A STUDY OF STEM ANATOMY IN BEGONIA L.*

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Begonia plants have been cultivated for ornamental purposes since their discovery early in the seventeenth century. The name Begonia, first given by Plumier, was published in 1700 by Tournefort in his Institutiones Rei Herbariae. Linnaeus introduced it officially in edition one of his Species Plantarum (1753), and it was in the fourth edition of his Genera Plantarum (1754).

The purpose of the present study was to investigate the anatomical variation in the stems of Begonia, and if any variations exist, to see whether there is correlation between these and the sections used in classifying the genus.

In the past anatomical studies for the most part concerned themselves with flowers and much less often with vegetative parts. Because the systematic value of reproductive organs has been emphasized by many botanists (Fellerer 1892; Klotzsch 1855, and many others), and because they have shown at least some superficial dissimilarity in vegetative characters, a further study of stem structure seemed desirable in understanding the genus Begonia.

Some publications have appeared previously in which the authors have tried to selve the questions of systematic position from a purely morphological or anatomical point of view. One of the first careful descriptions of a Begonia was in 1830, when the characteristics of the hairs, glands, and stem, of the long flower-stalked Begonia, B. longipes, was described by Hooker.

Hildebrand (1859) and Fellerer (1892) did outstanding work on the systematic anatomy of Begonia. They considered mainly the cystoliths and cystosphere-formation as a systematic characteristic in their analysis, the existence of which served them as a proof for a relationship with the Cucurbitaceae.

Haberlandt (1914) described the sclerenchyma of the species B. nelumbifolia Cham. et Schlecht, B. pustulata Liebm., and B. violifolia A DC.

Hallier (1903) tried to prove relationship of the anchor-hairs of some Begonia species with those of the compositaceous Hypochoeris aethnensis Benth. & Hook.

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Pneumatothodes have been described by Vouk (1912) in the stems of B. vitifolia Schott in Sprengel, where they resemble and replace typical lenticels. Metcalfe and Chalk (1957) said the pneumatothodes are composed of (i) an epidermis of small, thin-walled cells devoid of cuticle; (ii) stomata with poorly developed or occluded apertures; (iii) thin-walled photosynthetic tissue with a weakly developed intercellular system which constitutes the main portion of the penumatothodes.

Irmscher (1925) described various conditions of stems, flowers and leaves in classifying the sections. Bailey (1949) made a horticultural arrangement of species according to stem structure. Fotsch (1939) arranged much information concerning detailed Begonia anatomy, including that of the stems. After this no studies of Begonia stem anatomy were made except those included incidentally in brief descriptions of new species.

Trichomes of Begonia leaves were studied by Fellerer (1892) and Boghdan (1967). They described multicellular non-capitate, capitate, and some other modifications in trichomes. The same type of trichomes can be seen on the Begonia stems. Emergences have not been found on Begonia stems.

Multilayered epidermis in Begonia had been mentioned in passing by several plant anatomists. This condition was further studied by Boghdan and Barkley (1969), and by Barkley and Hozid (1971), who showed further examples of variation of the epidermis found in Begonia leaves, several species showing multilayered epidermis in the leaves. The development of the multiple epidermis in the leaf of B. floccifera Beddome was studied by Boghdan (1973).

Much attention was paid to the specialized stems of Begonia by many botanists and horticulturists. Many Begonia have more or less slender stems which grow upright, or tortuous, or even pendant. The slender stems of B. glabra Aublet and B. tropaeolifolia A. DC, climb up tree trunks by means of adventitious roots. Other Begonia such as the rhizomatous Begonia, B. acetosa Vellozo, have much thickened stems with short internodes and grow prostrate along the soil, but others of the rhizomatous Begonia having short internodes and thick stems, grow upright. Many, such as B. pustulata Liebm., have nodes far apart on thin prostrate stems and some have stolons on a grand scale, such as B. popenoei Standley. Then there are those in which the lower part of the stem becomes enlarged at the soil level or just below, the so-called semituberous Begonia, for example B. dregei Otto and Dietrich. Another unusual and unique stem modification is specialized thickened and succulent leaves produced at the soil level, resulting in a bulb in B. socotrana Hooker f. Such variation in stem structure obviously demonstrates need for further study.

The author wishes to express sincerest thanks to Dr. Fred A. Barkley for his continued counsel throughout this study and for the use of his private collections of Begonia which he made available for this study. The author is also indebted to Mr. Michael Kartuz of Kartuz' Greenhouses and to Mrs. Joy L. Martin of Logee's Greenhouses for several of the stems used in this study. The cooperation of the Gray Herbarium Library of Harvard University in allowing reference to the literature is most gratefully acknowledged.

Materials and Methods

The various Begonia stems used in this study were obtained from greenhouse-grown specimens. Table I shows the species studied, their taxonomic position in the genus and their geographic origins.

Stem portions of most species for the study were taken from the first (newest) internode and the fifth (older) internode (rarely in the sixth or seventh internode).

The specimens were killed in Craf I fixative and then transferred to Craf II solution (Sass 1958), (or rarely killed in Craf III), and immediately aspirated for two hours in vacuum to remove any air in the tissues. The tissues were dehydrated in graduations of ethyl alcohol following the schedule of Johansen (1940), changed to butyl alcohol and imbedded in paraplast. Ten to fifteen micron sections, both cross and longitudinal, were cut, stained with safranin and fast green, and mounted in Canada balsam for study.

Photomicrographs were made using a Polaroid Land Instrument Camera (Model ED-10) with Polaroid Black and White Film (Land Pack Film Type 107).

Drawings were made using a table projection of prepared slides with a Tri-Simplex Micro-Projector.

The nomenclature used in this study followed that published by Barkley (1972).

Observations

Microscopic observations at the first internode and at the fifth internode level of the collenchyma, sclerenchyma, secondary growth from vascular cambia, and from cork cambia (i.e. the phellogens), trichomes, the condition of the vascular ring, and of the vascular bundles, were made. Later comparisons were made between the stems of various species. Table II shows the abbreviations which are used for Table III.

TABLE I. The species of *Begonia* used in the present study of *Begonia* stems, the section of the genus to which each belongs and the locality where they are native.

