STUDIES IN THE GESNERIACEAE OF THE OLD WORLD XXXII: FOLIAR SCLEREIDS IN CYRTANDRA

M. H. BOKHARI & B. L. BURTT

ARTHACT. This is a preliminary survey. A brief outline of leaf histology in Cystandra is given. Seven types of foliar selectical are described and illustrated. These occur in various combinations in the leaves of different species and seven main patterns are recognised. The correlation of selected pattern with the tentative groupings of species made on morphological grounds suggests that they will prove important and useful taxonomic characterists.

INTRODUCTION

The fact that the fruit wall of Cyrtandra contains rod-shaped selereids has been known for some time. Dr. E. M. Rosser (unpubl.) found that they were dense in the rather crustaceous fruits of Malesian species, much sparser in the white fleshy fruits of the species further east, in the Pacific. Dr. Rosser also found nests of lignified brachysclereids, the outer ones with horse-shoe shaped thickening similar to that found in Aeschynanthus (Rosser and Butt, 1969), in the pith of a New Guinea species (Woods 101) and selereids in the cortex of a species from the Solomon Islands and in C. trisepala from Sarawak. We are here concerned, however, only with foliar sclereids.

There are two or three Malesian species such as C. elatostemoides,* C. gibbsiae and C. quinquenotata in which irregularly rod-shaped sclereids lying below the epidermis are easily observable in dried leaves. This was a routine observation in the course of herbarium work and for a long time it was taken on further. Recently, however, interest in the leaf sclereids of Limonium (Bokhari, 1970) led us to put the observation on an anatomical level. When this was done it was found that the rod-shaped sclereids lie in the hypodermis and are accompanied by branched sclereids in the mesophyll. Other species were naturally examined for comparison, and suddenly a whole new world of sclereids was opened up to us.

The main purpose of the present paper is to put the anatomical situation on record because it seems to be of such exceptional interest. We do not know of any other genus which shows such a diversity of leaf-selereids nor one where there are more patterns caused by the combination of different types of selerid. Doubtless it is only our ignorance that suggests that Cyrtandra is outstanding in these respects, but the wealth of characters which we now report should encourage others to seek to add further to the rather scanty knowledge of these interesting cells. Developmental studies in Cyrtandra have not been attempted, but the dendrosclereids (type 6, below) which grow down from the hypodermis into the mesophyll offer fascinating possibilities.

Cyrtandra is a very large genus and classificatory work on the Malesian species has still a long way to go. The discovery of these sclereids provides

^{*} All the species mentioned in this paper are annotated with references in that which follows. Some, however, can only be designated at present by collectors' numbers.

an anatomical character which may be of considerable help. Enough has been done to show that the sclereid-characters do fit to a considerable extent with the tentative morphological classification already devised, though they are not always diagnostic of a particular group. Sclereids are not always present in Cyrtandra leaves, and indeed we have not yet seen any in the Pacific species, of which only a very small sample has been examined. It should be emphasised that nearly all the specimens (rather less than 100) examined during this study are from recent collections made in Sarawak. Some taxonomic notes and a preliminary assessment follow the anatomical section.

There seems to be only one clear and detailed record of foliar sclereids in the Gesneriaceae. Solereder (1912) mentioned "spicular cells" in Hemiboea henryl C.B. Cl. These lie horizontally just below the epidermis and are visible with a hand lens on the dried leaf. We have examined these. They somewhat resemble the vermiform sclereids found in the hypodermis of Cyrtandra elatostemoides and related species (Type I below), but are short, rarely briefly forked at one end and are sharply pointed at both ends.

Foster has augmented his own original research on selercids in a number of different genera by useful summary accounts (Foster, 1944, 1947, 1955, 1956; cf. also Esau, 1965). Some selercids are merely parenchymatous cells which undergo belated selerosis without however growing out of the pattern of the surrounding cells: they may be somewhat larger than these if they cease cell division earlier. Such selercids are said to show co-ordinate growth. Other types however develop quite differently from the parenchymatous cells surrounding them; they elongate and often branch pushing their way through the intercellular spaces and between the walls of the neighbouring cells; these are said to show intrusive growth. Both types are found in Cyrtandra, and indeed it is difficult to decide which term to apply to the vesicular selercids (Type 3), while in the dendroselercids (Type 6), growth may be described as co-ordinate in the hypodermis but intrusive into the mesophyll.

