

THE SEED SURFACE MORPHOLOGY OF THE GESNERIACEAE
UTILIZING THE SCANNING ELECTRON MICROSCOPE AND
A NEW SYSTEM FOR DIAGNOSING SEED MORPHOLOGY

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ABSTRACT

The seed collection of the species of the Gesneriaceae on which this study is based was obtained, for the most part, during a number of visits to the herbaria of the Smithsonian Institution, Washington, D.C., and the Royal Botanical Garden of Kew, London, and Edinburgh, Scotland. The seed collection comprises well over 800 samples of about 700 species of the Gesneriaceae, representing 113 genera of the 127 in the family, and provides a good taxonomic representation of the Gesneriaceae. Following an examination of all the samples in the seed collection, over 300 species of the 113 genera were selected to represent the wide range of seed morphology characters observed among the examined species of the Gesneriaceae.

A system with which to analyze and diagnose seed surface morphology, designed by the author, is based on a format of six major categories and 60 tertiary terms of seed morphology characters and a companion diagnostic table. The categories are arranged in a sequence of increasingly smaller seed characters, ranging from seed shape to the ultrastructural characters of the individual cells. To ensure that the system would also apply to seed plants in general, the seeds, achenes and nutlets of a wide variety of species from families other than the Gesneriaceae were examined. Twenty species from 13 families other than the Gesneriaceae were then selected and are included in this study and, together with the Gesneriaceae, represent eight of the ten subclasses of the flowering plants (Cronquist 1968).

The seeds, achenes and nutlets of all the species included in this study are illustrated with SEM photomicrographs on the 54 plates of the Seed Atlas, and the seed morphology data of each species are recorded on the diagnostic tables that face each of the Atlas Plates. To facilitate the comparison of the taxa of the Gesneriaceae, and to assist in the identification of the seeds of the examined species of the Gesneriaceae, the seed morphology data are also recorded on a summary table at the genus, tribe, subfamily and family levels. The seed morphology of the Gesneriaceae is compared and contrasted with the current classifications of the family at the species, genus, tribe, subfamily and family levels.

The seed analysis system designed for this study has proven to be a rapid, efficient, uniform, objective method to deal with the analytical, diagnostic, and taxonomic aspects of an investigation of seed morphology. In addition, the system readily lends itself to the substitution or addition of terms and categories if needed, or to programming for a computerized analysis of seed morphology. It is hoped that the system will prove useful to other investigators, as well as prove helpful to standardize future investigations of seed morphology.

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TABLE I. SPECIES LIST

FAMILY GESNERIACEAE

Subfamily Cyrtandroideae

Subfamily Gesnerioideae

Tribes: Cyrtandreae Benth. & Hook.
Didymocarpeae Endl.
Klugieae B.L. Burtt
Trichosporeae Fritsch

Tribes: Anetantheae Fritsch
Bellonieae Fritsch
Beslerieae Fritsch
Coronanthereae Fritsch
Episcieae Endlicher
Gesnerieae G. Don
Gloxinieae Fritsch
Kohlerieae Fritsch
Mitrarieae B.L. Burtt
Sinningieae Fritsch
Solenophoreae Fritsch

Because of the large number of species included in this study, the species list is put at the beginning of the text to eliminate the necessity of putting the information, pertinent to each species, within the body of the text.

Species	Author	Collector and Number	Herbarium	Pl.-Fig. Number
<i>Acanthonema strigosum</i>	Hook.	Mann 1948	K	22-I
<i>Achimenes warszewicziana</i>	(Regel) H.E. Moore	Nelson 3084	US	36-D
<i>Aeschynanthus bracteatus</i>	Wall. ex DC.	G. Forrest	E	12-C
<i>Dichrotrichum chorisepalum</i>	Orr	Elmer 16171	US	12-D
<i>Aeschynanthus hartleyi</i>	P. Woods	Carr 12809	E	12-A
<i>A. hildebrandii</i>	Hemsl.	Iwatsuki 3650	K	11-F
<i>A. magnificus</i>	Stapf	Burtt B5226	E	12-B
<i>A. micranthus</i>	C.B. Cl.	Cult.	AGGS	11-G
<i>A. perrottetii</i>	A. DC.	Ramamurthy 18193	E	11-H
<i>Agalmyla clarkei</i>	(Elm.) B.L. Burtt	Elmer 19171	E	12-G
<i>A. species</i>	Bl.	Brass 27010	US	12-E
<i>Alloplectus cristatus</i> (paratype)	(L.) Mart.	Eggers 6160	US	43-A
<i>A. cucullatus</i>	Morton	Steyermark 44191	US	42-I
<i>A. ichthyoderma</i>	Hanst.	Langerhiem 3623	US	42-H
<i>A. tigrinus</i>	Hanst.	Williams 10577	US	43-B
<i>Alsobia punctata</i>	(Lindl.) Hanst.	Matuda 4864	US	51-H
<i>Ancylostemon saxatilis</i> (T)	Craib	Henry 7150	K	16-G
<i>Anetanthus gracilis</i> (a) (T)	Hiern	Hiern 18413	K	48-A
<i>A. gracilis</i> (b)	Hiern	Scolnick sn	US	48-D
<i>A. rubra</i>	L. Skog	Wurdak 1469	US	51-A
<i>Anna ophiorrhizoides</i> (T)	(Hemsl.) B.L. Burtt & R. Davids.	E. Faber 872	E	50-F
<i>Anodiscus xanthophyllus</i> (a)	(Poepp.) Mansf.	Allard 22168	US	34-H
<i>A. xanthophyllus</i> (b)	(Poepp.) Mansf.	Sagastegui (Peru)	US	34-I
<i>Asteranthera ovata</i>	(Cav.) Hanst.	sn	K	46-C
<i>Beccarinda cordifolia</i>	(Anthony) B.L. Burtt	Rea 17882	E	15-G
<i>Bellonia spinosa</i>	Sw.	Jimenez sn	US	33-A
<i>Besleria aggregata</i>	(Mart.) Hanst.	Cuatrecasas 10582	US	32-F
<i>B. barclayi</i>	L. Skog	Killip 35309	US	32-H
<i>B. connata</i>	Morton	Steyermark 55038	US	32-B
<i>B. formicaria</i>	Nowicke	Wiehler & Dressler 71279	US	32-G
<i>B. kalbreyeri</i>	Fritsch	Steyermark 56663	US	31-E
<i>B. lutea</i> (a)	L.	Stehle ex Bena 5345	US	32-A
<i>B. lutea</i> (b)	L.	Harris 6313	US	32-D
<i>B. macropoda</i>	J.D. Sm.	Tonduz 11358	US	32-C
<i>B. notabilis</i>	Morton	Standley & Valerio 47121	US	32-E
<i>B. reticulata</i> var. <i>venosa</i>	Morton	sn sn	US	31-D
<i>B. rhytidophyllum</i>	Hanst.	Tamoyo 1617	US	31-H
<i>B. solanoides</i>	Kunth	Arbelaez & Cuatrecasas 6090	US	31-I
<i>B. spinulosa</i>	Morton	Steyermark 62208	US	31-G
<i>Boea lawesii</i>	(F.V. Muell) H.O. Forbes	Wood 204	E	28-C
<i>B. magellanica</i> (a)	Lam.	Isles & Croft 32208	E	28-A
<i>B. magellanica</i> (b)	Lam.	Womersley 41207	E	28-B
<i>Boeica fulva</i> (T)	C.B. Cl.	Bootac 328	K	30-A
<i>B. hirsuta</i>	C.B. Cl.	Banks 1876	K	30-C
<i>B. filiformis</i>	C.B. Cl.	sn sn	K	30-D

TABLE I (continued)

Species	Author	Collector and Number	Herbarium	Pl.-Fig. Number
<i>Briggsia forrestii</i>	Craib	G.F. 25095	E	49-A
<i>Bucinellina nariniana</i>	(Wiehl.) Wiehl.	Wiehler W1624	W	49-I
<i>Capanea grandiflora</i>	(Kunth) Decne. ex Planch.	Woodson 656	US	38-A
<i>Championia reticulata</i> (syntypus)	Gardn.	C.P. 370	K	14-F
<i>Chirita asperifolia</i>	(Blume) B.L. Burt	Forbes 418	US	20-E
<i>C. eburnea</i>	Hance	Moore 196	US	20-D
<i>C. hamosa</i>	R. Br.	Henry 12,4430	K	19-F
<i>C. heterotricha</i>	Merr.	Lau 555	US	20-A
<i>C. lavandulacea</i>	Stapf	Moore 7012	Cult. US	19-G
<i>C. sinensis</i>	Lindl.	Champion sn	K	19-E
<i>C. walkeri</i>	Gardn.	Cramer 4198	US	20-B
<i>Chlamydobolea sinensis</i> (a)	Stapf	Henry 4158	K	28-F
<i>C. sinensis</i> (b)	Stapf	Lace 5502	K	28-G
<i>Chrysothemis rupestris</i>	(Benth.) Leeuw.	Wessels Boer 1409	K	42-A
<i>C. pulchella</i> (a)	(Donn ex Sims) Decne.	Schultes 7394	K	42-B
<i>C. pulchella</i> (b)	(Donn ex Sims) Decne.	Guilding 1822	K	42-C
<i>Codonanthe calcarata</i>	(Miq.) Hanst.	Chagas 725	US	45-F
<i>C. crassifolia</i>	(Focke) Morton	Tamayo 3147	US	45-E
<i>C. uleana</i>	Fritsch	Schultes 6861	US	45-D
<i>Colpogyne betsiliensis</i>	(Humbert) B.L. Burt	Humbert 30024	E	30-E
<i>Columnea angustata</i>	(Wiehl.) Skog	Skog sn	US	44-E
<i>C. anisophylla</i>	DC.	sn	US	44-D
<i>C. domingensis</i>	(Urb.) B. Morley	Howard & Howard sn	US	44-A
<i>C. florida</i>	Morton	Skog 4218	US	43-E
<i>C. nicaraguensis</i>	Oerst.	Skog sn	US	43-G
<i>C. purpurata</i>	Hanst.	Standley 33583	US	43-I
<i>C. sanguinea</i>	(Pers.) Hanst.	Gastony et al. 679	US	43-F
<i>C. schiedeana</i>	Schlecht.	Martinez-Calderon 34	US	43-H
<i>C. silvarum</i>	Morton	Mori & Kallunki 5498	US	44-B
<i>C. strigosa</i>	Benth.	Steyermark sn	US	44-F
<i>Conandron ramondiioides</i>	Sieb. & Zucc.	Togasi 1641	K	16-E
<i>Corallodiscus patens</i>	(Craib) B.L. Burt	Forrest 22260	E	50-C
<i>Coronanthera aspera</i>	C.B. Cl.	Leurmond 28.26	K	47-G
<i>C. deltoidifolia</i>	Vieill ex C.B. Cl.	Marseille 9-203	K	47-H
<i>C. grandis</i> (a)	Gillett	Whitmore 2417	K	47-E
<i>C. grandis</i> (b)	Gillett	Schodde 3838	K	47-F
<i>Cremosperma congruens</i>	Morton	sn sn	US	31-B
<i>C. jucundum</i> (T)	Morton	Kalbreyer 1821	US	31-A
<i>C. peruvianum</i> (a)	L. Skog	Wolfe 12288	US	51-E
<i>C. peruvianum</i> (b)	L. Skog	Dudley 13020	US	51-F
<i>Cyrtandra anthropophagorum</i>	Seem.	Parks 20276	US	10-B
<i>C. apiculata</i>	C.B. Cl.	Setchell & Parks 344	US	5-H
<i>C. brevicaulis</i>	Ridl.	Bartlett 876a	US	5-C
<i>C. compressa</i>	C.B. Cl.	Whistler W439	US	9-A
<i>C. cumingii</i>	C.B. Cl.	Elmer 8571	US	7-I
<i>C. didissandriiformis</i>	Merr.	Ramos 1833	US	8-H
<i>C. dolichocarpa</i>	A. Gray	Smith 612	US	7-F
<i>C. flabelligera</i>	Ridl.	Rahmat Si Boeea 6806	US	10-F
<i>C. garnotiana</i>	Gaudich.	Spezie 43	US	7-B
<i>C. gayana</i>	Heller	Darwin 1153	US	6-I
<i>C. humilis</i>	Blume	Martinele 35341	US	6-G
<i>C. hypochrysea</i>	Kranzl.	Foxworthy 42135	US	5-D
<i>C. hypochrysoides</i>	Kranzl.	Foxworthy 42135	US	8-B
<i>C. lagunae</i>	Kranzl.	Ramos 41543	US	5-G
<i>C. latebrosa</i>	Hilleb.	Hillebrand 417	US	6-A
<i>C. leucantha</i>	A.C. Sm.	Degener 14836	US	5-E
<i>C. lobbii</i>	C.B. Cl.	Ramos 20487	US	3-F
<i>C. longicarpa</i>	Merr.	Ramos 1833	US	5-A
<i>C. longiflora</i>	J.W. Moore	Grant 5149	US	9-D
<i>C. longifolia</i>	(Wawra) Hilleb. ex C.B. Cl.	Heller 2624	US	9-F
<i>C. lysiosepala</i>	A. Gray	Hillebrand 395	US	7-C
<i>C. mauiensis</i> v. <i>truncata</i>	Rock	Hitchcock 14911	US	7-D
<i>C. montana</i>	Gillespie	Smith 8833	US	10-E
<i>C. multiseptata</i>	Gillespie	Smith 6327	US	7-G
<i>C. oblongifolia</i>	(Bl.) C.B. Cl.	Bartlett 7955	US	8-C
<i>C. paludosa</i> v. <i>gayana</i>	(Heller) Rock	Stearn & Carlquist sn	US	7-A

TABLE I (continued)

Species	Author	Collector and Number	Herbarium	Pl.-Fig. Number
Cyrtandra parviflora	C.B. Cl.	McGregor 19750	US	9-E
C. parvifolia	Merr.	Merrill 225	US	5-I
C. pendula	Bl.	St. Tories 5226	US	6-C
C. pogonantha	A. Gray	Christopherson 2028	US	8-D
C. rarotongensis	Cheesem.	H. & S. Park 25591	US	8-G
C. reticulata	Gillett	Degener 14088	US	9-G
C. samoensis	A. Gray	Yunker 15,690	US	8-E
C. sandei	de Vriese	de Vriese sn	US	10-G
C. santosii	Merr.	Ramos 37699	US	6-D
C. sibuyanensis	Elm.	Ramos 40713	US	8-A
C. taviunensis	Gillespie	Smith 8234	US	10-D
C. tempestii	(Horne) C.B. Cl.	Smith 8388	US	9-C
C. todaensis	Kanehira	Kanehira 1854	K	50-A
C. trichophylla	A.C. Sm.	Smith 6246	US	10-A
C. victoriae	Gillespie	Smith 5081	US	9-H
C. wawrai	C.B. Cl.	Rock 5397	US	6-F
C. zamboangensis	Merr.	Ramos 36685	US	6-E
Depanthus glaber	(C.B. Cl.) S. Moore	Balanso 1346	E	49-C
Diastema longiflorum	Benth.	Pittier sn	US	38-D
D. rupestre	T.S. Brandeg.	MacDugall 73	US	38-G
D. vexans	H.E. Moore	Killip sn	US	38-E
Dichiloboea acaulis (holotype)	Barnett	Put 350	K	22-D
D. birmanica	Stapf	Henry 12,305	K	22-G
D. glabrescens	Barnett	van Brusekom 3740	K	22-F
D. speciosa	(Ridl.) Stapf	Curtis 2564	K	22-C
Didissandra elongata	(Jack) C.B. Cl.	sn sn	K	19-B
D. johorica	Ridl.	Kiah 32360	K	19-A
D. sprengelii	C.B. Cl.	Beccari 679	K	18-I
Didymocarpus cinerea	D. Don	D.H. sn	K	17-H
D. madagascariensis	C.B. Cl.	Humber 23028	K	18-E
D. platypus	C.B. Cl.	Burkhill HMB-1096	K	18-C
D. primulifolia	D. Don	sn sn	K	18-B
D. purpureo-bracteata	W.W. Smith	Henry 11,421	K	18-A
D. subalternans	C.B. Cl.	Strachey 3	K	17-G
Drymonia serrulata (a)	(Jacq.) Mart.	White 27 (Colombia)	US	43-C
D. serrulata (b)	(Jacq.) Mart.	Johnston 62 (Panama)	US	43-D
Episcia cupreata	(Hook.) Hanst.	Lehmann sn	K	41-C
E. fimbriata	Fritsch	Klug 2877	K	41-D
E. hirsuta (a)	Hanst.	Appun 976	K	41-E
E. hirsuta (b)	Hanst.	Engler 46452	K	41-H
E. lilacina	Hanst.	Collinette 4	US	41-F
E. reptans	Mart.	sn 2801	K	41-G
Epithema brunonis	Decne.	Elmer 8318	K	13-D
Eucodonia andrieuxii	(DC.) Wiehl.	Moore & Cetto 8181	US	36-E
Fieldia australis (a)	F.V. Muell.	Constable 47318	K	46-E
F. australis (b)	F.V. Muell.	Bynor W535	K	46-G
F. australis (c)	F.V. Muell.	Dunnington 00145	K	46-H
Gasteranthus acropodus	(J.D. Sm.) Wiehl.	Hammel et al. 4951	US	49-F
G. atratus	Wiehl.	Wiehler W2461	W	49-E
G. wendlandianus	(Hanst.) Wiehl.	Davidson & Jones 9375	US	49-D
Gesneria cuneifolia	(A.P. DC.) Fritsch	Cult. sn	LP	40-A
G. cuneifolia (cult)	(A.P. DC.) Fritsch	Cult. sn	LP	40-B
G. duchartreoides	(C. Wright) Urban	Alain & Lopez F.4640	US	40-C
G. haitiensis	L. Skog	sn	US	39-I
G. pumila	Sw.	Maxon 8863	US	39-G
G. viridiflora	(Decne.) O. Kuntze	Lopez F.2690	US	40-D
Gloxinia perennis	(L.) Fritsch	MacBride 4658	US	36-B
G. racemosa	(Benth.) Wiehl.	Haught sn	US	36-A
G. reflexa	Rusby	sn sn	US	34-A
G. sylvatica (a)	(Kunth) Wiehl.	Camp E-1561	US	35-H
G. sylvatica (b)	(Kunth) Wiehl.	Irwin & Soderstrom 7260	US	35-I
Goyazia petraea (holotype)	(S.M. Phillips) Wiehl.	D. Hunt & Ramos 6078	US	49-H
Haberlea rhodopensis	Friv.	Terril 1297	K	15-F
Hemiboea follicularis	C.B. Cl.	Balansa 776 (I-90)	E	19-D
Heppiella species	Regel	Anthony 236	US	35-G
Hexatheca fulva	C.B. Cl.	Anderson 27	K	10-H
Hypocyrta bradei (pollen)	Handro	sn	HBM	4-I
H. hirsuta	Mart.	sn	US	45-C

TABLE I (continued)

Species	Author	Collector and Number	Herbarium	Pl.-Fig. Number
<i>Isometrum farreri</i> (T)	Craib	Farrer & Purdom 262	E	50-B
<i>Jankaea heldreichii</i>	(Boiss.) Boiss.	Ophanides 625	K	15-E
<i>Koellikeria erinoides</i>	(DC.) Mansf.	Cult.	HBM	35-F
<i>Kohleria brachycalyx</i>	Fritsch	Haught 6012-A	US	38-I
<i>K. digitaliflora</i>	(Linden & Andre) Fritsch	Arbelaez & Cuatrecasas 5813	US	39-A
<i>Lembocarpus amoenus</i>	Leeuw.	Wessels Boer 1480	K	41-I
<i>Lenbrassia australiana</i> (a)	(C.T. White) Gillett	White 10548	K	46-I
var. <i>glabrescens</i>				
<i>L. australiana</i> (b)	(C.T. White) Gillett	Smith 10099	K	47-A
var. <i>australiana</i>				
<i>Leptoboea multiflora</i> (a)	Gamble	Ribu 3206	K	29-G
<i>L. multiflora</i> (b)	Gamble	Kerr 9232	K	29-H
<i>Lietzia brasiliensis</i>	Regel & Schmidt	Linden sheet #1	US	36-G
<i>Linnaeopsis alba</i> (T)	(E.A. Bruce) B.L. Burt	Burt 3470	K	22-A
<i>Loxocarpus caulescens</i>	B.L. Burt	Meijer 6893	K	27-B
<i>L. incanus</i>	R. Br.	Maingay 1228	K	26-I
<i>L. rufescens</i>	(C.B. Cl.) B.L. Burt	Ridley 1995	K	27-A
<i>L. verbeniflos</i> (T)	(C.B. Cl.) B.L. Burt	Burbridge 1877	E	26-H
<i>Loxonia hirsuta</i>	Jack	Jacobs 8367	K	14-E
<i>Loxostigma griffithii</i>	(Wight) C.B. Cl.	Keenan et al. 3716	E	50-G
<i>L. kurzii</i>	(C.B. Cl.) B.L. Burt	Wilson 1112	K	16-H
<i>Lysionotus serratus</i> (T)	D. Don	Smith & Abbey 6210	K	12-H
<i>Mitraria coccinea</i>	Cav.	Saratier sn (1897)	K	46-D
<i>Monopyle maxonii</i>	Morton	Tonduz 7457	US	34-D
<i>M. paniculata</i>	Benth.	sn	US	34-F
<i>M. puberula</i>	Morton	sn	US	34-G
<i>M. subdimidiata</i>	(Klotzsch ex Hanst.) Mansf.	sn	US	34-B
<i>Monophyllaea horsfieldii</i>	R. Br.	Wray 597	K	14-A
<i>M. singularis</i> (a)	(Balf.f. & W.W. Sm.) B.L. Burt	Kostermans 13556	K	13-G
<i>M. singularis</i> (b)	(Balf.f. & W.W. Sm.) B.L. Burt	Richards sheet #1	K	13-I
<i>Moussonia elegans</i>	Decne.	sn sn	US	38-H
<i>Napeanthus apodemus</i>	J.D. Sm.	Maj 6707	K	36-H
<i>N. subacaulis</i>	(Griseb.) Benth., J.D. Hook. ex O. Kuntze	Broadway 6738	K	36-I
<i>Nautilocalyx hirtiflorus</i>	(Spruce) Sprague	Ule 8960	K	42-E
<i>N. melittifolius</i>	(L.) Wiehl.	sn	K	42-F
<i>Creemosperma minutiflorum</i>	L. Skog	Steyermark 59284	US	51-D
<i>N. pictus</i>	(Hook.) Sprague	Engler	K	42-D
<i>N. villosus</i>	(Kunth & Bouche) Sprague	Aristigueita sn	K	42-G
<i>Negria rhabdothermoides</i>	F.V. Muell.	Rodd 1762	K	49-B
<i>Nematanthus gregarius</i>	D. Denh.	sn	US	45-B
<i>N. radicans</i>	Presl.	Cult.	FB	45-A
<i>Neomortonia nummularia</i>	(Hanst.) Wiehl.	Standley 42971	US	51-I
<i>N. rosea</i>	Wiehl.	Hugh-Jones 150	K	45-I
<i>Niphaea oblonga</i>	Lindl.	Standley 78576	US	33-C
<i>N. rubida</i>	Lindl.	Moore & Bunting 8696	US	33-D
<i>Oerstedina cerricola</i>	Wiehl.	sn sn	US	45-G
<i>Opithandra primuloides</i>	(Miq.) B.L. Burt	Togasi 622	E	17-E
<i>Orchadocarpa lilacina</i>	Ridl.	Robinson 31/3/3	K	18-H
<i>Oreocharis forrestii</i>	Skan	Scheider 3307	K	17-A
<i>Ornithoboea flexuosa</i> (a)	(Ridl.) B.L. Burt	Kerr sn	K	28-I
<i>O. flexuosa</i> (b)	(Ridl.) B.L. Burt	Hairff 640	K	29-A
<i>O. forrestii</i>	Craib	Forrest 929	K	28-H
<i>O. lanata</i> (T)	Craib	Kerr 2852	K	29-C
<i>O. leptanema</i>	(C.B. Cl.) B.L. Burt	Purch 4311	K	29-D
<i>O. parrishii</i> (T)	C.B. Cl.	Parrish 1862	K	29-B
<i>O. pseudoflexuosa</i> (holotype)	B.L. Burt	Put 964	K	29-F
<i>Paliavana prasinata</i>	(Ker-Gawl.) Benth.	Archer & M. Barreto 4939	US	37-I
<i>Paraboea laxa</i>	Ridl.	P. Lauk 3-9-1890	K	27-E
<i>P. tiumanica</i>	Burkill ex Ridl.	Symington 25863	K	27-D

TABLE I (continued)

Species	Author	Collector and Number	Herbarium	Pl.-Fig. Number
<i>Paradrymonia decurrens</i>	(Morton) Wiehl.	Skog 4191	US	44-G
<i>P. macrophylla</i>	Wiehl.	Skog 4118	US	44-H
<i>Parakohleria reticulata</i>	Fritsch	MacBryde 1550	US	51-B
<i>P. sprucei</i>	(Britton) Fritsch	Dudley 11579	US	51-C
<i>Pearcea hypocyrtiflora</i>	(Hook.) Regel	Steyermark 54889	US	49-G
<i>Petrocodon dealbatus</i>	Hance	Henry 7603	K	17-D
<i>Petrocosmea iodoides</i> (T)	Hemsl.	Henry 10,259	K	16-B
<i>P. kingii</i>	(C.B. Cl.) Chatterjee	Lace 6283	K	16-A
<i>P. martinii</i>	(Lev.) Lev.	Calaveri 837	K	16-C
<i>P. parryorum</i>	C.E.C. Fisher	sn 1955	K	16-D
<i>Pheidonocarpa corymbosa</i>	(Swartz) Skog	sn sn	US	39-D
subsp. <i>corymbosa</i>				
<i>Phinaea multiflora</i> (a)	Morton	Moore 8132	US	33-E
<i>P. multiflora</i> (b)	Morton	Moore 8237	US	33-G
<i>P. pulchella</i>	(Griseb.) Morton	Alain 4417	US	33-I
<i>Phylloboea amplexicaulis</i>	C.B. Cl.	Parrish 445	K	28-D
<i>Platystemma violoides</i>	Wall.	Gamble 27209	K	15-H
<i>Primulina tabacum</i>	Hance	Ford 131	K	21-D
<i>Ramonda myconi</i>	(L.) Reichenb.	Endref 1831	K	15-B
<i>R. nathaliae</i>	Pancic & Petrovic	Grebenschinoff 16-N-1537	K	15-A
<i>R. serbica</i>	Pancic	Baldacci 137	K	15-D
<i>Rechsteineria spicata</i>	(Vell.) Hoehne	sn	US	37-H
<i>R. umbellata</i>	(Decne.) Hjelmq.	Smith & Reitz 8853	US	37-G
<i>Reldia alternifolia</i>	Wiehl.	Skog 4189	US	32-I
<i>Resia nimbicola</i> (a) (isoparatype)	H.E. Moore	Schultes 1059	US	48-G
<i>R. nimbicola</i> (b)	H.E. Moore	Schultes 12121	US	48-I
<i>Rhabdothamnopsis sinensis</i> (a) (T)	Hemsl.	Prat 147	K	27-H
<i>R. sinensis</i> (b)	Hemsl.	Maine 658	K	27-I
<i>Rhabdothamnus solandri</i>	A. Cunn.	Sledge 72	K	47-C
<i>Rhynchoglossum azureum</i>	(Schlechtend.) Burt	Pittier 14154	US	51-G
<i>R. klugoides</i>	C.B. Cl.	Kadir A2086	K	13-C
<i>R. obliquum</i>	Bl.	Beccari 625	K	13-A
<i>Rhynchotechum discolor</i> (a)	(Maxim) B.L. Burt	Yamazaki 6877 (Japan)	K	11-A
<i>R. discolor</i> (b)	(Maxim) B.L. Burt	Price 1104 (N. Formosa)	K	11-D
<i>R. ellipticum</i>	DC.	Tsang sn	K	11-E
<i>Rhytidophyllum acunae</i> (holotype)	Morton	Morton & Alain 9181	US	40-F
<i>R. asperum</i>	Alain	Alain 17933	US	41-A
<i>R. auriculatum</i>	Hook.	US 1304242	US	40-H
<i>R. coccineum</i>	Urb.	Leon 18550	US	40-G
<i>R. crenulatum</i>	DC.	sn	US	40-E
<i>Rufodorsia minor</i>	Wiehl.	Cult. sn	FB	45-H
<i>Saintpaulia grandifolia</i>	B.L. Burt	Punter X58-3585	E	21-B
<i>S. grotei</i>	Engl.	HBM sn	Cult.	20-G
<i>S. inconspicua</i>	B.L. Burt	Poes 6296	E	20-F
<i>S. intermedia</i> (T)	B.L. Burt	Punter 1955	E	21-A
<i>S. magungensis</i>	E. Roberts	Punter SD3005/1	K	20-I
subsp. <i>occidentalis</i>				
<i>Sarmienta repens</i>	Ruiz & Pavon	Morrison 17566	K	46-A
<i>Schizoboea kamerunensis</i> (a)	Engl.	Breteler 220	K	18-D
<i>S. kamerunensis</i> (b)	Engl.	sn sn	K	18-G
<i>Sinningia barbata</i>	(Nees ex Mart.) Nichols.	Cult.	HBM	37-A
<i>S. cardinalis</i>	(Lehm.) H.E. Moore	Cult.	HBM	37-D
<i>S. eumorpha</i>	H.E. Moore	Cult.	HBM	37-B
<i>S. pusilla</i>	(Mart.) Baill.	Cult.	HBM	37-C
<i>S. tubiflora</i>	(Hook.) Fritsch	Cult.	AGGS	37-E
<i>Smithiantha multiflora</i>	(Martens & Gal.) Fritsch	Borgeau 3283	US	35-D
<i>S. zebrina</i>	(Paxt.) O. Kuntze	Cult.	FB	35-A
<i>Solenophora calycosa</i>	J.D. Sm.	sn sn	US	39-C
<i>Stauranthera cearulea</i>	Merr.	Ramos 1923	K	14-C
<i>S. grandifolia</i> (T)	Benth.	H.I. 6395	K	14-B
<i>Streptocarpus bambuseti</i>	B.L. Burt	Drummond 1988	E	24-A
<i>S. buchananii</i>	C.B. Cl.	Buchanan 410	E	24-H
(isotype)				
<i>S. candidus</i>	Hilliard	Hilliard sn	E	26-B

TABLE I (continued)

Species	Author	Collector and Number	Herbarium	Pl.-Fig. Number
<i>Streptocarpus caulescens</i>	Vatke	Falkner 1449	E	23-G
<i>S. caulescens</i>	Vatke	Burttt sn	E	23-C
var. <i>caulescens</i>				
<i>S. cyaneus</i>	S. Moore	Ross 1762	E	25-F
<i>S. davyi</i>	S. Moore	Hilliard 3068	E	26-A
<i>S. dunni</i>	J.D. Hook.	Hilliard 3665	E	25-D
<i>S. galpinii</i>	J.D. Hook.	Hilliard 3104	E	25-C
<i>S. gardenii</i>	J.D. Hook.	Burttt sn	E	26-G
<i>S. hildebrandtii</i>	Vatke	Cult. sn	E	26-E
<i>S. hilsenbergii</i>	R. Brown	Elliot 2121	E	23-B
<i>S. kirkii</i>	J.D. Hook.	R.K. Faden 70/750	E	25-A
<i>S. nobilis</i>	C.B. Cl.	Burttt sn	E	23-H
<i>S. pole-evansii</i>	Verdoorn	Hilliard 3018	E	25-E
<i>S. proxilus</i>	C.B. Cl.	Huntley 177	E	25-G
<i>S. rexi</i>	(Hook.) Lindl.	Hilliard sn	E	26-D
<i>S. saxorum</i>	Engl.	Drummond 1946	E	24-B
<i>S. silvaticus</i>	Hilliard	Hilliard-Burttt 5778	E	25-H
<i>S. stomandrus</i>	B.L. Burttt	Malberley 687C	E	24-C
<i>S. thompsonii</i>	R. Brown	Humbert 20532	E	23-A
<i>S. tsaratananensis</i>	Humbert ex B.L. Burttt	Humbert 18256	E	24-D
<i>S. variabilis</i>	Humbert	sn	AGGS	50-D
<i>Tetraphyllum bengalense</i> (T)	C.B. Cl.	E.I.T. 3830	K	14-G
<i>T. roseum</i>	Stapf	H. Nur 3695	K	14-I
<i>Titanotrichum oldhamii</i>	(Hemsl.) Soler.	Sasaki 21509	US	30-G
<i>Tremacron forrestii</i>	Craib	Rock 3307	K	17-B
<i>Trisepalum burmanicum</i>	(Craib) Stapf	Yu 1756D	E	21-E
<i>T. longipetalum</i>	B.L. Burttt	Larson 8601	E	21-F
<i>Tylopsacas cuneata</i>	(Gleason) Leeuw.	Maguire 23520	K	52-A
<i>Vanhouttea gardneri</i>	Fritsch	Anderson sn	US	38-C
<i>Whytockia sasaki</i>	(Hay.) B.L. Burttt	White 923	K	14-D

SPECIES TRANSFERRED FROM GESNERIACEAE TO SCHROPHULARIACEAE (BURTT 1963, 1967)				
<i>Charadrophila capensis</i>	Marl.	R. Rodin 3232	K	52-H
<i>Cyrtandromoea acuminata</i>	C.B. Cl.	Villos 1912	K	52-E
<i>C. decurrens</i>	(Bl.) Zoll.	Kurtz 26098	K	52-D
<i>Jerdonia indica</i>	Wight	Nicholson sn	K	52-C
<i>Rehmannia henryi</i>	N.E. Brown	Wilson 25	K	52-G

SELECTED SPECIES FROM FAMILIES OTHER THAN THE GESNERIACEAE REPRESENTING EIGHT OF THE TEN SUBCLASSES OF THE ANGIOSPERMS (CRONQUIST 1968)				
<i>Alisma triviale</i> (achene)	Pursh	sn	NC	3-B
<i>Anigozanthos flavidus</i>	Redoute	sn	RHS	2-H
<i>Aquilegia canadensis</i>	L.	sn	NC	3-D
<i>Arenaria serpyllifolia</i>	L.	sn	NC	2-A
<i>Cannabis sativa</i>	L.	sn	sn	3-F
<i>Eleocharis montevidensis</i> (nutlet)	Kunth	sn	NC	3-C
<i>Eucalyptus viminalis</i>	Labill.	sn	NC	2-B
<i>Fuchsia procumbens</i>	R. Cunn ex A. Cunn	sn	HBM	4-C
<i>Gentiana asclepiadea</i>	L.	sn	RHS	4-A
<i>Hackelia virginiana</i> (nutlet)	(L.) I.M. Johnston	sn	NC	2-C
<i>H. virginiana</i> (without trichomes) (nutlet)	(L.) I.M. Johnston	sn	NC	2-I
<i>Lophospermum purpusii</i>	(T.S. Brandeg.) Rothm.	sn	RHS	4-H
<i>Phygelius capensis</i>	E. Mey. ex Benth.	sn	HBM	4-B
<i>Spiranthes cernua</i>	(L.) Richard	sn	HBM	3-A
<i>Tetranema roseum</i>	(Mart. & Gal.) Standl. & Steyerl.	sn	HBM	4-G
<i>Vaccinium arboreum</i>	Marshall	sn	NC	3-G

INTRODUCTION

The Gesneriaceae

The angiosperm family Gesneriaceae Dum. (subclass Asteridae, order Scrophulariales, Cronquist 1968) is a large, evolutionally advanced taxon (Stebbins 1974, Burt 1977). The family contains approximately 125 genera with an estimated 2,000 species (Skog 1979). The genera are united into tribes according to various morphological differences (see Table III in the DISCUSSION.) The tribes are further united into two subfamilies, the Cyrtandroideae and the Gesnerioideae, based on the morphological differences in the cotyledonary development of the various species (Burt 1963). The family has a wide geographical distribution (Heywood 1978); its members occur in a variety of habitats and display a wide diversity of plant forms and other morphological characters.

The structural diversity of the Gesneriaceae includes herbs (monocarps and perennials), shrubs, lianas, and small trees. The seeds of the family are extremely numerous (per fruit) and range in size from 0.2 mm (*Streptocarpus* species) to 4 cm (including the hairlike appendages) in length (members of the Trichosporeae). Many of the arborescent species occur on Pacific islands that have rain-forest areas. Although the majority of the Gesneriaceae are native to the tropics and subtropics of the world, there are a few hardy genera that occur in the mountains of Europe and Japan. However, with the exception of Hawaii, there are no known gesneriad species native to the United States. The members of the Gesneriaceae occur in either terrestrial or epiphytic habitats (based on the herbarium specimens and literature examined, there are no known hydrophytic species in the family.) According to Skog (1979) gesneriad flowers are animal-pollinated, and the vectors are either bees, moths, butterflies, bats, or birds.

The Seeds of the Gesneriaceae

Despite the fact that the family is a large one, the seeds of the Gesneriaceae have not been studied very extensively, possibly because of their small size. Although the seed length range within the family varies from 0.2 mm to 4 cm, the seeds of the majority of the species examined varied from 0.2 mm to several millimeters in length. The seeds in the 4 cm range include those species of the Trichosporeae tribe, which have hairlike appendages on their apices. If the appendages are discounted however, the seeds of the Trichosporeae are comparable, in length, to seeds of the rest of the family. Because of their small size, seeds of many species are only barely visible to the naked eye. Although the overall shape of the seeds can usually be seen with the aid of the light microscope (hereafter simply LM), the surface morphology can be seen only with the aid of the scanning electron microscope (hereafter simply SEM).

Illustrations of gesneriad seeds in publications prior to the late 1960s consisted of drawings prepared with the use of the light microscope (LM) (Fritsch, 1894, Bouwer and Stahlin 1955, Ivanina 1967). In 1976, Skog used LM photomicrographs as well as a number of SEM photomicrographs. However, prior to 1977 (Beaufort-Murphy) SEM had apparently not been used as an observation tool except in an occasional species description (Nowicke 1974, Skog 1976).

In his description of the Gesneriaceae in 1894, Fritsch stated (translated from German) that "the small and numerous seeds have mostly a smooth testa with variously striped or netlike markings" (p. 141). He also mentioned that the Trichosporeae are distinguished by the hairlike appendages at both ends of the seeds. His description of the family included detailed drawings of the seeds of only three species.

Bouwer and Stahlin's *Handbook of Seeds* (1955) contains brief written descriptions of the seeds of ten gesneriads with rather indistinct drawings of only two of them.

Ivanina's carpological study of the family (1967) also included excellent drawings of the seeds of 76 species. Because the selected species are distributed throughout the family, the drawings give some indication of the morphological diversity of gesneriad seeds. However, 76 species is still a relatively small representation of such a large family. Ivanina (1966) described the gesneriad seeds as being "... mainly small and numerous" (p. 386), that the seed coats of the Cyrtandroideae are "... hard and thick, with surfaces that are either reticulate, pitted, prickly or tuberculate, while those of the Gesnerioideae are thin, and obliquely or longitudinally lined" (p. 386), and that the seeds of some of the advanced genera have aril-like appendages. Ivanina also pointed out that the seeds can be grouped according to size, whereby the increases in size are related, proportional to a decrease in their number in the fruit.

Skog's 1976 revision of the tribe Gesnerieae (which contains a total of 67 species in 3 genera) includes LM photomicrographs of the seeds of 14 species (from 2 genera), and SEM illustrations of the seeds of 4 species. Although the overall shape of the seeds is discernable in the LMs, the morphological features of the seed-surface are not apparent. On the other hand, the overall shape of the seeds is even more clearly defined in the SEM illustrations and the morphological features of the seed-surface are clearly defined. The superiority of SEM photomicrographs for revealing the morphological details of microscopic objects is further demonstrated by the SEM seed illustration included in Nowicke's original description of *Besleria subulata* (1974). The seed-surface morphology of *B. subulata* consists of distinct convoluted crests of the cell edges, which is illustrated in almost three-dimensional effect in the photomicrograph (Figure 6).

A preliminary SEM investigation (Beaufort-Murphy 1977) to determine the usefulness of a broad survey of Gesneriaceae from the seeds of 35 species of 16 genera revealed that the morphology of the seeds is as diverse as the morphology of the other plant parts of the family. The study also showed that surface morphology could be classified under three basic characteristics or patterns: 1. gross morphology or overall shape of the seeds; 2. primary surface reticulations; and 3. presence or absence of ultrastructural features.

From the preliminary 1977 SEM investigation, the gross morphological pattern of the seeds appeared to correspond to the family classification at the tribal level. On the other hand, primary surface reticulation patterns appeared to correspond to the accepted classification at the generic level. The ultrastructure of the seed surfaces was not studied for all of the species in the preliminary survey, but it will be very interesting to see if this character also corresponds to a particular classification level of the family. Beaufort-Murphy's study (1977) also confirmed the statement by Chuang and Heckard (1972) that "... seed surface patterns are both constant and characteristic for a given taxon" (p. 258).

A highly advanced family, such as the Gesneriaceae, with its wide ranges of structural diversity and geographical distribution, is an extremely interesting subject for an investigation of its seed-surface morphology. Such a study has been discussed in several personal conversations with B. L. Burt, S. Carlquist, Y. Sagawa, L. E. Skog, and G. L. Stebbins over the last few years, all of whom agreed that the investigation would make an important contribution to the knowledge of the phylogeny of the Gesneriaceae.

Research Objectives

Based on the results of the preliminary survey (Beaufort-Murphy 1977) a more extensive investigation of gesneriad seeds was undertaken. Seeds for the study were selected from species of all the available genera, to represent the taxonomic classification of the family. This selection comprises about 700 species, with a proportionally larger number of species chosen from the larger genera. Seeds of chosen species were investigated for gross morphological shape, primary surface patterns, and the presence or absence of ultrastructural features.

The results of the investigation will be used to:

1. Relate (and interpret, if possible) the pattern of seed-surface morphology to the taxonomic relationships within the Gesneriaceae.
2. Seek, by means of the scanning electron microscope, seed-surface morphology features that are representative of the Gesneriaceae.
3. Prepare a descriptive guide of the seeds of the Gesneriaceae based on SEM.

MATERIALS AND METHODS

The Use of SEM for the Study of Seed Morphology

In 1969, Heywood stated that "... the scanning electron microscope (SEM) is already proving to be the most exciting and significant tool so far produced for the study and evaluation of surface topography of solids" (p. 1). Heywood emphasized that there are a number of reasons for the potential importance of the SEM techniques in the study of plant materials. The main reason is that the surface morphology of seeds, fruits, and pollen grains is of major importance in systematic morphological and diagnostic botanical work.

Traditional biological illustrations have been either drawings or photographs prepared with the aid of a light microscope. Drawings are notably time-consuming and numerically slow to produce and require a skill that takes a long time to perfect, and in the end they are still the product of subjective decisions by the illustrator. The resolution of the light microscope is limited; therefore, photomicrographs taken with the use of a light microscope are restricted in an accurate representation of biological materials (Heywood 1969). However, the resolving power of the SEM permits a depth of field that can provide a photomicrograph that is detailed, accurate, and almost three-dimensional in appearance as well as being objective in its portrayal of the material.

At comparable magnification, the SEM provides photomicrographs that are far superior in resolution and depth of field to those from light microscopy. Beyond the range of the light microscope, SEM offers the potential of revealing unseen structures such as the ultrastructure of the seed or fruit surface. These are equally as good in resolution and depth of field as the SEM

photomicrographs made within the range of the light microscope (Heywood 1969). The SEM allows the user to take a photomicrograph of the material, examine it and redo it within minutes if needed. In addition to the speed with which a photomicrograph can be produced, there is also the advantage that the operation of the SEM does not take as long to learn as does the degree of expertise needed to produce excellent biological drawings.

The surface morphology of seeds, pollen grains, and small fruits is used extensively in taxonomic and biosystematic studies. Therefore, the correct identification of seeds is of major importance in agriculture, horticulture, pharmacology and forensic studies (Heywood 1969). Nevertheless, identification manuals usually rely on drawings and photographs (Gunn 1974, Ivanina 1967).

Despite Heywood's enthusiasm in 1969 about the potential of the SEM for illustrating biological material, Brisson and Peterson (1976) drew attention to the fact that there were, at that time, published SEM illustrations of seeds of about only 400 species of angiosperms. Most of these publications dealt with plants at the species level and none at the genus level, and none was of a monographic nature. Brisson and Peterson (1976) also stated that terminology, especially for seed-surface morphology, is urgently needed. They give examples of trichomes on seeds being referred to variously as hairs, prickles, hooks, or spines.

Examples of families, and the number of species within them, that have had publications on seeds illustrated with SEM photomicrographs are shown in Table II (numbers include all known publications on a given family, Brisson and Peterson 1976).

Table II. Families Published with SEM Illustrations of Seeds

Family	Species	Number of Species Published	Total Number of Species and Genera in Represented Families	
		Represented Genera	Species	Genera
Melastomaceae	25	24	4500	160
Cactaceae	29	29	2880	85
Liliaceae	43	25	4000	240

Hill (1976) stated that the study of seed testa features (on eleven species of *Mentzelia*, Loasaceae) showed that the taxa can be differentiated with the information gained from SEM. Reyre (1968) found an SEM study of gymnosperm pollen grains so informative that he proposed a new classification for the group he investigated. He also drew attention to "the inadequacies of morphological nomenclature established by light microscopes" (translated from French).

Chuang and Heckard's study (1972) of the seeds of 23 species of *Cordylanthus* revealed that the seed surface morphology patterns are constant for a given taxon. The same study showed that there were distinct differences in seed coats of species of different habitats. Davis and Heywood (1963) have suggested that the constancy of many of these seed characters may indicate a

high level of natural selection. However, as Brisson and Peterson (1976) pointed out, large (SEM assisted) monographic studies are needed to reveal more fully the extent of seed character consistency and to evaluate the full potential of SEM assisted investigations.

MATERIALS

Plant specimens were examined and seed samples for the SEM investigation were obtained mainly from the herbarium of the Department of Botany at the Smithsonian Institution in Washington, D.C. during a number of visits from 1976 until May, 1983. Additional specimens were examined and seed samples obtained from the herbaria of the Royal Botanic Gardens at Kew, England, and Edinburgh, Scotland, during the summer of 1977.

In order to undertake an investigation of biological material one must first obtain a representative sample of the desired specimens. Possibly the acquisition of such a collection of, say, the seeds of a local weedy species, might be relatively easy to obtain. However, the acquisition of a collection of seeds that are of sufficient quality and quantity, while at the same time providing an adequate representation of the taxonomy of the Gesneriaceae, proved to be extremely difficult, time-consuming, and expensive.

Herbaria are usually more than willing to select and send out herbarium sheets for taxonomic investigations. However, in order to obtain seeds suitable for an investigation, the sheets must contain mature fruits with ripe seeds that are in good morphological condition. Looking through an herbarium collection of a given taxon for the large number of seeds needed in an investigation such as this, would require far more time and staff than most herbaria have at their disposal. Mailing a large and valuable collection which can number into thousands of specimens would not be practical. Therefore, an investigator must collect the seeds on site. However, the personal investigation of the large herbarium collections of taxa can provide the material needed for a study as well as a better understanding of the characteristics and make-up of the group of plants under investigation. Visiting major herbaria also provides the opportunity to meet botanists who are already knowledgeable about the group of plants being studied.

The Smithsonian and Edinburgh herbaria have major collections of gesneriad specimens because each has (or has had) individuals on their staff who have spent many years specializing in the family (C. V. Morton and L. E. Skog at the Smithsonian and B. L. Burtt at Edinburgh). The Kew herbarium also has a very large gesneriad collection including quite a number of type specimens. The combined gesneriad collections of these herbaria provided a very good taxonomic representation of the family for the purposes of this study.

While a great many collectors look for plants with flowers, unfortunately very few seem to look for specimens with fruits or seeds because plants are usually classified by their flowers. The presence of fruit does not automatically imply usable seeds; at least it does not do so in the Gesneriaceae specimens. In fact, thousands of herbarium sheets had to be examined at the Smithsonian, Kew, and Edinburgh herbaria in order to obtain a collection of about 700 samples of seeds.

Seed collecting from herbarium sheets, especially with seeds as minute as those of the Gesneriaceae, can be made even more difficult by the fact that one deep breath or sneeze can instantly scatter thousands of seeds. In

addition, some of the herbaria, such as Kew, require that an investigator provide their herbarium with a duplicate set of packeted, labeled seeds, which adds considerably to the collecting time.

In addition to the seeds collected from the herbarium sheets, seeds of several species were donated for the investigation by B. L. Burt, Royal Botanic Garden, Edinburgh; L. E. Skog, Smithsonian Institution; and F. Batcheller, Durham, New Hampshire. Seeds of several additional species grown by the author were also included in the collection.

The final collection of seeds comprised well over 800 samples of about 700 species and included duplicate samples of certain species from multiple geographical locations. The 700 species of the seed collection represent 113 genera of the 127 making up the Gesneriaceae, thereby providing a very good taxonomic representation of the family. There were no seeds of the remaining 14 genera in the collections of the herbaria visited. However, should seeds of these genera become available, they will be examined and the results added to the study.

METHODS

Plant material (such as seeds, pollen grains and leaves) for examination with the scanning electron microscope (SEM) can be obtained from either fresh material or preserved herbarium specimens. However, because of certain problems that can be encountered when examining plant parts with the SEM, particularly with fresh material, pretreatment of the plant material is advisable.

Insufficiently pretreated material, such as an unfixed and/or too thinly coated specimen, can result in 'charging' or 'beam damage' (Hoyt 1974). Charging is the result of beam penetration of a specimen which can produce secondary electron emission from below the surface of the specimen. This can produce an extreme contrast in light and dark areas, with a complete loss of fine detail of the specimen. Charging can also result in 'spike brightness' (Hoyt 1974) in which the small areas emit an intense glow that prevents the examination of the specimen. Beam damage, a result of heating, can distort and/or crack the surface of the specimen and has been known to melt cuticular wax (Hoyt 1974).

Charging is more common with fresh material than preserved specimens, although preserved material can sometimes cause charging. Fresh untreated material can also contaminate the column of the SEM with the oils, resins and/or other chemicals present in the tissue of the specimen. In addition, fresh untreated material is more likely to collapse in the vacuum of the SEM than treated and/or preserved material.

The methods used for preparing seeds and/or other plant material varies from species to species and, unfortunately, there are no set procedures available to which an investigator can refer. Therefore, the method for each species has to be worked out by the investigator. Basically, the preparation methods for plant material include:

1. Fresh or dried material, untreated, uncoated then SEM
2. Fresh or dried material, untreated, coated then SEM
3. Fresh or dried material, fixed then SEM
4. Fresh or dried material, fixed, coated then SEM
5. Fresh or dried material, fixed, critical-point-dried, coated
 then SEM

Coating can be of carbon, silver, gold, gold-palladium alloy or platinum.

Coating mechanisms have either a revolving figure-eight platform or a stationary platform as on a sputter-coater. Both methods were tried.

All of the aforementioned methods (with the exception of platinum coating) were tried on sample specimens of gesneriad seeds (approximately 50 species), as well as pollen and leaf sections of selected species. The untreated plant material produced a high level of charging when scanned, that prevented either examination or photography of the specimens. Based on the results of these trials, the most satisfactory combination of methods for preparation of gesneriad seeds, either fresh or preserved, proved to be:

1. Attach a single-sided sticky copper tape, with sticky side exposed, to stubs with Dag 154* (for conduction and adhesion).
2. Attach seeds to exposed sticky surface of the tape using a light microscope (dissecting) to control positioning of the seeds.
3. Osmium fixation; stubs, with attached seeds, are put in a dessicator, with a watch glass containing approximately 5 ml of a 4% Os solution, and then exposed to the vapors for three hours in a vented chemical hood.
4. Coating: specimens are coated with carbon and gold (approximately 5 cm of wire) on a revolving-platform coater.
5. After coating, the specimens are kept in a clean, airtight container, preferably a dessicator. Scanning of the specimens should take place as soon as possible after the coating. Recoating with a small amount of gold might be necessary if specimens have been stored for several weeks or longer. However, specimens will not require refuming or further coating with carbon, even when kept for a year or more after treatment.

RESULTS

SEED ATLAS

Glossary Introduction

The author's examination of the seeds of more than 700 species of the Gesneriaceae revealed the wide diversity of seed morphology characters possessed by the various members of the family. In addition, she became even more aware of the enormous variety of seed morphology characters of the seeds plants as a whole when she organized and indexed the Herbarium Fruit and Seed Collection at North Carolina State University and photographed the seeds for *Identifying Seedlings and Mature Weeds* (Stucky et al. 1981.) Despite the very wide diversity of the morphological characters of seeds, a review of the existing literature demonstrated the paucity and inconsistent usage of terminology as applied to seed morphology. The lack of terminology was especially noticeable in relation to the ultrastructural level as seen with the SEM (Musselman and Mann 1976) and, as Heywood (1969) points out, "... seed details tend to be imprecise in taxonomic descriptions" (p. 7).

The investigations reviewed consisted of two basic types: those without a glossary of the terms discussed, such as Clark and Jernstedt 1978, and those with a glossary, such as Murley 1951. Murley's extensive glossary of seed morphology characters, based on the seeds of 92 species of the Brassicaceae and illustrated with drawings, is still used as the standard reference for seed morphology in current textbooks, such as Stearn's *Botanical Latin*

* Dag 154 is a trade name for a conductive-adhesive material consisting of graphite in isopropyl alcohol (Ted Pella, Inc.).

1978. However, the glossary was compiled before the advent of SEM-assisted investigations and does not, therefore, include ultrastructural features. In addition, Murley's glossary consists of a straight alphabetical list of the morphological characters discussed in the paper. Hunting through such a list for a character adds considerably to the time spent diagnosing seeds.

As a result of the literature review, the author realized that the monographic scope of her investigation, combined with the problems of existing terminology, emphasized the need for a comprehensive glossary of clearly defined, carefully illustrated characters with which to diagnose seed morphology. In addition, she decided that a glossary with an organized format, rather than a straight alphabetical list of characters such as Murley's (1951), would greatly facilitate seed morphology investigations.

Sources for terminology included Murrill (1905), Murley (1951), Featherly (1954), Kemp (1965), Burt (1975), and Stearn (1978). Stearn (1978) was also a reference for grammatical form to ensure a current and correct usage of the terms. The terms and/or their definitions have been selected and/or defined to describe seed morphology characters and some of them are a composite of several sources. The glossary of terms consists, for the most part, of existing terminology and is augmented with newly coined terms by the author where needed. However, the creation of the glossary format and its companion table and modifications, as well as the definition and usage of the categories and assignment of tertiary terms, are entirely the work of the author.

The glossary of terms is divided into six major categories, some of which are further divided into minor categories. Each of the categories, major and/or minor, contains a set of tertiary terms with which to define further the character in question. The categories are arranged in a sequence of increasingly smaller features ranging from the overall 'Seed Shape' (macro or LM level), through 'Cell Orientation' (LM level), to 'Primary' and 'Secondary Cell Characters' (SEM level). Major categories 1-3 deal with the multiple-cell features of seeds, while categories 4-6 deal with the morphological features of the individual cells. The glossary format readily allows for the addition and/or substitution of categories, such as would be needed for histological investigations with the transmission electron microscope (TEM), or tertiary terms, for taxa possessing characters not included in this glossary.

The glossary format is also represented by a companion table (see Atlas Table 2) which was designed to facilitate the recording of the diagnostic data obtained from a seed morphology investigation. The table can be readily modified to fit an investigator's needs. In this investigation, the table was used in its basic form to record the diagnostic data at the species level (see Atlas Tables 2-52). In one modification the table was used to record the diagnostic data and facilitate a summary of the investigation at the family, subfamily, tribal and genus levels (Summary Table), and in another modification the table was used as an index of the glossary terms and their illustrations (Atlas Table 1).

The morphology characters are defined in the Glossary of Terminology and illustrated with photomicrographs on Atlas Plates 1-a, 1-b, and 1-c. The definition of each character in the glossary is followed by the plate and figure number of its representative illustration (i.e., 'Seed Shape,' narrowly-elliptic, Plate 1-a, Fig. A). In addition, the 'Illustration Index of Morphological Characters for Seed (and/or Achenes and Nutlets)' (Atlas Table 1) provides a ready reference to the representative illustrations of the characters as well as the glossary format of categories and tertiary terms.

The glossary and its format were created primarily to diagnose the seeds of the Gesneriaceae. However, to ensure that it would also apply to seed plants in general, the author examined the seeds of a wide variety of species from other families. Seeds (nutlets or achenes) of 15 species were then selected to represent 8 of the 10 subclasses according to Cronquist (1968), and are included in this investigation (Atlas Plates and Tables 4-6). This selection represents only a small fraction of the enormous variety of the seed morphology characters possessed by seed plants but demonstrates that the glossary and its format can be used to assist in the diagnosis and/or identification of seeds of any of the seed plants.

Glossary of Terminology

1. Seed Shapes

Seed shapes can be defined by their basic outlines (using symmetrical plane figures) or by their three-dimensional shape (using solid figures). However, defining the shape of an object with many of these figures, such as ovate or obovate, requires that the basal apex of the object be known. Unfortunately the basal (chalazal) apex of small, unattached and/or highly sculptured seeds, such as many of the gesneriads, can be difficult to define. Therefore, for the purpose of this study, the majority of the seed shapes were defined by plane figures using the length versus width ratios, without regard to the position of the widest part of the seeds. These shapes include:

Narrowly elliptic	—	6:1 - 3:1
Elliptic	—	2:1 - 3:2
Broadly elliptic	—	6:5
Circular	—	1:1
Orbiculate	—	a somewhat flat body with a circular outline.
Reniform	—	kidney-shaped
* Carinate, as "Carinatus"	—	keeled, having a single projecting ridge (formed in the manner of a boat keel) along one side of a seed.
* Alate, as "Alatus"	—	winged, having thin, broad projections of the testa. The 'wings' can vary according to taxa, in shape, size, and number.
Irregular	—	lacking an apparent shape.

2. Apical Characters

Apical distinctions include:

Acute	—	terminating gradually to a point
Arillate	—	provided with an aril.
Constrictate	—	terminating as an abruptly constricted region that is not undulate as in Coronate.
Coronate	—	having crownlike projections at either or both apices.
Filiform	—	having hairlike projections at either or both apices.
Obtuse	—	terminating gradually in a rounded apex
Reniform	—	terminating in two rounded lobes.
Truncate	—	terminating abruptly as if cut off.
Premorse	—	terminating abruptly as if bitten off.
Irregular	—	lacking a consistent shape.

* — Ed.

3. Cell Orientations

The terms define the orientation of the cells in relation to the angle of divergence from the central axis of a seed, such as:

Straight	—	cell orientation parallel with the seed axis.
Slightly spiral	—	cell orientation slightly helical with the seed axis.
Spiral	—	cell orientation distinctly helical with the seed axis.
Irregular	—	cell orientation lacking an apparent pattern.

4. Individual Cell Shapes

The shapes of individual cells include polygonate variations (based on a plane closed figure bounded by three or more line segments having many angles), such as:

Narrowly lineate-polygonate	very narrow cells, the edges of which are contiguous or nearly so.
Lineate-polygonate	approximately 2:1 - 3:2 ratio.
Polygonate	approximately 6:5 ratio.

Additional cell shapes include:

Lobed	cell margins indented $1/8$ - $1/4$ distance to cell axis.
Parted	cell margins indented $1/2$ - $3/4$ distance to cell axis.
Irregular	lacking an apparent shape.

5. Primary Cell Characters

Facet	the visible (surface) portion of an individual cell.
Edges	extreme margins of a visible facet of an individual cell.
Crests	a structure formed by the contiguous edges of adjacent cells, a crest can be discrete, (not fused with each other), fused or composite (a crest which has both discrete and fused sections).
Face	central portion of the visible facet of a cell surrounded by the edges.
Edges and Faces	can be either elevated, level (on the same plane) or depressed in relation to each other.

6. Secondary Cell Characters

Ultrastructural features of the edges and/or faces of individual cells include:

Auriculate	furnished with earlike or lobed projections.
Colliculate	rounded projections closely spaced and covering the entire surface.
Face not visible	a cell with contiguous edges that conceal the face.
Foveate	a surface pitted with small indentations.
Level	on one plane.

