

THE PHYLOGENETIC SIGNIFICANCE OF STOMATA AND TRICHOMES IN THE LABIATAE AND VERBENACEAE

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Epidermal anatomy was surveyed in leaves of 127 genera of Labiatae and 59 of Verbenaceae *sensu lato*, with emphasis on the morphology of the stomatal complexes and the minute sessile glandular trichomes that are found in nearly all members of both families. The phylogenetic significance of the data above the genus level was analyzed, using the subfamilies of Verbenaceae as outgroups to the Labiatae, and the Scrophulariales as outgroup to the Verbenaceae. Many of the characters exhibited such a large amount of intrageneric variation that they have little value as phylogenetic indicators above the species level. In general, the presence/absence of stomatal types varied less within genera than presence/absence of glandular trichome types. Although the phylogenetic significance of these epidermal features must ultimately be evaluated in light of other characters, the derived states in parentheses suggest the existence of clades comprising the following taxa: *Brazoria*, *Macbridea*, and *Physostegia* (absence of anomocytic stomata); all Labiatae except the Prostanthereae and *Amethystea*, *Tetraclea*, *Tinnea*, and *Trichostema* of the Ajugeae (presence of diallelocytic stomata); *Phyla* (presence of two-armed unicellular trichomes; parallelocytic stomata); subfam. Verbenoideae, with the possible exception of four genera (absence of uniseriate "hairs" in nonglabrous species; i.e., only unicellular hairs occur); and all Chloanthoideae except *Nesogenes* (presence of branched, multicellular trichomes). The suite of stomatal types found in tribe Prostanthereae and *Tetraclea* and *Trichostema* of tribe Ajugeae differs markedly from that found in the rest of the Labiatae and resembles that in some Verbenaceae, particularly subfam. Chloanthoideae and tribe Clerodendreae. However, difficulty in assessing polarity of two of the relevant characters makes evaluation of cladistic relationships difficult.

In an earlier paper (Abu-Asab & Cantino, 1987a) the leaf anatomy of subtribe Melittidinae (Labiatae) was surveyed, and an attempt was made to evaluate the phylogenetic significance of anatomical variation in the group. This effort was hindered by a scarcity of published data on the leaf anatomy of other subgroups of the Labiatae. Assessment of character polarities within the ingroup was based on outgroup comparison, but the outgroups comprised a mere scattering of labiate genera for which anatomical data happened to be available. This is not an unusual problem since there are few comprehensive surveys of the leaf anatomy of large families.

The present survey is comprehensive to the extent that all major groups of the Labiatae and nearly all those of the Verbenaceae *sensu lato* have been

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included. However, the effort to maximize the breadth of the survey with regard to genera and suprageneric groups has resulted in a rather scanty sample of intrageneric variation, particularly within subfam. Nepetoideae (Labiatae). Moreover, not all aspects of epidermal anatomy were studied; emphasis was placed on those characters that Abu-Asab and Cantino (1987a) found to be of systematic significance. Despite these limitations, this survey is the only one available for the Labiatae or Verbenaceae as a whole and one of few available for a major angiosperm family. It is hoped that the data provided here will facilitate evaluation of the phylogenetic significance of leaf-epidermal variation within genera of both families.

TAXONOMIC BACKGROUND

It is widely accepted that the Labiatae evolved from the Verbenaceae (i.e., the immediate ancestors of the Labiatae, if alive today, would be assigned to the Verbenaceae). The two families form the core of the order Lamiales of Dahlgren (1980), Cronquist (1981), Thorne (1981), and Takhtajan (1986). The boundary between the Labiatae and the Verbenaceae is unclear. Traditionally, they have been distinguished on the basis of styler position—terminal in the Verbenaceae and gynobasic in the Labiatae. However, in the members of tribes Ajugeae and Prostanthereae of the Labiatae as well as some Verbenaceae, the gynoecium is intermediate in structure, the ovary being shallowly four-lobed and the style neither terminal nor fully gynobasic. Thus the taxonomic limits of the Labiatae are unclear, and there is no discrete character state (let alone a clearly derived one) supporting its monophyly. On the contrary, pollen morphology suggests that the Labiatae may be polyphyletic, with the more primitive genera having arisen from different subgroups of the Verbenaceae (Abu-Asab & Cantino, 1987b). Consequently, if a character survey of the Labiatae is to be useful in phylogenetic inference, it should include representatives of a wide variety of Verbenaceae as well.

The classification of the Verbenaceae used here is that of Moldenke (1971), except that Cronquist's (1981) broader circumscription of the family is adopted. Thus, the segregate taxa Avicennioideae, Chloanthoideae, Nyctanthoideae, Phrymoideae, Stilboideae, and Symphorematoideae, recognized as families by Moldenke, are treated as subfamilies here. This is done for convenience of data tabulation only and is not intended as a judgment on the relative merits of familial versus subfamilial rank for these taxa. For the Labiatae Erdtman's (1945) subfamilial classification (see Cantino & Sanders, 1986) has been adopted. Within subfam. Nepetoideae Benthams (1876) tribes are used (with corrected nomenclature of Sanders & Cantino, 1984), with the exception that those Pogostemoneae with tricolpate pollen are removed to the Lamioideae. Within subfam. Lamioideae five tribes are recognized here: Ajugeae *sensu* Benthams (1876), Prostanthereae *sensu* Benthams (1876), Lamieae *sensu* Abu-Asab and Cantino (1987a), Pogostemoneae (comprising *Colebrookea* Smith, *Comanthosphace* S. Moore, *Eusteralis* Raf., *Leucosceptrum* Smith, *Pogostemon* Desf., and *Rostrinucula* Kudo), and Scutellarieae (comprising *Scutellaria* L., *Salazaria* Torrey, and *Harlanlewisia* Epling). Although it would be simpler to adopt

Bentham's classification in its entirety, modifying it as is done here increases the proportion of the tribes for which there is evidence of monophyly. Nonetheless, certain infrafamilial taxa (designated with quotation marks in the tables) are recognized here in spite of their probable nonmonophyly because they have not yet been sufficiently studied to subdivide them in a way that better reflects phylogeny. Their use facilitates tabulation and summary of the data, but in recognition of their questionable status, their monophyletic component taxa are treated as separate units in the analysis.

MATERIALS AND METHODS

Leaf mounts were prepared from herbarium material by a procedure developed by Jon Hamer, modified from Abu-Asab and Cantino (1987a). Dried leaves were soaked overnight in a weak solution of Alconox soap in water, then transferred to five percent sodium hydroxide for twelve hours to three days, depending on leaf thickness. After being bleached in a 30 percent solution of household bleach (30 minutes to four hours, depending on the material), the leaves were placed in 50 percent ethanol for at least ten minutes, then stained with ferric tannate (2.5 percent tannic acid in 50 percent ethanol, followed by 2.5 percent ferric chloride in 50 percent ethanol; modified from Berlyn & Miksche, 1976) and mounted in surface view. A set of permanent slides is on deposit in the Bartley Herbarium of Ohio University (BHO).

The study set included representatives of 59 genera of the Verbenaceae *sensu lato* and 127 of the Labiatae. Within the latter, 69 genera of subfam. Lamioideae and 58 of subfam. Nepetoideae were included. Six additional genera of the Lamioideae and one of the Nepetoideae were examined by Abu-Asab and Cantino (1987a). When the two data sets are combined (see TABLES 1, 2), the total represents approximately 60 percent of the genera of Verbenaceae *sensu lato*, 73 percent of subfam. Lamioideae, and 36 percent of subfam. Nepetoideae (estimates of the number of genera in the Verbenaceae *sensu lato* and in the subfamilies of the Labiatae are derived from Moldenke (1971) and Cantino & Sanders (1986), respectively). A much higher proportion of the genera of the Verbenaceae and the Lamioideae were sampled than of the Nepetoideae because variation in the former groups may be particularly helpful in understanding the origin and early evolution of the Labiatae. (Subfamily Nepetoideae represents a single large clade that arose from within the paraphyletic or polyphyletic subfam. Lamioideae; see Discussion.) The list of voucher specimens was excluded from this report because of its length, but copies have been deposited in the libraries of the Harvard University Herbaria, the Missouri Botanical Garden, the New York Botanical Garden, and the United States National Herbarium. The vast majority of the specimens from which leaves were obtained are at A, BHO, and GH, but a few are at MO, NY, and US (abbreviations follow Holmgren *et al.*, 1981).

In the examination of the prepared slides, emphasis was placed on two sets of characters that Abu-Asab and Cantino (1987a) found to be of systematic significance in the Labiatae: the morphology of the stomatal complexes and the structure of the minute, sessile glandular trichomes that are character-

TABLE 1. Stomatal characters in Labiatae and Verbenaceae.

Taxa ^a	Stomatal Types ^{b,c}										Stom. Pos. ^d
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4		
Lamiaceae											
"Lamioideae"											
"Ajugeae"											
<i>Acrymia ajugiflora</i> Prain	-	-	-	-	-	-	+	+	*		hypo
<i>Ajuga chamaepitys</i> (L.) Schreber	+	+	-	-	-	-	*	+	-		amph
<i>A. genevensis</i> L.	+	-	-	-	-	-	*	+	-		amph
<i>A. laxmannii</i> Benth.	+	+	-	-	-	-	*	+	-		amph
<i>A. linearifolia</i> Pampan.	+	+	-	-	-	-	*	+	-		amph
<i>A. reptans</i> L. [§]	+	+	-	-	-	-	*	+	-		amph
<i>A. sciaphila</i> W.W.Smith	+	+	-	-	-	-	*	+	-		amph
<i>Amethystea coerulea</i> L. (#1)	*	+	-	r	-	+	+	-	-		hypo
<i>A. coerulea</i> L. (#2)	*	+	-	-	-	+	+	-	-		hypo
<i>Cymaria dichotoma</i> Benth.	+	+	-	-	-	r	*	r	-		hypo
<i>Kinostemon ningpoensis</i> (Hemsley) Kudo	+	+	-	-	-	-	+	*	+		hypo
<i>K. ornatum</i> (Hemsley) Kudo (#1)	+	-	-	-	-	-	*	+	+		hypo
<i>K. ornatum</i> (Hemsley) Kudo (#2)	+	-	-	-	-	-	+	*	+		hypo
<i>K. ornatum</i> (Hemsley) Kudo (#3)	+	+	-	-	-	-	+	*	+		hypo
<i>K. pernyi</i> (Franchet) Kudo	r	-	-	-	-	-	+	*	+		hypo
<i>Rubiteucris palmata</i> (Benth. ex Hook.f.) Kudo	*	+	-	-	-	-	+	+	-		hypo
<i>Schnabelia oligophylla</i> Hand.-Mazz.	*	?	?	?	?	?	+	?	?		hypo
<i>Tetraclea coulteri</i> A.Gray (#1)	*	+	-	+	-	+	-	-	-		amph
<i>T. coulteri</i> A.Gray (#2)	*	+	-	+	-	+	-	-	-		amph
<i>T. coulteri</i> A.Gray (#3)	*	+	-	+	-	+	r	-	-		amph
<i>Teucrium arduinii</i> L.	*	+	-	r	-	r	+	r	-		amph
<i>T. canadense</i> L. [§]	+	-	-	-	-	-	*	+	-		hypo
<i>T. chamaedrys</i> L. [§]	+	-	-	-	-	-	*	+	-		hypo
<i>T. integrifolium</i> F.Muell. ex Benth.	*	-	-	+	-	+	+	r	-		amph
<i>T. laciniatum</i> Torrey	+	+	-	-	-	r	*	+	-		amph
<i>T. marum</i> L.	+	?	?	?	?	?	*	+	?		hypo
<i>T. rotundifolium</i> Schreber	+	-	-	-	-	-	*	+	-		amph
<i>Tinnea aethiopica</i> Kotschy ex Hook.f. (#1)	*	+	-	-	-	r	+	-	-		hypo
<i>T. aethiopica</i> Kotschy ex Hook.f. (#2)	*	+	-	-	-	-	+	-	-		hypo
<i>T. antiscorbutica</i> Welw.	*	+	-	-	-	-	r	-	-		hypo
<i>T. apiculata</i> W.Robyns & Lebrun	*	+	-	-	-	-	+	-	-		hypo
<i>T. galpinii</i> Briq.	*	+	-	-	-	r	+	-	-		hypo
<i>T. rhodesiana</i> S.Moore (#1)	*	+	-	+	-	+	+	-	-		amph
<i>T. rhodesiana</i> S.Moore (#2)	*	+	-	-	-	-	+	-	-		hypo
<i>T. somalensis</i> Gurke ex Chiov.	*	+	-	-	-	-	+	-	-		hypo
<i>Trichostema arizonicum</i> A.Gray (#1)	*	+	-	+	-	+	-	-	-		amph
<i>T. arizonicum</i> A.Gray (#2)	*	-	-	+	-	+	-	-	-		amph
<i>T. brachiatum</i> L.	+	?	?	*	?	?	?	?	?		amph
<i>T. dichotomum</i> L. [§]	+	+	-	*	-	+	-	-	-		amph
<i>T. lanatum</i> Benth.	+	-	-	*	-	+	-	-	-		amph
<i>T. lanceolatum</i> Benth. [§]	*	-	-	+	-	+	+	-	-		amph
<i>T. lanceolatum</i> Benth.	+	?	?	+	?	?	+	?	?		amph
<i>T. setaceum</i> Houtt.	+	-	-	*	-	+	-	-	-		amph
Lamieae											
<i>Achyrosporum parviflorum</i> S.Moore	+	-	-	-	-	-	*	+	r		hypo
<i>A. schimperii</i> Perkins	r	-	-	-	-	-	+	*	r		hypo
<i>A. wallichianum</i> Benth. ex Hook.f.	+	+	-	-	-	-	+	*	+		hypo
<i>Acrotome angustifolia</i> G.Taylor	+	-	-	-	-	-	*	+	-		amph
<i>A. fleckii</i> (Gurke) Launert	+	-	-	-	-	-	*	+	-		amph
<i>A. hispida</i> Benth.	+	r	-	-	-	-	*	+	-		amph
<i>A. inflata</i> Benth.	+	-	-	-	-	-	*	+	+		amph

TABLE 1. (continued).

Taxa ^a	Stomatal Types ^{b,c}										Stom. Pos. ^d
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4		
<i>Ballota frutescens</i> (L.) J.Woods	*	+	-	-	-	-	r	-	-	amph	
<i>B. nigra</i> L. (#1)	+	+	-	-	-	-	*	+	-	hypo	
<i>B. nigra</i> L. (#2)	+	+	-	-	-	-	*	+	-	inte	
<i>B. pseudodictamnus</i> (L.) Benth.	*	+	-	-	-	-	+	+	-	hypo	
<i>Brazoria arenaria</i> Lundell [§]	-	-	-	-	-	-	*	+	-	amph	
<i>B. pulcherrima</i> Lundell [§]	-	-	-	-	-	-	*	+	-	amph	
<i>B. scutellarioides</i> Engelm. & A.Gray [§]	-	-	-	-	-	-	+	+	*	amph	
<i>B. truncata</i> (Benth.) Engelm. & A.Gray [§]	-	-	-	-	-	-	*	+	-	amph	
<i>Chamaesphacos ilicifolius</i> Schrenk	*	+	-	-	-	-	*	+	-	amph	
<i>Chelonopsis forrestii</i> Anthony [§]	*	+	-	-	-	-	+	-	-	hypo	
<i>C. lichiangensis</i> W.Smith	*	?	?	?	?	?	?	?	?	hypo	
<i>C. longipes</i> Makino	*	+	-	-	-	-	+	+	-	hypo	
<i>C. moschata</i> Miq.	+	?	?	?	?	?	+	?	?	hypo	
<i>C. moschata</i> Miq. [§]	*	?	?	?	?	?	+	?	?	hypo	
<i>C. odontochila</i> Diels	*	+	-	-	-	-	-	-	-	hypo	
<i>Colquhounia coccinea</i> Wallich	*	r	-	-	-	-	r	-	-	hypo	
<i>C. seguinii</i> Vaniot	+	+	-	-	-	-	*	+	-	hypo	
<i>Craniotome furcata</i> (Link) Kuntze	+	+	-	-	-	-	*	+	+	hypo	
<i>C. versicolor</i> Reichb. (#1)	+	?	?	?	?	?	+	+	+	hypo	
<i>C. versicolor</i> Reichb. (#2)	+	-	-	-	-	-	+	*	+	hypo	
<i>Eremostachys bachardenica</i> B.Fedtsch.	+	+	-	-	-	-	*	+	-	amph	
<i>E. iliensis</i> Regel	*	+	-	-	-	-	+	-	-	amph	
<i>E. isochila</i> Pazij & Vved.	+	-	-	-	-	-	*	+	-	amph	
<i>E. labiosa</i> Bunge	*	+	-	-	-	-	+	-	-	amph	
<i>E. regeliana</i> Aitch. & Hemsley	*	+	-	-	-	-	*	+	-	amph	
<i>E. speciosa</i> Rupr.	*	-	-	-	-	-	+	-	-	amph	
<i>E. tuberosa</i> (Pallas) Bunge	*	+	-	-	-	+	+	-	-	amph	
<i>Eriophyton wallichianum</i> Benth.	*	+	-	-	-	-	r	-	-	amph	
<i>Galeobdolon luteum</i> Hudson [§]	+	-	-	-	-	-	+	*	+	hypo	
<i>Galeopsis ladanum</i> L.	*	+	-	-	-	-	-	-	-	amph	
<i>G. ochroleuca</i> Lam.	*	-	-	r	-	-	+	-	-	amph	
<i>G. pubescens</i> Besser	*	+	-	-	-	-	+	-	-	hypo	
<i>G. tetrahit</i> L.	*	+	-	-	-	-	+	-	-	hypo	
<i>Gomphostemma chinense</i> Oliver	+	+	?	?	?	?	+	+	?	hypo	
<i>G. crinitum</i> Wallich	+	?	?	?	?	?	*	+	?	hypo	
<i>G. lucidum</i> Wallich	+	-	-	-	-	-	*	*	+	hypo	
<i>G. velutinum</i> Benth.	+	-	-	-	-	-	*	+	-	hypo	
<i>Lagochilus cabulicus</i> Benth.	*	-	-	-	-	-	*	+	-	amph	
<i>L. ilicifolius</i> Bunge	+	-	-	-	-	-	*	+	r	amph	
<i>L. platycalyx</i> Fischer & C.Meyer (#1)	+	+	-	-	-	-	*	+	-	amph	
<i>L. platycalyx</i> Fischer & C.Meyer (#2)	*	-	-	-	-	-	*	+	-	amph	
<i>Lagopsis supina</i> (Stephan) Ikonn.-Gal.	*	+	-	-	-	-	+	-	-	amph	
<i>Lamiophlomis rotata</i> (Benth.) Kudo	*	+	-	-	-	-	*	+	-	amph	
<i>Lamium album</i> L.	+	+	-	-	-	-	*	+	-	inte	
<i>L. maculatum</i> L. (#1)	+	+	-	-	-	-	*	+	-	hypo	
<i>L. maculatum</i> L. (#2)	+	-	-	-	-	-	+	*	+	hypo	
<i>L. moschatum</i> Miller	+	+	-	-	-	-	*	+	-	amph	
<i>L. pictum</i> Boiss. & Heldr.	+	+	-	-	-	-	*	+	-	amph	
<i>L. purpureum</i> L. [§]	+	+	-	-	-	-	*	+	-	amph	

TABLE 1. (continued).

