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DIVERSITY OF STOMATA AND TRICHOMES IN *EUPHORBIA* L. - I

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Abstract

Foliar epidermal features of 18 species of *Euphorbia* L. *s.l.* (Euphorbiaceae) are studied. While the anisocytic and anamocytic stomata are common in herbaceous members (*Euphorbia* subg. *Chamaesyce*), the paracytic type is predominant in succulent species (*Euphorbia* proper). The stomatal types, index and frequency, and the types of trichomes are explored on vegetative as well as floral parts to evaluate their possible taxonomic importance.

Introduction

Sufficient interest seems to have been revived during the past two decades on the role of internal organization of the individual organs of plants. Leaves occupy a prominent position in this regard and their various features such as venation, stomata and trichomes were found useful in solving taxonomic and phylogenetic issues. The utility of foliar epidermal features in distinguishing taxonomic groups was clearly established (Stace, 1965, 1984; Dilcher, 1974; Raju, 1981; Rao and Raju,1985, 1988; Mohan, 1994; Manohari, 2004).

In view of the above considerations, it was thought worthwhile to investigate the epidermology of the important genus *Euphorbia* L. *s.l.*, with 84 species occurring in India (Binojkumar and Balakrishnan, 2007, 2010). The great diversity in habit and adaptation exhibited by the species of the genus *Euphorbia* provide the added impetus for undertaking the present study. The structural diversity and distribution of trichomes are significant for taxonomic analysis, especially in tropical plants (Stace, 1965; Dilcher, 1974; Rao and Raju, 1985). The distribution and structure of trichomes and stomata are genetically controlled and consistent. The useful epidermal characters in systematics are the distribution of stomata over the two surfaces of the leaf, stomatal index and frequency, the nature of anticlinal walls of the epidermal cells and the types and distribution of trichomes. To fill the gaps in our knowledge in this regard concerning the genus *Euphorbia* sensu Linnaeus in India, the present study was undertaken. It is also intended to view whether these data support the realignments in the genus *Euphorbia* by Yang *et al*. (2012) with regard to the traditional subgenera *Eremophyton* and *Poinsettia*.

Materials and Methods

In the present investigation, 18 species of *Euphorbia* L. *s.l.* were studied for the organography of epidermal features (Table 1). The plant materials used in the present study were mostly shade dried and of pressed specimens. Whole plants were boiled in water with a few pellets (1 g) of NaOH at 30-40ºC. The peels were thoroughly washed and stained with safranin or acetocarmine and mounted in glycerin. The epidermal features such as cuticle, epidermal cells, stomata, and trichomes were observed on all the organs and measured using Nikon Eclipse, E-400 microscope.

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Ocular micrometer was used for measurement. The terminology adopted for the epidermal features is after Raju and Rao (1977, 1987) and Raju (1981). The species of *Euphorbia* studied were identified with the help of standard regional floras and experts (Ellis, 1990; Venkataraju and Pullaiah, 1995; Babu, 1995; Binojkumar and Balakrishnan, 2010), and the voucher specimens were deposited in the Sri Krishnadevaraya University Herbarium (SKU), Anantapur.

Results

The epidermis in *Euphorbia* bears a variety of trichomes and stomata dispersed all over the plant surface in a consistent pattern. The extent of variations in the shape of epidermal cells, nature of anticlinal walls, types of stomata, number of stomata per unit area and stomatal indices, and the types of trichomes (glandular and eglandular) observed in 18 species are documented in Tables 1 and 2.

Eleven species of *Euphorbia* bear trichomes on vegetative and floral parts and the remaining seven species are glabrous. The epidermal appendages vary in structure, form and distribution. The trichome types presently recorded in the members of *Euphorbia* are mostly multicellular. However, *Euphorbia agowensis* (Fig. 1A) bears unicellular cylindrical trichomes on vegetative as well as floral parts. A noteworthy feature of *Euphorbia* species currently recorded is the presence of glandular trichomes at nodes and bases of stipules. These can be found in *E. cristata* (Fig. 3A), *E. elegans* (Fig. 3B), *E. hirta* (Fig. 3E), *E. indica* (Fig. 3G), and *E. prostrata* (Fig. 3D) of subg. *Chamaesyce* and *E. heterophylla* (Fig. 3C) of subg. *Poinsettia*, which are often segregated as distinct genera. These glandular trichomes are multicellular, stalked and found to be species specific in regard to their size, shape and number per unit area. The stem of *E. hirta* (Fig. 2G) possesses two types of trichomes; they are multicellular forked with cuticular ornamentations and multicellular uniseriate osteolate ones. However, its involucre bears strictly two-celled cylindrical trichomes (Fig. 2H).

