HETEROSTYLISM IN *OLDENLANDIA UMBELLATA* L.

By BIR BAHADUR

Department of Botany, Osmania University, Andhra Pradesh, India

Remarkably little is known about heterostylism in tropical plants, and I know of no studies of natural populations comparable with those of Schoch-Bodmer (1938) on *Lythrum salicaria* L., Haldane (1938) on *Primula acaulis* and Crosby (1949) on *Primula vulgaris*. Prof. J. B. S. Haldane suggested that I might make such a study on one of the Rubiaceae, a family in which heterostyly is widespread, as Darwin (1892) pointed out in his classical book, *The different forms of flowers on plants of the same species.*

The genus Oldenlandia is represented by 200 species (Rendle, 1959) out of which 21 species display dimorphic heterostylism. Bremekamp (1952) has monographed the African species of this genus, in which he has shown the distribution of heterostyly and homostyly. Bremekamp (1956, 1958) reported some more species which are also heterostyled.

Oldenlandia umbellata L. shows dimorphic heterostylism, i.e., two types of flowers occur on separate plants, conventionally termed as "Thrum eyed", with short style and long anthers, and "Pin eyed", with long style and short anthers (see Plate 15).

Oldenlandia umbellata is common in the neighbourhood and accessible to me. It is a conspicuous white flowered annual, and a successful weed. At Adigmet (Osmania University Campus) the population was dense over a large area. At Himayat Sagar and Miraulam it was distributed over waste land and road sides, sometimes growing in sand or in rock crevices. At Narsapur it was not common in lawns, but occurred along dry water courses, confirming Ridley's (1930) statements as to the dispersal of its seeds by water.

Table 1 is a list of all species of Rubiaceae known to me in which heterostylism has been reported. These number 155 out of a total of about 5,500 species in the family.

Table 1. *Recorded cases of Heterostylism in the family Rubiaceae*

S. No.	Species	Tribe	Floral situation†	References
1.	**Cinchona micrantha.*	Cinchoneae.	D	Darwin (1892), East (1940)
2.	*Sipania sp.*	Rondeletieae.	D	Verdcourt (1958)
3.	*Pentas lanceolata.*	Hedyotideae.	T or D	Verdcourt (1953d), Baker (1958), Bir Bahadur (Pin form only)
	P. purseglovei.	,,	D	Verdcourt (1953d), Baker (1958)
	P. cteisostoma.	,,	D	Verdcourt (1953d)
	P. parviflora.	,,	D	Verdcourt (1953d), Hiern (1878)
	P. arvensis.	,,	D	Hiern (1878)
	P. zanzibarica.	,,	D	Verdcourt (1953d)
	P. pubiflora.	,,	D	,,
	P. decaryana.	,,	D	,,
	P. pseudomagnifica.	,,	D	quoted by Verdcourt (1953d)
	P. purpurea.	,,	D	Hiern (1878)

*East (1940): 40 species are heterosilylic.
†D Dimorphic, T Trimorphic.

Table 1. *Recorded cases of Heterostylism in the family Rubiaceae*—(*Contd.*)

