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Stomatal Observations in Dicotyledons

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Abstract: Since 1998, research into more than 470 plant species from some 65 families, found growing in a unique protected area of Irano-Torany, has examined diverse aspects of their anatomical and structural features and has studied the ecological implications of these finding for each species. The present paper, as a part of this research, focuses on the stomatal characters of 326 species from 36 families of dicotyledons, the majority of which are herbaceous species. The stomatal density, guard cell lengths on the adaxial and abaxial leaf epidermis and the stomatal type in each family is described and the relationship between stomatal density and guard cell size is reviewed. The stomatal characteristics presented here are a valuable research resource, allowing; I) the identification of basic stomatal types in these plants, II) the facilitation of their taxonomic classification and III) constitution of a baseline data set against which to monitor and evaluate environmental changes at these sites of international conservation interest.

Key words: Guard cells, herbaceous plants, leaf anatomy, protected area, stomatal density, type of stomata

INTRODUCTION

Stomata are considered to be one of the major structures within the leaf organ that have allowed the higher plants to adapt to virtually all terrestrial environments on the planet, by means of adjustment of their size, density and distribution (Zarinkamar, 2006b). An alteration of leaf stomatal density can be used as an indicator of environmental change (Case, 2004). Several researchers have shown that stomatal densities change in response to water availability (Edward and Meidner, 1978), light intensity (Retallk, 2001; Lu *et al.*, 1993), temperature (Ciha and Brun, 1975), geographical location (Retallk, 2001) and CO_2 concentration (Bristow and Looi, 1968; Woodward, 1987; Woodward and Bazzaz, 1988).

As environmental conditions affect stomatal density, this has implications for plant development. Collection of data on stomatal densities from sites which have experienced a minimum of environmental pollution and human impact can provide a baseline against which to assess anthropogenic impacts on these species elsewhere. This has the potential to facilitate appropriate monitoring and analysis of environmental changes, using stomatal characteristic as an indicator of physiological response. Suitable sites for such monitoring could be found amongst protected areas. These areas have experienced minimum levels of local environmental disturbance such as water and air contamination, waste pollution and human intervention.

MATERIALS AND METHODS

Some 320 species pertaining to 36 families of dicotyledons were selected to represent a broad spectrum of stomatal characteristics. All materials were identified by the Iranian central herbarium (TARI) and Department of Environment (DoE). To minimise misinterpretation, the central area of the leaf lamina from relatively mature leaves was selected for analysis and at each site, the data entry comprises an average of 30 samples taken from 6 plants of the same species. In order to study stomatal density, the diafanization technique was employed Stritmater (1973) and the results were observed using a light microscope. A combination of stomatal classification schemes of Dilcher (1974) and Wilkinson (1979) quoted by Stace (1989), were used as a basis to define the various stomatal forms encountered in this study. Most of stomatal types quoted by Stace are present in the plant families covered in the present report (shown in Fig. 1; A-R).

Most species in the present study are herbaceous; the exceptions are woody plants found in the following families; Aceraceae, Anacardiaceae, Caprifoliaceae, Cornaceae, Corylaceae, Fagaceae, Oleaceae, Rhamnaceae, Rosaceae and Ulmaceae. The study sites also contain the following endemic species: *Minuartia lineate*, *Silene persica* (Caryophyllaceae); *Centaurea aziziana*, *C. zuvandica* (Compositae); *Erysimum subulatum, Sterigmostemum contortuplicatum* (Cruciferae), *Hypericum linarioides* (Hypericaceae); *Scrophularia oxysepala* (Scrophulariaceae).

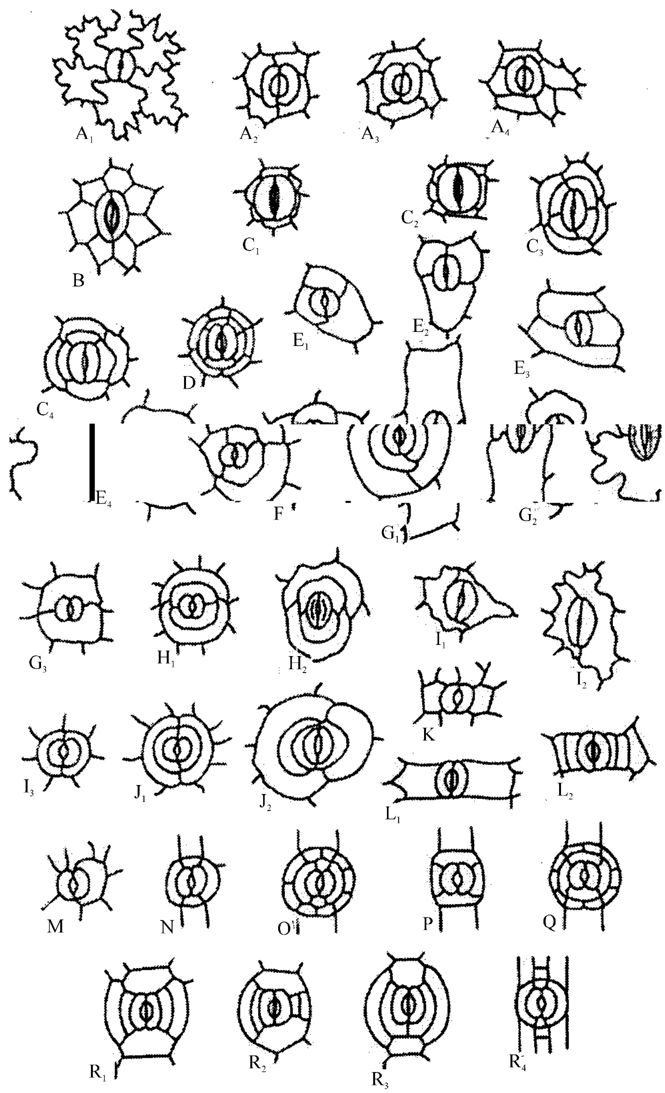

Fig. 1: Stomatal types: A1, Anomocytic; A (2,3,4), Staurocytic; B, actinocytic; C, (1,2), cyclocytic; C (3,4), tetracytic; D, amphicyclocytic, E, (1,2,3), anisocytic; E4, amphianisocytic; F, helicocytic; G, (1,2,3), diacytic; H, (1,2), amphianisocytic; I, (1,2), laterocyclic; I3, paracytic; J, (1,2), amphiparacytic; K, bracyparacytic; L, (1,2), amphibracyparacytic; M, hemiparacytic; N, paratetracytic; O, amhiparatetracytic; P, brachuparatetracytic; Q, amphibrachyparatetracytic, R (1,2,3) parahexacytic-monopolar; R4, parahexacytic-dipolar

RESULTS

Table 1 shows the stomatal densities and characteristics including type of stomata for all species studied. Metcalf and Chalk (1950) listed type of stomata in dicotyledons and based on that, Table 1 develops dominate and subordinate type of stomata as well as checking variation of stomatal type in the families under studies. The main observations from the Table are highlighted below; from this data, the following four groups can be distinguished.

Woody plants

Aceraceae: In the Aceraceae, stomata are present only on the abaxial surfaces and are found at relatively high densities. The highest densities are observed in *A. monspessulanum* at 510 per mm^2 and the lowest in *A. hyrcanum* at 366 per mm^2. Only anomocytic stomata are found in this family; guard cell lengths range between 22.06 and 23.14 μm and the stomatal apertures are unusually narrow.

Anacardiaceae: In the Anacardiaceae stomata are absent from adaxial surfaces, with the exception of

Table 1: Stomatal densities, Guard cell length for the adaxial and abaxial epidermis and type of stomata in dicotyledons (*=species showing a correlation between increased guard cell size and higher stomatal density: see discussion)

	Stomatal frequency (mm^2)		Guard cell length (µm)		Type of stomata	
Species	Adaxial	Abaxial	Adaxial	Abaxial	Dominant	Subordinate
Aceraceae						
Acer campestre	-	410	-	22.06	Anomocytic	
A. hyrcanum	-	366	-	23.14	Anomocytic	
A. monspessulanum	-	510	-	22.78	Anomocytic	
Anacardiaceae						
Cotinus coggygria	-	278.1	-	21.186	Anomocytic	
Pistacia atlantica	21.26	331.7	28.188	27.077	Anomocytic	
Rhus coriaria	-	195.5	-	29.667	Anomocytic	
Boraginaceae						
Asperugo procumbens	109.2	218.3	25.8	22.8	Anomocytic	
Bugloss ides arvensis	143.51	187.81	27.43	26.9	Anomocytic	
*Heliotropium ellipticum**	245.64	209.68	29.59	27.59	Anomocytic	
Lappula barbata	142.55	191.48	26.15	25.75	Anomocytic	
*Myosotis silvatica**	85.47	171.87	25.55	25.6	Anomocytic	Anisocytic
Onosma dichroanthum	350.4	496.9	21.8	20.02	Anomocytic	Anisocytic
*O. microcarpum**	227.7	297.5	22.02	24.25	Anomocytic	Anisocytic
Symphytum asperum	59.87	257.1	29.95	26.88	Anomocytic	Anisocytic, Diacytic
Campanulaceae						
Campanula glomerata	42.74	179.38	36.42	32.88	Anomocytic	
C. hohenackeri	64.05	165.2	30.09	29.88	Anomocytic	
C. rapunculoides	75.94	240.5	33.66	30	Anomocytic	
C. stevenii	81.68	146.07	35.47	34.56	Anisocytic	Anomocytic
Symphyandra armena	-	199.72	-	25.43	Anomocytic	
Caprifoliaceae						
Lonicera caucasica	-	364.9	-	21.28	Anomocytic	
L. iberica	-	223.92	-	24.365	Anomocytic	
Viburnum lantana	-	143.03	-	32.025	Anomocytic	Anisocytic hemiparacytic
Caryophyllaceae						
*Arenaria dianthoides**	95.42	122.5	32.18	36.35	Diacytic	
*A. gypsophiloides**	82.2	95	32.67	33.733	Anomocytic	
*A. serpyllifolia**	117.4	166.7	27.67	27.71	Diacytic	
*Cerastium glomeratum**	59.03	82.35	39.13	40	Anomocytic	
*C. holosteoides**	68	92	35	36	Anomocytic	
*C. szowitsii**	48	130	35	35.3	Anomocytic	
Dianthus cretaceus	127	86	32	33	Diacytic	
*D. crinitus**	81	83	33	35	Diacytic	
*Gypsophila elegans**	83	96	30	31	Diacytic	
Herniaria hirsuta	168	85	30	31	Anomocytic	
*H. incana**	146	99	26.2	26	Anomocytic	
*Minuartia acuminata**	88	71	34.2	34	Diacytic	
*M. lineata**	143	82	30.4	30.2	Diacytic	
*M. recurva**	170	110	30.03	30.01	Diacytic	
*Silene persica**	65	106	34	35	Anomocytic	Diacytic
*S. ruprechtii**	217	166	30.02	30	Diacytic	Anisocytic
S. spergulifolia	150	104	29	30	Diacytic	
*Stellaria media**	15	45	41.1	41.2	Anomocytic	
Chenopodiaceae						
*Chenopodium album**	93.2	123.33	28.4	28.5	Anomocytic	
Kochia prostrata	92.73	78.23	28.591	29.109	Bracyparacytic	
Noaea mucronata	132.38	150.73	27.112	24.305	Bracyparacytic	
Cistaceae						
Fumana procumbens	105.45	81.89	37.847	38.464	Anomocytic	Anisocytic
Helianthemum ledifolium	77.98	336.2	30.226	26.548	Anomocytic	
H. nummularium	92.81	231.35	29.206	28.645	Anomocytic	
*H. salicifolium**	73.33	138.33	28.35	30.15	Anomocytic	
Compositae						
*Achillea biebersteinii**	73.73	37	32.87	32.667	Anomocytic	
*A. millefolium**	89.68	39.73	35.528	35.317	Anisocytic	Anomocytic
Anthemis triumfettii	110.67	72.67	33.687	35.58	Anomocytic	
*Artemisia absinthium**	21.95	120.57	33.721	33.858	Anomocytic	
A. armeniaca	-	275.8	-	24.45	Anomocytic	Anisocytic

