

Phenology. Flowering: March–July. Fruiting: April, July, August, October, November.

Distribution. China (Yunnan), Myanmar (Mandalay Division and Shan State), and Thailand (Chiang Mai, Loei, and Mae Hong Son); Figure 5.

Habitat. In relatively sunny, mixed forests on mountain slopes; 700–1650(–2300) m.

Vernacular names. Zhou-ye-an-xi-xiang (Hwang, 1980), Zhou-ye-ye-mo-li (Anonymous, 1974).

Styrax rugosus occurs primarily in open forests at middle elevations in northwestern Thailand, central and southern Myanmar, and southern Yunnan Province, China. Numerous specimens are available from throughout most of the geographic range of this species, especially at the extreme northern (Jingdong Yizu Zizhixian, Yunnan Province) and southern (Chiang Mai Province, Thailand) edges. In addition to its close morphological similarity to *S. limprichtii* (see discussion under that species), *S. rugosus* is also sympatric with three other imbricate-flowered *Styrax* species in southern Yunnan Province (*S. hookeri, S. japonicus,* and *S. tonkinensis*), from which it is easily separated by the prominently long calyx teeth and rugose leaves. The longer pedicels and glabrous abaxial leaf surfaces of *S. japonicus,* the larger fruit of *S. hookeri,* and the longer petioles and tuberculate seeds of *S. tonkinensis* also can be used to distinguish these species from *S. rugosus.*

Additional specimens examined. CHINA. **Yunnan:** Jingdong Yizu Zizhixian, Cai-sheng-miao, *China-USSR team 18* (IBSC, PE); Chuing-tung, Cheng-nan, *M. K. Li 346* (IBK, IBSC, KUN); Xin-min, *H. Peng 445* (KUN); Cheng-xi, *H. Peng 1851* (KUN); near Jiu-tsun, Meng-ku-ho, *Y. Tsiang 12348* (IBSC, KUN, PE); Huang-cao-ling, *Z. H. Yang 101327* (KUN); *Z. H. Yang 101681* (KUN[2]); Menghai Xian, *K. L. Le 235* (KUN); Fo-hai, *C. W. Wang 74113* (A, IBSC, KUN, PE), *77088* (A, PE); Nan-chiao, *C. W. Wang 75068* (A, KUN, PE), *75198* (A, IBSC, KUN, PE); Mojiang Hanizu Zizhixian, betw. Mo-jiang & Pu-er, near Jiang-xi-zhai, *China-USSR team 217* (PE). MYANMAR. **Mandalay Division:** 1978, *M. Togashi s.n.* (TI); Maymyo, *Buchanan 25* (E); Maymyo, *C. E. Parkinson 680* (K). **Shan State:** Mt. Mo-la-hein, *F. G. Dickason 8750* (A, E, L); Laungyi, *A. Khalil DI189* (A); Paugmi State, near Leja, *W. A. Robertson 152* (K). **Locality unknown:** *C. B. Collett 800* (K); Thaymyo, *F. G. Dickason 6008* (A). THAILAND. **Chiang Mai:** forest station at Ban Bo Luang, *C. F. van Beusekom & C. Phengkhlai 1078, 1082* (AAU, C, E, K, L); Doi Intanon, *Danish Exp. (1958/1959) 3295* (C, K); Bo Luang, *Flora of Thailand Project Second Exp. (1968) 1913* (AAU, C, L); Doi Angka, Dci Pa Maun, *H. B. G. Garrett 376* (E, K, L); Chiang Dao Dist., Doi Sahm Meun Range, Doi Chiam, *A. Griffith 2* (CAS, L); Me Jun, *A. F. G. Kerr 6201* (BM, K), *6201A* (BM, E, K); from Sop Aep to Pha Mawn (Ban Yang), *G. Murata et al. T15602* (L); Mae Sanam, *C. Phengklai et al. 4150* (C, K, L). **Loei:** Jam yai, *collector unknown DI189* (A); Phukrading, *T. Smitinand 328* (A). **Mae Hong Son:** Jawm Tong, Mae Soi Ridge, Mae Soi Subdist., Awp Luang Natl. Park, near Ban Bah Gluay (Mong Village), *J. F. Maxwell 91535* (AAU, E, P, CAS), *93944* (CAS, L). **Locality unknown:** Bo Luang, *R. Geesink et al. 5776* (AAU, C, E), *T5776* (L), *A. F. G. Kerr 4201A* (K), *8855* (BM, K); Hoi, Pu Jang, *A. F. G. Kerr 8855A* (E, K).

13. Styrax shiraianus Makino, Bot. Mag. (Tokyo) 12: 50. 1898 [as *S.* "*Shiraiana*"]. *Strigilia shiraiana* (Makino) Nakai, Trees Shrubs Japan 1: 256. 1922. TYPE: Japan. Honshu: Shizuoka Pref., Sugura, Araizawa in Abe-gori, ***Herb. Sc. Coll. Imp. Univ. Tokyo s.n.*** (lectotype, designated here, TI!).

Styrax shiraianus var. *discolor* Nakai, J. Jap. Bot. 14: 631. 1938. TYPE: Japan. Kyushu: Kumamoto Pref., Higo Province, Itukimura, May 1908 (fl) and Aug. 1908 (fr), *T. Nakazima s.n.* (type material, TI missing).

Trees to 8 m tall. Young twigs purple-gray, yellow or brown stellate-tomentose; older twigs gray, glabrescent. Petiole of larger leaves 8–15 mm long, dilated at base and covering the bud. Two most proximal leaves on each shoot subopposite to opposite, smaller, with petioles not dilated at base or covering the bud. Lamina 8–10 × 7–9.5 cm, chartaceous, broadly obovate or rhomboid-orbicular; apex rounded or short-caudate; base cuneate or cuneate-rounded; adaxially deep green, with scattered simple or 2- or 3-armed to stellate trichomes, especially prevalent proximally, glabrescent; abaxially pale green to pale white, sparsely stellate-pubescent, glabrescent except in the axils of the midrib and secondary veins; margin proximally glandular-serrulate, distally irregularly grossly dentate; secondary veins 4 to 6 on each side of midvein; tertiary veins parallel, abaxially prominent. Fertile shoots 4–8 cm long, 2- to 4-leaved. Inflorescences arising from shoots of the current growing season; lateral racemes usually 1-flowered; pseudoterminal inflorescences racemose, 2–3 cm long, 3- to 11-flowered, distally congested, rachis yellow stellate-tomentose. Pedicel < 1 mm long, densely white and brown stellate-villous; bracteoles ca. 6 mm long, linear or setaceous, positioned at the base of pedicel, often those toward the base of the inflorescence leaf-like. Flowers 1.5–2 cm long. Calyx campanulate, 4–6.5 × 4–6 mm; adaxially densely appressed-pubescent with 2- or 3-armed or stellate

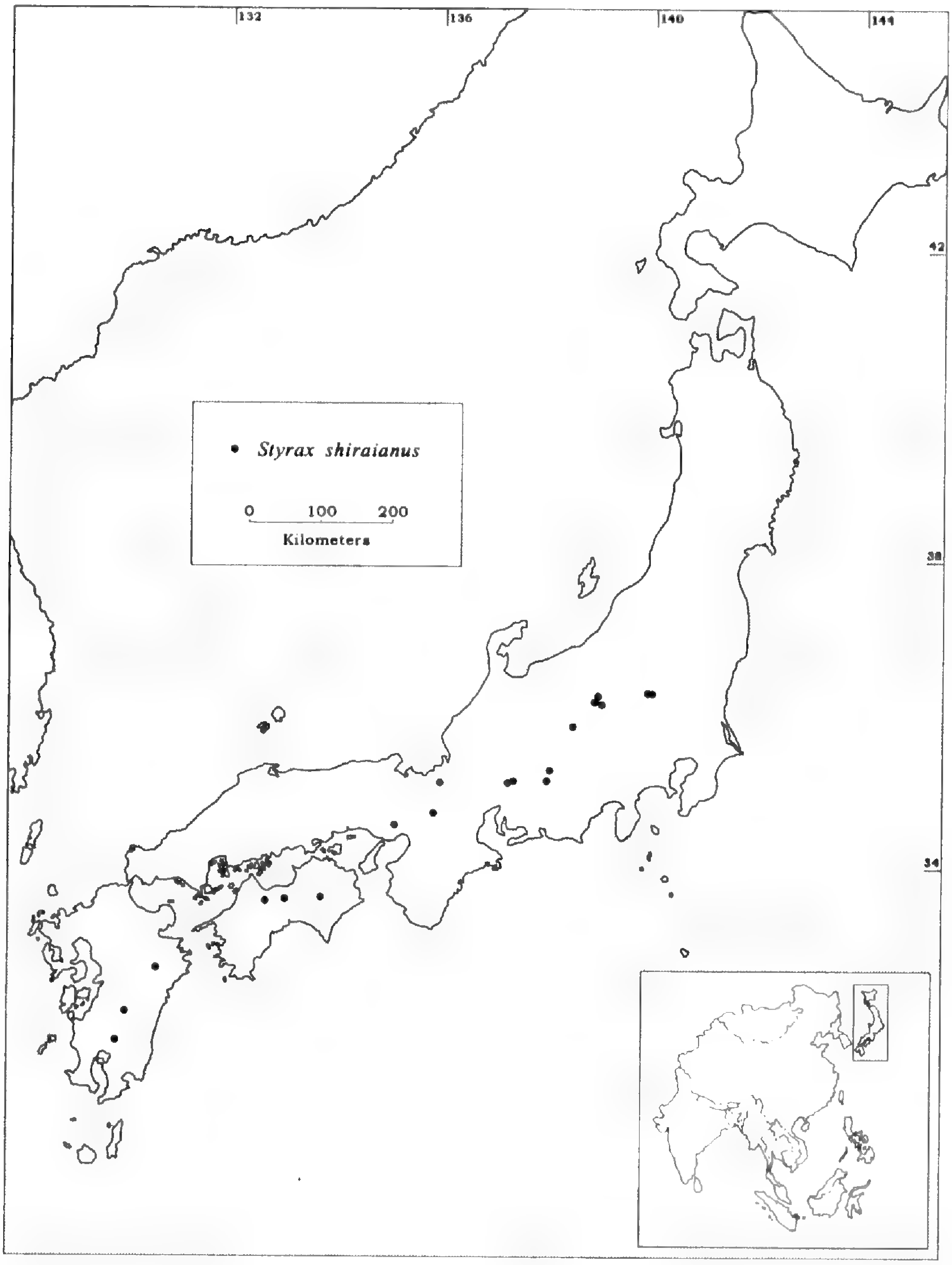

Figure 10. Geographic distribution of *Styrax shiraianus*.

trichomes; abaxially stellate-tomentose, often also with various amounts of larger yellow or brownish stiff stellate trichomes, especially proximally, within 1 mm from the margin more sparsely pubescent or glabrous, somewhat scarious, brown when dry; margin 5- to 8-toothed, teeth 1.5–2 mm long, deltoid, contiguous, apex acute. Corolla 1.0–1.5 cm long, white, tube 10–12 mm long, proximally glabrous, distally pubescent, lobes 5, 6–8 × 2.5–3 mm, ovate, apex acute, stellate-tomentose on both sides. Stamens 10; filaments 3–4 mm long, straight, of equal width throughout, sparsely stellate-pubescent; anthers 2–3 mm long, wider than distal portion of filament; connective glabrous; style proximally stellate-pilose, distally glabrous; stigma 0.4–0.6 mm wide, punctiform. Fruit 0.8–1.0 × 0.6–0.8 cm, ellipsoid to subglobose, apex rounded or apiculate, dehiscent by 2 or 3 valves from apex; pericarp dry, 0.3–0.7 mm thick, outside smooth, white stellate-tomentose, inside sparsely pubescent. Seeds brown, ellipsoid, smooth, glabrous.

Illustrations. Perkins in Engl., Pflanzenr. IV. 241 (Heft 30): 71, fig. 9. 1907; Nakai, Trees Shrubs Japan 1: 256, fig. 141. 1922 (as *Strigilia shiraiana*); Perkins, Übers. Gatt. Styrac.: fig. 9. 1928.

Phenology. Flowering: May, June. Fruiting: July–November.

Distribution. Japan (Honshu, Kyushu, and Shikoku); Figure 10.

Habitat. In open deciduous forests; 600–1500 m.

Vernacular names. Ko-hakuunboku (Japan; 1901, *T. Makino s.n.*), Uraziro-kohakuunboku (Japan; Nakai, 1938).

Styrax shiraianus is endemic to Japan (but see below), occurring on the islands of Honshu, Shikoku, and Kyushu. It appears to be a rare species, relatively little material being available for study. This species is easily distinguished from other species of *Styrax* series *Cyrta* by the racemes with distally congested flowers, long (10–12 mm) corolla tube, and very short pedicel (less than 1 mm). When only sterile specimens are available, the only other taxon with which *S. shiraianus* might possibly be confused is *S. obassia.* Both species have petioles that are dilated at the base and cover the bud, unlike all other species of *Styrax,* in which the bud is exposed. Sterile material of *S. shiraianus* can be distinguished from that of *S. obassia* by its smaller leaves that are abaxially glabrous or nearly so (vs. densely gray-white stellate-pubescent) and irregularly grossly deltoid-dentate (vs. subentire or remotely apiculate-dentate) leaf margins.

Apparently based on an erroneous observation of valvate corolla aestivation in *Styrax shiraianus,* Nakai (1922) transferred this species to *Strigilia* Cav., a genus described by Cavanilles (1789) and taken up by Miers (1859) to accommodate many South American species of *Styrax.* Later Nakai (1938) transferred it back to *Styrax.*

Styrax shiraianus has been reported from South Korea by Nakai (1938) on the basis of two collections from "Tiisan" (Chiisan) Mountain (*S. Okamoto s.n.* from "Zennan" (North Cholla) Province and *Tei-daigen s.n.* from "Keinan" (South Kyongsang) Province). Subsequently, the species was listed in three references on the Korean flora (T. B. Lee, 1989; W. T. Lee, 1996; Y. N. Lee, 1996), but locality or source information was not specified in any of these works. Nakai worked at TI until 1943, and from this we assume that the Korean material of *S. shiraianus* is stored at TI. We have not seen any material of *S. shiraianus,* however, from Korea among our loans from TI or other herbaria. Furthermore, we have not observed any photographs of living plants of *S. shiraianus* from Korea. The *Flora of Korea* (Y. N. Lee, 1996) contains color photographs of nearly all Korean species, including *S. japonicus* and *S. obassia,* but a photograph of *S. shiraianus* is notably lacking. No specimens of *Styrax* at SNU in Seoul, South Korea, have been identified as *S. shiraianus* (C.-W. Park, pers. comm.). We cannot be certain, therefore, that the Korean specimens cited by Nakai are not merely misidentified individuals of, e.g., *S. obassia.*

Four collections were cited in the protologue of *Styrax shiraianus*: Aug. 8, 1884, *T. Makino s.n.*; Aug. 1885, *T. Makino s.n., K. Watanabe s.n.*; and *Herb. Sc. Coll. Imp. Univ. Tokyo s.n.* The Makino herbarium (MAK) houses none of these specimens (M. Wakabayashi, pers. comm.), and TI has only the last of these (one sheet). Therefore, we have chosen to lectotypify on the only sheet of the syntypes known to exist among these herbaria. The TI herbarium does not have type material of *S. shiraianus* var. *discolor* (H. Ohba, pers. comm.).

Additional specimens examined. JAPAN. **Honshu:** Gifu Pref., Gifu-ken, Nakatugawa-shi, near Okunodaira, S foot of Mt. Ena, *K. Hidehiko 14* (KYO); Mino, *K. Shiota 2771, 5846, 6525, 7198, 9048* (A); Hyogo Pref., Mt. Setsuhiko, *H. Muroi 38* (A); Nagano Pref., Shinano, Ogawa, 1905, *J. G. Jack s.n.* (A, GH); Shinano, Ihida-shi, Mt. Surikogi Ohdaira, 1961, *F. Miyoshi s.n.* (A); Shinano, Nishichikuma-gun, Ohtaki-mura, *M. Mizushima 2379* (A); Kodzuke, Agatsuma-gun, Sawada-mura, Shima hot well, *M. Mizushima 2958* (A); Nishichikuma-gun, Okuwa-mura, Mt. Atera-yama, *G. Murata & H. Nishimura 906* (AAU, C, E, K, L, TI, UC); Shinano, *E. H. Wilson 7012* (A, BM, GH, K); Okayama Pref., Okayama-ken, Ushiroyama aidagun, 1951, *K. Uno s.n.* (A); Shiga Pref., Shiga-gun, Sgiga-cho, Yakumogahara in Hirasan Mts., *G. Murata 55807* (A, KYO); Tochigi Pref., Nikko, 1901, *collector unknown* (A), 1914, *collector unknown* (E), 1915, *collector unknown* (K), *T. Makino s.n.* (A, TI), *105785, 121299* (CAS), *105786* (A), 1904, *N. Mochizuki s.n.* (A), 1920, *H. Takeda s.n.* (BM), *E. H. Wilson 7710* (A); Nikko-shi, Mt. Nakimushi-yama, *Y. Tateishi 10287* (A). **Kyushu:** Kumamoto Pref., Mt. Ichibusa, Higo, 1908, *collector unknown* (E), 1947, *E. E. Harmsen s.n.* (L), 1910, *N. Mochizuki s.n.* (E), 1917, *Tashiro s.n.* (A); Sobosan, *Père U. J. Faurie 3272* (P); Kagoshima Pref., Mt. Kirishima, 1938, *T. Naito s.n.* (A). **Shikoku:** Tokushima Pref., Mt. Tsurugi, *M. Hiroe 13411* (C, UC); Ehimi Pref., Kamiukena-gun, Omogokei, 1940, *G. Murata s.n.* (A); Kochi Pref., Iyo sikoku, Yogo Ikkaku, *I. Yogo 9510* (A).

14. Styrax subpaniculatus Jungh. & de Vriese, in de Vriese, Pl. Nov. Ind. Bat. 9. 1845. *Styrax serrulatus* var. *mollissimus* Steenis, Bull. Jard. Bot. Buitenzorg, sér. 3, 12: 250. 1932. TYPE: Indonesia. Sumatra: province unknown, Tobing Dist., Battalands, 900 m, 1860–1862 (Steenis, 1932), *F. W. Junghuhn s.n.* (holotype, L [accession no. 90631-105]!; isotype, L [accession no. 908239-1494]!).

Styrax subdenticulatus Miq., Fl. Ned. Ind., Eerste Bijv. 474. 1860 [as *S. "subdenticulatum"*]. TYPE: Indonesia. Sumatra: province unknown, western Sumatra, Battang Baroes ["near Batang-barus"; protologue], 1856 (Steenis, 1932), *J. E. Teysmann 965HB* (holotype, U not seen; digital image of holotype!; isotype, BO not seen).

Styrax oliganthes Steenis, Bull. Jard. Bot. Buitenzorg, sér. 3, 12: 241. 1932. TYPE: Indonesia. Sumatra: Sumatera Barat, E coast, Manindjau, Kp. Silajang, 500 m, 7 July 1922, *Forest Research Institution b.b. 3965* (holotype, BO!; isotype, L!).

Trees to 33 m tall. Young twigs yellow-brown stellate-tomentose, terete; older twigs dark brown, glabrescent. Petiole 3–9 mm long. Two most proximal leaves on each shoot alternate. Lamina of fertile shoots 4–8.5 × 2–5 cm, those of sterile shoots 14.5 × 7.5 cm, membranaceous to thick-chartaceous, ovate, ovate-oblong, elliptic, or lanceolate; apex acuminate to caudate; base subrounded or broadly cuneate, slightly attenuate, sometimes oblique; adaxially subglabrous except on the midrib and the primary nerves, glabrescent; abaxially nearly glabrous to stellate-pubescent or -tomentose, the surface usually remaining visible through the pubescence; margin entire or indistinctly toothed, occasionally revolute; secondary veins 6 to 8 on each side of midvein; tertiary veins ± parallel and perpendicular to the secondaries. Fertile shoots (12–)15–21 cm long, (1- to)3- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- or 2-flowered or racemose, 3–8 cm long, (1- to)5- to 13-flowered; pseudoterminal inflorescences racemose or paniculate, 7–17 cm long, 9- to 20(to 23)-flowered, lateral branches 2 to 7, sometimes with 2 to 3 additional racemes from base of inflorescence, rachis and branches yellow-brown tomentose. Pedicel 4–6.5 mm long, stellate-tomentose; bracteoles 1–3 mm long, subulate or linear, mostly positioned at the base of the pedicel. Flowers 0.9–1.2 cm long. Calyx 3–4 × 3–4 mm, campanulate; adaxially glabrous or finely short-appressed-stellate-pubescent; abaxially yellow tomentose, arms of trichomes < 0.2 mm long, densely gray-white stellate-pubescent throughout; margin truncate, undulate, or irregularly lobed, the teeth minute, not contiguous if present. Corolla 0.5–0.8 cm long, white, tube 2.5–3 mm long, glabrous proximally; lobes 5, 7–9 × 2.5–3 mm, 2.3–2.8× as long as wide, oblong-elliptic, apex obtuse or acute, tomentose on both sides. Stamens 10; filaments 2.5–3 mm long, slightly flexuous at middle or occasionally straight, distally attenuate, densely white stellate-pubescent; anthers 3–4 mm long, equal to filament in width or narrower; connectives glabrous. Style glabrous; stigma 0.3–0.5 mm wide, punctiform. Fruit 0.7–1.0 × 0.6–0.8 cm, obovoid or globose, apex rounded or subacute, rarely also apiculate, indehiscent; pericarp dry, 0.2–0.5 mm thick, outside smooth, gray tomentose, inside downy-pubescent. Seed brown, ovoid, nearly smooth to irregularly rugose, glabrous.

Illustrations. Jungh. & de Vriese, in de Vriese, Pl. Nov. Ind. Bat.: pl. 3, 1–12. 1845; Steenis, Bull. Jard. Bot. Buitenzorg, sér. 3, 12: 222, fig. 3 (3). 1932 (as *S. oliganthes*); ibid.: 242, fig. 9. 1932 (as *S. oliganthes*).

Phenology. Flowering: February–April, October. Fruiting: May–August, October.

Distribution. Indonesia (Sumatra); Figure 4.

Habitat. In mesic, mixed primary forests, and in montane rain forests; 100–1600 m.

Vernacular names. Kajoe lomlang kajoe (*R. S. Boeea 9285*), kajoe komajan (*J. E. Teysmann 965HB*), or kajoe keminjan (Perkins, 1907 ex F. A. W. Miquel).

Styrax subpaniculatus is the only species of *Styrax* with imbricate corolla aestivation known from the island of Sumatra, Indonesia, where it is endemic. Steenis (1932) considered this species to be a variety of *S. serrulatus* (var. *mollissimus* Steenis), a species placed by Perkins (1907) in series *Valvatae* on the basis of its valvate corolla aestivation. Using the same reasoning as that outlined in the discussion of *S. porterianus,* we consider *S. subpaniculatus* a species distinct from *S. serrulatus.* The consistently imbricate corolla aestivation in *S. subpaniculatus* sharply delimits this species from *S. serrulatus,* which in our view possesses a subvalvate type of corolla aestivation. *Styrax serrulatus* is geographically distinct from *S. subpaniculatus,* occurring in the Himalayas and vicinity but not extending as far south as the Malay Peninsula or Sumatra. *Styrax subpaniculatus* can also be distinguished from *S. serrulatus* by its usually pubescent (vs. glabrous or nearly so) abaxial leaf surfaces and the truncate or undulate (vs. distinctly toothed) calyx margin.

Styrax porterianus has many features in common with *S. subpaniculatus,* but has shorter (2–4 vs. 7–17 cm long), strictly racemose (vs. often paniculate) inflorescences, and a fruit with a fleshy (vs. dry and rigid) pericarp that is deeply rugose (vs. smooth) in the dry state. In addition, the ranges of *S. subpaniculatus* and *S. porterianus* are completely nonoverlapping, the latter being restricted to the Malay Peninsula. *Styrax subpaniculatus* is also similar to *S. buchananii* and *S. odoratissimus* but distinguishable from both by its glabrous connectives and styles. In addition, the larger flowers (1.3–1.6 vs. 0.9–1.2 cm long) and longer anthers (6–7 vs. 3–4 mm) are useful characters to distinguish *S. buchananii* from *S. subpaniculatus,* whereas the wider petals (4–6 vs. 2.5–3 mm) and usually appressed-stellate-pubescent or lepidote (vs. glabrous) seeds readily distinguish *S. odoratissimus* from *S. subpaniculatus.*

Steenis (1932) described *Styrax oliganthes* based on a single fruiting collection from western Sumatra. Although hesitant to describe this species as new from only fruiting material, Steenis felt that the combination of densely pubescent abaxial leaf surfaces and apparent lack of any brown leaf pubescence (i.e., only white trichomes) provided sufficient justification for the recognition of a new species. Steenis postulated *Styrax benzoides* Craib and *S. tonkinensis* as close relatives of *S. oliganthes*, with *S. benzoides* distinguishable by its indehiscent fruit and *S. tonkinensis* by its tuberculate seeds. We agree that neither species could possibly be conspecific with *S. oliganthes*: besides its smooth seeds, *S. oliganthes* differs from *S. tonkinensis* in its truncate or undulate (vs. distinctly dentate) calyx margin and rounded (vs. rostrate) fruit apex. *Styrax benzoides* has the depressed-globose seeds of series *Benzoin* (see Fritsch, 1999); those of *Styrax oliganthes* are ellipsoid, clearly establishing its inclusion in series *Cyrta*.

Steenis did not consider a possible relationship of *Styrax oliganthes* with *S. subpaniculatus*. Nonetheless, there is ample evidence of affinity between these two entities. Both can reach a height of 30 m or more, which is uncommonly tall for species of *Styrax*; the leaves are of the same general dimensions, with equivalent numbers of secondary veins on each side of the midvein and an entire or indistinctly toothed margin; the fruiting calyx margins are truncate or undulate; the fruit is indehiscent, ± subglobose to slightly obovoid, smooth, and of similar general dimensions and color; the seeds are glabrous; finally, the locality of *S. oliganthes* is well-embedded within the general range of *S. subpaniculatus*, both being restricted to Sumatra.

Furthermore, characters that reportedly distinguish *Styrax oliganthes* from *S. subpaniculatus* are not reliable or otherwise do not serve to delimit the two taxa. The densely pubescent abaxial leaf surfaces in *S. oliganthes* differ from all collections of *S. subpaniculatus* known, but the degree of pubescence in *S. subpaniculatus* varies continuously from nearly none to nearly covering the entire surface. Variation in the amount of infraspecific abaxial leaf pubescence is common in species of *Styrax*, including several in this revision (e.g., *S. hemsleyanus, S. hookeri*). Steenis stated that there are only white trichomes on the abaxial leaf surface of *S. oliganthes*, but upon inspection at 64× magnification we observe scattered yellow, orange, and even brown stellate trichomes. The inflorescences of *S. oliganthes* are reportedly few-flowered, unlike the many-flowered condition of the pseudoterminal inflorescences of *S. subpaniculatus*. Only infructescences, however, are known in *S. oliganthes*. Typically, more flowers than fruits are borne on each reproductive structure in *Styrax*, and thus it is often difficult to infer the number of original flowers, or the structure and length of an inflorescence, from fruiting material. Furthermore, as in *S. subpaniculatus*, several pseudoterminal infructescences on the holotype of *S. oliganthes* are branched.

We examined several other features not mentioned by Steenis (1932) in considering the separation of the two species. The arms of the trichomes on the leaves abaxially average ca. 0.1 mm long in *S. oliganthes* versus those on most specimens of *S. subpaniculatus* (averaging ca. 0.4 mm long), but close inspection of all collections of *S. subpaniculatus* available to us indicates that trichome length is a continuously variable character. The leaves are thick-chartaceous in *S. oliganthes* whereas in most specimens of *S. subpaniculatus* they are membranaceous, but one specimen in bud (*Boeea 8857*) has leaves that are nearly as thick as *S. oliganthes* and several more have leaves that are notably thicker than usual. The seeds of *S. oliganthes* are irregularly rugose whereas those in *S. subpaniculatus* are smooth, but many species of *Styrax* exhibit infraspecific variation for this character (e.g., *S. japonicus*). Ultimately, we can detect no distinctive characters upon which to base the separation of *S. oliganthes* from *S. subpaniculatus*.

The only reference made to collections of *Styrax subdenticulatus* in the protologue is indicated with "(T.)," an abbreviation for J. E. Teysmann. According to Steenis (1932), Teysmann made three collections of *Styrax* from the type locality cited in the protologue. Two of these are identified by Steenis as *S. paralleloneurus* (*J. E. Teysmann 963* and *966*), and the third is specified by Steenis as the type of *S. subdenticulatus* (as "*Teysmann 965HB* [B, U])" (B in this case is BO, Herbarium of the Botanic Gardens, Buitenzorg, Java). Miquel's herbarium was U, but no indication of type status or any other annotation of Miquel exists on the U specimen of this collection. Although we have not seen the collections of *S. paralleloneurus* made by Teysmann from the type locality of *S. subdenticulatus*, the two species are easily distinguishable with vegetative characters. For example, the leaf surfaces of *S. subdenticulatus* are visible through the pubescence, whereas those of *S. paralleloneurus* are not. Thus, a mistake in identification of these specimens by Steenis is extremely unlikely. On this basis, we feel confident that the *Teysmann 965HB* specimen at U is the holotype of *S. subdenticulatus* (and thus there is no need to lectotypify in this case).

Additional specimens examined. INDONESIA. SUMATRA. **Aceh:** Saurauja, Blangkedjeren, *A. H. G. Alston 14716* (BM, L); Gajolanden, Goempang to Koengke, *C. G. G. J. Van Steenis 9802* (A, K, L); Gunung Leuser Natl.

Park, from Kutacane to Belangkejeren, Kulam, near Agusan, pass betw. Alas & Palok, *T. C. Whitmore TCW3348* (L); Gunung Leuser Nature Reserve, Gunung Mamas, 6 km SW from the mouth of Lau Ketambe, *W. J. J. O. de Wilde & B. E. E. de Wilde 15756* (BO, L); Gunung Leuser Nature Reserve, upper Mamas River Valley, ca. 15 km W Kutacane, *W. J. J. O. de Wilde & B. E. E. de Wilde 18342* (K, L). **Bengkulu:** G. Kaba, near Aer Angat, hot springs, *H. O. Forbes 2866* (BM, GH, L). **Sumatera Barat:** Ayer mancior, *O. Beccari 699* (BM, L); Pinang-Pinang plot, Ulu Gadut, *M. Hotta 26604* (BO); Pesisir Selatan, 12 km W of Muarasako, *Y. Laumonier YL5961* (K, L); Pajakumbuh, Mt. Sago, *P. Maradjo 87* (L), *W. Meijer 3175* (BO); Pajakumbuh, N slope of Mt. Sago, *W. Meijer 3186* (BM, L). **Sumatera Selatan:** Res. Palembang, Pasemah Lands, near Paoe, *H. O. Forbes 2335* (BM, GH, L[2]). **Sumatera Utara:** Tapanoeli, Kampoeng Sitoemba, *Forest Research Institution b.b. 5225* (L); Tapiannodi, Angkola & Sipirok, near Kampoeng Battang-Kola, *Forest Research Institution b.b. 5249* (L); Kampoeng Petjeren, *Forest Research Institution b.b. 6854* (L); Asahan, Pargambiran, *H. H. Bartlett 8077* (K, L); Kaban Djahe, *A. H. Batten-Pool 5* (L); Adian Rindang, Asahan, vicinity of Hoeta Tomoean Dolok, *R. S. Boeea 8857* (A, K, L, UC); Asahan (NE of Tomoean Dolok & W of Salabat), *R. S. Boeea 9285* (A, K, L, UC); S Tongkoh, Berastagi, Karoland, *J. Dransfield 3418* (L); NW Sibolangit, bank of the Betimoes, *J. A. Lörzing 5641* (L); Sibolangit, *J. A. Lörzing 14096* (K, L); Bandarbaru, near Sibolangit, *J. A. Lörzing 14129* (L); E Mt. Sibajak, *J. A. Lörzing 15167* (BO, K, L); Gunung Leuser Natural Park, Sekundur Forest Reserve, upper Besitang River area, *W. J. J. O. de Wilde & B. E. E. de Wilde 21156* (L). **Locality unknown:** Sumatra, *Ajoeb 728* (L); Sumatra, *H. O. Forbes 2835* (BM), *7866* (L); Karo Uplands, near Lake Laut Kawar & Kampoeng Sigarang, *Forest Research Institution b.b. 8618* (L); Sumatra, Langsdin, 1913, *J. C. v. der Meer Mohr s.n.* (L); Sumatra, E Batavae, 1857, *W. H. de Vriese s.n.* (L[6]); E coast of Sumatra, *H. S. Yates 1411* (BM, L, UC), *1467* (A, BM, IBSC, UC).

15. Styrax supaii Chun & F. Chun, Sunyatsenia 3: 34. 1935 [as *S.* "*Supaii*"]. TYPE: China. Guangdong: Ruyuan Yaozu Zizhixian, Chutsien Dun [Qi-xian-gou], 9 May 1934, *S. P. Kwok 80419* (lectotype, designated here, IBSC!; isotypes, A!, IBSC!).

Shrubs to 2 m tall or trees to 6 m tall. Young twigs brown or dark brown, densely stellate-pubescent; older twigs dark purple, glabrescent. Petiole 2–5 mm long. Two most proximal leaves on each shoot subopposite or opposite. Lamina 4–8 × 2–5 mm, chartaceous to thick-chartaceous, rarely membranaceous, ovate to obovate; base rounded to broadly cuneate; adaxially with a few simple or 2- or 3-armed to stellate trichomes when young, glabrescent; abaxially sparsely stellate-pubescent, glabrescent; margin coarsely serrate, deeply 3- to 5-dentate or lobed apically, lobes serrate-triangular or lanceolate, often remotely apiculate-serrate along the whole margin, up to 0.5 mm long; secondary veins 3 to 5 on each side of midvein; tertiary veins reticulate, adaxially plane, abaxially raised. Fertile shoots 2–5 cm long, 2- to 5-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- or 2-flowered; pseudoterminal inflorescences 2–3 cm long, 2- or 3-flowered, rachis and pedicel sparsely short-stellate-pubescent, with additional long simple or 2-armed trichomes. Pedicel 10–15 mm long; bracteoles 3–4 mm long, linear or subulate, positioned at the base or middle part of pedicel. Flowers 1.5–1.8 cm long. Calyx 5–6 (excluding teeth) × 4–5 mm, obconical; adaxially sparsely appressed-pubescent with long simple trichomes; abaxially with numerous simple or 2-armed trichomes ca. 1–1.5 mm long, stellate tomentum only sparsely distributed near the base, otherwise absent; margin distinctly dentate, the teeth 4–5 mm long, narrowly lanceolate or deltoid, unequal, contiguous. Corolla 0.9–1.3 cm long, white, tube ca. 3 mm, glabrous, lobes 5, 14–15 × 4–5 mm, lance-elliptic, adaxially sparsely pubescent with white 2- or 3-armed to stellate trichomes along the costae or distally, otherwise glabrous, abaxially densely stellate-pubescent. Stamens 10, conspicuously alternately unequal in length; filaments 4–5 mm long, straight, proximally broadened and white stellate-villous, distally attenuate and glabrous; anthers 4–6 mm long; connectives glabrous. Style glabrous; stigma 0.2–0.4 mm wide, punctiform. Fruit 1.0–1.5 × 0.7–0.9(–1.3) cm, ovoid or ellipsoid, apex apiculate to short-rostrate, dehiscent; pericarp dry, 0.3–0.6 mm thick, outside longitudinally striate and rugose, rarely smooth, densely white stellate-villous, inside glabrous. Seeds brown, ovoid, smooth, glabrous.

Illustrations. Chun & F. Chun, Sunyatsenia 3: pl. 3. 1935; Hu & Chun, Ic. Pl. Sin. 5: pl. 248. 1937; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1617, fig. 810. 1985; S. M. Hwang in F. H. Chen, Fl. Guangdong 1: 388, fig. 421. 1987; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 96, pl. 32 (1–7). 1987; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 201, fig. 201 (1–7). 2000.

Phenology. Flowering: May, June. Fruiting: June–November.

Distribution. China (Guangdong and Hunan); Figure 5.

Habitat. In mixed woods or near roadsides, and usually in relatively dry, disturbed habitats; 310–900 m.

Vernacular name. Lie-ye-an-xi-xiang (Hwang, 1980).

Styrax supaii is known only from the mountainous regions of Yizhang Xian, Hunan Province, and Ruyuan Yaozu Zizhixian, Guangdong Province, China. Based on the few specimens available for study, we believe this taxon must be a rare component of the vegetation. This distinctive species is easily identified by its long calyx teeth (4–5 mm) and a calyx covered with long simple trichomes (averaging 1.5 mm long), stellate calyx trichomes being absent nearly throughout. It also can easily be distinguished from sympatric species by its coarsely serrate to deeply 3- to 5-dentate or lobed leaves apically, and stamens alternately differing in length by 1–2 mm.

Additional specimens examined. CHINA. **Guangdong:** Ruyuan Yaozu Zizhixian, Daikiu [Da-qiao-qu, Hou-zhi-e], 1933 [5 June 1934; protologue], *S. P. Ko 52797* (IBK, IBSC[2], PE). **Hunan:** Yizhang Xian, Mang-shan, Rong-jia-dong, *S. Q. Chen 3552* (IBK, IBSC); Mang-shan, *B. G. Li 86* (IBSC); Dong-shan-keng, Mang-shan, *P. H. Liang 85344* (IBK, IBSC); Rong-jia-dong, *Q. Lin 167* (IBSC); Mang-shan, *Zhong-nan-lin-shi-xi-dui 94* (IBSC).

16. Styrax tonkinensis (Pierre) Craib ex Hartwich, Apotheker-Zeitung 28: 698. 1913. *Anthostyrax tonkinensis* Pierre, Fl. Forest. Cochinch. 4: t. 260. 1892 [as *A.* "*Tonkinense*"]. TYPE: Vietnam. Province unknown: Tu Phap, 12 May 1887, *B. Balansa 4332* (lectotype, designated by Svengsuksa & Vidal (1992), P not seen; isotype, P!).

Styrax hypoglaucus Perkins, Bot. Jahrb. Syst. 31: 486. 1902. TYPE: China. Yunnan: Simao Shi, eastern mountains, 1600 m, *A. Henry 12006* (lectotype, designated here, K!; isotypes, A!, E!, IBSC!, MO!, PE!).

Styrax subniveus Merr. & Chun, Sunyatsenia. 1: 78. 1930. TYPE: China. Guangdong: Lechang Shi, 24 May 1929, *C. L. Tso 20732* (holotype, IBSC!; isotype, PE!).

Trees to 30 m tall. Young twigs gray-brown stellate-tomentose, older twigs dark brown, glabrescent. Petiole 8–12(–15) mm long. Two most proximal leaves on each shoot alternate. Lamina 5–18 × 4–10 cm, chartaceous to thick chartaceous, elliptic to ovate; apex short-acuminate; base rounded to cuneate; adaxially glabrous except the major veins when young, glabrescent; abaxially gray or white stellate-tomentose, arms of trichomes very short, uniform, surface completely concealed by the tomentum; margin entire or apically 2- to 3-crenately toothed on young leaves; secondary veins 5 or 6 on each side of midvein; tertiary veins subparallel, adaxially plane or slightly sunken, abaxially prominent. Fertile shoots (7–)10–25 cm long, 3- or 4-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences 1- or 2-flowered or racemose, 3–5 cm long, 1- to 7-flowered; pseudoterminal inflorescences racemose or paniculate, (5–)7–20 cm long, (6- to)8- to 18(to 23)-flowered, lateral branches 2 to 5, sometimes with 2 or 3 lateral racemes from base of inflorescence, rachis and branches yellow-brown stellate-tomentose. Pedicel 5–10 mm long, yellow-brown stellate-tomentose; bracteoles 3–5 mm long, subulate or linear, positioned at the middle of pedicel or base of calyx. Flowers 1.2–1.5(–1.7) cm long. Calyx 3–4 × 2.5–3 mm, cupuliform; adaxially appressed-pubescent with white 2- or 3-armed or stellate trichomes; abaxially densely gray-white stellate-pubescent throughout; margin distinctly dentate, glandular-dotted, the teeth 0.3–0.7(–1.2) mm long, narrow-deltoid, usually contiguous or rarely separated by a shallow concave portion, unevenly distributed. Corolla 0.8–1.1(–1.3) cm long, white, tube 3–4 mm long, glabrous proximally, lobes 5, 10–15 × 3–4 mm, lance-ovate or oblong-elliptic, white stellate-tomentose on both sides. Stamens 10; filaments ca. 4 mm long, straight, of equal width throughout, moderately to densely white stellate-villous throughout, sometimes thinning apically; anthers ca. 5 mm long, as wide as filament; connective glabrous or short-stellate-pubescent. Style glabrous; stigma 0.2–0.5 mm wide, punctiform. Fruit 0.8–1.2 × 0.7–1.1 cm, subglobose, apex rostrate, irregularly dehiscent by 3 valves from apex; pericarp dry, 0.8–1.1 mm thick, outside nearly smooth, gray stellate-tomentose, inside sparsely downy-stellate-pubescent. Seeds brown or dark brown, ovoid, densely tuberculate, sometimes the tubercles arranged in stellate formations.

Illustrations. Pierre, Fl. Forest. Cochinch. 4: t. 260. 1892; Anonymous, Ic. Cormophyt. Sin. 3: 338, fig. 4630. 1974 (as *S. hypoglaucus*); C. Y. Wu, Fl. Yunnan. 3: 424, pl. 120 (1–6). 1983; L. Yang in Y. K. Li, Fl. Guizhou. 2: 548, fig. 234 (5–7). 1984; S. M. Hwang & C. J. Qi in W. C. Cheng, Sylva Sin. 2: 1603, fig. 798. 1985; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 85, pl. 28 (8–13). 1987; J. Q. Liu in L. G. Lin, Fl. Fujian. 4: 357, fig. 290. 1989; W. Q. Yin in Y. C. Xu, Ic. Arbor. Yunnan. 2: 892, pl. 470 (1–6). 1990; B. Svengsuksa & J. E. Vidal, Flore du Cambodge du Laos et du Viêtnam 26: 169, pl. 30, 4–7. 1992; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 197, fig. 197 (8–13). 2000.

Phenology. Flowering: April–July, September, November, December. Fruiting: January, February, April–December.

Distribution. China (Fujian, Guangdong, Guangxi, Guizhou, Hunan, Jiangxi, Yunnan, and Zhejiang), Laos (Houa Phan, Luang Prapang, Phongsali, and Xieng Khouang), and Vietnam (Bac Can, Cao Bang, Ha Tay, Lai Chau, Lao Cai, Ninh Binh,

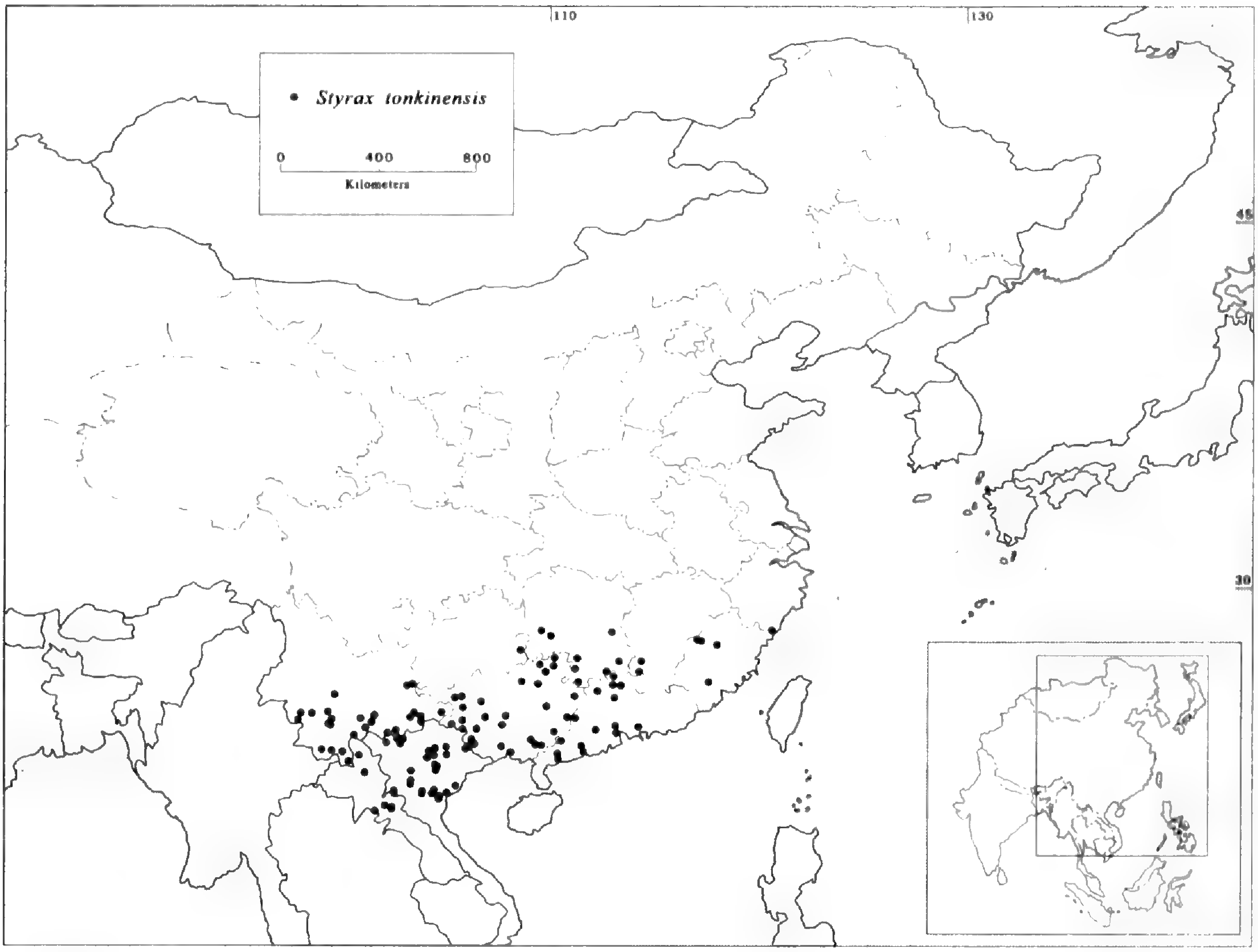

Figure 11. Geographic distribution of *Styrax tonkinensis*.

Phu Tho, Son La, Thanh Hoa, Tuyen Quang, and Yen Bai); Figure 11.

Habitat. In open forests on mountain slopes, and along edges of mixed forests in relatively disturbed sites; 30–2400 m.