Taxa ^a	Stomatal Types ^{b,c}										Stom. Pos. ^d
	ANO	ACT	CYC	ANI	HEL	PAR	D12	D13	D14		
<i>Leonotis latifolia</i> Gurke	*	+	-	-	-	-	+	-	-	inte	
<i>L. leonitis</i> R.Br.	+	+	-	-	-	-	*	r	-	amph	
<i>L. leonurus</i> (L.) R.Br. (#1)	+	?	?	?	?	+	+	?	?	amph	
<i>L. leonurus</i> (L.) R.Br. (#2)	*	+	-	-	-	-	+	-	-	inte	
<i>L. nepetaefolia</i> (L.) R.Br.	+	+	-	-	-	-	*	+	-	amph	
<i>Leonurus cardiaca</i> L. [§]	*	+	-	-	-	-	+	-	-	hypo	
<i>L. heterophyllus</i> Sweet	*	+	-	-	-	-	+	-	-	inte	
<i>L. macranthus</i> Maxim.	*	+	-	-	-	-	+	-	-	hypo	
<i>Leucas altissima</i> Engl.	+	?	?	?	?	?	*	?	?	amph	
<i>L. capensis</i> (Benth.) Engl.	*	+	-	-	-	-	+	+	-	amph	
<i>L. ciliata</i> Benth.	+	+	-	-	-	-	*	+	-	hypo	
<i>L. decemdentata</i> R.Br.	*	+	-	-	-	-	+	+	-	hypo	
<i>L. mildbraedii</i> Perkins	*	+	-	-	-	-	+	-	-	hypo	
<i>L. mollissima</i> Wallich	+	+	-	-	-	-	*	+	-	inte	
<i>Loxocalyx urticifolius</i> Hemsley	+	+	-	-	-	-	*	r	-	hypo	
<i>Macbridea alba</i> Chapman [§]	-	-	-	-	-	-	+	+	*	amph	
<i>M. caroliniana</i> (Walter) Blake [§]	-	-	-	-	-	-	+	*	+	amph	
<i>Marrubium desertii</i> Noë ex Cosson	*	+	-	-	-	-	+	+	-	amph	
<i>M. peregrinum</i> L.	*	+	-	-	-	-	+	-	-	amph	
<i>M. vulgare</i> L.	*	+	-	-	-	-	+	+	-	amph	
<i>M. vulgare</i> L. [§]	*	r	-	-	-	-	+	-	-	amph	
<i>Melittis melissophyllum</i> L. [§]	+	+	-	-	-	r	*	+	-	hypo	
<i>Metastachyidium sagittatum</i> (Regel) C.Y.Wu & Li	*	+	-	-	-	-	+	-	-	amph	
<i>Microtoena insuavis</i> (Hance) Prain ex Briq. (#1)	+	-	-	-	-	-	*	+	-	hypo	
<i>M. insuavis</i> (Hance) Prain ex Briq. (#2)	+	-	-	-	-	-	*	+	-	hypo	
<i>M. moupinensis</i> Franchet ex Prain	*	+	?	?	?	?	+	?	?	hypo	
<i>M. robusta</i> Hemsley	*	+	-	-	-	-	+	-	-	hypo	
<i>M. urticifolia</i> Hemsley	*	-	-	-	-	-	+	-	-	hypo	
<i>Moluccella laevis</i> L.	+	-	-	-	-	-	*	+	-	amph	
<i>M. spinosa</i> L.	+	-	-	-	-	-	*	+	r	amph	
<i>Notochaete hamosa</i> Benth.	*	+	-	-	-	-	+	+	-	hypo	
<i>Otostegia aucheri</i> Boiss.	+	-	-	-	-	-	*	-	-	amph	
<i>O. integrifolia</i> Benth.	*	?	?	?	?	?	+	?	?	inte	
<i>O. limbata</i> (Benth.) Benth. ex Hook.f.	+	+	-	-	-	-	*	+	-	amph	
<i>O. persica</i> (Burm.f.) Boiss.	*	+	-	-	-	-	+	-	-	amph	
<i>Panzeria argyrea</i> Kuprian.	*	+	?	?	?	?	?	?	?	inte	
<i>Paraphlomis javanica</i> (Blume) Prain ex Backer & Bakh.f.	r	-	-	-	-	-	*	*	r	hypo	
<i>P. rugosa</i> (Benth.) Prain	+	+	-	-	-	-	*	+	-	hypo	
<i>Phlomidioschema parviflorum</i> (Benth.) Vved.	+	-	-	-	-	r	*	+	-	amph	
<i>Phlomis agraria</i> Bunge	*	+	-	-	-	-	+	-	-	amph	
<i>P. bracteosa</i> Royle	*	+	-	-	-	-	+	+	-	amph	
<i>P. herba-venti</i> L.	+	+	-	-	-	-	*	+	-	hypo	
<i>P. maximoviczii</i> Regel	+	+	-	-	-	-	*	+	-	hypo	
<i>P. pratensis</i> Karelín & Kir.	*	+	-	-	-	-	+	-	-	amph	
<i>P. setigera</i> Falc. ex Benth.	*	r	-	-	-	-	+	r	-	inte	
<i>P. taurica</i> Hartw. ex Bunge	+	-	-	-	-	-	*	+	-	amph	
<i>P. tuberosa</i> L.	*	+	-	-	-	-	+	-	-	hypo	
<i>P. umbrosa</i> Turcz.	*	+	-	-	-	-	*	+	-	hypo	

TABLE 1. (continued).

Taxa ^a	Stomatal Types ^{b,c}										Stom. Pos. ^d
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4		
<i>Phyllostegia brevidens</i> A.Gray	+	+	-	-	-	-	*	+	-	hypo	
<i>P. grandiflora</i> (Gaudich.) Benth. (#1)	r	-	-	-	-	-	*	+	+	hypo	
<i>P. grandiflora</i> (Gaudich.) Benth. (#2)	+	-	-	-	-	-	*	*	+	hypo	
<i>P. hispida</i> Hillebrand	+	+	-	-	-	-	*	+	-	hypo	
<i>Physostegia angustifolia</i> Fern. [§]	-	-	-	-	-	-	+	*	+	amph	
<i>P. digitalis</i> Small [§]	-	-	-	-	-	-	-	*	+	amph	
<i>P. godfreyi</i> Cantino [§]	-	-	-	-	-	-	+	*	-	amph	
<i>P. leptophylla</i> Small [§]	-	-	-	-	-	-	+	*	+	amph	
<i>P. longisepala</i> Cantino [§]	-	-	-	-	-	-	-	+	*	amph	
<i>P. purpurea</i> (Walter) Blake [§]	-	-	-	-	-	-	+	*	+	amph	
<i>P. virginiana</i> (L.) Benth. [§]	-	-	-	-	-	-	+	*	+	amph	
<i>Prasium majus</i> L. (#1)	*	+	-	-	-	+	*	+	-	hypo	
<i>P. majus</i> L. (#2)	*	+	-	-	-	-	+	+	-	hypo	
<i>Roylea calycina</i> (Roxb.) Briq.	*	+	-	-	-	-	+	-	-	hypo	
<i>Sideritis ambigua</i> Fenzl	+	-	-	-	-	+	*	+	-	amph	
<i>S. hirsuta</i> L.	+	-	-	-	-	-	*	+	-	amph	
<i>S. ilicifolia</i> Willd.	+	-	-	-	-	-	*	+	-	amph	
<i>S. lagascana</i> Willk.	+	-	-	-	-	-	*	+	-	amph	
<i>S. lanata</i> L.	+	+	-	-	-	-	*	+	-	amph	
<i>S. montana</i> L.	+	-	-	-	-	-	*	+	-	amph	
<i>S. perfoliata</i> L.	+	-	-	-	-	-	*	+	-	amph	
<i>S. pullulans</i> Vent.	+	r	-	-	-	-	*	r	-	amph	
<i>Stachyopsis oblongata</i> (Schrenk) Popov & Vved.	*	+	-	-	-	-	+	-	-	inte	
<i>Stachys acerosa</i> Boiss.	+	-	-	-	-	-	*	+	-	amph	
<i>S. annua</i> (L.) L.	+	-	-	-	-	-	*	+	-	amph	
<i>S. betonica</i> Benth.	+	-	-	-	-	-	*	+	-	amph	
<i>S. betonicaeflora</i> Rupr.	+	-	-	-	-	-	*	+	-	amph	
<i>S. coccinea</i> Jacq.	+	-	-	-	-	-	*	+	-	amph	
<i>S. glutinosa</i> L.	+	-	-	-	-	r	*	+	-	amph	
<i>S. labiosa</i> Bertol.	+	-	-	-	-	-	*	+	-	amph	
<i>S. riddellii</i> House [§]	+	-	-	-	-	-	*	+	-	hypo	
<i>S. spathulata</i> Burchell ex Benth.	+	?	?	?	?	?	+	?	?	amph	
<i>S. spruneri</i> Boiss. ex Benth.	+	-	-	-	-	-	*	+	-	amph	
<i>S. tenuifolia</i> Willd. [§]	+	-	-	-	-	-	*	+	-	hypo	
<i>Stenogyne diffusa</i> A.Gray (#1)	+	-	-	-	-	-	*	*	+	hypo	
<i>S. diffusa</i> A.Gray (#2)	*	+	-	-	-	-	*	+	-	hypo	
<i>S. kamehamehae</i> Wawra	+	-	-	-	-	-	*	*	-	hypo	
<i>S. purpurea</i> H.Mann	+	-	-	-	-	-	+	*	+	hypo	
<i>S. rugosa</i> Benth.	+	+	-	-	-	-	*	+	-	hypo	
<i>Synandra hispidula</i> (Michx.) Baillon [§]	+	-	-	-	-	-	*	+	r	amph	
<i>Thuspeinanta brahuica</i> (Boiss.) Briq.	+	?	?	?	?	?	+	+	?	amph	
<i>T. persica</i> (Boiss.) Briq.	+	r	-	-	-	r	*	r	-	amph	
<i>Wiedemannia multifida</i> (L.) Benth.	r	r	-	-	-	-	*	+	-	amph	
Pogostemoneae											
<i>Colebrookea oppositifolia</i> Smith (#1)	*	?	?	?	?	?	+	?	?	hypo	
<i>C. oppositifolia</i> Smith (#2)	+	?	?	?	?	?	+	?	?	hypo	
<i>Comanthosphace stellipila</i> S.Moore	+	+	-	-	-	-	*	+	-	hypo	
<i>C. sublaceolata</i> (Miq.) S.Moore (#1)	+	+	-	-	-	-	*	+	-	hypo	
<i>C. sublaceolata</i> (Miq.) S.Moore (#2)	+	+	-	-	-	-	*	+	-	hypo	
<i>Eusteralis cruciata</i> (Benth.) Panigr.	r	-	-	-	-	-	+	*	-	hypo	
<i>E. sampsonii</i> (Hance) Panigr.	+	-	-	-	-	-	*	+	-	amph	
<i>E. stellata</i> (Lour.) Panigr. (#1)	-	-	-	-	-	-	+	*	+	amph	
<i>E. stellata</i> (Lour.) Panigr. (#2)	-	-	-	-	-	-	+	*	+	amph	

TABLE 1. (continued).

Taxa ^a	Stomatal Types ^{b,c}										Stom. Pos. ^d
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4		
<i>Pogostemon cablin</i> (Blanco) Benth.	r	-	-	-	-	-	+	*	+	inte	
<i>P. elsholtzioides</i> Benth.	r	-	-	-	-	-	*	+	-	hypo	
<i>P. glaber</i> Benth. (#1)	+	-	-	-	-	-	+	*	r	hypo	
<i>P. glaber</i> Benth. (#2)	+	-	-	-	-	-	+	*	+	inte	
<i>P. heyneanus</i> Benth. [§]	-	-	-	-	-	-	+	*	+	hypo	
<i>P. plectranthoides</i> Desf.	+	-	-	-	-	-	+	*	+	hypo	
<i>Rostrinucula dependens</i> (Rehder) Kudo	+	-	-	-	-	-	*	+	-	hypo	
Prostanthereae											
<i>Hemiandra pungens</i> R.Br.	r	-	-	*	-	r	-	-	-	amph	
<i>Hemigenia incana</i> Benth. (#1)	+	-	-	*	-	r	-	-	-	amph	
<i>H. purpurea</i> R.Br.	*	-	-	*	-	-	-	-	-	amph	
<i>H. saligna</i> Diels	+	-	-	*	-	-	-	-	-	amph	
<i>Microcorys brevidens</i> Benth.	*	-	-	+	-	+	-	-	-	amph	
<i>M. ericifolia</i> Benth.	*	-	-	+	-	-	-	-	-	amph	
<i>Prostanthera aspalathoides</i> Cunn. ex Benth.	*	-	-	*	-	+	-	-	-	amph	
<i>P. cuneata</i> Benth.	+	-	-	*	+	+	-	-	-	inte	
<i>P. euphrasioides</i> Benth.	+	-	-	*	+	-	-	-	-	amph	
<i>P. lasianthos</i> Labill. (#1)	*	-	-	*	r	+	r	-	-	hypo	
<i>P. lasianthos</i> Labill. (#2)	+	-	-	*	+	r	r	-	-	hypo	
<i>P. nivea</i> Cunn. ex Benth. (#1)	+	-	-	*	+	+	-	-	-	amph	
<i>P. nivea</i> Cunn. ex Benth. (#2)	*	-	-	*	+	+	-	-	-	amph	
<i>P. ovalifolia</i> R.Br.	*	+	-	+	-	+	-	-	-	hypo	
<i>P. rotundifolia</i> R.Br. [§]	*	+	-	+	-	r	+	-	-	amph	
<i>P. rotundifolia</i> R.Br.	*	+	-	*	-	+	-	-	-	inte	
<i>P. saxicola</i> R.Br.	+	+	-	*	+	+	-	-	-	amph	
Westringia											
<i>W. amabilis</i> J.Boivin	*	r	-	+	r	-	-	-	-	hypo	
<i>W. brevifolia</i> Benth.	*	*	-	r	-	-	-	-	-	hypo	
<i>W. cheelii</i> Maiden & Betche	*	+	-	-	-	-	-	-	-	amph	
<i>W. fruticosa</i> (Willd.) Druce	*	+	-	r	-	+	-	-	-	hypo	
Scutellarieae											
<i>Salazaria mexicana</i> Torrey (#1)	*	+	-	-	-	-	*	+	-	amph	
<i>S. mexicana</i> Torrey (#2)	+	+	-	-	-	-	*	+	-	amph	
<i>Scutellaria amoena</i> C.H.Wright	+	-	-	-	-	-	*	+	+	amph	
<i>S. elliptica</i> Muhlenb. [§]	+	-	-	-	-	-	+	*	+	hypo	
<i>S. gardoquioides</i> Benth.	*	-	-	-	-	-	+	-	-	hypo	
<i>S. hirtella</i> Juz.	?	?	?	?	?	?	*	+	?	inte	
<i>S. incana</i> Biehler [§]	+	+	-	-	-	-	*	+	r	hypo	
<i>S. integrifolia</i> L. [§]	+	-	-	-	-	-	*	*	r	inte	
<i>S. lateriflora</i> L. [§]	+	+	-	-	-	-	*	+	-	hypo	
<i>S. multicaulis</i> Boiss.	+	+	-	-	-	-	*	+	-	amph	
<i>S. nervosa</i> Pursh [§]	+	-	-	-	-	-	*	+	-	hypo	
<i>S. orientalis</i> L.	+	-	-	-	-	-	*	+	-	inte	
<i>S. ovata</i> Hill [§]	+	-	-	-	-	-	*	*	+	hypo	
<i>S. serrata</i> Andr. [§]	+	-	-	-	-	-	*	+	-	hypo	
Uncertain Tribal Affin.											
<i>Ajugoides humilis</i> (Miq.) Makino (#1)	+	+	-	-	-	-	*	+	-	hypo	
<i>A. humilis</i> (Miq.) Makino (#2)	*	+	-	-	-	-	*	+	-	hypo	
<i>Anisomeles heyneana</i> Benth.	+	-	-	-	-	-	*	+	-	hypo	
<i>A. indica</i> (L.) Kuntze (#1)	+	?	?	?	?	?	*	+	?	amph	
<i>A. indica</i> (L.) Kuntze (#2)	+	?	?	?	?	?	*	+	?	amph	
<i>A. malabarica</i> (L.) R.Br. ex Sims (#1)	+	-	-	-	-	-	*	+	-	hypo	
<i>Eurysolen gracilis</i> Prain (#1)	+	-	-	-	-	-	*	+	+	hypo	
<i>E. gracilis</i> Prain (#2)	+	+	-	-	-	-	*	+	-	hypo	
<i>Hypogomphia turkestanica</i> Bunge	+	-	-	-	-	-	*	+	-	amph	
<i>Suzukia shikikunensis</i> Kudo	+	+	-	-	-	-	*	+	-	hypo	

TABLE 1. (continued).

Taxa ^a	Stomatal Types ^{b,c}									Stom. Pos. ^d
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	
Nepetoideae										
"Mentheae"										
<i>Ceratomyinthe odora</i> (Griseb.) Hauman	+	+	-	-	-	-	*	-	-	hypo
<i>Collinsonia canadensis</i> L. (#1)	+	+	-	-	-	-	*	+	-	hypo
<i>C. canadensis</i> L. (#2)	+	+	-	-	-	-	*	+	-	hypo
<i>Cunila origanoides</i> (L.) Britt.	+	-	-	-	-	-	*	+	-	inte
<i>Cyclotrichium organifolium</i> (Labill.) Manden. & Scheng.	+	-	-	-	-	-	*	+	-	amph
<i>Elsholtzia patrinii</i> (Lepechin) Garcke	+	+	-	-	-	-	*	+	-	inte
<i>Hedeoma drummondii</i> Benth.	-	-	-	-	-	-	+	*	+	amph
<i>H. graveolens</i> Chapman ex A.Gray	+	-	-	-	-	-	*	+	-	amph
<i>H. nanum</i> (Torrey) Briq.	+	-	-	-	-	-	*	+	-	amph
<i>Keiskea japonica</i> Miq.	+	-	-	-	-	-	*	+	-	hypo
<i>Lepechinia hastata</i> (A.Gray) Epling	+	-	-	-	-	-	*	+	-	amph
<i>Lycopus americanus</i> Muhlenb.	+	-	-	-	-	-	*	+	-	inte
<i>L. rubellus</i> Moench	+	+	-	-	-	-	*	+	-	amph
<i>L. virginicus</i> L.	r	-	-	-	-	-	+	*	+	hypo
<i>Melissa officinalis</i> L. (#1)	+	-	-	-	-	-	*	+	-	hypo
<i>M. officinalis</i> L. (#2)	+	+	-	-	-	-	*	+	-	hypo
<i>Mentha arvensis</i> L.	r	-	-	-	-	-	*	*	-	hypo
<i>M. citrata</i> Ehrh.	r	-	-	-	-	-	*	+	+	hypo
<i>M. piperita</i> L.	r	-	-	-	-	-	*	+	-	hypo
<i>Micromeria biflora</i> Benth.	+	-	-	-	-	-	*	+	-	hypo
<i>M. punctata</i> Benth.	+	-	-	-	-	-	*	+	-	hypo
<i>Monardella odoratissima</i> Benth.	+	-	-	-	-	-	*	*	-	amph
<i>M. villosa</i> Benth.	+	-	-	-	-	-	*	+	r	amph
<i>Perillula reptans</i> Maxim. (#1)	+	-	-	-	-	-	+	*	r	hypo
<i>P. reptans</i> Maxim. (#2)	+	+	-	-	-	-	*	+	r	hypo
<i>Pogogyne zizyphoroides</i> Benth.	+	-	-	-	-	-	+	*	-	amph
<i>Poliomintha glabrescens</i> A.Gray ex Hemsl.	+	-	-	-	-	-	*	+	r	amph
<i>Pycnanthemum albescent</i> A.Gray	+	?	?	?	?	?	+	+	+	hypo
<i>P. floridanum</i> E. Grant & Epling	-	-	-	-	-	-	+	*	-	hypo
<i>P. aff. incanum</i> (L.) Michaux	+	-	-	-	-	-	+	*	-	hypo
<i>Rhabdocalyon strictum</i> (Benth.) Epling	-	-	-	-	-	-	+	*	-	hypo
<i>Rhododon ciliatus</i> (Benth.) Epling	r	-	-	-	-	-	*	+	-	amph
<i>Satureja arkansana</i> (Nutt.) Briq.	+	-	-	-	-	-	*	+	-	amph
<i>S. douglasii</i> (Benth.) Briq.	+	-	-	-	-	-	*	+	-	hypo
<i>S. parvifolia</i> (Philippi) Epling	+	+	-	-	-	-	*	+	-	hypo
<i>S. popovii</i> B.Fedtsch. & Gontch.	r	-	-	-	-	-	*	+	-	amph
<i>S. vulgaris</i> (L.) Fritsch	+	-	-	-	-	-	*	+	r	hypo
<i>Thymus serpyllum</i> L.	+	-	-	-	-	-	*	+	-	inte
Nepeteae										
<i>Agastache breviflora</i> (A.Gray) Epling	-	-	-	-	-	-	+	*	+	amph
<i>A. cana</i> (Hook.) Wooton & Standley	+	r	-	-	-	+	*	+	-	amph
<i>A. nepetoides</i> (L.) Kuntze	+	-	-	-	-	r	*	+	r	hypo
<i>A. pallidiflora</i> (A.A.Heller) Rydb.	+	-	-	-	-	-	*	+	-	amph
<i>A. scrophulariaefolia</i> (Willd.) Kuntze	+	+	-	-	-	-	*	*	+	hypo

TABLE 1. (continued).

Taxa ^a	Stomatal Types ^{b,c}										Stom. Pos. ^d
	ANO	ACT	CYC	ANI	HEL	PAR	D12	D13	D14		
<u>Cedronella canariensis</u> (L.) Webb & Berth. (#1)	+	+	-	-	-	-	*	+	-	hypo	
<u>C. canariensis</u> (L.) Webb & Berth. (#2)	+	+	-	-	-	-	*	+	r	hypo	
<u>Dracocephalum hemsleyanum</u> (Prain) Marquand	+	?	?	?	?	?	+	?	?	inte	
<u>D. heterophyllum</u> Benth.	r	r	-	-	-	-	*	+	+	amph	
<u>D. parviflorum</u> Nutt.	+	-	-	-	-	-	*	+	-	amph	
<u>D. ruyschiana</u> L.	+	+	-	-	-	+	*	+	-	inte	
<u>Glechoma hederacea</u> L.	+	-	-	-	-	-	*	*	+	hypo	
<u>Lophanthus chinensis</u> Benth.	+	-	-	-	-	-	*	+	-	amph	
<u>Meehania cordata</u> (Nutt.) Britton	-	-	-	-	-	-	+	*	r	hypo	
<u>Nepeta cataria</u> L.	+	-	-	-	-	-	*	+	-	amph	
<u>N. clarkei</u> Hook.f.	+	-	-	-	-	-	*	+	-	amph	
<u>N. curviflora</u> Boiss.	+	?	?	?	?	?	*	?	?	amph	
<u>N. discolor</u> Royle ex Benth.	+	-	-	-	-	-	*	+	-	amph	
<u>N. nepetella</u> L.	+	-	-	-	-	-	*	+	-	amph	
<u>Prunella vulgaris</u> L.	-	-	-	-	-	-	r	*	+	inte	
Ocimeae											
<u>Acrocephalus fruticosus</u> Dunn	+	-	-	-	-	-	*	+	-	amph	
<u>A. indicus</u> Kuntze	+	-	-	-	-	-	*	+	-	inte	
<u>Asterohyptis stellulata</u> (Benth.) Epling	+	+	-	-	-	-	*	+	-	inte	
<u>Catopheria capitata</u> Benth. ex Hemsley (#1)	r	-	-	-	-	-	*	+	r	hypo	
<u>C. capitata</u> Benth. ex Hemsley (#2)	?	?	?	?	?	?	+	*	?	hypo	
<u>Eriope crassipes</u> Benth.	+	-	-	-	-	-	*	+	-	amph	
<u>Eriopidion strictum</u> (Benth.) R.Harley	r	-	-	-	-	-	*	+	-	amph	
<u>Fuerstia africana</u> T.C.E.Fries	+	?	?	?	?	?	+	?	?	hypo	
<u>Haumaniastrum coeruleum</u> (Oliver) Duvign. & Plancke	-	-	-	-	-	-	+	*	+	amph	
<u>Hemizygia canescens</u> (Gurke) Ashby	-	-	-	-	-	-	+	*	+	amph	
<u>Holostylon strictipes</u> G.Taylor	+	-	-	-	-	-	*	+	-	amph	
<u>Hyptis alata</u> (Raf.) Shinn.	+	-	-	-	-	-	*	r	-	amph	
<u>H. emoryi</u> Torrey	*	-	-	-	-	-	+	+	-	amph	
<u>H. mutabilis</u> (Rich.) Briq.	+	-	-	-	-	-	*	+	-	inte	
<u>H. oblongifolia</u> Benth.	+	-	-	-	-	-	*	+	-	hypo	
<u>Icomum lineare</u> Burkill	-	-	-	-	-	-	*	+	-	amph	
<u>Lavandula multifida</u> L.	* ^e	-	-	-	-	-	+	+	-	amph	
<u>L. stoechas</u> L.	+	-	-	-	-	-	*	+	-	amph	
<u>Nautochilus labiatus</u> (N.E.Br.) Bremek.	+	+	-	-	-	-	*	+	-	hypo	
<u>Ocimum americanum</u> L.	+	-	-	-	-	-	*	+	-	amph	
<u>O. basilicum</u> L.	+	-	-	-	-	-	*	+	-	amph	
<u>O. gratissimum</u> L. (#1)	+	-	-	-	-	-	*	+	-	inte	
<u>O. gratissimum</u> L. (#2)	+	-	-	-	-	-	*	*	+	inte	
<u>Orthosiphon affinis</u> N.E.Br.	+	-	-	-	-	-	*	+	-	amph	
<u>O. aristatus</u> (Blume) Miq.	+	-	-	-	-	-	+	*	+	hypo	
<u>O. spiralis</u> (Lour.) Merr.	+	-	-	-	-	-	*	+	-	inte	
<u>Plectranthastrum clerodendroides</u> T.C.E Fries	-	-	-	-	-	-	+	*	+	hypo	

TABLE 1. (continued).