S. No.	Species	Tribe	Floral situation	References
	Pentas nobilis.	Hedyotideae.	D	Verdcourt (1953d)
	P. longiflora.	,,	T or D	,,
	P. coccinea.	,,	D	quoted by Baker (1958)
4.	*Parapentas battiscombei.*	,,	D	Verdcourt (1953c)
	P. setigera.	,,	T or D	,,
	P. gabonica.	,,	D	Bremekamp (1952)
5.	*Tapinopentas latifolia.*	,,	D	Verdcourt (1953c)
	T. ulugurica.	,,	D	,,
	T. cameronica.	,,	D	Bremekamp (1952)
6.	*Pentodon pentander.*	,,	D	,,
	P. laurentioides.	,,	D	,,
7.	*Dibrachinostylus kaessneri.*	,,	D	,,
8.	*Otomeria guineensis.*	,,	D	Verdcourt (1953a)
	O. lanceolata.	,,	D	,,
	O. madiensis.	,,	D	,,
	O. oculata.	,,	D	,,
9.	*Chamaepentas greenwayi.*	,,	D	Bremekamp (1952)
10.	*Sacosperma sp.*	,,	D	,,
11.	*Stephanococcus crepinianus.*	,,	D	,,
12.	*Manostachya sp.*	,,	D	,,
13.	*Hedythyrsus sp.*	,,	D	,,
14.	*Agathisanthemum bojeri.*	,,	D	,,
	A. angolense.	,,	D	,,
	A. chlorophyllum	,,	D	,,
	A. quadricostatum.	,,	D	,,
15.	*Eionitis sp.*	,,	D	,,
16.	*Amphiasma luzuloides.*	,,	D	,,
	A. redheadii.	,,	D	,,
	A. robijnsii.	,,	D	,,
	A. benguellense.	,,	D	,,
	A. merenkyanum.	,,	D	,,
	A. divaricatum.	,,	D	,,
17.	*Lelya osteocarpa.*	,,	D	,,
18.	*Pleiocraterium verticillare.*	,,	D	Bremekamp (1939)
19.	*Dirichletia sp.*	,,	D	Hiern (1878)
20.	*Pentanisia sp.*	,,	D	,,
21.	*Siderobombyx kinabalunisis.*	,,	D	Bremekamp (1947a)
22.	*Danais sp.*	,,	D	Verdcourt (1958)
23.	*Houstonia caerulea.*	,,	D	Darwin (1892), Stevens (1912), Robinson and Fernald (1908), Lewis (1961a)
24.	*Anotis nummularia.*	,,	D	Bond (1953)
	A. richardiana.	,,	D	,,
25.	*Schismatoclada trichopharynx.*	,,	D	Verdcourt (1958)
26.	*Oldenlandia cryptocarpa.*	,,	D	Bremekamp (1952)
	O. nervosa.	,,	D	,,
	O. chevallieri.	,,	D	,,
	O. ocellata.	,,	D	,,
	O. aretioides.	,,	D	,,
	O. pulvinata.	,,	D	,,
	O. monanthos.	,,	D	,,
	O. hockii.	,,	D	,,
	O. geophila.	,,	D	,,
	O. friesiorum.	,,	D	,,
	O. greenwayi.	,,	D	,,
	O. johnstonii.	,,	D	,,
	O. rupicola.	,,	D	,,
	O. muscosa.	,,	D	,,
	O. tenella.	,,	D	,,
	O. sipaneoides.	,,	D	,,
	O. tardavelina.	,,	D	,,

Table 1. *Recorded cases of Heterostylism in the family Rubiaceae*—(*Contd.*)

S. No.	Species	Tribe	Floral situation	References
	Oldenlandia taborensis.	Hedyotideae	D	Bremekamp (1952)
	O. duemmeri.	,,	D	,,
	O. scopulorum.	,,	D	,,
	O wiedemanii.	,,	D	,,
	O. icthyoderma.	,,	D	,,
	O. herbacea var. *holstii.*	,,	D	,,
	O. pringlai.	,,	D	,,
	O. saxifragoides.	,,	D	,,
	O. rosulata.	,,	D	,,
	O. microcalyx.	,,	D	,,
	O. affinis.	,,	D	Bremekamp (1952), Baker (1958)
	O. flosculosa.	,,	D	Bremekamp (1952)
	O. patula.	,,	D	,,
	O. umbellata.	,,	D	Bremekamp (1952), Bir Bahadur, Lewis (1961a)
	O. somala.	,,	D	Bremekamp (1952)
	O. eludens.	,,	D	,,
	O. marginata.	,,	D	Bremekamp (1958)
	O. oxycoccoides.	,,	D	,,
	O. verticillata.	,,	D	Bremekamp (1952)
	O. filipes.	,,	D	Bremekamp (1956)
	O. capensis.	,,	D	Post (1932)
	O. schimperi.	,,	D	Crowfoot (1928)
27.	*Hedyotis sp.*	,,	D	Darwin (1892)
	H. nigricans	,,	D	Lewis (1961b)
	H. humifusa	,,	D	,,
	H. purpurea.	,,	D	,,
28.	*Bouvardia leiantha.*	,,	D	Darwin (1892)
29.	*Knoxia sp.*	Knoxieae	D	Darwin (1892), East (1940)
	K. mollis.	,,	D	Fyson (1932)
	K. platycarpa.	,,	D	Bond (1953)
30.	*Cruckshankia glacialis.*	Cruckshankieae	D	Skottsberg (1915)
	C. hymenodon.	,,	D	Verdcourt (1958)
31.	*Mussaenda erythrophylla.*	Mussaendeae.	D	Baker (1958)
	M. elegans.	,,	D	Baker (1958), Hallé (1961)
	M. tenuiflora.	,,	D	Petit (1954)
	Mussaenda sp.	,,	D	Bremekamp (1947b)
	M. chippi	,,	D	Hallé (1961)
	M. erythrophylla	,,	D	,,
32.	*Pseudomussaenda stenocarpa.*	,,	D	Petit (1954), Hallé (1961)
	P. flava.	,,	D	Petit (1954)
33.	*Gouldia sp.*	,,	D	,,
34.	*Adenosacme longifolia.*	,,	T or D	Darwin (1892), Hooker (1882)
35.	*Aphaenandra uniflora.*	,,	D	Bremekamp (1937)
	Aphaenandra sp.	,,	D	Hallé (1961)
36.	*Coccocypselum sp.*	,,	D	Darwin (1892)
37.	*Pauridiantha sp.*	,,	D	Verdcourt (1958)
	P. hirtella.	,,	D	Hallé (1961)
38.	*Sabicea venosa.*	,,	D	,,
	S. hierniana.	,,	D	,,
39.	*Stipularia africana.*	,,	D	,,
40.	*Ecpoma apocynaceum.*	,,	D	,,
41.	*Temnopteryx sericea.*	,,	D	,,
42.	*Pentaloucha sp.*	,,	D	,,
43.	*Sacosperma paniculata*	,,	D	,,
44.	*Anthospermum herbaceum.*	Anthospermeae	D	Verdcourt (1958)
45.	*Coprosma sp.*	,,	D	Darwin (1892)
46.	*Mitchella repens.*	,,	D	Darwin (1892), Robinson and Fernald (1908)
47.	*Paederia sp.*	Paederieae	D	Verdcourt (1958)
48.	*Tricalysia sp.*	Ixoreae	D	Hiern (1878)