Vernacular names. Ba-fan-long (China, Yunnan; *W. X. Liu 694*), Bai-bei-an-xi-xiang (China, Guangdong; *Exp. Guangdong 587*), Bai-bei-mu, Bai-hua-mu (China, Guangxi; *S. Q. Zhong A63811*), Bai-hua-lang (China, Guangxi; *Y. X. Lin 16575*), Bai-hua-lang-shu (China, Guangdong; *W. T. Tsang 25866*), Bai-hua-shu (China, Yunnan; *W. X. Liu 566*), Bai-hua-shu-guo (China, Yunnan; *Exp. Wen-shan 259*), Bai-hua-zhan (China, Guangdong; *K. P. To et al. 12025*), Bai-mai-an-xi-xiang (Hwang, 1987), Bai-ye-an-xi-xiang (China, Guangdong; *Exp. Guangdong 70*), Bai-ye-ye-mo-li (China, Hunan; *Q. Z. Lin 514*), Da-qing-shan-an-xi-xiang (China, Guangxi; Hwang, 1987), Dian-gui-mo-li-hua (China, Guizhou; *P. C. Tsoong 1094*), Dian-gui-ye-mo-li (Hwang & Qi, 1985), Dou-zha-shu (China, Yunnan; *P. Y. Mao 2468*), Ge-jian-ge (China, Guangxi; *Y. K. Li P1122*), Jie-yong (China, Yunnan; *P. Y. Mao 2779*), Jing-guo (China, Guangxi; *Y. K. Li P901*), Mei-lu-zai (China, Guangxi; *Exp. Guangxi 3468*), Niu-you-shu (China, Yunnan; *P. Y. Mao 2941*), Qing-shan-an-xi-xiang (China, Guangxi; *H. N. Qin 245*), Shi-chi-yang (China, Guangxi; *F. H. Xie et al. 3727*), Tai-guo-an-xi-xiang (Hwang, 1987), Xiao-jie-yong (China, Yunnan; *K. M. Feng 5149*), Yue-nan-an-xi-xiang (Anonymous, 1974).

Styrax tonkinensis is a relatively common component of primary and secondary forests and disturbed sites across southern China and the northern regions of Laos and Vietnam. The gray to white stellate-tomentose abaxial surface of the lamina (often nearly glaucous in appearance) appears to be a constant character in *S. tonkinensis*, and serves to distinguish it from most other sympatric species of the imbricate members of series *Cyrta*. Three species occurring within the range of *S. tonkinensis* have at least some individuals with a stellate-tomentose abaxial laminar surface (*S. hookeri*, *S. limprichtii*, and *S. rugosus*). *Styrax limprichtii* and *S. rugosus* differ from *S. tonkinensis* by their smooth and glabrous (vs. tuberculate) seeds, leaves with shorter petioles and more prominent teeth, a calyx with scattered orange or brown stiff stellate pubescence, and a fruit with a rounded or apiculate (vs. rostrate) apex and a longitudinally striate (vs.

smooth or irregularly rugose) pericarp. *Styrax hookeri* differs by its truncate, undulate, or irregularly lobed calyx with the teeth not contiguous if present, and the outer surface of the calyx within 1 mm of the margin more sparsely pubescent than the rest of the calyx and somewhat scarious.

Styrax tonkinensis was described first as *Anthostyrax tonkinensis* Pierre from specimens collected in Vietnam (*B. Balansa 4332* and *4358*). Perkins (1902) may well have overlooked this taxon, because *S. macrothyrsus* Perkins was published from one of the type collections of *Anthostyrax tonkinensis* (*B. Balansa 4332*), and no reference was made to *Anthostyrax* Pierre in Perkins's 1907 monograph. Realizing Perkins's error, Hartwich (1913) made the transfer to *Styrax*. Perkins (1902) described *S. hypoglaucus* Perkins from a specimen collected from Simao Shi, Yunnan Province, China (*Henry 12006*). *Styrax hypoglaucus* supposedly differs from *S. tonkinensis* by its 6- to 10-flowered racemose or sparsely branched inflorescences 5–6 cm long (vs. multi-flowered paniculate inflorescences 17–18 cm long; Perkins, 1902, 1907). Merrill and Chun (1930) described *S. subniveus* Merr. & Chun based on a specimen collected from Lechang Shi, Guangdong Province (*C. L. Tso 20732*). They considered this species to be allied to *S. hypoglaucus* and *S. tonkinensis*. According to their protologue, *S. subniveus* has racemose or narrowly paniculate inflorescences 3–8 cm long with few to many flowers.

We agree with Hwang (1980) that both of these species are synonyms of *Styrax tonkinensis*. The constancy of such features as the entire or weakly toothed leaves that are densely pubescent abaxially, relatively small flowers, dentate calyx, glabrous style, rostrate fruit, and especially the tuberculate seeds (which occur nowhere else in the genus) all serve to delimit this species. As in *S. odoratissimus*, inflorescence length and flower number per inflorescence exhibit notable variation in *S. tonkinensis*. This is reflected in the key to species, in which *S. tonkinensis* falls out twice because of the variation in these characters.

Suvatti (1978) cited *Styrax tonkinensis* from eastern Thailand, but we have not seen any specimens of this taxon from that country. *Styrax tonkinensis* was introduced to the island of Java after World War II for reforestation purposes (Backer & van den Brink, 1965).

The holotype of *Styrax hypoglaucus* at B is presumably destroyed. Perkins may have only seen the specimen at B because none of the other sheets of *A. Henry 12006* that we have examined possess Perkins's annotation label. No herbaria are cited in either Perkins (1902) or Perkins (1907) to establish whether Perkins examined additional material. We have chosen the K specimen of *A. Henry 10644* as the lectotype because Kew was the location of Henry's headquarters.

Selected specimens examined. CHINA. **Fujian:** Hua'an Xian, Xin-kou, *P. C. Tsoong 635* (IBSC, PE); Jianning Xian, Wu-yi-shan, from Hong-du to Pi-keng, *H. Y. Zou 20266* (MO); Taining Xian, Xin-qiao-xiang, *G. D. Ye 2137* (IBSC). **Guangdong:** Fengkai Xian, Yu-lao-xiang, Huang-gang-shan, *C. Huang 164273* (IBSC, KUN); Gaozhou Shi, Fen-zhi-ling, *Y. Tsiang 2262* (IBK, IBSC, KUN, PE); Guangzhou Shi, *H. G. Yip 364* (A, BM, L); Huiyang Shi, San-keng-shi-tou-cun, Lian-hua-shan, *W. T. Tsang 25866* (A, CAS, E, IBSC); Huizhou Shi, Luo-fu-shan, *N. K. Chun 41251* (IBK); Lechang Shi, Yang-guo-tian, Zhong-shan, *S. P. Ko 54545* (IBK, IBSC, KUN, PE); Maoming Shi, Da-po-qu, Ge-chang-xiang, *L. Tang 2413* (IBSC, KUN, PE); Qujiang Xian, Lung-t'au-shan, near Iu, *K. P. To et al. 12267* (UC); Ruyuan Yaozu Zizhixian, Tian-jing-shan, *H. G. Liu 488* (IBSC, MO); Xinyi Xian, Ba-yi, *Exp. Guangdong 587* (IBSC); Yangchun Shi, He-tang-xiang, *C. Wang 41987* (IBK, IBSC, KUN); Yangjiang Shi, San-tang-xiang, Long-gao-shan, *C. Wang 41442* (IBK, IBSC[2], MO); Yangshan Xian, Wu-yuan-xiang, *L. Tang 1082* (IBSC, KUN); Yingde Shi, Sha-kou-xiang, Hua-shui-shan, *P. H. Liang 84294* (IBK, IBSC); Zhaoqing Shi, Ding-hu-shan, *G. L. Shi 13948* (IBSC). **Guangxi:** Bama Yaozu Zizhixian, Ling-lu-xiang, *Y. K. Li P1122* (IBK, IBSC, PE); Bobai Xian, Song-shan-xiang, *Y. X. Lin 16575* (IBSC, PE); Bose Shi, Ba-ko-shan, *R. C. Ching 7398* (A, IBSC, PE, UC); Cangwu Xian, Tong-luo-shan, *S. Q. Chen 10192* (IBK, IBSC); Daxin Xian, *H. N. Qin 245* (PE); Debao Xian, Huang-lian-shan, *C. C. Chang 13769* (IBK, IBSC); Hezhou Shi, Li-song-xiang, *H. C. Chen et al. 500132* (IBK, IBSC); Jingxi Xian, *Z. J. Li 1458* (IBK); Jinxiu Yaozu Zizhixian, Yao-shan, Tseung-yuen, *C. Wang 39419* (A, CAS, IBSC, L); Lingchuan Xian, Gong-ping-qu, *F. H. Xie et al. 3183* (IBK); Lingshan Xian, Yan-dun-xiang, *C. F. Liang 33787* (IBK); Lingyun Xian, Yu-hong-xiang, Lao-shan, *X. Q. Liu 28504* (IBK, IBSC, KUN, PE); Longlin Gezu Zizhixian, Ling-wan Dist., *S. K. Lau 28504* (A); Longsheng Gezu Zizhixian, Da-di-xiang, *Guang-fu Coll. Team 306* (IBK, IBSC, MO, PE); Longzhou Xian, Da-qing-shan, *C. C. Chang 11921* (IBSC, KUN); Nanning Shi, *R. C. Ching 7957* (A, IBSC, PE); Ningming Xian, Shang-si-xiang, *C. C. Chang 13025* (IBSC, KUN); Pingguo Xian, Na-lu-xiang, *Y. K. Li P901* (IBK, IBSC, PE); Pingxiang Shi, *Guangxi Institute of Botany 2* (IBK); Pubei Xian, Long-men-xiang, *W. C. Chen 61* (IBSC); Qinzhou Shi, San-wan-da-shan, *S. Q. Chen 4141* (IBSC); Rongshui Miaozu Zizhixian, Ping-shi-xiang, Jiu-wan-da-shan, *S. Q. Chen 16565* (IBK, IBSC, KUN, PE); Rong Xian, Ta-tseh-tsuen, *A. N. Steward & H. C. Cheo 1085* (A, BM); Shanglin Xian, Ta-ming-shan, *S. S. Sin 25360* (IBSC); Shangsi Xian, Deng-long-cun, Shi-wan-da-shan, *W. T. Tsang 24105* (A, IBSC, MO); Tianlin Xian, Mao-bi-liang, *Z. T. Li 600853* (IBK, IBSC, KUN, PE); Xing'an Xian, Liang-jin-kuang-xiang, Mao-er-shan, *Z. Z. Chen 51517* (IBSC, KUN); Yongfu Xian, Sheng-li-xiang, *J. F. Qin 700397* (IBK); Ziyuan Xian, Qi-gu-shan, *Z. Z. Chen 51906* (IBK). **Guizhou:** Xia-jiang, *P. C. Tsoong 1094* (PE[2]). **Hunan:** Dao Xian, *P. C. Tam 63707* (IBK); Dongkou Xian, Xue-feng-shan-qu, Ba-qu, Shui-wei, *C. T. Lee 2472* (IBSC, PE[2]); Hengshan Xian, Heng-shan, *C. J. Qi S8* (IBSC); Jianghua Yaozu Zizhixian, An-ning, *Hunan Forest Institute 6214*

(IBSC); Qianyang Xian, *C. T. Lee 2279* (IBSC); Shuangpai Xian, *Q. Z. Lin 341* (IBSC); Yizhang Xian, Mang-shan, *Q. Z. Lin 514* (IBSC); Zixing Shi, Ping-jiang-xiang, *P. H. Liang 86286* (IBSC, MO). **Jiangxi:** Dayu Xian, Zuo-bo-xiang, *M. Q. Nie et al. 9637* (IBK, IBSC, KUN); Shangyou Xian, from Sheng-shui to Xi-long, *Exp. Jiangxi 718* (PE). **Yunnan:** Cangyuan Wazu Zizhixian, Ban-hong-xiang, *Y. H. Li 11725* (IBSC, KUN); Funing Xian, Jar-gei, *C. W. Wang 89220* (IBSC, KUN, PE); Gengma Daizu Wazu Zizhixian, Xi-shan, *China-USSR team 5610* (IBSC, PE); Hekou Yaozu Zizhixian, Wu-tai-shan, *W. X. Liu 566* (IBSC, KUN, PE); Jianshui Xian, *H. T. Tsai 53147* (IBSC, KUN, PE); Jingdong Yizu Zizhixian, Wen-po-xiang, *Q. A. Wu 9040* (KUN); Jinggu Daizu Yizu Zizhixian, Weng-lang, *F. Konta & H. Takahashi CH3721* (KUN); Jinghong Shi, *C. W. Wang 73643* (A, KUN). Jinping Miaozu Yaozu Daizu Zizhixian, Yong-ping-xiang, *China-USSR team 1510* (IBSC, PE); Lüchun Xian, Fen-shui-ling, Lei-bo Valley, *D. D. Tao 164* (IBSC, KUN); Luoping Xian, Ba-da-he-qu, Beng-shan, *H. Sun 518* (KUN); Malipo Xian, Tung-ting, *K. M. Feng 13452* (A, KUN, PE); Menghai Xian, Fo-hai, *C. W. Wang 74118* (A, IBSC, KUN, PE[2]); Mengla Xian, Luo-shan, *S. K. Wu et al. 289* (KUN); Pingbian Miaozu Zizhixian, Liang-zi-xiang, San-cha-he, *P. Y. Mao 4083* (IBSC, KUN, PE); Pu'er Hanizu Yizu Zizhixian, Maretee, *A. Henry 13693* (A, E, K); Shizong Xian, *S. C. Ho 85251* (IBSC); Shuangjiang Lahuzu Wazu Bulangzu Daizu Zizhixian, Bang-tuo, *J. S. Xing 1082* (IBSC, KUN, PE); Simao Shi, Yi-xiang-qu, *P. Y. Mao 6173* (IBSC, KUN, PE); Wenshan Xian, Lao-jun-shan, *K. M. Feng 22614* (IBSC, KUN); Xichou Xian, Lian-hua-tang, Jin-ping-shan, *S. Z. Wang 889* (KUN); Yanshan Xian, Pie-shih-eih, *C. W. Wang 84747* (KUN, PE); Yuanjiang Hanizu Yizu Daizu Zizhixian, Xi-gui-he, *G. D. Tao 38695* (KUN); Yuanyang Xian, Fen-shui-ling, *S. C. Ho 85159* (IBSC). **Zhejiang:** Longquan Shi, Feng-yang-shan, *H. Y. Zou 454* (A). LAOS. **Houa Phan:** Tasseng de Samneua Muong de Samneua, *M. Borel 7* (P, UC). **Luang Prapang:** NE de Muong Ngoi, Louang Prabang, *E. Poilane 20726* (P). **Phongsali:** *E. Poilane 26003*. **Xieng Khouang:** km 226, betw. Vinh & Tranninh, *E. Poilane 16779* (P). VIETNAM. **Bac Can:** Dac Kiet, *E. Poilane 1831* (A, P). **Cao Bang:** Nangoa, 1997, *U. Kurosu s.n.* (CAS). **Ha Tay:** Da Chong, *P. A. Pételot 5755* (A, P). **Lai Chau:** betw. Tsinh Ho & Chinh Nua N of Lai Chau, *E. Poilane 25690* (P). **Lao Cai:** Chapa, *P. A. Pételot 3259* (CAS, P, UC). **Ninh Binh:** Phu Kho, Trung Giap, *F. Fleury 469* (P). **Phu Tho:** Phu Ho, *P. A. Pételot 1033* (P, UC). **Son La:** Pha Din, 1995, *U. Kurosu & S. Aoki s.n.* (CAS). **Thanh Hoa:** from Hoa Binh to Chobo, *E. Poilane 13018* (A, P). **Tuyen Quang:** Nui La, Ha Tuyen, *F. Fleury 37970* (P). **Yen Bai:** Bao Ha, *E. Poilane 25294* (P).

17. Styrax wilsonii Rehder, in Sarg., Pl. Wilson. 1: 293. 1912 [as *S.* "*Wilsonii*"]. TYPE: China. Sichuan: Baoxing Xian, Mu-pin, 1300–1700 m, June 1908, *E. H. Wilson 884* (lectotype, designated here, A [accession no. 18452]!; isotypes, A[3]!, BM!, E!, K[2]!).

Shrubs to 2 m tall. Young twigs densely ferrugineous stellate-pubescent. Older twigs dark brown, glabrescent. Petiole < 2 mm long. Two most proximal leaves on each shoot opposite to subopposite. Lamina 1–2.5(–4) × 0.7–2(–2.5) cm, chartaceous, obovate, rhomboid, or rarely elliptic-ovate; apex acute to short-acuminate; base cuneate; adaxially sparsely stellate-pubescent along the major veins, otherwise glabrous; abaxially finely gray-white stellate-tomentose, also with scattered yellow-brown or dark brown short stellate trichomes on major veins and the two most proximal leaves on each shoot; margin coarsely serrate or apically 2- to 4-dentate; secondary veins 4 to 6 on each side of midvein, adaxially slightly sunken, abaxially prominent; tertiary veins inconspicuous, plane or slightly sunken adaxially, faintly prominent abaxially. Fertile shoots 1–2.5 cm long, 2- to 4-leaved. Inflorescences arising from shoots of the current growing season; lateral inflorescences usually 1-flowered; pseudoterminal racemes 1–2 cm long, 3- to 5-flowered, rachis yellow stellate-tomentose. Pedicel 2–3 mm long, yellow or brown stellate-tomentose; bracteoles 0.5–1 mm long, subulate or linear, usually positioned at the middle of pedicel, sometimes those toward the base of the inflorescence leaf-like. Flowers 0.9–1.1(–1.3) cm long. Calyx 2–3 × 3–3.5 mm, cupuliform; adaxially sparsely white appressed-pubescent with 2- to 3-armed or stellate trichomes; abaxially gray-white stellate-tomentose throughout, often also with larger scattered orange or brown stiff stellate trichomes, especially proximally; margin distinctly dentate, the teeth narrow-deltoid, unevenly distributed, usually contiguous or rarely separated by a shallow concave portion. Corolla 0.6–0.8(–1.0) cm long, white, tube ca. 3 mm long, glabrous, lobes 5(6), 6–7 × 3.5–4 mm, narrowly oblong, adaxially sparsely pubescent except at the apex, abaxially pale yellow stellate-tomentose. Stamens 10(12); filaments 4.5–5 mm long, straight, distally slightly attenuate, ventrally white stellate-pubescent, becoming glabrous distally; anthers ca. 3 mm long, wider than distal portion of filament; connective glabrous. Style glabrous; stigma ca. 0.2 mm wide, punctiform. Fruit 0.5–0.6 × 0.4–0.5 cm, subglobose, apex rounded or apiculate, dehiscent; pericarp dry, 0.2–0.3 mm thick, outside longitudinally striate, gray tomentose, inside glabrous. Seeds brown, ovoid to globose, smooth, glabrous.

Illustrations. Prain, Bot. Mag. 148: t. 8444. 1912; F. T. Tai & T. C. Pan in W. P. Fang, Fl. Sichuan. 1: 420, fig. 162. 1981; S. M. Hwang, Fl. Reipubl. Popularis Sin. 60(2): 87, pl. 29 (1–6). 1987; Z. Y. [C. Y.] Wu & P. H. Raven, Fl. China Ill. 15: 198, fig. 198 (1–7). 2000.

Phenology. Flowering: May, June, September. Fruiting: April, September.

Distribution. China (Sichuan); Figure 2.

Habitat. In relatively sunny, open forests on mountain slopes; 700–1500 m.

Vernacular names. Ai-mo-li (Hwang, 1987), Xiao-ye-an-xi-xiang (Hwang, 1980), Xiao-ye-ye-mo-li (Anonymous, 1974).

Styrax wilsonii is known only from middle (1000–1700 m) elevations of Baoxing Xian, Sichuan Province, China. It is similar to the more widespread *S. limprichtii* in its shrub habit, scattered to dense orange or brown stiff stellate trichomes on the calyx, globose fruit with longitudinally striate pericarp, and flowering time usually before the full expansion of the leaves, such that we initially considered whether the two species might be best treated as varieties of a single species. *Styrax wilsonii* can be readily separated from *S. limprichtii*, however, by its smaller leaves, flowers, and fruit. In addition, the abaxial laminar surface of *S. wilsonii* possesses a tomentum of uniform height, whereas that of *S. limprichtii* possesses a layer of longer trichomes in addition to the white base tomentum, or is glabrous or nearly so. The apparent disjunction between these two species is likely to be real rather than an artifact of inadequate collecting because numerous collections of other species of *Styrax* have been made in the intervening areas of Sichuan Province. The morphological differences together with the discontinuous distribution provide sufficient evidence for treating *S. limprichtii* and *S. wilsonii* as separate species.

We have seen four sheets from A of *Styrax wilsonii* labeled as *E. H. Wilson 884*. Two of these indicate a collection date of June 1908, one a collection date of September 1908, and one a collection date of October 1910. The protologue indicates that *E. H. Wilson 884* is the type, but does not indicate a date of collection; thus, these sheets must be regarded as syntypes. We have chosen the June 1908 sheet with accession number 18452 as the lectotype because it possesses the best flowering material for examination. Furthermore, on the other June 1908 sheet (accession number 18453) is written "isotype" (with handwriting unknown but probably not Rehder's). Thus, alternatively designating 18453 as the lectotype would cause undue confusion.

Additional specimens examined. CHINA. **Sichuan:** Baoxing Xian, *C. Pei 8120* (PE), *T. P. Soong 9476* (IBSC, PE), *39476* (KUN), *T. T. Yü 1903* (IBSC, PE); Liang-he-kou, *X. B. Zhang & Y. X. Ren 4507* (PE); Wu-long, *X. B. Zhang & Y. X. Ren 4534* (PE); Ming-ling-xiang, Zhuang-zi-he-ba, *X. B. Zhang & Y. X. Ren 4640* (PE); Yan-bi-cun, *X. B. Zhang & Y. X. Ren 4957, 4982* (PE).

EXCLUDED NAME

Styrax bashanensis S. Z. Qu & K. Y. Wang, Bull. Bot. Res., Harbin 9(1): 27. 1989. TYPE: China. Shaanxi: Zhenping Xian, 1190 m, 28 May 1976, *K. Y. Wang 548* (holotype, NWFC lost).

We have located no authentic material referable to this name; the type is missing at NWFC. The description is consistent with the characters exhibited by some specimens of *S. hookeri* distributed near the periphery of this species' range (e.g., *X. H. Song 272* and *907, C. Wang 41180*; narrowly lance-elliptic, subcoriaceous leaves and/or relatively small fruits ca. 7 mm wide) where Wang's collection is located. There is sufficient uncertainty in the nature of these characters, however, to preclude the placement of this name in synonymy.

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Appendix 1. List of species.

1. *Styrax buchananii* W. W. Sm.
2. *Styrax chrysocarpus* H. L. Li
3. *Styrax curvirostratus* (B. Svengsuksa) Y. L. Huang & P. W. Fritsch
4. *Styrax hemsleyanus* Diels
5. *Styrax hookeri* C. B. Clarke
6. *Styrax japonicus* Siebold & Zucc.
7. *Styrax limprichtii* Lingelsh. & Borza
8. *Styrax macrocarpus* W. C. Cheng
9. *Styrax obassia* Siebold & Zucc.
10. *Styrax odoratissimus* Champ. ex Benth.
11. *Styrax porterianus* G. Don
12. *Styrax rugosus* Kurz
13. *Styrax shiraianus* Makino
14. *Styrax subpaniculatus* Jungh. & de Vriese
15. *Styrax supaii* Chun & F. Chun
16. *Styrax tonkinensis* (Pierre) Craib ex Hartwich
17. *Styrax wilsonii* Rehder

Appendix 2. Index to exsiccatae.

All specimens examined by the authors are listed alphabetically by collector, followed by collection numbers (and herbarium if anonymous). Numbers in parentheses correspond to those in the numerical list of species. If more than two persons participated in the collection, only the first collector listed on the label is cited.

236 Team 641 (10); 1251 (10); 1449 (10); 1944 (5). 713 Team 520 (5).

Ajoeb 728 (14). T. Akagi in 1985 (6). A. Aldridge in 1891 (6). C. d'Alleizette in 1908 (6); s.n. (4); s.n. (9). A. H. G. Alston 14716 (14). T. Amano 6962 (6). S. Amino et al. 192 (6). H. Ando in 1965 (6); in 1967 (6). Anonymous 3a (9) (IBSC); 3d (9) (IBSC); 1–32 (5) (KUN); 53 (16) (PE); 66 (4) (PE); 7824-70 (10) (PE); 86 (10) (IBK); 87 (6) (PE); 96 (6) (BM); 101 (6) (BM); 124 (16) (PE); 144 (16) (PE); 184 (5) (KUN); 186 (10) (PE); DI189 (12) (A); 195 (5) (KUN); 201 (6) (IBSC); 240 (6) (PE); 250 (9) (PE); 252 (6) (E); 265 (9) (PE); 273 (10) (PE); 279 (6) (C); 284 (9) (PE); 294 (10) (PE); L297 (6) (PE); 334 (6) (PE); 345a (6) (PE); 400 (10) (BM); 490 (6) (KUN); 522 (6) (KUN); 74-522 (6) (IBSC); 528 (6) (PE); 550 (10) (PE); H.III589 (5) (BM); 784 (5) (KUN); D941 (6) (PE); 1160 (6) (PE); 1189 (11) (K); 1326 (16) (IBK); 1344 (5) (E); 1369 (10) (PE); 1662 (5) (E); 1681 (16) (IBK); 1768 (10) (PE); H1795 (4) (A); 83-2052 (10) (PE); 2110 (16) (PE); 2160 (6) (BM, E); 2161 (6) (E); 2162 (6) (E); 2163 (6) (E); 2337 (9) (BR); 2346 (4) (A); 2705 (6) (KUN); 2742 (6) (PE); 3544 (6) (PE); 3584 (6) (PE); 3746 (1) (K); 4499 (16)

(IBK); 5093 (6) (IBSC); 6061 (9) (A); 6473 (16) (IBSC); 7047 (16) (IBSC); 10153 (6) (PE); 11840 (9) (A, MO); 12835 (9) (MO); 27495 (6) (PE); 31010 (9) (IBSC); 40225 (16) (P); 69965 (6) (IBK); 84100 (10) (KUN); 90244 (16) (IBSC); L8515037 (10) (PE); 8521239 (10) (PE). S. Arimoto in 1903 (9). L. Averyanov et al. VH4544 (3).

B. Balansa 4332 (16); 4339 (16); 4358 (16); 4365 (16); 12587 (16). S. Y. Bao 1 (7); 4 (5); 169 (6); 175 (6); 217 (6); 391 (5). S. P. Barchet in 1906 (10). B. Bartholomew 1916 (10). H. H. Bartlett 8077 (14). A. H. Batten-Pool 5 (14). R. K. Beattie & Y. Kurihara 10753 (6); 10814 (6). O. Beccari 699 (14). Beijing Youth Team (Guizhou, 1986) 54 (6). C. F. van Beusekom & C. Phengkhlai 1078 (12); 1082 (12). E. Beyer & Cowley 96 (9). J. Bisset 4605 (9). C. Bock & A. von Rosthorn 2423 (6). E. M. Bodinier in 1902 (6); s.n. (6); 1099 (10); 2221 (6). R. S. Boeea 8857 (14); 9285 (14). P. H. F. Bon 338 (10). A. Borel 8 (16); n8 (16). M. Borel 1 (16); 2 (16); 3 (16); 7 (16); 8 (16); 13 (16); 16 (16); 17 (16). D. E. Boufford & B. Bartholomew 24085 (6); 24853 (6). D. E. Boufford & E. W. Wood 25412 (9). D. E. Boufford et al. 25729 (6); 25808 (6); 26287 (6). F. S. A. Bourne in 1897 (6). H. S. Bowes 3199 (5). P. W. Bristol & P. W. Meyer 131 (9). W. P. Brooks 511 (9); 52511 (9). E. M. Buchanan 21 (1); 25 (12); 51 (1).

G. L. Cai 38 (10); 464 (6). K. H. Cai 850 (16); 1089 (16). T. R. Cao 90621 (10). Z. Y. Cao 191 (6). W. R. Carles 29 (6); 90 (6). J. Cavalerie 997 (6); 1062 (6); 3319 (6); 4526 (6); 8190 (6). C. H. Cave in 1912 (5); in 1913 (5); in 1917 (5); in 1919 (5); in 1922 (5). J. G. Champion 138 (10). D. Champluvier 5481 (6). T. R. Chand 1846 (5); 7065 (5); 7586 (5); C. C. Chang 602 (16); 11921 (16); 13025 (16); 13769 (16); 13901 (16); 13910 (16). C. E. Chang 2950 (6); 5547 (6); 6279 (6); 9719 (6); 15576 (6). H. T. Chang 3181 (6). J. H. Chang 19216 (16). R. E. Chang 4906 (6). S. Y. Chang 1512 (10); 1740 (6); 3319 (6); 5178 (10); 5822 (10); 6258 (10); 7772 (10); 8514 (10). Y. L. Chang 2512 (9). B. Y. Chen 2949 (10). C. Chen 1520 (10). G. R. Chen 2368 (10); 2442 (9). H. C. Chen et al. 500072 (10); 500132 (16); 500159 (10). L. X. Chen 500132 (16); 500159 (16). M. Chen 1061 (10); 1176 (10). S. Chen 519 (9). S. Q. Chen 674 (10); 2889 (8); 3431 (9); 3552 (15); 3573 (10); 4141 (16); 4875 (16); 5408 (8); 5649 (10); 10192 (16); 12850 (16); 13215 (16); 14263 (6); 14376 (5); 14420 (16); 14442 (6); 14692 (10); 14709 (6); 15240 (6); 15255 (16); 15281 (16); 15364 (6); 15367 (6); 15908 (6); 16408 (6); 16565 (16). S. Y. Chen 5649 (10). T. C. Chen 410 (6); 414 (10); 885 (16); 886 (6); 1028 (10). W. C. Chen 61 (16). Y. Chen & B. Bai 562 (5). Z. L. Chen 30585 (16); 30601 (10); 30603 (16); 30605 (10); 30610 (8); 30613 (10); 30614 (10). Z. Z. Chen 50892 (10); 50893 (10); 50983 (6); 50995 (10); 51016 (10); 51055 (6); 51074 (6); 51257 (6); 51517 (16); P51517 (16); 51906 (16); 52034 (6); 52458 (6); 52659 (10); 53822 (10). W. Cheng 103 (10). W. C. Cheng in 1937 (8); s.n. (8); 2926 (6); 3732 (10); 4588 (10); 6198 (5); 6332 (5); 6540 (5); 10388 (6); 10441 (4); 10638 (4); 11008 (4); 11022 (4). W. C. Cheng & C. T. Hwa 559 (6); 662 (6); 975 (6). X. Cheng et al. 1385 (16). Y. Q. Cheng 170066 (10); 170129 (10); 170262 (10); 170294 (10). H. C. Cheo & W. F. Wilson 229 (10). K. H. Cheo C302 (10). A. J. B. Chevalier 38674 (3); 41007 (16). C. C. Chi 5256 (10). C.-Y. Chiao 1634 (5); 2715 (6); 2800 (6); 2848 (6). C. P. Chien 623 (16). Chin & Shun 80 (4); 137 (4). China-USSR team 18 (12); 46 (16); 217 (12); 346 (6); 431 (6); 832 (6); 1510 (16); 1713 (10); 1853 (10); 1870 (16); 1876 (16); 2256 (5); 3070 (16); 3726 (16); 5570 (5); 5610 (16); 5958 (16); 6268 (5); 8531 (4); 9559 (16); 9688 (16); 185312 (10). China-Vietnam Exp. s.n. (16). Ching & Shun 80 (10). R. C. Ching 137 (4); 1415 (10); 1434 (10); 1622 (10); 1809 (10); 2080 (10); 2241 (10); 2911 (10); 3253 (9); 3273 (6); 4699 (10); 4825 (6); 5966 (6); 7096 (16); 7160 (6); 7398 (16); 7652 (16); 7957 (16); 8415 (16); 20264 (7); 20267 (7); 21670 (7); 22139 (7); 22316 (5); 22621 (5); 22673 (5); 24523 (7); 24887 (7). R. C. Ching & C. L. Tso 407 (10); 485 (10). L. H. Chiu 50078 (16). C. H. Chow 11767 (4). H.-C. Chow 832 (6); 7547 (10); 8016 (10). K. L. Chu 1266 (10); 2179 (6); 2963 (5). T. S. Chu 60946 (10). D. C. Chun 414 (10); 885 (16); 886 (6). N. K. Chun 41130 (16); 41251 (16); 41677 (10); 41913 (10). W.-Y. Chun 3699 (6); 3707 (6); 3708 (6); 4081 (6); 4159 (6); 4165 (6); 4990 (10); 5079 (10); 6051 (10); 7369 (16); 9744 (10); 9808 (10); 10623 (10). Chung In Cho 8276 (9). H. H. Chung 1345 (10); 1867 (10); 2615 (10); 2667 (10); 2742 (10); 2867 (10); 3438 (10); 7003 (10); 8455 (10). Z. S. Chung 81981 (10). Chungtien-Lijiang-Dali Exp. 1446 (5). C. B. Clarke 728B (5); 26889B (5); 27995B (5); 34944D (5); 43631A (5). Coll. Team for Oil Pl. 650302 (7); 650303 (7). C. B. Collett 800 (12). G. Congdon 507 (11). J. T. Conover 1171 (6). P. Courtois 25676 (10); 28596 (10); 36304 (6). J. M. Cowan s.n. (5). Cultuurtuin van Technische Gewassen in 1936 (6). C. Curtis 1538 (11).

L. Y. Dai & C. H. Qian 616 (6); 771 (6); 1484 (6); 1622 (6). T. L. Dai 1296 (4); 1511 (4); 1609 (4); 1689 (4); 100551 (4); 103315 (6); 105634 (4). J. M. Dalziel in 1906 (6). Danish Exp. (1958/1959) 3295 (12). K. Deguchi 4819 (6); 5737 (9). K. Deguchi & S. Tsugaru 3819 (6). J. M. Delavay in 1883 (7); 1017 (7); 2536 (7); 2782 (7); 2936 (7); 4354 (7); 4394 (7). R. P. Delavay s.n. (7). C. Y. Deng 2018 (6); 2505 (6). M. B. Deng 4134 (9); 4223 (9); 4263 (9); 4768 (10); 4803 (10); 11153 (10). M. P. Deng & K. Yao 79022 (6). X. F. Deng 4 (5); 791361 (5). P. Di 60022 (7). F. G. Dickason 6008 (12); 8750 (12). M. Dickins in 1877 (6). X. Y. Dong & Y. L. Xiong 93565 (10). P. H. Dorsett & W. J. Morse 719 (6). J. Dransfield 3418 (14). F. Ducloux 689 (6); 2291 (6); 2716 (6); 2717 (6); 4626 (5); 4627 (7); 4951 (5). S. T. Dunn 2897C (10).

E China Work Station 6855 (6); 7007 (9). Y. Z. E 77 (16). G. E. Edaño 79248 (6). H. J. Elwes & K. Watanabe in 1904 (6). Y. Endo in 1983 (6). Rev. Père J. H. Esquirol 408 (6). Exp. Anhui 59 (9); 219 (9); 359 (9); 423 (9); 1059 (10); 2344 (10); 2376 (10). Exp. An-shun 70 (6); 660 (6); 890 (5); 1353 (6). Exp. Bi-jie 358 (6); 847 (5); 1491 (6). Exp. Da-yao-shan 11118 (16); 11557 (16); 14243 (10). Exp. E-shan 88155 (5); 88441 (6). Exp. Fan-jin-shan & Feng-huang-shan 31159 (6); 32467 (6); 400532 (6); 400566 (6); 400838 (6); 400911 (6); 401959 (6); 402061 (6); 402110 (4); 402476 (10). Exp. Gao-li-gong-shan (1997) 9518 (5). Exp. Guangdong 70 (16); 144 (16); 249 (6); 445 (16); 587 (16); 1244 (10); 1265 (6); 5185 (8). Exp. Guangxi 455 (10); 627 (6); 3468 (16); 3627 (16). Exp. Guizhou 2924 (10); 3034 (10); 4042 (6); 4481 (6); 4737 (5); 4809 (6); 6836 (5); 7361 (6). Exp. Hainan 711 (6). Exp. Henan 714 (6); 868 (6); 945 (6); 1254 (6); 1405 (6); 1511 (4); 1905 (6); 2188 (6). Exp. Hokkaido EHOK105 (9). Exp. Hong-shui-he 89-999 (10); 1085 (10); 89-1109 (6); 2065 (6); 2336 (6); 2356 (5); 2943 (6). Exp. Hubei 14022 (6). Exp. Hunan 281 (6); 614 (6). Exp. Hunan & Guizhou 2626 (10); 3279 (6); 3802 (6). Exp. Jiangxi. 377 (6); 718 (16); 1411 (6); 1652 (6). Exp. Jin-fo-shan 477 (6); 1205 (6). Exp. Li-bo 1115 (6); 1188 (6); 2240 (6); 2248 (6). Exp. Long-sheng 55 (16); 151 (6). Exp. Lü-chun 43 (16); 803 (6); 866 (16); 902 (16); 1194 (16). Exp. N Guizhou 373 (6); 549 (6); 1360 (6); 1588 (6); 2046 (6). Exp. Nan-ling 55 (10); 272 (10); 560 (10). Exp. NE

Yunnan 137 (5); 309 (5); 568 (5); 905 (6); 1161 (4); 1163 (10). Exp. NW Yunnan 4010 (7); 6389 (7). Exp. Qinghai & Xizang 20 (7); 517 (7); 638 (7); 692 (7); 74-4029 (5); 6603 (5); 7245 (5); 9653 (5); 11362 (7). Exp. Qing-ling (No. 3 Team) 968 (4). Exp. S China 1996 (16); 2658 (10). Exp. S Guizhou 205 (5); 958 (6); 1104 (6); 1274 (6); 1590 (6); 1753 (6); 2008 (6); 2102 (6); 2182 (6); 2745 (6); 2902 (6); 3615 (6). Exp. Sang-zi 737 (4). Exp. SE Guizhou 50113 (6); 50609 (6); 50741 (6); 50915 (6); 50919 (6); 51245 (6). Exp. Sichuan & Guizhou 123 (6); 192 (6); 415 (6); 1774 (6); 1860 (6). Exp. SW China (Guizhou, Sichuan, Yunnan) in 1965 (7); 200 (7). Exp. W Hunan 81 (10); 495 (6); 1087 (6). Exp. Wen-shan 65-138 (16); 60243 (16); 60259 (16); 68275 (16). Exp. Wu-ling-shan 40 (6); 224 (6); 616 (6); 697 (6); 772 (6); 912 (6); 1989 (6); 2345 (6); 2598 (6). Exp. Wu-yi-shan 11 (10); 160 (10); 80-261 (6); 80-472 (6); 912 (6); 932 (6); 1624 (6); 1812 (6); 2409 (10); 6839 (10); 400668 (6); 400829 (6); 400912 (6); 401195 (10); 401260 (6). Exp. Yu-xi 2351 (5); 2373 (5); 2992 (6); 3055 (6); 3067 (6); 89480 (6). Exp. Zhan-jiang 2909 (16); 3648 (16). Exp. Zi-yun-shan 272 (6); 412 (6); 910 (6); 932 (6).

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APPENDIX 3. Index to scientific names. Numbers in parentheses correspond to taxon numbers in the text. Synonyms and excluded names are italicized.

PHYLOGENY OF CAMPANULACEAE S. STR. INFERRED FROM ITS SEQUENCES OF NUCLEAR RIBOSOMAL DNA[1]

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ABSTRACT

Ninety-three taxa comprising thirty-two genera (plus four outgroups from Lobeliaceae) were used to estimate a phylogeny of the Campanulaceae based on ITS sequences of nuclear ribosomal DNA. From 2629 most parsimonious trees, a strict consensus tree with bootstrap values was constructed, in addition to a phylogram showing branch lengths. The topologies of these two trees are discussed in relation to the pollen and capsule morphology within the family, in addition to chromosome number and geographical distribution. The results show that there is a major dichotomy between the colpate/colporate pollen alliance (platycodonoid taxa) and the porate pollen alliance (wahlenbergioid and campanuloid taxa). Both these major alliances are monophyletic. Within the porate alliance there are two major clades, the wahlenbergioids and the campanuloids. The campanuloid clade is further subdivided into two major clades representing the *Rapunculus* and the *Campanula* s. str. groups of taxa, plus three smaller clades that are considered as "transitional" taxa. It is argued that the family originated in a fragmenting West Gondwanaland and that tectonic processes are responsible for the major dichotomy in the family. The colpate/colporate platycodonoids subsequently remained relatively relictual in Asia, whereas the porate taxa spread over much of the Northern and Southern Hemispheres. The campanuloid lineage spread over the Northern Hemisphere from a major evolutionary center in the Mediterranean region and is represented in North America only by the *Rapunculus* group. The wahlenbergioid lineage is widely dispersed across the southern continents and oceanic islands but has a major secondary center of diversification in southern Africa. The use of ITS provides insights for future investigations and a phylogenetic framework that can be tested with other data sets. Its limitations for phylogeny reconstruction are briefly discussed. More extensive taxon sampling and additional data sets are required to refine these results and for a new classification of the Campanulaceae to be proposed.

Key words: Campanulaceae, evolution, Gondwanaland, ITS, nuclear-ribosomal DNA, phylogeny.

Classification systems of the bellflower family (Campanulaceae s. str.) have traditionally followed the arrangements of Boissier (1875, 1888) and Schönland (1889–1894) and, together with the refinements of Charadze (1949, 1970, 1976), Fedorov (1957), and others, can ultimately be traced back to the arrangement of De Candolle (1830) who divided the family into two subtribes, the Campanuleae and the Wahlenbergeae, based on the mode of capsule dehiscence (Table 1). Schönland divided the family into three subtribes, separating *Platycodon* A. DC., *Musschia* Dum., and *Microcodon* A. DC. in his subtribe Platycodinae on the basis of calyx lobe position in relation to the locules of the

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Table 1. Classification of Campanulaceae (A. P. de Candolle, 1830).

Subtribe I (Wahlenbergeae)	Subtribe II (Campanuleae)
Capsule with apical (valvate) dehiscence	Capsule with lateral (porate) dehiscence
Campanumoea Blume (baccate capsule)	*Adenophora* Fisch.
Canarina L. (baccate capsule)	*Campanula* L.
Cephalostigma A. DC.	*Merciera* A. DC. (indehiscent)
Codonopsis Wall.	*Michauxia* L'Her.
Jasione L.	*Musschia* Dum.
Lightfootia L'Her.	*Petromarula* Vent. ex Hedw. f.
Microcodon A. DC	*Phyteuma* L.
Platycodon A. DC.	*Specularia* A. DC.
Prismatocarpus L'Her.	*Symphyandra* A. DC.
Roella L.	*Trachelium* L.
Wahlenbergia W. Roth	

ovary (Table 2). Such natural classifications were essentially based on morphology of the calyx (e.g., the presence or absence of appendages between the lobes) or of the mode of capsule dehiscence (e.g., whether it is apical and valvate or lateral and porate). Many authors (e.g., Hutchinson, 1969; Carolin, 1978; Cronquist, 1988; Takhtajan, 1969) considered *Cyananthus* A. DC. to be the most primitive genus within the family based on its superior ovary.

These various classifications were generally useful in floristic works, especially during the 20th century when much of the research on the Campanulaceae was of a regional, floristic nature. Frequently, various authors have used their own modified system with many nomenclatural changes, and great confusion has resulted. Considerable conflict still exists as to the number of genera recognized. Generic distinctions in the family are often subtle, being based on a suite of characters best observed in living plants. In addition, species of the Campanulaceae appear to be prone to considerable phenotypic plasticity (Eddie, 1997; Eddie & Ingrouille, 1999) as well as ontogenetic variation, and this has led to a burgeoning of the literature with superfluous species names. The few generic monographs that have been completed, although excellent, often lacked a global perspective, and have contributed little to the establishment of a new, more generally accepted classification of the family. Reconstruction of the phylogeny of the Campanulaceae has been hindered by a lack of consensus as to what constitutes a genus and the failure to apply important character combinations (e.g., cytological and palynological characters), which could potentially

Table 2. Classification of the Campanulaceae (Schönland, 1889–1894).

Tribe Campanuleae		
Subtribe Campanulinae	Subtribe Wahlenberginae	Subtribe Platycodinae
Adenophora Fisch.	*Campanumoea* Blume	*Microdon* A. DC.
Campanula L.	*Cephalostigma* A. DC.	sect. *Eumicrocodon* A. DC.
sect. *Medium* Tourn.	*Codonopsis* Wall.	sect. *Caelotheca* A. DC.
sect. *Rapunculus* Boiss.	*Cyananthus* Wall.	*Musschia* Dum.
Canarina L.	*Githopsis* Nuttall	*Platycodon* A. DC.
Heterocodon Nuttall	*Hedraeanthus* Grisebach	
Michauxia L'Her.	*Heterochaenia* A. DC.	
Ostrowskia Regel	*Jasione* L.	
Peracarpa J.D. Hooker & T. Thoms.	*Leptocodon* (J. D. Hooker) Lem.	
Phyteuma L.	*Lightfootia* L'Her.	
sect. *Cylindrocarpa* Rgl.	*Merciera* A. DC.	
sect. *Hedranthum* G. Don	*Prismatocarpus* L'Her.	
sect. *Petromarula* A. DC.	*Rhigiophyllum* Hochst.	
sect. *Podanthum* G. Don	*Roella* L.	
sect. *Synotoma* G. Don	*Siphocodon*	
Symphyandra A. DC.	*Treichelia*	
Trachelium L.	*Wahlenbergia* W. Roth	

highlight major discontinuities at the generic, tribal, and subtribal levels. Many species have been placed, for convenience, in *Campanula* L., *Asyneuma* Grisebach & Schenk, and *Wahlenbergia* Schrad. ex W. Roth, and this has further complicated our understanding of phylogenetic relationships. Indeed, some of the intrageneric taxa in these large genera are probably more deserving of generic status than some of the currently recognized segregate genera. The so-called satellite genera of *Campanula* do not appear to be any closer to each other than they do to *Campanula*, and there is no evidence to suggest that *Campanula*, despite its numerical superiority, is ancestral to them. It is thus often easier to define what *Campanula* is not rather than what its actual boundaries are. Thus, to some extent, the genus *Campanula* is conceptually useless and its continued use as a "core" genus may be misleading. The same is probably true for *Asyneuma* and *Wahlenbergia*.

Knowledge of inter- and intrageneric relationships within the family has steadily increased during the latter half of the 20th century. Cytological studies, beginning with the seminal investigations of Gadella (1962, 1963, 1964, 1966, 1967), Contandriopoulos (1964, 1966, 1970, 1971, 1972, 1976, 1980a, b, 1984), Contandriopoulos et al. (1972, 1974, 1984), Damboldt (1965a, b, 1966, 1968, 1969, 1970, 1975, 1976, 1978a, b), Phitos (1963a, b, 1964a, b, 1965), and Podlech and Damboldt (1964) have vastly increased our knowledge of intrageneric relationships, particularly of the genus *Campanula*. The most common chromosome number in the Campanulaceae is $n = 17$, and this appears to have evolved independently several times in relatively unrelated genera (e.g., in *Campanula*, *Nesocodon* M. Thulin, *Ostrowskia* Regel, and *Canarina* L.). Forty-two percent of the published chromosome counts of the family Campanulaceae s.l. have this number (Lammers, 1992). The base number in the family has been suggested to be $x = 8$ (Böcher, 1964; Contandriopoulos, 1984), but Raven (1975) suggested that $x = 7$ is the ancestral number. An ancestral base number of $x = 7$ is supported by counts for *Cyananthus* (Kumar & Chauhan, 1975; Hong & Ma, 1991).