Foster (1955) has also differentiated between diffuse sclereids, which occur scattered through the parent tissue, and terminal sclereids, which develop in contact with the tracheary elements of the veinlet endings. So far all the sclereids found in Cvrtandra have proved to be of the diffuse type.

MATERIAL AND METHODS

The present account is entirely based on the study of leaves from herbarium material. Morphology and distribution were examined in cleared leaves and in hand sections. Individual selereids were examined in more detail from macerated tissue.

The techniques used for leaf clearing and preparing the herbarium material for section cutting were the same as those described for Limonium (Bokhari, 1970), but a rapid technique for macerating the tissue was used. The material was placed in a strong (20%) KOH solution for one hour and then washed with water. When thoroughly washed, it was transferred to Eau de Javelle. After one hour, the material was again washed with water and dehydrated with three changes of absolute aicohol. The dehydrated, macerated tissue was stained in safranin dissolved in absolute alcohol for five minutes. The stained tissue was placed on a slide, separated and mounted in euparal.

The advantages of this technique, besides its rapidity, are firstly, that it is very easy to separate and isolate the cells in euparal discarding the remaining tissue; secondly, there is no need to dehydrate the isolated cells after staining. a process which is lengthy and there is always a danger of losing some cells. The macerated tissue can be stored in stain for an indefinite period. Sections were taken from the middle of the leaf, including the midrib. It should be mentioned that in some leaves the sclereids are sparse and may be absent from individual sections; a portion of cleared leaf must be examined before their complete absence is recorded.

GENERAL HISTOLOGY OF THE LAMINA

Before giving details of the sclereids, it is necessary to give a brief desscription of the Cyrtandra leaf in which they are found. It is not possible at this stage to go into any great detail of foliar histology of a particular leaf nor to describe fully the rather considerable range of variation shown. Only the main general features can be mentioned now.

All the leaves are bifacial. Stomata are restricted to the under surface. They are anisocytic and all stomata have 2-3 rings of 3-subsidiary cells round them. Usually the stomata are level with the rest of the epidermis that is thus smooth. In some species however (for example Burtt 4940) the surrounding subsidiary cells are raised to form a turret on top of which the stoma itself is borne. This condition is widespread in other genera of Gesneriaceae and may give to the leaf a characteristic white-spotted appearance, due to the air in the stomatal cavity (at least in dried leaves), which may be mistaken at first glance for scattered scales. Most of the species have smooth leaves: others however are distinctly bullate (Burtt 4884) or even strongly "mamillate", pushed up into sharp peaks hollow underneath. This latter arrangement, characteristic of the widespread C, splendens, has the effect of increasing the leaf surface and must also provide surfaces which are temporarily at right angles to the light as it comes from changing directions. These leaves with irregular surfaces seem to be characteristically without

Epidermis. In nearly all the species examined the epidermal cells on both surfaces are barrel-shaped, giving a smooth surface. In a few species however, such as C. multibracteata and its allies (Burtt 5056, 5173), the epidermal cells on the upper surface have a conical outer wall. Leaves with an epidermis of this nature have a characteristic sheen in the living stage.

Hypodermis. A well-developed hypodermis of 1-5 layers is usually present. Its origin has not been investigated; but as the cells are not regularly aligned with those of the epidermis it is likely to be a true hypodermis rather than a multi-layered epidermis. In species lacking a hypodermis the epidermal cells seem to take over the function of water storage and are larger than usual: in fact the upper and lower epidermis together may make up the greater part of the leaf thickness (Burtt 4884).

Mesophyll. Palisade tissue is rather poorly developed and usually consists of a single layer of rather small cells. The cells of the spongy mesophyll are usually irregular in outline, enclosing a large number of intercellular air spaces, more or less elongated parallel to the surface of the leaf. In some species the cells are distinctly lobed and their orientation is irregular. Druses, if present, are confined to the mesophyll; they are principally found in the palisade but also occur in the spongy mesophyll in some species.

