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BY

CLIVE A. STACE
(University of Manchester)

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CUTICULAR STUDIES AS AN AID TO PLANT TAXONOMY

By CLIVE A. STACE

This review is an account of the systematic value of the epidermal characters of angiosperm leaves as they are seen on preparations of the cuticular membrane, and is based on a detailed study of about 250 species belonging to three families. The introductory sections outline the history of the taxonomic use of cuticular and epidermal characters, the anatomical background of the features observed on cuticular membranes, the methods employed in the isolation and mounting of the latter, and a suggested routine for their formal description. The main part of the work comprises a somewhat detailed account of the cuticular characters which have been found to be useful in identification and taxonomy, and of the variability that some of these exhibit in various conditions. The precautions necessary in the use of such characters are stressed. In the final section the place of cuticular characters in modern taxonomic work is discussed.

It is hoped that these comments will help to place the systematic use of the epidermis upon a firmer and more scientific basis than has hitherto been the case.

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I am indebted to the Keeper of Botany, British Museum (Natural History), for providing laboratory, library and herbarium facilities for the pursuit of this work, and to Dr. A. W. Exell for his very considerable help and valuable discussion at all stages. I am also grateful to those members of the Departments of Botany and Palaeontology, British Museum (Natural History), who have helped me with several problems, and to Mr. G. Grange, Department of Botany, University of Manchester, for preparing the photomicrographs.

References (by author and date) given in the text are to the list of Special Literature at the end of the paper.

§1. Preface

Plant taxonomy has undergone a great many changes since it was first treated as a scientific discipline in the seventeenth century, one of the major contributing factors being the discovery of the use of new fields of investigation to supplement the old. The ultimate aims of the majority of taxonomists have naturally also changed, the original hope of cataloguing every species of plant now embracing the idea that their evolutionary and genetic interrelationships should also be expressed. I accept that taxonomists should aim at devising " natural " classifications which attempt to indicate the phylogenetic position of each basic unit, although it seems to me certain that this goal will be in sight only when the genetical constitution of each taxon is known and can be expressed with something approaching the precision of a chemical formula, towards which the present binomial system of nomenclature is no more than a preliminary step.

Prior to the latter part of the nineteenth century taxonomists used only morphological (i.e. macroscopic) characters in their studies, and apart from the inclusion of the broadest vegetative features they confined themselves to the reproductive organs. It was not until about 1865 that anatomical (i.e. microscopic) characters were first used, and considerably later that this became usual practice. The volumes of Engler & Prantl's *Die natürlichen Pflanzenfamilien* (1887–1915) included a relatively large amount of anatomical and vegetative morphological details, and since then taxonomic monographs have been considered incomplete without them. Modern workers are constantly employing new diagnostic characters, and work of this kind will need to continue until every structural, physiological and biochemical feature has been utilized.

Parts of the plant which have been most successfully investigated from an anatomical rather than morphological viewpoint include the wood, primary vascular system, laticifer systems, crystals, epidermis (including stomata and trichomes), floral vascular supply, sclerenchyma, pollen-grains and chromosomes. A further group of characters, such as colour, chromosomal behaviour during meiosis, antigen-antibody reactions and chromatographic analyses of various chemical constituents, in fact represent plant structure at a third (i.e. sub-microscopic) level : that of the molecule. Only a synthesis of all this and other evidence will provide anything approaching a complete picture of each species, and thus an ideal classification. Even today there is a great reluctance by many taxonomists to make real use of any but macroscopic characters, and there are a large number who believe that vegetative features are to be used only as subsidiaries to evidence from floral studies.

Of all the types of somatic anatomy studied it seems clear that the less superficial layers of the plant have provided the best evidence for taxonomists, the wood, where present, perhaps being the most useful of all. The leaf epidermis, or its cuticle, has received relatively little attention from neobotanical taxonomists and most of the studies undertaken have been concerned with somewhat specialized groups of plants, e.g. *Gramineae*. Palaeobotanists, however, have used epidermal characters in classification since the beginning of this century, and today their use is practised as a routine procedure, although here the groups of plants concerned have usually been non-angiosperms. In recent years much more attention has been paid by both neobotanists and palaeobotanists to their use in angiosperms, but most of the studies are far from adequate and the subject is still in its infancy.

Except in fresh material of a relatively small proportion of species the leaf epidermis of modern angiosperms is extremely difficult or impossible to remove *in toto*. In fossil species, moreover, it is frequently not or only fragmentarily preserved, and most of the early work on fossil leaf forms was carried out solely with the aid of leaf impressions. The discovery that the cuticle, which covers the whole of the leaf epidermis, bears an imprint of the epidermal features was therefore of great importance, especially as it often remains on fossil leaves in a well-preserved state long after all cellular layers have disintegrated. Moreover, except in plants with a very thin cuticular covering, the cuticle can be removed from the fossil or modern leaf (whether fresh or as a herbarium specimen) in a continuous sheet, to which end several methods have been employed. Whilst some epidermal features are lost in cuticular preparations the cuticle does provide some extra characters, and the study of the cuticle rather than the epidermis places the work on a consistent and precisely definable basis which is comparable with palaeobotanical investigations. The present survey is concerned with the cuticle itself, although epidermal studies are of course highly relevant.

The level of knowledge now reached with regard to the systematic anatomy of the epidermis or cuticle is quite impressive in some groups, such as *Gramineae* or gymnosperms. In the dicotyledons and other monocotyledons, however, little extensive work has been attempted. Most investigations have been aimed at separating small groups of species or genera with little or no attempt at studying the degree of variation found within the taxa which are being separated. Much of the literature in the dicotyledons consists of short sections subsidiary to much wider studies of a more general nature. Work on fossil or recent plants by palaeobotanists has been solely for the purpose of identifying fossils by means of a comparison with living species rather than to investigate the intrinsic features of either group, and scarcely any mention is found of the possibilities of the presence of environmental or other variation. Many of the better surveys, even excluding the gymnosperms or *Gramineae*, appear to have been undertaken on plants with leathery, somewhat xeromorphic leaves (e.g. *Lauraceae*, *Magnoliales*). Such leaves have a thick cuticle which shows the epidermal cell pattern clearly, and for some reason these xeromorphs usually have a less variable pattern than mesomorphic species. Studies of the latter types have mostly been of a very limited scope, and in many cases a quite inadequate amount of material has been used as representative of each species.

Thus there is a considerable gap in the literature with regard to both the variation of cuticular patterns within a species and the types of characters and their degree of taxonomic usefulness which are to be found in " normal " mesomorphic dicotyledons. The series of investigations upon which this article is based was aimed directly at helping to fill this gap. The survey was intended to be intensive rather than extensive, for, whilst this narrows the range of experimental material, it was just this close study of a limited group of plants which was needed. Extensive investigations have been undertaken in the past by a few workers, mainly palaeobotanists, but they have invariably been too superficial for general use. The families of plants chosen for this programme, *Combretaceae*, *Rhizophoraceae* and *Avicenniaceae*, are almost wholly tropical. They contain about 550, 120 and 11 species in twenty, sixteen and one genera respectively, and although all are woody in habit the species show a great variety of growth forms, including trees, shrubs and lianes of all degrees of specialization occurring in all types of tropical habitat. All three families, of which the first two are regarded as very closely related but the third as very remotely so, contain mangroves. It is suggested that the results gained from the intensive study of these families have enabled a good number of general conclusions to be drawn which are applicable to all or most groups of dicotyledons.

A soundly based theory of cuticular patterns can be put to a good number of uses besides the obvious applications in identification, taxonomic research and phylogenetic investigations. These include peat stratigraphy, pharmacognostical analyses and animal foodstuff research. Only after thorough examination of all aspects of epidermal and cuticular variation can systematic cuticular evidence be legitimately used in these fields, and it is hoped that the following sections will go some way towards realizing that aim.

§2. HISTORICAL INTRODUCTION

A brief historical survey of the study of epidermal and cuticular anatomy throws much light on the situation at the present day, and is a considerable help in understanding the areas in which work is now most needed.

The earliest reference to fossil cuticles is apparently the note by Brodie (1842) " When the sandstone is freshly broken the epidermis of the fossil frequently peels off . . .", but this observation was not followed up. Three years later Goeppert & Berendt (1845) figured cuticular fragments of one species of conifer and two species of angiosperm which they found preserved in amber. These figures appear in a large volume primarily concerned, amongst plants, with twigs and leaf impressions, and this is the case with the later cuticular diagrams of Schleiden (1846), Unger (1853) and Wessel & Weber (1856). In all four cases the figures are crude and highly diagrammatic, and except where the material has been available for subsequent study the true identity of the plants is obscure. For example the leaves described by Unger as a *Potamogeton* have been found to belong to a member of the *Loranthaceae*, whilst those figured by Schleiden are not identifiable at all (Edwards, 1935). Wessel & Weber described and figured a number of dicotyledons which they referred, in most instances, to living species, whilst Goeppert & Berendt more advisedly used generic names, such as *Alnites*, which were not applicable to living plants.

The first really important work on the systematic treatment of cuticles was that of Bornemann (1856), describing fossil cuticles of cycads from the neighbourhood of Thüringen. He was the first person to realize the exact nature of the cuticles which he studied, and went to great pains to explain the relation between them and the leaves which bore them. He wrote : " The outline of the cell walls of the epidermis is almost always shown on the (cuticular) membrane by a network of dark brown lines, which apparently represent the cell walls, but which are much thinner than these would have been. These brown lines are to be regarded as parts of a homogeneous cuticle . . ." (transl.).

From then onwards a large number of works, from short notes to large volumes, began to appear on the subject of fossil cuticles. Even so, systematic studies on the surface features of angiosperms generally made use of the whole epidermis, and such investigations in the latter half of the nineteenth century were very numerous. One of the earliest of these was the investigation by Prillieux (1856) into the types of peltate trichomes found in various members of the *Oleaceae*, and he was actually able to separate all 23 species examined on the structure of these trichomes alone.

The first taxonomist to make constant use of anatomical characters for his diagnoses was apparently Bureau (1864) in his revision of the *Bignoniaceae*, although these characters naturally formed but a very minor part of the descriptions. Soon after this anatomical characters began to appear more widely in taxonomic treatments, reaching a climax in Engler & Prantl's *Die natürlichen Pflanzenfamilien* (1887–1915). Conversely anatomists were becoming more aware of the systematic value of many of their studies, and a number of extremely useful surveys appeared at that time, several of which are unknown to many present-day workers. Weiss (1865) produced a monumental account of the sizes, numbers and distribution of stomata in a large number of dicotyledons ; Bokorny (1882) surveyed the distribution and occurrence of pellucid spots in dicotyledon leaves, classifying them according to their causes ; Bachmann (1886) gave a beautifully illustrated account of all the types of peltate hairs known, in systematic arrangement ; Grob (1896) provided a very useful early account of grass-leaf epidermides ; and von Minden (1899) thoroughly covered the different types of water-secreting organs (e.g. water stomata, hydathodes) found in dicotyledons. It was perhaps this productive period which led Fritsch (1903) to summarize the most important systematic anatomical characters to which taxonomists might pay more attention, and in many instances his comments still apply today. Solereder's encyclopaedic volumes on dicotyledon systematic anatomy, first published in 1898–99, represent the epitome of anatomical works at that time, and together with a supplement were translated into English by Boodle & Fritsch (1908). They remain a standard reference today, one of their most valuable aspects being the detailed survey of the principal families in which a wide range of anatomical characters are to be found.

Although works on fossil cuticles from Bornemann's (1856) time onwards were equally numerous very few of great value were produced before the present century, and scarcely any of these were concerned with angiosperms. Schenk (1869–71) included some drawings of cuticles in his studies of Wealden plants, but of course none of these was an angiosperm. Zeiller (1882) wrote what must be regarded as the first review on cuticular studies, and his article brings together much useful information with many supplementary original facts on cuticles of fossil ferns and conifers. Perhaps the most important of the early cuticular studies, however, were those of Nathorst (1907–12). His *Paläobotanische Mitteilungen* represents the first work which reported a long series of cuticular studies on a large number of species, and should be considered as the consolidation of this subject as a truly scientific discipline.

One of the most important features of Nathorst's work is the improvement in various techniques, and these were quickly assimilated by palaeobotanists elsewhere in Europe and in America. This resulted in a considerable number of studies entirely devoted to cuticles, rather than studies using cuticular characters as supplementary evidence as had previously been usual. Thompson (1912), for instance, studying Cretaceous conifers, re-examined the genus *Frenelopsis* and concluded that Zeiller (1882) was wrong in believing that its stomata had the unusual number of four guard-cells : in fact these four cells are the subsidiary cells, the guard-cells being quite normal.

The first noteworthy cuticular investigations by British workers were those of Thomas & Bancroft (1913) on cycads. They compared cuticles of fossil and recent species with an emphasis on stomatal characters, and thus uncovered a considerable amount of detail regarding the relationships of the fossil types. Some of the first good photomicrographs of cuticles were included in this publication, and others were produced by Wills (1914) who reported on fossils from British coal-measures. Thomas (1930) later produced an article supplementing the knowledge of Mesozoic cycadean fronds set out in the earlier work. To exemplify the spread of cuticular studies from continental Europe Holden's (1915) paper may be cited, being one of the first works on Asian cuticles. From her study of Indian fossil conifers she concluded that epidermal leaf characters may often be of great value in specific determination, but that they seem of little use as phylogenetic evidence.

By far the most important cuticular investigations are those of Florin, who for the past forty years has produced a large number of excellent accounts of recent and fossil gymnosperm cuticles, together with first-class photographs and drawings. One of his earliest important papers (Florin, 1920) was concerned with a comparison of fossil conifer cuticles with those of modern conifers, and most of his subsequent work has been developed along these lines. Florin's most important work on modern conifers (1931) includes descriptions of the cuticles of almost every known species, with particular reference to stomata, and a section is also included on the stoma types of the major gymnospermous fossil and recent groups for comparative purposes. Later (1938–45) he produced an even larger work on Upper Carboniferous and Lower Permian conifers, including full details of their cuticles, but this work also embraces the reproductive structures and other vegetative organs than the leaves. Perhaps his most important work on non-coniferous cuticles was the account of the stomata of Mesozoic cycads (Bornemann's subject in 1856) and *Bennettitales*, attempting to shed some light on the relationships of these groups (Florin, 1933). More recently Florin has devoted most of his time to studying conifer cone-structures, and it is fortunate that he continued to investigate conifer relationships rather than turn his attention to angiosperm cuticles as Edwards (1935) once suggested.

Bandulska (1923) investigated the cuticular anatomy of dicotyledon and conifer leaves found in Eocene deposits at Bournemouth, and was able to place one of the latter into an already known fossil species. The dicotyledons, which were unidentified at the time, were placed into a new fossil form-genus, *Dicotylophyllum*. In her following four papers Bandulska described a series of cuticles of modern dicotyledons and in several genera she placed species which she had previously described under *Dicotylophyllum*. These genera were *Nothofagus* and *Fagus* in the *Fagaceae* (1924) ; *Aniba*, *Lindera*, *Litsea* and *Neolitsea* in the *Lauraceae* (1926) ; *Cinnamomum* also in the *Lauraceae* (1928) ; and *Tristania* and *Rhodomyrtus* in the *Myrtaceae* (1931). This work was the first important investigation of modern dicotyledon cuticles to be attempted, and it clearly showed that with a great deal of patience conclusive and positive results can be obtained from this approach.

Odell (1932) published a highly controversial paper which not only condemned the identification of fossil leaves by their gross form (shape and venation), but also severely attacked the use of cuticular characters for this purpose. She apparently originally attempted to identify the older Eocene fossils of the Bournemouth deposits, where Bandulska had first investigated the younger Eocene leaves, but concluded that the variation shown in all characters which were normally used to this end made it an impossible task. The bulk of her paper consists of a series of conclusions drawn from the study of 170 species of modern angiosperms, but unfortunately she does not state the extent of her sample of each species. Her method of argument is to take each character used in cuticular differentiation separately, discuss the evidence for the fact that this character is known to vary under environmental or other conditions, or that completely unrelated species are identical (or, conversely, closely related species quite different) in that character, and conclude that it is taxonomically worthless. One could, of course, equally well do this with any other character that has ever been used taxonomically, but because (for example) *Ranunculus ficaria* L. possesses about seven to twelve petals one cannot conclude that petal number is of no diagnostic importance, either in this or in any other group.

It is perhaps worth mentioning two of the twelve or so characters which Odell considered, as more or less random examples. With regard to the presence and types of subsidiary cells around the stomata she states that the three main types recognized by Solereder are not found especially in any taxonomic groups, but are distributed variously in different genera and families. Moreover in some species only the stomata on the stems are associated with subsidiary cells. Thus " the presence or absence of *subsidiary cells bordering the stoma* can be of little systematic value ". In the case of non-glandular hairs Odell mentions that the arrangements and numbers per unit area on a leaf vary tremendously, and are affected by environmental factors such as sunlight, humidity, wind and altitude. Their abundance also varies on different parts of the same plant or even of the same leaf. Types of hair often differ within a family, and there is often more than one type even on one leaf, so that the types of hair are not connected with taxonomic categories. She therefore decided that " *clothing hairs* cannot be used in the identification of the vegetative parts of Angiosperms ", and that their " structure has been found of no diagnostic value ". Her final conclusions were that " any feature of the epidermis of the vegetative parts of living Angiosperms is unsatisfactory for diagnostic work ", and that " the modern method of naming fossil Angiosperms from a combination of the form, venation, and epidermal structure of their vegetative organs is quite inadequate for specific or even generic diagnosis ".

In almost all instances Odell's statement of fact must be regarded as correct, but it is in some of her extraordinary conclusions that she is obviously in error. If she was attempting to show that it is in general impossible to place a vegetative portion of a plant into its correct family or order on a single epidermal character (or even on a combination of such characters) then one would readily agree with her, but to assert that each of the twelve or so characters is " of no diagnostic value ", or " cannot be used in determinative work ", is obviously quite illogical. Odell appears to have overlooked two important basic points in drawing her conclusions. First of these is that the compilation of diagnoses and hence the identification of species should not be undertaken with a single character, but with a combination of as many characters as possible. Although two families, genera or species may not be separable by a single character a combination of several characters will often enable separation to be effected. Secondly a range of form is often more important taxonomically than is a fixed type. For example the possession of a variable number of petals by *Ranunculus ficaria* is a notable taxonomic feature of this species, not a reason to doubt the systematic value of petal number. Further criticism of Odell's remarks is unnecessary. In general one would agree with her that cuticular characters are usually not useful at the family level or above, but it is unfortunate that she does not differentiate between those cases where the characters are useful in phylogenetic classification and those where they are useful for identification.

Belying Odell's claim that stomatal structure " cannot be regarded as of systematic value " just four of several publications may be cited. Carolin (1954), working with *Dianthus*, found that contrary to the usual findings (see below) neither stomatal size nor frequency could be used to indicate the level of ploidy. However, within the diploid and within the hexaploid groups most investigated species could be separated by a series of size, frequency and morphological characters. Stebbins & Khush (1961) surveyed the " stomatal complex " of most families of monocotyledons. They found that characters such as the number and type of subsidiary cells gave valuable clues to the affinities of the plants, so that each family had a predominant type or arrangement. Watson (1962) found that in the *Epacridaceae* the stomatal distribution and orientation on the perianth and leaves, and also the broad structural types of stomata, were mostly differentiated at the generic or a higher level, and in the *Ericaceae* '(Watson, 1965) the stomata provided equally important taxonomic evidence although in several instances there was little or no correlation with the usually accepted classification.

Pharmacognosists have frequent need to identify leaves or fragments of leaves used as herbs, and, as the number of species is relatively small, epidermal features have often made identification possible. Timmerman (1927) produced an early analysis of one of the characters used in pharmacognosy, namely stomatal frequency. Using *Datura* she found that stomata were more frequent at the leaf apex than in the middle, whilst the ratio on the two epidermides also altered in different parts of the leaf. She therefore concluded that stomatal frequency was generally of no use for identifying leaf fragments in this genus, although she was able to separate one species from the rest of those examined by this character. In the same year, working from a different angle, Salisbury (1927) also investigated the constancy of stomatal frequency, adding environmental effects to the positional factors considered by Timmerman. Salisbury found much the same variation as Timmerman, except that the proportions on the two epidermides did not appear to alter. He found that if the proportion of stomata to epidermal cells (the stomatal index, i.e. $100S/E+S$) was measured instead of the stomatal frequency the variation produced by environment and position could be completely cancelled, apart from the effect of humidity. He was able, in fact, to measure the environmental humidity by means of the stomatal index. This very simple information was of extreme importance to taxonomists, and the stomatal index is now used as a routine procedure in palaeobotany (cf. Harris, 1944). Salisbury's use of the stomatal index had been foreshadowed, however, by Loftfield (1921), who noticed that the ratio of stomata to epidermal cells often remained constant when the stomatal frequency varied.

A less reliable method of overcoming the variation in stomatal frequency was also used by Baranov (1924), who found that the stomatal frequency of the middle portion of leaves half-way up the stem was equal to the average frequency of all parts of all leaves. This does not take into account the fact that most fossils are only fragmentary, nor the effects of environment.

Working much later than the above, Gupta (1961) also found a considerable variation in stomatal frequency on leaves from different parts of the plant, and demonstrated a negative correlation between this and the lamina size. He thus used an Absolute Stomatal Number, the product of the stomatal frequency and the lamina size, as a constant, this being comparable to the stomatal index.

Sax & Sax (1937) and Sax (1938) reported on some very interesting and now almost classic studies on the effect of polyploidy on stomatal size and frequency. They found a positive correlation between each of these two variables and polyploidy, and could usually separate the diploids and tetraploids in any given series of plants. Modern Floras now often contain characters such as stomatal size and stomatal index in the separation of closely related species where one is a polyploid (e.g. *Rorippa nasturtium-aquaticum* (L.) Hayek and *R. microphylla* (Boenn.) Hyland.).

The great mass of anatomical work which marked the end of the last century seems to have largely ceased with the publication of Solereder's work and supplement (1908). Rehfous (1917), however, provided a very useful survey of work on stomata. In the 1930's systematic anatomy, together, in fact, with taxonomic studies in general, began to regain popularity, and from then on the number of systematic studies has increased quite steadily.

Meyer (1932, 1932a) investigated the *Alismataceae*, firstly for taxonomic and secondly for phylogenetic reasons. Most of the genera and species Meyer examined could be separated by anatomical features, but he found little evidence suggesting close relation between the *Alismataceae* and *Ranunculaceae* ; the stomata, for instance, are quite different. This work was connected with the commencement of a *Systematische Anatomie der Monokotyledonen* by Solereder & Meyer (1928–33), of which only a very small proportion appeared.

Prat (1932) published an extremely important work surveying the systematic value of grass epidermides, this family without doubt being the most amenable amongst the angiosperms to epidermal classification. Several important taxonomic changes have been foreshadowed in the *Gramineae* by epidermal considerations, such as the exclusion of *Nardus* from the *Hordeeae* or of *Eragrostis* from the *Festuceae*, a situation only elsewhere paralleled in some gymnosperms. Many more recent works on this subject have appeared, but the exceptional nature of the *Gramineae* precludes the necessity of their being considered fully here. The most important work is that of Metcalfe (1960), which is a complete survey of almost all genera and of all the literature. Some recent papers which show the amazing systematic value that can confidently be placed on minute features of grass epidermides are those of Tateoka *et al.* (1959) and Borrill (1961). In all cases, however, students of grass epidermal anatomy have used the whole epidermis in preference to the cuticle.

In the last twenty years a great many systematic anatomical studies have been undertaken, and the resulting publications provide sections on epidermal and cuticular characters varying in length with their taxonomic importance in the group concerned. Mention may be made of the work of Bailey & Nast (1944, 1948) in the *Winteraceae, Illiciaceae* and *Schisandraceae*, Heintzelman & Howard (1948) in the *Icacinaceae*, Morley (1953) in the *Melastomataceae*, Tomlinson (1959) in the *Musaceae*, and Paterson (1961) in the *Epacridaceae*. The degree of use which can be obtained from the epidermis varies considerably in these groups, as would be expected. Thus Tomlinson was able to use a number of general and special epidermal characters to great effect in delimiting at the generic level, but Bailey & Nast, who were two of the few anatomists to isolate the cuticle and study it as such, found that apart from its very distinctive appearance throughout the *Winteraceae* it did not furnish good taxonomic characters.

Over forty years after Solereder's volumes (1908) Metcalfe & Chalk (1950) published along similar lines a modern survey of dicotyledon systematic anatomy. The literature survey is essentially concerned with work done since Solereder's time, and many details of structure mentioned by the latter are omitted where no further examinations have been undertaken. The greatest improvements and additions are to be found in the sections on secondary-xylem structure, upon which emphasis is justifiably placed. With regard to the epidermis and cuticle Solereder's work is therefore frequently the more informative. In reviewing characters of taxonomic importance Metcalfe & Chalk obviously consider wood and associated tissues to be of the highest importance, and epidermal characters are dismissed in a few paragraphs. With regard to stomata they quite correctly state that the number per unit area is too variable to be of any great importance, but it is strange that they do not mention the usefulness of the stomatal index. More recently Metcalfe has commenced a comparative *Anatomy of the Monocotyledons*, of which to this date volumes have appeared on the *Gramineae* (Metcalfe, 1960) and the *Palmae* (Tomlinson, 1961). Without such an important basis as Solereder's dicotyledon volumes the compilation of a systematic anatomy of the monocotyledons is a considerably greater task, and when completed will probably prove even more valuable.

In 1954 Metcalfe published a paper which may be compared with one by Fritsch (1903) half a century before. This set out to indicate the main lines along which systematic anatomy could be developed, and in the next year (1955) he summarized recent work on this subject in the monocotyledons, especially the grasses. More recently Metcalfe (1963) has elaborated his opinions on the desirable trends in modern comparative plant anatomy.

From about the time of Bandulska's work (1923–31) onwards a considerable number of articles on fossil dicotyledons began to appear in the literature, in several cases obviously directly inspired by her publications. Stockmans (1932) reported on two species discovered in Belgium : a *Litsea* and a *Dewalquea*. The first genus, a member of the *Lauraceae*, had been discovered in England by Bandulska (1926), whilst the extinct genus *Dewalquea* had been previously found in Ireland by Johnson & Gilmore (1921). Discussions by Stockmans and Johnson & Gilmore, in both cases well illustrated, on the affinities of this genus produced little concrete theory, several diverse families being mentioned. Since not all of the species of *Dewalquea* possessed peltate scales on the leaf it was suggested that they were perhaps representatives of two different genera. Whether or not this is true it must be remembered that other genera known today (e.g. *Combretum* and *Rhododendron*) possess scaly and scale-less species.

Hofmann produced a valuable series of papers from 1926 to 1932 (cf. Hofmann, 1932) on plant remains in early Tertiary formations. In her earlier works she attempted to give names of living genera or species to the cuticles, and in 1926 she described fossil plants in ten living genera from these deposits. In 1932, however, she changed to the more advisable system of describing these old leaves in a fossil form-genus. Her choice of name for this was *Folium*, which is nomenclaturally superfluous owing to Bandulska's early name *Dicotylophyllum* for the same purpose. Edwards (1935) justifiably comments that her descriptions of new fossil leaves are somewhat inadequate, but she gives some good photographs.

Kubart (1927) found great difficulty in distinguishing between the fossil leaves of

Fraxinus (*Oleaceae*) and *Umbellaria* (*Lauraceae*) which he discovered in North America. He pointed out, however, that had the cuticles been preserved there would have been no difficulty in discrimination as the epidermal structure of the two genera is quite different. In support of this he figured a series of recent species of each genus, showing the great divergence between them. Also working on Tertiary plants, Straus (1930) was able to identify a number of species with modern genera, and in the cases of the two better-preserved genera (*Juglans* and *Populus*) he gave some good high-powered photographs. Straus pointed out the need for microscopic examination of the cuticle in cases where two fossil leaves appeared to be closely similar.

In recent years the great majority of works on fossil cuticles has been concerned with pre-Tertiary plants, mostly gymnosperms. Perhaps the most important publications have been those of Harris (1942→), who has covered a wide range of topics on the Jurassic flora of Yorkshire in several scores of articles, many of these including cuticular studies which have often proved of considerable diagnostic value.

Cookson (1953) reported on a relatively recent (early Tertiary) cycad from Australia which, on the basis of its cuticular characters, could be referred to the genus *Macrozamia*, which still occurs in Australia today. Cuticles of this fossil and of the living *M. hopei* W. Hill ex F. M. Bailey are shown, and due to the great similarity between them the former is named *M. hopeites* Cookson.

Apart from Europe and North America some of the most important cuticular studies have emanated from India, and as examples two of the papers on the Indian *Glossopteris* flora by Srivastava and his colleagues may be cited. Srivastava (1956) produced a most thorough account of all the species of *Glossopteris*, *Gangomopteris* and *Palaeovittaria*, with very clear descriptions, drawings and photographs. All species could quite easily be separated on cuticular characters alone, a whole series of features, concerning epidermal cells, stomata and venation, being employed. Surange & Srivastava (1956) concurrently considered the generic limits in this group of leaves. They concluded that the three genera, which were delimited on frond shape, could be better divided into six genera using the cuticular characters. These six genera did not correspond in any way to the three established genera, and pending further information no new generic names were proposed.

Apparently the only general review of cuticular studies in angiosperms is that of Edwards (1935). He gives an extremely useful survey of the literature to that date, which has obviated the necessity of very detailed accounts of the earlier work in this introduction. The account treats recent and fossil monocotyledons and dicotyledons in four separate sections, those on monocotyledons being mostly concerned with grasses. Many of his citations are annotated with some sort of assessment on their importance or validity, but in the case of Odell's (1932) paper he quite justifiably records strong protest with a series of objections, mostly in the form of counter-evidence. One would concur with almost all of his opinions on this and other papers, but as mentioned previously I prefer to attack Odell's deductions and conclusions rather than her statement of fact. In several instances it is obvious that Edwards held almost as extreme ideas as Odell, though in a completely opposite direction. He was clearly convinced of the tremendous and widespread usefulness of cuticular characters in the angiosperms, which is perhaps to be expected of a palaeobotanist whose cuticular studies had mostly been concerned with gymnosperms. Had he made extensive investigations in the angiosperms he would have met, in many instances, with a much wider range of variation than is found in any gymnosperm, and than he seemed to admit as existing in the angiosperms. For instance, in criticizing Odell's statement that the leaves of *Campanula latiloba* A. DC. and *Inula salicina* var. *denticulata* Borbás are identical, he found that there were in fact good microscopic differences between them, and he also suggested that Odell's " own drawings do not suggest identity of epidermal structure ". Odell's figures differ only in the thickness and degree of undulation of the epidermal cell walls, and had Edwards been familiar with the range of variation of the cuticles of many angiosperms he would have realized that most species show a wider range of variation than Odell's two drawings. Thus, although in fact the two species do apparently differ in cuticular structure (*fide* Edwards), Odell's figures certainly do not suggest it. Apart from a few criticisms such as the above, Edwards's paper is a valuable and critical review. His conclusion may be quoted : " given careful and critical work on well-preserved material, together with a detailed comparison with a wide range of living forms, results obtained from a study of fossil angiosperm cuticles will be as valuable as those derived from any other fossil remains, and certainly far more reliable than those founded on leaf impressions alone ".

Edwards did not mention any articles concerned solely with modern dicotyledon cuticles, and the first that the writer has traced is the account by Rao (1939) of the order *Magnoliales* in the sense of Hutchinson (1926), a very heterogeneous assemblage of families about which Rao concludes: " From the point of view of epidermal studies, the Magnoliales do not represent a co-sanguinary group, but indicate a convergence ". Rao's paper presents a detailed description of the cuticles of over 50 species representing more than half the genera of the order, but since he admitted that in most cases only a single leaf of each species was examined the results must be treated with extreme caution. Objection must be made to some of Rao's conclusions, although a detailed criticism will not be attempted here. Rao implied, for instance, that the cuticular striations found in some species of *Magnoliales* are phylogenetically related to those of the *Cycadales*. However, representatives of many dicotyledon families possess cuticular striations which are identical with those of the *Magnoliales*. Even if cuticular striations in the two orders were phylogenetically related, and this seems unlikely and in any case could never be proved, no such inference could be drawn merely from their presence in both groups. Rao strongly stressed further evidence of a connexion between the *Magnoliales* and gymnosperms from his stomatal studies. Using Florin's (1931) two categories of stomatal development Rao claimed that two genera of *Magnoliales*, *Euptelea* and *Cercidiphyllum*, possessed haplocheile stomata, which according to Rao were otherwise virtually unknown in the dicotyledons yet were typical of all gymnosperms except the *Bennettitales*, *Welwitschiales* and *Gnetales*. Later work has shown many of Rao's conclusions regarding stomatal types to be erroneous, and a modern stomatal survey of the *Magnoliales* is badly needed. Jalan (1962), for example, has found that the stomata of *Schisandra* are haplocheilic (as, in fact, they are in a great many dicotyledons), and the same is true of *Gnetum* (Maheshwari & Vasil, 1961). In *Magnolia* and *Michelia* species the stomata on the leaves are syndetocheilic, but those on the flowers haplocheilic (Paliwal & Bhandari, 1962). The need for developmental studies rather than observations of mature structure cannot be overemphasized, and the approach of several Indian workers in this field is encouraging (cf. Pant, 1965). Further reference to this is made in the section on stomata.

Ahmad (1964, 1964b, 1964c) has investigated the cuticular and epidermal anatomy of 17 genera of *Solanaceae*, and found that a number of characters concerning the stomata, trichomes, epidermal anticlinal cell walls and cuticular striations are very useful in identification. The same characters enabled 28 species of *Solanum* and 23 of *Cestrum* to be differentiated.

Sinclair & Dunn (1961), on the other hand, working in the monocotyledons, appear to have made conclusions regarding the usefulness of cuticular characters at the family and generic levels which are not justified on present information.

It is perhaps largely by chance that the *Lauraceae* have been studied more frequently than any other dicotyledon family with regard to their cuticular characters. Studies already mentioned have been those of Bandulska (1926, 1928), Kubart (1927) and Stockmans (1932), and there have been other less important ones besides. Kostermans (1957), in his taxonomic studies of the *Lauraceae*, mentioned the usefulness of cuticular characters, but pointed out the care necessary in the interpretation of the results of these investigations. He was referring mostly to Bandulska's work. Marlier-Spirlet (1945) investigated the epidermal anatomy of *Cinnamomum* more thoroughly than did Bandulska, and produced many figures. He also showed vertical sections of the leaf to demonstrate the derivation of various features of the cuticular preparations which were not readily interpretable from surface views alone. It was found to be possible to separate many of the eighteen species investigated, and three broad groups were recognized, containing four, three and eleven species respectively. The most useful taxonomic criteria appear to be the shape of the upper epidermal cells and the types of stomata. A continuation of this study would be of considerable interest and value. Dilcher (1963) undertook a " cuticular analysis " of an Eocene species of *Ocotea*, and after a study of its variation and of the living taxa concluded that it should be considered a distinct species.

Martin (1955) used cuticular anatomy to a most novel and useful end to which there appear to be no subsequent references. Previously Parkinson & Fielding (1930 ; *fide* Martin, 1955) had compiled notes of some epidermal characters of the plants used as cattle food, using the solid leaf fragments. In order to study the diet that sheep choose in various pastures Martin examined the rumen contents and faeces of these animals to ascertain quantitatively the species of plants represented by their cuticles. In the upland pastures in which the work was pursued the number of species was rather limited and few species were closely related ; thus Martin was able to separate all forty likely plants by cuticular anatomy and determine them quantitatively in the faeces. He gives brief descriptions and photographs of twelve representative species. Of these forty species only sixteen were recognized in the stomach contents or faeces, including four grasses, two sedges, three rushes, two mosses and five dicotyledons. Except in the case of two species of *Juncus* each genus was represented by only a single species, although other genera were represented by two or more species among the originally investigated group of forty plants. It seems likely, however, that some or many mesomorphic herbs would never be represented due to their extremely thin cuticle, although the only known cutinase enzyme has been isolated for certain solely from *Penicillium spinulosum* Thom (Heinen, 1960, 1961).

This work is a further indication of the economic use to which cuticular studies may be put, and emphasizes the need to discover the basic principles underlying the possible application of this method in various directions.

§3. ANATOMICAL INTRODUCTION

Some idea of the precise relationship between the cuticle and the underlying epidermal cells is essential to a full understanding of the nature of the patterns seen on acellular cuticular preparations and their interpretation in terms of a cellular layer.

Although Bornemann (1856) obviously understood the cuticular-epidermal relationship fully the first good general anatomical accounts are those of de Bary (1871, 1884), and Höhnel (1878) appears to be the first to have described the chemistry of the cuticle. During the past thirty years our knowledge of the cuticle and of its essential constituent, *cutin*, has steadily grown, accelerated by two major technical advances. The first of these, polarizing microscopy, became available in the 1920's and its use is shown in the work of several Continental writers. The second, electron microscopy, a post-war development, has been utilized in cuticular studies mainly by Roelofsen and a number of American workers.

In all vascular plants the basic chemical component of all the cell walls is cellulose, whose long-chain molecules exist as long compound microfibrils. In the interfibrillar spaces are a number of substances, including other polysaccharides, fatty materials, water and inorganic and organic solutes. Separating two such walls of adjacent cells is a cellulose-free layer known as the middle lamella, consisting basically of calcium and magnesium pectates. The outer face of an epidermal cell, however, is unusual in being adjacent to the environment rather than to another cell, and it is on this face that the cuticle is found. The precise structure of the latter was first ascertained by means of polarizing microscopy (e.g. Meyer, 1938 ; Roelofsen, 1952) and was confirmed later by electron microscopy (Roelofsen, 1959).

External to the normal cellulose cell wall of the outer face of each epidermal cell is found a thin layer of pectic material which is presumably continuous with the middle lamellae of the anticlinal walls of the underlying epidermal cells (Fig. 1).

Outside this is a usually two-layered wall, which according to the nomenclature of Roelofsen (1952, 1959) may be termed the *cuticular membrane.* The inner portion of this, the *cuticular layer,* is composed essentially of a cellulosic framework between the microfibrils of which are *encrusted* large amounts of cutin. The outer part is a usually thinner layer, the *cuticle* proper, which lacks cellulose and is composed mainly of cutin, which is *adcrusted* on to the cuticular layer. Esau (1953) refers to the process of encrustation as *cutinization,* and that of adcrustation as *cuticularization.* The above terminology is adopted hereinafter. In a number of plants, usually those with leathery leaves, the four layers exterior to each epidermal cell lumen are simplified insofar as a cellulose-free pectic layer is absent, the cutin-free innermost cellulose wall gradually merging into the outermost cellulose-free cutin layer. Rarely are all four layers as sharply defined as suggested in Fig. 1, but in general it can be said that the innermost layers lack cutin and the outermost layers lack cellulose. Chemically cutin consists of a number of highly polymerized long-chain hydroxy-fatty acids.

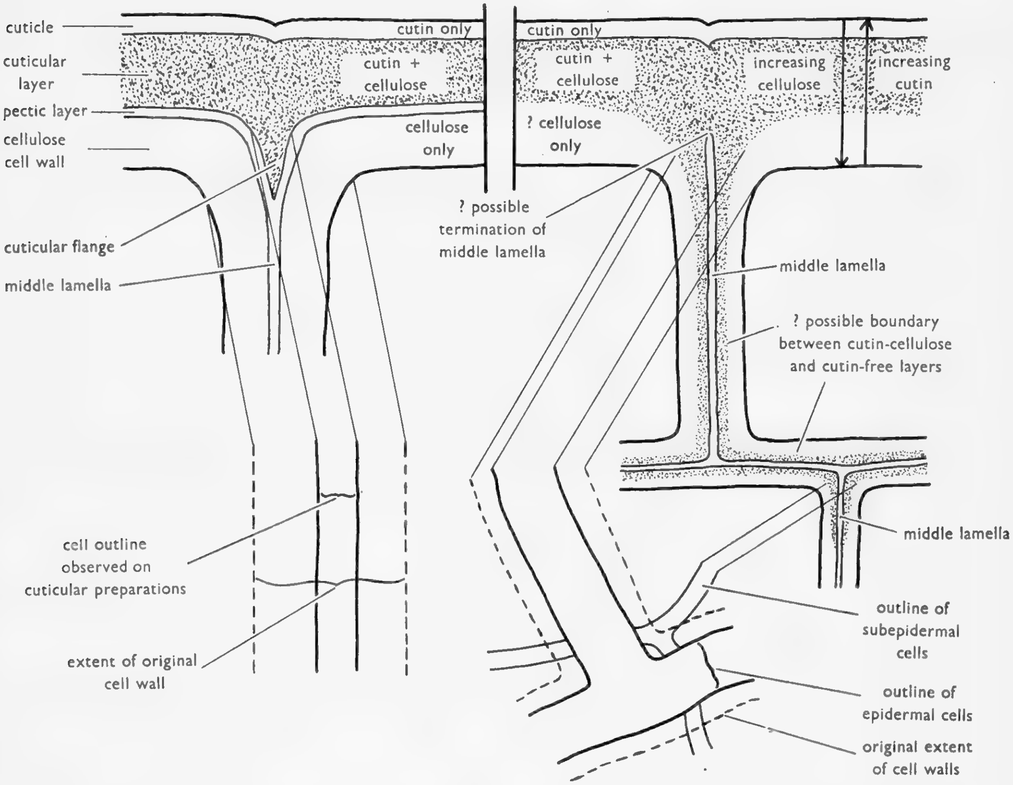


FIG. 1. The organization and interpretation of cuticular membranes and preparations : sections of epidermides with normal and abnormally extensive cutinization are shown, together with diagrams showing the significance of the patterns observed on the respective cuticular preparations.

Where the outer walls of two epidermal cells meet, the pectic layer, if present, may form a T-shaped juncture with the middle lamella of the vertical walls of the cells. In most cases, however, the cuticular layer projects down between the two cellulose cell walls for some way, forming the three-dimensional network of so-called *cuticular flanges* (Fig. 1). The length of the cuticular flanges varies from their virtual absence to their reaching all the way to the inner wall of the epidermis. In some leaves a greater proportion of the epidermis may be cutinized, in extreme cases the cell walls on all faces of the epidermal cells and even the outer walls of the subepidermal layer being encrusted with a certain amount of cutin. This internal cutinization is a feature of many xeromorphic plants.

Cuticular flanges are formed by the cuticular layer alone, and the cuticle remains a thin uninterrupted membrane. Indeed, the cuticular membrane as a whole is a continuous and virtually extra-cellular sheet, and should be thought of as something additional to the cell wall. It completely covers the leaf, usually including any trichomes which may be present, being interrupted only by the stomata. In a herbaceous plant it appears to surround the whole of the aerial shoot, including the apical meristems and flowers, although some workers have stated that certain trichomes lack a cuticular covering. With regard to the root system there is less certainty, opinions differing whether it is only the root tip and root hairs or nearly all the root that lacks a cuticular membrane (Lee & Priestley, 1924 ; Priestley, 1943 ; Esau, 1953). At each stoma the cuticular membrane follows the contours of the guard-cells, and often ends on their inner walls. In some cases, however, it is more extensive, covering also the adjacent mesophyll cells. Cutinized cell walls have also been found in more internal regions of the plant (cf. Arzt, 1934), and Lamarlière (1906) found a " cuticule interne " lining the aerenchyma of water plants.

Right from the time that the leaf is a minute primordium in the apical meristem it is covered by the rudiments of the cuticular membrane in the form of a very thin and pliable yet continuous fatty layer. These fatty substances obviously migrate through the cell wall from the cytoplasm, although there are no visible pores in the former for the passage of the cutin. On exposure to air the cutin hardens to a varnish-like cuticle by polymerization. A reasonably hardened cuticular membrane is present long before the epidermal cells have attained full size, and the problem is thus one of increasing the surface area of a relatively non-stretchable substance. Some workers suggest that the epidermal cells may grow in surface area only at their edges, so that the already hardened cuticular membrane remains undisturbed (e.g. Schieferstein & Loomis, 1959).

Not only is wax present within cell walls and cuticular membranes but it is also found in a fairly pure state on the surface of the cuticle of many plants. In recent years these deposits, which are the cause of the " bloom " on the surfaces of many leaves, have been studied in considerable detail, since they are important to the understanding of water repellency. Fairly comprehensive accounts are given by Mueller *et al.* (1954), Schieferstein & Loomis (1956, 1959), Scott *et al.* (1958), Juniper & Bradley (1958), Roelofsen (1959) and Juniper (1959, 1959a, 1960). It is interesting to note that the type of deposit (frequently variously shaped rods and plates) appears to be largely characteristic of each plant species. The deposits, when washed, dissolved or brushed off growing leaves, re-form quite rapidly and in exactly the same form as previously, and although their abundance varies with the environment and other factors their non-varying form is obviously in some way genetically regulated. What determines the form which the wax assumes is of course unknown, and moreover different parts of the plant (e.g. stem and leaf epidermides) may have totally different patterns. This subject is obviously of some taxonomic interest though doubtfully of any widespread practicability, and it is not considered further in this review.

In studying the cuticular membrane various methods may be employed to isolate it from the rest of the leaf. All make use of one or both of two important structural features of the epidermis which will have become apparent from the preceding paragraphs : firstly, the cuticular membrane is in most plants separated from the cellulose cell wall within by a thin layer of pectic material ; and secondly, the cuticle and the bulk of the mature cuticular layer are essentially composed of a substance (cutin) of very different chemical structure from the main constituent of the cell wall (cellulose). Isolation of the cuticular membrane may be effected with either of two types of substance : an enzymic preparation, either a pectinase which digests the pectic layers and so frees the cuticular membrane from the underlying cells and these from each other (Orgell, 1955), or a cruder hemicellulase-cellulase-pectinase mixture which additionally digests the cell walls (Skoss, 1955) ; or a macerating solution, composed usually of strong acids, which completely dissolves away all polysaccharide leaving only cutin unaffected. Very much later the acid also dissolves the cutin. The enormous resistance of cutin to the effects of age, micro-organisms and chemicals is, in fact, its greatest attribute with regard to the present study. Only one organism (*Penicillium spinulosum*) is known to be able to break down cutin (Heinen, 1960, 1961). The advantage of the above enzymic method is that the cutin is always completely unchanged, and in biochemical studies of the cuticular membrane this method is the only one to be recommended. On the other hand the macerating solutions are very much quicker and simpler to use, and the speed of reaction may be adjusted more easily. The cuticular membranes are also better for microscopic examination since they are considerably cleaner.

The upper surface of such preparations is smooth, or minutely striate or papillose, whereas the lower surface is protracted into a reticulate series of flanges which represent the position of the epidermal cell walls. When viewed from above or below the cuticular membrane is much thicker at the position of these flanges, which therefore show up, especially if the cutin is stained, as a series of narrow darker lines representing the shapes of the original epidermal cells (Fig. 1). It is important to realize that these lines only show the position of the central region of each double cell wall, and that the original walls were present for a considerable thickness on either side of them. In those cases where there are no cuticular flanges the cuticular preparations will of course lack the cell outlines, but it is apparently rare in woody plants for at least the faintest and most fragmentary of outlines not to be present.

As mentioned previously some plants have a heavily cutinized epidermis, the whole of the outer, vertical and inner walls and even the top of the vertical walls of the subepidermal layers being encrusted with cutin. In these cases the preparations have cuticular flanges which are very long and join up at their bases, and in surface view a second fainter outline, that of the subepidermal layer, may be visible below the epidermal outline. There is some evidence that the cuticular membrane is more or less completely lacking in cell outlines, or is not even able to be isolated in a continuous sheet, in many though by no means all herbaceous dicotyledons. In these cases the whole epidermis, or plastic moulds of it, must be studied.

§4. Materials and methods

For the purposes of obtaining cuticular preparations leaves may be used in any state (fresh, spirit-preserved or dried) and it is fortunate that herbarium specimens even over 100 years old produce at least as satisfactory preparations of the cuticular membrane as fresh leaves, exactly the same techniques being used. It is important, if studies of cuticular membranes are to be used as routine taxonomic procedure, that the methods involved in their isolation should be simple, quick and reliable.

With regard to the choice of material it is essential to ensure that a representative sample of each species is examined, and this involves a considerable amount of preliminary investigation into the variability of the taxa concerned. Thus the amount of material which can be considered truly representative will vary greatly, but in the present study I found it necessary to examine only one leaf of each specimen, except in cases of obviously different-aged leaves. The number of specimens of each species which was investigated varied according to the amount of material available, the degree of macroscopic variation apparent, and the ecological and geographical range of the species concerned. Three to five specimens were usually found to be a sufficient sample, but care was taken to select those with the widest morphological and ecological variation. In many cases, however, fewer specimens were available, while on the other hand special circumstances sometimes necessitated the examination of up to twenty.

The first task in investigating the taxonomic use of a new character is obviously to check it with the other characters already used, and for this correctly named material is absolutely essential. In the present series of investigations the families concerned are rather well covered in the literature, although the lack of knowledge concerning two genera necessitated a complete revision of all the species (Exell & Stace, 1963), and in some families this problem is so marked that it would become the limiting factor. Other genera of the three families studied still badly require revision. Whatever the state of knowledge of the classification of the taxon concerned differences of opinion may exist and occur, and a careful record of the actual specimens examined is essential. All the permanent slides prepared by me are marked with the collector, the number, year and country of collection, and the herbarium from which the material was obtained. This enables the identification to be checked whenever required.

Many different macerating techniques have been employed to isolate the cuticular membrane. Enzymic maceration is not suitable for taxonomic work as the conditions (temperature, pH, concentration) have to be carefully controlled and the method is very slow, and in fact in many thick leaves a clean preparation cannot be obtained. Of the milder chemical macerating solutions Eau de Javelle ($CaCl_2$ and K_2CO_3 solutions) is the most used (Nathorst, 1907 ; Bather, 1908 ; Bandulska, 1923), but for present purposes strong acids are preferable. Schulze's Solution (Schulze, 1855), concentrated HNO_3 with a few $KClO_3$ crystals added, is the most popular, and several improvements and variations have been suggested (e.g. Bather, 1908 ; Thomas, 1912 ; Thomas & Bancroft, 1913 ; Gothan, 1915 ; Harris, 1926). I found, however, that a slight modification of Jeffrey's Solution (Jeffrey, 1917), equal parts of 10% chromic and bench concentrated nitric acids, gave the best preparations in the shortest time, and it has been used without exception. This mixture was variously diluted to conveniently regulate the time taken for maceration to about sixteen hours, i.e. overnight, and in all 250 or so species examined the method was entirely successful. Care must be taken not to allow maceration to continue for too long since over-macerated cuticular membranes are unsuitable for future manipulation and examination.

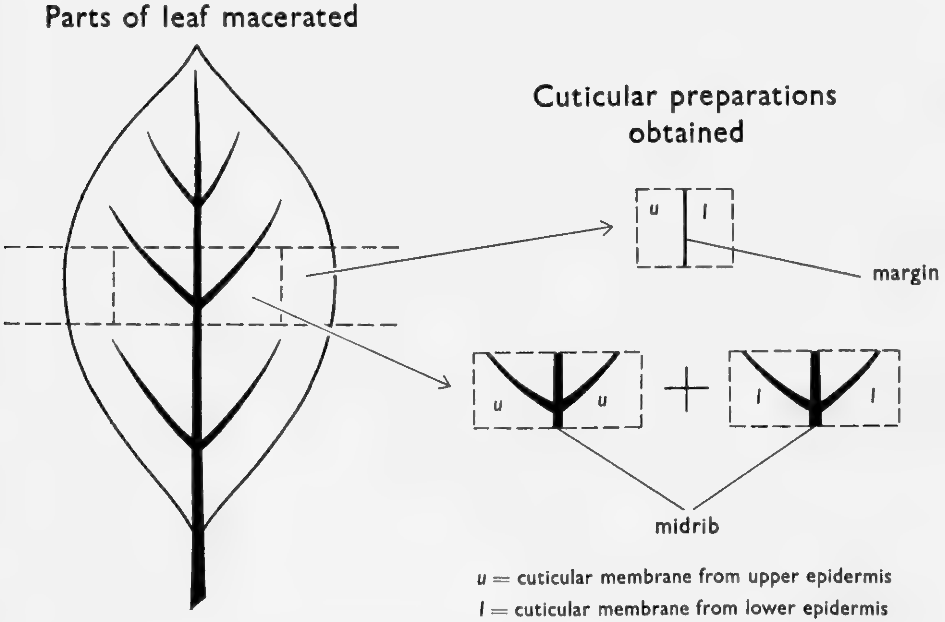


FIG. 2. Diagram illustrating the origin of cuticular preparations.

For purposes of conformity identical regions of each leaf were macerated (Fig. 2), so that three pieces of cuticular membrane were made into separate permanent mounts.

In some cases it is necessary to examine the cuticular pattern of species not available for maceration, or of species whose cuticular membrane cannot be removed as a continuous sheet. For this purpose the preparation of a plastic epidermal cell mould can prove of value, the plastic, usually cellulose acetate or nitrate, being either painted on to the leaf as a solution or pressed on as a thin sheet and then partly and temporarily redissolved (e.g. Nathorst, 1907, 1907a ; Bather, 1907 ; Thomas, 1912 ; Long & Clements, 1934 ; Sinclair & Dunn, 1961), making use of the fact that the outer surface of the cuticle usually follows the contour of the epidermal cells to some extent. The version of this method considered most suitable is that of North (1956), who used the formula 2 gms. of cellulose acetate and 0·7 gms. of gentian violet in 100 mls. of acetone, the stain improving the contrast. Herbarium specimens, whether dry or boiled, rarely give such good results as fresh leaves, but they are usually quite usable. The method is useless for most thick-cuticled leaves, which do not show the lines of the epidermal cells on the outer cuticular surface, and for pubescent leaves, although in the latter case the hairs can sometimes be removed. Occasionally transparent cell moulds are found already prepared on herbarium specimens in the form of flakes of old dried herbarium gum, which may show the epidermal cell outline very clearly.

Frequently sections of leaves must be prepared in order to interpret the observed cuticular patterns. Fresh or spirit-preserved leaves are naturally easier to section, but herbarium leaves of great antiquity, after boiling in water for a while, usually provide good sections when cut by hand or with a freezing-microtome. It is often more expedient to isolate the whole epidermis rather than the cuticular membrane alone, this method being particularly applicable to *Gramineae*. Lactic acid is generally used to separate the epidermis from the subepidermal layers, and the epidermis may then be stained with any general botanical stain (Clarke, 1960).

The technique employed to prepare permanent mounts was again designed to meet the three requisites of speed, simplicity and reliability. The best stain was found to be Sudan IV (1% solution in 70% alcohol) which has the advantage of being progressive, so that overstaining does not occur, but the disadvantage that dehydration and thus mounting in canada-balsam or similar media is impossible since the stain is re-dissolved from stained preparations by absolute alcohol. Thus glycerin-jelly was used as the mountant, and although this is not completely permanent most preparations are still perfect after at least thirty years and can at any time be remounted. Since the cuticular preparations are acellular sheets rather than pieces of tissue the number of stages from water to alcohol, alcohol to water, and water to glycerol can be reduced to a minimum, and each stage to a few seconds. The procedure adopted for preparing permanent mounts may be summarized : leaf fragments macerated in suitably diluted Jeffrey's Solution in an open watch-glass ; cuticular membranes washed in water, re-macerated in undiluted solution and re-washed in water if some cellular tissue remains, and transferred to a slide in 70% alcohol ; 70% alcohol replaced by Sudan IV solution for fifteen to thirty minutes ; slide irrigated with water, with 50% glycerol, and then with 100% glycerol ; and cuticular membranes finally mounted in glycerin-jelly.

Cuticular preparations can be kept indefinitely, before staining and mounting, in 70% alcohol ; placed in water they become excellent cultures of bacteria, fungi and protozoa (which feed on the adhering polysaccharides, not on the cutin) in a day or two.

§5. Survey of cuticular characters

The present section is a catalogue of the main characters which are present in cuticular preparations, together with some idea of the extent of their variation from species to species. In general the ranges of variation discussed indicate those normally encountered without examining plants of an extreme facies or with a very specialized adaptation, so that no mention is made of unusual extremes of structure or of features of very restricted occurrence. Any combination and number of these characters may be of diagnostic value in a particular group of plants. The first task is thus to survey the features found on cuticular membranes, and then to investigate the degree of variation each exhibits. After analysing the causes of variation the systematic value can be ascertained. Most of the comments made have been drawn from my experience in investigations of the three families mentioned previously, and, whenever relevant, examples are usually given from these groups.

Such a general and, it is hoped, purely objective survey of cuticular characters has not been previously compiled, and thus the different terms which have been introduced into the literature are quite uncorrelated. In many cases, for instance, several descriptive terms exist for a single situation (e.g. cuticular flanges, teeth, pegs or ribs). When an acceptable and non-ambiguous descriptive term is already available this has been adopted, but in some cases terms had to be coined, or existing unsuitable ones replaced. All accepted terms are printed in italics, and it is hoped that this will encourage nomenclatural stability.

Of the characters observed during microscopic examination of cuticular preparations some are quite easily observed on whole leaves with an ordinary hand-lens, or with the naked eye. In these cases microscopic examination usually gives a more quantitative or precise assessment of the character, although some points (such as the colour or " texture " of the indumentum, e.g. silky, bristly or velvety) may be lost with this medium. Other characters are wholly microscopic in nature, and it is convenient here to treat the two groups separately.

A. Macroscopic characters.

The four features discussed here are treated only from the microscopic viewpoint, although preliminary study of a leaf with a hand-lens or low-power binocular microscope should always be undertaken.

(1) *Leaf venation.*

The venation of a leaf, second to its general shape, is frequently the most obvious character, and descriptions of all new plants contain (or should contain) a note of its organization. The type of venation is often typical of broad taxonomic groups. In general, dicotyledons have leaves (or leaflets) with a single central main vein which is a continuation of the petiole, if this is present. This is known as a *midrib*, costa or main vein. In some leaves two or more main veins may be present, although that situation is more characteristic of monocotyledons. Branching from the midrib are a number of lesser *veins* or nerves of successively smaller order. Those branching directly from the midrib may be termed *lateral veins*, and they are usually very numerous. However, a limited number, from two or three to a score or more, are generally much more conspicuous than the rest and are here described as *major lateral veins*, as opposed to the less distinct *minor lateral veins*. In most descriptions " lateral veins " usually refers to the former only. The number of major lateral veins, their spacing, whether they arise in pairs or independently on either side of the midrib, the angle at which they arise, the curvature along their length, and their method and position of ending are all taxonomic features.

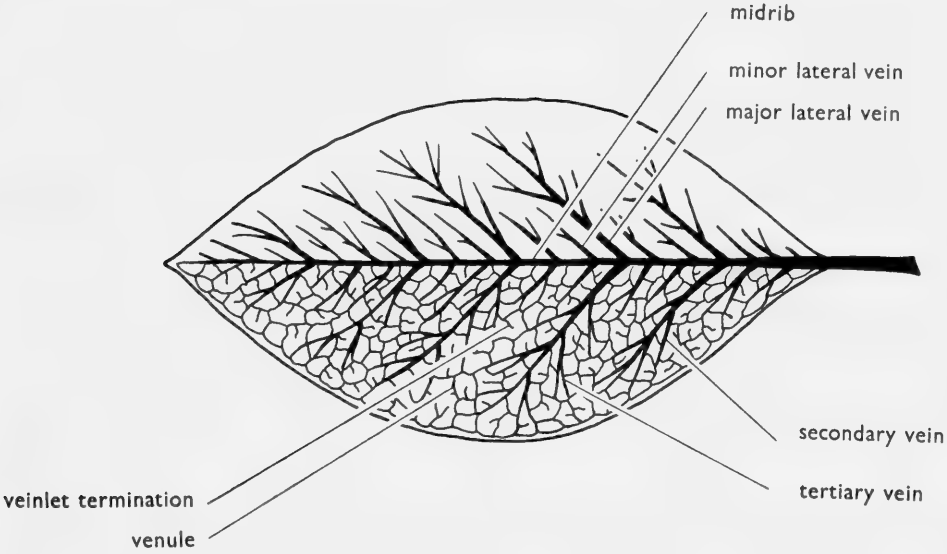
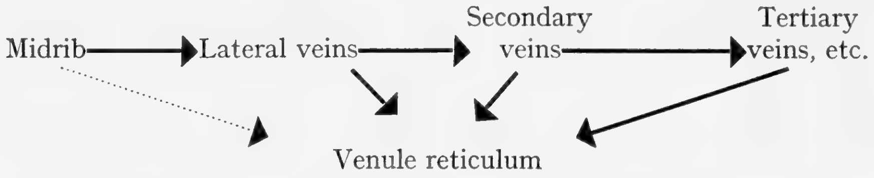


FIG. 3. Terminology of leaf venation.

Such a venation system is *pinnate*, but *palmate* systems also exist. In the latter case there are a number of main veins all arising from a single point and diverging outwards, and each usually has an accessory venous system resembling that of a pinnately veined leaf.

Generally, arising from the lateral veins is a series of *secondary veins*, from these *tertiary veins*, and so on. Unlike the branching of a tree, however, the smallest veins, the *venules* or veinlets, in most cases do not possess terminations, but usually join up to form an extensive *venule reticulum*. The number of orders of veins between the midrib and the venules is usually one or two only, but it may be more. The term venule is reserved for the smallest veins with no directional tendency. Whatever the number of orders of veins, however, there is in these types of leaves usually a system of venules which emanates directly from the midrib, and almost always one from all other orders of veins. The venation system (Fig. 3) may thus be represented :



The above systems of venation, terminated by a venule reticulum, are termed *closed*, but *open* systems, where a reticulum is not present, are found in some dicotyledons.

The spaces in the venule reticulum are known as *areolae*, veinlet-islands, vein-islets or inter-reticular spaces. Their shape and size vary considerably and, although difficult to measure, are often the cause of the different appearance of various leaves. Levin (1929) found that the average " vein islet area " is of considerable taxonomic importance.

Although most, or all, venules join up to form the venule reticulum there are often a number which end blindly, projecting into areolae, these being termed *veinlet terminations* (venule terminations). Hall & Melville (1951) calculated the " veinlet termination number " (number of veinlet terminations per square millimetre of leaf surface) and found it of diagnostic importance. It was stated to be uncorrelated with the number of areolae per square millimetre, and less variable over different parts of the same leaf and hence of greater systematic value. Later work by the same authors (1954) confirmed that the veinlet termination number was more constant than the number of areolae, but found that the two showed a slight positive correlation, and both a negative correlation with leaf size. Gupta (1961) improved Hall & Melville's methods by devising the " absolute vein-islet number " and " absolute veinlet termination number ", the product of the respective numbers and the leaf area. This, of course, cancels the variation due to leaf size and, although more laborious to calculate, should always be used when whole leaves are available. In certain disciplines, such as pharmacognosy and palaeobotany, however, whole leaves are often not available ; in these cases the non-absolute numbers should be used with the greatest caution.

Leaf venation is treated from a different aspect below, when its position as a cuticular character will become clear.

(2) *Distribution of trichomes.*

The very different degrees of pubescence shown by plants have given rise to a great variety of descriptive terms (e.g. hirsute, pubescent, pilose, ciliate, puberulent, etc.) which unfortunately have no universally recognized meaning. Using cuticular preparations the precise distribution and frequency of hairs and other trichomes can be measured, i.e. the individual trichomes can be counted and their positions noted. Taking into account the enormous variation that is encountered, only differences of a considerable degree are likely to be of taxonomic value, and the extremes of a range must be noted.

Precise data may thus sometimes replace such statements as " almost glabrous " or " sparsely pubescent ", but in general their compilation will not be worth the labour involved. Besides variation apparently uncorrelated with other factors the degree of pubescence is dependent more than most characters upon the environmental conditions and the age of the leaf.

Of much more value than simple trichome frequency is the relative frequency of trichomes on different parts of the same leaf. As is well known, hairs are usually more abundant on the midrib and veins of a leaf, and these regions are usually the last to become glabrous as the leaf ages. However, this is by no means always the situation. In the *Combretum psidioides* Welw. aggregate, for example, there are three taxa (treated by Exell (1961) as subspecies of *C. psidioides*) which differ only in their distribution of indumentum on the lower leaf surface : one taxon has a densely pubescent venule reticulum and sparsely pubescent to glabrous areolae (subsp. *psidioides*) ; the second a glabrous venule reticulum and tomentose areolae (subsp. *kwinkiti* (De Wild.) Exell) ; and the third a tomentose venule reticulum and areolae (subsp. *dinteri* (Schinz) Exell). Moreover, a further species in this aggregate, *C. grandifolium* F. Hoffm., differs not only in its larger leaves but also in having glabrous areolae and a sparsely pubescent to glabrous venule reticulum. This taxon, demonstrating the fourth combination, appears to be a further subspecies of *C. psidioides*. Dr. Exell and I have found that all four taxa belonging to this group have apparently no other constant differences, either macroscopic or microscopic, than the distribution of hairs. In many plant groups the distribution of hairs on the leaf margin is frequently also a diagnostic character.

The broad type of trichome, e.g. sessile glands, stalked glands, branched hairs, peltate hairs, long straight hairs or short curly hairs, etc., is also a character often used without resorting to the use of a microscope, although this is not to be encouraged. Small differences, often vital, may be not apparent with a hand-lens or binocular microscope, and very distinct taxa can easily be classed together. The key to the genera of *Sapotaceae* by Hutchinson & Dalziel (1931), for instance, is completely misleading due to a mis-statement on the type of hair present. I have found that the hairs described as " simple (not medifixed) " (as opposed to medifixed, stalked and thus " T-shaped " hairs) are in fact medifixed but sessile. Such errors would have been avoided if a microscope had been employed. There have been many erroneous statements concerning the trichomes of the *Combretaceae*. A hand-lens should only be relied upon when two or more very different types of trichomes are being searched for (e.g. in *Epilobium*), or special distinctive trichomes are sought (e.g. in *Urtica*).

As previously mentioned, characters of the texture or overall appearance (including colour) of the indumentum are lost in cuticular preparations.

(3) *Cork-warts and similar structures.*

Very frequently there are to be found on the cuticular preparations of leaves structures which are usually referable to wounds of one sort or another, but which, in some cases, represent cork-warts or related structures. Cork-warts are not abundant in nature, and they are usually constant in occurrence, so they are frequently useful in identification. In the mangrove genera of the *Rhizophoraceae,* for instance, they are present in all species of *Rhizophora* but in none of the other three genera. In West Africa, moreover, they are larger in *R. mangle* L. than in the other two species of that genus found there, and are said to be diagnostic in the field (Keay, 1953). They appear as small convex warts of corky tissue up to about 2 mm. across.

Microscopically the position of a cork-wart on the cuticular membrane is marked by a circular or less regular hole surrounded by modified epidermal cells (Plate 1 A). The latter are usually, though not always, thicker-walled and much smaller than the normal epidermal cells, and they are arranged in strict rows radiating for some distance from the hole. It appears as if the radiating cells are meristematic, being produced to repair the hole. These areas are thus very characteristic and conspicuous.

Unfortunately three types of wounds are extremely similar to the cork-warts. Purely mechanical accidents are marked by variously shaped, but usually long and scar-like, areas, the surrounding cells being identical to those of the cork-warts. In many cases, presumably in the case of more ancient wounds, or perhaps when only part of the outer wall of the epidermis has been removed or damaged, a very thin cuticular membrane, usually scarcely stainable, has grown over the wound, this being either amorphous or with very thin cell walls. The cells on these areas, if present, are usually normal-sized, although small cells would have been expected if they were meristematic. Insect punctures are also frequently found on leaves, these more often resembling cork-warts than accidental injuries, and probably not being distinguishable from the former. They are of the same order of size as a small cork-wart, and usually smoothly circular in outline. They were also reported by Orgell (1955), who observed an identical structure. Moreover he found that they frequently became occupied by corky or gummy plugs, showing a very close analogy to cork-warts. The third type of wound which I have observed is a fungal attack, found in the form of hemispherical shining excrescences on both leaf surfaces of one specimen of *Buchenavia kleinii* Exell. The hole left by these fruiting bodies after maceration is surrounded by the radiating rows of small cells typical of cork-warts (Plate 1 B).

Although cork is more or less resistant to the macerating solutions used in the present study, owing to its chemical similarity to cutin, it is not preserved on the cuticular preparations as the wart or plug is not connected to the cuticular membrane, but falls away during maceration. Where a wound has healed over, and occasionally a cork-wart has dropped out, however, the tissues may become covered with a thin cuticular membrane, as observed above.

Thus, although wounds have no intrinsic taxonomic value, they are important as they closely resemble cork-warts, and thus render the latter considerably less useful in systematics. This equally applies to macroscopic and microscopic studies.

Other types of structures found on leaves, although often not macroscopic characters, are sufficiently similar to cork-warts to be mentioned here. In many cases they may be referred to excretory glands (e.g. salt glands, chalk glands, sessile hydathodes, etc.), which may be macroscopically very conspicuous. The actual gland is frequently only very thinly covered with a cuticular membrane, and the adjacent cells may be radially arranged or otherwise modified. Holes may also be found in the cuticular membrane due to the presence of modified epidermal cells (e.g. calcified or silicified cells) which have no cuticular covering, but these are usually surrounded by normal epidermal cells, as are the terminations of long idioblasts. Cells containing crystals frequently break through to the surface of the leaf, and these are often surrounded by radially arranged cells, as in wounds. In this connexion the minute pimples and translucent spots common on some leaves and often used by taxonomists may be mentioned. They are not epidermal characters : the former are due to abnormally large epidermal or subepidermal cells, usually containing crystals ; the latter to similar cells which interrupt the mesophyll. In fact in most cases the translucent spots correspond with small pimples, although either one may be present in the absence of the other, or rarely both exist together on the same leaf but are unconnected.

Wound-like structures are frequently present on cuticular preparations in such a regular manner that they are almost certainly not wounds, but no macroscopic equivalent is visible and no microscopic subepidermal structures seem to be connected with them. In *Terminalia catappa* L., for example, all specimens examined showed ragged holes along the leaf margin (Plate 1 C), and *T. chebula* Retz. possesses similar areas there and on the lower epidermis (but not the upper). In *T. bursarina* F. Muell. similar areas are present in the major lateral vein axils on the upper epidermis, corresponding to the presence of domatia on the lower epidermis. They are caused by the growing of the domatia (see below) right through the leaf to the upper surface.

Besides hydathodes, other water-secreting organs are the *water-stomata*, which are usually distinctly different from the normal stomata in some way (e.g. by their smaller or larger size). They are, of course, not macroscopic structures, although they are in some families united into groups which appear as small surface spots (Solereder, 1908). In the two Combretaceous mangrove genera, *Lumnitzera* and *Laguncularia*, large stomata which may be water-stomata are found scattered over the leaf surface. Usually they are surrounded by enormous subsidiary cells, and around the latter the epidermal cells may be radially arranged (Plate 1 D). In extreme cases the radially arranged cells form an extensive area resembling those around a wound or cork-wart, and indeed in some instances the large stoma has disappeared, leaving a hole. Solereder (1908), in fact, states that stomata may become underlaid with a development of cork which ultimately erupts to give rise to a cork-wart. Cork-warts have not been recorded from the *Combretaceae*, however, and any connexion between the observed structures and cork is conjectural.

In addition *Lumnitzera* possesses wound-like areas along the leaf margin (cf. *Terminalia catappa*) which appear to be distinct from those developing around the large stomata, and which are also unconnected with the shallow marginal pits thought to be domatia.

Finally, the presence in many instances of thin-walled areas, often only a few cells in size, on the leaf epidermis may be noted. In some cases the component cells are much more or much less undulate-walled than the rest of the epidermal cells. Their origin is unknown.

It may thus be seen that the presence of " spots ", " pimples " or " warts " on leaves may be due to any one of a whole range of epidermal (or subepidermal) structures, which only a microscopic examination will determine. Their study is, however, hampered by the presence of various types of wounds and punctures of external cause which may extremely closely resemble the structural features and thus limit the determinative value of the latter.

(4) *Domatia.*

The term *domatium* is used to denote a small cavity of very varying form, found on almost any vegetative part of the plant, which is inhabited, or thought to be inhabited, by some type of animal. Domatia have been almost completely neglected from a taxonomic viewpoint in the past, and so limited is our knowledge of them that they are treated rather fully here. It will be seen that on occasions they may be of great diagnostic significance.

Domatia vary from cavernous passages in rhizomes, stems or petioles to minute pits or hair-tufts on the under surfaces of leaves. The former are usually occupied by ants, and the literature concerning these so-called myrmecodomatia is fairly extensive (see Uphof, 1942). The smaller domatia, which may be up to about 4 mm. in diameter, are often said to be occupied by mites or similar arthropods, although good evidence for this is usually lacking. They are, however, called acarodomatia, a term suggested by Lundström (1887), and the plants on which they occur acarophytes or acarophilous plants. Elliot (1911) stated that the mites could be seen scurrying away from the appropriate regions of the leaves of many common English trees when the former were disturbed with a needle, and Mani (1964) reported that acarodomatia may be inhabited by mites such as species of *Tarsonemus*.

The literature relevant to acarodomatia is remarkably scanty, the only important papers being a biological study by Lundström (1887) and a review by Penzig & Chiabrera (1903). The latter account is excellent from many aspects, and thus any sort of systematic review is unnecessary here. The authors reported acarodomatia from about 425 species and 175 genera in 44 families, all woody dicotyledons. They are most abundant in the *Rubiaceae*, in which Penzig & Chiabrera recorded 54 acarophilous genera. As these authors predicted, since 1903 many additional genera have been shown to possess acarodomatia, but few are of very special note.

An exception is *Dioscorea*, which is the only monocotyledonous genus and also the only herbaceous one known to possess acarodomatia.

Apart from the fact that they are more or less confined to woody dicotyledons there is no connexion whatsoever between the type of leaf and the presence or type of domatia. They do perhaps tend to be rarer on leaves with inconspicuous venation, but they are not absent from these and any generalization would have a number of exceptions.

The commonest types of acarodomatia are small pockets or pits in the axils of the main veins with the midrib on the lower leaf surface. Since the whole domatium, whatever its shape, is lined with epidermis throughout, cuticular preparations provide excellent transparent models of the domatia and afford the best method of studying their anatomy. The preparations can be studied both with a high-power and a binocular microscope. The domatia are very conspicuous on the cuticular preparations since, where there is an extended piece of leaf tissue overarching the main bulk, the cuticular membrane overlaps and so is three layers in thickness.

There is in all probability no system of classification that will accommodate all types and grades of domatium. The usefulness of some sort of classification is, however, obvious, and the one which I use to cover leaf domatia has proved relatively satisfactory. Two main types of domatium are recognized (Fig. 4):

Marsupiform (*pocket-shaped*) *domatium* (*domatium marsupiforme*) (Plate 2 A, B).

All grades, from an extremely highly developed " pocket " to a situation which is scarcely able to be called a domatium exist. They are found in the axils of the major lateral veins with the midrib, or more rarely of secondary veins with major lateral veins. In a leaf with very conspicuously raised veins a cuticular preparation will always show folding of the epidermis of the veins over that of the areolae, and this effect is of course doubled at a vein branch, especially the branchings from the midrib. Leaves of *Buchenavia reticulata* Eichl., for instance, show this to a marked degree. In some leaves this folding is only evident in the major lateral vein axils, and here a V-shaped suggestion of a domatium is to be seen, as, for example, in *Terminalia mollis* Laws. Penzig & Chiabrera (1903) classed this species as domatium-bearing, but the case is debatable. In the genus *Terminalia*, as probably in many others, a whole series of types from that of *T. mollis* to the most complex pocket-shaped domatium is to be seen. This gradation can be visualized as the gradual filling-in of the notch of the V to form a ▽-shaped triangular pocket where all traces of the " arms " of the V have disappeared. These latter types bear no relation at all to the conspicuousness of the veins, often being found on leaves with an almost planar venation. The basal point of the triangle points towards the vein axil, and the mouth of the domatium, forming one side of the triangle, away from it. Thus the depth of the domatial cavity, which lies between the leaf surface and the triangular area of tissue, is parallel to the leaf surface. The mouth of the pocket-shaped domatium is therefore at its broadest and most distal point.

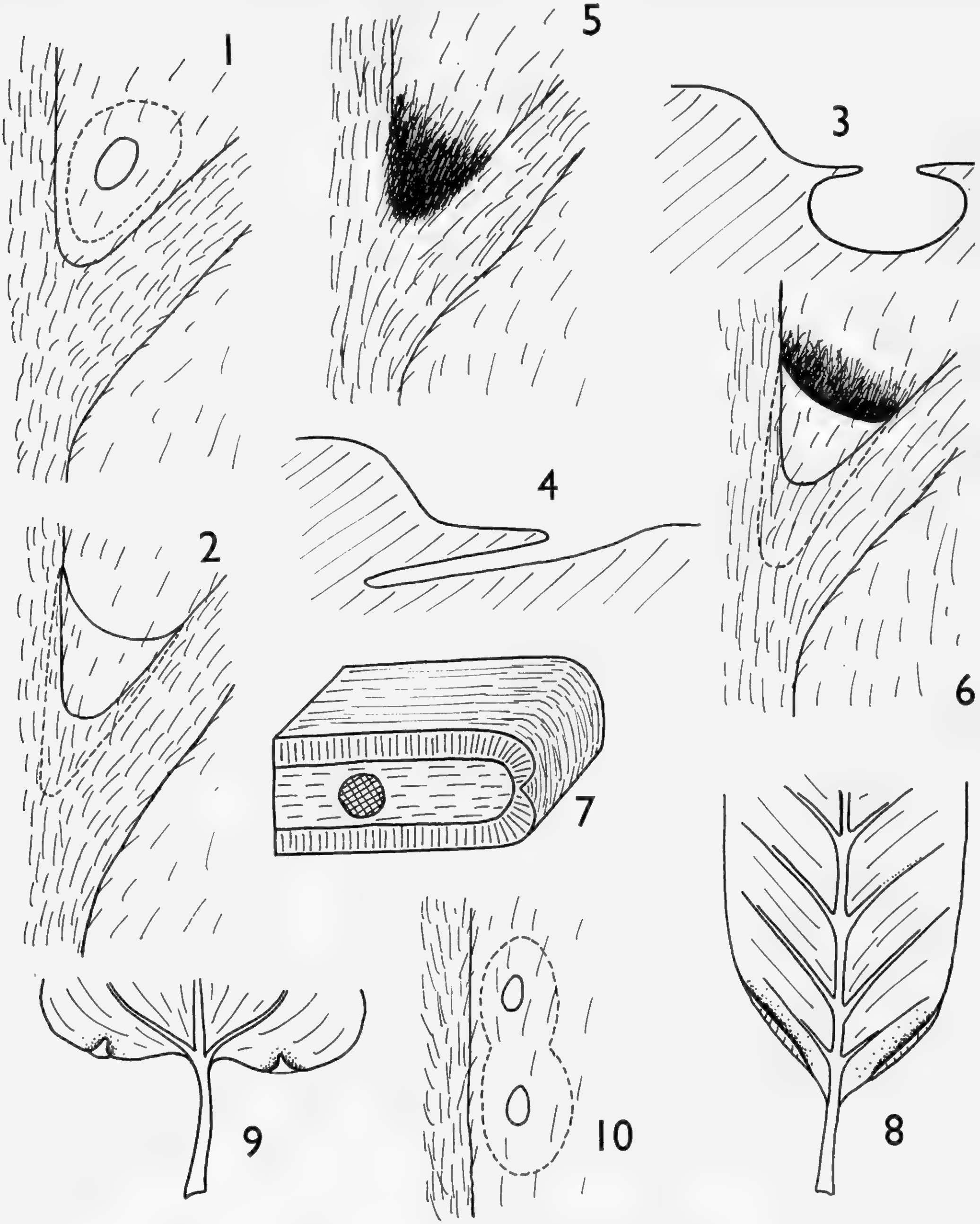


Fig. 4. Types of domatia: 1, primary-axillary lebetiform. 2, primary-axillary marsupiform. 3, 4, vertical sections of 1 and 2 respectively, at angle bisecting the vein axil. 5, primary-axillary hair-tuft. 6, primary-axillary pubescent-marsupiform. 7, marginal lebetiform, in section (*Lumnitzera*). 8, baso-laminar revolute (*Strephonema*). 9, baso-laminar revolute (*Dioscorea*). 10, twinned supernumerary lebetiform (*Terminalia catappa*).

Lebetiform (*bowl-shaped*) *domatium* (*domatium lebetiforme*) (Plate 2 C, D).

As with the preceding type all grades of bowl-shaped domatia are to be found, the simplest of which might be visualized as a shallow depression in the leaf surface. Such shallow depressions are found in *Lumnitzera*, on the leaf margin, and have been referred to as domatia by Backer (*fide* van Steenis, *in litt.*). In most cases, however, bowl-shaped domatia are found in the axils of veins. In *Terminalia plagata* Merr. well-developed domatia are present in the major lateral vein axils, but in the secondary vein axils reduced forms, the shallow depressions visualized above, are to be found. A series may again be traced where the opening of the hollow becomes smaller, and/or the hollow itself becomes deeper and wider, the genus *Terminalia* showing all types of intermediates. As noted by Penzig & Chiabrera (1903), in some cases (e.g. *T. microcarpa* Decne.) the pore of the domatium may be at the level of the rest of the leaf surface, the pit being entirely internal, whereas in other cases (e.g. *T. catappa*) the pit is only partially sunken into the leaf tissue, the pore being at the apex of a small dome. In the best-developed bowl-shaped domatia the pore is extremely small in proportion to the large pit beneath (e.g. *T. microcarpa*). In the present type the depth of the domatium is thus at right-angles to the leaf surface. The pore is usually in the centre of the domatium as viewed from above, but it may be placed elsewhere. In some abnormal forms of domatium in *T. catappa* there are two pores. The pore may be circular, elliptic or slit-like : in the last case it is most frequently found on elongated domatia, the elongation of both domatium and pore being parallel to the lateral vein.

The above two types of domatium are nearly always distinct, and it is suggested that they arose independently, from the overarching veins and the shallow hollow respectively. Intermediates, although rare, are apparently present, but they are thought more likely to represent the points of convergence than of divergence. As shown above, increasing stages in complexity of both types can be traced which are difficult to interrelate. In apparently intermediate types (e.g. *Terminalia moluccana* Lam.) the bowl-shaped domatium has a large pore which is distal to the vein axil, and the cuticular membrane is often not trebled at its distal edge. The trebled membrane thus forms a crescent rather than a circle, and moreover the depth of the domatium appears to be parallel to the leaf surface, although it may not be so. This type obviously closely resembles the pocket-shaped domatium. The latter may also approach the intermediate situation by the narrowing of the opening. The domatium of *Buchenavia fanshawei* Exell & Maguire, which is classed as the bowl-shaped type, may possibly be a modified pocket-shaped type as all other species of *Buchenavia* which possess domatia have the latter type.

Two other types of domatium may be recognized : the first often very well defined ; the second of a highly dubious nature.

Revolute (*rolled-margin*) *domatium* (*domatium revolutum*).

In this type the leaf margin is inrolled, or folded under like the flap of an envelope. Inrolled domatia are found in such plants as *Hevea brasiliensis* (Kunth) Muell. Arg.

(Penzig & Chiabrera, 1903) and *Strephonema* spp. (De Wildeman, 1923 ; confirmed by my own examination). The inrolling is present at the base of the lamina, just above the petiole on either side. The degree of inrolling varies considerably, and the status of the domatium is thus dubious. In the flap-like domatia a specialized portion of the lamina is folded under ; if this is folded back it forms a regularly shaped projection from the leaf margin. It was found in dicotyledons (e.g. *Ilex* sp.) by Lundström (1887) and later in *Dioscorea* by De Wildeman (1904). The latter author described the structure in *D. smilacifolia* De Wild., in a new species (*D. acarophyta* De Wild.), and subsequently, from 1912 to 1914, in ten other new taxa. Burkill (1939) showed that these twelve represented three species only : *D. smilacifolia*, *D. minutiflora* Engler and *D. pynaertii* De Wild., but he discovered domatia in a fourth closely related species, *D. praehensilis* Benth.

Hair-tuft domatium (*domatium fasciculatum*).

The vein axils of the otherwise sparsely pubescent or glabrous leaves of a large number of species of trees may be densely pubescent or pilose, and these tufts of hairs have been considered to be domatia by Lundström (1887) and others. If mites do take refuge in them this may be accepted. Amongst British trees *Tilia*, *Alnus* and *Corylus* are examples. In this type there is no modification of leaf tissue other than the development of the hairs. Although many trees have leaves which are at first densely pubescent and later scarcely so, and the last areas to lose the indumentum are the veins of the lower leaf surface, the hair-tuft domatia are often well defined, even if their association is dubious. They are frequently found in connexion with the slightest development of a pocket-shaped domatium.

Lundström (1887) recognized more or less the same four types of domatia as I do, although a much smaller range of forms was considered. Penzig & Chiabrera (1903) closely followed Lundström, but described six types. The " hollow "-shaped (*fossette*) and " pocket "-shaped (*tasche* or *borsette*) domatia were each divided into two categories according to the presence or absence of hairs. It is not, however, advisable to distinguish between glabrous and pubescent types because the difference is apparently of no consequence and every type of intermediate is to be found. Penzig & Chiabrera appear to separate the " hollows " from the " pockets " in that the former are sunken into the leaf tissue with their openings on the level of the leaf surface, whilst the latter (which may be either bowl-shaped or pocket-shaped in my system) are raised above the leaf surface. Intermediates are, however, as common as either extreme, and the classification is considered inferior to that used in the present study. It so happens that Lundström's scheme does not commit itself to agreement with either Penzig & Chiabrera's system or mine, since all his " hollows " were in fact wholly sunken into the leaf, no raised hollows (as in *Terminalia catappa*) being noted.

The latinized terms have been given for the convenience of concise description. The position of the domatia can also be described by the following terms : *marginal*, for those at the leaf margin (e.g. *Lumnitzera*) ; *primary-axillary*, for those in the major lateral vein axils (the most common type) ; *secondary-axillary,* for those in the secondary or lesser vein axils (e.g. *Tilia* spp., *Terminalia oreadum* Diels and *T. plagata*) ; *baso-laminar,* for those on either side of the lamina base (e.g. *Quercus robur* L., *Strephonema* spp. and *Dioscorea* spp.) ; *extra-axillary,* for those just below each major lateral vein axil (e.g. *Rudgea lanceolata* Benth.) ; and *supernumerary,* for those not associated with any particular part of the lamina (e.g. *Terminalia catappa,* where they are found scattered up the side of the midrib apart from the vein axils ; and *T. grandiflora* Benth. and *Conocarpus* spp., where they are found very sparsely scattered over the lower leaf surface). They are occasionally also found elsewhere : for example in *Schinus terebinthifolia* Raddi domatia revoluta are found on leafy wings to the rhachis of the pinnate leaves ; and in one or two genera they have been reported from young twigs and petioles.

In most cases the epidermis lining and around the domatia is little or not modified. In the axils of major lateral veins there is usually a patch of small straight-walled isodiametric cells, and when a primary-axillary domatium is present this area is merely enlarged, and this type of epidermis lines the domatium. In some cases, however, the cells do differ in some way from those surrounding the domatium, usually being smaller. In *Terminalia catappa* the adjacent cells are often arranged in radial files for a short distance. In *Conocarpus erectus* L. var. *erectus* the epidermis is absolutely identical in, near and away from the domatia, even to the extent of the possession of stomata. In *C. erectus* var. *sericeus* Forsstr. ex DC. the epidermis is very densely pubescent, but that lining the domatia is more or less glabrous, as in var. *erectus.*

In many cases the domatia are associated with an abnormal amount of hair development in, on or around the actual structure. In some species, e.g. *Thiloa gracilis* (Schott) Eichl., the hairs are of a peculiar type not found elsewhere on the leaf. In a few species gland-like structures are to be found in the domatium. These were noted in *Anacardium* by Lundström (1887), and in the *Combretaceae* they have been found in *Buchenavia parvifolia* Ducke and *Terminalia archboldiana* Exell, though not very frequently. The nature and function of their secretion, if any, are unknown. It is just possible that the deeply sunken glands found on the leaves of *Laguncularia* are homologous with domatia, but this is not likely as they are found on both epidermides and have an extremely narrow slit-like opening at the surface.

The examples cited above clearly show that domatia may have a considerable value in taxonomy, although they have rarely been used. An extreme case is perhaps that of *Buchenavia fanshawei* which has well-developed domatia lebetiformia. Of the other 22 species examined in this genus 13 have domatia marsupiformia and nine lack domatia altogether. Thus much use of this fact was made in constructing a key to the genus (Exell & Stace, 1963). In the *Combretaceae* domatia revoluta are found in all six species of *Strephonema,* which is usually treated as a separate subfamily from the other genera, all of which lack these domatia. The remaining genera belong to three groups, of which two contain eight genera each. In one of these groups (*Terminalieae*) four genera possess domatia (three lebetiform and three marsupiform); whilst in the other (*Combreteae*) all eight genera possess marsupiform domatia only. The third group (*Laguncularieae*) consists of three genera, of which one possesses peculiar marginal lebetiform domatia. Thus in the *Combretaceae* the occurrence of the various types of domatia to some extent agrees with the generally accepted subdivision of the family. This is not the usual situation, however. Penzig & Chiabrera (1903) recorded all six of their types from the *Rubiaceae*, and four from several genera, and in general domatia are useful in identification at the specific level only.

There is no reason not to believe that all specimens of a domatium-bearing species do possess domatia, although these may be sparser in some cases and may be lacking altogether on some parts of the plant such as the sucker shoots. Bloembergen (*fide* van Steenis, *in litt.*) found that *Alangium chinense* (Lour.) Harms and *A. kurzii* Craib possess domatia in most of Asia, but not in Malaysia, but, as this situation has never been reported elsewhere, the absence of domatia in Malaysia or the identity of the species in the two areas needs careful checking. In the genus *Terminalia*, of which I investigated 160 species, no such geographical variation was noted. For example *T. catappa*, a native of Asia and Australasia, possesses very typical domatia whether in its native countries or planted in Africa or America ; and *T. arjuna* (Roxb.) Wight & Arn., a native of India, lacks them there or when planted elsewhere in Asia, Africa or America. A different type of geographical variation, however, was discovered in *Terminalia*. Of the 160 species studied 50 (31%) possess domatia, of which 16 (32%) have domatia marsupiformia and 34 (68%) domatia lebetiformia. However, in Australasia 21 (62%) of the 34 examined species possess domatia, and the figures for other continents are : Malaysia 19 (58%) out of 33 ; Asia 4 (13%) out of 34 ; Africa 1 (3%) out of 39 ; and America 7 (23%) out of 30. Thus as one travels east or west from the islands between Australia and Malaysia the percentage of domatium-bearing species drops sharply. The proportion of the two types of domatia does not significantly differ from continent to continent.

Extremely little is known about the formation or function of acarodomatia, but despite suggestions to the contrary it is obvious that mites play no part in their formation. It is more likely that the mites inhabiting the domatia (if this is a regular occurrence) are in a purely chance association. It is possible that they may enlarge the domatia somewhat once they have taken possession of them, and this may be the cause of the deep domatia in *Terminalia bursarina* which sometimes reach the upper epidermis. There is no necessity, however, to consider that this is not a natural plant process. Lundström (1887) claimed that the domatia of *Psychotria*, *Coprosma* and *Rhamnus* developed in the absence of mites, but, although he was doubtless correct, his experiments have never been repeated under the exacting conditions necessary to exclude all mites. Mani (1964) also stated that the mites did not participate in domatium formation. Bailey (1924) showed that American myrmecodomatia developed in the absence of ants. Whilst it is true that seedlings (and often suckers) lack domatia, these developing only at a later stage, seedling and sucker leaves often differ in many ways from the other leaves, and van Steenis (1953) states that in *Nothofagus* domatia develop by the young sapling stage.

Good evidence for the non-participation of mites in domatium formation is that domatia are definitely formed in predisposed places: e.g. at the bases of the laminae in *Dioscorea,* or just below each major lateral vein axil in *Rudgea.* If the domatia were formed by mites they would not be so distributed, and neither would they be so constant in their presence (on all individuals in all geographical areas) and structure. In the case of primary-axillary domatia these are not always found in all major lateral vein axils. They are always better-developed towards the lamina base, but in some species, e.g. *Terminalia bursarina, T. grandiflora* and *Nothofagus menziesii* Oerst., they are found only in the lowest axil on each side of the midrib, or in the latter two sometimes also in the next axil. Furthermore, only certain species in any one genus may possess domatia, e.g. only two species out of about 40 in *Nothofagus* (van Steenis, 1953) and four out of several hundred in *Dioscorea* (Burkill, 1939). The domatia are often very hairy, and since many mite-produced galls also possess this character, definitely as a direct result of the animals' activities, it has been suggested that pubescent domatia are also formed in this way. There is no reason to believe this, however, and in most *Combretaceae,* at least, the pubescent domatia (often the only pubescent parts of the leaf) are relics of a wholly pubescent juvenile state, and the hairs may wear off even here at senescence.

The very young leaf develops domatia marsupiformia by an extension of the pocket tissue over the vein axil, but, if domatia lebetiformia evolved in the manner previously suggested, ontogeny does not repeat phylogeny as the pits do not appear to develop by an extension of tissue encroaching over a hollow. In the cases examined (especially *Conocarpus erectus*) the pit forms internally, and at first is only marked by a primary axillary pimple. Later a pore develops in the top of the pimple, and this enlarges to a varying degree. The hollow appears to develop internally. Different stages may be seen on one leaf, development being acropetal. This is an important argument against any participation by mites in domatium formation. Holtermann (1893), however, seems to suggest that the pits of *Conocarpus* do develop by means of an epidermal intucking, and not as I have observed.

The situation regarding domatia has been discussed at some length, although numerous other points could have been included, since little is known of them in general, and they have been largely neglected by taxonomists. With regard to their position and structure they may be very useful in identification, but their biological significance is highly obscure. They are doubtless often used as a shelter by mites and other similar minute arthropods, but in the great majority of cases no animals have been connected with them. This is in marked contrast to the case regarding myrmecodomatia. The prefix " acaro- " is thus best rejected and replaced by one suggestive of the organ on which the domatia are found, e.g. *phyllodomatia.*

B. MICROSCOPIC CHARACTERS.

(1) *Epidermal cells.*

There are a large number of directions of variation to be found with respect to the epidermal cells, even omitting the several characters which are not apparent from a purely surface examination, but they have rarely been used by taxonomists.

In certain regions the epidermal cells are modified, notably over the veins and leaf margin and around the stomata and trichome-bases. This section deals only with the areas not so modified.

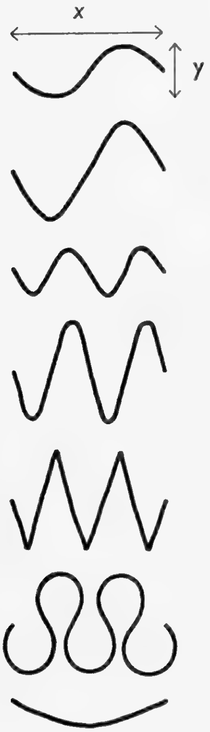
Although the shape, size and other characters of the epidermal cells exhibit a wide range of genotypic variation, which in many cases has definite taxonomic application, the cells certainly show an extreme degree of phenotypic variation which is elsewhere only paralleled by characters such as pubescence and petal colour, etc.

One of the most obvious features of the epidermal cells is their shape ; this is often quite different on the two epidermides. This fact is often of systematic importance, although Odell (1932) decided that it indicated that cell shape was " of no diagnostic value ". The cells are usually *isodiametric*, i.e. more or less the same in length and width, with any scattered elongated cells randomly orientated. In some dicotyledon leaves, however, as well as in many groups of monocotyledons, the epidermal cells are predominantly elongated. This feature usually occurs in narrow leaves, the cells lying parallel to, or less often at right-angles to, the leaf axis. In cases of isodiametric-celled epidermides some species have a characteristically low (e.g. *Guiera senegalensis* J. F. Gmel., Plate 4 D) or high number of walls to each cell, this factor markedly altering the appearance of the epidermis.

In some species the epidermal cells are arranged in small groups separated by thicker than normal cell walls, where it appears that an originally single cell has retained its identity after many subsequent divisions. Species of *Avicennia* show this feature well. A related phenomenon is the anticlinal division of the epidermal cells, where cells are divided by one or more thin straight walls which cut a normal-sized cell into two or more parts. Such secondary division (i.e. occurring after normal epidermal cell division has ceased, and not being accompanied by an increase in size) is often taxonomically important. In the genus *Laguncularia*, for example, it is absolutely constant, and it is not well developed elsewhere in the family *Combretaceae*.

The term " wall " is here used as an abbreviation for the apparent cell wall produced by the cuticular flanges, and it should always be borne in mind that the actual cell wall was present for some distance on either side of these. For this reason some workers prefer the term " cell outline ".

The anticlinal walls of the epidermal cells are either *straight*, *curved* or variously *undulate* or sinuate (cf. Plate 3 A, B). This is undoubtedly of taxonomic use in some instances : it has been used as a major character in *Lemna* and is useful in many groups of *Combretum*. For some unknown reason straight-walled epidermal cells are commoner in xeromorphic plants than in mesomorphic ones, which typically have undulate cell walls. The relative advantages and disadvantages of undulate walls are unknown, but Wylie (1943), who attributes a conductive function to the epidermis, suggests that their advantage is to increase the area of contact between adjacent cells. If this is so it is surprising that undulate walls are not commoner in xerophytes. The type of undulation is very various ; the " waves " may be most easily measured in exactly the same terms as light waves, i.e. in the three variables *frequency*, *amplitude* and *wave-length*. In the present study the frequency was usually expressed in terms of wave-lengths per wall, but in some cases it seems that the number of peaks (i.e. half wave-lengths) per cell may be a less variable value. There may be considerable or very little variation in the degree of undulation on one leaf, but the undulation often markedly decreases towards the leaf margin and veins. It will be seen from Fig. 5 that the three variables mentioned above aptly express all the characters of the undulations but one, i.e. the shape of the waves. These may usually be described as U-shaped, V-shaped or Ω-shaped. In some species peculiar shapes of undulation are found with ornamentations, in the form of knobs, ridges or T-shaped thickenings, on the outer side of the crest of each wave. Curved epidermal cell walls may be described as having half a wave-length.



Frequency	Wave-length	Amplitude
1·0	x	y
1·0	x	$2y$
2·0	$x/2$	y
2·0	$x/2$	$2y$
2·5	$2x/5$	$2y$
2·5	$2x/5$	$2y$
0·5	$2x$	y

FIG. 5. Types of cell-wall undulation.

The exact causes of epidermal cell-wall undulation are unknown, the two main theories involving the suggestions that it is due to the tensions set up between the mesophyll and the epidermis, and that it is caused by the method of hardening of the differentiating cuticular membrane (Watson, 1942). It has been found that whereas many leaves have the epidermal cells undulate-walled throughout the height of the cells, some have only the outer part of the wall undulate, and thus the second hypothesis is by far the more likely. Sifton (1963) has provided further evidence supporting Watson's theory. Amongst species examined in the present study the situation where only the outer part of the wall is undulate is very conspicuous in *Ramatuella*. Watson, however, was able to produce either condition in mature ivy leaves by varying the illumination during development, so that the character is probably rarely of taxonomic use. In some species with straight walls the isolated cuticular membranes show the tips of the cuticular flanges to be irregularly undulate, but this is probably due to the effect of removing the epidermal cells. It is especially noticeable in *Conocarpus erectus*.

As mentioned above, the cell shape is often different on the two epidermides, the chief varying factor being the degree of undulation. In almost all undulate-walled leaves the amount of undulation is greater on the lower than on the upper epidermis. In many cases the former is markedly undulate-walled and the latter straight-walled. Odell's (1932) remark that a few leaves of *Acer pseudoplatanus* L. may show the reverse of this situation, which the bulk of the leaves exhibit, needs to be checked. Some species, however, do possess a markedly more undulate-walled upper epidermis than lower, e.g. *Terminalia microcarpa*, *T. plagata* and others.

Epidermal cells vary tremendously in size, average widths being about 20–30 μ. Even on typically large-celled epidermides, however, small cells are usually to be found scattered. Some epidermides, in fact, are characterized by their extremely variable-sized cells. That cell size might be of taxonomic value is indicated by the knowledge that polyploids usually have larger cells than diploids, although this is better shown by the stomata than other epidermal cells. Solereder (1908) mentions the fact that certain species are characterized by a particularly small- or large-celled epidermis, and this has been noted in the present study. *Avicennia marina* var. *rumphiana* (Hallier f.) Bakh., for example, has a notably smaller-celled epidermis than other varieties of this species. *Lumnitzera littorea* (Jack) J. O. Voigt has a smaller average cell size than has *L. racemosa* Willd., although some overlap occurs and this character, like all others, fails to separate the two species on surface cuticular characters in all cases. The cell size is frequently different on the two epidermides, as is cell shape. Solereder (1908) states that in general the upper epidermis is composed of larger cells than the lower, but the opposite was found in the present study. Characters such as the comparative sizes of parts of the same leaf are extremely useful as the different parts are all equally affected by external conditions, e.g. the presence of upper epidermal cells twice as large as the lower epidermal cells is a better diagnostic character than the presence of upper epidermal cells of an average length of 40 μ. The cell size usually decreases towards the leaf margin and apex.

Although the boundary between the cuticular membrane and the cellulose cell wall is usually a smooth line, interrupted only by the cuticular flanges, in some species regular cellulose pegs protrude outwards into the cuticular membrane, which becomes very thin in these regions. This may or may not be accompanied by an extension outwards of the cell lumen in the corresponding position. In either case small elliptic or circular areas are seen on the cuticular membranes where the thin membrane is less deeply stained. Such areas are very well developed in *Combretum obanense* (Baker f.) Hutch. & Dalziel and certain of its relatives, but in all other species of this genus they are unknown. The thin areas are frequently present in the bulge of each undulation, and in *C. obanense* they are so conspicuous that the normal differentiation between cuticular flanges and non-flange areas is entirely masked, except on the veins. The epidermis in this case appears to be composed of minute cells about 5–10 μ across, with extremely thick walls. Other situations have been described where the outer epidermal cells contain large pores, the cell contents having been lost. The origin of the pores in the cuticular preparations of *Cinnamomum* obtained by Marlier-Spirlet (1945) is obscure.

The surface of each epidermal cell may be flat or convex, or bear a small conical process. The latter is known as a *papilla,* and the epidermides or cells which bear papillae are said to be papillate, but unless the papillae exceed a certain length they are not seen on surface preparations of cuticular membranes. They may, however, be viewed on folded-over pieces of membrane. All gradations from simple conical papillae to long structures better described as hairs exist, and if they are long enough to become folded over on cuticular preparations they are visible in surface views. They are often considered to be taxonomically important. The papillae are usually centrally placed on the epidermal cell, but they may be found on one corner of each cell, as in *Combretum zenkeri* Engler & Diels. Elsewhere in this large genus papillae have been recorded in less than half a dozen species, e.g. *C. lanceolatum* Pohl ex Eichl., and in all cases are of the central type.

(2) *Leaf venation.*

The epidermal cells above and below the veins are usually variously modified, so that leaf venation is a cuticular character. Characters of the venation which are microscopic alone, as opposed to the type of venation (which is a macroscopic character), are the extent and nature of the modification of the epidermal cells.

The midrib and the lateral, secondary, etc. veins are usually enclosed or capped by sclerenchyma, which may or may not reach either epidermis. In any case the epidermis above and below these veins is usually markedly modified, in the majority of cases the cells being elongated parallel to the veins. These elongated cells are usually rectangular, and, even if the epidermal cells of the areolae have undulate walls, straight-walled. In general the more xeromorphic a leaf the less conspicuous are the veins on the epidermis. Usually the degree of modification of the epidermis is proportional to the prominence of the veins, hence there tends to be a much greater modification on the lower than on the upper epidermis, although this is not always so. In most cases a more modified epidermis has more narrowed and elongated cells over the veins. The ends of the cells may be truncate, oblique or almost pointed and interlocking (prosenchymatous) ; and the cells arranged end to end in numerous parallel rows, or less regularly placed. In many cases, especially when the midrib is well developed on the epidermis but the cells are not very narrow, the cells are secondarily subdivided at right-angles to the midrib, and in these cases the cells may be squarish or even broader than long. Some leaves, most frequently rather xeromorphic leaves with a prominent midrib but rather inconspicuous veins and venules, have the epidermis modified over the former into strict rows of broader-than-long cells, the primary and secondary cell divisions being indistinguishable because all the cuticular flanges are equally thick. Examples found in the *Combretaceae* are *Strephonema* spp., *Combretum demeusei* De Wild., *Terminalia laxiflora* Engler and many others. This effect is almost always more greatly developed on the upper epidermis, and furthermore the cells of the veins of lesser prominence show it to a progressively lesser degree.

The lesser veins and venules showing no directional tendencies have a different anatomical structure. Above and below, or below only, many of them are bounded by a dorsiventral extension, the *vein-extension* or vein-rib, which consists of living cells elongated parallel to the venules and abutting on to the epidermis below and often also above. Wylie (1943) considers that these, as well as the epidermis, constitute a conductive system supplementary to the venous system. When a venule is connected to the epidermis in this way the latter is modified. Thus it may be seen that, as with the major veins and the midrib, the upper epidermis is modified to an equal or lesser extent than the lower epidermis over the lesser veins and venules. The modification of the cells over the venules (Plate 5 B) is similar to but much less developed than that over the midrib, etc. The cells are generally elongated, to varying extents, although secondary division of them is rare or absent. When the epidermis is mostly composed of undulate-walled cells the venule cells are usually straight-walled, but sometimes they are slightly, or even equally, undulate-walled. In the latter case only their elongation and, on the lower epidermis, the lack of stomata make them distinguishable.

Thus every intermediate between the very long and narrow midrib cells to the scarcely modified venule cells exists. The cells in the centre of each vein are mostly greatly modified, the edges of the veins gradually or abruptly merging into the normal epidermal cells. The most modified midribs are several hundreds of cells wide, the smallest venules only one or two. In an average mesomorphic leaf such as those of many species of *Combretaceae* the following degree of modification is seen : midrib composed of about 50 parallel rows of narrow elongated straight-walled cells ; major lateral veins about half as wide, the cells shorter and wider ; secondary veins about 10–15 cells wide, the cells only about twice as long as broad ; lesser veins about 5–10 cells wide ; venules forming venule reticulum about 2–3 cells wide, the cells little longer than broad, many with slightly undulate walls. Variation in one extreme is shown by strongly xeromorphic leaves, e.g. of *Laguncularia*, where only the midrib is modified on the epidermis, and that not conspicuously ; and in the other extreme by species with strongly reticulate leaves, e.g. *Buchenavia reticulata*, where the venules forming the reticulum are 5 or more cells wide, the cells being straight-walled and somewhat narrow and elongated. In all cases the lower epidermis is more greatly modified than the upper, so that the venation of the upper epidermis of a leaf would resemble that of the lower epidermis of a more xeromorphic leaf, and so on.

From the preceding paragraphs it can be seen that the three variables mentioned (i.e. the venation pattern ; the degree to which the venation system is recognizable on the epidermis ; and the type of modification of the cells) are completely independent of each other. Because of this, caution must be exercised in interpreting the extent of the venation system seen on the epidermis as that to be found in the leaf : it is frequently not so. The smallest veins represented on an epidermis, whether they are in fact the smallest venules of the leaf or of a much larger order, tend to be of the 2–3-wide slightly elongated-cell type. Thus a venule reticulum with areolae 3000μ across seen on an epidermis might represent this structure in the leaf, or smaller venules may be present but not differentiated on the epidermis. According to the excellent figures of Wylie (1943), and to my own observation, the ultimate veinlet terminations rarely have vein-extensions, and are thus rarely visible on an epidermis. Apparent veinlet terminations seen on the epidermis are due to venules which are not represented in full.

Although the vein-like structures seen on the epidermis are of course only modified epidermal cells, they are for convenience referred to as midribs, veins and venules, etc. Thus the " upper epidermal midrib " or " lower epidermal venules " may be referred to in descriptions. The unmodified epidermal islands within the venule reticulum may likewise be referred to as the areolae. In cases where the venules are not well represented on the epidermis, and the venation system is thus apparently open rather than closed, the unmodified epidermal cells may be referred to as the *non-venous areas*. In general the differentiation of the veins on the epidermis is subject to rather more phenotypic variation than is the organization of the actual veins themselves, calling for a greater measure of caution in their taxonomic use.

(3) *Leaf margin.*

The epidermis is continuous over the leaf margin, connecting the upper and lower epidermides, but its cells are modified at these positions, providing useful taxonomic characters. Towards the margin the cells of both epidermides are frequently smaller and thicker-walled, and if the normal cells are undulate-walled the undulations become less pronounced. Thus the marginal cells either abruptly or gradually merge into the normal epidermal cells.

The width of the margin, of course, is partly dependent upon the thickness of the leaf, and may be of diagnostic value. In most mesomorphic leaves the margin is not very wide, often not exceeding 5 or 6 cells across. The cells are in most cases rectangular, straight-walled and variously elongated (Plate 3 c). Secondary division of these cells may be apparent, giving rise to squarish or broader-than-long cells. The margin is thus frequently very similar to a venule, and may be indistinguishable but for its continuous straight appearance and the absence of other venules branching from it.

In certain cases, especially in xeromorphic leaves, other types of leaf margin are to be found. One of the most common of these is composed of small isodiametric cells, frequently with very thick walls and more or less circular lumina. Sometimes these are arranged into parallel rows as is normally the case, but in other leaves they may be quite irregularly arranged. All intermediates are to be found, but in some cases the margin provides valuable systematic characters. The two Combretaceous mangrove genera, *Lumnitzera* and *Laguncularia*, for example, are closely similar in cuticular characters, but one of the three main differences lies in the leaf margin. In *Laguncularia* (Plate 3 D) the cells are much smaller than those elsewhere, have thick walls and circular lumina and are arranged completely at random. In *Lumnitzera*, however, the marginal cells are scarcely smaller than the other epidermal cells, have little-thicker walls, have angular lumina, are rectangular and slightly to conspicuously longer than broad, and are always arranged end to end in parallel rows.

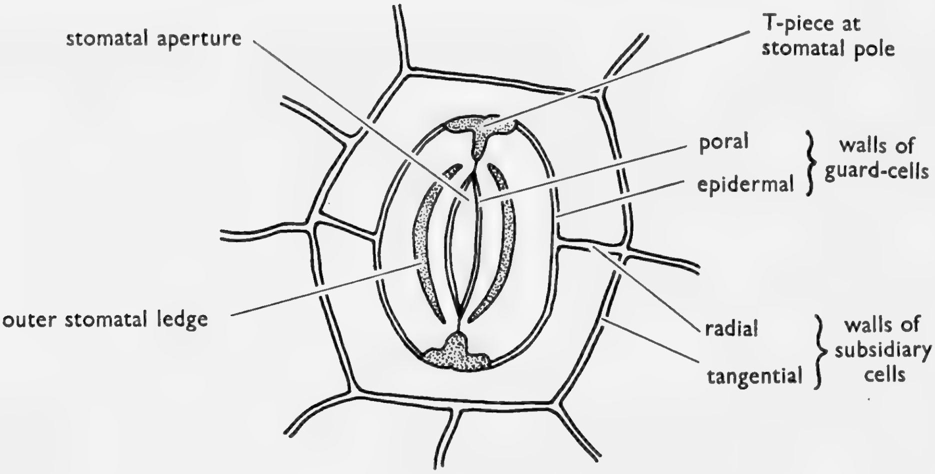


Fig. 6. Terminology of stoma as seen in surface view.

(4) *Stomata.*

The term *stoma* is here taken to include the pair of *guard-cells* with the *stomatal aperture* or pore between them. In all vascular plants there are normally two guard-cells to each stoma, these arising from a single stomatal mother-cell at an early stage of leaf development, although abnormalities with one or three or more guard-cells do rarely occur (Dehnel, 1961; Ahmad, 1964a; Pant, 1965) and may even be of diagnostic value. Other cases have been described of bistratose guard-cells which have divided by a periclinal wall (Rehfous, 1914). The guard-cells are surrounded by normal or modified epidermal cells, which in the latter case are termed *subsidiary cells* or accessory cells. The whole system is known as the *stomatal complex* or stomatal apparatus. In surface view the guard-cells, in the great majority of vascular plants, and in almost all dicotyledons, are vaguely reniform. The anticlinal wall on the side towards the pore is here described as the *poral wall*, and that towards the rest of the epidermis the *epidermal wall*. If subsidiary cells are present their anticlinal walls abutting on the guard-cells may be known as *radial walls*, and those adjacent to the rest of the epidermis as *tangential walls* (Fig. 6).

In vertical transverse section the guard-cells show an extremely various construction which is surprising in view of their relative constancy in surface view (Fig. 7). The guard-cells vary in three main directions: their position relative to the subsidiary or other adjacent cells; the relative thickenings of the various walls of the guard-cells; and the pattern of cuticular ornamentation of the guard-cells. All these are important taxonomic characters. In most mesomorphic plants the guard-cells are on a level with or very slightly sunken below or raised above the rest of the epidermis, but in some xeromorphic plants they are often sunken to a considerable degree. In many conifers, as well as in a number of angiosperms, the guard-cells are very deeply sunken and completely overarched by the subsidiary cells, so that in a surface view the former are almost invisible, their position being marked by a ring of subsidiary cells (known as a *poral ring*) around a nearly circular pore. In other plants the subsidiary cells are also sunken. The thickenings of the guard-cell walls are very uneven in distribution, being connected with the physiology of the stomatal movements. In general, however, the poral and epidermal walls are rarely thickened, the former never, whilst the other two walls (i.e. the *outer wall*, adjacent to the environment, and the *inner wall*, adjacent to the inner regions of the leaf) are variously thickened. In some species, mostly xeromorphic, the thickenings are very considerable, and the cell lumen may be reduced to an extremely

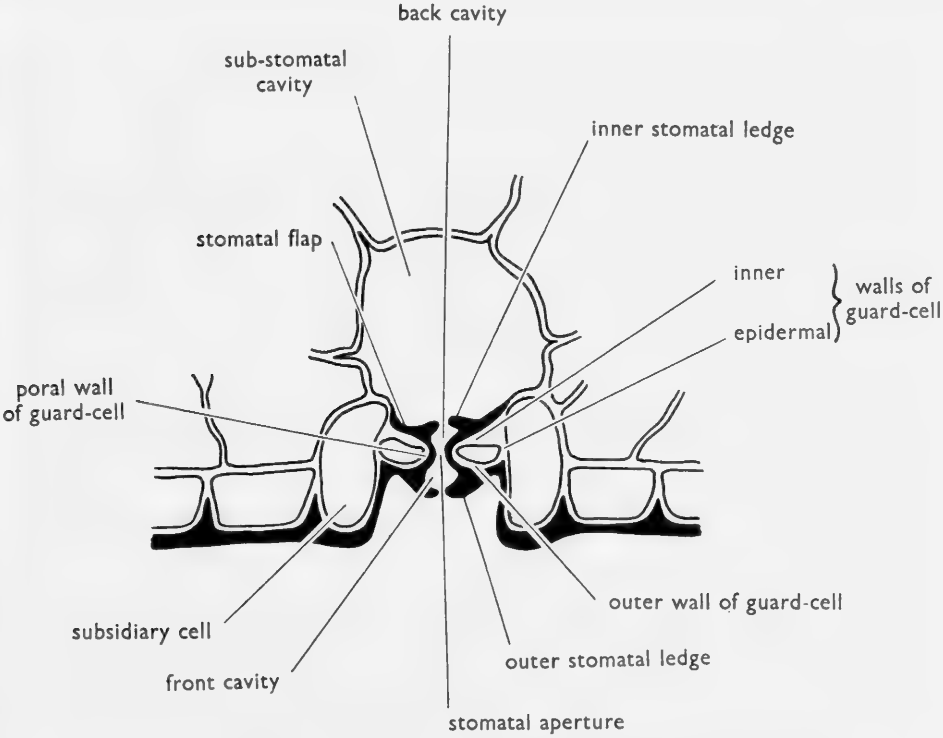


FIG. 7. Terminology of stoma as seen in transverse vertical section.

small proportion of the cell volume. The amount of cuticular ornamentation of the guard-cells is frequently proportional to the thickening of the cell walls, and hence to the degree of xeromorphism. The cuticular membrane which covers the epidermis is continuous over the subsidiary and guard-cells, and either ends where the inner and epidermal walls meet or also covers a varying amount of the subepidermal cells which line the space which usually exists below the stoma (the *sub-stomatal cavity*). In most cases the cuticular membrane is very thin on the poral walls, but thick on the outer and inner walls, especially where each of these meets the poral wall. Here the cuticular membrane may be protracted into a pair of cuticular or *stomatal ledges*, ridges, horns, rims or hooks, which may be termed *outer* and *inner* respectively. This is found in many xeromorphic plants, but more frequently only the outer stomatal ledge is present. When the stoma is closed the poral walls of the two guard-cells meet, and above and below this point the outer and inner stomatal ledges also, if present, meet, or nearly so. Thus two extensions of the stomatal pore are delimited : a *front cavity* and a *back cavity* (Fig. 7). In some plants, e.g. *Bruguiera* spp. (Areschoug, 1902) and *Ceriops* spp. (Stace, 1963), there are actually two pairs of outer stomatal ledges subdividing the front cavity into two portions.

In cuticular preparations the stomata are usually well preserved, and they provide valuable systematic characters (cf. Plate 3 A, B). Because much stomatal variation is in the third dimension (depth), however, a number of characters are not usually observable on cuticular preparations. It is often very difficult to ascertain the exact relative positions of the guard-cells and their neighbouring cells and the precise structure beneath the outer stomatal ledge. The cuticular membrane below the latter, since it curves back over the inner stomatal wall, is conspicuous on many preparations as a pair of *stomatal flaps*. A very good idea of the degree of cuticularization and sunkenness of the guard-cells and subsidiary cells may often be obtained by examining cuticular preparations with the membranes folded over on themselves inside outermost (Plate 5 C). Also a surprising amount of structure can be observed once the many lines and ridges on the preparation have been interpreted by means of vertical sections. This approach was useful in the Rhizophoraceous mangroves, which have many diagnostic details of stomatal structure. The single known epidermal difference between *Lumnitzera littorea* and *L. racemosa*, the shape of the guard-cells and subsidiary cells in section, however, was not visible from surface views of either cuticular preparations or whole epidermides.

However, in surface view the most obvious cuticular characters are present on the outer walls of the guard-cells. The shape of the guard-cells as a whole is a useful criterion which is usually constant within species. The commonest shapes are circular, elliptic and oblong, but some stomata may even be broader than long, and sometimes angular. The *stomatal poles* where the two guard-cells meet may be obtuse, truncate, rounded or retuse, the last apparently being the case in many xeromorphic plants. The appearance of various thickenings on the outer guard-cell walls is also of importance. The outer stomatal ledge is usually visible from surface views, and its thickness and relative distance between the epidermal and poral walls are characters of significance. When this ledge is directly over the poral wall of the guard-cells it forms a thick rim to the stomatal aperture which Bandulska (1923, etc.) called the poral rim. At the stomatal poles there may be developed a T-shaped thickening or *T-piece*, much used by Bandulska (1924) as a character in the *Fagaceae*. Sometimes only the upright or the cross-piece of this is present. In some groups there is a small thin area at the polar end of each guard-cell, being circular, elliptic or comma-shaped. Solereder (1908) mentioned several examples and Rao (1939) found them commonly in the *Magnoliales*. A few genera are known to possess peculiar lobe-like extensions of the guard-cell epidermal walls, and these were noted in *Strephonema*.

Perhaps of more significance than any of the above characters, however, are the presence and types of subsidiary cells around the stomata. In his various studies Florin (1931, 1933) distinguished two types of stomatal development in the gymnosperms, based on whether or not the guard-cells and subsidiary cells originate from the same mother-cell (syndetocheile and haplocheile respectively), and these types can usually be seen in the mature state because the former has two adjacent subsidiary cells and the latter a variable greater number. Although it was frequently necessary for Florin to draw conclusions concerning ontogeny by examining the mature anatomy, since many of his plants were fossils, it is unfortunate that it was so because the two terms are now more often used for describing the mature anatomy than the developmental sequence, and it has been shown by many workers that the presence of subsidiary cells does not necessarily signify a syndetocheile ontogeny, nor does their absence always indicate a haplocheile one. Thus the terms syndetocheile and haplocheile are better abandoned, and the cells neighbouring a stoma (whether they be subsidiary cells, i.e. different from the other epidermal cells, or not) described as *mesogenous* or *perigenous* according to whether or not they arise from the same mother cell as the stoma. These terms were first used by Florin (1933). In addition Pant (1965) proposed the term *mesoperigenous* for those situations where one neighbouring cell is mesogenous and the rest perigenous. This terminology has the advantages that it is equally applicable to all groups of plants rather than primarily to the gymnosperms, and that it allows for the fact that mesogenous subsidiary cells may become indistinguishable from other epidermal cells, or that perigenous cells may become specialized as subsidiary cells. The last term has no ontogenetic implications.

The earliest system of subsidiary cell classification was adopted by Solereder (1908) from the work of Prantl (1872) and Vesque (1889). Six ontogenetic categories were recognized, three of which were perigenous and three mesogenous. Due to convergence during maturation only four types were recognizable in the mature state, being termed Ranunculaceous, Rubiaceous, Caryophyllaceous and Cruciferous. Metcalfe & Chalk (1950) completely ignored the modes of development and renamed these four categories as follows: *anomocytic*, with no distinctive subsidiary cells (Plate 4 A); *paracytic*, with 2 subsidiary cells lying parallel to the guard-cells (Plate 4 C); *diacytic*, with 2 subsidiary cells lying transversely to the guard-cells; and *anisocytic*, with 3 subsidiary cells of which one is distinctly larger or smaller than the other two.

These groups are often of considerable taxonomic significance, in many cases one type being characteristic of a whole genus or family. In the *Combretaceae*, for instance, *Strephonema* is the only genus with paracytic stomata, and this agrees with the usual treatment of *Strephonema* as a separate subfamily. Apart from the four types of situation mentioned above there are other arrangements of subsidiary cells for which no terms are generally available, although for descriptive purposes they are obviously desirable. The term *actinocytic* was proposed by Metcalfe & Chalk (1950) for cases where the subsidiary cells, usually four or more in number, are elongated radially to each stoma, and *cyclocytic* by Stace (1963), where a similar number of cells forms a narrow ring round each stoma. Both terms have subsequently been used by other workers, although they probably refer to mere modifications of the anomocytic type. Of the 19 genera of *Combretaceae* without paracytic subsidiary cells, in fact, two (*Lumnitzera* and *Laguncularia*) are cyclocytic (Plate 4 B) and the rest anomocytic. Bandulska (1931) also found cyclocytic subsidiary cells (" girdle cells ") in various genera of *Myrtaceae*. More usually, however, differentiation by subsidiary cell types is only at the specific level, or is even here absent. In *Anopyxis klaineana* (Pierre) Engler (*A. ealaensis* (De Wild.) Sprague), for example, paracytic, anisocytic and anomocytic stomata are said to occur on the same leaf (Metcalfe & Chalk, 1950), and other members of the *Rhizophoraceae* also show varying arrangements. It seems probable that only one basic mode of development is involved, but that the degree of subdivision of the subsidiary cells finally differs, producing the different arrangements.

A reliable ontogenetic classification is highly desirable, and that proposed by Pant (1965) seems to be satisfactory. Ten categories are recognized, of which one is perigenous, three mesoperigenous, and six mesogenous. This nomenclature is quite separate from one based upon mature topography. The latter scheme would involve a larger number of categories (perhaps about 15), several of which could be derived from several different modes of development. Apart from the six terms mentioned previously one other has so far been named: *tetracytic* (Metcalfe, 1963), for cases where there are four subsidiary cells, two polar and two lateral, as in many monocotyledons. Terms such as paracytic, tetracytic, etc., could conveniently be prefixed by meso-, peri-, etc., once the mode of development was known. Members of the *Rubiaceae* are meso-paracytic (Pant, 1965), for instance, and of the *Gramineae* peri-paracytic (Stebbins & Jain, 1960; Stebbins & Shah, 1960; Stebbins & Khush, 1961). All investigated monocotyledons, in fact, have been found to be perigenous. It seems clear that the developmental studies at present being carried out mainly by Pant and his compatriots (e.g. Pant, 1965; Pant & Mehra, 1963; Pant & Verma, 1963) will provide valuable evidence for a classification of stomata which will prove to be of considerable taxonomic and phylogenetic value.

In some plants the subsidiary cells are furnished with distinct papillae, which may be absent elsewhere on the leaf. These may be quite long and overarch the stomatal aperture (Solereder, 1908).

Stomata vary considerably in size and this is often a character of some importance. The relation between the level of ploidy and stomatal size is well known, but stomatal size does not always indicate the former (Carolin, 1954). In many species the stomatal size also varies on a single leaf, but this may not prevent it from being an important taxonomic feature. On many leaves abnormally large stomata are to be found, and these are often, if not almost always, *water-stomata*, which are supposed to secrete drops of liquid water. Their presence is noteworthy. Water-stomata, or *water-pores* if the surrounding cells are not obviously guard-cells, may also be smaller than the normal stomata, and sometimes occur in groups (Solereder, 1908).

The distribution and frequency of stomata are their most conspicuous characters, and are often of considerable systematic value. They are very often, of course, connected with the ecology of the species, and thus not likely to be of great phylogenetic importance. In many hydrophytes, for example, stomata are either absent or infrequent and vestigial. In some terrestrial plants also some stomata may be vestigial, and Solereder (1908) describes situations where they may be plugged with a resinous mass. In plants with floating leaves they are usually on the upper epidermis only, and the same is true of other species with variously modified leaves which for some reason have a more concealed lower than upper epidermis, or even with apparently normal leaves (Solereder, 1908). In most dicotyledons, however, the stomata are more or less confined to the lower epidermis, although it appears to be usual to find a few scattered along the vicinity of the upper epidermal midrib of mesomorphic leaves. Solereder also noted this, and wisely pointed out that it could have " no great systematic value ". They are present there in most species of *Combretaceae*, and are frequently abnormally elongated. They are sometimes present upon the midrib itself, rather than beside it, and cannot here be functional. All intermediate situations from the complete absence of stomata on the upper epidermis to their presence as abundantly as on the lower epidermis are to be found, even within the *Combretaceae* alone. *Lumnitzera* spp., in fact, have stomata more abundant on the upper than on the lower epidermis. Species showing a slight increase from normal in the abundance on the upper epidermis have stomata scattered quite frequently alongside the midrib, more sparsely alongside the veins, and very sparsely in the rest of the areolae, and the further from the midrib they are situated the less abnormal is their anatomy. On the lower epidermis stomata are usually confined to the areolae, or non-venous areas, but sometimes they are to be found scattered on the midrib. They have seldom been recorded from the leaf margin of a dorsiventral leaf, or from the venules and veins of the lower epidermis.

Thus stomata are typically found in the areolae of the lower epidermis, and usually only very sparsely anywhere else. In leaves showing various xeromorphic characters, especially where a closed system of venules is not apparent on the epidermides, they may be otherwise distributed. In the latter case they are frequently found all over the epidermis, except for the veins and midrib, but in some species they may be present only in special areas, e.g. longitudinal grooves, or depressions. These latter situations are not found in the *Combretaceae*, although here there are some species with very prominent reticulations and thus sunken areolae. The position and types of sunken areas, the *stomatal crypts* or stomatal pits, may be very useful in taxonomy (cf. Morley, 1953). They are quite independent of the individually sunken stomata found in a number of xeromorphic leaves.

In leaves with stomata confined to areolae or to stomatal crypts the stomata are not regularly orientated, their long axes being quite randomly directed. In some leaves, however, especially narrow leaves or those with stomata present in longitudinal grooves, the stomata are all orientated parallel to the leaf axis. In a still smaller group of species the stomata are orientated at right-angles to the leaf midrib, e.g. *Laguncularia racemosa* (L.) Gaertn. f. These characters are usually of absolute constancy and of sufficient scarcity to be valuable in identification.

The frequency of stomata, either in the areolae or in the non-venous areas, is a much used character, and frequently misused. A large number of workers have used the stomatal frequency in order to distinguish between species, with varying degrees of success. Timmerman (1927), for example, found the character of little use in *Datura* since the frequency varied considerably on different portions of the leaf. Environmental and other factors also cause variation in frequency. Valuable taxonomic evidence, however, may often be obtained if the stomatal index ($100S/E+S$), based on the proportion of stomata to epidermal cells, is used instead of the frequency per unit area (Salisbury, 1927), as has been shown by various workers in modern and fossil plant taxonomy. In *Lumnitzera*, however, the two species only differ on stomatal frequency since the stomatal indices of the two species are identical, the stomatal frequency being greater in one due to the smaller size of all the cells.

(5) *Types of trichomes and trichome-bases.*

Despite some attempts by Odell (1932) to prove otherwise, trichome anatomy provides a very important group of taxonomic characters. The definition of *trichomes* as outgrowths of the epidermis is not absolute as there is every grade between these and the so-called emergences which differ in also involving some subepidermal layers in the outgrowth, but in the present context both types are included.

The extent to which trichomes are cuticular characters depends upon the degree to which they are cuticularized. In the case of most emergences and of trichomes with multiseriate basal parts a high proportion of the outgrowth is preserved on cuticular preparations, and the structure can be observed quite easily. Thus the whole or most of such outgrowths is cuticularized, only the more distal regions being sometimes not so covered. In the case of trichomes with pauci- or uni-seriate basal parts a similar proportion of the outgrowth may be cuticularized, but quite frequently only the very basal parts or even none at all possess a cuticular membrane. There are, of course, many exceptions to these generalizations ; for example the very long unicellular hairs of *Macropteranthes leichhardtii* F. Muell. are well cuticularized along their whole length. Where cuticularization is extensive cuticular preparations may provide the best means of studying the trichome anatomy.

Outgrowths with large multiseriate bases are not readily broken off at the base, but when this happens an irregular hole appears in the cuticular preparation. Trichomes with pauci- or uni-seriate bases are much more easily removed *in toto* from the epidermis, the appearance of the remaining *trichome-base* (i.e. the adjacent modified region of the epidermis, exclusive of any parts of the trichome itself) depending upon the original organization of the basal parts of the trichome, of which there are two main situations (Fig. 8). Firstly the trichome may rest upon a normal or modified epidermal cell or group of cells, or, in the case of some unicellular trichomes such as root-hairs, the trichome may in fact not be separated from the epidermal cell by a cell wall. In these types the former position of a lost trichome will be indicated on the cuticular membrane by a modified epidermal cell or cells, by a hole in an epidermal cell, or will not be visible at all. Secondly the base of the trichome may be inserted between the epidermal cells, or may replace an epidermal cell, so that a lost trichome leaves a pore in the cuticular preparation.

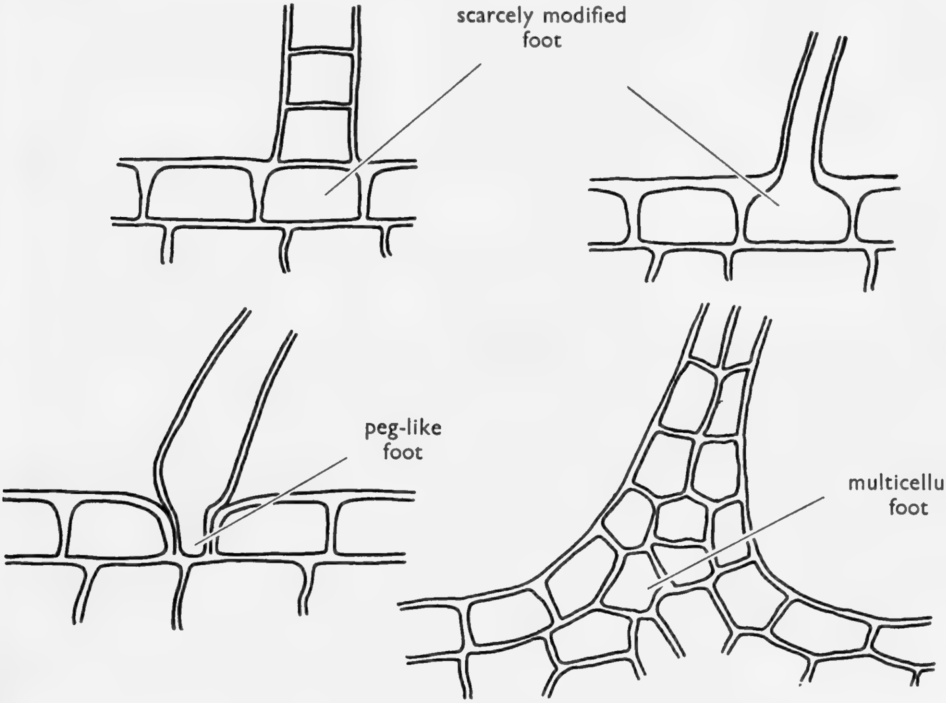


FIG. 8. Four types of trichome-base as seen in vertical section.

Trichome-bases (hair-bases, gland-bases, etc.) of the above types are common features of cuticular preparations, especially as the trichomes are usually covered with a thinner cuticular membrane than the rest of the epidermis so that slight over-maceration removes the trichome completely. Their organization provides useful diagnostic characters, and it has been found necessary to create a terminology for the parts of the trichome-base (Fig. 9). The *trichome-base cells* may or may not surround a *pore*. In the former case the trichome-base cell walls may be termed *poral*, *radial* and *epidermal*, the first of these often being considerably thickened and then known as the *poral rim*.

A trichome occupying the pore of a trichome-base therefore consists of two parts : the *foot*, which is inserted into the pore ; and the *body*, which extends above the epidermis. The foot may thus be a single cell, a small group of cells, or a peg-like basal portion of a cell. The parts of the body of the trichome have been given very different names by various authors according to the trichome structure (e.g. stalk, head, branches, arms, disk, fringe, rim, etc.) and generalization is impossible and in fact undesirable.

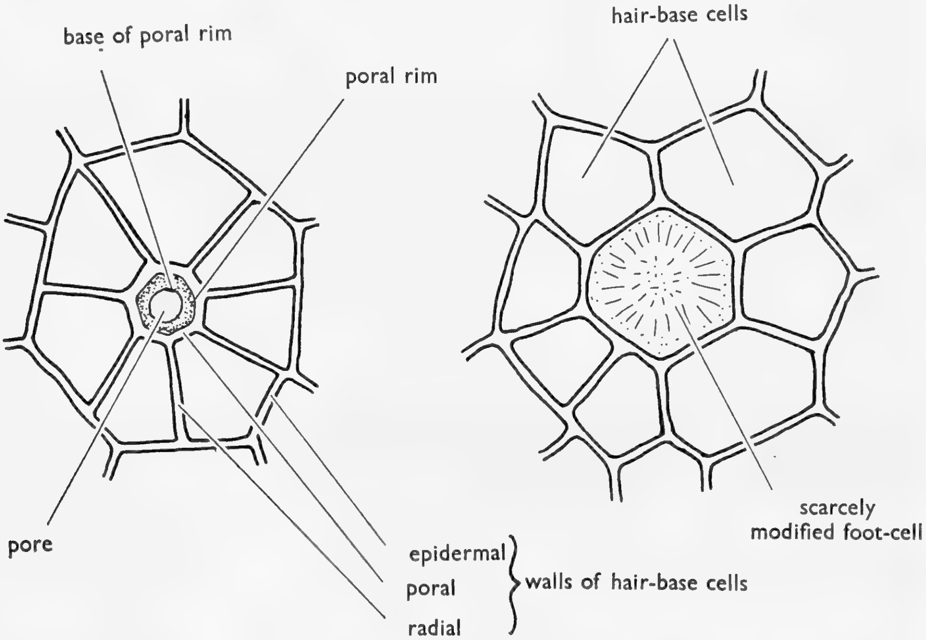


FIG. 9. Terminology of two main types of trichome-base.

There have been many attempts to classify trichomes (cf. Bachmann, 1886 ; Solereder, 1908 ; Foster, 1949 ; Seithe, 1960, 1962 ; etc.) but none has been generally successful. As mentioned previously, not only does each trichome type grade into the next but there is no real distinction between papillae, trichomes and emergences. The most usual division, between glandular and non-glandular types, suffers from the same disadvantages as other systems in that there is no sharp distinction between the groups, and in any case the division often separates obviously very closely related types. Furthermore, within each group or subgroup the directions of variation are often quite different in various plant taxa, so that the only way to avoid the situation where a single trichome could belong to more than one group on different points of anatomy would be to create a system with many groups each with numerous parallel subgroups. It is thus quite clear that no useful general classification of trichomes can be constructed, but that instead it is advisable to create systems for each particular plant group investigated as it becomes necessary, and to employ special descriptive terms in each case without attempting to correlate the terms from taxon to taxon. This has the advantage that newly discovered types can easily be fitted into the system at any time.

Good accounts of the ranges of variation and of the details of anatomy and functioning of trichomes are given by Solereder (1908) and Netolitzky (1932) respectively, and so no sort of review is given here. Instead an indication of the types of problems and the degree of taxonomic usefulness which may be involved in trichome studies is given by a brief statement of two major points of interest in the *Combretaceae*. In all twenty genera of this family peculiar unicellular hairs with distinctive basal components (known as " Combretaceous hairs ") occur, elsewhere being known only in a few genera of the *Myrtaceae* and of the *Cistaceae*. These are of great interest for they virtually delimit the *Combretaceae* from all other families except the other two mentioned above, and thus indicate a monophyletic origin of this family. The *Myrtaceae*, moreover, are generally considered to be closely related to the *Combretaceae*, and the hairs thus support this view. The presence of the hairs in the *Cistaceae*, however, is difficult to understand since this family has never been considered at all closely related to the *Combretaceae*. The identity of the Combretaceous and Cistaceous hairs thus needs to be investigated. In *Strephonema*, a Combretaceous genus usually placed in a separate subfamily from all the other genera, typical Combretaceous hairs are present in one of the species, thus confirming its inclusion in this family. In the other four species, however, they are absent and are replaced by hairs unique in the *Combretaceae*, so that the hairs also support the treatment of *Strephonema* as a separate subfamily.

The second point concerns the presence of " scales " (Plate 5 A), which are short-stalked trichomes with a disk-shaped multicellular head found in a wide range of plant families (Bachmann, 1886). These trichomes are often extremely distinctive, but in some families they intergrade with stalked globular glands, with stellate hairs, or with cup-shaped hairs. In the *Combretaceae* scales are found in all species of the small genera *Thiloa*, *Calycopteris* and *Guiera*, and in over half of the large genus *Combretum*. These four genera all belong to the same tribe (*Combreteae*), and the scales do seem to indicate, therefore, that this classification is well founded. In the *Combretaceae* the disk of the scales is always one cell thick, but varies in the degree and manner of subdivision, giving rise to a very wide range of types. In *Rhododendron*, a genus of the very distant family *Ericaceae*, however, the main direction of variation is in the overall organization of the scale rather than in its division in one plane, producing an equally varied range of forms (Cowan, 1950 ; Seithe, 1960). Furthermore, in *Rhododendron* there are intermediates between all of the numerous (25 according to Cowan ; 43 to Seithe) types of trichomes, whereas in the *Combretaceae* there are three main types (Combretaceous hairs, scales and stalked glands) which are always quite distinct (Stace, 1965). Thus Cowan concluded that all the trichomes of *Rhododendron* are phylogenetically directly related, especially as they all appear to pass through identical early stages of ontogeny. Although this may be correct in *Rhododendron* I do not consider it to be the case in *Combretum*, where it is not possible to construct a " phylogenetic tree " of trichome types as did Cowan.

The stalked glands of the *Combretaceae* (Plate 5 B) are found in all the scale-less genera of *Combreteae* except *Pteleopsis*, in all the scale-less species of *Combretum* itself, and also in *Conocarpus*, a genus in another tribe. Their presence in the last genus and absence from *Pteleopsis* is puzzling, since the two tribes are otherwise well defined on a number of characters. The presence and types of stalked glands or scales are thus very useful taxonomic criteria in *Combretum* and in other genera of the *Combreteae* (Stace, 1961, 1963, 1965; Exell, 1963). In both *Combretum* and *Rhododendron* the major taxonomic positions of trichome differentiation are at the subgeneric and sectional level, and where a section contains species with unexpectedly divergent trichome types there is good reason to doubt the homogeneity of that group.

Compared with trichome structure trichome size is relatively unimportant, but nevertheless at times very useful. For example the Combretaceous hairs of the *Combretaceae* are relatively very uniform in structure, but those of *Macropteranthes leichhardtii* are very distinct in their large size, and those of *Guiera senegalensis* extremely so in their very small size. The length of hairs generally is, of course, a frequently used taxonomic character.

The trichome-base frequently provides characters of importance, most notable of which is the shape (i.e. the degree of modification) of the trichome-base cells. In some cases they are scarcely modified from normal epidermal cells, but usually they are elongated radially to the pore, when this is present. If the normal epidermal cells are undulate-walled the radial walls of the trichome-base cells are very often straighter or straight, and frequently their epidermal walls also. Although the number of trichome-base cells varies considerably within one species, in many cases there is a typical range, of which 5–8 is the commonest, which may aid in the diagnosis of the plant. Some species, for example, have a characteristically low or high number of trichome-base cells. In some species the trichomes are so numerous that almost every epidermal cell is a trichome-base cell, and radially elongated. In *Guiera* (Plate 4 D) many upper epidermal cells are adjacent to two or three hair-bases, and there are no unmodified upper epidermal cells. The latter are thus typically elongated in two or three directions, and the cuticular preparations of this genus are quite distinct in the whole family. In many *Combretum* species (e.g. *C. glutinosum* Perrott. ex DC. and several related species) almost all of the lower epidermal cells are scale-base or hair-base cells.

Quite frequently, especially in xeromorphic species, the trichome-base cells are not radially elongated, but have become tangentially divided so that there are several rings of modified cells, the inner of which is composed of cells longer in the tangential than in the radial plane. The cuticular flanges of these walls are usually thick and straight. Sometimes the two different types of trichome-bases mentioned above form valuable diagnostic characters between species, although in other cases this is not so and too much emphasis should not be placed on them. In *Terminalia glabrescens* Mart., for example, both extremes and all degrees of intermediates may be found.

The size of the pore, where present, varies considerably, but in some cases may characterize species. In *Anogeissus acuminatus* (Roxb. ex DC.) Wall. ex Bedd., for example, the pores are very large (often over 50μ across) and are a quite distinctive character of this species. The thickness of the poral rim varies in two dimensions, i.e. towards the centre of the pore (Plate 5 A), and towards the centre of the leaf. In the former case it may result in a very small pore of only 1–2μ in diameter. The thick rims are frequently, though not always, accompanied by a considerable thickening of the radial walls of the trichome-base cells, so that a stellate pattern of thickening is obtained. In extreme cases, where the trichome-base cells are of the tangentially subdivided type, all the walls of the trichome-base are conspicuously thicker than the rest of the epidermal cell walls. The poral rim often becomes deeper by a development of cuticular membrane around the foot of the trichome, often up to the inner wall of the epidermis. The diameter of the pore is nearly always narrower at the base than at the apex, so that the sides and base of the pore can be seen in surface view.

Where there is more than one type of trichome on a leaf the types of trichome-bases bearing them are often different (Plate 5 D). In *Combretum*, for example, where hairs are always accompanied by either stalked glands or scales, the poral rims of the latter are much thicker and deeper than those of the hair-bases, and the two can be readily distinguished. Moreover the distribution of the scales is different from that of the stalked glands, the latter being commoner on the veins, the former in the areolae. Thus the abundance and distribution of each type of trichome can be ascertained even if the trichomes have been lost. In *Conocarpus erectus* there are two types of bases : those with radially and those with tangentially elongated cells. Stalked glands are found on all of the latter types, on intermediate types and on a few of the former types ; whilst Combretaceous hairs are confined to the former types of bases. Thus in this genus the difference is not so well marked.

(6) *The cuticle.*

Besides providing a means of studying epidermal anatomy in the absence of any cellular layers the cuticle often possesses characters of its own on its outer surface, and the cuticular membrane also varies in the degree of its development. All these characters are worthy of study as potential taxonomic criteria.

The most obvious feature is the degree of development of the cuticular membrane, as has been mentioned in several preceding sections, notably the cuticular ornamentation of the guard-cells and trichome-bases. The thickness of the cuticular membrane over the normal epidermal cells is also a character of diagnostic importance. In most cases thicker membranes are characteristic of plants of drier habitats, and are thus a measure of xeromorphy, although this is not always so. In *Lumnitzera racemosa* and *Macropteranthes kekwickii* F. Muell., for instance, the wall between the lumen of the epidermal cells and the exterior is quite thick, as might be expected in these two xeromorphs. However, in the former the cuticular membrane is thick and has long stout cuticular flanges, whilst in the latter the cuticular membrane is thin with scarcely any flanges, the non-cutinized epidermal wall accounting for the greater part of the thickness of the outer compound wall. Because of its relation to the environment, however, the degree of development of the cuticular membrane is liable to considerable phenotypic variation, and great care must be exercised in its use in taxonomy. The cuticular flanges show the same degrees of genetic and phenotypic variation and may also prove of diagnostic value in some cases, besides determining the over-all appearance of the cuticular preparation and whether or not the epidermal cell outlines are visible (Plate 5 c). In *Combretum psidioides*, for example, the cellular organization of the scales is always more or less completely indiscernible, whilst in all other closely related groups it is clearly visible on cuticular preparations. Again, xeromorphic species usually have well-developed flanges, but some species have thick cuticular membranes yet very short and narrow flanges.

The other character of the cuticular membrane is the type of minute ornamentation of the outer surface of the cuticle, this having been used by a number of past workers. The vast majority of plants have a smooth or minutely granulated cuticle when viewed with a light microscope, and no use can be made of this fact beyond the absence of any definite markings. The latter, as seen in many mesomorphic plants, take the form of a series of minute grooves and ridges which are commonly termed striations from their appearance in surface view. Their presence and degree of development do not always seem to be related to xeromorphy, although some species of *Combretaceae* have been found in which the degree of striation is not constant. In their less-developed state the striations are usually found running parallel to the midrib and veins, and radially to the trichome-bases and stomata, and the presence of such a pattern is probably of little importance. In general the striations bear no relation to the cell outlines, each marking passing over a number of cells, but exceptions have been found where each striation is always contained within a single cell outline. When the striations are better developed they appear on the non-venous areas unconnected with the trichomes or stomata, and their orientation, arrangement and degree of development may be very various. Where they are found in areolae they are usually contained within one areola, i.e. they do not continue across the venules. Where the veins are less extensive on the epidermis the striations may be much longer. They are extremely conspicuous, for example, in *Macropteranthes kekwickii* and *M. montana* (F. Muell.) F. Muell., where they are found on all parts of the epidermis. In section the surface of the cuticle appears papillate. In extreme cases, several of which have been found in *Combretum*, the whole cuticle is covered with striations, those radial to the trichomes and stomata and those parallel to the veins being continuous over other areas of the epidermis (Plate 5 D). Sometimes the striations are so strong, and the cuticular flanges so weak, that the former obscure all signs of the cell outlines.

In *Combretum zenkeri* the long papillae have a conspicuously echinate cuticle. The series of raised cuticular anastomosing ridges reported by Solereder (1908) in several families appear to be rare.

§6. DESCRIPTION OF CUTICULAR CHARACTERS

Just as the formal description of a new plant species follows a well-defined and well-known pattern, so should the characterization of a cuticular membrane, although hitherto this has not been the case. Two types of description are required for various purposes : a relatively full account of the cuticular membrane characters ; and an abbreviated account or diagnosis. A suggested form for the former, after many adjustments, is as follows :

1. Distribution of species ; habitat.
2. Morphology of the leaf :
   - a. general morphology as seen with the naked eye.
   - b. special morphology—venation pattern and prominence, trichome types and distribution, clear spots, pimples, etc.
3. Account of the cuticular membrane :
   - a. general features—thickness, ease and quality of preparation.
   - b. shape, arrangement and size of upper epidermal cells of :
     - i. venation system ;
     - ii. non-venous areas.
   - c. shape, arrangement and size of lower epidermal cells of :
     - i. venation system ;
     - ii. non-venous areas.
   - d. shape, arrangement and size of margin cells.
   - e. distribution, frequency, orientation, size and structure of stomata, including the subsidiary cells.
   - f. distribution, frequency, size and structure of trichomes and trichome-bases.
   - g. presence of any other features, e.g. cork-warts, hydathodes, water-stomata, domatia.
   - h. presence of markings, e.g. striations, on the cuticle.
4. If necessary : interpretation of surface cuticular characters, primarily of the stomata, by means of leaf sections. A brief mention of the organization of the hypodermal and inner layers of the leaf might not be out of place as a general background to the cuticular characters.

Such a description is an obvious prerequisite for the use of cuticular characters in taxonomy and identification, and full allowance must be made for environmental and other variation. Characters which are thought to be likely to vary beyond the limits observed should be indicated.

For the purposes of a diagnosis the third section above, i.e. the description of the cuticular characters themselves, should alone be used, and this in an abbreviated though essentially similar form to that above. To this end certain abbreviations may be employed, comparable to lvs., fls. and fr. in other descriptions. The following are suggested : epid. (epiderm-is, -ides or -al) ; l. and u. (lower and upper) ; cutic. (cuticle(s), cuticular or cuticular membrane(s), unless these need to be distinguished) ;

stom. (stom-a, -ata or -atal); ven. (venule(s)); ret. (reticulum); w.l./wall (wavelengths per wall) ; ampl. (amplitude) ; isod. (isodiametric) ; 2ry (secondary) ; lat. (lateral(ly)) ; longit. (longitudinal(ly)) ; trans. (transverse(ly)) ; tang. (tangential (ly) ; rad. (radial(ly)).

In some cases these procedures may need to be modified, just as with normal taxonomic descriptions, but in general their use would lead to a greater uniformity and thus ease of reference and comparison. A diagnosis of a typically mesomorphic species is given here :

Diagnosis of *Combretum fruticosum* (Loefl.) Stuntz.

Cutic. medium thickness ; features clear. U. epid. : midrib broad and conspicuous, of many longit. rows of narrow elongated cells ; lat. veins conspicuous but narrower ; minor veins and some ven. distinguishable but ven. ret. absent or fragmentary ; cells of non-venous areas averaging c. 30 μ across, isod., with straight walls, or less often with undulate walls with up to 1½ w.l./wall and 5 μ ampl. L. epid. : midrib and lat. veins broader and more conspicuous than on u. epid. but minor veins and ven. not so much more conspicuous and ven. ret. still ill-defined ; cells of areolae averaging c. 20–25 μ across, isod., with faint undulate walls with up to 2½ w.l./wall and 8 μ ampl. Margin of a very few rows of slightly elongated rectangular, straight-walled cells. Stom. very frequent in non-venous areas of l. epid., sparse alongside u. epid. midrib, randomly orientated on l. epid., c. 22–30 × 15 μ ; epid. walls very faint ; poral walls quite conspicuous ; stom. ledges absent ; poles mostly rounded, sometimes retuse or obtuse ; adjacent epid. cells 4–7, unmodified. Combretaceous hairs frequent on midribs and lat. veins of both epid., but sparse elsewhere ; hair-bases with pore c. 10–25 μ across ; poral rim somewhat thickened ; hair-base cells mostly 5–9 and slightly rad. elongated, with straight, slightly thickened rad. walls ; internal compartments long and pointed. Scales bowl-shaped with raised convex cutic. membrane, frequent in l. epid. areolae, sparse on l. epid. venous areas and on u. epid., there frequently commoner on or near midrib ; scale-bases with pore c. 10–25 μ across ; poral rim considerably thickened ; scale-base cells c. 8–13, considerably rad. elongated with thin straight rad. walls ; scales c. 100–200 μ across, circular in surface view, scalloped at margin, divided into c. 35–70 cells by rad. walls alone, few of the cells reaching the scale centre, all reaching the scale margin ; stalk of scale uniseriate.

§7. VARIATION OF CUTICULAR CHARACTERS

The main disadvantage of many taxonomic characters is that they will vary independently of the genotype, and it is thus important to discover to what extent and under which conditions this variation will occur. In all groups certain characters vary so much that they are useless in taxonomy, but since these characters are not the same ones in every plant group every character is worthy of study. With regard to cuticular characters variation is due to three major causes : the age of the leaf, or rather its degree of maturity ; the environment in which the plant is situated ; and the position of the leaf upon the plant, that is to say the internal and external environment of the leaf. In general the characters affected by these three factors are those of size, frequency and degree rather than the actual anatomy or organization of the particular structures. Thus the majority of the characters previously discussed show relatively little of this type of variation. Much of the variation shown within species is of course genetically controlled ; this must be equally carefully studied, and, if possible, distinguished from the environmental and developmental variation.

