FOLIAR SCLEREIDS IN THE MARCGRAVIACEAE

A. C. DE ROON

(Botanical Museum and Herbarium, Utrecht)

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ABSTRACT

A survey is given of the types of the sclereids and the sclereid patterns occurring in the leaves of the Marcgraviaceae. Eight main categories of sclereids are distinguished on the base of the morphology of the sclereids. A comparison is made with the foliar sclereids found in some other families. The systematic value and the function of the sclereids are briefly discussed. Some new combinations of names are published.

INTRODUCTION

'Sclerenchymatic idioblasts', i.e. the kind of cells which are usually indicated by the name 'sclereids', are very common in the *Marcgraviaceae*. They are found in a great diversity of forms and often in large numbers in various parts of the plants, viz. in the cortex and the medulla of the shoots, in the leaves, in the nectaries and in the perianth, the pistil and the pericarp. In this paper we will confine ourselves mainly to the foliar sclereids.

The presence of idioblastic sclereids in leaves and other parts is a phenomenon found in species belonging to many different families. In the works of SOLEREDER (1899) and of METCALF and CHALK (1950) a large number of examples are to be found. Also a large amount of data are given in papers published in various periodicals. For surveys we can refer to FOSTER (1944, 1949), RAO (1951a, 1957b), for the older literature moreover to WIJNAENDTS FRANCKEN (1890) and for sclereids occurring in conifers to STERLING (1947) and to AL-TALIB and TORREY (1961).

In recent studies on sclereids attention is drawn in particular to three aspects of this subject, namely the morphology, the ontogeny and the taxonomic value. For several purposes a practical classification of the sclereids based on their morphology can be of use. However in view of the enormous variability found among the sclereids, it seems advisable to name only the main categories. And as the distinguishable types are almost always connected to each other by intermediate forms, it will often be necessary to add a qualifying description. It seems to me that this is preferable to the elaboration of a classification which aims at completeness but would lose a good deal of its usefulness. A natural classification of the sclereids can not be based on their morphology alone, therefore other characters such as the structure and the ontogeny must be considered (cf. FOSTER, 1949; RAO, 1951a, 1957b). The great diversity in form

shown by the sclereids has led to a chaotic terminology (cf. FOSTER, 1944) and to avoid a further increase of this chaos we have confined ourselves, where possible, to the general terminology used by TSCHIRCH (1889) and FOSTER (1949) and to the terminology used by RICHTER (1916, 1917, 1920) for the sclereids found in the *Marcgraviaceae*.

The first one who set up a classification of sclereids was TSCHIRCH (1889). He distinguished four main categories of sclereids, viz. 'brachysclereids', 'macrosclereids', 'osteosclereids' and 'astrosclereids'. As clearly appears from the examples given by him, he used these terms in a very broad sense, broader than most of the authors after him did. A classification of foliar sclereids is made by RAO (1951a, 1957b) who distinguishes as form types: 'spheroidal sclereids', 'osteosclereids', 'fusiform sclereids', 'filiform sclereids', 'astrosclereids' and 'crystalliferous sclereids', which are classified in three main groups on the basis of their ontogeny. The general morphological classification of TSCHIRCH (1889) proves still to be usable though a certain modification is necessary. So it might be advisable to treat the non-idioblastic, tissue-forming sclerenchyma cells as a separate category along with the categories of the idioblastic sclereids and the fibers.

In the studies on the ontogeny of foliar sclereids two problems had special attention, the origin of the sclereid initials with their possible relation to the terminations of the veinlets and the method of growth of the cells. FOSTER (1946, 1947) discovered that beside a random distribution, foliar sclereids can be restricted to the ends of the veinlets. In several genera such terminal sclereids are a common phenomenon. In the *Marcgraviaceae* the foliar sclereids are transformed palisade or spongy parenchyma cells; their distribution is diffuse and there is no evidence for an ontogenetic relation with the vascular bundles. However, as no ontogenetic investigations are made, these and other remarks in this paper regarding the origin of the sclereids are only based on the form and the position of the sclereids and must therefore be taken with some reservation. The necessity for this caution is illustrated by the following examples: the osteosclereids found in the leaves of *Mouriria huberi* Cogn. (FOSTER, 1947), which connect the upper with the lower epidermis like pillars, develop from initials found in the spongy parenchyma region at the terminus of the procambial strands and the similar type of sclereids found in the leaves of *Olea dioica* Roxb. (RAO and KULKARNY, 1952) represent transformed palisade cells. The Marcgraviaceous 'palosclereids' very probably are transformed palisade parenchyma cells but a similar type of sclereids occurring in the palisade layer of the leaves of *Diospyros discolor* develop from initials situated in the spongy mesophyll (RAO, 1951c).

Determination of sclereid initiation has become subject to experimental manipulation (FOARD, 1958, 1959; AL-TALIB and TORREY, 1961). AL-TALIB and TORREY concluded from their experiments that the determination of sclereid initials in foliar leaves of *Pseudosuga menziesii* is clearly under some precise control of changing physiological conditions active during leaf and shoot development. Insofar as there

is evidence on the matter, it would seem probable that hormonal factors, especially auxins, may play a role in determining when and where sclereid initials will develop. Their experiments suggest that auxin levels in the leaf influence the development of sclereids, with high auxin levels tending to suppress sclereid development. I think that for the taxonomist these experiments are of great interest and importance as will be discussed in the chapter on the taxonomic value of sclereids.

In the present article the results of a study of the foliar idioblastic sclereids of the *Marcgraviaceae* are presented. This study covered the form and the classification of the sclereids, their distribution and their arrangement into patterns. A comparison is made with the foliar sclereids of some other families. The value of sclereids as a taxonomic character is discussed. Some remarks are made on the possible function of foliar sclereids.

Material and methods

The investigations are based on the study of leaves of herbarium specimens of a great number of species. The sclereids were studied in cleared leaf sectors, in hand sections and after isolation from macerations. The leaves were cleared following the technique of Foster (1946, 1949) and mostly stained with saffranine. Macerations were made by one of the usual methods.

As it is intended to give in this paper a general survey only, and no detailed studies on the sclereid patterns of the individual species, no list of all the specimens studied is given but the specimens sclereids of which are figured are mentioned in the explanation of the figures.

New combinations

For a correct citation of some species it is necessary to publish here some new combinations of names, anticipating a monographic treatment of the family which is in preparation. This regards the following species:

Souroubea bicolor (Bentham) de Roon comb. nov.
Basionym: *Ruyschia bicolor* Bentham, Bot. Voy. Sulph.: 73, t. 29. 1844.

Souroubea loczyi (Al. Richter) de Roon comb. nov.
Basionym: *Norantea loczyi* Al. Richter in Math. u. Naturw. Berichte aus Ungarn 31: 115. 1920.
Synonym: *Souroubea triandra* Lundell in Phytologia 1: 244. 1937.

Souroubea platyadenia (Gilg) de Roon comb. nov.
Basionym: *Ruyschia platyadenia* Gilg in Engler, Bot. Jahrb. 25, Beibl. 60: 34. 1898.

Norantea brachystachya (Rusby) de Roon comb. nov.
Basionym: *Souroubea brachystachya* Rusby in Bull. N.Y. Bot. Garden 8: 103. 1912.

Norantea jimenezii (Standley) de Roon comb. nov.
Basionym: *Ruyschia jimenezii* Standley in Field Mus. Bot. 18: 699. 1937.

Marcgravia goudotiana (Triana et Planchon) de Roon stat. nov.
Basionym: *Marcgravia rectiflora* Triana et Planchon var. goudotiana Triana et Planchon in Ann. Sc. Nat. ser. 4, 17: 366. 1862.

Marcgravia leticiana (Macbride) de Roon stat. nov.
Basionym: *Marcgravia flagellaris* Poeppig ex Wittmack var. *leticiana* Macbride in Candollea 5: 387. 1937.
Synonym: *Marcgravia trinitatis* Presl var. *leticiana* Macbride in Field Mus. Bot. 13A, 2: 707. 1956.

Survey of the types of sclereids found in the Marcgraviaceae

Among the foliar sclereids of the *Marcgraviaceae* a high degree of diversity is found. On the base of their form they may be arranged in eight main categories, three of which were already distinguished by Tschirch, viz.: 'brachysclereids', 'astrosclereids' and 'osteosclereids', completed with five categories distinguished by Richter, viz.; 'ophiurosclereids', 'librosclereids', 'palosclereids', 'rhizosclereids' and 'idiosclereids'.

The wall of the sclereids may be thickened to a varying degree and it often shows a distinct lamellation which becomes still more clearly visible in polarised light. The outside of the sclereids is usually smooth, spicules as were found by Foster (1944) on the sclereids of *Camellia japonica*, were never met with. Pits may be present in all the various types. In the sclereids provided with long projections pits are only found in the 'central body'.

The simplest type among sclereids is that found in the '*brachysclereids*' or 'stone cells'. Sometimes they are no larger than the surrounding parenchyma cells, but often they exceed these in size considerably. Two forms of brachysclereids are found in the *Marcgraviaceae*. Brachysclereids with a rather thin wall and a wide lumen are found in the spongy parenchyma in the leaves of several species, mostly in small numbers only and sometimes united into small clusters. Brachysclereids with very thick and conspicuously lamellated and pitted walls are frequently found in various parts e.g. the cortex and the pith of the shooth, the sepals and the pericarp; they are often united into clusters. In the corolla of the *Marcgravia* species they form a hard solid layer. In the leaves they are sometimes crowded around the hypophyllous glands and immediately below the midrib they may be numerous too; here transitions between them and macrosclereids and astrosclereids are frequently met with. In wound tissue and other abnormal cork developments brachysclereids are often seen as well; mostly they have the same form as the cork cells; Richter (1917) speaks in this case of '*phellosclereids*'.

The final form of a sclereid depends greatly upon the tissue in which it develops, particularly on the shape of the cells out of which

such a tissue is formed. So in the palisade parenchyma of part of the *Norantea* and *Souroubea* species sclereids are found which agree in shape with the surrounding parenchyma cells. They are sometimes arranged in clusters or rows but mostly they are isolated. The thickening of their walls varies from slight to very strong, and the width of the cell lumen, accordingly, from wide to narrow; the pits in the walls are very conspicuous (Plate I, Figs. 1–3). In the classification of TSCHIRCH these rod-shaped 'palisadic sclereids' belong to the category of the macrosclereids. TSCHIRCH used the term macrosclereid for the columnar non-idioblastic sclereids which form a palisade layer in the testa of many Papilionaceae, as well as for idioblastic foliar and cortical sclereids (TSCHIRCH, 1889, fig. 347). In my opinion it would be better to keep the non-idioblastic, tissue-forming sclereids out of a classification of idioblastic sclereids, and to use the term 'malpighian cells' for the above mentioned sclerenchyma cells of seed coats.

Richter proposed the term *'palosclereids'* for the sclereids of the palisade parenchyma described above, which term is adopted in the present article, and by which therefore is meant macrosclereids situated in the palisade parenchyma, whether they have retained the shape and the size of the parenchyma cells or not.

A special form of palosclereids is found in *Norantea spiciflora* and in various species of *Souroubea*, e.g. *S. crassipes*, *S. pachyphylla*, *S. didyma*, *S. bicolor* and *S. vallicola*. They are of the same height as the surrounding palisade cells, but their diameter is larger to very much larger than that of these cells. In transverse sections they are usually rectangular. They often form rows running in the direction from the base to the top. The walls are often but slightly thickened and they are therefore not always easily recognisable as sclereids. In *Norantea spiciflora* and *Souroubea vallicola*, and occasionally also in some other species, the walls are more strongly thickened, and in that case the pits and the lamellated structure of the wall are quite conspicuous (Plate I, Fig. 7; Plate II, Figs. 2, 3). In the above mentioned *Souroubea* species, in which the palisade parenchyma consists of two layers, the palosclereids are always found in the layer adjoining the epidermis.

Palosclereids provided with short protrusions and showing therefore a development in the direction of the rhizosclereids which will be discussed below, have been found in *Norantea cuneifolia* and in *N. spec.*, Cuatrecasas 16618 (Plate I, Figs. 1, 2).

The *'rhizosclereids'* or 'rooting sclereids' consist of a central part comparable in form to a palosclereid and occupying a similar position between the palisade cells, a number of root-like protrusions extending into or on top of the spongy parenchyma, and often also some, usually shorter, processes extending between the epidermis and the top of the palisade cells. The processes at the upper end may differ considerably in length; occasionally they extend into the longitudinal direction of the leaf (Plate VI, Figs. 4–7). Sometimes they are bent downwards at the end, and then the hooklike top penetrates between the palisade cells (plate V, Fig. 8).

Within the category of the rhizosclereids three types are distinguished in the *Marcgraviaceae*. In the first type the projections at the lower end of the central part extend into the direction of the lower epidermis, and they are mostly somewhat spreading (e.g. Plate III, Figs. 9–13; Plate IV, Figs. 4–6; Plate V, Figs. 6–10; Plate VI, Figs. 10–14). In the second type the projections may all or in part extend in a longitudinal direction on the top of the spongy parenchyma (Plate VI, Figs. 20, 21, 23). In the most deviating type the central part is shortened and more or less contracted in the middle, hour-glass-shaped, and the protrusions at the top as well as at the base are long and extending in the longitudinal direction; the number of them, as well at the top as at the base, is moreover reduced to two to four (Plate VI, Fig. 22).

Rhizosclereids are found in *Ruyschia* and *Souroubea* (type 1) and in *Norantea* subgen. *Marcgraviastrum* (type 1, 2, and 3). In some *Marcgravia* species sclereids are met with which extend partly into the palisade parenchyma, but they are of another type than the rhizosclereids described above. They will be described in detail further on.

In the spongy parenchyma the sclereids show a much greater diversity; they are, moreover, much less regular in form. In the first place we will mention here the large group of the '*astrosclereids*', in which all sclereids are included with an irregular shape caused by the presence of ramifications or of shorter or longer projections or arms. This is a very heterogenous assemblage, so that the term can be used only in a rather vaguely descriptive way. The many kinds of astrosclereids which are encountered in the *Marcgraviaceae*, may be arranged in a few series, the members of which gradually pass from the star-shaped form of the typical astrosclereid into more specialized types like the ophiurosclereids, the librosclereids and the idiosclereids.

In the typical form of astrosclereids met with in the *Marcgraviaceae* there is a central part provided with a less strongly to very strongly thickened wall and an usually rather small to very small cell lumen and with a number of projections extending in all directions and rather short, their length not exceeding more than a few times the diameter of the central part (Plate IV, Figs. 7–12; Plate V, Figs, 11, 12, 14; Plate VI, Fig. 15). This type of astrosclereids is connected by transitions with the brachysclereids. They occur in the spongy parenchyma of the majority of the species belonging to the genus *Ruyschia* and in a fair number of the species belonging to other genera. They are not confined to the leaves but occur also in other parts, so e.g. in the cortex of the shoots, in the pedicels, sepals, etc., and they are often present in large numbers and often crowded.

In some astrosclereids of this type there is a tendency towards reduction of the size of the central part and towards an increase in length of the projections. If this tendency becomes more pronounced the astrosclereids pass into the type for which RICHTER used the name '*ophiurosclereids*'. The latter possess a relatively small central

part and are provided with very long projections, i.e. that the length of these arms exceeds the diameter of the central part many times; the arms are situated, as a rule, in a plane which runs parallel to the surface of the leaf (Plate III, Figs. 14–16; Plate IV, Figs. 14, 18–23; Plate V, Figs. 13, 23, 24, 27). This type of sclereid is included by TSCHIRCH in his category of the astrosclereids. RICHTER used the name ophiurosclereids for the very same type of sclereids as JÖNSSON (1880), who introduced this term in his study of the leaf anatomy of the *Proteaceae*.

Often ophiurosclereids are met with in which some of the arms are very strongly elongated, whereas the other projections are much shorter; in this case the elongated arms extend in opposite directions (e.g. Plate III, Figs. 16–18; Plate V, Fig. 22).