Veins. The midrib and lateral veins have collateral bundles which are accompanied by sclereids in the ground tissue.

TYPES OF SCLEREIDS

The selereids in Cyrtandra exhibit a wide diversity in their form and distribution. Sclereids may be confined to the hypodermis or to the mesophyll alone or found both in the hypodermis as well as the mesophyll. When sclereids are present in the hypodermis and also in the mesophyll, they occur in various specific combinations (as will be discussed below) and show distinctive distribution pattern. The foliar sclereids in Cyrtandra can be conveniently classified into the following types.

Type 1. Vermiform sclereids. These are probably the largest known sclereids; they are of intrusive growth and may attain a length of 1400 µm. In macerated leaf tissue and in cleared leaves they can be easily seen with the naked eye and are conveniently isolated for detailed study. They are unbranched with rounded ends, having slightly wavy walls with sharp crests and a broad lumen of uniform width, varying considerably in size and shape in different species as well as in the same species (plate 1, B, C & fig. 1, Aa, Ba, Ca). In C. elatostemoides these are short and much broader with distinct pores in the walls (plate 1, C & fig. 1, Ca). These sclereids are confined to the hypodermis and as their size would suggest they are oriented parallel to the epidermis.

Type 2. Osteosclereids. These are unbranched cells of co-ordinate growth, they are bone-shaped, more or less expanded at both ends and have a broad lumen of uniform width. They vary considerably in shape and size. At one extreme they are quite long with more or less wavy cell walls and comparatively narrow lumen, at the other extreme they are more or less squarish in outline, having very broad lumen and smooth cell walls. There are, of course various intermediate forms between these two extremes (fig. 1, Ga-la). Osteosclereids are present only in the hypodermis and their orientation is invariably at right angles to the epidermis. The two extremes of the osteo-sclereids are accompanied by particular types of astrosclereids in the meso-phyll.

Type 3. Vestcular type. They appear as sclerotic parenchymatous cells which are usually unbranched but variously lobed. They were noted only in the mesophyll, diffused amongst the spongy tissue, but more abundant around the veins, in C. horizontalis (plate 1, H & fig. 1, E). They are little different from the neighbouring cells and do not show intrusive growth.

Type 4. Astrosclereids. They are irregularly branched cells and fluctuate greatly in their size, degree of branching, lumen of the main cell body and their position. They are confined to the mesophyll and show strong intrusive growth. Astrosclereids possessing very long branches have a narrow lumen

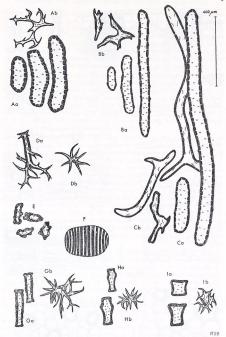


Fig. 1. Selereids isolated from the macerated lamina showing morphological diversities in different Cyramára species. As-b. C. elabateramides: Aa, verniform selereids of hypodermis: Ab, polymorphic selereid of the mesophyll. Ba-b. C. gibbsiae: Ba, verniform selereids of the mesophyll. Ca-b. C. polymorphic selereids of the hospotypli. Ca-b. C. propropried selereids of the mesophyll. Ca-b. C. polymorphic selereids of the mesophyll. Ca-b. C. propropried selereids of the selective selection of the selective selecti

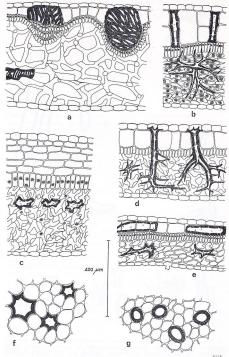


Fig. 2. a, transverse section of the lamina of *Cyrtandra hoseana*. b, T. S. of lamina of *C. bracheia*. c, T. S. of lamina of *C. horizontalis*. d, T. S. lamina of *C. axillaris*. e, T. S. lamina of *C. axillaris*. e, T. S. lamina of *C. probiaia*. f, T. S. of ground tissue of midrib of *C. bracheia*. g, T. S. of ground tissue of midrib of *C. pibbsiae*.