Taxa ^a	Stomatal Types ^{b,c}										Stom. Pos. ^d
	ANO	ACT	CYC	ANI	HEL	PAR	D12	D13	D14		
<i>Plectranthus forsteri</i> Benth.	r	-	-	-	-	-	*	*	r		amph
<i>P. scutellarioides</i> (L.) R.Br.	+	-	-	-	-	-	*	+	-		hypo
<i>Rabdosia excisa</i> (Maxim.) H.Hara	+	+	-	-	-	-	*	r	-		hypo
<i>R. inflexa</i> (Thunb.) H.Hara	*	+	-	-	-	-	*	+	-		hypo
<i>R. nervosa</i> (Hemsley) C.Y.Wu & Li	*	+	-	-	-	-	*	+	-		inte
<i>Solenostemon scutellarioides</i> L.Codd (#1)	+	-	-	-	-	-	*	*	-		amph
<i>Syncolostemon densiflorus</i> Benth.	+	-	-	-	-	-	*	+	-		amph
"Salviaeae"											
<i>Arischrada bucharica</i> (Popov) Pobed.	r	-	-	-	-	-	+	*	+		amph
<i>Blephilia hirsuta</i> (Pursh) Benth. ⁵	+	r	-	-	-	-	*	+	-		hypo
<i>Monarda clinopodia</i> L.	+	-	-	-	-	-	*	+	-		hypo
<i>M. fistulosa</i> L. ⁵	?	?	?	?	?	?	?	*	?		hypo
<i>M. punctata</i> L.	+	-	-	-	-	-	*	+	-		amph
<i>Perovskia abrotanoides</i> Karelin	+	+	-	-	-	-	*	+	-		amph
<i>P. atriplicifolia</i> Benth.	+	+	-	-	-	-	*	+	-		amph
<i>Salvia carnososa</i> Douglas	+	?	?	?	?	?	+	?	?		amph
<i>S. farinacea</i> Benth.	+	-	-	-	-	-	*	+	-		amph
<i>S. lyrata</i> L.	-	-	-	-	-	-	*	*	r		amph
<i>S. reflexa</i> Hornem.	+	-	-	-	-	-	*	*	-		amph
Verbenaceae											
Avicenniioideae											
<i>Avicennia nitida</i> Jacq.	+	-	-	-	-	-	*	-	-		hypo
Caryopteridoideae											
Caryopterideae											
<i>Caryopteris grata</i> Benth.	*	+	-	-	-	-	+	-	-		hypo
<i>C. incana</i> (Thunb.) Miq. (#1)	+	+	?	?	?	?	?	?	?		hypo
<i>C. mongholica</i> Bunge (#1)	*	+	-	+	-	-	-	-	-		amph
<i>C. mongholica</i> Bunge (#2)	*	+	-	+	-	-	-	-	-		amph
<i>C. nepetaefolia</i> (Benth.) Maxim.	*	+	-	-	-	r	+	-	-		hypo
<i>C. odorata</i> (Ham.) Robinson	+	+	-	-	-	-	*	+	-		hypo
<i>C. terniflora</i> Maxim.	+	r	-	-	-	-	*	+	-		hypo
<i>Glossocarya siamensis</i> Craib	*	+	-	+	-	-	-	-	-		hypo
<i>Petraeovitex kinabaluensis</i> Munir	+	-	-	-	-	+	*	+	-		hypo
<i>P. multiflora</i> (Smith) Merr.	*	+	-	-	-	+	+	-	-		hypo
Teijsmanniodendreae											
<i>Teijsmanniodendron ahernianum</i> (Merr.) Bakh.	*	+	-	-	-	-	-	-	-		hypo
<i>T. subspicatum</i> (H.Hallier) Kosterm.	*	+	-	-	-	+	r	-	-		hypo
Chloanthoideae											
Achariteae											
<i>Nesogenes dupontii</i> Hemsley	*	-	-	-	-	-	r	-	-		amph
<i>N. euphrasioides</i> (Hook. & Arn.) A.DC.	*	-	-	-	-	-	-	-	-		amph
<i>Spartothamnella puberula</i> (F.Muell.) Maiden & Bette (#1)	*	-	-	+	-	+	-	-	-		hypo
<i>S. puberula</i> (F.Muell.) Maiden & Bette (#2)	*	+	-	+	-	+	r	-	-		hypo
<i>S. puberula</i> (F.Muell.) Maiden & Bette (#3)	*	+	-	+	-	-	-	-	-		inte
Chloantheae											
<i>Chloanthes stoechadis</i> R.Br.	+	-	-	*	-	-	-	-	-		hypo
<i>Cyanostegia angustifolia</i> Turcz.	*	-	-	+	-	+	-	-	-		amph
<i>C. microphylla</i> S.Moore	+	-	-	*	+	-	-	-	-		amph

TABLE 1. (continued).

Taxa ^a	Stomatal Types ^{b,c}										Stom. Pos. ^d
	ANO	ACT	CYC	ANI	HEL	PAR	D12	D13	D14		
Physopsidaeae											
<u>Dicrastylis</u> <u>exsuccosa</u> (F.Muell.) Druce	*	-	-	+	-	-	-	-	-	-	amph
<u>Newcastelia</u> <u>cephalantha</u> F.Muell.	r	-	-	*	+	-	-	-	-	-	amph
Nyctanthoideae											
<u>Nyctanthes</u> <u>arbor-tristis</u> L.	*	+	-	-	-	-	-	-	-	-	hypo
Phrymoideae											
<u>Phryma</u> <u>leptostachya</u> L.	*	+	-	r	-	-	r	-	-	-	hypo
Symphorematoideae											
<u>Congea</u> <u>chinensis</u> Mold.	+	+	-	*	-	+	-	-	-	-	hypo
<u>C.</u> <u>forbesii</u> King & Gamble	*	+	-	+	-	+	-	-	-	-	hypo
<u>C.</u> <u>tomentosa</u> Roxb.	*	+	?	+	?	?	?	?	?	?	hypo
<u>Sphenodesme</u> <u>ferruginea</u> (Griffith) Briq.	+	?	?	?	?	*	?	?	?	?	hypo
<u>S.</u> <u>pentandra</u> Jack	*	-	-	-	-	+	-	-	-	-	hypo
<u>Symphorema</u> <u>luzonicum</u> (Blanco) Fernandez-Villar	+	+	-	-	-	*	-	-	-	-	hypo
Verbenoideae											
Citharexyleae											
<u>Citharexylum</u> <u>affine</u> D.Don	*	+	-	-	-	-	-	-	-	-	inte
<u>C.</u> <u>berlandieri</u> Robinson	*	+	-	+	-	-	-	-	-	-	hypo
<u>C.</u> <u>caudatum</u> L.	*	r	-	+	-	-	-	-	-	-	hypo
<u>C.</u> <u>ligustrinum</u> Van Houtte	*	+	-	-	-	-	-	-	-	-	hypo
<u>C.</u> <u>punctatum</u> Greenman	+	*	-	-	-	-	-	-	-	-	hypo
<u>Duranta</u> <u>mandonii</u> Mold.	*	-	+	-	-	+	-	-	-	-	hypo
<u>D.</u> <u>mutisii</u> L.f.	*	+	+	-	-	+	-	-	-	-	hypo
<u>D.</u> <u>peruviana</u> Mold.	*	-	+	-	-	+	-	-	-	-	hypo
<u>D.</u> <u>repens</u> L. (#1)	*	-	-	+	+	+	-	-	-	-	hypo
<u>Rehdera</u> <u>trinervis</u> (S.F.Blake) Mold.	*	+	-	-	-	-	-	-	-	-	hypo
<u>Rhaphithamnus</u> <u>spinosus</u> (A.L.Juss.) Mold.	*	+	-	-	-	-	-	-	-	-	hypo
Lantaneae											
<u>Aloysia</u> <u>gratissima</u> (Gill. & Hook.) Tronc.	*	?	?	?	?	?	?	?	?	?	amph
<u>Bouchea</u> <u>fluminensis</u> (Vell.Conc.) Mold.	+	-	-	-	-	-	*	+	-	-	hypo
<u>B.</u> <u>prismatica</u> (L.) Kuntze	*	+	-	-	-	-	*	+	-	-	amph
<u>Diostea</u> <u>juncea</u> (Gillies & Hook.) Miers	*	*	-	-	-	-	-	-	-	-	amph
<u>Lantana</u> <u>horrida</u> Kunth (#1)	*	+	-	r	-	r	*	-	-	-	amph
<u>L.</u> <u>horrida</u> Kunth (#2)	*	+	-	+	-	r	+	r	-	-	amph
<u>L.</u> <u>involucrata</u> L.	*	-	-	+	-	+	+	-	-	-	inte
<u>Lippia</u> <u>graveolens</u> Kunth	*	r	-	-	-	-	+	-	-	-	hypo
<u>Phyla</u> <u>incisa</u> Small	+ ^e	-	-	-	-	+	*	+	-	-	amph
<u>P.</u> <u>lanceolata</u> (Michaux) E.Greene [§]	+ ^e	-	-	-	-	r	*	*	r	-	amph
<u>P.</u> <u>nodiflora</u> (L.) E.Greene	+ ^e	-	-	-	-	*	*	+	-	-	amph
<u>Priva</u> <u>aspera</u> Kunth	*	+	-	-	-	r	+	-	-	-	amph
<u>P.</u> <u>grandiflora</u> (Ortega) Mold.	*	+	?	?	?	?	?	?	?	?	amph
<u>Stachytarpheta</u> <u>frantzii</u> Polak.	+	+	-	-	-	-	*	r	-	-	inte
<u>S.</u> <u>jamaicensis</u> (L.) Vahl	+	+	-	-	-	-	*	r	-	-	amph
Monochileae											
<u>Amasonia</u> <u>campestris</u> (Aublet) Mold.	*	+	-	-	-	-	*	+	-	-	hypo
<u>A.</u> <u>hirta</u> Benth.	+	+	-	-	-	-	*	+	-	-	amph

TABLE 1. (continued).

Taxa ^a	Stomatal Types ^{b,c}									Stom. Pos. ^d
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	
Petreeae										
<i>Casselia hymenocalyx</i> Briq.	+	-	-	-	-	-	*	r	-	hypo
<i>Petrea amazonica</i> Mold.	+	-	-	-	-	-	+	*	+	hypo
<i>P. arborea</i> Kunth	+	?	?	?	?	?	+	?	?	hypo
<i>P. volubilis</i> L. (#1)	+	-	-	-	-	-	*	-	-	hypo
<i>P. volubilis</i> L. (#2)	+	+	-	-	-	+	*	-	-	hypo
Verbeneae										
<i>Glandularia bipinnatifida</i> (Nutt.) Nutt.	*	-	-	-	-	-	+	-	-	amph
<i>G. canadensis</i> (L.) Small	*	+	-	-	-	-	-	-	-	amph
<i>Hierobotana inflata</i> (Kunth.) Briq.	+	?	?	?	?	?	?	?	?	hypo
<i>Junellia ligustrina</i> (Lagascana) Mold.	*	+	-	-	-	-	-	-	-	amph
<i>Tamonea curassavica</i> (L.) Pers.	+	?	?	?	?	?	*	?	?	amph
<i>Verbena hastata</i> L. [§]	*	r	-	-	-	-	+	-	-	hypo
<i>V. litoralis</i> Kunth	*	+	-	+	-	r	r	-	-	amph
<i>V. macdougalii</i> A.A.Heller	*	+	-	+	-	-	r	-	-	amph
<i>V. pumila</i> Rydb.	*	+	-	-	-	-	+	-	-	amph
<i>V. urticifolia</i> L. [§]	*	+	-	-	-	-	-	-	-	hypo
Viticoideae										
Callicarpeae										
<i>Aegiphila aculeifera</i> Mold.	+	*	-	-	-	-	-	-	-	hypo
<i>A. deppeana</i> Steudel	+	+	-	*	+	-	-	-	-	hypo
<i>A. pendula</i> Mold.	*	+	-	+	-	-	+	-	-	hypo
<i>Callicarpa americana</i> L.	*	+	-	-	-	-	+	-	-	hypo
<i>C. dichotoma</i> (Lour.) K.Koch	*	+	?	?	?	?	?	?	?	hypo
<i>C. mollis</i> Siebold & Zucc.	*	+	-	-	-	-	+	-	-	hypo
Clerodendreae										
<i>Clerodendrum aculeatum</i> (L.) Schldl.	*	+	-	-	-	-	-	-	-	hypo
<i>C. anafense</i> Britton & P.Wilson	*	+	-	+	-	+	-	-	-	hypo
<i>C. capitatum</i> (Willd.) Schum. & Thonn.	*	+	-	-	-	-	-	-	-	hypo
<i>C. cuneatum</i> Gurke	+	+	-	-	-	r	*	+	r	amph
<i>C. floribundum</i> R.Br.	*	+	-	r	-	+	-	-	-	amph
<i>C. glabrum</i> E.Meyer	*	+	-	-	-	-	-	-	-	inte
<i>C. inerme</i> (L.) Gaertner	*	*	-	r	-	-	-	-	-	hypo
<i>C. myricoides</i> (Hochst.) R.Br.	*	+	-	-	-	-	*	+	-	hypo
<i>C. philippinum</i> Schauer	*	+	-	+	-	-	-	-	-	hypo
<i>C. squiresii</i> Merr.	*	+	-	-	-	+	-	-	-	hypo
<i>C. trichotomum</i> Thunb.	*	+	-	-	-	-	-	-	-	hypo
<i>Faradaya amicornum</i> (Seemann) Seemann	*	+	-	-	-	-	-	-	-	hypo
<i>F. ovalifolia</i> (A.Gray) Seemann	*	-	-	+	-	-	-	-	-	hypo
<i>F. splendida</i> F.Muell.	*	+	-	-	-	-	-	-	-	hypo
<i>Holmskioldia sanguinea</i> Retz. (#1)	*	+	-	+	-	-	-	-	-	hypo
<i>H. sanguinea</i> Retz. (#2)	*	+	-	+	-	r	+	-	-	hypo
<i>H. sanguinea</i> Retz. (#3)	*	+	-	+	-	-	r	-	-	hypo
<i>H. tettensis</i> (Klotzsch) Vatke	+	*	-	r	-	-	-	-	-	hypo
<i>Kalaharia spinescens</i> Gurke	*	-	-	+	-	+	-	-	-	amph
<i>Karomia fragrans</i> Dop	*	+	-	+	-	+	r	-	-	hypo
<i>Oxera morierii</i> Vieill.	+	-	-	*	+	+	-	-	-	hypo
<i>O. neriifolia</i> Beauv.	+	+	-	*	+	+	-	-	-	hypo
<i>O. sulfurea</i> Dubard	+	+	-	*	+	+	-	-	-	hypo
<i>Teucrium parvifolium</i> Hook.f.	*	+	-	+	-	-	+	-	-	hypo

TABLE 1. (continued).

Taxa ^a	Stomatal Types ^{b,c}									Stom. Pos. ^d
	ANO	ACT	CYC	ANI	HEL	PAR	DI2	DI3	DI4	
Viticeae										
<i>Cornutia grandiflora</i> (Cham. & Schldl.) Schauer	*	+	-	-	-	-	+	-	-	hypo
<i>C. pyramidata</i> L.	*	?	?	?	?	?	+	?	?	hypo
<i>Garrettia siamensis</i> Fletcher	+	?	?	?	?	?	?	?	?	hypo
<i>Gmelina delavayana</i> Dop	*	+	-	-	-	-	-	-	-	hypo
<i>G. moluccana</i> (Blume) Backer	*	+	-	-	-	+	-	-	-	hypo
<i>G. racemosa</i> (Lour.) Merr.	*	+	?	?	?	?	?	?	?	hypo
<i>Premna barbata</i> Wallich	+	-	-	-	-	-	*	+	-	hypo
<i>P. corymbosa</i> Willd.	+	-	-	-	-	-	*	*	+	hypo
<i>P. foetida</i> Reinw.	+	-	-	-	-	-	*	+	-	hypo
<i>P. japonica</i> Miq.	*	+	-	-	-	-	+	-	-	hypo
<i>P. octonervia</i> Merr. & Metcalf	*	+	-	-	-	-	*	-	-	hypo
<i>Pseudocarpidium avicennioides</i> (A.Rich.) Millsp.	*	+	-	-	-	-	-	-	-	hypo
<i>P. wrightii</i> Millsp.	*	+	-	-	-	-	-	-	-	hypo
<i>Tsoongia axillariflora</i> Merr.	+	-	-	*	-	+	-	-	-	hypo
<i>Vitex agnus-castus</i> L.	*	+	-	-	-	-	-	-	-	hypo
<i>V. cannabifolia</i> Siebold & Zucc.	*	+	-	+	-	r	-	-	-	hypo

^aIf name is followed by the symbol \$, data are from Abu-Asab and Cantino (1987a). All other data are from the present survey. #1, #2, etc. refer to different specimens of a species; the numbers correspond to entries in the voucher list deposited in four major botanical libraries (see Materials and Methods).

^bStomatal Types: ANO, anomocytic; ACT, actinocytic; CYC, cyclocytic; ANI, anisocytic; HEL, helicocytic; PAR, paracytic; DI2, diacytic (2 subsidiary cells); DI3, 3-celled diallelocytic; DI4, 4-celled diallelocytic.

^cSymbols: *, commonest type(s); +, present; r, rare (no more than two examples found); -, absent; ?, unknown whether present or absent (stomata are poorly stained or obscured by dense trichomes).

^dStomatal Position: amphistomatic, hypostomatic, or intermediate (i.e., a few stomata on the adaxial surface).

^eRare stomatal types: staurocytic, in *Lavandula multifida*; parallelocytic, in the three species of *Phyla*.

istic of the Labiatae. The fundamental structure of the nonglandular trichomes (i.e., unicellular vs. multicellular and simple vs. branched) was also noted. The classification system developed by Abu-Asab and Cantino (1987a) for the sessile glandular trichomes in subtribe Melittidinae was found to apply well to the Labiatae as a whole and is used here (see the APPENDIX). For it to extend to the Verbenaceae, an additional gland type (type 11) was added.

RESULTS

TABLES 1 and 2 require some introductory comments. Because the leaves of some species stained poorly, and the sessile glands and stomata in others were obscured by a dense layer of nonglandular trichomes, the tables are heavily laden with question marks. Even when the data are incomplete, however, some information may be inferred. For example, type 5 glands were definitely present

on the leaves of *Tinnea apiculata* (see TABLE 2, under "Ajugeae"), and more complex glands were present as well, but it was unclear whether they were type 8, 9, or 10. On the other hand, types 1-4, 6, 7, and 11 were definitely absent.

A species has been included in a table only if there were clear observations to tabulate with regard to the characters of concern. Each table therefore includes some species not found in the other. For example, *Acrotome angustifolia* is present in TABLE 1 but not TABLE 2 because the stomatal complexes stained sufficiently for their configurations to be discerned but the sessile glands did not stain well enough to be classified as to type.