If the number of the elongated arms is reduced to four, three or two, we arrive at a type for which RICHTER introduced the name '*librosclereids*' or 'fibre-shaped sclereids'. The typical librosclereids are provided with a very small central part and two very long arms extending in opposite directions and occasionally accompanied by a few extremely small projections; this type therefore shows a striking resemblance to a fibre (Plate II, Fig. 10; Plate III, Figs. 26–28; Plate IV, Fig. 25; Plate V, Figs. 25, 28; Plate VI, Figs. 28–37). They may reach a considerable length; in *Norantea spec.*, Killip and Cuatrecasas 39159 for instance, they are circa 6 mm long. A type with usually four arms, and therefore more or less H-shaped is also often encountered (Plate III, Figs. 22–25; Plate V, Fig. 26; Plate VI, Figs. 31, 34). This type of sclerenchyma cell is also indicated as 'poil interne en H' by VAN TIEGHEM (1866, 1891), as 'trichoblast' by SACHS (1874) and as 'trichosclereid' by BLOCH (1946). Librosclereids in the leaf are always oriented lengthwise, i.e. parallel to the midrib.

Large ophiurosclereids and librosclereids with slender arms are found, all or not in combination, in *Ruyschia phylladenia*, several *Souroubea* species, e.g. *S. guianensis*, *S. corallina*, *S. bicolor* and *S. sympetala*, and most of the *Norantea* species belonging to the subgenus *Marcgraviastrum*.

Ophiurosclereids and librosclereids, especially the H-shaped ones, are often found in the cortex and occasionally also in the medulla of young shoots; in the peduncle and in the axis of the inflorescence and in the pedicels they may also be present. In some species of *Souroubea* and of *Marcgravia* and in the subgenus *Marcgraviastrum* of *Norantea* they are a conspicuous feature of these parts.

A category of sclereids for which RICHTER proposed the name '*idiosclereids*' is met with in a fairly large number of *Marcgravia* species but outside this genus only in *Norantea spiciflora* and *N. jimenezii*. The sclereids of this category are very polymorphic and very variable in shape and size. Some types can be distinguished by the structure of the wall and the ramification of the cell (Plate I, Fig. 8; Plates VII-X). In the classification of TSCHIRCH these sclereids belong to the category of the astrosclereids but in my opinion it is better to treat the idiosclereids as a distinct category and to assign to the

astrosclereids only the more or less pure stellate forms. RAO (1950b) named similar types of sclereids of the leaves of the Proteacea *Leucospermum hypophyllum* R. Br. 'polymorphic sclereids'.

Finally there is the category of the '*osteosclereids*', columnar sclereids with mostly dilatated, lobed or ramified ends, to which TSCHIRCH (1889) assigns both tissue forming sclereids from seed coats and idioblastic foliar sclereids. Osteosclereids are known from the leaves of a few *Marcgravia* species where they connect the upper and the lower epidermis like pillars, e.g. in *M. brownei*, *M. goudotiana* and *M. schippii* (Plate XII).

Below the midrib the sclereids often show a deviating form; these sclereids have been left out of consideration in the survey given above. Near the margin of the leaf usually but few or hardly any sclereids are seen, though occasionally some large brachysclereids or macrosclereids are found here (Plate II, Figs. 4, 8). Another noteworthy feature is that in some species some of the cells of the spongy parenchyma, occasionally even a large part of them, possess a thickened wall with remarkable large pits (Plate I, Fig. 4).

The various types of sclereids can be placed in morphological series which show the relations among the types and their possible derivation. For the sclereids which occur in the genera *Norantea*, *Ruyschia* and *Souroubea* this is shown on Plate XIII.

In the genus *Marcgravia* the sclereids deviate in their form, as a rule, rather strongly from those occurring in the other genera. The delimitation of the various types is more difficult, and within the categories the diversity is mostly larger. Palosclereids and rhizosclereids are entirely lacking in the genus, whereas the astrosclereids, the ophiurosclereids and the librosclereids are represented by forms which deviate from those found in the other genera. The idiosclereids are found in the genus in an enormous variability.

Brachysclereids like those of *M. soropaniana*, and two other species figured on Plate VII (Figs. 1–3, 7), may be regarded as representing the basic form from which the others can be derived. By way of the intermediate idiosclereidlike forms provided with a larger number of protrusions and with a wide cell lumen found in *M. gentlei* (Fig. 8), *M. williamsii* (Fig. 9) and *M. coriacea* (Figs. 13, 14) we arrive at the large and long idiosclereids provided with a rather wide cell lumen found e.g. *M. spec.*, Killip and Cuatrecasas 39100, (Fig. 15), *M. lineolata* (Figs. 18, 19) and *M. evenia* (Fig. 17), whereas by the way of the sclereids of *M. mexicana* (Plate VIII, Figs. 6, 8, 9) we come to the elongated, unbranched or but slightly branched idiosclereids of *M. angustifolia* (Figs. 1, 2), *M. magnibracteata* (Figs. 4, 5), *M. crenata* (Fig. 2), and the more branched sclereids like those of *M. comosa* (Figs. 7, 10, 12). In *M. spec.*, Skutch 3762 (Plate IX, Fig. 1), *M. macrophylla* (Figs. 2, 3), *M. rectiflora* (Figs. 4, 5), *M. oblongifolia* (Figs. 8–13) and *M. flagellaris* (Fig. 14) we note a gradual increase in the number of projections and in their length, leading to an irregular, often very disorderly form.

All the sclereids figured on Plate IX are shown as they appear to

us in a transverse section of the leaf. With the exception of the one shown in Fig. 14 they are all oriented perpendicular to the surface of the leaf. The longer projections are usually oriented parallel to the surface.

Starting from these forms there seems to be a differentiation in two directions. The central part may grow out perpendicular to the surface of the leaf with the result that either its upper end or one or more of the protrusions reach the upper epidermis. This kind of differentiation is shown by the forms figured on Plate X. A portion of the central part and occasionally some of the projections penetrate in this case between the palisade cells, and, due to this, these sclereids remind us more or less of rhizosclereids. However, it does not seem probable that they developed out of cells belonging to the palisade tissue, as they ought to have done if they really were rhizosclereids. The end of these sclereids which abuts on the epidermis is often more or less flattened, and the extension of the projections more or less parallel to the surface of the leaf is sometimes quite considerable (Plate X, Fig. 9), but this is not always so. On Plate XII a number of forms are figured in which the elongation perpendicular to the surface of the leaf has proceeded so far that these sclereids form a kind of pillars resting on the lower epidermis and bearing the upper one. In *M. goudotiana* (Figs. 2, 3) these osteosclereids still possess some lateral projections, but in the other forms which are shown on this plate, these lateral projections are completely lacking. These osteosclereids may perhaps be derived from idiosclereids like those which are found in the leaves of *M. magnibracteata* (Plate VIII, Fig. 5), but the affinity with a type like that found in *M. spec.*, Cowan 38207 (Plate X, Fig. 1) is probably more pronounced.

A differentiation in the other direction is found in the forms shown in the Figures 6–14 of Plate IX. These sclereids too are oriented with the central part more or less perpendicular to the surface of the leaf, but they show an ever increasing expansion in the direction parallel to the surface. Fig. 14 shows a transition towards the large astro- and ophiurosclereids shown on Plate XI. These kinds of sclereids (Plate XI) are usually somewhat coarser and less regular in shape, and are often provided with a larger number of projections directed towards the surface of the leaf as compared to the ophiurosclereids occurring in the genera *Norantea* and *Souroubea*.

Foliar sclereid patterns

For the characterisation of the species it is not only the form of the sclereids which is of importance but also their frequency, varying from scattered to densely crowded, their orientation in the leaf, e.g. perpendicular to the epidermis or parallel with the latter, and the occurrence of one type or a combination of different types of sclereids in the leaf, in brief all the characters which together constitute the 'sclereid pattern'.

The following descriptions of sclereid patterns must be regarded

with some reserve, since often only a few leaves or even just one leaf could be studied. A thorough study of the variation of the sclereid pattern in the leaves of the individual and within the species is desirable but could be made here only in a few species. In these species the sclereid pattern appears to be rather constant, though a certain variation exists possibly related to ecological factors. This problem will be discussed elsewhere in this paper.

Striking distributional patterns with a concentration of sclereids in a certain zone of the leaf as are e.g. found by FOARD (1959) in the leaves of *Camellia japonica* or by KITAMURA (1956) in the leaves of *Sciadopitys verticillata* are not met with in the *Marcgraviaceae*. The midrib region and the outmost marginal zone, however, are different from the rest of the leaf and must let out of consideration.

In the leaves of all *Ruyschia* species which could be investigated, with the sole exception of those of *R. phylladenia*, large numbers of rhizosclereids (type 1) are inserted between the palisade cells, whereas in the spongy parenchyma many coarse and thickwalled astrosclereids and occasionally transitions between the latter and ophiurosclereids are met with. *R. phylladenia*, however, occupies a particular position in the genus in this respect, for in the leaves of this species slender rhizosclereids with usually long projections extending into the spongy parenchyma, and most of them also with long projections below the epidermis are found, whereas in the spongy parenchyma a large number of ophiurosclereids and of librosclereids are found.

On account of the characters shown by the sclereids the species of the genus *Souroubea* may be divided into three groups which appear to differ also in other morphological features. The first group, which comprises the species *S. dasystachya*, *S. exauriculata*, *S. gilgii*, *S. loczyi*, *S. platyadenia* and *S. venosa*, is characterized by the scarcity or complete absence of sclereids in the leaves. However in *S. gilgii*, and occasionally also in *S. exauriculata*, the sclereids are found to be somewhat more numerous; in this two species some palosclereids and, in the spongy parenchyma, also brachysclereids are found, the latter are mostly confined to the vicinity of the midrib, though in *S. gilgii* they are also found occasionally in other parts of the leaf. In *S. gilgii* the diversity in form is also greater than in the other species; in the vicinity of the leaf margin some large brachysclereids are found (Plate II, Fig. 8), and elsewhere transitions are seen from brachysclereids by the way of ophiurosclereids to librosclereids; librosclereids themselves are also present; none of these types, however, is found in large numbers (Plate II, Fig. 10).

In the second group of species which may be distinguished in the genus *Souroubea*, and which comprises the species *S. bicolor*, *S. crassipes*, *S. didyma*, *S. pachyphylla*, *S. vallicola* and *S. spec.*, Bang 2401, the palisade parenchyma, which in this group consists of two layers of cells, very often contains large palosclereids which are often arranged in rows. Very large palosclereids are found in *S. bicolor* (Plate I, Fig. 2), whereas those of *S. vallicola* have the thickest walls (Plate II, Fig. 1; Plate XV, Fig. 4). The spongy parenchyma of *S. spec.*, Bang 2401,

contains no sclereids at all, that of *S. vallicola* (Plate IV, Fig. 10) and *S. crassipes* rather small astrosclereids, that of *S. pachyphylla* and *S. didyma* contains astrosclereids and transitions to ophiurosclereids (Plate IV, Figs. 11–13, 15) and that of *S. bicolor* big ophiurosclereids (Plate IV, Figs. 9, 14, 22, 23). A transverse section through the leave of *S. vallicola* is given on Plate XV, Fig. 4.

The third group, which comprises the species *S. corallina*, *S. guianensis*, *S. sympetala*, two not yet described species and probably *S. peruviana*, is characterized by the presence of rhizosclereids, usually in rather larger numbers, but sometimes, e.g. in *S. sympetala*, in a small number only. In the spongy parenchyma of the species belonging to this group typical ophiurosclereids and/or librosclereids and transitions between these two types are found (Plate III, Figs. 14–28; Plate IV, Figs. 14, 18–25; Plate XV, Fig. 3).

Within the genus *Norantea* rather considerable differences in the number and shape of the sclereids are encountered. In the leaves of the species belonging to the subgenus *Sacciophyllum*, as well as those of *N. brasiliensis* and of *N. adamantium*, the sclereids are almost entirely limited to a few brachysclereids, sometimes accompanied by a few sclereids of another type in the vicinity of the midrib. This applies also to the species belonging to the subgenus *Pseudostachyum*, although the leaves of some of the species of this subgenus contain a fairly large number of palosclereids.

N. cuneifolia, *N. spiciflora* and *N. jimenensis* occupy an isolated position in this genus. The leaves of *N. cuneifolia* contain numerous palosclereids provided with rudimentary protrusions and showing therefore an approach to rhizosclereids; other kinds of sclereids are lacking. An undescribed species (Cuatrecasas 16618), probably belonging to the genus *Norantea*, resembles *N. cuneifolia* in the structure of the palosclereids, but in its spongy parenchyma large and rather irregular astrosclereidlike sclereids with a wide cell lumen are present which sometimes show an approach to idiosclereids (Plate I, Fig. 2). In *N. jimenezii* the spongy parenchyma contains rather large, irregularly shaped sclereids with disorderly and rather short protrusions and a relative thin wall (Plate I, Fig. 6). This type of sclereid is difficult to include in one of the distinguished categories. In *N. spiciflora* the palosclereids (Plate I, Fig. 7) are remarkable large, and possess a rather wide cell lumen and a thick wall; they vary strongly in size and are several times larger than the surrounding palisade cells; they show a fairly strong resemblance to the palosclereids found in *Souroubea vallicola*. The spongy parenchyma in this species contains a large number of rather densely packed idiosclereids which are oriented perpendicular to the surface (Plate I, Figs. 8, 9); they belong to a type which is well represented in the genus *Marcgravia*.

The subgenus *Marcgraviastrum* differs strongly from the other subgenera of Norantea as to the sclereids. In the leaves of all its species we find a large number of sclereids belonging to at least two types forming a pattern which lend the leaf a characteristic structure (Plate XVI). The leaves of some species, e.g. *N. brenesii*, *N. wed-*

delliana, *N. macrocarpa* and *N. costaricensis* contain rhizosclereids of type 1 as well as astrosclereids or ophiurosclereids (Plate XVI, Fig. 3), those of other species, e.g. *N. obovata*, *N. pendula*, *N. peduncularis*, *N. subsessilis* and *N. sodiroi* contain rhizosclereids of the types 1, 2 and 3, as well as librosclereids, the latter often in two tiers, immediately below the palisade layer and just above the upper epidermis (Plate XVI, Fig. 1). Sometimes, e.g. in *N. subsessilis* and in *N. sodiroi*, the leaves contain astrosclereids or ophiurosclereids and brachysclereids too (Plate XVI, Fig. 2).

The genus *Marcgravia* too contains some groups of species in which the leaves show a characteristic sclereid pattern; however they are less sharply defined than the patterns found in the other genera. The species belonging to these groups often agree in other taxonomical important characters too, but this does not apply to all of them.

Within the section *Orthothalamium* three groups may be distinguished. The first group, which comprises the species *M. angustifolia*. *M. comosa*, *M. crenata*, *M. macrophylla*, *M. magnibracteata*, *M. mexicana*, and *M. spec.*, Skutch 3762 is characterised by the presence of numerous regularly spread or sometimes scattered idiosclereids which are usually elongated and not at all or only slightly ramified, provided with a rather narrow cell lumen and a thick wall and which are oriented perpendicular to the surface of the leaf (Plate XIV, Figs. 1,2).

In the second group which is formed by *M. brownei*, *M. myriostigma*, *M. goudotiana*, *M. schippii* and *M. spec.*, Cuatrecasas 16890 the leaves contain a large number of osteosclereids which are separated from each other by small intervals and which connect the lower epidermis with the upper one as pillars (Plate XIV, Fig. 5).

The third group, which is less uniform than the two other ones, consists of the species *M. flagellaris*, *M. leticiana*, *M. rectiflora*, *M. trinitensis*, *M. spec.*, Aristeguieta 4460, *M. spec.*, Cowan 38207 and *M. spec.* Mexia 7109. Here we usually find a large number of irregularly branched sclereids which form a dense network. *M. rectiflora*, which in other respects agrees well with the species of this group, is provided with sclereids which show a much less differentiated form (Plate IX, Figs. 4, 5); their projections are shorter than those of the sclereids of the other species of the group with the result that these sclereids are quite free from each other; they form, therefore, a pattern which shows a stronger resemblance to that found in the first group. In *M. trinitatis* the sclereids are provided with long branches and projections spreading in all directions; there is a slight indication that part of them are oriented more or less perpendicular to the surface of the leaf, whereas another part runs more or less parallel to the latter (Plate IX, Figs. 6, 7; Plate XI, Fig. 9). In the other species this difference in orientation is more pronounced; the sclereids which are oriented parallel to the surface run mainly in the longitudinal direction of the leaf. The sclereids in these species are all very irregular in form, and remind us of rhizosclereids, ophiurosclereids and librosclereids (Plates X, XI). Together they form a dense tangle in which the individual cells are hardly recognizable (Plate XIV, Figs. 3, 4).

