

GENERAL CONSIDERATIONS

We should endeavour to determine how few, not how many species are comprised in the Malaysian flora.

In writing the following chapters I have kept in mind the exemplary 'Introductory Essay' of J. D. HOOKER in his 'Flora Indica' (1855), the precursor of the 'Flora of British India'.

For the same reasons that moved HOOKER, I felt obliged to introduce the Flora Malesiana proper by some general considerations especially intended for co-operators less fortunate than I have been in acquiring an experience of long standing in the field. I may add that field experience often is invaluable when studying dried, always fragmentary, materials in the Herbarium.

Some of the subjects HOOKER treated are now too large to be included in one essay and, therefore, the *survey of the Malaysian collections*, the *physiognomy of the vegetation*, and the *genetic and floristic plant geography* occupy the (introductory) volumes 1-3 of this work.

The present essay will be entirely devoted to topics directly bearing on the study of systematic botany. Some of them I have previously discussed, or touched on, in my study of the origin of the Malaysian mountain flora.¹

As my intention is to further the study of Malaysian botany, I shall discuss only points of which a clear understanding is essential to the Malaysian naturalist. I will try to illustrate each case by reference to plants of this region.

These points are: *individual variation and racial segregation, variation caused by the environment, the problem of speciation and specific centres, hybridization, views on the status of the species and subspecies, migration and adaptation*, and the way to interpret these concepts.

These theoretical points are inseparable from a philosophical study of plants, and I believe it to be essential for systematists to explain the principles which have guided them in the execution and design of their work.

HOOKER's general instructions have guided me in my work, and I am convinced that in the *flux* of botanical conceptions in general aspects the words of the Master still hold their own. I desire to express here my admiration for this classic work by quoting *literatim* some passages of his essay.

"It may seem almost chimerical to look forward to a time when all the species of the vegetable world shall have been classified upon philosophical principles, and accurately defined; and it must be confessed that the present state of descriptive botany does not hold out much prospect of the realization of so very desirable an object. This, we think, is in a great measure due, not to any want of students willing and anxious to take up the subject, but rather to a gradually increasing misapprehension of the true aim and paramount importance of systematic botany, and of the proper mode of pursuing the study of the laws that govern the affinities of plants. We are therefore desirous, at the outset of a work which is devoted to these subjects,

of explaining our views on them; and as we trust that our work will fall into the hands of many beginners who are anxious to devote themselves usefully to the furtherance of botanical science, but who have not an opportunity of acquiring in any other way its fundamental principles, we shall make no excuse for dwelling at some length on the subject. We are also anxious to refute the too common opinion (which has been productive of much injury to the progress of botany) that the study of systems presents no difficulties, and that descriptive botany may be undertaken by any one who has acquired a tolerable familiarity with the use of terms."

"There can be no doubt that any observant person may readily acquire such a knowledge of external characters, as will in a short time enable him to refer a considerable number of plants to their natural orders; though even for this first step more knowledge of principles is required, than to make an equal advance in the animal kingdom: but to go beyond this,—to develop the principles of classification, to refer new and obscure forms to their proper places in the system, to define natural groups and even species on philosophical grounds, and to express their relations by characters of real value and with a proper degree of precision, demands a knowledge of morphology and anatomy and often of physiology, which must be completely at command, so as to be brought to bear, when necessary, upon each individual organ of every species in the group under consideration. To follow the laws that regulate the growth of all parts of the plant, especially the structure of stems, the functions of leaves, the development and arrest of floral organs, and the form, position, and minute anatomy of the pollen and ovule, and to trace the whole progress of the ovule and its integuments to their perfect state in the seed, ought all to be familiar processes to the systematic botanist who proceeds upon safe principles; but no progress can be made by him who confines his attention chiefly to the modification of these organs in individual or natural orders."—So far HOOKER.

Variability in characters of minor importance and description of extreme forms have led to a rather confused state of affairs. I believe that among the scores of species described many microspecies should be reduced to a much smaller number of true species, with a normal area of distribution and a normal variability in characters typical for Linnean populations which are intermediate between the species of extreme 'splitters' and extreme 'lumpers'. Much 'splitting' has been caused by describing single extreme forms not exactly agreeing with the type or type-description; for practical purposes it is sometimes required to describe such forms as new species and to recognize them provisionally as new 'entities'; the author's conscience and eagerness to finish his task are thus temporarily satisfied. This method has proved a failure and a serious handicap to the progress of tropical plant knowledge.

(1) Bull. Jard. Bot. Btjg III, 13 (1935) 358-407.

There are three methods of handling new collections, all being equally unsatisfactory. Firstly, provisional rapid identification of the material as to genus, or to species as far as is possible, and its insertion in the herbarium; collectors in general do not favour this method as only few final names can be provided on a cursory examination. Secondly, a collection may be worked through by rough comparisons to named specimens and with standard literature. This second method is rapid but all extreme forms and forms belonging to large genera or to difficult families which cannot be identified from the available literature, are described as new (*specimen description*). By this method collectors get immediate results but science is burdened with a host of 'endemic' species which, as experience has shown, disappear by the score when a thorough monograph is made. Thirdly, a collection may be thoroughly studied, delaying results, as the identification of extremes means in nearly every genus a preliminary revision.

HOOKER continues (*l.c.*):—"A knowledge of the relative importance of characters can only be acquired by long study; and without a due appreciation of their value, no natural group can be defined. Hence many of the new genera which are daily added to our lists rest upon trivial characters, and have no equality with those already in existence. A proneness to imitation leads to a gradual increase in their numbers, without a corresponding increase of sectional groups. Indeed, even when the sectional groups are well defined, and the genera in themselves natural, a too great increase in the number of genera is detrimental, by keeping out of view those higher divisions which are of greater importance. The modern system of elevating every minor group, however trifling the characters by which it is distinguished, to the rank of a genus, evinces, we think, a want of appreciation of the true value of classification. The genus is the group which, in consequence of our system of nomenclature, is kept most prominently before the mind, and which has therefore most importance attached to it."¹

(1) "We may make our meaning more clear by a few examples. The genus *Ficus* is surely more natural than the subgenera *Pogonotrophe*, *Covellia*, *Urostigma*, &c, into which it has been subdivided. So with the genera *Anemone*, *Hedyotis*, *Erica*, *Andromeda*, and others which have been split into many by modern systematists." R. BROWN, G. BENTHAM, J. D. HOOKER and others, in all their works, laboured to keep this important principle in view, and to impress it upon others; they have, however, failed to check the prevalent tendency to the multiplication of genera.

I add here other examples of genera occurring in Malaysia which are separated by trifling characters: *Voandzeiu* differs from *Vigna* only in fruit biology, viz its globular pods ripening subterraneously. In *Urena* and *Pavonia* now only one fruit character remains the decisive distinction, *Dillenia* and *Wormia* are distinguished only in their fruit biology, *Berberis* and *Mahonia* are distinct solely in the foliage, *Kibessia* and *Pternandra* differ only

"The rashness of some botanists is productive of still more detrimental effects to the science in the case of species; for though a beginner may pause before venturing to institute a genus, it rarely enters into his head to hesitate before proposing a new species. Hence the difficulty of determining synonymy is now the greatest obstacle to the progress of systematic botany; and this *incubus* unfortunately increases from day to day, threatening at no very distant period so to encumber the science,² that a violent effort will be necessary on the part of those who have its interests at heart, to relieve it of a load which materially retards its advancement. The number of species described is now so very great, and the descriptions are scattered through such a multitude of books, that even after long research it is difficult to avoid overlooking much that is already known; and when botanists with limited libraries and herbaria institute new species, it is almost certain that the latter will be found to have been already characterized. To such an extent is this carried, that we could indicate several works, in which one half and even more of the species are proposed in ignorance of the labours of other botanists. Indian Botany unfortunately, far from forming an honourable exception in this particular, presents a perfect chaos of new names for well-known plants, and inaccurate or incomplete descriptions of new ones".

"It must be remembered too that the Linnean canon, by which twelve words were allowed for a specific character, is now becoming quite inadequate to the requirements of the science; and that the brief descriptions, which are now so generally substituted for definitions, unless prepared with the greatest skill, as well as care, and after an inspection of very numerous specimens, seldom express accurately the essential characters of a plant. It is indeed becoming more and more evident, that in the great majority of instances no definition is sufficient to enable inexperienced botanists to determine with accuracy the species of a plant, even when the whole genus is well known; much more is this the case in genera, many of whose species are yet undiscovered; and most of all, in those where the forms, though sufficiently well known, are liable to much variation. In the last case their determination becomes a special study;

in unimportant characters of the calyx tube, etc. The separating characters are far less important than those which, in other genera, serve to divide sections or subgenera.

The more species are described the more differences originally accepted as of generic rank tend to disappear. A redefinition of the generic characters is often delayed, and the attitude in 'local-monographs' is mostly to keep at all costs the old delimitation in order to avoid laborious monographic work. Suggestive casual remarks are often made in local works, but decisions deferred.

(2) In entomology this has led to an intolerable chaos (*cf.* The New Systematics 1940, p. 475-491). The same holds for several large groups of the Fungi.

and when attempted without access to authentic specimens, leads to inextricable confusion, and its evil effects are not confined to specific botany, but extend to all departments."

"The pages of our Indian Flora will supply numerous illustrations of these remarks, and we would direct the attention of those commencing the study to the lesson to be derived from these instructive errors; for where the first botanists of the day have failed, beginners cannot be expected to succeed. It cannot be too strongly impressed upon all students of botany, that it is only after much preliminary study, and with the aids of a complete library, and an herbarium containing authentic specimens of a very large proportion of known species, that descriptive botany can be effectively carried out; and it would be well for science if this were fully understood and acted upon."

"The prevailing tendency on the part of students of all branches of natural history, to exaggerate the number of species, and to separate accidental forms by trifling characters, is, we think, clearly traceable to the want of early training in accurate observation, and of proper instruction in the objects and aim of natural science. Students are not taught to systematize on broad grounds and sound principles, though this is one of the most difficult processes, requiring great judgement and caution; or, what is worse, they are led by the example if not by the precepts of their teachers, to regard generic and specific distinctions as things of little importance, to be fixed by arbitrary characters, or according to accidental circumstances. As a consequence, the study of systematic botany is gradually taking a lower and lower place in our schools; and, being abandoned by many of those who are best qualified to do it justice, it falls into the hands of a class of naturalists, whose ideas seldom rise above species, and who, by what has well been called *hair-splitting*, tend to bring the study of these into disrepute."

"We therefore earnestly recommend to the Indian botanist the detailed study of individuals and their organs with the view of determining their limits of variation."

WIGHT and ARNOTT¹ formulated their warning to beginners as follows:—

"We shall perhaps be severely censured for cutting down species. We have all along considered it as trifling with nature to separate species on slight or variable grounds, nor could we ever understand the '*cui bono*' for which so much ingenuity in splitting hairs has been wasted. Before we determined what was a species, we examined with care numerous specimens from the same and different localities; and so far we have had an advantage over many other of the European botanists who have described Indian plants, they having only seen one or two isolated specimens. Numerous observations too were made in the plants in their natural situation, the result of which went to prove, what we have frequently endeavoured to enforce by

examples throughout the present volume, that no precise shape of leaf or quantity of pubescence is of any value, although both of these seem in each species to be limited within certain variations. With regard to varieties, we have seldom distinguished any unless well marked and tolerably constant; we are aware, indeed, that these correspond to what some naturalists call species, but our own observations have convinced us, that varieties and forms, as well as species, may be constant in similar situations, and even in widely different situations, for many years, if raised from seeds either obtained from the original locality or from cultivated plants; the cultivated cerealia and garden vegetables ought to lead to such an hypothesis without any additional proof." So far WIGHT and ARNOTT.

HOOKEER continues:—

"In relative size especially, the observer will find immense variation; for, unlike the animal creation, proportional dimensions are of small moment in the vegetable kingdom. This fact, so familiar to the botanist of experience, is always a puzzle to the zoologist, who fancies he perceives a vagueness and want of exactness in all botanical writings (except in those of the too numerous class that make a parade of measuring to lines organs that vary inches), that contrasts unfavourably with descriptive zoology. Symmetry is again only a relative term amongst plants, for even such leaves as grow in pairs are never alike, and often differ much in form, texture, and colour; whilst the various sepals, petals, *etc.* of an individual flower, never so exactly correspond as the relative members of an animal do; and there are still greater differences between these organs, when taken from different flowers."

"It is hardly necessary to allude to the desirability of studying the various forms induced by artificial causes: the browsing of cattle on shrubs, for instance, which is almost invariably followed, by an abnormal state of foliage on the subsequently developed shoots, has been a prolific source of bad species; while there is scarcely an operation of man that does not tend to produce change in the vegetation surrounding him."

"It will generally be found that botanists who confine their attention to the vegetation of a circumscribed area, take a much more contracted view of the limits of species, than those who extend their investigations over the whole surface of the globe. This is partly, no doubt, owing to the force of bad example; and partly to the fact that the student who takes up the study of the flora of his native country, finds that the species are all tolerably well known, and that no novelty is to be discovered. There is therefore a natural tendency to make use of trifling differences, from the scope which they afford for minute observation and critical disquisition; whilst the more close comparison of the few species which come under his investigation, leads the local botanist to attach undue importance to differences which the experienced observer knows may be safely attributed to local circumstances. To this tendency there can be no limit, when the philosophy of system is not understood; the distinctions which appeared trifling to

(1) Prod. Fl. Pen. Ind. Or. 1 (1834) p. xxxi.

botanists a quarter of a century ago, are at the present day so magnified by this class of observers, that they constantly discover novelties in regions which have been thoroughly well explored; considering as such, forms with which our predecessors were well acquainted, and which they rightly regarded as varieties.¹

"Another result of the depreciated state of systematic botany is, that intelligent students, being repelled by the puerilities which they everywhere encounter, and which impede their progress, turn their attention to physiology before they have acquired even the rudiments of classification, or an elementary practical acquaintance with the characters of the natural orders of plants. Unfortunately, in botany, as in every other branch of natural science, no progress can be made in the study of the vital phenomena except the observer have a previous accurate acquaintance with the various modifications under which the individual organs of plants appear in the different natural orders, and such an appreciation of the comparative value, structural and morphological of these modifications, as can only be obtained by a careful study of the affinities of their genera and species. Ignorance of these general laws leads to misinterpretation of the phenomena investigated by the physiologist, and to that confusion of ideas which is so conspicuous in the writing of some of the astute physiological observers of the day."

"The modern system of botanical instruction attempts far too much in a very limited space of time, and sends the student forth so insufficiently grounded in any branch of the science, that he is unprepared for the difficulties which he encounters, let his desire to progress be ever so great. The history of botanical discovery, and the philosophy of its advance, form instructive chapters for the student in any department of natural science."

"We owe to LINNÆUS the establishment of the doctrine of the sexuality of plants; and we find by the writings of the same great naturalist, that besides foreseeing many physiological discoveries, he preceded GOETHE in the discovery of morphology, a doctrine which, more than any other, has tended to advance scientific botany. A third great discovery, that of the nature of the ovule, and the relation of the pollentube to the ovary, received its principal illustration at the hands of BROWN, our chief English systematist, and of BRONGNIART, also a practised botanist."

"It should not be forgotten, that the relative importance of physiology is very different in the animal and vegetable kingdoms. In the former, structure and function operate so directly upon one another, that the great groups are, to a certain extent, defined by well-marked external characters, which are at once recognizable by the student, and are familiar, or at least intelligible, to those even

who have paid no attention to natural history. In the vegetable kingdom this is by no means the case: the processes of assimilation and secretion present but little of that complication which renders the study of animal physiology so important; they are, on the contrary, uniform almost throughout its whole extent, and moreover so simple in their *modus operandi*, that this very simplicity prevents their being rightly understood. In consequence, even the two great classes of Monocotyledons and Dicotyledons are not distinguishable without considerable practice and study; and were we dependent upon actual inspection of the organs whence the essential characters of these groups are drawn, for the means of recognizing, Systematic Botany would be an impracticable study."

"Herein lies one great obstacle which meets the beginner on the very threshold of his botanical studies: he sees the great divisions of the animal kingdom to be recognizable by mere inspection, and that familiar characters are also natural, and available for purposes of classification: the very names of the groups convey definite information, and to a great extent give exact ideas. Birds, fishes, reptiles, *etc.* are all as natural as they are popular divisions; but what have we in the vegetable kingdom to guide the student through the two hundred and fifty natural orders of flowering-plants? As with a new language, he must begin from the very beginning, and also avail himself of artificial means to procure as much superficial knowledge of structure and affinity as shall enable him to see that there is a way through the maze. Hence the obvious necessity of an artificial system of some sort to the beginner, who has, at the same time, to master a terminology, which, if not so complex as that of zoology, is more difficult at the outset, from the want of standards of comparison between the organs of plants and those he is familiar with in himself as a member of the sister kingdom. Applying these remarks to practice, the botanical student finds that he has much to unlearn at the very outset; in many cases he has misapplied the terms root, stem, leaf, *etc.*, and contracted most erroneous ideas of their structure and functions; while he is startled to find that the popular divisions of plants into trees, shrubs, and herbs, —leafy and leafless, water and land, erect, climbing, or creeping,—are valueless even as guides to the elements of the science."

"It is not however to be supposed, because pure physiology is of secondary importance to the right understanding of the affinities of plants, that botany is therefore a less noble or philosophical study than zoology; since we find anatomy, development, and morphology, occupying a very far higher rank in proportion. Being deprived, as he is in most cases, of all technical aids to the determination even of the commoner exotic natural families, the systematist is compelled to commence with the knife and microscope, and can never relinquish these implements. Systematic Botany is indeed based upon development; and no one can peruse, however carelessly, the most terse diagnosis of a natural order or genus of plants, without being

(1) "Many of the species which have been revived in modern times were indicated by HALLER, RAY, TOURNEFORT, and other ancient botanists, but were reduced to the rank of varieties, when the science was reformed by LINNÆUS."

struck with the variety and extent of knowledge embodied as *essential* to its definition and recognition. Not only are the situation and form, division or multiplication, relative arrest or growth, of the individual organs exactly defined, in strictly scientific and scrupulously accurate language, but the development of each is recorded from an early stage: the vernation and stipulation of the leaves; the aestivation of the young calyx and corolla, and their duration relatively to other organs; the development and cohesion of the stamens; the position and insertion of the anther; its pollen; the cohesion or separation of the carpels, and the stages of their development from the bud to the mature fruit, and from the ovule to the ripe seed, are all essential points; all however minute, must in many cases be actually inspected before the position of a doubtful genus can be ascertained in the Natural System; and this is not the exception, but the rule."

"The necessity for acquiring so extensive and detailed a knowledge indicates a power of variation in those organs from which the natural characters are drawn, that defeats any attempt to render one, or a few of them only, available for the purposes of classification; and hence it is that the study of morphology or the homologies of the organs, becomes indispensable to the systematist; by this he reduces all anomalies to a common type, tests the value of characters, and develops new affinities. The number, form, and relative positions of organs may supply technical characters, by which observers of experience recognize those natural orders under which a great number of plants arrange themselves; but a knowledge of structure and anatomy alone enable the botanist to progress beyond this, and to define rigidly: whilst the study of development affords him safe principles upon which to systematize and detect affinities, and morphology supplies the means of testing the value of the results, and reveals the harmony that reigns throughout the whole vegetable world."

"Physiology, again, is a branch of botany very much apart from these: its aim is the noblest of all, being the elucidation of the laws that regulate the vital functions of plants. The botanical student of the present day, however, is too often taught to think that getting up the obscure and disputed speculative details of physiology, is the most useful elementary information he can obtain during the short period that is given him to devote to botany; and that, if to this he adds the scrutiny of a few of the points under a microscope, he has made real progress as an observer. This, we maintain, is no more botany, than performing chemical experiments is chemistry, or star-gazing astronomy. A sound elementary knowledge of vegetable physiology is essential to the naturalist, and should indeed be a branch of general education, as it requires nothing but fair powers of observation and an ordinary memory to acquire it. For the student to confine his attention to this knowledge of the vegetable world, and to try and improve upon it by crude experiments of his own, undertaken in ignorance of the branches of pure botany

we have enumerated, is a very rational amusement, but nothing more."

"The students are indeed, in too many cases, perfectly ignorant of the elements of natural science, and require some practical acquaintance with plants and their organs, before they can appreciate the relations of the different branches of botany to one another, or discriminate between what is essential to understand first, and what is better acquired afterwards. Were the elements of science taught at schools, this would not be so: we should then have the student presenting himself at the botanical lectures fully prepared for the more difficult branches of science, and for making that progress in them for which the professor's aid is indispensable. A sound practical knowledge of system we hold to be an essential preliminary to the study of the physiology of plants—a study which requires also a practical acquaintance with organic chemistry, consummate skill in handling the dissecting knife, and command over the microscope, a good eye, a steady hand, untiring perseverance, and above all, a discriminating judgment to check both eye, hand and instrument. A combination of these rare qualities makes the accomplished vegetable physiologist, and their indispensability gives physiology its pre-eminence in practice."

"It has been with no desire of obtruding our views upon our readers that we have ventured to discuss these obscure subjects with relation to Indian plants, but from a conviction, that in the present unsatisfactory state of systematic botany it is the duty of each systematist to explain the principles upon which he proceeds; and we do it not so much with the intention of arguing the subject, as of pointing out to students the many fundamental questions it involves, and the means of elucidating them."

"To every one who looks at all beneath the surface of descriptive botany, it cannot but be evident that the word *species* must have a totally different signification in the opinion of different naturalists; but what that signification is, seldom appears except inferentially. After having devoted much labour in attempting to unravel the so-called species of some descriptive botanist, we have sometimes been told that the author considers all species as arbitrary creations, that he has limited the forms he has called species by arbitrary characters, and that he considers it of no moment how many or how few he makes. So long as this opinion is founded on conviction, we can urge no reasonable objection against its adoption; but it is absolutely necessary that the principle should be avowed, and that those who think the contrary should not have to waste time in seeking for nature's laws in the works of naturalists who seek to bind nature by arbitrary laws. So again with regard to specific centres; except we are agreed with an author as to whether the same species has been created in one or more localities, and at one or more times, we shall be at cross purposes when discussing points and principles relating to identity of species and geographical distribution."

"Great differences of opinion have from the

earliest days of science always existed on the nature of species. The prevalent opinion has undoubtedly at all times been, that a species is a distinct creation, distinguishable from all others by certain permanent characters. Many eminent philosophers, however, have taken a contrary view; of these the best known have been LAMARCK, and more recently the anonymous author of the 'Vestiges of Creation'."—So far HOOKER.

Modern biological science has progressed rapidly in the last decades through the results of experimental genetics. Though it is far from easy to weld the often contradictory opinions into a satisfactory whole, views relating to matters of variation have much gained. In the following pages I will try to discuss on this new basis the value to be attributed to characters of less than specific importance and a number of considerations which may lead to increased accuracy in judging specific delimitation.

Trifling characters, such as *peloric* and *cleistogamous flowers*, have led to the creation of worthless new genera; *galls*, *insect bites*, and *parasitic fungi* have been mis-interpreted and caused the publication of new species of Phanerogams. *Individual variations*, either intrinsic or extrinsic have, in a similar way, induced systematists working on tropical plants to distinguish more species than Nature intended.

It is not our intention to limit phytography to a merely administrative function in the study of botany, but to treat it as an essential of natural philosophy. The systematist ought to keep pace with cytogenetics, physiology and morphology,¹ phytochemistry, phytogeography, ecology, genetics, *i. e.* experimental taxonomy.

Inadequate material² and information are the chief causes which prevent the phyto-systematist from applying the results obtained by these branches of botanical science.

The systematist is seldom favourably regarded by the layman or student of directed botany. They are opposed to changes in nomenclature, being unable to gauge the force of the arguments for a 'new' name for a familiar plant and so rarely accept the judgment of taxonomists. When, on the other hand taxonomic problems are tackled by applied scientists nomenclature and specific distinction become chaotic; entomology, mycology, forestry, agriculture and horticulture supply many examples. A wish for simplification, impatience, or even personal vanity or the desire for pecuniary gain have caused hosts of 'species' to be added to our lists

(1) For the value of wood anatomy in taxonomy, see DEN BERGER, in Handel. 4e N.I. Natuurwet. Congres (1926) 397.

(2) Cf. WIGHT, in a letter to GRIFFITH, dated April 15, 1842:—"How people can work on dry plants I cannot imagine. I am daily convinced of the poverty of the study from such materials, unless a man has seen much of living structure." MIQUEL ignored this remark, and on sterile and inadequate material based a host of species from Sumatra which even at present are not wholly elucidated.

by applied workers. Not long ago a forestry officer made a study of *Agathis*³ in Malaysia in which 13 species and 2 doubtful ones, that is 15 entities, were distinguished. In the same material the late Dr DANSER, whose judgment and experience cannot be doubted, distinguished only 3 divergent species with a number of local geographic variations. He found it very difficult to define the latter. Additional material showed that the keys and distinctions presented for the 13 species did not hold to the satisfaction of the Forest Research Station, from which this work emanated. In plant families of economic importance particularly in *Gramineae*, *Rutaceae*, and *Leguminosae*, similar work has resulted in multitudes of microspecies provided with binomials; by such a proceeding nothing is gained and much lost.

An example of the difficulties arising between taxonomy and an applied science when a good revision is absent, is the following:—a *Clausena* of unknown origin was cultivated for economic purposes at Buitenzorg. I referred it to *Clausena anisum-olens* (BLCO)MERR. but the phytochemist was dissatisfied, the properties of the oil did not tally with data recorded from the same species in the Philippines. I then sent ample material with full notes to Dr TANAKA, Dr SWINGLE, and to the Kew and Paris Herbaria, for identification. The answers were all different and the phytochemist was, of course, disgusted with the practical results of taxonomy, because now he had the choice among 5 names for his plant. By way of comfort I expressed the hope that a systematist would some day make a satisfactory monograph of the genus.⁴ In order not to raise his hopes too high I remarked that even then some research from *him* would be needed to establish the assumed constancy of the oil properties as a specific character. I also informed him that taxonomy has sometimes scored by predicting phytochemical facts, *e.g.* when HALLIER supposed the presence of valerianic acid in *Viburnum*⁵ on phylogenetic grounds only.

In the following two chapters general information on variation as a source of superfluous binomials is collected for the benefit of those with no field experience of the Malaysian flora. I distinguish variations induced by the environment from those belonging to the genetic composition of populations, and I have tried to illustrate them by examples in Malaysian phytography.

Often the number of examples is too small, and chapters overlap, but in the course of time every student of Malaysian botany will meet with other equally telling cases. May they stimulate the wish to avoid lapses of this character by conscientious treatment of the revisions in Flora Malesiana.

(3) Bull. Jard. Bot. Btzig III, 16 (1938) 455-474.

(4) Compare R. WIGHT in a letter to GRIFFITH, dated March 30, 1841:—". . . "as you say Botany is difficult, and increasingly so, but Botanists are to blame for this. No remedy will be so effectual as the publication of Monographs."

(5) Med. Rijksherb. Leiden no 14 (1912) 36; *ibid.* 37 (1918) 92. Cf. also *V. valerianoides* ELM.

VARIATIONS MOSTLY INDUCED BY THE ENVIRONMENT
(*Phenotypic modifications*)

Phenotypic modification is the response to environmental conditions, such as climate, soil, exposure, altitude, temperature, wind, fire and living organisms. The genetic qualities govern the character of the plant, but the environment in which the plant develops determines the actual and final appearance of the individual. The changes or differences from the 'normal plant' are called *modifications*. Such changed characters are not themselves inherited, however, though the manner in which a plant reacts to environmental conditions is. In some cases an external change may be reversed by a change in the environment during the development of the individual but in other cases, when factors act in the seedling stage only, the effects in the individual are irreversible.

It is necessary to agree about the concept 'normal plant'. This is far from easy, as each specimen grows under a different combination of CEB-factors (Climatic, Edaphic, Biotic). We might ap-

proach the idea by saying that "the normal plant results from a genetically average individual under average natural environmental conditions", average to be understood in the sense of optimal. This 'normal' individual is never a reality but remains an abstraction.

Though the difference between phenotypic and genotypic variation is clear, the field botanist—and still more the herbarium botanist—is not always able to recognize it. Only experiments may furnish proof. For instance a dwarf shrub in an area subject to fire or browsing animals may assume this stunted form through these CEB-factors but it is also possible that the stunted form is a specialized race adapted to these conditions and thus selected by nature itself from the specific population. Experimental breeding must decide its constancy.