Ocellate	an elevated ringlike projection surrounding a depressed area.
Papillate	small rounded projections.
Rough	an uneven surface that lacks distinctively shaped features.
Smooth	lacking surface texture.
Stellate-glochidate trichomes	trichomes with star-shaped apices, the rays of which are reflexed and terminate in sharp points.
Striate	longitudinal or transverse ridges (and/or grooves) on the edges and/or faces of the cells.
Tetragonate	based on a solid figure (tetragon) having three mutually perpendicular axes, two of which are of equal length and the third longer or shorter.
Tholiform	dome shaped, a broad shallow dome
Tuberculate	rounded to distinctly tubelike projections (larger than Papillate).
Undulate	wavy, having an uneven, alternately concave and convex margin.
Verrucate	with irregular warty projections.

SEED MORPHOLOGY SCALE

The scale of the seed morphology is indicated by the hatch mark at the bottom of each photomicrograph. For example, the "100.0 μ —" on Pl. Ia, fig. B, indicates that the hatch mark is equal to 100 microns.

DISCUSSION

The classification systems in Table III represent investigations that included taxa of each of the subfamilies of the Gesneriaceae. As can be seen from the table, the tribes Anetantheae, Beslerieae, Columneae, Mitrarieae, and Coronanthereae have been transferred back and forth between the subfamilies on the basis of morphological differences among the tribes in question. On the other hand, regardless of the morphological characters used for comparative purposes, all of the investigators have retained the tribes Cyrtandreae, Trichosporeae, Klugieae, and Didymocarpeae of the subfamily Cyrtandroideae, and Bellonieae, Gloxinieae, Kohlerieae, Solenophoreae, Sinningieae, and Gesnerieae of the subfamily Gesnerioideae in the subfamilies in which they were originally placed by Fritsch (1893). The classification system followed in this study is the same as that of Wilson (1974) with the exception of the reinstatement of the tribe Anetantheae. The order in which the tribes are arranged in Table III is to emphasize the differences between the systematic treatments of the various authors and, in my case at least, does not necessarily imply a particular order of affinity of the tribes.

Table IV lists the selected species from families other than the Gesneriaceae representing eight of the ten subclasses of the angiosperms (Cronquist 1968) included in this study. The seeds of the species are illustrated and recorded on Atlas Plates and Tables 4-6.

TABLE III. Gesneriaceae Dum. (1822)

G. Don (1838) included all known genera of the family; his classification was based on presence or absence of endosperm and geographical distribution.

	Fritsch 1893-4	Burtt 1963	Melchior 1964	Ivanina 1966	Wilson 1974	Beaufort-Murphy 1983
	Based on ovary position, fruit and disk morphology.	Based on seedling morphology.	Based on ovary position, fruit, disks, and leaf arrangement.	Based on carpel morphology.	Based on floral anatomy.	Based on seed morphology.
Sub-family	18 tribes	15 tribes-1963 14 tribes-1977	17 tribes	17 tribes	14 tribes	15 tribes
CYRTANDROIDEAE	Cyrtandreae	Cyrtandreae	Cyrtandreae	Cyrtandreae	Cyrtandreae	Cyrtandreae
	Trichosporeae	Trichosporeae	Aeschynanthaeae	Trichosporeae	Trichosporeae	Trichosporeae
	Klugieae	Klugieae† Loxoniaeae†	Klugieae	Klugieae	Klugieae	Klugieae
	Didymocarpeae	Didymocarpeae	Didymocarpeae	Didymocarpeae	Didymocarpeae	Didymocarpeae
	Streptocarpeae			Saintpaulieae		
	Hemiboeae		Hemiboeae	Rhynchotecheae		
	Ramondeae		Ramondeae	Ramondeae		
	Championaeae		Championaeae			
	Anetanthaeae*			Mitrarieae*		
	Beslerieae*		Beslerieae*			
	Columnaeae*	(†-combined as Klugieae 1977)	Columnaeae*			
EPISCIOIDEAE	Coronanthereae*		Coronanthereae*	Coronanthereae*		
				Episcieae* Columnaeae*		
GESNERIOIDEAE		Beslerieae* Columnaeae* Coronanthereae* Mitrarieae*			Beslerieae* Columnaeae* Coronanthereae* Mitrarieae*	Anetanthaeae* Beslerieae* Episcieae* Coronanthereae* Mitrarieae*
	Bellonieae		Bellonieae	Bellonieae	Bellonieae	Bellonieae
	Gloxinieae		Gloxinieae	Gloxinieae	Gloxinieae	Gloxinieae
	Kohlerieae		Kohlerieae	Kohlerieae	Kohlerieae	Kohlerieae
	Solenophoreae		Solenophoreae	Solenophoreae		Solenophoreae
	Sinningieae		Sinningieae		Sinningieae	Sinningieae
	Gesnerieae		Gesnerieae	Gesnerieae	Gesnerieae	Gesnerieae
				Rechsteinerieae		

*-Tribes that have been transferred back and forth between subfamilies.

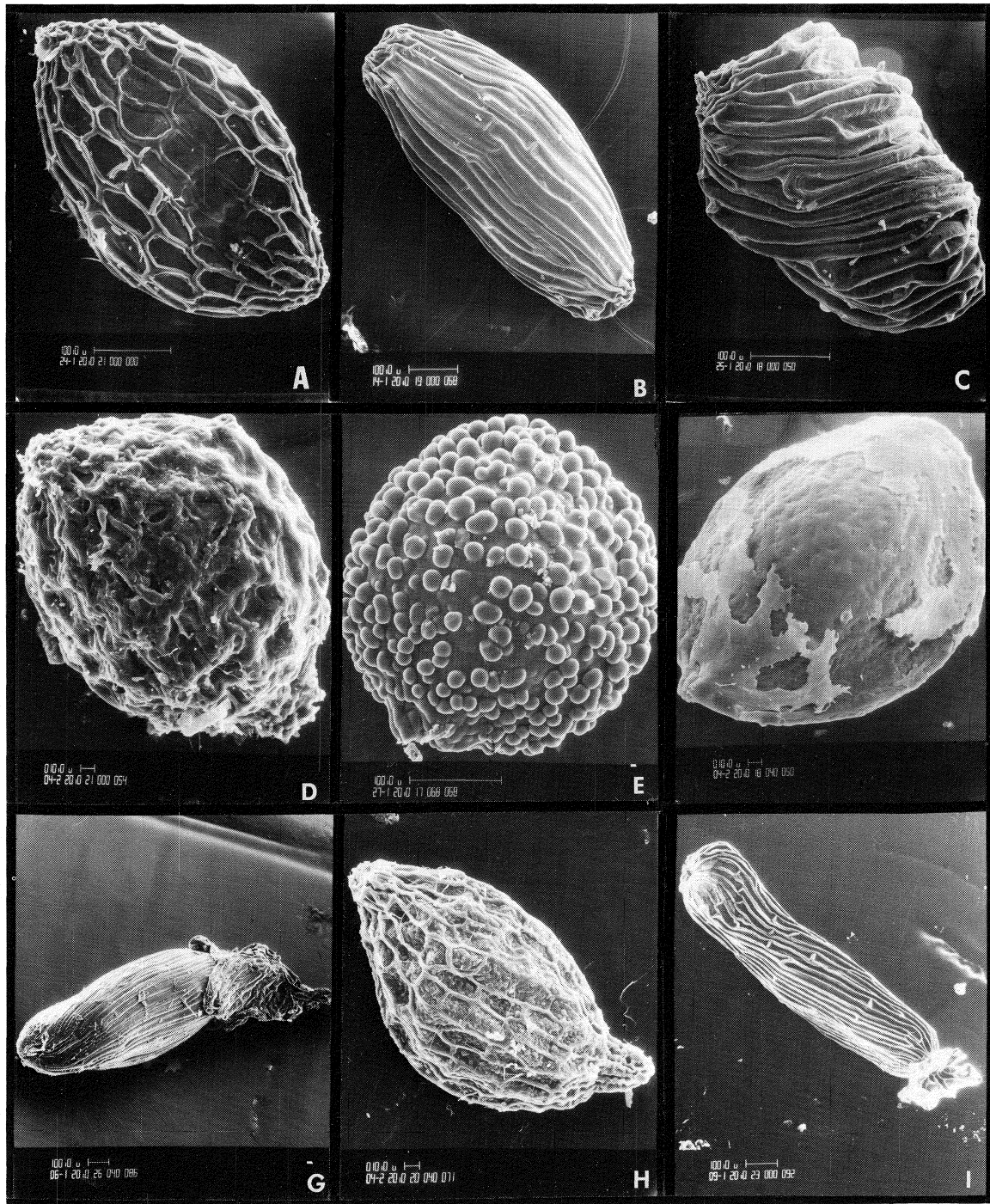
TABLE IV. Selected Species from Families Other Than the Gesneriaceae Representing Eight of the Ten Subclasses of the Angiosperms (Cronquist 1968).

	Genus, species	Families	Orders	Subclasses
<u>Monocots</u>				
Nutlets	<i>Eleocharis montevidensis</i>	Cyperaceae	Cyperales	Commelinidae
Achene	<i>Alisma triviale</i>	Alismataceae	Alismatales	Alismatidae
Seeds	<i>Spiranthes cernua</i>	Orchidaceae	Orchidales	Liliidae
<u>Dicots</u>				
Seeds	<i>Aquilegia canadensis</i>	Ranunculaceae	Ranunculales	Magnoliidae
Seeds	<i>Cannabis sativa</i>	Moraceae	Urticales	Dilleniidae
Seeds	<i>Vaccinium arboreum</i>	Ericaceae	Ericales	Dilleniidae
Seeds	<i>Arenaria serpyllifolia</i>	Caryophyllaceae	Caryophyllales	Caryophyllidae
Seeds	<i>Eucalyptus viminalis</i>	Myrtaceae	Myrtales	Rosidae
Seeds	<i>Fuchsia procumbens</i>	Onagraceae	Myrtales	Rosidae
Nutlet	<i>Hackelia virginiana</i>	Boraginaceae	Polemoniales	Asteridae
Seeds	<i>Gentiana asclepiadea</i>	Gentianaceae	Gentianales	Asteridae
Seeds	<i>Lophospermum purpusii</i>	Scrophulariaceae	Scrophulariales	Asteridae
Seeds	<i>Tetranema roseum</i>	Scrophulariaceae	Scrophulariales	Asteridae
Seeds	<i>Phygellus capensis</i>	Scrophulariaceae	Scrophulariales	Asteridae

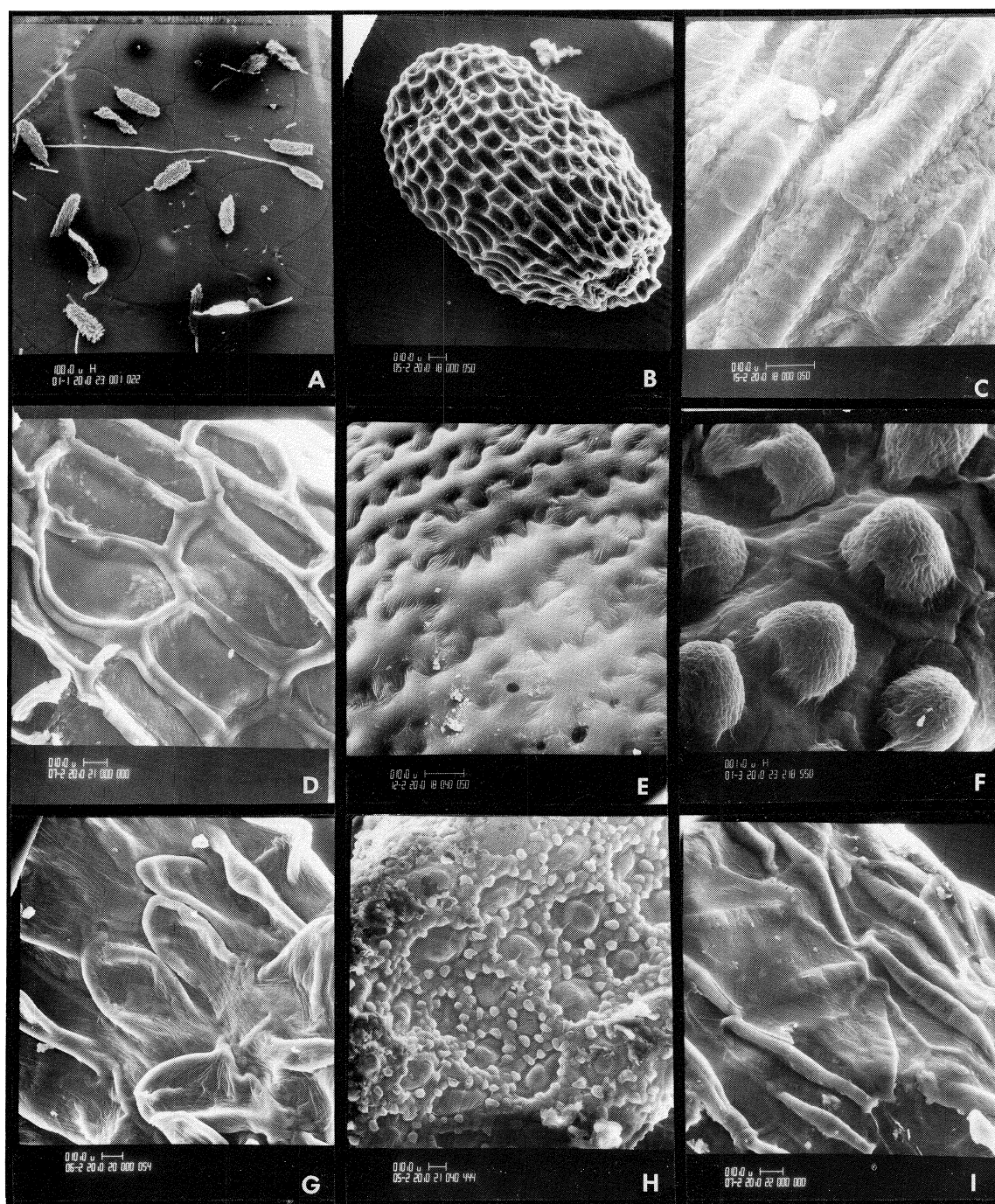
ATLAS TABLE 1 ILLUSTRATION INDEX OF MORPHOLOGICAL CHARACTERS
FOR SEEDS (AND/OR ACHENES AND NUTLETS)

		Characters	Representative illustrations	Plate	Fig.
1	Seed Shapes	Narrowly-elliptic	<i>Fieldia australis</i>	AP 1a	B
		Elliptic	<i>Cyrtandra mauiensis</i>	AP 1a	A
		Broadly-elliptic	<i>Cyrtandra zamboangensis</i>	AP 1a	D
		Circular	<i>Tylopsacas cuneata</i>	AP 1a	E
		Orbiculate	<i>Anetanthus gracilis</i>	AP 1a	F
		Reniform	<i>Arenaria serpyllifolia</i>	AP 2	A
		Carinatus(C), Alatus(A)	<i>Aquilegia canadensis</i> (C)	AP 3	D
			<i>Anetanthus gracilis</i> (A)	AP 1a	F
		Irregular	not illustrated in glossary plates	-	-
2	Apical Characters	Acute	<i>Cyrtandra mauiensis</i>	AP 1a	A
		Arillate	<i>Nematanthus radicans</i>	AP 1a	G
		Constrictate	<i>Ornithoboea leptanema</i>	AP 1a	H
		Coronate	<i>Sinningia cardinalis</i>	AP 1a	I
		Filiform	<i>Aeschynanthus javanicus</i>	AP 1b	A
		Obtuse	<i>Rhynchosoglossum obliquum</i>	AP 1b	B
		Reniform	<i>Arenaria serpyllifolia</i>	AP 2	B
		Truncate(T), Premorse(P)	<i>Cannabis sativa</i> (T)	AP 3	F
			<i>Alisma triviale</i> (P)	AP 3	B
		Irregular	not illustrated in glossary plates	-	-
3	Cell Orientation				
		Straight	<i>Cyrtandra mauiensis</i>	AP 1a	A
		Slightly-spiral	<i>Fieldia australis</i>	AP 1a	B
		Spiral	<i>Gesneria pumila</i>	AP 1a	C
		Irregular	<i>Tylopsacas cuneata</i>	AP 1a	E
4	Cell Shapes				
		N-lineate-polygonate	<i>Fieldia australis</i>	AP 1a	B
		Lineate-polygonate	<i>Cyrtandra multiseptata</i>	AP 1a	C
		Polygonate	<i>Cyrtandra mauiensis</i>	AP 1b	D
		Lobed(L), Parted(P)	<i>Arenaria serpyllifolia</i> (L)	AP 2	D
			<i>Anetanthus gracilis</i> (P)	AP 1b	E
		Irregular	not illustrated in glossary plates	-	-
5	Primary Cell Characters	Edges			
		Elevated	<i>Cyrtandra mauiensis</i>	AP 1b	D
		Depressed	<i>Saintpaulia grotei</i>	AP 1b	F
		Irregular	not illustrated in glossary plates		
		Crests	<i>Cyrtandra mauiensis</i>	AP 1b	D
		Fused	<i>Ramonda myconi</i>	AP 1b	G
		Composite	<i>Cyrtandra longifolia</i>	AP 1b	I
		Face	<i>Saintpaulia grotei</i>	AP 1b	F
		Depressed	<i>Cyrtandra mauiensis</i>	AP 1b	D
6	Secondary Cell Characters	Edge Characters			
		Foveate	<i>Vaccinium arboreum</i>	AP 3	H
		Papillate	<i>Chirita hamosa</i>	AP 1b	H
		Auriculate	<i>Ramonda myconi</i>	AP 1b	G
		Undulate	<i>Phinaea pulchella</i>	AP 1c	A
		Verrucate	<i>Cyrtandra multiseptata</i>	AP 1b	C
		Striate	<i>Boeica fulva</i>	AP 1c	B
		Rough	<i>Streptocarpus bambuseti</i>	AP 1c	D
		Smooth	<i>Cyrtandra mauiensis</i>	AP 1b	D
		Face Characters			
		Face not visible	<i>Phinaea pulchella</i>	AP 1c	A
		Level	<i>Opithandra primuloides</i>	AP 1c	C
		Tholiform	<i>Petrocodon dealbatus</i>	AP 1c	E
		Colliculate	<i>Tylopsacas cuneata</i>	AP 1a	E
		Papillate	<i>Chirita lavandulacea</i>	AP 1c	G
		Tuberculate	<i>Saintpaulia grotei</i> & <i>Aeschynanthus bracteatus</i>	AP 1b, c	F, H
		Auriculate	<i>Trisepalum longipetalum</i>	AP 1c	I
		Ocellate	<i>Streptocarpus bambuseti</i>	AP 1c	D
		Tetragonate	<i>Ornithoboea pseudoflexuosa</i>	AP 2	G
		Verrucate	<i>Rhynchosoglossum klugoides</i>	AP 1c	F
		Striate	<i>Boeica fulva</i>	AP 1c	B
		Rough	<i>Opithandra primuloides</i>	AP 1c	C
		Smooth	<i>Vaccinium arboreum</i>	AP 3	H
		Stellate-glochidate	<i>Hackelia virginiana</i>	AP 2	C

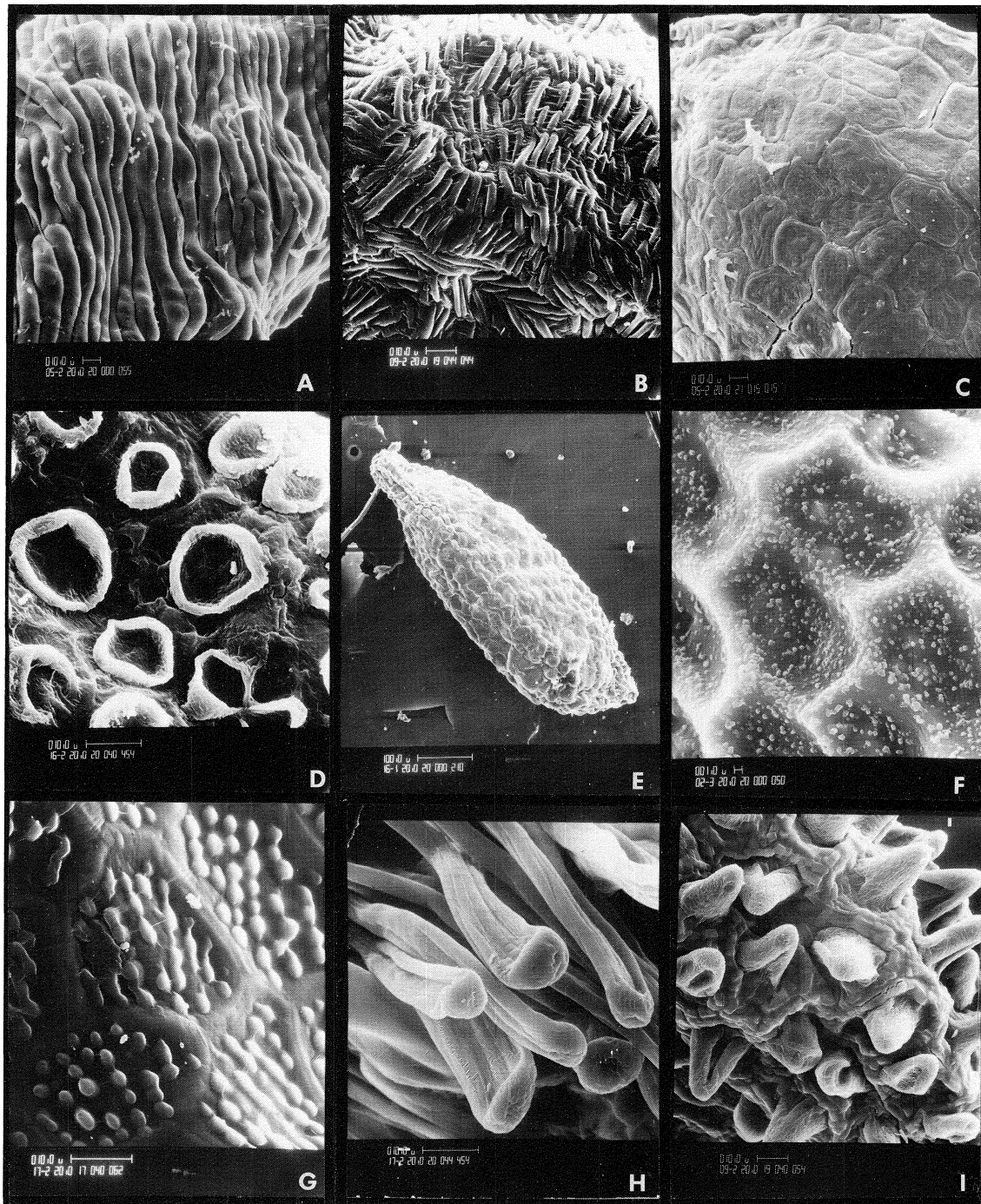
ATLAS PLATE 1a



ATLAS PLATE1b

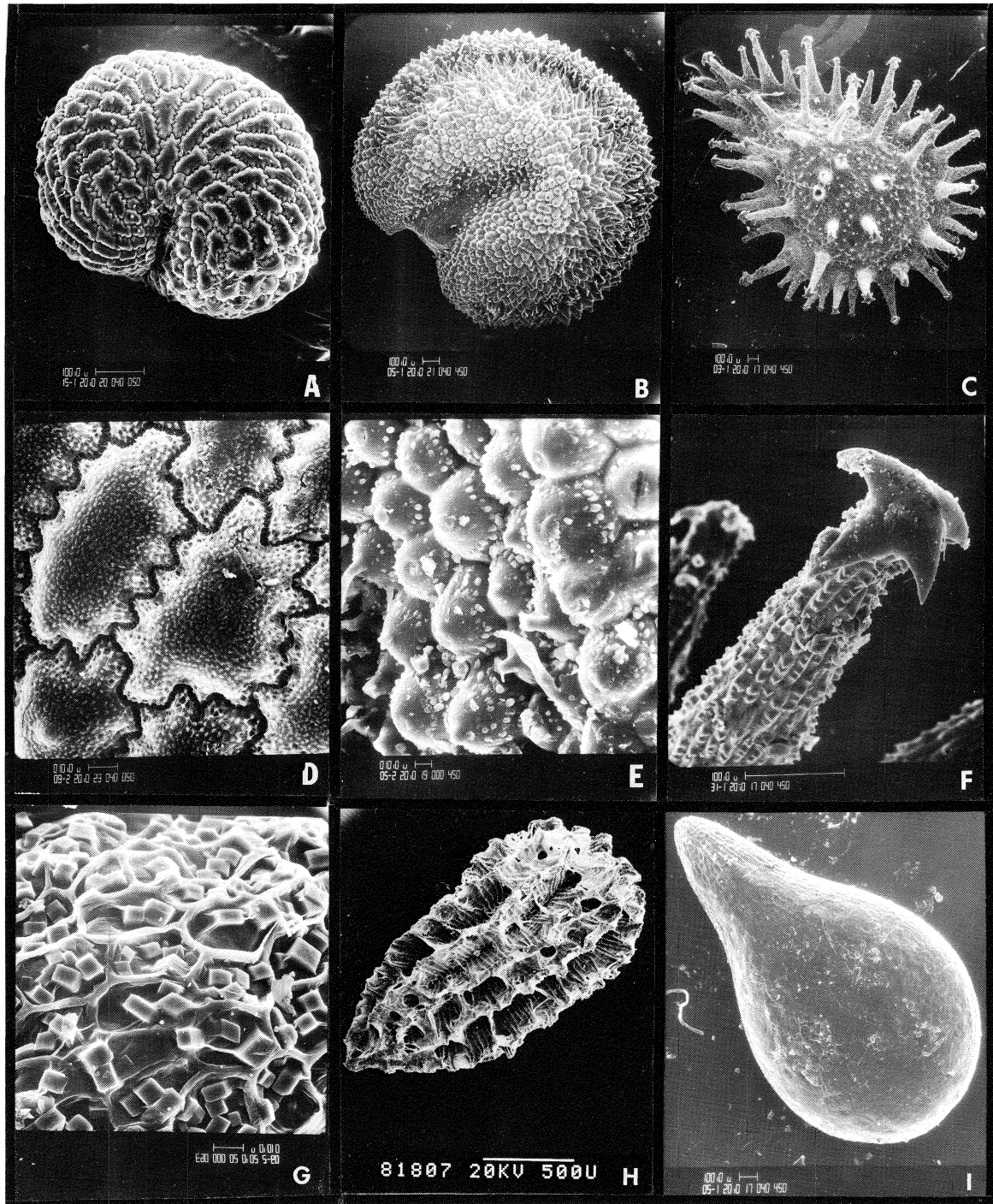


ATLAS PLATE 1c



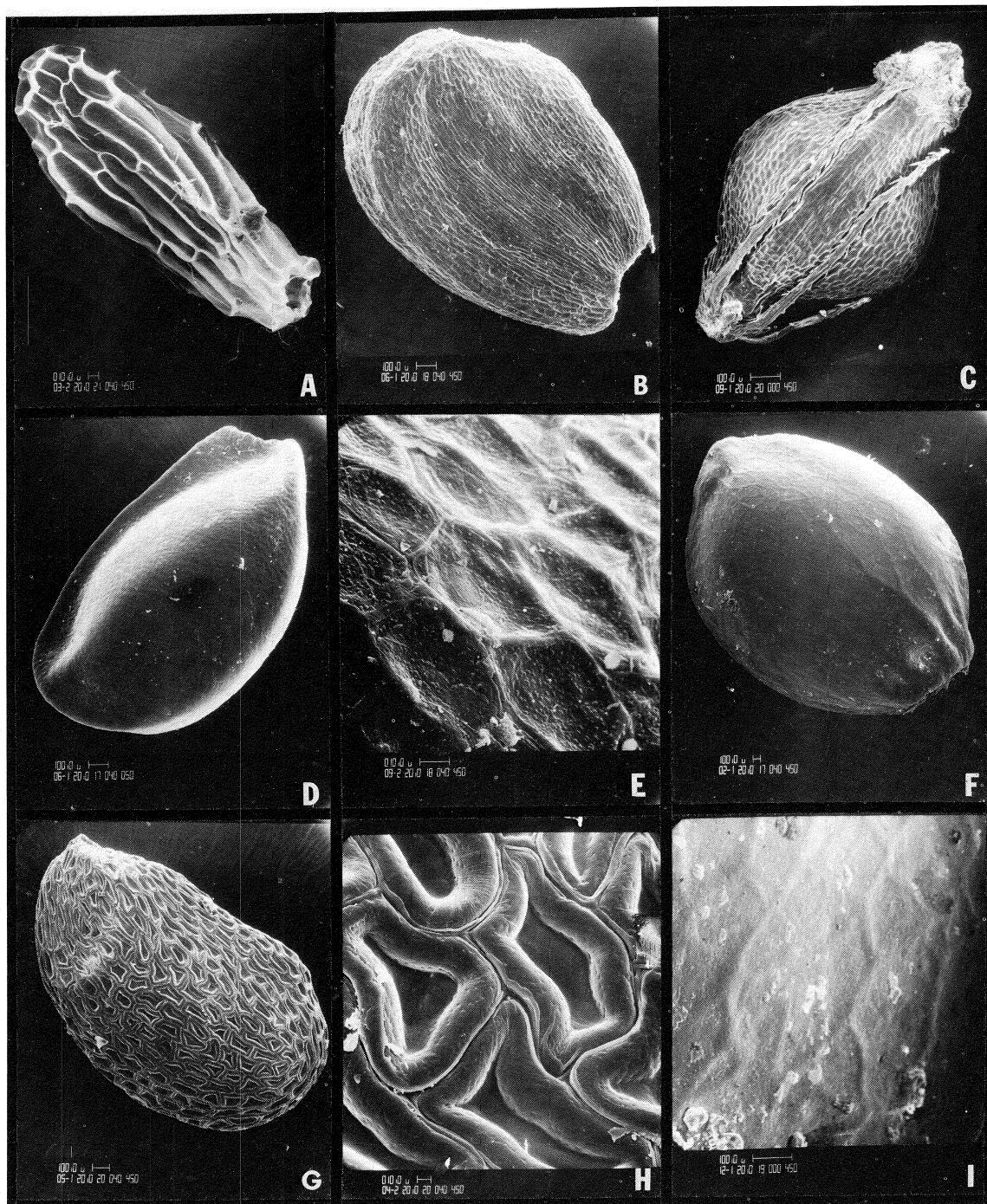
ATLAS TABLE 2			<i>Arenaria serpyllifolia</i> <i>Eucalyptus viminalis</i> <i>Hackelia virginiana</i> <i>Arenaria serpyllifolia</i> <i>Eucalyptus viminalis</i> <i>Hackelia virginiana</i> <i>Ornithoboea pseudoflexuosa</i> (holotype) <i>Anigozanthos flavidus</i> <i>Hackelia virginiana</i> (without trichomes)								
			A	B	C	D	E	F	G	H	I
Seed Shapes		Narrowly-elliptic				CU	CU	CU	CU		
		Elliptic			3:2					2:1	3:2
		Broadly-elliptic	6:5	6:5							
		Circular									
		Orbiculate									
		Reniform	+	+							
		Carinarus(C), Alatus(A)								A	
Apical Characters		Irregular									
		Acute			+					+	+
		Arillate									
		Constrictate									
		Coronate									
		Filiform									
		Obtuse	+	+	+					+	+
Cell Orientation		Reniform	+	+							
		Truncate(T), Premorse(P)									
		Irregular									
Cell Shapes		Straight	+							+	
		Slightly-spiral									
		Spiral									
		Irregular		+	+						+
Primary Cell Characters		N-lineate-polygonate								+	
		Lineate-polygonate									
		Polygonate	+	+							
		Lobed(L), Parted(P)	L								
Secondary Cell Characters		Irregular			+						
		Edges			+					+	+
		Elevated									
		Depressed	+	+							
		Irregular									
		Crests									
		Discrete	+	+							
Secondary Cell Characters		Fused								+	
		Composite									
		Face									
		Elevated	+	+							
		Depressed			+					+	+
		Edge Characters									
		Foveate									
		Papillate									
		Auriculate									
		Undulate									
		Verrucate	+	+							
		Striate									
		Rough			+					+	+
		Smooth									
		Face Characters									
		Face not visible									
		Level									
		Tholiform									
		Colliculate		+							
		Papillate									
		Tuberculate									
		Auriculate									
		Ocellate									
		Tetragonate									
		Verrucate	+	+							
		Striate									
		Rough			+					+	+
		Smooth									
		Stellate-glochidate			+						

ATLAS PLATE 2



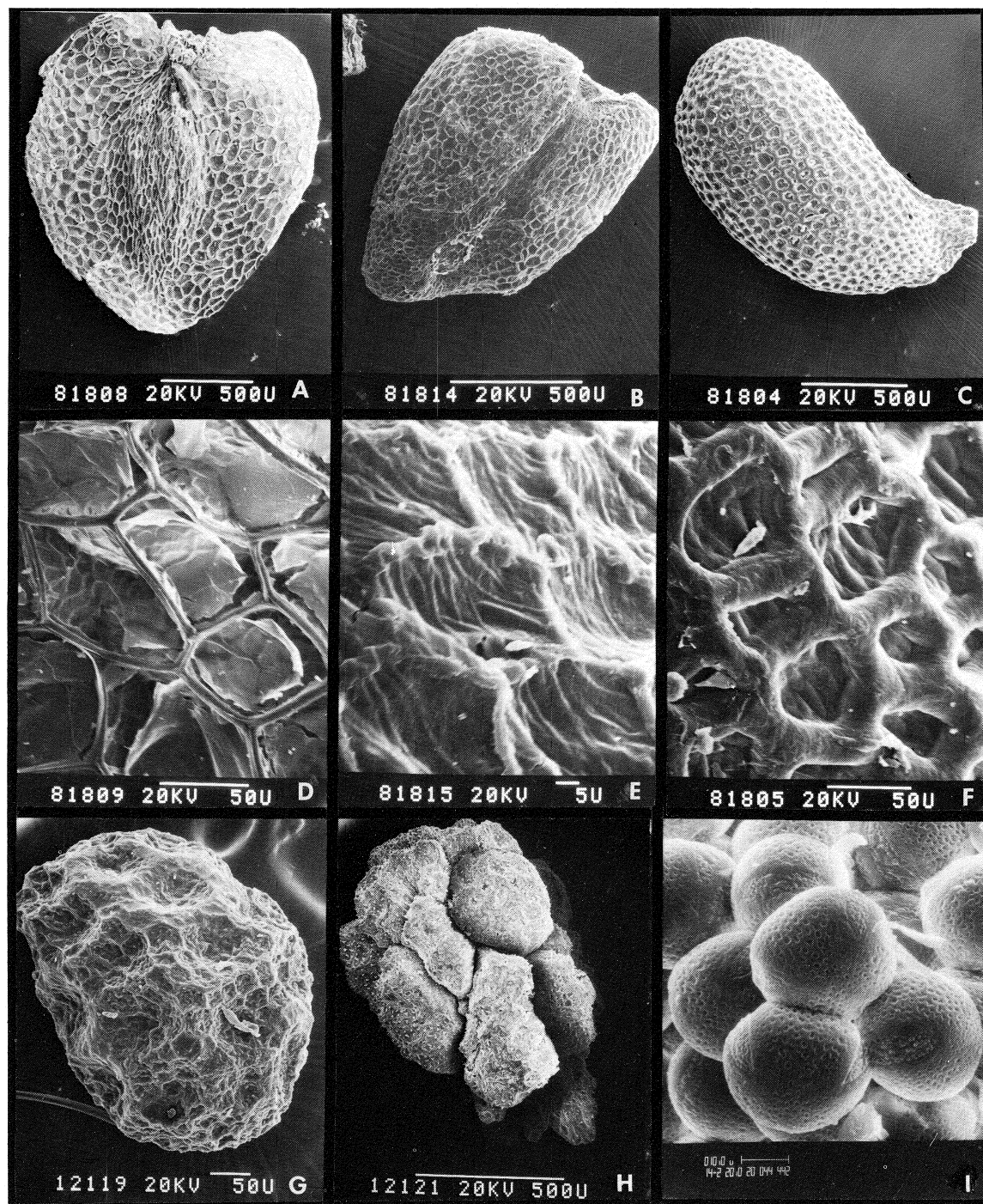
ATLAS TABLE 3			Cannabis sativa Vaccinium arboreum Vaccinium sativa Cannabis sativa Alisma canadensis Aquilegia montevidensis (nutlet) Eleocharis (achene) Alisma triviale Spiranthes cernua										
			A	B	C	D	E	F	G	H	I		
Seed Shapes		Narrowly-elliptic	3:1			5:3	5:3	CU		5:3		CU	
		Elliptic				5:3							
		Broadly-elliptic		5:4				6:5					
		Circular											
		Orbiculate											
		Reniform											
		Carinatus(C), Alatus(A)				C							
Apical Characters		Irregular											
		Acute			+	+		+	+				
		Arillate											
		Constrictate											
		Coronate											
		Filiform											
		Obtuse	++	+	+	+				+			
Cell Orientation		Reniform											
		Truncate(T), Premorse(P)		P					T				
		Irregular											
		Straight	+	+	+								
		Slightly-spiral											
		Spiral											
		Irregular				+		+	+				
Cell Shapes		N-lineate-polygonate											
		Lineate-polygonate	+										
		Polygonate		+	+	+		+	+				
		Lobed(L), Parted(P)											
		Irregular											
Primary Cell Characters		Edges	Elevated	+	+	+			+	+			
		"	Depressed										
		"	Irregular				+						
		Crests	Discrete		+					+			
		"	Fused	+		+			+				
		"	Composite										
Secondary Cell Characters		Face	Elevated						+				
		"	Depressed	+						+			
		Edge Characters	Foveate								+		
			Papillate										
			Auriculate										
			Undulate										
Verrucate			+										
Striate													
Rough					+		+						
Face Characters		Smooth	+		+								
		Face not visible											
		Level											
		Tholiform											
		Colliculate											
		Papillate											
		Tuberculate											
		Auriculate											
		Ocellate											
		Tetragonate											
		Verrucate		+									
		Striate											
		Rough			+	+		+					
		Smooth	+							+			
Stellate-glochidate													

ATLAS PLATE 3

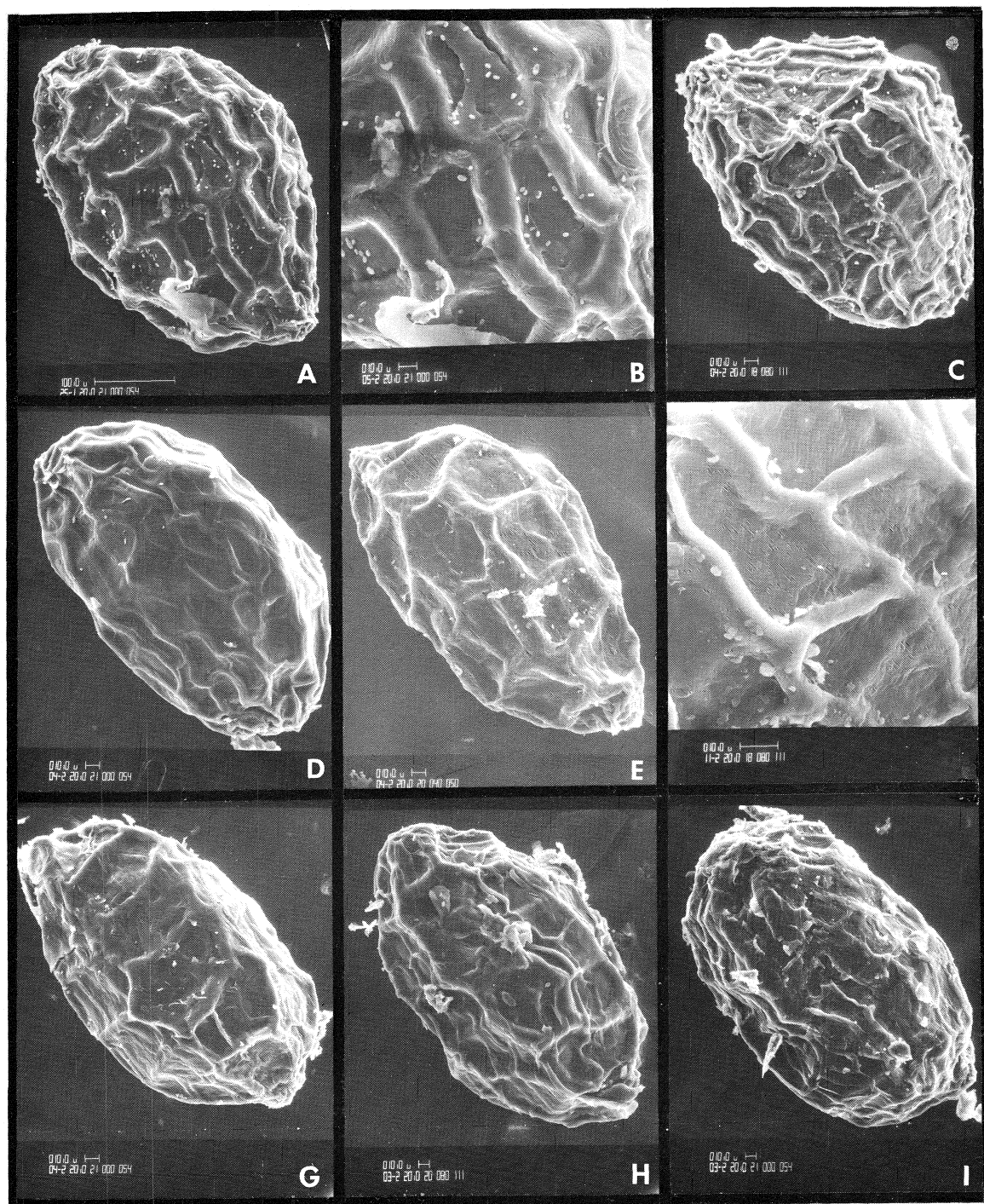


ATLAS TABLE 4			Gentiana asclepiadea	Phygellus capensis	Fuchsia procumbens	Gentiana asclepiadea	Phygellus capensis	Fuchsia procumbens	Tetranema procumbens	Lophospermum roseum	Hypocyrta bradei (pollen)			
			A	B	C	D	E	F	G	H	I			
Seed Shapes		Narrowly-elliptic				CU	CU	CU						
		Elliptic			3:2						5:3			
		Broadly-elliptic								7:5				
		Circular												
		Orbiculate												
		Reniform												
		Carinatus(C), Alatus(A)									A			
Apical Characters		Irregular (Cordate)	1:1c	5:3c										
		Acute	+	+						+	+			
		Arillate												
		Constrictate			+									
		Coronate												
		Filiform												
		Obtuse			+					+	+			
Cell Orientation		Reniform	+	+										
		Truncate(T), Premorse(P)												
		Irregular												
Cell Shapes		Straight												
		Slightly-spiral												
		Spiral												
		Irregular	+	+	+					+	+			
Primary Cell Characters		N-lineate-polygonate												
		Lineate-polygonate												
		Polygonate	+	+	+					+				
		Lobed(L), Parted(P)												
		Irregular									+			
Secondary Cell Characters	Edge Characters	Edges												
		Elevated	+	+	+					+	+			
		Depressed												
		Irregular								+	+			
		Crests												
		Discrete	+											
		Fused		+	+					+				
Secondary Cell Characters	Face Characters	Composite									+			
		Face												
		Elevated												
		Depressed	+	+	+					+	+			
		Foveate												
		Papillate								+				
		Auriculate		+										
		Undulate												
		Verrucate												
		Striate		+										
		Rough			+					+	+			
		Smooth	+											
		Face not visible												
		Level												
		Tholiform												
		Colliculate												
		Papillate								+				
		Tuberculate												
		Auriculate												
		Ocellate												
		Tetragonate												
		Verrucate												
		Striate		+	+									
		Rough								+	+			
		Smooth	+											
		Stellate-glochidate												

ATLAS PLATE 4

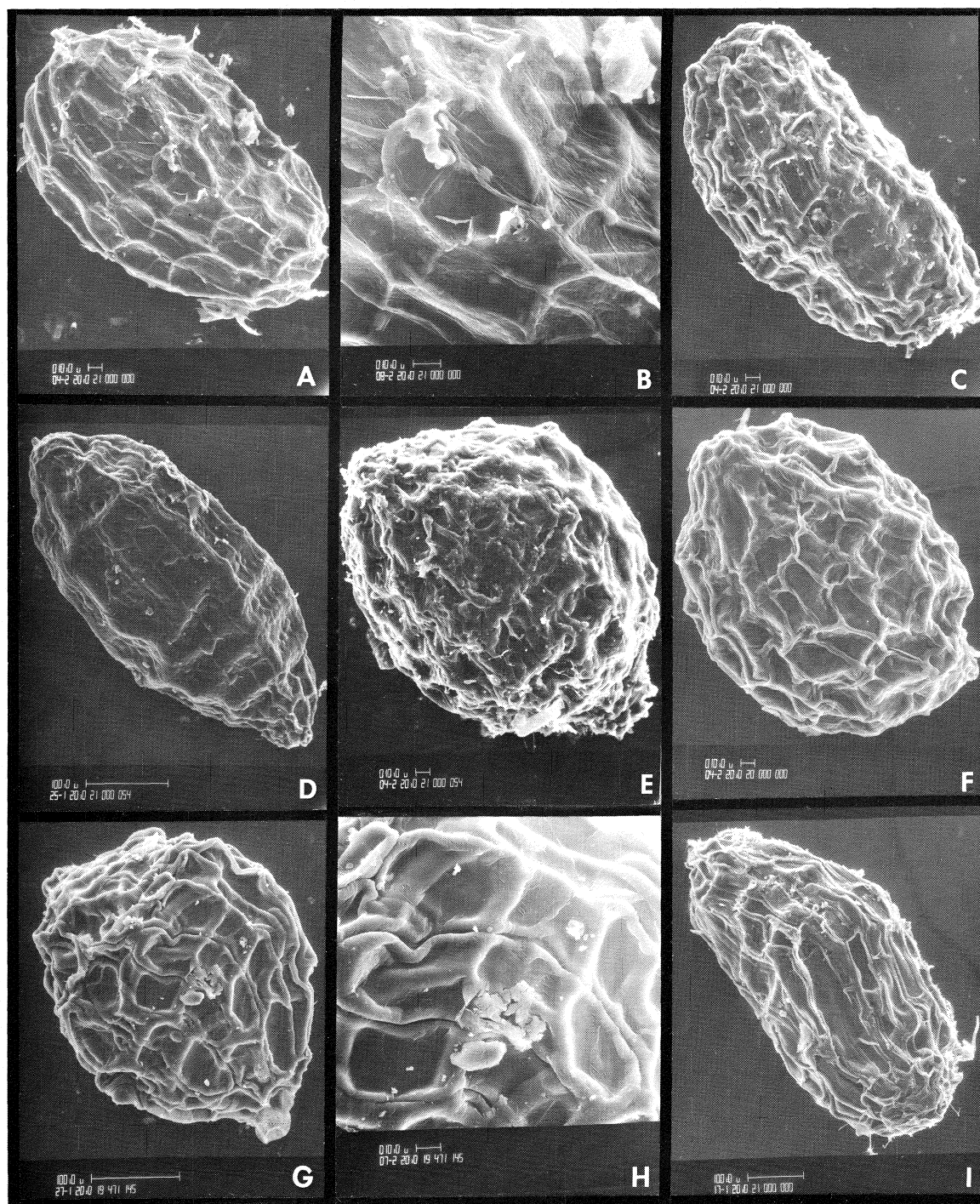


ATLAS PLATE 5

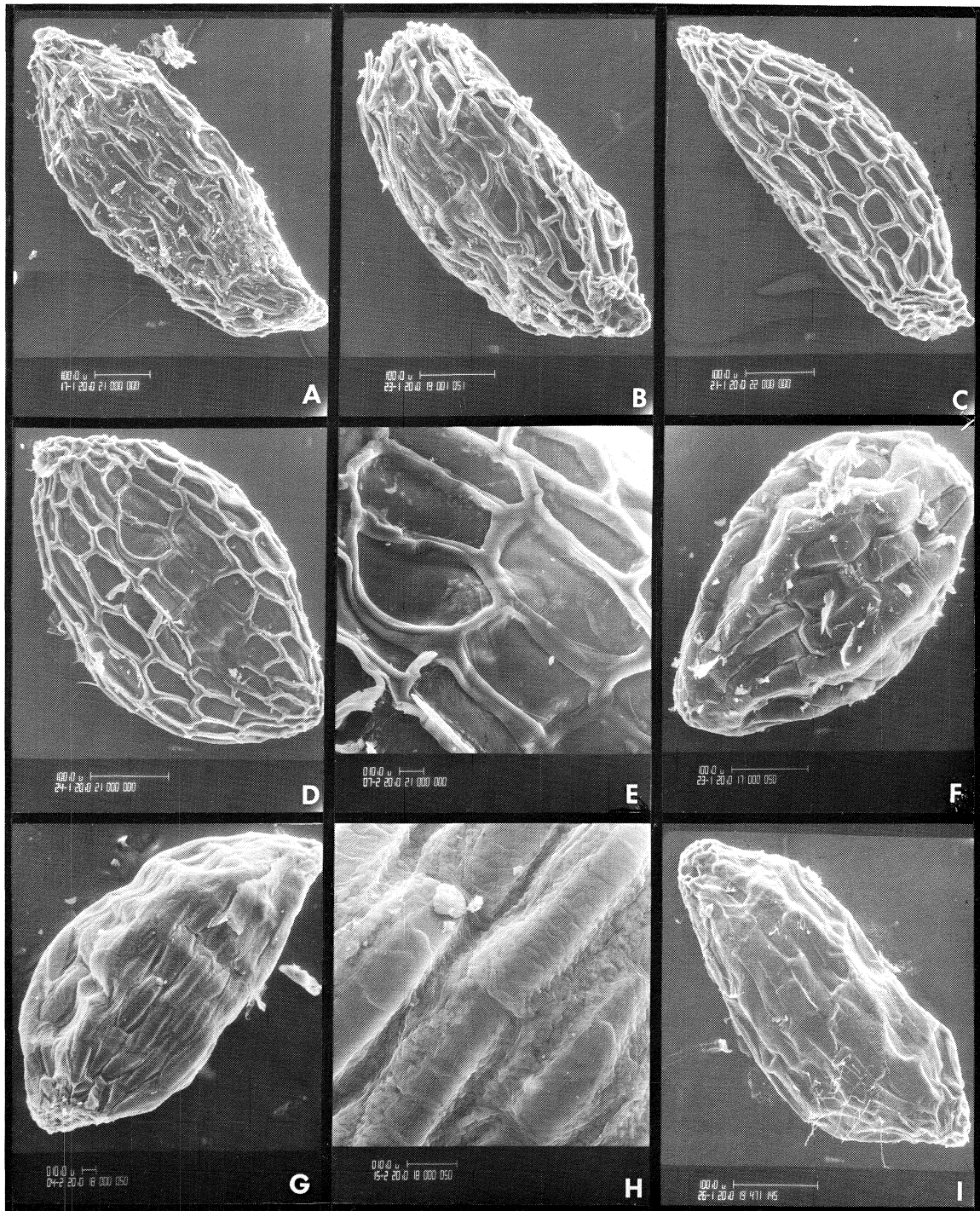


[illegible]

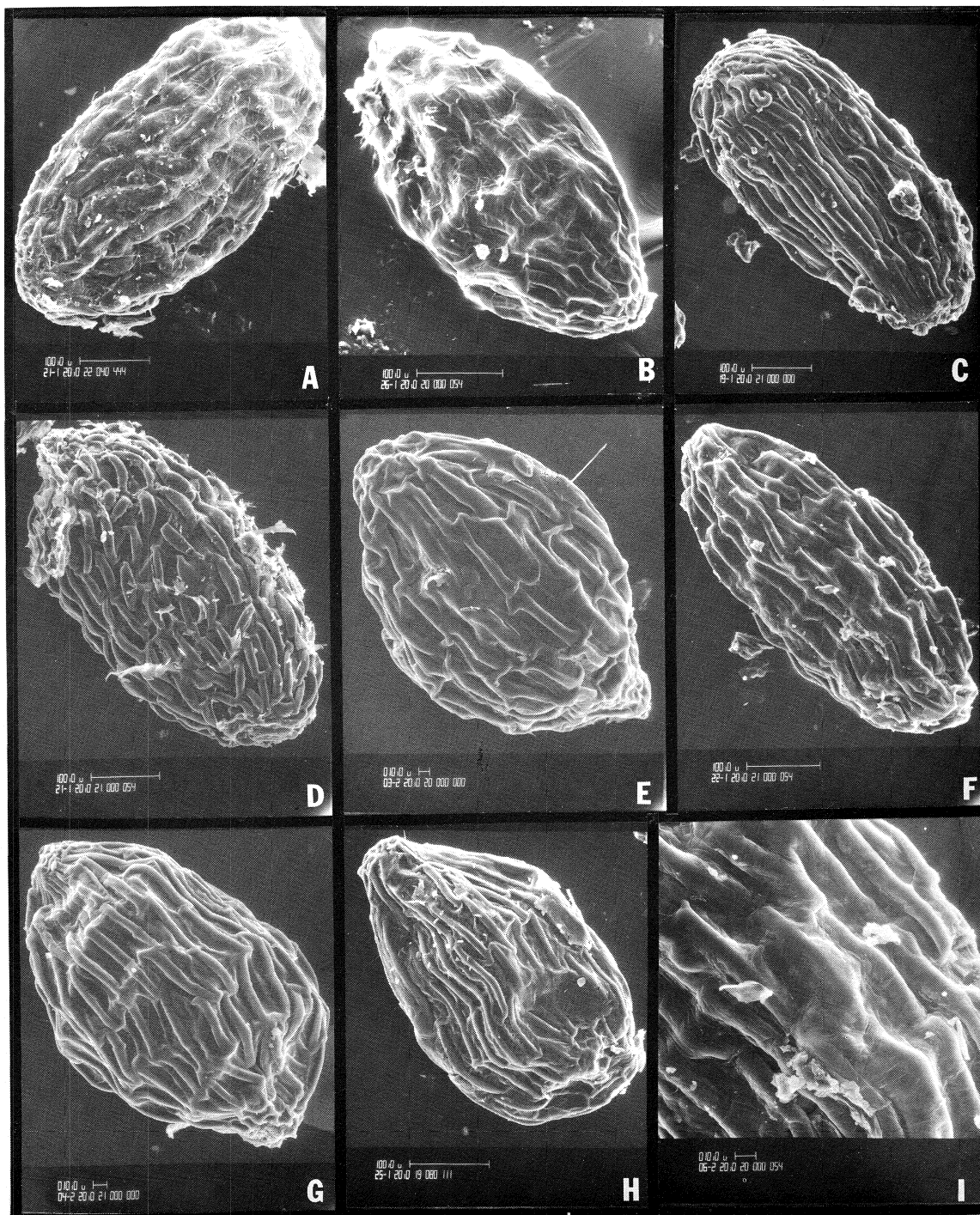
ATLAS PLATE 6



ATLAS PLATE 7

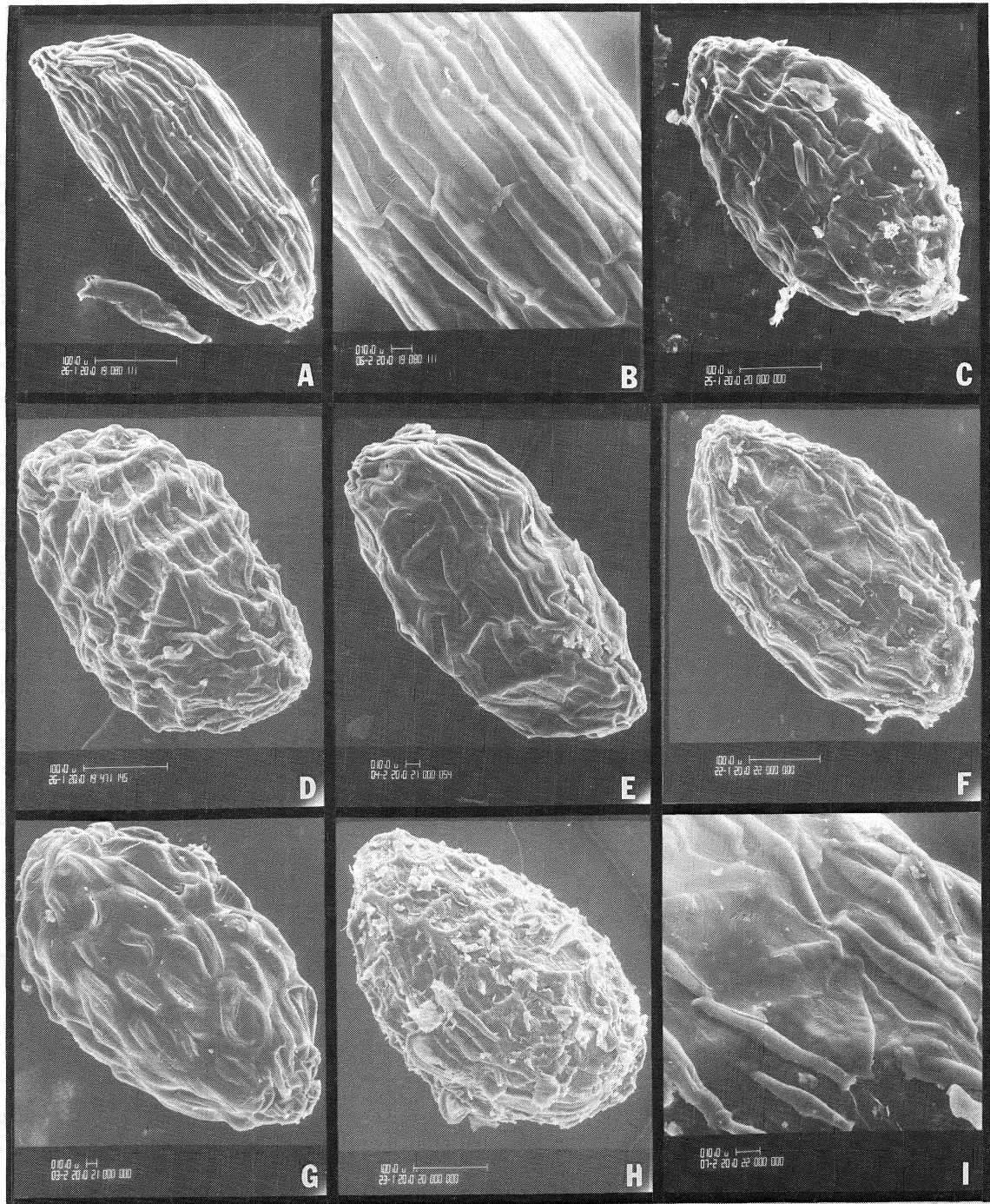


ATLAS PLATE 8



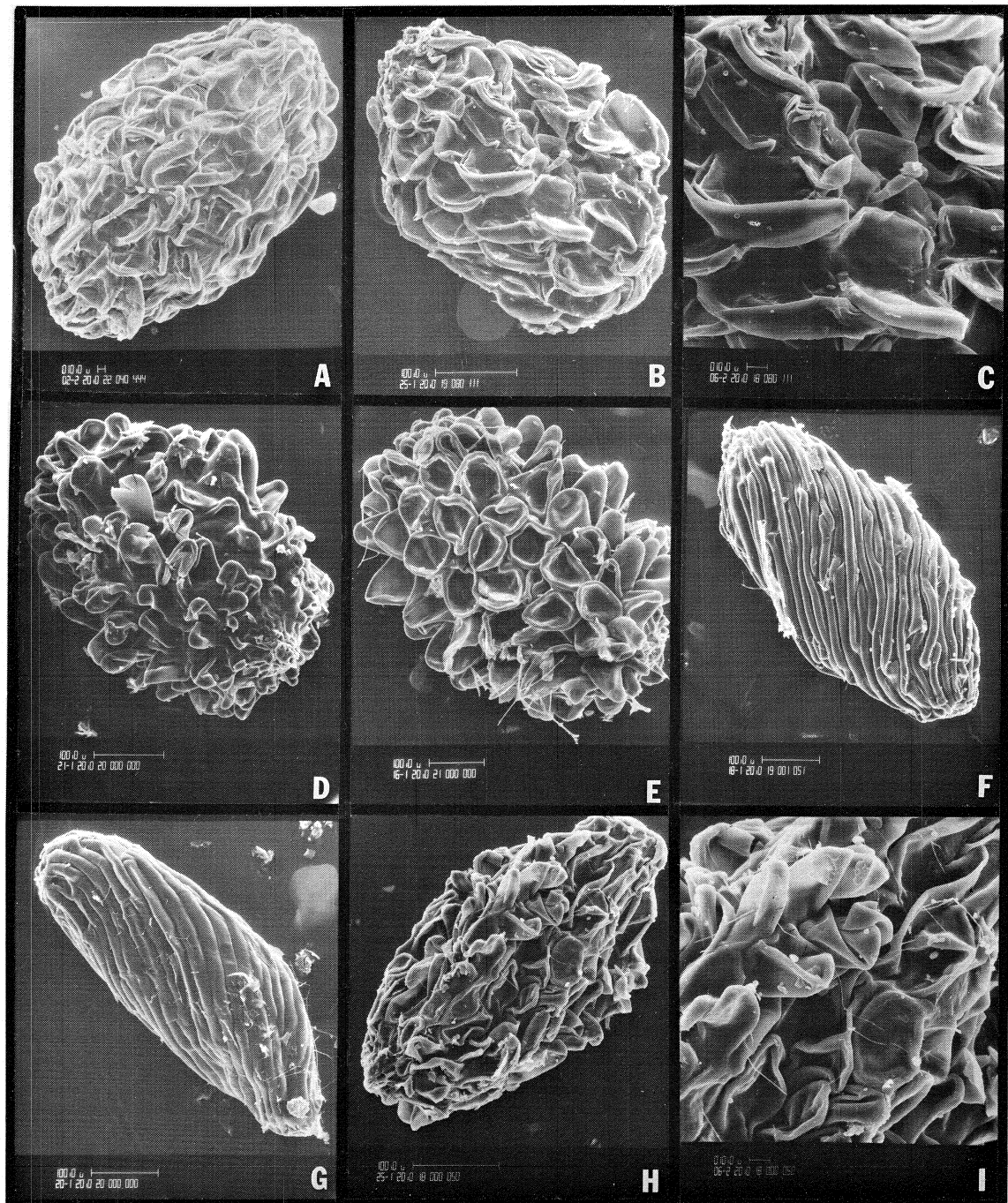
ATLAS TABLE 9			Cyrtandra longifolia Cyrtandra victoriae Cyrtandra reticulata Cyrtandra longifolia Cyrtandra parviflora Cyrtandra longifolia Cyrtandra tempestii Cyrtandra compressa Cyrtandra compressa Cyrtandra compressa										
			A	B	C	D	E	F	G	H	I		
Seed Shapes		Narrowly-elliptic	3:1	CU								CU	
		Elliptic			5:3	5:3	2:1	5:3	5:3	2:1			
		Broadly-elliptic											
		Circular											
		Orbiculate											
		Reniform											
Apical Characters		Carinatus(C), Alatus(A)											
		Irregular											
		Acute	++		++								
		Arillate											
		Constrictate											
		Coronate											
		Filiform											
		Obtuse				++	++	++	++	++			
Cell Orientation		Reniform											
		Truncate(T),Premorse(P)											
		Irregular											
		Straight	+		+	+		+	+				
Cell Shapes		Slightly-spiral											
		Spiral											
		Irregular								+			
		N-lineate-polygonate											
		Lineate-polygonate	+										
Primary Cell Characters		Polygonate			+	+							
		Lobed(L), Parted(P)											
		Irregular					+	+	+	+			
		Edges	Elevated	+		+	+						
		" "	Depressed										
		" "	Irregular				+	+	+	+			
		Crests	Discrete			+	+						
		" "	Fused	+									
		" "	Composite					+	+	+			
		Face	Elevated										
Secondary Cell Characters	Edge Characters	Depressed	+		+	+							
		Foveate											
		Papillate											
		Auriculate			+				+	+			
		Undulate											
		Verrucate											
		Striate											
		Rough								+			
	Face Characters	Smooth	+		+	+	+	+	+				
		Face not visible											
		Level											
		Tholiform											
		Colliculate											
		Papillate											
		Tuberculate											
		Auriculate											
		Ocellate											
		Tetragonate											
		Verrucate											
		Striate	+			+							
Rough			+					+					
Smooth	+			+	+	+	+						
Stellate-glochidate													