Species	Section	Geographic origin
B. acetosa Vellozo	Pritzelia	Brazil
B. aconitifolia A. DC.	Latistigma	Brazil
B. angularis Raddi	Begonia	Brazil
B. boliviensis A. DC.	Barya	Bolivia
B. coccinea Hooker	Pritzelia	Brazil
B. convolvulacea A. DC.	Enita	Brazil
B. crispa Krel	Begonia	(Cult.)
B. cubincola A. DC.	Begonia	Cuba
B. cucullata var. *hookeri* Smith & Schubert	Begonia	Brazil
B. domingensis Grisebach	Begonia	Santo Domingo
B. echinosepala Regel	Pritzelia	Brazil
B. egregia N. E. Brown	Tetrachia	Brazil
B. engleri Gilg	Rostrobegonia	Tropical Africa
B. epipsila Brade	Pritzelia	Brazil
B. fagifolia Fischer	Enita	Brazil
B. floccifera Beddome	Reichenheimia	India
B. foliosa HBK	Lepsia	Colombia
B. glabra Aublet	Pritzelia	West Indies, Brazil, Mexico
B. goegoensis N. E. Brown	Reichenheimia	Sumatra
B. grandis Dryander	Knesebeckia	China, Japan
B. incana Lindley	Knesebeckia	Guatemala
B. incarnata Link & Otto	Knesebeckia	Mexico
B. involucrata Liebmann	Gireoudia	Costa Rica
B. lobata Schott *in* Sprengel	Ewaldia	Costa Rica
B. maculata Raddi	Gaerdtia	Brazil
B. mannii Hooker *f.*	Tetraphila	Tropical Africa
B. mazae Ziesenhenne	Gireoudia	Mexico
B. metallica Regel	Gireoudia	Mexico
B. parilis Irmscher	Pritzelia	Brazil
B. parva Merrill	Diploclinium	Philippines
B. polygonoides Hooker *f.* *in* Oliver	Tetraphila	Tropical Africa
B. pustulata Liebmann	Weilbachia	Mexico
B. richardsoniana Merrill & Perry	Petermannia	New Guinea
B. roxburghii A DC.	Sphenanthera	Burma
B. rubro-venia Planchon	Platycentrum	Himalaya
B. scharffiana Regel *ex* Hooker *f.*	Ewaldia	Brazil
B. schmidtiana Regel	Begonia	Brazil
B. serratipetala Irmscher	Petermannia	New Guinea
B. solananthera A. DC.	Solananthera	Brazil
B. stipulacea Willdenow	Begonia	Brazil
B. ulmifolia Willdenow	Donaldia	Venezuela
B. undulata Schott & Sprengel	Gaerdtia	Brazil
B. venosa Skan *ex* Hooker *f.*	Gireoudia	Brazil
B. viscida Ziesenhenne	Begonia	Mexico
B. vitifolia Schott *in* Sprengel	Pritzelia	Brazil

Explanation of Figures.

Fig. 1. Medullary bundle (Collateral) in B. parilis Irmscher (X.S., X 88).

Fig. 2. Medullary bundle (Amphivasal) in B. parilis (X.S., X 88).

Fig. 3. Medullary bundle with limited secondary growth in B. roxburghii A.DC. (X.S., X 35).

Fig. 4. Cross section of the first internode showing capitate trichomes, B. crispa Krel (X.S., X 100).

Fig. 5. Cross section of the first internode showing cortex with dense protoplasm, B. epipsila Brade (X.S., 5a X 88, 5b 350).

Fig. 6. Cortical bundle which is a leaf-trace in the cortex, B. floccifera Beddome (X.S., X 88).

Fig. 7. Vascular bundle showing pericyclic fibers and lignified tracheids, B. venosa Skan ex Hooker f, (X.S., X 88).

Fig. 8. Vasculer bundle showing pericyclic fibers and lignified tracheids, B. dietrichiana Irmscher (X.S., X 88)

Fig. 9. Big trichome in the first internode, B. viscida Ziesenhenne (X.S., X 70).

Fig. 10. Branched trichome in the first internode, B. roxburghii (X.S., X 70).

Fig. 11. Non-capitate, whiplash trichome and hemispherical wen-like structure in second inte node, B. pustulata Liebm. (X.S., X 88).

Fig. 12. Cross section of non-capitate trichome and capitate trichome with head, B. maculata Raddi (X.S., X 350).

Fig. 13. Whiplash trichome in the first internode, B. lobata Schott in Sprengel (X.S., X 350).

Fig. 14. Short-stalked, capitate trichome in the first internode, B. crispa Krel (X.S., X 350).

Fig. 15. Cross section of the fifth internode showing medullary bundles, B. parilis Irmscher (X.S., X 35).

Fig. 16. Medullary and cortical bundles, B. angularis Raddi (X.S., X 35).

Fig. 17. Medullary bundle, B. stipulacea Willdenow (X.S., X 35).

Fig. 18. Irregularly thickened stone-cells in the cortex, B. mannii Hooker f. (X.S., X 35).

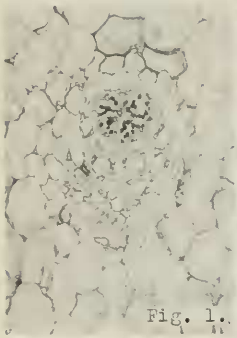
Fig. 19. Stone-cells, B. coccinea Hooker (X.S., X 35).

Fig. 20. Stone-cells and starch grains, B. undulata Schott in Sprengel (X.S., X 35).

Fig. 21. Indented vascular cylinder including two-sized bundles, B. vitifolia Schott in Sprengel (X.S., X 25).

Fig. 22. Discontinuous vascular cylinder, B. viscida Ziesen. (X.S., X 100).