It was Avetisian (1948, 1967, 1973, 1986) who first drew attention to the different pollen morphologies within the family and gave a schematic presentation of pollen evolution based on aperture types. She further pointed out that pollen with colpate and colporate apertures are typical of those taxa found in the tropics, whereas those with porate apertures are typical of taxa from temperate regions. Dunbar (1973a, b, c, 1975a, b, 1981, 1984) and Dunbar and Wallentinus (1976) extended Avetisian's work by providing excellent surveys of pollen from numerous genera of the Campanulaceae, and this has been augmented by Morin (1987), Nowicke et al. (1992), and Morris and Lammers (1997). Several of these studies suggest that some of the genera are artificially grouped together in De Candolle's and in Schönland's arrangements because of the limited criteria used as the basis for their classification systems.

Seed morphology has been examined for a number of taxa, principally those of North America (Shetler & Morin, 1982, 1986) and Eurasia (Belyaev, 1984a, b, 1985, 1986; Oganesian, 1985). Life-form in the Campanulaceae has been studied intensively by Shulkina (1974, 1975a, b, 1977, 1978, 1979, 1980a, b, c, 1986a, b, 1988) and Shulkina and Zykov (1980), but these data have not been incorporated into a cladistic analysis. Serological studies have been done on the tribe Phyteumatae (Gudkova & Borshchenko, 1991), while Gorovoi et al. (1971) conducted a limited chemotaxonomic survey of Russian Far-Eastern taxa. Kolakovsky (1980, 1982, 1986a, 1986b, 1987), Kolakovsky and Serdyukova (1980), and Lakoba (1986) did some pioneering carpological investigations of the family, but so far this work has not been corroborated and it remains to be seen whether their segregate genera will be accepted.

Few molecular phylogenetic studies of the Campanulaceae have been undertaken. Cosner (1993) and Cosner et al. (2004) used chloroplast DNA (cpDNA) structural rearrangements to establish a phylogeny of the family based on 18 genera, while Cosner et al. (1994) determined *rbc*L sequences for several genera as part of a study of interfamilial relationships of the Campanulales. Eddie (1997, and unpublished data), using cladistic and phenetic methodologies, investigated the morphology of most of the genera of the Campanulaceae, in addition to molecular variation of 23 to 29 taxa using internal transcribed spacers (ITS) and *mat*K/*trn*K-intron sequence data from nuclear ribosomal (nrDNA) and cpDNA, respectively. For molecular variation within and between genera, ITS sequences have been used by Ge et al. (1997) for *Adenophora* Fisch. and by Kim et al. (1999) for *Hanabusaya* Nakai. Haberle (1998) examined relationships among the families Campanulaceae, Cyphiaceae, Nemacladaceae, Cyphocarpaceae, and Lobeliaceae using ITS sequence data.

This study is an attempt to reconstruct the phylogeny of the Campanulaceae s. str. using nrDNA ITS sequences and to compare the results with certain characters that have traditionally been used in the classification of the Campanulaceae (i.e., capsule morphology and presence/absence of calyx appendages in addition to chromosome numbers, pollen, and geographical distribution). It is the first time that molecular methods have been applied to a broad sample of taxa (93 species in 32 genera) within the family. This study is also the first part of more extensive investigations of the Campanulaceae using a variety of molecular markers, including the sequences of chloroplast genes *mat*K and *rbc*L, as well as chloroplast genome rearrangements and morphological data. Ultimately these studies should lead to a new comprehensive classification of the Campanulaceae.

MATERIALS AND METHODS

TAXA SAMPLED AND SOURCES OF PLANT MATERIAL

ITS sequences for 93 taxa of the Campanulaceae were used, including a number of which were previously published and available from Genbank (Fu et al., 1999; Ge et al., 1997; Kim et al., 1999; Schultheis, 2001; K. Dotti, unpublished data) (see Appendix 1). Many of the samples represent taxa that are commonly accepted as genera or sections within genera because of their obvious morphological discontinuities and that provide a broad sample of the family. The nomenclature used in this study is based on the classification system used by Fedorov (1957), but the names given to the major groups or clades are merely for convenience and not based on any particular classification system. Added to the data set were four outgroups from the Lobeliaceae (*Downingia bacigalupii* Weiler, *Lobelia aberdarica* R. E. Fries & T. C. E. Fries, *L. tenera* Kunth, and *L. tupa* L.), bringing the total number of taxa in the data set to 97. There is overwhelming evidence from both morphological (Lammers, 1992; Gustafsson & Bremer, 1995) and molecular (Cosner et al., 1994; Gustafsson et al., 1996; Jansen & Kim, 1996; Albach et al., 2001) studies that the Lobeliaceae are an appropriate outgroup for the Campanulaceae sensu stricto. DNA samples were obtained from living plants cultivated at The Institute of Cell and Molecular Biology (ICMB), University of Edinburgh, Scotland, U.K., The Royal Botanic Garden Edinburgh (RBGE), Scotland, U.K., The University of Texas at Austin (UT), U.S.A., and the Missouri Botanical Garden (MO), St. Louis, U.S.A. For sources of material and location of vouchers, see Appendix 1.

DNA ISOLATION, AMPLIFICATION, AND SEQUENCING

Genomic DNA was extracted following the CTAB protocol of Doyle and Doyle (1987) or with minor modifications such as the addition of PVP-40 and/or BSA. Double-stranded DNA from the ITS and the intervening 5.8S subunit of the 18S–26S nr DNA was amplified using standard PCR procedures (Kim & Jansen, 1994). The basic primer sequences were those of White et al. (1990) or the modifications by Yokota et al. (1989). Purification of the PCR products was by means of Qiagen QIAquick spin columns (Qiagen Corp.), and sequences were obtained from ABI Prism 377 Automatic DNA Sequencers (Perkin Elmer, Applied Biosystems Division). For each taxon, forward and reverse sequences were obtained, and the results were saved as electropherograms and edited using the programs SEQUENCHER, vers. 3.0 and 4.1.2 (Gene Codes Corp.), EDITVIEW, ver. 1.0.1, and SEQUENCE NAVIGATOR, ver. 1.0.1 (Perkin Elmer, Applied Biosystems Division).

SEQUENCE ALIGNMENT

The boundaries for the ITS region were determined by comparisons with published ITS sequences of *Nicotiana rustica* L. (Solanaceae, Venkateswarlu & Nazar, 1991), *Krigia* Schreb. (Asteraceae, Kim & Jansen, 1994), Madiinae Benth. (Asteraceae, Baldwin, 1992), and *Gentiana* L. (Gentianaceae, Yuan et al., 1996). Alignment of ITS proved to be problematic, particularly at the 3′ end of the ITS2 region close to the 26S subunit. Due to a high level of ambiguity, this region was deleted at 205 bases downstream from the start of the ITS2 region. The highly conserved 5.8 subunit was not available for all taxa and therefore was not included in phylogenetic analyses. The multiple alignment used in this study was created by CLUSTALX (ver. 1.64b; Thompson et al., 1997) in several stages using the Slow/Accurate dynamic programming option. Divergent sequences (> 40%) were delayed in the alignment procedure. Insertions from individual taxa, which created gaps and had no apparent homology with the rest of the taxa, were removed, and another round of alignment was initiated. A range of gap penalties from 5.00 to 20.00 and gap extension penalties from 3.00 to 8.00 were initially tried with various combinations until a consistent alignment was established using a gap penalty of 8.00 and a gap extension penalty of 5.00. Minor final adjustments to the alignment were done manually. The alignment is available at: <http://www.biosci.utexas.edu/IB/faculty/jansen/lab/personnel/eddie.htm>. All new sequences have been submitted to Genbank.

Table 3. Base composition and nucleotide divergence in the aligned partial sequences of ITS1 and ITS2 regions of nr DNA in the Campanulaceae.

Sequence parameter		ITS1 + partial ITS2		
Aligned length		497		
Constant sites		81		
Variable sites		416 (75 uninformative)		
Informative sites		345		
G + C content (%)		59.8		
Unambig. transitions		627		
Unambig. transversions		500		
Ts/Tv ratio		1.254		
Avg. base frequencies*	A = 20.8	C = 30.6	G = 29.2	T = 19.3

* Missing data and gaps excluded.

PHYLOGENETIC ANALYSES

A search for the most parsimonious tree was initiated using the PARSIMONY option of PAUP 4.068 (Swofford, 2001) with ACCTRAN, MULTREES, TBR, and COLLAPSE ZERO LENGTH BRANCHES options. All characters were given equal weight and were unordered. Gaps were treated as missing data. The HEURISTIC search algorithm was chosen, with 1000 random addition replicates and with a limit of 2000 trees saved per replicate. The amount of support for monophyletic groups was evaluated by 1000 bootstrap replicates and a 50% cut-off value for the bootstrap consensus tree (Felsenstein, 1985). Consistency Indices (CI) (Kluge & Farris, 1969) were also computed. The Retention Index (RI) and the g1 statistic (Hillis & Huelsenbeck, 1992) were also computed, the latter after computing the tree-length distribution of 100,000 random parsimony trees by means of the RANDOM TREES command.

RESULTS AND DISCUSSION

The total aligned length of the ITS1 and partial ITS2 (including gaps) was 497 bp. There were 81 constant characters, 71 variable characters that were parsimoniously uninformative, and 345 parsimoniously informative characters (Table 3). Parsimony analyses generated 2629 trees with 2130 steps, a CI of 0.3703 (excluding uninformative characters), and RI of 0.7583 (Figs. 1, 2). The g1 statistic for 100,000 trees randomly sampled was −0.327694 indicating that the ITS data set is significantly skewed from random and contains considerable phylogenetic information (Hillis & Huelsenbeck, 1992). For other statistics of the aligned sequences see Table 3. Multiple ITS types were not detected, and in one case there were two separate samples of the same species (*Adenophora divaricata* Franch. & Sav.) that did not come out together. The branch lengths are very short for the *Adenophora* clade overall, which indicates that most of the species have very similar ITS sequences. The differences between the two samples of *A. divaricata* suggest either misidentification of the original sample or population differences in the ITS sequences.

The taxonomic categories used in classifications are unequivocal and the amount of molecular divergence (and hence phylogenetic signal) within and between taxa at each level in the taxonomic hierarchy varies. For a family such as the Campanulaceae, which has numerous monophyletic genera and sections, the use of ITS sequences is justified by the phylogenetic signal obtained, but there may be substantial trade-off due to problems with alignments. The difficulties associated with sampling across a wide spectrum of taxa in the Campanulaceae should lessen as we are able to refine our molecular analyses at different levels in the taxonomic hierarchy, in conjunction with other sources of data. Due to high ambiguity at the generic level in the Campanulaceae, ITS sequence data may be approaching the limits of usefulness for phylogenetic reconstruction, whereas at the species level, there may not be enough signal, and many species may be spuriously placed with each other. For extensive discussion of the utility and limitations of the ITS region in the reconstruction of angiosperm phylogeny, see Baldwin et al. (1995), Coleman (2003), and Goertzen et al. (2003).

MAJOR CLADES IN THE ITS TREE

The topology of the strict consensus tree (Fig. 1) shows that there are two major clades of the Campanulaceae. This major dichotomy in the family is supported by pollen data. For convenience, these two major clades are referred to as alliances and are named on the basis of their pollen types. The taxa in the smaller of these two alliances comprise

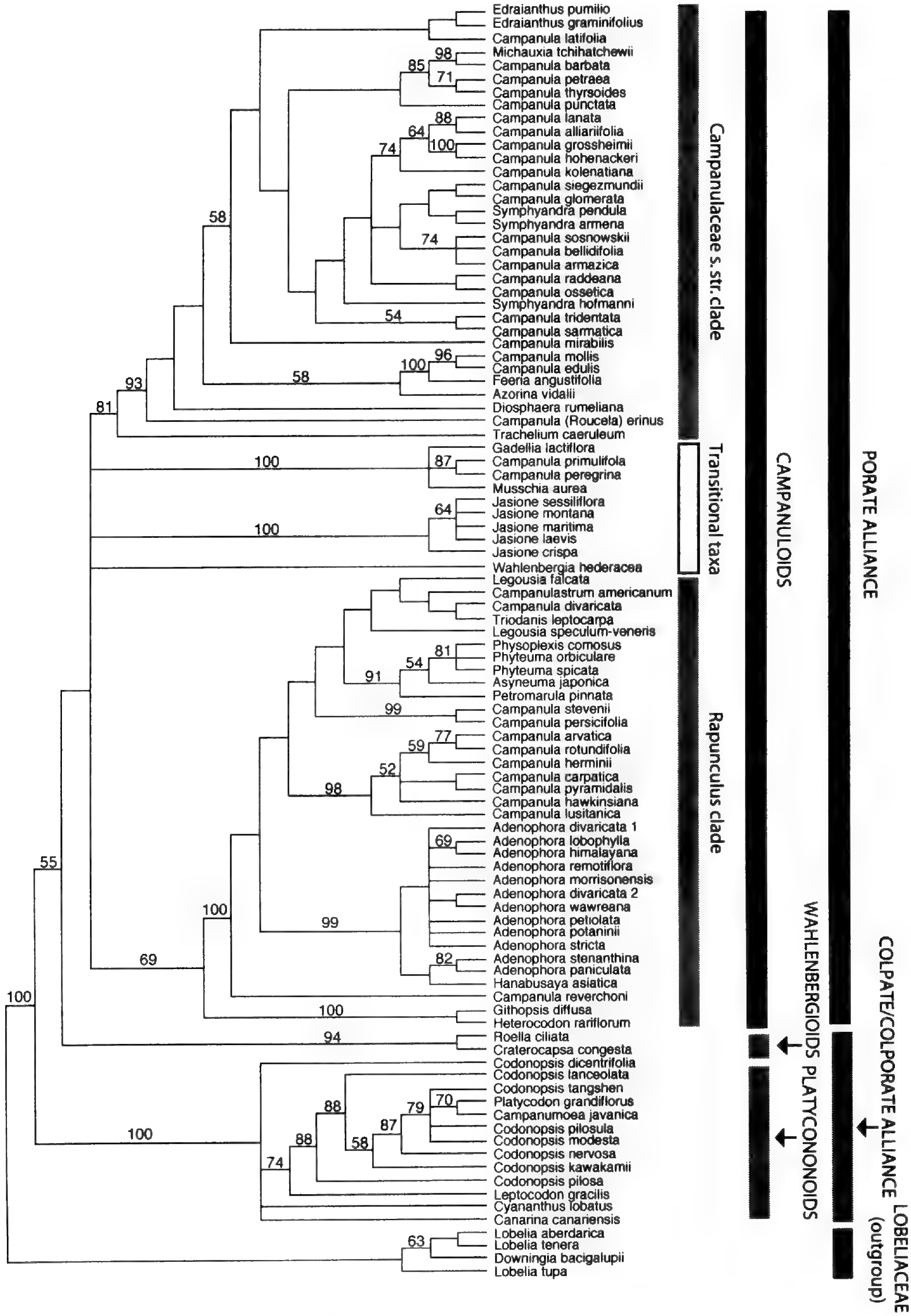

Figure 1. Strict consensus of 2629 most parsimonious trees with 2130 steps for 93 taxa of the Campanulaceae and 4 outgroups of the Lobeliaceae based on parsimony analysis of the combined ITS1 and ITS2 sequence data. The numbers above the nodes are bootstrap percentages of 1000 replicates. [CI = 0.3703 (excluding uninformative characters), RI = 0.7583.] Nodes without bootstrap values had less than 50% support.

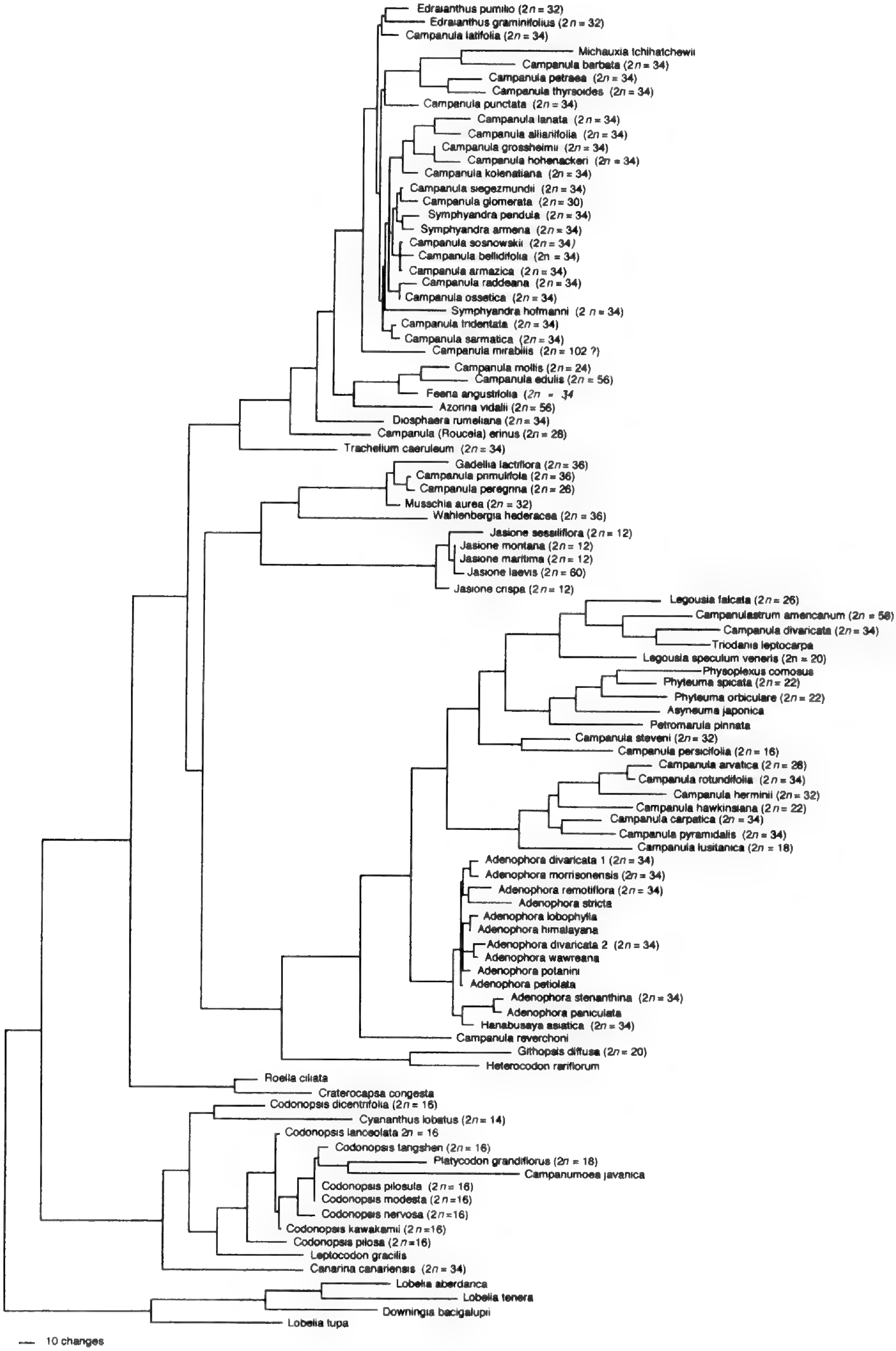

Figure 2. Phylogram of one of the 2629 equally parsimonious trees for 93 taxa of the Campanulaceae and 4 outgroups of the Lobeliaceae based on parsimony analysis of the combined ITS1 and partial ITS2 sequence data. A scale bar representing 10 changes is shown on bottom left corner.

genera such as *Codonopsis, Platycodon, Canarina,* etc., which are all distinguished by their possession of either colpate or colporate pollen (Avetisian, 1948, 1967, 1973, 1986; Dunbar, 1973a, b, c, 1975a, b, 1981, 1984) and are also referred to as the platycodonoid group in this paper. The colpate/colporate alliance is strongly supported with a 100% bootstrap value and is the only clade with taxa that have baccate fruits (*Canarina, Campanumoea* Blume, and *Cyclocodon* W. Griff.), although the majority have dry capsules. Geographically, the colpate/colporate alliance is mostly distributed in the tropics or subtropics, from Southeast Asia and the western Himalayas to Ussuriland, Korea, and Japan, and from Indonesia and the Philippines to New Guinea. The genus *Canarina* is unique within this alliance in being essentially African, but it is disjunct, with one species in Macaronesia and two species in the mountains of East Africa. The taxa in the larger alliance comprise the remainder of the Campanulaceae, and they are distinguished by their porate pollen. The porate alliance has only weak support with a 55% bootstrap value. It is far larger numerically than the colpate/colporate alliance and is divided into two major groups, the wahlenbergioids and the campanuloids. This huge alliance is distributed mostly in the temperate regions of the world, although a few wahlenbergioid and campanuloid taxa extend to the tropics. All taxa within these two groups have capsules that are predominantly dry and dehiscent. In the discussion that follows, we describe the major groups in the two alliances and how they compare with data from morphology, chromosome number, and geography.

THE COLPATE/COLPORATE ALLIANCE (THE PLATYCODONOID GROUP)

There is strong support (100%) for the monophyly of the colpate/colporate alliance, although the major clades within this alliance are only partially resolved. *Canarina, Cyananthus,* and *Codonopsis* Wall. subg. *Obconicapsula* D. Y. Hong form a polytomy with the remainder of taxa, including *Codonopsis, Leptocodon* (J. D. Hooker) Lem., *Platycodon,* and *Campanumoea javanica* Blume. *Codonopsis* subg. *Obconicapsula* is somewhat isolated morphologically and, to a lesser extent, geographically (central Himalayas) from the rest of *Codonopsis.* It has an ovary that bulges upward above the level of the calyx lobes and an incomplete nectar dome. These features, together with the overall appearance of the flower, recall *Platycodon. Cyananthus* comprises highly adapted perennial and annual species of very high elevations in the mountains of southern Asia. Because of its superior ovary and low chromosome number of $2n = 14$, it has traditionally been considered the most ancestral genus of the Campanulaceae (Hutchinson, 1969; Cronquist, 1988; Takhtajan, 1969). However, it also has specialized ecological characters such as deep taproots and prostrate lateral branching, both of which are characteristic of alpine plants. The isolated position of *Canarina* is supported by both geography and chromosome number. *Canarina canariensis* (L.) Vatke has $2n = 34$, while the remainder of the platycodonoids have $2n = 16$ or 18. Bootstrap support for the clade comprising *Leptocodon,* the remainder of *Codonopsis,* plus *Campanumoea javanica* and *Platycodon* is moderate (74%). Support for the minor clade containing the bulk of *Codonopsis* plus *Platycodon* and *C. javanica* is strong (88%), but the clade with only the latter two genera is moderately supported (70%). The taxa of *Codonopsis* are morphologically less divergent from each other, whereas *C. javanica* and *Platycodon* are considerably divergent. Hong and Pan (1998), on the basis of pollen morphology, seed coat, and gross morphology, restored the genus *Cyclocodon,* which was formerly included in *Campanumoea* s.l. as *C. celebica* Blume and *C. lancifolia* (Roxb.) Merr. They considered *Cyclocodon* to be more closely related to *Platycodon* than to *Campanumoea* s. str. (i.e., *C. javanica* Blume and *C. inflata* (Hook. f.) C. B. Clarke). *Campanumoea* and *Cyclocodon* have baccate fruits but would appear to be rather distant from *Canarina.*

THE PORATE ALLIANCE (THE WAHLENBERGIOID AND CAMPANULOID GROUPS)

The monophyly of the porate alliance is weakly supported (55%) and it comprises two very unequal clades, the wahlenbergioids and the campanuloids. This is undoubtedly an artifact of the undersampling of wahlenbergioid taxa.

The wahlenbergioid group. The sister relationship of the two wahlenbergioid taxa, *Craterocapsa* Hilliard & B. L. Burtt and *Roella* L., has strong bootstrap support (94%). These two genera have traditionally been considered closely related (Hilliard & Burtt, 1973). Both are from southern Africa, although *Craterocapsa* ranges north to the mountains of eastern Zimbabwe. Since only three traditionally accepted wahlenbergioid genera were available for molecular analysis, the discussion of the results for this group is relatively straightforward, but caution should be observed for such a small sample. *Wahlenbergia hederacea* L. falls within the campanuloid group and is therefore distant from the other two wahlenbergioid genera. This is surprising because this species has traditionally been considered as typically wahlenbergioid. It has a chromosome number of $2n = 36$, which is not particularly unusual, but it is isolated in western Europe, and has a vegetative morphology that is rather atypical for the wahlenbergioids. Although all modern European workers have never questioned the wahlenbergioid nature of *W. hederacea*, this species was recognized as a separate genus by some early workers (*Schultesia* Roth, *Valvinterlobus* Dulac, *Aikinia* Salisb. ex A. DC.) and it was assigned to *Roucela* by Dumortier (1827). The majority of species of *Wahlenbergia* are distributed in the Southern Hemisphere. Some species (e.g., *W. trichogyna* Stearn) have $2n = 36$, but the majority have $2n = 18$ (see also Petterson et al., 1995; Crawford et al., 1994; Anderson et al., 2000). In the study of Cosner et al. (2004), the Australian species, *W. gloriosa* Lothian (not sampled), was found to be in the same clade as *Roella ciliata* L.

*The campanuloid group (*Campanula *s. str., "transitional" taxa, and* Rapunculus *clades).* This huge group forms an unresolved polytomy consisting of two major clades and three smaller ones. This basic division is partially in agreement with mode of capsule dehiscence (there are exceptions such as *Edraianthus* in the *Campanula* s. str. clade and *Adenophora* and subsection *Heterophylla* in the *Rapunculus* clade) and presence or absence of calyx appendages, two characters that have traditionally been used in intrageneric classifications of *Campanula* (Boissier, 1875, 1888; Fedorov, 1957). One large, well-supported clade (81%) comprises those taxa centered around *Campanula* s. str. (i.e., mostly those taxa belonging to the sect. *Medium* DC.), but also genera such as *Trachelium, Diosphaera, Azorina,* etc. The second large clade has moderate support (69%) and comprises those taxa centered around *Campanula* sect. *Rapunculus* (Fourr.) Boiss. (the *Rapunculus* clade). Two smaller clades have strong support (100%) and consist of several transitional genera such as *Jasione* L., *Musschia,* and *Gadellia* Shulkina, while the third small clade comprises *Wahlenbergia hederacea* alone.

THE *CAMPANULA* S. STR. CLADE

The *Campanula* s. str. clade includes a small number of mostly monotypic genera that are considerably more divergent than the majority of taxa in this clade. Some have upright flowers (e.g., *Trachelium caeruleum* L., *Diosphaera rumeliana* (Hampe) Bornm., *Feeria angustifolia* (Schousb.) Buser, *Campanula* [subg. *Roucela* (Dumort.) J. Damboldt] *erinus* L., *Campanula mollis* L., and *Campanula edulis* Forssk.), but *Azorina vidalii* (Wats.) Feer, with its nodding flowers, is a conspicuous exception. With *Trachelium* removed, bootstrap support for this clade is 93%. *Campanula* (subg. *Roucela*) *erinus* ($2n = 28$) belongs to a rather distinct group of annual campanuloids of the Mediterranean, which superficially resemble *C. mollis* and *C. edulis*, but its capsules are discoid and the calyx appendages are absent. The corolla approaches the hypercrateriform shape of *Trachelium* corollas to some extent. The flowers of *Diosphaera* Buser are quite similar to those of *Trachelium* and it has the same chromosome number ($2n = 34$), but there are conspicuous differences between the two genera, both vegetatively and in the form of the inflorescence. The two genera are often united, but they are disjunct geographically in the Mediterranean. Calyx appendages are absent in both genera.

Azorina Feer is quite isolated morphologically (vegetatively and in branching pattern), but its vague resemblance to *Campanula bravensis* Bolle and *C. jacobaea* C. Smith of the Cape Verde Islands, together with its chromosome number of $2n = 56$, may link it rather tenuously to *Campanula* subsect. *Oreocodon* Fed. (but see also Thulin, 1976: 354). Support for the clade that comprises *Azorina, Feeria, Campanula mollis,* and *C. edulis* is weak (58%), but when *Azorina* is removed support for the remaining taxa is 100%. *Feeria angustifolia* has traditionally been associated with *Trachelium,* but morphologically it is quite distinct. In some respects, particularly the globular, more compact shape of the inflorescence, and the valvate apical dehiscence, it approaches *Jasione* L., but the chromosome number for *Feeria angustifolia* is $2n = 34$ (vs. $2n = 12$ for *Jasione*). The similarity of its ITS sequences with those of both *Campanula mollis* and *C. edulis* does not accord with its morphology. *Campanula mollis* and *C. edulis* are probably closely related to each other, and this relationship is strongly supported in the ITS tree (96%). These two species belong to a group of annual and perennial campanuloids ($2n = 24$, 28, 54, 56), which range from Macaronesia, North Africa, and the Iberian Peninsula south to the equator in Tanzania. They have basal dehiscence and appendages between the calyx lobes (Maire, 1929; Quézel, 1953; Thulin, 1976). This group probably links up with *Campanula* subsect. *Oreocodon* of the western Himalayas and south-central Asia, which is characterized by species such as *C. incanescens* Boiss., *C. cashmeriana* Royle, and *C. colorata* Wall.

The remaining taxa in the *Campanula* s. str. clade are weakly supported (58%) as a monophyletic group. They are mostly Eurasian and North African, although at least one species in this alliance occurs as far east as the Aleutian Islands (*C. chamissonis* Fed. subsect. *Scapiflorae* (Boiss.) Fed., not sampled), and another south to the equator in northern Tanzania (*C. keniensis* Thulin, also not sampled). The isolated species *C. mirabilis* Albov (subsect. *Spinulosae* (Fom.) Fed.) is the sister taxon to all the others. The small clade formed by *Edraianthus pumilio* (Schultes) A. DC., *E. graminifolius* (L.) A. DC., and *C. latifolia* L. is weakly supported (< 50%). The two species of *Edraianthus* (A. DC.) DC. are confined to the mountains of southeastern Europe, and are rather dissimilar morphologically. *Edraianthus pumilio* has solitary flowers on multiple inflorescence stems, whereas *E. graminifolius* has a glomerulate inflorescence. Morphologically, *E. pumilio* may be closer to *Campanula* (*Petkovia* Stefanoff) *orphanidea* Boiss. (not sampled), which has a similar mode of capsule dehiscence (Hartvig, 1991) and similar corollas (*C. orphanidea* has $2n = 26$). *Edraianthus* was formerly considered to be wahlenbergioid because of the apical rupture of its capsule, but its overall morphology is very similar to *Campanula* and its chromosome number ($2n = 32$) is more typical of campanuloid taxa. *Campanula latifolia* is rather isolated in the *Campanula* s. str. clade. It belongs to a distinct group of tall mesophytic species from Eurasia that lack appendages and have nodding flowers on long spicate inflorescences (e.g., *C. trachelium* L., *C. bononiensis*, *C. rapunculoides* L., etc.). In general morphology this group (subsect. *Eucodon* (A. DC.) Fed.) resembles *Adenophora*.

Several other minor groups within the *Campanula* s. str. clade have moderate to strong support. *Michauxia tchihatchewii* Fisch. & C. A. Meyer and *C. barbata* L. have a bootstrap value of 98%. This relationship is surprising since the morphology of these two species is very divergent. The monophyly of the two, yellow-flowered species from the European Alps, *C. thyrsoides* L. and *C. petraea* L., is moderately supported (71%). Collectively, these four taxa form a strongly supported clade (85%). The long branches (Fig. 2) show clearly that these four taxa are all very divergent from each other. In some cases, relationships in the *Campanula* s. str. clade are in accord with classification of Fedorov (1957), whereas in other instances there is conflict. For example, *C. armazica* Kharadze, *C. sosnowskii* Kharadze, and *C. bellidifolia* Adam have a support value of 74%, which agrees with their placement in section *Scapiflorae* (Boiss.) Fed. In contrast, *C. hohenackeri* Fisch. & C. A. Mey. (subsect. *Triloculares* Boiss.) and *C. grossheimii* Kharadze (subsect. *Eucodon*) have bootstrap support of 100%, but their relationship conflicts with Fedorov's arrangement.

THE "TRANSITIONAL" TAXA

The clade comprising *Musschia*, *Gadellia*, and the two species of *Campanula* sect. *Pterophyllum* Damboldt (*C. peregrina* L. and *C. primulifolia* L.) is strongly supported (100%). *Musschia aurea* Dumort. is an endemic of Madeira together with its congener, *M. wollastoni* Lowe, whereas *C. peregrina* and *C. primulifolia* are disjunct between the eastern Mediterranean region and the western Iberian Peninsula, respectively. *Gadellia lactiflora* (M. Bieb.) Shulkina is endemic to the Caucasus region. Morphologically, *Musschia* is different from the other three taxa except for a vague similarity of form, robustness, and disposition of the stigmatic lobes. Its capsule is 5-loculed, prismatic, and opens with numerous transverse slits. Its chromosome number is $2n = 32$. *Gadellia* was erected by Shulkina (1979) for *Campanula lactiflora* M. Bieb. based on its distinct growth form and chromosome number ($2n = 36$). It has open, upright flowers and dehisces somewhat medially/apically. *Campanula primulifolia* was placed in the genus *Echinocodon* (= *Echinocodonia* Kolak.) by Kolakovsky (1986b). *Campanula peregrina* was acknowledged to be very close to *C. primulifolia* by Damboldt (1978b) and was placed in the section *Pterophyllum*. Bootstrap support for a close relationship between these two species is 87%. Despite their strong resemblances, the chromosome number for *C. primulifolia* is $2n = 36$, while *C. peregrina* is recorded as $2n = 26$ (Gadella, 1964). However, Marchal (1920) recorded the former also as $2n = 26$, so these findings require clarification.

The genus *Jasione* L. is strongly supported as a monophyletic group (100%). Within the genus, *J. crispa* (Pourr.) Samp. is sister to all the others sampled, but the clade formed by them is weakly supported (64%) and relationships among species within the group are unresolved. The relationship of *Jasione* to other taxa of Campanulaceae is unresolved in the ITS tree. *Jasione* has most frequently been associated with the wahlenbergioid alliance, although it does bear some resemblance to *Feeria* Buser with which it shares a similar mode of capsule dehiscence, but it has a chromosome number of $2n = 12$ (vs. $2n = 34$ for *Feeria*).

THE *RAPUNCULUS* CLADE

The *Rapunculus* clade has moderate support (69%) and has a number of smaller clades that are all relatively divergent from each other morphologically. In terms of branch length, the taxa within the *Rapunculus* clade are much more divergent overall than the taxa within the *Campanula* s. str. clade (Fig. 2). *Githopsis* Nuttall and *Heterocodon* Nuttall are rather divergent in morphology from each other, particularly that of the capsule (see McVaugh, 1945), but are probably closely related and have strong bootstrap support (100%). They are sister to the remaining members of the *Rapunculus* clade. Most of these taxa are either Mediterranean or North American in distribution. The majority of taxa within this clade have open, upright flowers that are rather stellate in form, and the capsule opens apically or medially by a pore, but there are conspicuous exceptions (see below). None of the taxa in the *Rapunculus* clade has calyx appendages. The irregular rupture of the capsule apex in *Githopsis* may represent a derived condition, but this is not to imply that its ancestral state was lateral (e.g., it may be derived from an apical valvate condition similar to that present in the wahlenbergioid alliance). In *Adenophora, Hanabusaya,* and *Campanula rotundifolia* L. (the sole representative of the harebell group sampled, *Campanula* subsect. *Heterophylla* Fed.), the flowers are campanulate and nodding and the capsule opens basally. The inclusion of these taxa within the *Rapunculus* clade is surprising. Morphologically these taxa seem to be more closely allied to groups within the *Campanula* s. str. clade (e.g., *C. latifolia* and its allies in sect. *Eucodon*).

When *Githopsis* and *Heterocodon* are removed, the remaining taxa of the *Rapunculus* clade have 100% bootstrap support. Within this clade the Texan endemic annual *Campanula reverchoni* A. Gray is sister to all the remaining taxa, although support for this group is weak (< 50%). Within this clade there are several small groups with moderate to strong support. The clade comprising *Adenophora* and *Hanabusaya* is strongly supported (99%), although species relationships are largely unresolved. This confirms the close relationship between *Hanabusaya* and *Adenophora* suggested previously by Eddie (1997) and by Kim et al. (1999), and it tentatively suggests that *Hanabusaya* is closest to the two species *A. stenanthina* (Ledeb.) Kitagawa and *A. paniculata* Nannf. (sect. *Thyrsanthe* (Borb.) Fed.). Support for the clade uniting these three taxa is weak (< 50%). The remaining species of *Adenophora* form an unresolved polytomy, although there is weak support for a group consisting of *A. himalayana* Feer (sect. *Pachydiscus* Fed.) and *A. lobophylla* D. Y. Hong (sect. *Microdiscus* Fed.).

The sister group to the *Adenophora*/*Hanabusaya* clade is only weakly supported, but it contains several well-supported smaller groups. These taxa are divergent morphologically and have a wide range of chromosome numbers. The group containing the serpentine endemic from the Balkans, *C. hawkinsiana* Hausskn. & Heldreich ($2n = 22$), and Iberian endemics *C. lusitanica* Loefl. ($2n = 18$), *C. herminii* Hoffmanns & Link. ($2n = 32$), and *C. arvatica* Lag. ($2n = 28$), is strongly supported (98%), while the clade with *C. stevenii* M. Bieb. ($2n = 32$) and *C. persicifolia* L. ($2n = 16, 18$) has a support value of 99%. The two morphologically divergent species, *C. arvatica* and *C. rotundifolia* ($2n = 34$), are sister species with 77% bootstrap support. *Campanula carpatica* Jacq. (subsect. *Rotula* Fed.) does not appear to be as close to *C. pyramidalis* L. ($2n = 34$), but it does resemble *C. herminii* from the Iberian Peninsula. *Campanula pyramidalis* is part of the "isophylloid" group of species (e.g., *C. isophylla* Moretti, *C. garganica* Tenore, *C. versicolor* Andrews [not sampled], etc.), which is centered in Italy and the western Balkan Peninsula and is somewhat intermediate between the *Phyteuma* L./*Asyneuma* alliance and those species that could be considered as typically rapunculoid (e.g., *Campanula carpatica,* etc.) (see also Damboldt, 1965a). However, many species in this group hybridize freely, and numerous hybrids involving *C. carpatica* are known in cultivation (Lewis & Lynch, 1989). Thus, the ITS data suggest that this grouping is a natural one. Broader sampling would perhaps have helped clarify the positions of the "isophylloid" and *Heterophylla* groups.

The *Phyteuma* clade includes morphologically similar species and has strong bootstrap support (91%). *Petromarula* Vent. ex Hedw. f. is sister to all the other taxa, followed by *Asyneuma japonicum* (Miq.) Briq. The clade comprising *Physoplexis* (Endl.) Schur and *Phyteuma* has a bootstrap support of 81%, but relationships within this group are unresolved. The long branches in this clade (Fig. 2) suggest these taxa are relatively divergent. The sister group of *Phyteuma* and closely related genera includes Eurasian genera such as *Legousia* Dur. and several diverse North American taxa, such as *Triodanis* Raf., *Campanula divaricata* Michx., and *Campanulastrum americanum* (L.) Small. This clade is weakly supported with a bootstrap value of less than 50%. Apart from *Triodanis,* which is sometimes considered to be congeneric with *Legousia* (McVaugh, 1945, 1948), these taxa are all rather divergent morphologically. In *Asyneuma, Phyteuma, Petromarula, Physoplexis,* the "isophylloid" species such as *Campanula pyramidalis,* and the American taxa such as *Campanulastrum* and *Triod-*

anis, the capsule opens apically or medially by a more irregular pore. Morphologically, *C. divaricata* resembles *Adenophora* somewhat, and the capsule opens basally. In other respects, such as the open stellate shape and upward orientation of the flower, the majority of the other taxa in this clade are typically rapunculoid (e.g., *C. rapunculus* L., *C. patula* L., etc.).

CONCLUSIONS

Overall, there is a remarkable congruence between the ITS tree and traditional ideas on species relationships within the Campanulaceae (Eddie, 1999). The insights of early workers such as De Candolle and Boissier have proved to be remarkably clear, and their classification systems have, on the whole, been logically consistent with our findings on phylogeny. This study also supports the serological studies of Gudkova and Borshchenko (1991) and the cpDNA phylogenies of Cosner (1993) and Cosner et al. (2004).

The ITS trees indicate that the colpate/colporate alliance (the platycodonoids) is sister to the remainder of the Campanulaceae (Eddie, 1997, 1999; Shulkina & Gaskin, 1999). This is in agreement with phylogenies of the Campanulaceae based on cpDNA structural rearrangements (Cosner et al., 2004). In comparison with the porate taxa, the colpate/colporate taxa show considerably more molecular divergence, although the wahlenbergioid taxa were under-sampled. As a group, the colpate/colporate alliance has not radiated into drier, more temperate regions and its area of greatest diversity remains the region between the eastern Himalayas and southwest China. It is hypothesized that *Ostrowskia* (not sampled) represents a minor element of this alliance, which has evolved in the dry, temperate, and highly seasonal environments of Central Asia and thus displays features that parallel certain porate taxa, particularly the mode of capsule dehiscence. *Canarina* is clearly part of this alliance and was misplaced in the classifications of De Candolle (1830) and Schönland (1889–1894), although its chromosome ($2n = 34$) is anomalous within the platycodonoid group. These results also suggest that baccate fruits evolved several times in the colpate/colporate taxa (see Hong & Pan, 1998). Within this alliance there are combinations of certain morphological features that also occur in the porate taxa, e.g., valvate apical dehiscence, a nectary protected by expanded basal filaments (nectar dome), and colored pollen, and these may afford some clues about possible links between the two major alliances of the family.

The wahlenbergioids probably branched off early in the evolution of the porate alliance and constitute the only major group in the Southern Hemisphere. They have radiated most in southern Africa, although distinctive taxa occur on islands of the Atlantic, Indian, and Pacific Oceans. Several species of *Wahlenbergia* have ovaries that are almost superior, while *Nesocodon* from Mauritius has flowers that recall some species of *Codonopsis* in the colpate/colporate alliance. In contrast, the campanuloids are dominant over much of the Northern Hemisphere. The relative isolation of monotypic or small, distinctive genera within the two main campanuloid clades (e.g., the *Rapunculus* and *Campanula* s. str. clades) suggests that the group as a whole evolved in the Mediterranean Basin and spread rapidly over the Northern Hemisphere. The *Rapunculus* clade is considerably heterogeneous both cytologically and morphologically, although all taxa within this clade are exappendiculate. Many of the species were included in section *Rapunculus* (Fourr.) Boiss. (Boissier, 1875). It is the most geographically widespread clade, most diverse in the Mediterranean Basin, and the only one that has spread into North America (apart from *Campanula chamissonis* in the Aleutian Islands). The numerically small but diverse campanulaceous taxa of North America probably contain many relicts from pre-glacial times and represent several relatively independent groups derived from the main rapunculoid radiation in Eurasia (Shetler, 1979). An early radiation of the *Rapunculus* group in the Northern Hemisphere would explain the distinctiveness of subgroups (e.g., *Phyteuma*, *Petromarula*, and related genera) that are associated with the European Alpine orogenic events and fluctuating Mediterranean sea levels during the Tertiary period (Eddie, 1984; Favarger, 1972; Greuter, 1979). It would also explain the presence of endemic genera such as *Githopsis* in California and the other rather heterogeneous taxa in North America, e.g., *Heterocodon* and diverse *Campanula* annuals in California (see Morin, 1980), China, and southern Asia (e.g., *Homocodon* D. Y. Hong and *Peracarpa* J. D. Hooker & T. Thoms.). The ancestral group(s) that eventually gave rise to *Adenophora*, *Hanabusaya*, and the harebell group (subsect. *Heterophylla*) may be related to some of the North American taxa such as *C. divaricata* and *C. robinsiae* Small (not sampled), and may also have been ancestral to the predominantly appendiculate *Campanula* s. str. group, of which the mesophytic, exappendiculate species such as *C. latifolia*, *C. trachelium*, etc. (sect. *Eucodon*), may be the least morphologically modified descendants.

Species of the *Campanula* s. str. clade are mostly appendiculate, have basal dehiscence, and are cytologically more homogeneous, particularly those species in *Campanula* and *Symphyandra*. Many of them were included in *Campanula* sect. *Medium* (DC.) Boiss. (Boissier, 1875). Much of the radiation of this group is associated with the mountain-building processes of Eurasia, from the Atlas Mountains in the west to the western Himalayas. Subcenters of high diversity for the *Campanula* s. str. clade include the Balkan Peninsula, Anatolia, and the Caucasus Mountains. *Campanula*, as it is currently constituted, is clearly polyphyletic. The more divergent taxa in this clade are found mainly in the Mediterranean basin and are placed in small or monotypic genera (e.g., *Azorina*, *Diosphaera*, *Edraianthus*, *Feeria*, and *Michauxia*). Since De Candolle's monograph of 1830, *Edraianthus* has been associated with the wahlenbergioid group, but it is clearly campanuloid, although its exact relationships within the *Campanula* s. str. clade remain unclear (see also Hilliard & Burtt, 1973).

Symphyandra A. DC. is now generally considered to be artificial (Greuter et al., 1984; Oganesian, 1995), and this analysis supports that conclusion. However, the four sections of the genus recognized by Fedorov (1957) are all quite distinct, and we suggest that the species formerly included in this genus should be re-examined and not necessarily included in *Campanula* without substantial evidence. The generic status of *Symphyandra odontosepala* (Boiss.) E. Esfandiari (not sampled) and the Iranian endemic genus *Zeugandra* P. H. Davis (not sampled) also need to be reassessed. *Symphyandra hofmanni* Pant. seems to be rather distant from the bulk of species in *Campanula*, whereas *S. pendula* (M. Bieb.) DC. and *S. armena* (Stev.) A. DC. are much closer.

Several genera may best be regarded as transitional between the wahlenbergioid group and the campanuloid group. *Musschia* is probably better placed with the campanuloids, but it is somewhat intermediate morphologically between the two major porate groups and shows some resemblance to wahlenbergioids such as *Heterochaenia* A. DC. from Réunion. It does not appear to be close to *Platycodon* or *Microcodon* A. DC. as in the arrangement of Schönland (1889–1894). On the basis of ITS sequence similarity to *Gadellia*, we suggest that the distinct morphological evolution of *Musschia* on Madeira was relatively rapid. *Jasione* also appears to be basal within the complex of Northern Hemisphere genera but its exact relationships remain unclear. On the whole it appears to have more affinities with campanuloid taxa. In the cpDNA tree of Cosner et al. (2004), *Jasione* forms an unresolved polytomy with *Symphyandra*, *Edraianthus*, *Campanula*, and *Trachelium*.