ATLAS PLATE 9



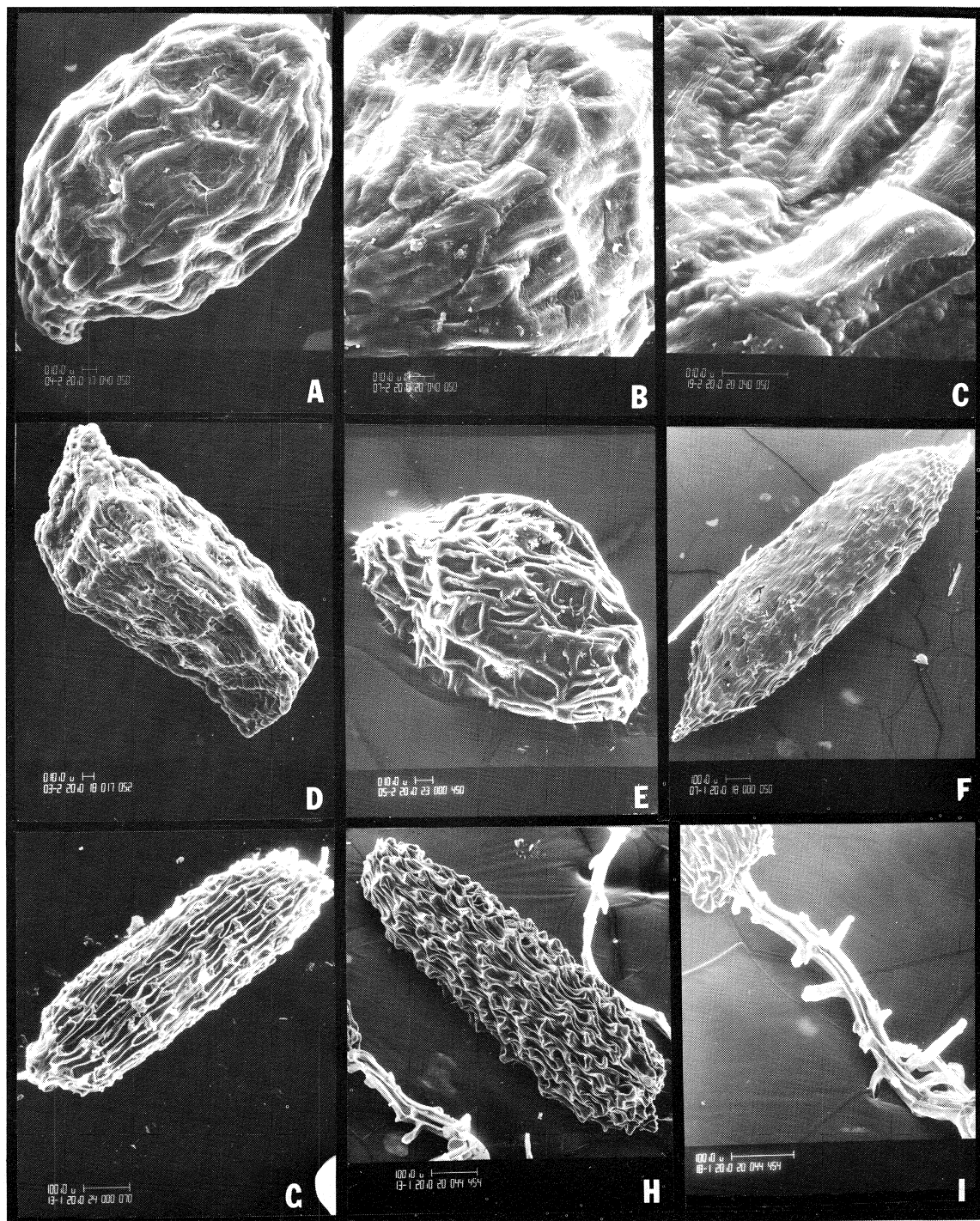
ATLAS TABLE 10			Cyrtandra trichophylla	Cyrtandra anthropophagorum	Cyrtandra taviunensis	Cyrtandra montana	Cyrtandra flabelligera	Hexatheca sandei	Hexatheca fulva	Cyrtandra fulva						
			A	B	C	D	E	F	G	H	I					
Seed Shapes		Narrowly-elliptic			CU					3:1		CU				
		Elliptic	5:3	3:2		2:1		4:3		2:1						
		Broadly-elliptic					6:5									
		Circular														
		Orbiculate														
		Reniform														
		Carinatus(C), Alatus(A)														
Apical Characters		Irregular														
		Acute						+	+							
		Arillate														
		Constrictate														
		Coronate														
		Filiform														
		Obtuse	++	++		++	++	+	+	++						
Cell Orientation		Reniform														
		Truncate(T), Premorse(P)														
		Irregular														
		Straight	+	+		+	+				+					
Cell Shapes		Slightly-spiral														
		Spiral						+	+							
		Irregular														
		N-lineate-polygonate						+	+							
		Lineate-polygonate														
Primary Cell Characters	Edges	Polygonate				+	+				+					
		Lobed(L), Parted(P)														
		Irregular	+	+												
	Crests	Elevated	+	+				+	+	+	+	+				
		Depressed				+	+									
		Irregular	+	+												
		Discrete														
Face	Fused	+	+		+	+	+	+	+	+						
	Composite															
Secondary Cell Characters	Edge Characters	Elevated				+	+									
		Depressed	+	+				+	+	+	+					
		Foveate														
		Papillate														
		Auriculate	+	+		+	+				+					
		Undulate														
		Verrucate														
		Striate														
	Face Characters	Rough														
		Smooth							+	+						
		Face not visible							+	+						
		Level														
		Tholiform														
		Colliculate														
		Papillate														
		Tuberculate				+	+									
		Auriculate	+	+		+	+				+					
Ocellate																
Tetragonate																
Verrucate																
Striate																
Rough																
Smooth																
Stellate-glochidate																

ATLAS PLATE 10

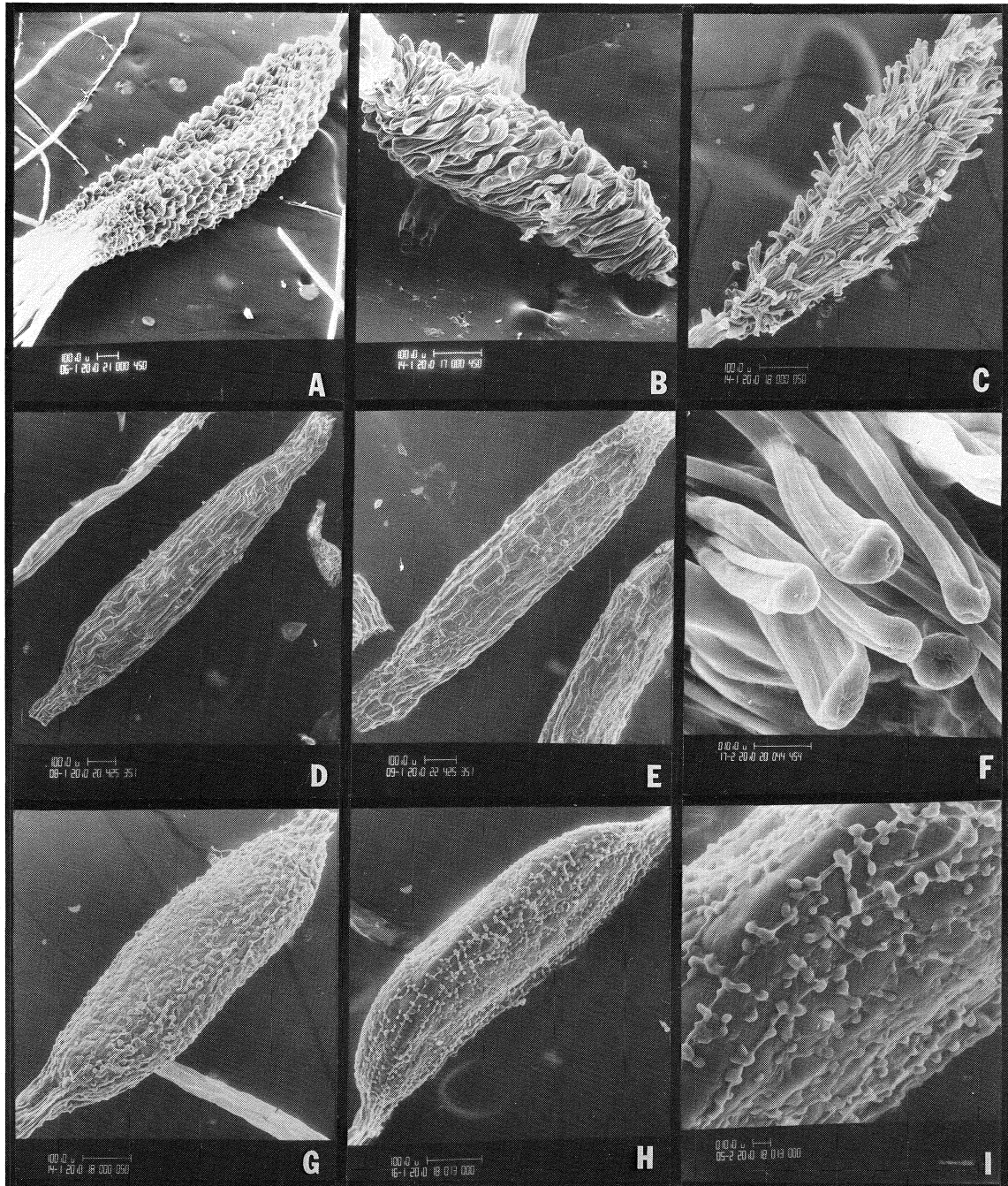


[illegible]

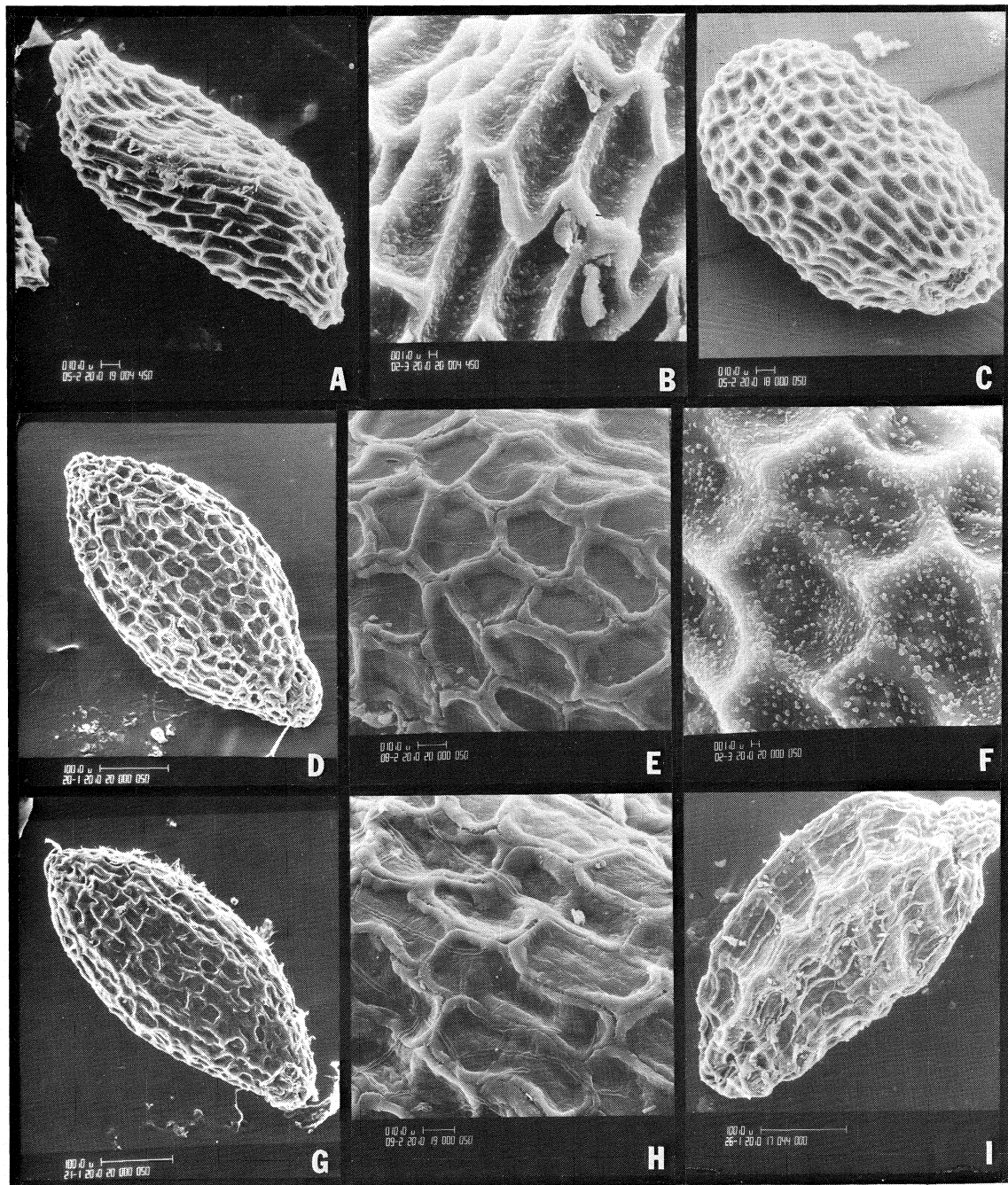
ATLAS PLATE 11



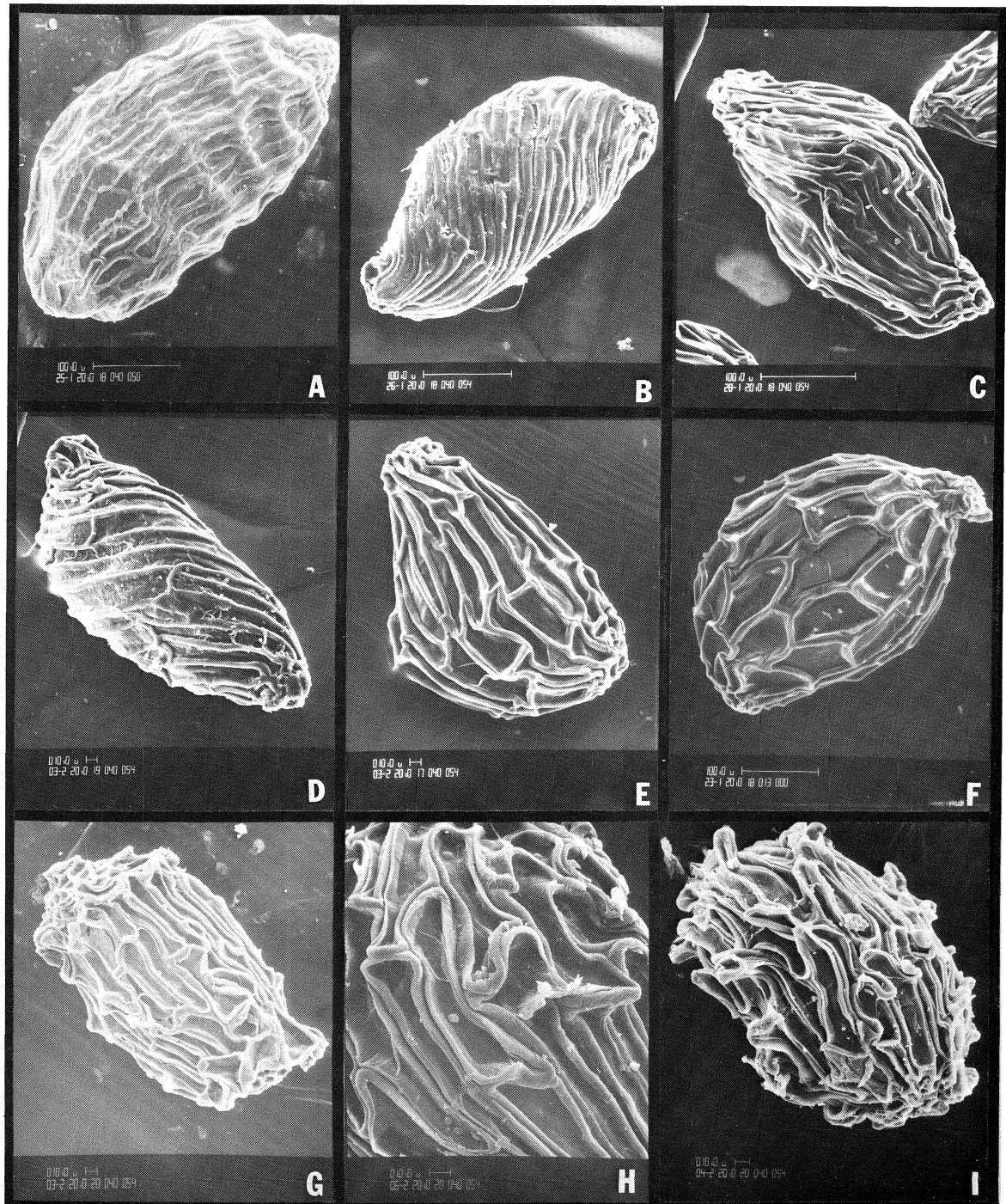
ATLAS PLATE 12



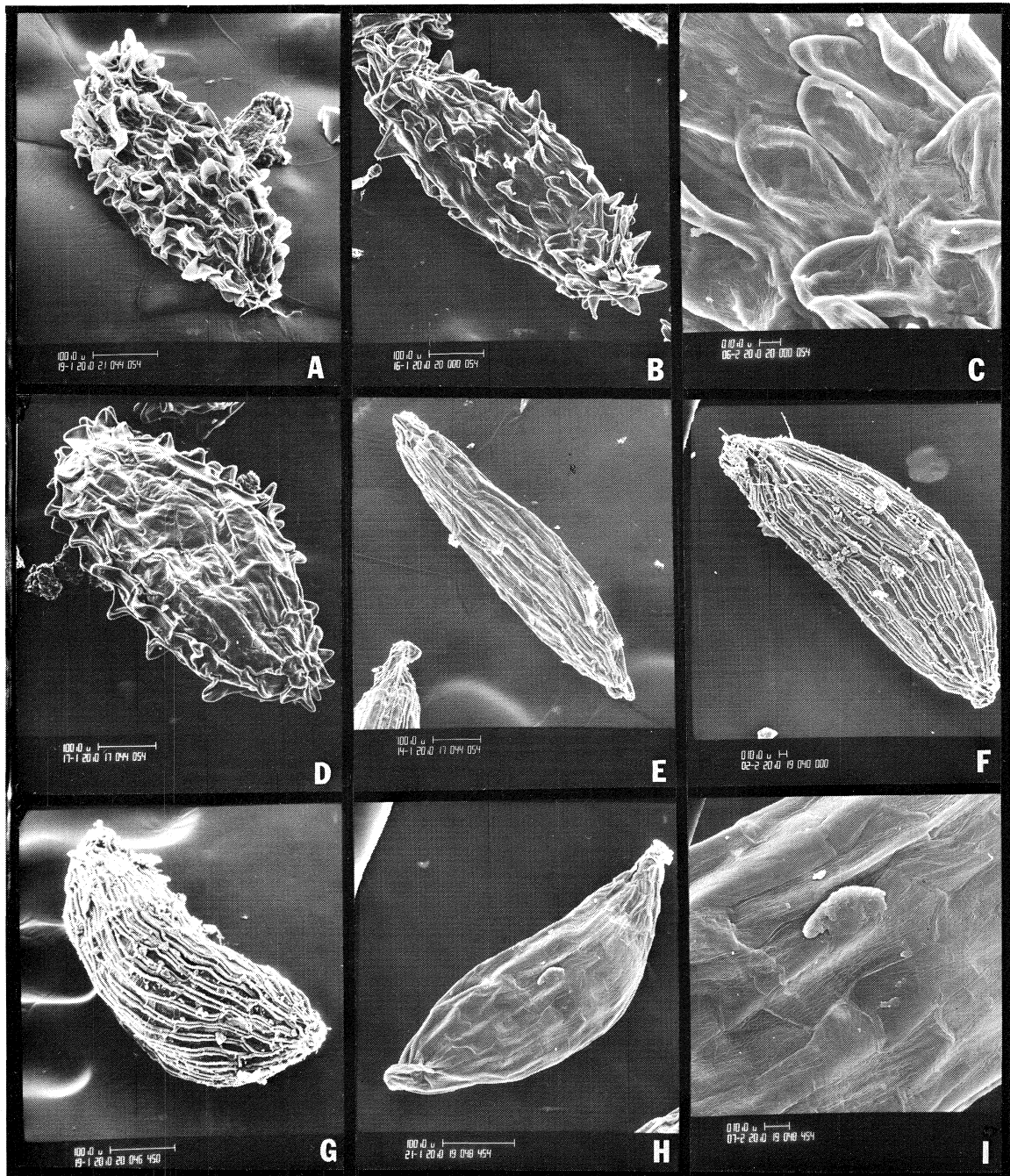
ATLAS PLATE 13



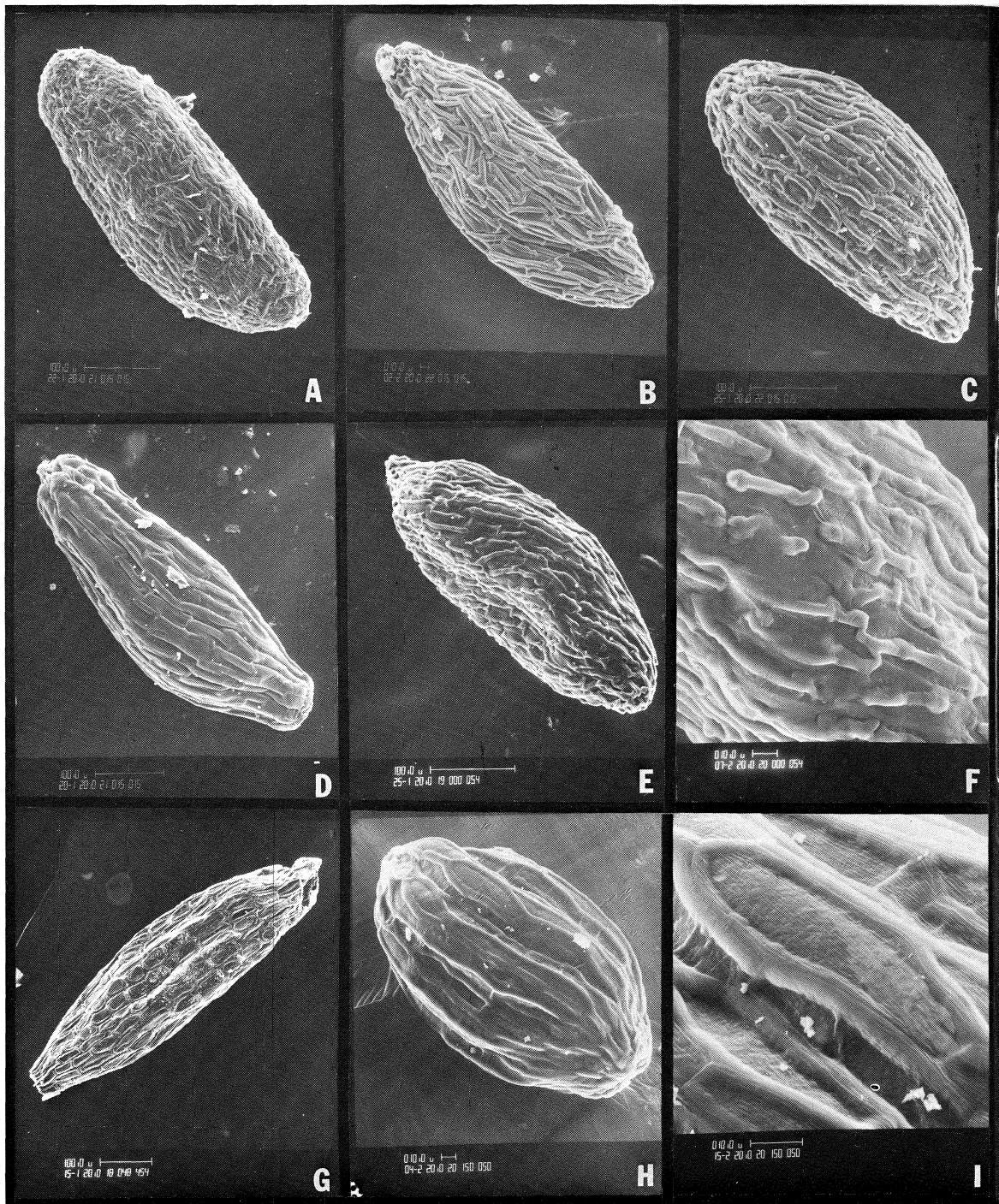
ATLAS PLATE 14



ATLAS PLATE 15

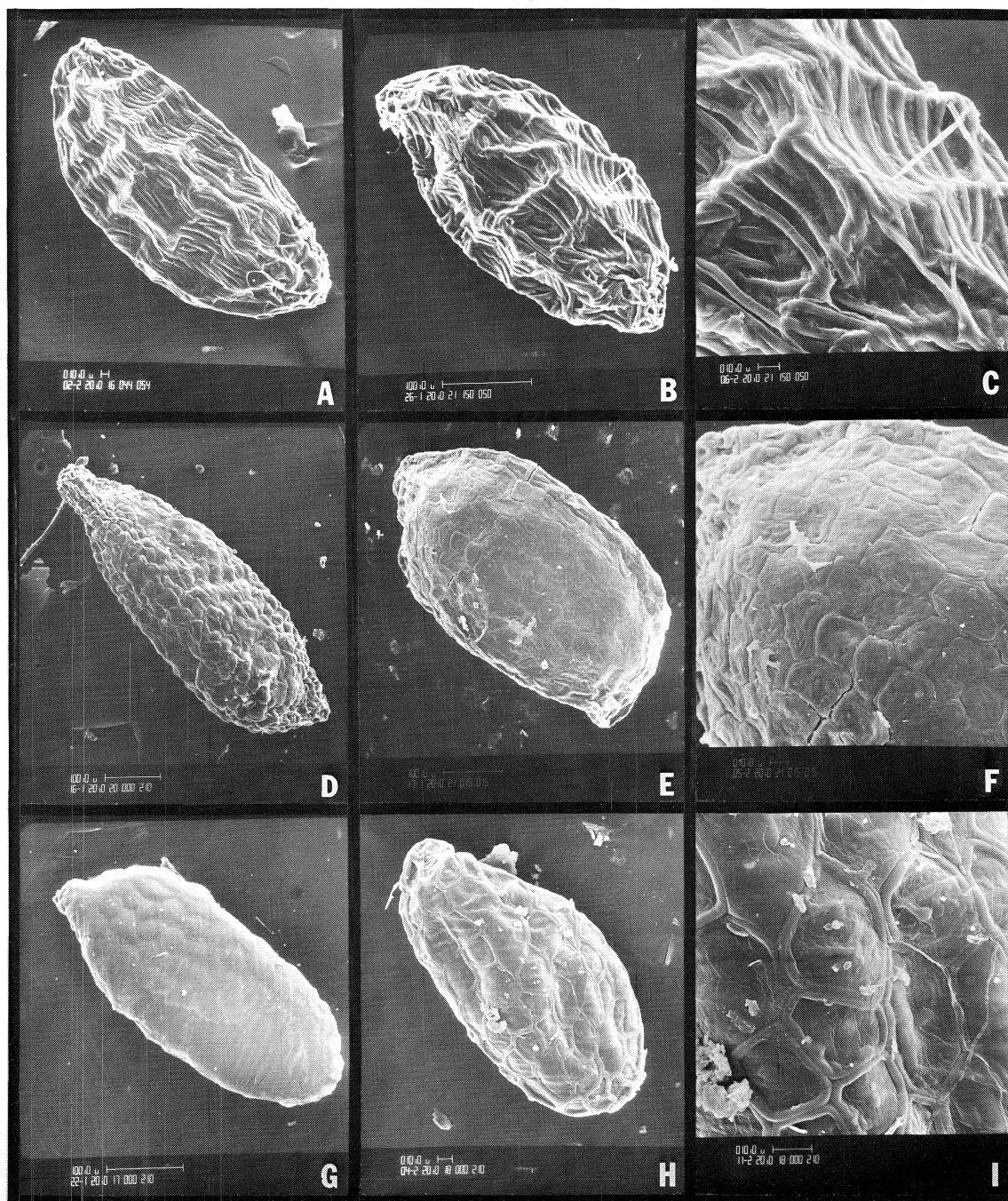


ATLAS PLATE 16



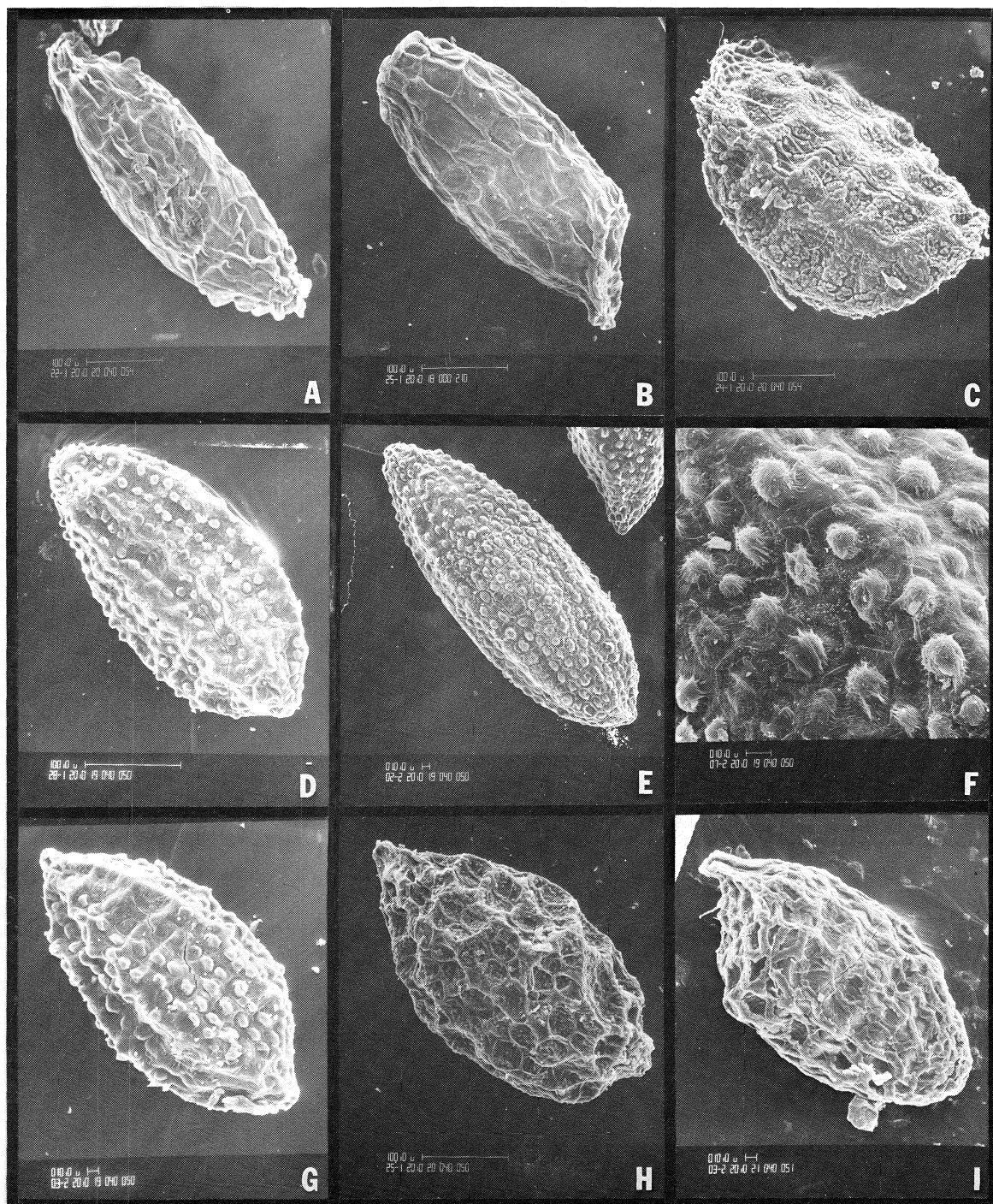
ATLAS TABLE 17			Didymocarpus cinerea Didymocarpus subalternans Didymocarpus primuloides Opithandra primuloides Opithandra dealbiatus Petrocodon forrestii Tremacron forrestii Tremacron forrestii Oreocharis forrestii										A	B	C	D	E	F	G	H	I
Seed Shapes		Narrowly-elliptic			CU	3:1		CU						CU							
		Elliptic	2:1	2:1				2:1		2:1	2:1										
		Broadly-elliptic																			
		Circular																			
		Orbiculate																			
		Reniform																			
		Carinatus(C), Alatus(A)						C													
Apical Characters		Irregular																			
		Acute				+	+														
		Arillate																			
		Constrictate		+		+			+	+											
		Coronate																			
		Filiform																			
		Obtuse	++	+			+		+	+											
Cell Orientation		Reniform																			
		Truncate(T), Premorse(P)																			
		Irregular																			
		Straight	+	+		+	+		+	+											
Cell Shapes		Slightly-spiral																			
		Spiral																			
		Irregular																			
		N-lineate-polygonate																			
		Lineate-polygonate	+	+																	
Primary Cell Characters		Polygonate				+	+			+	+										
		Lobed(L), Parted(P)																			
		Irregular																			
		Edges	Elevated	+	+		+					+									
		"	Depressed					+		+											
		"	Irregular																		
		Face	Crests	Discrete				+	+		+	+									
"	Fused		+	+																	
"	Composite																				
"	Elevated						+		+												
Secondary Cell Characters	Edge Characters	Depressed	+	+		+					+										
		Foveate																			
		Papillate																			
		Auriculate																			
		Undulate																			
		Verrucate																			
		Striate																			
		Rough																			
		Smooth	+	+		+	+		+	+											
	Face Characters	Face not visible																			
		Level					+		+		+										
		Tholiform					+														
		Colliculate																			
		Papillate																			
		Tuberculate																			
		Auriculate																			
		Ocellate																			
		Tetragonate																			
		Verrucate		+																	
		Striate																			
		Rough					+	+		+	+										
		Smooth	+																		
		Stellate-glochidate																			

ATLAS PLATE 17



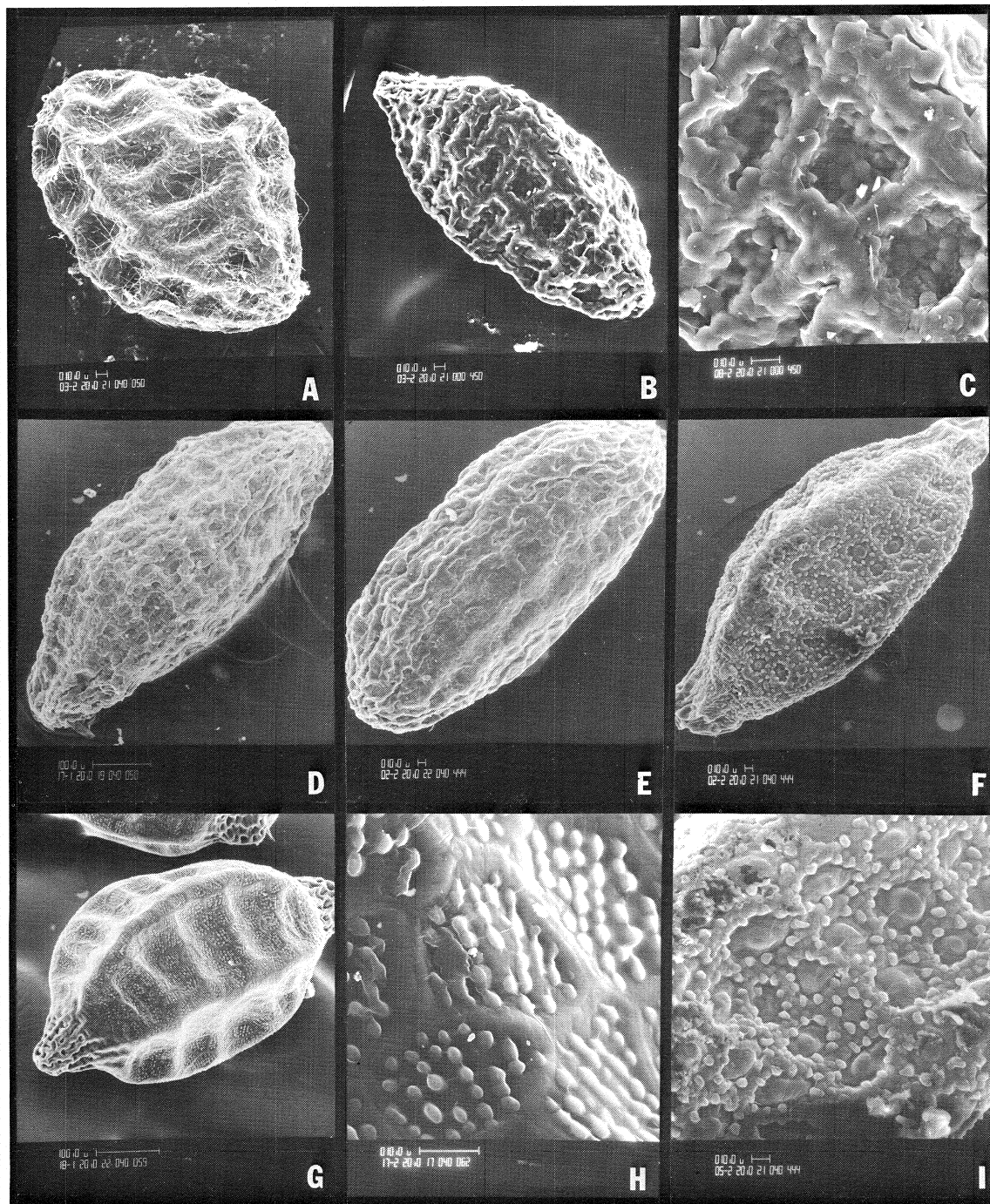
[illegible]

ATLAS PLATE 18

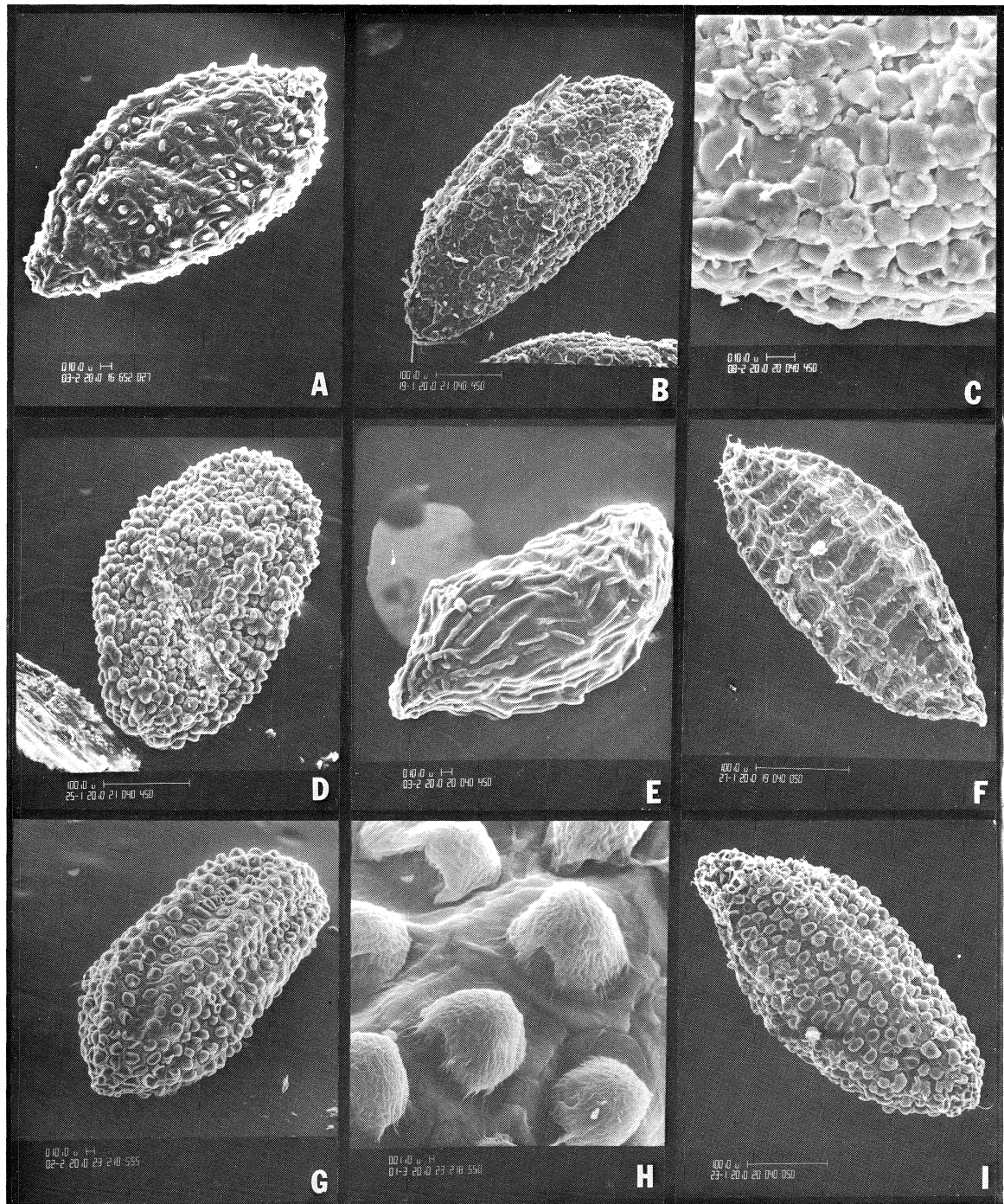


ATLAS TABLE 19			Hemiboea elongata		Chirita sinensis		Chirita hamosa		Chirita lavandulacea		Chirita hamosa		Chirita lavandulacea		Didissandra johorica		Didissandra elongata		Didissandra johorica	
			A	B	C	D	E	F	G	H	I	A	B	C	D	E	F	G	H	I
Seed Shapes		Narrowly-elliptic			CU	3:1		3:1		CU	CU									
		Elliptic		2:1				2:1		2:1										
		Broadly-elliptic	5:1																	
		Circular																		
		Orbiculate																		
		Reniform																		
		Carinatus(C), Alatus(A)																		
Apical Characters		Irregular																		
		Acute		+				+												
		Arillate																		
		Constrictate		+		+		++	++											
		Coronate																		
		Filiform																		
		Obtuse	++			+	+													
Cell Orientation		Reniform																		
		Truncate(T),Premorse(P)																		
		Irregular																		
		Straight	+	+		+	+	+	+											
Cell Shapes		Slightly-spiral																		
		Spiral																		
		Irregular																		
		N-lineate-polygonate																		
		Lineate-polygonate																		
Primary Cell Characters		Polygonate	+	+		+	+	+	+											
		Lobed(L), Parted(P)																		
		Irregular																		
		Edges	Elevated	+	+		+	+	+	+										
		"	Depressed																	
		"	Irregular																	
		Crests	Discrete																	
Face		Fused	+	+		+	+	+	+											
		Composite																		
		Elevated																		
Secondary Cell Characters	Edge Characters	Depressed	+	+		+	+	+	+											
		Foveate																		
		Papillate		+				+												
		Auriculate																		
		Undulate																		
		Verrucate	+			+	+													
		Striate																		
		Rough																		
	Smooth																			
	Face Characters	Face not visible																		
		Level																		
		Tholiform																		
		Colliculate																		
		Papillate		+																
		Tuberculate							+											
		Auriculate																		
		Ocellate																		
		Tetragonate																		
		Verrucate	+			+	+													
		Striate																		
Rough																				
Smooth																				
Stellate-glochidate																				