The epidermal cells may be rectangular and polygonal in outline. Depending upon the location on the leaf, i.e., the midrib, margin and apex, their shapes tend to vary. The anticlinal walls are straight to variously arcuate.

The anticlinal walls are straight in *E. dracunculoides, E. deccanensis* var. *nallamalayana* (Fig. 1M), *E. nivulia* (Fig.1H), *E. perbracteata* (Fig. 1L, adaxial) and *E. tirucalli* (Fig. 1K). Most of the stomatal types noted for Dicotyledonae (Magnoliopsida) are met within the genus, with anamocytic, anisocytic and paracytic being most preponderant or basic (Sehgal and Paliwal, 1974; Raju and Rao 1977, 1987). Stomata of more than one types have been encountered on the same leaf surface in *E. hyssopifolia, E. longistyla* (Fig. 1I) and *E. thymifolia* (Fig. 1J), as reported earlier by Raju and Rao (1977, 1987) for the other species of *Euphorbia*. In *E. caducifolia* (Fig. 1B) at places, the stomata are just represented by persistent stomatal initials (due to arrested stomatal development c.f. Raju and Rao, 1977). In *E. tirucalli*, sometimes, the stomatal complex has single guard cell. With regard to the position of stomata to the level of epidermis, different depths of sunkenness have been observed in various succulent *Euphorbia* species (Fig. 1B, H). Obviously, these epidermal features can be usefully employed for diagnostic purposes in *Euphorbia*.

Discussion

The foliar epidermis offers a number of noteworthy taxonomic characters. The biosystematic and taxonomic studies of a number of families established the importence of leaf epidermis (Baranova, 1972; Raju, 1981; Stace, 1984). Although the taxonomists realized lately the importance of micromorphology of the epidermis, the taxonomic monographs are now considered

Table 1. Analysis of foliar stomatal diversity in 18 taxa of *Euphorbia* L.

No.	Taxon		Stomatal types	Percentage of richness	Stomatal index		Stomatal frequency		Source and voucher specimen number
					Adaxial	Abaxial	Adaxial (μm^2)	Abaxial (μm^2)	
	Subg. **Esula**		Anamocytic	54%	11.11	16.96	0.004	0.006	Sanjamula, Kurnool (31412)
1	*E. dracunculoides* Lam.		Anisocytic	32%					
			Paracytic	14%					
2	*E. perbracteata* Gage	Vegetative leaf	Anamocytic	66%	20.312	17.30	0.009	0.006	Sanjamula, Kurnool (31411)
			Anisocytic	44%					
		Floral leaf	Anisocytic	58%	18.00	18.35	0.006	0.007	
			Anamocytic	42%					
	Subg. **Euphorbia** L.								
3	*E. caducifolia* Haines		Paracytic	100%	8.571	7.691	0.082	0.692	Rachakunta palle, Kadapa (31416)
4	*E. nivulia* Buch.-Ham.		Paracytic	100%	8.00	11.11	0.002	0.003	Srisailam, Kurnool (31417)
5	*E. tirucalli* L.		Paracytic	100%	9.836	13.432	0.826	0.123	Ramagiri, Anantapur (31418)
	Subg. **Chamaesyce** Raf. Sect. **Scatorhizae** Y. Yang & P.E. Berry								
6	*E. agowensis* Hochst *ex* Boiss.		Paracytic	82%	21.608	22.608	0.130	0.179	Srisailam, Kurnool (31410)
			Anisocytic	18%					
	Sect. **Anisophyllum** Roep.								
7	*E. deccanensis* V.S. Raju var. *nallamalayana* (Ellis) V.S. Raju		Anamocytic	73%	15.789	18.852	0.061	0.096	Nallamalais, Kurnool (31402)
			Anisocytic	27%					
8	*E. corrigioloides* Boiss.		Anisocytic	66%	17.89	18.584	0.006	0.007	Vemula, Kadapa (31415)
			Anamocytic	44%					
9	*E. cristata* Heyne *ex* Roth		Anisocytic	81%	18.584	14.893	0.144	0.096	Gooty hills, Anantapur (31409)
			Anamocytic	19%					
10	*E. elegans* Spreng.		Anisocytic	57%	10.344	11.578	0.061	0.075	Chelama, Kurnool (31404)
			Anamocytic	43%					

Table 1 contd.