I have arranged the phenotypic modifications under several headings—which partly overlap and interlock—in the following sequence:

Intrinsic	} Ontogeno-morphosis .	1. Juvenile forms	p. xix
		2. Precocious flowering (<i>paedogenesis</i>)	xxi
		3. Dimorphous foliage	xxii
		4. Dimorphous seeds and fruits	xxiv
		5. Dimorphous flowers	xxv
		6. Cleistogamous flowers	xxv
		7. Teratological forms	xxv
Climatic	} Hypselo-morphosis .	8. Phenotypic effect of altitude	xxvi
		9. Epiphytes	xxviii
		10. Shade forms	xxix
		11. Influence of drought	xxix
		12. Seasonal variation	xxix
Edaphic	} Edapho-morphosis .	13. Wind forms	xxx
		14. Fumarole plants	xxx
		15. Rock plants; calcareous and silicious soils	xxxii
Biotic	} Hydro-morphosis .	16. Solfataral plants	xxxiii
		17. Water and swamp plants	xxxiv
	} Phyto-morphosis .	18. Fungus and bacterial diseases, and symbiosis	xxxv
		19. Ant plants (<i>myrmeco-morphosis</i>)	xxxv
		20. Galls deceptive to phytographers (<i>cecidio-morphosis</i>)	xxxvi
		21. Influence of browsing animals (<i>pascoo-morphosis</i>)	xxxvi
		22. Influence of fire (<i>pyro-morphosis</i>)	xxxvii
		23. Pioneer plants	xxxviii
Anthropo-morphosis	xxxviii		
		24. Savannah trees	xxxviii

Ontogeno-morphosis

1. Juvenile forms

Juvenile forms often differ widely from the mature plant. Seedlings of many *Leguminosae* differ greatly from the adult in foliage and other characters. The youth form of *Cassia javanica* L. possesses large metamorphosed twigs acting as thorns (1). Thorny juvenile specimens are also found in *Alangium*.

In general, flowering twigs have smaller leaves than sterile branches; this often gives rise to diffi-

culty in identifying non-flowering material and so one of the pitfalls if new species are based on sterile material. An example is *Campnosperma acutiauris* BOERL. & KOORD. (*Anacardiaceae*) described on sterile juvenile material from Sumatra. The leaves are large and conspicuously auriculate-amplexicaulous. A similar juvenile form was later found in West Java, together with mature trees. These possessed much smaller non-auriculate leaves (fig. 2). The plant appeared to represent a species of *Tristania* (*Myrtaceae*)(2); its specific identity will probably remain obscure, however, as several species produce similar juvenile forms.

Youth forms of *Myrica longifolia* T. & B. differ strongly from mature specimens in possessing distinct stipules and incised larger leaves.

Incised leaves of seedlings occur in a score of arboreal plants, e.g. many *Bignoniaceae*, *Proteaceae*, *Gmelina*, *Lonicera*, *Alangium*, *Vitex*, &c. Leaves of young trees of *Pangium edule* REINW.

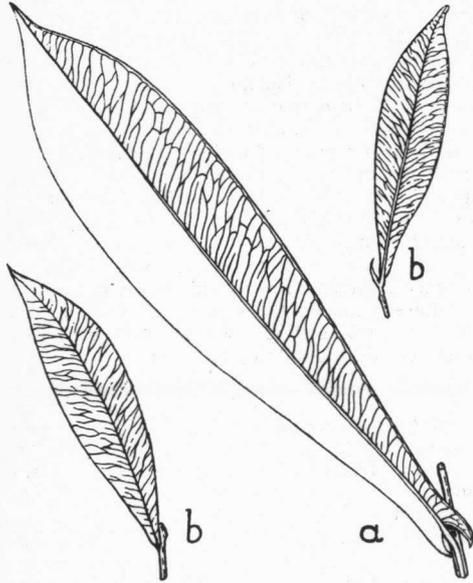


Fig. 2. Large leaf of a juvenile specimen, small leaves of a mature tree of *Tristania* sp. (Myrt.) in W. Java, $\times \frac{1}{3}$.

are 3-lobed whereas the leaves of mature trees are entire.

The growth of different parts of the plant is often very disproportionate. In some *Symplocos* species I found the leaf teeth were mature and large in young leaves but inconspicuous in mature foliage: they possibly have some (?excretive) function during youth only. BACKER (3) found the leaf tip earlier developed than the blade in some species of *Dioscorea*; it disappears also sooner. A peculiar development occurs in the growing leaves of some *Meliaceae*, e.g. *Chisocheton* (fig. 3).

Very peculiar juvenile forms greatly differing from the later normal foliage, have been described in various climbing plants such as some spp. of *Adenia*, *Medinilla*, *Macrozamia*, *Piper*, *Araceae*, *Ficus*, &c. Juvenile specimens of these trunk climbers are always sterile. Their foliage is mostly broader than that of mature plants, and is appressed to rocks or tree trunks. The similarity in their appearance may cause considerable confusion as e.g. is shown by the type specimen of *Ficus peltata* BL. which was recently proved to represent a juvenile specimen of some climbing species of *Piper*.

In several *Malvaceae*, *Leguminosae*, *Sterculiaceae*, *Tiliaceae*, juvenile leaves are often different

from mature ones (fig. 4). *Sterculia polyphylla* R. BR. is a juvenile stage of *St. foetida* L.; young trees often possess leaves having 10-15 narrow leaflets, mature trees have mostly 5-9-foliolate leaves with broader segments. Young *Lasia spinosa* THW. is very different from the mature plant. *Ficus basidentula* MIQ. is merely the juvenile form of *F. callosa* WILLD.; it is quite common in the hedges at Buitenzorg. The polymorphy in the habit and foliage of *Ficus quercifolia* ROXB. and *F. heterophylla* L.f. is unbelievable.

In juvenile forms of *Nepenthes* the shape of the pitchers may considerably differ from that in mature plants; as a result juvenile *Nepenthes* cannot with certainty be identified.

In *Carallia lucida* ROXB. leaves of mature trees are oblong to obovate with very shallowly serrate to entire margins; saplings, however, have oblong to lanceolate leaves distinctly serrate (4).

Other cases of old mature plants differing from young ones are found among lianas in which the shape of the stem may change considerably: *Cissus tuberculata* BL. has terete tuberculate stems but they later become flat and, in older stems, up to 60 cm broad looking like gigantic ribbons! The latter were described as a separate species, *Vitis lanceolaria* WALL., but the two forms are merely two stages of one species. The stems of lianas generally change greatly with age, through the development of corky warts and wings, together with secondary wood not present in young flowering twigs. Spines sometimes disappear in lianas and trees with age; in some cases, on the other hand, they enlarge considerably. A peculiar case is represented in two undescribed Cucurbitaceous lianas from the Lesser Sunda Islands, both having a

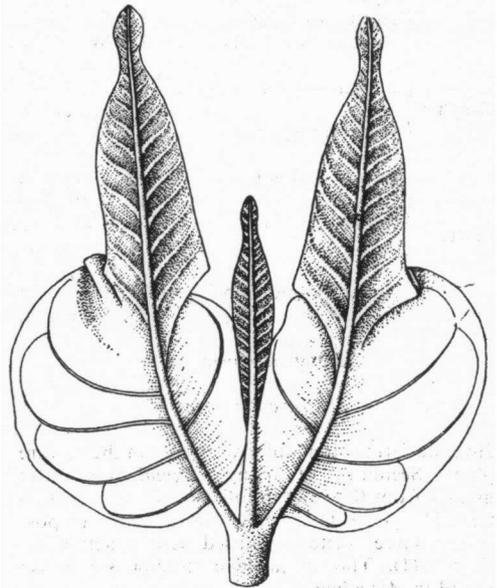


Fig. 3. Growing leaf tip of *Chisocheton* sp. (Meliac.) (bb. 23227), $\times 3$.

swollen base; in *Gynostemma* sp. this 'podagric' base is smooth, in *Alsomitra* sp. it is spiny (5).

Habit also sometimes changes with age: *Ancistrocladus* is sometimes a shrub in youth whereas later it becomes distinctly scandent. Climbers which have no support may sometimes grow into semi-erect shrubs; this I once observed in a plant

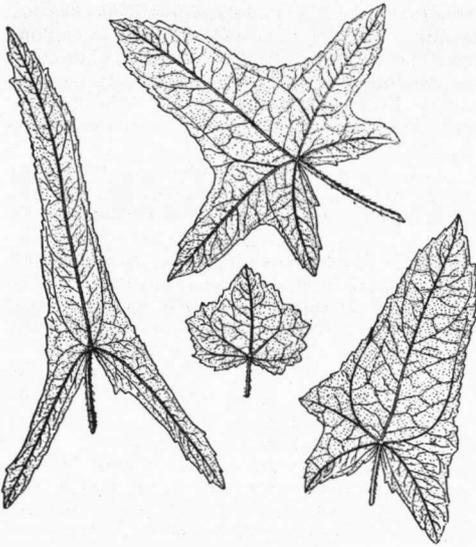


Fig. 4. *Hibiscus sagittifolius* KURZ (*Malvac.*), leaves from one specimen (Indramajoe, W. Java), $\times \frac{1}{2}$.

of *Smilax modesta* DC. in a grass field on Mt Dieng.

Spotted leaves often occur only or predominantly in juvenile specimens. *Strobilanthes picta* KOORD. was a new species proposed on account of silvery spots on the leaves. However, it is a juvenile stage of *Str. cernuus* BL. Similar cases are known in *Begonia*, *Cissus*, and other genera where these spots may disappear with age. In greenhouses these juvenile forms are preferred for ornamental purposes.

Juvenile forms of plants with pinnate leaves sometimes have a much larger number of pinnæ e.g. *Campsis pandorana* (ANDR.)STEEN. c.n. (6).

An example of a new species based on a juvenile plant is found in *Dacrydium*: the type specimens of *Dacrydium junghuhnianum* MIQ. from Sumatra consist of juvenile specimens of *D. elatum* WALL. with long loosely set needles.

In the herbarium flowers sometimes open during drying and create the impression of being mature. This is specially the case with flowers having valvate terete corollas e.g. *Symplocos* § *Cordyloblaste*, *Styrax*, *Polyosma*, *Proteaceae*, *Loranthaceae*, &c.

MIQUEL described a new species of *Lonicera* from Sumatra *L. sumatrana* MIQ. In his description short corollas are mentioned; owing to this mistake the species was subsequently placed in the wrong section and described twice again, once from Burma

and once from Sumatra (7). The examination of MIQUEL's type specimen revealed that he described immature flowers, in fact buds which had opened in the herbarium. Immature woody capsules or strobili of *Myrtaceae*, *Theaceae*, *Coniferae*, *Casuarina*, &c. also tend to open after drying.

There is often a great similarity in the leaves of watersprouts of mature trees with those of saplings: large size, deeper incised teeth, thinner texture, e.g. in *Symplocos*, *Ficus*, *Sapotaceae*, *Dipterocarpaceae*, etc.

A still unsolved case is that of *Evonymus japonicus* THUNB. of which a sterile slender climbing and rooting form is frequently found in the Javan mountain forests. I originally took it for a juvenile shade form (8). Not until 1941 did I succeed in finding it flowering and fruiting on the open summit of Mt Jang. It is unknown whether the shade conditions in the juvenile stage determine the later morphology.

Cited literature: (1) A. J. KOENS, De Trop. Natuur 2 (1913) 174; see also KOORDERS, Bull. Jard. Bot. Btzg. III, 1 (1919) 168. (2) *Tectona* 22 (1929) 1336-1340. (3) *Handboek Flora Java* pt 3 (1924) 109. (4) *Schoolflora voor Java* (1911) 486. (5) *Figured in De Trop. Natuur* 29 (1940) 6. (6) *Bignonia pandorana* ANDR. (7) *Journ. Arnold Arbor.* 27 (1946) 441, 445. (8) *De Trop. Natuur* 22 (1933) 175-176.

2. Precocious flowering (paedogenesis)

In several Malaysian plants precocious flowering is observed. COSTERUS (1) recorded flowering seedlings in *Melia arguta* DC. (fig. 5). BACKER found them in *Melia azedarach* L. and J. J. SMITH described (2) the same phenomenon in *Murraya paniculata* L. In *Cocos nucifera* L. precocious flowering is often seen. The late Dr A. RANT observed flowering seedlings in *Cinnamomum zeylanicum* THW. (oral comm.). Other plants in Malaysia in which precocious flowering has been observed are *Swietenia mahagoni* JACQ., *Coffea robusta*, *Citrus decumana* L., *Nicotiana tabacum* L., *Sesbania sericea* DC., *Vigna sinensis* ENDL., *Teramnus labialis* SPRENG., *Tectona grandis* L.f., *Kalanchoe pinnata* PERS., and *Ailanthus* sp.

In plants which flower strictly periodically precocious flowering is sometimes controlled by the date of sowing. If sown too late they flower together with full-grown plants sown earlier. This is a fact well-known to agriculturists (in Java e.g. in *Hibiscus* spp.).

Precocious flowering may also be caused by poor soil or some

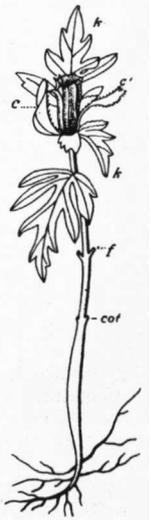


Fig. 5. Precocious flowering (paedogenesis) in *Melia arguta* DC. (*Meliac.*) (after COSTERUS)

methods of pruning. An example of the former cause is *Osbeckia pusilla* ZOLL. which is a flowering dwarf of *O. chinensis* L. on poor soils.

Sometimes dwarfed plants flower when very small and represent distinct varieties or strains, e.g. the dwarf of *Canangium odoratum* BAILL. f. *pumila* (3) grown in pots in Malaysia (introduced

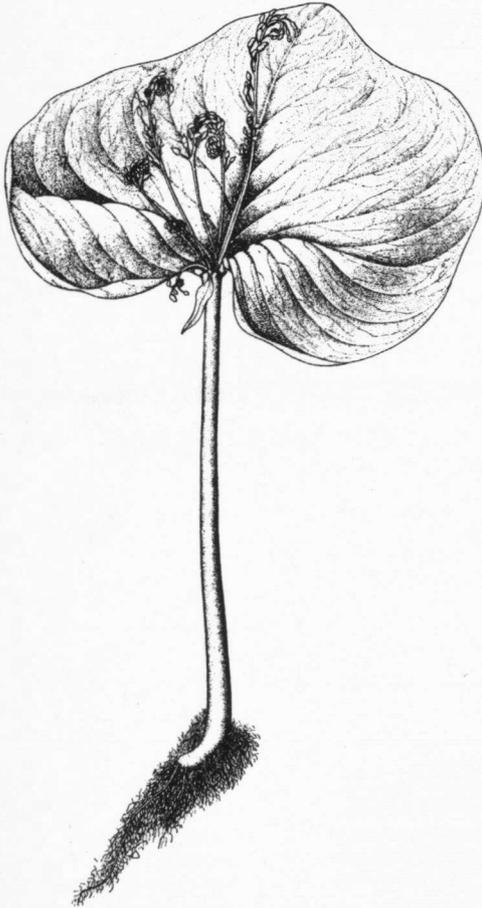


Fig. 6. *Monophyllaea horsfieldii* R.Br. (*Gesn.*), adult plant, one cotyl large and leafy, the other (in front) bract-like, soon disappearing (W. Java, Kalapa Noenggal), $\times 2/5$.

from China), *Aglata odorata* LOUR. var. *microphyllina* DC., and a dwarf of *Punica granatum* L. The skill of Chinese and Japanese horticulturists in raising dwarfs is due partly to the selection of pygmy varieties but more important is their skill in impoverishing the plant without starving it (4).

Many dwarfs are found near solfatara, on rocks, and on silicious soils (cf. § 15-16).

Flowering juvenile forms are comparable to the neoteny found in the animal kingdom.

Pteridophytes generally are apparently more plastic with regard to precocity than *Phanerogams*,

and several species are known to form spores in dwarf or juvenile specimens which have sometimes been described as distinct species. It has been assumed that pygmy species in *Antrophyum* may possibly represent neotenuous stages of other species. COPELAND described in 1939 (5) a dwarf fern from Borneo as *Holttumia*, but it is Dr DONK's contention that this fern is a precocious stage of a *Taenites*. In the genera *Teratophyllum*, *Stenochlaena* and *Lomariopsis*, HOLTUM (6) was able to demonstrate that a great deal of confusion is caused by the description of juvenile stages; being familiar with the living plants in the field he clarified the true status and affinities of a number of obscure species.

DIELS (7) compiled an instructive book on juvenile forms, giving instances where the juvenile foliage persists in the mature flowering plant, a course of development comparable to neotenuous forms in zoology. Australian and New Zealand botanists have written a great deal about this phenomenon of heteroblasty which in those floras has apparently an important bearing on speciation (8). I cannot remember a Malaysian plant suspected to represent such a case. Yet such strange plants as *Monophyllaea* (fig. 6) and allied genera of the *Gesneraceae* living on the enlarged cotyledons might be examples.

Cited literature: (1) Rec. Trav. Bot. Néerl. 1 (1904) 128. (2) De Trop. Natuur 1936, Jub. uitg. p. 73. (3) Now described as a separate species *Canangium fruticosum* CRAIB (Kew Bull. 1922, p. 166) being cultivated in Siam. (4) Compare F. A. McCLURE, in Lingn. Sci. Journ. 12 (1933) Suppl. p. 119-149. (5) Philip. Journ. Sci. 74 (1941) 153-156. (6) Gard. Bull. Str. Settlm. 5 (1932) 245 seq.; *ibid.* 9 (1937) 139 seq. (7) Jugendformen und Blütenreife im Pflanzenreich 1905. (8) cf. COCKAYNE, 13th Meeting Australas. Ass. Adv. Sci. (1912) 217 seq.

3. *Dimorphous foliage*

It was observed by F. W. WENT (1) that in trees generally the foliage of the lower branches is larger than that of the upper twigs. He ascribes this to the amount of water available to different shoots (internal water-conducting capacity); so, in mature trees the upper foliage would be insufficiently provided with water. The leaves of water sprouts, on the other hand, are mostly exceedingly large as their water supply is abundant. Leaves of these shoots are mostly hardly recognizable in the herbarium, as they may reach disproportionate dimensions. Foliage for description in the herbarium ought therefore to be comparable and preferably that of flowering twigs.

The dimorphy of the foliage is mostly linked up with a difference between flowering and non-flowering parts of the plant, similar to that found in *Hedera*. It is conspicuous in several climbing *Ficus*, *Piper*, *Araceae*, and in some *Conifers*. A striking example of plagiotropically flowering twigs is that of *Abroma angusta* L.f.

A good illustration is also *Luvunga sarmentosa* (BL.) KURZ (*Rutaceae*). The stem shoots of this

liana possess large straight axillary thorns and 1-foliolate leaves. The climbing shoots, however, possess conspicuously curved thorns and 3-foliolate leaves and the flowering parts of these are often unarmed. *L. eleutherandra* DALZ. was based on a type different from BLUME's but is actually the same species, as was found by KURZ (2).



Fig. 7. Heterophylly in *Ficus deltoidea* JACK (= *F. diversifolia* BL.) (Morac.), Mt Gedeh, W. Java, $\times \frac{2}{3}$.

Putting into practice what he had read of *Hedera helix* in a botanical manual, Mr BOLT made a remarkable application of the dimorphy of *Piper cubeba* L. Near Semarang, instead of cultivating it as a climber he took cuttings of the flowering twigs, and got shrublets which, though small, produced abundantly 'tail pepper'.

Plants with dimorphous foliage are very numerous in Malaysia and species are frequently named after this peculiarity. *Ficus deltoidea* JACK (= *Ficus diversifolia* BL., fig. 7) is one of them; L. VAN DER PUIJ (3) could not find any regularity in its heterophylly. In *Faradaya dimorpha* PULLE from New Guinea there are two kinds of twigs, with decussate and with 3-whorled leaves of different shape. *Phytocrene macrophylla* BL. has both entire and 3-lobed leaves on one individual, as have *Broussonetia sumatrana* MIQ., *Knema heterophylla* WARB., several species of *Gmelina* and *Sterculiaceae*, *Tiliaceae*, *Artocarpus varians* MIQ. A good case is also *Uvaria picta* Desv. (fig. 8). Heterophylly is common in ferns.

Polymorphy in leaf shape among different individuals of a population is a subject which ought to have a separate heading. It is of universal occurrence in the Malaysian flora, and has (e.g. in *Cucurbitaceae*) given rise to a multiplication of names. In *Coccinea*, MIQUEL (4) distinguished two species, one with incised leaves and one with angular entire leaves: according to BACKER they are identical, the incised leaves mostly belong to juve-

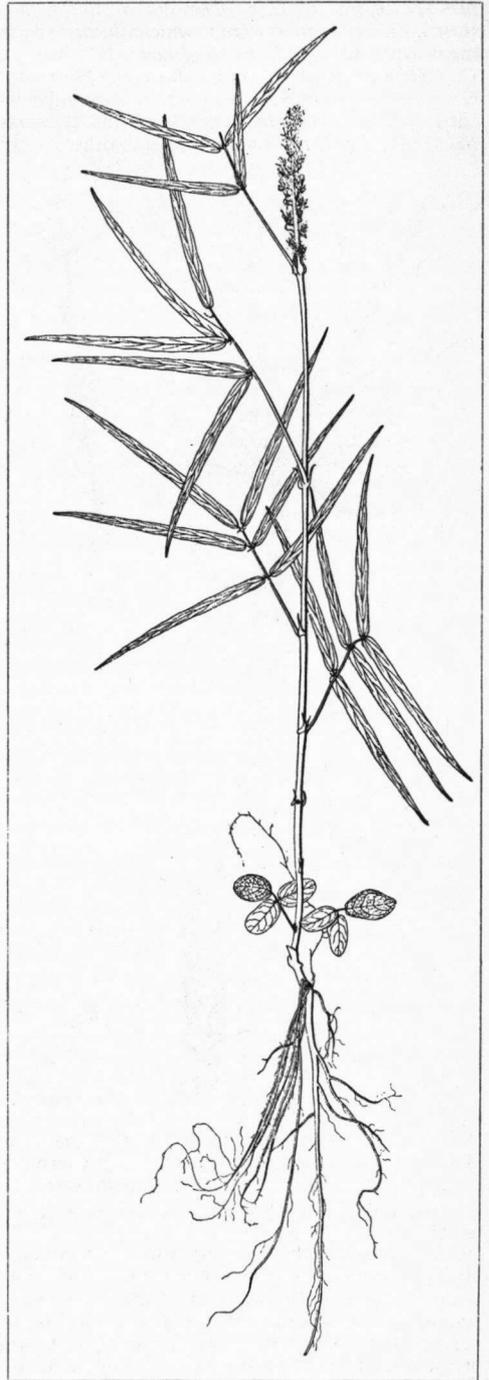


Fig. 8. *Uvaria picta* DESV. (Legum.), with heterophyllous foliage, Kangean Island, moist Imperata fields at low alt., $\times \frac{1}{2}$.

nile specimens. In *Gymnopetalum cochinchinense* (LOUR.) KURZ there is even more confusion: specimens with incised leaves have been described as *G. septemlobum* MIQ., *G. quinquelobum* MIQ. and *G. quinquelobatum* COGN., those with angular or entire leaves as *G. piperifolia* MIQ. and *G. horsfieldii* MIQ. There is probably a host of other names



Fig. 9. Macrobiocarpy in *Callistemon speciosus* DC. (*Myrt.*) with 3 sets of fruits below the terminal bud, originating from 3 previous flowering periods, $\times \frac{1}{4}$.

for this species which is very variable in foliage. In *Trichosanthes* a similar polymorphy of the foliage caused superfluous description of species. *Tr. grandiflora* BL. is, according to BACKER, a form of *Tr. globosa* BL. with lobed leaves. In *Gynostemma* CLARKE and BACKER assume a variability in foliage (3-foliolate to pedately lobed leaves) which will cause a considerable reduction of the number of species. Similarly scores of superfluous names are found in polymorphic species such as *Urena lobata*

L. etc. In the *Oleaceae*, *Nyctanthes dentata* BL. is only a dentate-leaved form of *N. arbor-tristis* L.

In some Pteridophytes heterophyllous leaves are well known. The most striking examples occur in the genera *Teratophyllum*, *Stenochlaena* and *Lomariopsis* where according to HOLTUM (5) heterophylly has caused much taxonomic confusion. An other striking case is that of the plant which is mostly cited as *Lindsaya repens* (BORY) BEDD. as demonstrated by W. TROLL (6).

Cited literature: (1) Handel. 5e Ned. Ind. Nat. Wet. Congres (1928) 385-392 (1929). (2) Journ. As. Soc. Beng. 39 (1870) 69. (3) De Trop. Natuur 27 (1938) 89. (4) Flora Ind. Bataviae 1, 1 (1855) 673. (5) Gard. Bull. Str. Settle. 5 (1932) 245; *ibid.* 9 (1937) 139. (6) Flora 126 (1932) 408.

4. Dimorphous seeds and fruits

Of *heterocarpy* (1) only few examples are known in the Malaysian flora. In some *Compositae* the marginal fruits are sometimes strikingly different from those produced by the central tubular flowers, as was described for *Synedrella nodiflora* GAERTN. by A. ERNST (2). It is also known that in *Tragia volubilis* L. normal and 2-hooked one-seeded fruits may occur together.

In *Umbelliferae* normal fruits and fruits with one half reduced may sometimes be observed.

In *Leguminosae* also different types of fruit are sometimes found on one plant. In *Desmodium heterocarpum* DC. the lower pods are 1-seeded, the upper 5-7-seeded.

Dimorphous fruits and seeds are known in *Aeschynomene spp.* and in the genus *Jussiaea*.

One of the most curious cases of dimorphous fruits is that detected by BACKER (3) in the common *Acalypha indica* L. in Java where the tip of the male spikelets is crowned by a single female flower developing into a T-shaped fruit with a central fertile and 2 lateral sterile cells; the central cell seems to be sunken in the tip of the axis of the rachis. The normal capsule consists of 3 equal cocci.

A special case is that of *macrobiocarpy* (4) when not all fruits dehisce at the end of the season but a number remain closed on the plant and grow for years larger and woody. Sometimes fruits of 3-4 seasons are found on one twig, which thus keeps a reserve of seeds. Macrobiocarpy seems to be mainly restricted to the semi-arid climates and is of definite advantage in fire-swept areas. It is very common in some genera of capsular *Myrtaceae* (fig. 9), viz *Leptospermum*, *Eucalyptus*, *Melaleuca*, *Agonis*, *Metrosideros*, *Syncarpia*. It possibly also occurs in some *Proteaceae*, *Coniferae*, *Casuarina*, and some *Rubiaceae*.

The woody structure, large size and modified shape of the fruits formed in previous seasons must be allowed for in identifying the species. Inadequate material may cause considerable confusion.

Cited literature: (1) DELPINO, Mem. R. Ac. Sc. Inst. Bologna V, 4 (1894). (2) Ber. Deutsch. Bot. Ges. 24 (1906) 450-459. (3) Onkruidflora Jav. Suiker. (1930) 406-407. (4) WINKLER, Ann. Jard. Bot. Btzg 20 (1905) 37-41.

5. Dimorphous flowers

A most peculiar case of flower dimorphy occurs in some *Orchidaceae* viz in *Renanthera lowii* RCHB. f. (1) and *Grammatophyllum speciosum* BL. (2). The shape and colour of the lower flowers in a raceme are very much different from those of the upper ones. In these Orchids the occurrence of aberrant lower flowers is a normal phenomenon. It seems also to occur in some species of *Arachnis* and less obviously in some species of *Bulbophyllum*.

In *Oberonia imbricata* LINDL. the upper flowers of the spike are abnormal and their gynaeceum is reduced.

Dimorphous flowers are also frequently found in dioecious and polygamous plants. Male and female flowers are sometimes very different in shape and size, e.g. in *Mangifera*, *Brucea*, *Hevea*, &c.

In thyrsoid inflorescences the marginal flowers are often different from the central ones, or sometimes the central ones are reduced or deformed. A conspicuous instance is *Mussaenda* where some flowers of the inflorescences have one calyx lobe large and leafy. Other cases are found in *Hydrangea*, *Sambucus javanica* REINW., some *Umbelliferae*, some *Araliaceae*, e.g. *Boerlagiodendron*, and some *Mimosaceae*.

Cited literature: (1) WINKLER, Ann. Jard. Bot. Btzg 20 (1906) 1. (2) COSTERUS, Dodonaea 6 (1894) 24.

6. Cleistogamous flowers

Cleistogamous flowers occur frequently in the Malaysian flora. A general survey has hitherto not been compiled.

They were described in *Clitoria* by HARMS (1) and RANT (2) where they are sometimes more frequent than normal flowers. The description of specimens with cleistogamous flowers has led here to phyto-graphical confusion: the American genus *Martia* LEAND. SACR. was based on a cleistogamous leguminous plant which is, actually, according to BENTHAM and HARMS (*l.c.*) nothing but the cleistogamous state of *Clitoria*.