Table 1: Continued

	Stomatal frequency (mm²)		Guard cell length (µm)		Type of stomata	
Species	adaxial	abaxial	adaxial	abaxial	dominant	subordinate
*A. chamaemellifolia**	37.22	127.83	31.231	33.184	Anomocytic	
*A. fragrans**	136.77	141.84	25.087	26.95	Anomocytic	
*A. scoparia**	112.49	131.25	26.506	26.61	Anomocytic	Anisocytic
*A. splendens**	74.8	108.13	35.963	36.04	Anomocytic	
*Calendula persicaria**	53	56.96	44.5	44.87	Anomocytic	
Carduus pycnocephalu	90.66	219.4	33	31	Anomocytic	Anisocytic
C. seminidus	33.01	126.5	35	34.44	Anomocytic	Anisocytic
C. thoermeri	125	339.2	31.27	24.6	Anomocytic	
*Carthamus lanatus**	168.4	245.7	27.11	27.37	Anisocytic	Anomocytic
*Centaurea aziziana**	145.48	162	23.65	23.99	Anomocytic	
C. macrocephala	68.14	181	26.27	25.22	Anomocytic	
*C. rhizantha**	214.6	238.33	23.97	26.05	Anomocytic	
*C. solstitialis**	190	196.67	16.2	17.14	anomo=aniso	
*C. sosnovskyi**	151.4	158.17	31.489	32.772	anomo=aniso	
*C. zuvandica**	68.65	409.5	23.897	23.96	Anomocytic	Anisocytic
Cirsium echinus	100.83	311.7	30.22	25.8	Anomocytic	Anisocytic
C. osseticum	18.26	334.4	25.513	20.252	Anomocytic	
Causinia belangeri	80.8	195	26.233	24.133	Anomocytic	
*Crepis foetida**	149.05	179.02	30.743	30.843	Anomocytic	
*C. sancta**	156.53	205.9	30.2	30.367	Anomocytic	
*Crupina crupinastrum**	81.7	88.15	29.712	31.587	anomo=aniso	
Doronicum hyrcanum	35.67	91	39.087	36.207	Anomocytic	
*Erigeron acer**	48.1	99.39	29.633	30.967	Anomocytic	
*Filago pyramidata**	78.56	114.45	23.705	24.187	Anomocytic	
Helichrysum plicatum	139.7	162	23.787	22.5	Anomocytic	Anisocytic
*Hieracium pilosella**	203.33	210.83	26.983	27	Anomocytic	
*H. procerum**	70.61	94.55	32.436	32.66	Anomocytic	
Inula oculus-christii	130.83	169.58	27.429	26.81	Anomocytic	
I. vulgaris	20.26	182.77	28.086	26.20	Anomocytic	
*Koelpinia linearis**	102.27	95.93	32.67	30.67	Anomocytic	
Lapsana communis	18.98	114.48	28.767	27.13	Anomocytic	
*Leontodon asperrimus**	112.81	138.18	29.767	31.76	Anomocytic	
*Scorzonera laciniata**	125	151.67	30.75	30.9	Anomocytic	
Serratula quinquefolia	3.786	206.9	27.57	24.342	Anomocytic	
Sonchus asper	42.19	42.19	30	29.333	Anomocytic	Anisocytic
*Tanacetum chiliophyllum**	69.52	66.24	36.733	36.655	Anomocytic	
*T. parthenium**	25.73	58.23	33.867	34.133	Anomocytic	
*T. graminifolius**	109.14	137.1	24.417	24.5	Anomocytic	
*Tragopogon kemulariae**	83.3	96.67	24.6	27.9	Anomocytic	Anisocytic
*T. pterocarpus**	67.47	88.6	26.33	29	Anomocytic	
*T. reticulatus**	117.73	120.5	31.313	31.493	Anomocytic	
Xeranthemum annum	71	184	21.487	20.46	Anomocytic	Anisocytic
Convolvulaceae						
*Convolvulus arvensis**	220	189.7	26.693	25.613	paracytic	Anisocytic
*C. cantabrica**	141.93	156.55	26.909	26.985	paracytic	Anisocytic
*C. lineatus**	143.2	164.03	28.436	28.615	paracytic	
Cornaceae						
Cornus australis	-	172.11	-	24.398	Anomocytic	
C. mas	-	93.5	-	31.86	Anomocytic	
Corylaceae						
Carpinus betulus	61.18	136.9	33.867	29.293	Anomocytic	brachy-paracytic
Corylus avellana	-	101.67	-	26.07	Anomocytic	
Crassulaceae						
*Sedum spurium**	53.19	57.32	34.848	34.988	Anisocytic	
*S. subulatum**	36.87	36.9	31	31.33	Anisocytic	
Cruciferae						
*Alliaria petiolata**	9.81	163.16	10.11	20.54	Anisocytic	Anomocytic
Alyssum desertorum	69.57	189.8	26.66	26.33	Anisocytic	
*A. linifolium**	186	473.3	20.1	21.96	Anisocytic	Anomocytic
*A. longistylum**	98.07	210.9	20.16	22.16	Anisocytic	
*A. minutum**	122.9	263.6	22.74	25.45	Anisocytic	
*A. sibiricum**	151	279.8	21.037	21.787	Anisocytic	Anomocytic
*A. strigosum**	122.29	210.35	24.474	24.652	Anisocytic	Anomocytic
Arabis sagittata	172.3	282.7	19.647	17.693	Anisocytic	Anomocytic

Table 1: Continued

Species	Stomatal frequency (mm²) adaxial	Stomatal frequency (mm²) abaxial	Guard cell length (µm) adaxial	Guard cell length (µm) abaxial	Type of stomata dominant	Type of stomata subordinate
Clypeola jonthlaspi	-	189.83	-	20.33	Anisocytic	
*Erysimum subulatum**	103.57	223.1	24.524	25.095	Anisocytic	
*Hesperis hyrcana**	12	62	35.7	39.64	Anisocytic	Anomocytic
*Neslia apiculata**	248.3	320	21.9	22.5	Anisocytic	
Rapistrum rugosum	269.5	337.1	24.048	22.69	Anisocytic	
*Sterigmostemum contortuplicatum**	125.33	140.33	30.34	32.93	Anisocytic	
*Thlaspi arvensis**	212.23	210.54	21.267	20.133	Anisocytic	
*Turritis glabra**	63.78	88.3	21.583	23.917	Anisocytic	
Dipsacaceae						
*Scabiosa amoena**	125.33	154.33	29.84	29.94	Anisocytic	
*S. caucasica**	86.33	124.87	36.3	38.28	Anisocytic	
S. crinita	129.53	294.5	32.4	30.06	Anisocytic	Anomocytic
*S. olivieri**	181.4	254	21	22.33	Anisocytic	
*S. persica**	138.1	183.97	33.14	33.52	Anisocytic	
*Cephalaria hirsuta**	58.2	85.81	40.73	41.73	Anisocytic	Anomocytic
Fagaceae						
Quercus macranthera	-	559.1	-	25.6	Anomocytic	
Q. petraea	-	613.2	-	25.1	Anomocytic	
Gentianaceae						
*Gentiana cruciata**	16	83.67	38.26	39.05	Anomocytic	
*G. gelida**	5.05	55.44	40.4	40.86	Anomocytic	Anisocytic
Geraniaceae						
Erodium cicutarium	170.49	202.43	26.43	26.02	Anomocytic	
Geranium lucidum	47.55	225.9	27.8	25.82	Anomocytic	
G. pratense	-	273.15	-	26.86	Anomocytic	
G. robertianum	2	114.5	27.67	24.47	Anomocytic	
G. rotundifolium	-	104.74	-	26.51	Anomocytic	
Hypericaceae						
*Hypericum hirsutum**	7.28	161.21	23.86	24.97	Anisocytic	Anomocytic
H. linarioides	3.67	229.15	26.11	24.05	Anisocytic	Anomocytic
*H. perforatum**	5	261.8	24.14	24.37	Anisocytic	Anomocytic
Labiatae						
*Ajuga comata**	47.37	154	26.417	26.5	Diacytic	
A. orientalis	76.88	227.6	27.917	26.45	Diacytic	
Betonica grandiflora	27	220.33	31.88	29.45	Diacytic	Anisocytic
Clinopodium vulgare	-	200.91	-	22.9	Diacytic	
*Lamium album**	33.07	245.5	28.73	28.75	Diacytic	
*L. amplexicaule**	73.16	185.65	26.66	29	Diacytic	Anisocytic
Marrubium astracanicum	87.23	275.8	22.05	20.55	Diacytic	
Mentha longifolia	7.01	229.2	29.7	25.17	Diacytic	
Nepeta betonicifolia	86.01	175.38	26.217	24.38	Diacytic	
N. haussknechtii	68	288.3	25.22	23.42	Diacytic	
Origanum vulgare	33.81	253.12	23.8	23.17	Diacytic	Anisocytic
Phlomis herba-venti	34.76	214.8	31.33	28.11	Diacytic	Anisocytic
P. tuberosa	13.93	343.8	23.82	21.77	Diacytic	
*Prunella vulgaris**	28.01	195.3	28.46	30.53	Diacytic	
*Salvia atropatana**	118.5	272	22.19	23.76	Diacytic	
*S. nemorosa**	67.47	308	24.16	24.66	Diacytic	Anisocytic
S. sclarea	105.2	319.8	23.34	21.44	Diacytic	
*S. verticillata**	204.9	436.9	23.42	23.63	Diacytic	Anisocytic
S. viridis	110.65	212.82	27.62	25.66	Diacytic	
*Satureja macrantha**	91.07	90.36	25.73	25.25	Diacytic	
Scutellaria pinnatifida	63.29	428.4	22.3	20.92	Diacytic	
*Sideritis montana**	60.17	117.81	28.19	28.54	Diacytic	
*Stachys asterocalyx**	102.91	281.2	24.6	24.8	Diacytic	
S. byzanthina	130.38	286.1	25.47	23.82	Diacytic	
*S. lavandulifolia**	78	177.22	25.39	25.87	Diacytic	Anisocytic
S. schtschegleevii	-	399.8	-	20.34	Diacytic	
*Teucrium chamaedrys**	85.7	291.7	27.11	27.76	Diacytic	
T. polium	4.27	312.47	22.42	21.21	Diacytic	Anisocytic
Thymus kotschyanus	93.59	173.53	28	25	Diacytic	
Ziziphora capitata	86.06	279.9	24.42	22.36	Diacytic	
Z. clinopodioides	146.58	247.6	24.56	23.68	Diacytic	Anisocytic