17

and extend their branches to the lower epidermis and to the palisade tissue as in C. bracheia (fig. 2, b). In some of the species the sclereids possess short branches with a broad lumen and their branches are confined to the mesophyll as in C. adnua (plate 1, F). In all the specimens studied, irrespective of the size of the sclereids, the main cell body of the astrosclereid is in the spongy mesophyll and invariably the sclereid branches intrude into the palisade tissue. Astrosclereids may be present alone in the mesophyll or they are accompanied by different types of sclereids in the hypodermis.

Type 5, Polymorphic sclereids. These sclereids vary considerably in size, form of cell body and degree of branching. In the simplest type they are dichotomously branched or lobed at one end as in C. quinquenotata (fig. 1, Cb). In other species they are variously branched but unlike astrosclereids they usually branch in one plane and their ultimate branches are very short as in C. elatostemoides (plate 1, D & fig. 1, Ab) and in C. gibbsiae (plate 1, B & fig. 1, Bb). Like astrosclereids they are present only in the spongy mesophyll and show marked intrusive growth.

Type 6. Dendrosclereids. In Cyrtandra there are usually distinct types of sclereids confined either to the hypodermis or to the mesophyll. Dendrosclereids, however, originate in the hypodermis and unlike osteosclereids which remain confined to the hypodermis, grow through the mesophyll to the lower epidermis. In the hypodermis they are usually unbranched (or with few small branches), but are profusely branched in all directions in the mesophyll. They have thick walls and a narrow lumen which is continuous from the unbranched portion to the ultimate branches. Dendrosclereids are usually accompanied by astrosclereids in the mesophyll (plate 2, A & fig. 1, Da). It may be mentioned here that the sclereids in Boscia (Capparidaceae) are the only sclereids noted in the literature which approach the dendrosclereids of Cyrtandra. In Boscia the sclereids branch also only in the mesophyll, but unlike Cyrtandra the sclereids are produced from the upper and lower epidermis of the leaf into the mesophyll and they ramify only in one plane (Pestolozzi, 1898).

Type 7. Tracheoids. This type consists of idioblasts resembling tracheids in their annular thickened or pitted walls, but differing from typical tracheary elements in their form, size and general topography. They are reported to occur in many diootyledonous genera (Solereder, 1908, p. 1902, Haberlandt, 1924, p. 378 & Pirwitz, 1931). In the majority of the cases the tracheoids are more or less isolated, occurring either in the middle of the ground tissue or in connection with the vascular system or secretory organs. In Cyrtandra they are confined to the hypodermis, sometimes accompanied by astrosclereids in the mesophyll (plate 2, E–H & fig. 1, F). Their growth is coordinate, but they may bulge down into the palisade tissue which then forms a bowl-like depression to accommodate them as in C. hoseana (plate 2, G & fig. 2, a). In rare cases, the sclereids in the mesophyll develop tracheoid-like thickenings.

POSITION AND COMBINATIONS OF SCLEREIDS IN THE LAMINA

As has already been mentioned, distinct types of sclereids are confined either to the hypodermis or to the mesophyll only, but in most of the cases sclereids are present in the hypodermis as well as the mesophyll and they show distinctive combinations. The situations regarding the position and combinations of sclereids that have been found so far are enumerated below.

Pattern I. Vermiform sclereids in the hypodermis and polymorphic types in the mesophyll

Vermiform sclereids can be easily spotted from the dried herbarium leaves with a hand lens. In surface view they radiate from the midrib to the margin of the leaf following the veins. In cross sections they occur in the hypodermis and are always placed parallel to the epidermis. Vermiform sclereids are invariably found to be associated with polymorphic sclereids in the mesophyll as in C. quinquenotata (plate 1, A), and C. gibbsiae (fig. 2, e). In Cyrtandra species having vermiform sclereids in the hypodermist, the leaf midrib always has vermiform sclereids which appear rounded in cross-section as in C. gibbsiae (fig. 2, g).