Cleistogamy also occurs in Malaysian species of *Viola*. It is stated by BECCARI (3) to occur in several Bornean *Annonaceae*.

A very typical example is described in *Commelina benghalensis* L. by J. VAN WELSEM (4): cleistogamous flowers are present on subterranean shoots.

Another well known case in a common plant is *Ruellia tuberosa* L. mentioned by VAN WELSEM (5) and A. F. G. KERR (6).

Cleistogamous (better: *cleistopetalous*) flowers are common in *Orchidaceae* as J. J. SMITH and R. SCHLECHTER both frequently mentioned. The former gives a list of cases known to him in connection with his experience on autogamy (8); the latter studied the occurrence of cleistogamy especially in New Guinea (7) and found it in several genera, and both in the lowland and in the mountains. Sometimes in several specimens all the flowers are cleistogamous, e.g. in *Eria rugosa* LINDL. and *Dendro-*

bium gemellum LINDL. SMITH even found species which are only known in the cleistogamous state (8, p. 138), or of which normal flowers have only occasionally been found.

SMITH suggests that cleistogamy is more common in the rainy season, and he mentions that R. SCHLECHTER also got the impression that cleistogamy was common in very wet places in Sumatra and in the mossy forests of New Guinea more frequent in the rainy season than in the dry period. The same phenomenon has been observed by C. A. BACKER (9) for cleistogamy in *Dicliptera canescens* NEES (*Acanth.*) in Java; in moist countries or during wet periods in the dry season this plant produces minute white cleistogamous flowers the corollas of which drop in the early morning.

It is certainly noteworthy that a single trivial character like cleistogamy can so upset taxonomical judgment that a new genus has been based on this abnormal state of a plant; this character changes the whole floral development, and suppresses the manifestation of numerous genome tendencies in the mature plant. Physiologically this can only be explained by some break in the physiological chain reactions in an early stage of the development of the flower. The field observations mentioned above may show how this problem may be studied experimentally.

Cited literature: (1) Ber. Deutsch. Bot. Ges. 25 (1907) 165-176. (2) Ann. Jard. Bot. Btzg 44 (1935) 239-242; Bull. Jard. Bot. Btzg III, 4 (1922) 241. (3) Wanderings in the great forests of Borneo (1904) 402. (4) De Trop. Natuur 4 (1915) 142; see also BACKER, Handb. Flora Java pt 3 (1924) 25. (5) De Trop. Natuur 2 (1913) 53-58, 68. (6) Journ. Siam Soc. Nat. Hist., Suppl. 10 (1935) 66-67. (7) Die Orchid. Deutsch Neu Guinea, FEDDE, Report. Beih. 1 (1914) p. 1-li. (8) Natuurk. Tijdschr. Ned. Ind. 88 (1928) 122-140, Orch. Rev. 37 (1929) 75, Nova Guinea 14 (1929) 359. (9) Onkruidflora Jav. Suiker (1931) 676, *in nota*.

Teratologo-morphosis

7. Teratological forms

Malaysia can boast of a series of good articles by J. J. SMITH & J. C. COSTERUS (1) dealing with teratological phenomena in plants.

Though several of these teratological forms are due to some hereditary factor, others are apparently caused by external factors. Some are possibly the result of a fungus's attack though no fungus has been found.

Pometia pinnata FORST. almost always has peculiar large brown structures like witches' brooms by which the tree can easily be recognized in the riverine forest: they suggest inflorescences.

Invirescentia are quite a common phenomenon in several *Compositae* (fig. 10); the fact that they are often found together in colonies in several different species suggests that they may be due to some virus (?).

Monstrous flowers occur rather frequently in *Orchidaceae* and have often confused systematists.

J. J. SMITH (2) has given an interesting account of them. The absence of a rostellum is closely connected with autogamy. As a result the flowers often hardly open, do not develop well, and their colour is paler than normal e.g. in *Phajus tankervilleae* BL.



Fig. 10. Invirescence of *Emilia sonchifolia* DC. (Comp.) from Mt Abang, Bali, sandy riverbed, ca 1000 m, $\times \frac{1}{2}$.

Sumatran specimens are apparently more normal than Javan. Of quite a number of these abnormal *Orchidaceae* no normal specimen is as yet known.

Another abnormality is a variation in the number of anthers, which, in *Dilochia pentandra* RCHB. f., is five; this 'species' is, however, a mere form of *D. wallichii* LINDL. In other cases the third stigmatic lobe is changed into a rostellum and the rostellum has become a stigmatic lobe.

J. J. SMITH remarks that the phenomenon of peloria occurs in different degrees. Mostly the peculiarities of the labellum disappear, sometimes the tepals show some characteristics of the labellum. As peloria is for the most part inherited these

forms are treated in more detail in the following chapter, paragraph 2.

Teratological aberrations frequently cause such large changes in the structure of flowers that they strongly suggest some taxonomic novelty. An additional example is: an interesting 3-seeded coconut (3). DE WIT & POSTHUMUS collected at Buitenzorg, Sept. 1944, a specimen of *Cassia mimosoides* L. of which each flower possessed 2 ovaries. This character is considered to be primitive or ancient in the *Leguminosae*; it has been reported to occur in several *Caesalpiniaceae*, e.g. in African *Schwartzia* (6) and Indian *Caesalpinia* (7). In *Archidendron*, a genus of *Mimosaceae* centred in New Guinea, it is a generic character.

Monstrous forms occur frequently in *ferns* where the plasticity seems greater than in *Spermatophyta*. Forked, lobed, and crisped leaves occur in many genera. Sometimes these monstrosities seem to be inherited and of racial rank (4). Even precocious spore formation may be partly inherited.

Teratological aberrations merge gradually into *individual variations*. It is questionable whether an individual of *Cassia mimosoides* L. with two ovaries is to be classed as a teratological or individual variation.

I will mention only a few examples of individual variation. MELCHIOR found (5) some flowers in *Aphania masakapu* MELCH. with free anthers. BACKER found individuals of *Alysicarpus rugosus* DC. with 2-3-foliolate leaves. The leaves of *Cissampelos pareira* L. are sometimes both peltate and non-peltate in one plant. Some specimens of *Amaranthus spinosus* L. are unarmed.

There is no end to this kind of individual variation which sometimes affects typically structural characters. Experiments are needed to ascertain whether these aberrant plants are sports of the genom and hereditary or not.

Cited literature: (1) Ann. Jard. Bot. Btzg vols 13, 19, 23, 24, 28, 29, 32, 33, 39, 42 (1895-1931). (2) Natuurk. Tijdschr. Ned. Ind. 88 (1928) 122-140. (3) Natuurwet. Tijdschr. Ned. Ind. 101 (1941) 144. (4) O. POSTHUMUS, De Trop. Natuur 25 (1936) 177-178. (5) Notizbl. Berl.-Dahl. 10 (1928) 277. (6) JACQUES-FÉLIX, Bull. Soc. Bot. Fr. 92 (1945) 158. (7) WIGHT & ARNOTT, Prod. Fl. Pen. Ind. Or. (1834) 281.

Hypselo-morphosis

8. Phenotypic effect of altitude

G. BONNIER, and later F. E. CLEMENTS, experimented on the effect of altitude on plants. BONNIER even assumed that species might change under prolonged exposure to different conditions into other species but it seems that his experiments are untrustworthy (1).

In the Malaysian mountains where collectors are often compelled to follow ridges, plants from exposed situations are frequently brought home. Their foliage is often reduced, the leaves roundish, margins recurved, texture coriaceous, venation prominent, petioles reduced, habit compact. It is

not always certain that these characters are a 'normal feature' of the species. It is, therefore, of the greatest importance to try to collect such species from less exposed habitats (light, wind, poor soil), *i.e.* from the more fertile, sheltered, though less



Fig. 12. *Histiopteris alte-alpina* v. A. v. R. (Polypod.), an altitudinal form of *H. incisa* J. Sm., in its habitat between 'sterile' rocks on the summit of Mt Kerintji, W. Sumatra, ca 3750 m alt. (FREY WÜSSLING)

accessible slopes. Extensive notes and large collections may show that such variability exists and serve to define the position of transitional specimens. The same species may be a crooked gnarled shrub when growing on a ridge and a moderately tall tree 50 m lower on the slope.

The dwarfing of trees towards the summits of mountains and ridges is chiefly due to the gradual disappearance of the bole with increasing altitude. This is partly a consequence of the development of the young plants under a gradually increasing light intensity which stimulates branching close to the base. I observed a striking example in the field of dwarfing in *Casuarina junghuhniana* MIQ. on Mt Soeket, Idjen volcano, E. Java. Herbs too are generally dwarfed at high altitude, *e.g.* *Erigeron linifolius* WILLD.

I studied an instructive case of variation induced by altitude combined with poor rocky soil in the grass *Isachne pangerangensis* Z. M. (fig. 11). A large series of transitions from tall to dwarfed specimens were represented.

An example of a 'hypselo-morphosis' which has been described as a local-endemic species is that of the fern *Histiopteris alte-alpina* v. A. v. R. (fig. 12) from the summit of Mt Kerintji, West-Central Sumatra, which is found at ca 3700 m alt., on a barren rocky ridge. This is certainly only a form of the common volcanophile *H. incisa* J. Sm.

It is difficult, however, to single out the various factors associated with increasing altitude *viz* more wind, sudden and large changes of temperature, strong insolation, poorer soils, lower atmospheric

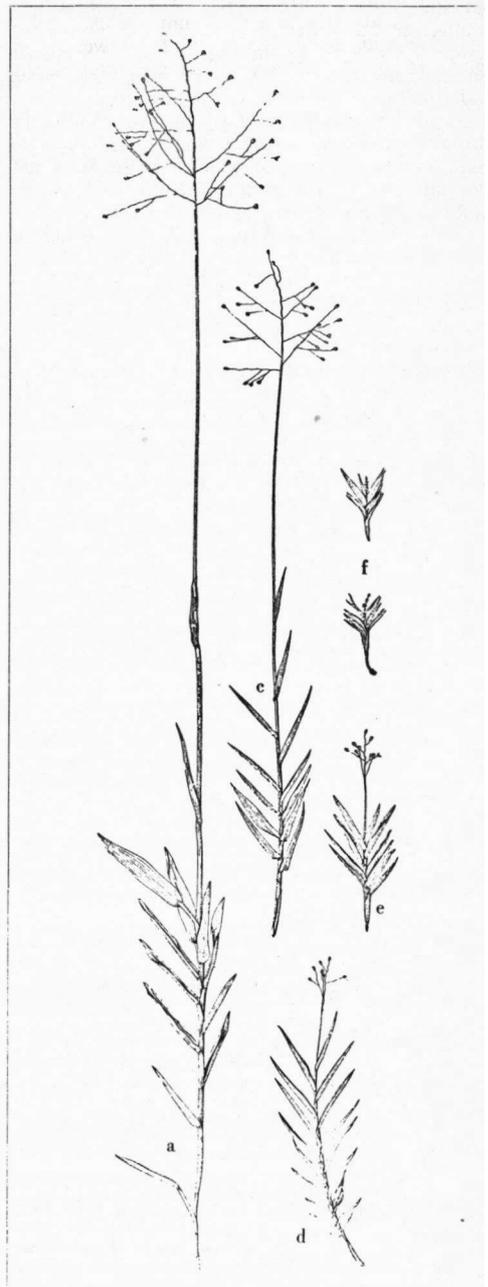


Fig. 11. Variable habit of *Isachne pangerangensis* Z. M. (Gram.) in N. Sumatra, Mt Losir, *a.* on burnt ridge in thick humus, 1500 m, *c.* on ridge with ericoid scrub, half-shade, thinner soil, 2000 m, *d-e.* open sandy flats on poor soil, 3000 m, *f.* on rocky windswept summit, soil nearly absent, 3440 m, $\times 1/4$.

pressure, different fluctuations of atmospheric humidity, greater difference between day and night temperatures, &c. In the absence of experiments one can only make some suggestion, in many cases based on observation in the field only.

I know of only few species which are hairier in the mountains than in the lowland, e.g. *Hydrocotyle sibthorpioides* LAMK, of which BLUME described the hairy form as *H. hirsuta* BL. *non al.* However, glabrous forms of this species also occur on the mountains! An other example is that of *Dodonaea viscosa* (L.) JACQ.

KURZ (2) in his 'Sketch of the Vegetation of the Nicobar Islands' has remarked on the apparent absence of any general relation between hairiness and environment.

There is no general rule that flowers are brighter coloured in the mountains. *Ageratum houstonianum* MILL. has larger capitules and brighter blue flowers in the mountains than at low altitude but on Mt Pakiwang, S. Sumatra, I found the reverse (3), *Scutellaria javanica* JUNGH. var. *sumatrana* BACKER having here blue flowers at the base of the peak but white ones towards the summit.

Of *Dendrobium jacobsonii* J. J. S. (§ *Pedilonum*) from the *Casuarina* forests 2400–2900 m alt. in East Java, J. J. SMITH says that at Bandoeng at 700 m alt. cultivated specimens had smaller and paler coloured flowers with a slightly different flower shape: mentum not bent and differences in the labellum; the inflorescences were, moreover, sometimes 2-flowered (4).

Fruiting and flowering are also strongly influenced by altitude, as I demonstrated elsewhere (5).

Experiments on the influence of altitude, the morphological and physiological behaviour of Malaysian plants have been scarcely made. TEYSMANN made some observations in his pioneer work on Mt Gedeh in West Java but did not comment; COSTER (6) wrote a note on the beech specimen planted by the former.

In the Malay Peninsula RIDLEY (7) made some notes on the acclimatization of plants and the ways in which they can be accommodated at low altitude.

Cited literature: (1) The New Systematics 1940, p. 55 seq. (2) Journ. Asiat. Soc. Beng. new ser. pt II, 45 (1876) 126. (3) Bull. Jard. Bot. Btzg III, 13 (1933) 16. (4) Bull. Jard. Bot. Btzg II, no 26 (1918) 41. (5) Bull. Jard. Bot. Btzg III, 13 (1935) 331–343. (6) Ann. Jard. Bot. Btzg 35 (1926) 105. (7) Agric. Bull. Str. & Fed. Mal. St. volumes 6–7 (1907–08).

Photo-morphosis

9. Epiphytes

It is sometimes wrongly assumed that epiphytism is confined to specific plants which are restricted to this mode of life. The amount of light appears to be the main factor. On the floor of closed forest the shade prevents epiphytes from making use of patches of bare soil, which in primary forest are always present. Exposed places, such as rocks, lava streams, landslides, poor silicious soils, mud

streams and solfatara, however, offer conditions suitable for their growth, and are indeed often the places where many epiphytes are assembled, i.e. selected from the neighbouring forest. Though epiphytes may withstand dry conditions well, they mostly need a rather high atmospheric humidity which, in these exposed places, becomes a limiting factor. Most astonishingly rich communities of epiphytes I found on the often misty slopes of Mt Tèlong in N. Sumatra which from 1800 m upwards is like a rock garden carpeted with normally epiphytic orchids amidst luxuriant dripping cushions of hepatics and mosses with some isolated dwarf *Rhododendrons*. It is sometimes contended that these terrestrial epiphytes are *epilithes* but I have

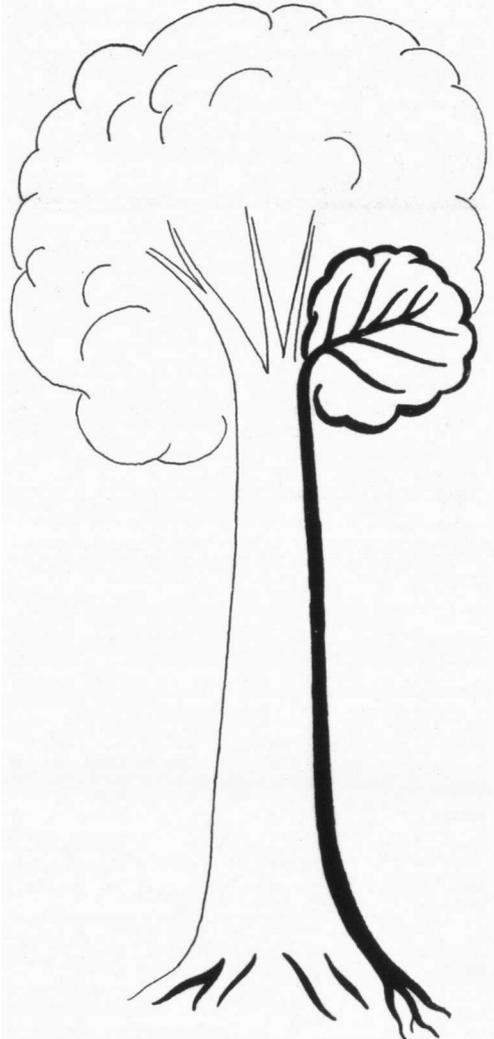


Fig. 13. *Vaccinium laurifolium* MIQ. (*Eric.*) as a hemi-epiphyte, height ca 5 m, along a road above Trètès, 1500 m, N. slope of Mt Ardoeno, E. Java.

also found them in deep humic soil between the rocks. I did not succeed in detecting any essential differences in habit between terrestrial and epiphytic specimens.

In other species, though, the terrestrial speci-

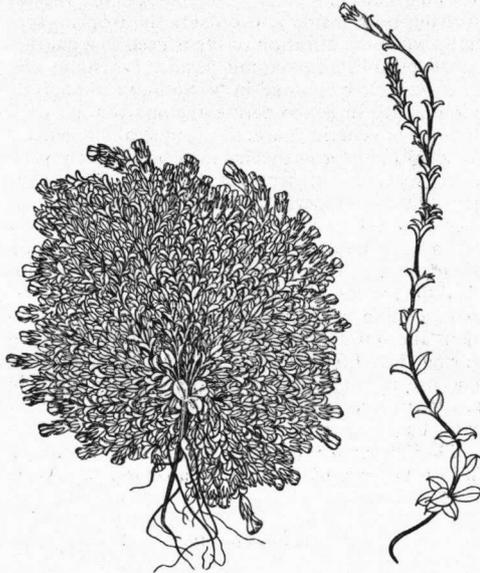


Fig. 14. Habitat variations of *Gentiana quadrifaria* BL. (*Gent.*) in Java. The condensed pin-cushion shape is found on open dry windswept habitats, the loose habit on marshy or slightly shady soil, $\times 1/2$.

mens may differ considerably in habit from epiphytic; they become more rigid and condensed, often fastigate. *Vaccinium lucidum* (BL.) MIQ., as an epiphyte is a loosely and irregularly branched shrublet with a tuberous woody base. Terrestrial specimens on ridges are mostly cupressus-shaped miniature trees without the woody tuberous base. Similar differences are found in *Ficus deltoidea* JACK of which the epiphytic and terrestrial specimens may differ considerably in habit.

It goes without saying that a proposal by NAKAI (2) to distinguish the Ericaceous *Agapetes* and *Vaccinium* by a terrestrial habit in the latter and an epiphytic habit in the former did not meet with the approval of SLEUMER.

Some species begin their life as epiphytes but, when their roots subsequently reach the soil, they may grow into trees and sometimes show no sign of their early history. Such is found e.g. in *Ficus*, *Fagraea*, *Schefflera*, *Wightia* (1), and I even found it once in *Vaccinium laurifolium* MIQ. (fig. 13). Many, however, are equally able to germinate terrestrially and grow normally to trees. This is, in *Wightia*, even more common than the hemi-epiphytic habit. As a small tree it is gregarious on the sunbaked lava streams of Mt Idjen in East Java, but on the forested outer slopes of the same mountain it is a hemi-epiphyte.

Cited literature: (1) Revision of *Wightia*, Bull. Jard. Bot. Btzg III, 18 (1948) in the press. (2) Japan. Journ. Bot. 12 (1936) 37-38.

10. Shade forms

Shade forms are found both in the lowland and the mountains. In general they possess larger, thinner leaves, longer internodes, &c. Shade and normal leaves may occur in one individual. A very good example is *Gentiana laxicaulis* Z.M. described from Java, which appears to be a shade form of *G. quadrifaria* BL. Sometimes compact tussocks of the latter bear on one side shoots of 'laxicaulis' in one individual plant (fig. 14).

Slender modifications of herbs can be observed in tall grass fields, comparable with those in temperate corn fields. These weeds growing in the damp dark micro-climate between the closely set culms of *Saccharum spontaneum* L., *Andropogon amboinicus* (L.) MERR., etc. strive for light. They show reduced leaves and inflorescences in relation to their lank habit. All herbs unable to emerge from the tops of the grasses show a similar habit, a kind of etiolated growth combined with some degree of nanism.

For the effect of light on the habit of forest trees see the paragraph on savannah trees.

Hygro-morphosis

11. Influence of drought

Hardly anything is known of the influence of drought, and the changes induced by it in the morphology and physiology of Malaysian plants. In *Gerbera jamesonii* BOLUS I observed in the dry year 1945 at Buitenzorg an astonishing reduction in length of the peduncles in relation to leaf length. The size of the leaves was very much reduced during the same period in *Turnera subulata* SM. (*T. trioniflora* AIT.).

Similar behaviour is mentioned by BACKER (1) in *Jatropha gossypifolia* L. var. *elegans* M.A., a plant which is thoroughly naturalized in the dry regions of Java and the Lesser Sunda Islands; during the driest period of the dry season only minute, short-petiolate dark-brown leaves are produced.

Flowering of some trees, e.g. *Dipterocarpaceae*, and probably *bamboos* coincides with unusually dry years. Higher fungi fructify after a dry spell.

Cited literature: (1) Onkruidflora Jav. Suiker. (1930) 411.

Hora-morphosis

12. Seasonal variation

Seasonal variation as described in Europe (1) I have not found recorded from Malaysia. In the cultivated *Hibiscus sabdariffa* L. I have seen fruiting specimens flowering a second time; these flowers, however, were only half the normal size and, also, paler in colour. Field botanists should search for 'autumn forms' in periodically dry regions.

Seeds of seasonal plants germinating in the wrong season may sometimes grow into dwarfs. I observed such forms also in *Hibiscus sabdariffa* L. at Buitenzorg. These dwarfs were 10–15 cm high and

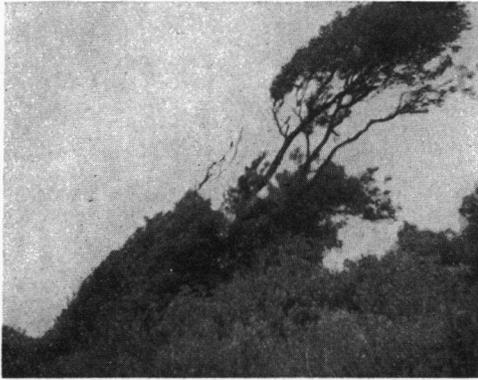


Fig. 15. Oblique, wind-trimmed *Tamarindus indica* L. (Leg.) on a ridge at ca 600 m on Noesa Penida, SE of Bali Island (DE VOOGD)

had 2-3 flowers producing good seeds; the flowers were mostly much smaller than those of specimens flowering in the optimal season.

Of leaf-shedding trees flowers are often collected with immature foliage which may deviate considerably from mature leaves. A peculiar case is that

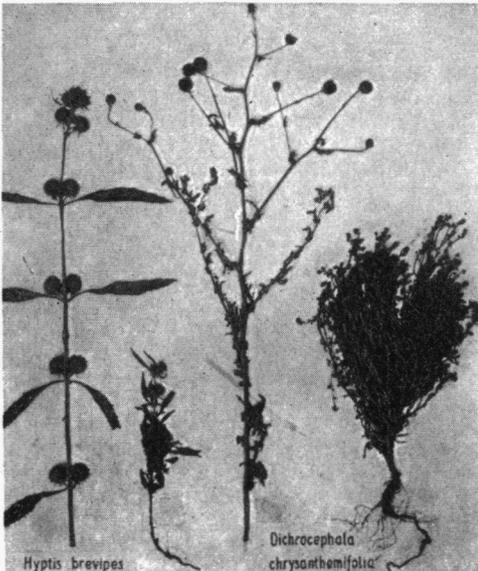


Fig. 16. Compact dwarfing of plants near the fumaroles on the summit of Mt Kembar, Ardjoeno, E. Java, 3100 m alt. Normal specimens left, dwarfed ones right, $\times \frac{1}{3}$.

of some leguminous trees which produce leaves in flushes; the latter consist of pale or white or even pink-coloured limply hanging leaves which only slowly get their normal texture (*Maniltoa*).

The distinction between annuals, biennials and perennials causes many difficulties in species growing both inside and outside the tropics, specially when the duration of life is used as a character to establish taxonomic limits. I assume e.g. *Centrolepis* to be annual in N. Sumatra, though its perenniality in S. temperate regions is used as a distinctive generic character against allied genera. In some *Gramineae* species may be similarly variable, specially in tropical localities, and thus deviate from temperate representatives of the same species in a character which is, in grasses, generally assumed to be of importance for the delimitation of species if it runs parallel with other morphological differential characters. It is puzzling me how it is possible to interpret from herbarium specimens the duration of life of perennials flowering during their first year and collected in that state. The use of the duration of life as a character in keying out species must be limited to very clear cases based on wide experience.

Cited literature: (1) R. v. WETTSTEIN, Unt. ü. d. Saison-Dimorphismus im Pflanzenreiche. Wien 1900. 42 pp.

Anemo-morphosis

13. Windforms

A peculiar aberrant habit in shrubs and trees can be caused by constant winds. I have described this from Noesa Penida and Bali (1) in *Terminalia catappa* L., *Barringtonia asiatica* (L.) KURZ, *Calophyllum inophyllum* L., *Bischofia javanica* BL., *Ficus* sp., and *Tamarindus indica* L. (fig. 15). Other more recent examples are *Dodonaea viscosa* JACQ. near the Wijnkoops Bay, S. Java, and plants from Padang Bolak in N. Sumatra described by M. VAN DER VOORT (2). These plants possess sometimes a peculiar oblique condensed one-sided habit and always show a decreased leaf size apparently owing to desiccation of the buds. They are found both on seashores and inland.

Cited literature: (1) De Trop. Natuur 26 (1937) 69–78, 14 fig. (2) De Trop. Natuur 28 (1939) 201–209.

Edapho-morphosis

14. Fumarole plants

I have described (!) very aberrant modifications from some mountain summits viz Mt Ardjoeno in East Java (2) and Mt Agoeng in Bali (3) at 2900–3000 m alt. Some common lowland weeds, have through chance dispersal by wandering pilgrims and/or by deer established themselves in the immediate neighbourhood of fumaroles. Owing to the heat and moisture emitted by the fumaroles they are able to grow at these high altitudes. They are very much reduced in size and in habit very condensed, and their leaves are very small (fig. 16). Without

flowers their identification would be difficult. They live in what may be called 'open air hothouses' in the subalpine zone, and the altitude, insolation, &c. are doubtless the factors which have induced their



Fig. 17. Dwarf of *Pemphis acidula* FORST. (Lythr.) in flower and fruit, seashore of Oedjoeng Koelon, W. Java, $\times 2\frac{1}{2}$.

aberrant mode of growth and resulted in what seems to be an 'alpine habit'.

The species concerned were: *Hyptis brevipes* POIR., *Dichrocephala chrysanthemifolia* (BL.) DC., *Lycopodium cernuum* L., *Emilia sonchifolia* DC., *Bidens pilosus* L., *Oldenlandia herbacea* ROXB., *Fimbristylis capillaris* A. GRAY, *Lindernia crustacea* F. v. M.



Fig. 18. Full-grown specimen of *Pemphis acidula* FORST., NE. coast of P. Tioman, Mal. Peninsula. (CORNER)

Cited literature: (1) The Gard. Bull. Str. Settlem. 9 (1935) 63-69. (2) De Trop. Natuur 23 (1934) 119-120. (3) De Trop. Natuur 25 (1936) 158-159.

15. Rock plants; calcareous and silicious soils

Both rocks and silicious soils may bring about rather conspicuous changes of habit in some plants, apparently owing to the small amount of nutrients available. These modifications can occur either at low or high altitude.



Fig. 19. Flowering and fruiting dwarf of *Leptospermum flavescens* J.SM. (Myrt.) on dry sterile sands of Toba highlands, Central Sumatra, in a heath-like vegetation, $\times \frac{1}{2}$.

Mr C. N. A. DE VOGD collected dwarf specimens of *Pemphis acidula* FORST. (fig. 17) on the rocky coast of SW. Java resembling subalpine 'Spaliersträucher'; normally this littoral species is a bush or small tree (fig. 18).