Chromosome numbers (Fig. 2) are lowest overall in the colpate/colporate alliance, although the lowest recorded diploid number is for *Jasione* ($2n = 12$). Within the *Rapunculus* clade, with the exception of the clade comprising *Adenophora* and *Hanabusaya*, the chromosome numbers are diverse and are consistently lower than numbers recorded for the *Campanula* s. str. clade, which are predominantly $2n = 34$. If we accept the premise that there has been a general increase in chromosome number during the evolution of the Campanulaceae, then the platycodonoids are ancestral to all other groups and the wahlenbergioids and rapunculoids are ancestral to the campanuloids s. str. This accords well with our knowledge of pollen morphology and evolution in the family, as well as the morphology of the capsule in the different groups. However, the diploid number $2n = 34$ occurs in several unrelated lineages (*Campanula*, *Nesocodon*, *Canarina*, and *Ostrowskia*) and probably evolved independently in each of these genera.

This analysis suggests that the ancestral home of the Campanulaceae may be in the region of eastern Asia (of current geography) (see also Hong, 1995; Cosner et al., 2004), but such an interpretation cannot be easily reconciled with the distribution of many genera within the family or with closely related families such as the Lobeliaceae, Cyphiaceae s. str., or Nemacladaceae (Eddie, 1984, 1997, 1999). Carolin (1978), citing the distribution of *Cyananthus* in India, concluded that the Campanulaceae are essentially an African family that evolved primarily in western Gondwanaland. Bremer and Gustafsson (1997), using nucleotide substitutions in *rbc*L, suggested an East Gondwanaland origin at the end of the Cretaceous for the asteraceous alliance of families, and that the group subsequently diversified and expanded to West Godwanaland before the breakup of the supercontinent. On the basis of *atp*B-*rbc*L spacer sequence data, E. B. Knox (pers. comm.) has stated, ". . . The interpretation is that *Cyphia* and the Lobeliaceae originated in southern Africa because the eight 'basal' lineages are entirely or predominantly African, and many of these are restricted to southern Africa."; ". . . The Lobeliaceae, Cyphiaceae, and Campanulaceae go back at most 40–50 MYA, and I do not think that the biogeographic patterns can be attributed to Gondwanaland." If the family had arisen in Asia one would have expected platycodonoids to be represented in Eurasia and in North America. The presence of the colporate genus *Canarina* in

Africa and Macaronesia suggests that the family may have been more widespread in Africa and around the Indian Ocean than now, but this additional hypothesis does not conflict with an Asian, African, or a Gondwanaland origin for the family. The major dichotomy in the family between the colpate/colporate and the porate taxa suggests that major tectonic processes in the early to mid Tertiary period are implicated in its evolutionary history. A fragmenting West Gondwanaland origin, with the Asian platycodonoid taxa as relictual in land masses that now form the region of the eastern Himalayas and western China, seems a more likely scenario, and this would accord well with the hypothesis (Eddie, 1997) that the more basal members of the wahlenbergioid group are essentially southern or oceanic in their distribution (e.g., *Nesocodon*, *Heterochaenia*, *Berenice* L. R. Tulasne, and the shrubby species of *Wahlenbergia* from New Zealand, St. Helena, and the Juan Fernandez Islands). The endemic genera of the Cape Region of South Africa probably represent a very early radiation of the wahlenbergioid group in the fynbos vegetation as the climate there cooled and became more arid during the mid to late Tertiary (Eddie & Cupido, 2001).

The ITS phylogeny does not necessarily reflect a species phylogeny (Doyle, 1992), but it does provide a basis for inferring possible relationships within and between taxa at several taxonomic levels and provides insights for future investigations. It also provides a phylogenetic framework that can be tested with other data sets. We must await more extensive taxon sampling and data from other genes (both nuclear and chloroplast), as well as intrageneric analyses and chloroplast genome rearrangement studies in order to refine these results. At the same time it must be emphasized that refined data sets of floral morphology and developmental studies are also desirable before a new classification of the Campanulaceae can be proposed.

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Appendix 1. Taxa sequenced for the ITS region of nr DNA, listed alphabetically by genera and species within the Campanulaceae and Lobeliaceae. Institutional abbreviations are: Royal Botanic Gardens Edinburgh (RBGE); Royal Botanic Gardens, Kew (RBGK); Missouri Botanical Garden (MO); Tblisi (TBI); National *Campanula* Collection, Cambridge (NCC); University of Texas, Austin (UT); Plant Resources Center, University of Texas, Austin (TEX); and University of Edinburgh (EGHB). Accession numbers follow the abbreviations for Botanical Gardens. Material with voucher specimens is followed by collector, collection number, and herbarium acronym. Sources of material for published sequences can be found in the cited publications.

Taxon name and authority	DNA accession number and (repository)	Voucher information, botanical garden accession number, or reference for published sequences (country of origin when available)	Genbank accession number (ITS1, ITS2)
Campanulaceae			
Adenophora divaricata Franch. & Sav.	Eddie 96086 (UT)	RBGE 19875003	AY322005, AY331418
Adenophora divaricata Franch. & Sav.		Ge et al. (1997)	AF090710, AF09071
Adenophora himalayana Feer		Ge et al. (1997)	AF090716, AF09071
Adenophora lobophylla D. Y. Hong		Ge et al. (1997)	AF090706, AF09070
Adenophora morrisonensis Hayata		Ge et al. (1997)	AF090718, AF09071
Adenophora paniculata Nannf.		Ge et al. (1997)	AF090714, AF09071
Adenophora petiolata Pax & Hoffm.		Ge et al. (1997)	AF090700, AF09070
Adenophora potaninii Korsh.		Ge et al. (1997)	AF090704, AF09070
Adenophora remotiflora (Sieb. & Zucc.) Miq.	Eddie 96087 (UT)	RBGE 19900973 (Japan)	AY322006, AY331419
Adenophora stenanthina (Ledeb.) Kitagawa		Ge et al. (1997)	AF090708, AF09070
Adenophora stricta Miq.		Ge et al. (1997)	AF090712, AF09071
Adenophora wawreana Zahlbr.		Ge et al. (1997)	AF090702, AF09070
Asyneuma japonicum (Miq.) Briq.		Kim et al. (1999)	AF183437, AF18343
Azorina vidalii (Wats.) Feer	Eddie 4548404814 (UT)	*Eddie 4548404814* (EGHB)	AY322007, AY331420
Campanula alliariifolia Willd.	Cosner *s.n.* (UT)	RBGK 16225	AY322008, AY331421
Campanula armazica Charadze	Gaskin: 463 (UT)	*T. Shulkina s.n.* (Caucasus, Georgia, MO)	AY322009, AY331422
Campanula arvatica Lag.	Eddie 94003 (UT)	NCC 94003 (EGHB)	AY322010, AY331423
Campanula barbata L.	Eddie 251.700 (UT)	*J. Archibald 251.700* (Italy, TEX)	AY322011, AY331424
Campanula bellidifolia Adams	Gaskin: 115 (UT)	*Gaskin s.n.* (Caucasus, Georgia, TBI)	AY322012, AY331425
Campanula carpatica Jacq.	Cosner *s.n.* (UT)	*Lammers 8858* (USA, Illinois, F)	AY322013, AY331426
Campanula divaricata Michx.	Haberle (UT)	*R. C. Haberle 150* (USA, Virginia, TEX)	AY322014, AY331427
Campanula edulis Forssk.	Eddie 96055 (UT)	*S. Collenette 8782* (Saudi Arabia, TEX)	AY322015, AY331428
Campanula erinus L.	Eddie 95016 (UT)	*Eddie 95.016* (Turkey, TEX)	AY322016, AY331429
Campanula glomerata L.	Eddie 98016 (UT)	*Eddie 98016* (EGHB)	AY322017, AY331430
Campanula grossheimii Kharadze	Gaskin 2084 (MO, UT)	*M. Merello 2084* (Caucasus, Georgia, MO)	AY322018, AY331431
Campanula hawkinsiana Hausskn. & Heldreich	Eddie 94002 (UT)	NCC 94002, *Eddie 94002* (EGHB)	AY322019, AY331432
Campanula herminii Hoffmans. & Link.	Neves 227 (UT)	*S. Neves 227* (Portugal, TEX)	AY322020, AY331432
Campanula hohenackeri Fisch. & C. A. Mey.	Gaskin 205 (UT)	*M. Merello 2194* (Caucasus, Georgia, MO)	AY322021, AY331434

Appendix 1. Continued.

Taxon name and authority	DNA accession number and (repository)	Voucher information, botanical garden accession number, or reference for published sequences (country of origin when available)	Genbank accession number (ITS1, ITS2)
Campanula kolenatiana C. A. Mey.	Gaskin 466 (UT)	*T. Shulkina 18* (Caucasus, TBI)	AY322022, AY331435
Campanula lanata Friv.	Eddie 96051 (UT)	NCC 96092, *Eddie 96051* (EGHB)	AY322023, AY331436
Campanula latifolia L.	Cosner *s.n.* (UT)	Lammers, no voucher	AY322024, AY331437
Campanula lusitanica Loefl.	Neves 226 (UT)	*S. Neves 226* (Portugal, TEX)	AY322025, AY331438
Campanula mirabilis Albov	Eddie 96056 (UT)	RBGE 19972042	AY322026, AY331439
Campanula mollis L.	Neves 230 (UT)	*S. Neves 230* (Spain, TEX)	AY322027, AY331440
Campanula ossetica Bieb.	Gaskin 468 (UT)	*T. Shulkina 58* (Caucasus, TBI)	AY322028, AY331441
Campanula peregrina L.	Eddie 95007 (UT)	*Eddie 95007* (Turkey, TEX)	AY322029, AY331442
Campanula persicifolia L.	Eddie 95027 (UT)	RBGE 1969372, *Eddie 95027* (EGHB)	AY322030, AY331443
Campanula petraea L.	Eddie *s.n.* (UT)	RBGE 19860223 (France)	AY322031, AY331444
Campanula primulifolia L.	Neves 229 (UT)	*S. Neves 229* (Portugal, TEX)	AY322032, AY331445
Campanula punctata Lam.	Eddie 96092 (UT)	NCC 96092, *Eddie 96092* (EGHB)	AY322033, AY331446
Campanula pyramidalis L.	Eddie 96089 (UT)	NCC, *Eddie 96089* (EGHB)	AY322034, AY331447
Campanula raddeana Trautv.	Gaskin 57 (UT)	*T. Shulkina s.n.* (Caucasus, Georgia, TBI)	AY322035, AY331448
Campanula reverchoni A. Gray	Eddie 00004 (UT)	*Eddie 00004* (USA, Texas, TEX)	AY322036, AY331449
Campanula rotundifolia L.	Cosner *s.n.* (UT)	*Lammers 8714* (USA, F)	AY322037, AY331450
Campanula samatica Ker-Gawl.	Gaskin 458 (UT)	*T. Shulkina s.n.* (Caucasus, Georgia, TBI)	AY322038, AY331451
Campanula siegizmundii Fed.	Gaskin 462 (UT)	*T. Shulkina s.n.* (Caucasus, TBI)	AY322039, AY331452
Campanula sosnowskyi Charadze	Gaskin 314 (UT)	*J. Gaskin 442* (Caucasus, Georgia, TBI)	AY322040, AY331453
Campanula steveni M. Bieb.	Gaskin 302 (UT)	*J. Gaskin 158* (Caucasus, Georgia, TBI)	AY322041, AY331454
Campanula thyrsoides L.	Eddie *s.n.* (UT)	NCC, *Eddie s.n.* (EGHB)	AY322042, AY331455
Campanula tridentata Schreb.	Gaskin 417 (MO,UT)	*J. Gaskin 417* (Caucasus, Georgia, MO)	AY322043, AY331456
Campanulastrum americanum (L.) Small	Eddie 96050 (UT)	NCC, *Eddie 96050* (TEX)	AY322044, AY331457
Campanumoea javanica Blume		Fu et al. (1999)	AF134862
Canarina canariensis (L.) Vatke	Eddie 96048 (UT)	RBGE 19770035 (Spain, Canary Islands)	AY322045, AY331458
Codonopsis dicentrifolia W. W. Sm.	Eddie 95022 (UT)	RBGE 19920352 (Nepal)	AY322046, AY331459
Codonopsis kawakamii Hayata	Cosner *s.n.* (UT)	*Lammers 8439* (Taiwan, F)	AY322047, AY331460
Codonopsis lanceolata (Sieb & Zucc.) Benth. & Hook.f.	Eddie 95023 (UT)	RBGE 19870950	AY322048, AY331461
Codonopsis modesta Nannf.		Fu et al. (1999)	AF134859
Codonopsis nervosa Nannf.		Fu et al. (1999)	AF136237
Codonopsis pilosa Chipp		Fu et al. (1999)	AH008217
Codonopsis pilosula Nannf.		Fu et al. (1999)	AF134860
Codonopsis tangshen Oliv.		Fu et al. (1999)	AF134861

Appendix 1. Continued.

Taxon name and authority	DNA accession number and (repository)	Voucher information, botanical garden accession number, or reference for published sequences (country of origin when available)	Genbank accession number (ITS1, ITS2)
Craterocapsa congesta Hilliard & B. L. Burtt	Eddie 0448 (UT)	*Hirst & Webster D. 448* (Lesotho, EGHB)	AY322049, AY331462
Cyananthus lobatus Wall. ex Benth.	Cosner *s.n.* (UT)	*Cosner 179* (OS)	AY322050, AY331463
Diosphaera rumeliana (Hampe) Bornm.	Eddie 95045 (UT)	*Eddie 95045* (EGHB)	AY322051, AY331464
Edraianthus graminifolius (L.) A. DC.	Eddie 95029 (UT)	RBGE 19860931	AY322052, AY331465
Edraianthus pumilio (Schultes) A. DC.	Eddie 940119 (UT)	RBGE 19940119	AY322053, AY331466
Feeria angustifolia (Schousb.) Buser	Eddie 98004F (UT)	*S. L. Jury et al. 17429* (Morocco, TEX)	AY322054, AY331467
Gadellia lactiflora (M. Bieb.) Schulkina	Eddie 95009 (UT)	RBGE 19693714	AY322055, AY331468
Githopsis diffusa A. Gray	Cosner *s.n.* (UT)	Morin, no voucher	AY322056, AY331469
Hanabusaya asiatica Nakai	Eddie 95018 (UT)	RBGE 19872386 (South Korea)	AY322057, AY331470
Heterocodon rariflorum Nutt.	Haberle 149 (UT)	*R. C Haberle 149* (USA, California, TEX)	AY322058, AY331471
Jasione crispa (Pourr.) Samp.	Eddie 95083 (UT)	*Eddie 95003* (EGHB, TEX)	AY322059, AY331472
Jasione laevis Lam.	Eddie 95035 (UT)	*Eddie 95035* (EGHB)	AY322060, AY331473
Jasione maritima (Duby) L. M. Dufour ex Merino	Eddie 49 (UT)	*Sales & Hedge 98.49* (Spain, RBGE)	AY322061, AY331474
Jasione montana L.	Eddie 98 (UT)	*Sales & Hedge 98.98* (Spain, RBGE)	AY322062, AY331475
Jasione sessiliflora Boiss. & Reut.	Eddie 13 (UT)	*Sales & Hedge 98.13* (Spain, RBGE)	AY322063, AY331476
Legousia falcata (Ten.) Fritsch	Eddie 97017 (UT)	*Eddie 97017* (EGHB, TEX)	AY322064, AY331477
Legousia speculum-veneris (L.) Fisch.	Eddie 95034 (UT)	*Eddie 95034* (EGHB, TEX)	AY322065, AY331478
Leptocodon gracilis Lem.	Eddie 95021 (UT)	RBGE 198921881 (Nepal)	AY322066, AY331479
Michauxia tchihatchewii Fisch. & C. A. Mey.	Eddie *s.n.* (UT)	RBGE *s.n.*	AY322068, AY331480
Musschia aurea Dumort.	Eddie 95030 (UT)	*Eddie 95030* (EGHB, TEX)	AY322067, AY331481
Petromarula pinnata (L.) A. DC.	Eddie 96066 (UT)	*Eddie 96066* (Greece, TEX)	AY322069, AY331482
Physoplexis comosa (L.) Schur	Eddie 95008 (UT)	RBGE 19771648	AY322070, AY331483
Phyteuma orbiculare L.	Cosner *s.n.* (UT)	*Lammers 9993* (F)	AY322071, AY331484
Phyteuma spicata L.	Eddie 96090 (UT)	RBGE 19782029 (Spain)	AY322072, AY331485
Platycodon grandiflorus (Jacq.) A. DC.	Eddie 96076 (UT)	*Eddie 96076* (EGHB)	AY322073, AY331486
Roella ciliata L.	Cosner *s.n.* (UT)	*T. Ayers s. n.* (BH)	AY322074, AY331487
Symphyandra armena (Stev.) A. DC.	Eddie 760258 (UT)	RBGE 19760258	AY322075, AY331488
Symphyandra hofmanni Pant.	Eddie 750893A (UT)	RBGE 19750893	AY322076, AY331489
Symphyandra pendula (Bieb.) A. DC	Gaskin 255(UT)	*T. Shulkina s.n.* (Caucasus, TBI)	AY322077, AY331490
Trachelium caeruleum L.	Eddie 98008T (UT)	*Eddie 98008T* (EGHB)	AY322078, AY331491
Triodanis leptocarpa (Nutt.) Nieuwl.	Haberle 132 (UT)	*R. C. Haberle 132* (USA, Texas, TEX)	AY322079, AY331492
Wahlenbergia hederacea L.	Eddie 98004W (UT)	*Eddie 98004W* (Scotland, TEX)	AY322080, AY331493

Appendix 1. Continued.

Taxon name and authority	DNA accession number and (repository)	Voucher information, botanical garden accession number, or reference for published sequences (country of origin when available)	Genbank accession number (ITS1, ITS2)
Lobeliaceae			
Downingia bacigalupii Weiler		Schultheis (2001)	AF176900
Lobelia aberdarica R. E. Fries & T. C. E. Fries		Schultheis (2001)	AF163435
Lobelia tupa L.		Schultheis (2001)	AF163436
Lobelia tenera Kunth		Dotti (1998)	AF054938

MORPHOLOGICAL STUDIES TOWARD AN IMPROVED CLASSIFICATION OF CAMPANULACEAE S. STR.[1]

Tatyana V. Shulkina,[2] John F. Gaskin,[2,3] and W. M. M. Eddie[4]

ABSTRACT

Growth and seedling morphology of 144 species representing 30 genera of Campanulaceae s. str. were studied. Two types of seedlings were found: Group A, with an elongated epicotyl and elongated internodes, and Group B, with a shortened (not visible) epicotyl and usually shortened internodes. These two types appear to be correlated with other vegetative characters. Thus, plants from Group A have an opposite leaf arrangement (at least early in ontogenesis), rhythmic seasonal growth with a long dormant period, and sympodial branching. Plants from Group B have a spiral leaf arrangement, continuous growth (at least in the non-flowering period), and sympodial and monopodial branching. Taxa in Group A are distributed mostly in Asia, whereas representatives in Group B occur almost worldwide. The two groups do not coincide with current taxonomic classifications but correspond remarkably well with the distribution of other characters such as pollen-grain morphology and correlate with groups based on molecular analysis; therefore, these two groups may reflect two lineages. Growth and seedling morphology are of taxonomic significance in Campanulaceae and can be used for treatments in conjunction with other characters. Taxonomic changes, which are supported by molecular data, are proposed.

Key words: Campanulaceae, growth and seedling morphology and development, taxonomy.

Campanulaceae herein are treated in a narrow circumscription (without Lobeliaceae) as a monophyletic group with a distinct geographical distribution and with well-defined morphological characters. Campanulaceae s. str., despite their size and importance in temperate floras, remain unrevised. This family, with about 50 genera and 800 species distributed worldwide, is the largest and most primitive and basal one within the order Campanulales (Lammers, 1992; Takhtajan, 1997). Although representatives of the family occur on all continents except Antarctica, the vast majority of genera and species are found in temperate regions of the Old World. Raven and Axelrod (1974) considered the family to have a Laurasian–African origin. The centers of distribution and diversity include the Mediterranean, East Asia, and South Africa (Shulkina, 1978; Kolakovsky, 1995; Hong, 1995; Eddie, 1997).

De Candolle's (1830) comprehensive monograph on the Campanulaceae provided a solid basis for all subsequent works. He divided the family into two tribes and later added a third tribe to accommodate *Merciera* (De Candolle, 1839). Schönland (1889) also divided the tribe Campanuloideae (Campanulaceae s. str. here) into three groups, based on mode of dehiscence and ovary position, but these three groups differed in composition from those of De Candolle. These two classifications became the basis for all future treatments (Table 1). Although the current systems differ greatly from the old ones in number of genera, as many taxa have been added during the last century, it is easy to understand what classification each particular author is following. Schönland's treatment has been used often and remains a currently useful reference.

Fedorov (1957), on the contrary, followed in general De Candolle's position and published a detailed classification for Campanulaceae growing in the former Soviet Union (FSU). Fedorov proposed 8 tribes (6 new) based on capsule dehiscence, corolla shape, and presence and shape of appendages between the calyx lobes. Kolakovsky (1995) proposed a new system with 4 subfamilies and 22 tribes based on internal fruit structure. He

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Table 1. Treatment of genera in Campanulaceae.

De Candolle (1830, 1839)	Schönland (1897)
Fam. Campanulaceae	Subfam. Campanuloideae
Tribe Campanuleae	Subtribe Campanulinae
Adenophora	*Adenophora*
Campanula	*Campanula*
Musschia	*Heterocodon*
Michauxia	*Michauxia*
Petromarula	*Ostrowskia*
Phyteuma	*Peracarpa*
Symphyandra	*Phyteuma*
Trachelium	*Legousia*
	Symphyandra
	Trachelium
Tribe Wahlenbergieae	Subtribe Wahlenberginae
Campanumoea	*Campanumoea*
Canarina	*Cephalostigma*
Cephalostigma	*Codonopsis*
Codonopsis	*Cyananthus*
Edraianthus	*Edraianthus*
Jasione	*Heterochaenia*
Lightfootia	*Jasione*
Microcodon	*Leptocodon*
Platycodon	*Merciera*
Prismatocarpus	*Prismatocarpus*
Roella	*Rhigiophyllum*
Wahlenbergia	*Roella*
	Siphocodon
	Treichelia
	Wahlenbergia
Tribe Merciereae	Subtribe Platycodinae
Merciera	*Microcodon*
	Musschia
	Platycodon

described 9 new genera within *Campanula*, which have not yet been included in the *Vascular Plants of Russia and Adjacent Countries* (Czerepanov, 1995) due to their contradictory descriptions. Takhtajan (1997) divided the family into 4 subfamilies and 16 tribes, taking into consideration not only the fruit structure but also pollen-grain structure, ovary position, as well as the presence or absence of appendages between the calyx lobes. Subfamily Cyananthoideae includes the genera *Cyananthus*, *Codonopsis*, *Campanumoea*, *Leptocodon*, and *Platycodon*; subfamilies Ostrowskioideae and Canarinoideae are monotypic. The last subfamily, Campanuloideae, consists of 12 tribes and includes all remaining genera. Genera described by Kolakovsky were not included in the system. Hong (1995) tentatively divided the genera into 6 unnamed groups based primarily on various morphological characters. Eddie (1997) divided the family into two major tribes, with the differences between them considered to not warrant subfamilial status. Eddie's Platycodoneae subdivided into the following subtribes: Ostrowskiinae, Cyananthinae, Echinocodinae, Codonopsinae, Platycodinae, Campanumoeinae, and Canarininae. His Campanuleae comprised the following: Wahlenberginae, Jasioneinae, Musschiinae, Azorininae, and Campanulinae.

There is considerable disagreement among all prior classifications of Campanulaceae. Furthermore, there is no common opinion about generic limits or higher relationships among the major subdivisions of the family. Taxonomic problems in this family can be explained by the fact that nearly all of these earlier classifications had a geographical rather than biological basis. Thus, floristic treatments differ considerably in the generic delimitation of the Campanulaceae for the former U.S.S.R. (Fedorov, 1957), Europe (Fedorov & Kovanda, 1976; Tutin, 1976), Turkey (Damboldt, 1976), and China (Hong, 1983).

Genera crossing diverse geographical regions need multidisciplinary study, including research on the development of vegetative organs, morphology and anatomy of fruits and seeds, pollen grain structure, as well as molecular and serological data. As stated by Takhtajan (1997: 6), "We cannot establish phyletic relationships and construct phyletic lineages using only floral characters. It is all the more impossible to reconstruct phyletic lineages on the basis of the characters of the vegetative organs only." The greater the number of characters from different correlation groups taken into consideration, the closer we can approximate the evolutionary phylogeny of the family.

Vegetative characters in higher plants are accorded only a limited place in classification, despite the angiosperms being first divided into two great subclasses according to the number of cotyledons as early as the 13th century by Albertus Magnus. Publications in which the importance of vegetative characters is supported are not numerous (e.g., Stebbins, 1974; Tomlinson, 1984). However, life forms and growth patterns, ultimately influencing the structure of the mature plant, are often ignored or little emphasized because of the common opinion that all these characters are adaptive. However, life forms include many distinctive vegetative characters that can be taxonomically valuable if they are stable.

The goals of this study are (1) to study vegetative organs and development of life forms in representative species across Campanulaceae; (2) to select characters that are common to species groups that may have taxonomic value; (3) to compare the groups suggested by these characters with formal classifications for congruence with other morphological and molecular data.

We examined seedling morphology, growth patterns, leaf arrangement, seasonal development and behavior, and branching patterns before and after first flowering in studied plants. Special attention was paid to genera whose placement varies in current systems: *Azorina, Campanulastrum, Canarina, Edraianthus, Musschia, Ostrowskia,* and *Platycodon.* Also included were representatives of recently segregated genera: *Annaea* (= *Campanula*), *Gadellia* (= *Campanula*), *Hemisphaera* (= *Campanula,* subsect. *Scapiflorae*), *Neocodon* (= *Campanula,* sect. *Rapunculus*), and *Theodorovia* (= *Campanula*).

MATERIAL AND METHODS

Plants of 144 species in 30 genera were examined (Table 2). The studied genera represent taxa from 2 tribes of De Candolle (1830), 3 subtribes of Schönland (1889), 8 subtribes of Fedorov (1957), 17 tribes of Kolakovsky (1995), and 14 tribes of Takhtajan (1997), and they provide a representative sample of the Campanulaceae. Almost half of the studied taxa were formed by the species of *Campanula* (65) and other genera (13) of the flora of the FSU. All new genera described by Kolakovsky were split from *Campanula* as well. As the most complete classification for this group was made by Fedorov (1957), the list of studied species was mainly arranged according to the system published in the *Flora of the U.S.S.R.* All plants were grown at the Komarov Botanical Institute (St. Petersburg, Russia) and a few (*Azorina vidalii, Campanulastrum americanum, Campanula kemulariae, C. punctata, Canarina canariensis*) also at the Missouri Botanical Garden (St. Louis, Missouri, U.S.A.). The taxonomic identity of all plants was confirmed when flowering. Vouchers are partly deposited in the general herbarium at the Komarov Botanical Institute (LE) (e.g., *Canarina canariensis,* Shulkina, 1978; with no numbers as is typical in Russian herbaria), and partly in the herbarium at the Department of Living Plants collections at the Komarov Botanical Institute.

Plants were grown outdoors or in greenhouses, depending on the plant's requirements. Seeds were collected in nature throughout the former Soviet Union and the midwestern United States by the senior author. They were also obtained from other collectors undertaking field trips on the islands of Macaronesia, or in the Middle East or South Africa, as well as from different botanical gardens. Seeds were sown in the greenhouses at the Komarov Botanical Institute in early spring (March) during 1973–1990. Observations were made every other day during germination and early stages of seedling growth and once a week for maturing plants. Sample size per collection (species investigated) was 20 to 50 plants whenever possible, but in some cases fewer seedlings were available. The period of germination and cotyledon size and shape were noted, and the first leaves were examined. Seedlings were illustrated when they had first leaves and fully developed cotyledons, approximately one, rarely two, months after first appearance. At this time seedlings were transplanted into larger pots.

Most plants were planted in summer in an experimental plot in the open air, but some (*Azorina, Canarina, Diosphaera, Musschia, Roella*) were kept in greenhouses. Some portions of outside plants were brought back into greenhouses in late autumn to study the presence and length of their dormant period. Leaf arrangement and branching patterns were examined throughout the year as were the presence of green leaves or renewal buds during the winter months. The timing and position of new growth were recorded in early spring. Plants were dug out, and the development of their underground organs was checked in the first year and while flowering. Life forms of some species (above- and underground organs) were also studied in nature by the senior author in the Caucasus, southern Siberia, Central Asia, the Russian Far East, the Carpathians, the Mediterranean, and the midwestern United States.

RESULTS AND DISCUSSION

GROSS MORPHOLOGY

The Campanulaceae include plants with varied life forms. As shown in previous studies (Shulkina, 1978) most species, including members of about 30 genera, are perennial herbs, and these are found throughout the range of the family. Annuals, mainly in the Mediterranean region and the New World, rarely in East Africa and Australia, also very rarely in East Asia, are present in 11 genera. Some African annuals are relatively long-lived plants (e.g., *Wahlenbergia undulata* lives 10–12 months), whereas the Mediterranean annuals are usually short-lived (e.g., *Brachycodonia fastigiata,* 1–2.5 months). Thirteen genera consist completely or partly of arborescent and semi-arborescent plants. These dwarf trees and shrubs occur in the Azores, Madeira, the Mascarenes, Reunion, and South Africa (e.g., *Azorina, Musschia, Heterochaenia, Berenice, Prismatocarpus*). Three genera include her-

Table 2. List and location of taxa studied, number of species used/general number of species in each genus. All vouchers are at the Komarov Botanical Institute, St. Petersburg, Russia (LE). Type species are in bold.

Adenophora 8/40, Eurasia		
A. stenanthina (Ledeb.) Kitag.	Perennial	Altay
A. kurilensis Nakai	Perennial	Korea*
A. liliifolia (L.) A. DC.	Perennial	E Europe
A. nikoensis Franch. & Sav.	Perennial	Korea*
A. pereskiifolia (Fisch. ex Roem. & Schult.) G. Don	Perennial	Siberia
A. tetraphylla (Thunb.) Fisch.	Perennial	Sakhalin
A. trachelioides Maxim.	Perennial	Far East
A. triphylla (Thunb.) A. DC.	Perennial	China*
Asyneuma 4/50, Disjunct, Europe & E Asia		
A. japonicum (Miq.) Briq.	Perennial	Far East
A. otites (Boiss.) Bornm.	Biennial	France*
A. pulchellum (Fisch. & Mey.) Bornm.	Biennial	E Caucasus
A. salignum (Waldst. & Kit. ex Besser) Fed.	Perennial	E Caucasus
Azorina 1/1, Azores		
A. vidalii (Wats.) Feer	Dwarf tree	Portugal*
Brachycodonia 1/1, Mediterranean, E Caucasus, C Asia		
B. fastigiata (Dufour ex A. DC.) Fed.	Annual	C Asia
Campanula L. 70/300, Northern Hemisphere		
section *Campanula*		
subsection *Quinqueloculares* Boiss.		
C. medium L.	Biennial	France*
C. crispa Lam.	Biennial	Caucasus
subsection *Spinulosae* (Fomin) Fed.		
C. mirabilis Albov	Perennial	W Caucasus
subsection *Triloculares* Boiss.		
C. sibirica L.	Perennial	Siberia
C. caucasica Bieb.	Perennial	E Caucasus
C. hohenackeri Fisch. & C. A. Mey.	Perennial	Caucasus
C. komarovii Maleev	Perennial	W Caucasus
C. longistyla Fomin	Perennial	W Caucasus
subsection *Phasidianthe* Fed.		
C. imeretina Rupr.	Perennial	W Caucasus
subsection *Tulipella* Fed.		
C. punctata Lam.	Perennial	Far East
subsection *Dasystigma* Fed.		
C. alpina Jacq.	Perennial	Carpathians
subsection *Annuae* (Boiss.) Fed. = *Roucella* Dumort.		
C. erinus L.	Annual	France*
C. propinqua Fisch. & C. A. Mey.	Annual	Armenia
subsection *Campanula*		
C. latifolia L.	Perennial	Caucasus
C. bononiensis L.	Perennial	N Caucasus
C. cordifolia C. Koch	Perennial	W Caucasus
C. megrelica Manden. & Kuth.	Perennial	W Caucasus
C. odontosepala Boiss.	Perennial	E Caucasus
C. rapunculoides L.	Perennial	E Europe
C. trachelium L.	Perennial	E Europe
subsection *Involucratae* (Fomin) Fed.		
C. glomerata L.	Perennial	E Europe

Table 2. Continued.

C. cephalotes Nakai	Perennial	China*
C. oblongifolia (C. Koch) Charadze	Perennial	S Caucasus
C. trautvetteri Grossh. & Fed.	Perennial	S Caucasus
subsection *Cordifolia* (Fomin) Fed.		
C. alliariifolia Willd.	Perennial	Caucasus
C. dolomitica E. Busch	Perennial	Caucasus
C. makaschvilii E. Busch	Perennial	W Caucasus
subsection *Latilimbus* Fed.		
C. collina Bieb.	Perennial	Caucasus
C. albovii Kolak.	Perennial	W Caucasus
C. irinae Kuth.	Perennial	W Caucasus
C. sarmatica Ker-Gawl.	Perennial	C Caucasus
C. sommieri Charadze	Perennial	N Caucasus
subsection *Trigonophyllon* Fed.		
C. dzychrica Kolak.	Perennial	W Caucasus
C. autraniana Albov	Perennial	W Caucasus
subsection *Symphyandriformes* (Fomin) Fed.		
C. kolenatiana C. A. Mey. ex Rupr.	Perennial	Tbilisi*
C. bayerniana Rupr.	Perennial	S Caucasus
C. choziatowskyi Fomin	Perennial	S Caucasus
C. kemulariae Fomin	Perennial	W Caucasus
C. ossetica Bieb.	Perennial	Tbilisi*
C. raddeana Trautv.	Perennial	Caucasus
subsection *Oreocodon* Fed.		
C. incanescens Boiss.	Perennial	C Asia
C. kachetica Kantsch.	Perennial	Caucasus
C. kantschavelii Zagareli	Perennial	Caucasus
subsection *Scapiflorae* (Boiss.) Fed. = *Hemisphaera* Kolak		
C. anomala Fomin	Perennial	N Caucasus
C. aucheri A. DC.	Perennial	Caucasus
C. bellidifolia Adams	Perennial	Caucasus
C. biebersteiniana Roem. & Schult.	Perennial	Caucasus
C. chamissonis Fed.	Perennial	Far East
C. ciliata Steven	Perennial	E Caucasus
C. saxifraga Bieb.	Perennial	N Caucasus
C. tridentata Schreb.	Perennial	Caucasus
subsection *Rupestris* (Boiss.) Fed.		
C. karakuschensis Grossh. = *Theodorovia* Kolak.	Perennial	S Caucasus
C. lehmanniana Bunge = *Hyssaria* Kolak.	Perennial	C Asia
subsection *Hypopolion* Fed.		
C. hypopolia Trautv.	Perennial	Caucasus
subsect. *Heterophylla* (Nym.) Fed.		
C. rotundifolia L.	Perennial	E Europe
C. polymorpha Witasek	Perennial	Carpathians
section *Rapunculus* (Fourr.) Boiss.		
subsection *Campanulastrum* Fed.		
C. rapunculus L. = *Neocodon* Kolak.	Perennial	N Caucasus
C. abietina Griseb. & Schenk = *Neocodon* Kolak.	Perennial	Carpathians
C. alberti Trautv. = *Neocodon* Kolak.	Perennial	C Asia
C. altaica Ledeb. = *Neocodon* Kolak.	Perennial	S Siberia
C. beauverdiana Fomin = *Neocodon* Kolak.	Perennial	S Caucasus
C. hemchinica C. Koch = *Neocodon* Kolak.	Perennial	W Caucasus

Table 2. Continued.

C. hieracioides Kolak. = *Annaea* Kolak.	Perennial	W Caucasus
C. lambertiana A. DC. = *Neocodon* Kolak.	Perennial	N Caucasus
C. patula L. = *Neocodon* Kolak.	Perennial	E Europe
C. persicifolia L. = *Neocodon* Kolak.	Perennial	E Europe
C. pontica Albov = *Neocodon* Kolak	Perennial	W Caucasus
C. stevenii Bieb. = *Neocodon* Kolak.	Perennial	S Caucasus
C. turzcaninovii Fed.	Perennial	S Siberia
subsection *Rotula* Fed.		
C. carpatica Jacq.	Perennial	Carpathians
subsection *Melanocalyx* Fed.		
C. uniflora L.	Perennial	N Siberia
subsection *Odontocalyx* Fed.		
C. lasiocarpa Cham.	Perennial	Far East
Campanulastrum 1/1, North America		
C. americanum (L.) Small	Biennial	MO, U.S.A.
Canarina 2/3, Canary Islands, disjunct E Africa		
C. canariensis (L.) Vatke	Perennial	Spain*
C. eminii Aschers.	Perennial	France*
Codonopsis 6/30, E and C Asia		
C. clematidea (Schenk) C. B. Clarke	Perennial	C Asia
C. ovata Benth.	Perennial	China*
C. pilosa Chipp	Perennial	England*
C. pilosula (Franch.) Nannf.	Perennial	Far East
C. ussuriensis (Rupr. & Maxim.) Hemsl.	Perennial	Far East
C. vincifolia Kom.	Perennial	Japan
Cyananthus 4/23, E Asia		
C. lobatus Wall. ex Benth.	Perennial	Great Britain*
C. inflatus Hook.f. & Thomson	Perennial	Great Britain*
C. integer Wall. ex Benth.	Perennial	Austria*
C. microphyllus Edgew.	Perennial	Great Britain*
Diosphaera 1/3, Middle East		
D. hysterantha Rech.f. & Schiman-Czeika	Perennial	Spain*
Edraianthus 4/24, E Mediterranean		
E. graminifolius (L.) A. DC.	Perennial	Italy*
E. horvatii Lakusic	Perennial	Yugoslavia*
E. pumilio (Portenschlag) A. DC.	Perennial	Yugoslavia*
E. sutjeskae Lakusic	Perennial	France*
E. tenuifolius (Waldst. & Kit.) A. DC.	Perennial	France*
Gadellia 1/1, Caucasus		
G. lactiflora (Boiss.) Schulkina	Perennial	Caucasus
Githopsis 3/4, W North America		
G. calycina Benth.	Annual	W North America
G. diffusa A. Gray	Annual	W North America
G. pulchella Vatke	Annual	W North America
G. specularioides Nutt.	Annual	W North America
Jasione 3/20, Europe, N Africa		
J. heldreichii Boiss. & Orph.	Biennial	France*
J. laevis Lam.	Ann., bien.	France*
J. montana L.	Biennial	Switzerland*
Legousia 3/20, Europe, N Africa, Americas		
L. falcata (Ten.) Fritsch	Annual	Spain*

Table 2. Continued.

L. hybrida (L.) Delarbe	Annual	Greece*
L. pentagonia (L.) Druce	Annual	France*
Leptocodon 1/2, E Asia		
L. gracilis (Hook.f.) Lem.	Perennial	Great Britain*
Michauxia 1/7, E Mediterranean		
M. laevigata Vent.	Perennial	Caucasus
Musschia 2/2, Madeira Islands		
M. aurea (L.) Dum.	Shrublet	Great Britain*
M. wollastonii Lowe	Dwarf tree	Great Britain*
Ostrowskia 1/1, C Asia, Afghanistan		
O. magnifica Regel	Perennial	Central Asia
Peracarpa 1/1, E Asia		
P. circaeoides (F. Schmidt) Feer	Perennial	Russian Far East
Physoplexis 1/1, Europe (Alps)		
P. comosa (L.) Schur	Perennial	Switzerland*
Phyteuma 7/40, Europe		
P. betonicifolium Vill.	Perennial	France*
P. globulariifolium Sternb. & Hoppe	Perennial	France*
P. orbiculare L.	Perennial	E Europe
P. spicatum L.	Perennial	E Europe*
P. vagneri A. Kern.	Perennial	E Europe*
Platycodon 1/1, E Asia		
P. grandiflorus (Jacq.) A. DC.	Perennial	Russian Far East
Popoviocodonia 1/1, Russian Far East		
P. uyemurae (Kudo) Fed.	Perennial	Russian Far East
Roella 1/25, South Africa		
R. ciliata L.	Perennial	South Africa
Sergia 1/2, C Asia		
S. sewerzowii (Regel) Fed.	Perennial	C Asia
Symphyandra 4/12, E Mediterranean		
S. armena (Steven) A. DC.	Perennial	Caucasus
S. cretica A. DC.	Perennial	Greece*
S. hofmannii Pant.	Biennial	France*
S. pendula (Bieb.) A. DC.	Perennial	Switzerland*
Trachelium 2/7, Mediterranean		
T. caeruleum L.	Shrublet	Italy*
T. rumelianum Hampe	Shrublet	Italy*
Wahlenbergia 6/150, Southern Hemisphere, Europe, SE Asia		
W. albomarginata Hook. f.	Ann., per.	Great Britain*
W. gracilis (Forst.) A. DC.	Ann., per.	Great Britain*
W. hederacea (L.) Reichenb.	Ann., per.	Great Britain*
W. procumbens A. DC.	Ann., per.	Great Britain*
W. undulata (L. f.) A. DC.	Ann., per.	South Africa
Zeugandra 1/2, Middle East (Iran)		
Z. iranica P. H. Davis	Perennial	Iran

Number of species follows Mabberley (1997), except *Cyananthus* (Shrestha, 1992) and *Edraianthus* (Lakušić, 1974). Taxonomic division within *Campanula* follows Fedorov (1957).

* Species of cultivated origin.

baceous vines (*Campanumoea, Canarina, Codonopsis*).

The different life forms in the Campanulaceae have been accommodated within several commonly used gross morphological systems (Du Rietz, 1931; Raunkiaer, 1934; Serebrjakov, 1962). Comparison between these gross morphological groups and taxonomic classifications shows no agreement. The same life form may be present in different tribes, and individual tribes may include more than one life form. A single genus can include life forms with different life spans (e.g., *Campanula* includes perennials, biennials, and annuals). Closely related species sometimes have different types of adaptation (e.g., *C. hohenackeri* has a well-developed primary root system, whereas mature plants of *C. caucasica* have rhizomes, and both species belong to the same subsection *Triloculares*). Therefore, the life form groups arranged according to existing morphological systems do not correlate with Campanulaceae taxonomic classifications, and perhaps the current taxonomic systems do not reflect natural groups within the family.

SEEDLING MORPHOLOGY

The initial and early stages of plant growth are significant to the survival of seedlings in various kinds of environments (Stebbins, 1971, 1974). Seedling morphology (along with other characters) has been useful for the delimitation of taxa above the generic level in some families such as Crassulaceae (Ohba, 1978), Gesneriaceae (Burtt, 1977), and Sapotaceae (Bokdam, 1977), at the generic level within the tribe Cynometreae of the Fabaceae (Léonard, 1957), and species level in the genus *Calophyllum* (Stevens, 1980).

All species studied in Campanulaceae have epigeal (aboveground) germination (Fig. 1), with cotyledons usually oval in shape with an apical notch. Cotyledons may be as large as 6.3 × 8.3 mm (*Canarina canariensis*) and as small as 1.5 × 1.0 mm (*Gadellia lactiflora*). The primary leaves emerge in two or three weeks, and cotyledons persist during the first two months of development. The position of the primary leaves varies, and as a result there are two different types of seedlings within the family (see Table 3).

The first seedling group, "Group A," has an elongated epicotyl (1–11 cm long) and elongated first internodes. The length of the epicotyl and internodes may vary even in one species under different conditions. Young plants of some species can produce shorter internodes when occurring in unfavorable habitats. Thus, *Ostrowskia magnifica* grown in the open air in St. Petersburg might have internodes 2–3 cm long, whereas in greenhouses and in its native habitat in Central Asia the internodes are 10 cm or more. Although the length of the epicotyl and internodes may vary, they are always present.

A second group, "Group B," has no visible epicotyl, and the first internodes are practically absent. Leaves appear immediately above cotyledons and form a rosette.

Seedling morphology in each genus is relatively uniform. It is true not only with oligotypic genera such as *Canarina, Musschia, Sergia,* and *Trachelium,* but also with rich genera such as *Campanula* and *Phyteuma*. Species of *Campanula* studied here belong mostly to the flora of the FSU and include representatives of both sections and the 24 subsections of Fedorov's (1957) classification. *Campanula* is morphologically heterogeneous, and seedlings differ markedly in size, first leaf shapes, and development patterns. However, they all form rosettes at the beginning of growth. All examined species do not have an epicotyl and the first internodes are very short. On the basis of seedlings, *Annaea, Hemisphaera, Neocodon, Theodorovia*—genera described by Kolakovsky—do not stand apart noticeably from the other *Campanula* species. The only *Campanula* that has an elongated seedling is *C. lactiflora,* which is now segregated in *Gadellia.*

Other consistent characters of vegetative and reproductive organs are common to species of each seedling group. In Group A, the plant is sympodial and its leaves are opposite (*Campanumoea, Canarina, Codonopsis, Cyananthus, Leptocodon, Ostrowskia, Platycodon*), at least in ontogenesis. In such mature plants the leaf arrangement may remain opposite or become whorled (*Canarina, Ostrowskia*) or spiral (some species of *Cyananthus*). These species are perennials; only *Legousia* and some *Cyananthus* species are annuals (Shrestha, 1992). All have sympodial growth patterns, and shoots die every year even if they do not terminate in a flower, and the next year's shoots come from axillary buds. Following the first year's growth, the plants are dormant during the unfavorable season, be it cold or dry. Thus, *Codonopsis, Leptocodon,* and *Platycodon,* which occur in eastern Asian regions without snow cover, have a deep dormant period in winter. *Canarina* (Canary Islands and East Africa) and *Ostrowskia* (Central Asia) are both geophytes growing in a climate with a long dry period (spring and summer for *Canarina* and summer for *Ostrowskia*), during which they are dormant. Even in the greenhouses with constant warmth and humidity these plants have a deep dormant period.

In seedling Group B, all plants have a rosette of

Figure 1. Seedling morphology. Examples of plants with shortened epicotyl (a to l). First row: —a. *Campanula latifolia.* —b. *Symphyandra armena.* —c. *Brachycodonia fastigiata.* —d. *Adenophora liliifolia.* —e. *Popoviocodonia uyemurae.* Second row (scale as above): —f. *Michauxia laevigata.* —g. *Phyteuma spicatum.* —h. *Asyneuma salignum.* —i. *Sergia sewerzowii.* —j. *Edraianthus graminifolius.* Third row: —k. *Campanulastrum americanum.* —l. *Peracarpa circaeoides.* Examples of plants with an elongated epicotyl (m to t). —m. *Gadellia lactiflora.* —n. *Azorina vidalii.* —o. *Musschia aurea.* Fourth row: —p. *Platycodon grandiflorus.* —q. *Codonopsis pilosula.* —r. *Cyananthus microphyllus.* —s. *Canarina canariensis.* —t. *Ostrowskia magnifica,* with cotyledons in the first year and primary stem the next year. All plants taken from collections at LE.