No.	Taxon	Stomatal types	Percentage of richness	Stomatal index		Stomatal frequency		Source and voucher specimen number
				Adaxial	Abaxial	Adaxial (μm^2)	Abaxial (μm^2)	
11	*E. hirta* L.	Anisocytic Anamocytic	60% 40%	21.568	22.707	0.227	0.289	Anantapur (31407)
12	*E. hyssopifolia* L	Anisocytic Anamocytic Paracytic	79% 13% 8%	8.108	9.333	0.061	0.096	Palamaneru, Chittoor (31407)
13	*E. indica* Lam.	Anisocytic Anamocytic	88% 12%	15.714	21.787	0.151	0.268	Sanjamula, Kurnool (31420)
14	*E. longistyla* (Boiss.) Croizat	Anisocytic Anamocytic Diacytic	92% 5% 3%	10.769	12.50	0.048	0.061	Palakonda hills, Kadapa (31406)
15	*E. prostrata* Aiton	Anisocytic Anamocytic	58% 42%	22.535	20.37	0.220	0.151	Batrepalle, Anantapur (31401)
16	*E. serpens* Kunth	Anisocytic Anamocytic Paracytic	66% 23% 11%	19.727	20.43	0.199	0.261	Kalasamudram, Anantapur (31421)
17	*E. thymifolia* L.	Anisocytic Diacytic Paracytic	58% 22% 20%	20.987	17.62	0.234	0.144	S.K. University campus, Anantapur (31422)
	Sect. **Poinsettia** (Graham) Baill.	Anamocytic	72%	16.097	19.923	0.022	0.358	S.K. University campus, Anantapur (31423)
18	*E. heterophylla* L.	Anisocytic	28%					

Infrageneric classification after Binojkumar and Balakrishnan (2010), and Yang *et al.* (2012).

Table 2. Diversity and distribution of trichomes of 18 taxa of *Euphorbia* L.

Taxon	Plant part	Function of Trichomes	Trichome type	Size
Subg. **Esula** 1. *E. dracunculoides*		absent on all the organs		
2. *E. perbracteata*	Floral leaf adaxial	Eglandular trichomes	Multicellular uniseriate cylindrical	0.4 mm
	Floral leaf abaxial	”	”	0.6 mm
	Capsule	”	Unicellular cylindrical	0.8-0.9 mm
Subg. **Euphorbia** 3. *E. caducifolia*		Absent on all the organs		
4. *E. nivulia*		Absent on all the organs		
5. *E. tirucalli*	Capsule	Eglandular trichomes	Multicellular uniseriate cylindrical	1.5-1.9 mm
Subg. **Chamaesyce**	Stem	Eglandular	Unicellular cylindrical	189-191 µm
Sect. **Scatorhizae**	Leaf abaxial	”	”	190-200 µm
6. *E. agowensis*	Involucre	”	”	183-184.5µm
	Capsule	”	”	172.8-176.2 µm
Sect. ***Anisophyllum*** 7. *E. deccanensis* var. *nallamalayana*		Absent on all the organs		
8. *E. corrigioloides*	Stem	Eglandular trichomes	Multicellular cylindrical	75.6 µm
	Leaf abaxial	”	Unicellular cylindrical	56.7 µm
	Involucre	”	”	59.4 µm
	Capsule	”	”	62.1 µm
9. *E. cristata*	Stem	Eglandular	Multicellular uniseriate cylindrical	1.2 mm
	Stipular base	Glandular	Multicellular stalked	0.8-1.0 mm
	Leaf adaxial	Eglandular	Multicellular osteolate	1.0-1.2 mm
	Leaf abaxial	”	”	1.1-1.3 mm
	Involucre	”	Multicellular cylindrical	0.9 mm
	Capsule	”	”	1.0-1.1 mm
10. *E. elegans*	Stem	Eglandular	Multicellular uniseriate cylindrical	2 mm
	Stipular base	Glandular	Multicellular stalked	0.4 mm
	Leaf abaxial	Eglandular	Multicellular uniseriate cylindrical	0.9-1.0 mm
	Involucre	”	”	0.6-0.8 mm
	Capsule	”	”	0.8-1.2 mm

Table 2 contd.