On the so-called 'padangs', the gravelly or sandy flats of various geological history which sometimes occupy large areas in Sumatra and Borneo, many species are dwarfed: *Leptospermum flavescens* SM. when growing under optimal conditions is a medium sized cedar-like tree (fig. 20); here it is a dwarf, 10-20 cm high, which flowers and fruits abundantly (fig. 19). Many other species behave similarly. If herbarium specimens are not provided with good field notes, a botanist who has never visited the tropics is of course confronted with a puzzle. He may even find some other slight charac-

ter not known to occur in the normal population and may think that they represent a different species: in this way another 'paper species' is created. Residents in the tropics ought to experiment with seeds gathered from dwarf individuals. Abandoned mining grounds in Banka, Billiton and Borneo are rich in dwarf forms of the most diverse species, which flower precociously as very small individuals (1).

flowers, an unusual character in the species (2). Though no experiments have been made it is likely to be an edaphical form only.

Scores of dwarfed species, mostly of shrubs or small trees but also of herbs (e.g. *Dianella nemorosa* LAMK. f. *nana* SCHLITTL. from Camarines and *f. monophylla* SCHLITTL. from New Guinea) occur in the Philippine Islands, and especially in New Guinea on ridges in the mossy forest and the sub-

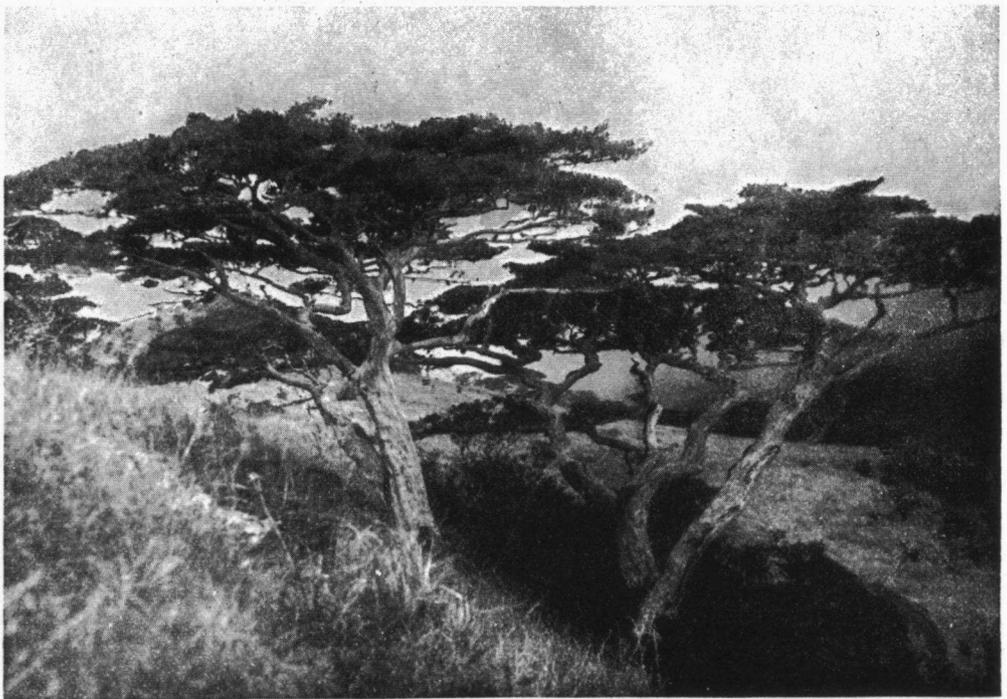


Fig. 20. Full-grown specimens of *Leptospermum flavescens* J.Sm. (Myrt.) on the slopes of Mt Bonthain, SW. Celebes. (L. VAN DER PIJL)

On poor unweathered volcanic ash on the slopes of mountains the vegetation as a whole is dwarfed, e.g. on the slopes of the easily accessible Mt Lamongan, E. Java. Here the black gravel and sand is continually rejuvenated and gradually runs down. On these ash slopes all the common Javan mid-mountain trees and shrubs are dwarfed but flower and fruit profusely e.g. *Radermachera gigantea* (BL.) MIQ., *Parasponia parviflora* MIQ., and *Weinmannia blumei* (BL.) PLANCH., &c. flower and fruit on 1-2 m high shrubs. This observation induces me to suspect that *Radermachera brachybotrys* MERR. from Leyte merely represents a dwarf specimen of some other species; KORTHALS found a similar specimen in the padangs of Borneo.

I have also found dwarfs on wooded limestone cliffs in NW. Bali at 100-200 m mostly of herbaceous species. One of them was so aberrant that I described it as a new variety, *Anisomeles indica* (L.) O.K. var. *biflora* STEEN.; this had solitary

alpine zone. No experiments have been done and the 'normal' habit of these plants is thus unknown.

On rock cones, e.g. Mt Idjen, E. Java (fig. 21) and Mt Agoeng, Bali, I found *Casuarina* (fig. 22), *Vaccinium*, *Rhododendron* as extremely small shrubs and ascribed this to the very poor soil, though on these cones the influence of climate and soil are not readily separable.

W. TROLL found precocious spore formation in *Gleichenia vulcanica* BL. on Mt Gedeh. This was certainly not caused by altitude but by the locally poor rocky soil. In cracks of rock on the summit Argapoera, of Mt Jang, E. Java, I have collected microphyllous specimens of a *Polygonum* which I originally took for *P. chinense* L. but which DANSER afterwards identified as an aberrant form of *P. runcinatum* DON (fig. 23). On Mt Kerintji were found minute fruiting specimens of *Aralia ferox* BL. which I have distinguished as *f. nana* (3).

Cited literature: (1) TEYSMANN, Nat. Tijdschr. Ned. Indië 32 (1873) 84; DUNSELMAN, De Trop. Natuur 27 (1938) 97-104. (2) Bull. Jard. Bot. Btzg III, 17 (1948) 389. (3) Bull. Jard. Bot. Btzg III, 17 (1948) 394.

16. Solfataras plants

Specimens collected in craters are often of a surprisingly dwarfed habit even when old. SCHRÖTER (1) figured a dwarf plant of *Vaccinium varingifolium* MIQ. of East Java which was probably 50 years old and had the appearance of some alpine 'Spalierstrauch'. At a short distance from these strongly insolated, edaphically dry and often wind-swept barren rocky places on slopes or summits, the same species occurs in hollows or other sheltered places as well-developed shrubs or small trees. The dwarf shrubs of craters are often wholly appressed to the soil (with rooting branches!), with a matted and prostrate habit. Owing to the poisonous gases emitted by the solfataras or effect of the wind on ridges, their surfaces are flat and look as if clipped



Fig. 21. *Vaccinium varingifolium* MIQ. (*Eric.*) as poor prostrate shrubs ('Spaliersträucher') near Kawah Idjen, E. Java, ca 2000 m alt. Exceedingly poor, eroded, very young volcanic soil. This species also grows in the mountain forest on the ridge behind in ca 3-6 m tall trees.

or pruned (2) (fig. 21, 24). The solfataras may shift its outlet and so release these plants from its influence: I found some partly grown into a fresh bush, proving that the plant had recently escaped from the reach of the gases, the prostrate section being the oldest part. The reverse may also occur; erect shrubs may be affected later by crater gases (3) which makes them one-sided (fig. 25).

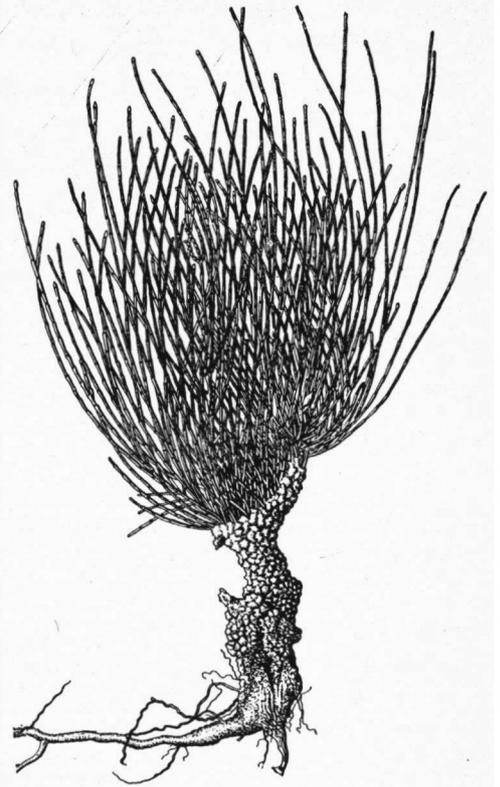


Fig. 22. *Casuarina junghuhniana* MIQ. (*Casuar.*). Old dwarf from the summit of Mt Agoeng, Bali Island, 3100 m, on a rocky windswept cone, $\times \frac{1}{2}$.

Solfataras plants thus represent forms different in habit, and herbarium botanists must handle these materials cautiously. In a general sense the 'poor soil'-conditions cause nanism.

In Malaysia adaptability to habitat and variability in habit under extreme conditions is far greater than the average herbarium botanist suspects. It is difficult to interpret aberrant specimens from remote regions without a thorough field knowledge. Unfortunately this has led to the description of many 'paper species' which may seem specifically distinct but, when studied under various natural environments appear gradually to merge in the range of modifications existing in many Linnean populations.

Cited literature: (1) Vierteljahrshr. Naturf. Ges. Zürich 73 (1928) 584. (2) De Trop. Natuur 24 (1935) 142-144, fig. 2-5. (3) SO₂, H₂S, Cl₂, &c.

Hydro-morphosis

17. Water- and swamp plants

Phenotypic variations comparable to those known in Europe are also known in the Malaysian flora. *Jussieu repens* L., when growing on muddy soil

through the lowering of the water level, changes into a conspicuously different land form with minute hairy leaves and very condensed habit; it takes some time to recognize this land form (1). Land forms are also known in *Potamogeton*, e.g. from Sumatra, and in *Utricularia*.

Of *Neptunia plena* BTH. a land form is known. BACKER suggests that the endemic *N. javanica* MIQ., a terrestrial endemic species in Java, is merely a land form of the common *N. oleracea* LOUR. (2).

Limnophila sessiliflora BL. and *L. indica* (L.) DRUCE, in shallow water, have deeply divided leaves below the surface with gradual transitions to lobed and toothed upper leaves above the water level. In very deep water pinnatifid leaves predominate, but in marshy grass fields only pinnatisect to dentate leaves are present.

The amount of aerenchyma is closely related to the depth of the water.

Many swamp plants fail to flower in deep water, but come rapidly into bloom when the water recedes (*Lemna*, *Blyxa*, *Pistia*, *Azolla*, *Salvinia*, *Marsilea*, &c.).

Swamp forest trees are also affected by the amount of water in the soil. A conical base to the trunk, so well known in *Taxodium*, is found frequently in other swamp species e.g. in *Gluta reinghas* L., *Alstonia spathulata* BL., &c. but, in non-inundated soils, the swollen base of the trunk is not or scarcely developed.

The same is true of aerial roots at the base of the trunk. In deep swamps they may resemble the stilt roots of mangrove. Such roots may not develop in the same species when it is growing on dry land e.g. *Acmena (Eugenia) operculata* (ROXB.) MERR. & PERRY. Root production in these cases is doubtless a direct response to the habitat.

Cited literature: (1) De Trop. Natuur 2 (1913) 83, fig. 3. (2) Schooflora voor Java (1911) 428.



Fig. 23. *Polygonum runcinatum* DON. (*Polygonum*). Below: apex of a normal plant. Above: a very uncommon form of Mt Argapoera (Jang massif, E. Java) from clefts in rocks (St. 10960), $\times 2/3$.

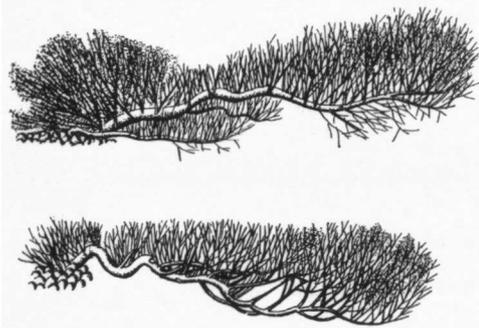


Fig. 24. Sketches of prostrate clipped habit of shrubs in the crater of Mt Papandajan, W. Java, ca 2000 m, through the combined action of wind and sulphurous vapours from solfatara. Above: *Vaccinium varingifolium* MIQ., below: *Rhododendron retusum* (BL.) BENN. (*Eric.*) (drawn after photographs).



Fig. 25. Oblique growth of *Vaccinium varingifolium* MIQ. caused by sulphurous gases of the crater of Mt Papandajan, W. Java, ca 2000 m alt., ca 1 m high.

Phyto-morphosis

18. *Fungus and bacterial diseases, and symbiosis*

Malformations caused by fungi have led to some errors in identifying Malaysian plants. *Loranthus maculatus* BL. is, according to DANSER, the common *Dendrophthoe pentandra* MIQ. with a fungus on the leaves causing black spots (1).

In specimens of *Cassytha filiformis* L. from New Guinea Dr HATUSIMA found some tetramerous



Fig. 26. Pseudo-flowering of bamboo; galls caused by *Epichloe treubii* (Fungi). Bot. Gardens, Buitenzorg, Java.

flowers with a central column marked by little pits. The slender inflorescence was glabrous and the rest of the plant hairy. It was evidently a malformation caused by a *Peziza*-like *Ascomycete*.

Root deformities caused by *Cyanophyceae* are found in *Jycas*, *Gunnera*, &c.

Structures like witches' broom are often found in bamboos, and often regarded as immature flowering parts. These pseudo-flowers are galls caused by a fungus (fig. 26).

A curious malformation in *Pilea trinervia* WIGHT consisting of conspicuous swellings of the internodes was described by Mrs WEBER VAN BOSSE (2) and is caused by a parasitic alga: *Phytophysa treubii* W. v. B.

In *Pavetta*, bacteria cause dark often thickened spots in the leaves. According to BREMEKAMP the symbiosis is mostly restricted to particular species. Similar bacteria are found in species of *Psychotria*,

Ardisia, the tips of the leaves of *Smilax*, &c. The presence or absence of bacterial nodules is used in the identification of *Rubiaceae*, a rather singular method.

Cited literature: (1) Compare BOEDIJN, Bull. Jard. Bot. Btzg III, 13 (1935) 497-501, fig. 1. (2) Ann. Jard. Bot. Btzg 8 (1890) 165-186.

Zoo-morphosis

19. *Ant plants (myrmeco-morphosis)*

Several Malaysian plants are inhabited by ants. TREUB (1) proved that the cavities in which the ants live in the tubers of *Myrmecodia* and *Hydnophytum* are also formed in the absence of ants.

In other instances, however, ants presumably bite their way into internodes and remove and carry away the pith. This was shown to occur in *Endospermum moluccanum* T. & B. (*E. formicarum* BECC.) by DOCTERS VAN LEEUWEN (2); I am able to confirm this. DOCTERS VAN LEEUWEN also found some specimens uninhabited by ants. In *Endospermum*, therefore, whether the internodes are hollow or not is certainly not a good specific distinction, though used by PAX in his key to the species of

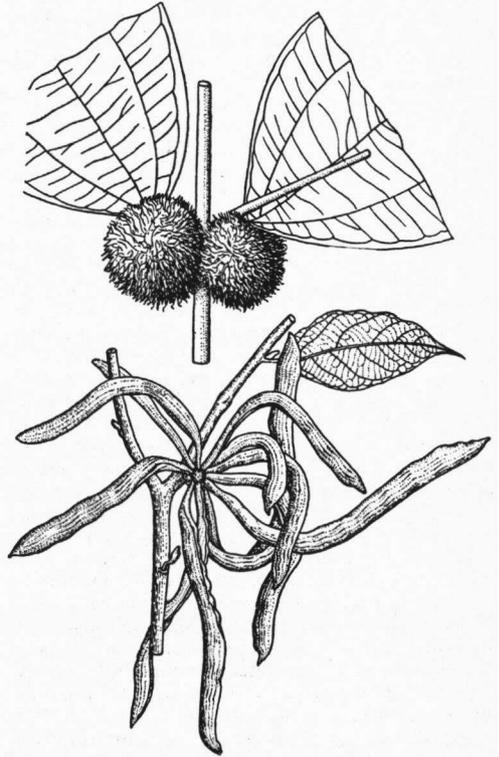


Fig. 27. Above: *Kibessia sessilis* BL. (*Melast.*) being based on a galled swollen fruit of *K. azurea* BL. (W. Java). Below: peculiar galls of *Styrax benzoin* DRYAND. (*Styrac.*) from Sumatra, $\times \frac{2}{3}$.

Endospermum subg. *Capellenia* (3). Moreover, as the other character used by PAX, viz the number of cocci in the fruit, varies from 3–5, through ignorance of data on points the collector ought to have noted on the label, the whole key breaks down.

In *Wightia borneensis* HOOK. f. some individuals are attacked by ants which remove the pith from the upper internodes. The withdrawal of the inner tissue causes the hollow internodes to assume a cigar-like shape.

Cited literature: (1) Ann. Jard. Bot. Botz 3 (1883) 129–153. (2) *Treubia* 10 (1929) 1–7. (3) Pfl. Reich Heft 52 (1912) 34.

20. *Galls deceptive to phyto-graphers* (*cecidio-morphosis*)

Cecidia caused by animals have sometimes deceived botanists when describing plants. An example is *Ceratostachys arborea* BL., a genus based on a galled fruit of *Nyssa javanica* (BL.) WANG.

Kibessia sessilis BL. is merely the galled and enlarged fruit of *K. azurea* BL. (fig. 27).

According to RIDLEY (1) *Apteron lanceolatum* KURZ, described as a distinct genus, is identical with *Ventilago kurzii* RIDL.; KURZ mistook some insect galls for the ripe fruit.

MIQUEL described (2) an abnormal tree from Sumatra which was actually a species of *Styrax*, a genus in which most peculiar galls (fig. 27) are very common.

Otopetalum micranthum MIQ. is an *Apocynaceae* described from Java. According to BOERLAGE (3) the plant was referred to the wrong tribe because MIQUEL erroneously took galled flowers for 1-seeded berries; the former author suspects that it is related to *Micrechites*.

Insects (mostly cicads and larvae of Hemiptera) cause a singular malformation of the flowers in some species of the genus *Sterculia*. H. C. CAMMERLOHER (5) observed that they are attracted to so-called 'sugar hairs' which occur on the inside of the perianth. The insects injure both the hairs and the outer tissue in an early stage of development of the flower. The calyx becomes enlarged, thicker and tough, and opens hardly in anthesis; its lobes remain short and triangular, and the tube is relatively large. These flowers are conspicuously different from the normal 'uninhabited' flowers and, according to ADELBERT (6), ought not to be used when describing or identifying plants.

BACKER (7) described in *Hibiscus schizopetalus* (MAST.) HOOK. f. malformations of the vegetative parts and of the flowers caused by plant lice.

The Philippine species *Euphoria malaanonan* was described by BLANCO and by him referred to *Sapindaceae* but MERRILL stated (8) that it is merely based on specimens of the echinate galls of *Shorea guiso* BL. of the *Dipterocarpaceae*.

W. M. DOCTERS VAN LEEUWEN has published (4) an illustrated book on zoococcidia of Indonesia.

Cited literature: (1) *Flora of the Malay Peninsula* 5 (1925) 300. (2) *Linnaea* 26 (1853) 285. (3) *Hand-leiding Fl. Ned. Ind.* 2² (1899) 380. (4) *The Zoococcidia of the Netherlands Indies, Batavia* 1926;

Supplement, Ned. Kruidk. Arch. 51 (1941) 122–251. (5) *De Trop. Natuur* 22 (1923) 147. (6) In BACKER, *Flora van Java, Nooduitg. IVb* (1944) fam. 107, p. 18. (7) *Flora van Java, Nooduitg. IVc* (1943) fam. 109, p. 27. (8) *Spec. Blanc.* (1918) 33.

21. *Influence of browsing animals* (*pascuo-morphosis*)

In some parts of Malaysia browsing cattle and deer (1) can induce changes in the morphology of plants which might be termed *pascuo-morphosis*. In

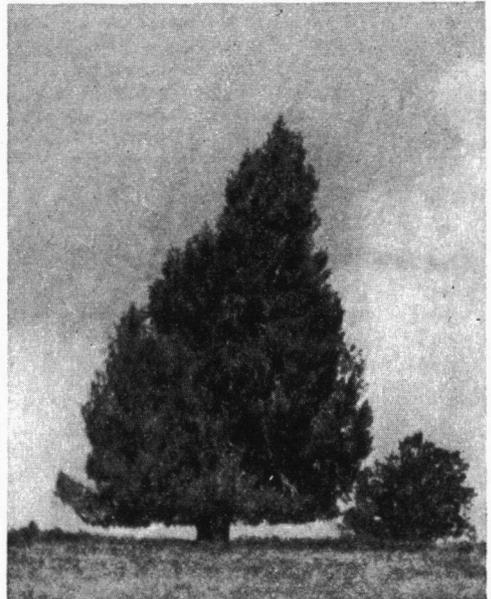


Fig. 28. *Casuarina junghuhniana* MIQ. (*Casuar.*) on Mt Jang, E. Java; crown trimmed below by deer.

the deerpark of the Buitenzorg Palace, deer regularly feed on the pendent air roots of *Ficus* and prevent them from reaching the soil. The trees therefore remain single-stemmed and do not form thickets of pillar-like roots.

A similar effect is caused by deer on Mt Jang, in East Java, where deer eat the hanging branches of *Casuarina junghuhniana* MIQ. as high as they can reach (fig. 28). The trees look as if clipped (2) at the underside of the crown like those on the lawns at Buitenzorg. Much the same was observed on Mt Rindjani, Lombok Island (3). The broom-like appearance of the grass *Pogonatherum panicum* HACK. on Mt Diëng was ascribed to grazing cattle by the late Mr LOOGEN (4), an excellent amateur field botanist.

Browsing of animals has in general the same effect on the vegetation as frequent burning: the plants acquire a low habit and flower at an early age (pseudo-nanism). This occurs very commonly on the closely cropped fields of fine grass of Mt

Jang. It is only in hedges, on steep slopes or somewhere out of reach of deer that plants grow to normal dimensions.

In Central and East Java, and the Lesser Sunda Islands *pascuo-morphosis* is due to browsing of cattle in the dry season; it is known in *Zizyphus jujuba* L., *Streblus asper* L. and other shrubs. These assume a fastigate habit as high as the browsing animals can reach: above about 2 m the twigs are again spreading and form a globular crown.

A transition to anthropo-morphosis is the clipping and pruning of plants which can sometimes produce an aberrant habit. According to BACKER (5) repeated cutting of plants along roadsides produced a peculiar table-shaped densely branched

form in *Sida retusa* L. near Batavia. In the Lesser Sunda Islands cattle are sometimes fed in the dry season with leaves of trees, as is done in Africa. For this purpose the people lop the lower branches of trees in order that cattle may reach the foliage. This causes a tendency to umbrella-shaped trees. Deer may cause the same change of habit.

Cited literature: (1) Mentioned for India by HOOKER & THOMSON, *Flora Indica* (1855) 29. (2) *De Trop. Natuur* 21 (1932) 27. (3) *De Trop. Natuur* 30 (1941) 123. (4) *De Trop. Natuur* 30 (1941) 70. (5) *Flora van Batavia* (1907) 102.

Anthropo-morphosis

22. Influence of fire (*pyro-morphosis*)

The changes in habit and structural characters induced by fire were named *pyro-morphosis* by PERRIER DE LA BÂTHIE who made observations in the island of Madagascar. In Malaysia there are few reliable data. One of the changes induced by regular burning of the vegetation is that plants are stunted, and flower when small.

Owing to the damage done to the surface part of the plant the underground parts thicken, and the upper portion of the rootsystem and lower portion of the stem form gradually a thickened half-subterranean 'lignotuber', which sprouts after fires have swept the plains. I made some observations in the Indramajoe plains (W. Java), where species of *Grewia*, *Butea*, *Dillenia*, *Morinda*, *Phyllanthus emblica*, *Zizyphus*, &c. sprouted from these thickened bases (1) (fig. 29).

Some instances of phytographical importance have come to my knowledge. RANT found (2, 3) that *Psidium cujavillus* BURM. f. can originate spon-

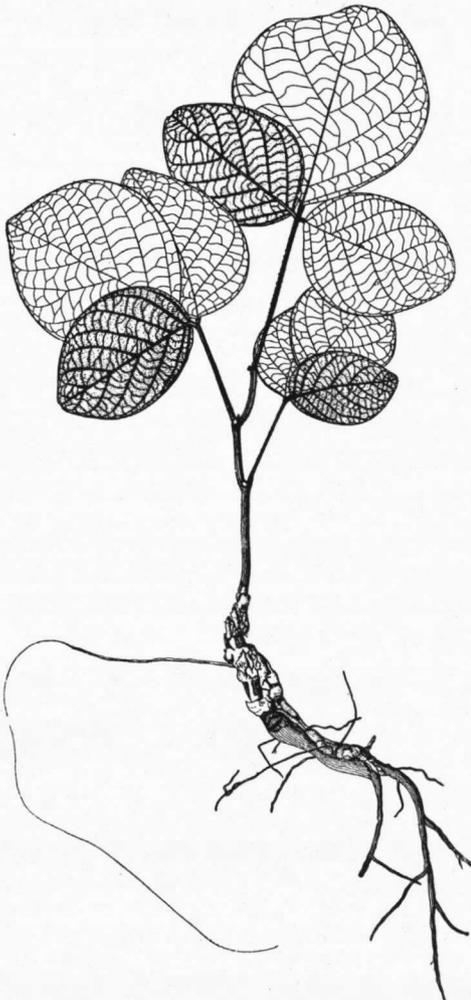


Fig. 29. Seedling of *Butea monosperma* TAUB. (*Leg.*) sprouting in its 3rd year in the fire-swept savannahs of Indramajoe, W. Java, and developing a lignotuber, $\times \frac{1}{3}$.



Fig. 30. Park-like savannah in SW. Soembawa; trees with short boles and rounded crowns. (DE VOOGD)

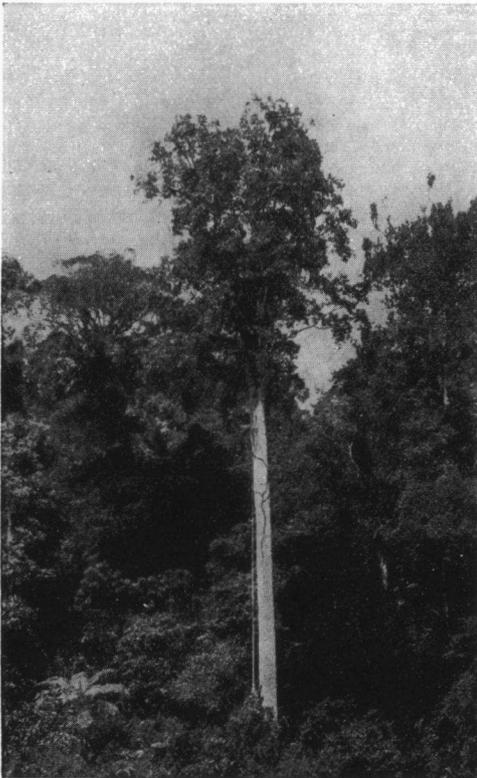
taneously from root shoots of *Ps. guajava* L. It is distinguished from *Ps. guajava* L. mostly by differences of size. *Ps. cujavillus* BURM. f. must, therefore, be reduced to a sport of *Ps. guajava*.

Fire-resistant trees are often crippled beyond recognition. Plants described from semi-arid (4) regions where fires occur annually are sometimes known only in this crippled state, e.g. *Fordia fruticosa* CRAIB, from N. Siam, described (5) as a shrublet 40 cm tall. The late A. F. G. KERR, a most able and experienced field botanist, stressed in a note made in the field that the plant was growing in an area subject to fire; this may explain such a habit in this otherwise arboreal genus. The normal plant will, in all probability, prove to be a tree.

Cited literature: (1) De Trop. Natuur 25 (1936) Jub. nummer, p. 117-118. (2) Ann. Jard. Bot. Btzg 41 (1930) 27-32. (3) Natuurk. Tijdschr. Ned. Ind. 94 (1934) 112. (4) That is: regions which are periodically wet and dry, and show two distinct seasons coinciding with the monsoons. (5) Kew Bull. 1927, 60; Fl. Siam. En. I (1928) 395.