In the case of variation due to age it is obvious that in extremely young leaves every cuticular character would be quite unlike that character on a mature leaf, and such immature leaves are usually of no taxonomic use with regard to either macroscopic or microscopic features. The present section therefore only deals with leaves that are likely to be chosen for cuticular examination, i.e. leaves which are over half-grown.

The relevant literature shows a generalized sequence of the development of the various cellular layers of a typical simple leaf to be established (Avery, 1933 ; Esau, 1953 ; Slade, 1957 ; etc.). The leaf primordium arises as a bud-like outgrowth of the apical meristem of the stem, and develops by its own apical meristem into a finger-like projection which corresponds to the petiole and midrib. The lamina later grows out from this as a pair of lateral wings, this activity of a marginal meristem usually commencing before the cessation of that of the apical meristem, in most cases before the leaf is a millimetre long. When apical growth has ceased the leaf elongates by intercalary growth. The thickness of the lamina in terms of cell number is determined at a very early stage in development, when the leaf is a few millimetres long, and subsequent increase in cell number is solely by anticlinal divisions. Very soon after the lamina has begun to develop the major lateral veins appear in its central portion, branching from the midrib and keeping pace with the lamina extension by intercalary growth. The lesser veins and venules develop similarly at progressively later stages. Recent work (Pray, 1963) has shown that the veinlet terminations also develop in the same manner, and not by dissociation of parts of the venule reticulum in the expanding leaf as was formerly thought to be the case.

Before the leaf approaches its mature size cell division ceases altogether, the remaining increase in leaf size being by cell expansion alone, and, although some of the layers are distinguishable before cell division ceases, most of them acquire their characteristic form after this point. The first parts of the leaf to end cell division are the two epidermides, followed by the spongy mesophyll and lastly the palisade mesophyll. Not all regions of the leaf stop producing more cells at the same time, moreover, the leaf apex reaching maturity first and the base last, and superimposed on this sequence the leaf margin continues cell division longer than the midrib region. The tip of the leaf is thus the most mature, and the marginal parts the least. Since the epidermis is the first layer to show a cessation of cell division, cell enlargement shows its greatest development there. Stomata develop from epidermal initials soon after the number of cells in the lamina thickness has been established, and their mature shape is attained in most cases before that of the other epidermal cells. The times and rates of trichome development usually appear to run parallel to those of the stomata, and in almost all the cases investigated trichomes and stomata had reached their mature structure before the leaf was its mature size. Thus one of the latest features of the epidermis to appear is the mature epidermal cell shape and size.

Examination of data from a wide range of taxa has led to the conclusion that there are six cuticular characters which are regularly to be expected to show sufficient environmental and developmental variation to pose serious taxonomic difficulties. These are discussed separately.

A. Epidermal cell size.

A number of workers (e.g. Yapp, 1912 ; Salisbury, 1927 ; Watson, 1942) have found that the epidermal cells are larger on leaves in more humid or more shaded situations, and Odell (1932) cites workers who also discovered a decreasing cell size with excess carbon dioxide, drier air, drier soil and greater altitude. In general these size differences are proportional to a change in leaf area. The cell size also decreases with an increased height of insertion upon the axis of many herbs (Yapp, 1912 ; Stober, 1917 ; Odell, 1932 ; Turrell, 1942 ; Ashby & Wangermann, 1950 ; etc.). Although this might seem to reflect the more shaded and humid environment of lower leaves Ashby & Wangermann (1950) concluded that the difference in cell size was not dependent upon the climate when the leaf unfolds, even though in *Ipomoea* at least the later the time of seed sowing the larger were the epidermal cells, but found (1950a) that the factors affecting this character operate mainly by increasing the period of cell division in upper leaves. Ashby (1948) discovered that the decrease in cell size was accompanied by a decrease in leaf area and cell number, and although the latter were affected by water supply the former was not, since plants in dry and wet conditions produced the same-sized epidermal cells. This is contrary to the results of most of the above workers.

Some investigations into the relation between cell size and leaf maturity were made by me on a number of species, using North's cellulose acetate film technique (North, 1956). In the two main species investigated, *Quercus robur* and *Carpinus betulus* L., the leaves grow by cell division and enlargement until they are about one-third their mature size, when cell division ceases and subsequent leaf enlargement is entirely due to cell enlargement. In species with undulate epidermal cell walls, e.g. *C. betulus*, the cells appear for a time to be enlarging more rapidly than the leaves. This apparent anomaly is due to the fact that cells can increase in length and breadth without any increase in area while the wall undulations are developing (cf. Fig. 10).

Secondly, the nature of the abnormally small leaves found at the base of most sucker shoots was investigated in *Quercus robur*, *Buchenavia capitata* (Vahl) Eichl. and *Platanus* × *hybrida* Brot., cells from fully mature leaves of as wide a size range on the same sucker as possible being examined. No significant cell-size difference whatsoever was found, an increase in mature leaf size of a factor of three producing no increase at all in the cell size in all three species. Representative figures obtained from *Quercus* and *Buchenavia* are:

Quercus		*Buchenavia*	
Lf. size	Av. cell lgth.	Lf. size	Av. cell lgth.
9·0 × 5·0 cm.	30·0 μ	3·5 × 2·0 cm.	42·5 μ
6·0 × 3·0 cm.	28·0 μ	2·5 × 1·3 cm.	41·5 μ
4·5 × 3·0 cm.	31·0 μ	1·0 × 0·6 cm.	40·5 μ
3·3 × 2·0 cm.	28·5 μ		

This is in direct contrast to the results obtained by Turrell (1942) and others working with herbs showing typical heteroblastic development (i.e. varying leaf types up the stem) where the upper and lower leaves differed in a number of size characters besides the overall leaf size, and thus indicates that the small leaves at the base of suckers do not represent normal heteroblastic growth. Since different-sized leaves on a single sucker differ in cell number but not cell size the factors regulating the mature leaf size must take effect early on by determining the point at which cell division stops. The same results were obtained from abnormal suckers on coppiced trees of *Quercus* which possessed leaves over twice as long and twice as broad as those on normal suckers, yet which had epidermal cells of the same size.

Finally, the average epidermal cell sizes of different parts of a single leaf were measured, when in every case the cells increased in size with the distance from the leaf apex and from the leaf margin. Representative measurements for *Quercus robur* are : extreme leaf apex, $29 \times 22\ \mu$; extreme lamina base, $36 \times 31\ \mu$; extreme margin, half-way from base to apex, $30 \times 20\ \mu$; half-way from base to apex and from margin to midrib, $34 \times 27\ \mu$.

These observations merely serve to emphasize the variability of epidermal cell size not only with age and minor genetic variation but with the environment, position of the leaf on the shoot and the position of the cells in the leaf. However, there does appear to be less variation than might be expected with respect to the cells of leaves on a single shoot which attain different sizes at maturity, and this is encouraging from the angle of systematic anatomy. Should the character appear to be of taxonomic use great care must be taken to use strictly comparable mature material, and to ascertain the degree of variation to be found. Thus with herbarium material this feature should not be used unless very well marked.

An additional complication, the secondarily subdivided epidermis, is unlikely to cause any confusion as the nature of the extra walls is usually obvious (see §2 above). They presumably develop long after normal cell division has stopped, and represent a renewal of meristematic activity.

A very similar situation to the above exists regarding stomatal size, although in this case the leaf size is not wholly and directly dependent upon the character. Measurements indicate, in fact, that the stomata may become mature in size and anatomy before the epidermal cells have fully expanded, and so the use of absolutely mature leaves may not be so essential. Various workers, especially those previously mentioned, have found that stomata become longer nearer the base of a herbaceous plant, in shade, in moist air and in moist soil. These results are not always capable of repetition, however, and some workers (e.g. Odell, 1932) found no difference in stomatal size on sun and shade leaves. Thus the variation of this character in the particular group concerned should be fully ascertained before it is taxonomically employed, but the evidence does suggest that the average stomatal size is less subject to phenotypic variation than that of the epidermal cells.

B. STOMATAL FREQUENCY.

Since the number of stomata that appear on a leaf is determined at the end of the period of cell division, long before a leaf reaches its full size, the stomatal frequency expressed as the number of stomata per unit area clearly decreases as the leaf expands. Again, therefore, only mature leaves are suitable for comparative measurements of stomatal frequency. Moreover the stomatal frequency often varies considerably on different parts of the same leaf, and on different leaves of the plant. Salisbury (1927) found that the lowermost leaves of a plant, and the basal and the midrib regions of the leaf, had a lower stomatal frequency, which was reflected to an equal extent on both epidermides when the upper epidermis possessed stomata. The increased frequency of stomata on higher (smaller) leaves of herbs has also been noted by Yapp (1912), Stober (1917), Rea (1921) and Turrell (1942), but Odell (1932) and others have found that the frequency increases towards the base and midrib of each leaf.

Environmental factors also regulate the stomatal frequency, the latter being lowered by humid air, wet ground, shade from sun and wind, lower altitude, and a lesser concentration of carbon dioxide (*fide* Odell, 1932).

Fortunately, however, the above variation can apparently be almost entirely cancelled by recording stomatal frequency in terms of the proportion of stomata to epidermal cells :

$$\frac{\text{No. of stomata}}{\text{No. of stomata} + \text{No. of epidermal cells}} \times 100 = \text{Stomatal Index.}$$

Since the variation in stomatal frequency caused by the above factors is apparently due to the increase or decrease in epidermal cell (and to a lesser extent stomatal) size, but not to cell number, the stomatal index is not affected. Salisbury (1927), who was the first to use this value, found that one factor did, however, alter the stomatal index—the humidity. It is not known how widespread this phenomenon is, but it seems that the diverse variation shown by stomatal frequency can often be more or less overcome. More work is needed, however, to establish that the stomatal index is always as invariable as has been claimed : Yapp's (1912) data, for example, would suggest that it is not. Gupta (1961) also used a value which cancelled the effect of the position and environment—the absolute stomatal number. This is obtained by calculating the product of the stomatal frequency per unit area and the leaf area, and can therefore be used as an alternative to the stomatal index. Reyenga & Karstens (1964) described an unusual situation in the sepals of *Hydrangea*, which are small and pink during anthesis, but which afterwards turn green and enlarge considerably. This period of growth includes not only the formation of new stomata but also the disintegration and disappearance of some of the original ones, the stomatal index rising due to the predominance of the former process. Moreover, the original stomata have actinocytic subsidiary cells with radial cuticular striations, whilst those of the later stomata are anomocytic and not striated. Furthermore, Dehnel (1960) reported in *Begonia* the disintegration of stomata which have been wounded. Phenomena of this kind are probably exceptional, however, and need rarely enter into consideration.

Rea (1921) found that in *Campanula rotundifolia* L. the hydathodes showed the same positional and environmental variation as the stomata.

C. TRICHOME FREQUENCY.

The general situation regarding trichome density is similar to that of stomatal frequency in that usually the number of organs is determined when the leaf is very young and the frequency thus drops as the leaf expands. Thus a densely pubescent young leaf may develop into a sparsely pubescent mature leaf. Yapp (1912), however, found that in *Filipendula ulmaria* (L.) Maxim. there was an additional development of hairs after the leaf began to unfold, the original pubescence being developed in the leaf bud. As in the case of stomata the pubescence often varies from leaf to leaf, from one part of a leaf to another, and under a variety of environmental conditions. The variation in trichome frequency on different parts of one leaf is a well-known and important taxonomic character. Yapp (1912) and Stober (1917) both found that the pubescence on plants generally rose with increasing distance up the aerial shoot : in many plants, in fact, the radical leaves are almost glabrous and the upper cauline leaves conspicuously pubescent. The inner radical leaves are also usually more pubescent than the outer.

The same workers, in general, as those who have found a variation in other characters, have also documented the variation of trichomes in different environmental conditions (*fide* Odell, 1932). Hairs have been found to be more abundant in greater sunlight, greater wind exposure, drier air, drier soil and greater altitude. McDougall (1927), however, reported that far more hairs developed in reduced sunlight in *Lactuca biennis* (Moench) Fernald (*L. spicata* auct.). It is possible that in some of these cases the proportion of hairs to cells does not vary, but at least in many instances it does. In general there is no possibility, therefore, of the use of a trichome index comparable to the stomatal index ; trichome density is a much more variable character than stomatal frequency, and its taxonomic use is thus more restricted. Only differences of a considerable degree or differences in the relative distribution of trichomes are reliable. The one advantage of a measurement of hair density in terms of hairs per cell rather than of hairs per unit area is that the former cancels the effect of age in any one leaf, except as noted below. As in the case of stomata the number of hairs per epidermal cell may remain constant as the leaf expands, and it is unfortunate that this value does not also remain constant in different environmental conditions and positions on the plant.

A further complicating factor concerned with trichome frequency is the phenomenon of glabrescence : the gradual loss of hairs with age. As explained previously most hairs may be localized on cuticular preparations by the presence of a hair-base, the centre of this often being occupied by a pore. It was thought that the number of hair-bases per epidermal cell might remain constant throughout the life of a leaf, even if most of the hairs themselves dropped off. Unfortunately in most cases this was found to be untrue. Observations were made chiefly on a number of species of *Buchenavia, Conocarpus* and *Combretum* ranging from extremely small young leaves, from which cuticular membranes were difficult to prepare, to senescent leaves that had begun to fall from the trees. In the species of *Buchenavia* examined, notably *B. capitata* and *B. kleinii*, the very young leaves are uniformly densely pubescent or sericeous, whilst the very old leaves are mostly glabrous with a few hairs still remaining on the midribs and major lateral veins. Microscopic examination of the former showed that almost every epidermal cell was adjacent to one or more hair-bases, but as the leaf expanded and the hairs began to fall off the hair-bases gradually became occluded, and in the mature state the majority were not visible at all. The more actively growing (i.e. the more immature) a leaf the more quickly occluded are unoccupied hair-bases. Occlusion is effected by the hair-base cells encroaching inwards until no pore remains. When loss of the trichomes is delayed until after leaf growth has ceased, however, the vacated hair-bases often remain distinct thereafter, as is the case with the diagnostically important scales of *Combretum* spp., although this is not true of the hairs of *Conocarpus erectus* var. *sericeus*.

Thus the use of trichome frequency as a taxonomic character must be preceded by an exhaustive series of observations on a wide range of material in order to discover the cuticular changes accompanying growth and senescence, as well as the degrees of phenotypic variation.

D. Epidermal cell shape.

The epidermal cells gain their characteristic shape gradually from the time that cell division ceases onwards, and in general this is completed before the process of cell expansion has ended. Certain types of cell shape, however, may be finally assumed after the leaf has reached full size. The only important example of this is the undulation of the lateral epidermal cell walls. Since the undulations occur equally on either side of an imaginary mid-line, i.e. into each of the two adjacent cells, the apparent length of the cell can increase (by twice the value of half the amplitude) without any increase in volume (Fig. 10).

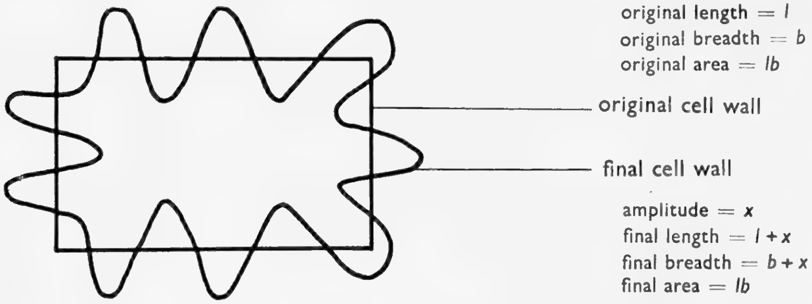


Fig. 10. Diagram illustrating growth of cell-wall undulations.

In most cases examined, however, the development of undulations takes place whilst the leaf is expanding, and can give rise to the apparent phenomenon that the cells are growing faster than the leaf. The final amplitude of the undulations is usually reached as the cells (and the leaf) attain full size, although the maximum growth of the undulations ceases some time before this. In *Buchenavia capitata*, however, the leaves at flowering time, which are fully grown but considerably thinner and more pubescent than when mature, have conspicuously less undulate walls than those at fruiting time, and in this case at least the undulations do increase in amplitude without any increase in cell area. This is most apparent on the upper epidermis. According to Watson (1942) it is the stresses set up by the hardening cuticular membrane which cause the plastic cell walls to become undulate, and when the cells have become mature their walls are too rigid to allow further increase of undulation. It is thus clear that absolutely mature leaves must be examined in order to ascertain the degree of undulation of the cell walls.

Much variation in this undulation has been noted in various environmental conditions, strongly undulate to straight walls often being observed within a single species. Brenner (1900), amongst the earlier workers, found that considerable differences could be found between plants in " normal " and damp conditions : in two species of *Crassulaceae* the normally straight-walled cells were converted to markedly undulate-walled cells, and in a third species the exactly opposite result was obtained. A considerable number of workers have noted that the amplitude of the undulations increases with increased shade, humidity and soil dampness (Odell, 1932). Watson (1942) found that epidermal cells of *Hedera* in sunny situations had 6·3 crests per cell, whilst those in shade had 8·7. Moreover the latter extended throughout the height of the cells, whereas the former were confined to their outer edge. This was explained on the basis that in the sun the cells become mature and rigid more quickly, so that the hardening cuticular membrane does not have an effect to such a great depth as in the shade.

Yapp (1912), Stober (1917) and other workers (*fide* Odell, 1932) have found that the undulation of the cells of many species decreases the higher the point of insertion on the stem, in some cases radical leaves having undulate-walled cells and cauline leaves straight-walled cells.

With regard to other features of cell shape Brenner (1900) claimed that *Crassula portulacea* Lam. has strongly papillose cells in damp conditions, but flat cells in " normal " situations.

Few other characters of the epidermis show as much variation as the cell-wall undulation, and although this has been used taxonomically in a number of groups its use requires the most extreme caution.

E. LEAF VENATION.

Variation in the actual venation of leaves is apparently not very frequent, and when it does occur not drastic. The characters found to vary, if any, are exemplified by the situation found in *Medicago sativa* L. by Turrell (1942), where the larger leaves, which had larger epidermal cells and stomata than normal, possessed larger areolae, i.e. the number of veins and venules was not different, but the spaces between them were larger. Levin (1929) and Hall & Melville (1951) claimed that the areola size was diagnostically important, but the latter authors (1954) and Gupta (1961) later found that it in fact varied with leaf size.

The most variable venation character with regard to the present study is the degree to which the various orders of veins are represented on the epidermis. This feature appears as the epidermal cells are enlarging, but its exact time of development probably varies from group to group. In *Buchenavia capitata* and *B. kleinii*, for instance, it develops earlier on the lower epidermis, where it is quite well developed well before the cells are full-sized, than on the upper epidermis, where it has not fully developed when the leaves are fully grown: in the latter case both the smaller venules and undulations of the cells develop as the full-sized leaf matures. In fact it is the non-appearance of undulations on the venule cells which causes them to be distinguished so easily.

No comments concerning the phenotypic variation of the epidermal veins seem to have been made in the literature, but considerable variation was in fact found in a number of species. Since the species in which this was noted were all of tropical origin the reasons could not be definitely explained, but there is little doubt that they are partly environmental and positional in origin. The differences were concerned with the size of the smallest venules distinguishable on the epidermis, and thus with the sizes of the areolae and the degrees to which the venous system appeared to be open or closed. Usually the range of variation within a species gives extremes with different-sized areolae only, but in some cases a species shows open and closed venous systems of all degrees.

It appears that the environmental conditions producing a leaf with fewer veins discernible on the epidermis in fact act primarily by producing a thicker leaf due to the larger cells and inter-cellular spaces. This in some way seems to permit fewer of the vein extensions to extend from the venules as far as the epidermis, so that fewer venules produce epidermal cell modifications. Greater shade and humidity are the commonest conditions which cause these effects.

F. Development of cuticular membrane.

The mature thickness of the cuticular membrane is not attained until a fairly late stage, when cell enlargement is completed. The membrane is, however, thick enough to be isolated *in toto* even before cell division has stopped, and the cuticular flanges are then well enough developed to show quite clearly the outlines of the cells. Nevertheless absolutely mature leaves are essential for comparative taxonomic purposes.

Furthermore environmental conditions are known to affect the cuticular membrane thickness and cuticular-flange length. Skoss (1955) found that the " cuticle " was thicker in leaves exposed to the sun, and the same was discovered by a number of other workers who also correlated a thicker cuticular membrane with a drier soil, drier air, more exposure to wind, a higher altitude and other factors (*fide* Odell, 1932).

Also the cuticular membrane is usually thicker on the upper stem leaves than on the lower stem or radical leaves (Yapp, 1912) but Stober (1917) reported that in some plants it was thickest on the lower stem and upper radical leaves. This cuticular thickness is accompanied by a thickening of the outer epidermal cellulose cell wall.

Variation may also be caused by other, unknown, conditions, since Stevens (1932) noted a fluctuation in the cuticular thickness on cranberry fruits (*Vaccinium macrocarpon* Aiton) from year to year which was not correlated with fruit size or climate, and which was exactly repeated in 33 different varieties of the plant. In *Lumnitzera racemosa*, a mangrove with a normally very thick cuticular membrane, a single specimen was encountered with very abnormally thin leaves due to the sparse development of the usually abundant water-storage tissue. This specimen had a very much thinner cuticular membrane than usual, but the epidermal anatomy was otherwise quite typical, and the habitat gave no clue to the reason for the peculiarity.

Conspicuous cuticular striations are absent from most leaves, but when they are present they do not develop until a relatively late stage, and their usefulness is restricted to mature leaves. They are, however, of great taxonomic value in some groups, being highly characteristic of three of the four species of *Macropteranthes*, for example. No very young leaves of markedly striate species of the *Combretaceae* were available, but Martens (1934) has followed the development of the cuticular striations on certain petals. There is, however, a considerable variation in the degree of development of the cuticular striations in some species, and full account of this must be taken. In *Combretum molle* R. Br. ex G. Don, for example, the only known gathering from South West Africa is most distinctive in its extremely conspicuously striated cuticle, the striations being so strong as to obscure the cell outlines (Stace, 1961). In tropical Africa, however, where this species is very abundant, all degrees of striation are found from the previous situation to the presence of only a few striations placed radially to each trichome-base, a situation present in many or even most species of the genus. Since the cell outlines in the latter cases are very clear, the two extremes have an entirely different aspect. The cause of this variation is, of course, unknown, but would seem likely to be environmental as the climate of the South West African habitat is relatively very dry.

G. SUMMARY.

It is clear that a great deal of variation is to be encountered within one species in certain cuticular characters, although little or none may be found in others. Variation may be attributed to minor genetic (genotypic) differences or to certain measurable influences, both genotypic and phenotypic, of three main types—developmental, positional and environmental. Obviously variation due to all of these factors must be fully considered before the characters are utilized taxonomically.

In many or most plants the lower leaves are in a different environment from the upper, and their structure often reflects this. In *Filipendula ulmaria*, for example, the lower leaves are in a much more shaded and humid situation, and the type of variation from the upper leaves which they show is similar to that which is shown by upper leaves of other plants which are in a wholly damper environment, although this is not to say that the characteristics of the lower leaves are actually caused by their environment, as are those of upper leaves of plants in damp, shaded situations. The characters of these leaves are nevertheless to be regarded as relatively mesomorphic, and those of leaves in drier conditions as xeromorphic. The commonest mesomorphic cuticular characters are : a thinner cuticular membrane and shorter flanges ; more undulate epidermal cell walls ; fewer hairs ; less densely situated stomata ; larger epidermal cells and stomata ; and larger areolae.

A third level of differentiation of mesomorphic and xeromorphic characters, beyond various parts of one plant and plants of one taxon, is between different species of one larger taxon. In this case the characters are genetically regulated, and they differ to some extent from those mentioned above, mainly in that they are concerned with structure to a greater extent than size and frequency, but they do show a number of similarities. The xeromorphic characters as exemplified by the *Combretaceae* are : a thicker cuticular membrane and longer cuticular flanges ; straighter cell walls ; more hairs (in a group in which hairs are of frequent occurrence the more xeromorphic species are usually the most pubescent, but in other groups xeromorphs are frequently extremely glabrous, e.g. mangroves) ; lesser development of veins and venules on the epidermis ; presence of stomata on both leaf surfaces (in those groups in which there is a tendency for stomata to appear on the upper epidermis the character is usually most developed in the most xeromorphic species, but in other groups the stomata of xeromorphs are frequently more limited in distribution on the lower epidermis alone, e.g. they may be confined to grooves or crypts) ; more sunken guard-cells ; and, within the anomocytic stomatal group, the tendency to develop distinctive epidermal cells adjacent to the guard-cells.

It is the task of the taxonomist to distinguish between phenotypic and genotypic variation. In the former case the problem is to correlate it with specific environmental or other factors and to ascertain the degree of the variation, and in the latter to decide at what taxonomic levels it should be recognized, if at all.

§8. General conclusions

It cannot be too heavily emphasized that there are no guiding principles enabling assessment of the taxonomic usefulness of a given character in a taxon in which it has not been previously utilized ; neither are there any means of predicting the characters most likely to prove of greatest diagnostic importance in an uninvestigated group. It is thus unwise and unjustifiable to draw on experience in one taxon and to apply it to another, even if the two plant groups are very closely related. In the *Combretaceae,* for instance, the flowers and trichomes provide the most useful systematic characters in the tribe *Combreteae,* the fruits being relatively uniform in structure ; whereas in the closely related *Terminalieae* the fruits and the epidermis are the only organs showing a large number of known taxonomic criteria. The diagnostic value of pollen-grains, chromosomes and wood anatomy in this family has as yet been little studied. Furthermore, in general, characters tend to vary and assume a greater or lesser taxonomic importance quite independently of one another, and there is no single character which universally or even usually overrides all others in importance. Even in the case of the chromosomes, for which the latter has most frequently been claimed, there are very many taxa in which characters other than the number and morphology of these organelles are of greatest significance, indicating that the genetic information in the chromosomes is no more manifested in their over-all shape than in that of the flowers, fruits, leaves or other organs.

There is, therefore, no reason to doubt the validity of epidermal features merely because in some groups they do vary greatly or do not agree with differentiation by other means. If it is possible for two taxa to differ solely on the shape of the stamens or leaves then it is possible for two others to be distinguished only on the form of their hairs or epidermal cells. It is very doubtful, however, whether a difference in a single feature of one organ (whatever that organ) will differentiate between taxa at a higher level than " minor genetic variants ", and almost certainly not between " species " as normally understood. In reaching taxonomic conclusions evidence from as many sources as possible should be incorporated into the catalogue of information which will lead to the proposed classification. No facet of the plant, morphological, physiological, biochemical or genetic, should be omitted. This becomes abundantly clear when the case of taxa whose systematic position varies with the character selectively utilized (e.g. *Pteleopsis* and *Calycopteris* in the *Combretaceae*) is considered.

Undoubtedly minor exceptions to these generalizations exist, though by no means disproving the rule. There does appear, for instance, to be some degree of correlation between the diagnostic value of the epidermal cells and stomata and the degree of xeromorphy of the taxon. Most groups which have been found to possess taxonomically valuable epidermal characters are xeromorphic to some extent, e.g. gymnosperms, *Lauraceae*, *Magnoliaceae*, *Ericaceae*, *Epacridaceae*, various mangroves, and others. This is perhaps an expression of the idea that plants which are more highly specialized tend to be less variable, potentially as well as actually. It seems obvious that the greater the complexity of an organ the more features there are to be used by taxonomists, and thus the greater the diagnostic value of that organ. There is, in addition, the commonly held belief that characters of apparently little or no differential survival value (e.g. pollen-grain sculpturing, delimitation of cells of certain trichomes) are those with the greatest systematic and phylogenetic significance.

Attempts have often been made to generalize on the taxonomic level at which various diagnostic characters differentiate. Fritsch (1903), for example, concluded that gland anatomy was more indicative above the generic level, and the presence or absence of papillate epidermal cells at the specific level. Edwards (1935), however, pointed out that in different groups stomatal frequency can be a family, generic or specific criterion, or of no systematic importance at all. This is true of almost every character as the many exceptions to Fritsch's and others' claims testify. Thus, apart from noting that in a particular family or other group certain characters are more important than others at the various taxonomic levels little or no valid generalization can be made. A good example illustrating this point is the possession of a very densely or very sparsely pubescent leaf epidermis : in *Ramatuella* it serves to distinguish between *R. argentea* Kunth and *R. virens* Spruce ex Eichl. ; in *Hibiscus vitifolius* L. between subsp. *vitifolius* and subsp. *vulgaris* Brenan & Exell ; in *Conocarpus erectus* between var. *sericeus* and var. *erectus* ; and in many species of *Epilobium* between no more than various phenotypic modifications. In these cases, therefore, the level at which the character differentiates is presumably dependent upon the other characters with which it is correlated, and with the causes of the differences. Similarly, the presence of stomata on the upper epidermis is important at the family level within the mangrove habit, but amongst the non-mangrove members of the *Combretaceae* it is of little significance, varying from species to species or often even infraspecifically. Stomatal size is frequently directly the result of the level of ploidy, and indicates a second reason for the fact that characters differentiate at varying taxonomic levels : namely that taxonomists have often failed to accord similar ranks to groups of taxa showing exactly the same differences. Thus *Rorippa microphylla* and *R. nasturtium-aquaticum, Galium palustre* L. subsp. *palustre* and subsp. *tetraploideum* Clapham, and *Ranunculus ficaria* var. *ficaria* and var. *bulbifer* Marsden-Jones are three pairs of taxa of which the first is diploid and the second tetraploid, although the resultant stomatal size differences apparently show differentiation at three distinct levels, if the taxonomic ranks assigned above are accepted[1].

The need to investigate exhaustively all aspects of the genotypic and phenotypic variation of a " new " character has been previously stressed. In cases where characters have been used before this preliminary survey has been undertaken the identifications attempted have often proved faulty, and have cut across decisions based on other characters. When the potentiality of the character is understood, however, and accurate identification is possible, the taxonomy of the group may on occasions be improved in the light of the discoveries. The present cuticular study has resulted in several such proposals in the classification of the *Combretaceae.* It is not to be expected that the new evidence will cause a drastic re-classification to become desirable, but rather that the new character might so shift the balance of the evidence from all sources that in some places taxonomic adjustments seem advisable. Entirely new classifications based on one type of evidence are usually shorter-lived than the original.

Epidermal characters, then, are likely to provide not only a means of identification (especially of sterile material) but also as valuable taxonomic and phylogenetic clues as most other characters, and they exhibit much the same characteristics with respect to their pattern of variability. Edwards (1935) commented that the

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[1] *Rorippa microphylla* was in fact first described as a variety of *R. nasturtium-aquaticum*, and *Ranunculus ficaria* var. *bulbifer* has been raised to subspecific rank as *R. ficaria* subsp. *bulbifer* (Marsden-Jones) Lawalrée.

cuticular differences between closely related species or infraspecific taxa are usually slight or absent. This is by no means always so. When all the differences between two closely allied taxa are analysed it is usually found that a few characters are conspicuously different, many slightly or scarcely so, and others identical. Thus, although it is most likely in such a case that the cuticular characters will also be only slightly or not different, the same is true of any other single feature. Occasionally, however, it is just that particular character being studied that shows the greatest difference between the two taxa. Several examples where this is true of the cuticular characters have been discovered within the *Combretaceae*. It seems that a knowledge of the relative usefulness and an understanding of the level of differentiation of cuticular characters in the angiosperms as a whole will only be objectively obtained when cuticular studies have been absorbed into the general practice of plant taxonomy.

I do not claim that cuticular characters are of any outstandingly fundamental or all-important significance, as did some of the early exponents of the taxonomic use of pollen-grain or chromosome features. They are, however, to be regarded as characters of undoubted importance as further pieces of the jigsaw of complete systematic evidence, and at times they are in fact of greater value in identification and taxonomy than are any other characters of which we know.

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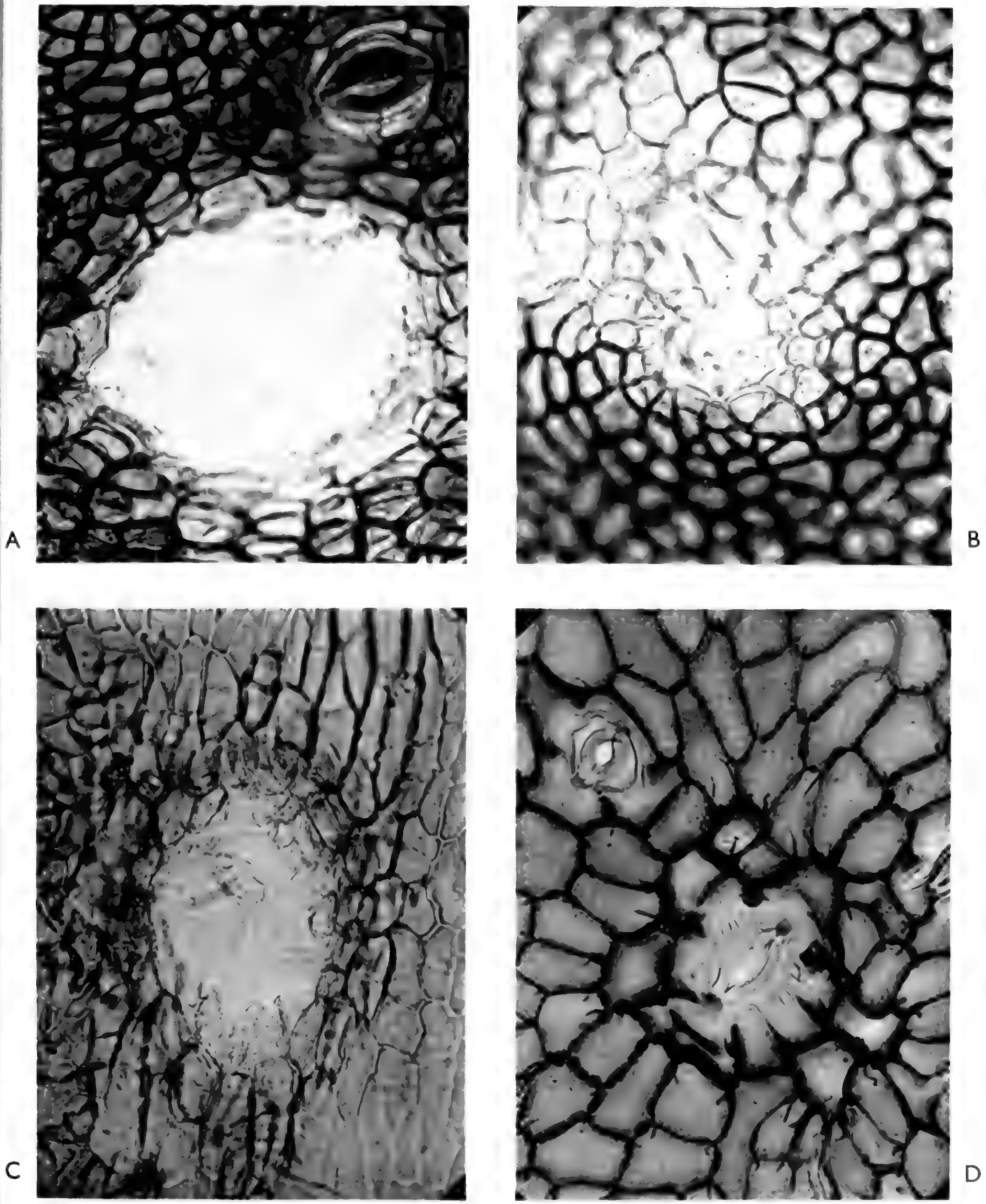
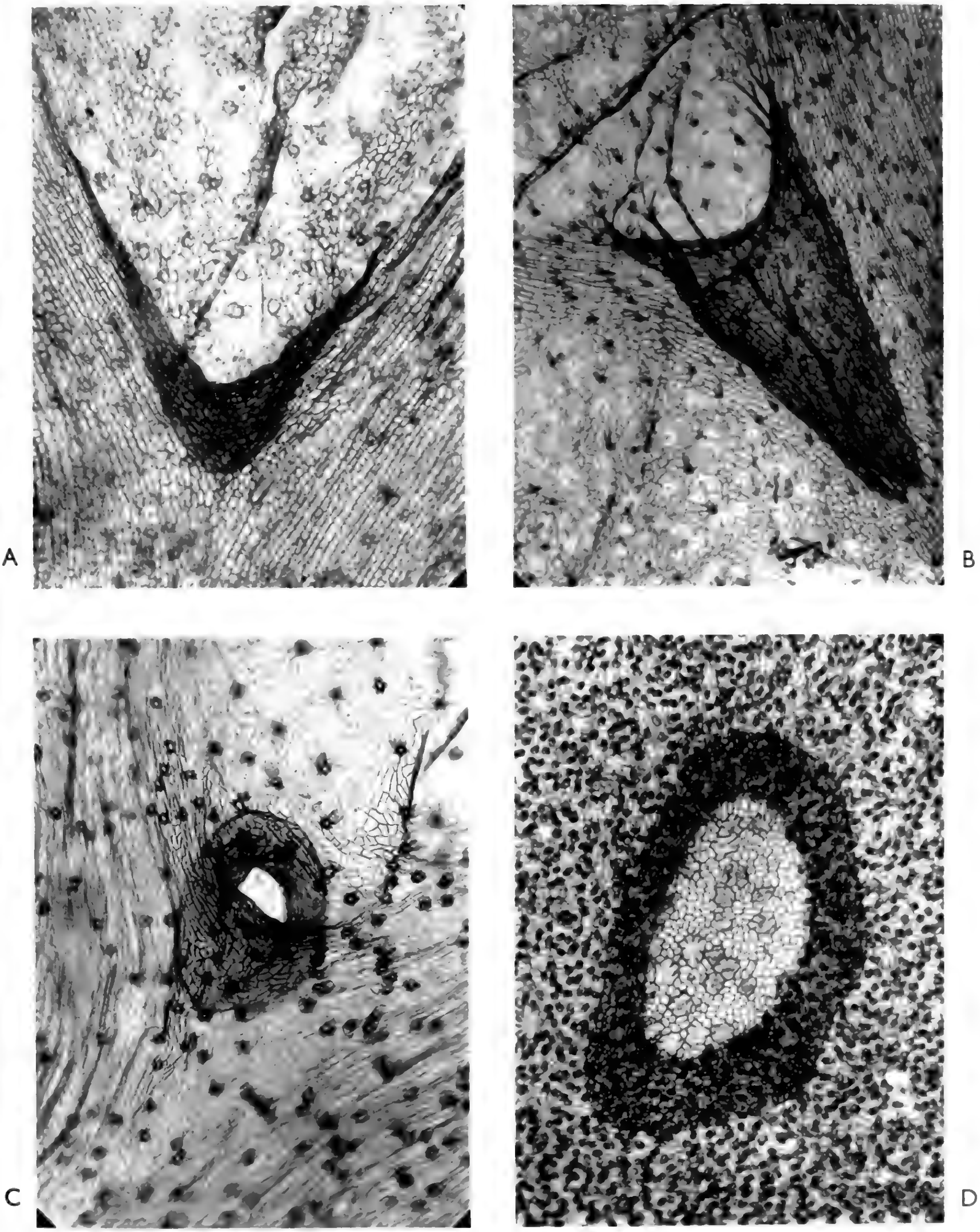
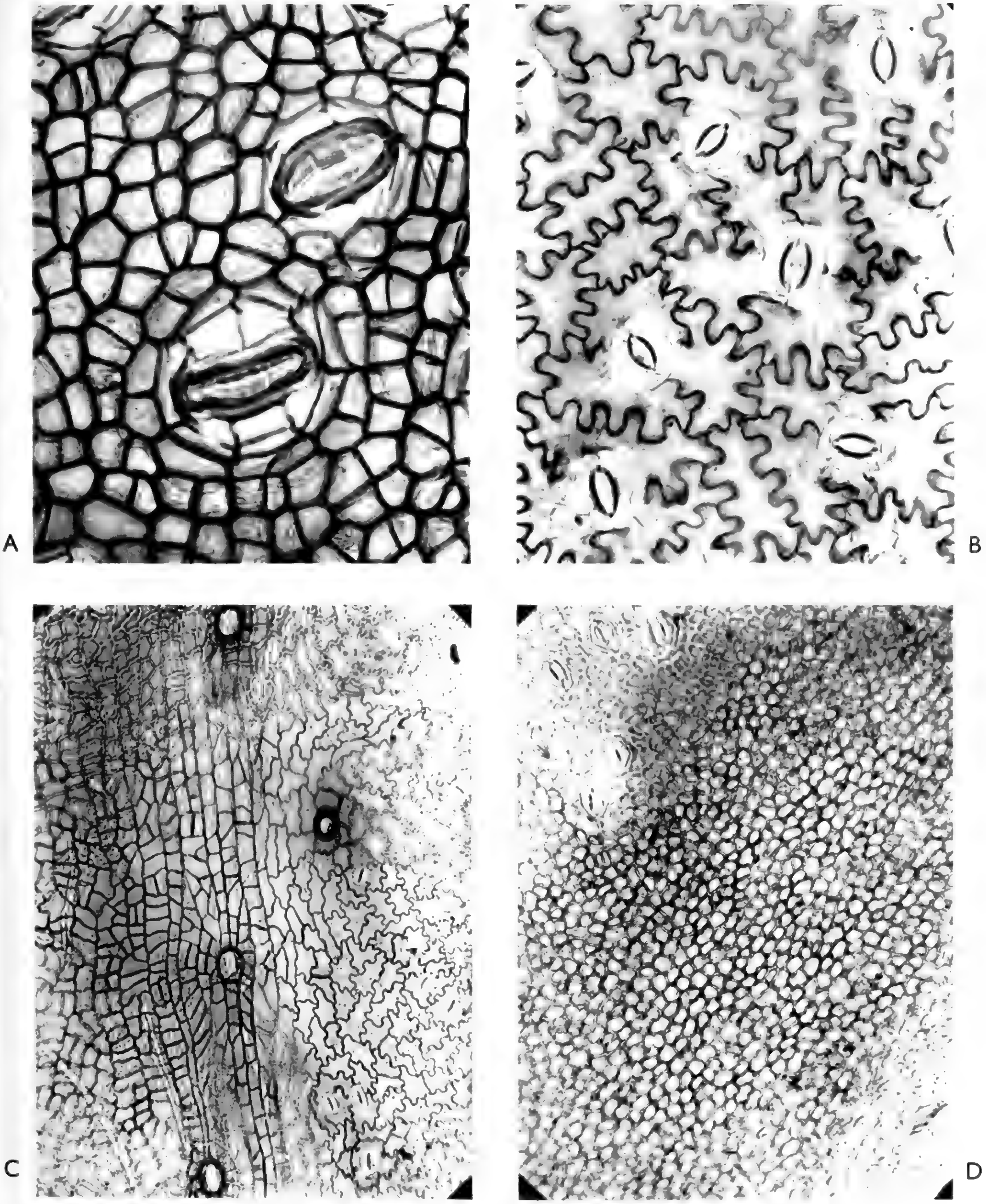


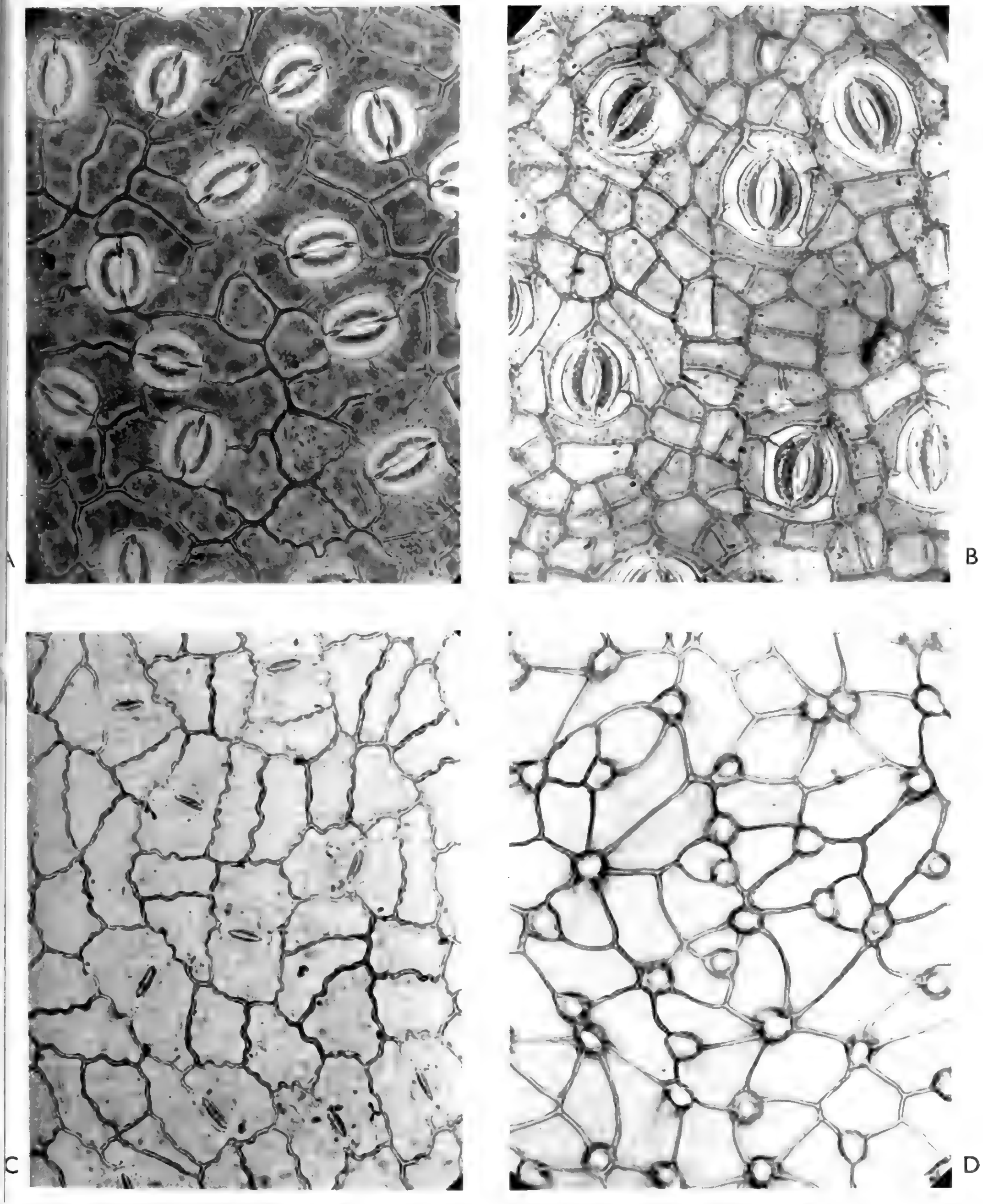
A, *Rhizophora mucronata* Lam. : lower epidermis of leaf, showing cork-wart (×420). B, *Buchenavia kleinii* Exell : upper epidermis of leaf, showing wound caused by fungal attack (×420). C, *Terminalia catappa* L. : leaf margin, showing characteristic hole (×420). D, *Lumnitzera racemosa* Willd. : lower epidermis of leaf, showing water-stoma (×420).



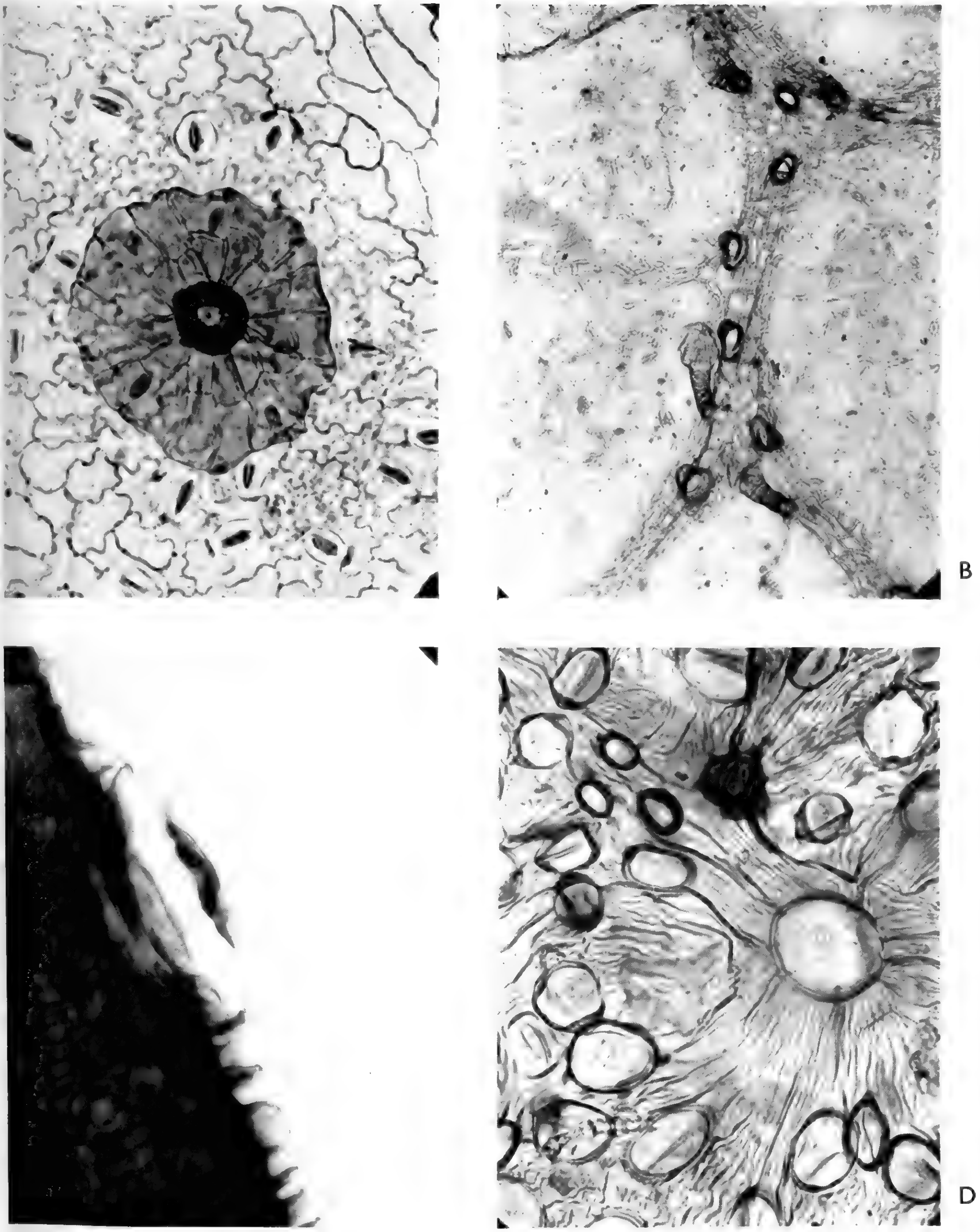
A, *Buchenavia grandis* Ducke : lower epidermis of leaf, showing marsupiform domatium (×80). B, *B. capitata* (Vahl) Eichl. : lower epidermis of leaf, showing marsupiform domatium (×60). C, *Terminalia catappa* L. : lower epidermis of leaf, showing lebetiform domatium (×80). D, *Conocarpus erectus* var. *sericeus* Forsstr. ex DC. : lower epidermis of leaf, showing lebetiform domatium (×60).



A, *Rhizophora mangle* L. : lower epidermis of leaf, showing strongly cuticularized stomata and straight epidermal cell walls (×420). B, *Buchenavia fanshawei* Exell & Maguire : lower epidermis of leaf, showing thinly cuticularized stomata and undulate epidermal cell walls (×420). C, *Combretum nigrescens* King : leaf margin (×170). D, *Laguncularia racemosa* (L.) Gaertn. f. : leaf margin (×170).



A, *Ramatuella virens* Spruce ex Eichl. : lower epidermis of leaf, showing anomocytic stomata (×420). B, *Laguncularia racemosa* (L.) Gaertn. f. : lower epidermis of leaf, showing cyclocytic stomata (×420). C, *Strephonema sericeum* Hook. f. : lower epidermis of leaf, showing paracytic stomata (×420). D, *Guiera senegalensis* J. F. Gmel. : upper epidermis of leaf, showing numerous simple hair-bases (×420).



A, *Thiloa glaucocarpa* (Mart.) Eichl. : lower epidermis of leaf, showing scale with strongly cuticularized scale-base (×420). B, *Combretum obovatum* F. Hoffm. : lower epidermis of leaf, showing stalked glands on the raised venule reticulum (×170). C, *Ceriops tagal* (Perrott.) C. B. Robinson : lower epidermis of leaf, showing stoma and cuticular flanges in profile on cuticular membrane folded inside outermost (×420). D, *Quisqualis hensii* (Engler & Diels) Exell : upper epidermis of leaf, showing cuticular striations and three types of trichome-base (×420).

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W. A. SLEDGE

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THE GENUS *ELAPHOGLOSSUM* IN THE INDIAN PENINSULA AND CEYLON

By W. A. SLEDGE

In a comment on the systematic list of ferns in a paper by Manton and myself on the cytology and taxonomy of the pteridophytes of Ceylon, I expressed the view (Phil. Trans. Roy. Soc., ser. B. 238 : 158 (1954)), that the names currently employed for the four species of *Elaphoglossum* were in need of revision. It subsequently became apparent that both the taxonomy and the nomenclature of the Indian species also required re-examination.

The names employed in Beddome's works are mostly those originally given to African or tropical American plants with which Indian ones were at that time considered identical. The same names are now used in a more restricted sense and the discrimination of several species with more limited distributions within the areas of the aggregate species has left in doubt the correct names to be assigned to Indian and Ceylon species. So far as I am aware the only paper on Indian species of *Elaphoglossum* which has appeared since the time of Beddome is one by Biswas (Bull. Misc. Inf. Kew 1939 : 237–241 (1939)) in which two new species are described. Both of these supposed new species however are unnecessary renamings of species already described by Blume and Fée.

In his *Ferns of Southern India*, Beddome described under the name *Elaphoglossum conforme* a species which appears to be not uncommon in the Nilgiri Hills. Biswas, who described it as new, was correct in rejecting this identification but appears not to have questioned the identification of another species growing in the Nilgiri and adjoining hills which Beddome and later authors called *E. stigmatolepis* (Fée) Moore ; indeed he makes no reference anywhere in his paper to this species. Beddome's *E. conforme* was in fact based on specimens of the same species as that first described by Fée as *Acrostichum stigmatolepis*, and it is therefore Beddome's *E. stigmatolepis* which requires a new name. In his *Handbook to the Ferns of British India, Ceylon and the Malay Peninsula* (1883), Beddome amplified the distribution credited to *E. conforme* to include the Himalayas, Ceylon and Malaya. The plant from the Himalayas is *E. marginatum*, which had long been regarded as a synonym of *E. conforme* but which Biswas correctly reinstated as a distinct species. Neither *E. stigmatolepis* nor *E. marginatum* occur either in Ceylon or Malaya and these regions were included through errors of identification and do not cover a third species unaccounted for amongst those described by Beddome.

The Indian specimens which Beddome originally referred to *E. laurifolium* (changed in his *Handbook* to *E. latifolium*) are identical with Blume's Javan *Acrostichum angulatum*, which name he cited as a synonym of *E. laurifolium* in his *Ferns of Southern India*. This is the other species which Biswas needlessly described as a new species. *E. angulatum* is an easily recognized species on account of its long-creeping rhizome and very distinctive rhizome scales, yet most Ceylon gatherings of this species are identified in herbaria not as *E. laurifolium* but as *E. conforme.* The true *Acrostichum laurifolium* of Thouars is confined to Tristan da Cunha and Gough Island, and another species from Ceylon and southern India with short-creeping rhizome, closely placed fronds and different rhizome scales, which is usually labelled *E. laurifolium* in herbaria, is *E. commutatum*, a species which was founded by Mettenius partly on a Ceylon gathering made by Thwaites but which is not illustrated in Beddome's works.

As regards the ferns that Beddome called *E. squamosum*, this name was currently used to cover superficially similar plants ranging from tropical America eastwards to southern India and Ceylon. African, Madagascan and Mascarene representatives of the aggregate species have since been split off from Jamaican plants, whence the type was described. The Nilgiri and Ceylon plants which were united under the same name by Beddome are certainly distinct from one another and as neither can be matched by African or Mascarene gatherings, I have described these as two new species, using names already given to herbarium specimens at Kew by Krajina but never published by him.

Of the names used by Beddome, only *E. spatulatum* stands unchanged and even this very distinct species has recently been incorrectly excluded as a Ceylon species by Madame Tardieu-Blot (Not. Syst. 15 : 432 (1959)), and the equally distinct Madagascan *E. schizolepis* has erroneously been substituted for it.

The confusion which has surrounded the application of so many of these names is discussed in more detail later in this paper under the individual species ; but it may be useful to list here the illustrations and names given in Beddome's *Ferns of Southern India* together with their correct identifications :

F.S.I. t. 196 as *E. viscosum* = *E. stelligerum* (Wall. ex Baker) Alston & Bonner
F.S.I. t. 197 as *E. squamosum* = *E. nilgiricum* Krajina ex Sledge
F.S.I. t. 198 as *E. conforme* = *E. stigmatolepis* (Fée) T. Moore
F.S.I. t. 199 as *E. stigmatolepis* = *E. beddomei* Sledge
F.S.I. t. 200 as *E. laurifolium* = *E. angulatum* (Blume) T. Moore
F.S.I. t. 213 as *E. spathulatum* = *E. spatulatum* (Bory) T. Moore
No illustration in F.S.I. { *E. marginatum* (Wall. ex Fée) T. Moore
E. commutatum (Mett.) Alderw. van Rosenb.
E. ceylanicum Krajina ex Sledge

At the time of writing, a proposal (Anderson in Regn. Veg. 40 : 18 (1965)) to conserve the generic name *Elaphoglossum* Schott ex J. Smith (Hooker's Journ. Bot. 4 : 148 (Aug. 1841)) against *Aconiopteris* C. Presl (Tent. Pterid. : 236 (1836)) is under consideration. It has been approved by the Special Committee for Pteridophyta (Taxon 15 : 333 (1966)) but awaits ratification.

My grateful thanks are tendered to the Directors and Curators of the herbaria at the British Museum (Natural History) (BM), the Botany School, University of Cambridge (CGE), the Royal Botanic Garden, Edinburgh (E), the Royal Botanic

Gardens, Kew (K) and the Division of Systematic Botany, Peradeniya, Ceylon (PDA) for access to, or for the loan of, specimens in their charge.

Key to the Species

Fronds coriaceous or at least stiff in texture, margins with a cartilaginous border, surfaces glabrous or with minute scales.
  Rhizome long-creeping, fronds spaced.
    Rhizome scales papery, broad, pale brown ; lamina 2·5–4·5 cm. broad 1. *E. angulatum*
    Rhizome scales not papery, dark brown or black ; lamina 1·5–2·5 cm. broad 2. *E. stigmatolepis*
  Rhizome short-creeping, fronds crowded.
    Rhizome scales entire, linear (5–10 times as long as broad), stipes much shorter than lamina . . . . 3. *E. beddomei*
    Rhizome scales more or less fimbriate, narrow (4–5 times as long as broad), stipes up to half as long as lamina.
      Rhizome scales dark brown, 5 mm. long, acuminate 4. *E. marginatum*
      Rhizome scales brown, 10 mm. long, attenuate with crisped tips 5. *E. commutatum*
Fronds thickly herbaceous or soft in texture, margins without a cartilaginous border, surfaces conspicuously scaly or hairy.
  Scales of stipe and lamina stellate with long rays . . 6. *E. stelligerum*
  Scales not stellate.
    Scales ovate with long marginal teeth.
      Fronds densely paleate, the lower surface wholly obscured by imbricating scales ; scales of stipe broad, mostly concolorous 7. *E. nilgiricum*
      Fronds paleate but neither surface obscured by scales ; scales of stipe narrow, mostly with their borders and teeth dark-coloured 8. *E. ceylanicum*
    Scales filiform, hair-like . . . . 9. *E. spatulatum*

1. **Elaphoglossum angulatum** (Blume) T. Moore, Index Fil. : 5 (1857).

Acrostichum angulatum Blume, Enum. Pl. Jav. : 101 (1828) ; Fl. Jav., Fil. : 25, t. 6 (1829).—Fée, Mém. Fam. Foug. 2 : 32 (1845).—Kunze in Linnaea 24 : 248 (1851).—Christ in Neue Denkschr. Schweiz. Ges. Naturw. 36 (1, 2) : 46, 49 (1899).
Olfersia angulata (Blume) C. Presl, Tent. Pterid. : 234 (1836).
Acrostichum conforme sensu Hook., Sp. Fil. 5 : 198 (1864) pro parte ; non Swartz.—Hook. & Baker, Synops. Fil. : 401 (1868) pro parte.
Acrostichum marginatum sensu Thw., Enum. Pl. Zeyl. : 380 (1864) ; non Wall. ex Fée.
Elaphoglossum laurifolium sensu Bedd., Ferns S. Ind. : 67, t. 200 (1864) ; non T. Moore.
Elaphoglossum latifolium sensu Bedd., Handb. Ferns Brit. Ind. : 416 (1883) ; non J. Smith.
Elaphoglossum ogatai C. Chr., in Dansk. Bot. Ark. 9 (3) : 67 (1937).
Elaphoglossum krajinae Biswas in Bull. Misc. Inf. Kew 1939 : 240, t. 1 fig. 2 (1939).

Rhizome long-creeping with stipes 1–3 cm. apart, clothed with *pale, rufous-brown, papery, thin-walled, broadly ovate, acute scales*, 5 × 2 mm., with *subentire margins.* Fronds stalked 15–35 (45) cm., stipe of sterile fronds up to 15 cm. or more, often as long as the lamina but sometimes only half or less their length, scaly, the scales like those of the rhizome but with *irregularly fringed margins* ; lamina elliptic, 2·5–5 cm. broad, apex acute, base narrowed and shortly decurrent on the stipe, margins with a cartilaginous, revolute border, lower surface with scattered, minute, brown, more or less stellately-laciniated scales, midrib with a few larger irregularly laciniate scales ; texture coriaceous. Fertile fronds on stalks about as long as or longer than the sterile ones, 2–3 cm. broad. Spores 27–30 × 18–21 μ.

South India : Anamallays, 1,800 m., on trees, " F.S.Ind. f. 200 *Elaphoglossum laurifolium*" *Beddome* (BM). Kudiabad, Sispara Rd., 2,400 m., Nov. 1883, *Gamble 13473* (K). Bear Shola, Kodaikanal, Pulney Hills, 19 May 1898, *Bourne 4972* (K). Kodaikanal Waterfall, Pulney Hills, 30 May 1898, *Bourne 4973* (K).

Ceylon : *Thwaites C.P. 1311* (BM ; CGE ; K ; PDA). *Gardner 1165* (BM ; CGE, Nuwara Eliya, on trees, 1,500–2,100 m., Sept. 1844 ; E ; K). *Gardner 1310* (E ; K). Nuwara Eliya, *Thomson* (K). Same locality, *Freeman 369A, 370B, 371C* (BM). Same locality, *Day* in *Herb. Henderson* (E.). Same locality, creeping over tree trunks, 9 May 1906, *Matthew* (K). Pedrotalagala, 2,100 m., on mossy trees, 26 Dec. 1950, *Holttum* (SING). Adams Peak, on trees, 2,100 m., 14 Feb. 1908, *Matthew* (K). Same locality, 1,950 m., 14 Dec. 1950, *Sledge 615* (BM). Namunukula, Uva Province, 1,950 m., 24 Feb. 1954, *Sledge 1208* (BM). 1855, *R. W. Rawson 1039* (BM). *Mrs. Carr* ex *Herb. T. Moore* (K). *Wall* in *Herb. Henderson* and in *Herb. Neill Fraser* (E).

South India (Nilgiri, Pulney and Anamallay Hills), Ceylon, Sumatra, Java, Borneo, New Guinea, Philippine Islands, Tonkin, Formosa.

The long-creeping rhizome and broad, membranous, pale brown or rufous-brown, concolorous scales readily distinguish *E. angulatum* from all other Asiatic species. It differs also from all other Indian or Ceylonese species in having the veins united by a connecting strand at their extremities—a character of the *Aconiopteris* (*E. nervosum* (Bory) Christ) group. This structural feature is however invisible in living and herbarium specimens and can only be seen after treatment with a clearing agent. Its spores are smaller than those of the other marginate-leaved species occuring in India and Ceylon. *E. stigmatolepis*, which it most resembles in growth habit, may be distinguished by its dark rhizome scales and the narrower fronds appearing punctate beneath on account of the more peltate scales and the black points of attachment left where these have been shed.

Ceylon gatherings of this fern are usually named *E. conforme* and Indian ones either *E. conforme* or *E. laurifolium* (or *E. latifolium*). They certainly resemble African *E. conforme* but they agree far better and are indeed indentical with authentic specimens of Blume's *A. angulatum* at Kew and with other gatherings from Java. Kunze (loc. cit.) long ago reached the same conclusion when he referred a Nilgiri gathering (*Schmid 65*) to this species. *A. angulatum* was later merged in *A. conforme* by Hooker in the *Species Filicum*, and subsequent authors followed Hooker in their treatment of Ceylon and Indian plants.

Beddome's illustrations of what he names *E. conforme* and *E. laurifolium* in his *Ferns of Southern India* and the descriptions in his *Handbook* have been the greatest source of confusion surrounding the taxonomy of Indian *Elaphoglossums*. In the former work his illustration (t. 198) and description, purporting to be *A. conforme* Swartz, were based on plants on a sheet in the Kew collection annotated by him " type of tab. 198 F.S.I. ". The specimens on this sheet represent unmistakable though small and not very characteristic examples of *E. stigmatolepis* (Fée) Moore. (Beddome's illustration (t. 199) of what he calls *E. stigmatolepis* Fée represents another species.) The two different scales depicted represent examples taken from the rhizome and, in the case of the shorter and broader one with markedly jagged margins, from the stipe or midrib of the frond. The enlargement of a portion of the underside of the frond shows stellate scales quite different from the minute peltate scales with shortly fimbriate margins which characterize *E. stigmatolepis*, and this drawing could not possibly have been made from any of the fronds on the sheet referred to. There is moreover no reference in the accompanying description or in the later description in the *Handbook* to the presence of stellate scales on the fronds. The earlier work similarly contains no description of the form or colour of the rhizome scales, but in the *Handbook* these are referred to as " blackish " in colour, a description which is applicable to the specimens on the sheet and appropriate for *E. stigmatolepis* (and even, though somewhat less accurately, for *E. marginatum*, which, from the amplified distribution assigned in the *Handbook* to " *conforme* ", he now included in that species) but which is completely false for *E. angulatum* or for the true African *E. conforme*.

It is clear from the evidence provided by Beddome's own specimens at Kew and the British Museum that he was unfamiliar with *E. angulatum* for, whereas *E. stigmatolepis* (i.e. Beddome's *E. conforme*) is stated to be " very common " and is represented by several gatherings of his, he appears to have collected *E. angulatum* once only. This single gathering is in the British Museum collection, the sheet being labelled by Beddome " Anamallays. 6,000 ft., on trees. *Elaphoglossum laurifolium* (Thouars) F.S.Ind. f. 200 ". The description of *E. laurifolium* in the *Ferns of South. India* is followed by the citation of " *E. angulatum* Bl. En. 201 [sic] : Id. Fl. Jav. 25, t. 6 " in synonomy and the reference to the rhizome as " wide-creeping with bright chestnut or golden scales " and the other distinctions attributed in the *Handbook* to his *E. conforme* and *E. latifolium* (the name there substituted for *E. laurifolium* of the *Ferns of Southern India*) become explicable when it is realized that his *E. conforme* is based on *E. stigmatolepis* and his *E. laurifolium* (or *E. latifolium*) is based on *E. angulatum*.

Christensen states (in Gard. Bull. Str. Settl. 7 : 291 (1934)) *a propos* of Blume's figures of his *A. conforme* (i.e. *E. commutatum*) and *A. angulatum*, " I am by no means sure that the two ' species ' illustrated by Blume are really different ". And so it might seem from the plates themselves, for whilst the plate of the latter is an admirable representation of *E. angulatum*, that of the former is less characteristic of *E. commutatum* particularly in the spacing and small size of the fronds. Blume's drawings and descriptions of the rhizome scales of his two species however indicate such considerable differences and they agree so very closely with the scales of *E. commutatum* and *E. angulatum* that I have no hesitation in accepting the descriptions and the plates as illustrations of these two species. Fée's plate of *A. laurifolium* does not represent the same species. It is a Mascarene plant which has since been described by Mme. Tardieu-Blot (Not. Syst. 15 : 433 (1959)) as *E. alstonii*.

The type of *E. ogatai* is at the British Museum. Of this Christensen (Dansk Bot. Ark. 9 (3) : 67 (1937)) says " it is extremely like *E. angulatum* (Bl.) Moore . . . differs however in its remarkably thin texture and the distinctly but shortly decurrent lamina ". Tagawa, who is familiar with the living plant, states (in Mem. Coll. Sci. Univ. Kyoto, ser. B, 20 : 28 (1951)) that its fronds are thin-coriaceous and that no distinction can be drawn in the other respects. One of Bourne's Indian plants (Bear Shola, Pulney Hills) also has quite thin fronds, and the more ovate rather than elliptic fronds which look distinctive in the type specimen of *E. ogatai* can be matched by a specimen of Matthew's from Adam's Peak, Ceylon. I therefore accept Tagawa's reduction of *E. ogatai* to a synonym of *E. angulatum*.

Biswas's *E. krajinae* is quite clearly no more than a redescription of *E. angulatum*, which he evidently never took into consideration when separating Indian and Ceylon plants from African *E. conforme*.

2. **Elaphoglossum stigmatolepis** (Fée) T. Moore, Index Fil.: xvi, 15 (1857), 368 (1862).—Christ in Neue Denkschr. Schweiz. Ges. Naturw. 36 (1, 2) : 52 (1899).

Acrostichum stigmatolepis Fée, Mém. Fam. Foug. 2 : 62, t. 24 f. 2 (1845).—Hook., Sp. Fil. 5 : 216 (1864).
Elaphoglossum conforme sensu Bedd., Ferns S. Ind. : 67, t. 198 (1864) ; Handb. Ferns Brit. Ind. : 416, fig. 247 (1883) pro parte ; non J. Smith.
Elaphoglossum ballardianum Biswas in Bull. Misc. Inf. Kew 1939 : 239, t. 1 fig. 1 (1939).

Rhizome long-creeping, stipes 5–10 mm. apart, clothed with *ovate-lanceolate scales*, 3–5 × 1–2 mm., brown at the base and *blackish above, with subentire or sparsely fringed margins* and acute tips. Fronds stalked, 15–35 cm. long, *stipes of sterile fronds* variable in length, sometimes as long as the lamina but commonly much less, *scaly*, at least when young, *with* rather *broad scales* with jagged margins ; lamina narrowly elliptic, 1·5–2·5 cm. broad, apex acuminate, base narrowed and decurrent on the stipe, margins with a narrow, revolute, cartilaginous border, *midrib sparsely scaly beneath with short broad scales like those on the stipe, lower surface clothed with minute, dark, peltate scales with fimbriate margins*, upper surface with scattered scales of the same form when young, becoming smooth with age ; texture stiffly membranaceous to subcoriaceous. Fertile fronds on stipes normally exceeding those of the sterile fronds, 1–2 cm. broad. Spores (39) 42–45 (48) × 27–30 μ.

South India : " Ind. Orient Neilgherries, 159 " (CGE, ?isotype). Nilgiris, 2,100 m., " type of tab 198 F.S.I.", *Beddome* (K). Same locality, 1860, *Beddome 5* (K). Same locality, 2,100 m., Oct. 1889, *Gamble 21420* (K). Same locality, 2,100 m. Nov. 1870, *Henderson* (E). Same locality, *Wight 50* (K). Same locality, on trees and rocks, 1842, *Gough 3234/58* (K). Ootacamund, 2,100 m., Oct. 1885, *Gamble 16963* (BM). Same locality and date, *Gamble* in *Herb. Blanford* (E). Same locality, 2,100 m., Aug. 1885, *Gamble 16661* (K). Same locality, *Babcock* (K). Same locality, *Cockburn 85* (BM). Dodabetta, Nilgiri District, 2,550 m., June 1883, *Gamble 12038* (E). Kudiabad, Sispara Road, 2,400 m., Nov. 1883, *Gamble 13474* (K).

Moir Point, Pulney Hills, 2,340 m., stream, July 1937 and May 1938, *Aroticasamy 10* (BM).

South India (Nilgiri and Pulney Hills).

Elaphoglossum stigmatolepis differs from the other marginate-leaved species in its narrower, less coriaceous fronds, which are more tapering above and studded beneath with minute disc-like scales with shortly fimbriate margins. The points of attachment to the lamina appear as black dots when the scales have been shed. These are referred to by Fée as "petits points qui paraissent être de nature glanduleuse: ne serait-ce pas la base persistante des squames?". Young fronds show more sparsely distributed scales on the upper surface and in older fronds, where they have been shed, similar minute black scars are recognizable. Fée does not allude to these in his description but they are correctly shown in his illustration.

The rhizome scales are more pointed than those of *E. angulatum*, pale brown at the base but almost black, and often somewhat glossy, in the upper parts, and hence through imbrication they appear darker than the uniformly pale, rufous-brown and thinner, more papery scales of *E. angulatum*. As in that species, the stipe bears broad, brown scales with jagged margins and these are continued on to the lower part of the midrib. The spores are considerably larger than in *E. angulatum*, agreeing in size with those of *E. marginatum*, from which, and from *E. commutatum*, it differs in its more strongly creeping rhizome, in its frond form and texture, and in its scale characters.

Fée's description of *E. stigmatolepis* was based on a gathering " *in herb.* de Lessert., [sic] *sub* no. 159 ". The collector's name was evidently not stated on the label but the provenance is given as " in Indiis orientalibus, Neilgherries ". There is in the Cambridge University collection a sheet bearing a complete and well-preserved plant with three sterile and one fertile frond attached to a long-creeping rhizome 15 cm. long. No collector's name is inscribed on the label but this also reads " Ind. orient Neilgherries 159 ". The specimen agrees so exactly with Fée's description and plate that it is almost certainly an isotype. *Wight 50* in herb. Kew is also an excellent match for Fée's illustration and the Cambridge plant.

In Fée's description the fronds are said to be " membranaceis, papyraceis " and he does not include this species in the coriaceous-leaved group to which *A. marginatum*, *A. conforme* and *A. laurifolium* are referred. At the same time the fronds are described as narrowly revolute, and revolute edges are commonly associated with the stiff-leaved species. I have seen no living plants of *E. stigmatolepis* but to judge from herbarium specimens the fronds are thin but stiff and are distinctly less coriaceous than those of the other marginate-leaved species.

E. ballardianum Biswas is merely a redescription of *E. stigmatolepis* and inaccurate in the statement that the fronds lack a border. One of the gatherings which Biswas cites is labelled *Acrostichum stigmatolepis* and another has had the same name pencilled on the sheet, yet Biswas makes no reference to this species anywhere in his paper, though he could hardly have failed to note its description in the literature which he cites or that it was founded on plants from the identical area of his own supposed new species.

3. ***Elaphoglossum beddomei*** Sledge, sp. nov.

Elaphoglossum stigmatolepis sensu Bedd., Ferns S. Ind.: 67, t. 199 (1864); Handb. Ferns Brit. Ind.: 418 (1883); non T. Moore.

Acrostichum stigmatolepis sensu Baker in Hook. & Baker, Synops. Fil., ed. 2: 521 (1874); non Fée.

Rhizoma repens, *paleis linearibus brunneis marginibus integris* 6–9 mm. longis basi 1 mm. latis vestitum, stipitibus crebrioribus. Frondes stipitatae, 20–35 cm. longae; *stipites frondium sterilium* plerumque breves et 3–6 cm. longi, vel, si longiores, dimidia parte longitudinis laminae breviores, juventutes *paleaci paleis linearibus* fimbriis marginalibus paucis; lamina coriacea, anguste elliptica, 2–3 cm. lata, in apicem acutum diminuta, *basi gradatim decrescens et in alas angustas aut cristas in stipite decurrens*, marginibus angustis revolutis cartilagineis, infra paleis minutis stellatis vestita, supra in frondibus junioribus paleis similibus vestita, in vetustioribus glabrescens. Frondes fertiles eas steriles longitudine tota aequantes sed stipes quam lamina aequaliter longus; lamina 1·5–2·5 cm. lata. Sporae (36) 39–42 (45) × 24–30 μ.

South India: Anamallays, 1,050 m., " F.S.Ind. f. 199 *Elaphoglossum stigmatolepis* Kunze ", *Beddome* (BM, holotype). Palghat Hills, 1,500 m., *Beddome* (K). Nilgiri Hills, 2,100 m., *Beddome* (K). Same locality, *Beddome 6* (K). Same locality 1,500 m., 1870, *Henderson* (E). Sispara Ghat, Nilgiri District, Nov. 1883, *Gamble 13418* (K).

South India (Nilgiri, Anamallay and Palghat Hills).

Elaphoglossum beddomei differs from *E. stigmatolepis* in its longer and narrower, uniformly brown rhizome scales, the margins of which are entire or at most with an occasional marginal fimbriation. Its shortly stalked more coriaceous fronds are decurrent on the stipes, forming narrow wings or ridges often extending to the base, and the minute scales on the under surfaces of the fronds are stellately laciniated. The stipes bear linear scales markedly different from those of *E. stigmatolepis,* in which they are short and broad and are continued on to the midrib of the lower surface of the fronds.

Beddome's illustration well portrays the habit of this species. In one of the three sterile fronds depicted the narrow wing extending downwards from the decurrent lamina to the base of the stipe is correctly shown. Sometimes the stipes are considerably longer than those illustrated, and then the decurrent wings merge into ridges on the sides of the stipes. The fringed scale represents one of those clothing the stipe, as the rhizome scales have margins which are mostly quite entire though a few fimbriations may sometimes be present.

When Beddome first used the name *E. stigmatolepis* for this species he added a query both after the name and following the citation of Fée's figure. Baker's annotations on Beddome's specimens at Kew and his citation of Beddome's illustration show that this was the plant which he had in mind when adding *Acrostichum stigmatolepis* to the second edition of the *Synopsis Filicum* and, following Baker, the query was dropped by Beddome in his *Handbook.* Two distinct species however occur in the Nilgiri and adjoining hills in South India and the true *E. stigmatolepis* is the plant which was subsequently distinguished by Biswas as *E. ballardianum.* He evidently accepted the present species, on the evidence of Beddome's illustration and the named sheets at Kew, as being *E. stigmatolepis*, though he makes no reference to this species anywhere in his paper but compares *E. ballardianum* with *E. conforme*, to which its relationship is certainly more remote.

4. ***Elaphoglossum marginatum*** (Wall. ex Fée) T. Moore, Index Fil.: 8, 11 (1857), 361 (1862).

Acrostichum marginatum Wall., Numer. List: 2, n. 17 (1829), *nom. nud.*
Acrostichum marginatum Wall ex Fée, Mém. Fam. Foug. 2 : 31 (1845), excl. syn. Blume.
Acrostichum conforme sensu Hook., Sp. Fil. 5 : 198 (1864) pro parte.—Hook. & Baker, Synops. Fil. : 401 (1868) pro parte.
Elaphoglossum conforme sensu Bedd., Handb. Ferns Brit. Ind. : 416 (1883) pro parte minore et excl. fig. 247 ; non J. Smith.—Tagawa in Mem. Coll. Sci. Univ. Kyoto, Ser. B, 20 : 29 (1951).
Elaphoglossum fuscopunctatum Christ in Bull. Herb. Boiss. 6 : 867 (1898) ; in Neue Denkschr. Schweiz. Ges. Naturw. 36 (1, 2) : 51 (1899).

Rhizome stout, *short-creeping, stipes close,* clothed with *dark brown, thick-walled, narrow, lanceolate, attenuate, shortly and irregularly fringed scales,* 4–5 × 1–1·5 mm. Fronds stalked, 20–50 cm., stipe of sterile frond up to half as long as lamina but often much less, deciduously scaly ; lamina elliptic, 2–4 (5) cm. broad, apex acute, base gradually narrowed and decurrent on the stipe, margins with a translucent cartilaginous border, lower surface with scattered minute, more or less stellately laciniated, brown scales, upper surface glabrous ; texture coriaceous. Fertile fronds on longer stalks than the sterile ones, lamina slightly narrower. Spores 42–45 × 27–30 μ.

NEPAL : Sheopore, 1829, *Wallich 17* (K). *Wallich 174* (BM). Sheopuri Lekh, Katmandu, 1,350 m., 19 Aug. 1954, *Stainton, Sykes and Williams 6917* (BM). Between Torke and Okhaldunga, 1,950 m., 2 Nov. 1954, *Zimmermann 1997* (BM).

SIKKIM : Darjeeling, 2,280 m., 9 Aug. 1875, *C.B. Clarke 26913* (K). Same locality, 1,800 m., Oct. 1881, *Gamble 9884* (K). Kohima, 1,800 m., 21 Oct. 1885, *C. B. Clarke 40971* (K). Neebay (?), 2,250 m., 16 Oct. 18—, *C. B. Clarke 25337* (BM). Jeylep Rd., 1,800 m., Nov. 1880, *Gamble 9938* (K). *Treutler 988* (K). 2,100 m., Sept. 1882, *Levinge* (K). *Jerdon* (K).

BHUTAN : Kancham, Punakha, 1,950 m., 28 Aug. 1914, *Cooper 3058* (BM). Trashiyangsi Valley, Tobrang, on rock faces, dense jungle, 29 Aug. 1934, *Ludlow & Sherriff 902* (BM ; E).

ASSAM : Sohra River, 1,500 m., 16 Oct. 1872, *C. B. Clarke 19239* (BM ; K). Same locality, 1,500 m., 28 Nov. 1871, *C. B. Clarke 14778* (K). Same locality, 1,350 m., 15 Oct. 1872, *C. B. Clarke 18826* (K). Vale of Rocks, Sept. 1886, *C. B. Clarke 45828* (K). Suruseem, Khasia, 1,200–1,800 m., 26 May 1850, *Hooker & Thomson* (K). Kalapanee, Khasia 1,650 m., 6 Aug. 1850 and 28 Oct. 1850, *Hooker & Thomson* (K). Assam, 1870–80, *G. Mann* (K). Ukhrul, Manipur State, on rocks in the forest, 1,800 m., 12 Aug. 1948, *Kingdon Ward 17935* (BM).

Himalayas eastwards from Nepal, Sikkim, Bhutan, Khasi Hills, Manipur, Yunnan, Formosa.

Elaphoglossum marginatum differs from the other coriaceous-leaved species in its thicker, more shortly creeping rhizome with more crowded stipes. *E. angulatum* is readily distinguished by its long-creeping habit with well-spaced fronds and much broader, thinner and light brown rhizome scales. *E. stigmatolepis* also differs in its more rampant habit, its narrower fronds, which are more tapering above and below, and by the different form of the scales on the lower surface. Both Fée and Moore included Java in the distribution of *E. marginatum* through inclusion of the plants later distinguished by Mettenius as *Acrostichum commutatum*. From this *E. marginatum* is best distinguished by its stouter rhizome and more clustered fronds and its darker coloured rhizome scales, which lack the long-attenuate flexuose and curled apices and long marginal fimbriations of *E. commutatum*.

Christ makes no mention of *Acrostichum marginatum* in his monograph of *Elaphoglossum*, but his *E. fuscopunctatum* described from Yunnan I consider the same as Wallich's plant. There are specimens at Kew and the British Museum of *Henry 9158*, on which Christ's species was based, and these are, to me, indistinguishable from some Himalayan gatherings of *E. marginatum* (e.g. *Hooker & Thomson*, from Khasia in Herb. Kew ; *Ludlow & Sherriff 902* from Bhutan in Herb. Edin.). The scales in several other collections of *E. marginatum* give a conspicuously fuscopunctate appearance to the undersides of the fronds. Tagawa (loc. cit.) reduced both to forms of *E. conforme*.

5. **Elaphoglossum commutatum** (Mett.) Alderw. van Rosenb., Malayan Ferns, Suppl. 1 : 427 (1917).

Acrostichum conforme sensu Blume, Enum. Pl. Jav. 2 : [275] (1828) (errore "*aemulum*" in p. 101) ; Fl. Jav., Fil. : 23, t. 5 (1829) ; non Swartz.—Hook., Sp. Fil. 5 : 198 (1864) pro parte.—Hook. & Baker, Synops. Fil. : 401 (1868) pro parte.
Acrostichum marginatum Fée, Mém. Fam. Foug. 2 : 31 (1845) pro parte, incl. syn. Blume.
Elaphoglossum laurifolium sensu T. Moore, Index Fil. : 359 (1862) pro parte, quoad specim. ex India, Ceylon, Java ; non T. Moore, op cit. : xvi (1857).
Acrostichum laurifolium sensu Thw., Enum. Pl. Zeyl. : 380 (1864) ; non Thou.
Acrostichum commutatum Mett. apud Kuhn in Ann. Mus. Bot. Lugd.-Bat. 4 : 292 (1869).

Rhizome creeping, stipes rather close, clothed with *narrow, brown scales with fimbriate margins and long-attenuate, flexuose and twisted tips*, 10 × 2 mm. Fronds stalked, 15–30 (50) cm., stipe of sterile fronds variable in length, up to half as long as the lamina but often much less, scaly when young with spreading, linear, fimbriate, dark brown scales and with smaller, appressed, stellately laciniated scales, but becoming smooth with age ; lamina elliptic, 2–5 (6) cm. broad, apex acute, base gradually narrowed and decurrent on the stipe, margins with a translucent, cartilaginous, revolute border, lower surface with scattered, minute, more or less stellately laciniated scales, upper surface with similar scales when young, becoming glabrous; texture coriaceous. Fertile fronds on stalks normally exceeding those of the sterile ones and sometimes the stipes longer than the sterile fronds, 1·5–3·0 cm. broad. Spores 33–36 × 24–27 μ.

SOUTH INDIA : Bolampatty Hills, 1,500 m., *Beddome* (K). Nilgiri Hills, 1,200 m., Nov. 1870, *Henderson* (E).

CEYLON : *Thwaites C.P. 1310* (BM ; CGE ; E ; K ; PDA). Hoolankande Peak, Matale, 10 Jan. 1862, *Brodie* (E). Nuwara Eliya, *Freeman 368 A* (BM). Kabot's Gap, Rangala, 8 Sept. 1927, *Alston 2375* (PDA). Knuckles, 1881, no collector's name (PDA). Ramboda Pass, 1,650 m., epiphytic on tree trunk by stream in jungle, 17 Dec. 1950, *Sledge 646* (BM). Hoolankande, 1,350 m., 20 Jan. 1954, *Sledge 1010* (BM). Jungle above Le Vallon Estate, 1,500 m., 9 Feb. 1954, *Sledge 1116* (BM). Parawella Falls, Kandapola, near Nuwara Eliya, 1,425 m., 19 March 1954, *Sledge 1329* (BM). *Robinson 20* (K). Central Prov., *Naylor Beckett* (K). 1871, *Randall* in *Herb. R. W. Rawson 3285* (BM). *R. W. Rawson 1027–1802* (BM). *Henderson* (E). *Anderson* (E).

South India (Nilgiri Hills), Ceylon, Java.

Elaphoglossum commutatum is intermediate in habit between *E. marginatum* and *E. angulatum*, with less crowded stipes than the former but with shorter internodes than the latter, in which the fronds are 1–2 cm. or more apart. It differs from *E. marginatum* in its rhizome scales as described under that species, and in its smaller spores. From *E. angulatum*, apart from its much less widely creeping rhizome, it differs in its markedly narrower, darker brown, finely acuminate and strongly fimbriate rhizome scales. The stipes bear similar linear dark-coloured scales intermixed with small appressed stellate scales like those of the under surface of the blades, which spread down the stipes, though in old fronds the stipes may be practically naked. In *E. angulatum* the broad, pale brown scales which clothe the rhizome spread up the stipe and are continued on the lower part of the midrib of the lamina, becoming narrower and more laciniated upwards and gradually merging into the minute stellate scales of the under surface. Stellate scales are absent on the stipes of *E. angulatum*.

Mettenius based his description (loc. cit.) on plants of Blume's from Java and on *Thwaites C.P. 1310* from Ceylon. His references to Thwaites's numbered collection and to the description and figure of Blume's *A. conforme* and his own accurate description of the rhizome scales fix the identity of the species. Van Alderwereldt van Rosenburg validly transferred the specific epithet to *Elaphoglossum* though the plants he had in mind were doubtfully the same as those of Mettenius. The species has been treated in most works as a synonym of *E. laurifolium* (Thou.) Moore, which was described from Tristan da Cunha. Christensen (Res. Norw. Sci. Exped. Tristan da Cunha, 1937–38, 6 : 19 (1940)) expressed the view that *E. laurifolium* was endemic to Tristan da Cunha. Through the kindness of Mr. James Dickson I have been able to examine good specimens of *E. laurifolium* collected by him on Tristan da Cunha in 1962. These and other gatherings from Tristan and from Gough Island stand well apart from Ceylon and South Indian plants in their wide-creeping habit with long internodes, their dark brown-black rhizome scales, which lack the fimbriated edges and crisped apices of *E. commutatum*, and their larger spores (45–48 × 30–33 μ).

E. commutatum stands between *E. laurifolium* and *E. callifolium*, the latter being a larger plant with bigger rhizome scales (up to 2 cm. long), which have entire margins. Backer and Posthumus (Varenflora voor Java: 251 (1939)) maintained *E. commutatum* (sub. nom. *E. laurifolium*) and *E. callifolium* as distinct species, though they express the view that the former may be no more than a form of the latter. I have no doubt as to Ceylon and South Indian plants being distinct from *E. callifolium* but I am much less sure if plants from Java and elsewhere in Indonesia which have been called *E. laurifolium* are identical with those from India and Ceylon. Specimens so named from Java, Sumatra, Borneo and Indo-China have rhizome scales the margins of which are less irregular and they lack the frizzed tips of those of *E. commutatum*. They approach *E. callifolium* in these respects though the scales are narrower and shorter.

I suspect *E. permutatum* Alderw. van Rosenb. (Bull. Jard. Bot. Buitenz., ser. 2, 16 : 13 (1914)) to be synonymous with *E. commutatum*. There is an isotype (*Matthew 696* from Mt. Sago, Sumatra) at the British Museum and this has rhizome scales with fimbriate margins and crisped apices although the description states that the scales are " integerrimis ". In its other characters the cotype does not appear to me to be significantly different from *E. commutatum*.

6. **Elaphoglossum stelligerum** (Wall. ex Baker) T. Moore ex Alston & Bonner in Candollea 15 : 216 (1956).

Acrostichum neriifolium Wall., Numer. List : 2, n. 16 (1829), *nom. nud.*
Acrostichum stelligerum Wall., op. cit. : 65, n. 2167 (1830), *nom. nud.*
Elaphoglossum stelligerum T. Moore, Index Fil. : 15 (1857), 368 (1862), *nom. nud.*
Acrostichum viscosum sensu Hook., Sp. Fil. 5 : 220 (1864) pro parte ; non Swartz.
Elaphoglossum viscosum sensu Bedd., Ferns. S. Ind. : 67, t. 196 (1864) ; Handb. Ferns Brit. Ind. : 420 (1883) ; non J. Smith.
Acrostichum stelligerum Wall. ex Baker in Hook. & Baker, Synops. Fil, ed. 2 : 521 (1874).
Acrostichum yunnanense Baker in Bull. Misc. Inf. Kew 1898 : 233 (1898).
Elaphoglossum yunnanense (Baker) C. Chr. in Contrib. U.S. Nat. Herb. 26 : 327 (1931).

Rhizome creeping with stipes close together, clothed with *linear, attenuate, dark castaneous, glossy scales*, 3–5 × 0·5 mm., with occasional fimbriations in their lower parts, elsewhere with entire or obscurely dentate margins. Fronds stalked, 20–40 cm. long, *stipes* of sterile fronds densely scaly *with a mixture of stellate scales with slender rays and lanceolate scales with long-fimbriate margins* ; lamina narrowly elliptic 1–2·5 cm. broad, apex acute, base gradually narrowed and decurrent on the stipe, *lower surface with abundant, loose, reddish-brown, stellate scales with long rays which diverge from the leaf surface*, the midrib with similar scales intermixed, especially in the lower part, with broader-centred ones with long-fimbriate margins ; upper surface stellate-pubescent when young, becoming more or less smooth with age, the scales paler than those on the lower surface ; texture thin but firm. Fertile fronds on longer stipes than the sterile ones, lamina narrower, to 1 cm. broad. Spores 42–45 × 30 μ.

NEPAL : 1820, *Wallich 16* (BM ; E ; K). *Wallich* ex coll. *Hooker f. & Thomson 96* (E). Panapa, 1,546 m., 6 Sept. 1954, *Zimmermann 1036* (BM). Between Manebhanjyang and the Sun Kosi, 1,500 m., 5 Nov. 1954, *Zimmermann 2058 B* (BM).

SIKKIM : 600 m., *Beddome* (BM). 2,400 m., 1868, *Henderson* (E). 1871, *Levinge* (K). Darjeeling, 1871, *Hope* (E). Same locality, coll. *Levinge*, ex *Herb. Hope* (E). Same locality, Oct. 1873, *C. B. Clarke 21486* (K). Goke, 17 July 1880, *Levinge* (E).

Bhutan: Towards Kolepani, 3 Nov. 1835, *Griffith* (K).

Assam: Khasia, 1,350 m., *Hooker & Thomson* (E; K). Same locality, 1,200 m., 16 Sept. 1850, *Hooker & Thomson 2285* (K). Same locality, 1,200 m., 16 Nov. 1871, *C. B. Clarke 14678* (K). Jowye, Jainteas, 1,200 m., 19 Oct. 1867, *C. B. Clarke 5938* (K). Mariao, 1,200 m., 7 Nov. 1871, *C. B. Clarke 15369* (BM; E). Bogapani, Khasia, 1,050 m., 29 Oct. 1871, *C. B. Clarke 16367* (K). Same locality, 1,200 m., July 1890, *G. Mann* (E).

South India: Pulney Mts., Sept. 1836, *Wight 51* (K). Same locality, 1,800 m., *Beddome* (BM; K). Periya Shola, Pulneys, 21 Apr. 1898, *Bourne 4971* (K). Kodaikanal, Pulney Hills, 1,960 m., May 1937, *Aroticasamy 7* (BM). Nilgiri, 1860, *Beddome 4* (K). Anamallays, 1,350 m., " F.S.Ind. f. 196 ", *Beddome* (BM). Same locality, 1864, *Henderson* (E). Shevaroy Hills 1,200 m., 1898, coll. *J. W. Furrell 66* ex *Herb. Hope* (E). Massif du Shevaroy, 10 Oct. 1939, *Faucheux* (BM). Honey Rock stream, Yercaud, Shevaroy Hills, 1,100 m., 25 Oct. 1962, *Ghatak G195A* (BM).

Yunnan, Indo-China.

Elaphoglossum stelligerum is readily distinguished from all other Indian species by its loose, rufous-brown, stellate scales with long rays which are not appressed to the surfaces of the stipes or fronds. The linear, dark-coloured, somewhat glossy rhizome scales are also markedly different from those of other species. It is closely related to *E. petiolatum* (Swartz) Urban, described from Jamaica and formerly credited with a pantropic distribution.

I see no significant difference between *E. stelligerum* and Baker's *Acrostichum yunnanense.* Baker's description states " ad *A. stigmatolepidem*, Fée, magis accedit; frondibus linearibus ad marginem paleis parvis ciliatis et paleis facialibus profunde stellatim fissis differt " ; but the comparison with *E. beddomei*—*A. stigmatolepis* sensu Baker being *E. beddomei* mihi—is incomprehensible since the plant Baker had before him is manifestly far closer to, and is indeed in my opinion specifically identical with, *E. stelligerum.* Ching evidently dismissed it as a valid species since there is a second sheet of *Henry 10310*, the type gathering of *A. yunnanense*, in the same folder at Kew which he has labelled *E. petiolatum* (Sw.) Urban. Christensen upheld *E. yunnanense* (in Contrib. U.S. Nat. Herb. 26 : 327 (1931)) but his comments on the distinction between it and *E. petiolatum* are equally applicable to *E. stelligerum*, which he did not distinguish. Nor do I agree with Holttum (Fl. Malaya 2 : 455 (1954)) that Malayan specimens agree better with the type of *E. yunnanense* than with South Indian specimens. They are more robust than either Henry's Yunnan collection or Indian gatherings.

E. stelligerum is very closely related to *E. blumeanum* (Fée) J. Sm. from Malaysia and *E. salicifolium* (Willd. ex Kaulf.) Alston from the Mascarene Islands (type from Réunion) and Africa, all being formerly included in *E. petiolatum* Swartz, which was described from Jamaica. Malaysian plants are larger than those from India and the scales on the two surfaces of the sterile fronds are dissimilar. Indian and Mascarene plants have the scales on the two surfaces alike and differences between them are so slight that they probably represent no more than geographical variants. The names are retained however pending a much-needed revision of the whole *E. petiolatum* complex.

7. ***Elaphoglossum nilgiricum*** Krajina ex Sledge, sp. nov.

Elaphoglossum squamosum sensu Bedd., Ferns S. Ind.: 67, t. 197 (1864); Handb. Ferns Brit. Ind.: 420, fig. 251 (1883) excl. specim. ex Ceylon; non J. Smith.

Rhizoma breviter repens, paleis anguste lanceolatis vel linearis, pectinato-dentatis, fusco-castaneis, marginibus nigris, nitidis, vestitum. Frondes caespitosae, breviter stipitatae, 5–25 (40) cm. longae; stipites paleis ovatis vel late ovatis, pallido-ferrugineis in margine dentibus setiformibus praelongis, densissime obtecti; lamina anguste oblonga vel longitudo-ligulata, 1–2 cm. lata, apice obtusa, in basi sensim attenuata, in marginibus et utraque superficie copiose squamosa, infra paleis brunneis, mollibus, lanceolatis ad late ovatis, margine dentibus setiformibus fimbriata, confertis imbricatis occultata, supra paleis similibus minus confertis, pallidioribus, aliquibus paleis in ambitu plus-minusque orbiculatis sed in margine radiis tenuibus longis instructis; textura crassiter herbacea. Forma frondium fertilium ut in sterilibus.

SOUTH INDIA: Sisparah Ghat, Nilgiris, 1,500 m., " type of tab 197. FSI.", *Beddome* (K, holotype). Same locality, 1,800 m., Nov. 1883, *Gamble 13468* (K). Same locality, *Miss Cockburn 81* (BM). Nilgiri, 1860, *Beddome 7* (K). Pykara Falls, Nilgiri District, 1,800 m., June 1883, *Gamble 12009* (K). Nediwattan, Nilgiri Hills, 1,800 m., May 1866, *Gamble* ex *Herb. Blanford* (E). Nilgiri Hills, *Henderson* (E).

Endemic to Nilgiri Hills.

The type of *Elaphoglossum hirtum* (Swartz) C. Chr. was described from Jamaica. This name, or the synonym *E. squamosum* (Swartz) Urban, was formerly used in a collective sense to cover plants ranging from tropical America eastwards to southern India and Ceylon, which are the only regions in Asia whence plants have been found. Several species based on collections from Africa, Madagascar, and the Mascarene Islands have since been given independent rank. As South Indian and Ceylon plants not only differ from each other but cannot be matched satisfactorily with any Jamaican, African or Mascarene gatherings which I have examined, I have adopted the unpublished names affixed to the Kew sheets by Krajina in 1937.

Specimens from the Nilgiri Hills are very uniform and they differ consistently from Ceylon plants in the scales of the stipes being markedly broader with their margins and setiform teeth rarely dark-coloured as in *E. ceylanicum*, save at the base of the stipe adjacent to the rhizome. They also differ in their much more densely paleate fronds, the lower surfaces of which are hidden beneath the closely imbricating pale-brown scales.

Beddome's illustration (Ferns S. Ind.: t. 197 (1864)), is a fair representation of the species except that the stipes are unaccountably portrayed as smooth and glabrous whereas his description states that they are " very scaly " and both in his own and all other gatherings they are invariably densely paleate with patent scales. The isolated, long, falcate and apparently glabrous frond depicted on the left-hand side of the plate is meaningless and, not surprisingly, is omitted from the reproduction of this plate in the Handbook.

8. ***Elaphoglossum ceylanicum*** Krajina ex Sledge, sp. nov.

Rhizoma breviter repens, paleis linearibus pectinato-dentatis fusco-castaneis vel nigris vestitum. Frondes caespitosae, breviter stipitatae, 5–25 cm. longae ; stipites paleis anguste lanceolatis, attenuatis, acutis, ferrugineis, in margine dentibus setiformis praelongis, plerumque marginibus dentibusque fuscis, obtecti ; lamina oblongo-elliptica, 1–2 cm. lata, in apice acuta vel acuminata, in basi sensim attenuata, in marginibus et utraque superficie paleis tenuibus brunneis; supra pallidioribus vestita, sed infra, praeter in juventute, non paleis occultata.

CEYLON : *Gardner 1164* (BM ; CGE on trees in dark forests at Nuwara Eliya, Sept. 1844 ; K, holotype). *Thwaites, C.P. 3292* (BM ; CGE ; E ; PDA). Central Province, on trees and rocks, *Naylor Beckett 401* (K). Peacock Hill, Pussilawa, 1870, *Randall* in *Herb. R. W. Rawson 3284* (BM). Pundaloya, 1,500 m., *Freeman 372A, 374A, 375B* (BM). Nuwara Eliya, *Freeman 373B* (BM). *Walker* (K). *Robinson 22* (K). Rocks by stream at Lonach near Norton Bridge, Central Province, 900 m., 13 Dec. 1950, *Sledge 598* (BM). Ramboda, on mossy rock by stream in jungle, 1,650 m., 17 Dec. 1950, *Sledge 648* (BM). Kuda Oya, Ramboda, on rocks in shade by stream through jungle, 1,725 m., 28 Dec. 1950, *Sledge 769* (BM).

Endemic.

The distinctions between this species and *E. nilgiricum* are referred to under the previous species. The fully developed fronds are acute at the apex and green in colour since neither surface is covered by a continuous coating of scales as is the lower surface of the frond in *E. nilgiricum*. Young fronds however are very scaly. In both species the lamina scales vary in shape, the body of the scales being mostly broadly to narrowly ovate in outline but some are more or less orbicular. All have the margins fringed by long setiform teeth.

E. ceylanicum seems to come closest to *E. deckenii* var. *rufidulum* (Willd. ex Kuhn) Tardieu-Blot (Not. Syst. 15 : 430, t. 4 f. 6–10 (1959) =*E. hirtum* var. *rufidulum* (Willd. ex Kuhn) C. Chr. in Dansk. Bot. Ark. 7 : 170 (1932)) from Madagascar and Réunion. In that species, however, the fronds are borne on long stipes and the shape of the rhizome scales and their marginal teeth are different.

Plants from Madeira and the Azores have jet black scales on the stipes and under surface of the costae, intermixed with ferrugineous ones with and without thickened and darkened margins. Such scales are not present in *E. nilgiricum* or *E. ceylanicum*. Specimens from Madeira and the Azores are closest to *E. splendens* (Bory) Brackenr. from Réunion and Mauritius but are better treated as a separate species.[1]

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[1] **Elaphoglossum paleaceum** (Hook. & Grev.) Sledge, *comb. nov.*

Acrostichum paleaceum Hook. & Grev., Ic. Fil. 2 : t. 235, Alph. Index et Syst. Index (1831) (errore "*vestitum*" in expl. tab.).

It would seem that Hooker and Greville realized during the preparation of the *Icones Filicum* that Lowe's manuscript name *Acrostichum vestitum* was a later homonym. Its appearance in the text accompanying the plate, in spite of the fact that *A. paleaceum* is used on the plate and in the indexes, is to be regarded as an error.

9. **Elaphoglossum spatulatum** (Bory) T. Moore, Index Fil.: 14 (1857).—Bedd., Ferns S. Ind.: 71, t. 209 (err. 213) (1864).

Acrostichum spatulatum Bory, Voy. Mers d'Afriq. 1 : 363, t. 20 f. 1 (1804).—Fée, Mém. Fam. Foug. 2 : 51, t. 14 f. 3 (1845).
Acrostichum acutum Fée ex Kuhn in Linnaea 36 : 44 (1869).

Rhizome creeping with stipes rather close together, clothed at the apex with filiform, rufous scales. *Sterile fronds up to 10 cm. long, stipes* about equalling the lamina in length and *covered with patent, reddish, setaceous scales* ; lamina lanceolate to rhomboid-lanceolate, 1–1·5 cm. broad, base narrowed into the stipe, apex usually acute sometimes obtuse, margins and *both surfaces covered with hair-like scales* ; texture rather thickly herbaceous. Fertile fronds smaller than the sterile ones and on much longer stipes, lamina broadly oval or almost orbicular, conduplicately folded when young and often splitting at the apex when mature.

CEYLON : *Thwaites C.P. 989* (BM ; E ; K ; PDA). Adam's Peak, *Moon* (BM). Nuwara Eliya, *Rawson W. Rawson 1041* (BM). Same locality, *Freeman 376A, 377B* (BM). Sita Eliya, Hakgala, March 1885 (PDA). Hawa Eliya, 25 Aug. 1926, *J. M. de Silva* (PDA). Kuda Oya, Ramboda Pass, 1,700 m., in shady places on rocks by stream in jungle, 28 Dec. 1950, *Sledge 771* (BM). 1,500–1,800 m. " Type of tab 209 FSI ". *Thwaites* in *Herb. Beddome* (K). 1870, *Thwaites* in *Herb. Henderson* (E). On wet rocks at about 1,800 m., *Hutchison* (E.). *Wall* (E). *Robinson 23* (K). *Gardner* (K).

Africa (N. & S. Rhodesia, Transvaal, Natal, Cape), Madagascar, Réunion.

A very distinct species, much smaller than all other Indian and Ceylon species. Closely related plants, which have often been treated as belonging to the same species, occur in tropical America and Tristan da Cunha ; but Christensen (Res. Norw. Sci. Exped. Tristan da Cunha, 1937–38, 1 (6) : 20 (1940)) considered the species on that island, *E. obtusatum* (Carm.) C. Chr., to be " certainly quite different from *E. spathulatum* ".

Madame Tardieu-Blot (Not. Syst. 15 : 432 (1959) ; in Humbert, Fl. Madag., Polypod. 2 : 49 (1960)) has erroneously transferred the Ceylon records of *E. spatulatum* to *E. schizolepis* (Baker) Christ. The type of the latter—from Madagascar—is at Kew and is quite unlike any Ceylon plant.

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FRANCES L. BALFOUR-BROWNE

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THE BRITISH MUSEUM (NATURAL HISTORY)
BOTANY Vol. 4 No. 3
LONDON: 1968

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Pp. 97–141; 4 *Text-figures*

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THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

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THE BRITISH MUSEUM (NATURAL HISTORY)

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FUNGI OF RECENT NEPAL EXPEDITIONS

By FRANCES L. BALFOUR-BROWNE

THE fungi recorded below were collected during four general botanical expeditions made in the Nepal highlands by (1) J. D. A. Stainton, W. R. Sykes and L. H. J. Williams in 1954, (2) J. D. A. Stainton in 1956, (3) A. H. Norkett in 1961–62 and (4) J. D. A. Stainton in 1962. Expeditions (1) and (4) were in Central Nepal while the other two were mainly in Eastern Nepal.

The collections were made at altitudes between 300 m. and 5,000 m. At the highest levels were Conifer and Rhododendron forests with Evergreen Oaks coming in from below, and the lower levels were characterized by rice terraces, bamboos, ferns and *Castanopsis* forest. Sheals & Inglis (1965) give details of the local geography and the nature of the terrain encountered in Expedition (3).

In this account references have been restricted to the authorities of the names used and to the more significant or well-known synonyms. For additional references to most of the species the revised (1960) edition of Butler & Bisby's indispensable *Fungi of India* by Vasudeva should be consulted.

In some groups the delimitation of genera is very controversial and consequently the classification and the names employed are very much a personal matter of opinion with very little agreement amongst workers. This is particularly so for the Polyporaceae. During the last twenty years new systems of classification for this group have been published by Pilát (1936–42, Europe), Cunningham (1947, 1947–50, 1965, New Zealand), Corner (1932, 1953, general), Overholts (1953, America), Imazeki (1943, Japan), Donk (1933, 1960, general), Singer (1962, general), Bondartzev (1953, Russia), Nobles (1958, Canada), Pinto-Lopez (1952, Portugal), Kotlaba & Pouzar (1957, Europe), Teixeira (1962, Brazil). These systems have been based on a variety of criteria: general anatomical and morphological structure, hymenial structure, hyphal structure, biosystematics, hyphal thickening and the presence or absence of clamps, and physiological characters. Significant as are these characters, nevertheless owing to the difference in emphasis placed upon them by different authors, considerable difficulty arises in attempting to derive a stable or consistent nomenclature. Here, therefore, the well-known, old or mainly Friesian subdivisions have been used for the Polyporaceae and the less conservative names included in the synonymy.

Recently suggested, but still tentative, relationships of certain agarics (so hitherto regarded) with polypores rather than with other agarics, or *vice versa*, are also not taken up here. The second edition of R. Singer's *The Agaricales in Modern Taxonomy* (1962) should be referred to for new ideas on the classification of this group.

As regards the Clavariaceae, these have been named by Dr. E. J. H. Corner of Cambridge, and each identification for which he is responsible is indicated by his initials in parentheses.

In mountainous countries such as Nepal with an annual rainfall in some areas of 500 cm., the difficulty is to get the plants dry. The tendency is therefore to press them too enthusiastically, with the consequence that some of the agarics and

Clavariae were tissue-paper thin and their hyphal structure indiscernible. To off-set this it would have been valuable to have had some of the soft and fleshy fungi preserved in fluid, and full notes as to colour, texture and shape when fresh are always much desired. For the rest, the material was in good condition and together represents the largest collection so far from this difficult and until recently almost inaccessible region: 160 species excluding some immature and over-ripe specimens which so far have resisted identification. Previous records consist of about two dozen species collected by Sir Joseph D. Hooker over a century ago and described by Berkeley (1850, 1851, 1852, 1854) and about 70 species collected by Polunin, Sykes and Williams in 1952 and reported in a previous number of this journal (Balfour-Browne, 1955).

All the specimens cited in this paper are in the herbarium of the British Museum (Natural History).

PHYCOMYCETES

ALBUGINACEAE

Albugo bliti (Biv.) Kuntze, Revis. Gen. Pl. 2 : 658 (1891).—Best. Biga in Sydowia 9 : 347 (1955).

Uredo bliti Biv., Stirp. Rar. Sicil. 3 : 11 (1815).
Cystopus bliti (Biv.) De Bary in Ann. Sci. Nat., Sér. 4, Bot. 20 : 131, tab. 13 figs. 13–15 (1863).
Caeoma amaranthi Schwein. in Trans. Amer. Phil. Soc., New Ser., 4 : 292 (1832).
Cystopus amaranthi (Schwein.) Berk. in Grevillea 3 : 58 (1874).

Nepal: Bhurungdi Khola, 1,600 m., on *Amaranthus lividus* L., 20th May, 1954, *Stainton, Sykes & Williams 5342*.

Distribution: Worldwide.

For a recent review of the genus *Albugo* consult Bestagno Biba (tom. cit.: 339–58).

PERONOSPORACEAE

Sclerospora graminicola (Sacc.) Schroet. in Cohn, Krypt.-Fl. Schles. 3 (1) : 236 (1886).

Protomyces graminicola Sacc. in Nuov. Giorn. Bot. Ital. 8 : 172 (1876).

Nepal: Bongakhani, 2,130 m., on grass, 22 Aug. 1954, *Stainton, Sykes & Williams 3943*.

Distribution: America, Europe, Africa, India, Australia.

PYTHIACEAE

Phytophthora infestans (Mont.) De Bary in Journ. Roy. Agric. Soc., Ser. 2, 12 : 240 (1876).

Botrytis infestans Mont. in L'Institut, Sect. 1, 13 : 313 (1845).

Nepal: Murigurja Gad, 2,500 m., on potato, 27 July 1954, *Stainton, Sykes & Williams 3654*.

Distribution: Worldwide.

ASCOMYCETES

MORCHELLACEAE

Morchella elata Fries, Syst. Mycol. 2 : 8 (1822).

Nepal: Siklis, north of Pokhara, 3,000 m., on rotten tree trunk, 21 Apr. 1954, *Stainton, Sykes & Williams 4956*.

Distribution: America, Europe, India, China, Japan, Australia.

HELVELLACEAE

Helvella crispa Fries, Syst. Mycol. 2 : 14 (1822).

Nepal: Lete, 2,600 m., beneath conifers, 27 Aug. 1954, *Stainton, Sykes & Williams 7501*.

Distribution: Worldwide; previously recorded from Nepal in 1955.

HUMARIACEAE

Aleuria aurantia (Fries) Fuckel in Jahrb. Nass. Ver. Naturk. 23–24 : 325 (1870).

Peziza aurantia Fries, Syst. Mycol. 2 : 49 (1822).

Nepal: Ghar Khola, 2,130 m., 14 June 1954, *Stainton, Sykes & Williams 5759*.

Distribution: Worldwide.

GEOGLOSSACEAE

Geoglossum affine (Durand) Sacc. & Trav. in Sacc., Syll. Fung. 19 : 756 (1910).—Maas Geest. in Persoonia 4 : 23 (1965).

Gloeoglossum affine Durand in Ann. Mycol 6 : 420 (1908).

Nepal: Annapurna Himal, Seti Khola, 3,830 m., on shady banks, 28 July 1954, *Stainton, Sykes & Williams 6540*. South of Gurjakhani, 4,000 m., among dwarf Rhododendron, 17 Aug. 1954, *Stainton, Sykes & Williams 3879*.

Distribution: United States, Himalayas.

These specimens were examined and identified by Dr. Maas Geesteranus.

Mitrula rosea Lloyd, Mycol. Not. 61 : 885, t. 129 fig. 1529 (1919).

Nepal: Gosainkund, Malemchi, 2,800 m., on bare earth, 30 May 1962, *Stainton 3789*.

Distribution: India.

Pale rose coloured ascophores about 1 cm. tall with smooth or contorted caps.

SCLEROTINIACEAE

Rutstroemia sp. cf. **firma** (Fries) Karst. in Bidr. Känn. Finl. Natur & Folk 19 : 108 (1871).

Peziza firma Fries, Syst. Mycol. 2 : 117 (1822).
Ciboria firma (Fries) Fuckel, Symb. Mycol. : 312 (1869).
Phialea firma (Fries) Gill., Champ. Fr., Discom. : 101, t. 74 fig. 2 (1883).

NEPAL: Dhankuta Province, near Mahe, 1,300 m., on dead twig, 20 Sept. 1961, *Norkett 5175 B.*

Distribution (of *R. firma*): Worldwide.

The fungus agrees well with this species except that its spores are somewhat short, 9–11 × 4–5 μ. The material, however, is barely ripe.

HYALOSCYPHACEAE

Perrotia malemchiensis Balfour-Browne, sp. nov. (Fig. 1.)

Apothecia sparsa, superficialia, sessilia, carnosa, uda pallide brunnea, sicca cinnabarina, extus villosa, 500–1,000 μ diam.; setae cylindraceae ad basim ± cohaerentes apice liberae et acutae, septatae, minute granulosae, pallide ochraceae; asci clavati, recti vel curvuli, octospori, 80–110 × 9–10 μ; sporae clavatae vel fusoideae, hyalinae, 5–7 septatae, 20–30 × 4–5 μ; paraphyses filiformes, septatae, hyalinae.

Ad ligna et cortices arborum frondosarum.

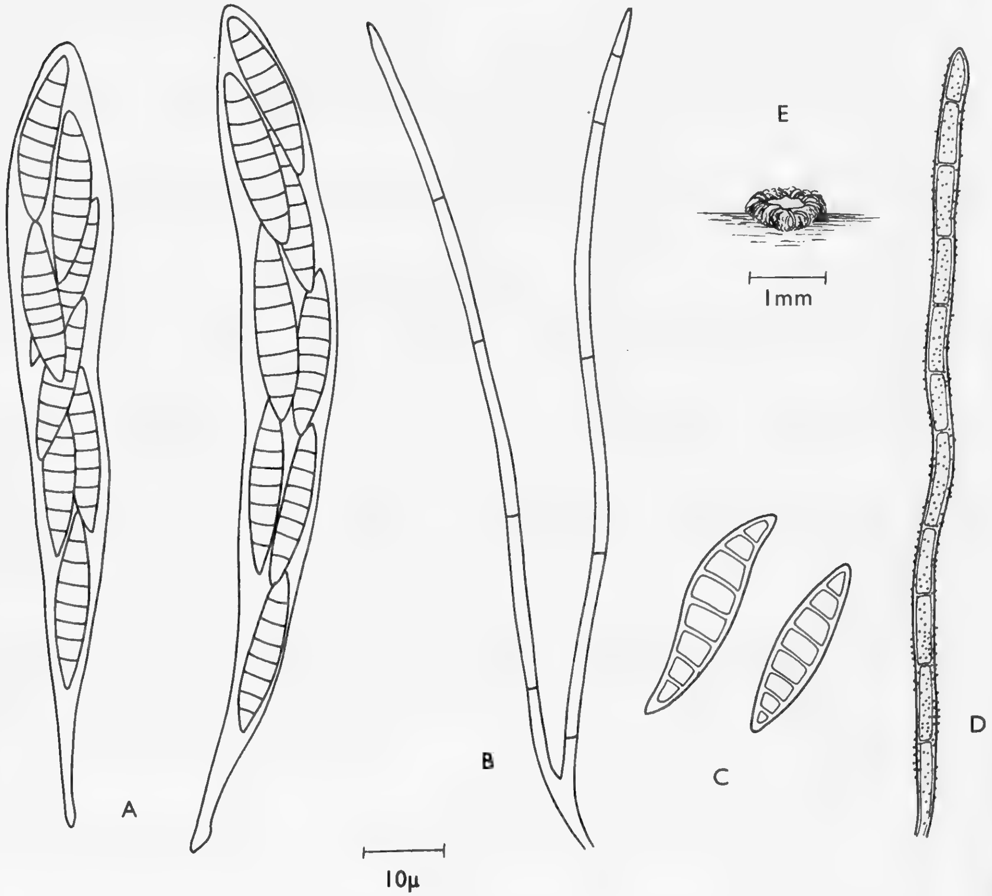

FIG. 1. *Perrotia malemchiensis* Balfour-Browne. A, asci containing ascospores; B, paraphyses; C, ascospores; D, external hair; E, apothecium. *Stainton 3768.*

NEPAL: Gosainkund, Malemchi, 2,400 on a dead tree, 29 May 1962, *Stainton, 3768* (holotype).

This differs from related species not only in colour and measurements but in spore septation: *P. fusca* Müll. & Dennis, 1-septate; *P. lutea* (Phill.) Dennis, up to 31-septate; *P. himalayensis* Müll. & Dennis, 3-septate.

DERMATEACEAE

Mollisia dhankutae Balfour-Browne, sp. nov. (Fig. 2.)

Apothecia superficialia, sessilia, usque ad 1·5 mm. diam., disco sordide flavido-albo; excipulo fusco-brunneo, pseudoparenchymatico; asci cylindraceo-clavati, octospori, poro jodo tincto, 80–90 × 9–10 μ; ascosporae biseriatae, elongato-

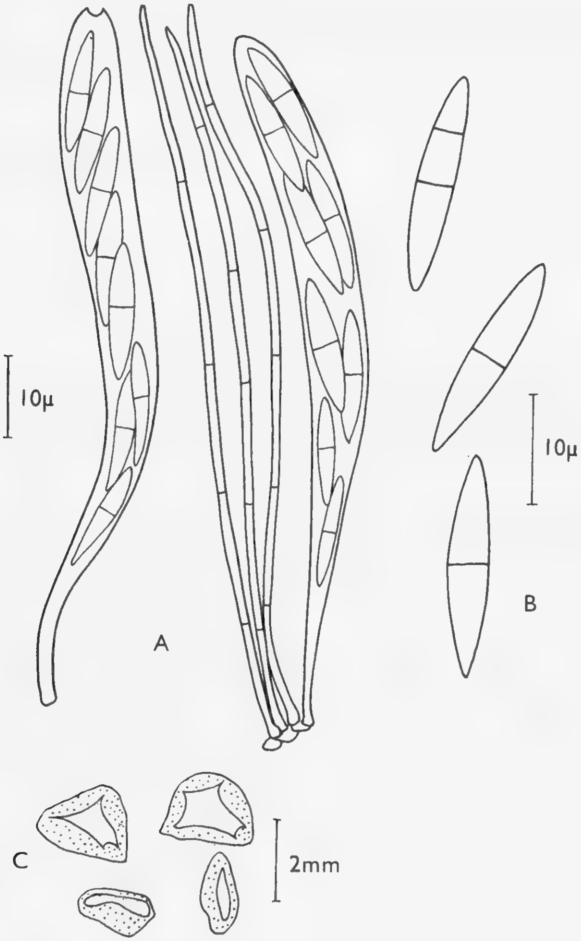

FIG. 2. *Mollisia dhankutae* Balfour-Browne. A, asci and paraphyses; B, ascospores; C, apothecia. *Norkett 7751 A.*

fusoideae, uniseptatae, hyalinae, 16–20 × 3·5–4 μ; paraphyses filiformes, septatae, 2 μ, supra usque 3·5 μ.

In ramis siccis *Bambusae.*

NEPAL: Dhankuta Province, Taplejung district, Sanghu, 1,750 m., on dead bamboo stump, 19 Nov. 1961, *Norkett 7751 A* (holotype). Sanghu, 2,060 m., 9 Nov. 1961, *Norkett 7349.*

Although very close to *Mollisia caesia* var. *andina* Dennis (Kew Bull. 14 : 441 (1960)) from Venezuela, it differs in the absence of a whitish margin to the receptacle, in the slightly larger and more acutely pointed spores and in the different host. It differs also from *Cenangella bambusicola* Rick (Broteria 5 : 37 (1906)), which was described from living bamboo in South America, in that the paraphyses do not form an epithecium and the apothecia are not at first white, but externally very dark brown with an off-white disc.

OSTROPACEAE

VIBRISSEA TRUNCORUM Fries, Syst. Mycol. 2 : 31 (1822).

NEPAL: Rambrong, Lamjung Himal, 4,500 m., on dead roots of Rhododendron, 10 July 1954, *Stainton, Sykes & Williams 6269.*

Distribution: America, Europe. Apparently not previously recorded from Nepal or neighbouring countries, possibly because it is easily overlooked, being small and generally found on roots, frequently submerged in water, or on debris.

Apothecia scattered or in groups, with orange discs, 3–5 mm. diam., seated on pale stalks, blackish below, 15 × 2–3 mm. Asci 250–300 × 6–8 μ; ascospores acicular, hyaline, multiseptate, 180–200 × 1·5 μ. Paraphyses branched, filiform with spherical heads.

DIATRYPACEAE

DIATRYPE CHLOROSARCA Berk. & Broome in Journ. Linn. Soc. Lond., Bot. 14 : 123 (1873).

NEPAL: Tumlingtar, Arun ravine, on dead twigs, 23 Dec. 1961, *Norkett 9060.*

Distribution: Ceylon and India.

The Nepal collection agrees with the type material described from Ceylon: spores 7–9 × 2–2·5 μ, hyaline to light brown.

HYPOCREACEAE

cf. BALANSIA ANDROPOGONIS Syd. apud H. & P. Syd. & Butl. in Ann. Mycol. 9 : 395 (1911).—Patel, Gokh. & Kulk. in Indian Phytopath. 4 : 65 (1951).

NEPAL: Mayangdi Khola, 1,000 m., on inflorescence of *Chrysopogon aciculatus,* 4 Sept. 1954, *Stainton, Sykes & Williams 4137.*

Distribution (of *B. andropogonis*): India, Philippines.

The inflorescence of the host is so deformed and shrouded by the fungus as to give the appearance of quite a different genus of grass. Only the *Ephelis* stage of the fungus is represented: conidia acicular, 20–24 × 1·5 μ.

EPICHLOE CINEREA Berk. & Broome in Journ. Linn. Soc. Lond., Bot. 14 : 111 (1873).

NEPAL: Taplejung district, Dhankuta Province, Sanghu, 2,000 m., on an indeterminable grass haulm, 17 Oct. 1961, *Norkett 5696 C*.

Distribution: Previously recorded from Ceylon. Sydow and Butler's record from Mysore (Ann. Mycol. 9 : 394 (1911)) appears to be a different species, as Petch (Ann. Roy. Bot. Gdns. Peradeniya 7 : 88 (1920)) has noted.

PHYLLACHORACEAE

CATACAUMA REPENS (Corda) Theiss. & Syd. in Ann. Mycol. 13 : 383 (1915).

Sphaeria repens Corda, Icones Fung. 4 : 42, tab. 9 fig. 123 (1840).
Phyllachora repens (Corda) Sacc., Syll. Fung. 2 : 597 (1883).

NEPAL: Phewa Tal, 800 m., on fallen leaves of *Ficus religiosa*, 6 May 1954, *Stainton, Sykes & Williams 5254*.

Distribution: Cuba, Natal, India.

Several species of *Catacauma* have been described from *Ficus* spp. but this Nepal collection is quite typical of *C. repens*.

XYLARIACEAE

HYPOXYLON MULTIFORME (Fries) Fries, Summa Veg. Scand. : 384 (1849).

Sphaeria multiformis Fries, Syst. Mycol. 2 : 334 (1823).

NEPAL: Taplejung, Mewa Khola, 2,750 m., on moss-covered branch (? birch), 22 Jan. 1962, *Norkett 9300*. Ganesh Himal, Ankhu Khola, 2,130 m., on rotting log, 12 May 1962, *Stainton 3694*.

Distribution: Widespread in Northern hemisphere; previously recorded from Nepal.

HYPOXYLON TRUNCATUM (Schwein.) J. H. Mill. in Trans. Brit. Mycol. Soc. 17 : 130 (1932); Monogr. World Sp. Hypoxylon : 95 (1961).

Sphaeria truncata Schwein. in Schr. Naturf. Ges. Leipz. 1 : 44 (1822).—Fries, Syst. Mycol. 2 : 442 (1823).

NEPAL: Bakhri Kharka, north of Pokhara, 2,000 m., 25 Apr. 1954, *Stainton, Sykes & Williams 5065*.

Distribution: Tropical and semitropical; America, Africa, China, Japan.

Miller (loc. cit., 1961) should be consulted for an account of this species and its considerable synonymy.

XYLOSPHAERA HYPOXYLON subsp. **ADSCENDENS** (Fries) Dennis in Bull. Jard. Bot. Bruxelles 31 : 124 (1961).

Sphaeria adscendens Fries in Linnaea 5 : 537 (1830).
Xylosphaera adscendens (Fries) Dennis in Kew Bull. 13 : 102 (1958).
Xylaria hypoxylon f. *tropica* H. & P. Syd. & Butl. in Ann. Mycol. 9 : 418 (1911).
Xylaria hypoxylon var. *tropica* (H. & P. Syd. & Butl.) Balf.-Browne in Bull. Brit. Mus. (Nat. Hist.), Bot. 1 : 216 (1955).

NEPAL: South of Gurjakhani, 3,500 m., 18 Aug. 1954, *Stainton, Sykes & Williams 3897*.

Distribution: South America, West Indies, Africa, India, Nepal, Indonesia.

This is the fungus previously recorded from Nepal as *Xylaria hypoxylon* var. *tropica* (Balfour-Browne, loc. cit.). Dennis (loc. cit., 1961) considers that it should be treated as a separate subspecies of *Xylosphaera hypoxylon* Dumort. Dennis had not seen the type specimen of *Xylaria hypoxylon* forma *tropica* and left open the question of whether that name was a synonym of *Xylosphaera hypoxylon* subsp. *adscendens*. I too have not seen the type, but I follow Dennis in considering that this is a separate subspecies.

XYLOSPHAERA MELLISSII (Berk.) Dennis in Kew Bull. 13 : 104 (1958); in Revista Biol. 1 : 186 (1958).

Hypoxylon mellissii Berk. in Melliss, St. Helena : 379 (1875).
Xylaria mellissii (Berk.) Cooke in Grevillea 11 : 85 (1883).
Xylaria arbuscula Sacc. in Michelia 1 : 249 (1878).—J. H. Mill. in Bothalia 4 : 265 (1942).

NEPAL: Dhankuta Province, Chainpur district, Tumlingtar, Sabhaya Khola, 600 m., " growing out of a niche in rock ", 8 Dec. 1961, *Norkett 8471 A*.

Distribution: Generally common in the tropics and subtropics, but not previously reported from the Himalayan region.

The Nepal collection consists of branched stromata with long slender stalks and short cylindrical heads; ascospores are 14–16 × 4·5 μ.

XYLOSPHAERA POLYMORPHA (St. Amans) Dumort., Comment. Bot. : 92 (1822).—Dennis in Bull. Jard. Bot. Bruxelles 31 : 140 (1961).

Sphaeria polymorpha St. Amans, Fl. Agenaise : 520 (1821).
Xylaria polymorpha (St. Amans) Grev., Fl. Edinensis : 355 (1824).

NEPAL: Arun Valley, Sabhaya Khola, 2,300 m., on tree trunk in forest, 7 Sept. 1956, *Stainton 1607*.

Distribution: Worldwide.

For a recent account and complete synonymy see Dennis (loc. cit.).

XYLOSPHAERA TELFAIRII (Berk.) Dennis in Kew Bull. 13 : 106 (1958); in Bull. Jard. Bot. Bruxelles 31 : 119 (1961).

Sphaeria telfairii Berk. in Ann. Nat. Hist. 3 : 397 (1839).
Xylaria telfairii (Berk.) Fries in Nov. Acta Reg. Soc. Sci. Upsal., Ser. 3, 1 : 127 (1851).

NEPAL: Arun Valley, Kasuwa Khola, 2,800 m., on tree trunk in forest, 11 Sept. 1956, *Stainton 1619*. Arun Valley, Hatiar, 2,600 m., 21 Aug. 1956, *Stainton 1408*.

Distribution: Africa, Ceylon, India, Indonesia, Australia.

For a recent account of the species, Dennis (loc. cit.) should be consulted.

Ustulina deusta (Fries) Petrak in Ann. Mycol. 19 : 279 (1921).

Sphaeria deusta Fries, Syst. Mycol. 2 : 345 (1823).
Ustulina vulgaris Tulasne frat., Sel. Fung. Carp. 2 : 23, tab. 3 figs. 1–6, (1863), *nom. superfl.*

Nepal: Bakhri Kharka, north of Pokhara, 2,000 m., 25 April 1954, *Stainton, Sykes & Williams 5056.*

Distribution: Worldwide.

CORONOPHORACEAE

Coronophora epistroma Syd. apud. Syd., Mitter & Tand. in Ann Mycol. 35 : 231 (1937).

Nepal: Sanghu, gulley below camp, 2,000 m., on dead twig, 21 Dec. 1961, *Norkett 6390.*

Distribution: Originally recorded from Allahabad, and not reported since.

This species was originally described as parasitic in the stromata of *Haplosporella phyllanthina* and again in the present gathering it is growing within the remains of a fungal pycnidium, but the identity of the latter could not be determined, nor that of the host twigs.

PLEOSPORACEAE

Fenestella fenestrata (Berk. & Broome) Schroet. in Cohn, Krypt.-Fl. Schles. 3(2) : 435 (1897). (Fig. 3).

Valsa fenestrata Berk. & Broome in Ann. Mag. Nat. Hist., Ser. 3, 3 : 366, t. 10 fig. 14 (1859).
Fenestella princeps Tulasne frat., Sel. Fung. Carp. 2 : 207 (1863), *nom. superfl.*

Nepal: Dhankuta district, Chitre, on dead twig, 2,000 m., 20 Sept. 1961, *Norkett 5159 A.*

Distribution: N. America, Europe.

The fungus occurs on an unidentified dicotyledonous twig. The pseudothecia are superficial, ± stipitate, arising in small groups on an inconspicuous stroma. Asci cylindrical, 250 × 20 μ approx. Ascospores 30–50 × 12–14 μ, broadly fusiform, dark brown, the end cells being ± hyaline; there are 3 main and several lesser transverse septa and several longitudinal septa.

Petrak (Sydowia 8 : 165 (1954)) describes *Cucurbitaria pakistanica* from Choa Saidan Shah, on *Acacia modesta*. This resembles the Nepal fungus in general structure but its spores are considerably smaller, the average size being 13–22 × 8–10 μ.

VENTURIACEAE

Rehmiodothis osbeckiae (Berk. & Broome) Theiss. & Syd. in Ann. Mycol. 12 : 192 (1914).

Dothidea osbeckiae Berk. & Broome in Journ. Linn. Soc. Lond., Bot. 14 : 134 (1873).

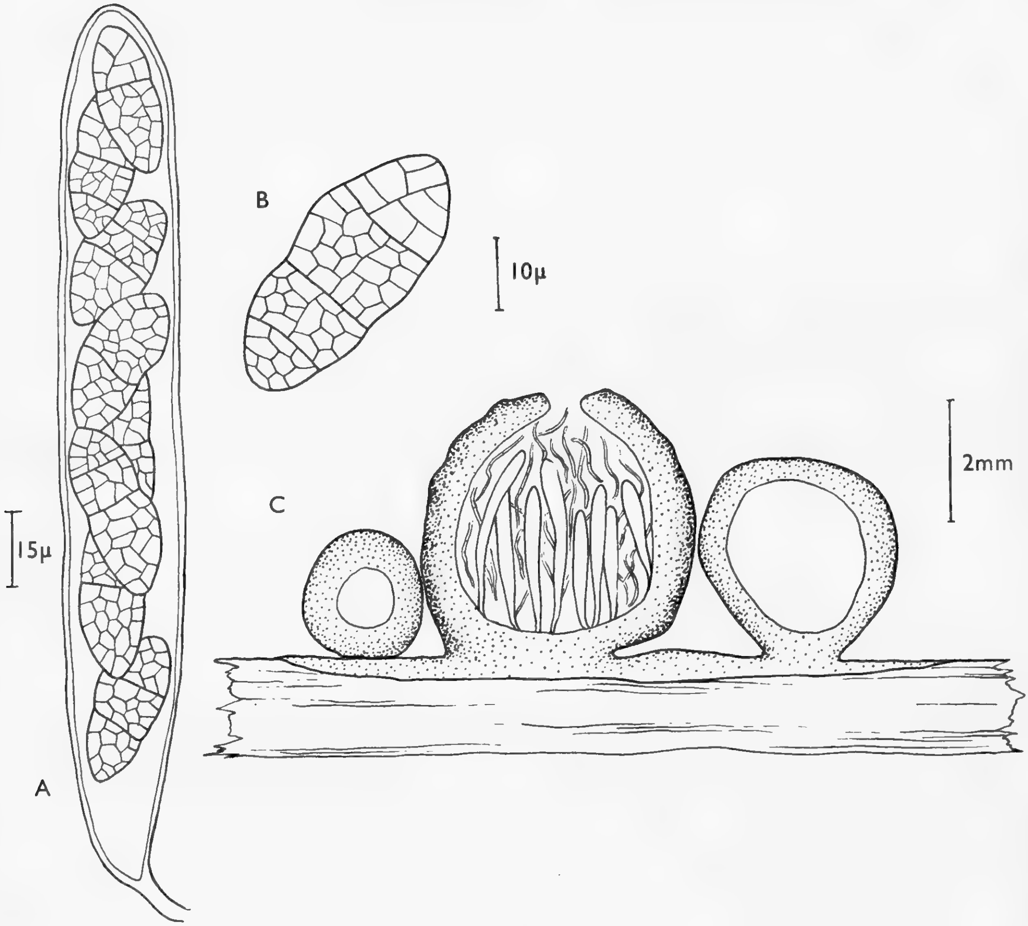

FIG. 3. *Fenestella fenestrata* (Berk. & Broome) Schroet. A, asci containing ascospores; B, ascospore; C, stroma with pseudothecia. *Norkett 5159 A*.

NEPAL: Dhankuta Province, Taplejung district, Sanghu, 2,000 m., on *Osbeckia* sp., 4 Oct. 1961, *Norkett 5696 D*.

Distribution: Previously recorded only from Ceylon.

POLYSTOMELLACEAE

SCHNEEPIA sp. cf. DISCOIDEA (Racib.) Racib. ex Theiss. & Syd. in Ann. Mycol. 13 : 203 (1915).

Parmularia discoidea Racib., Parasit. Algen & Pilze Java's 2 : 21 (1900).

NEPAL: Dhankuta Province, Taplejung district, Sanghu, 1,600 m., on fern, *Davallia* sp., 7 Jan. 1962, *Norkett 8552*.

Distribution (of *S. discoidea*): Previously recorded on *Polypodium longissimum* from Java.

The Nepal material is not quite ripe, but appears to represent the above species. Its rounded black stromata occur on the underside of the fronds and are somewhat raised in the centre. The asci and the 1-septate brownish spores, which are not fully mature, measure approximately 35 × 8 μ and 10 × 4 μ respectively.

Several black stromatic Ascomycetes with 1-septate spores have been described on ferns. Careful comparison of type and authentic material is needed and would probably reveal that a number of names are synonyms.

BASIDIOMYCETES

USTILAGINACEAE

CINTRACTIA CARICIS (Pers.) Magnus in Verh. Bot. Ver. Prov. Brandenb. 37 : 79 (1896).

Uredo caricis Pers., Syn. Meth. Fung. : 225 (1801).

NEPAL: Lamjung Himal, 4,500 m., on inflorescence of Cyperaceae, 14 July 1954, *Stainton, Sykes & Williams 6350*. East of Chalike Pahar, 4,500 m., 4 Aug. 1954, *Stainton, Sykes & Williams 3743*.
Distribution: Worldwide.

FARYSIA OLIVACEA (DC.) H. & P. Syd. in Ann. Mycol. 17 : 41 (1919).

Uredo olivacea DC., Fl. Franç. 6 : 78 (1815).

NEPAL: Bhurungdi Khola, 1,600 m., smut balls in inflorescence of *Carex cruciata* Wahl., 20 May 1954, *Stainton, Sykes & Williams 5336*. Near Lumsum, 2,300 m., 24 Oct. 1954, *Stainton, Sykes & Williams 9127*.
Distribution: Worldwide.

SPHACELOTHECA HYDROPIPERIS (Schumach.) de Bary, Vergl. Morph. Biol. Pilze : 187 (1884).

Uredo hydropiperis Schumach., Enum. Pl. Saell. 2 : 234 (1803).

NEPAL: Southwest of Gurjakhani, 3,300 m., in flower of *Polygonum campanulatum*, 20 Oct. 1954, *Stainton, Sykes & Williams 9104*. Dhankuta Province, Taplejung district, Sanghu, 2,000 m., 25 Nov. 1961, *Norkett 7532 A*.
Distribution: Worldwide on *Polygonum* sp. Previously recorded from Nepal in 1955.

SPHACELOTHECA REILIANA (Kühn) Clint. in Journ. Mycol. 8 : 141 (1902).

Ustilago reiliana Kühn in Rabenh., Fung. Eur. : No. 1998 (1875).

NEPAL: Murigurja Gad, 2,500 m., on *Zea mays*, 27 July 1954, *Stainton, Sykes & Williams 3653*.
Distribution: Recorded in most countries where maize is grown.

USTILAGO BISTORTARUM (DC.) Körn. in Hedwigia 16 : 38 (1877).

Uredo bistortarum DC., Fl. Franç. 6 : 76 (1815).

NEPAL: East of Chalike Pahar, 4,830 m., on leaves of *Polygonum affine*, 22 Sept. 1954, *Stainton, Sykes & Williams 4541*.

Distribution: Worldwide.

Forming in this material elongated pustules over the under surface of the leaf lamina, and not occurring on the margins. The spores are pale purple, angular to globose, 10–16 μ, minutely verrucose.

This species, common in most parts of the world, appears not to have been recorded previously from India or neighbouring countries.

Ustilago hordei (Pers.) Lagerh. in Mitt. Badischen Bot. Ver. [2](59) : 70 (1889), non *Ustilago hordei* Bref. (1888).

Uredo segetum var. *hordei* Pers., Syn. Meth. Fung. : 224 (1801).

NEPAL: Gurjakahni, 2,800 m., on barley inflorescence, 1 June 1954, *Stainton, Sykes & Williams 2941*. Tegar, north of Mustang, 6 Aug. 1954, *Stainton, Sykes & Williams 2252*.

Distribution: Worldwide.

The name used for this species is illegitimate, being a later homonym of *Ustilago hordei* Bref. (in Nachr. Klub Landwirthe Berl. 221 : 1593 (28 June 1888)), which was based on the loose smut of barley, as a name for which it antedated *U. nuda* (Jensen) Kellerm. & Swingle (see below). Before the correct names of these two species can be established, it is necessary to fix the application of the name *Uredo segetum* Pers. (Syn. Meth. Fung. : 224 (1801)), and also to investigate the status and application of the names *Uredo carbo-tritici* and *Uredo carbo-hordei* quoted by Kellerman & Swingle (in Annu. Rep. Exp. Stat. Kansas State Agric. Coll. 2 : 262, 269, 278 (1890)) from a work by Philippar not available to me. I therefore adopt for the present the names in current use.

USTILAGO MORINAE Padw. & Azmat. Khan in Mycol. Pap., Imp. Mycol. Inst. 10 : 1 (1944).

NEPAL: Above Seng Khola, 4,500 m., in flowers of *Morina*, 25 June 1954, *Stainton, Sykes & Williams 3254*.

Distribution: Recorded from Kashmir in 1944 on *Morina longifolia*.

Ustilago nuda (Jens.) Kellerm. & Swingle in Annu. Rep. Exp. Stat. Kansas State Agric. Coll. 2 : 277 (1890).

Ustilago segetum var. *nuda* Jens. in Journ. Roy. Agric. Soc., Ser. 2, 24 : 406 (1888).
Ustilago nuda Rostr. in Tidsskr. Landøkon 8 : 745 (1889), *nom. nud.*

NEPAL: Chimgoan, north of Tukucha, 3,000 m., on barley in field, 3 June 1954, *Stainton, Sykes & Williams 904*. Gurjakhani, 2,830 m., on wheat, 1 June 1954, *Stainton, Sykes & Williams 2940.* Tamur valley, Mewa Khola, on wheat, 17 May 1956, *Stainton* 343.

Distribution: Worldwide.

For the status of this name, see under *Ustilago hordei* above.

USTILAGO PIPERI Clint. in Proc. Boston Soc. Nat. Hist. 31 : 382 (1904).—G. W. Fisch., Man. N. Amer. Smut Fungi : 291, fig. 123 D (1953).

NEPAL: Near Seng Khola, 4,600 m., on *Polygonum rumicifolium,* 9 Aug. 1954, *Stainton, Sykes & Williams 3809.*

Distribution: United States of America.

The Nepal collection agrees well with this species; it forms large pustules on the underside of the leaves; the spores are pinkish purple, spherical or subspherical, 7–9 μ diam., marked with striae. This species differs from *U. bistortarum* in the distinctly smaller spores.

TILLETIACEAE

MELANOTAENIUM SELAGINELLAE Henn. & Nyman in Warb., Monsunia 1 : 2 (1900).

NEPAL: Dhankuta Province, Taplejung district, Sanghu, on *Selaginella* sp., 27 Oct. 1961, *Norkett 6551 A.*

Distribution: Previously recorded from Tjibodas in Java.

In the present collection the smut occurs mostly on the basal portion of the leaves, but occasionally it covers the whole leaf surface. Spores dark brown, globose, coarsely verrucose, 15–18 μ diameter.

MELAMPSORACEAE

COLEOSPORIUM BARCLAYENSE Bagchee in Ind. Forest Rec., New Ser., Bot. 4 : 53 (1950).

NEPAL: Annapurna Himal, Mardi Khola, 4,160 m., on *Senecio alatus* Wall. ex DC., 20 Sept. 1954, *Stainton, Sykes & Williams 8528.*

Distribution: India.

The teleutospore stage is represented in this collection. Morphologically, the *Coleosporium* species on *Senecio* are difficult to separate, but, on the basis of inoculation experiments carried out by Bagchee (loc. cit.) on rusts on different species of *Senecio,* that on *S. alatus* would appear to be his *C. barclayense.*

COLEOSPORIUM CAMPANULAE (Pers.) Kickx, Fl. Crypt. Flandres 2 : 54 (1867).—Gaüm. in Beitr. Krypt.-Fl. Schweiz 12 : 113, fig. 99–100 (1959).

Uredo campanulae Pers., Syn. Meth. Fung. : 217 (1801).

NEPAL: Near Jagat, 2,800 m., on *Campanula* sp., 5 July 1954, *Stainton, Sykes & Williams 3376.* Above Lumsum, 3,700 m., on *Campanula* seedlings, 23 Oct. 1954, *Stainton, Sykes & Williams 9122.* Rambrong, Lamjung Himal, 3,000 m., on *Lobelia seguinii* var. *doniana* (Skottsb.) Wimm., 27 Oct. 1954, *Stainton, Sykes & Williams*

8306. Annapurna Himal, Mardi Khola, 2,600 m., on *Lobelia* sp., 20 Sept. 1954, *Stainton, Sykes & Williams 8531.* Baglung, 1000 m., on *Wahlenbergia gracilis* DC., 20 Apr. 1954, *Stainton, Sykes & Williams 548.*

Distribution: Widely represented in the Northern hemisphere and previously recorded from Nepal.

The uredospores occurred on stems as well on both leaf surfaces. A greater proportion of the spores on *Wahlenbergia* were oblong and elongated compared with those on *Campanula.* Probably two biological forms are represented. Gaümann (loc. cit.) should be consulted for an account of at least six such forms which have been isolated from different genera and species of Campanulaceae.

COLEOSPORIUM INULAE Rabenh. in Bot. Zeit. 9 : 455 (1851).—P. & H. Syd., Monogr. Ured. 3 : 609 (1915).—Vasud. in Butl. & Bisby, Fungi of India, Rev. Ed. : 85 (1960).

Uredo inulae Kunze in Klotsch, Herb. Viv. Mycol., No. 589 (1844), *nom. nud.*

NEPAL: Pasgam, 1,500 m., on *Inula cappa* DC., 25 June 1954, *Stainton, Sykes & Williams 5938.*

Distribution: Europe, North Africa, Asia Minor, India.

The uredo stage is represented and this chiefly on the upper surface of the leaves, with very few pustules on the lower.

COLEOSPORIUM PEDICULARIDIS Tai in Farlowia 3 : 100 (1947).

NEPAL: Taglung, south of Tukucha, Kali Gandaki, 4,000 m., on leaves of *Pedicularis* sp., 22 Sept. 1954, *Stainton, Sykes & Williams 7987.* Panchasi, 2,300 m., on *Pedicularis* sp., 15 Oct. 1954, *Stainton, Sykes & Williams 8944.*

Distribution: China.

There is little doubt that the Nepal fungus represents this species. The uredosori are chiefly on the under surface of the leaves, light yellow and soon pulverulent. The uredospores are coarsely and densely echinulate, 18–30 × 12–20 μ, oblong to irregularly globose.

COLEOSPORIUM PLECTRANTHI Barcl. in Journ. Asiatic Soc. Bengal 59 (2): 89 (1890).

NEPAL: Sattewati, 2,000 m., on *Plectranthus* sp., 12 Oct. 1954, *Stainton, Sykes & Williams 8950.*

Distribution: India, Japan.

COLEOSPORIUM SENECIONIS (Pers.) Fries, Summa Veg. Scand. : 512 (1849).

Uredo farinosa var. *senecionis* Pers., Syn. Meth. Fung. : 218 (1801).

NEPAL: Above Lumsum, 3,160 m., on *Senecio graciliflorus* DC., 10 Sept. 1954, *Stainton, Sykes & Williams 4327.* Dhankuta Province, Milke Danda, 3,160 m., on *Senecio graciliflorus* DC., 16 Nov. 1961, *Norkett 7121 A.*

Distribution: Worldwide.

Uredospore stage. See note under *Coleosporium barclayense.*

Hyalopsora polypodii (Pers.) Magn. in Ber. Deutsch. Bot. Ges. 19 : 582 (1902).

Uredo linearis var. *polypodii* Pers., Syn. Meth. Fung. : 217 (1801).

Nepal: Annapurna Himal, Seti Khola, 4,160 m., on *Polypodium malacodon*, 3 Aug. 1954, *Stainton, Sykes & Williams 6603*.

Distribution: North America, Europe, India, Japan.

Melampsora sp. cf. **hirculi** Lindr. in Acta. Soc. Fauna & Flora Fenn. 22 (3) : 19 (1902).

Nepal: Annapurna Himal, 4,150 m., on *Saxifraga moorcroftiana* Wall., 2 Aug. 1954, *Stainton, Sykes & Williams 6587*.

Distribution (of *M. hirculi*): Europe (Finland, Russia, Switzerland).

Although this species so far has apparently only been recorded from Europe, the Nepal collection agrees very closely with the original description of *M. hirculi*, but the fungus occurs not only on the under surfaces, but more frequently on the upper leaf surfaces, which become considerably discoloured and blotchy. Uredospores are globose, ovate or ellipsoid, minutely verrucose, 16–25 × 14–18 μ; paraphyses are abundant and capitate or clavate, 35–60 × 10–20 μ with a thick wall. The teleutospores are brown, oblong, 35–55 × 8–12 μ.

Milesina sp. cf. **exigua** Faull in Journ. Arnold Arb. 12 : 218 (1931).

Nepal: Dhankuta Province, Taplejung district, 1,950 m., on *Diplazium* sp., 9 Jan. 1962, *Norkett 8642 A*.

Distribution (of *M. exigua*): Poland, Japan and the Siberian coast.

Uredosori only are represented; they occur in brown discoloured areas on both sides of the fronds. Many of the spores are somewhat irregularly polygonal in shape. They measure 28 × 15 μ (average) and are quite smooth.

PUCCINIACEAE

Frommea duchesneae (Arth.) Arth. in Bull. Torrey Bot. Club 44 : 504 (1917); in N. Amer. Fl. 7 : 731 (1925).

Kuhneola duchesneae Arth. in N. Amer. Fl. 7 : 185 (1912).
Frommea obtusa [var.] *duchesneae* (Arth.) Arth., Man. Rusts U.S. & Canada : 93 (1934).—Gäum. in Beitr. Krypt.-Fl. Schweiz 12 : 1177 (1959).
Frommea obtusa-duchesneae Vienn.-Bourg. in Rev. Path. Vég. Entom. Agric. Fr. 33 : 38 (1954), *nom. superfl.*

Nepal: Ghar Khola, 1,600 m., on *Duchesnea indica*, 14 June 1954, *Stainton, Sykes & Williams 5767*.

Distribution: Nepal, and North America and France, where the host is naturalized.

It seems that Arthur in 1934 (loc. cit.) had second thoughts about treating the rust on *Duchesnea indica* as a full species and, describing it as a " less robust form " compared with *F. obtusa*, regarded it merely as a variety of the latter species.

In the Nepal collection the uredo-sori are abundant, the uredospores measure

9–14 × 18–20 μ, distinctly small for *F. obtusa* (which occurs on *Potentilla* sp.) but in agreement with the spores described on *Duchesnea* from America by Arthur and from France by Viennot-Bourgin. No other spore form was present on the Nepal plants. In the absence of firm evidence to support synonymy with *F. obtusa* the name *F. duchesneae* is retained here. This is the first record of the rust in what is considered to be the host plant's centre of origin.

GYMNOSPORANGIUM PADMARENSE Balf.-Browne in Bull. Brit. Mus. (Nat. Hist.) 1 : 205, fig. 2 (1955).

NEPAL: Near Gurjakhani, 3,000 m., on *Juniperus wallichiana*, 3 June 1954, *Stainton, Sykes & Williams 2969.*

Distribution: Nepal.

The material under consideration is old, the sori are broken up and the teleutospores have lost their pedicels.

GYMNOSPORANGIUM CUNNINGHAMIANUM Barcl. in Sci. Mem. Med. Off. Army Ind. 5 : 78, t. 1–3 (1890).

NEPAL: Village south of Chakure Lekh, 6 Apr. 1952, *Polunin, Sykes & Williams 1870.*

Distribution: India, Nepal.

PHRAGMIDIUM INCOMPLETUM Barcl. in Journ. Asiatic Soc. Bengal 59 (2) : 83 (1890).

NEPAL: Siklis, north of Pokhara, 3,000 m., on *Rubus* sp., 21 Apr. 1954, *Stainton, Sykes & Williams 4950.*

Distribution: India.