Taxon	Plant part	Function of Trichomes	Trichome type	Size
11. *E. hirta*	Stem	Eglandular trichomes	Multicellular uniseriate osteolate and multicellular biforked osteolate trichomes with cuticular ornamentation	0.7-1.2 mm & 0.8-1.3 mm
	Stipule	”	Multicellular uniseriate osteolate	0.4 mm
	Leaf adaxial	”	”	0.4-0.9 mm
	Leaf abaxial	”	”	0.4-0.9 mm
	Involucre	”	Two celled uniseriate cylindrical	73-78 µm
	Capsule	”	”	60 µm
	Stipular base	Glandular trichomes	Multicellular stalked	0.6-0.8 mm
12. *E. hyssopifolia*			Absent on all the organs	
13. *E. indica*	Stem	Eglandular	Multicellular uniseriate osteolate	0.2-0.3 mm
	Leaf abaxial	”	”	0.3 mm
	Capsule	”	”	0.4 mm
	Involucre	”	”	0.5 mm
	Stipular base	Glandular	Multicellular stalked	0.4-1.2 mm
14. *E. longistyla*	Petiole	Eglandular	Multicellular uniseriate cylindrical	0.1 mm
15. *E. prostrata*	Stem	Eglandular	Multicellular uniseriate cylindrical	0.2-0.4 mm
	Capsule	”	”	81-88 µm
	Leaf abaxial	”	Multicellular uniseriate osteolate	0.7-0.9 mm
	Stipule	”	”	1.0 -1.2 mm
	Involucre	”	”	86.4-87.0 µm
	Stipular base	Glandular	Multicellular stalked	161 µm
16. *E. serpens*			Absent on all the organs	
17. *E. thymifolia*	Stem	Eglandular	Multicellular uniseriate cylindrical	0.8-1.0 mm
	Leaf abaxial	”	”	0.8 mm
	Involucre	”	”	0.6 mm
	Capsule	”	”	0.9 mm
Sect. ***Poinsettia***	Stem	Eglandular	Multicellular uniseriate cylindrical	0.3-0.6 mm
18. *E. heterophylla*	Petiole	”	Multicellular uniseriate osteolate	0.6-0.8 mm
	Leaf adaxial	”	”	0.8-1.0 mm
	Leaf abaxial	”	”	0.9-1.0 mm
	Node	Glandular	Multicellular stalked	0.4 mm