23. Pioneer plants

In the preceding paragraphs 9, 14-16, and 22, several examples have already been given of pioneer



plants. I am decidedly of the opinion that this term should not be restricted to plants peculiar to landslides and other bare soils. Trees settling in savannahs or devastated areas, epiphytes settling on rocks, &c. are just as well 'pioneer plants'. They constitute seral vegetation types. In the initial stages of revegetation forest trees may appear as pioneer shrubs, flowering and fruiting early. It is rather baffling to find *Schima noronhae* REINW. flowering and fruiting as a lax shrub 2 m tall, when one is familiar with the gigantic full grown tree in the forest (height sometimes over 50 m, columnar bole over 1 m diam.). BACKER found (1) near Batavia flowering specimens 15 cm tall of *Grewia microcos* L., usually a tree up to 17 m high. The same phenomenon can occur in *Adinandra*, various *Urticaceae*, *Leguminosae*, *Ulmaceae*, &c. In New Guinea some endemic species were originally described as tall trees but Mr BRASS has recently found them as gregarious pioneer shrubs in different seral vegetation types.

A promising shade plant, *Albizia sumatrana* STEEN., described from the Westcoast of Sumatra, was found to be a forest tree. In the plantations it is a weed tree flowering and fruiting at a very early age. In the forest, its native habitat, flowering is apparently suppressed by the deep shade, the seedlings grow into pole trees, slender and tall with a minute crown and real growth only starts when the crownlet emerges from the canopy. The behaviour and appearance of forest trees when growing in the open cannot be predicted. The adaptive capabilities of most Malaysian forest trees are unknown, though data on these points would be of great importance for practical forestry. See also chapt. 2 on precocious flowering, a phenomenon frequently observed in pioneer plants.

Cited literature: (1) Flora van Batavia (1907) 196.

24. Savannah trees

Trees of the savannah generally differ in habit from trees of the closed forest in their short bole and spherical crown (fig. 30). If young forest trees



Fig. 31. *Altingia excelsa* NOR. (*Hamam*.) at Tjibodas, W. Java, ca 1450 m. Left: forest-grown tree, clear bole ca 25 m. Right: planted on the lawns of the mountain garden, at ca 200 m distance.

in deforested areas become exposed, or when they are planted as roadside trees, they acquire this shape: a striking example is *Altingia excelsa* NOR., a forest giant of the West Java midmountain forest between 600-1600 m. The clear bole is usually a characteristic feature of the tree; it is columnar, up to 1½ m in diameter, and up to 20-30 m from the ground unbranched (fig. 31). Specimens 50 years old, however, planted on the lawns at Tjibodas mountain garden, have grown into low spreading trees with hardly any bole at all (fig. 31). Descriptions of the habit of trees and shrubs taken from specimens grown in private and botanic gar-

dens, will therefore generally not agree with those taken from specimens in the forest. THORENAAR made similar observations in Javan oaks, and other trees such as *Podocarpus imbricata* BL., *Quercus*, etc. The habit of trees grown in open gardens resembles the shape of trees of the savannahs where the rounded crowns on a short bole often characterize the physiognomy of the open savannah forest. Physiologically this tree form is in all probability determined by the high amount of light present during the juvenile stages of growth. The crowns of mature forest giants exposed after deforestation also tend to become rounded.

VARIATIONS BOUND TO THE GENOTYPE

(Genotypic variation)

1. General remarks	xxxix	9. Centres of generic development in Malaysia	lv
2. Peloric flowers	xli	10. Local-endemic species and genera	lvi
3. Other teratological or deviating forms	xlii	11. Parallel or homologous variation	lvii
4. Distribution of the sexes	xliii	12. Reticulate affinities	lviii
5. Geographical segregation of Malaysian specific populations	xliv	13. Vicarism in the Malaysian flora	lix
(a) Ecological	xlvi	14. Adaptation and migration	lx
(b) Regional	xlvii	15. Hybrids in the Malaysian flora	lxii
(c) Topographical	xlix	16. Polyembryony, parthenogenesis and apogamy	lxiv
6. The problem of speciation	li	17. The origin of native aliens	lxv
7. The effect of isolation	lii	18. The origin of Malaysian cultigens	lxvi
8. Centres of speciation in the Malaysian flora	lii	19. Extinct plant groups in Malaysia	lxviii

Variation bound to the genotype is intimately related to the species concept and to geographical distribution. The ideas advanced by J. D. HOOKER in his introductory essay to the 'Flora Indica' (1855) have gained in 'philosophical' importance through the progress of basic research in experimental taxonomy in the last decades in Europe and the United States, in particular by E. BAUR, F. v. WETTSTEIN, N. H. NILSSON, G. TURESSON, A. MÜNTZING, Ö. WINGE, G. D. KARPECHENKO, B. H. DANSER, W. B. TURRILL, J. CLAUSEN, J. P. LOTSY, H. DE VRIES, N. I. VAVILOV, and many others. This work is summarized in several useful symposia and textbooks such as 'The New Systematics' edited by J. HUXLEY, CAIN's 'Foundations of Plant Geography' and CLAUSEN's *c.s.* 'Experimental Studies on the Nature of Species' (1945).

It lies outside the scope of this essay to consider the various view points on these subjects. Some of them I have already touched on in a study of Malaysian mountain plants.¹

Now I will try to explain briefly some current views, including my own, and will illustrate them by examples taken from Malaysian botany.

1. General remarks

Scientific names of species rest on the 'International Rules of Nomenclature' and depend on the identity of the 'type specimen'. This need not imply that only studies in which all type specimens have been

examined, full synonymy is given, in which nomenclature is in accordance with the Rules, and in which new species or other *taxa* have been described by careful Latin descriptions, are sound and durable. I know some excellent works in which nomenclature is neglected and synonymy is obsolete but in which botanical distinction and description are superb, and specific delimitation is carefully drawn. Such books give the impression that the author is master of his art.

I become more and more convinced that in the past two decades the care for outward appearance has come to take a too predominant share of the attention of some botanists who wrongly assumed that the examination of type specimens is the last word in real taxonomical research. It is sometimes not realized that *type specimens often are only deficient, poor and miserably dried single plants chosen at random from billions of specimens growing in Nature in the past, the present and the future*, which, together, according to the Linnean principle, compose the specific population. Very often these type specimens by no means represent the 'average' or 'most common type' of the population. The '*α*-typica'-distinction, therefore, has only nomenclatural, *i.e.* administrative but no botanical value.

It needs no comment that an up to date nomenclature is a *conditio sine qua non* for any taxonomic work, and it will be tried to reach a high standard in this Flora. At the same time, however, is it hoped that the contributors will not be satisfied when writing formally correct revisions, but also carefully consider the status of both genera and

(1) Bull. Jard. Bot. Btzig III, 13 (1935) 358-391.

species and the structural differences distinguishing them, not merely limiting themselves to the distinction of *taxa* for reasons of convenience.

Inadequacy of material and lack of field knowledge are both sources for the provisional distinction of 'species of convenience', which mark, in tropical floras, as a rule the initial stage of exploration.

Whilst the inadequacy of material is an insurmountable obstacle, and not every revisor will have the privilege to acquire field knowledge, a large fund of experience has been collected on the subject of variation in tropical plants.

The following pages contain a discussion, valuation, and illustration of variation in Malaysian plants.

In general the new systematics, based on modern experimental taxonomy holds that a narrow species concept is not in accordance with the structure of nature.

Modern insight offers no support to so-called 'splitters', one of whom declared to me as his 'principle' that he felt obliged to distinguish the smallest distinguishable entities and to assign to these a binomium. On the average the standard of the specific concept proposed by LINNAEUS in his works and rules cannot be questioned and for binomiums the Linnean canon has *priority of conception*. I fail to understand how that conscientious splitter who in matters of nomenclature adheres strictly to priority and applies the binomial system of LINNAEUS can simultaneously call wide-spread polymorphic populations 'collective species'. To do so is intentionally to depreciate the time-honoured and scientifically sound Linnean standards.

The difficulties confronting the systematist are manifold; no clue exists to the causes of polymorphy. Systematists are still far from being able to explain why some species are polymorphic and variable and why others show a narrow amplitude of divergency. This is a fundamental barrier to the methods of 'weighing and measuring', a common basis in the natural sciences generally. Polymorphy is apparently not related to speciation, as monospecific units such as *Homo sapiens*, *Cocos nucifera*, &c. are very variable and species of large genera are sometimes not very polymorphic, though it will be observed that in most genera at least one species is widely distributed and rather polymorphic.

Ignorant of the laws underlying his taxonomic distinctions, the systematist should be aware that he deals with *unequal* entities, though we may try to shape them as consistently as possible.

A basic research in this connection is the work of the late E. BAUR, the geneticist, who made unsurpassed long-range efforts in the combined fields of taxonomy, field-work and experiments, to disentangle the genus *Antirrhinum sect. Antirrhinastrum* (1). This section had some dozens of local species described from the West Mediterranean distinguished by characters which were the despair of taxonomists. BAUR proved that the population of the section falls apart in numerous 'colonies' or 'partial populations' which are isolated and cross

mutually (*convivia, sensu* DANSER). Each colony has its own type, the larger the colony the wider the local diversity (fig. 33c). All these local types can be freely intercrossed with fertile offspring, and there is no doubt that, if not isolated in nature, they would together merge into a still more diverse population with transitions and intermediates. BAUR, moreover, obtained experimentally many forms *not* realized in nature (*l.c.* p. 289), showing that the potential variability (2) or polymorphy (3), *i.e.* the total number of possible forms (genetic capabilities) is not exhaustively represented. There is a *great reserve* of possible combinations, and the genus manifests itself to us at present under a limited number of combinations.

Hardly any plant species is evenly spread within its area, and many occur in aggregates or colonies. BAUR's findings are thus of the utmost value for the Malaysian archipelago where isolation is a normal factor in specific populations, in the lowland owing to the insular discontinuous nature of this region and in the mountains still more accentuated by the often long distances between the summits. We cannot expect that the whole plant world will be subjected to accurate and thorough experimental research like BAUR's *Antirrhinum*-studies, but, judging from his results, it appears that *geographical distribution is an important argument when determining the status of taxa*. Well-defined allied species possess in general overlapping areas of distribution proving the independence of the populations. If, however, several allied species exclude each other geographically one must be on the alert, and check the differential characters again because the specific population may well be differentiated into a number of races, subspecies, or ecotypes.

Especially along the *frontier*—horizontal and altitudinal—of the area, a species population has a different *facies* from that at its centre. KERNER (4) showed that in *Cytisus sect. Tubocystis* aberrant forms occurred along the border of the area (fig. 33e). Migrating plant individuals (seeds, spores, fruits, root-stocks, &c.) carry only a part of the potential polymorphy of the genus, and their offspring will possess a special *facies*. Hence, along the frontiers, combinations can be expected which are not realized within the centre of the population. According to VAVILOV such pioneer aggregates are found to be recessive homozygous; this is of great practical importance.

It is worthy of note, as was pointed out by E. C. ANDREWS (5) that BENTHAM realized long ago that the geographical station of a waif or colonist imposes variations upon it almost from the moment of its arrival. ANDREWS adds, that Eucalypts planted in New Zealand, California, *etc.* present marked differences in general appearance from the same species in Australia.

Stimulated apparently by HOOKER (6), HUGO DE VRIES (7), the Master of experimental taxonomic botany, remarked that the initial stages of new species will be found most easily in luxuriant alien vegetations. His classic example, *Oenothera*, showed these 'mutations'—which they indeed are if the

mutation concept is accepted, in a wide sense, as a discontinuity in the sense of BATESON. In Malaysia, an example is perhaps the occasional occurrence, about 15 years after its arrival as a waif, of a yellow-flowered variety of *Gynura crepidioides* BTH. amongst the millions of specimens which possess the normal brick-red coloured capitules (8).

Anthropogenous *convivia* do not differ essentially in their behaviour from native *convivia*; they are partial populations isolated from breeding with the main population. Through inbreeding the partial polymorphy and the environment together will, in a few generations, determine the final composition of the colony or aggregate, and each *convivium* will represent a special local 'race'. Stray colonists or waifs from such *convivia* will show little differences in general in various localities, their characteristics having already been fixed. An experienced botanist thoroughly acquainted with a species is often able to determine the locality from which a specimen was obtained by means of its appearance.

Several aliens are known only as aliens and most probably represent combinations which do not persist in the parent population. Cultivated plants also are an essentially identical case. Kapok, *Ceiba pentandra* GAERTN., indigenous in the New World, is represented in the Old World by a subspecies, possessing recessive characters, which is not known in the New World (9). *Rumex obovatus* DANSER is a species known only as an alien, a nomad of the plant kingdom. Another example is *Kosteletzkya batacensis* (BLCO) F.-VILL.; according to MERRILL (10) it was certainly introduced from Mexico into the Philippines in post-Columbian time, but is as yet unmatched by any known Mexican species. MERRILL states (11) that *Prosopis vitaliana* NAVES forms dense thickets immediately behind the beach in the Manila Bay region, and is also found in Basilan. It is unquestionably introduced from Mexico, probably from the vicinity of Acapulco, and was reduced to *P. juliflora* DC. by several authors but according to MERRILL it is not identical with it.

The genus *Elephantopus* is certainly not native in the Indo-Australian region; *E. scaber* L., however, is widely spread in Malaysia but found only as an alien (already recorded by BONTIUS, 1629) and apparently not known as a native species in the New World; it is alien there also (12).

A slightly different but interesting case is that of the New World genus *Turnera subulata* SM. (= *trioniflora* SIMS) and *T. ulmifolia* L. s. str. These two taxa, both alien in Malaysia (13), doubtless behave there as quite distinct species. In the West Indies, however, intermediate forms are so numerous that URBAN has not kept the two as separate species.

Among cultivated species selected by chance ages ago is e.g. a nearly etiolated form of *Pisonia sylvestris* T. & B., already mentioned by RUMPHIUS as 'Moluccan cabbage tree' and described as *P. alba* SPAN. It flowers seldom and differs considerably in habit from the rare wild form. Several *Pandanus* species cultivated in Java are unknown

in the fertile state. The cultivated clove, *Eugenia aromatica* O.K. has never been found wild in its native habitat, the Moluccas; the favourite clove of Zanzibar is derived from the Moluccan. The wild form of *Eugenia aromatica* O.K. is quite distinct from the cultigen in its much larger fruits, coarser foliage and lack of oil (9, p. 25). In the *Cucurbitaceae* and *Araceae* many forms are not known in a wild state, and their native country is unknown. The same applies to the *coconut* which is a very variable plant. BECCARI mentions peculiar forms of wild forest palms and other plants which he found selected and in cultivation only near the dwellings of the inland Dyak people in Borneo.

Another still unsolved problem is that of *Helliconia* (*Musaceae*) which occurs semi-naturalized in E. Malaysia. BACKER, who studied it, found that it is was distinctly different from the American species (14). The plant was already recorded by RUMPHIUS.

The taxonomic units of the Malaysian flora next in rank to the genera are the species, that is, the specific populations. Their delimitation must be carefully considered. It is to be expected that the insular character of the Malaysian archipelago, its intricate geography, topography, and climate, and its complicated geological past, have given rise to great ecological variety and furnished ample opportunity for segregation within the limits of species populations. Sometimes adaptive segregation under special ecological circumstances can be traced. The majority of segregational phenomena remain unexplained at present.

In the following chapters some characteristic types of divergence in populations will be considered and examples given of each.

Cited literature: (1) Zeitschr. f. Ind. Abst. & Vererb. 63 (1932) 256-302. (2) HAGEDOORN, The relative value of the processes causing evolution (1921) 104. (3) DANSER, Ann. Jard. Bot. Btzg 40 (1929) 34. (4) Die Abhängigkeit der Pflanzengestalt von Klima und Boden &c. 1869. 48 pp. (5) Proc. 6th Pac. Sci. Congr. 4 (1940) 617. (6) Flora Indica (1855) 30. (7) Über das Aufsuchen von Artanfängen. Veröff. Geobot. Inst. Rübél 3 (1925) 567-570. (8) Current Science 8 (1939) 421; De Trop. Natuur 28 (1939) 173. (9) H. J. TOXOPEUS, Natuurwet. Tijdschr. Ned. Ind. 101 (1941) 23. (10) Enumeration Philip. Flow. Pl. 3 (1923) 41. (11) Enumeration Philip. Flow. Pl. 2 (1923) 251. (12) KOSTER, Blumea 1 (1935) 460. (13) De Trop. Natuur 20 (1931) 227-231. (14) Bull. Jard. Bot. Btzg III, 2 (1920) 315-319.

2. Peloric flowers

In addition to the *teratologo-morphosis* I have tentatively arranged under this heading examples of peloria in Malaysian plants, since these belong—at least partly—to the inherited type of variation. Future experimental breeding experiments will certainly elucidate their significance and *status* of which, at present, we are sometimes ignorant.

Peloric flowers have been described in various articles on tropical teratology by J. C. COSTERUS

& J. J. SMITH (1). They are specially common in Malaysian orchids, and have caused much confusion in phytography. In actinomorphic flowers the spur is absent or nearly so.

The following examples taken from J. J. SMITH's compilation on teratological orchids of Malaysia (2), may serve as illustrations.

A Papuan orchid was described as *Aulostylis papuana* SCHLTR., a new genus. According to J. J. SMITH (3) it is the peloric form of a *Calanthe* (*C. papuana* (SCHLTR.) J.J.S.).

Uropedium LINDL. is synonymous with *Phragmopedilum* ROLFE.

The monotypic *Argyrorchis javanica* BL. (*Macodes javanica* HOOK. f.) is the peloric form of *Macodes petola* LINDL. var. *argenteo-reticulata* J.J.S.

Lobogyne SCHLTR. is a teratological state of *Appendicula* BL.

The monotypic *Chlorosa javanica* BL. is probably a peloric form of *Cryptostylis arachnites* (BL.) LINDL.

Chitonochilus SCHLTR. is synonymous with *Agrostophyllum* BL.

The genus *Paxtonia* LINDL. is according to SCHLECHTER (4) a peloric form of *Spathoglottis*.

The genus *Eucosia* (*Euc. carnea* BL.) is possibly a monstrous form of *Goodyera viridiflora* BL.

Dendrobium atavus J. J. S. is a peloric monstrous form of an orchid unknown in the normal state, it approaches *D. normale* FALC.

Epipogium roseum (D. DON) LINDL. is often spurless and peloric.

Peloric forms have been described in *Dendrobium normale* FALC., some species of *Appendicula* (3), *Stereosandra*, *Agrostophyllum* (4), &c.

Goodyera parviflora BL. is probably a peloric of *F. procera* HOOK. f.

Of *Dendrobium tetradon* RCHB. f. a peloric form is common in Java of which the flowers mostly remain closed and are self-fertilized.

In *Oberonia imbricata* LINDL. the upper flowers of the spike are abnormal and the gynaeceum is reduced.

Owing to the absence of a rostellum, autogamy is prevalent in several Malaysian *Orchidaceae* of which normal flowers are not yet known. This phenomenon has certainly a genetic basis.

Abnormal orchids with an enlarged number of anthers are sometimes also known only in that state (J. J. SMITH, *l.c.* p. 131).

Peloric orchids are often not known in their normal structure (J. J. SMITH *l.c.* p. 133-137). Sometimes the variation is geographic, e.g. in *Agrostophyllum denbergeri* J.J.S. which is in Java normal, but in Krakatau peloric.

In other cases it is peculiar to the individual e.g. in *Eria oblitterata* RCHB. f. which J. J. SMITH cultivated at Buitenzorg for a long time but remained peloric; it was later redescribed as a new species *E. isochila* KRZL. The same was the case with *Eria teysmannii* J.J.S. from Borneo, from which J. J. SMITH cultivated both a normal and a peloric form together; this plant also was described as a new species, *Trichotosia dajakorum* KRZL. A

peloric of the Sumatran *Dendrobium indragiriense* SCHLTR. was described as a separate species *D. isomerum* SCHLTR. J. J. SMITH assumes *Lecanorchis javanica* BL. to represent a peloric form of *L. pauciflora* J.J.S.

Peloric forms have been described in non-orchidaceous plants, e.g. in *Clitoria*. They have not yet been reported to my knowledge from Malaysia in other families with zygomorphic flowers as the *Gesneraceae* and *Scrophulariaceae*.

Discoid capitula of normally ray-flowered *Compositae* can also be regarded as peloric forms. Artificial keys to the genera fail when identifying such specimens. I suspect that some genera composed of species of reduced habit and subantarctic affinities may be only chance groupings of species occurring in the discoid form only.

These examples clearly show that the occurrence of monstrous forms presents a difficulty in identifying Malaysian plants. The fact that a single character has proved to upset taxonomy to such an extent that even new genera are based on these monstrous forms should encourage to more caution in the future.

Cited literature: (1) Ann. Jard. Bot. Btzg. vols 19, 23, 24, 28, 29, 32, 33, 34, 42 (1904-1931). (2) Natuurk. Tijdschr. Ned. Ind. 88 (1928) 122-140, specially p. 128, 131, 137. (3) Nova Guinea 14, p. 359. (4) Die Orchid. v. Deutsch Neu Guinea (1914) p. xlviii-xlix.

3. Other teratological or deviating forms

Phenotypic variation and inherited teratological and monstrous forms are often difficult to distinguish. Juvenile forms with lobed leaves, or with whorled leaves, and the like, are sometimes partly inherited, or the potentiality for producing them under certain ontogenic circumstances is inherited. This plastic variation is e.g. generally found in ferns where both dichotomous and lobed leaves occur in numerous genera. The tendency to lobing is sometimes even of racial character and may predominate in part of a population. In *Polypodium feei* METT., POSTHUMUS (1) found that the degree of lobation of the leaves gradually increases in Java from the West towards the East and the Lesser Sunda Islands, also from West Java towards North Sumatra (fig. 32). Forked leaflets frequently occur as individual variations, but, e.g. in *Asplenium dicranurum* C. CHR. of Celebes, they are as far as known a regular specific character, even in mature specimens.

There is a clone of *Hevea brasiliensis* M.A. in Java always possessing large simple leaves when young; the total surface of these simple leaves is nearly equal to the combined surfaces of the leaflets in divided leaves. One-foliolate leaves occur in several genera with compound leaves (*Leea*, *Aglaia*, *Allophylus*, &c.). A closer study of the ontogeny of these species seems to be needed.

An other phenomenon is found in *Boehmeria biloba* MIQ. (2) from Java, in which some specimens have forked leaves.

An example of a deviating form with variegated

leaves is *Coffea sundana* MIQ. from Sumatra; it is a variegated form of *C. arabica* L. *Pandanus variegatus* MIQ. was reduced by BACKER to *P. tectorius* PARK. as a variegated form; it remains sterile, and is only known as a cultigen. The soil has sometimes a great influence on the degree of variegation; poor soils stimulate the variegation in the leaves of *Caladium*, by manuring (N-compounds) this disappears to a large extent.

Hardly anything is known about these aberrant forms and experimental data are needed before a final conclusion can be drawn.

Cited literature: (1) De Trop. Natuur 25 (1936) 177-178. (2) MOR. Syst. Verz. (1845) 100, *syn. B. bifida* BL. Mus. Bot. II, 222, *non* WEDD., Ann. Sci. Nat. IV, 1 (1854) 199, from Japan.

4. Distribution of the sexes

In the Malaysian flora many plants possess unisexual or polygamous flowers. The shape and size of flowers of different sex sometimes differ widely (*Mangifera*, *Hevea*, *Diospyros*, *Brucea*, &c.). The mode of distribution of the sexes is not homogeneous within a single genus, but differs from species to species, and even within one species (*Carica*).



Fig. 32. *Polypodium feel* METT. (*Polypod.*), a typical fern of a crater vegetation, *a.* from Mt Papandajan, typical W. Java form with entire leaves, *b.* from Moengal pass, E. Java, *c.* from Geli Moetoe, Flores Island. All specimens at ca 1500-2000 m (after POSTHUMUS), $\times 1/5$.

In *Casuarina* the beach 'tjemara' (*Cas. equisetifolia* L.) is monoecious, whereas the mountain 'tjemara' (*Cas. junghuhniana* MIQ.) is typically dioecious.

Sex is mostly dependent on a single Mendelian character and so the two sexes in dioecious plants will tend to be present in equal numbers; cases are known of a 3 : 1 proportion.

In polygamous plants where σ and φ and σ flowers occur, the proportions are sometimes difficult to understand. Dr H. C. D. DE WIT recently found that in several species of *Eurya* no σ flowers are known (1). The distribution of the σ flowers in this genus is peculiar; sometimes a few scattered σ flowers occur among the $\varphi\varphi$ on one twig, sometimes there are σ and φ twigs, but σ flowers are always in the minority.

He also reports to me that in *Bauhinia malabarica* ROXB. the flowers have 10 stamens, as a rule all fertile. Sometimes all 10 stamens are reduced to staminodes; there are no intermediate stages, all stamens are either fertile or sterile. In all probability, if the stamens are reduced all flowers in one plant have reduced stamens. This induced BLANCO (16) to describe the female plants as *Bauhinia castrata*, and HASSKARL, unaware of BLANCO's name, again gave this the same name, *Bauhinia castrata* (17); now it was treated as a Javan species. ROXBURGH observed more or less the reverse in *Bauhinia acuminata*: in a number of flowers abortion of the ovary leaves the flowers male. WIGHT and ARNOTT (18) quoted GRAHAM's observation that 'for some reason (*Bauhinia malabarica*) has never borne fruit in the Calcutta Botanic Garden'.

In several species of *Dioscorea* BACKER (2) found male specimens much more common than female specimens.

HILDE SCHRÖTER & HUB. WINKLER found (15) in 100 sheets of *Elatostema rostratum* (BL.) HASSK., a common Javan species, the following remarkable figures for the distribution of the sexes: 4 σ , 6 sheets with mixed σ and φ flowers in one axillary inflorescence, and 90 sheets pure φ . This is probably connected with apogamy which phenomenon was in other species recorded by TREUB.

In polygamous flowers it is often difficult to say whether the ovary remains rudimentary or not.

In *Arisaema* I found (14) a peculiar distribution of the sexes in the spadices; σ was predominant! In *A. filiforme* BL. I examined 108 spadices: σ 75, φ 31, φ 2. In *A. barbatum* BUCHET I examined 36 spadices: σ 29, σ 1, φ 6. Dr H. J. TOXOPEUS has suggested to me that in *Araceae* this might be due to the great loss of vegetable matter in the φ rootstocks and tubers through the production of seeds. φ and σ plants would probably flower less frequently than σ . This is a very reasonable explanation, which must, however, be tested experimentally.

The *Ebenaceae*, numerous *Euphorbiaceae*, *Cucurbitaceae*, *Myristicaceae*, &c. are consistently dioecious.

These plants are often difficult to classify, and whether σ and φ flowered specimens ought to be referred to one species should be considered with great care. In most families the male flowers are more important, in others the female give the better

clue to the relationship. Descriptions based on inadequate material are, in dioecious genera and plants with uni-sexual flowers, decidedly insufficient. An example of the dangers involved in describing plants of one sex only is the following: BOERLAGE and KOORDERS described a small Euphorbiaceous tree from Sumatra on fruiting material only, and placed it in *Erismanthus* as *E. leembrugianus* BOERL. & KOORD. MERRILL, much later, described on flowering material, a new genus *Moultonianthes borneensis* MERR. The type specimens of these striking plants are identical. The confusion came from the fact that the subtribes of the *Cluytiaeae* are mainly separated on the structure of the male flowers.

In many cases two keys must be made for the identification, one based on ♂ and another based on ♀ characters.

In some plants it is still not known whether polygamy occurs. ENGLER (3) still supposed the flowers of *Weinmannia* to be bisexual, but KOORDERS and VALETON (4), BACKER (5), and the present writer (6) found polygamy at least in *W. blumei* PLANCH. and *W. clemensiae* STEEN. In *Myristica fatua* HOUTT. ♀ trees have sometimes some ♂ flowers and sometimes ♀. 'Male nutmegs' ('pala lelaki') were already known to RUMPHIUS; popular credulity caused them to be used as an aphrodisiac by the garrison at Sintang (7). These male nutmegs belong, however, to another species: *M. argentea* WARRB.

In Malaysia several species are only known either as male or female plants. BACKER mentions that in *Lannea coromandelica* (HOUTT.) MERR. only female specimens occur, which fruit very seldom (5).

In *Garcinia mangostana* L. apparently only ♀ specimens are known to occur (8); according to BACKER (5, p. 91) male flowers have not been recorded in the past century.

Heterostyly occurs in quite a number of Malaysian plants. The Javan *Primula imperialis* JUNGH. is different from the Khaysan *P. prolifera* WALL. only in having monomorphic (homostylous) sexual organs, and is therefore—in my opinion wrongly—kept specifically separate from the Asiatic race (9).

Several *Rubiaceae*, *Allaeophania* (10), etc., are heterostylous, of course also *Oxalis*. In heterostylous *Eichhornia crassipes* SOLMS (2, p. 41) only the medium-styled form is spread in Malaysia. Heterostyly also occurs in *Connaraceae* and in *Averrhoa* (11).