In most of the species belonging to the section *Plagiothalamium* the leaves chiefly contain idiosclereids which although differing in form, size and number, do not form such marked patterns as are found in the section *Orthothalamium*. *M. coriacea* and its allies as e.g. *M. romaimana* and *M. williamsii*, nevertheless form a distinct group. Their sclereids are large, irregularly shaped idiosclereids, provided with a wide cell lumen and many rather long projections (Plate VII, Figs. 9, 13–15). The distances by which they are separated from each other are small, and occasionally, e.g. in *M. coriacea* and in *M. williamsii*, they are arranged more or less in two tiers (Plate XV, Fig. 2). The sclereids of *M. spec.*, Cuatrecasas and Killip 39100, seem to be somewhat longer (Plate VII, Fig. 15), and those of *M. roraimana* are, as a rule, somewhat smaller, provided with lesser and shorter projections and with a narrower cell lumen than the preceeding species.

Among the remaining species of the section *Plagiothalamium* a number have but few or hardly any sclereids in their leaves; those present look more or less like brachysclereids or transitions from the latter to astrosclereids or idiosclereids, and are found near the midrib; if their number is somewhat larger, they may be spread throughout the leaf, and in this case they belong to the category of the idiosclereids (some of the latter are shown in Plate VII, Figs. 5, 6, 10, 11, 12 and 16). To this group of species, which however is not yet thoroughly studied, belong among others the species *M. parviflora*, *M. gracilis*, *M. purpurea*, *M. pedunculosa*, *M. weberbaueri* and *M. eichleriana*. The sclereid pattern of these group remind us, if sclereids are present, of that found in the first group of the section *Orthothalamium*. In a number of species, e.g. *M. evenia*, *M. domingensis*, *M. sintenisii* and *M. lineolata*, the sclereids are somewhat more robust (Plate VII, Figs. 17, 18, and 19), more numerous and therefore nearer to each other. *M. spec.*, Fanshawe and Maguire 23467, differs from the other species by the presence of a pecular type of brachysclereid which is provided with a thin wall and a large cell lumen (Plate VII, Fig. 7); they are rather numerous and regularly distributed in the leaf. Similar sclereids are met with in *M. soropaniana*, but here they are found only in the vicinity of the midrib and here in a small number only. *M. gentlei* has rather characteristic astrosclereids in its leaves; they show a wide cell lumen (Plate VII, Fig. 8); and *M. waferi* differs from the other species in its astrosclereid-like sclereids which, especially in the vicinity of the midrib, are provided with long projections.

Comparison of the foliar sclereids of the Marcgraviaceae with those found in some other families

As already mentioned foliar sclereids are found in a great number of families. In few families however they are such an important feature as in the *Marcgraviaceae*, this is e.g. the case in the *Theaceae* (Wijnaendts Francken, 1890; Pekelharing, 1908; Cavara, 1897;

BEAUVISAGE, 1920; FOSTER, 1944; RAO, 1952; BARUA and WIGHT, 1959; BARUA and DUTTA, 1960; KENG, 1962), the *Proteaceae* (JÖNSSON, 1880; WIJNAENDTS FRANCKEN, 1890; TSCHIRCH, 1881; RAO, 1950b); the Oleaceae (TSCHIRCH, 1881, 1885; KRISHNASWAMY 1942; RAO, 1947, 1948, 1949, 1950a, 1957b; RAO and KULKARNY, 1952; ARZEE, 1953a, b) and the genera *Mouriria* and *Memecylon* of the Melastomataceae (VAN TIEGHEM, 1891; FOSTER, 1946, 1947; SUBRAHMANYAN and RAO, 1949; RAO, 1950b, 1951c, 1957a; MORLEY, 1953; RAO and DAKSHNI, 1963), although in none of these families do they show such a variation in form and pattern as they do in the *Marcgraviaceae*.

Brachysclereids or stone cells are widely distributed and so well known that it is not necessary to give examples.

Astrosclereids are well known too, typical astrosclereids are e.g. those found in the *Nymphaeaceae* (MALAVIYA, 1962).

Ophiurosclereids which show a strong resemblance to those of the *Marcgraviaceae* are found in the leaves of the Proteacea *Isopogon petrophiloides* R. Br. (JÖNSSON, 1880; SOLEREDER, 1899, fig. 173B; ENGLER, 1894, fig. 89C).

Long straight librosclereids as occur in the leaves and the cortex of the shoots of many species of the *Marcgraviaceae* are rare in other families. They are known from the cortex and the leaves of *Pelliciera rhizophorae* Tr. et Pl. (SOLEREDER, 1899; BEAUVISAGE, 1920) and from *Araceae*, especially *Monsteroideae* (VAN TIEGHEM, 1866; RICHTER, 1899; BLOCH, 1947; NICOLSON, 1960). Long filiform sclereids are e.g. known from species of *Mouriria* (FOSTER, 1946, figs. 22–30, 39) and *Memecylon* (RAO, 1951c, 1957a), from *Olea europaea* L. (TSCHIRCH, 1881; ARZEE, 1953a), from species of *Linociera* (RAO, 1957b) and from some *Annonaceae* (RAO and WEE, 1966), but these sclereids are bent and twisted irregularly and usually they run in a criss-cross manner through the leaf. Some authors (e.g. KAUSMANN, 1963) regard this type of sclereids as fibers.

Sclereids which show much resemblance to the idiosclereids found in *Norantea spiciflora* and many species of *Marcgravia* are known from the leaves of a great number of species belonging to different families. These sclereids are often indicated as astrosclereids and sometimes as polymorphic sclereids. This type of sclereid is common in the *Theaceae*; they are found e.g. in various species of the genera *Ternstroemia* (BEAUVISAGE, 1920, figs. 11 and 12) and *Camellia* (TSCHIRCH, 1889, fig. 348; BARUA and WIGHT, 1959, figs. 9 and 10; BARUA and DUTTA, 1960). Other species from which idiosclereid-like sclereids are known are e.g. the Rhizophoracea *Rhizophora conjugata* L. (SOLEREDER, 1899, fig. 74A; METCALF and CHALK, 1950, fig. 133A), the Capparidacea *Niehbuhria apetala* Dunn (RAO and KELKAR, 1951, figs. 1–14), the Proteacea *Leucospermum hypophyllum* R. Br. (RAO, 1950b, fig. 2), the Oleaceae *Linociera macrophylla* Wall and *L. intermedia* Wight (RAO, 1950a, figs. 1–20).

Osteosclereids extending in the leaf from the lower epidermis to the upper one are found in several families where they show a rather great diversity in form and structure. In the leaves of some species

e.g. in the genus *Camellia*, osteosclereids are found together with idiosclereids, whereby the only difference between these types is that the latter do not reach the epidermis (TSCHIRCH, 1889, fig. 348). Species from which foliar osteosclereids are described are e.g. the Theaceae *Camellia thea* Link. (TSCHIRCH, 1889, fig. 348), *C. irrawadiensis* Barue (BARUA and WIGHT, 1959, figs. 1–8, fig. 11), *Gordonia lasianthus* L. (BEAUVISAGE, 1920, fig. 54), *Lacanthea pubescens* L'Hér. (BEAUVISAGE, 1920, fig. 52), and *Schima noronhae* Reinw. (BEAUVISAGE, 1920, fig. 46), the Cornacea *Nyssa caroliniana* Poir. (SOLEREDER, 1899, fig. 99A; METCALF and CHALK, 1950, fig. 174A), the Capparidacea *Capparis odoratissima* Jacq. (SOLEREDER, 1899, fig. 18B; METCALF and CHALK, 1950, fig. 24B), the Oleacea *Olea dioica* Roxb. (KRISHNASWAMY, 1942, figs. 1 and 2; RAO, 1951a, fig. 4; RAO and KULKARNY, 1952, figs. 12, 13 and 17), the Proteacea *Hakea suaveolens* R. Br. (TSCHIRCH, 1881, fig. 23) the Annonacea *Popowia pisocarpa* (Bl.) Endl. and the Melastomataceae *Mouriria cauliflora* DC., *M. pusa* Gardn. and *M. huberi* Gogn. (FOSTER, 1946, figs. 35, 36 and 37; FOSTER, 1947) and *Memecylon scutellatum* (Lour) Naud. and *M. cuneatum* Thw. (RAO, 1957a, figs. 34 and 35). In particular the sclereids found in the leaves of the three species of *Mouriria* mentioned above and in *Schima noronhae* remind us strongly of those found in *Marcgravia brownei* and its allies (Plate XII). In *Olea dioica* the osteosclereids branch at both ends with long projections running under the epidermis.

Palosclereids and rhizosclereids of the kind found in the genera *Ruyschia*, *Souroubea* and *Norantea* are probably rare in other families. Typical palosclereids are found in the leaves of the Oleacea *Nyctanthes arbor-tristis* L. (RAO, 1947, fig. 1; RAO, 1951a, fig. 2). Palosclereids showing a strong resemblance to those figured on Plate I, Fig. 2 are known from the Theacea *Freziera undulata* Sw. (SOLEREDER, 1899, fig. 29B; METCALF and CHALK, 1950, fig. 44B). Palosclereids somewhat extending into the spongy region are described from the leaves of the Ebenacea *Diospyros discolor* Willd. (RAO, 1951b) which sclereids however are developed from initials situated in the spongy region of the leaves. More or less true rhizosclereids, i.e. sclereids of the palisade layer with rootlike projections extending into the spongy parenchyma are met with in the leaves of the Theaceae *Adinandra jackiana* Korth. and *A. dumosa* Jacq. (BEAUVISAGE, 1920, Figs. 21 and 23) and *Cleyera grandiflora* Hook. f. et Thoms. (SOLEREDER, 1899, figs. 29C and D; METCALF and CHALK, 1950, figs. 44C and D).

A remarkable type of 'T' shaped sclereids is described from the leaves of *Olea europaea* L. (ARZEE, 1953a). They have a basal part with the size of a palisade cell in the palisade layer, no projections into the spongy region but two very long projections running underneath the epidermis (ARZEE, 1953a, figs. 4–6 and 8H).

Not only the sclereids but also the sclereid patterns found in many species of *Marcgravia* find a counterpart in those found in species of other families. Several *Theaceae* have a foliar sclereid pattern similar to that found in one or more species of *Marcgravia*. The intricate network of filiform sclereids observed in the leaves of e.g.

Mouriria anomala Pulle and its allies (Foster, 1946, plate VII-IX) and *Olea europaea* L. (Tschirch, 1881, fig. 22; 1885, fig. 31; Arzee, 1953a, figs. 1 and 2) show a superficial resemblance to the patterns of tangled sclereids as are found in *Marcgravia flagellaris* and related species where, however, the sclereids show a greater diversity in form.

The sections through the leaves of *Schima noronhae* Reinw., *Mouriria pusa* Gardn. and *Memecylon scutellatum* (Lour) Naud. and *M. cuneatum* Thw. (Rao, 1957a, figs. 34 and 35) respectively figured by Beauvisage (1920, fig. 46) and Foster (1946, fig. 16), show a striking resemblance in sclereid pattern to *Marcgravia brownei* (Plate XIV, Fig. 5).

The sclereid patterns composed of different types of sclereids as are found in the genera *Ruyschia*, *Souroubea* and *Norantea* subgenus *Marcgraviastrum*, however form a feature confined to the leaves of these *Marcgraviaceae*.

The systematic value of sclereids

Opinions about the systematic value of sclereids found in the literature are rather contradictory and in most cases guardedly formulated. Solereder (1899) and Van Tieghem (1891) adjudged the sclereids to be of value at the specific level. Bailey and Nast (1944) in their study on the *Winteraceae*, point to the instability and variability of internal characters of the leaf and the consequential danger in using them for taxonomic purposes. Morley (1953) made an extensive study of the systematic anatomy of the genus *Mouriria*. He concluded that the great variety of form in the genus and the relative consistency of form within the species make sclereid morphology a very valuable diagnostic character. The more distinct types will sometimes indicate the section and even the species of a specimen. However, owing to the occurrence of like forms in different sections and the tendency of the majority of the species in a section to have much the same sclereid morphology, this character, like most others, cannot be relied upon alone, but must be used in conjunction with one or more other characters. Rao (1957), who contributed very much to our knowledge of foliar sclereids, in his study on *Memecylon* states that though a cautious use of this character is needed, the sclereids should form a part of any thorough taxonomic analysis. Keng (1962) in his study on the anatomy of the *Theaceae* stated that in general the presence or absence and the shape and the size of foliar sclereids seem to be rather constant characters. Species of the same genus, with few exceptions, have essentially similar patterns of sclereids and this similarity is also found among many species of different but related genera. Barua and Dutta (1960) found that three varieties of *Camellia sinensis* are characterised by the form and the number of the foliar sclereids. In these taxa the form of the sclereids appeared to be a useful taxonomic character which appeared to be correlated with the presence or absence of taxonomically important chemical substances. In Camellia the sclereids seem to be a valuable taxonomic character at the specific

as well as at the infra-specific level. NICOLSON (1960) on the contrary found that in the *Monsteroideae* the distribution and frequency of trichosclereids in various organs of a given species may not be constant and that presence or absence of trichosclereids should not be used alone as a diagnostic or key character at any classification level in *Araceae*.

The results of my study of the foliar sclereids of the *Marcgraviaceae* lead to conclusions which in general agree with those of most of the above mentioned authors. In the *Marcgraviaceae* the difference in form and pattern of the sclereids among different specimens of the same species is probably only slight in most species but in some species it may be rather considerable. In only few species, however, could this variation be studied more or less satisfactorily. In *Souroubea guianensis*, a wide spread species, there exists a rather great variation in form and number of the sclereids and especially in the ratio of the different types. The sclereid pattern in this species consists of rhizosclereids combined with ophiurosclereids, librosclereids and transitional forms between the last two categories. There exists a variation in the form and the density of the rhizosclereids and in the ratio between ophiurosclereids and librosclereids which varies from nearly 100% librosclereids to nearly 100% ophiurosclereids. This difference in sclereid pattern is correlated with differences in other characters and therefore can serve as a basis for the subdivision of the species. In some species of the *Marcgraviaceae* the form or structure of the sclereids or the sclereid pattern is so characteristic that the species is easily recognisable by it, but often related species show less difference in form or pattern of the sclereids. The complete variation in form and pattern of sclereids in the species of the *Marcgraviaceae* needs further investigation. A number of groups of species appear to have a similar sclereid pattern which is correlated with other characters. As already mentioned there exist great differences in sclereid forms and patterns between *Marcgravia* and the other genera. In the *Marcgraviaceae* the sclereid pattern forms, in general, a good character in defining species, sections and even genera. However, as it happens in nearly every taxonomic unit, like a section or a genus, that one or more species deviate in this character from the general trend – a phenomenon which may present itself also in other characters – it is advisable to use this character only in combination with others. Taxonomy can never be based on a single character but only on the totality of the characters, an opinion generally accepted but often forgotten in practice. The overestimation of a character, as is done by RICHTER (1920) with regard to the sclereids of the *Marcgraviaceae*, may lead to a highly unnatural classification as is found e.g. in his subdivision of the genus *Norantea*.

Our conclusion must be that it is difficult to ascertain the real value of foliar sclereids as a taxonomic character, especially the value which can be attached to quantitative differences. It is absolutely necessary to have sufficient data about the possible variation of form, frequency and distribution of the sclereids in the leaves of the

individual plant as well as in the species before conclusions can be made. It is still questionable whether and to what extent form, frequency and distribution of sclereids are influenced by environmental factors. To gain a better view and a more funded opinion on this problem it is necessary to know what internal or external factors might play a role, either directly or indirectly, in the initiation and ontogeny of sclereids. It is therefore that experiments as those of FOARD (1958, 1959) and of AL-TALIB and TORREY (1961) are of great interest for the taxonomist too, though they are only the first step towards the solution of the problems.

THE FUNCTION OF FOLIAR SCLEREIDS

A discussion of the problem of the possible functions of foliar sclereids is given by RAO (1957b), to which we also referred for a review of the literature. An excellent treatment of the mechanical functions of sclereids is given by WIJNAENDTS FRANCKEN (1890). In many cases the mechanical function of the sclereids is evident, with regard to the *Marcgraviaceae*, this has already been observed by RICHTER (1920). Sclereid patterns, particularly as figured on the Plates XIV, Figs. 3, 4; XV, Fig. 3 and XVI, Fig. 1–3, give these leaves great strength.