Table 1: Continued

Species	Stomatal frequency (mm²) adaxial	Stomatal frequency (mm²) abaxial	Guard cell length (µm) adaxial	Guard cell length (µm) abaxial	Type of stomata dominant	Type of stomata subordinate
Linacea						
*Linum nervosum**	81.33	72.73	31.73	31.17	laterocyclic	
L. nodiflorum	70.06	67.44	37.91	39.57	laterocyclic	
L. tenuifolium	185.17	14.05	30.46	32.62	laterocyclic	
Oleaceae						
Fraxinus excelsior	-	227.63	-	23.9	actinocytic	
Jasminum fruticans	13.03	250.52	32.06	27.35	staurocytic	cyclocytic
Ligustrum vulgare	-	200.02	-	28.71	actinocytic	
Papaveraceae						
*Papaver glaucum**	93.62	107.97	34.53	37.53	Anomocytic	
P. orientale	-	176.65	-	38.6	Anomocytic	
Papilionaceae						
Anthyllis biossieri	240.72	147.08	24.81	26.41	Anomocytic	Anisocytic
*Astragalus alyssoides**	174.15	133.01	24.18	23.99	Anisocytic	Anomocytic
*A. aureus**	284.3	222.3	19.52	18.14	Anisocytic	
*A. bicolor**	170.17	158.67	23.59	22.63	Anisocytic	
A. glycyphyllus	-	109.96	-	31.39	Anomocytic	Anisocytic
*A. hamosus**	204.1	198.9	24.67	23.92	Anomocytic	
*A. hirticalyx**	349.5	384.07	18.98	19.45	Anisocytic	Anomocytic
*A. macrourus**	184.9	179.52	20.92	20.13	Anisocytic	Anomocytic
*A. microcephalus**	241.59	201.32	20.64	20.56	Anisocytic	Anomocytic
*A. onobrychioides**	167.31	120.2	24.88	23.77	Anisocytic	Anomocytic
*A. pinetorum **	176.21	174.41	23.56	23.45	Anisocytic	Anomocytic
*A. schistosus**	161.01	159.79	27.84	27.2	Anisocytic	
*A. tribulodies**	231.1	393.9	20.66	20.66	Anomocytic	Anisocytic
*Colutea cilicica**	77.67	174.3	23.27	23.82	Anomocytic	Anisocytic
Coronilla scorpioides	280.4	185.4	21.44	23.46	Anisocytic	Anomocytic
*C. varia**	191.5	199.4	24.35	24.51	Anomocytic	Anisocytic
Dorycnium intermedium	157.5	144.2	21.28	22.65	Anomocytic	Anisocytic
Hippocrepis unisiliquosa	212.2	200.9	20.21	20.83	Anisocytic	Anomocytic
Lathyrus cyaneus	110.54	95.35	30.2	32.46	Anisocytic	
L. laxiflorus	121.69	74.43	30.6	32.73	laterocyclic	Anisocytic,
*L. pratensis**	60.5	69.77	27.86	29.33	Anisocytic	Anomocytic
*L. rotundifolius**	148.3	65	31.2	30.9	laterocyclic	Anisocytic
Lotus corniculatus	165.19	137.72	24.72	26.14	Anomocytic	Anisocytic
*Medicago minima**	270.74	279.54	18.07	18.79	Anisocytic	Anomocytic
*M. rigidula**	226.3	268.7	18.33	19.42	Anomocytic	
M. sativa	244.02	290.43	18.88	17.11	Anomocytic	
*Onobrychis bungei**	352.8	206.68	20.52	20.07	Anomocytic	
*O. cornuta**	299.22	193.03	20.68	20.29	Anomocytic	
*O. hohenackeriana**	261.2	192.82	23.4	22.8	Anomocytic	
O. michauxii	310.7	292.7	21.65	23.12	Anomocytic	
Securigera securidaca	154	140.88	23.09	23.25	Anomocytic	
Trifolium arvense	212.23	210.54	20.13	21.26	Anomocytic	
T. campestre	169.57	145.51	17.33	20.13	Anomocytic	
T. canescens	276.5	215.3	17.15	20.31	Anomocytic	Anisocytic
T. hybridum	387.33	372.7	14.45	16.19	Anomocytic	Anisocytic
T. montanum	397.7	235.2	20.7	24.97	Anisocytic	Anomocytic
*T. pratense**	163.5	216.8	19.25	20.16	Anomocytic	Anisocytic
*T. repens**	139.19	205.94	17.33	17.4	Anomocytic	Anisocytic
T. scabrum	304.44	252.5	17.44	19.11	Anomocytic	
Trigonella brachycarpa	233.28	282.7	20.5	20.12	Anomocytic	Anisocytic
T. calliceras	231.39	165	19.88	22.85	Anomocytic	
T. gladiata	206.7	205.63	24.33	24	Anomocytic	Anisocytic
T. monspeliaca	297.46	187.8	23	25	Anomocytic	Anisocytic
T. spicata	305.3	244.3	19.38	22.1	Anomocytic	Anisocytic
*Vicia grandiflora**	46	178.3	22.8	23.7	laterocytic	Anisocytic
*V. hybrida**	67.7	83	28.7	28.76	laterocytic	Anisocytic
*V. truncatula**	32.17	62.71	28.85	30.28	laterocytic	Anisocytic
*V. variegata**	76.15	81.6	26.8	27.23	Anomocytic	Anisocytic
Plantaginaceae						
Plantago lanceolata	234.6	267.3	25.04	24.42	Diacytic	Anisocytic
*P. ovata**	155	139.1	28.16	27.17	Diacytic	Anomocytic
P. psyllium	190.93	152.11	28.18	29.67	Diacytic	Anomocytic

Table 1: Continued

	Stomatal frequency (mm^2)		Guard cell length (µm)		Type of stomata	
Species	adaxial	abaxial	adaxial	abaxial	dominant	subordinate
Polygonaceae						
Atraphaxis spinosa	118.03	150.9	30.06	29.53	Anisocytic	Anomocytic
Polygonum alpestre	81.03	116.28	33.82	33.04	Anisocytic	
Rumex acetoselloides	74.4	85.5	42.62	39.78	Anisocytic	Anomocytic
R. tuberosus	59.8	89.05	38.56	37.67	Anisocytic	
Primulaceae						
Anagallis arvensis	35.15	83.71	42.58	38.33	Anomocytic	
Androsace villosa	63.79	60.55	35.69	37.007	Anomocytic	
Primula auriculata	38.53	117.37	30.9	28.82	Anomocytic	
P. macrocalyx	18.28	115.82	30.88	27.851	Anomocytic	
Ranunculaceae						
*Adonis aestivalis**	46.41	27.42	65.5	61.33	Anomocytic	
*Anemone albana**	120	161.7	33.9	38.4	Anomocytic	
Delphinium tuberosum	-	82.52	-	49.98	Anomocytic	
*Ranunculus caucasicus**	66.92	98.58	35.51	36.03	Anomocytic	
*R. polyanthemos**	30.33	77	50.11	50.25	Anomocytic	
*R. strigillosus**	96.31	68.96	40.02	39.99	Anomocytic	
Thalictrum minus	-	248.5	-	23.48	Anomocytic	
Rhamnaceae						
Paliurus spine Christi	-	437.8	-	21.52	Anomocytic	
Rhamnus catharica	-	256.87	-	26.06	Anomocytic	
R. pallasii	48.04	259.09	29.52	27.67	Anomocytic	
Rosaceae						
Agrimonia eupatoria	0.188	230.76	28.5	26.819	Anomocytic	
Alchemilla fluminea	53.58	270.88	28.2	28.46	Anomocytic	
A. erythropoda	78.52	248.95	26.1	24.76	Anomocytic	
A. persica	76.25	255	24.7	22.56	Anomocytic	
A. pseudo-cartalinica	40.87	228.05	26.06	25.73	Anomocytic	
A. sericata	75.24	231.2	29.19	27.91	Anomocytic	
Amygdalus fenzliana	-	207.6	-	37.133	Anomocytic	
Cerasus avium	-	259.54	-	27.01	Anomocytic	
C. incana	-	199.99	-	28.33	Anomocytic	
Cotoneaster nummularioides	-	217	-	27.144	Anomocytic	
C. nummularia	-	177.8	-	34.702	Anomocytic	
Crataegus meyeri	-	126.76	-	38.98	Anomocytic	
Filipendula vulgaris	2.96	398.3	24.04	23.75	Anomocytic	
Fragaria vesca	-	317.5	-	21.44	Anomocytic	
Geum rivale	33.75	351	26.53	24.3	Anomocytic	
G. urbanum	5.2	127.21	28.41	26.22	Anomocytic	
Mespilus germanica	-	226.9	-	25.78	Anomocytic	
Potentilla aucheriana	59.29	298.6	31.43	29.2	Anomocytic	
P. inclinata	28.55	292.79	27.37	25.6	Anomocytic	
P. recta	64.05	258.12	27.45	26.21	Anomocytic	
P. szovitsii	26.4	395.1	25.836	25	Anomocytic	
Prunus divaricata	-	408.2	-	23.69	Anomocytic	
P. spinosa	-	272.7	-	27.73	Anomocytic	
Pyrus syriaca	-	133.3	-	29.7	Anomocytic	
Rosa canina	-	150.74	-	28.05	Anomocytic	
R. iberica	-	133.27	-	27.73	Anomocytic	
R. pimpinellifolia	-	78.33	-	31.8	Anomocytic	
Sanguisorba minor	40.84	401.7	24.62	23.51	Anomocytic	
Sorbus torminalis	-	170.66	-	26.95	Anomocytic	
*Spiraea crenata**	0.68	234.5	19	22.89	Anomocytic	
*S. hypericifolia**	13.97	296.14	20.2	20.85	Anomocytic	
Rubiaceae						
*Asperula glomerata**	66.21	80.07	38.169	39.48	laterocyclic	
A. molluginoides	1.41	70.64	46.67	34.6	laterocyclic	
Callipeltis cucullaris	49.06	122.6	38.97	34.79	laterocyclic	
*Cruciata laevipes**	32	90.5	27.3	29.76	laterocyclic	
C. taurica	-	136.25	-	29.09	laterocyclic	
*Galium aparine**	6.94	56.99	33.63	39.07	laterocyclic	
G. odoratum	-	61.2	-	32.08	laterocyclic	
G. verum	3.24	233.78	37.83	30.02	laterocyclic	
*Sherardia arvensis**	88	169.06	29.75	30.52	laterocyclic	