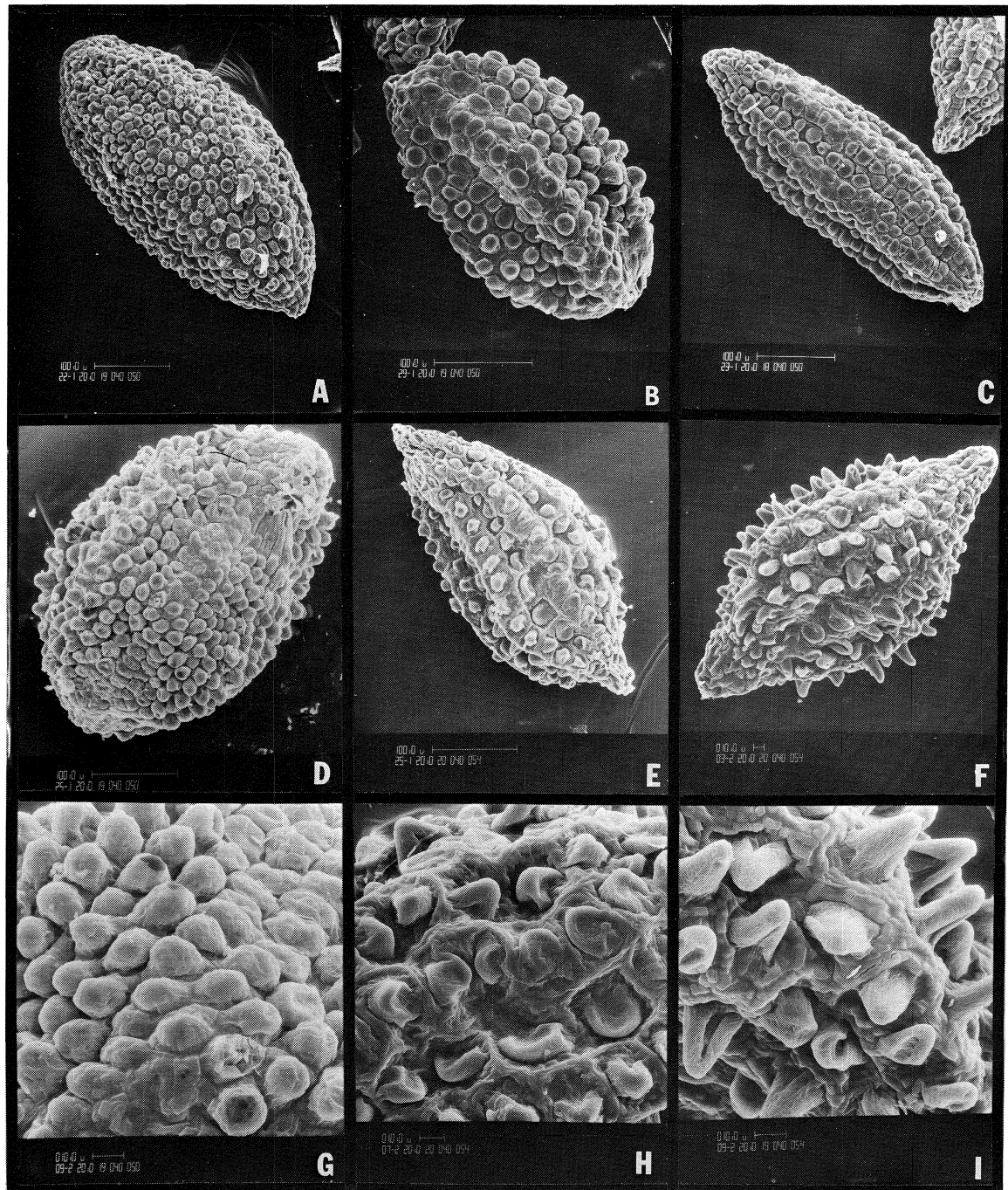
ATLAS PLATE 19



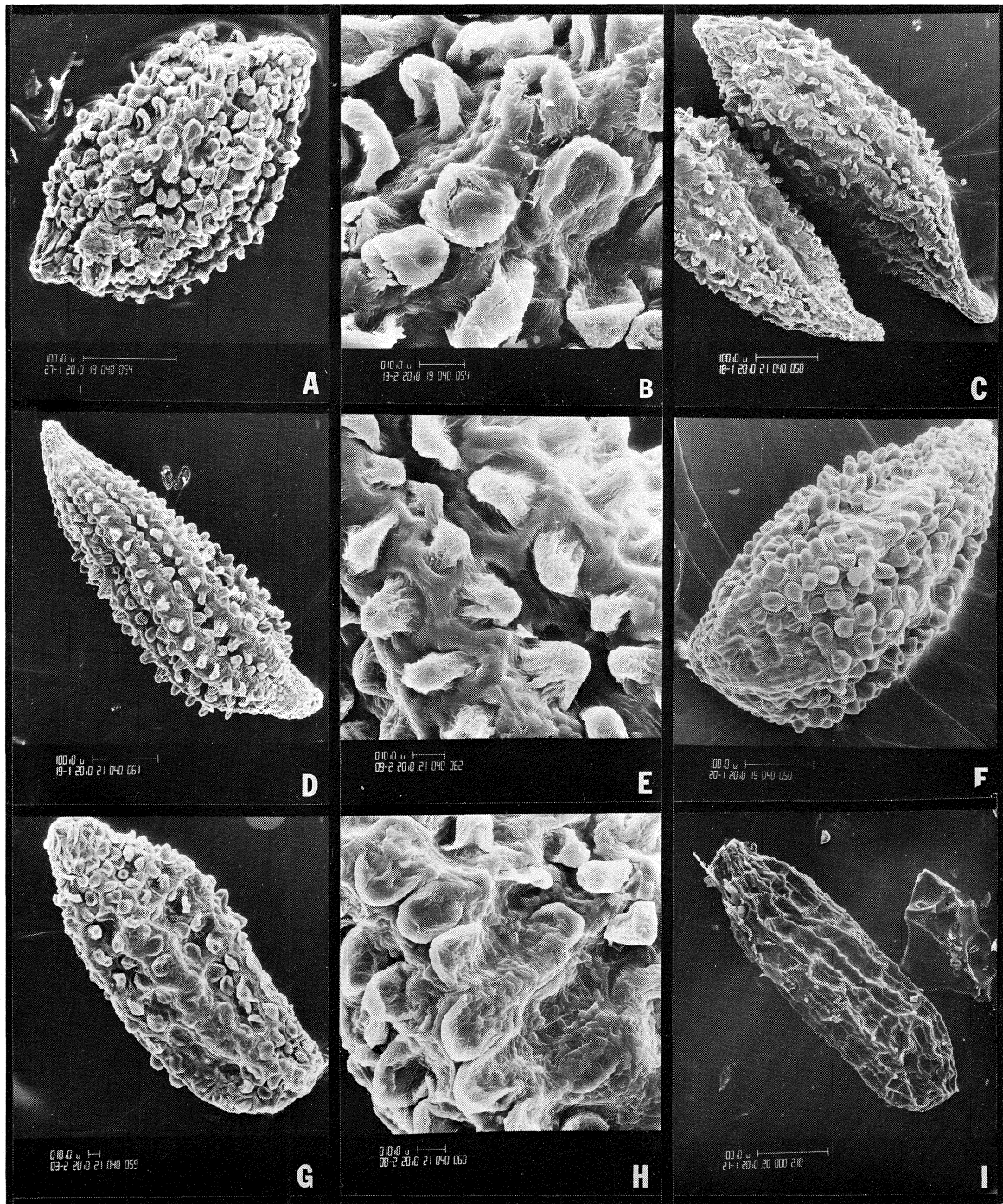
ATLAS PLATE 20



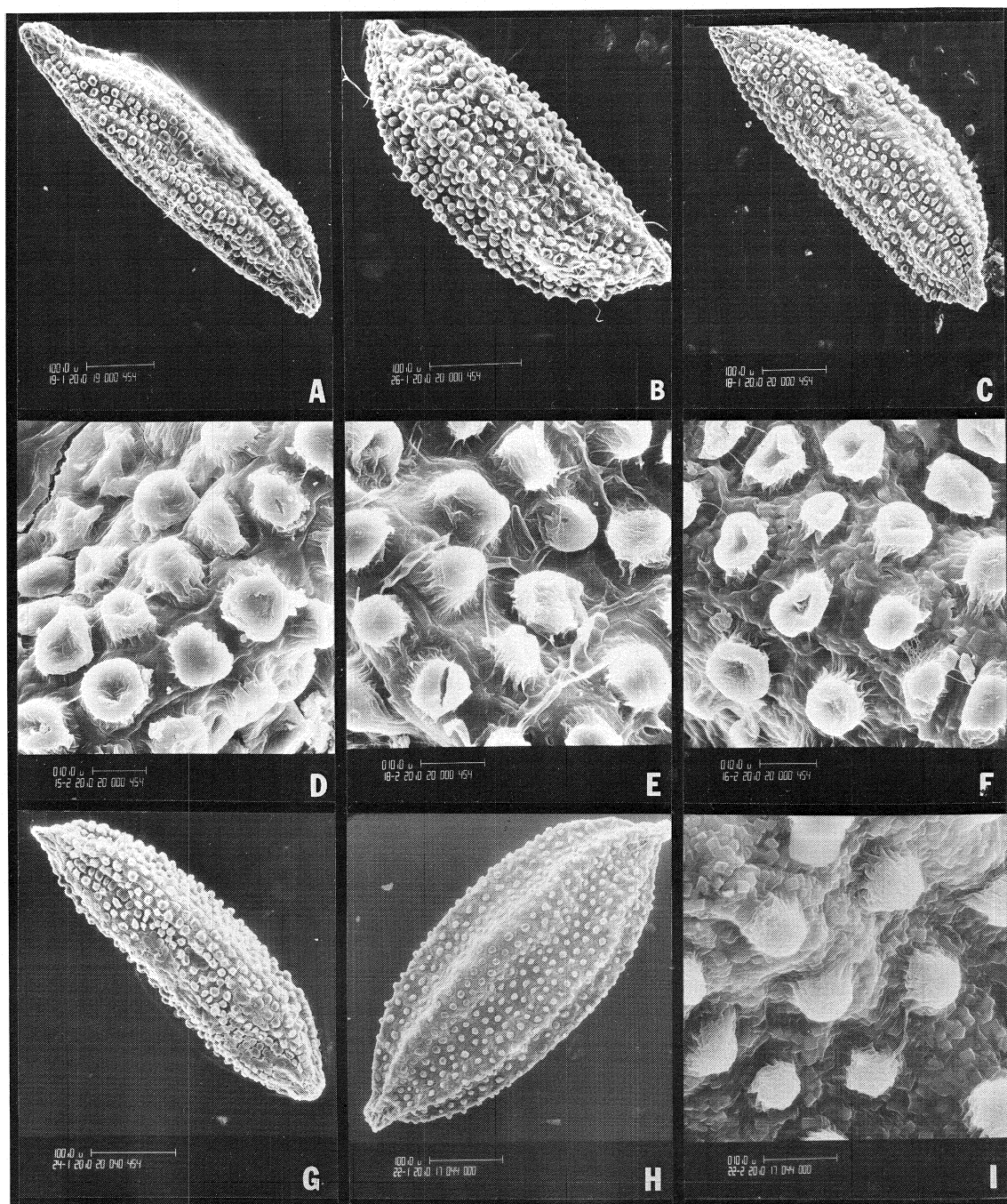
ATLAS PLATE 21



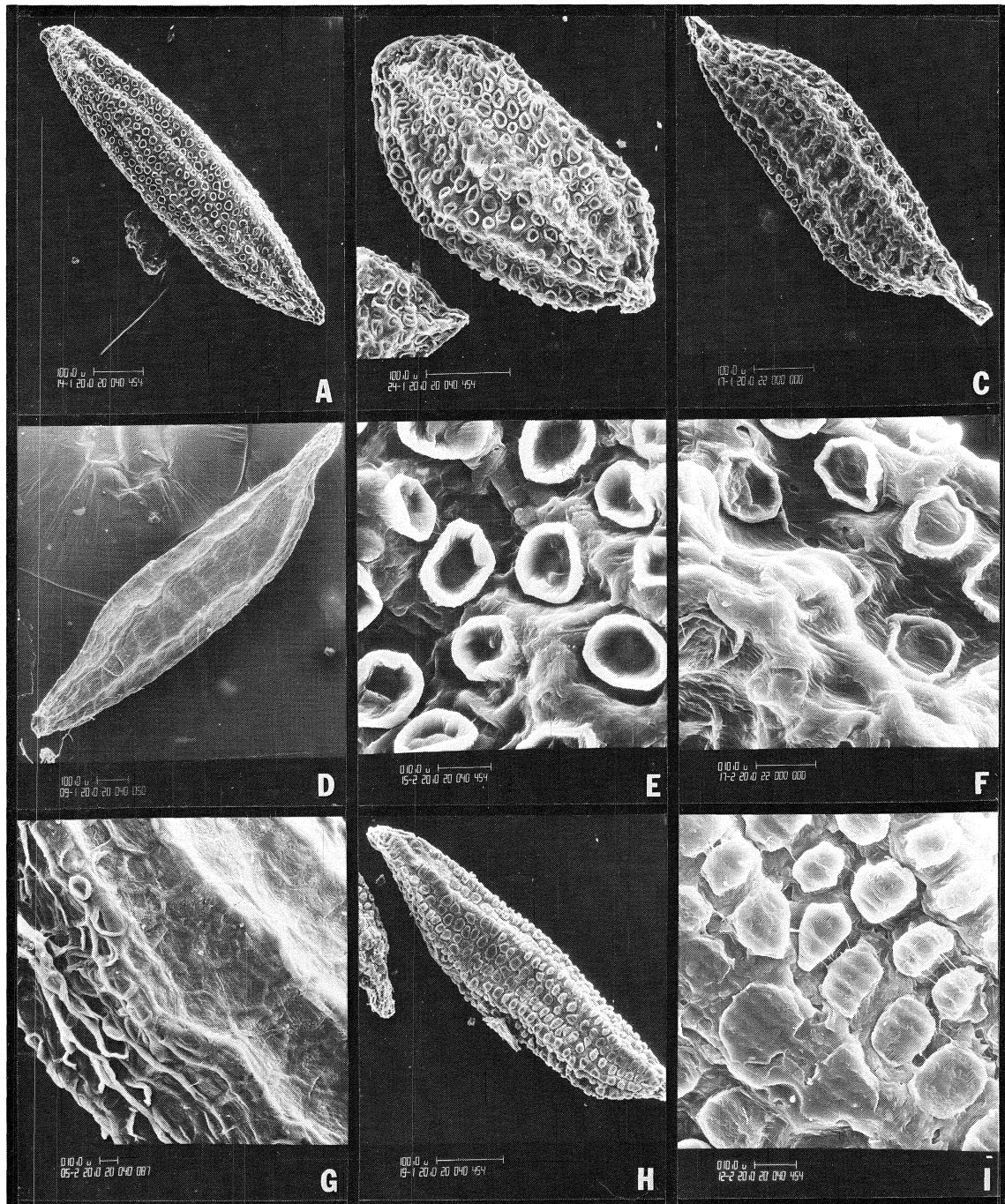
ATLAS PLATE 22



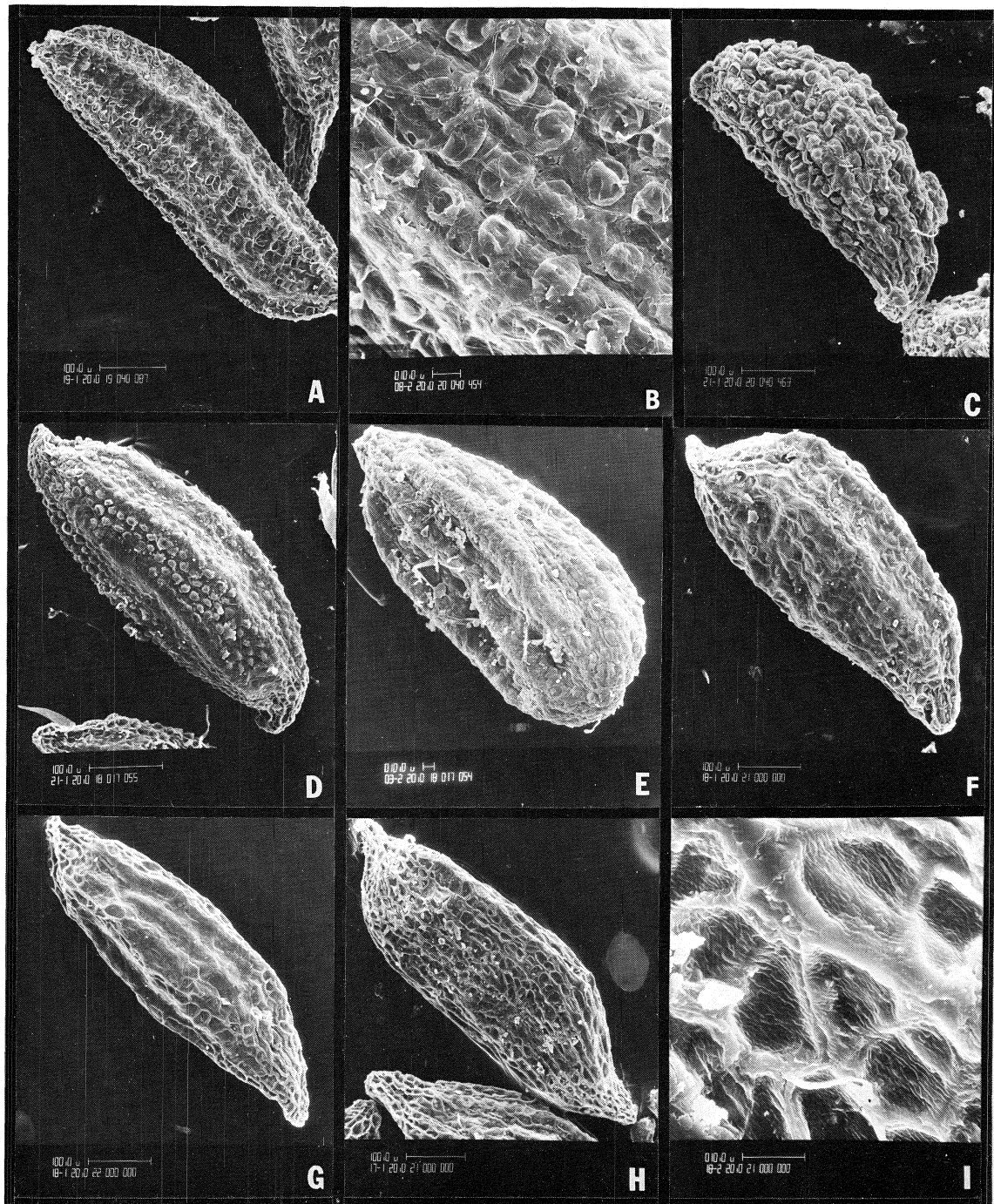
ATLAS PLATE 23



ATLAS PLATE 24

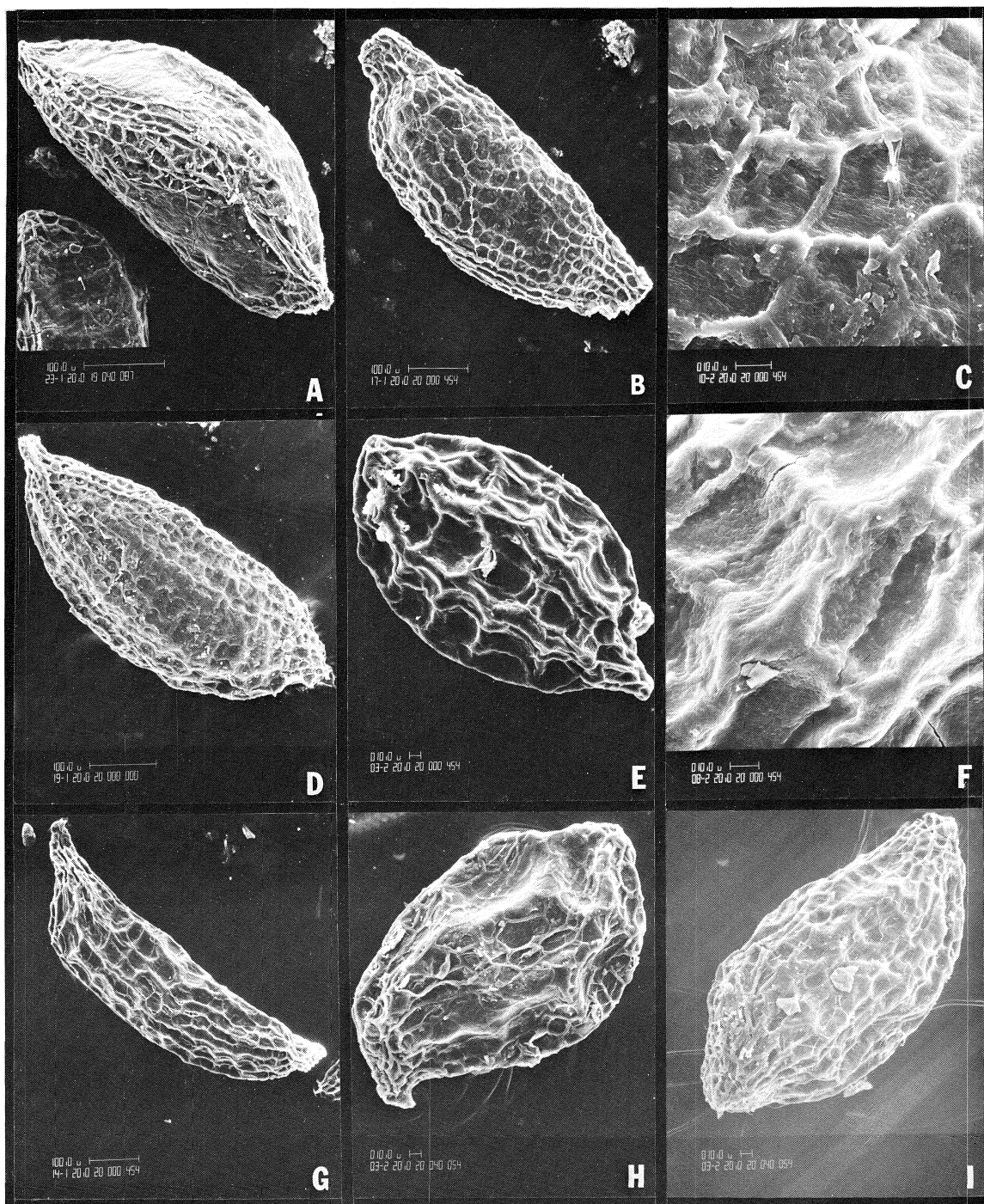


ATLAS PLATE 25

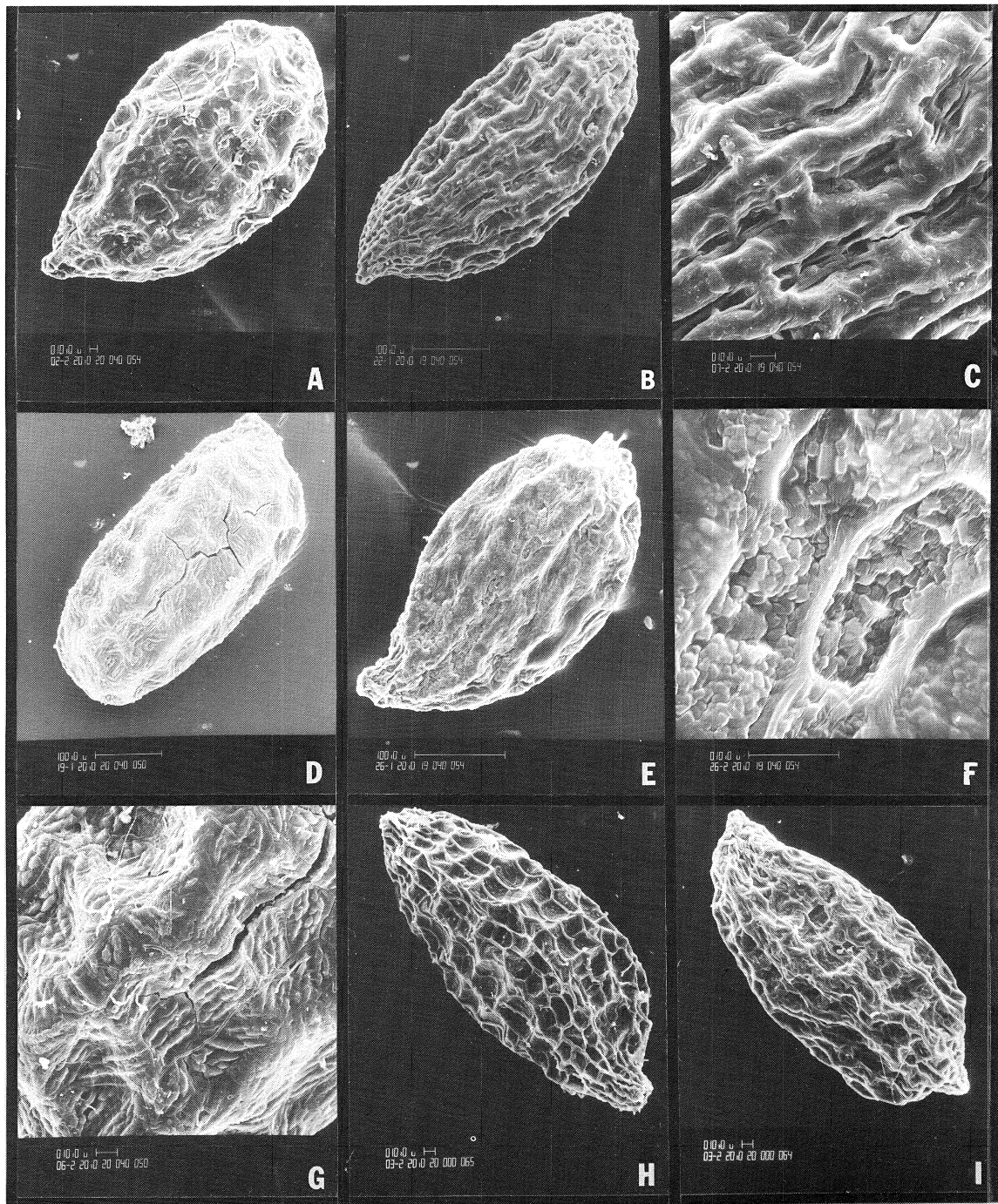


[illegible]

ATLAS PLATE 26

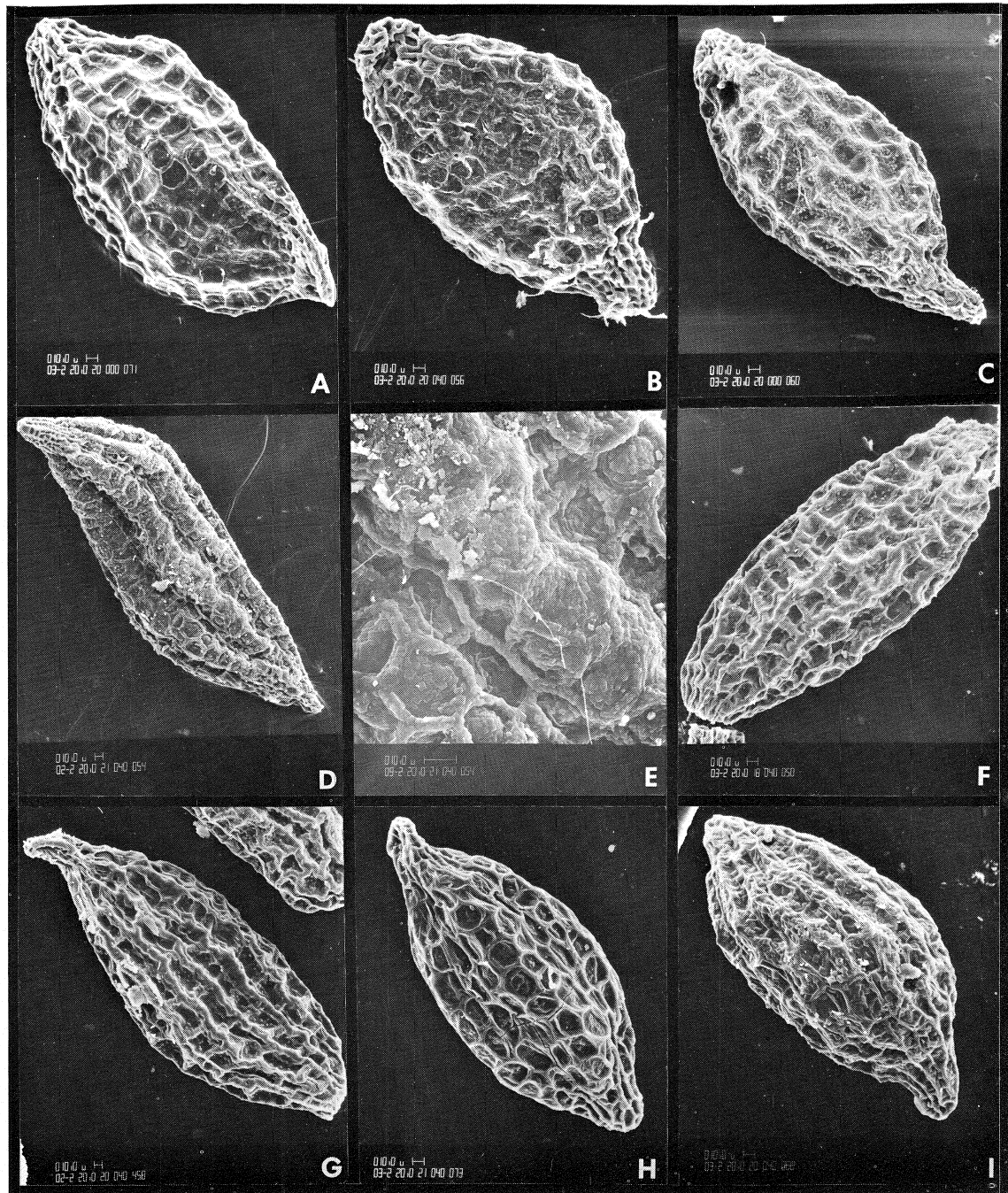


ATLAS PLATE 27

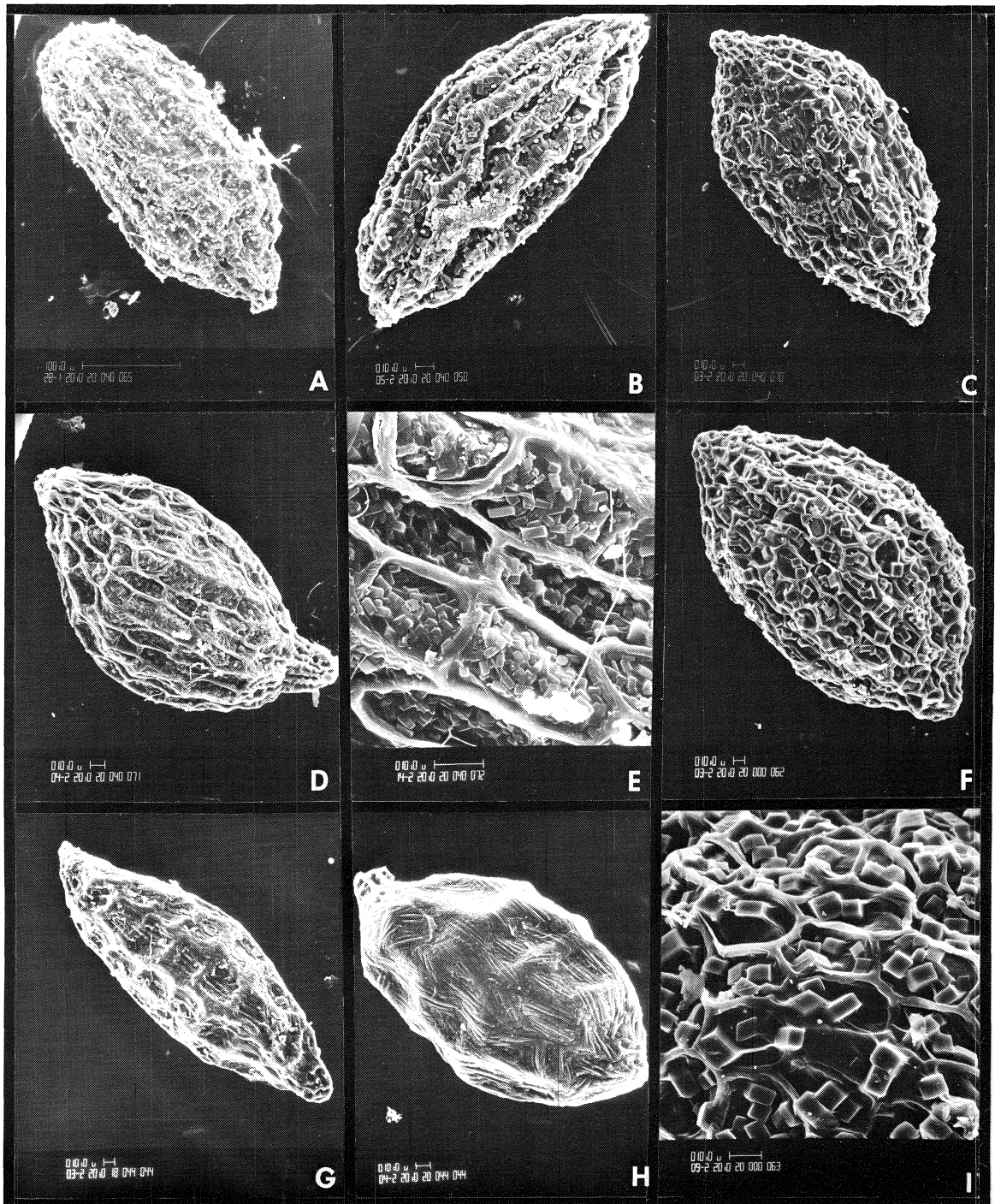


[illegible]

ATLAS PLATE 28

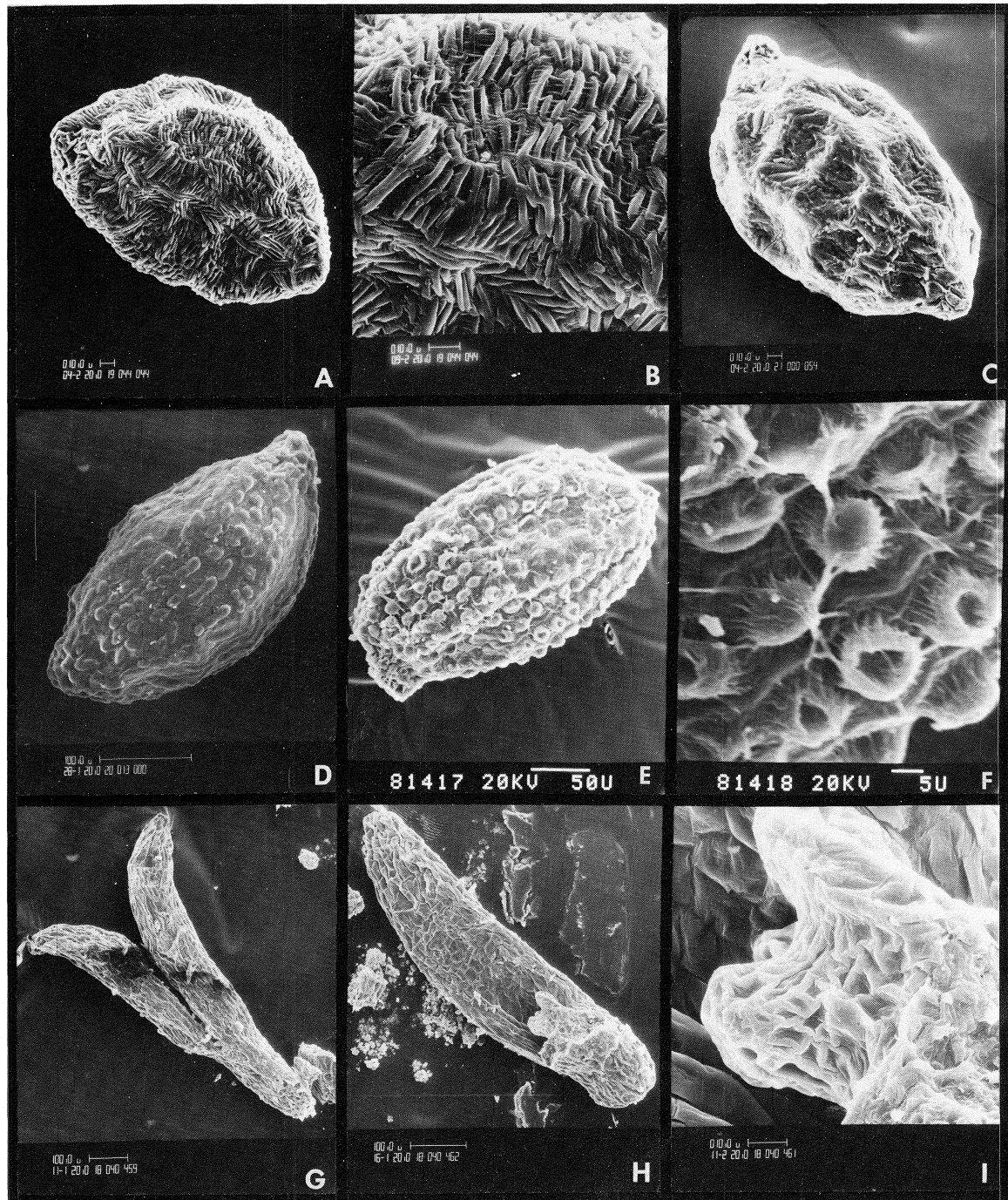


ATLAS PLATE 29

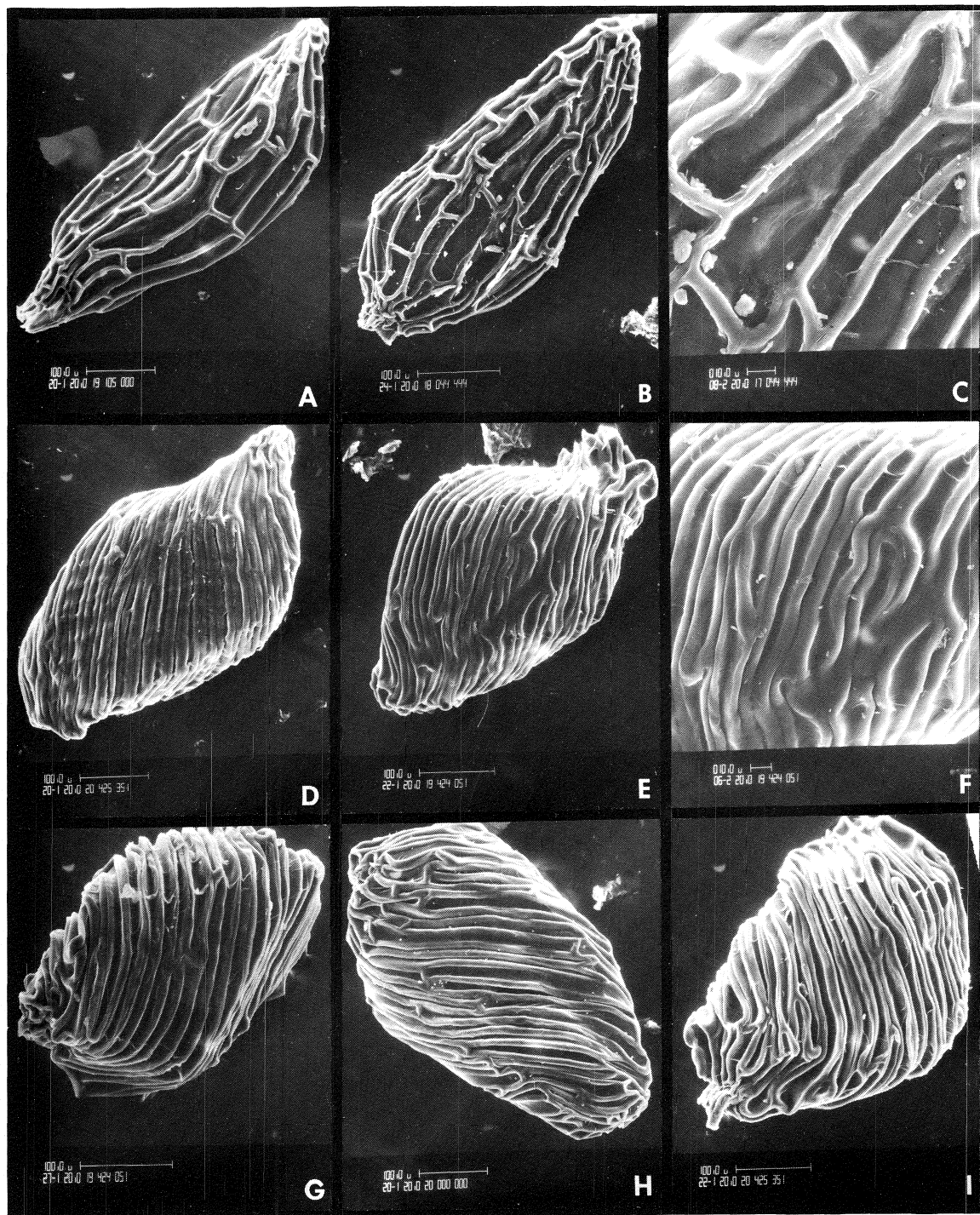


ATLAS TABLE 30			Boeica fulva	Boeica fulva (T)	Boeica hirsuta	Boeica filiformis	Colpogyne betsiensis	Titanotrichum oldhamii	Titanotrichum oldhamii	Titanotrichum oldhamii	Titanotrichum oldhamii	Titanotrichum oldhamii	Titanotrichum oldhamii	Titanotrichum oldhamii	
			A	B	C	D	E	F	G	H	I				
Seed Shapes		Narrowly-elliptic		CU											
		Elliptic	5:3		5:3	2:1	2:1	CU		Propagules only					
		Broadly-elliptic								no seeds					
		Circular								available					
		Orbiculate													
		Reniform													
		Carinatus(C), Alatus(A) Irregular					G	G							
Apical Characters		Acute													
		Arillate													
		Constrictate			+	+	+								
		Coronate													
		Filiform													
		Obtuse	++		+	+	+								
		Reniform													
Cell Orientation		Truncate(T),Premorse(P)						T							
		Irregular													
		Straight	+		+	+	+								
		Slightly-spiral													
Cell Shapes		Spiral													
		Irregular													
		N-lineate-polygonate													
		Lineate-polygonate	+		+	+									
Primary Cell Characters		Polygonate						+							
		Lobed(L), Parted(P)													
		Irregular													
		Edges													
		"													
		"													
Secondary Cell Characters		Depressed	+		+		+								
		Irregular	+		+	+	+								
		Crests													
		"													
		"													
		"													
Secondary Cell Characters	Edge Characters	Composite	+		+		+								
		Face													
		"													
		Depressed	+		+		+								
		Foveate													
		Papillate													
		Auriculate													
		Undulate													
	Face Characters	Verrucate													
		Striate	+		+		+								
		Rough				+									
		Smooth													
		Face not visible													
		Level													
		Tholiform													
		Colliculate													
		Papillate													
Tuberculate					+	+									
Auriculate															
Ocellate							+								
Tetragonate															
Verrucate															
Striate	+		+												
Rough															
Smooth															
Stellate-glochidate															

ATLAS PLATE 30

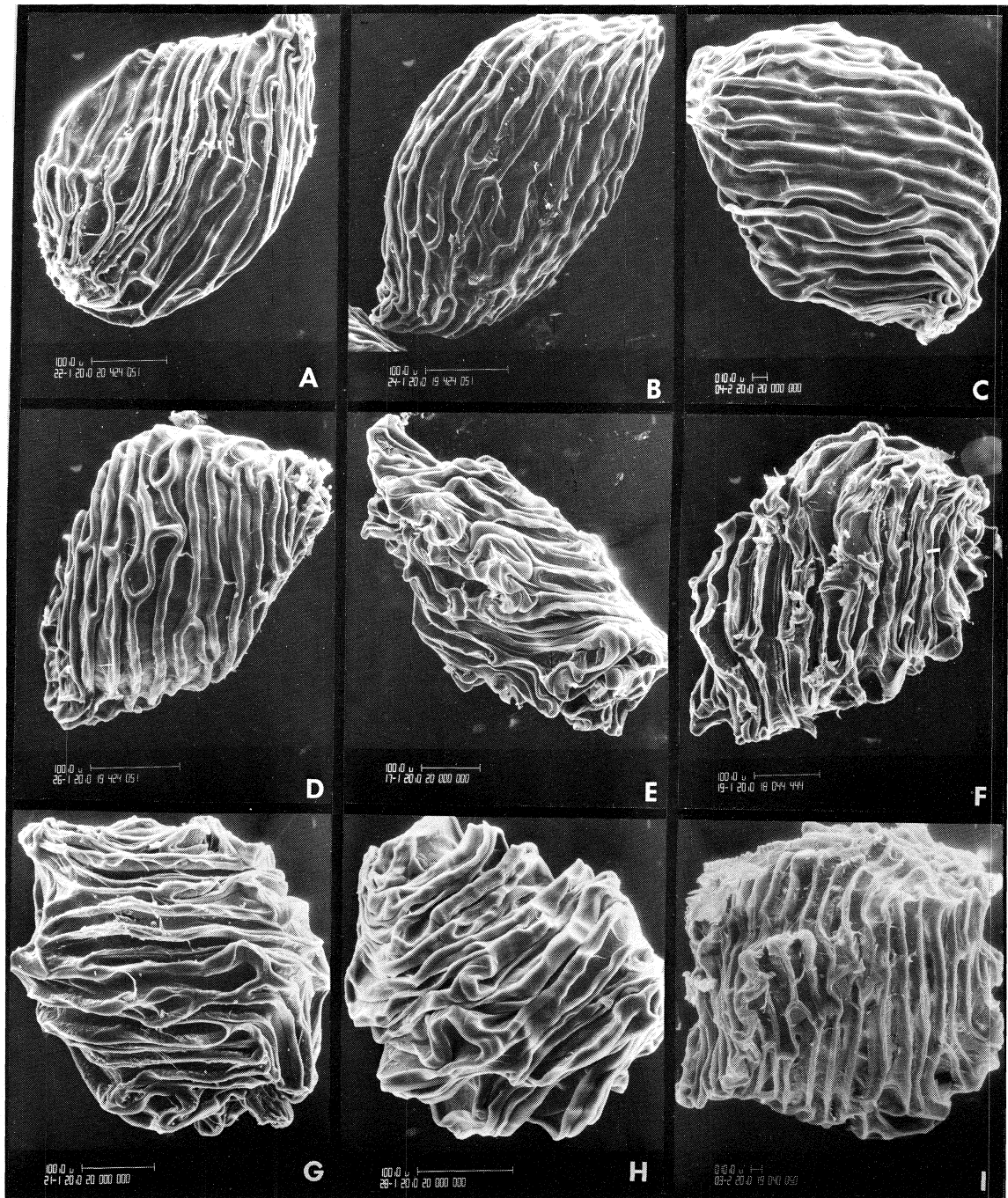


ATLAS PLATE 31

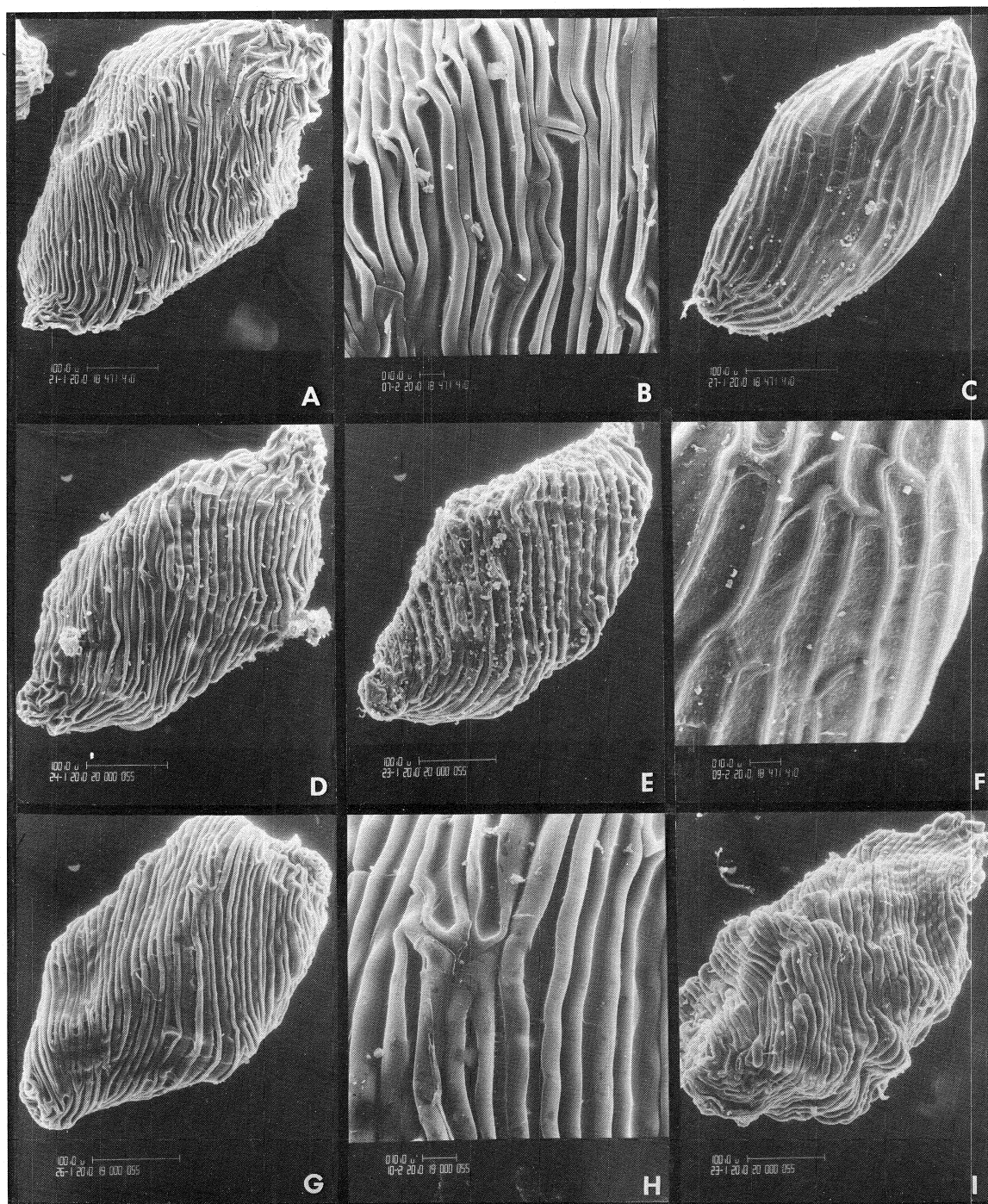


ATLAS TABLE 32			Besleria lutea (a)Besleria connataBesleria macropodaBesleria lutea (b)Besleria notabilisBesleria aggregataBesleria formicariaReldia alternifoliaBesleria barclayi								
			A	B	C	D	E	F	G	H	I
Seed Shapes		Narrowly-elliptic									
		Elliptic	5:3	2:1	5:3	5:3	2:1	5:3	3:2		
		Broadly-elliptic								7:6	7:6
		Circular									
		Orbiculate									
		Reniform									
		Carinatus(C), Alatus(A)									
Apical Characters		Irregular									
		Acute	+	+			+				
		Arillate									
		Constrictate									
		Coronate						+			
		Filiform									
		Obtuse	+		+	+					
Cell Orientation		Reniform									
		Truncate(T), Premorse(P)									
		Irregular		+	+	+	+	+	++	++	++
		Straight									
		Slightly-spiral		+							
		Spiral	+		+	+	+	+	+	+	+
		Irregular									
Cell Shapes		N-lineate-polygonate								+	
		Lineate-polygonate	+	+	+	+	+	+	+		+
		Polygonate									
		Lobed(L), Parted(P)									
		Irregular									
Primary Cell Characters	Edges	Elevated	+	+	+	+	+	+	+	+	+
		Depressed									
	Crests	Irregular									
		Discrete	+	+	+	+	+	+	+	+	+
	Face	Fused									
		Composite									
Secondary Cell Characters	Edge Characters	Elevated									
		Depressed	+	+	+	+	+	+	+	+	+
		Irregular									
		Discrete	+	+	+	+	+	+	+	+	+
		Fused									
		Composite									
		Elevated									
		Depressed	+	+	+	+	+	+	+	+	+
		Foveate									
	Face Characters	Papillate									
		Auriculate									
		Undulate	+	+	+	+	+	+	+	+	+
		Verrucate									
		Striate									
		Rough									
		Smooth									
		Face not visible									
		Level									
		Tholiform									

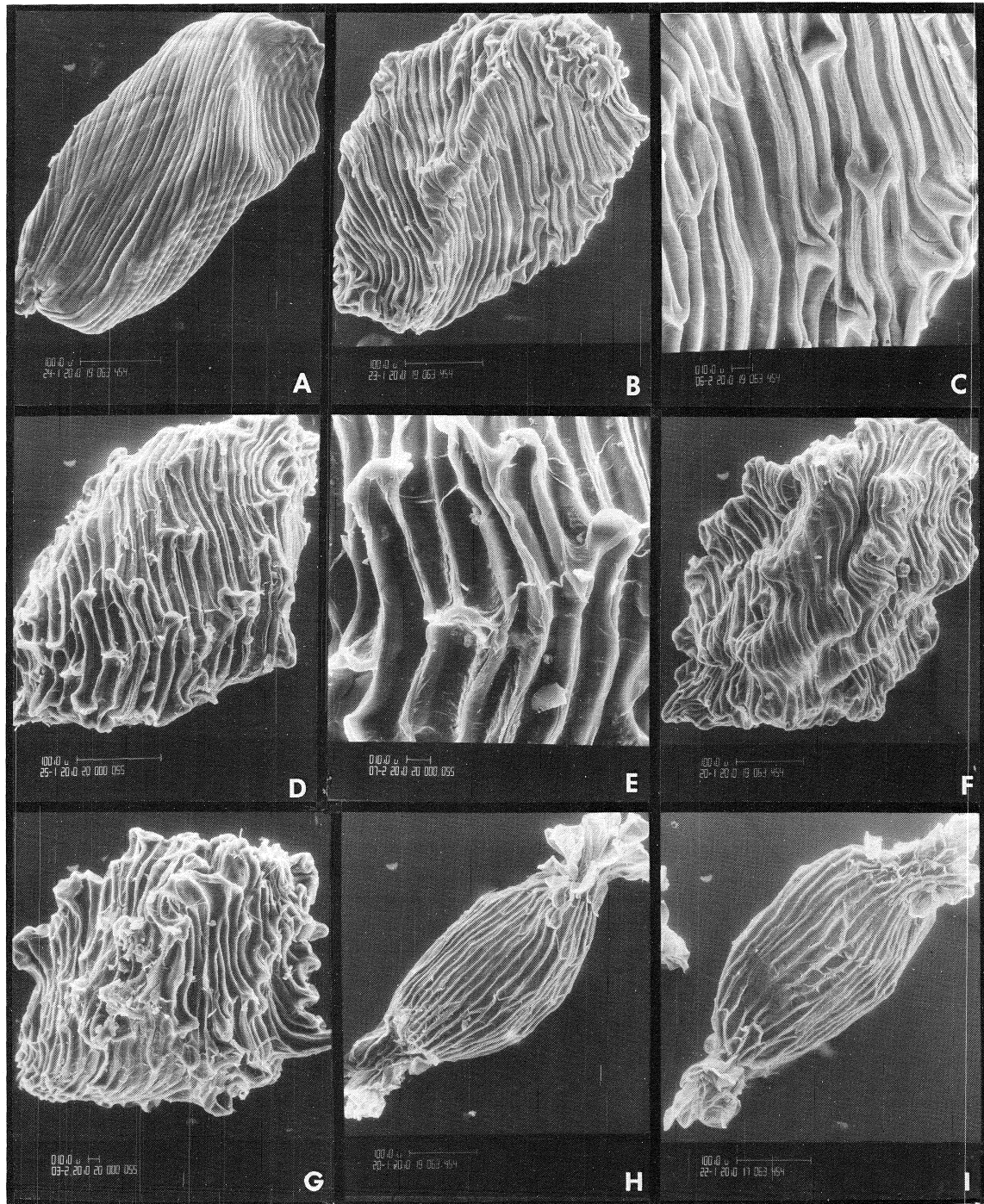
ATLAS PLATE 32



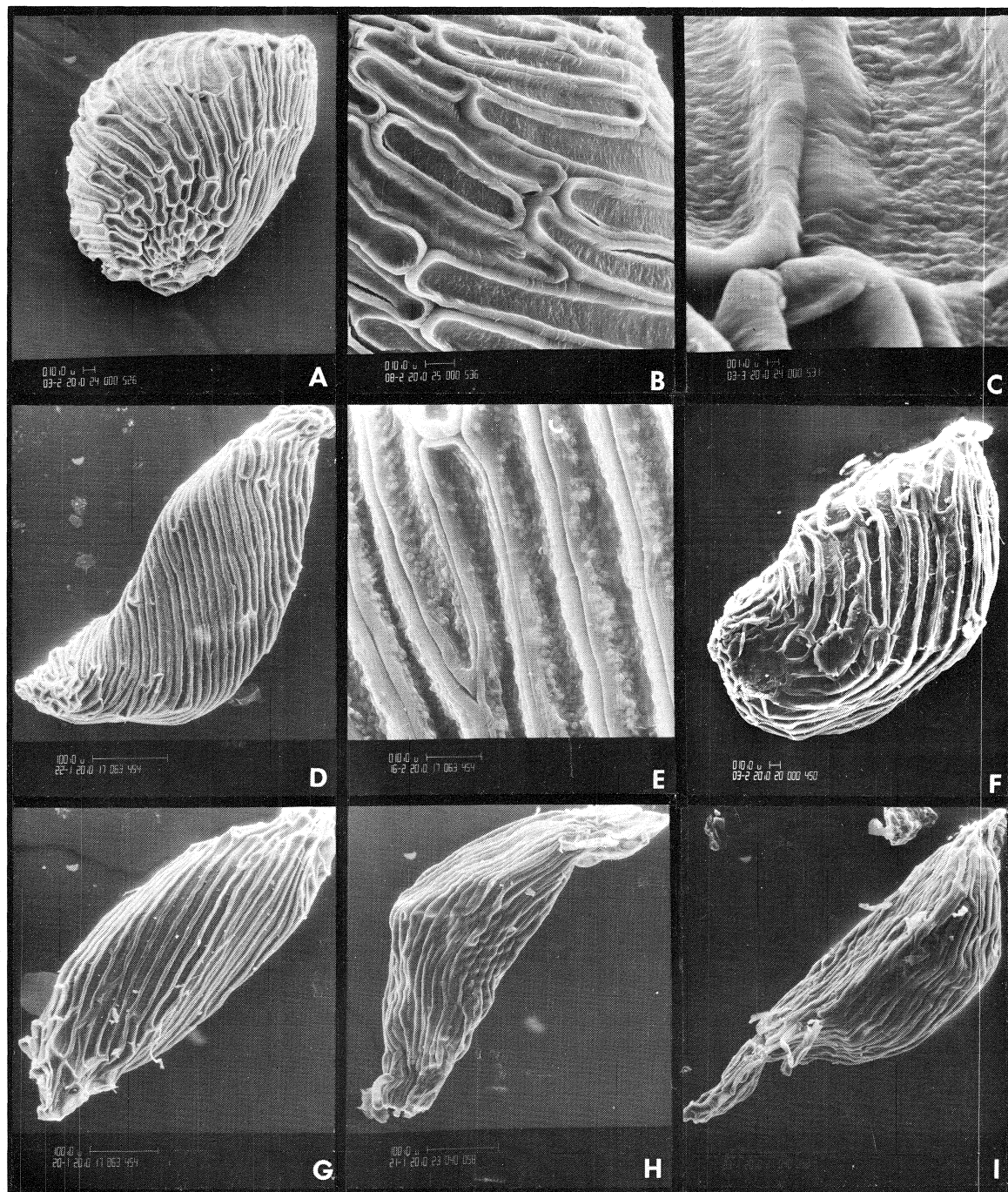
ATLAS PLATE 33



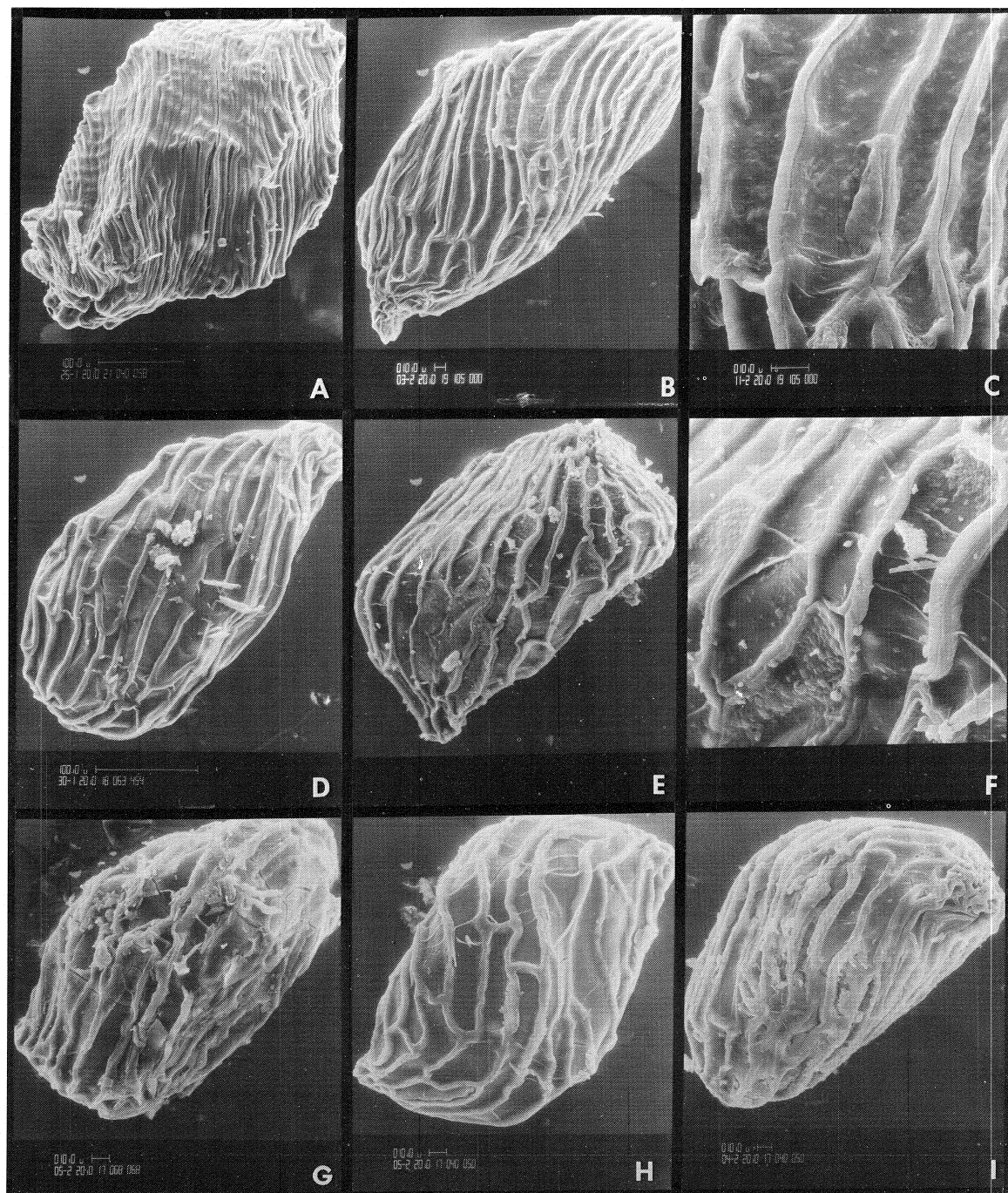
ATLAS PLATE 34



ATLAS PLATE 35

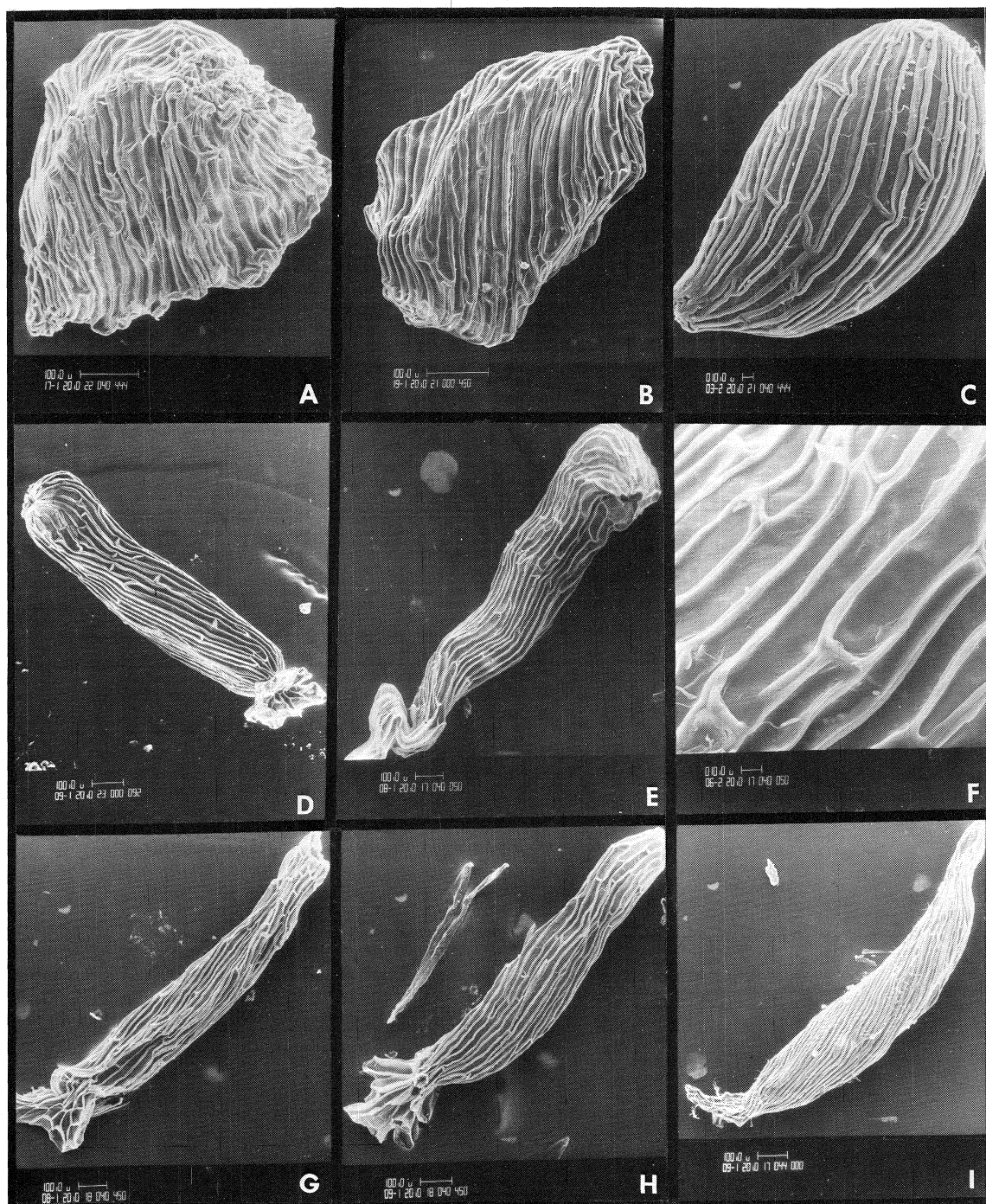


ATLAS PLATE 36



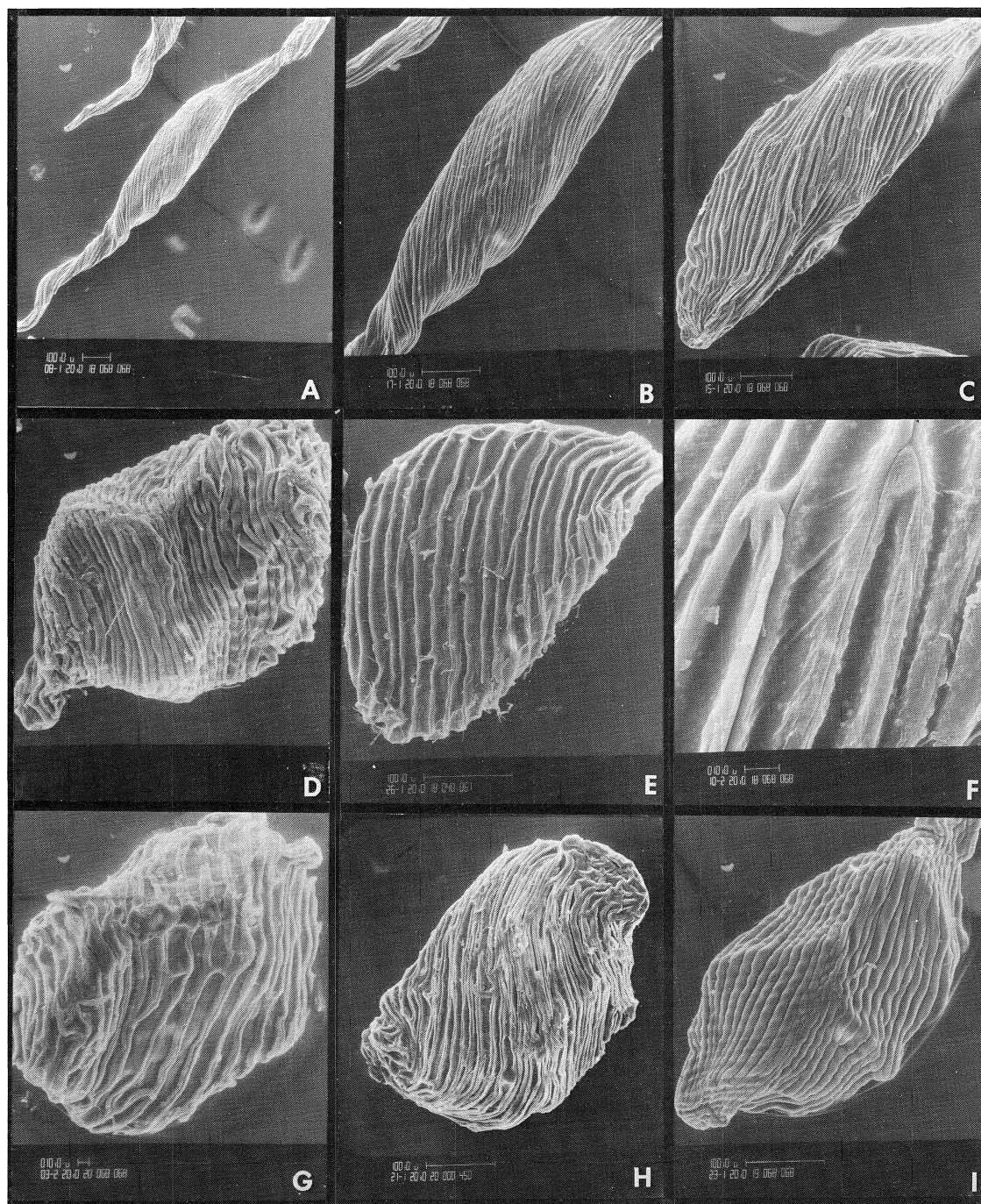
[illegible]