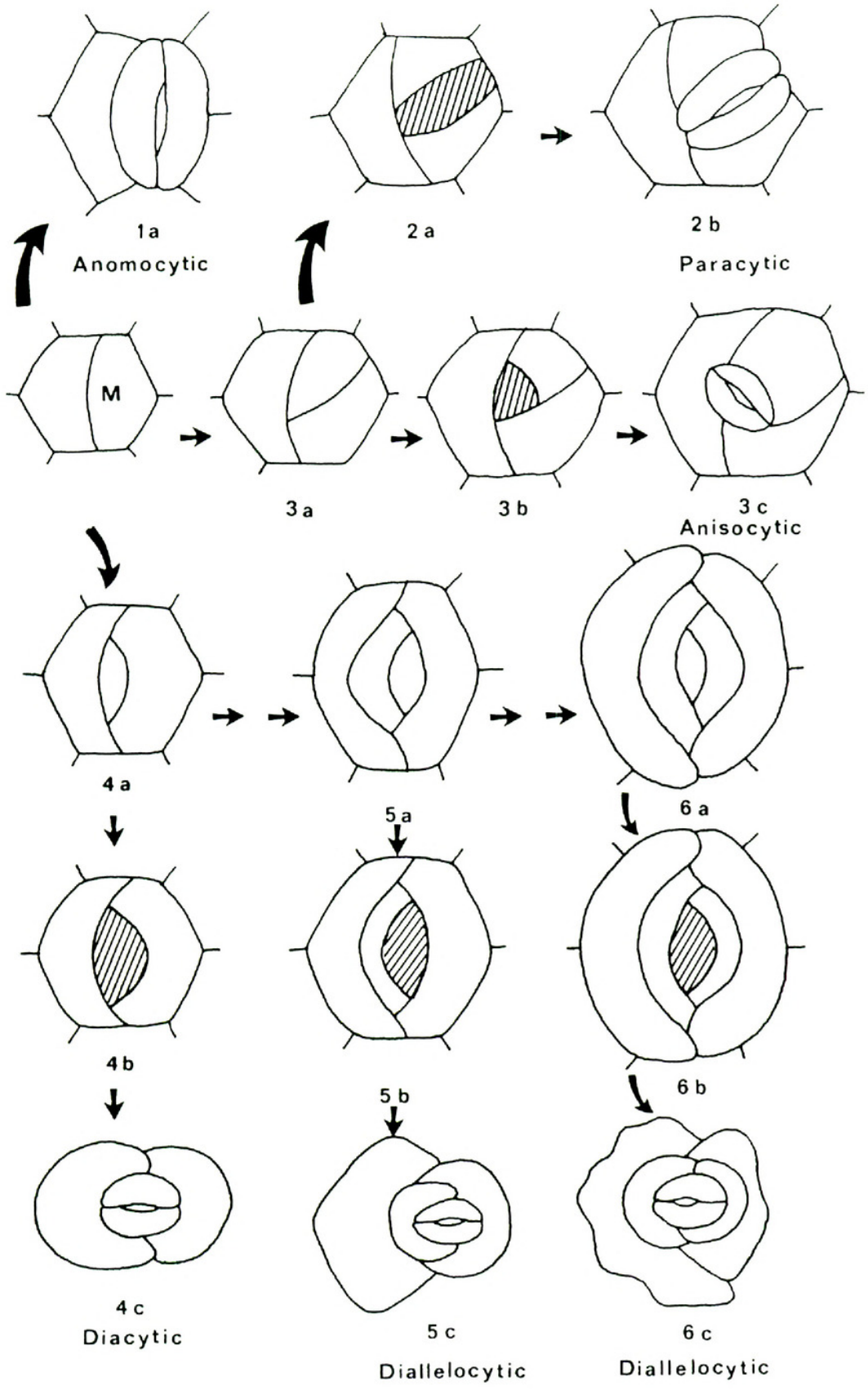
For sessile glands and stomatal complexes I have indicated relative abundance by designating with an asterisk the most common gland and stomatal types in a species. If no asterisk is present, it may be because sessile glands were so infrequent that a meaningful estimate of relative abundance could not be made or, alternatively, because such a high proportion of the glands (or stomata) were poorly stained or hidden by nonglandular trichomes that relative abundance could not be estimated. If two or more types of stomata or glands are marked with an asterisk, they were roughly equal in abundance on the leaf surface (or, occasionally, one type was most abundant on the abaxial surface and another on the adaxial).

In order to provide a more comprehensive survey and facilitate comparison of taxa, data published by Abu-Asab and Cantino (1987a) are included in the tables. Because actinocytic stomata were not distinguished from anomocytic in the earlier study (discussed below), the slides used by Abu-Asab and Cantino were reexamined to determine the distribution of actinocytic stomata. In the process, a few other errors of omission were discovered. When discrepancies exist between the earlier paper and this one, the data here should be assumed to be correct.

In TABLES 1 and 2 the names of a few suprageneric taxa of Labiatae (Lamioideae, Ajugeae, Mentheae, Salviae) are placed in quotation marks to indicate that these taxa are probably not monophyletic (see Taxonomic Background). No attempt was made to do the same for the Verbenaceae, in which phylogenetic relationships are less well understood.

STOMATA

Ten types of stomatal complexes were observed (definitions adapted from Payne, 1970, Dilcher, 1974, and Wilkinson, 1979): actinocytic (stoma surrounded by a single ring of five or more radially elongate cells enclosing the guard cells); anisocytic (stoma surrounded by three subsidiary cells, one of which is markedly smaller than the other two); anomocytic (stoma surrounded by cells that are indistinguishable from other epidermal cells); cyclocytic (stoma surrounded by a single ring of small subsidiary cells); diacytic (stoma enclosed by a pair of subsidiary cells whose common walls are perpendicular to the guard cells); diallelocytic (stoma enclosed by an alternating complex of three or more C-shaped subsidiary cells of graded sizes oriented perpendicular to the guard cells); helicocytic (stoma surrounded by a helix of four or more cells); paracytic (stoma bordered on either side by one or more subsidiary cells whose



long axes parallel those of the guard cells; subsidiary cells may or may not meet over the poles); parallelocytic (stoma with an alternating complex of three or more C-shaped subsidiary cells of graded sizes oriented parallel to the guard cells); staurocytic (stoma surrounded by three or four similar subsidiary cells with anticlinal walls arranged crosswise to the guard cells).

The actinocytic type, scored as anomocytic by Abu-Asab and Cantino (1987a), is recognized here with reservations. The term has been used differently by different authors (discussed by Baranova, 1987) and is considered by Stace (1965) to be a mere modification of the anomocytic type. As a rule of thumb, I have scored a stomatal complex as actinocytic if there are at least five radially elongate subsidiary cells that are longer than the other epidermal cells. Using this definition, however, many stomatal complexes were scored as actinocytic that closely resemble what Wilkinson (1979, fig. 10.3a) considered to be anomocytic. Others scored here as actinocytic might be classified by some workers as stephanocytic, a newly described stomatal complex (Baranova, 1987) that is intermediate between the actinocytic and cyclocytic types. Wilkinson (1979, p. 99) noted that "giant or hydathodic stomata" are frequently actinocytic. Those observed in the present study were frequently, but not invariably, larger than the other stomata on the leaf.

As discussed by Abu-Asab and Cantino (1987a), two kinds of diallelocytic stomata occur in the Labiatae, one with three subsidiary cells and the other with four. Because they do not always occur together (the latter is much rarer than the former), they have been listed separately in TABLE 1.

Stomatal ontogeny was not systematically studied, but ontogenies could sometimes be inferred from the morphology of mature stomatal complexes. The ontogenetic pathways of most stomatal types that are common in the Labiatae and Verbenaceae are shown in FIGURE 1.

Anomocytic and diacytic stomata were the most frequently encountered types in both the Labiatae and the Verbenaceae (see TABLE 1). The former were observed in all Verbenaceae and the vast majority of Labiatae examined, the latter in slightly more than half the genera of Verbenaceae and all genera of Labiatae except in tribe Prostanthereae, where they were rare.

Diallelocytic stomata are far more frequent in the Labiatae than in the Verbenaceae. In the Labiatae diallelocytic stomata with three subsidiary cells were found in nearly all species of subfam. Nepetoideae and tribes Pogostemoneae and Scutellarieae, in most genera of Lamieae, and in six genera of Ajugeae, but they have not been found in tribe Prostanthereae. In the Verbenaceae three-celled diallelocytic stomata were found in all examined species of *Amasonia* L. f., *Bouchea* Cham., *Phyla* Lour., *Stachytarpheta* M. Vahl, and *Clerodendrum* L. subg. *Cyclonema* (Hochst.) Gurke, three species of *Premna*

FIGURE 1. Stomatal ontogenetic pathways: anomocytic (1a), paracytic (2a, b), anisocytic (3a-c), diacytic (4a-c), diallelocytic with 3 subsidiary cells (5a-c), diallelocytic with 4 subsidiary cells (6a-c). (M = meristemoid, *sensu* Fryns-Claessens & Van Cotthem, 1973.) (Ontogenies of diacytic and 4-celled diallelocytic stomata adopted from Payne, 1970. Figure originally published in Abu-Asab & Cantino, 1987a.)

L., two species of *Caryopteris* Bunge, and four other scattered species. Diallelocytic stomata with four subsidiary cells are very rare in the Verbenaceae. In the Labiatae they are widespread, occurring in every tribe except the Prostanthereae, but their distribution within genera is very inconstant: although observed in 44 genera of the family, in only four were they found in all examined species (excluding those in which only one species was studied).

Anisocytic stomata are widespread in the Verbenaceae and particularly common in the Chloanthoideae and the Clerodendreae. In the Labiatae they are essentially restricted to the two tribes that lack a gynobasic style—the Ajugeae and the Prostanthereae. Particularly characteristic of the Prostanthereae, anisocytic stomata were found in nearly every species and were the most common type in three of the five genera examined. In the Ajugeae they were found in all examined specimens of *Tetraclea* A. Gray and *Trichostema* L. but were rare or absent in the other genera. Anisocytic stomata can be derived via several ontogenetic pathways (Payne, 1970). The ontogeny documented by Abu-Asab and Cantino (1987a) and shown in FIGURE 1, which if extended can give rise to helicocytic stomata (see below), is responsible for most or all of the stomata scored here as anisocytic. Superficially similar stomatal complexes that appeared to have been derived via other ontogenetic pathways (e.g., see Payne, 1970, figs. 25–27) were scored as anomocytic rather than anisocytic.

Helicocytic stomata, found in five genera of the Verbenaceae and two of the Prostanthereae but rarely in all species of a genus, occur only when anisocytic stomata are present and usually when they are the most common type. This association was also noted by Wilkinson (1979), and the ontogenetic connection between the two types has been documented by Payne (1970).

Paracytic stomata are widespread in the Verbenaceae, somewhat less widespread in subfam. Lamioideae, and very rare in subfam. Nepetoideae. They are particularly characteristic of *Prostanthera* Labill. and *Trichostema* in the Labiatae and of *Duranta* L., *Petraeovites* Oliver, *Phyla*, *Oxera* Labill., and subfam. Symphorematoideae in the Verbenaceae. Payne (1970) commented that the paracytic type is ontogenetically the most variable stomatal complex in the dicotyledons. In the Labiatae and the Verbenaceae stomata scored as paracytic develop through at least two and perhaps more ontogenetic pathways. In the majority of genera where it is a common type, it appears to have an ontogeny whose initial steps are shared with the anisocytic stoma (see FIGURE 1). In other genera, in which anisocytic stomata are absent and diacytic and diallelocytic types are common, paracytic stomata may have an ontogeny similar to that of diacytic stomata (see FIGURE 1), differing only in the final division, the guard-cell mother cell dividing parallel to the subsidiary cells instead of perpendicular to them. This hypothesis is supported by the occurrence of occasional intermediates between diacytic and paracytic stomata, in which the guard cells lie at an oblique angle to the subsidiary cells (Pant & Kidwai, 1964; Inamdar & Bhatt, 1972). In *Sphenodesme* Jack and *Symphorema* Roxb. paracytic stomata are abundant and neither anisocytic nor diacytic types were found, suggesting that paracytic stomata may arise via a third, unknown pathway in these genera.

Actinocytic stomata are widespread in both the Labiatae and the Verbenaceae

but are seldom particularly common on a given leaf. The remaining three stomatal types were found in very few species: cyclocytic in three species of *Duranta*, staurocytic in *Lavandula multifida*, and parallelocyctic in the three examined species of *Phyla*.

Amphistomatic leaves are slightly more frequent than hypostomatic ones in the Labiatae, but both conditions occur in every tribe (see TABLE 1). In contrast, over 70 percent of the species of Verbenaceae investigated, including all examined members of the Symphorematoideae, Callicarpeae, Petreeae, and Viticeae, and all but one species of the Caryopteridoideae and Citharexyleae, had hypostomatic leaves. Amphistomatic leaves predominate in the Chloanthoideae, Lantaneae, and Verbenaceae. Variation within genera is common, both conditions being found in 20 genera of the Labiatae and five of the Verbenaceae. The difference between the Labiatae and the Verbenaceae in the proportion of species with each condition may be an ecological correlate. The Labiatae are much better represented than the Verbenaceae in arid and semiarid regions, and amphistomatic leaves tend to occur more commonly in xeric habitats (Parkhurst, 1978).

SUBSESSILE GLANDULAR TRICHOMES

Subsessile glandular trichomes have been widely reported in the Labiatae and the Verbenaceae under a variety of names, including peltate hairs, glandular dots, and glandular scales (Solereder, 1908; Metcalfe & Chalk, 1950; Huang & Cheng, 1971; Bosabalidis & Tsekos, 1982; Werker, Ravid, & Putievsky, 1985a). The adjective "subsessile" was applied by Abu-Asab and Cantino (1987a) because the glands may appear sessile in surface view but can be seen in cross section to have a short, usually discoid stalk cell (Fahn, 1979, *fig. 92*; Abu-Asab & Cantino, 1987a, *fig. 3*). The same term was employed for similar glands in the Acanthaceae by Ahmad (1978) and Karlström (1978, 1980). In many Labiatae the subsessile glands function in the secretion and storage of the essential oils (volatile terpenoids) that characterize the family (Fahn, 1979; Bosabalidis & Tsekos, 1982; Bruni & Modenesi, 1983; Werker, Ravid, & Putievsky, 1985a). Their ontogeny has been well documented (Bosabalidis & Tsekos, 1982, 1984; Bruni & Modenesi, 1983). Because subsessile glandular trichomes occur in nearly all Labiatae but vary in structure, they would seem to offer considerable potential as taxonomic characters. Abu-Asab and Cantino (1987a) developed a classification of subsessile gland types based on the number of cells and the cell-wall configurations in the head of the gland. This classification, modified to include a gland type found only in the Verbenaceae, has been adopted here (see FIGURE 2, APPENDIX).

Capitate glandular trichomes—i.e., those whose stalk is long in relation to the size of the head—are also widespread in the Labiatae but were not included in this survey because it was clear at the outset that they exhibit too much intrageneric variation to be of much use as phylogenetic indicators above the species level. Their presence complicated the scoring of subsessile gland types, however, because they occasionally intergrade. The intermediates have a stalk that is elongate rather than discoid but shorter than the head. As a rule of

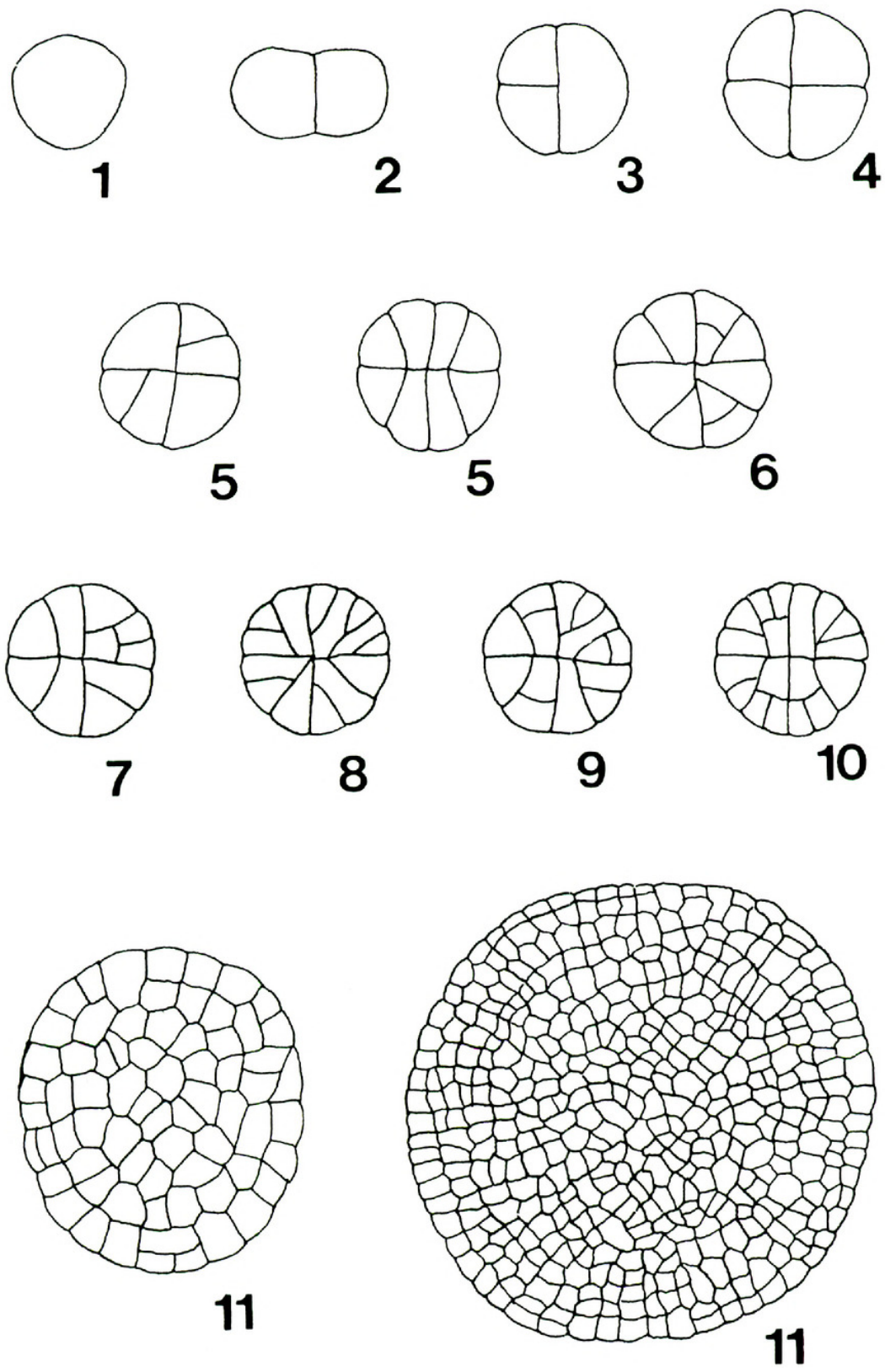


FIGURE 2. Examples of the 11 types of subsessile glandular trichomes in the Labiatae and Verbenaceae, as seen in surface view (see also APPENDIX).

thumb, these were counted as subsessile and included in TABLE 2 if the length of the stalk was no more than half the height of the head.

Subsessile glands are present in nearly all the Labiatae and Verbenaceae (see TABLE 2) but vary greatly in abundance. They are generally more common on the abaxial than the adaxial surface of the leaf. In some specimens only one or two glands were found in spite of much searching, and they were not found at all in three species of Verbenaceae (*Gmelina moluccana*, *Nesogenes dupontii*, *Premna octonervia*) and one of Labiatae (*Trichostema lanceolatum*). The glands occur in other species of each of these genera, and it is possible that they simply are very sparse in these four species and would be found if more leaves were examined. In *Trichostema lanceolatum* capitate glandular trichomes are abundant on the leaves and have been shown by Heisey and Delwiche (1984) to contain a phytotoxic essential oil. Thus the leaves of all examined species of Labiatae had glandular trichomes of some kind.

Types 4 and 5 were the most frequently observed subsessile glands in both families. Within the Verbenaceae type 4 was recorded in 78 percent and type 5 in 71 percent of the genera; within the Labiatae these figures were 76 and 72 percent, respectively (genera for which presence or absence could not be determined are excluded from percentage calculations here and elsewhere). In view of the frequency of type 4 glands in both families, their rarity in the Mentheae is noteworthy.

Type 2 glands are the third most frequent type in both families, occurring in 41 percent of the genera of Verbenaceae and 48 percent of the Labiatae, but at the tribal level they are less uniformly distributed than types 4 and 5. Type 2 glands are most common in subfam. Nepetoideae (except tribe Mentheae), tribe Lantaneae, and the genera *Ajuga* L., *Anisomeles* R. Br., *Eusteralis*, *Kinostemon* Kudo, *Leucas* R. Br., *Phlomis* L., *Pogostemon*, *Sideritis* L., and *Teucrium* L. in subfam. Lamioideae. They were infrequently encountered in subfam. Viticoideae and tribes Citharexyleae, Prostanthereae, and Mentheae and were not found at all in the Symphorematoideae or the Viticeae.

Type 1 glands were present in only six genera of Verbenaceae, four of them in the Lantaneae, but a wider distribution in the Verbenaceae was reported by Robert (1912; discussed below). In the Labiatae they were encountered frequently in tribe Mentheae and moderately so elsewhere in subfam. Nepetoideae. In subfam. Lamioideae they were found only in *Anisomeles*, *Eusteralis*, and *Pogostemon*.

Type 3 glands were observed in about a third of the genera of both families but were never very common when present, were rarely found in all examined species of a genus, and were only found when type 2 or 4 was present as well. Type 3 is probably an occasional derivative of the ontogenetic pathways that lead to types 2 and 4 glands and, as such, may be expected to occur irregularly in any species in which type 2 or 4 is common.