Table 3. Seedling grouping in Campanulaceae.

Group A (elongated epicotyl)	Group B (reduced epicotyl, rosette-formers)
Azorina	*Adenophora*
Campanumoea	*Asyneuma*
Canarina	*Brachycodonia*
Codonopsis	*Campanula*
Cyananthus	*Campanulastrum*
Gadellia	*Cryptocodon*
Legousia	*Cylindrocarpa*
Leptocodon	*Diosphaera*
Musschia	*Githopsis*
Ostrowskia	*Edraianthus*
Platycodon	*Jasione*
	Michauxia
	Peracarpa
	Physoplexis
	Popoviocodonia
	Roella
	Sergia
	Symphyandra
	Trachelium
	Zeugandra

leaves or at least the first internodes are shortened in early ontogenesis. Plants have spirally arranged leaves. The group includes annuals, biennials, perennials, and semi-arborescent forms with various types of seasonal development and branching. Annuals can have 2 to 4 leaves in a rosette, and the epicotyl axis terminates in a flower. All subsequent reproductive branches usually arise from the meristems in the upper leaf axils just beneath the terminal flower, e.g., *Campanula erinus, Githopsis calycina.*

In biennials an epicotyl axis produces a rosette of leaves during the first year (up to 100 leaves in *Campanula medium*) and elongated internodes the next year that terminate in a flower or in thyrsoid inflorescences, e.g., *Asyneuma pulchellum, Campanula barbata, C. crispa, C. medium, Michauxia laevigata.*

In many perennials, e.g., *Adenophora liliifolia, Asyneuma japonicum, Campanula latifolia, C. glomerata, C. alliariifolia,* the main stem comes into flower after the production of short nodes over 2–4 years of growth. Further stem growth occurs from axillary buds after a dormant period. In some species mature plants do not have aboveground rosettes of leaves, but two or three pairs of scale leaves, below ground, e.g., all examined species of *Adenophora.* In the Mediterranean region, some plants retain green leaves not only in a basal rosette, but also at the mid-fertile nodes, and subsequent branches derive from axillary buds. Their perennial stems are lignified, forming arborescent semi-shrubs, e.g., *Trachelium caeruleum.*

There are also many species of Group B with an indeterminate apical meristem. Many of these Campanulaceae develop a basal rosette that can overwinter under the snow. Reproductive branches are axillary, often leafless. In this case the branching pattern is clearly monopodial, e.g., *Campanula anomala, Edraianthus graminifolius.* The main rosette can persist or be replaced by axillary ones that also grow monopodially and bear second-order reproductive leafless stems. In some cases plants are monopodial but reproductive stems are leafy, e.g., species from subsection *Trigonophyllon,* such as *Campanula autraniana.* The other extreme is *Campanula karakushensis,* where the main rosette produces cataphylls only, and it is the axillary stems that are leafy and bear an inflorescence. In *Campanula polymorpha, C. rotundifolia,* and *C. uniflora* the apical meristem does not participate in formation of the plant body. The epicotyl axis produces a rosette of two or three leaves, after which the apical meristem diminishes. Axillary elongated stems are produced by basitonic (sympodial) branching terminating in inflorescences. Successive branches are produced from lower leaf axils on these second-order reproductive stems, and the branching pattern becomes basically sympodial. All examined species of each subsection of *Campanula* have a similar branching pattern, and this character is of taxonomic value within this genus.

Perennials of *Adenophora, Astrocodon, Asyneuma,* many species of *Campanula, Cryptocodon,* some *Phyteuma,* and *Popoviocodonia* enter dormancy after their initial anthesis. Also, perennial *Cylindrocarpa, Diosphaera, Edraianthus, Jasione, Physoplexis, Sergia, Symphyandra, Trachelium,* and some *Campanula* remain evergreen, but some have a short, easily interrupted dormant period. Although life form and seasonal rhythm vary widely within Group B, all plants of this group, including biennials and annuals, start as rosette plants.

An interesting correlation was found between seedling types and pollen grains. Dunbar (1973) and especially Avetisjan (1986, 1988) studied pollen within the family, the latter describing four groupings divided into nine types. These roughly sort into two assemblages corresponding to or coincident with seedling Groups A and B (see Fig. 2). The first pollen assemblage includes meridional-zonocolpate, equatorial-colporate, and colporoidate pollen grains and includes *Cyananthus, Codonopsis, Leptocodon, Ostrowskia, Platycodon,* and *Canarina.* The second pollen assemblage has porate grains and includes *Asyneuma, Azorina, Bra-*

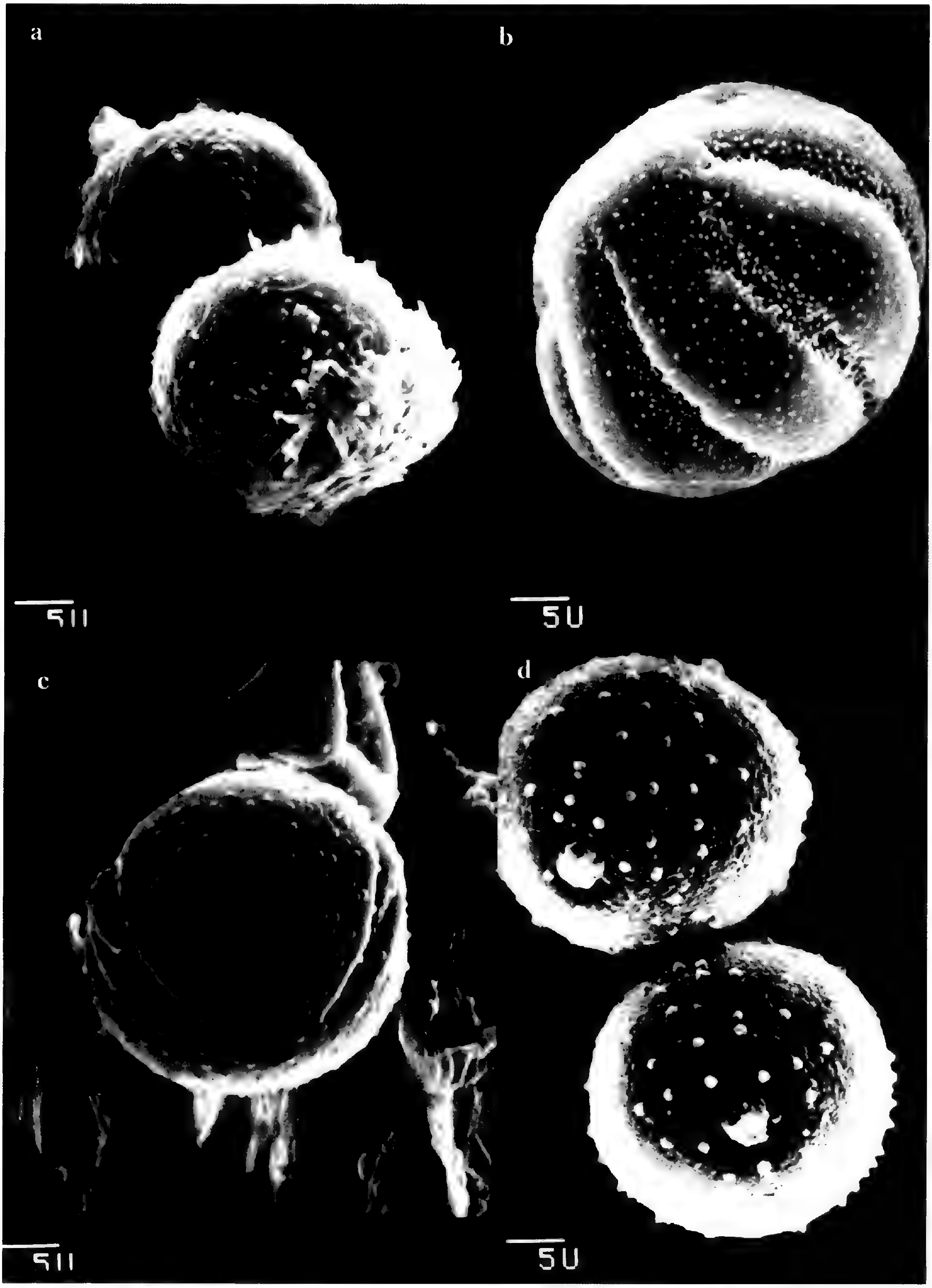

Figure 2. Pollen grains: a. *Musschia aurea*, porate, *Lowe 161283* (MO). —b. *Codonopsis clematidea*, colpate, Central Asia, Turkestan Range, *Shulkina s.n.* (LE). —c. *Canarina canariensis*, colporate, *Crosby 11425* (MO). —d. *Gadellia lactiflora*, porate, Caucasus, Teberda, *Shulkina s.n.* (LE).

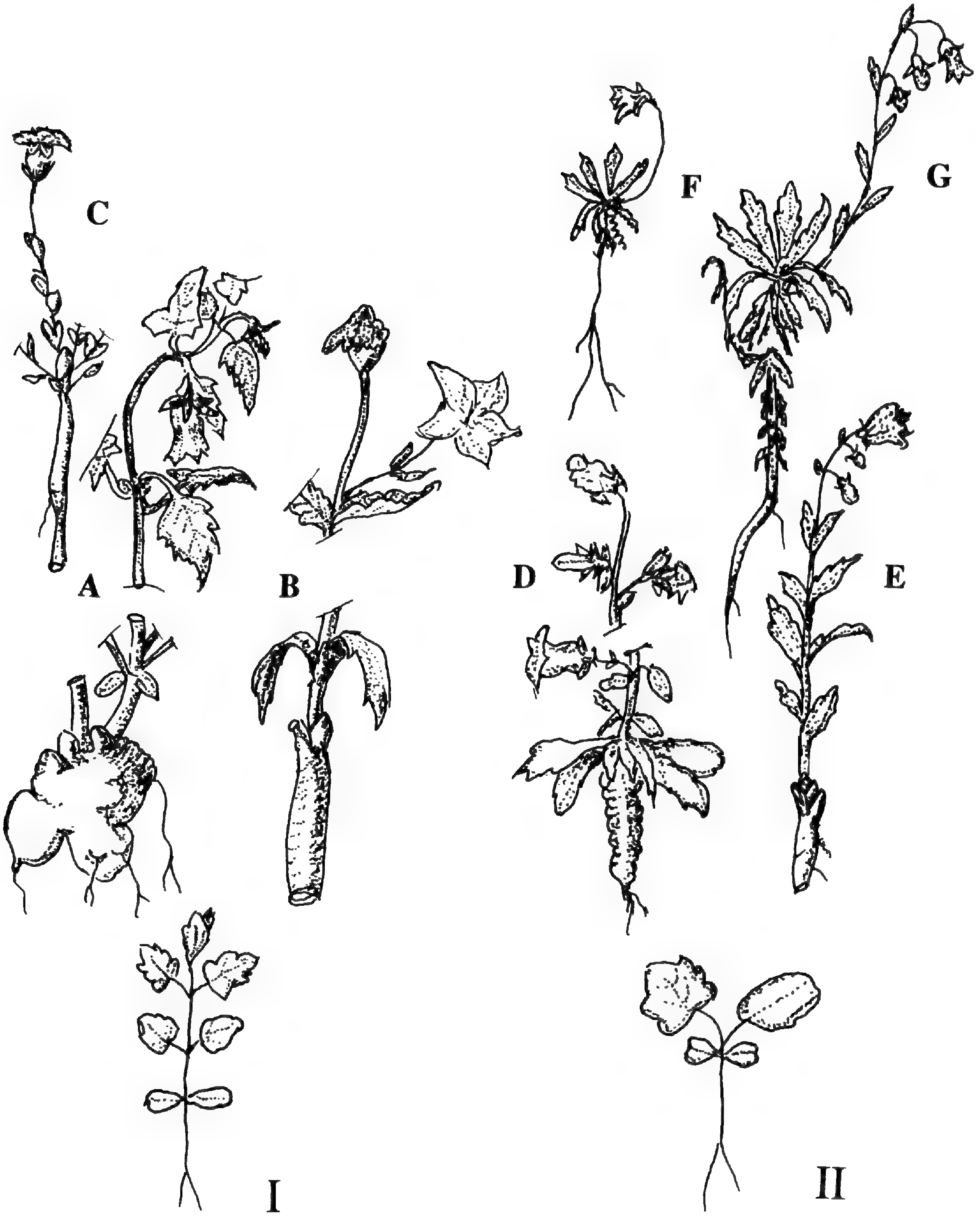

Figure 3. Two groups of plants within the Campanulaceae family. I. Plants with elongated seedlings: *Canarina canarioides* (A), *Platycodon grandiflorus* (B), *Cyananthus integer* (C). II. Plants with rosette seedlings: *Campanula mirabilis* (D), *Adenophora tetraphylla* (E), *Campanula tridentata* (F), *Azorina vidalii* (G).

chycodonia, Campanula, Campanulastrum, Edraianthus, Gadellia, Jasione, Legousia, Michauxia, Musschia, Peracarpa, Popoviocodonia, Roella, Sergia, Symphyandra, and *Trachelium,* covering those species of *Campanula* that were segregated into *Annaea, Hemisphaera, Neocodon,* and *Theodorovia.*

Almost all species of seedling Group A have colpate, colporate, and colporoidate pollen grains, whereas species of seedling Group B have only porate pollen grains (Fig. 3). There are some exceptions: species of *Azorina, Gadellia, Musschia,* and *Legousia* develop an elongated epicotyl (seedling

Group A), though their pollen grains are porate, as in seedling Group B. Three of these genera, *Azorina, Gadellia,* and *Musschia,* have spiral leaves in the earliest seedling stages. *Azorina* and *Musschia* both occur in a warm unseasonable climate and have continuing monopodial growth throughout the year, exceptional within Group A. The only character that associates *Azorina* and *Musschia* with group A is their elongated stem in the first year, which is pronounced to as long as 50–70 cm. Species of these two genera have arborescent life forms unusual within Campanulaceae. *Azorina vidalii,* which grows in the Azores Islands, is a dwarf tree or shrub to 1.5 m high (Feer, 1890; Vasilevskaya & Shulkina, 1976). During the first year it develops an elongated epicotyl and stem with elongated internodes. Subsequently, the internodes become shortened, but the main stem remains vegetative, and the axillary branches, all with elongated nodes, produce inflorescences in 2 to 3 years and die after fruiting. Two species of *Musschia* occur on the Madeira Archipelago. *Musschia wollastonii* is a monocarpic, unbranched dwarf tree to 1.5 m tall when flowering, with a rosette of large leaves (to 70 cm long) elevated above ground. The stems produce elongated internodes during the first year and shortened ones in following years. It comes to flower in 2 to 5 years and the flowering period lasts 4 to 6 months. The stems are crowned by long inflorescences (70–90 cm), and plants die after fruiting. *Musschia aurea* is a dwarf shrub 0.4–0.7 m high. The main stem has elongated internodes in the first year and rather shortened ones in the following years. All axillary branches are equivalent in length to the main one. The plant grows 2 to 5 years before flowering and inflorescences are terminal on the reproductive branches, which are monocarpic and die after fruiting. Molecular data from ITS sequences also support the position of *Azorina* (Shulkina & Gaskin, 1999) and *Musschia* (Eddie, 1984; Eddie et al., 2003 this issue) within Group B.

Endemic to the Caucasus, *Gadellia lactiflora* (seedling Group A herein) was segregated from *Campanula* (Shulkina, 1979). *Gadellia* has elongated seedlings, an unusual growth pattern with a dormant period and sympodial growth after the first year; an unusual chromosome number ($2n = 36$) and morphology (Gadella, 1964); some peculiarity in flowers such as narrow filaments; pollen grains with two pores (Shulkina, 1979); and an unusual septicidal fruit, which is dehiscent by pores and regularly cracks along the septa up to the axis column (Kolakovsky, 1986). Molecular (Eddie et al., 2003), serological (Gudkova & Borschenko, 1986), and seed morphology (Belyayev, 1984, 1985) data also support its segregation from *Campanula.* At the same time, it has many characters in common with *Campanula,* including its spiral leaf arrangement, which proves that its elongated stem is of secondary origin.

One last exception in seedling Group A is the genus *Legousia,* the taxonomic position of which has been controversial (McVaugh, 1948; Fedorov, 1957) within Campanulaceae. The prismatic capsules and almost rotate corollas distinguish it from all other related taxa, sensu Phyteumateae (Fedorov, 1957). Shetler and Morin (1986), who investigated the seed structure of the North American Campanulaceae, also concluded that the taxonomic position of *Legousia* is unclear and more study is needed. Serological studies revealed differences separating *Legousia* from other genera within Phyteumateae (Gudkova & Borshchenko, 1991), and its elongated seedling is also a character that suggests reconsideration of its taxonomic position. Molecular studies (Eddie et al., 2003) show *Legousia* is nearer to *Campanulastrum* than *Phyteuma.*

This division within Campanulaceae based on seedling type almost completely coincides with De Candolle's (1830, 1839) system. De Candolle's work included only half the genera now known, but the comparison is potentially useful. De Candolle recognized two major groups: Wahlenbergieae and Campanuleae (a third tribe, Merciereae, includes a single South African genus, *Merciera,* with 3 species, which was unfortunately unavailable for this study). The tribe Wahlenbergieae includes genera with "capsula apice dehiscens," whereas the tribe Campanuleae has plants with "capsula lateralitier dehiscens" (De Candolle, 1830). Almost all plants from his tribe Wahlenbergieae have "elongated" seedlings (Group A), whereas plants from Campanuleae have a "rosette" type of seedling (Group B).

A few exceptions need further discussion. De Candolle's division was based on external fruit structure. He placed *Edraianthus* and *Jasione* in the tribe Wahlenbergieae because both have apically dehiscent capsules. Kolakovsky (1982, 1995), who studied internal fruit structure, showed that fruits of many genera in Campanulaceae have a special organ (special tissue) that helps to open a capsule. The list of genera with an axicorn (as it was named by Kolakovsky) includes *Adenophora, Asyneuma, Campanula, Michauxia, Phyteuma, Popoviocodonia, Sergia,* and also *Edraianthus* and some other genera of Group B. This axicorn opens a pore on the lateral wall of the fruit in *Campanula* and other mentioned genera, while in *Edraianthus* it irregularly tears apart the membranous top of the capsule. Thus, capsules in *Edraianthus* and *Cam-*

panula open in different places but by the same mechanism. An explanation probably lies in a type of inflorescence of *Edraianthus*. All species of this genus have capitate inflorescences surrounded by bracts (Lakušić, 1973), and the apical opening of the fruit facilitates seed dispersal more readily than a basal or lateral opening. Therefore, the capsule of *Edraianthus* differs in its dehiscence mechanism from those of other genera with apical valves. Indeed, *Edraianthus* is related to our seedling group with basal rosettes, and this relationship is supported by molecular data (Eddie et al., 2003).

On the other hand, the groups in Shönland's system are very heterogeneous in growth and seedling characters. Thus, according to morphological division *Canarina* should be excluded from the *Campanula* alliance. *Edraianthus* is closely related to *Campanula* and not to genera with apical capsule dehiscence and should be excluded from the subtribe Wahlenberginae. *Musschia* should be excluded from subtribe Platycodinae. The taxonomic position of *Legousia* should be reconsidered.

There is greater similarity between our morphological groups and Takhtajan's (1997) system. His first three subfamilies (Cyanthoideae, Ostrowskioideae, Canarinoideae) include genera with an elongated epicotyl, our Group A. All studied species within our Group B, with a shortened epicotyl, belong to his subfamily Campanuloideae. Anomalous taxa (*Azorina*, *Musschia*) in which the elongated epicotyl may be of secondary origin are also in this subfamily, but isolated in separate tribes.

Data from molecular biology, such as chloroplast DNA structural changes, can contribute to Campanulaceae classification and have already been used in phylogenetic reconstruction of the Lobeliaceae (Knox et al., 1993). Recent molecular analyses of the Campanulaceae based on *rbc*L sequences (Cosner et al., 1994) and nuclear ribosomal DNA ITS sequence data of 93 taxa (Eddie et al., 2001, 2003) support two major lineages within the family (Shulkina & Gaskin, 1999).

CONCLUSIONS

Seedling morphology appears to be a useful character for the classification of Campanulaceae, with two major groups evident. The first one, seedling Group A (*Campanumoea*, *Canarina*, *Codonopsis*, *Leptocodon*, *Ostrowskia*, *Platycodon*, and *Cyananthus*) share elongated seedlings, opposite leaves (at least in the early stage), sympodial branching, and dormancy after the first year. Flowers are mostly in cymose inflorescences (*Platycodon*, *Canarina*, *Ostrowskia*), rarely solitary in the high mountain species (*Cyananthus*). The ovary is superior, half-inferior, or inferior. The pollen grains range from 6- to 10-colpate (*Cyananthus*), colporate (*Canarina*, *Platycodon*), or colporoidate (*Campanumoea*), seen as primitive types within the Campanulaceae (Avetisjan, 1988). Capsule dehiscence is mostly apical by valves (*Codonopsis*, *Leptocodon*, *Platycodon*, *Cyananthus*), or lateral by cracks (*Ostrowskia*); there is no axicorn. Almost all taxa are diploid, with $2n = 14, 16, 18$ (Arano & Saito, 1979). Vessels with scalariform perforation plates are found in *Cyananthus*, *Platycodon*, and *Canarina* (Shulkina & Zykov, 1980). Genera of this group occur mostly in East Asia, and only *Canarina* has a disjunct distribution (Macaronesia and eastern Africa). Most genera are monotypic or oligotypic (*Canarina*, *Leptocodon*, *Ostrowskia*, *Platycodon*, *Campanumoea*), and many are considered paleorelicts with unclear relationships (Hedberg, 1961; Popov, 1963); their taxonomic positions vary in different systems.

"Group B" in Campanulaceae includes genera with rosette seedlings, spiral leaf arrangement, and different branching patterns (sympodial, monopodial). Immature plants of this group show no fixed dormancy; mature plants have various seasonal growth patterns and different life forms. The flowers are usually in cymose inflorescences modified into umbel-like, spike-like, and solitary forms. The ovary is inferior. All studied species have porate (including zonoporate and pantoporate) pollen grains. Fruit dehiscence varies, but the capsules never have apical valves; an axicorn is sometimes present. The chromosome numbers vary greatly, with numerous polyploid lines, but $x = 17$ in many (Gadella, 1964). The representatives of this group are widely distributed. Taxonomically the group includes the tribes Campanuleae (6 genera) and Phyteumateae (6 genera), among them large genera such as *Campanula* (300 spp.), *Asyneuma* (50 spp.), *Adenophora* (40 spp.), and *Phyteuma* (40 spp.). The numerous smaller genera with restricted ranges are *Githopsis* (western North America), *Edraianthus* (Apennines and Balkan Peninsula), and *Michauxia* (Turkey, the southern Transcaucasus, Iran). There are also monotypic and oligotypic genera: *Azorina* (Azores), *Cryptocodon* (Pamiro–Alay Mountains), *Cylindrocarpa* (Karatau, Tien Shan), *Musschia* (Madeira Islands), *Physoplexis* (southern Alps), *Popoviocodonia* (Russian Far East), *Sergia* (Tien Shan), and *Zeugandra* (northern Iran), etc. These habitats and environmental conditions obviously vary greatly, and the plants of the group have numerous life forms. All data lead us to conclude that the basal rosette and a shortened type of seedling represent morphological apomorphies. There is strong evidence that the "elongated" type of seedling is plesiomorphic and characterizes more primitive Campanulaceae forms.

Therefore, two evolutionary directions, two lineages, can be traced within the family which correspond to the above two groups and probably reflect differences in the environments occupied by ancestral types. The recently recognized genus *Gadellia* (Shulkina, 1979) and the critical *Campanulastrum* (Small, 1903) are supported by morphological and molecular data, and both fall outside of *Campanula* s. str. The sister taxa to *Gadellia* in the ITS study (Eddie et al., 2003) is *Musschia aurea*, and this supports *Gadellia* as a genus distinct from *Campanula*. *Campanulastrum americanum* (*Campanula americana*) of the "rosette Group B" is not close to the *Campanula* alliance. Studies of pollen grain (Avetisjan, 1988), chromosome number and morphology (Gadella, 1964), seed-coat morphology (Shetler & Morin, 1986), and molecular data (Eddie et al., 2003) support segregation of *Campanulastrum*. The genus *Campanula* is highly heterogeneous and should be studied carefully. Further morphological and molecular investigations are needed to increase our understanding of monophyletic groups within this family. In Campanulaceae similarities due to convergent and parallel evolution occur both in reproductive and vegetative structures. All characters should be used in conjunction with others.

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PHYLOGENY OF SAURURACEAE BASED ON MORPHOLOGY AND FIVE REGIONS FROM THREE PLANT GENOMES[1]

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ABSTRACT

Phylogenetic relationships of the six extant species of four genera of the Saururaceae are resolved based on sequence data: 18S and ITS from the nuclear genome; *rbc*L and *trn*L-F from the chloroplast genome; and *mat*R from the mitochondrial genome. *Zippelia begoniaefolia,* from a genus of Piperaceae, is used as an outgroup. Results are presented in separate and combined analyses of sequence data. Forty-nine morphological characters reconstruct the phylogeny in this family, again using *Zippelia* as outgroup. Whether the topologies of Saururaceae are based on individual genomic data sets, the combined DNA sequence data sets, morphological data sets, or the combined DNA sequence and morphological data sets, all are closely congruent. In all analyses, the monophyly of *Saururus* and *Gymnotheca,* respectively, is strongly supported, and the sister relationship between *Gymnotheca* and *Saururus* is well supported. In the analysis of nuclear DNA data sets, *Anemopsis* is the sister group to all other Saururaceae, with *Houttuynia* then sister to *Saururus* and *Gymnotheca,* and with *Saururus* sister to *Gymnotheca*; however, in the analyses of the other data sets, *Anemopsis* is the sister group of *Houttuynia,* and the *Anemopsis–Houttuynia* clade lies sister to the *Saururus–Gymnotheca* clade. The result that the *Anemopsis–Houttuynia* clade comprises the sister group of *Saururus–Gymnotheca* clade is novel and differs from previous phylogenetic opinion.

Key words: *Anemopsis,* genomes, *Gymnotheca, Houttuynia,* morphology, multigene data, phylogeny, Saururaceae, *Saururus.*

Saururaceae are a core member of the paleoherbs (Tucker & Douglas, 1996) and are an ancient family with six species in the four relictual genera *Saururus, Gymnotheca, Anemopsis,* and *Houttuynia* (Liang, 1995). These are all perennial herbs with simple flowers that bear bracts without perianths. Saururaceae have an East Asian–North American disjunction, with *Anemopsis californica* Hook. & Arn. and *Saururus cernuus* L. in North America, *Houttuynia cordata* Thunb., *Gymnotheca chinensis* Decne., *Gymnotheca involucrata* Pei, and *Saururus chinensis* (Lour.) Baill. in East Asia. Due to their basal systematic position and interesting geographical pattern of distribution, Saururaceae have been of much phylogenetic interest, although they are a small family including six species. Current viewpoints on the phylogeny of Saururaceae diverge, based on gross morphology, cytology, and floral morphogenesis. Wu and Wang (1957) included *Saururus, Circaeocarpus, Anemopsis, Gymnotheca,* and *Houttuynia* in Saururaceae and thought that *Circaeocarpus, Anemopsis, Gymnotheca,* and *Houttuynia* derived directly from *Saururus* one after another. Later, they (Wu & Wang, 1958) realized that the recently published *Circaeocarpus* (Wu & Wang, 1957) was in fact a member of Piperaceae, and *Circaeocarpus saururoides* C. Y. Wu and *Zippelia begoniaefolia* Blume ex Schult. & L. H. Schult. were synonymous. Considering their biogeography, Wu (1984) later thought *Anemopsis* and *Houttuynia* to be products of a vicariance event, and *S. chinensis* and *S. cernuus* were products of another

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Table 1. List of species and vouchers** for Saururaceae and its outgroup (Piperaceae).

Species	Origin	Collection no.	18S	ITS
Ingroup				
Anemopsis californica Hook. & Arn.	U.S.A. Louisiana.	*Liang 97017*	AF197576*	AF21592
Gymnotheca chinensis Decne.	China. Yunnan: Xuanwei.	*Meng 99003*	AY032643	AF20362
Gymnotheca involucrata Pei	China. Sichuan: Emei.	*Liang 97015*	AY032644	AF20362
Houttuynia cordata Thunb.	China. Guizhou: Xingyi.	*Meng 99301*	AY032645	AF20362
Saururus cernuus L.	U.S.A. Louisiana.	*Liang 97016*	AY032646	AF22330
Saururus chinensis (Lour.) Baill.	China. Yunnan: Mengla.	*Meng 99525*	AY032647	AF21592
Outgroup				
Zippelia begoniifolia Blume ex Schult. & L. H. Schult.	China. Yunnan: Menglun.	*Meng 99715*	AY032648	AF20363

** All vouchers are deposited at KUN.
* Obtained from GenBank.

vicariance event. Based on basic chromosome numbers of *Saururus, Anemopsis,* and *Houttuynia,* Okada (1986) proposed that *Anemopsis* and *Houttuynia* were derived from *Saururus.* Lei et al. (1991) supported Okada's opinion and thought that *Gymnotheca* was the more derived taxon based on chromosome number. Based on a cladistic analysis of morphological and ontogenetic characters, Tucker et al. (1993) inferred that *Saururus* was the first to diverge from the ancestral Saururaceae, followed by *Gymnotheca,* with *Houttuynia* and *Anemopsis* as sister taxa. Combining data from gross morphology, anatomy, embryology, palynology, cytology, and flower development (Liang & Tucker, 1990; Liang, 1991, 1992, 1994, 1995), Liang (1995) proposed that the ancestors of Saururaceae were divided into two lineages: *Gymnotheca–Anemopsis* and *Saururus–Houttuynia.*

In spite of the fact that certain Saururaceae, such as *Saururus, Anemopsis,* and *Houttuynia,* have been represented in recent studies of higher-level phylogenetic relationships within the angiosperms (e.g., Chase et al., 1993; Soltis et al., 1997; Mathews & Donoghue, 1999; Qiu et al., 1999; Soltis et al., 2000), further investigation into the molecular systematics of Saururaceae has been needed to determine phylogenetic relationships within this family of basal angiosperms. Our phylogenetic assessment of Saururaceae is based on five genic regions from all three plant genomes: the 18S ribosomal RNA gene and ITS spacer (including 5.8S) from the nuclear genome; *rbc*L and *trn*L-F, its intron and gene spacer, from the chloroplast genome; and *mat*R from the mitochondrial genome. Forty-nine morphological characters were also selected for phylogenetic analysis (Appendix 1). These morphological characters were comprised of subsets from gross morphology, anatomy, embryology, palynology, cytology, and flower development. Generally, 18S, *rbc*L, and *mat*R genes have been used to reconstruct higher-level phylogeny, such as relationships among orders, families, or distantly related genera (e.g., Chase et al., 1993; Soltis et al., 1997; Qiu et al., 1999), while ITS and *trn*L-F have commonly been used for genera, species, and lower-level questions (Baldwin et al., 1995; Bayer & Starr, 1998). We selected these five gene regions because taxa in this family likely diverged at diverse points in time.

MATERIALS AND METHODS

PLANT MATERIALS

All six species of the ingroup, *Anemopsis californica, Gymnotheca chinensis, G. involucrata, Houttuynia cordata, Saururus cernuus, S. chinensis,* and one designated outgroup, *Zippelia begoniaefolia* of Piperaceae, were collected from natural populations. Vouchers are deposited in the herbarium of Kunming Institute of Botany (KUN), Chinese Academy of Sciences, Kunming (see Table 1). The GenBank accession numbers of all relevant sequences are included.

DNA EXTRACTION, PCR, AND SEQUENCING

Genomic DNA was extracted from silica-gel-dried or fresh leaves using a modified CTAB procedure (Doyle & Doyle, 1987). PCR amplifications were conducted at a thermocycler (Perkin-Elmer 9600). It consisted of initial denaturization at 94°C (4 min.), followed by 35 cycles of 94°C denaturization (1 min.), 55°C annealing (1 min.), and 72°C extension (90 sec.), with a final extension for 7 min. at 72°C. The 18S primers used for amplification and sequencing were 5′ CTAGAGCTAATA-

CGTGCAAC 3′ (121F) and 5′ GATAAGGTTCAGTGGACTTC 3′ (1692R). The primers of ITS, *rbc*L, *trn*L-F, and *mat*R followed White et al. (1990), Feng et al. (1998), Taberlet et al. (1991), and Meng et al. (2002), respectively. PCR products were separated with 1.5% agarose TAE gel and were purified using Wizard PCR Preps DNA Purification System. Sequencing reactions were performed using PRISM Dye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, Inc.). The products of sequencing reaction were electrophoresed on an ABI PRISM 310 Genetic Analyzer (Applied Biosystems, Inc.), which performs capillary electrophoresis and can ensure accurate base stretch above 1200 bp in one sequencing (guidebook about sequencing from Applied Biosystems, Inc.). Each studied DNA segment is sequenced twice from two ends in opposite directions.

SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSES

Contiguous DNA sequences were compiled using Seq^{Ed} (Applied Biosystems, Inc.). All sequences were aligned using Clustal X (Thompson et al., 1997) and Mega 2b3 (Sudhir et al., 2000). Maximum parsimony analyses were performed using PAUP 4.0 b10 (Swofford, 2001). We used the branch-and-bound search option with furthest addition sequence. Gaps were treated as missing data. A bootstrap analysis was performed with 1000 replicates (Felsenstein, 1985).

COMBINED DNA DATA ANALYSIS

We first analyzed individual genomic data sets after combining 18S and ITS to represent nrDNA, combining *rbc*L and *trn*L-F to represent cpDNA, and finally using *mat*R DNA to represent mitochondrial genomic data. All DNA sequence data were then combined into one matrix to analyze. These combined data sets were analyzed using the same settings as the individual genomic data sets. After the phylogenetic tree was reconstructed from the combined DNA data sets, the matrix of all DNA sequences was re-analyzed with characters reweighted according to rescaled consistency indices (RC) (Farris, 1989).

Separate matrixes of each genomic data set as well as the matrix of combined DNA data sets are available upon request from the corresponding author.

MORPHOLOGICAL DATA ANALYSIS

Forty-nine morphological characters were selected to reconstruct the phylogeny in this family (Appendix 1). These characters were derived from herbarium specimens and literature (e.g., Liang & Tucker et al., 1990, 1995; Liang, 1991, 1992, 1994, 1995; Tucker, 1975, 1980, 1981, 1982a, b, 1985; Tucker et al., 1993; Lei et al., 1991; Carlquist et al., 1995; Meng & Liang, 1997). Six characters were vegetative; 3 were from stem anatomy; 15 were from floral morphology; 10 were from floral anatomy; 5 were from pollen; 8 were from embryology; and 2 were from cytology. Within this morphological character matrix (Appendix 2), 37 characters were treated as binary and 12 as multi-state. The analysis of Saururaceae was conducted using PAUP 4.0 b10 (Swofford, 2001). All characters were first equally treated as weighted and unordered. Other settings are the same as those for the molecular data. After a morphological phylogenetic tree was reconstructed using the above setting, the morphological matrix was also analyzed with characters reweighted according to rescaled consistency indices.

ANALYSIS OF THE COMBINED DNA AND MORPHOLOGICAL DATA

After replacing A, G, C, T from DNA sequence with 0, 1, 2, 3, respectively, we combined all DNA data sets with the morphological one into a common matrix and re-analyzed. All characters were unordered and equally weighted. Other settings in PAUP 4.0 were the same as those for the combined molecular data.

RECONSTRUCTION OF CHARACTER EVOLUTION

Using the program WinClada v. 0.9.99m 7.5 beta (Nixon, 1999), we analyzed the morphological matrix again and recovered a phylogenetic tree topology similar to that from the PAUP 4.0 analysis. The distribution of each morphological character was then analyzed to investigate the evolution of each morphological character in Saururaceae. The combination of this heuristic search, 1000 replications, with one starting tree per replication, using a multiple TBR and TBR search strategy, with zero random seed, and a slow optimization, was used in the maximum parsimony analysis.

RESULTS

NUCLEAR GENOME DATA ANALYSIS

The alignment of 7 sequences resulted in a matrix of 2279 aligned positions, of which 195 were

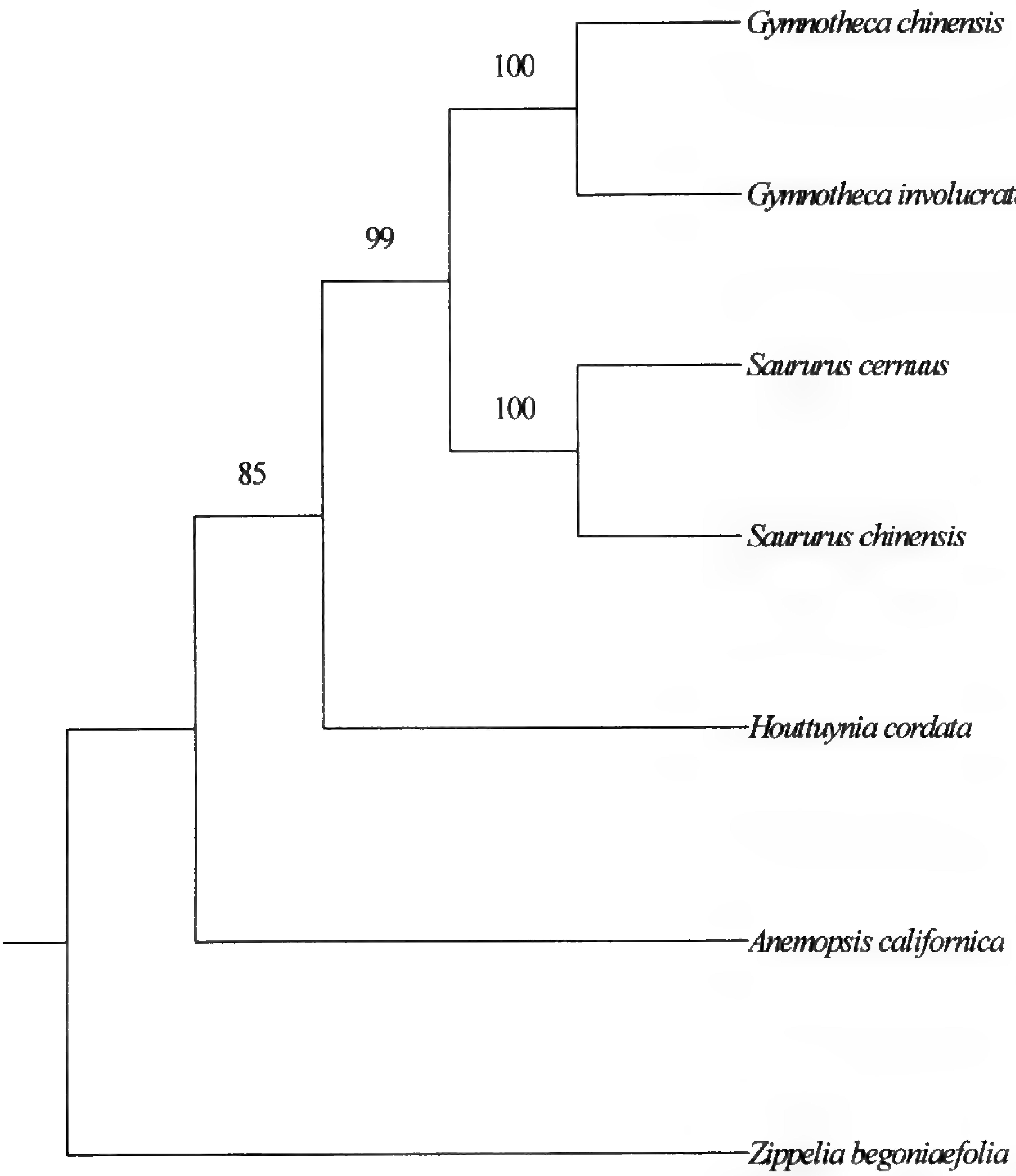

Figure 1. The single most parsimonious tree for Saururaceae based on nuclear genome data. Tree length = 434, CI = 0.8963, RI = 0.7384, and RC = 0.6618. Bootstrap values are found above branches.

variable and uninformative but 137 were parsimony-informative. Our percentage of phylogenetic-informative sites was 6%. The uncorrected sequence divergence ranged from 0.09% to 6.517% within Saururaceae and from 9.233% to 10.11% between the outgroup and the ingroups. Pairwise distance comparisons of all data sets, including the individual genomic DNA data sets, the combined DNA data sets, and the morphological data sets, are available from the corresponding author.

A single most parsimonious tree of 434 steps was obtained from nrDNA (18S and ITS), with CI = 0.8963, RI = 0.7384, and RC = 0.6618 (Fig. 1). The monophyly of *Saururus* (100% BS: bootstrap percentage) and *Gymnotheca* (100% BS) was strongly supported. *Anemopsis californica* was the sister group of other Saururaceae. *Houttuynia cordata* was sister to the *Saururus–Gymnotheca* clade (85% BS). *Saururus* was sister to *Gymnotheca* (99% BS).

CHLOROPLAST GENOME DATA ANALYSIS

Sequence alignment yielded 2400 bp, 166 of which were variably uninformative and 76 of which were parsimony-informative. The percentage of phylogenetic-informative sites was 3.167%. The uncorrected sequence divergence ranged from 0.043% to 2.543% among Saururaceae sampled and from 7.846% to 8.38% between the outgroup in Piperaceae and the ingroup taxa.

A single most parsimonious tree of 270 steps was yielded for cpDNA data sets (CI = 0.9444, RI = 0.8315, and RC = 0.7853; Fig. 2). The monophyly

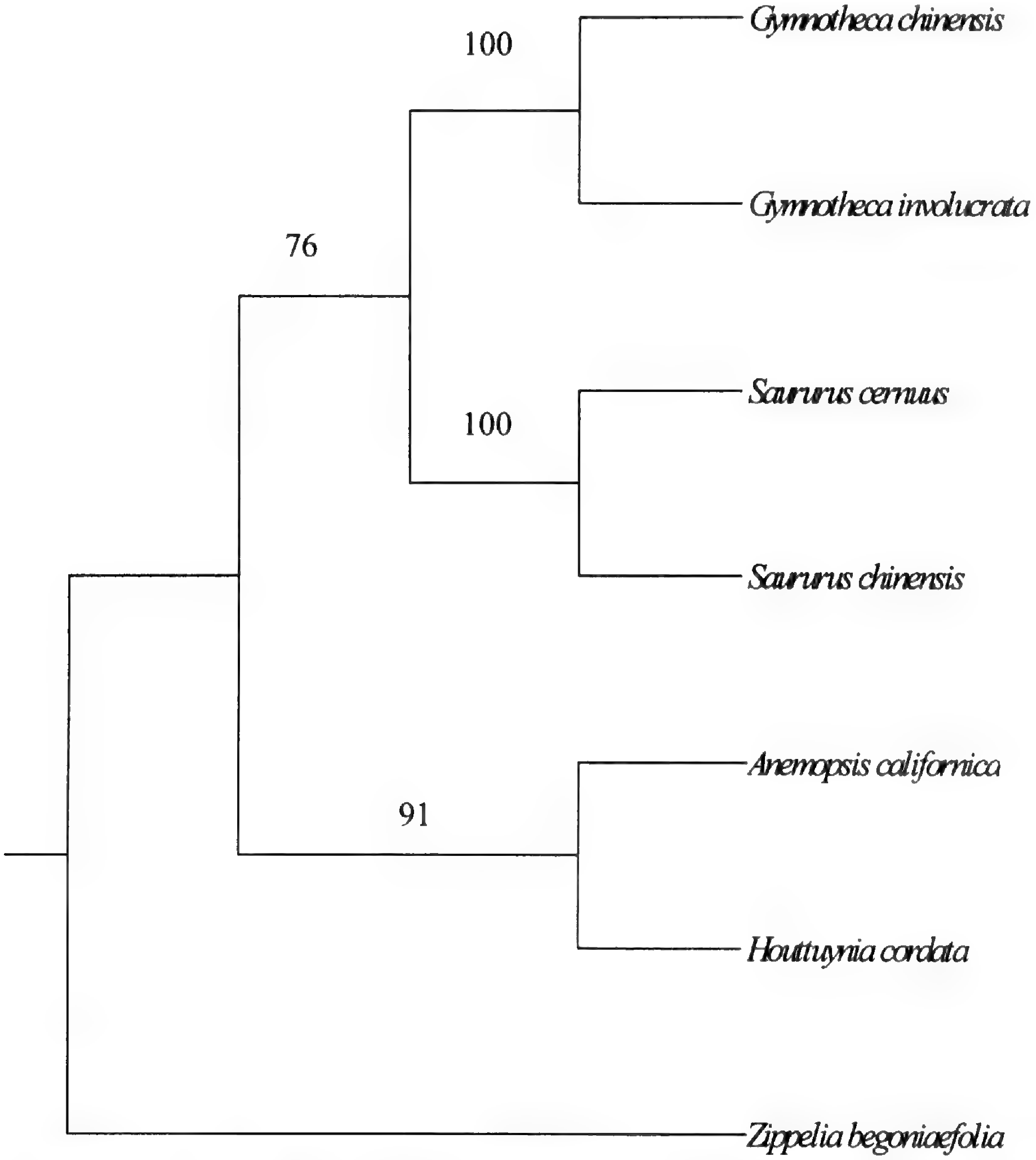

Figure 2. The single most parsimonious tree for Saururaceae based on chloroplast genomic data. Tree length = 270, CI = 0.9444, RI = 0.8315, and RC = 0.7853. Bootstrap values are found above branches.

of *Gymnotheca* (100% BS) and *Saururus* (100% BS) was strongly supported. Moreover, *A. californica* was the sister group of *H. cordata* (91% BS), and the *Anemopsis–Houttuynia* clade was sister to the *Saururus–Gymnotheca* clade. The sister relationship of *Saururus* and *Gymnotheca* was supported (76% BS).

MITOCHONDRIAL GENOME DATA ANALYSIS

Sequence alignment yielded 1777 bp, 59 of which were at variable sites and 19 at parsimony-informative sites. The percentage of phylogenetically informative sites was 1.07%. The uncorrected sequence divergence ranged from 0 to 1.753% among Saururaceae sampled and from 1.439% to 2.064% between the outgroup and the ingroup taxa.

A single most parsimonious tree of 63 steps was yielded for mitochondrial genomic data (*mat*R), and the topology of the tree matches Figure 2, with CI = 0.9524, RI = 0.8696, and RC = 0.8282. The monophyly of *Gymnotheca* (99% BS) and *Saururus* (99% BS) was resolved with strong internal support. *Anemopsis californica* was the sister group of *H. cordata* (73% BS). The *Anemopsis–Houttuynia* clade was sister to the *Saururus–Gymnotheca* clade. *Saururus* was sister to *Gymnotheca* (74% BS).