A strange case of abnormal geographical distribution of the sexes is found in *Balanophora globosa* JUNGH. This species is known from the Malay Peninsula and West Java, but in Java only the ♀ form is found and is according to LOTSY (12) apogamous. In the Malay Peninsula, however, both female and male plants have been collected.

Another case is that of *Brucea amarissima* Desv. which in Malaysia is mostly monoecious; in Central- and E. Java ♂ and ♀ specimens occur, according to BACKER (5, p. 192, footnote; 13). A similar peculiarity in geographic distribution of sexual forms is seen in *Lannea grandis* ENGL. of which the flowers are unisexual. The Javan specimens are all

dioecious, and only female specimens have been found (5, p. 281).

Cited literature: (1) Bull. Jard. Bot. Btzg III, 17 (1947) 332. (2) Handboek Flora Java pt 3 (1924) 109. (3) Nat. Pfl. Fam. ed. II, 18a (1930) 250. (4) Bijdr. Boomsoorten Java 5 (1900) 398, 401. (5) Schoofflora voor Java (1911) 471–2. (6) Journ. Bot. 72 (1934) 5. (7) Geneesk. Tijdschr. Ned. Ind. 13 (1868) 361. (8) Science 92 (1940) 359. (9) Ber. Schweiz. Bot. Ges. 48 (1938) 156–165. (10) DOCTERS VAN LEEUWEN, Verh. Kon. Akad. Wet. A'dam 31 (1933) 232. (11) BURCK, Ann. Jard. Bot. Btzg 6 (1887) 251–254. (12) Ann. Jard. Bot. Btzg 16 (1899) 174–185. (13) Flora Batavia (1907) 260. (14) Bull. Bot. Gard. Btzg III, 17 (1948) 449. (15) in FEDDE, Rep. Beih. 83, 2 (1936) 93. (16) Fl. Filip. 1 (1837) 337. (17) Flora 25 (1842) Beibl. II, 54. (18) Prodr. Fl. Pen. Ind. Or. (1834) 295.

5. Geographical segregation in Malaysian specific populations

Geographic segregation is the fact that the hereditary characteristics within a population are not homogeneously distributed over the specific area. This uneven representation of the genotypic types manifests itself both morphologically and ecologically (physiologically).

It is clear that the pattern of the types in general will coincide with the pattern of the environments. The environment itself seems to a certain degree responsible for this coincidence or, in other words, the *principle of tolerance of the plants is expressed by means of selection by the environment*. In a large N-S directed area like North America the hardest types of a population will be found in the northern parts of its area and the southern types will, in all probability, be unable to stand a severe winter. Northern types planted in the south will, however, show other deficiencies and, probably, be unable to stand long hot summers. This has in fact been found experimentally in forest trees in the U.S.A. as Dr H. M. RAUP, professor of plant geography, Harvard University, kindly informed me. The same holds for altitudinal types within species of wide altitudinal range. In short, it is the rule wherever a widely distributed species has had to withstand differences in soil and climate.

It is not necessary *a priori* that physiological differences should create or accompany morphological differences. Ecologically distinct races, therefore, may not always be morphologically distinguishable; the differences may be 'invisible'. However, in practice in the majority of physiological races some minor morphological differences can be traced though they are not always clearly defined.

The wider a species has spread the more tolerance it has, apparently, towards various climates and soils, and the higher is, on the whole, its variability; these facts are causally related.

Valuable practical use can be made of this differentiation in a population. If seedling Eucalypts are required for afforestation in a rather wet climate, it is important to collect seeds from trees growing under conditions which closely approach

the conditions of the new forest. If *Pinus merkusii* JUNGH. & DE VR. is used for afforestation in the mountains seed collected at high altitude will give the best results; for afforestation in the lowlands seed-parents must be chosen at low, or the lowest possible altitude.

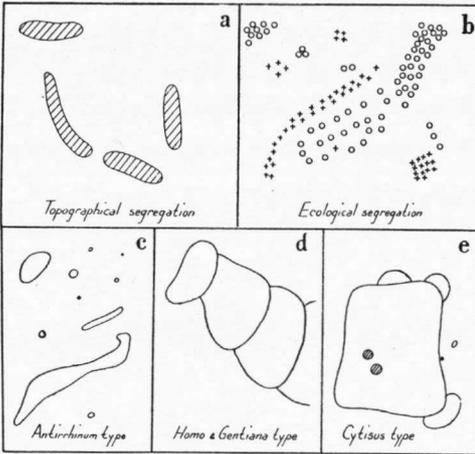


FIG. 33. Some imaginary types of racial differentiation:

- a. **Topographical segregation:** the areas exclude one another by topographical barriers (seas, mountain ranges, deserts, etc.).
- b. **Ecological segregation:** the subspecies or races exclude one another through edaphic factors, e.g. dry-land against inundated land, etc.
- c. **Specific area consisting of a number of isolated colonies,** each occupied by a separate race, each colony with its own facies; no intermediates. *Antirrhinum* type.
- d. **Specific area consisting of a number of regional exclusive races bordering on the area of neighbouring races.** Intermediates are found at the frontiers shared by 2 types. Frequent type of segregation in birds and butterflies. *Homo* and *Gentiana* type.
- e. **Widely distributed specific population with marginal and/or altitudinal races or subspecies.** The shaded areas represent altitudinal races. *Cytisus* type.

It is a striking fact that the amplitude of ecological behaviour is very narrow in some large and widely distributed genera. Examples are *Primula*, *Gentiana*, *Geranium*, *Pedicularis*, &c.; all are strictly microtherm. Apparently their basic genom pattern lacks the potentiality to produce derived types able to withstand a constant high temperature. In the tropics they occur only at high altitude.

This contrasts sharply with equally wide distributed genera like *Quercus*, *Hydrocotyle*, *Myrica*, *Hypericum*, *Ajuga*, *Salvia*, *Rosa*, *Vaccinium*, &c. which are essentially temperate but also contain tropical lowland species.

In some genera only certain sections possess this

potentiality in their genom pattern, e.g. *Carex*, *Rubus*, *Clematis*, *Daphne*, *Lobelia*, &c. (1).

The same applies to the capacities of megatherm families and genera. In the large family of *Dipterocarpaceae*, occurring from the Himalayan tracts and Ceylon to the Louisiades, no species is able to withstand cold; in Malaysia hardly any species oversteps the 1000 m contour.

Other genera, though typically tropical, such as *Calophyllum*, *Garcinia*, *Symplocos*, *Pandanus*, &c. have produced a number of species occurring at high altitude in the tropics. It is remarkable that these have mostly *not* spread into temperate countries but remained in the tropics.

Within specific populations there are three types of racial or subspecific differentiation.

Firstly there is *segregation of parts of the populations by different ecological stations*. The segregates may occur in the same geographical area but are confined to restricted habitats; so, as regards distribution, they form two or more complementary mosaic patterns in the same area. This type of segregation is mostly due to differences in edaphic conditions (fig. 33b).

Secondly *the areas occupied by the subspecies may be regional, and the areas exclude each other either altitudinally or horizontally*, but their frontiers touch as in a jigsaw puzzle. This kind of segregation is mostly due to climatic conditions (fig. 33d).

Thirdly *the areas of the subspecies or races may exclude each other as in the second case but their frontiers do not touch each other as the subspecific areas are separated by topographical conditions* (fig. 33a).

In one species more than one type of segregation may be present, e.g. in *Impatiens platypetala* LINDL. (2). The 'normal' form in Java of this widely distributed species has large purple flowers; it favours moist places, descending seldom below 500 m (mostly along streams and only in continuously wet climates); it ascends to 2500 m alt. In Central and East Java another form occurs, named by MIQUEL *I. nematoceras*; this occurs mainly in the northern portion of Java from Cheribon eastward in grass fields between 50 and 850 m alt. and is confined to regions subjected to a dry season; it is also found in Madoera and the Lesser Sunda Islands. In habit it is frail and lank, its leaves and purple flowers are always smaller and rather typically ephemeral in appearance; it is the only *Impatiens* found in teak forests and the only species known from dry Madoera Island (fig. 34). The 'normal' form and *I. nematoceras* exclude each other geographically and differ in habitat (climatic and altitudinal) and build (mostly size). Intermediate specimens are very scarce; I myself have seen none. The differential characters are certainly not of specific rank and both BACKER and I are convinced that *I. platypetala* and *I. nematoceras* are races of one population i.e. regional subspecies; here differentiation results in two climatically limited areas.

In Celebes there is a third race, confined to that island, with slightly smaller, plain orange coloured

flowers, formerly described as *I. aurantiaca* T. & B. ex KOORD. and as *I. celebica* MIQ. This form differs from the others practically only in the colour of the flowers, hardly by any structural characters. This is clearly an instance of a topographical race, belonging to type 3. It has a similar ecology as the 'normal' *I. platypetala* in Java.

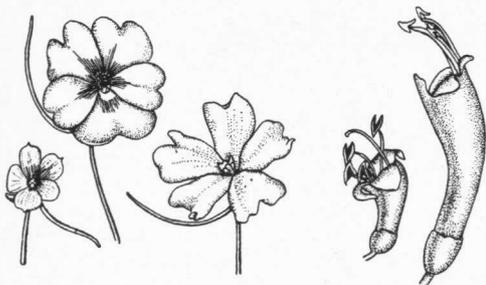


Fig. 34. Left: flowers of 3 subspecies of *Impatiens platypetala* LINDL. (Bals.), from left to right: *ssp. nematoceras*, *ssp. genuina*, *ssp. aurantiaca*. Right: flowers of the two Malaysian subspecies of *Wightia borneensis* HOOK. *f. (Scroph.)*, from left to right: *ssp. ottolanderi*, *ssp. genuina*, $\times 1/2$.

The study of the problems connected with riaciation are in Malaysia far less advanced in botany than e.g. in entomology, and our knowledge is mostly based on field observations and herbarium study, rarely on experiments.

The examples given in the following chapters must, therefore, be considered in the light of this fact.

(a) *Ecological segregation (mostly edaphic ecotypes, races or subspecies)* (fig. 33b). Under this heading some examples of ecologically segregated populations will be enumerated. The areas of the races or subspecies overlap, but if the boundaries are accurately marked on a map their growing localities exclude each other, forming a mosaic pattern. Only a very few cases have been mentioned in literature or have come to my knowledge, and the intimate relationships have not yet been studied in the field and experimentally.

Hanguana (Susum) is a genus of *Flagellariaceae* of which two species have been distinguished in Malaysia, viz: *H. anthelminthicum* BL. and *H. malayanum* (HOOK.) MERR. The former is a characteristic gregarious swamp plant of deep water in most parts of Malaysia. It produces numerous stolons and its inflorescences are large and stout, 1½–2 m tall with glabrous panicles and flowers inserted on lateral branches of second and third order.

H. malayanum is a typical terrestrial forest plant of much smaller dimensions. It does not produce stolons during anthesis; only one stolon is formed after the setting of fruit. It is never found in flooded or temporarily flooded places and is not gregarious (presumably owing to the absence of stolons); it is 40–100 cm tall. The panicles are at first more or

less hairy, later glabrescent. The flowers are inserted mostly on branches of the first partly also on those of the second order. These distinguishing characters seem small and inessential, but the plants can be separated quite easily both in the herbarium and in the field (3).

In Java no transitions have been found but BACKER says they occur in Sumatra (4). In Java, therefore, the two plants behave as good species, but not in Sumatra. BACKER therefore reduced them to the rank of 'forms', in the sense of races or subspecies which is, as far as our knowledge goes, apparently the appropriate status.

A more or less gradual geographical change in a population is found in the fern *Polypodium feei* METT. as shown in fig. 32.

Among the grasses endless varieties and forms have been distinguished, according to BACKER's excellent treatment of the Javan members of this family. In general they exclude each other horizontally. There are also ecological races, e.g. in *Coix lacryma-jobi* L., a polymorphous species cultivated from early times and doubtfully native in Malaysia. The common form is *f. agrestis* BACKER (*C. agrestis* LOUR.), *f. ma-yuen* STAFF is only cultivated. In the Danoe swamp in W. Java there is a tall ecotype *f. palustris* BACKER (*C. palustris* KOORD.), in the Pening swamp in Central Java another form with floating stems *f. aquatica* BACKER (*C. aquatica* ROXB.) and in N. Sumatra near Toba Lake still another form, *f. ouwehandii* (KOORD.) BACKER; all these are distinguished by minor morphological characters. The floating habit seems far from constant, as the Pening form when cultivated at Buitenzorg gave an erect strongly stooling plant 1 m high (4).

A form of *Spinifex littoreus* (BURM.) MERR. is recognized as *var. longifolius* BACKER (formerly distinguished as a distinct species *Sp. longifolius* R. BR.). It occurs in the Lesser Sunda Islands and E. Java, and in Australia. BACKER (4, p. 188) says that this variety is usually easy to distinguish from the main type, but generally does not grow mixed with it and apparently occupies a slightly different habitat. He also found intermediates.

A typical ecotype in Java is a very slender brittle form of the variable common weed *Emilia sonchifolia* (L.) DC. with narrow-lanceolate to linear leaves. It has been described as *E. flaccida* MIQ. but its real status is still unknown to me; it may be identical with *E. angustifolia* (WALL.) DC. which is sometimes reduced to *E. prenanthoidea* MIQ. It is very distinct in the field and seems to be definitely native, though in Java the common weed *E. sonchifolia* is an introduced alien, along roadsides, in fields, gardens and plantations. The form described as *E. flaccida* MIQ. occurs in Java only in the marginal reed and sedge vegetation of mountain swamps and lakes.

Another case is that of *Melaleuca leucadendron* L. which is a variable plant throughout its area in Queensland and Malaysia, apparently split into races or subspecies. In East Malaysia at least two subspecific entities occur, viz a dry-land savannah form from which the essential 'kajoe poetih' oil

is prepared in the islands of Boeroe and Ceram, and a form confined to forested swamps. In New Guinea both forms occur, but strictly exclude each other as regards habitat. In West Malaysia (Sumatra, Malay Peninsula, Borneo, West Java) only the swamp race is present. The latter does not yield essential oil for commercial purposes. Morpholo-

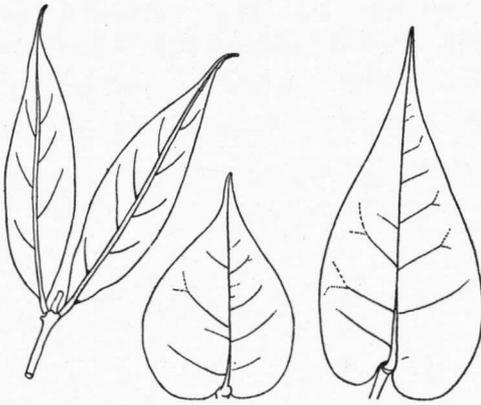


Fig. 35. Leaf types of the two races of *Macrosolen pseudoperfoliatus* MIQ. (*Loranth.*). Left: a pair from Mt Ardjoeno, right: 2 leaves from specimens of Mt Tengger, $\times 1/2$.

gically the swamp forest race has broader leaves than the savannah race; but otherwise the differences are trivial.

(b) *Regional segregation.*

(b¹) *Horizontal segregation* (mostly climatic ecotypes) (fig. 33d, e). An illustrative example is the Loranthaceous *Macrosolen pseudoperfoliatus* (ZOLL.) MIQ. which DANSER says (5) is endemic in East Java on the two neighbouring mountain massifs Tengger and Ardjoeno. The forms on each massif differ strikingly only by the shape of the leaves, which in Ardjoeno specimens is lanceolate or ovate-lanceolate with attenuate base, but in Tengger specimens cordate-amplexicaulous (fig. 35). No intermediate forms occur, but as no floral differences have been observed, DANSER does not separate them. This is certainly a very instructive case of racial differentiation, though unexplained, as the climate, altitude, &c. of these mountains are exactly alike.

A remarkable case is that of *Wightia* (21), a woody genus of the *Scrophulariaceae* (fig. 36). A thorough study revealed the length of the corolla as the only really constant difference between the two Malaysian species described: *W. borneensis* HOOK. f. from Borneo, and *W. ottolanderi* KOORD. from E. Java (fig. 34). This character is sufficient to separate the forms easily and no intermediates have been found. The distributional data also demonstrate, however, a peculiar difference in ecology, as *W. borneensis* (elongate corolla) is only found in the rain forests and forest margins of

Borneo, the Malay Peninsula, Sumatra, and West Java, whereas the small-flowered *W. ottolanderi*, occurs only from Central to East Java and in the Lesser Sunda Islands in places subjected to a pronounced dry season during the East monsoon. No immediate adaptive relation seems to exist between the morphology and the climate; the foliage is similar, and both species are deciduous. I accept them as of subspecific rank.

Racial differentiation is also described in *Alangium* by BLOEMBERGEN (6) viz in *A. salvifolium* (L. f.) WANG. of which *ssp. decapetalum* is known from the Comores to SE. Asia and *ssp. sundanum* from the SW. part of the Deccan peninsula, Ceylon, the Andamans, and Malaysia. According to BLOEMBERGEN'S map (6, p. 148) the subspecies exclude one another completely.

The subspecies of *Polygonum* apparently have no ecologically different habit. In *Polygonum barbatum* L. DANSER (7) distinguishes a *ssp. gracile* differing from the main population by a slenderer less ramose habit, less numerous spikes, and somewhat narrower leaves with rotundate or cordate base. It does not differ, however, in geographical distribution and even occurs in the same spots as the main species. This is certainly not a subspecies in the present meaning. Similar subspecies are distinguished in *P. caespitosum* BL. DANSER found intermediates fertile with the main population and this prevented him from accepting it as a separate species. *P. caespitosum ssp. yokusaianum* is known only from Sumatra; DANSER supposes this to be a subspecies, that is, in his sense, a clearly distinguishable but not sharply separable race with a certain measure of independence, behaving locally like a

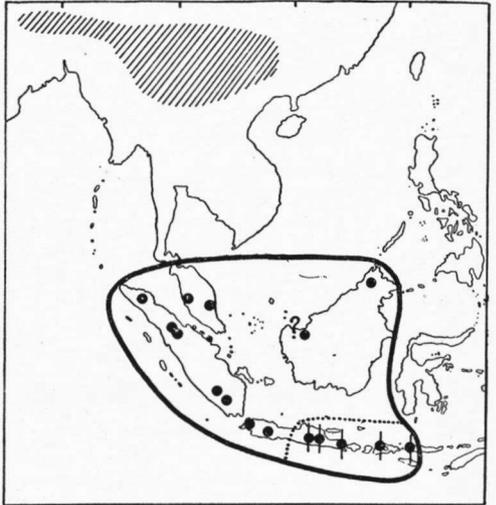


Fig. 36. Distribution of the genus *Wightia* (*Scroph.*), the shaded area is that of *W. speciosissima* (D. DON) MERR. sens. ampl. The \pm disjunct Malaysian species consists of 2 subspecies of *W. borneensis* HOOK. f.; dots: *W. borneensis s.str.* and crossed dots: *ssp. ottolanderi*.

species. Judging from the localities there is no apparent difference in ecotype. In *P. pulchrum* BL., DANSER distinguished one subspecies, *hallierii*, from Borneo, which is the only representative of the species in Borneo; it is therefore a marginal race.

In *P. minus* HUDS., DANSER has arranged all Malaysian specimens in 5 different subspecies mostly based on 5 former species. Several are clearly connected by intermediates. In mapping the subspecies it appears that *micranthum* and *depressum* are both practically limited to Sumatra-Malacca-Java, *procerum* is exclusively found in Borneo and from there eastwards, *subsessile* is found in New Guinea and Australia; forms intermediate between *subsessile* and the Australian *decipiens* also occur in New Guinea. Between *subsessile* and *procerum* there are intermediates in New Guinea. These subspecies exclude each other geographically quite consistently and have the character of races.

In *P. hydro Piper* L. there is a peculiar geographical racial differentiation. The large-fruited *ssp. megalocarpum* is found in the temperate regions of Europe and Asia, and in temperate Australia. The tropics in between have only the small-fruited *ssp. microcarpum* which is represented in Malaysia by the lenticular-fruited variety occurring in Malacca and N. Sumatra, and further only by the triquetrous-fruited variety. This is a distinct geographical segregation; the large-fruited subspecies is found only in the temperature outposts of the distributional area.

In *P. pubescens* BL. (SE.-E. Asia and Malaysia) a subspecies *prianganicum* is distinguished, occurring only in the mountainous W. part of Java, but found together with the main population on some mountains there. There is no geographical segregation.

In *P. runcinatum* D. DON (SE.-E. Asia, Sumatra and Java) the main form occurs only on Mt Diëng (Central Java) while the other Javan specimens are distinguished as *ssp. javanum*. This subspecies is so different from the Asiatic population that DANSER would have raised it to specific rank had not some forms been found in Asia approaching *ssp. javanum*.

In *Pimpinella pruatjan* MOLK. all specimens found in its westernmost locality in Java, Mt Pangrango, have rooting inflorescences. Though I agree with BUWALDA in reducing *P. leeuwenii* WOLFF, which is based on this ecotype, to *P. pruatjan*, the fact remains that the trivial racial differences are probably hereditary (8).

In *Anaphalis javanica* SCH. BIP., specimens found on Mt Tengger have a peculiar yellowish tomentum in the inflorescence, in contrast with the snow-white one of specimens from elsewhere. The ecotype is local.

In *Berberis sect. Mahonia* specimens from N. Sumatra (described as a separate species) differ from those of Java mainly in the very large leaves, but I believe both to represent two distinct races of *B. nepalensis* SPR. Scores of slightly different forms in Southeastern Asia have been described as 'species' by SCHNEIDER, FEDDE, and TAKEDA. It is astonishing to learn that these species are mostly known from one or a few specimens only. It is

significant that the area of these 'species' is local, and further that no overlapping of the areas occurs. The absence of a sound key to the species in TAKEDA's revision shows the feeble position of the distinctions which is further illustrated by his numerous drawings.

Racial differentiation in Malaysian plants is further described by WASSCHER (9) in *Podocarpus*, by VAN OOSTSTROOM (10) in *Evolvulus alsinoides* L., by Miss KOSTER (11) in several genera of *Compositae*, e.g. *Centratherum* and *Vernonia*, by DE WIT (2) in *Eurya*, by BACKER (12) in *Forrestia* and *Gramineae*, and is further known in *Swertia*, *Malvaceae* and a number of other plants.

Exclusive areas of distribution do not always prove groups to be of less than specific rank. DANSER distinguishes in *Agathis* three species viz *A. borneensis* WARB. from Sumatra, the Malay Peninsula and Borneo; *A. alba* FOXW. from the Philippines, Celebes and the Moluccas; and *A. labillardieri* WARB. from New Guinea and adjacent islands. These three species exclude each other topographically and represent vicariads. According to DANSER each is differentiated in a number of ill-defined geographical variations.

(b¹¹) *Altitudinally differentiated populations* (fig. 33e).—Altitudinal differentiation is often difficult to evaluate as in most species a distinct change in habit and foliage with altitude is observed which is certainly sometimes only a modification or adaptation; the leaves become smaller and more leathery, leaf margins tend to recurve, the blade grows broader proportionally, &c.

Transitional forms are often found between those of the hills and the summits. In the absence of experiments it is often difficult to judge whether the differences are of modificational, racial or specific rank. Characters of leaf and habit are, in my opinion, certainly not sufficient for specific distinction if there are no additional structural differences in the floral parts.

In Japan *Fritillaria camschatcensis* KER-GAWL em. SWEET occurs in two forms, viz a dwarf alpine ecotype and a lowland type. MATSUURA (13) has found the alpine subspecies to be polyploid and derivative.

A good example of an altitudinal subspecies in Malaysia is, I think, a peculiar form of *Schima noronhae* REINW. which was described from Mt Kinabalu as *Sch. brevifolia* HOOK. f. In 1937 I collected this small tree also in N. Sumatra (Losir highlands). Its leaves are rounded, crowded and sessile, its habit compact; I could not find sufficient floral differences, and STAFF also remarked that it was very closely allied to *Sch. noronhae* REINW., but a distinct series of intermediates was not found. For these reasons I have reduced this summit form to the rank of a subspecies (1, p. 51).

It is an unsolved problem whether these altitudinal subspecies behave distributionally as species, or whether they are a result of independent polytopic segregation on different mountain complexes; in the latter case they would be autochthonous polytopic segregations. There is, I believe,

only one way to solve this question, viz by means of a 'tracer'-character in the populations. Assuming that in the Bornean population of *Sch. noronhae* a small morphological character could be demonstrated which is absent in the Sumatran population, then this would point to polytopic origin of *ssp. brevifolia*. If, however, this 'tracer'-character were

summits) has some minute characteristic in common with West Java *spicata* (from the hills) which fails to occur in both Central Javan summit *sessilifolia* and Central Javan hill *spicata*.

A remarkable altitudinal segregation exists in *Dodonaea viscosa* JACQ. in Java; it is either found near the sea shore in a glabrous form or in the mountains, between 1100 and 3300 m, in a hairy form.

Other examples are species of *Cardamine*, and specially *Plantago major* L. s.l. The latter species has been described under various names from Java and elsewhere in Malaysia. Phenotypically it is very changeable but it has also certainly been segregated in local races. PILGER (14) has not been able to separate *P. asiatica* L. from *P. hasskarlii* DECNE and *P. incisa* HASSK. in his key. All species together form an exceedingly polymorphous ubiquitous population described under many names.

Altitudinal exclusion, on the other hand, is not always a proof that entities are of less than specific standing. This is demonstrated by the genus *Lonicera* of which only two native species occur in Java (15), both with good floral and vegetative characters. In fig. 37 I have marked the occurrence of the species on the summits of Java, and it appears that the altitudinal areas touch only on Mt Gedeh in W. Java where, however, no intermediates are found. This is clearly a case of altitudinal vicariism of two distinct species.

(c) *Topographical segregation* (historical raciation) (fig. 33a, c).—Under this heading I have arranged examples of type 3, that is subspecies, or races, excluding each other geographically but whose boundaries do not coincide, or touch. They remain separated by topography or mere distance. Naturally, Malaysia, consisting as it does mostly of islands, is topographically most suitable to this kind of segregation.

In the introduction to this chapter I mentioned that the purple-flowered Javan *Impatiens platyptala* LINDL. is represented in Celebes by an orange-flowered race (subspecies).

A similar more complicated racial differentiation was described by Dr BLOEMBERGEN in his revision (6, p. 197) of the genus *Alangium*, viz in *A. villosum* (BL.) WANG. in which he distinguished no less than 11 subspecies, mostly confined to a single island, island group, or part of an island.

In the genus *Pahudia* (now *Azelia*) DR DE WIT found that of *P. javanica* MIQ. a large-flowered form is found in Sumatra (Eastcoast Residency) far from the Javan population. The size of the flowers is the only reliable difference from the Javan species (16).

In the mountains topographical segregation is of very common occurrence. This is readily understood when it is realized that the flora of the summits is comparable to the plant-cover of scattered islets in a sea of lowland megatherm vegetation. Though apparently not so pronounced as in animals, in plants also all specimens from one summit or a mountain massif frequently show a certain *local facies* in minor characters. In *Primula proli-*

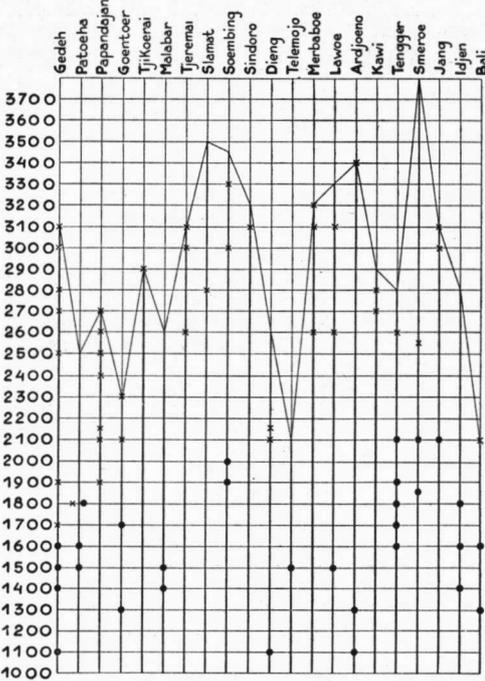


Fig. 37. Altitudinal localities (in metres) of *Lonicera acuminata* WALL. (X) and *L. javanica* (•) (*Caprif.*) in Java and Bali. Mountains arranged from W towards E. Thickened vertical lines indicate the altitude of the summits.

present only in the Sumatran highland *brevifolia* and not in the Sumatran lowland and hill populations of *Sch. noronhae* it would point to an independent distributional behaviour of *ssp. brevifolia*. The 'tracer'-character could, of course, equally well be present in the Sumatran population and Borneo *brevifolia*, but be absent from the Bornean hill and lowland populations. The solution of the question whether these altitudinal subspecies can emerge locally and independently from lowland populations requires a very detailed morphological study based on abundant materials and wide field studies. The outcome might have very important theoretical results.