ATLAS PLATE 37



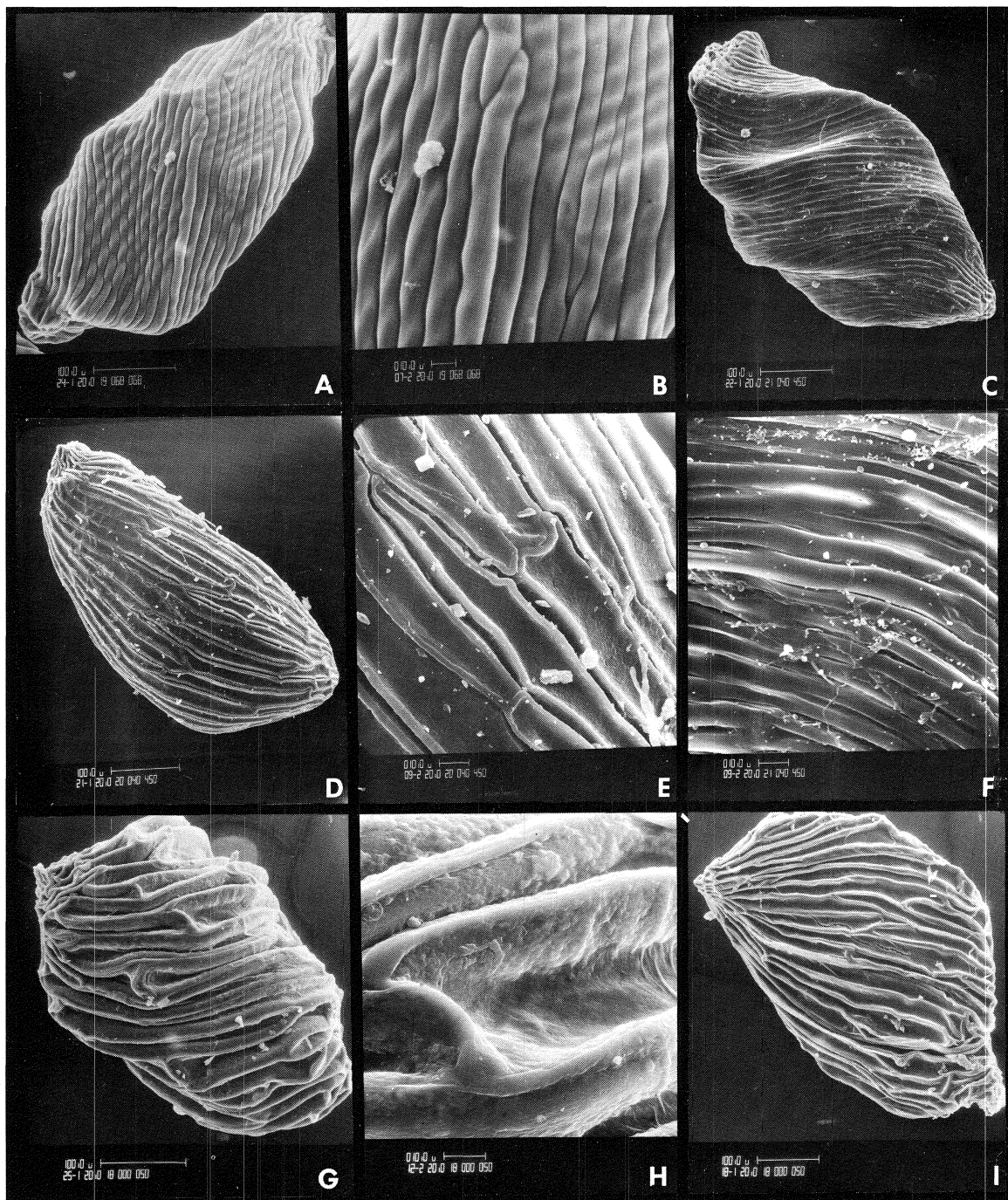
ATLAS TABLE 38			Capanea grandiflora	Capanea grandiflora	Vanhouttea gardneri	Diastema longiflorum	Diastema vexans	Diastema gardneri	Moussonia rupestre	Kohleria brachycalyx					
			A	B	C	D	E	F	G	H	I				
Seed Shapes		Narrowly-elliptic	10:1	CU	3:1				CU						
		Elliptic				5:3	5:3			2:1	5:3	2:1			
		Broadly-elliptic													
		Circular													
		Orbiculate													
		Reniform													
		Carinatus (C), Alatus (A)													
Apical Characters		Irregular													
		Acute			++										
		Arillate													
		Constrictate				+	+		+	++	++				
		Coronate													
		Filiform	++												
		Obtuse				+	+		+						
		Reniform													
Cell Orientation		Truncate (T), Premorse (P)													
		Irregular													
		Straight													
		Slightly-spiral													
Cell Shapes		Spiral	+		+	+	+		+	+	+				
		Irregular													
		N-lineate-polygonate	+		+	+	+			+	+	+			
		Lineate-polygonate								+					
		Polygonate													
Primary Cell Characters		Lobed (L), Parted (P)													
		Irregular													
		Edges	Elevated	+		+	+	+		+	+	+			
		"	Depressed												
		"	Irregular												
		Crests	Discrete	+		+	+	+		+	+	+			
Secondary Cell Characters		"	Fused												
		"	Composite												
		Face	Elevated												
		"	Depressed	+		+	+	+		+	+	+			
		Edge Characters	Foveate												
			Papillate												
Auriculate															
Undulate	+			+	+			+	+	+					
Verrucate															
Striate															
Rough							+								
Smooth	+			+	+			+	+	+					
Face Characters		Face not visible	+												
		Level													
		Tholiform													
		Colliculate													
		Papillate													
		Tuberculate													
		Auriculate													
		Ocellate													
		Tetragonate													
		Verrucate													
		Striate													
		Rough						+	+		+	+	+		
		Smooth				+									
Stellate-glochidate															

ATLAS PLATE 38

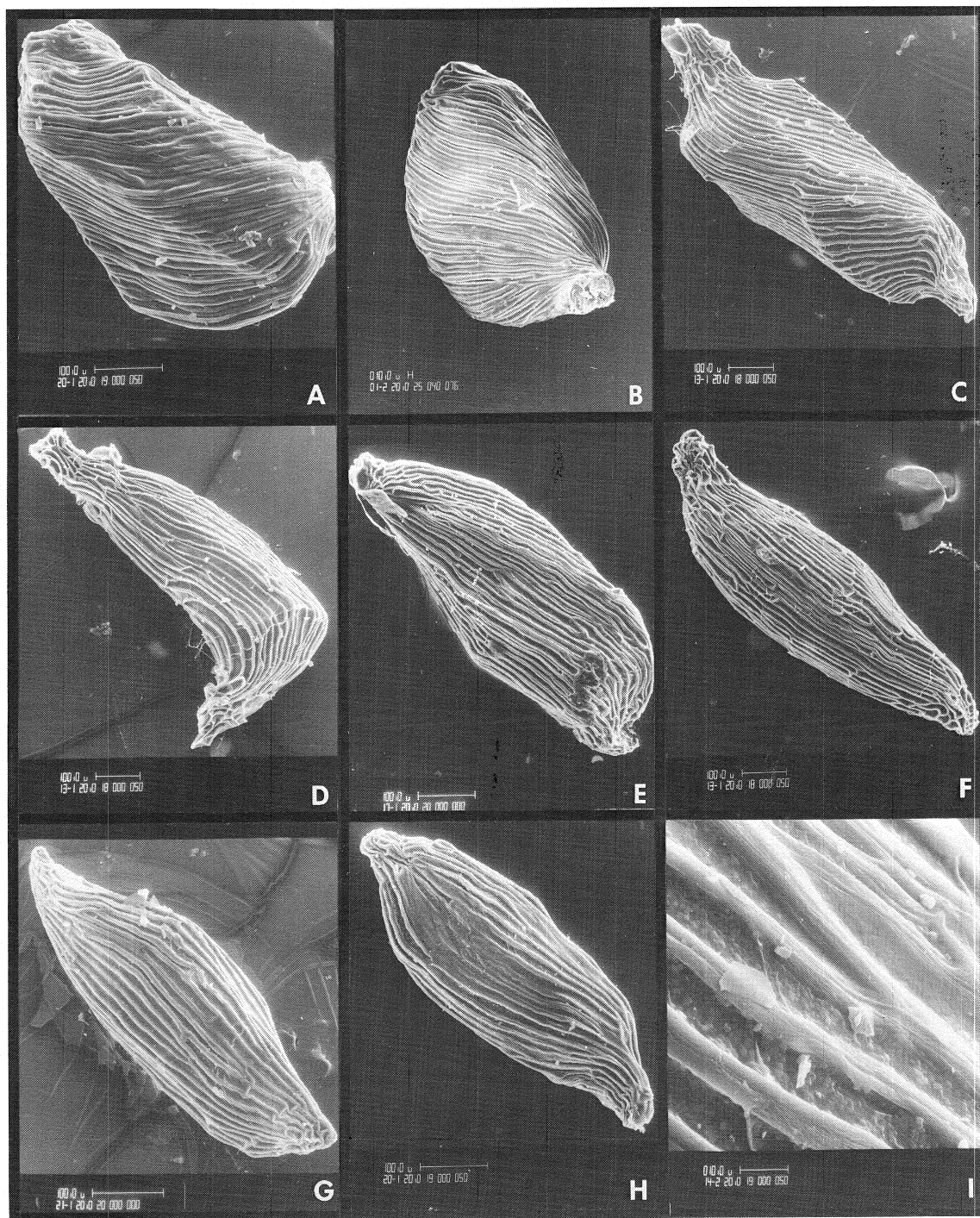


[illegible]

ATLAS PLATE 39

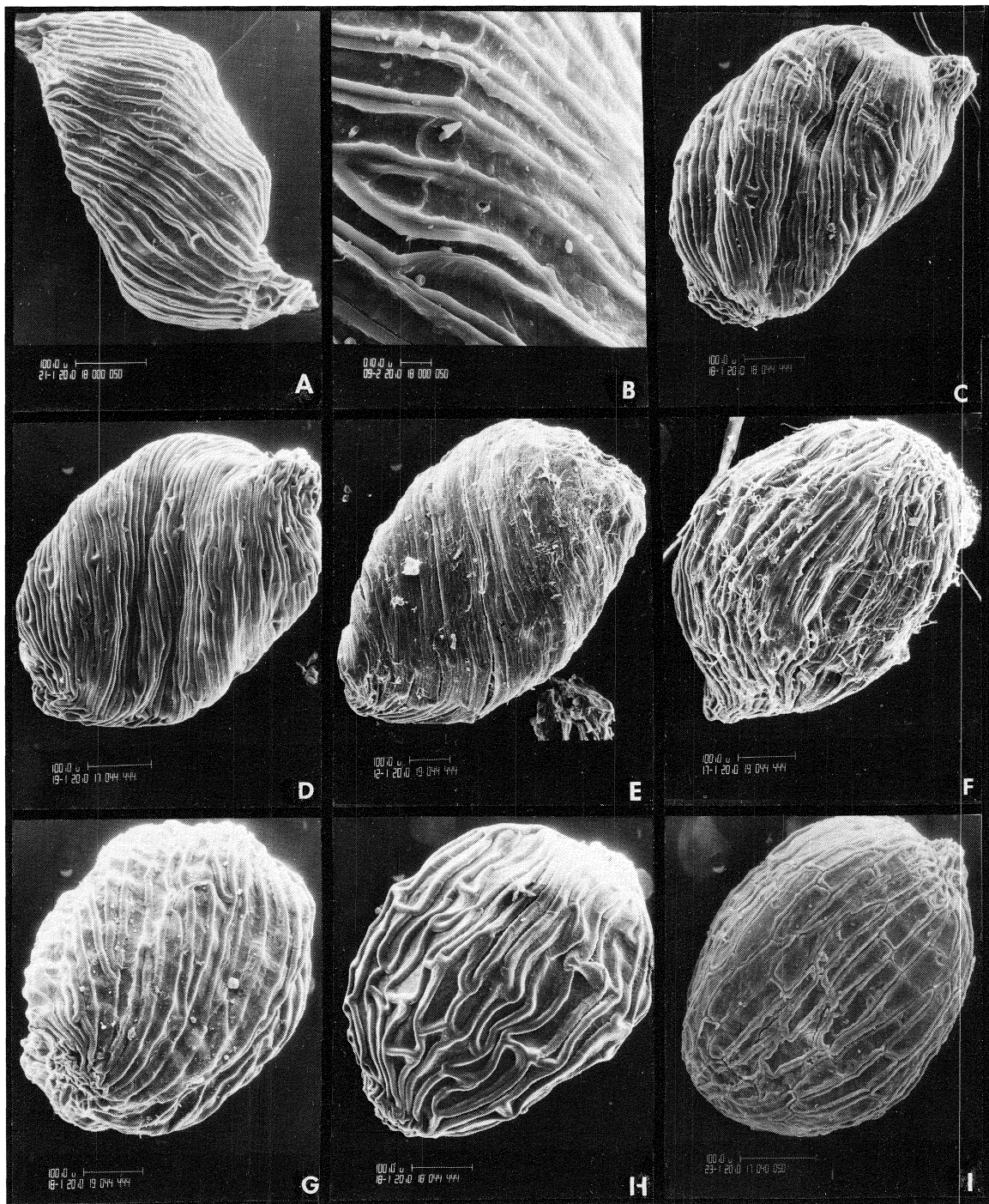


ATLAS PLATE 40



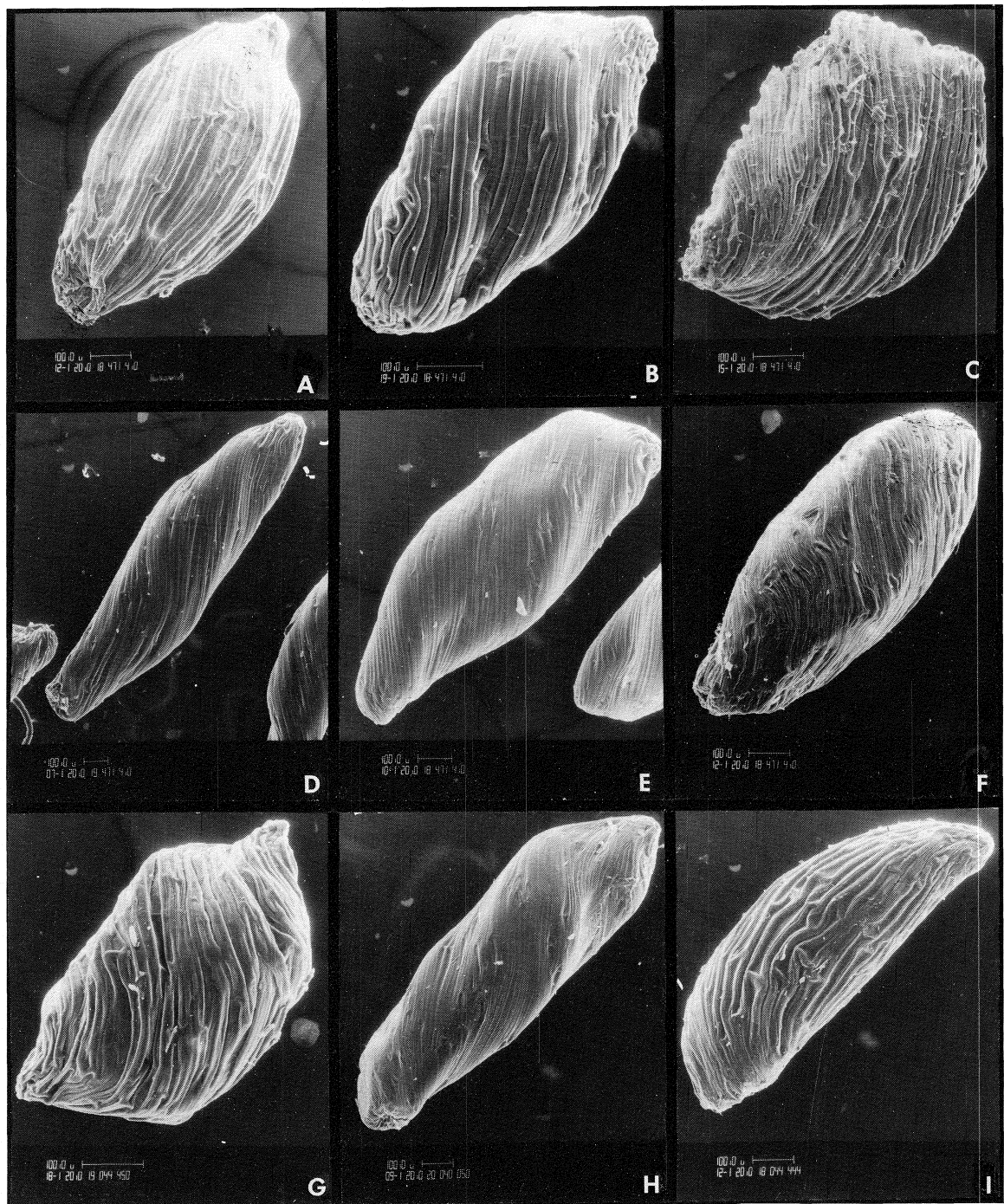
ATLAS TABLE '41			Episcia hirsuta (a) Episcia lilacina Episcia cupreata Episcia fimbriata Episcia hirsuta (b) Lembocarpus amoenus Lembocarpus reptans Rhytidophyllum asperum Rhytidophyllum cupreum Rhytidophyllum asperum									
			A	B	C	D	E	F	G	H	I	
Seed Shapes		Narrowly-elliptic	3:1	CU								
		Elliptic				5:3	3:2	5:3	3:2	3:2		
		Broadly-elliptic									6:5	6:5
		Circular										
		Orbiculate										
		Reniform										
		Carinatus(C), Alatus(A) Irregular										
Apical Characters		Acute										
		Arillate										
		Constrictate	++		+	+	+	+	+	+	+	+
		Coronate										
		Filiform										
		Obtuse			+	+	+	+	+	+	+	+
		Reniform										
Truncate(T), Premorse(P) Irregular												
Cell Orientation		Straight										
		Slightly-spiral						+	+	+	+	
		Spiral	+		+	+	+					
		Irregular										
Cell Shapes		N-lineate-polygonate			+	+	+					
		Lineate-polygonate	+					+	+	+	+	
		Polygonate										
		Lobed(L), Parted(P)										
		Irregular										
Primary Cell Characters	Edges " "	Elevated	+		+	+	+	+	+	+	+	
		Depressed										
		Irregular										
	Crests " "	Discrete	+		+	+	+	+	+	+	+	
		Fused										
	Face "	Composite										
Elevated												
Secondary Cell Characters	Edge Characters	Depressed	+		+	+	+	+	+	+	+	
		Smooth	+		+	+	+	+	+	+	+	
		Foveate										
		Papillate										
		Auriculate										
		Undulate										
		Verrucate										
		Striate										
	Face Characters	Rough										
		Smooth										
		Face not visible			+	+	+					
		Level										
		Tholiform										
		Colliculate										
		Papillate										
		Tuberculate										
		Auriculate										
		Ocellate										
		Tetragonate										
		Verrucate	+									
Striate												
Rough	+						+	+	+			
Smooth												
Stellate-glochidate												

ATLAS PLATE 41



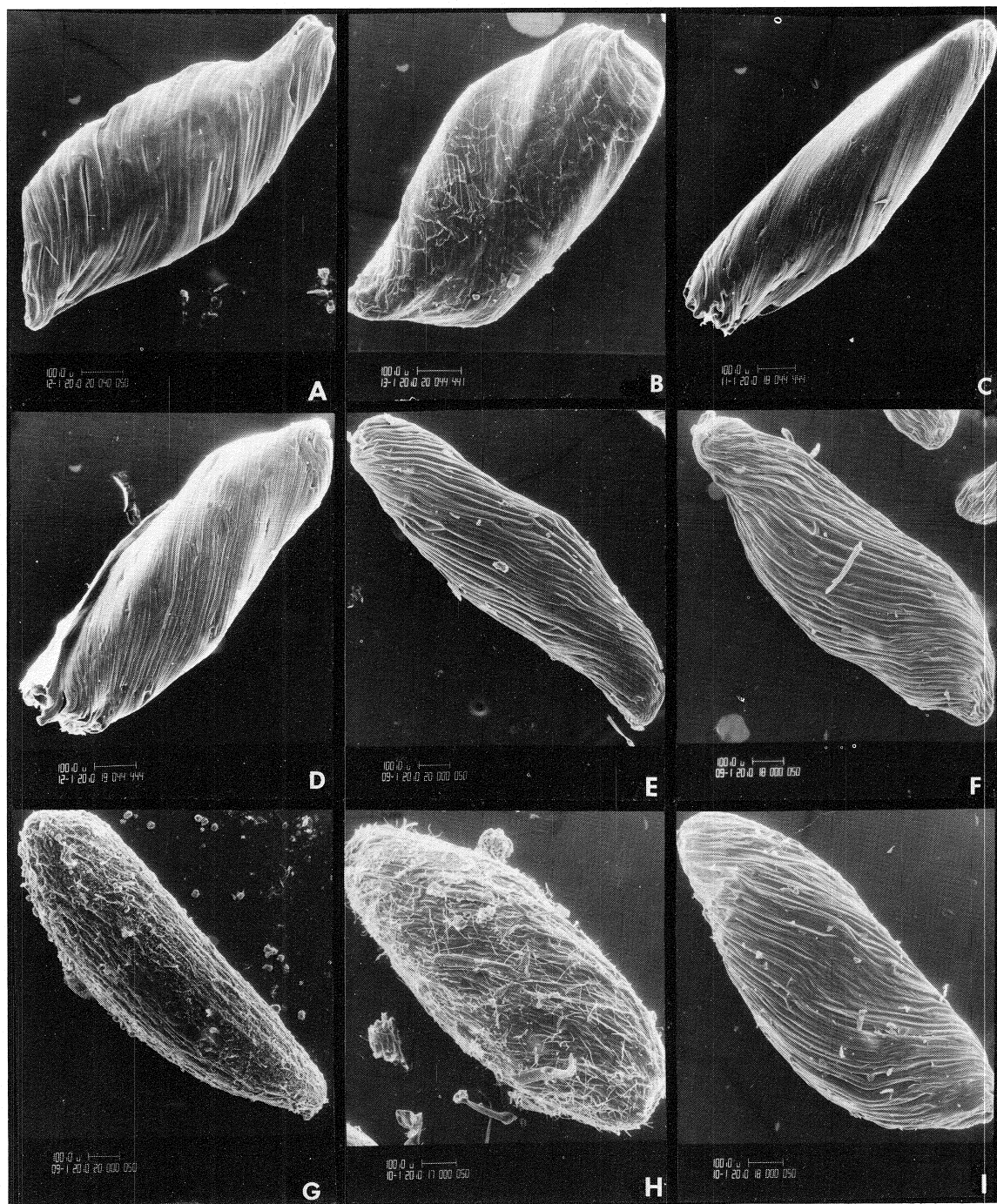
[illegible]

ATLAS PLATE 42



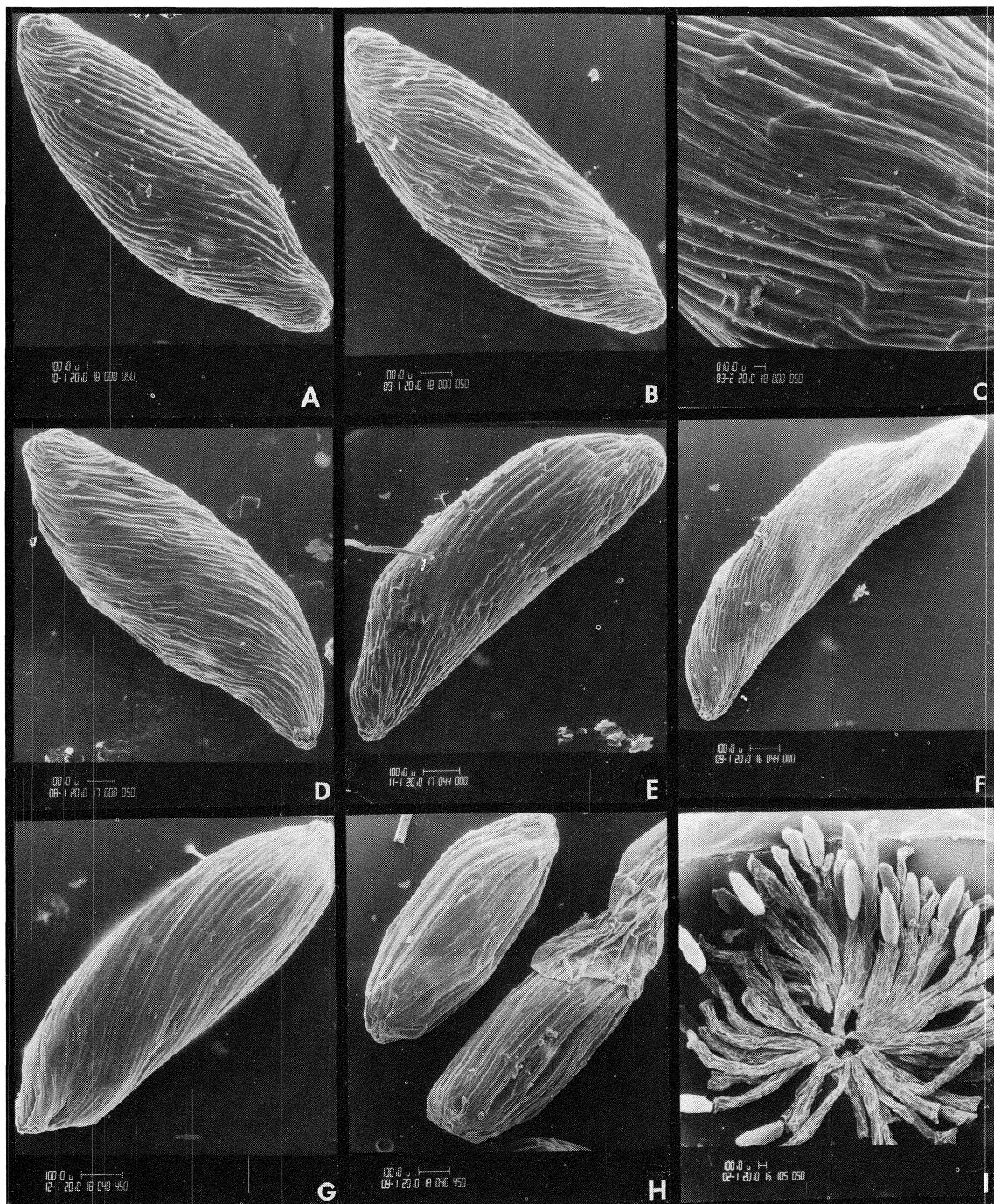
[illegible]

ATLAS PLATE 43

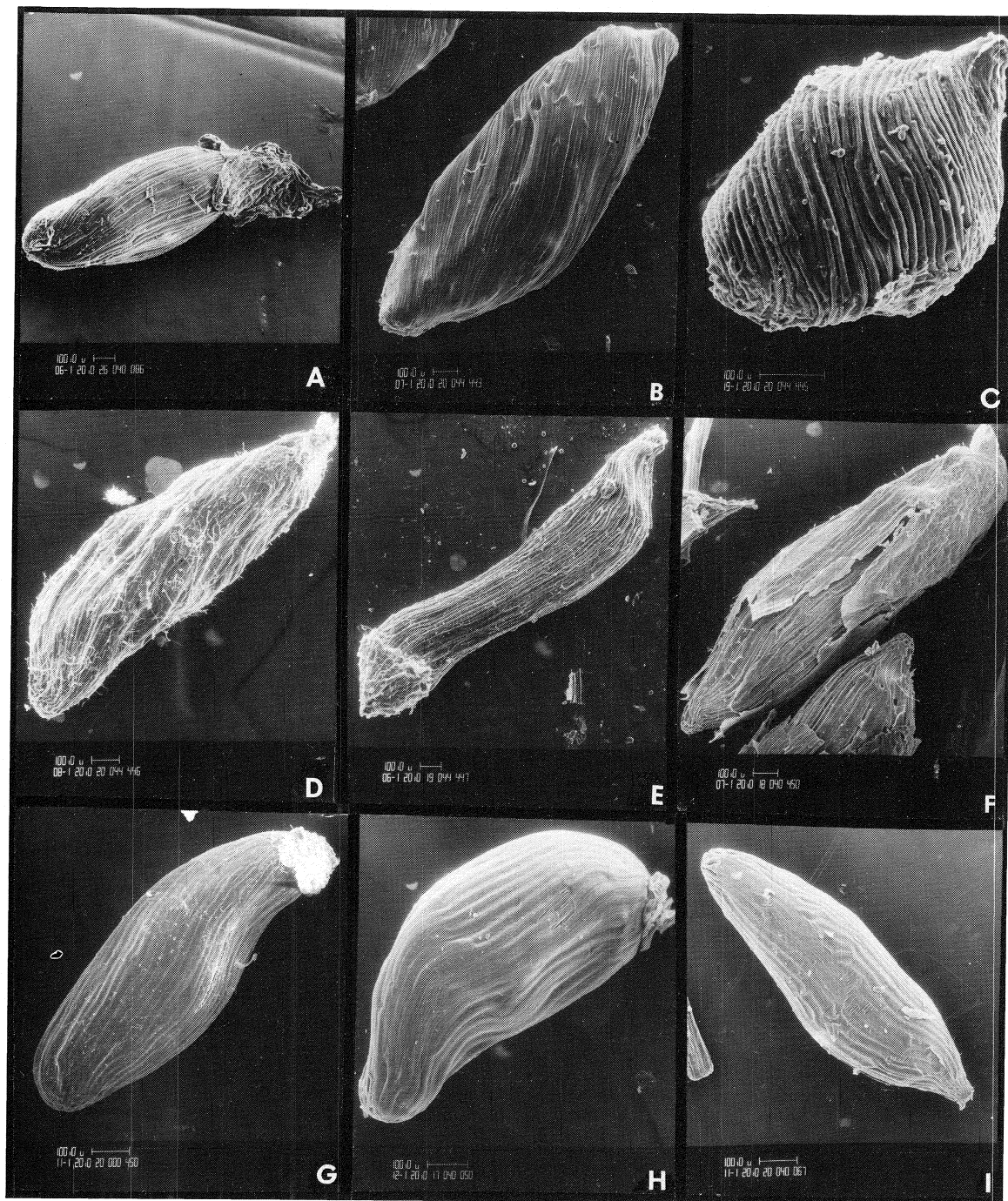


[illegible]

ATLAS PLATE 44

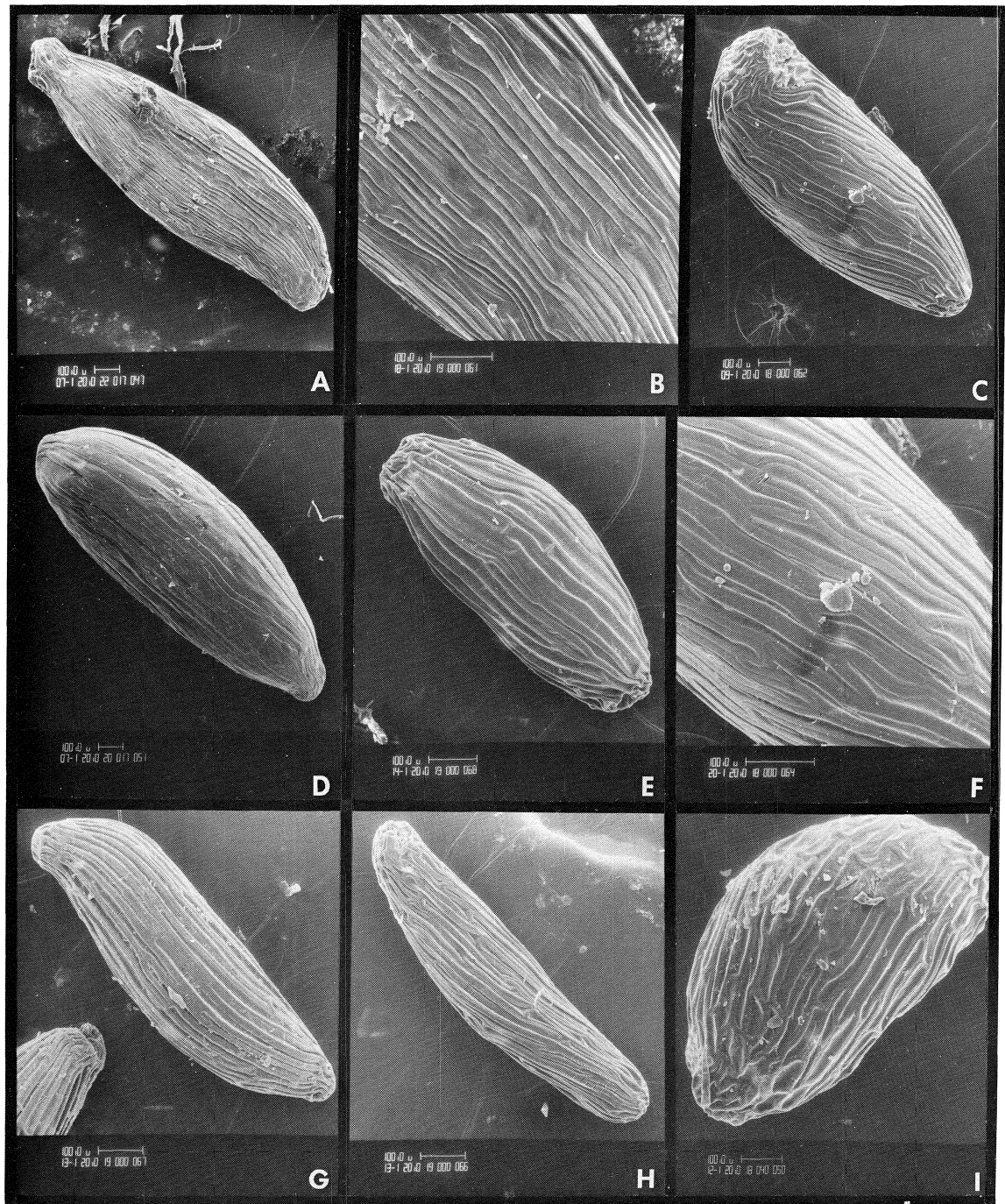


ATLAS PLATE 45

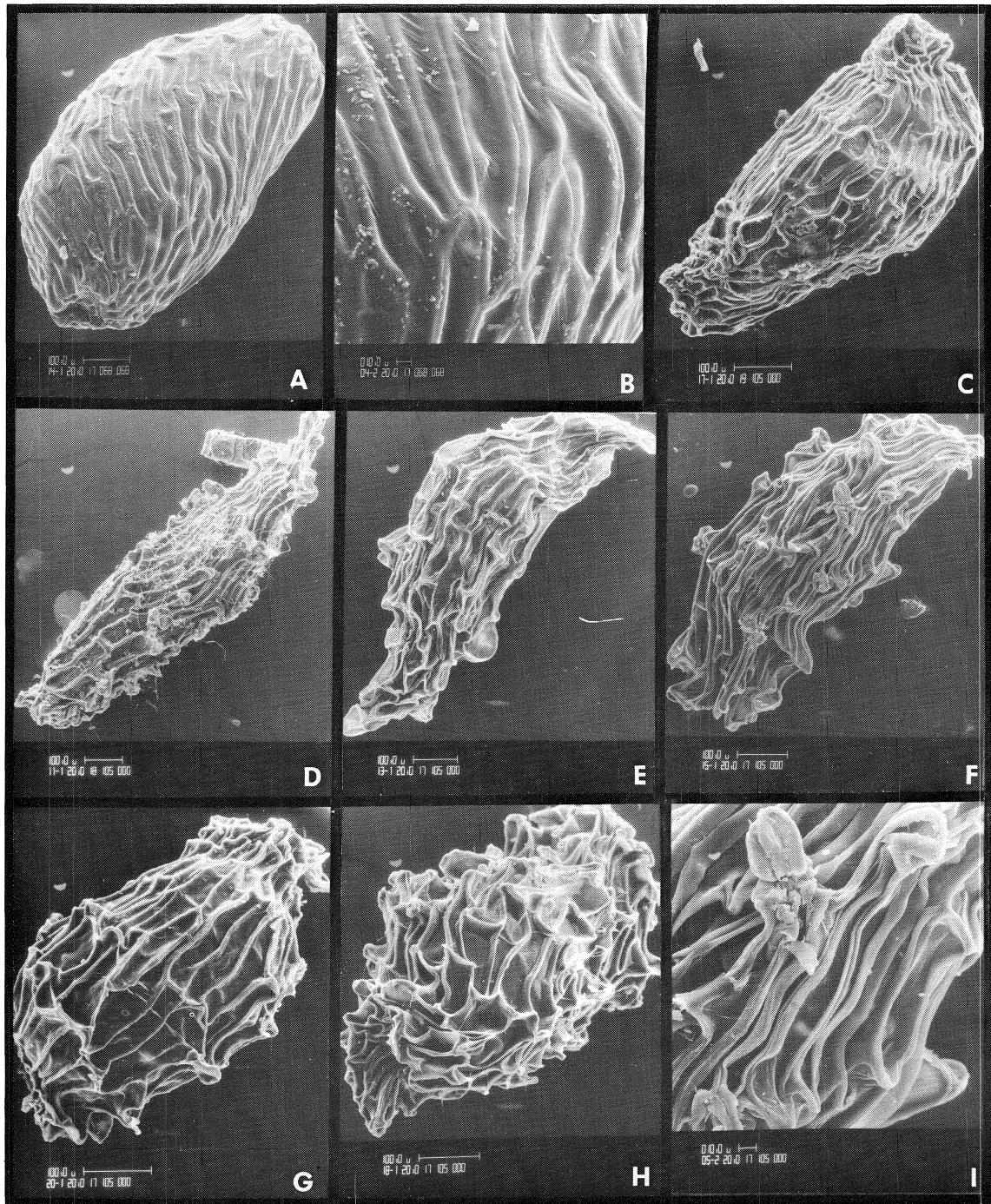


[illegible]

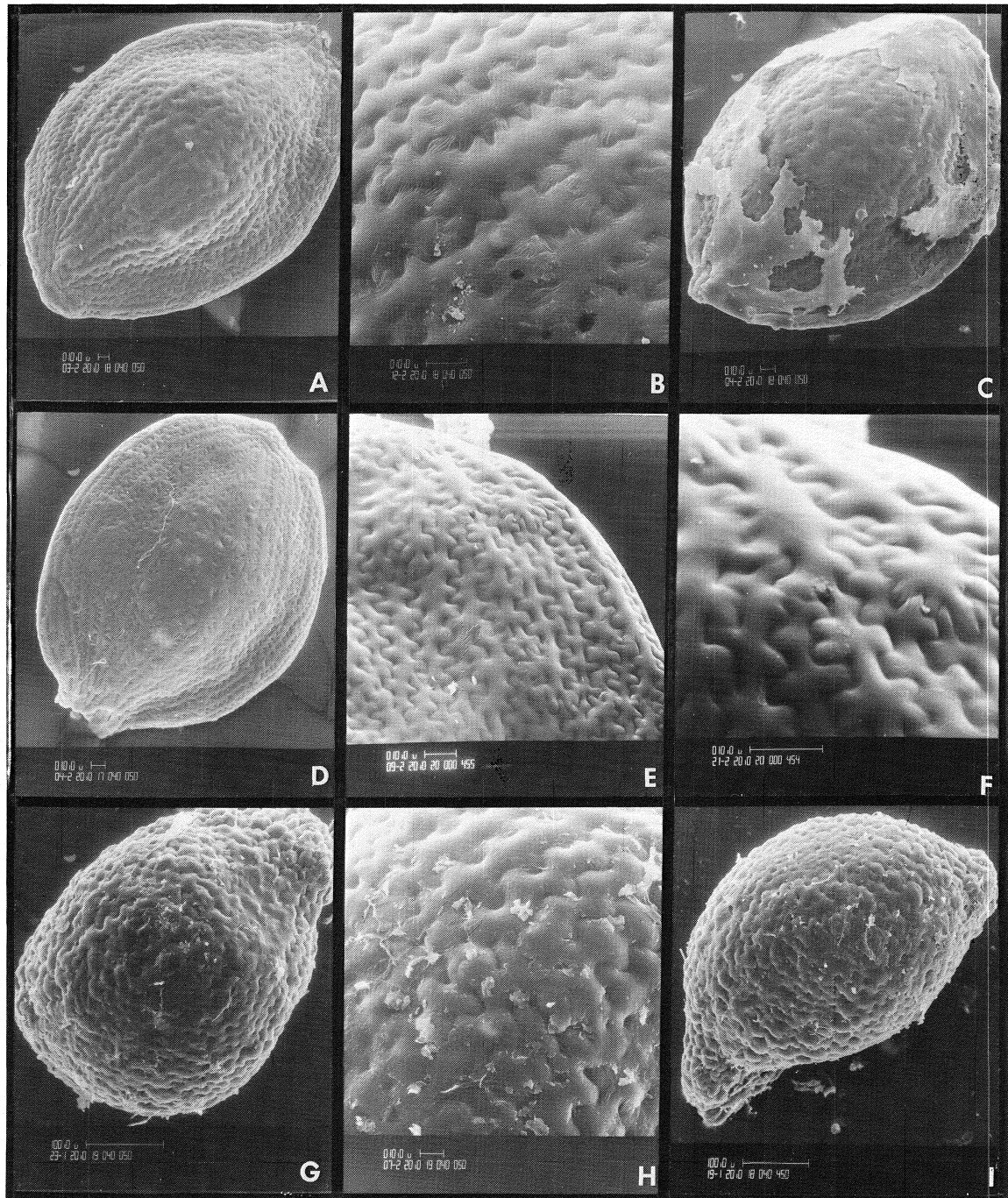
ATLAS PLATE 46



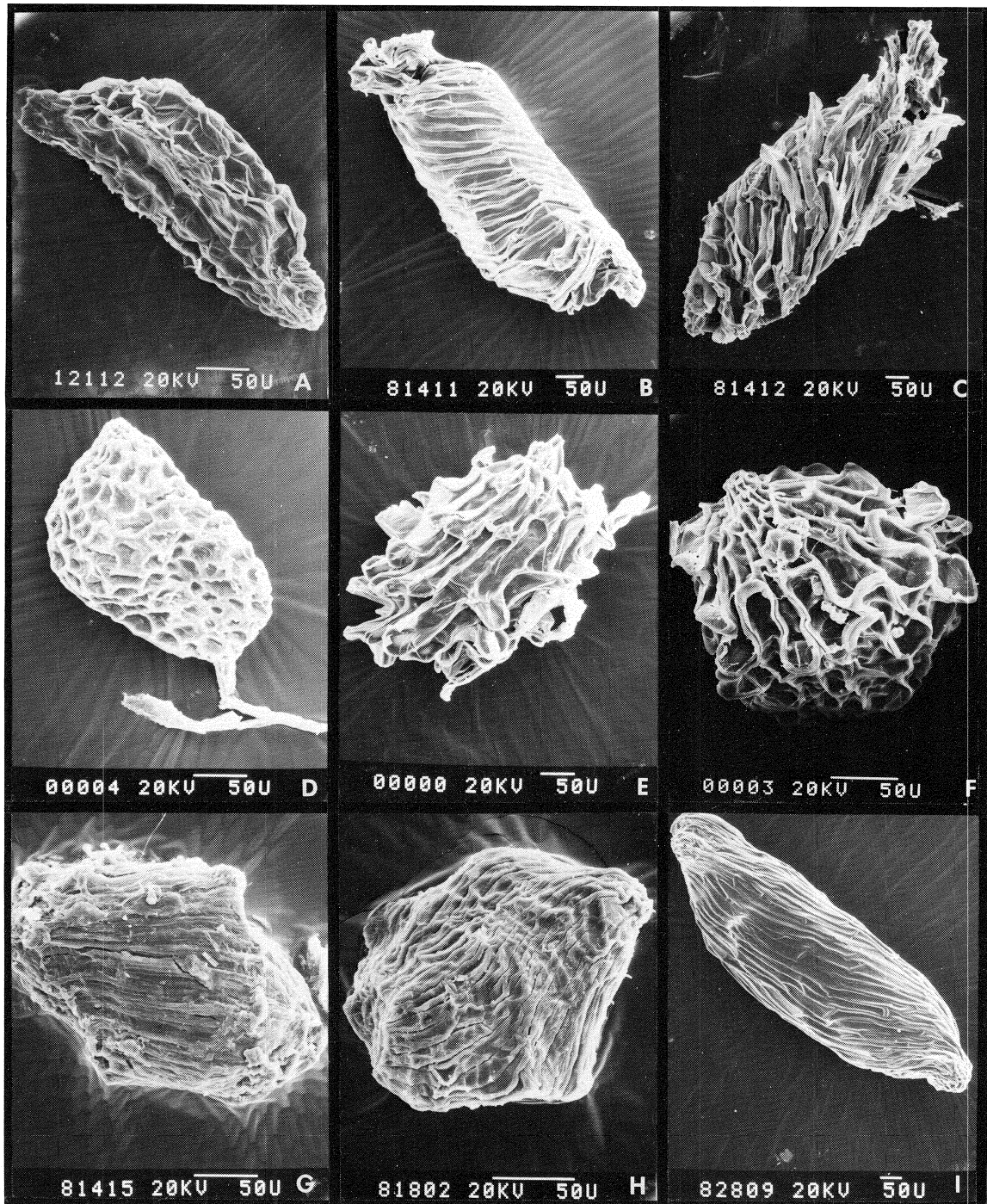
ATLAS PLATE 47



ATLAS PLATE 48

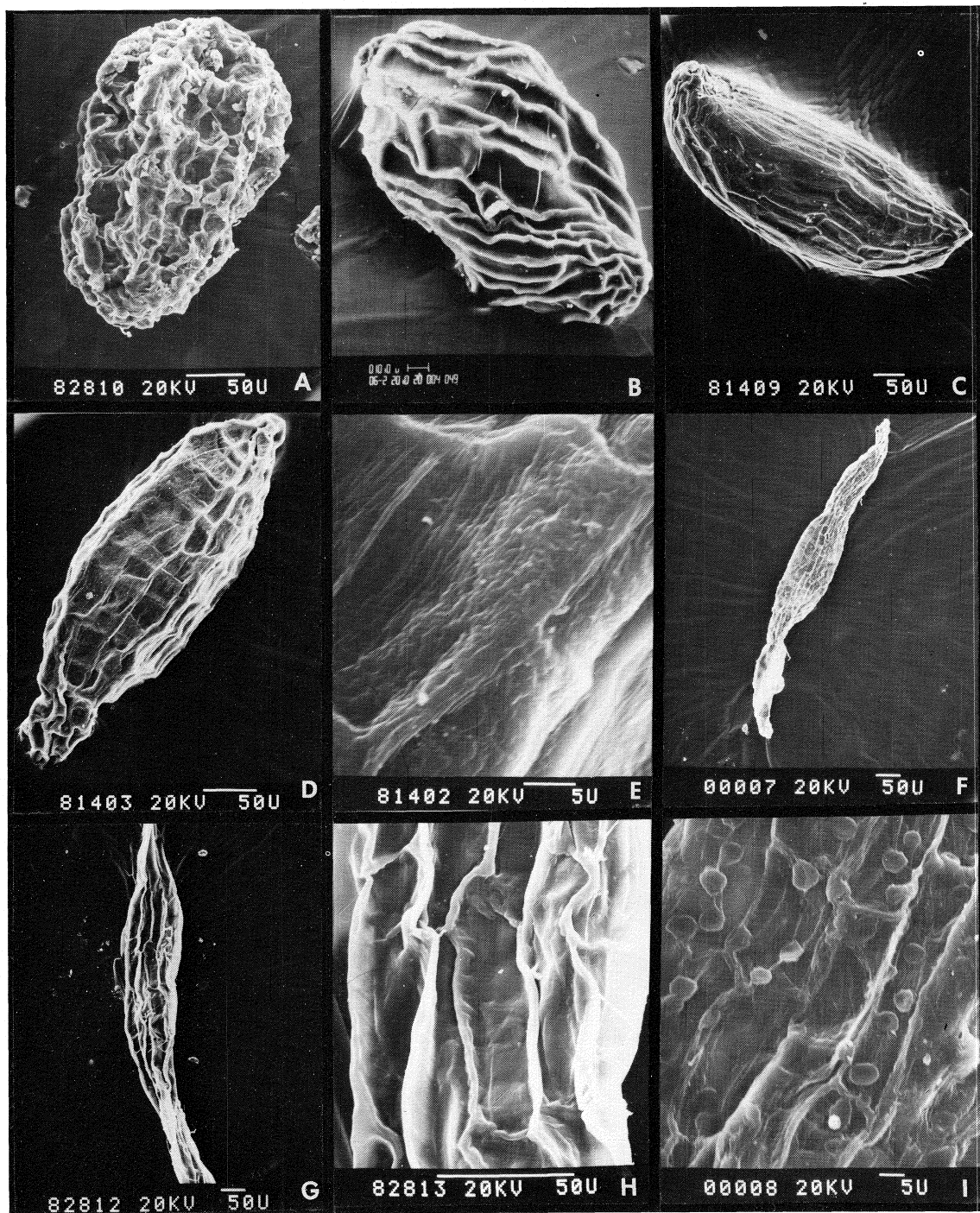


ATLAS PLATE 49



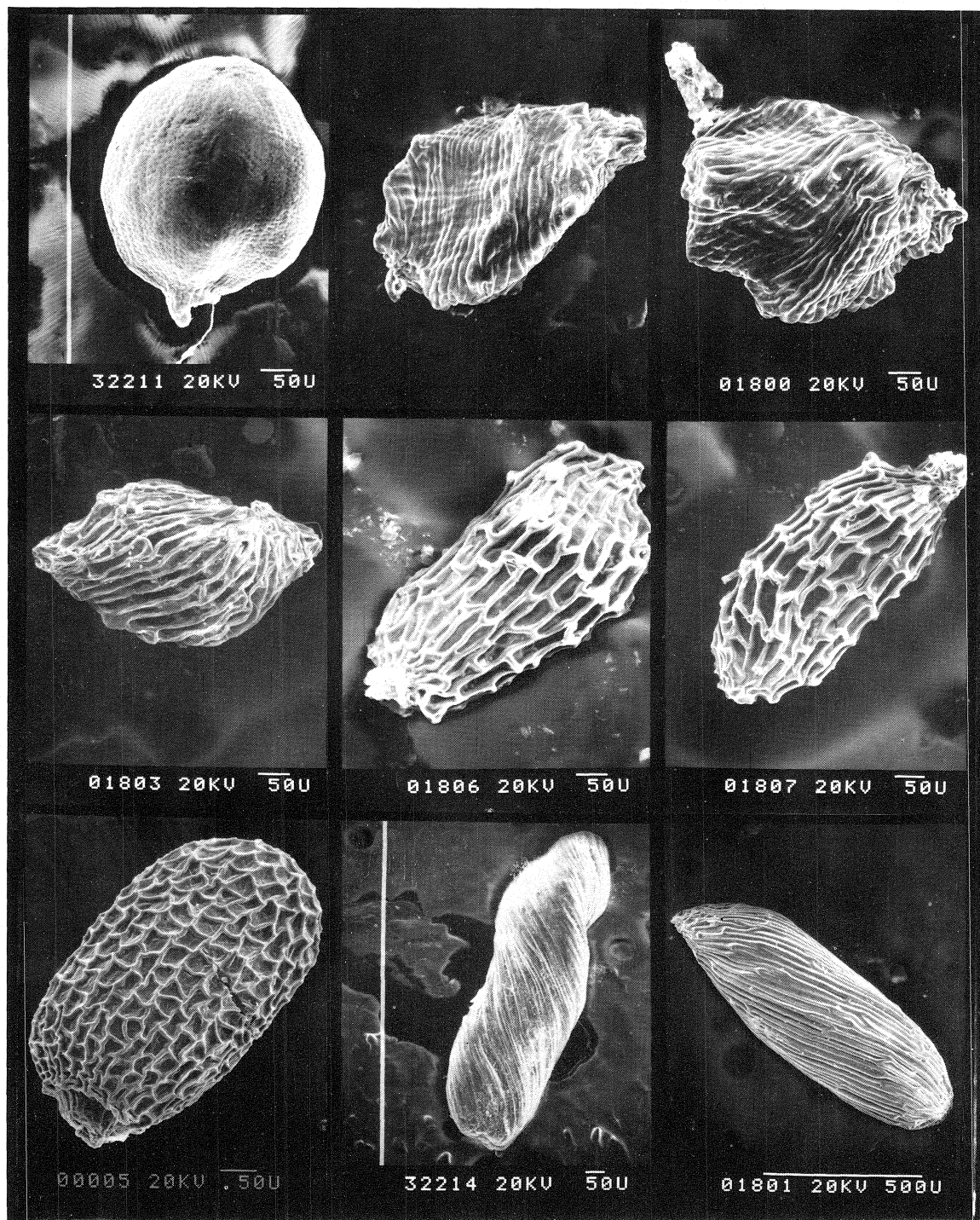
ATLAS TABLE 50			<i>Cyrtandra todalensis</i> <i>Isometrum farreri</i> <i>Corallodiscus patens (T)</i> <i>Streptocarpus variabilis</i> <i>Streptocarpus variabilis (T)</i> <i>Anna ophiorrhizoides (T)</i> <i>Loxostigma griffithii</i> <i>Loxostigma griffithii (T)</i> <i>Anna ophiorrhizoides (T)</i>								
			A	B	C	D	E	F	G	H	I
Seed Shapes		Narrowly-elliptic			3:1	3:1	CU	7:1	7:1	CU	CU
		Elliptic	5:3	2:1							
		Broadly-elliptic									
		Circular									
		Orbiculate									
		Reniform									
		Carinatus(C), Alatus(A)									
Apical Characters		Irregular									
		Acute			+						
		Arillate									
		Constrictate		+		++					
		Coronate									
		Filiform						++	++		
		Obtuse	++	+	+						
Cell Orientation		Reniform									
		Truncate(T), Premorse(P)									
		Irregular									
Cell Shapes		Straight	+		+	+		+	+		
		Slightly-spiral		+							
		Spiral									
		Irregular									
Primary Cell Characters	Edges	N-lineate-polygonate									
		Lineate-polygonate		+	+	+		+	+		
		Polygonate	+								
		Lobed(L), Parted(P)									
		Irregular									
	Crests	Elevated	+	+	+	+		+	+		
		Depressed									
		Irregular									
		Discrete			+	+					
		Fused	+					+			
Secondary Cell Characters	Face	Composite		+					+		
		Elevated									
		Depressed	+	+	+	+		+	+		
	Edge Characters	Foveate									
		Papillate						+			
		Auriculate									
		Undulate									
		Verrucate									
		Striate									
		Rough	+			+			+		
		Smooth		+	+						
	Face Characters	Stellate-glochidate									
		Face not visible									
		Level									
		Tholiform									
		Colliculate									
		Papillate						+			
		Tuberculate									
		Auriculate									
		Ocellate									
		Tetragonate					+				
		Verrucate									
		Striate									
		Rough	+		+			+	+		
		Smooth		+							

ATLAS PLATE 50

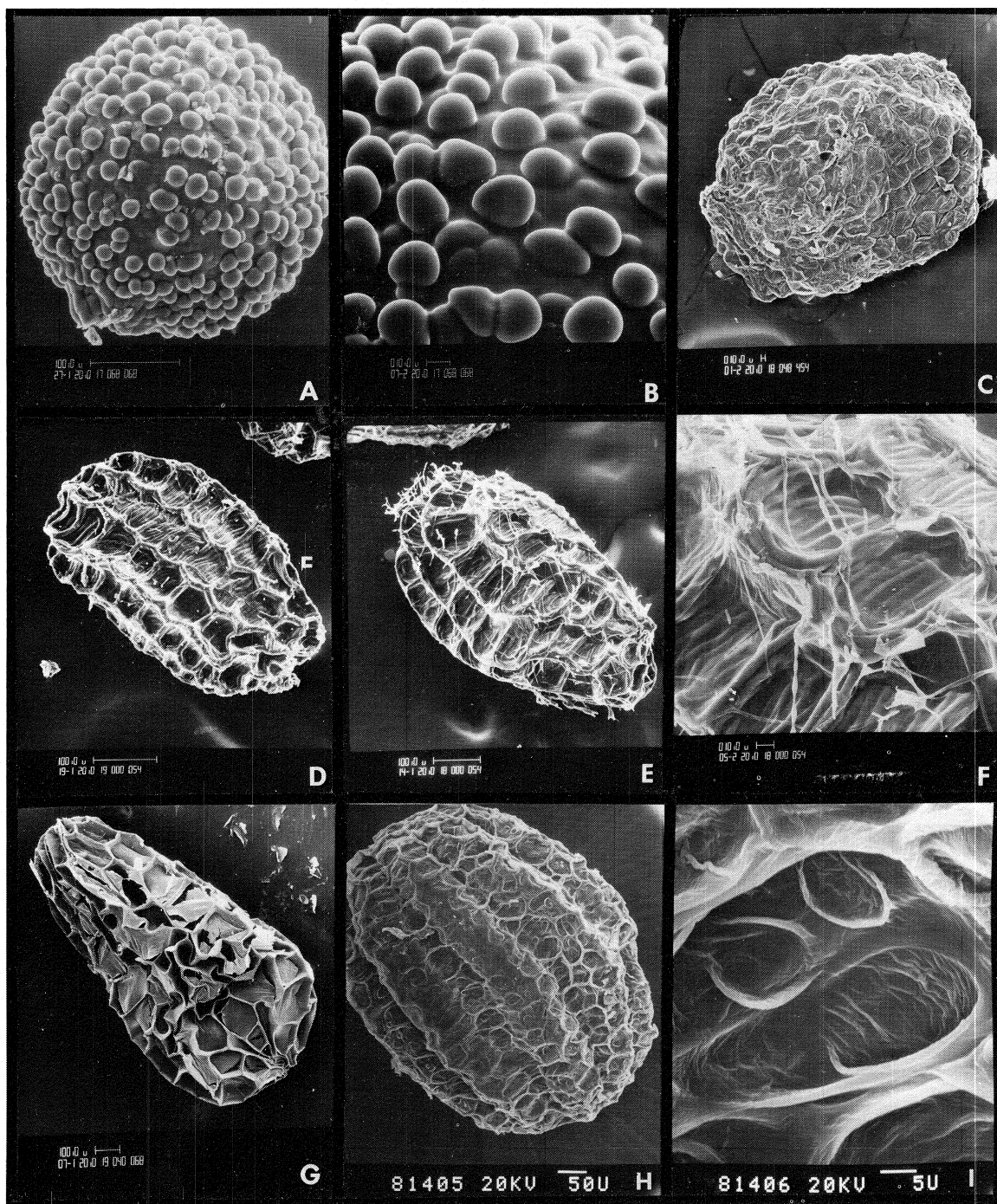


ATLAS TABLE 51			Neomortonia nummularia Alsobia punctata Rhynchosglossum azureum Cremosperma peruvianum (a) Cremosperma minutiflorum Cremosperma sprucei Parakohleria reticulata Parakohleria rubra Aneranthus rubra									
			A	B	C	D	E	F	G	H	I	
Seed Shapes		Narrowly-elliptic								3:1	3:1	
		Elliptic		5:3			2:1	2:1	2:1			
		Broadly-elliptic			6:5	3:2						
		Circular										
		Orbiculate	1:1									
		Reniform										
Apical Characters		Carinatus(C), Alatus(A)										
		Irregular			+							
		Acute				+					+	
		Arillate										
		Constrictate					+	+	+			
		Coronate				+						
		Filiform										
		Obtuse	+				+	+	+	+	+	
Cell Orientation		Reniform										
		Truncate(T),Premorse(P)								P		
		Irregular		++	++							
		Straight	+				+	+	+			
Cell Shapes		Slightly-spiral									+	
		Spiral		+	+	+				+		
		Irregular										
		N-lineate-polygonate		+	+					+	+	
		Lineate-polygonate				+	+	+				
Primary Cell Characters	Edges " "	Polygonate					+	+	+			
		Lobed(L), Parted(P)	P									
		Irregular					+	+				
	Crests " "	Elevated				+	+	+	+	+	+	
		Depressed	+	+	+							
		Irregular										
		Discrete								+	+	
Face "	Fused					+	+	+				
	Composite				+							
	Elevated	+	+	+								
Secondary Cell Characters	Edge Characters	Depressed				+	+	+	+	+	+	
		Foveate										
		Papillate										
		Auriculate				+						
		Undulate				+						
		Verrucate							+			
		Striate										
		Rough										
	Face Characters	Smooth	+				+	+		+	+	
		Face not visible										
		Level										
		Tholiform										
		Colliculate										
		Papillate										
		Tuberculate										
		Auriculate										
		Ocellate										
		Tetragonate								+		
		Verrucate								+		
		Striate										
		Rough										
		Smooth	+	+	+	+	+	+		+	+	
		Stellate-glochidate										

ATLAS PLATE 51



ATLAS PLATE 52



FAMILY GESNERIACEAE
SUBFAMILY CYRTANDROIDEAE

Atlas Plates and Tables 5-20, figs. A-I; 30, figs. A-F; 49, fig. A; 50, figs. A-I; and 51, fig. G.

The subfamily Cyrtandroideae comprises four tribes: Cyrtandreae, Trichosporeae, Klugieae, and Didymocarpeae (Burt 1963). All of the tribes are represented in this study. (Atlas Plates and Tables 5-20, figs. A - I; 30, figs. A - F; 49, fig. A; 50, figs. A - I; and 51, fig. G.)

TABLE V. TRIBE 1: CYRTANDREAE - Atlas Plates and Tables 5-10, figs. A-I; 11, figs. A-E; and 50, fig. A. Representative genera: *Cyrtandra*, *Hexatheca*, and *Rhynchotechum*.

Burt (1963) assigned five genera to the tribe Cyrtandreae: *Hexatheca*, *Rhynchotechum*, *Protocyrtandra*, *Sepikaea*, and *Cyrtandra*. However, Gillett (1970) combined *Protocyrtandra* with *Cyrtandra* making the tribe a unit of four genera. This study contains representative species of all the genera with the exception of *Sepikaea* of which seeds were not available.

Seed Shapes

The seeds of the species of the Cyrtandreae vary from narrowly elliptic (*Cyrtandra compressa* Pl. 9, fig. A), to broadly elliptic (*Cyrtandra zamboangensis* Pl. 6, fig. E).

Apical Characters

The seed apices of the species of the tribe Cyrtandreae are either acute and/or obtuse with the exception of *Cyrtandra* (Pl. 6, figs. E, F, G) and *Rhynchotechum* (Pl. 11, figs. A, D), the seeds of which are constrictate at one apex.