Fig. 23. Discontinuous vascular cylinder, B. incarnata Link & Otto (X.S., X 35).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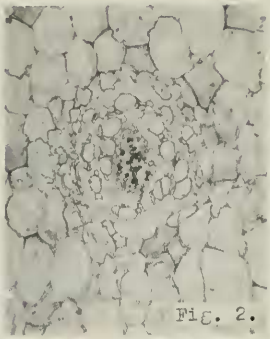
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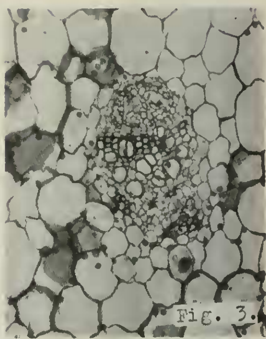
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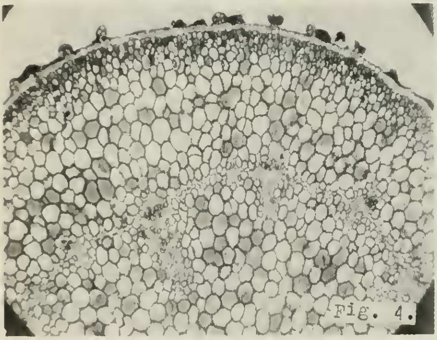
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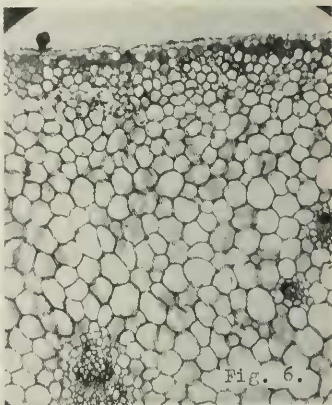
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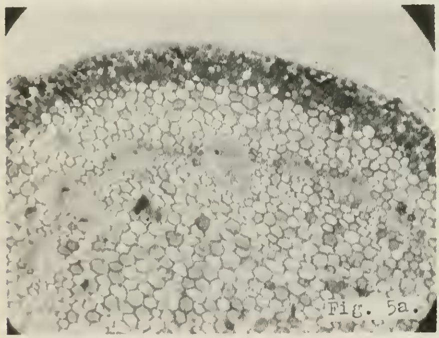
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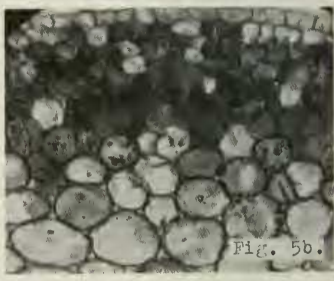
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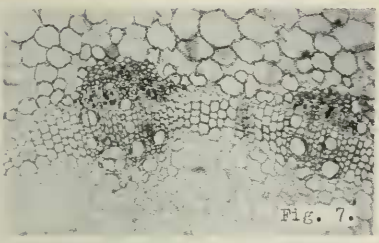
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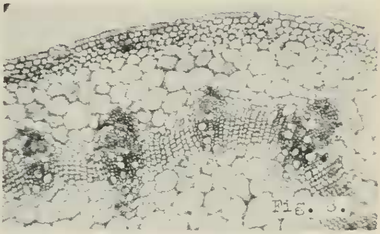
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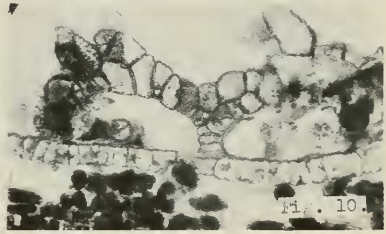
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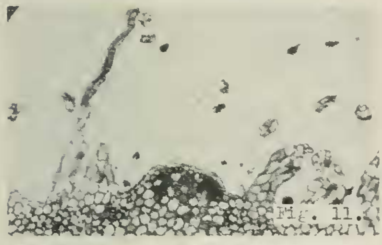
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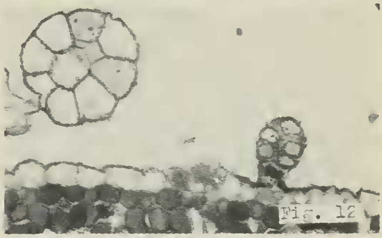
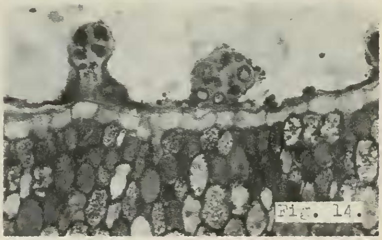


Fig. 12


Fig. 13.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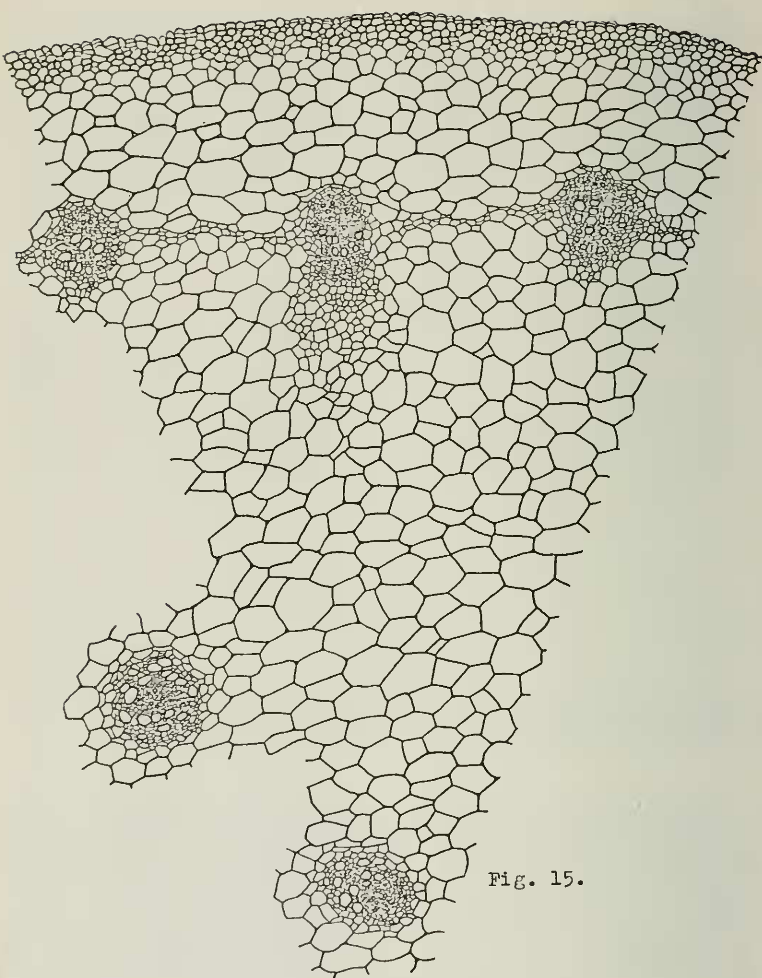