Table 1. *Recorded cases of Heterostylism in the family Rubiaceae*—(Contd.)

S. No.	Species	Tribe	Floral situation	References
49.	*Craterispermum laurinum.*	Craterispermeae	D	Verdcourt (1958)
50.	*Rudgea jasminoides.*	Coussareae	D	Baker (1956)
	R. coriacea. (*R. eriantha.*)	,,	D	Baker (1956) "Darwin's (1892) *Faramea sp.*"
51.	*Psychotria vogeliana.*	Psychotrieae	D	Baker (1958)
	Psychotria sp.	,,	D	Darwin (1892)
	P. benthamiana.	,,	D	Baker (1958)
	P. warnecki.	,,	D	,,
	P. malyana.	,,	D	Ernst (1932)
	P. elongata.	,,	D	Fyson (1932)
52.	*Uragoga nimbana.*	,,	D	Schnell (1953) quoted by Baker (1958)
	U. peduncularis.	,,	D	Baker (1958)
53.	*Lasianthus capitdatus.*	,,	D	Bir Bahadur (Pin form only)
54.	*Mapouria sp.*	,,	D	Bremekamp (1961)
55.	*Grumilea sp.*	,,	D	,,
56.	*Geophila sp.*	,,	D	Baker (1958) (Pin form only)
57.	*Borreria sp.*	Spermacoceae	D	Darwin (1892)
58.	*Diodia sp.*	,,	D	Darwin (1892), Baker (1958)
59.	*Spermacoce sp.*	,,	D	Darwin (1892)
60.	*Selonocera sp.*	,,	T	Willis (1931)
61.	*Suteria sp.*	,,	D	Darwin (1892)
62.	*Lipostoma sp.*	,,	D	,,
63.	*Schwendenera sp.*	,,	D	East (1940)
64.	*Perama sp.*	,,	D	,,
65.	*Nertera sp.*	?	D	Darwin (1862)
66.	*Manettia sp.*	?	D	,,

During September and December 1960, the collections of plants were made in the localities mentioned in Table 2. As the species is a strict annual, there was never any doubt as to what constituted a single plant, as there is in perennials such as *Primula acaulis* and *Lythrum salicaria*. I carried two bags, into one of which I put long styled plants into the other short styled plants. The counts are given in Table 2. There is an excess of "Pin" or long styled plants, which is highly significant ($\chi^2_1=44.7$). But the different populations are extremely heterogeneous ($\chi^2_5=72{\cdot}37$) and it is quite possible that "Thrum" or short styled plants might predominate in a larger total sample, as they did in two of my six. This inequality or anisoplethy and heterogeneity is very different from Haldane's (1938) finding in *Primula acaulis*.