The uredospore stage only is present, and it agrees well with the original account, except that it is chiefly epiphyllous. Uredospores have a thick, 3–4 μ, epispore, which is warted. There are no paraphyses.

PHRAGMIDIUM sp. cf. NEPALENSE Barcl. in Journ. Asiatic Soc. Bengal 60 (2) : 220 (1891).

NEPAL: Bhuji Khola, 2,800 m., on *Potentilla nepalensis*, 16 Oct. 1954, *Stainton, Sykes & Williams 9058.*

Distribution (of *P. nepalense*): India.

Uredosori only are represented. In the original description it was not stated whether the epispore is smooth or echinulate. Padwick & Azmatullah Khan (Mycol. Papers, Imp. Mycol. Inst. 10 : 4 (1944)) record this species and describe the uredospores as finely echinulate. This agrees with those on the present collection, and the measurements are similar.

PUCCINIA CARICIS var. HIMALAYENSIS (Barcl.) Padw. & Azmat. Khan in Mycol. Papers, Imp. Mycol. Inst. 10 : 9 (1944).

Aecidium urticae var. *himalayense* Barcl. in Sci. Mem. Med. Off. Army Ind. 2 : 29, t. 4, 5 figs. 8–17 (1887); in Journ. Asiatic Soc. Bengal 56 (2) : 368 (1887).

NEPAL: Jagat, 2,600 m., on *Urtica* sp., 5 July 1954, *Stainton, Sykes & Williams 3364.*
Distribution: India, Himalayas.
Cf. Padwick & Azmatullah Khan (loc. cit.) for an account of the somewhat confused synonymy.

PUCCINIA FAGOPYRI Barcl. in Journ. of Bot. 28 : 261 (1890).

NEPAL: Dhankuta Province, Taplejung district, Sanghu, 2,000 m., on *Fagopyrum,* 11 Nov. 1961, *Norkett 7173 A.*
Distribution: India.

PUCCINIA GENTIANAE (Strauss) Link in L., Sp. Pl., Ed. 4, 6 (2) : 73 (1825).

Uredo gentianae Strauss in Ann. Wetter. Ges. 2 : 102, t. 11 fig. 33 (1811).

NEPAL: South of Gurjakhani, 4,000 m., on *Gentiana* sp., 8 June 1954, *Stainton, Sykes & Williams 3071.*
Distribution: Widely distributed in the northern Hemisphere.
Only the aecidial stage is represented in the Nepal material.

PUCCINIA GLUMARUM (J. K. Schmidt) Erikss. & Henn. in Medd. K. Landtbr.-Akad. Exp. 38 : 141 (1896).

Uredo glumarum J. K. Schmidt in Allgem. Ökonom.-Tech. Flora 1 : 27 (1827).

NEPAL: Gurjakhani, 2,800 m., on *Triticum vulgare,* 1 June 1954, *Stainton, Sykes & Williams 2939.*
Distribution: Worldwide.

PUCCINIA GRAMINIS Pers., Syn. Meth. Fung. : 228 (1801).

NEPAL: Ghasa, Kali Gandaki Valley, 2,500 m., on *Berberis* sp., 31 May 1954, *Stainton, Sykes & Williams 5499*; same locality and host, 13 June 1954, *Stainton, Sykes & Williams 5750.*
Distribution: Worldwide.
Some of the pustules were a bright pink and considerably swollen.

PUCCINIA LANTANAE Farl. in Proc. Amer. Acad. Arts & Sci. 18 : 83 (1883).—G. Laund. in Mycol. Papers, Commonw. Mycol. Inst. 89 : 43 (1963).

NEPAL: Sanghu, Dhankuta Province, 2,000 m., on *Justicia diffusa,* 15 Oct. 1961, *Norkett 6124.*
Distribution: North and South America, India, Indonesia, Philippines, China, Japan.

PUCCINIA LEUCOPHAEA H. & P. Syd. & Butl. in Ann. Mycol 10 : 258 (1912).

NEPAL: Ghar Khola, 2,000 m., on *Colquhounia coccinea,* 14 June 1954, *Stainton, Sykes & Williams 5758.*

Distribution: India.

Aecidial stage only and chiefly epiphyllous; only a few isolated sori on the lower surface and on the petioles. In the original account the aecia were said to be hypophyllous.

PUCCINIA POLYGONI-AVICULARIAE Pers., Syn. Meth. Fung. : 227 (1801).

> *Puccinia polygoni* Alb. & Schwein., Consp. Fung. : 132 (1805), *nom. superfl.*—Gäum. in Beitr. Krypt.-Fl. Schweiz 12 : 775 (1959).

NEPAL: Dhankuta Province, Taplejung district, Sanghu, 2,000 m., on *Polygonum nepalense*, 25 Nov. 1961, *Norkett 7530 A*.

Distribution: Worldwide.

The teleutospore stage is represented. This species and *P. polygoni-amphibii* are united by some mycologists but treated as separate by others. The two species are maintained here not only on biological grounds but also on account of definite small morphological distinctions, which apply not only to European plants, as generally stated, but also to American specimens as exemplified in the British Museum herbarium. In *P. polygoni-amphibii*, usually occurring on *Polygonum amphibium*, *P. lapathifolium* and related species, the teleutosori remain for long covered by the epidermis and form small pimply pustules, and the spores are frequently somewhat bent and easily lose their pedicels. On the other hand, in *P. polygoni-aviculariae*, usually on *Polygonum dumetorum* and *P. convolvulus*, the pustules rapidly burst through the epidermis of the host, leaving smooth black cushions of straight, stalked teleutospores.

In the present instance the host, *Polygonum nepalense*, resembles in general appearance and texture *Polygonum convolvulus*, and the teleutospores and sori of the fungus agree exactly with those described for *P. polygoni-aviculariae*.

PUCCINIA PULVERULENTA Grev., Fl. Edin. : 432 (1824).—Gaüm. in Beitr. Krypt.-Fl. Schweiz 12 : 929 (1959).

NEPAL: Near Dogadi Khola, 4,300 m., on *Epilobium* sp., 23 June 1954, *Stainton, Sykes & Williams 3226*.

Distribution: Worldwide.

PUCCINIA USTALIS Berk. in Hook., Journ. Bot. 6 : 207 (1854).

> *Puccinia songarica* Jacz. in Hedwigia 39 : (130), fig. 1 (1900).

NEPAL: Rambrong, Lamjung Himal, 4,000 m., on *Ranunculus* sp., 29 June 1954, *Stainton, Sykes & Williams 6016*.

Distribution: India, Turkestan, Mongolia.

RAVENELIA EMBLICAE Syd. apud H. & P. Syd. & Butl. in Ann. Mycol. 4 : 438 (1906). —P. & H. Syd., Monogr. Ured. 3 : 293 (1914).

NEPAL: Chainpur path, Tumlingtar, 800 m., on *Phyllanthus emblica*, 21 Dec. 1961, *Norkett 8100*.

Distribution: Previously recorded from India and Burma.

Ravenelia phyllanthi Mundk. & Thirum. (Mycol. Papers, Imp. Mycol. Inst. 16 : 24, fig. 18 (1946)) seems to be synonymous. This was described on *Phyllanthus polyphyllus* from Mysore.

UREDINALES—Form Genera

AECIDIUM CRINI Kalchbr. in Grevillea 11 : 26 (1882).—Mundk. & Thirum. in Mycol. Papers, Imp. Mycol. Inst. 16 : 16 (1946).

Aecidium amaryllidis H. & P. Syd. & Butl. in Ann. Mycol. 10 : 274 (1912).

NEPAL: Dana, Kali Gandaki Valley, 1,600 m., on *Crinum amoenum* Roxb. ex Ker-Gawl., 13 June 1954, *Stainton, Sykes & Williams 5738.*

Distribution: India, South Africa.

AECIDIUM INFREQUENS Barcl. in Journ. Asiatic Soc. Bengal, 59 (2) : 105 (1890).

NEPAL: Nr. Dogadi Khola, 4,300 m., on *Geranium collinum* Steph. ex Willd., on open slopes, 23 June 1954, *Stainton, Sykes & Williams 3227.*

Distribution: India, Nepal, Japan.

The aecidia cover considerable areas of the lower side of the leaves, showing as light brown patches on the upper surface. Each aecidium is 250–300 μ diam. The size, ornamentation, colouring of the aecidia and aecidiospores correspond exactly with those originally described for *A. infrequens* by Barclay on a *Geranium* sp. (? *nepalensis*) from Simla. The present fungus agrees also with the details given for *A. sanguinolentum* on other *Geranium* spp. in Finland, Russia and America by Lindroth (Bot. Notiser 1900 : 241), and he suggested this might be a synonym of Barclay's rust.

Polunin, Sykes & Williams 4765, recorded in 1955 in this Journal (Balfour-Browne, 1955) as *A. infrequens* is microscopically similar to the fungus now reported, but differs in that the aecidia are grouped in orbicular patches with a small bare spot in the centre of each patch, i.e., as described by Lindroth for the less heavily infected specimens of his *A. sanguinolentum.* The host of this earlier collection, which has now been identified also as *G. collinum,* is more elegant and slender. Possibly the heavy rust infection is responsible for the coarser growth of the host specimen of *Stainton, Sykes & Williams 3227.*

A. sanguinolentum, in consequence of inoculation experiments from *Geranium* spp. of European origin (Lindroth, *loc. cit.*), has been described as a stage in life history of *Puccinia polygoni-amphibii* Pers. However, until experiments are made using specimens of the Nepal fungus, no certain conclusions can be drawn as to its relationships or alternative host plants.

In the meantime *A. infrequens* Barcl. is the name preferred on grounds of distribution and would be also on grounds of priority should this species prove to be identical with *A. sanguinolentum.*

Aecidium scutellariae Syd. apud H. & P. Syd. & Butl. in Ann. Mycol. 5 : 504 (1907).

Nepal: Ghar Khola, 1,800 m., on *Scutellaria scandens* D. Don., 14 June 1954, *Stainton, Sykes & Williams 5763.*
Distribution: Himalayas.

A similar fungus, *Aecidium scutellariae-indicae* Dietel, has been described from Japan on *Scutellaria indica* var. *japonica.* This may be identical with the above species (P. & H. Syd., Monogr. Ured. 4 : 115 (1923)).

Peridermium orientale Cooke in Ind. Forester 3 : 91 (1877) " orientalis ".

Aecidium complanatum Barcl. in Journ. Asiatic Soc. Bengal 59 (2) : 101 (1890).

Nepal: Dhaibungkot, 1,600 m., on dead pine needles, 31 May 1949, *Polunin 041.* Near Beni, 1,300 m., on needles of *Pinus longifolia*, 23 May 1954, *Stainton, Sykes & Williams 2794.*
Distribution: India, Nepal, Bhutan.

Uredo hyperici-mysorensis Petch in Ann. R. Bot. Gdns. Peradeniya 6 : 213 (1917).

Nepal: Sanghu, Dhankuta Province, 1,400 m., on *Hypericum* sp., 12 Nov. 1961, *Norkett 7088.*
Distribution: Ceylon, India.

AURICULARIACEAE

Auricularia delicata (Fries) Henn. apud Bresad., Henn. & Magn. in Engl., Bot. Jahrb. 17 : 492 (1893).

Laschia delicata Fries in Linnaea 5 : 533 (1830).
Laschia tremellosa Fries, Summa Veg. Scand. : 325 (1849).

Nepal: Ranipauwa, north of Beni, Kali Gandaki, 1,000 m., 3 Sept. 1954, *Stainton, Sykes & Williams 7629.*
Distribution: mostly tropical; America, Africa, India, Australia, Pacific.

Auricularia mesenterica Pers., Mycol. Eur. 1 : 97 (1822).

Nepal: Arun Valley, Num, 1,500 m., on tree trunk, 30 Aug. 1956, *Stainton 1459.*
Distribution: America, Europe, India, Indonesia, Australia.

The fructifications are broadly attached, many more or less disciform, and they therefore superficially resemble *A. peltata* Lloyd. However the hairs are much longer, up to 500 μ.

Auricularia polytricha (Mont.) Sacc. in Atti R. Ist Veneto, Ser. 6, 3 : 722 (1885).

Exidia polytricha Mont. in Bélang., Voy. aux Indes-Or. 2 : 154 (1834).
Hirneola polytricha (Mont.) Fries in K. Vet.-Akad. Handl. 1848 (1) : 146 (1849).

Nepal: Tamrang Khola, 2,300 m., on branch of tree, 21 Nov. 1961, *Norkett 7889.*
Distribution: Worldwide.

TREMELLACEAE

GUEPINIA HELVELLOIDES (Fries) Fries, Elenchus Fung. 2 : 31 (1828).

Tremella helvelloides Fries, Syst. Mycol. 2 : 211 (1822).
Phlogiotis helvelloides (Fries) Martin in Amer. Journ. Bot. 23 : 628 (1936).
Tremella rufa Pers., Mycol Eur. 1 (1) : 103 (1822).
Gyrocephalus rufus (Pers.) Bref. in Unters. Gesammtgeb. Mykol. 7 : 131 (1888).

NEPAL: Taglung, Kali Gandaki, 3,500 m., 22 Sept. 1954, *Stainton, Sykes & Williams 7990*.

Distribution: North America, Europe, China, India.

TREMELLA MESENTERICA Fries, Syst. Mycol. 2 : 214 (1822).

NEPAL: Dhankuta Province, near Mahe, 1,300 m., on dead tree, 20 Sept. 1961, *Norkett 5175 D*.

Distribution: Worldwide.

EXOBASIDIACEAE

EXOBASIDIUM sp.

NEPAL: Lete, Kali Gandaki Valley, 3,800 m., on *Rhododendron campanulatum*, 4 June 1954, *Stainton, Sykes & Williams 5607*. Above Sauwala Khola, 3,800 m., on *Rhododendron lepidotum*, 15 Sept. 1954, *Stainton, Sykes & Williams 4430*. Near Lumsum, 2,300 m., on *Rhododendron* seedlings, 24 Oct. 1954, *Stainton, Sykes & Williams 9132*.

Specific identification could not be made as the collections in all cases were very over-ripe. Several species of *Exobasidium* have been described on *Rhododendron*. References to the literature on *Exobasidium* can be found in Sundström (Phytopath. Zeitschr. 40 : 213–17 (1960)) and in McNabb (Trans. R. Soc. N.Z., Bot. 1 : 267 (1962)).

AGARICACEAE

ARMILLARIA MELLEA (Fries) Kummer, Führ. Pilzk. : 134 (1871).

Agaricus melleus Fries, Syst. Mycol 1 : 30 (1821).

NEPAL: Arun Valley, Kasuwa Khola, on tree trunk in forest, 11 Sept. 1956, *Stainton 1618*.

Distribution: Worldwide.

CLITOCYBE TABESCENS (Fries) Bresad., Fung. Trident. 2 : 84, t. 197 (1900).

Agaricus tabescens Fries, Hymenomyc. Eur., Ed. 2 : 111 (1874).

NEPAL: Lete, Kali Gandaki Valley, 2,600 m., in leaf mould at base of *Pinus chylla*, 3 June 1954, *Stainton, Sykes & Williams 5551*.

Distribution: Worldwide.

Coprinus comatus (Fries) Gray, Nat. Arrang. Brit. Pl. 1 : 633 (1821).

Agaricus comatus Fries, Syst. Mycol. 1 : 307 (1821).

Nepal: Chimgaon (north of Tukucha), Kali Gandaki, 4,500 m., 17 July 1954, *Stainton, Sykes & Williams 1846*.

Distribution: Worldwide.

Coprinus disseminatus (Fries) Gray, Nat. Arrang. Brit. Pl. 1 : 634 (1821).

Agaricus disseminatus Fries, Syst. Mycol. 1 : 305 (1821).
Psathyrella disseminata (Fries) Quél. in Mém. Soc. Émul. Montbéliard, Ser. 2, 5 : 153 (1872) (reimpr. quam Champ. Jura Vosg. : 123 (1872)).

Nepal: Arun Valley, Hatiar, 2,300 m., on fallen tree in forest, 20 Aug. 1956, *Stainton 1394*.

Distribution: Worldwide.

Crepidotus mollis (Fries) Staude in Festg. Mitgl. XIX Versamml. deutsch. Land- und Forstwirthe Coburg : 71 (1857) (reimpr. quam Schwämme Mitteldeutschl. : 71 (1858)).

Agaricus mollis Fries, Syst. Mycol. 1 : 274 (1821).

Nepal: Arun Valley, Kasuwa Khola, 2,800 m., on tree trunk in forest, 11 Sept. 1956, *Stainton 1617*.

Distribution: America, Europe, China, Japan, Australia.

Very badly crushed in pressing but the layers of parallel and gelatinous hyphae were readily observed; spores 9 × 5 μ, smooth.

Gomphus floccosus (Schwein.) Sing. in Lloydia 8 : 140 (1945).

Cantharellus floccosus Schwein. in Trans. Amer. Phil. Soc., New Ser. 4 : 153 (1832).

Nepal: Above Sauwala Khola, 3,300 m., on earth bank in *Quercus* forest, 13 Sept. 1954, *Stainton, Sykes & Williams 4375*.

Distribution: Recorded from North America, China, Japan, as well as from Nepal (1955).

Laccaria laccata (Fries) Cooke in Grevillea 12 : 70 (1884).

Agaricus laccatus Fries, Syst. Mycol. 1 : 106 (1821).

Nepal: Arun Valley, Barun Khola, 4,000 m., in short grass, pinkish brown, 15 Sept. 1956, *Stainton 1662*.

Distribution: Worldwide.

Lactarius pubescens (Krombh.) Fries, Epicrisis Syst. Mycol. : 335 (1838).

Agaricus pubescens Krombh., Naturg. Abbild. & Beschreib. Essb., Schädl. & Verdächt. Schwämme 2 : 24, t. 13 figs. 1–14 (1832).

NEPAL: Arun Valley, Barun Khola, 4,000 m., in short grass, 15 Sept. 1956, *Stainton 1660.*

Distribution: Apparently worldwide, but it is uncertain how many records under the name of the coarser *L. torminosus* (Fries) Gray, from which many mycologists have not separated this species, refer to it. Very few species of *Lactarius* have as yet been recorded from India or any of the neighbouring countries.

LEPIOTA ERMINEA (Fries) Gill., Hyménomycètes : 59 (1874).

Agaricus ermineus Fries, Syst. Mycol. 1 : 22 (1821).

NEPAL: Mathand, near Pokhara, 1,120 m., on shady bank, " white except top of cap which is brown ", 22 June 1954, *Stainton, Sykes & Williams 5852.*

Distribution: Europe, India, Australia.

MARASMIUS CRINIS-EQUI F. von Muell. ex Kalchbr. in Grevillea 8 : 153 (1880).

Marasmius equicrinis F. von Muell. ex Berk. in Journ. Linn. Soc. Lond., Bot. 18 : 383 (1881), *nom. superfl.*

NEPAL: Murigurja Gad, 2,500 m., on dead vegetation near ravine track, 27 July 1954, *Stainton, Sykes & Williams 3647.*

Distribution: America, India, Ceylon, Philippines, Australia.

Panus polychrous (Lév.) Singer ex Balfour-Browne, comb. nov.

Lentinus polychrous Lév. in Ann. Sci. Nat., Ser. 3, Bot. 2 : 175 (1844).
Lentinus vellereus Berk. & Curt. in Journ. Linn. Soc. Lond., Bot. 10 : 301 (1868).
Lentinus kurzianus Currey in Trans. Linn. Soc. Lond., Ser. 2, Bot. 1 : 120, t. 20 fig. 11 (1876).
Panus polychrous Sing., Agaricales in Modern Taxonomy, Ed. 2 : 172 (1962), *nom. invalid.*

NEPAL: Tumlingtar, Sabhaya Khola, 600 m., on dead tree, 20 Dec. 1961, *Norkett 8108.*

Distribution: Cuba, India, Nepal, Ceylon, Philippines, Australia.

A few additional synonyms are given by Singer (loc. cit.).

PANUS TIGRINUS (Fries) Sing. in Lilloa 22 : 275 (1951).

Agaricus tigrinus Fries, Syst. Mycol. 1 : 176 (1821).
Lentinus tigrinus (Fries) Fries, Epicrisis Syst. Mycol. : 389 (1838).

NEPAL: Midam Khola, Chisankhu, 650 m., on dead tree trunk, 4 May 1954, *Stainton, Sykes & Williams 5214.*

Distribution: Worldwide.

PHOLIOTA SQUARROSA (Fries) Kummer, Führ. Pilzk. : 84 (1871).

Agaricus squarrosus Fries, Syst. Mycol. 1 : 243 (1821).

NEPAL: Chimgaon (north of Tukucha), Kali Gandaki, 3,500 m., in forest, at base of conifer, 14 Sept. 1954, *Stainton, Sykes & Williams 7830.*

Distribution: North America, Europe, Japan.

SCHIZOPHYLLUM COMMUNE Fries, Syst. Mycol 1 : 330 (1821).

NEPAL: Ranipauwa (north of Beni), Kali Gandaki, 1,000 m., on tree, 12 Sept. 1954, *Stainton, Sykes & Williams 7818.* Tumlingtar, Sabhaya River, Chainpur district, 600 m., 12 Dec. 1961, *Norkett 8480.* Hinwan Khola, Chainpur, 660 m., on dead stick, 21 Dec. 1961, *Norkett 9024.*
Distribution: Worldwide.

HYDNACEAE

HERICIUM ERINACEUS (Fries) Pers., Mycol. Eur. 2 : 153 (1825).

Hydnum erinaceus Fries, Syst. Mycol. 1 : 407 (1821).

NEPAL: Above Sauwala Khola, 3,300 m., on *Quercus* in thick forest, 15 Sept. 1954, *Stainton, Sykes & Williams 4415.* Chimgaon, Kali Gandaki, 3,300 m., 14 Sept. 1954, *Stainton, Sykes & Williams 7821.*
Distribution: America, Europe, India, Japan, China.

HYDNELLUM ZONATUM forma VESPERTILIO (Berk.) Coker & Beers, Stipitate Hydnums of Eastern U.S. : 80 (1951).

Hydum vespertilio Berk. in Hook., Journ. Bot. 6 : 167 (1854).

NEPAL: Taglung, Kali Gandaki, 3,500 m., 22 Sept. 1954, *Stainton, Sykes & Williams 7991.*
Distribution: America, Europe, India.

POLYPORACEAE

AMAURODERMA RUGOSUM (Blume & Nees) Torrend in Broteria, Ser. Bot. 18 : 127 (1920).

Polyporus rugosus Blume & Nees in Nov. Act. Phys.-Med. Acad. Caes. Leop.-Car. 13 : 21, t. 7 (1826).

NEPAL: Dhankuta Province, below Sanghu, on roots of bamboo, 1,800 m., 27 Feb. 1962, *Norkett 10233.*
Distribution: Mostly tropical; Madagascar, India, Ceylon, Java, Philippines.

GANODERMA APPLANATUM (Pers.) Patouill. in Bull. Soc. Mycol Fr. 5 : 67 (1889).—Humphr. & Lewis in Philipp. Journ. Sci. 45 : 514 (1931).

Polyporus fomentarius var. *applanatus* Pers., Mycol. Eur. 2 : 80 (1825).
Polyporus applanatus (Pers.) Wallr., Fl. Crypt. Germ. 2 : 591 (1833).

NEPAL: Bakhri Kharka, north of Pokhara, 1,800 m., on rotten tree trunk, 24 April 1954, *Stainton, Sykes & Williams 5060.* Taglung, Kali Gandaki, 3,300 m., 19 Oct. 1954, *Stainton, Sykes & Williams 8198.* Dharan Bazar, Terai forest, south of Gopa Gurkha Camp, 250 m., on old tree, 27 Feb. 1962, *Norkett 10234.*
Distribution: Worldwide.

GANODERMA LUCIDUM (Fries) Karst. in Rev. Mycol. 3 (9) : 17 (1881).

Polyporus lucidus Fries, Syst. Mycol. 1 : 353 (1821).

NEPAL: Bakhri Kharka, north of Pokhara, 2,000 m., on rotten tree trunk, 25 April 1954, *Stainton, Sykes & Williams 5075.*
Distribution: Worldwide

FOMES PECTINATUS (Klotzsch) Gill., Hyménomycètes : 686 (1874).

Polyporus pectinatus Klotzsch in Linnaea 8 : 485 (1833).

NEPAL: Between Bakhri Kharka and Rambrong, 2,300 m., on rotten tree trunk, 26 Apr. 1954, *Stainton, Sykes & Williams 5081.*
Distribution: America, Europe, India, Australia, Philippines.

FOMES MARGINATUS (Fries) Gill., Hyménomycètes : 683 (1874).

Polyporus marginatus Fries, Syst. Mycol. 1 : 372 (1821).

NEPAL: Taglung, Kali Gandaki, 3,300 m., on forest tree, 11 July 1954, *Stainton, Sykes & Williams* 1751. Also at 3,500 m., 22 Sept. 1954, *Stainton, Sykes & Williams 7992.*
Distribution: America, Europe, India, Nepal, China, Japan.

POLYPORUS ARCULARIUS Fries, Syst. Mycol. 1 : 342 (1821).

Polyporellus arcularius (Fries) Pilát in Kav. & Pilát, Atlas Champ. 3 : 75, t. 30–31, fig. 18 (1936).

var. ARCULARIUS.

NEPAL: Midam Khola, Chisankhu, 660 m., 4 May 1954, *Stainton, Sykes & Williams 5210.* Kabre, Kali Gandaki, 2,000 m., 13 June 1954, *Stainton, Sykes & Williams 5742.* Dhankuta Province, Chainpur district, Tumlingtar, 600 m., on dead trunk, 13 Dec. 1961, *Norkett 8109 B; 8815 A;* and on 14 Dec. 1961, *Norkett 8107 B.*
Distribution: Worldwide; previously recorded from Nepal.

var. STRIGOSUS Bourd. & Galz., Hymenomyc. Fr. : 532 (1928).

NEPAL: Chipli, North of Pokhara, 2,600 m., on rotten tree trunk, 18 Apr. 1954, *Stainton, Sykes & Williams 4882.*
Distribution: Worldwide.
Distinguished by its marginal hairs.

POLYPORUS PARGAMENUS Fries, Epicrisis Syst. Mycol. : 480 (1838).—Overh., Polyp. U.S., Alaska & Canada : 336 (1953).

NEPAL: Sanghu, Milke Danda Forest, 2,900 m., on old dead tree, 16 Nov. 1961, *Norkett* 7129.

Distribution: Widespread in temperate and tropical regions.

The material is in good condition but not sporing. There is much confusion over the use of this name, *P. biformis* Klotsch and *P. cervinus* Fries. It is hoped to make a more critical study of the problem shortly. Meanwhile Overholt's interpretation of *P. pargamenus* is adopted.

POLYPORUS CORRUGATUS Pers. apud Gaud. in Freyc., Voy. aut. Monde Uranie & Physicienne, Bot. : 172 (1826).

Earliella corrugata (Pers.) Murrill in Bull. Torrey Bot. Cl. 34 : 468 (1907).
Polystictus persoonii Cooke in Grevillea 14 : 85 (1886).
Daedalea sanguinea Klotsch in Linnaea 8 : 481 (1833).

NEPAL: Chainpur district, Tumlingtar, Dhankuta Province, 600 m., on dead tree, 13 Dec. 1961, *Norkett 8109 E.*

Distribution: West Indies, India, Nepal, East Indies and throughout most of the tropics.

POLYPORUS PICIPES Fries, Epicrisis Syst. Mycol. : 440 (1838).—Overh., Polyp. U.S., Alaska & Canada : 262 (1953).

Polyporellus picipes (Fries) Karst. in Bidr. Känn. Finl. Natur. & Folk 37 : 31 (1882).—Pilát in Kav. & Pilát, Atlas Champ. 3 : 99, t. 44 fig. 1–3, t. 46 fig. b, fig. 24, p. 105 fig. B (1937).

NEPAL: Ghar Khola, 3,100 m., on dead trunk, 15 June 1954, *Stainton, Sykes & Williams 5769.* Arun Valley, Kasuwa Khola, 2,800 m., 11 Sept. 1956, *Stainton 1624.*

Distribution: Worldwide.

POLYPORUS SQUAMOSUS Fries, Syst. Mycol. 1 : 343 (1821).

NEPAL: Rambrong ridge, north of Pokhara, 3,300 m., on rotten tree trunk, 27 Apr. 1954, *Stainton, Sykes & Williams 5103.*

Distribution: Worldwide.

POLYPORUS SULPHUREUS Fries, Syst. Mycol. 1 : 357 (1821).

Grifola sulphurea (Fries) Pilát in Beih. Bot. Centralbl. 52 (B) : 39 (1934).
Laetiporus sulphureus (Fries) Bondartz. & Sing. in Ann. Mycol. 39 : 51 (1941).

NEPAL: Chimgaon, Kali Gandaki, 3,500 m., 14 Sept. 1954, *Stainton, Sykes & Williams 7828.* Arun Valley, Kasuwa Khola, 2,800 m., on tree in forest, 11 Sept. 1956, *Stainton 1621.*

Distribution: Worldwide; previously recorded from Nepal.

POLYPORUS ZONALIS Berk. in Ann. & Mag. Nat. Hist. 10 : 375, t. 10 fig. 5 (1843).

NEPAL: Karelung, Madi Khola, 660 m., on rotten branch, 23 June 1954, *Stainton, Sykes & Williams 5911.*

Distribution: tropical and semi-tropical; Central and South America, Cuba, India, Indonesia, China, Australia.

Resembles the type but is a little thicker. Spores globose and no cystidia.

POLYSTICTUS AFFINIS (Blume & Nees) Fries in Nov. Act. Soc. Sci. Upsal., ser. 3, 1 : 75 (1851).

Polyporus affinis Blume & Nees in Nov. Act. Phys.-Med. Acad. Caes. Leop.-Car. 13 : 18, t. 4 (1826).
Microporus affinis (Nees) Kuntze, Revis. Gen. Pl. 3 (2) : 495 (1898).

NEPAL: Arun Valley, Sashaya Khola, 660 m., on tree trunk in forest, 4 Sept. 1956, *Stainton 1578*. Dharan Bazar, Terai Forest, south of Gopa Gurkha Camp, 250 m., 27 Feb. 1962, *Norkett 10224*.

Distribution: widespread in tropical and subtropical regions; previously recorded from Nepal.

POLYSTICTUS CINNAMOMEUS (Gray) Sacc., Syll. Fung. 6 : 210 (1888).

Strilia cinnamomea Gray, Nat. Arrang. Brit. Pl. 1 : 645 (1821).
Polyporus cinnamomeus (Gray) Fries, Epicrisis Syst. Mycol. : 468 (1838).—Overh., Polyp. U.S., Alaska & Canada : 386 (1953).
Coltricia cinnamomea (Gray) Murrill in Bull. Torrey Bot. Cl. 31: 343 (1904).

NEPAL: Taglung, Kali Gandaki, 3,500 m., in wood, 22 Sept. 1954, *Stainton, Sykes & Williams 7991*.

Distribution: Worldwide; previously recorded from Nepal.

Very close to *P. perennis* but distinguished by its more uniform and silkier cap.

POLYSTICTUS HIRSUTUS (Fries) Fries in Nov. Act. Soc. Sci. Upsal., ser. 3, 1 : 86 (1851).

Polyporus hirsutus Fries, Syst. Mycol. 1 : 367 (1821).
Coriolus hirsutus (Fries) Quél., Enchir. Fung. : 175 (1886).—Bourd. & Galz., Hyménomyc. Fr. : 561 (1928).

NEPAL: Dhankuta Province, Milke Danda Forest, 260 m., 29 Nov. 1961, *Norkett 8307 A*.

Distribution: Worldwide.

POLYSTICTUS PERULA (Fries) Fries in Nov. Act. Soc. Sci. Upsal., ser. 3, 1 : 73 (1851).

Polyporus perula Fries, Syst. Mycol. 1 : 349 (1821).
Polyporus xanthopus Fries, Syst. Mycol. 1 : 350 (1821).
Polystictus xanthopus (Fries) Fries in Nov. Act. Soc. Sci. Upsal., ser. 3, 1 : 74 (1851).
Microporus perula (Fries) Hariot in Bull. Soc. Mycol. Fr. 7 : 206 (1891).

NEPAL: Rupakot Tal, 800 m., on rotten branch, 5 May 1954, *Stainton, Sykes & Williams 5233*. Arun Valley, Hinwan Khola, 800 m., on rotten log, 4 Sept. 1956, *Stainton 1533.* Sanghu, 3,000 m., on tree stump, 2 Oct. 1961, *Norkett 5540.* Chainpur district, Tumlingtar, 600 m., 13 Dec. 1961, *Norkett 8109 C.*

Distribution: Widespread in tropical and sub-tropical areas; previously recorded from Nepal.

POLYSTICTUS SANGUINEUS (Fries) Fries in Nov. Act. Soc. Sci. Upsal., ser. 3, 1 : 75 (1851).

Polyporus sanguineus Fries, Syst. Mycol. 1 : 371 (1821).
Pycnoporus sanguineus (Fries) Murrill in Bull. Torrey Bot. Cl. 31 : 421 (1904).

NEPAL: Midam Khola, Chisankhu, 660 m., 4 May 1954, *Stainton, Sykes & Williams 5218.* Midam Khola, Karelung, 600 m., 23 June 1954, *Stainton, Sykes & Williams 5910.* Kusma, 660 m., 2 Nov. 1954, *Stainton, Sykes & Williams 9270.* Sanghu, 3,000 m., 6 Oct. 1961, *Norkett 5709.*

Distribution: Mostly tropical and sub-tropical.

The Nepal material is thin and smooth and conforms with *P. sanguineus. P. cinnabarinus* Fries, at one time considered to be a synonym, has been shown to be distinct on the basis of cultural interfertility tests (McKay in Mycologia, 51 : 465–73 (1959)).

POLYSTICTUS SUBAFFINIS Lloyd, Mycol. Not. 40 : 550, fig. 755 (1916).

NEPAL: Surauti Khola, 660 m., on dead bamboo, 12 Aug. 1954, *Stainton, Sykes & Williams 6869.*

Distribution: Japan, Java, Madagascar.

The present collection appears to agree completely with Lloyd's species as he figured it from Umemura's Japanese specimen, but it is doubtful whether this species is distinct from *Polystictus affinis* (Fries) Fries.

POLYSTICTUS TABACINUS (Mont.) Sacc., Syll. Fung 6 : 280 (1888).

Polyporus tabacinus Mont. in Ann. Sci. Nat., Ser. 2, Bot. 3 : 349 (1835).

NEPAL: Siklis, north of Pokhara, 2,100 m., on rotten tree trunk, 22 Apr. 1954, *Stainton, Sykes & Williams 4974.* Gurjagaon, 3,000 m., on dead tree, 25 Sept. 1961, *Norkett 5481.* Milke Danda Forest, 3,000 m., on old dead tree, 16 Nov. 1961, *Norkett 7127.*

Distribution: South America, Africa, India, East Indies, China, Australasia.

9–10 pores per mm., setae subulate, dark brown. This species differs from *P. iodinus* in having smaller pores.

POLYSTICTUS TEPHROLEUCUS (Berk.) Sacc., Syll. Fung. 6 : 275 (1888).

Trametes tephroleuca Berk. in Hook., Journ. Bot. 6 : 165 (1854).
Coriolus tephroleucus (Berk.) Bondartz., Trutov. Ghrib. Evr. Chasti S.S.S.R. & Kavk. : 492, fig. 126 (1953).
Coriolus favoliporus Pilát in Bull. Soc. Mycol. Fr. 52 : 313, t. 3 figs. 3–4 (1937).
Trametes favolipora (Pilát) Pilát in Kav. & Pilát, Atlas Champ. 3 : 267, t. 182, fig. 105 (1939).

NEPAL: Lulo Khola, 16 Sept. 1952, *Polunin, Sykes & Williams 3448*. Near Lumsum, 2,300 m., on dead tree stump, 24 Oct. 1954, *Stainton, Sykes & Williams 9137*.

Distribution: Asia: Kazakstan, India and East Nepal.

Fine specimens but the pores in *Stainton, Sykes & Williams 9137* are mostly discoloured owing to a mycelial growth over the hymenium.

POLYSTICTUS VERSATILIS (Berk.) Fries in Nov. Act. Soc. Sci. Upsal., Ser. 3, 1 : 92 (1851).

Trametes versatilis Berk. in Lond. Journ. Bot. 1 : 150 (1842).
Polyporus versatilis (Berk.) Romell in Bih. K. Svensk. Vet. -Akad. Handl. 26, (3, 16) : 35 (1901).—Lloyd, Mycol. Not. 50 : 703, figs. 1049–50 (1917).—Overh., Polyp. U.S., Alaska & Canada: 325 (1953).

NEPAL: Ghar Khola, 2,600 m., 3 May 1954, *Stainton, Sykes & Williams 5444*. Maikot, 2,600 m., on stump, 4 July 1954, *Stainton, Sykes & Williams 3363*. Tumlingtar, Chainpur, 600 m., on old tree in ravine, 9 Dec. 1961, *Norkett 8693*. Dharan Bazar, Terai forest, south of Gopa Gurkha Camp, 230 m., 27 Feb. 1962, *Norkett 10232*.

Distribution: America, Madagascar, India, Malaya, Indonesia, Japan, China.

POLYSTICTUS VERSICOLOR (Fries) Fries in Nov. Act. Soc. Sci. Upsal., Ser. 3, 1 : 86 (1851).

Polyporus versicolor Fries, Syst. Mycol. 1 : 368 (1821).
Coriolus versicolor (Fries) Quél., Enchir. Fung. : 175 (1886).

NEPAL: Ranipauwa, Kali Gandaki, 1,000 m., 3 Sept. 1954, *Stainton, Sykes & Williams 7637*. Lete, Kali Gandaki, 2,800 m., 17 Sept. 1954, *Stainton, Sykes & Williams 7893*. Bakhri Kharka, Pokhara, 2,000 m., 25 Apr. 1954, *Stainton, Sykes & Williams 5073*. Arun Valley, Hatiar, 2,600 m., 21 Aug. 1956, *Stainton 1412*. Taplejung, above Sanghu, Milke Danda Forest, 3,000 m., 16 Nov. 1961, *Norkett 7124 A*. Mewa Khola, 2,700 m., 23 Jan. 1962, *Norkett 9345* and *9345 A*.

Distribution: Worldwide; previously reported from Nepal.

DAEDALEA UNICOLOR Fries, Syst. Mycol. 1 : 336 (1821).—Overh., Polyp. U.S., Alaska & Canada : 125 (1953).

Coriolus unicolor (Fries) Patouill., Ess. Tax. Fam. & Genr. Hyménomyc. : 94 (1900).

NEPAL: Sanghu, 3,000 m., 1 Nov. 1961, *Norkett 6728*.

Distribution: America, Europe, North Africa, China, Australia.

TRAMETES CERVINA (Schwein.) Bresad. in Ann. Mycol. 1 : 81 (1903).

Boletus cervinus Schwein. in Schrift. Naturf. Ges. Leipz. 1 : 96 (1822).
Coriolus cervinus (Schwein.) Bondartz., Trutov. Ghrib. Evr. Chasti S.S.S.R. & Kavk. : 493, fig. 127 (1953).
Polyporus biformis sensu Berk. in Ann. & Mag. Nat. Hist. 3 : 392 (1839), non Klotzsch.

NEPAL: Ulleri, north of Kusma, Kali Gandaki, 2,600 m., on tree in wood, 1 Nov. 1954, *Stainton, Sykes & Williams 8275*.

Distribution: Europe, Russia, India, Ceylon, China, Australia.

For nomenclature of this fungus see note under *Polyporus pargamenus* (p. 123).

TRAMETES GIBBOSA (Fries) Fries, Epicrisis Syst. Mycol. : 492 (1838).

Daedalea gibbosa Fries, Syst. Mycol. 1 : 338 (1821).
Pseudotrametes gibbosa (Fries) Bondartz. & Sing. in Ann. Mycol. 39 : 60 (1941).

NEPAL: Siklis, north of Pokhara, 21 Apr. 1954, *Stainton, Sykes & Williams 4957*.

Distribution: Europe, Africa, India, China.

LENZITES BETULINA (Fries) Fries, Epicrisis Syst. Mycol. : 405 (1838).

Daedalea betulina Fries, Syst. Mycol. 1 : 333 (1821).
Trametes betulina (Fries) Pilát in Kav. & Pilát, Atlas Champ. Eur. 3 : 327, t. 220, fig. 142 (1940).

NEPAL: Arun Valley, Hatiar, 2,600 m., on tree trunk, 21 Aug. 1956, *Stainton 1412*. Siklis, north of Pokhara, 2,500 m., on rotten tree trunk, 19 Apr. 1954, *Stainton, Sykes & Williams 4926*.

Distribution: Worldwide.

LENZITES PALISOTII (Fries) Fries, Epicrisis Syst. Mycol. : 404 (1838).

Daedalea palisotii Fries, Syst. Mycol. 1 : 335 (1821) "*Palisoti*".
Daedalea applanata Klotzsch in Linnaea 8 : 481 (1833).
Lenzites repanda Fries, Epicrisis Syst. Mycol. : 404 (1838).
Lenzites applanata (Klotzsch) Fries, Epicrisis Syst. Mycol. : 404 (1838).

NEPAL: Arun Valley, Sabhaya Khola, 800 m., on tree trunk, 3 Sept. 1956, *Stainton 1576*. Dhankuta Province, Chainpur district, Tumlingtar, 600 m., on dead branch, 13 Dec. 1961, *Norkett 8109 A*.

Distribution: Widespread, especially in the southern hemisphere.

LENZITES SUBFERRUGINEA Berk. in Hook., Journ. Bot. 6 : 134 (1854).

Gloeophyllum subferrugineum (Berk.) Bondartz., Trutov. Ghrib. Evr. Chasti S.S.S.R. & Kavk. : 50 (1953).

NEPAL: Lete, Kali Gandaki Valley, 2,600 m., on rotten tree trunk, 12 June 1954, *Stainton, Sykes & Williams 5730*; same locality, 8 July 1954, *Stainton, Sykes & Williams 1639*. Taglung, Kali Gandaki, 27 Aug. 1954, *Stainton, Sykes & Williams 7494*.

Distribution: India, Nepal, Philippines, Japan.

No spores were found in any of the gatherings. *Stainton, Sykes & Williams 5730* has a grey cap, *1639* has grey cap with wide brown margin, and in *7494* the cap is entirely brown.

THELEPHORACEAE

CORTICIUM CAERULEUM (Pers.) Fries, Epicrisis Syst. Mycol. : 562 (1838).

Thelephora caerulea Pers., Mycol. Eur. 1 : 147 (1822).—Fries, Elench. Fung. 1 : 202 (1828).

NEPAL: Ganesh Himal, Ankhu Khola, 2,800 m., on bark in broad-leaved forest, 17 May 1962, *Stainton 3731*.
Distribution: America, Europe, India, Australia, Japan.

HYMENOCHAETE MOUGEOTII (Fries) Cooke in Grevillea 8 : 147 (1880).

Thelephora mougeotii Fries, Elench. Fung. 1 : 188 (1828).

NEPAL: Annapurna Himal, on branches of *Rhododendron campanulatum*, 30 Aug. 1954, *Stainton, Sykes & Williams 6641*. Rambrong, Lamjung Himal, on branch of *Betula utilis*, 7 July 1954, *Stainton, Sykes & Williams 6202*. Mewa Khola, 1,300 m., on dead wood, 1 Feb. 1962, *Norkett 9182*. Ganesh Himal, Ankhu Khola, 2,800 m., on bark in broad-leaved forest, 17 May 1962, *Stainton 3732*. Ganesh Himal, Mailung Khola, 4,000 m., 20 May 1962, *Stainton 3744*.
Distribution: Europe, India, Nepal, Australia, New Zealand, China.

HYMENOCHAETE RHEICOLOR (Mont.) Lév. in Ann. Sci. Nat., Ser. 3, Bot. 5 : 151 (1846).

Stereum rheicolor Mont. in Ann. Sci. Nat., Ser. 2, Bot. 18 : 23 (1842).
Stereum tenuissimum Berk. in Hook., Lond. Journ. Bot. 6 : 510 (1847).
Hymenochaete sallei Berk. & Curt. in Journ. Linn. Soc. Lond., Bot. 10 : 333 (1868).
Hymenochaete tenuissima Berk. apud Berk. & Curt. in Journ. Linn. Soc. Lond., Bot. 10 : 333 (1868) *nom. nud.*
Hymenochaete tenuissima (Berk.) Berk. & Broome in Journ. Linn. Soc. Lond., Bot. 14 : 67 (1873).
Stereum elegantissimum Spegazz. in An. Soc. Cient. Argent. 17 : 78 (1884).

NEPAL: Dhankuta Province, Taplejung district, Sanghu, 2,000 m., 17 Oct. 1961, *Norkett 5696 B*; same locality, 15 Nov. 1961, *Norkett 7112 C*.
Distribution: North and South America, Africa, West Indies, India.

HYMENOCHAETE RUBIGINOSA (Fries) Lév. in Ann. Sci. Nat., Ser. 3, Bot. 5 : 151 (1846).

Thelephora rubiginosa Fries, Syst. Mycol. 1 : 436 (1821).

NEPAL: Chainpur district, Tumlingtar, 600 m., on dead tree, 13 Dec. 1961, *Norkett 8109 D*; same locality, 16 Dec. 1961, *Norkett 8567*.
Distribution: Worldwide.

HYMENOCHAETE TABACINA (Fries) Lév. in Ann. Sci. Nat., Ser. 3, Bot. 5 : 152 (1846).

Thelephora tabacina Fries, Syst. Mycol. 1 : 437 (1821).
Stereum tabacinum (Fries) Fries, Epicrisis Syst. Mycol. : 550 (1838).

NEPAL: Annapurna Himal, on branches of *Rhododendron campanulatum*, 3 Aug. 1954, *Stainton, Sykes & Williams 6642*. Near Dogadi Khola, 4,300 m., on dead shrubs, 11 Aug. 1954, *Stainton, Sykes & Williams 3818*.

Distribution: Worldwide.

LOPHARIA CRASSA (Lév.) Boidin in Bull. Soc. Mycol. Fr. 74 : 479 (1958).

Thelephora crassa Lév. in Ann. Sci. Nat., Ser. 3, Bot. 2 : 209 (1844).
Stereum umbrinum Berk. & Curt. apud Berk. in Grevillea 1 : 164 (1873).
Hymenochaete vinosa Cooke in Grevillea 8 : 149 (1880).
Laxitextum crassum (Lév.) Lentz in U.S. Dept. Agric., Agric. Monogr. 24 : 20 (1955).

NEPAL: Dhankuta Province, Dhankuta, near Mahe, 1,300 m., 20 Sept. 1961, *Norkett 5157 C*. Sombu, 1,600 m., 23 Sept. 1961, *Norkett 5289*. Dhankuta Province, Taplejung district, Sanghu, 3,000 m., 3 Oct. 1961, *Norkett 5639 A*; same locality, 2,000 m., 15 Nov. 1961, *Norkett 7112 C*.

Distribution: America, Europe, Africa, India, Australia, New Zealand.

STEREUM OSTREA (Fries) Fries, Epicrisis Syst. Mycol. : 547 (1838).

Thelephora fasciata Schwein. in Schrift. Naturf. Ges. Leipz. 1 : 106 (1822).
Thelephora ostrea Fries, Elench. Fung. 1 : 175 (1828).
Thelephora versicolor var. *fasciata* (Schwein.) Fries, loc. cit.
Stereum fasciatum (Schwein.) Fries, Epicrisis Syst. Mycol. : 546 (1838).

NEPAL: Arun Valley, Khandbari, 2,300 m., on rotting log, 31 Aug. 1956, *Stainton 1472*.

Distribution: widespread; previously recorded from the Himalayas.

Since Fries did not treat *Thelephora fasciata* Schwein. as a separate species in his *Elenchus*, which is part of the starting-point for the *Fungi caeteri*, the epithet of his *T. ostrea* must be adopted when the two names are regarded as synonyms.

STEREUM HIRSUTUM (Fries) Gray, Nat. Arrang. Brit. Pl. 1 : 653 (1821).

Thelephora hirsuta Fries, Syst. Mycol. 1 : 439 (1821).

NEPAL: Chipli, north of Pokhara, 3,600 m., 18 Apr. 1954, *Stainton, Sykes & Williams 4885*. Arun Valley, Hatiar, 2,600 m., on rotting log, 21 Aug. 1956, *Stainton 1410*. Arun Valley, Sibrung, 27 Aug. 1956, *Stainton 1447*. Kasuwa Khola, 3,300 m., 12 Sept. 1956, *Stainton 1637*. Milke Danda Forest, 3,000 m., 16 Nov. 1961, *Norkett 7125*. Sanghu, 2,300 m., 23 Nov. 1961, *Norkett 8196*.

Distribution: Worldwide.

STEREUM ROSEO-CARNEUM (Schwein.) Fries, Acta Soc. Sci. Upsala, Ser. 3, 1 : 112 (1851).

Thelephora roseo-carnea Schwein. in Schrift. Naturf. Ges. Leipz. 1 : 107 (1822).
Laxitextum roseo-carneum (Schwein.) Lentz in U.S. Dept. Agric., Agric. Monogr. 24 : 22 (1955).

NEPAL: Dhankuta Province, Taplejung district, Sanghu 2,060 m., 15 Nov. 1961, *Norkett 7112 B.*

Distribution: North and South America, Japan, China.

The fructifications are pinkish buff, resupinate on twigs; the paraphyses have branching tips; spores 8 × 4·5 μ.

STEREUM SANGUINOLENTUM (Fries) Fries, Epicrisis Syst. Mycol. : 549 (1838).

Thelephora sanguinolenta Fries, Syst. Mycol. 1 : 440 (1821).

NEPAL: Gurjakhani, 3,160 m. on small branches, 30 July 1954, *Stainton, Sykes & Williams 3678.*

Distribution: North America, Europe, South Africa, Australia, New Zealand.

STEREUM SUBPILEATUM Berk. & Curt. apud Berk. in Hook., Journ. Bot. 1 : 238 (1849).—Lentz in U.S. Dept. Agric., Agric. Monogr. 24 : 36 (1955).

Stereum insigne Bresad. in Nuovo Giorn. Bot. Ital. 23 : 158 (1891).
Xylobolus subpileatus (Berk. & Curt.) Boidin in Rev. de Mycol. 23 : 336 (1958).—Lentz in Sydowia 14 : 118 (1960).

NEPAL: Bakhri Kharka, north of Pokhara, on rotten tree trunk, 24 Apr. 1954, *Stainton, Sykes & Williams 5059.* Milke Danda Forest, Dhankuta Province, 2,800 m., 2 Nov. 1961, *Norkett 6806 A*; same area, 3,000 m., 16 Nov. 1961, *Norkett 7124.*

Distribution: America, Europe, India, Indonesia, China, Japan.

Lentz and Boidin should be consulted for modern interpretations of this aggregate species.

STEREUM sp. cf. SULCATUM Burt apud Peck in New York State Mus. Annu. Rep. 54, 1, App. 1 : 154 (1901).

NEPAL: South of Gurjakhani, 3,600 m., on tree in *Abies* forest, 16 Aug. 1954, *Stainton, Sykes & Williams 3868.*

Large robust sporophores superficially like those of a large *S. princeps* (Jungh.) Lév. but having a tomentose sulcate pileus, coarse, more or less parallel skeletal hyphae intermingled with generative hyphae, and no acanthophyses as such, but merely some slightly granular cystidial hyphae. The spores, irregularly globose, smooth or very faintly punctate and amyloid, 4·5–6 μ diameter, resemble those of *S. sulcatum* Burt and those of *S. taxodii* Lentz & McKay (Mycologia 52 : 262 (1960)), two species recently transferred by H. L. Gross to his genus *Echinodontium* (Mycopath. & Mycol. Appl. 24 : 8, 11 (1964)). The Nepal fungus however differs in the absence of large encrusted cystidia and in the possession of large flabelliform reflexed pilei. In view of the large and conspicuous fructifications it would seem unlikely that this fungus has not been recorded previously. I therefore defer describing it as new to science.

THELEPHORA CARYOPHYLLAEA Fries, Syst. Mycol. 1 : 430 (1821).

Phylacteria caryophyllea Patouill., Hym. Eur. : 154 (1887), *nom. nud.*
Phylacteria caryophyllea (Fries) Patouill. ex Bourd. & Maire in Bull. Soc. Mycol. Fr. 36 : 76 (1920).

NEPAL: Taplejung district, above Sanghu, 2,000 m., amongst moss on earth, 12 Oct. 1961, *Norkett 5927 A.*

Distribution: Worldwide.

VARARIA RHODOSPORA (Wakef.) G. H. Cunn. in Proc. Linn. Soc. N.S.W. 77 : 291 (1953); in N.Z. Dept. Sci. Industr. Res. Bull. 145 : 100 (1963).

Stereum duriusculum sensu Bresad. in Ann. Mycol. 6 : 43 (1908), non Berk. & Broome.
Asterostromella rhodospora Wakef. in Kew Bull. 1915 : 372 (1915).—Banergee in Journ. Ind. Bot. Soc. 14 : 45 (1935).
Asterostromella dura Bourd. & Galz. apud Bourd. & Maire in Bull. Soc. Mycol. Fr. 36 : 74 (1920).
Dichostereum durum (Bourd. & Galz.) Pilát in Ann. Mycol. 24 : 223 (1926).

NEPAL: Sanghu, 820 m., 9 Nov. 1961, *Norkett 7324.*

Distribution: America, Europe, Africa, India, Japan, Australia, New Zealand.

The species was recorded from India by Banergee. The Nepal collection consists of tough, resupinate thalli covering earth beneath tree roots, about 2–3 mm. thick, mid-brown, of stratose context. Only a few basidia were observed embedded in the dichophysoid paraphyses; spores globose, straw-coloured, echinulate, 5–6 μ diameter; context hyphae brown, dendroidly and dichotomously branched, most markedly and densely in the hymenial layer, where they form the brown dendrophyses and dichophyses; intermingled with them are finer, readily stained hyphae. Rogers & Jackson (Farlowia 1 : 309 (1943)), treat *Dichostereum durum* as a synonym of *Vararia pallescens* (Schwein.) Rog. & Jacks. Type material of *Thelephora pallescens* Schwein. in the B.M. Herbarium differs in several particulars, notably its finer context, and would appear to be not merely a different growth-form, as these authors suggested, but a distinct species.

CLAVARIACEAE

CLAVULINA MUSSOORIENSIS Corner, Thind & Dev in Trans. Brit. Mycol. Soc. 41 : 204 t. 8 fig. 3, text-fig. 1 (1958).

NEPAL: Near Gurjakhani, 2,800 m., among grass on open slope, 28 July 1954, *Stainton, Sykes & Williams 3670.*

Distribution: India.

(E.J.H.C.)

Clavulina alta Corner, sp. nov.

Receptacula ad 11 cm. alta, alba, sicco luride flava; stipite 2–6 cm. × 3–8 mm., bene evoluto; ramulis inferioribus polychotomis v. applanato-multifidis, superioribus 1 mm. latis dichotomis v. cristatis, axillis inferioribus 3–6 mm. latis. Sporae 9·5–14 × 7·5–9 μ, subglobosae, lacrymiformes v. pyriformes, apiculo 1 μ longo. Basidia 6·5–7·5 μ lata, bispora. Hymenium incrassatum; cystidiis nullis; hyphis subhymenialibus 6–17 μ latis, fere pseudoparenchymaticis. Hyphae 3–12 μ latae, fibulatae, tenue tunicatae, cellulis potius brevibus.

NEPAL: Chimgaon, north of Tukucha, Kali Gandaki, 3,500 m., on ground beneath conifers, 14 Sept. 1954, *Stainton, Sykes & Williams 7825*. (Herb. Mus. Brit. holotype).

This resembles *C. rugosa* (Fries) Schroet. in the large spores and wide subhymenial hyphae, and *C. cristata* var. *coralloides* Corner in the form of the fruit-body. I have not seen such a distinct form before, and the spores are constantly rather narrow for their length.

(E.J.H.C.)

Lentaria macrospora Corner, sp. nov.

Receptacula ad 10 cm. alta, gregaria v. caespitosa, carneoflavida; stipite ad 25 × 2–4 mm., axillas inferiores polychotomas versus plus minus dilatato; ramulis superioribus teretibus dichotomis strictis ascendentibus, 1–2 mm. latis. Sporae 20–30 × 3·7–5·5 μ, hyalinae, cylindricae, v. subclavatae, saepe curvatae v. sigmoideae, et allantiformes, tenue tunicatae, haud amyloideae. Basidia ad 45 × 9–10·5 μ; sterigmatibus 2–4, 7–8 μ longis. Hymenium incrassatum; cystidiis nullis. Hyphae 2·5–7 μ latae, fibulatae, tunicis ad 0·5 μ vix incrassatis; in mycelio 2·5–4 μ latae, fibulatae, monomiticae, tunicis tenacibus sed vix incrassatis, passim partibus ampulliformibus ad 15 μ latis inflatae, crystallis sphaeroideis 2–7 μ latis inter hyphas numerosis.

NEPAL: Tamur Valley, Ghunsa, east of Walungchung Gola, 4,300 m., on ground under conifers, 27 July 1956, *Stainton 1145*. (Herb. Mus. Brit. holotype).

This resembles in shape and colour the common tropical *L. surculus* (Berk.) Corner but the spores are much longer, the hyphal walls are scarcely thickened, and the habitat seems to be humicolous. Many basidia had 1–3 long spiculiform sterigmata, but they may have been abnormal and formed after collection.

(E.J.H.C.)

RAMARIA aff. BOTRYTOIDES (Peck) Corner, Monogr. Clavaria, Ann. of Bot., Mem. 1 : 562 (1950).

Clavaria botrytoides Peck in N.Y. State Mus., Mus. Bull. 94 : 49, t. 93 figs. 5–7 (1905).

NEPAL: Taglung, south of Tukucha, Kali Gandaki, 3,300 m., on ground beneath trees, 11 July 1954, *Stainton, Sykes & Williams 1691*.

Distribution (of *Ramaria botrytoides*): America, southern parts of Australia and Tasmania, Japan; when the species is interpreted in a wide sense.

(E.J.H.C.)

RAMARIA SUECICA (Fries) Donk in Med. Bot. Mus. Herb. Rijks Univ. Utrecht 9 : 105 (1933).—Corner, Monogr. Clavaria, Ann. of Bot., Mem. 1 : 629 (1950).

Clavaria suecica Fries, Syst. Mycol. 1 : 469 (1821).
Clavariella suecica (Fries) Karst. in Bidr. Känn. Finl. Natur. & Folk 37 : 187 (1882).

NEPAL: South of Gurjakhani, 3,300 m., on damp shady forest bank, 18 Aug. 1954, *Stainton, Sykes & Williams 3902.*

Distribution: Europe, China, Canada, Northern U.S.A.

(E.J.H.C.)

RAMARIA FLACCIDA (Fries) Ricken, Vadem. Pilzfr.: 254 (1918).

Clavaria flaccida Fries, Syst. Mycol. 1 : 471 (1821).

NEPAL: Taglung, south of Tukucha, Kali Gandaki, 3,300 m., in pine wood, 22 Sept. 1954, *Stainton, Sykes & Williams 7971.*

Distribution: America, Europe, South Africa, Australia, China, Japan.

(E.J.H.C.)

RAMARIA OBTUSISSIMA (Peck) Corner, Monogr. Clavaria, Ann. of Bot., Mem. 1 : 609 (1950).

Clavaria obtusissima Peck in N.Y. State Mus., Mus. Bull. 167 : 39 (1913).

NEPAL: Taglung, south of Tukucha, Kali Gandkai, 3,000 m., beneath conifers, 12 July 1954, *Stainton, Sykes & Williams 1790.*

Distribution: U.S.A. and Canada.

The pink form is represented.

(E.J.H.C.)

RAMARIA SUBAURANTIACA Corner apud Balf.-Browne in Bull. Brit. Mus. (Nat. Hist.), Bot. 1 : 200 (1955).

NEPAL: North of Barse, 4,000 m., on *Abies* stump, 14 Aug. 1954, *Stainton, Sykes & Williams 3851.*

Distribution: Tibet.

Spores 10·5–15 × 5–6 μ, rather coarsely subverrucose. No clamps.

(E.J.H.C.)

CYPHELLACEAE

Chromocyphella bryophyticola Balfour-Browne, sp. nov.

Fungus cupulatus, cupulis sessilis, levis, griseo-albis, 0·5 mm. diam.; contextis tenuis, mollis, 15 μ latis ex hyphis elongatis efformatis; hymenio levo, brunneo; basidiis cylindricis, 15–16 × 4–5 μ; sporis globosis, 5–7 μ diam., brunneis, punctatis.

NEPAL: Sanghu, 1,800 m., on moss, *Pterobryopsis*, and on an intermingled liverwort, on shady rock, 8 Nov. 1961, *Norkett 7292.* (Herb. Mus. Brit. holotype).

This fungus is not unlike *Cyphella chromospora* Patouill. (Tab. Anal. Fung. 1 : 19, fig. 32 (1883)), but the spores are larger. It differs from *Chromocyphella burtii* Bridge Cooke (Sydowia, Beiheft 4 : 137 (1961)), in its smaller basidia and its definitely punctate spores.

This appears to be the first record of a " Cyphella " in the Himalayan region.

SCLERODERMATEACEAE

SCLERODERMA AURANTIUM Pers., Syn. Meth. Fung. : 153 (1801).

NEPAL: Mathand, near Pokhara, 1,160 m., on shady bank, 22 June 1954, *Stainton, Sykes & Williams 5851.*

Distribution: Worldwide.

Spores 8–10 μ, reticulated.

LYCOPERDACEAE

BOVISTA sp. cf. BOVISTOIDES (Cooke & Massee) Ahmad, Gasteromycetes W. Pakistan, Publ. Dept. Bot. Univ. Panjab 11 : 16 (1952).

Mycenastrum bovistoides Cooke & Massee in Grevillea 16 : 26 (1887).

NEPAL: Above Dogadi Khola, amongst short grass on exposed slope, 21 June 1954, *Stainton, Sykes & Williams 3211.*

Distribution (of *Bovista bovistoides*): India.

The Nepal collection appears to be very close to this species but has very slightly warted spores, whereas Ahmad described them as smooth. The capillitium threads agree in being chestnut brown and unpitted.

BOVISTA ECHINELLA Patouill. in Bull. Soc. Mycol. Fr. 7 : 165 (1891).

Bovistella echinella (Patouill.) Lloyd, Mycol. Notes 23 : 286, t. 89 figs. 1–2 (1906).
Lycoperdon echinella (Patouill.) Ahmad in Journ. Ind. Bot. Soc. 20 : 138 (1941).

NEPAL: Chainpur district, Tumlingtar, 600 m., on earth near base of cliff of Sabhaya River, 9 Dec. 1961, *Norkett 8682 A.*

Distribution: North and South America, Jamaica, Europe, Pakistan.

The spores are smooth, not echinulate as described by Patouillard, but show " lines " beneath the outer membrane which at a certain focus appear like spines; the pedicels are mostly 6 μ long.

GEASTRUM FIMBRIATUM (Fries) E. Fisch. in Engl. & Prantl, Nat. Pflanzenfam., 2 Aufl., 7a : 73 (1933).

Geaster fimbriatus Fries, Syst. Mycol. 3 : 16 (1829).

NEPAL: Tukucha, Kali Gandaki, 3,600 m., 12 Oct. 1954, *Stainton, Sykes & Williams 8212.*

Distribution: America, Europe, Africa, India, Australia.

GEASTRUM HARIOTII (Lloyd) E. Fisch. in Engl. & Prantl, Nat. Pflanzenfam., 2 Aufl., 7a : 73 (1933).

Geaster hariotii Lloyd, Mycol. Not. 25 : 311, t. 99 figs. 7–9 (1907).

NEPAL: Tumlingtar, Sabhaya Khola, 600 m., on earth beneath bamboo, 20 Dec. 1961, *Norkett 9002*.

Distribution: South America, West Indies, Europe, Ceylon, Australia (according to Cunningham, v. below).

The eight specimens from Nepal resemble the descriptions of *Geastrum hariotii* very closely in being non-hygroscopic, in having a sessile endoperidium, dark, sulcate peristome and small, 3–3·5 μ diam., minutely verrucose spores. But the surface of the endoperidium is furfuraceous or granular rather than pitted as described by some authors (Cunningham, Gasteromycetes Austral. and N.Z. : 165 (1942)).

LYCOPERDON PYRIFORME Pers., Syn. Meth. Fung. : 148 (1801).

NEPAL: Tukucha, Kali Gandaki, 3,500 m., 12 Sept. 1954, *Stainton, Sykes & Williams 7806*.

Distribution: Worldwide.

FUNGI IMPERFECTI

SPHAEROPSIDACEAE

CONIOTHYRINA AGAVES (Durieu & Mont.) Petr. & Syd. in Beih. Rep. Spec. Nov. Regn. Veg. 42 : 322 (1927).

Phoma agaves Durieu & Mont. in Mont., Syll. Pl. Crypt.: 271 (1856).
Coniothyrium agaves (Durieu & Mont.) Sacc., Syll. Fung. 3 : 318 (1884).

NEPAL: Sanghu, 2,000 m., on Agave, 17 Nov. 1961, *Norkett 7154*; Sombu, 1,600 m., on *Agave*, 23 Sept. 1961, *Norkett 5313*.

Distribution: America, South Europe, Africa, India.

NECTRIOIDACEAE

ASCHERSONIA sp. cf. VIRIDANS (Berk. & Curt.) Patouill. in Bull. Soc. Mycol. Fr. 7 : 48 (1891).

Hypocrea viridans Berk. & Curt. in Journ. Linn. Soc. Lond., Bot. 10 : 376 (1868).
Aschersonia disciformis Patouill. in Bull. Soc. Mycol. Fr. 8 : 136 (1892).
Aschersonia viridula Sacc. in Ann. Mycol. 11 : 547 (1913).

NEPAL: Phewa Tal, 800 m., on leaves of *Castanopsis* sp., 8 May 1954, *Stainton, Sykes & Williams 5272 (a)*.

Distribution (of *A. viridans*): Central America (Trinidad, Vera Cruz, Cuba, Ecuador), Brazil, Mexico.

The Nepal fungus was growing on white fly. It differs from previous accounts in the greater number of pycnidia to each stromatic cushion, which is completely dotted over with the greenish ostioles; conidia 12–16 × 1·5–2 μ.

Another *Aschersonia* also was collected on *Castanopsis* leaves; this appears to be close to *A. caespiticia* Syd. (in Engl., Bot. Jahrb. 54 : 260 (1916)), but differs in the rough surface of the tubercles and its small basal cushions. Tilhar, 3 Nov. 1954, *Stainton, Sykes & Williams 9251* (*a*).

LEPTOSTROMATACEAE

MELASMIA SALICINA Tulasne frat., Sel. Fung. Carp. 3 : 119, t. 15 figs. 15–17 (1865).

NEPAL: East of Chalike Pahar, 4,160 m., on *Salix* sp., 25 Sept. 1954, *Stainton, Sykes & Williams 4587*.

Distribution: not previously collected in this part of the world but its perfect state, *Rhytisma salicinum* Fries, has been recorded from the Punjab.

MELANCONIACEAE

Mastigonetron americanum (Mont.) Balfour-Browne, comb. nov.

Pestalotia americana Mont. in Gay, Hist. Chile, Bot. 7 : 481 (1850).—Guba, Monogr. Monochaetia & Pestalotia : 268 (1961).

Seiridium liquidambaris Berk. & Curt. apud Berk. in Grevillea 2 : 154 (1874).

Mastigonetron fuscum Klebahn in Myc. Centralbl. 4 : 18, fig. 37–38 (1914).

Monochaetia liquidambaris (Berk. & Curt.) Guba, loc. cit. (1961), *nom. synon.*

NEPAL: Taplejung district, Sanghu, Tamrang Khola, 2,000 m., on dead twigs, 19 Oct. 1961, *Norkett 6319 A*.

Distribution: North and South America.

The acervuli, about 0·5 mm. in diameter, are scattered over the twigs and resemble lenticels in appearance. The conidia, 20–27 × 9–10·5 μ, are dark brown, unicellular, ovoid or ellipsoid, each with a hyaline apical appendage 30–40 × 2 μ, and a pedicel 12 × 2 μ, approximately.

The fungus agrees exactly with Klebahn's species and apparently also with the type of *P. americana* (in spite of Montagne's description of the conidia as biseptate) since Guba, loc. cit., states that " Montagne's drawings of the fungus and my study show dark colored 1-celled ellipsoid conidia ". The drawing mentioned is apparently unpublished.

In view of its unicellular conidia the species cannot be included in either *Monochaetia* or *Pestalotia*. As for *Seiridium* Nees & Henry, (Syst. Pilze : 18, t. 3 (1837)), arguments can be brought forward for retaining it as an earlier name for *Mastigonetron* if one regards as accurate the elder Nees's (Syst. Pilze & Schwämme : 22 (1816), t. 1 fig. 19 (1817)) description and drawing of unicellular appendaged conidia. This non-septate condition of the conidia was accepted by Berkeley & Curtis when they selected this genus for the fungus on *Liquidambar*. Alternatively, *Seiridium* can be regarded as an older name for *Monochaetia* if Fries's (Syst. Mycol. 3 : 473 (1832)) statement that his examination of Nees's material showed multiseptate conidia is taken as correct. The original collection appears to be lost but other collections since then and reputed to be the same species, i.e. *S. marginatum*, are invariably described as having a brown septate conidium with a transparent apical seta. The probable explanation for this discrepancy is that Nees chanced to examine and illustrate the unripe fungus, i.e. before the conidia became septate, while they were still unicellular, spindle-shaped and contained grey granular protoplasm. Fries, on the other hand, and all subsequent workers have described the mature fungus, which represents what is now generally regarded as typical *Monochaetia*. Taking this latter view, or better still treating *Seiridium* as a *nomen confusum*, this generic name cannot be used in place of *Mastigonetron* and therefore the correct name for the Nepal fungus becomes *Mastigonetron americanum*, as cited above.

STILBACEAE

ARTHOBOTRYUM NILGIRENSE Subram. in Proc. Ind. Acad. Sci., Sect. B, 46 : 324, fig. 1 (1957).

NEPAL: Chainpur, Tumlingtar, 660 m., on old bamboos, 15 Dec. 1961, *Norkett 8868.*

Distribution: Previous record and original description from bamboo, Sim's Park. Coonoor, Madras, 1956.

Podosporium himalensis Balfour-Browne, sp. nov. (Fig. 4).

Synnemata atrobrunnea numerosa et effusa ex hyphis parallelibus juxtapositis efformata. Conidia atrobrunnea, 1–12 septata, obclavata, leniter curvata et irregulariter disposita, 9–15 × 16–100 μ.

NEPAL: Lamjung Himal, 4,500 m., black woolly growth on branches of *Rhododendron campanulatum*, 14 July 1954, *Stainton, Sykes & Williams 6341.* (Herb. Mus. Brit., holotype).

The general form of the synnemata is similar to that described by Subramanian (Journ. Ind. Bot. Soc. 35 : 73 (1956)) for his *Prathoda saparva*; the conidia however are different and the conidiophores hardly distinct from the hyphae and not geniculate. The Nepal material resembles an extremely luxuriant form of *Podosporium rigidum* Schwein., originally described from Carolina. The hyphae are hormiscium-like and very probably any portion breaking away can regenerate fresh growth, independently of conidial reproduction.

STILBUM CINNABARRINUM Mont. in Ann. Sci. Nat., Ser. 2, Bot. 8 : 360 (1837).

Stilbum lateritium Berk. in Ann. Nat. Hist. 4 : 291, pl. 8 fig. 2 (1840).

NEPAL: Tumlingtar, by shore of Sabhaya Khola, 600 m., 11 Dec. 1961, *Norkett 8107 C.*

Distribution: North and South America, Cuba, Dominica, Africa, Nepal, India, Ceylon, Australia.

Pleonectria pseudotrichia (Schwein.) Wollenw. is its perfect form. The present collection occurs on unnamed bark and is very sparing.

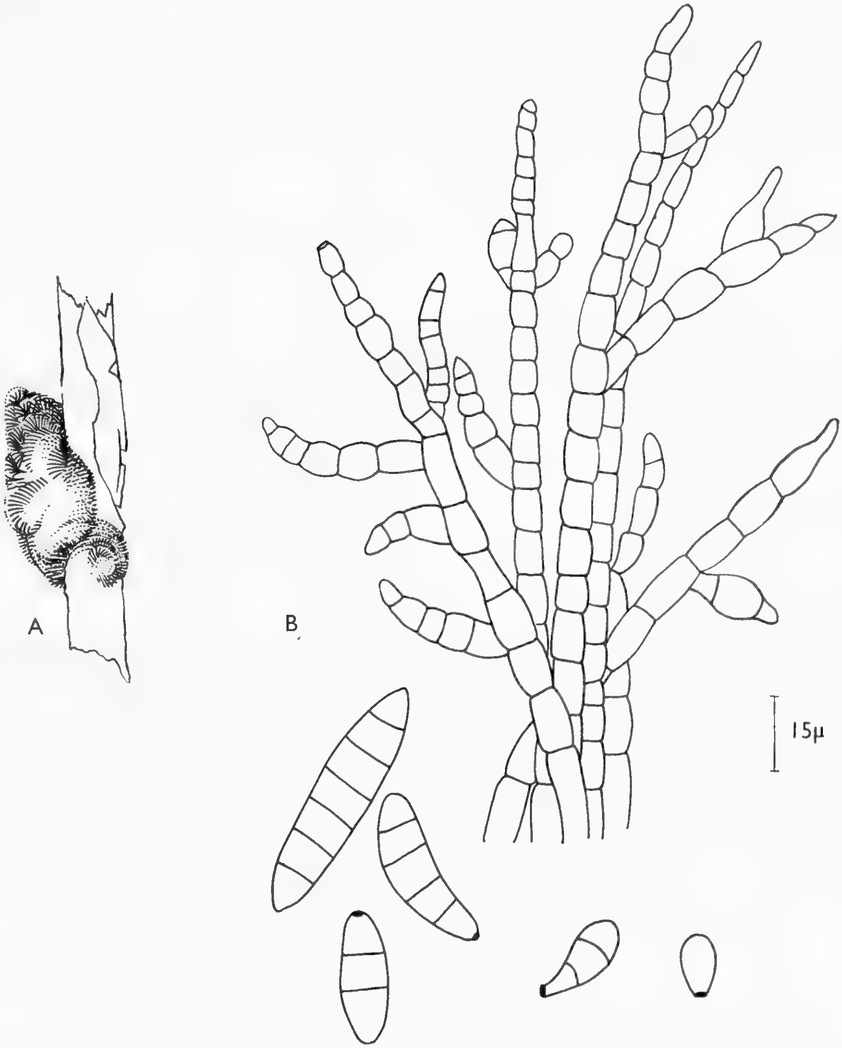

FIG. 4. *Podosporium himalensis* Balfour-Browne. A, general aspect; B, conidia and conidiophorous hyphae. *Stainton, Sykes & Williams 6341.*

STILBUM INCONSPICUUM Currey in Trans. Linn. Soc. Lond., Ser. 2, Bot. 1 : 129 (1876).

Stilbum kurzianum Cooke in Grevillea 16 : 71 (1888).

NEPAL: Sanghu, 2,000 m., 17 Nov. 1961, *Norkett 7153*.
Distribution: India.
On dead twigs of *Rosa* sp. Synnemata 3–4 mm. tall, pale orange soon becoming cinereous; conidia rod-shaped 7–9 × 3 μ.

TUBERCULARIACEAE

Epicoccum andropogonis (Rabenh.) Schol-Schwarz in Trans. Brit. Mycol. Soc. 42 : 171, t. 9 fig. 11 (1959).

Cerebella andropogonis Rabenh. in Bot. Zeit. 9 : 669 (1851).

Nepal: Bhadauri, near Pokhara, 2,000 m., on inflorescence of a grass, 1 Nov. 1954, *Stainton, Sykes & Williams 8326*.

Distribution: Worldwide but chiefly in the tropics and subtropics.

This genus has been revised recently by Langdon (Mycol. Commonw. Mycol. Inst. Papers, 61 : 1–18 (1955) under the name *Cerebella*), and by Schol-Schwarz (tom. cit. : 149–173).

Epicoccum purpurascens Schlechtend., Fl. Berol. 2 : 136 (1824).—Link in L., Sp. Pl., Ed. 4, 6 (2) : 108 (1825).

Epicoccum nigrum Link, loc. cit.—Schol-Schwarz in Trans. Brit. Mycol. Soc. 42 : 170 (1959).

Nepal: Argam, near Pokhara, 830 m., on leaves and stems of *Acrocephalus indicus* (Burm.) O. Kuntze, 10 Sept. 1954, *Stainton, Sykes & Williams 7146*.

Distribution: Worldwide.

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WILLIAM THOMAS STEARN Xref.

Pp. 143–173; 25 *Text-figures*; *Plates* 6–13

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By WILLIAM T. STEARN

SUMMARY

The family *Myrsinaceae* is represented in Jamaica by three genera, *Ardisia, Wallenia* and *Myrsine* (including *Rapanea*). Recognition of the species presents especial difficulty in *Wallenia*, which is dioecious; some taxa are known only from specimens with male flowers or female flowers or fruits, i.e. in only one of three states needed for adequate discrimination; few are known in all three; 15 species, two occurring also in Cuba, the others endemic, are listed here. *Ardisia* is represented by eight species, one (*A. solanacea*) introduced and naturalized; *Myrsine* by two, which Mez placed in *Rapanea*. Keys, synonymy and statements of distribution are given. *Ardisia brittonii* and *A. byrsonimae* are described as new; *A. rosea* Urban (1908), non *A. rosea* King & Gamble (1905), is renamed *A. urbanii*.

INTRODUCTION

STUDENTS of the family *Myrsinaceae* tend to be censorious of the work of Carl Mez (1864–1944) on this difficult and to most botanists unattractive family, wherein, as C. L. Lundell (1966*a*) has remarked, " most generic characters are weak and those separating species are often weaker." Nevertheless, they must needs be grateful to Mez for his comprehensive survey of its West Indian members published in Urban's *Symbolae Antillanae* 2 : 389–433 (1901) and for his world monograph in Engler's *Das Pflanzenreich* IV.236 (1902), in which he provided a helpful basic classification, co-ordinated the extensive literature, and enumerated and described the material then available. The subsequent great increase of specimens in herbaria and a more critical attention to matters of nomenclature and typification than prevailed then have, however, made necessary many alterations and some drastic revisions of Mez's treatment; moreover, some characters emphasized by him in his keys have been found impracticable. E. Y. Hosaka, for example, in his account of the Hawaiian species of *Myrsine* sensu lato (in Occ. Pap. B.P. Bishop Mus. 16 : 25–76 (1940)) concluded that *Rapanea, Suttonia* and *Myrsine*, kept as separate genera by Mez, overlap so much in their characters that they should be combined in one genus, *Myrsine*, as indeed they were by Bentham & Hooker in 1873; H. C. D. de Wit (in Bull. Jard. Bot. Bruxelles 27 : 233–242 (1957)) has united *Heberdenia* with *Ardisia*. On the other hand, Lundell (in Wrightia 3 : 88 (1963)) has raised Mez's *Ardisia* sect. *Synardisia* to generic rank as *Synardisia*. A few examples may suffice to indicate the nomenclatural rectifications needed. The name *Ardisia coriacea* Swartz (1788), based on Jamaican material, was misapplied by Mez to a species which does not occur in Jamaica, i.e. *A. obovata* Ham. (*A. guadalupensis* Griseb.). The name *Ardisia sanguinolenta* Blume (1825) is the correct name for *A. zollingeri* A.DC. (1844): *A. wallichii* A.DC is the correct name for *A. sanguinolenta* Wall. ex Mez (1902). Merrill has called attention (in Lingnan Sci. Journ. 11 : 50 (1932) and in Contrib. Arnold Arb. 8 : 131 (1934)) to Mez's misinterpretation of *A. humilis* Vahl (1794), which, according to Merrill, is the same as *A. hainanensis* Mez (1902), while

A. humilis sensu Mez is *A. elliptica* Thunb. (1795) (syn. *A. obovata* Blume (Dec. 1825–March 1826), non *A. obovata* Ham. (Nov. 1825)). As regards the East Asiatic *Myrsinaceae*, a much needed nomenclatural and taxonomic overhaul has been made by E. H. Walker (in Philipp. Journ. Sci. 73 : 1–258 (1940), with supplementary notes in Journ. Arnold Arb. 23 : 344–355 (1942), in Bot. Mag. Tokyo 67 : 105–111, 155–162, 203–213, 247–255 (1954) and in Quart. Journ. Taiwan Mus. 12 : 161–194 (1959)). Unfortunately, there exists no comprehensive survey of the American *Myrsinaceae* later than Mez's of 1902, although many new species have been published since by Urban, Standley and C. L. Lundell, who has also revised the genus *Parathesis* (Lundell, 1966*b*) and the Guatemalan members of the family (Lundell, 1966*a*). The author of a local Flora is accordingly obliged to make a study more or less independent of Mez's work and to extend his enquiries beyond his own geographical area. The following synopsis of Jamaican *Myrsinaceae* is a by-product of preparing a more detailed account for the *Flora of Jamaica*; descriptions and particulars of localities to be given there in detail are either summarized below or omitted.

Mez in 1901 based his account of the *Myrsinaceae* occurring in Jamaica on 14 wild and two cultivated gatherings of *Ardisia*, 15 of *Wallenia*, 13 of *Rapanea* (i.e. *Myrsine*), i.e. 42 in all. For the *Flora of Jamaica* I have examined at least 120 Jamaican gatherings of *Ardisia*, 130 of *Wallenia*, and 50 of *Myrsine*, i.e. in all more than 300 gatherings. This increase in material has made evident the distribution of the *Myrsinaceae* in Jamaica, but has not greatly simplified the problems of their classification. Thus, despite much field work, the female flowers of *Wallenia clusioides*, *W. crassifolia*, *W. discolor*, *W. erythrocarpa* and *W. xylosteoides* and the male flowers of *W. discolor*, *W. elliptica*, *W. erythrocarpa*, *W. punctulata* and *W. sylvestris* have apparently missed collection; they have not been observed in the material studied, which, in addition to that of the British Museum (Natural History), London (cited below as BM), has included the specimens of the Systematisch-Geobotanisches Institut, Universität Göttingen (GOET), the Institute of Jamaica, Kingston, Jamaica (IJ), the Royal Botanic Gardens, Kew (K), the New York Botanical Garden (NY) and the University of the West Indies, Mona, Jamaica (UCWI) and the lectotype of *Wallenia grisebachii* at the Botanische Staatssammlung, Munich. Thanks are here expressed to the Directors of these Institutions for their invaluable co-operation in lending or making available for study this extensive material. Nevertheless, the following account as regards the status and distinctive characters of some taxa is necessarily provisional.Text-figures 21–25 have been drawn by Joanna C. Webb (Mrs. D. Erasmus).

HISTORY

The first members of the *Myrsinaceae* to be recorded from Jamaica, indeed from all America, were *Ardisia tinifolia* and *Wallenia laurifolia* gathered by Hans Sloane in 1688 or 1689. He collected the *Ardisia* " on the Mountains near Mr. Elletson's Plantation in Liguanee ", i.e. in the parish of St. Andrew, Jamaica, and published it in his *Catalogus Plantarum*: 169 (1696) and *Voyage to the Islands Madera* etc. 2 : 98, t. 205 f. 2 (1725) as " Jasminum forte, arboreum, foliis laurinis obtusis latioribus atrovirentibus, flore pentapetalo racemoso purpureo reflexo". Concerning this, Sloane wrote: "This Tree riseth to about thirty Foot high, having a Clay or Ash-colour'd pretty smooth Bark; its Twigs are set about with Leaves which are very smooth, of a dark green Colour, having a quarter of an Inch long Footstalks, being four Inches long and two broad in the Middle, where broadest, having an eminent middle Rib. The Flowers stand on several little Branches, being pentapetalous, purplish, bow'd back, having yellow Stamina in their Middle." Olof Swartz found the same species "in aridis submontosis Jamaicae" during his stay in the West Indies from 1784 to 1786, and gave it the binomial *Ardisia tinifolia* when founding the genus *Ardisia* in his *Nova Genera et Species Plantarum seu Prodromus* : 48 (1788).

Swartz referred five species to *Ardisia*: 1. *A. tinifolia* from Jamaica; 2. *A. coriacea* (now regarded as conspecific with *A. tinifolia*), its provenance vaguely recorded by him as "India occidentalis"; 3. *A. serrulata* (now *Parathesis serrulata* (Swartz) Mez) from Hispaniola, these three being of his own collecting; 4. *A. laterifolia* (now *Stylogyne laterifolia* (Swartz) Mez), vaguely recorded as from "India occidentalis"; 5. *A. parasitica* (now *Grammadenia parasitica* (Swartz) Griseb.) from "Montserrat" (later corrected to Dominica); these last two were known to him only from specimens in the herbarium of Sir Joseph Banks, now at the British Museum (Natural History), as the asterisk against the diagnosis indicates. Later authors have accepted *A. tinifolia* as the type-species of *Ardisia*. Swartz's description of the species in his *Flora Indiae Occidentalis* 1 : 468 (1797) is fairly detailed and accompanied by a reference to his "Icon. fasc. 3". Unfortunately, this third fascicle of his *Icones Plantarum incognitarum* (fasc. 1, 1794; fasc. 2, 1800) was never published, although Swartz sent the illustrations and text to Schreber in Erlangen for publication. Schreber died in 1810, Swartz in 1818; the Palmische Verlagsbuchhandlung in Erlangen published a note in *Flora (Regensburg)* 3 : 144 (March 1820) offering these illustrations to whoever would undertake their publication, but no one responded. Their subsequent history is unknown until about 1890 when the Berlin botanist Ignaz Urban acquired a volume containing presumably all that had survived of Swartz's 200 drawings of West Indian plants. They are cited in Urban's *Symbolae Antillanae* (cf. 1 : 164 (1898)) as "Sw. Ic. ined", and in Fawcett & Rendle's *Flora of Jamaica* (1 : xviii, etc. (1910)) as "Sw. Icon. ined:". They could not be traced at the Botanisches Museum, Berlin-Dahlem after the 1939–45 war and hence were believed to have been destroyed by bombing in March 1943, as stated in Sitwell and others, *Great Flower Books* : 77 (1956). Luckily, however, Urban had sold this precious volume in 1922 (cf. Journ. Bot. (Lond.) 60 : 361 (1922)) to C. A. Lindman in Stockholm and it is now preserved in the library of the Royal Swedish Academy of Sciences; Plates 6 and 7 are reproduced here from these drawings by permission of the Royal Swedish Academy of Sciences, to which grateful acknowledgement is made. Sets of photographs of Swartz's unpublished drawings have been deposited in the libraries of the British Museum (Natural History), London, the Institute of Jamaica, Kingston, Jamaica, and the Hunt Botanical Library, Pittsburgh, U.S.A. Swartz's coloured drawings representing *Ardisia tinifolia* and *A. coriacea*, together with *A. serrulata* and *A. parasitica*, leave no doubt as to the application of the names. Swartz applied the name *A. coriacea* to a Jamaican plant (without evident veining of the leaves but otherwise very similar to his *A. tinifolia*) which was described by Mez in 1901 as *A. harrisiana*; hence, as pointed out by Urban (Symb. Antill. 3 : 330 (1902); op. cit. 8 : 519 (1921)), Mez used the name *A. coriacea* wrongly for a species of the Lesser Antilles, i.e. *A. obovata* (*A. guadalupensis*).

According to Sloane's account (Voy. Nat. Hist. Jam. 1 : 234 (1707)) of the Jamaican plant now known as *Wallenia laurifolia*, but recorded by him as " Bryonia nigra fruticosa, foliis laurinis, floribus, racemosis, speciosis ", he " gathered it, if I rightly remember, in St. Maries, near Cabeça del oro in the North-side of this Island amongst the Woods "; he described the flowers simply as " at the top of the Branch... standing in a bunch together, being many very beautiful and small ". On this species Swartz in 1788 (Nov. Gen. & Sp. Pl. : 2, 31) founded the genus *Wallenia*, naming it in honour of Matthew Wallen, from whom Swartz received much hospitality while in Jamaica. Meanwhile, Jacquin had published in his *Selectarum Stirpium Americanarum Historia* : 17 (1763) the provisional designation *Petesioides laurifolium* referring to incomplete material collected by him in Santo Domingo (Haiti) between 1755 and 1759, and *Petesioides* was accordingly cited in the 1952, 1956, and 1961 editions of the International Code of Botanical Nomenclature, under No. 6304, as a nomen genericum rejiciendum necessitating the conservation of Swartz's *Wallenia*. Linnaeus had, however, ruled in *Critica botanica* : 34 (1737) that " nomina generica in *oides* desinentia, e foro Botanico releganda sunt " (generic names ending in *oides* are to be banished from the botanical forum). Hence, when Linnaeus himself used designations such as *Baccharioides*, *Bannisteroides*, *Cornutioides*, *Euonymoides*, *Hibiscoides*, *Oxycoccoides*, *Senecioides* etc. in his *Flora Zeylanica* (1747) for obscure plants and when loyal followers of Linnaean method and nomenclature such as Jacquin, Loefling and Rottböll used designations such as *Celosioides*, *Diodiodes*, *Malpighioides*, *Sideroxyloides*, *Staehelinoides* and *Viscoides*, they did not intend them to be permanent names for the genera concerned but merely as provisional or token names indicating resemblance; they intended that these *-oides* designations should later be replaced by correctly formed names. Jacquin's description of his *Petesioides* indicates that he possessed only a specimen with functionally female flowers; he believed that it represented a new genus which could not be properly established until fruits became available; accordingly, in his own words, " ego interea ab habitu nomen fluxum imposui " (I meanwhile, from its habit of growth, have given it a perishable name). Such token designations are in a different category from the pre-Linnaean generic names ending in *-oides*, such as *Capnoides*, *Ficoides*, *Nymphoides*, brought into post-Linnaean use as definite generic names by Miller, Hill, Adanson, Medicus and others. In a like spirit Rottböll in 1772 described *Schoenoides* and *Scirpoides* as new genera to which names would be given later; in 1773 he named the first *Kyllinga*, the second *Fuirena*. Swartz thus acted rightly according to the procedure of his times in replacing *Petesioides* by *Wallenia* and Jacquin evidently approved Swartz's action, for he himself adopted the name *Wallenia* in his *Plantarum rariorum Horti Caesarei Schoenbrunnensis Descriptiones* 1 : 13, t. 30 (1797). Valid publication of " *Petesiodes* Jacq." as a real generic name dates from Otto Kuntze's adoption of it in 1891 (Revis. Gen. Pl. 2 : 402).

In 1788 Swartz named, as *Samara coriacea* (Nov. Gèn. & Sp. Pl. : 32), a third

Jamaican member of the family, referring it to the Linnaean genus *Samara*, which is now included in *Embelia* Burman f. This species, found " in sylvis montium Jamaicae australis ", is congeneric with *Rapanea guianensis* Aublet, as Swartz noted, but *Rapanea* itself is not well separated from *Myrsine* L.

The collections including *Myrsinaceae* made in Jamaica during the first half of the nineteenth century by Macfadyen, Alexander, McNab, Nathaniel Wilson, March, and Purdie and used by Grisebach in preparing his *Flora of the British West Indian Islands* : 392–397 (1861) provided the material for publication there of *Wallenia clusiifolia*, *W. venosa*, *Ardisia xylosteoides*, and *A. clusioides*, and the record of *A. humilis* (actually *A. solanacea*) as naturalized in Jamaica. Grisebach's book (cf. Stearn, 1965) seems to have given the impression for many years that no further collecting need be done in the West Indies. William Harris's collecting from 1894 onwards brought about a new era in the botanical exploration of Jamaica, revealing the existence there of a multitude of new species which had escaped the notice of earlier collectors (cf. Urban, Symb. Antill. 6 : 70–86 (1909)). In 1895 Krug & Urban, working out Harris's collections from the Blue Mountains, Jamaica, published two further species, *Myrsine acrantha* and *Ardisia densiflora*. Mez in 1901 recorded from Jamaica four species of *Ardisia*, *A. harrisiana* being proposed as new, eight species of *Wallenia*, and four of *Rapanea*. At the same time he defined more satisfactorily the genera, by transferring to *Wallenia* some species which Grisebach had included in *Ardisia*, although he separated *Rapanea* from *Myrsine*, reducing the latter to four African and Asiatic species typified by *M. africana* L.

The acquisition of new Jamaican material, mostly collected by Harris and by N. L. Britton of the New York Botanical Garden, and the re-study of the older material seen by Mez led Urban between 1908 and 1915 to describe as new *Ardisia dictyoneura*, *A. troyana*, *Wallenia calyptrata*, *W. corymbosa*, *W. discolor*, *W. elliptica*, *W. erythrocarpa*, *W. punctulata* and *W. sylvestris* and Britton to describe *Petesioides subverticillata* (now *Wallenia subverticillata*). Urban's descriptions are wonderfully accurate, clear and detailed and are accompanied by helpful critical notes in which he made the most of inadequate material, but as usual he never provided a key to aid their recognition. The construction of such a key has indeed proved very difficult, partly because some taxa are only known in one of their three possible states—thus of the 16 species of *Wallenia* distinguished here, only six have been collected in their staminate, pistillate and fruiting states—but also because of the variation among these plants, which makes every gathering seem a little different from other gatherings. This is discussed further below under *Wallenia*.

GEOGRAPHICAL DISTRIBUTION

Four, if not five, of the Jamaican members of the *Myrsinaceae* occur outside the island. These are *Ardisia compressa*, which extends from Mexico to northern South America, *Myrsine coriacea*, which extends from Cuba over Jamaica, Hispaniola, Puerto Rico and the Lesser Antilles, and from Mexico over Central America, to Bolivia and Argentina, *Wallenia laurifolia*, which occurs also in Cuba and Hispaniola, and *W. subverticillata*, which also occurs in Cuba. *Ardisia densiflora* is closely allied to *A. spicigera* of Mexico and *A. gentlei* of British Honduras; indeed, according to Lundell (1966*a*) the three are conspecific. The ornamental Asiatic species *A. solanacea* (Text-fig. 8) has become naturalized in several places. All the others appear to be endemic to Jamaica, although *Myrsine acrantha* may probably be found on other islands; specimens of it are likely to be referred to *Myrsine* (*Rapanea*) *guianensis*. Members of the family may be found in Jamaica at any altitude from sea-level to the top of Blue Mountain Peak (7,400 ft., 2,250 m.).

Although it would be premature to define types of distribution within Jamaica on the basis of present material, this is adequate to indicate relative ranges. Thus *Myrsine acrantha* (Text-fig. 20), *M. coriacea* (Text-fig. 19), *Ardisia tinifolia* (Text-figs. 1–4), *Wallenia laurifolia* (Text-fig. 17), and *W. venosa* (Text-fig. 14) have comparatively wide ranges extending both east and west. A few are localized in the east, i.e. *Ardisia brittonii* (Text-fig. 5), *Wallenia sylvestris* (Text-fig. 18), and *W. subverticillata* (Text-fig. 9). Some others are restricted to the higher parts of the Blue Mountains, i.e. *Ardisia densiflora* (Text-fig. 6), *Wallenia calyptrata* (Text-fig. 13), *W. crassifolia* (Text-fig. 10), and *W. fawcettii* (Text-fig. 16). As far as is known, *Ardisia byrsonimae* (Text-fig. 5), *A. urbanii* (Text-fig. 5), *Wallenia corymbosa* (Text-fig. 11), *W. elliptica* (Text-fig. 9), and *W. punctulata* (Text-fig. 13) are restricted to the middle of the island. *Ardisia dictyoneura* (Text-fig. 6), *Wallenia grisebachii* (Text-fig. 15), and *W. purdieana* (Text-fig. 16) occur both in the middle and west, *Ardisia compressa* (Text-fig. 7), *Wallenia clusioides* (Text-fig. 9), and *W. erythrocarpa* (Text-fig. 12) only in the west. As there has obviously been no bias in making the collections here analysed, the species such as *Ardisia brittonii* (Text-fig. 5), *A. byrsonimae* (Text-fig. 5), *A. urbanii* (Text-fig. 5), *Wallenia discolor*, *W. elliptica* (Text-fig. 9), *W. erythrocarpa* (Text-fig. 12), and *W. punctulata* (Text-fig. 13), which are known only from single gatherings or from gatherings made at the same place, must be of very limited range.

Specimens are cited below under Jamaican parishes, proceeding usually from west to east or from north to south within the parish.

Family Characters

The family *Myrsinaceae* as represented in the West Indies consists of small trees or shrubs, with the leaves usually alternate, rarely whorled, and without stipules. The flowers are regular, bisexual or unisexual, with parts in fours or fives, and are grouped in axillary or terminal racemes or panicles sometimes condensed into fascicles or umbels. The calyx is persistent, with segments free or basally connate, imbricate or valvate. The corolla is usually gamopetalous but in *Myrsine acrantha* parted to the base. The stamens are inserted on the corolla, opposite to and the same number as the lobes of the corolla, with the anthers opening introrsely by lengthwise slits or apical pores. The ovary, superior in West Indian genera, is one-chambered with a free central placenta, into which the few or many ovules are sunk, appearing as slight or distinct bulges on its surface; the style may be short or long, with the stigma undivided or lobed or fimbriate. The fruit in West Indian genera is a more or less globose drupe. The family as a whole includes about 900

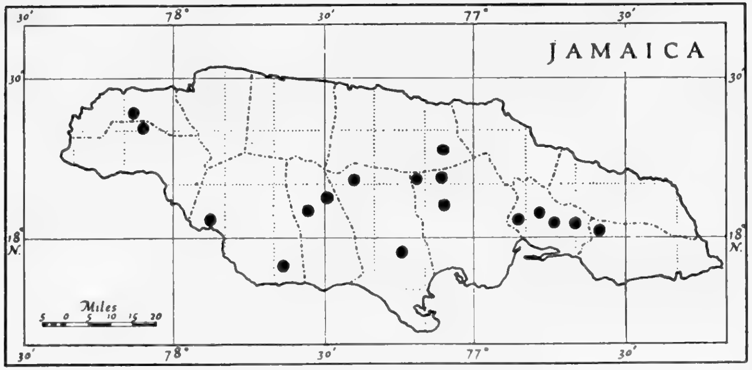

FIG. 1. *Ardisia tinifolia* var. 1.

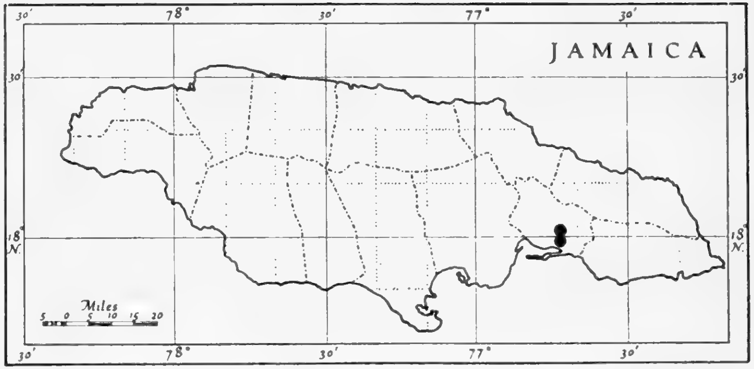

FIG. 2. *Ardisia tinifolia* var. 2.

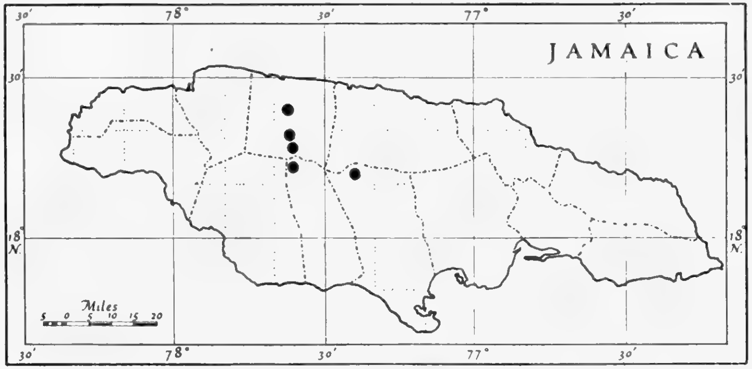

FIG. 3. *Ardisia tinifolia* var. 3.

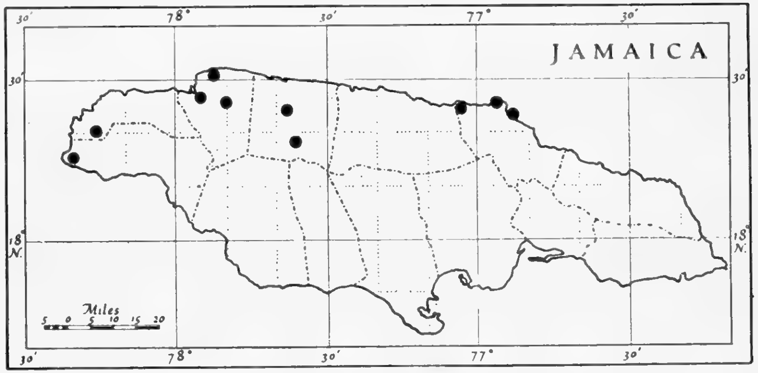

FIG. 4. *Ardisia tinifolia* var. 4.

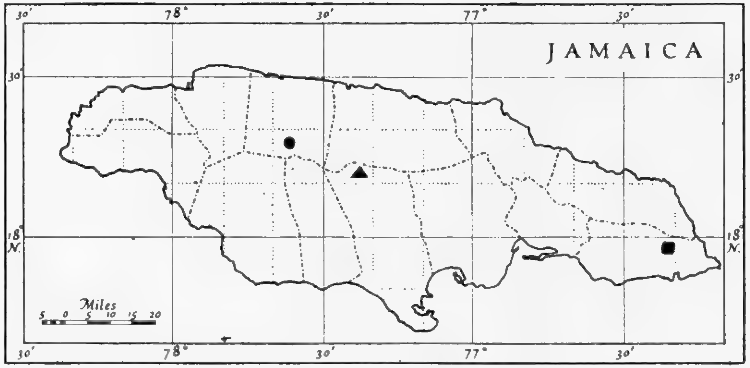

FIG. 5. *Ardisia urbanii* ●; *A. byrsonimae* ▲; *A. brittonii* ■.

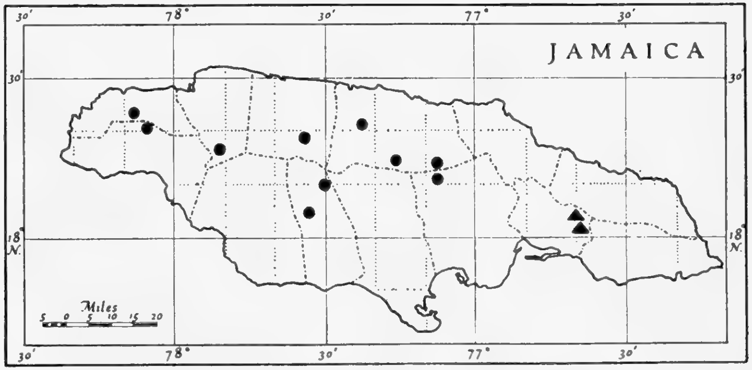

FIG. 6. *Ardisia dictyoneura* ●; *A. densiflora* ▲.

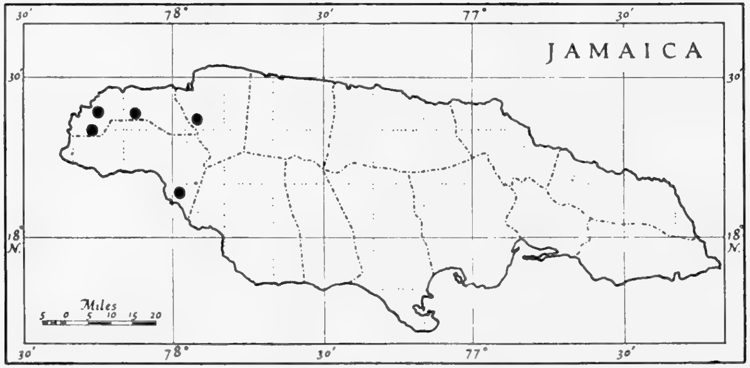

FIG. 7. *Ardisia compressa*.

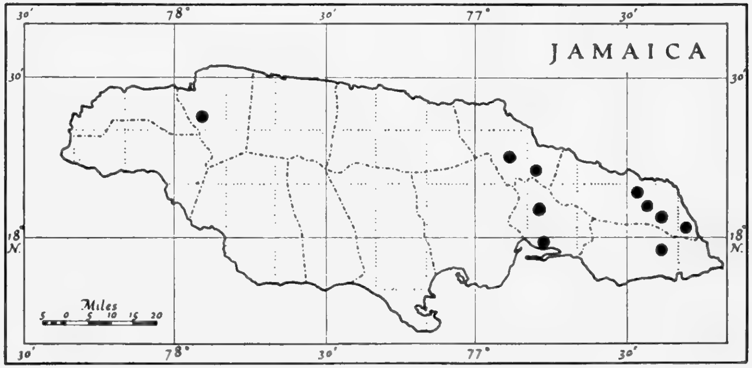

FIG. 8. *Ardisia solanacea*.

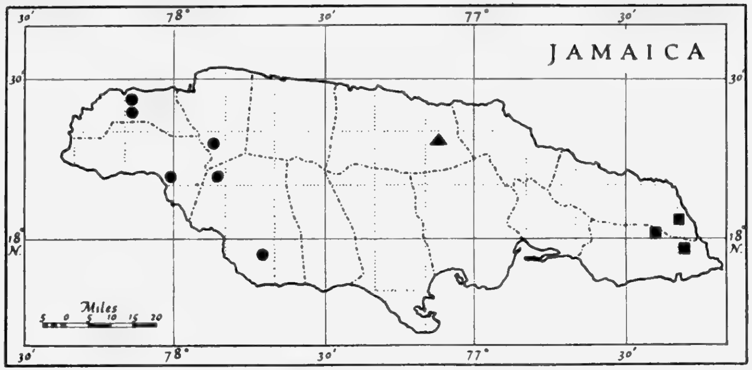

FIG. 9. *Wallenia clusioides* ●; *W. elliptica* ▲; *W. subverticillata* ■.

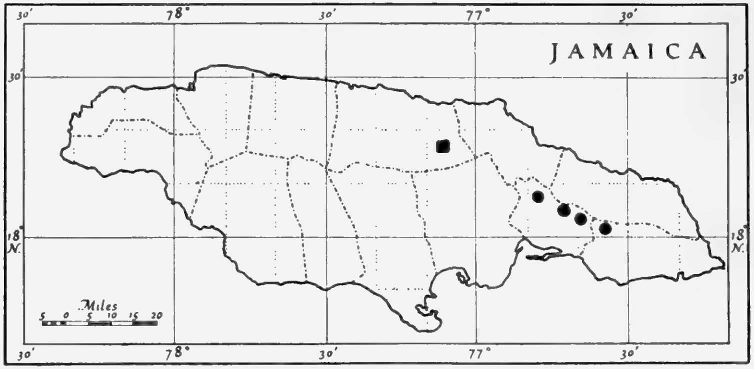

FIG. 10. *Wallenia crassifolia* ●; *W. xylosteoides* ■.

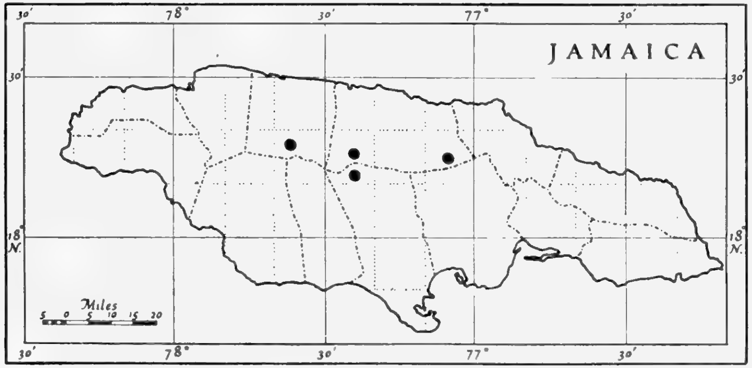

FIG. 11. *Wallenia corymbosa.*

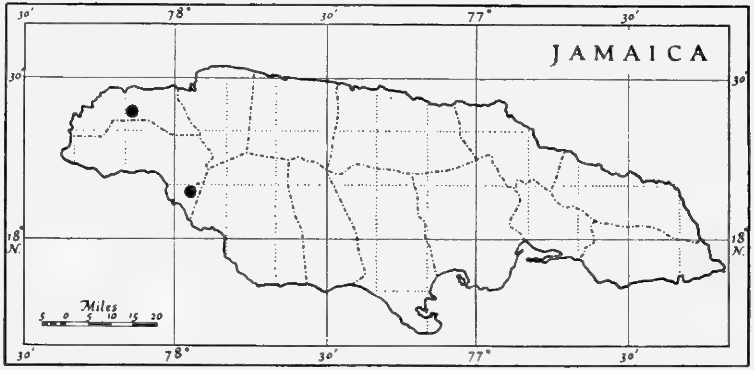

FIG. 12. *Wallenia erythrocarpa.*

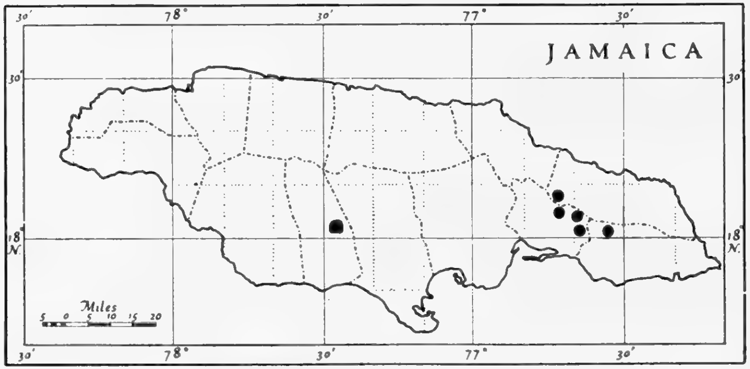

FIG. 13. *Wallenia calyptrata* ●; *W. punctulata* ■.

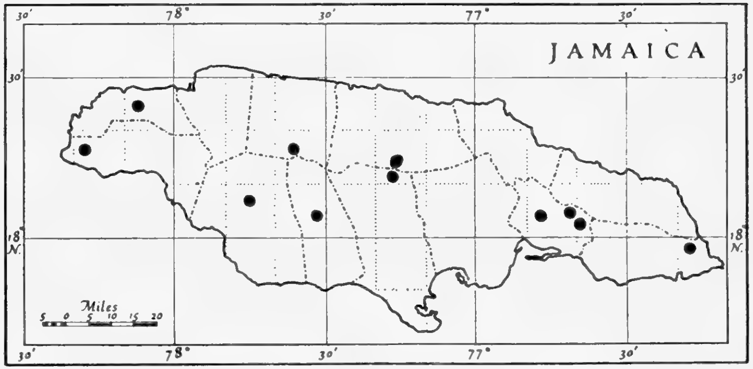

FIG. 14. *Wallenia venosa.*

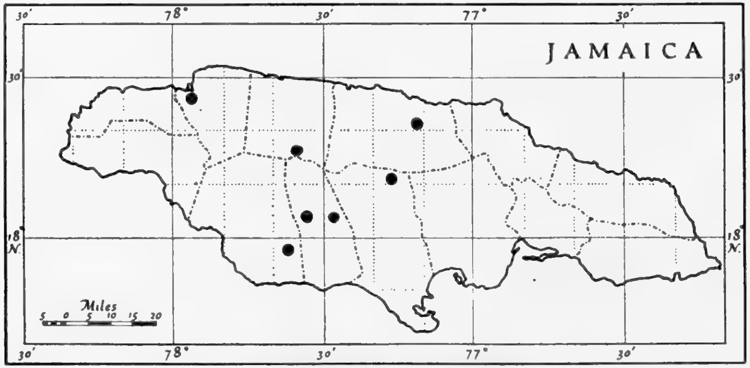

FIG. 15. *Wallenia grisebachii.*

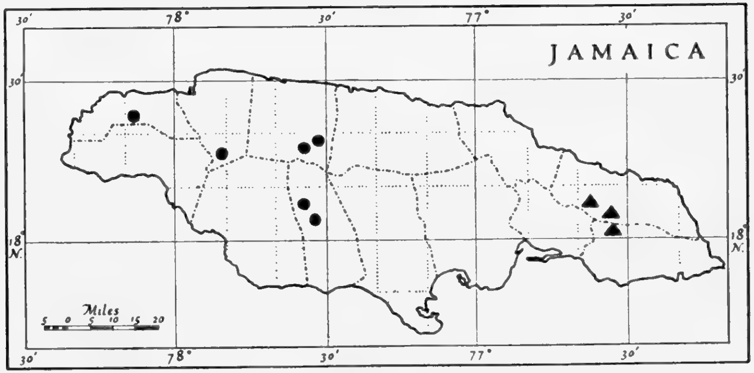

FIG. 16. *Wallenia purdieana* ●; *W. fawcettii* ▲.

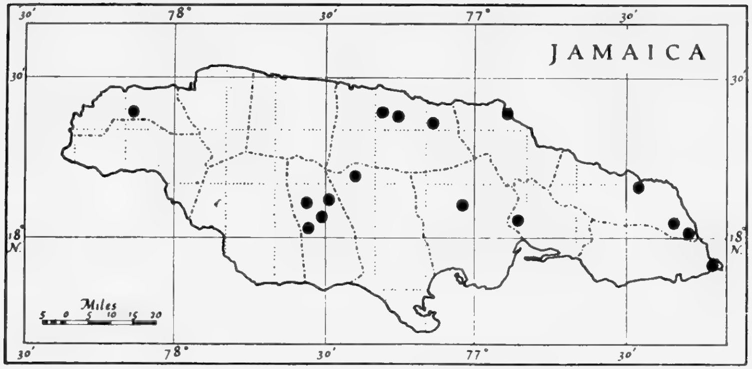

FIG. 17. *Wallenia laurifolia.*

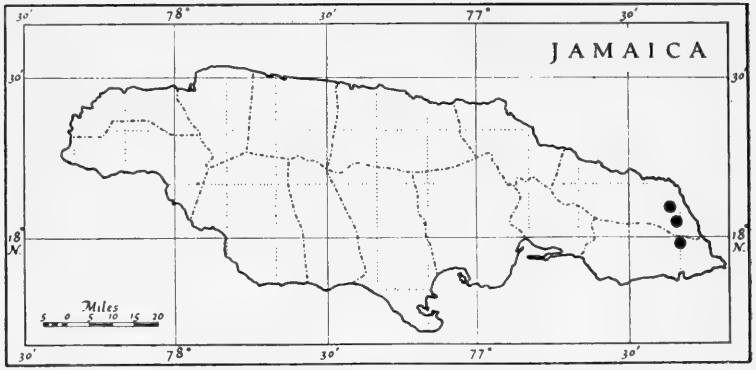

FIG. 18. *Wallenia sylvestris.*

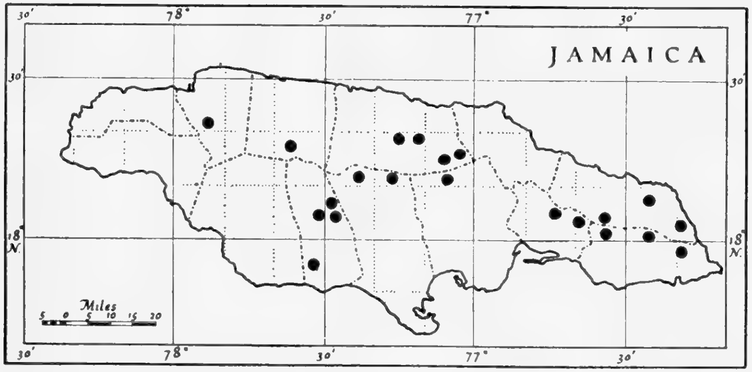

FIG. 19. *Myrsinecoriacea.*

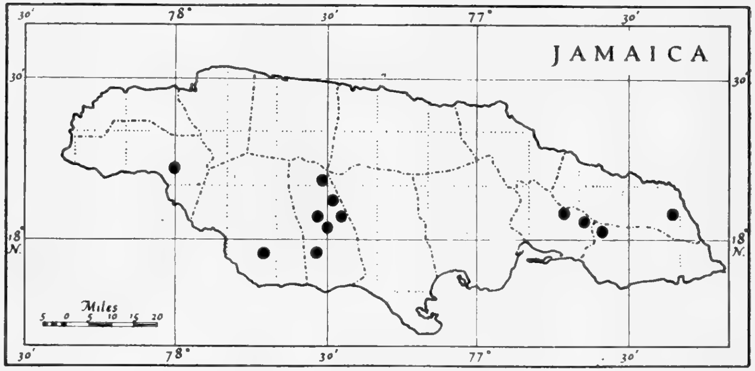

FIG. 20. *Myrsine acrantha.*

species and occurs in the tropics and sub-tropics of the Old and the New World. Of its 30 or so genera, nine are represented in the West Indies as a whole but only three in Jamaica. Those absent from Jamaica are *Parathesis* (Cuba, Hispaniola, Puerto Rico), *Stylogyne* (Lesser Antilles), *Conomorpha* (Lesser Antilles), *Weigeltia* (Lesser Antilles), *Cybianthus* (Trinidad) and *Grammadenia* (Puerto Rico, Lesser Antilles).

Key to Jamaican Genera

Flowers in usually terminal (sometimes axillary and then long-pedunculate) racemes or panicles; style slender; stigma inconspicuous.

  Flowers bisexual, with stamens and style both well developed in the same flower; corolla c. 6–12 mm. long; ovules numerous, scattered in several series over the placenta . . . . 1. *Ardisia*

  Flowers unisexual, dioecious, the male flowers with well developed exserted stamens, the female flowers with abortive included stamens but exserted styles; corolla 1·5–6 mm. long; ovules 3–4 in a single horizontal row on the placenta . . . . 2. *Wallenia*

Flowers in umbellate clusters on very short, scaly axillary spurs; style short or none (in American species); stigma conspicuous . . . . 3. *Myrsine*

1. ***ARDISIA*** Swartz

Ardisia Swartz, Nov. Gen. & Sp. Pl. : 3, 48 (1788); Fl. Ind. Occ. 1 : 467 (1797); nomen conservandum No. 6285.

Lectotype: *A. tinifolia* Swartz.

Key to Jamaican Species

Inflorescences all axillary; pedicels 1–4 cm. long, clustered almost umbellately at the end of the peduncle; anthers 5–6 mm. long . . . 8. *A. solanacea*

Inflorescences terminal (sometimes with a few axillary inflorescences below); pedicels mostly 1–7 mm. long, sometimes to 12 mm. long but then racemosely arranged along the lateral peduncle; anthers 1·5–5 mm. long:

  Lateral peduncles compound, i.e. bearing 3 to 4 secondary peduncles each umbellately 2–6-flowered; leaves 7–16 cm. long, the blades narrowly obovate to oblanceolate; filaments of stamens 0·5 mm. long . . 7. *A. compressa*

  Lateral peduncles simple, i.e. directly bearing 3 to 28 pedicelled flowers but no secondary peduncles; leaves mostly less than 12 cm. long, the blades various; filaments of stamens 1–5 mm. long:

    Leaves closely clustered at the tips of shoots, less than 5·5 cm. long; inflorescence contracted, less than 4 cm. long and broad, the branches 3–6-flowered, the pedicels 1–4 mm. long; central Jamaica . . . 6. *A. byrsonimae*

    Leaves more widely spaced, some or all more than 5·5 cm. long; inflorescence more than 4 cm. long and broad, the branches usually many-flowered, the pedicels 2–15 mm. long:

Inflorescence somewhat fastigiate, the densely many-flowered branches ascending at c. 40°; corolla c. 5 mm. long; anthers c. 1·5 mm. long, much shorter than the filaments; Blue Mountains . . 5. *A. densiflora*

Inflorescence looser, the branches spreading at c. 50–60°; corolla 7–12 mm. long; anthers 2·5–5 mm. long, equalling or longer than the filaments:

- Pedicels 1–4 mm. (rarely to 5 mm.) long; leaf-blades with well-marked reticulate venation . . . . . . 4. *A. dictyoneura*
- Pedicels 4–15 mm. long; leaf-blades not markedly reticulate:
  - Sepals 2·5–4 mm. broad:
    - Anthers 4·5–5 mm. long, apically dehiscent; sepals almost or quite glabrous; eastern Jamaica . . . . 2. *A. brittonii*
    - Anthers 3–3·5 mm. long, laterally dehiscent almost to the base; sepals ciliate; western Jamaica. . . . . 3. *A. urbanii*
  - Sepals 1–2 mm. broad:
    - Sepals ovate or broadly ovate:
      - Anthers 3–3·5 mm. long . . . . 1. *A. tinifolia* var. 1
      - Anthers 4–5 mm. long . . . . *A. tinifolia* var. 2
    - Sepals mostly narrowly ovate or oblong-lanceolate:
      - Leaf-blades mostly less than 6 cm. long; sepals 2–2·5 mm. long *A. tinifolia* var. 3
      - Leaf-blades 7–12 cm. long; sepals 2·5–3 mm. long *A. tinifolia* var. 4

Subgenus 1. *ARDISIA*

ARDISIA subgenus ARDISIA; subgenus typicum generis.

Ardisia Swartz, Nov. Gen. & Sp. Pl. : 3, 48 (1788), sensu stricto.
Pickeringia Nutt. in Journ. Acad. Sci. Philad. 7 : 95 (1834).
Ardisia sect. *Euardisia* Endl., Gen. Pl. : 736 (1839).
Ardisia subgenus *Pickeringia* (Nutt.) Mez in Urban, Symb. Antill. 2 : 396 (1901); in Engler, Pflanzenr. IV. 236 : 79 (1902).

Lectotype: *A. tinifolia* Swartz.

Inflorescence always terminal; branches simply racemose. Stamens with conspicuous filaments. Species all American.

1. ***Ardisia tinifolia*** Swartz, Nov. Gen. & Sp. Pl. : 48 (1788); Fl. Ind. Occ. 1 : 468 (1797).—Griseb., Fl. Brit. W. Ind. Is. : 396 (1861).—Mez in Urban, Symb. Antill. 2 : 400 (1901); in Engler, Pflanzenr. IV. 236 : 83, fig. 11 F–K (1902). (Text-fig. 23G, H; pl. 6, 7.)

Ardisia coriacea Swartz, Nov. Gen. & Sp. Pl. : 48 (1788); Fl. Ind. Occ. 1 : 470 (1797).
Ardisia harrisiana Mez in Urban, tom. cit. : 401 (1901); in Engler, tom. cit. : 83 (1902).
Ardisia troyana Urban, Symb. Antill. 5 : 455 (1908).
" Jasminum forte, arboreum, foliis laurinis obtusis latioribus atrovirentibus, flore pentapetalo racemoso purpureo reflexo " Sloane, Cat. Pl. Jam.: 169 (1696); Voy, Jam. Nat. Hist. 2: 98, t. 205 fig. 2 (1725).

The species *Ardisia tinifolia* as here accepted includes plants diverging in form and size of leaf, in number of flowers, shape of sepals and length of anthers. Selected specimens, e.g. *Harris 8741* (type-collection of *A. troyana*) from near Troy, Central

Jamaica, with very small leaves, *Proctor 16621* from Orange River Valley, St. James, with comparatively elongated sepals, and *Loveless 1198* from the Long Mountain, near Kingston, with long anthers, could reasonably be regarded as exemplifying independent species and were indeed treated by the writer as such until the difficulty of finding stable combinations of characters and of allocating specimens intermediate in one character or another to these supposed taxa made it more practical to place them all in one species, within which four major populations (Text-figs. 1–4) are more or less distinguishable though not easily defined. They are simply given numbers below. Swartz's original diagnosis of his *A. tinifolia* in 1788 is brief but the more detailed description in his *Flora Indiae Orientalis*, and his unpublished illustration (Pl. 6, see p. 147) and authentic specimens (BM) clearly establish the identity of the plant he had in mind. A representative modern gathering is *Harris 12087*, collected between Constant Spring and Bardowie, St. Andrew, with veining on the lower surface of the leaf plainly evident. It typifies the population (var. 1 below) found in the southern parishes of Jamaica, with an altitudinal range of 50 ft. (15 m.) to 3,500 ft. (1,070 m.). Here belongs Swartz's *A. coriacea* with veining on the lower leaf-surface faint or not evident, likewise represented by an unpublished drawing (Pl. 7). Diverging from typical *A. tinifolia* principally by having somewhat longer anthers is the population (var. 2 below) characteristic of the Long Mountain near Kingston, at 500 ft. (150 m.) to 1,000 ft. (300 m.). Small short-petioled leaves evidently veined characterize plants of central Jamaica (var. 3 below) named *A. troyana* by Urban, which also differ from typical *A. tinifolia* in having shorter branches of the inflorescence. These occur at 700 ft. (210 m.) to 2,500 ft. (750 m.). Their range slightly overlaps that of a population (var. 4 below) with larger longer-petioled leaves, looser many-flowered inflorescences and slightly shorter filaments, found in the northern parishes of Jamaica from almost sea-level to 700 ft. (210 m.). They occur in the same area at Sherwood Content, Trelawny, and merit particular study there in the field.

Together the plants here placed in *Ardisia tinifolia* thus give the impression of a population within which morphologically and geographically differentiated taxa have been formed but have not achieved complete independence.

Var. 1.

A. tinifolia Swartz, loc. cit. (1788).
A. coriacea Swartz, loc. cit. (1788).
A. harrisiana Mez, loc. cit. (1901).

Leaf-blades mostly elliptic, sometimes narrowly obovate, the apex obtuse or acute, 5–12 cm. long, 1·5–7 cm. broad. Sepals imbricate, ovate or broadly ovate, rounded, c. 1·5–2·5 mm. long, 1·2–2 mm. broad. Anthers 3–3·5 mm. long.

St. Elizabeth: *Proctor 15419* (BM; IJ), *Proctor 11344* (BM; IJ).

Clarendon: *Proctor 22739* (BM; IJ), *Proctor 9712* (IJ), *Proctor 10233* (IJ), *Stearn 1044* (BM), *Adams 8424* (UCWI).

St. Ann: *Alexander* (K).

St. Catherine: *Proctor 9310* (BM; IJ), *Proctor 8373* (IJ), *Proctor 22739* (IJ).

St. Andrew: *Britton 3461* (NY), *Stearn 59* (BM), *Proctor 11428* (IJ), *Harris 5970*

(BM; NY), *Harris 11137* (NY; UCWI), *Newill 5449* (IJ), *Harris 5926* (NY), *Harris 12081* (BM; NY; UCWI), *Harris 9033* (BM; NY; UCWI), *Powell 850* (IJ), *Proctor 23694* (IJ), *Harris 6600* (BM; NY; UCWI: type-collection of *Ardisia harrisiana* Mez), *Britton 2987* (NY), *Proctor 24511* (BM), *Proctor 23982* (BM).

ST. THOMAS: *Adams 12579* (UCWI).

Var. 2.

Leaf-blades elliptic or broadly elliptic, a few broadly obovate, the apex obtuse or rounded, 4–9 cm. long, 2–6 cm. broad. Sepals imbricate, ovate or broadly ovate, c. 2–2·5 mm. long, 1·5–2 mm. broad. Anthers 4–5 mm. long.

KINGSTON and ST. ANDREW: *Britton 377* (NY), *Robbins 1496* (UCWI), *Proctor 7386* (IJ), *Webster 4986* (BM), *Loveless 1198* (UCWI), *Yuncker 17315* (BM), *Anderson & others 626* (UCWI).

Var. 3.

Ardisia troyana Urban, loc. cit. (1908).

Leaf-blades elliptic, the apex obtuse, c. 3–10 cm. long, 1·5–6 cm. broad (usually less than 6 cm. long, 3·5 cm. broad). Sepals narrowly ovate, 2–2·5 mm. long, 1- 1·5 mm. broad. Anthers 3–3·5 mm. long.

TRELAWNY: *Harris 8741* (BM; NY; UCWI: type-collection of *A. troyana* Urban), *Britton 605* (NY), *Harris 9473* (NY; UCWI), *Howard, Proctor & Stearn 14677* (BM), *Howard, Proctor & Stearn 14679* (BM; IJ), *Proctor 11060* (BM; IJ), *Proctor 22543* (BM; IJ), *Proctor 24458* (BM; IJ), *Proctor 25676* (IJ).

CLARENDON: *Harris 12769* (NY; UCWI), *Proctor 9772* (IJ), *Proctor 10233* (IJ).

MANCHESTER: *Proctor 25625* (BM; IJ).

Var. 4.

Leaf-blades narrowly obovate or elliptic, the apex acute or shortly acuminate, 5–12 cm. long, 2–6 cm. broad. Sepals scarcely or not imbricate, ovate to obovate-lanceolate, obtuse, c. 1·5–2·5 mm. long, 1–1·5 mm. broad. Anthers c. 3 mm. long.

HANOVER: *Proctor 11280* (BM; IJ).

WESTMORELAND: *Harris 10220* (BM; K; NY; UCWI).

ST. JAMES: *Harris 10318* (BM; NY; UCWI), *Britton & Hollick 2355* (NY), *Proctor 16621* (BM; IJ), *Proctor 24292* (BM; IJ).

TRELAWNY: *Proctor 11062* (BM; IJ).

ST. MARY: *Loveless 2437* (UCWI), *Proctor 7546* (IJ), *Yuncker 17838* (BM).

2. **Ardisia brittonii** Stearn, sp. nov. (Text-fig. 21; Pl. 8a)

Arbor parva ad 4·5 mm. alta, *ramulis* hornotinis primo ferrugineis pulverulentisque, annotinis nigrescentibus glabrisque. *Folia* dissita, c. 4–8 mm. inter se distantia, magna, patentia, longipetiolata; *lamina* oblongo-elliptica, apice obtusa, margine integra, basi cuneata in petiolum attenuata, 8–17 cm. longa, 3–8 cm. lata, glabra, utrinque punctata, coriacea, venis numerosis utrinque prominulis marginem versus reticulate anastomosantibus; *petiolus* 1–2·2 cm. longus. *Inflorescentiae* terminales multiflorae laxae, c. 15 cm. longae, 10 cm. latae, supra glabrae, inferne minute pubescentes, ramulis patentibus ad 9 cm. longis racemose 8–12-floris; *pedicelli inferiores* ad 1·5 cm. longi. *Calyx* c. 4·5–5 mm. longus; *sepala* imbricata parum inaequalia, ovata vel late oblonga, rotundata, c. 4–4·5 mm. longa, 2·5–3 mm. lata, punctata, margine glabra. *Corolla* rosea, c. 1·3 cm. longa; *petala* in 1/4 altitudinis coalita, apice obtusa, parte libera oblonga c. 4 mm. lata, per anthesin revoluta, nigro-punctata et lineolata. *Stamina* quam petala breviora, c. 1·5 mm. supra corollae basin inserta; *antherae* anguste triangulares, c. 4·5–5 mm. longae, apice obtusa rimis brevibus dehiscentes, basi cordatae; *filamenta* 3 mm. longa. *Ovarium* late ovoideum; stylus c. 9 mm. longus, stigmate minuto.

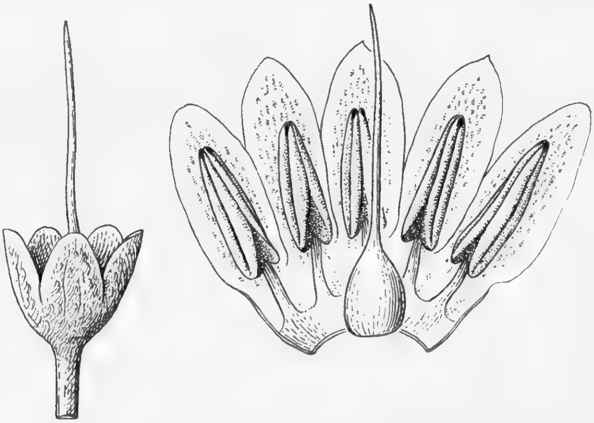

FIG. 21. Dissected flower of *Ardisia brittonii* Stearn (*Harris & Britton 10558*), × 3.

ST. THOMAS: Bath to Cuna Pass, Sept., 1908, *Harris & Britton 10558* (NY, holotype: BM; K; UCWI).

This species of eastern Jamaica has been named in honour of Nathaniel Lord Britton (1859–1934), founder of the New York Botanical Garden and author of many botanical works on the eastern United States and the West Indies; see *National Acad. Sci. U.S.A. Biogr. Mem.* 19 : 147–202 (1938) for a biography by E. D. Merrill and a bibliography by J. H. Barnhart.

Ardisia brittonii differs from the widespread *A. tinifolia* principally in its broader sepals and in having somewhat larger flowers and longer anthers than is usual in *A. tinifolia*. It agrees more closely with *A. urbanii* of central Jamaica but may be distinguished from that by its glabrous calyx and its longer anthers, which dehisce only at the apices.

3. **Ardisia urbanii** Stearn, nom. nov. (Text-fig. 22.)

Ardisia rosea Urban, Symb. Antill. 5 : 456 (1908); non *A. rosea* King & Gamble (1905).

TRELAWNY: *Harris 9419* (BM; NY; type-collection), *Harris 9418* (BM; NY; UCWI), *Britton 659* (NY).

Ardisia urbanii is known only from collections made at Troy on the southern side of the Cockpit Country by Harris & Britton in 1906 at about 1,600 ft. (530 m.). The size of the calyx (with sepals 3–5 mm. long, 2·5–4 mm. broad) distinguishes it from *A. tinifolia*; the ciliated sepals and the anthers dehiscent to the base distinguish it from *A. brittonii* of eastern Jamaica. According to Harris, it forms a small tree to 25 ft. (7·5 m.) high, with rosy flowers. It is named in honour of Ignaz Urban (1848–1936), the author of many important works on the West Indian flora; see *Ber. Deutsch. Bot. Ges.* 48 : (205)–(225) (1931) for a biography and bibliography by Th. Loesener.

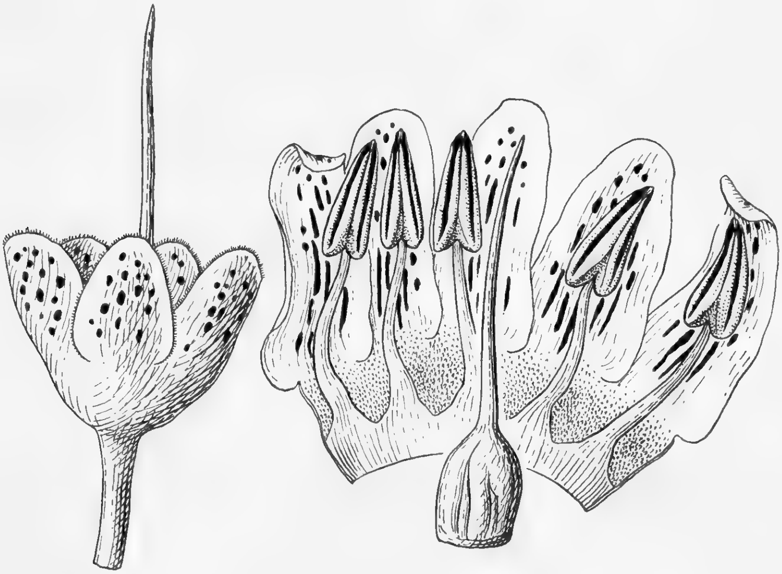

FIG. 22. Dissected flower of *Ardisia urbanii* Stearn (*Britton 659*), × 4.

4. **Ardisia dictyoneura** Urban, Symb. Antill. 6 : 28 (1909).

HANOVER: *Harris 10345* (BM; NY; UCWI; type-collection), *Proctor 11316* (BM; IJ), *Britton 2277* (NY).

WESTMORELAND: *Proctor 7321* (BM; IJ).

ST. JAMES: *Proctor 22979* (BM; IJ).

TRELAWNY: *Proctor 10610* (BM; IJ).

MANCHESTER: *Proctor 11028* (BM; IJ), *Proctor 11036* (BM; IJ), *Proctor 18299* (IJ), *Stearn 351* (BM).

ST. ANN: *Purdie* (K), *Proctor 22835* (BM; IJ), *Proctor 26724* (BM), *Stearn 567* (BM), *Proctor 11896* (IJ), *Howard & Proctor 15039* (IJ), *Proctor 7494* (IJ).

ST. CATHERINE: *Howard & Proctor 13620* (IJ; NY).

Ardisia dictyoneura is a species of western and central Jamaica at 1,000–3,000 ft. (300–900 m.). The type collection was made by Harris in 1908 at Fray Woods in Hanover. It has often been collected in fruit, only twice in flower, and is notable for its profusely and finely reticulate-veined coriaceous mostly obovate or narrowly obovate leaves and its comparatively large fruits, 6·5–8 mm. in diameter when mature, borne on pedicels only 1–4 mm. long.

5. ***Ardisia densiflora*** Krug & Urban in Notizbl. Bot. Gart. & Mus. Berlin 1 : 79 (1895).—Urban, Symb. Antill. 1 : 385 (1899); op. cit. 6 : 28 (1909).—Mez in Urban, Symb. Antill. 2 : 398 (1901); in Engler, Pflanzenr. IV. 236 : 82 (1902).—C. L. Lundell in Fieldiana, Bot. 24 (8) : 141 (1966). (Text-fig. 23F.)

Ardisia spicigera Donn. Smith in Bot. Gaz. 27 : 434 (1899), fide Lundell, loc. cit. (1966).
Ardisia gentlei C. L. Lundell in Field & Lab. 13 : 11 (1945), fide Lundell, loc. cit. (1966).

St. Andrew: *Harris 5227* (K; UCWI), *Harris 5431* (BM; K; type collection), *Harris 7657* (BM; K; NY; UCWI), *Harris 6578* (BM; UCWI), *Harris 10029* (BM; NY; UCWI), *Harris 6077* (NY; UCWI), *D. Watt 8225* (NY; UCWI), *Maxon & Killip 1343* (NY), *Proctor 24511* (BM; IJ), *Proctor 25610* (BM; IJ).

The discovery in 1894 of *Ardisia densiflora* in the Blue Mountains of Jamaica, on which it grows at about 3,000–4,000 ft. (900–1,200 m.), was one of the early results of the renewed collecting in Jamaica at the end of the nineteenth century. It is a well-marked species with a densely many-flowered inflorescence, the branches of which are ascending, almost fastigiate, and which bear up to 25 small white flowers on pedicels 1–6 mm. long. The filaments of the stamens are much longer than the longitudinally dehiscent anthers. According to Lundell, *A. spicigera* from Mexico and *A. gentlei* from British Honduras are both conspecific with *A. densiflora*, which thus has a fairly wide but sparse Central American distribution comparable with that of *Achimenes erecta* (Lam.) H. P. Fuchs, a gesneriad restricted in Jamaica to the Blue Mountains.

6. ***Ardisia byrsonimae*** Stearn, sp. nov. (Text-fig. 23A–E; Pl. 8b).

Arbor parva ad 4·5 m. alta, *ramulis* hornotinis ferrugineis pulverulentisque, annotinis cinereis glabrisque. *Folia* pro genere parva, ad apices ramulorum conferta, 1–5 mm. inter se distantia, ascendentia, brevipetiolata; *lamina* obovata, apice rotundata interdum emarginata, margine integra, basi cuneata, c. 3–5·5 cm. longa, 1·3–3·5 cm. lata, glabra, utrinque punctata, coriacea, venis vix prominulis; *petiolus* 2–5 mm. longus. *Inflorescentiae* terminales fere sessiles multiflorae densae, c. 3 cm. longae et latae, primo pulverulentae, ramulis ascendentibus ad 3 cm. longis racemose 3–6-floris; *pedicelli* 1–4 mm. longi. *Calyx* c. 3 mm. longus; *sepala* imbricata, ovata, rotundata, c. 2–2·5 mm. longa, 1·5–2 mm. lata, margine scariosa ciliataque. *Corolla* rosea, c. 7–8 mm. longa; *petala* in 1/4 altitudinis coalita, apice acuta, parte libera lanceolata, 2–2·5 mm. lata, per anthesin recurvata, punctata. *Stamina* quam petala breviora, c. 1·5–2 mm. supra corollae basin inserta; *antherae* anguste triangulares, c. 3–5·5 mm. longae, apice mucronatae et rimis brevibus quasi poratim dehiscentes, basi cordatae; filamenta c. 2 mm. longa. *Ovarium* late ovoideum; stylus c. 8–9 mm. longus, stigmate minuto. *Fructus* transverse late ellipsoideus, c. 4–5 mm. altus, 5–6 mm. latus, glanduloso-punctatus, styli basi c. 1 mm. longa coronatus.

Clarendon: Peckham Woods, 760 m., Dec. 1917, *Harris 12799* (BM; NY; UCWI), same locality, Aug. 1954, *Webster & Proctor 5428* (BM), same locality, Jan. 1955, *Proctor 9743* (BM; IJ), same locality, Dec. 1955, *Stearn 9* (BM, holotype; K), *Proctor 11408* (IJ).

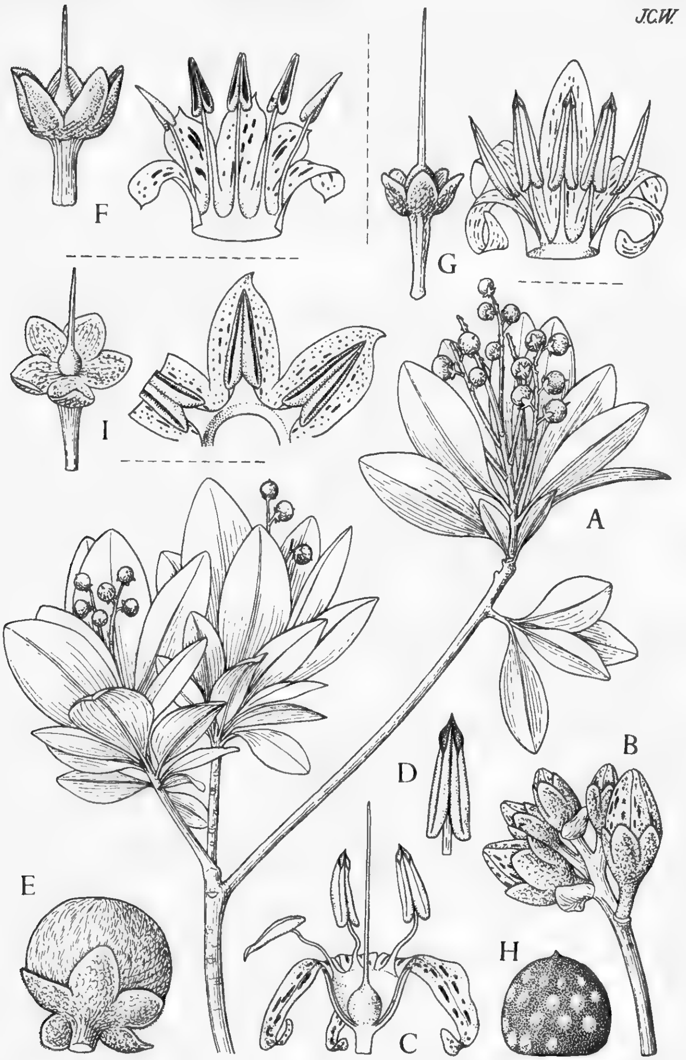

FIG. 23. *Ardisia byrsonimae* Stearn: A, fruiting specimen (*Stearn 9*), × ½; B, buds (*Proctor 9743*), × 2; C, dissected flower (*Stearn 9*), × 3; D, anther (*Stearn 9*), × 5; E, fruit (*Stearn 9*), × 4. *Ardisia densiflora* Krug & Urban: F, dissected flower (*Harris 10029*), × 4. *Ardisia tinifolia* Swartz; G, dissected flower (*Harris 12081*), × 3; H, placenta with ovules (*Harris 12081*), × 20. *Ardisia solanacea* Roxb.; I, dissected flower (*Harris 11637*), calyx and ovary × 1·5, corolla and stamens × 2.

Ardisia byrsonimae is a slow-growing tree endemic to wooded limestone hill-tops in upper Clarendon, Jamaica. It differs from other Jamaican species in its comparatively small leaves crowded at the ends of the shoots and its contracted inflorescences with very short pedicels. From *A. tinifolia* var. 3 (*A. troyana* Urban), likewise inhabiting the western interior of Jamaica, it may also be distinguished by its markedly imbricate and more rounded sepals. The epithet *byrsonimae* was given to this species by N. L. Britton under *Icacorea* but never published by him. It refers to a resemblance in habit between it and certain West Indian species of *Byrsonima* (*Malpighiaceae*), notably *B. lucida* (Mill.) Rich., with small obovate leaves usually clustered at the ends of the shoots.

Subgenus 2. ***ICACOREA*** (Aublet) Pax

Ardisia subgen. Icacorea (Aublet) Pax in Engler & Prantl, Nat. Pflanzenfam. 4 (1): 94(1889).—Mez in Urban, Symb. Antill. 2 : 391(1901).

Icacorea Aublet, Hist. Pl. Guiane Franç. 2, Suppl. : 1 (1775).
Ardisia sect. *Icacorea* (Aublet) Griseb., Fl. Brit. W. Ind. Is. : 395 (1861).

Type (by monotypy): *Ardisia guianensis* (Aublet) Mez (*Icacorea guianensis* Aublet).

Inflorescences terminal or both axillary and terminal; branches compoundly racemose, bearing several umbellate or corymbose clusters. Stamens with short filaments. Species all American.

7. ***Ardisia compressa*** Kunth, Nov. Gen. & Sp. Pl. 3 : 245 (1819).—Mez in Urban, Symb. Antill. 2 : 393 (1901); in Engler, Pflanzenr. IV. 236 : 89 (1902).—C. L. Lundell in Fieldiana, Bot. 24 (8) : 139 (1966).

Ardisia decipiens sensu Griseb., Fl. Brit. W. Ind. Is. : 395 (1861); non A. DC.
Icacorea compressa (Kunth) Standley in Contrib. U.S. Nat. Herb. 23 : 1110 (1924).

Hanover: *Proctor 10013* (BM; IJ), *Harris 10253* (BM; K; NY), *Britton & Hollick 2129* (NY), *Britton & Hollick 2164* (NY).

Westmoreland: *Proctor & Mullings 22060* (BM; IJ).

St. James: *Proctor 16166* (BM; IJ).

Ardisia compressa ranges from Mexico to northern South America, including Trinidad, but is not recorded from any other West Indian island. Humboldt and Bonpland collected the type near Caripe, Venezuela. Most continental specimens have the apex of the leaf more gradually tapered than have Jamaican specimens, which approximate most to some from British Honduras. The Jamaican specimens are all from the west of the island. The British Museum (Natural History) possesses an unlocalized specimen from Jamaica collected by William Wright who was in Jamaica in 1765–76 and 1782–85, living most of the time at Hampden, in Trelawny, and Mez suggests that this was of cultivated origin, which, however, seems unlikely. It is easily distinguished from other Jamaican species by its more intricately branched inflorescence, the lateral peduncles of which bear three or four secondary peduncles each with two to six small, whitish, brown-flecked flowers; the filaments of the stamens are about 0·5 mm. long, and much shorter than the anthers.

Subgenus 3. ***TINUS*** Mez

Ardisia subgen. Tinus Mez in Engler, Pflanzenr. IV. 236 : 124 (1902).
Lectotype: *Ardisia elliptica* Thunb. (*A. humilis* sensu Mez, pro parte; non Vahl).

Inflorescences axillary. Stamens with very short filaments. Species Asiatic and Australian, one often naturalized elsewhere.

8. ***Ardisia solanacea*** Roxb., Pl. Coast Coromand. 1 : 27, t. 27 (1795).—Sims in Curt. Bot. Mag. 40 : t. 1677 (1814).—Mez in Urban, Symb. Antill. 2 : 402 (1901); in Engler, Pflanzenr. IV. 236 : 132 (1902).—E. H. Walker in Philipp. Journ. Sci. 73 : 58 (1940). (Text-fig. 23 I.)

Ardisia humilis sensu A.DC. in DC., Prodr. 8 : 129 (1844); non Vahl.—Wight, Ic. Pl. Ind. Br. 4 : t. 1212 (1848).—Griseb., Fl. Brit. W. Ind. Is. : 396 (1861).—C. B. Clarke in Hook. f., Fl. Brit. Ind. 3 : 529 (1882).—De Wild., Ic. Select. Hort. Thenen. 1 : 79, t. 19 (1900).
Icacorea solanacea (Roxb.) Britton, Fl. Berm. : 284 (1918).

ST. JAMES: *Proctor 16461* (BM; IJ).

ST. MARY: *Harris 11637* (NY; UCWI), *Proctor 20615* (BM; IJ), *Adams 12076* (UCWI).

ST. ANDREW: *Grabham* (NY), *Adams 10094* (BM).

PORTLAND: *Powell 717* (BM; IJ; NY), *Proctor 16546* (BM; IJ; NY), *Proctor 19723* (BM; IJ; NY), *Marble 852* (NY), *Yuncker 18826* (BM), *Adams 11482* (BM; UCWI).

ST. THOMAS: *Nichols 191* (NY), *Powell 854* (IJ), *Harris & Britton 10585* (NY; UCWI), *Proctor 9217* (BM; IJ), *Webster & Wilson 5218* (BM; IJ), *Howard, Proctor & Stearn 14809* (BM; IJ), *Proctor 16450* (BM; IJ), *Yuncker 17523* (BM), *Yuncker 18826* (BM; UCWI), *Harris 6040* (NY), *Britton 3555* (NY), *Adams 10471* (UCWI).

A native of India, Malaya and China, long cultivated in tropical gardens, this has become naturalized here and there in Jamaica, usually along streams or on shaded road banks, and is sometimes called " Blackberry " or " Craingcraing ". It is easily recognized by its axillary few-flowered inflorescences with comparatively large pale rose flowers clustered almost umbellately at the end of the long peduncle.

2. *WALLENIA* Swartz

WALLENIA Swartz, Nov. Gen. & Sp. Pl. : 2, 31 (1788); Fl. Ind. Occ. 1 : 247 (1797); nomen conservandum No. 6304.

Petesioides Jacq. ex Kuntze, Revis. Gen. Pl. 2 : 402 (1891), nom. superfl.

Type (by monotypy): *W. laurifolia* Swartz (*Petesioides laurifolium* Jacq.)

Wallenia belongs to the tribe *Myrsineae* characterized by having the ovules few and arranged in a single series around the placenta. Both it and *Myrsine* can be readily distinguished by their small flowers, with the corolla 1·5–6 mm. long, from *Ardisia* of the tribe *Ardisieae*, characterized by having numerous ovules arranged in several series or apparently scattered over the placenta. The loose many-flowered inflorescence of *Wallenia* readily distinguishes it from *Myrsine* (*Rapanea*) which has flowers crowded in axillary clusters. The Jamaican species all belong to the subgenus *Wallenia* (subgenus *Euwallenia* Mez) which is confined to Jamaica, Cuba and Hispaniola and has an erect terminal paniculate inflorescence; the other subgenus, *Homowallenia* Mez, with pendulous axillary racemose inflorescences, occurs in Cuba, Hispaniola, Puerto Rico, and the Lesser Antilles but not in Jamaica.

The dioecious nature of *Wallenia* possibly militates against the formation of well-defined taxa within the genus; it certainly makes difficult the correlation of characters in herbarium material. The corolla of male flowers is much longer than the calyx; the anthers are borne on long exserted filaments. The corolla of female flowers is shorter or little longer than the calyx; the filaments are very short and the anthers aborted. Consequently female flowers are much less conspicuous than male flowers and are liable to be passed over by collectors as not being fully developed. Thus there is rarely available, from the same locality, male and female flowering material and mature fruiting material obviously belonging to the same species, which would provide the means of correlating other material. Instead some members of the genus are only known in one of these three possible states. The variability of the genus, presumably maintained by " out-breeding ", is such that two gatherings rarely match completely. Mez and Urban accordingly tended to describe each new gathering as representing a new species distinguished from its congeners by a combination of subtle rather than well-marked characters, the latter being few within the subgenus *Wallenia* (*Euwallenia* Mez). The lack of comparable material makes it difficult to assess the worth of such characters. In preparing the present account it has not been possible to devise a key making full use of floral characters and unfortunately the vegetative characters used tend either to overlap or to be difficult to express without appearing too definite and exclusive or too vague and hence useless. Thus while the key should lead to the identification of typical material of the species, it would be too optimistic to expect conclusive results with all specimens. *Wallenia laurifolia* occurs in Cuba, Hispaniola and Jamaica, *W. subverticillata* in Cuba and Jamaica; the other species accepted here are apparently endemic to Jamaica.