Cell Orientation

The cell orientation of the species of this tribe is either straight (*Cyrtandra longicarpa* Pl. 5, fig. A) or irregular (*Cyrtandra parvifolia* Pl. 5, fig. I), with the exception of *Cyrtandra sandei* (Pl. 10, fig. G) and *Cyrtandra flabelligera* (Pl. 10, fig. F) in which the cell orientation is spiral.

Cell Shapes and Primary (PCC) and Secondary (SCC) Cell Characters

There are five basic cell shapes among the species of the Cyrtandreae, with a wide diversity of primary and secondary cell characters in types 2 through 5.

1. Narrowly lineate-polygonate.

PCC: Edges elevated.
Faces depressed.
Crests fused.

SCC: Edges smooth.
Faces not visible.

Type 1 includes two species only: *Cyrtandra flabelligera* and *Cyrtandra sandei* (Pl. 10, figs. F, G).

2. Lineate-polygonate.

PCC: Edges shallowly elevated (*Cyrtandra compressa* Pl. 9, fig. A) to depressed (*Cyrtandra multiseptata* Pl. 7, fig. G).

Faces shallowly depressed to distinctly elevated, with linear striae which can vary from narrow (*Cyrtandra compressa* Pl. 9, fig. A) to wide (*Cyrtandra multiseptata* Pl. 7, fig. G).

SCC: Edges smooth.

Faces range from smooth (*Cyrtandra compressa* Pl. 9, fig. A) to verrucate (*Cyrtandra multiseptata* Pl. 7, fig. G).

Type 2 includes 12 species of *Cyrtandra* (Pl. 7, fig. F to Pl. 9, fig. A), and *Rhynchoechum discolor* (Pl. 11, figs. A-D).

3. Polygonate. (*Cyrtandra longicarpa* Pl. 5, figs. A, B).

PCC: Edges distinctly elevated.

Faces distinctly depressed.

Crests fused.

SCC: Edges varying from rough to smooth.

Faces rough.

Type 3 includes 11 species of *Cyrtandra* (Pl. 5, fig. A to Pl. 6, fig. D, and Plate 50, fig. A).

4. Polygonate. (*Cyrtandra mauiensis* var. *truncata* Pl. 7, figs. D, E).

PCC: Edges distinctly elevated.

Faces distinctly depressed.

Crests discrete.

SCC: Edges and/or faces rough to smooth.

Type 4 includes 8 species of *Cyrtandra* (Pl. 6, fig. E to Pl. 7, fig. E).

5. Polygonate. (*Cyrtandra anthropophagorum* Pl. 10, figs. B, C).

PCC: Edges and/or faces irregularly elevated and/or depressed.

SCC: Edges and/or faces irregular, ranging from shallow and irregular crests of *Cyrtandra longifolia* (Pl. 9, figs. F, I) through slightly auriculate (*Cyrtandra anthropophagorum* Pl. 10, figs. B, C), to distinctly auriculate and/or tuberculate (*Cyrtandra montana* Pl. 10, fig. E).

Type 5 includes 11 species of *Cyrtandra* (Pl. 9, fig. C to Pl. 10, Fig. E) and *Hexatheca fulva* (Pl. 10, fig. H).

The genus *Cyrtandra* is a very large assemblage of some 600 species (Gillett 1973). However, Gillett pointed out that the extant infrageneric classifications of the genus *Cyrtandra* had been based on inadequate or biased samples of the genus, and that the use of any infrageneric classification of the genus would be inappropriate until an extensive investigation had been made of the entire genus. I agree with Gillett, and because a definitive study on the genus has yet to be undertaken, the results of this study have not been compared with any of the extant infrageneric classifications. However, I am currently conducting an ongoing investigation of the genus *Cyrtandra* that may determine if the seed morphology of the genus *Cyrtandra* supports the other morphological characters of the genus, as does the seed morphology of the tribes Klugieae and Trichosporeae.

The species of *Cyrtandra* included in this study were selected from well over 100 species examined, to show the range of seed characters observed throughout the genus.

Rhynchoechum discolor was classified as *Isanthera discolor* (Maxim.) B. L. Burtt until Burtt (1962) united the genus *Isanthera* with *Rhynchoechum*. The secondary cell characters of the seeds of *Rhynchoechum discolor* (Pl. 11, figs. A, B, C) are similar to those of several of the species of

Cyrtandra in type 2, such as *Cyrtandra multiseptata* (Pl. 7, figs. G, H); however, the secondary cell characters of *Rhynchotechum ellipticum* (Pl. 11, fig. E) are quite different from those of *R. discolor* but are similar to those of *Cyrtandra garnotiana* in type 4 (Pl. 7, fig. B). The seeds of the third genus in the tribe (*Hexatheca fulva*), are remarkably similar to those of *Cyrtandra anthropophagorum* (Pl. 10, figs. B, C).

Within the Gesneriaceae the seeds of the species of the tribe Cyrtandreae are second only to those of the tribe Didymocarpeae in their extremely wide range of character diversity; the characters are exhibited in a variety of combinations and trends throughout the tribe.

The cell orientation of the examined species of the tribe is either straight or irregular, with the exception of *Cyrtandra sandei* and *C. flabelligera* in which the cell orientation is spiral. These two species of *Cyrtandra* are also distinct from the rest of the tribe at the cell shape, primary and secondary cell character levels and compose shape type 1.

The cell shapes of the tribe exhibit a trend from narrowly lineate-polygonate to irregularly polygonate and within the framework of this trend can be divided into five basic cell shape types. The primary and secondary cell characters of the species of each of the five cell shape types are diverse among themselves but distinct as a group from those of the other types. For instance, types 3, 4, and 5 are similar to each other with a polygonate cell shape but distinct from each other at the primary cell character level. The primary and secondary cell characters of the types 2 through 5 are especially diverse and exhibit a number of trends in character expression.

The distinctive lineate-polygonate cells with elevated faces and depressed edges exhibited by some of the species of type 2, such as *Cyrtandra multiseptata* (Pl. 7, figs. G, H) and *Rhynchotechum discolor* (Pl. 11, figs. A-D) are unique, within the Gesneriaceae, to the tribe Cyrtandreae. In addition, the auriculate and/or tuberculate cell faces of the species in cell type 5 are also unique to the tribe Cyrtandreae, although they are somewhat similar to those of some of the species of the tribe Didymocarpeae. Being able to see secondary cell characters of type 5 is one more example of the advantage of the use of the SEM. Under the light microscope, the seed surfaces of the species in type 5 of this tribe and those of the species of *Ramonda* (in the tribe Didymocarpeae) are practically indistinguishable, whereas they are in fact quite different as can be seen from the photomicrographs of the species in question. For example, *Ramonda myconi* (Pl. 15, fig. B) and *Cyrtandra montana* (Pl. 10, fig. E).

The seed morphology of the examined species of the tribe Cyrtandreae supports the unity of the group with a common cell orientation with only two exceptions: the overall and consistent trend of cell shapes from lineate-polygonate to polygonate, and the expression of the secondary cell characters in a variety of combinations and trends throughout the tribe.

The members of the tribe Cyrtandreae exhibit certain seed characters that are unique to the tribe as discussed above. The seeds of *Cyrtandra flabelligera* and *C. sandei* are distinct from the rest of the tribe but similar to those found in other tribes. The similarities of these two *Cyrtandra* species to species in other tribes will be discussed later.

TABLE VI. TRIBE 2: TRICHOSPOREAE - Atlas Plates and Tables 11, figs. F - I; and 12, figs. A - I. Representative genera: *Aeschynanthus*, *Agalmyla* and *Lysionotus*.

The tribe Trichosporeae comprises four genera: *Aeschynanthus*, *Agalmyla*, *Lysionotus*, and *Micraeschynanthus* (Burt and Woods 1975). This study contains representative species of all of the genera with the exception of *Micraeschynanthus* of which seeds were not available.

Seed Shapes

The seeds of all of the examined species of the Trichosporeae are narrowly elliptic in shape.

Apical Characters

The seeds of all of the examined species of this tribe had filiform apical appendages on both apices of the seeds. The appendages vary from a flat, single appendage (*Agalmyla clarkei* Pl. 12, fig. G) to the multiple hairlike projections of *Aeschynanthus hartleyi* (Pl. 12, fig. A). Some of the appendages are branched as on *Aeschynanthus perrottetii* (Pl. 11, figs. H, I). The apical appendages were removed from most of the seeds to facilitate examination with the SEM.

Cell Orientation

The basic cell orientation of the Trichosporeae seeds is straight, with the exception of *Aeschynanthus magnificus* (Pl. 12, fig. B) which has a spiral cell orientation.

Cell Shapes and Primary (PCC) Cell Characters

The cell shapes of this tribe range from narrowly lineate-polygonate (*Aeschynanthus micranthus* Pl. 11, fig. G) to lineate-polygonate (*Agalmyla clarkei* Pl. 12, fig. G).

- PCC: Edges elevated on all examined species of the tribe.
Faces depressed on all examined species of the tribe.
Crests fused on all examined species of the tribe.

Secondary (SCC) Cell Characters

The edge characters in this tribe are extremely diverse and consist of two distinct types.

- SCC: 1. Edges exhibit a very diverse trend ranging from basically shallow edges with slightly auriculate cell apices (*Aeschynanthus micranthus* Pl. 11, fig. G) through increasingly more prominent edges (Pls. 11-12) to the very distinctive tuberculate cells of *Aeschynanthus bracteatus* (Pl. 12, fig. C), in which the cell edges and faces elongate to produce one of the most elaborate seed surfaces in the family.

Faces smooth to rough and/or finely striate where visible.

Type 1 includes the genus *Aeschynanthus* (Pls. 11 and 12).

2. Edges shallow, evenly elevated and distinctively papillate. The papillae are unique in that they are astride the cell crests.

Faces basically smooth and sparsely papillate.

Type 2 includes the species of *Agalmyla* and *Lysionotus* (Pl. 12).

The consistent occurrence among the Trichosporeae genera of elongate fruits that contain seeds with apical appendages, epiphytic or climbing habit, certain unusual anatomical features (Rosser and Burt 1969), as well as a basic chromosome number of $n = 16$ (Ratter 1975), are some of the characters that support the unity of the tribe as a natural group. The seed morphology of the tribe, in addition to the occurrence of apical appendages, also supports the concept of the tribe as a natural group with the similarity of seed shapes, cell orientation, cell shapes, and primary cell characters of its members.

The floral and leaf morphology (Burt 1969) and certain anatomical features of the tribe are similar but distinct, in varying degrees, from genus to genus and indicate that *Aeschynanthus* and *Agalmyla* share a closer affinity with each other than with the other members of the tribe (Rosser and Burt 1969). In addition, the cortical cell sheaths of *Aeschynanthus* distinguish it completely from the other genera of the tribe (Rosser and Burt 1969). The seed morphology, in addition to supporting the unity of the group, as above, also distinguishes the genus *Aeschynanthus* (secondary cell character type 1) from *Agalmyla* and *Lysionotus* (secondary cell character type 2).

The five sectional divisions of the genus *Aeschynanthus* are based on apical appendage types (Burt and Woods 1975) and the selection of twenty *Aeschynanthus* species, of which seeds were examined for this study, included at least one species from each of the sections. Unfortunately, the seeds of *Aeschynanthus miniata* (the only representative obtained of section *Aeschynanthus*) were too immature to be of any use in this study. In addition, the seeds of the other species available did not include enough representatives of the remaining four sections to determine if consistent sectional seed character distinctions exist among the species other than the apical appendage types.

The species of the *Aeschynanthus* represented in this study were selected, from the larger number examined, to include the range of seed characters observed throughout the genus. The seeds of certain species (Pl. 12, fig. C) are more distinctive than others, but none of the species examined possesses seeds that are identical to those of another species.

The tribe Trichosporeae is unique in the family in that the seeds of all the species have filiform appendages on both apices and all are of a uniform narrowly elliptic shape. The seeds of the genus *Aeschynanthus* are unique in the extremely wide range of secondary cell character elaborations exhibited by the species. Certain seed characters of the examined species of *Agalmyla* and *Lysionotus* are similar to those found in the Didymocarpeae.

Mature seeds of this tribe are particularly difficult to obtain because the ripe seed is soon dispersed in the wild (Burt and Woods 1975), and the author's experience has shown, all too often, that seemingly ripe fruits from an herbarium sheet contain only very immature seed. In addition, the filiform appendages of this tribe are extremely fragile, especially on seeds obtained from herbarium sheets and/or transported after removal from the fruits, as were the seeds for this study. Unfortunately, the length of the appendages necessitated their removal to facilitate examination with the SEM. Therefore, for the purpose of this study, the seeds of this tribe were examined for the possession of apical appendages, but the appendage diversity was not included in the investigation. Nevertheless, the diversity of the Trichosporeae seeds and their apical appendages observed during this investigation indicates that an additional SEM investigation of the Trichosporeae seeds and appendages, with a wider range of the *Aeschynanthus* species, would provide a valuable addition to the body of existing information of the group.

The members of the tribe Trichosporeae exhibit certain characters that are unique to the tribe as discussed above; the similarities to seed characters found in other tribes will be discussed later.

TABLE VII. TRIBE 3: KLUGIEAE - Atlas Plates and Tables 13, figs. A-I; 14, figs. A-E; and 51, fig. G. Representative genera: *Epithema*, *Loxonia*, *Monophyllaea*, *Stauranthera*, *Whytockia*, and *Rhynchoglossum*.

All of the Klugieae genera (Burt 1975) are represented in this study. Burt (1977) stated that the Klugieae were "... a small tribe of six genera with a remarkable range of morphological characters." The same statement holds true for the seed characters of the tribe.

Seed Shapes

The seed shapes of this tribe range from narrowly elliptic (*Rhynchoglossum* Pl. 13, fig. A) to elliptic (*Epithema* Pl. 13, fig. D).

Apical Characters

The apical characters of this tribe include acute, constrictate (*Epithema* Pl. 13, fig. D), and obtuse (*Rhynchoglossum* Pl. 13, fig. C), and are similar to those found throughout the family.

Cell Orientation, Cell Shape and Primary (PCC) and Secondary (SCC) Cell Characters

The elevated edges and depressed faces (primary cell characters) of the cells are basically uniform throughout the tribe. The widest character diversity and/or uniqueness of the seeds of this tribe are demonstrated by cell orientation, cell shape, cell crests (primary cell characters) and secondary cell characters.

The cell orientation of the tribe exhibits a trend from straight to spiral and, within the framework of this trend, can be divided into three basic types.

1. Straight.

Cell shape: Lineate-polygonate to polygonate.

PCC: Crests discrete.

SCC: Edges and faces variably rough to sparsely verrucate.

Type 1 includes species of *Epithema* and *Monophyllaea* (Pls. 13, 51).

2. Straight to spiral.

Cell shape: Lineate-polygonate.

PCC: Crests fused.

SCC: Edges and faces distinctively verrucate.

Type 2 includes *Rhynchoglossum* species (Pl. 13).

3. Spiral.

Cell shape: Narrowly lineate-polygonate.

PCC: Crests discrete.

SCC: Edges and faces smooth.

Type 3 includes species of *Stauranthera*, *Whytockia*, and *Loxonia*.

Each of the three types of cell orientation of the Klugieae tribe has a distinct combination of cell shape, cell crests (primary cell characters), and secondary cell characters, and each type shares some characters with the genera of other types. In addition, the seeds of the individual species are distinct

from each other by the character variations illustrated and defined on Atlas Plates and Tables 13 and 14.

The seed characters exhibited by *Epithema* and *Monophyllaea* (type 1) are similar to those of some of the species in the tribes Cyrtandreae and Didymocarpeae.

The genus *Rhynchoglossum* (type 2) is unique among the Gesneriaceae with its very wide disjunct distribution; it occurs from West Africa to the Solomon Islands in the Pacific and also in Central and South America (Burt 1977). The seeds of the *Rhynchoglossum* are also unique within the family with straight (*R. klugoides*) and spiral (*R. obliquum*) cell orientation on seeds that are otherwise extremely similar. The particular combination of characters that demonstrates the similarity (lineate-polygonate cells, fused crests and distinctively verrucate cell edges) is also unique within the family. *Rhynchoglossum azureum* (Pittier 14154 US), (Pl. 51) is from Costa Rica, Central America, and *R. klugoides* is from Sumatra, and yet the seed morphology of the two species is extremely similar except for a difference in cell shape. *Rhynchoglossum azureum* and *R. klugoides* even share the same apical character, which is unique within the family to the genus *Rhynchoglossum*. The constricted portion of the seed apex is somewhat sunken into the end of the seed and is surrounded by a collar of protruding cells. In addition, the distinctive characters of the cell faces are shared by all of the examined species of *Rhynchoglossum*. Of additional interest are the tetragonate projections on the cell faces of *R. azureum*; this is the only species, outside of the tribe Didymocarpeae, to possess this particular character, which suggests an apparent affinity of the genus *Rhynchoglossum* with the tribe Didymocarpeae. The seeds of the examined species of *Rhynchoglossum* certainly provide a very strong confirmation for Chuang and Heckard's statement "... that seed surface patterns are characteristic and constant for a given species or a group of species" (1972, p. 258).

The *Rhynchoglossum* species (type 2) share verrucate cell surfaces and straight cell orientation with type 1 and spiral cell orientation with type 3. The fused crests of the cell edges of the examined species of *Rhynchoglossum* (type 2) distinguishes the genus from the species of the genera in types 1 and 3, which have discrete crests.

The genera in type 3 (*Stauranthera*, *Whytockia*, and *Loxonia*) were classified as belonging to the Loxonieae (Burt 1963) until Weber (1976) showed that the anatomical and floral morphology of *Whytockia* and *Monophyllaea* (of the Klugieae) provided evidence of a close affinity between the two genera. Burt (1977) united the genera of these tribes making Klugieae a small tribe of six genera: *Epithema*, *Monophyllaea*, *Rhynchoglossum*, *Loxonia*, *Stauranthera*, and *Whytockia*. Weber (1977) concluded that an investigation of the shoot morphology and inflorescence of *Loxonia*, *Stauranthera*, *Whytockia*, *Epithema*, and *Rhynchoglossum* indicated a close relationship between *Loxonia* and *Stauranthera* and that they may have been derived from a *Whytockia*-like ancestor. The results of his study also suggested a close affinity between the two genera and *Rhynchoglossum* as well as *Epithema*.

The seed morphology of the tribe supports the unity of the Klugieae, as defined by Burt (1977), with the overall trend of the cell orientation exhibited by the species, the overlapping or shared characters of the three cell orientation types, and the uniformity of the edges and faces at the primary cell character level.

The seed morphology also confirms and strengthens Weber's conclusions (1976, 1977). The discrete cell crests of cell orientation types 1 and 3 sup-

port the concept of an affinity between *Whytockia* and *Monophyllaea* (Weber 1976). The cell orientation diversity of the *Rhynchoglossum* species demonstrates the affinity of the genus to *Loxonia*, *Stauranthera*, and *Epithema* (Weber 1977). *Rhynchoglossum obliquum*, *Loxonia*, and *Stauranthera* have spiral cell orientation, while *R. klugioides* and *Epithema* have straight cell orientation. The affinity between *Rhynchoglossum* and *Epithema* is further strengthened by the verrucate cell surfaces of the two genera. In addition, the seed characters exhibited by *Stauranthera* and *Whytockia* (of type 3) are similar to those of some of the species of the subfamily Gesnerioideae.

The members of the tribe Klugieae exhibit certain character combinations that are unique to the tribe as discussed above. The similarities to seed characters found in other tribes will be discussed later.

TABLE VIII. TRIBE 4: DIDYMOCARPEAE - Atlas Plates and Tables 14, figs. F-I; 15-29, figs. A-I; 30, figs. A-F; 49, fig. A; and 50, figs. B-I. Representative genera: *Championia*, *Tetraphyllum*, *Ramonda*, *Jankaea*, *Haberlea*, *Beccarinda*, *Platystemma*, *Petrocosmea*, *Conandron*, *Ancylostemon*, *Loxostigma*, *Oreocharis*, *Tremacron*, *Petrocodon*, *Opithandra*, *Didymocarpus*, *Orchadocarpa*, *Didissandra*, *Hemiboea*, *Chirita*, *Saintpaulia*, *Primulina*, *Tri-sepalum*, *Linneaopsis*, *Dichiloboea*, *Acanthonema*, *Streptocarpus*, *Loxocarpus*, *Paraboea*, *Rhabdothamnopsis*, *Boea*, *Phylloboea*, *Chlamydoboea*, *Ornithoboea*, *Leptoboea*, *Boeica*, *Colpogyne*, *Isometrum*, *Anna*, *Corallo-discus*, *Briggsia*, and *Schizoboea*.

The above genera, with the exception of *Loxostigma*, *Schizoboea*, and *Colpogyne* were included in the Didymocarpeae by Burt (1963) when he published his *Tentative Keys to the Tribes and Genera* of the Old World Gesneriaceae. Burt segregated *Colpogyne* from *Streptocarpus* (1971) and *Schizoboea* from *Didymocarpus* (1974), and transferred *Loxostigma* from the tribe Trichosporeae to the tribe Didymocarpeae (1975).

This study does not include representative species of the genera *Cathayanthe*, *Dasydesmus*, *Bournea*, *Codonoboea* or *Tengia* because seeds of these genera were not available.

Seed Shapes

The seed shapes of the tribe Didymocarpeae vary from narrowly lineate-polygonate (*Jankaea* Pl. 15) to elliptic (*Ramonda* Pl. 15), and one species of *Didissandra* (Pl. 19) is broadly elliptic. The range from narrowly elliptic to elliptic is found even within some of the genera, such as *Chirita*, *Didymocarpus*, and *Streptocarpus*, as well as within the tribe as a unit.

Apical Characters

The apical characters of this tribe include acute, constrictate, filiform, and obtuse. Constrictate is the most common apical character in the Didymocarpeae and varies from slightly constrictate (*Schizoboea* Pl. 18, fig. G) to distinctly constrictate (*Dichiloboea* Pl. 22, fig. G). The filiform apices of *Loxostigma* (Pl. 50, fig. G) and *Anna* (Pl. 50, fig. F) are the only examples of filiform apices found in the Cyrtandroideae outside of the Trichosporeae.

Cell Orientation

The cell orientation of the seeds of this tribe includes: Straight — all of

the genera with the exceptions of *Petrocosmea*, *Conandron*, and *Isometrum*. Straight to slightly spiral and irregular — a trend found within the species of *Petrocosmea* (Pl. 16). Slightly spiral — the species of *Conandron* (Pl. 16) and *Isometrum* (Pl. 50).

Primary (PCC) Cell Characters

The primary cell characters of this tribe do not correlate with the cell shape and secondary characters. Therefore, these are detailed below. The primary cell characters consist of three basic types.

- PCC:
1. Edges distinctively elevated.
Faces distinctively depressed.
Type 1 includes all of the species of the tribe with the exception of those in types 2 and 3.
 2. Edges elevated to irregularly elevated.
Type 2 includes all of the species of *Streptocarpus* (Pls. 23-26) and *Conandron* (Pl. 16), as well as *Chirita asperifolia* (Pl. 20, fig. E).
 3. Edges depressed.
Faces elevated.
Type 3 includes the species of *Primulina* (Pl. 21) and *Opi-thandra* (Pl. 17).

Cell Shapes and Secondary (SCC) Cell Characters

The widest character diversity and/or uniqueness of the seeds of this tribe are demonstrated by the cell shapes and secondary cell characters. Based on these characters the members of this tribe can be divided into two basic groups. The seeds of the genera in group 1 exhibit similar cell shapes and a moderate range of cell edge character diversity but very little cell face character diversity. On the other hand, the seeds of the genera in group 2 exhibit a common cell shape and a small range of cell edge character diversity but an extremely wide range of very elaborate cell face character diversity.

Group 1.

Cell shapes

1. Narrowly lineate-polygonate, all of the examined species of *Jankaea*, *Haberlea*, and *Beccarinda* (Pl. 15).
2. Narrowly lineate-polygonate, a trend within the species of *Petrocosmea* (Pl. 16).
3. Lineate-polygonate, all of the examined species of *Tetraphyllum* (Pl. 14), *Ramonda* (Pl. 15), *Platystemma* (Pl. 15), *Conandron* (Pl. 16), *Loxostigma* (Pls. 16, 50), *Ancylostemon* (Pl. 16), *Oreocharis* (Pl. 17), *Tremacron* (Pl. 17), *Isometrum* (Pl. 50), *Corallodiscus* (Pl. 50), *Anna* (Pl. 50), and *Briggsia* (Pl. 49).

SCC: Edges. Papillate, the species of *Conandron* (Pl. 16) and *Anna* (Pl. 50).

Auriculate, a trend from slightly to distinctly auriculate and/or undulate, the species of *Tetraphyllum* (Pl. 14), *Ramonda* (Pl. 15) and *Jankaea* (Pl. 15).

Rough to Smooth, all of the examined species in this tribe with the exception of the five genera immediately above.

Faces. Striate, *Loxostigma* (Pl. 16).

Rough to Smooth, all of the examined species of this tribe with the exception of *Loxostigma*.

Group 1 includes the genera: *Jankaea*, *Haberlea*, *Beccarinda*, *Petrocosmea*, *Tetraphyllum*, *Briggsia*, *Isometrum*, *Platystemma*, *Anna*, and *Corallo-discus* (see above for plate numbers).

Group 2.

Cell Shapes: Polygonate, all of the examined species of the genera in this group.

The secondary cell characters of this group are the most diverse in the family. The secondary cell characters are illustrated and recorded at the species level on the Atlas Plates and Tables, and summarized at the genus and tribal level on the Summary Tables. However, to demonstrate further the character diversity of this very large group and the manner in which the characters are exhibited among the genera, a specific example of each character is given (genus, plate and figure number) followed by the genera in which the character occurs. (Species shown with a photomicrograph of a whole seed as well as a close-up of the cells.)

SCC: Edges. Papillate, *Chirita* (Pl. 19, figs. G, H), *Chirita*, *Didissandra* and *Anna*.

Auriculate, *Didymocarpus* (Pl. 18, fig. A, this example does not have a close-up).

Verrucate, *Streptocarpus* (Pl. 23, figs. C, F), *Hemiboea*, *Chirita*, *Saintpaulia*, *Trisepalum*, *Dichiloboea*, *Streptocarpus*, *Paraboea*, *Boea*, and *Phylloboea*.

Striate, *Paraboea* (Pl. 27, figs. D, G), *Paraboea*, *Saintpaulia*, and *Colpogyne*.

Smooth, *Championia* (Pl. 14, fig. F, this example does not have a close-up).

Rough to Smooth, all of the remaining examined species of this group.

Faces. Papillate, *Chirita* (Pl. 19, figs. G, H), *Chirita* and *Didissandra*. Tuberculate, *Saintpaulia* (Pl. 20, figs. G, H), *Didissandra*, *Chirita*, *Saintpaulia*, *Didymocarpus*, *Primulina*, *Dichiloboea*, *Streptocarpus*, *Boeica*, *Colpogyne*, and *Schizoboea*. Auriculate, *Trisepalum* (Pl. 21, figs. F, I), *Trisepalum* and *Linneaopsis*.

Ocellate, *Streptocarpus* (Pl. 24, figs. B, E), *Streptocarpus* and *Colpogyne*.

Tetragonate, *Ornithoboea* (Pl. 29, figs. F, I), *Streptocarpus*, *Paraboea*, *Boea*, *Chlamydoboea*, and *Ornithoboea*.

Verrucate, *Didymocarpus* (Pl. 18, fig. C), *Phylloboea*, *Orchadocarpus*, *Hemiboea*, *Chirita*, *Dichiloboea*, *Boea*, *Chlamydoboea*, and *Ornithoboea*.

Striate, *Boeica* (Pl. 30, figs. A, B), *Boeica*, *Leptoboea*. The striae are irregularly oriented and range from shallow to very distinctively striate. The seeds of *Boeica fulva* (Pl. 30, fig. A, B) are among the most elaborate in the family.

Rough to Smooth, the remaining examined species of the group.

Group 2 includes the genera: *Championia* (Pl. 14), *Petrocodon* (Pl. 17), *Opithandra* (Pl. 17), *Didymocarpus* (Pls. 17, 18), *Schizoboea* (Pl. 18), *Orchadocarpa* (Pl. 18), *Didissandra* (Pls. 18, 19), *Hemiboea* (Pl. 19), *Chirita* (Pls. 19, 20), *Saintpaulia* (Pls. 20, 21), *Primulina* (Pl. 21), *Trisepalum* (Pl. 21), *Linneaopsis* (Pl. 22), *Dichiloboea* (Pl. 22), *Acanthonema* (Pl. 22), *Streptocarpus* (Pl. 23-26), *Loxocarpus* (Pl. 26, 27), *Paraboea* (Pl. 27), *Rhabdothamnopsis* (Pl. 27), *Boea* (Pl. 28), *Phylloboea* (Pl. 28), *Chlamydoboea* (Pl. 28), *Ornithoboea* (Pls. 28, 29), *Leptoboea* (Pl. 29), *Boeica* (Pl. 30), and *Colpogyne* (Pl. 30).

Recent and definitive investigations of the tribes Trichosporeae (Rosser and Burt 1968, Ratter 1975) and Klugieae (Weber 1976) have resulted in a body of taxonomic information with which studies on those groups can be compared. Unfortunately, there are no similar studies on the tribe Didymocarpeae as a whole, but within the tribe there are several studies on the genera.

Group 1.

The seeds of the species of this group vary from narrowly lineate-polygonate to lineate-polygonate and the cell orientation of this group is straight, with the exception of the species of *Conandron*, *Petrocosmea*, and *Isometrum*.

The cell edges of the species of *Conandron* and *Anna* are papillate, while the cell edges of the examined species of the remaining genera range from shallow to distinctly auriculate and/or undulate. The cell faces of the genera in this group vary from rough to smooth with the exception of *Loxostigma* in which the cell faces are finely striate.

The seeds of the examined species of this group, while distinct from species to species, share some similarities; namely, basic cell shape, cell orientation, and cell face characters.

The genus *Beccarinda* is a group of rosulate species considered by Burt (1963) to be a "... natural assemblage of species." However, as Burt points out, the species can, at times, present difficulties in keying because the plants can elongate under certain light conditions, and when the plants are elongated they are very similar to the species of *Didissandra*. This similarity led Burt (1963) to question the distinction of the two genera. However, the seeds of the two genera are completely different from each other (*Beccarinda* Pl. 15, and *Didissandra* Pls. 18-19) and support the distinction of the two genera as separate taxa.

The seeds of the examined species of *Petrocosmea*, *Conandron* and *Anna*, which are distinct from the rest of the tribe in cell orientation and secondary cell characters, are similar in certain respects to some of the species of the tribes Cyrtandreae and Trichosporeae. For example, the secondary cell characters of *Conandron* and *Anna* are similar to those found among the species of the tribe Trichosporeae, and the cell orientation as well as the primary and secondary cell characters of the examined species of *Petrocosmea* resemble those exhibited among the species of the tribe Cyrtandreae.

Group 2.

The seeds of all of the examined species of this group have straight cell orientation and polygonate cell shapes. The seeds of the genera in this group possess the most elaborate and diverse secondary cell characters in the family.

The papillae on the cell edges of *Chirita* and *Didissandra* (Pl. 19) occur along the inner walls of the cell edges, but they do not sit astride the cell crest as do the papillae on the cell crests of *Conandron* (Pl. 16) and *Anna* (Pl. 48) in group 1. The auriculate cell edges of the seeds of *Didymocarpus purpureobracteata* (Pl. 18, fig. A) are similar to those of the species of *Ramonda* (Pl. 15) and unlike the seeds of any other examined species in group 2.

The secondary cell characters of the species in group 2 express a trend from level, through shallow domes, to papillate, tuberculate, ocellate and auriculate as well as tetragonate and verrucate. These characters are expressed in a very wide variety of combinations and trends throughout the group as a unit as well as within the various genera.

As can be seen from the tabular summary, some of the genera, such as *Saintpaulia* and *Chirita*, possess more than one secondary cell face character. This does not imply that all of the species of each genus exhibit all of the characters under which they are listed. For instance, of the six species of *Saintpaulia* that are included in this study (Pl. 20-21), five of the species have seeds with tuberculate faces and one species has verrucate cell faces.

The seeds of the species of *Chirita* and *Didissandra* (Pl. 19) that have papillate cells provide excellent examples of the overwhelming advantage of the combination of a verbal description and an SEM photomicrograph over a verbal description alone and/or with light microscope photographs or camera lucida drawings. The papillae on the cells of *Chirita hamosa* (Pl. 19, figs. F, I), while similar to those of *Didissandra elongata* (Pl. 19, figs. B, C), are quite different from those of *Anna ophiorrhizoides* (Pl. 50, fig. I). The term papillate defines the basic character but the SEM photomicrograph is necessary to reveal the subtle differences of the papillae from one species to another.

The species of *Chirita* (Pls. 19-20) exhibit a trend from papillate, through mixed papillate and tuberculate, to tuberculate, with the exception of *Chirita asperifolia* (Pl. 20, fig. E) which is quite different from the other examined species of the genus. However, the seeds of *Chirita asperifolia* are quite similar to some of the species of the tribe Cyrtandreae. Wood (1974) pointed out that *Chirita asperifolia* was a taxonomically confusing species with an obscure affinity to the section in which it is classified, and that the species might repay further investigation. The distinction of the seeds of this species from that of the rest of the genus certainly confirms Wood's statements and suggests that its affinity might even be with other members of the Cyrtandroideae.

During the course of his revision of the genus *Chirita*, Wood (1974) combined *Chirita blumei* with *Chirita asperifolia*. Seeds of specimens that were formerly *C. blumei* were examined as a part of this study and were found to be identical with those of *C. asperifolia*, confirming Wood's combination of the species. The species of *Chirita* represented in this study were selected from a much larger number examined, and include species from all three of the sections of the genus (Wood 1974) as well as the range of seed characters observed throughout the genus.

Burt (1974) segregated *Schizoboea kamerunensis* (Pl. 18, fig. D) from the genus *Didymocarpus* and suggested that it may have an affinity with *Saintpaulia* through *S. inconspicua* (Pl. 20, fig. F). The seeds of *Schizoboea kamerunensis* have distinctively tuberculate cell faces, as do those of the examined species of *Saintpaulia*, with the exception of *S. inconspicua*. The seeds of *Didymocarpus madagascariensis* (Pl. 18, fig. E) are also similar to those of *Schizoboea* but unlike the other examined species of *Didymocarpus*. The seeds of *Colpogyne* (also from Madagascar, Pl. 30) and some of the species of *Streptocarpus*, from the African continent as well as Madagascar, are also similar to those of *Schizoboea*.

Ocellate cell faces are unique, within the Gesneriaceae, to the Didymocarpeae. The ocellate cells occur on the seeds of *Colpogyne* (Pl. 30) and a number of the species of *Streptocarpus*. The amount of ocellate cells per seed is apparently species specific and ranges from about 100% on the seeds of *Colpogyne* (Pl. 30) and *Streptocarpus saxorum* (Pl. 24, fig. E), through mixed ocellate and tuberculate (*Streptocarpus hilsenbergii* Pl. 23, fig. B) to *Streptocarpus tsaratananensis* (Pl. 24, fig. D) on which there is only an occasional ocellate cell. The ocellate and/or tuberculate cells occur on the seeds

of the majority of the examined species of the subgenus *Streptocarpella*, but on only a few of the examined species of the subgenus *Streptocarpus* (Hilliard and Burt 1971). The seeds of the species of *Streptocarpus* that lack ocellate and/or tuberculate cells are very similar to those of *Saintpaulia inconspicua* (Pl. 20, fig. F).

The term tetragonate was coined by the author to define the tetragonal-shaped projections that occur on the cell faces of the genera listed above. So far as is known, tetragonate cell characters have not been reported for the seeds of any other family. The tetragonate cell character is unique, within the Gesneriaceae, to the Didymocarpeae. The shape of the projections suggests that they may be the result of a mineral deposit, possibly a pigment such as dunnione (Burt 1971). But the answer to their origin and composition, and whether or not tetragonate cells occur in other families will have to wait for a future investigation. Meanwhile, it is of interest to note that the tetragonate cell character is exhibited by some of the species in a number of genera, as listed above. That the character is unique to this tribe but occurs among the species of a number of genera suggests a particular affinity between the genera in question.

The seeds of the species of the tribe Didymocarpeae exhibit an amazing variety of combinations and trends of seed characters. The distinction between the seeds of the species of groups 1 and 2 suggests that the species of each group may share a closer affinity with each other than with the species of the other group. In addition, the expression of the secondary cell characters among the genera of group 2 suggests that some of the genera share a particularly close affinity to those with similar cell characters, while at the same time the species as a group represent a natural assemblage as a taxon.

The members of the tribe Didymocarpeae exhibit certain seed characters that are unique to the tribe as discussed above; the similarities to the seed characters found in other tribes will be discussed later.

SUBFAMILY GESNERIOIDEAE

The subfamily Gesnerioideae as here defined comprises 11 tribes: Beslerieae, Bellonieae, Gloxinieae, Sinningieae, Kohlerieae, Solenophoreae, Gesnerieae, Episcieae, Mitrarieae, Coronanthereae and Anetantheae. All of the tribes are represented in this study. (Atlas Plates and Tables 31-48, figs. A-I; 49, figs. B-I; and 51, figs. A-F, H-I.)

TABLE IX. TRIBE 5: BESLERIEAE - Atlas Plates and Tables 31-32, figs. A-I; 49, figs. D, E, F; and 51, figs. D-F. Representative genera: *Cremosperma*, *Besleria*, *Reldia*, and *Gasteranthus*.

Fritsch (1893), Morton (1939), Melchior (1964) and Wilson (1974) maintained the tribe Beslerieae in the subfamily Cyrtandroideae; however, it seems more appropriate at this time to replace it in the subfamily Gesnerioideae (Hanstein 1853).

The examined species of the tribe Beslerieae can be divided into two distinct groups based on distinctions between the seed shapes, apical characters, cell orientation and cell shapes as well as primary and secondary cell characters.

Group 1.

Seed Shapes

The seed shapes of this group range from narrowly elliptic to elliptic.

Apical Characters

The apical characters of group 1 include acute, constrictate, and obtuse.

Cell Orientation

The cell orientation of group 1 is straight.

Cell Shape and Primary (PCC) and Secondary (SCC) Cell Characters

Cell shape: Lineate-polygonate to polygonate.

PCC: Edges elevated.
Faces depressed.
Crests discrete.

SCC: Edges smooth.
Faces smooth.

Group 1 includes the examined species of *Cremosperma* (Pls. 31 and 51) with the exception of *Cremosperma minutiflorum* (Pl. 51).

Group 2.

Seed Shapes

The seed shapes of this group range from elliptic (*Besleria kalbreyeri* (Pl. 31, fig. E) to broadly elliptic (*Besleria* and *Reldia* Pl. 32).

Apical Characters

The apical characters of group 2 include acute, constrictate, coronate, and obtuse.

Cell Orientation

The cell orientation of group 2 ranges from slightly spiral to tightly spiral.

Cell Shape and Primary (PCC) and Secondary (SCC) Cell Characters

There are two basic cell shapes among the species of group 2, with a diversity of primary and secondary cell characters in each type:

1. Cell shape: Narrowly lineate-polygonate to lineate-polygonate.

PCC: Edges elevated.
Faces depressed.
Crests discrete.

SCC: Edges, a trend from smooth (*Besleria* Pl. 31) to distinctly auriculate and/or undulate (*Besleria*, *Reldia* Pls. 31-32; and *Cremosperma minutiflorum* Pl. 51).
Faces rough.

Type 1 includes the examined species of *Besleria*, *Reldia* (Pls. 31-32) and *Cremosperma minutiflorum* (Pl. 51).

2. Cell shape: Lineate-polygonate to polygonate.

PCC: Edges elevated.
Faces depressed.
Crests discrete.

SCC: Edges smooth to extremely auriculate and/or undulate.
Faces rough.

Type 2 includes the examined species of *Gasteranthus* (Pl. 49).

Group 2 includes the examined species of *Besleria*, *Reldia*, and *Gasteranthus* (Pls. 31-32, 49) and *Cremosperma minutiflorum* (Pl. 51).

The seed morphology of the examined species of the tribe Beslerieae shows that the genera of the tribe can be divided into two distinct groups based on apical characters, cell orientation and cell shapes as well as primary and secondary cell characters. Group 1 contains the genus *Cremosperma* and group 2 consists of the examined species of *Besleria*, *Reldia* and *Gasteranthus*.

Group 1.

The seeds of the examined species of *Cremosperma* (*C. congruens*, *C. jucundum* and *C. peruvianum*) are quite distinct in every respect from those of the examined species of *Besleria*, *Reldia*, and *Gasteranthus*. Morton (1939) segregated the species of *Cremosperma* from the genus *Besleria* on the basis of morphological differences, but he also considered the two genera to be closely related to each other. The distinct differences between the seeds of the examined species of *Besleria* and the above three species of *Cremosperma* support Morton's separation of the taxa but do not support the concept of an apparent affinity between the genera. However, the seeds of *C. minutiflorum* are similar to those of the examined species of *Besleria* and will be discussed in group 2.

With only a few exceptions, the seeds of the examined species of the subfamily Gesnerioideae, including those of the genera *Besleria*, *Reldia*, and *Gasteranthus*, possess a spiral cell orientation. The cell orientation of the seeds of the above three species of *Cremosperma* (*C. congruens*, *C. jucundum* and *C. peruvianum*) are most decidedly straight (Pls. 30, 51). In addition, the seeds of these three species of *Cremosperma* are also distinct from those of *Besleria*, *Reldia* and *Gasteranthus* as well as the rest of the examined species of the subfamily Gesnerioideae, in their apical characters, seed and cell shapes, as well as primary and secondary cell characters. On the other hand, the seeds of the above three species of *Cremosperma* are very similar in all of the above characters to those of several of the species of *Cyrtandra* (Pl. 7), such as *C. lysiosepala* (Pl. 7, fig. C).

That the seed morphology of *Cremosperma congruens*, *C. jucundum*, and *C. peruvianum* are so very distinct from that of the subfamily Gesnerioideae but so very similar to those of some of the members of the subfamily Cyrtandroideae, certainly raises a question regarding the natural position of the species within the classification of the family. However, as Skog (personal communication 1983) points out, "the apparent resemblances between *C. congruens* and *C. jucundum* on one hand and *Cyrtandra lysiosepala* on the other hand, go only so far as having white corollas and long peduncles." Nevertheless, the striking resemblances of the seeds of the species in question are extremely interesting and will be discussed again in this paper.

Group 2.

The species of the genus *Besleria* are distinct from those of the *Gasteranthus* by stomata, fruit and nectary differences (Wiehler 1975). The genus *Besleria* is a large assemblage of some 200 species and considered by Morton (1939) and Wiehler (1979) to be a natural and clearly defined unit. The species of *Besleria* included in this study were selected, from a much larger number of species examined, to include the range of seed characters observed throughout the genus.

The cell orientation of the examined species of *Besleria* ranges from slightly to distinctly spiral and the primary and secondary cell characters exhibit a trend from moderately elevated and smooth to distinctly elevated and auriculate and/or undulate. The seeds of *Reldia alternifolia* (Pl. 31, fig. I) are very similar, in all respects, to those of *Besleria formicaria* (Pl. 32, fig. G).

When Skog (1974) described *Nautilocalyx minutiflorus*, he mentioned that the inflorescence of the species resembled that of some of the members of *Cremosperma* but that the corolla and nectary glands of the species were similar to those found among the species of *Nautilocalyx*. Wiehler (1978) transferred the species to *Cremosperma*. However, the seeds of *C. minutiflorum* do not resemble either those of the examined species of *Nautilocalyx* or the other examined species of *Cremosperma*. The seeds of four collections of *C. minutiflorum* were examined for this study.

The only similarity found among the seeds of *Cremosperma minutiflorum* and those of the examined species of *Nautilocalyx* is the spiral cell orientation, but that type of cell orientation is also typical of the majority of the examined species of the subfamily Gesnerioideae. In addition, the seeds of *C. minutiflorum* possess coronate apices, a character not found among the examined species of *Nautilocalyx* or any other member of the tribe Episcieae, nor has it been found among the other examined species of *Cremosperma*. On the other hand, coronate apices have been found among the species of *Besleria* and *Reldia* of the tribe Beslerieae.

The seeds of *Cremosperma minutiflorum* are completely unlike those of the other examined species of *Cremosperma* (Pls. 31, 51); also, as previously mentioned, the seeds of *C. congruens*, *C. jucundum* and *C. peruvianum* are distinct from the other examined species of the subfamily Gesnerioideae in all respects. On the other hand, the seeds of *C. minutiflorum* are very similar, in all respects, to those of *Reldia alternifolia* (Pl. 32) and some of the examined species of *Besleria* such as *B. kalbreyeri* (Pl. 31) and *B. formicaria* (Pl. 32).

According to Skog (personal communication 1983), *Cremosperma minutiflorum* is similar to *Reldia alternifolia* in other morphological characters as well. Unfortunately, the details of the cytology and pollen morphology of *C. minutiflorum* and *R. alternifolia* have not been published as of the time of this writing. However, the results of this study, in conjunction with other morphological characters (Skog, personal communication 1983), may suggest that *C. minutiflorum* shares an affinity with *Besleria* and an even closer affinity with the genus *Reldia*. An investigation of the pollen and cytology of *C. minutiflorum* and *R. alternifolia* would, no doubt, help to resolve the question of the natural position of *C. minutiflorum* within the Gesneriaceae.

The seed characters of the examined species of *Besleria*, *Reldia*, *Cremosperma minutiflorum* and *Gasteranthus* (group 2) express an overall trend that suggests an apparent affinity between the genera and support the concept of the genera as a natural unit. In addition, the various combinations and trends in which the characters are expressed distinguish the species and genera from each other and support the separation of the genus *Gasteranthus* from *Besleria* (Wiehler 1975). For instance, the seeds of the examined species of *Gasteranthus* (Pl. 49) differ from those of *Besleria* and *Reldia* (Pls. 31, 32) in cell shapes and secondary cell characters. The auriculate extensions of the cells exhibited by some of the species of *Gasteranthus* are much more elaborate than those of any of the examined species of *Besleria*.

The seeds of the examined species of *Gasteranthus* are similar in cell shape, as well as in primary and secondary cell characters, to those of some species of the tribe Coronanthereae (also of the subfamily Gesnerioideae) and Didymocarpeae of the subfamily Cyrtandroideae.

The coronate apical characters that occur among the species of *Besleria*, *Reldia*, *Cremosperma minutiflorum* and *Gasteranthus* are unique, within the Gesneriaceae, to the subfamily Gesnerioideae, and occur in a wide range of variations among the species of the tribes Bellonieae, Gloxinieae, Sinningieae,

Kohlerieae and Coronanthereae as well as Beslerieae. However, the coronate apices have not been found among the examined species of the tribes Episcieae or Mitrarieae.

The characters shared among the members of the Beslerieae and those of other tribes, as mentioned above, suggest that the members of the Beslerieae share a closer affinity with some of the tribes of the subfamily Gesnerioideae than with others.

The seed morphology of the examined species of the tribe Beslerieae supports the concept of an affinity between the genera *Besleria*, *Reldia*, *Cremosperma minutiflorum* and *Gasteranthus*, but not between those genera and *Cremosperma congruens*, *C. jucundum*, and *C. peruvianum*.

The tribe Beslerieae has been transferred back and forth between the two subfamilies (Hanstein 1853, Fritsch 1893, Morton 1939, Burt 1963, Melchior 1964, and Wilson 1974) on the basis of morphological characters shared by the tribe Beslerieae with each of the subfamilies. The seed morphology of the Beslerieae shows that the members of the tribe exhibit seed characters similar to those found in both of the subfamilies. This similarity of seed characters certainly poses a number of interesting possibilities: Does the tribe actually share an affinity with both of the subfamilies? Is the tribe a link between the subfamilies? Are any of the genera misclassified?

There is no one seed character unique to the tribe Beslerieae; the similarities to those found in other tribes will be discussed again later.

TABLE X. TRIBE 6: BELLONIEAE - Atlas Plates and Tables 33, figs. A-I; 34, figs. B-I. Representative genera: *Bellonia*, *Niphaea*, *Phinaea*, *Monopyle*, and *Anodiscus*.

Seed Shapes

The seed shapes of the Bellonieae include narrowly elliptic (*Anodiscus* Pl. 34, figs. H, I), and elliptic to circular, a trend exhibited by the species of *Bellonia*, *Niphaea*, *Phinaea*, and *Monopyle* (Pls. 33, 34).

Apical Characters

The apical characters of the examined species of the tribe Bellonieae include constrictate, coronate, obtuse, and irregular. The coronate apices exhibited among the examined species of this tribe range from slightly coronate to distinctly coronate and occur on one or both apices of the seeds, depending on the taxon.

Cell Orientation

The cell orientation of the examined species of this tribe includes:

1. Straight (*Anodiscus* Pl. 34).
2. Spiral, the examined species of *Bellonia*, *Niphaea*, *Phinaea*, and *Monopyle* (Pls. 33, 34).

Cell Shapes, Primary (PCC) and Secondary (SCC) Cell Characters

The cell shapes of the examined species of this tribe range from narrowly lineate-polygonate (*Bellonia* Pl. 33) to lineate-polygonate (*Niphaea* Pl. 33).

PCC: Edges elevated, the examined species of the tribe Bellonieae.

Faces depressed, the examined species of the tribe Bellonieae.

Crests fused (*Anodiscus* Pl. 34, figs. H, I).

Crests discrete, the examined species of *Bellonia*, *Niphaea*, *Phinaea*, and *Monopyle* (Pls. 33, 34).

SCC: Edges smooth (*Anodiscus* Pl. 34, figs. H, I).

Edges, a trend from smooth to distinctly undulate and/or auriculate, the examined species of *Bellonia*, *Niphaea*, *Phinaea* and *Monopyle* (Pls. 33, 34).

The seed characters of the examined species of the tribe Bellonieae express an overall trend that supports the concept of the tribe as a natural unit. The various combinations and trends in which the characters are expressed distinguish the species and genera from each other.

The seed morphology of the examined species of *Monopyle* (Pl. 34) is an excellent example of a trend of character expression by the species of a genus. The cell shapes range from narrowly lineate-polygonate to lineate-polygonate, and the cell edges vary from moderately elevated and smooth to very distinctly elevated and auriculate and/or undulate. Among the species of the Gesneriaceae, the particular type of undulate cell edges exhibited by *Phinaea pulchella* (Pl. 33, fig. I) and *Monopyle paniculata* (Pl. 34, fig. F) is unique to the tribe Bellonieae. In addition, the trend of character expression exhibited by the species of *Phinaea* is similar to that of the species of *Monopyle*. That the morphology of the two genera is so similar suggests that the genera may share a particularly close affinity with each other.

The cell crests of *Niphaea*, *Phinaea*, and *Monopyle* are discrete. However, those of *Anodiscus xanthophyllus* are fused. In addition, *A. xanthophyllus* is one of the few examined species of the subfamily Gesnerioideae with seeds that have a straight cell orientation. However, the coronate apices, cell shape and secondary cell characters are similar to those found among the examined species of the tribe Bellonieae as well as a number of other tribes of the subfamily Gesnerioideae. Of the many species of the Gesnerioideae that possess coronate apices, those of *A. xanthophyllus* are the most elaborate.

The seed morphology of the specimens of *A. xanthophyllus* (Pl. 34, figs. H, I) confirm Chuang and Heckard's statement "... seed surface characters are characteristic and constant for a given species . . ." (1972, p. 258), and demonstrate that the overall seed morphology is also constant and characteristic for a taxon. The seeds of *A. xanthophyllus* specimen 'a' and 'b' are, to all intents and purposes, identical and yet specimen 'a' (*Allard 22168*) and specimen 'b' (*Sagastequi s.n.*) came from different collections.

The coronate apices found among the species of the tribe Bellonieae also occur, in a wide range of variations, among the tribes Beslerieae, Gloxinieae, Sinningieae, Kohlerieae, and Coronanthereae.

The overall trend of seed shape, apical characters, cell orientation (except for *Anodiscus*), and cell shape as well as primary and secondary cell characters are similar to those found among the examined species of Beslerieae, Gloxinieae, Sinningieae, Kohlerieae, Solenophoreae and Gesnerieae.

TABLE XI. TRIBE 7: GLOXINIAE - Atlas Plates and Tables 34, fig. A; 35, figs. A-I; 36, figs. A-F; and 41, fig. I. Representative genera: *Smithiantha*, *Koellikeria*, *Heppiella*, *Gloxinia*, *Achimenes*, *Eucondonia* and *Lembocarpus*.

Seed Shape

The seed shapes of this tribe range from narrowly elliptic (*Heppiella* Pl. 35) to broadly elliptic (*Lembocarpus* Pl. 41).

Apical Characters

The apical characters of this tribe include: acute (*Smithiantha* Pl. 35, fig. A), constrictate (*Gloxinia* Pl. 36, fig. B), obtuse (*Smithiantha* Pl. 35, fig. A), and coronate. The coronate apices vary from slightly coronate (*Gloxinia* Pl. 36, fig. A) to elongated coronate (*Gloxinia* Pl. 35, figs. H, I).

Cell Orientation

1. Straight, *Lembocarpus* (Pl. 41).
2. Slightly spiral, *Gloxinia sylvatica* (Pl. 35, figs. H, I).
3. Spiral, the remaining examined species of *Gloxinia* and the examined species of *Koellikeria*, *Heppiella*, *Eucodonia*, and *Achimenes*.

Cell Shapes, Primary (PCC), and Secondary (SCC) Cell Characters

The cell shapes of the examined species of this tribe range from narrowly lineate-polygonate to lineate-polygonate.

PCC: Edges elevated.

Faces depressed.

Crests discrete.

The primary cell characters of all of the examined species of the tribe Gloxinieae are similar.

SCC: Edges rough and/or smooth, all examined species of this tribe.

Faces verrucate, the verrucae can cover the entire face (*Smithiantha* Pl. 35) or be confined to a patch at one apex of each cell face (*Eucodonia andrieuxii* Pl. 36, figs. E, F).

The seed morphology of the examined species of the tribe Gloxinieae are diverse from species to species, but the similarity of characters shared among the genera supports the concept of the group as a natural unit.

Wiehler (1976) segregated the species of *Eucodonia* from *Achimenes*, but considered that the two genera were closely related. The examined species of *Achimenes* and *Eucodonia* are similar in cell orientation, cell shape and primary cell characters, but are distinguished from each other by the differences of apical and secondary cell characters. The seed character similarities shared by the two genera confirm an apparent affinity between the genera, and the distinctions between the seeds of *Achimenes* and *Eucodonia* confirm the separation of the genera by Wiehler (1976).

The seeds of *Eucodonia andrieuxii* (Pl. 36, fig. E) are unique among the examined species of the tribe Gloxinieae because of the distinctive opposite oblique orientation of the seed apices, as well as the small patches of verrucae which are confined to one apex of each cell (Pl. 36, fig. F). Verrucate cell faces also occur among the examined species of *Smithiana* and *Koellikeria*, but in these instances the entire cell faces are verrucate.

Leeuwenberg (1958) suggested that the genus *Lembocarpus* was distantly related to *Gloxinia* and shared an affinity with *Episcia* through *Rhoogeton*. *Lembocarpus amoenus* (Pl. 41, fig. I) is one of the few species of the examined species of the subfamily Gesnerioideae with seeds that have straight cell orientation. The cell orientation of the examined species of the tribes Gloxinieae and Episcieae, with the exception of *L. amoenus*, range from slightly spiral to spiral. The seed shape of *L. amoenus* resembles that of some of the examined species of *Episcia* (Pl. 41), but is not similar to any of the examined species of *Gloxinia* (Pls. 35, 36). The cell shape, as well as primary and secondary cell characters of *L. amoenus* are quite different from those of the examined species of *Gloxinia* and *Episcia*, but similar to those of *Smithiantha zebrina*, which is a member of the tribe Gloxinieae.

The character similarities shared between *L. amoenus* and *Episcia* on the one hand and *L. amoenus* and *Smithiantha zebrina* on the other hand support Leeuwenberg's suggestion that *Lembocarpus* may share an apparent affinity with the genera *Episcia* and *Gloxinia*. Despite the straight cell orientation of *L. amoenus*, the distinctive cell shape and primary and secondary cell characters confirm the affinity of the genus with the subfamily Gesnerioideae. Nevertheless, the particular combination and expression of the overall seed morphology of *L. amoenus* distinguish it from the other examined species of the subfamily Gesnerioideae and suggest that the species may share a rather isolated position within the family.

The details of the cytogenetics and pollen morphology of *L. amoenus* would help to resolve the perplexing problem of the natural position of the species within the subfamily Gesnerioideae. Unfortunately this information has not been reported as of the time of this writing (May 1983). As live material of this species is available, an investigation of the cytogenetics and pollen morphology of *L. amoenus* may be conducted in the near future.

The overall trend of seed characters expressed by the examined species of the tribe Gloxinieae is similar to those of the tribes Beslerieae, Bellonieae, Sinningieae, Kohlerieae, Solenophoreae and Gesnerieae, and confirm the concept of the affinity of the tribe within the subfamily Gesnerioideae.

TABLE XII. TRIBE 8: SINNINGIEAE - Atlas Plates and Tables 36, figs. G-I; and 37, figs. A-H. Representative genera: *Lietzia*, *Napeanthus*, *Sinningia*, and *Rechsteineria*.

Primary Cell Characters (PCC)

The elevated cell edges and depressed cell faces are basically uniform throughout the examined species of the tribe Sinningieae.

Seed Shapes, Apical Characters, Cell Orientation, and

Secondary Cell Characters (SCC)

The seed shapes of this tribe are exhibited in a trend from narrowly elliptic to elliptic and, within the framework of this trend, can be divided into three basic types.

1. Narrowly elliptic.

Apical Characters: The apical characters of this type include distinctly coronate, filiform, and obtuse.

Cell Orientation: Slightly spiral.

Cell Shapes: Narrowly lineate-polygonate.

SCC: The cell edges and faces are rough and/or smooth.

Type 1 includes *Sinningia cardinalis*, *S. tubiflora*, and the examined species of *Rechsteineria* (Pl. 37).

2. Elliptic.

Apical Characters: The apical characters of this type include obtuse and irregular (opposite oblique).

Cell Orientation: Spiral.

Cell Shapes: Lineate-polygonate.

SCC: The cell edges and faces are rough.

Type 2 includes the examined species of *Lietzia* and *Napeanthus* (Pl. 36).

3. Ranges from elliptic to broadly elliptic.

Apical Characters: The apical characters of this type include slightly coronate and obtuse.

Cell Orientation: Spiral.

Cell Shapes: Variable, from narrowly lineate-polygonate to lineate-polygonate.

SCC: The cell edges and faces are rough.

Type 3 includes the examined species of *Sinningia* with the exception of those in type 1.

Type 1.

The seed morphology of the species in type 1 is distinct from that in types 2 and 3 in apical characters, cell orientation and cell shapes. The fili-form apices of *Sinningia tubiflora* (Pl. 37) are similar to but distinct from the flat hyaline apices of *Agalmyla* of the tribe Trichosporeae of the subfamily Cyrtandroideae (Pl. 12).

Type 2.

Fritsch (1893) placed the genus *Napeanthus* in the tribe Klugieae of the subfamily Cyrtandroideae. On the other hand, Leeuwenberg (1958) considered that *Napeanthus* belonged in the subfamily Gesnerioideae; in addition, he suggested that the genus occupied a rather isolated position within the Gesnerioideae.

The seed morphology of the examined species of *Napeanthus* (Pl. 36) clearly demonstrates an apparent affinity of the genus with the subfamily Gesnerioideae. The cell orientation and cell shapes as well as the primary and secondary cell characters of the examined species of *Napeanthus* fit within the overall trend of seed morphology of the subfamily Gesnerioideae and bear no resemblance to that of the examined species of the subfamily Cyrtandroideae.

The seed and cell shapes as well as apical characters of the examined species of *Napeanthus* are similar to those of *Lietzia* (Pl. 36). In addition, the seeds of the examined species of *Lietzia* and *Napeanthus* (Pl. 36) are similar in seed and cell shapes as well as apical characters to those of the examined species of *Eucodonia* and *Achimenes* (Pl. 36) of the tribe Gloxinieae. The particular combination and expression of characters exhibited by the examined species of *Lietzia*, *Napeanthus*, *Eucodonia* and *Achimenes* suggest an apparent affinity among the four genera. However, the details of the cytogenetics and pollen morphology of *Lietzia* and *Napeanthus* have not been reported as of the time of this writing (May 1983), so the natural position of *Lietzia* and *Napeanthus* within the Gesnerioideae is still in question.

Type 3.