Mention may be made of Fabergé (1959) who recently counted populations of Oxalis, a trimorphic genus. He counted the populations of *Oxalis grandis* and *Oxalis suksdorfii*, in which he found anisoplethy as against isoplethy (the equilibrium condition according to certain theories). His counts are given below (Table 3).

To investigate the mode of inheritance of style length, long and short styled plants were crossed and selfed in the combinations shown in Table 4. The cross P×T is more fertile than T×P as deduced from the greater seed set per capsule. Selfing pin and thrum produced very few or no seeds. Occasionally long styled plants set 2-5 seeds. Thus the incompatibility in thrum is absolute, and in the case of pin is relaxed a little.

Table 2. *Counts of Natural populations of* Oldenlandia umbellata

Locality	Pin eyed	Thrum eyed	Total	% of Pins	% of Thrums
1. Adigmet	337	150	487	69·20	30·80
2. Miraulam	146	112	258	56·59	43·41
3. Narsapur	111	133	244	45·49	54·51
4. Falaknuma	78	120	198	39·39	60·61
5. Himayat Sagar	125	100	225	55·56	44·44
6. S.V.U. Campus	296	186	482	61·41	38·59
Total	1,093	801	1,894	57·709	42·291

Table 3

Species	Locality	Long styled	Mid styled	Short styled
1. *Oxalis grandis*	Southern Indiana	1305	661	623
2. *O. suksdorfii*	Oregon	246	453	207

To confirm the self-incompatibility I isolated 15 long and 15 short styled plants, but none of them produced seeds. I also bagged inflorescences of thrum and pin plants with small butter paper bags, and thus confirmed the incompatibility.

Tale 4. *Fruit and seed production in pollination experiments with* Oldenlandia umbellata

Pollination	Flowers pollinated	Capsules set	Average seed set per capsule
Thrum × Thrum (cross) ..	5	1	0
,, ,, (self)	80	2	1
Pin × Pin (cross)	6	0	0
,, ,, (self)	76	5	2
Pin × Thrum	26	23	45·4
Thrum × Pin	29	26	37·5

The mean lengths of styles, anthers, and stigmatic papillae of thrum and pin eyed plants of *O. umbellata* are given is Table 5. The stigmatic papillae are smaller in thrum than pin, and thrum pollen grains are larger than pin grains (Plate 15).

Table 5. *The morphology of distyly in* Oldenlandia umbellata

Flower type	Style length in mm.	Anther height in mm.	Length of stigmatic papillae in μ
Pin eyed	2·5	0·84	130
Thrum eyed	0·8	2·56	80

I measured 2,043 polar and 2,007 equatorial diameters of pollen grains from 20 plants of each type. Pollen was taken from developed buds and open flowers. Table 6 shows the distribution of measurements in microns. Measurements were taken in ocular micrometer divisions, each division being equal to 2·5μ.

Table 6. *Means and variances of pollen grain diameters in microns*

Flower type	Polar diameter			Equatorial diameter		
	Mean	S.E. of mean	Standard deviation	Mean	S.E. of mean	Standard deviation
Thrum	22·165	0·117	3·80	19·239	0·077	2·39
Pin	20·769	0·087	2·68	17·450	0·059	0·67

The mean volume of thrum and pin pollen grains are respectively about 67,000 and 52,000 cubic microns assuming them to be spheroids, and multiplying means, which is not quite accurate. However the mean volume of a thrum grain is about 129% of that of a pin grain. This is usually the case in heterostyled plants, and is of course believed to be an adaptation to the need of thrum grains to produce longer tubes.

The significance of the differences in Table 6 is high, those of the mean polar and equatorial diameters being 9·24 and 18·6 times their standard errors respectively. However, if the mean values for different plants differed sufficiently, even such large differences as these could be fortuitous. The means for each of the 40 plants were calculated (Tables 7 and 8). They varied a great deal within each group. Thus the polar diameters of thrums ranged from 10·95$\pm$0·14 scale divisions to 7·28$\pm$0·18, those of pins from 9·04$\pm$0·12 to 7·00$\pm$0·15. Given such variation the simplest test of significance is to order the plants in terms of pollen grain size.