COMBINED MOLECULAR DATA ANALYSIS

After all molecular data were combined, there were 6456 bp in the matrix: 633 of them were variable, 232 were parsimony-informative. The percentage of phylogenetic-informative sites was 3.59%. The uncorrected sequence divergence ranged from 0.111% to 3.365% among included

Saururaceae and from 6.712% to 7.073% between the outgroup and the ingroups.

A single most parsimonious tree of 775 steps was obtained for the combined molecular data sets, with the topology of the tree as in Figure 2, with CI = 0.9084, RI = 0.75, and RC = 0.6813. The monophyly of *Saururus* (100% BS) and *Gymnotheca* (100% BS) was strongly supported. *Anemopsis californica* was the sister group of *H. cordata* (52% BS), and the *Anemopsis–Houttuynia* clade sister to the *Saururus–Gymnotheca* clade. *Saururus* was then sister to *Gymnotheca* (100% BS).

A stable topology was generated after the matrix of combined DNA data sets was re-analyzed once with characters reweighted according to RC (base weight = 2). The topology was still identical to the previous one (Fig. 2). However, the following parameters and bootstrap values were much higher: tree length = 1276, CI = 0.9953, RI = 0.9839, and RC = 0.9792. Again, the monophyly of *Saururus* (100% BS) and *Gymnotheca* (100% BS), and sister-group relationships between *Saururus* and *Gymnotheca* (100% BS), and between *Anemopsis* and *Houttuynia* (100% BS), were strongly supported.

MORPHOLOGICAL DATA ANALYSIS

Of the 49 characters considered, 19 were variable-uninformative and 29 were parsimony-informative. The percentage of phylogenetic-informative characters was 59.18%. The uncorrected character divergence ranged from 2.041% to 61.702% within the Saururaceae and from 53.061% to 63.83% between the outgroup and the ingroups.

A single most parsimonious tree of 71 steps was produced for the morphological matrix, and the topology of the tree was again congruent with Figure 2, with CI = 0.8451, RI = 0.7442, and RC = 0.6289. The monophyly of *Saururus* (100% BS) and *Gymnotheca* (83% BS) was strongly supported, with *A. californica* sister to *H. cordata* (72% BS), and *Anemopsis–Houttuynia* sister to *Saururus–Gymnotheca*. The sister relationship between *Saururus* and *Gymnotheca* was weakly supported (57% BS).

After the morphological matrix was re-analyzed, with characters reweighted according to RC (base weight = 2), a stable topology was obtained. This also resembled previous topologies. However, the following parameters were much higher: tree length = 101, CI = 0.9703, RI = 0.94, and RC = 0.9121. Again, the monophyly of *Saururus* (100% BS) and *Gymnotheca* (95% BS), and sister-group relationships between *Saururus* and *Gymnotheca* (93% BS), and between *Anemopsis* and *Houttuynia* (99% BS), were strongly supported.

ANALYSIS OF THE COMBINED DATA SETS OF DNA AND MORPHOLOGY

After the molecular and the morphological data were combined, there were 6505 bp in the matrix, 681 of which were variable and 261 of which were parsimony-informative. The percentage of phylogenetic-informative sites was 4.01%. The uncorrected sequence divergence ranged from 0.157% to 3.799% among Saururaceae sampled and from 7.137% to 7.479% between the outgroup and the ingroups.

A single most parsimonious tree of 846 steps was obtained for the combined molecular and morphological data sets, and the topology of the tree corresponded to Figure 2: CI = 0.9031, RI = 0.7492, and RC = 0.6766. The monophyly of *Saururus* (100% BS) and *Gymnotheca* (100% BS) was strongly supported. *Anemopsis californica* was the sister group of *H. cordata* (82% BS), with *Anemopsis* and *Houttuynia* sister to *Saururus* and *Gymnotheca*. *Saururus* was the sister group of *Gymnotheca* (100% BS).

ANALYSIS OF MORPHOLOGICAL CHARACTERS

A phylogenetic tree was obtained when we analyzed the morphological matrix using WinClada v. 0.9.99m 7.5 beta, with its topology corresponding to Figure 2. After analyzing the distribution of each character and its state on the phylogenetic tree, characters 3, 12, 14, 16, 19, 28, 30, 33, 35, 36, and 39 were realized as homoplasious, with the other characters homologous in Saururaceae (Fig. 3). A "homoplasious character" means that its diverse states are due to convergent, parallel, or reverse evolution and not due to inheritance from a common ancestor. Such a character still contributes to constructing the phylogenetic tree in a cladistic analysis (see Fig. 3), but it is prone to mislead if overweighted in building a phylogeny.

DISCUSSION

THE PHYLOGENY OF SAURURACEAE

In all analyses, the monophyly of *Saururus* and *Gymnotheca* is resolved with high bootstrap support. The combined analysis of molecular data and morphological data strongly supports the monophyly of *Saururus* and *Gymnotheca*, and the sister-group relationships between *Anemopsis* and *Houttuynia*, between *Gymnotheca* and *Saururus*, and between the *Anemopsis–Houttuynia* clade and the

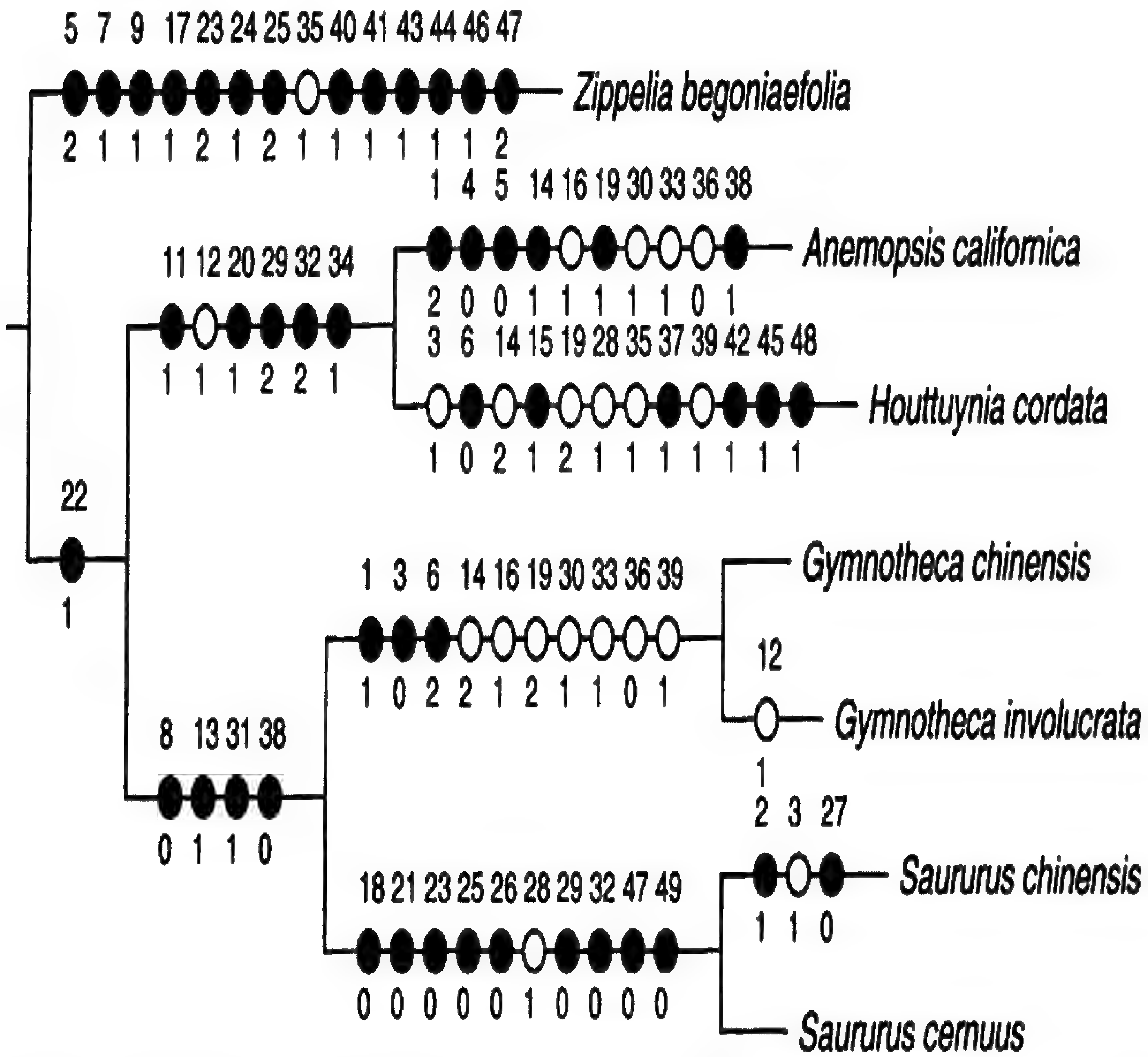

Figure 3. Distribution of morphological character states. The numbers above branches indicate characters; the numbers below branches refer to corresponding character states. Solid black circles represent homologous characters with empty circles representing homoplasious characters.

Gymnotheca–Saururus clade. Similarly, strong support is seen separately from analyses of chloroplast genomic data, mitochondrial genomic data, morphological data, and combined DNA data. Departure occurs in our analysis of the nuclear genome data sets (18S, ITS): *Anemopsis* is the sister group of all other plants of Saururaceae, with *Houttuynia* then sister to *Saururus* and *Gymnotheca*, and *Saururus* sister to *Gymnotheca* (Fig. 1). These results are surprising and differ from all the other phylogenetic opinions on Saururaceae based on morphological data (Wu & Wang, 1957, 1958; Okada, 1986; Lei et al., 1991; Tucker et al., 1993; Liang, 1995).

Our results disagree with the phylogenetic tree of Saururaceae of Wu and Wang (1957, 1958), but partly confirm their relationships as seen by Wu (1984), who proposed that *Anemopsis* and *Houttuynia* may be vicariant genera, and *S. chinensis* and *S. cernuus* may be vicariant species. Vicariant genera and species may be interpreted as "sister groups" in a phylogenetic sense because whether they are two vicariant genera or two vicariant species, they are from an immediate common ancestor. The sister-group relationships between *Anemopsis* and *Houttuynia*, and between *S. chinensis* and *S. cernuus* are well supported in our study. Our results are not congruent with Okada (1986) and Lei et al. (1991), who considered *Saururus* as the basal genus of Saururaceae, and *Anemopsis* and *Houttuynia* to be derived from an ancient *Saururus*. Lei et al. (1991) further suggested that *Gymnotheca* was most distantly derived from any ancestral *Saururus*, as was supported by Tseng (1982) in the *Flora Reipublicae Popularis Sinicae* and by Xia and Brach (1999) in the *Flora of China*. In terms of the close relationship of *Anemopsis* and *Houttuynia,* our results partly agree with Tucker et al. (1993), who generated a tree similar to our combined molecular tree (compare Fig. 2 herein and fig. 5 in Tucker et al., 1993), but with low bootstrap values; they treated *Saururus* as the first derived genus in Saururaceae and believed that *Saururus* bore many plesiomorphies. Tucker et al. (1993) used *Magnolia, Cabomba, Chloranthus, Lactoris,* and *Saruma* as outgroups of Saururaceae and Piperaceae. According to the present understanding of angiosperm phylogeny (APG, 1998), *Chloranthus, Cabomba,* and *Magnolia,* lying too distant from Saururaceae, may not be the best choices for outgroups of Saururaceae, although *Lactoris* and *Saruma* may serve as outgroups of Saururaceae (Parkinson et al., 1999; Graham & Olmstead, 2000; González & Rudall, 2001). However, Piperaceae are preferable to *Lactoris* and *Saruma* to function as the outgroup of Saururaceae (APG, 1998; Mathews & Donoghue, 1999; Qiu et al., 1999; Soltis et al., 2000). Also at issue is the interpretation of character 20 in Tucker et al. (1993: 621), whether a pair of stamens originated from separate primordia or from a common primordium. The stamens of *Houttuynia* have been confirmed to originate from separate primordia (Tucker, 1981; Liang, 1995). However, this character was variably coded in Tucker et al. (1993). When we correct for this and re-analyze, using Piperaceae as outgroup, the topology resembles Figure 2, and the bootstrap supports rise.

Liang (1995) weighted the rhizomatous character to support the monophyly of Saururaceae. She (1995: 261) treated "stoloniferous" and "separate initiation of bract-flower" as synapomorphies that supported the sister relationship of *Gymnotheca* and *Anemopsis,* and treated "common primordium initiation of bract-flower" as a synapomorphy for *Saururus* and *Houttuynia.* However, the ontogeny of the bract-flower in Saururaceae was homoplasious.

SELECTION OF THE OUTGROUP IN THE PHYLOGENETIC RECONSTRUCTION OF SAURURACEAE

Hennig (1966) pointed out that a sister group is the preferred outgroup, and one of the main tasks of phylogenetic analysis is to look for these. What then is the sister group of Saururaceae? Hutchinson (1959) and Cronquist (1981) both treated Piperaceae, Saururaceae, and Chloranthaceae in Piperales. Melchior (1964) circumscribed Saururaceae, Piperaceae, Chloranthaceae, and Lactoridaceae in Piperales. For Dahlgren (1983), Thorne (1983), and Takhtajan (1987), Piperales were restricted to Saururaceae and Piperaceae, although Takhtajan (1997) further distinguished Peperomiaceae from Piperaceae. Chase et al. (1993) supported the sister relationship between Piperaceae and Saururaceae in *rbc*L analysis, as did Hoot et al. (1999), including *atp*B, *rbc*L, and 18S. Additional support was provided by Mathews and Donoghue (1999) using duplicate phytochrome genes (PHYA and PHYC), from Qiu et al. (1999) for *rbc*L, *atp*B, 18S, *mat*R, and *atp*1, spanning three genomes, as well as Soltis et al. (2000) from *atp*B, *rbc*L, and 18S. In conclusion, the sister relationship between Piperaceae and Saururaceae has been well established (Tucker et al., 1993; Wu et al., 1998; APG, 1998; Mathews & Donoghue, 1999; Qiu et al., 1999; Soltis et al., 2000). Piperaceae are the sister group of Saururaceae, confirmed not only by morphology but also molecular systematics, and therefore the better outgroup for study.

IS *SAURURUS* THE SISTER GROUP OF THE REST OF SAURURACEAE?

Previous authors (Wu & Wang, 1957, 1958; Okada, 1986; Lei et al., 1991; Tucker et al., 1993; Liang, 1995) postulated that the ancestral Saururaceae were similar to extant *Saururus* in having free carpels, free stamens, and superior ovaries. *Saururus* was considered to have the following ancestral features: a stamen number of 6 (character 15, Appendix 1); stamens free (character 16) and hypogynous (character 14); carpels superior (character 19) and free (character 21); stamens and carpels free and not adnate (character 18); and placenta marginal (character 23). These morphological characters and others in Appendix 1 were scored following traditional opinion about morphological character evolution. Nonetheless, our analysis herein differs from previous phylogenetic trees based on morphology (Wu & Wang, 1957, 1958; Okada, 1986; Lei et al., 1991; Tucker et al., 1993; Liang, 1995), in that the *Anemopsis–Houttuynia* clade lies sister to the *Gymnotheca–Saururus* clade. We think the difference is due to the following three reasons at least. First, our morphological characters exceed others, in that 49 from diverse sources were considered. Okada (1986) and Lei et al. (1991) mainly used chromosome numbers to reconstruct the phylogeny of Saururaceae. Tucker et al. (1993) used 35 characters restricted to morphology and ontogeny. Second, the method of analysis is different. Wu and Wang (1957, 1958), Okada (1986), Lei et al. (1991), and Liang (1995) did not use cladistic analysis, whereas Tucker et al. (1993) and our study did. Third, certain morphological characters are homoplasious in Saururaceae, e.g., characters 14 (stamen position), 16 (stamen fusion), and 19 (ovary position) (Fig. 3). However, hypogynous stamens (our character 14), free stamens (our character 16), and superior ovary (our character 19) were overweighted by previous researchers (Wu & Wang, 1957, 1958; Liang, 1995). In our included analyses, *Saururus* is not the first derived genus within Saururaceae (Figs. 1, 2). Our analysis is supported by the following documents. Tutupalli and Chaubal (1975) studied the constituents of essential oils of *A. californica, H. cordata,* and *S. cernuus.* They pointed out that each species in Saururaceae had its own characteristic essential oil type, and that *Saururus* was not the least specialized genus according to its chemosystematics. After comparing wood and stem anatomy of *A. californica, H. cordata,* and *S. cernuus,* Carlquist et al. (1995) thought that *Anemopsis* possessed likely ancestral character states, such as relatively abundant secondary growth and tracheids. Buddell and Thieret (1997) put *Anemopsis* before *Saururus* when they described Saururaceae in the *Flora of North America.*

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APPENDIX 1

MORPHOLOGICAL CHARACTERS AND THEIR CHARACTER STATE CODES.

Vegetative

1. Stem: erect (0), stolon (1), short stem with one node (2).
2. Terminal leaf of stem in reproductive period: green (0), white (1).
3. Tomentum on lamina: none (0), restricted to underside (1), on both sides (2).
4. Leaf venation: pinnate (0), palmate (1).
5. Secondary venation: none (0), dichotomous (1), not dichotomous (2).
6. Areoles: incomplete (0), incomplete or imperfect (1), imperfect or perfect (2).

Stem Anatomy

7. Number of stem vascular cylinders: 1 (0), 2 (2).
8. Fiber in stem: discontinuous (0), continuous (1).
9. Perforation plate type in vessel members: scalariform (0), simple (1).

Floral Morphology

10. Floral symmetry: radial (0), dorsiventral or zygomorphic (1).
11. Abnormal regular flower: none (0), present (1).
12. Color of inflorescence involucrum: green (0), not green, showy (1).

13. Flower-bract stalk: absent (0), present (1).
14. Stamen position: hypogynous (0), perigynous (1), epigynous (2).
15. Number of stamens: 6 (0), 3 (1).
16. Stamen fusion: free (0), connate (1).
17. Anther dehiscence: stomium along entire length of anther (0), predominantly in proximal position (1), in distal position (2).
18. Adnation of stamens and carpels: free (0), partial fusion (1).
19. Ovary position: superior (0), perigynous (1), inferior (2).
20. Number of carpels: 4 (0), 3 (1), 1 (2).
21. Carpel adnation: free (0), fully adnate (1), single carpel (2).
22. Style presence: none (0), present (1).
23. Placenta: marginal (0), parietal (1), basal (2).
24. Ovules per carpel: greater than or equal to 3 (0), less than 1 (1).

Floral Anatomy

25. Number of carpel vascular bundles: 2 (0), coadnate (1), 1 (2).
26. Vascular bundle fusion of stamens and carpels: free (0), partial fusion (1).
27. Fusion of adaxial and abaxial carpel bundle: free (0), partial fusion (1).
28. Genesis of bract-flower: discrete bract and flower initiation (0), common primordial initiation (1).
29. Genesis order of carpels: middle primordium first (0), bilateral primordium first (1), simultaneous appearance or single or common primordium (2).
30. Genesis of stamens: discrete primordium (0), common primordium (1).
31. Genesis ordering of stamens: bilateral stamens first (0), middle stamens first (1).
32. Genesis pattern of median sagittal stamens: in pair (0), adaxial axis first (1), no adaxial or abaxial stamen (2).
33. Genesis pattern of bilateral stamen pair: discrete primordium (0), common primordium (1).
34. Median sagittal carpels: adaxial and abaxial carpels (0), adaxial only (1).

Pollen

35. Germinal aperture: anasulcate (0), anasulcate and anatrichotomosulcate (1), inaperturate (2).
36. Small verruculae at the edge of foveolae of pollen tectum: absent (0), present (1), narrow belt of granule on tectum (2).
37. Microspore genesis: simultaneous (0), successive (1).
38. Type of minor tetrad: bilateral symmetry, T shape and + shape (0), bilateral symmetry and + shape (1), bilateral symmetry (2).
39. Pollen abortion: absent (0), present (1).

Embryology

40. Layers of ovule integument: two (0), outer layer present but degraded (1), only inner layer present (2).
41. Micropyle: both inner and outer integuments (0), inner integument only (1).
42. Nucellus: crassinucellate (0), tenuinucellate (1).
43. Functional megaspore: from micropylar or chalazal megaspore (0), from megaspore tetrad (1).
44. Embryo sac: *Polygonum* type (0), *Drusa* or *Peperomia* type (1), *Fritillaria* type (2).
45. Apomixis: absent (0), present (1).
46. Perisperm: cellular type (0), nuclear type (1).
47. Fruit type: capsule (1), berry (2).

Cytology

48. Ploidy: diploid (0), polyploid (1).
49. Base chromosome number: 11 (0), not 11 (1).

Appendix 2. The matrix of coded morphological characters.

Taxon/Characters	1111111111222222222233333333334444444444 1234567890123456789012345678901234567890123456789
Zippelia begoniaefolia	0021211111000000110010212110100100110201101101201 1
Anemopsis californica	20200?0?0011010101111110111021021100010000000000101 1
Houttuynia cordata	0011100100110210012111101111200201111210010010111 1
Saururus chinensis	0111110001001000000000100000100100001000000000000
Saururus cernuus	0021110001001000000000100001100100001000000000000
Gymnotheca chinensis	1001120001001201012011101110111110000010000000101
Gymnotheca involucrata	1001120001011201012011101110111110000010000000101

PHYLOGENETIC POSITION AND GENERIC LIMITS OF *ARABIDOPSIS* (BRASSICACEAE) BASED ON SEQUENCES OF NUCLEAR RIBOSOMAL DNA[1]

Steve L. O'Kane, Jr.[2] *and Ihsan A. Al-Shehbaz*[3]

ABSTRACT

The primary goals of this study were to assess the generic limits and monophyly of *Arabidopsis* and to investigate its relationships to related taxa in the family Brassicaceae. Sequences of the internal transcribed spacer region (ITS-1 and ITS-2) of nuclear ribosomal DNA, including 5.8S rDNA, were used in maximum parsimony analyses to construct phylogenetic trees. An attempt was made to include all species currently or recently included in *Arabidopsis,* as well as species suggested to be close relatives. Our findings show that *Arabidopsis*, as traditionally recognized, is polyphyletic. The genus, as recircumscribed based on our results, (1) now includes species previously placed in *Cardaminopsis* and *Hylandra* as well as three species of *Arabis* and (2) excludes species now placed in *Crucihimalaya, Beringia, Olimarabidopsis, Pseudoarabidopsis,* and *Ianhedgea*.

Key words: *Arabidopsis, Arabis, Beringia,* Brassicaceae, *Crucihimalaya,* ITS phylogeny, *Olimarabidopsis, Pseudoarabidopsis.*

Arabidopsis thaliana (L.) Heynh. was first recommended as a model plant for experimental genetics over a half century ago (Laibach, 1943). In recent years, many biologists worldwide have focused their research on this plant. As indicated by Patrusky (1991), the widespread acceptance of *A. thaliana* as a model organism is attributed to the discovery that it has one of the smallest genomes of any flowering plant, a low chromosome number ($n = 5$), and that its genome contains few repetitive sequences and little intergenic spacer DNA. A surprising recent finding by Blanc et al. (2000), however, showed that although *A. thaliana* has a remarkably small genome, much of the DNA is present in more than one copy. In addition to these important attributes, *A. thaliana* has a short generation time (four to six weeks), a small size (dozens can be grown in a small pot), and can easily be grown on synthetic media (Meyerowitz, 1989; Meyerowitz & Pruitt, 1985). The species has been used extensively in developmental, evolutionary, and genetic studies and has played a major role in understanding the various biological processes in higher plants (see references in Somerville & Meyerowitz, 2002). The intraspecific phylogeny of *A. thaliana* has been examined by Vander Zwan et al. (2000). Despite the acceptance of *A. thaliana* as a model organism and the sequencing and mapping of its nuclear genome (The Arabidopsis Genome Initiative, 2000; Cooke et al., 1996), little is known about the other species of *Arabidopsis* sensu lato, and their closest relatives.

A small number of molecular phylogenetic studies have included a few members of *Arabidopsis* Heynh. sensu lato (Price et al., 1994; O'Kane et al., 1996; Galloway et al., 1998; Koch et al., 1999, 2000, 2001; Yang et al., 1999). However, none of these studies attempted to examine all of the taxa either currently or previously included in the genus, and they included only a small number of other, sometimes distantly related, genera. The last comprehensive taxonomic account (Schulz, 1924),

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which recognized 11 species, is unsatisfactory. As many as 50 species have been placed in the genus, and, although many of these are now placed in other genera (Al-Shehbaz et al., 1999), their phylogenetic relationships remain unresolved. Monophyly of the genus has not yet been critically determined, and even basic biological information, such as chromosome numbers, generation time, and breeding system of the members of the genus, is lacking.

Generic delimitation is perhaps one of the most difficult and frequently encountered problems in the systematics of the Brassicaceae (Al-Shehbaz, 1973; Rollins, 1993), and *Arabidopsis* clearly demonstrates this problem. There has been a lack of agreement among taxonomists on the number of species that belong to *Arabidopsis* and on the characters that indicate its generic boundaries (e.g., Ball, 1993; Löve, 1961; Rollins, 1993). The generic limits of *Arabidopsis* have been highly unnatural, and there were no well-defined characters separating it from several closely associated genera (but see our taxonomic revision based on the results of this current work, O'Kane & Al-Shehbaz, 1997; Al-Shehbaz & O'Kane, 2002a). Some individual *Arabidopsis* species have been transferred among several other genera. An example is *A. thaliana*, which on the basis of Schulz's (1924) synonymy was previously placed in at least nine other genera, including *Arabis* L., *Conringia* Adans., *Crucifera* E. H. L. Krause, *Erysimum* L., *Hesperis* L., *Nasturtium* R. Br., *Pilosella* Kostel., *Sisymbrium* L., and *Stenophragma* Čelak.

Arabidopsis has been closely associated with three different genera, *Cardaminopsis* (C. A. Mey.) Hayek, *Arabis* L., and *Halimolobos* Tausch. Schulz (1924, 1936) considered its nearest relative to be *Halimolobos*, and separated the latter as being coarser herbs with the styles much narrower than the fruit, as opposed to *Arabidopsis*, which were seen as slender herbs with the styles slightly narrower than the fruit. These alleged differences are not mutually exclusive, and species recognized by him in one genus can easily be accommodated in the other. Löve (1961) and Hylander (1957) indicated a relationship with *Cardaminopsis* based on natural interspecific hybridization. Hedge (1968) suggested a closer relationship between *Arabidopsis* and *Arabis* and indicated that the two differ only in the cotyledonary position. He further suggested that *Arabidopsis wallichii* (Hook. f. & Thoms.) Busch probably represents the link between the two genera. An (1987) and Jafri's (1973) transfer of several species from *Arabis* to *Arabidopsis* was probably influenced by Hedge's view.

Molecular-based results (O'Kane et al., 1996; Kamm et al., 1995; Mummenhoff & Hurka, 1994) agree with Löve's (1961) and Hylander's (1957) hypothesis in showing *A. thaliana* to be most closely related to species placed in *Cardaminopsis*. In anticipation of results published here and to make the names available for floristic works in progress, we previously published the needed nomenclatural innovations for the genus *Arabidopsis* (O'Kane & Al-Shehbaz, 1997) and have established several new genera to accommodate excluded species (Al-Shehbaz et al., 1999). In brief, *Arabidopsis* includes only *A. thaliana* and species previously included, or suggested to be, in *Cardaminopsis* (Jones & Akeroyd, 1993a, 1993b). Species now excluded from *Arabidopsis* are placed in *Thellungiella* O. E. Schulz (Al-Shehbaz & O'Kane, 1995), *Neotorularia* Hedge & J. Léonard (Al-Shehbaz & O'Kane, 1997), *Ianhedgea* Al-Shehbaz & O'Kane (Al-Shehbaz & O'Kane, 1999), *Crucihimalaya* Al-Shehbaz et al., *Olimarabidopsis* Al-Shehbaz et al., and *Pseudoarabidopsis* Al-Shehbaz et al. (Al-Shehbaz et al., 1999), and *Beringia* Price et al. (Price et al., 2001).

Our primary objectives are to determine the generic limits of a morphologically coherent, monophyletic *Arabidopsis* and to reconstruct a robust interpretation of its phylogenetic neighborhood. A well-corroborated phylogeny of the group will allow better evolutionary interpretations to be made of the massive amounts of data now accumulating for *A. thaliana*. Workers will know which species to compare to *A. thaliana* when making interpretations of evolutionary processes. Furthermore, these initial steps will provide a better understanding of morphological character evolution in the Brassicaceae, a family of great economic importance fraught with taxonomic problems related to an under-developed understanding of character evolution and generic delimitation.

MATERIALS AND METHODS

TAXON SAMPLING

We included representatives of all taxa (at least at the generic level) that are now or have been included in *Arabidopsis* (e.g., Schulz, 1924; Hedge, 1965; Jafri, 1973; Al-Shehbaz, 1988; Ball, 1993). Taxa shown to lie near *Arabidopsis* in other molecular studies have also been included (Price et al., 1994; O'Kane et al., 1996; Galloway et al., 1998), as have a sampling of taxa from elsewhere in the Brassicaceae. Phylogenetic trees were initially rooted by *Cleome lutea* Hook. of the Cleomaceae, a family basal to the Brassicaceae (Rodman et al., 1993; Judd et al., 1994; Hall et al., 2002). Included taxa, as well as voucher information and some nomenclatural comments, are given in Table 1. Where possible, plant materials were collected in the field and dried in powdered silica gel. In some cases tissue was obtained from plants grown from seeds. Where fresh or dried material was not available, we used tissue from herbarium specimens; the sequence for *Arabis scabra* All. was obtained from GenBank.

DNA EXTRACTION, PCR AMPLIFICATION, AND SEQUENCING

Total DNA was extracted from dried tissue ground in a pinch of sterile sand by a modified CTAB procedure as previously described (O'Kane et al., 1996). Amplification of the internal transcribed spacer region (including ITS-1, 5.8S, and ITS-2) was done using the conditions given in O'Kane et al. (1996) except that some ITS regions were amplified as a single unit using primer ITS1–18S (5′ CGTAACAAGGTTTCCGTAGG 3′) and ITS-4 (White et al., 1990) rather than as two overlapping pieces. PCR products were purified from 0.8% agarose gels containing 1X TAE using Wizard PCR Preps (Promega). Sequences were obtained either manually using the *fmol*™ DNA Sequencing System (Promega) or from the automated sequencer at the University of Iowa using the same primers as were used to amplify the product. GenBank accession numbers are given in Table 1. Sequences of the allotetraploid *Arabidopsis suecica* (Fries) Norrl. were obtained from cloned PCR products as previously reported (O'Kane et al., 1996).

SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSES

Sequences were aligned with the computer program MALIGN 2.7 (Wheeler & Gladstein; available at <ftp://ftp.amnh.org/pub/people/wheeler/malign/>) using the following empirically determined parameters: internal 7, extragap 5, leading 3, trailing 3, matrix 0 3 2 3 3 0 3 2 2 3 0 3 3 2 3 0, aspr, spr, quick, keepa2, keept3, and score 2. The matrix parameters weight transversions as 3, transitions as 2, intitial gaps as 7, gap extensions as 5, and initial and ending gaps as 3 (not a factor in our sequences). Most-parsimonious trees were found using PAUP* 4.0b4 (Swofford, 2000). In our analyses all characters were considered to be of equal weight and gaps were coded as missing data. Two hundred and fifty replicates of random addition using Fitch parsimony were performed using Tree Bisection Reconnection (TBR), Mulpars, multistate = polymorphism, gaps coded as missing, and Collapse branches if maximum length is zero. Bootstrap support was obtained from 500 replicates using a single round of simple taxon addition. Decay values (Bremer, 1988; Donoghue et al., 1992) were found using the AutoDecay program 4.01 of Eriksson (1998). Clade Significance (Lee, 2000) was implemented in PAUP by the AutoCladeS program (T. Eriksson; available at <http://www.bergianska.se/index_forskning_soft.html>). We found that this new measure of support indicates those clades that have the highest support based on the other two measures. The information content of the data was assessed by the g1 statistic (Hillis & Huelsenbeck, 1992) based on 100,000 random trees and by the Permutation Tail Probability (PTP) (Faith & Cranston, 1992) based on 200 heuristic searches of randomized data (PAUP* parameters as above except simple addition was used rather than random addition).

RESULTS

In nearly all samples there was no evidence of heterogeneity among individual ITS copies. Rarely, two different bases were present at a given position as indicated by two bands on an autoradiograph or as two clear peaks on a chromatogram. In these cases the base position was coded using the appropriate ambiguity code. We interpret this rare "heterozygosity" as incomplete homogenization of the ITS copies and not as evidence of hybridization; an individual sequence would show much more variation if hybridization were involved. Although initial analyses used *Cleome lutea* as the outgroup, inclusion of this taxon added to the complexity of sequence gaps and to areas with ambiguous alignments. Of the taxa included in this study, *Berteroella maximowiczii* (Palib.) O. E. Schulz was found to be strongly supported as the basal-most taxon. Further analyses, then, used *B. maximowiczii* as the outgroup. The resulting multiple alignment of the internal transcribed spacer region (ITS) was 716 base-pairs in length. Sequences are deposited in GenBank (accession numbers in Table 1), and the full alignment is available from the first author. Two regions of the alignment that were extremely sensitive to alignment parameters and could not be improved by eye (114–139 and 461–507) were not used in the phylogenetic analyses. In all, 384 bases were invariant, 79 were parsimony uninformative, and 253 were parsimony informative.

Parsimony searches yielded 24 distinct most-parsimonious trees of length 951, consistency index (CI) 0.48, consistency index excluding uninformative characters (CIU) 0.43, retention index (RI) 0.73, and rescaled consistency index (RC) of 0.35. The g1 statistic of the data was −0.5982, which

Table 1. Voucher information and GenBank accession numbers for samples included in this study. Voucher information is given as collector, collector number, and herbarium of deposit; identical superscripts indicate samples with identical rDNA sequences.

Taxon	Voucher information	Source locality	Number
Arabidopsis arenosa (L.) Lawalrée	*O'Kane & Mirek 3650* (MO)[1]	Poland	U52188
	Tzvelev et al. 79 (LE)[1]	Russia	U52187
	O'Kane & Kuciel 3664 (MO)[1]	Poland	U43233
A. cebennensis (DC.) O'Kane & Al-Shehbaz	*Coste s.n.* (1890))BUCS)	France	AF137545
A. croatica (Schott) O'Kane & Al-Shehbaz	*Kummert s.n.* (1977) (W)	Yugoslavia	AF137546
A. halleri (L.) O'Kane & Al-Shehbaz subsp. *gemmifera* (Matsum.) O'Kane & Al-Shehbaz	*O'Kane 3693* (MO)[2]	Japan	AF137544
	O'Kane & Berkutenko 3678 (MO)[2]	Russian Far East	AF137542
	O'Kane & Probatova 3683 (MO)[2]	Russian Far East	AF137543
A. halleri (L.) O'Kane & Al-Shehbaz subsp. *halleri*	*Koteja 123* (MO)	Poland	AF137541
A. halleri (L.) O'Kane & Al-Shehbaz subsp. *ovirensis* (Wulfen) O'Kane & Al-Shehbaz	*O'Kane & Dihoru 3611* (MO)	Romania	AF137540
A. lyrata (L.) O'Kane & Al-Shehbaz subsp. *kamchatica* (Fisch. ex DC.) O'Kane & Al-Shehbaz	*O'Kane & Berkutenko 3679* (MO)[3]	Russian Far East	U96266
	O'Kane 3684 (MO)[3]	Japan	U96268
	O'Kane & Berkutenko 3681 (MO)[3]	Russian Far East	U96267
A. lyrata (L.) O'Kane & Al-Shehbaz subsp. *petraea* (L.) O'Kane & Al-Shehbaz	*Kharkevich et al. 22-7-83* (VLA)[4]	Russian Far East	AF137539
	Barkalov & Bezdeleva 6-8-89 (VLA)[4]	Russian Far East	U96270
	Probatova & Seledets 7-8-80 (VLA)[4]	Russian Far East	U96269
A. neglecta (Schult.) O'Kane & Al-Shehbaz	*Horníčkova s.n.* (1977) (BRA)[1]	Slovakia	U52186
A. suecica (Fr.) Norrl.	*Lampinen 2450* (H)	Finland	U52185
A. thaliana (L.) Heynh. (sample 1)	*Podlech 17544* (MO)	Afghanistan	U43225
(sample 2)	*O'Kane & Krahulec 3638* (MO)	Czech Republic	U43224
Arabis alpina L.	*O'Kane & Dihoru 3618* (MO)	Romania	AF137559
Arabis drummondii S. Watson	*O'Kane 3676* (MO)	Montana, U.S.A.	AF137575
Arabis flagellosa Miq.	*O'Kane & Kato 3689* (MO)	Japan	AF137560
Arabis lyallii S. Watson	*O'Kane 3673* (MO)	Montana, U.S.A.	AF137561
Arabis nuttallii B. L. Rob.	*O'Kane 3672* (MO)	Montana, U.S.A.	AF137562
Arabis pendula L.	*O'Kane & Berkutenko* 3682 (MO)	Russian Far East	AF137572
Arabis scabra All.	From GenBank		X98630
Beringia bursifolia (DC.) R. A. Price, Al-Shehbaz & O'Kane subsp. *bursifolia*	*Abolin 53* (LE)	Russia	AF137557
Berteroella maximowiczii (Palib.) O. E. Schulz	*Cheo & Yen 208* (GH)	China	AF137573
Braya glabella (Richardson) S. Watson	*Neely 3174* (CS)	Colorado, U.S.A.	AF137578
Camelina microcarpa Andrz. ex DC.	*O'Kane & Dihoru 3596* (MO)	Romania	AF137574
Capsella bursa-pastoris (L.) Medik.	*Al-Shehbaz & O'Kane 9401* (MO)	Missouri, U.S.A.	AF137570
Cleome lutea Hook.	*O'Kane 3773* (ISTC)	Utah, U.S.A.	AF137588
Crucihimalaya himalaica (Edgew.) Al-Shehbaz, O'Kane & R. A. Price	*Al-Shehbaz 9354* (MO)	China	AF137553

Table 1. Continued.

Taxon	Voucher information	Source locality	Number
Crucihimalaya kneuckeri (Bornm.) Al-Shehbaz, O'Kane & R. A. Price	*Kaiser 632* (S)	Egypt (Sinai)	AF137550
Crucihimalaya lasiocarpa (Hook. f. & Thoms.) Al-Shehbaz, O'Kane & R. A. Price	*Al-Shehbaz 9333* (MO)	China	AF137556
Crucihimalaya mollissima (C. A. Mey.) Al-Shehbaz, O'Kane & R. A. Price	*Wendelbo & Ekberg 9642* (E)	Afghanistan	AF137552
Crucihimalaya ovczinnikovii (Botsch.) Al-Shehbaz, O'Kane & R. A. Price	*Kamelin s.n.* (LE)	Tajikistan	AF137551
Crucihimalaya stricta (Cambess.) Al-Shehbaz, O'Kane & R. A. Price	*Rechinger 30655* (W)	Pakistan	AF137554
Crucihimalaya wallichii (Hook. f. & Thoms.) Al-Shehbaz, O'Kane & R. A. Price	*Palmer 66* (K)	Afghanistan	AF137555
Dichasianthus subtilissimus (Popov) Ovcz. & Junussov	*Chukavinah & Kenzikaeva 5473* (LE)	Tajikistan	AF137594
Dimorphocarpa wislizenii (Engelm.) Rollins	*Porter 4467* (SJC)	New Mexico, U.S.A.	AF137593
Dithyrea californica Harv.	*Heil 6401* (SJC)	Mexico	AF137592
Drabopsis nuda (Belang. ex Boiss.) Stapf	*Rechinger 54514* (MO)	Iran	AF137577
Eutrema penlandii Rollins	*O'Kane 2157* (CS)	Colorado, U.S.A.	AF137580
Halimolobos palmeri (Hemsl.) O. E. Schulz var. *acutiloba* Rollins	*Magaña 5961* (MO)	Mexico	AF137569
Halimolobus diffusa A. Gray var. *jaegeri* (Munz) Rollins	*Morefeld et al. 4549* (MO)	Nevada, U.S.A.	AF137567
Ianhedgea minutiflora (Hook. f. & Thoms.) Al-Shehbaz & O'Kane	*Rasoul 3541* (W)	Afghanistan	AF137568
Lyrocarpa coulteri Hook. & Harv.	*Heil 6399* (SJC)	Mexico	AF137591
Neotorularia gamosepala (Hedge) Al-Shehbaz & O'Kane	*Podlech 12379* (E)	Afghanistan	AF137565
Neotorularia humilis (C. A. Mey.) Hedge & J. Léonard	*Shao-Xing s.n.* (PE)	China	AF137566
Neotorularia torulosa (Desf.) Hedge & J. Léonard	*Rechinger 40534* (W)	Iran	AF137571
Nerisyrenia linearifolia (S. Watson) Greene	*Sawyer 77* (SJC)	New Mexico, U.S.A.	AF137587
Neslia paniculata (L.) Desv. subsp. *paniculata*	*Bzowska & Rabczak 329* (MO)	Poland	AF137576
Olimarabidopsis cabulica (Hook. f. & Thoms.) Al-Shehbaz, O'Kane & R. A. Price	*Grubov et al. s.n.* (LE)	Kyrgyzstan	AF137548
Olimarabidopsis pumila (Stephan) Al-Shehbaz, O'Kane & R. A. Price	*Hedge & Wendelbo W8650* (E)	Afghanistan	AF137549
Olimarabidopsis umbrosa (Botsch. & Vved.) Al-Shehbaz, O'Kane & R. A. Price	*Rechinger 18359* (US)	Afghanistan	AF137547
Paysonia densipila (Rollins) O'Kane & Al-Shehbaz	*Rebman & Dierig 2894* (ISTC)	Tennessee, U.S.A.	AF137586
Paysonia stonensis (Rollins) O'Kane & Al-Shehbaz	*Rebman 2892* (ISTC)	Tennessee, U.S.A.	AF137585
Physaria acutifolia Rydb.	*O'Kane 3706* (ISTC)	Utah, U.S.A.	AF137582
Physaria didymocarpa (Hook.) A. Gray var. *didymocarpa*	*O'Kane 3794* (ISTC)	Montana, U.S.A.	AF137583
Physaria pruinosa (Greene) O'Kane & Al-Shehbaz	*O'Kane & Anderson 3739* (ISTC)	Colorado, U.S.A.	AF137584
Pseudoarabidopsis toxophylla (M. Bieb.) Al-Shehbaz, O'Kane & R. A. Price	*Skvortsov s.n.* (1987) (MO)	Kazakstan	AF137558
Smelowskia calycina (Stephan ex Willd.) C. A. Mey.	*O'Kane 3675* (MO)	Montana, U.S.A.	AF137581
Sphaerocardamum macropetalum (Rollins) Rollins	*Rollins & Roby 7489* (MO)	Coahuila, Mexico	AF137589
Synthlipsis greggii A. Gray	*Rollins & Tryon 5893* (MO)	Nuevo Leon, Mexico	AF137590
Thellungiella halophila (C. A. Mey.) O. E. Schulz	*Pavlov et al. 1192* (LE)	Kazakstan	AF137563
Thellungiella parvula (Schrenk) Al-Shehbaz & O'Kane	*Davis & Dodds 18677* (BM)	Turkey	AF137579
Thellungiella salsuginea (Pall.) O. E. Schulz	*Ledingham 7937* (MO)	Canada	AF137564

indicates strong phylogenetic signal in the data ($P < 0.01$). The Permutation Tail Probability (PTP) also indicated strong signal ($P = 0.005$). Figure 1 shows the strict consensus tree of the 24 most parsimonious trees.

DISCUSSION

RELATIONSHIPS AND CIRCUMSCRIPTION OF *ARABIDOPSIS*

The relationships among the species included in this study are almost entirely consistent with results previously published for smaller taxon samples in the Brassicaceae focusing on *Arabidopsis* (e.g., Price et al., 1994; Galloway et al., 1998; Koch et al., 1999, 2000, 2001; Yang et al., 1999). Like those studies, our research indicates that *Arabidopsis* as traditionally circumscribed is a highly artificial group. In fact, even the tribe Sisymbrieae, the traditional placement for *Arabidopsis* (Schulz, 1924, 1936; Al-Shehbaz, 1984, 1988), is itself artificial. The confused circumscription of *Arabidopsis*, as based on morphological grounds, was noted in previous taxonomic treatments. Hylander (1957: 602), for example, recognized that if *Cardaminopsis* and *Arabidopsis* are combined, as seemed likely, the limits of *Arabidopsis* "would thereby be considerably widened—or, perhaps more correctly, drawn in quite another way." Jones (1964) also indicated that two species of *Arabis*, *A. pedemontana* Boiss. and *A. cebennensis* DC., might best be included in *Cardaminopsis*. Thus, at least as early as 1964, taxonomic problems were anticipated in *Arabidopsis*, *Cardaminopsis*, and *Arabis*.

Results from our study are sufficient to allow a revision of the taxonomy of the genus *Arabidopsis*. A strongly supported clade (bootstrap support 97%, decay index 6, clade support 0.014; see Fig. 1) containing *A. thaliana*, the type species of the genus, defines the limits of a recircumscribed genus *Arabidopsis*. As stated above, we have anticipated the publication of these results by redefining the circumscription of *Arabidopsis* (O'Kane & Al-Shehbaz, 1997), transferring species to previously recognized genera (Al-Shehbaz & O'Kane, 1995, 1997), and lastly by erecting several new genera for species previously included in *Arabidopsis* (Al-Shehbaz et al., 1999; Al-Shehbaz & O'Kane, 1999, 2002a; Price et al., 2001). Names in bold type in Figure 1 represent new genera erected for species previously included in *Arabidopsis* by other authors, and the bold letter "A" indicates species previously included in *Arabidopsis*. In every case we have made genera monophyletic (sensu Hennig, 1966; holophyletic of Ashlock, 1971). Species previously included in *Arabidopsis* are now placed in *Beringia*, *Crucihimalaya*, *Olimarabidopsis*, *Pseudoarabidopsis*, *Ianhedgea*, *Neotorularia*, and *Thellungiella*. *Arabidopsis* sensu novo is distinguished from other genera in the Brassicaceae by having short petiolate but not auriculate or amplexicaul cauline leaves, the presence of simple trichomes, these often mixed with few-forked ones but not stellate hairs, well-defined basal rosettes at least in young plants, white to lavender (rarely almost purple) but never yellow flowers, erect to slightly ascending non-saccate or slightly saccate inner sepals, siliques at least slightly torulose, much longer than they are wide and glabrous, compressed (rarely subterete to terete), seeds uniseriate in the silique, and cotyledons accumbent or rarely incumbent (O'Kane & Al-Shehbaz, 1997). Habit ranges from annual to short- or long-lived perennials. Chromosome numbers vary from $x = n = 5$ in *A. thaliana* to $x = 8$ in the remaining species except for *A. suecica*, which is an allotetraploid ($2n = 26$) derived from *A. thaliana* ($2n = 10$) and *A. arenosa* (L.) Lawalrée ($2n = 16$) (Mummenhoff & Hurka, 1994; O'Kane et al., 1996, and references therein). Keys to the species and subspecies are given in O'Kane and Al-Shehbaz (1997). As circumscribed here, the genera *Cardaminopsis* and *Hylandra* Á. Löve are united with *Arabidopsis*. *Arabidopsis* is a monophyletic genus consisting of *A. arenosa*, *A. cebennensis* (DC.) O'Kane & Al-Shehbaz, *A. croatica* (Schott) O'Kane & Al-Shehbaz, *A. halleri* (L.) O'Kane & Al-Shehbaz, *A. lyrata* (L.) O'Kane & Al-Shehbaz, *A. neglecta* (Schultes) O'Kane & Al-Shehbaz, *A. suecica*, and *A. thaliana*. Although we have no sequences of *A. pedemontana* (Boiss.) O'Kane & Al-Shehbaz, it, too, clearly belongs in *Arabidopsis* based on its morphological relationship to *A. cebennensis*.