TSCHIRCH (1881) was of the opinion that the presence of foliar sclereids in many species is an adaption of the plants to a dry environment because they help to prevent the deformation of the leaf and especially of the photosynthetic tissue by a temporary desiccation. Examples to illustrate this are found in many *Oleaceae* and *Proteaceae*.

Although the *Marcgraviaceae* are all inhabitants of regions with a wet climate it is not impossible that the above mentioned opinion of Tschirch applies to at least a part of the *Marcgraviaceae* provided with foliar sclereids too. This may be the case in the species which by their epiphytic habitat are exposed to short periods of drought and in the species from e.g. montane rain forests where owing to the low temperature and often strong winds one might speak of a physiological drought. The question of the function of foliar sclereids, however, needs further investigation, both as to the suggested mechanical function and as to possible other functions e.g. that of water storage cells.

EXPLANATION OF PLATES

PLATE I

Sclereids of *Norantea* species. Palosclereids from the palisade parenchyma are figured as they appear to us seen through the epidermis of the cleared leaf and in transverse sections. Fig. 1 — *N. cuneifolia* Delp., Gardner 333, palosclereids.Figs. 2, 5 — *N. spec.*, Cuatrecasas 16618; Fig. 2: palosclereids; Fig. 5: sclereids from the spongy mesophyll. Figs. 3, 4 — *N. spec.*, Phelps & Hitchcock 422; Fig. 3: palosclereids; Fig. 4: sclerified cells from the spongy parenchyma. Fig. 6 — *N. jimenezii* (Standley) de Roon, Standley & Valerio 49160, sclereids from the spongy mesophyll. Figs. 7, 8 — *N. spiciflora* (Juss.) Kr. et Urb., Stehlé 328; Fig. 7: palosclereids; Fig. 8: idiosclereids.

(continued on p. 619)