When this is done we find that of the forty mean polar diameters the ten largest belong to thrum plants, of the forty equatorial diameters, the eleven largest belong to thrums. After this the order is unclear, the smallest polar diameter but one, and the smallest equatorial but three being found in thrum plants. This is explicable if about half the plants produced enough pollen grains which were small for various non-genetical reasons to lower their mean values appreciably. The probability that the first ten polar diameters should belong to thrum plants if thrums were no likelier to

Table 7 *Thrum plants*

Plant No.	n	Polar diameter Mean	Range	Variance	n	Equatorial diameter Mean	Range	Variance
1	58	10·95	8-13	1·160	58	8·00	6 -10	1·075
15	50	10·13	8-12	1·769	50	8·52	7 -10	0·335
4	30	9·97	8-11	0·433	30	7·93	6 - 9	0·602
8	50	9·68	7-12	1·008	50	7·94	7 - 9	0·423
3	50	9·42	7-11	0·501	51	7·71	6 - 8	0·298
19	51	9·42	8-11	0·484	44	8·43	7 -10	0·586
12	50	9·28	6-12	1·388	50	7·49	6 - 9	0·475
2	54	9·17	7-12	2·233	50	6·60	5 - 8	0·417
20	53	9·07	6-11	2·725	60	8·80	8 -10	0·446
10	61	9·05	7-11	0·929	61	7·61	6 - 8	0·426
18	44	9·00	7-11	0·871	43	8·81	7 -10	0·738
16	59	8·93	7-10	0·912	49	8·76	7 -10	0·522
13	60	8·67	5-14	4·990	55	7·25	5·5- 8·5	0·341
11	65	8·55	7-10	0·793	65	7·51	6 - 9	0·358
17	52	8·27	7-10	0·980	59	8·46	7 -10	0·307
14	67	8·24	6-10	1·768	67	6·97	6 - 8	0·219
5	53	8·02	6-10	1·226	53	6·97	6 - 8	0·151
6	52	8·02	6-10	1·583	52	6·96	6 - 8	0·347
9	67	7·58	6-11	2·360	57	7·25	6 - 8	0·266
7	64	7·28	6-10	2·144	57	6·73	6 - 9	0·757

Table 8. *Pin plants*

Plant No.	n	Polar diameter Mean	Range	Variance	n	Equatorial diameter Mean	Range	Variance
7	39	9·04	7-10	0·527	40	7·56	6 -8	0·233
1	73	9·03	8-12	0·929	76	6·97	6 -9	0·323
5	21	8·76	6-10	1·567	21	7·19	6 -8	0·454
13	54	8·67	6-10	0·798	53	7·15	5 -8·5	0·826
3	34	8·65	7- 9·5	0·213	34	6·96	5·5-8	0·375
2	45	8·60	6-10	1·080	43	6·44	5 -8	0·645
20	50	8·54	7-11	0·742	55	7·11	6 -8	0·053
14	57	8·53	7-10	0·599	57	7·04	6 -8	0·077
18	54	8·39	6-10	1·215	50	7·36	6 -8	0·198
6	40	8·36	7-10	0·410	39	7·14	6 -8	0·219
16	66	8·27	6-10	1·080	66	6·86	6 -8	0·342
9	47	8·22	7-10	0·415	47	7·05	6 -8	0·506
15	49	8·16	6-10	0·909	49	7·22	6 -8	0·198
19	45	8·00	7-10	0·962	56	6·82	5 -8	0·901
10	44	8·00	7- 9	0·242	44	7·18	7 -8	0·064
12	56	7·83	6-10	1·601	48	6·86	6 -8	0·073
17	56	7·73	6-10	1·535	56	6·52	5 -8	0·498
11	58	7·47	5-10	1·749	58	6·78	5 -8	0·620
4	34	7·43	6-10	1·006	33	7·03	6 -8	0·418
8	31	7·00	6- 9	0·733	31	6·55	6 -7·5	0·206

produce large pollen than pins is $\frac{30!20!}{40!10!}$, or $\frac{1}{4,588}$, and the corresponding probability for the equatorial diameters is $\frac{1}{3}$ of this, or $\frac{1}{13,764}$. Thus the difference is very highly significant. However if only one thrum and one pin plant had been compared or even a pair of each, nothing definite could be said. Thus Thrum 6 has smaller mean polar and equatorial diameters than Pin 5, though neither is an extreme variant.

Summary

A brief review of heterostylic species of Rubiaceae has been made. Counts of natural populations of the distylic *Oldenlandia umbellata* have been made from six localities. Out of a total of 1,894 plants counted, there were 1,093 long styled plants and 801 short styled plants.

Long and shortstyled plants are self incompatible. Seeds are set only in legitimate crosses. Biometrical data pertaining to the pollen grains of the long and short styled plants has been analysed. Short styled pollen grains are larger than long styled. Measurements of styles, anthers, and stigma papillae are also given.