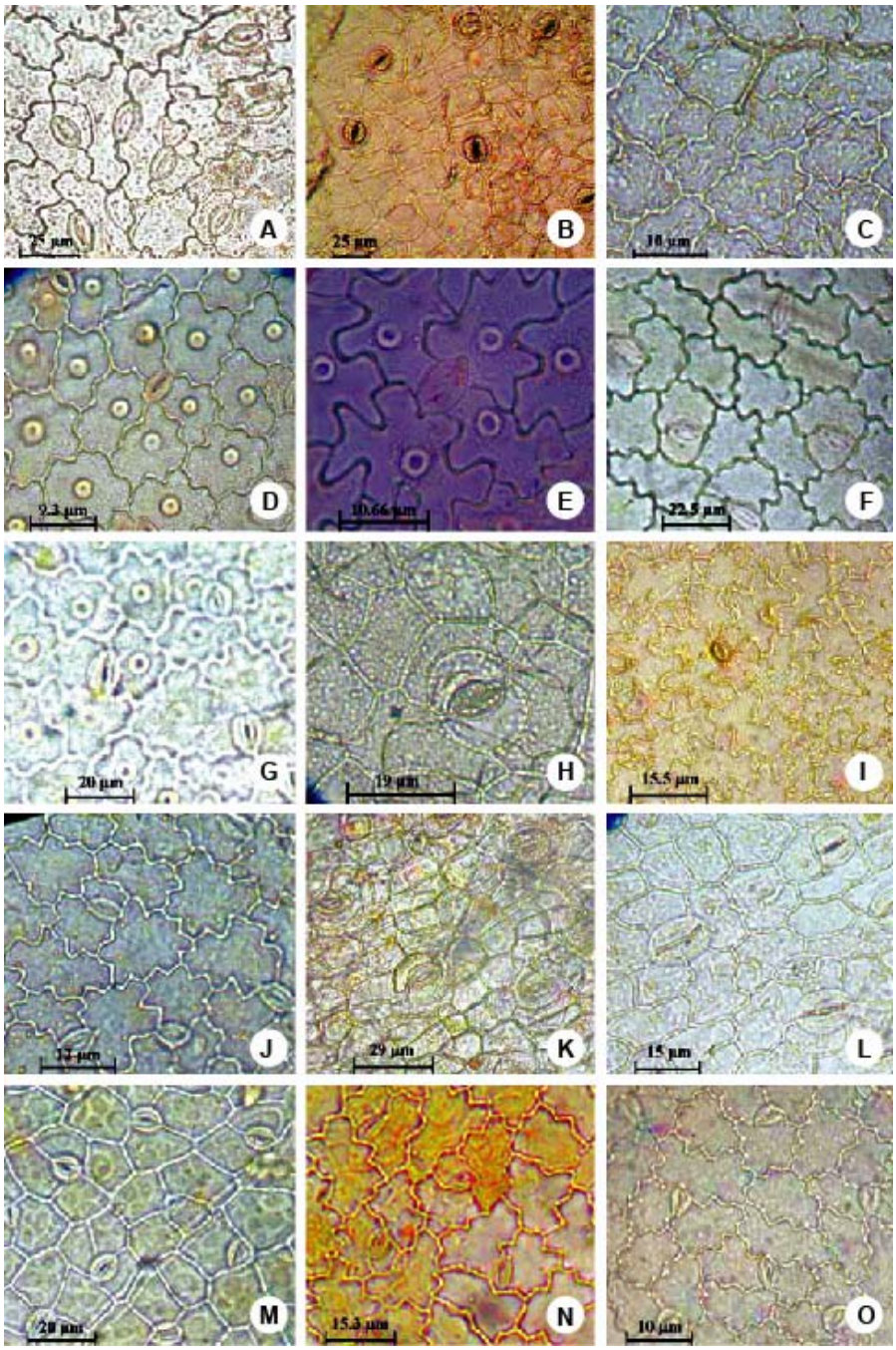

Fig. 1. Organography of epidermal structures in *Euphorbia*. A) *E. agowensis*, B) *E. caducifolia*, C) *E. corrigioloides*, D) *E. cristata*, E) *E. elegans*, F) *E. heterophylla*, G) *E. indica*, H) *E. nivulia*, I) *E. longistyla*, J) *E. thymifolia*, K) *E. tirucalli*, L) *E. perbracteata*, M) *E. deccanensis* var. *nallamalayana*, N) *E. prostrata*, O) *E. serpens.*