Type 6 glands are much more frequent in the Labiatae than in the Verbenaceae, where they were found in only ten genera, usually in only one species per genus. In the Labiatae they were most frequently present in subfam. Nepetoideae, although rare in tribe Ocimeae. In subfam. Lamioideae they were ob-

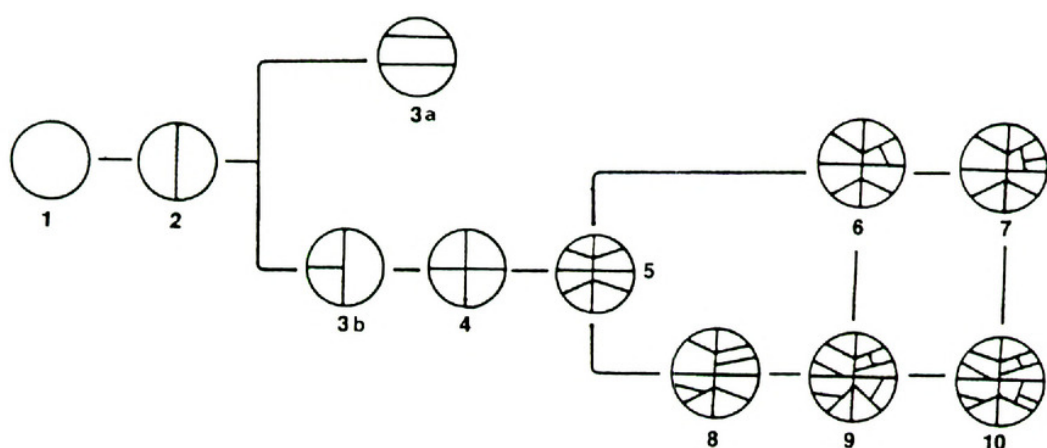


FIGURE 3. Hypothesized transformation series of subsessile glandular trichome types 1-10. (Figure originally published in Abu-Asab & Cantino, 1987a.)

served in over a third of the examined genera, but usually in only a single species.

Type 7 glands were found in nine species of Labiatae scattered through six tribes, no two species in the same genus. None were found in the Verbenaceae. Never common, type 7 glands occur only when type 6 is present as well and are best viewed as a rare derivative of the ontogenetic pathway that produces type 6 glands.

Type 8 glands were found in 11 genera of Verbenaceae and 20 of Lamioideae but in only one genus of Nepetoideae. They were seldom observed throughout a genus. The only genera in which type 8 glands appear to be characteristic (i.e., present in most or all examined species or, if only one species was examined, then the most common gland type in that species) are *Callicarpa* L. and *Citharexylum* L. in the Verbenaceae and *Brazoria* Engelm. ex A. Gray, *Craniotome* Reichb., *Cymaria* Benth., *Prostanthera*, *Scutellaria*, and *Tinnea* Kotschy & Peyr. in the Labiatae.

Type 9 glands are also much more common in the Labiatae than in the Verbenaceae. In the Labiatae they occur most frequently in the Mentheae and least frequently in the Ajugeae, the Ocimeae, and the Pogostemoneae. Based on their structure, it appears that type 9 glands may arise via two different ontogenetic pathways: through the development of one or more tangential walls in what would otherwise be a type 8 gland, or the development of tertiary radial walls in what would otherwise be a type 6 gland (see FIGURE 3). Based on the co-occurrence of type 6 or 8 glands with type 9 it appears likely that type 9 glands have arisen via the type 6 pathway in subfam. Nepetoideae, where type 8 glands are very rare, as well as in some genera of the Lamieae. They have apparently arisen via the type 8 pathway in a scattering of Verbenaceae and Lamioideae (e.g., *Duranta*, *Tinnea*). However, there are many species in which type 9 glands are associated with both types 6 and 8 or neither, preventing indirect inference of the developmental pathway.

Type 10 glands were found in five species of Verbenaceae scattered among four genera. In the Labiatae they were encountered in about 20 percent of the

genera of both subfamilies but usually not throughout a genus. The only genera in which type 10 glands are "characteristic" (defined above in discussion of type 8 glands) are *Brazoria*, *Hemiandra* R. Br., and *Macbridea* Elliott ex Nutt. in the Labiatae and *Holmskioldia* Retz. in the Verbenaceae. In general, type 10 glands probably develop as an extension of the type 9 pathway (see FIGURE 3), but they may also develop from type 7 glands through the addition of tertiary radial walls. This may be the case in *Hemigenia saligna*, where types 7 and 10 glands occur but not type 9.

Type 11 glands are broad and scalelike, varying greatly in size even on a single leaf but always much larger than the other subsessile glands. Viewed with a dissecting microscope, they are yellowish or brownish and sometimes glistening (and therefore presumably glandular), but it is unclear whether they are fundamentally similar to the other subsessile gland types (hence their exclusion from FIGURE 3). They occur only in the Verbenaceae, where they were encountered in 30 percent of the genera but often in only one species per genus. They are most widespread in the Viticoideae and the Citharexyleae and were not found in the Chloanthoideae or the Verbeneae. Because they are sparse when present at all (rarely more than three seen on a slide), they may have been overlooked in some species and thus be of wider occurrence than TABLE 2 suggests. Glands of similar construction were documented by Robert (1912) in some species of *Clerodendrum*, *Duranta*, *Faradaya* F. Mueller, *Lippia* L., and *Stachytarpheta*. Their functional significance is unclear, but Fedorowicz (1916) referred to similar structures in *Melampyrum* L. (Scrophulariaceae) as extrafloral nectaries. Metcalfe and Chalk (1950) stated that extrafloral nectaries are common in *Clerodendrum*.

NONGLANDULAR TRICHOMES

Nonglandular trichomes were found in most species (see TABLE 2). Species with glabrous leaves (subsessile glandular trichomes are ignored in the definition of "glabrous" used here) were encountered in nearly a quarter of the genera of Verbenaceae examined but only one tenth of the genera of Labiatae. In the latter glabrousness is commonest in the Prostanthereae and rarest in the Ajuceae and the Nepetoideae.

The leaves of the vast majority of Labiatae and nonverbenoid Verbenaceae bear simple, multicellular (i.e., uniseriate) "hairs." The rarity of these trichomes in the Verbenoideae and the Prostanthereae is, in contrast, noteworthy. Excluding these two groups, nearly all other Verbenaceae and Labiatae that lack uniseriate hairs are either glabrous or bear branched, multicellular trichomes, which presumably evolved from uniseriate hairs. In most nonglabrous Prostanthereae and Verbenoideae, however, the hairlike trichomes are unicellular. Unicellular hairs are widespread in other groups of the Labiatae and the Verbenaceae as well; thus it is the absence of multicellular hairs in nonglabrous species rather than the presence of unicellular ones that characterizes the Verbenoideae and the Prostanthereae.

Branched, multicellular trichomes were found in 20 percent of the genera of Verbenaceae and 16 percent of the genera of Labiatae examined. They are

TABLE 2. Distribution of nonglandular trichomes and sessile glands in Labiatae and Verbenaceae.

Taxa ^a	Subsessile Glands ^b											Nonglandular ^c			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
Lamiaceae															
"Lamioideae"															
"Ajugeae"															
<i>Acrymia ajugiflora</i> Prain	-	*	+	+	+	-	-	-	-	-	-	+	+	-	-
<i>Ajuga chamaepitys</i> (L.) Schreber	-	*	+	+	+	-	-	-	-	-	-	-	+	-	-
<i>A. genevensis</i> L.	-	+	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>A. laxmannii</i> Benth.	-	*	-	+	-	-	-	-	-	-	-	-	+	-	-
<i>A. linearifolia</i> Pampan.	-	*	+	+	+	-	-	-	-	-	-	+	+	-	-
<i>A. reptans</i> L. [§]	-	*	-	+	-	-	-	-	-	-	-	-	+	-	-
<i>A. sciaphila</i> W.W.Smith	-	*	-	+	-	-	-	-	-	-	-	-	+	-	-
<i>Amethystea coerulea</i> L. (#1)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>A. coerulea</i> L. (#2)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>Cymaria dichotoma</i> Benth.	-	-	-	+	+	-	-	*	-	-	-	+	+	-	-
<i>Kinostemon ningpoensis</i> (Hemsley) Kudo	-	+	+	*	-	-	-	-	-	-	-	-	+	-	-
<i>K. ornatum</i> (Hemsley) Kudo (#1)	-	*	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>K. ornatum</i> (Hemsley) Kudo (#2)	-	+	+	*	+	-	-	-	-	-	-	+	+	-	-
<i>K. ornatum</i> (Hemsley) Kudo (#3)	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>K. pernyi</i> (Franchet) Kudo	-	+	+	*	+	-	-	-	-	-	-	+	+	-	-
<i>Rubiteucris palmata</i> (Benth. ex Hook.f.) Kudo	-	+	+	*	-	-	-	-	-	-	-	-	+	-	-
<i>Schnabelia oligophylla</i> Hand.-Mazz.	-	-	+	*	-	-	-	-	-	-	-	-	+	-	-
<i>Tetraclea coulteri</i> A.Gray (#1)	-	-	-	+	*	-	-	-	-	+	-	+	+	-	-
<i>T. coulteri</i> A.Gray (#2)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>T. coulteri</i> A.Gray (#3)	-	-	-	+	*	-	-	-	-	+	-	+	+	-	-
<i>Teucrium arduinii</i> L.	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>T. canadense</i> L. [§]	-	*	+	*	+	-	-	-	-	-	-	-	+	-	-
<i>T. chamaedrys</i> L. [§]	-	*	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>T. integrifolium</i> F.Muell. ex Benth.	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
<i>T. laciniatum</i> Torrey	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>T. marum</i> L.	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>T. rotundifolium</i> Schreber	-	*	-	+	+	-	-	-	-	-	-	-	+	-	-
<i>Tinnea aethiopica</i> Kotschy ex Hook.f. (#1)	-	-	-	-	+	-	-	*	+	-	-	-	+	-	-
<i>T. aethiopica</i> Kotschy ex Hook.f. (#2)	-	-	-	+	*	-	-	-	-	-	-	-	+	-	-
<i>T. antiscorbutica</i> Welw.	-	-	-	-	+	-	-	*	-	-	-	+	+	-	-
<i>T. apiculata</i> W.Robyns & Lebrun	-	-	-	-	+	-	-	?	?	?	-	+	+	-	-
<i>T. galpinii</i> Briq.	-	-	-	-	*	+	-	+	+	-	-	-	+	-	-
<i>T. rhodesiana</i> S.Moore (#1)	-	-	-	+	+	-	-	*	+	-	-	+	+	-	-
<i>T. somalensis</i> Gurke ex Chiov.	-	-	-	-	+	-	-	+	*	+	-	+	+	-	-
<i>Trichostema arizonicum</i> A.Gray (#1)	-	+	+	*	+	-	-	-	-	-	-	+	+	-	-
<i>T. arizonicum</i> A.Gray (#2)	-	+	+	*	-	-	-	-	-	-	-	-	+	-	-
<i>T. brachiatum</i> L.	-	+	+	*	+	-	-	-	-	-	-	+	+	-	-
<i>T. dichotomum</i> L. [§]	-	-	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>T. lanatum</i> Benth.	-	-	-	+	*	-	-	-	-	-	-	-	+	-	-
<i>T. lanceolatum</i> Benth. [§]	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>T. lanceolatum</i> Benth.	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>T. setaceum</i> Houtt.	-	-	-	*	-	-	-	-	-	-	-	-	+	-	-
Lamieae															
<i>Achyropermum parviflorum</i> S.Moore	-	-	-	+	*	-	-	-	-	-	-	-	+	-	-
<i>A. schimperi</i> Perkins	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
<i>A. wallichianum</i> Benth. ex Hook.f.	?	?	?	*	?	?	?	?	?	?	-	+	+	-	-
<i>Acrotome fleckii</i> (Gurke) Launert	-	+	-	+	*	+	+	+	+	-	-	+	+	-	-
<i>A. hispida</i> Benth.	-	-	-	*	+	?	?	?	?	-	-	+	+	-	-
<i>A. inflata</i> Benth.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-

TABLE 2. (continued).

Taxa ^a	Subsessile Glands ^b											Nonglandular ^c			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
<i>Ballota frutescens</i> (L.) J.Woods	-	-	+	*	+	-	-	-	-	-	-	-	+	-	-
<i>B. nigra</i> L. (#1)	-	-	*	+	-	-	-	-	-	-	-	+	+	-	-
<i>B. pseudodictamnus</i> (L.) Benth.	?	?	?	?	+	?	?	?	?	?	?	-	-	-	+
<i>Brazoria arenaria</i> Lundell [§]	-	-	+	*	-	-	+	+	+	-	-	-	+	-	-
<i>B. pulcherrima</i> Lundell [§]	-	-	+	*	-	-	+	+	+	-	-	-	+	-	-
<i>B. scutellarioides</i> Engelm. & A.Gray [§]	-	-	*	+	+	-	-	+	+	-	-	+	+	-	-
<i>B. truncata</i> (Benth.) Engelm. & A.Gray [§]	-	-	+	*	-	-	+	+	+	-	-	-	+	-	-
<i>Chamaesphacos ilicifolius</i> Schrenk	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-
<i>Chelonopsis forrestii</i> Anthony [§]	-	+	-	*	+	-	-	-	-	-	-	-	+	-	-
<i>C. lichiangensis</i> W.Smith	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
<i>C. longipes</i> Makino	-	-	-	+	+	+	-	+	-	-	-	-	+	-	-
<i>C. odontochila</i> Diels	-	-	-	*	-	-	-	-	-	-	-	-	+	-	-
<i>Colquhounia coccinea</i> Wallich	-	-	-	+	+	?	?	?	?	?	-	-	-	-	+
<i>C. seguinii</i> Vaniot	-	-	-	+	*	+	-	-	-	-	-	+	+	-	-
<i>Craniotome furcata</i> (Link) Kuntze	-	-	-	+	+	?	?	?	?	+	?	+	+	-	-
<i>C. versicolor</i> Reichb. (#3)	-	-	-	+	+	+	-	*	+	-	-	-	+	-	-
<i>Eremostachys bachardenica</i> B.Fedtsch.	-	-	-	+	+	-	-	-	-	-	-	-	+	-	-
<i>E. iliensis</i> Regel	-	*	+	+	-	-	-	-	-	-	-	-	+	-	-
<i>E. labiosa</i> Bunge	?	+	?	?	?	?	?	?	?	?	-	-	-	-	+
<i>E. regeliana</i> Aitch. & Hemsley	-	+	-	*	+	-	-	-	-	-	-	-	+	-	-
<i>E. speciosa</i> Rupr.	?	?	?	?	+	?	?	?	?	?	-	+	+	-	-
<i>Eriophyton wallichianum</i> Benth.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>Galeobdolon luteum</i> Hudson [§]	-	-	-	*	+	+	-	-	+	-	-	-	+	-	-
<i>Galeopsis ladanum</i> L.	-	-	-	-	*	+	-	-	+	-	-	-	+	-	-
<i>G. ochroleuca</i> Lam.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>G. pubescens</i> Besser	-	-	-	-	+	*	-	-	*	-	-	+	+	-	-
<i>G. tetrahit</i> L.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>Gomphostemma crinitum</i> Wallich	-	-	+	*	+	-	-	-	-	-	-	+	+	-	+
<i>G. javanicum</i> (Blume) Benth.	-	-	-	+	?	?	?	?	?	?	-	-	+	-	+
<i>G. lucidum</i> Wallich	-	-	-	*	+	-	-	-	-	-	-	?	?	-	+
<i>G. velutinum</i> Benth.	?	?	?	?	?	+	?	?	?	?	?	-	+	-	+
<i>Haplostachys haplostachya</i> (A.Gray)	-	*	+	-	-	-	-	-	-	-	-	-	+	-	-
St. John	-	*	+	-	-	-	-	-	-	-	-	-	+	-	-
<i>H. linearifolia</i> (Drake) Sherff	?	?	?	+	+	+	?	?	?	?	?	-	-	+	-
<i>Lagochilus cabulicus</i> Benth.	-	-	-	-	+	-	-	*	+	-	-	+	+	-	-
<i>L. diacanthophyllus</i> (Pallas) Benth.	?	?	?	?	+	?	?	?	+	+	?	+	+	-	-
<i>L. ilicifolius</i> Bunge	-	-	-	+	*	+	-	-	-	-	-	+	-	-	-
<i>L. knorringianus</i> Pavlov	-	-	-	-	-	-	-	-	*	+	-	+	-	-	-
<i>L. platycalyx</i> Fischer & C.Meyer (#2)	-	-	-	*	+	-	-	-	*	-	-	+	-	-	-
<i>Lagopsis supina</i> (Stephan) Ikonn.-Gal.	-	-	-	+	-	-	-	+	*	+	-	+	+	-	-
<i>Lamiophlomis rotata</i> (Benth.) Kudo	-	-	+	*	-	-	-	-	-	-	-	-	+	-	-
<i>Lamium album</i> L.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>L. maculatum</i> L. (#1)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>L. maculatum</i> L. (#2)	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
<i>L. moschatum</i> Miller	-	-	-	*	-	-	-	-	-	-	-	+	+	-	-
<i>L. pictum</i> Boiss. & Heldr.	-	-	-	*	+	+	-	-	+	-	-	+	+	-	-
<i>L. purpureum</i> L. [§]	-	+	+	*	+	+	-	-	-	-	-	+	+	-	-
<i>Leonotis latifolia</i> Curke	-	-	-	-	*	+	-	-	+	-	-	-	+	-	-
<i>L. leonitis</i> R.Br.	-	-	+	+	*	-	-	-	-	-	-	-	+	-	-
<i>L. leonurus</i> (L.) R.Br. (#1)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>L. leonurus</i> (L.) R.Br. (#2)	-	-	-	*	+	+	-	-	+	-	-	-	+	-	-

TABLE 2. (continued).

Taxa ^a	Subsessile Glands ^b											Nonglandular ^c			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
<i>Leonurus cardiaca</i> L. [§]	-	+	+	+	+	+	*	+	-	-		-	+	-	-
<i>L. heterophyllus</i> Sweet	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>Leucas altissima</i> Engl.	-	+	-	+	*	-	-	-	-	-	-	-	+	-	-
<i>L. capensis</i> (Benth.) Engl.	-	+	+	*	+	-	-	-	-	-	-	?	+	-	-
<i>L. ciliata</i> Benth.	-	+	+	+	*	-	-	-	-	-	-	-	+	-	-
<i>L. decedentata</i> R.Br.	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
<i>L. mildbraedii</i> Perkins	-	+	-	*	+	-	-	-	-	-	-	-	+	-	-
<i>L. mollissima</i> Wallich	?	?	?	*	?	?	?	?	?	?	-	+	+	-	-
<i>Loxocalyx urticifolius</i> Hemsley	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>Macbridea alba</i> Chapman [§]	-	-	-	+	*	+	-	+	+	+	-	-	-	-	-
<i>M. caroliniana</i> (Walter) Blake [§]	-	-	-	+	*	*	-	-	+	+	-	-	-	-	-
<i>Marrubium desertii</i> Noë ex Cosson	-	-	-	+	*	-	-	-	-	-	-	-	-	-	+
<i>M. peregrinum</i> L.	-	+	+	*	+	-	-	-	-	-	-	-	-	-	+
<i>M. vulgare</i> L.	-	+	+	*	+	-	-	-	-	-	-	-	+	-	+
<i>M. vulgare</i> L. [§]	-	+	+	*	+	-	-	-	-	-	-	-	+	-	+
<i>Melittis melissophyllum</i> L. [§]	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
<i>Metastachydium sagittatum</i> (Regel) C.Y.Wu & Li	-	-	+	*	-	-	-	-	-	-	-	+	+	-	+
<i>Microtoena insuavis</i> (Hance) Prain ex Briq. (#1)	-	-	-	*	*	-	-	-	-	-	-	+	+	-	-
<i>M. moupinensis</i> Franchet ex Prain	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
<i>M. robusta</i> Hemsley	-	-	+	+	-	-	-	-	-	-	-	-	+	-	-
<i>M. urticifolia</i> Hemsley	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
<i>Moluccella laevis</i> L.	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-
<i>M. spinosa</i> L.	-	-	-	+	*	-	-	-	-	-	-	-	+	-	-
<i>Notochaete hamosa</i> Benth.	-	*	+	+	-	-	-	-	-	-	-	+	+	-	+
<i>Otostegia aucheri</i> Boiss.	-	-	-	*	+	-	-	-	*	+	-	+	+	-	-
<i>O. integrifolia</i> Benth.	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
<i>O. limbata</i> (Benth.) Benth. ex Hook.f.	-	-	-	+	*	-	-	-	-	-	-	-	+	-	-
<i>O. persica</i> (Burm.f.) Boiss.	-	-	-	+	*	+	-	+	-	-	-	-	+	-	-
<i>Panzeria argyracea</i> Kuprian.	?	?	?	?	?	?	?	?	?	?	-	-	+	-	-
<i>Paraphlomis javanica</i> (Blume) Prain ex Backer & Bakh.f.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>P. rugosa</i> (Benth.) Prain	-	-	-	*	*	+	-	-	-	-	-	+	+	-	-
<i>Phlomidioschema parviflorum</i> (Benth.) Vved.	?	?	?	?	?	?	?	?	?	?	?	-	-	-	+
<i>Phlomis agraria</i> Bunge	-	*	-	*	-	-	-	-	-	-	-	+	+	-	+
<i>P. bracteosa</i> Royle	-	*	+	-	-	-	-	-	-	-	-	-	+	-	+
<i>P. herba-venti</i> L.	-	*	+	+	-	-	-	-	-	-	-	-	-	-	+
<i>P. maximoviczii</i> Regel	-	*	-	+	-	-	-	-	-	-	-	-	-	-	+
<i>P. pratensis</i> Karelín & Kir.	-	*	+	+	-	-	-	-	-	-	-	-	+	-	+
<i>P. setigera</i> Falc. ex Benth.	-	*	+	+	-	-	-	-	-	-	-	+	+	-	+
<i>P. taurica</i> Hartw. ex Bunge	?	+	?	?	?	?	?	?	?	?	?	-	-	-	+
<i>P. tuberosa</i> L.	-	*	-	-	-	-	-	-	-	-	-	-	+	-	+
<i>P. umbrosa</i> Turcz.	-	*	+	+	-	-	-	-	-	-	-	+	+	-	+
<i>Phyllostegia brevidens</i> A.Gray	-	-	-	+	*	-	-	-	-	-	-	-	+	-	-
<i>P. grandiflora</i> (Gaudich.) Benth. (#1)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>P. grandiflora</i> (Gaudich.) Benth. (#2)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>P. hispida</i> Hillebrand	-	-	-	+	*	+	-	+	+	-	-	-	+	-	-
<i>P. lantanoides</i> Sherff	-	-	+	*	-	-	-	-	-	-	-	+	+	-	-

TABLE 2. (continued).