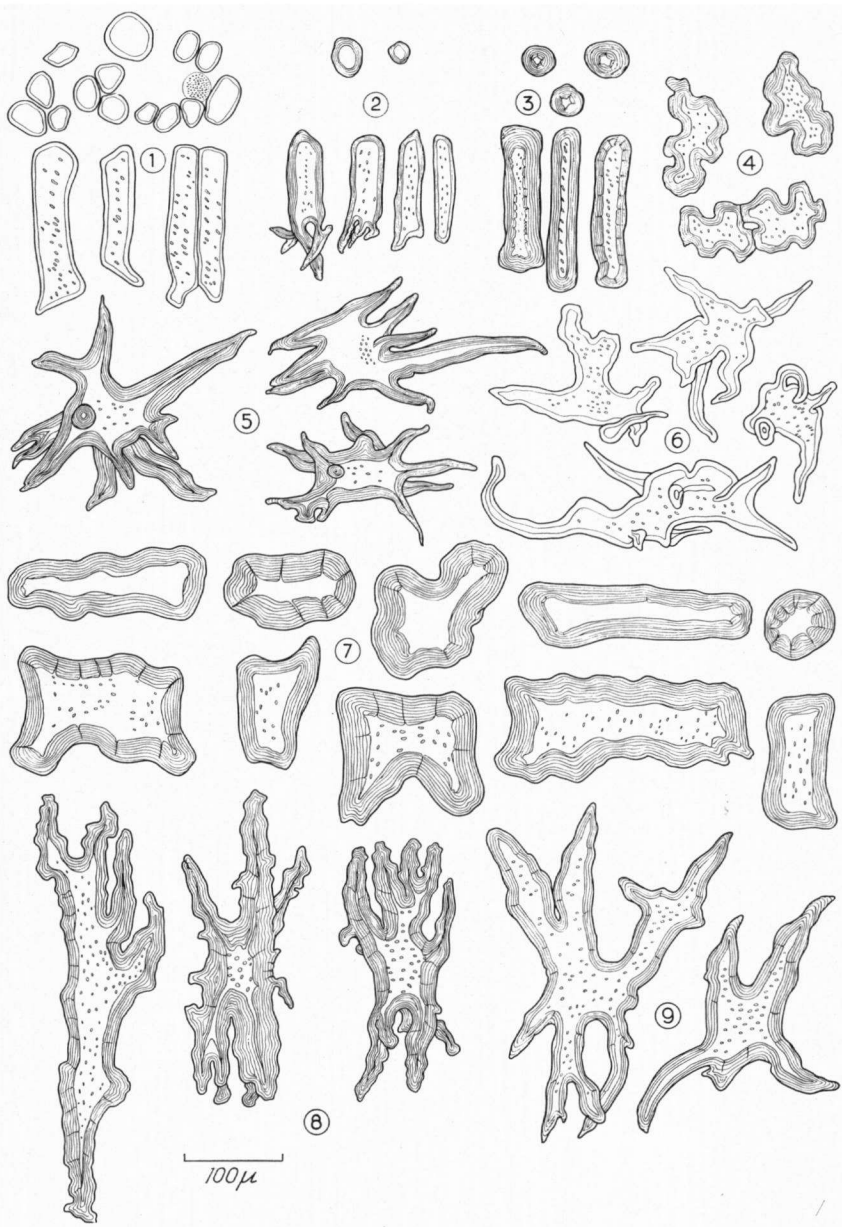

PLATE I Foliar sclereids of Norantea species

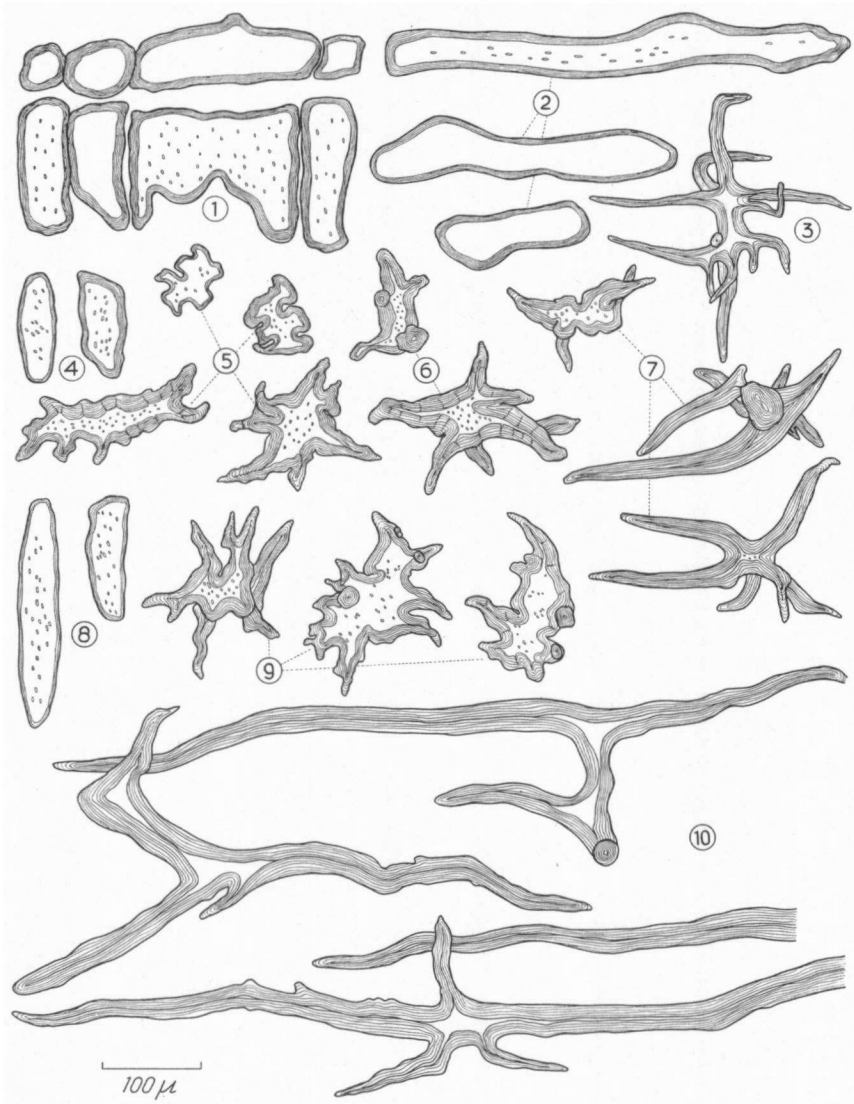

PLATE II Foliar sclereids of Souroubea species

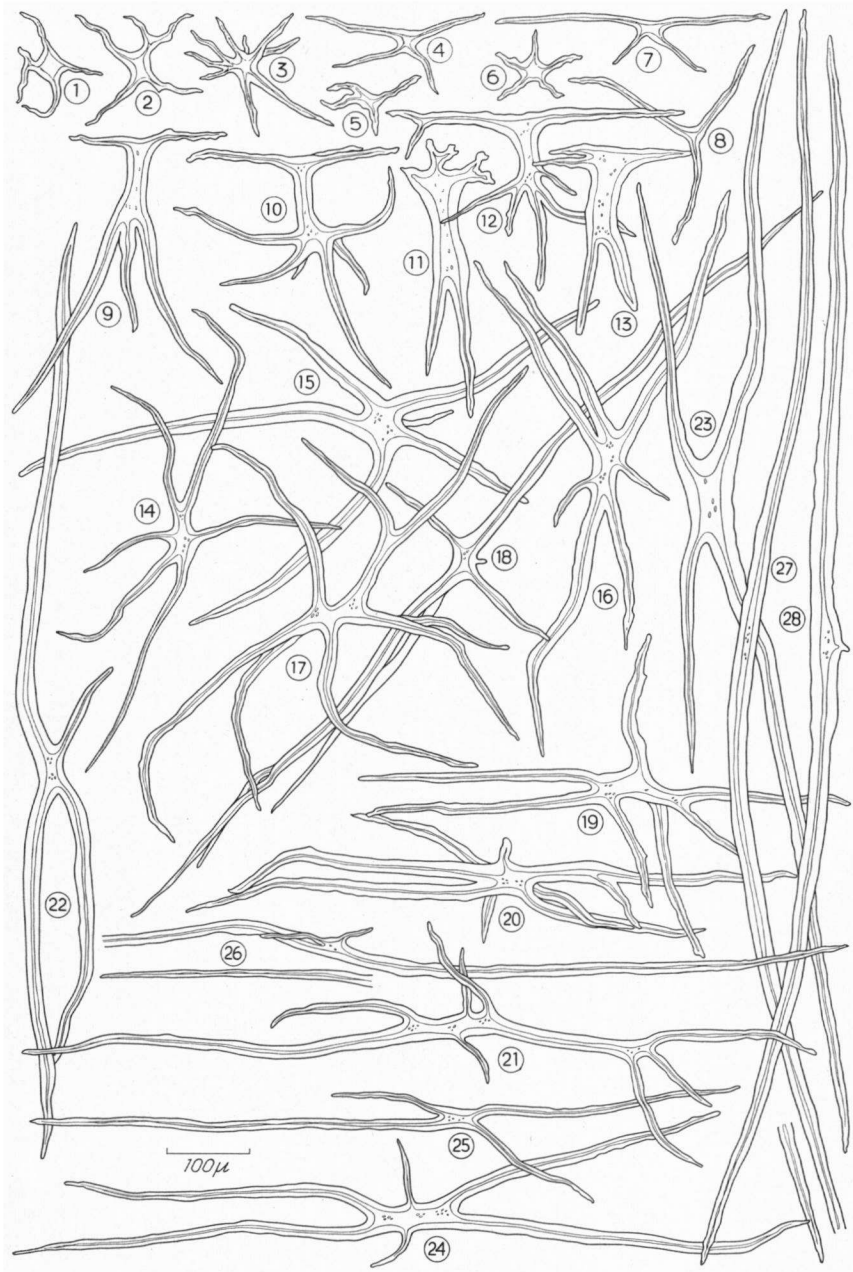

PLATE III Foliar sclereids of Souroubea guianensis

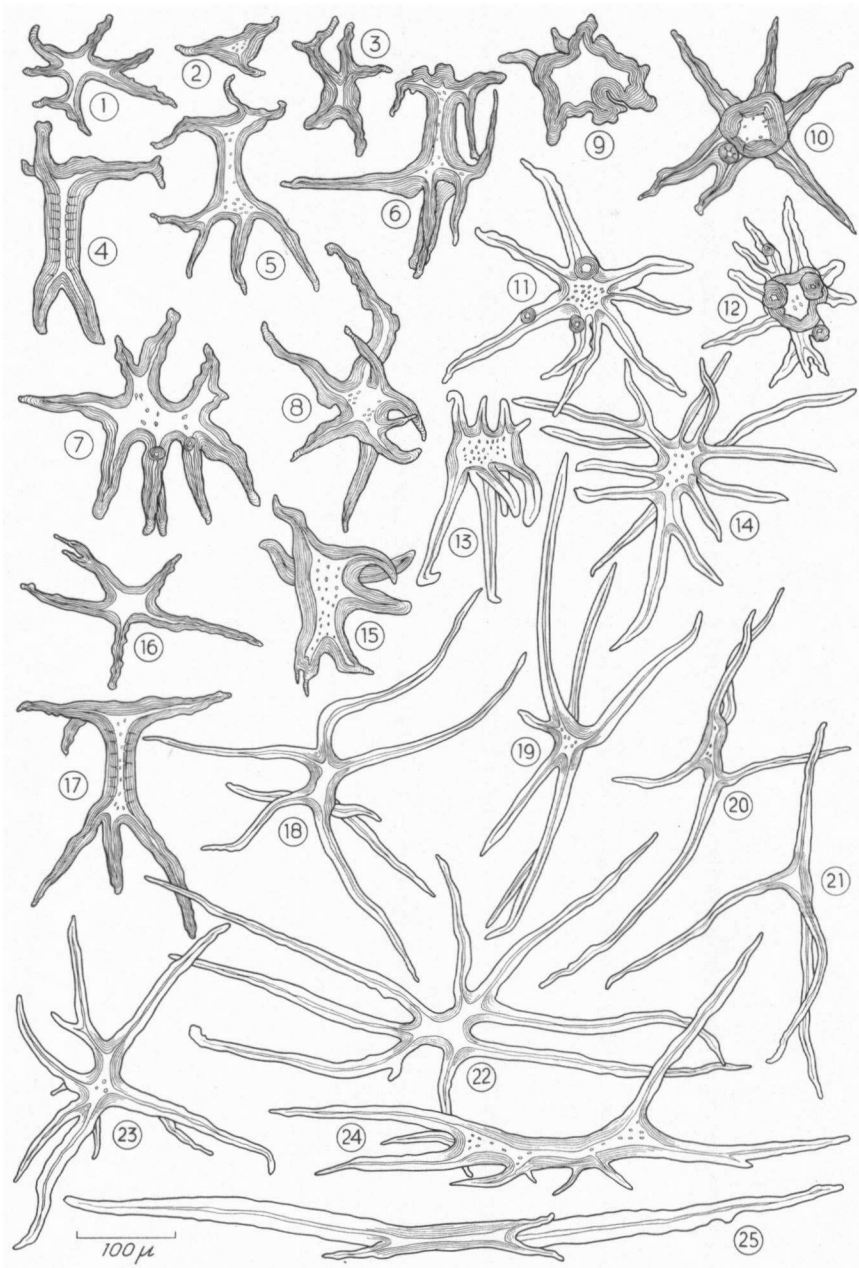

PLATE IV Foliar sclereids of Ruyschia and Souroubea species

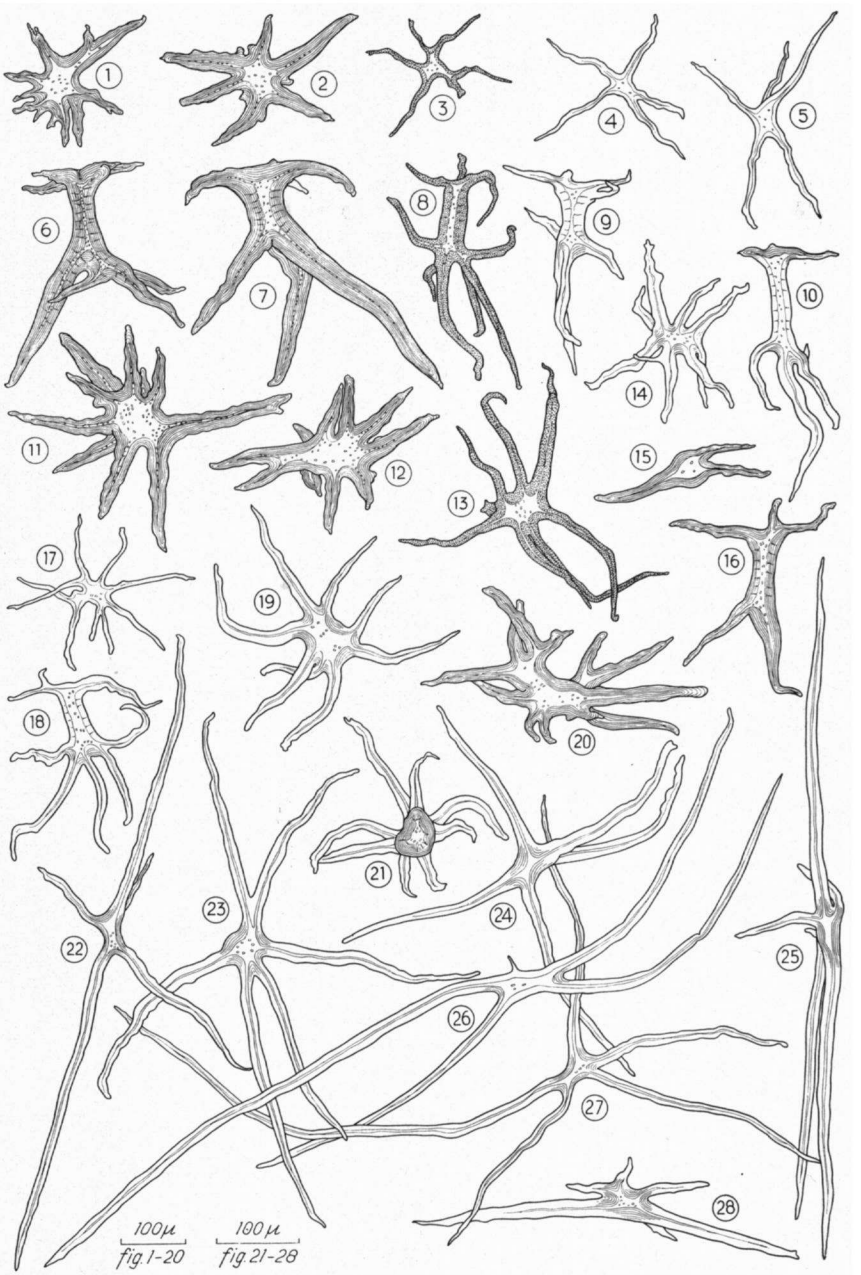

PLATE V Foliar sclereids of species of Norantea subg. Marcgraviastrum

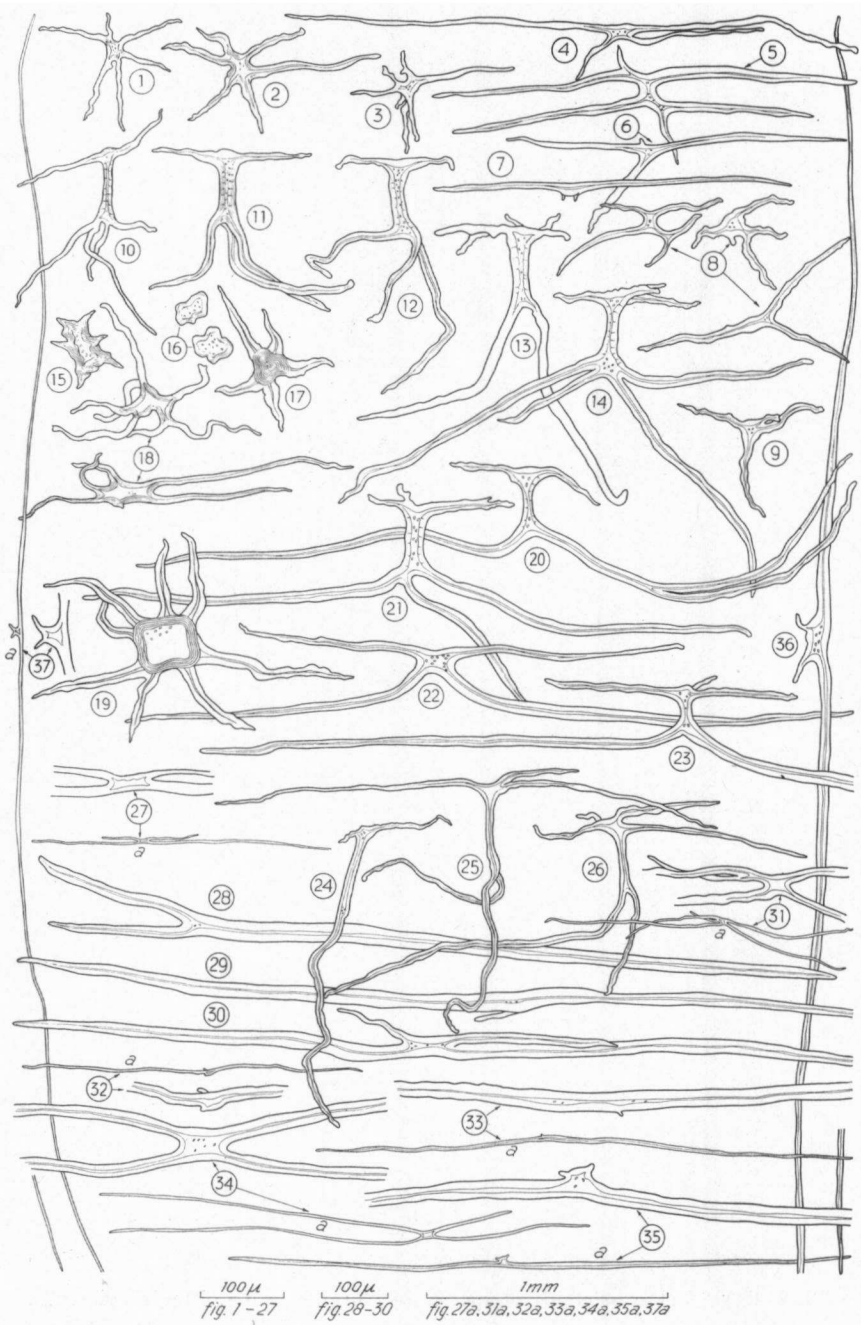

PLATE VI Foliar sclereids of species of Norantea subg. Marcgraviastrum

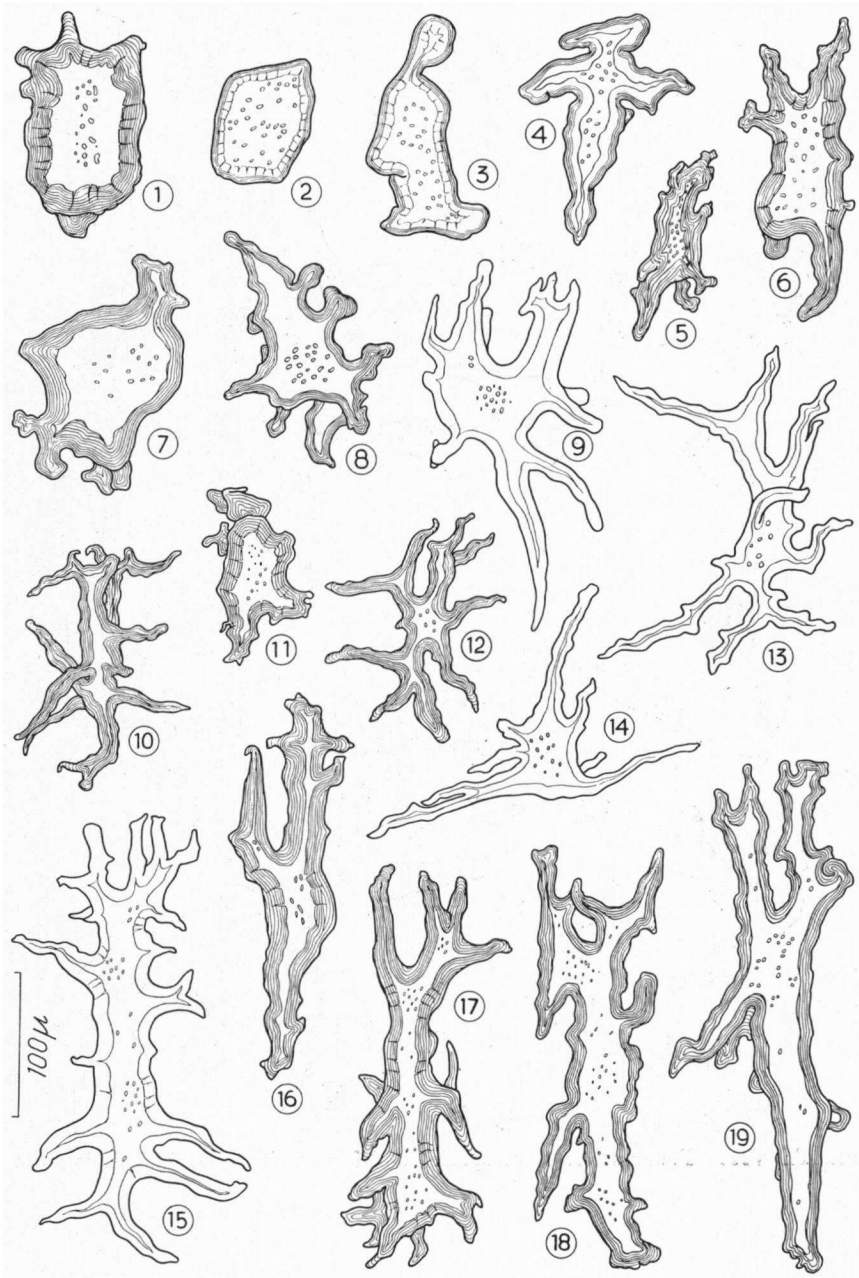

PLATE VII Foliar sclereids of species of Marcgravia sect. Plagiothalamium

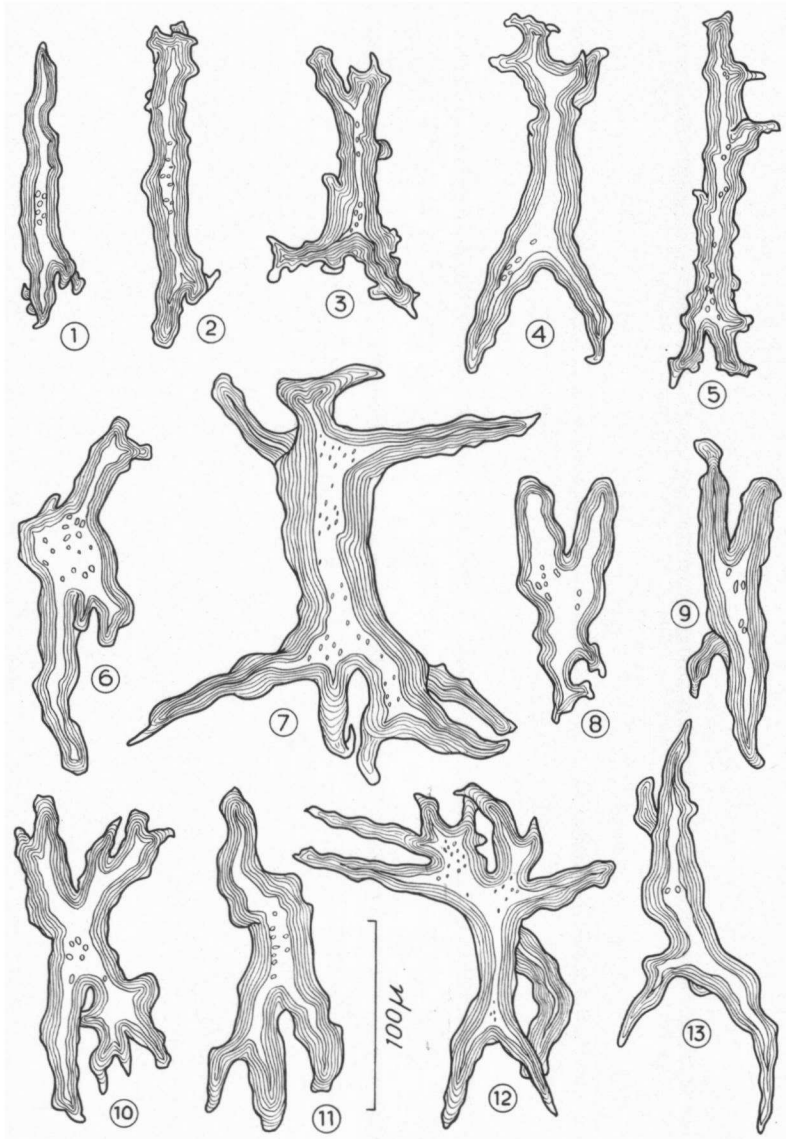

PLATE VIII Foliar sclereids of species of Marcgravia sect. Orthothalamium

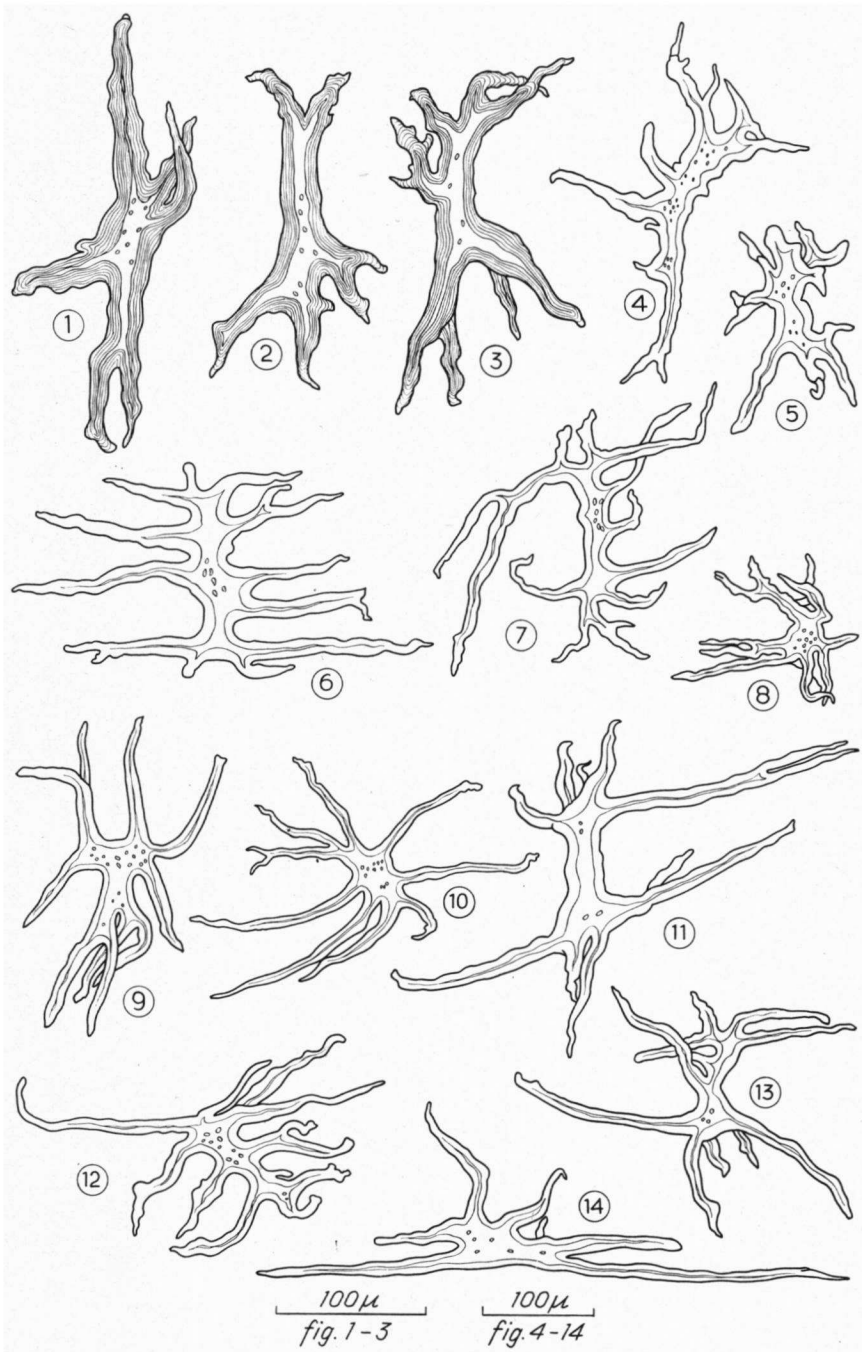

PLATE IX Foliar sclereids of species of Marcgravia sect. Orthothalamium

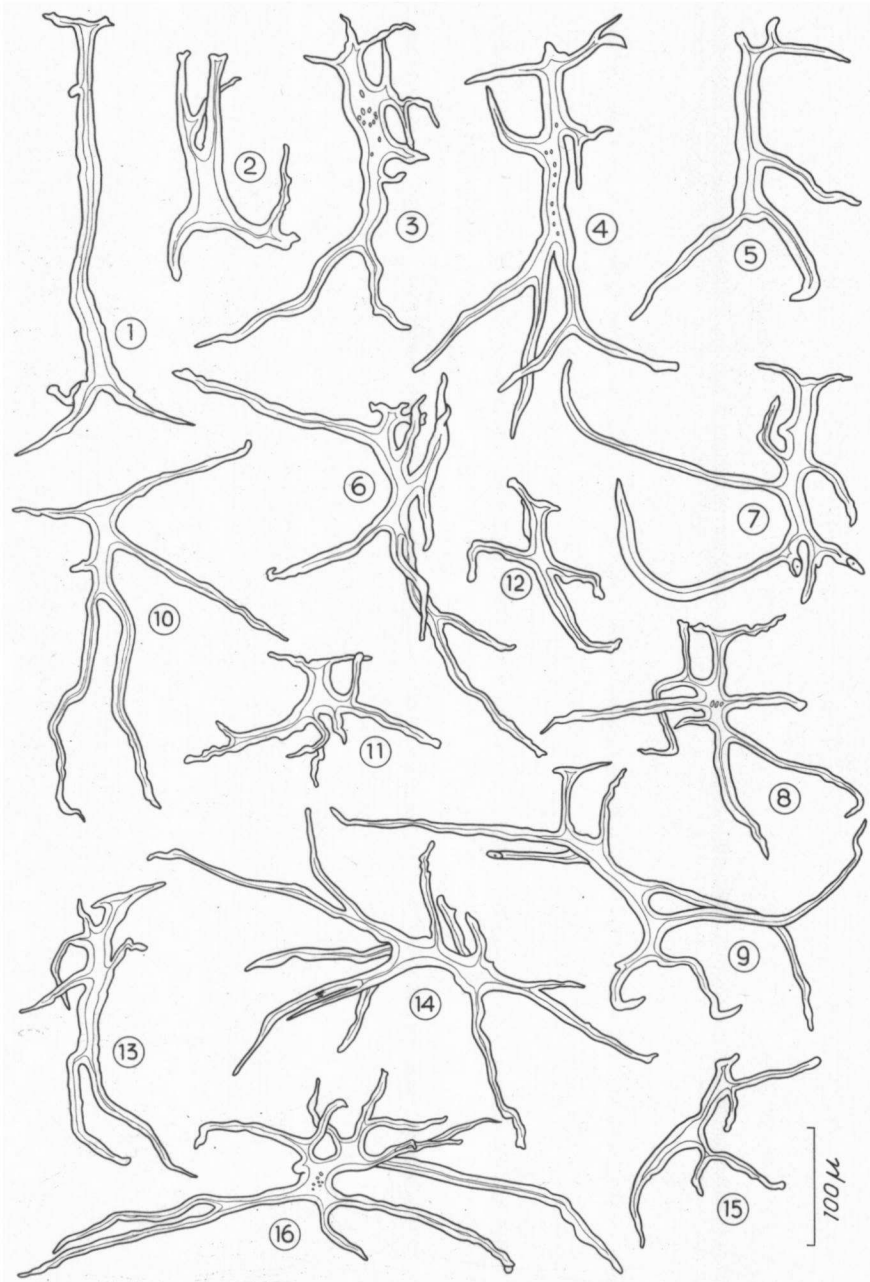