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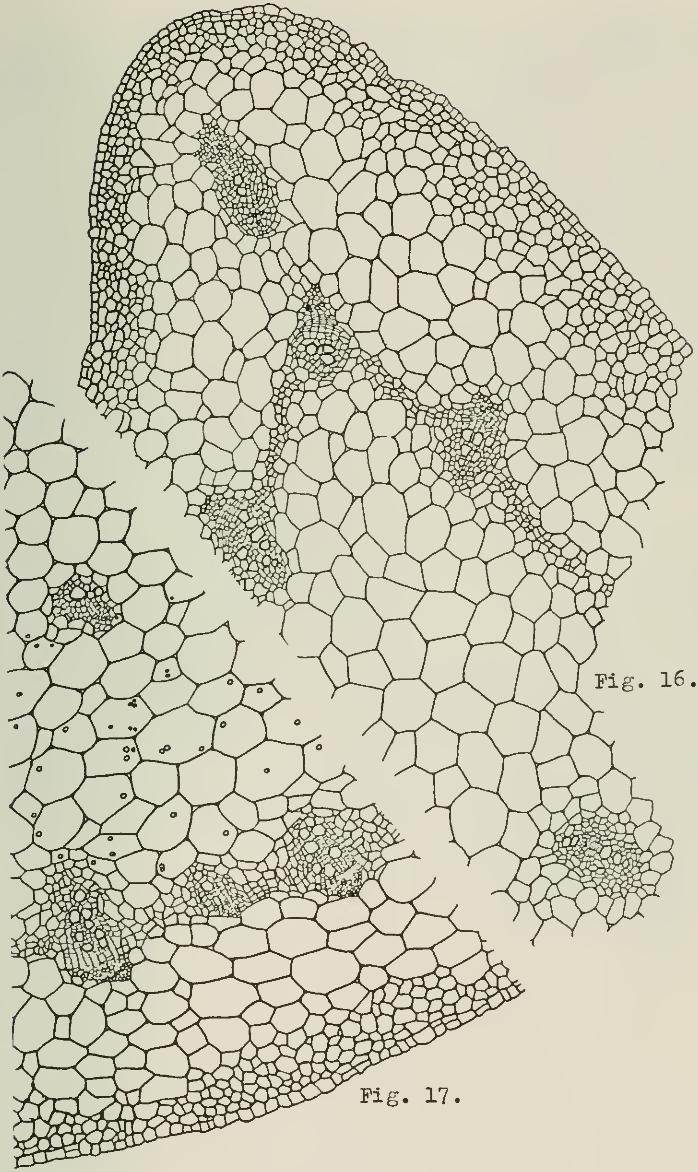

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Fig. 17.

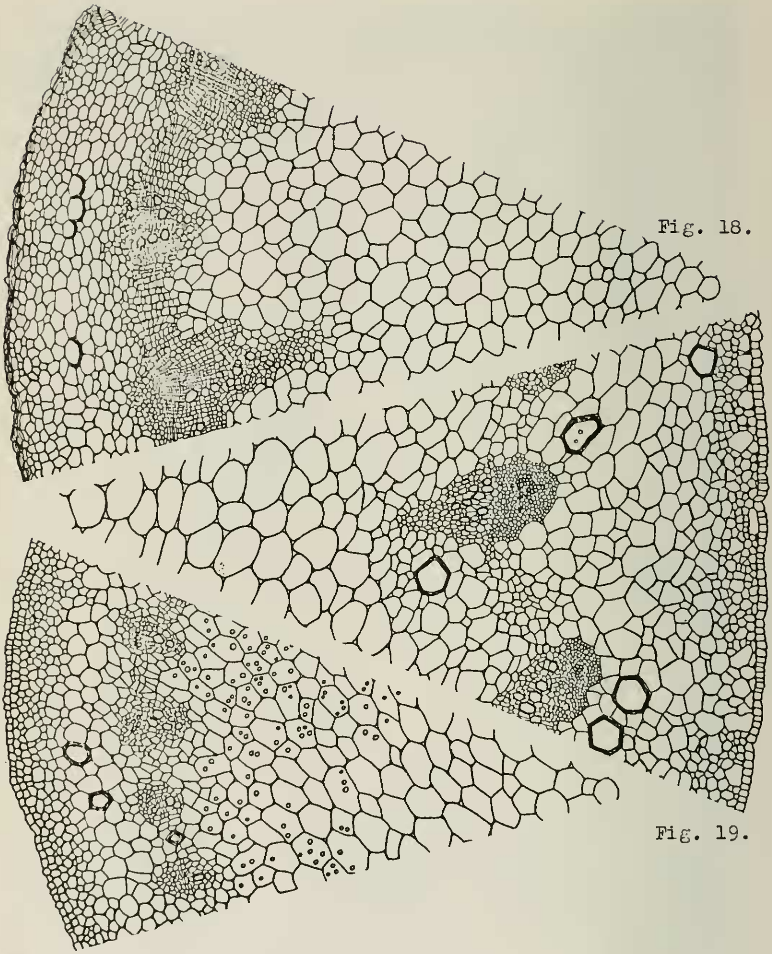

Fig. 18.

Fig. 19.

Fig. 20.

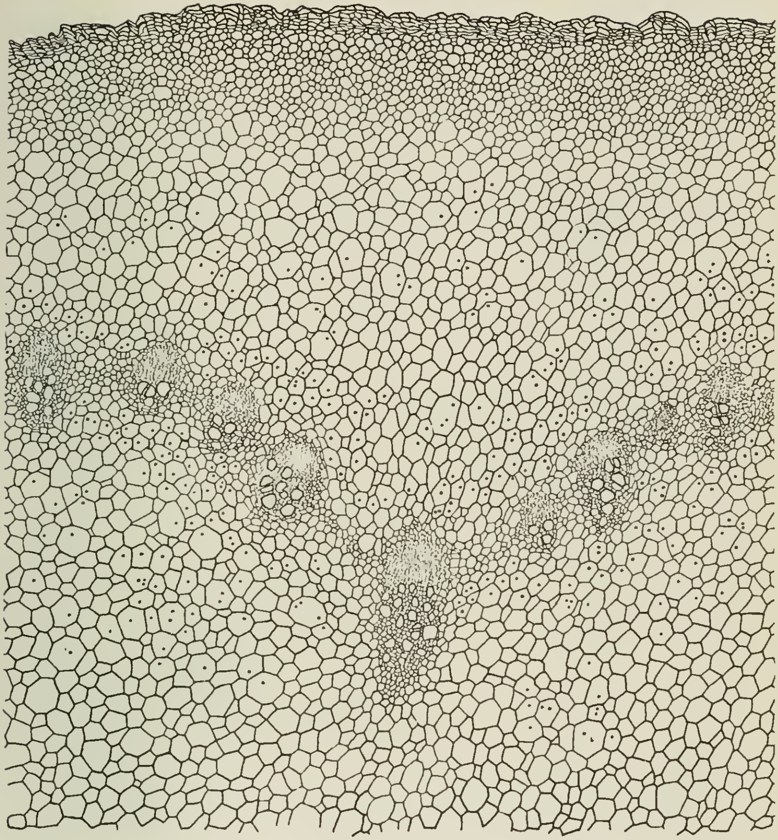

Fig. 21.