Key to Jamaican Species

Leaves with base broadly rounded and slightly cordate, paired or in whorls of three together, fairly large (3–17 cm. broad), the petiole short (less than 6 mm. long) or lacking:
  Leaves rounded at the apex, 7–17 cm. broad:
    Leaves sessile . . . . 1. *W. clusioides*
    Leaves with 3–6 mm. long petiole . . . . . . 2. *W. elliptica*
  Leaves narrowed towards the acute or obtuse apex, 3–6 cm. broad
    3. *W. subverticillata*
Leaves with base cuneate or attenuate, rarely rounded (the petiole then 1 cm. or more long), usually alternate, only occasionally paired or whorled, the petiole short or long:
  Leaves reticulate-veined beneath, with slightly raised cross-veins between the main lateral veins:
    Petiole short, c. 1–8 mm. long; blades under 11 cm. long:
      Leaves mostly broadest at the middle and gradually narrowed from there to the apex:
        Petiole very short, 1–4 mm. long; blade inconspicuously punctate beneath
        4. *W. fawcettii*

Petiole longer (5–8 mm. or more long); blade conspicuously punctate beneath . . . . 10. *W. venosa*

Leaves mostly broadest above the middle with the apex rounded or obtuse:

Leaf-blades 2–8 cm. long, less than 3·5 cm. broad; crest of Blue Mountains 5. *W. crassifolia*

Leaf-blades larger (5–11 cm. long):

Leaves coriaceous, firm, greyish or glaucescent; female calyx c. 1·4 mm. long . . . . 6. *W. corymbosa*

Leaves chartaceous, thinner:

Leaves drying light green; female calyx c. 1·5 mm. long 11. *W. purdieana*

Leaves drying brownish; female calyx 1 mm. long 7. *W. xylosteoides*

Petiole longer (c. 8–30 mm. long); blades mostly more than 11 cm. long:

Leaf-blades nearly three times as long as broad, mostly narrowly elliptic:

Base of blade narrowly cuneate or attenuate . . 8. *W. erythrocarpa*

Base of blade rounded or abruptly contracted . . 12. *W. grisebachii*

Leaf-blades about twice as long as broad, mostly elliptic or narrowly obovate:

Lateral veins spreading outwards from the midrib at an angle of about 40° 9. *W. punctulata*

Lateral veins spreading outwards from the midrib at an angle of about 50–70°:

Male flower with calyx 1·5–2·5 mm. long, corolla 2·5–4 mm. long; persistent fruiting calyx not more than 1·5 mm. long:

Leaves usually densely blackish-punctate and somewhat mottled beneath, strongly veined, the base cuneate . 10. *W. venosa*

Leaves inconspicuously punctate and not mottled beneath, lightly veined, the base cuneate or rounded or abruptly contracted:

Leaves drying light green; inflorescence glabrous, loose; male flower with corolla yellowish, not punctate; style about 0·8 mm. long 11. *W. purdieana*

Leaves drying brownish; inflorescence minutely pubescent, compact; male flower with corolla reddish, distinctly punctate; style about 1·5 mm. long . . . . . 12. *W. grisebachii*

Male flower with calyx c. 3 mm. long, corolla 5–6 mm. long; persistent fruiting calyx about 2·5 mm. long . . 13. *W. calyptrata*

Leaves pinnately veined beneath, i.e. without raised cross-veins between the main lateral veins:

Blades of some or all leaves abruptly contracted at base into the petiole; inflorescence usually minutely pubescent . . . 12. *W. grisebachii*

Blades of all leaves gradually narrowed into the petiole; inflorescence glabrous:

Blades of leaves mostly less than 12 cm. long, 6 cm. broad; petiole not more than 1 cm. long . . . . 14. *W. laurifolia*

Blades of leaves up to 25 cm. long, 11 cm. broad, mostly more than 12 cm. long, 6 cm. broad; petiole 1–2 cm. long:

Fruits vertically ribbed	15. *W. sylvestris*
Fruits not ribbed	16. *W. discolor*

1. **Wallenia clusioides** (Griseb.) Mez in Urban, Symb. Antill. 2 : 411 (1901); in Engler, Pflanzenr. IV. 236 : 245 (1902).

Ardisia clusioides Griseb., Fl. Brit. W. Ind. Is. : 396 (1861) excl. specim. Alexander.

HANOVER: *Harris 10333* (BM; NY), *Proctor 10028* (IJ), *Proctor 26590* (IJ).
WESTMORELAND: *Purdie* (K, lectotype), *Harris 10210* (BM; NY).
ST. JAMES: *Harris 9177* (BM; NY).
ST. ELIZABETH: *Harris 9761* (NY), *Britton 1110* (NY), *Proctor 26530* (IJ).

W. clusioides is a species of western Jamaica notable for its very large sessile and subcordate leaves 15–31 cm. long, 7–17 cm. broad. It forms a small tree or tall shrub 6–20 ft. (2–6 m.) high. The female flowers are unknown. The greenish-yellow male flowers have the calyx 1·5–2 mm. long, the corolla about 2·5 mm. long.

2. **Wallenia elliptica** Urban, Symb. Antill. 6 : 30 (1909). (Pl. 9a.)

Ardisia clusioides Griseb., Fl. Br. W. Ind. Is. : 396 (1861) pro parte, quoad specim. Alexander.

ST. ANN: *Alexander 569* (K; NY; type-collection), *Britton & Hollick 2776* (NY).

An obscure species described by Urban on a specimen collected by Alexander at Grierfield near Moneague, St. Ann, *W. elliptica* is provisionally kept apart from *W. clusioides* on account of the shortly petioled leaves. The male flowers are unknown. The female flowers have the calyx and corolla about 1·5 mm. long.

3. **Wallenia subverticillata** (Britton) Ekman ex Urban, Symb. Antill. 9 : 412 (1925).—Alain in León & Alain, Fl. Cuba 4 : 111 (1957). (Text-fig. 24K.)

Petesioides subverticillatum Britton in Bull. Torrey Bot. Club 37 : 355 (1910).

PORTLAND: *Proctor 22102* (IJ).
ST. THOMAS: *Britton 3937* (NY), *Harris & Britton 10694* (NY, holotype; UCWI), *Harris & Britton 10701* (K; NY), *Britton 4049* (NY), *Proctor 28681* (BM).

Wallenia subverticillata, a species of mountain woods at 1,000–2,000 ft. (300–600 m.), is distinguished by having its leaves grouped in pairs or threes; they are almost sessile and are much narrower and more attenuate towards the apex than those of *W. clusioides* but are nevertheless extremely variable in shape and size, e.g. 5–20 cm. long, 3–5 cm. broad on the same plant. The type was collected by Harris and Britton on a slope below Big Level, eastern St. Thomas. Rather surprisingly, specimens of what appear to be the same species have been collected in Las Villas, Cuba, by Ekman. The calyx of male flowers is 2–2·5 mm. long, of female flowers about 1 mm. long; the corolla of male flowers is about 2·5 mm. long, of female flowers about 1 mm. long, slightly longer than the calyx.

4. **Wallenia fawcettii** Mez in Urban, Symb. Antill. 2 : 408 (1901); in Engler, Pflanzenr. IV. 236 : 244 (1902). (Pl. 9b.)

PORTLAND: *Maxon & Killip 714* (NY).

PORTLAND or ST. THOMAS: *Harris 5422* (NY, type collection).

ST. THOMAS: *Proctor 9684* (IJ).

From other relatively small-leaved and short-petioled species, *Wallenia fawcettii* may be recognized by its more attenuate leaves, which are gradually narrowed above the middle to a usually acute apex. It is known only from the crest of the Blue Mountains, at about 5,000–5,500 ft. (1,500–1,700 m.); the type was collected by Harris near Portland Gap but whether on the Portland or St. Thomas side is uncertain. The calyx of male flowers is about 1·5 mm. long, of female flowers about 1 mm. long; the corolla of male flowers is about 2·5 mm. long, of female flowers unknown.

5. ***Wallenia crassifolia*** Mez in Urban, Symb. Antill. 2 : 409 (1901); in Engler, Pflanzenr. IV. 236 : 244 (1902). (Pl. 10a.)

Wallenia venosa Griseb., Fl. Brit. W. Ind. Is. : 394 (1861) pro parte, excl. specim. Wilson.

ST. ANDREW: *Proctor 9890* (IJ; NY), *Proctor 9524* (BM; IJ), *Maxon & Killip 1026* (NY), *Philipson 932* (BM), *E. G. Britton 3866* (NY), *Purdie* (K, holotype).

ST. THOMAS: *Webster & Wilson 5445* (IJ), *Proctor 9207* (IJ), *Stearn 101* (BM), *Proctor 11458* (IJ).

Wallenia crassifolia inhabits mountain rain forest along the crest of the Blue Mountains between 4,750 and 6,500 ft. (1,400–2,000 m.). That the smallness of its elliptic or narrowly elliptic leaves is not simply a reduction occasioned by its high mountain environment is shown by the occurrence of the large-leaved and undoubtedly distinct *W. calyptrata* in the same habitat. The type-locality of *W. crassifolia* is Morces Gap, where it was first collected by William Purdie in 1843. The calyx of male flowers is about 2 mm. long, of female flowers about 1 mm. long, the corolla of male flowers about 4 mm. long, of female flowers unknown.

6. ***Wallenia corymbosa*** Urban, Symb. Antill. 5 : 457(1908). (Text-fig. 24A–J.)

TRELAWNY: *Harris 8720* (BM; NY; UCWI; type-collection), *Harris 9095* (NY; UCWI).

CLARENDON: *Harris 10864* (NY), *Harris 10996* (NY), *Harris 12781* (BM; NY; UCWI), *Harris 12803* (NY; UCWI).

ST. ANN: *Howard & Proctor 15037* (IJ), *Howard & Proctor 15170* (BM; IJ), *Proctor 26739* (BM).

Typical *Wallenia corymbosa* inhabits the central hills of Jamaica at about 2,000–2,500 ft. (600–760 m.), probably extending well into the Cockpit Country, and is notable for its thick greyish or glaucescent narrowly obovate leaves.

The type-locality is on Crown Lands near Troy, where William Harris collected it at 2,500 ft. (760 m.) in 1904. Subsequent collections in the same area have provided an unusually adequate representation of it in male and female flower and in fruit. The flowers are described as " pale yellow with red spots " or " cream with red stripes". The calyx of male flowers is 1·5–2 mm. long, of female flowers about 1·4 mm. long, the corolla of male flowers 3–4 mm. long, of female flowers about 2·5 mm. long. The fruits are about 3·5 mm. broad.

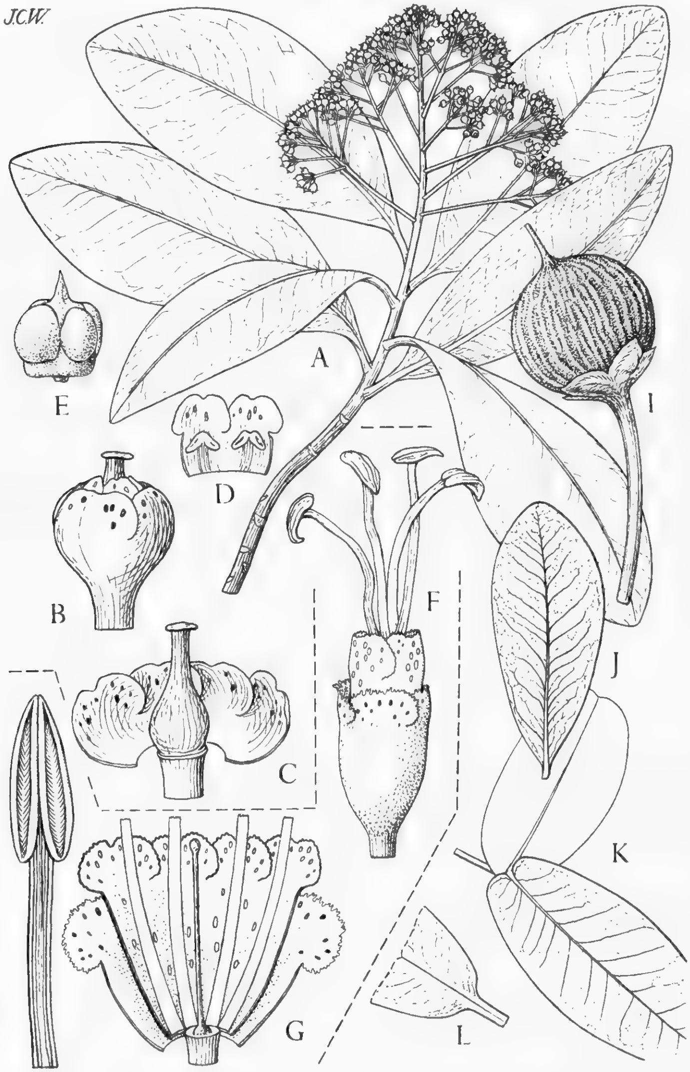

FIG. 24. *Wallenia corymbosa* Urban: A, female flowering specimen (*Harris 12803*), × ½; B, female flower (*Harris 12803*), × 6; C, dissected calyx and gynoecium of female flower (*Harris 12803*), × 8; D, dissected corolla of female flower with aborted stamens (*Harris 12803*), × 8; E, placenta of female flower (*Harris 12803*), × 20; F, male flower (*Harris 12819*), × 8; G, dissected corolla of male flower with aborted gynoecium (*Harris 12819*), × 8; H, anther of male flower (*Harris 12819*), × 20; I, fruit (*Harris 12781*), × 5; J, leaf (*Harris 12781*), × ½. *Wallenia subverticillata* (Britton) Ekman: K, leaves (*Harris & Britton 4049*), × ½. *Wallenia grisebachii* Mez: L, leaf-base (*Proctor 8247*), × ½.

7. ***Wallenia xylosteoides*** (Griseb.) Mez in Urban, Symb. Antill. 2 : 409 (1901); in Engler, Pflanzenr. IV. 236 : 244 (1902). (Pl. 10b.)

Ardisia xylosteoides Griseb., Fl. Br. W. Ind. Is. : 395 (1861) tantum quoad pl. Jamaic.

St. Ann: *Alexander 568* (K, lectotype).

Grisebach reported his *Ardisia xylosteoides* from " Haiti!; Mexico!; New Granada! " as well as Jamaica; these records cannot apply all to one species. Mez in 1901 restricted the epithet *xylosteoides* to Jamaican material collected by Alexander on St. Ann's Road, Moneague. The same species is represented by *Jamaican Plants 1118* (UCWI) and *1141* (K) without locality. The calyx of female flowers is about 1 mm. long, the corolla scarcely longer. Male flowers and fruit are unknown. The epithet indicates a resemblance in leaf-form to *Lonicera xylosteum* L., the *Xylosteum* of pre-Linnaean authors.

8. ***Wallenia erythrocarpa*** Urban, Symb. Antill. 6 : 29 (1909). (Pl. 11a.)

Hanover: *Harris 10343* (BM; NY; UCWI; type-collection).
Westmoreland: *Harris 7080* (UCWI).

This species is still only known from material collected by Harris, the type from Fray Woods at 1,650–1,800 ft. (500–550 m.) in 1908; he gathered other material at Grandvale at 500 ft. (150 m.) in 1898. It is notable for its large but relatively narrow long-petioled leaves with prominent reticulate veining, their narrowly elliptic-oblong shape and their size (11–21 cm. long, 4·5–7·5 cm. broad) distinguishing it from *W. venosa*. The calyx in fruit is about 1 mm. long. Male and female flowers are unknown.

9. ***Wallenia punctulata*** Urban, Symb. Antill. 7 : 322 (1912). (Pl. 11b.)

Manchester: *Britton 3281* (NY; type collection).

Wallenia punctulata is another little-known species, known only from the type-collection gathered by N. L. Britton in 1908 between Brown's Town and Porus, but distinguished from other species with prominently reticulate-veined leaves by its more oblique lateral veins which pass outwards from the midrib at an angle of about 40°. The calyx in fruit is about 2 mm. long, the corolla of female flowers according to Urban about 1·7 mm. long.

10. ***Wallenia venosa*** Griseb., Fl. Brit. W. Ind. Is. : 394 (1861) quoad specim. Wilson.—Mez in Urban, Symb. Antill. 2 : 410 (1901); in Engler, Pflanzenr. IV. 236 : 245 (1902).—Urban, Symb. Antill. 7 : 322 (1912). (Pl. 13a.)

Hanover: *Britton 2425* (NY), *Britton 2292* (NY), *Britton 2326* (NY).
Westmoreland: *Harris 10248* (BM; NY).
Trelawny: *Harris 8768* (BM; NY; UCWI).
St. Elizabeth: *Harris 9925* (BM; K; NY; UCWI).
Manchester: *Britton 3712* (NY).
Clarendon: *Proctor 18400* (BM; IJ), *Proctor 26514* (BM; IJ), *Proctor 27637* (BM; IJ).
St. Ann: *Proctor 26514* (BM).

St. Andrew: *Harris 5633* (BM; NY; UCWI), *Harris 6126* (BM), *Harris 16032* (BM; NY; UCWI), *Adams 11845* (UCWI).

St. Thomas: *Harris & Britton 10745* (NY), *Britton 3963* (NY), *Britton 3988* (NY), *Britton 4145* (NY).

The lectotype of this widespread species is *Wilson 388* (GOET, K), collected in 1858 without specified locality, which was designated by Mez in 1901. *Wallenia venosa* has prominently reticulate-veined leaves with black dots beneath sometimes so numerous as to give it a somewhat mottled appearance. The calyx of male flowers is 1·5–2 mm. long, of female flowers 0·8 mm. long, the corolla of male flowers about 3 mm. long, of female flowers about 1 mm. long. The *Alexander* specimen (GOET) from the Blue Mountains cited by Grisebach under *W. venosa* belongs to *W. crassifolia*.

11. ***Wallenia purdieana*** Mez in Urban, Symb. Antill. 2 : 408 (1901); in Engler, Pflanzenr. IV. 236 : 243 (1902). (Pl. 12a.)

Hanover: *Harris 10305* (BM; UCWI), *Proctor 11301* (IJ).

St. James: *Proctor 22992* (BM; IJ).

Trelawny: *Harris 9096* (UCWI), *Britton 510* (NY), *Proctor 15663* (BM; IJ), *Howard, Proctor & Stearn 14663* (BM; IJ).

Manchester: *Purdie* (K, type), *Proctor 16118* (BM; IJ), *Howard, Proctor & Wagenknecht 20520* (NY), *Harris & Britton 10601* (BM; NY; UCWI), *Robertson 5416* (UCWI).

Wallenia purdieana is a species of western and central Jamaica between 1,000 ft. (300 m.) and 3,000 ft. (900 m.). The type was collected by William Purdie in Manchester, but without specified locality. The leaves on drying retain their green colour unlike those of other species which become brownish or grey. The calyx of male flowers is about 2 mm. long, of female flowers about 1·5 mm. long, the corolla of male flowers about 3 mm. long, of female flowers about 1·5–2 mm. long.

12. ***Wallenia grisebachii*** Mez in Urban, Symb. Antill. 2 : 411 (1901) quoad specim. Wullschlägel 1338; in Engler, Pflanzenr. IV. 236 : 245 (1902).—Urban, Symb. Antill. 6 : 31 (1909). (Text-fig. 24L; Pl. 12b.)

Wallenia laurifolia sensu Griseb., Fl. Brit. W. Ind. Is. : 394 (1861) pro parte; non Swartz.

St. James: *Proctor 22154* (BM; IJ).

St. Elizabeth: *Howard & Proctor 13745* (IJ; NY), *Howard & Proctor 13755* (IJ).

Trelawny: *Perkins 1385* (K).

Manchester: *Wullschlägel 1338* (Munich, lectotype), *S. Brown 300* (NY), *Robertson 5470* (UCWI), *Adams 10116* (UCWI), *Adams 11766* (UCWI).

Clarendon: *Proctor 8247* (IJ).

St. Ann: *Britton & Hollick 2776* (NY; UCWI).

The species *W. grisebachii* as accepted here consists of plants with fairly large coriaceous leaves having the rounded base contracted abruptly into the petiole and becoming brownish on drying. Mez separated *W. grisebachii* from among material included by Grisebach in *W. laurifolia*. Urban further divided this, restricting the name *W. grisebachii* to the taxon represented by ***Wullschlägel 1338*** collected at

Fairfield, Springfield, in Manchester parish, between 1847 and 1849. The inflorescence is compact; the flowers are rusty brown. The calyx of male flowers is 2 mm. long, of female flowers 1·5–2 mm. long, the corolla of male flowers about 4 mm. long, of female flowers about 1·5 mm. long.

13. ***Wallenia calyptrata*** Urban, Symb. Antill. 5 : 458 (1908); in Fedde, Repert. Sp. Nov. 13 : 469 (1915).

St. Andrew: *Shreve s.n.* (NY), *J. A. Harris & Lawrence 15490* (NY), *Adams 7440* (UCWI).

Portland: *Proctor 26717* (BM; IJ).

St. Thomas: *Proctor 9638* (IJ), *Proctor 9683* (IJ; NY), *Stearn 104* (BM), *Proctor 11457* (IJ).

Although the type-gathering of *W. calyptrata* made by Rehder in 1903 at Morces Gap has not been seen, the agreement of Urban's description with the other material collected along the crest of the Blue Mountains leaves no doubt as to its identity. Its range here seems to be between 5,000 ft. (1,500 m.) and 7,000 ft. (2,100 m.) in mountain mist-forest. It has prominently reticulate-veined leaves 8–14 cm. long, 3·5–6 cm. broad, and larger male flowers than other species. The calyx of male flowers is 3–3·5 mm. long, of female flowers 2·5 mm. long, the corolla of male flowers 5–6 mm. long, of female flowers 3 mm. long.

14. ***Wallenia laurifolia*** Swartz, Nov. Gen. & Sp. Pl. : 31 (1788); Fl. Ind. Occ. 1 : 248 (1797).—Mez in Urban, Symb. Antill. 2 : 407 (1901); in Engler, Pflanzenr. IV. 236 : 243 (1902).—Urban, Symb. Antill. 8 : 521 (1921).—Alain in León & Alain, Fl. Cuba 4 : 110, fig. 42 (1957).

Petesioides laurifolium Jacq., Select. Stirp. Amer. Hist. : 17 (1763), nom. invalid.
Wallenia clusiifolia Griseb., Fl. Brit. W. Ind. Is. : 394 (1861).
" Bryonia nigra fruticosa, foliis laurinis, floribus racemosis speciosis " Sloane, Cat. Pl. Jam. : 106 (1696); Voy. Jam. Nat. Hist. 1 : 234, t. 145 f. 2 (1707).

Hanover: *Proctor 10035* (BM; IJ).

Manchester: *S. Brown 138* (NY), *Proctor 24175* (BM; IJ), *Crawford 775* (NY), *Farr & Sanderson 22334* (IJ), *Harris & Britton 10613* (NY; UCWI), *Howard & Proctor 14964* (IJ), *Howard, Proctor & Wagenknecht 20520* (BM; IJ), *Harris 12862* (BM; NY), *Howard, Proctor & Stearn 14708* (BM; IJ).

Clarendon: *Harris 11188* (NY; UCWI).

St. Ann: *Stearn 603* (BM), *Proctor 11907* (IJ), *Proctor 8632* (IJ), *Proctor 16142* (IJ).

St. Catherine: *Britton 2616* (NY).

St. Mary: *Sloane, Herb. IV. 494* (BM), *Proctor 7554* (NY; IJ).

St. Andrew: *Harris 6880* (BM; NY; UCWI).

Portland: *Stearn 538* (BM), *Proctor 11841* (IJ), *Wight 195* (NY), *Maxon & Killip 830* (NY), *Harris & Britton 10767* (K; NY), *Proctor 11347* (BM; IJ), *Proctor 11352* (IJ), *Proctor 16259* (IJ), *Howard, Proctor & Stearn 14758* (BM; IJ), *Stearn 226* (BM; UCWI), *Britton 4121* (NY).

St. Thomas: *Britton 4109* (NY), *Powell 1647* (BM; IJ).

This widespread species, first described from Hispaniola and also known from Cuba, is mainly distinguished by its relatively inconspicuous veining with the areas between the main lateral veins flat, not reticulate with prominent veinlets. The material from the upper part of the John Crow Mountains exemplified by *Proctor 9822* gathered at 1,500–2,500 ft. (450–750 m.), with very small leaves (to 6 cm. long) and reduced inflorescence, differs much in appearance from that of the coast, exemplified by *Stearn 226*, but these differences are assumed to result from the diversity of habitat, as small leaves approaching these are to be found on some specimens from elsewhere referred to this species, e.g. *Howard, Proctor & Stearn 14708* from Manchester, *Proctor 8632* from St. Ann, and *Proctor 10035* from Hanover, and intermediates occur moreover on the John Crow Mountains. The calyx of male flowers is 1·5–2·5 mm. long, of female flowers about 1·5 mm. long, the corolla of male flowers 2·5–3 mm. long, of female flowers about 1·5 mm. long.

15. ***Wallenia sylvestris*** Urban in Fedde, Repert. Sp. Nov. 13 : 468 (1915). (Pl. 13b.)

PORTLAND: *Proctor 10477* (IJ; NY), *Proctor 16258* (IJ), *Proctor 5266* (BM; IJ), *Proctor 5244* (IJ).

PORTLAND or ST. THOMAS: *Harris & Britton 10720* (NY, type-collection), *Harris & Britton 10690* (K; NY; UCWI), *Harris & Britton 10776* (NY; UCWI).

This species is apparently confined to mountain woods on the John Crow Mountains at 1,500–2,500 ft. (450–750 m.). The type-locality is the southern end of the John Crow Mountains near the boundary of the parishes of Portland and St. Thomas. It is notable for its large long-petioled leaves with elliptic or narrowly elliptic (rarely obovate or narrowly obovate) blades up to 22 cm. long, 9 cm. broad. The calyx and corolla of female flowers are about 2 mm. long. The male flowers are unknown. The subglobose fruits are slightly punctate and vertically ribbed.

16. ***Wallenia discolor*** Urban, Symb. Antill. 6 : 29 (1909).

ST. ANN: *Alexander* (fide Urban).

Described by Urban from fruiting material collected by Alexander, probably in St. Ann but without recorded locality, this appears to be distinguished from *W. laurifolia* by its larger leaves (18–25 cm. long), shorter pedicels (0·5–3 mm. long) and coarsely punctate but not ribbed fruits. Male and female flowers are unknown.

3. *MYRSINE* L.

MYRSINE L., Sp. Pl. 1: 196(1753), Gen. Pl. ed. 5: 90(1754).

Type (by monotypy): *M. africana* L.

The genus *Myrsine* as accepted here includes the groups kept apart by Mez as *Myrsine, Rapanea* and *Suttonia.*

KEY TO JAMAICAN SPECIES

Young shoots and petioles minutely pubescent; leaf-blades mostly narrowly elliptic and mostly less than 2·5 cm. broad; corolla lobes joined for the lower 0·5 mm. or more . . . . 1. *M. coriacea*

Young shoots and petioles glabrous; leaf-blades mostly obovate or narrowly obovate and mostly more than 2·5 cm. broad; corolla lobes free to the base
2. M. acrantha

1. ***Myrsine coriacea*** (Swartz) R. Br. ex Roem. & Schult. in L., Syst. Veg., ed. nov. 4 : 511 (1819).—A. DC. in DC., Prodr. 8 : 99 (1844). (Text-fig. 25E–H.)

Samara coriacea Swartz, Nov. Gen. & Sp. Pl. : 32 (1788); Fl. Ind. Occ. 1 : 261 (1797).
Caballeria ferruginea Ruiz & Pavon, Syst. Veg. Fl. Peruv. & Chil. 1 : 280 (1798).
Myrsine ferruginea (Ruiz & Pavon) Spreng. in L., Syst. Veg., ed. 16, 1 : 664 (1825).
Myrsine laeta sensu Griseb., Fl. Brit. W. Ind. Is. : 392 (1861); non A.DC.
Rapanea coriacea (Swartz) Mez in Urban, Symb. Antill. 2 : 428 (1901); in Engler, Pflanzenr. IV. 236 : 380 (1902).
Rapanea ferruginea (Ruiz & Pavon) Mez in Urban, Symb. Antill. 2 : 429 (1901); in Engler, Pflanzenr. IV. 236 : 381 (1902).—Urban, Symb. Antill. 8 : 522 (1921).—Britton & Wilson in Sci. Surv. Puerto Rico 6 : 61 (1925).—Alain in León & Alain, Fl. Cuba 4 : 112, fig. 43 (1957).—J. F. Macbr. in Publ. Field Mus. Nat. Hist., Bot. 13 (5) : 168 (1959).—Little & Wadsworth, Common Trees of Puerto Rico : 432, fig. 203 (1964).

ST. JAMES: *Norman 50* (BM).

TRELAWNY: *Webster, Proctor & Powell 5355* (BM; IJ), *Britton 486* (NY), *Adams 12413* (UCWI).

MANCHESTER: *Proctor 21920* (BM; IJ), *Britton 3216* (NY), *Adams 8466* (UCWI), *Proctor 23118* (BM; IJ).

CLARENDON: *Proctor 9723* (IJ), *Proctor 8427* (IJ), *Proctor 15905* (BM; IJ; UCWI).

ST. ANN: *Proctor & Howard 14992* (IJ), *Howard, Proctor & Stearn 14607* (BM; IJ), *Proctor 7471* (BM; IJ), *Skelding 3016* (UCWI), *Adams 12698* (UCWI).

ST. CATHERINE: *Howard & Proctor 13599* (IJ).

ST. ANDREW: *Adams 12675* (UCWI), *Britton 147* (NY).

PORTLAND: *Philipson 933* (BM), *Proctor 10110* (IJ; NY), *Howard, Proctor & Stearn 14767* (BM; IJ).

ST. THOMAS: *Webster & Wilson 5454* (IJ), *Stearn 111* (BM), *Proctor 11463* (IJ), *Maxon 9442* (US), *Proctor 1108* (IJ), *Stearn 505* (BM).

A widely ranging species, recorded in the West Indies from Cuba, Hispaniola, Jamaica, Puerto Rico and the Lesser Antilles and on the American mainland from Mexico to Peru, Chile, Bolivia and Argentina, this is commonly known as *Rapanea ferruginea*, a name based on Peruvian material; Swartz's *Samara coriacea*, based on Jamaican material being, in my opinion, conspecific, his epithet is adopted here. It is sometimes called " colic wood " in Jamaica, according to Proctor.

2. ***Myrsine acrantha*** Krug & Urban in Notizbl. K. Bot. Gart. Mus. Berlin 1 : 79 (1895); in Urban, Symb. Antill. 1 : 380 (1899). (Text-fig. 25A–D.)

Myrsine coriacea sensu Griseb., Fl. Brit. W. Ind. Is. : 392 (1861); non (Swartz) R. Br.
Rapanea guianensis Mez in Urban, Symb. Antill. 2 : 431 (1901); in Engler, Pflanzenr. IV. 236 : 392 (1902) pro parte, quoad pl. Jamaic.; non Aubl.
Rapanea acrantha (Krug & Urban) Mez in Urban, Symb. Antill. 2 : 433 (1901); in Engler, Pflanzenr. IV. 236 : 376 (1902).

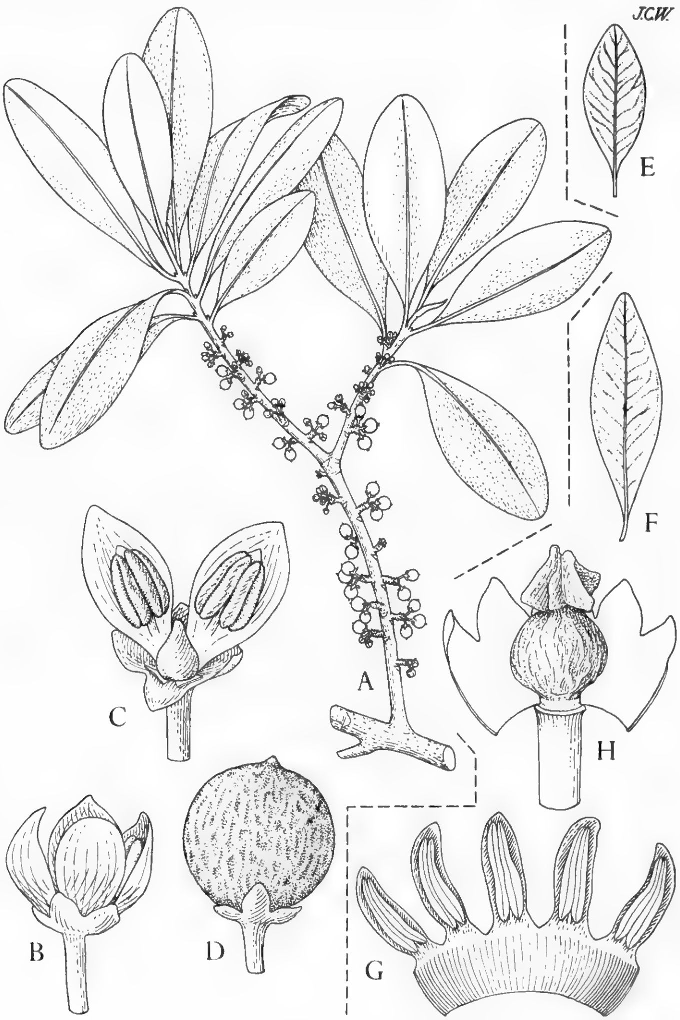

FIG. 25. *Myrsine acrantha* Krug & Urban: A, fruiting specimen (*Robertson 5372*), × ½; B, flower (*Harris 8295*), × 10; C, dissected flower with aborted gynoecium (*Harris 8295*), × 10; D, fruit (*Harris 7061*), × 5. *Myrsine coriacea* Swartz: E, leaf (*Stearn 111*), × ½; F, leaf (*Stearn 505*), × ½; G, dissected corolla with stamens (*Stearn 111*), × 10; H, dissected calyx with gynoecium (*Stearn 111*), × 10.

WESTMORELAND: *Proctor & Mullings 22061* (BM; IJ).

ST. ELIZABETH: *Britton 1320* (NY), *Proctor 7754* (BM; IJ), *Howard & Proctor 13682* (IJ).

MANCHESTER: *Howard, Proctor & Wagenknecht 20521* (BM; NY; UCWI), *Robertson 5372* (BM; K; UCWI), *Harris 8295* (BM; NY; UCWI), *Proctor 21908* (BM; IJ), *Proctor 11619* (BM; IJ), *S. Brown 159* (NY), *Adams 10114* (UCWI), *Proctor 23130* (IJ).

St. Andrew: *Harris 6072* (NY), *Harris 5398* (K; NY; UCWI; type-collection of *Myrsine acrantha*), *Harris 5398 bis* (BM; UCWI), *A. von der Porten 2035* (IJ), *Harris 5528* (NY; UCWI), *Loveless 1502* (IJ; UCWI).

Portland: *Proctor 19737* (BM; NY; UCWI).

St. Thomas: *Proctor 9580* (BM; IJ).

Myrsine acrantha has hitherto been regarded as a rare and obscure species, known only from the type and topotype collections gathered by Harris in 1894 and 1895 at Strawberry Hill Cottage high in the Blue Mountains of St. Andrew. Mez distinguished it by its free petals from the two other Jamaican species accepted by him under the names *Rapanea ferruginea* and *R. guianensis*. Thus according to his own generic key in the *Pflanzenreich* IV. 236 : 15 (1902) it should be referred to the otherwise Pacific Ocean group *Suttonia*! In fact all the Jamaican specimens hitherto referred to *Myrsine* (or *Rapanea*) *guianensis* agree with *M. acrantha* in having obovate or narrowly obovate leaves, flowers borne on very short bract-covered lateral shoots, and free petals. *Myrsine guianensis* (Aubl.) Kuntze does not occur in Jamaica; it was described by Aublet in 1775 (Hist. Pl. Guiane Franç. 1 : 121; 3 : t. 46) as *Rapanea guianensis* from French Guiana and is accepted by Mez as ranging from Florida over the West Indies to the Guianas and over Mexico and Central America to Bolivia. Typical *M. guianensis* as represented by specimens from French Guiana (*Aublet! Sagot 913! Martin!*) is notable for its large obovate leaves up to 10 cm. long, 7 cm. broad, with a glossy almost varnished upper surface and distinctly punctate lower surface; plants of similar character occur in Bolivia, Colombia, British Guiana, and Surinam. Very similar to this but distinguishable by the leaves being marked with short lines beneath is *M. trinitatis* A.DC. occurring in Trinidad, Tobago, Grenada, Martinique and Puerto Rico. Plants from Hispaniola, Cuba, Jamaica, the Bahamas and Florida stand apart from these in their smaller leaves, rarely more than 8 cm. long, 2·5 cm. broad, less glossy above, punctate but not lined beneath. Whether more than one taxon is represented in this mostly sterile material is uncertain. Some specimens from Cuba, e.g. *Ekman 15603* (Oriente province), and from Haiti, e.g. *E. C. Leonard 8456* (Departement du Nord) in their leaves and short spurs unfortunately lacking flowers, closely resemble the Jamaican *M. acrantha*. In the Bahamas and Florida the plants of this alliance as represented by *A. Curtiss 44* from New Providence, Bahamas, and *R. A. Howard 8047* and *Tracy 7454* from Florida have their five corolla-lobes fused at the base for about 0·4–0·5 mm., as figured by Small (Man. Southeast Fl. : 1029 (1933)). They represent a species distinct from *M. acrantha* for which the correct name appears to be *Myrsine punctata*.*

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* ***Myrsine punctata*** (Lam.) Stearn, comb. nov.
Sideroxylum punctatum Lam., Tabl. Encyc. & Méth., Bot. 2: 42 (1794) [from Carolina, *Michaux*].
Bumelia punctata (Lam.) Roem. & Schult. in L., Syst. Veg., ed. nov. 4 : 498 (1819).
Myrsine floridana A.DC. in Trans. Linn. Soc. London 17 : 107 (1834); in DC., Prodr. 8 : 98 (1844) [from Florida].
Rapanea guyanensis sensu Small, Man. Southeast Fl. : 1029, fig. (1933); non Aublet.

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DR. WILLIAM T. STEARN, D.Sc., Sc.D.
Dept. of Botany
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD, LONDON, S.W.7

Ardisia tinifolia Swartz; original drawing by Swartz.

PLATE 7

Ardisia tinifolia Swartz; original drawing by Swartz representing *A. coriacea* Swartz.

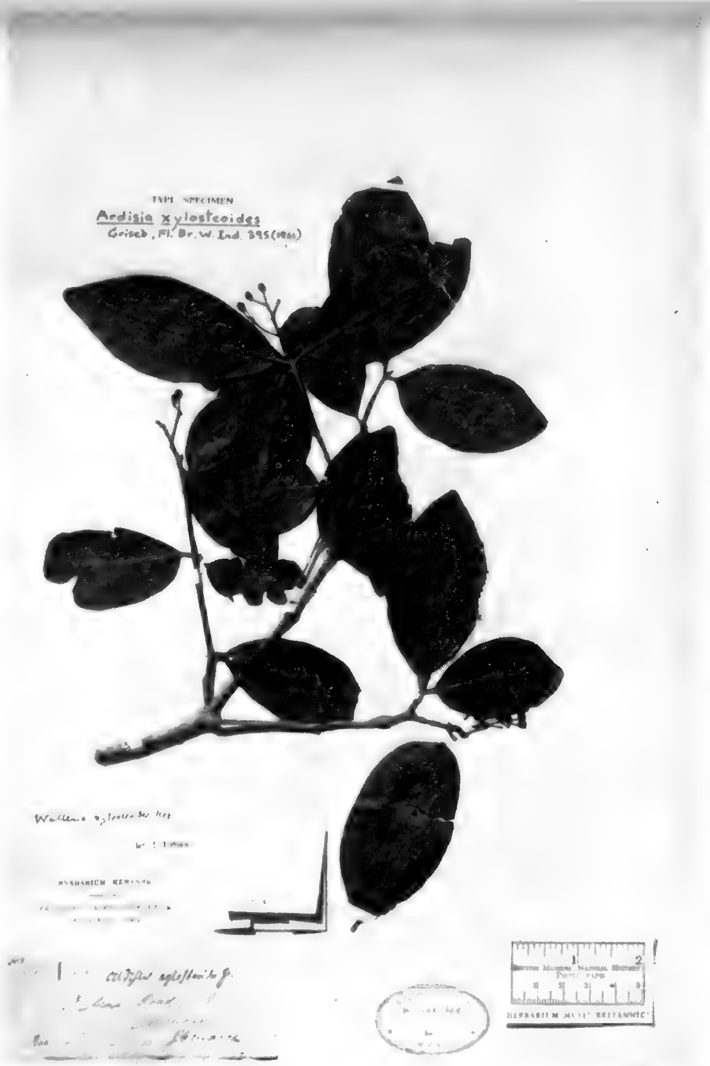
(b) *Ardisia byrsonimae* Stearn; holotype (*Stearn 9*).

(a) *Ardisia brittonii* Stearn; holotype (*Harris & Britton 10558*).

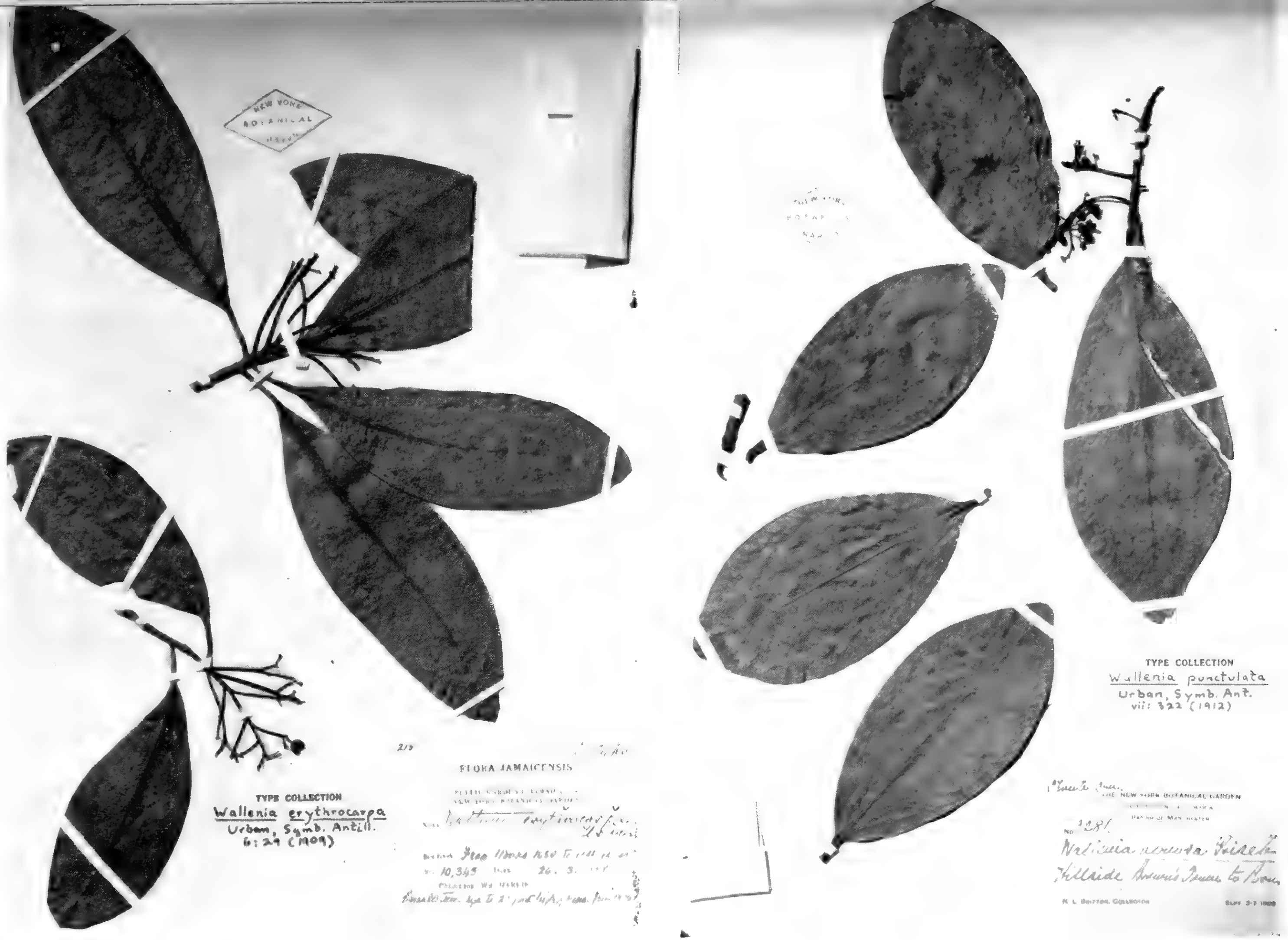
(a) *Wallenia elliptica* Urban; isotype (*Alexander*).

(b) *Wallenia fawcettii* Mez; isotype (*Harris 5422*).

(a) *Wallenia crassifolia* Mez; below, lectotype (*Purdie*); above, representative specimen (*Stearn 101*).



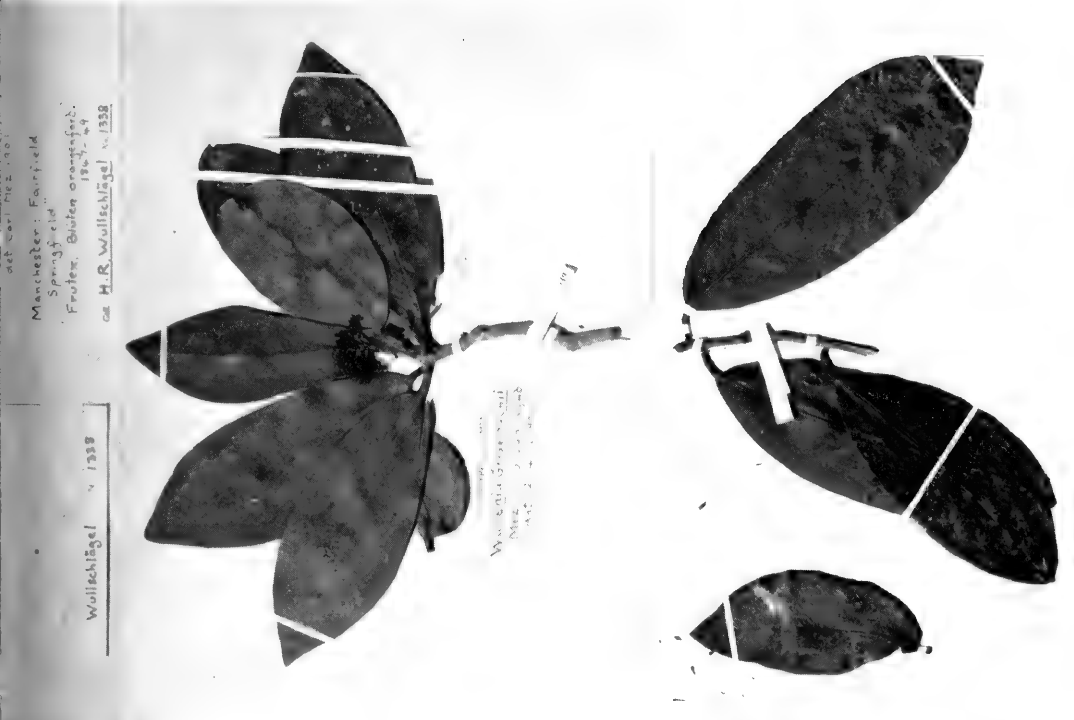
(b) *Wallenia xylosteoides* (Griseb.) Mez; lectotype (*Alexander 568*).



(a) *Wallenia erythrocarpa* Urban; isotype (*Harris 10343*).

(b) *Wallenia punctulata* Urban; isotype (*Britton 3281*).

(a) *Wallenia purdieana* Mez; holotype (*Purdie*).



(b) *Wallenia grisebachii* Mez; lectotype (*Wullschlägel 1338*).

(a) *Wallenia venosa* Griseb.; lectotype (*Wilson 388*).

(b) *Wallenia sylvestris* Urban; isotype (*Harris & Britton 10720*).

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Xref.

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THE JAMAICAN SPECIES OF *COLUMNEA* AND *ALLOPLECTUS* (GESNERIACEAE)

By WILLIAM T. STEARN

With Notes on CYTOLOGY and CHEMOTAXONOMY

By BRIAN D. MORLEY

SUMMARY

Eleven species of *Columnea* L., together with hybrids between two species (*C. rutilans* and *C. urbanii*), and two species of *Alloplectus* Mart. occur in Jamaica. All are endemic and have distinctive ranges within the island. *Columnea proctorii* and *C. urbanii*, here described as new species, have previously been misidentified.

The present paper deals with their history and morphological characteristics, the typification of the names *Columnea*, *Achimenes* and *Alloplectus*, the definition of the genera *Columnea* and *Alloplectus*, and the effect of pollination by humming-birds on their evolution; it also provides notes on cytology and chemotaxonomy as well as a key, descriptions and enumerations of specimens. Diagnostic features of pubescence and calyx are illustrated. A survey by methods of numerical taxonomy (taxonometrics) using both a wide range of characters and a reduced range gave a classification of the species in general agreement with one reached by traditional methods.

INTRODUCTION

THE following paper on the Jamaican species of *Columnea* and *Alloplectus* is the outcome of the preparation of the text on the Gesneriaceae for Fawcett and Rendle's *Flora of Jamaica*, volume 6. A study of all the available herbarium material before my visit to Jamaica in 1955–56 (cf. Stearn, 1959) indicated the need for further collecting and study of the species, despite the excellence of Morton's careful and critical revisions of 1944, and I gathered specimens of them whenever I came across them. Thanks to the co-operation of Mr. George R. Proctor of the Institute of Jamaica I was able to see most of them in their type localities or nearby. Subsequent collecting by Proctor has further increased our knowledge of their distribution. In 1965 Dr. Brian Morley visited Jamaica to study the cytology of the genus *Columnea*, using wild material. His field work revealed the existence of hybridization between *C. rutilans* and *C. urbanii* and he was able to introduce most of the species into cultivation at the Royal Botanic Gardens, Kew. Study of the abundant material now available made evident the need also to consider the definition of the genera *Columnea* and *Alloplectus* on a wider basis. It provided data which appeared suitable for testing taxonometric analysis as a means of classifying the species. These matters are dealt with below.

THE TYPE OF *COLUMNEA*

The genus *Columnea* L. (sensu stricto) comprises more than 100 species, all native to tropical America. It attains its greatest morphological diversity and breaks up into its greatest number of species in northern South America and Central America: 17 species, for example, are recorded from Costa Rica alone. In the West Indies as a whole it is represented by some 16 species, one of which, *C. scandens* L., is the type-species by monotypy. Charles Plumier collected this between 1689 and 1697 " in locis insulae martinicanae ", i.e. in Martinique, Lesser Antilles, and founded a new genus upon it dedicated to the Italian botanist Fabius Columna (i.e. Fabio Colonna, 1567–1650). He published a brief description, together with an engraving showing floral details, in his *Nova Plantarum Americanarum Genera* : 28, t. 33 (1703) as follows:

" Columnea est plantae genus flore monopetalo, personato, cujus labium superius non nihil fornicatum & excavatum, inferius vero tripartitum. Ex calyce autem surgit pistillum, posticae floris parti, ad instar clavi infixum, quod deinde abit in fructum globosum, mollem, seminibusque plenum exiguis, & oblongis.

Columneae species sunt.
Columnea scandens, phaeniceo flore, fructu albo,
Columnea scandens, flore lutescente, fructu albo."

Plumier had, however, drawn up a much more detailed description and had made a coloured drawing depicting the flowers as red, the original of which is at the Muséum National d'Histoire Naturelle, Paris, but of which there are copies in the University Library, Groningen, the Herbarium Library of the Royal Botanic Gardens, Kew (Plum. MSS. 2 : 117), and the Department of Botany, British Museum (Natural History), London (Plum. MSS. 2 : 104). That now at Groningen forms part of the set of copies of Plumier's drawings originally made for Boerhaave, which passed after his death to Johannes Burman, Linnaeus's friend, at Amsterdam. In 1756 Burman published an engraving made from it, excellently portraying the habit of the whole plant, in *Plantarum Americanarum Fasciculus quartus*: t. 89. Lamarck's account in the *Encyclopédie méthodique, Botanique* 2 : 66 (1786), which is fuller than any previously published, was based on Plumier's manuscript material in Paris. Plumier's plant with yellowish flowers is assumed to be a rare colour form.

Linnaeus himself possessed no specimens of *Columnea* and he based his description of the genus in his *Genera Plantarum*: 373 no. 921 (1737), 5th ed.: 286 no. 710 (1754) and likewise his protologue of *C. scandens* in the *Species Plantarum* 2 : 638 (1753) primarily on Plumier's published text and figures, although it is evident that between the preparation of the first edition (1737) and the second edition (1742) of the *Genera Plantarum* he saw herbarium material of a *Columnea* which enabled him to amend his 1737 statement " STAM: *Filamenta* duo (pingit, an quatuor) ", based on Plumier's figure which portrays only two stamens, to " STAM. *Filamenta* quatuor, quorum duo longiora, sub labio superiore recondita. *Antherae* simplices " in 1742. He may well have seen material during his visit to Paris in 1738. In any event he stated " Habitat in Gallia aequinoctiali ", meaning the French possessions in tropical America. The traditional use of the name *Columnea scandens* L. for the red-flowered species occurring in Martinique is thus well-founded. This ranges in the Lesser Antilles from Montserrat, by way of Martinique, St. Vincent and Grenada, to Trinidad and Tobago, but does not occur in the Greater Antilles.

SLOANE'S JAMAICAN MATERIAL

The first record of any species now included in the genus *Columnea* was made not by Plumier but by Hans Sloane and resulted from his stay in Jamaica from December 1687 to March 1689. He found " in montosis Insulae Jamaicae sylvis " a species which he listed as " Rapunculus fruticosus foliis oblongis integris villosis ex adverso sitis flore purpureo villoso " in his *Catalogus Plantarum quae in Insula Jamaica sponte proveniunt* : 58 (1696). This entry would be completely cryptic but for the description and the rather crude engraving in his later *Voyage to the Islands Madera . . . and Jamaica* 1 : 157, t. 100 f. 1 (1707) and the specimen in Herb. Sloane 3 : fol. 21 at the British Museum (Natural History) on which these were based. Sloane's artist Everard Kickius unfortunately failed to distinguish the calyx from the corolla, both being very hairy, but examination of Sloane's specimen shows his plant to be *Columnea fawcettii* (Urban) Morton, which was not distinguished as a species until 1944. Sloane probably collected it on Mount Diablo.

THE TYPE OF *ACHIMENES*

Patrick Browne, failing to connect Linnaeus's genus *Columnea* with any Jamaican plant, established a new genus *Achimenes* in his *Civil and Natural History of Jamaica* : 270, t. 30 (1756). He included two species. The first of these, his " Achimenes major, herbacea, subhirsuta, oblique assurgens " to which he referred Sloane's " Rapunculus fruticosus . . ." is undoubtedly a *Columnea*, probably *C. fawcettii*, since he mentions it as " most commonly met with in the woods of *New Liguanea* and *St. Ann's* " and describes the " divisions of the cup ", i.e. calyx-segments, as " pinnated at the sides, somewhat like those of the garden rose ". Browne's generic description was based on this species, as is evident, for example, from his account of the irregular corolla: " *limbus* erectus, in quatuor lacinias inaequales, inaequaliter sectus; *lacinia* superior recta, latiuscula, profunde crenata, sive bifida; *laterales* oblongae & a superiori oblique decendentes; *infima* anguste patula, ad medietatem floris incisa, longissima." Hence *Achimenes* P. Browne (1756) as to type is congeneric with *Columnea* L. Browne's second species " Achimenes minor, erecta, simplex . . ." is the plant commonly known as *Achimenes coccinea* (Scop.) Pers. or *A. pulchella* (L'Hérit.) Hitchc., but whose correct name is *A. erecta* (Lam.) H. P. Fuchs. Browne regarded it as agreeing " in the most essential parts [of the flower] with the foregoing ", although it has an almost regular corolla. When Persoon dealt with these two Brownean species in his *Synopsis Plantarum* 2 : 164 (1806) he referred Browne's first species to *Columnea*, as Burman had already done in 1756 and Swartz in 1788, but he retained the name *Achimenes* for the second species, at the same time providing a new generic description referring to this alone: " *Cal.* superus 5-phyllus. *Cor.* infundibuliformis; limbus planus, 5-lobus, subaequalis. *Rudimentum* filamenti 5-ti. *Antherae* connexae. *Caps.* bilocularis." Under the name *Achimenes* Persoon in fact established a new genus distinct from *Achimenes* P. Browne (sensu stricto) and the name *Achimenes* has been consistently used for it. This now includes about 25 species, of which 13 are in cultivation, together with many cultivars, some of hybrid origin. Being a later homonym of *Achimenes* P. Browne, it needs conservation; the type-species of *Achimenes* Pers. is *A. coccinea* (Scop.) Pers., i.e. *A. erecta* (Lam.) H. P. Fuchs.

THE TYPE OF *ALLOPLECTUS*

The genus *Alloplectus* was founded by Martius, *Nov. Gen. Sp. Pl. Brasil.* 3 : 53 (1829), with the following differential character: " Calyx liber, coloratus, pentaphyllus, foliolis imbricatis, plus minus connatis, duobus interioribus. Corolla infera, tubulosa vel claviformis, rectiuscula, limbo brevi quinquelobo aut quinquedentato. Stamina quatuor didynama, cum quinti postici rudimento minimo, e basi tubi. Annulus hypogynus in glandulam posticam tumens. Capsula baccans, ovata, coriacea, unilocularis, bivalvis, seminibus numerosis oblongis." He included two Brazilian species, both described and illustrated in detail, *A. sparsiflorus* Mart. and *A. circinatus* Mart.

In the list of conserved generic names in the *International Code of Botanical Nomenclature* the name *Alloplectus* Mart. (1829) is conserved under No. 7860 against *Crantzia* Scop. (1777) and *Vireya* Raf. (1814) and its lectotype given as *A. sparsiflorus* Mart. (= *A. hirtellus* (Schott) Preston), although *A. circinatus* would have been a better choice since Martius saw no mature fruits of *A. sparsiflorus* but had both flowering and fruiting material of *A. circinatus* and described the fruits and seeds of *Alloplectus* from this species. His two Brazilian species are, however, closely allied and differ in several characters from many species now referred to the genus *Alloplectus*. If, however, a broad concept of the limits of *Alloplectus* is accepted, as in the present paper, *Dalbergaria* Tussac (Fl. Antilles 1 : 141 (1811–13) must be added to its synonomy as a *nomen rejiciendum*, since its type, *D. phaenicea* Tussac, loc. cit. (1811–13) is the same Hispaniola species (*Alloplectus sanguineus* (Pers.) DC., Prodr. 7 : 546 (1839))* as Rafinesque's *Vireya sanguinolenta*, i.e. the type of *Vireya* Raf. already listed as a *nomen rejiciendum*. The short-lived Palermo *Specchio delle Scienze o Giornale enciclopedico di Sicilia*,† wherein (1 : 194 (June, 1814)) Rafinesque published *Vireya*, is an extremely scarce periodical and his account is accordingly reprinted here:

" VIREYA. Cal. 5partitus, lac. equal. laciniatis, Corolla peripetala tubulosa 5dentata, basi gibbosa; Stam.4. didynamica inclus. Ov. liberum oblong. basi monadeno, stigma 2lamellat. Capsula 1.locul. 4valve polysperma, semina recept. 4. longitudinal. affixa. *Planta, fol. oppos. flor. axillaris.* — Oss. Mi. fù comunicato questo nuovo genere del Sign. Turpin col. barbaro nome di *Caonabo*, al quale hò sostituito il nome dell' egregrio moderno naturalista e filosofo Virey. Si appartiene alla mia seconda Classe *Mesogynia*, 5. Ordine *Epidia*, Famiglia *Didynamia*: ha delle affinità colli generi *Browallia*, e *Lindernia*.

Vireya sanguinolenta. Caule erecto simplex, foliis oppositis, alternis multo major, oblongis integris acutis sub-villosis subtus sanguinolentis, florib. axillarib. solitaris sessilis. — Oss. Nasce nell'Isola di S. Domingo offerisce le singolari particolarità di

---

* Martius, Nov. Gen. & Sp. 3 : 57 (1829) suggested that *Besleria sanguinea* Pers. belonged to *Alloplectus* but he did not make the combination *A. sanguineus* attributed to him by Jackson (Index Kew. 1 : 84 (1893)), Urban (Symb. Antill. 2 : 358 (1901)), and Morton (Contr. U.S. Nat. Herb. 29 : 4 (1944)).

† The British Museum (Natural History) now possesses a photostat copy.

avere alternativamente le foglie dieci volte più grande delle opposte, e coperte al di sotto di una larga macchia sanguinosa: hà le corolle d'un giallo lividó."

Vireya Raf. is thus a synonym of *Dalbergaria*.

RECORDS OF *COLUMNEA* AND *ALLOPLECTUS* IN JAMAICA

The first post-Linnaean author to deal with the Jamaican species of *Columnea* was Olof Swartz, who travelled extensively in Jamaica between 1784 and 1786 and succeeded in finding an extraordinary number of rare plants. His journeys took him into the parishes of Trelawny, Hanover, St. Elizabeth, St. Andrew, St. Catherine and St. Thomas. His collections included three new species of *Columnea*, i.e. *C. hirsuta*, *C. hispida* and *C. rutilans*, of which he published diagnoses in his *Nova Genera et Species Plantarum seu Prodromus* : 94 (1788) and detailed descriptions in his *Flora Indiae Occidentalis* 2 : 1080–1086 (1800). Under his *C. hirsuta* he cited as synonyms Sloane's " Rapunculus fruticosus . . ." and Browne's " Achimenes major herbacea . . .", but from the significant note in his description, " Hirsuties pulchre articulata," and his specimen in the British Museum (Natural History) it is clear that he based his *C. hirsuta* on material of the species growing high in the Blue Mountains which has conspicuous multicellular hairs on the leaves. To this species the name *C. hirsuta* has always been attached. Swartz himself ascended Blue Mountain Peak in 1785 and, while a guest of Matthew Wallen at Coldspring, St. Andrew, in the Blue Mountains, he had other opportunities of collecting the species. In the west of Jamaica he collected *C. rutilans*, conspicuous for its leaves red beneath. Swartz's third species, *C. hispida*, was long enigmatic. He himself collected it only in fruit " in montibus altis Jamaicae occidentalis, ad rupes umbrosas ". Its flowers in fact remained unknown until February 1957; the flowering material collected by Wullschlägel in Manchester which Grisebach in 1862 (Fl. Brit. W. Ind. Is. : 465) referred to *C. hispida* belongs to another species, *C. urbanii*. Swartz's own description and his specimens at the British Museum (Natural History) and the Rijksmuseet, Stockholm, show *C. hispida* to be a very distinct species and justify Morton's comment in 1944: " From description I am not able to identify this with any of the species known from Jamaica. It is perhaps a valid species, not collected again." Swartz, as was unfortunately his custom, gave no precise locality. In 1784 he travelled across western Jamaica from Montego Bay on the north coast to Savanna-la-Mar on the south coast and it would seem probable that he then came across this very rare and local species, for White Rock Hill, St. James, where Proctor and I had the good fortune to rediscover it in March 1956, lies near a route between these towns.

Grisebach's account of *Columnea* in his *Flora of the British West Indian Islands* : 464–465 (1862) added a further species, *C. argentea* Griseb., notable for its sericeous leaves and other parts, which the missionary Heinrich Rudolf Wullschlägel (1805–64) of the Moravian Brothers had collected in 1849 at Nazareth, Manchester. Evidently unaware of Grisebach's publication, Hanstein described it anew in 1865 as *C. wullschlaegeliana*. This again is a very local species. In 1956 I was overjoyed to find it growing among rocks near the Moravian Chapel at Nazareth, which must have been the very place where Wullschlägel gathered it. As noted above, Grisebach included under *C. hispida* Swartz a species here named *C. urbanii*.

Grisebach placed three Jamaican species in the genus *Pterygoloma,* which was founded by Hanstein in 1854 (Linnaea 26 : 211) on a species described and illustrated in *Bot. Mag.* 72 : t. 4250 (1846) as *Alloplectus repens* Hook. and there stated to have been collected by William Purdie " in the ascent of the Sierra Nivada, Santa Martha ", Colombia. The first of these, which Grisebach erroneously identified with *Pterygoloma repens* (Hook.) Hanstein and enumerated as such, is a dwarf creeping species, with flowers not so markedly zygomorphic as in typical species of *Columnea*; it had been collected in Jamaica both by Wullschlägel and Purdie. In 1901 Urban distinguished it as *Columnea jamaicensis.* Grisebach's two other species, *P. pubescens* from western Jamaica and *P. cristatum* from central Jamaica, based on collections by Wilson, Purdie, Alexander and Wullschlägel, agreed with the first in their low creeping habit but differed in having almost cylindrical or clavate corollas with very short almost equal rounded lobes. They are easily distinguished from one another by the calyx-segments, entire in *P. pubescens*, pinnatifid with spreading lobes in *P. cristatum.* Fawcett listed all three under *Alloplectus* (see p. 234) in 1893. The association of the three accords with the results of a taxonometric analysis of the group (see p. 213).

Nothing more was published on the Jamaican species of *Columnea* until 1901, when Urban included them in his " Enumeratio Gesneriacearum " (Symb. Antill. 2 : 344–388 (1901)). He revised nomenclature, listed synonyms and specimens, and amended previous descriptions in the careful and scholarly manner which makes his contributions to West Indian botany so valuable as quarries of information, but as usual he failed to provide a key to the plants concerned, an omission which detracts so much from the practical utility of his work. He recorded five species as Jamaican, expressing his opinion about their distinctness by the comment " Fortasse omnes *Columneae* species in Jamaica obviae formis intermediis inter sese conjunctae sunt, *C. jamaicensi* excepta ". There are indeed some specimens intermediate between recognized species, but these would appear to result from hybridization. All the species accepted by Urban have definite characters associated with distinctive geographical ranges which justify their separation. *C. hirsuta* he regarded as a very variable species, within which, despite the limited material then available, he distinguished seven taxa. On the basis of the much more abundant and adequate material now at hand, it seems more reasonable to refer Urban's varieties and forms of *C. hirsuta* to four species as follows:

var. *genuina* (p. 361) = *C. hirsuta* Swartz
var. *pallescens* (p. 362) = *C. hirsuta* Swartz
var. *concolor* (p. 362) = *C. hirsuta* Swartz
var. *subintegra* (p. 362)
  forma *wullschlaegelii* (p. 362) = *C. urbanii* Stearn
  forma *hansenii* (p. 363) = ? *C. harrisii* (Urban) Britton ex Morton
  forma *harrisii* (p. 363) = *C. harrisii* (Urban) Britton ex Morton
var. *fawcettii* (p. 363) = *C. fawcettii* (Urban) Morton

In 1909 Urban added another species, *Columnea brevipila,* collected by Harris on Bluefields Mountains, Westmoreland.

Morton in 1944 (*a, b*) revised the West Indian species of *Columnea* and *Alloplectus.* With much more material for study than Urban had, most of it collected by Harris and by Britton, he described seven Jamaican species of *Columnea* in detail, raising two of Urban's varieties of *C. hirsuta* to specific rank as *C. harrisii* and *C. fawcettii* and adding a new species, *C. subcordata,* from Windsor, Trelawny. Unlike Urban, he provided a key to all the West Indian species of both *Columnea* and *Alloplectus.* Examination of living material during my visit to Jamaica in 1956 (cf. Stearn, 1959) confirmed the taxonomic soundness of Morton's work, already evident from a prior survey of herbarium material.

DEFINITION OF *COLUMNEA* AND *ALLOPLECTUS*

The difficulties of defining the American genera of Gesneriaceae, among them *Columnea* and *Alloplectus,* are reflected in the different views of authors on their generic limits. As stated by Leeuwenberg (1958 : 293), " there are several cases of close inter-relationship of species usually placed in separate genera, rendering the boundaries between those genera vague or even untenable. Judging from these cases alone one would be compelled to unite large groups of genera or even complete tribes under one genus; this is particularly true for the *Columneinae.* The typical species of the genera are however so different that such a procedure would be quite undesirable. But part of those generic limits are based rather on convenient characters than on conspicuous discontinuities of features. A consequence of this state of affairs is the presence of what may be called ' borderline species ', i.e. species that have some characters of one and some of an other genus." Such a species in Jamaica is *Columnea jamaicensis,* referred by Grisebach to *Pterygoloma,* by Fawcett to *Alloplectus,* by Urban to *Columnea.* The two Brazilian species (see above) on which Martius founded the genus *Alloplectus* in his *Nova Genera et Species Plantarum Brasiliensium* 3 : 53, t. 223 (1829) are markedly different from *Columnea* in their narrowly tubular rather ventricose corolla with the limb almost regular and very shortly lobed, i.e. shallowly 5-toothed or 5-lobed, the lobes almost equal, in their free anthers and their rather fleshy 2-valved capsule, but these distinctions have not remained clear-cut as more and more species of the group have been discovered. A few examples will serve to indicate the lack of correlated differences. Thus a species such as *Columnea aureonitens* Hook. (Bot. Mag. 73 : t. 4294 (1847)) has a narrowly tubular corolla with very short almost equal lobes, but four of the anthers cohere as in typical zygomorphic species of *Columnea,* while *C. kalbreyeri* Hook. f. (Bot. Mag. 108 : t. 6633 (1882)) has a zygomorphic corolla but the four anthers are completely free from one another. *C. guianensis* Morton, illustrated by Leeuwenberg (1958 : 387, fig. 16), agrees with many typical species of *Columnea* in having the leaves of a pair markedly unequal in size, but its corolla is narrowly cylindrical with a small almost regular limb of five short erect lobes, the two dorsal ones however connate, and the anthers are free from one another as in a typical *Alloplectus.* The same is true of *C. sanguinea* (Pers.) Hanstein (*Dalbergaria phaenicea* Tussac) with markedly unequal leaves but a regular cylindrical corolla and anthers cohering only in pairs. *Alloplectus savannarum* Morton (illustrated by Leeuwenberg, 1958 : 365, fig. 9) has unequal leaves and cohering anthers but a cylindrical corolla and a two-valved capsule as in typical *Alloplectus*. A possible distinction based on the form of the corolla tube, i.e. gradually widened and not contracted at the mouth in *Columnea*, ventricose with a contracted mouth in *Alloplectus*, is obscured by such species as *Columnea filipes* Oliver (Hook., Ic. Pl. 25 : t. 2428 (1896)) with ventricose tube but connate anthers. Characters of the fruit, an almost globose berry in typical *Columnea*, a capsule separating into two fleshy or thick valves in typical *Alloplectus*, might provide means of separation, but *A. domingensis* with a regular corolla has a berry-like fruit like a typical *Columnea* and the fruits of many species placed currently in *Columnea* or *Alloplectus* are unknown; the correlation of carpological, habit and floral characters in the group as a whole is accordingly doubtful. Attempts to separate the two genera by referring those with a coloured calyx and free anthers to *Alloplectus*, the type of which, *A. hirtellus*, has a dark red calyx, and those with a green calyx and connate anthers to *Columnea* are frustrated by such a species as *C. scheideana* Schlecht. (illustrated in Bot. Mag. 70 : t. 4045 (1843)) with a large purplish-red calyx as in *Alloplectus* but a markedly zygomorphic 2-lipped corolla and connate anthers typical of *Columnea*. Anisophylly is likewise unavailing, since the type-species of both *Columnea* and *Alloplectus* have the two leaves of a pair equal.

In short there is no apparent discontinuity between *Columnea* and *Alloplectus*. O. Kuntze in 1891 (Rev. Gen. Pl. 2 : 470) united the two, together with *Hypocyrta* and *Nematanthus*, into one genus, *Columnea* (sensu lato), which would now include about 220 species, defined as follows: " Ovarium omnino superum. Disci glandula postica magna ceterae 0 vel parvae. Stamina 4. Antherarum loculi paralleli. Filamenta basi dilatata unilateraliter connata cum corolla breviter connata. Calyx 5-partitus vel alte 5-fidus. Corolla apice variabilis exappendiculata. Fructus subbaccatus vel demum bivalvis." This course certainly has simplicity to recommend it as regards nomenclature but obscures the special character of *Columnea* (sensu stricto) as a highly developed group. The prevailing gamopetalous type of corolla found in Gesneriaceae and allied families consists of a fairly long tube with a spreading limb which is shorter than the tube and slightly or distinctly two-lipped; the two upper lobes form an upper lip while the lower lobe and the two lateral lobes together form a lower lip which serves as a landing platform for insects seeking nectar at the base of the tube. The stamens are usually included within the corolla-tube and self-pollination is often possible; it occurs, for example, in *Alloplectus* species under cultivation. The fruit is usually a capsule. *Alloplectus* (sensu stricto) represents this general unspecialized type. The corolla of *Columnea* (sensu stricto) represents a reversal of the trend towards development of an expanded lower lip able to support the weight of a bee. In *Columnea* the upper side of the corolla has become prolonged forward, the two uppermost lobes being fused and enlarged into a hood sheltering the exserted anthers and stigma; the two lateral lobes are reduced and they spread either sideways or upwards; the lower lip is also reduced and turned down or back. By these features, together with the horizontal poise of the flowers and their usually conspicuous red or yellow colouring, the flower of *Columnea* (sensu stricto) has become perfectly adapted to pollination by nectar-seeking humming-birds on the wing (Text-fig. 5). The reduced lower lip and lateral lobes offer no obstacle to the bird as it flies under the lengthened upper lip and thrusts its beak and tongue down to the abundant nectar at the base of the tube, while its wings beat unimpeded on both sides of the lip. The anthers and stigma, being directly under the upper lip, are so placed that they touch the top of the head of the hovering bird. The coherence of the anthers ensures that they deposit the maximum of pollen in one area on the bird's head where the stigma of another flower will first come into contact with it. The corolla as a whole is firm enough in texture to sustain vibration by the wing-beats of a humming-bird (mostly 20–25 beats per second, but ranging from 8 to 80 according to the size of the bird; cf. Greenewalt, 1960). Such a flower well exemplifies " the syndrome of ornithophily " as characterized by Faegri & van der Pijl (1966 : 109). This has been achieved by the successful association of several divergences from the almost regular flower typical of *Alloplectus*, which divergences have evidently also occurred separately and independently, as the anomalous intermediate species mentioned above indicate.

The proposal is accordingly made that *Columnea* should be defined more narrowly than is customary, by including within it only species of this ornithophilous habit, characterized by having a distinctly bilabiate red or yellow corolla, with the four upper (posterior) lobes fused and extended into a galea, the lower (anterior) lobe narrow and bent downwards, and having exserted stamens with the four anthers initially connate. Those species not satisfying this definition should be transferred to *Alloplectus** or possibly other genera. Thus *Alloplectus* might likewise be more narrowly defined and restricted to species with a regular corolla and a capsular fruit akin to the type-species. To accommodate the species not fitting into this and *Columnea* (sensu stricto), *Dalbergaria* and possibly also *Pterygoloma* might then be restored.

A situation of this kind, in which a well-marked specialized offshoot, such as *Columnea* (sensu stricto), is still connected to a generalized stock, such as *Alloplectus*

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* Acceptance of this viewpoint makes it necessary to transfer to *Alloplectus* the following West Indian, Guianaian and Venezuelan species allocated to *Columnea* by Morton and by Leeuwenberg:

Alloplectus affinis (Morton) Stearn, comb. nov.
Columnea affinis Morton in Fieldiana 28 : 529 (1953).

Alloplectus aureonitens (Hook.) Stearn, comb. nov.
Columnea aureo-nitens Hook. in Bot. Mag. 73 : t. 4294 (1847).—Leeuwenberg in Act. Bot. Neerl. 7 : 383 (1958).

Alloplectus calotrichus (Donn. Smith) Stearn, comb. nov.
Columnea calotricha Donn. Smith in Bot. Gaz. 40 : 9 (1905).—Leeuwenberg, tom. cit. : 385 (1958).

Alloplectus cubensis (Urban) Stearn, comb. nov
Columnea sanguinea var. *cubensis* Urban, Symb. Antill. 2 : 359 (1901).
Columnea cubensis (Urban) Britton in Torreya 5 : 215 (1905).—Morton in Contr. U.S. Nat. Herb. 29 : 5 (1944).—Alain in León & Alain, Fl. Cuba 4 : 472 (1957).

Alloplectus guianensis (Morton) Stearn, comb. nov.
Columnea guianensis Morton in Bull. Torrey Bot. Club 75 : 564 (1948).—Leeuwenberg, tom. cit. : 386 (1958).

(sensu lato), by a few species showing intermediate stages of development, does not permit of a solution both logical and convenient and hence proves disconcerting to a tidy-minded taxonomist intent on emphasis of discontinuity, but it is all the more interesting and worthy of study as indicating possible lines of evolution within the group. The most practical procedure would seem to be to recognize as genera both the large heterogeneous groups manifesting a wide range of characters occurring in many different combinations without consistent correlations and also at the same time the allied apparently monophyletic groups separated from them by possessing consistent correlations of characters whereby these form biologically important or conveniently distinguishable entities, the few intermediate species being referred to the more heterogeneous groups. The case of *Alloplectus* and *Columnea* parallels in some ways that of *Lilium* and *Nomocharis* (cf. Sealy, 1950) where a solution according with this viewpoint has proved satisfactory.

The Jamaican species, apart from *Columnea jamaicensis*, fit readily into *Columnea* with a strongly bilabiate corolla and *Alloplectus* with a regular cylindrical corolla. *C. jamaicensis* is like *A. pubescens* and *A. grisebachianus* in its low creeping habit and has the bilabiate character of the corolla less marked than in typical *Columnea*, but the tube expands gradually, the upper lip consists of two fused lobes with two spreading lateral lobes, and the four anthers are connate. These associated floral characters justify the allocation of *C. jamaicensis*, and hence of *Pterygoloma*, to *Columnea*, as defined here, even though on the sum of its other characters, as is shown by taxonometric analysis, it has more in common with the Jamaican species of *Alloplectus*.

Characters distinguishing the species

The Jamaican species of *Columnea* and *Alloplectus* are soft-wooded plants of creeping or sprawling habit, rather sparingly branched, with stems which may even reach a length of several metres in some robust specimens, the leaves then being clustered near the growing tip and the branchlets marked with the conspicuous scars of the fallen leaves. *Columnea jamaicensis* (Pl. 14), *Alloplectus pubescens* and *A. grisebachianus* have slender creeping branchlets only 1–3 mm. thick, whereas the others have much stouter branchlets about 5–10 mm. thick, initially erect but drooping downwards with age when the plants grow as epiphytes on trees. The leaves are paired, those of a pair being almost equal in size and shape, as in *C. urbanii* (Pl. 16), to markedly unequal, as in *C. proctorii* (Pl. 17) and *C. rutilans* (Pl. 21), the smaller leaf of the pair having a shorter petiole as well as a shorter blade and often falling earlier than the larger leaf. This anisophylly, although used by Leeuwenberg (1958 : 295) in his study of Guiana Gesneriaceae to separate *Alloplectus* sect. *Alloplectus* with the leaves of a pair almost equal from *Columnea* sect. *Collandra* with leaves of a pair markedly unequal, varies in the Jamaican species, being apparently constant in some, such as *C. hispida*, *C. subcordata* and *C. harrisii*, but variable in others such as *C. fawcettii* and *C. hirsuta*, which may have the leaves of a pair almost equal or markedly unequal. The difference between the large and small leaves is particularly evident in *C. rutilans*, *C. proctorii* and *C. subcordata*.

The proportions as well as the actual dimension of the leaf-blade provide characters of some diagnostic value, as Morton demonstrated by measuring 50 representative leaves of each species when he had enough material available. Thus in *Columnea jamaicensis*, *C. hirsuta* and *C. subcordata*, the blades average about two times as long as broad, in *C. fawcettii*, *C. brevipila* and *C. harrisii*, between 2·4 and 2·7 times as long as broad, and in *C. rutilans* and *C. argentea*, about 3·4 to 3·7 times as long as broad. The leaf-base is remarkably asymmetric in *C. harrisii* and *C. hispida* *C. rutilans* stands apart from the others in having the underside of the leaf either completely red or else conspicuously red-veined, and this red colouring is evident in some of the hybrids between *C. rutilans* and *C. urbanii*.

Diversity of hair-covering provides features of diagnostic value, notably the hair-covering on the upper surface of the leaf-blade, where four main types of hairs may be distinguished (Text-fig. 1, p. 192):

1. Hairs erect, 8–9-celled, red, to 3·5 mm. long, e.g. *Columnea hispida* (Text-fig. 1A), in which also occur minute erect colourless, 3-celled hairs.
2. Hairs erect, 5–10-celled, colourless, 0·8–2·5 mm. long, e.g. *C. hirsuta* (Text-fig. 1C), *C. proctorii*, *C. subcordata*, *C. urbanii* (Text-fig. 1B); in *C. hirsuta* these are associated with minute almost appressed 2-celled hairs.
3. Hairs bent forward and somewhat or almost appressed, 4–6-celled, colourless, scarcely 1 mm. long, e.g. *C. argentea* (Text-fig. 1F), *C. harrisii* (Text-fig. 1E) and *C. rutilans* (Text-fig. 1D), in all of which they are associated with minute almost appressed 2-celled hairs.
4. Hairs bent forward, almost appressed, 2-celled, colourless, 0·2–0·4 mm. long, exclusively present in *C. brevipila* (Text-fig. 1D) and *C. fawcettii* (Text-fig. 1H), associated with longer hairs in *C. argentea* (Text-fig. 1F), *C. hirsuta* (Text-fig. 1C), *C. harrisii* (Text-fig. 1E), and *C. rutilans* (Text-fig. 1G).

Suppression of the long hairs in *C. hirsuta* would produce leaves like those of *C. fawcettii*.

The flowers are axillary, with one to five in an axil, on pedicels 1–3 cm. long, varying from species to species in the type of hair-covering.

The most useful characters for specific distinction are provided by the calyx (Text-fig. 2). The segments may increase a little in size after flowering as the fruit matures but retain their shape, being, for example, about 12 mm. long in flower but 16 mm. long in fruit in *Columnea jamaicensis*, about 2·5 cm. in flower but 3·5 cm. in fruit in *C. rutilans*. They are mostly between 2 and 3 cm. long. *C. subcordata* (Text-fig. 2G) stands apart from the other species, in which the five segments are free almost to the base, by having four segments united for about the lower third of their length and the fifth almost free.

The segments are linear and entire in *C. hispida* (Text-fig. 2A) and lanceolate or narrowly lanceolate and entire or scarcely toothed in *C. argentea* (Text-fig. 2C), *C. brevipila*, *C. harrisii*, *C. proctorii* (Text-fig. 2B), *C. urbanii* (Text-fig. 2H) and *A. pubescens* (Text-fig. 29G). In *C. hirsuta* and *C. fawcettii* (Text-fig. 2D; Text-fig. 28B) the segments bear one to three remote but usually well-marked teeth on each margin. In *C. rutilans* (Text-fig. 2F) and *A. grisebachianus* (Text-fig. 29C) they are laciniate in the lower part, with 3–5 prominent teeth on each margin. These differences in shape, together with differences in hair-covering, enable most species to be recognized by the calyx alone. The hairs of the calyx are red in *C. hispida*, *C. fawcettii*, C. *hirsuta*, *C. hispida* and *C. rutilans*, colourless in the others.

The corolla as mentioned above (p. 186) is small, narrowly tubular and regular in *Alloplectus grisebachianus* (Text-fig. 29A, B) and *A. pubescens* and slightly 2-lipped

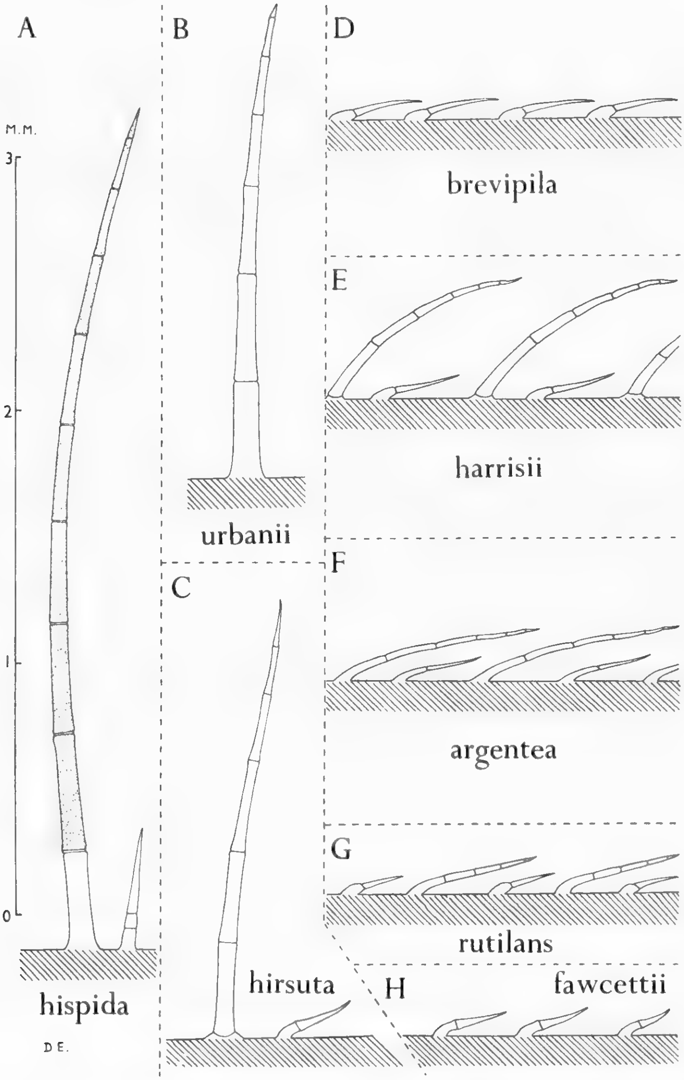


FIG. 1. Hairs on upper leaf-surface of: A, *Columnea hispida* Swartz; B, *C. urbanii* Stearn; C, *C. hirsuta* Swartz; D, *C. brevipila* Urban; E, *C. harrisii* (Urban) Morton; F, *C. argentea* Griseb.; G, *C. rutilans* Swartz; H, *C. fawcettii* (Urban) Morton. (All drawn from living plants cultivated at Kew.)

in *Columnea jamaicensis* (Text-fig. 28H), but larger and strongly 2-lipped in the other species. It is completely yellow in *C. argentea* (Text-fig. 5), *C. brevipila*, *C. hispida* *C. subcordata* and *C. urbanii* (Text-fig. 28G) but longitudinally striped with red in the others, including many of the hybrids between *C. rutilans* and *C. urbanii*.

The filaments of the stamens are glabrous in *Columnea argentea* and *C. brevipila* but pubescent in most other species.

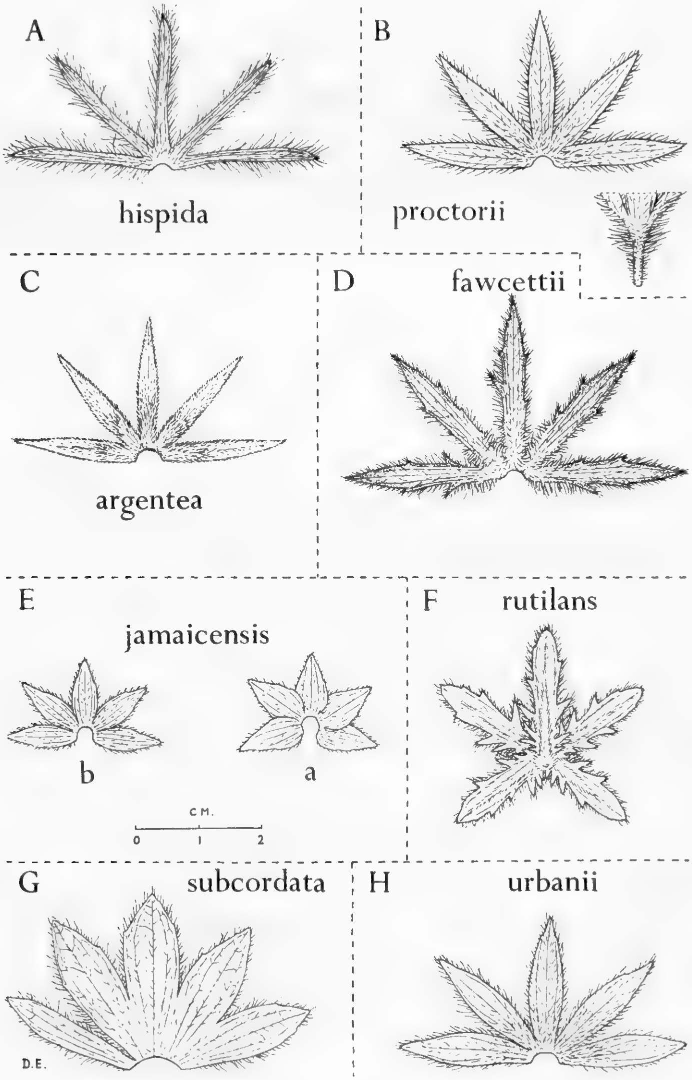


Fig. 2. Calyx of: A, *Columnea hispida* Swartz (*Stearn 449*); B, *C. proctorii* Stearn, with apex of pedicel (*Stearn 451*); *C. argentea* (*Stearn 359*); D, *C. fawcettii* (*Stearn 157*); E, *C. jamaicensis* Urban, a (*Wullschlägel 1290*), b (*Stearn 928*); F, *C. rutilans* Swartz (*Stearn 453*); G, *C. subcordata* Morton (*Stearn 472*); H, *C. urbanii* Stearn (*Stearn 361*).

Certain species can thus be easily recognized by distinctive and unusual characters. For example, *Columnea jamaicensis* has small leaves about 3·5 cm. long, a short calyx and a small corolla not strongly bilabiate. *C. rutilans* stands apart from other species in having its leaves red below and its calyx-segments partly laciniate. *C. subcordata* has a bilabiate calyx with four segments fused for their lower third. *C. fawcettii* with toothed calyx-segments and *C. brevipila* with entire calyx-segments differ from other species in having only very short appressed 2-celled hairs on the upper surface of the leaf. *C. argentea* has relatively narrow leaves silvery-grey with long somewhat appressed sericeous hairs. *C. hispida* is notable for the long erect reddish hairs covering the upper side of the leaf as well as the calyx and for the relatively small corolla.

CYTOLOGY

By BRIAN D. MORLEY

The chromosome numbers of species of *Columnea* have been reported by Rogers (1954), Eberle (1956), Fussell (1958), Lee (1962*a*, *b*, 1964, 1966, 1967), Morton (1963), Lee & Grear (1963) and Morley (1967). Investigation of the chromosome numbers of ten Jamaican species and four natural hybrids selected from a hybrid swarm between *C. rutilans* and *C. urbanii* confirms the reports for *C. brevipila*, *C. fawcettii* and *C. hispida* by Lee (1964, 1966) and shows that all the Jamaican species have a diploid number of 2n = 18 and that their basic number is the same as that of other *Columnea* species, x = 9. The plants studied were as follows:

Species	Locality	Plant reference no.	2n
C. hirsuta	Hardwar Gap, St. Andrew–Portland.	Morley 33	18
C. fawcettii	Mount Diablo, St. Ann.	Morley 2 (coll. E. Lodge)	18
C. rutilans	Ramgoat Cave, Trelawny.	Morley 3	18
		Morley 35	18
C. rutilans	Near Catadupa, St. James.	Morley 20	18
C. argentea	Shooters Hill, Manchester.	Morley 36	18
C. urbanii	Top Hill, Manchester.	Morley 14	18
		Morley 442	18
C. urbanii	Near Newport, Manchester.	Morley S.6	18
C. urbanii	Rose Hill Village, Manchester.	Morley S.7	18
C. proctorii	Near Troy, Trelawny.	Morley S.17 (coll. C. D. Adams)	18
C. proctorii?	Ramgoat Cave, Trelawny.	Morley 5	18
C. hispida	Near Catadupa, St. James.	Morley 40	18
C. harrisii	Seven Rivers, St. James.	Morley 23	18
C. harrisii	Near Leamington, Westmoreland.	Morley S.11	18
C. brevipila	Cho Cho Gulley, Westmoreland.	Morley 24	18
C. jamaicensis	Near Leamington, Westmoreland.	Morley 27 (coll. C. D. Adams)	18

C. jamaicensis	Near Leamington, Westmoreland.	Morley S.10	18
C. rutilans × *urbanii* hybrid 4	Top Hill, Manchester.	Morley 16, 44, 45	18
C. rutilans × *urbanii* hybrid 6	Top Hill, Manchester.	Morley 47	18
C. rutilans × *urbanii* hybrid 8	Top Hill, Manchester.	Morley 15, 46	18
C. rutilans × *urbanii* hybrid 11	Top Hill, Manchester.	Morley 48	18
A. grisebachianus	Mount Diablo, St. Ann.	Morley s.n. (coll. E. Lodge)	18

Although the chromosomes are small, they display sufficient morphological diversity to allow recognition of the following three karyotype series. A metacentric position is defined as an approximate position of 50% along the length of a chromosome and submetacentric as 60%–70% along a chromosome.

Series 1. Karyotypes with large chromosomes, i.e. longer and thicker, where the smallest chromosome is always longer than broad. Two pairs of chromosomes with submetacentric centromere position, seven pairs of chromosomes with metacentric centromere position; see Text-fig. 3.
Species: *C. hirsuta*, *C. fawcettii*, *C. urbanii* (from an area north of Mandeville).

Series 2. Karyotypes with large chromosomes, i.e. longer and thicker, where the smallest chromosome is always longer than broad. Three pairs of chromosomes with submetacentric centromere position, six pairs of chromosomes with metacentric centromere position; see Text-fig. 3.
Species: *C. urbanii* (from an area south of Mandeville), *C. brevipila*, *C. rutilans*, *C. jamaicensis*.

Series 3. Karyotypes with small chromosomes, i.e. shorter and thinner, where the smallest chromosome is always as long as broad. Three pairs of chromosomes with submetacentric centromere position, six pairs of chromosomes with metacentric centromere position; see Text-fig. 4.
Species: *C. argentea*, *C. hispida*, *C. harrisii*, *C. proctorii*.

Series 1 karyotypes characterize the species *Columnea hirsuta* and *C. fawcettii*, which are morphologically and biochemically distinct from other Jamaican species and are only found in eastern Jamaica. Most *C. urbanii* karyotypes belong to Series 2, with the exception of one plant which had a Series 1 karyotype.

Although *Columnea jamaicensis* is included in Series 2, it is unlike any other Jamaican species, having a different phenotype and a karyotype with two pairs of satellites. The metacentric satellite pair of *C. urbanii* (66.1460) requires further analysis.

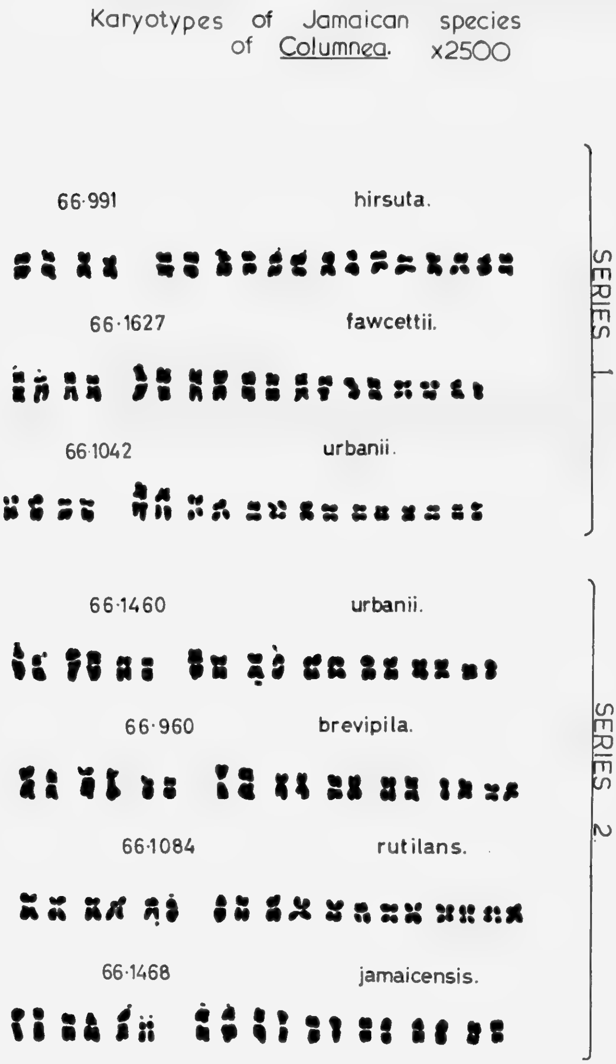


FIG. 3. Karyotypes of some Jamaican species of *Columnea.*

The hybrids between *Columnea rutilans* and *C. urbanii* have karyotypes intermediate in morphological details between those of the parents; see Text-fig. 4.

The Jamaican species with smaller and more asymmetric karyotypes, i.e. *Columnea argentea*, *C. hispida* and *C. harrisii* in Series 3, have the more limited distributions in Jamaica.

While, on evidence so far available, no changes in chromosome number have accompanied the evolution of *Columnea*, changes in chromosome structure have occurred, as is evident from gross morphological studies of Jamaican and Central American *Columnea* karyotypes.

FIG. 4. Karyotypes of some Jamaican species and hybrids of *Columnea*.

CHEMOTAXONOMY

By BRIAN D. MORLEY

Cultivation of the Jamaican species of *Columnea* at Kew enabled Dr. J. B. Harborne to carry out on fresh leaves three chromatographic tests for flavones, orobanchin, and cinnamics, and also to test for saponin. The substances detected in these tests were characterized as follows:

I. *Flavone a*: Rf 0·35 in butanol-acetic acid-water, Rf 0·05 in 5% acetic acid; colours in ultra-violet light + NH_3: dark brown–bright yellow; possibly luteolin 7-glucoside.
Flavone b: Rf 0·13 in 5% acetic acid; colours as flavone a.
Flavone c: Rf 0·23 in 5% acetic acid; colours as flavone a.
Flavone d: Rf 0·25 in butanol-acetic acid-water, Rf 0·05 in 5% acetic acid; colours as flavone a, but more intense.
II. *Orobanchin*: A complex ester of caffeic acid (see Harborne, 1966*a*).
III. *Cinnamics, Blue Spot*: Rf 0·69 in butanol-acetic acid-water; colours in ultra-violet light: colourless–blue; possibly a p-coumaric acid ester.
Cinnamics, Turquoise Spot: Rf 0·24 in butanol-acetic acid-water.
IV. *Saponin*: Detected by the presence of frothing when an aqueous leaf extract was shaken up.

These tests yielded the following results:

		I Flavones				II Orobanchin	III Cinnamics		IV Saponin
Species	Plant reference number	a	b	c	d		Blue spot	Turquoise spot	
C. hirsuta	Morley 33	+	+	—	—	+	—	—	—
C. fawcettii	Morley 34	+	+	—	—	+	—	—	—
C. proctorii	Morley S.17	—	—	—	—	+	+	+	+
C. urbanii	Morley 12	—	—	—	—	+	+	+	+
C. harrisii	Morley 6	+	+	—	+	+	+	+	—
C. argentea	Morley 36	—	—	tr	—	+	+	+	—
C. hispida	Morley 40	—	tr	tr	—	+	+	—	—
C. rutilans	Morley 3	—	tr	—	—	+	—	—	—
C. brevipila	Morley 24	tr	—	—	—	+	—	—	—
C. jamaicensis	Morley 27	+	—	—	—	+	—	+	—

Where + = present; — = absent; tr = trace.

The leaf-flavone attributes of *Columnea hirsuta* and *C. fawcettii* are similar and distinct from those of the other species; they support their taxonomic separation from other Jamaican species on the basis of calyx characters. Certain cytological features of the two species also distinguish them from the others in Jamaica. *C. urbanii* and *C. proctorii* have similar leaf-flavone attributes, and this parallels their morphological similarities. The leaf-flavone attributes of *C. urbanii* and *C. brevipila* are nearly similar, which adds some evidence for their general affinity to that provided by morphological and cytological data. The remaining species show a reticulate pattern of flavone attributes. *C. harrisii* was found to have a flavone attribute not observed in leaves of the other Jamaican species tested.

The tests for cinnamics and saponin give results in accordance with those for flavones in the case of the species pairs *Columnea hirsuta* and *C. fawcettii*, and *C. urbanii* and *C. proctorii*, the first pair being negative and the second positive. The resemblance in flavone attributes between *C. urbanii* and *C. brevipila* is not paralleled in the case of cinnamics and saponin. *C. rutilans* was found to have columnin in the leaves, a 3-desoxyanthocyanin, as reported by Harborne (1966*b*), which is responsible for the red pigmentation of the abaxial leaf surface in this species.

Columnea argentea and *C. harrisii* have common saponin and cinnamics attributes paralleling the densely hairy leaves found only in these species; thus the sensitivity of the biochemical tests is shown by their discrimination of particular species within a group of closely related endemic species. As noted above, they provide further evidence of affinity between *C. hirsuta* and *C. fawcettii*, between *C. urbanii* and *C. proctorii*, and to a lesser extent between *C. brevipila* and *C. urbanii*, and between *C. argentea* and *C. harrisii*.

Investigation of the cinnamics and saponin attributes of material from a hybrid swarm at Top Hill, Manchester, gave the following results. The hybrids are arranged in a series suggested by their degree of morphological agreement relative to their parents; the biochemical attributes broadly parallel this arrangement.

		Cinnamics		
Taxon	Plant reference number	Blue spot	Turquoise spot	Saponin
C. rutilans	Morley 19	−	−	−
Hybrid 11	Morley 48	+	−	−
Hybrid 10	Morley 46	−	−	+
Hybrid 6	Morley 47	+	−	−
Hybrid 4	Morley 8	+	−	+
Hybrid 1	Morley 43	+	−	+
C. urbanii	Morley 31	+	+	+

The leaf-flavone attributes of *Columnea rutilans* and *C. urbanii* are too similar to warrant their examination in the hybrids, but the saponin and cinnamics attributes of the hybrids were found to differ. The turquoise spot attribute in *C. urbanii* was not found in any of the hybrids and it may be genetically recessive. It is possible that backcrossing has occurred in the hybrid swarm and this may have complicated a simple pattern of gradation of the parental saponin and cinnamics attributes as found in hybrids 10 and 11. With a sufficiently comprehensive set of tests it might be possible to trace a backcrossing system in the hybrid swarm, particularly if synthetic backcrosses were made and used as marker plants.

Harborne (1966*b*) reported that biochemical tests distinguished between the subfamilies Gesnerioideae and Cyrtandroideae. The present study has shown that biochemical tests are also sensitive at specific and intraspecific levels; leaf flavones provide attributes for the identification of Jamaican species of *Columnea*, and leaf-saponin and cinnamic attributes identify different hybrid phenotypes in a hybrid swarm.

Harborne (1966*b*) has suggested that there may be correlation between the possession of 3-desoxyanthocynanins and ornithophilous pollination in the Gesnerioideae, as brightly coloured flowers are attractive to birds and plants synthesizing those pigments in larger quantities would have a selective advantage.

ECOLOGY AND DISTRIBUTION

All the Jamaican species of *Columnea* are endemic. Although they do not vie in brilliancy of colour with such conspicuous Central American species as *C. crassifolia*, *C. gloriosa*, *C. hirta*, *C. microphylla* and *C. oerstediana* (cf. Moore, 1957; Raymond, 1965), they are nevertheless attractive and interesting plants. They often grow as epiphytes high on trees and are then usually associated with bromeliads, notably clumps of *Hohenbergia*, thus easily passing unnoticed, but they also grow on rocks or stone walls when the rainfall is high enough to permit the luxuriant growth of mosses and the deposit of humus. Evidently they need good drainage and a moist or intermittently moist atmosphere.

The large zygomorphic yellow or red flowers have protruding stamens and style, and secrete nectar at the base of the corolla-tube and are visited by humming-birds. Three species of humming-bird (Trochilideae) inhabit Jamaica (cf. Bond, 1947), namely the Jamaican Mango Humming-bird (*Anthracothorax mango*) with a beak about 2·5 cm. long, the Streamertail (*Trochilus polytmus*) with a beak about 2 cm. long and the Vervain Humming-bird (*Mellisuga minima*) with a beak about 9 mm. long. Of these, the Streamertail has been observed visiting flowers of *Columnea* (cf. Morley, 1966). The corolla-tube in most Jamaican species of *Columnea* averages about 2 cm. long; indeed the general size of the corolla appears to be correlated with the length of the beak and head of the Streamertail (Text-fig. 5), which has thus probably been a major factor in the evolution of the Jamaican species, apart from *C. hispida* and *C. jamaicensis*. If the Streamertail became extinct, most of the Jamaican species of *Columnea* would probably also become extinct.

Humming-birds are strongly territorial in their habits. Thus a single bird feeds within a limited area and drives other humming-birds from it, thereby restricting pollination of ornithophilous flowers to plants within this feeding area (cf. Pitelka,

FIG. 5. Flower of *Columnea argentea* and head of Streamertail Humming-bird (*Trochilus polytmus*).

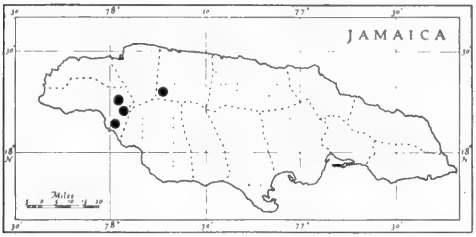
1942). Grant & Grant (1966 : 55), for example, record humming-birds each individually guarding its own patch of *Zauschneria latifolia* in flower and chasing other humming-birds from its preserve. These territorial habits of humming-birds presumably favour the inbreeding of plant colonies, which may be very important in the earlier stages of species development. As, however, unlike bees, humming-birds have no flower constancy but dart indiscriminately from one nectar-yielding species to another, they are likely to cross-pollinate quickly any two species flowering at the same time in a given feeding area. The numerous seeds contained in the white or pink berries of *Columnea* are presumably distributed from tree to tree by other birds; the association of *Columnea* with bromeliads may possibly result from birds drinking water and collecting insects at the bromeliad pitchers. Ants, however, find the seeds attractive, according to Morley, as they do those of other Gesneriaceae, and thus could aid dissemination over the same tree or rocky slope.

Although the Jamaican species have much the same ecological preferences, they differ markedly in range (Text-figs. 6–19) and exhibit the general tendency of the family Gesneriaceae towards much local endemism. Longitude 77° 20′ approximately halves the island of Jamaica. West of it occur *Columnea rutilans*, *C. harrisii*, *C. jamaicensis*, *C. urbanii* (with a slight extension of range east of it), *C. hispida*, *C. proctorii*, *C. brevipila*, *C. subcordata* and *C. argentea*, to the east of it *C. fawcettii* (with a slight extension of range west of it), *C. hirsuta* and *Alloplectus pubescens*, as also *Achimenes erecta* (Text-fig. 20), the early history of which is entangled with that of *Columnea*. *Alloplectus grisebachianus* has a central position. Hybridization is easily effected in cultivation but rarely occurs in the wild because, although the ranges of some species overlap, usually only one grows in a particular locality. Dr. Brian Morley collected at Top Hill, Manchester, near Walderston (Text-fig. 16), in a man-disturbed habitat, where both *C. rutilans* (Text-fig. 17) and *C. urbanii* (Text-fig. 9) occur, a series of intermediate plants evidently resulting from their hybridization. There may also be some ecological separation. Thus *C. hirsuta* (Text-fig. 14) grows mostly between 900 m. (3 ,000 ft.) and 1,500 m. (5,000 ft.), although descending in Portland and St. Thomas to 600 m. (2,000 ft.). *C. fawcettii* (Text-fig. 15), which is closely allied and has been long confused with it, grows mostly between 400 m. (1,400 ft.) and 900 m. (3,000 ft.) in the same general area as *C. hirsuta* but extends far beyond the range of this. Some species are clearly very restricted in range, e.g. *C. argentea* (Text-fig. 12) and *C. hispida* (Text-fig. 7), though the reasons are not evident.

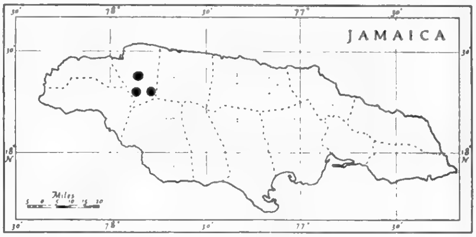
TAXONOMETRIC SURVEY

Before the computer-aided techniques of numerical taxonomy (taxonometrics) can be used with confidence to classify taxa belonging to difficult or obscure groups, by assessing the relative over-all similarity of these taxa and then arranging them hierarchically in accordance with their degree of similarity and divergence, it is necessary to test the validity and sensitivity of such techniques by applying them to better understood groups already satisfactorily classified by traditional methods and represented by adequate material. A computer-aided technique which for such a group produces a classification essentially similar to or as reasonable as a well

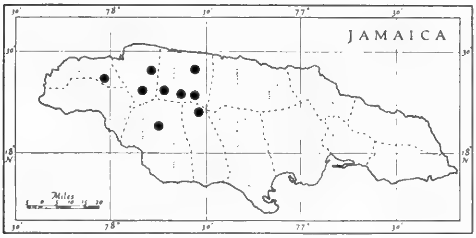
COLUMNEA



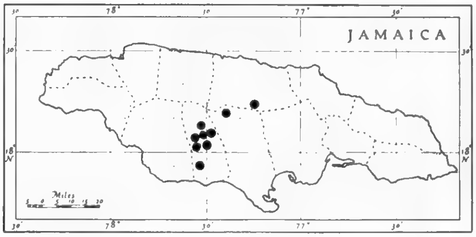
6 jamaicensis



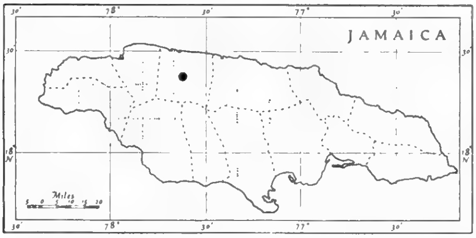
7 hispida



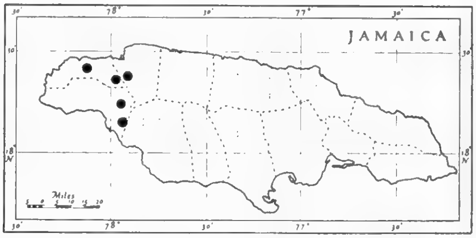
8 proctorii



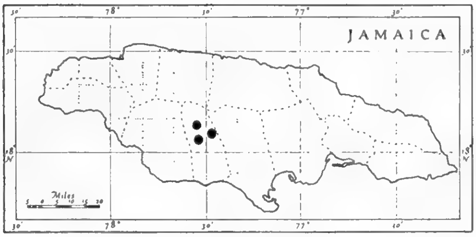
9 urbanii



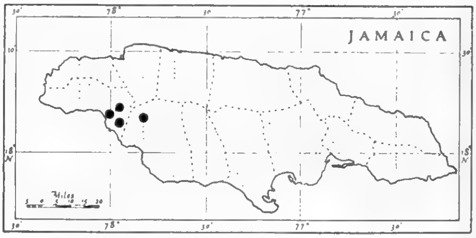
10 subcordata



11 harrisii



12 argentea

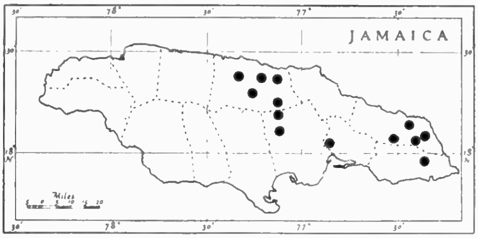


13 brevipila

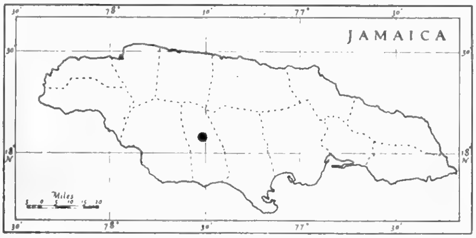
FIGS. 6–13. Distribution of *Columnea* in Jamaica: Fig. 6, *C. jamaicensis*; Fig. 7, *C. hispida*; Fig. 8, *C. proctorii*; Fig. 9, *C. urbanii*; Fig. 10, *C. subcordata*; Fig. 11, *C. harrisii*; Fig. 12, *C. argentea*; Fig. 13, *C. brevipila*.

Columnea

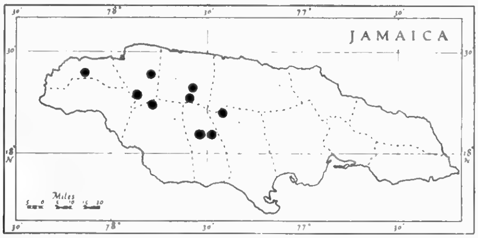
14 **hirsuta**



15 **fawcettii**

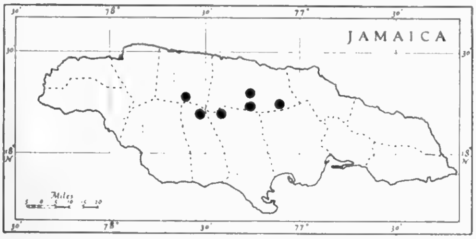


16 **hybrid (rutilans x urbanii)**

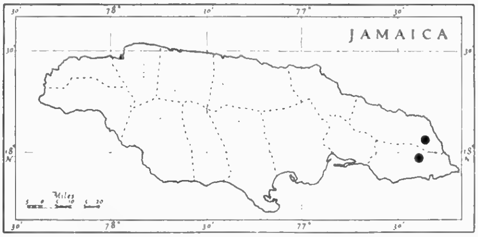


17 **rutilans**

Alloplectus

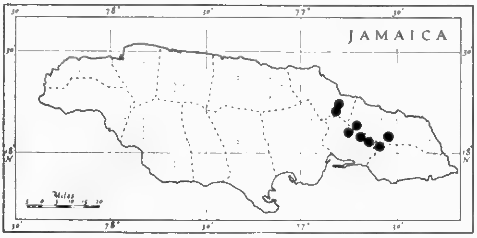


18 **grisebachianus**



19 **pubescens**

Achimenes



20 **erecta**

Figs. 14–20. Distribution of *Columnea*, *Alloplectus* and *Achimenes* in Jamaica: Fig. 14, *Columnea hirsuta*; Fig. 15, *C. fawcettii*; Fig. 16, *C. rutilans* × *urbanii*; Fig. 17, *C. rutilans;* Fig. 18, *Alloplectus grisebachianus*; Fig. 19, *A. pubescens*; Fig. 20, *Achimenes erecta*.

grounded existing one obviously commends itself for use in other investigations. Conversely a technique which makes nonsense when dealing with the known is unlikely to do better with the unknown. Application of taxonometric methods to different groups has given results of varied acceptability. Thus a comparison by Kendrick and Weresub (1966) of members of orders within the Basidiomycetes, using 67 haphazardly assembled equally weighted characters, resulted in a haphazard classification, seemingly of no value for any purpose. Watson, Williams & Lance (1967), using 38 characters, produced a classification of the genera of Ericales which bears only a limited resemblance to the one generally accepted; they regard, however, the new scheme as more convincing, " since it provides a convenient summary of the information put into it and makes sense of observations other than those on which it was based, while the traditional scheme does neither." Sheal's taxonometric survey of mesostigmatid mites of the *Hypoaspis-Androlaeleps* complex, using 62 characters, gave results in good agreement with a recent revision by traditional methods (Sheals, 1965; cf. also British Museum (Natural History), 1966). Likewise an arrangement of the genera of megascolecoid earthworms (Oligochaeta Megascolecidae) by computer technique, using 43 characters, gave results coinciding largely with one of the previously proposed classifications (Sims, 1966).

A major difficulty in numerical taxonomy is finding enough attributes for computation; obviously the smaller the number, the greater the risk of results distorted by abnormalities. Between 40 and 100 characters have been postulated as necessary to give results statistically valid (Sokal & Sneath, 1963), but in practice it is often difficult or impossible to provide so many characters; the diversity within small groups does not stretch that far. Hence it is desirable to ascertain empirically whether a much smaller number of characters will yield results which, even if not so detailed and meaningful as those derived from a large number of characters, can nevertheless be helpful by grouping together organisms with over-all resemblance and separating those which differ. It is also desirable to ascertain the extent to which a reduced set of selected characters and an equally reduced set of characters picked at random agree in their results with each other and with a maximum set.

The information available about the Jamaican species of *Columnea* and *Alloplectus* seemed to be broadly enough based and adequate enough in quantity to provide such comparisons and to test the ability of a computer-aided taxonometric procedure to classify these species. By including cytological, biochemical and anatomical data along with gross morphological data it was possible to tabulate 51 characters varying from species to species, i.e. constant within a given species but not for the whole group. This full set of characters was the basis of one computation; 27 of them had been used in a key and thus formed a reduced set weighted in favour of readily observed macroscopic characters, on which indeed most angiosperm taxonomy is necessarily based. These were used for a second computation. For comparison, 27 characters were taken at random, i.e. by assigning number to each of the full 51 characters and picking blindfold 27 cards out of 51 bearing these numbers; 13 were found to coincide with those of the other set. These were used for a third computation. Such characters for coding purposes may be divided into three groups (cf. Watson, Williams & Lance, 1967): *qualitative* (or *discrete*) *two-state* (or *dichotomous*), in which a character exists in one or other of two states; *qualitative multi-state,* in which a character exists in one of three or more states; *quantitative* (or *continuous*) comprising characters within which several measurable or assessable though less clear-cut and sometimes overlapping states may be distinguished. For some characters their allocation to one or other of these groups is arbitrary. Those used in this survey were as follows:

TWO-STATE

1.* *Stem thickness*: less than 5 mm.; more than 5 mm.
2.* *Leaves*: isophyllous; anisophyllous.
3.* *Leaf base*: symmetric; asymmetric.
4.* *Leaf underside*: green; red.
5.* *Hairs of leaf*: colourless; red.
6. *2–3-celled hairs on leaf upperside*: absent; present.
7. *Other hairs on leaf upperside*: 4–7-celled; 8–10-celled.
8.* *2–3-celled hairs on leaf underside*: absent; present.
9. *Other hairs on leaf underside*: 4–7 celled; 8–10-celled.
10. *Pedicels*: always 1; 1–several.
11. *Hairs of pedicels*: colourless; red.
12.* *Calyx-segments*: all free; 4 fused, 1 free.
13.* *Calyx*: green; wholly or partly red.
14.* *Hairs of calyx*: long; short.
15. *Long hairs of calyx*: erect; otherwise.
16. *Short hairs of calyx*: few; many.
17.* *Hairs of calyx*: colourless; red.
18.* *Corolla*: completely yellow; yellow and red.
19.* *Corolla length*: 3 cm. or less; 4 cm. or more.
20.* *Corolla-tube length*: 1 cm.; 1·4–2·5 cm.
21. *External hairs of corolla*: 2–6-celled; 6–12-celled.
22. *External hairs of corolla*: colourless; red.
23. *External hairs of corolla*: appressed; spreading.
24. *External hairs of corolla*: few; many.
25. *Internal hairs of corolla*: 1–3-celled; 3–6-celled.
26.* *Filaments of stamens*: glabrous; hairy.
27. *Non-glandular hairs on style*: absent; present.
28. *Submetacentric chromosome pairs*: 2; 3.
29. *Saponin*: absent; present.
30.* *Corolla*: regular; zygomorphic.
31. *Anthers*: almost square; oblong.

MULTI-STATE

32. *Flavone*: none; A; B; C.

QUANTITATIVE

33.* *Leaf-blade length/breadth*: 1·5–2; 2·4–2·7; 3·4–4.
34.* *Leaf-blade length*: under 5·5 cm.; 5·5–12 cm.; more than 12 cm.
35. *Length of long petiole*: almost nil; to 1 cm.; to 1·5 cm.; to 3·5 cm.
36.* *Vein pairs of leaf*: 3; 4–5; 5–7; 7–8.
37.* *Hair density on leaf upperside per sq. cm.*: 0–25; 26–100; 101–400; 401–800; 801–1,600.
38.* *Hairs on leaf upperside*: erect; strongly curved; appressed.
39. *Hair density on leaf underside per sq. cm.*: 0–25; 26–100; 101–400; 401–800; 801–1,600.
40.* *Hairs on leaf underside*: erect; strongly curved; appressed.
41. *Palisade layer*: in upper $\frac{1}{2}$; at middle; in lower $\frac{1}{2}$.
42. *Cell width in palisade layer*: narrow; medium; broad.
43. *Pedicel length*: 2–10 mm.; to 25 mm.; to 30 mm.
44.* *Hairs on pedicel*: appressed; ascending; erect.
45.* *Length of calyx-segments*: 1–1·4 cm.; 1·5–1·9 cm.; 2–2·4 cm.
46.* *Calyx-segments*: entire or almost so; toothed; laciniate.
47.* *Length of upper lip of corolla*: nil; 2–2·4 cm.; 2·5–3 cm.; 3·1–3·4 cm.
48. *Length of mid lobe of corolla*: nil; 3–5 mm.; 10–15 mm.; 16–18 mm.
49. *Length of lower lip of corolla*: nil; 1 cm. or less; 1·5 cm. or more.
50.* *Ovary*: glabrous; hairy above; completely hairy.
51. *Cinnamic*: absent; scanty; abundant.

These characters were ascertained from living and herbarium material and coded numerically, e.g. hairs colourless = 0, hairs red = 1, hairs appressed = 0, hairs strongly curved = 1, hairs erect = 2, then tabulated as a species/data matrix, all being included in the full matrix, but only the 27 marked * in the reduced matrix of selected characters (reduced key matrix). For many quantitative characters, an average from a number of specimens was taken and the coding based on this. Computation of the above data on an Orion electronic computer at the Rothamsted Experimental Station, Harpenden, Herts., England, by G. Ross, using Gower & Ross's program CLASP, gave the " median sort " results expressed as dendrograms (phenograms) in Text-figs. 21–23.

Since certain species are obviously closely linked in their morphological characters, e.g. (1) *Columnea hirsuta* and *C. fawcettii*, (2) *C. subcordata* and *C. proctorii*, (3) *C. argentea*, *C. brevipila* and *C. harrisii*, and others are relatively isolated, e.g. *C. hispida*, *C. jamaicensis*, *A. grisebachianus*, it was postulated before computation that, unless the resulting dendrograms linked and separated such species accordingly, they would have little or no relevance to the actual situation within the genus. In fact all three dendrograms make these associations and distinctions. The dendrogram (Text-fig. 21) from the full matrix (51 characters) achieves, however, the most satisfactory differentiation, then comes that from the reduced random matrix (Text-fig. 22), both being superior to that from the reduced key matrix of 27 characters (Text-fig. 23). Thus, whereas the dendrogram from the reduced key matrix

(Text-fig. 23) simply places together at a similarity coefficient (phenon level) of 80% *C. fawcettii*, *C. harrisii*, *C. hirsuta*, *C. proctorii* and *C. subcordata* without further distinction and separates from them at the 75% level *C. argentea* and *C. brevipila*, the full one and the reduced random one put these species in three groups, the full one (Text-fig. 21) at the 75% level, the random (Text-fig. 22) at the 70% level, i.e. (1) *C. hirsuta* and *C. fawcettii* together, (2) *C. subcordata* and *C. proctorii* with *C. urbanii*, (3) *C. argentea* and *C. brevipila* with *C. harrisii*; the dendrogram from the full matrix goes further by associating *C. hirsuta*, *C. fawcettii* and *C. rutilans*. In

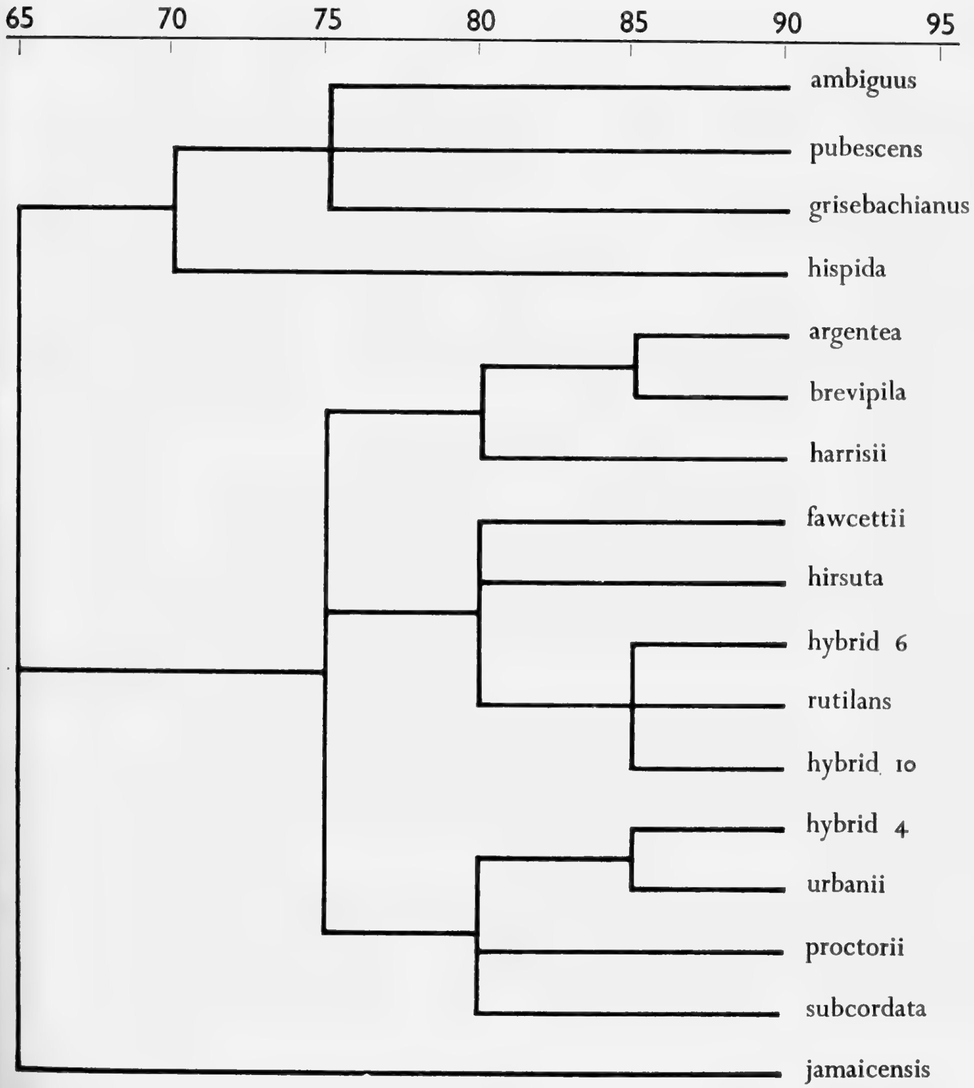


FIG. 21. Dendrogram showing the percentage of similarity of 17 species and hybrids of *Columnea* and *Alloplectus* computed from a matrix of 51 characters (cf. Fig. 24).

these instances, a taxonometric method has thus created from an assemblage of numerous unweighted characters a classification basically the same as one made by traditional methods. All dendrograms emphasize the distinctness of *C. jamaicensis* from other Jamaican species of *Columnea* by separating it at the 65% (full and reduced random matrices) and 70% (reduced key matrix) levels; no dendrogram, however, indicates any resemblance of this to the *Alloplectus* species *A. ambiguus*, *A. grisebachianus* and *A. pubescens*. All associate the hybrids with one or other of their parents. The superiority of the dendrogram based on 27 random characters (Text-fig. 22) over that based on 27 selected characters (Text-fig. 23) would appear to result from the first including biochemical, anatomical and cytological characters as opposed to the purely morphological characters of the second. The difference between them is in line with the general view of taxonomists that certain characters

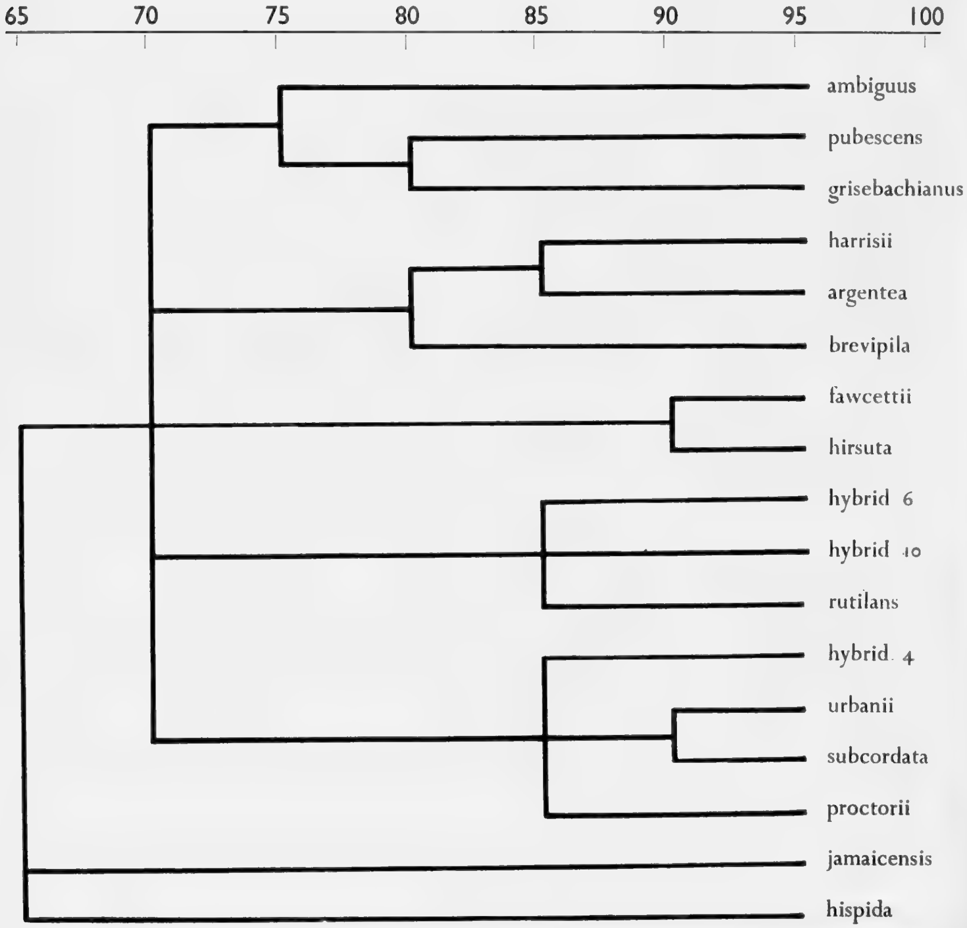


FIG. 22. Dendrogram showing the percentage of similarity of 17 species and hybrids of *Columnea* and *Alloplectus* computed from a matrix of 27 characters taken at random (cf. Fig. 25).

reflect more strongly than others the genetic composition of taxa but it also indicates that such characters are not all of them consciously used by taxonomists.

A dendrogram provides a convenient expression of relationship by degree of similarity, since this similarity presumably arises from and expresses a similarity of genes, but it suffers from the disadvantages inevitable in a linear sequence. A more revealing view of relationships may be obtained by producing from the similarity matrix, by means of Gower's method of Principal Co-ordinates Analysis (Gower,

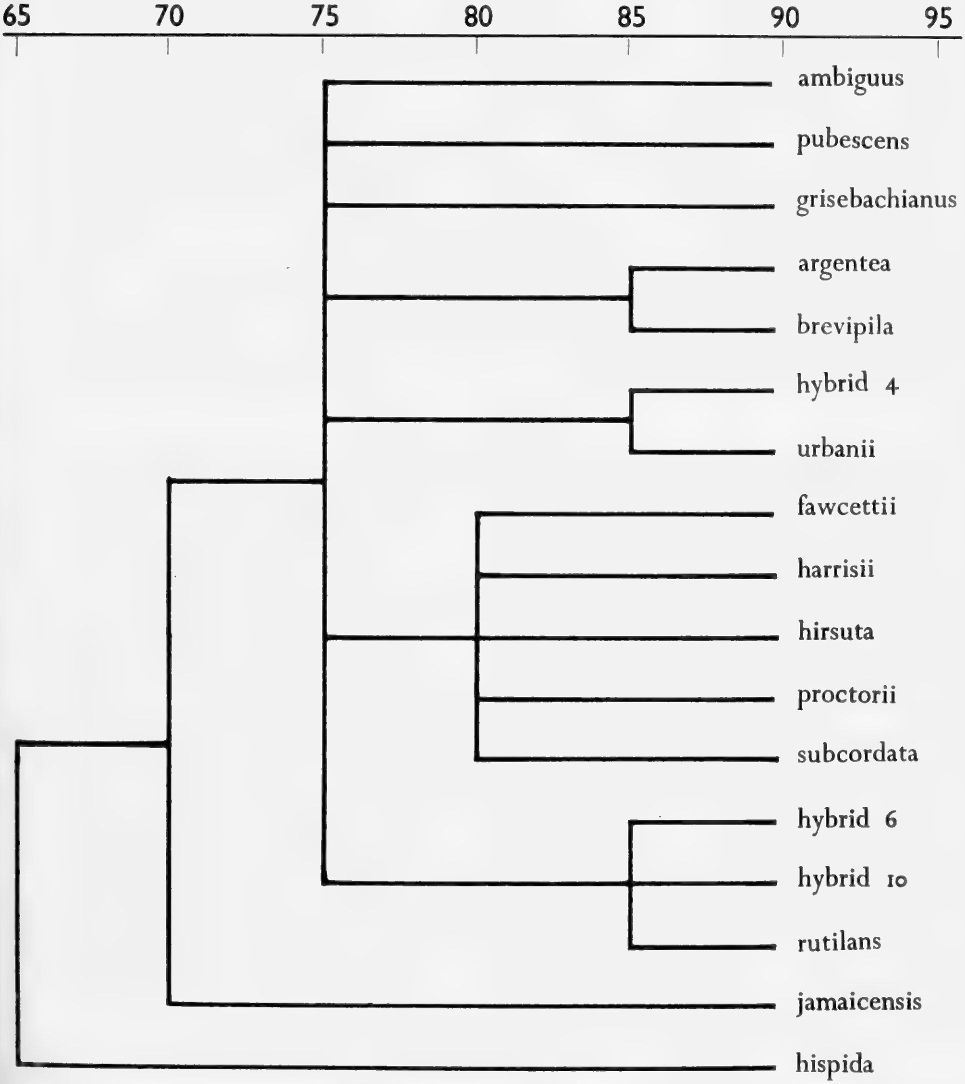


FIG. 23. Dendrogram showing the percentage of similarity of 17 species and hybrids of *Columnea* and *Alloplectus* computed from a matrix of 27 characters used in a key for their recognition (cf. Fig. 26).

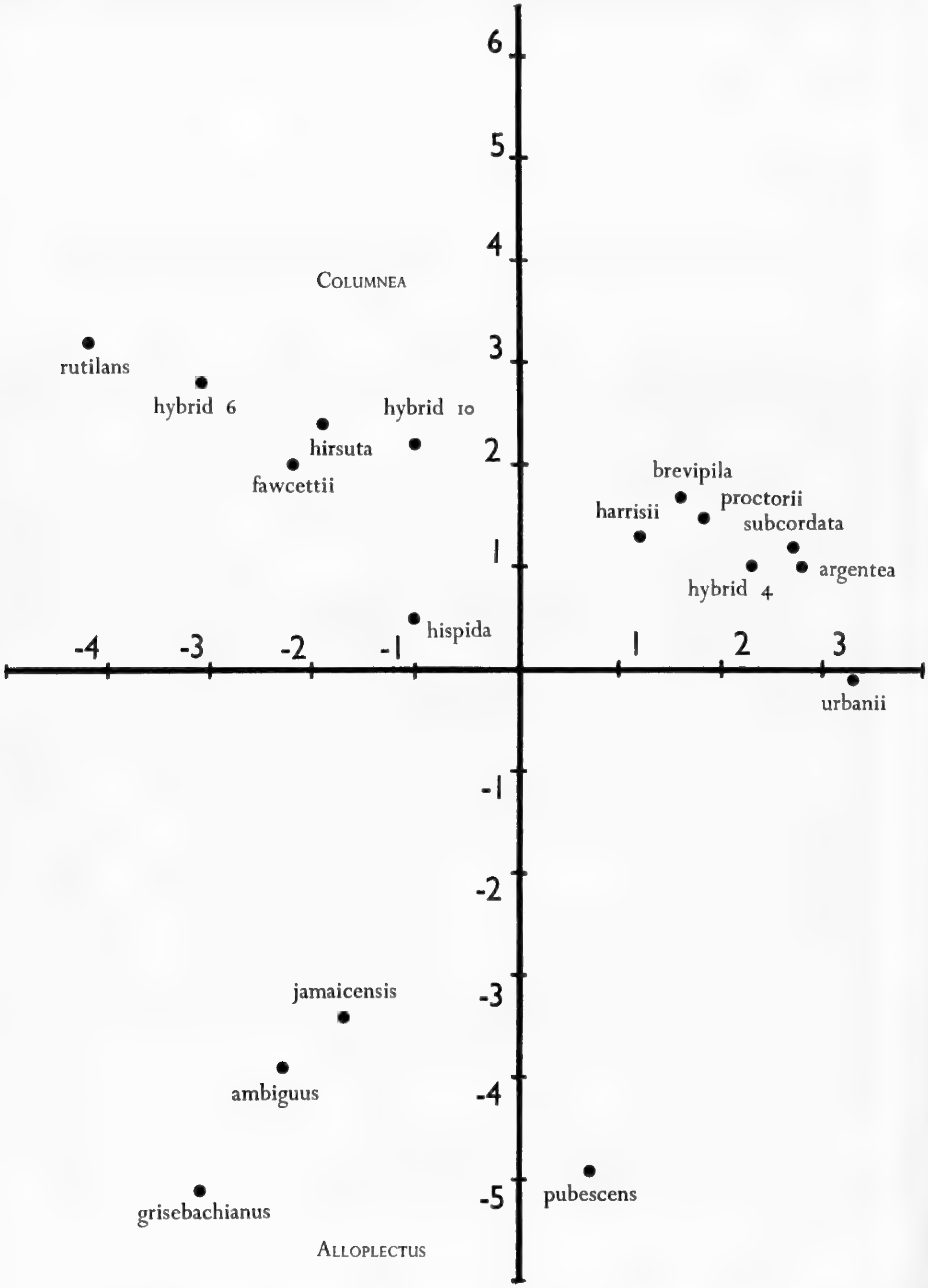


Fig. 24. Vector diagram showing relative similarity of 17 species and hybrids of *Columnea* and *Alloplectus* computed from a matrix of 51 characters (cf. Fig. 21); the vertical co-ordinates are the vectors corresponding to the first latent roots, the horizontal co-ordinates those of the second latent roots, of the transformed matrix.

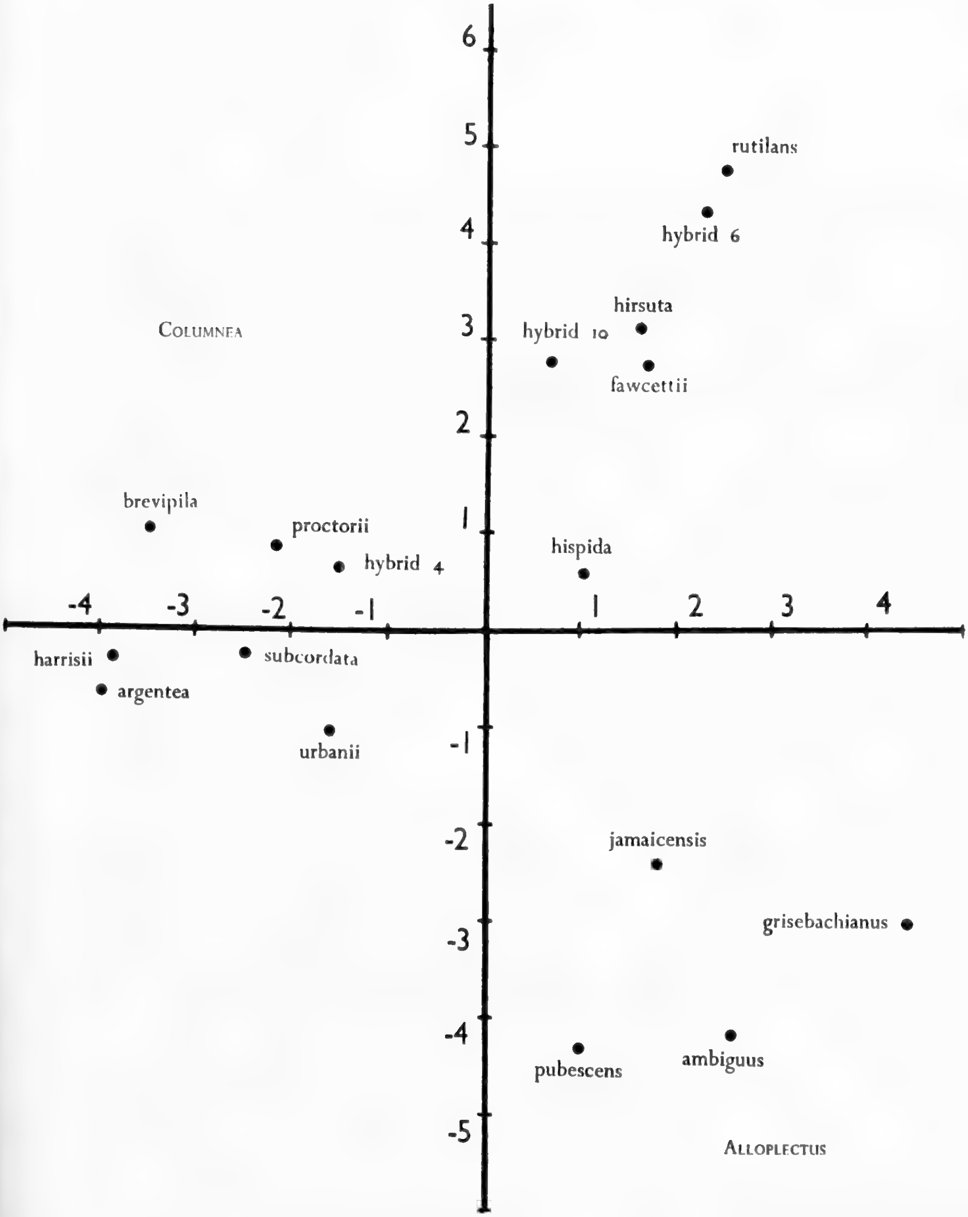


FIG. 25. Vector diagram showing relative similarity of 17 species and hybrids of *Columnea* and *Alloplectus* computed from a matrix of 27 characters taken at random (cf. Fig. 22); co-ordinates as in Fig. 24.

1966), a scatter diagram with the scaled first and second vectors of the transformed matrix as co-ordinate axes. In this vector diagram the distances between the units are proportional to the square root of their dissimilarity. Those resulting from the full and reduced matrices (Text-figs. 24–26) differ very much less than might be expected; indeed the major differences between the three are in the relation of the units to the axes and not to one another, as becomes evident by rotating the diagram of the reduced key matrix (Text-fig. 26) through about 45 degrees to the left and by

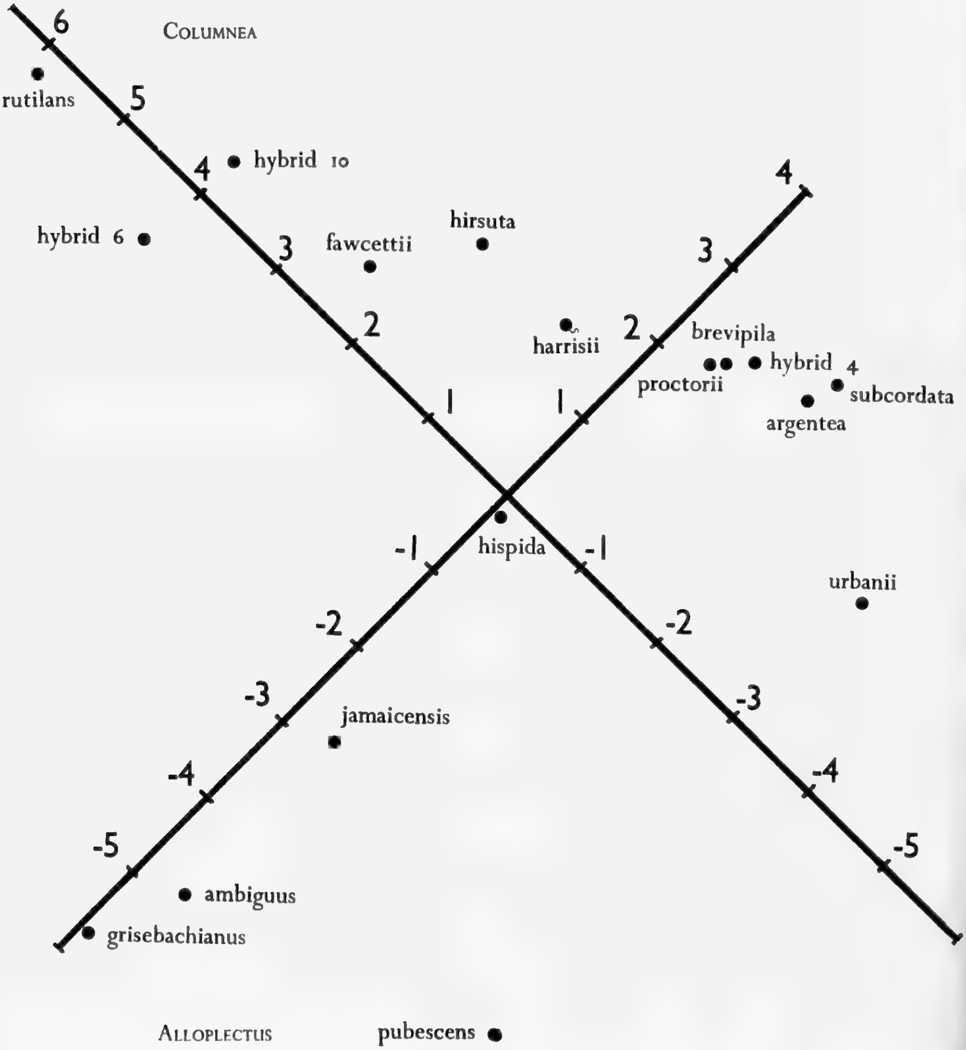


Fig. 26. Vector diagram showing relative similarity of 17 species and hybrids of *Columnea* and *Alloplectus* computed from a matrix of 27 characters used in a key for their recognition (cf. Fig. 23); the right to left co-ordinates are derived from the first latent roots, the left to right co-ordinates from the second latent roots (cf. Fig. 24).

transposing from left to right and vice versa the units of the diagram of the reduced random matrix (Text-fig. 25). They all convey much the same general information. In all three diagrams, *Columnea hirsuta* and *C. fawcettii* are brought closer to *C. rutilans* than is apparent in the dendrogram from the reduced matrices; *C. rutilans* and *C. urbanii* are well isolated and their hybrids spaced between them. All diagrams place fairly close together *C. proctorii*, *C. brevipila*, *C. subcordata*, *C. argentea* and hybrid 4, an assemblage which should, however, on morphological grounds be separated into three groups. The configuration of species becomes here more meaningful if the third latent vector is brought into consideration by being treated as a third dimension. Thus, in the data derived from the full matrix, the third latent vector of — 0·25 for *C. proctorii* brings this close to *C. subcordata* with a vector of — 0·24, while *C. brevipila*, with a vector of 0·25, and *C. argentea*, with a vector of 0·23, stand apart from them both and from hybrid 4, with a vector of 0·11; consideration of the third latent vector thus separates them into three groups agreeing with their general morphological characters.

The units on the vector diagrams resolve into a general pattern which appears significant. The typical species of *Columnea* with large zygomorphic flowers stretch together across the upper part of the diagram of the full matrix (Text-fig. 24) in a sequence passing from *C. urbanii* with green isophyllous leaves and entire calyx-segments to *C. rutilans* with markedly anisophyllous leaves red below and laciniate calyx-segments, and they undoubtedly form a natural group, the evolution of which has probably been partly controlled by the Jamaican endemic Streamertail Humming-bird (Text-fig. 5). From this group *C. hispida* stands somewhat apart, and in view of its short and more dingy corolla it probably has a different pollinating agent. Far below them and well separated from each other in every diagram are the species of *Alloplectus*, i.e. *A. ambiguus*, *A. grisebachianus* and *A. pubescens*, probably self-pollinated, with *C. jamaicensis* brought much closer to them than to the typical species of *Columnea*, a placing which agrees well with its general morphology but is not evident from the dendrograms.

The vector diagrams give indeed the general impression that, whereas the typical *Columnea* species of Jamaica can well be regarded as derivatives of a single stock, *C. jamaicensis* represents an independent and florally less developed offshoot of *Alloplectus*.

A dendrogram simply indicates degree of similarity without necessarily placing the units of a particular group into a meaningful sequence within it, whereas a scatter diagram places them in two-dimensional relation to one another and hence can be used as a better basis for arranging the units in a sequence indicative of resemblance and possibly of genetic affinity. The dendrogram derived from the full matrix arranged in this way (Text-fig. 27) by reference to the corresponding scatter diagram (Text-fig. 24) gives an arrangement which coincides almost exactly with the taxonomic arrangement previously made by traditional methods.

This survey thus confirms the view that taxonometric methods when applied to an adequate body of data can produce a grouping of species certainly as satisfactory as one obtained by traditional methods and possibly more suggestive of their course of development; moreover such groupings can result from the computation of much less than the postulated necessary 40 characters, particularly when the characters used are diverse enough to epitomise the whole organization of the species.

SYSTEMATIC ACCOUNT

MATERIAL STUDIED

This account has been based on the collection in the Department of Botany, British Museum (Natural History), London (BM) together with material lent by the

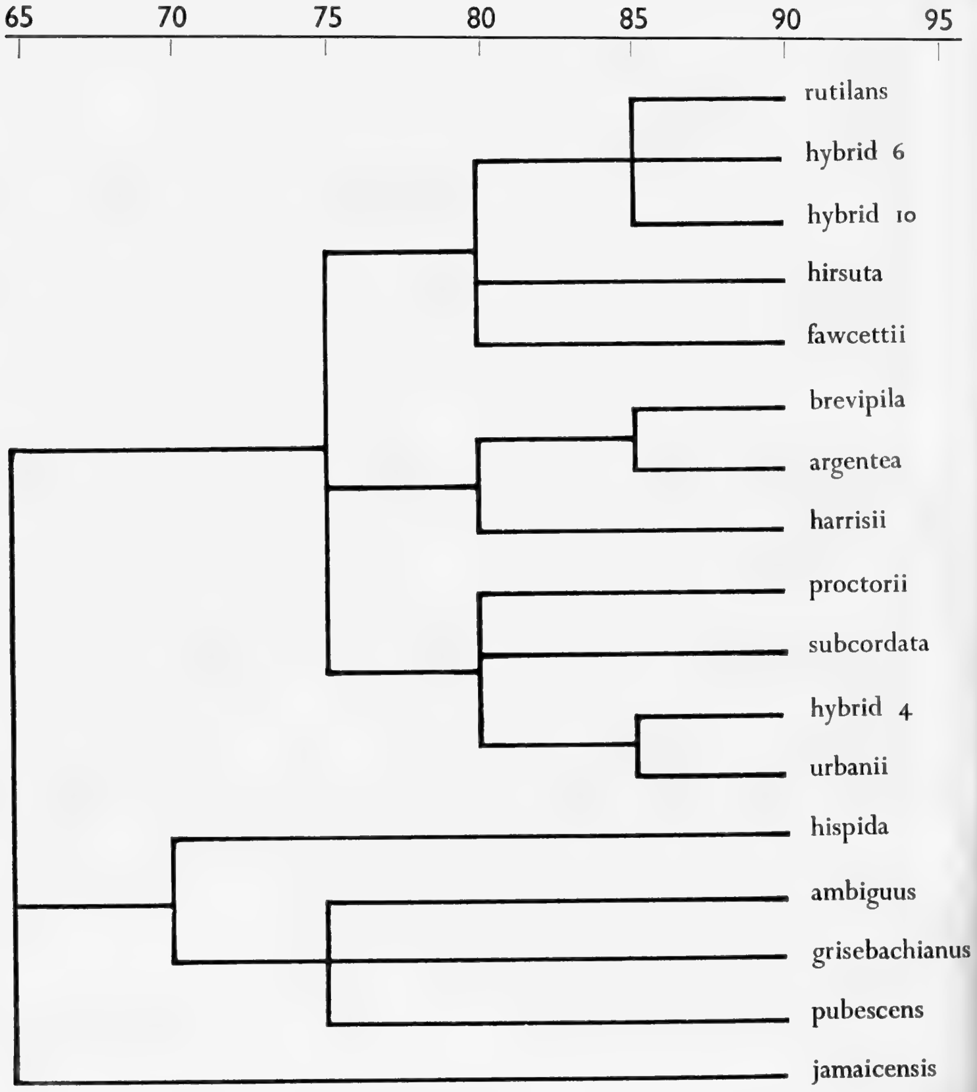


FIG. 27. Dendrogram showing phenetic affinity of 17 species and hybrids of *Columnea* and *Alloplectus* computed from a matrix of 51 characters and arranged in a sequence based on a vector diagram from the first and second latent roots (cf. Figs. 21, 24).