PLATE X Foliar sclereids of species of Marcgravia sect. Orthothalamium

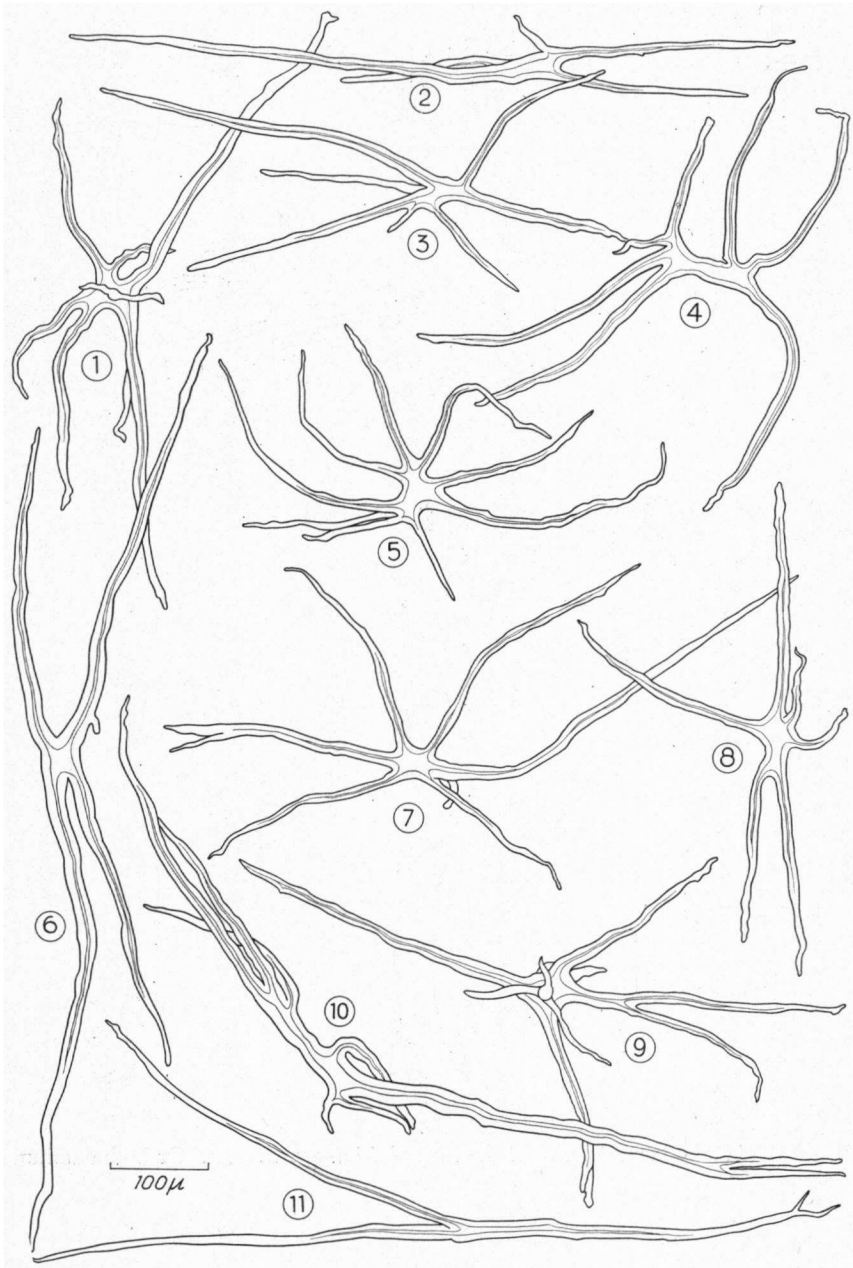

PLATE XI Foliar sclereids of species of Marcgravia sect. Orthothalamium

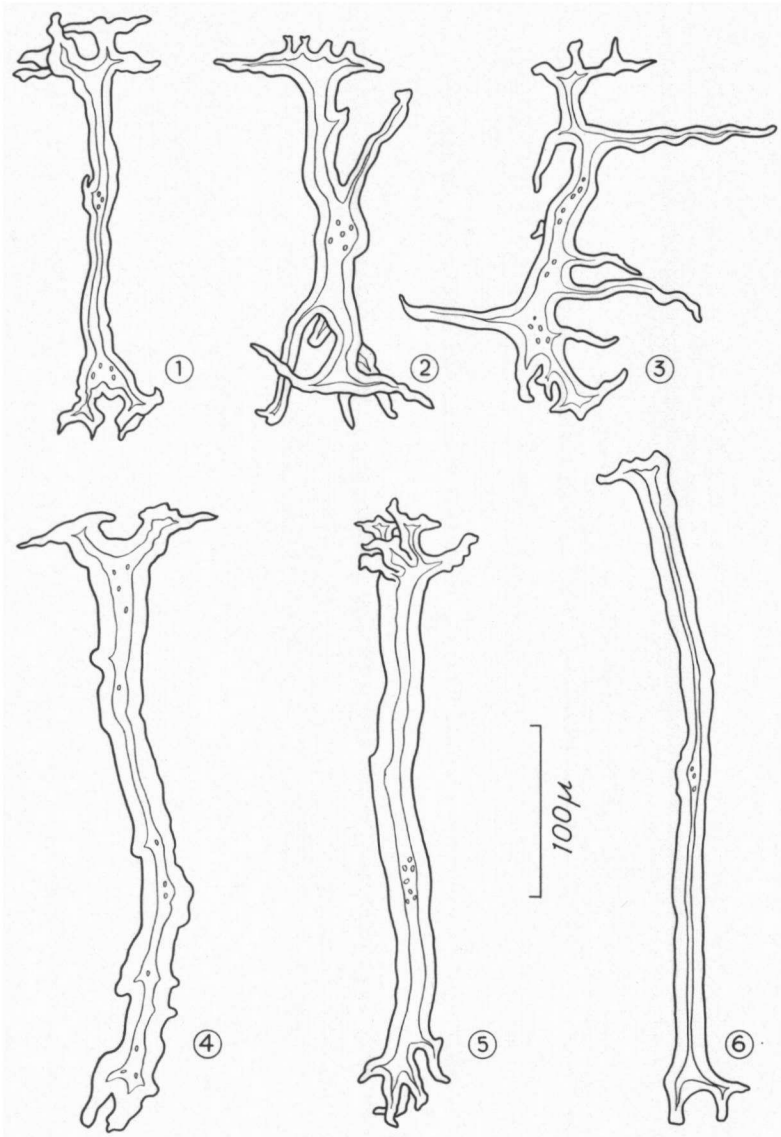

PLATE XII Foliar sclereids of species of Marcgravia sect. Orthothalamium

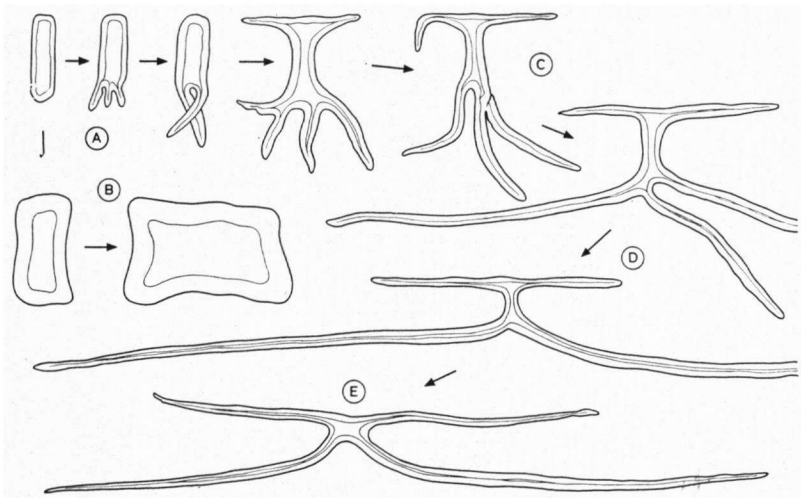

Fig. 1

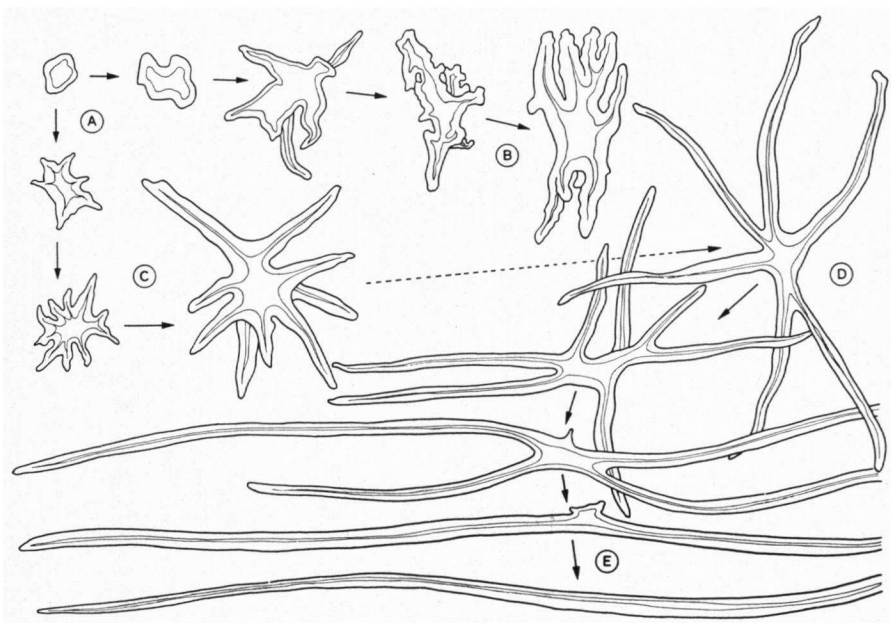

Fig. 2

PLATE XIII Fig. 1. Morphological series showing the derivation of the types of sclereids from the palisade parenchyma in the genera Ruyschia, Souroubea and Norantea. Fig. 2. Morphological series showing the derivation of the types of sclereids from the spongy parenchyma in the genera Ruyschia, Souroubea and Norantea.

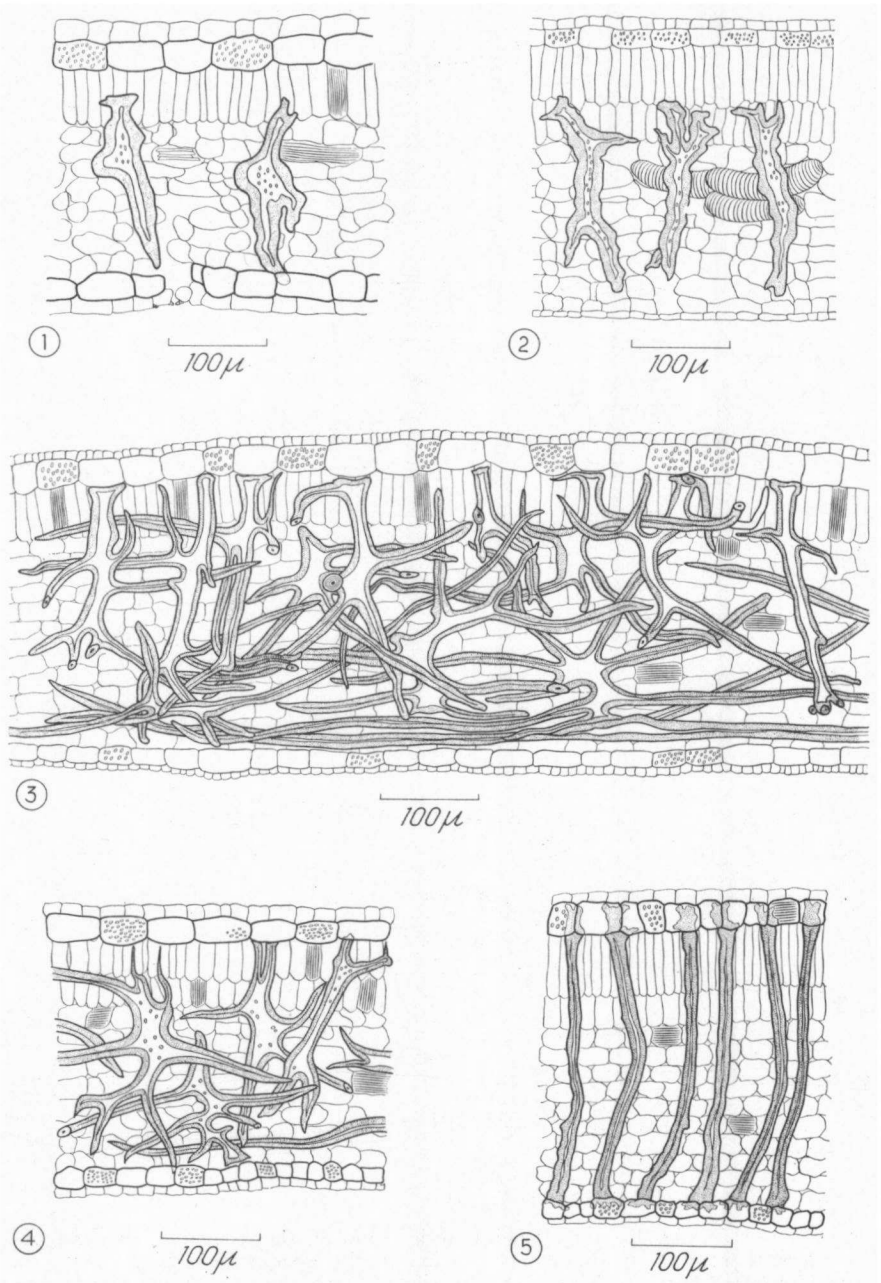

PLATE XIV Transverse sections through the leaves of Marcgravia mexicana (Fig. 1), M. magnibracteata (Fig. 2), M. leticiana (Fig. 3), M. spec. (Fig. 4) and M. brownei (Fig. 5) showing the sclereid pattern. Semidiagrammatic.