Table 1: Continued

Species	Stomatal frequency (mm²) adaxial	Stomatal frequency (mm²) abaxial	Guard cell length (μm) adaxial	Guard cell length (μm) abaxial	Type of stomata dominant	Type of stomata subordinate
Scrophulariaceae						
Digitalis nervosa	6.67	110.86	39.6	34.9	Anisocytic	Anomocytic
*Linaria kurdica**	125.27	115.98	31.9	31.86	Anisocytic	Anomocytic
Pedicularis sibthorpii	-	302	-	28.07	Anomocytic	
P. wilhelmsiana	-	353.8	-	24.59	Anomocytic	
Scrophularia oxysepala	52.7	333.3	33.33	27	Anomocytic	
S. umbrosa	2.1	279.3	26.5	21.86	Anomocytic	
S. variegata	108.89	141.1	29.99	29.6	Anisocytic	Anomocytic
*Verbascum orientale**	127.6	150.6	26.34	27.04	Anomocytic	
*V. suworowianum**	108.42	182.55	27.51	27.67	Anomocytic	
V. speciosum	88.1	255.4	27.71	26.51	Anomocytic	Anisocytic
*Veronica anagallis-aquatica**	107.44	110.22	29	31.9	Anomocytic	Anisocytic
V. gentianoides	80.95	117.2	38.39	36.39	Anomocytic	
*V.multifida**	58.11	158.37	32.5	33.05	Anomocytic	Anisocytic
V.polita	84.3	135	32.55	24.5	Anomocytic	
Ulmaceae						
Celtis caucasica	-	742.4	-	20.66	Anomocytic	
Ulmus glabra	-	280.37	-	33.67	cyclocytic	
U. minor	-	434.4	-	33.35	cyclocytic	
Umbelliferae						
Albovia tripartita	3.7	144.8	29.62	25.32	Diacytic	Anisocytic
Bupleurum falcatum	210	126.67	17.7	19.2	Anisocytic	Anomocytic
*B. geradii**	183.46	165.56	20.66	17.66	Anisocytic	Anomocytic
*Carum carvi**	117.5	289.2	26.1	27.367	Anisocytic	Anomocytic Diacytic
Caucalis platycarpos	91.8	225.7	27.83	26.333	Diacytic	
Chaerophyllum aureum	4.44	326.7	21.76	21.37	Anisocytic	Anomocytic Diacytic
Cymbocarpum anethoides	111.81	107.59	30.73	32.46	Anomocytic	
Daucus broteri	216.7	300	25.2	20.23	Diacytic	
*Eryngium caucasicum**	91.61	107.53	25.38	26.16	Anisocytic	
*Falcaria vulgaris**	88.06	107.9	22.66	23.3	Diacytic	
Heracleum pastinacifolium	122.85	298.47	28.33	27	Anisocytic	Anomocytic Diacytic
H. persicum	117.14	275.5	24.61	23.35	Anisocytic	Anomocytic, Diacytic
Laser trilobum	-	108.87	-	29.62	Anomocytic	
Peucedanum caucasicum	-	173.4	-	22.76	Anomocytic	
Pimpinella aurea	105	533.3	21.6	20.7	Anisocytic	Anomocytic
*P. tragium**	101.32	157.5	26.531	26.6	Diacytic	Anisocytic
*Prangos ferulacea**	50	50	38.1	45.3	Anisocytic	Anomocytic
Sanicula europaea	-	90.35	-	22.96	Anomocytic	
Seseli peucedanoides	-	222.86	-	28.7	Anisocytic	Anomocytic
*Trinia leiogona**	87.55	93.88	28.33	26.66	Anisocytic	Anomocytic
Valerianaceae						
Valerianella dactylophylla	54.8	83.27	37	34	Anomocytic	Anisocytic
V. lasiocarpa	81.17	102.8	31.5	26.83	Anomocytic	Anisocytic
Violaceae						
Viola arvensis	65.33	94.9	37.67	35.16	Anisocytic	
V. odorata	15.23	135.27	29.41	27.06	Anisocytic	

Pistacia atlantica which has stomata on both surfaces. Stomatal densities within the family range from 195 per mm² for *Rhus coriaria* to 331 per mm² for *P. atlantica*. The stomatal type is usually anomocytic and guard cells vary between 21.18 and 29.66 μm in length.

Caprifoliaceae: In the three species of Caprifoliaceae represented here, stomata are observed only on abaxial surfaces. The highest density is observed in *Lonicera caucasica* with an average of 364 per mm². The dominant stomatal type is anomocytic. In *Viburnum lantana*, anisocytic and hemiparacytic stomata are also present as subordinate types. The guard cell length is between 21.28 and 32.02 μm.

Cornaceae: In the Cornaceae, stomata are found only on abaxial surfaces. The stomatal density is 93-172 per mm². The dominant stomatal type is anomocytic. Guard cell length is between 24.39 and 31.86 μm.

Corylaceae: In the Corylaceae, *only abaxial* stomata are present, except in *Carpinus betulus* which has stomata on both surfaces; in this species, the average densities are 61 per mm^2 and 136 per mm^2 for adaxial and abaxial surfaces, respectively. Stomatal density is low in comparison with other woody plants. The dominant stomatal type is anomocytic, though in *C. betulus* brachyparacytic stomata are also present. Guard cell average length is 33.86 μm on adaxial surfaces and between 26.7 and 29.29 μm on abaxial surfaces for the two species studied.

Fagaceae: In the Fagaceae, stomata are observed only on abaxial surfaces. The stomatal density is high, averaging at 613 per mm^2. The stomatal type is anomocytic and guard cell average length approximates to 25 μm.

Oleaceae (Fig. 2A-I): In the Oleaceae, stomata are absent from adaxial surfaces, with the exception of *Jasminum fruticans*. Abaxial average densities are between 200-250 per mm^2. Stomata are anomocytic, with actinocytic, staurocytic or cyclocytic arrangements in different species. Guard cell average length is 32.06 μm on adaxial surfaces and 23.9 μm on abaxial surfaces.

Rhamnaceae: In the Rhamnaceae, stomata are present only on abaxial surfaces, with the exception of *Rhamnus pallasii*. The highest stomatal density is observed in *Paliurus spina-chiristi* at 437 per mm^2. Stomatal type is anomocytic. Guard cell lengths vary between 29.52 and 21.52 μm.

Rosaceae: In the Rosaceae, stomata are observed on both laminar surfaces in the genera *Alchemilla, Geum,*

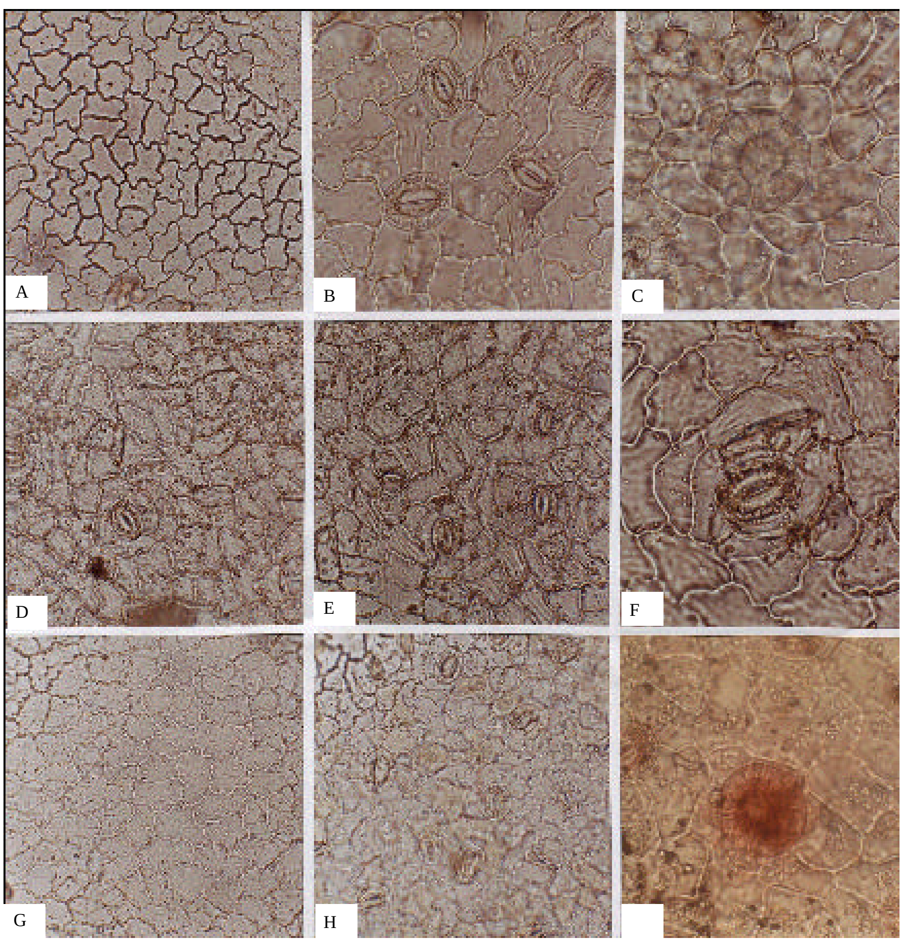

Fig. 2: A-I, epidermis in superficial view of the Oleaceae; A-C, *Fraxinus excelsior*; A, adaxial; B, C, abaxial; C, glandular trichome; D-F, *Jasminum fruticans*; D, adaxial; E, F, abaxial; G-I, *Ligustrum vulgare*; G, adaxial; H, I, abaxial; I, glandular trichome; A, D, E, G, H, (×150); B, C, F, I, (×300)

Potentilla and *Spirea*, whilst in *Amygdalus*, *Cerasus*, *Cotoneaster*, *Prunus* and *Rosa*, they are found only on abaxial surfaces. The abaxial stomatal densities are always higher than those of the adaxial surfaces; the highest density is observed in *Prunus* at an average of 408 per mm^2. Stomatal type is anomocytic. Where stomata are present on both surfaces, the adaxial guard cells are larger (average 31.43 μm) than those of the abaxial surface (average 21.44 μm), though in the genus *Spiraea*, this is vice-versa.

Ulmaceae (Fig. 3A-G): In the Ulmaceae, stomata are present only on the abaxial surfaces. The stomatal densities are high, ranging between 280 per mm^2 for *Ulmus glabra* and 742 per mm^2 for *Celtis caucasica*. Stomata are anomocytic in *C. caucasica* whilst in the genus *Ulmus*, cells are cyclocytic. Guard cell lengths vary between 20.66 and 33.67 μm.

Herbaceous species with stomatal characteristics comparable to woody plants

Campanulaceae: In the Campanulaceae, with the exception of *Symphyandra armena*, stomata are present on both surfaces. Abaxial stomatal frequencies are usually higher than those of the adaxial surfaces; these differences can be up to four-fold, as in *Campanula glomerata*. The average stomatal densities are 42 per mm^2 for adaxial surfaces and 240 per mm^2 for abaxial surfaces. The dominant type of stomata is anomocytic, with the exception of *C. stevenii* where anisocytic patterning is dominant over the anomocytic arrangement. Guard cells on adaxial surfaces (average 36.42 μm) are longer than those of the abaxial surface (average 25.43 μm).