The seed morphology of the species in type 3 ranges from a spiral cell orientation with lineate cells that are basically smooth, to a tightly spiraled cell orientation with cells that are auriculate and/or undulate. This trend of character expression is also found among the genera of a number of the other tribes in the subfamily Gesnerioideae, such as Beslerieae.

The species of *Sinningia* in types 1, 2, and 3 were selected from a larger number examined to represent the range of seed characters observed throughout the genus. The similarity of the seed morphology of *Sinningia cardinalis* and the examined species of *Rechsteineria* (Pl. 37) is particularly interesting because *S. cardinalis* was formerly classified as a species of *Rechsteineria* until it was transferred by Moore (1973). However, although the species of *Sinningia* in type 1 are distinct from those in type 3 in certain respects, the seeds of the genus *Sinningia*, when viewed as a unit, are expressed in an overall

trend that supports the concept of the genus as a natural unit.

The coronate apices found among the genera of the tribe Sinningieae, with the exception of *Lietzia* and *Napeanthus*, also occur in a wide range of variations among the species of the tribes Beslerieae, Gloxinieae, Kohlerieae, and Coronanthereae.

The overall trend of seed shape, apical characters, cell orientation, and cell shape as well as primary and secondary cell characters of the examined species of the tribe Sinningieae, are similar to that found among the tribes Beslerieae, Gloxinieae, Kohlerieae, Solenophoreae, and Gesnerieae.

TABLE XIII. TRIBE 9: KOHLERIEAE - Atlas Plates and Tables 37, fig. I; 38, figs. A-I; 39, figs. A, B; 49, figs. G, H; and 51, figs. B, C. Representative genera: *Paliavana*, *Capanea*, *Vanhouttea*, *Diastema*, *Moussonia*, *Kohleria*, *Pearcea*, *Goyazia*, and *Parakohleria*.

Seed Shapes

The seed shapes of this tribe consist of two types: narrowly elliptic (the examined species of *Paliavana*, Pl. 37; *Capanea* and *Vanhouttea*, Pl. 38), and elliptic to broadly elliptic (the examined species of *Diastema*, *Moussonia*, *Kohleria*, *Goyazia* and *Pearcea*, Pls. 38, 39, 49).

Apical Characters

Apical characters of this tribe include: acute (*Vanhouttea* Pl. 38), constrictate (*Diastema*, Pl. 38), coronate (*Paliavana* Pl. 37), filiform (*Capanea* Pl. 38), obtuse (*Diastema* Pl. 38) and irregular.

Cell Orientation

The cell orientation for all of the examined species of this tribe is spiral.

Primary (PCC) and Secondary (SCC) Cell Characters

The primary and secondary cell characters of this tribe consist of two types:

1. PCC: Edges depressed.
Faces elevated.
Crests not visible.
SCC: Edges not visible.
Faces smooth with transverse grooves.
Type 1 consists of the examined species of *Kohleria* (Pls. 38, 39) and *Parakohleria* (Pl. 51).
2. PCC: Edges elevated.
Faces depressed.
Crests discrete.
SCC: Edges smooth and irregularly undulate.
Faces verrucate.
Type 2 consists of all of the examined species of the tribe Kohlerieae with the exception of the species of *Kohleria* and *Parakohleria* in type 1.

The filiform seed apices of *Capanea* (Pl. 38, figs. A, B) are the most elaborate among the examined species of the subfamily Gesnerioideae and are similar to, but distinct from, those found among the species of the tribe Trichosporeae of the subfamily Cyrtandroideae, such as *Agalmyla* (Pl. 12). However, except for the filiform apices, the seeds of *Capanea* are similar in seed and cell shape and cell orientation as well as primary and secondary cell characters to those of *Paliavana* and *Vanhouttea* (Pls. 37, 38). The similarity

of the seeds of *Paliavana*, *Vanhouttea* and *Capanea* suggests an apparent affinity among the genera. The seeds of these genera are also similar to those of several of the species in the tribe Sinningieae, such as *Rechsteineria spicata* (Pl. 37, fig. H).

The seeds of the examined species of *Diastema*, *Moussonia* (Pl. 38), *Pearcea* and *Goyazia* (Pl. 49) are extremely similar to each other in shape, apical characters, cell orientation, and cell shapes as well as primary and secondary cell characters. On the other hand, although the seeds of the examined species of *Kohleria* and *Parakohleria* share similar shape, apical characters, cell orientation and cell shape with the genera *Diastema*, *Moussonia*, *Pearcea*, and *Goyazia*, they are quite different from them at the primary and secondary cell levels. The cell edges of the examined species of *Kohleria* and *Parakohleria* are depressed and the cell faces are elevated (the reverse of the above four genera). This particular combination of characters is unique among the examined species of the subfamily Gesnerioideae to the species of *Kohleria*, *Parakohleria* and *Solenophora* of the tribe Solenophoreae. That the character is unique and shared among the species of *Kohleria*, *Parakohleria* and *Solenophora* suggests that the genera may share a particularly close affinity with each other.

The species of *Moussonia* were separated from *Kohleria* on the basis of morphological and cytological differences among the species of *Kohleria* (Wiehler 1975). The seed character differences between the examined species of *Kohleria* and *Moussonia* support the separation. Wiehler later (1978) separated the species of *Parakohleria* from *Kohleria* on the basis of morphological differences. However, the two genera are similar in having an $n = 13$ chromosome count. The seeds of *Kohleria* and *Parakohleria* are very similar to each other in overall morphology and, in addition, they share the unique primary and secondary cell characters that are found only among the examined species of these two genera and *Solenophora* (tribe Solenophoreae). Therefore, neither the seed morphology nor the cytology of the genera supports the separation of *Parakohleria* from *Kohleria*.

The seeds of *Goyazia petraea* (Pl. 49) provide another example of the advantage of the SEM for the examination of small structures. Wiehler (1976) describes the seeds of *Goyazia petraea* as "... ellipsoid, with flattened surfaces and not striate" (p. 394). Whereas the SEM photomicrograph shows that the seeds are broadly elliptic, the surface is far from flat, and on an overall basis the spiral cell orientation forms a striate pattern on the surface of the seeds. However, these features are not readily apparent when viewed under a light microscope.

The seed morphology of the tribe Kohlerieae is expressed in an overall trend that supports the concepts of the tribe as a natural unit. However, the distinction of the primary and secondary cell characters of the examined species of *Kohleria* and *Parakohleria* suggests that the genera *Paliavana*, *Capanea*, *Vanhouttea* and *Diastema* may share a closer affinity with each other than with the genera *Kohleria* and *Parakohleria*.

TABLE XIV. TRIBE 10: SOLENOPHOREAE - Atlas Plates and Table 39, figs. C, F. Representative genus: *Solenophora*.

Seed Shape

The seed shape for the examined species is elliptic.

Apical Character

The apical character of the examined species is constrictate.

Cell Orientation

The cell orientation is spiral for the examined species of this tribe.

Cell Shape, Primary (PCC) and Secondary (SCC) Cell Characters

Cell Shape: Narrowly lineate-polygonate.

PCC: Edges depressed.
Faces elevated.
Crests not visible.

SCC: Edges not visible.
Faces smooth.

Solenophora calycosa was the only species of which seed was available for this study.

The seeds of *Solenophora calycosa* (Pl. 39, figs. C, F) are similar in shape, cell orientation and cell shape to those found among the examined species of the tribes Beslerieae, Bellonieae, Sinningieae, Kohlerieae and Gesnerieae. However, the primary and secondary cell characters resemble those of the examined species of *Kohleria* in the tribe Kohlerieae. The depressed cell edges and elevated cell faces of the examined species of *Kohleria*, *Parakohleria* and *Solenophora* are restricted within the subfamily Gesnerioideae, suggesting that the three genera may share a particularly close affinity with each other.

The overall seed morphology that *Solenophora* shares with the species of the tribes Beslerieae, Bellonieae, Sinningieae, Kohlerieae, and Gesnerieae supports the concept of its affinity with the subfamily Gesnerioideae.

TABLE XV. TRIBE 11: GESNERIEAE - Atlas Plates and Tables 39, figs. D, E, G-I; 40, figs. A-I; and 41, figs. A, B. Representative genera: *Pheidonocarpa*, *Gesneria*, and *Rhytidophyllum*.

All of the genera of the tribe Gesnerieae are included in this study (Skog 1976).

Seed Shapes

The seed shapes of this tribe include two basic types: narrowly elliptic (the examined species of *Gesneria duchartreoides* Pl. 40, fig. C and *Rhytidophyllum* Pls. 40, 41) and elliptic (the examined species of *Pheidonocarpa* Pl. 39, fig. D, and the other species of *Gesneria* Pl. 39, figs. G-I, and 40, figs. A, B).

Apical Characters

The apical characters of the examined species of this tribe include: acute, (*Pheidonocarpa* Pl. 39, fig. D), constrictate (*Gesneria* Pl. 40, fig. A), and obtuse (*Gesneria* Pl. 39, fig. G).

Cell Orientation

The cell orientation of the examined species ranges from slightly spiral to spiral, a trend exhibited throughout the tribe.

Cell Shapes

The cell shapes of this tribe include two basic types:

1. Narrowly lineate-polygonate.

Type 1 includes all of the examined species of this tribe with the exception of *Pheidonocarpa*.

2. Lineate-polygonate.

Type 2 includes the examined species of *Pheidonocarpa* (Pl. 39).

Primary (PCC) and Secondary (SCC) Cell Characters

The primary cell characters are uniform throughout the examined species of the tribe Gesnerieae, and there is only a small range of variation from species to species at the secondary cell level.

PCC:	Edges elevated. Faces depressed. Crests discrete.
SCC:	Edges basically smooth with some of the cell apices projecting slightly (<i>Pheidonocarpa</i> Pl. 39, figs. D, E). Faces variable from rough (<i>Pheidonocarpa</i> Pl. 39, figs. D, E) to verrucate (<i>Gesneria</i> Pl. 39, fig. G).

When Skog (1976) revised the tribe Gesnerieae, he segregated the species of *Pheidonocarpa* from the genus *Gesneria* on the basis of crystal, leaf and floral differences among the species. The seeds of the examined species of *Pheidonocarpa* (Pl. 39) differ from those of the examined species of *Gesneria* (Pls. 39, 40) in cell shape and secondary cell characters, and support the separation of the genera. The representative species of *Gesneria* were selected, from a much larger number examined, to include the range of seed characters observed throughout the genus.

The overall trend of seed morphology of the tribe Gesnerieae is of particular interest because of the similarities that it shares with other tribes. The seed morphology of the examined species of the tribe Gesnerieae exhibits a very wide trend of seed shape and cell orientation, ranging from elliptic seed shape and tightly spiral cell orientation (*Gesneria pumila* Pl. 39, figs. G, H) to narrowly elliptic seed shape and slightly spiral cell orientation (*Rhytidophyllum auriculatum* Pl. 40, figs. H, I). The species with the tightly spiral cell orientation resemble the overall morphology exhibited among the species of the tribes Beslerieae, Bellonieae, Sinningieae, Gloxinieae and Kohlerieae. On the other hand, the overall seed morphology of the species with the slightly spiral cell orientation and narrowly elliptic seeds, such as *Rhytidophyllum auriculatum*, resembles the overall seed morphology found among the species of the tribes Episcieae (*Columnnea strigosa* Pl. 44, fig. F) and Mitrarieae (*Sarmienta repens* Pl. 46, fig. A).

In addition, the bluntly angled seed apices of *Gesneria viridiflora* and *Rhytidophyllum crenulatum* (Pl. 40, figs. D, E) resemble those of *Negria rhabdothamnoides* (Pl. 49, fig. B).

The overall trend of seed characters exhibited by the examined species of the tribe Gesnerieae supports the concept of the tribe as a natural unit (Skog 1976), and the combinations and trends of characters distinguish the genera and species from each other.

The distinguishing features of the seed morphology of the tribe Gesnerieae have been discussed above. The similarities of seed characters shared by the species of the tribe Gesnerieae with those of other tribes will be discussed later.

TABLE XVI. TRIBE 12: EPISCIEAE - Atlas Plates and Tables 41, figs. C-H; 42-45, figs. A-I; 49, fig. I; and 51, figs. H, I. Representative genera: *Episcia*, *Chrysothemis*, *Nautilocalyx*, *Alloplectus*, *Drymonia*, *Columnnea*, *Paradrymonia*, *Nematanthus*, *Codonanthe*, *Oerstedina*, *Rufodorsia*, *Neomortonia*, *Bucinellina*, *Alsobia*, and *Hypocyrtia*.

The combinations of genera that share a given character vary from character to character in the tribe Episcieae.

Seed Shapes

There are three basic groups of seed shapes in the tribe Episcieae.

1. Narrowly elliptic.

Group 1 includes the examined species of *Drymonia* (Pl. 43), *Columnnea* (Pls. 43, 44), *Paradrymonia* (Pl. 44), *Codonanthe* (Pl. 45), *Oerstedina* (Pl. 45), *Neomortonia* (Pls. 45, 51) *Bucinellina* Pl. 49), and *Alsobia* (Pl. 51).

2. Narrowly elliptic to elliptic, trends within the genera.

Group 2 includes the examined species of *Chrysothemis* (Pl. 42), *Nautilocalyx* (Pl. 42), *Alloplectus* (Pls. 42, 43), and *Nematanthus* (Pl. 45).

3. Elliptic to broadly elliptic, a trend within the genus.

Group 3 includes the examined species of *Episcia* (Pl. 41).

Cell Orientation

The cell orientation of the tribe Episcieae includes three basic types:

1. Slightly spiral.

Type 1 includes the examined species of *Paradrymonia*, *Oerstedina*, *Rufodorsia*, *Neomortonia*, and *Bucinellina*.

2. Slightly spiral to spiral.

Type 2 includes the examined species of *Episcia*, *Chrysothemis*, *Alloplectus*, *Columnnea*, *Nematanthus*, and *Codonanthe*.

3. Spiral.

Type 3 includes the examined species of *Nautilocalyx*, *Drymonia* and *Alsobia*.

Cell Shapes

The cell shapes of all of the examined species of the tribe Episcieae are narrowly lineate-polygonate.

Apical Characters

The apical characters of this tribe include acute, arillate, constrictate, obtuse and premorse.

Constrictate: the examined species of *Episcia* and among the species of *Chrysothemis*, *Alloplectus*, *Codonanthe*, and *Neomortonia*.

Arillate: among the examined species of *Paradrymonia*, *Nematanthus*, *Codonanthe*, *Oerstedina* and *Rufodorsia*.

Premorse: the examined species of *Drymonia*.

Primary (PCC) and Secondary (SCC) Cell Characters

PCC: Edges elevated.
Faces depressed.
Crests discrete.

Includes all of the examined species of this tribe.

There are two basic types of secondary cells in this tribe.

- SCC; 1. Edges basically smooth to rough.
Faces smooth to rough where visible.
Type 1 includes all of the examined species of this tribe with the exceptions of the species of *Episcia* and one species of *Alloplectus*.
2. Edges undulate and/or slightly auriculate cell apices.
Type 2 includes the examined species of *Episcia* and *Alloplectus cucullatus* (Pls. 41, 42).

The seeds of the examined species of the tribe Episcieae exhibit a trend of seed shapes from narrowly elliptic to broadly elliptic. However, within the majority of the genera the seed shapes are rather conservative. For instance, the seeds of the examined species of *Drymonia*, *Columnea*, *Paradrymonia*, *Codonanthe*, *Oerstedina* and *Neomortonia* vary from narrowly elliptic to elliptic, but the species that are elliptic are near the narrowly elliptic ratio. Therefore, the basic seed shape for these genera is narrowly elliptic, or nearly so. The seeds of the examined species of *Episcia* vary from elliptic to broadly elliptic. However, the species that are elliptic are near the broadly elliptic ratio (*Episcia cupreata* Pl. 41, fig. C). Therefore, the basic seed shape for this genus is broadly elliptic or nearly so. The seeds of *Chrysothemis* are elliptic but vary from species to species. On the other hand, the examined species of *Nautilocalyx*, *Alloplectus* and *Nematanthus* exhibit a distinct trend within each genus from narrowly elliptic to elliptic.

The cell orientation of the examined species of the tribe Episcieae is exhibited in an overall trend from slightly spiral to tightly spiral. However, within the majority of the genera the cell orientation is rather conservative and ranges from slightly spiral to spiral. On the other hand, the examined species of *Chrysothemis*, *Alloplectus* and *Nematanthus* exhibit a broad trend within each genus from slightly spiral to tightly spiral.

Within the family Gesneriaceae, the arillate apices found among the species are unique to the tribe Episcieae. The arils vary from a very short frill (*Rufodorsia minor* Pl. 45, fig. H) to those that almost enclose the entire seed (*Codonanthe calcarata* Pl. 45, fig. F). Genera found to include species with arillate seeds are *Paradrymonia*, *Nematanthus*, *Oerstedina* and *Rufodorsia*. *Neomortonia rosea* (Pl. 45, fig. I) is reported to possess arillate seeds (Skog 1979, Wiehler 1975). However, the seeds of *N. rosea* that I obtained for this study (*Hugh-Jones 150K*) did not have arillate seeds.

Within the subfamily Gesnerioideae, the premorse apices as found in *Drymonia serrulata* (Pl. 43, figs. C, D) are unique to the examined species of *Drymonia* (Pl. 43) and *Alsobia* (Pl. 51). The only other examined species of the family Gesneriaceae found to possess seeds with premorse apices was *Acanthonema strigosum* (Pl. 22, fig. I) in the tribe Didymocarpeae of the subfamily Cyrtandroideae. However, the premorse apices of these species are quite distinct from each other. The two specimens of *D. serrulata* are another example of the conservative nature of seed morphology. Specimen 'a' (*White 27*) is from Colombia and specimen 'b' (*Johnston 62*) is from Panama, and yet the seeds of the specimens are, to all intents and purposes, identical to each other.

Although neither uniform nor distinctive, constrictate apices were found to occur on all of the examined species of *Episcia* and among the species of *Chrysothemis*, *Alloplectus*, *Codonanthe* and *Neomortonia*.

The secondary cell characters of the examined species of the tribe Episcieae vary from rough to smooth with the exceptions of *Alloplectus cucullatus* and some of the species of *Episcia* which include auriculate and undulate cell edges (Pls. 41, 42).

Group 3.

The seed shape of the examined species of *Episcia* is broadly elliptic. Leeuwenberg (1958) pointed out that the genus *Lembocarpus* shared an affinity with both *Episcia* and *Gloxinia*. The seed shape of *Lembocarpus amoenus* (Pl. 41, fig. I) is similar to those of the examined species of *Episcia*.

However, as previously mentioned, the cell shape and primary and secondary cell characters of *L. amoenus* are similar to those of *Smithiantha zebrina* of the tribe Gloxinieae.

The examined species of the genus *Episcia* share the overall cell orientation, cell shape and primary cell characters of the other genera of the tribe Episcieae but are distinct from the other genera of the tribe with a basically broadly elliptic seed shape and range of cell characters. The examined species of *Episcia* exhibit a wider range of cell widths than do the species of groups 1 and 2. In addition, the distinctive auriculate and/or undulate cell edges, such as those of *E. hirsuta* (Pl. 41, fig. H) have not been found among the examined species of the other genera of the tribe Episcieae. However, the cell edges of *Alloplectus cucullatus* are slightly auriculate and/or undulate. The seeds of *E. hirsuta* specimen 'a' (Appun 976, Pl. 41, fig. E) and specimen 'b' (Engler 46452, Pl. 41, fig. H) are very unusual in that the seeds of the two specimens are quite distinct from each other. Of the numerous examples of multiple specimens of a given species examined during the course of this study, the seeds of *E. hirsuta* were the only example in which there was such a distinct morphological difference between the specimens. That the difference between the specimens was so unusual suggests that one of the herbarium specimens was incorrectly identified.

Group 2.

The seed morphology of the genera in group 1 (*Drymonia*, *Columnnea*, *Paradrymonia*, *Rufodorsia*, *Oerstedina*, *Bucinellina* and *Neomortonia*; Pl. 43-45, 49, and 51) and group 3 (*Episcia* Pl. 41) is rather conservative in comparison with that of the genera in group 2 (*Chrysothemis*, *Nautilocalyx*, *Alloplectus* and *Nematanthus*; Pl. 42, 43, and 45).

The seed morphology of the examined species of *Chrysothemis* (Pl. 42), *Nautilocalyx* (Pl. 42), *Alloplectus* (Pls. 42, 43) and *Nematanthus* (Pl. 45) resemble each other in that each species exhibits a common trend of similar seed shapes, cell orientation and cell shapes as well as primary and secondary cell characters. Within each genus the cell orientation of these four genera is expressed as a wide trend ranging from slightly spiral to tightly spiral. Usually among these genera, it is of particular interest that the tighter the degree of the spiral of the cell orientation, the wider the individual cells are.

The cell characters of *Alloplectus* and *Nautilocalyx* (Pls. 42, 43) of group 2 and *Drymonia* (Pl. 43) from group 1 are extremely interesting. The cells of the examined species of these genera are all narrowly lineate-polygonate but vary from species to species from those in which the cells are extremely narrow with the cell edges closely contiguous with each other and the cell faces not visible (*Nautilocalyx hirtiflorus* Pl. 42, fig. E) to those in which the cells are wider and the faces are visible (*Nautilocalyx pictus* Pl. 42, fig. D). In addition, the cell edges of some of the species of *Nautilocalyx*, *Alloplectus*, and *Drymonia* (Pls. 42, 43) are extremely uniform in elevation and so closely contiguous with each other that the seed surfaces appear to be completely flat when viewed under the LM. However, the high power of the SEM shows that the seed surfaces are far from flat. Within the Gesneriaceae, the particular combination of primary and secondary cell characters of these genera is unique to some of the species of *Nautilocalyx*, *Alloplectus*, and *Drymonia* of the tribe Episcieae.

Group 1.

The seeds of the examined species of *Drymonia*, *Columnnea*, *Paradrymonia*, *Codonanthe*, *Oerstedina*, *Neomortonia*, *Bucinellina* and *Alsobia* re-

seem each other in shape (basically narrowly elliptic), a similar trend of cell orientation, and cell shapes as well as primary and secondary cell characters. The exception to these resemblances is the unique secondary cell characters of *D. serrulata* which were discussed in group 2. There are apical character distinctions among some of the genera in this group which are recorded on Atlas Tables 43-45, 49, and 51, listed and discussed on Table XVI and in the description following Table XVI.

Alsobia punctata (Lindl.) Hanst. is the type species of *Alsobia* Hanst. *Alsobia punctata* (Hanstein 1854, Wiehler 1973) has also been classified as *Drymonia punctata* Lindl. (Lindley 1842, 1844), *Episcia punctata* (Lindl.) Hanst. (Hanstein 1865), and *Columnea septentrionalis* Morton (Morton 1967). The shifting of this species from genus to genus is of particular interest. The specific combination in which the seed characters of *A. punctata* are exhibited distinguishes the species from the examined species of the other genera of the Episcieae. On the other hand, a number of the seed characters exhibited by *A. punctata* are shared among the examined species of several of the other genera of the Episcieae. For instance, the seed shape and pre-morse apex of *A. punctata* is similar to that of the examined species of *Drymonia* (Pl. 43); the seed shape, primary and secondary cell characters are similar to those of *Columnea florida* (Pl. 43), and the seed shape is also similar to that of *Alloplectus ichthyoderma* (Pl. 42). However, the overall seed morphology of *Alsobia punctata* is completely different from the examined species of *Episcia* (Pl. 41). Therefore, the seed morphology of *A. punctata* confirms the concept of the genus as a taxon and suggests that the genus may share a closer affinity with some of the genera of the Episcieae than with others.

After much consideration, Morton (1971b) concluded that the elongate appendages between the corolla lobes of the species of *Trichantha* (the only characters separating *Trichantha* from *Columnea*) "... were not of fundamental importance in delimiting genera ..." (p. 223) and reduced the genus *Trichantha* to *Columnea*. The results of numerous other investigations (Byrne and Morley 1976; Jones and Rich 1972; Morley 1972, 1973a, 1973b; Morton 1971a; Sherk 1960; Skog 1979; and Stearn 1969) have concurred with Morton's conclusion and supported the concept of the genus *Columnea* sensu lato. On the other hand, Wiehler (1973) divided the species of the genus sensu lato into an alliance of a number of closely related genera.

The genus *Columnea* sensu lato fits the pattern of a genus having variable plant and corolla forms but an identical chromosome number, $n = 9$, (Skog 1980). The genus *Sinningia* fits a similar pattern with a chromosome number of $n = 13$ (Clayberg 1968, 1970) as does the genus *Nematanthus* which has a chromosome number of $n = 8$ (Saylor 1979). However, the seed morphology of the examined species of *Columnea* is remarkably uniform throughout the genus, and that of *Sinningia* and *Nematanthus* includes a wide range of character diversity within each genus.

The species of *Columnea* represented in this study (Pls. 43, 44) were selected from a much larger number examined to include the range of seed characters observed throughout the genus. Based on the seed morphology of the species of other genera examined during the course of the study, the seeds of the species of *Columnea* are an unusually uniform group, especially for such a large genus (160 species, Skog 1978). The seed shapes, apical characters, cell orientation and cell shape as well as primary and secondary cell characters are basically uniform throughout the examined species of the genus. The only differences observed were a slight variation in the seed shape

ratios and degree of cell orientation spiral from one species to another and the fibrous covering on the seed of *C. nicaraguensis* and *C. schiedeana* (Pl. 43, figs. G, H). The nature and/or origin of the fibrous material has not yet been determined. However, a developmental investigation of living material would no doubt resolve the problem.

In contrast to the uniformity of the seed morphology of *Columnea*, other large genera in the Gesneriaceae such as *Streptocarpus* (132 species according to Hilliard and Burt 1971) and *Besleria* (over 150 species, Skog 1978), have been found to exhibit a wide range of seed character diversity. The uniformity of the seed morphology of the examined species of *Columnea*, in conjunction with the cytological and other morphological characters of the genus (Byrne and Morley 1976; Jones and Rich 1972; Morley 1972, 1973a, 1973b; Morton 1971a, 1971b; Sherk 1960; Skog 1978; and Stearn 1969), suggest an apparent close affinity among the species and support the concept of the genus *Columnea* sensu lato.

The seed morphology of *Neomortonia rosea* (Pl. 45, fig. I) is of particular interest because of the flattened cell crests exhibited by this species. *Neomortonia rosea* shares an overall seed shape, cell orientation, cell shape and primary and, in general, secondary cell characters with the other examined species of the genera in group 3. However, the seeds of *N. rosea* are distinguished from those of the other genera in the group because the cell crests of *N. rosea* are distinctively flattened while those of the other species in the group are not.

The seeds of *N. rosea* are similar also to those of the examined species of *Sarmienta*, *Mitraria*, *Asteranthera* and *Fieldia* (Pl. 46) of the tribe Mitrarieae in seed shape, cell orientation and primary cell characters as well as the distinctive flattened cell crests which, among the examined species of the Gesneriaceae, are unique to these four genera. The seeds of *N. rosea* are distinguished from those of *Sarmienta*, *Mitraria*, *Asteranthera* and *Fieldia* in having somewhat wider cells that are consistently slightly undulate. The cells of *Sarmienta*, *Mitraria*, *Asteranthera* and *Fieldia* are extremely narrow and usually straight with only an occasional cell edge being very slightly undulate.

Neomortonia rosea occurs from Costa Rica and Panama southward to the western part of Colombia. *Sarmienta* and *Mitraria* are from southern Chile, *Asteranthera* is from southern Chile and adjacent Argentina, and *Fieldia* is from Australia. These last four genera are monotypic taxa that possess fleshy fruits as does *N. rosea*.

The distinctively undulate cell edges of *Episcia hirsuta* (Pl. 41) are somewhat similar but more elaborate than those of *Lenbrassia australiana*, another monotypic genus from Australia of the tribe Mitrarieae. The similarities of seed characters, in conjunction with other morphological characters shared among the species of the tribes Episcieae and Mitrarieae, suggest an apparent affinity between the two tribes.

When Wiehler (1978) revised the genera *Episcia*, *Alsobia*, *Paradrymonia* and *Nautilocalyx*, he concluded that as a group the genera did not appear to share a particularly close affinity with each other. On the other hand, he also concluded that *Nautilocalyx* and *Alloplectus* (Pls. 42, 43) probably shared a close relationship with each other. The seed morphology of these genera supports Wiehler's conclusions. The seed morphologies of *Episcia* (group 3), *Paradrymonia* and *Nautilocalyx* (group 2) are distinct from each other in certain respects although each genus fits within the overall trend of seed mor-

Gillett (1974) described *Lenbrassia* as a monotypic genus. Morley (1978) described two varieties of the species, *L. australiana* var. *glabrescens* (Pl. 46, fig. I) and *L. australiana* var. *australiana* (Pl. 47, figs. A, B). The herbarium specimens of the two varieties represented in this study were among those included in Morley's investigation. *Lenbrassia australiana* var. *glabrescens* (White 10548) came from Mt. Spurgeon and *L. australiana* var. *australiana* (Smith 10099) is from Cook. In his description of the two varieties, Morley points out that "... the morphological differences do not seem to intergrade to any appreciable extent in the apparently similar rain forest habitat shared by the two sorts of plants" (p. 187). As can be seen from the photomicrographs, the seeds of the two varieties are, to all intents and purposes, identical demonstrating that while the morphological distinctions (leaf, floral, indumentum, etc.) support the concept of the varieties within the species, the uniformity of the seed morphology exhibited throughout the species confirms the concept of the genus as a natural taxon.

Fieldia australis specimen 'a' (Constable 47318) is from the Blue Mountains of New South Wales and specimen 'c' (Dunnington 00145) is from Moreton, Queensland. The locale for specimen 'b' is not known. On the overall basis the seed shapes of the specimens exhibit a trend from narrowly elliptic to elliptic. However, the seed shape for each specimen is distinct from those of the other specimens. Although the seeds of the individual specimens differ from each other in length-width ratios, the cell orientation and cell shapes as well as the primary and secondary cell characters are uniform throughout the species and support the concept of the genus as a natural taxon.

The similarity of the overall seed morphology exhibited by the species of the tribe Mitrarieae supports the classification of the tribe (Burt 1963), lends additional support to the concept of the tribe as a natural taxon, and distinguishes it from the other tribes. On the other hand, the distinctive cell crests and overall seed morphology shared among the species of *Sarmienta*, *Mitraria*, *Asteranthera* and *Fieldia* and with the species of *Neomortonia* of the tribe Episcieae suggest that these genera may share an especially close affinity with each other.

In addition, the seed shapes, cell orientation, cell shapes, and primary cell characters found among the species of Mitrarieae are similar to those found among other genera of the tribe Episcieae (e.g., *Paradrymonia decurrens* Pl. 44, fig. G) as well as the tribe Gesnerieae (e.g., *Rhytidophyllum coccineum* Pl. 40, fig. G). The seeds of the tribe Mitrarieae are also similar to the examined species of the tribes Episcieae and Gesnerieae in that none was found to possess coronate apices.

The similarities of seed characters shared among the species of Mitrarieae, Episcieae and Gesnerieae suggest that the three tribes may share a closer affinity with each other than with the other tribes of the subfamily Gesnerioideae. However, the overall seed morphology of the tribe Mitrarieae clearly demonstrates the affinity of the tribe with the subfamily Gesnerioideae and supports Burt's transfer of the tribe from the subfamily Cyrtandroideae to the Gesnerioideae.

The similarity of the seed morphology exhibited by the species of the tribe Mitrarieae is particularly interesting because of the wide disjunct distribution of its members and provides an excellent example of the consistency of seed characters for a given taxon.

TABLE XVIII. TRIBE 14: CORONANTHEREAE - Atlas Plates and Tables 47, figs. C-I and 49, figs. B, C. Representative genera: *Rhabdothamnus*, *Coronanthera*, *Negria* and *Depanthus*.

All of the genera of the tribe Coronanthereae (Burt 1963) are included in this study.

Seed Shapes

The seed shapes of this tribe vary, within individual genera as well as within the tribe as a whole, from narrowly elliptic to elliptic (*Coronanthera* Pl. 47).

Apical Characters

The apical characters of this tribe include acute, coronate, and obtuse. Coronate is the most common apical character among the examined species of this tribe.

Cell Orientation

There are two basic types of cell orientation in the Coronanthereae.

1. Slightly spiral.

Type 1 includes the examined species of *Rhabdothamnus* and *Coronanthera*.

2. Spiral.

Type 2 includes the examined species of *Negria* and *Depanthus*.

Cell Shapes and Primary (PCC) and Secondary (SCC) Cell Characters

Cell shapes: Lineate-polygonate and irregular. The irregularity of the cell shapes varies from slightly irregular (*Negria* Pl. 49) to distinctly irregular (*Coronanthera* Pl. 47).

Includes all examined species of this tribe.

PCC:

Edges elevated.

Faces depressed.

Crests discrete.

Includes all examined species of this tribe.

SCC:

There are two types of secondary cell types in the tribe.

1. Edges smooth and undulate and/or auriculate.

Faces smooth.

Type 1 includes the examined species of *Rhabdothamnus*, *Coronanthera*, and *Depanthus* (Pl. 47, 49).

2. Edges smooth.

Faces smooth.

Type 2 includes the examined species of *Negria* (Pl. 49).

The tribe Coronanthereae as described by Burt (1963) consists of *Coronanthera* (11 species) from New Caledonia and the Solomon Islands; three monotypic genera: *Negria* from Lord Howe Island; *Depanthus* from the Solomon Islands; and *Rhabdothamnus* from North Island of New Zealand. The genera of the tribe Coronanthereae are characterized as having cymose inflorescences and dry, capsular, dehiscent fruit with wind dispersed seeds (Burt 1963, Gillett 1974).

The seed morphology of the Coronanthereae is as distinctive as the fruits of the tribe. The seed shapes of the tribe range from narrowly elliptic to elliptic, and the cell orientation varies from slightly spiral to tightly spiral. The very irregularly shaped cells of this tribe are among the most elaborate secondary cell characters in the family. In addition, coronate apices are found

among the examined species of *Coronanthera*, *Depanthus* and *Negria*. The cell edge elaborations vary from the undulate cell edges of *Rhabdothamnus solandri* (Pl. 47, fig. C) to the extremely elongated cell apices of *D. glaber* (Pl. 49, fig. C). The seeds of *N. rhabdothamnoides* (Pl. 49, fig. B) have one coronate apex and one abruptly angled apex. The abruptly angled apex is very similar to that of *Rhytidophyllum crenulatum* (Pl. 40, fig. E) of the tribe Gesnerieae. The coronate apices exhibited among the examined species of *Negria*, *Depanthus*, and *Coronanthera* are similar to those found among the examined species of the tribes Beslerieae, Bellonieae, Sinningieae, Gloxinieae and Kohlerieae.

The examined species of *Coronanthera* are from widely separated locations; nevertheless, the distinctive seed characters of the examined species of *Coronanthera* (Pl. 47) are exhibited within an overall trend of very similar characters. The consistency of these distinctive characters exhibited throughout the examined species of *Coronanthera* provides another example of the conservative nature of seed morphology. Of particular interest is the fact that the seeds of the examined species of *Coronanthera* are similar in cell shape, primary and secondary cell characters to those found among the examined species of *Gasteranthus* of the tribe Beslerieae (Pl. 49) as well as the examined species of *Tetraphyllum* (Pl. 14) of the tribe Didymocarpeae and subfamily Cyrtandroideae.

The seed apices and primary and secondary cell characters exhibited among the examined species of the tribe Coronanthereae are quite distinct from those of the tribe Mitrarieae and support the concept of the two tribes as separate taxa (Burt 1963, Gillett 1974). The seed characters shared among the members of the tribe Coronanthereae and those of other tribes, as mentioned previously, suggest that the tribe Coronanthereae may share a much closer affinity with some tribes of the subfamily Gesnerioideae, such as Beslerieae, Bellonieae, Gloxinieae, Sinningieae, Kohlerieae, and Gesnerieae, than with other tribes such as Episcieae and Mitrarieae. However, the overall seed morphology exhibited among the examined species of the tribe Coronanthereae fits within the overall trend of seed characters exhibited by the members of the subfamily Gesnerioideae and supports Burt's transfer of the tribe (1963) from the subfamily Cyrtandroideae to the subfamily Gesnerioideae. The seed characters shared among the examined species of *Coronanthera*, *Gasteranthus* (tribe Beslerieae) and *Tetraphyllum* (tribe Didymocarpeae) will be discussed again later.

TABLE XIX. TRIBE 15: ANETANTHEAE - Atlas Plates and Tables 48, figs. A-I; and 51, fig. A. Representative genera: *Anetanthus* and *Resia*.

Seed Shape

The seed shape of the examined species of this tribe range from orbiculate to suborbiculate (*Anetanthus* Pl. 48, 51) and elliptic (*Resia* Pl. 48).

Apical Characters

The apical characters of the examined species of this tribe include obtuse and constrictate.

Cell Orientation

The cell orientation is straight for all the examined species of this tribe.

Cell Shapes, Primary (PCC) and Secondary (SCC) Cell Characters

Cell shape: Parted.

- PCC: Edges depressed.
Faces elevated.
Crests discrete.
- SCC: Edges rough.
Faces smooth to slightly rough.
- Includes all the examined species of this tribe.

As described by Fritsch (1893-94) the tribe Anetantheae contained one genus, *Anetanthus*, and was placed in the subfamily Cyrtandroideae. Melchior (1964) retained the genus in the Cyrtandroideae but placed it in the tribe Ramondieae. The genus was not included in the studies of Burt (1963), Ivanina (1966), or Wilson (1974).

Howard (1975) pointed out that resolving the question of the familial association of *Anetanthus* was more difficult than with certain other genera of the family, such as *Goyazia*, but he made no mention of a possible affinity of the genus with a particular tribe and/or subfamily. Wiehler (1976) described *Anetanthus* as a monotypic genus and mentioned that the genus would be placed in the tribe Beslerieae of the subfamily Gesnerioideae in a new classification of the subfamily. Although this classification has been mentioned numerous times, from as early as 1973, it has not been published as of the time of this writing (May 1983), so the basis for the proposed assignment is not known. When Skog (1982) described a new species of *Anetanthus* (*A. rubra* Pl. 51, fig. A), he drew attention to the fact that the seeds of the genus *Anetanthus* appeared to be anomalous in the Gesneriaceae, but that several other morphological characters of the genus confirmed the affinity of the genus in this family.

Moore (1962) described *Resia* as a new genus, but he did not assign it to a tribe although he mentioned that there were superficial resemblances between *Resia* and some of the Columneae as well as *Tylopsacus*. Leeuwenberg (1968) described an additional species of *Resia* (*R. ichthyoides*), but he did not suggest a possible tribal affinity for the genus.

The orbiculate to suborbiculate winged seed shapes of the species of *Anetanthus* (Pls. 48, 51) are restricted, within the examined species of the Gesneriaceae, to the genus *Anetanthus*. The constricted apices of the examined species of *Resia* make the seeds elliptic in shape. Nevertheless, discounting the winged portions of the seeds of *Anetanthus* and the constrictate apices of the seeds of the examined species of *Resia*, the seeds of the two genera are similar in shape. The cell orientation of the seeds of *Anetanthus* and *Resia* is straight.

The excellent drawings of the seeds of *A. rubra* that accompany Skog's (1982) description of the species illustrate the seed shape and the proportion of wing to overall seed size. However, because the camera lucida drawings were done with the aid of an LM, they do not show the orientation or shape of the cells. The most striking character of the seeds of the examined species of *Anetanthus* and *Resia* is the parted cell shapes which are completely different from any other cell shape found among the examined species of the Gesneriaceae. The parted cell shapes of the examined species of *Anetanthus* and *Resia* are similar to, but distinct from, each other. That the cell shapes of *Anetanthus* and *Resia* are so very similar to each other but so very distinct from those of the rest of the family suggests that the genera probably share a very close affinity with each other. The parted cell shapes of *Anetanthus* and *Resia* have not been mentioned in previous studies of the genera.

A seed character unique to the species of *Anetanthus* is the covering that encloses the seeds (Pl. 48, fig. C). The origin and/or nature of the covering is not known at this time. However, when live material of *Anetanthus* becomes available, an investigation to determine the origin and/or development of the seed covering will make a most interesting study. This seed covering has not been mentioned in previous studies on the genus.

Moore (1962) suggested that *Resia* appeared to be closely related to *Napeanthus* (Pl. 36), but the seed morphology of the examined species of the two genera are quite distinct from each other and do not support the concept of such a relationship. Wiehler (1976) suggested that *Anetanthus* and *Resia* shared a close relationship with the members of the tribe Beslerieae, but the seed morphology of the two genera is completely different from that of the examined species of the Beslerieae and does not support Wiehler's suggestion.

The morphological characters of *Anetanthus* and *Resia*, exclusive of the seeds, are shared among the genera of both the Cyrtandroideae and Gesnerioideae. For instance, the parietal placentation of the two genera is characteristic for the family Gesneriaceae in general. The superior ovaries of *Anetanthus* (Melchior 1964) and *Resia* (Moore 1962) are characteristic of the subfamily Cyrtandroideae while the coherent anthers of *Anetanthus* (Wiehler 1976) and *Resia* (Moore 1962) are found among the species of the subfamily Gesnerioideae. On the other hand, the loculicidal capsules of *Anetanthus* (Skog 1982) and *Resia* (Moore 1962) occur only among the species of the tribe Coronanthereae, subfamily Gesnerioideae (Wiehler 1976).

Neither the details of the cytological characters and the seedling morphology of *Anetanthus* and *Resia* nor the pollen morphology of *Resia* have been published as of the time of this writing (May 1983). Howard (1975) included photomicrographs of the pollen of *A. gracilis* and *A. alatus*, but unfortunately the pollen grains were collapsed and portions of the pollen were concealed. Recent developments of improved pre-SEM-treatment techniques for pollen (Williams 1982) have resulted in pollen grains that are fully expanded which allows a more complete analysis to be made of the pollen morphology. An investigation of the pollen morphology utilizing these techniques in conjunction with an investigation of the seedling and cytogenetic characters of *Anetanthus* and *Resia* will provide valuable information that may resolve the question of the natural position of these two very interesting genera in the Gesneriaceae. Because of the anomalous nature of these two genera, such information may well provide additional insight regarding the evolution of the family and its relationship to other closely related families.

The overall seed morphology of *Anetanthus* and *Resia* is anomalous within the Gesneriaceae. The straight cell orientation of the seeds of *Anetanthus* and *Resia* is common among the examined species of the Cyrtandroideae but rare among the examined species of the Gesnerioideae. Within the examined species of the Gesnerioideae, the parted cell shapes are unique to these two genera.

The seed morphology of *Anetanthus* and *Resia*, in conjunction with other morphological characters, makes the genera distinct enough as a group to justify their being classified as a separate taxon. Therefore, the tribe Anetantheae (Fritsch 1893-94) is being reinstated at this time to contain these two genera.

Fritsch (1893-94) and Melchior (1964) classified the tribe Anetantheae in the subfamily Cyrtandroideae. The subfamily classification of the Gesneriaceae is based on the development of the cotyledon after germination

(Burt 1963), but unfortunately the cotyledonary development of *Anetanthus* and *Resia* has not been published at the time of this writing (May 1983). In addition, as previously mentioned, certain morphological characters of these two genera are found in each of the subfamilies.

Because *Anetanthus* and *Resia* are among the New World genera of the Gesneriaceae, the tribe Anetantheae is being placed, tentatively, in the Gesnerioideae. The details of the cytogenetics and pollen and seedling morphology when they become known, will help to resolve the natural position of the tribe within the Gesneriaceae. Maybe the genera of this tribe will prove to be a link between the two subfamilies.

TABLE XX. GENERA ANOMALA - Atlas Plates and Tables 30, figs. G-I, and 52, figs. A, B. Representative genera: *Titanotrichum* and *Tylopsacas*.

Seeds of *Titanotrichum oldhamii* were not available for this study. However, a sterile 'flower' is illustrated on Atlas Plate 30, figs. G-I.

The seed morphology characters of *Tylopsacas cuneata* are as follows:

Seed Shape

The seed shape is circular and globose like a sphere, not flattened.

Apical Characters

The apical characters of *Tylopsacas cuneata* are obtuse and constrictate.

Cell Orientation

The cell orientation of this species is irregular.

Cell Shapes, Primary (PCC) and Secondary (SCC) Cell Characters

Cell shapes: Irregular.

PCC: Edges not visible.

Faces elevated.

Crests not visible.

SCC: Edges not visible.

Faces colliculate and smooth.

Unfortunately an examination of all of the available herbarium specimens of *Titanotrichum oldhamii* at the herbaria of the Smithsonian, Kew and Edinburgh failed to produce any seeds. According to Burt (1963), *T. oldhamii* has not been known to produce seeds in cultivation, although Sealy (1949) mentions that propagation of the species can be effected from leaf cuttings, rhizomes or seeds so apparently seeds can be produced. However, my cultivated plants have not produced any seeds during the course of this study.

In addition to producing a normal flowering inflorescence, the plants of *T. oldhamii* sometimes bear long spikes of thickly clustered sterile flowers. According to Sealy (1949), the sterile spikes, which are often seen on collected specimens, had not been produced in cultivation in Britain. However, these sterile spikes have been produced on my cultivated plants, in the late fall, in both North Carolina and Florida. An individual 'flower' from a sterile spike (from Sasaki 21509 US) is illustrated on Plate 30. Figure G is a complete 'flower'; in figure H one 'bract' was removed to show the central shoot, and figure I is a close-up of the central shoot.

As Burt (1963) pointed out, the subfamily affinity of *T. oldhamii* cannot be decided without the details of the cotyledonary development of this

species. When fertile seeds become available, the seedling morphology will help to resolve the subfamily classification of *T. oldhamii*, and seed and pollen morphology, in conjunction with a complete analysis of the other morphological characters of *T. oldhamii*, will help to define the tribal affinity of the species. For the time being *T. oldhamii* remains an anomalous genus of the Gesneriaceae.

In his revision of the Gesneriaceae of Guiana, Leeuwenberg (1958) separated *Episcia cuneata* from the genus *Episcia* on the basis of inflorescence, nectary gland and seed morphology distinctions, and put the species into a new genus *Tylosperma* (later changed to *Tylopsacas*). However, he did not suggest a tribal association for the genus. The seed morphology of *T. cuneata* is quite distinct, in all respects, from that of the examined species of *Episcia* and supports Leeuwenberg's segregation of the genus from the *Episcia*.

Wiehler (1976) described the seeds of *Tylopsacas* as round and flat. However, as can be seen from the photomicrograph (Pl. 52), the seeds of *T. cuneata* are round and globose and not flattened at all. Wiehler suggested that *Tylopsacas* shared an affinity with the tribe Beslerieae and appeared to be the genus most closely related to *Anetanthus*. However, the seed morphology of *Tylopsacas* (Pl. 52) bears no resemblance whatsoever to that of the examined species of the tribe Beslerieae (Pls. 31, 32) or to *Anetanthus*, tribe Anetantheae (Pls. 48, 51) and does not support Wiehler's suggestions.

The seed morphology of *Tylopsacas cuneata* is completely different from any other examined species of the family Gesneriaceae. In all of the other examined species of the family, the individual cells are quite distinct from each other. In *T. cuneata* the cell edges are not discernible (see close-up on Pl. 52, fig. B). In addition, the seed shape, cell orientation, primary and secondary cell characters are also completely different from the other examined species of the family. That the seed morphology of *T. cuneata* is so very distinct from that of the rest of the examined species of the family suggests that the genus may occupy a rather isolated position within the Gesneriaceae.

The details of the cytology and seedling and pollen morphology of *T. cuneata* have not been reported as of the time of this writing (May 1983). When live material of *T. cuneata* becomes available, the details of the cytology and seedling and pollen morphology of this genus may help to resolve the question of the natural position of the genus within the family. Meanwhile it seems appropriate at this time not to assign the genus to a tribe.

TABLE XXI. SUBFAMILY CYRTANDROIDEAE - Atlas Plates and Tables 5-29, figs. A-I; 30, figs. A-F; 49, fig. A; 50, figs. A-I; and 51, fig. G.

The Cyrtandroideae consists of four tribes (Burt 1963): 1. Cyrtandreae, 2. Trichosporeae, 3. Klugieae, and 4. Didymocarpeae; all of the tribes are represented in this study.

Except where stated, the listing of a tribal name after a character does not imply that the character occurs in all of the examined species and/or genera of that tribe but rather that it has been found to occur among some of the examined species of that tribe.

Seed Shapes

The seed shapes of the examined species of the subfamily Cyrtandroideae include:

Narrowly elliptic: Trichosporeae.

Narrowly elliptic, elliptic and broadly elliptic: Cyrtandreae and Didymocarpeae.

Broadly elliptic: Klugieae.

The seed shapes listed are exhibited by all of the examined species of the listed tribes.

Apical Characters

The apical characters of the examined species of the subfamily Cyrtandroideae include:

Acute, constrictate, obtuse: Cyrtandreae, Klugieae and Didymocarpeae.

Filiform: all of the examined species of the tribe Trichosporeae.

Filiform and premorse: Didymocarpeae (in addition to the characters listed above).

Cell Orientation

The cell orientations of the examined species of the Cyrtandroideae include:

Straight: Cyrtandreae, Trichosporeae, Klugieae, and Didymocarpeae.

Slightly spiral: Klugieae and Didymocarpeae.

Spiral: Cyrtandreae (2 species only), Trichosporeae, and Klugieae.

Irregular: Cyrtandreae.

The most common cell orientation found among the examined species of the subfamily Cyrtandroideae is straight.

Cell Shapes

The cell shapes of the examined species of the Cyrtandroideae include:

Narrowly lineate-polygonate: Cyrtandreae, Trichosporeae, Klugieae and Didymocarpeae.

Lineate-polygonate: Cyrtandreae, Klugieae, and Didymocarpeae.

Irregular: Cyrtandreae, Trichosporeae and Didymocarpeae.

Primary (PCC) and Secondary (SCC) Cell Characters

The primary and secondary cell characters of the examined species of the Cyrtandroideae can be divided into two basic groups:

1. PCC: Edges elevated, depressed or irregular.
Crests fused or discrete.
Crests composite (found only among the examined species of the Didymocarpeae).
SCC: Edges papillate, auriculate, verrucate, striate, rough and smooth.
Except where noted, the above primary and secondary cell characters are found among the examined species of Cyrtandreae and Didymocarpeae.
SCC: Faces tuberculate, auriculate, verrucate, striate, rough and smooth: Cyrtandreae and Didymocarpeae.
Faces not visible: Cyrtandreae (2 species only).
Faces level, tholiform, papillate, ocellate and tetragonate: Didymocarpeae.
2. PCC: Edges elevated: Trichosporeae and Klugieae.
Crests fused: Trichosporeae.
Crests fused or composite: Klugieae.
Faces depressed: Trichosporeae and Klugieae.
SCC: Edges papillate, rough: Trichosporeae and Klugieae.
Edges auriculate: Trichosporeae.
Edges verrucate, smooth: Klugieae.
Faces verrucate: Klugieae.
Faces smooth: Trichosporeae.

SUBFAMILY CYRTANDROIDEAE

TRIBE 1: CYRTANDREAE

The cell orientation of the examined species of the tribe Cyrtandreae, with the exception of two species, is either straight or irregular. The cell shapes range from lineate-polygonate to polygonate and irregular, and there is a wide diversity of cell edge elaborations. The seed morphology of the examined species of the tribe Cyrtandreae is second only to that of the Didymocarpeae in diversity. However, the seeds of the examined species of the Cyrtandreae lack the extremely wide range of secondary cell face characters found among the examined species of the Didymocarpeae.

The seed morphology of *Cyrtandra sandei* and *C. flabelligera* (Pl. 10) is completely different from that of the other examined species of the subfamily Cyrtandroideae. However, the spiral cell orientation and narrowly lineate-polygonate cells with concealed faces that are exhibited by these two species are very similar to those found among the subfamily Gesnerioideae, such as *Besleria reticulata* var. *venosa* (Pl. 31) of the tribe Beslerieae. That the seed morphology of these two species of *Cyrtandra* is so distinct from that of the other examined species of the genus, tribe, and subfamily in which they are classified and so similar to that found among the examined species of the Gesnerioideae raises a question concerning the classification of the species. No obvious difference between the morphology of these two species and that of the other species of *Cyrtandra* was observed during the course of obtaining the seeds from the herbarium sheets. An additional examination of the herbarium specimens of these species (Skog, personal communication) also failed to show any readily apparent difference. A further examination of these two species is planned as a part of my ongoing study of the genus *Cyrtandra*. The results of such an examination, in conjunction with the details of the cytology and seedling development, when live material becomes available, will help to resolve the question of the natural position of the two species within the Gesneriaceae.

TRIBE 2: TRICHOSPOREAE

The filiform apical characters that are exhibited by all of the examined species of the Trichosporeae, in conjunction with the narrowly lineate-polygonate to lineate-polygonate cells and straight to slightly spiral cell orientation, distinguish the examined species of the tribe from the other examined species of the Cyrtandroideae. The papillate projections on the cell crests of the examined species of *Dichrotrichum*, *Agalmyla*, and *Lysionotus* are restricted to these genera and two of the examined species of the Didymocarpeae.

TRIBE 3: KLUGIEAE

There is no one character common to all of the examined species of the Klugieae that is unique to the tribe. However, within the examined species of the Cyrtandroideae, the combination of verrucate cell faces, fused crests and a variable cell orientation that is exhibited among the examined species of *Rhynchoglossum*, is restricted to the Klugieae. In addition, there is a much higher percentage of seeds with a spiral cell orientation among the examined species of the tribe Klugieae than among the examined species of the other tribes of the Cyrtandroideae. However, the cell orientation of the examined species of *Monophyllaea* is straight.

TRIBE 4: DIDYMOCARPEAE

The examined species of this tribe exhibit the most elaborate and diverse range of seed morphology found among the examined species of the Gesneriaceae, although there is no one seed character common to all of the examined species of the Didymocarpeae that is restricted to the tribe. However, the very elaborate secondary cell characters of the cell faces exhibited by the examined species of this tribe distinguish it from the other tribes of the Cyrtandroideae. These distinguishing features include level, tholiform, papillate, ocellate and tetragonate cell face characters as well as the transverse striae of the cell edges and faces. There are two distinct groups of cell shapes among the examined species of the Didymocarpeae — Group 1 exhibits variable cell shapes, whereas those of Group 2 are uniformly polygonate.

Genera with examined species that exhibit seed characters that are distinct among the examined species of the Didymocarpeae but similar to those found in other tribes include *Petrocosmea*, *Conandron*, *Anna*, *Chirita*, *Loxostigma* and *Tetraphyllum*.

The overall trend of seed characters exhibited by the examined species of *Petrocosmea* (Pl. 16), tribe Didymocarpeae, is very similar to that of the species of *Cyrtandra* that comprise type 2 of the tribe Cyrtandreae (Table V: Pls. 7, 8, and 9). Chromosome counts of $n = 17$ and $2n = 34$ have been reported for *Petrocosmea parryorum* and *P. kerrii* (Skog 1981). The same $n = 17$ and $2n = 34$ has also been reported for 21 of the 25 species of *Cyrtandra* that have been published so far (Skog 1981). This includes *C. oblongifolia* (Pl. 8) which is one of the species of *Cyrtandra* having seed morphology similar to the examined species of *Petrocosmea*.

The similarity of seed characters, in conjunction with similar cytological counts where known, suggests that the genera *Petrocosmea* and *Cyrtandra* may share an affinity with each other. These similarities raise a number of questions regarding the natural position of *Petrocosmea* within the Gesneriaceae. For instance, is the genus *Petrocosmea* more closely related to the members of the tribe Didymocarpeae or Cyrtandreae, and/or is the genus a link between the two tribes?

The distinctive seed characters of *Anna*, *Conandron* and *Loxostigma* are of particular interest because these genera have provided classification problems, based on other morphological characters, in past investigations.

Conandron is an Asiatic genus of three species (Kao and DeVol 1972). Both Hooker (1882) and Moore (1957) drew attention to the distinctions of the floral and plant form characters between *C. ramondioides* and the other members of the Gesneriaceae. Fritsch (1893-94) considered the genus distinct enough from the other members of the tribe Didymocarpeae to classify it as the only genus in the subtribe Conandrinae.

Anna ophiorrhizoides was first described as *Lysionotus ophiorrhizoides* (Hemsley 1890) and later transferred to the genus *Anna* (Burt and Davidson 1955) and placed in the tribe Didymocarpeae (Burt 1963). On the other hand, Wang (1980) considered that the species should be classified as *Didissandra sinoophiorrhizoides*. However, the seed morphology is completely different from that of the examined species of *Didissandra* (Pls. 18, 19) and does not support the concept of the inclusion of the species in that genus. Therefore it seems more appropriate at this time to consider the species as *Anna ophiorrhizoides*.

In his revision of the Asiatic genus *Loxostigma*, Burt (1975) transferred the genus from the tribe Trichosporeae to the Didymocarpeae and

drew attention to the fact that the genus shared morphological characters with each of the tribes. When Burttt revised *Loxostigma* he made it a genus of four species and pointed out that *L. griffithii* had been previously placed in the *Didymocarpus* and *Dichrotrichum* and, as herbarium specimens, had been referred to as *Chirita* as well as *Lysionotus*. Additional genera to which the other species of this genus have been previously assigned include *Didissandra* and *Briggsia*. These various genera with which the species of *Loxostigma* have been previously associated span two tribes, the Trichosporeae (*Dichrotrichum* and *Lysionotus*) and the Didymocarpeae (*Didymocarpus*, *Chirita*, *Didissandra* and *Briggsia*).

The seed morphology of the examined species of *Conandron*, *Anna*, and *Loxostigma* of the Didymocarpeae is distinct from the other examined species of the Didymocarpeae, but is similar, in many respects, to that of the examined species of *Agalmyla*, *Dichrotrichum* and *Lysionotus* of the tribe Trichosporeae.

The seed apices of *Anna ophiorrhizoides* and *Loxostigma griffithii* are filiform, as are those of the examined species of *Dichrotrichum*, *Agalmyla*, and *Lysionotus*; those of *Conandron ramondiioides* are not filiform, but one apex extends out to a distinct point. The apices of *Loxostigma kurzii* are obtuse and acute. The cell orientation of *Anna ophiorrhizoides* and the examined species of *Loxostigma* are straight, as are those of *Dichrotrichum*, *Agalmyla*, and *Lysionotus*, while that of *Conandron ramondiioides* is very slightly spiral. The cell shapes of the examined species of *Conandron*, *Anna*, *Loxostigma*, *Dichrotrichum*, *Agalmyla*, and *Lysionotus* are lineate-polygonate. The primary cell characters of the examined species of *Anna*, *Loxostigma*, *Dichrotrichum*, *Agalmyla*, and *Lysionotus* consist of distinctly elevated edges and depressed faces while those of *Conandron ramondiioides* are irregular. The most interesting of the characters shared among the examined species of *Anna*, *Conandron*, *Dichrotrichum*, *Agalmyla*, and *Lysionotus* are the papillate projections that occur astride the cell crests and on the cell faces. The amount of papillae per cell ranges from dense (*Agalmyla clarkei*, Pl. 12) to sparse (*Dichrotrichum chorisepalum*, Pl. 12). The examined species of *Loxostigma* do not possess these papillae. The occurrence of papillate projections astride the cell crests is restricted, among the examined species of the Gesneriaceae, to the examined species of *Conandron*, *Anna*, *Agalmyla*, *Dichrotrichum*, and *Lysionotus*. As pointed out above, the seeds of *Conandron*, *Anna*, *Loxostigma*, *Dichrotrichum*, *Agalmyla* and *Lysionotus* share a number of characters in common, and the distinctive papillae are exhibited in a trend from very frequent to sparse and are lacking in the examined species of *Loxostigma*. The seeds of *Loxostigma kurzii* are distinct from the other mentioned species in that the cells are covered in fine, linearly oriented striae.

In addition to the similarity of the seed characters shared among the examined species of *Conandron*, *Anna*, *Loxostigma*, *Dichrotrichum*, *Agalmyla* and *Lysionotus*, the chromosome counts of *C. ramondiioides*, $n = 16$ and $2n = 32$ (Skog 1981), are the same as those of the reported species of *Dichrotrichum* (Skog 1981), *Agalmyla* (Skog 1980), and *Lysionotus* (Skog 1981). Chromosome counts for the species of *Anna* and *Loxostigma* have not been reported as of the time of this writing (May 1983). The geographical distribution of some of the species of *Conandron* and *Lysionotus* (Kao and DeVol 1972, Burttt 1975) overlap in Vietnam and Japan, and *Loxostigma griffithii* has been reported from North Vietnam (Burttt 1975). The species of *Conandron*, *Loxostigma*, and *Lysionotus* are also similar to each other in having rhizomes and/or creeping stems.