Taxa ^a	Subsessile Glands ^b											Nonglandular ^c			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
<i>Physostegia angustifolia</i> Fern. [§]	-	-	-	*	+	-	-	+	+	+	-	-	-	-	-
<i>P. digitalis</i> Small [§]	-	-	-	+	*	-	-	-	-	-	-	-	-	-	-
<i>P. godfreyi</i> Cantino [§]	-	-	-	+	*	-	-	+	-	-	-	-	-	-	-
<i>P. leptophylla</i> Small [§]	-	-	-	*	+	+	-	-	-	-	-	-	-	-	-
<i>P. longisepala</i> Cantino [§]	-	-	-	*	+	-	-	-	-	-	-	-	-	-	-
<i>P. purpurea</i> (Walter) Blake [§]	-	-	-	+	*	-	-	-	-	-	-	-	-	-	-
<i>P. virginiana</i> (L.) Benth. [§]	-	-	-	*	+	-	-	-	+	+	-	-	-	-	-
<i>Prasium majus</i> L. (#1)	-	-	-	-	*	?	?	?	-	?	?	-	+	-	-
<i>P. majus</i> L. (#2)	-	-	-	-	*	-	-	-	+	-	-	-	-	-	-
<i>Pseuderemostachys sewertzowii</i> (Herder) Popov	?	?	?	?	?	?	?	?	?	?	?	-	-	-	+
<i>Roylea calycina</i> (Roxb.) Briq.	-	-	+	+	*	+	-	+	+	-	-	+	+	-	-
<i>Sideritis hirsuta</i> L.	-	+	-	+	+	+	-	+	*	+	-	-	+	-	-
<i>S. ilicifolia</i> Willd.	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
<i>S. lagascana</i> Willk.	-	*	-	+	+	*	-	-	-	-	-	+	+	-	-
<i>S. lanata</i> L.	-	*	+	+	-	-	-	-	-	-	-	-	+	-	-
<i>S. montana</i> L.	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
<i>S. perfoliata</i> L.	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
<i>S. pullulans</i> Vent.	-	*	+	+	+	-	-	-	-	-	-	-	+	-	-
<i>S. romana</i> L.	-	*	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>Stachyopsis oblongata</i> (Schrenk) Popov & Vved.	-	-	-	*	-	-	-	-	-	-	-	+	+	-	-
<i>Stachys acerosa</i> Boiss.	-	-	-	+	+	+	?	?	?	?	-	+	+	-	-
<i>S. annua</i> (L.) L.	-	+	-	*	+	+	+	-	-	-	-	+	+	-	-
<i>S. betonicaeflora</i> Rupr.	-	+	-	+	*	+	-	+	+	-	-	+	+	-	+
<i>S. coccinea</i> Jacq.	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>S. glutinosa</i> L.	?	?	?	?	+	?	?	?	?	?	-	-	-	-	-
<i>S. inflata</i> Benth.	?	?	?	?	?	?	?	?	?	?	?	-	-	-	+
<i>S. labiosa</i> Bertol.	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>S. riddellii</i> House [§]	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>S. spathulata</i> Burchell ex Benth.	?	+	+	+	?	?	?	?	?	?	-	-	-	-	+
<i>S. spruneri</i> Boiss. ex Benth.	-	*	-	+	-	-	-	-	-	-	-	+	+	-	-
<i>S. tenuifolia</i> Willd. [§]	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
<i>Stenogyne diffusa</i> A.Gray (#1)	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>S. diffusa</i> A.Gray (#2)	-	-	-	*	-	-	-	-	-	-	-	+	+	-	-
<i>S. kamehamehae</i> Wawra	-	-	-	+	+	-	-	-	-	-	-	-	+	-	-
<i>S. purpurea</i> H.Mann	-	-	-	*	+	-	-	-	-	-	-	-	-	-	-
<i>S. rugosa</i> Benth.	-	-	-	*	-	-	-	-	-	-	-	-	+	-	-
<i>Synandra hispidula</i> (Michx.) Baillon [§]	-	-	-	*	+	+	+	+	-	+	-	-	+	-	-
<i>Thuspeinanta brahuica</i> (Boiss.) Briq.	-	-	-	-	+	*	-	-	+	-	-	-	+	-	-
<i>T. persica</i> (Boiss.) Briq.	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-
<i>Wiedemannia multifida</i> (L.) Benth.	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
Pogostemoneae															
<i>Colebrookea oppositifolia</i> Smith (#1)	?	?	?	?	?	+	?	?	?	+	+	+	+	-	-
<i>C. oppositifolia</i> Smith (#2)	?	?	?	?	+	*	?	?	?	?	?	+	+	-	-
<i>Comanthosphace stellipila</i> S.Moore	-	-	-	+	*	-	-	-	-	-	-	-	+	-	+
<i>C. subanceolata</i> (Miq.) S.Moore (#1)	-	-	-	+	*	-	-	-	-	-	-	-	+	-	-
<i>C. subanceolata</i> (Miq.) S.Moore (#2)	-	-	-	+	*	-	-	-	-	-	-	-	+	-	+
<i>Eusteralis cruciata</i> (Benth.) Panigr.	+	*	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>E. sampsonii</i> (Hance) Panigr.	?	+	?	?	?	?	?	?	?	?	?	-	-	-	-
<i>E. stellata</i> (Lour.) Panigr. (#1)	*	+	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>E. stellata</i> (Lour.) Panigr. (#2)	+	*	-	-	-	-	-	-	-	-	-	+	-	-	-

TABLE 2. (continued).

Taxa ^a	Subsessile Glands ^b											Nonglandular ^c			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
<i>Pogostemon auricularius</i> (L.) Hassk.	*	*	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>P. brachystachyus</i> Benth.	*	+	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>P. cablin</i> (Blanco) Benth.	*	*	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>P. elsholtzioides</i> Benth.	*	+	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>P. glaber</i> Benth. (#1)	*	*	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>P. glaber</i> Benth. (#2)	*	*	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>P. heyneanus</i> Benth. [§]	*	*	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>P. plectranthoides</i> Desf.	*	*	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>Rostrinucula dependens</i> (Rehder) Kudo	-	-	-	+	*	+	-	-	-	-	-	-	-	-	+
<i>R. sinensis</i> (Hemsley) C.Y.Wu	?	?	?	?	?	?	?	?	?	?	?	-	-	-	+
Prostanthereae															
<i>Hemiandra pungens</i> R.Br.	-	-	-	-	-	-	-	-	+	*	-	-	-	-	-
<i>Hemigenia incana</i> Benth. (#1)	-	-	+	*	-	-	-	-	-	-	-	-	+	-	-
<i>H. incana</i> Benth. (#2)	-	+	+	*	+	-	-	-	-	-	-	-	+	-	-
<i>H. saligna</i> Diels	-	-	-	-	-	+	+	-	-	*	-	+	-	-	-
<i>Microcorys brevidens</i> Benth.	-	-	-	?	?	-	-	-	-	-	-	-	-	-	-
<i>Prostanthera cuneata</i> Benth.	-	-	-	?	?	?	?	+	?	?	-	-	-	-	-
<i>P. lasianthos</i> Labill. (#1)	-	-	-	-	*	?	?	?	?	?	-	-	-	-	-
<i>P. lasianthos</i> Labill. (#2)	-	-	-	-	*	+	?	*	+	?	-	-	-	-	-
<i>P. nivea</i> Cunn. ex Benth. (#1)	-	-	-	*	+	-	-	-	-	-	-	+	-	-	-
<i>P. nivea</i> Cunn. ex Benth. (#2)	-	-	+	*	+	-	-	+	-	-	-	+	-	-	-
<i>P. ovalifolia</i> R.Br.	-	-	-	+	+	?	?	?	+	?	?	-	-	-	-
<i>P. rotundifolia</i> R.Br. [§]	-	-	+	+	?	?	?	*	?	?	?	-	-	-	-
<i>P. rotundifolia</i> R.Br.	-	-	-	+	?	?	?	+	?	?	?	-	-	-	-
<i>P. saxicola</i> R.Br.	-	-	+	*	-	-	-	-	-	-	-	+	-	-	-
<i>Westringia amabilis</i> J.Boivin	-	-	-	-	+	*	-	+	+	-	-	-	-	-	-
<i>W. cheeli</i> Maiden & Betche	-	-	-	-	-	-	-	-	?	+	-	+	-	-	-
<i>W. fruticosa</i> (Willd.) Druce	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-
Scutellarieae															
<i>Salazaria mexicana</i> Torrey (#1)	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
<i>S. mexicana</i> Torrey (#2)	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
<i>Scutellaria amoena</i> C.H.Wright	-	-	-	-	*	+	-	+	+	-	-	+	+	-	-
<i>S. elliptica</i> Muhlenb. [§]	-	-	-	*	-	-	-	+	-	-	-	-	+	-	-
<i>S. gardoquioides</i> Benth.	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
<i>S. hirtella</i> Juz.	?	?	?	?	+	+	?	?	?	?	?	-	+	-	-
<i>S. incana</i> Biehler [§]	-	-	-	+	+	+	-	*	+	-	-	+	+	-	-
<i>S. integrifolia</i> L. [§]	-	-	-	+	*	-	-	+	-	-	-	+	+	-	-
<i>S. lateriflora</i> L. [§]	-	+	+	*	-	-	-	-	-	-	-	-	+	-	-
<i>S. multicaulis</i> Boiss.	-	-	+	+	*	+	-	+	+	-	-	+	+	-	-
<i>S. nervosa</i> Pursh [§]	-	-	-	*	+	-	-	+	-	-	-	+	+	-	-
<i>S. ovata</i> Hill [§]	-	-	+	*	+	+	+	+	-	-	-	-	+	-	-
<i>S. serrata</i> Andr. [§]	-	+	+	*	+	-	-	-	-	-	-	-	+	-	-
Uncertain Tribal Affin.															
<i>Ajugoides humilis</i> (Miq.) Makino (#1)	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>A. humilis</i> (Miq.) Makino (#2)	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>Anisomeles heyneana</i> Benth.	*	+	+	-	-	-	-	-	-	-	-	-	+	-	-
<i>A. indica</i> (L.) Kuntze (#1)	*	+	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>A. indica</i> (L.) Kuntze (#2)	*	+	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>A. malabarica</i> (L.) R.Br. ex Sims (#1)	*	+	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>A. malabarica</i> (L.) R.Br. ex Sims (#2)	*	+	-	-	-	-	-	-	-	-	-	-	+	-	-
<i>Eurysolen gracilis</i> Prain (#1)	-	-	+	+	+	+	?	+	+	?	-	-	+	-	-
<i>E. gracilis</i> Prain (#2)	?	?	?	?	?	+	+	?	?	?	?	+	+	-	-
<i>Hypogomphia turkestanica</i> Bunge	-	-	-	+	-	-	-	-	-	-	-	-	+	-	-
<i>Leucosceptrum canum</i> Smith	?	?	?	?	+	?	?	?	?	?	?	-	-	-	+
<i>Suzukia shikikunensis</i> Kudo	?	?	?	?	+	+	?	?	?	?	?	-	-	+	-

TABLE 2. (continued).

Taxa ^a	Subsessile Glands ^b											Nonglandular ^c			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
Nepetoideae															
"Mentheae"															
<u>Ceratomythe odora</u> (Griseb.) Hauman	*	-	-	?	+	?	?	?	?	-		+	+	-	-
<u>Cyclotrichium origanifolium</u> (Labill.) Manden. & Scheng.	-	-	-	-	*	-	-	+	+	-		-	-	-	-
<u>Elsholtzia fruticosa</u> (D.Don) Rehder	-	*	+	?	?	?	?	?	+	?	-	+	+	-	+
<u>E. patrinii</u> (Lepechin) Garcke	-	*	-	?	?	?	?	?	+	?	-	+	+	-	-
<u>Hedeoma graveolens</u> Chapman ex A.Gray	-	-	-	-	*	+	-	+	+	-		+	+	-	-
<u>H. nanum</u> (Torrey) Briq.	*	-	-	-	+	?	?	?	?	?	-	+	+	-	-
<u>Keiskea japonica</u> Miq.	-	-	-	-	*	?	?	?	?	?	-	+	+	-	-
<u>Lepechinia hastata</u> (A.Gray) Epling	+	-	-	-	*	+	-	-	-	-	-	-	-	-	+
<u>Lycopus americanus</u> Muhlenb.	-	+	-	+	*	-	-	-	-	-	-	+	+	-	-
<u>L. rubellus</u> Moench	?	?	-	-	*	-	-	-	-	-	-	+	+	-	-
<u>L. virginicus</u> L.	-	*	-	+	+	-	-	-	-	-	-	+	+	-	-
<u>Melissa officinalis</u> L. (#1)	-	-	-	-	*	*	-	-	+	-	-	+	+	-	-
<u>Mentha arvensis</u> L.	?	?	?	?	?	+	?	?	?	?	-	+	+	-	-
<u>M. citrata</u> Ehrh.	?	?	?	?	?	+	?	?	?	?	-	-	+	-	-
<u>M. piperita</u> L.	?	?	?	?	?	+	+	?	?	?	-	-	+	-	-
<u>Monardella odoratissima</u> Benth.	+	-	-	-	-	+	+	-	*	+	-	+	+	-	-
<u>M. villosa</u> Benth.	+	-	-	-	?	*	?	?	+	?	-	+	+	-	-
<u>Perillula reptans</u> Maxim. (#1)	-	*	+	-	*	-	-	-	-	-	-	+	+	-	-
<u>P. reptans</u> Maxim. (#2)	+	*	-	-	+	?	?	?	?	?	-	+	+	-	-
<u>Pogogyne zizyphoroides</u> Benth.	+	-	-	-	+	-	-	-	-	-	-	+	-	-	-
<u>Poliomintha glabrescens</u> A.Gray ex Hemsl.	*	-	-	-	*	?	?	?	?	?	-	+	+	-	-
<u>Pycnanthemum floridanum</u> E.Grant & Epling	-	-	-	-	*	?	?	?	?	?	-	+	+	-	-
<u>P. aff. incanum</u> (L.) Michaux	-	-	-	-	*	?	?	?	?	?	-	+	+	-	-
<u>Rhododon ciliatus</u> (Benth.) Epling	*	-	-	-	+	?	?	?	?	?	-	-	+	-	-
<u>Satureja arkansana</u> (Nutt.) Briq.	*	-	-	-	*	+	?	?	?	?	-	+	-	-	-
<u>S. douglasii</u> (Benth.) Briq.	*	-	-	-	+	*	-	+	-	-	-	+	+	-	-
<u>S. parvifolia</u> (Philippi) Epling	*	-	-	-	?	*	?	?	+	?	-	+	+	-	-
<u>S. popovii</u> B.Fedtsch. & Gontch.	+	-	-	-	-	*	-	-	+	-	-	+	+	-	-
<u>Thymus serpyllum</u> L.	+	?	?	?	?	+	?	?	?	?	-	+	+	-	-
Nepeteae															
<u>Agastache breviflora</u> (A.Gray) Epling	-	+	-	-	+	+	?	+	?	?	-	-	+	-	-
<u>A. cana</u> (Hook.) Wooton & Standley	-	*	-	-	?	+	?	?	?	?	-	+	+	-	-
<u>A. nepetoides</u> (L.) Kuntze	?	?	?	?	?	+	?	?	?	?	-	+	+	-	-
<u>A. pallidiflora</u> (A.A.Heller) Rydb.	?	*	?	?	?	+	?	?	?	?	-	+	+	-	-
<u>Cedronella canariensis</u> (L.) Webb & Berth. (#1)	-	-	-	-	-	+	?	?	?	+	+	+	+	-	-
<u>Dracocephalum heterophyllum</u> Benth.	-	*	-	+	-	+	+	+	-	-	-	+	+	-	-
<u>D. parviflorum</u> Nutt.	?	+	?	?	?	+	?	?	?	?	-	+	+	-	-
<u>D. ruyschiana</u> L.	-	*	-	-	+	+	-	-	-	-	-	+	+	-	-
<u>Glechoma hederacea</u> L.	-	*	-	-	+	+	-	-	-	-	-	+	+	-	-
<u>Lophanthus chinensis</u> Benth.	*	+	-	-	-	-	-	-	-	-	-	+	+	-	-
<u>Meehanian cordata</u> (Nutt.) Britton	?	?	?	?	+	?	+	?	?	?	-	+	+	-	-

Taxa ^a	Subsessile Glands ^b											Nonglandular ^c			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
<hr/>															
<i>Rabdusia excisa</i> (Maxim.) H.Hara	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
<i>R. inflexa</i> (Thunb.) H.Hara	-	-	+	*	-	-	-	-	-	-	-	-	+	-	-
<i>R. nervosa</i> (Hemsley) C.Y.Wu & Li	-	+	+	*	-	-	-	-	-	-	-	-	+	-	-
<hr/>															
<i>Rabdosiella calycina</i> (Benth.) Codd	-	+	+	*	+	-	-	-	-	-	-	-	+	-	-
<i>Solenostemon scutellarioides</i> (L.) Codd (#1)	-	+	-	*	+	-	-	-	-	-	-	+	+	-	-
<i>S. scutellarioides</i> (L.) Codd (#2)	-	+	-	*	-	-	-	-	-	-	-	+	+	-	-
<i>Syncolostemon densiflorus</i> Benth.	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
<hr/>															
"Salviaeae"															
<i>Arischrada bucharica</i> (Popov) Pobed.	-	*	-	-	-	+	+	-	+	+	-	-	+	-	-
<i>Blephilia hirsuta</i> (Pursh) Benth. [§]	-	-	-	?	+	?	?	?	?	?	-	+	+	-	-
<i>Monarda clinopodia</i> L.	?	+	?	?	?	+	?	?	?	?	-	-	+	-	-
<i>M. fistulosa</i> L. [§]	?	?	?	?	?	+	?	?	?	?	-	+	+	-	-
<i>M. punctata</i> L.	?	?	?	?	?	+	?	?	?	?	-	+	+	-	-
<i>Perovskia abrotanoides</i> Karelin	+	+	+	+	+	*	-	-	*	*	-	+	-	-	+
<i>P. atriplicifolia</i> Benth.	-	*	+	+	+	+	-	-	+	-	-	-	-	-	+
<i>Rosmarinus officinalis</i> L.	?	?	?	?	?	?	?	?	?	?	?	?	?	-	+
<i>Salvia carnosa</i> Douglas	-	-	-	+	*	+	-	-	-	-	-	+	-	-	-
<i>S. farinacea</i> Benth.	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>S. reflexa</i> Hornem.	-	*	-	*	+	-	-	-	-	-	-	-	+	-	-
<hr/>															
Verbenaceae															
Avicenniioideae															
<i>Avicennia nitida</i> Jacq.	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
<hr/>															
Caryopteridoideae															
Caryopterideae															
<i>Caryopteris divaricata</i> (Siebold & Zucc.) Maxim.	?	?	?	+	+	?	?	?	?	?	-	-	+	-	-
<i>C. forrestii</i> Diels (#1)	?	?	?	*	?	?	?	?	?	?	-	+	+	-	-
<i>C. forrestii</i> Diels (#2)	?	?	?	*	?	?	?	?	?	?	-	+	+	-	-
<i>C. grata</i> Benth.	-	+	-	+	*	-	-	-	-	-	-	-	+	-	-
<i>C. incana</i> (Thunb.) Miq. (#2)	?	+	?	+	?	?	?	?	?	?	-	+	+	-	-
<i>C. mongholica</i> Bunge (#2)	?	?	?	+	?	?	?	?	?	?	-	?	+	-	-
<i>C. nepetaefolia</i> (Benth.) Maxim.	-	-	-	*	-	-	-	-	-	-	-	-	+	-	-
<i>C. odorata</i> (Ham.) Robinson	-	+	-	*	-	-	-	-	-	-	-	-	+	-	-
<i>C. terniflora</i> Maxim.	-	+	+	*	-	-	-	-	-	-	-	+	+	-	-
<i>Glossocarya siamensis</i> Craib	-	+	+	+	*	+	-	-	-	-	-	+	+	-	-
<i>Peronema canescens</i> Jack	?	?	?	+	?	?	?	?	?	?	?	+	+	-	-
<i>Petraeovitea kinabaluensis</i> Munir	-	-	-	+	*	-	-	-	-	-	-	-	-	-	-
<i>P. multiflora</i> (Smith) Merr.	-	-	-	-	*	+	-	+	+	+	+	-	-	-	-
<hr/>															
Teijsmanniodendreae															
<i>Teijsmanniodendron ahernianum</i> (Merr.) Bakh.	-	-	-	+	+	-	-	-	+	*	-	-	+	-	-
<i>T. subspicatum</i> (H.Hallier) Kosterm.	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-
<hr/>															
Chloanthoideae															
Achariteae															
<i>Nesogenes jupontii</i> Hemsley	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>N. euphrasioides</i> (Hook. & Arn.) A.DC.	-	-	-	-	+	-	-	-	-	-	-	+	+	-	-
<i>Pityrodia atriplicina</i> (F.Muell.) Benth.	?	?	+	+	?	?	?	?	?	?	?	-	-	-	+
<i>P. dilatata</i> (F.Muell.) Benth.	?	?	?	+	+	?	?	?	?	?	?	-	-	-	+
<i>P. paniculata</i> (F.Muell.) Benth.	-	*	+	-	-	-	-	-	-	-	-	-	-	-	+

TABLE 2. (continued).