Fig. 22.

Fig. 23.

TABLE II. Explanations of the abbreviations used in the discussions of observations.

1. Vascular ring.

VC_1: a continuous vascular cylinder in which the ring is almost round in cross section.

VC_2: a continuous vascular cylinder in which the ring is wavy in cross section.

VC_3: a continuous vascular cylinder in which the ring in cross section is angular and somewhat square or trapezoid.

VC_4: a discontinuous vascular cylinder in which the primary vascular tissues form a system of strands, the interfascicular cambia produce almost only ray parenchyma, and therefore, the secondary vascular tissues appear as strands.

2. Secondary growth.

OSGF: no secondary growth in the fascicular regions.

OSGI: no secondary growth in the interfascicular regions.

ISGF: initiation of secondary growth in the fascicular regions.

ISGI: initiation of secondary growth in the interfascicular regions.

SGFO: mature secondary growth in the fascicular regions without tracheids having lignified secondary wall.

SGIO: mature secondary growth in the interfascicular regions without tracheids having lignified secondary wall.

SGFT: mature secondary growth in the fascicular regions with tracheids having lignified secondary wall.

SGIT: mature secondary growth in the interfascicular regions with tracheids having lignified secondary wall.

3. Vascular bundle.

MB: additional vascular bundles in the pith.

CB: additional vascular bundles in the cortex.

VB_1 to VB_5 show in (i) to (v).

p: phloem, c: cambium, x: xylem with well-developed vessels,
pf: phloem fibers, t: tracheid with lignified thick wall,
per.f.: pericyclic fibers.

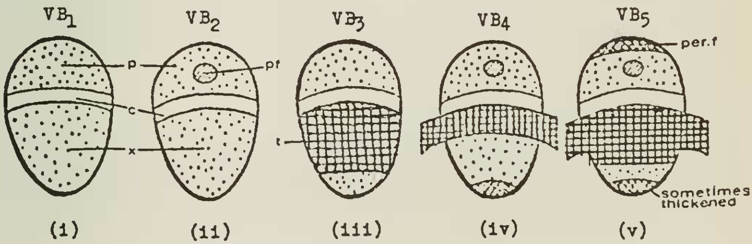

Table III-a. A tabular representation of the characteristics of the stems of the Begonia selected for study.

botanical name & section	collenchyma (5th inter-node level)	trichomes	sclerenchyma (5th inter-node level)	vascular bundle condition	secondary growth: vascular cambial activity: first internode: fascicular regions	secondary growth: vascular cambial activity: first internode: inter-fascicular regions	secondary growth: vascular cambial activity: 5th internode level: fascicular regions	secondary growth: vascular cambial activity: 5th internode level: inter-fascicular regions	secondary growth: cork cambial activity (5th internode level)
B. boliviensis A.DC. (Barya)	2-3 layers angularly thickened			VC_1 ISGF O(I)SGI VB_1	− *	−	+++	−	
B. angularis Raddi (Begonia)	4-5 layers angularly thickened	capitate(short-stalked) & non-capitate		VC_3 SGFT SGIT VB_3 MB CB	−	−	++++	+++	partly initiated in epiderm-al layer
B. cubincola A.DC. (Begonia)	2-3 layers little thickened	capitate(short-stalked) & non-capitate	pericyclic fibers.	VC_1 SGFT SGIT VB_5	−	−	++++ +++	++++ +++	several layers
B. crispa Krel (Begonia)	3-4 layers angularly thickened	capitate(short-stalked) & non-capitate		VC_1 SGFO ISGI VB_2	+	−	++	+	
B. domingensis A.DC. (Begonia)	5-6 layers angularly thickened	capitate(short-stalked) & non-capitate some scale-like	pericyclic fibers, stone-cells	VC_1 SGFT SGIT VB_5	+	−	+++++	+++++	several layers
B. schmidtiana Regel (Begonia)	2-3 layers angularly thickened	capitate(short-stalked),many		VC_1 SGFT SGIT VB_4	+	−	++++	+++	
B. cucullata var. hookeri (Begonia)	2 layers angularly thickened small	capitate(short-stalked)	pericyclic fibers	VC_1 SGFO(T) ISGI VB_5	++	−	+++	+	
B. stipulacea Willdenow (Begonia)	5-6 layers angularly thickened		pericyclic fibers	VC_1 SGFT SGIO VB_5 MB CB	+	−	++++	++++	partly initiated in epiderm-al layer
B. viscida Ziesenhenne (Begonia)	1-2 layers little, equally thickened	non-capitate(whiplash),very big,many		VC_1 ISGF OSIT VB_2	−	−	++	−(+)	
B. parva Merrill (Diploclinium)	4 layers angularly thickened	non-capitate	irregularly thickened stone-cells	VC_1 SGFT SGIT VB_3	+++	++	+++++	+++++	several layers

Table III-b. A tabular representation of the characteristics of the stems of the <u>Begonia</u> selected for study.

<u>B. ulmifolia</u> Willdenow (Donaldia)	4-5 layers angularly thickened	non-capitate (2 rowed)		VC_1 SGFO O(I)SGI VB_2	−	−	+++	+(−)	partly initiated in epidermal layer
<u>B. convolvulacea</u> A.DC. (Enita)	4-5 layers angularly thickened	capitate(short-stalked) & non-capitate, few		VC_1 SGFO ISGI VB_2	−	−	++	−	
<u>B. scharffiana</u> Regel ex Hooker (Ewaldia)	4-5 layers angularly thickened	capitate(non- or short-stalked) & non-capitate		VC_1 SGFT SGIT VB_5	++	−	+++	+++	partly dev.
<u>B. lobata</u> Schott in Sprengel (Ewaldia)	3-4 layers angularly thickened	capitate(short-stalked) & non-capitate(whip-lash)		VC SGFT SGIT VB_5 MB	−	−	+++	+++	partly dev.
<u>B. maculata</u> Raddi (Gaerdtia)	3-5 layers angularly thickened	capitate(short-stalked) & non-capitate	irregularly thickened stone-cells	VC_1 SGFO O(I)GIO VB_2	−	−	+++	++	partly dev.
<u>B. undulata</u> Schott in Sprengel (Gaerdtia)	3-4 layers little thickened	non-capitate, few	stone-cells	VC_1 SGFO S(I)GIO VB_2	−	−	++	++	partly dev.
<u>B. involucrata</u> Liebmann (Gireoudia)	8-9 layers little thickened	capitate(short-stalked) & non-capitate some scale-like		VC_1 SGFT SGIO VB_3 MB	+	−	++	−	partly dev.
<u>B. erzae</u> Ziesenhenne (Gireoudia)	4-5 layers little thickened	non-capitate		VC_1 SGFT SGIO VB_3	−	−	+++	+++	
<u>B. metallica</u> Regel (Gireoudia)	3-4 layers angularly thickened	capitate(short-stalked) & non-capitate(multi-, & single-rowed)	pericyclic fibers	VC_2 SGFT SGIT VB_5 MB	−	−	++++ ++	++++ ++	partly dev.
<u>B. venosa</u> Skan <u>ex</u> Hooker <u>f.</u> (Gireoudia)	4-9 layers little, equally thickened	capitate(short-stalked) & non-capitate(multi-, & single-rowed)	pericyclic fibers	VC SGFT SGIT VB_5 MB	+	−	+++++	+++++	partly initiated in epidermal layer
<u>B. grandis</u> Dryander (Knesebeckia)	3-4 layers angularly thickened	capitate(short-stalked) & non-capitate, many		VC_1 SGFO SGIO VB_1 MB	+	−	++	+	partly dev.
<u>B. incana</u> Lindley (Knesebeckia)	6-7 layers almost none	non-capitate, many		VC_1 SGFO ISGI VB_2	+	−	+++	+	partly dev.