Systematisch-Geobotanisches Institut, Universität, Göttingen (GOET), the Science Museum, Institute of Jamaica, Kingston, Jamaica (IJ), the Royal Botanic Gardens, Kew (K), the Botanische Staatssammlung, Munich (M), the New York Botanical Garden (NY), the Department of Botany, University of the West Indies, Mona, Jamaica (UCWI) and the United States National Herbarium, Smithsonian Institution, Washington, D.C. (US).

Specimens are listed by the parishes of Jamaica, beginning with Hanover and Westmoreland in the west and ending with Portland and St. Thomas in the east (cf. Stearn, 1959 : 134, fig. 1a).

As an indication of how our knowledge of the Jamaican species of *Columnea* and *Alloplectus* has grown, it is of interest to note that Grisebach (in 1862) distinguished seven species on 15 gatherings, Urban (in 1901) seven species on 20 gatherings, Morton (in 1944) ten species on 54 gatherings; the present account distinguishing 13 species has been based on 190 gatherings. Our understanding of the group in Jamaica would appear more likely now to benefit from field observations on pollination and dissemination than from further collecting.

ACKNOWLEDGEMENTS

Grateful thanks are here expressed to those in charge of the above herbaria for the opportunity to study their material. I am indebted especially to Mr. George R. Proctor for his help to me while collecting Columneas and other plants in Jamaica. Dr. Brian D. Morley has generously made available the results of his extensive cytological and other research and contributed the sections on cytology and biochemistry above. He and Miss Barbara Heywood also assisted me in ascertaining and tabulating the characters used in the taxonometric analysis above, which is the result of computation by Mr. Gavin J. S. Ross at the Department of Statistics, Rothamsted Experimental Station; it has benefited much from the advice of Dr. J. G Sheals. Mr. D. Erasmus drew the text-figures. The co-operation of them all is much appreciated.

KEY TO JAMAICAN SPECIES OF *COLUMNEA* AND *ALLOPLECTUS*

Corolla tubular or narrowly funnel-shaped, the limb not markedly 2-lipped, the lobes of the limb only 2–8 mm. long; leaf-bearing branches slender (1–3 mm. diam.); all leaf-blades small (mostly under 5 cm. long, 3 cm. broad):
  Calyx-segments laciniate with four or five prominent teeth either side; central Jamaica . . . . 2. *Alloplectus grisebachianus*
  Calyx-segments entire or with one or two minute teeth either side:
    Leaves and calyx densely hirsute; corolla-lobes almost uniform, about 1–2 mm. long; eastern Jamaica . . . . 1. *A. pubescens*
    Leaves and calyx apparently glabrous but with ciliate margins and short inconspicuous hairs on surface; corolla-lobes forming two lips, the lower lip about 6 mm. long; western Jamaica . . 1. *Columnea jamaicensis*

Corolla markedly 2-lipped, the lobes of the limb 1 cm. or more long; leaf-bearing branches stout (5–10 mm. diam.); leaf-blade of at least one leaf of a pair larger (longer than 5 cm. or broader than 3 cm.):

Leaf-blades partly or completely red beneath or coloured red along the veins:

Calyx-segments deeply toothed along the margin, the lowermost teeth to 5 mm. long; larger leaf-blades three to four times as long as broad 11. *C. rutilans*

Calyx-segments entire or shortly toothed, the teeth to 2 mm. long; larger leaf-blades about two times as long as broad . . *C. rutilans × urbanii*

Leaf-blades green or silvery beneath, not red-veined or red:

Hairs on upper side of leaf minute, 0·2–0·3 mm. long, 2-celled, inconspicuous:

Calyx-segments entire, green, inconspicuously hairy with short rather appressed hairs:

Pedicels with minute appressed hairs 0·4 mm. or less long; Westmoreland, St. Elizabeth . . . . 8. *C. brevipila*

Pedicels with longer somewhat spreading hairs to 1 mm. long; Manchester *C. rutilans × urbanii*

Calyx-segments with one to three linear teeth to 2 mm. long on each margin, red in upper part, densely hirsute . . . . 9. *C. fawcettii*

Hairs on upper side of leaf 1 mm. or more long, 3–8-celled, conspicuous:

Calyx sericeous with dense appressed silvery hairs:

Leaf-blades densely sericeous beneath, three to five times as long as broad, with four or five primary veins either side, almost symmetric at base; corolla yellow . . . . 6. *C. argentea*

Leaf-blades with short curved hairs not completely covering the surface beneath, about two to three times as long as broad, with six to eight primary veins either side, markedly asymmetric at base; corolla red and yellow . . . . 6. *C. harrisii*

Calyx not sericeous but hispid or pilose with long, spreading, often glandular, hairs:

Calyx-segments with one to three linear teeth on each margin and with attentuate red tips; eastern Jamaica . . . . 9. *C. hirsuta*

Calyx-segments entire or only minutely toothed, green, the tips not attenuate; central and western Jamaica:

Leaves and calyx with conspicuous red hairs; corolla about 2·5 cm. long 2. *C. hispida*

Leaves and calyx with colourless (not red) hairs; corolla 4–5 cm. long:

Four calyx-segments joined at base for 5 to 8 mm., the fifth (posterior) one free from them; leaf-blades sometimes subcordate at base, usually asymmetric . . . . 5. *C. subcordata*

All calyx-segments free almost to the base; leaf-blades rounded to cuneate at base:

Leaves of a pair markedly unequal in size, the largest asymmetric at base and usually 8–14 cm. long, hirsute below with abundant long spreading hairs; corolla striped red and yellow throughout 4. *C. proctorii*

Leaves of a pair almost equal in size, the largest symmetric at base and at most 8 cm. long, usually much less, strigillose below with very short appressed hairs; corolla yellow or with red markings at base only:

Corolla yellow; style yellow . . . . . 3. *C. urbanii*

Corolla yellow with red stripes on base, or, if entirely yellow, style red . . . . *C. rutilans* × *urbanii*

COLUMNEA L.

Columnea L., Sp. Pl. 2 : 638 (1753); Gen. Pl. ed. 5 : 286 (1754).

Shrubs. Leaves opposite, those of a pair equal to markedly unequal, usually shortly petiolate. Flowers solitary or fasciculate in leaf-axils, with or without bracts. Calyx 5-partite. Corolla inferior, erect in the calyx, gibbous but not spurred at base, the tube gradually expanded upwards, long, the limb 2-lipped, the upper lip 3-lobed with the middle lobe formed from two united lobes into a notched galea or hood and with two lateral lobes spreading from it, the lower lip entire and recurving or reflexed. Stamens 4, didynamous, the filaments united in the lower part, free and filamentous above, the anthers of all four stamens cohering at anthesis, their loculi parallel, longitudinally dehiscent; fifth stamen represented by a staminode. Disc gland large and dorsal, sometimes accompanied by two to four smaller glands. Ovary superior; stigma usually 2-lobed. Fruit a fleshy berry; seeds minute, longitudinally or obliquely striate.

Type-species by monotypy: *C. scandens* L.

The above description does not cover the anomalous non-Jamaican species with regular corolla mentioned above (p. 187).

1. ***Columnea jamaicensis*** Urban, Symb. Antill. 2 : 359 (1901).—Morton in Contr. U.S. Nat. Herb. 29 : 3 (1944).—Stearn in Proc. Linn. Soc. Lond. 170 : 141 (1959). (Pl. 14; Text-figs. 2E, 6, 28H.)

Pterygoloma repens sensu Griseb., Fl. Brit. W. Ind. Is. : 464 (1862) pro parte, quoad pl. Jamaic.; non Hanstein.

Shrub of dwarf creeping habit, the stems grey, slender, c. 2 mm. thick, pilose with reddish hairs when young, later glabrous. *Leaves* paired, those of a pair unequal, sparsely setose on both surfaces, dark green above, paler green below, the larger leaf of the pair long-stalked, the blade narrowly ovate, asymmetric, with the apex shortly acuminate or acute, the margin almost entire or remotely serrulate, the base cuneate, 2·5–5·5 cm. long, 1–2·3 cm. broad, the smaller leaf soon falling, short- or long-stalked, the blade 0·5–3 cm. long, 0·5–1·5 cm. broad; petiole of larger leaves 5–11 mm. long, of smaller leaves 1–3 mm. long. *Flowers* solitary in leaf-axils. *Pedicel* 1·5–3 cm. long, strigillose with very short appressed hairs. *Calyx* divided to the base, reddish or green, sparsely and shortly pilose and ciliate outside; *segments* narrowly ovate or lanceolate, acute, 8·5–12 mm. long in flower, to 16 mm. long in fruit, entire or with one or two minute teeth on each margin. *Corolla* tubular, gradually widened, 2·5–

3 cm. long, crimson or orange yellow streaked with red bands, the tube much longer than the calyx, the upper lip about 0·5–1 cm. long, 3-lobed, the lower lip 5–8 mm. long, narrowly oblong. *Stamens* slightly exserted; filaments glabrous; anthers about 1 mm. long. *Ovary* glabrous except for a few sparse hairs near the apex; style glandular-pilose. *Berry* white, c. 5 mm. across.

WESTMORELAND: Springfield, 1849, *Wullschlägel 1290* (M; GOET, type of *C. jamaicensis*). Bluefields Mountain, four miles from the sea, 600 m., *Purdie* (K).

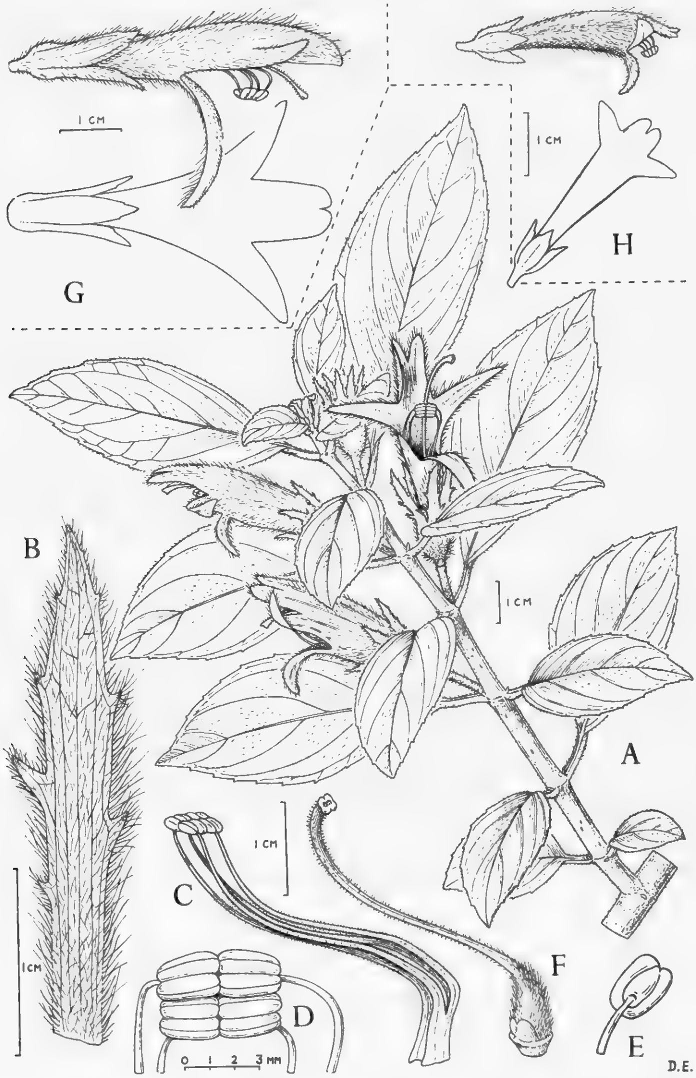


FIG. 28. *Columnea fawcettii* (Urban) Morton: A, flowering shoot; B, calyx-segment; C, stamens; D, anthers; E, anther showing insertion of filament; F, gynoecium, with disc-gland (*Stearn 255*). *Columnea urbanii* Stearn; G, flower (*Stearn 361*, spirit material). *Columnea jamaicensis* Urban: H, flower (*Stearn 928*, spirit material).

Three miles west of New Works, Bluefields Hill, 680 m., July 1954, *Farr 5643* (IJ). Two and a half miles northeast of Bluefields P.O., 700 m., July 1954, *Webster & Wilson 1954* (AA). Kentucky Hill, Bluefields Mountain, 600–760 m., March 1908, *Harris 10200* (BM; NY). Woodstock, near Newmarket, 420 m., Sept. 1907, *Britton 1571* (NY; US), *Harris 9836* (NY). Same locality, Oct. 1960, *Proctor 21518* (BM). Near Woodstock, 360 m., Dec. 1965, *Adams 12794* (BM). One mile west-northwest of Hopewell, 530 m., Nov. 1955, *Proctor 11232* (BM; IJ).

TRELAWNY: Cockpit Country, at Black Banana Hole, five miles north of Accompong, 330 m., April, 1956, *Stearn 928* (BM). Red Mud Hole, six miles north-northwest of Accompong, 330 m., April 1956, *Stearn 964* (BM).

Urban based his *C. jamaicensis* on specimens collected by Wullschlägel at " Springfield ", presumably Springfield in Westmoreland parish, although there are at least 20 other places in Jamaica named Springfield. Grisebach had earlier (Fl. Brit. West. Ind. Is. : 464 (1892)) listed this as *Pterygoloma repens* (Hook.) Hanstein, which is figured in *Botanical Magazine* 72 : t. 4250 (1846) as *Alloplectus repens* from Colombia. Among Jamaican species of *Columnea* it is notable for its very slender creeping stems, small leaves and almost tubular narrow corolla with a short only slightly bilabiate limb. The type-specimen (*Wullschlägel 1290*, GOET) has red narrowly ovate sepals about 12 mm. long, 4–6 mm. broad at anthesis, and similar specimens have been collected in Westmoreland. Specimens collected by me in the Cockpit Country diverge in having green lanceolate sepals 8·5–10 mm. long, 3·5–4 mm. broad at anthesis. It grows on damp walls, moss-covered rocks and trees, in western Jamaica (Text-fig. 6).

Hooker's *Alloplectus repens*, i.e. *C. repens* (Hook.) Hanstein (in Linnaea 34 : 395 (1865)) was based on a cultivated plant said to have been introduced by Purdie from Colombia. It comes so close to *C. jamaicensis*, however, as to arouse suspicion that Hooker may have had an unusual variant of *C. jamaicensis* mislabelled as to origin. If no such plant as Hooker's occurs in Colombia, then the correct name for the Jamaican species will be *C. repens*. Some of Purdie's Colombian specimens have been attributed to Jamaica by Grisebach; hence the possibility of some of his Jamaican material being attributed to Colombia.

2. **Columnea hispida** Swartz, Nov. Gen. & Sp. Pl. : 94 (1788); Fl. Ind. Occ. 2 : 1085 (1800).—Griseb., Fl. Brit. W. Ind. Is. : 465 (1862) excl. descript.—Urban, Symb. Antill. 2 : 364 (1901).—Stearn in Proc. Linn. Soc. Lond. 170 : 141 (1959). (Pl. 15; Text-figs. 1 A, 2 A, 7.)

Shrub, the stems brownish grey, stout, hispid with stiff spreading hairs to 3 mm. long. *Leaves* paired, those of a pair markedly unequal, dark green above, paler green below, hirsute on the upper surface and at the margin with long erect reddish hairs to 4 mm. long, hirsute on the lower surface along the veins with similar long hairs and hispid on the surface itself with short colourless hairs to 0·5 mm. long, the larger leaf of the pair relatively long-stalked, asymmetric, the blade more or less elliptic or obovate, with the apex obtuse, the margin remotely and shallowly serrate or almost entire, the base asymmetric, its lower side broadly cuneate, its other side narrowly cuneate and arising from the midrib about 5–10 mm. higher, 6–15 cm. long, 4–7 cm. broad, with four to six curved veins impressed each side of the midrib above, the smaller leaf 2–6 cm. long, 1·5–3·5 cm. broad; petiole of larger leaf 1–2 cm. long, of smaller leaf 5–10 mm. long. *Flowers* up to three in a leaf-axil. *Pedicels* c. 5 mm. long, densely hispid. *Calyx* divided to the base, very pale green but hispid outside with long reddish hairs; *segments* very narrowly oblong, c. 15 mm. long in flower to 2 cm. long in fruit, 3 mm. broad, entire. *Corolla* strongly 2-lipped, dull golden yellow, c. 2·5 cm. long, densely hispid on the back with hairs to 3 mm. long, the tube a little shorter than the calyx, c. 1 cm. long, the upper lip c. 1·5 cm. long and trilobed with a notched middle lobe and two rounded lateral lobes c. 4 mm. long, the lower lip c. 1 cm. long, 4 mm. broad, recurved. *Stamens* exserted; filaments minutely and sparsely hairy; anthers c. 2 mm. long. *Ovary* covered with long ascending bristles; style glandular-pubescent.

St. James: White Rock Hill, one mile south of Sweetwater, 600 m., March 1956, *Stearn 449* (BM). Same locality, Feb. 1957, *Proctor 16158* (BM; IJ). Half mile south of Point P.O., 500–550 m., 1961, *Proctor 22577* (IJ). Near Catadupa (*fide* Morley).

Unlocalized: *Swartz* (BM, type-collection).

This species was described by Swartz from fruiting specimens collected by himself " in montibus altis Jamaicae occidentalis, ad rupes umbrosas " and it remained thus vaguely localized and not again collected, despite the wide-ranging activities of Purdie, Harris and Britton in Jamaica, until found by Proctor and myself in 1956, growing on shaded limestone cliffs in the west of the island (Text-fig. 7), as indicated by Swartz. The flowers were unknown until 1957. It has since been cultivated at Kew and Montreal botanic gardens. From other Jamaican species it is easily distinguished by the long reddish hairs on the upper surface of the leaves and by the small flowers.

3. **Columnea urbanii** Stearn, sp. nov. (Pl. 16; Text-figs. 1B, 2H, 9, 28G.)

Columnea hispida sensu Griseb., Fl. Brit. W. Ind. Is. : 465 (1862) pro parte maj.; non Swartz.

Columnea hirsuta sensu Hanstein in Linnaea 34 : 413 (1865) pro parte quoad *Wullschlägel 959*; non Swartz.

Columnea hirsuta var. *subintegra* f. *wullschlaegelii* Urban, Symb. Antill. 2 : 363 (1901).

Suffrutex, caulibus ascendentibus 4–6 mm. crassis, primo pilis patentibus ad 2 mm. longis hirsutis, demum griseis glabratis, internodiis 0·5–4 cm. longis, cicatricibus prominentibus. *Folia* ad apicem ramulorum conferta, per paria aequalia, subsessilia, plerumque late elliptica sed interdum rotunda vel late obovata, apice obtusa vel rotundata, margine subintegra, basi late cuneata raro asymmetrica, 3–8 cm. longa, 2·5–5·5 cm, lata, in vivo utrinque pallide viridia, nervis lateralibus utroque latere costae 4–5 arcuatis, supra pilis erectis incoloribus plerumque 5-cellularibus c. 2 mm. longis hirsuta, subter pilis plerumque multo brevioribus appressis c. 0·5 mm. longis strigulosa; petiolus c. 1–4 mm. longus. *Flores* axillares 1–2. *Pedicelli* c. 8–15 mm. longi, hirsuti. *Calyx* viridis, extus hirsutus; segmenta libera subaequalia lanceolata acuta, anthesi 10–15 mm. longa, post anthesin ad 25 mm. longa, 3·5–5 mm. lata, integra. *Corolla* valde bilabiata, c. 5 cm. longa, flava, dorso pilis patentibus ad

2·5 mm. longis hirsuta; tubus basi postice saccatus gradatim ampliatus c. 22 mm. longus calyce fere duplo longior; labium superum c. 18–25 mm. longum, trilobatum, lobo medio emarginato c. 10 mm. lato, lobis lateralibus anguste triangularibus patentibus; labium inferum c. 18 mm. longum, 3 mm. latum, recurvatum. *Stamina* exserta, filamentis glabris, antheris oblongis c. 1·5–2 mm. longis. *Ovarium* apice hirsutum; stylus pubescens.

Shrub, the stems ascending, grey, stout, 4–6 mm. thick, hirsute, with spreading hairs to 2 mm. long when young, later glabrous. *Leaves* paired, those of a pair almost equal, short-stalked or almost sessile, the blade mostly broadly elliptic but varying from rotund to broadly obovate, with the apex obtuse or rounded, the margin almost entire, the base broadly cuneate, sometimes asymmetric, 4–12 cm. long, 2·5–5·5 cm. broad, light green on both surfaces, with 4–5 curved veins each side of the midrib impressed deeply above, hirsute above with erect mostly 5-celled hairs c. 2 mm. long, strigose below with numerous short hairs c. 0·5 mm. long, together with some longer hairs; petiole 1–4 mm. long. *Flowers* 1 or 2 in a leaf-axil. *Pedicels* c. 8–15 mm. long, hirsute. *Calyx* divided to the base, green, densely hirsute outside, less so inside; *segments* lanceolate, acute, 10–15 mm. long in flower, 3–5 mm. broad, to 25 mm. long in fruit, entire. *Corolla* strongly 2-lipped, pale yellow, c. 5 cm. long, hirsute on the back with long spreading hairs to 2·5 mm. long, the tube nearly twice as long as the calyx, c. 22 mm. long, the upper lip c. 18–25 mm. long, trilobed, with a notched middle lobe c. 10 mm. broad and two spreading narrowly triangular acute lateral lobes, the lower lip c. 18 mm. long, 3 mm. broad, recurved. *Stamens* exserted; filaments glabrous; anthers c. 1·5–2 mm. long. *Ovary* hirsute at the apex; style pubescent.

MANCHESTER: Top Hill, 820 m., March 1966, *Morley 325* (BM). Fairfield, 1849, *Wullschlägel 959* (GOET; M; type-collection of *C. hirsuta* var. *subintegra* f. *wullschlaegelii*). Along road between Fairfield and Huntley, 800–900 m., Jan. 1957, *Proctor 16109* (IJ). Huntley, 900 m., 25 Feb. 1956, *Stearn 361* (BM, holotype), *Proctor 11621* (IJ). Near Christiana, May 1901, *Fawcett 8145* (UCWI). Upper slopes and summit of Heron's Hill (Shooter's Hill, Martin's Hill), 900–940 m., March 1958, *Proctor 17489* (BM; IJ). Banana Ground, 900 m., Dec. 1961, *Adams 10127* (UCWI). Oatlands, north-west of Rose Hill, 830 m., Jan. 1961, *Proctor 21915* (BM).

ST. ANN: Mason River district, three to four miles northwest of Kellits, 760 m., March 1957, *Proctor 16201* (BM; IJ).

CLARENDON: Peckham Woods, 760 m., March 1954, *Proctor 8422* (IJ). Knox College, Spaldings, 850 m., March 1952, *Proctor 6345* (IJ).

This species was first collected by the Moravian missionary Wullschlägel in 1849 and identified by Grisebach with the very different *C. hispida*. Urban recognized its distinctness but, having only Wullschlägel's limited material at hand, described it briefly as a form of *C. hirsuta*, which is confined to the Blue Mountains of Jamaica. In a living state the leaves are a bright green with the veins deeply impressed above, and the flowers are pale yellow. It grows among both rocks and trees, and sometimes on stone walls, in central Jamaica (Text-fig. 9). Fairfield, where Wullschlägel collected his specimens, and Huntley, where I collected mine, are about five miles apart and near the western boundary of Manchester. It is named in honour of Ignaz Urban (1848–1931), the most scholarly, industrious and scientifically prolific of the many botanists who have studied West Indian plants; a short survey of his career by R. A. Howard will be found in E. Carroll and S. Sutton, *Cumulative Index to the nine Volumes of the Symbolae Antillanae* : 1–5 (1965). Among hybrids between this species and *C. rutilans* are some plants clearly intermediate, others approximating more closely to one or other parent species, probably as a result of back-crossing. Those nearest to *C. urbanii* in leaf-size and pubescence may nevertheless usually be distinguished from it by having the base of the leaf-blade more attenuate and the corolla partly red, although sometimes they agree with it in almost all characters but have only minute bristles on the upper surface of the leaf.

4. ***Columnea proctorii*** Stearn, sp. nov. (Pl. 17, 18; Text-figs. 2B, 8.)

Suffrutex, caulibus ascendentibus c. 5 mm. crassis, pilis patentibus ad 3 mm. longis hispidis, internodiis longis, cicatricibus prominentibus. *Folia* ad apicem 5–14 cm. longum ramulorum disposita, per paria valde inaequalia, folio majore breviter petiolato asymmetrico, lamina ovata ad obovata, apice acuta vel breviter acuminata, margine subintegra, basi uno latere rotundato, altero cuneato, 5–10 cm. longa, 2·5–6·5 cm. lata, pallide viridia, nervis lateralibus utroque latere costae 4–6 arcuatis supra profunde impressis, utrinque pilis erectis incoloribus plerumque 5-cellularibus 1·5–2·5 mm. longis hirsuta, folio minore fere sessili orbiculato 1–3·5 cm. longo latoque, similiter vestito; petiolus folii majoris 2–8 mm. longus. *Flores* axillares 1–3. *Pedicelli* 12–20 mm. longi, dense hirsuti. *Calyx* viridis, extus pilis longis glandulosis hirsutus; *segmenta* libera subaequalia anguste lanceolata acuta, anthesi c. 2 cm. longa, post anthesin c. 3 cm. longa, 2–3 mm. lata, integra. *Corolla* valde bilabiata, c. 4–5 cm. longa, flava rubrovittata, dorso pilis patentibus glandulosis ad 2 mm. longis dense hirsuta; tubus basi postice saccatus gradatim ampliatus c. 18–25 mm. longus calycem aequans; labium superum c. 18 mm. longum, trilobatum, lobo medio emarginato c. 7 mm. lato, lobis lateralibus anguste triangularibus vel fere lanceolatis obtusis patentibus; labium inferum c. 12 mm. longum, 4 mm. latum, recurvatum. *Stamina* exserta, filamentis glabris, antheris oblongis 2 mm. longis. *Ovarium* basi glabrum, supra medium pubescens; stylus glanduloso-pubescens.

Shrub, the stems grey, stout, c. 5 mm. thick, hispid with spreading hairs to 3 mm. long. *Leaves* occupying the terminal 5–14 cm. of the shoots, paired, those of a pair markedly unequal, light green, hirsute on both surfaces with erect colourless hairs 1·5–2·5 mm. long, the larger leaf of the pair short-stalked, asymmetric, the blade more or less ovate to obovate, with the apex acute or shortly acuminate, the margin almost entire, the base asymmetric, its lowest side rounded, the other cuneate and arising from the midrib about 5 mm. higher, 5–10 cm. long, 2·5–6·5 cm. broad, with four to six curved veins each side of the midrib impressed deeply above, the smaller leaf almost sessile and orbicular, 1–3·5 cm. long and broad; petiole of larger leaf 2–8 mm. long. *Flowers* 1–3 in a leaf-axil. *Pedicels* 12–20 mm. long, hirsute. *Calyx* divided to the base, light green, hirsute with long glandular hairs, the segments narrowly lanceolate, acute, c. 2 cm. long, 2–3 mm. broad in flower to 3 cm. long in fruit, entire. *Corolla* strongly 2-lipped, pale yellow with longitudinal red stripes, c. 4–5 cm. long, densely hirsute on the back with long spreading glandular hairs to 2 mm. long, the tube almost as long as the calyx, c. 18–25 mm. long, the upper lip c. 18 mm. long, trilobed, with a notched middle lobe about 7 mm. broad and two spreading narrowly triangular to almost lanceolate obtuse lateral lobes, the lower lip c. 12 mm. long, 4 mm. broad, recurved. *Stamens* exserted; filaments glabrous; anthers 2 mm. long. *Ovary* glabrous in the lower part, pubescent in the upper part style glandular-pubescent.

HANOVER: Ramble, March 1905, *Fawcett 8916* (UCWI).

ST. JAMES: Chatsworth district one and a half miles north-north-west of Maroon Town, 480 m., March 1956, *Stearn 451* (BM, holotype; K), *Proctor 11753* (IJ). White Rock Hill, one mile south of Sweet Water, 600–670 m., Feb. 1957, *Proctor 16160* (IJ). Same locality, Dec. 1962, *Proctor 23009* (BM; IJ).

ST. ELIZABETH: Maggotty Falls, by the Black River, 120 m., May 1956, *Stearn 1039* (BM), *Proctor 15382* (IJ).

TRELAWNY: Cockpit Country at Black Banana Hole, about five miles north of Accompong, 330 m., April 1956, *Stearn 938* (BM). Cockpit Country, near Red Mud Hole, about six miles north-north-west of Accompong, 330 m., April 1956, *Stearn 957* (BM; K). Cockpit Country, at Ramgoat Cave, 460 m., Jan. 1956, *Howard, Proctor & Stearn 14645* (BM; IJ). Miss Laura's Hill, Wilson Valley district, one mile north of Warsop, 600–670 m., Jan. 1964, *Proctor 24452* (BM; IJ). Island View Hill, Wilson Valley district, one and a half miles north of Warsop, 600–670 m., March 1960, *Proctor 20756* (BM; IJ). Five miles northwest of Troy, 530 m., Sept. 1963, *Adams 12420* (BM).

MANCHESTER: Half a mile northwest of Christiana, 900 m., Oct. 1958, *Proctor 18288* (BM; IJ). Same locality, Feb. 1960, *Proctor 20595* (BM; IJ). One mile southeast of Pike, 900 m., Oct. 1958, *Proctor 18308* (BM; IJ).

This species is widespread in the Cockpit Country and adjacent areas of western Jamaica (Text-fig. 8) and is apparently more northern in distribution than *C. urbanii*, from which it differs in having the leaves of a pair markedly unequal in size and hirsute below, and the corolla usually striped longitudinally with red; the five free calyx-segments distinguish *C. proctorii* from *C. subcordata*. I have named it in honour of George Richardson Proctor, author of *A Preliminary Checklist of Jamaican Pteridophyta* (1953), *Additions to the Flora of Jamaica* (1967) and other publications on Jamaican plants, whose collecting activities, extended since 1949 over almost the whole of Jamaica, have so notably increased knowledge of the distribution of species within the island and in whose company in 1956 I had the privilege of collecting the type material of this species.

5. **Columnea subcordata** Morton in Contr. U.S. Nat. Herb. 29 : 6 (1944).—Stearn in Proc. Linn. Soc. Lond. 170 : 141 (1959). (Pl. 19; Text-figs. 2G, 10.)

Shrub, the stems grey or brownish, stout, c. 5 mm. thick, hispid when young with long mostly spreading brownish multicellular hairs c. 2–3 mm. long. *Leaves* paired, those of a pair unequal, all short-stalked, green and hirsute with sparse long whitish multicellular hairs 0·8–1·8 m . long on both surfaces, the blade of the larger leaf of the pair more or less oblong-elliptic, with the apex abruptly and shortly acuminate, the margin entire and long-ciliate, the base subcordate and slightly oblique, 8–14 cm. long, 4·5–6·5 cm. broad, the blade of the smaller leaf (which usually falls quickly) broadly ovate or broadly obovate, 2·5–3·5 cm. long, 2 cm. broad; petiole 3–10 mm. long. *Flowers* 1–4 in a leaf-axil. *Pedicels* 1·5–2 cm. long, hirsute. *Calyx* 2-lipped, the four anterior segments joined from the base for 5 mm. (in flower) to 8 mm. but the posterior segment free to the base, light green, hispid with long whitish hairs on both surfaces, 1·5–2·2 cm. long, the four free segments narrowly oblong-lanceolate 2·5–4·5 mm. broad, acute, the posterior segment linear-tapering, all entire. *Corolla* strongly 2-lipped, light yellow, glandular-pilose, 4–4·8 cm. long, the tube mostly covered by the calyx, the upper lip c. 2·5 cm. long with a deeply notched middle lobe and two spreading oblong lateral lobes, the lower lip c. 1·5 cm. long, narrowly oblong, reflexed. *Stamens* exserted; filaments pubescent; anthers 2 mm. long. *Ovary* sericeous; style glandular-pilose.

TRELAWNY: Mount Ridgway Road, Windsor, 100–150 m., April 1931, *G. S. Miller 1556* (US, type). Windsor House estate, 120 m., March 1956, *Stearn 472* (BM; K).

Columnea subcordata stands apart from all other Jamaican species of *Columnea* in the fusion of the four anterior calyx-segments into one for the lower third of their length, with the posterior one remaining completely free. It probably arose as a mutation from *C. proctorii*. At the type-locality, Proctor and I found it growing high on trees, the sparingly branched stems hanging to a length of six feet. The leaves are dark green above, the hairs colourless, the corolla light yellow (Chinese yellow). It is evidently confined to a small area of western Jamaica (Text-fig. 10).

6. ***Columnea harrisii*** (Urban) Britton ex Morton in Contr. U.S. Nat. Herb. 29 : 10 (1944).—Stearn in Proc. Linn. Soc. Lond. 170 : 141 (1959). (Text-fig. 1E, 11.)

Columnea hirsuta var. *subintegra* f. *harrisii* Urban, Symb. Antill. 2 : 363 (1901).

Shrub, the stems grey, fairly slender, pilose with whitish hairs. *Leaves* paired, those of a pair unequal or almost equal, green and sericeous with numerous slightly arched more or less appressed multicellular hairs on both surfaces, the larger leaf of an unequal pair asymmetric, the blade more or less narrowly elliptic-oblong, with the apex shortly acuminate, the margin remotely and shallowly toothed, the base rounded on the outer side, acute on the inner side, 7·5–13 cm. long, 3–5 cm. broad, the smaller leaf broadly or narrowly ovate or almost orbicular, 1·5–4·5 cm. long, 1·0–2·3 cm. broad; petiole of larger leaves 3–8 mm. long, of smaller leaves 1–3 mm. long. *Flowers* 1 to 3 in a leaf axil. *Pedicels* 5–25 mm. long, hirsute. *Calyx* divided to the base, green, densely sericeous on both surfaces; segments lanceolate to narrowly lanceolate, 1·8–2·5 cm. long, c. 4 mm. broad, entire or with one or two minute teeth on each margin. *Corolla* strongly 2-lipped, yellow striped with red, 3·8–5 cm. long, sericeous outside with long whitish hairs, the tube almost covered by the calyx, the upper lip c. 2·3 cm. long with a notched middle lobe and two spreading narrowly-oblong lateral lobes, the lower lip c. 12–15 mm. long, narrowly oblong, recurved. *Stamens* exserted; filaments glabrous; anthers c. 1·8 mm. long. *Ovary* sericeous; style glandular-pilose.

HANOVER: Belvedere, 160 m., Jan. 1899, *Harris 7522* (BM, isotype). Same locality, March 1903, *Fawcett 8480* (BM; NY). Hills near Kempshot, March 1908, *Britton 2438* (NY; US). Shettlewood, 350–450 m., Feb. 1961, *Proctor & Mullings 22016* (BM; IJ).

WESTMORELAND: Newmarket, Sept. 1907, *Britton 1576* (NY). Woodstock, 400 m., Aug. 1907, *Harris* (UCWI). Same locality, 360–420 m., Oct. 1960, *Proctor 21519* (BM; IJ).

ST. JAMES: One mile southwest of Montpelier, 110 m., Feb. 1961, *Proctor & Mullings 22010* (BM; IJ).

Columnea harrisii, although placed by Urban under *C. hirsuta*, is abundantly distinct in its sericeous pubescence, entire calyx-segments and glabrous stamens, its distribution, and its ecology, as pointed out by Morton. It is a lowland species confined to the west of the island (Text-fig. 11), where it is epiphytic on large trees and often associated with bromeliads. Its name commemorates William Harris (1860–1920), for many years Superintendent of Public Gardens in Jamaica, whose extensive collections from 1890 onwards led to the discovery in Jamaica of approaching 400 species above those recorded for the island in Grisebach's *Flora* (1859–64).

7. **Columnea argentea** Griseb., Fl. Brit. W. Ind. Is. : 465 (1862).—Urban, Symb. Antill. 2 : 361 (1901).—Morton in Contr. U.S. Nat. Herb. 29 : 9 (1944).—Stearn in Proc. Linn. Soc. Lond. 170 : 141 (1959). (Pl. 20; Text-figs. 1F, 2C, 5, 12.)

C. wullschlaegeliana Hanstein in Linnaea 34 : 414 (1865).

Shrub, the stems stout, c. 5 mm. thick, silky at the apex with white hairs. *Leaves* paired, those of a pair almost equal, the blade very narrowly elliptic, narrowly elliptic or oblanceolate, with the apex shortly acuminate, the margin remotely and shallowly toothed, almost entire, the base rounded or cuneate, 7·5–17 cm. long, 2·5–4 cm. broad, grey-sericeous on both surfaces; petiole 4–10 mm. long. *Flowers* 1 to 4 in a leaf axil. *Pedicels* 5–25 mm. long, sericeous. *Calyx* divided to the base, densely sericeous on both surfaces; *segments* equal, oblong-linear, c. 14–18 mm. in flower to 20–24 mm. long in fruit, 2–4 mm. broad, entire. *Corolla* strongly 2-lipped, pale yellow, 4–5 cm. long, densely white-sericeous outside, the tube slightly longer than the calyx, c. 2·0–2·5 cm. long, the upper lip c. 2·0–2·5 cm long, with a notched middle lobe and two narrowly triangular lateral lobes, the lower lip 15–18 mm. long, oblong-linear, reflexed. *Stamens* exserted; filaments glabrous; anthers 1·5 mm, long. *Ovary* sericeous; style glandular-pilose. *Berry* ellipsoid, pink, c. 11 mm. long, 8 mm. broad.

MANCHESTER: Nazareth, 1849, *Wullschlägel 959* (GOET, holotype of *C. argentea*; M, holotype of *C. wullschlaegeliana*). Nazareth, among rocks behind the Moravian Church, one mile south of Maidstone P.O., 880 m., Feb. 1956, *Stearn 359* (BM; K; topotype of *C. argentea* and *C. wullschlaegeliana*), *Proctor 11615* (IJ). Alumina Jamaica property near Kirkvine Works, Shooters Hill, 380–460 m., Jan. 1958, *Howard & Proctor 14944* (BM; IJ). Bath district, along Somerset Road southeast of

Johns Hall, 700 m., Jan. 1961, *Proctor 21883* (BM; IJ). New Green, Sept. 1908, *Britton 3755* (NY). Clones, Ballynure to Malton, 700 m., April 1962, *Adams 11018* (BM).

Columnea argentea is an attractive and easily recognized species, notable for the silvery and silky pubescence which clothes the relatively long and narrow leaves, the calyx and the outside of the pale clear yellow corolla. At the type-locality I found it growing among rocks. Howard & Proctor record it as epiphytic on clumps of *Hohenbergia* in trees. All collections have come from within ten miles of one another in central Manchester (Text-fig. 12).

8. **Columnea brevipila** Urban, Symb. Antill. 6 : 41 (1909).—Morton in Contr. U.S. Nat. Herb. 29 : 9 (1944).—Stearn in Proc. Linn. Soc. Lond. 170 : 141 (1959). (Text-fig. 1D, 13.)

Shrub, the stems grey, stout, 5–8 mm. thick, strigillose when young with minute white appressed hairs and with lines of more villous hairs between the leaf-insertions, later glabrous. *Leaves* paired, those of a pair almost equal, shortly stalked, the blade narrowly oblong-elliptic or narrowly elliptic, with the apex shortly acuminate, the margin remotely and obscurely toothed, the base cuneate, 5–11 cm. long, 2–5 cm. broad, green and strigillose on both surfaces with minute whitish appressed hairs c. 0·2 mm. long; petiole 7–11 mm. long. *Flowers* 1 to 5 in a leaf-axil. *Pedicels* 1–2 cm. long, strigillose. *Calyx* divided to the base, green, minutely strigillose on both surfaces; *segments* narrowly lanceolate, acute, 2–3 cm. long, 3–5 mm. broad, entire. *Corolla* strongly 2-lipped, completely yellow, 4·5–5 cm. long, sericeous outside with long whitish hairs, the tube mostly covered by the calyx, the upper lip c. 2–2·5 cm. long, with a strongly notched middle lobe and two spreading and ascending oblong lateral lobes, the lower lip to 1·5 cm. long, narrowly oblong, reflexed. *Stamens* exserted; filaments glabrous; anthers 2 mm. long. *Ovary* densely hirsute; style glandular-pilose.

WESTMORELAND: Kentucky Hill, Bluefields Mountains, 600–760 m., March 1908, *Harris 10199* (NY; UCWI; US; type-collection). Hills west of Bognie, Bluefields Mountains, 700–760 m., Feb. 1961, *Proctor & Mullings 22043* (BM). Teague Gully, 300–400 m., Feb. 1961, *Proctor & Mullings 22062* (BM). Cairn Curran district, two and a half miles west-north-west of Hopewell, 530 m., March 1956, *Stearn 433* (BM; K), *Proctor 11719* (IJ).

ST. ELIZABETH: One mile north of Redgate, 150 m., March 1956, *Stearn 438* (BM).

Columnea brevipila agrees with *C. fawcettii* in having the upper surface of the leaf beset with minute appressed hairs but differs completely in its entire sepals. It is confined to southwestern Jamaica (Text-fig. 13). Some hybrids between *C. rutilans* and *C. urbanii* come close to it in general character but differ in having their pedicels and sepals clothed with spreading hairs.

9. **Columnea hirsuta** Swartz, Nov. Gen. & Sp. Pl. : 94 (1788); Fl. Ind. Occ. 2 : 1080 (1800) excl. syn.—Hook. in Curtis, Bot. Mag. 58 : t. 3081 (1831).—Griseb., Fl. Brit. W. Ind. Is. : 465 (1862) excl. parte.—Hanstein in Linnaea 34 : 413

(1865) excl. parte.—Urban, Symb. Antill. 2 : 361 (1901) excl. var. *subintegra* & var. *fawcettii*.—Morton in Contr. U.S. Nat. Herb. 29 : 7 (1944).—Stearn in Proc. Linn. Soc. Lond. 170 : 141 (1959). (Text-fig. 1C, 14.)

Eusynetra bicolor Raf., Fl. Tellur. 2 : 57 (1837), nom. superfl.
Columnea hirsuta var. *genuina* Urban, tom. cit. : 361 (1901).
Columnea hirsuta var. *pallescens* Urban, tom. cit. : 362 (1901).
Columnea hirsuta var. *concolor* Urban, tom. cit. : 362 (1901).

Shrub, the stems brownish grey, moderately slender, densely hirsute when young with long multicellular hairs. *Leaves* paired, those of a pair unequal, green and hirsute on both surfaces with long multicellular flaccid hairs together with short 2–3-celled hairs, the blade of the larger leaf oblong-elliptic to narrowly obovate, with the apex acute or shortly acuminate, the margin shallowly serrate, the base rounded or cuneate, 4·5–12 cm. long, 2·5–5·5 cm. broad, the blade of the smaller leaf elliptic or broadly elliptic, 2–6 cm. long, 1·8–3·8 cm. broad; petiole c. 15 mm. long. *Flowers* 1–3 in a leaf-axil. *Pedicels* 1–2 cm. long, hirsute. *Calyx* divided to the base, red or green, densely hirsute on both surfaces with long multicellular red or colourless hairs; *segments* linear, slightly uneven, c. 2 cm. long in flower to 4 cm. long in fruit, 2–4 cm. broad, remotely toothed with one to three teeth on each margin. *Corolla* strongly 2-lipped, red with broad yellow longitudinal stripes, c. 4·5–5 cm. long, the tube mostly covered by the calyx, c. 2 cm. long, the upper lip c. 2·5 cm. long, with a deeply notched middle lobe and two spreading narrowly triangular lateral lobes, the lower lip c. 2·2 cm. long, oblong-linear, reflexed. *Stamens* exserted; filaments sparsely pubescent; anthers 1·8–2·5 mm. long. *Ovary* sericeous; *style* densely glandular-pilose. *Berry* white.

ST. ANDREW: Moresham River, quarter mile above Hermitage Dam, 350 m., March 1956, *Stearn 412* (BM). Hardwar Gap, 1,200 m., Sept. 1952, *Robbins 1511* (UCWI). Summit of Catherine's Peak, 1,540 m., Nov. 1952, *Proctor 7341* (IJ). West slope of Catherine's Peak, 1,300 m., Jan. 1961, *Proctor 21954* (BM). Catherine's Peak, Jan. 1888, *Eggers 3603* (US, type-collection of *C. hirsuta* var. *pallescens*). Vicinity of St. Helen's Gap, 1,475 m., March 1920, *Maxon & Killip 591* (US). Morces Gap, 1,520 m., July 1903, *Nichols 15* (K; US). Same locality, 1,500 m., March 1920, *Maxon & Killip 1722* (US). Along trail between Cinchona and Morces Gap, 1,520 m., Feb. 1941, *Burrowes 3563* (IJ). Near Cinchona, 1,600 m., June 1896, *Fawcett 6366* (BM, type-collection of *C. hirsuta* var. *concolor*). Cinchona, windward slopes, Feb. 1915, *Harris & Lawrence C 15158* (US).

PORTLAND: Trail from Morces Gap to Vinegar Hill, 1,175–1,500 m., March 1920, *Maxon & Killip 694* (US). Near Mabess River, 780 m., Dec. 1905, *Harris 9123* (NY). Lower eastern ridge of Mossman's Peak, 1,600–1,700 m., May 1926, *Maxon 9665* (US). East slope of the John Crow Mountains two miles southwest of Ecclesdown, 600 m., March 1951, *Proctor 5703* (IJ). Same locality, Jan. 1956, *Howard, Proctor & Stearn 14790* (BM). Upper north slope of Silver Hill Gap, along track toward Big Level, 1,100 m., Feb. 1963, *Proctor 23255* (BM; IJ).

ST. THOMAS: Near Whitfield Hall, 1,400 m., Jan. 1956, *Stearn 123* (BM). Portland Gap, 1,640 m., Dec. 1954, *Proctor 9615* (BM). Same locality, Jan. 1956, *Stearn 94* (BM). Northwest slope of Yallahs Hill, 600 m., April 1956, *Stearn 677* (BM).

UNLOCALIZED: 1777, *Shakespear* (BM). *W. Wright* (BM). *Swartz* (BM, type-collection of *C. hirsuta*). 1843, *Lane* (K). *Purdie* (K). *March* (K).

An eastern Jamaican species characteristic of the Blue Mountains (Text-fig. 14), *Columnea hirsuta* is easily distinguished from its closest ally, *C. fawcettii*, by the long multicellular hairs on the upper leaf-surface. The leaves green beneath separate these species at a glance from *C. rutilans*, which has also more deeply toothed calyx-segments.

Usually *C. hirsuta* grows as an epiphyte, the vegetative shoots clinging like ivy to mossy tree trunks while the flowering shoots spread horizontally outwards, but it may sometimes be found growing terrestially among rocks.

10. ***Columnea fawcettii*** (Urban) Morton in Contr. U.S. Nat. Herb. 29 : 8 (1944).—Stearn in Proc. Linn. Soc. Lond. 170 : 141 (1959).—Raymond in Mém. Jard. Bot. Montréal 57 : 13, t. 6 (1965). (Text-fig. 1H, 2D, 15, 28.)

Columnea hirsuta sensu Griseb., Fl. Brit. W. Ind. Is. : 465 (1862) pro parte; non Swartz.
Columnea hirsuta var. *fawcettii* Urban, Symb. Antill. 2 : 363 (1901).
Rapunculus fruticosus foliis oblongis integris villosis etc. Sloane, Cat. Pl. Jam. : 58 (1696); Voy. Nat. Hist. Jam. 1 : 157, t. 100 f. 1 (1707).

Shrub, the stems grey, fairly slender, pilose with whitish hairs. *Leaves* paired, those of a pair equal to very unequal, green and shortly strigillose on both surfaces, the hairs of the upper surface 2-celled, 0·3–0·4 mm. long, the blade of the larger leaf mostly elliptic or narrowly elliptic, with the apex shortly acuminate, the margin remotely and obscurely toothed, the base asymmetric, cuneate, 6–10·5 cm. long, 2·5–4·5 cm. broad, the blade of the smaller leaf in shape like the larger, 3–4·5 cm. long; petiole of larger leaves 8–16 mm. long, of smaller 2–4 mm. long. *Flowers* 1 to 3 in a leaf-axil. *Pedicels* 12–15 mm. long, hirsute. *Calyx* divided to the base, red, densely hirsute on both surfaces; segments slightly uneven, narrowly lanceolate, 2·3–2·8 cm. long, 3–4 mm. broad, remotely toothed, with two or three linear teeth to 2 mm. long on each margin. *Corolla* strongly 2-lipped, red with yellow longitudinal stripes, c. 4·5–5 cm. long, sericeous with long whitish hairs, the tube covered by the calyx, the upper lip c. 2·8 cm. long, with a strongly notched middle lobe and two spreading narrowly triangular lateral lobes, the lower lip c. 2 cm. long, narrowly oblong, reflexed. *Stamens* exserted; filaments slightly pubescent; anthers c. 1·5 mm. long. *Ovary* sericeous; style glandular-pilose. *Berry* ovoid, white.

ST. ANN: Interior Road, near Browns Town, Feb. 1897, *Fawcett 6587* (BM, type-collection). Dry Harbour Mountains, two miles west of Albion, 760 m., Jan. 1956, *Stearn 157* (BM). Vicinity of Lydford Post Office, Governor's Hill, 560 m., Dec. 1953, *Howard & Proctor 13570* (IJ). Reynolds Mine Area near Lydford Post Office, 360–420 m., Jan. 1956, *Howard, Proctor & Stearn 14602* (BM). Averham Park, 560 m., March 1956, *Stearn 585* (BM). Soho, 430 m., May 1915, *Harris 11993* (NY). St. Ann's Road, four miles from Moneague, Dec. 1849, *Alexander* (K). Union Hill, near Moneague, April 1908, *Britton & Hollick 2741* (NY). Grierfield, near Moneague, April 1908, *Britton 2659* (NY). Lower part of road to Holly Mount, 400 m., March 1956, *Stearn 576* (BM). Near Camperdown School, one and a half miles southwest of Gibralter, 420 m., March 1956, *Stearn 568* (BM; K).

St. Catherine: Vicinity of Holly Mount, Mount Diablo, 750 m., May 1904. *Maxon 2334* (US). Same locality, Feb. 1905, *Harris 8896* (K; NY). Mount Diablo, Feb. 1916, *Ridley* (K). Upper slopes of Mount Diablo, 500–800 m., Feb. 1920, *Maxon & Killip 429* (NY; US). Between Point Hill and Juan de Bolas Peak, 610–820 m., March 1958, *Yuncker 18374* (BM).

St. Andrew: Cooper's Hill, Red Hills, 670–760 m., March 1954, *Proctor 8488* (IJ; NY). Same locality, Feb. 1956, *Stearn 255* (BM; K).

Portland: Port Antonio–Moore Town Road, March 1924, *Norman 225* (BM). Uncommon Hill, above Fruitful Vale Post Office, 670–760 m., April 1954, *Proctor 8579* (IJ). Seamen's Valley, 150–250 m., Feb. 1920, *Maxon & Killip 81* (NY; US). Alligator Church district, one mile south of Seamen's Valley, 70–150 m., March 1960, *Proctor 20640* (BM). Northwest slope of Joe Hill, 300–670 m., April 1955, *Proctor 10102* (IJ). Same locality, Feb. 1956, *Stearn 243* (BM). Vicinity of Millbank, 200–300 m., Feb. 1920, *Maxon & Killip 133* (NY; US). East slope of John Crow Mountains, one to one and a half miles southwest of Ecclesdown, 300–460 m., April 1954, *Proctor 8603* (IJ). Same locality, 460–600 m., Aug. 1954, *Webster 5579* (BM). Same locality, Jan. 1955, *Proctor 9798* (IJ). Ten miles southwest of Priestmans River, 460–760 m., Jan. 1951, *Proctor 5255* (IJ).

St. Thomas: Maccasucker Bump, 825–1,025 m., June 1926, *Maxon 9523* (US). Ridge east of Cuna Cuna Gap, 750–840 m., June 1926, *Maxon 9407* (US). North slope of Corn Puss Gap, 600 m., Jan. 1945, *Barry 1058* (IJ). Sulphur Creek, above Fountain Inn [Bath Fountain], 150–200 m., Nov. 1957, *Yuncker 17486* (BM).

Unlocalized: *Sloane, Herb. 3 : fol. 21* (BM). 1859–60, *Metcalfe* (BM). *Purdie* (K).

Columnea fawcettii is the most widespread Jamaican species of *Columnea* (Text-fig. 15) and was the first to be collected and recorded, having been gathered by Sir Hans Sloane as long ago as 1688–89 and illustrated by him, albeit crudely, in 1707. Nevertheless, because it closely resembles *C. hirsuta*, it remained without varietal or specific designation until 1901, when Urban named it *C. hirsuta* var. *fawcettii*; not indeed until 1944 was its true status recognized, Morton then giving Urban's variety specific rank as *C. fawcettii*. It differs from *C. hirsuta* principally in having only short appressed hairs on the upper surface of the leaves. Its name commemorates William Fawcett (1851–1926), from 1880–86 assistant botanist at the British Museum, a period during which the botanical collections were transferred from Bloomsbury to South Kensington, then from 1887 until his retirement in 1908 Director of Botanic Gardens and Plantations in Jamaica. When in Jamaica he became especially interested in the Orchidaceae of the island and his monograph, prepared in collaboration with A. B. Rendle (1865–1938), was converted into the first volume (published in 1910) of the *Flora of Jamaica*. He worked continuously on this Flora at the British Museum (Natural History) until his death in 1926.

11. **Columnea rutilans** Swartz, Nov. Gen. & Sp. Pl. : 94 (1788); Fl. Ind. Occ. 2 : 1083 (1800).—DC., Prodr. 7 : 542 (1839).—Griseb., Fl. Brit. W. Ind. Is. : 465 (1862).—Hanstein in Linnaea 34 : 415 (1865).—Urban, Symb. Antill. 2 : 363 (1901).—Morton in Contr. U.S. Nat. Herb. 29 : 5 (1944).—Stearn in Proc. Linn. Soc. Lond. 170 : 141 (1959). (Pl. 21; Text-figs. 1G, 2F, 17.)

Shrub, the stems grey, stout, when young strigose or almost tomentose with reddish hairs, later sparingly strigose. *Leaves* paired, those of a pair unequal, the upper surface dark green and strigillose with short multicellular hairs, the lower surface red-veined or completely red, pilose and almost sericeous, the larger leaf of the pair long-stalked, the blade lanceolate or narrowly lanceolate, with the apex shortly acuminate, the margin remotely serrulate, the base asymmetric, acute, 7–18 cm. long, 2·5–6 cm. broad, smaller leaf of the pair soon falling, short-stalked, the blade 2–4·5 cm. long, 1·5–2·5 cm. broad; petiole of larger leaves 1–2·5 cm. long, of smaller leaves 3–5 mm. long, sericeous. *Flowers* 1 to 4 in a leaf-axil. *Pedicels* 1–2 cm. long, strigillose. *Calyx* divided to base, pilose on both surfaces with long red hairs; segments 2–2·5 cm. long in flower to 3·5 cm. long in fruit, pinnately cleft with three acute teeth on each margin. *Corolla* strongly 2-lipped, red with longitudinal orange stripes, 4·5–5·5 cm. long, the tube covered by the calyx, the upper lip to 3 cm. long, with a strongly notched galea and two spreading narrowly triangular lateral lobes, the lower lip to 2·5 cm. long, narrowly oblong, reflexed. *Stamens* exserted; filaments glabrous or slightly hairy, pale yellow; anthers 2·5 mm. long. *Ovary* sericeous; style glandular-pilose. *Berry* white, globose, c. 12 mm. broad, pilose.

HANOVER: Northwestern slope of Dolphin Head, May 1906, *Harris 9265* (NY; US). Interior summit slopes of Dolphin Head, 460–520 m., April 1955, *Proctor 10036* (BM; IJ). Same locality, March 1960, *Proctor 20689* (BM; IJ).

ST. JAMES: Chatsworth district, one and a half miles north-north-west of Maroon Town, 490 m., March 1956, *Stearn 453* (BM).

ST. ELIZABETH: Near Accompong, 400 m., April 1956, *Stearn 1005* (BM). Cooks Bottom, east of Elderslie, 490–520 m., May 1960, *Proctor 20864* (BM).

TRELAWNY: Near Troy, 600 m., April 1906, *Harris 9370* (BM; K; NY). Same locality, 600–660 m., June 1906, *Maxon 2852* (NY; US). Bartley's Run, three miles north-north-west of Troy, 520 m., April 1956, *Stearn 927* (BM). Tyre district, two miles north of Troy, 530 m., March 1955, *Proctor 9926* (IJ). Six miles from Troy, April 1954, *Robertson 1058* (UCWI).

MANCHESTER: Feb. 1844, *Purdie* (K). Near Christiana, May 1901, *Fawcett 8144* (UCWI). Heron's Hill (Shooter's Hill, Martin's Hill), 910–940 m., March 1958, *Proctor 17482* (BM). Top Hill, 820 m., March 1966, *Morley 344* (BM).

CLARENDON: Peckham Woods, 750 m., May 1912, *Harris 11092* (NY; US). Same locality, March 1954, *Proctor 8424* (IJ). Same locality, May 1955, *Robertson 2034* (K). Knox College, Spaldings, 850 m., May 1949, *Dignum 34* (IJ). Bull Head, March 1903, *Fawcett 8465* (UCWI).

UNLOCALIZED: 1787, *Swartz* (BM, type-collection).

Columnea rutilans is a western Jamaican species (Text-fig. 17) easily recognized by the conspicuous red colouring on the under-side of the leaves and the calyx. The calyx-segments are, moreover, deeply and pinnately lobed and clothed with long reddish hairs. Although occasionally epiphytic, it mostly grows in pockets of humus on limestone rocks. Despite its distinctness from other species, it hybridizes with *C. urbanii* when, as at Top Hill, Manchester, it grows at the same place.

HYBRIDS

Columnea rutilans* × *urbanii (Text-fig. 16).

A number of hybrids between ornamental cultivated species of *Columnea* has been raised in gardens, among those named for horticultural purposes being *C.* × *banksii* Lynch (*C. oerstediana* Klotzsch ex Oerstedt × *C. schiedeana* Schlechtendal), *C.* × *euphora* H. E. Moore (*C. gloriosa* Sprague × *C. lepidocaula* Hanst.), *C.* × *lemoinei* Garnier (*C. glabra* Oersted × *C. magnifica* Oersted) and *C.* × *vedrariensis* Mottet (*C. magnifica* × *C. schiedeana*). Unless, however, plants of two species grow together or within the territory of one individual humming-bird, hybridization is unlikely often to take place in the wild. Jamaica provides the first recognized example of its occurrence.

In April, 1962, Dr. C. D. Adams collected at Top Hill near Walderston, Manchester (Text-fig. 16) a *Columnea* (*Adams 11085*; UCWI) which agreed with *C. rutilans* in having its leaves red beneath but diverged in its shorter leaves with longer hairs on the upper surface and its toothed rather than laciniate calyx-segments. He surmised that it might be a hybrid of *C. rutilans* with another species. He also collected between Contrivance and Top Hill a *Columnea* (*Adams 11077*; UCWI) with leaves like *C. urbanii* but flowers longitudinally red-striped which likewise did not fit any recorded species. Earlier, in 1924, C. Norman (*Norman 69*; BM) collected near Mandeville, Manchester, an anomalous specimen.

Investigation of the Top Hill area by Dr. Brian D. Morley in 1966 revealed the existence here of both *C. rutilans* and *C. urbanii* and a series of intermediate plants evidently derived from their hybridization. These two species are so distinct in the shape, size, colour and pubescence of their leaves and calyx-segments, as well as the colour of the corolla, that an isolated intermediate specimen of unknown provenance could easily be taken to represent an independent species not closely connected with either. Such a specimen, for example, is *Morley 334, hybrid 6*, having elliptic leaf-blades 6–9 cm. long, 3·5–4·5 cm. broad, reddish below, also slightly toothed calyx-segments covered with minute bristles and long reddish multicellular hairs, and a yellow corolla with similar reddish hairs. The ranges of *C. rutilans* and *C. urbanii* overlap in Manchester and upper Clarendon and it is within these parishes that the plants combining their characters occur, sometimes where neither of the two species is now present. This may be due to the disappearance of these species but it may also result from the dispersal of seed of hybrid origin by birds and later by self-pollination and inbreeding of a colony thus established outside the original locality. Morley collected ten nothomorphs at Top Hill in which the characters of *C. rutilans* and *C. urbanii* were variously mingled.

The following gatherings also appear to show traces of hybrid origin, although much closer to *C. urbanii* than to *C. rutilans*:

MANCHESTER: Grounds of West Indian Training College near Mandeville, 760 m., March 1958, *Proctor 17455* (BM; IJ). Providence, one and a half miles west-south-west of Newport, 800–820 m., Jan., 1961, *Proctor 21905* (IJ). Rose Hill, 760 m., Oct. 1965, *Morley 274C* (BM). Moorlands estate, two miles northeast of Spur Tree, 760 m., Jan. 1956, *Howard, Proctor & Stearn 14701* (IJ). Newport, 680–760 m., Feb. 1966, *Powell & Green 1663* (IJ).

CLARENDON: Peckham Woods, 760 m., March 1956, *Robertson 2720* (UCWI; IJ).

ALLOPLECTUS Mart.

ALLOPLECTUS Mart., Nov. Gen. & Sp. Pl. Brasil. 3 : 53 (1829), nom. cons.

Shrubs or herbs. Leaves opposite, those of a pair equal to unequal, usually long-petiolate. Flowers solitary or fasciculate in leaf-axils or borne in short axillary racemes, with bracts. Calyx 5-partite. Corolla inferior, erect or oblique in the calyx, gibbous but not spurred at base, the tube cylindric or ventricose, contracted or not expanded in the throat, the limb regular or almost so with five short rounded lobes. Stamens four, didynamous, the filaments united in the lower part, free and filamentous above, the anthers free or cohering in pairs, their loculi parallel, longitudinally dehiscent. Disc gland large and dorsal, sometimes accompanied by smaller glands. Ovary superior; stigma usually 2-lobed. Fruit a capsule or berry; seeds minute, longitudinally or obliquely striate.

Lectotype (see p. 184): *A. sparsiflorus* Mart. (= *A. hirtellus* (Schott) Preston).

The genus *Alloplectus* as defined above comprises about 80 species, native to tropical America, including the Caribbean islands.

1. ***Alloplectus pubescens*** (Griseb.) Fawcett, Provis. List Flow. Pl. Jam. : 28 (1893).—Urban, Symb. Antill. 2 : 358 (1902).—Morton in Contr. U.S. Nat. Herb. 29 : 15 (1944). (Text-figs. 19, 29G–H.)

Pterygoloma pubescens Griseb., Fl. Brit. W. Ind. Is. : 464 (1862).
Columnea pubescens (Griseb.) Kuntze, Rev. Gen. Pl. 2 : 472 (1892).

Shrub of dwarf creeping habit, the stems grey, slender, 2–3 mm. thick, hirsute with colourless hairs. *Leaves* paired, those of a pair almost equal to markedly unequal, short-stalked, green and densely hirsute on both surfaces, some of the hairs on the upper surface glandular, the larger leaf with the blade elliptic or narrowly obovate, symmetric, the apex acuminate, the margin inconspicuously denticulate, the base cuneate, 4·5–8 cm. long, 2–3 cm. broad, the smaller leaf often half as long as the larger leaf; petiole 2–10 mm. long. *Flowers* solitary in leaf-axils. *Pedicel* 7–15 mm. long, hirsute. *Calyx* divided to the base, green, hirsute on both surfaces with colourless glandular hairs; *segments* narrowly elliptic, acuminate, c. 1 cm. long, entire. *Corolla* tubular, slightly swollen at the middle, c. 2 cm. long, reddish orange, the tube c. 4 mm. broad at the middle, strigose outside, the lobes almost equal, 1–2 mm. long. *Stamens* included; filaments glabrous; anthers c. 1·1 mm. long. *Ovary* glabrous; style glabrous. *Berry* pink or purplish, c. 5 mm. broad.

PORTLAND: 610 m., *Wilson* (K; GOET, type). John Crow Mountains, one and a third miles south-west of Ecclesdown, 460–610 m., Aug. 1954, *Webster 5569* (BM; IJ). Same locality, Dec. 1955, *Proctor 11346* (IJ). Same locality, Jan. 1956, *Howard, Proctor & Stearn 14792* (IJ).

Alloplectus pubescens is a rare and inconspicuous species confined to the rain forest of the mountains in the extreme east of Jamaica (Text-fig. 19) and differs from other West Indian species of *Alloplectus* in its entire sepals, which are hirsute on both surfaces. The corolla is variously described as " pale orange ", " orange " and " pale salmon-pink ", the fruit as " pink " or " light rose-purple ".

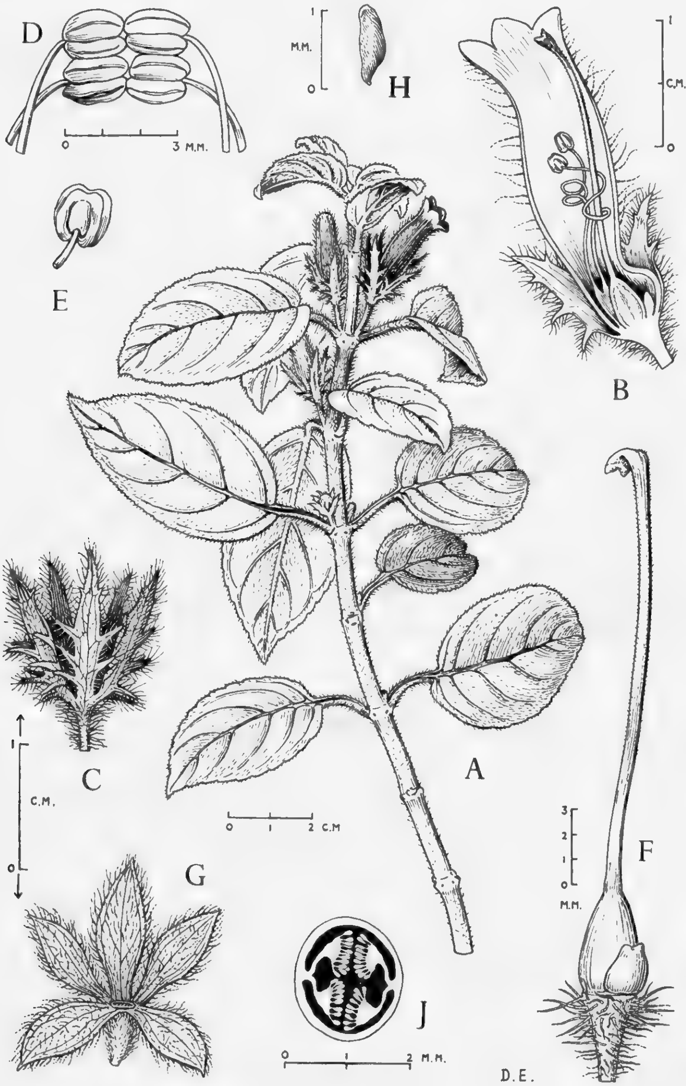


FIG. 29. *Alloplectus grisebachianus* (Kuntze) Urban: A, flowering shoot (*Proctor 22648, 16539*); B, section of flower after anthesis (*Harris 555*); C, calyx (*Harris 555*); D, anthers (*Harris 555*); E, anther, back view (*Harris 555*); F, gynoecium (*Harris 555*); *Alloplectus pubescens* (Griseb.) Fawcett: G, calyx (*Wilson*); H, seed (*Webster 5569*). *Alloplectus ambiguus* Urban: J, section of ovary (after H. E. Moore, 1957).

2. ***Alloplectus grisebachianus*** (Kuntze) Urban, Symb. Antill. 2 : 357 (1901).—Morton in Contr. U.S. Nat. Herb. 29 : 18 (1944). (Text-figs. 18, 29A–F.)

Pterygoloma cristatum Griseb., Fl. Brit. W. Ind. Is. : 464 (1862).
Columnea grisebachiana Kuntze, Rev. Gen. Pl. 2 : 472 (1892).
Alloplectus cristatus (Griseb.) Fawcett, Provis. List Flow. Pl. Jam. : 28 (1893); non *A. cristatus* (L.) Mart. ex G. Don (1838).
Alloplectus grisebachianus var. *ochrotrichus* Urban, Symb. Antill. 5 : 497 (1908).—Morton, loc. cit. (1944).
Columnea hunnewellii L. B. Smith in Rhodora 39 : 275 (1937).

Shrub of dwarf creeping habit, branched, sometimes forming a bush with descending shoots, the stems grey, slender, 2–3 mm. thick, densely hirsute when young with reddish hairs or colourless hairs, the leaf-scars prominent. *Leaves* paired, those of a pair mostly unequal, short- or long-stalked, green and hirsute on both surfaces with long rather appressed hairs, the larger leaf of the pair with the blade elliptic or ovate, slightly or distinctly asymmetric, the apex shortly acuminate, the margin shallowly denticulate, the base rounded, 2·5–6 cm. long, 1·5–3 cm. broad, the smaller leaf sometimes half as long as the larger leaf and falling earlier; petiole 3–10 mm. long. *Flowers* solitary in the leaf-axils. *Pedicel* 2–10 mm. long, hirsute. *Calyx* divided to the base, green, hirsute outside with long reddish hairs or colourless hairs, glabrous inside; segments laciniate, c. 10–12 mm. long, with two to five prominent teeth on each side. *Corolla* tubular, slightly swollen at the middle, c. 2 cm. long, dull purplish red, the tube c. 5–6 mm. broad at the middle, hirsute outside with long spreading hairs and very minute appressed hairs, the lobes almost equal, c. 1 mm. long. *Stamens* included; filaments glabrous; anthers c. 1 mm. long. *Ovary* glabrous; style minutely pubescent in the upper part. *Berry* white, c. 7 mm. broad.

TRELAWNY: near Troy, 610 m., May 1903, *Harris 8549* (BM; US; lectotype collection of *Alloplectus grisebachianus* var. *ochrotrichus*).

MANCHESTER: Olive River, Christiana district, 910 m., Oct. 1901, *Harris 8413* (BM).

CLARENDON: Peckham Woods, 750 m., Dec. 1917, *Harris 12766* (K; US). Same locality, Dec. 1955, *Stearn 10* (BM).

ST. ANN: Albion, March 1850, *Purdie 555* (K, lectotype of *Pterygoloma cristatum*). Dry Harbour Mountains, two miles west of Albion, 600 m., Jan. 1956, *Stearn 158* (BM; K). Mount Diablo, Feb. 1916, *Ridley* (K). Same locality, Jan. 1938, *Hunnewell* (BM; K; US). Union Hill, near Moneague, 750 m., *Britton & Hollick 2744* (NY). Hollymount, Feb. 1905, *Harris 8891* (NY). Same locality, Sept. 1906, *Britton 718* (NY). Along the road to Hollymount, Mount Diablo, 800 m., Aug. 1957, *Proctor 16539* (BM). Ramble, Claremont, 450 m., Jan. 1898, *Fawcett & Harris 7168* (BM).

UNLOCALIZED: *Alexander* (GOET). *Wullschlägel* (GOET)

The transfer by Fawcett in 1893 of Grisebach's epithet *cristatus* from *Pterygoloma* to *Alloplectus* created a later homonym of *Alloplectus cristatus* (L.) Mart. ex G. Don, based on *Besleria cristata* L. (1753). In 1892, however, Kuntze united *Alloplectus*, *Nematanthus* and *Hypocyrta* with *Columnea* and as he could not use Grisebach's epithet owing to the prior claim of Linnaeus's published under *Besleria*, which resulted in the name *Columnea cristata* (L.) Kuntze, he coined the new name *Columnea grisebachiana* for *Pterygoloma cristatum* Griseb. Thereby he provided a legitimate epithet for use under *Alloplectus*. For a biography and bibliography of August Heinrich Rudolf Grisebach (1814–79), the Göttingen professor of botany whom the name commemorates, see *Journ. Arnold Arb.* 46 : 245–260 (1965).

Alloplectus grisebachianus is restricted to the central uplands of Jamaica (Text-fig. 18). The typical and commonest form of the species is notable for the long reddish multicellular hairs which clothe the branchlets, petioles, leaf-blades, pedicels, calyx and corolla. To this belongs the type-specimen of *Columnea hunnewellii* L. B. Smith collected by Hunnewell and Griscom in March 1936, on Mount Diablo. In specimens collected by Harris at Troy (*Harris 8549*) and at Olive River (*Harris 8413*) the hairs are colourless and Urban distinguished them as *A. grisebachianus* var. *ochrotrichus* in 1908. A gathering made by Hunnewell in January 1938 on Mount Diablo includes, however, both forms; the loss of colour in the hairs has probably taken place independently in several localities.

Alloplectus ambiguus Urban is a species not of Jamaica but of Puerto Rico; because it is adequately known from wild and cultivated material and is allied to the Jamaican species, it has been included above in the taxonometric survey (pp. 207–214) to increase the representation of *Alloplectus* and in Fig 29 (p. 233) to illustrate the placentation of these plants.

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W. T. STEARN, D.Sc., Sc.D.
Dept. of Botany
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON, S.W.7

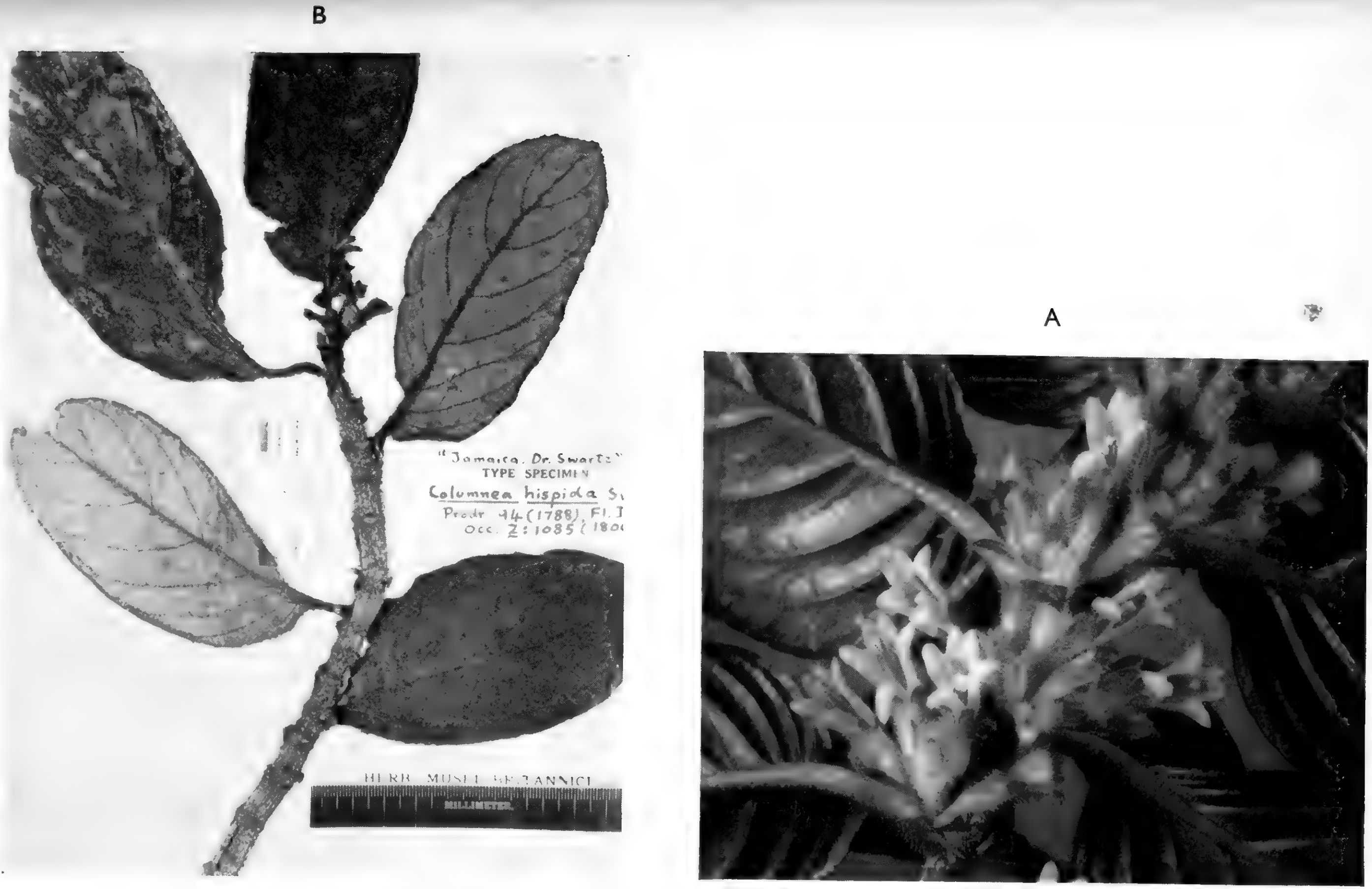
for FLORA OF JAMAICA
Columnea jamaicensis Urban
var jamaicensis
det W. T. Stearn 196

JAMAICA

INSTITUTE OF JAMAICA
FLORA OF JAMAICA
Parish: WESTMORELAND

Name: Columnea jamaicensis Urb.
Locality: 1 mile W.N.W. of HOPEWELL.
Altitude: 1750 ft. Date November 21, 1955
Habitat: Wooded limestone hillside.
Notes: Trailing epiphyte; calyx red; corolla yellow, streaked with orange.
Collector: George R. Proctor No. 11232

Columnea jamaicensis Urban (*Proctor 11232*; representative specimen in Herb. Brit. Mus. (Nat. Hist.), London).



A. Living plant of *Columnea hispida* Swartz cultivated at Montreal Botanic Garden. Photo M. Raymond.

B. Holotype of *Columnea hispida* Swartz (*Swartz*; Herb. Brit. Mus. (Nat. Hist.), London).

Columnea urbanii Stearn (*Stearn 361*; holotype in Herb. Brit. Mus. (Nat. Hist.), London).

FLORA OF JAMAICA

Columnea (new species)

PARISH St. James ALT. 1600 ft DATE 10 March 1956

LOC. Chatsworth district, 1½ miles N.N.W. of Maroon Town

Epiphytic with long branched spreading stems; leaves [illegible] green, [illegible] veins, the hairs profuse, erect, colourless; pedicels green; calyx light green with colourless hairs. Corolla yellow overlaid with longitudinal red streaks and stripes; pollen yellow

COLL. W. T. STEARN NO. 451

Columnea proctorii Stearn (*Stearn 451*; holotype in Herb. Brit. Mus. (Nat. Hist.), London).

Columnea proctorii Stearn (*Stearn 451*; isotype in Herb. Brit. Mus. (Nat. Hist.), London).

Columnea subcordata Morton (*Miller 1556*; holotype in U.S. Nat. Herb., Washington).

FLORA OF JAMAICA
Columnea argentea Griseb. (TOPOTYPE)
PARISH Manchester ALT. 2900 ft. DATE 25. II. 1956
LOCALITY Nazareth, among rocks behind the Moravian Church at top of hill.
Shoots grey, to 70 cm. long; leaves spreading, silky, the longest to 17 cm. long, 5 cm. broad; calyx light green; corolla pale yellow; fruit ellipsoid, pink, 11 mm. long, 8 mm. broad.
COLL. W. T. STEARN NO. 359

Columnea argentea Griseb. (*Stearn 359*; topotype in Herb. Brit. Mus. (Nat. Hist.), London).

Columnea rutilans Swartz (*Stearn 1005*; representative specimen in Herb. Brit. Mus. (Nat. Hist.), London).

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NEW OR LITTLE KNOWN HIMALAYAN SPECIES OF *SWERTIA* AND *VERATRILLA* (GENTIANACEAE)

H. SMITH

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
BOTANY Vol. 4 No. 6
LONDON : 1970

NEW OR LITTLE KNOWN HIMALAYAN SPECIES OF *SWERTIA* AND *VERATRILLA* (GENTIANACEAE)

BY
HARRY SMITH
Institute of Systematic Botany, University of Uppsala

Pp. 237–258 ; 7 *Text-figures, Plates* 22–37

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THE BRITISH MUSEUM (NATURAL HISTORY)

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NEW OR LITTLE KNOWN HIMALAYAN SPECIES OF *SWERTIA* AND *VERATRILLA* GENTIANACEAE

By HARRY SMITH

SUMMARY

TEN species of *Swertia* : *S. acaulis*, *S. grandiflora*, *S. virescens*, *S. pseudo-hookeri*, *S. staintonii*, *S. assamensis*, *S. crossoloma*, *S. splendens*, *S. gracilescens* and *S. burmanica* are described as new. The first eight of these, with *S. hookeri* C. B. Clarke and *S. candelabrum* H. Smith, form a distinct group within *Swertia* sect. *Swertia* and a key is provided for this group. The new name *S. franchetiana* is proposed for *S. stricta* Franch., a later homonym of *S. stricta* Collett & Hemsl. *Kingdonwardia codonopsidoides* Marq. is shown to be a synonym of *Swertia racemosa* (Griseb.) C. B. Clarke and reasons are given for not maintaining *Kingdonwardia* as a genus distinct from *Swertia*. Extensions of range are recorded for *S. kiharae* Kitam. and the previously described species mentioned above.

Certain errors in Franchet's original account of *Veratrilla* are pointed out, *Swertia mekongensis* Balf. f. & Forr. is treated as a synonym of *Veratrilla baillonii* Franch. and *Swertia burkilliana* W. W. Smith is transferred to *Veratrilla*. Extensions of range of both species are recorded.

INTRODUCTION

Until this century the world's herbaria contained few specimens of plants from the Himalayan region. In the last few decades, however, a very considerable amount of material has been collected in Tibet, Assam, Bhutan, Sikkim, and, more recently, Nepal, much of this in the course of expeditions under the auspices of the British Museum (Natural History). This paper deals with those specimens of the genera *Swertia* and *Veratrilla* that have been collected in those countries and that either represent new species or provide new information about species previously described. Except for a few specimens from the Royal Botanic Garden, Edinburgh, indicated by " (E) ", all those cited are in the herbarium of the British Museum (Natural History) ; there are duplicates of the great majority in Uppsala.

SWERTIA L.

Swertia L., Sp. Pl. 1 : 226 (1753) ; Gen. Pl., ed. 5 : 107 (1754).

Sectio *SWERTIA*

Swertia subgen. *Euswertia* C. B. Clarke in Hook. f., Fl. Brit. Ind. 4 : 127 (1883), *nom. invalid.*
Swertia sect. *Euswertia* Gilg in Engl. & Prantl, Naturl. Pflanzenfam. 4 (2) : 88 (1895), *nom. invalid.*

Swertia kiharae Kitam. in Acta Phytotax. & Geobot. 16 : 133 (1956). (Plate 22 ; Text-fig. 1.)

Chitral : Gangallat Gol, S.W. of Chitral, 2,700 m., amongst shrubs at edge of stream, petals and filaments white, anthers black, 18 June 1958, *Stainton 2708.* Golan Gol, 3,000 m., edge of stream, white, 13 July 1958, *Bowes-Lyon 63.*

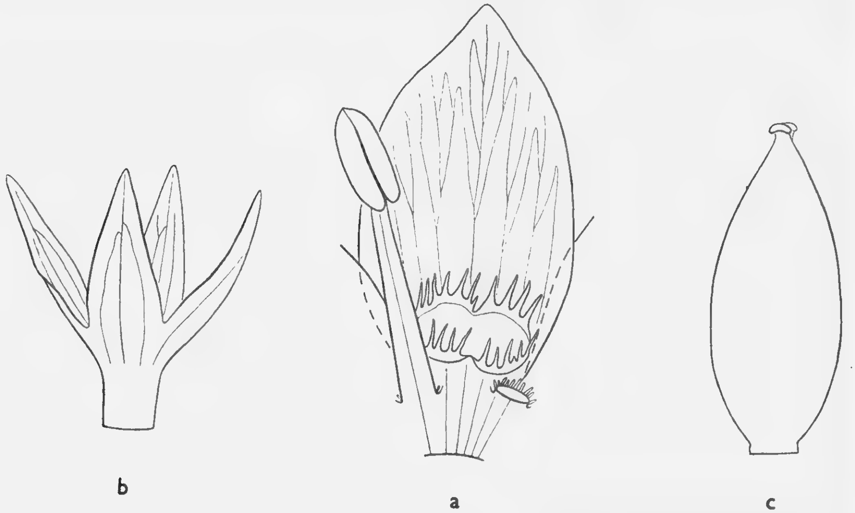


Fig. 1. *Swertia kiharae* Kitam. : a, corolla lobe with nectary and stamen ; b, calyx ; c, ripening capsule (*Stainton 2708*). All × 5.

These are interesting finds of a species originally described from Afghanistan. No species of the *Swertia aucheri* Boiss. group has been recorded until now from the Indian sub-continent.

THE *SWERTIA HOOKERI* GROUP OF SPECIES

The botanical explorations in the remote parts of the Himalayas during this century have shown that *Swertia hookeri* C. B. Clarke, originally described from a single collection from Sikkim, is not an isolated species but is instead a member of a complex group consisting of not less than ten distinct species, all obviously of close affinity. Unfortunately the material in herbaria is not rich ; collectors do not relish putting such robust and unwieldy plants in the press.

This group is well differentiated from other members of the section *Swertia* by the following characters : 4-merous fairly large to very large flowers, single nectary, robust growth, thick hollow stem, which can be 0·8 m. high or more (the abbreviated *S. acaulis* H. Smith excepted), and seeds globose and unwinged or much flattened and winged.

A distinctive character of unusual nature divides this group into two parts, each with five species. In the first part the margin of the leaves and sepals is glabrous, though a cellular papillosity is visible at a high magnification (text-fig. 2, b). In the other the margin is cut into hair-like, chlorophyllaceous lacinules only 0·3–0·5 mm. long (text-fig. 4, b, c). No specimen has been found that deviates in the slightest way from one or other of these two patterns. The species development seems to have followed parallel lines in these two groups. In both we have species with naked or with fimbriate nectaries, and species with cymose or with pyramidal inflorescences. Whether there is a similar parallelism in types of seed cannot yet be determined ; there are four species of which there is not available ripe seed nor ovules so far advanced that the shape of the seed can be safely presumed. At present we know that globose wingless seeds are present in both groups but flattened winged seeds are so far known only in the first.

The following is a key to this Group of species:

Margin of leaves and sepals entire, with obsolete cellular papillae (text-fig. 2, b):
  Nectary naked:
    Inflorescence cymose, many-flowered ; seed flattened :
      Plant 20–80 cm. tall ; inflorescence of distant axillary cymes, rarely moderately branched ; seed discoid, circularly winged . *S. hookeri*
      Plant subacaulous, stem at most 2 cm. tall ; seed oval, the obtuse ends unequally and irregularly winged . . . . *S. acaulis*
    Inflorescence pyramidal ; seed globose, not winged :
      Large robust plant 60 cm. or more tall ; petals reddish, 3 cm. long by 1·6 cm. broad ; inside base of sepals with a ring of black hairs *S. grandiflora*
      Plant 20–30 cm. tall ; petals greenish, 1·2–2·0 cm. long by 0·7–1·2 cm. broad ; inside base of sepals glabrous . . . . *S. virescens*
  Nectary densely fimbriate ; plant 30–40 cm. tall ; inflorescence pyramidal ; flowers yellowish-greenish, with glabrous and scarcely winged pedicels; seeds globose, not winged . . . . . *S. pseudo-hookeri*
Margin of leaves and sepals minutely and somewhat irregularly lacinulate, lacinules chlorophyllaceous, hair-like, 0·3–0·5 mm. long (text-fig. 4, b, c) :
  Nectary naked, its margin smooth :
    Stem deeply 5-grooved ; inflorescence pyramidal, copiously branching from base and nodes ; wings of stem and pedicels ciliate ; petals 2 cm. long by 1·7 cm. broad ; seed globose, not winged . . . *S. staintonii*
    Stem terete or nearly so ; inflorescence of axillary cymes not or moderately branched ; wings of stem and pedicels glabrous ; petals 2·5 cm. long by 2 cm. broad ; (seed not seen) . . . . . *S. assamensis*
  Nectary toothed or fimbriate at the margin :

Margin of nectary toothed with pointed projections not more than 0·5 mm. long, less than 1/3rd of the diameter of the nectary ; flowers few on robust, curvingly ascendent branches . . . . *S. candelabrum*

Margin of nectary fimbriate with filamentous projections 1–2 mm. long, ½ or more of the diameter of the nectary ; inflorescence pyramidal :

Connective of anthers prolonged, often claw-like ; flowers pale creamy green ; petals 1·9 cm. long by 1·0 cm. broad ; wings of pedicels ciliate *S. crossoloma*

Connective of anthers not prolonged ; flowers brick red ; petals 2·5 cm. long by 2·0 cm. broad ; wings of pedicels glabrous except at point of junction with the decurrent sepals . . . . *S. splendens*

SWERTIA HOOKERI C. B. Clarke in Hook. f., Fl. Brit. Ind. 4 : 127 (1883). (Plate 23 ; Text-fig. 2 a–d.)

TIBET : Kongbo, Doshong La, 4,000 m., on grassy slope at base of precipice, herb to 1 m., calyx green, corolla greenish yellow with faint browny purple veins, filaments and ovary purple-black, anthers dull yellow, 15 July 1938, *Ludlow, Sherriff and Taylor 5256.* Same locality, amongst shrubbery, calyx green, corolla yellowish green, anthers and ovary dark green, 16 Aug. 1947, *Ludlow, Sherriff and Elliot 14376.*

NEPAL : Barun Khola, N. of Num, Arun Valley, 3,800 m., on open slopes, corolla greenish brown, filaments white, 12 June 1956, *Stainton 641.* S. of Topke Gola, Arun-Tamur watershed, 4,300 m., on open slopes, corolla, filaments and anthers bronze-coloured, 9 July 1956, *Stainton 903.*

SIKKIM : Changu, 3,700 m., in turfy level space on hill, red flowers, spikes 60–90 cm., 8 Sept. 1913, *R. E. Cooper 832.* North Chakung Chu, 4,000 m., on peat hillside, 1 m. tall, red flowers, many whorls, 20 Sept. 1913, *R. E. Cooper 918.*

BHUTAN : Ju La Mangde Chu, 4,300 m., in open alpine zone, calyx green, corolla brownish red, 19 July 1949, *Ludlow, Sherriff & Hicks 16892.* Parshong, 4,000–3,800 m., tall, red, 27 July 1914, *R. E. Cooper 1993.*

Clarke's original description, although based on only two gatherings, is very accurate and complete and there can be no doubt about the identity of his plant.

Swertia acaulis H. Smith, sp. nov. (Plate 24 ; Text-fig. 2e.)

Swertia acaulis H. Smith ex Nilsson in Grana Palyn. 7 : 111 (1967), *nom. nud.*

Omnino glabra, radix validus verticalis, caulis valde abbreviatus 1–2 cm. altus, flores numerosos, cymosos, subaequaliter 3–4 cm. longe pedicellatos edens. Habitu *S. multicaulis* D. Don[1] subsimilis sed distat : floribus multo majoribus albis (nec caeruleis), nectario perfecte nudo (nec fimbriato), seminibus complanatis, ambitu ovalibus, in apicibus inaequaliter alatis (nec subglobosis exalatis).

Folia rosularia desunt, caulina aggregata, numerosa, lanceolata, acuta, trinervia,

---

[1] C. B. Clarke in Hook. f., Fl. Brit. Ind. 4 : 129 (1883) says that *S. multicaulis* is 5-merous, whereas it is 4-merous, as correctly stated in the original diagnosis by D. Don, Prodr. Fl. Nepal : 128 (1825).

5–7 cm. longa, ad 0·9 cm. lata, lamina in petiolum subaequilongum sensim angustata. *Flores* 4-meri ; calyx fere ad basin fissus, lobi ovati, acuti, 11–16 mm. longi et 5–7 mm. lati ; corollae tubus perbrevis, lobi obovati, rotundato-truncati, apice minute lacerulati, 18 mm. longi et 11 mm. lati, nectario nudo nigro ; stamina tubo adnata, filamentis liberis 11 mm. et thecis 2 mm. longis, connectivo antherarum fere 0·5 mm. longe aristulatim protracto ; ovarium anguste ovatum in stigmas sessiles angustatum ; semina complanata, ambitu ovalia, 1·0 × 0·6 mm. magna, in apicibus valde inaequaliter alata.

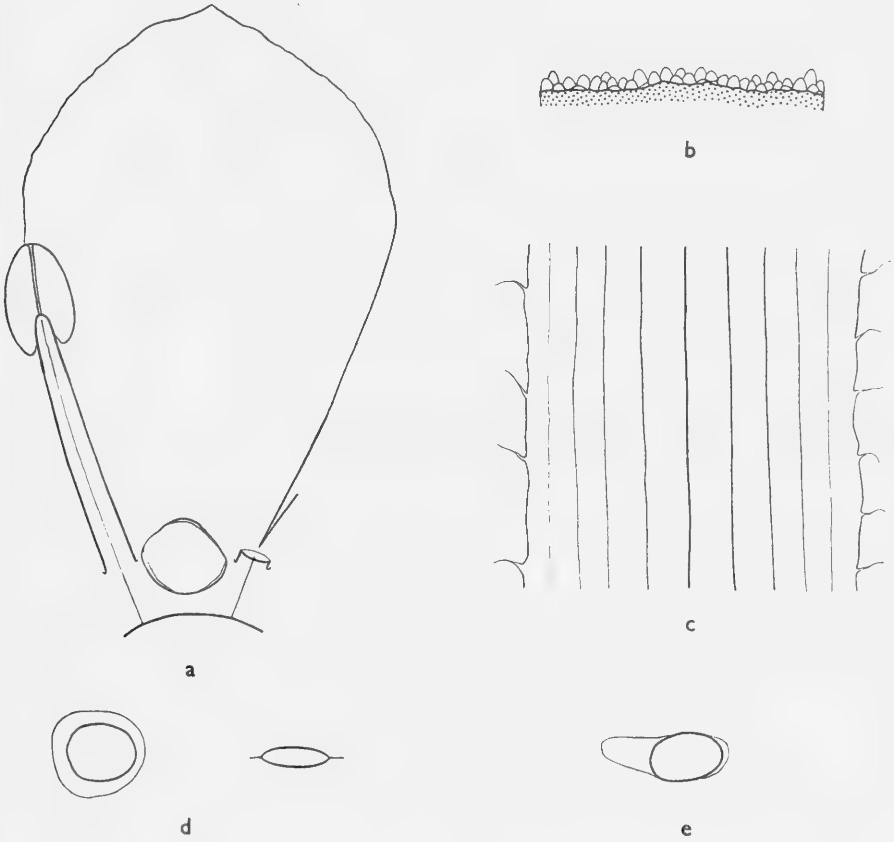


FIG. 2. *Swertia hookeri* C. B. Clarke : a, corolla lobe with nectary and stamen ; b, margin of leaf, with chlorophyllaceous area dotted ; c, middle part of rosular petiole (*Ludlow, Sherriff & Elliot 14376*) ; d, seed from above and in cross section (holotype) *Swertia acaulis* H. Smith : e, seed from above (*Lall Dhowj 0291*). b × 50, e × 10, a, c, d × 5.

NEPAL : Foot of Rolwaling, 3,700–5,500 m., yellow, 1930, *Lall Dhowj 0291* (holotype). Dudkund, 5,500 m., yellow, 24 Aug. 1932, *K. N. Sharma E504*. Wabak Khola, east of Num, Arun Valley, 4,600 m., on open slopes, petals white, filaments and anthers blue, 12 Aug. 1956, *Stainton 1334*.

Swertia grandiflora H. Smith, sp. nov. (Plate 25.)

Planta 60 cm. vel ultra alta *S. candelabro* H. Smith subsimilis, sed distat : margine foliorum et sepalorum integro (nec lacinulato), floribus majoribus 3 cm. longis, calycis lobis late ovalibus obtusis (nec cordato-triangularibus, acutis).

Caulis robustus ad 1·6 cm. diametiens, ut rami et pedicelli modeste quadrialatus, glaber. Inflorescentia pyramidalis, ramis robustis, paucifloris e nodis 2 arcuatim adscendentibus. *Folia* margine integra, rosularia ad 18 cm. longa et 6 cm. lata, 7–13 nervia, lamina elliptica apice acuta in petiolum latum brevem vel longiorem angustata, caulina perpauca ad 9·5 cm. longa et 6 cm. lata, sessilia, nervis c. 9 *Flores* patuli ad 5·5 cm. diametientes, rubroviride striati ; calycis tubus perbrevis basi interno breviter nigro-barbatus, lobi inaequales, duo majores ad 1·9 cm. longi et 1·5 cm. lati, ovales, obtusi vel subobtusi, glabri ; corollae tubus brevis, lobi oblongi, apice rotundati, ad 3 cm. longi, superiori parte 1·5–1·7 cm. lati, nectario nudo subquadrangulari margine paullo elevato cincto ; stamina tubo adnata, filamentis liberis crassis 10 mm. longis, antheris caeruleis 3 mm. longis ; ovarium conicum stigmatibus parvis sessilibus coronatum ; capsula matura (e *Ludlow & Sherriff 1040*) 2 cm. longa, valvis apice recurvantibus, pedicellis ad 4–10 cm. prolongatis ; semina ovali-globosa, exalata, 1·7–2·0—1·4–1·6 mm. magna, testa levi.

BHUTAN : Shingbe, Me La, 4,000 m., on open hillside, very common, flowers striped dull red and green, 14 June 1949, *Ludlow, Sherriff & Hicks 20732* (holotype). Me La 4,300 m., open grassy hillside above tree line, 6 Oct. 1934, *Ludlow & Sherriff 1040*.

Swertia virescens H. Smith, sp. nov. (Plate 26 ; Text-fig. 3c, d.)

Swertia virescens H. Smith ex Nilsson in Grana Palyn. 7 : 112 (1967), *nom. nud.*

Species 15–20 cm. alta, *S. hookeri* C. B. Clarke affinis sed distat : planta multo minore, inflorescentia pyramidale, floribus vix 1·5 cm. longis, foliis omnibus obtusis (nec subacutis) caulinis sessilibus (nec longe petiolatis).

Caulis glaber, quadrialatus, superiori dimidia parte 3-nodosus, e nodo infimo rami 4, pluriflori, suberecti, florendi tempore 4–6 cm. longi editi, in nodo supremo flores numerosi cymosi, omnes graciliter pedicellati, pedicellis glabris modeste quadrialatis. *Folia* rosularia numerosa, lamina ovali, obtusa, 7-nervia, margine integra, c. 5 cm. longa et 2·5 cm. lata, in petiolum ad 1·5 cm. longum et 1 cm. latum, margine densius ciliato, attenuata, folia caulina ovato-ovalia sessilia. *Flores* virescentes, brunneo-striati, nutantes ; calycis tubus perbrevis, lobi ovati, acuti vel subobtusi, ad 10 mm. longi et 5–7 mm. lati, margine integri ; corollae tubus vix 2 mm. longus, lobi cuneato-obovati, apice rotundati et minutissime erosulati, ad 12 mm. longi et 5–7 mm. lati, nectario nudo subrotundato ; stamina tubo 1·5 mm. alte adnata, filamentis liberis 5 mm. longis, antheris 2·3 × 1·7 mm. magnis ; ovarium anguste ovatum, stigmatibus subsessilibus orbicularibus ; capsula, semina non visa, ovulis semievolutis, ut videtur, subglobosis exalatis.

BHUTAN : Tsampa (Tolegang), Pangotang, 4,400 m. on open hillside, locally common, corolla green striated red brown, 3 July 1949, *Ludlow, Sherriff & Hicks 19323* (holotype).

The following two collections are closely allied to *Swertia virescens* : Tibet, Chickchar, Tsari, 4,600 m., on open grassy hillside above rhododendrons, pale cream green, filaments dull green, anthers dark brown, stigma pale green, 13 June 1936, *Ludlow & Sherriff 2149* ; Bhutan, Tsampa, Pangotang, 4,300 m., in open wet stony place, corolla white with striations inside, 16 June 1949, *Ludlow, Sherriff & Hicks 19168.* These are both low-growing but very robust plants that are just beginning to flower ; their flowers are bigger than those of *Swertia virescens* and differ in colour, and the

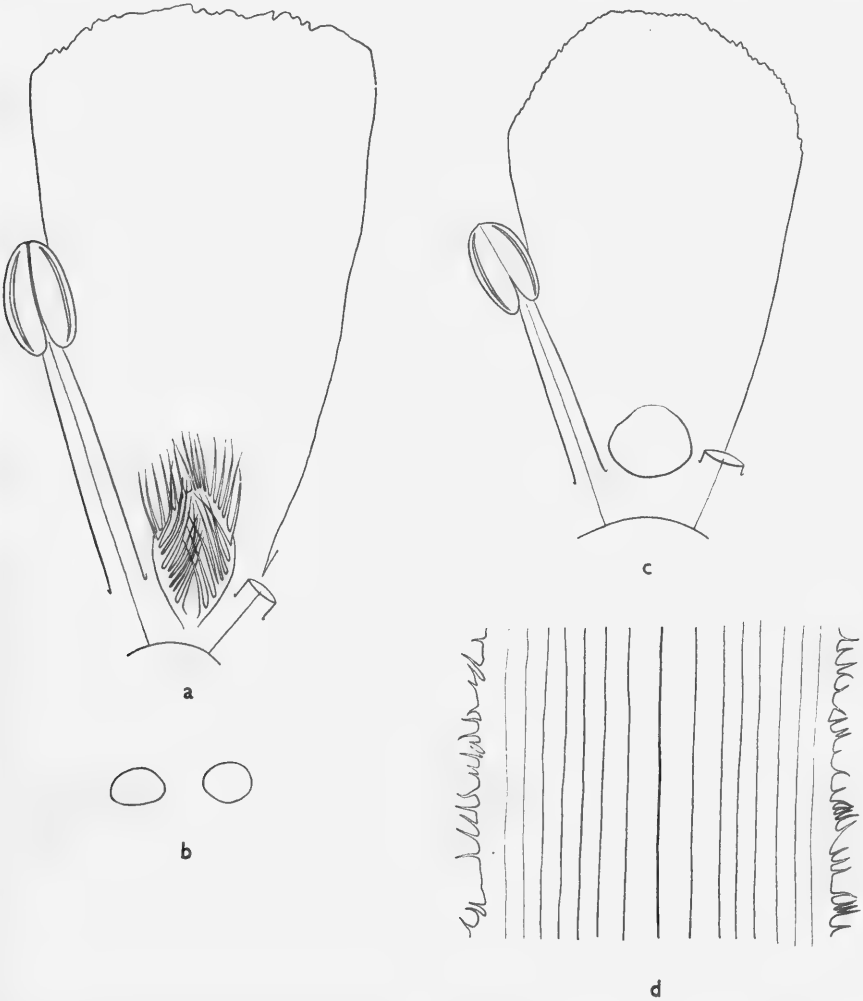


FIG. 3. *Swertia pseudo-hookeri* H. Smith : a, corolla lobe with nectary and stamen ; b, seed (*Ludlow, Sherriff & Hicks 19414*). *Swertia virescens* H. Smith : c, corolla lobe with nectary and stamen ; d, middle part of rosular petiole (*Ludlow, Sherriff & Hicks, 19323*). All × 5.

striation of the petals is hardly noticeable. They probably represent an undescribed species which cannot be published as new on the unsatisfactory material yet available.

Swertia pseudo-hookeri H. Smith, sp. nov. (Plate 27 ; Text-fig. 3a–b.)

Swertia pseudo-hookeri H. Smith ex Nilsson, Grana Palyn. 7 : 111 (1967), *nom. nud.*

Planta 30–40 cm. alta, caulis teres, inflorescentia laxa e nodis 3–4 anguste pyramidalis. Habitu *S. virescenti* H. Smith subsimilis sed nectario longe nigro-fimbriato (nec nudo) inter alia distincta.

Folia rosularia ad 12 cm. longa, lamina elliptica subacuta c. 5 cm. longa et 1·5 cm. lata, margine integra, in petiolum latum margine glabrum laminam longiorem vel breviorem sensim attenuata, folia caulina sessilia, sursum decrescentia, in nodis paria. *Flores* albo-virides marginem versus purpureo-striati, 1–5 cm. longe pedicellati, pedicellis glabris obsolete alatis ; calycis tubus brevissimus, lobi subaequimagni ovati obtusi, c. 10 mm. longi et 5–7 mm. lati, margine integri ; corollae tubus perbrevis, lobi obcuneati, apice truncati et parum erosulati, 1·5 cm. longi et 0·9 cm. lati, nectario ovali c. 2 mm. longe nigro-fimbriato, basi non clauso ; stamina tubo adnata, filamentis liberis 8 mm. longis et thecis 3·0 × 1·6 mm. magnis ; ovarium ovatum, stigmatibus parvis subsessilibus ; capsula (e *Ludlow, Sherriff & Hicks 19801*) angusta, 1·5 cm. longa, carpellis apice excurvantibus, seminibus ovato-globosis exalatis c. 1·4 × 1·2 mm. magnis.

BHUTAN : Tsampa, Marlung, 4,400 m., on open grassy hillside, corolla pale green, finely striated purple, 12 July 1949, *Ludlow, Sherriff & Hicks 19414* (holotype). Upper Mangde Chu, Saga La, 4,700 m., 14 July 1949, ravines in alpine zone, herb 60 cm. or more in height, calyx pale green, corolla greenish white finely striated purple at edges of segments, filaments purplish, anthers black, ovary and style greenish blue, 14 July 1949, *Ludlow, Sherriff & Hicks 16817*. Mangde Chu, Namdating, 4,300 m., on steep open hillside, flowers over, 3 Oct. 1949, *Ludlow, Sherriff & Hicks 19801*. Pumthang, Tibdeh La, 4,000 m., on peaty slopes, showy pyramid of white and pale blue flowers, 1 Sept. 1915, *R. E. Cooper 4769*.

Swertia staintonii H. Smith, sp. nov. (Plate 28 ; Text-fig. 4.)

Swertia staintonii H. Smith ex Nilsson in Grana Palyn. 7 : 112 (1967), *nom. nud.*

Planta c. 30 cm. alta, inflorescentia pyramidalis e basi et nodis 3–4 ramosa, ramis et ramulis suberectis. Species *S. crossolomae* H. Smith subsimilis sed distat : caule, praesertim inferiori parte, alte 5-sulcato (nec subtereti), floribus majoribus, nectario nudo (nec fimbriato), connectivo antherarum subplano (nec protracto, saepe uncinato).

Caulis, rami et pedicelli ciliato-alati, alis caulinis in sulcis nec in angulis locatis. *Folia* rosularia numerosa, subacuta, 6–10 cm. longa et 1–2 cm. lata, lamina in margine dense lacinulata, lacinulis robuste piliformibus 0·3–0·4 mm. longis, in petiolum subaequilongum sensim angustata, petiolo in margine laxe ciliato ; folia caulina infimi nodi 5-verticillata, subacuta, lanceolata, c. 7 × 2 cm. magna, breviter petiolata. *Flores* rosei (e collectore) 1–2 cm. longe pedicellati ; calycis tubus perbrevis, lobi ovato-triangulares, acuti, dense lacinulati, 1·5 cm. longi et 1 cm. lati, marginibus basalibus in alas pedicelli decurrentibus ; corollae tubus vix 2 mm. longus, lobi obcuneati margine fere integri, ad 2 cm. longi et 1·7 cm. lati, nectario nudo basi rotundato apice subacuto ; stamina tubo 1·5 mm. alte adnata, filamentis liberis 1 cm. longis, antheris 3×2 mm. magnis minutissime apiculatis ; ovarium anguste ovatum, stigmatibus orbicularibus subsessilibus ; semina (ex *Cooper 1994* et *2990*) subglobosa, exalata, 1·5–1·9×1·2–1·4 mm. magna.

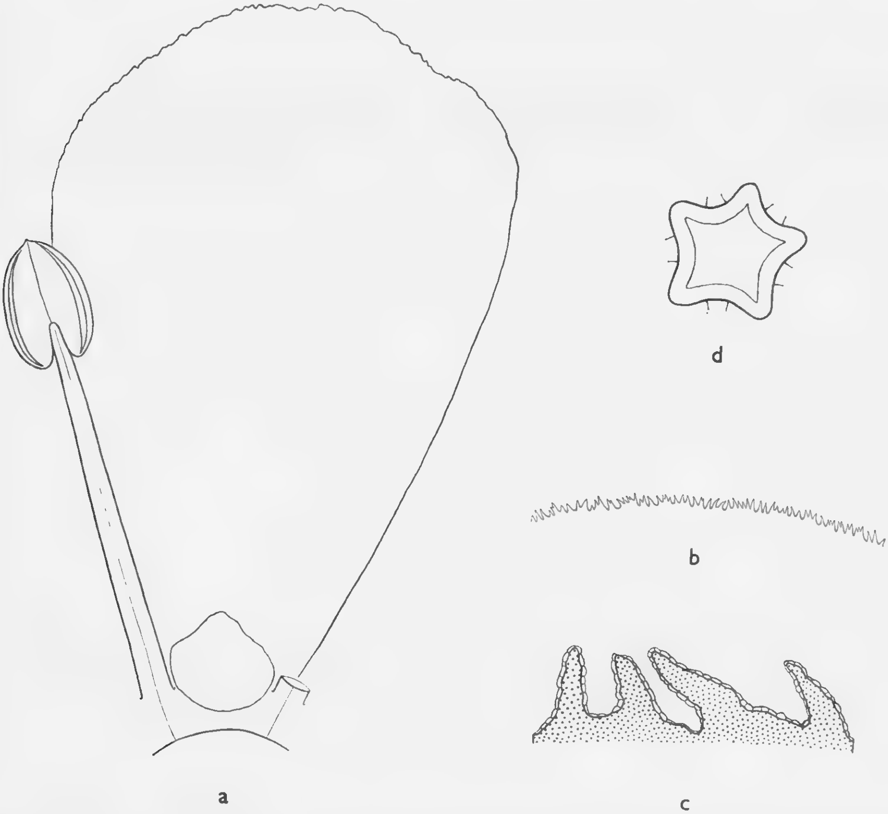


Fig. 4. *Swertia staintonii* H. Smith : a, corolla lobe with nectary and stamen ; b, margin of leaf ; c, the same, with chlorophyllaceous area dotted (*Stainton 755*) ; d, cross section of lower part of stem (*Cooper 1994*). a, b ×5, c ×50, d ×2½.

Nepal : Arun Valley, Chhoyang Khola, west of Num, 3,800 m., on open slopes, corolla pink, filaments black, anthers white, 23 June 1956, *Stainton 755* (holotype).

Bhutan : Parshong Timpu, 4,000 m., on peaty gravel, common in this one place, flowers white, 27 July 1914, *R. E. Cooper 1994*(E). Same loc., in alpine turf, pyramid of white flowers, 25 Sept. 1914, *R. E. Cooper 2990*(E).

I have no doubt that Cooper's two gatherings belong to the same species as Stainton's. All three have exactly the same unusual morphological organization.

The difference in colour is of little account. The Cooper specimens are both in a far advanced fruiting condition ; the flowers are shrivelled, the leaves withered or gone, the capsules mostly empty, but the important characteristics are still there. The peculiar arrangement with the deeply groved stem and the 5-verticillate lower cauline leaves is exactly the same as in the Stainton plant. So are also the shape and margin of the leaves and sepals and the size and form of the petals and nectaries.

Cooper's notes on the labels " pyramid of white flowers " and " common in this one place " show that he was well acquainted with the plant. It is certainly to be supposed that he also collected flowering specimens, but no such specimen ever reached Edinburgh. Possibly some packages of his got lost on their way during the troubled year of 1915.

Swertia assamensis H. Smith, sp. nov. (Plate 29.)

Planta robusta c. 30 cm. alta, habitu *S. hookeri* C. B. Clarke subsimilis, sed inter alia distat : floribus majoribus, marginibus foliorum sepalorumque dense lacinulatis (nec integris).

Caulis glaber modeste alatus. *Folia* omnia et sepala lacinulata, lacinulis piliformibus vix 0·5 mm. longis ; folia rosularia ad 9 cm. longa, lamina elliptica subobtusa 2–2·5 cm. lata, in petiolum subaequilongum sensim attenuata, petiolo margine sparse ciliata. *Flores* in cymis 3 distantibus, raro breviter ramosis, dispositi, subpatuli, magni, c. 1 cm. longe pedicellati, pedicellis quadrialatis glabris ; calycis lobi duo majores triangulari-ovati ad 13 mm. longi et basi 12 mm. lati, duo minores angustiores et breviores ; petala late obcuneata ad 2·5 cm. longa et apicem versus 2 cm. lata, margine minutissime lacerulata, nectario singulo, nudo, margine basali membranaceo modice elevato ; stamina tubo brevissimo adnata, filamentis liberis 10 mm. longis, thecis robustis 4 mm. longis ; stigmata subsessilia ; capsula, semina non visa.

ASSAM : Poshing La, 4,000 m., on cliff ledges and turf slopes, " (= 13797) ", 22 July 1938, *Kingdon-Ward 14008* (holotype). Bhutan frontier, Orka La, 3,400–4,000 m., abundant in alpine pastures where cattle feed, comes up in colonies where scrub is cleared, height 25–35 cm., flowers yellow, streaked red, 7 June 1938, *Kingdon-Ward 13797*.

SWERTIA CANDELABRUM H. Smith in Notes Roy. Bot. Gard. Edinb., 26 : 255, pl. 34, fig. 8 d–f (1965).

A specimen which may belong to this species is : Bhutan, Sakden, Nyuksang La, 3,700 m., open hillside among rhododendron scrub, pale greenish yellow streaked pale reddish purple, 6 July 1934, *Ludlow & Sherriff 601*. It differs from the type of *S. candelabrum*, which comes from central Nepal, in the colour of its flowers, whitish blue in the type, and in the membraneous margin of the nectary, which is less laciniate. In other respects it is very similar ; its water-swelled ovules are ellipsoidal and not winged.

Swertia crossoloma H. Smith, sp. nov. (Plate 30 ; Text-fig. 5.)

Planta florendi tempore 22 cm. alta, *S. staintonii* H. Smith subsimilis sed distat : caule subtereti (nec alte sulcato), nectario fimbriato (nec nudo), connectivo antherarum protracto, saepe uncinatim curvato (nec subplano), floribus minoribus.

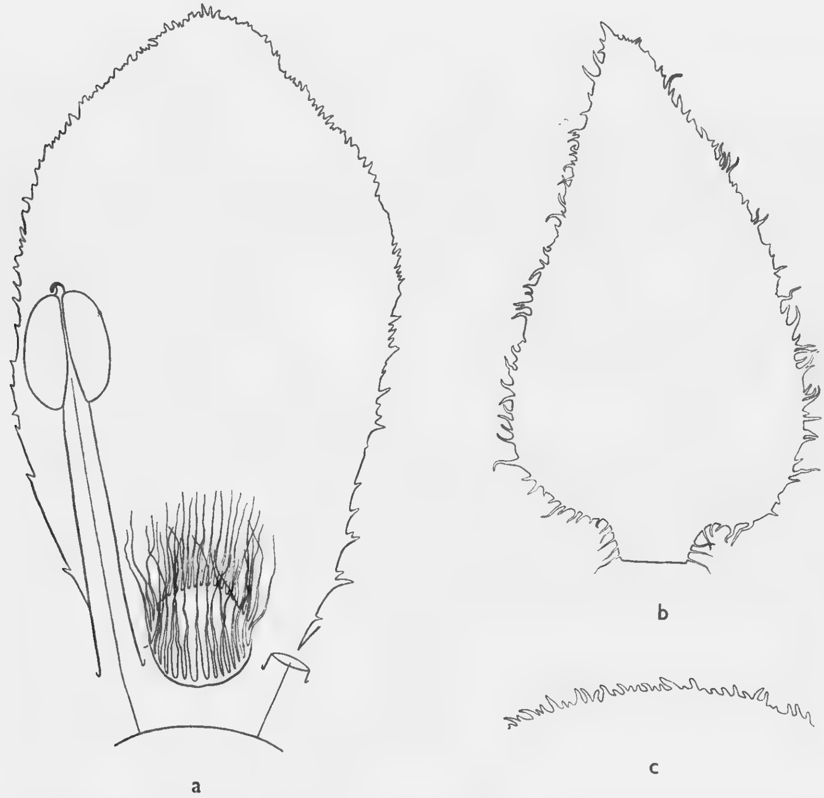


FIG. 5. *Swertia crossoloma* H. Smith : a, corolla lobe with nectary and stamen ; b, outline of calyx lobe ; c, margin of leaf (*Ludlow & Sherriff 421*). All × 5.

Caulis subteres, basin versus 4-alatus, alis ciliatis ; inflorescentia pyramidalis e basi et nodis 3 ramosa, ramis, ramulis et pedicellis ciliato-alatis. *Folia* rosularia ad 11 cm. longa, lamina late lanceolata, acuta, ad 2 cm. lata, in petiolum subaequilongum sensim attenuata, margine crebre lacinulata, lacinulis piliformibus 0·3–0·4 mm. longis. *Flores* pallide albo-virescentes (e collectore) ; calycis lobi subaequales, c. 7 mm. longi et 3·5 mm. lati, ovato-triangulares, subobtusi vel acutiusculi, margine irregulariter lacinulati, basin versus etiam ciliati, marginibus basalibus in alas pedicelli decurrentibus ; corollae lobi subobovales ad 1·9 cm. longi et 1·0 cm. lati, superiori parte minute, deorsum grossius lacerulati, nectario orbiculari circum longe fimbriato ; stamina tubo adnata, filamentis liberis 10 mm. longis, thecis c. 3 × 2 mm. magnis, connectivo antherarum protracto saepe uncinatim curvato. Capsula, semina non visa.

Bhutan : Me La, 4,300 m., open grassy hillside, pale creamy green, striped blue at base, 6 Aug. 1933, *Ludlow & Sherriff 421* (holotype).

Swertia splendens H. Smith, sp. nov. (Plate 31; Text-fig. 6.)

Planta plus quam 40 cm. alta (parte basali deficiente), ex affinitate *S. crossolomae* H. Smith, a qua distat : planta multo majore, inflorescentia laxiore, floribus lateritiis, 2·5 cm. longis (nec virescentibus, 1·7 cm. longis), corollae lobis late obovatis subtruncatis (nec ovalibus), connectivo antherarum abbreviato (nec uncinatim protracto), fimbriis nectarii inflexis 1 mm. longis (nec erectis 2 mm. longis).

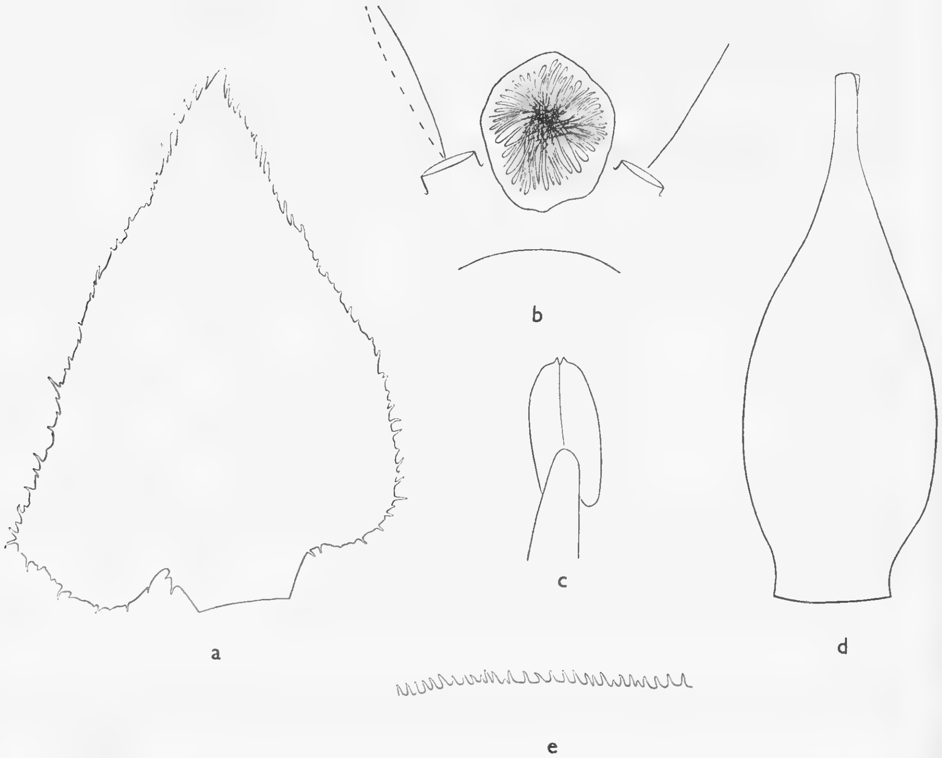


Fig. 6. *Swertia splendens* H. Smith : a, outline of calyx lobe ; b, base of corolla lobe with nectary ; c, anther ; d, ovary ; e, margin of leaf (*Ludlow & Sherriff 654*). All ×5.

Caulis (pars florifera solum adest) robustus, obsolete quadri-alatus, alis sparsissime sed robuste ciliatis ; nodi 3 inflorescentiae pyramidalis distantes, rami infimi arcuatim adscendentes 2–5-flori, in nodo supremo flores plures (ad 10) cymosi. *Folia* rosularia (duo adsunt) spathulata, 7-nervia, lamina obovata, subacuta, 8 et 12 cm. longa, c. 5·5 cm. lata, margine crebre lacinulata, lacinulis piliformibus c. 0·3 mm. longis, in petiolum latum, subaequilongum attenuata, petiolo in margine sparse, basi intus densius ciliato. *Flores* ampli lateritii 1–3·5 cm. longe pedicellati, pedicellis quadrialatis glabris ; calycis tubus perbrevis, lobi triangulari-cordati, majores ad 1·6 cm. longi, 1·0 cm. lati, margine minute lacinulati basin versus etiam ciliati ; corollae tubus brevis, lobi late obovati, 2·3 cm. longi et 2·0 cm. lati, margine apicaliter minutissime lacerulati, nectario orbiculari fimbriis inflexis 1 mm. longis cincto ; stamina tubo 2 mm. alte adnata, filamentis liberis 11 mm. longis, thecis 3·5 mm. longis, apicibus thecarum connectivo abbreviato liberis ; ovarium ovatum, stylo cum stigmatibus parvis 2 mm. longo ; capsula, semina non visa, ovula, ut videtur, subglobosa exalata.

TIBET : Milakatong La, near Tawang, 4,000 m., open stony hillside, brick red, 14 July 1934, *Ludlow & Sherriff 654* (holotype).

Sectio *OPHELIA*

Swertia sect. *Ophelia* (D. Don ex G. Don) Gilg in Engler & Prantl, Naturl. Planzenfam. 4 (2) : 88 (1895).

Ophelia D. Don ex G. Don, Gen. Syst. 4 : 178 (1837).
Swertia series *Ophelia* (D. Don ex G. Don) Benth. & Hook., Gen. Pl. 2 : 817 (1876).
Swertia subgen. *Ophelia* (D. Don ex G. Don) C. B. Clarke in Hook. f., Fl. Brit. Ind. 4 : 121 (1883).

Swertia franchetiana H. Smith, nom. nov. (Plate 32.)

Swertia stricta Franchet in Bull. Soc. Bot. France 46 : 322 (1900) ; non *S. stricta* Collett & Hemsl. in Journ. Linn. Soc. Lond., Bot. 28 : 91 (1890).

TIBET : Hills north of Lhasa, 3,800 m., on open sandy banks, flowers pale blue violet striated darker, 31 Aug. 1943, *Ludlow & Sherriff 9907*. Lhakang, 3,700 m., open hillside, very pale blue, veins mauve, 2 Sept. 1933, *Ludlow & Sherriff 518*. Kongbo, Lhatra Chu (Pangkar), 4,100 m., on dry ground, calyx green, corolla bluish white, filaments blue, anthers very dark brown, style green, stigma very dark brown, 7 Sept. 1947, *Ludlow, Sherriff & Elliot 15694*. Kongbo, Temo La, 3,200–3,400 m., on grassy banks in forest, calyx green, petals pale watery blue with dark blue veins, two lateral lines of purple hairs at base, stamens pale blue, anthers purple, ovary light green at base, darker above, 7 Sept. 1938, *Ludlow, Sherriff & Taylor 6992*. Kongbo, Tsangpo Valley, Pe, 2900 m., in grass by streams, calyx green, corolla slaty blue veins darker, 23 Aug. 1947, *Ludlow, Sherriff & Elliot 14436*.

Franchet described this species from western China ; it has not previously been recorded outside China proper.

Swertia gracilescens H. Smith, sp. nov. (Plate 33.)

Planta hapaxantha, *S. paniculatae* Wall. affinis, sed gracilior, flores minores, emaculati, eleganter dispersi (nec in cymas modice contracti), folia angustiora, rarissime ad 3 mm. lata.

Caulis erectus ad 35 cm. altus, basin versus ad 2 mm. crassus, in lineis decurrentibus brevissime ciliolatus vel glabrescens, e nodis 10–13 pyramidatim ramosus, ramis numerosis, gracilibus, inferioribus maximis ad 10 cm. longis et 0·5 mm. crassis, suberectis vel subpatentibus, sursum gradatim deminuta. *Folia* caulina lanceolato-linearia, uninervia, media maxima ad 2·5 cm. longa, circ. 2 mm. lata, marginibus glabra. *Flores* albi, emaculati, 5–6 mm. longi, 5-meri, uninectariati, gracillime 4–6 mm. longe pedicellati ; calycis tubus perbrevis, lobi attenuato-lineares, 4·5–5 mm. longi, basi 0·5–1 mm. lati, emucronati ; corollae tubus minus quam 1 mm. longus, lobi lanceolato-ovati, acuti, ad 5·5 mm. longi et 4 mm. lati, nectario glabro, orbiculato, margine superiori elevato ; stamina tubo 0·7 mm. alte adnata, filamentis liberis non dilatatis 3·5 mm. longis, thecis 0·8 × 0·3 mm. magnis ; ovarium anguste ovoideum in stylum 1·5 mm. longum contractum, stigmatibus vix 0·5 mm. longis. Capsula, semina non visa.

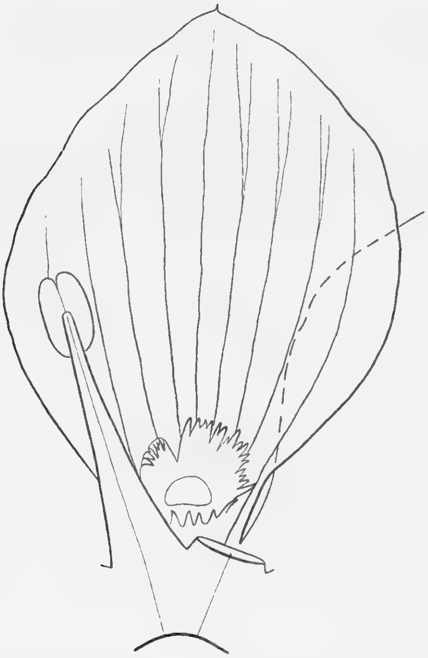


FIG. 7. *Swertia burmanica* H. Smith : corolla lobe with nectary and stamen. × 5.

NEPAL : Bhuji Khola, 2,100 m., open slope by track, flowers white, 15 Oct. 1954, *Stainton, Sykes & Williams 9049* (holotype). Near Gurjakhani, 2,600 m., exposed grass slope, flowers white, 17 Sept. 1954, *Stainton, Sykes & Williams 4470*. Kali Gandaki Valley, Taglung, south of Tukucha, 3,700 m., on grass slopes, petals and filaments white, anthers black, 22 Sept. 1954, *Stainton, Sykes & Williams 7970*.

Swertia burmanica H. Smith, sp. nov. (Plate 34 ; Text-fig. 7.)

Swertia burmanica H. Smith ex Nilsson in Grana Palyn. 7 : 110 (1967), *nom. nud.*

Planta hapaxantha *Swertia racemosae* (Griseb.) C. B. Clarke affinis et habitu similis, tamen distat : foliis subcoriaceis, lineari-lanceolatis, media parte (nec basin versus) latissimis, ad 2·5 cm. longis et 0·5–0·7 cm. latis, pagina inferiori conspicue flavescente ; floribus amplioribus ad 1·5 cm. longis, calyce turbinato (nec campanulato), tubo calycis breviore, 1·5–2·5 mm. longo (nec 2–5 mm.) ; corolla fere ad basin filamentorum partita, lobis late ovalibus, acutis, minute mucronulatis, margine obsolete microciliatis, ad 13 mm. longis et 10 mm. latis, tubo 5-plo longioribus (nec sublongioribus), indusio nectarii robusto, squamiforme, margine libero partim incurvante breviter laciniato, laciniis ecoloratis (nec tenero, magis diviso, laciniis vulgo nigrescentibus) ; filamentis deorsum valde incrassatis, basi approximatis sed non connatis (nec basi fere 1 mm. longe tubiforme connatis).

BURMA : Mt. Victoria Ridge, 2,600 m., a gregarious weed growing all along the ridge and on turf slopes in thousands, flowers 5-petalled, purple, 26 Oct. 1956, *Kingdon-Ward 22747* (holotype).

On the type sheet there are 3 individuals present. Two of them are more or less densely ciliate on the wings of the stem, on the surface and base of the under-side of the leaves, and on the calyx. The third specimen is nearly glabrous except on the wings of the stem. The degree of hairiness seems to be of small taxonomic importance, as is also the case in *S. racemosa* (below).

SWERTIA RACEMOSA (Griseb.) C. B. Clarke in Hook. f., Fl. Brit. Ind. 4 : 124 (1883).

Swertia racemosa Wall., Numer. List : 154, n. 4377 (1831), *nom. nud.*
Ophelia racemosa Griseb., Gen. & Sp. Gentian. : 319 (1838).
Kingdon-Wardia codonopsidoides Marquand in Journ. Linn. Soc. Lond., Bot. 48 : 207 (1929) ; in Hook. Icon. Pl. 32 : t. 3163 (1932).

TIBET : Kongbo, Pa La (Tra La), 3,700 m., in colonies in damp shady situations, flowers pale dull purple, 26 Sept. 1924, *Kingdon-Ward 6205* (isotype of *Kingdon-Wardia codonopsidoides*). Kongbo, Bo La, 4,300 m., under bushes in light forest, calyx light green, corolla purplish white, filaments pale blue, anthers black, 9 Sept. 1947, *Ludlow, Sherriff & Elliot 15705*. Kongbo, Nambu La, 4,400 m., on grassy banks in juniper forest, corolla pinkish mauve, 31 Aug. 1938, *Ludlow, Sherriff & Taylor 6951*. Tsari valley, 4,000–4,300 m., on alpine meadow slopes, 11 Sept. 1935, *Kingdon-Ward 12324*. Tsari, Podzo Sumdo, 3,500 m., by the side of a stream in dense forest, corolla palest mauve, 5 Sept. 1936, *Ludlow & Sherriff* 2544.

NEPAL : Deoli Patan, S.E. of Jumla, 3,800 m., growing on open slopes, corolla mauve, stamens blue, 5 Sept. 1952, *Polunin, Sykes & Williams 3189*. Rohagaon, Suli Gad, 3,400 m., open slopes, corolla mauve, nectaries at base of lobes green with fringe of dark blue hairs, filaments blue at apex, anthers brown, style blue, 14 Sept. 1952, *Polunin, Sykes & Williams 3386*. Near Seng Khola, 4,100 m., grass gullies, flowers pale mauve, 3 Oct. 1954, *Stainton, Sykes & Williams 4688*. Near Phagune

Dhuri, 3,500 m., sheltered gully, flowers lilac, 12 Oct. 1954, *Stainton, Sykes & Williams 4799*. Above Dogadi Khola, 4,600 m., exposed earth pockets near ridge, flowers mauve, calyx and pedicels dark purple, 12 Aug. 1954, *Stainton, Sykes & Williams 3834*. Same loc., 4,000 m., among dwarf *Rhododendron*, flowers light purple, 1 Oct. 1954, *Stainton, Sykes & Williams 4661*. Dhorpatan, 2,900 m., among shrubs on bank, flowers mauve, 16 Oct. 1954, *Stainton, Sykes & Williams 9056*. Above Sauwala Khola, 3,400 m., grass slopes on ridge, flowers mauve, 13 Sept. 1954, *Stainton, Sykes & Williams 4381*. Same loc., 4,000 m., among short grass on ridge top, abundant, flowers mauve, 13 Sept. 1954, *Stainton, Sykes & Williams 4389*. N.W. of Gurjakhani, 3,500 m., grassy slope, flowers white, 20 Sept. 1954, *Stainton, Sykes & Williams 4502*. Same loc., 3,700 m., near grazing encampment, abundant, flowers dark mauve, 20 Sept. 1954, *Stainton, Sykes & Williams 4512*. Kali Gandaki Valley, Samargaon, north of Tukucha, 4,900 m., on steep grass slopes, calyx mauvish green and hairy, corolla, filaments and anthers pale mauve, 16 Aug. 1954, *Stainton, Sykes & Williams 7249*. Kali Gandaki Valley, Sangdah, north of Tukucha, 4,100 m., open grass slopes, calyx green, corolla, filaments and anthers whitish blue, 18 Aug. 1954, *Stainton, Sykes & Williams 7309*. Kali Gandaki Valley, Tukucha, 3,700 m., open grass slopes, calyx greenish mauve, corolla and filaments pale mauve, lower leaves reddish green, 9 Sept. 1954, *Stainton, Sykes & Williams 7735*. Same loc., 3,700 m., open grass slopes, calyx greenish white, corolla and filaments white, anthers black, 9 Sept. 1954, *Stainton, Sykes & Williams 7737*. Same loc., 3,100 m., open grass slopes, corolla white, 15 Oct. 1954, *Stainton, Sykes & Williams 8157*. Kali Gandaki Valley, Taglung, south of Tukucha, 3,700 m., open grass slopes, petals and filaments white, anthers black, 20 Sept. 1954, *Stainton, Sykes & Williams 7945*. Sabze Khola, 4,000 m., among low bushes in moist ground and by stream side, flowers pale lilac or mauve, leaves and stem stained red, 6 Sept. 1950, *Lowndes L1491*. Khangsar, 4,300–4,600 m., open dryish hillside, in great quantity, flowers pale lilac or mauve, leaves and stem stained red, 9 Sept. 1950, *Lowndes L1502*. Bimtakothi, 4,000 m., damp hillsides, flowers whitish, 12 Sept. 1950, *Lowndes L1539*. Baraha Pokhri ridge, 4,000 m., open grassy hillside, flowers greyish white, 19 Sept. 1950, *Lowndes L1526*. Mardi Khola, Annapurna Himal, 3,500 m., among shrubs, corolla pale blue, 17 Sept. 1954, *Stainton, Sykes & Williams 8465*. Rambrong, Lamjung Himal, 3,700 m., on open hillside, corolla pale blue, 18 Sept. 1954, *Stainton, Sykes & Williams 8631*. Kyangjin Ghyang, 4,000 m., grassy ground, pale purple, *O. Polunin 1909*. " Gossain Thar " [? = Gosainkund], *Wallich 4377* (isotype of *Swertia racemosa*). Gosainkund, 4,900 m., 28 Oct. 1935, *F. M. Bailey's collectors 60*. E. of Num, Maghang Khola, Arun valley, 3,500 m., on open slopes, corolla mauve, 15 Sept. 1956, *Stainton 1737*. Sabel, 4,000 m., 18 Sept. 1937, *K. N. Sharma 63/94*. Chocho, 3,500 m., 27 Sept. 1937, *K. N. Sharma 56/94*. Gupchet, 3,700 m., 13 Sept. 1935, *F. M. Bailey's collectors s.n.* Chilung Pati, 4,100 m., 25 Oct. 1935, *F. M. Bailey's collectors 49*. Rolwaling valley, 3,800 m., 28 Sept. 1960, *Swan R 90*.

SIKKIM : Changu, 3,700 m., on loamy and sandy banks, blue, 25 cm. tall, 27 Sept. 1913, *Cooper 954*.

BHUTAN : Lingshi, 4,100 m., shrubbery, flowers dull purple, 24 Sept. 1967, *Bowes*

Lyon 5135. Thimpu, 3,100 m., on dry loam, blue to purple flowers, 25 cm. tall, slender, 5 Nov. 1914, *R. E. Cooper 3549*. Kopub, 3,400 m., in mould and leaves, etc., at edge of forest, flowers pale blue and white, 24 Sept. 1914, *R. E. Cooper 2141*. Lhabja, 3,800 m., on moist soil under forest, flowers blue, 30 cm. tall, 22 Sept. 1914, *R. E. Cooper 2187*. Waitang, Tsampa, 4,000 m., in dense vegetation of steep hillside, flowers pale pink with a tinge of blue, up to 40 cm. tall, 19 Sept. 1949, *Ludlow, Sherriff & Hicks 19753*. Tolegang, Tsampa, 4,300 m., among dwarf rhododendron on the open hillside, corolla pale slaty blue, 10 Sept. 1949, *Ludlow, Sherriff & Hicks 19730*.

ASSAM : Near Orka La, 3,700–4,000 m., alpine turf slopes along the ridge, flowers purple, 26 Sept. 1938, *Kingdon-Ward 14292*.

The genus *Kingdon-Wardia* is said by its author to be intermediate in position between *Gentiana* and *Swertia*, differing from the former by the presence of a fimbriate nectary at the base of each corolla lobe and from the latter by " the conspicuous calyx tube surmounted by triangular lobes and the well-marked corolla tube." The distinction from *Gentiana* certainly holds true, but the separation from *Swertia* is not convincing. Marquand was obviously not acquainted with *Swertia racemosa*, a species little known in 1928 and represented in the Kew herbarium at that date by only the Wallich type specimen and by the specimen from Tibet to which Burkill had given the manuscript name *Swertia codonopsidoides*.

The only statement in the diagnosis of *Kingdon-Wardia* that does not fit *Swertia racemosa* is : " corolla circa ad ¼ lobata ". This statement is, however, not correct ; a more exact one would be : corolla ad ½ vel paullo ultra lobata. The figure subsequently published by Marquand in *Hooker's Icones* shows the lobes and the tube to be of equal length, but the previous incorrect statement is repeated in the text. In the isotypes that I have seen my own measurements show that the lobes are in fact constantly a trifle longer than the tube, exactly as in *Swertia racemosa*, with which species *Kingdon-Wardia codonopsidoides* is undoubtedly conspecific.

Swertia racemosa has a slightly isolated position in the genus, differing from other species of *Swertia* sect. *Ophelia* by the less divided corolla and by the well developed calyx tube, but it is not divergent in any other respect. Its affinity with such species as *S. ciliata* (G. Don) Burtt and *S. hispidicalyx* Burk. is indicated by the shape of the nectary, stamens and style. It is even closer to *S. burmanica*, which is very similar in appearance. The calyx and deeply cleft corolla of that species conform to the normal pattern found in *S.* sect. *Ophelia* and it thus links *S. racemosa* with the other members of the section.

Plentiful material of *Swertia racemosa* has been collected in recent years, especially by the British Museum expeditions to the Himalayas. In that herbarium there are 32 gatherings from Nepal, 1 from Sikkim, 6 from Bhutan, 5 from S.E. Tibet and 1 from Assam. This ample material shows that *S. racemosa* has an unusually wide range of variability. The corolla lobes vary from distinctly to only slightly longer than the tube ; the calyx varies from 5 to 2 mm. in length, the calyx lobes are usually much longer than the tube and distinctly unequal, but they may also be shorter than the tube and of subequal size, and the angles between the lobes vary from broadly rounded to narrowly acute ; the stigma is sometimes subsessile, but commonly the style is more or less prolonged and may reach a length of 5 mm. ; the petals average in length 11 mm. (5–14) ; the calyx, the margins and upper surface of the leaves vary from densely or sparingly long- or short-ciliate to perfectly glabrous. All these variations seem to be independent of each other, and the extremes are connected by intermediate stages. To name such indistinct forms would be meaningless. It may nevertheless be mentioned that really long-styled specimens are not found outside Nepal, but this may be due to the fact that the plant has been collected over 30 times there and only 13 times elsewhere.

VERATRILLA (Baillon) Franchet

VERATRILLA (Baillon) Franchet in Bull. Soc. Bot. France 46 : 310 (1900).

Swertia sect. *Veratrilla* Baillon in Bull. Mens. Soc. Linn. Paris 1 : 730 (1888).

At a session of the Linnean Society of Paris on 6 April 1888, Baillon demonstrated a gentianaceous plant collected by Delavay in Yunnan. He gave a description, pointing out that it had certain characters in common with *Jæschkea, Obolaria, Bartonia* and *Gentiana,* but concluded " . . . *Swertia* proprement dits, et c'est a ce genre que le *Veratrilla,* si singulier qu'il puisse paraître, devra se rapporter comme section." This must be regarded as valid publication of the name *Swertia* sect. *Veratrilla.* The sectional epithet was chosen on account of the resemblance of this plant to *Veratrum* L. Baillon proposed no specific name for this plant.

In the following year, Baillon (Hist. Pl. 10 : 142 (1889)) expressed uncertainty about the taxonomic status of the Delavay plant, saying in a footnote to *Swertia* " aut generis sectio, aut generis proprium erit *Veratrilla* H. Bn. . . ., cujus flores dioeci, sæpe 4-meri . . . Species asiaticae multae novae hanc plantam cum *Frasera* et *Swertiis* legitimis nihilhominus connectunt."

Franchet, who had at an earlier date, probably in 1885, given a manuscript name under *Swertia* to the Delavay specimen in the Paris herbarium, obviously became convinced that it represented a separate genus and published it in 1900 at that rank and, ignoring his earlier manuscript epithet, published the name *Veratrilla baillonii* for the species. I quote his diagnosis in extenso ; there are two statements in it that should be altered. It seems as if Franchet had by that time lost interest in the plant ; the description is not of the same high class as one is used to from him :

" Veratrilla, an generis sectio an genus proprium Baillon, *Hist. des pl.* X, 142 et *Bull. Soc. Linn. de Paris,* 729.

" Flores dioeci, sæpius 4-meri ; corolla tubuloso-rotata, staminibus inferne cum tubo connatis juxta sinum tantum liberis, brevibus ; stylus brevis (vix 1 mm.) stigmate bilobo, lobis ovatis patentibus ; capsula ovata, breviter attenuata ; semina late ovata, levia.—Planta glabra, elata veratriformis ; folia inferiora longe petiolata, omnia opposita, anceolata [sic], inferiora vaginata ; inflorescentia e racemis densis pyramidam longam, angustam efformantibus ; corolla luteoviridis, 6 mm. longa et lata.

" V. Bailloni sp. nov.

" Hab.—La Chine occidentale, Yunnan, dans les broussailles, au-dessus du col de Yen-tze-hai, alt. 3500 mètres (Delavay) ; prairies humides de Tsang-chan, près de l'arête (Delavay n. 147).

" Genre remarquable, à cause de sa dioïcité ; les étamines sont insérées comme celle des *Jæschkea.*"

Baillon said in his original account " ses fleurs sont ordinairement tétramères, plus rarement pentamères, principalement dans le pied femelle " and in the *Histoire des Plantes* " flores . . . saepe 4-meri ", and Franchet said " flores . . . saepius 4-meri ", but I have examined 16 different collections and have never found a single flower that was not tetramerous. Kingdon-Ward, however, recorded pentamerous flowers in a field note (see below).

Franchet's description of the seeds reads "semina late ovata, levia". A more accurate one would be : semina complanata, ambitu subovalia, circum anguste alata c. 3 × 1·5–2 mm. magna, ala 0·3–0·5 mm. lata.

The great difference in appearance between the male and female plants must also be pointed out. The female plant has the long narrow pyramid of Franchet's description ; each bract supports one or two short upright branches bearing fewer than ten pedicelled flowers. The inflorescence of the male plant is robust and spreading, several hundreds of small flowers without pedicels being massed together on the stout and more or less patent branches. This difference is well demonstrated by the specimens of this species from China that are illustrated as plates 35–36. Those from Tibet or Assam are not so satisfactory for photography.

VERATRILLA BAILLONII Franchet in Bull. Soc. Bot. France 46 : 311 (1900) (" bailloni "). (Plates 35, 36.)

Swertia mekongensis Balf. f. & Forr. in Notes R. Bot. Gard. Edinb. 4 : 80, t. 19 (1907).

S.E. TIBET : Mt. Kenichunpo, Salween and Irrawaddy divide, 4,600 m., limestone crags, alpine region, plant fleshy, flowers yellow, May–July 1932, *Rock 21938.*

ASSAM : Orka La, Bhutan frontier, 4,000 m., pastures, flowers 4-merous, sometimes 5-merous, *Kingdon-Ward 13725.*

Veratrilla baillonii had not previously been recorded outside China proper, the identity of *Swertia mekongensis* with it not having been recognized. It is now recorded for S.E. Tibet and Assam.

Veratrilla burkilliana (W. W. Smith) H. Smith comb. nov. (Plate 37.)

Swertia burkilliana W. W. Smith in Journ. Asiat. Soc. Bengal, new ser. 7 : 78, t. 1, fig. i–iii (1911).
Veratrilla burkilliana H. Smith apud Nilsson in Grana Palyn. 7 : 113 (1967), *nom. nud.*

S.E. TIBET : Tsari, Tomtsang, 4,300 m., on open grassy hillside, corolla dull purple margined with green and slightly streaked with greenish purple, anthers blue purple, 23 June 1936, *Ludlow & Sherriff 2204.* Same loc., 4,300 m., on open grassy hillside, flower over, 13 Sept. 1936, *Ludlow & Sherriff 2578.* Chubumbu La, Langong, 4,000 m., common in open swampy meadows, corolla pale green, tinged dull slate blue at base, 2 June 1938, *Ludlow, Sherriff & Taylor 3943*.

SIKKIM : Changu, 3,700 m., in turf on lake side, green flowers, black marks, blue stamens, 1 July 1913, *R. E. Cooper 92*. Same loc., 3,700 m., on lake border, greenish flowers with spots, 20 Aug. 1913, *R. E. Cooper 565*.

BHUTAN : Pung La, 3,700 m., open marshy places near top of pass, flowers blue marked with green, 9 July 1949, *Ludlow, Sherriff & Hicks 20903*.

This second species of *Veratrilla* agrees exactly in all generic characteristics with *V. baillonii*, but it is quite distinct specifically. The plant is much smaller and less robust, only 15–30 cm. tall as against 30–50 cm. The cauline leaves are shorter and relatively broader. The seeds are slightly smaller, nearly circular in outline and with a slightly broader wing. The difference in appearance between male and female plants is strongly marked in this species also. The excellent figure accompanying the original description of the species represents the female plant. In the male the inflorescence is spreading, up to 4 cm. wide by 6 cm. long.

DR. H. SMITH
INSTITUTE OF SYSTEMATIC BOTANY OF THE UNIVERSITY OF UPPSALA
BOTANICAL GARDEN AND BOTANICAL MUSEUM
UPPSALA 1
SWEDEN

Swertia kiharae Kitam. (*Stainton 2708* in Herb. Brit. Mus.)

Swertia hookeri C. B. Clarke (*Ludlow, Sherriff & Elliot 14376* in Herb. Brit. Mus.)

Swertia acaulis H. Smith (*Lall Dhowj 0291* ; holotype in Herb. Brit. Mus.)

FLORA OF BHUTAN No. 20733

Loc. SHINGBE ME LA N E BHUTAN Alt. 13,000' Date 14/6/49

Lat. Long

Flowers striped dull red & green - growing on open hillside - Very common

Swertia grandiflora H. Sm.

Determ. H. SMITH, Upsala 1965

Coll. F. LUDLOW, G. SHERRIFF & J. H. HICKS

HOLOTYPE
Swertia grandiflora H. Smith

Swertia grandiflora H. Smith (*Ludlow, Sherriff & Hicks 20732*; holotype in Herb. Brit. Mus.)

Swertia virescens H. Smith (*Ludlow, Sherriff & Hicks 19323* ; holotype in Herb. Brit. Mus.)

Swertia pseudo-hookeri H. Smith (*Ludlow, Sherriff & Hicks 19414*; holotype in Herb. Brit. Mus.)

Swertia staintonii H. Smith (*Stainton* 755 ; holotype in Herb. Brit. Mus.)

Swertia assamensis H. Smith (*Kingdon-Ward 14008* ; holotype in Herb. Brit. Mus. The printed number on the ticket has been deleted in blue ink and *14008* substituted, but this has not reproduced on the photograph.)

Swertia crossoloma H. Smith (*Ludlow & Sherriff 421*; holotype in Herb. Brit. Mus.)

Swertia splendens H. Smith (*Ludlow & Sherriff 654* ; holotype in Herb. Brit. Mus.)

F. LUDLOW—G. SHERRIFF.
Locality Lhalung. S. Tibet No. 518
Alt. 13000' Date 2.9.33.
Description
Very pale blue, veins mauve.
Open hillside.

Swertia lactea Franch.

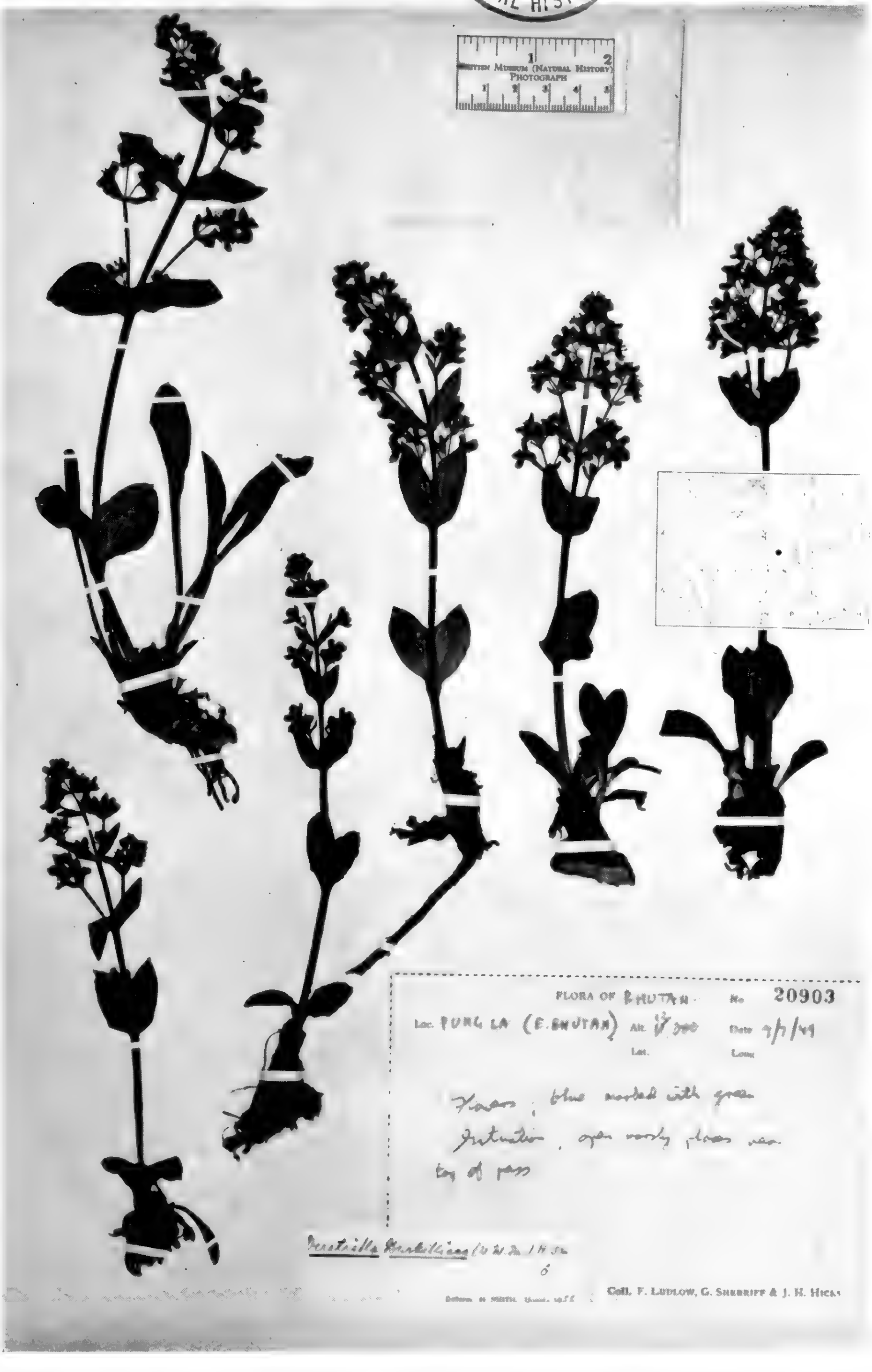
Swertia franchetiana H. Smith (*Ludlow & Sherriff 518* in Herb. Brit. Mus.)