Taxa ^a	Subsessile Glands ^b											Nonglandular ^c			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
<u>Spartothamnella puberula</u> (F.Muell.)															
Maiden & Betché (#1)	?	?	?	?	+	?	?	?	?	?	-	+	+	-	+
<u>S. puberula</u> (F.Muell.)															
Maiden & Betché (#2)	-	+	+	*	-	-	-	-	-	-	-	+	+	-	+
<u>S. puberula</u> (F.Muell.)															
Maiden & Betché (#3)	-	+	-	*	-	-	-	-	-	-	-	+	+	-	+
Chloantheae															
<u>Chloanthes stoechadis</u> R.Br.	?	?	?	?	?	?	?	?	?	?	?	-	+	-	+
<u>Cyanostegia angustifolia</u> Turcz.	?	?	?	?	+	?	?	?	?	?	?	-	-	-	-
<u>C. microphylla</u> S.Moore	?	?	?	?	+	?	?	?	?	?	?	-	+	-	-
Physopsidae															
<u>Dicrastylis exsuccosa</u> (F.Muell.) Druce	-	*	+	+	?	?	-	-	-	-	-	-	-	-	+
<u>Lachnostachys eriobotrya</u> (F.Muell.) Druce	?	?	?	?	?	?	?	?	?	?	?	-	-	-	+
<u>Mallophora globiflora</u> Endl.	?	?	?	?	?	?	?	?	?	?	?	-	-	-	+
<u>Newcastelia cephalantha</u> F.Muell.	*	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Nyctanthoideae															
<u>Nyctanthes arbor-tristis</u> L.	+	+	+	*	+	-	-	-	-	-	-	+	-	-	-
Phrymoideae															
<u>Phryma leptostachya</u> L.	-	*	-	-	-	-	-	-	-	-	-	-	+	-	-
Symphorematoideae															
<u>Congea chinensis</u> Mold.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-
<u>C. forbesii</u> King & Gamble	-	-	-	*	-	-	-	-	-	-	+	-	+	-	-
<u>C. tomentosa</u> Roxb.	-	-	-	*	+	-	-	-	-	-	-	-	+	-	+
<u>Sphenodesme ferruginea</u> (Griffith) Briq.	?	?	?	?	?	?	?	?	?	?	?	-	+	-	+
<u>S. pentandra</u> Jack	-	-	-	+	*	-	-	-	-	-	+	-	+	-	-
<u>Symphorema luzonicum</u> (Blanco)															
Fernandez-Villar	?	?	?	?	+	?	?	?	?	?	?	-	-	-	-
Verbenoideae															
Citharexyleae															
<u>Citharexylum affine</u> D.Don	-	-	-	-	*	-	-	-	-	-	+	+	-	-	-
<u>C. berlandieri</u> Robinson	-	-	-	-	*	-	-	+	+	-	-	+	-	-	-
<u>C. caudatum</u> L.	-	-	-	-	*	+	-	+	+	-	-	+	-	-	-
<u>C. ligustrinum</u> Van Houtte	-	-	-	-	+	-	-	*	-	-	-	-	-	-	-
<u>C. punctatum</u> Greenman	-	-	-	-	*	-	-	*	+	-	-	+	-	-	-
<u>Duranta mandonii</u> Mold.	-	-	-	-	+	-	-	*	+	-	-	-	+	-	-
<u>D. mutisii</u> L.f.	-	-	-	-	+	-	-	+	*	+	+	?	?	-	-
<u>D. peruviana</u> Mold.	-	-	-	-	*	?	?	?	?	?	-	-	+	-	-
<u>D. repens</u> L. (#1)	-	-	-	+	*	-	-	-	-	-	+	+	+	-	-
<u>D. repens</u> L. (#2)	-	-	-	+	*	-	-	-	-	-	+	-	+	-	-
<u>Rehdera trinervis</u> (S.F.Blake) Mold.	-	*	-	+	-	-	-	-	-	-	-	-	-	-	-
<u>Rhaphithamnus spinosus</u> (A.L.Juss.) Mold.	-	-	+	*	-	-	-	-	-	-	+	+	-	-	-
Lantaneae															
<u>Aloysia gratissima</u> (Gill. & Hook.) Tronc.	*	-	-	+	-	-	-	-	-	-	-	+	-	-	-
<u>A. wrightii</u> (A.Gray) A.A.Heller	*	-	-	-	-	-	-	-	-	-	-	+	-	-	-
<u>Bouchea prismatica</u> (L.) Kuntze	-	*	+	+	+	-	-	-	-	-	-	+	-	-	-
<u>Diostea juncea</u> (Gillies & Hook.) Miers	?	?	?	?	?	?	?	?	?	?	?	+	-	-	-
<u>Lantana horrida</u> Kunth (#1)	+	*	+	+	+	-	-	-	-	-	-	+	-	-	-
<u>L. horrida</u> Kunth (#2)	+	*	-	+	+	-	-	-	-	-	-	+	-	-	-
<u>L. involucrata</u> L.	*	+	-	+	-	-	-	-	-	-	-	+	-	-	-

TABLE 2. (continued).

Taxa ^a	Subsessile Glands ^b											Nonglandular ^c			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
<i>Lippia graveolens</i> Kunth	*	+	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Phyla incisa</i> Small	?	?	?	?	?	?	?	?	?	?	?	-	-	+	-
<i>P. lanceolata</i> (Michaux) E. Greene [§]	*	+	-	+	-	-	-	-	-	-	-	-	-	+	-
<i>P. nodiflora</i> (L.) E. Greene	?	+	?	?	+	?	?	?	?	?	-	-	-	+	-
<i>Priva aspera</i> Kunth	-	*	-	+	-	-	-	-	-	-	-	+	-	-	-
<i>P. grandiflora</i> (Ortega) Mold.	-	*	+	+	+	-	-	-	-	-	-	+	-	-	-
<i>Stachytarpheta frantzii</i> Polak.	-	*	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>S. jamaicensis</i> (L.) Vahl	-	-	+	*	-	-	-	-	-	-	-	-	-	-	-
Monochileae															
<i>Amasonia campestris</i> (Aublet) Mold.	-	-	-	+	*	-	-	-	-	-	+	+	+	-	-
<i>A. hirta</i> Benth.	?	?	?	+	+	?	?	?	?	?	+	-	+	-	-
Petreeae															
<i>Casselia hymenocalyx</i> Briq.	-	*	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Petrea arborea</i> Kunth	?	?	?	+	?	?	?	?	?	?	-	+	-	-	-
<i>P. volubilis</i> L. (#1)	-	-	-	+	*	-	-	-	-	-	-	+	-	-	-
<i>P. volubilis</i> L. (#2)	-	-	-	+	*	-	-	-	-	-	-	+	-	-	-
<i>Recordia boliviana</i> Mold.	?	?	?	?	?	?	?	?	?	?	?	+	+	-	-
Verbeneae															
<i>Glandularia bipinnatifida</i> (Nutt.) Nutt.	-	-	-	*	-	-	-	-	-	-	-	+	-	-	-
<i>G. canadensis</i> (L.) Small	-	-	-	*	-	-	-	-	-	-	-	+	-	-	-
<i>Hierobotana inflata</i> (Kunth.) Briq.	?	?	?	?	?	?	?	?	?	?	?	+	-	-	-
<i>Junellia ligustrina</i> (Lagascana) Mold.	-	+	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Tamonea curassavica</i> (L.) Pers.	-	*	-	+	+	-	-	-	-	-	-	+	-	-	-
<i>Verbena hastata</i> L. [§]	-	-	-	+	*	-	-	-	-	-	-	+	-	-	-
<i>V. litoralis</i> Kunth	?	?	?	+	?	?	?	?	?	?	-	+	-	-	-
<i>V. maddougallii</i> A.A.Heller	-	-	+	*	-	-	-	-	-	-	-	+	-	-	-
<i>V. pumila</i> Rydb.	-	-	-	*	-	-	-	-	-	-	-	+	-	-	-
<i>V. urticifolia</i> L. [§]	-	-	+	*	+	-	-	+	-	-	-	+	-	-	-
Viticoideae															
Callicarpeae															
<i>Aegiphila aculeifera</i> Mold.	-	-	-	*	+	-	+	+	-	-	-	-	+	-	-
<i>A. deppeana</i> Steudel	-	-	+	+	*	-	-	-	-	-	-	-	+	-	-
<i>A. pendula</i> Mold.	-	+	+	*	+	-	-	-	-	-	+	+	+	-	-
<i>Callicarpa americana</i> L.	-	-	-	+	+	+	-	*	+	-	+	-	+	-	+
<i>C. dichotoma</i> (Lour.) K.Koch	-	-	-	+	+	-	-	*	+	+	+	+	+	-	-
<i>C. mollis</i> Siebold & Zucc.	?	?	?	+	?	?	?	?	?	?	?	+	+	-	+
<i>Geunsia farinosa</i> Blume	?	?	?	?	?	?	?	?	?	?	-	+	+	-	+
Clerodendreae															
<i>Clerodendrum aculeatum</i> (L.) Schldl.	-	-	-	+	*	-	-	?	?	?	-	-	+	-	-
<i>C. anafense</i> Britton & P.Wilson	-	-	-	-	*	+	-	-	-	-	+	-	+	-	-
<i>C. capitatum</i> (Willd.) Schum. & Thonn.	-	-	-	-	+	?	?	?	?	?	-	-	+	-	-
<i>C. cuneatum</i> Gurke	-	-	-	+	*	-	-	-	-	-	-	-	+	-	+
<i>C. floribundum</i> R.Br.	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-
<i>C. glabrum</i> E.Meyer	-	-	-	-	*	-	-	+	-	-	-	-	-	-	-
<i>C. inerme</i> (L.) Gaertner	-	-	+	*	+	-	-	-	-	-	-	-	+	-	-
<i>C. philippinum</i> Schauer	-	-	-	+	*	-	-	-	-	-	+	+	+	-	-
<i>C. squiresii</i> Merr.	-	+	+	*	+	-	-	-	-	-	+	-	+	-	-
<i>Faradaya amicomum</i> (Seemann) Seemann	-	-	-	-	*	+	-	-	-	-	-	-	-	-	-
<i>F. splendida</i> F.Muell.	?	?	?	?	+	+	?	?	?	?	-	-	-	-	-

TABLE 2. (continued).

Taxa ^a	Subsessile Glands ^b											Nonglandular ^c			
	1	2	3	4	5	6	7	8	9	10	11	su	sm	bu	bm
<i>Holmskioldia sanguinea</i> Retz. (#1)	-	-	-	+	-	-	*	-	-	-	-	-	+	-	-
<i>H. sanguinea</i> Retz. (#2)	-	-	-	*	-	-	+	+	+	-	-	-	+	-	-
<i>H. sanguinea</i> Retz. (#3)	-	-	-	+	-	-	+	+	+	-	-	-	+	-	-
<i>H. tettensis</i> (Klotzsch) Vatke	-	-	-	+	+	-	-	*	+	-	-	+	+	-	-
<i>Kalaharia spinescens</i> Gurke	-	-	-	*	-	-	+	-	-	+	-	+	+	-	-
<i>Karomia fragrans</i> Dop	-	-	-	*	+	-	-	-	-	-	-	-	-	-	-
<i>Oxera morierli</i> Vieill.	-	-	-	-	+	-	*	-	-	-	-	-	-	-	-
<i>O. nerifolia</i> Beauv.	-	-	+	*	+	-	-	-	-	+	-	-	-	-	-
<i>O. sulfurea</i> Dubard	-	-	-	+	*	-	-	-	-	-	-	-	-	-	-
<i>Teucrium parvifolium</i> Hook.f.	-	+	+	*	-	-	-	-	-	-	-	-	+	-	-
Tectoneae															
<i>Petitia domingensis</i> Jacq.	-	-	-	*	+	-	-	-	-	-	-	-	+	-	-
Viticeae															
<i>Cornutia grandiflora</i> (Cham. & Schldl.) Schauer	?	?	?	?	+	?	?	?	?	?	-	-	+	-	-
<i>C. pyramidata</i> L.	-	-	+	*	+	-	-	-	-	-	+	+	+	-	-
<i>Garrettia siamensis</i> Fletcher	-	-	-	+	*	-	-	-	-	-	+	-	+	-	-
<i>Gmelina delavayana</i> Dop	?	?	+	+	+	?	?	?	?	?	+	-	-	-	-
<i>G. moluccana</i> (Blume) Backer	-	-	-	-	-	-	-	-	-	-	-	+	+	-	-
<i>Premna barbata</i> Wallich	-	-	-	*	+	-	+	-	-	-	-	-	+	-	-
<i>P. corymbosa</i> Willd.	-	-	-	-	*	-	-	+	-	-	-	+	+	-	-
<i>P. foetida</i> Reinw.	-	-	-	*	-	-	-	-	-	-	-	-	+	-	-
<i>P. japonica</i> Miq.	-	-	-	*	+	-	+	+	-	-	-	-	+	-	-
<i>P. octonervia</i> Merr. & Metcalf	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudocarpidium avicennioides</i> (A.Rich.) Millsp.	?	?	?	+	?	?	?	?	?	?	-	+	-	-	-
<i>P. wrightii</i> Millsp.	-	-	-	*	-	-	-	-	-	-	-	-	-	-	-
<i>Tsoongia axillariflora</i> Merr.	-	-	-	+	*	-	-	-	-	-	-	+	+	-	-
<i>Vitex agnus-castus</i> L.	-	-	-	*	-	-	-	-	-	-	-	+	+	-	-
<i>V. cannabifolia</i> Siebold & Zucc.	-	-	-	*	+	-	-	-	-	-	-	+	+	-	-

^aIf name is followed by the symbol §, data are from Abu-Asab and Cantino (1987a). All other data are from the present survey. #1, #2, etc. refer to different specimens of a species; the numbers correspond to entries in the voucher list deposited in four major botanical libraries (see Materials and Methods).

^bSubsessile Gland Types defined in Appendix 1. Symbols: *, commonest type(s); +, present; -, absent; ?, unknown whether present or absent (glands are poorly stained or obscured by dense trichomes).

^cNonglandular Trichomes: su, simple unicellular; sm, simple multicellular (uniseriate); bu, branched unicellular; bm, branched multicellular. Symbols: +, present; -, absent; ?, presence uncertain.

most widespread in the Chloanthoideae and were not observed in the Verbenoideae, Ajugeae, Prostanthereae, Scutellariaeae, or Nepeteae. However, Robert (1912) reported them in some species of *Citharexylum* (Verbenoideae), and within the Prostanthereae they are known from two species of *Prostanthera* (Conn, 1984) and at least two species of *Hemigenia* R. Br. (Bentham, 1870; B. Conn, pers. comm.). Outside the Chloanthoideae, genera whose leaves are

characteristically clothed with branched, multicellular trichomes include *Comanthosphace*, *Gomphostemma* Benth., *Leucosceptrum*, *Marrubium* L., *Perovskia* Karel., *Phlomis*, and *Rostrinucula* (see TABLE 2; Bokhari & Hedge, 1971; Azizian & Cutler, 1982; Press, 1982). Branched, unicellular (two-armed) trichomes were found only in *Phyla*.

DISCUSSION

SAMPLE SIZE LIMITATIONS

Because this survey was motivated by an interest in phylogenetic relationships among genera and suprageneric groups, particularly within subfam. Lamioideae and related Verbenaceae, taxonomic breadth of coverage was emphasized at the expense of depth. Very few species are represented by more than a single specimen. Consequently, the data in the tables should not be used to characterize species or infer interspecific relationships, although they may suggest avenues for further research in certain genera. However, the sample sizes for many genera of Lamioideae and for suprageneric groups in both families are sufficient to provide a general picture of the distribution of trichome and stomatal types in the Lamiales.

In most genera of subfam. Nepetoideae, the number of species sampled is too low to be any more than suggestive about the epidermal anatomy of the genus. Although perhaps disappointing to those whose primary interest lies in this subfamily, the shallow sampling of this group is justifiable in relation to the ultimate objective of the survey—an improved understanding of the origin of the Labiatae and of relationships among its basal clades (which lie within the paraphyletic or polyphyletic subfam. Lamioideae). Although subfam. Nepetoideae includes well over half the genera of Labiatae, it represents but a single clade (Cantino & Sanders, 1986) whose closest relatives lie somewhere within subfam. Lamioideae. Knowledge of its character-variation pattern is therefore no more nor less critical to an understanding of the origin and early evolution of the Labiatae than is that of any single genus in the Lamioideae.

COMPARISON WITH PUBLISHED DATA

There has been no broad survey of the morphology of trichomes in the Labiatae or the morphology of stomata in the Verbenaceae. El-Gazzar and Watson (1968) investigated stomatal configurations in a wide range of Labiatae but listed only the predominant type in each genus. Furthermore, their observations regarding many genera of the Lamioideae conflict markedly with my own (discussed below). Robert's (1912) study of trichome morphology in the Verbenaceae provides extensive data on the nonglandular trichomes and capitate glandular trichomes of some 55 genera, but the descriptions and illustrations of the more complex subsessile glands (except type 11) are, for the most part, inadequate to classify them according to the system used here. Nonetheless, the study is a useful complement to the present one in that the nonglandular trichomes are described in far more detail than they are in this paper. Moreover,

Robert included 11 genera in his survey that are not covered here, most of them in the Chloanthoideae and the Stilboideae.

In addition to these two surveys, some information is available on individual genera or groups of genera (Labiatae—Mayer (1909), Bech (1963), Kaleva (1967), Wieffering (1970), Bokhari & Hedge (1971, 1976), Inamdar & Bhatt (1972), Heinrich (1973), Rudall (1980, 1986), Azizian & Cutler (1982), Press (1982), Sharma & Shome (1982), Bruni & Modenesi (1983), Manzanares *et al.* (1983), Shah & Naidu (1983), Bosabalidis & Tsekos (1984), Werker, Putievsky, & Ravid (1985), Werker, Ravid, & Putievsky (1985a, b); Verbenaceae—Mullan (1931), Pant & Kidwai (1964), Kundu & De (1968), Inamdar (1969a), Ramayya & Rao (1969), Inamdar *et al.* (1976), Fahn & Shimony (1977), Puff (1978), Trivedi & Upadhyay (1978), Bhatt *et al.* (1979), Mathew & Shah (1981, 1983), Shah & Mathew (1982a, b)).

By and large, the data provided in these publications are consistent with those reported here, but some disagreements and additions to the data base warrant discussion. Robert (1912) reported type 1 subsessile glands in nine genera of the Verbenaceae in which I either failed to find them (*Avicennia* L., *Casselia* Nees & C. Martius, *Dicrastylis* J. L. Drumm. ex Harvey, *Petitia* Jacq., *Priva* Adanson, *Stachytarpheta*, and *Verbena* L.) or could not determine whether they were present or absent (*Peronema* Jack), or that I did not study (*Hemiphora* F. Mueller). Type 1 glands were reported in *Avicennia* by Mullan (1931) as well, but not in the very thorough study by Fahn and Shimony (1977), so this discrepancy probably represents genuine intrageneric variation rather than error. In the Labiatae type 1 glands have been reported from some species of *Phlomis* (Bech, 1963; Azizian & Cutler, 1982), a genus in which I failed to find them, as well as from numerous genera of subfam. Nepetoideae (see below).

Studies of the subsessile glands of tribe Mentheae (Mayer, 1909; Kaleva, 1967; Bruni & Modenesi, 1983; Bosabalidis & Tsekos, 1984; Werker, Putievsky, & Ravid, 1985; Werker, Ravid, & Putievsky, 1985a), including five genera not examined here, confirm that the group is characterized by the absence of type 4 glands and the presence of both type 1 glands and those with tangential walls (usually types 6 and/or 9). Type 1 glands were also reported from the majority of the Ocimeae studied by Shah and Naidu (1983) and in subtribe Hyptidinae (Ocimeae) by Rudall (1980). In tribe Salviae glandular trichomes that appear to be type 1 have been reported in *Dorystaechas* Boiss. & Heldr. ex Benth, *Horminum* L., *Meriandra* Benth, *Perovskia*, *Salvia* L., and *Zhumeria* Rech. f. & Wendelbo (Bech, 1963; Bokhari & Hedge, 1971, 1976; Sharma & Shome, 1982). Thus type 1 glands occur widely in subfam. Nepetoideae and may be better thought of as characterizing this more inclusive group rather than tribe Mentheae alone.

It is difficult to evaluate the apparent conflicts in the distribution of stomatal types in the Verbenaceae—among published works and between some of them and the present study—because of differences in how authors classified the stomatal complexes. For example, Mathew and Shah (1981) reported anisocytic stomata in more genera of Verbenaceae than I have, but upon examination of their illustrations, it appears that they have classified as anisocytic many stomata that I would have scored as anomocytic—stomata that happen to be in

contact with three surrounding cells, but these (some or all of them) not distinguishable from the other epidermal cells. Several other stomatal types (e.g., haplocytic, tetracytic) recognized by Shah and Mathew in this and other papers (1982a, b) were also treated as anomocytic in the present study. On the other hand, stomata that I would have scored as actinocytic are treated by Mathew and Shah as anomocytic in some cases and cyclocytic in others.