All other species previously included in *Arabidopsis* are more distantly related, especially those Himalayan species now included in *Crucihimalaya* and the Middle Eastern and central Asian *Olimarabidopsis*. Morphologically, *Crucihimalaya* differs from *Arabidopsis* in that it has at least some stellate trichomes, whereas *Arabidopsis* has forked trichomes. *Olimarabidopsis* differs from *Arabidopsis* in its yellow, rather than white or lavender petals, pubescent, rather than glabrous fruits, and auriculate rather than attenuate or petiolate cauline leaves. Al-Shehbaz et al. (1999) presented an analysis of all species formerly placed in *Arabidopsis*. Based on the results presented here, *Arabidopsis* is a genus of circumboreal and circum-north-temperate species. Most species, however, are confined to Europe. Workers conducting comparative research us-

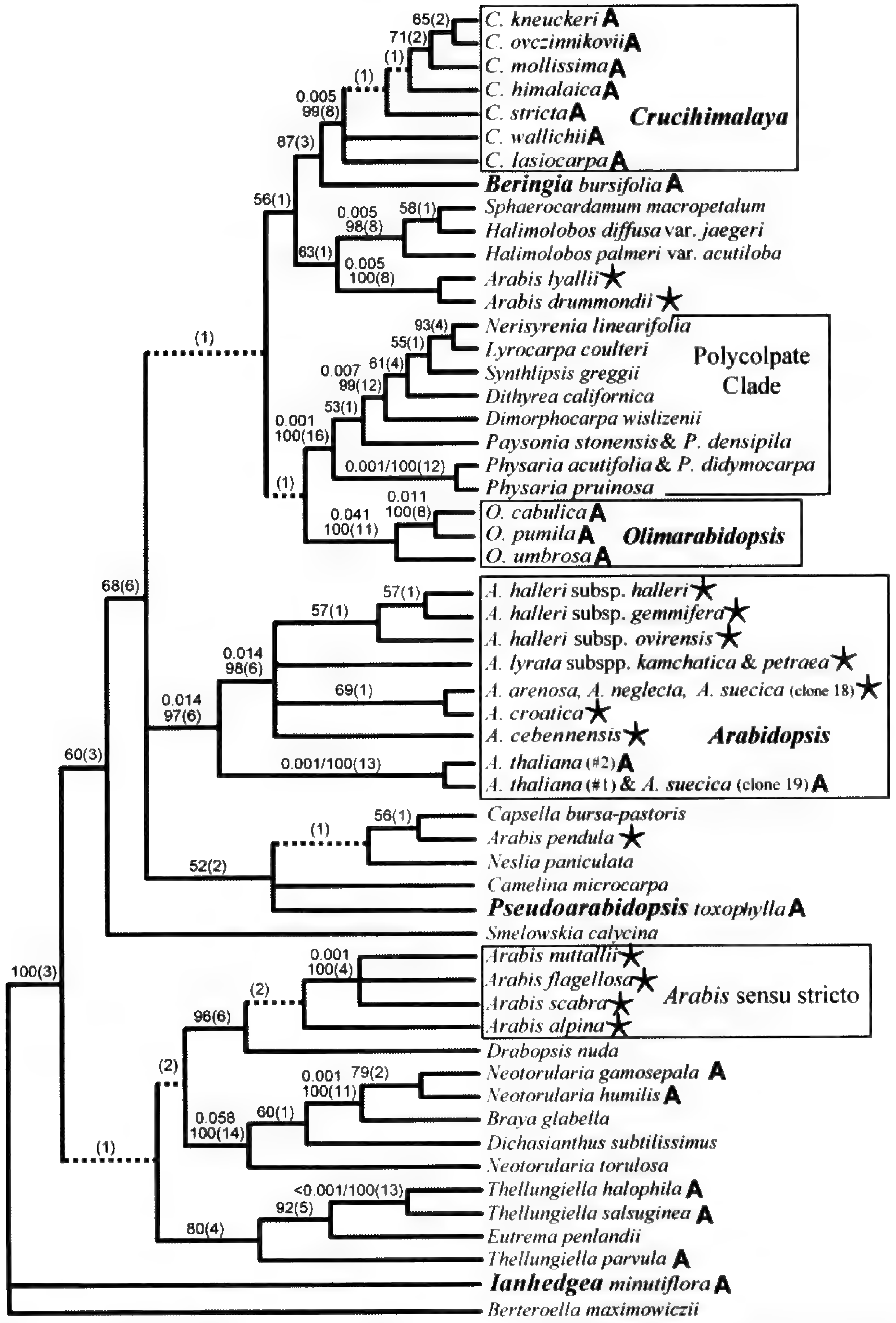

Figure 1. Strict consensus tree of 24 most-parsimonious trees. Whole numbers indicate bootstrap support; values in parentheses are the Decay Index; decimal values are Clade Significance. Dashed branches indicate branches with < 50% bootstrap support. Large bold "A" indicates species variously placed in *Arabidopsis* in previous taxonomic treatments. Large asterisks indicate species traditionally placed in *Arabis*. Genera in bold type are segregates from *Arabidopsis* named elsewhere as a result of these analyses (see Discussion).

ing *A. thaliana* as a model organism can now confidently use the other species of a better-circumscribed *Arabidopsis*, all of which are found in the sister group to *A. thaliana*, as experimental organisms. This sister group relationship implies that all species of *Arabidopsis* are equally related to *A. thaliana*. Unfortunately, the sister group to the genus *Arabidopsis* cannot be given with confidence. A trichotomy appears below *Arabidopsis* (Fig. 1): (*Arabidopsis* clade)("*Capsella–Pseudoarabidopsis*" clade)("*Crucihimalaya–Olimarabidopsis*" clade). Galloway et al. (1998), using sequences of arginine decarboxylase and a much smaller taxon sample (28 species from throughout the family), confidently placed *Capsella* in a sister group relationship to *Arabidopsis*. Unfortunately, their analysis did not include any members of the "*Crucihimalaya–Olimarabidopsis*" clade. Koch et al. (1999) found, using ITS sequences (and with low bootstrap support), *Capsella* to be sister to *Arabidopsis* and *Olimarabidopsis*, but their analysis did not include any members of *Crucihimalaya*. Koch et al. (2001) obtained similar results using plastidic *mat*K and nuclear *Chs* sequences. Additional work is needed to resolve this issue, but assuming that the "*Capsella–Pseudoarabidopsis* clade" is sister to *Arabidopsis* appears to be a valid working hypothesis.

TAXONOMIC IMPLICATIONS ELSEWHERE IN THE BRASSICACEAE

Although our intent was not to study the genus *Arabis* in any detail, our results mirror those of Koch et al. (1999, 2000, 2001) in showing *Arabis*, as traditionally recognized, to be polyphyletic even after *A. lyrata* L., *A. pedemontana*, and *A. cebennensis* are transferred to *Arabidopsis* (Fig. 1). In our analysis, the genus *Boechera* Á. Löve & D. Löve seems to be the proper home for $x = 7$ species like *A. lyallii* A. Gray and *A. drummondii* S. Watson, though not all of the necessary generic transfers have been made. *Arabis* in its strictest interpretation will consist only of those species in the clade with *A. alpina* L., the lectotype of *Arabis*. *Arabis glabra* (L.) Bernh. belongs to *Turritis* L. and *A. pauciflora* (Grimm) Garcke belongs to *Fourraea* Greuter & Burdet (Koch et al., 1999). But to which genus does *A. pendula* L. or *A. turrita* L. belong (Koch et al., 1999)? Including species once thought to be related to *Arabidopsis* in our study has also raised other taxonomic questions. *Neotorularia*, *Braya* Sternb. & Hoppe, and *Dichasianthus* Ovcz. & Junussov form a well-supported clade (Fig. 1) with *Neotorularia* being paraphyletic. *Thellungiella* and *Eutrema* R. Br. also form a well-supported clade, with *Thellungiella* being paraphyletic.

A surprising result of our study was the discovery of a clade of species all possessing pollen with more than the usual three colpi (see Polycolpate clade, Fig. 1). Palynological studies (Rollins, 1979; Rollins & Banerjee, 1979) showed that among some genera thought not to be closely related in the Brassicaceae, colpi range from four to ten. These genera, according to Schulz (1936), are as follows: *Physaria* (Nutt. ex Torr. & A. Gray) A. Gray (tribe Lepidieae, subtribe Physariinae), *Dithyrea* Harv. and its recent segregate *Dimorphocarpa* Rollins (Lepidieae, Iberidinae), *Lyrocarpa* Hook. & Harv. (Lepidieae, Lyrocarpinae), *Nerisyrenia* Greene (as *Greggia* A. Gray) and *Synthlipsis* A. Gray (Lepideae, Capsellinae), and *Lesquerella* S. Watson (Drabeae). The results presented here also suggest that within this "polycolpate clade" taxonomic revisions are needed in *Lesquerella* and *Physaria*. We have recently united these two genera (Al-Shehbaz & O'Kane, 2002b), except that the auriculate-leaved species formerly placed in *Lesquerella* are recognized as a distinct genus, *Paysonia* O'Kane & Al-Shehbaz (O'Kane & Al-Shehbaz, 2002).

Future work in the family will certainly yield further taxonomic alignments since there is rampant morphological convergence (Al-Shehbaz et al., 1999; Koch et al., 1999) and because previous taxonomy in the family has relied heavily on fruit morphology (e.g., Rollins, 1993; Al-Shehbaz, 1984) to the exclusion of floral and vegetative features (Al-Shehbaz et al., 1999). Molecular techniques in concert with a reevaluation of morphological characters are rapidly reshaping our understanding of the family (e.g., Bailey & Doyle, 1999; Bailey et al., 2002; Bowman et al., 2000; Koch et al., 1999, 2000, 2001; Mummenhoff & Koch, 1994; Mummenhoff et al., 1997a, b, 2001a, b; Price & Palmer, 1996; Rodman et al., 1996; Warwick & Black, 1993, 1997). Characterizing the membership of *Arabidopsis* and sketching its relationships to related genera, we believe, contributes to this growing body of knowledge.

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Note added in proof.

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EVOLUTION OF FLORAL NECTARIES IN IRIDACEAE[1]

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ABSTRACT

New data on nectaries in Iridaceae are presented in combination with a literature review, in the context of systematics and pollination biology. Iridaceae are a highly diverse family with respect to nectar production, reflecting the wide range of pollination syndromes within the family. Based on outgroup comparison, presence of septal nectaries is probably the plesiomorphic condition for Iridaceae, despite their absence from the putatively basal genus *Isophysis.* Within Iridaceae, septal nectaries are present in the largest subfamily Crocoideae (Ixioideae) and also in *Diplarrhena,* which is putatively sister to all other Iridoideae, but absent from the rest of Iridoideae. Within the paraphyletic Nivenioideae (six genera), septal nectaries are absent from *Aristea, Geosiris,* and *Patersonia* and present in the three shrubby Cape genera *Klattia, Nivenia,* and *Witsenia.* Perigonal nectaries and elaiophores (oil-producing hairs) are mostly confined to the subfamily Iridoideae, where they take many different forms, although some Iridoideae lack nectaries entirely. In different species of *Iris,* nectaries are present either on the base of the perianth tube or around the base of the style, or sometimes in a continuous region between the two. In many other Irideae they are located at the bases of the outer tepals (most species of *Moraea*) or the bases of all six tepals (e.g., *Ferraria*). In *Olsynium douglasii* and *O. junceum* (Sisyrinchieae) nectar is apparently secreted directly from the filament column, and in *Sisyrinchium* subg. *Sisyrinchium* elaiophores are present on the lower part of the filament column. Perigonal nectaries may have evolved from septal nectaries by developmentally later formation of nectaries in a more distal position on organ primordia (i.e., heterochrony).

Key words: *Diplarrhena,* epigyny, heterochrony, *Isophysis,* perigonal nectary, septal nectary, systematics.

Iridaceae are a cosmopolitan family comprising about 65 genera and 1850 species that are most abundant and diverse in the Southern Hemisphere, especially Africa. They represent an unusually coherent family among lilioid monocots, possessing several reliable morphological synapomorphies, including the presence of isobilateral unifacial leaves, styloid crystals, and flowers with only three stamens (i.e., lacking the inner staminal whorl). Recent molecular analyses of monocotyledons (e.g., Chase et al., 1995, 2000) have consistently placed Iridaceae in the order Asparagales, among the lower asparagoid grade, associated with families such as Doryanthaceae (*Doryanthes*), Ixioliriaceae (*Ixiolirion*), and Tecophilaeaceae. Iridaceae and Orchidaceae represent easily the largest families of Asparagales (indeed, orchids are arguably the second-largest angiosperm family). Despite their readily diagnostic features, both families are unusually diverse in terms of morphological features, and both share some characters with the order Liliales, including the presence of perigonal nectaries in some taxa. For this reason they were formerly thought (e.g., by Dahlgren & Clifford, 1982; Dahlgren et al., 1985) to be closely related to some families of Liliales, although molecular analyses have now clarified their placement in Asparagales (APG, 1998).

Septal nectaries are a characteristic feature of flowers of many monocotyledons (Van Heel, 1988; Schmid, 1985, 1988; Endress, 1995; Simpson, 1993, 1998; Smets et al., 2000). They result from incomplete fusion of a small region of the carpel margins, which are otherwise fused. In contrast, perigonal (stamen and tepal) nectaries occur mainly in the orders Asparagales and Liliales, but are concentrated in Liliales, where septal nectaries are entirely absent (Rudall et al., 2000). Septal nectaries and perigonal nectaries rarely (or possibly never) occur together in the same flower in monocots (Smets et al., 2000). Iridaceae are highly unusual (possibly unique) in that both types occur in different genera within the family, some members of which also have oil-producing epidermal cells and trichomes (elaiophores), all probably related to different pollination syndromes. This paper reviews

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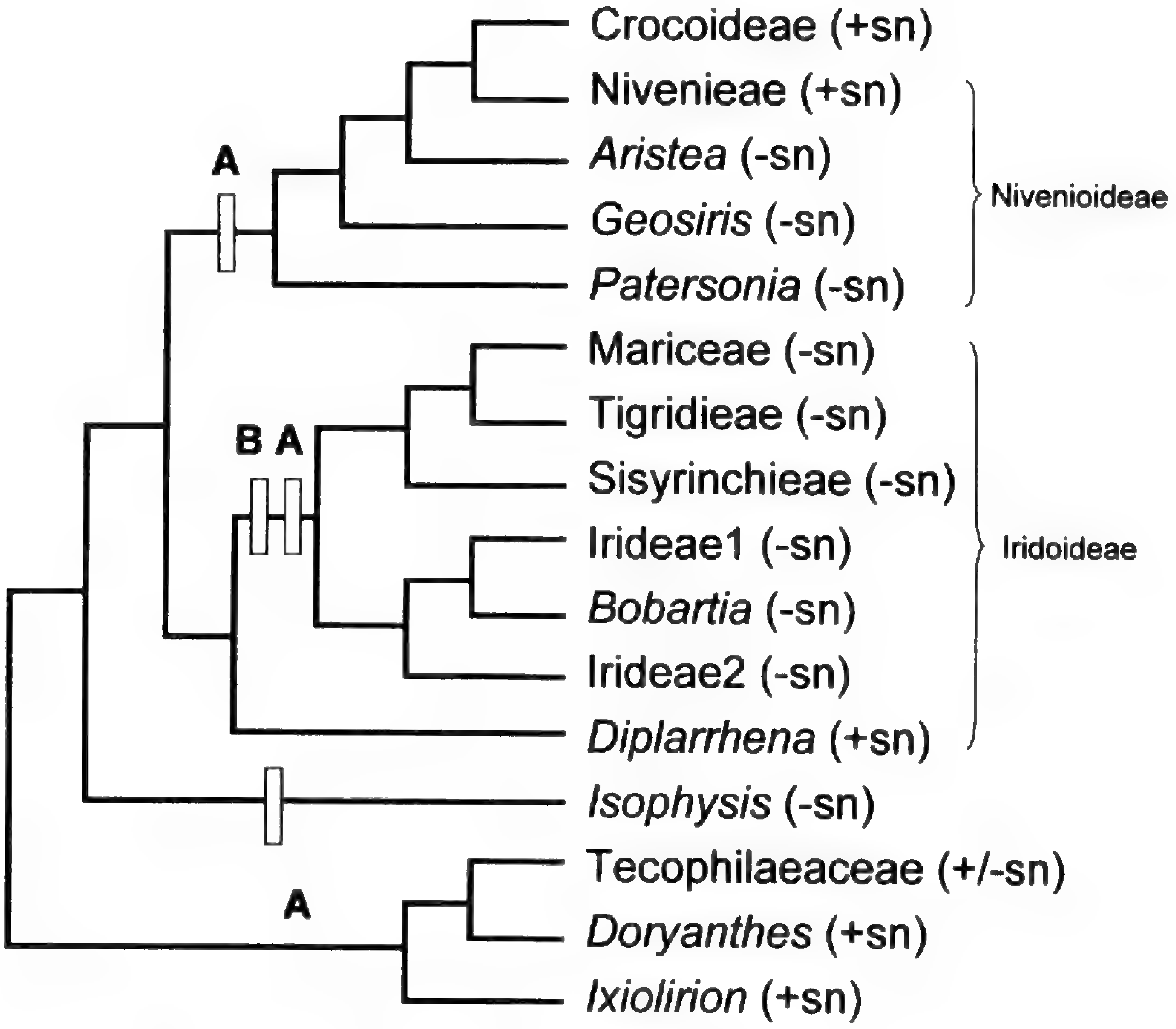

Figure 1. Diagram of relationships in Iridaceae, based on a combined molecular tree presented by Reeves et al. (2001), showing characters optimized. A = loss of septal nectaries (i.e., complete fusion of carpel margins); B = perigonal nectaries present (not in all taxa); sn = septal nectaries. An equally parsimonious option would be loss of septal nectaries on the branch leading to Iridaceae, with at least two subsequent regains (but see discussion).

the distribution of these characters in a systematic context, in order to assess their evolution within Iridaceae. Particular reference is made to a recent combined molecular analysis of Iridaceae using four plastid DNA data sets (two protein coding genes: *rps*4, *rbc*L, the *trn*L intron, and the *trn*L-F inter-gene spacer: Reeves et al., 2001; Fig. 1).

MATERIALS AND METHODS

Material examined was taken from sources indicated in Table 1. Flowers were fixed in FAA (formalin acetic alcohol) and stored in 70% ethanol before processing. Flowers were embedded in Paraplast using standard methods of wax embedding and serially sectioned using a rotary microtome. Paraffin sections were stained with safranin O and Alcian blue 8GX, dehydrated through an alcohol series to 100% ethanol then Histoclear, mounted in Euparal or DPX mountant, and examined using normal bright-field optics.

RESULTS

The systematic distribution of nectaries in Iridaceae is summarized in Table 2 using the classification of Goldblatt (1990, 1998a). Within the largest subfamily Crocoideae (Ixioideae, including ca. 28 genera of Africa and Eurasia), septal nectaries are present in representative species of all genera examined (Tables 1, 2; Daumann, 1970; de Vos, 1974a, b, 1982, 1984, 1985) (Figs. 1A, B, 5C, 6A, C). The so-called stylar nectaries described by Daumann (1970) for *Lapeirousia laxa* (Thunb.) N. E. Br. and *L. cruenta* (Lindl.) Baker (= *Freesia laxa* (Thunb.) Goldblatt & J. C. Manning: Goldblatt & Manning, 1995) are probably septal nectaries with pores opening close to the base of the style. Nectar production is suppressed in some Crocoideae, notably *Ixia* subg. *Ixia* (Goldblatt et al., 2000a), but non-functional septal nectaries are apparently present in these taxa, for example, in *I. maculata* L. and *I. viridiflora* (Daumann, 1970).

Septal nectaries are also present in *Diplarrhena* (Fig. 5B) but absent from all other members of subfamily Iridoideae (sensu Goldblatt, 1998a) examined here (Figs. 2C, D, F, 3E, 5A, 6B, 7A, 8A). Within subfamily Nivenioideae, which includes six genera (Goldblatt, 1998a), septal nectaries are absent from *Aristea* (Fig. 4B), *Geosiris* (Fig. 4C), and *Patersonia*, and nectar is not produced in most *Aristea* species (but see below). However, septal nectaries are present in the shrubby Cape genera *Klat-*

Table 1. List of species examined, with sources of plant material. For Iridaceae classification used here, see Goldblatt (1990, 1998a).

Taxon	Collection data
Subfamily Isophysidoideae	
Isophysis tasmanica (Hook.) T. Moore	Australia, Tasmania, *Jarman s.n.* (MO)
Subfamily Nivenioideae	
Aristea ecklonii Baker	Cultivated material, NBG Kirstenbosch, South Africa
Aristea ecklonii Baker	Cultivated material, RBG Kew, U.K.
Geosiris madagascariensis Baill.	Madagascar, *Dorr et al. s.n.* (MO)
Klattia stokoei L. Guthrie	South Africa, W. Cape, *Goldblatt 8347* (MO)
Klattia flava (G. J. Lewis) Goldblatt	South Africa, W. Cape, *Goldblatt 8656* (MO)
Nivenia binata Klatt	South Africa, W. Cape, *Goldblatt 7959* (MO)
Nivenia stokoei (L. Guthrie) N. E. Br.	South Africa, W. Cape, *Goldblatt 7628* (MO)
Patersonia longifolia R. Br.	Australia, New South Wales, *Ladd s.n.* (NBG)
Witsenia maura (L.) Thunb.	South Africa, W. Cape, *Goldblatt & Gentry 1600* (NBG)
Subfamily Iridoideae	
Tribe Diplarrheneae	
Diplarrhena latifolia Benth.	Cultivated material, RBG Kew, U.K. (1980–2283)
Tribe Sisyrinchieae	
Libertia grandiflora Sweet	Cultivated material, RBG Kew, U.K.
Olsynium douglasii A. Dietr.	U.S.A., Washington, *Goldblatt 11642* (MO)
Olsynium junceum (E. Mey. ex Presl) Goldblatt	Cultivated material, RBG Kew, U.K.
Orthrosanthus laxus (Endl.) Benth.	Cultivated material, RBG Melbourne, Australia
Orthrosanthus sp.	Cultivated material, RBG Kew, U.K.
Sisyrinchium striatum Sm.	Cultivated material, RBG Kew, U.K.
Sisyrinchium sp.	Cultivated material, RBG Kew, U.K.
Tribe Irideae	
Belamcanda chinensis (L.) DC.	Cultivated material, University of Durban-Westville, S. Africa
Bobartia gladiata (L.f.) Ker-Gawl.	South Africa, W. Cape, *Boucher 5263* (NBG)
Dietes grandiflora N. E. Br.	Cultivated material, NBG Kirstenbosch, South Africa
Ferraria crispa Burm.	South Africa, W. Cape, *Goldblatt & Manning 11665* (MO)
Ferraria foliosa G. J. Lewis	South Africa, W. Cape, *Goldblatt & Porter 11888* (MO)
Ferraria ferrariola (Jacq.) Willd.	South Africa, N. Cape, *Goldblatt & Porter 11765* (MO)
Ferraria divaricata Sweet subsp. *divaricata*	South Africa, N. Cape, *Goldblatt & Manning 10176* (MO)
Ferraria schaeferi Dinter	South Africa, W. Cape, *Goldblatt & Porter 11734* (MO)
Moraea collina Thunb.	South Africa, W. Cape, *Goldblatt 2132* (MO, NBG)
Moraea spathulata (L.f.) Klatt	South Africa, E. Cape, *Goldblatt 12232* (MO)
Tribe Tigridieae	
Alophia drummondii (Graham) R. C. Foster	Cultivated material, Missouri BG, U.S.A.
Ennealophus euryandrus (Griseb.) P. Ravenna	Cultivated material, RBG Kew, U.K.
Gelasine elongata (R. Grah.) P. Ravenna	Cultivated material, ex hort. B. Mathew, Surrey, U.K.
Tigridia meleagris (Lindl.) Nichols.	Mexico, Kenton, *Rudall & Howard 49-319* (K)
Tribe Trimezieae	
Pseudotrimezia planifolia P. Ravenna	Brazil, *Harley et al. 25445* (K)
Subfamily Crocoideae (Ixioideae)	
Tribe Pillansieae	
Pillansia templemannii L. Bolus	South Africa, W. Cape, *Goldblatt 7907A* (MO, NBG)

Table 1. Continued.

Taxon	Collection data
Tribe Watsonieae	
Lapeirousia neglecta Goldblatt & J. C. Manning	South Africa, W. Cape, *Goldblatt & Manning 9022* (MO)
Micranthus alopecuroides (L.) Rothm.	South Africa, *Goldblatt & Manning 10431* (NBG)
Thereianthus racemosus (Klaff) G. J. Lewis	South Africa, W. Cape, *Manning s.n.* (NBG)
Watsonia angusta Ker-Gawl.	South Africa, W. Cape, *Snijman 971* (NBG)
Tribe Ixieae	
Babiana sinuata G. J. Lewis	South Africa, W. Cape, *Goldblatt 2545* (MO, NBG)
B. stricta (Aiton) Ker-Gawl.	South Africa, W. Cape, *Goldblatt & Manning 10343* (NBG)
Crocus sieberi Gay	Cultivated material, RBG, Kew, U.K.
Dierama pendulum (L. f.) Walp.	Cultivated material, NBG Kirstenbosch, South Africa
Freesia alba (G. L. Meyer) Gumbleton	Cultivated material, NBG Kirstenbosch, South Africa
F. grandiflora (Baker) Klaff	Cultivated material, NBG Kirstenbosch, South Africa
Geissorhiza ornithogaloides Klatt	South Africa, W. Cape, *Manning 2026* (NBG)
Gladiolus gracilis Jacq.	South Africa, W. Cape, *Manning 2016* (NBG)
Hesperantha falcata (L. f.) Ker-Gawl.	South Africa, near George, *Goldblatt & Manning s.n.*
Ixia polystachya L.	South Africa, ex hort. Kirstenbosch
Melasphaerula ramosa (Burm. f.) N. E. Br.	South Africa, W. Cape, Cape Peninsula, *Goldblatt & Manning s.n.*
Romulea rosea (L.) Eckl.	South Africa, W. Cape, *Manning 2017* (NBG)
Sparaxis grandiflora (D. Delaroche) Ker-Gawl.	Cultivated material, NBG Kirstenbosch, South Africa
Tritonia squalida (Aiton) Ker-Gawl.	South Africa, W. Cape, near Albertinia, *Goldblatt & Manning s.n.*
Tritoniopsis parviflora (Jacq.) G. J. Lewis	South Africa, *Goldblatt & Manning 2283* (NBG)
Tritoniopsis burchellii (N. E. Br.) Goldblatt	South Africa, W. Cape, *Goldblatt & Manning 9869* (NBG)
Xenoscapa fistulosa (E. Mey. ex Klaff) Goldblatt	South Africa, W. Cape, *Manning 2028* (NBG)

tia, *Nivenia*, and *Witsenia* (Figs. 3A, F, G, 4D, E), which together form a clade (Manning & Goldblatt, 1991; Reeves et al., 2001). Septal nectaries are absent from the monogeneric subfamily Isophysidoideae (*Isophysis*) (Fig. 2E).

Perigonal nectaries and elaiophores (oil-producing hairs) are mostly confined to subfamily Iridoideae, in which septal nectaries are always absent (except *Diplarrhena*; see above). However, there are at least two examples of perigonal nectaries or elaiophores in taxa outside Iridoideae: (1) one species of Nivenioideae (*Aristea spiralis* (L.f.) Ker-Gawl.) produces nectar that is secreted from small perigonal nectaries on the short perianth tube below the base of the free parts of the tepals (Fig. 4A); Daumann (1970) also reported perigonal nectaries in *A. africana* (L.) Hoffmanns. (2) In *Tritoniopsis parviflora* (Jacq.) G. J. Lewis (subfamily Crocoideae), floral oils are produced from a glandular epithelium at the base of the free parts of the tepals and in the mouth of the perianth tube (Manning & Goldblatt, 2002). Oil secretion is supplemented by production of sugary nectar from septal nectaries.

Within subfamily Iridoideae, perigonal nectaries and elaiophores take several different forms. Daumann (1935) illustrated highly vascularized nectariferous regions present on different parts of the flower surface in different species of *Iris*. These included:

(1) Nectaries present on the base of the perianth tube (comprising fused perianth and staminal tissue), especially (but not exclusively) in the interstaminal regions (e.g., in *I. douglasiana* Torr., *I. ensata* Thunb., *I. foetidissima* L., *I. graminea* L., *I. pseudacorus* L., *I. sibirica* L., and also in two allied monotypic genera, *Belamcanda* and *Hermodactylis*).

(2) Nectaries present around the base of the style (e.g., in *I. dichotoma* Pall.).

(3) Nectaries present in a continuous region extending from around the base of the perianth tube to around the base of the style (e.g., in *I. chamaeiris* Bertol., *I. germanica* L., *I. kolpakowskiana* Regel, *I. pumila* L., *I. stolonifera* Maxim., *I. tectorum* Maxim., *I. tingitana* Boiss. & Reut., *I. warleyensis* Foster, *I. xiphioides* Ehrh.) extending onto the bases of the inner tepals in *I. sisyrinchium* L. These are not

Table 2. Distribution of nectaries in Iridaceae (arranged according to the classification of Goldblatt, 1990, 1998a).

Taxon	Septal nectaries	Other floral secretory structures
Isophysidoideae (*Isophysis*)	absent (Fig. 5A)	absent
Nivenioideae	absent from *Aristea* (Fig. 4B), *Geosiris* (fig. 4C), *Patersonia*, present in *Klattia*, *Nivenia* (Fig. 3F, G), *Witsenia* (Fig. 4D, E)	absent, except in *Aristea spiralis*, in which small perigonal nectaries present (Fig. 4A)
Iridoideae	absent (except in *Diplarrhena*: Fig. 5B)	often present
Bobartia	absent (Fig. 5A)	absent
Dietes	absent (Fig. 6B)	absent
Diplarrhena	present (Fig. 5B)	absent
Iridoideae–Sisyrinchieae	absent (Figs. 2C, D, 3E, 7A, 8A)	nectar secreted from filament column in *Olsynium* (Figs. 7, 8); elaiophores present on filament column in many species of *Sisyrinchium* subg. *Sisyrinchium* (Fig. 3C–E)
Iridoideae–Irideae	absent (Figs. 5A, 6B)	perigonal nectaries present in *Moraea* (Fig. 6D) and *Ferraria*, or on the walls of the perianth tube in *Iris*
Iridoideae–Tigridieae	absent (Fig. 2F)	elaiphores present on tepal claws in some species (Figs. 3B, 9)
Iridoideae–Trimezieae	absent	elaiophores present on tepal claws in some species
Crocoideae	present in all taxa (Figs. 2A, B, 5C, 6A, C)	absent

septal nectaries, because they do not extend into the unfused regions of the carpel margins within the ovary, but they could easily be mistakenly identified as such in the absence of anatomical sections.

Among other members of the Old World and North American tribe Irideae, in *Moraea* and *Ferraria* the smooth glistening perigonal nectaries, when present, can readily be seen with the naked eye; they are located at the bases of the outer tepals (in most species of *Moraea*) or at or near the bases of all six tepals (in *Ferraria* and many *Moraea* spp.) (Vogel, 1954; Daumann, 1970; de Vos, 1979; Goldblatt, 1986, 1987; Goldblatt & Manning, unpublished data). In some species of *Ferraria* the nectaries may cover more than half the area of the tepal claws and measure up to 4 × 3 mm. Species of *Dietes* and *Bobartia* apparently lack nectaries entirely (Figs. 5A, 6B) and produce no nectar, as indicated by visual observation and the taste test (applying likely nectar-bearing parts of the flower to the tongue) (Goldblatt, unpublished data). This observation refutes Daumann's (1970) reports of perigonal nectaries in *Dietes bicolor* (Lindl.) Sweet and *D. iridoides* (L.) Sweet ex Klatt (as both *D. vegeta* (L.) N. E. Br. and *Moraea iridoides* L.). In *Moraea ochroleuca* (Salisb.) Drapiez and *M. lurida* Ker-Gawl. nectar is produced along the length of all six tepal claws above the vascular strands but no nectariferous glands are evident (Goldblatt et al., 1998; Goldblatt & Manning, 2002). Nectaries are not developed in several species of *Moraea* that are pollinated by hopliine scarab beetles, e.g., *M. cantharophila* Goldblatt & J. C. Manning, *M. tulbaghensis* L. Bolus, and *M. villosa* Ker-Gawl. (Goldblatt et al., 1998; Goldblatt & Manning, 2002; Steiner, 1998).

The New World Iridoideae are currently distributed among tribes Sisyrinchieae, Trimezieae, and Tigrideae (Goldblatt, 1990, 1998a). These include numerous species that produce nectar from various different parts of the flower, although some apparently lack nectar entirely; for example, Cocucci and Vogel (2001) reported that *Olsynium philippi* (Klatt) Goldblatt (Sisyrinchieae) does not produce nectar. In many Iridoideae (and other Iridaceae) the stamen filaments are free in the upper half and fused into a filament column at their base. In *O. douglasii* A. Dietr. the outer surface of the filament column is smooth, with large epidermal cells and dark-staining highly vascularized tissue beneath, indicating a nectary (Fig. 7A–D). The inner surface of the filament column is highly convoluted and thin-walled. The filament column is swollen just above the base; nectar presumably accumulates in a subepidermal space in this region. After exudation, nectar then accumulates in a semi-enclosed cham-

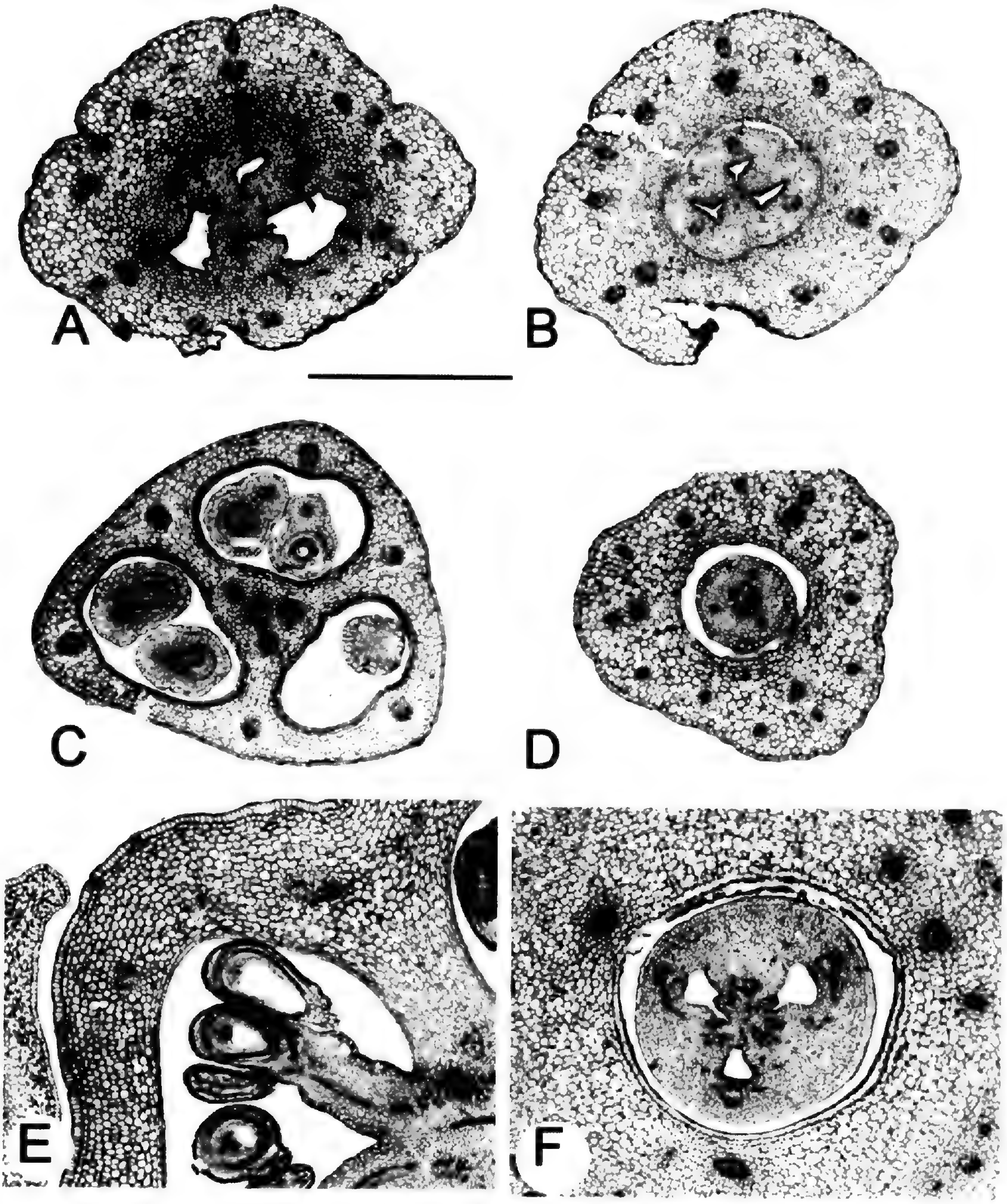

Figure 2. —A, B. *Crocus sieberi* (Crocoideae), transverse sections (TS) of flower through base of ovary (A) and top of ovary (B); septal nectaries arrowed. —C, D. *Orthrosanthus laxus* (Iridoideae–Sisyrinchieae), TS of flower through ovary (C) and style plus perianth tube (D); nectaries absent. —E. *Isophysis tasmanica* (Isophysidoideae), TS of superior ovary; nectaries absent. —F. *Gelasine elongata* (Iridoideae–Tigridieae), TS of top of ovary, nectaries absent. Scale = 0.5 mm for all images.

ber around the narrow basal part of the column. This nectar chamber (also present in some *Moraea* species, e.g., *M. miniata* Andr.; Goldblatt & Bernhardt, 1999) is enclosed by the short perianth tube (in *Olsynium*), the walls of which are almost in contact with the swollen portion of the filament column, or by the short tepal claws that abut the swollen lower portion of the filament column (in *Moraea*). Other species of *Olsynium* have a similar swollen base to the filament column and a perianth tube and most likely also produce nectar in the manner described for *O. douglasii.* At least *O. junceum* (E. Mey. ex Presl) Goldblatt is known to produce nectar (Forcone et al., 1998), which is presumably secreted from anticlinally elongated epidermal cells on both surfaces of the filament tube (Fig. 8).

Many other New World Iridoideae bear trichome elaiophores, which are invariably unicellular and

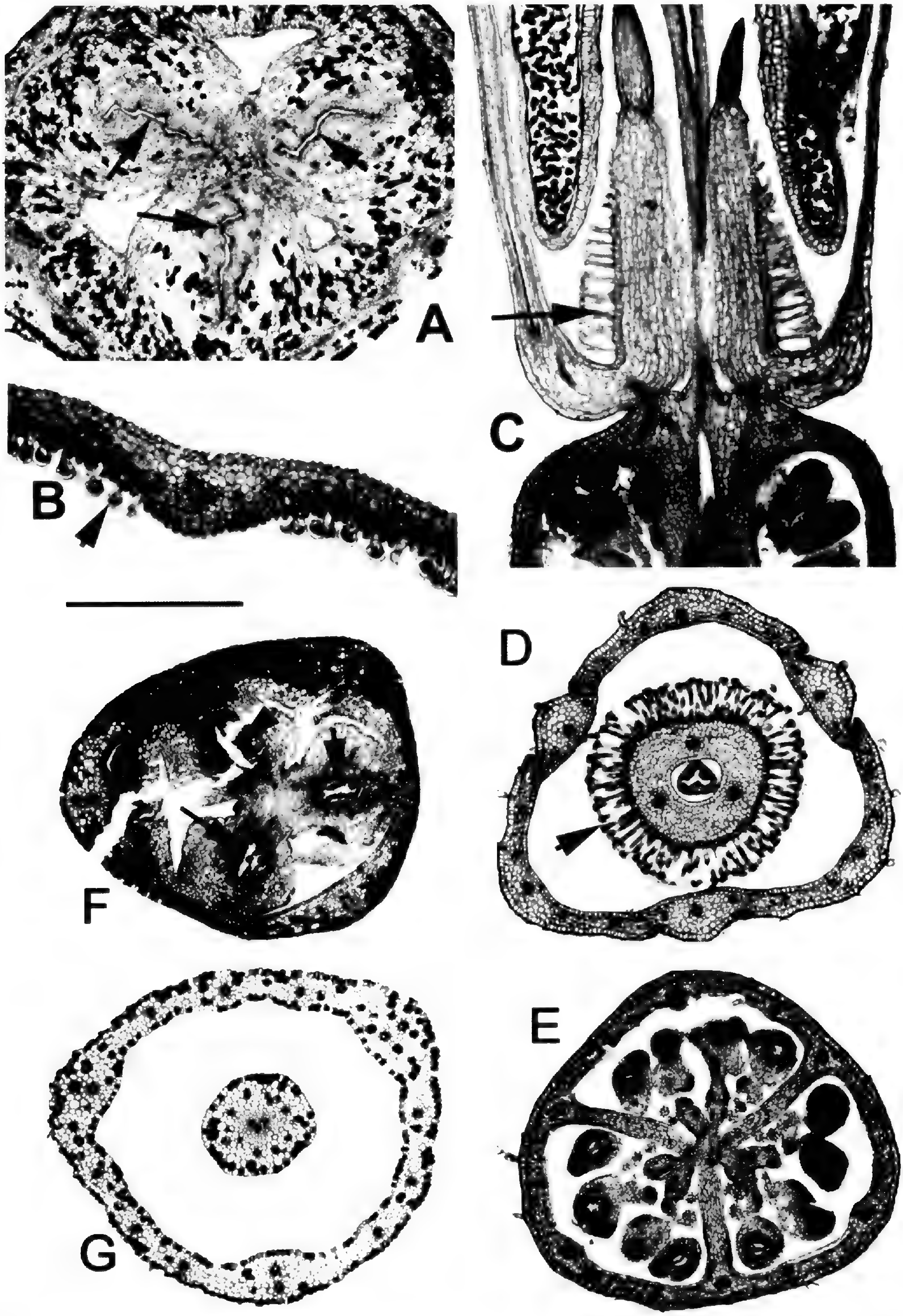

Figure 3. —A. *Klattia stokoei* (Nivenioideae), TS of flower just proximal to top of semi-inferior ovary, showing septal nectaries (arrowed). —B. *Tigridia meleagris* (Iridoideae–Tigridieae), TS of inner tepal with oil-producing trichomes (elaiophores). C–E. *Sisyrinchium* sp. (Iridoideae–Sisyrinchieae). —C. Longitudinal section (LS) of flower showing distal end of inferior ovary and proximal end of perianth tube, staminal column, and central style, with elaiophores present on staminal column. —D. TS of staminal column (with elaiophores) and central style. —E. TS of ovary, lacking septal nectaries. F, G. *Nivenia binata* (Nivenioideae). —F. TS of flower just proximal to top of semi-inferior ovary, showing septal nectaries (arrowed). —G. TS of perianth/stamen tube and style. Scale = 0.5 mm for all images.