Swertia gracilescens H. Smith (*Stainton, Sykes & Williams 9049* ; holotype in Herb. Brit. Mus.)

Swertia burmanica H. Smith (*Kingdon-Ward 22747* ; holotype in Herb. Brit. Mus.)

Veratrilla baillonii Franchet, male plant (*Forrest 6983* in Herb. Brit. Mus.)

Veratrilla baillonii Franchet, female plant (*Yu 13514* in Herb. Brit. Mus.)



Veratrilla burkilliana (W. W. Smith) H. Smith, male plants (*Ludlow, Sherriff & Hicks 20903* in Herb. Brit. Mus.)

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A SURVEY OF THE TROPICAL GENERA *OPLONIA* AND *PSILANTHELE* (ACANTHACEAE)

W. T. STEARN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
BOTANY Vol. 4 No. 7
LONDON : 1971

A SURVEY OF THE TROPICAL GENERA *OPLONIA* AND *PSILANTHELE* (ACANTHACEAE)

BY

WILLIAM THOMAS STEARN

Pp. 259–323 ; 18 *Text-figures* ; *Plates* 38–47

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A SURVEY OF THE TROPICAL GENERA *OPLONIA* AND *PSILANTHELE* (ACANTHACEAE)

By WILLIAM T. STEARN

SUMMARY

On grounds of priority the generic name *Oplonia* Raf. (1838) replaces *Anthacanthus* Nees (1847) ; both have the same type, *Justicia spinosa* Jacq. The genus *Psilanthele* Lindau (1897) is restricted to its type-species, *P. eggersii* Lindau of Ecuador ; the Peruvian and Jamaican species put in *Psilanthele* by Lindau are transferred to *Oplonia*, the supposed distinction between the " Rahmenpollen " of the one and " Spangenpollen " of the other being illusory. *Forsythiopsis* Baker (1883), hitherto considered endemic to Madagascar, is here united with *Oplonia*, as they agree in habit, floral structure, capsule, and pollen. The genus *Oplonia* thus extended consists of one species in Peru, eight in the West Indies, none in Central America, and five in Madagascar, which, like Cuba and Jamaica, is a major centre of endemism. Recognition of taxa within the group is very difficult owing to extensive but seemingly uncorrelated variation in habit of growth, pubescence of shoots, and size and shape of leaves. The spines provide useful diagnostic characters. Floral dimorphism, i.e. the occurrence of long-stamened short-styled flowers and of short-stamened long-styled flowers on different individuals of the same taxon in the same district, is demonstrated, possibly for the first time in the *Acanthaceae* ; otherwise the genus manifests very little floral diversity. Most species grow in dry open habitats as part of scrub forest. Their evolution would appear to be from a mesophytic spineless South American ancestor, resembling the small-flowered species of *Odontonema*, by progressive reduction in size of leaf, by contraction of the inflorescence from a narrow panicle or raceme into a few-flowered axillary fascicle or a solitary axillary flower, and by conversion of lateral branches into spines, by which changes they became xerophytic. The most primitive species on this assumption are *O. grandiflora* of Peru and *O. jamaicensis* of Jamaica. Parallels in distribution with *Neriacanthus*, *Heppiella*, *Huerta* and *Purdiaea* indicate ancient floristic links between the Greater Antilles and north-western South America independent of Central America and the Lesser Antilles and suggest that a major part of the Greater Antillean flora may be descended from plants of a land-mass now sunk which occupied the position of the present Caribbean Sea.

The presence of congeneric species in tropical America and Madagascar but not in continental Africa, as exemplified by *Oplonia*, *Oliganthes*, and *Ravenala*, is attributed to continental drift and subsequent extinction on the African mainland, as there exist genera with ranges intermediate between the extreme discontinuity of these and the continuous range of, e.g., *Sabicea*.

New nomenclatural combinations are: *Oplonia acicularis* (*Justicia acicularis* Swartz), *O. armata* (*J. armata* Swartz), *O. grandiflora* (*Psilanthele grandiflora* Lindau), *O. linifolia* (*Forsythiopsis linifolia* Benoist), *O. microphylla* (*J. microphylla* Lam.), *O. minor* (*F. minor* Benoist), *O. minor* var. *meridionalis* (*F. vincoides* var. *meridionalis* Benoist), *O. minor* var. *vestita* (*F. vincoides* var. *vestita* Benoist), *O. nannophylla* (*Anthacanthus nannophyllus* Urban), *O. purpurascens* (*A. purpurascens* Griseb.), *O. vincoides* (*J. vincoides* Lam.). *O. tetrasticha* var. *polyece* from Oriente province, Cuba, and *O. acuminata* and *O. puberula*, both from Madagascar, are described as new ; *Psilanthele minor* Lindau is renamed *O. armata* var. *pallidior*. Descriptions, synonymy and distributional data are provided.

As a guide to the capacity of computer-aided taxonometric (numerical taxonomic) methods to facilitate the sorting of relatively intractable specimens into groups definable and acceptable as taxonomic units, two of these methods (using programmes CLASP and Taximetric Similarity

Graph-clustering) were applied to *Oplonia* specimens providing a matrix of 24 unweighted characters. The results, expressed as stages of clustering, as a dendrogram and as a minimum scanning tree converted into a pictorialised scatter diagram, demonstrated their value as aids to understanding assemblages wherein most distinctions lie in a diversity of minute characters neither simultaneously observable nor easily correlated. The stage-by-stage clustering, with progressive reduction of the degree of similarity necessary for admission of specimens to clusters, portrayed graphically by the Taximetric Similarity Graph-clustering programme, commended itself as a time-saving substitute for part of the process of searching for correlations.

HISTORICAL INTRODUCTION

THE genus *Oplonia* is a small group of woody much-branched usually spiny small-flowered tropical plants belonging to the family *Acanthaceae* subfamily *Ruelloideae* tribe *Odontonemateae*. The flowers are solitary in the leaf-axils or borne in comparatively few-flowered axillary fascicles with minute bracts, this much-reduced inflorescence distinguishing *Oplonia* from *Odontonema* Nees (*Thyrsacanthus* Nees), which has terminal racemes or panicles. The calyx, as in *Odontonema*, is cleft into five narrow segments. The corolla (Text-fig. 1, B) is zygomorphic, usually lilac or red, but sometimes white, with a slender tube and a two-lipped limb, the upper lip two-lobed, the lower lip three-lobed. There are two stamens, which may be exserted or included, and two staminodes. One species, *Oplonia grandiflora*, grows in northern

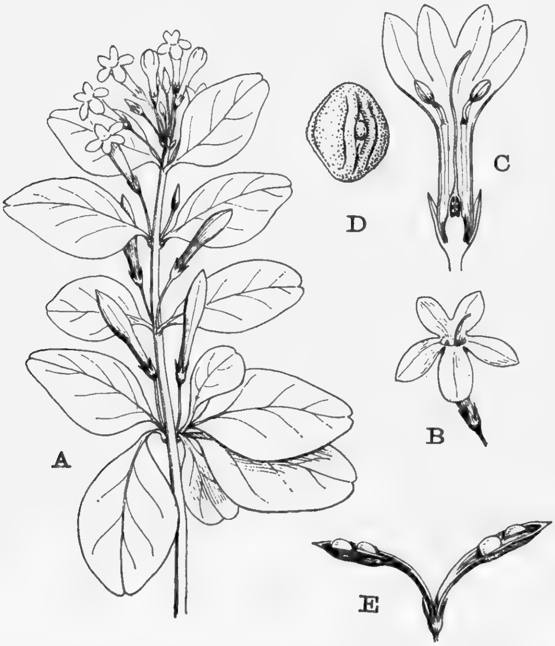

FIG. 1. *Oplonia armata* var. *pallidior* Stearn : A, Habit, × 2/3 ; B, corolla, × 1 ; C, flower of long-styled form cut lengthwise, × 2 ; D, pollen grain, × 300 ; E, capsule, × 1 (*Harris 10257*).

Peru ; the others are West Indian or Madagascan. Most of these can be distinguished from other West Indian members of the *Acanthaceae* by their opposite axillary spines (Text-fig. 2), which are modified shoots, not modified leaves as are the paired spines of *Barleria* and *Barleriola.* They supply the major taxonomic features of the species and vary from the forbidding rigid four-ranked stiletto-like thorns up to 3 cm. long of *O. tetrasticha* to the short prickles, sometimes under 4 mm. long, of *O. nannophylla.* The generic names *Oplonia* and *Anthacanthus* and the epithets *acicularis, armata, polyece* and *spinosa* all refer to this armature.

Although pre-Linnaean collectors gathered a few specimens of *Oplonia microphylla* in Antigua and Jamaica, the first species to be scientifically recorded was *O. spinosa* collected by Nicolaus Joseph von Jacquin near Port-au-Prince, Haiti, in 1757-58 and published by him in 1760 as *Justicia spinosa* (Pl. 43 a). On this species Rafinesque founded the genus *Oplonia* in 1838, his characteristically contracted diagnosis being as follows :

> " 987. Oplonia R. (weapons) diff. *Justicia,* cor. hypocraterif, tubo tereto, limbus 5 lobo, bilabiato, lab. sup. bilobo plano. Type *Opl. spinosa* R. Justicia do. L. auct. Prickly shrub, and probably all the prickly American sp. J. microphylla, armata, acicularis &c. "

Probably Rafinesque never saw any of the plants concerned, which are all West Indian and were then rare in herbaria. However he never hesitated about founding new genera on the illustrations and descriptions of more cautious authors* and he could have drawn more than enough information for his diagnosis from Vahl's *Enumeratio Plantarum* 1 : 167–169 (1804), where *J. spinosa, J. microphylla, J. armata* and *J. acicularis* are described. The epithets *spinosa, armata* and *acicularis* presumably suggested the generic name *Oplonia,* derived, like the name *Oplopanax* (Torr. & Gray) Miq., from the Greek *ὅπλον,* " implement of war, weapon, armour ", and thus cognate with the word " hoplite " ; *Hoplonia* would indeed have been a better rendering. Rafinesque's *Flora Telluriana* (Philadelphia, 1837–38) is a very rare work, of which apparently only two copies were available in Europe until the publication in 1946 of a photographic facsimile. Certainly C. G. Nees von Esenbeck knew nothing of it when in 1847 he separated these same prickly species from *Justicia* and *Eranthemum* and named the genus *Anthacanthus,* from *ἀνθος* " flower " and *ἀκάνθος,* " spine ". Nees distinguished within *Anthacanthus* a section *Armati* consisting of the spine-bearing West Indian species (*A. spinosus, A. armatus, A. acicularis, A. microphyllus, A. lycioides, A. cuneatus, A. emarginatus* and a " species dubia ", *A. sprengelii,* actually a member of the *Rubiaceae*) and a section *Inermes* consisting of unarmed species (*A. vincoides* from Madagascar, *A. sinuatus* and *A. repandus* from the New Hebrides) which could well have been left in *Eranthemum*

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* In his *Flora Telluriana* 4 : 64, n.986 (1838), Rafinesque with customary recklessness also published a genus *Crateola* to include two little-known species, " Types the J. *vincoides,* J. *parviflora* Ortega non Retz.", of which he had read the brief descriptions in Vahl, Enum. Plant. 1 : 166–167 (1804), and characterized it as "diff. *Justica,* cor. hypocraterif. tubo brevis basi inflato, limbo plano 5 lobo vel 5 partito equalis ". As Vahl described the corolla of *Justicia vincoides* Lam. as " infundibiliformis "(its tube is in fact narrowly cylindric and not swollen at base) but stated that *J. parviflora* Ortega had "corollae tubus basi ampliatus ", I accordingly designate *J. parviflora* as the lectotype of *Crateola* Raf. Nees placed this obscure species in the genus *Dipteracanthus* Nees (1832), although Hemsley suggested that it might belong to *Hemigraphis* Nees (1847). The name *Crateola* thus typified cannot displace either *Oplonia* or *Forsythiopsis* ; should it compete with *Hemigraphis,* the latter name should be conserved.

(see p. 320) as accepted then.* In 1920 Britton and Millspaugh designated *Anthacanthus spinosus* (*Justicia spinosa* Jacq.) as the lectotype of *Anthacanthus*. Since, however, the genus *Anthacanthus* as originally circumscribed by Nees included the designated type of *Oplonia* Raf., the name *Anthacanthus* was technically a superfluous name when published and its type has always been *Justicia spinosa* Jacq. (see *Int. Code Bot. Nomencl.* Art 7, Note 4.)

Subsequent botanists dealing with the family *Acanthaceae* have maintained the genus and, with the exception of Otto Kuntze, have adopted the name *Anthacanthus* for it. In 1839 Endlicher divided the genus *Eranthemum* into three groups of unspecified rank, namely *Euranthemum* of the East Indies, *Planetanthemum* of Africa and Australia and *Hesperanthemum* of the West Indies. He did not list their species but his group *Hesperanthemum*, comprising " frutices antillani spinosi " with " pedunculi axillares, subuniflori ", obviously refers to the group typified by *Eranthemum spinosum* (Jacq.) R.Br. ex Roem. & Schult., i.e. *Justicia spinosa* Jacq. Kuntze raised this group to generic rank in 1891 as *Hesperanthemum*, thereby creating a superfluous new name. At the same time, obviously knowing nothing about the plants themselves covered by this nomenclatural exercise, Kuntze described as *Jasminum coeruleum* the only one he himself had collected on St. Thomas in the West Indies. As pointed out by Green (1969), there are no *Jasminum* species native to the New World, *J. fluminense* Vell. being a naturalized African species, and Kuntze's *Jasminum coeruleum* is here regarded as conspecific with *Oplonia spinosa*.

Although the genus *Oplonia* is easily recognised and defined, the species are far otherwise. Gustav Lindau in 1895 described it as having " 6 (oder mehr) schwer zu trennende, westindische Arten ". The difficulty of separating the nine species named by earlier authors led him in 1900 to reduce them to three distinguished on characters so unreliable that he might just as well have been content with one. Lindau regarded *A. armatus* as a species endemic to Jamaica, which it is, but he treated *A. acicularis*, in fact also a Jamaican endemic, as " eine sehr variabele Species " extending from the Bahamas over Cuba, Jamaica, Hispaniola, St. Thomas and Antigua to Guadeloupe and Marie Galante. To *A. spinosus* he attributed a similar range, from the Bahamas over the Greater and Lesser Antilles to Guadeloupe and Martinique. Specimens with puberulous flowers he referred to the one, those with glabrous flowers to the other, a procedure of no value whatever.

Meanwhile Lindau described in 1897 a new genus *Psilanthele*, based on a new species , *P. eggersii*, collected by Baron Henrik Eggers (*Eggers 15129*) in the province Manabi of Ecuador, which has very small flowers, the corolla being about 4 mm. long, in 10–20-flowered raceme-like panicles terminating axillary shoots (Pl. 47). The generic name, unexplained by Lindau, is evidently from ψιλός, " smooth, bare ", ἀνθήλη, " blossom, panicle ". Since he considered its pollen to be of the " Rahmenpollen " type typical of the *Graptophylleae*, whereas *Anthacanthus* and *Odonto-*

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* As accepted by Nees, the genus *Eranthemum* L., of which the type species is *E. capense* L., included not only species of *Eranthemum* sensu stricto (*Daedalacanthus* T. Anderson) but also of *Pseuderanthemum* Radlkofer (" *Eranthemum* " sensu T. Andersoni, non L.), as explained by Stapf in *Bot. Mag.* 135 : t.8239 (1909) and *Ruspolia* Lindau (cf. Milne-Redhead in *Kew Bull.* 1936 : 255–274 (1936)). *Oplonia*, *Psilanthele* and *Odontonema* are related to *Pseuderanthemum* and not to *Eranthemum*, of which one species, *E. pulchellum* Andrews (*E. nervosum* (Vahl) R. Br. ex Roem. & Schult., *Daedalacanthus nervosus* (Vahl) T. Anderson), is naturalized in the West Indies.

nema were characterized by " Spangenpollen ", Lindau did not associate it with the latter but with *Carlowrightia*, *Anisacanthus* and *Harpochilus*.

In 1904 Lindau added to his genus *Psilanthele* a second species, *P. grandiflora* (Pl. 42) collected by Ernst Ule (*Ule 6493*) in north-eastern Peru, which differed from the type-species in having larger flowers, the corolla being about 1 cm. long, in condensed axillary fascicles. He noted that this had two minute staminodes and " pollinis granula typica, fere globosa, c. 38 μ diam. " In the following account, *Psilanthele* is restricted to its type species and *P. grandiflora* is transferred to *Oplonia*.

The extensive collections made by William Harris in the interior of Jamaica brought to Lindau's attention a species agreeing in its contracted inflorescence with the Peruvian *P. grandiflora* but having larger flowers, the corolla being nearly 2 cm. long, although with " pollinis granula iis *Graptophyllearum* conformia, subglobosa, 46–50 μ diam. " Lindau named this *P. jamaicensis* in 1908. That year Harris collected material of an allied plant on the coast of Jamaica which Lindau described in 1912 as *P. minor* (Text-fig. 1). He then pointed out that *Psilanthele* resembled *Anthacanthus* so closely in habit and flower that only the constant lack of spines in the former and a difference in pollen separated them : " *Psilanthele* zeigt stets deutlichen Rahmenpollen, *Anthacanthus* nur Spangenpollen ". A Jamaican specimen without spines (*Harris 10224*) and identical with *P. minor* but possessing " Spangenpollen " he accordingly referred to *Anthacanthus*. Lindau took this as evidence of the over-riding importance of the character of the pollen grain, as opposed to general resemblance, in the classification of the *Acanthaceae*. With equal cogency he could have taken it to exemplify the danger of over-emphasis on a slight difference in the marking of the pollen grain when countered by resemblances in everything else.

Increase in the number of specimens available for study has increased, not lessened, the difficulty of defining taxa within this group. When travelling and collecting in Jamaica in 1955–56 (cf. Stearn, 1959) I collected specimens of these plants in many parts of the island. A low-growing white-flowered species occurring in the parishes of St. Thomas and Portland, subsequently identified as Swartz's *Justicia acicularis* (now *Oplonia acicularis*), was easily recognizable in the field as distinct from the other members of the genus ; a taller-growing species, now referred to *O. microphylla*, with very small leaves and pale lilac flowers found on coastal limestone near Kingston has also a distinctive appearance. The large leaves and numerous flowers of *O. jamaicensis* set this apart from the others, as regards which there appeared to be no evident pattern of variation with convenient discontinuities. Instead the specimens collected merely indicated the existence of numerous local populations, probably themselves more or less homogeneous and with their own assemblage of minute characters but not well differentiated from other local populations. Preparation of an account of the *Acanthaceae* for the continuation of Fawcett and Rendle's *Flora of Jamaica* made it necessary to classify this bewildering and exasperating material. Questions of nomenclature then arose, which involved taxonomic decisions ; whether, for example, early names based on material from other West Indian islands could be applied to Jamaican taxa. In dealing with these it became painfully clear that a revision of the group over its whole range from the Bahamas to the Grenadines and into Peru could not be avoided. The present paper is the outcome of this survey and is based on about 250 gatherings. In 1900 Lindau based his account on some 60 gatherings ; Nees von Esenbeck in 1847 had about 12 gatherings. The close resemblance of Jamaican species placed in *Oplonia* and Madagascan species placed in *Forsythiopsis* was quite unexpected and did not become evident until long after the completion of the account of the American group.

TAXIONOMIC CHARACTER

Lindau (1900) wrote of his " *Anthacanthus acicularis* " that it was " eine sehr variabele Species, sowohl was Behaarung wie auch Blattgrösse betrifft. Dadurch, dass die Dornen bald lang bald kurz, bald gerade abstehend oder im Winkel abstehend, bald etwas gebogen, bald sehr dünn, bald holzig dick sind, wechselt der Habitus ungemein. " Within this he included the plants distinguished by other authors as *Anthacanthus microphyllus*, *A. cuneatus*, *A. lycioides*, *A. purpurascens* and *A. tetrastichus*, although not, as it happens, any specimens of the true *A. acicularis*! He thus dismissed as having no taxonomic value their diversity in form and length of spines. Of his *A. spinosus* he wrote similarly ; " Ebenso wie vorige Art sehr variabel im Habitus. Die Veränderlichkeit erstreckt sich auf die Stacheln und die Blätter ". He was left with " flores ± puberuli " as the distinguishing feature of *A. acicularis* and " flores semper glaberrimi " of *A. spinosus*. The characters mentioned above cover the major variation within the genus. They may be summarized as follows :

Habit of Growth.
Most members of the genus are shrubs up to 2 metres high. The extremes are represented by *Oplonia nannophylla* (Pl. 45) of Cuba, a shrublet only 4–8 cm. high with internodes 1–3 mm. long, and *O. armata* var. *pallidior* of Jamaica, which may grow into a small tree. Possibly each species when living has a distinctive habit. As noted above, I found *O. acicularis* easily recognizable in Jamaica by its low, much-branched growth as well as by its white flowers.

Pubescence of Branches and Spines.
With age the shoots of *Oplonia* lose their original epidermis, this being replaced by a thin bark, and become glabrous. As in *Thymus* (*Labiatae*) and *Epilobium* (*Onagraceae*), the young four-sided stems may be holotrichous, i.e. with hairs on all sides, or goniotrichous, i.e. with the two opposite sides immediately below the leaves glabrous and the two opposite intervening sides hairy, their position thus alternating from node to node. The hairs themselves may be relatively long (up to 0·5 mm. long) or much shorter (down to 0·1 mm. long), dense or sparse, horizontally spreading or slightly or distinctly upcurved.

Variation in the pubescence of shoots is well illustrated by a series of specimens belonging to a small-leaved taxon (here included in *Oplonia microphylla*) which grows on the dry limestone over a limited area of south-eastern Jamaica near Kingston (Text-fig. 2J–M). The type-specimen of *Anthacanthus cuneatus* Nees (*Macfadyen s. n.* in Herb. Kew) exemplifies one extreme : white spreading hairs up to 0·5 mm. long cover densely all four sides of the shoots, while the spines are densely pubescent with

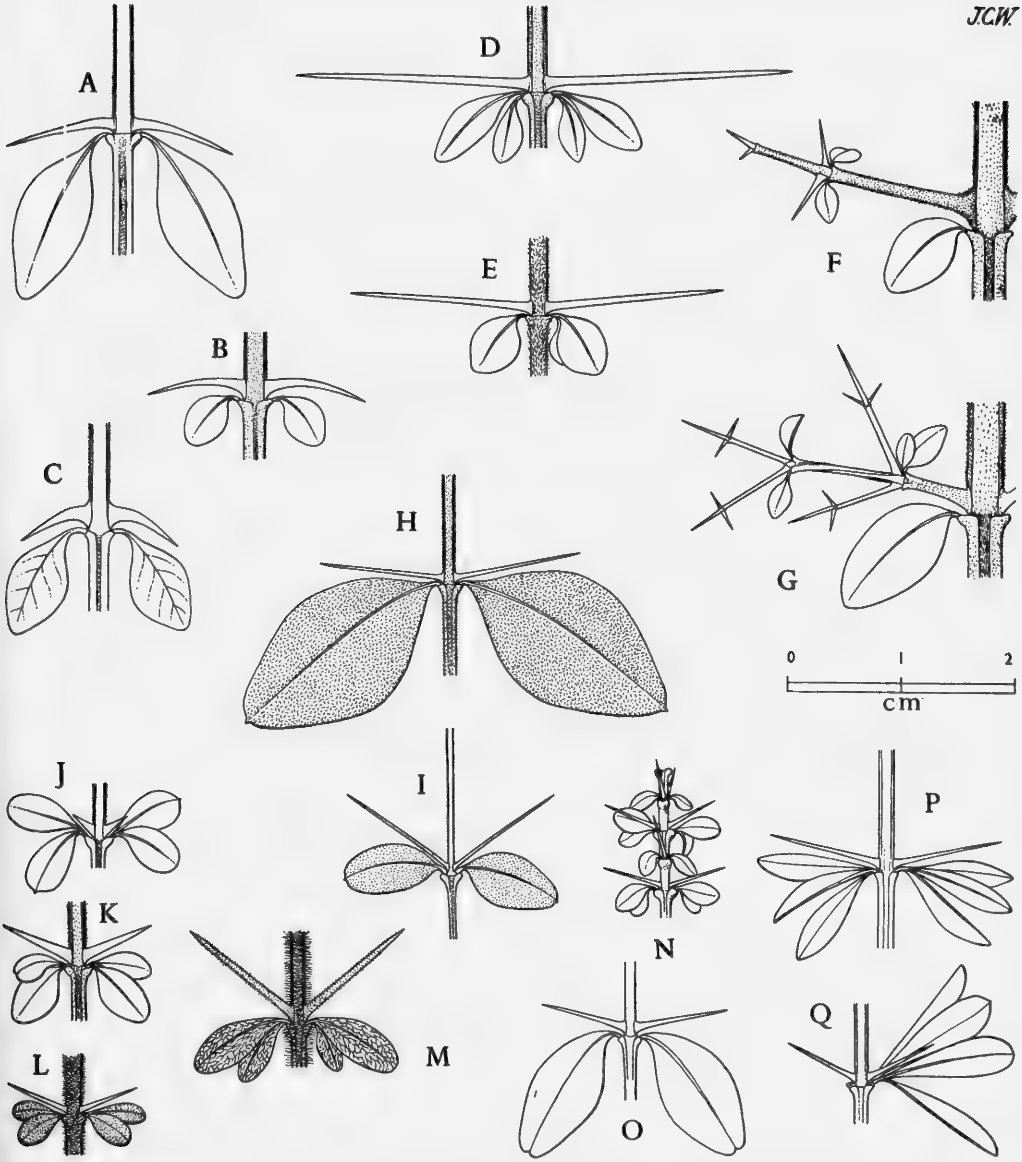

FIG. 2. Spines and leaves of *Oplonia* : A,B,C, *O. spinosa* (Jacq.) Raf. (A, *Buch 1851*, Haiti ; B, *Curtiss 133*, New Providence ; C, *Marie-Victorin et al. 21625*, Cuba) ; D,E, *O. tetrasticha* (Griseb.) Stearn var. *tetrasticha* (D, *Proctor 16430*, Cuba ; E, isotype, *Wright 3067*, Cuba) ; F,G, *O. tetrasticha* var. *polyece* Stearn (F, *Clemente 5014*, Cuba ; G, holotype, *Clemente 5657*, Cuba) ; H,I, *O. acicularis* (Swartz) Stearn (H, authentic specimen, *Swartz*, Jamaica ; I, *Stearn 498*, Jamaica) ; J,K,L,M, *O. microphylla* (Lam.) Stearn (J, isotype, *Richard*, St. Croix ; K, *Howard 10916*, Grenadines ; L, *Araque-Molina & Barkley 22J448*, Jamaica ; M, holotype of *Anthacanthus cuneatus*, *Macfadyen*, Jamaica) ; N, *O. nannophylla* (Urban) Stearn (holotype, *Ekman 16532*, Cuba) ; O, *O. armata* var. *pallidior* Stearn (*Stearn 863*, Jamaica) ; P,Q, *O. purpurascens* (Griseb.) Stearn (isotypes, *Wright 3066*, Cuba) ; all × 1½. Cystoliths are present on all leaves but are indicated only in figs. H and I.

shorter hairs. Similar abundant pubescence of branches and spines occurs in *Araque-Molina & Barkley 22J448* and *Proctor 10195*, both gatherings from near localities in Kingston and St. Thomas ; *Proctor 9971* and *Asprey 2059* from St. Catherine and *Proctor 18268* from St. Thomas have the shoots likewise densely hairy but the spines glabrous ; *Harris 9606, Proctor 11436, Stearn 66*, and *Stearn 830*, all from the Long Mountain, Kingston and St. Andrew, have two opposite sides densely hairy but the other two sides almost glabrous and the spines glabrous. In *Harris 8609* from St. Andrew the hairs are much more abundant on two opposite sides than on the intervening sides but the hairs are only 0·1 to 0·2 mm. long. Thus three types of hair covering, which in some genera, e.g. *Thymus*, would be taken as evidence of specific distinctness, here occur on plants of similar habit growing under similar conditions in the same region.

Spines.

The spines of *Oplonia* (Text-fig. 2 ; Pl. 45) are reduced shoots ; hence they arise singly and opposite one another in the axils of leaves, each node having but one pair. The apparent exception, Grisebach's *Anthacanthus bispinosus* with two pairs of spines at a node, does not belong to *Oplonia*, its spines being modified leaves, and proves to be *Barleriola solanifolia* (L.) Oerstedt, specimens of which may be found in herbaria determined as *Anthacanthus spinosus* (e.g. *J. H. Jack 5596*) and *A. tetrastichus* (e.g. *A. Gonzales 672*). Spines appear to be constantly absent from the mesophytic *O. jamaicensis* and *O. grandiflora*. Among the specimens referred to *O. armata* var. *pallidior* some have no spines, other have well developed spines ; indeed the same bush may bear spiny and spineless shoots, as on *Stearn 863* from St. Elizabeth. Spines are usually well developed in the xerophytic species. They then supply some conspicuous diagnostic characters. Thus spines spreading horizontally but with a slight downward curve or curved so strongly as to be hooked or deflexed characterize *O. spinosa* as accepted here. Such spines are found on specimens collected from the Bahamas to the Virgin Islands but not on any Jamaican specimens. Very long, straight, usually stout and rigid spines, varying between 1 cm. and 3·5 cm. in length, distinguish *O. tetrasticha* of Cuba ; spines more than 1·4 cm. long are unknown outside Cuba. Spines very slender for their length, i.e. 8 mm. to 14 mm. long but about 0·3 mm. thick, help to give *O. acicularis* of Jamaica its distinctive habit. In *O. microphylla* they are shorter and more rigid. The development of pairs of short subsidiary spines on the ordinary spines is characteristic of *O. tetrasticha* var. *polyece*. The Madagascan species have no spines.

Leaves.

The largest leaves of the genus are found in *O. grandiflora* (Pl. 42) and *O. jamaicensis* where they vary on the same plant from 2 cm. to 10 cm. in length and to 3 cm. or more in width. At the other extreme are *O. nannophylla, O. linifolia* and *O. microphylla* with leaves only 2–10 mm. long. On many specimens the leaves seem fairly constant in size and shape but on others there may be remarkable diversity. Thus a gathering made on St. John, Virgin Islands (*Robertson 26*), here referred to *O. spinosa*, has the leaves almost circular or very broadly ovate, the length and breadth being almost the same with the greatest breadth at or below the middle. On a gathering by A. C. Smith (*A. C. Smith 10562*) from Virgin Gorda, Virgin Islands, also referred to *O. spinosa*, some leaves are likewise broadly ovate but others are elliptic or narrowly obovate, i.e. proportionally narrower with the greatest breadth at or above the middle. Such specimens connect with the narrowly elliptic and oblanceolate leaves of *O. spinosa* on specimens collected in Haiti and the Bahamas. The apex of the leaf is acute to acuminate in *O. acuminata* and *O. grandiflora*. The Madagascan *O. linifolia* has linear leaves. The others have the apex itself rounded and usually slightly or distinctly indented, sometimes with a distinct mucro.

The veining (Pl. 43b) is evident in some specimens, faint or invisible in others, and seemed at first to offer characters of possible taxonomic value. Using the clearing technique described by Arnott (1959), preparations were made of leaves from a diversity of plants, these inserted in a microfiche viewer, and their veining then drawn on a vastly enlarged scale. It proved to be brachydromous in all, i.e. with about 6 to 11 lateral veins on each side of the midrib running slightly obliquely almost to the margin, then bending abruptly forward and joining the bend of the lateral vein immediately above, thus making a closed series of loops more or less parallel to the margin. Variation in the number of veins and their angle of divergence from the midrib was slight.

Number of Flowers.

The inflorescence of *Oplonia* occasionally develops into a short lateral raceme but is usually reduced to a sessile axillary fascicle, which may bear up to 15 flowers in the large-leaved *O. jamaicensis* but is commonly only one- or two-flowered in species with leaves less than 2·5 cm. long.

Pedicels.

The pedicels are mostly much longer than the calyx and up to 1 cm. long. In *O. purpurascens*, however, the flowers are almost sessile with pedicels 1–1·5 mm. long and thus shorter than the 3–4 mm.-long calyx. Specimens of *O. microphylla* sometimes have pedicels as short, but longer pedicels are usually to be found on the same plant. They are usually glabrous, but occasional individuals have hairs on the pedicels.

Calyx.

The calyx is parted almost to the base into 5 narrow segments which are linear in *O. grandiflora* but very narrowly triangular (subulate) in the others. The calyx is usually about 3·5 mm. long. Its length does not seem correlated with other characters. In specimens referred to *O. armata* var. *pallidior* it varies from 2 mm. (*Howard, Proctor & Stearn 14740, Norman 100*) to 5 mm. (*Stearn 863*).

Corolla

The corolla (Text-fig. 1, 3) is surprisingly uniform in size and form and consists of a slender tube slightly expanded above the insertion of the stamens on its upper part and a spreading two-lipped limb with two ascending more or less fused upper lobes and three descending distinct lower lobes. Tube and limb are almost equal in length. In *O. grandiflora*, so inappropriately named, the tube is only 4–4·5 mm. long, in *O. acicularis* 4–6·5 mm., in the others 6–10 mm. long. Although Lindau clutched at the presence or absence of hairs on the corolla in despair of finding any other character for specific distinction, this seems of trivial value. The hairs are very small and are present or absent without correlation with any other characters.

The red colour of the corolla of *O. armata* var. *armata* readily distinguishes it in a living state from all other members of the genus. In these the corolla is mostly a bluish lilac or bright purple having at the base of the lower lip a pale area marked with dots or streaks of purple, which presumably serve as nectar guides. In *O. acicularis* the corolla is normally white.

Length of Stamens and Style

In some flowers of *Oplonia* the stamens project conspicuously from the tube of the corolla, in others they scarcely reach beyond its mouth (Text-fig. 3). This diversity seemed at first to offer welcome specific characters but undoubtedly expresses floral dimorphism, merely separating individuals within the same population, such as occurs in many gamopetalous families, notably the *Rubiaceae* (cf. Burck, 1883–4 ; Bahadur, 1963), although not previously recorded for the family *Acanthaceae*. Thus

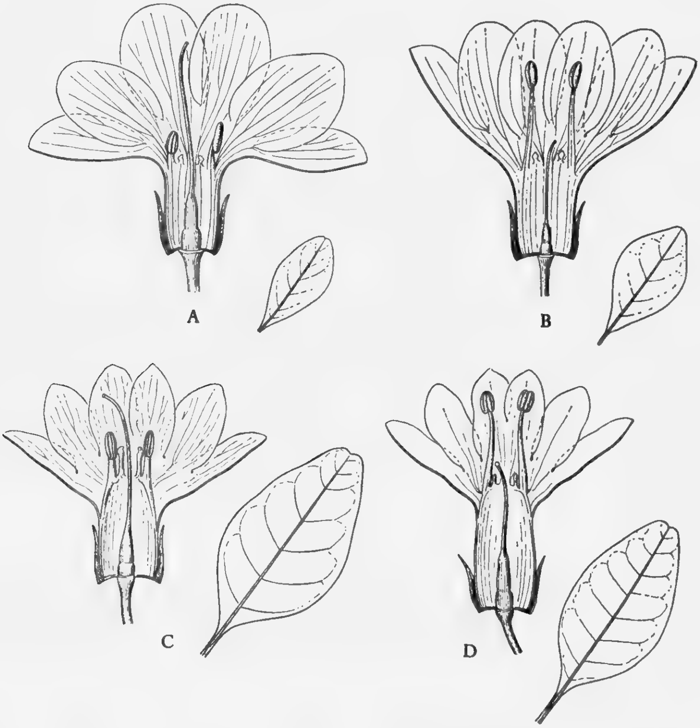

FIG. 3. Floral dimorphism in *Oplonia armata* (Swartz) Stearn ; flower cut lengthwise : A,B, *O. armata* var. *pallidior* Stearn (A, *Adams 11147*, Round Hill, Clarendon, Jamaica ; B, *Adams 11143*, same locality) ; C,D, *O. armata* var. *armata* (C, *Adams 11062*, between Aenon Town and McKay, Clarendon, Jamaica ; D, *Adams 11060*, same locality). Flower, × 2, leaves × 1.

in the specimens of south-eastern Jamaica mentioned above as referred to *O. microphylla* and agreeing closely in habit, some have short stamens and long styles, others long stamens and shorter styles. For example, *Proctor 18268* from St. Thomas, *Harris 8609* from Kingston and St. Andrew, *Asprey 2059* and *Proctor 9971* from St. Catherine have the filaments about 1·2–1·5 mm. long, the style 7–9 mm. long. *Araque-Molina & Barkley 22J448* from St. Thomas, *Proctor 11436*, *Stearn 66* and *Stearn 830* from Kingston and St. Andrew have the filaments about 5–5·5 mm. long, the style 4·5–5 mm. long. Both types occur on the Long Mountain near Kingston. Among specimens of *O. armata* var. *pallidior*, *Stearn 726* has the filaments 1·5 mm. long, the style 10 mm. long, but *Proctor 16655* has the filaments 5·5 mm. long, the style 6 mm. long. Likewise, of specimens of *O. armata* var. *pallidior* collected by Dr. C. D. Adams on Round Hill, Clarendon on 13 May 1962, *Adams 11147* has long-exserted stamens and a short style, *Adams 11143* short stamens and a long-exserted style (Text-fig. 3, A,B). Similar dimorphism is found in *O. armata* var. *armata* collected by Adams between Aenon Town and McKay, Clarendon, *Adams 11062* (with light crimson corolla) having long-exserted stamens and a short style, *Adams 11060* (with rich-violet corolla), short stamens and a long-exserted style (Text-fig. 3, C, D).

The same floral dimorphism is evident in Cuban material of *O. spinosa* all from the Moa region of Oriente province. Thus *Victorin, Clemente & Alain 21621* and *21625* have the filaments about 2 mm. long, the style 10 mm. long, but in *Clemente 3665* and *3646* the filaments are about 4·5 mm. long, the style about 5–6·5 mm. long. Such floral dimorphism probably occurs throughout the genus ; several specimens agreeing in other respects and from the same district or, better, the same locality are needed to demonstrate this. Its development is of great evolutionary interest. Its presence in *Oplonia* raises the question whether it may not have been overlooked elsewhere in the family and have thus led to unjustified separation of long-stamened and short-stamened forms as different species, although, as Darwin (1877 : 136)* pointed out, in the *Rubiaceae* " this character, which is not even of specific value in the heterostyled species, is often of generic value in other members of the family ". It also occurs in Madagascan specimens formerly placed in the genus *Forsythiopsis*. Thus in a gathering of *O. minor* (*Humbert 2506*) one specimen has the filaments about 2·5 mm. long and the style 7 mm. long, another has the filaments about 5 mm. long and the style 5 mm. long. A specimen of *O. vincoides* collected near Fort Dauphin by Cloisel (*Cloisel 209*) has the filaments about 3 mm. long, the style about 10 mm. long, while another, also from Fort Dauphin, collected by Scott Elliott (*Scott Elliott 2586*) has the filaments about 6 mm. long, the style 6–8 mm. Thus heterostylous floral dimorphism probably occurs throughout the genus.

Pollen

Lindau attributed " Spangenpollen " to *Oplonia* and " Rahmenpollen " to *Psilanthele*, using this as a generic distinction. Actually the difference between " Rahmenpollen " and " Spangenpollen " is by no means clear-cut. The pollen grains of typical species of *Oplonia* such as *O. microphylla* (Text-fig. 4) and *O. armata*

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* The " *Faramea* " described by Darwin has been discussed by H. G. Baker, " Pollen dimorphism in the Rubiaceae ", *Evolution* 10 : 23–31 (1956), 340 (1956) and proves to be *Rudgea jasminoides* Muell.-Arg.

var. *pallidior* (Pl. 38) are spheroid or prolate, 30–50 μ m. in diameter, with three germ pores each in a longitudinal furrow (mesocolpium) reaching almost to the pole, the grain thus being primarily three-furrowed (tricolpate), but with a shorter subsidiary longitudinal furrow (pseudocolpus) on each side of the main furrow ; all nine furrows are separate and do not join. They are " Spangenpollen ", as figured by Lindau (1893 : 38, fig. 1 L, t.2 fig. 62 ; 1900 : 173, fig. 12, 13), since the subsidiary furrows remain distinct and do not continue towards the poles and there fuse. In " Rahmenpollen ", as figured by Lindau (1893 : fig. 1 O, t.1 fig. 49–51 ; 1900 : 173, fig. 10, 11) and attributed by him to *Psilanthele*, the two adjacent subsidiary furrows meet near the poles, thus joining into three pairs. If these furrows converge but do not quite touch, then presumably the grain belongs to the " Spangenpollen " type (cf. Pl. 38, 40) ; if they join, then it belongs to the "Rahmenpollen" type (cf. Pl. 39).

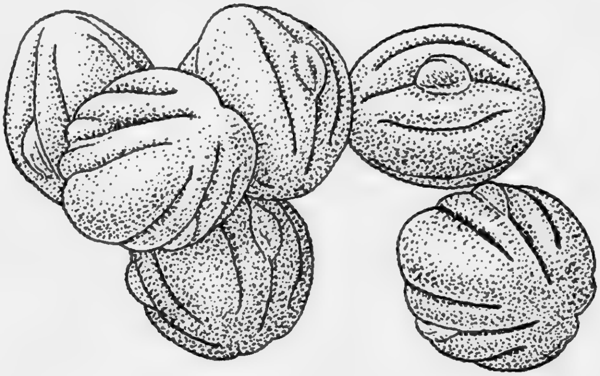

FIG. 4. Pollen grains (" Spangenpollen ") of *Oplonia microphylla* (Lam.) Stearn (*Stearn 66* ; drawing based on Stereoscan photograph), × 700.

This distinction is not always easy to observe even on grains stained and magnified × 1500, yet it is the only one, following Lindau, by which the Jamaican species referred to *Psilanthele* can be distinguished generically from *Anthacanthus*, i.e. *Oplonia*. Actually there is no difference in pollen grains between *Oplonia* and *Psilanthele*. Photographs made with the scanning electron microscope (Cambridge Instrument Co. Stereoscan), at magnifications between × 500 and × 5,700, of pollen grains of *Oplonia microphylla* (*Stearn 66*), *O. armata* var. *armata* (*Proctor 21407*), *O. armata* var. *pallidior* (*Stearn 726*), *O. acicularis* (*Britton 2894*), *O. jamaicensis* (*Harris 8968*), *O. grandiflora* (*Ule 6493*), the Madagascan *O. vincoides* (*Baron 1937*, *McWhirter & Capuron 184*) and *Psilanthele eggersii* (*Eggers 15129*) show them to be essentially uniform in form, although varying in size, with their subsidiary furrows sometimes joining but usually not quite reaching each other. The type species of *Psilanthele* (*P. eggersii* of Ecuador) differs from Lindau's Peruvian and Jamaican species not in pollen grains but in its loose inflorescence and very small flowers with the two loculi (thecae) of the anther separated a little, not absolutely parallel and contiguous as in *Oplonia*. Hence the genus *Psilanthele* is here restricted to *P. eggersii* and the other species are transferred to *Oplonia*.

Variation in size of pollen within a species can be illustrated from Jamaican material of *O. microphylla*, measurements taken by Dr. S. Sengupta from 10 grains each of 8 specimens being as follows :

1. *Proctor 18268* : diameter range 33·3 μm–36·0 μm ; spheroid.
2. *Proctor 24186* : diameter range 34·2 μm–36·0 μm ; spheroid.
3. *Stearn 66* : diameter range 31·5 μm–32·4 μm ; prolate, with length range 43·2 μm–50·4 μm.
4. *Webster, Ellis & Miller 8364* : diameter range 28·8 μm–29·7 μm ; prolate with length range 45·0 μm–49·5 μm.
5. *Harris 9606* : diameter range 28·8 μm–29·7 μm ; prolate, with length range 40·5 μm–43·2 μm.
6. *Araque-Molina & Barkley 22J448* : diameter range 32·4 μm–36·0 μm ; spheroid.
7. *Stearn 830* : diameter range 35·2 μm–37·8 μm ; prolate-spheroid, with length range 38·7 μm–40·5 μm.
8. *Proctor 9971* : diameter range 27·0 μm–28·8 μm ; prolate-spheroid, with length range 28·8 μm–32·4 μm.

TAXONOMIC PROCEDURE

As noted above, the plants of this group show diversity in habit, in length, form and direction of spines, hairiness of branches, form and size of leaves, number of flowers at an axil, length of pedicel, length of calyx, colour and pubescence of corolla, and length of filaments and style, without there being much readily evident correlation between the characters of one organ and those of another. The difficulty of perceiving associations is increased by the smallness of the organs themselves, which require examination one by one with a lens ; each character thus presents itself to the mind as a separate entity not linked with others. Lindau's treatment of 1900 brought together under one species a multitude of very unlike specimens while at the same time referring almost identical specimens to different species. Dissatisfied by this and by the evident confusion, I decided to ignore for the time being all literature about the group and all determinations on the herbarium sheets, and instead to begin anew by treating each specimen as if it were a new and independent taxon, tabulating its characters and then trying to ascertain how these were correlated with others. This proved a laborious and time-consuming procedure, despite the independent use of three complementary techniques, i.e. punched cards, metroglyphs and correlation coefficients. Firstly, characters of potential utility were recorded on marginally punched cards. These made it possible to check the distribution of characters and to test likely combinations, usually with negative results ! Secondly, a chart was made by expressing a few salient characters of each specimen (e.g. the size and shape of the leaves, the type of pubescence and the colour of the corolla) as pictorialized scatter diagrams or metroglyphs (cf. Text-fig. 7 B), following Edgar Anderson (1952 ; 1957 ; see also Hatheway, 1962.) Thirdly, with the help of Dr. P. H. A. Sneath, a range of 33 character states on 68 specimens were coded for computer-aided single-linkage cluster analysis ; Sneath then calculated their correlation coefficients (cf. Sneath, 1962) and produced a dendrogram indicating overall similarity in the characters taken. Those available in *Oplonia* fell far below the postulated minimum of forty characters and some unexpected associations resulted. Metroglyphs seemed to provide the best method of grasping the essentials of this complex taxonomic situation, punched cards a means of quickly retrieving the information, correlation coefficients a means of grouping objectively the specimens or taxa. In fact none of these methods gave a satisfying arrangement by itself. They resulted, however, in bringing together piles of specimens having many characters in common, which it had been difficult or impossible to associate by simple observation, since there were too many inconspicuous variables concerning too many specimens for them all to be kept in mind at the same time. It then became possible to take more or less homogeneous clusters of specimens and associate other specimens with them, later uniting these groups with other groups as the discontinuities between the groups were obliterated or bridged. Before this process merged the twenty or so provisional West Indian taxa into one, the dominance of an easily observable feature in a particular group and its absence from others, e.g. very small leaves, hooked or decurved spines, very long spines, numerous flowers in a fascicle, or red corolla, became evident. Most of the material could then be placed into groups characterized by these features ; ambiguous specimens were referred to them on a basis of general resemblance to already placed specimens from the same island or district. The result has led me to accept nine generally recognizable but not always clearly distinguishable American groups treated below as species.

TAXONOMETRIC SURVEY

The most difficult task when classifying apparently rather uniform biological material, such as that of *Oplonia*, wherein most distinctions lie in a diversity of minute characters neither simultaneously observable nor easily correlated, is that of putting the specimens into small relatively homogeneous groups which can later be joined into larger groups as defining attributes become evident ; obviously then, the study of such material would be eased by the use of an efficient computer-aided method of assembling the specimens into successively united groups (clusters) characterized at first by high overall resemblance between the members of each group, a resemblance which would decrease progressively as more groups were united. Hence it seemed worthwhile, as a guide for future procedure in dealing with intractable groups like *Oplonia*, to apply such methods to an assemblage of specimens of *Oplonia*.

Availability of computers and exercise of mathematical ingenuity have now led to the creation of possible numerical methods bewildering in their number and claims (cf. Johnson, 1968, for comment and extensive bibliography ; also Cole, 1969). Assessment of their respective merits for a given task must depend upon practical experience. They need to be tested by application to group upon group (cf. Stearn, 1969).

The following observations relate to a method of cluster analysis based on graph theory, to which Professor D. J. Rogers (then at the New York Botanical Garden, now at the University of Colorado) drew my attention in 1964, after the present study, mostly done in 1961–62, had been virtually completed. This method has since been expounded mathematically by Estabrook (1966) and applied by Wirth, Estabrook and Rogers (1966) to *Orchidaceae* subtribe *Oncidiinae*, by Irwin and Rogers (1967) to *Cassia* sect. *Apoucouita* and by Prance, Rogers and White (1969) to *Chrysobalanaceae* tribe *Hirtellae*. It groups objects into clusters, defined by similarity of their members, with stage-by-stage reduction in the degree of similarity necessary for objects to be placed in the same cluster. It is a process wherein hitherto unclustered objects are progressively admitted into earlier-formed clusters through linkage by resemblance to objects already in the cluster. Thus small clusters become linked to larger clusters ; as a cluster enlarges through incorporation of other clusters, so the amount of similarity between all members of the resulting cluster lessens at each stage until ultimately the objects all come together into one large cluster. The computer print-out for the whole process records it as a series of stages of clustering. The taxonomist must decide which of the intermediate stages, when there exist several or many clusters of specimens, have the most relevance to his needs.

The first task, as in other taxonometric procedures, consists of listing all the available characters and their states differing from specimen to specimen ; these are then tabulated for each specimen being studied. Comparison by the computer pairs the specimens according to their mutual similarity. This stage, the first partition, divided the material into the basic classes. The principles governing procedure, as stated by Estabrook (1966), are :

" (1) a biological classification for a collection of objects is a series of partitions for this collection, classes under later partitions consisting wholly of classes under earlier partitions. (For example, genera consist wholly of species.)

" (2) For any given partition in this series, two similar objects should not be placed in different classes (this assumes that no knowledge of evolution is available).

" (3) The classes of a given partition should be isolated from one another ; that is, there should be some phenotypic discontinuity between members of different classes. "

As the original clusters (disjoint partitions) merge into the ultimate single cluster (conjoint partition), by coming together at given degrees of lessening similarity, the greater the overall resemblance between specimens the earlier will be the stage at which they are linked into a common cluster ; conversely, the greater their divergence so much the later will be their linkage. Part of the task of preparing a taxonomic revision of a group has always been a search for such resemblances and divergences, followed by hierarchic ranking of the sub-groups detected. A machine technique quickly displaying these relations can thus significantly lessen the labour of research ; it may even indicate correlations of characters which otherwise would not have been perceived.

To test this computer-aided hierarchical clustering technique based on graph theory, the characters, 26 in all, of 35 specimens of *Oplonia* representing the geographical and morphological extremes of the group as well as numerous intermediate states were tabulated by me and then computed (using Taximetric Similarity Graph-Clustering programme on CDC 1604 computer at New York)* by Rogers, who converted the computer print-out into a series of diagrams (subgraphs), each represent-

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* This study was run on a Control Data 1604 under the direction of D. J. Rogers of the Taximetrics Laboratory then located at the New York Botanical Garden but now at the University of Colorado, Boulder, Colorado, U.S.A. The programmes are operative on IBM 7000 series + 360/75 and CDC 6400.

ing one partition of 21 stages (levels) of clustering. These specimens (to which the scientific name now adopted has been added) were as follows :

1. *Britton 2877* ;	Jamaica ;	*O. acicularis*
2. *Stearn 550* ;	Jamaica ;	*O. acicularis*
3. *Britton 2894* ;	Jamaica ;	*O. acicularis*
4. *Proctor 8433* ;	Jamaica ;	*O. jamaicensis*
5. *Stearn 454* ;	Jamaica ;	*O. jamaicensis*
6. *Harris 8968* ;	Jamaica ;	*O. jamaicensis* (isotype)
7. *Proctor 16430* ;	Cuba ;	*O. tetrasticha* var. *tetrasticha*
8. *León 3326* ;	Cuba ;	*O. tetrasticha* var. *tetrasticha*
9. *Curtiss 133* ;	Bahamas ;	*O. spinosa*
10. *Robertson 26* ;	Virgin Islands ;	*O. spinosa*
11. *Stearn 726* ;	Jamaica ;	*O. armata* var. *pallidior*
12. *Proctor 21407* ;	Jamaica ;	*O. armata* var. *armata*
13. *Box 757* ;	Antigua ;	*O. microphylla*
14. *Howard 10916* ;	Petit St. Vincent ;	*O. microphylla*
15. *Araque-Molina & Barkley 22J448* ;	Jamaica ;	*O. microphylla*
16. *Proctor 9971* ;	Jamaica ;	*O. microphylla*
17. *Stearn 830* ;	Jamaica ;	*O. microphylla*
18. *Norman 100* ;	Jamaica ;	*O. armata* var. *pallidior*
19. *Stearn 863* ;	Jamaica ;	*O. armata* var. *pallidior*
20. *Ekman 15042* ;	Cuba ;	? *O. tetrasticha* var. *tetrasticha*
21. *Marie-Victorin, Clemente & Alain 21625* ;	Cuba ;	*O. spinosa*
22. *Leonard & Leonard 13674* ;	Hispaniola ;	*O. spinosa*
23. *Valeur 724* ;	Hispaniola ;	*O. microphylla*
24. *Ekman 16534* ;	Cuba ;	*O. nannophylla* (type)
25. *Clemente 5657* ;	Cuba ;	*O. tetrasticha* var. *polyece* (type)
26. *Buch 1851* ;	Hispaniola ;	*O. spinosa*
27. *Proctor 10236* ;	Jamaica ;	*O. armata* var. *armata*
28. *Schomburgk 107* ;	Hispaniola ;	*O. spinosa*
29. *Stearn 486* ;	Jamaica ;	*O. armata* var. *armata*
30. *Wright 3067* ;	Cuba ;	*O. tetrasticha* var. *tetrasticha* (isotype)
31. *Clemente 5014* ;	Cuba ;	*O. tetrasticha* var. *polyece*
32. *Stearn 455* ;	Jamaica ;	*O. armata* var. *armata*
33. *Proctor 8830* ;	Turks & Caicos Islands ;	*O. spinosa*
34. *Stearn 498* ;	Jamaica ;	*O. acicularis*
35. *Ule 6493* ;	Peru ;	*O. grandiflora* (isotype)

Study of Rogers's series of diagrams (subgraphs) in association with the specimens themselves revealed particularly the utility of the middle stages (levels) of clustering as an aid to perceiving and distinguishing the main components of the group. Text-fig. 5, for example, represents the clustering reached at stages 6 and 12. The first partition (stage 1) made according to a very high degree of resemblance brought together the almost identical Jamaican specimens (Nos. 15, 16, 17) now referred to *O. microphylla*. By stage 6 Jamaican specimens (Nos. 11, 12 and 18, 19) now referred to *O. armata* had been placed in two clusters, Lesser Antillean specimens (Nos. 13, 14) referred to *O. microphylla* in another, Cuban specimens (Nos. 7, 8) referred to *O. tetrasticha* and Jamaican specimens (Nos. 4, 5) referred to *O. jamaicensis* in yet others. By stage 12 the grouping and linking have gone far enough to make a significant arrangement of most of the specimens. Thus Nos. 13, 14, 15, 16, 17, and 23 when put side by side agree in having very small leaves and short ascending spines and constitute a taxon for which the earliest epithet is *microphylla* ; Nos. 7, 8, 20, 25 and

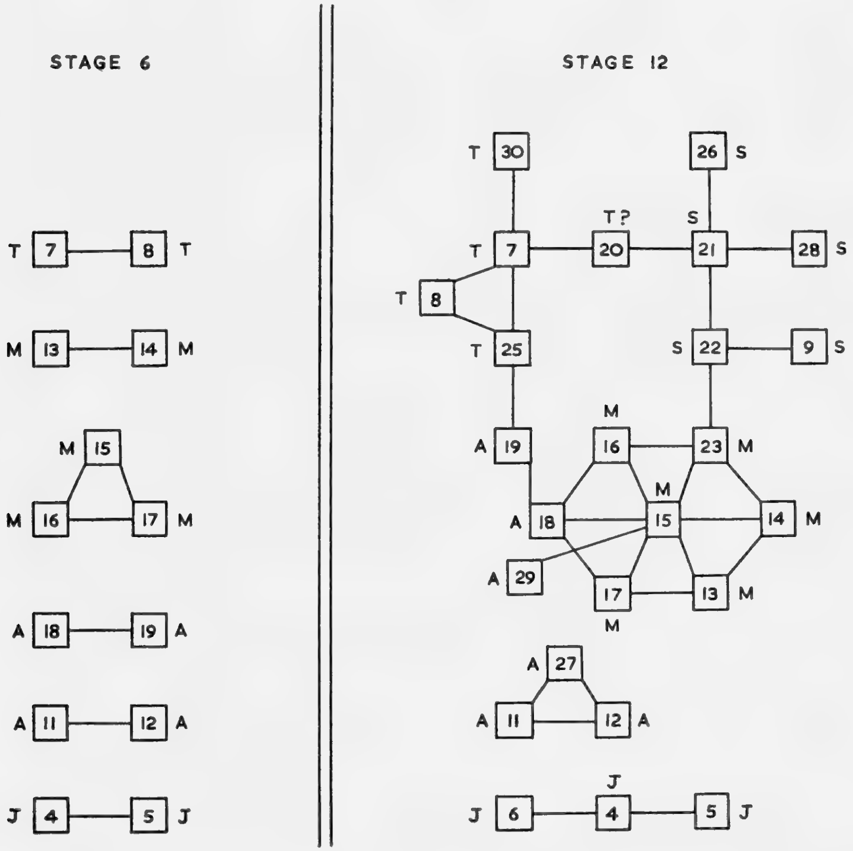


FIG. 5. Stages 6 and 12 of 1–22 sequence in cluster analysis of 35 specimens of *Oplonia* (listed by numbers on p. 276) by graph-theory method as computed by D. J. Rogers ; A, specimens classified as *O. armata* ; J, as *O. jamaicensis* ; M as *O. microphylla* ; S as *O. spinosa* ; T as *O. tetrasticha.*

30, all from Cuba, with their long straight horizontal spines form another group, for which the epithet is *tetrasticha* ; Nos. 9, 21, 22, 26, and 28 with their mostly curved horizontal or deflexed spines likewise form a group, to be called *spinosa* ; Nos. 4, 5 and 6, all from Jamaica, with large leaves and many flowers represent the easily distinguishable *jamaicensis*. Among the specimens unclustered at this stage, No. 24 (*nannophylla*), Nos. 1, 2, 3 and 34 (*acicularis*) and 35 (*grandiflora*) strike the eye as well distinct from the others, while Nos. 32 (*armata*), 10 (*spinosa*) and 33 (*armata*) show resemblance to some specimens already clustered. The last specimen to enter was No. 35 (*grandiflora*), from Peru, which accords with its morphological and geographical distinctness. The logical coherence of this grouping made me regret that the technique used had not been available much earlier ; it would have provided a means of grouping fairly quickly the specimens into the taxa ultimately adopted without so much time-consuming search for correlations. The computer run dealing with this material took 3 minutes 47 seconds, an infinitesimal amount of time compared with that of ascertaining and tabulating data and that of expressing and considering the results. The method commends itself for its graphic portrayal of classification as a stage-by-stage process and corresponds closely enough in its working to the mental acts of a working taxonomist to be able to serve as a time-saving substitute for some of them. Thus in dealing with a large confused group it is convenient to pick out various types and use these as focal points to which specimens can be referred by resemblance, thereby creating assemblages from which concepts of taxa can take shape and definitions be formulated. This computer method creates such assemblages in the same typological manner, presents them to the eye pictorially, and thus prepares the way for defining their circumscription and ascertaining the characters by which they can be distinguished.

The reasonableness of the classifications of genera (cf. Sims, 1966) and species (cf. Wilkinson, 1967 ; Stearn, 1969) produced by computation using the computer programme CLASP indicated the desirability of testing it as a means of classifying individual specimens, i.e. of arranging them into groups to be treated as species or subspecies, by taking each specimen as a separate operational taxonomic unit (OTU) for association with other specimens on a basis of overall shared characters, as had been done using the different technique outlined above. Accordingly essentially the same characters (24) of the same specimens (35, plus one of *O. purpurascens* from Cuba earlier inadvertently omitted) were coded and tabulated for computation as follows :

TWO-STATE (BINARY)

1. *Habit* : tall ; low.
2. *Internodes* : 5 mm. long or less ; more than 5 mm. long.
3. *Hairs of stem* : present ; absent.
4. *Hairs of stem* : short ; long.
5. *Hairs of stem* : on 2 sides ; on 4 sides.
6. *Spines* : present ; absent.
7. *Spines* : short ; long.
8. *Spines* : fine ; stout.

9. *Spines* : simple ; branched.
10. *Leaf-base* : cuneate ; rounded.
11. *Leaf-apex* : emarginate ; not emarginate.
12. *Leaf-apex* : mucronate ; not mucronate.
13. *Flowers* : 1 or 2 ; more than 2.
14. *Pedicel* : shorter than calyx ; longer than calyx.
15. *Pedicel* : pubescent ; glabrous.
16. *Sepals* : subulate ; linear.
17. *Corolla* : pubescent outside ; glabrous.
18. *Corolla-tube* : to 4·5 mm. ; more than 4·5 mm.

Multi-state (Qualitative)

19. *Spines* : deflexed or curved ; horizontal ; ascending.
20. *Leaf* : broadest below middle ; at middle ; above middle.
21. *Corolla* : white ; blue ; red.

Quantitative

22. *Leaf length, maximum* ; less than 12 mm. ; 12–25 mm. ; more than 25 mm.
23. *Leaf breadth, maximum* : less than 6 mm. ; 6–18 mm. ; more than 18 mm.
24. *Sepal length* : 2–2·5 mm. ; 2·5–4 mm. ; more than 4 mm.

A few specimens, being incomplete, did not provide all the information desired and these deficiencies, it was understood, had later to be kept in mind since they might affect not only the subsequent placing of such specimens but also the linkage of others ; thus Nos. 20 and 24 lacked flowers.

Computation of this data was made by Mr. G. J. S. Ross at the Rothamsted Experimental Station, Harpenden, Herts. using an Orion electronic computer. The resulting classification, as expressed in a dendrogram (cf. Text-fig. 6) and a minimum spanning tree (cf. Text-fig. 7), agreed in general with that obtained by other means and undoubtedly would have been very helpful if initially available. The anomalous placing, however, of some specimens led to re-examination of their coding. This showed that a few attributes had been originally defined somewhat ambiguously or too arbitrarily ; thus some spines intermediate in length between the undoubtedly long spines of *O. tetrasticha* and the undoubtedly short spines of *O. microphylla* had been classified as " long " for some specimens but " short " for others, thereby causing inconsistency and so making non-valid or exaggerated distinctions ; moreover a few attributes, it must be confessed, had been erroneously coded. Since variability within a population may not be evident from the relatively few specimens available in herbaria for some groups, characters were taken, from the individual specimens, which *a priori* might have been of taxonomic value but which are now known to vary from individual to individual within a population, e.g. the presence of hairs on two or four sides of the stem, on the pedicels and on the outside of the corolla. In a small sample, using few characters, these may have a distorting effect and, when the aim is to define populations, would seem best ignored. In the dendrogram a specimen (No. 6) of the very distinct *O. jamaicensis* was not associated as closely with Nos. 4 and 5 as it should have been, simply because it had pubescent instead of glabrous shoots and flowers. The anomalous placing of specimens caused by the unsatisfactory coding of a few characters indicates the closeness of affinity

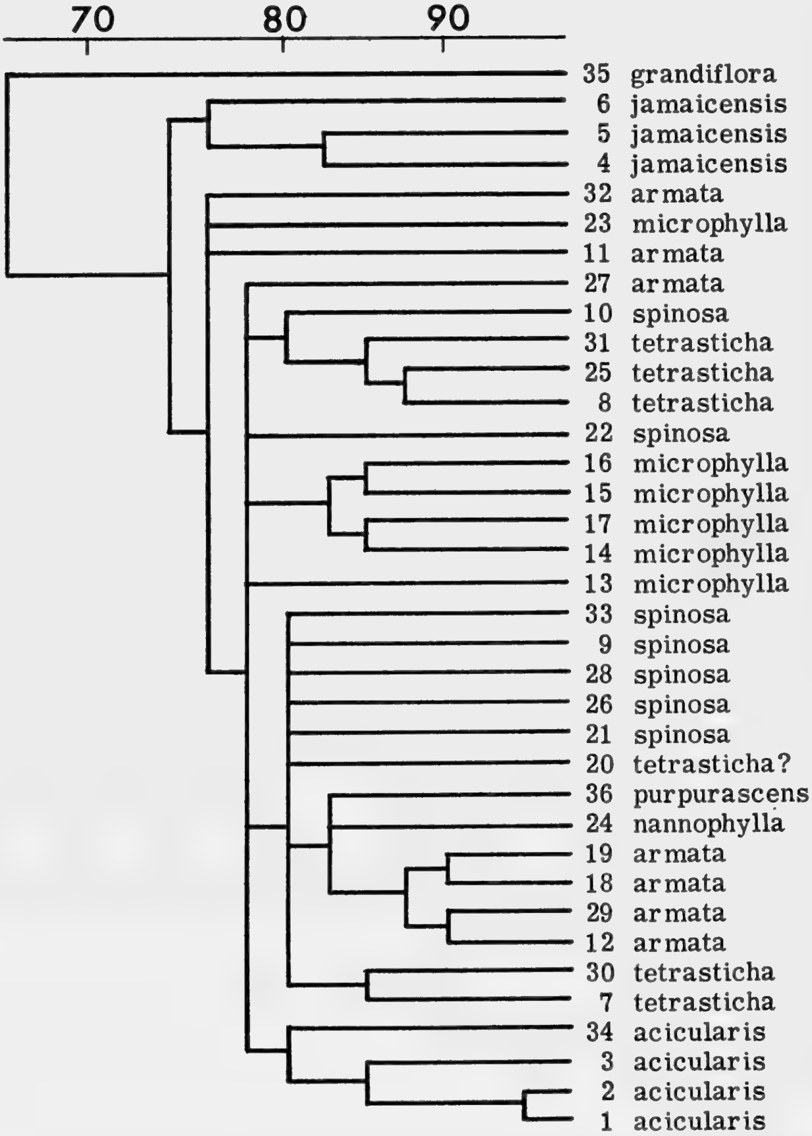


FIG. 6. Dendrogram showing overall phenetic similarity of 36 specimens of *Oplonia* (listed by numbers on p. 276) as computed from a matrix of 24 characters by G. J. S. Ross.

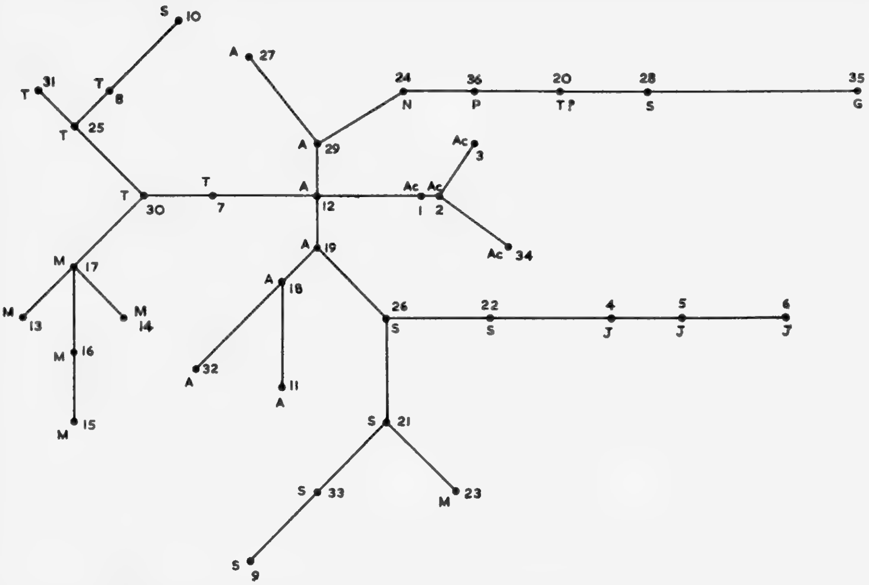
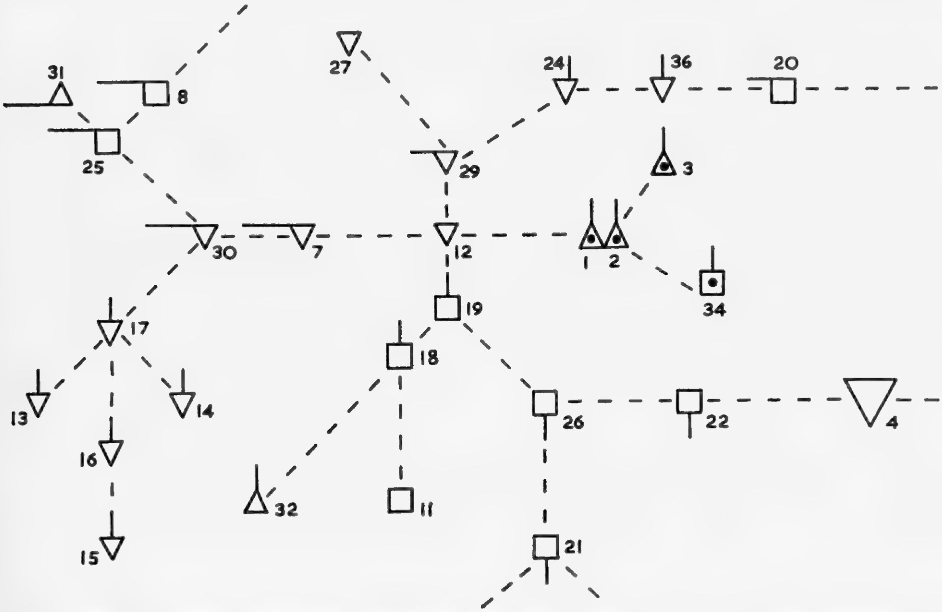


FIG. 7. (A). Minimum spanning tree uniting 36 specimens of *Oplonia* (listed by numbers on p. 276), the lengths of segments indicating phenetic distances between specimens as computed from a matrix of 24 characters by G. J. S. Ross ; A, specimens classified as *O. armata* ; Ac as *O. acicularis* ; G. as *O. grandiflora* ; J as *O. jamaicensis* ; M as *O. microphylla* ; N as *O. nannophylla* ; P as *O. purpurascens* ; S as *O. spinosa* ; T as *O. tetrasticha*.



(B). Part of above minimum spanning tree converted into pictorialized scatter diagram ; △ leaves broadest below middle, □ at middle, ▽ above middle ; | upward, spines ascending, | downward, spines downwards curved, – spines horizontal ; ● flowers white.

within the group. It also serves as a warning of the narrow margin of error in treating closely knit groups and the need for care in defining attributes so that essentially similar ones are similarly coded ; inconsistencies in these as well as slight errors of observation or recording may have their effect disproportionately magnified through lack of compensating other characters within a low range of characters. Taking, however, the dendrogram (Fig. 6) as a whole, it emphasizes the distinctness of the Peruvian *O. grandiflora* (No. 35) from the Caribbean group and it brings together enough specimens of *O. acicularis* (Nos. 1, 2, 3, 34), of *O. armata* (Nos. 12, 18, 19, 29), of *O. jamaicensis* (Nos. 4, 5, 6), of *O. microphylla* (Nos. 14, 15, 16, 17), of *O. spinosa* (Nos. 9, 21, 26, 28, 33), and of *O. tetrasticha* (Nos. 8, 25, 31, and 7, 30) to form a basis for classification, though it is not acceptable as a whole without re-allocation of some specimens.

A minimum spanning tree (cf. Gower & Ross, 1969 ; Ross in Cole, 1969) constructed from the same data provides alternative pictorial expression of phenetic linkage and distance (Text-fig. 7) when, as here, principal co-ordinate analysis does not help very much because the first five latent roots are nearly equal and a plain vector diagram (Text-fig. 8) consequently has no clearly informative pattern and gives a confused impression. It should be noted that, in a minimum spanning tree, the linkages between units and the distances separating them along the branches are significant, not the direction and relative spacing of branches which are simply a matter of convenience in drawing the diagram. Thus, in Text-fig. 7A, Nos. 1, 2, 3 and 34 are closely and directly linked but their proximity to Nos. 36 and 22 is purely coincidental and has no significance, because these are only distantly and indirectly linked, i.e. through No. 12. Here *O. grandiflora* (No. 35) is again given an isolated position. *O. jamaicensis* (Nos. 4, 5 and 6) links on to *O. spinosa* (Nos. 22, 26, 21, 33, 9) and so to *O. armata* (Nos. 19, 12, 29, 27, 18, 11, 32) which has a central pivotal place in the genus and from which some others such as *O. acicularis* (Nos. 1, 2, 3, 34), *O. tetrasticha* (Nos. 7, 30, 25, 31, 8) and *O. microphylla* (Nos. 17, 13, 14, 16, 15) as well as *O. nannophylla* (No. 24) and *O. purpurascens* (No. 30) could be derived. Anomalously placed specimens are No. 20 (incomplete, now referred to *O. tetrasticha* with doubt), No. 28 (now referred to *O. spinosa*), No. 10 (now referred to *O. spinosa*) and No. 23 (now referred to *O. microphylla*).

A minimum spanning tree or principal co-ordinate analysis graph can be converted into a pictorialized scatter diagram more helpful for correlations of characters simply by adding to each position representing a specimen certain symbols indicating character states likely to have taxonomic importance, e.g. a triangle for leaves broadest below the middle, an inverted triangle for those broadest above the middle, a red mark for red flowers, a blue one for blue, lilac or purple flowers, a dot for white ones, small symbols for small leaves, larger for large leaves, etc. (cf. Text-fig. 7B).

To utilize the results of these computer-produced diagrams in practical taxonomy the simplest procedure is to lay out the specimens on a large table in a sequence or disposition corresponding to the diagrams and then by scanning and study to find the major characters diagnostic of the groups and the discontinuities between them. Marked discontinuities are almost nonexistent in *Oplonia* but the minimum spanning tree (Text-fig. 7A) can then be seen to have eight major elements. Excluding No. 35

(*O. grandiflora*) and Nos. 5, 4, 6 (*O. jamaicensis*) on account of their very large leaves and No. 24 (*O. nannophylla*) for its condensed growth, the most evident common denominator for the specimens assembled in each other group is the character of the spine, even though in coding this accounted for only 4 of the attributes. Using spine characters for diagnosis and now considering also the provenance of the specimens, No. 28 from Hispaniola with downward-curved spines and No. 10 from the Virgin Islands with some spines likewise downward-curved fit into the *spinosa* group and No. 23 from Hispaniola with fine ascending spines fits into the *microphylla* group. The same result would have been attained had spine characters received special weighting when coded.

FIG. 8 Vector diagram showing lack of easily discernible patterns of correlated variation in 36 specimens of *Oplonia* (listed by numbers on p. 276) as computed from a matrix of 24 characters by G. J. S. Ross ; the vertical co-ordinates are the vectors corresponding to the first latent roots, the horizontal co-ordinates those of the second latent roots, of the transformed matrix.

Long experience has convinced taxonomists that characters are of unequal value in classification ; to produce a reasonable systematic arrangement by taxonometric methods they could well be unequally weighted, but unfortunately such weighting cannot usually be made before decision as to the nature of the group. Hence, since the main purpose of these methods is to aid decision-making, *a priori* weighting or advance decision would reduce their effectiveness ; characters need to be weighted *a posteriori* according to their distribution in the groups formed on the basis of overall similarity. Apparently the best course would be to accept as a basis the main groupings produced from an unweighted coding, then to investigate the content of these groups and modify them, if need be, according to the concepts of unequal taxonomic value of characters which emerge from this study.

GEOGRAPHICAL DISTRIBUTION AND ECOLOGY

The situation thus demonstrated in *Oplonia* parallels in some respects that described for the perennial species of *Ziziphora* (*Labiatae*) by I. C. Hedge (1961). The general habitat of these plants of the Near and Middle East is arid steppe and dry alpine slopes ; that of *Oplonia* is generally dry rocky slopes. In *Ziziphora* the plants are small-leaved and have small zygomorphic flowers showing sexual states which had not previously been recognized as such, again much as in *Oplonia*. The occurrence within a single *Ziziphora* population of forms having very diverse hair-covering, together with scarcely correlated differences in habit of growth, proportion of leaf, length of calyx and shape of calyx-teeth, led Hedge to the conclusion that, despite some forty specific names applied to these plants, they form one actively evolving genetic unit in which certain phenotypic trends are apparent but are not yet marked by discontinuities justifying their specific or infra-specific designation. He found it impossible to construct a satisfactory key to the variants of *Ziziphora* but accepted a number of reference points within the multiplicity of trends in variation. This likewise is largely true of *Oplonia*. Many combinations or intergradations of character are possible but some are represented by few or no individuals. *Ziziphora* inhabits a continuous landmass extending from Bulgaria over Turkey, the Caucasus and northern Persia to the Western Himalaya and the Altai mountains. The main territory of *Oplonia* is the Antillean chain of islands, most of which have long been separated from one another and others, e.g. the Lesser Antilles, have always been independent (cf. Alston, 1952 ; Schuchert, 1935). Thus conditions here favour differentiation. Cuban species, such as *Oplonia nannophylla* and *O. tetrasticha*, and Jamaican species, such as *O. acicularis*, *O. armata* and *O. jamaicensis*, individually possess morphological features unknown in the other islands. There are, however, forms extending from the Bahamas to the Virgin Islands and from Cuba to the Grenadines which do not make a homogeneous series or even a cline and do not break up into consistently distinct populations, but which include here and there forms so different that considered apart from the whole assemblage they would seem to merit specific rank and have indeed sometimes been given it. In a genus of closely allied plants, independent homologous and parallel variation is to be expected ; thus similar-looking plants of different immediate phylogeny may occur in areas remote from one another. The classification adopted here is, it is hoped, less arbitrary than

Lindau's but is likely to be arbitrary nevertheless in that, by attempting to assemble specimens linked by overall resemblance into groups which can be recognized by a few fairly well-marked and constant features and be named according to the nomenclatural types coming within their circumscription, no account is or can be taken of parallel or convergent evolution ; moreover not all specimens manifest clearly the chosen diagnostic features. With these reservations the genus, as stated above, has been divided into 14 species, which although not always easy to distinguish seem to have geographical as well as morphological justification.

The genus *Oplonia* as defined and classified here consists of one species (*O. grandiflora*) in northern Peru, three species (*O. acicularis*, *O. armata* and *O. jamaicensis*) confined to Jamaica, three species (*O. nannophylla*, *O. purpurascens* and *O. tetrasticha*) confined to Cuba, two species of much wider Antillean range, i.e. *O. spinosa*, which extends from the Bahamas over Cuba, Hispaniola and Puerto Rico (but not Jamaica) to the Virgin Islands, and *O. microphylla*, which extends from eastern Jamaica to the Grenadines in the Lesser Antilles, and, by the inclusion of *Forsythiopsis*, also five species from Madagascar. They usually inhabit the drier regions of these islands, their normal habitats being on limestone cliffs or rocky slopes thinly covered with scrub forest and thus well-drained, open and sunny. The xerophytic features characteristic of most species, i.e. the marked development of spines and reduction of leaf size and inflorescence, accord with their ecology but are uncommon within the family *Acanthaceae* as a whole. It is essentially these features of reduction which separate them from the small-flowered species of *Odontonema*, such as *O. nitidum*, which are of mesophytic habit, with relatively large leaves, numerous flowers in racemes or narrow panicles and no spines. *Psilanthele eggersii* of Ecuador approaches closest to *Odontonema*. Within *Oplonia* itself, *O. grandiflora* of Peru, *O. jamaicensis* of Jamaica and *O. acuminata* of Madagascar approximate most to the presumed archetype of the group in having a mesophytic habit, relatively large leaves, no spines and several or many flowers in axillary fascicles which are evidently condensed racemes.

The occurrence of species showing relatively primitive features, as *Psilanthele eggersii* and *Oplonia grandiflora*, within the region of northwestern South America (northern Peru, Ecuador and Colombia ; Text-fig. 9), which has been an area of major development for the *Acanthaceae*—thus 39 native genera of *Acanthaceae*, with 365 species, are recorded from Colombia by Leonard (1951–58)—points to this as being the area where *Oplonia* had its origin, even though it has reached its greatest morphological diversity in Cuba and Jamaica. It misses the Central American mainland entirely. In this it is far from unique phytogeographically. As Seifriz (1943) mentions, the plant life of Cuba shows great similarity to that of South America, less to Central America and little to North America, and the same is probably true of the other Greater Antillean islands, Jamaica, Hispaniola and Puerto Rico. There are certainly floristic links between South America and the Greater Antilles which are unlikely to have been made by way of a former land connection between Honduras and the Greater Antilles (regarding which cf. Schuchert, 1935 ; Asprey & Robbins, 1953). Thus the genus *Neriacanthus* (*Acanthaceae*) consists of *N. grandiflorus* Leonard in Colombia, *N. lehmannianus* (Lindau) Lindau in Colombia and Peru, and *N. purdieanus* Benth. in Jamaica. *Heppiella* (*Gesneriaceae*) has about ten species in tropical South America, none in Central America, *H. corymbosa* (Swartz) Urban in south-eastern Jamaica and *H. cubensis* Morton in Cuba (Oriente province). *Huertea* (*Staphyleaceae*) has one species, *H. glandulosa* Ruiz & Pavon, in Peru, none in Central America, and one, *H. cubensis* Urban, in Cuba and Hispaniola. Of the genus *Purdiaea* (*Cyrillaceae*), according to J. L. Thomas (1960, 1961), there is one species, *P. nutans* Planchon, in Peru, Colombia and Venezuela and another one, *P. belizensis* (Smith & Standl.) J. L. Thomas, in British Honduras, whereas Cuba possesses ten species, of which one, *P. cubensis* (A. Rich.) Urban, grows in the Isle of Pines and Pinar del Rio province and of which the other nine are endemic to Oriente province.

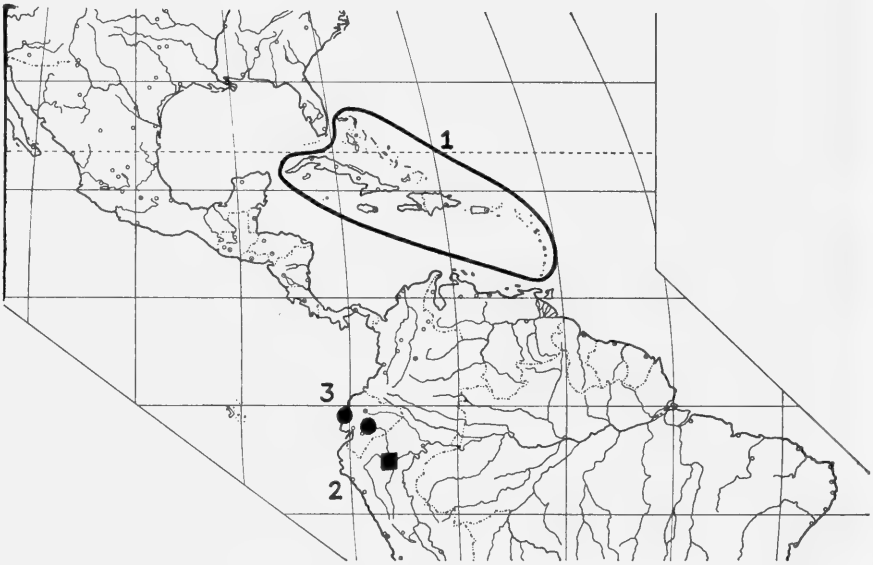


FIG. 9. Distribution of *Oplonia* and *Psilanthele* in tropical America ; 1, West Indian species of *Oplonia* ; 2, *Oplonia grandiflora* in Peru ; 3, *Psilanthele eggersii* in Ecuador. (*Goode Base Map, University of Chicago*).

Thomas (1960) states : " there are several trends of specialization in *Purdiaea* which indicate that the South American species, *P. nutans*, is the most primitive species in the genus ". The *Melastomataceae* provide further examples of floristic linkage. Thus *Clidemia grisebachii* Cogn. of Jamaica and *C. cruegerana* of Trinidad and Venezuela are closely related, likewise *Miconia nubicola* Proctor of Jamaica and certain species of the Venezuelan coastal Cordillera and the Andes with no close relatives elsewhere (J. J. Wurdack in litt.). *Henrietta sessilifolia* Triana occurs in Jamaica, Trinidad and Venezuela, *H. ramiflora* (Swartz) DC. in Jamaica, Trinidad, Venezuela, the Guianas and Brazil.

Such facts taken from a diversity of families speak for a former direct way of floristic migration between north-western South America and the Greater Antilles in which Central America had little or no part. Despite the limited collecting then available, Grisebach as long ago as 1865 alluded to such a " besondere Wanderungslinie" connecting the Andes of South America with the mountains of Jamaica and Cuba. Croizat (1952 : fig. 71), arguing largely from the distribution of some Cactaceae, also postulates a Peru–West Indies track across Venezuela direct to the Greater Antilles.

Moreover it seems improbable that the rich and diversified endemic flora of the Greater Antilles evolved on so limited an area as this flora now occupies and likewise improbable that the ancient floristic connections of the Greater Antilles and northern South America were made by long-distance leaping dispersal across the great expanse of the Caribbean Sea, although floating seeds carried by sea currents must have taken a number of coastal plants from island to island and light air-borne seeds, e.g. of members of the *Apocynaceae*, have been swept over the area by high winds. In general, the biological facts seem to favour the hypothesis that " until the end of the Cretaceous a continental landmass occupied the position of the present-day Caribbean Sea " (cf. Weyl, 1965), and this landmass (*Caribia*) subsided during the Cretaceous and Tertiary periods. The submergence of almost the whole area, including Jamaica and Cuba, by Oligocene times would have led to the extinction of the major part of its flora but much of the present Greater Antillean flora may nevertheless be descended from the plants of this lost territory which presumably both contributed to and received from the flora of South America and contributed to that of Central America. Such a hypothesis provides a plausible background to facts of Caribbean phytogeography at present otherwise inexplicable, among them the distribution of *Oplonia*. Croizat (1952 : 368) has indeed gone so far as to describe " the tale of dispersal in the Caribbeans " as " the record how a land once filling the extant sea crumbled front by front, thereby creating huge gaps in distribution. "

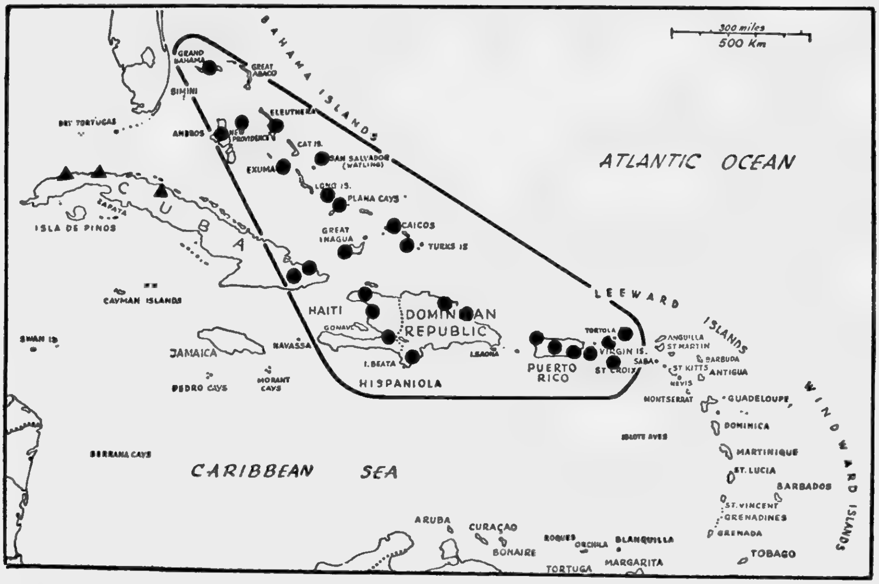


FIG. 10. Distribution of *Oplonia nannophylla* ▲ ; *O. spinosa* ●.

Jamaica and Cuba are the major islands of development for *Oplonia*. The species show different patterns of distribution (see Text-figs. 10–14).

In Jamaica, *O. microphylla* (Text-fig. 12) inhabits the very hot and dry honeycomb limestone along the southern coast from St. Thomas to St. Catherine, which has a characteristic scrub forest flora described by Asprey and Robbins (1953). *O. acicularis* (Text-fig. 12), with an evident preference for moister and even somewhat shaded habitats, has a remarkably disjunct distribution, one area in the east and another in

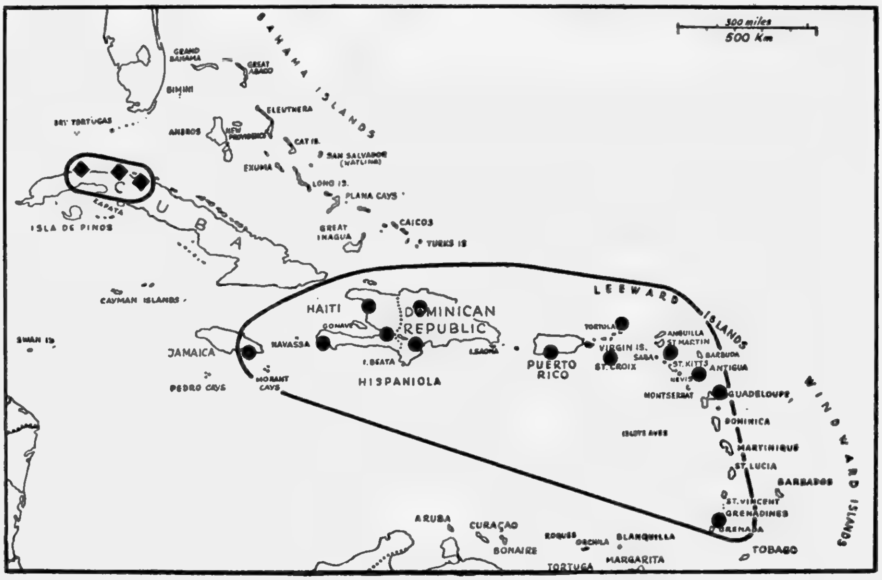


FIG. 11. Distribution of *Oplonia purpurascens* ◆ ; *O. microphylla* ●.

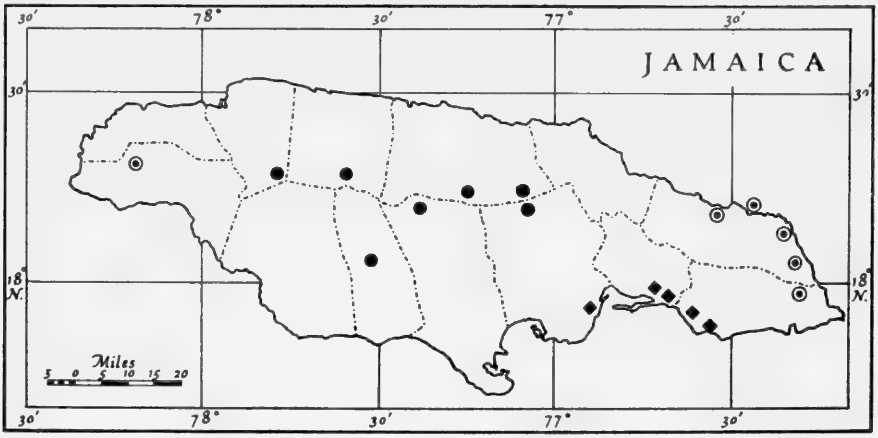


FIG. 12. Distribution of *Oplonia acicularis* ⊙ ; *O. jamaicensis* ● ; *O. microphylla* (in Jamaica) ◆.

the west but not in the middle of the island. *O. jamaicensis* (Text-fig. 12), considered the most primitive Antillean species, grows only in the moist interior upland region. *O. armata* (Text-fig. 13), as accepted here, presents much diversity in habit and leaf-form with geographical differentiation mostly in colour of the corolla. Red flowers occur only on plants inhabiting the interior (var. *armata*), paler bluish or lilac flowers only on those nearer or at the coast (var. *pallidior*).

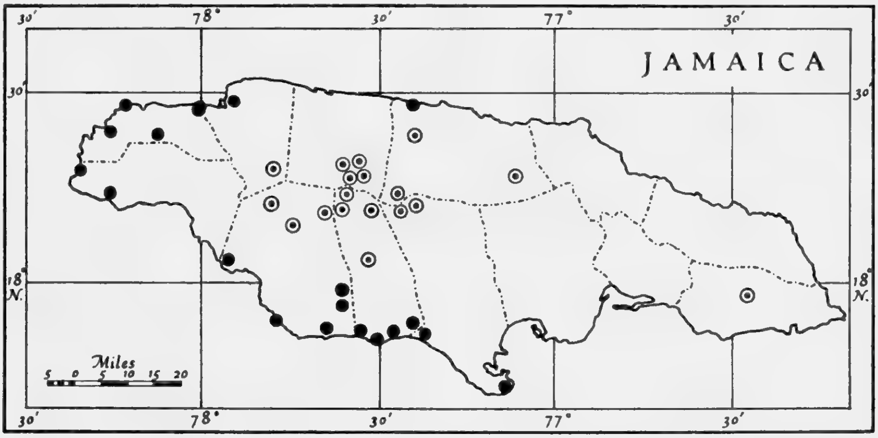


FIG. 13. Distribution of *Oplonia armata* ; var. *pallidior* ● ; var. *armata* ⊙.

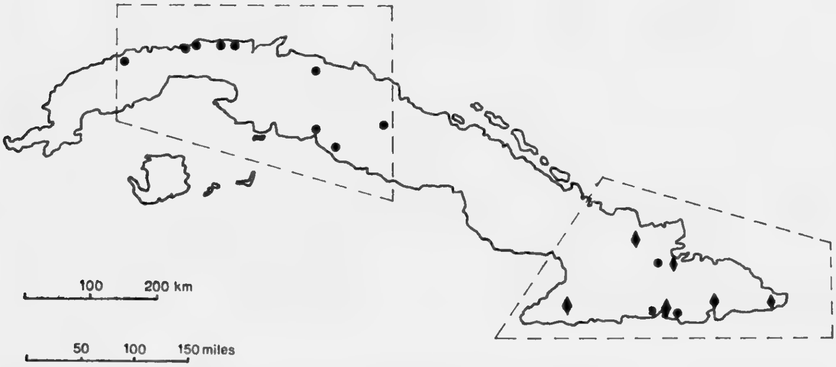


Fig. 14. Distribution of *Oplonia tetrasticha* ; var. *tetrasticha* ● ; var. *polyece* ◆.

Cuba divides conveniently into four botanical regions (cf. Conde, 1952, also Alain, 1953, 1958) ; 1 : Occidente, comprising the provinces of Pinar del Rio, Habana and Matanzas ; 2 : Las Villas, the former province of Santa Clara ; 3 : Camaguey ; 4 : Oriente. *O. purpurascens* (Text-fig. 11) is apparently endemic to the mogotes, the precipitous limestone " haystack hills " (cf. Seifriz, 1943 : 394 ; Lehmann, 1954) of Pinar del Rio around Viñales. *O. nannophylla* (Text-fig. 10) occurs in Pinar del Rio, Habana and Las Villas. *O. tetrasticha* var. *tetrasticha* (Text-fig. 14), with simple spines, likewise occurs in Pinar del Rio, Habana, Las Villas and Oriente, but is largely replaced in Oriente province, rightly described by Croizat as a "hotbed of endemism" by *O. tetrasticha* var. *polyece* with branched spines. *Oplonia* has not yet been collected in Camaguey. In Oriente occur also plants referred to *O. spinosa* (Text-fig. 10) (see p. 307), a species which extends over the low-lying Bahama Islands northward to Grand Bahama and New Providence and eastward to the Virgin Islands. Within Oriente province it appears to be confined to the Moa region on the north coast.

O. microphylla (Text-fig. 11), which has not colonized the Bahamas, extends the range of the genus beyond the Greater Antilles to the Grenadines in the Lesser Antilles, which are of volcanic origin, but it does not reach Barbados, Tobago or Trinidad. The absence of the genus from these three islands, which lie on the continental shelf of north-western South America, as also from Venezuela, makes it as improbable that it migrated from South America by way of the Lesser Antilles as that it did so along the isthmian route leading to the presumed Antillean-Honduran land bridge.

From the above survey it would appear that the genus *Oplonia* may have had its origin in South America from mesophytic shrubs resembling *Psilanthele eggersii* or small-flowered species of *Odontonema*, that it reached the Greater Antilles by way neither of Central America and the Honduran land-bridge nor of the Lesser Antilles but by a former direct long-vanished link, and that its major development has taken place in Jamaica and Cuba with little change in floral structure but with increasing vegetative adaptation to xerophytic conditions.

PHYTOGEOGRAPHICAL LINKAGE OF TROPICAL AMERICA AND MADAGASCAR

A remarkable discontinuity of range associated with little morphological divergence becomes apparent when the American species of *Oplonia* are compared with the Madagascan species currently referred to *Forsythiopsis*. Since their resemblances in habit, floral structure, capsule and pollen together leave no characters available for generic separation, they are here placed in the same genus despite their geographical remoteness. Use of different generic names for the American and Madagascan plants respectively has obscured their affinity. Baker would surely never have described *Forsythiopsis* as an independent genus in 1883 had he not then compared Baron's Madagascan specimens, the type material of *Forsythiopsis baronii* Baker, with *Ruellia* instead of with *Anthacanthus* (i.e. *Oplonia*), to which Nees von Esenbeck had already in 1847 referred Lamarck's conspecific *Justicia vincoides*, likewise from Madagascar. Moreover, the pollen of *Forsythiopsis*, as is evident from that of the holotype of *F. baronii* (*Baron 1937*), the holotype of *F. linifolia* (*Humbert & Swingle 5507*), an authentic specimen of *F. australis* (*Scott-Elliott 270*) and other specimens (*McWhirter & Capuron 184*, *Humbert 2606*) studied with the scanning electron microscope at magnifications between × 500 and 5,400, agrees with the pollen of West Indian *Oplonia* specimens ; it is prolate or spheroid, 3-colporate, each colpus flanked by a pseudo-colpus extending almost to the poles, the surface pitted with minute lumina (Pl. 41); it in no way resembles the reticulate pollen of *Ruellia*. Similar pollen occurs in *Pseuderanthemum* and also the continental African genus *Ruttya*, within which C. B. Clarke would have incorporated *Forsythiopsis*, but this has larger flowers with monothecous (unilocular) anthers (whence Hochstetter's name *Haplanthera*), possibly derived from a *Pseuderanthemum*- or a *Forsythiopsis*-like stock with dithecous (bilocular) anthers.

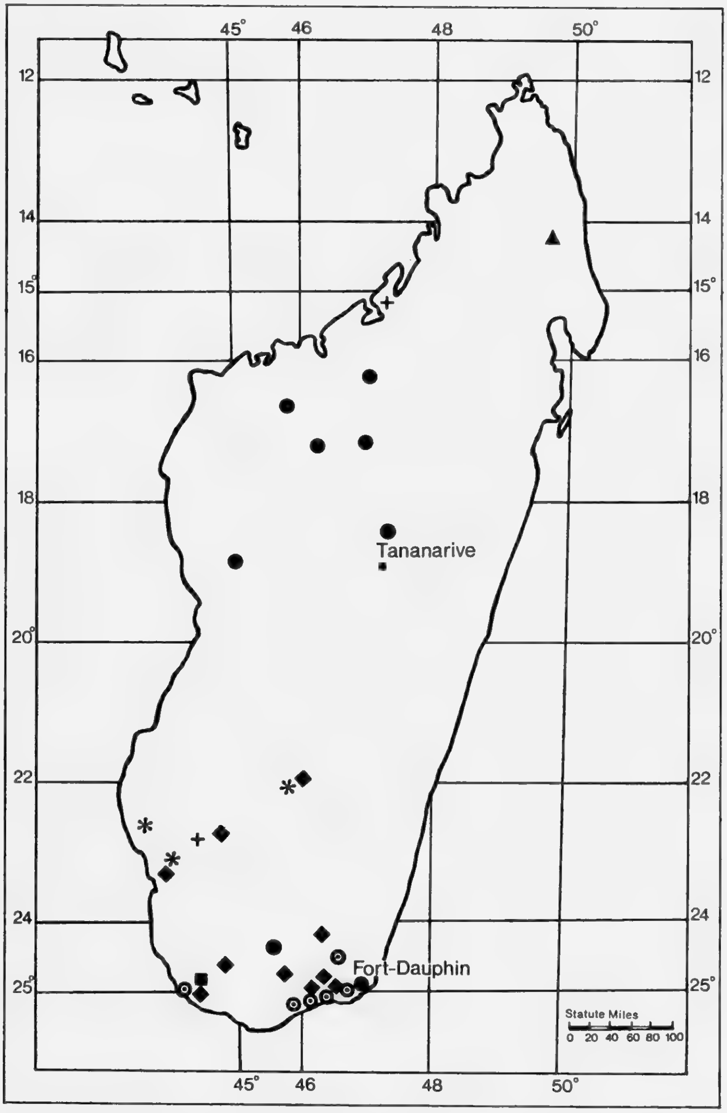


FIG. 15. Distribution of *Oplonia* in Madagascar ; *Oplonia vincoides* ● ; *O. minor* var. *minor* ◆ ; *O. minor* var. *meridionalis* ⊙ ; *O. minor* var. *vestita* ∗ ; *O. linifolia* ■ ; *O. acuminata* + ; *O. puberula* ▲.

In Madagascar (Text-fig. 15) the species grow mostly within Humbert's phytogeographical domains Sud and Ouest (cf. Blanc, 1971, for maps and climatological data), arid and semi-arid regions with open xerophytic scrub and savanna vegetation;

they thus appear to have much the same ecological requirements as most West Indian species of *Oplonia*. Madagascar, with some 400 species of *Acanthaceae* to an area of 228,000 square miles, has been a major centre of development for the family, outrivalling even Colombia, with some 370 species to 462,000 square miles.

No species congeneric with *Oplonia* (including *Forsythiopsis*) are known from continental Africa. In manifesting such discontinuity *Oplonia* does not stand alone. There are other links, few but definite, between the floras of tropical America and Madagascar which testify to a much wider primaeval range of certain groups forming part of Perrier de la Bathie's " elément austral " in the Madagascar flora, " témoins résiduels d'une flore antique en voie d'extinction " (Perrier de la Bathie, 1936 : 139–140). Thus *Ravenala* (*Musaceae*) has one species, *R. madagascariensis* Sonnerat, the well-known " Traveller's Tree " in Madagascar ; its only close ally is a species of tropical America (Brazil, Guiana), *R. guianensis* (L. C. Rich.) Petersen ; the latter having five stamens (instead of six) can be put in a genus by itself as *Phenakospermum guianense* (L. C. Rich.) Miq., but, whether the two are treated as forming one genus with two species or as two monotypic genera, their affinity and their distinctness from all other genera remain beyond dispute. *Oliganthes* (*Compositae*), with 9 species in Madagascar and 12 in tropical America but none elsewhere, provides another example of such linkage, as do *Clara* (*Herreria* Ruiz & Pavon, non Adans.; *Liliaceae*) with 5 or 6 species in South America and *Herreriopsis* with one species in Madagascar. *Gladiopappus* (*Compositae*) of Madagascar is allied exclusively to the tropical American genera *Richterago* (*Seris* Less. non Willd.), *Hyalis* and *Hecastocleis*. These anomalous ranges only become explicable when considered in relation to those of genera or groups of closely allied genera occurring not only in tropical America and Madagascar but also in continental Africa. For example, the genus *Sabicea* (including *Stipularia; Rubiaceae*) has about 50 species in tropical America (including Peru, Ecuador, Colombia and the West Indies), 85 in continental tropical Africa and 5 in Madagascar. A year before the publication of Alfred Wegener's book on continental drift, and long before it had become generally known, characters common to various American and African species of *Sabicea* led Wernham (1914) to the opinion that " the genus existed simultaneously in Africa and America as an ancestral race (*Primosabicea*) with lax inflorescence, represented at the present day by e.g. *S. venosa* in Africa and *S. paraensis* in America ". It has maintained a continuity of range in Africa, unlike, for example, the genus *Hirtella* (*Chrysobalanaceae*) with approaching 100 species in tropical America, 2 in tropical East Africa, of which one occurs in Madagascar but none in West Africa. *Mendoncia* (*Acanthaceae*) has about 90 species in tropical America, 4 in tropical West Africa (but not East Africa) and 3 in Madagascar. *Symphonia* (*Guttiferae*) is remarkable in having one species (*S. globulifera* L.f.) common to tropical America and tropical West and Central Africa and 15 species recorded from Madagascar. An even more remarkable range has been attained and maintained by *Christiana africana* DC. (*Tiliaceae* ; cf. *Kew Bull.* 17 : 501 (1964)), which occurs in tropical America, tropical West, Central and East Africa and Madagascar ; the one other species of the genus is Brazilian. *Genlisea* (*Lentibulariaceae*), with 15 species, also occurs in tropical America, tropical continental Africa and Madagascar. *Savia* (*Euphorbiaceae*) has two main centres of diversity, with 12 species in the West Indies and 9 in Madagascar, but their discontinuity is slightly lessened by 2 species in Brazil and one in South Africa ; one species extends into southern U.S.A. The *Velloziaceae* display a likewise significant pattern of distribution linking tropical America, continental Africa and Madagascar, as noted, for example, by Camp (1947). The family consists of *Vellozia* and *Barbaceniopsis*, which are exclusively tropical American, and *Barbacenia* (sensu lato, including *Xerophyta*) which has about 75 species in tropical America, about 40 species in continental Africa, 3 in Madagascar, one in southern Arabia. Several consistent features distinguish American *Barbacenia* (sensu stricto) from African *Xerophyta* ; one African species (*Vellozia elegans* Oliver of Natal), in the opinion of L. B. Smith and E. Ayensu (in litt.), constitutes an intermediate monotypic genus (*Talbotia* Balf. f., non S. Moore) combining several primitive features, which suggest that the family originated in Africa ; but whether the African species are included in *Barbacenia* or separated from it generically is irrelevant from a phytogeographical standpoint in view of the undoubted affinity of the American and African groups. A somewhat like affinity is that of *Aphelandra* (*Acanthaceae*), having about 200 species in tropical America, with *Stenandriopsis* having 5 species in tropical West Africa, one in East Africa and 8 in Madagascar (cf. Heine in Aubréville, *Fl. Gabon* 13 : 99 ; 1966). The genera *Agarista* (*Ericaceae*) and *Agauria* provide another example ; *Agarista* (cf. Stevens, 1970) has about 34 species, mostly in South America but with a few in Central America and the southern United States ; the closely allied genus *Agauria*, according to Sleumer (1938), consists of one polymorphic species divisible into 20 intergrading infraspecific taxa, a few occurring widely separated in West Africa, more on the East African mountains, most of them in Madagascar.

Equally significant is the existence of other groups connecting tropical America and Madagascar which have more restricted ranges evidently resulting from the fragmentation and reduction of former more extensive ranges. Thus the genus *Erblichia* (or *Piriqueta* sect. *Erblichia* ; *Turneraceae*) has one species in Central America, one in southern Africa, three in Madagascar. Another phytogeographically relevant group is that formed of three closely allied monotypic genera of *Compositae* described by Lawralrée (1943), i.e. *Eleutherantha* in tropical America, *Hoffmanniella* in Cameroons and Congo, *Exomiocarpon* in Madagascar. A rather similar linkage is to be found in the *Dichapetalaceae* with *Stephanopodium* in tropical America, *Tapura* in tropical America and continental Africa, *Falya* in Madagascar. The *Canellaceae*, one of the nine exclusively Amerafran families*, exemplifies the same general floristic linkage, with *Canella*, *Cinnamodendron* and *Pleodendron* in tropical America, *Warburgia* in tropical East Africa and *Cinnamosma* in Madagascar. The genus *Carpodiptera* (*Tiliaceae*) does not reach Madagascar but nevertheless manifests a distribution of the same type as *Hirtella* by having species in Central America and the West Indies, tropical East Africa, and the Comoro Islands

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* Angiosperm families occurring both in tropical America and Africa but not known elsewhere are *Bromeliaceae*, *Canellaceae*, *Caricaceae*, *Humiriaceae*, *Hydnoraceae*, *Mayacaceae*, *Rapataceae* and *Vochysiaceae* (cf. Vester, 1940 : 527–529, 567–569, maps 238–241, 245–248). *Loasaceae* and *Velloziaceae* occur in tropical America and Africa but extend from east Africa into southern Arabia (cf. Vester, 1940 ; maps 243, 244). To these can be added *Strelitziaceae* if separated from *Musaceae*.

north of Madagascar (cf. map in J. Hutchinson, *Evolution and Phylogeny of Flowering Plants* : 232 (1969)).

There are also families and genera occurring both in tropical America and West Africa (cf. Hepper, 1965) which do not reach Madagascar but nevertheless emphasize the floristic affinity of the two continents. One such is *Cienfuegosia* (cf. Fryxell, 1969) in the *Malvaceae* with 16 American and 8 African species.

Taken together these diverse ranges form a series manifesting stage by stage the reduction from a wide continuous range, such as that of *Sabicea* (America, continental Africa, Madagascar), by way of intermediate discontinuous ranges, such as those of *Erblichia* and *Hirtella*, to the extremely discontinuous ranges of *Ravenala, Oliganthes* and *Oplonia*. These floristic linkages must have had their origin in the far distant past, presumably long before the end of the Cretaceous period, when the continuity of the Amerafran landmass (cf. maps in Bullard, Everett & Smith, 1965 ; Smith & Hallam, 1970 ; Dietz & Holden, 1970), later separated into South America and Africa, still provided the opportunity for (or the narrowness of the South Atlantic Ocean made no obstacle against) the spread of extreme western-originated groups eastward across that vast landmass, the interior of which must have been very dry, however, before separation, and the spread of eastern-originated groups westward, since climatic conditions were presumably more favourable for the evolution and preservation of diversity towards the periphery than towards the centre. If so, the groups concerned have kept their generic characters, or at least many characters indicative of affinity, essentially unchanged for probably 90 million years or more ; indeed Hawkes and Smith (1965) have argued from the taxonomy and distribution of *Bromus*, *Gossypium* and *Solanum* that these genera existed already in the early Cretaceous, some 100 to possibly 135 million years ago.

Madagascar has certainly been isolated for a long time. If, as stated by Flories (1970), the rift which became the Mozambique Channel separating Madagascar from continental Africa had been completed by the end of the Cretaceous period, i.e. some 70 million years ago, at which time modern orders and families of angiosperms were already differentiated (cf. Muller, 1970), then the ancestors of the Madagascan plants whose nearest allies now inhabit tropical America must have already acquired the characters still common to the Madagascan and American plants or at least a close genetical similarity determining later parallel development. This conclusion, if correct, implies the origin of the *Acanthaceae* long before that part of the Miocene epoch, some 12–20 million years ago, to which belongs the earliest available palaeontological evidence of its existence, i.e. pollen of the *Justicia*-type named *Multiareolites formosus* and of the *Trichanthera*-type named *Multimarginites vanderhammenii* (cf. Germeraad et al., 1968: 302, t.6) from Venezuela; phytogeographical evidence indicates a Cretaceous origin.

Acceptance of the view that the angiosperms originated on the Gondwanaland continent and that many genera existing today had acquired their distinctive characteristics before it broke into several continental landmasses (cf. Melville 1966 ; Schopf, 1970) harmonizes many otherwise seemingly inexplicable facts of angiosperm distribution. The drifting apart of Africa and South America, together with the associated far-reaching climatic disturbance, must have led to the extinction or reduction of range of some groups while promoting the development and spread of others. Evidently those groups such as *Oliganthes* and *Oplonia*, now with representatives in tropical America and Madagascar but not elsewhere, owe the isolation of these to continental drift which divided the original stock into American and African populations, to the spread of the African population across Africa and over to Madagascar or of a Madagascar-originated population across Africa to America, to climatic changes, which led to extinction in continental Africa, and to peripheral survival in America and Madagascar, with the larger area and more varied habitats of tropical America favouring greater specific development and range extension.

ACKNOWLEDGMENTS

The preparation of this survey of *Oplonia* and *Psilanthele* would probably have been simpler had a revision of the whole group been planned from the start instead of undertaken reluctantly as the only way of elucidating nomenclatural problems affecting Jamaican species. No attempt has been made to borrow for study all the material available from islands other than Jamaica. My thanks are due to the directors and curators of the following institutions for the privilege of examining specimens in their charge : the Arnold Arboretum of Harvard University, Cambridge, Mass. (cited as A) : the Field Museum of Natural History, Chicago (F) ; the Gray Herbarium of Harvard University (GH) ; the Science Museum, Institute of Jamaica, Kingston, Jamaica (IJ) ; the Royal Botanic Gardens, Kew (K) ; Herbario de la Salle, Habana (LS ; temporarily deposited in NY) ; the Institute Botanique, Université de Montréal, Montreal (MT) ; the New York Botanical Garden, New York (NY) ; Laboratoire de Phanérogamie, Muséum National d'Histoire Naturelle, Paris (P) ; the Botanical Department, Naturhistoriska Riksmuseum, Stockholm (S) ; Department of Botany, University of the West Indies, Mona, Jamaica (UCWI).

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The photographs of pollen grains illustrating this paper have been made with the

" Stereoscan " electron microscope in the Electron Microscopy Unit, British Museum (Natural History) and I thank Miss P. A. Sims and Dr. S. Sengupta for their valuable technical assistance in this and other palynological work.

Miss Beatrice M. Corfe drew Text-fig. 1, Miss Joanna C. Webb (Mrs. D. Erasmus) Text-figs. 2 and 3, Mr. Derrick Erasmus Text-figs. 4 and 16 and Miss Victoria Goaman Text-figs. 17 and 18.

PSILANTHELE Lindau

Psilanthele Lindau in Bull. Herb. Boiss. 5 : 663 (1897).

Shrubs without spines. Leaves small, shortly petiolate, entire ; cystoliths present. Flowers small, pedicellate in short-pedunculate few-flowered loose raceme-like cymose inflorescences terminating short axillary branches. Bracts minute. Calyx 5-parted, c.2 mm. long, the tube very short, the segments almost equal, narrow, acute. Corolla zygomorphic, bluish, c.5 mm. long ; tube narrow, cylindric, almost straight ; limb spreading, 2-lipped, the upper lip shortly 2-lobed, the lower lip 3-parted, the segments almost equal. Stamens 2, inserted above the middle of the corolla-tube ; filaments short ; anthers with 2 spurless equal disjunct loculi ; staminodes 2, extremely minute. Pollen prolate, 3-colporate, each colpus flanked by 2 pseudocolpi, reticulate with minute lumina. Ovary with 2 ovules in each loculus ; style relatively long. Capsule clavate, stipitate, 4-seeded. Type-species by monotypy : *Psilanthele eggersii* Lindau.

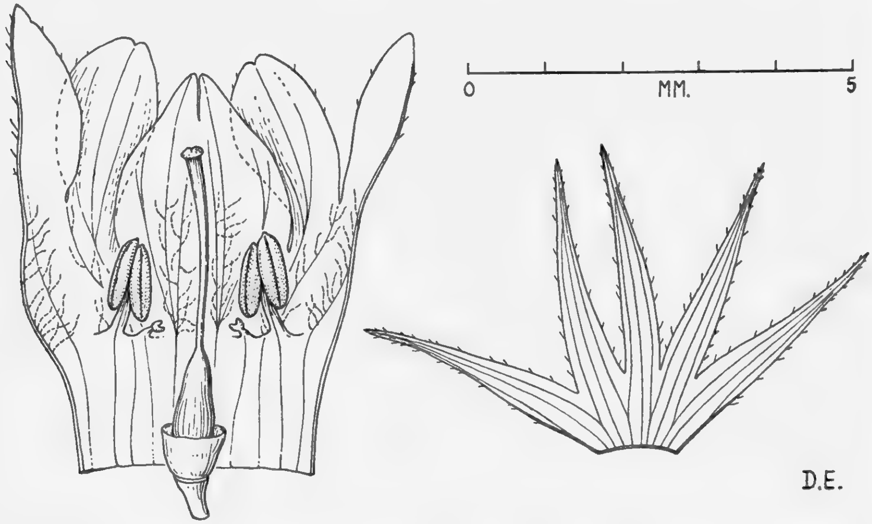

Fig. 16. Flower of *Psilanthele eggersii* Lindau (*Eggers 15129*) cut lengthwise.

Only known species the following :

1. ***Psilanthele eggersii*** Lindau in Bull. Herb. Boiss. 5 : 664 (1897).—Mildbraed apud Diels in Bibl. Bot. 116 : 148 (1937). (Text-fig. 16 ; Pls. 40a, 46).

Shrub to 2 m. high ; *branches* slender, ascending, sparsely and minutely pubescent, red-brown (fide Diels) when young, becoming yellowish with age. *Leaves* short-stalked, the blade narrowly elliptic or lanceolate, the apex acuminate, the base attenuate, c. 1·5–5 cm. long, 5–15 mm. broad, glabrous and with numerous cystoliths above, glabrous below, thin, the veining evident. *Flowers* in 16–20-flowered inflorescences 1–2 cm. long ; *pedicels* 2–3 cm. long. *Calyx* c.2 mm. long, the segments very narrowly triangular. *Corolla* blue (fide Lindau) or white with red streaks on lower lip (fide Diels), minutely pubescent, c.5 mm. long, the tube 2·5 mm. long, the segments 2·5 mm. long. *Stamens* almost included, the filaments 0·7 mm. long, the anthers 1 mm. long.

ECUADOR : *Manabi* : probe Hacienda El Recreo, 16 July 1898, *Eggers 15129* (F ; K ; isotypes). *Chimborazo* : im Gebiet des R. Chanchan bei Naranjapata, 530m., Sept. 1933, *Diels 1192* (fide Mildbraed, loc. cit).

The above account is based on Lindau's original description and isotypes in the Kew and Chicago herbaria. As the type was collected by Baron Henrik Franz Alexander Eggers (1844–1903) in western Ecuador near the coast at El Recreo (0° 27′S) south of Cape Pasado, and Mildbraed records it from central Ecuador at Naranjapata (2° 17′S), it would seem to be a species widely distributed in Ecuador but rarely collected, the flowers being inconspicuous and its habit of growth in no way remarkable. Eggers was a Danish professional soldier, who served in Mexico and the Danish West Indian islands (St. Croix, 1869–72, 1873–74, St. Thomas, 1872–73, 1874–1885) and who managed while so engaged to collect botanical specimens on many West Indian islands. In 1891–99 he travelled and collected in South America (Venezuela, Ecuador). An account of his career will be found in Urban, *Symb. Antill.* 3 : 40–43 (1902).

A photograph of the holotype (formerly in Berlin-Dahlem) is available in Field Museum of Natural History, Chicago, photograph 8737.

OPLONIA Raf.

OPLONIA Raf., Fl. Tellur. 4 : 64 (1838).

Eranthemum c. *Hesperanthemum* Endl., Gen. Pl. : 706 (1839).

Anthacanthus Nees in DC., Prodr. 11 : 460 (1847) *nom. superfl.*, excl. § 2.—Griseb., Fl. Brit. W. Ind. Is. : 457 (1862).—Benth. in Benth. & Hook., Gen. Pl. 2 : 1097 (1876).—Lindau in Engler & Prantl, Nat. Pflanzenfam. iv. 3b : 335 (1895) ; in Urban, Symb. Antill. 2 : 214 (1900).—Britton & Millsp., Bahama Fl. : 402 (1920).—Britton & Wils. in Sci. Surv. Porto Rico & Virgin Is. 6 : 212 (1925).—Alain in León & Alain, Fl. Cuba 4 : 498 (1957).

Forsythiopsis Baker in Journ. Linn. Soc. Lond., Bot. 20 : 218 (1883).—Benoist in Humbert, Fl. Madag. 182 : 106 (1967).

Hesperanthemum (Endl.) Kuntze, Revis. Gen. Pl. 2 : 490 (1891), *nom. superfl.*

Shrubs or small trees, mostly with opposite axillary spines, sometimes spineless. Leaves usually small, shortly petiolate or almost sessile, entire, often fascicled when two or more pairs arise on the same extremely short axillary branch ; cystoliths present, often abundant. Flowers small, pedicellate, solitary and axillary, or in sessile or short-pedunculate axillary fascicles. Bracts minute. Calyx 5-parted, 3–6 mm. long, the tube very short, the segments almost equal, narrow, acute.

Corolla zygomorphic, white, bluish, purple or red, 8–18 mm. long ; tube narrow, cylindric, almost straight, slightly expanded above ; limb spreading, 2-lipped, the upper lip 2-lobed, the lower lip 3-parted, the segments almost equal ; aestivation imbricate. Stamens 2, inserted above the middle of the corolla-tube, included or exserted ; filaments slender, short or long ; anthers with 2 parallel spurless equal loculi ; staminodes 2, minute. Pollen spheroid or prolate, 3-colporate, each colpus flanked by 2 pseudocolpi, pitted with minute lumina. Ovary with 2 ovules in each loculus ; style long, the stigma slightly thickened and almost entire. Capsule clavate, stipitate, 2–4-seeded. Seeds somewhat flattened, almost circular in outline, 2–3 mm. broad, borne on acute retinacula.

Type-species by original designation : *Oplonia spinosa* (Jacq.) Raf. based on *Justicia spinosa* Jacq.

Species variable and difficult to define, fourteen accepted here, one from Peru, eight West Indian, ranging from the Bahamas and Cuba to the Grenadines in the Lesser Antilles, and five Madagascan.

As Brizicky (1969) has pointed out, it is impossible to decide the rank of Endlicher's subdivisions of genera.

Key to Species of Oplonia

Spines up to 3 cm. long and mostly more than 1·5 cm. long, spreading horizontally or slightly ascending, straight, rigid ; Cuba . . . . 6. *O. tetrasticha*
  Spines all unbranched . . . . 6a. var. *tetrasticha*
  Spines mostly bearing 2–4 subsidiary spines . . . 6b. var. *polyece*
Spines absent, or, if present, mostly less than 1·2 cm. long, or, if longer, deflexed or curved or very slender :
  Spines present, some or all slightly or distinctly curved, spreading almost horizontally or recurving ; Bahamas to Virgin Islands . . 4. *O. spinosa*
  Spines absent or, if present, straight and spreading horizontally or ascending :
    Shrub of very dwarf habit, 4–8 cm. high, with internodes 1–3 mm. long; Cuba. 9. *O. nannophylla*
    Shrub taller and looser in habit, the internodes more than 1 cm. long :
      Pedicels shorter than the calyx:
        Spines present ; western Cuba . . . . 8. *O. purpurascens*
        Spines absent ; Madagascar. . . . . . . 13. *O. minor*
      Pedicels some or all longer than the calyx :
        Corolla white ; stamens always included, the filaments c.0·8 mm. long, shorter than the anthers ; low spreading shrub under 60 cm. high, with leaves mostly broadest below the middle ; Jamaica 7. *O. acicularis*
        Corolla red, purple, pale violet or blue, very rarely white ; stamens exserted or included, the filaments 1·5–7 mm. long, longer than the anthers ; shrubs mostly 1–2 m. or even small trees to 6 m. high, with leaves variable but often broadest at or above the middle:
          Leaves all very small (not more than 12 mm. long, 6 mm. broad):
            Leaves linear; Madagascar . . . . . 14. *O. linifolia*

Leaves elliptic to narrowly obovate:

Spines present ; Jamaica to the Grenadines . 5. *O. microphylla*

Spines absent ; Madagascar . . . . 12. *O. minor*

Leaves larger, some or all more than 12 mm. long or, if less, then broadest at or below the middle:

Apex of leaf acuminate or acute ; calyx segments about as long as the 4·5–5-mm. long corolla tube:

Flowers 7–10 at each axil ; leaf blade narrowly cuneate at base ; Peru . . . . 1. *O. grandiflora*

Flowers 1–3 at each axil ; leaf blade rounded at base ; Madagascar . . . . . . 10. *O. acuminata*

Apex of leaf usually obtuse or rounded, rarely acute ; calyx segments shorter than the 5–10-mm. long corolla tube:

Corolla segments longer than tube ; style hairy ; Madagascar:

Mature leaves mostly 3–9 cm. long:

Calyx segments narrowly triangular, sparsely hairy. 11. *O. vincoides*

Calyx segments narrowly oblong, densely hairy. 12. *O. puberula*

Mature leaves less than 3 cm. long . . . 13. *O. minor*

Corolla segments slightly shorter than tube ; style glabrous; Jamaica:

Leaves mostly 3–10 cm. long, 1·8–4·5 cm. broad ; flowers in each fascicle numerous (4–15) ; interior of Jamaica, mostly above 500 m. . . . . . . 2. *O. jamaicensis*

Leaves smaller, mostly 1–2·5 cm. long, 0·4–2 cm. broad, if longer then broadest above the middle and flowers solitary ; flowers solitary or few (2–4) in each fascicle. 3. *O. armata*

Corolla red ; leaves often broadest above the middle; plants of the interior . . . . . 3a. var. *armata*

Corolla pale purple, lilac or almost white : leaves mostly broadest at the middle ; plants occurring below 500 m., usually coastal . . . 3b. var. *pallidior*

1. ***Oplonia grandiflora*** (Lindau) Stearn, comb. nov. (Pls. 40b, 42).

Psilanthele grandiflora Lindau in Bull. Herb. Boiss., Sér. 2, 4 : 401 (1904).

Shrub 1–4 m. high ; *branches* stout, greyish, at first sparsely pilose with long hairs, later glabrous ; *spines* absent. *Leaves* short-stalked, the blade very variable in size in the same fascicle, mostly lanceolate, sometimes narrowly elliptic, the apex acute, the base narrowly cuneate, c.2–10 cm. long, 0·5–3 cm. broad, glabrous except for sparse more or less appressed hairs on the veins below and along the margin, the veining evident with 6–8 lateral veins each side of the midrib ; petiole 5–10 mm. long. *Flowers* 7–10 in sessile axillary fascicles ; *pedicels* 1–2 cm. long, glabrous. *Calyx* 4·5–6 mm. long, the segments linear, acute. *Corolla* white with violet markings (fide

E. Ule), glabrous, the tube 4–4·5 mm. long, the upper lip slightly 2-lobed, c. 5 mm. long, the lower lip 3-parted with obtuse segments to 6·5 mm. long, 4 mm. broad. *Stamens* included, the filaments c. 1 mm. long, the anthers scarcely 1 mm. long.

Endemic to Peru.

PERU : *San Martin* : prope Fuan-Guerra ad Tarapoto, " Strauch 1–4 m., Bl. weiss mit violetter Zeichnung ", Oct. 1902, *E. Ule 6493* (K, isotype).

O. grandiflora is a geographically isolated species differing from other members of the genus in its acute leaves, its linear more or less parallel-sided calyx-segments, which equal the corolla-tube in length, and its smaller corollas, but it approaches *O. jamaicensis* in its comparatively large and broad leaves and many-flowered fascicles. There seems no adequate basis for the generic separation of this Peruvian species from the Jamaican species which Lindau associated with it under the name *Psilanthele*, even though this raises the problem of the presence of ancient South American elements in the Jamaican flora (see p. 285).

When transferred to the genus *Oplonia*, the epithet *grandiflora* is misleading as the species has smaller flowers than any other. Lindau, however, contrasted it not with members of *Oplonia* (*Anthacanthus*) but with *Psilanthele eggersii*, which has even smaller flowers.

A photograph of the holotype (formerly in Berlin-Dahlem) is available in Field Museum of Natural History, Chicago, photograph 8738.

2. **Oplonia jamaicensis** (Lindau) Stearn, comb. nov. (Pl. 39).

Psilanthele jamaicensis Lindau in Urban, Symb. Antill. 5 : 501 (1908).

Sparse straggling shrub to 4 m. high ; *branches* rather stout, light brown and minutely pubescent with very short upcurved hairs when young, later greyish and glabrous, somewhat broadened and flattened below the nodes ; *spines* usually absent. *Leaves* short-stalked, the blade narrowly obovate, oblanceolate or elliptic, the apex rounded or obtuse and often emarginate, sometimes mucronate, the base cuneate or attenuate, 3–10 cm. long, 1·8–4·5 cm. broad, glabrous above, sometimes sparsely pubescent along the nerves below, the veining usually prominent below ; petiole c.5 mm. long. *Flowers* 4–15 in sessile axillary fascicles ; *pedicels* 5–12 mm. long, minutely pubescent or glabrous. *Calyx* c.5 mm. long, the segments very narrowly triangular or subulate. *Corolla* purplish or lavender blue with purple blotches at the base of the lobes, pubescent, the tube c.10 mm. long, the segments 7–9 mm. long. *Stamens* almost included or long-exserted, the filaments c.2 mm. or 6 mm. long, the anthers 1·5 mm. long. *Capsule* c.1·5–2 cm. long.

Endemic to inland woods of Jamaica at about 350–800 m.

JAMAICA : *St. James* : White Rock Hill, 1 mile S. of Sweetwater, 640 m., 10 Mar. 1956, *Stearn 454* (BM ; S), *Proctor 11745* (*IJ*). *Trelawny* : Tyre, near Troy, 600 m., 24 Apr. 1906, *Harris 9362* (BM ; K ; NY) ; 3 Apr. 1917, *Perkins 1323* (K). 2 miles N. of Troy, 530 m., 14 Mar. 1955, *Proctor 9949* (IJ) ; ½ mile N. of Troy, 480 m., 14 Mar. 1955, *Proctor 9924* (IJ). *Manchester* : Vicinity of Mandeville, Feb. 1910, *S. Brown 264* (NY). *Clarendon* : Peckham Woods, 760 m., May 1912, *Harris 11060* (NY) ;

10 Mar. 1954, *Proctor 8433* (BM ; IJ) ; May 1955, *Robertson 1992* (UCWI). Aenon Town to McKay, 600 m., Apr. 1962, *Adams 11034* (UCWI). *St. Ann* : Mason River District, 3–4 miles NW. of Kellits P.O., 2 Mar. 1957, *Proctor 16216* (IJ). Along road to Hollymount, Mount Diablo, 820 m., 6 Aug. 1957, *Proctor 16523* (IJ) ; 680 m., Mar. 1962, *Adams 10830* (UCWI). *St. Catherine* : Hollymount, Mount Diablo, 760 m., 11 Aug. 1908, *Harris 8968* (NY, lectotype ; BM ; F) ; 15 Feb. 1905, *Harris 8888* (BM; NY).

This species was first collected by Swartz but was confused, it would seem, with *O. armata*. It stands apart from other Jamaican species in its large leaves and numerous flowers. The corolla is described as " lavender blue " by Perkins, as " purple " or " violet " or " pale lavender " by Proctor, as " purple " by Robertson.

3. **Oplonia armata** (Swartz) Stearn, comb, nov.

Justicia armata Swartz, Nov. Gen. & Sp. Pl. : 13 (1788) ; Fl. Ind. Occ. 1 : 28 (1797).—Vahl, Enum. Pl. 1 : 168 (1804).

Eranthemum armatum (Swartz) R. Br. ex Roem. & Schult. in L., Syst. Veg., ed. nov. 1 : 176 (1817).

Anthacanthus armatus (Swartz) Nees in DC., Prodr. 11 : 460 (1847).—Griseb., Fl. Brit. W. Ind. Is. : 457 (1862).—Lindau in Urban, Symb. Antill. 2 : 217 (1900).

Hesperanthemum armatum (Swartz) Kuntze, Revis. Gen. Pl. 2 : 490 (1891), excl. syn. Neesii.

Sparse straggling or erect shrub or small tree (in var. *pallidior*) ; *branches* slender, arching or spreading, pubescent when young on two opposite sides with short or very short ascending or upcurved hairs, the other two opposite sides almost or quite glabrous ; *spines* often absent but when present slender, rigid, 5–10 mm. (rarely to 20 mm.) long, spreading at an angle of c.75°, glabrous or minutely pubescent. *Leaves* short-stalked, very variable in size and shape, the blade ovate or narrowly ovate, elliptic or narrowly obovate or oblanceolate, the apex obtuse or rounded, usually emarginate, the base cuneate or attenuate, 0·5–4 cm. long, 0·3–2 cm. broad, glabrous above, sometimes sparsely pubescent along the nerves below, the veining below scarcely evident to prominent ; petiole 2–5 mm. long. *Flowers* solitary or 2–4 in sessile axillary fascicles ; *pedicels* 5–15 mm. long, glabrous or minutely pubescent. *Calyx* 4–6 mm. long, the segments very narrowly triangular or subulate. *Corolla* deep pink, rose or red-purple (in var. *armata*), lavender-blue, pale purple or almost white (in var. *pallidior*), pubescent or glabrous, the tube 8–10 mm. long, the segments 4–8 mm. long. *Stamens* almost included or long-exserted, the filaments c.1·5–2 mm. or 5–7 mm. long, the anthers c.1–1·5 mm. long. *Capsule* c. 1·5–2 cm. long.

Endemic to Jamaica, var. *pallidior* at sea-level to 400 m., var. *armata* at 150–850 m.

3a. **Oplonia armata** var. **armata** (Text-fig. 3 C, D ; Pl. 43b).

Shrub 1·5–3 m. high. *Leaf-blades* narrowly ovate, narrowly elliptic or narrowly obovate, the base cuneate or attenuate. *Flowers* mostly solitary, sometimes 2–4 in a fascicle. *Corolla* red, variously described as deep rose-pink, red-purple, cerise and crimson.

Forma 1. *Leaf-blades* mostly narrowly ovate, 1–2·5 cm. long, 0·5–1·5 cm. broad. *Corolla* deep pink or bright cerise.

Jamaica : *St. James* : White Rock Hill, 1 mile S. of Sweetwater, 640 m., 10 Mar. 1956, *Stearn 455* (BM). *St. Elizabeth* : Balaclava, 150 m., 25 Mar. 1917, *Perkins 1413* (GH ; K). *Trelawny* : Boothe district, 3 miles N. of Troy, 490 m., 14 Mar. 1955, *Proctor 9957* (IJ). Troy, 13–18 Sept. 1906, *Britton 589* (F ; NY). *Manchester* : Halifax, 26 July 1952, *West & Arnold 896* (BM). *Clarendon* : Peckham Woodland, 760–850 m., 2 Mar. 1910, *Harris 10877* (GH ; K ; NY ; UCWI ; US).

Forma 2. *Leaf-blades* varying from narrowly ovate to narrowly obovate, mostly more or less elliptic, 0·7–2·5 cm. long, 0·4–1 cm. broad. *Corolla* deep rose or red-purple (" deep lilac ").

Jamaica : *Trelawny* : End of Crown Lands Road coming from Peckham, 300–600 m., Mar. 1954, *Robertson 2079* (UCWI). *St. Elizabeth* : Ipswich, 150–210 m., 7 Mar. 1917, *Harris 12508* (BM ; GH ; K ; NY ; UCWI ; US). Maggotty, 5 July 1928, *Orcutt 2123* (BM). *St. Ann* : Moneague Hills, 1850, *Alexander* (K). Somerton district, 500 m., 28 Mar. 1956, *Stearn 608* (BM) ; *Proctor 11921* (IJ). *Manchester* : Mandeville, Oct. 1886, *Hart 1545* (K). *Clarendon* : Aenon Town to McKay, 700 m., Apr. 1962, *Adams 11060* (UCWI), *Adams 11062* (UCWI) ; Feb. 1961, *Adams 9002* (UCWI). Peckham Woods, 300–600 m., Mar. 1956, *Robertson 2485* (UCWI).

Forma 3. *Leaf-blades* mostly narrowly obovate, 1–2·5 cm. long, 0·4–1 cm. broad. *Corolla* rose-pink, red-purple, bright rose or crimson.

Jamaica : *Trelawny* : Island View Hill, Wilson Valley district, 1½ miles N. of Warsop, 600–670 m., 13 Oct. 1960, *Proctor 21407* (BM ; IJ) ; 30 Apr. 1964, *Proctor 24826* (BM ; IJ). Ramgoat Cave District, 450 m., 4 July 1955, *Howard & Proctor 14406* (BM ; IJ ; LS) ; 19 Jan. 1956, *Howard, Proctor & Stearn 14674* (A ; BM ; IJ). Norwood to Bailey, 770 m., Apr. 1963, *Adams 12474* (UCWI), *12479* (UCWI). *Manchester* : Glasgow near Troy, 400 m., 18 Sept. 1906, *Harris 9478* (BM ; NY ; UCWI). Troy to Oxford, Sept. 1906, *Britton 678* (NY). *Clarendon* : Peckham Woods, 760 m., 26 May 1955, *Proctor 10236* (BM ; IJ) ; May 1955, *Robertson 1985* (UCWI). *St. Thomas* : Between Whitehall and Big Hill, 300–900 m., 12 Feb. 1953, *Proctor 7668* (IJ ; LS ; NY). Gorge of Plantain Garden River, 330 m., 15 Mar. 1956, *Stearn 486* (A ; BM ; UCWI).

3b. ***Oplonia armata*** var. **pallidior** Stearn, stat. & nom. nov. (Text-figs. 1, 2 O, 3 A, B ; Pl. 38).

Anthacanthus acicularis sensu Lindau in Urban, Symb. Antill. 2 : 214 (1900) pro parte min., tantum quoad specim. *Harris 6324* ; non (Swartz) Nees.
Psilanthele minor Lindau in Urban, Symb. Antill. 7 : 383 (1912).

Shrub or small tree to 6 m. high. *Leaf-blades* mostly ovate or elliptic, sometimes broadly elliptic or narrowly obovate, the base rounded to attenuate, 0·5–4 cm. long, 0·3–2 cm. broad, the veining faint or not evident beneath. *Corolla* pale purple or lilac or almost white with purplish markings.

Jamaica : *Hanover* : Green Island, Fish River, in coastal thicket, 15 Mar. 1908, *Harris 10257* (BM ; F ; K ; NY ; US ; isotypes of *Psilanthele minor*). Upper S. slope of Dolphin Head, 370–490 m., 11 Apr. 1955, *Proctor 10018* (BM ; GH). Coastal thicket, Pedro Point, Mar. 1908, *Britton 2184* (NY). Wooded limestone sea-cliffs ½ mile NW. of mouth of the Great River, 3–15 m., 15 Sept. 1957, *Proctor 16655* (BM ; IJ). Lucea to Montego Bay, Mar. 1908, *Britton 2195* (NY). *Westmoreland* : Sea-coast, Negril, 10 Mar. 1908, *Harris 10224* (NY ; UCWI ; US) ; *Britton & Hollick 2073* (NY). Little Bay, 15 m., Dec. 1961, *Adams 10169* (UCWI). *St. James* : Glen Devon Road, Montego Bay, 1924, *Norman 100* (BM). Hills overlooking Ironshore estate, 60–240 m., 16 Feb. 1963, *Proctor 23236* (IJ). *St. Elizabeth* : Coast about 2 miles E. of White House, 22 Feb. 1958, *Yuncker 18012* (BM ; F ; S). Vicinity of Merriman's Point, in dry coastal woodland, 9 m., 10 May 1956, *Stearn 863* (A ; BM ; UCWI) ; *Proctor 15337* (IJ). Near Fort Charles, 8 Jan. 1959, *Robertson 5390* (UCWI). Between Southfield and Pedro Cross, 360 m., 9 May 1956, *Stearn 843* (BM). Lover's Leap, Santa Cruz Mountains, Sept. 1907, *Britton 1151* (IJ). Yardley Chase, limestone cliff, 490 m., 4 Sept. 1907, *Harris 9675* (NY ; UCWI ; US). 1 mile NW. of Alligator Pond, 14 Sept. 1954, *Howard & Proctor 13807* (IJ). 0·6 mile W. of Lititz, 240 m., 21 Jan. 1956, *Howard, Proctor & Stearn 14740* (A ; BM ; IJ) ; Sept. 1907, *Harris 9675* (NY ; US). Kaiser mine area S. of Gutters, 13 Sept. 1954, *Howard & Proctor 13760* (IJ ; NY). *Manchester* : Alligator Pond, 1 May 1896, *Harris 6324* (NY ; UCWI). Near Great Bay, 3 miles SE. of Alligator Pond, 15 m., 3 Apr. 1956, *Stearn 641* (BM). 1 mile ESE. of Gods Well, on N. side of Round Hill, 90 m., 3 Apr. 1956, *Proctor 11942* (BM ; IJ). *St. Ann* : Dry coastal thorn forest near the sea, Reynolds bucket line, 20–21 Dec. 1953, *Howard & Proctor 13577* (IJ). Fort Point, Dry Harbour (Discovery Bay), 3 m., 12 Apr. 1956, *Stearn 726* (BM). 1 mile W. of Discovery Bay, 30 m., Apr. 1960, *Adams 6855* (UCWI). *Clarendon* : E. end of Portland Ridge, 15 m., 18 Mar. 1943, *Lewis 104* (IJ). Round Hill near Milk Pen, 45 m., May 1962, *Adams 11143* (UCWI), *11147* (UCWI). Milk River, 3–6 m., 5 June 1965, *Proctor 26894* (BM).

O. armata as accepted here includes plants of such diversity in habit, size and shape of leaf, and colour of corolla that Lindau referred them to three species and two genera. The numerous specimens collected in Jamaica since Lindau's publications have increased rather than diminished the difficulty of classifying them. Swartz's original diagnosis of his *Justicia armata* reads : " I. fruticosa, aculeata, foliis oblongis emarginatis coriaceis nitidis. Jamaica ". The description in his *Flora Indiae Occidentalis* attributes to it " Caulis fruticosus, 3–4 pedalis . . . Folia breviter petiolata cuneato-obovata, emarginata, nervosa . . . Aculei gemini . . . spinaeformes . . . Flores axillares, solitarii, pedunculati, coccinei " and gives its habitat as " in rupibus montium Jamaicae septentrionalis ". Red-flowered plants of this character occur in the interior of Jamaica, e.g. at White Rock Hill, which may possibly be the type-locality, as it stands by a route between Montego Bay and Savanna La Mar ; Swartz travelled across the island from the one to the other during his stay in Jamaica (cf. Stearn, 1965). The number of flowers may vary up to four in a fascicle. Leaves of such red-flowered plants vary in size from 0·2 cm. to 2·5 cm. long, and display astonishing diversity in shape : three main types, described above as forms 1–3, may be distinguished under var. *armata*. Except in colour of corolla, it does not seem possible to distinguish from these a very variable assemblage of plants, here put under var. *pallidior*, occurring mostly at or near the coast and having pale purple, lavender-blue or almost white flowers ; one of these, in a spineless state, was described by Lindau in 1912 as *Psilanthele minor*, the specific epithet of which is certainly inappropriate for a variant of *O. armata* forming " a small tree up to 20 feet high in coastal thickets ", as noted by Harris for the type-collection (*Harris 10257*) ; Harris recorded it as having " flowers pale blue ". This, however, is also evidently allied closely to plants inhabiting the interior of Jamaica and possessing larger leaves and more numerous flowers (4–15 in a fascicle) described by Lindau in 1908 as *P. jamaicensis*. The latter occurs in at least one locality, White Rock, with *O. armata* var. *armata* f. 1 ; according to the limited material from this place, they here keep distinct, the difference in flower colour probably serving to prevent cross-pollination.

Swartz's description of his *Justicia armata* as having solitary red flowers excludes *O. jamaicensis*. A specimen presented by him to Sir Joseph Banks as his *J. armata* unfortunately lacks corollas. It has glabrous shoots, spines about 5 mm. long, solitary flowers with pedicels to 1 cm. long and calyx about 5 mm. long, but oblanceolate or narrowly obovate leaves, varying from 2·5 cm. long, 1 cm. broad to 5·5 cm. long, 2 cm. broad. No specimen exactly corresponding to this has been seen among the numerous collections now available from Jamaica. In its solitary flowers it agrees with *O. armata* as accepted here on the basis of Swartz's description ; in its large leaves it comes closer, however, to *O. jamaicensis*. It might possibly represent a hybrid between them. Its existence suggests that *O. jamaicensis* could be united with *O. armata*, but in view of the distinctness of all the other specimens they are here kept apart. In Swartz's herbarium at the Riksherbarium, Stockholm, there are four pieces labelled " armata ", evidently part of the same gathering, one piece with a spine to 1 cm. long, another with four pedicels arising from the same axil. This agrees with *O. jamaicensis*. The descriptions in Swartz's *Flora Indiae Occidentalis* for the most part are evidently based on notes made directly from living plants in Jamaica and, as far as they go, are quite accurate. The explanation of the discrepancy between Swartz's description and his now available material may be that he described his *armata* from one living plant and kept dried specimens from another.

4. **Oplonia spinosa** (Jacq.) Raf., Fl. Tellur. 4 : 65 (1838). (Text-figs. 2 A, B, C ; Pl. 43a).

Justicia spinosa Jacq., Enum. Syst. Pl. Carib. : 11 (1760) ; Select. Stirp. Amer. : 2, t.2 fig. 1 (1763) ; Select. Stirp. Amer. Ic. Pict. : 7, t.2 (1780).—L., Sp. Pl., ed. 2, 2 : 1663 (1763) excl. pl. Milleri.—Swartz, Obs. Bot. : 12 (1791).—Willd. in L., Sp. Pl., ed. 4, 1 : 100 (1797). —Vahl, Enum. Pl. 1 : 167 (1804).

Eranthemum spinosum (Jacq.) R.Br. ex Roem. & Schult. in L., Syst. Veg., ed. nov. 1 : 176 (1817).

Eranthemum emarginatum Link in Jahrb. Gewächsk. 1 (3) : 47 (1820).—Schult., Mant. 1 : 154 (1822).

Anthacanthus spinosus (Jacq.) Nees in DC., Prodr. 11 : 460 (1847).—Lindau in Urban, Symb. Antill. 2 : 216 (1900) excl. parte.—Britton & Millsp., Bahama Fl. : 403 (1920).—Urban, Symb. Antill. 8 : 655 (1921).—Britton & Wils. in Sci. Surv. Porto Rico & Virgin Is. 6 : 212 (1925).—Alain in León & Alain, Fl. Cuba 4 : 500 (1957).—P. S. Green in Kew Bull. 23 : 275 (1969).

Anthacanthus spinosus var. *horridus* Nees, loc. cit. (1847).
Anthacanthus emarginatus (Link) Nees, tom. cit. : 461 (1847).
Jasminum coeruleum Kuntze, Revis. Gen. Pl. 2 : 410 (1891).
Hesperanthemum spinosum (Jacq.) Kuntze, tom. cit. : 490 (1891).

Shrub of variable habit, usually erect, sometimes dwarf but up to 3 m. (9 ft.) high : *branches* ascending, slender, glabrous on 2 opposite sides and pubescent on the 2 intervening sides with short spreading hairs or densely and minutely pubescent all round, sometimes with the hairs on two sides slightly longer ; *spines* curved or directed downwards slightly or strongly, sometimes almost straight and horizontal, 4–12 mm. long, at base c.0·5–0·7 mm. thick, glabrous or minutely pubescent. *Leaves* short-stalked, the blade very variable in shape and size, mostly narrowly elliptic or narrowly obovate, sometimes broadly ovate or elliptic, the apex obtuse or rounded and almost truncate, entire or emarginate, the base cuneate, c.8–20 mm. long (including the 1–1·5 mm. long petiole), 3–9 mm. broad, glabrous, the veining below faint or evident. *Flowers* solitary or 2–6 in sessile axillary fascicles ; *pedicels* 3–9 mm. long. *Calyx* 3–5 mm. long, the segments narrowly triangular or subulate. *Corolla* bluish purple or lavender, glabrous or pubescent, the tube c. 6–9 mm. long, the segments 6–7 mm. long. *Stamens* included or exserted, the filaments 1·5–2 mm. or 6 mm. long ; anthers c.1·8 mm. long. *Style* 9–10 mm. or 6 mm. long. *Capsule* c.1·2 cm. long.

Bahamas, from Grand Bahama, New Providence and Andros, over eastern Cuba, Hispaniola and Puerto Rico, to the Virgin Islands, mostly on coastal limestone, but ascending to 900 m.

BAHAMAS : *Grand Bahama* : Barnett's Point, 5–13 Feb. 1905, *Britton & Millspaugh 2711* (F). *New Providence* : 13 Mar. 1888, *Eggers 4487* (BM : K). Near Nassau, 24 Mar. 1903, *Curtiss 133* (BM ; F ; GH ; K) ; 8 Mar. 1905, *Wight 174* (GH ; K). Point Montague, 27 Aug. 1904, *Britton & Brace 311* (F). Rifle Range, 3 Feb. 1905, *E. G. Britton 3279* (F). *Andros* : Mangrove Cay, Aug.–Sept. 1906, *Brace 4926* (F) ; 16–19 Jan. 1910, *Small & Carter 8471* (F ; K). Fresh Creek, 10 June 1890, *Northrop & Northrop 396* (F ; GH) ; 12 Sept. 1937, *Matthews 131* (K). Nicols Town, 8 Apr. 1890, *Northrop & Northrop 396A* (K). *Eleuthera* : fide Britton & Millspaugh, loc. cit. (1920). *San Salvador* (*Watling Island*) : Graham Harbour to Cockburn Town, 15 Mar. 1907, *Britton & Millspaugh 6192* (F). Cockburn Town and vicinity, 12–13 Mar. 1907, *Britton & Millspaugh 6099* (F). *Rum Cay* : Sclater's Hill, 4 Dec. 1905, *Brace 3949* (F). Port Nelson, 23 Mar. 1966, *Gillis 6298* (A). *Exuma* : Cay N. of Wide Opening, 18 Feb. 1905, *Britton & Millspaugh 2783* (F). *Crooked Island* : Landrail Point, Jan. 1906, *Brace 4560* (F). *Long Cay* : Dec. 1905, *Brace 4108* (F.). *Acklins Island* : Spring Point, Dec. 1905–Jan. 1906, *Brace 4281* (F.) *Caicos Islands* : Bellemont, North Caicos, 2 Mar. 1911, *Millspaugh & Millspaugh 9188* (F). Jacksonville, East Caicos, 26 Feb. 1911, *Millspaugh & Millspaugh 9083* (F). Vicinity of Cockburn Harbour, South Caicos, 17 June 1954, *Proctor 8830* (IJ). *Great Inagua Island* : Between Matthew Town and Lighthouse, 14 Oct. 1904, *Nash & Taylor 1053* (F ; K). Salt Pond Hill, 12 Oct. 1904, *Nash & Taylor 993* (F ; K).

CUBA : *Oriente* : Mayari, Charrascos cerca de la crestas del Cristal, 2–7 Apr. 1956, *Alain, Acuna & Lopez Figueiras 5701* (LS), *5703* (LS), *5708* (LS), *5810* (LS). Cerro de Miraflores, Cananova, July 1942, *Léon & Mentero 21152* (LS). Moa, lieux rocheux, 16–23 Apr. 1943, *Marie-Victorin, Clemente & Alain 21485* (LS ; MT), *21778* (LS). Moa, Chemins de Cayo Chiquito, 18 May 1944, *Clemente 3646* (LS ; MT). Moa, bois en arrière de la Mine Franklin, 20 May 1944, *Clemente 3665* (LS ; LT). Moa, Playa la Vaca, Apr. 1943, *Marie-Victorin, Clemente & Alain 21503* (LS). Rio Yagrumaje, 16–23 Apr. 1943, *Marie-Victorin, Clemente & Alain 21621* (LS), *21625* (MT). Moa, chemin de la mine Delta, à l'est de la vallée du Rio Cayoguán, *Marie-Victorin & Clemente 21778* (LS ; MT). Moa, Orillas del Rio Cayoguán, 13 July 1949, *Clemente & Alain 880* (LS). Moa, curso del Rio Cayoguán, 13 July 1949, *Alain & Clemente 856* (LS). Sierra de Nipe, 24 July 1914, *Ekman 2179* (S). Sierra de Nipe, headwaters of Rio Piloto, 750 m., 15 May 1915, *Ekman 5701* (S) ; 375 m., 3 June 1924, *Ekman 9170* (S). Headwaters of Brazo Dolores, 925 m., 15 Oct. 1914, *Ekman 3117* (S). Charrasco, Peña Prieta, Magdalena, 30 July 1953, *Alain 3491* (LS).