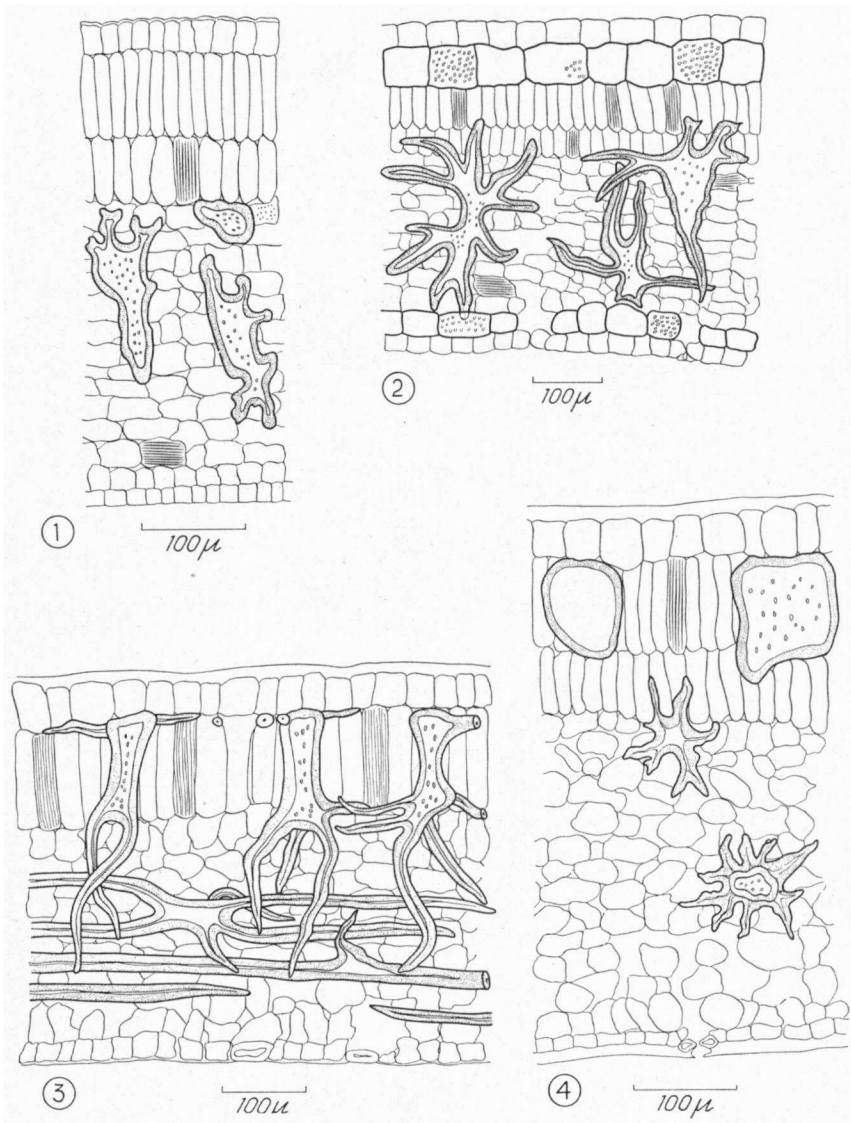

PLATE XV Transverse sections through the leaves of Marcgravia gentlei (Fig. 1,) M. coriacea (Fig. 2), Souroubea guianensis (Fig. 3) and S. vallicola (Fig. 4) showing the sclereid pattern. Semidiagrammatic.

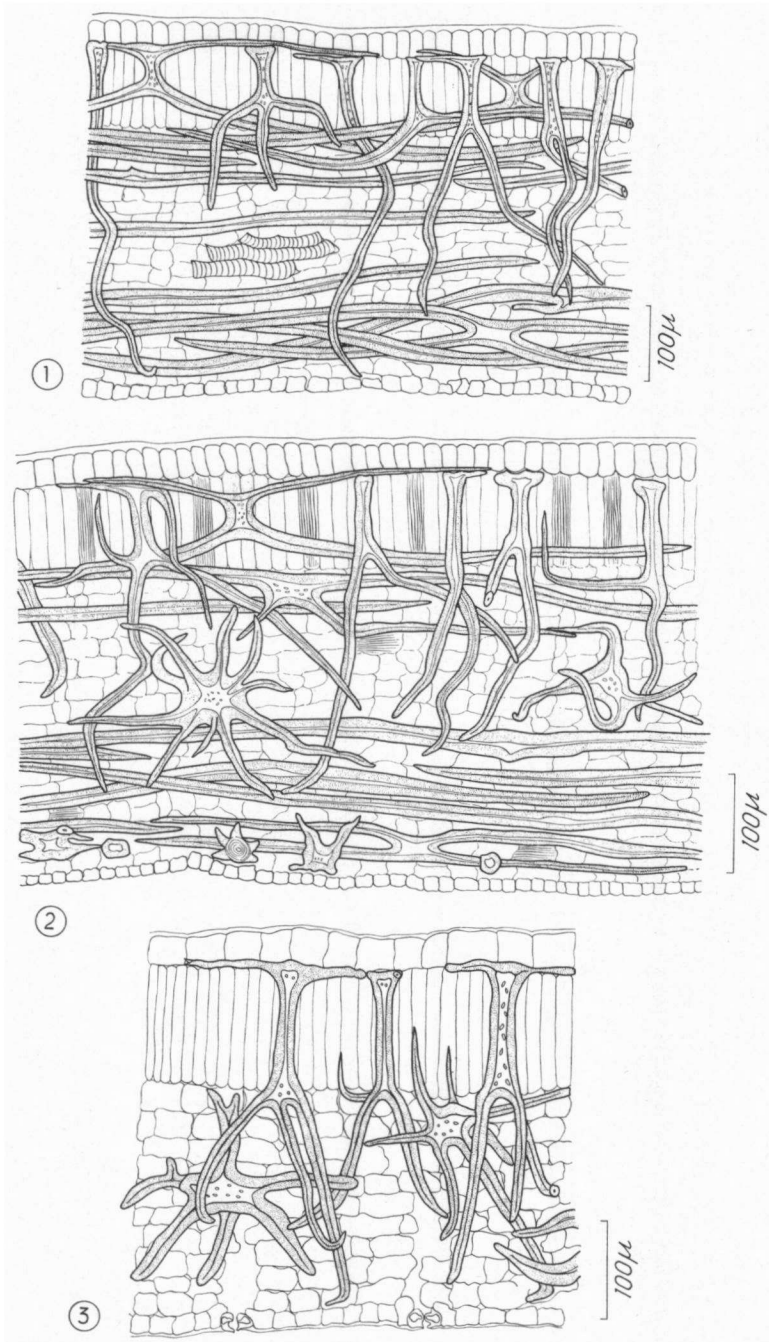

PLATE XVI Transverse sections through the leaves of Norantea peduncularis (Fig. 1), N. sodiroi (Fig. 2) and N. weddelliana (Fig. 3) showing the sclereid pattern. Semidiagrammatic.

EXPLANATION OF PLATES (continued)

PLATE II

Sclereids of *Souroubea* species. Fig. 1 — *S. vallicola* Woodson, Allen 3541, palosclereids shown as they are seen through the upper epidermis of the cleared leaf and in transverse sections. Figs. 2, 3 — *S. bicolor* (Bentham) de Roon, Killip & Garcia 33206; Fig. 2: palosclereids seen through the upper epidermis; Fig. 3: sclereid from the spongy mesophyll. Fig. 4–6 — *S. exauriculata* Delp., Matuda 1853; Fig. 4: sclereids from the marginal region; Figs. 5, 6: sclereids from the spongy mesophyll. Fig. 7 — *S. dasystachya* Gilg, Schunke 20, sclereids from the spongy mesophyll near the midrib. Figs. 8–10 — *S. gilgii* Al. Richter, Woodson 1899, sclereids from the spongy mesophyll; Fig. 8: marosclereids from the marginal region; Fig. 9: irregularly shaped astrosclereid-like sclereids; Fig. 10: librosclereids.

PLATE III

Sclereids of *Souroubea guianensis* Aublet. Selection showing the great variation of form of sclereids within this species. Figs. 1–8 — rhizosclereids seen through the upper epidermis of cleared leaves showing the projections spreading under the epidermis. Figs. 9–13 — rhizosclereids seen in transverse sections. Figs. 14–16 — typical ophiurosclereids. Figs. 17–21 — transitions between ophiurosclereids and librosclereids. Figs. 22–25 — H-shaped librosclereids. Figs. 26–28 — typical librosclereids.

PLATE IV

Sclereids of *Ruyschia* and *Souroubea* species. The rhizosclereids from the palisade parenchyma are figured as seen through the upper epidermis of the cleared leaf, showing the projections underspreading the epidermis (Figs. 1–3, 16) and as seen in transverse sections (Figs. 4–6, 17). The other types are figured as seen in cleared leaves or in macerations. Figs. 1, 4, 7 — *R. pilophora* Tr. et Pl., von Schneidern s.n.; Figs. 1, 4: rhizosclereids; Fig. 7: astrosclereid. Figs. 2, 5 — *R. tremadena* (Ernst) Lundell, Steyermark 55105, rhizosclereids. Figs. 3, 6, 8 — *R. clusiaefolia* Jacq., Duss 278; Figs. 3, 6: rhizosclereids; Fig. 8: astrosclereid. Figs. 9, 14, 22 and 23 — *S. bicolor* (Bentham) de Roon, Killip & Garcia 33206, astro- and ophiurosclereids. Fig. 10 — *S. vallicola* Woodson, Allen 3541, astrosclereid. Figs. 11–13 — *S. pachyphylla* Gilg, Spruce 4469, Ule 6320, Williams 7013, astrosclereids and transitions towards ophiurosclereids. Fig. 15 — *S. didyma* (Wittm.) Gilg, Kanehira 198, astrosclereid. Figs. 16, 17, 24, 25 — *S. spec.*, Krukoff 11037, Gay 843; Figs. 16, 17: rhizosclereids; Figs. 24, 25: librosclereids. Figs. 18–21 — *S. peruviana* (Wittm.) Gilg, Mexica 8310, ophiurosclereids.

PLATE V

Sclereids of species of *Norantea* subg. *Marcgraviastrum*. The rhizosclereids are figured as seen through the upper epidermis of the cleared leaf, showing the projections underspreading the epidermis (Figs. 1–5, 15, 17) and as seen in transverse sections (Figs. 6–10, 16, 18). The other types from the spongy parenchyma are figured as they are seen intransverse sections or in macerations. Figs. 1, 6, 11 — *N. pardoana* Gilg, Uribe Uribe 1953; Figs. 1, 6: rhizosclereids; Fig. 11: astrosclereid. Figs. 3, 8, 13 — *N. brenesii* Gilg, Brenes 5570; Figs. 3, 8: rhizosclereids; Fig. 13: ophiurosclereid. Figs. 4, 9 — *N. brachystachya* (Rusby) de Roon, Williams 1461, rhizosclereids. Figs. 5, 10, 14, 24, 25, 28 — *N. weddelliana* Baillon, Bang 290; Figs. 5, 10: rhizosclereids; Fig. 14: astrosclereid; Fig. 24: ophiurosclereid; Fig. 25: librosclereid; Fig. 28: short librosclereid from the midrib region. Figs. 15, 16, 20 — *N. spec.*, Cuatrecasas 23618; Figs. 15, 16: rhizosclereids; Fig. 20: astrosclereid. Figs. 17–19, 21–23, 26, 27 — *N. macrocarpa* G. Don, Pavon s.n., Nuñez 704; Figs. 17, 18: rhizosclereids; Figs. 19, 21: transitional forms between astro- and ophiurosclereids; Figs. 23, 27: ophiurosclereids; Figs. 22, 26: librosclereids.

PLATE VI

Sclereids of species of *Norantea* subg. *Marcgraviastrum*. The rhizosclereids are figured as seen through the upper epidermis of the cleared leaf, showing the projections underspreading the epidermis (Figs. 1–9) and as seen in transverse sections (Figs.

10–14, 20–26). The other types from the spongy mesophyll are figured as seen in cleared leaves or in macerations. Figs. 1, 4, 10, 15, 27 — *N. sodiroi* Gilg; Acosta Solis 6153; Figs. 1, 4, 10: rhizosclereids; Fig. 15: astrosclereid; Fig. 27: librosclereid. Figs. 2, 5, 11, 16–19, 28–30 — *N. subsessilis* (Bentham) Donn. Smith, Killip & Garcia 33217; Figs. 2, 5, 11: rhizosclereids; Figs. 16: brachysclereids; Figs. 17–19: astro-ophiurosclereids; Figs. 28–30: librosclereids. Figs. 3, 6, 12, 20, 22, 36 — *N. pendula* Lanj. et v. Heerdt, B.W. 5682; Figs. 3, 6, 12: rhizosclereids; Fig. 20: rhizosclereid type 2; Fig. 22: rhizosclereid type 3; Fig. 36: librosclereid. Figs. 7–9, 13, 14, 21, 23, 33–35 — *N. spec.*, Schultes & Cabrera 14931; Figs. 7–9, 13, 14: rhizosclereids; Figs. 21, 23: rhizosclereids type 2; Figs. 33–35: librosclereids. Figs. 24–26, 31, 32 — *N. spec.*, Cuatrecasas 15456; Figs. 24–26: rhizosclereids; Figs. 31, 32: librosclereids. Fig. 37 — *N. spec.*, Killip & Cuatrecasas 39159, librosclereid.

PLATE VII

Sclereids of *Marcgravia* sect. *Plagiothalamium*. All the sclereids are figured as they are seen in transverse sections. Fig. 1 — *M. sororopaniana* Steyerm., Steyermark 60127, brachysclereid. Figs. 2–4 — *M. spec.*, Fagerlind & Wibom 1166B, brachysclereids and idiosclereid from the midrib region. Fig. 5 — *M. spec.*, Steyermark 75089, idiosclereid. Fig. 6 — *M. eichleriana* Wittm., Schultes & Cabrera 10105C, idiosclereid. Fig. 7 — *M. spec.*, Fanshawe & Maguire 23467, brachysclereid. Fig. 8 — *M. gentlei* Lundell, Gentle 3176, astrosclereids. Fig. 9 — *M. williamsii* Macbride, Cuatrecasas 11251, idiosclereid. Figs. 10–12 — *M. spec.*, Core 1545, idiosclereids from the midrib region. Figs. 13–14 — *M. coriacea* Vahl, Archer 7986, idiosclereids. Fig. 15 — *M. spec.*, Killip & Cuatrecasas 39100, idiosclereids. Fig. 16 — *M. spec.*, Fendler 2281, idiosclereid. Fig. 17 — *M. evenia* Kr. et Urb., Alain & Lopez 19646, idiosclereid. Figs. 18, 19 — *M. lineolata* Urb., Box 1941, idiosclereids.