Table III-c. A tabular representation of the characteristics of the stems of the Begonia selected for study.

B. incar nata Link & Otto (Knesebeckia)	5-6 layers angularly thickened	non-capitate, few		VC_1 SGFO OSGI VB_1	+	−	+++	−	
B. aconitifolia A.DC. (Latistigma)	4-5 layers angularly thickened		stone-cells	VC_1 SGFO O(I)SGI VB_1	−	−	++	−	several layers
B. foliosa HBK (Lepsia)	2-3 layers angularly thickened	non-capitate, few		VC_1 SGFO O(I)SGI VB_1	−	−	+++	+(−)	
B. richardsoniana Merrill & Perry (Petermannia)	4-5 layers little, equally thickned	non-capitate, few		VC_1 SGFO ISGI VB_1	−	−	++	++	several layers
B. serratipetala Irmscher (Petermannia)	2-3 layers angularly thickened	capitate(short-stalked) & non-capitate		VC_1 SGFO ISGI VB_2	++	−	+++	+(−)	partly dev.
B. rubro-venia Hooker (Platycentrum)	4-5 layers angularly thickened	capitate(short-stalked) & non-capitate	pericyclic fibers	VC_1 SGFT SGIT VB_5 MB	−	−	+++	+	partly initiated in epiderm-al layer
B. acetosa Velloza (Pritzelia)	4-5 layers little thickened	capitate(short-stalked) & non-capitate, few	pericyclic fibers	VC_1 SGFT SGIO VB_5	−	−	++	++	partly dev.
B. coccinea Hook f. (Pritzelia)	3-4 layers little equally thickened	capitate(short-stalked) & non-capitate	stone-cells	VC_1 SGFO OSGI VB_2	−	−	+++	−	
B. echinosepala Regel (Pritzelia)	3-4 layers angularly thickened	capitete(short-stalked) & non-capitate		VC_1 SGFO SGIO VB_2	++	−	+++	−	partly dev.
B. epipsila Brade (Pritzelia)	5-7 layers angularly thickened	non-capitate, few, branched	pericyclic fibers	VC_1 SGFT SGIT VB_5	−	−	+++++	+++++	partly initiated in epiderm-al layer
B. fagifolia Fischer in Otto (Pritzelia)	5-7 layers angularly thickened	non-capitate		VC_1 SGFT SGFO VB_2	+++	−	+++++	+++++	partly initiated in epiderm-al layer
B. glabra Aublet (Pritzelia)	3-4 layers angularly thickened	capitate(non-, & short-stalk-ed) & non-capitate	pericyclic fibers	VC_1 SGFT SGIT VB_5	−	−	+++	+(−)	
B. parilis Irmscher (Pritzelia)	4-7 layers angularly thickned	capitate(short-stalked) & non-capitate(single rowed), many		VC_1 SGFO ISGI VB_1 MB	+	−	++++	+	few layers

Table III-d. A tabular representation of the characteristics of the stems of the Begonia selected for study.

B. vitifolia Schott in Sprengel (Pritzelia)	8-13 layers angularly thickened	capitate(short- & non-stalked) & non-capitete(short multi-, & long uni-rowed)		VC_2 SGFO ISGI VB_2	+	+(-)	++	+(-)	several layers
B. floccifera Bedome (Reichenheimia)	6-8 layers little equally thickened		stone-cells	VC_1 SGFT SGIO VB_3	+	–	+++	++	
B. goegoensis N.E.Brown (Reichenheimia)	none	capitate(short-stalked) & non-capitate in very early stage		VC_1 SGFT SGIO VB_3 MB CB	–	–	+++	+++	several layers
B. engleri Gilg (Rostrobegonia)	4-5 layers angularly thickened	non-capitate wen-like		VC_1 SGFO ISGI VB_2	–	–	++	+	
B. solananthera A.DC. (Solananthera)	1-2 layers angularly thickened		pericyclic fibers	VC_1 SGFT SGIT VB_5	+	–	+++++	+++++	
B. roxburghii A.DC. (Sphenanthera)	7-12 layers angularly thickened	capitate(non-, short- & long-branched stalked) & non-capitate (single rowed)	pericyclic fibers unbranched, fibers	VC_1 SGFT SGIT VB_5 MB	–	–	+	+	
B. egregia N.E.Brown (Tetrachia)	8-9 layers angularly thickened	capitate(short-stalked) & non-capitate(single rowed)		VC_1 SGFO SGIO VB_1	+++	+	+++++	+	several layers
B. mannii Hooker f. (Tetraphila)	3-4 layers angularly thickened	capitate(short-stolked) in very early stage	stone-cells(regularly & irregularly thickened)	VC_1 SGFT SGIT VB_3	++	+(-)	++++	++++	several layera
B. polygonoides Hooker f. in Oliver (Tetraphila)	4-5 layers little thickened		stone-cells	VC_1 SGFT SGIT VB_4	–	–	+++++	+++++	several layers
B. pustulata Liebmann (Weilbachia)	4-5 layers angularly thickened	capitate(short-stelked) & non-capitate(multi-rowed & whiplash)		VC_1 SGFT SGIO VB_1	+	–	+++	+	

* The symbol "+" means secondary growth, additional "+'s" roughly indicate the comparative amount of secondarygrowth and "_" is the symbol indicating absence of secondary growth.