HAITI : Without precise locality, *Poiteau* (BM ; P) ; *Schomburgk 107* (BM). *Département du Nord Ouest* : Vicinity of Jean Rabel, 1–13 Mar. 1929, *Leonard & Leonard 13674* (A ; GH). Vicinity of Port à l'Ecu, Mar. 1929, *Leonard & Leonard 13876* (K). *Département de l'Artibonite* : Plaisance, Gonaives, 400 m., May 1900, *Buch 375* (IJ). *Département de l'Ouest* : Duchené, Port au Prince, 800 m., Mar. 1920, *Buch 1851* (IJ). Massif de la Selle, Port au Prince, 300 m., 21 Apr. 1926, *Ekman 5923* (K). Massif de la Hotte, gr. Morne Rochelois, Miragoane, 25 Mar. 1927, *Ekman 7896* (S).

DOMINICAN REPUBLIC : Without precise locality, 1852, *Schomburgk* (BM). Puerto Playa, sea-level, 1 May 1959, *Jimenez 3931* (BM). Opposite San Gabriel, S. side of Samana Bay, sea-level, 10 April 1921, *Abbott 1293* (GH). Barahona, Enriquillo (Petit Trou), sea-level to 100 m., 15 Feb. 1922, *Abbott 1756* (GH).

PUERTO RICO : *Aquadilla*: Cape Borinquen, 2 Mar. 1929, *Britton & Britton 9283* (F ; GH). Quebradillas, 2 Mar. 1914, *Britton, Britton & Cowell 1958* (F). *Bayamon* : Hills near Bayamon, 20 m., 23 Feb. 1900, *Heller 4688* (A ; F ; GH). *Humacao* : Punto Cabalero, 29 Sept. 1886, *Sintenis 5202* (BM ; GH). *Arecibo* : Prope Utuado ad Los Angelos, 17 Jan. 1887, *Sintenis 5913* (K). *Vieques Island* : Cayo Puerto Real, 7, Feb. 1914, *Shafer 2753* (GH).

ST. THOMAS : Without precise locality, *Herb. Willdenow 276* (B, type of *Eranthemum emarginatum* ; BM, photo) ; Feb. 1874, *Kuntze* (K, isotype of *Jasminum coeruleum*) ; Feb. 1887, *Eggers 630* (A ; P). Cowells Hill, Jan. 1881, *Eggers 203* (K).

ST. JOHN : Without precise locality, 1 March 1957, *Robertson 26* (A).

VIRGIN GORDA : North Sound, 29 Oct. 1918, *Fishlock 6* (A ; GH). Eastern slope of Virgin Peak, 150–420 m., 15 Apr. 1956, *A. C. Smith 10562* (A ; K ; IJ).

ST. CROIX : Without precise locality, *L. C. Richard* (P) ; May 1896, *Ricksecker 335* (F ; GH). E. slope of Mount Eagle, 230 m., 21 Dec. 1959, *Proctor 20448* (A ; BM ; IJ). Near Kingshill, 20 Jan. 1961, *Howard 15658* (A).

Jacquin's epithet *spinosa* is the earliest one given to a member of the group ; his original diagnosis under *Justicia spinosa* being but three words long, " Justicia monanthera, spinosa ", this epithet has excusably been applied to a diversity of plants. The term " monanthera " as used here means that the two loculi (thecae) of the anther are at the same level and opposite one another, thus obviously being part of one anther, in contrast to the term " dianthera " referring to stamens in which the two loculi are at different heights, the filament thus appearing to possess two anthers. Jacquin's diagnosis served to distinguish his species from all the species until then referred to *Justicia* ; it fits, however, almost all the members of the genus *Oplonia* and its application would be obscure indeed but for the detailed description and the illustration published three years later in his *Selectarum Stirpium Americanarum Historia.* This establishes the name as based on a shrub up to 1·5 m. high with more or less elliptic or narrowly ovate leaves about 1·5 cm. long and cuneate at base, with spreading spines shorter than the leaves, one to four flowers at an axil, a short calyx only half the length of the corolla-tube, and a purple corolla, its habitat being " in fruticetis & arbustis maritimis circa Portum Principis in Domingo ". There can be no doubt that a plant collected at Duchené, Port au Prince, Haiti, by W. Buch (*Buch 1851* in IJ) represents Jacquin's *Justicia spinosa.* While some spines on this specimen spread horizontally, most of them curve markedly downwards and they vary from 8 to 15 mm. in length. The leaves range from 1 to 2 cm. in length, 2·5 to 7 mm. in width. There does not seem any justification for separating specifically from this gathering other Haitian specimens with downwards curved spines, e.g. *Buch 375* from Gonaives, which has, however, small ovate leaves rounded at base, and *Leonard & Leonard 13674* from Jean Rabel, which has lanceolate, narrowly elliptic and narrowly oblanceolate leaves. Buch's Duchené material links up, however, with comparatively large-leaved specimens from the Moa district of Cuba (e.g. *Marie-Victorin, Clemente & Alain 21778*) on which the leaves vary from elliptic to ovate and narrowly obovate and from 7 mm. to 35 mm. long. The range of variation within a a series of specimens collected in the Moa district does not make it feasible to separate specifically the plant from St. Thomas on which the names *Eranthemum emarginatum* Link and *Jasminum coeruleum* Kuntze are based. Leonard and Leonard's small-leaved material from Jean Rabel in turn links up with the small-leaved plants characteristic of the Bahamas. There is indeed surprisingly little difference between some specimens from New Providence, Bahamas (e.g. *Curtiss 133*) and some from St. John, Virgin Islands (e.g. *Robertson 26*).

5. **Oplonia microphylla** (Lam.) Stearn, comb. nov. (Text-figs. 2 J–M, 4 ; Pl. 44).

Justicia microphylla Lam. in Tab. Encycl. Méth., Bot. 1 : 37 (1791).—Vahl, Eclog. Amer. 2 : 1 (1798) ; Enum. Pl. 1 : 168 (1804).
Eranthemum microphyllum (Lam.) R.Br. ex Roem. & Schult. in L., Syst. Veg., ed. nov. 1 : 176 (1817).
Eranthemum lycioides Link in Jahrb. Gewächsk. 1 (3) : 47 (1820).
Anthacanthus microphyllus (Lam.) Nees in DC., Prodr. 11 : 461 (1847).—Griseb., Fl. Brit. W. Ind. Is. : 457 (1862).—Duss in Ann. Inst. Colon. Marseille 3 : 427 (1897).
Anthacanthus lycioides (Link) Nees, loc. cit. (1847).
Anthacanthus cuneatus Nees, loc. cit. (1847).
Hesperanthemum microphyllum (Lam.) Kuntze, Revis. Gen. Pl. 2 : 490 (1891).
Anthacanthus acicularis sensu Lindau in Urban, Symb. Antill. 2 : 214 (1900) pro parte ; non (Swartz) Nees.

Erect much-branched spiny shrub to 1·5 m. high ; *branches* spreading almost horizontally or ascending, slender, brownish or grey when young, glabrous on 2 opposite sides and pubescent on the 2 alternating sides, with short or moderately long spreading or ascending whitish hairs 0·1–0·3 mm. long, or pubescent all round, the internodes 3–15 mm. long ; *spines* ascending or almost horizontally spreading, straight 3–12 mm. long, glabrous or pubescent. *Leaves* short-stalked, the blade elliptic or narrowly elliptic or narrowly ovate to oblanceolate or narrowly obovate, the apex rounded or almost truncate, slightly emarginate and mucronate, the base cuneate, c.3–12 mm. long (including the 0·5–1 mm. long petiole), 1·5–6 mm. broad, glabrous above, glabrous or occasionally pubescent below along the midrib, the veining faint not evident. *Flowers* solitary or paired ; *pedicels* 2–7 mm. long, glabrous. *Calyx* 2–3·5 mm. long, the segments narrowly lanceolate. *Corolla* pale purple, lilac or almost white with purple dots on the lower lip, minutely pubescent, the tube c.6–7 mm. long, the segments 5–6 mm. long. *Stamens* almost included or long-exserted, the filaments c.1·5 mm. or 4–5 mm. long, the anthers 1·5 mm. long. *Capsule* c.1–2 cm. long ; seeds c.2 mm. long.

South-eastern Jamaica, Hispaniola and Puerto Rico, Lesser Antilles south to the Grenadines, at sea-level to about 600 m., mostly under 200 m.

JAMAICA : Without precise locality, 1730, *Houstoun* (BM) ; *W. Wright* (BM) ; *Macfadyen* (K, type of *Anthacanthus cuneatus*). *St. Catherine* : Port Henderson Hills, Nov. 1954, *Asprey 2059* (UCWI). Lazaretto, above Port Henderson, 30–75 m., 27 Mar. 1955, *Proctor 9971* (BM ; IJ). *Kingston & St. Andrew* : E. of Militia Rifle Range, 45 m., 8 Jan. 1904, *Harris 8609* (NY). Long Mountain, S. side, 90 m., 3 July 1907, *Harris 9606* (BM ; K ; NY ; UCWI) ; 90–220 m., 19 June 1959, *Webster, Ellis & Miller 8364* (BM). W. slope of Long Mountain, along road to Wareika, 75–370 m., 7 May 1954, *Farr 5133* (IJ) ; 140 m., 3 Jan. 1956, *Stearn 66* (A ; BM ; UCWI) ; *Proctor 11436* (IJ) ; 150 m., 7 May 1956, *Stearn 830* (A ; BM). Gorge of the Cane River, 75–120 m., 22 May 1955, *Proctor 10195* (IJ) ; 29 Oct. 1957, *Yuncker 17215* (F). *St. Thomas* : Four Mile Wood, between Bull Bay and Grant's Pen, 150 m., 28 Nov. 1958, *Proctor 18268* (A ; BM ; IJ). Grant's Pen, 6 m., Dec. 1959, *Adams 5665* (UCWI). Yallahs, 30 m., 16 June 1952, *Araque-Molina & Barkley 22J448* (BM ; IJ). Vicinity of Gypsum mines, 1 mile N. of Eleven Mile, 150 m., 8 Nov. 1963, *Proctor 24186* (BM).

HAITI : *Département de l'Artibonite* : André, Gonaives, 200 m., Apr. 1899, *Buch 144* (IJ). *Département de l'Ouest* : Plaine Cul-de-Sac, near Gauthier, 24 Feb. 1925, *Ekman 3321* (GH ; F ; K ; S). *Département du Sud* : Prope Port à Piment, Aug. 1917, *Ekman 698* (A ; S). Inter Cahauane et Aux Anglais, July 1917, *Ekman 378* (S).

DOMINICAN REPUBLIC : Without precise locality, 1852, *Schomburgk 37* (BM). *Barahona* : Barahona, Las Salinas, 40 m., May 1911, *Fuertes 1105* (A ; P). *Santiago* : distr. of San José de las Matas, 600 m., 12 Oct. 1931, *Valeur 724* (A ; BM ; F ; K ; S). Pico Diego de Ocampo, 1220 m., 3 Mar. 1957, *Jimenez 3455* (BM).

PUERTO RICO : *Ponce* : Ponce to Playa Las Cucharas, 13 Mar. 1913, *Britton, Britton & Marble 1948* (A ; F). Ponce to Penuelas, 22 Mar. 1906, *Britton & Cowell 1271* (F). *Culébra* : Mar. 1906, *Britton & Wheeler 23* (F). *Vieques* : Jan. 1876, *Eggers* (GH).

ST. CROIX : Without precise locality, *L. C. Richard* (P, isotype of *Justicia microphylla*).

TORTOLA : Coastal hill, 1918, *Fishlock 105* (K).

ST. BARTHÉLEMY : Morne de Grand Fond, 250 m., 11 Oct. 1951, *Le Gallo 311* (A ; LS ; NY). Grand Platon, 150–200 m., 30 Oct. 1952, *Le Gallo 1057* (LS ; NY) ; 12 Nov. 1953, *Le Gallo 2180* (A).

ANTIGUA : Without precise locality, *Wullschlägel 452* (GOET) ; *Nicholson* (K). Santa Maria Hill, 25 Apr. 1937, *Box 757* (A ; BM). Little Cove near Half Moon Bay, July 1960, *D. R. Harris 34* (BM).

GUADELOUPE : *La Désirade* : *Duchaissang 461* (GOET) ; 10–150 m., Nov. 1935, *Stehlé 424* (IJ) ; 100 m., *Stehlé & Stehlé 7091* (A) ; 8 June 1960, *Proctor 21212* (A).

GRENADINES : *Petit St. Vincent* : East end, Mar.-Apr. 1950, *Howard* 10916 (A ; BM). *Little Martinique* : Mar. 1950, *Howard 10933* (A ; GH).

O. microphylla was published by Lamarck in 1791 under the name *Justicia microphylla* with an extremely brief diagnosis and a vague indication of its provenance as follows : " J. fruticosa, foliis obovatis coriaceis, spinis axillaribus brevissimis, pedunculis unifloris lateralibus. Ex insulis Caribaeis. *Richard. an justicia armata* Swartz. " The type-specimen in Lamarck's herbarium, now at the Muséum National d'Histoire Naturelle, Paris, gives no more precise information about its place of collection but fortunately it matches so exactly a localized specimen, under another name, in L. C. Richard's own herbarium, likewise at Paris, that they presumably formed part of the same gathering made " in fruticetis sepibus Stae Crucis ", i.e. on the island of St. Croix, Virgin Islands, which Richard visited between February 1786 and November 1787 (cf. Urban, *Symb. Antill.* 3 : 111 (1902)). Richard's material has light brown branches which are almost glabrous on two opposite sides but pubescent on the other two sides with moderately long whitish hairs to 0·3 mm. long ; the short stout slightly ascending spines are up to 3 mm. long ; its numerous, narrowly obovate leaves are 4–10 mm. long, 3–6 mm. broad, and sometimes have a few hairs along the midrib below. The small leaves and open habit, with branches spreading laterally from the main stem at an angle of about 60°–80°, give it a distinctive appearance which it shares with other specimens from the Lesser Antilles ; these diverge from it principally in having somewhat longer (5–12 mm. long) spines. On the dry coastal limestone of south-eastern Jamaica grow similar small-leaved plants with, however, more erect branches which ascend from the main stem at an angle of about 50° or less. There is much variation in degree of hairiness within this Jamaican population. *Anthacanthus cuneatus* was founded on a gathering by James Macfadyen with markedly hairy shoots, spines and leaves ; among modern Jamaican collections this is represented by *Araque-Molina & Barkley 22J448* from Yallahs, St. Thomas. It does not seem possible, however, to make any satisfactory distinction between this and other less hairy Jamaican specimens of the same area : distinctions between specimens from Jamaica and those from Hispaniola and Puerto Rico are likewise not clear-cut. Hence the epithet *microphylla* is here used to cover them all.

6. **Oplonia tetrasticha** (C. Wright ex Griseb.) Stearn, comb. nov.

Anthacanthus tetrastichus C. Wright ex Griseb., Cat. Pl. Cub. : 198 (1866).—Alain in León & Alain, Fl. Cuba 4 : 500, fig. 219 (1957).
Hesperanthemum tetrastichum (C. Wright ex Griseb.) Kuntze, Revis. Gen. Pl. 2 : 490 (1891).
Anthacanthus acicularis sensu Lindau in Urban, Symb. Antill. 2 : 214 (1900) pro parte min. ; non (Swartz) Nees.

Much branched spiny shrub, up to about 2 m. high ; *branches* stout, yellowish when young and pubescent all round or only on two opposite sides with short spreading hairs, the internodes 5–15 mm. long ; *spines* horizontally spreading or very slightly ascending straight, rigid, 1–3·5 cm. long, to 1 mm. thick, simple (var. *tetrasticha*) or branched (var. *polyece*), glabrous or minutely pubescent. *Leaves* short-stalked, the blade narrowly obovate to narrowly elliptic, the apex rounded, slightly mucronate, the base cuneate, 6–10 mm. long (including the 1–3 mm. long petiole), 2–3 mm. broad much shorter than the spines, glabrous, the veining not evident. *Flowers* solitary in the axils ; *pedicels* 4–6 mm. long, glabrous. *Calyx* c.3–5 mm. long, the segments subulate. *Corolla* lilac or "bright violet with white purple-dotted patch in throat" (fide Proctor), glabrous or pubescent, the tube 4·5–10 mm. long, the segments c.3–5 mm. long. *Stamens* included or exserted, the filaments c.1 or 4 mm. long, the anthers c.1·5 mm. long.

Endemic to Cuba.

6a. **Oplonia tetrasticha** var. **tetrasticha** (Text-figs. 2 D, E).

Spines all simple, not branched.

CUBA : Without precise locality : 1860–64, *C. Wright 3067* (BM ; K ; S, isotypes). *Pinar del Rio* : Cuabales al Este de la Loma de Cajálbana, La Palma, 10 June 1950, *Alain & Acuña 1395* (LS) ; 3 Apr. 1954, *Alain 3909* (LS). Norte del Pan de Guajaibón, 5 Apr. 1952, *Alain 2423* (LS). *Habana* : Guanabacoa, Lomas de las Jatas, 3 June 1923, *Ekman 16530* (S). Cojimar, 24 May 1914, *Ekman 1101* (S). Columbia, Habana, 22 June 1912, *León 3326* (LS ; P). Valle del Almendares, Dec. 1908, *León 465* (LS). Loma S. de la Jata, Guanabacoa, 4 Jan. 1912, *León 2865* (LS). Loma de Machado, Jibacoa, 2 Jan. 1929, *León & Roig 13756* (LS). *Matanzas* : Camarioca, 1849, *Rugel 249* (K). Cerca de la Boca de Canasi, 17 Oct. 1928, *León 13696* (LS). *Las Villas* (*Santa Clara*) : Sabana de Motembo, 2 Jan. 1919, *León & Fortem 8579* (LS). Loma de Belén, cerca de Santa Clara, 28 June 1931, *León 14947* (LS). Cienfuegos Bay, dry east-facing slopes of Loma San Juan, 11 July 1947, *Wood & Atchison 7416* (IJ). Gavilán, Cienfuegos, 13 Mar. 1928, *Jack 5815* (A ; LS). Alto de Farallón, Ensenada de Guajimico, S. de Cienfuegos, 21 Mar. 1953, *Alain, Clemente & Walsingham 2839* (LS). Guajimico Bay, on coast S.E. of Cienfuegos, 3–15 m., 23 Mar. 1957, *Proctor 16430* (IJ). *Oriente* : El Cobre, 6 Oct. 1916, *Ekman 7832* (S). Santiago, in limestone hills W. of Playa Siboney, 8 Nov. 1917, *Ekman 8723* (S). Santiago, pr. Aquadores, 1922, *Ekman 15631* (S). Sierra de Nipe, between Rio Bayate and Rio Piedra, 8 Sept. 1922, *Ekman 15042* (BM ; S).

6b. ***Oplonia tetrasticha*** var. ***polyece*** Stearn, var. nov. (Text-figs, 2 F, G.)

Spinae primariae rectae lignosae 1–3·5 cm. longae plerumque ramosae spinas secundarias plerumque 2 interdum 4 geminatas 1–12 mm. longas vel tantum gemmas minutas geminatas ferentes.

Primary spines straight, 1–3·5 cm. long, usually branched and bearing 2–4 paired spines 1–12 mm. long or in their place minute paired buds.

CUBA : *Oriente* : Sierra Maestra, on the edge of Arroyo Corojo, a tributary of Yara, near Nagua, c.150 m., 5 Aug. 1922, *Ekman 14735* (BM). Cuabales de serpentina, Holguin, May 1939, *León & Carabia 18981* (LS). Pinal Mayari, Sierra de Nipe, 7 Apr. 1941, *León, Marie-Victorin, Clemente & Alain 19920* (LS). Renté, Bahia de Santiago, 1 May 1943, *Clemente 2680* (LS). Club de Punta Gorda, Bahia de Santiago de Cuba, 1 Mar. 1953, *López Figueiras 911* (LS). Manigua costera de Santiago de Cuba, Mar. 1954, *López Figueiras 1131* (LS). Antigua linea de Firmeza, Santiago de Cuba, May 1946, *Clemente 5014* (LS). Manigua de Ciudamar, June 1946, *Clemente 5039* (BM ; LS). Camino viejo del Morro, Oct. 1947, *Clemente 5657* (BM, holotypus ; LS) ; July 1943, *Clemente 2906* (LS). Manigua de Aguadores, Santiago de Cuba, May 1946, *Clemente 5021* (LS). Punta de la Gaviota junto a la Playa de Siboney, Santiago de Cuba, 24 Feb. 1952, *López Figueiras 359* (LS). Farallon de la Perla, 14 Feb. 1911, *Shafer 8772* (GH ; K). La Perla, prope villam Monte Verde, 1859, *C. Wright 369* (GH ; K). Las Ninfas, Guantánamo, Feb. 1919, *Hioram 2354* (LS). Macambo, Via Azul, 28 Dec. 1954, *Alain & López Figueiras 4210* (LS). Charrascos de Jauco, July 1924, *León 1191* (LS). Region de Baracoa, entre Jauco y Cajobabo, July–Aug. 1924, *León 11987* (LS), *12079* (LS), *12031* (LS).

The long and rigid sharply pointed spines projecting from the branches in four ranks (whence the epithet *tetrasticha*) have earned this species the Cuban vernacular name " no-me-toques ". They are longer than in any other species of *Oplonia*. The type collected by Charles Wright somewhere in western Cuba has simple stiletto-like spines, as have other specimens collected outside of the Oriente province. Within that province, along the south coast, there is a marked tendency for these major spines to bear a pair or two pairs of subsidiary spines which are usually short but may be up to 12 mm. long. Numerous specimens with such branched spines have been collected around Santiago de Cuba. Many of them have the shoots hairy on two opposite sides only, the two sides alternating with these being glabrous, but some (e.g. *López Figueiras 359* from Siboney, near Santiago de Cuba) are hairy all round. The leaves of main shoots vary from 5 to 12 mm. in length ; those on the spines are much smaller. The plant would appear to initiate a lateral branch, then halt its development after producing a pair or less often two pairs of short spines, then stop its development entirely by making it terminate as a sharp spine. The few corollas examined of this variant have been glabrous, whereas the few corollas examined of typical *O. tetrasticha* have been minutely pubescent. A specimen of the Baracoa region, Oriente, collected by León (*León 12031*), appears at first to have long simple spines as in typical *O. tetrasticha*, but these bear nevertheless a pair of minute buds corresponding to the secondary spines of other specimens collected in this area by León. The Oriente population with branched spines is accordingly here distinguished as var. *polyēcē*, the epithet from πολυ- (" many ") and -ηκη (" pointed ") being formed by analogy with εὐήκη '(" well-pointed ") and λεπτηκή (" fine-pointed ").

Usually the spines are more than 1·5 cm. long. A specimen from Habana province, collected by Ekman (*Ekman 1101*) at Cojmar, which it does not seem possible to refer to any species but *O. tetrasticha*, nevertheless has straight slightly ascending spines with the smallest down to 3 mm., the longest to 2 cm. long. Another Ekman gathering (*Ekman 15042*) from Oriente province has more slender spines than is typical and approaches *O. microphylla.*

7. **Oplonia acicularis** (Swartz) Stearn, comb. nov. (Text-fig. 2 H, I).

Justicia acicularis Swartz, Nov. Gen. & Sp. Pl. : 13 (1788) ; Fl. Ind. Occ. 1 : 29 (1797).—Vahl, Enum. Pl. 1 : 169 (1804).

Eranthemum aciculare (Swartz) R. Br. ex Roem. & Schult. in L., Syst. Veg., ed. nov. 1 : 177 (1817).

Anthacanthus acicularis (Swartz) Nees in DC., Prodr. 11 : 460 (1847) excl. parte.

Anthacanthus jamaicensis Griseb., Fl. Brit. W. Ind. Is. : 457 (1862), *nom. superfl.*

Hesperanthemum aciculare (Swartz) Kuntze, Revis. Gen. Pl. 2 : 490 (1891).

Anthacanthus spinosus sensu Lindau in Urban, Symb. Antill. 2 : 216 (1900) pro parte min. ; non (Jacq.) Nees.

Low spreading much branched spiny shrub, mostly under 30 cm. high ; *branches* slender, brownish when young and pubescent with minute upward-pointing hairs on 2 or all sides ; *spines* very slender, 8–14 mm. long, c. 0·3 mm. thick. *Leaves* short-stalked, the blade ovate to narrowly lanceolate, the apex obtuse, mucronate, the base cuneate or rounded, 7–25 mm. long (including the c.1 mm. long petiole), 4–10 mm. broad, glabrous, the veining not evident. *Flowers* solitary in the axils ; *pedicels* c.3–4 mm. long, minutely pubescent. *Calyx* 2·2–4 mm. long, the segments very narrowly lanceolate or subulate, ciliate. *Corolla* white, glabrous, the tube cylindrical c.4–6·5 mm. long, the limb spreading with segments oblong, c.4–6 mm. long, 2·5–3 mm. broad, obtuse. *Stamens* included, inserted on the upper third of the corolla-tube, the filaments c.0·8 mm. long, the anthers 1·4 mm. long. *Capsule* c.1·5 cm. long ; *seeds* c.2·5 mm. long, rugose.

Endemic to Jamaica.

JAMAICA : Without precise locality : 1862, *March* (K) ; *Swartz* (S, type collection) ; *Wilson 453* (GOET ; K). *Westmoreland* : Between Grange Hill and Glasgow, Mar.–Apr. 1908, *E. G. Britton 2894* (NY). Hills near Bulstrode, 12 Mar. 1908, *E. G. Britton 2877* (K ; NY). *Portland* : Gorge of the Swift River at Eden, ½ mile N. of Paradise, 30 m., 19 Mar. 1956, *Stearn 550* (BM), *Proctor 11866* (IJ). Navy Island, June 1897, *Fredholm 3073* (NY ; US). Friendship Valley district near Ecclesdown, 330–360 m., 23 May 1967, *Proctor 27920* (IJ). Priestman's River, Nov. 1886, *Hart 1545* (K) ; 3 m., 13 Aug. 1957, *Proctor 16574* (IJ) ; 18 Mar. 1958, *Yuncker 18421* (IJ). Lawrence Bottom, 370 m., Mar. 1961, *Adams 9258* (UCWI). *St. Thomas* : Big Level district, S.E. end of John Crow Mountains, 450–600 m., 16 Mar. 1956, *Stearn 498* (BM), *Proctor 11818* (IJ).

Although *O. acicularis* has been recorded (as *Anthacanthus acicularis*) from many West Indian islands, through confusion with other species, it is, in fact, a Jamaican endemic characterized by low growth, slender needle-like spines, mostly ovate leaves and small white flowers which make it easily distinguishable in a living state from other Jamaican species. It often grows in somewhat shaded places. Swartz's original diagnosis of his *Justicia acicularis* reads : " I. fruticosa, diffusa, spinosa, spinis setaceis, floribus pedunculatis axillaribus solitariis. Jamaica ". Later he supplemented this in his *Flora Indiae Occidentalis* with a detailed description, giving particulars such as " Fruticulus pedalis . . . Folia petiolata, opposita ovata minora, apice acumine brevissimo . . . Spinae oppositae, setaceae . . . Flores . . . parvi, albidi " etc., which together apply only to the Jamaican species described above. It has a remarkably disjunct distribution within the island, most specimens having been collected on the extreme east and a few in the west but none in the middle.

8. **Oplonia purpurascens** (Griseb.) Stearn, comb. nov. (Text-fig. 2 P, Q.)

Anthacanthus purpurascens Griseb., Cat. Pl. Cub. : 197 (1866).—Alain in León & Alain, Fl. Cuba 4 : 500 (1957).
Hesperanthemum purpurascens (Griseb.) Kuntze, Revis. Gen. Pl. 2 : 490 (1891).
Anthacanthus acicularis sensu Lindau in Urban, Symb. Antill. 2 : 214 (1900) pro parte min. ; non (Swartz) Nees.

Shrub ; *branches* ascending, slender, purplish, glabrous on 2 opposite sides, minutely pubescent on the 2 other sides when young ; *spines* ascending at an angle of c.48–58°, slender, straight, 4–8 mm. long, at base 0·5 mm. thick. *Leaves* short-stalked, the blade obovate or oblanceolate, the apex obtuse, entire or slightly emarginate, the base narrowly cuneate, 6–15 mm. long, 1·5–6 mm. broad, glabrous, the veining scarcely evident ; petiole 1–3 mm. long. *Flowers* solitary or paired in the axils ; *pedicels* c.1–1·5 mm. long. *Calyx* c.3–4 mm. long, the segments very narrowly lanceolate or subulate. *Corolla* " pale purple ", minutely pubescent, the tube c.8–9 mm. long, the segments c.6 mm. long. *Stamens* included.

Endemic to Cuba.

CUBA : Without precise locality, 1860–64, *C. Wright 3066* (BM ; K ; S, isotypes). *Pinar del Rio* : Sierra de Viñales, 8 June 1923, *Ekman 16582* (BM). Mogote de la Bandera, Viñales, 9 Mar. 1924, *Ekman 18658* (LS). Ensenada de los Muertos, Mogote de la Bandera, Viñales, 29 Mar. 1953, *Alain 2860* (LS). Ensenada de la Bandera, Mogote de la Bandera, Viñales, Mar. 1953, *Alain 2892* (LS).

O. purpurascens is a species characteristic of the mogotes (" haystack hills " or " Kegel-karst ") of north-western Cuba. The very short pedicels distinguish it from allied species. Possibly here belongs a specimen collected in the district of Cienfuegos, Santa Clara by R. Combs (*Combs 567* ; K).

9. **Oplonia nannophylla** (Urban) Stearn, comb. nov. (Text-fig. 2 N, Pl. 45).

Anthacanthus nannophyllus Urban in Fedde, Repert. Sp. Nov. 20 : 350 (1924).

Low spreading shrublet branched from the base, 4–8 cm. high ; *branches* spreading or arching, slender, minutely pubescent when young, the internodes 1–3 mm. long ; *spines* almost horizontally spreading or ascending, straight or very slightly curved, slender, 2·5–11 mm. long, at base to 0·5 mm. thick. *Leaves* short-stalked, almost sessile, much shorter than the spines, the blade obovate or narrowly elliptic, the apex obtuse, the base broadly cuneate, 2–5 mm. long, 1–3 mm. broad, glabrous, the cystoliths numerous, the veining not evident, rigid ; petiole c.0·5 mm. long. *Flowers* unknown.

Endemic to Cuba.

CUBA : *Pinar del Rio* : Cuabales, Oeste de la Loma de Cajálbana, La Palma, 3 Apr. 1954, *Alain 3901* (LS) ; Feb. 1953, *Alain 2757* (LS). *Habana* : prope Guanacaboa in Lomas de la Yatas, 3 June 1923, *Ekman 16534* (S, type). *Las Villas* (*Santa Clara*) : Manigua, Sabana de Motembe, 28 Aug. 1922, *Léon 11385* (GH ; LS).

O. nannophylla is an inconspicuous plant of extremely reduced habit and probably slow growth, with minute leaves and short internodes, which has not yet been collected in flower. It is apparently restricted to north Cuba between 80° and 84°W.

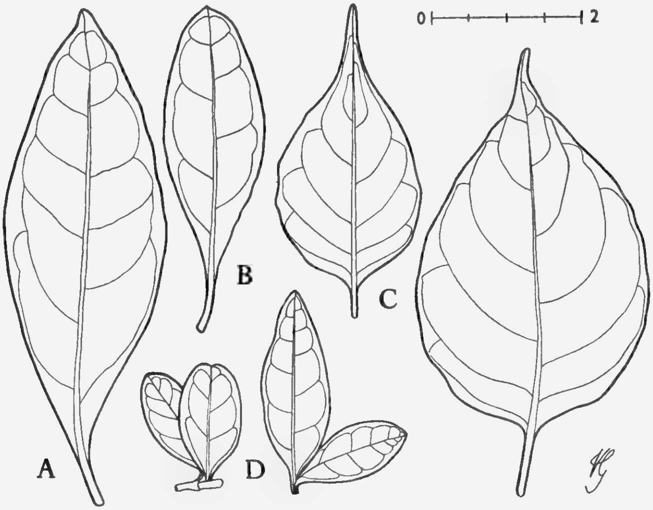

FIG. 17. Leaves of *Oplonia* from Madagasgar. A, B, *O. vincoides* ; C, *O. acuminata* ; D. *O. minor* var. *meridionalis*.

10. *Oplonia acuminata* Stearn, sp. nov. (Text-fig. 17 C)

Frutex 1–3 m. altus, inermis ; *ramuli* hornotini in sicco atri glabri [vel pubescentes], annotini graciles pallidi, internodiis plerumque elongatis ad 9 cm. longis. *Folia* manifeste petiolata ; *lamina* ovata, apice acuminata, basi rotundata in petiolum ad 1 cm. longum abrupte angustata, c. 2–5 cm. longa, acumine 5–9 mm. longo inclusa, 1–4 cm. lata, glabra [vel supra sparse subter magis praecipue secus venas puberula], cystolithis tantum sub lente visibilibus sed numerosis, papyracea, venis arcuatis conspicuis. *Flores* axillares 1–3 ; *pedicelli* 7–9 mm. longi, glabri. *Calyx* c.5 mm. longus, sparse puberulus [vel glaber], segmentis subulatis. *Corolla* alba, bilabiata ; tubus c.4·5 mm. longus, sparse puberulus ; labium superum ascendens c. 8 mm.

longum, segmentis duobus supra medium coalitis quamobrem bilobatum lobis liberis c.3·5 mm. longis 2 mm. latis ; labium inferum descendens trifida, segmentis anguste ovatis acutis c. 8–9 mm. longis, 4 mm. latis ; segmenta extra intraque praecipue apicem versus puberula. *Stamina* in fauce affixa, exserta ; *filamenta* laevia, in typo 5·5 mm. longa ; *antherae* purpureae, c.2 mm. longae ; *staminodia* minuta. *Ovarium* glabrum ; *stylus* puberulus, c.12 mm. longus. [*Capsula* c.1·7–2·5 cm. longa].

Shrub 1–3 m. high ; *branches* slender, glabrous or pubescent when young ; *spines* absent. *Leaves* short-stalked, the blade ovate, the apex acuminate, the base rounded and abruptly narrowed into the petiole, 2–5 cm. long (including the 5–9 mm. long elongated tip), 1–4 cm. broad, almost glabrous or else pubescent particularly below along the veins ; petiole 5–10 mm. long. *Flowers* 1–3 in the axils ; pedicels 7–9 mm. long, glabrous. *Calyx* c.5 mm. long, sparsely puberulous or glabrous, the segments subulate. *Corolla* white, puberulous, the tube c.4·5 mm. long, the segments 8–9 mm. long, 4 mm. broad, the upper two united to above the middle. *Stamens* exserted, the filaments (on the type) c.5·5 mm. long, smooth, the anthers c.2 mm. long. *Style* puberulous. *Capsule* 1·7–2·5 cm. long.

Endemic to western Madagascar.

MADAGASCAR : Environs de Majunga ; arbuste 1–3 m., fleur blanche à 2 lèvres, la supérieure entière, l'inférieure trilobée ; Nov. 1914, *Perrier de la Bathie 12908* (P, holotype). Vallée du Fiherenana, à 15–25 kil. en amont de Tuléar ; arbuste 2 m., corolle à lèvre inférieure blanche, lèvre supérieure blanc-verdâtre, anthères pourpres ; vers 200 m., Mar. 1934, *Humbert 14357* (K).

This is separated from *O. vincoides* by its somewhat broader, ovate, distinctly acuminate leaves which are also thinner in texture. The two upper segments of the corolla are united for more than half their length to form an apically bilobed upper lip. The only two known localities are some 500 km. apart. Details added from Humbert's specimen are cited in the Latin description in square brackets e.g. [vel pubescentes].

11. **Oplonia vincoides** (Lam.) Stearn, comb. nov. (Pl. 41, 46 ; Text-fig. 17A, B).

Justicia vincoides Lam. in Encycl. Méth. Bot. 1 : 628 (1785).—Vahl, Enum. Pl. 1 : 167 (1804).

Eranthemum vincoides (Lam.) R. Br. ex Roem. & Schult. in L., Syst. Veg., ed. nov. 1 : 176 (1817).

Anthacanthus vincoides (Lam.) Nees in DC., Prodr. 11 : 461 (1847).

Forsythiopsis baronii Baker in Journ. Linn. Soc. Lond., Bot. 20 :219, t.27 (1883) " *baroni* ".

Forsythiopsis australis Scott Elliot in Journ. Linn. Soc. Lond., Bot. 29 : 37 (1891).

Forsythiopsis vincoides (Lam.) Benoist, Cat. Pl. Madag., Acanth.: 15 (1939).—Benoist in Humbert, Fl. Madag. 182 : 106, fig. 18 no. 10–13 (1967), excl. var. *minor*.

Much-branched shrub 1–3 m. high ; *branches* slender, pilose when young ; *spines* absent. *Leaves* short-stalked, the blade narrowly elliptic to narrowly obovate, the apex usually obtuse, often emarginate, the base cuneate or attenuate, 2–9 cm. long, 0·6–3 cm. broad, conspicuously veined, puberulous when young, later almost glabrous ; petiole 2–6 mm. long. *Flowers* solitary or 2–3 in axillary fascicles ;

pedicels 1–3 cm. long. *Calyx* 4·5–6 mm. long, the segments very narrowly triangular, sparsely puberulous. *Corolla* white, blue or violet, glabrous or pubescent, the tube c.5–8 mm. long, the segments c.8–12 mm. long, 3·5–5 mm. broad, the upper two free to the lower 2·5 mm. *Stamens* almost included or long-exserted, the filaments c.1·5–3 mm. or 6–8 mm. long, papillose, the anthers 1·5–2 mm. long. *Style* puberulous. *Capsule* c.2–2·5 cm. long.

Endemic to Madagascar.

MADAGASCAR : Without locality, but apparently from Fort Dauphin, *Commerson* (P, type collection of *Justicia vincoides*). Fort Dauphin, *Scott Elliot 2586* (BM ; K, lectotype of *Forsythiopsis australis*), *2701* (K) ; *Cloisel 209* (BM). 10 km. W. of Fort Dauphin, 0–12 m., 2 Sept. 1968, *McWhirter & Capuron 184* (K). Central Madagascar [Imerina], *Baron 1937* (K, type of *F. baronii*). Ankorafantsika, Ambalo-Boeni, 10 Oct. 1950, *Ramamoufisoa 2058* (P).

Lamarck described his *Justicia vincoides* from herbarium material collected in Madagascar by Philibert Commerson, who spent the last three months of 1770 botanizing around the French settlement, Fort Dauphin, in the extreme southeast of the island. Here, therefore, must be its type-locality. No specimen now exists in Lamarck's private herbarium and possibly he never possessed one but based his description of *J. vincoides* on the Commerson specimen still existing in the herbarium of the Museum National d'Histoire Naturelle, Paris (Pl. 46). In 1847 Nees referred it to the genus *Anthacanthus* after studying another Commerson specimen in Vahl's herbarium at Copenhagen. The epithet *vincoides* was suggested by a general resemblance in leaf to a periwinkle, probably *Vinca minor* L. The leaves of the Commerson specimen in Paris are elliptic, narrowly elliptic or narrowly obovate, cuneate at base, obtuse at the apex, with a minute apiculus, 2–4 cm. long, 7–15 mm. broad, prominently veined and glabrous. The flowers are clustered in short-peduncled axillary cymes. The corolla is pubescent inside and out, the tube about 5 mm. long, the segments about 8 mm. long, 4 mm. broad ; the two segments of the upper lip are fused for the lower 2·5 cm. The filaments of the stamens are about 1.5 mm. long. Likewise short stamens occur on a specimen collected near Fort Dauphin by Cloisel (*Cloisel* 209). It is almost identical with the specimens collected near Fort Dauphin by Scott Elliot on which in 1891 he based his *Forsythiopsis australis* ; these, however, have filaments about 5 mm. long. This Madagascan species thus manifests the same floral dimorphism, some individuals having long stamens and short styles, others short stamens and long styles, as the West Indian species of *Oplonia*.

In 1883 Baker founded the genus *Forsythiopsis* with one species, *F. baronii*, on specimens collected by the English missionary Richard Baron in central Madagascar, the precise locality in the Imerina region unfortunately not recorded. Whereas in the Fort Dauphin material of *O. vincoides* the leaves are evidently mature, on Baron's specimen the leaves are only partly developed, the longest only 2·5 cm. long, 1–2 cm. broad, which may be associated with a local difference of climate. The corolla is pubescent, with the tube about 7 mm. long, the segments about 10–11 mm. long, 4·5 mm. broad, the two segments of the upper lip being united for about the lower

2 mm. The filaments of the stamens are about 2·5 mm. long. A specimen with similar immature leaves was collected by Ramamoufisoa. Benoist in 1939 equated it with Lamarck's *Justicia vincoides* and Scott Elliot's *Forsythiopsis australis*. Baker compared his *Forsythiopsis* with *Ruellia* and Benoist in 1967 similarly placed it in the " Tribu des Ruelliées " next to *Strobilanthus*. On account of its 3-colporate usually prolate pollen, with a pseudocolpus (colpoid streak) each side of the colpus, and other characters, including imbricate aestivation, it belongs, however, to the subfamily *Ruelloideae* tribe *Ruellieae* subtribe *Odontoneminae* as defined by Bremekamp (1965), not to his subtribe *Ruellinae* or subtribe *Strobilanthidinae*, and it cannot be separated from *Oplonia*. The unlikelihood of Madagascan material having any affinity with American and the consequent neglect of comparison together account for the acceptance of *Forsythiopsis* as an endemic Madagascan genus.

Although the application of the epithet *vincoides* to the taxon of the Fort Dauphin area with narrowly elliptic leaves up to 9 cm. long, 3 cm. broad, is thus certain, the circumscription of the species presents much difficulty. Thus Benoist in 1930 described a *Forsythiopsis minor* with obovate or narrowly obovate leaves only 2–7 mm. long, 1–4 mm. broad, which in 1967 he treated as *F. vincoides* var. *minor*. In 1949 he described under *F. vincoides* two varieties, one with glabrous leaves, his var. *meridionalis*, the other with densely hairy leaves, his var. *vestita*, both with obtuse leaves not more than 3 cm. long. He also included in *F. vincoides* material with ovate distinctly acuminate leaves. His 1967 concept of *F. vincoides* thus embraced several distinguishable taxa, which seem to represent at least three species.

12. **Oplonia puberula** Stearn, sp. nov. (Text-fig. 18).

Frutex (liana caule crasso, fide Humbert et Capuron), inermis ; *ramuli* pallidi, hornotini puberuli, annotini decorticantes glabri, internodis ad 5 cm. longis. *Folia* breviter petiolata ; *lamina* anguste obovata, apice rotundata, obtusa vel acuta, basi cuneata, immatura c.2–4·5 cm. longa, 1–2 cm. lata, supra sparse puberula, subter praecipue secus venas multo magis puberula, venis arcuatis conspicuis utroque latere costae 5–7 ; petiolus ad 6 mm. longus, dense puberulus. *Flores* axillares plerumque 4 ; *pedicelli* 5–10 mm. longi, dense puberuli. *Calyx* 2·5–3 mm. longus, omnino dense puberulus, segmentis anguste oblongis obtusis. *Corolla* violacea (fide Humbert et Capuron), bilabiata ; tubus c.7–8 mm. longus, puberulus ; labium superum ascendens c. 12 mm. longum, segmentis duobus fere ad medium coalitis quamobrem bilobatum lobis liberis c. 7 mm. longis, 3 mm. latis ; labium inferum descendens trifida, segmentis ellipticis obtusis c. 12 mm. longis, 5·5 mm. latis ; segmenta extra intraque puberula. *Stamina* in fauce affixa, exserta ; *filamenta* valde papillosa, in typo 4 mm. longa ; *antherae* olivaceae (fide Humbert et Capuron), c.1·5 mm. longae ; *staminodia* minuta. *Ovarium* glabrum ; *stylus* dense puberulus, c.12 mm. longus.

Shrub (a thick-stemmed liane according to Humbert & Capuron) ; *branches* puberulous when young ; *spines* absent. *Leaves* short-stalked, the blade narrowly obovate, the apex rounded, obtuse or acute, the base cuneate, about 2–4·5 cm. long, 1–2 cm.

broad in an immature state, above sparsely puberulous, below much more thickly puberulous, particularly along the veins ; petiole to 6 mm. long. *Flowers* about 4 in the axils ; pedicels 5–10 mm. long, densely puberulous. *Calyx* 2·5–3 mm. long, densely puberulous all over, the segments narrowly oblong. *Corolla* violet, puberulous, the tube 7–8 mm. long, the segments c.12 mm. long, 3–5·5 mm. broad, the upper two united almost to the middle. *Stamens* exserted, the filaments (on the type) c.4 mm. long, the anthers c.1·5 mm. long. *Style* densely puberulous.

Endemic to northern Madagascar.

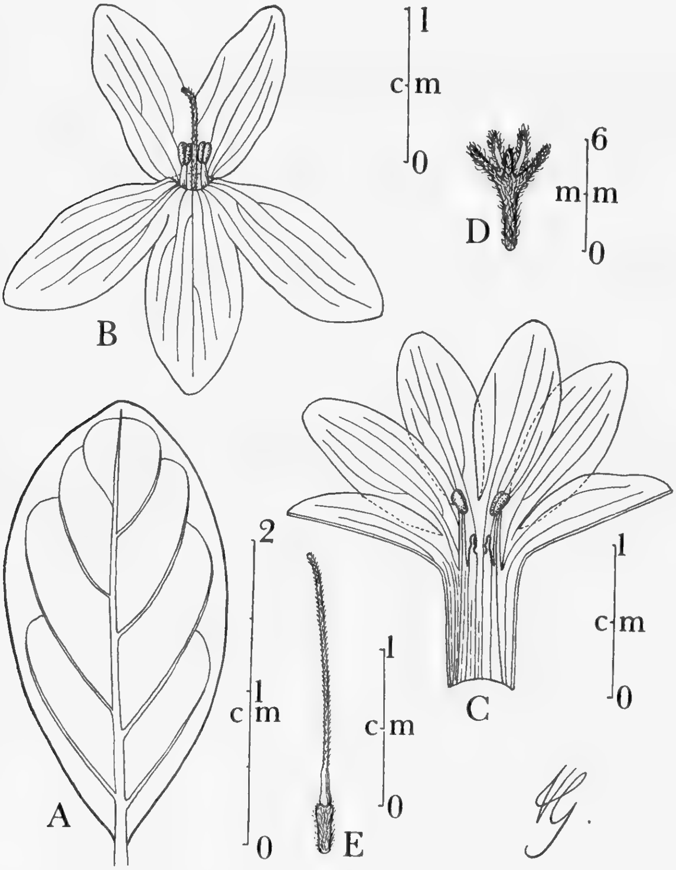

Fig. 18. *Oplonia puberula* Stearn. A, leaf; B, flower in front view; C, corolla in longitudinal section; D, calyx; E, gynoecium.

Madagascar : Vallée inférieure de l'Androranga, affluent de la Bemarivo (nord-est) aux environs d'Antongondriha, Mont Anjenabe, forêt ombrophile sur gneiss ; grande liane à tige épaisse, écorce subereuse, corolle violette, anthères olivâtres, style blanc ; 750 m., 3–7 Nov. 1950, *Humbert & Capuron 24103* (P, holotype ; BM).

This taxon comes very close to *O. vincoides*, from which it may be distinguished by its narrowly oblong calyx-segments completely and densely covered outside with very short erect hairs ; those of *O. vincoides* are narrowly triangular with much sparser hairs not completely covering their surface. It is everywhere hairier than *O. vincoides* and has a slightly shorter calyx and slightly larger corolla. There would also appear to be a difference in habit if Humbert and Capuron's description of it as a large liane is correct and applies to other specimens. On these grounds it is here given separate specific rank. The type-gathering evidently represents a long-styled state ; the style itself is more densely hairy and slightly longer (i.e. c.12 mm. long as against 8–9 mm.) than in long-styled *O. vincoides*.

13. ***Oplonia minor*** (Benoist) Stearn, comb. nov.

Forsythiopsis minor Benoist in Bull. Soc. Bot. France 76 : 1033 (1930).
Forsythiopsis vincoides var. *meridionalis* Benoist in Mém. Soc. Bot. France 1949 : 94 (1949).—Benoist in Humbert, Fl. Madag. 182 : 108 (1967).
Forsythiopsis vincoides var. *vestita* Benoist, loc. cit. (1949).—Benoist, loc. cit. (1967).
Forsythiopsis vincoides var. *minor* (Benoist) Benoist in Humbert, Fl. Madag. 182 : 109 (1967).

Shrub ; *branches* slender, pubescent when young ; *spines* absent. *Leaves* short-stalked, the blade obovate or narrowly obovate, the apex obtuse, the base cuneate, c.2–30 mm. long, 1–10 mm. broad, puberulous when young, later glabrous or puberulous ; petiole c.1 mm. long. *Flowers* solitary or paired ; *pedicels* 7–9 mm. long. *Calyx* 2–4 mm. long, the segments subulate. *Corolla* pale violet or lilac, pubescent, the tube c.5–6 mm. long, the segments c.8–10 mm. long, 3–4 mm. broad, the upper two united at base for the lower third of their length. *Stamens* almost included or long-exserted, the filaments c.2·5 mm. or 5 mm. long, papillose, the anthers c.1·5 mm. long. *Style* puberulous or almost glabrous. *Capsule* c.1·5 cm. long.

Var. ***minor***

F. minor Benoist, loc. cit. (1930).

Leaves 2–9 mm. long, 1–4 mm. broad, puberulous when young, later glabrous. *Calyx* 2–3 mm. long, glabrous.

Madagascar : Fort Dauphin, Behara, 10 July 1926, *Decary 4273* (BM ; K). Environs de Tuléar, 10–200 m., Sept. 1924, *Humbert & Perrier de la Bathie 2506* (K). Many other localities are cited by Benoist (1967).

Var. ***meridionalis*** (Benoist) Stearn, comb. nov. (Text-fig. 17D).

F. vincoides var. *meridonalis* Benoist, loc. cit. (1949).

Leaves 12–25 mm. long, 4–10 mm. broad, becoming glabrous. *Calyx* c.3 mm. long, almost glabrous.

Madagascar : Fort Dauphin, c. 1890, *Cloisel 9* (BM). Amborombe, 7 Aug. 1931, *Decary 9118* (BM ; K). Massif de l'Andohahelo, au-dessus de Pisopiso (Beake), 1000–1100 m., Jan. 1934, *Humbert 13676* (K, isotype of *F. vincoides* var. *meridionalis*).

Var. **vestita** (Benoist) Stearn, comb. nov.

F. vincoides var. *vestita* Benoist, loc. cit. (1949).

Leaves 8–30 mm. long, 3–15 mm. broad, puberulous on both surfaces, densely so along the veins below. *Calyx* 2·5–6 mm., puberulous.

MADAGASCAR : Basse valléee du Fiherenana, 50–200 m., Nov. 1933, *Humbert 11535* (K, isotype of *F. vincoides* var. *vestita*). Forêt de Besomaty entre le Fiherenana et l'Isahaina (Mangoky), 750–800 m., Oct. 1933, *Humbert 11272* (P). La Table Tuléar, *Dequaire 329* (P). Au delta de la Linta, au nord d'Itampolo, 1–10 m., Aug. 1928, *Humbert & Swingle 5382* (P).

The plants assembled here under the name *O. minor* are primarily distinguished from *O. vincoides* by their much smaller leaves and somewhat smaller flowers. Since they vary between themselves and merit study with more extensive material, it has seemed best to indicate variation as above, following Benoist, with some hesitation and doubt as to the validity of these taxa.

14 ***Oplonia linifolia*** (Benoist) Stearn, comb. nov.

Forsythiopsis linifolia Benoist in Notulae Syst. Paris 12 : 11 (1945).—Benoist in Humbert, Fl. Madag. 182 : 109, fig. 18 no. 14 (1967).

Shrub ; *branches* slender, glabrous ; *spines* absent. *Leaves* sessile, linear, the apex acute, the base cuneate, 5–10 mm. long, scarcely 1 mm. broad, glabrous. *Flowers* solitary ; pedicels 3–6 mm. long, glabrous. *Calyx* 2 mm. long, glabrous, the segments narrowly triangular. *Corolla* lilac, pubescent, the tube c.5 mm. long, the segments c.6 mm. long. *Stamens* slightly exserted ; filaments c.1 mm. long ; anthers c.1 mm. long. *Style* puberulous. *Capsule* c.1·5 cm. long.

MADAGASCAR : Bassin de la Linta, plateau calcaire à l'est du delta, 200–250 m., August 1928, *Humbert & Swingle 5507* (P, holotype).

This minute and rare species, only known from one locality in southern Madagascar, stands apart from all others by its very narrow linear leaves.

EXCLUDED SPECIES

Anthacanthus bispinosus Griseb. in Mem. Amer. Acad. Arts & Sci., New Ser. 8 : 525 (1862) from Cuba (Oriente) = *Barleriola solanifolia* (L.) Oerst. ex Lindau in Engler, Bot. Jahrb. 18 : 63 (1893), based on *Barleria solanifolia* L., Sp. Pl. 2 : 636 (1753) ; cf. Lindau in Urban, Symb. Antill. 2 : 204 (1900). Oersted described the genus *Barleriola* in Vidensk. Medd. Naturh. For. Kjöbenh. 1854 : 136 (1855) but did not publish the combination *Barleriola solanifolia* often cited from there.

Anthacanthus repandus (Forst. f.) Nees in DC., Prodr. 11 : 462 (1847), based on *Justicia repanda* Forst. f., Florul. Ins. Austr. Prodr. : 3 (1786), from Tanna, New Hebrides = *Eranthemum repandum* (Forst. f.) R.Br. ex Roem. & Shult. in L., Syst. Veg., ed. nov. 1 : 175 (1817) ; cf. Seem., Fl. Vit. : 185 (1866) = *Pseuderanthemum repandum* (Forst. f.) Guillaumin in Ann. Mus. Colon. Marseille, ser. 6, 5–6 : 49 (1948).

Anthacanthus sinuatus Nees in DC., Prodr. 11 : 462 (1847), based on *Justicia sinuata* Vahl, Symb. Bot. 2 : 11 (1791), *nom. superfl.* = *Eranthemum longifolium* (Forst. f.) Seem., Fl. Vit. : 185 (1866), based on *Justicia longifolia* Forst. f., Florul. Ins. Austr. Prodr. : 4 (1786), from Tanna, New Hebrides. = *Pseuderanthemum longifolium* (Forst. f.) Guillaumin in Bull. Mus. Hist. Nat. Paris, Ser. 2, 14 : 456 (1943).

Anthacanthus sprengelii Nees in DC., Prodr. 11 : 461 (1847), *nom. superfl.* based on *Eranthemum acanthodes* Spreng. in L., Syst. Veg., ed. 16, 1 : 88 (1824), from Hispaniola = *Scolosanthus acanthodes* (Spreng.) Urban, Symb. Antill. 1 : 481 (1900). This belongs to *Rubiaceae.*

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WILLIAM T. STEARN, D.Sc., Sc.D.
Department of Botany
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
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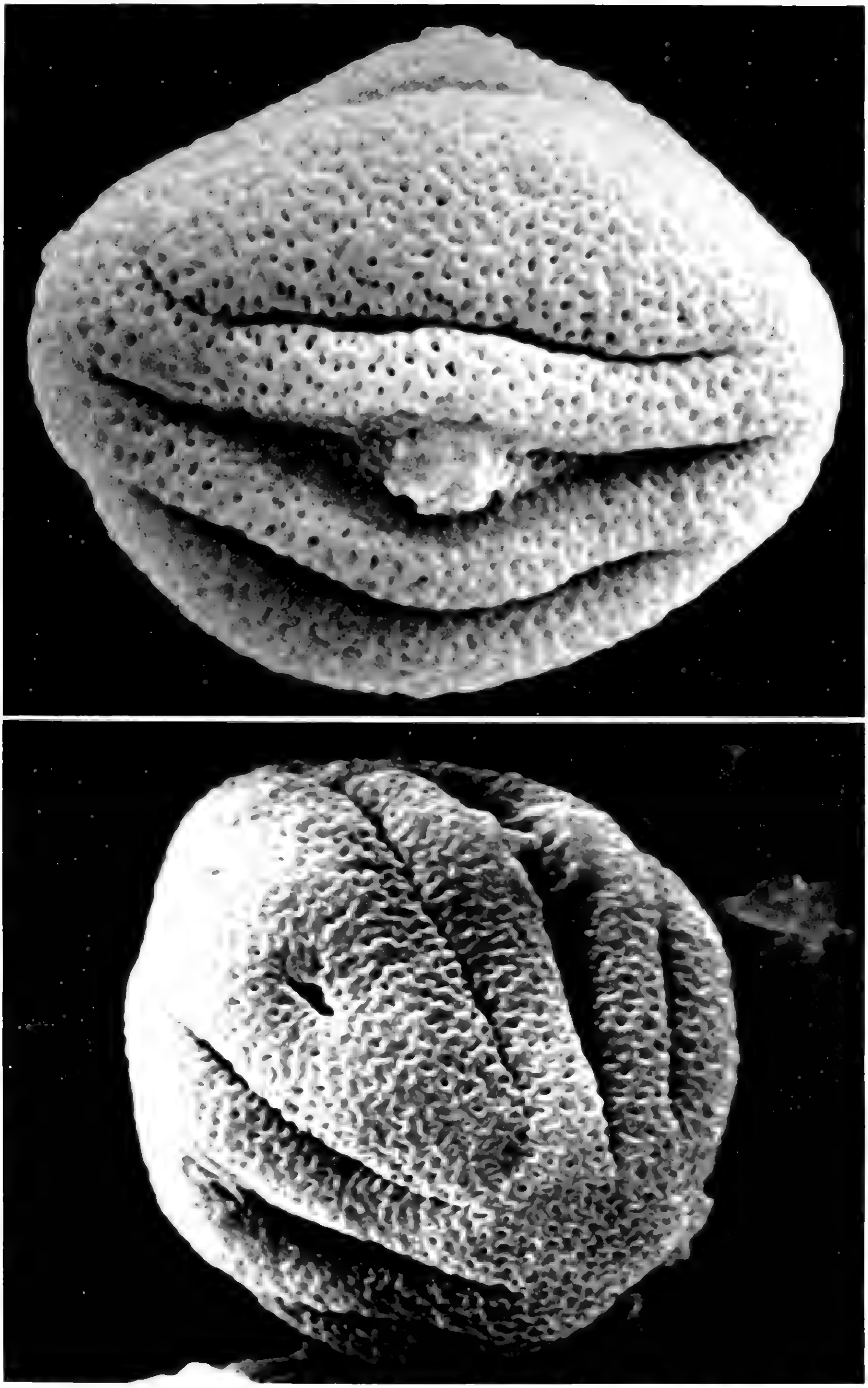
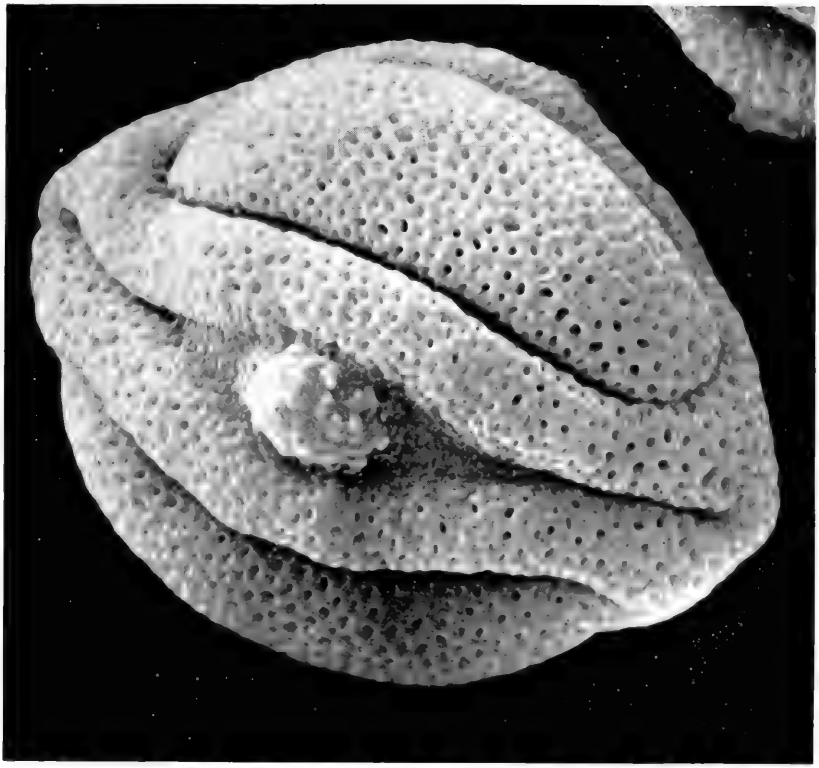
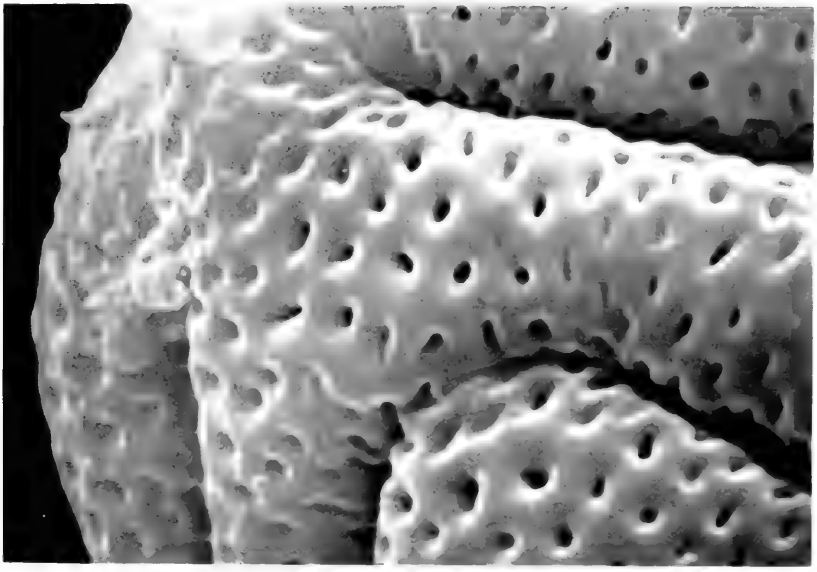
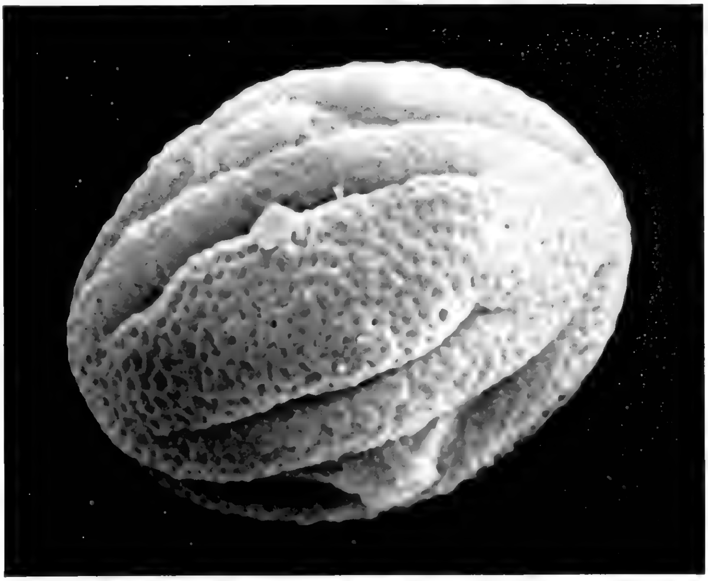


Pollen grain of *Oplonia armata* var. *pallidior* Stearn (*Stearn 726*) ; above, equatorial view, × 2000 ; below, polar view, × 2000.

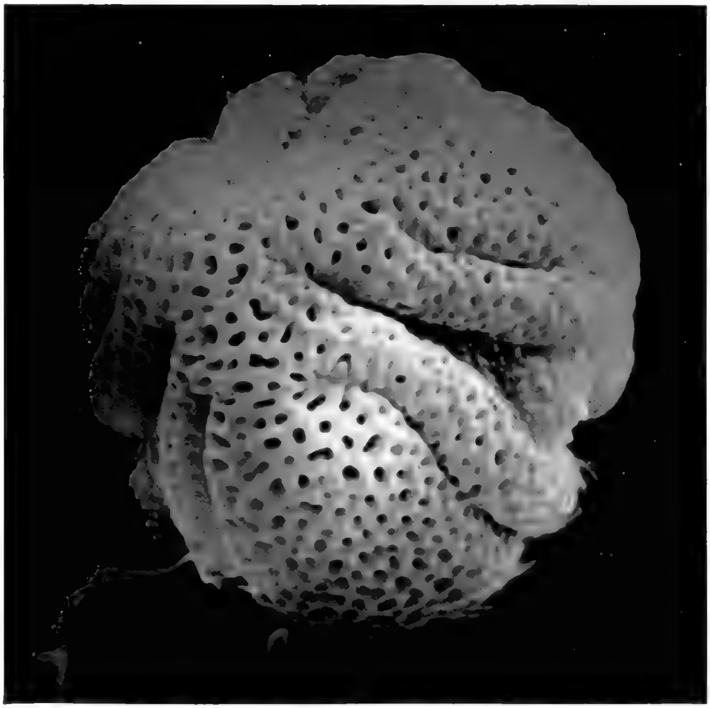




Pollen grain of *Oplonia jamaicensis* (Lindau) Stearn (*Proctor 8423*) ; above, equatorial view, × 2000 ; below, surface, × 6500.

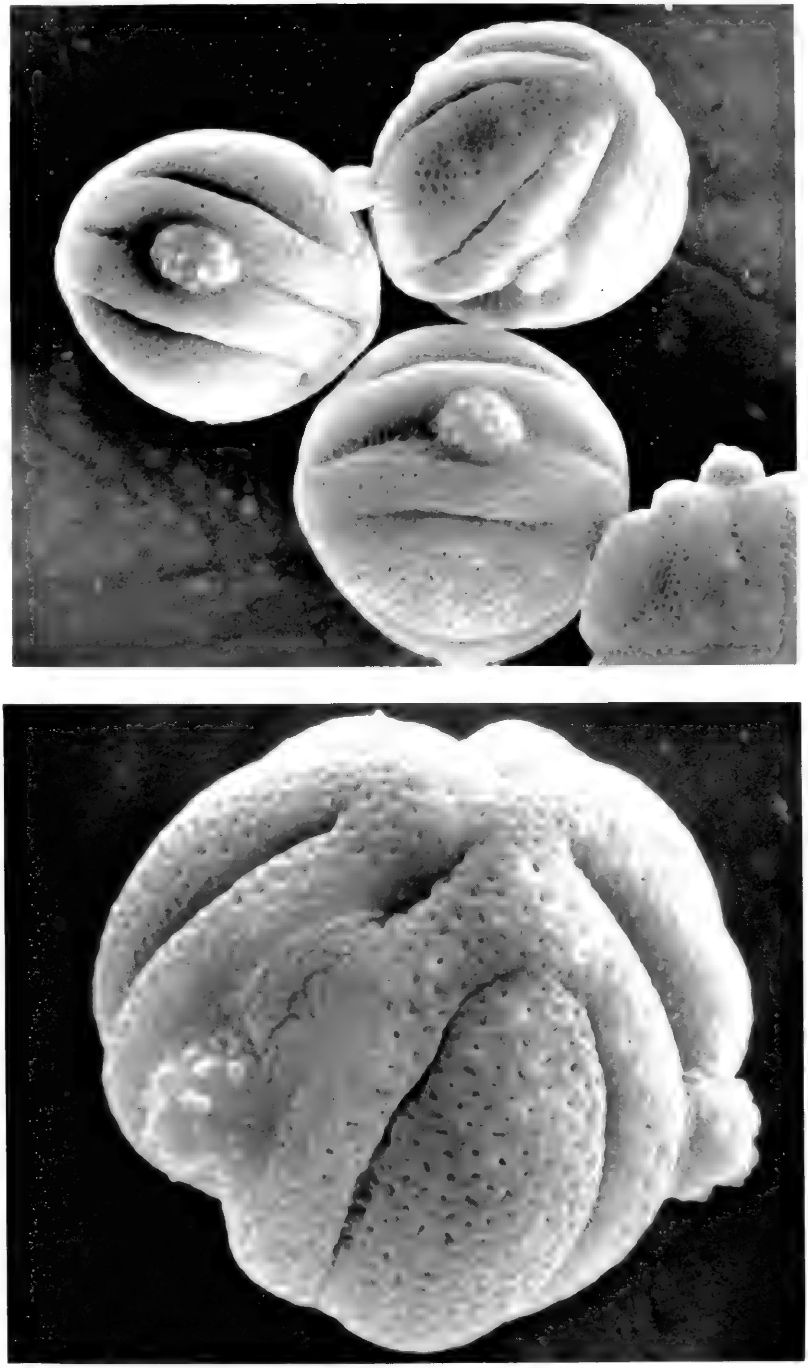


(a)



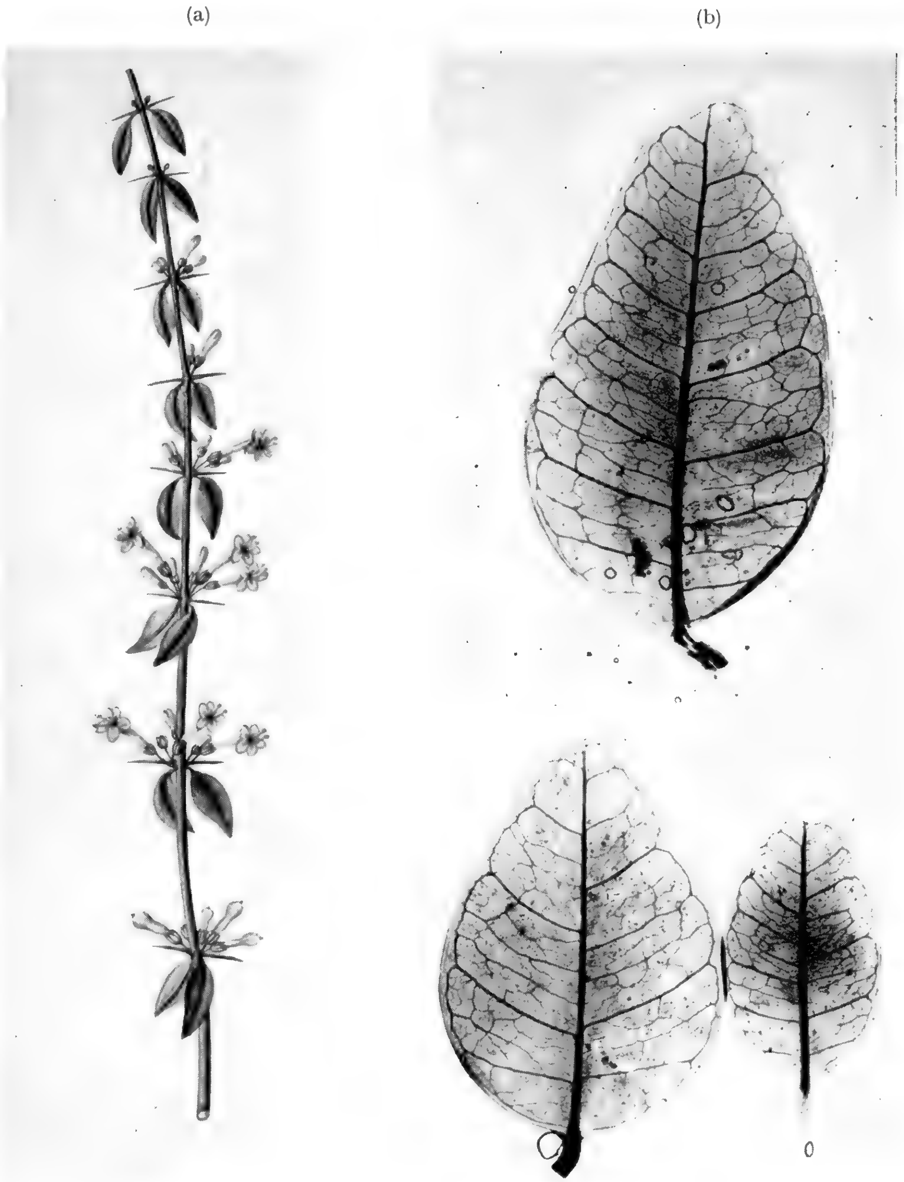
(b)

(a) Pollen grain of *Psilanthele eggersii* Lindau (*Eggers 15129*) ; equatorial view, × 2850.
(b) Pollen grain of *Oplonia grandiflora* (Lindau) Stearn (*Ule 6493*) ; polar view, × 3000.



Pollen grains of *Oplonia vincoides* (Lam.) Stearn (*McWhirter & Capuron 184*) ; above, × 1000 ; below, polar view, × 2000.

Oplonia grandiflora (Lindau) Stearn ; isotype (*Ule 6493*).



(a) *Oplonia spinosa* (Jacq.) Raf. ; drawing from Jacquin, *Select. Stirp. Amer. Pict.* (1780) representing *Justicia spinosa* Jacq. ; × ½.
(b) Cleared leaves of *Oplonia armata* var. *armata* (*Proctor* 9957) to illustrate veining characteristic of genus *Oplonia* ; × 3.

Oplonia microphylla (Lam.) Stearn ; isotype (*Richard*).

Oplonia nannophylla (Urban) Stearn ; holotype (*Ekman 15634*).

Oplonia vincoides (Lam.) Stearn; syntype (Madagascar, *Commerson*).

Psilanthele eggersii Lindau ; isotype (*Eggers 15129*).

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BOTANY Vol. 4 No. 8
LONDON : 1973

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BY

ARTHUR WALLIS EXELL

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Pp 325–411

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ANGIOSPERMS OF THE ISLANDS OF THE GULF OF GUINEA (FERNANDO PO, PRÍNCIPE, S. TOMÉ, AND ANNOBON)

By ARTHUR W. EXELL

THE time has come when it seems useful to give an up-to-date list of the flowering plants of the Guinea Islands. There have been many supplements etc. since the publication in 1944 of the *Catalogue of the Vascular Plants of S. Tomé* (*with Principe and Annobon*) (1),[1] many changes recorded in the second edition of the *Flora* of *West Tropical Africa* (10, 12, 17, 18, 21), various publications by Portuguese authors (8, 9, 13), by Emilio Guinea (2, 3, 4, 5, 6, 7) and Antonio Escarré (19), as well as changes proposed by specialists in certain families or genera. Furthermore, there has been considerable additional collecting.

Fernando Po has now been added because the only way to get a clear picture of the flora of that island is to extricate the information from F.W.T.A. ed. 2 (10, 12, 17, 18, 21) and, as will be seen from the present work, this is at times incomplete.

FLORA OF FERNANDO PO

A clear distinction must be made between Fernando Po, only 32 km from the mainland, and the other three islands. The latter (Príncipe, S. Tomé and Annobon) can scarcely be classified as 'oceanic islands' and as I know of no appropriate term in use I shall call them 'maritime islands' and Fernando Po a 'littoral island'. Of the three maritime islands only Annobon, the smallest and the furthest from the mainland, has some of the characteristics of an oceanic island, especially in its high proportion of Pteridophyta and of widespread species of Angiosperms.

The flora of Fernando Po is unlikely to have been much affected by the narrow strip of water separating it from the continent. Fairly convincing proof of this will be given later. I have noticed, however, in Africa that even a short stretch of water may prove a barrier to many Leguminosae (except for littoral species). I attribute this to the comparatively heavy seeds unsuitable for wind distribution and not, as far as I know, much distributed by birds. On the three maritime islands, although the list of Leguminosae may seem extensive, if all the introduced species, the littoral species carried by ocean currents and the doubtfully indigenous cosmopolitan, pan-tropical or American weeds are excluded, the family is poorly represented compared with the adjacent mainland. Although Fernando Po has more Leguminosae, its flora still seems impoverished with respect to this family.

The Compositae, excellently distributed by wind, are quite well represented in Fernando Po but poorly so on the maritime islands when only species with some claim to be indigenous are considered. This apparent discrepancy is almost certainly due to the presence of montane or submontane grassland (Moka, etc.) in Fernando Po and its almost complete absence in the maritime islands.

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[1] For references, see Bibliography, pp. 333–336.

Rubiaceae, Euphorbiaceae and Orchidaceae are well represented both in Fernando Po and in the maritime islands.

Endemism in Fernando Po, as befits a littoral island, is much lower than in the maritime islands. For the relevant figures and the relationship between the islands see the Statistical Summary below.

As usual in floristic comparisons one can seldom isolate the statistical behaviour due to separate factors but in comparing these islands at least differences due to climate are probably minimal, though Annobon is rather drier than the other three.

INTRODUCED PLANTS

All introduced plants of which I have seen records or specimens have been included. Species are marked with an asterisk in the Systematic List whenever there is a high probability that they are not indigenous. There are of course very many other species (mainly weeds) where the evidence is not conclusive. One reason for including the introduced species in the list is to facilitate the naming of future collections as a glance at the list may save a lot of trouble.

The introduced species fall into the following main categories :

(1) The successful introductions grown as crops for export, such as cocoa and coffee.

(2) Unsuccessful introductions for the same purpose. In the early days of Portuguese colonization there are records of many attempted introductions (wheat, rye, etc.) at a period when there was no experience of tropical agriculture to act as a guide. Many such species probably no longer exist on the islands.

(3) Species introduced as shade plants for cocoa or as ground cover.

(4) Species grown as local food plants (bananas, breadfruit, pineapples, etc.).

(5) Ornamental plants.

(6) Accidentally introduced tropical American weeds (usually clearly not indigenous).

(7) A few European or cosmopolitan weeds (such as *Plantago major*) very improbably indigenous.

There is of course another large category of weeds and widespread species which are probably introduced but could be indigenous.

It will be noticed that there are relatively far more introduced species for S. Tomé (and to a lesser extent for Príncipe) than for the other two islands. The reasons for this are historical. Both S. Tomé and Príncipe have been highly cultivated for about four centuries. By 1550 two-thirds of S. Tomé were said to be under cultivation and these islands were probably the first places where tropical agriculture for export was carried on. Fernando Po was much less exploited and I do not know of any serious export from Annobon. Nor has this small island many introduced ornamental plants.

STATISTICAL SUMMARY

I have been interested for over forty years in the problem of comparing floras of similar or different sizes inhabiting areas of similar or different sizes in order to obtain Quotients of Affinity and Quotients of Similarity (see especially Exell and

Wild in *Kirkia* **2** : 108–130 (1961)). In the work cited we discussed in some detail the various quotients which have been employed at different times and the justification for the use of the simple formula referred to as QA (EW) which is the expression of the number of species common to two floras as a percentage of the smaller one. This is used in the present work and is here simply called QA (Quotient of Affinity). After further thoughts about this formula (since 1961) I have now the impression that it tends to become less meaningful when a very small flora is compared with a very large one. In the ultimate case, when the flora of an island or region is compared with the flora of the whole of the rest of the world we get a QA which is exactly the inverse of the proportion of endemism in the small flora (i.e. with no endemics the QA becomes 100). Thus when there is a very great disparity of size between the floras under consideration the relative abundance or absence of endemism begins to loom very large in the QA figures and to obscure other factors.

Where the QA employed is at its most useful and most accurate is in comparing the flora of a given region with those of neighbouring regions not differing greatly from it or from each other in size. I have borne this in mind in the statistical comparison of the floras of the four islands with the mainland flora and confined this comparison to the Southern Nigeria and West Cameroon regions, and a combination of the two (which already begins to get too large). To extend the comparison to the whole tropical West African flora would be to approach the situation I have indicated above where the figures would do little beyond reflecting the different degrees of endemism on the different islands and be merely an immensely laborious way of arriving at such a result.

The Quotients of Affinity of the islands with one another and with the mainland regions are set out in Table I. It should be stated that the figures given in this table are not absolutely correct because of slight adjustments made to the systematic list right up to the time of going to press. The mathematical discrepancy is, however, negligible, especially in view of the considerable and unavoidable subjective factor involved in choosing which taxa to exclude (such as possibly introduced or too doubtfully identified species).

TABLE I

Quotients of Affinity of the flora of the islands of the Gulf of Guinea and the adjacent mainland

	FP	P	ST	A	SN	WC	SN + WC
FP	—	59·0	47·8	56·25	68·5	71·5	89·0
P	59·0	—	67·9	44·7	73·2	60·2	78·9
ST	47·8	67·9	—	71·5	64·4	52·6	71·9
A	56·25	44·7	71·5	—	72·1	55·8	77·9

FP, Fernando Po, 1105 species; P. Príncipe, 314 species; ST, S. Tomé, 601 species; A, Annobon, 208 species; SN, Southern Nigeria, 'S. Nig.' of the *Flora of West Tropical Africa*; WC, West Cameroon, 'Brit. Cam.' '[Br.] Cam.' and 'W. Cam.' of the various volumes of the Flora of West Tropical Africa.

If the QA figures between the various islands are compared with similar statistics given in the past (see especially Exell and Wild, *loc. cit.* Table I, column QA (EW)) it will be seen that relationships between Príncipe, S. Tomé and Annobon have not altered appreciably although the total number of species recorded for each island has increased. The figures for Fernando Po have, however, changed significantly. This is mainly due to a complete re-appraisal of the Fernando Po flora in the second edition of the *Flora of West Tropical Africa.* This has resulted in a great increase in the QA's between Fernando Po and the three maritime islands correlated with a marked decrease in the percentage of species considered endemic to Fernando Po (from 12 per cent in 1944 to 3·6 per cent now) ; this is due partly to taxonomic changes (reduction of endemics to synonymy), partly to the discovery on the mainland of species formerly thought to be endemic and partly to an increase of non-endemic species recorded. The same process has occurred to a lesser extent in the other three islands (fairly significantly in Annobon) as Table II shows.

TABLE II

Percentage of species considered as endemic in the flora of the islands of the Gulf of Guinea

	1944	1971
Fernando Po	12·0	3·6 (3·8)
Príncipe	12·7	9·9 (13·7)
S. Tomé	19·4	15·4 (17·8)
Annobon	14·8	7·7 (11)

The figures in brackets in the last column are those obtained if species occurring on more than one island but not elsewhere are reckoned as endemics.

The decrease in Annobon is due almost entirely to the fact that the recorded non-endemic flora has nearly doubled since 1944.

Relatively few new endemic species have been described to counterbalance the tendencies mentioned above. There is little hope, however, that the present figures represent anything like finality. There are many more discoveries still to make.

In the past there have not been sufficiently accurate data available to work out the QA's between the various islands and selected regions of the mainland. This has now been largely remedied with regard to Southern Nigeria and West Cameroon by the publication of the second edition of the *Flora of West Tropical Africa.*

It is perhaps worth mentioning that the statistics were first worked out separately for the Dicotyledons and Monocotyledons but no significant difference was found. The Monocotyledons do not behave statistically as a separate unit. The Orchidaceae, for example, with many endemics, behave much as the Melastomataceae, Rubiaceae and Euphorbiaceae while the Gramineae and Cyperaceae behave very like the Leguminosae and the Compositae.

It is now easiest to consider each of the four islands separately.

Fernando Po

The QA of Fernando Po with the adjacent coastal region as a whole (SN + WC of Table I) is 89. This is very high indeed. For comparison, the highest QA obtained in a statistical analysis of a sample of the flora of the region covered by *Flora Zambesiaca* was 87 between the Eastern Division of Rhodesia and the southern part of Mozambique, two adjacent and floristically closely related regions on the mainland of Africa. The only QA higher than 89 that I have yet recorded is 92·4 between the floras of Guernsey and Alderney (Channel Islands). This QA of 89 between Fernando Po and SN + WC gives statistical proof of what has long been recognized, that Fernando Po does not have an insular flora but is floristically part of the mainland.

The QA 71·5 of Fernando Po with West Cameroon is slightly higher than the QA 68·5 between the island and Southern Nigeria, indicating a fairly equal derivation of the flora of Fernando Po from West Cameroon and Southern Nigeria, but, if the species contributing to these two QAs are studied in detail, the impression is gained that the slight difference in favour of West Cameroon should really be greater than it is for it is certainly based on more significant distribution patterns. Among the species common to Fernando Po and Southern Nigeria there are far more widespread species and weeds, and many of these probably occur also in West Cameroon, which appears to be somewhat under-collected.

Príncipe

The QA of this island's flora with that of the adjacent coastal region as a whole (SN + WC) is 78·9, showing a high affinity between the two, but clearly indicating that the flora of Príncipe is more insular than that of Fernando Po. The QA with Southern Nigeria is 73·2 and that with West Cameroon 60·2, very considerably different from the figures for Fernando Po, for they show that Southern Nigeria is a more important source than West Cameroon for the flora of Príncipe. The QA of 59·0 with Fernando Po and 67·9 with S. Tomé are both fairly high, as compared for example with a QA of 47·8 between Fernando Po and S. Tomé, and seem to indicate some derivation of the flora of Príncipe from the two larger islands between which it lies.

S. Tomé

The QA between this island and the adjacent coastal region as a whole (SN + WC) is 71·9, appreciably lower than the islands nearer the mainlaind and probably fairly typical of an insular flora with considerable endemism. The QA 64·4 with Southern Nigeria is considerably higher than the QA 52·6 with West Cameroon, indicating that Southern Nigeria is the more important as a source of the flora of S. Tomé.

Annobon

This, although further from the mainland than S. Tomé, has a higher QA, 77·9, with the adjacent coastal region as a whole (SN + WC). Here we begin to get, I believe, a partial 'oceanic island' effect, a somewhat impoverished flora with a higher proportion of widespread species and rather fewer endemics. The affinity with Southern Nigeria (QA 72·1) is much higher than that with West Cameroon (QA 55·8).

A special feature of the Annobon figures is the high QA, 71·5, with S. Tomé, and this appears to be a real affinity, indicating that the small Annobon flora has been partly derived from the much larger and comparatively near-by island of S. Tomé.

The QA of 56·25 between Annobon and Fernando Po seems abnormally high for that between the two most widely separated islands, especially when it is compared with QA 47·8 between S. Tomé and Fernando Po. Detailed study indicates that is partly an 'oceanic island' effect, the flora of Fernando Po being more than five times the size of that of Annobon, and partly the result of a few anomalous distributions, which may not all be genuine.

General

There has been no change in the general hypothesis that in the main each island received its flora independently from the adjacent regions of the mainland, each receiving a considerably different selection so that the QAs with the mainland are usually higher than those between one island and another. Each island mostly produced its own endemics. There are relatively few cases of species endemic to more than one island and some of these may not survive future investigation and further collecting (i.e. they may yet be found on the mainland). A few, especially those common to S. Tomé and Annobon, are probably genuine.

I hope that it will be apparent that the comparisons given above, and in fact most of the discussion, would be almost impossible without using the QA concept. Whether the QA used here is the best one available is not so certain and any suggested improvement will always merit examination.

SYSTEMATIC LIST

This list is mainly a compilation of published records of taxa from the islands but I have been fortunate in getting assistance, for which I am most grateful, from specialists in a number of families and from other colleagues. Acknowledgements are made after the bibliography. The list is very condensed in form but it is possible from the bibliographical references and some short notes appended under the species to obtain fairly full nomenclatural data and records of specimens.

An asterisk * indicates an introduced species. It is often impossible to be certain whether a taxon such as a widespread weed is indigenous or not. It is fairly certain that all the species marked * are introduced but it is by no means certain that all the species not so marked are truly indigenous.

The bibliographical references are given by number in the central column. To avoid unnecessary complication, where infraspecific categories are now recognized, the older bibliographical references have been placed where they almost certainly belong. This usually consists of putting the reference under the typical subspecies or variety when only the specific name was originally given in the work cited. The same has been done in a few cases where it seems quite clear to which infraspecific taxon (other than the typical one) the work cited must refer even when this was not mentioned or had not been established at the time.

The letters FP, P, ST, A in the right-hand column indicate Fernando Po, Príncipe, S. Tomé and Annobon respectively and the letter E in the right-hand margin indicates an endemic taxon.

In the case of Fernando Po (FP) I have indicated all records additional to or omitted from the second edition of the *Flora of West Tropical Africa* (except in the case of introductions). These fall into very different categories. Some are evident accidental omissions (when, for example, the type is from Fernando Po), some are new and probably correct records, others are very doubtful indeed (especially those to which I have given question marks).

ANNOTATED BIBLIOGRAPHY OF WORKS PUBLISHED FROM 1944 ONWARDS

References to works prior to 1944 will mainly be found in 1, 10, 11, 12, 17, 18, 21.

Different numbers are given to the separate volumes (or parts) of the second edition of the *Flora of West Tropical Africa* in order to maintain chronological sequence and to facilitate reference.

1. A. W. Exell. *Catalogue of the Vascular Plants of S. Tomé (with Príncipe and Annobon).* 1944.

References to works prior to 1944, species references and fairly full synonymies. Contributors (Angiosperms) other than the author were: Leguminosae (partly by E. G. Baker and D. Hillcoat); Rubiaceae (by G. Taylor); Apocynaceae (by W. R. Philipson); Asclepiadaceae (partly by C. Norman); Loganiaceae (by W. R. Philipson); Acanthaceae (partly by E. Milne-Redhead); Labiatae (by G. Taylor); Euphorbiaceae (partly by J. Hutchinson); Ulmaceae (by G. Taylor); Moraceae (by G. Taylor); Urticaceae (by G. Taylor); Cannabaceae (by G. Taylor); Monocotyledones (by J. E. Dandy, with V. S. Summerhayes assisting with Orchidaceae).

2. E. Guinea Lopez. *Ensayo Geobotánico de la Guinea Continental Española.* 1946.

The relevant part is the 'Catálogo Florístico', pp. 218–368, in which Fernando Po records are given and some references made to the other islands.

3. E. Guinea (Lopez). Agrostigrafia fernandina e hispano-guineanae. *An. Agr. Territ. Españ. del Golfo de Guinea* 1947, publ. 13 : 95–164. 1948.

4. E. Guinea (Lopez). Juncaceae, Cyperaceaeque Fernandopoinae. *An. Jard. Bot. Madrid* 9 : 335–360. 1950.

5. E. Guinea (Lopez). Melastomataceae Fernandopoanae. *Bol. Real Soc. Esp. Hist. Nat.* 49 : 175–187. 1951.

6. E. Guinea (Lopez). Asteraceae (Compositae) Fernandopoanae. *An. Inst. Bot. Cavan.* 1 : 301–340. 1951.

7. E. Guinea Lopez. Esquema de la Vegetación de Fernando Póo. *Conferencia Internacional de Africanistas Occidentales* (1951). Circular Paper. 1951.

This includes some lists of plants collected by Guinea in Fernando Po. The work is repeated in Spanish (41–45), French (52–56), English (62–66) and Portuguese (73–77). The Araliaceae (*Polyscias fulva, Schefflera mannii, S. ledermannii*) are omitted from the English version.

8. L. G. Sobrinho. Vascular Plants from S. Tomé. *Port. Act. Biol.* (B), 3 : 392–401. 1953.

The date on the title-page of the separate is 1952 but it was apparently published in 1953 (see p. 392). This work records plants collected in Príncipe and S. Tomé by d'Oliveira and Noronha in 1951.

9. L. G. Sobrinho. Vascular Plants from Ano Bom and Príncipe Islands. *Port. Act. Biol.* (B) 4 : 177–190. 1953.

This records plants (now at LISU) collected by F. Newton in Annobon in 1893 and a few specimens collected by de Souza Jr in Príncipe in 1880. The existence of these specimens was unknown to me at the time of the publication of (1). There are many new records from Annobon.

10. J. Hutchinson and J. M. Dalziel. *Flora of West Tropical Africa* 1 (1), ed. 2, revised by R. W. J. Keay. 1954.

Authors of various families other than Keay are indicated in the work. I am much indebted to this excellent second edition and the Fernando Po records have been largely extracted from this and the succeeding volumes.

11. A. W. Exell. *Supplement to the Catalogue of the Vascular Plants of S. Tomé* (with Principe and Annobon). 1956.

This brought (1) up to date by including the records in (8) and (9) and a considerable collection made in S. Tomé by Espírito Santo. Acknowledgement to collaborators is made in the introduction. This opportunity is taken to correct two formulae on p. 4 in the discussion on statistics. These should read : (1) the increase in number of species by adding area B to area A $= T - a = \alpha \log_e [(A + B)/A]$ and (2) similarly the increase of species by adding area A to area B $= T - b = \alpha \log_e [(A + B)/B]$.

12. As (10). Vol. 1 (2). 1958.

13. H. Lains e Silva. *São Tomé e Príncipe e a Cultura do Café.* 1958.

This important work has much information about the vegetation of the two islands, the ecology and the introduced species. It should be noted that the 'Nomes latinos das especies vegetais' on p. 405 does not refer only to species occurring in the islands but includes a few species from other parts of the world mentioned in the text. There are a number of new records. I have not myself seen the specimens of these.

14. A. W. Exell and A. Rozeira. Aditamento à Flora das Ilhas de S. Tomé e do Príncipe. *6 Conferencia Internacional dos Africanistas Ocidentais* (Ilha de S. Tomé, 1956) 3 : 77–92. 1958.

Spermatophyta by A. W. Exell. This mainly consists of new records from the collections of A. Rozeira in Príncipe and S. Tomé. I was not shown any proofs of this publication and regret a number of typographical errors for which I was not responsible.

15. A. W. Exell. Additions to the Flora of S. Tomé and Príncipe. *Bull. I.F.A.N.* 21, sér. A, 2 : 439–476. 1959.

Mainly an account of new records from collections by Th. Monod made in Príncipe and S. Tomé in 1956.

16. A. W. Exell. Angiosperms of the Cambridge Annobon Island Expedition. *Bull. Br. Mus. nat. Hist.* (*Bot.*), 3 : 93–118 (1963).

This listed new and interesting plants collected by F. A. Melville and T. C. Wrigley in Annobon in 1959. Certain families not by the author were contributed as follows: Loganiaceae (by J. Lewis) ; Solanaceae (by W. T. Stearn) ; Piperaceae (by W. T. Stearn) ; Loranthaceae (by W. T. Stearn) ; Orchidaceae (by V. S. Summerhayes) ; Gramineae (by W. D. Clayton).

17. As (10) but revised by F. N. Hepper. Vol. 2. 1963.

18. As (17). Vol. 3 (1). 1968.

19. A. Escarré. *Aportaciones al Conocimento de la Flora de Fernando Poo.* I—Araliaceae, Umbelliferae. 1968. II—Piperaceae, Urticaceae. 1969.

20. W. W. Sanford. The Orchid Flora of Equatorial Guinea in relation to that of West Africa. *Mitt. Bot. StSamml. Münch.* 10 : 287–298. 1971.

21. As (18). Vol. 3 (2). 1972.

22. J. H. P. de Barros Ferreira. Contribuição para o Estudo das Malváceas de S. Tomé e Príncipe. *Garcia de Orta,* 11 : 27–55. 1963.

23. J. H. P. de Barros Ferreira. Contribuição para o Estudo das Begoniáceas de S. Tomé e Príncipe. *Garcia de Orta,* 13 : 525–543. 1965.

24. J. H. P. de Barros Ferreira. Contribuição para o Estudo das Melastomataceae de S. Tomé e Príncipe. *Garcia de Orta,* 16 : 69–86. 1968.

Includes *Tristemma thomensis* Barros Ferreira published by the author on p. 66 of the same volume.

25. J. do Espírito Santo. Nomes crioulos e vernáculos de algumas plantas de S. Tomé e Príncipe. *Bolm cult. Guiné port.* 24 : 193–211. 1969.

In spite of the title the plants recorded are all from S. Tomé. The author states in a footnote to the first page of (27) that the 'prospecção botânica' of 1968 did not get to Príncipe. Numerous spelling mistakes, etc. are mainly corrected in the Corrigenda to (27).

26. J. do Espírito Santo. Algumas Plantas medicinais e venenosas de S. Tomé e Príncipe. *Bolm cult. Guiné port.* 24 : 917–940. 1969.

Notes to (25) apply equally to this.

27. J. do Espírito Santo. Aditamento a Flora de S. Tomé. *Bolm cult. Guiné port.* 25 : 489–511. 1970.

New records are mainly introduced species but there are a few interesting indigenous ones. *Erythroxylum emarginatum, Ilex mitis* and *Alangium chinense* add new families to those recorded from S. Tomé. The specimens are at LISJC and most of them also at LISC. This work corrects many mistakes in (25) and (26) but adds a few more most of which are fairly obvious.

ACKNOWLEDGEMENTS

S. Balle : Loranthaceae.
J. P. M. Brenan : various.
J. F. M. Cannon : Araliaceae, Umbelliferae.
W. D. Clayton : Gramineae.
J. E. Dandy : various.
A. Escarré : Piperaceae, Urticaceae and various.
A. & R. Fernandes : Barringtoniaceae, Melastomataceae, Onagraceae.
F. N. Hepper : various.
C. Jeffrey : Compositae, Cucurbitaceae.
E. Launert : various.
J. Léonard : Euphorbiaceae.
Maria Cândida Liberato : Leguminosae.
J. B. Marshall : Compositae.
E. Milne-Redhead : various.
D. Napper : Acanthaceae.
R. M. Polhill : Leguminosae.
J. Raynal : Cyperaceae.
N. K. B. Robson : Hypericaceae.
R. Ross : for much help throughout.
W. W. Sanford : Orchidaceae.
P. Taylor : Amaranthaceae.

NEW NAMES PUBLISHED IN THIS WORK

Pauridiantha camposii (G. Tayl.) Exell, comb. nov. (Rubiaceae).
Psychotria hierniana Exell, nom. nov. (Rubiaceae).

DICOTYLEDONES

1. ANNONACEAE

Annona arenaria Thonn.	1			ST ?		
*Annona cherimola L.	25			ST		
*Annona glabra L.	1, 10			ST		
*Annona muricata L.	1, 2, 16, 25, 26	FP	P	ST	A	
*Annona reticulata L.	1, 16, 25		P	ST	A	
*Annona squamosa L.	1, 25			ST	A	
Artabotrys macrophyllus Hook. f.	2, 10	FP				E
Artabotrys sp.		FP				
FP : *Mildbraed 6412*						
*Asimina triloba (L.) Dunal	1		P ?			
*Cananga odorata (Lam.) Hook. f. & Thomson	2, 11, 25	FP		ST		
Cleistopholis patens (Benth.) Engl. & Diels	2	FP				
FP : Bokoko, *Burchardt*. Not recorded from FP in 10.						
Enantia chlorantha Oliver	10	FP				
Monodora brevipes Benth.	1, 2, 10	FP	P			
Monodora myristica (Gaertn.) Dunal	1, 2, 7, 25, 26	FP	P	ST		
Not recorded from FP in 10.						
Monodora tenuifolia Benth.	2, 10	FP				
Monodora zenkeri Engl.	2	FP				
Not in 10.						

Oxymitra gracilipes Benth.	10	FP				E
Oxymitra gracilis (Hook. f.) Sprague & Hutch.		FP				
Unona millenii Engl. & Diels	2					
Not recorded from FP in 10.						
Oxymitra hirsuta (Benth.) Sprague & Hutch.	2, 10	FP				
Polyalthia oliveri Engl.	1, 2			ST		
Popowia sp.		FP				
FP: Bokoko, *Mildbraed 6869*						
Uvaria sp.	27			ST		
Uvariodendron connivens (Benth.) R. E. Fries	10	FP				
Uvaria connivens Benth.	2					
Uvariodendron fuscum (Benth.) R. E. Fries	10	FP				
Uvaria fusca Benth.	2					
Uvariodendron letestui (Pellegrin) R. E. Fries	10	FP				
Uvaria mannii Hutch. & Dalz.	2					
Xylopia aethiopica (Dunal) A. Rich.	1, 2, 25, 26		P	ST		
Xylopia africana (Benth.) Oliver	1, 2, 10	FP	P	ST		
FP: Moka, *Mildbraed 7025*. Not recorded from FP in 10.						
Xylopia quintasii Engl. & Diels	1, 2, 10	FP		ST		
X. striata Engl.	2					
Not recorded from FP in 10.						

2. MONIMIACEAE

Glossocalyx longicuspis Benth.	2, 10	FP				
Xymalos monospora (Harv.) Baillon ex Warb.	2, 10	FP				

3. LAURACEAE

*Cinnamomum burmanni (C. & T. Nees) Blume	1			ST		
*Cinnamomum camphora (L.) T. Nees & Eberm.	1, 25			ST		
*Cinnamomum zeylanicum Garc. ex Blume	1, 2, 13		P	ST		
*Persea americana Miller	1, 13, 16, 25	FP	P	ST	A	
P. gratissima Gaertn. f.	2					

4. HERNANDIACEAE

Hernandia beninensis Welw. ex Henriq.	1, 2, 7, 10	FP		ST		E

5. MYRISTICACEAE

Coelocaryon preussii Warb.		FP				
FP: Bokoko, *Mildbraed 6856*. Not recorded from FP in 10.						
*Myristica fragrans Houtt.	1			ST		
Pycnanthus angolensis (Welw.) Warb.	1, 10, 11	FP		ST		
P. kombo (Baillon) Warb.	2					
Not recorded from FP in 10.						
Pycnanthus microcephalus (Benth.) Warb.	2, 10	FP				
Staudtia kamerunensis Warb.	2	FP				
FP: Bokoko, *Mildbraed 6883*, on which the record in 2 is probably based. Not recorded from FP in 10.						
Staudtia pterocarpa (Warb.) Warb.	1, 25			ST		E
Staudtia stipitata Warb.		FP				
S. gabonensis Warb.	2					
Not recorded from FP in 10.						

6. RANUNCULACEAE

Clematis hirsuta Guillemin & Perrottet	8, 11, 15			ST		
Clematis simensis Fresen.	10	FP				
C. altissima Hutch.	2					
Ranunculus extensus (Hook. f.) Schube ex Engl.	2, 10	FP				
'*Rubus extensus* Schube ex Engl.', *Index Kewensis*, Suppl. 1 : 370 (1906), cited from FP but entirely mythical; *Ranunculus extensus* was undoubtedly intended.						
Thalictrum rhynchocarpum Dillon & Rich.	10	FP				
T. mannii Hutch.	2, 7					

7. NYMPHAEACEAE

Nymphaea lotus L.	10	FP				
N. lotus var. *sinoeensis* Stapf	2					

8. MENISPERMACEAE

Chasmanthera dependens Hochst	27			ST		
Cissampelos owariensis Beauv. ex DC.	10	FP				
Dioscoreophyllum volkensii var. fernandense (Hutch. & Dalziel) Troupin	12	FP				
D. fernandense Hutch. & Dalziel	2					
D. tenerum var. *fernandense* (Hutch. & Dalziel) Troupin	10					
Jateorhiza macrantha (Hook. f.) Exell & Mendonça	2, 10	FP				
Penianthus longifolius Miers	2, 10	FP				
Stephania abyssinica (Dillon & Rich.) Walp. var. abyssinica	2, 10	FP				
Stephania cyanantha Welw. ex Hiern	12	FP				
Stephania dinklagei (Engl.) Diels	15		P			
Stephania laetificata (Miers) Oliver	2	FP				
Not recorded from FP in 10. The holotype, *Mann 236*, is from FP.						
Syrrheonema fasciculatum Miers	2, 10	FP				
Triclisia coriacea Oliver	2, 10	FP				E
Triclisia macrophylla Oliver	2, 10	FP				
Recorded as endemic to FP in 10, but the distribution has since been found to extend to Sierra Leone and Cameroons Mt.						

9. ARISTOLOCHIACEAE

Aristolochia littoralis Parodi				ST		
A. elegans Mast.	11					
Pararistolochia goldieana (Hook. f.) Hutch. & Dalziel	2, 10	FP				

10. PIPERACEAE

Peperomia fernandopoiana C.DC.	2, 7, 10, 15, 19	FP	P			
Peperomia hygrophila Engl.	1, 10, 16			ST	A	
P. annobonensis Mildbr.	1, 2					
Peperomia kamerunana C.DC.	10, 19	FP				
'Peperomia lucida'	7	FP				
Probably *P. pellucida* was intended.						

Peperomia mannii Hook. f. ex C.DC.	2, 10, 19	FP				
Peperomia molleri C.DC.	1, 10, 19	FP	P	ST		
Peperomia pellucida (L.) Kunth	1, 2, 7, 10, 11, 19, 25, 26	FP	P	ST		
Peperomia reflexa (L.f.) A. Dietr.	1, 15			ST		
Peperomia thomeana C.DC.	1			ST		E
Peperomia vaccinifolia C.DC.	10, 19	FP				
Peperomia sp.	1				A	
Piper capense L.f.	1, 2, 10, 11, 19	FP	P	ST		
Piper guineense Schumacher	1, 2, 7, 10, 19, 25	FP	P	ST		
P. clusii C.DC.	2					
Piper umbellatum L.	1, 10, 11, 19, 25, 26	FP	P	ST	A	
P. subpeltatum C.DC.	2					

11. PAPAVERACEAE

*Argemone mexicana L.	1, 25, 26			ST		

12. FUMARIACEAE

*Fumaria muralis Sonder ex Koch	1			ST		

13. CAPPARACEAE

Buchholzia coriacea Engl.	27			ST		
B. macrophylla sensu Espírito Santo	25					
Capparis tomentosa Lam.	1			ST		
Cleome rutidosperma DC.	16	FP	P	ST	A	
C. ciliata Schumacher	1, 2, 9, 10, 11, 25					
Gynandropsis gynandra (L.) Briq.	1	FP		ST		
Pedicellaria pentaphylla Schrank	2					
Not recorded from FP in 10.						
Ritchiea erecta Hook. f.	2, 10	FP				E
Ritchiea polypetala Hook. f.	10	FP				
R. fragrans sensu Mildbr. ?						
R. cf. *glossopetala* Gilg						
FP : Bokoko, *Burchardt.*						
R. obanensis Hutch. & Dalziel	2					

14. CRUCIFERAE

*Brassica juncea (L.) Czerniak	1, 15			ST		
*Brassica oleracea L.	2	FP				
*Capsella bursa-pastoris (L.) Medik.	1			ST		
Cardamine africana L.	1, 10, 13	FP		ST		
C. africana var. *pubescens* Hook. f.	2					
Cardamine hirsuta L.	2, 7, 10			ST		
*Coronopus didymus (L.) Smith	1, 11			ST		
*Diplotaxis tenuisiliqua Delile	1			ST		
*Lobularia maritima (L.) Desvaux	15			ST		
*Raphanus sativus L.	1, 13			ST		
Rorippa humifusa (Guillemin & Perrottet) Hiern		FP				
Nasturtium humifusum Guillemin & Perrottet	2					
Not recorded from FP in 10.						

Rorippa indica (L.) Hiern	16			ST		
Nasturtium sinapis (Burm. f.) O. E. Schulz	11, 14					
Rorippa sinapis (Burm. f.) Ohwi & Hara	15					
*Rorippa nasturtium-aquaticum (L.) Hayek	15, 25, 26	FP		ST		
Nasturtium officinale R.Br.	1, 2					
*Sinapis alba L.	2	FP				

15. VIOLACEAE

Hybanthus enneaspermus (L.) F. v. Muell.	10	FP				
Rinorea angustifolia (Thouars) Baillon				ST	A	
R. molleri Brandt	1, 9, 11					
R. ardisiiflora sensu Guinea	2					
See Tennant in *Kew Bull.* 16 : 412 (1962).						
Rinorea chevalieri Exell	1			ST		E
Rinorea dentata (Beauv.) Kuntze	2, 7, 10	FP				
R. bipindensis Engl.	2					
Rinorea insularis Engl.	1		P			E
Rinorea longisepala Engl.	2	FP				
Not recorded from FP in 10.						
Rinorea thomensis Exell	1			ST		E
Viola abyssinica Steudel ex Oliver	2, 10	FP				
V. emirnensis (Engl.) Guinea	2					

16. POLYGALACEAE

Carpolobia glabrescens Hutch. & Dalziel	2, 10	FP				

17. CRASSULACEAE

*Bryophyllum pinnatum (Lam.) Oken	1, 11, 25, 26	FP	P	ST	A	
B. germinans sensu Guinea	2					
Crassula alsinoides (Hook. f.) Engl.	2, 7	FP				
Not recorded from FP in 10. The type is from FP.						
Kalanchoe crenata (Andr.) Haw.	1, 10, 11, 16, 27			ST	A	
Kalanchoe crenata var. verea (Jacq.) Cufod. in *Bull. Jard. Bot. Brux.* 27 : 714 (1957).				ST		
ST : *Menyharth 24* (WU).						
Kalanchoe laciniata (L.) DC.		FP				
FP : Moka, *Exell 796* (BM.). Not recorded from FP in 10.						

18. HYDRANGEACEAE

*Hydrangea sp.	1			ST ?		

19. PODOSTEMACEAE

Tristicha trifaria (Bory) Sprengel	10	FP				
T. hypnoides (St.-Hil.) Sprengel	2					

20. CARYOPHYLLACEAE

Cerastium indicum Wight & Arn.	10	FP				
Drymaria cordata (L.) Willd.	1, 2, 8, 10, 11, 13, 25	FP	P	ST		
Sagina abyssinica Hochst. ex A. Rich.	2, 10	FP				
Stellaria mannii Hook. f.	1, 10, 11, 13	FP		ST		
*Stellaria media (L.) Vill.	1	FP		ST		
FP : *Guinea 2057*.						

21. AIZOACEAE

Sesuvium portulacastrum (L.) L.	1			ST	

22. PORTULACACEAE

Portulaca oleracea L.	1, 2, 10, 13, 15, 16, 25	FP		ST	
Portulaca quadrifida L.	13			ST	
*Talinum triangulare (Jacq.) Willd.	1, 2, 11, 16, 25	FP		ST	

23. POLYGONACEAE

*Antigonon leptopus Hook. & Arn.		FP		ST	
A. cordatum Martens & Galeotti	2, 13				
Polygonum nepalense Meissner	10	FP			
P. alatum (Buch.-Ham. ex D. Don) Sprengel	2				
Polygonum nyikense Baker	10	FP			
Polygonum salicifolium Brouss. ex Willd.	1				A
Polygonum senegalense Meissner	1			ST	
Rumex abyssinicus Jacq.	1, 2	FP		ST	
Not recorded from FP in 10.					

24. PHYTOLACCACEAE

Phytolacca dodecandra var. apiculata Baker & Wright	1, 11, 13			ST	

25. CHENOPODIACEAE

Chenopodium album L.	1			ST	
*Chenopodium ambrosioides L.	1, 11, 13, 25, 26		P	ST	

26. AMARANTHACEAE

Achyranthes aspera L.	1, 2, 16, 25	FP		ST	A
Not recorded from FP in 10.					
Achyranthes bidentata Blume	2, 10	FP			
Aerva lanata (L.) Juss. ex J. A. Schultes	2 ('*Aurea*')	FP			
FP: *Guinea 1123*. Not recorded from FP in 10.					
Alternanthera maritima (Mart.) St.-Hil.	16	FP	P	ST	A
Telanthera maritima (Mart.) Moq.	1, 14				
FP: *Guinea 875*. Not recorded from FP in 10.					
Alternanthera pungens Kunth			P	ST	
A. repens (L.) Link, non *A. repens* J. F. Gmelin	1, 11, 13				
Alternanthera sessilis (L.) R. Br. ex DC., *Cat. Hort. Monspel.*: 77 (1813).	1, 8, 10, 11, 16	FP	P	ST	A
Amaranthus graecizans L.				ST	
A. blitum sensu auctt.	13				
The record in 13 is probably *A. graecizans*.					
Amaranthus hybridus subsp. incurvatus (Timeroy ex Grèn. & Godron) Brenan		FP			
A. paniculatus L.	2				
Not in 10.					
Amaranthus spinosus L.	1, 2, 10, 13, 16	FP	P	ST	A
Amaranthus viridis L.	1, 2, 16	FP		ST	A
Not recorded from FP in 10.					
*Celosia argentea L.	1, 2	FP		ST	
Probably introduced.					

Celosia bonnivairii Schinz	10	FP				
Celosia laxa Schumacher	2, 10	FP				
Celosia leptostachya Benth.	1, 2, 10, 11, 13	FP		ST		
Celosia trigyna L.	1, 10	FP			A	
Cyathula achyranthoides (Kunth) Moq.	2, 10	FP				
Cyathula cylindrica var. mannii (Baker) Suesseng.	10	FP				
C. mannii Baker	2					
Cyathula fernandopoensis Suesseng. & Friedrich	10	FP				E
Cyathula pedicellata C. B. Clarke	10	FP				
Cyathula prostrata (L.) Blume	1, 10, 13, 16	FP	P	ST	A	
Deeringia amaranthoides (Lam.) Merr.	1		P			
*Gomphrena globosa L.	1, 2	FP		ST		
*Iresine herbstii Hook.	1			ST		
Nothosaerva brachiata (L.) Wight		FP				
FP: *Escarré 361, 373, 375*. Not recorded from FP in 10.						
Philoxerus vermicularis (L.) Beauv.	1, 19	FP		ST		
FP: *Escarré 360*. Not recorded from FP in 10.						
Pupalia lappacea (L.) Juss.	1, 2, 9, 11, 25	FP		ST	A	
Not recorded from FP in 10.						
Sericostachys scandens Gilg & Lopr.	10	FP				

27. BASELLACEAE

*Basella alba L.	1, 16			ST	A	
Probably introduced.						

28. GERANIACEAE

Geranium arabicum Forssk.		FP				
G. simense Hochst. ex A. Rich.	2, 7, 10					
See Laundon in *Bol. Soc. Brot.*, sér. 2, 35 : 59 (1961).						

29. OXALIDACEAE

Oxalis corniculata L.	1, 2, 10, 11, 12, 13	FP	P	ST	A	
*Oxalis corymbosa DC.	1, 11, 13, 25		P	ST		

30. AVERRHOACEAE

*Averrhoa carambola L.	2, 13, 25	FP		ST		

31. BALSAMINACEAE

*Impatiens balsamina L.	1, 13			ST		
Impatiens buccinalis Hook. f.	1, 11			ST		E
Impatiens filicornu Hook. f.	2, 10	FP				
(Omitted from index to 10; text p. 162.)						
Impatiens hians Hook. f.	2, 10	FP				
Impatiens kamerunensis Warb.	10	FP				
Impatiens macroptera Hook. f.	2, 10	FP				
Impatiens mannii Hook. f.	2, 10	FP				
I. affinis Warb.	2					
Impatiens manteroana Exell	1, 14		P			E
Impatiens niamniamensis Gilg	10	FP				
I. dichroa Hook. f. ex Gilg	2					
Impatiens sakerana Hook. f.	10	FP				
Impatiens tamsiana Exell	1		P			E
Impatiens thomensis Exell	1, 14			ST		E

32. LYTHRACEAE

*LAWSONIA INERMIS L.	11		P			

33. PUNICACEAE

*PUNICA GRANATUM L.	2, 13, 16	FP		ST	A	

34. ONAGRACEAE

LUDWIGIA ERECTA (L.) Hara	14			ST		
Jussiaea erecta L.	1					
LUDWIGIA HYSSOPIFOLIA (G. Don) Exell	14, 15		P	ST		
Jussiaea linifolia Vahl	1, 8, 13					
LUDWIGIA LEPTOCARPA (Nutt.) Hara	14			ST		
Jussiaea leptocarpa Nutt.	1					
LUDWIGIA OCTOVALVIS (Jacq.) Raven subsp. OCTOVALVIS		FP		ST		
Jussiaea suffruticosa L.	1					
Ludwigia pubescens (L.) Hara	14					
FP: San Carlos, *Mildbraed 6781*.						
Neither *Ludwigia* nor *Jussiaea* is recorded from FP in 10.						

35. HALORAGACEAE

*LAUREMBERGIA cf. TETRANDRA (Schott) Kanitz	10	FP				

36. THYMELAEACEAE

DICRANOLEPIS DISTICHA Planchon	10	FP				
D. mannii Baillon	2					
DICRANOLEPIS GRANDIFLORA Engl.	2, 10	FP				
DICRANOLEPIS STENURA Gilg ex Engl.	2	FP				E ?
Not in 10, but probably = *D. vestita*.						
DICRANOLEPIS THOMENSIS Engl. & Gilg	1			ST		E
DICRANOLEPIS VESTITA Engl.	2, 10	FP				
PEDDIEA FISCHERI Engl.		FP				
FP: *Melville & Wrigley 632* (K.). Not recorded from FP in 10.						
PEDDIEA PARVIFLORA Hook. f.	2, 10	FP				E
PEDDIEA THOMENSIS Exell	1, 13			ST		E

37. NYCTAGINACEAE

BOERHAVIA COCCINEA Miller	16		P	ST	A	
B. diffusa sensu Exell pro parte et sensu Lains & Silva.	1, 13, 26					
BOERHAVIA COCCINEA var. VISCOSA (Lag. & Rodriguez) Moscoso		FP				
B. viscosa Lag. & Rodriguez	2					
Not recorded from FP in 10.						
BOERHAVIA DIFFUSA L.	1, 16, 25, 26		P	ST	A	
*BOERHAVIA PANICULATA Rich.	1			ST		
*BOUGAINVILLEA GLABRA Choisy	2	FP				
*BOUGAINVILLEA SPECTABILIS Willd.	1, 2, 13	FP	P	ST		
*MIRABILIS JALAPA L.	1, 2, 11, 26	FP		ST	A	

38. PROTEACEAE

*GREVILLEA ROBUSTA Cunn.	13			ST		

39. DILLENIACEAE

*DILLENIA INDICA L.	1, 27			ST		
TETRACERA ALNIFOLIA Willd.	1, 2, 7, 10, 16	FP	P		A	
TETRACERA ERIANTHA (Oliver) Hutch.	2, 10	FP				

40. PITTOSPORACEAE

PITTOSPORUM MANNII Hook. f. subsp. MANNII	2, 10	FP				

41. BIXACEAE

*BIXA ORELLANA L.	1, 9, 10, 11, 13, 25, 26	FP	P	ST		

42. FLACOURTIACEAE (incl. SAMYDACEAE)

CALONCOBA GLAUCA (Beauv.) Gilg	10	FP				
*CALONCOBA WELWITSCHII (Oliver) Gilg	2	FP				
CAMPTOSTYLUS MANNII (Oliver) Gilg	10	FP				
Caloncoba mannii (Oliver) Gilg	2					
CASEARIA BARTERI Mast.	1, 11, 25			ST		
CASEARIA MANNII Mast.	1		P			E
FLACOURTIA FLAVESCENS Willd.	11			ST		
? HOMALIUM AFRICANUM (Hook. f.) Benth.	2	FP ?				
Record probably based on a misidentification of *H. letestui*.						
HOMALIUM HENRIQUESII Gilg ex Engl.	11			ST		E
H. africanum sensu Exell	1					
HOMALIUM LETESTUI Pellegrin	10	FP				
H. dolichophyllum Gilg ex Engl.	2, 7					
HOMALIUM SARCOPETALUM Pierre	10	FP				
LINDACKERIA DENTATA (Oliver) Gilg		FP				
FP: Bokoko, *Burchardt*. Not recorded from FP in 10.						
ONCOBA SPINOSA Forssk.	1, 2, 25, 26	FP		ST		
Not recorded from FP in 10.						
OPHIOBOTRYS ZENKERI Gilg	11, 25, 27			ST		

43. PASSIFLORACEAE

ADENIA CISSAMPELOIDES (Planchon ex Benth.) Harms	2, 10, 26	FP	P ?	ST ?		
ADENIA CYNANCHIFOLIA (Benth.) Harms	2, 10	FP				E
ADENIA LOBATA (Jacq.) Engl.	1, 2, 10, 11	FP	P	ST	A	
BARTERIA FISTULOSA Mast.	2, 10	FP				
BARTERIA NIGRITANA Hook. f.	10	FP				
*PASSIFLORA EDULIS Sims	1, 11, 25			ST		
*PASSIFLORA FOETIDA L.	1, 8, 10, 25, 26	FP	P	ST		
*PASSIFLORA QUADRANGULARIS L.	1		P	ST		

44. CUCURBITACEAE

General reference: C. Jeffrey, 'Key to the Cucurbitaceae of West Tropical Africa, with a guide to the localities of rare and little-known species' in *Journ. W. Afr. Sci. Assn.* 9: 79–97 (1965).

CAYAPONIA AFRICANA (Hook. f.) Exell	1, 9, 10, 11			ST	A	
CITRULLUS LANATUS (Thunb.) Matsum. & Nakai		FP	P ?			
C. vulgaris Schrader	2					
Colocynthis citrullus (L.) Kuntze	1					
Not recorded from FP in 10.						

Coccinia barteri (Hook. f.) Keay	10	FP				
Physedra barteri (Hook. f.) Cogn.	2					
Cucumeropsis edulis (Hook. f.) Cogn.	2	FP				
Not recorded from FP in 10.						
Cucumis metulifer E. Meyer ex Naudin	1			ST ?		
*Cucumis sativus L.	1			ST		
*Cucurbita maxima Duchesne	2	FP				
Diplocyclos palmatus (L.) C. Jeffrey	16	FP		ST		
Bryonopsis laciniosa Naudin pro parte	1, 10					
Lagenaria breviflora (Benth.) Roberty	16	FP	P	ST	A	
Adenopus breviflorus Benth.	1, 2, 25					
Not recorded from FP in 10.						
Lagenaria siceraria (Molina) Standley	16, 25	FP		ST	A	
L. vulgaris Ser.	2, 13					
*Luffa acutangula Roxb.	2	FP				
Luffa aegyptiaca Miller	1, 10, 16	FP		ST	A	
L. cylindrica M. Roemer	2					
Momordica cabrae (Cogn.) C. Jeffrey		FP				
Dimorphochlamys mannii Hook. f.	2, 10					
Momordica charantia L.	1, 2, 9, 10, 13, 25, 26	FP	P	ST	A	
Momordica charantia var. abbreviata Ser.	1, 9, 11	FP	P	ST	A	
Momordica cissoides Planchon ex Benth.	2, 10	FP				
Momordica foetida Schumacher	2, 10	FP				
M. mannii Hook. f.	2					
Momordica multiflora Hook. f.	2, 10	FP				
Oreosyce africana Hook. f.	2, 10	FP				
Peponium vogelii (Hook. f.) Engl.	2, 10, 16	FP		ST		
P. bracteatum (Cogn.) Cogn.	1					
Raphidiocystis mannii Hook. f.	2, 10	FP				
Ruthalicia longipes (Hook. f.) C. Jeffrey		FP				
Physedra longipes Hook. f.	10					
*Sechium edule Swartz	1, 2	FP		ST		
Telfairia occidentalis Hook. f.	2, 10	FP				
Zehneria capillacea (Schumacher) C. Jeffrey		FP				
Melothria capillacea (Schumacher) Cogn.	2, 10					
Zehneria gilletii (De Wild.) C. Jeffrey	16			ST		
Melothria capillacea sensu Exell	1					
Zehneria minutiflora (Cogn.) C. Jeffrey		FP				
FP: *Wrigley 516* (K). Not recorded from FP in 10.						
Zehneria scabra (L. f.) Sonder	16	FP		ST		
Melothria minutiflora sensu Exell	1					
M. fernandensis Hutch. & Dalziel	2, 10					

45. BEGONIACEAE

Begonia ampla Hook. f.	1, 2, 7, 10, 23, 25	FP	P	ST	A	
Begonia annobonensis A.DC.	1, 2, 10, 11, 23		P	ST	A	
Begonia baccata Hook. f.	1, 11, 23			ST		E
B. crateris Exell	1, 13, 25					
I agree that *B. crateris* is no more than a form of *B. baccata*.						
Begonia eminii Warb.	10	FP				
Begonia fusialata Warb.	23		P			

Begonia furfuracea Hook. f.	2, 10	FP				E
Begonia gilgii Engl.	2, 10	FP				
Begonia gladiifolia Engl.	2, 10	FP				
Begonia loranthoides Hook. f.	1, 23		P	ST		E
B. henriquesii C.DC.	1					
Begonia macambrarensis Exell	1, 13, 23			ST		E
Begonia mannii Hook.	2, 10	FP				
B. epiphytica Hook. f.	2					
B. excelsa Hook. f.	2					
Begonia molleri (C.DC.) Warb.	1, 13, 23			ST		E
Begonia oxyloba Welw. ex Hook. f.	2, 10	FP				
Begonia poculifera Hook. f.	2, 10	FP				
Begonia prismatocarpa Hook.	2, 10	FP				
Begonia sessilifolia Hook. f.	2, 10	FP				
Begonia thomeana C.DC.	1			ST		E
Begonia sp. 1	1		P			
Begonia sp. 2	1			ST		
Begonia sp. 3	1			ST		
Begonia sp. 4	1			ST		
*Begonia sp.	11, 23			ST		
Begonia sp. cf. macropoda Gilg	10	FP				

46. CARICACEAE

*Carica papaya L.	1, 16, 25		P	ST	A	

47. CACTACEAE

*Opuntia dillenii (Ker-Gawl.) Haw.		FP				
O. horrida Salm-Dyck	2					
Rhipsalis baccifera (J. S. Miller) Stearn	11	FP	P	ST	A	
R. cassutha Gaertn.	1, 2, 10					

48. OCHNACEAE

Ochna membranacea Oliver	16			ST	A	
O. quintasii (Tieghem) Exell	1, 13					
O. cf. *gilgiana* Engl.	1					
Ouratea affinis (Hook. f.) Engl.	2, 10	FP				
? Ouratea brachybotrys Gilg	2	FP				
FP: Bokoko, *Mildbraed 6866*. A doubtful record. Not in 10.						
Ouratea brunneopurpurea Gilg	1, 2, 14	FP	P	ST		
Not in 10.						
Ouratea calophylloides Hutch. & Dalziel	2, 10	FP				E
Ouratea elongata (Oliver) Engl.	2, 10	FP				
Ouratea flava (Schumacher) Hutch. & Dalziel ex Stapf	10	FP				
O. reticulata sensu Guinea	2	FP				
Ouratea mannii (Oliver) Engl.	2, 10	FP				
Ouratea micrantha (Hook. f.) Hutch. & Dalziel	2, 10	FP				E
Ouratea molleri (Tieghem) Exell	1, 11, 13		P	ST		E ?
Campylospermum vogelii var. *molleri* (Tieghem) Farron in *Bull. Jard. Bot. Brux.* 35 : 404 (1965).						
Ouratea nutans (Hiern) Exell	1, 11		P			E
Ouratea quintasii (Tieghem) Exell	1, 13			ST		E ?
Rhabdophyllum arnoldianum var. *quintasii* (Tieghem) Farron, *tom. cit.* : 391 (1965).						

49. MYRTACEAE

*EUCALYPTUS ROBUSTUS Smith	2	FP				
*EUCALYPTUS sp.	13			ST		
*EUGENIA BRASILIENSIS Lam.	13			ST		
*EUGENIA DOMBEYI (Sprengel) Skeels	27			ST		
EUGENIA ELLIOTII Engl. & Brehmer	11			ST		
EUGENIA FERNANDOPOANA Engl. & Brehmer	2, 10	FP				E
EUGENIA OBANENSIS Baker f.	2, 10	FP				
*EUGENIA UNIFLORA L.	1, 2, 25	FP	P	ST		
*MYRCIARIA CAULIFLORA O. Berg	13			ST		
*PSIDIUM GUAJAVA L.	1, 2, 13, 25, 26	FP	P	ST	A	
*SYZYGIUM AROMATICUM (L.) Merr. & Perry	27			ST		
SYZYGIUM GUINEENSE (Willd.) DC.	2, 15, 25, 26, 27	FP		ST		
SYZYGIUM GUINEENSE var. LITTORALE Keay	10	FP				
*SYZYGIUM JAMBOS (L.) Alston		FP	P	ST	A	
Eugenia jambos L.	1, 2					
*SYZYGIUM MALACCENSE (L.) Merr. & Perry		FP				
Eugenia malaccensis L.	2					
SYZYGIUM STAUDTII (Engl.) Mildbr.	10	FP		ST		
ST : *Monod 11929.*						

50. BARRINGTONIACEAE

NAPOLEONAEA MANNII Miers	2, 10	FP				E
N. cuspidata sensu Guinea	2					

51. MELASTOMATACEAE

AMPHIBLEMMA CYMOSUM var. BOLIVARI Brenan & Guinea, *nom. provis.*	5	FP				
A. Fernandes (in litt.) suggests that this may be *A. mildbraedii*.						
AMPHIBLEMMA MILDBRAEDII Gilg ex Engl.	2, 10	FP				
CALVOA CONFERTIFOLIA Exell	1, 24			ST		E
CALVOA CRASSINODA Hook. f. & Triana	1, 13, 24			ST		E
CALVOA GRANDIFOLIA Cogn.	1, 8, 13, 24			ST		E
CALVOA HENRIQUESII Cogn.	1, 11, 13, 15, 24		P	ST		E
CALVOA HIRSUTA Hook. f.	2, 5, 10	FP				
CALVOA INTEGRIFOLIA Cogn.	1, 24			ST		E
CALVOA MOLLERI Gilg	1, 11, 15, 24			ST		E
CALVOA SINUATA Hook. f. ex Triana	1, 24		P			E
CALVOA aff. TROCHAINII Jacques-Félix	5, 10	FP				
C. ignatii-bolivari Guinea, *nom. provis.*	5					
C. polychoeta Guinea, *nom. invalid.*	5					
Referred to in the legend of the plate on p. 179 but not in the text, and presumably the same as *C. ignatii-bolivari*.						
CALVOA UROPETALA Mildbr.	1, 2				A	E
DICELLANDRA BARTERI Hook. f.	2, 5, 7, 10	FP				
DICELLANDRA SCANDENS Gilg ex Engl.	2, 10	FP				E
DINOPHORA SPENNEROIDES Benth.	2, 10	FP				
DISSOTIS BARTERI Hook. f. ex Triana	1, 24		P			E
DISSOTIS DECUMBENS (Beauv.) Triana	2, 5, 10	FP				
DISSOTIS ROTUNDIFOLIA (Smith) Triana	1, 5, 7, 10, 24	FP	P	ST		

Guyonia ciliata Hook. f.	10	FP				
Afzeliella bolivari Brenan & Guinea, *nom. provis.*	5					
Afzeliella sp. aff. *ciliata*	5					
Medinilla mannii Hook. f.	2, 10	FP				E
Memecylon fernandianum Gilg ex Engl.	2, 10	FP				E
Memecylon membranifolium Hook. f.	2, 10	FP				
Memecylon memecyloides (Benth.) Exell	1, 10, 24, 25	FP	P			
M. vogelii Naudin						
Memecylon aff. strychnoides Baker	1				A	
Memecylon tessmannii Gilg ex Engl.	2	FP				
Not in 10.						
Myrianthemum mirabile Gilg	2, 10	FP				
Tristemma coronatum Benth.	24		P			E
Tristemma hirtum Beauv.	1, 2, 5, 10, 13, 14, 15, 24	FP	P	ST		
Tristemma incompletum R. Br.	1, 5, 8, 9, 10, 11, 13, 14, 15, 24	FP	P	ST		
Tristemma littorale Benth.	1, 2, 5, 7, 10, 24	FP	P			
Tristemma mildbraedii Gilg ex Engl.	2, 10, 24	FP		ST		
Tristemma oreothamnus Mildbr.	1, 2, 5, 16				A	E
Tristemma radicans Gilg ex Engl.	2, 10	FP				E
Tristemma thomensis Barros Ferreira	24			ST		E

52. COMBRETACEAE

Combretum bracteatum (M. A. Lawson) Engl. & Diels	10	FP				
Combretum confertum (Benth.) M. A. Lawson	2, 10	FP				
Combretum cuspidatum Planchon ex Benth.	2, 10	FP				
Combretum insulare Engl. & Diels	2, 10	FP				
Combretum paniculatum Vent.	1, 2, 10, 11	FP	P			
? Combretum platypterum (Welw.) Hutch. & Dalziel	1		P ?			
A doubtful record.						
Combretum racemosum Beauv.	2, 10	FP				
Conocarpus erectus L.	1, 7	FP		ST		
Not recorded from FP in 10.						
Laguncularia racemosa (L.) Gaertn. f.	2, 7	FP				
Not recorded from FP in 10.						
*Quisqualis indica L.	1	FP		ST		
*Terminalia catappa L.	1, 2, 16	FP	P	ST	A	

53. RHIZOPHORACEAE

Anisophyllea cabole Henriq.	1, 13, 25			ST		E
Anisophyllea setosa Mildbr., *nom. nud.*	10	FP				E ?
FP: Bokoko, *Mildbraed 6836*.						
Anisophyllea sp.	15		P			
Cassipourea annobonensis Mildbr.	1, 2, 16				A	E
Cassipourea glomerata Alston	1			ST		E
Cassipourea gummiflua var. mannii (Hook. f. ex Oliver) J. Lewis				ST		
C. mannii Hook. f. ex Oliver	1, 13					
Rhizophora harrisonii Leechm.	11, 13, 15		P	ST		
R. racemosa sensu Exell	1					
Rhizophora mangle L.	7	FP ?				
This may be *R. harrisonii*. The genus is not recorded from FP in 10.						

54. HYPERICACEAE

Harungana madagascariensis Lam. ex Poiret	1, 8, 10, 11, 13, 25	FP	P	ST	
H. paniculata Pers.	2				
Hypericum peplidifolium A. Rich.	10	FP			
Hypericum revolutum Vahl		FP			
H. lanceolatum Lam.	2, 7, 10				
H. sp.	10				

55. GUTTIFERAE

Allanblackia monticola Mildbr. ex Engl.	2, 10	FP			
Garcinia kola Heckel	2	FP			
Not recorded from FP in 10.					
*Garcinia mangostana L.	13			ST	
Garcinia mannii Oliver	2	FP			
Not recorded from FP in 10.					
Garcinia polyantha Oliver	1, 2, 10	FP	P ?		
Garcinia sp.		FP			
FP: Bokoko, *Burchardt.*					
Mammea africana Sabine	1, 10, 15, 27		P	ST	
Pentadesma butyraceum sensu Exell et al.	1, 11, 13, 25				
Mammea klaineana Pierre	2				
? Pentadesma butyraceum Sabine		FP ?			
See 'Antidesma butyraceum', p. 352.					
Symphonia globulifera L. f.	10, 26, 27	FP		ST	
S. gabonensis (Vesque) Pierre	1				
FP: Bokoko, *Mildbraed 6886, 6965.* Not recorded from FP in 10.					

56. SCYTOPETALACEAE

Rhaptopetalum coriaceum Oliver	2, 12	FP			
Scytopetalum kamerunianum Engl.	25, 27			ST	
Scytopetalum sp.	11			ST	
This may be *S. kamerunianum.*					

57. TILIACEAE

*Berria cordifolia (Willd.) Burret		FP			
B. amomnilla Roxb.	2				
Corchorus aestuans L.	1			ST	A
Corchorus capsularis L.	2	FP			
Not in 12.					
Corchorus olitorius L.	1, 2	FP		ST	
Not recorded from FP in 12.					
Duboscia macrocarpa Bocquet	2	FP			
Not recorded from FP in 12.					
Glyphaea brevis (Sprengel) Monachino	12	FP			
Grewia carpinifolia Juss.	1, 13			ST	
Grewia floribunda Mast.	1			ST	
Grewia malacocarpa Mast.	12			ST	
Grewia oligoneura Sprague	2, 12	FP			
Triumfetta cordifolia A. Rich.	2, 12	FP			
Triumfetta eriophlebia Hook. f.	2, 12	FP			
Triumfetta rhomboidea Jacq.	1, 2	FP		ST	A
Not recorded from FP in 12.					

58. STERCULIACEAE

Cola acuminata (Beauv.) Schott & Endl.	1, 2, 12, 13, 15	FP	P	ST		
C. pseudoacuminata Engl.	2					
Cola digitata Mast.	1		P	ST		
Cola ficifolia Mast.	2, 12	FP				
Cola nitida (Vent.) Schott & Endl.	12	FP				
C. acuminata var. *latifolia* K. Schum.	2					
C. vera K. Schum.	2					
Cola obtusa Engl. & Krause	2	FP				
Not in 12.						
? Cola sphaerocarpa A. Chev.	1			ST ?		
Said to be endemic but a very doubtful species.						
Cola verticillata (Thonn.) Stapf ex A. Chev.	2	FP				
Not recorded from FP in 12.						
Leptonychia adolfi-friederici Engl. & Krause	2, 12	FP				E
Leptonychia batangensis (C. H. Wright) Burret	12	FP				
Leptonychia densivenia Engl. & Krause	12	FP				E
L. urophylla sensu Guinea	2					
Leptonychia fernandopoana Engl. & Krause ex Mildbr., *nom. nud.*	12	FP				E
FP: Bokoko, *Mildbraed 6823, 6862.*						
Leptonychia lanceolata Mast.	2, 12	FP				E
Leptonychia pallida K. Schum.	12	FP				
Melochia corchorifolia L.	1			ST		
*Pterygota alata (Roxb.) R.Br.	2	FP				
? Sterculia bequaertii De Wild.	25			ST		
*Sterculia foetida L.	2	FP				
Sterculia oblonga Mast.	2, 12	FP				
If the genus *Eribroma* Pierre be maintained, the name for this is *E. oblonga* (Mast.) Bodard						
Sterculia tragacantha Lindl.	1, 2	FP	P	ST		
Not recorded from FP in 12.						
*Theobroma cacao L.	1, 2, 11, 13, 25	FP	P	ST	A	
Waltheria indica L.		FP				
FP: *Wrigley & Melville 704* (K). Not recorded from FP in 12.						

59. BOMBACACEAE

adansonia digitata L.	1, 9, 25, 26	FP	P	ST	A	
A. digitata var. *congolensis* A. Chev.	1, 13					
Not recorded from FP in 12.						
Bombax buonopozense Beauv.	2	FP				
Not recorded from FP in 12.						
*Bombax kimuenzae De Wild. & Dur.	2	FP				
Ceiba pentandra (L.) Gaertn.	1, 2, 7, 13, 25	FP	P	ST	A	
Not recorded from FP in 12.						

60. MALVACEAE

*Abelmoschus esculentus (L.) Moench	22		P	ST		
Hibiscus esculentus L.	1, 25					
Abelmoschus moschatus Medik.	2, 22	FP		ST		
Hibiscus abelmoschus L.	1					
Abutilon grandiflorum G. Don	1, 22, 25, 26			ST		

*Abutilon grandifolium (Willd.) Sweet				ST	
A. mollissimum (Cav.) Sweet	1, 22				
See R. Fernandes in *Anu. Soc. Brot.* 25 : 29 (1959).					
*Abutilon venosum Lemaire	1, 22			ST	
*Gossypium barbadense L.	1, 16, 22		P	ST	A
*var. brasiliense (Macfad.) J. B. Hutch.	12	FP			
G. brasiliense Macfad.	2				
G. arboreum sensu Guinea	2				
*Gossypium hirsutum L.	1, 22			ST	
*Hibiscus acetosella Welw. ex Hiern	11, 15, 22, 25		P	ST	
Hibiscus donianus D. Dietr.	1, 22			ST	
*Hibiscus mutabilis L.	15, 22		P	ST	
Hibiscus physaloides Guillemin & Perrottet	1, 9, 11, 22			ST	A
*Hibiscus rosa-sinensis L.	1, 22		P	ST	
*Hibiscus sabdariffa L.	2, 14, 22	FP		ST	
*Hibiscus schizopetalus (Mast.) Hook. f.		FP			
FP : *Guinea* 97.					
Hibiscus surattensis L.	1, 2, 22	FP	P	ST	
Not recorded from FP in 12.					
*Hibiscus syriacus L.	2	FP			
Hibiscus tiliaceus L.	1, 2, 7, 12, 22	FP	?	ST	
*Malvastrum coromandelianum (L.) Garcke	15, 22		P	ST	
Pavonia urens Cav. var. urens	12	FP			
Pavonia urens var. glabrescens (Ulbr.) Brenan	12	FP			
P. schimperana sensu Guinea	2				
Sida acuta Burm. f.	1, 8, 9, 11, 12, 13, 22, 25	FP	P	ST	A
Sida acuta var. carpinifolia K. Schum.	2	FP			
Sida alba L.	1, 22	FP			A
FP : Moka, *Tessmann 2817*. Not recorded from FP in 12.					
Sida cordifolia L.	1, 2, 9, 11, 22	FP		ST	A
Not recorded from FP in 12.					
Sida rhombifolia L.	1, 12, 13, 16, 22	FP	P	ST	A
Sida rigida (D. Don) D. Dietr.	1, 22			ST	
Sida stipulata Cav.	12	FP			
Sida urens L.	1, 22			ST	
Sida veronicifolia Lam.	1, 22			ST	
Urena lobata L.	1, 9, 11, 12, 13, 22, 25	FP	P	ST	A
Wissadula rostrata (Schumacher) Hook. f.	15, 22, 25	FP	P	ST	A
W. amplissima var. *rostrata* (Schumacher) R. E. Fries	1, 9, 11, 12				
W. heterosperma Hochst. ex Mast.	2				

61. MALPIGHIACEAE

Acridocarpus longifolius (G. Don) Hook. f.	1, 2, 12	FP	P	ST
Flabellaria paniculata Cav.	2, 12	FP		
Heteropteris leona (Cav.) Exell	1, 12		P	ST

62. HUMIRIACEAE

Sacoglottis gabonensis (Baillon) Urban	2, 12	FP

63. ERYTHROXYLACEAE

*ERYTHROXYLUM COCA Lam.	1			ST		
ERYTHROXYLUM EMARGINATUM Thonn.	9, 11, 27			ST	A	

64. LINACEAE (HUGONIACEAE)

HUGONIA PLATYSEPALA Welw. ex Oliver	1, 12	FP	P			
HUGONIA SPICATA Oliver var. SPICATA	2, 12	FP				E
The type variety is endemic.						

65. EUPHORBIACEAE

ACALYPHA ANNOBONAE Pax & Hoffm.	1, 2, 16				A	E
ACALYPHA CILIATA Forssk.	1			ST		
ACALYPHA MANNIANA Müll. Arg.	12	FP				
ACALYPHA ORNATA Hochst. ex A. Rich.	2	FP				
Not recorded from FP in 12.						
ACALYPHA RACEMOSA Wall. ex Baillon	12	FP				
A. paniculata Miq.	2					
ALCHORNEA CORDIFOLIA (Schumacher) Müll. Arg.	1, 12, 13, 25, 26	FP	P	ST		
ALCHORNEA FLORIBUNDA Müll. Arg.	2, 12	FP				
ALCHORNEA HIRTELLA Benth.	1		P			
ALCHORNEA LAXIFLORA (Benth.) Pax & Hoffm.				ST		
Lepidoturus laxiflorus Benth.	1					
*ALEURITES CORDATA (Thunb.) R. Br. ex Steudel	13			ST		
ANTHOSTEMA AUBRYANUM Baillon	1, 11, 12		P	ST		
'Antidesma butyraceum'	7	FP				
Possibly *Pentadesma butyraceum* was intended. If so, it is a new record of that species from FP.						
ANTIDESMA LACINIATUM Müll. Arg. var. LACINIATUM	2, 12	FP				
ANTIDESMA MEMBRANACEUM Müll. Arg.	1			ST	A	
ANTIDESMA OBLONGA (Hutch.) Keay		FP				
FP: *Wrigley & Melville 633* (K). Not recorded from FP in 12.						
*BREYNIA NIVOSA (W. G. Smith) Small	27			ST		
Phyllanthus nivosus W. G. Smith	13					
BRIDELIA STENOCARPA Müll. Arg.	7, 11, 25	FP	P	ST	A	
B. micrantha sensu Exell	1, 2, 7					
Not recorded from FP in 12.						
CAPERONIA LATIFOLIA Pax	1, 2, 12			ST		
CAVACOA QUINTASII (Pax & Hoffm.) J. Léonard	15			ST	A	
Grossera quintasii Pax & Hoffm.	1					
CLEISTANTHUS LIBERICUS N. E. Brown	1, 16, 27			ST		
C. polystachyus sensu Hutch.	11, 12, 25, 27					
*CODIAEUM VARIEGATUM (L.) Blume	1, 16			ST	A	
*CROTON DRACONOPSIS Müll. Arg.	1			ST		
CROTON LOBATUS L.	12	FP				
CROTON STELLULIFER Hutch.	1		P			E
CROTONOGYNE MANNIANA Müll. Arg. subsp. MANNIANA	2, 7, 12	FP				
DISCOCLAOXYLON HEXANDRUM (Müll. Arg.) Pax & Hoffm.	2, 16	FP				
Claoxylon hexandrum Müll. Arg.	12					
DISCOCLAOXYLON OCCIDENTALE (Müll. Arg.) Pax & Hoffm.	1, 2, 13, 16			ST		E
DISCOCLAOXYLON PEDICELLARE (Müll. Arg.) Pax & Hoffm.	2, 16	FP				E
Claoxylon pedicellare Müll. Arg.	12					

Discoclaoxylon pubescens (Pax & Hoffm.) Exell	16				A	E
D. occidentale var. *pubescens* Pax & Hoffm.	1					
For a general discussion of *Discoclaoxylon* see 16.						
Discoglypremna caloneura (Pax) Prain	1, 2, 11, 12, 25			ST	A	
Drypetes fernandopoana Brenan	12	FP				E
D. glomerata (Müll. Arg.) Hutch.	2					
Drypetes glabra (Pax) Hutch.	1			ST		E
Drypetes henriquesii (Pax) Hutch.	1			ST		E
Drypetes laciniata (Pax) Hutch.	1			ST	?	
Drypetes occidentalis (Müll. Arg.) Hutch.	2, 12	FP				E
Drypetes principum (Müll. Arg.) Hutch.	1, 2, 12	FP	P			
Elaeophorbia drupifera (Thonn.) Stapf	1, 25, 26		P	ST		
Erythrococca anomala (Juss. ex Poiret) Prain	12	FP				
Erythrococca columnaris (Müll. Arg.) Prain	1		P			E
Erythrococca mannii (Hook. f.) Prain	2, 12	FP				E
Athroandra mannii (Hook. f.) Pax & Hoffm.	2					
Erythrococca molleri (Pax) Prain	1, 11			ST		E
Erythrococca pallidifolia (Pax & Hoffm.) Keay	12	FP				E
Athroandra pallidifolia Pax & Hoffm.	2					
Euphorbia cervicornu Baillon	1, 12			ST		
Euphorbia glaucophylla Poiret	7	FP				
Not recorded from FP in 12.						
Euphorbia hirta L.	1, 9, 11, 12, 25, 26	FP	P	ST	A	
Euphorbia hyssopifolia L.	11, 12		P	ST		
E. hypericifolia sensu Exell	1					
*Euphorbia peplus L.	1			ST		
Euphorbia prostrata Aiton	1, 9, 11, 12, 13, 25, 26	FP	P	ST	A	
*Euphorbia pulcherrima Willd. ex Klotzsch	16				A	
Euphorbia schimperana G. H. A. Scheele		FP				
E. ampla Hook. f.	2					
FP: Moka, *Exell 845* (BM). Not recorded from FP in 12.						
*Euphorbia serpens Kunth	26			ST		
Euphorbia thymifolia L.	1				A	
*Euphorbia tirucalli L.	14			ST		
E. rhipsaloides Welw. ?	1					
Excoecaria guineensis (Benth.) Müll. Arg.			P			
Sapium guineense (Benth.) Kuntze	1, 12					
See J. Léonard in *Bull. Soc. Bot. Brux.* 29 : 138 (1959).						
Grossera elongata Hutch.	1		P			E
Grossera sp.	1			ST		
*Hevea brasiliensis (Kunth) Müll. Arg.	1, 2	FP		ST		
*Hevea guianensis Aubl.	1			ST		
*Jatropha curcas L.	1, 9, 11, 12	FP		ST	A	
*Jatropha multifida L.	1, 11, 16, 25, 26		P	ST	A	
Klaineanthus gaboniae Pierre ex Prain	11, 12			ST		
Macaranga monandra Müll. Arg.	11, 25			ST		
Macaranga occidentalis (Müll. Arg.) Müll. Arg.	2, 12	FP				
Macaranga spinosa Müll. Arg.	2, 12	FP				
Maesobotrya dusenii (Pax) Hutch.	12	FP				
Maesobotrya glabrata (Hutch.) Exell	15		P			E
Thecacoris glabrata Hutch.	1					
Maesobotrya 'sp. nov.'	1					

MAESOBOTRYA sp.	14, 15			ST		
Thecacoris stenopetala sensu Exell pro parte	1					
MALLOTUS SUBULATUS Müll. Arg.	2, 12	FP				
*MANIHOT ESCULENTA Crantz	1, 13			ST	A	
*MANIHOT GLAZIOVII Müll. Arg.	1		P	ST		
MANNIOPHYTON FULVUM Müll. Arg.	12		P	ST		
M. africanum Müll. Arg.	1, 2					
MAREYA MICRANTHA (Benth.) Müll. Arg. subsp. MICRANTHA	12	FP				
M. spicata Baillon	2					
MARGARITARIA DISCOIDEA (Baillon) Webster			P	ST		
Phyllanthus discoideus (Baillon) Müll. Arg.	1, 11, 25					
MICRODESMIS PUBERULA Hook. f. ex Planchon	12	FP				
NEOBOUTONIA MANNII Benth.	1, 2, 12	FP	P	ST		
PHYLLANTHUS AMARUS Schumacher	2, 9, 11, 12, 13	FP		ST	A	
PHYLLANTHUS CAPILLARIS Schumacher	7, 12	FP				
PHYLLANTHUS MUELLERANUS (Kuntze) Exell	1, 12	FP		ST		
PHYLLANTHUS NIGERICUS Brenan	12	FP				
PHYLLANTHUS ODONTADENIUS Müll. Arg.	1, 11, 12	FP	P	ST		
P. niruri sensu Exell	1					
PHYLLANTHUS PENTANDRUS Schumacher	1, 9, 11				A	
PHYLLANTHUS PHYSOCARPUS Müll. Arg.	1		P			E
PHYLLANTHUS RETICULATUS Poiret	16				A	
PHYLLANTHUS TESSMANNII Hutch.	1			ST		
PROTOMEGABARIA MACROPHYLLA Hutch.	1, 12		P	ST		
PSEUDAGROSTISTACHYS AFRICANA (Müll. Arg.) Pax & Hoffm. subsp. AFRICANA	1, 2, 12	FP		ST		
PYCNOCOMA MACROPHYLLA Benth. var. MACROPHYLLA	12	FP				
RICINODENDRON HEUDELOTII subsp. AFRICANUM (Müll. Arg.) J. Léonard	12	FP				
R. africanum Müll. Arg.	7					
See J. Léonard in *Bull. Soc. Bot. Brux.* 31 : 398 (1961).						
*RICINUS COMMUNIS L.	1, 13, 16		P	ST	A	
SAPIUM ELLIPTICUM (Hochst.) Pax	1, 12	FP		ST		
SPONDIANTHUS PREUSSII Engl. var. PREUSSII	12	FP				
TETRACARPIDIUM CONOPHORUM (Müll. Arg.) Hutch. & Dalziel	2, 12	FP				
TETRORCHIDIUM DIDYMOSTEMON (Baillon) Pax & Hoffm.	1, 11, 12, 25	FP		ST		
THECACORIS ANNOBONAE Pax & Hoffm.	1, 16				A	E
THECACORIS MANNIANA (Müll. Arg.)Müll. Arg.	1, 13, 15			ST		E
THECACORIS MEMBRANACEA Pax	1			ST		E
THECACORIS STENOPETALA (Müll. Arg.) Müll. Arg.	1 (p.p.), 2, 12	FP	P			
TRAGIA BENTHAMII Baker	2, 12	FP				
TRAGIA TENUIFOLIA Benth.	1			ST		
*TRAGIA VOLUBILIS L.	2, 12	FP				
UAPACA GUINEENSIS Müll. Arg.	12, 27	FP		ST		
Uapaca sp.	25					
UAPACA STAUDTII Pax	2, 12	FP				

66. ROSACEAE

ALCHEMILLA CRYPTANTHA Steudel ex A. Rich.	1, 12, 13	FP		ST		
A. tenuicaulis Hook. f.	2					
*CYDONIA OBLONGA Miller	13			ST		
Pyrus cydonia L.	13					

*ERIOBOTRYA JAPONICA (Thunb.) Lindl.	1, 13, 15		ST	
*MALUS PUMILA Miller	1		ST ?	
A doubtful record.				
*PRUNUS CERASUS L.	1		ST ?	
A doubtful record.				
*PRUNUS DOMESTICA L.	13		ST ?	
*PRUNUS DULCIS (Miller) D. A. Webb			ST	
P. amygdalus Batsch	13			
*PRUNUS PERSICA (L.) Batsch	1, 11, 13		ST	
PYGEUM AFRICANUM Hook. f.	2, 12, 15	FP	ST	
If transferred to *Prunus* this becomes *P. africana* (Hook. f.) Kalkman				
*ROSA CHINENSIS Jacq.	1		ST	
*ROSA LAEVIGATA Michaux	1		ST	
*ROSA MULTIFLORA Thunb.	15		ST	
*RUBUS DISCOLOR Weihe & Nees	2	FP		
'Rubus extensus Schube ex Engl.' *Index Kew.*, Suppl. 1 : 370 (1906), cited as 'in Abh. Preus. Akad. Wiss. 1891 (1892) 212.—Ins. Fernando Po'. A manifest error for *Ranunculus extensus* Schube ex Engl., *tom. cit.* : 218.				
RUBUS PINNATUS var. AFROTROPICUS (Engl.) Gustafsson	1, 2, 12, 13	FP	ST A	
Rubus afrotropicus (Engl.) Guinea	2			
*RUBUS ROSIFOLIUS Smith	1, 8, 11, 13	FP P	ST	
RUBUS sp.	15		ST	

67. CHRYSOBALANACEAE

ACIOA MANNII (Oliver) Engl.	2, 7, 12	FP		
CHRYSOBALANUS ELLIPTICUS Solander ex Sabine	12	FP		
? CHRYSOBALANUS ORBICULARIS Schumacher	7	FP ?		
Probably *C. ellipticus*.				
PARINARI EXCELSA Sabine	1, 13		ST ?	
A doubtful record.				
PARINARI MACROPHYLLA Sabine	1, 12		ST ?	
A doubtful record.				
PARINARI MOBOLA Oliver	13		ST ?	
A doubtful record.				