Cistaceae (Fig. 4A-I): In the Cistaceae, stomata are observed on both surfaces. The abaxial stomatal densities are greater than on those of the adaxial surfaces with the

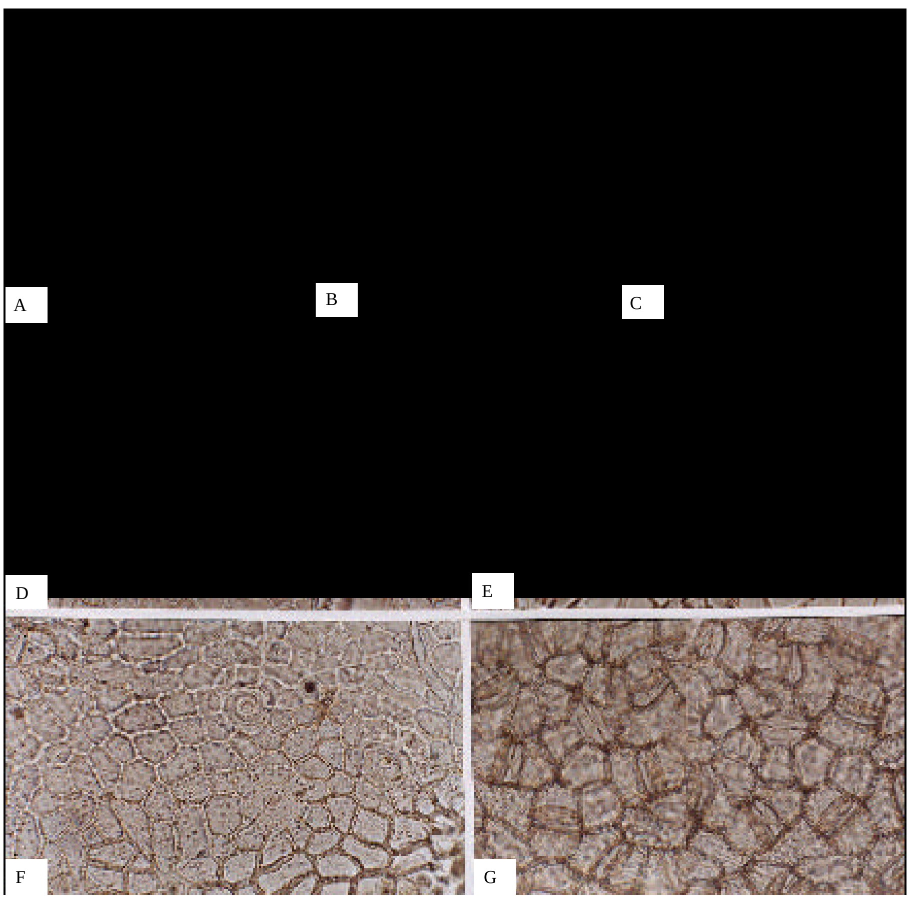

Fig. 3: A-G, epidermis in surface view of the Ulmaceae; A-C, *U. minor*; A, B, adaxial; C, abaxial; D, E, *U. glabra*; D, adaxial; E, abaxial; F, G, *Celtis caucasica*; F, adaxial; G, abaxial; A, (×75); B, D, F, (×150); C, E, G, (×300)

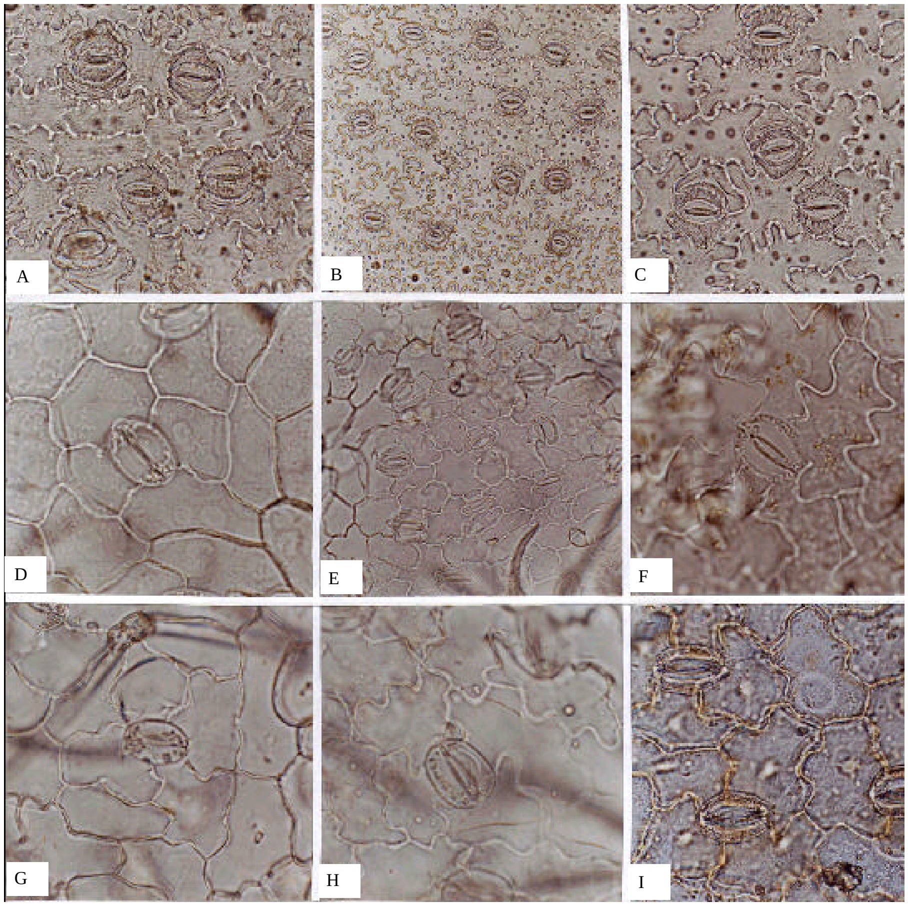

Fig. 4: A-I, epidermis in superficial veiw of the Cistaceae; A-C, *Fumana procumbens*; A, adaxial; B, C, abaxial; D-F, *Helianthemum ledifolium*; D, adaxial; E, F, abaxial; G, H, *H. salicifolium*; G, adaxial; H, abaxial; I, adaxial surface of *H. nummularium*; A, C, E, (×150); B, (×75); D, F-I, (×300)

exception of *Fumana procumbens*. The density differences between adaxial and abaxial surfaces can be up to four-fold, as in *Helianthemum ledifolium,* which at an average of 336 per mm^2 shows the highest density of the four species studied. The dominant stomatal type is anomocytic, though in *F. procumbens* anisocytic patterning is also observed. The guard cell lengths range between 26.54 and 38.46 μm for abaxial surfaces.

Geraniaceae: In the Geraniaceae, with the exceptions of *G. pratense* and *G. rotundifolium*, stomata are found on both surfaces. The abaxial stomatal densities are higher than those of adaxial surfaces. The difference between surfaces is considerable; higher densities on the abaxial side range between 104 and 273 per mm^2. The stomatal type is anomocytic. Guard cells on adaxial surfaces (average 27.8 μm) are longer than those of the abaxial surfaces (average 24.47 μm).

Polygonaceae (Fig. 5A-I): In the Polygonaceae, stomata are present on both laminar surfaces. Abaxial stomatal densities (average 150 per mm^2) are higher than those of the adaxial surfaces (average 59 per mm^2). The dominant stomatal type is anisocytic, with anomocytic stomata present as a subordinate pattern. Guard cell lengths on adaxial surfaces (average 42.62 μm) are greater than abaxial guard cell average lengths (29.53 μm).

Primulaceae: In the Primulaceae, stomata are observed on both laminar surfaces, with higher abaxial stomatal densities except in *Androsace villosa*. Average densities for the four species studied are 18 per mm^2 for adaxial

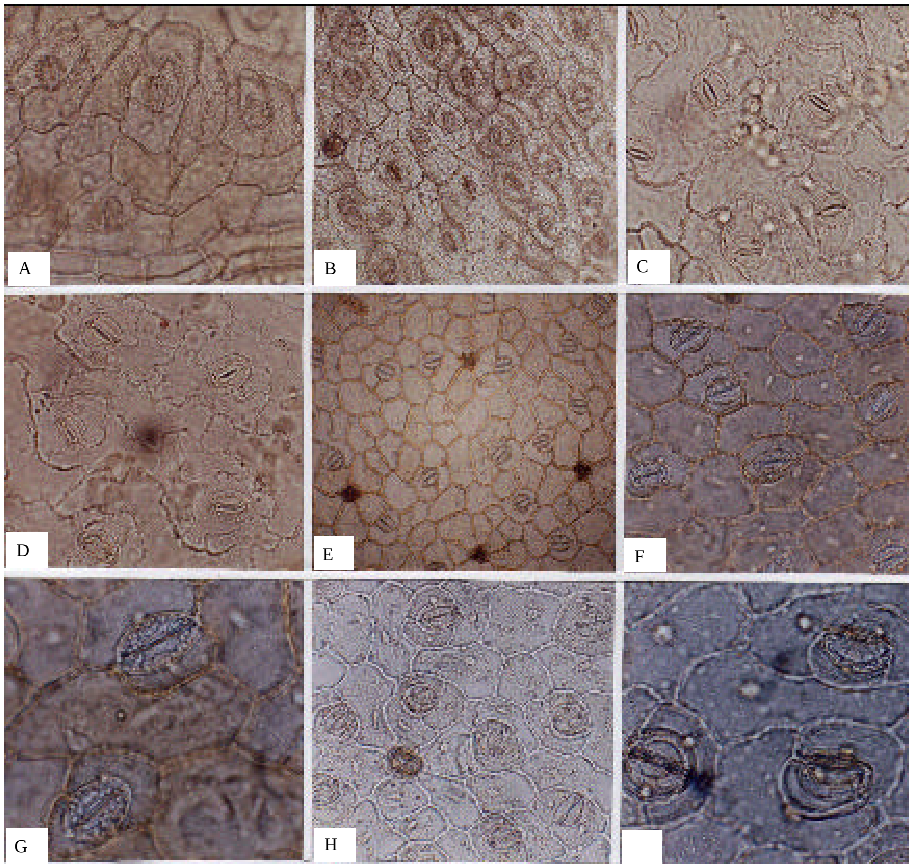

Fig. 5: A-I, epidermis in superficial view of the Polygonaceae; A, B, *Atraphaxis spinosa*; A, adaxial; B, abaxial; C, D, *Polygonum alpestre*; C, adaxial; D, abaxial; E-G, *Rumex acetosa*; E, adaxial; F, G, abaxial; H, I, *R. tuberosus*; H, adaxial; I, abaxial; A, C, D, F, H, (×150); B, E, (×75); G, I, (×300)

surfaces and 117 per mm^2 for abaxial surfaces. The differences in density between these surfaces can be up to six times, as in *P. macrocalyx*. Stomata are anomocytic throughout the family. Guard cell average length for the adaxial surfaces (42.58 μm) is greater than the abaxial average (27.85 μm).

Valerianaceae: In the Valerianaceae, stomata are present on both surfaces, with higher-abaxial stomatal densities (102 per mm^2) than those of the adaxial surfaces (54 per mm^2). The dominant stomatal type is anomocytic; anisocytic cells are also present as a subordinate category. Adaxial guard cell lengths are greater (average 37 μm) than abaxial cell lengths (average 26.83 μm).

Violaceae: In the Violaceae, stomata are present on both surfaces; with higher average abaxial (135 per mm^2) than adaxial densities (15 per mm^2). Stomatal type is anisocytic. The largest guard cells are always found on adaxial surfaces; cell lengths vary between 37.67 μm for adaxial and 27.06 μm for abaxial guard cells.

Families of herbaceous species with characters distinct from woody plants

Caryophyllaceae: In the Caryophyllaceae, special arrangements of stomata are evident in a genus- specific manner; e.g. in *Herniaria, Minuartia* and *Silene* (with the exception of *S. persica)* stomatal frequencies on adaxial surfaces are greater than those of abaxial surfaces, whilst in *Arenaria* and *Cerastium* these are vice-versa. In *Dianthus*, *Minuartia*, *Arenaria* (with the exception of *A. gypsophiloides)* and *Silene* (with the exception of *S. persica)* the dominant stomatal type is diacytic, whilst in *Cerastium* and *Herniaria*, anomocytic cells dominate. Usually abaxial stomata (average length 41.2 μm) are equal to or larger than the adaxial stomata (26.2 μm), e.g., in *Cerastium* and *Silene*, differences in guard cell lengths between adaxial and abaxial surfaces are minor. The size of stomata is similar on both surfaces in *Stellaria media* and in all representatives of the genus *Minuartia* (Zarinkamar, 2001).