In spite of these classification problems, which apply mainly to the papers by Shah and Mathew, published illustrations provide some genuine additions to the data base. Stomata that I would have scored as anisocytic are documented for seven genera in which I did not record them (*Bouchea*, *Gmelina* L., *Petrea* L., *Phyla*, *Premna*, and *Stachytarpheta*) or that I did not study (*Tectona* L. f.) (Pant & Kidwai, 1964; Inamdar *et al.*, 1976; Bhatt *et al.*, 1979; Mathew & Shah, 1981). In addition, diacytic stomata have been recorded from *Citharexylum*, *Gmelina*, and *Nyctanthes* L. (Trivedi & Upadhyay, 1978; Bhatt *et al.*, 1979; Mathew & Shah, 1981), paracytic from *Nyctanthes*, *Premna*, and *Tectona* (Inamdar *et al.*, 1976; Trivedi & Upadhyay, 1978; Mathew & Shah, 1981), and cyclocytic from a few species of *Clerodendrum* (Shah & Mathew, 1982a).

With regard to the Labiatae, there is universal agreement that the diacytic types of stomata (including diallelocytic) predominate in subfam. Nepetoideae, but El-Gazzar and Watson's (1968, 1970) observations on subfam. Lamioideae conflict markedly with my own. The data in TABLE 1 do not support their assertion (1970, p. 476) that if *Prunella* L., *Cleonia* L., and the North American Melittidinae are excluded, anomocytic stomata "are the rule" in Bentham's "Stachydeae" (Lamieae). Both diacytic and anomocytic stomata occur in all examined genera of the group thus circumscribed by El-Gazzar and Watson (i.e., excluding *Prunella*, etc.), and diacytic stomata are as or more common than anomocytic in about two thirds of them. Furthermore, El-Gazzar and Watson (1968) listed *Achyrosperrum* Blume, *Acrotome* Bentham ex Endl., *Ajuga*, *Anisomeles*, *Comanthosphace*, *Craniotome*, *Galeobdolon* Adanson, *Gomphostemma*, *Moluccella* L., *Phyllostegia* Bentham, *Rostrinucula*, *Sideritis*, *Thuspeinanta* T. Durand, and *Wiedemannia* Fischer & C. Meyer (not all in Bentham's Lamieae) as having predominantly anomocytic and/or anisocytic stomata, whereas I found diacytic and/or diallelocytic stomata to be commonest in these genera and did not find anisocytic stomata in any of them.

PHYLOGENETIC SIGNIFICANCE

This is one of several character surveys being conducted in preparation for a cladistic analysis of the Lamiales. Although the phylogenetic significance of the data in TABLES 1 and 2 can best be assessed in the context of such an analysis, Hennigian reasoning can be applied to single characters to yield tentative suggestions about their significance. Thus if it can be shown that a character state is derived in a particular group, it may be treated as a potential synapomorphy for a clade within that group unless the distribution of other characters indicates that such a conclusion is unparsimonious. This approach will be employed here.

Outgroup comparison (Watrous & Wheeler, 1981; Maddison *et al.*, 1984)

will be used to assess character polarity. It is generally recognized that the Labiatae arose from the Verbenaceae (Cronquist, 1981), which is consequently paraphyletic, but the affinities of the Labiatae are difficult to identify more precisely. Pollen morphology (Raj, 1983) and gynoecial structure (Junell, 1934) suggest that the closest relatives of the Labiatae lie within the Viticoideae and/or the Caryopteridoideae and that the Verbenoideae are unlikely to be closely related. The other subfamilies, except perhaps the Chloanthoideae, seem to have little in common with the Labiatae. In evaluating the polarity and phylogenetic significance of characters within the Labiatae, one must therefore pay particular attention to their occurrence in the Viticoideae and the Caryopteridoideae.

The Scrophulariales is the best-supported sister group of the Lamiales (Cantino, 1982; Frohlich, 1987) and will be treated here as the sole outgroup. More distant outgroups will not be considered because higher-level relationships in the Asteridae are poorly resolved. The distributions of stomatal and trichome types are reasonably well documented in the Acanthaceae (De, 1967; Ahmad, 1974, 1978; Karlström, 1978, 1980) and the Gesneriaceae (Rosser & Burtt, 1969; Van Cotthem, 1971; Sahasrabudhe & Stace, 1974; Herat & Theobald, 1979; Yuen & Dehgan, 1982; Wiehler, 1983), but extensive surveys have not been published for the other families of Scrophulariales. In the discussion that follows, statements about the epidermal anatomy of these families are based on the summaries provided by Solereder (1908) and Metcalfe and Chalk (1950), the distributions of stomatal types tabulated by Wilkinson (1979), and studies of particular genera or groups of genera (Bignoniaceae—Paliwal (1970), Jain (1978), Elias & Newcombe (1979), Henrickson (1985); Lentibulariaceae—Casper (1966), Komiya (1972), Trinta (1979), Fineran (1985); Myoporaceae—Dell & McComb (1977); Pedaliaceae (including Martyniaceae)—Mullan (1936), Inamdar (1969b), Karatela & Gill (1984); Plantaginaceae—Andrzejewska-Golec & Swietoslawski (1987); Scrophulariaceae—Fedorowicz (1916), Spoerri (1930), Bhatt & Inamdar (1975), Stefanova-Gateva & Boeva (1979), Doaigey & Harkiss (1982), Henrickson & Flyr (1985)).

Anomocytic stomata, found in all examined species of Verbenaceae and nearly all Labiatae, are the most widespread stomatal type in the Scrophulariales as well, occurring commonly in every family except the Acanthaceae (absent) and the Plantaginaceae (rare). Hence the hypothesis that their presence is ancestral (and their absence derived) in the Labiatae is parsimonious, regardless of whether the Labiatae are monophyletic or polyphyletic and of which groups of Verbenaceae are most closely related to the Labiatae. It is also worth noting that presence/absence of anomocytic stomata exhibits less intrageneric variation than most other characters in this study and is therefore of particular value in assessing intergeneric phylogenetic relationships. In tribe Lamieae anomocytic stomata are universally present in 42 of the 45 investigated genera and universally absent in the other three (*Brazoria*, *Macbridea*, and *Physostegia* Benth). Absence of anomocytic stomata is thus a corroborating synapomorphy for a clade proposed by Abu-Asab and Cantino (1987a) comprising these three genera. It may be of some phylogenetic significance in subfam.

Nepetoideae as well, but the much poorer sample of this subfamily makes evaluation difficult.

Diallelocytic stomata are common in the Acanthaceae but rare to absent in the other families of the Scrophulariales. If the Acanthaceae were the basal clade of the Scrophulariales, polarity of this character within the Lamiales would be equivocal. However, assuming the Acanthaceae are not basal (a reasonable assumption; see Cronquist, 1981), it is most parsimonious to hypothesize that absence of diallelocytic stomata is the ancestral condition in the Lamiales and that their presence is derived. The three-celled diallelocytic type is of special interest as the only epidermal feature whose distribution parallels relatively closely the traditional boundary between the families; i.e., it is very common in the Labiatae but infrequent in the subfamilies of the Verbenaceae that appear to be most closely related to them. Its phylogenetic significance is discussed below (see Circumscription of Labiatae). Four-celled diallelocytic stomata can be hypothesized to represent a derived state as well, again assuming that the Acanthaceae is not the basal family of the Scrophulariales, but because this character exhibits far more intrageneric variation than the previous one, it is of little phylogenetic significance above the genus level.

In the Scrophulariales cyclocytic stomata have been reported only from the Bignoniaceae, where they are apparently infrequent. Their presence in three of the four examined species of *Duranta* is therefore hypothesized to be derived. The other species (*D. repens*) has quite a different set of stomatal types (anisocytic and heliocytic but not cyclocytic), a distinction that might be of systematic value within the genus and warrants further study. It should be noted, though, that many stomata in the former three species of *Duranta* have an incomplete or irregular circle of subsidiary cells and thus seem to be intermediate between anomocytic and cyclocytic. Study of stomatal ontogeny in this genus is needed before any systematic conclusions are drawn. Two other rare stomatal types, staurocytic and parallelocytic, also appear to be derived states and of possible phylogenetic significance, the former at the species level within *Lavandula* L. and the latter as a synapomorphy for *Phyla*.

The distributions of the other stomatal types are of limited phylogenetic value above the genus level because of difficulties in assessing polarity, questions of homology, and/or high intrageneric variability. Actinocytic stomata have been reported only a few times in the Scrophulariales (in a few members of the Bignoniaceae, Gesneriaceae and Lentibulariaceae), but it is unclear whether they are genuinely rare or have been classified as anomocytic by most authors. Moreover, the ontogeny of actinocytic stomata in the Lamiales is unknown; thus they cannot necessarily be considered homologous in the taxa where they occur. A more definite homology problem exists in the case of paracytic stomata, which appear to develop via several different ontogenetic pathways in the Lamiales (discussed above).

Anisocytic stomata are the predominant type in the Gesneriaceae; they also occur at least occasionally in the Bignoniaceae, Scrophulariaceae, Pedaliaceae, and Myoporaceae but never in the other families of Scrophulariales. Hence it is unclear whether presence or absence is ancestral in the Lamiales. Similarly,

diacytic stomata are common in the Acanthaceae and the Plantaginaceae, at least occasional in the Lentibulariaceae, the Pedaliaceae, and the Scrophulariaceae, and rare to absent in the other families of the Scrophulariales. Again, polarity in the Lamiales cannot be assessed without knowing something about cladistic topology within the Scrophulariales. Nor can polarity be assessed within the Labiatae, because both anisocytic and diacytic stomata occur widely, but far from universally, in the two subfamilies of the Verbenaceae that are thought to be closest to them. This is unfortunate, because the two characters exhibit relatively little intrageneric variation within the Labiatae and an intriguing, inversely correlated distribution pattern. In the Prostanthereae and two genera of the Ajugeae (*Tetraclea* and *Trichostema*), diacytic stomata are rare while anisocytic stomata are nearly universally present and often the most common stomatal type. In the rest of the Ajugeae and all gynobasic-styled Labiatae, the reverse is true. From a phenetic standpoint at least, these characters neatly distinguish the Prostanthereae from the gynobasic-styled Labiatae and also give cause to question whether *Tetraclea* and *Trichostema* belong in the family (further discussed below). The inverse correlation between anisocytic and diacytic stomata is weaker in the Verbenaceae, where many genera have neither, and a few (e.g., *Holmskioldia* and *Lantana*) have both. The group of Verbenaceae in which anisocytic stomata are most consistently present is subfam. Chloanthoideae. Their absence in *Nesogenes* A. DC., which also lacks the branched trichomes characteristic of the Chloanthoideae (see below), is consistent with its exclusion from this group (as by Marais, 1981).

Stomatal position (leaves hypostomatic vs. amphistomatic) is of little value as a phylogenetic indicator because of its high intrageneric variability, the existence of an intermediate condition with a few stomata on the adaxial surface of the blade, and the apparent correlation with environmental factors (discussed above). This correlation appears to hold in the Scrophulariales as well: hypostomatic leaves predominate in the families best represented in the humid tropics (Acanthaceae, Gesneriaceae, Bignoniaceae), while amphistomatic ones are commonest in those well represented in xeric habitats (Myoporaceae, Pedaliaceae, Plantaginaceae). Both conditions occur widely in the Scrophulariaceae.

Subsessile glands, nearly universally present in the Labiatae and the Verbenaceae, are equally characteristic of the Scrophulariales, where they are frequent in all families except the Myoporaceae and the Plantaginaceae. Type 4 is the most common type in the Scrophulariales and therefore probably represents an ancestral condition in the Lamiales, where it was found in more than three quarters of the genera of both families. The absence of type 4 glands in nearly all examined Mentheae can thus reasonably be hypothesized to be a derived state and may be of help in circumscribing this poorly defined tribe. The character's value as a phylogenetic indicator is reduced, however, by its relatively high intrageneric variability elsewhere in the Labiatae and the Verbenaceae. Sessile glandular trichomes of types 1, 2, and 5 are also quite widespread in the Scrophulariales but are not so universal as to permit polarity assessment in the Lamiales.

The more complex gland types (6–11) are generally rare in the Scrophulariales (except that type 11 is widespread in the Bignoniaceae). It is reasonable to

hypothesize that all are derived in the Lamiales. However, these characters exhibit so little constancy within genera (and sometimes even within species; e.g., types 8 and 9 in *Tinnea aethiopica*, types 8 and 10 in *Holmskioldia sanguinea*) that their phylogenetic significance above the species level is probably minimal. Moreover, types 9 and 10 may arise through more than one ontogenetic pathway (see FIGURE 3 and associated text) and are thus not necessarily homologous where they do occur. In view of these problems, the presence of type 10 glands in all species of *Brazoria* and *Macbridea* and some species of *Physostegia*, invoked by Abu-Asab and Cantino (1987a) in support of a clade composed of these three genera, must be considered very weak evidence. This clade is more convincingly supported by the absence of anomocytic stomata, as discussed above.

Nonglandular trichomes, both simple-unicellular and uniseriate, occur widely in the Scrophulariales, the latter type being found in nearly all nonglabrous members of the order. The presence of both kinds of "hairs" is thus probably ancestral in the Lamiales. There is a great deal of intrageneric variation in presence vs. absence of unicellular trichomes in the Lamiales, but much less so for uniseriate trichomes. The rarity of uniseriate trichomes in the Verbenoideae is therefore of interest. Presence of *only* unicellular hairs (i.e., absence of uniseriate hairs in nonglabrous species) may represent a synapomorphy, and the taxonomic position of the few genera of Verbenoideae in which uniseriate trichomes were observed (*Amasonia*, *Duranta*, *Recordia* Mold., *Stachytarpheta*) should be examined. Indeed, the pollen morphology of *Amasonia* (but not of the other three genera) suggests that it belongs with the Viticoideae or the Caryopteridoideae rather than the Verbenoideae (Raj, 1983). The rarity of multicellular foliar hairs in the Verbenoideae has also been noted by Robert (1912) and El-Gazzar (1974). This character may be of phylogenetic significance in the Prostanthereae as well, but with over half the examined species being glabrous, the sample size of those with hairs of any kind was too small to draw any conclusions.

Branched, multicellular trichomes occur in a scattering of genera in the Scrophulariales but are not common in the major families; they are unlikely to be ancestral in the Lamiales. Their presence in most Chloanthoideae may be a synapomorphy for a large subgroup composed of all genera except *Nesogenes*. (Although the foliage of *Cyanostegia* Turcz. is glabrous or nearly so, branched hairs are present on the ovaries and fruits (Munir, 1978).) Presence of branched, multicellular trichomes is also a probable synapomorphy uniting the species of individual genera such as *Phlomis* and *Perovskia*—genera that, on the basis of other characters, are unlikely to be closely related to each other. Unicellular, two-armed trichomes occur in one genus of Acanthaceae (Solereder, 1908) but are clearly a derived condition in the Lamiales, where they represent a synapomorphy of *Phyla*.

CIRCUMSCRIPTION OF THE LABIATAE

This study was originally undertaken in the hope that it might contribute to an understanding of phylogenetic relationships among the basal clades of the

Labiatae. Several stomatal characters have turned out to be of interest in this regard. As discussed above, the presence of diallelocytic stomata can reasonably be hypothesized to be a derived state. As such, it would seem to support a clade composed of the gynobasic-styled Labiatae (i.e., subfam. Nepetoideae, subfam. Lamioideae tribes Lamieae, Pogostemoneae, and Scutellarieae, and the genera of "uncertain tribal affinities" in TABLE 1) plus *Acrymia* Prain, *Ajuga*, *Cymaria*, *Kinostemon*, *Rubiteucris* Kudo, and *Teucrium* of the Ajugeae. In the Verbenaceae diallelocytic stomata were found in seven genera of subfam. Verbenoideae, two of Caryopteridoideae, and two of Viticoideae (see TABLE 1). On the basis of pollen and gynoecial morphology (Junell, 1934; Raj, 1983), the Verbenoideae are unlikely to be closely related to the Labiatae, so the occurrence of diallelocytic stomata in this group is probably due to parallelism. A close phylogenetic relationship between one or more of the other verbenaceous genera in which diallelocytic stomata occur (i.e., *Caryopteris* (sect. *Pseudocaryopteris* Briq. only), *Clerodendrum* (subg. *Cyclonema* only), *Petraeovitex*, and *Premna*) and the Labiatae that share this derived state is somewhat more plausible but may be unparsimonious when other characters are considered.

Although diallelocytic stomata were not found in all species of the Lamieae, Scutellarieae, and Nepetoideae, they occur in the vast majority of the members of these three groups, each of which is defined as a clade on the basis of other (nonepidermal) characters. The presence of diallelocytic stomata is thus a "non-universal derived state" shared by a set of clades and, as argued by Cantino (1985), provides evidence for a larger clade composed of them. The critical requirements are that the state be derived and that the groups united on the basis of it each be supported as a clade by other characters. A shared, nonuniversal derived state constitutes weaker evidence of phylogenetic relationship than a shared, universal derived state—i.e., one found throughout the groups it unites (Cantino, 1985).

The distributions of anisocytic and diacytic stomata exhibit a pattern that is highly congruent with that of the diallelocytic stomata, although it is not known whether presence or absence of the former two types is derived. In the Labiatae with a gynobasic style and most Ajugeae, anisocytic stomata are rare and diacytic stomata are nearly universally present. All three stomatal characters (two of them used only in a phenetic sense, since their polarity cannot be assessed) delimit a group composed of all gynobasic-styled Labiatae plus some Ajugeae. Tribe Prostanthereae is consistently excluded from this group, as are *Tetraclea* and *Trichostema* of tribe Ajugeae. Among the other Ajugeae, all three characters support the inclusion of *Acrymia*, *Ajuga*, *Cymaria*, *Kinostemon*, and *Rubiteucris*. The stomatal characters conflict or are ambiguous with regard to the other four genera. *Schnabelia* Hand.-Mazz. has diacytic stomata, but the slide was too poor to determine whether anisocytic or diallelocytic stomata were present as well. In *Amethystea* L. diacytic stomata are present, diallelocytic stomata absent, and anisocytic stomata rare. *Teucrium* consistently has diacytic and diallelocytic stomata, but anisocytic ones were found in two species. *Tinnea* consistently has diacytic stomata and lacks diallelocytic; anisocytic stomata were found in one species only. The strong positive correlation between the occurrences of diacytic and diallelocytic stomata is hardly

surprising since the initial steps in their ontogenies are the same (Payne, 1970), but there is no reason to expect the observed negative correlation between diacytic and anisocytic stomata. Indeed, this correlation is much weaker in the Verbenaceae.

The relationships suggested by these characters must be evaluated in the light of others, and recircumscription of the Labiatae at this time would be highly premature. However, those taxa whose epidermal anatomy is divergent from the rest of the Labiatae should be carefully examined. One of these (*Tetraclea*) has been assigned to the Verbenaceae by some authors (e.g., Moldenke, 1971), and the flowers of another (*Trichostema*) bear a striking resemblance to those of *Caryopteris* sect. *Pseudocaryopteris* in the Verbenaceae. The supratectal spinelike projections on the pollen of *Tetraclea* (Raj, 1983) and *Trichostema* (Abu-Asab & Cantino, 1989), as well as a few other genera of Ajugeae, constitute a derived feature shared by many Verbenaceae (Raj, 1983) and entirely unlike the exine sculpturing of the gynobasic-styled Labiatae (Abu-Asab & Cantino, 1987b).

The Prostanthereae have traditionally been placed in the Labiatae because the ovary is moderately lobed (with the style somewhat sunken but not gynobasic) and matures to form four nutlets. However, the characteristic suite of stomatal types in the Prostanthereae, with anisocytic stomata abundant in all but one genus (they are present but uncommon in *Westringia* Smith), diacytic stomata rare, and diallelocytic stomata absent, differs markedly from that in the gynobasic-styled Labiatae and resembles certain groups of Verbenaceae—particularly subfam. Chloanthoideae and tribe Clerodendreae. This is intriguing from a biogeographic standpoint since the Prostanthereae and most genera of Chloanthoideae are Australian endemics, while the Labiatae (other than Prostanthereae) are rather poorly represented in Australia (Bentham, 1870). In a numerical phenetic analysis of Labiatae and Verbenaceae (El-Gazzar & Watson, 1970), the Prostanthereae, Chloanthoideae, and Stilboideae clustered together tightly. It is not clear that the similar suites of stomatal types in the Prostanthereae and Chloanthoideae reflect cladistic relationship, since absence of diallelocytic stomata is an ancestral state and the polarity of the other two characters cannot be assessed without knowing more about cladistic topology of the Verbenaceae and/or the Scrophulariales, but the possibility that these two Australian groups may be more closely related than generally thought warrants study.

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APPENDIX 1. Classification of subsessile glandular trichomes in the Labiatae and Verbenaceae.*

- TYPE 1. Head composed of one cell.
- TYPE 2. Head composed of two cells.
- TYPE 3. Head divided by three radial walls to form three cells, one twice as large as the other two.
- TYPE 4. Head composed of four cells.
- TYPE 5. Head of more than four cells, usually divided by four primary radial walls that are more or less perpendicular to each other; tertiary and tangential walls absent; no more than one secondary radial wall arising on a given side of any primary radial wall.
- TYPE 6. As in type 5, but with tangential walls present; partial and tertiary radial walls absent.
- TYPE 7. As in type 6, but with partial radial walls present.
- TYPE 8. Head of more than four cells; tertiary radial walls present and/or more than one secondary radial wall arising on the same side of at least one primary radial wall; tangential walls absent.
- TYPE 9. As in type 8, but with tangential walls present; partial radial walls absent.
- TYPE 10. As in type 9, but with partial radial walls present.
- TYPE 11. More complex than type 10, with many tangential walls forming concentric layers of cells.

*Illustrated in FIGURE 2; adapted from Abu-Asab and Cantino (1987a).



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