Pattern II. Osteosclereids in the hypodermis and astrosclereids in the mesophyll Osteosclereids are always present in the hypodermis and are oriented at right angles to the epidermis and hence appear more or less angular from the surface view in cleared leaves (plate 1, G). Two variations may be distinguished:

IIa, long osteosclereids with wavy outer walls accompanied in the mesophyll by very much branched astrosclereids, whose branches usually extend to the lower epidermis, as in *C. bracheia* (plate 1, E & fig. 2, b); IIb, short and more or less squarish osteosclereids accompanied in the mesophyll by astrosclereids with short branches which remain confined to the mesophyli, as in *C. admata* (plate 1, F). The midribs of leaves that have astrosclereids in the mesophyll have short-rayed astrosclereids in the ground tissue (fig. 2, f).

Pattern III. Dendrosclereids usually accompanied by astrosclereids in the mesophyll Dendrosclereids are usually accompanied (III a) by astrosclereids with

long branches in the mesophyll as in C. axillaris (plate 2, A-B; fig. 1, Da-b; fig. 2, d). In C. lambirensis (III b) dendrosclereids seem to occur alone, without astrosclereids.

Pattern IV. Tracheoids in the hypodermis and astrosclereids in the mesophyll Tracheoids with annular or pitted thickenings are present in most of the hypodermal cells. In some they enlarge into the palisade tissue. The astrosclereids accompanying tracheoids are usually short-rayed cells with a broad lumen as in C. andersonii (plate z, E), and C. hoseane (plate z, G & fig. z, a). These leaves have short-rayed astrosclereids as well as tracheoids interspersed in the ground tissue of the midrib.

Pattern V. Vesicular sclereids in the mesophyll only

Vesicular sclereids are confined to the middle of the spongy mesophyll increasing in number around the veins. They have been noted so far only in C. horizontalis (plate 1, H & fig. 2, c).

Pattern VI. Astrosclereids only in the mesophyll

Astrosclereids in the mesophyll which are unaccompanied by any types of sclereids in the hypodermis are usually small in size with a broad lumen and

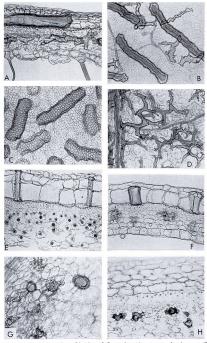


PLATE 1. A, transverse section of lamina of Cyttandra quinquenotata showing vermiform sclereids in the hypodermis and polymorphic sclereids in the mesophyll. B, part of cleared leaf of C. glabshiae showing vermiform and polymorphic sclereids. C, part of cleared leaf of C. elatostemoides showing vermiform sclereids in the hypodermis. D, part of cleared leaf of C. elatostemoides showing polymorphic sclereids in the mesophyll. E, T. S. lamina of C. aduata with osteosclereids in the mesophyll. E, T. S. lamina of C. aduata with osteosclereids in the hypodermis and astrosclereids in the mesophyll. G, part of cleared leaf of C. aduata showing osteosclereids and astrosclereids in surface view. H, T. S. of lamina of C. horizontalis having vesicular sclereids only in the mesophyll. All X 20.

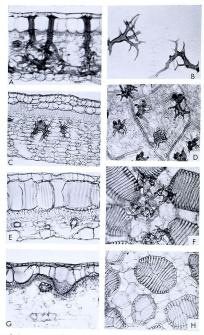


PLATE 2. A. transverse section of lamina of Cyrnonira arillaris with dendrosclereids. B. siolated dendrosclereids of C. arillaris from macerteed tissue. C., T. S. lamina of C. ditterial flowing astrosclereids only in the mesophyrate part of cleared leaf of C. ditterial flowing astrosclereids with short branches. E. T. pt. tof cleared leaf of C. molerosmit and astrosclereids in the mesophyll. F. and the continuation of C. hoseana with tracheoids of an attrosclereids in surface view. G. T. S. lamina of C. hoseana with tracheoids and astrosclereids in surface view. G. T. S. lamina of C. hoseana with tracheoids and satir tracheoids. All X 200.

short branches which are confined to the mesophyll only, as in C. digitaliflora (plate 2, C, D).