Discussion

The genus Begonia has been the classical example of multi-layered epidermis (Fellerer 1892, Solereder 1908, Haberlandt 1928, Metcalfe & Chalk 1957, Foster & Gifford 1959, Esau 1965, Boghdan & Barkley 1969, Barkley & Hozid 1971 and many others). This is in contrast with single-layered epidermis recognized as the almost universal structure of leaves of Anthophyta. Metcalfe & Chalk (1957) described multilayered epidermis consisting of one to four layers in Begonia stems. Barkley & Hozid (1971) illustrated the various multilayered epidermis in the leaves of B. acetosa Vellozo, B. venosa Skan ex Hooker f., B. floccifera Beddome, B. mannii Hooker f. , B. parilis Irmscher, B. ulmifolia Willdenow, etc. Although sometimes a few individual cells of the epidermis undergo periclinal divisions (Fig. 15), multilayered epidermis was not found in the present study of stem anatomy, even in those having multilayered epidermis in the leaves. These divisions were shown in the cross section of the fifth internode levels in such species as B. angularis Raddi, B. fagifolia Fischer, B. stipulacea Willdenos and B. ulmifolia Willd. These divisions are thought to be the initiation of phellogen. It was considered the first periderm because this kind of divisions did not occur throughout the epidermis, but only in particular areas. In most stems the phellogen is initiated in the hypodermis (subepidermal layer), but rarely the epidermal cells give rise to the phellogen (as in the genera Nerium or Pyrus (Esau 1965)). In some species of Begonia the phellogen appeared to be initiated in the epidermis.

Just inside of the epidermis there is a narrow cylinder of collenchyma cells. The inner portion of the cortex is composed of large parenchyma cells. As seen in the cross sections in many species (Begonia acetosa Vellozo, B. angularis Raddi, B. boliviensis A. DC., B. crispa Krel, B. epipsila Brade (Fig. 5), B. lobata Schott in Sprengel, B. maculata Raddi and B. metallica Regel), the collenchyma cells showed very dense protoplasm in the first internode, and the fifth internode levels still remained densely cytoplasmic. The differences in cell-type and in the number of layers in the cross sections varied considerably. The number of peripheral layers of the collenchyma ranged from zero to thirteen layers. Some rhizomatous Begonia have little thickening in the collenchyma cells. No collenchyma was observed microscopically in B. goegoensis N. E. Brown. B. acetosa Vellozo, B. floccifera Beddome, B. involucrata Liebm., B. polygonoides Hooker f. in Oliver, B. richardsoniana Merrill & Perry, B. viscida Ziesen. and others have a little angularly thickened or a little equally thickened collenchyma (Table III).

In the first internode of Begonia, the maturation of the primary vascular elements in the procambial strand or cylinder clearly showed the outline and internal pattern of the vascular system. In many cases secondary growth in the fascicular regions (sometimes both in the fascicular and interfascicular regions) showed considerable growth. Extremely active vascular cambial activity in the fascicular regions at the first internode was seen in B. cucullata var. hookeri Smith & Schubert, B. scharffiana Regel ex Hooker f., B. fagifolia Fischer, B. serratipetala Irmscher, B. echinosepala Regel, B. egregia N. E. Brown and B. mannii Hooker f. Between the first and fifth internode level, the cells of stelar parenchyma adjacent to the dividing cells of the fascicular cambium begun to divide, forming a layer of interfascicular cambium. The fifth internode level was considered as a critical age to observe the secondary growth in the vascular cambium of Begonia stems. Considerable secondary growth in the interfascicular regions was found there in B. cubincola A. DC., B. metallica L. Smith, B. domingensis A. DC., B. stipulacea Willd., B. parva Merrill, B. venosa Skan., B. epipsila Brade, B. fagifolia Fischer, B. solananthera A. DC., B. mannii Hooker f., and B. polygonoides Hooker f., whereas a lack of interfascicular growth was found, or was unclear, in B. boliviensis A. DC., B. viscida Ziesen., B. ulmifolia Willd., B. convolvulacea A. DC., B. involucrata Liebm., B. grandis Dryander, B. incarnata Link & Otto, B. aconitifolia A. DC., B. foliosa HBK., B. serratipetala Irmscher, B. coccinea Hooker, B. echinosepala Regel, B. glabra Aublet and B. vitifolia Schott in Sprengel. In some medullary bundles, secondary growth also occurred although the amount was not great (Fig. 3).

In type of the vascular bundle, the Begonia group has collateral bundles which are a distinctive type in the dicotyledons and gymnosperms. They have closed collateral bunles in which cambium differentiates only within the vascular strand, or an open collateral bundle in which cambium differentiates laterally, connecting with the cambium of adjacent bundles. The secondary growth in them is very limited. B. crispa Krel., B. incarnata Link & Otto (Fig. 23) and B. viscida Ziesen. (Fig. 22) at the fifth internode showed absolutely independent bundles not connected with interfascicular cambium. Therefore, in these there is no demarcation between the cortex and pith (VC_4 in Table II) in the interfascicular regions. However, most members of Begonia have a continuous vascular cylinder in which the ring in cross section is almost round because of secondary growth in both the fascicular and interfascicular regions. A continuous vascular cylinder often is indented as in B. metallica L. Smith, B. vitifolia Schott or angular as in B. angularis Raddi (Fig. 16). The complexities of development and of mature structure of the primary vascular system result, in part, from the circumstance that sometimes this system is initiated before the shoot completes its primary growth in both width and length (Esau 1965).