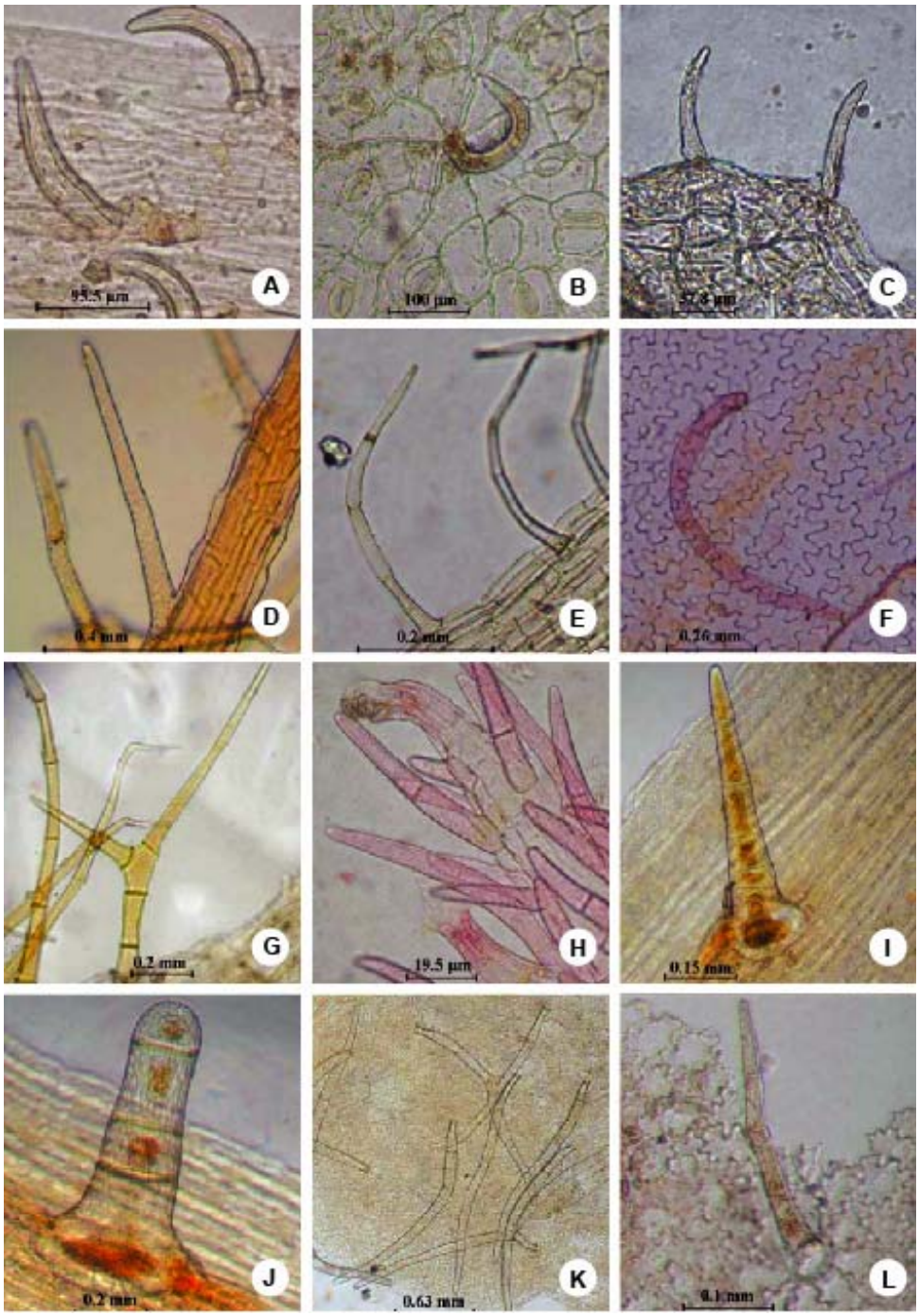

Fig. 2. Trichome diversity in *Euphorbia*. A) & B) *E. agowensis* (stem & leaf), C) *E. corrigioloides* (stem), D) *E. cristata* (appendages), E) *E. prostrata* (stem), F) *E. elegans* (leaf abaxial), G) & H) *E. hirta* (stem & involucre), I) & J) *E. heterophylla* (stem), K) *E. tirucalli* (capsule), L) *E. indica* (leaf abaxial).

incomplete without it (Rejdali, 1991). The diversity and distributional pattern of stomata and trichomes can be viewed from different perspectives and used as a model system for investigations into developmental biology, ecology, physiology, morphology and evolution.