Pattern VII. Tracheoids in the hypodermis unaccompanied by any sclereids in the mesophyll

Such tracheoids are usually larger is size and generally replace the majority of the hypodermal cells. They were found to have annular-thickened walls as in *C. sarawakensis* (plate 2, H & fig. 1, F).

Pattern VIII. Sclereids absent.

TAXONOMIC NOTES (by B. L. B.)

The tentative nature of these taxonomic notes must be strongly emphasised. No useful purpose would be served in this preliminary account by giving full details of every specimen examined. However it should be said that while the statements about some species are based on the examination of two or three different collections, in other cases only a single leaf has been studied. A great deal more work will have to be done, but it is clear that the foliar sclereids of Cyrtandra do provide taxonomic features that may be a great help in understanding and classifying this difficult genue.

As might be expected, certain sclereid patterns occur only in a single group of species: others are found in more than one group and these may not be closely related. Where species-groups have a certain ecological uniformity it is particularly interesting to find that they are supported by the evidence from leaf sclereids. For example tracheoids, which occur only in patterns IV and VII, are apparently restricted to plants on sand or sandy clav.

There are far less patterns available than there are groups of species. It is useless to speculate on the interrelationships of the various patterns until a full survey of the genus has been completed.

It is too early yet to try to communicate the correlation between the sclereids present in the leaf and the leaf-texture, but this can be quite distinctive. Already the pattern of sclereids that will be found has several times been correctly forceast from the general appearance of the dried leaf on a herbarium specimen. It may therefore be possible to devise a catalogue of descriptive terms for leaf texture which can be anatomically defined. Of course sclereids are not the only element of leaf structure that contributes to texture and it is clear that a full investigation of leaf anatomy will have to be made.

Pattern I. Three named species are referable here: C. elatostemoides, C. gibbsiae and C. guinquenotata. In these the vermiform selereids are superficially visible with a hand lens and this feature was used in grouping the species together. However they hold well in other characters: marked anison phylly, indumentum, large tubular calys and large corolla with bristly hairs on the outside. This group of species is, as far as is known at present, restricted to the island of Palawan, Sabah and northern Sarawak.

Pattern IIa. The plants here are members of what I had roughly called the C. decurrens group (Clarke's section Decurrentes in part); rather coarse plants with large corollas having long silky hairs on the outside. It turns out however, that the type of C. decurrens De Vriese, a Moluccan species, has sclereids only in the mesophyll (Pattern VI). The different pattern in these Sarawak plants helps to confirm that they should not be placed in C. decurrens. Species to be placed here are C. bracheia, C. subgrandis, C. woodsii and some others not yet named.

Pattern IIb. This pattern, short broad hypodermal ostoosclereids and shortly branched astrosclereids in the mesophyll, seems to occur in several distinct taxonomic groupings. Some of the plants belong to the "C. decurrens" group as do those of pattern IIa; these include C. erectipila, C. adnata, C. vulpina and other unnamed plants. Then C. microcarpa has small pink subglabrous flowers in dense axillary clusters. Finally there are two specimens (Burtt 5012, 5056) belonging to the group of C. trisepala. This is distinguished by small white rather fleshy corollas and a bilabiate calyx, the three upper lobes being united into a dorsal trilobed lip, the two lower remaining free to the base.

Pattern IIIa. Dendrosclereids accompanied by astrosclereids in the mesophyll are characteristic, it seems, of two species that I had placed close together—

C. latens and C. axillaris; there are also unnamed specimens (Burtt 2636, 4763) which I would be happy to have placed in this affinity.

Pattern IIIb. Dendrosclereids alone have so far been found only in C. lambirensis a species that is morphologically isolated. Possible affinities that had been entertained with C. eximia or C. yelutina obtain no support from the sclereid character as both lack foliar sclereids altogether.