In *Symplocos* closer study may give a key to this 'tracer' problem. The summit species *S. sessilifolia* (BL.) GÜRKE is distinguished from *S. spicata* ROXB. (= *S. laurina* (RETZ) WALL.), mainly by a condensed habit, and sessile or subsessile coriaceous broad leaves. The West Javan *sessilifolia* (from the

fera WALL. the Javan specimens from Mts Pangrango, Papandajan and Jang differ from one another in small characters (17). The form from Mt Jang, the most eastern extremity of the generic area in Malaysia, is also the most deviating! The Malaysian *Primula prolifera* population as mentioned above differs essentially from the remote Himalayan-Chinese *P. prolifera* only in its monomorphous-homostylous flowers (18) (fig. 38).

Pleiocraterium—preferably a section of *Hedyotis*—I found on two mountains in N. Sumatra about 80 km apart. The colonies were different in minor respects, which induced BREMEKAMP to recognize them as different species (19). This I am prepared to accept only if it is proved that they do not hybridize when growing in company. Moreover, I am firmly convinced that when the other summits in N. Sumatra have been searched, it will be found that each summit possesses its own race of *Pleiocraterium*.

A somewhat complicated situation exists in genera containing a widely distributed continental specific population which has spread into Malaysia by two different tracks (pincer-migration). An example is *Ainsliaea pteropoda* DC. which is found widely distributed in SE. Asia, in West Malaysia (Sumatra, and the Malay Peninsula) and in North Malaysia (Philippine Islands).

It stands to reason that the Philippine specimens originated from Formosan-Chinese sections of the continental population, and that the Malay Peninsula specimens migrated from the Burmo-Siamese section of the continental population. The continental populations of widely distributed species are often regionally divergent. It is thus to be expected that the Philippine groups will be somewhat different from the West Malaysian specimens. In fact they have been described under different names, but it is extremely likely that there are no greater differences between them than will be found to exist in a comprehensive study of the continental population.

Another type of topographical race formation is the occurrence of partial populations distinctly deviating from the continental specimens, of species wide-spread in Asia but occurring in Malaysia in a single island.

Pirola japonica SIEB. is for example mainly distributed in Japan but is known in continental Asia from Manchuria and Korea. The race in Korea is a distinct subspecies, and ANDRES (20) considers the Malaysian entity, from N. Sumatra, to be a separate species: it is distinguished by the leaf shape, leaf colour, leaf size, and colour of the flowers. ANDRES accepts it as related to the 'Formenkreise' of *P. japonica*.

Many SE. Asiatic mountain plants are common to the Himalayan and Khasyan tracts as well as to Sumatra and Java; minor differences are often observed between the continental and the Malaysian specimens, but they are *not* connected by intermediates. This feature of topographical segregation did not deceive HOOKER, and his collaborators in their attempts to verify the identity of the Indian and Javan specimens and species.

Examples of racial differentiation in mountain plants could be cited by the dozen. The above-mentioned will suffice to illustrate their presence in the Malaysian flora.

This local differentiation is often a *crux botanicorum*. In genera like *Potentilla*, *Ranunculus*, *Gentiana*, *Euphrasia*, &c. every mountain massif has

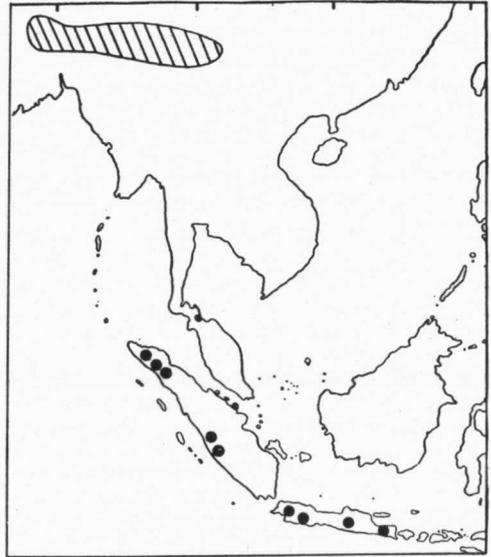


Fig. 38. Distribution of *Primula* sect. *Candelabra*; in Malaysia only one species.

its own type and intermediates are mostly not found. Each form must be carefully considered to define its rank. Monographic study is indispensable; local studies alone will not yield satisfactory results.

Cited literature: (1) A discussion of some of these problems is found in my study of Malaysian mountain plants, *cf.* Bull. Jard. Bot. Btzg III, 13 (1934) 141–146. (2) Bull. Jard. Bot. Btzg III, 17 (1948) 385. (3) Data after BACKER, Handboek Flora Java pt 3 (1924) 3. (4) BACKER, Handboek Flora Java pt 2 (1925) 33–34. (5) Bull. Jard. Bot. Btzg III, 11 (1931) 296. (6) Bull. Jard. Bot. Btzg III, 16 (1939) 10–7210. (7) Bull. Jard. Bot. Btzg III, 8 (1927) 146. (8) Blumea 2 (1936) 192. (9) Blumea 4 (1941) 359–481. (10) Monogr. (1934); Blumea 3 (1938) 74. (11) Blumea 1 (1935) 351–512. (12) Handboek Flora Java pt 3 (1924) 33; pt 2 (1928). (13) Journ. Fac. Sci. Hokkaido Imp. Univ. 3 (1935) 219–232. (14) Pfl. Reich Heft 102 (1937). (15) Journ. Arn. Arbor. 27 (1946) 442–452. (16) Bull. Jard. Bot. Btzg III, 17 (1941) 146. (17) De Trop. Natuur 19 (1930) 81–82. (18) A. ERNST, Ber. Schweiz. Bot. Ges. 48 (1938) 156–165. (19) Rec. Trav. Bot. Néerl. 36 (1939) 438, 445. (20) Bull. Jard. Bot. Btzg III, 14 (1936) 4–7. (21) Bull. Bot. Gard. Btzg, III, 18 (1949) 213–227.

6. The problem of speciation

A mass of literature exists on the origin of new species and the specific concept. It is outside the scope of this introduction to evaluate all the recent, and often brilliant, advances in this field of research. I have already commented on this in my study on the origin of the Malaysian mountain flora (1).

According to BATESON, DOLLO, DE VRIES, and LOTSY the discontinuity in the characters or complexes of characters of the organisms enables us to distinguish species. An *abrupt origin of new forms* is consequently suggested, *i.e.* mutation *sensu amplissimo*.

No objection is raised against the assumption of a gradual dynamic change and shift in units or populations after they have been (abruptly) established. This may be caused by dispersal into some new environment and, eventually by secular changes in conditions of growth.

The consequence of the principle of discontinuity and mutation principles is that *no aeons are necessary for the origin of new species; they may originate abruptly*.

This is exactly what has been found experimentally in recent decades. In the single source of speciation now known beyond any doubt, *i.e.* hybridization connected with a duplication of the genome, the abruptness of the process is demonstrated. Since 1912, when DISBY described the raising of the 'constant hybrid' *Primula kewensis* W. WATSON, a polyploid new species, numerous examples of this kind have been found. LOTSY predicted the hybrid origin of *Spartina townsendii* GROVES. Later, thoroughly investigated additional instances have been described in *Salix*, *Nicotiana*, *Solanum*, *Brassica*, *Rosa*, *Digitalis*, *Phleum*, *Triticum*, *Secale*, *Saxifraga*, *Aegilops*, &c. Classical examples were those of HERIBERT NILSSON who raised an artificial *Salix cinerea* L., and of MÜNTZING who succeeded in producing *Galeopsis tetrahit* L. artificially, both species being generally recognized in West European floras. KARPECHENKO even managed to breed a constant intergeneric polyploid between *Raphanus* and *Brassica*. The new polyploids breed true and are separated by a sterility barrier from the parent species.

The occurrence of numerous genera in nature showing polyploid series of species suggests that, at last, part of the veil concealing the origin of new species of plants has been lifted. The disintegration of these highly complex genomes may be found to be another source of new combinations and may perhaps explain the peculiar dysploid series of chromosome numbers found in genera like *Carex*.

Mutation *sensu strictissimo*—the abrupt change of single genes—has also been demonstrated, but in all cases described these changes are below specific rank.

The outcome is that new polyploid species can be produced in 2 generations, that is, in the case of herbs in a few years, in the case of trees in less than a century. No Lamarckian periods are needed for species formation, in contrast to the views held by some zoologists who often postulate a gradual

change of an entire population into a new species. The parent species thus disappears. In plants, the polyploid stands quite independently from the parent species; it has its own range of variability and its own ecological needs. It thrives independently of the parent species and there is no reason to expect a close competition between them. Balanced and unbalanced polyploids probably spring into existence and, subsequently, varying disintegration of the genome may take place.

It stands to reason that *polytopic* origin will be frequent, though it may escape actual observation and must be inferred. It might seem that such polytopy would throw plant geography into confusion, in particular as regards the explanation of disjunctions. This is, however, not the case because at the place and moment of the origin of a new species *both* parent species must have been present.

A test case for the actual occurrence of polytopy could be made out by *tracer*-characters *e.g.* between two specific populations A and B which are both racially differentiated into two races which may be indicated as A^c and A^d, and B^x and B^y, with the polyploid combinations A^cB^x and A^dB^y. If experimental taxonomy could analyse such a case, it would almost amount to a proof of a polytopic origin of the polyploid population consisting of the races A^cB^x and A^dB^y.

Additional possibilities are manifold. One parent species may become extinct, followed by isolation of the new species from the other parent; subsequent geological discontinuation of this isolation and the entrance of a new wave of pioneer or marginal elements of the generic population may or may not occur, and recombinations within the limits of the partial generic polymorphy in the area; then, also, geological change (*orogenesis*) may give an opportunity to formerly unviable combinations, &c. An unending vista of possibilities thus opens; much must be assumed and little can or will be proved by the laborious and painstaking methods of experimental taxonomy.

Few Malaysian plants have been studied cytologically, and little is known of the occurrence of polyploidy which must certainly exist in the large genera of the Malaysian flora. In these genera one often meets some species aberrant in size. My list of suspected records is unfortunately lost; from memory I quote *Anellema giganteum* R. BR., *Urtica grandidentata* MIQ., *Macaranga sp. div.*, *Homalanthus giganteus* Z.M.

It must be added that, though the *origin* of new *taxa* will generally be sudden, the rate at which the new forms will multiply and spread under natural conditions from the place of origin may greatly vary, and range from nil to some unknown quantity. This will depend mainly on the ecological potentialities of the *taxon* (*i.e.* its capacities for adaptation, dispersal and tolerance) and the eventual accessibility of 'ecological niches'. Experience has convinced me that closely related species may show a widely different ecological behaviour. I am principally opposed, therefore, to WILLIS's contention that—among closely related species—the size of the area of distribution depends only or

mainly on 'age'. A close comparison and careful valuation of the distribution of species in *Nepenthes*, *Dolichandrone* and others in Malaysia show the untenability of the assumed universal application of 'age and area' when explaining origin in conjunction with distribution. WILLIS's is a mathematical, not a biological trend of thought.

Cited literature: (1) Bull. Jard. Bot. Btzg III, 13 (1935) 358-385, with list of literature.

7. The effect of isolation

Isolation has been accepted as an important source of the origin of new species. It was assumed that an isolated group of plants would evolve independently, in the course of long periods, diverging in appearance from the parent population.

These views are derived from the theories of LAMARCK, DARWIN, and WALLACE and still find followers among zoologists.

In the light of experimental botanical taxonomy, however, it appears, *firstly*, that acons are unnecessary for the origin of new forms below the rank of a species, and of species themselves: *a few generations are sufficient*; and *secondly* it is highly improbable that single isolated, genetically well balanced species will give rise to constant new *taxa*.

Several allied species, however, growing together in geographical isolation from the ancestral populations may produce combinations not realized in the original centre, because they represent only a portion of the potential polymorphy of the genus and, at the same time, are closely allied and isolated when breeding. The probability of new *taxa* is increased the nearer this 'isolated affinity' is to the margin of the area occupied by the parent population, this marginal population being always distinctly different from that in the centre. Here recessive characters become predominant. Such a local development of an 'isolated affinity' may constitute a secondary centre of speciation. If the isolation is geologically ancient, archaic characters will be preserved as the isolated population remains untouched by the effacing influences of the original centre of speciation. Local and exceptional factors of climate and soil, aided by selection, will determine the constitution and general aspect of the isolated populations.

To measure the period of isolation by the number of deviating species present in an isolated area (a lake, a summit, an island) seems an uncertain procedure, since experimental taxonomy shows that speciation itself is a rapid process. Judgment is highly subjective and the effects of geological and climatic changes and other accidental factors influencing the life of isolated populations cannot be accurately estimated; reference may be made to what was said on geographical segregation in the introduction.

The most important function of isolation is the *preservation of types, gene complexes and genom combinations*, which may become lost in the dynamics of the remainder of the population.

An excellent opportunity for the study of the

effects of isolation is furnished by Australia where many plants were introduced, intentionally or unintentionally, in former centuries. In the Queensland flora several species are mentioned which are otherwise known only from Europe, and many others only from Asia. The Queensland forms are sometimes described as separate species, e.g. *Trigonella suavissima* LINDL. According to BENTHAM, this is closely allied to some South European species, but not quite identical with any of them. The same is the case with *Lavatera plebeja* SIMS, *Glycirrhriza psoraleoides* BTH., *Zinnia australis* BAILEY (genus otherwise neotropical), *Erythraea australis* R. BR., *Lycium australe* F.V.M., *Datura leichhardtii* F.V. M., &c.

Others are identical, or nearly so, with widely remote populations, such as *Static australis* SPRENG. (also recorded from E. Asia), *Alyssum linifolium* STEPH., *Gypsophila tubulosa* BOISS., *Saussurea carthamoides* BTH. None of these were collected at an early date and they are certainly not recent intruders. None has ever been found in Malaysia!

A closer study of this problem ought to comprise both herbarium and library work combined with field work and experiments. It may be that some of the above-mentioned species represent natural disjunct areas, but I find it extremely difficult to accept this for the majority.

8. Centres of speciation in the Malaysian flora

It is an established fact that the distribution of species within a generic area is mostly far from gradual and regular. Genera with a rich development of species specially show a specific differentiation in one or more centres radiating into neighbouring countries and become gradually or abruptly poorer towards the generic boundary. One could speak of the *decrease of the potential polymorphy of the genus* from the centre towards the boundary. *Isoflors* can be distinguished, that is, areas with the same number of species of one genus.

As a rule the outermost isoflor contains only one species which is generally also the most widely distributed. The natural explanation is to assume its emergence from the richer isoflors, *i.e.* from the centre of the genus.

(a) *The centre of speciation is situated outside Malaysia.* This is true of practically all microtherm plants (1), and is demonstrated e.g. by the genus *Primula* of which two species are recorded from Malaysia. One of these *P. sumatrana* MERR., is of uncertain affinity but approaches the type of *P. auricula* L., and is only found in the extreme north of Sumatra. The second species, *P. prolifera* WALL., belongs to *sect. Candelabra* which comprises some 25 *spp.* in SE. Asia, mainly in W. China. It occurs on the mountains of Sumatra and Java (fig. 38). The richest centre of specific and sectional development of the genus is SE. Asia (Himalaya-W. China).

The Malaysian species are obviously isolated outliers. The Malaysian localities are arranged

along a very definite line and this induced me to assume that the Malaysian species formerly migrated along a *migratory track* from the centre to reach their present stations at the limit of the generic area (1).

Similar examples are known in many other genera centered outside Malaysia, and I have therefore

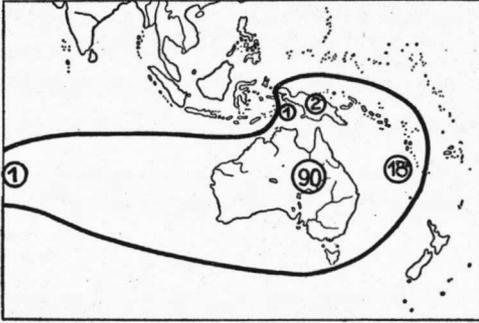


Fig. 39. Geographical distribution of the genus *Hibbertia* (Dill.), centre in Australia, one species in Madagascar.

concluded that at least 3 migratory tracks existed, the *Sumatran track*, the *Formosa-Luzon track* and the *New Guinea track*.

An example of a migrant along the Formosa-Luzon track is *Lilium*. This genus has 70 species in the N. hemisphere. Its subg. *Eulirion* sect. *Leucolirion* has 13 spp. in the Old World, to which the single Malaysian species *L. philippinense* BAKER from Formosa and Luzon belongs.

An example of a species following the New Guinea track is e.g. *Hibbertia* (Dill.), genus with ca 110 spp. of which 90 occur in Australia, 18 in New Caledonia, 1 in Madagascar, and 1 in New Guinea and Aroe Isl. The last is closely allied to one of the Queensland-New South Wales species (fig. 39).

The past history of the area and specific development in the genera *Primula*, *Lilium*, and *Hibbertia* are not known with certainty. Nevertheless judging from the present distribution, it seems clear that the marginal species are outliers spreading from the centre of specific development in each genus. Sometimes more than one species occupies the boundary area.

(b) *Genera with one centre of specific differentiation outside and another inside Malaysia.* Among Asiatic genera there are few examples of clearly marked centres. The number of Indian and Malaysian species belonging to such genera often gradually changes in various directions within the generic area as a whole. A remarkable case of several separate centres is *Rhododendron*, which has its richest centre in Himalaya-W. China with secondary centres in Borneo and New Guinea. Though exact figures are not known there is certainly *no gradual decrease* in the number of species from SE. Asia towards New Guinea. *Rubus*, *Poten-*

tilla, and *Gentiana* also have secondary centres in New Guinea.

Among plants with SE. affinities several good examples may be mentioned: *Trachymene* which contains appr. 20 spp. in Australia, 1 in New Caledonia, 1 in Fiji, 10 in New Guinea, 1 in the Moluccas, 1 in the Lesser Sunda Islands, 6 in Celebes, 1 in the Philippines and 1 in Br. N. Borneo. The orchid genus *Corybas*, with a rich centre in New Guinea is another striking instance (fig. 40).

A still more widely distributed genus is *Drimys* which extends from Mexico to Tierra del Fuego, and further to New Zealand, Australia, New Caledonia, New Guinea, the Moluccas, Celebes, Philippines, and Borneo. It has a separate centre in the S. Pacific and another in New Guinea.

A typical case of abrupt centres of specific development is *Euphrasia*, a microtherm genus almost confined to the N. hemisphere but with a distinct track across the Sunda bridge via Australia to New Zealand and Juan Fernandez, Tierra del Fuego, and Chile. From Borneo, Celebes, the Philippines and Moluccas only one species or subspecies is recorded, but in New Guinea a number of species occur in a secondary centre; a third is found in New Zealand (fig. 41).

It is difficult to see how these disrupt isoflora, and the formation of secondary centres could be caused otherwise than by past changes in the geography of the region concerned.

The only method of tracing the origin of new species of which factual proof is available is through hybridization combined with polyploidy. This demands that at least two species be present for the formation of new ones. If part of the generic area, e.g. New Guinea, is cut off from contact with the main centre of the population for a long period, some combinations which are not preserved in the main centre may maintain themselves. If at a later period another migration wave is made possible through geological changes, a further portion of the potential polymorphy may at length penetrate into the area and so take part in renewed speciation. This opens the possibility of new com-

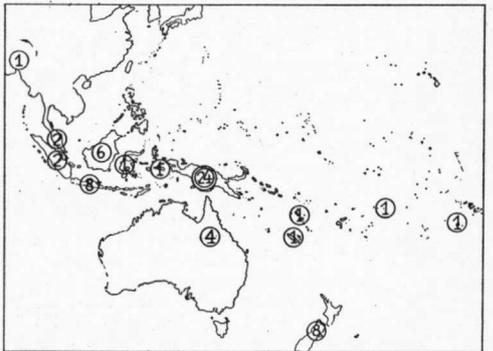


Fig. 40. Area of distribution of the genus *Corybas* (*Corysanthes*) (Orchid.). Centre in New Guinea, two secondary centres in W. Malaysia and New Zealand.

binations never realized in the original centre. The outcome might be the origin of a new secondary centre of speciation.

In the light of these hypothetical considerations the existence of secondary centres must indicate a complicated geological history of the area.

Similar pictures could be drawn for genera like *Dimorphanthera*, *Haplolobus*, *Xanthomyrtus* (fig. 43) *Palmeria*, &c., which centre in New Guinea and radiate into the Philippines, Celebes, and in some cases even into Borneo.

The richness of the centres in Malaysia is not

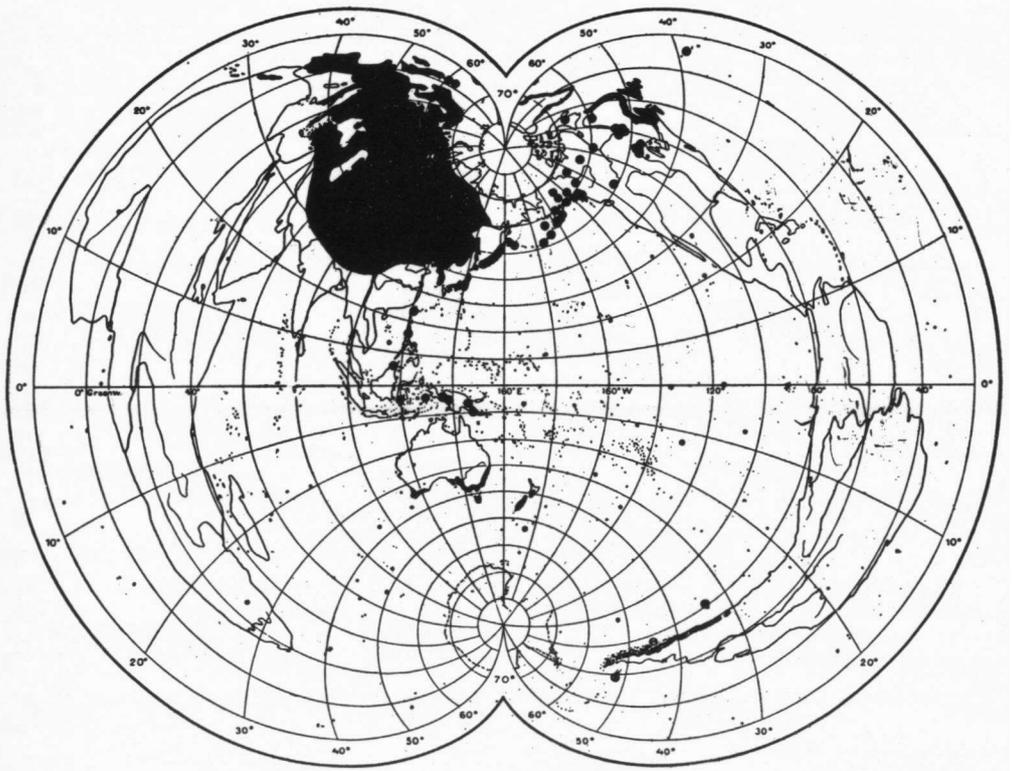


Fig. 41. Distribution of the genus *Euphrasia* L. (*Scroph.*). (after DU RIETZ, 1940)

(c) *Genera with a single centre of specific development in Malaysia.* An obvious example is the genus *Sericolea* (*Elaeocarpaceae*), with at least 17 spp., confined to New Guinea. A more advanced stage is seen in genera which have spread from their centre into other parts of Malaysia e.g. the genus *Archidendron* (*Leguminosae*) (2) (fig. 42). It is closely allied to *PitheceHobium* but differs in several flower and fruit characters, and shows the ancient condition of having more than one ovary.¹ The islands adjacent to New Guinea all have distinct species except for that of the Aru Islands which is also found on the main land.

(1) I wish to draw attention to the occurrence of essentially the same aberrant character in *Zoellera*, a *Boraginacea* from New Guinea. *Zoellera* was even proposed as the type of a separate tribe on account of its several carpels, but according to JOHNSTON'S opinion it is merely a remarkable pleiocarpous species of *Trigonotis*.

accurately known, the figures depending on the judgment of the monographer; most genera have not been recently revised. Though it is a common experience that when revisions are made many local endemics appear to be better reduced, it may be said that rich centres of specific development are situated in the West Malaysian province, specially Borneo, the Malay Peninsula, and the Philippines, and to a lesser extent in Sumatra. These centres, however, are mostly rich in the same genera and are better regarded as a single large centre.

The South Malaysian province (Java and the Lesser Sunda Islands) on the contrary, is exceedingly poor in centres of specific development, and does not represent a composite centre at all. New Guinea, in the East Malaysian province, appears to be a rich centre of the same rank as the whole West Malaysian province while the Moluccas and Celebes are poor and their vegetation mainly derivative.

Especially on the old continental shelf areas

specific development reaches its climax. This seems in contradiction to an almost generally accepted rule that a high percentage of specific endemism is typical of a young development. I refrain from commenting on this point, so as to avoid premature guess work.

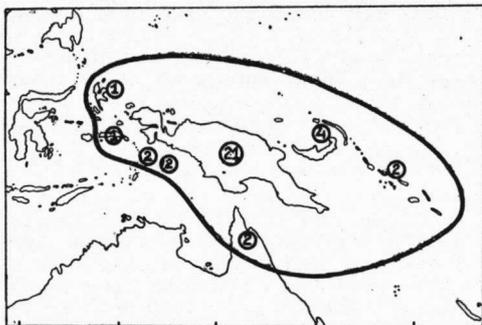


Fig. 42. Geographical distribution of the genus *Archidendron* (Leg.). Centre in New Guinea, with radiations into the adjacent regions.

The case of *Dryobalanops* may serve as a warning against drawing hasty conclusions. This is one of the well developed genera of dipterocarps in the West Malaysian province. The genus consists of 7 species found in a coherent area in Central Sumatra, the Malay Peninsula, and Borneo (fig. 44). There are no floristic or geographical characters to indicate that this genus is ancient, and its position among the genera *Shorea*, *Dipterocarpus*, *Vatica*, &c. which are far more differentiated is not isolated. Now, finds of fossil wood show that in the Tertiary *Dryobalanops* was abundant in South Sumatra and West Java. At present, therefore, it occupies a relic area.

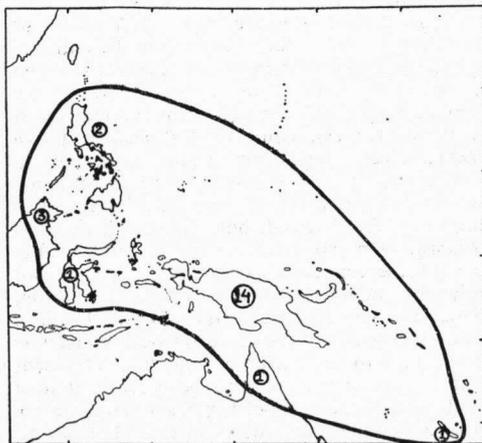


Fig. 43. Geographical distribution of the genus *Xanthomyrtus* (Myrt.). Centre in New Guinea, with radiations into the surrounding regions.

Most probably the centres of specific development are mixed, containing both progressive and relic species. To judge from the affinities, New Guinea harbours many old types belonging to a great number of families.

If the abundance of local endemics, so-called 'swarms', indicates a young flora, all tropical floras being very rich, must be young. I am not prepared to accept this assumption which implies that temperate floras are all of great antiquity.

It is sometimes assumed that rich specific development runs parallel with great diversity of habitat, varied topography and geology, and a variety of climatic conditions. Dr G. L. STEBBINS Jr alluded to this relation during the AAAS-meetings at Boston (Dec. 1946). The wet lowland forests of West Malaysia, on the other hand, show an intense speciation in e.g. *Dipterocarpaceae*, *Myristicaceae*, *Ebenaceae*, *Calamus*, *Canarium*, &c. although the environment has been extremely monotonous and uniform from an early period. Variability and

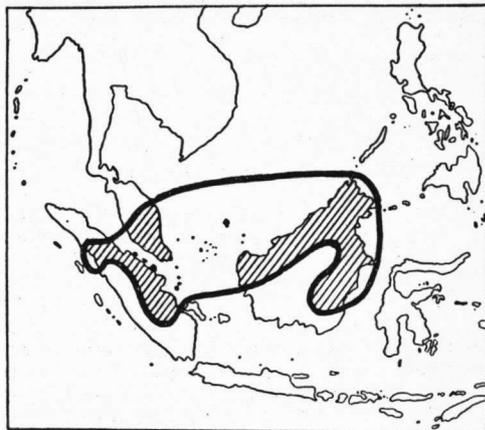


Fig. 44. Present area (shaded) of the genus *Dryobalanops* (Dipt.). Fossil records in S. Sumatra and W. Java.

change of environment are certainly not the only factors responsible for speciation.