The work done on the stomata and trichomes was well-documented by Metcalfe and Chalk (1950) and reviewed by Raju and Rao (1977) and Rao and Raju (1985, 1988). The present study fills up the gaps in our knowledge of the other species of the genus *Euphorbia* after Sehgal and Paliwal (1974), Raju and Rao (1977) and Raju (1981) in India. Different species of *Euphorbia* have been found to possess anamocytic, anisocytic and paracytic types of stomata, indicating that Linnean *Euphorbia* is heterogeneous. Therefore, this diversity is of use for infrageneric delimitation. The species of *Euphorbia* subg. *Chamaesyce* such as *E. hyssopifolia*, *E. longistyla* and *E. thymifolia* showed combinations of two or more types of stomata on the same leaf surface. Despite the variation, a single stomatal type is preponderant in any particular Euphorbiaceous taxon (Raju and Rao, 1977). In the case of *Euphorbia* subg. *Chamaesyce,* it is the trilabrate anisomesogenous type. Anisocytic stomata are dominant (Table 1) in the foliar epidermis of *E. longistyla* (92%) followed by *E. indica* (88%), *E. cristata* (81%) and *E. prostrata* (73%). While anamocytic stomata are predominantly found in *E. deccanensis* var. *nallamalayana* (73%), *E. heterophylla* (72%), *E. perbracteata* (66%) and *E. dracunculoides* (54%), paracytic stomata are preponderant in tree species and shrubs like *E. caducifolia*, *E. nivulia* and *E. tirucalli* (Table 1).

Papillate epidermal cells were found in the abaxial surface of leaves of *Euphorbia* subg. *Chamaesyce*, as seen in *E. cristata, E. elegans* (Fig. 1D, E) and *E. indica* (Fig. 1G). In *E. perbracteata*, the anticlinal walls are straight in the adaxial foliar epidermis while they are undulate to highly wavy abaxially, as noted in the other Euphorbiaceae (Raju and Rao, 1977). Similarly, more than seven types of eglandular trichomes and three types of glandular trichomes are found on vegetative and floral parts of the Linnean *Euphorbia*.

Taxonomic Treatment

The diversity in stomata and trichomes is useful for infrageneric distinctions. However, their importance as taxonomic criteria will be greatly enhanced if the information can be interpreted with supportive evidence.

Binojkumar and Balakrishnan (2010) recognised 10 subgenera under *Euphorbia* for the Indian species. The species of *Euphorbia* studied now belong to five subgenera, *viz.*, *Chamaesyce, Eremophyton, Esula, Euphorbia* and *Poinsettia. Euphorbia* subg. *Chamaesyce* exibits distinct taxonomic features like varied forms of glandular trichomes at stipular bases, more than four types of eglandular trichomes and four types of stomata, whereas the subg. *Eremophyton* is distinct from the other groups by bearing unicellular trichomes on all vegetative and floral parts, and the predominant paracytic stomata. The subg. *Esula* shows two stomatal types, the abaxial anticlinal walls wavy and adaxial ones straight, while the subg. *Euphorbia* is characterized by paracytic and sunken stomata. The subg. *Poinsettia* exhibits two types of trichomes (eglandular and glandular) and the predominant advanced anamocytic stomata. Yang *et al*. (2012) based on molecular evidence, re-circumscribed the genus *Euphorbia* subg. *Chamaesyce*. They reduced the traditional subgenera *Eremophyton* and *Poinsettia* as sections under *Euphorbia* subg. *Chamaesyce. E. agowensis* was placed under subg. *Euphorbia* sect. *Scatorhizae.* However, *E. agowensis* is not allied to the core sect. *Anisophyllum* in its basic stomata and trichome types besides being ecarunculate and non-kranz species (Tables 1 & 2). As a section, *Poinsettia* (*E. heterophylla*) also makes the subg. *Chamaesyce* heterogeneous with its species bearing coloured floral bracts, basic anamocytic stomata (Table 1) and two types of trichomes on the stem (Table 2). Therefore, the micromorphological evidence supplemented with other morphological data are not in agreement with the re-alignment made for these two sections by Yang *et al*. (2012), and instead, the data are