Pattern IV. Tracheoids in the hypodermis accompanied by astrosclereids in the mesophyll are characteristic of *C. andersonii* and of *C. schizostyla* with which it had already been associated: an unnamed plant (*Butt* 4,944) with the same pattern seems to be of this affinity also. The morphological features are large cream flowers with yellow bars in the throat, dwarf habit, rather thick coarsely hairy leaves and laciniate bracts.

Pattern V. Vesicular tracheids have so far been found only in *C. horizon-talls*, which on other grounds seems related to *C. oblongifolia* and *C. angularis*. These two species lack sclereids altogether.

Pattern VI. Astrosclereids in the mesophyll only. This may, in a sense, be regarded as the most generalized pattern. It is therefore not surprising to find it is shown by more than one taxonomic group. C. cretacea and some other limestone plants belong here; the type of C. decurrens De Vriese from the Moluccas, and also the type of C. pilosa Bl. from Java; one Bornean member of the "C. decurrens" group showing this pattern is C. gracilenta. C. digitalifyora is apparently allied to C. radiciflora (an example of affinity between a plant with basal flowers and one having them borne higher up the stem) and both have selereids of this pattern.

Pattern VII. This pattern confirms the taxonomic grouping: C. sarawakensis and C. pendulflora are certainly allied species although the former has almost sessile clusters of flowers and the latter has them trailing on the ground on a long peduncle. Because of these basal flowers Kraenzlin esta-

blished a distinct section for plants showing this feature. However this is taxonomically a complete jumble of species as basal flowers, which are very common amongst tropical plants, occur in a number of quite unrelated groups of Cyrtandra.

C. hoseana differs from C. sarawakensis and C. penduliflora by the way in which the tracheoids bulge into the palisade tissue; however it was already associated with these two species in the herbarium and this affinity therefore receives general support.

Pattern VIII. Some seventeen specimens examined (in addition to one or two from New Guinea and the Pacifio) showed no foliar schereids. Named species included C. oblongifolia, C. angularis, C. velutina, C. impar, C. eximia, C. megalocrater, C. farinosa and C. splendens. Some of these have already been mentioned in discussing the affinity of species possessing sclereids: C. impar belongs to the C. trisepala group (Pattern IIb). C. megalocrater and C. farinosa are allied and have inflorescences enclosed by cupular brates. No doubt small groups of species that always lack sclereids will be characterized as the study proceeds.

REFERENCES

- BOKHARI, M. H. (1970). Morphology and taxonomic significance of foliar sclereids in Limonium. Notes R. B. G. Edinb. 30: 43-53.
- Esau, K. (1965). Plant Anatomy, 2nd edition, New York.
- FOSTER, A. S. (1944). Structure and development of sclereids in the petiole of Camellia japonica L. Bull. Torrey Bot. Club 71: 302-306.
- (1947). Structure and ontogeny of terminal sclereids in the leaf of Mouriria huberi Cogn. Amer. Jour. Bot. 34: 501-514.
- (1955). Comparative morphology of foliar sclereids in Boronella Bail.

 Jour. Arnold Arb. 36: 189-198.
- (1956). Plant idioblasts: remarkable examples of cell specialization.
 Protoplasma 46: 184-193
- HABERLANDT, G. (1924). Physiologische Pflanzenanatomie. 6 Aufl. Leipzig. PESTALOZZI, A. (1898). Die Gattung Boscia Lam. Bull. Herb. Boiss. 6, Appendix 3.
- Appendix 3.

 PIRWITZ, K. (1931). Physiologische und anatomische Untersuchungen an Speichertracheiden und Velamen. Planta 14: 19–76.
- ROSSER, E. M. & BURIT, B. L. (1969). Studies in the Gesneriaceae of the Old World, XXX: anatomical characters in the tribe Trichosporeae. Notes R. B. G. Edinb. 29: 39-48.
- SOLEREDER, H. (1908). Systematic anatomy of dicotyledons, trans. Boodle & Fritsch. Oxford.
- (1912). Über die Gattung Hemiboea. Beih. Bot. Centralb. 29, 2: 117-126.