Compositae: In the Compositae, stomata are present on both surfaces, with the exception of *Artemisia armeniaca*. The stomatal densities of on abaxial surfaces are usually higher than those of the adaxial surfaces, with some exceptions (*Achillea* and *Anthemis)*. The species *A. armeniaca*, *Carduus thoermeri*, *Centaurea zavandica*, *Cirsium osseticum*, *Crepis sancta*, *Hieracium pilosella*, *Inula vulgaris*, *Tanacetum graminifolius* and *Tragopogon reticulatus* have the highest stomatal densities in their respective genera. *C. zavandica*, with an average of 409 per mm^2 on abaxial surfaces, has the highest stomatal density of any member of the *Compositae* family included in the present study. In this family, only anomocytic and anisocytic stomatal forms are evident. In the genera *Artemisia*, *Centaurea*, *Hieracium*, *Tragopogon* and *Tanacetum*, the abaxial guard cells are equal to or larger than adaxial cells, whilst in *Carduus*, *Cirsium* and *Inula* this is vice-versa. Stomatal size is similar on both surfaces in *Achillea millefolium* and in the genus *Crepis*.

Convolvulaceae: Throughout this family, stomata are observed on the both surfaces of the leaf. Abaxial stomatal densities are higher than those of the adaxial surfaces, with the exception of *Convolvulus arvensis*. Density differences between both surfaces are minor. The dominant stomatal form is paracytic, whilst anisocytic cells are also observed in two of the three species studied. Guard cell sizes are similar on both surfaces (with the exception on *C. arvensis)*. The guard cell lengths range between 25.61 and 28.61 μm; longer guard cells are associated with higher stomatal densities.

Crassulaceae: In the Crassulaceae, stomata are present on both leaf surfaces. A similar adaxial and abaxial stomatal size and density is usually observed; the two species studied have an average stomatal density of between 36 and 57 per mm^2. Stomatal type is anisocytic and guard cell lengths are between 31.00 and 34.98 μm.

Cruciferae: In the Cruciferae, stomata are present on both leaf surfaces, with the exception of *Clypeola jonthlaspi*. The stomatal densities of abaxial leaf surfaces are usually greater than those of the adaxial surfaces; differences can be up to two-fold as in the genus *Alyssum*, or can be roughly equivalent, as in *Thlaspi arvense*. The highest density is observed in *A. linifolium* at 473 per mm^2 on the abaxial surface and the lowest in *Hesperis hyrcana*, with 12 per mm^2 on adaxial surfaces and 62 per mm^2 on abaxial surfaces. The dominant stomatal type is anisocytic, with anomocytic cells also present in some species. Abaxial guard cell lengths (39.64 μm) are equal to or larger than adaxial guard cells (10.11 μm), with the exceptions of *Arabis sagittata*, *Rapistrum rugosum* and *Thlaspi arvense*.

Dipsacaceae (Fig. 6A-I): In the Dipsacaceae, stomata are observed on both surfaces, with greater abaxial than adaxial densities; differences between surfaces vary within the family. The highest, in *Scabiosa crinita* has an abaxial average of 294 per mm^2, which is twice that of the adaxial surface (129.53 per mm^2). The lowest difference between surfaces is seen in *Cephalaria hirsuta* (58 per mm^2 adaxial and 85 per mm^2 abaxial). The dominant stomatal type is anisocytic, whilst anomocytic cells are occasionally subordinate. Abaxial guard cells lengths are greater (average 41.73 μm) than adaxial guard cells (average 21 μm), with the exception of *S. crinita*. Longer guard cells are usually associated with higher stomatal frequencies.

Gentianaceae: In the Gentianaceae, stomata are present on both surfaces. The overall stomatal density is low, especially on adaxial surfaces. Average densities are between 5 and 16 per mm^2 on adaxial surfaces and from 55 to 83 per mm^2 on abaxial surfaces. The dominant stomatal type is anomocytic, whilst anisocytic cells are present as a subordinate category in *G. gelida*. Abaxial guard cells are longer (average 40.86 μm) than adaxial cells (average 38.26 μm).

Hypericaceae: In the family Hypericaceae, stomata are present on both leaf surfaces; abaxial are higher than adaxial stomatal densities, with most stomata present on abaxial surfaces (abaxial averages range between 161 and 261 per mm^2). The dominant type is anisocytic, with anomocytic stomata also evident. Guard cell lengths on abaxial surfaces are greater than those of adaxial surfaces, with the exception of *H. linarioides*. Guard cell average lengths for the three species studied are between 23.86 and 26.11 μm (both of these are measurements of cells from adaxial surfaces).

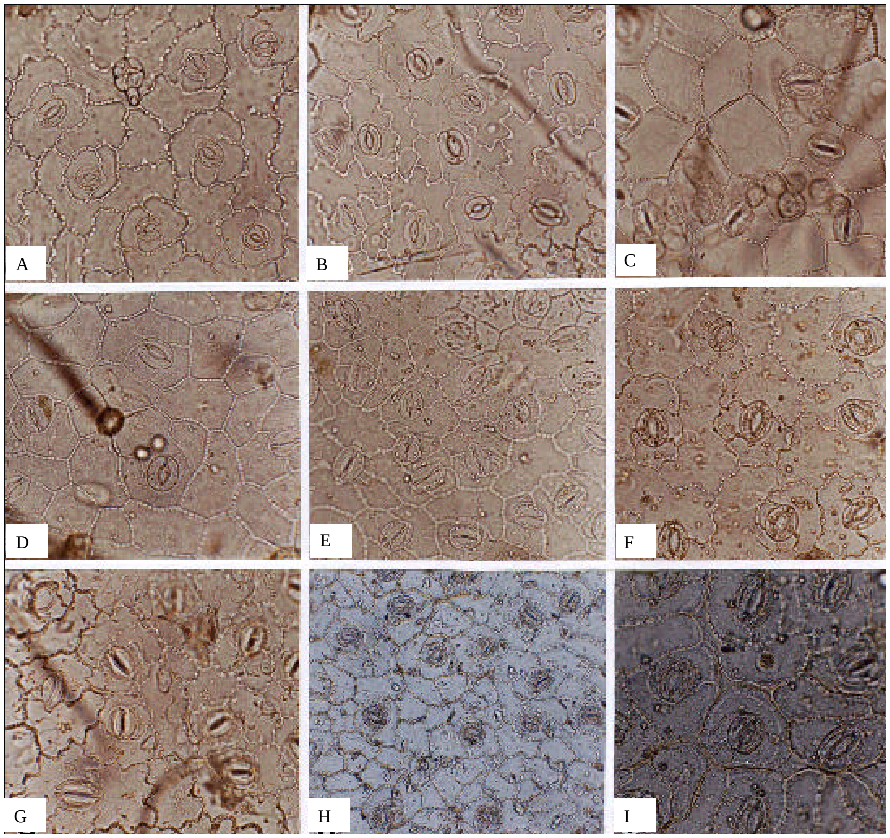

Fig. 6: A-I, epidermis in superficial view of *Scabiosa* sp.; A, B, *S. olivieri*; A, adaxial; B, abaxial; C, adaxial epidermis of *S. amoena*; D, E, *S. crinita*; D, adaxial; E, abaxial; F, G, *S. persica*; F, adaxial; G, abaxial; H, I, *S. caucasica*; H, adaxial; I, abaxial; A-G, I, (×150); H, (×75)

Papilionaceae (Fig. 7, A-H): The Papilionaceae, are well represented in this study, with 48 species examined. Stomata are observed on both surfaces throughout the family, with the exception of *Astragalus glycyphyllus*. Stomata show unusually wide variability and lack any genus-specific occurrence of a distinctive stomatal form; also the numbers of stomata per unit area are often higher on the adaxial surfaces. The highest density is observed in *Trifolium* (139 to 397 per mm^2 on adaxial surfaces); and the lowest in the genus *Vicia* (32 per mm^2 and 178 per mm^2 on adaxial and abaxial surfaces, respectively). The dominant stomatal type in *Astragalus* is anisocytic; whilst in *Trifolium* and *Trigonella* anomocytic cells are most frequent. In *Lathyrus* and *Vicia,* laterocyclic cells are observed together with other two types. Guard cells are smaller in comparison with other families studied, ranging in length between 14.45 μm on the adaxial surface of *Trifolium hybridum*, to 32.73 μm on the abaxial surface of A. *glycyphyllus*.

Ranunculaceae: In the Ranunculaceae, stomata are found on both surfaces. The difference in density between adaxial and abaxial surfaces is minor, with the exceptions of *Delphinium tuberosum* and *Thalictrum minus* where stomata are completely absent from the adaxial surface. Generally abaxial stomatal densities are higher than those of the adaxial surfaces, except in *Adonis aestivalis* and *Ranunculus strigillosus* where this is vice-versa. The highest density is observed in *T. minus* (with 248 per mm^2 on the abaxial surfaces) and the lowest in *A. aestivalis* (with 46 per mm^2 on adaxial surfaces and 27 per mm^2 on abaxial surfaces). Stomata are anomocytic in all species studied and abaxial guard cells are longer (average 61.33 μm) than adaxial cells (average 33.9 μm), except in the species *A. aestivalis*.

Families of herbaceous species whose stomatal characters differ greatly between genera of the same family and also within species of the same genus

Boraginaceae: In the Boraginaceae, stomata are observed

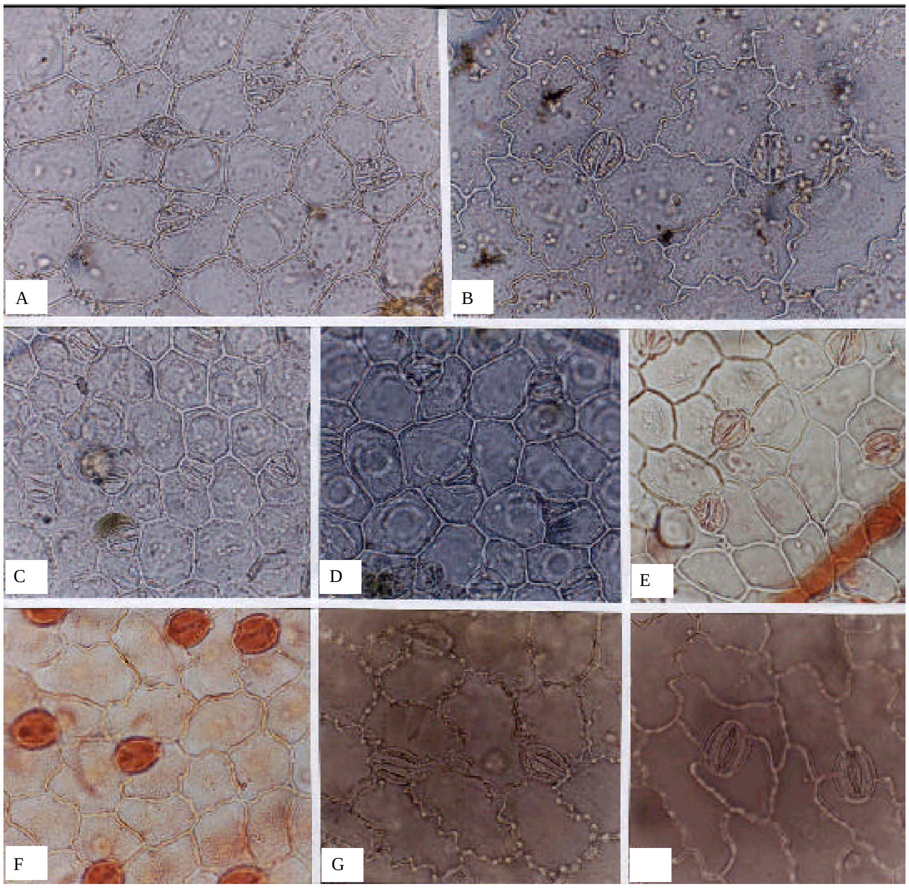

Fig. 7: A-H, epidermis in superficial view of *Trifolium* sp.; A, C, E, adaxial; B, D, F, G, H, abaxial; A, B, *T. pratense*; C, D, *T. hybridum*; E, F, *T. canescens*; G, *T. arvense*; H, *T. repens*; A-H, (×300)

on both leaf surfaces, though are always most abundant on the abaxial epidermis, with the exception of *Heliotropium ellipticum*. In some species this difference is between two-to four-folds, as in *Asperugo procumbens*, *Myosotis silvatica* and *Symphytum asperum*. The highest stomatal densities are observed in *Onosma dichroanthum* (350 per mm^2 on adaxial and 496 per mm^2 on abaxial surfaces) and the lowest in *M. silvatica* (85 per mm^2 on adaxial and 171 per mm^2 on abaxial surfaces). The dominant stomatal type is anomocytic, with anisocytic cells present as a subordinate type in some species such as *M. silvatica, O. dichroanthum* and *O. microcarpum*. In *S. asperum,* diacytic cells are also observed together with the other two types. Guard cell average length on adaxial surfaces (29.95 μm) is greater than abaxial surfaces (20.2 μm), with the exception of *O. microcarpum*.