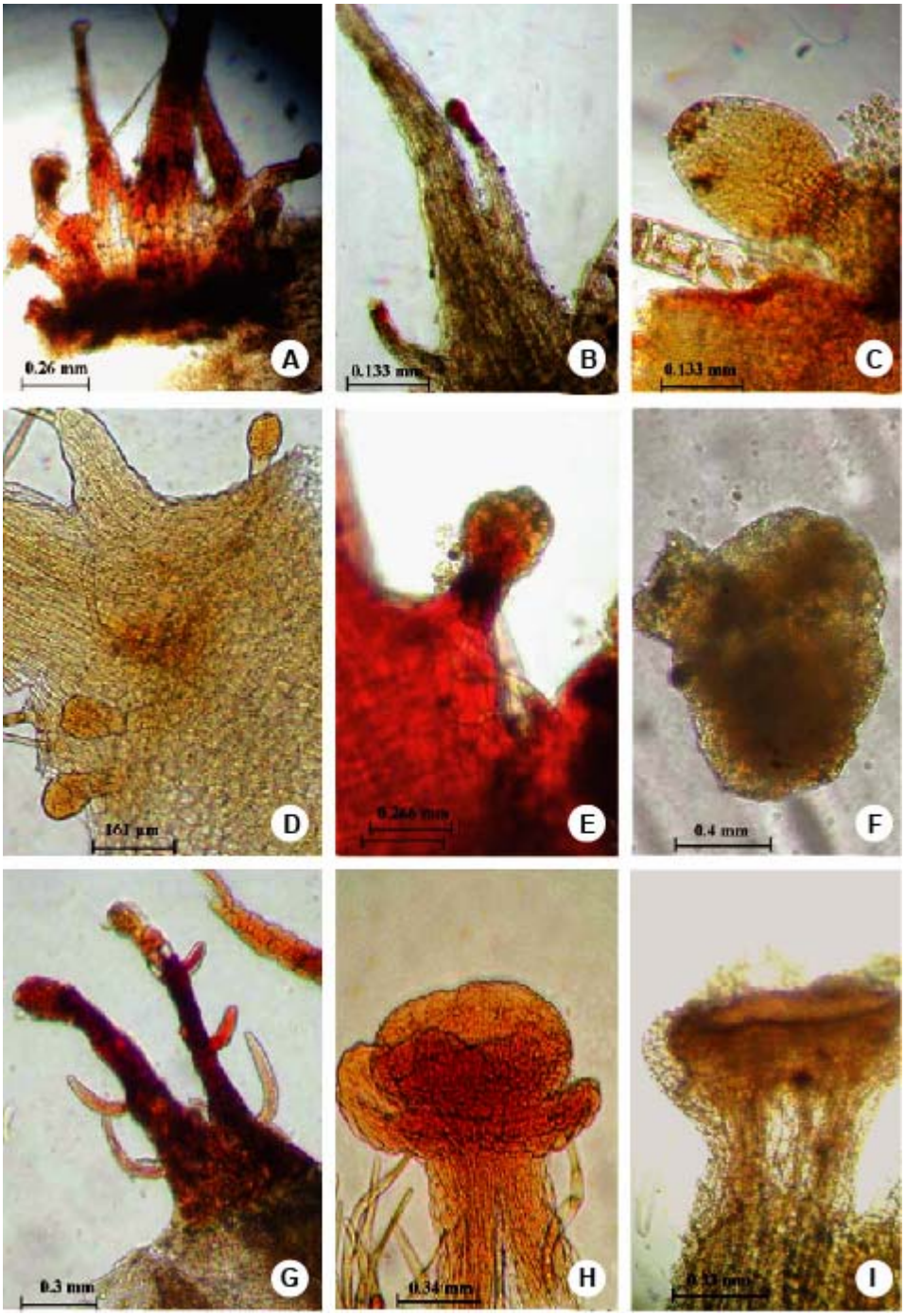

Fig. 3. Vegetative and floral glands in *Euphorbia*. A) *E. cristata*, B) *E. elegans*, C) *E. heterophylla*, D) *E. prostrata*, E) *E. hirta*, F) *E. agowensis* (leaf), G) *E. indica*, H) *E. prostrata* (involucral gland), I) *E. serpens* (involucral gland).

compatible with the traditional treatment adopted by Binojkumar and Balakrishanan (2010), for the species examined.

The present study reveals that the epidermal characters are of taxonomic significance in the members of the *Euphorbia* examined. Despite the fact that the epidermis is being influenced by environmental factors, the traits employed are stable with regard to the mature stomatal type and distribution on different organs. Therefore, the stomata, trichomes and epidermal cells can be effectively used to identify and distinguish different plant species and draw parallels or convergence with the molecular evidence.

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