PLATE VIII

Idiosclereids of species of *Marcgravia* sect. *Orthothalamium*. All the sclereids are figured as they are seen in transverse sections. Figs. 1, 2 — *M. angustifolia* Ruiz et Pavon apud López, Pavon s.n. Fig. 3 — *M. crenata* Poeppig ex Wittm., Poeppig 1477. Figs. 4, 5 — *M. magnibracteata* Lanj. et v. Heerdt, B.W. 4119. Figs. 6, 8, 9 — *M. mexicana* Gilg, Wawra 1132. Figs. 7, 10, 12 — *M. comosa* Presl, R.B. 48131. Figs. 11, 13 — *M. spec.*, Skutch 3762.

PLATE IX

Idiosclereids of species of *Marcgravia* sect. *Orthothalamium*. All the sclereids are figured as they are seen in transverse sections. Fig. 1 — *M. spec.*, Skutch 3762. Figs. 2, 3 — *M. macrophylla* (Wittm.) Gilg, Poeppig 2005. Figs. 4, 5 — *M. rectiflora* Tr. et Pl., Sintenis 269. Figs. 6, 7, 11 — *M. trinitatis* Presl, Duss 4629. Figs. 8–13 — *M. oblongifolia* Pavon ex Wittm., Ruiz 157. Fig. 14 — *M. flagellaris* Poeppig ex Wittm., Poeppig 2026.

PLATE X

Idiosclereidlike sclereids of species of *Marcgravia* sect. *Orthothalamium*. All the sclereids are figured as they are seen in transverse sections. They are all oriented more or less vertically and all, except those shown in Figs. 14 and 16, are touching the upper epidermis. Figs. 1–4, 16 — *M. spec.*, Cowan 38207. Fig. 5 — *M. spec.*, Mexia 7109. Figs. 7–9 — *M. leticiana* (Macbr.) de Roon, Krukoff 8491, Kuhlmann 1248. Figs. 10–15 — *M. flagellaris* Poeppig ex Wittm., Poeppig 2026, Ule 5635.

PLATE XI

Ophiurosclereid- and librosclereid-like sclereids from the spongy parenchyma of species of *Marcgravia* sect. *Orthothalamium*. All the sclereids are figured as they are seen in cleared leaves or in macerations. They are oriented parallel to the epidermis. Figs. 1, 2, 5–7 — *M. flagellaris* Poeppig ex Wittm., Poeppig 2026, Ule 5635. Figs. 3, 11 — *M. leticiana* (Macbr.) de Roon, Krukoff 8491, Kuhlmann 1248. Figs. 4, 10 — *M. spec.*, Mexia 7109. Fig. 8 — *M. spec.*, Aristeguieta 4460. Fig. 9 — *M. trinitatis* Presl, Duss 4629.

PLATE XII
Osteoclereids of species of *Marcgravia* sect. *Orthothalamium*. All the sclereids are figured as they are seen in transverse sections. Figs. 1, 4 — *M. brownei* (Tr. et Pl.) Kr. et Urb., Williams 10435, Killip 5577. Figs. 2, 3 — *M. goudotiana* (Tr. et Pl.) de Roon, Goudot s.n. Fig. 5 — *M. myriostigma* Tr. et Pl., Cuatrecasas 15597. Fig. 6 — *M. spec.*, Cuatrecasas 16890.

PLATE XIII
Morphological series showing the derivation of the types of sclereids from the palissade parenchyma (Fig. 1) and the spongy parenchyma (Fig. 2) in the genera *Ruyschia*, *Souroubea* and *Norantea*. Figs. 1A and B: palosclereids; C: rhizosclereid type 1; D: rhizosclereid type 2; E: rhizosclereid type 3. Figs. 2A: brachysclereid; B: idiosclereid; C: astrosclereid; D: ophiurosclereid; E: librosclereid.

PLATE XIV
Transverse sections through the leaves of *Marcgravia* species showing the sclereid pattern. Semidiagrammatic. Fig. 1 — *M. mexicana* Gilg. Fig. 2 — *M. magnibracteata* Lanj. et v. Heerdt. Fig. 3 — *M. leticiana* (Macbr.) de Roon. Fig. 4 — *M. spec.*, Aristeguieta 4460. Fig. 5 — *M. brownei* (Tr. et Pl.) Kr. et Urb.

PLATE XV
Transverse sections through leaves of *Marcgravia* and *Souroubea* species showing the sclereid pattern. Semidiagrammatic. Fig. 1 — *M. gentlei* Lundell. Fig. 2 — *M. coriacea* Vahl. Fig. 3 — *S. guianensis* Aubl. Fig. 4 — *S. vallicola* Woodson.

PLATE XVI
Transverse sections through leaves of *Norantea* species showing the sclereid pattern. Semidiagrammatic. Fig. 1 — *N. peduncularis* Poeppig ex Wittm. Fig. 2 — *N. sodiroi* Gilg. Fig. 3 — *N. weddelliana* Baillon.

REFERENCES

AL-TALIB, KHALIL H. and JOHN G. TORREY. 1961. Sclereid distribution in the leaves of Pseudotsuga under natural and experimental conditions. Am. Jour. Bot. **48**: 71–79.

ARZEE, TOVA. 1953a. Morphology and ontogeny of foliar sclereids in Olea europaea. I. Distribution and structure. Am. Jour. Bot. **40**: 680–687.

———. 1953b. Morphology and ontogeny of foliar sclereids in Olea europaea. II. Ontogeny. Am. Jour. Bot. **40**: 745–752.

BAILEY, I. W. and CHARLOTTE G. NAST. 1944. The comparative morphology of the Winteraceae. V. Foliar epidermis and sclerenchyma. Jour. Arnold Arb. **25**: 342–348.

BARUA, P. K. and W. WIGHT. 1959. Leaf sclereids in the taxonomy of Thea Camellias. I. Wilson's and related Camellias. Phytomorphology **8**: 257–264.

——— and A. C. DUTTA. 1960. Leaf sclereids in the taxonomy of Thea Camellias – II. Camellia sinensis L. Phytomorphology **9**: 372–382. 1959.

BEAUVISAGE, L. 1920. Contribution à l'étude anatomique de la famille des Ternstroemiaceae. Thèse. Poitiers.

BLOCH, R. 1946. Differentiation and pattern in Monstera deliciosa. The idioblastic development of trichosclereids in the air root. Am. Jour. Bot. **33**: 544–551.

CARLQUIST, SHERWIN. 1961. Comparative Plant Anatomy. New York.

CAVARA, F. 1897. Contributo alla morfologia ed alla sviluppo degli idioblasti delle Camelliee. Atti Ist. Bot. Pavia **4**: 61–87.

ENGLER, A. 1894. Proteaceae in Engler and Prantl, Die natürl. Pflanzenfam. III, **1**: 119–156.

ESAU, K. 1953. Plant Anatomy. New York.

FOARD, DONALD E. 1958. An experimental study of sclereid development in the leaf of Camellia japonica. Plant Physiol. **33** (suppl.): xli.

FORD, DONALD E. 1959. Pattern and control of sclereid formation of Camellia japonica. Nature **184**: 1663–1664.
FOSTER, A. S. 1944. Structure and development of sclereids in the petiole of Camellia japonica L. Bull. Torrey Bot. Club **71**: 302–326.
———. 1945a. The foliar sclereids of Trochodendron aralioides Sieb. and Zucc. Jour. Arnold Arb. **26**: 155–162.
———. 1945b. Origin and development of sclereids in the foliage leaf of Trochodendron aralioides Sieb. and Zucc. Am. Jour. Bot. **32**: 456–468.
———. 1946. Comparative morphology of the foliar sclereids in the genus Mouriria Aubl. Jour. Arnold Arb. **27**: 253–271.
———. 1947. Structure and ontogeny of the terminal sclereids in the leaf of Mouriria huberi Cogn. Am. Jour. Bot. **34**: 501–5–4.
———. 1949. Practical Plant Anatomy. New York.
———. 1955a. Comparative morphology of the foliar sclereids in Boronella Baill. Jour. Arnold Arb. **36**: 189–198.
———. 1955b. Structure and ontogeny of terminal sclereids in Boronia serrulata. Am. Jour. Bot. **42**: 551–560.
———. 1956. Plant idioblasts: remarkable examples of cell specialisation. Protoplasma **46**: 184–193.
GAUDET, JOHN. 1960. Ontogeny of foliar sclereids in Nymphaea odorata. Am. Jour. Bot. **47**: 525–532.
JÖNSSON, B. 1880. Bidrag till kännedomen om bladets anatomiska byggnad hos Proteaceerna. Lund.
KAUSSMANN, B. 1963. Pflanzenanatomie. Jena.
KENG, H. 1962. Comparative morphological studies in Theaceae. Univ. Calif. Publ. Bot. **23**: 269–383.
KITAMURA, R. 1956. Development of foliar sclereids in Sciadopitys verticillata Sieb. et Zucc. Bot. Magazine (Tokyo) **69**: 519–523.
MALAVIYA, M. 1962. A study of sclereids in three species of Nymphaea. Proc. Indian Acad. Sci. **B 56**: 232–236.
———. 1963a. Study of sclereids in Nymphoides cristatum (Roxb.) O. Kuntz. Proc. Indian Acad. Sci. **B 57**: 223–229.
———. 1963b. On the distribution, structure and ontogeny of stone-cells in Avicennia officinalis Linn. Proc. Indian Acad. Sci. **B 58**: 45–50.
MIA, A. J. 1964. Ontogeny and differentiation of sclereids in Rauwolfia. Am. Jour. Bot. **51**: 78–87.
MELCHIOR, H. 1925. Theaceae in Engler, Die natürl. Pflanzenfam. ed. 2, **21**: 109–154.
METCALF, C. R. and L. CHALK. 1960. Anatomy of the Dicotyledons. Oxford.
MORLEY, T. 1953. The genus Mouriri (Melastomataceae): a sectional revision based on anatomy and morphology. Univ. Calif. Publ. Bot. **26**: 223–312.
NICOLSON, DAN H. 1960. The occurrence of trichosclereids in the Monsteroideae (Araceae). Am. Jour. Bot. **47**: 598–602.
PEKELHARING, N. R. 1908. Systematisch-anatomisch onderzoek van den bouw der bladschijf in de familie der Theaceae. Diss. Groningen.
RAO, A. N. and WEE YEOW CHIN. 1966. Foliar sclereids in certain members of Annonaceae and Myristicaceae. Flora **B 156**: 220–231.
RAO, T. ANANDA. 1947. On the occurrence of sclerosed palisade cells in the leaf of Nyctanthes arbor-tristis L. Curr. Sci. **16**: 122–123.
———. 1949. Foliar sclereids in the Oleaceae. 1. On the occurrence of sac-like spicular cells in the leaf of Schrebera swietennoides Roxb. Jour. Indian Bot. Soc. **28**: 251–254.
———. 1950a. Foliar sclereids in the Oleaceae. 2. Occurrence of terminal foliar sclereids in some species of the genus Linociera Swartz. Jour. Indian Bot. Soc. **29**: 220–224.
———. 1950b. Studies on the foliar sclereids in Dicotyledons (2). On sclereids in species of Leucospermum (Proteaceae), Mimusops (Sapotaceae) and Memecylon (Melastomataceae). Jour. Univ. Bombay **19**: 25–31.
———. 1951a. Studies on foliar sclereids. A preliminary survey. Jour. Indian Bot. Soc. **30**: 28–39.
———. 1951b. Studies on foliar sclereids in Dicotyledons I. Structure and

ontogeny of sclereids in the leaf of Diospyros discolor Willd. Proc. Indian Acad. Sci. **B 34**: 92–98.

RAO, T. ANANDA. 1951c. Studies on foliar sclereids in Dicotyledons V. Structure and development of the terminal sclereids in the leaf of Memecylon heyneanum Benth. Proc. Indian Acad. Sci. **B 34**: 329–334.

————. 1952. Studies on foliar sclereids in Dicotyledons IV. Structure and development of sclereids in the leaf of Ternstroemia japonica L. Proc. Nat. Inst. Sci. India **18**: 233–239.

————. 1957a. Comparative morphology and ontogeny of foliar sclereids in seed plants. I. Memecylon L. Phytomorphology **7**: 306–330.

————. 1957b. Comparative morphology and ontogeny of foliar sclereids in seed plants. II. Linociera Swartz. Proc. Nat. Inst. Sci. India **23 B**: 152–164.

———— and K. M. M. DAKSHNI. 1963. Systematics of Memecylon. A preliminary survey based on the slereid morphology. Proc. Indian Acad. Sci. **B 58**: 28–35.

———— and S. S. KELKAR. 1951. Studies on foliar sclereids in Dicotyledons III. On sclereids in species of Loranthus (Loranthaceae) and Niebuhria apetala (Capparidaceae). Jour. Univ. Bombay **20** (**3**) **B**: 16–20.

———— and G. Y. KULKARNY. 1952. Foliar sclereids in the Oleaceae. III. Ontogeny of the sclereids in two species of the genus Olea L. Jour. Univ. Bombay **20** (**5**) **B**: 52–57.

———— and K. J. MODY. 1961. On terminal sclereids and tracheoid idioblasts. Proc. Indian Acad. Sci. **B 53**: 257–262.

———— and M. MALAVIYA. 1962. The distribution, structure and ontogeny of sclereids in Dendropthae falcata (L.f.) Ettings. Proc. Indian Acad. Sci. **B 55**: 239–243.

RICHTER, ALADÁR. 1899. Adatok a Marcgraviaceae és az Aroideae physiologiai-anatomiai és systematikai ismeretéhez. (Beiträge zur physiologisch-anatomischen und systematischen Kenntnis der Marcgraviaceen und Aroideen). Természetrajzi Füzetek **22**: 27–87.

————. 1916. A Marcgraviaceae néhány új alakjaról, a származásés az összehasonlitó alkattan alapjan (Über einige neuere Formen der Marcgraviaceen auf entwicklungsgeschichtlicher und vergleichend-organologischer Grundlage). Math. Term. Értesitö **34**: 551–586, 801–820, 821–839.

————. 1917. Két ritka Norantea philogeniájárol. (Über die Phylogenie zwei seltener Norantea Arten). Math. Term. Értesitö **35**: 159–184.

————. 1920. Über einige neue Glieder der Marcgraviaceen, auf Basis der Phylogenie und der vergleichende Anatomie. Math. Naturw. Berichte Ungarn **31**: 65–146.

SACHS, J. 1874. Lehrbuch der Botanik. Vierte Auflage. Leipzig.

SOLEREDER, H. 1899. Systematische Anatomie der Dikotyledonen. Stuttgart.

STERLING, CLARENCE. 1947. Sclereid formation in the shoot of Pseudotsuga taxifolia. Am. Jour. Bot. **34**: 45–52.

TIEGHEM, PH. VAN. 1866. Recherches sur la structure des Aroidéés. Ann. Sc. Nat., **Sér. 5, 6**: 72–210.

————. 1891. Sur la structure et les affinités des Mémécylées. Ann. Sc. Nat. **Sér. 7, 13**: 23–91.

TOMLINSON, P. B. 1959. Structure and distribution of sclereids in the leaves of palms. New Phytol. **58**: 253–266.

TUCKER, SHIRLEY C. 1964. The terminal idioblasts in Magnoleaceous leaves. Am. Jour. Bot. **51**: 1051–1062.

TSCHIRCH, A. 1881. Ueber einige Beziehungen des anatomischen Baues der Assimilationsorgane zu Klima und Standort, mit spezieller Berücksichtigung des Spaltöffnungsapparates. Linnaea **43**: 139–252.

————. 1885. Beiträge zur Kenntniss des mechanischen Gewebesystems der Pflanzen. Jahrb. Wiss. Bot. **16**: 303–335.

————. 1889. Angewandte Pflanzenanatomie. Wien und Leipzig.

WIJNAENDTS FRANCKEN, C. J. 1890. De sclereiden. Diss. Utrecht.