Chenopodiaceae: In the Chenopodiaceae, stomata are present on both surfaces, with greater abaxial than adaxial densities, except in *Kochia prostrata*. The differences between adaxial and abaxial surfaces are usually minor. Of the three species studied, densities are highest in *Noaea mucronata* (abaxial average of 150 per mm^2) and lowest in *K. prostrata* (abaxial average of 78 per mm^2). The dominant type of stomata in *Chenopodium album* is anomocytic, whilst in *K. prostrata* and *N. mucronata* bracyparacytic cells are most frequent. Guard cell average length is between 24.30 and 29.1 μm in these three species (Zarinkamar, 2006a).

Labiatae (Fig. 8A-J): In the Labiatae, stomata are found on both surfaces, except in *Clinopodium vulgar* and *Stachys schtschegleevii*, where adaxial stomata are completely absent. Abaxial stomatal densities are higher than those of the adaxial surfaces; the highest of these is observed in *Salvia verticillata* (436 per mm^2) with significant differences between surfaces for all species studied. The dominant stomatal type is diacytic, with

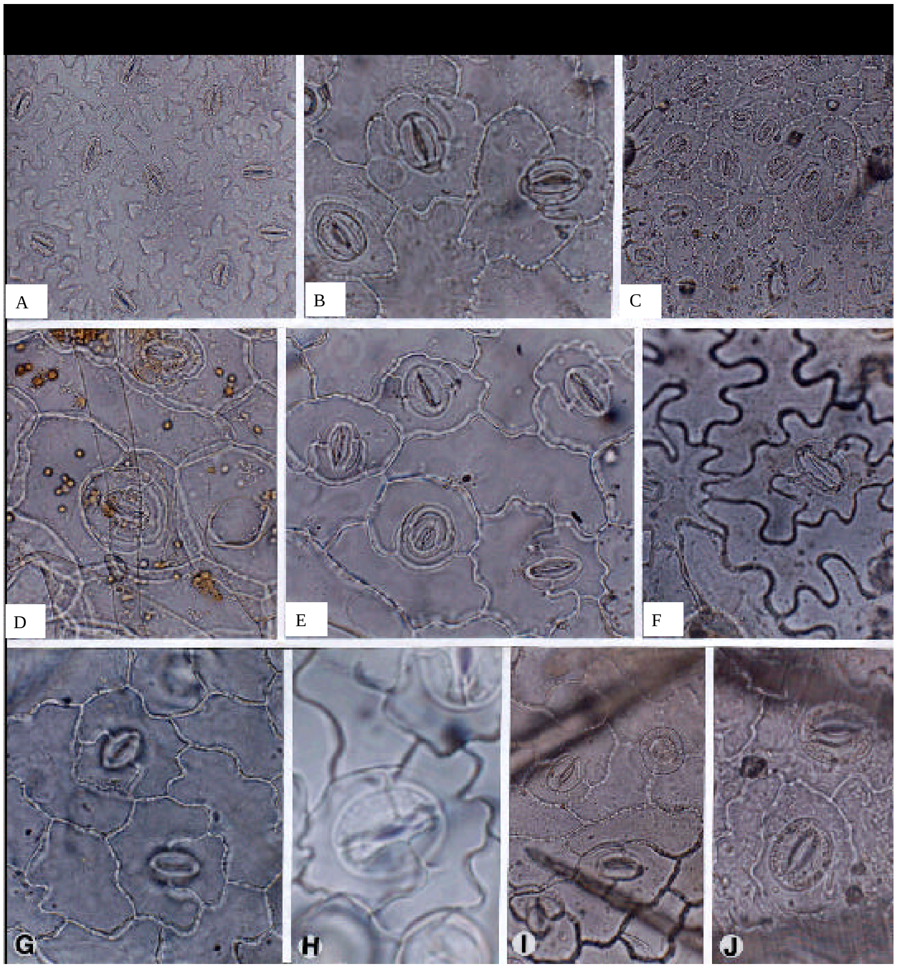

Fig. 8: A-J, epidermis in superficial view of the Labiatae; A, abaxial epidermis of *Lamium album*; B, adaxial epidermis of *Nepeta betonicifolia*; C, abaxial epidermis of *Ziziphora clinopodioides*; D, E, *Salvia atropatana*; D, adaxial; E, abaxial; F, abaxial epidermis of *Mentha longifolia*; G, H, *Scutellaria pinnatifida*; G, adaxial; H, abaxial; I, J, *Betonica grandiflora*; I, adaxial; J, abaxial; A, C, I, (×150); B, D-G, J, (×300), H, (×750)

anisocytic forms present as a subordinate pattern. Guard cell lengths on adaxial surfaces (average 31.88 μm) are usually equal to or larger than abaxial cell lengths (average 20.34 μm).

Linaceae: In the Linaceae, stomata are present on both surfaces. Adaxial stomatal densities (between 70 and 185 per mm^2) are higher than those of abaxial surfaces. Density differences between surfaces are minor in *Linum nervosum* and *L. nodiflorum*, but vary greatly in *L tenuifolium*. Stomatal type is laterocyclic. Guard cells are large, averaging between 30.46 and 39.57 μm in length.

Papaveraceae: Two species of Papaveraceae occur in this study: of these, stomata are present on both surfaces in *P. glaucum*, whilst in *P. orientale* they are found only on the abaxial surfaces. The average densities for these two species are 93.62 per mm^2 for adaxial surfaces and 176.65 per mm^2 for abaxial surfaces. Stomatal type is anomocytic. Guard cell average length is 34.53 for adaxial cells and 38.6 μm for abaxial cells.

Plantaginaceae: In the *Plantaginaceae,* stomata are present on both surfaces in all species studied. Adaxial stomatal densities are higher than abaxial densities, with the exception of *Plantago lanceolata*. Densities range between 139 and 267 stomata per mm^2 and differences between both surfaces are minor. The dominant stomatal type is diacytic; anomocytic and anisocytic forms are also present. Adaxial guard cells are often larger than abaxial cells; lengths range between 24.42 and 29.67 μm.

Rubiaceae: In the herbaceous members of the Rubiaceae studied here, stomata are present on both surfaces and abaxial densities are higher than those of the adaxial surfaces. *Cruciata taurica* and *Galium odoratum* have a shrubby growth form in this environment and in these species stomata are completely absent from the adaxial surface. The highest density of stomata is found on the abaxial leaf surfaces of *G. verum* with an average of 233 per mm^2 and the difference between both surfaces is high. Stomata throughout this family are laterocyclic and are consistently large; the guard cell lengths range from 29.09 μm for abaxial cells, to 46.67 μm for adaxial cells.

Scrophulariaceae (Fig. 9A-I): In the Scrophulariaceae, stomata are found on both surfaces except in the genus *Pedicularis*. Abaxial stomatal densities are higher than those of the adaxial surface, except in *Linaria kurdica*. The highest overall average density is observed on the abaxial surfaces of species in the genus *Pedicularis*, at 353 per mm^2. Density differences between both surfaces show variability throughout this family, without any genus specific patterns. In most of the species studied, stomata are anomocytic; anisocytic cells are variably present as a subordinate type. Guard cell average lengths range from (abaxial) 21.86 μm to (adaxial) 39.60 μm.

Umbelliferae (Fig. 10A-H): In the Umbelliferae, most species, studied have stomata on both surfaces; the exceptions are *Laser trilobum*, *Peucedanum caucasicum*,

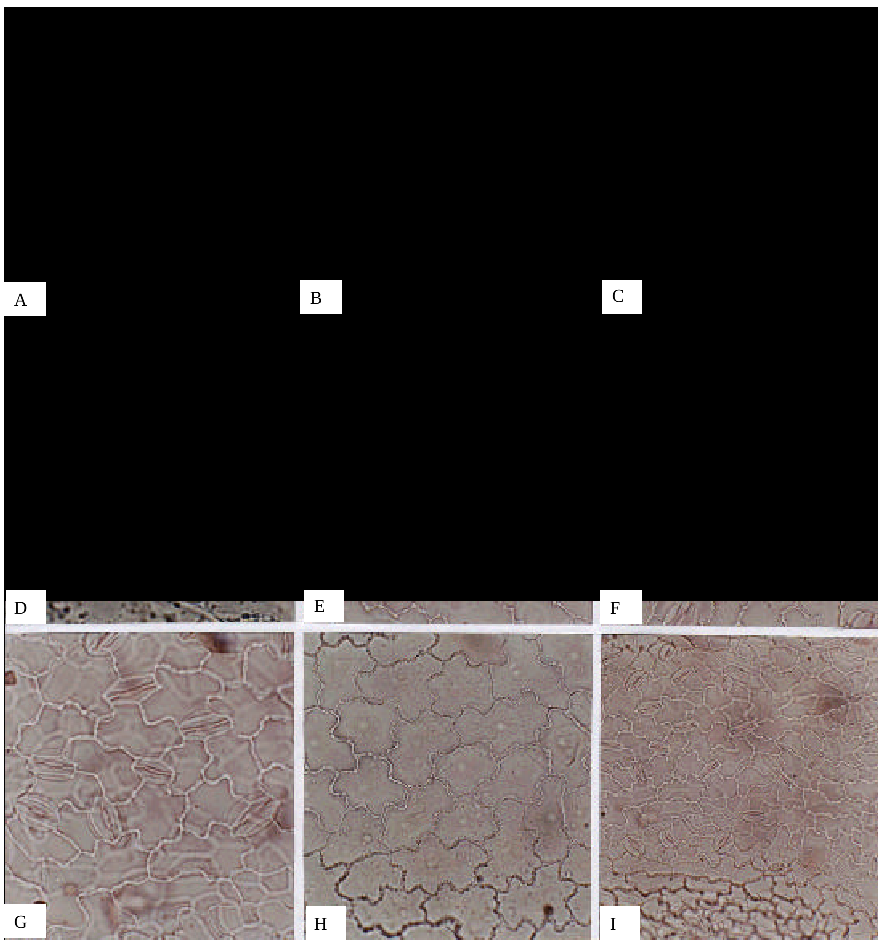

Fig. 9: A-I, epidermis in superficial view of the Scrophulariaceae; A, B, *Digitalis nervosa*; A, adaxial; B, abaxial; C, abaxial epidermis of *Veronica anagallis-aquatica*; D, adaxial epidermis of *V. polita*; E, F, *V. gentianoides*; E, adaxial; F, abaxial; G, abaxial epidermis of *Pedicularis sibthorpii*; H, I, *P. wilhelmsiana*; H, adaxial; I, abaxial; A-C, E, F, H, (×150); D, G, (×300); I, (×75)