68. DICHAPETALACEAE

DICHAPETALUM AFFINE Planchon ex Benth.	12	FP		E
DICHAPETALUM BOCAGEANUM (Henriq.) Engl.	1		ST	E
DICHAPETALUM FLORIBUNDUM (Planchon) Engl.	2, 12	FP		
DICHAPETALUM KAMERUNENSE Engl.		FP		
FP : San Carlos, *Mildbraed 6793*. Not in 12.				
DICHAPETALUM OBLONGUM (Hook. f.) Engl.	2, 12	FP		
DICHAPETALUM SUBCORDATUM (Hook. f.) Engl.	2, 12	FP		E
DICHAPETALUM TOMENTOSUM Engl.		FP		
D. acutifolium Engl.				
FP : Bokoko, *Burchardt*. Not recorded from FP in 12.				
TAPURA AFRICANA Oliver	2, 12	FP		

69. LEGUMINOSAE

ABRUS PRECATORIUS L.	1, 9, 11, 12	FP	ST A	
*ACACIA FARNESIANA (L.) Willd.	1, 2, 25	FP	ST	
ACACIA KAMERUNENSIS Gandoger	15		ST	
A. pennata sensu auctt., pro parte	1, 25			

ACACIA PENTAGONA (Schumacher) Hook. f.	15		P		
A. pennata sensu auctt., pro parte	1				
*ADENANTHERA PAVONINA L.	2, 13	FP		ST	
ADENOCARPUS MANNII (Hook. f.) Hook. f.	2, 7, 12	FP			
AESCHYNOMENE INDICA L.	1, 13		P	ST	
AIRYANTHA SCHWEINFURTHII subsp. CONFUSA (Hutch. & Dalziel) Brummitt		FP			
Baphia confusa Hutch. & Dalziel	2				
Baphiastrum confusum (Hutch. & Dalziel) Pellegrin	12				
Baphia spathacea Hook. f.	2				
See Brummitt in *Kew. Bull.* 22 : 381 (1968).					
*ALBIZIA FALCATA (L.) Backer	11, 13			ST	
*ALBIZIA LEBBECK (L.) Benth.	2, 11, 12	FP		ST	
*ALBIZIA MOLUCCANA Miq.	2	FP			
*ALBIZIA PROCERA (Roxb.) Benth.	11			ST	
ALBIZIA ZYGIA (DC.) J. F. Macbride		FP			
A. brownei (Walp.) Oliver	2				
Not recorded from FP in 12.					
ALYSICARPUS VAGINALIS (L.) DC.	1, 9, 11			ST	A
ANTHONOTHA MACROPHYLLA Beauv.	12	FP			
Macrolobium palisotii Benth.	2				
*ARACHIS HYPOGAEA L.	1, 3, 16, 25	FP		ST	A
BAIKIAEA INSIGNIS Benth. subsp. INSIGNIS	2, 12	FP			
BAPHIA CAPPARIDIFOLIA subsp. POLYGALACEA (Hook. f.) Brummitt		FP			
B. polygalacea (Hook. f.) Baker	2, 12				
BAPHIA NITIDA Lodd.	12	FP		ST	
ST : *Espirito Santo 4422.*					
*BAUHINIA PURPUREA L.	1, 11			ST	
*BAUHINIA TENUIFLORA Watt ex C. B. Clarke	2	FP			
*BAUHINIA TOMENTOSA L.	27			ST	
BERLINIA BRACTEOSA Benth.	2, 12	FP			
CAESALPINIA BONDUC (L.) Roxb.	1, 9, 11, 12, 25	FP		ST	A
C. crista sensu Guinea	7				
*CAESALPINIA PULCHERRIMA (L.) Swartz	1, 2, 11, 12, 16	FP	P	ST	A
*CAJANUS CAJAN (L.) Millsp.	1, 16, 25	FP	P	ST	A
C. indicus Sprengel	2				
*CALOPOGONIUM MUCUNOIDES Desvaux	27			ST	
CANAVALIA ENSIFORMIS (L.) DC.	1, 2	FP		ST	
Not recorded from FP in 12.					
CANAVALIA MARITIMA (Aubl.) Urban	27	FP		ST	A
C. rosea (Swartz) DC.	1, 13				
C. obtusifolia DC. pro parte	7				
Not recorded from FP in 12.					
*CASSIA ALATA L.	2, 27	FP		ST	
CASSIA KIRKII Oliver	12	FP			
*CASSIA LAEVIGATA Willd.	1, 2, 11, 12	FP		ST	A
CASSIA MANNII Oliver	1, 11, 12		P	ST	
CASSIA MIMOSOIDES L.	1	FP		ST	
FP : Moka, *Tessmann 2868.* Not recorded from FP in 12.					
CASSIA OBTUSIFOLIA L.	16	FP		ST	A
C. tora sensu auctt.	1, 12				
See Brenan in *Kew Bull.* 13 : 248 (1958).					

*CASSIA OCCIDENTALIS L.	1, 2, 11, 12, 16, 25, 26	FP	P	ST	A
CASSIA PODOCARPA Guillemin & Perrottet	1, 2, 12, 25, 26	FP		ST	
*CASSIA SIAMEA Lam.	27			ST	
CASSIA SIEBERANA DC.	1			ST ?	
*CASSIA SOPHERA L.	1, 2, 25	FP	P	ST	
*CASSIA SPECTABILIS DC.	27			ST	
*CENTROSEMA PLUMIERI (Turpin ex Pers.) Benth.	11			ST	
*CENTROSEMA PUBESCENS Benth.	11			ST	
*CERCIS SILIQUASTRUM L.	13			ST	
*CLITOREA TERNATEA L.	2, 11	FP		ST	
COLOPHOSPERMUM MOPANE (Benth.) Kirk ex J. Léonard				ST ?	
Copaifera mopane Benth.					
Helder Lains e Silva (13) records *Copaifera mopane* ('pau ferro') as one of the important timber trees of S. Tomé, but no one else to my knowledge has ever recorded it from the island and I have seen no specimens.					
CROTALARIA DONIANA Baker				ST	
ST : *Espírito Santo 66.*					
CROTALARIA GOREENSIS Guillemin & Perrottet	12	FP			
*CROTALARIA LANCEOLATA E. Meyer	2	FP			
Not recorded from FP in 12. If correctly named, not indigenous.					
CROTALARIA MUCRONATA Desvaux	1, 9, 11		P	ST	A
CROTALARIA OCHROLEUCA G. Don	1, 12			ST	
CROTALARIA RETUSA L.	1, 2, 13	FP	P	ST	
P : *Rozeira 452.* Not recorded from FP in 12.					
*CROTALARIA ZANZIBARICA Benth.	15			ST	
C. thomensis Baker f.	1, 11, 14				
CRUDIA KLAINEI Pierre ex De Wild.	2, 12	FP			
C. senegalensis sensu Guinea	2				
CYNOMETRA MANNII Oliver	1, 9, 11, 12, 13, 25			ST	
DALBERGIA ECASTAPHYLLUM (L.) Taub.	1, 2, 11, 12, 13	FP	P	ST	A
*DALBERGIA MONETARIA L.	2	FP			
DANIELLIA OBLONGA Oliver	2, 12	FP		ST ?	
D. thurifera sensu Exell	1				
DANIELLIA OGEA (Harms) Rolfe ex Holland	12	FP			
*DELONIX REGIA (Bojer ex Hook.) Raf.	1	FP		ST	
Poinciana regia Bojer ex Hook.	2				
*DESMANTHUS VIRGATUS (L.) Willd.	11, 13, 15, 25		P	ST	
DESMODIUM ADSCENDENS (Swartz) DC. var. ADSCENDENS	1, 2, 12, 13	FP	P	ST	A
DESMODIUM ADSCENDENS var. ROBUSTUM Schubert	12	FP			
DESMODIUM CANUM (J. F. Gmelin) Schinz & Thell.	1, 8, 9, 11, 12, 13	FP	P	ST	A
D. incanum DC.	2				
DESMODIUM GANGETICUM (L.) DC.	1		P		A
P : *Gossweiler s.n., Rose 487, Rozeira 4220.*					
DESMODIUM PROCUMBENS (Miller) A. S. Hitchc.	11				A
D. ospriostreblum Steudel ex Chiov.	1, 9				
DESMODIUM RAMOSISSIMUM G. Don	11, 12, 16	FP	P	ST	A
D. mauritianum sensu Exell	1, 13				
DESMODIUM REPANDUM (Vahl) DC.	11, 12	FP		ST	
D. scalpe DC.	1, 2, 13				

DESMODIUM TORTUOSUM (Swartz) DC.				ST	
ST : *Espirito Santo 4203, Rozeira 5072.*					
DESMODIUM TRIFLORUM (L.) DC.	13	FP ?	P	ST	
? *D. trifolium* sensu Guinea	2				
DESMODIUM VELUTINUM (Willd.) DC.	11	FP	P	ST	A
D. lasiocarpum (Beauv.) DC.	1, 9, 13				
D. latifolium DC.	2				
Not recorded from FP in 12.					
DIALIUM GUINEENSE Willd.	1, 7, 11, 12, 25	FP	P	ST	
Not recorded from FP in 12.					
DIOCLEA REFLEXA Hook. f.	1, 12, 25	FP	P	ST	
DISTEMONANTHUS BENTHAMIANUS Baillon	2	FP			
Not recorded from FP in 12.					
DREPANOCARPUS LUNATUS (L. f.) G. F. W. Meyer	1		P	ST	
ST : *Rozeira 4403.*					
ENTADA AFRICANA Guillemin & Perrottet	2	FP			
Not recorded from FP in 12.					
ENTADA GIGAS (L.) Fawcett & Rendle	12	FP			
E. scandens sensu Guinea	2				
ENTADA MANNII (Oliver) Tisserant	12	FP			
Piptadenia mannii Oliver	2				
ERIOSEMA GLOMERATUM (Guillemin & Perrottet) Hook. f.	16				A
? ERIOSEMA PARVIFLORUM E. Meyer subsp. PARVIFLORUM	12	FP ?			
A doubtful record.					
? ERYTHRINA CAFFRA Thunb.	1		P ?		
* ERYTHRINA DROOGMANSIANA De Wild. & Dur.	27			ST	
Probably introduced.					
ERYTHRINA GILLETII De Wild.	2	FP			
Not in 12.					
*ERYTHRINA INDICA Lam.	13, 14, 15		P	ST	
*ERYTHRINA POEPPIGIANA (Walp.) O. F. Cook	15			ST	
? ERYTHRINA SENEGALENSIS DC.	2	FP ?			
This may be *E. vogelii.*					
*ERYTHRINA UMBROSA Kunth	13			ST	
*ERYTHRINA VELUTINA Willd.	1, 13			ST	A
ERYTHRINA VOGELII Hook. f.	12	FP			
ERYTHROPHLOEUM GUINEENSE G. Don	2	FP			
Not recorded from FP in 12.					
GLYCINE WIGHTII (Wight & Arn.) Verdc.				ST	
G. javanica sensu Exell	11				
GRIFFONIA PHYSOCARPA Baillon	2, 12	FP			
*HAEMATOXYLUM CAMPECHIANUM L.	27			ST	
INDIGOFERA ASTRAGALINA DC.				ST	
ST : *Espirito Santo 4214.*					
INDIGOFERA COLUTEA (Burm. f.) Merr. var. COLUTEA				ST	
ST : *Espirito Santo 4228.*					
INDIGOFERA HIRSUTA L.	1			ST	
INDIGOFERA SPICATA Forssk.	11, 13			ST	A
I. hendecaphylla Jacq.	1, 9				
INDIGOFERA SUFFRUTICOSA Miller	11, 25			ST	
INDIGOFERA TINCTORIA L.	1, 9, 11, 25		P	ST	A
INDIGOFERA TRITA var. SUBULATA (Vahl ex Poiret) Ali				ST	
ST : *Rozeira 4416.*					
*INGA EDULIS Mart.	15, 25, 27			ST	

*INGA sp.	13			ST		
LABLAB PURPUREUS (L.) Sweet		FP				
Dolichos lablab L.	2					
Not recorded from FP in 12.						
LEPTODERRIS BRACHYPTERA (Benth.) Dunn	2, 12	FP				
L. africana (Baker) Harms	2					
*LEUCAENA LEUCOCEPHALA (Lam.) De Wit		FP	P	ST		
L. glauca sensu Benth.	1, 2, 12, 13					
LEUCOMPHALUS CAPPARIDEUS Benth. ex Planchon	2, 12	FP				
LONCHOCARPUS CYANESCENS (Schumacher) Benth.	2, 12	FP				
LONCHOCARPUS GRIFFONIANUS (Baillon) Dunn	2, 7, 12	FP		ST		
? *Millettia thonningii* sensu Guinea	2					
ST : *Espírito Santo 4553.*						
LONCHOCARPUS SERICEUS (Poiret) Kunth ex DC.	1, 11, 12, 13	FP	P	ST		
MILLETTIA BARTERI (Benth.) Dunn	1			ST		
MILLETTIA MACROPHYLLA Benth.	2, 12	FP				
MILLETTIA MANNII Baker	2	FP				
Not recorded from FP in 12.						
MILLETTIA MILDBRAEDII Harms	2	FP				E ?
FP : San Carlos, *Mildbraed 6975*. Not in 12.						
MILLETTIA SANAGANA Harms	2, 12	FP				
MILLETTIA THONNINGII (Schumacher) Baker	1, 12, 25	FP		ST		
*MIMOSA POLYDACTYLA Humb. & Bonpl. ex Willd.	1		P	ST		
*MIMOSA PUDICA L.	2, 27	FP		ST		
M. pigra sensu Espírito Santo	25					
This may be *M. polydactyla.*						
MUCUNA FLAGELLIPES T. Vogel ex Hook. f. & Benth.	2, 12	FP				
MUCUNA PRURIENS (L.) DC.	1, 2, 25	FP		ST		
M. utilis sensu Guinea	2 (photo)					
Not recorded from FP in 12.						
MUCUNA SLOANEI Fawcett & Rendle	12, 16, 25	FP		ST	A	
M. urens sensu Exell	1					
ORMOCARPUM SENNOIDES subsp. HISPIDUM (Willd.) Brenan & Léonard				ST		
O. cochinchinense (Lour.) Merr.	1, 11					
See Brenan & Léonard in *Bull. Jard. Bot. Brux.* 24 : 104 (1954).						
ORMOCARPUM VERRUCOSUM Beauv.	1, 2, 12	FP	P	ST		
*ORMOSIA DASYCARPA Jackson	13			ST		
OSTRYOCARPUS RIPARIUS Hook. f.	2, 12	FP				
PARKIA CLAPPERTONIA Keay		FP				
? *P. africana* sensu Guinea	2					
Not recorded from FP in 12.						
PARKIA OLIVERI J. F. Macbride	1, 9, 11, 13			ST	A	
*PELTOPHORUM PTEROCARPUM (DC.) Backer ex K. Heyne		FP				
P. ferrugineum (Decaisne) Benth.	2					
PENTACLETHRA MACROPHYLLA Benth.	1, 2, 7, 12, 13, 25	FP	P	ST	A	
PHASEOLUS ADENANTHUS G. F. W. Meyer	1			ST		
PHASEOLUS LUNATUS L.	1, 2, 12	FP		ST	A	
*PHASEOLUS VULGARIS L.	1			ST		
PHYSOSTIGMA VENENOSUM Balf.	2, 12	FP				
? PILIOSTIGMA RETICULATUM (DC.) Hochst.	27	FP ?		ST ?		
Bauhinia reticulata DC.	2					
Not recorded from FP in 12.						

PIPTADENIASTRUM AFRICANUM (Hook. f.) Brenan		FP			
Piptadenia africana Hook. f.					
FP : Bokoko, *Burchardt.* Not recorded from FP in 12.					
PSOPHOCARPUS SCANDENS (Endl.) Verdc.	27			ST	
*PTEROCARPUS INDICUS Willd.				ST	
ST : *Espírito Santo 4388.*					
PTEROCARPUS MILDBRAEDII Harms	2, 12	FP			
*PUERARIA JAVANICA Benth.	13			ST	
RHYNCHOSIA DENSIFLORA (Roth) DC.	12			ST	
R. debilis G. Don	1				
RHYNCHOSIA MANNII Baker	2, 12	FP			
RHYNCHOSIA MINIMA (L.) DC.				ST	A
R. memnonia sensu Exell	1, 9, 11				
RHYNCHOSIA PREUSSII (Harms) Taub. ex Harms	12	FP			
R. cyanosperma Benth. ex Baker pro parte	2				
RHYNCHOSIA PYCNOSTACHYA (DC.) Meikle	12	FP			
SAMANEA SAMAN (Jacq.) Merr.		FP		ST	
Pithecellobium samana (Jacq.) Benth.	2, 13				
SCORODOPHLOEUS ZENKERI Harms	2	FP			
Not in 12.					
SESBANIA SERICEA (Willd.) Link				ST	A
S. pubescens DC.	1, 9, 11, 12				
SOPHORA TOMENTOSA L.				ST	
S. occidentalis L.	1, 12				
*TAMARINDUS INDICA L.	1, 2, 13, 25, 26	FP	P	ST	A
*TEPHROSIA CANDIDA (Roxb.) DC.	11, 25			ST	
TEPHROSIA NOCTIFLORA Bojer ex Baker				ST	
ST. : *Espírito Santo 4324, Rozeira 775, 1231.*					
TEPHROSIA PLATYCARPA Guillemin & Perrottet				ST	
T. flexuosa G. Don	1, 12				
TEPHROSIA PURPUREA subsp. LEPTOSTACHYA var. PUBESCENS Baker	1			ST	
TEPHROSIA UNIFLORA Pers.				ST	
ST : *Espírito Santo 4636.*					
TEPHROSIA VOGELII Hook. f.	1, 2, 11, 12, 25, 26	FP	P	ST	
TERAMNUS LABIALIS (L. f.) Sprengel	1, 9, 11, 15		P	ST	A
TETRAPLEURA TETRAPTERA (Schumacher) Taub.	1, 12, 13			ST	
TRIFOLIUM RUEPPELLIANUM var. PREUSSII (Taub. ex Baker f.) J. B. Gillett	12	FP			
T. preussii Taub. ex Baker f.	2				
TRIFOLIUM SIMENSE Fresen.	2, 12	FP			
T. subrotundum Steudel ex Hochst.	2				
TRIFOLIUM USAMBARENSE Taub.	12	FP			
T. mannii Guinea, *nom. nud.*	7				
URARIA PICTA (Jacq.) DC.	1, 9, 11			ST	A
*VICIA FABA L.	13			ST	
VIGNA ALBA (G. Don) Planchon ex Baker f.	1, 13			ST	
VIGNA GRACILIS (Guillemin & Perrottet) Hook. f.	12		P		
V. occidentalis Baker f.	1				
VIGNA MULTIFLORA Hook. f.	2, 12	FP			
VIGNA OBLONGA Benth.	2	FP		ST	
V. marina sensu Exell	1, 12				

VIGNA RACEMOSA (G. Don) Hutch. & Dalziel	1, 8, 11, 13		P	ST	
P : *Rozeira 3932, 3991.*					
VIGNA UNGUICULATA (L.) Walp.	16	FP			A
V. sinensis Endl. ex Hassk.					
FP : *Mann 415*. Not recorded from FP in 12. See Baker in Oliver, *Fl. Trop. Afr.* 2 : 205 (1871).					
VIGNA VEXILLATA (L.) A. Rich.	12	FP			
V. thonningii Hook. f.	2				
ZENKERELLA CITRINA Taub.	12	FP			
Cynometra leptoclada Harms	2				
ZENKERELLA PAUCIFLORA Harms		FP			
Cynometra pauciflora (Harms) Harms	2				
Not in 12.					

70. BUXACEAE

*BUXUS SEMPERVIRENS L.	1			ST ?	

71. MYRICACEAE

MYRICA ARBOREA Hutch.	12	FP			

72. ULMACEAE

CELTIS GOMPHOPHYLLA Baker				ST	
C. durandii Engl.	1, 11. 12, 13, 25, 27				
CELTIS INTEGRIFOLIA Lam.	13			ST ?	
CELTIS MILDBRAEDII Engl.	12, 25, 27			ST	
C. soyauxii sensu G. Taylor	1, 13				
CELTIS PRANTLII Priemer ex Engl.	1, 9, 11, 27		P	ST	A
C. insularis Rendle	2				
This is considered by Letouzey (*Fl. Cameroun* 8 : 26 (1968)) to be *C. philippensis* Blanco.					
CELTIS WRIGHTII Planchon		FP			
C. brownii Rendle	12				
C. prantlii sensu Guinea	2				
C. rendleana G. Taylor	1, 11				
See Polhill in *Kew Bull.* 19 : 141 (1964). Letouzey (*loc. cit.*) considers that this also is *C. philippensis* Blanco.					
CHAETACME ARISTATA E. Meyer ex Planchon	1, 12				A
TREMA ORIENTALE (L.) Blume		FP	P	ST	A
T. guineense (Schumacher) Ficalho	1, 2, 7, 12, 13				

73. MORACEAE

ANTIARIS AFRICANA Engl.	2	FP			
Not recorded from FP in 12.					
ANTIARIS sp.		FP			
FP : Bokoko, *Mildbraed 6880.*					
*ARTOCARPUS ALTILIS (S. Parkinson) Fosberg		FP	P	ST	A
A. communis J. R. & G. Forster	1, 13, 16, 25				
A. incisus (Thunb.) L. f.	2				
*ARTOCARPUS HETEROPHYLLUS Lam.	16, 25	FP	P	ST	A
A. integer sensu G. Taylor	1, 13				
A. integrifolius sensu Guinea	2				

BOSQUEIA ANGOLENSIS Ficalho	1, 12				A	
*CASTILLOA ELASTICA Cerv.	1, 11		P	ST		
*CECROPIA PELTATA L.	11, 25			ST		
CHLOROPHORA EXCELSA (Welw.) Benth.	1, 2, 7, 11, 12, 13, 25	FP	P	ST		
DORSTENIA BARTERI Bur.	2, 12	FP				
DORSTENIA ELLIPTICA Bur.	2, 12	FP				
DORSTENIA PROREPENS Engl.	2, 12	FP				
FICUS ANNOBONENSIS Mildbr. & Hutch.	1, 2, 11	FP	P	ST	A	E
Not in 12. Recorded from FP in 1, fide G. Taylor.						
FICUS CAMPTONEURA Mildbr.	2, 12	FP				
FICUS CAMPTONEUROIDES Hutch.	2, 12	FP				
FICUS CAPENSIS Thunb.	1, 25			ST		
*FICUS CARICA L.	13			ST		
FICUS CHLAMYDOCARPA Mildbr. & Burret	12	FP	P	ST	A	
F. clarencensis Mildbr. & Hutch.	1, 2, 13					
*FICUS ELASTICA Roxb.	1			ST		
FICUS ERIOBOTRYOIDES Kunth & Bouché var. ERIOBOTRYOIDES	12	FP				
FICUS EXASPERATA Vahl	1, 2, 7, 12, 25	FP		ST		
FICUS FERNANDESIANA Hutch.	11			ST		E
FICUS GLOBICARPA Warb. ex Guinea, *nom. nud.*	2	FP				
I cannot trace that this name, listed by Guinea in 2, has been validly published.						
FICUS KAMERUNENSIS Warb. ex Mildbr. & Burret	1, 12, 25			ST		
FICUS MACROSPERMA Warb. ex Mildbr. & Burret		FP				
FP: *Melville & Wrigley 622* (K). Not recorded from FP in 12.						
FICUS MALLOTOCARPA Warb.	2, 12	FP				
FICUS MUCUSO Welw. ex Ficalho	1, 12	FP		ST		
FICUS NATALENSIS Hochst.	2, 12	FP				
FICUS OTTONIIFOLIA (Miq.) Miq.	2, 12	FP				
FICUS OVATA Vahl	2, 7, 12	FP				
FICUS PRATICOLA Mildbr. & Hutch.	2, 12	FP				
FICUS PREUSSII Warb.	2	FP				
Not recorded from FP in 12.						
*FICUS PUMILA L.	27			ST		
'Ficus scabra (var. Jacq. nec Wild.)'	2	FP				
I do not know what this is.						
FICUS SIDIFOLIA Welw. ex Hiern	9, 11, 13			ST	A	
FICUS SPIROCAULIS Mildbr., *nom. nud.*	2, 12	FP				E ?
? *F. urceolaris* sensu Guinea	2, 7					
FP: Musola, *Mildbraed 7010*.						
FICUS THONNINGII Blume	12	FP				
F. microcarpa Vahl	2					
FICUS VOGELIANA (Miq.) Miq.	2, 7, 12	FP				
FICUS VOGELII (Miq.) Miq.	1, 12	FP		ST		
F. vogelii var. *pubicarpa* Mildbr. & Burret	2					
FICUS WILDEMANIANA Warb.	2	FP				
Not in 12.						
MESOGYNE HENRIQUESII Engl.	1, 11			ST		E
MUSANGA CECROPIOIDES R.Br.	1, 7, 11, 12, 13, 25	FP		ST		
M. smithii R.Br.	2					

Myrianthus preussii Engl.	12	FP				
Treculia africana Decaisne var. africana	1, 7, 11, 12, 13, 25	FP	P	ST		
Not recorded from FP in 12.						

74. URTICACEAE

*Boehmeria nivea (L.) Gaudich.	1, 2, 13	FP		ST		
Boehmeria platyphylla D. Don	1, 2, 12, 19	FP		ST		
Droguetia iners (Forssk.) Schweinf.	19	FP				
Not recorded from FP in 12.						
Elatostema mannii Wedd.	2, 12, 19	FP				
Elatostema monticola Hook. f.	12, 19	FP				
Elatostema paivaeanum Wedd.	2, 12, 19	FP				
Elatostema thomense Henriq.	1, 13			ST		E
Perhaps a form of *E. paivaeanum*.						
Elatostema welwitschii Engl.	1, 2, 7, 11, 12, 13, 19	FP		ST		
E. henriquesii Engl.	2					
Laportea aestuans (L.) Chew		FP	P	ST	A	
Fleurya aestuans (L.) Gaudich. ex Miq.	1, 2, 11, 12, 13, 19, 26					
Laportea alatipes Hook. f.	19	FP				
Not recorded from FP in 12.						
Laportea ovalifolia (Schumacher) Chew		FP				
Fleurya ovalifolia (Schumacher) Dandy	12, 19					
F. podocarpa Wedd.	2					
Lecanthus peduncularis (Royle) Wedd.	2, 12, 19	FP				
Parietaria debilis Forster f.	19	FP				
P. laxiflora Engl.	2, 12					
Pilea manniana Wedd.	1, 13			ST		E
Pilea microphylla (L.) Liebm.	2, 12, 19	FP				
Pilea rivularis Wedd.	19	FP		ST		
P. ceratomera Wedd.	1, 2, 12, 13					
Pilea sublucens Wedd.	2, 12, 19	FP				
Pilea tetraphylla (Steudel) Blume	12, 19	FP				
Pouzolzia guineensis Benth.	1, 2, 11, 12, 13, 19	FP		ST		
Pouzolzia parasitica (Forssk.) Schweinf.	19	FP				
Not recorded from FP in 12.						
Procris crenata C. B. Robinson	1, 12, 19	FP	P	ST	A	
P. laevigata sensu Guinea	2					
Urera batesii Rendle	2, 12, 19	FP				
Urera cameroonensis Wedd.	1, 2, 12, 16, 19	FP		ST	A	
Urera mannii (Wedd.) Benth. & Hook. ex Rendle	1, 2, 12, 19	FP	P	ST	A	
Urera repens (Wedd.) Rendle	2, 12, 19	FP				
Urera thonneri De Wild. ex T. Dur.	19	FP				
FP: *Escarré 451*. Not in 12.						

75. CANNABACEAE

*Cannabis sativa L.	1, 13			ST		

76. AQUIFOLIACEAE

Ilex mitis (L.) Radlk.	12, 27	FP		ST		

77. CELASTRACEAE (incl. HIPPOCRATEACEAE)

Campylostemon angolense Welw. ex Oliver	12	FP				
Hippocratea indica Willd.	12	FP				
H. loesenerana Hutch. & Moss	2					
Hippocratea velutina Afzel.	1, 12			ST		
Maytenus annobonensis (Loes. & Mildbr.) Exell	16				A	E
Gymnosporia annobonensis Loes. & Mildbr.	1, 2					
Maytenus buchananii (Loes.) R. Wilczek		FP				
FP: *Wrigley & Melville 673* (K.) Not in 12.						
Maytenus monodii Exell	15			ST		E
Salacia cf. cuspidicoma Loes.		FP				
FP: Bokoko, *Burchardt.*						
Salacia debilis (G. Don) Walp.	2, 12	FP				
Salacia mannii Oliver	2, 12	FP				
Salacia pyriformis (Sabine) Steudel	1, 12			ST		

78. ICACINACEAE

Desmostachys tenuifolius Oliver	2, 12	FP				
Lasianthera africana Beauv.	2, 12	FP				
Lavigeria macrocarpa (Oliver) Pierre	12	FP				
Icacina macrocarpa Oliver	2					
Neostachyanthus zenkeri (Engl.) Exell & Mendonça	12	FP				
Rhaphiostylis ferruginea Engl.		FP				
FP: Bokoko, *Burchardt.* Not recorded from FP in 12.						

79. OLACACEAE

Heisteria parvifolia Smith	1, 7, 12	FP	P	ST	A	
Olax gambecola Baillon	11			ST	A	
O. viridis Oliver	1, 9					
Strombosia grandifolia Hook. f. ex Benth.	2, 12	FP				
Strombosia scheffleri Engl.	12	FP				
Strombosia sp.	1				A	
Ximenia americana L.	1, 25, 26				A	

80. OPILIACEAE

Urobotrya minutiflora Stapf		FP				
Opilia minutiflora (Stapf) Engl.	2					
Not recorded from FP in 12.						

81. LORANTHACEAE

General reference: S. Balle, 'Les Loranthacées d'Afrique portugaise. I. Guinée et San Tomé' in *Bolm. Soc. Broter.*, sér. 2, 38: 9–80, t. 1–16 (1964).

? Globimetula braunii (Engl.) Tieghem		FP ?				
Loranthus zenkeri Engl.	2					
Not recorded from FP in 12. Balle considers it unlikely that the species occurs in FP.						
Helixanthera mannii (Oliver) Danser var. mannii	11, 12, 13			ST		
Loranthus mannii Oliver	1					
Loranthus ternatus Tieghem	1					
Helixanthera mannii var. *ternata* (Tieghem) Balle	11					
Phragmanthera capitata (Sprengel) Balle		FP				
Loranthus capitatus (Sprengel) Engl.	2					
Loranthus incanus Schumacher	2					
Phragmanthera incana (Schumacher) Balle	12					

Phragmanthera nitidula (Sprague) Balle		FP				
Loranthus nitidulus Sprague	2					
Phragmanthera polyscripta Balle pro parte	12					
Tapinanthus bangwensis (Engl. & Krause) Danser	12	FP				
Viscum engleri Tieghem	16				A	
Viscum triflorum DC.				ST		
V. nervosum var. *angustifolium* Sprague	1					

82. SANTALACEAE

Thesium tenuissimum Hook. f.	2, 12	FP				

83. RHAMNACEAE

Gouania longipetala Hemsley	12	FP				
Lasiodiscus mannii Hook. f.	1, 12		P			
Lasiodiscus mildbraedii Engl.	1, 12			ST		
Lasiodiscus rozeirae Exell	14			ST		E
Maesopsis eminii Engl.	2, 12, 27	FP		ST		
Ventilago diffusa (G. Don) Exell	1, 11, 12			ST		
Ziziphus abyssinica Hochst. ex A. Rich.	25			ST		
*Ziziphus mauritiana Lam.	13			ST		

84. VITACEAE

Ampelocissus cavicaulis (Baker) Planchon	2	FP				
Not recorded from FP in 12.						
Ampelocissus macrocirrha Gilg & Brandt	2, 12	FP				
Stated in 12 to be doubtfully distinct from *A. cavicaulis*.						
Cissus adenopoda Sprague		FP				
FP: *Melville & Wrigley 455b* (K). Not recorded from FP in 12.						
Cissus aralioides (Welw. ex Baker) Planchon	1		P ?	ST		
Cissus arguta Hook. f.	2	FP ?				
Recorded from FP in *Fl. W. Trop. Afr.*, ed. 1, 1 : 475 (1928) but not in 12. The FP plant may be *C. producta*.						
Cissus barbeyana De Wild. & Dur.	1, 12		P	ST		
Cissus barteri (Baker) Planchon	2, 12	FP				
Cissus curvipoda (Baker) Planchon	1			ST		E
Cissus debilis (Baker) Planchon	1, 2, 12, 13	FP		ST		
Cissus diffusiflora (Baker) Planchon	2, 12	FP				
Cissus glaucophylla Hook. f.	2, 12	FP				
Cissus gracilis Guillemin & Perrottet	2, 12	FP				
Cissus lageniflora Gilg & Brandt	12	FP				
Cissus mannii (Baker) Planchon	12	FP				
Cissus oliveri (Engl.) Gilg	1			ST		
Cissus aff. petiolata Hook. f.	1			ST		
Cissus producta Afzel.	1, 2, 12	FP		ST		
Cissus vogelii Hook. f.	2, 12	FP				
*Vitis vinifera L.	1, 13			ST		

85. LEEACEAE

Leea guineensis G. Don	1, 2, 12	FP		ST		
Leea tinctoria Lindl. ex Baker	1, 13, 25			ST		E

86. RUTACEAE

Afraegle mildbraedii Engl.	2, 12	FP				E
*Citrus aurantifolia (Christm.) Swingle	1, 16		P		A	
*Citrus aurantium L.	1, 2, 13	FP		ST	A	
*Citrus grandis (L.) Osb.	2, 13	FP		ST		
*Citrus limon (L.) Burm. f.		FP				
C. limonum Risso	2					
*Citrus nobilis Lour.	1			ST		
Clausena anisata (Willd.) Hook. f. ex Benth.	2, 7, 12	FP				
Fagara annobonensis Mildbr.	1, 2				A	E
Fagara macrophylla Engl. Not recorded from FP in 12.	1, 7, 12, 13, 25	FP	P	ST		
Fagara rubescens (Planchon ex Hook. f.) Engl.	12			ST		
F. melanacantha (Planchon ex Oliver) Engl.	1, 13					
F. welwitschii Engl.	1, 13					
Fagara thomensis Engl.	1			ST		E
Glycosmis ? africana Hook. f.	1			ST		
*Ruta chalepensis L.	13			ST ?		
Teclea verdoorniana Exell & Mendonça	12	FP				
T. grandifolia sensu Guinea	2					

87. SIMAROUBACEAE

Brucea guineensis G. Don *B. paniculata* sensu Mildbr. in *Notizbl. Bot. Gart. Berl.* 12 : 185 (1934) is almost certainly *B. guineensis*. Not recorded from FP in 12.		FP				
Hannoa klaineana Pierre & Engl. FP : Bokoko, *Burchardt*. Not recorded from FP in 12.		FP				
*Quassia amara L.	13			ST		

88. IRVINGIACEAE

Desbordesia glaucescens (Engl.) Tieghem Not recorded from FP in 12.	2	FP				
Irvingia gabonensis (Aubry-Lecomte ex O'Rorke) Baillon	1, 12		P			

89. BURSERACEAE

Canarium schweinfurthii Engl. Not recorded from FP in 12.	2	FP				
Canarium velutinum Gilg Not in 12.	2	FP				
Dacryodes edulis (G. Don) H. J. Lam	12, 25, 27	FP	P	ST		
Pachylobus edulis G. Don	1, 11, 13					
P. edulis var. *mubafo* Engl. Not recorded from FP in 12.	2					
Santiria trimera (Oliv.) Aubrév.	25, 26, 27		P	ST		
Santiriopsis trimera (Oliv.) Guillaumin ex Engl.	1					

90. MELIACEAE

Carapa procera DC.	1, 2, 12, 25	FP		ST		
*Cedrela odorata L.	13			ST		
C. toona sensu Exell	11					
Entandrophragma angolense (Welw.) C.DC.	12	FP				

Guarea glomerulata Harms	2, 12	FP				
Heckeldora staudtii (Harms) Staner		FP				
Guarea staudtii Harms	2					
Not recorded from FP in 12.						
*Melia azedarach L.	1, 2, 25	FP	P	ST		
*Toona ciliata M. Roem.	25, 27			ST		
Cedrela toona Roxb. ex Willd.	1					
Trichilia grandifolia Oliver	1			ST		E
Trichilia macrophylla Oliver ex Guinea, *nom. nud.*, non *T. macrophylla* Benth.	2	FP ?				
Apparently an erroneous citation.						
Trichilia monadelpha (Thonn.) J. De Wilde		FP				
T. heudelotii Planchon ex Oliver	2, 12					
Trichilia rubescens Oliver	2, 12	FP				
Turraea glomeruliflora Harms	1, 2, 16				A	E
Turraea vogelii Hook. f. ex Benth.	1, 2, 9, 11, 12, 13	FP	P	ST		

91. SAPINDACEAE

Allophylus africanus Beauv.	1, 11, 13, 25, 26	FP		ST		
FP: Bokoko, *Mildbraed 6792*; Musola, *Mildbraed 7018*. Not recorded from FP in 12.						
Allophylus grandifolius (Baker) Radlk.	1, 11		P	ST		
Allophylus hirtellus (Hook. f.) Radlk.	2, 12	FP				
Allophylus oreodryadum Gilg ex Mildbr., *nom. nud.*	2, 12	FP				
FP: *Mildbraed 6406*.						
Blighia sapida C. Koenig	1		P	ST		
Cardiospermum corindum L.	1				A	
Cardiospermum halicacabum L.	1, 2, 12	FP		ST		
Chytranthus mannii Hook. f.	1, 11, 13, 25		P	ST		E
Deinbollia insignis Hook. f.	2, 12	FP				
Eriocoelum kerstingii Gilg ex Engl.	2	FP				
Not recorded from FP in 12.						
Eriocoelum macrocarpum Gilg ex Engl.		FP				
FP: Bokoko, *Burchardt*. Not recorded from FP in 12.						
Eriocoelum sp.	12	FP				
Laccodiscus ferrugineus (Baker) Radlk.	2, 12	FP				
Lychnodiscus reticulatus Radlk.	2, 12	FP				
Paullinia pinnata L.	1, 2, 9, 12	FP	P	ST		
*Sapindus saponaria L.	1				A	

92. MELIANTHACEAE

Bersama abyssinica subsp. paullinioides (Planchon) Verdc.	12	FP				
B. paullinioides (Planchon) Baker	2					

93. ANACARDIACEAE

*Anacardium occidentale L.	1, 2, 25	FP	P	ST	A	
Antrocaryon klaineanum Pierre	2, 12	FP				
Lannea welwitschii (Hiern) Engl.	1				A	
*Mangifera indica L.	1, 2, 16	FP	P	ST	A	
Pseudospondias microcarpa (A. Rich.) Engl.	1, 2, 11, 12, 13, 25	FP	P	ST	A	

SORINDEIA GRANDIFOLIA Engl.	1, 12, 13			ST		
? SORINDEIA JUGLANDIFOLIA Planchon	2			ST ?		
Record probably based on a misidentification of *S. grandifolia*.						
*SPONDIAS CYTHEREA Sonnerat	1, 11, 13, 25		P	ST		
S. dulcis Forster f.	2					
*SPONDIAS MOMBIN L.	1, 11, 12, 25, 26		P	ST	A	
TRICHOSCYPHA BIJUGA Engl.	2, 12	FP				

94. CONNARACEAE

AGELAEA ANNOBONENSIS Schellenb.	1, 2				A	E
AGELAEA COCCINEA Exell	1		P			E
AGELAEA OBLIQUA var. CORDATA (Schellenb.) Exell	1, 12			ST		
AGELAEA OVALIS Schellenb.	1, 2, 16				A	E
AGELAEA PHAEOCARPA Exell	1		P			E
AGELAEA PILOSA Schellenb.		FP				
FP: *Melville & Wrigley 638* (K). Not recorded from FP in 12.						
AGELAEA PRINCIPENSIS Exell	1		P			E
AGELAEA PSEUDOBLIQUA Schellenb.	2, 12	FP				
AGELAEA RETICULATA Exell	1		P			E
BYRSOCARPUS DINKLAGEI (Gilg) Schellenb. ex Hutch. & Dalziel	2, 12	FP				
CNESTIS FERRUGINEA DC.	1, 12	FP	P	ST		
FP: *Veitch* (fide Schellenb. in Engl., *Pflanzenr.* IV, 127 : 33 (1938)). Not recorded from FP in 12.						
? CNESTIS URENS Gilg	2	FP ?				
Not in 12.						
CONNARUS AFRICANUS Lam.	1			ST		
CONNARUS GRIFFONIANUS Baillon	1, 2, 12	FP	P			
PAXIA ZENKERI Schellenb.	2	FP				
Not in 12 and not recorded from FP by Schellenberg.						

95. ALANGIACEAE

ALANGIUM CHINENSE (Lour.) Harms	12, 27	FP		ST		
A. begoniifolium (Roxb.) Baillon	2					

96. ARALIACEAE

*HEDERA HELIX L.	1, 3, 15			ST		
POLYSCIAS FULVA (Hiern) Harms	2, 7, 12, 19	FP				
*POLYSCIAS GUILFOYLEI var. LACINIATA L. H. Bailey	16				A	
POLYSCIAS QUINTASII Exell	1, 11, 13, 15, 25		P	ST		E
SCHEFFLERA BARTERI (Seem.) Harms var. BARTERI	1, 12, 19	FP	P	ST		
S. henriquesiana Harms ex Henriq.	1, 11					
Tennant (in *Kew Bull.* 15 : 332 (1961)) considers that this is a synonym of *S. barteri* var. *barteri*.						
Not recorded from FP in 12.						
SCHEFFLERA HIERNIANA Harms	12, 19	FP				
S. ledermannii Harms	2, 7					
Tennant (*loc. cit.*) refers this with doubt to *S. barteri* var. *barteri*; he does not mention *S. hierniana*, to which it is referred in 12.						
SCHEFFLERA MANNII (Hook. f.) Harms	1, 2, 7, 12, 13, 14, 19	FP		ST	A	

97. UMBELLIFERAE

Apium leptophyllum (Pers.) F. v. Muell. ex Benth.	1		P		
Caucalis melanantha (Hochst.) Benth. & Hook. ex Hiern	2, 7, 12, 19	FP			
C. gracilis sensu Guinea	2				
Centella asiatica (L.) Urban	1, 11, 12, 19, 25, 26	FP	P	ST	
Cryptotaenia africana (Hook. f.) Drude	12, 19	FP			
***Eryngium foetidum** L.	1, 2, 8, 11, 12, 13, 19, 25	FP	P	ST	
***Foeniculum vulgare** Miller	2	FP			
Hydrocotyle bonariensis Lam.	1, 13, 19	FP	P	ST	
Hydrocotyle mannii Hook. f.	1, 2, 12, 19	FP		ST	
Hydrocotyle sibthorpioides Lam.	12, 19	FP			
H. monticola Hook. f.	2				
***Petroselinum crispum** (Miller) A. W. Hill		FP		ST	
P. sativum Hoffm.	2				
P. hortense auctt.	13				
Peucedanum winkleri H. Wolff	12, 19	FP			
Pimpinella oreophila Hook. f.	2, 7, 12, 19	FP			
P. petitianum sensu Guinea	2				
Sanicula elata Buch.-Ham. ex D. Don	12, 19	FP			
S. europaea var. *elata* (Buch.-Ham. ex D. Don) H. Wolff	2				
S. europaea sensu Guinea	7				

98. THEACEAE

Balthasaria mannii (Oliver) Verdc.				ST	E
Adinandra mannii Oliver	1, 13				
Melchiora mannii (Oliver) Kobuski	15				
***Camellia japonica** L.	1			ST	
***Camellia sinensis** (L.) Kuntze				ST	
Thea sinensis L.	1				

99. ERICACEAE

Agauria salicifolia (Commerson) Hook. f. ex Oliver	2, 7, 17	FP			
Blaeria mannii (Engl.) Engl.	2, 7, 17	FP			
B. dicranotricha Mildbr.					
Philippia mannii (Hook. f.) Alm & Fries	2, 7, 17	FP			
Philippia thomensis Henriq.	1, 13, 15			ST	E
***Rhododendron mucronatum** (Blume) G. Don	1			ST	

100. EBENACEAE

? **Diospyros elliotii** (Hiern) F. White		FP			
Maba mannii Hiern	2				
Not recorded from FP in 17. According to F. White almost certainly *D. piscatoria*.					
Diospyros ferrea (Willd.) Bakh.				ST	
Maba buxifolia (Rottb.) Pers., non *Diospyros buxifolia* (Blume) Hiern	1				
Diospyros melocarpa F. White	17	FP			

DIOSPYROS PISCATORIA Gürke		FP				
Maba bipindensis Gürke						
FP: Bokoko, *Mildbraed 6950*. Not recorded from FP in 17.						

101. SAPOTACEAE

CHRYSOPHYLLUM ALBIDUM G. Don	1, 13, 27		P	ST		
Gambeya albida (G. Don) Aubrév. & Pellegrin	25					
CHRYSOPHYLLUM CALOPHYLLUM Exell	1		P			E
CHRYSOPHYLLUM DELEVOYI De Wild.	17, 27	FP		ST		
C. africanum sensu Baker in Oliver, *Fl. Trop. Afr.* 3 : 500 (1877) et auctt. (? *C. africanum* A.DC.).						
It is impossible to decide to what species the name *Chrysophyllum africanum* A.DC. applies; see J. H. Hemsley in *Kew Bull.* 20 : 461–465 (1966).						
CHRYSOPHYLLUM HENRIQUESII Engl.	1		P			E
CHRYSOPHYLLUM PRUNIFOLIUM Baker	2, 17	FP				
CHRYSOPHYLLUM sp.	15			ST		
MANILKARA MULTINERVIS (Baker) Dubard	25, 27			ST		
MIMUSOPS cf. LACERA Baker	1				A	
OMPHALOCARPUM ELATUM Miers	7, 17	FP				
VINCENTELLA DENSIFLORA (Baker) Pierre	1			ST		E
VINCENTELLA REVOLUTA (Baker) Pierre	17	FP				
Bakerisideroxylon revolutum (Baker) Engl.	2					

102. MYRSINACEAE

AFRARDISIA CYMOSA Mez	1, 17			ST		
AFRARDISIA STAUDTII (Gilg) Mez		FP				
FP: Musola, *Mildbraed 7003* (as *A. haemanthus* (Gilg) Mez). The genus is not recorded from FP in 17.						
MAESA BORJAEANA Henriq.		FP		ST		
M. kamerunensis Mez	7, 17					
M. lanceolata sensu Exell	1, 2, 11, 13					
MAESA LANCEOLATA Forssk.	17	FP				
RAPANEA NEUROPHYLLA (Gilg) Mez	17	FP				
RAPANEA THOMENSIS Exell	1, 13			ST		E

103. LOGANIACEAE

ANTHOCLEISTA MICROPHYLLA Wernham	17	FP	P	ST		
A. macrocalyx Philipson	1, 11, 13					
A. micrantha Gilg & Mildbr. ex Hutch. & Dalziel	2					
A. stenantha Philipson	1, 14					
ANTHOCLEISTA SCANDENS Hook. f.	1, 2, 13, 17	FP		ST		
A. exelliana Monod	13, 15					
A. sp. nov.	1					
NUXIA CONGESTA R.Br. ex Fresen. var. CONGESTA	16, 17	FP			A	
Lachnopylis annobonensis Mildbr.	1					
Nuxia annobonensis Mildbr., *nom. nud.*	2					
NUXIA CONGESTA var. THOMENSIS (Philipson) J. Lewis	16			ST		
Lachnopylis thomensis Philipson	1, 15					
STRYCHNOS ACULEATA Solereder	2, 17	FP				
STRYCHNOS ISABELINA Gilg	2	FP				
FP: *Mildbraed 6353*. Not in 17.						

STRYCHNOS QUADRANGULARIS Mildbr., *nom. nud.*, non *S. quadrangularis* A. W. Hill	2	FP				
FP: Bokoko, *Mildbraed 6817*. Not in 17.						

104. OLEACEAE

JASMINUM FLUMINENSE Vell.	11			ST		
J. mauritianum Bojer ex DC.	1					
JASMINUM THOMENSE Exell	11			ST		E
*OLEA EUROPAEA L.	13			ST		
OLEA HOCHSTETTERI Baker	15, 26			ST		
OLEA WELWITSCHII (Knobl.) Gilg & Schellenb.	17, 25, 27			ST	A	
Steganthus welwitschii (Knobl.) Knobl.	1, 13					

105. APOCYANACEAE

ALAFIA MULTIFLORA (Stapf) Stapf	17	FP				
Holalafia multiflora Stapf	2					
*ALLAMANDA CATHARTICA L.	16				A	
BAISSEA MULTIFLORA A.DC.	2	FP				
Not recorded from FP in 17.						
*CATHARANTHUS ROSEUS (L.) G. Don	1, 16	FP		ST	A	
Lochnera rosea (L.) Reichenb. f.	2					
*ERVATAMIA DIVARICATA (L.) Burkill	15		P			
E. coronaria (Jacq.) Stapf	1					
FUNTUMIA AFRICANA (Benth.) Stapf	1, 7, 11, 17, 25	FP	P	ST		
Kickxia africana Benth.	2					
FUNTUMIA ELASTICA (Preuss) Stapf	13	FP		ST		
Kickxia elastica Preuss	2					
Not recorded from FP in 17.						
*LANDOLPHIA DAWEI Stapf	1			ST		
*NERIUM OLEANDER L.	1, 2	FP		ST		
*PLUMERIA ALBA L.	2	FP				
*PLUMERIA RUBRA L.	1	FP		ST	A	
RAUVOLFIA DICHOTOMA K. Schum.	1, 11, 13, 25			ST		
RAUVOLFIA MACROPHYLLA Stapf	1, 11, 13, 17, 25			ST		
RAUVOLFIA VOMITORIA Afzel.	1, 7, 9, 11, 13, 17	FP	P	ST	A	
Not recorded from FP in 17.						
STROPHANTHUS BULLENIANUS Mast.	2, 17	FP				
STROPHANTHUS PREUSSII Engl. & Pax	17	FP				
TABERNAEMONTANA BRACHYANTHA Stapf	2, 7, 17	FP				
Conopharyngia brachyantha (Stapf) Stapf	2					
TABERNAEMONTANA EGLANDULOSA Stapf	17	FP				
Gabunia eglandulosa (Stapf) Stapf	2					
TABERNAEMONTANA PACHYSIPHON Stapf				ST		
Conopharyngia pachysiphon (Stapf) Stapf	1, 13, 25					
TABERNAEMONTANA STENOSIPHON Stapf				ST		E
Conopharyngia stenosiphon (Stapf) Stapf	1, 13					
TABERNAEMONTANA sp. aff. STENOSIPHON			P			
Conopharyngia sp. nov. ?	1, 15					
TABERNAEMONTANA sp. ?				ST		
Conopharyngia sp.	1					
*THEVETIA NERIIFOLIA Juss.	2					
VOACANGA AFRICANA Stapf	1, 2, 17, 25	FP		ST		
VOACANGA LEMOSII Philipson	1			ST		E

106. ASCLEPIADACEAE

*ASCLEPIAS CURASSAVICA L.	1, 2, 8, 11, 13, 16, 17	FP		ST	A	
'*Asclepias sericea*'	2	FP				
I cannot trace this name. *A. serica* Raf., a synonym of *A. syriaca* L., may be intended.						
*CALOTROPIS PROCERA (Aiton) Aiton f.	2, 17	FP				
CYNANCHUM ADALINAE (K. Schum.) K. Schum. subsp. ADALINAE	2, 17	FP				
GONGRONEMA LATIFOLIUM Benth.				ST		
Marsdenia latifolia (Benth.) K. Schum.	1, 25, 26					
MARSDENIA EXELLII C. Norman	1, 14			ST		E
ONCOSTEMMA CUSPIDATUM K. Schum.	1	FP		ST		
FP: Bokoko, *Mildbraed 6948*. Not recorded from FP in 17.						
RHYNCHOSTIGMA RACEMOSUM Benth.	17	FP				
TYLOPHORA OBLONGA N. E. Brown	2	FP				
Not recorded from FP in 17. The type (*Mann 277*) is from FP.						
TYLOPHORA OCULATA N. E. Brown	2	FP				
Not recorded from FP in 17.						
TYLOPHORA SYLVATICA Decaisne	2, 17	FP				

107. RUBIACEAE

AIDIA GENIPIFLORA (DC.) Dandy	17	FP				
Randia genipiflora DC.	2					
AIDIA PALLENS (Hiern) G. Taylor	1			ST		E
AIDIA QUINTASII (K. Schum.) G. Taylor	1			ST		E
AIDIA WATTII G. Taylor	1			ST		E
ANTHOSPERMUM ASPERULOIDES Hook. f.	2, 17	FP				
ARGOSTEMMA AFRICANUM K. Schum.		FP				
FP: *Mildbraed 6308*. Not recorded from FP in 17.						
AULACOCALYX LE-TESTUI (Pellegrin) E. Petit				ST		
Dorothea le-testui Pellegrin	1					
BELONOPHORA COFFEOIDES Hook. f.	1			ST		E
BERTIERA ANNOBONENSIS G. Taylor	1, 16				A	E
BERTIERA LAXA Benth. var. LAXA	2, 17	FP				
BERTIERA PEDICELLATA (Hiern) Wernham	1			ST		E
BERTIERA RACEMOSA (G. Don) K. Schum. var. RACEMOSA	1, 13, 17	FP	P	ST		
B. montana Hiern	2					
BERTIERA RETROFRACTA K. Schum.	2, 17	FP				
B. obversa K. Krause	2					
BORRERIA OCYMOIDES (Burm. f.) DC.	1, 8, 17	FP	P	ST	A	
BORRERIA PRINCEAE var. PUBESCENS Hepper	17	FP				
BORRERIA SCABRA (Schumach.) K. Schum.	17	FP				
B. monticola Mildbr.	2					
BORRERIA VERTICILLATA (L.) G. F. W. Meyer	1, 8, 11, 13, 14		P	ST		
CANTHIUM DUNLAPII Hutch. & Dalziel	17	FP				
CANTHIUM HENRIQUESIANUM (K. Schum.) G. Taylor	1, 17			ST		
CANTHIUM SETOSUM Hiern	17	FP				
CANTHIUM SUBCORDATUM DC.				ST		
C. glabriflorum Hiern	1, 2, 11, 13, 25					
CANTHIUM sp. aff. ANOMOCARPUM DC.	1		P			

Canthium sp. aff. glabriflorum Hiern	13			ST		
Canthium sp.	1		P			
Canthium sp.	13			ST		
Cephaelis mannii (Hook. f.) Hiern	17	FP				
Uragoga mannii (Hook. f.) Hutch. & Dalziel	2					
Cephaelis peduncularis Salisb.	1, 13		P	ST	A	
Uragoga membranifolia Mildbr., *nom. nud.*	2					
Cephaelis peduncularis var. hypsophila (Schum. & Krause) Hepper	17	FP				
Cephaelis spathacea Hiern	1, 11, 13			ST		
Chassalia cristata (Hiern) Bremek.	17	FP				
Chassalia doniana (Benth.) G. Taylor	1, 11			ST		
Chassalia hiernii (Kuntze) G. Taylor var. hiernii	1, 11		P			
Chassalia hiernii var. glandulosa G. Taylor	1		P			
Chassalia kolly (Schumach.) Hepper	17	FP				
Psychotria benthamiana Hiern	2					
Chassalia subherbacea (Hiern) Hepper	17	FP				
Psychotria subherbacea Hiern	2					
*Cinchona						
Numerous cultivated species are grown in ST ; see 1.						
*Coffea arabica L.	1, 2, 11, 13, 17, 25	FP	P	ST		
*Coffea liberica Bull ex Hiern	1, 2, 13, 16, 25	FP	P	ST	A	
Coffea macrochlamys K. Schum.	17	FP				
*Coffea stenophylla G. Don	1, 2, 11, 13, 25			ST		
Many other introduced species and varieties of *Coffea* are listed in 2 and 13.						
Corynanthe sp. ?		FP				
FP : Bokoko, *Burchardt.*						
Craterispermum montanum Hiern	1, 13		P	ST	A	E
Cremaspora thomsonii Hiern		FP				
FP : *Burchardt.* Not recorded from FP in 17.						
Cuviera subuliflora Benth.	2, 17	FP				
Dictyandra arborescens Welw. ex Hook. f.	7, 17	FP				
Diodia scandens Swartz	17	FP				
Diodia serrulata (Beauv.) G. Taylor	1		P	ST		
Ecpoma cauliflorum (Hiern) N. Hallé in Adansonia 3 : 173 (1963).				ST		E
Sabicea cauliflora Hiern	1, 11					
ST : *Rose 208,* fide N. Hallé (additional record).						
Ecpoma gigantistipulum (K. Schum.) N. Hallé, *loc. cit.*	17	FP	P			
Sabicea gigantistipula K. Schum.	17					
P : *Rose 419,* fide N. Hallé.						
Galium simense Fresen.	17	FP				
Galium thunbergianum Ecklon & Zeyher	17	FP				
G. biafrae Hiern	2					
Gardenia nigrificans Wernham	2	FP				
Not in 17.						
Geophila afzelii Hiern	17		P			
G. cordiformis A. Chev. ex Hutch. & Dalziel	1					
Carinta cordiformis (A. Chev. ex Hutch. & Dalziel) G. Taylor	11, 14					
Geophila neurodictyon (K. Schum.) Hepper	16		P			
Psychotria neurodictyon K. Schum.	1, 2					

GEOPHILA OBVALLATA (Schumacher) Didrichsen	1, 2, 17	FP	P			
Carinta obvallata (Schumacher) G. Taylor	11					
GEOPHILA REPENS (L.) I. M. Johnston			P	ST		
G. uniflora Hiern	1					
Carinta uniflora (Hiern) G. Taylor	11					
HEINSIA CRINITA (Afz.) G. Taylor var. CRINITA	1, 17	FP	P			
H. pulchella K. Schum.	2					
? HEINSIA EPIDENDRON Mildbr.	2	FP				
Not in 17. Probably an error for *Hymenodictyon epidendron* Mildbr. (= *H. biafranum* Hiern).						
HYMENODICTYON BIAFRANUM Hiern	1, 17	FP	P			
IXORA BREVIFLORA Hiern	2, 17	FP				
*IXORA COCCINEA L.	11, 16			ST	A	
IXORA FOLIOSA Hiern		FP				
FP: Moka, *Tessmann 2896*. Not recorded from FP in 17.						
IXORA GUINEENSIS Benth.	17	FP				
I. riparia Hiern	2					
IXORA NEMATOPODA K. Schum	17	FP				
I. rosea K. Schum.	2					
IXORA THOMEANA (K. Schum.) G. Taylor	1			ST		E
LASIANTHUS AFRICANUS Hiern	1, 15		P	ST		E
LASIANTHUS aff. MANNII Wernham	17	FP				
MASSULARIA ACUMINATA (G. Don) Bullock ex Hoyle	17	FP				
Randia acuminata (G. Don) Benth.	2					
MITRAGYNA CILIATA Aubrév. & Pellegrin	17	FP				
MITRIOSTIGMA BARTERI Hook. f. ex Hiern	2, 17	FP				E
MORINDA LONGIFLORA G. Don	2, 17	FP				
MORINDA LUCIDA Benth.	1, 2, 17, 25, 26	FP	P	ST		
MORINDA MORINDOIDES (Bak.) Milne-Redh.	17	FP				
M. confusa Hutch.	2					
MUSSAENDA ARCUATA Lam. ex Poiret	2, 17	FP				
MUSSAENDA ELEGANS Schumacher	2	FP				
Not recorded from FP in 17.						
MUSSAENDA ERYTHROPHYLLA Schumacher	2	FP				
Not recorded from FP in 17.						
MUSSAENDA ISERTIANA DC.	2, 17	FP				
MUSSAENDA LANCIFOLIA K. Krause	2, 17	FP				E
MUSSAENDA POLITA Hiern		FP				
FP: Bokoko, *Mildbraed 6814*. Not recorded from FP in 17.						
MUSSAENDA TENUIFLORA Benth. var. TENUIFLORA	2, 17	FP				
MUSSAENDA TENUIFLORA var. PRINCIPENSIS G. Taylor	1		P			E
MUSSAENDA TENUIFLORA var. THOMENSIS G. Taylor	1			ST		E
MUSSAENDA aff. AFZELII G. Don	13		P			
NAUCLEA LATIFOLIA Smith		FP				
Sarcocephalus esculentus Afzel. ex Sabine	2					
Not recorded from FP in 17.						
OLDENLANDIA CORYMBOSA L.	1, 2, 11, 17	FP	P	ST	A	
OLDENLANDIA HERBACEA (L.) Roxb.	16				A	
OLDENLANDIA LANCIFOLIA (Schumacher) DC.	17	FP				
OTOMERIA CAMERONICA (Bremek.) Hepper	17	FP	P			
O. guineensis sensu G. Taylor	1					
Tapinopentas latifolia Verdc.	11					

Oxyanthus formosus Hook. f. ex Planchon	2, 17	FP				
O. breviflorus Benth.	2					
Oxyanthus gracilis Hiern	2, 17	FP				
Oxyanthus speciosus DC.	1, 9, 11, 13, 17			ST	A	
Oxyanthus sp. A	17	FP				
Parapentas setigera (Hiern) Verdc.	17	FP				
Virecta setigera Hiern	2					
Pauridiantha camposii (G. Taylor) Exell, comb. nov.				ST		E
Urophyllum camposii G. Taylor in Exell, *Cat. Vasc. Pl. S. Tomé* : 202 (1944).	1					
Holotype : *Campos 71* (COI).						
Pauridiantha canthiiflora Hook. f.	17	FP				
Urophyllum canthiiflorum (Hook. f.) Hutch. & Dalziel	2					
Pauridiantha floribunda (Schum. & Krause) Bremek.	17		P	ST	A	
Urophyllum floribundum Schum. & Krause	1, 11, 13					
U. annobonense Mildbr., *nom. nud.*	2					
Pauridiantha hirtella (Benth.) Bremek.		FP				
FP : Bokoko, *Mildbraed 6938.* Not recorded from FP in 17.						
Pauridiantha insularis (Hiern) Bremek.				ST		E
Urophyllum insulare Hiern	1, 13					
Pauridiantha paucinervis (Hiern) Bremek.	17	FP				
Urophyllum paucinerve Hiern	2					
Pauridiantha rubens (Benth.) Bremek.	17	FP		ST		
Urophyllum rubens Benth.	1, 2					
Pavetta bidentata Hiern	2, 17	FP				
Pavetta brachycalyx Hiern	2	FP				
FP : Bokoko, *Mildbraed 6812.* Not recorded from FP in 17.						
Pavetta corymbosa (DC.) F. N. Williams		FP				
P. nitida (Schumach.) Hutch. & Dalziel	2					
Recorded from FP in *Fl. W. Trop. Afr.*, ed. 1, but not in 17.						
Pavetta glaucescens Hiern	2, 17	FP				
Pavetta hispida Hiern	2, 17	FP				
Pavetta hookerana Hiern	17	FP				
P. exellii Bremek.	2					
Pavetta monticola Hiern	1, 11, 13			ST	A	E
P. dermatophylla Mildbr., *nom. nud.*	2					
Pavetta neurocarpa Benth.	2, 17	FP				
Pavetta oresitropha Bremek.	2, 17	FP				E
Pavetta owariensis Beauv.	17	FP				
Pavetta rigida Hiern	2, 17	FP				
Pentas schimperana subsp. occidentalis (Hook. f.) Verdc.	17	FP		ST		
P. occidentalis (Hook. f.) Benth. & Hook. ex Hiern	1, 11, 13					
Pentodon pentandrus (Schumacher) Vatke	17			ST		
Oldenlandia macrophylla DC.	1					
Polycoryne fernandensis (Hiern) Keay	17	FP				
Gardenia fernandensis Hiern	2					
Pouchetia confertiflora Mildbr.	1, 2				A	E
Pouchetia parviflora Benth.	1, 2, 17	FP	P	ST		

Preussiodora sulphurea (K. Schum.) Keay	17	FP			
Randia exserta K. Schum.	2				
? Psilanthus bicarinatus Mildbr., *nom. nud.*	2	FP			
Perhaps an error for *Psychotria bicarinata* Mildbr. (= *Psychotria recurva* Hiern).					
? Psilanthus epiphyticum Mildbr., *nom. nud.*	2	FP			
Probably an error for *Psychotria epiphytica* Mildbr.					
Psilanthus mannii Hook. f.	17	FP			
Heinsia jasminiflora sensu A. Chev.	2				
Psychotria bifaria Hiern	2, 17	FP			
Psychotria brachyantha Hiern	2, 17	FP			
Psychotria calva Hiern	2, 17	FP			
Psychotria cornuta Hiern	2, 17	FP			E
Psychotria crassicalyx K. Krause	2, 17	FP			E
Psychotria epiphytica Mildbr., *nom. nud.*, non *P. epiphytica* K. Krause nec *P. epiphytica* Elmer	2, 17	FP			
FP: *Mildbraed 6433, 7189*.					
Psychotria erythropus K. Schum.		FP			
FP: *Mildbraed 6327*. Not recorded from FP in 17.					
Psychotria euchlora K. Schum.	1, 13			ST	E
Psychotria fernandopoensis E. Petit	17	FP		ST ?	
? *Grumilea* sp. aff. *sphaerocarpa* Hiern	1				
Psychotria sphaerocarpa (Hiern) Hutch. & Dalziel, non *P. sphaerocarpa* Wall.	2				
Psychotria guerkeana K. Schum.	1, 13			ST	E
Psychotria henriquesiana K. Schum.	1			ST	E
Psychotria hierniana **Exell, nom. nov.**				ST	E
Grumilea macrocarpa Hiern in Oliver, *Fl. Trop. Afr.* 3 : 217 (1877), non *Psychotria macrocarpa* Hook. f. (1880).	1				
Holotype: *Mann* (K), from S. Tomé					
? Psychotria insidens Hiern	2, 17	FP			
E. Petit considers this to be a new genus of Rubiaceae. The specimen of this species recorded in 17 as *Mann 301* has been renumbered *Mann 301a*, as there is also a specimen of *P. pteropetala* numbered *Mann 310*.					
Psychotria latistipula Benth.	2, 17	FP			
Psychotria leptophylla Hiern	17	FP			
P. setacea Hiern	2				
Psychotria lucens Hiern	1		P		E
Psychotria malchairei De Wild.	17	FP			
Psychotria molleri K. Schum.	1			ST	E
Psychotria mollipes K. Krause	2	FP			
FP: above Basilé. *Mildbraed 6360*. Not in 17.					
Psychotria nubicola G. Taylor	1, 13			ST	E
Psychotria principensis G. Taylor	1		P		E
Psychotria pteropetala K. Schum.	2, 17	FP			
Psychotria recurva Hiern	2, 17	FP			
Psilanthus carinatus Mildbr., *nom. nud.*					
Psychotria sciadephora Hiern		FP			
FP: Bokoko, *Mildbraed 6853*. Not recorded from FP in 17.					
Psychotria subobliqua Hiern	1, 2, 11, 13, 17	FP	P	ST	
Psychotria thomensis G. Taylor	1			ST	E

PSYCHOTRIA VENOSA (Hiern) E. Petit	17	FP		ST		
Grumilea venosa Hiern	1, 2, 11, 25					
PSYCHOTRIA sp.		FP				
FP : Musola, *Mildbraed 7042*, as *Grumilea* sp.						
ROTHMANNIA LONGIFLORA Salisb.	17	FP				
Randia maculata DC.	2					
ROTHMANNIA MACROCARPA (Hiern) Keay		FP				
Randia myrmecophylla De Wild.	2					
Not in 17.						
ROTHMANNIA OCTOMERA (Hook.) Fagerl.	17	FP				
Randia octomera (Hook.) Hook. f.	2					
ROTHMANNIA URCELLIFORMIS (Schweinf. ex Hiern) Bullock ex Robyns	15			ST		
R. arcuata Bremek.	11					
? ROTHMANNIA WHITFIELDII (Lindl.) Dandy		FP ?				
FP : Bokoko, *Mildbraed 6947*, identification doubtful. Not recorded from FP in 17.						
RUTIDEA DECORTICATA Hiern		FP				
FP : Bokoko, *Mildbraed 6822* ; Musola, *Mildbraed 7012*. Not recorded from FP in 17, but perhaps these specimens are *R. syringoides*.						
RUTIDEA SMITHII Hiern	1, 17				A	
The Annobon plant may be *R. smithii* var. *welwitschii*.						
RUTIDEA SMITHII var. WELWITSCHII Scott Elliot	15			ST		
RUTIDEA SYRINGOIDES (Webb) Bremek.	17	FP				
RYTIGYNIA CONCOLOR (Hiern) Robyns	1		P		A ?	
SABICEA AFRICANA (Beauv.) Hepper		FP				
Stipularia africana Beauv.	7					
Not recorded from FP in 17.						
SABICEA CALYCINA Benth.	2, 17	FP				
SABICEA CAPITELLATA Benth.	2, 17	FP				
SABICEA EXELLII G. Taylor	1			ST		E
SABICEA HIERNIANA Wernham		FP				
FP : *Mildbraed* 6288. Not in 17.						
SABICEA INGRATA K. Schum.	1			ST		E
SABICEA INSULARIS (Wernham) G. Taylor	1			ST	A	E
S. annobonensis Mildbr., *nom. nud.*	2					
SABICEA SCHAEFERI Wernham	17	FP				E ?
Also in Cameroon fide N. Hallé.						
SABICEA URBANIANA Wernham	2, 17	FP				E
SABICEA URCEOLATA Hepper	17	FP				
SABICEA aff. CAULIFLORA Hiern	13		P			
Presumably a species of *Ecpoma*.						
SACOSPERMA PANICULATUM (Benth.) G. Taylor	1, 11, 17	FP	P	ST		
Oldenlandia peltospermum Hiern	2					
SCHUMANNIOPHYTON MAGNIFICUM (K. Schum.) Harms		FP				
FP : Bokoko, *Mildbraed 6350, 6936*. Not recorded from FP in 17.						
TARENNA BIPINDENSIS (K. Schum.) Bremek.	17	FP				
Ixora bipindensis (K. Schum.) K. Schum. ex Hutch. & Dalziel	2					
TARENNA CONFERTA (Benth.) Hiern	2, 17	FP				
TARENNA GRANDIFLORA (Benth.) Hiern	2, 17	FP				
TARENNA NITIDULOIDES G. Taylor	1, 15			ST		E

Tarenna sp. 1	1		P			
Tarenna sp. 2	1			ST		
Tarenna sp. 3	1			ST		
Tricalysia biafrana Hiern		FP				
FP: Bokoko, *Mildbraed 6962*. Not recorded from FP in 17.						
Tricalysia oligoneura K. Schum.		FP ?				
FP: Bokoko, *Mildbraed 6909*; a doubtful record. Not recorded from FP in 17.						
Tricalysia pallens Hiern	2, 17	FP				
Uncaria africana G. Don var. africana	16				A	
? Urogoga nutans K. Krause	2	FP				
Presumably either *Cephaelis mannii* or *C. peduncularis*.						
Virectaria major (K. Schum.) Verdc. var. major	17	FP				
Virectaria procumbens (Smith) Bremek.	17	FP				

108. CAPRIFOLIACEAE

*Sambucus canadensis L.		FP				
FP: Santa Isabel, *Mildbraed 6483*.						

109. COMPOSITAE

*Acanthospermum hispidum DC.	1, 25		P	ST		
Adenostemma mauritianum DC.	2, 17	FP				
Adenostemma perrottetii DC.	1, 6, 11, 13, 16, 17, 25	FP		ST	A	
Ageratum conyzoides L.	1, 2, 6, 9, 11, 13, 17, 25, 26	FP	P	ST	A	
Ambrosia maritima L.	1		P	ST		
Aspilia rudis Oliver & Hiern subsp. rudis	1		P			
Bidens pilosa L.	1, 6, 8, 9, 11, 13, 17, 25, 26	FP	P	ST	A	
Blumea aurita (L. f.) DC.	2	FP				
Not recorded from FP in 17.						
*Chrysanthemum indicum L.	1			ST		
*Cichorium intybus L.	1			ST		
Conyza bonariensis (L.) Cronq.			P	ST		
Erigeron sumatrensis Retz.	1					
Conyza clarenceana (Hook. f.) Oliver & Hiern	3, 6, 17	FP				E
Conyza floribunda Kunth		FP				
Erigeron floribundus (Kunth) Schultz Bip.	6, 17					
Conyza persicifolia (Benth.) Oliver & Hiern	2, 6, 17	FP		ST		
Eschenbachia persicifolia (Benth.) Exell	1, 8, 11, 13, 25					
Conyza steudelii Schultz Bip. ex A. Rich.		FP				
FP: *Escarré k-57*. Not recorded from FP in 17.						
Conyza theodori R. E. Fries		FP				
FP: *Escarré e-2*. Not recorded from FP in 17.						
Crassocephalum biafrae (Oliver & Hiern) S. Moore	6, 17	FP		ST		
Senecio biafrae Oliver & Hiern	1					
Crassocephalum bougheyanum C. D. Adams	17	FP				
Crassocephalum crepidioides (Benth.) S. Moore	6, 11, 15, 17	FP				
Gynura crepidioides Benth.	1					
Crassocephalum gracile (Hook. f.) Milne-Redh. ex Guinea	6, 17	FP				

Crassocephalum mannii (Hook. f.) Milne-Redh.	6, 17	FP			
Senecio mannii Hook. f.	2				
Crassocephalum montuosum (S. Moore) Milne-Redh.	15, 17	FP		ST	
Crassocephalum picridifolium (DC.) S. Moore	6, 17	FP			
Crassocephalum rubens (Juss. ex Jacq.) S. Moore		FP			
FP: Moka, *Tessmann 2872*. Not recorded from FP in 17.					
Crassocephalum vitellinum (Benth.) S. Moore	6, 17	FP			
Gynura vitellina Benth.	2				
Dichrocephala chrysanthemifolia (Blume) DC.	2, 6, 17	FP			
Dichrocephala integrifolia (L. f.) Kuntze	16, 17	FP		ST	
D. bicolor (Roth) Schlechtendal	1, 11, 13				
Eclipta prostrata (L.) L.	1		P	ST	A
Elephantopus mollis Kunth	1, 6, 11, 13, 17, 25	FP	P	ST	
*Eleutheranthera ruderalis (Swartz) Schultz Bip.	16, 17	FP			A
Emilia coccinea (Sims) G. Don	17	FP		ST	
E. flammea Cass.	13				
E. sagittata DC.	2, 13				
Emilia praetermissa Milne-Redh.		FP			
FP: fide Escarré. Not recorded from FP in 17.					
Emilia sonchifolia (L.) DC.	1, 2, 6, 14, 17	FP	P	ST	
Enydra fluctuans Lour.	2, 17	FP			
*Epaltes brasiliensis DC.	1		P	ST	
Ethulia conyzoides L.f.	1, 17	FP		ST	
FP: *Melville & Wrigley 627* (K). Not recorded from FP in 17.					
*Galinsoga ciliata (Raf.) Blake		FP			
FP: fide Escarré.					
*Galinsoga parviflora Cav.	1			ST	
Gnaphalium luteo-album L.	1, 6, 13, 14, 17	FP	P	ST	
Helichrysum cymosum (L.) Less.	17	FP			
H. fruticosum Vatke	2, 6				
Helichrysum foetidum (L.) Moench	1, 2, 6, 17	FP		ST	
Helichrysum globosum Schultz Bip. ex A. Rich.	2, 6, 17	FP			
Helichrysum mannii Hook. f.	2, 6, 17	FP			
Helichrysum odoratissimum (L.) Less.	17	FP			
Achyrocline hochstetteri Schultz Bip.	2, 6				
Lactuca capensis Thunb.	6, 17	FP			
Lactuca glandulifera Hook. f. var. glandulifera	6, 17	FP			
Laggera alata var. montana C. D. Adams	6, 17	FP			
Melanthera scandens (Schumacher) Roberty	17	FP			
M. brownei (DC.) Schultz Bip.	2, 6				
Microglossa densiflora Hook. f.	6, 17	FP			
Microglossa pyrifolia (Lam.) Kuntze	1, 15, 17	FP	P	ST	
Mikania cordata (Burm. f.) B. L. Robinson var. cordata	11, 16, 17	FP	P		A
M. scandens sensu auctt.	1, 2, 6, 7				
Mikania sp.	11			ST	A
M. scandens sensu Exell	1				
Mikaniopsis paniculata Milne-Redh.	11, 15, 17	FP		ST	
FP: *Melville & Wrigley 625* (K). Not recorded from FP in 17.					
Senecio clarenceanus Hook. f	2, 6, 17	FP			

Sonchus oleraceus L.	1, 6, 13, 17	FP		ST		
Sonchus schweinfurthii Oliver & Hiern	FP					
FP: fide Escarré. Not recorded from FP in 17.						
Spilanthes filicaulis (Schumacher) C. D. Adams	17	FP	P	ST		
S. acmella sensu Exell	1, 6					
S. caulirhiza sensu Exell	11					
Struchium sparganophora (L.) Kuntze	1, 6, 9, 11, 13, 17, 25, 26	FP	P	ST		
Sparganophorus vaillantii Crantz	2, 7					
Synedrella nodiflora (L.) Gaertn.	1, 6, 11, 13, 16, 17, 25	FP	P	ST	A	
*Tagetes erecta L.	6	FP				
Triplotaxis stellulifera (Benth.) Hutch.	1, 2, 6, 11, 13, 17	FP	P	ST		
Vernonia amygdalina Delile	1, 2, 6, 13, 17, 25, 26	FP		ST	A	
? *V. senegalensis* sensu Guinea	2					
Vernonia biafrae Oliver & Hiern	2, 6, 17	FP				
Vernonia blumeoides Hook. f.	6	FP				
Not recorded from FP in 17.						
Vernonia conferta Benth.	2, 6, 7, 17	FP				
Vernonia insignis (Hook. f.) Oliver & Hiern		FP				
FP: *Escarré e-29*. Not recorded from FP in 17.						
Vernonia mokaensis Mildbr. & Mattf.	2, 6, 17	FP				E
Vernonia myriantha Hook. f.	2, 17	FP				
*Zinnia peruviana (L.) L.	1, 6	FP		ST		

110. GENTIANACEAE

Canscora decussata (Roxb.) J. A. & J. H. Schultes	16				A	
Exacum quinquenervium Griseb.	16				A	
Neurotheca loeselioides (Spruce ex Progel) Baillon	2, 17	FP				
Sebaea brachyphylla Griseb.	17	FP				
S. multinodis N. E. Brown	2, 7					
Swertia abyssinica Hochst.	17	FP				
S. clarenceana Hook. f.	2, 7					
'*Swertia camerunensis*'	7	FP				
I cannot trace this name.						

111. PRIMULACEAE

Ardisiandra sibthorpioides Hook. f.	2, 7, 17	FP				

112. PLUMBAGINACEAE

*Plumbago auriculata Lam.				ST		
P. capensis Thunb.	1, 11					
Plumbago zeylanica L.	1, 17	FP		ST		

113. PLANTAGINACEAE

*Plantago major L.	1, 15		P	? ST		
Plantago palmata Hook. f.	2, 17	FP				

114. CAMPANULACEAE

Cephalostigma perrottetii A.DC.	16				A	
Wahlenbergia arguta Hook. f.	2, 17	FP				
Wahlenbergia mannii Vatke	2, 17	FP				

115. LOBELIACEAE

Dielsantha galeopsoides (Engl. & Diels) E. Wimmer	17	FP				
Lobelia acutidens Hook. f.	2, 17	FP				E
Lobelia barnsii Exell	1, 13, 15			ST		E
Lobelia columnaris Hook. f.	2, 7, 17	FP				
Lobelia kamerunensis Engl. ex Hutch. & Dalziel	17	FP				
Lobelia molleri Henriq.	1, 17	FP		ST		
Monopsis stellarioides var. schimperana (Urban) E. Wimmer	17	FP				

116. GOODENIACEAE

Scaevola plumieri (L.) Vahl	1			ST		

117. BORAGINACEAE

Cordia aurantiaca Baker	2, 17	FP				
*Cordia gerascanthus L.	13, 27			ST		
Cordia platythyrsa Baker	27	FP		ST		
C. odorata Gürke						
Cordia sp.	25					
FP: Bokoko, *Mildbraed 6939*. Not recorded from FP in 17.						
Cordia senegalensis Juss.		FP				
FP: San Carlos, *Mildbraed 6932*. Not recorded from FP in 17.						
Cynoglossum lanceolatum Forssk.	2	FP				
Not recorded from FP in 17.						
Ehretia scrobiculata Hiern	1		P			E
Ehretia zenkeri Gürke ex Baker & Wright	11, 27			ST		
E. scrobiculata sensu Espírito Santo	25					
Treated in 17 as a variety of *E. cymosa* Thonn.						
Heliotropium indicum L.	1, 11, 13, 25	FP	P	ST		
FP: fide Escarré. Not recorded from FP in 17.						
Myosotis abyssinica Boiss. & Reuter	2, 17	FP				

118. SOLANACEAE

*Browallia americana L.	11			ST		
B. demissa L.	8					
*Brunfelsia uniflora (Pohl) D. Don				ST		
Franciscea uniflora Pohl	13					
Capsicum annuum L.	1, 2, 16, 25	FP		ST	A	
Not recorded from FP in 17.						
Capsicum frutescens L.	1, 2, 13, 25	FP	P	ST		
Not recorded from FP in 17.						
*Cestrum laevigatum var. puberulum Sendtner	1, 11, 13, 25	FP	P	ST		
Now quite spontaneous in ST.						
*Cyphomandra betacea (Cav.) Sendtner	1			ST		
*Datura candida (Pers.) Saff.	11, 16	FP		ST	A	
FP: Moka, *Exell 777*. Common as a bush in the grassland and as a small tree in the woodland. Used by the Bubis to make fences for their villages.						
*Datura metel L.	1, 2, 25, 26	FP		ST		
*Datura stramonium L.	2	FP				
Discopodium penninervium Hochst.	2, 17	FP				

*Lycopersicum esculentum var. cerasiforme (Dunal) Alef.	1, 2, 16	FP	P	ST	A
L. cerasiforme L.	2				
Solanum lycopersicum L.	2				
*Nicandra physaloides (L.) Gaertn.	1, 11, 25, 26	FP	P	ST	
Physalis peruviana sensu Guinea	2				
*Nicotiana tabacum L.	1, 2, 16	FP		ST	A
*Physalis angulata L.	1, 2, 13, 16, 17	FP	P	ST	A
Physalis micrantha Link	16				A
Solanum aculeatissimum Jacq.	1		P		
Solanum dasyphyllum Schumacher	16	FP	P		A
S. duplosinuatum Klotzsch	1, 2				
Not recorded from FP in 17.					
Solanum indicum L.	1, 2	FP		ST	
Solanum indicum var. grandemunitum Bitter	17	FP			
Solanum indicum var. modicearmatum Bitter	17	FP			
Solanum macrocarpon L.	1, 2	FP		ST	
Not recorded from FP in 17.					
*Solanum melongena L.	1, 2	FP		ST	
Solanum nigrum L. sens. lat.	1, 2, 8, 9, 11, 17	FP	P	ST	A
S. nodiflorum Jacq.	16				
The specimens from our area are probably all referable to *S. americanum* Mill.					
Solanum terminale subsp. inconstans (C. H. Wright) Heine	17	FP			
S. inconstans C. H. Wright	2, 7				
Solanum terminale Forssk. subsp. terminale				ST	
S. bifurcatum Hochst. ex A. Rich.	1				
Solanum terminale subsp. welwitschii (C. H. Wright) Heine	17	FP			
S. welwitschii var. *strictum* C. H. Wright	2				
Solanum torvum Swartz	2, 17	FP			
*Solanum tuberosum L.	1			ST	

119. CONVOLVULACEAE

*Ipomoea alba L.	16	FP	P	ST	A
Calonyction aculeatum (L.) H. D. House	1				
C. bona-nox (L.) Bojer	2				
Not recorded from FP in 17.					
Ipomoea batatas (L.) Lam.	1, 2, 11, 13	FP	P	ST	
Not recorded from FP in 17.					
Ipomoea cairica (L.) Sweet	1, 2, 17	FP	P	ST	
Ipomoea eriocarpa R. Br.	1, 9, 11	FP		ST	A
I. hispida (Vahl) Roemer & Schultes, *non* Zuccagni	2				
Not recorded from FP in 17.					
*Ipomoea hederifolia L.		FP	P	ST	
Quamoclit coccinea sensu Exell	1, 11				
Ipomoea involucrata Beauv.	2, 16, 17	FP			A
Ipomoea mauritiana Jacq.	15, 16, 17	FP		ST	A
I. digitata sensu Exell	1, 2, 7				
? *Convolvulus paniculatus* sensu Guinea	2				
Ipomoea nil (L.) Roth	16	FP			A
I. hederacea sensu Baker & Rendle					
FP : *Buchholz*. Not recorded from FP in 17.					

IPOMOEA PES-CAPRAE subsp. BRASILIENSIS (L.) Van Ooststr.	1, 2, 7, 9, 11, 13, 17	FP	P	ST	A	
*IPOMOEA PURPUREA Roth	2	FP				
IPOMOEA QUAMOCLIT L.	2, 17	FP	P	ST		
Quamoclit vulgaris Choisy	1, 11					
IPOMOEA RUBENS Choisy		FP	?	ST		
I. lilacina Blume, *non* Schrank	2					
I. riparia G. Don	1					
Not recorded from FP in 17, but the FP record is doubtful.						
*IPOMOEA SETIFERA Poiret	1		P			
IPOMOEA STOLONIFERA (Cyr.) J. F. Gmel.	1, 7	FP		ST		
Not recorded from FP in 17.						
*IPOMOEA TILIACEA (Willd.) Choisy	1, 17		P			
*IPOMOEA TUBEROSA L.	2	FP				
MERREMIA AEGYPTIA (L.) Urban	1			ST		
*MERREMIA DISSECTA (Jacq.) Hallier f.	2, 17	FP				
MERREMIA PTERYGOCAULOS (Choisy) Hallier f.	2	FP				
FP: *Buchholz*. Not recorded from FP in 17.						
MERREMIA TRIDENTATA subsp. ANGUSTIFOLIA (Jacq.) Van Ooststr.	11			ST		
M. angustifolia (Jacq.) Hallier f.	1					
MERREMIA UMBELLATA (L.) Hallier f. subsp. UMBELLATA	1, 2, 11, 17	FP	P			

120. SCROPHULARIACEAE

ALECTRA SESSILIFLORA var. MONTICOLA (Engl.) Melch.	16, 17	FP	P		A	
A. communis Hemsley	1					
CELSIA DENSIFOLIA Hook.	17	FP				
'*Celsia densiflora* Hook. f.'	2					
*LENDNERIA VERTICILLATA (Mill.) Britton		FP				
Stemodia verticillata (Mill.) Boldingh	17					
LIMOSELLA AUSTRALIS R.Br.		FP				
L. subulata Ives	17					
L. tenuifolia Nutt.	2					
LINDERNIA DIFFUSA (L.) Wettst. var. DIFFUSA	1, 16, 17	FP	P	ST	A	
LINDERNIA DIFFUSA var. PEDUNCULATA (Benth.) Skan	1, 11, 16, 17			ST	A	
L. stictantha (Hiern) Skan	8					
LINDERNIA VOGELII Skan	17	FP				
*RUSSELIA EQUISETIFORMIS Schlectendal & Cham.	11, 13		P	ST		
R. juncea Zucc.	8					
SCOPARIA DULCIS L.	1, 25		P	ST	A	
SIBTHORPIA EUROPAEA L.	17	FP				
S. australis Hutch.	2					
THUNBERGIANTHUS QUINTASII Engl.	1			ST		E
TORENIA DINKLAGEI Engl.	17	FP				
T. parviflora sensu Guinea	2					
TORENIA THOUARSII (Cham. & Schlecht.) Kuntze	1		P	ST		
VERONICA MANNII Hook. f.	2, 17	FP				

121. LENTIBULARIACEAE

UTRICULARIA MANNII Oliver	14, 15, 17	FP	P	ST		
U. bryophila Ridley	1, 13					
UTRICULARIA STRIATULA Smith	1, 15, 17	FP	P			

122. GESNERIACEAE

Acanthonema strigosum Hook. f.	2, 17	FP			
Didymocarpus kamerunensis Engl.	17	FP			
Epithema tenue C. B. Clarke	1, 2, 17	FP		ST	
Streptocarpus elongatus Engl.		FP			
FP: fide Escarré. Not recorded from FP in 17.					
Streptocarpus insularis Hutch. & Dalziel	7, 17	FP			E
S. denticulatus Engl., *non* Turrill	2				
Streptocarpus nobilis C. B. Clarke	14, 17			ST	
Streptocarpus thomensis Exell	1, 13			ST	E

123. BIGNONIACEAE

*Jacaranda mimosifolia D. Don	27			ST	
Kigelia africana (Lam.) Benth.	17	FP			
K. impressa Sprague	2				
K. pinnata (Jacq.) DC.	2				
Markhamia lutea (Benth.) K. Schum.	2, 7, 17	FP			
Newbouldia laevis (Beauv.) Seem. ex Bur.	1, 2, 7, 13, 17, 25	FP		ST	
*Parmentiera alata (Kunth) Miers		FP			
Crescentia alata Kunth	2				
Spathodea campanulata Beauv.	2, 17, 27	FP		ST	
*Spathodea nilotica Seem.	15			ST	

124. PEDALIACEAE

Sesamum radiatum Schumacher	2, 17	FP			

125. ACANTHACEAE

Acanthopale decempedalis C. B. Clarke	2, 17	FP			
Acanthopale sp.		FP			
FP: *Boughey 136.*					
Acanthus montanus (Nees) T. Anders.	1, 2, 7, 11, 13, 17	FP			
Adhatoda maculata C. B. Clarke	2, 17	FP			
Adhatoda orbicularis (Lindau) C. B. Clarke	2, 17	FP			
Adhatoda robusta C. B. Clarke	2, 17	FP			
Adhatoda tristis Nees	2, 17	FP			
Afrofittonia silvestris Lindau	17	FP			
Asystasia gangetica (L.) T. Anders.	1, 13, 17	FP	P	ST	
Asystasia macrophylla (T. Anders.) Lindau	2, 17	FP			
Asystasia vogeliana Benth.	2, 17	FP			
Brachystephanus longiflorus Lindau	2, 17	FP			
Brachystephanus occidentalis Lindau	1			ST	E
Brillantaisia lamium (Nees) Benth.	1, 2, 9, 11, 13	FP ?	P	ST	
Not recorded from FP in 17. The record from FP in 2 may be based on *Fl. West Trop. Afr.*, ed. 1, where the distribution is given as 'Biafran Is.'					
Brillantaisia madagascariensis T. Anders. ex Lindau	17	FP			
Brillantaisia nitens Lindau	2	FP			
Not recorded from FP in 17.					
Brillantaisia cf. owariensis Beauv.		FP			
FP: *Escarré j-6.*					

BRILLANTAISIA PATULA T. Anders.	1			ST		
BRILLANTAISIA VOGELIANA (Nees) Benth.	1, 2, 11, 13, 17	FP		ST		
CROSSANDRELLA DUSENII (Lindau) S. Moore	2	FP				
Not recorded from FP in 17.						
DICLIPTERA LAXATA C. B. Clarke	17	FP				
DICLIPTERA VERTICILLATA (Forssk.) Christensen	16		P	ST	A	
D. umbellata (Vahl) Juss.	1, 15					
DISCHISTOCALYX THUNBERGIIFLORUS (T. Anders.) Benth.	2, 17	FP				
ELYTRARIA MARGINATA Vahl	11, 17, 25, 26	FP	P	ST		
E. acaulis sensu Exell	1, 2					
? FILETIA AFRICANA Lindau		FP				
FP: Musola, *Mildbraed 7001*. Not recorded from FP in 17. This may be *Asystasia decipiens* Heine, but that species is also not recorded from FP.						
*GRAPTOPHYLLUM PICTUM (L.) Nees ex Griff.	1, 2, 14	FP	P	ST		
HETERADELPHIA PAULOWILHELMIA Lindau	1			ST		E
HYPOESTES ARISTATA (Vahl) Solander ex Roemer & Schultes	17	FP				
H. insularis T. Anders.	2					
HYPOESTES TRIFLORA (Forssk.) Roemer & Schultes '*trifolia*' in 2	2, 17	FP				
HYPOESTES sp.	1			ST		
ISOGLOSSA GLANDULIFERA Lindau	2, 17	FP				
ISOGLOSSA sp. B	17	FP				
JUSTICIA EXTENSA T. Anders.		FP				
Duvernoia extensa (T. Anders.) Lindau	2					
Not recorded from FP in 17. This may be *J. laxa*.						
JUSTICIA INSULARIS T. Anders.	2, 17	FP				
JUSTICIA LAXA T. Anders.	2, 17	FP				
JUSTICIA MANNII T. Anders.		FP				E ?
The type is from FP but is apparently untraceable. Anderson himself named two sheets of *Mann 1435* (K) as this but, according to E. Milne-Redhead (in litt.), they are definitely not the species described but are *Adhadota orbicularis*.						
JUSTICIA PREUSSII (Lindau) C. B. Clarke		FP				
FP: Musola, *Mildbraed 7047*. Not recorded from FP in 17.						
JUSTICIA TENELLA (Nees) T. Anders.	1, 17	FP	P	ST		
JUSTICIA THOMEENSIS Lindau	1			ST		E
MENDONCIA GILGIANA (Lindau) Benoist		FP				
FP: Musola, *Mildbraed 6990*; between Musola and Concepción, *Wrigley & Melville 549* (K). Not recorded from FP in 17.						
MIMULOPSIS SOLMSII Schweinf.	17	FP				
M. violacea Lindau	2					
NELSONIA CANESCENS (Lam.) Sprengel	1, 17	FP	P			
OREACANTHUS MANNII Benth.	2, 17	FP				
PHAULOPSIS FALCISEPALA C. B. Clarke	17	FP				
PHAULOPSIS MICRANTHA (Benth.) C. B. Clarke	1, 16, 25			ST	A	
PSEUDERANTHEMUM LUDOVICIANUM (Büttner) Lindau	17	FP				
Eranthemum ludovicianum Büttner	2					
PSEUDERANTHEMUM TUNICATUM (Afzel.) Milne-Redh.	17	FP				
P. nigritianum (T. Anders.) Radlk.	2					

RHINACANTHUS VIRENS (Nees) Milne-Redh. var. VIRENS	11, 17	P ST ?
R. dewevrei De Wild. & Dur.	1	
This is recorded from ST in 17 but I have no evidence of its occurrence in that island.		
*RUELLIA GRAECIZANS Backer	15	ST
RUELLIA PRIMULOIDES (T. Anders. ex Benth.) Heine		FP
Endosiphon primuloides T. Anders. ex Benth.	2, 17	
RUNGIA PAXIANA (Lindau) C. B. Clarke	2, 17	FP
SCHAUERIA POPULIFOLIA C. B. Clarke	2, 17	FP
SCLEROCHITON PREUSSII (Lindau) C. B. Clarke	2	FP
Not recorded from FP in 17.		
STENANDRIOPSIS GUINEENSIS (Nees) Benoist		FP
Crossandra guineensis Nees	2, 17	
STENANDRIOPSIS THOMENSIS (Milne-Redh.) Heine		ST
Crossandra thomensis Milne-Redh.	1, 15, 17	
*THUNBERGIA ALATA Bojer ex Sims	1, 8	ST
THUNBERGIA VOGELIANA Benth.	2, 17	FP
WHITFIELDIA ELONGATA (Beauv.) De Wild. & Dur.	17	FP
W. longifolia T. Anders. (incl. var. *perglabra* (C. B. Clarke) Hutch. & Dalziel)	2	

126. VERBENACEAE

CLERODENDRUM BIPINDENSE Gürke	2, 17	FP
CLERODENDRUM CAPITATUM (Willd.) Schumacher		FP
FP: Musola, *Mildbraed 7043*. Not recorded from FP in 17.		
CLERODENDRUM DUSENII Gürke	17	FP ST
C. thomasii Moldenke	1	
Premna macrosiphon Baker	2	
Not recorded from FP in 17.		
CLERODENDRUM GLOBULIFLORUM B. Thomas	17	FP
CLERODENDRUM GRANDIFOLIUM Gürke		FP
FP: *Mildbraed 6345*. Not in 17.		
*CLERODENDRUM JAPONICUM (Thunb.) Sweet		ST
C. fragrans var. *pleniflorum* Schauer	11	
CLERODENDRUM MELANOCRATER Gürke	17	FP
CLERODENDRUM SILVANUM Henriq.	1	FP ST A
C. buchholzii Gürke	17	
*CLERODENDRUM SPECIOSISSIMUM Van Geert ex Morren	1, 11	FP ST
C. fallax Lindl.	2	
Not listed in 2 but see photograph following p. 352.		
CLERODENDRUM SPLENDENS G. Don	2, 7	FP
Not recorded from FP in 17.		
CLERODENDRUM THOMSONIAE Balf. f.	11	ST
C. scandens sensu Exell	1	
CLERODENDRUM UMBELLATUM Poiret	17	FP
C. scandens Beauv.	2	
CLERODENDRUM VOLUBILE Beauv.	1, 17	FP P
*DURANTA REPENS L.	1, 11	ST
*LANTANA CAMARA L.	1, 13, 25	ST
PREMNA ANGOLENSIS Gürke	11, 25	ST
PREMNA MILNEI Baker	2, 17	FP
STACHYTARPHETA INDICA (L.) Vahl	17	FP

VITEX LEHMBACHII Gürke		FP				
FP: Bokoko, *Burchardt*. Not recorded from FP in 17.						
VITEX MILNEI Pieper	17	FP				E ?
V. cienkowskii sensu Guinea	2					

127. AVICENNIACEAE

AVICENNIA GERMINANS (L.) L.	14, 15, 16	FP		ST	A	
A. africana Beauv.	1, 13, 17					
A. nitida Jacq.	2, 7					

128. LABIATAE

ACHYROSPERMUM OBLONGIFOLIUM Baker	1, 2, 17	FP		ST		
COLEUS aff. PREUSSII Gürke		FP				
FP: Moka, *Mildbraed 7103*. *Coleus preussii* is not mentioned in 17 although the syntypes are from Buea. It is presumably a species of *Plectranthus*.						
*'*Coleus tuberosus*'	2	FP				
Perhaps *C. parviflorus* Benth.						
ELSHOLTZIA sp.	1		P ?			
HOMALOCHEILOS RAMOSISSIMUS (Hook. f.) J. K. Morton	17	FP				
Plectranthus ramosissimus Hook. f.	2					
HOSLUNDIA OPPOSITA Vahl	9, 11, 17	FP			A	
H. verticillata Vahl	2					
HYPTIS LANCEOLATA Poiret	17	FP				
LEONOTIS NEPETIFOLIA (L.) Aiton f.	1, 2, 11, 13, 17, 25, 26	FP	P	ST	A	
Not recorded from FP in 17.						
LEUCAS DEFLEXA Hook. f.	17	FP				
LEUCAS MARTINICENSIS (Jacq.) Aiton f.	17	FP				
*MENTHA ROTUNDIFOLIA (L.) Huds.	13			ST		
*OCIMUM BASILICUM L.	1, 2, 13, 16, 17, 25	FP		ST	A	
OCIMUM CANUM Sims	2, 17	FP				
*OCIMUM GRATISSIMUM L.	17	FP	P	ST	A	
O. viride Willd.	1, 2, 11, 13, 25, 26					
PLATOSTOMA AFRICANUM Beauv.	1, 2, 17	FP		ST		
PLECTRANTHUS ASSURGENS (Baker) J. K. Morton	17	FP				
PLECTRANTHUS DECURRENS (Gürke) J. K. Morton	17	FP				
Coleus decurrens Gürke	2					
PLECTRANTHUS ESCULENTUS N. E. Brown		FP				
Coleus dazo A. Chev.	2					
Not recorded from FP in 17.						
PLECTRANTHUS GLANDULOSUS Hook. f.	2, 17	FP				
PLECTRANTHUS INSIGNIS Hook. f.		FP				
FP: *Melville & Wrigley 589* (K); *Mildbraed 7143*. Not recorded from FP in 17.						
PLECTRANTHUS PUNCTATUS L'Hérit. subsp. PUNCTATUS	17	FP				
PYCNOSTACHYS MEYERI Gürke	17	FP				
P. volkensii Gürke	2					
*SALVIA COCCINEA Buc'hoz ex Etlinger	1			ST		
SATUREJA PSEUDOSIMENSIS Brenan	17	FP				
Calamintha simensis sensu Guinea	2					

Solenostemon mannii (Hook. f.) Baker	17	FP				
Solenostemon monostachyus (Beauv.) Briq. subsp. monostachyus	1, 11, 13, 17, 25	FP	P	ST	A	
Solenostemon repens (Gürke) J. K. Morton	17	FP				
Stachys aculeolata Hook. f.	2, 17	FP				
*Stachys arvensis (L.) L.	11			ST		

MONOCOTYLEDONES

129. HYDROCHARITACEAE

Ottelia ulvifolia (Planchon) Walp.	18	FP				

130. POTAMOGETONACEAE

Potamogeton scheweinfurthii A. Benn.	18	FP ?				

131. COMMELINACEAE

Aneilema beniniense (Beauv.) Kunth	1, 2, 18	FP	P			
Aneilema dispersum Brenan	18	FP				
Aneilema umbrosum (Vahl) Kunth subsp. umbrosum	2, 18	FP				
A. nigritianum (C. B. Clarke) Hutch.	2					
Buforrestia mannii C. B. Clarke	2, 18	FP				
'*Commelina africana* C. B. Clarke'	2	FP				
Possibly *C. africana* L. var. *mannii* (C. B. Clarke) Brenan is intended. This is not recorded from FP in 18.						
Commelina benghalensis L.	2, 16	FP			A	
Not recorded from FP in 18.						
Commelina cameroonensis J. K. Morton	18	FP				
Commelina capitata Benth.	2, 18	FP				
Commelina congesta C. B. Clarke	18	FP		ST		
C. condensata C. B. Clarke	1, 2, 25					
Commelina diffusa Burm. f. subsp. diffusa	1, 8, 13, 18	FP	P	ST	A	
C. nudiflora L. pro parte	2, 25					
Commelina diffusa subsp. montana J. K. Morton	18	FP				
Commelina erecta L. subsp. erecta	18	FP				
C. vogelii C. B. Clarke	2					
Cyanotis barbata D. Don	18	FP				
C. mannii C. B. Clarke	2					
Palisota barteri Hook.	2, 18	FP				
? Palisota bicolor Mast.	2, 18	FP				
Palisota bracteosa C. B. Clarke	1, 2, 18			ST		
Palisota hirsuta (Thunb.) K. Schum.	18	FP				
P. thyrsiflora Benth.	2					
Palisota mannii C. B. Clarke	2, 18	FP				
Palisota pedicellata K. Schum.	1, 13		P	ST	A	E
Palisota preussiana K. Schum. ex C. B. Clarke	18	FP				
Pollia condensata C. B. Clarke	1, 2, 8, 18	FP	P	ST		
Pollia mannii C. B. Clarke	1, 2, 18			ST		
Polyspatha paniculata Benth.	2, 7, 18	FP				
P. glaucescens (C. B. Clarke) Hutch.	2					
*Rhoeo spathacea (Swartz) Stearn		FP		ST ?		
R. discolor (L'Herit.) Hance	1, 2					
Stanfieldiella brachycarpa var. hirsuta (Brenan) Brenan	18	FP ?				

Stanfieldiella imperforata (C. B. Clarke) Brenan	16	FP ? P ST
Buforrestia imperforata C. B. Clarke	1, 2, 13	
Brenan (in *Kew Bull.* 14 : 285 (1960)) states that one of the syntypes is from FP, but he considers that it may be *S. brachycarpa* var. *hirsuta* (see above).		
*Zebrina pendula Schnizl.	1, 13	P ST

132. FLAGELLARIACEAE

Flagellaria guineensis Schumacher	2	FP
Not recorded from FP in 18.		

133. ERIOCAULACEAE

Eriocaulon zambesiense Ruhl.	18	FP
Mesanthemum radicans (Benth.) F. Körnicke	2, 18	FP

134. BROMELIACEAE

*Ananas comosus (L.) Merr.	1	FP P ST A
A. sativus Lindl.	2	

135. MUSACEAE

*Musa chinensis Sweet	2	FP
*Musa paradisiaca L.	1, 2, 13, 25	FP P ST A
*Musa paradisiaca var. sapientum (L.) Kuntze	2	FP ST
M. sapientum L.	13	
M. paradisiaca subsp. *sapientum* (L.) K. Schum.	25	
*Musa paradisiaca var. vittata (W. Ackerm. ex Rodigas) K. Schum.	1	ST
*Musa rosacea Jacq.	1	ST
*Musa textilis Née	2	FP
*Musa ventricosa Welw.	13	ST
*Ravenala madagascariensis Sonnerat	2	FP
*Strelitzia reginae Banks	2	FP

136. ZINGIBERACEAE

Aframomum chlamydanthum Loes. & Mildbr.	18	FP
Aframomum daniellii (Hook. f.) K. Schum.	1, 2, 8, 9, 11, 13, 18, 25, 26	FP P ST
Aframomum keniense R. E. Fries		FP
FP : *Melville & Wrigley 487* (K.) Not in 18.		
Aframomum limbatum (Oliver & Hanb.) K. Schum.	2, 7, 18	FP
Aframomum melegueta (Roscoe) K. Schum.	1, 2, 18	FP P ST
Aframomum pilosum (Oliver & Hanb.) K. Schum.	2, 18	FP
Aframomum sceptrum (Oliver & Hanb.) K. Schum.		FP
FP : *Melville & Wrigley 555* (K). Not recorded from FP in 18.		
Costus afer Ker-Gawl.	1, 2, 11, 18, 25, 26	FP P ST
Costus engleranus K. Schum.	18	FP
Costus giganteus Welw. ex Ridley	1, 11, 13, 25	P ST A
Costus lucanusianus J. Braun & K. Schum.	2, 18	FP
Costus spectabilis (Fenzl) K. Schum.	1	ST
*Curcuma domestica Valeton	1	P
*Elettaria repens (Sonnerat) Baillon	1	ST ?

*HEDYCHIUM CORONARIUM Koenig	1, 2, 11	FP	P			
RENEALMIA AFRICANA Benth. & Hook.	2, 18	FP				
RENEALMIA CINCINNATA (K. Schum.) T. Dur.	1		P			
RENEALMIA GRANDIFLORA Baker	1			ST		E
Alpinia africana Ridley	2					
RENEALMIA MACROCOLEA K. Schum.	2	FP				
Probably the same as *R. africana.*						
RENEALMIA MANNII Hook. f.	2, 18	FP				E
*ZERUMBET SPECIOSUM Wendl.				ST		
Alpinia speciosa (Wendl.) K. Schum.	13					
*ZINGIBER OFFICINALE Roscoe	1, 2, 13, 25	FP	P	ST		
*ZINGIBER ZERUMET (L.) Smith	2	FP				

137. CANNACEAE

*CANNA INDICA L.	1, 11, 13		P ?	ST	A	
This should perhaps be treated as a distinct African species, *C. bidentata* Bertol.						

138. MARANTACEAE

HALOPEGIA AZUREA (K. Schum.) K. Schum.	7	FP				
Not recorded from FP in 18.						
'*Hybophrynium mannianum*'	7	FP				
I cannot trace this name. Perhaps it is an error for *H. braunianum* (see *Trachyphrynium* below).						
*MARANTA ARUNDINACEA L.	1		P	ST	A	
MARANTOCHLOA FILIPES (Benth.) Hutch.	18	FP				
Clinogyne filipes (Benth.) K. Schum.	2					
? MARANTOCHLOA FLEXUOSA (Benth.) Hutch.		FP ?				
Clinogyne flexuosa (Benth.) K. Schum.	2					
This species was recorded from FP in *Fl. W. Trop. Afr.*, ed. 1, but in 18 it was divided between *M. leucantha* (K. Schum.) Milne-Redh. and *M. purpurea* (Ridley) Milne-Redh. and neither of these species was recorded from FP.						
MARANTOCHLOA LEUCANTHA (K. Schum.) Milne-Redh.		FP				
FP: *Melville & Wrigley 554* (K). Not recorded from FP in 18.						
MARANTOCHLOA MANNII (Benth.) Milne-Redh.	18	FP				
Phrynium mannii (Benth.) K. Schum.	2					
MARANTOCHLOA RAMOSISSIMA (Benth.) Hutch.	18	FP				
Clinogyne ramosissima (Benth.) K. Schum.	2					
SARCOPHRYNIUM BRACHYSTACHYS (Benth.) K. Schum.		FP				
Phrynium brachystachys (Benth.) Körnicke	2					
Not recorded from FP in 18.						
THAUMATOCOCCUS DANIELLII (Benn.) Benth.	1, 2, 7, 9, 18	FP	P	ST		
Not recorded from FP in 18.						
TRACHYPHRYNIUM BRAUNIANUM (K. Schum.) Baker	18	FP				

139. LILIACEAE

*ASPARAGUS OFFICINALIS L.	13			ST		
CHLOROPHYTUM SPARSIFLORUM Baker	2, 18	FP				
GLORIOSA SIMPLEX L.	2	FP				
Not recorded from FP in 18.						

Gloriosa superba L.	2	FP				
Not recorded from FP in 18.						
Wurmbea tenuis (Hook. f.) Baker	2, 18	FP				

140. SMILACACEAE

Smilax kraussiana Meissner	18	FP				

141. ARACEAE

Amorphophallus mannii N. E. Brown	2, 18	FP				E
Anchomanes difformis var. pallidus (Hook.) Hepper	2 ?, 18	FP				E
A. petiolatus (Hook.) Hutch.	2, 7					
The plant recorded as *A. difformis* (Blume) Engl. in 2 is likely to be this variety.						
Anubias barteri Schott	2, 18	FP				
Anubias heterophylla Engl.	2	FP				
Not in 18.						
*Caladium bicolor (Aiton) Vent.	1, 2, 13	FP	P	ST		
Cercestis stigmaticus N. E. Brown	2, 18	FP				
C. dinklagei Engl. pro parte	2					
*Colocasia esculenta (L.) Schott	1, 2, 13	FP	P	ST		
Culcasia angolensis Welw. ex Schott	1, 2, 7, 18	FP		ST		
Culcasia lancifolia N. E. Brown	18	FP				
C. insulana N. E. Brown	2					
Culcasia parviflora N. E. Brown	2, 18	FP				
Culcasia scandens Beauv.	1			ST		
Cyrtosperma senegalense (Schott) Engl.	2, 18	FP				
Nephthytis constricta N. E. Brown	2, 18	FP				
Nephthytis poissonii (Engl.) N. E. Brown	18	FP				
Pistia stratiotes L.	2	FP				
Not recorded from FP in 18.						
Rhaphidophora africana N. E. Brown	18	FP				
Afrorhaphidophora africana (N. E. Brown) Engl.	2					
Rhektophyllum mirabile N. E. Brown	2, 7, 18	FP				
Sauromatum venosum (Aiton) Kunth	18	FP				
Jaimenostea fernandopoana Guinea & Moreno	2					
Stylochiton zenkeri Engl.	2, 18	FP				
*? Xanthosma sagittifolium (L.) Schott	13, 16			ST	A	
This may be *X. mafaffa* Schott.						
*Xanthosma violaceum Schott	2	FP				

142. LEMNACEAE

Lemna perpusilla Torrey	15			ST		

143. AMARYLLIDACEAE

*Allium cepa L.	2, 13	FP		ST		
*Allium sativum L.	13			ST		
*Crinum asiaticum L.	1			ST ?		
Crinum jagus (Thompson) Dandy	1	FP		ST		
C. giganteum Andr.	2					
Not recorded from FP in 18, presumably in error, as it is recorded in *Fl. W. Trop. Afr.*, ed. 1, under *C. giganteum*, on the basis of *Exell 768*, the sheet of which in BM bears a ticket reading 'Seen for Revised Edition of F.W.T.A.'						

Crinum natans Baker	2, 18	FP				
Haemanthus cinnabarinus Decaisne	2, 18	FP				
Haemanthus multiflorus Martyn	18	FP				
*Hippeastrum puniceum (Lam.) Urban	1		P	ST		
Hymenocallis littoralis (Jacq.) Salisb.	16				A	

144. IRIDACEAE

Acidanthera divina Vaupel	2, 18	FP				
*Neomarica caerulea (Lodd.) Sprague	1, 11	FP	P	ST		
Marica sabinii Lindl.	2					

145. DIOSCOREACEAE

*Dioscorea alata L.	1, 11, 13, 16, 25			ST	A	
Dioscorea bulbifera L.	1, 2, 13	FP		ST		
Not recorded from FP in 18.						
*Dioscorea cayenensis Lam.	1, 9, 11, 13, 16		P ?	ST	A	
Dioscorea dumetorum (Kunth) Pax	1, 2, 11, 13, 16, 25, 26	FP		ST	A	
Not recorded from FP in 18.						
Dioscorea elephantipes (L'Hérit.) Engl.		FP				
D. elephantopus Sprengel	2					
Dioscorea minutiflora Engl.	1, 2, 13	FP ?		ST		
The record from FP in 2 is probably based on a misidentification of *D. smilacifolia*.						
Dioscorea preussii Pax	2	FP				
Not recorded from FP in 18.						
Dioscorea sansibarensis Pax	1, 11, 13, 25			ST		
D. macroura Harms	25, 26					
Dioscorea smilacifolia De Wild.	18	FP				

146. AGAVACEAE

*Agave sisalana Perrine	1			ST ?		
*Cordyline fruticosa (L.) A. Chev.	16				A	
Dracaena adamii Hepper	18	FP				
Dracaena arborea (Willd.) Link	1, 11, 25		P	ST		
Dracaena bicolor Hook.	2, 18	FP				
Dracaena fragrans (L.) Ker-Gawl.	2	FP				
FP: Moka Lake, *Exell 809* (BM). Not recorded from FP in 18.						
Dracaena laxissima Engl.	1, 13		P	ST		
Dracaena monostachya Baker	1		P			E
Dracaena phrynioides Hook.	2, 18	FP				
? Dracaena usambarensis Engl.	2, 7	FP ?				
Not in 18. An unlikely record unless introduced.						
Dracaena viridiflora Engl. & Krause	2	FP				
Not recorded from FP in 18.						
*Furcraea foetida (L.) Haw.	1			ST ?		
Sansevieria guineensis (L.) Willd.	2	FP ?				
Not in 18. Record in 2 perhaps based on a misidentified specimen of *S. trifasciata* Prain.						
Sansevieria longiflora var. fernandopoensis N. E. Brown	2, 18	FP				E
Sansevieria metallica Gérôme & Labroy	16				A	

147. PALMAE

Ancistrophyllum opacum (Mann & Wendl.) Drude	2, 18	FP				
Ancistrophyllum secundiflorum (Beauv.) Wendl.		FP				
A. acutiflorum Becc.	2					
Not recorded from FP in 18.						
*Areca catechu L.	2	FP				
Borassus aethiopum Mart.	1, 13, 25			ST		
*Butia ereospatha (Mart.) Becc.	1			ST ?		
*Caryota urens L.	1			ST ?		
*Cocos nucifera L.	1, 2, 13	FP	P	ST	A	
Elaeis guineensis Jacq.	1, 2, 7, 13, 25	FP	P	ST	A	
Oncocalamus mannii (Wendl.) Wendl.	2	FP				
Not recorded from FP in 18.						
*Oreodoxa regia Kunth	2	FP				
*Phoenix dactylifera L.	2, 13	FP		ST		
Podococcus barteri Mann & Wendl.	2	FP				
Not recorded from FP in 18.						
Raphia hookeri Mann & Wendl.	18	FP				
Raphia vinifera Beauv.	2, 18	FP				
Sclerosperma mannii Wendl.	2	FP				
Not recorded from FP in 18.						

148. PANDANACEAE

Pandanus candelabrum Beauv.	1	FP	P			
Not recorded from FP in 18, although the type of *P. barteranus* Rendle, cited as a synonym, comes from FP.						
Pandanus thomensis Henriq.	1, 13, 25			ST		E
Pandanus sp. nov. ?	15		P			

149. TACCACEAE

Tacca leontopetaloides (L.) Kuntze	1			ST ?		

150. ORCHIDACEAE

Aerangis flexuosa (Ridley) Schlechter	1			ST		E
A. elegans (Rolfe) Dandy	1					
Aerangis gravenreuthii (Kränzlin) Schlechter	18, 20	FP				
Aerangis megaphylla Summerh.	1				A	E
Aerangis phalaenopsis Schlechter	2				A ?	
Record probably based on a misidentified specimen of *A. megaphylla*. There is no evidence of more than one species of *Aerangis* on Annobon.						
Ancistrochilus thomsonianus (Reichenb. f.) Rolfe	20	FP				
Not recorded from FP in 18.						
Ancistrorhynchus capitatus (Lindl.) Summerh.	18, 20	FP				
Ancistrorhynchus metteniae (Kränzlin) Summerh.	11, 18			ST		
Cephalangraecum metteniae (Kränzlin) Schlechter	1					
Ancistrorhynchus serratus Summerh.	18, 20	FP				
Angraecopsis dolabriformis (Rolfe) Schlechter	1, 11			ST		E
Angraecopsis ischnopus (Schlechter) Schlechter	20	FP				
Not recorded from FP in 18.						
Angraecopsis tridens (Lindl.) Schlechter	2, 18, 20	FP				
Angraecum tridens Lindl.	2					
Angraecum affine Schlechter	20	FP				
Not in 18.						

Angraecum aporoides Summerh.	18, 20	FP	P			
A. distichum var. *grandifolium* (De Wild.) Summerh.	15					
Angraecum astroarche Ridley	1			ST		E
Angraecum birrimense Rolfe	20	FP				
Not recorded from FP in 18.						
Angraecum chevalieri Summerh.	18, 20	FP				
Angraecum distichum Lindl.	1, 2, 11, 18		P	ST		
Angraecum doratophyllum Summerh.	1			ST		E
Angraecum infundibulare Lindl.	1, 18		P			
Angraecum pungens Schlechter	18, 20	FP				
Angraecum subulatum Lindl.	2, 18, 20	FP				
Ansellia africana Lindl.	2, 18, 20	FP				
Bolusiella talbotii (Rendle) Summerh.	16, 18, 20	FP			A	
Bolusiella sp.	20	FP				
FP: *Sanford 5919, 5920.*						
Brachycorythis basifoliata Summerh.	1		P			E
Bulbophyllum bequaertii De Wild.	18, 20	FP				
Bulbophyllum bufo (Lindl.) Reichenb. f.	18, 20	FP				
Bulbophyllum calamarium Lindl.	20	FP				
Not recorded from FP in 18.						
Bulbophyllum calyptratum Kränzlin	15		P			
Bulbophyllum cochleatum Lindl.	2, 15, 18, 20	FP		ST		
Bulbophyllum cocoinum Bateman ex Lindl.	1, 11, 18, 20				A	
Bulbophyllum comatum Lindl.	12, 18, 20	FP				
Bulbophyllum distans Lindl.	18, 20	FP				
Bulbophyllum falcatum (Lindl.) Reichenb. f.	1, 15, 18, 20	FP	P	ST		
Bulbophyllum fernandopoanum Schlechter, *nom. nud.*	2, 20	FP				
FP: Bokoko, *Mildbraed 6892.* Not in 18.						
Bulbophyllum flavidum Lindl.	1, 11, 18, 20	FP		ST		
Bulbophyllum fuerstenbergianum (De Wild.) De Wild.	18, 20	FP				
Bulbophyllum fuscoides J. B. Petersen	18, 20	FP				
Bulbophyllum gravidum Lindl.	2, 18, 20	FP				
Bulbophyllum insulanum Schlechter, *nom. nud.*	2, 20	FP				
FP: Bokoko, *Mildbraed 6935.* Not in 18.						
Bulbophyllum intertextum Lindl.	18, 20	FP				
Bulbophyllum mannii Hook. f.	18, 20	FP				
Bulbophyllum maximum (Lindl.) Reichenb. f.	1		P	ST		
Bulbophyllum mediocre Summerh.	15		P	ST		E
B. recurvum sensu Dandy	1					
Bulbophyllum melanorrhachis (Reichenb. f.) Reichenb. f.	16, 18, 20				A	
Bulbophyllum oreonastes Reichenb. f.	18, 20	FP				
Bulbophyllum oxypterum (Lindl.) Reichenb. f.	18, 20				A	
Bulbophyllum quintasii Rolfe	1		P			E
Bulbophyllum recurvum Lindl.	18, 20	FP				
Bulbophyllum resupinatum Lindl.	1			ST		E
Bulbophyllum schultzeanum Schlechter, *nom. nud.*	2, 20	FP				
FP: Bokoko, *Mildbraed 6951.* Not in 18.						
Bulbophyllum tenuicaule Lindl.	1, 2, 18, 20	FP		ST		
Bulbophyllum thomense Summerh.	1			ST		E
Bulbophyllum velutinum (Lindl.) Reichenb. f.	14, 15, 18			ST		
Bulbophyllum winkleri Schlechter	20	FP				
Not recorded from FP in 18.						

CALANTHE CORYMBOSA Lindl.	1, 2, 7, 11, 18, 20	FP		ST	A	
CALYPTROCHILUM EMARGINATUM (Swartz) Schlechter	18, 20	FP				
CEPHALANGRAECUM ACRODONTUM Schlechter ex Mildbr., *nom. nud.*		FP				
Ancistrorhynchus acrodontum Sanford, *nom. nud.*	20					
FP: *Mildbraed 7149*. Not in 18.						
CHAMAEANGIS THOMENSIS (Rolfe) Schlechter	1			ST		E
CHAMAEANGIS VAGANS (Lindl.) Schlechter	1		P			E
CHAMAEANGIS VESICATA (Lindl.) Schlechter	18, 20	FP				
CHAMAEANGIS sp.						
FP: *Sanford 4291*.	20	FP				
CHEIROSTYLIS LEPIDA (Reichenb. f.) Rolfe	1, 11, 18, 20	FP		ST		
CORYMBORKIS CORYMBOSA Thouars	16, 18, 20	FP		ST	A	
C. welwitschii (Reichenb. f.) Kuntze	1, 2					
CYNORKIS ANACAMPTOIDES Kränzlin	18, 20	FP				
CYNORKIS CALCARATA (Reichenb. f.) Schlechter 'Cynosorchis'.	20	FP				
FP: Moka, *Tessmann 2891*. Not in 18.						
CYNORKIS DEBILIS (Hook. f.) Summerh.	1, 11, 18, 20	FP		ST		
CYNORKIS GABONENSIS Summerh.	15		P			
CYRTORCHIS ACUMINATA (Rolfe) Schlechter	1		P		A	E
CYRTORCHIS HENRIQUESIANA (Ridley) Schlechter	1		P			E
CYRTORCHIS MONTEIROAE (Reichenb. f.) Schlechter	18		P			
CYRTORCHIS RINGENS (Reichenb. f.) Summerh.	15, 18, 20	FP		ST		
C. bistorta (Rolfe) Schlechter	1					
Not recorded from FP in 18.						
DIAPHANANTHE ACUTA (Ridley) Schlechter	1			ST		E
DIAPHANANTHE BIDENS (Swartz) Schlechter	18, 20	FP				
DIAPHANANTHE BREVIFOLIA (Summerh.) Summerh.				ST		E
Rhipidoglossum brevifolium Summerh.	1					
DIAPHANANTHE CURVATA (Rolfe) Summerh.	15		P			
DIAPHANANTHE KAMERUNENSIS (Schlechter) Schlechter	20	FP				
Not recorded from FP in 18.						
DIAPHANANTHE PAPAGAYI (Reichenb. f.) Schlechter	1		P			E
DIAPHANANTHE PELLUCIDA (Lindl.) Schlechter	1, 11, 15, 18, 20		P		A	
DIAPHANANTHE QUINTASII (Rolfe) Schlechter	1, 11, 18, 20	FP		ST		
DIAPHANANTHE RUTILA (Reichenb. f.) Summerh.	18			ST		
Rhipidoglossum rutilum (Reichenb. f.) Schlechter	1, 2, 11					
DIAPHANANTHE SUBCLAVATA (Rolfe) Schlechter	1, 20	FP		ST		
FP: San Carlos, *Mildbraed 6787*. Not in 18.						
DISPERIS MILDBRAEDII Schlechter ex Summerh.	2, 18, 20	FP				
DISPERIS REICHENBACHIANA Welw. ex Reichenb. f.	1, 11			ST		
DISPERIS THOMENSIS Summerh.	1, 11, 18, 20	FP		ST		
EPIPOGIUM ROSEUM (D. Don) Lindl.	2, 16, 18, 20	FP			A	
EULOPHIA BOULIAWONGO (Reichenb. f.) Raynal	20	FP				
E. oedoplectron Summerh.	18					
Lissochilus giganteus Welw.	2					
See Raynal in *Rev. Soc. Sav. Haute Normandie*, 39 : 47 (1966).						
EULOPHIA CRISTATA (Swartz) Steudel		FP				
Lissochilus purpuratus Lindl.	2					
Not recorded from FP in 18 or 20, therefore doubtful.						
EULOPHIA HORSFALLII (Bateman) Summerh.	2, 7, 18, 20	FP				

EULOPHIA MILNEI Reichenb. f.	18, 20	FP				
EULOPHIDIUM LATIFOLIUM (Rolfe) Summerh.	15, 18			ST		
Eulophia latifolia Rolfe	1, 11					
EULOPHIDIUM MACULATUM (Lindl.) Pfitzer	18		P	ST		
E. ledienii (Stein ex N. E. Brown) De Wild.	1, 11					
EULOPHIDIUM SAUNDERSIANUM (Reichenb. f.) Summerh.	18, 20	FP				
EURYCHONE ROTHSCHILDIANA (O'Brien) Schlechter	18, 20	FP				
GENYORCHIS MICROPETALA (Lindl.) Schlechter	2, 18, 20	FP				
Polystachya micropetala (Lindl.) Rolfe	2					
GENYORCHIS PLATYBULBON Schlechter	2	FP				
FP: *Gomez Moreno.* Not recorded from FP in 18 or 20.						
GENYORCHIS PUMILA (Swartz) Schlechter	15, 18, 20	FP	P			
GRAPHORKIS LURIDA (Swartz) Kuntze	11, 18, 20	FP		ST		
HABENARIA ATTENUATA Hook. f.	2, 18, 20	FP				
HABENARIA BARRINA Ridley	1, 11, 18, 20	FP		ST		
HABENARIA BRACTEOSA Hochst. ex A. Rich.	18, 20	FP				
HABENARIA BUETTNERANA Kränzlin	14			ST		
HABENARIA GABONENSIS Reichenb. f.	1, 11, 18, 20	FP	P			
HABENARIA MANNII Hook.	2, 18, 20	FP				
HABENARIA MICROCERAS Hook. f.	18, 20	FP				
HABENARIA STENOCHILA Lindl.	1, 11, 18		P			
HABENARIA THOMANA Reichenb. f.	1, 13			ST		
HETAERIA HETEROSEPALA (Reichenb. f.) Summerh.	1, 11, 18			ST		
HETAERIA MANNII (Reichenb. f.) Dur. & Schinz	20	FP				
FP: *Mildbraed 6400.* Not recorded from FP in 18.						
HETAERIA STAMMLERI (Schlechter) Summerh.	1, 18, 20	FP	P			
LIPARIS DEISTELII Schlechter	18, 20	FP				
LIPARIS GOODYEROIDES Schlechter	15		P			
Malaxis sp.	1					
LIPARIS GRACILENTA Dandy	1		P			E
LIPARIS NERVOSA (Thunb.) Lindl.	20	FP	P	ST	A	
L. guineensis Lindl.	1, 2, 11, 18					
LIPARIS TRIDENS Kränzlin	18, 20	FP				
LIPARIS WELWITSCHII Reichenb. f.	16				A	
LIPARIS sp.	20	FP				
FP: *Sanford 4084.*						
MALAXIS MACLAUDII (Finet) Summerh.	18, 20	FP				
MALAXIS PROREPENS (Kränzlin) Summerh.	20	FP				
Not recorded from FP in 18.						
MALAXIS WEBERBAUERANA (Kränzlin) Summerh.	18, 20	FP				
MANNIELLA GUSTAVII Reichenb. f.	1, 2, 13, 18, 20	FP		ST		
MICROCOELIA sp.	20	FP				
FP: *Sanford 4167.*						
NERVILIA ADOLPHII Schlechter	20	FP				
Not recorded from FP in 18.						
NERVILIA RENIFORMIS Schlechter	20	FP				
Not recorded from FP in 18.						
NERVILIA UMBROSA (Reichenb. f.) Schlechter	1, 11, 13		P	ST		
OBERONIA DISTICHA (Lam.) Schlechter	1			ST		
ORESTIAS STELIDOSTACHYA (Reichenb. f.) Summerh.	1, 11, 13		P	ST		E
PLATYLEPIS GLANDULOSA (Lindl.) Reichenb. f.	1, 2, 11, 16, 18, 20	FP	P	ST	A	
PODANGIS sp.	1			ST		

Polystachya affinis Lindl.	15				A	
Polystachya albescens Ridley subsp. albescens	1, 13, 15, 18, 20	FP	P	ST	A	
P. epidendroides Schlechter ex Mildbr., *nom. nud.*	2					
P. imbricata Rolfe	1, 11, 13					
Polystachya alpina Lindl.	2, 18, 20	FP				
Polystachya bicalcarata Kränzlin	18, 20	FP				
Polystachya bifida Lindl.	1, 2, 11, 13, 18, 20	FP		ST		
Polystachya calluniflora Kränzlin	20	FP				
Not recorded from FP in 18.						
Polystachya caloglossa Reichenb. f.	2, 18, 20	FP				
Polystachya calyptrata Kränzlin	20	FP				
P. elegans pro parte in 18, quoad *Sanford 4013*.						
Not in 18.						
Polystachya camaridioides Summerh.	20	FP				
Not recorded from FP in 18.						
Polystachya cultriformis (Thouars) Spreng.	18, 20	FP				
Polystachya disticha Rolfe	1			ST		
Polystachya elegans Reichenb. f.	18, 20	FP				
Excl. *Sanford 4013* in 18.						
Polystachya expansa Ridley	1			ST		
Polystachya fractiflexa Summerh.	20	FP				
Not recorded from FP in 18.						
Polystachya fusiformis (Thouars) Lindl.	18, 20	FP				
P. composita Kränzlin	2					
Polystachya laxiflora Lindl.	2, 18, 20	FP				
Polystachya nyanzensis Rendle	20	FP				
Not in 18.						
Polystachya odorata Lindl. var. odorata	2, 18, 20	FP				
Polystachya oligantha Schlechter, *nom. nud.*	2, 20	FP				
FP: *Mildbraed 7131*. Not in 18.						
Polystachya parviflora Summerh.	1			ST		E
Polystachya polychaete Kränzlin	2, 18, 20	FP				
Polystachya rhodoptera Reichenb. f.	1, 15, 18, 20	FP	P	ST		
Not recorded from FP in 18.						
Polystachya ridleyi Rolfe	1, 13, 16			ST	A	E
Polystachya setifera Lindl.	1		P			E
Polystachya superposita Reichenb. f.	18, 20	FP				
Polystachya tessellata Lindl.	1, 2, 11, 18, 20	FP		ST	A	
Polystachya thomensis Summerh.	15			ST		E
Polystachya cf. mukandaensis De Wild.	15			ST		
Polystachya sp.	1			ST		
Polystachya sp.	20	FP				
FP: *Sanford 5922*.						
Rangaeris brachyceras (Summerh.) Summerh.	1, 11, 18			ST		
Rangaeris aff. trilobata Summerh.	1			ST		
Sarcorhynchus polyanthus (Kränzlin) Schlechter	18, 20	FP				
Satyrium sp.	20	FP				
FP: *Tessmann 2890*.						
Solenangis scandens (Schlechter) Schlechter	15, 18			ST		
Stolzia elaidum (Lindl.) Summerh.	18		P			
Bulbophyllum elaidum Lindl.	1					
Tridactyle anthomaniaca (Reichenb. f.) Summerh.	20	FP				
Not recorded from FP in 18.						

Tridactyle tridactylites (Rolfe) Schlechter	1, 15, 18, 20	FP	P	ST		
Tridactyle aff. bicaudata (Lindl.) Schlechter	20	FP				
FP : *Sanford 5998.*						
Tridactyle aff. fusifera Mansf.	15			ST		
Tridactyle sp.	1			ST		
Tridactyle sp.	20	FP				
FP : *Sanford 4162.*						
*Vanilla crenulata Rolfe	1, 18, 25		P			
Vanilla grandifolia Lindl.	1, 11, 25		P			
*Vanilla planifolia Andr.	1, 2, 11, 25		P	ST		
Zeuxine elongata Rolfe	1, 18, 20		P	ST	A	
The record of this from FP in 20 is apparently an error. It is not recorded from FP in 18.						

151. JUNCACEAE

Luzula campestris var. mannii Buchenau	1, 2, 4, 13, 21	FP		ST		

152. CYPERACEAE

Bulbostylis densa (Wall.) Hand.-Mazz. var. densa	21	FP				
B. capillaris sensu Guinea	2					
Bulbostylis erratica (Hook. f.) C. B. Clarke	2, 21	FP				
Carex echinochloe Kunze		FP				
C. chlorosaccus C. B. Clarke	2, 21					
Carex leptocladus C. B. Clarke	1, 13			ST		E
Carex mannii E. A. Bruce	2, 4, 21	FP				
Cyperus articulatus L.	1, 2, 21	FP	P			
Cyperus atroviridis C. B. Clarke	2, 21	FP				
Cyperus baronii C. B. Clarke	1, 13	FP		ST		
C. mannii C. B. Clarke	2, 4, 21					
Cyperus compressus L.	1, 4	FP			A	
Not recorded from FP in 21.						
Cyperus cuspidatus Kunth					A	
A : *Melville 148* (P).						
Cyperus difformis L.	1			ST		
Cyperus diffusus subsp. buchholzii (Boeck.) Kükenthal	1, 2, 21	FP	P			
Cyperus distans L. f.	1, 2, 9, 11, 13, 21	FP	P	ST	A	
Cyperus esculentus L.	1		P	ST		
Cyperus exaltatus Retz.	1			ST		
Cyperus haspan L.	14			ST		
*Cyperus luzulae (L.) Retz.				ST		
ST : Perseverança, *Rose 535* (P). An American species probably introduced.						
Cyperus renschii Boeck.	4	FP				
Not recorded from FP in 21.						
Cyperus rotundus L.	1, 13		P	ST		
Cyperus sphacelatus Rottb.	1, 2, 4, 9, 11, 21	FP	P	ST	A	
Cyperus sylvicola Ridley	1			ST		E
Eleocharis geniculata (L.) Roemer & Schultes	21	FP		ST		
E. caribaea (Rottb.) Blake	4					
ST : Perseverança, *Rose 539* (P).						
Eleocharis mutata (L.) Roemer & Schultes		FP				
FP : *Melville 713* (K). Not recorded from FP in 21.						

Fimbristylis cymosa R.Br.			P			
F. obtusifolia Kunth	13					
Fimbristylis dichotoma (L.) Vahl var. dichotoma	1, 2, 4, 9, 11, 21	FP	P	ST	A	
Fimbristylis ferruginea (L.) Vahl	1, 4	FP		ST		
Not recorded from FP in 21.						
Fimbristylis ovata (Burm. f.) Kern				ST	A	
Abildgaardia monostachya (L.) Vahl	1, 9, 11					
Fuirena umbellata Rottb.	1			ST		
Hypolytrum grande (Uitt.) Koyama	16		P			E
Principina grandis Uitt.	1					
Hypolytrum heteromorphum Nelmes	2, 4, 11, 15	FP	P	ST		
H. africanum sensu Dandy	1, 2					
Not recorded from FP in 21.						
Hypolytrum purpurascens Cherm.	21	FP				
H. heterophyllum sensu Guinea	2					
Kyllinga appendiculata K. Schum.	21	FP				
? *K. cylindrica* sensu Guinea	2					
Kyllinga elatior Kunth	21	FP				
Kyllinga erecta Schumacher	4	FP				
Not recorded from FP in 21.						
Kyllinga nemoralis (J. R. & G. Forster) Dandy			P	ST		
Cyperus kyllingia Endl.	1					
Kyllinga odorata Vahl	2, 21	FP				
Kyllinga peruviana Lam.	4	FP	P	ST		
Cyperus peruvianus (Lam.) F. N. Williams	1					
Not recorded from FP in 21.						
Kyllinga pumila Michaux	2, 4, 21	FP	P	ST		
Cyperus tenuifolius Dandy pro parte, quoad specim.	1					
Kyllinga robusta Boeck.	21	FP				
Mapania amplivaginata K. Schum.		FP				
M. oblonga C. B. Clarke	4					
Not recorded from FP in 21.						
Mapania ferruginea Ridley	11		P	ST		E
M. aschersoniana sensu Dandy	1, 13					
M. subcomposita C. B. Clarke	1					
P: *Monod 12126.*						
Mapania macrantha (Boeck.) H. Pfeiffer		FP				
M. deistelii K. Schum.	4					
Not recorded from FP in 21.						
Mariscus alternifolius Vahl	21	FP	P	ST	A	
Cyperus sublimis (C. B. Clarke) Dandy	1, 9, 11, 13					
M. umbellatus sensu Guinea	4					
Mariscus dubius (Rottb.) Hutch.			P	ST	A	
Cyperus dubius (Rottb.) C. E. Fischer	1, 9, 11					
Mariscus flabelliformis Kunth var. flabelliformis	21	FP	P	ST		
Cyperus tenuis Swartz	1, 13					
Mariscus ligularis (L.) Urban	2, 21	FP	P	ST	A	
Cyperus ligularis L.	1					
M. rufus Kunth	4					
Mariscus longibracteatus Cherm.	21	FP		ST		
ST: Boa Entrada, *Chevalier 13706* (P).						
Mariscus luridus C. B. Clarke		FP				
FP: Moka, *Tessmann 67*. Not recorded from FP in 21.						

Mariscus tomaiophyllus (K. Schum.) C. B. Clarke	2, 21	FP			
Pycreus elegantulus (Steudel) C. B. Clarke	21	FP			
P. cimicinus sensu Guinea	2, 4				
Pycreus polystachyos Rottb.		FP	P	ST	
Cyperus polystachyos (Rottb.) Beauv.	1, 4				
Not recorded from FP in 21.					
Pycreus smithianus (Ridley) C. B. Clarke	2, 21	FP			
Remirea maritima Aubl.	1, 4, 14	FP	P		A
Cyperus pedunculatus (R.Br.) Kern	16				
Not recorded from FP in 21.					
Rhynchospora corymbosa (L.) Britton	8, 11			ST	
Scirpus brachyceras Hochst.	2, 4, 21	FP			
S. inclinatus (Delile) Aschers. & Graebner may prove to be an earlier name for this species.					
Scleria boivinii Steudel	21	FP			
S. barteri Boeck.	2				
Scleria lagoensis Boeck.					A
S. canaliculato-triquetra Boeck.	2				
Scleria naumanniana Boeck.	1		P		
Torulinium odoratum (L.) Hooper		FP	P		
Cyperus odoratus L.	1				
Not recorded from FP in 21.					

153. GRAMINEAE

Acroceras zizanioides (Kunth) Dandy	1, 2, 3, 7, 13, 21	FP		ST	
Agrostis mannii (Hook. f.) Stapf	2 3, 21	FP			
? Agrostis tropica Beauv.	1, 13		P ?		
Andropogon amethystinus Steudel	21	FP			
A. abyssinicus sensu Guinea	3				
Andropogon gayanus var. squamulatus (Hochst.) Stapf	3	FP			
Not recorded from FP in 21.					
Andropogon macrophyllus Stapf	21	FP			
Andropogon mannii Hook. f.	2, 3, 21	FP			
Anthephora cristata (Doell) Hackel ex De Wild. & Dur.	8, 11, 16			ST	A
Aristida adscensionis L.	9, 11				A
*Axonopus compressus (Swartz) Beauv.	8, 11			ST	
Axonopus flexuosus (Peter) C. E. Hubbard ex Troupin	14, 21	FP	P		
*Bambusa vulgaris Schrader ex Wendl.	1, 3, 13, 16		P	ST	A
Beckeropsis laxior W. D. Clayton	16, 21			ST	A
B. nubica sensu Dandy	1, 13				
Dandy followed Stapf & Hubbard (in Prain, *Fl. Trop. Afr.* 9 : 952 (1934)), who included in *B. nubica* (Hochst.) Fig. & De Not. the West African plants later segregated by Clayton as *B. laxior*.					
Brachypodium flexum Nees	2, 21	FP			
Bromus leptoclados Nees		FP			
B. scabridus Hook. f.	2				
Not recorded from FP in 21.					
Centotheca lappacea (L.) Desvaux	1, 2, 3, 8, 11, 13, 21	FP	P	ST	
Chloachne oplismenoides (Hackel) Stapf ex Robyns	21	FP			
Chloris pilosa Schumacher	1, 2, 13, 15, 21	FP	P	ST	
Chloris pycnothrix Trin.	1, 2, 15		P	ST	

*COIX LACRYMA-JOBI L.	1, 3, 16	FP		ST	A
CTENIUM NEWTONII Hackel	21	FP			
*CYMBOPOGON CITRATUS (DC.) Stapf	1. 2. 3, 16	FP	P	ST	A
CYNODON DACTYLON (L.) Pers.	1, 2, 3, 13	FP		ST	
Not recorded from FP in 21.					
CYRTOCOCCUM CHAETOPHORON (Roemer & Schultes) Dandy		FP			
C. setigerum Stapf	7				
Not recorded from FP in 21.					
DACTYLOCTENIUM AEGYPTIUM (L.) Beauv.	14			ST	
DESCHAMPSIA CESPITOSA (L.) Beauv.	2, 3, 21	FP			
DIGITARIA HORIZONTALIS Willd.	1, 8, 9, 11, 21	FP	P	ST	A
D. velutina sensu Guinea	2, 3				
DIGITARIA LONGIFLORA (Retz.) Pers.	14			ST	
ECHINOCHLOA COLONUM (L.) Link	13, 14			ST	
ELEUSINE INDICA (L.) Gaertn.	1, 3, 7, 11, 13, 15, 21	FP	P	ST	A
E. indica forma *unispicata* Sobrinho	8				
ERAGROSTIS DOMINGENSIS (Pers.) Steudel	21			ST	
E. linearis (Schumach.) Benth.	1, 14				
ERAGROSTIS MOKENSIS Pilger	2, 3, 21	FP			
ERAGROSTIS SUPERBA Peyr.	14			ST	
ERAGROSTIS TENELLA (L.) Beauv. ex Roemer & Schultes	3, 13, 15	FP	P	ST	
Not recorded from FP in 21.					
ERIOCHLOA NUBICA (Steudel) Hackel & Stapf ex Thell.	1, 9, 11	FP		ST	A
Not recorded from FP in 21.					
FESTUCA ABYSSINICA Hochst. ex A. Rich.	21	FP			
F. schimperana A. Rich.	2, 3				
FESTUCA CAMUSIANA subsp. CHODATIANA St.-Yves	21	FP			
F. simensis sensu Guinea	2, 3				
FESTUCA MEKISTE W. D. Clayton	21	FP			
F. gigantea sensu Guinea	2, 3				
HELICTOTRICHON MANNII (Pilger) C. E. Hubbard	2, 3, 21	FP			
HETEROPOGON CONTORTUS (L.) Beauv. ex Roemer & Schultes	1		P	ST	A
*HORDEUM VULGARE L.	13			ST	
HYPARRHENIA DIPLANDRA (Hackel) Stapf	1			ST	
HYPARRHENIA RUFA (Nees) Stapf var. RUFA	1, 9, 11			ST	A
HYPARRHENIA RUFA var. MAJOR (Rendle) Stapf	1			ST	
ISACHNE BUETTNERI Hackel	1, 2, 3, 7, 13, 21	FP	P	ST	
ISACHNE MAURITIANA Kunth	21	FP		ST	
I. aethiopica Stapf & Hubbard	1, 13				
LEERSIA HEXANDRA Swartz	3, 21	FP			
LEPTASPIS COCHLEATA Thwaites	1, 3, 7, 21	FP	P	ST	
L. conchifera Hackel	2				
MEGASTACHYA MUCRONATA (Poiret) Beauv.	21	FP			
Centotheca mucronata (Poiret) Kuntze	3				
C. urekana Guinea	3				
MELINIS MINUTIFLORA Beauv.	1, 3, 7, 13	FP		ST	A
Not recorded from FP in 21.					
OLYRA LATIFOLIA L.	1, 2, 7, 9, 11, 21	FP	P	ST	
OPLISMENUS BURMANNI (Retz.) Beauv.	1, 2, 3, 9, 11, 14, 21	FP		ST	A
OPLISMENUS HIRTELLUS (L.) Beauv.	1, 2, 3, 7, 8, 11, 13, 16, 21	FP	P	ST	A

*Oryza sativa L.	2, 3, 13	FP		ST		
*Oxytenanthera abyssinica (A. Rich.) Munro	3	FP				
Panicum acrotrichum Hook. f.	7, 21	FP				
P. acrotrichum var. *pubescens* Guinea	3					
Panicum brevifolium L.	1, 2, 3, 7, 8, 13, 16, 21	FP	P	ST	A	
Panicum hochstetteri Steudel	1, 2, 3, 8, 13, 21	FP		ST		
Panicum maximum Jacq.	1, 2, 8, 13, 14	FP	P	ST	A	
Not recorded from FP in 21.						
Panicum monticola Hook. f.	21	FP				
P. macrophyllum Guinea ex W. D. Clayton	7					
Paspalum conjugatum Bergius	1, 2, 3, 7, 8, 13, 16, 21	FP	P	ST	A	
Paspalum orbiculare Forster f.	21	FP		ST	A	
P. commersonii Lam.	1, 16					
P. scrobiculatum var. *commersonii* (Lam.) Stapf	2, 3					
Paspalum paniculatum L.	1, 8, 11, 13, 21	FP	P	ST		
Paspalum vaginatum Swartz	1, 2, 3, 9, 11, 14, 21	FP		ST	A	
Pennisetum hordeoides (Lam.) Steudel	2, 3, 21	FP				
Pennisetum monostigma Pilger	2, 3, 21	FP				
Pennisetum polystachion (L.) Schultes	1, 13, 14, 16		P	ST	A	
Pennisetum purpureum Schumacher	1, 3, 7, 11, 21	FP		ST		
? Phragmites karka (Retz.) Trin. ex Steudel		FP				
P. vulgaris sensu Guinea ?	3					
Not recorded from FP in 21. The plant recorded by Guinea is much more likely to be this species than *P. australis* (Cav.) Trin. ex Steudel.						
Poa annua L.	1, 3, 11, 21	FP	P	ST		
Poa leptoclada Hochst. ex A. Rich.	21	FP				
Pseudechinolaena polystachya (Kunth) Stapf	1, 3, 13, 21	FP		ST		
Puelia ciliata Franchet		FP				
P. acuminata Pilger	3					
Not recorded from FP in 21.						
Rhynchelytrum repens (Willd.) C. E. Hubbard	1		P			
Rhynchelytrum reynaudioides C. E. Hubbard	1, 2				A	E
Rottboellia exaltata (L.) L. f.	1, 3, 8, 21	FP		ST	A	
*Saccharum officinarum L.	1, 3, 13	FP	P	ST	A	
Sacciolepis africana C. E. Hubbard & Snowden	1			ST		
Schizachyrium brevifolium (Swartz) Nees ex Büse	16				A	
*Secale cereale L.	13			ST		
Setaria barbata (Lam.) Kunth	1, 2, 3, 8, 9, 11, 21	FP	P	ST	A	
Setaria caudula Stapf	21	FP				
Setaria chevalieri Stapf	1, 2, 8, 11, 13, 21	FP	P	ST		
Setaria longiseta Beauv.	1, 9, 11, 13		P	ST	A	
Setaria megaphylla (Steud.) Dur. & Schinz	1, 2, 3, 9, 11, 21	FP	P			
Setaria mildbraedii Mez ex C. E. Hubbard	1				A	E
Setaria sp. aff. mildbraedii Mez ex C. E. Hubbard	14			ST		
Sorghum arundinaceum (Desvaux) Stapf	1, 2, 3, 9, 11, 13, 21	FP		ST	A	
*Sorghum drummondii (Steudel) Nees ex Millsp. & Chase	1, 2		P			

SPOROBOLUS MOLLERI Hackel	1, 3, 7, 21	FP P ST
SPOROBOLUS PYRAMIDALIS Beauv.	1, 3	FP P ST
Not recorded from FP in 21.		
SPOROBOLUS ROBUSTUS Kunth	3, 7	FP
Not recorded from FP in 21.		
SPOROBOLUS TENUISSIMUS (Schrank) Kuntze	21	FP ST
S. minutiflorus (Trin.) Link	8, 9, 11, 13	
SPOROBOLUS VIRGINICUS (L.) Kunth	1, 3, 9, 11, 13	FP P ST A
Not recorded from FP in 21.		
STENOTAPHRUM SECUNDATUM (Walt.) Kuntze	1, 3, 7, 13	FP P ST A
Not recorded from FP in 21.		
STREBLOCHAETE LONGIARISTATA (A. Rich.) Pilger	21	FP
STREPTOGYNA CRINITA Beauv.	2, 21	FP
S. gerontogaea Hook. f.	3	
*TRITICUM AESTIVUM L.		ST
T. vulgare Vill.	13	
*ZEA MAYS L.	1, 3, 13	FP P ST

NOTE

Whilst this work was in the press the following was received:

M. C. Liberato. *Flora de S. Tomé e Principé* Papilionaceae. 1972.

Additional records contained in it, kindly communicated by its author, are included in this paper.

INDEX TO THE FAMILIES AND GENERA IN THE SYSTEMATIC LIST

Synonyms are printed in *italics*. In the text the genera and species are arranged alphabetically in each family. When a species is not to be found under the genus in which it was originally recorded it will usually have been transferred to another genus and will probably be found under one of the references to the original genus as a synonym.

Arthur W. Exell
Church Gates
Blockley
Moreton-in-Marsh, Glos.

INDEX TO VOLUME 4

The page numbers of the principal references and the new taxonomic names are printed in **bold-face** type, synonyms in *italics*. Names of intraspecific taxa are indexed only when they are new or are synonyms.

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