As discussed above, the seed morphology of the examined species of *Anna*, *Conandron* and *Loxostigma* includes certain characters that are restricted to these three genera among the examined species of the Didymocarpeae. On the other hand, the straight cell orientation and lineate cell shapes of those genera are found among other examined species of the tribes Cyrtandreae, Didymocarpeae and Klugieae and confirm the affinity of these genera within the subfamily Cyrtandroideae.

The shared seed characters, in conjunction with the other shared similarities mentioned above, suggest that these six genera may share a particularly close affinity with each other. The seed morphology of the examined species of *Loxostigma* supports Burt's (1975) concept of the genus as a link between the tribes Didymocarpeae and Trichosporeae. The seed characters in conjunction with previously mentioned similarities suggest that *Conandron* and *Anna* may also be a link between these two tribes. However, the seed morphology and other shared similarities suggest that as a group the tribal affinity of *Conandron*, *Anna*, and *Loxostigma* may be with the tribe Trichosporeae rather than with the Didymocarpeae.

When material becomes available, the details of the cytology of *Anna* and *Loxostigma* and the pollen morphology of *Conandron*, *Anna*, and *Loxostigma* will help to resolve the very interesting problems of the natural positions, generic and/or tribal, of the species of these genera within the Gesneriaceae.

Chirita asperifolia (Pl. 20) has been described under a number of synonyms (Wood 1974) and in his revision of the genus, Wood (1974) pointed out that the affinity of *C. asperifolia* with the other species of the section *Chirita* was obscure. The seed morphology of *C. asperifolia* is completely different from that of the other examined species of *Chirita* as well as that of the other examined species of the tribe Didymocarpeae. On the other hand, the seed morphology of *C. asperifolia* is very similar to that of *Cyrtandra parvifolia* (Pl. 5, fig. 1) of the tribe Cyrtandreae in all respects. The similarity of the seed morphology of *Chirita asperifolia* and *Cyrtandra parvifolia* may indicate that *Chirita asperifolia* shares a closer affinity with the genus *Cyrtandra* than with the genus *Chirita*. A comparison of the other morphological characters of these two species including pollen, in conjunction with the cytology of *Cyrtandra parvifolia* when live material is available, will help to resolve the natural position of *Chirita asperifolia* within the Gesneriaceae.

The strikingly similar seed morphology shared among the examined species of *Tetraphyllum* (Pl. 14) and two genera of the subfamily Gesnerioideae (*Gasteranthus*, Pl. 49, of the Beslerieae and *Coronanthera* Pl. 47, of the Coronanthereae) is especially interesting. The specimens of the examined species of *Tetraphyllum* were collected in Asia. The species of *Gasteranthus* occur from Peru to Guatemala (Wiehler 1975) and those of *Coronanthera* occur on a number of the Pacific Islands (Gillett 1967).

The tribes Beslerieae and Coronanthereae were placed in the subfamily Cyrtandroideae based on ovary position by Fritsch (1893-94) and Melchior (1964). Ivanina (1967) placed the Coronanthereae in the Cyrtandroideae but submerged the species of Fritsch's Beslerieae in the Episcieae and placed the tribe in the subfamily Episcioideae. On the other hand, the tribes Beslerieae and Coronanthereae were placed in the Gesnerioideae based on seedling morphology (Burt 1963, Wilson 1974). The overall seed morphology and the coronate apices of the examined species of *Gasteranthus* and *Coronanthera* support the classification of the genera in the Gesnerioideae.

The overall seed morphology exhibited by the examined species of *Tetraphyllum*, *Gasteranthus*, and *Coronanthera* fits within the basic framework

of the seed morphology of the Gesneriaceae. Nevertheless, the particular combination and expression of seed characters exhibited among the examined species of these three genera distinguish them, as a group, from the other examined species of the family. On the other hand, the differences at the secondary cell character level distinguish the genera from each other.

That certain seed characters shared among the examined species of these three genera are so similar in each of the genera and so distinct from those of the other examined species of the family may suggest that the genera share an affinity with each other despite their disjunct distributions. The similarities may also suggest that the genera are links among the subfamilies.

As can be seen from the Summary Table, the various seed characters of the examined species of the Cyrtandroideae are shared in a wide variety of combinations among the four tribes of the subfamily. The occurrence of such diverse and overlapping combinations strengthens the concept of the affinity of the tribes and/or genera with each other as members of a natural taxon. The examined species of the Cyrtandreae and Didymocarpeae share more characters with each other than with the Trichosporeae or Klugieae but are distinguished from each other as previously discussed.

The seed morphology of the examined species of the four tribes of the Cyrtandroideae fits within an overall trend of characters that supports the concept of the subfamily as a natural unit (Burt 1963). On the other hand, the combinations and expression or elaboration of the characters exhibited among the examined species of the four tribes distinguish each tribe from the others.

TABLE XXII. SUBFAMILY GESNERIOIDEAE - Atlas Plates and Tables 31-48, figs. A-I; 49, figs. B-I; and 51, figs. A-F, H-I.

The subfamily Gesnerioideae, as defined here, comprises 11 tribes: 5. Beslerieae, 6. Bellonieae, 7. Gloxinieae, 8. Sinningieae, 9. Kohlerieae, 10. Solenophoreae, 11. Gesnerieae, 12. Episcieae, 13. Mitrarieae, 14. Coronanthereae, 15. Anetantheae, making a total of 15 tribes for the Gesneriaceae.

Except where stated, the listing of a tribal name after a character does not imply that the character occurs on all of the examined species and/or genera of that tribe, but rather that it has been found to occur among some of the examined species of that tribe.

Seed Shapes

The seed shapes of the examined species of the subfamily Gesnerioideae include:

Narrowly elliptic and/or elliptic: Beslerieae, Bellonieae, Gloxinieae, Sinningieae, Kohlerieae, Solenophoreae, Gesnerieae, Episcieae, Mitrarieae and Coronanthereae.

Broadly elliptic: Beslerieae, Gloxinieae, Sinningieae and Episcieae.

Circular: Beslerieae.

Orbiculate: Anetantheae.

Apical Characters

The apical characters most commonly found among the examined species of the Gesnerioideae include acute, obtuse, and constrictate. Distinctive apical characters include:

Arillate: Episcieae.

Coronate: Beslerieae, Bellonieae, Gloxinieae, Sinningieae, Kohlerieae, and Coronanthereae.

- Filiform: Sinningieae and Kohlerieae.
Irregular: Gloxinieae and Sinningieae.

Cell Orientation

The cell orientation of the examined species of the Gesnerioideae includes:

- Straight: Beslerieae, Sinningieae, Episcieae, and Anetantheae.
Slightly spiral: Bellonieae, Gloxinieae, Sinningieae, Gesnerieae, Episcieae, Mitrarieae, and Coronanthereae.
Spiral: Beslerieae, Bellonieae, Gloxinieae, Sinningieae, Kohlerieae, Solenophoreae, Gesnerieae, Episcieae, Mitrarieae and Coronanthereae.

Cell Shapes

The cell shapes exhibited among the examined species of the Gesnerioideae include:

- Narrowly lineate-polygonate to lineate-polygonate: Beslerieae, Bellonieae, Gloxinieae, Kohlerieae, Solenophoreae, Gesnerieae, Episcieae, Mitrarieae, and Coronanthereae.
Polygonate: Beslerieae.
Parted: Anetantheae.

Primary (PCC) and Secondary (SCC) Cell Characters

- PCC: Edges depressed, faces elevated: Kohlerieae and Solenophoreae.
Edges elevated, faces depressed: the other examined species of the Gesnerioideae.
Crests discrete: Beslerieae, Bellonieae, Gloxinieae, Sinningieae, Kohlerieae, Gesnerieae, Episcieae, Mitrarieae and Coronanthereae.
Crests fused: Beslerieae, Bellonieae, Kohlerieae, Solenophoreae, Gesnerieae, and Episcieae.
Crests composite: Bellonieae, Gloxinieae, Sinningieae, and Gesnerieae.
- SCC: The secondary cell characters of the edges and faces common among the examined species of the Gesnerioideae include rough and smooth. Distinctive secondary cell characters include:
Edges auriculate: Beslerieae, Bellonieae, Sinningieae, Kohlerieae and Coronanthereae.
Edges undulate: Beslerieae, Bellonieae, Gloxinieae, Sinningieae, Episcieae, Mitrarieae and Coronanthereae.
Edges and/or faces verrucate: Gloxinieae, Sinningieae and Gesnerieae.

SUBFAMILY GESNERIOIDEAE

With the exceptions of the examined species of the tribe Anetantheae, there is no one seed character common to all of the species of any one of the other ten tribes of the Gesnerioideae that is restricted to a particular tribe. The similarity of seed characters shared among some of the examined species of all of the tribes of the Gesnerioideae, with the exception of Anetantheae, confirms the inclusion of the tribes Beslerieae, Bellonieae, Sinningieae, Gloxinieae, Solenophoreae, Kohlerieae, Gesnerieae, Episcieae, Mitrarieae, and Coronanthereae within the Gesnerioideae and the classification of the

subfamily as a natural taxon. The combinations and/or expressions of the seed characters exhibited among the examined species of the various tribes of the Gesnerioideae distinguish the tribes from each other, and some of the tribes are more distinct than others.

TRIBE 5: BESLERIEAE

The overall seed morphology of the examined species of *Besleria*, *Reldia*, *Gasteranthus* and *Cremosperma minutiflorum* consists of a particularly wide range of seed characters. The seed characters found among the above mentioned taxa are similar to those found among some of the examined species of the other tribes of the Gesnerioideae, with the exception of the Aneanthaeae. However, the seed morphology of the examined species of *Cremosperma*, with the exception of *C. minutiflorum*, is completely different from that of any of the other examined species of the Gesnerioideae.

The coronate apices exhibited among the examined species of the Beslerieae are similar to those found among some of the examined species of the Bellonieae, Gloxinieae, Sinningieae, Kohlerieae, and Coronanthereae. Individual genera with examined species that exhibit seed characters that are distinct among the examined species of the Beslerieae, but similar to those found among the examined species of other tribes, include *Gasteranthus* and *Cremosperma*.

The overall seed morphology of the examined species of *Gasteranthus* fits within the trend of seed characters exhibited among the examined species of the Beslerieae. Within the examined species of the Beslerieae, the combination of cell orientation, cell shapes and distinctively auriculate cell apices is restricted to *Gasteranthus*. The particular combination of primary and secondary cell characters found among the examined species of *Gasteranthus* is similar to that of the examined species of *Coronanthera* of the Coronanthereae of the subfamily Gesnerioideae as well as those of *Tetraphyllum* of the Didymocarpeae of the subfamily Cyrtandroideae. The seed character similarities shared among the examined species of *Gasteranthus*, *Coronanthera*, and *Tetraphyllum* were dealt with in detail in the discussion of the subfamily Cyrtandroideae (following Table XXI).

As mentioned in the main discussion of the tribe Beslerieae (following Table IX), the seed morphology of *Cremosperma congruens*, *C. jucundum*, and *C. peruvianum* is completely different in every respect from that of the other examined species of the Gesnerioideae but is very similar to that of a number of the examined species of *Cyrtandra*, such as *C. lysiosepala*, of the Cyrtandreae in the subfamily Cyrtandroideae. That the seed morphology of these three species of *Cremosperma* is so distinct from that of the other examined species of the Gesnerioideae, and so similar to that of some of the examined species of *Cyrtandra*, suggests that these three species of *Cremosperma* may share a closer affinity with the *Cyrtandra* than with the members of the Beslerieae.

Wiehler (1978) transferred *Cremosperma minutiflorum* from *Nautilocalyx* to *Cremosperma*. However, the seed morphology of this species is completely different from that of the other examined species of *Cremosperma* and does not support the concept of an affinity between *C. minutiflorum* and the other examined species of the genus. On the other hand, the seed morphology of *C. minutiflorum* is similar to that of *Reldia alternifolia*, which suggests that these two species may share an affinity with each other. Based on the consistency of the seed characters exhibited among the various

genera examined during the course of this study, the marked distinctions between the seed morphology of *C. minutiflorum* and the other examined species of the *Cremosperma* may suggest that either *C. minutiflorum* or the other examined species of the genus are incorrectly classified.

The seed morphology of the tribe Beslerieae, in conjunction with other morphological characters (Hanstein 1853, Fritsch 1893, Morton 1939, Burt 1963, Melchior 1964 and Wilson 1974), suggests that the tribe may share an affinity with both the Cyrtandroideae and the Gesnerioideae and may be a link between the two subfamilies.

Neither the cytogenetic details nor the morphological characters of the pollen and seedlings of the species of *Gasteranthus* and *Cremosperma* as well as the several species of *Cyrtandra* in question, *Trisepalum* or *Coronanthera* have been reported as of the time of this writing (May 1983). When live material of these taxa is available, the details of the cytogenetics, the seedling and pollen morphology, in conjunction with other morphological characters, will help to resolve some very interesting problems. For instance: whether there are affinities, as suggested by the seed morphology, among the taxa; the natural positions of the taxa within the Gesneriaceae; and whether or not the tribe Beslerieae is a link between the subfamilies of the Gesneriaceae.

TRIBE 6: BELLONIEAE

The combinations, trends and expression of the seed characters exhibited among the examined species of the Bellonieae distinguish the tribe from the other tribes of the Gesnerioideae.

The seed morphology of the examined species of the *Monopyle* provides an excellent example in which the seeds of the species of a genus demonstrate a continuum over a wide range in the expression of a particular combination of characters. The gradation of seed characters ranges from the medium spiral cell orientation, narrowly lineate-polygonate cell shapes and basically smooth cell edges of *M. subdimidiata* (Pl. 34) to the tightly spiraled cell orientation, considerably wider cell shapes and extremely elaborate auriculate and/or undulate cell edges of *M. puberula* (Pl. 34). The seed morphology of the examined species of the other examined genera of the Bellonieae fits within the trend of characters exhibited by the examined species of *Monopyle* and supports the concept of an affinity among the genera of the Bellonieae.

The seeds of *Niphaea oblonga* (Pl. 33) and *Anodiscus xanthophyllus* (Pl. 34) are similar to each other in overall morphology but are distinguished from each other in cell orientation and apical characters. For instance, the cell orientation of the seeds of *N. oblonga* is slightly spiral while that of *A. xanthophyllus* is straight. Coronate apices are exhibited in a very wide range of variations among the examined species of six of the tribes of the Gesnerioideae, and those of *A. xanthophyllus* are the most elaborate. On the other hand, the seed apices of *N. oblonga* lack any cell elaboration and are simply acute and obtuse. The seed morphology of these two species provides an example in which the examined species of related genera have been found to exhibit an overall similar seed morphology, but are distinguished from each other in certain characters and/or combinations of characters.

The coronate apices exhibited among the examined species of the Bellonieae are similar to those found among the examined species of the Beslerieae, Gloxinieae, Sinningieae, Kohlerieae and Coronanthereae.

TRIBE 7: GLOXINIEAE

The coronate apices exhibited among the examined species of the Gloxinieae are similar to those found among the examined species of the Beslerieae, Bellonieae, Sinningieae, Kohlerieae and Coronanthereae. Individual genera of the Gloxinieae with examined species that exhibit distinctive seed characters similar to those found among the examined species of other tribes include *Lembocarpus*, *Achimenes*, and *Eucodonia*.

The seed shape of *Lembocarpus amoenus* (Pl. 41) is similar to that of the examined species of *Episcia* of the tribe Episcieae. The straight cell orientation of this species is fairly rare among the examined species of the Gesnerioideae but very common among the examined species of the Cyrtandroideae. However, the seed shape and primary and secondary cell characters are typical of those found among the examined species of the Gesnerioideae and quite different from those found among the examined species of the Cyrtandroideae. The anomalous combination of seed characters exhibited by *L. amoenus* suggests that the species may share an isolated position within the Gesnerioideae. However, when live material of this species is available, the details of the cytology and pollen morphology of this species may help to resolve the natural position of this species within the Gesnerioideae.

The particular combination of seed characters exhibited by the examined species of *Achimenes* and *Eucodonia* is similar to that of the examined species of *Lietzia* and *Napeanthus* of the tribe Sinningieae. These similarities will be discussed in the section about Sinningieae which follows.

TRIBE 8: SINNINGIEAE

The coronate apices exhibited among the examined species of the Sinningieae are similar to those found among the examined species of Beslerieae, Bellonieae, Gloxinieae, Kohlerieae, and Coronanthereae. Individual genera of the Sinningieae with examined species that exhibit distinctive seed characters similar to those found among the examined species of other tribes are *Lietzia*, *Napeanthus*, *Sinningia* and *Rechsteineria* (Pls. 36, 37).

Verrucate cell faces occur among some of the examined species of the Gloxinieae, Sinningieae and Gesnerieae. The verrucate cell faces found among the examined species of the Gesnerieae will be discussed in the summary of that tribe (Tribe 11). Verrucate cell faces occur among the examined species of *Eucodonia* of the Sinningieae as well as the examined species of *Smithiantha* and *Koellikeria* of the Gloxinieae. The verrucae cover the entire cell faces and/or edges of the examined species of *Smithiantha* and *Koellikeria*, but occur only as a distinct patch on one apex of each cell face of the examined species of *Eucodonia*. These distinctive verrucate patches are restricted within the Gesneriaceae to the examined species of the *Eucodonia* (Pl. 36).

As mentioned in the main discussion of the Sinningieae (Table XII), Fritsch (1893) placed the genus *Napeanthus* in the tribe Klugieae of the subfamily Cyrtandroideae. Leeuwenberg (1958) considered that *Napeanthus* belonged in the subfamily Gesnerioideae, but he did not assign the genus to a tribe. The overall seed morphology of the examined species of *Napeanthus* is typical of that exhibited among the examined species of the Gesnerioideae and supports Leeuwenberg's assignment of the genus to that subfamily. However, because the very distinctive combination of seed characters of the examined species of *Napeanthus* is extremely similar in all respects to that of *Lietzia* in the tribe Sinningieae, it seems appropriate at this time to place the genus *Napeanthus* tentatively in the Sinningieae. The details of neither the

cytology nor the pollen morphology of the species of *Napeanthus* and *Lietzia* have been reported as of the time of this writing (May 1983). However, when live material is available, the details of the cytology as well as the pollen morphology of *Lietzia* and *Napeanthus* in conjunction with other morphological characters may show whether or not these two genera share an affinity with *Achimenes* and *Eucodonia*. This information will also help to resolve the question of the natural position of *Lietzia* and *Napeanthus* within the Gesneriaceae.

The particular combination of seed shapes, apical characters and an otherwise similar seed morphology exhibited by *Sinningia cardinalis*, *S. tubiflora*, *Rechsteineria umbellata* and *R. spicata* (Pl. 37) of the Sinningieae and *Paliavana prasinata* and *Capanea grandiflora* (Pls. 37, 38) of the Kohlerieae is restricted to these species within the examined species of the Gesneriaceae. The chromosome numbers of *Sinningia cardinalis* have been reported as $n = 13$ and $n = 14$ (Skog 1982), those of *Sinningia tubiflora* as $2n = 26$ and $2n = 28$ (Skog 1982), while those of *Capanea grandiflora* (Skog 1980) and *Paliavana prasinata* (Skog 1981), as $n = 13$. The chromosome numbers for the above two species of *Rechsteineria* have not been reported as of the time of this writing (May 1983). That the above species share a similar distinctive seed morphology and similar chromosome numbers (where known) suggests that these species may share a particularly close affinity with each other.

TRIBE 9: KOHLERIEAE

The coronate apices exhibited among the examined species of the Kohlerieae are similar to those found among the examined species of the Beslerieae, Bellonieae, Gloxinieae, Sinningieae and Coronanthereae. Individual genera of the Kohlerieae with examined species that exhibit distinctive seed characters that are similar to those found among the examined species of other tribes include *Kohleria*, *Paliavana* and *Capanea* (Pls. 37-39).

The distinctive primary and secondary cell characters of the examined species of *Kohleria* of the Kohlerieae and *Solenophora* of the Solenophoreae are restricted to these two genera within the examined species of the Gesnerioideae. That the characters are unique and shared among only the examined species of these two genera suggests that the genera may share a particularly close affinity with each other.

The seed character distinctions of the examined species of *Paliavana* and *Capanea* have already been discussed in the section about the tribe Sinningieae (Tribe 8).

TRIBE 10: SOLENOPHOREAE

Solenophora calycosa (Pl. 39, fig. C) is the only representative species of the Solenophoreae included in this study.

The distinctive primary and secondary cell characters of *Solenophora calycosa* (depressed cell edges and elevated faces) are restricted to *S. calycosa* and the examined species of *Kohleria* and *Parakohleria* of the Kohlerieae within the examined species of the Gesnerioideae. Except for these distinctive cell characters, the overall seed morphology of *Solenophora calycosa* is very similar to that found among the examined species of the Beslerieae, Bellonieae, Sinningieae, Gloxinieae, Kohlerieae, and Gesnerieae.

TRIBE 11: GESNERIEAE

All of the genera of the Gesnerieae (Skog 1976) are included in this study. The combinations of seed characters exhibited among the examined

species of the Gesnerieae are of particular interest because of the manner in which the combinations are shared among the examined species of some of the other tribes of the Gesnerioideae. The combinations and/or expression of seed characters exhibited among the examined species of the Gesnerieae also help to distinguish the tribe from the other tribes of the Gesnerioideae. The seed morphology of the examined species of the Gesnerieae, in conjunction with the other morphological features of the species (Skog 1976) and chromosome numbers (Skog, 1981a, 1981c), supports the concept of the tribe as a natural taxon.

All of the genera of the Gesnerieae (Skog 1976), namely *Pheidonocarpa*, *Gesneria* and *Rhytidophyllum* (Pls. 39-41), have species that exhibit seed character combinations similar to those found among the examined species of the other tribes of the Gesnerioideae. The overall seed morphology of the examined species of *Gesneria* that possess elliptic seed shapes and a tightly spiral cell orientation (Pls. 39, 40) is similar to that found among the examined species of Beslerieae, Bellonieae, Sinningieae, Gloxinieae and Kohlerieae. On the other hand, the overall seed morphology of the examined species of *Gesneria* and *Rhytidophyllum* that possess narrowly elliptic seed shapes and a slightly spiral cell orientation (Pl. 40) is similar to that found among the examined species of the Episcieae and Mitrarieae. The bluntly angled apices exhibited among the examined species of *Gesneria* and *Rhytidophyllum* (Pl. 40) are similar to those of *Negria rhabdothamnoides* (Pl. 49) of the Coronanthereae. The overall seed morphology of *Pheidonocarpa corymbosa* subsp. *corymbosa* (Pl. 39) is similar to, but quite distinct from that of *Niphaea oblonga* of the Bellonieae at the primary and secondary cell levels. The verrucate cell edges and/or faces exhibited among the examined species of *Gesneria* and *Rhytidophyllum* (Pls. 39, 40) are similar to, but distinct from those found among the examined species of the Gloxinieae (Pl. 35, 36) and Sinningieae (Pl. 37).

TRIBE 12: EPISCIEAE

There are a number of characters exhibited among the examined species of the Episcieae that are restricted to the Episcieae within the examined species of the Gesnerioideae. For instance: the distinctive combination of cell characters found among the examined species of *Nautilocalyx* and *Alloplectus*; the arillate apices found among the examined species of *Codonanthe*, *Nematanthe*, *Oerstedina* and *Rufodorsia*; and the distinctive premorse apices of the examined species of *Drymonia*.

There are a number of seed characters and/or combinations of seed characters exhibited among the examined species of the Episcieae that are similar to those found among some of the examined species of other tribes in the Gesnerioideae. For instance, characters shared among the examined species of the Episcieae and Mitrarieae include: the similar seed shape shared among a large proportion of the examined species of both of the tribes; similar cell shapes; similar cell orientation; the distinctive flattened cell crests which are restricted to some of the examined species of these two tribes within the examined species of the Gesnerioideae. Additional characters exhibited among the examined species of the Episcieae and shared among the examined species of some of the other tribes of the Gesnerioideae will be discussed in the summary of the subfamily.

TRIBE 13: MITRARIEAE

All of the genera of the Mitrarieae (Burt 1963, Gillett 1974) are represented in this study.

The distinctive flattened cell crests exhibited by the examined species of *Sarmienta*, *Asteranthera*, *Mitraria* and *Fieldia* (Pl. 46) of the Mitrarieae are also exhibited by the examined species of *Neomortonia* (Pls. 45, 51) of the Episcieae. This particular cell crest character is restricted to these two tribes within the examined species of the Gesnerioideae. The particular combination of seed shapes, cell orientation and cell shapes exhibited among the examined species of the Mitrarieae are very similar to those exhibited among some of the examined species of the Episcieae. Additional characters exhibited among the examined species of the Mitrarieae and shared among the examined species of some of the other tribes of the Gesnerioideae will be discussed in the summary of the subfamily.

TRIBE 14: CORONANTHEREAE

The coronate apices exhibited among the examined species of the Coronanthereae are similar to those found among the examined species of the Beslerieae, Bellonieae, Sinningieae, Gloxinieae and Kohlerieae.

The particular combination and expression of the primary and secondary cell characters exhibited among the examined species of *Coronanthera* (Pl. 47) are very similar to those of the examined species of *Gasteranthus* (Pl. 49) of the tribe Beslerieae as well as *Tetraphyllum* (Pl. 14) of the Didymocarpeae of the subfamily Cyrtandroideae. These similarities were discussed in detail in the summary of the tribe Didymocarpeae (Tribe 4).

TRIBE 15: ANETANTHEAE

Within the examined species of the Gesneriaceae, the parted cell shapes of the examined species of the Anetantheae are restricted to this tribe and readily distinguish the members of this tribe from the examined species of the rest of the tribes of the family. The orbiculate seed shapes of the examined species of *Anetanthus* (Pl. 48, 51) are also restricted to the Anetantheae within the examined species of the Gesneriaceae.

The terms 'straight cell orientation' and 'discrete cell crests' can be applied to the seeds of the examined species of the Anetantheae. However, the expression of these characters among the examined species of the Anetantheae is completely different from that found among any of the other examined species of the Gesneriaceae and can be readily distinguished from those of the other examined species of the family.

SUBFAMILY GESNERIOIDEAE

The seed morphology exhibited by the examined species of the Gesnerioideae, with the exception of the Anetantheae, fits within an overall trend of characters and/or combinations of characters that supports the concept of the subfamily as a taxon. Of particular interest is the manner in which the seed characters are shared among the examined species of the tribes.

One of the objectives of this study was to compare the seed morphology of the Gesneriaceae with the current classification of the family. As can be seen from Table III, the classification used for comparative purposes is basically that of Burt (1963) and Wilson (1974) with the exception of the reinstatement of the tribe Anetantheae. Wiehler has mentioned a new classification of the subfamily Gesnerioideae being prepared, from as early as 1973, but it has not been published as of the time of this writing (May 1983) and is therefore not available for comparative purposes.

Wiehler (1976) merged the tribes Bellonieae, Sinningieae, Solenophoreae and Kohlerieae, as defined in this study, with the Gloxinieae. However, the

seed morphology of these taxa is not distinguished, as a unit, from that of the rest of the Gesnerioideae and therefore does not support Wiehler's classification.

Of particular interest is the manner in which the seed characters are shared among the tribes. There is a consistent occurrence of coronate apices, in conjunction with a very similar overall seed morphology, among the examined species of the Beslerieae, Bellonieae, Gloxinieae, Sinningieae, Kohlerieae and Coronanthereae. The seeds of the examined species of Solenophoreae lack coronate apices, but the overall seed morphology of the examined species of this tribe is otherwise very similar to that of the examined species of the tribes in which coronate apices do occur.

The examined species of Episcieae and Mitrarieae and Gesnerieae also lack coronate apices. However, as mentioned in the tribal summary of the Gesnerieae (Tribe 11), there are seed characters and/or combinations of characters exhibited by some of the examined species of the Gesnerieae that are similar to those of the tribes in which coronate apices do occur, as well as other characters exhibited by other examined species of the Gesnerieae that are similar to those found among the examined species of the Episcieae and Mitrarieae.

In addition to the seed morphology shared among the examined species of the Episcieae and Mitrarieae that was discussed in the tribal summaries of those tribes (Tribes 12 and 13, respectively), the seed morphology of the examined species of these two tribes is also similar in each in that they lack the highly elaborate cell edges and/or crests found among the examined species of the Beslerieae, Bellonieae, Sinningieae, Gloxinieae, Kohlerieae, Gesnerieae and Coronanthereae.

The seed morphology of the examined species of the Gesnerioideae suggests that the examined species of the Beslerieae, Bellonieae, Gloxinieae, Sinningieae, Solenophoreae, Kohlerieae and Coronanthereae may share a closer affinity with each other than with those of some of the other tribes. The seed morphology of the subfamily also suggests that the examined species of the Episcieae and Mitrarieae may also share a closer affinity with each other than with those of some of the other tribes. In addition, the seed morphology of the examined species of the Gesnerioideae suggests the examined species of the Gesnerieae may be a link between the two groups of tribes mentioned above.

The seed morphology of the examined species of the Anetantheae does not indicate with which subfamily the tribe shares an affinity. In addition, the seed morphology of this tribe suggests that the tribe may occupy a rather isolated position within the family.

The overall seed morphology of the Gesnerioideae however, provides a very strong support for the concept of the subfamily as a natural taxon.

TABLE XXIII. FAMILY GESNERIACEAE - Atlas Plates and Tables 5-52.

The family Gesneriaceae as defined here comprises two subfamilies: Cyrtandroideae and Gesnerioideae (Fritsch 1893, Burt 1963, Melchior 1964 and Wilson 1974).

Except where stated, the listing of a subfamily name after a character does not imply that the character occurs in all of the species, genera and/or tribes of that subfamily, but rather that it has been found to occur among some of the examined species of that subfamily.

Seed Shapes

- Narrowly elliptic, elliptic, broadly elliptic: Cyrtandroideae and Gesnerioideae.
- Circular: Gesnerioideae.
- Keeled: Cyrtandroideae.
- Orbiculate: Gesnerioideae.

Apical Characters

- Acute, constrictate, filiform, premorse, obtuse: Cyrtandroideae and Gesnerioideae.
- Arillate and coronate: Gesnerioideae.

Cell Orientation

- Straight, slightly spiral and spiral: Cyrtandroideae and Gesnerioideae.

Cell Shapes

- Narrowly lineate-polygonate, lineate-polygonate and polygonate: Cyrtandroideae and Gesnerioideae.
- Parted: Gesnerioideae.

Primary Cell Characters

- PCC: Edges elevated or depressed.
- Crests discrete, fused and/or composite.
- Faces elevated or depressed.

All of the above primary cell characters have been found to occur among some of the species of both the Cyrtandroideae and the Gesnerioideae.

Secondary Cell Characters

- SCC: Edges auriculate, verrucate, rough and smooth: Cyrtandroideae and Gesnerioideae.
- Faces not visible, verrucate, rough and smooth: Cyrtandroideae and Gesnerioideae.
- Faces level, tholiform, papillate, tuberculate, auriculate, ocellate, tetragonate, and striate: Cyrtandroideae.

FAMILY GESNERIACEAE

As outlined in Table III (see DISCUSSION), the family Gesneriaceae comprises either two (Fritsch 1893, Burt 1963, Melchior 1964, and Wilson 1974) or three (Ivanina 1965) subfamilies and a variable number of tribes, depending on the morphological characters upon which a particular system is based. Five of the tribes — Anetantheae, Beslerieae, Episcieae, Coronantherae and Mitrarieae — have been transferred back and forth between the subfamilies, whereas the remaining tribes have always been retained within the subfamily to which they were originally assigned (Fritsch 1893, Burt 1963, Melchior 1964, Ivanina 1965, and Wilson 1974).

Based on the carpel morphology of the examined taxa, Ivanina (1965) considered that the Gesneriaceae consisted of three subfamilies, the Cyrtandroideae, the Episcioideae, and the Gesnerioideae. She separated the taxa of the two tribes of the Episcioideae from the subfamily Cyrtandroideae on the basis of distinctive carpological characters found among the examined taxa. The overall seed morphology of the species included in Ivanina's Episcioideae that were examined for this study is quite distinct from that of the examined species of the Cyrtandroideae and supports the separation of the taxa from the Cyrtandroideae.

With the exception of *Besleria*, *Pterobesleria*, (in 1979 Wiehler reduced *Pterobesleria* to *Besleria*), *Napeanthus*, *Tylopsacas*, and *Jerdonia*, the genera

included in Ivanina's Episcioideae are among those included in the Episcieae (as defined here) of the Gesnerioideae. The seed morphology of the examined species of *Besleria*, *Napeanthus*, *Tylopsacas* and *Jerdonia* is quite distinct from that of the examined species of the other genera included in the tribe Episcieae (as defined here). The seed morphology of the examined species of *Besleria* is similar to that of the other examined species of the tribe Beslerieae and supports the affinity of the genus to the other members of that tribe. As previously discussed, the seed morphology of the examined species of *Napeanthus* is similar to that of some of the examined species of the Sinningieae and Gloxinieae which suggests that the *Napeanthus* may share an affinity with either or both of these tribes. The seed morphology of *Tylopsacas cuneata* is anomalous within the Gesneriaceae and does not indicate a tribal or subfamilial affinity for the species within the family, and *Jerdonia* has since been transferred to the Scrophulariaceae (Burt 1977).

The overall seed morphology of some of the examined species of the Episcieae (which includes the genera of Ivanina's Episcioideae with the exception of the genera mentioned above) is very similar to that of the examined species of the Mitrarieae. That there are distinctive seed characters shared among some of the examined species of the Episcieae and Mitrarieae suggests that the two tribes may be closely allied. The seed morphology of the examined species of the Episcieae and Mitrarieae is distinct in certain respects from that of the other examined species of the Gesnerioideae. However, the overall seed morphology of the examined species of these two tribes fits readily within the trend of the seed morphology of the examined species of the Gesnerioideae (as defined here) and supports the concept of the subfamily based on seedling morphology (Burt 1963) and floral anatomy (Wilson 1974).

An information sheet distributed by Wiehler at Les Florales Internationales de Montreal in May 1980 outlined a proposed classification system of the subfamily Gesnerioideae. The outline consisted of a list of generic, tribal and subfamilial names but did not contain any background information regarding the basis for the system. In the outline, the subfamily Gesnerioideae, as defined by Burt (1963) and Wilson (1974), was divided into two subfamilies: the Gesnerioideae and the Coronantheroideae. Also in the outline, the subfamily Coronantheroideae consisted of a single tribe because the tribes Coronanthereae and Mitrarieae, as defined by Burt (1963), Ivanina (1965), Wilson (1974), and Gillett (1974), were merged into one tribe, the Coronanthereae. In addition, the genus *Napeanthus* was classified in the outline as a unigeneric tribe, the Napeantheae, of the Gesnerioideae.

As previously discussed, the seed morphology of the examined species of *Napeanthus* is very similar in all respects to that of the examined species of *Lietzia* of the Sinningieae, and similar in certain very distinctive characters to that of the examined species of *Eucodonia* and *Achimenes* of the Gloxinieae. The shared similarities suggest that the genus *Napeanthus* may share an affinity with either or both the Sinningieae and the Gloxinieae. In addition to the distinctions just mentioned, the overall seed morphology of the examined species of *Napeanthus* fits within the overall trend of that exhibited among the examined species of the Beslerieae, Bellonieae, Sinningieae, Gloxinieae and Kohlerieae and does not support the concept of the separation of the genus as an isolated unigeneric tribe as suggested in Wiehler's outline.

The tribes Bellonieae, Sinningieae, Gloxinieae, Solenophoreae and Kohlerieae were merged into one tribe in Wiehler's outline, and the seed morphol-

ogy of the examined species of these taxa is indeed similar. However, the seed morphology of the examined species of these five tribes is also very similar to that of the Beslerieae, and in certain respects to the examined species of the Coronanthereae and the Gesnerieae. Therefore, the seed morphology in conjunction with other morphological characters (Fritsch 1893, Melchior 1964, Ivanina 1965, and Wilson 1974) of the examined species of these tribes does suggest a close affinity among the above mentioned tribes, but not necessarily in the manner indicated in Wiehler's outline.

The seed character distinctions, in conjunction with other distinctive morphological differences (Burt 1963, Ivanina 1965, Wilson 1974 and Gillett 1974) exhibited among the examined species of the Coronanthereae and Mitrarieae, support the concept of the two tribes as separate taxa, and do not support merging the tribes into a single tribe as indicated in Wiehler's outline. In addition, the seed morphology of the examined species of the Coronanthereae and Mitrarieae fits readily within the trend of seed morphology of the examined species of the Gesnerioideae, as defined here, and does not support the classification of the taxa as a separate subfamily as indicated in Wiehler's outline. On the other hand, the similarity of the seed morphology exhibited among the examined species of the Gesnerioideae, in conjunction with other morphological characters, does provide a very strong support for the concept of the Gesnerioideae as a natural taxon as defined by Burt (1963) and Wilson (1974).

The parted cell shapes and seed morphology of the examined species of the Anetantheae distinguish the tribe from the rest of the examined species of the Gesneriaceae. However, polygonate and parted cell shapes that are somewhat similar to, but quite distinct from, those found among the examined species of the Gesneriaceae, occur among the reported species of the genus *Mentzelia* of the Loasaceae (Hill 1976). Whether both polygonate and parted cell shapes have also arisen among the species of families other than the Loasaceae is not known at this time. There is a variation of parted cell shapes exhibited among the published species of *Mentzelia* (Hill 1976), so maybe the current and recent explorations of South America will result in new taxa of the Gesneriaceae that exhibit further variations of the seed types of the Anetantheae. Such additional new taxa in conjunction with the cytological details of the known taxa of the tribe may help to resolve the problem of the affinity of the tribe Anetantheae within Gesneriaceae.

As can be seen from the Summary of the Seed Morphology Characters of the Gesneriaceae (Table XXV), some of the seed characters are exhibited among the examined species of both of the subfamilies, while others are restricted to either one or the other of the subfamilies.

Within the overall trend of seed morphology exhibited among the examined species of the Gesneriaceae, there are a number of combinations of characters and/or expressions of the characters that distinguish the subfamily Cyrtandroideae from the Gesnerioideae. These distinctions include differences in the cell orientations, cell shapes and secondary cell characters. For instance, the proportions of the cell orientation types exhibited among the examined genera of the Cyrtandroideae range from straight (85%) to slightly spiral (7.5%) and spiral (7.5%). Conversely the proportions of cell orientation types exhibited among the examined genera of the Gesnerioideae range from straight (4%) to slightly spiral (37%) and spiral (58%). In addition, there is a smaller proportion of narrowly lineate-polygonate cell shapes (14%) than lineate-polygonate (36%) and polygonate (70%) exhibited among

the examined genera of the Cyrtandroideae, whereas among the examined genera of the Gesnerioideae the proportions of the cell shapes range from narrowly lineate-polygonate (53%) to lineate-polygonate and polygonate only (1%).

The subfamilies are also distinguished from each other by the secondary cell characters exhibited among the examined species of the family. For instance, there is a very wide range of extremely diverse cell face elaboration characters exhibited among the examined species of the Cyrtandroideae, but only a very minor range of cell face characters exhibited among the examined species of the Gesnerioideae. The cell face characters that are restricted among the examined species of the Gesneriaceae to the Cyrtandroideae include level, tholiform, papillate, tuberculate, auriculate, ocellate, tetragonate, and striate. On the other hand, the cell edges of the examined species of the Cyrtandroideae are not nearly as highly or distinctively elevated or elaborated as are those of many of the examined species of the Gesnerioideae. These very distinctive cell edges of the Gesnerioideae, in conjunction with a similar overall seed morphology are found, for the most part, among the examined species of the Beslerieae, Bellonieae, Sinningieae, Gloxinieae, Kohlerieae, Gesnerieae and Coronathereae.

The seed morphology distinctions exhibited among the examined species of the Cyrtandroideae and Gesnerioideae support the concept of the division of the Gesneriaceae into two subfamilies based on seedling morphology (Burt 1963) and floral morphology (Wilson 1974). The distinctions found among the chromosome numbers of each of the subfamilies also support the concept of the division of the Gesneriaceae into the Cyrtandroideae and Gesnerioideae. For instance, the compendia of published chromosome numbers of the Gesneriaceae (Skog, 1980a, 1980b, 1981a, 1981b, 1981c, 1982a, 1982b) show that there is a much wider range of chromosome numbers found among the examined species of the Cyrtandroideae than among the examined species of the Gesnerioideae. The compendia also show that there can be a very wide range of chromosome number variations found among the examined species of a genus and/or tribe of the Cyrtandroideae whereas the chromosome numbers of the examined species of the Gesnerioideae are usually consistent among the species of a genus and/or tribe.

Distinctive seed characters shared among the examined species of the Cyrtandroideae and the Gesnerioideae include the particular combinations of seed characters exhibited among the examined species of *Tetraphyllum* of the Didymocarpeae of the Cyrtandroideae and *Gasteranthus* of the Beslerieae and *Coronanthera* of the Coronathereae of the Gesnerioideae. These shared characters are of particular interest because the tribes Beslerieae and Coronathereae are among the tribes that have been transferred back and forth, depending on the morphological characters used to separate the subfamilies, between the Cyrtandroideae and the Gesnerioideae (Fritsch 1893, Ivanina 1966 and Melchior 1964). Burt (1963) and Morley (1978) pointed out that very little is actually known about the interrelationships among the taxa of the Gesneriaceae. However, that there are distinctive seed characters shared among some of the examined species of the Didymocarpeae, Beslerieae and Coronathereae suggests that in conjunction with other morphological characters (Fritsch 1893, Ivanina 1966 and Melchior 1964), some of the species of these tribes may be links between the subfamilies.

The manner in which the combinations and expression of the seed characters are exhibited among the examined species of the Gesneriaceae helps to

distinguish the taxa at the various levels of classification within the family. The trend of the seed morphology exhibited among the examined species of the Gesneriaceae, within which the various combinations of seed characters fit and/or overlap, supports the concept of the Gesneriaceae as a natural taxon as defined by Dumortier (1822), G. Don (1838), Fritsch (1893), Burt (1963), Melchior (1964), Ivanina (1966) and Wilson (1974).

TABLE XXIV. GENERA EXCLUDENDA - Atlas Plate and Table 52, figs. C-I. Representative genera: *Jerdonia*, *Cyrtandromoea*, *Rehmannia* and *Charadrophila*.

Seed Shapes

The seed shapes of these genera include elliptic and broadly elliptic.

Apical Characters

The apical characters of these genera include constrictate and obtuse.

Cell Orientation

The cell orientation of these genera include two types:

1. Straight: the examined species of *Cyrtandromoea* and *Charadrophila*.
2. Irregular: the examined species of *Jerdonia* and *Rehmannia*.

Primary (PCC) and Secondary (SCC) Cell Characters

The primary and secondary cell characters of these genera can be divided into two basic types:

1. PCC: Edges irregular.
Crests discrete.
Faces elevated.
- SCC: Edges rough.
Faces tholiform and rough.
Type 1 consists of *Jerdonia indica*.
2. PCC: Edges elevated: the examined species of *Cyrtandromoea*, *Rehmannia* and *Charadrophila*.
Crests discrete: the examined species of *Cyrtandromoea* and *Charadrophila*.
Crests fused: *Rehmannia henryi*.
Faces depressed: the examined species of *Cyrtandromoea*, *Charadrophila* and *Rehmannia*.
- SCC: Edges striate: the examined species of *Cyrtandromoea*.
Edges rough: the examined species of *Charadrophila*.
Edges smooth: *Rehmannia henryi*.

The genera *Jerdonia*, *Cyrtandromoea*, *Rehmannia* and *Charadrophila* are of particular interest in this study because they were formerly classified as members of the Gesneriaceae (Burt 1963). Then in 1965, Burt transferred *Cyrtandromoea*, on the basis of possessing isocotylous seedlings, to the Scrophulariaceae and in 1977, also on the basis of possessing isocotylous seedlings, Burt transferred *Jerdonia*, *Charadrophila*, *Rehmannia* and *Brookea* to the Scrophulariaceae. Seeds of *Brookea* were not available for this study. However, *Jerdonia*, *Cyrtandromoea*, *Rehmannia* and *Charadrophila* are included in this study, and the seeds of these genera are illustrated and recorded on Atlas Plate and Table 52.

The cell shapes and primary cell characters of *Jerdonia indica* are somewhat similar to but distinct from those of *Petrocodon dealbatus* (Pl. 17, fig. D) and *Opithandra primuloides* (Pl. 17, fig. E). However, the cell orientation

of *J. indica* is irregular whereas that of *P. dealbatus* and *O. primuloides* is straight. Other than the similarities mentioned above, the seeds of *J. indica* are quite distinct from those of the examined species of the Gesneriaceae.

The seed shapes, straight cell orientation and cell shapes of the examined species of *Charadrophila* and *Cyrtandromoea* are similar to but quite distinct from those of the examined species of the Gesneriaceae. For instance, the examined species of *Cyrtandromoea* have discrete cell edges and very distinct striae that encircle the circumference of the cell edges and are transverse across the cell faces (Pl. 52, figs. D, E, F). In contrast, the cells of *Boeica fulva*, Didymocarpeae, subfamily Cyrtandroideae (Pl. 30, fig. A), have fused crests with distinct striae that are transverse across both the cell edges and faces. In addition, the fibrous extensions on the cell edges of the examined species of *Cyrtandromoea* have not been found among the examined species of the Gesneriaceae.

The examined species of *Charadrophila* have discrete cell crests with transverse striae and multiple ocellate projections on the cell faces and smooth cell edges, a combination of characters that has not been found among the examined species of the Gesneriaceae. Some of the species of *Streptocarpus*, such as *S. saxorum* (Pl. 24, fig. B), have single ocellate projections on the cell faces, but none of the examined species of the Gesneriaceae have been found to exhibit multiple ocellate projections on the cell faces, with or without transverse striae.

The irregular cell orientation and cell shapes of *Rehmannia henryi* are quite distinct from those of the examined species of the Gesneriaceae. In addition, the outer layer (or layers?) of the seeds of *R. henryi* break down by the time the seeds are mature and leave a 'broken window' effect in many of the cells (Pl. 52, fig. G). This broken window effect has not been found among the examined species of the Gesneriaceae. However, it is similar to that found on the seeds of *Gentiana asclepiadea* (P. 4, figs. A, D) of the Gentianaceae.

The similarity of certain seed characters exhibited by the examined species of *Jerdonia*, *Cyrtandromoea*, *Rehmannia* and *Charadrophila* to those found among the examined species of the Gesneriaceae confirms the affinity of the Gesneriaceae with the Scrophulariaceae (Burt 1963, Heywood 1978). On the other hand, the differences of the seed characters and the combinations of characters exhibited by the examined species of these four genera from those found among the examined species of the Gesneriaceae support Burt's transfer (1963, 1977) of the genera to the Scrophulariaceae.

RELATIONSHIPS OF THE GESNERIACEAE TO OTHER FAMILIES

The Gesneriaceae are considered to be closely related to the Scrophulariaceae (Heywood 1978), the Bignoniaceae and probably the Orobanchaceae (Lawrence 1951). The Scrophulariaceae is a large family of some 220 genera and 3,000 species, the Bignoniaceae comprises 120 genera and 650 species and the Orobanchaceae consists of 14 genera and 180 species (Heywood 1978).

There are 8 species in 7 genera of the Scrophulariaceae included in this study (Pls. 4, 52). The combined SEM investigations of Chuang and Heckard (1972), Tomb (1974), and Musselman and Mann (1976) included details of the seed morphology of 49 species in 14 genera of the Scrophulariaceae. The SEM investigation of Hesse and Morowitz (1980) included details of the seeds of 21 species in 3 genera of the Bignoniaceae, and that of Musselman and Mann (1976) included 2 species in 2 genera of the Orobanchaceae.

At the time of their investigation, Musselman and Mann (1976) pointed out that terminology needed to describe seed surface characters adequately had not yet been evolved. Heywood (1969) and Hill (1976) also drew attention to the problems and confusion caused by the lack of precise terminology with which to describe seed characters. However, in order to keep the language of the following comparisons uniform with the rest of the study, the seed terminology used in the comparisons is that of the glossary of terminology defined for and used throughout this study and not necessarily that used by the authors of the various investigations discussed.

A. SCROPHULARIACEAE

Cordylanthus, 23 species (Chuang and Heckard 1972).

The elliptic seed shape of *Cordylanthus parviflorus* (Ferris) Wiggins and *C. pringlei* A. Gray is somewhat similar to but quite distinct from some of the seeds found among some examined species of the Gesneriaceae because of the irregular shape. However, the reniform seed shapes, the extremely irregular, lineate-polygonate cell shapes, the highly elevated cell crests, the secondary cell characters, such as multiple honeycomb reticulations exhibited on the individual cell faces, the elongated, pointed tuberculae, and the particular type of papillate cell face characters exhibited among the illustrated species of *Cordylanthus*, are all quite different from those observed on any of the examined species of the Gesneriaceae.

Leucophyllum, 2 species; *Faxonantha*, 1 species (Tomb 1974). Close-ups of cells only.

The cell shapes of the illustrated species of *Leucophyllum* and *Faxonantha* are very similar to those of the examined species of *Cyrtandromoea* (Pl. 52). The similarity confirms Burt's (1965) transfer of the *Cyrtandromoea* from the Gesneriaceae to the Scrophulariaceae. The papillate cell crests of the illustrated species of *Leucophyllum* and *Faxonantha* are somewhat similar to those exhibited by some of the examined species of the Trichosporeae in the Gesneriaceae, subfamily Cyrtandroideae, such as *Lysionotus*. However, the surface texture of the cell crests and cell face characters are quite different from those observed on any of the examined species of the Gesneriaceae.

Agalinis, *Aureolaria*, *Buchnera*, *Castilleja*, *Dasistoma*, *Macranthera*, *Malampyrum*, *Pedicularis*, *Schwalbea*, *Seymeria* and *Striga*, 23 species in 11 genera (Musselman and Mann 1976).

Seed character similarities shared among the examined species of the Gesneriaceae and those of the illustrated species of the genera listed above include the seed shapes of *Rhynchoglossum klugoides* of the tribe Trichosporeae, subfamily Cyrtandroideae, and those of *Pedicularis canadensis* L. The seed and cell shapes of some of the examined species of *Cyrtandra*, tribe Cyrtandreae, subfamily Cyrtandroideae, are somewhat similar to those of *Agalinis tenella* Penn. However, for the most part, the seed morphology of the illustrated species of the genera listed above is quite distinct from that of the examined species of the Gesneriaceae. Examples of seed character distinctions exhibited among some of the illustrated species of the above genera that have not been observed among any of the examined species of the Gesneriaceae include distinctive papillate cell crests (*Striga*), very highly elevated cell crests (*Seymeria*), 'broken window' effect of the cell surfaces (*Seymeria*), and multiple honeycomb reticulations of the individual cell faces (*Seymeria*).

Included in this study were *Jerdonia*, *Cyrtandromoea*, *Charadrophila* and *Rehmannia* (Pl. 52), transferred from the Gesneriaceae to the Scrophulariaceae (Burt 1963, 1967), and *Phygelius*, *Lophospermum* and *Tetranema* (Pl. 4). The deeply rugose surface of the seeds of *L. purpusii* (Pl. 4, fig. H) is completely different from that of any of the other species examined during the course of this investigation. The secondary cell characters of *P. capensis* (Pl. 4, fig. B) are similar to that of the examined species of *Cyrtandromoea* (Pl. 52) and *Cordylanthus orcuttianus* A. Gray (Chuang and Heckard 1972). The striate cell face characters of *T. roseum* (Pl. 4, fig. F) are very similar to those of the examined species of *Cyrtandromoea* (Pl. 52). The 'broken window' effect of the cell surfaces of *R. henryi* are very similar to those of some of the illustrated species of *Seymeria* (Musselman and Mann 1976). The multiple reticulations of the cell faces of the examined species of *Charadrophila* are similar to those among the illustrated species of *Cordylanthus*, and the cell shapes of *J. indica* (Pl. 52, fig. C) are also similar to those of some of the illustrated species of *Cordylanthus* (Chuang and Heckard 1972).

The seed character similarities shared among the examined species of *Jerdonia*, *Cyrtandromoea*, *Charadrophila*, and *Rehmannia* (Pl. 52) with the other examined or illustrated species of the Scrophulariaceae confirm Burt's transfer of those genera from the Gesneriaceae to the Scrophulariaceae (1963 and 1967) and add support to the concept of the Scrophulariaceae as a natural taxon. The particular combinations and types of multiple projections on the individual cell faces exhibited among a number of the examined or illustrated species of the Scrophulariaceae may prove to be distinctive characters of the family. However, this will not be known until the seeds of a much larger number of the species of the family have been investigated. The seed characters shared among some of the examined species of the Gesneriaceae with some of the examined or illustrated species of the Scrophulariaceae support the concept of an affinity between the families (Heywood 1978). On the other hand, the seed character differences exhibited among the examined or illustrated species of the two families support the concept of the two families as separate and natural taxa (Heywood 1978).

B. BIGNONIACEAE

Jacaranda, 16 species, and 1 species each of *Tabebuia*, *Digomphia*, and *Tecoma* (Hesse and Morowitz 1980); close-ups of secondary cell characters.

The very distinctive stellate projections on the cell faces of the illustrated species of *Jacaranda* were not found on any of the examined species of the Gesneriaceae. The primary and secondary cell characters of the illustrated species of *Digomphia*, *Tecoma*, and *Tabebuia* were also quite different from those of any of the examined species of the Gesneriaceae.

C. OROBANCHACEAE

Epiphagus, 1 species, and 1 species of *Conopholis* (Musselman and Mann 1976).

The seeds of *Epiphagus virginiana* (L.) Bart. are somewhat similar to those of *Cremosperma congruens* and *C. jucundum*, tribe Beslerieae, subfamily Gesnerioideae, in seed and cell shapes but are quite distinct from them at the primary and secondary cell character levels. The seed morphology of *Conopholis americana* (L.) Wallr. appears to be quite distinct from that of the examined species of the Gesneriaceae (the photo is not as distinct as it might be) but similar to that of *Tetranema roseum* (Pl. 4).

The small number of species of the Scrophulariaceae, Bignoniaceae and Orobanchaceae of which the details of the seed morphology have been either

published or included in this study, does not, of course, provide sufficient information on which to base comparisons of the seed morphology of the three families. However, based on the seed morphology of the examined species of the Gesneriaceae and the small number of species of the Scrophulariaceae, Bignoniaceae and Orobanchaceae discussed above, the seed morphology of the Gesneriaceae is distinct from that of the other three families in a number of characters or combinations of characters. Any meaningful comparisons of the seed morphology of the Gesneriaceae with that of other families will have to wait until after family-wide seed investigations are conducted.

DISTINCTIVE SEED CHARACTERS OF FAMILIES OTHER THAN THE GESNERIACEAE

Additional distinctive seed characters found among some of the examined species of families other than the Gesneriaceae, that are different from those found among the examined species of the Gesneriaceae include:

1. *Hackelia virginiana* (family Boraginaceae). This species produces dimorphic nutlets, and the nutlets of both types (Pl. 2, figs. C, I) are similar in shape. However, the surface of one type is covered with very prominent and distinctive stellate-glochidate trichomes (Pl. 2, fig. F, close-up) while the surface of the other type (Pl. 2, fig. I) is smooth and lacks trichomes.

2. *Arenaria serpyllifolia* (family Caryophyllaceae). The reniform seed shape of this species is completely different from that of any of the examined species of the Gesneriaceae, but the lobed cell shapes of *A. serpyllifolia* (Pl. 2, fig. A) are somewhat similar to the parted cell shapes of the examined species of *Anetanthus* and *Resia*, tribe Anetantheae, subfamily Gesnerioideae. However, the parted cell shapes of the examined species of *Anetanthus* and *Resia* are narrowly lineate-polygonate, and the cell margins are indented $1/2$ to $3/4$ to the axis of the cell. The protruding portions of the cell margins of the examined species of *Anetanthus* are expanded and fit into the indentation of the adjoining cells (Pl. 48, figs. E, F, close-ups) in the manner of a jigsaw puzzle. On the other hand, the lobed cells of *Arenaria serpyllifolia* are irregular-polygonate in shape, the cell margins are indented about $1/8$ to $1/4$ the distance to the axis of the cell, and the protruding portion of the cell margins are not expanded. The lobed cell shapes and primary and secondary cell characters of *A. serpyllifolia* are very similar to those observed on the dozen or so other species of the Caryophyllaceae examined during the course of this investigation.

3. *Eucalyptus viminalis* (family Myrtaceae). The cell faces of this species (Pl. 2, figs. B, E) are distinctively elevated and have a fairly regular pattern of papillae on the surface of each cell face (Pl. 2, fig. E, close-up). There had been a trichome at the center of each of the cell faces but, unfortunately, most of the trichomes had been broken off.

4. *Gentiana asclepiadea* (family Gentianaceae: Pl. 4, figs. A, D) and *Phygeliopsis capensis* (family Scrophulariaceae: Pl. 4, figs. B, E). The seeds of these two species are very similar to each other in seed shapes, cell orientation, cell shape and primary cell characters. However, as can be seen from the close-ups of the cells of these two species (Pl. 4, figs. D, E), the secondary cell characters of these two species are quite different from each other.

The 6 major categories, several minor ones and 60 individual seed characters that make up the seed identification and analysis system that was

created for this study has provided the means to diagnose a very wide range of combinations and expressions of the seed morphology exhibited among the examined species of the Gesneriaceae. One of the most interesting and rewarding results of this study has been to discover that, in most cases, it was the manner in which the combinations and expressions of the various seed characters, not just a single character, defined the taxa at various levels.

The seeds that were examined during the course of this study were pre-treated for SEM as well as scanned and photographed with the SEM by the author, and the plates that illustrate this study were made by the author.

CONCLUSION

The research objectives of this study were to (1) prepare a descriptive guide of the seeds of the examined species of the Gesneriaceae based on SEM; (2) relate, and interpret if possible, the patterns of seed morphology of the examined species of the Gesneriaceae to taxonomic relationships within the Gesneriaceae; and (3) seek, by means of the SEM, seed morphology features that are representative of the Gesneriaceae.

Because of the paucity and inconsistent usage of seed terminology in the existing literature, a system with which to analyze and diagnose the seed surface morphology of the examined species of the Gesneriaceae was designed by the author. To ensure that the system would also apply to the seed morphology of seed plants in general, the seeds, or achenes and nutlets, of a wide variety of species from families other than the Gesneriaceae were examined. The seeds, achenes and nutlets of 15 species from 13 families were selected from the species examined to represent 8 of the 10 subclasses of the flowering plants (Cronquist 1968) and were included in this study. An additional 5 species that were transferred from the Gesneriaceae to the Scrophulariaceae (Burt 1963, 1967) made a total of 20 species from families other than the Gesneriaceae included in this study.

The Seed Atlas (Glossary and Atlas Plates and Tables) of this study consists of an illustrated, descriptive guide of the examined species of the Gesneriaceae as well as the non-gesneriaceous species included in this study. The seeds, achenes and nutlets of the examined species included in this study are illustrated with SEM photomicrographs and the diagnostic data of each species are recorded on the Atlas Tables that face each of the Atlas Plates. To facilitate the comparison of the taxa and to assist in the identification of the seeds of a species, the seed morphology data of the examined species of the Gesneriaceae are also recorded on the Summary Table (Table XXV) at the genus, tribal, subfamily, and family levels.

The seed morphology of the examined species of the Gesneriaceae is compared and contrasted with the current classifications of the family in the DISCUSSION, at the species, generic, tribal, subfamily and family levels. Each of the sections of the DISCUSSION includes a summation table of the seed characters of the taxa at that particular classification level. In addition, the seed morphology of the examined species of the Gesneriaceae is compared with that of the species included in published SEM investigations of the Scrophulariaceae (Musselman and Mann 1976, Tomb 1974, and Chuang and Heckard 1972), Bignoniaceae (Hesse and Morowitz 1980) and the Orobanchaceae (Musselman and Mann 1976).

Therefore the study has fulfilled all of the proposed research objectives. The study has also resulted in a system that was designed by the author to facilitate a rapid, efficient, uniform, objective method with which to deal

with the analytical, diagnostic, identification and taxonomic comparison aspects of an investigation of seed morphology. In addition, the system readily lends itself to the substitution and addition of categories and terms if needed as well as to programming for computerized analysis of seed morphology such as outlined by Gunn and Seldin (1977).

The seed analysis system designed for this study has proved to be an extremely useful tool in my investigation of the seed morphology of the Gesneriaceae. It is hoped that the system will prove to be useful to other investigators as well as to help standardize future investigations of seed morphology. The relationships between the seed morphology patterns and the geographical distributions of the examined species of the Gesneriaceae included in this study will be the subject of a later paper.

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