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Note added in Proof

While my paper was in press, Khoshoo and Bhatia (1963) have found heterostyly in *Hamiltonia suaveolens*, *Mussaenda luteola*, *M. frondosa*, and *Leptodermis lanceolata* while studying the cytology of the flora of the N. W. Himalayas.

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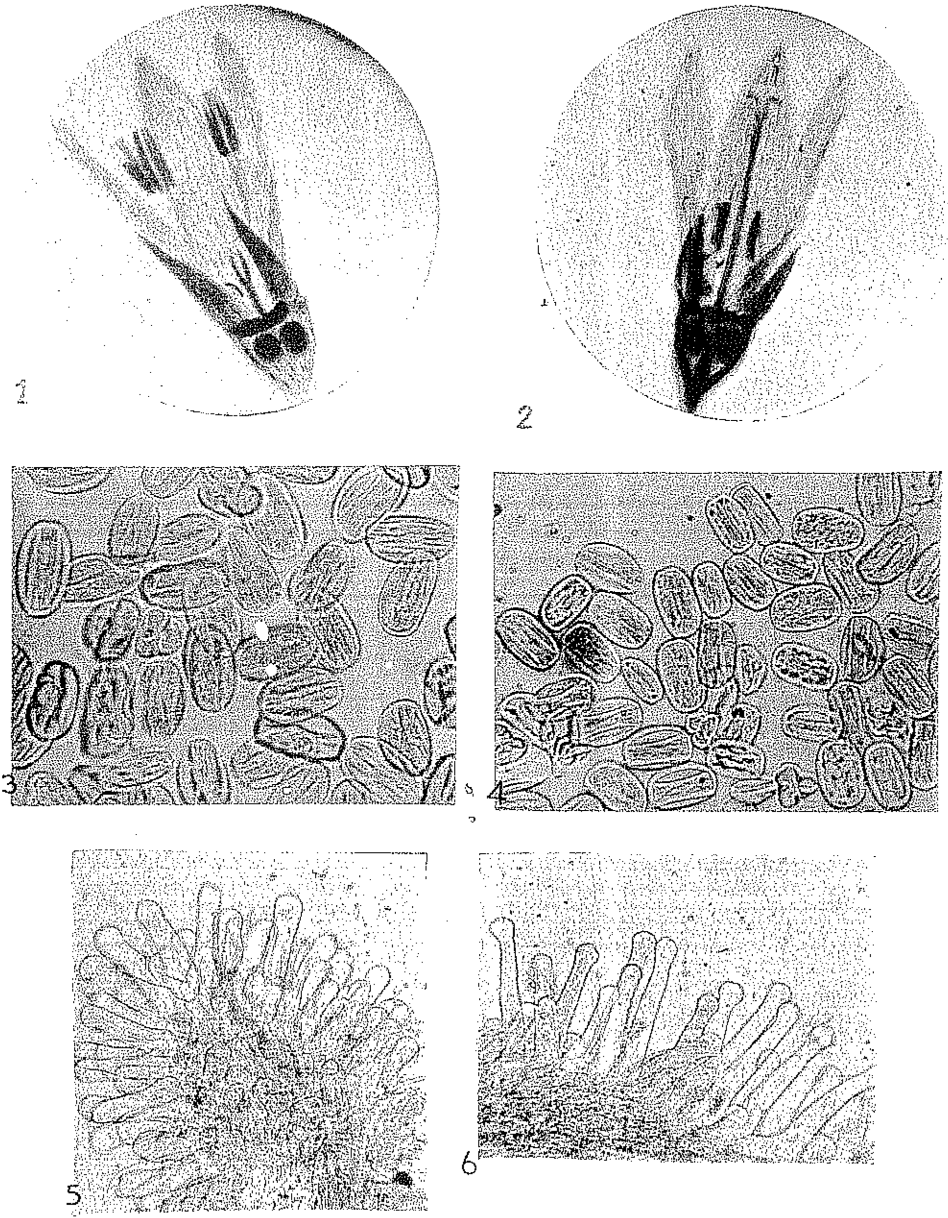
*Original not seen.

PLATE 15



Figs. 1-2. Clear mounts of short and long styled flowers of *Oldenlandia umbellata*.
Fig. 3. Pollen grains from short styled flower. ×635.
Fig. 4. Pollen grains from long styled flower. ×635.
Fig. 5. Stigmatic papillae from short styled flower. ×300.
Fig. 6. Stigmatic papillae from long styled flower. ×300.