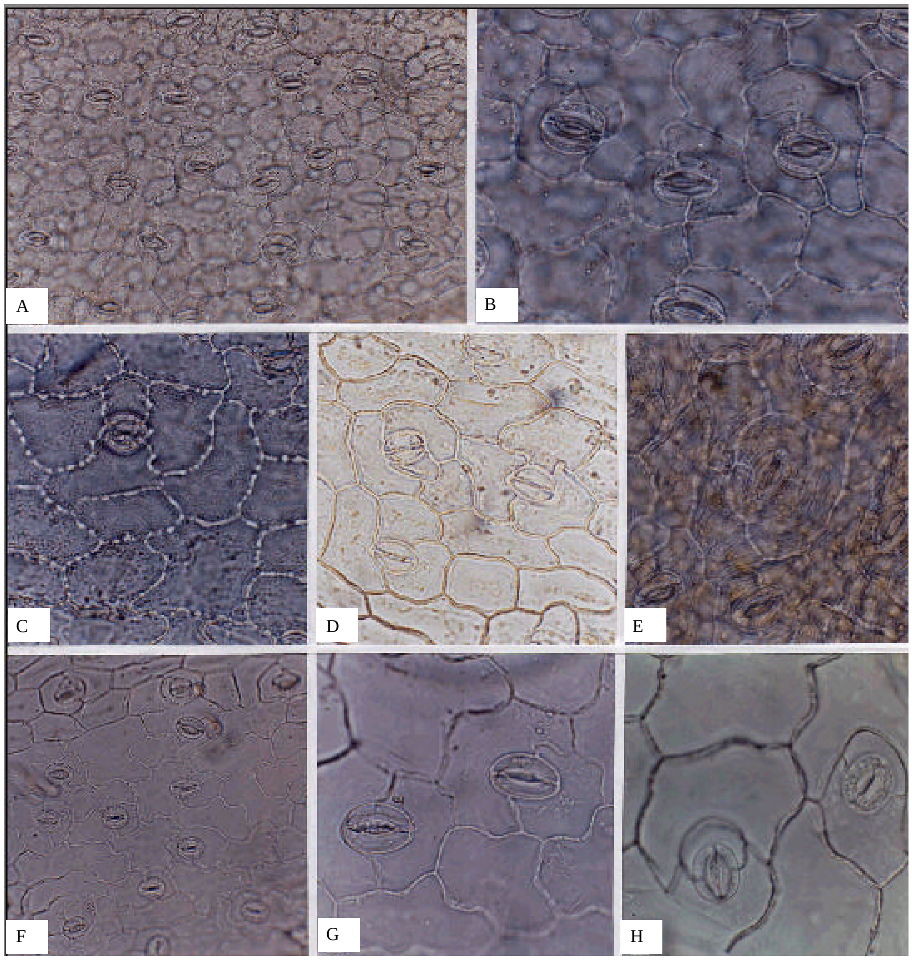

Fig. 10: A-H, epidermis in superficial view of the Umbelliferae; A-E, G, abaxial; F, H, adaxial; A, B, *Carum carvi*; C, *Bupleurum falcatum*; D, *B. geradii*; E, *Pimpinella tragium*; F, G, *Daucus broteri*; H, *Caucalis platycarpos*; A, F, (×150); B-E, G, H, (×300)

Sanicula europaea and *Seseli peucedanoides*. Abaxial stomatal densities are greater than those of the adaxial surfaces except in the genus *Bupleurum*. The highest observed abaxial density is found in *Pimpinella aurea*, at an average of 533 per mm^2. Stomatal density differences between leaf surfaces illustrate the variability between species e.g., in *Prangos ferulacea* adaxial and abaxial surfaces are similar, whilst in *Chaerophyllum aureum* adaxial stomata are very sparse (4.44 per mm^2) and the abaxial density is unusually high for the family (326.7 per mm^2). Species in this family were found in a variety of different habitats and the types and sizes of stomata are variable both inter- and intra-specifically. For example in *Chaerophyllum aureum,* the commonest stomatal form recorded is the anisocytic pattern at (40%), followed by anomocytic (30%), then diacytic (20%) and last finally paracytic cells (10%); because of variation due to environmental influences, taxonomic classification is particularly difficult. Guard cell lengths range between 17.66 μm and 45.3 μm; both of these values represent abaxial stomata. In the Umbelliferae, stomatal types provide a valuable indicator for easier identification and classification at the species level.

As indicated, in Table, the types of stomata are highly variable between herbaceous species and so could be a valuable tool in informing their taxonomic classification.

Stomatal types in woody plants are mostly anomocytic; these plants show little variation compared with herbaceous species. Herbaceous plants include a much greater diversity of stomatal forms. These are, in decreasing order of occurrence, anomocytic, anisocytic, diacytic and paracytic. The family Umbelliferae encompass the greatest variety in stomatal form, whilst the least variation in form is seen in the families Ranunculaceae and Rubiaceae.

DISCUSSION

The numbers of stomata present on leaf surfaces vary widely amongst different species of plants. Generally the abaxial epidermis has higher numbers of stomata than the adaxial surface. According to Eames (1947), stomata on the leaves of woody plants are more frequent on the lower (abaxial) surfaces of leaves and the numbers per unit area tend to be greater than in herbaceous plants. Table 1 show that a higher density of stomata is observed in species where stomata are present only on one leaf surface.

Although the data generally confirm Eames' observations, some herbaceous species show a stomatal distribution similar to that of woody plants, due to an absence of stomata on their adaxial surfaces. This is clearly evident in, for example in *Artemisia armeniaca* (Compositae), *Clypeola jonthlaspi* (Cruciferae), *Galium* sp., *Cruciata taurica* (Rubiaceae) and *Laser trilobum, Peucedanum caucasicum, Sanicula europaea* and *Seseli peucedanoides* (Umbelliferae).

Interesting observations from this study include;

- In the Linacea, Plantaginaceae and the majority of Papilionaceae families, in contrary to the general features of herbaceous species studied, the adaxial stomatal densities are higher than those of the abaxial surfaces and
- The similarity of stomatal sizes and densities on both surfaces of the Crassulaceae family.

The highest recorded adaxial stomatal densities are found in *Trifolium montanum* (Papilionaceae), at 397 stomata per mm^2. The highest densities for an abaxial surface are observed in *Celtis caucasica* (Ulmaceae) at 742 per mm^2. The largest observed guard cell length is 65.5 μm in *Adonis aestivalis* (Ranunculaceae) and the smallest is 10.11 μm in *Alliaria petiolata* (Cruciferae); both of these measurements are from adaxial surfaces.

According to Willmer (1996), stomatal frequency and guard cell size are interdependent and the stomatal size usually decreases with increasing stomatal density. However the data presented in this paper shows that guard cells on lower leaf surfaces are equal to or smaller in size than those of the upper surfaces in some families. Table 1 show that Willmer's observations apply generally to the woody plants, although some exceptions occur such as *Alchemilla fluminea*, *Spiraea crenata* and *S. hypericifolia* (Rosaceae). In these exceptions, in spite of low stomatal densities on the adaxial surfaces, the abaxial guard cells are larger than those of the adaxial surface.

In this study, an assessment of the validity of Willmer's theory of the interdependence of guard cell size and stomatal density, demonstrates the following three phenomena:

- Willmer's theory correlates generally to the stomatal patterning seen in first group (the woody plants) and in the following herbaceous families from group two of the results section; Campanulaceae, Cistaceae, Geraniaceae, Polygonaceae, Primulaceae, Valerianaceae and Violaceae.

In many of these herbaceous species, there are major differences in stomatal density between adaxial and abaxial surfaces; these patterns are close to those observed in woody plants.

Willmer's proposal is confirmed by the general observations from the first and second groups of families. The stomatal characters common to the second group species are as follows;

- Stomata are observed on both sides of leaves.
- Abaxial stomatal densities are higher than adaxial densities.
- The differences in density between both surfaces are high, tending towards greater stomatal densities on abaxial surfaces; this can be up to six-fold as in *Primula macrocalyx* (Primulaceae) or four-fold in *Helianthemum ledifolium* (Cistaceae); *Campanula glomerata* (Campanulaceae).and *Geranium lucidum* (Geraniaceae).
- Stomatal type is anomocytic or anisocytic.
- The largest guard cells are always found on the adaxial surfaces.
- Stomatal size usually decreases with increasing stomatal frequency.

- The third group of plant families demonstrates a patterning phenomenon that is in contrast to Willmer's findings, characterised by a correlation between increased guard cell size and increased stomatal density. This group includes the following families; Caryophyllaceae, Compositae, (with the exception of the genera Inula, Carduus and Cirsium), Convolvulaceae, Cruciferae, Dipsacaceae, Gentianaceae, Hypericaceae, Papilionaceae and Ranunculaceae. In most of these species, the stomatal density differences between adaxial and abaxial surfaces are minor:

Common stomata characters in this group, in contrast with Willmer's hypothesis, are as follows;

- Stomata are present on both surfaces.
- Abaxial stomatal densities are higher than on adaxial densities, except some genera from the Caryophyllaceae and the majority of Papilionaceae.
- The density differences between both surfaces are minor, except in the Hypericaceae and Gentianaceae.
- The abaxial guard cells are larger than adaxial cells.
- Longer guard cells are associated with higher stomatal densities.
- The types of stomata are variable within families.

- The fourth group of plant families demonstrate variable phenomena within the same genus; some species show characteristics of group II, in line with Willmer's theory, whilst other species show the opposing pattern as in group III above. This category includes genera from the following families: Boraginaceae, Chenopodiaceae, Labiatae, Linaceae, Papaveraceae, Plantaginaceae, Rubiaceae, Scrophulariaceae and Umbelliferae.

Previous studies of various herbaceous species have shown that if stomata are found on both surfaces of the leaf, then usually the adaxial guard cells are larger than those of the abaxial surface. The data in Table 1 demonstrate that, contrary to Willmer's observations, in certain herbaceous species a higher stomatal density is associated with increased guard cell size. These are indicated in the Table 1; with an asterisk. In almost all of these, the density differences between adaxial and abaxial surfaces are minor. This suggests that the relationship between density and guard cell size is strongly related to density differences and distribution of stomata over both leaf surfaces in herbaceous plants.

The adaptive significance of the presence of stomata over one or both leaf surfaces is unclear. According to Parkhurst (1978), herbaceous plants increase CO_2 uptake by reducing the length of the CO_2 diffusion pathway to the mesophyll. It may be that in herbaceous species, the efficiency of photosynthesis is potentially higher than that of woody plants, because of the existence of stomata on both surfaces of the leaf.

Although the rate of photosynthesis in woody plants may be less per unit area than in herbaceous species, the absence of stomata on the adaxial surfaces and the variable densities of these abaxial stomata, suggest a greater capacity for response and adaptation to environmental conditions, as seen in the xerophytes growth form.

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