Table V. The groups of the vascular bundles found in the *Begonia* studied

VB_1:	Barya	*B. bolviensis* A. DC.
	Knesebeckia	*B. grandis* Dryander
	Tetrachia	*B. egregia* N. E. Brown
	Weilbachia	*B. pustulata* Liebmann
VB_2:	Begonia	*B. angularis* Raddi, *B. crista* Krel, *B. viscida* Ziesenhenne
	Donaldia	*B. ulmifolia* Willdenow
	Enita	*B. convolvulacea* A. DC.
	Gaerdia	*B. maculata* Raddi, *B. undulata* Schott *in* Sprengel
	Knesebechia	*B. incana* Lindley, *B. incarnata* Link and Otto
	Latistigma	*B. aconitifolia* A. DC.
	Lepsia	*B. foliosa* HBK
	Petermannia	*B. richardsoniana* Merrill and Perry, *B. serratipetala* Irmscher
	Pritzelia	*B. coccinea* Hook *f.*, *B. echinosepala* Regel, *B. fagifolia* Fischer
		B. parilis Irmscher, *B. vitifolia* Schott *in* Sprengel
	Bostrobegonia	*B. engleri* Gilg
VB_3:	Diplocloclinium	*B. parva* Merrill
	Gireoudia	*B. involucrata* Liebmann, *B. nazae* Ziesenhenne
	Reichenheimia	*B. floccifera* Beddome, *B. goegoensis* N. E. Brown
	Tetraphila	*B. mannii* Hooker *f.*
VB_4:	Begonia	*B. schmidtiana* Regel
	Tetraphila	*B. polygonoides* Hooker *f. in* Oliver
VB_5:	Begonia	*B. cubincola* A. DC., *B. cucullata* var. *hookeri*, *B. domingensis* Grisebach
		B. stipulata Willdenow
	Enita	*B. scharffiana* Regel *ex* Hooker
	Ewaldia	*B. lobata* Schott *in* Sprengel
	Gireoudia	*B. metallica* Regel, *B. venosa* Skan *ex* Hooker *f.*
	Platycentrum	*B. rubro-venia* Planchon
	Pritzelia	*B. acetosa* Vellozo, *B. epipsila* Brade, *B. glabra* Aublet
	Sphenanthera	*B. roxburghii* A. DC.
	Solananthera	*B. solananthera* A. DC.

Different forms of the vascular ring in the same plant could be looked upon as expressions of different degree of development of stem. This expression can often be seen at the fifth internode level in cross sections of Begonia stems (Table III). In many species, especially B. cubincola A. DC., B. domingensis Grisebach, B. mannii Hooker f. (Fig. 18) and B. solananthera A. DC. developed tracheids having lignified secondary walls in both the fascicular and interfascicular regions.

The vascular bundles may be grouped into five categories: VB_1 to VB_5 (Table II-3. (i) to (v)). In comparing the vascular bundle anatomy of the Begonia studied, no particular intrasectional relationship was found (Table IV). In cross sections of B. vitifolia Schott (Fig. 21) and B. roxburghii A. DC. the bundles of two sizes occurred in the lobed vascular cylinder. In the fifth internode the larger bundles were located in the indentations of the vascular cylinder (Fig. 21) and the small bundles, which were not distinguishable in the first internode, were distributed along the lobes between the main bundles. The small bundles in B. vitifolia Schott were secondarily formed by the interfascicular cambium after the formation of the principal bundles.

Vascular bundles in the pith are often regarded as anomalous formations, although they may occur in otherwise typically formed stem. In the dicotyledons, the medullary bundles are commonly concentric, especially amphivasal (Esau 1965). The medullary bundles encountered in some Begonia are with few exceptions, commonly collateral. This collateral type, however, has a tendency to become concentric as they mature in the older internodes. Those in B. parilis Irmscher or B. stipulacea Willd. showed both collateral and and amphivasal (Fig. 1, 2) bundles. Bicollateral bundles, as well as collateral, were found in B. rubrovenia Planchon and B. venosa Skan. ex Hooker f. Two bundles joined to one another by the xylem were observed in the pith of B. angularis Raddi and B. rubrovenia Planchon. In the mature region of the stem of Begonia, the medullary bundles are highly variable. Some are arranged with the xylem on the inner face, the others conversely.

In Begonia. the medullary and cortical bundles showed no discernible pattern in relation to taxonomic position. It was thought that the medullary bundles might be associated with specific adaptations. For instance, many of the medullary bundles are often found in a very succulent stems. More than twenty medullary bundles were counted in the pith of B. roxburghii and more than ten in B. rubrovenia Planchon. The number of medullary bundles changes from the younger internodes to the older ones.

Two particular cell-types of sclerenchyma were observed: (i) the pericyclic fibers of the bundle cap were developed by the fifth internode level as found in B. domingensis Griesbach, B. solananthera A. DC., B. venosa Skan. in Hooker f. and many others; and (ii) the stone-cells which were equally thickened secondarily with lignin, were distributed in the cortex and occasionally in the pith. The stone-cells had living protoplasm and also often contain some starch grains (Fig. 19). In certain species as B. maculata Raddi, B. mannii Hooker f. (Fig. 18) and B. parva Merrill, the cell walls of the stone-cells were irregularly thickened in the direction of the pith.

One of the most common features of Begonia is the epidermal appendages, technically called trichomes (emergences, seemingly are found in Begonia on leaves of some species, but not on stems). The distribution of trichomes in the first internode of the Begonia stem often shows them as very dense and usually becomes less abundant as the internode grows older (in part by the increase in the epidermal area and in part by shedding). Trichomes were not found on the stems of B. boliviensis A. DC., B. stipulacea Willd., B. aconitifolia A. DC., B. floccifera Beddome, B. solananthera A. DC. and B. polygonoides Hooker f. Metcalfe & Chalk (1957) described the hairs of the Begoniaceae as being of two types, non-capitate (non-secretory) and capitate (secretory). Esau (1965) classified plant hairs into unicellular and multicellular trichomes, and these may be either unbranched or branched. As far as observed in this study, all trichomes of Begonia stems were multicellular. The trichomes most often observed were the non-capitate trichomes with long axis, such as were found on B. fagifolia Fischer, B. pustulata Liebm (Fig. 11), B. viscida Ziesen. (Fig. 22), and many others. Some additional species with similar trichomes formed by a single row of cells are B. metallica L. Smith, B. parilis Irmscher, B. vitifolia Schott., B. roxburghii A. DC., and B. egregia N. E. Brown. Sometimes the trichomes made a long whiplash axis. This type occurred on B. pustulata Liebm. (Fig. 11), B. viscida Ziesen. and B. lobata Schott. These hairs vary not only in length, but also in abundance on the first internode of stems.

Another type of trichome is capitate, and has some secretory function regardless of the substance secreted. The capitate trichome could be distinguished easily by a secretory structure called the 'head' (Figs. 12, 14), which was absent on the non-capitate trichomes (Solereder 1908; Boghdan 1967).

Most variation in stem anatomy found in this study showed a great range and presents no discernible pattern from either taxonomic position nor geographic origin.

When we consider the systematic classification of the genus Begonia closely, we are perhaps astoniched that a genus which is so rich in species and varieties has not been subdivided into smaller systematic groups. This has been done frequently with large genera, as for example Prunus and genera in the Cactaceae. Attempts have actually been made in a similar direction (cf. Klotzsch 1855), but without satisfactorily fruitful results. These studies indicate that further investigations of the nodal anatomy, the leaf traces, and a more comprehensive study of the vascular elements would be very desirable, especially in relation to sectional classification in the group.

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