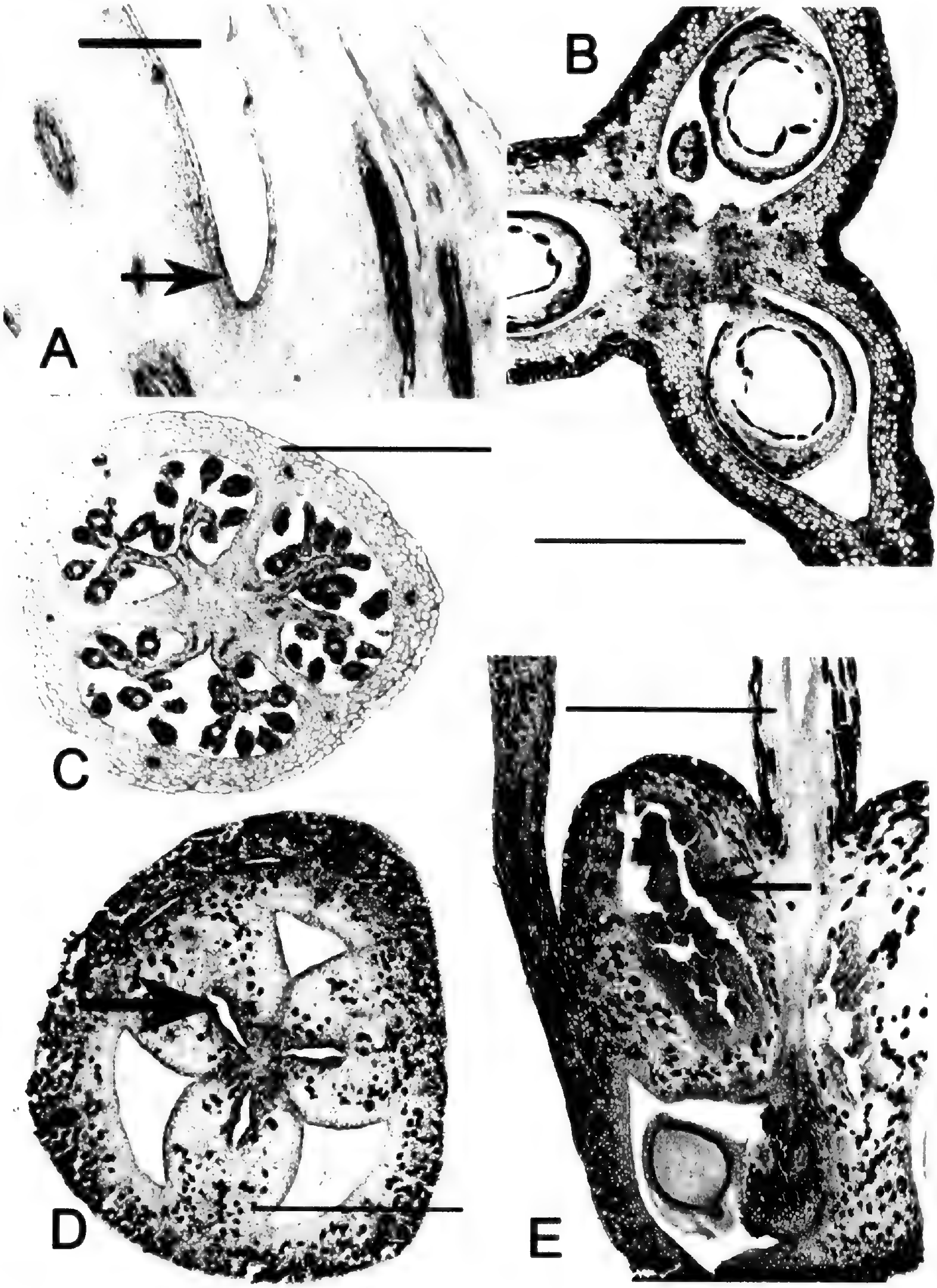

Figure 4. —A. *Aristea spiralis* (Nivenioideae), LS of top of ovary with perigonal nectary at base of perianth tube arrowed. —B. *Aristea ecklonii* (Nivenioideae), TS of ovary, lacking septal nectaries. —C. *Geosiris madagascariensis* (Nivenioideae), TS of ovary, lacking septal nectaries. D, E. *Witsenia maura* (Nivenioideae). —D. TS of top part of ovary, with one of three septal nectaries arrowed. —E. LS of ovary, with one of three septal nectaries arrowed. Scales: in A = 100 μm; in B–E = 0.5 mm.

club-shaped, with a rounded tip. In *Sisyrinchium* subg. *Sisyrinchium* trichomes (elaiophores) present on the lower part of the filament column (Fig. 3C, D) secrete floral oils; this was first reported by Vogel (1971, 1974) and described in detail by Cocucci and Vogel (2001). Similar trichome elaiophores also occur on the tepal claws in Tigridieae, including *Alophia* (syn. *Eustylis*), *Cypella*, *Ennealophus* (Fig. 9), *Fosteria* (a genus closely allied to, if not nested in *Tigridia*: Goldblatt, 1998a), *Gelasine*, *Herbertia*, many species of *Tigridia* (Fig. 3B), and Trimezieae, including *Neomarica* (Molseed,

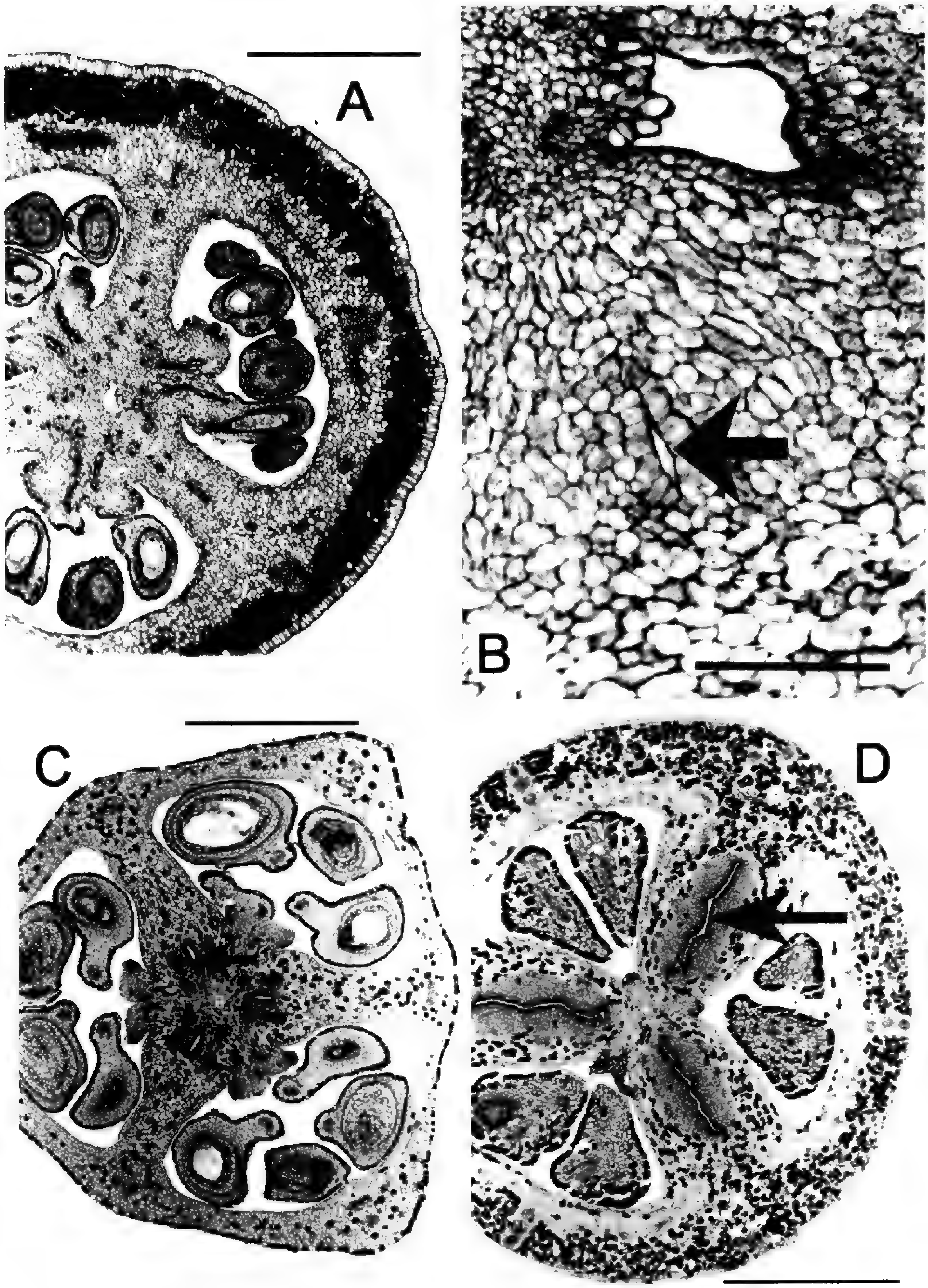

Figure 5. —A. *Bobartia gladiata* (Iridoideae–Irideae), TS of ovary, lacking septal nectaries. —B. *Diplarrhena latifolia* (Iridoideae–Diplarrheneae), TS of septal nectary (arrowed). —C. *Babiana stricta* (Crocoideae), TS of ovary, with one of three septal nectaries arrowed. —D. *Tritoniopsis burchellii* (Crocoideae), TS of ovary, with one of three septal nectaries arrowed. Scales: in A, C, D = 0.5 mm; in B = 100 µm.

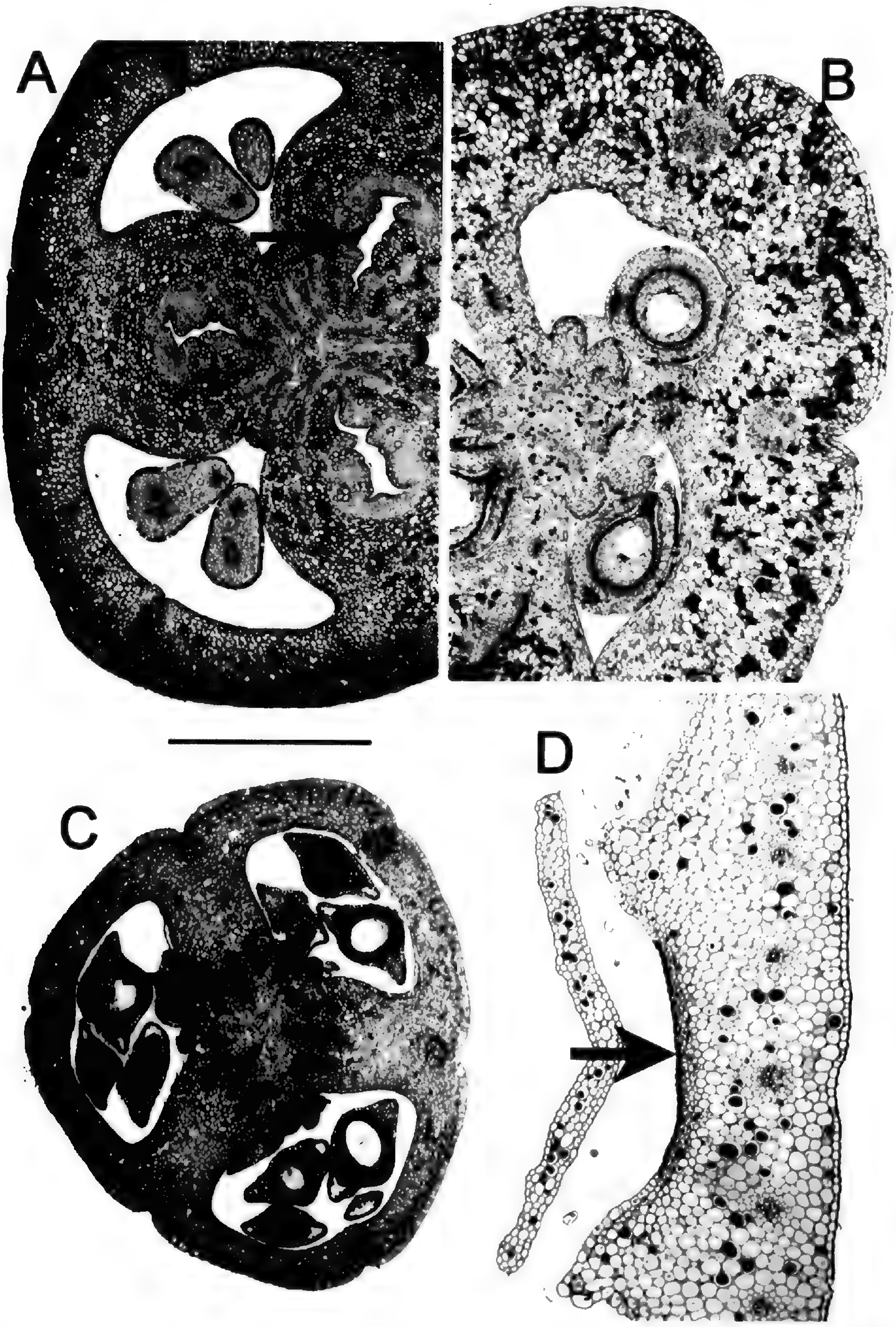

Figure 6. —A. *Watsonia angusta* (Crocoideae), TS of ovary, with one of three septal nectaries arrowed. —B. *Dietes grandiflora* (Iridoideae–Irideae), TS of ovary, lacking septal nectaries. —C. *Gladiolus gracilis* (Crocoideae), TS of ovary, with one of three septal nectaries arrowed. —D. *Moraea spathulata* (Iridoideae–Irideae), TS of tepals, with perigonal nectary arrowed. Scale = 0.5 mm.

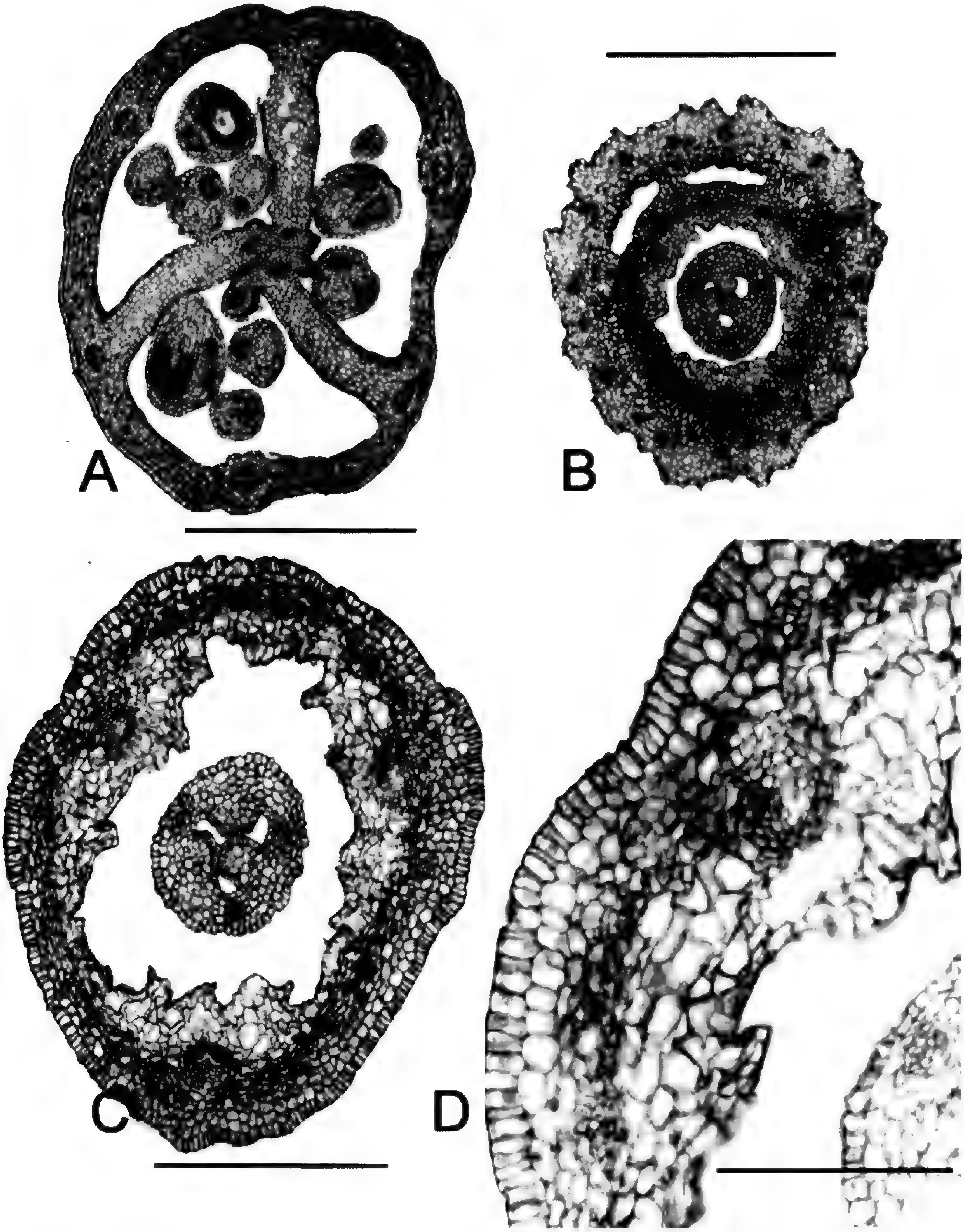

Figure 7. *Olsynium douglasii* (Iridoideae–Sisyrinchieae), serial TS of flower. —A. TS of ovary, lacking septal nectaries. —B. Just above top of inferior ovary, showing central style surrounded by staminal column partially fused with perianth tube. —C. More distal section showing central style surrounded by staminal column in which the outer epidermal cells are axially elongated and the inner epidermis is thin-walled and convoluted. —D. Enlarged view of part of staminal column showing extensive vascular tissue beneath outer epidermis. Scales: in A–C = 0.5 mm; in D = 100 μm.

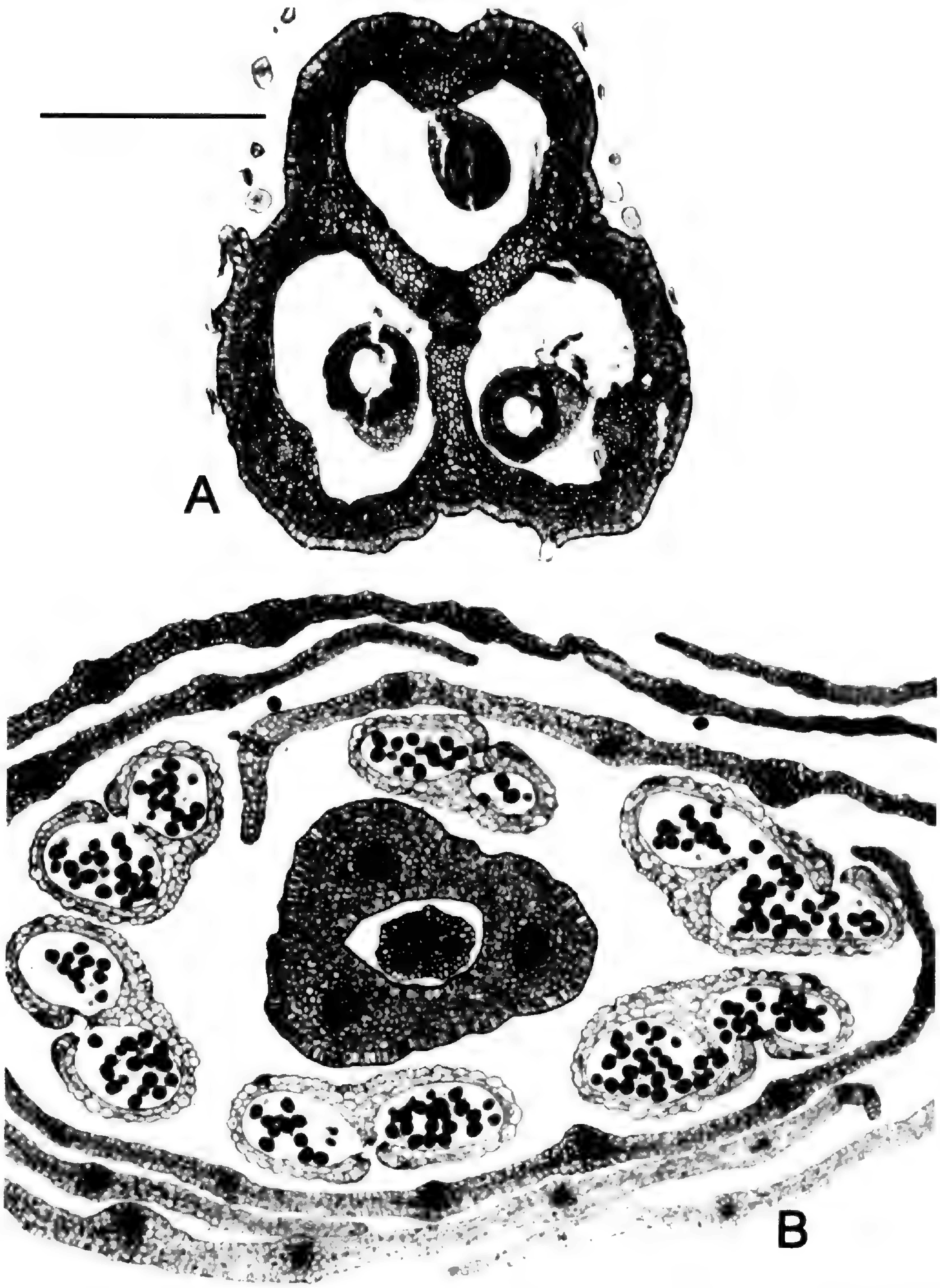

Figure 8. *Olsynium junceum* (Iridoideae–Sisyrinchieae), TS of flower. —A. TS of ovary, lacking septal nectaries. —B. TS above top of inferior ovary, showing central style surrounded by staminal column in which both outer and inner epidermal cells are axially elongated. Scale = 0.5 mm.

1968, 1970; Vogel, 1974; Lee, 1994). The elaiophores develop from epidermal cells rather late in development, shortly prior to anthesis. Their distribution on the tepals varies, although in general the zone of glandular trichomes is restricted to the adaxial surfaces of the smaller inner tepals, often concentrated in pouches at the juncture of the tepal claw and limb. In *Herbertia* there are nectaries on

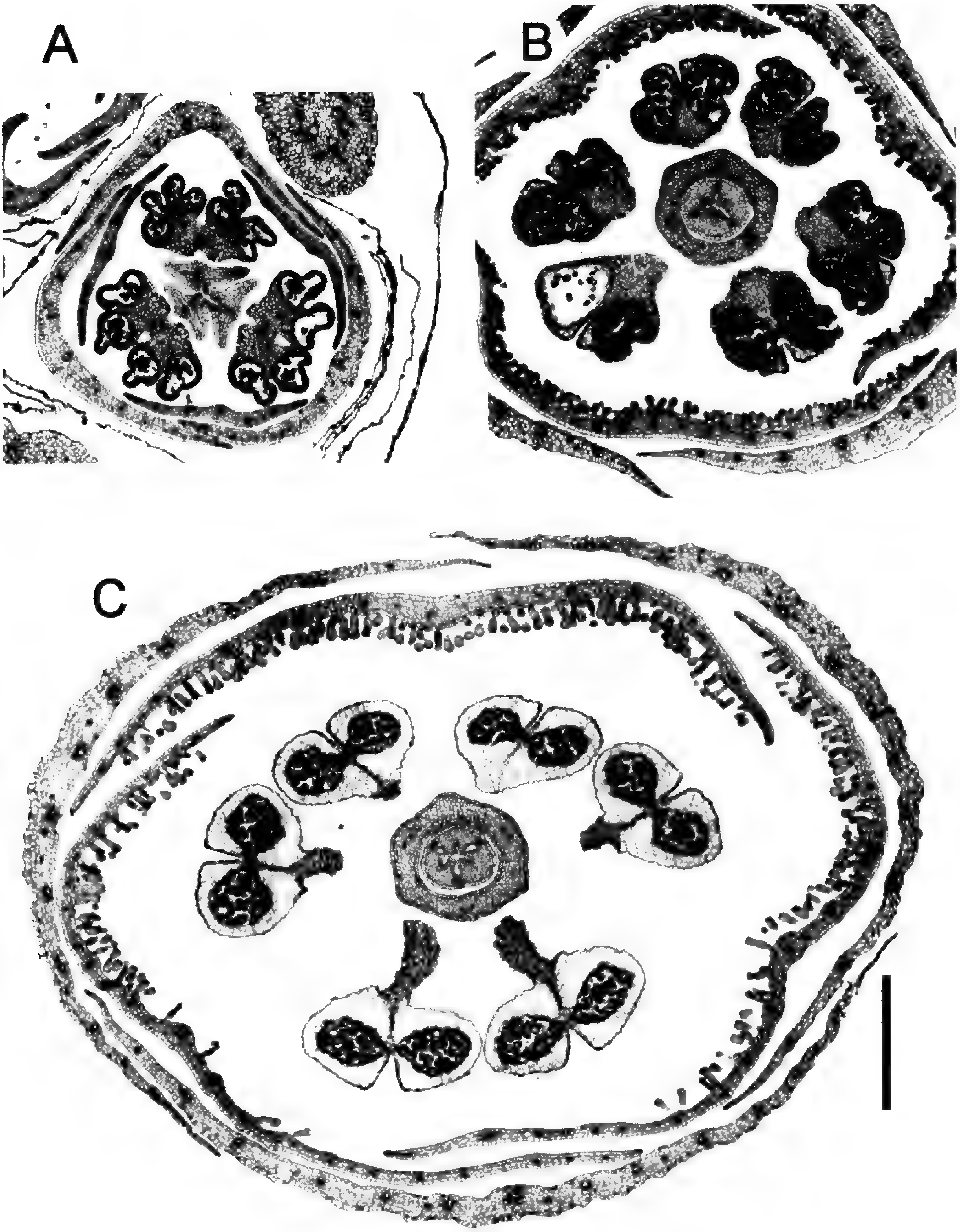

Figure 9. *Ennealophus euryandrus* (Iridoideae–Tigridieae), TS of flowers through style. —A. TS of young bud; perigonal trichomes not developed. —B. TS of older bud; short perigonal trichomes (elaiophores) present on inner surface of inner tepals. —C. TS of bud just before anthesis; longer trichomes (elaiophores) present on inner surface of inner tepals. Scale = 0.5 mm.

the smaller inner tepals and the claws of the outer tepals. At least two genera of the tribe apparently lack nectaries: *Sessilanthera* and *Cobana*, which have porose anthers and on this basis are expected to be buzz pollinated. Absence of nectar is often associated with buzz pollination, and information available indicates that these two genera lack nectaries and elaiophores (Molseed & Cruden, 1969; Ravenna, 1974). *Eleutherine* and *Nemastylis* also evidently lack nectaries (Molseed, 1970) but these species have conventional longitudinal anther dehiscence.

Red-flowered and presumably hummingbird-pollinated species of *Tigridia,* which were formerly placed in a separate genus, *Rigidella* (Goldblatt, 1998a), secrete copious amounts of sugary nectar from nectaries on the inner tepal claws (Cruden, 1971). Other Tigridieae may also secrete nectar from perigonal nectaries, although this is not adequately documented. Molseed (1970) mentioned fly and wasp visitors in some small-flowered species of *Tigridia;* as far as we know flies and wasps do not take floral oils as a reward.

Lee (1994) described a novel mode of nectar production in *Alophia drummondii* Grah. in which the expanded, fiddle-shaped anther connectives secrete a sticky mucilage with dilute sugar content. During the later stages of anthesis this is concentrated by evaporation to form an alternative nectar source. The primary role of the mucilage is reportedly to promote pollen adherence on the dorsal thorax of visiting bees.

DISCUSSION

SEPTAL NECTARIES IN ASPARAGALES

An understanding of sister-group relationships is critical for optimization of characters onto an existing phylogeny. However, this is problematical for Iridaceae because relationships among the various lower asparagoid clades are still not satisfactorily resolved, partly because *Ixiolirion* is a "wildcard" taxon on a very long branch in molecular analyses (Fay et al., 2000), tending to destabilize tree topology. Three taxa, *Ixiolirion* (Ixioliriaceae), *Doryanthes* (Doryanthaceae), and Tecophilaeaceae, are commonly placed close to Iridaceae in cladistic analyses (e.g., Chase et al., 1995; Rudall et al., 1997; Fay et al., 2000). Of these, the Australian bird-pollinated genus *Doryanthes* (ca. two spp.) is a good candidate for a sister group relationship with Iridaceae because it shares some synapomorphies, including presence of styloid crystals (and absence of raphides). Within Iridaceae, raphides are invariably absent and almost all taxa have styloids (Goldblatt et al., 1984) with the exception of *Sisyrinchium* and its close allies, which lack crystals altogether (a synapomorphy for this group: Rudall et al., 1986; Goldblatt et al., 1990). On the other hand, raphides are present (and styloids absent) in both *Ixiolirion* and Tecophilaeaceae (Prychid & Rudall, 1999). Furthermore, both *Doryanthes* and Iridaceae have extrorse anther dehiscence, a character that is otherwise unusual in Asparagales. *Ixiolirion* is a small Eurasian genus of ca. three species with epigynous flowers with septal nectaries in the top half of the ovary (Simpson & Rudall, 1998; Rudall, 2002). Fay et al. (2000) placed *Ixiolirion* with *Doryanthes* in an equally weighted multigene analysis and with Tecophilaeaceae in a successively weighted analysis. Analysis of morphological data (Rudall, 2002b) supported a close association between *Ixiolirion* and *Doryanthes,* although *Ixiolirion* shares a corm with Tecophilaeaceae (Kubitzki, 1998; Simpson & Rudall, 1998), while *Doryanthes* has a short vertical rhizome (Clifford, 1998).

Septal nectaries are absent from some Tecophilaeaceae (Simpson & Rudall, 1998), but present in both *Doryanthes,* in which copious nectar is secreted (Newman, 1928; Patil & Pai, 1981; Kocyan & Endress, 2001) and *Ixiolirion* (Rudall, 2002a). Loss of septal nectaries has apparently occurred *de novo* several times within Asparagales (Rudall, 2002a), including at least once in both Tecophilaeaceae and Iridaceae. Therefore, despite their absence from the putatively basal genus, *Isophysis* (see below, and introduction), the most likely scenario is that presence of septal nectaries is the plesiomorphic condition for Iridaceae (Fig. 1).

Total absence of septal nectaries (i.e., complete fusion of carpel margins) occurs sporadically within Asparagales (sensu APG, 1998), in contrast to the related order Liliales, where absence of septal nectaries and presence of perigonal nectaries both represent highly consistent synapomorphies (Rudall et al., 2000). Total absence of nectar often indicates an alternative pollination mode; for example, several asparagoid families with vibratile (buzz) pollination and *Solanum*-type flowers lack nectaries entirely, including some Laxmanniaceae (e.g., *Arthropodium*), some Hemerocallidaceae, some Tecophilaeaceae, and apostasioid orchids (Vogel, 1981; Dressler, 1993; Bernhardt, 1995, 1996; Kocyan & Endress, 2001; Rudall, 2001, 2002a). Septal nectaries are often absent from epigynous taxa (Rudall, 2002a) and always absent from "hyper-epigynous" taxa with gynostemia such as Orchidaceae (Rudall & Bateman, 2002).

NECTARIES IN IRIDACEAE

Within Iridaceae, there is some topological conflict at the deeper nodes resulting from analyses of different data sets, especially between molecules and morphology, although even the molecular topologies differed in some respects (Reeves et al., 2001). Analysis of four plastid DNA data sets (*rbc*L, *rps*4, *trn*L, *trn*L-F) for 57 genera of Iridaceae plus outgroups, found that in each of the individual trees, some genera or groups of genera were misplaced relative to morphological cladistic studies, but the combined analysis produced a tree in which all subfamilies were resolved as monophyletic, except that Nivenioideae formed a grade in which Crocoideae (Ixioideae) were embedded (Reeves et al., 2001). Among other genera of disputed affinities, *Geosiris* was placed within the nivenioid grade (Goldblatt et al., 1987), *Isophysis* was sister to the rest of the family, and *Diplarrhena* was placed in a well-supported position as sister to Iridoideae (Rudall & Goldblatt, 2001). *Bobartia* (formerly Sisyrinchieae: Goldblatt & Rudall, 1992) has found support as a member of Irideae (Iridoideae), by both Reeves et al.'s (2001) study and a molecular analysis of the ITS2 gene (Donato et al., 2000).

Assuming that the combined (successively weighted) molecular topology of Reeves et al. (2001) is correct, with the Tasmanian genus *Isophysis* as the basal taxon (Fig. 1), and also that the presence of septal nectaries is the plesiomorphic condition for Iridaceae (see above), then there are two possible evolutionary scenarios for this character within the family: (1) suppression of septal nectaries in the ancestor of Iridaceae plus at least two *de novo* developments of septal nectaries, in Nivenioideae/Crocoideae and *Diplarrhena* (and probably a subsequent secondary loss in Iridoideae), or (2) separate suppressions of septal nectaries in *Isophysis*, the basal Nivenioideae (*Aristea, Geosiris,* and *Patersonia*), and Iridoideae, as illustrated in Figure 1. The latter scenario would involve several separate losses of septal nectaries in *Isophysis, Aristea, Geosiris,* and *Patersonia.* However, it is possible that *Aristea, Geosiris,* and *Patersonia* may ultimately form a clade, since Reeves et al. (2001) suggested that the existing topology, which conflicts with morphological data for these taxa, is questionable due to high levels of sequence divergence. In any case, this hypothesis, although less parsimonious, is perhaps ultimately more plausible, especially if (as seems likely) perigonal nectaries evolved from septal nectaries (see below).

Nivenioideae and Crocoideae. The subfamily Nivenioideae is a relatively heterogeneous group with respect to several characters, including nectaries (Table 2). Reeves et al. (2001), in analyses of molecular data from four gene loci, found Nivenioideae to be paraphyletic to Crocoideae (Ixioideae), although the three shrubby Cape genera *Klattia* (3 spp.), *Nivenia* (10 spp.), and *Witsenia* (1 sp.) together formed a well-supported clade. *Klattia, Nivenia,* and *Witsenia* all have septal nectaries (Figs. 3A, F, G, 4D, E). In *Nivenia,* nectar ranges from 1 to 2 μl in volume, has a relatively high sugar concentration, and is sucrose-rich (Goldblatt, 1993). In contrast, nectar volumes in *Klattia* and *Witsenia* are substantial; as much as 77.9 μl of nectar per flower has been recorded in *W. maura* Thunb. and 46.9 μl nectar in *K. stokoei* Guthrie (Goldblatt, 1993). In these genera nectar sugar concentrations are low, 12–15% sucrose equivalents, and nectars are hexose (glucose plus fructose)-dominant. Larger volumes of nectar, low sugar concentrations, and dominance of hexose sugars in these two genera are associated with sunbird pollination compared with anthophorine bee and/or long-proboscid fly pollination in *Nivenia* (Goldblatt, 1993).

Most species of the Afro-Madagascan *Aristea* (ca. 50 spp.; Nivenioideae) do not produce nectar and lack septal nectaries; the presence of perigonal nectaries in *A. spiralis* is apparently an autapomorphy for this species. *Aristea spiralis* is embedded within the derived subgenus *Pseudaristea,* which is characterized by derived large pollen grains with specialized 2-zonasulcate apertures (Goldblatt & LeThomas, 1997). Nectar production in *A. spiralis* appears to be correlated with its pollination by long-proboscid flies, evidently unique in the genus (Johnson, 1992; Goldblatt & Manning, 1997). Of the remaining genera of Nivenioideae, nectaries are absent from the Madagascan saprophyte *Geosiris,* and the salverform flowers of the Australasian *Patersonia,* which have a long perianth tube. In this genus the tube evidently serves to raise the nearly sessile flowers out of the long inflorescence spathes that enclose the flower buds.

Within subfamily Crocoideae (28 genera, currently arranged in three tribes), nectar characteristics are highly variable in volume and concentration, but are typically sucrose-rich to sucrose-dominant. This is associated with the diverse pollination systems found in most genera of the subfamily (Goldblatt et al., 1995, 1998, 2001, in press; Goldblatt & Manning, 2000; Bernhardt & Goldblatt, 2000). The only significant departure from the pattern of high sucrose concentration is in some (but not all) sunbird-pollinated species (Goldblatt et al., 1999, 2001). Discharge of nectar from septal nectaries is highly variable (Smets et al., 2000). Suppression of nectar production in some species of *Ixia* subg. *Ixia* is associated with a shift in pollination strategy from anthophorine bees to hopliine beetles in section *Ixia* (hopliines have no interest in nectar and use flowers largely as sites for assembly, mate selection, and copulation) (Goldblatt et al., 2000a). As far as is known, species of the other section *Dichone* of *Ixia* subg. *Ixia* are buzz pollinated by female anthophorine bees, and pollen is the sole floral reward (Goldblatt et al., 2000a). In subgenus *Ixia,* suppression of nectar secretion is correlated with the narrowing of the diameter of the perianth tube so that its walls tightly surround the style. The tube in these species effectively functions as a stalk (pseudopedicel) for the outspread tepals. The narrowing of the tube so that it clasps the style occurs in species of several other genera, notably in *Romulea* and *Sparaxis*, but usually traces of nectar are still secreted and presented at the mouth of the tube (Goldblatt et al., 2000a, b), and de Vos (1972) has confirmed that septal nectaries are present in *Romulea*. Often, no trace of nectar can be detected in flowers of these species, presumably because the nectar has already been removed by visiting bees. In two species of *Hesperantha*, however, nectar secretion appears to be completely suppressed and pollination is accomplished by deceit, the flowers of these species resembling others that do secrete nectar (Goldblatt et al., in press).

In *Tritoniopsis parviflora*, production of floral oils from glandular epithelium at the base of the free parts of the tepals (Manning & Goldblatt, 2002) is apparently unique among Crocoideae. This species is pollinated over part of its range by the oil-collecting melittid bee, *Rediviva gigas*. Species of *Rediviva* are assumed to use floral oils as part of the food supply for larvae (Steiner & Whitehead, 1988, 1990).

Iridoideae: Diplarrhena. The presence of septal nectaries in *Diplarrhena* argues against its inclusion in the subfamily Iridoideae, which otherwise entirely lack them. Rudall and Goldblatt (2001) erected a new tribe, Diplarrheneae, for this genus but noted that its phylogenetic position remains uncertain. Molecular data did not fully resolve the positions of either *Diplarrhena* or *Patersonia*, since they occupied reversed positions in the *rps*4 topology with respect to the *rbc*L and *trn*L-F trees (Reeves et al., 2001), although in the combined (successively weighted) molecular analysis their positions were strongly supported (BS > 96%) with *Diplarrhena* as sister to Iridoideae, and *Patersonia* sister to the remaining Nivenioideae/Crocoideae.

On the other hand, the presence of septal nectaries in Nivenioideae/Crocoideae plus *Diplarrhena* tends to support the *rps*4 topology (*Diplarrhena* as sister to Nivenioideae/Crocoideae) rather than the combined topology (Fig. 1), although *Diplarrhena* lacks the repeated codon of the *rps*4 gene that is found in the Nivenioid–Crocoid clade (Souza-Chies et al., 1997). *Diplarrhena* shares morphological similarities with some Nivenioideae; for example, pollen of *Diplarrhena* strikingly resembles that of *Patersonia*, both having distinctive inaperturate pollen with a vermiform surface patterning (Rudall & Goldblatt, 2001). Flowers of *Diplarrhena* differ from those of most other Iridoideae, especially in the style branches, which are flat lobes, unlike the tubular style branches (sometimes with apical appendages) and terminal or subterminal stigma lobes typical of Iridoideae.

Conversely, the leaf anatomy of *Diplarrhena* is rather similar to that of *Libertia* (Iridoideae–Sisyrinchieae) (Rudall, 1986, 1994), and the simple rhipidial inflorescences are consistent with those of other Iridoideae. Furthermore, although the subfamily Nivenioideae lacks clear synapomorphies and may well be paraphyletic (Reeves et al., 2001), *Diplarrhena* differs from them in some respects, notably inflorescence morphology, having flowers in simple rhipidia rather than the paired (or binate) rhipidia of all Nivenioideae (Goldblatt, 1990; Manning & Goldblatt, 1991). *Diplarrhena* also differs from Nivenioideae in that the root metaxylem vessels in all Nivenioid genera have only scalariform perforation plates, whereas in most other Iridaceae, including *Diplarrhena*, they are simple (Cheadle, 1963). Clearly, no single character can independently test relationships, and a revised morphological analysis of Iridaceae in the light of new data may help to resolve this conundrum.

Perigonal nectaries within Iridoideae. Among other Iridoideae, there is apparently a preadaptation to production of perigonal secretory structures (character B in Fig. 1), since both perigonal nectaries and elaiophores (oil-producing glands) are widespread in the subfamily but otherwise unusual within Asparagales (although some Orchidaceae have nectariferous tepaline spurs).

The presence of sugary nectar (as opposed to oil) secreted from the filament column is an autapomorphy for *Olsynium*. The "diffuse" nectaries that occur in *Moraea lurida* and *M. ochroleuca* appear to be unique in the family, yet must have arisen independently from each other, since the two species belong in different subgenera (Goldblatt, 1986, 1998b). However, given their topological similarity and close phylogenetic relationship, it seems likely that the elaiophores found in some *Sisyrinchium* species may have evolved from perigonal nectaries.

Daumann's (1935) detailed work on nectaries in many different species of *Iris* (Iridoideae) may help to elucidate nectary evolution in Iridaceae. In some *Iris* species the nectariferous regions extend from around the base of the perianth/stamen tube and around the base of the style, so that the nectary exudes nectar at the same place as it would in an epigynous flower that possessed septal nectaries (e.g., in members of subfamily Crocoideae, or in *Dioscorea*, Dioscoreaceae: Caddick et al., 2000). This raises the intriguing possibility that perigonal nectaries may have evolved from septal nectaries by heterochrony (temporal shifts), or possibly heterotopy (Alberch et al., 1979; Bateman, 1994; Baum & Donoghue, 2002; Rudall & Bateman, 2002), specifically reflecting later formation of nectaries that are expressed in a more distal position on organ primordia. This hypothesis, which requires testing in a molecular-developmental context, is dependent on taxa with perigonal nectaries having evolved from ancestors with septal nectaries (as shown in Fig. 1) rather than from taxa that lacked septal nectaries entirely. It is noteworthy that perigonal nectaries, which are relatively uncommon in monocots, are frequently associated with epigyny (e.g., in Iridaceae and Orchidaceae), although exceptions include some taxa of the order Liliales, in which perigonal nectaries are common and both epigyny and hypogyny occur (Rudall et al., 2000). Van Heel (1988) examined gynoecial and septal nectary development in some hypogynous Asparagales, but there have been very few such developmental studies on epigynous Asparagales, although Payer (1857) illustrated organogenesis in *Gladiolus communis* (Iridaceae) and Mogensen (1969) in *Agave* (Agavaceae). Rudall (2002a) examined floral development in the taxonomically isolated lower asparagoid genus *Xanthorrhoea* (Xanthorrhoeaceae), in which the ovary is hypogynous at anthesis but epigynous at early development stages, and septal nectaries are extensive. These investigations all showed initial free development of organ primordia (two peripheral tepal whorls, two stamen whorls, and finally three free carpels) and subsequent axial elongation of the receptacular/placental region by elongation of their common bases.

Furthermore, it seems unlikely that a *de novo* nectar source should have evolved in Iridaceae at the same time as suppression of septal nectaries, unless there is some developmental relationship between the two structures. Perigonal nectaries appear to be simply an alternative source of nectar for the same insects, including bees of various families, that also pollinate flowers of some Crocoideae, where nectar from septal nectaries is proffered. The absence or paucity of flowers adapted for specialized pollinators in Iridoideae, including long-proboscid flies, sunbirds, moths, and large butterflies, so common in Crocoideae, seems related to the presence of a well-developed perianth tube and widespread floral zygomorphy in Crocoideae and not directly to nectary type. However, the source of nectar is in the ovary, and thus at the base of the perianth tube where nectar is retained and beyond the reach of short-tongued or short-proboscid insects. This factor is obviously significant in the development of the specialized pollination strategies so common within Crocoideae (Bernhardt & Goldblatt, 2000).

It is also predictable that within Asparagales trichome elaiophores were exploited only in a subfamily in which perigonal nectaries were developed (i.e., Iridoideae). Oil collection is a widely exploited syndrome in the Neotropics and adjacent temperate zones to the north and south, and bees of several genera in different families utilize floral oils, hence the disproportionate development of oil secretion in the New and Old Worlds. In contrast to the situation in the New World, in which literally hundreds of Iridaceae secrete floral oils, in the Old World only one species of Iridaceae (*Tritoniopsis parviflora*) is known to do so, and only one genus of bees is adapted to exploit floral oil secretion.

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Statistical Summary of Some of the Activities in the Missouri Botanical Garden Herbarium, 2002

	Vascular	Bryophyte	Total
Acquisition of Specimens			
Staff Collections	36,701	3,355	40,056
Purchase	3,510	0	3,510
Exchange	25,162	1,208	26,370
Gifts	8,405	995	9,400
Total acquisitions	73,778	5,558	79,336
Mountings			
Newly mounted at MO	90,652	19,980	110,632
Specimens mounted when acquired	30,441	0	30,441
Repairs			
Specimens repaired	22,982	n/a	22,982
Specimens stamped	1,622	n/a	1,622
Total repairs	24,604	0	24,604
Specimens Sent			
On exchange	34,185	4,576	38,761
As gifts	13,798	1,622	15,420
Total	47,983	6,198	54,181
Loans Sent			
Total transactions	320	19	339
Total specimens	24,400	1,393	25,793
To U.S. institutions			
Transactions	165	7	172
Specimens	11,971	176	12,147
To foreign institutions			
Transactions	155	12	167
Specimens	12,429	1,217	13,646
To student investigators			
Transactions	37	0	37
Specimens	3,868	0	3,868
To professional investigators			
Transactions	283	19	302
Specimens	20,532	1,393	21,925
Loans Received			
Transactions	252	9	261
Specimens	18,519	624	19,143
	From U.S.A.	From abroad	Total
Visitors	226	106	332

During 2002, 142,695 specimens were accessioned into the herbarium: 110,632 mounted at MO, 30,441 mounted when acquired, and 1622 old MO specimens stamped (and numbered). The total number of mounted, accessioned specimens in the herbarium on 1 January 2003 was 5,361,911 (4,954,890 vascular plants and 407,021 bryophytes).

The 30,441 vascular plants listed as "mounted when acquired" are all from the Reed Herbarium, purchased in 2001, and represent about 20 percent of that acquisition.

The Garden's herbarium is closely associated with its database management system, TROPICOS (see ⟨www.mobot.org/mobot/research⟩). The charts below summarize some of the statistics from TROPICOS both for the calendar year 2002 and as year-end totals. Note that the specimen records in TROPICOS are primarily based on MO specimens, meaning that about thirty-eight percent of the bryophytes (an increase of about one percent over 2001) and thirty-three percent of the vascular plants (an increase of about one percent) in the herbarium are now computerized, with an overall total of about thirty-four percent (an increase of about two percent).

TROPICOS records—Calendar Year 2002 Additions

	Bryophytes	Vascular Plants	Total
Specimens	13,318	111,708	125,026
Names	3,202	17,261	20,463
Synonyms	4,840	14,307	19,147
Distributions	3,822	24,398	28,220
Types	1,311	13,004	14,315
Bibliography	1,782	2,318	4,100

TROPICOS records—Year-End 2002 Totals

	Bryophytes	Vascular Plants	Total
Specimens	156,616	1,659,817	1,816,433
Names	103,633	812,662	916,295
Synonyms	68,255	406,549	474,804
Distributions	42,850	823,163	866,013
Types	8,894	291,621	300,515
Bibliography	25,056	66,972	92,028
Specimens in herbarium	407,021	4,954,890	5,361,911
Percent of specimens computerized	38	33	34

In TROPICOS, literature-based Synonymy is always linked to a reference in Bibliography and directly with at least two records in Names, the synonym, often a basionym, and the correct name according to the reference. Additional synonymy may be derived from these direct links, e.g., all other combinations of a basionym treated as a synonym of a given name are also synonyms of it.

—Marshall R. Crosby

ANNALS OF THE MISSOURI BOTANICAL GARDEN: CHECKLIST FOR AUTHORS

The *Annals* publishes original articles in systematic botany and related fields. Papers whose purpose is the establishment of new nomenclatural entities in vascular plants and bryophytes are not accepted. Rather, they should be submitted to *Novon* for consideration. (*Novon* instructions are available on the Web or from the managing editor.)

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Authors are urged to contact the managing editor prior to submitting manuscripts. Because the electronic file will be used by the printer for typesetting, it is important to adhere to the items listed in the format section of the checklist. Authors' electronic files are formatted by the editors and are sent to the printer in electronic form (not as camera-ready pages). Every electronic file sent by the author should be clearly labeled with the first author's last name, the first four letters of the taxon involved, and an indication of the file's contents (i.e., text, figure, table, etc.).

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1. General

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☐ Electronic file of manuscript is labeled with first author's last name, first four letters of the taxon involved, and an indication of what the file contains, e.g., Celis Cipu text.doc, Celis Cipu Figure1.tif, Celis Cipu Table1.doc, etc.

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☐ Original illustrations, photostats, or their electronic equivalents are included with the original submission, with the understanding that these may have to be revised based on review. [JPEG images are permissible for the review process, if necessary, but are not acceptable for submission to the printer. See the printer's electronic illustration requirements, below.]

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☐ Right-hand margin is not justified, and words are not hyphenated there.

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5. Abstract & Key Words

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