Cited literature: (1) Bull. Jard. Bot. Btzg III, 13 (1934) 146. (2) DE WITT, Bull. Jard. Bot. Btzg III, 17 (1942) 256-271.

9. Centres of generic development in Malaysia

The centres of generic development show a similar picture as the centres of speciation; some notes will be given here.

In 1944, a survey of genera restricted to one island or island group resulted in the accompanying map (fig. 45). It appears that New Guinea is richest of all, and of the same rank as the total of the Sunda Islands and the Malay Peninsula together. Java, the Lesser Sunda Islands, Celebes, and the Moluccas prove to be poor. The estimates given in this map are generous because several

imperfectly known genera are included in the low figures. Sumatra in relation to its large surface is also rather poor in endemic genera. Borneo was possibly much richer in endemic genera formerly than it is now. During the Pleistocene Ice Age when the Sunda Islands were connected by dry land a number of endemic genera may have migrated out of Borneo and are now no longer endemics.

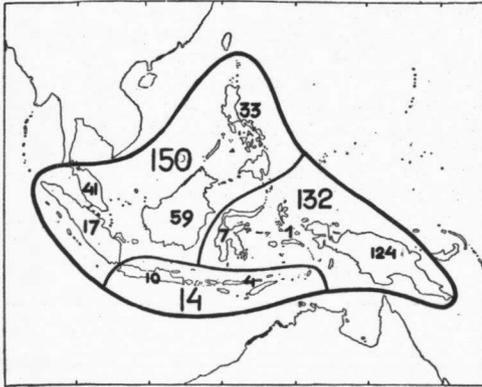


Fig. 45. Number of endemic genera of Phanerogams in the several islands and island groups of Malaysia, according to a census made in 1944.

Again the continental (shelf) areas, the Sunda Islands and Malay Peninsula in West Malaysia, and New Guinea in East Malaysia, are richest.

The figures must not be taken too strictly since they are not final and the revisions in the Flora Malesiana will effect changes in details. Moreover, no distinction is made between taxonomically very important genera (e.g. *Scyphostegia* in Borneo and *Papuzilla* in New Guinea) and those separated from large genera for convenience which represent merely derivative segregates.

10. Local-endemic species and genera

To a botanist experienced in tropical field work, records of strictly local-endemic species seem absurd. Nobody who ever looks down from a summit on a vast tract covered by luxuriant tropical forest untrod by a collecting botanist, can escape the thought that it is impossible to comb this welter of vegetation. In my experience novelties and new records are usual on every trip. Most mountains are climbed along one or, at best, very few trails, and even these frequented bridle paths continue to yield new finds and records at any time.

It is therefore scientifically inadmissible to discuss tropical local-endemic species.

A local-endemic species is one which has hitherto been found only in one single spot or island seems the only justified definition.

Botanists who have worked in the tropics are well aware of this but those acquainted only with the temperate vegetation seldom realize the true state of affairs.

In a tropical forest it is hardly possible to locate specimens of lianas, epiphytes and tall trees. Among all three classes some species are common and others are rare. To locate the rare or less common ones is impossible over more than a very limited area as for this purpose the vegetation must be cut down. How can one search for rare plants over hundreds of thousand square kilometres of forest vegetation?

Sometimes it is supposed that the flora of Java is completely known but, though Java is better known than any other large island in Malaysia, our knowledge is far from complete. Only a few years ago my colleague Dr BLOEMBERGEN was introduced to forest exploration work by a trained forester. In an area chosen at random in West Java for practice they found a large tree which proved to be a new species of *Vatica*. Only a single tree could be located. Another example is that of *Sophora wightii* BAKER discovered by JUNGHUHN a century ago in a mountain forest of West Java which is often assumed to be completely known. The small but conspicuous treelet has only been found once again. Of *Symplocos henschelii* (MOR.) BTH. from the same type of forest, also a small-sized conspicuous tree, in a century of botanical exploration in Java less than 10 individual trees have been located. Above Tjibodas, the mountain botanic garden in West Java, there are a few trees of *Ormosia incerta* KOORD. a 'local-endemic', which never flowered in 15 years. The monotypic Javan genus *Tetradia* R. BR. was once collected by HORSFIELD, and a century later one other tree was located in East Java. These are only random examples from a well-explored area. In the rich centres of development mentioned in the foregoing paragraphs the progress of collecting is *a fortiori* much slower.

The same holds still more true of the exact delimitation of the geographical distribution of species, even in Java. Owing to the habit of always keeping to the beaten track a small swamp in the Tjibodas Forest Reserve was never explored though lying only a few metres from the path below the well-known Tjibeureum waterfalls. When searched, *Xyris* and *Juncus* were found to grow there in profusion, both new records for this part of West Java (1). Until 1930 *Primula prolifera* WALL., a very conspicuous plant, was known in Java only from Mt Gedeh in West and Mt Jang, in East Java. A few years later two intermediate localities were detected, both by tips of amateur botanists. On Mt Papandajan, I could readily locate some dozens of species at that time known only from Central or East Java and, in addition, made some new records for the flora of Java (2).

Another source of error due to so-called endemic species adds to the urgency of compiling the present flora. Hosts of species have been ascribed to a single locality but reappear under different names in various other places in or outside Malaysia although they belong to the same, widely scattered population. This refers especially to the floras of the Malay Peninsula, the Philippines, and New Guinea, which have been studied without con-

sidering the whole Malaysian material. In revisions local-endemic species usually vanish by the dozen.

In the light of such facts it seems impossible to use data on tropical local-endemics in support of far-fetched and sometimes highly hypothetical speculations concerning basic problems of the origin and distribution of species (*cf.* Dr WILLIS's theory of 'Age and Area'). Reliable objective data on the exact distribution of tropical species suitable for highly specialized scientific analysis are not available; they are certainly not precise enough to serve as the foundation of theories depending on the accuracy of the details.

Cited literature: (1) *De Trop. Natuur* 30 (1941) 170-172. (2) *De Trop. Natuur* 19 (1930) 73-91; *ibid.* 21 (1932) 101-108.

11. Parallel or homologous variation

Parallelism is the phenomenon that similar characters, or combinations of such, occur in otherwise

different plants or plant groups of the same rank. The characters vary from modificational to structural importance. Parallelism is most conspicuous when it occurs in closely allied species or genera in the same geographical area.

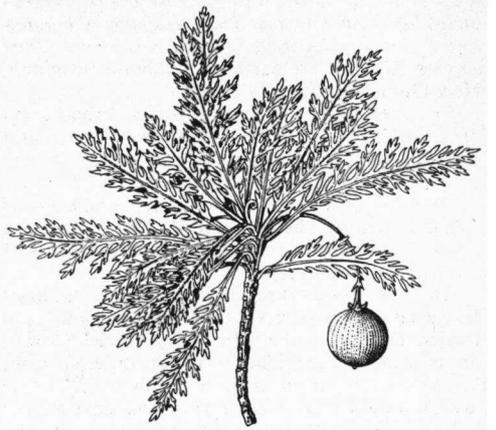


Fig. 47. *Discocalyx dissecta* KAN. & HAT. (*Myrs.*) from New Guinea, mossy forest, 1900 m, $\times 2/3$.



Fig. 46. Malaysian rheophytes: stenophyllous foliage as a common morphological 'adaptation' in systematically remote plants. a. *Nephrodium stenophyllum* BAKER (*Polypod.*), b. *Ardisia tahananica* K. & G. (*Myrs.*), c. *Ophioglossum inconspicuum* V.A.V.R. (*Ophiogl.*), d. *Boerlagiodendron borneense* (SEEM.) MERR. (*Aral.*), e. *Homonota riparia* LOUR. (*Euph.*), f. *Neonauclea chalmersii* (F.V.M.) MERR. (*Rub.*), g. *Aglaia ijzermannii* BOERL. & KOORD. (*Meliac.*). All $\times 1/4$, except d, $\times 1/6$.

Rheophytes are plants restricted to riverbeds within the reach of swiftly running water (1). They have several characters in common among which the most prominent are stream-lined leaves approaching the *Salix*-type, a strongly developed root system, and mostly a sympodial branching resulting in a flat-topped habit. BECCARI called them *stenophyllous plants*. Species of genera with pinnate leaves tend to have simple leaves under these conditions. These stenophyllous plants belong to about 80 different families and to a still larger number of genera. In several large genera more than one species of this habit is known *e.g.* *Ficus*, *Syzygium*, *Neonauclea*, *Aglaia*, &c. (fig. 46).

In many mountain plants the leaves are roundish with a cordate, pseudo-amplexicaulous base, prominent nervation, and a coriaceous texture (*Ericaceae*, *Guttiferae*, *Symplocaceae*, *Myrtaceae*, &c.). It is surprising to observe these features in Bornean *Ericaceae*: *Rhododendron*, *Costera*, *Diplycosia*, *Vaccinium*; this proves it not to be limited to mountain species, and that these features are not simply 'adaptive'.

In New Guinea a peculiar series of plants occurs belonging to families which characteristically have simple leaves; here the leaves are pinnatifid. The genera *Ardisia*, *Discocalyx*, *Begonia*, *Cyrtandra*, *Elatostema* are examples; in most genera more than one species shows similarly incised leaves. Why this convergent development should occur preferably in Papuan plants remains obscure (fig. 47).

In Bornean plants I believe to have traced a remarkable series of species in the most diverse families all possessing a peculiar long brown indumentum. These plants occur both in shady forests

and on light mountain slopes. The hairiness recurs in a large number of plant groups of very remote systematic position.

The same can be observed in other morphological characters, e.g. *cauliflory*, *flagelliflory*, *geocarp*, the *cycadoid habit*, *exceedingly large leaves*, the *presence of tubers*, and the *occurrence of exceedingly long caudate-acuminate leaf-tips* ('Träufelspitze'), *macrobiocarp*, and *microphyllous dwarf species*. The last are particularly abundant among New Guinean mountain plants.

NAUDIN (2) drew attention to numerous cases of parallel variation in the *Cucurbitaceae* and DUVAL-JOUVE (3) mentioned instances in the *grasses*, and in *Juncus*.

DARWIN (4) termed such variation *analogous* or *parallel variation*; he observed it often in different races of one species, more rarely in descendants of remotely allied species.

HUGO DE VRIES (5) regarded the results of parallel variations as derived true varieties, and contrasted them with the elementary species (Jordanonts) which he considers as of quite different rank.

VAVILOV (6) in an essay on what he calls 'the law of homologous series in variation' gave a large body of new examples in the *grasses*, *cucurbits* and *leguminous plants*. He assumes that each family has a 'cycle' or 'series' of variability present in all its genera.

VAVILOV's idea was that these genera have an inner stable hereditary set of '*radicals*' governing the major structural characters. Besides, numberless other factors act in varying ways, but more superficially (like slight variations in embroidery on a basic underlying pattern). *Radicals* and *variable characters* (specific complexes of morphological and physiological nature) would thus be essentially different.

In a most interesting study of the 90 known genera of the *Annonaceae* DIELS (7) opposed the views of DE VRIES and VAVILOV. He found that the characters used to separate genera are not '*radicals*' but that each genus is characterized by a complex of '*varying characters*'. If, in the *Annonaceae*, concluded DIELS, one wishes to speak of radicals, then there is only one radical; the family character (structure). He pointed to the fact that VAVILOV himself shows some uncertainty when attempting to trace a sharp distinction between radicals and varying characters. He also opposed VAVILOV's thesis that only radicals are important in taxonomy and phylogeny and that therefore the systematics of the *Cruciferae* is wholly at fault (being based on varying characters) in contrast to the *Ranunculaceae* where the genera are separated on structural differences. DIELS pointed out that these families cannot be compared and contends that the degree of sharpness in demarcation depends on the absence or presence of intermediate homologous variants, or, possibly on our ignorance of the existence of such 'links'. For the *Annonaceae* DIELS tabulated the following characters: 1. aestivation; 2. dimery against trimery; 3. perianth partly connate or free; 4. anthers locellate or not, 5. distribution of the sexes (polygamous, monoecious,

dioecious); 6. insertion of the flowers (on leafy twigs, or cauliflorous to flagelliflorous). Each genus is in this way represented by a certain formula. It appears that very few possible combinations are not realized in nature; some exist but have only recently been collected, e.g. *Mezzettiopsis*, in 1912, in Borneo, with formula P | 1 O. Hence very few are extinct. The present 'completeness' and 'prosperity' of this pantropical family in the recent flora is a highly interesting phenomenon as it is generally believed to be of ancient ancestry. The formula Ka Pr O ∞ ascribed to the theoretical ancestor of the *Annonaceae* is still shown by several genera distributed over the whole of the tropics. Parallel variation causes a reticulate structure of affinities. From an evolutionary point of view one generally assumes a 'pluripotent ancestor'.

Genom complexes (HAYATA) (8), or 'Artengene' of HERIBERT NILSSON (9) seem to be more or less independent and may be combined into different formulas. HAYATA is therefore probably right in assuming so-called analogies to be not essentially different from homologies.

Cited literature: (1) Bull. Jard. Bot. Btzg III, 12 (1932) 196-201. (2) Ann. Sci. Nat. IV, vols 6, 7, 12, 16. (3) Bull. Soc. Bot. France 12 (1865) 196-211. (4) Variation, 1 (1868) 442-458; 2 (1888) 340-345 (2nd Engl. ed.). (5) Die Mutationstheorie 1 (1901) 454. (6) Journ. Heredity 12 (1922) 75. (7) Sitz. Ber. Preuss. Akad. Wiss. 1932, Math. Phys. Kl. p. 77-85, specially p. 81. (8) Icon. Plant. Formos. 10 (1921) 76-234. (9) Lunds Univ. Årsskr. N. F. Avd. 2, 27 (1930) 3-4.

12. Reticulate affinities

Reticulate affinities occur chiefly in moderately large to large genera of plants. Normally a large group of allied species is intimately interrelated and shows different combinations of a relatively limited number of more or less equally important characters. Reticulate relationship makes a natural classification very difficult and is unsuitable for a linear arrangement. A division of the group into sections and subsections is hardly possible.

According to DANSER *Nepenthes* is a case in point; the species are often closely allied to one another, division into subgenera or sections is impossible (1), but the genus itself is a most natural unit.

A similar state of affairs is found in large groups of the genera *Begonia*, *Ficus*, *Vaccinioideae*, *Rhododendron*, *Syzygium*, *Symplocos s.str.*, *Saurauia*, and others, all showing an abundant development of species in Malaysia.

Reticulate affinities probably indicate 'fully expressed' potentialities.

It is not certain, of course, that all potentialities in every plant group are viable, and may have existed or will exist, or will exist at the same time. Gaps may persist by inner genetic necessity.

I am not prepared to answer the question whether this must be considered to be a 'young' or an 'old' feature. The development itself has probably been accomplished rapidly. Its preservation has pro-

bably depended on the dynamics of disturbing environmental factors. Damp tropical hothouse conditions are more apt to preserve uncommon combinations than any other environment, and organisms with poor prospects of survival may find an ecological niche here and survive.

Cited literature: (1) Bull. Jard. Bot. Btzg III, 9 (1928) 403.

13. Vicariism in the Malaysian flora

Vicariism is the phenomenon that two species which are *inter se* distinctly closer related than to any other member of their group, replace one another with exclusion of their area geographically or altitudinally. Vicariism occurs both in the lowlands and the mountains, and between lowland and mountain plants.

Whether one should speak of subspecific segregation or of racial differentiation in delimiting such species is sometimes merely a matter of taste. In the latter case geographical exclusion is necessarily present. Therefore, it seems preferable to apply the term 'vicariads' only to taxa which are by general consent lineonets.

Typical cases of vicariism are found in mangroves. VAN SLOOTEN (1) has demonstrated that the two allied species of *Lumnitzera* exclude each other almost consistently. A similar case of exclusion is found in the genus *Camptostemon* between *C. philippinensis* (VIDAL) BECC. and *C. schultzei* MAST. (2).

Still more remarkable behaviour is shown by *Aegialitis*. The two species in this genus are both restricted to the mangrove, one occurring from Bengal to Mergui and the other in East Malaysia and Queensland (fig. 48).

In *Gossampinus* two species occur in Java, viz *G. malabarica* (DC.)ALST. and *G. valetonii* (HOCHR.)BAKH. which exclude each other, *G. malabarica* preferring the semi-arid central and eastern regions, *G. valetonii* being confined to the everwet western parts. In Central Java few inter-

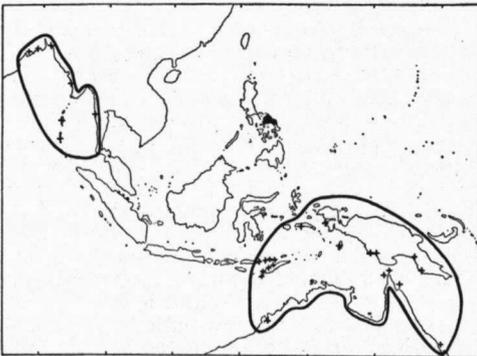


Fig. 48. Geographical distribution of the genus *Aegialites* (Plumb.). The Asiatic species *Aeg. rotundifolia* (Pr.) ROXB., the Australian-East Malaysian *Aeg. annulata* R.Br.

mediate specimens have been found and are assumed to be hybrids.

Vicariism also occurs in mountain plants; a few examples may demonstrate this. *Gynura aurantiaca* (BL.)DC. occurs in Java from Mt Gedeh eastward to Mt Willis between 850 and 2400 m, the species replacing it in East Java is *G. densiflora* MIQ. which is found from Mt Lawoe eastwards, between 2200 and 2800 m (3).

A similar replacement is found in *Anaphalis*. *A. javanica* SCH.BIP. occurs in West to Central Java and *A. viscida* DC. replaces it in East Java (4) and North Central Java.

Closely allied species, but never found close together, are *Polygala pulchra* HASSK. and *P. venenosa* (BL.)JUSS., the first is practically confined to ridges and summits, the latter to the forest borders and gently sloping forest; they possess the same size and habit.

In *Agathis*, DANSER distinguishes 3 Malaysian species viz *A. borneensis* WARB. in the Malay Peninsula, Sumatra, and Borneo, *A. alba* (LAMK.)FOXW. in the Philippines, Celebes, and Moluccas, and *A. labillardieri* WARB. in New Guinea and adjacent islands. Each of these three allied species excludes the others from its area of distribution but they all occupy the same place in the vegetation.

Typical cases of altitudinal vicariism are also known. Two species of *Sopubia* occur in Malaysia, *S. stricta* DON in SE. Asia also occurring in Madoera Island (E. Java), in lowland grassfields. *S. trifida* HAM. is a mountain plant known from Africa through trop. Asia and Malaysia to Australia. In Malaysia its altitudinal range is 950-1800 m. In Java it is found in one place, due S of Madoera Island on Mt Idjen, also in grassfields, at 1000 m.

In *Orchidaceae*: *Bulbophyllum tenellum* LINDL. occurs in Java between 1000 and 1500 m, but according to J.J. SMITH its closest ally, *B. xylocarpit* J.J.S., is confined to mangrove forests. Both are epiphytes.

In Java and the Lesser Sunda Islands two native species of *Casuarina* occur, the first, *C. equisetifolia* L., confined to the coastal regions or the beach and the second, *C. junghuhniana* MIQ. (= *C. montana* MIQ.), occurring exclusively in the mountains and, although its lower limit descends from W to E, the two species never occur mixed.

In Timor and adjacent islands at least two species of *Eucalyptus* occur: the white-stemmed *Euc. alba* REINW. in the lowlands and the dark-stemmed *Euc. cf. platyphylla* F.v.M. (an *Eucalyptus decaisneana* BL.) in the mountains. Occasionally populations adjoin but they are never found mixed.

Similar cases are known in the genus *Styphelia*, of which allied species occur in the lowland and the mountains.

The Javan *Loniceras* have already been mentioned in the paragraph on altitudinal racial differentiation. *L. acuminata* WALL. and *L. javanica* (BL.)DC. occupy corresponding places in the mountain forest but their areas do not overlap altitudinally (fig. 35).

How vicariads would behave if they would not be separated is a very interesting question both

from the taxonomical and the phytogeographical point of view. In some cases SAX (5) found a high degree of fertility (*Platanus*, *Campsis*, *Larix*) between geographically remote species. Recently E. C. SMITH proved in *Catalpa*, that in species which have been isolated during a considerable period a complete interspecific fertility may have been preserved (6). It is not clear what the aspect of the population would become when these species would be in close contact.

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14. *Adaptation and migration*

The concept *adaptation* is closely interwoven with that of 'natural selection' which causes it to be often misunderstood. On the other hand it ought not to be discarded; after all, plants are adapted to the place where they grow. They are able to tolerate the limiting factors of their particular station because they possess certain genom structures which provide the individuals during their development with physiological and morphological characters enabling them to grow and propagate.

Adaptation is not an innate purposeful change, and selection is a merciless agent directed by the environment, unyielding in its basic demands for adjustment to its minimum factors. The plant is left no way out, it has to comply or to perish on the spot. Each plant is, therefore, of necessity adapted to its habitat, that is: in accordance with the local minimum factors indispensable for its survival and propagation.

The only 'active' principles of the plant as a passive object are the genetic dynamism of the population which produces new combinations, partly viable partly lethal, and also its population 'pressure' leading to dispersal resulting in migration.

The phrase that plants 'have adapted' themselves, then, means that the population has managed to produce combinations capable of meeting the minimum claims of the environment.

Adaptation is therefore selection based on tolerance, a general principle affecting every plant species, and every vegetation type (1).

A species migrating into a semi-arid savannah area burned yearly must possess properties to withstand this savannah environment. It must either be able to sprout from a rootstock, a bulb or a tuber, or its stem must be corky, its seeds must be able to germinate in the open and withstand fire, its root system must be able to get water even during a long dry period, &c. These demands are also met by ephemerals which complete their life cycle within the short period of the rainy season.

Forests also offer a special environment; its

species must be able to germinate, flower, and fruit in the shade. Similarly in case of mountains, swamps, solfatara, &c.

This harmony between plant and *monde ambiante*, as an implied result of the tolerance of plants under the selective agency of the environment is, to a certain extent, reflected in the biological spectra of RAUNKIAER. It is essentially the same as R. D'O. GOOD's 'Principle of Tolerance', and the general conception of natural selection by DARWIN. The environment is thus partly directive.

These considerations, however, do not exclude the possibility that plants possess *characters which have no relation with the demands of the environment*. Indeed most structural characters are unaffected by the environment *e.g.* the type of inflorescence, the phyllotaxis, the number and attachment of ovules, whether the ovary is superior or inferior, whether the stamens are diplostemonous or obdiplostemonous, the habit arboreous or herbaceous, &c. The plant will thrive if, within its range of tolerance, it can adjust itself to the conditions of life in its environment, if not it will inevitably perish.

The harmony between plant and habitat does not imply that the nature of the habitat of a plant can be deduced from its appearance. Physiology apparently admits diverse means of adjustment. We find, *e.g.* in the microphyllous stunted forest of the Papuan Alps large-leaved species of *Schefflera* and *Olearia* at 4000 m altitude, and equally hygrophilous large-leaved species of *Alpinia*, *Cyrtandra*, and *Saurauia* at 3000 m altitude on the summits of Celebes. In Java at the same altitude we find with the dominant microphyllous *Vaccinium*, *Leptospermum*, and *Rapanea* trees, typical hygrophytes as *Neillia thyrsiflora* DON, *Prenanthes rostrata* BL., and mesophyllous large-leaved *Photinia notoniana* WALL.

We should be wrong to infer the habitat of *Taxotrophis*, which sometimes dominates the undergrowth of everwet Malaysian forests, from its morphology; the very hard thorny leaves would suggest it to be a species of semi-arid thorny jungle.

Hairiness is also no indication whatever of habitat. S. KURZ (2) already commented on this with regard to *Semecarpus* of the Nicobar islands. He says: "This tendency to become pubescent is peculiar to a great number of tropical trees, and is not attributable, as some may suggest, to a drier or sunny station, but seems to be rather idiosyncrasy. For we often find the two states growing side by side in the densest shade of the tropical forests. This is the case, *e.g.* with *Micromelum pubescens*, while the perfectly glabrous and the almost villous-pubescent form... of *Vangueria spinosa* grow similarly associated in the dry hot forests of Prome. Other examples of the same phenomenon are afforded by *Garuga pinnata* and *G. mollis*, *Chickrassia tabularis* and *Ch. velutina*, *Schrebera swietenia* and *Schr. pubescens*, *Holarhena codaga* and *H. antidysenterica*, *Trewia nudiflora* and the glabrous form, *Berrya ammonilla* and *B. mollis*, *Grewia laevigata* and its pubescent form,

Walsura trijuga and *W. pubescens*, *Amoora rohituka* and *A. aphanomyxis*, *Terminalia catappa* and its pubescent form, and numerous others. In two only of these, viz in *Berrya* and *Micromelum*, have I observed real intermediate and therefore connecting states. In most of these cases not only are the vegetative parts affected but the calyx and the corolla also." Another typical case from Java may be added. *Dodonaea viscosa* JACQ. occurs behind the beach in a glabrous form and on the mountains between 1100 and 3300 m in a hairy form!

A consistently microphyllous type of vegetation is found on the sandy padang soils of Banka, dominated by *Baeckea frutescens* L., *Eugenia bankensis* (HASSK.) BACKER, *Styphelia malayana* (JACK) J.J.S. and *Leptospermum flavescens* J.Sm. The leaves of these plants are typical of micro-sclerophyllous scrub of xerophilous habitat. The habitat is in fact everwet tropical lowland, suitable for coconut and pepper.

One of the wildest theories I ever met in literature was proposed by the geographer W. VOLZ. He supposed that during the Upper Pliocene there was an arid climate in North Sumatra (3), basing, or mainly sustaining, this theory on the statement that the present vegetation of *Pinus merkusii* JUNGH. & DE VR., *Saccharum spontaneum* L., *Imperata cylindrica* P.B., *Pteridium aquilinum* KUHN, and a spiny 'Acacia' consists of relics from an arid period, these being 'xerophilous' plants. This absurdity needs no further comment here; it is a layman's fancy when, in the field on a hot sunny day, trying to understand narrow leaves.

These examples show the uncertainty of deducing a climate from the morphology and size of leaves only. This is important especially in palaeontology, particularly because in general only the thicker leaf types will be preserved.

Adaptation, then, exists but in the restricted sense discussed above. Its manifestation is quite different from what is often popularly described and illustrated by picked cases. Life apparently has many means to meet the demands of the environment.

Migration is not a purposed but a passive dynamic process affecting all plants. Each plant tends to (not intends to) expand its area from the mere fact that seeds or spores are produced and disseminated by each generation in various ways and through various agencies. If conditions in the area are uniform this extension will be circular, as a fungus spreads on an agar plate.

In nature the expansion will be modified by the surrounding barriers e.g. a mountain plant on an elongated range will 'follow' the range. Such \pm linear radiations have been found to exist in Malaysia. I have named them 'tracks', along which plants wandered, dissemination being the only impulse for progress.

If the environment becomes active—changes abruptly or secularly, which certainly happens continually—plants are driven from their original sites. With the change in the environment, the demands change. Suppose that in some region a secular change of the climate towards more arid

conditions takes place. This desiccation will cause the gradual multiplication of the most drought-resistant combinations, and there is much shifting. It is conceivable that these drought-adapted combinations had formerly no chance of survival under moist conditions and always perished *in situ*. Under the new conditions they have a chance of survival and a new species or subspecies is created. Other species which could just survive earlier moist conditions, and occurred in small numbers in the driest stations, multiply gradually at the cost of those species which were at their optimum under the moist conditions. Species unable to produce arid-tolerant races will become exceedingly rare, or disappear entirely. Thus the whole community is affected by the shift due to climatic change.

Another kind of change in the environment is orogenesis (mountain formation); this has played an important role in the composition of the Malaysian plant communities. The environment will now select hardy types because temperature tolerance is most important in plants. Orogenesis opens the possibility of the origin of new combinations either of specific or infra-specific rank. The facts support this view: many typically tropical genera and families mainly developed in the tropical lowlands have shown ability to produce mountain species (*Pandanus*, *Macaranga*, *Albizia*, *Casearia*, &c).

Conversely, typically microtherm genera have produced species able to thrive in the tropical lowland (*Corybas*, *Ajuga*, *Lysimachia*, *Salix*, *Salvia*, *Rosa*, *Ulmus*, *Clematis*, &c.).

The abrasion of Malaysian mountains by rapid tropical erosion causes, in addition, a gradual shifting of the mountain vegetation from cool zones to the subtropical and tropical climates (4). This is not mere hypothesis, it has actually occurred on large massifs now demolished or reduced to medium height. In particular, this process is still going on in the Malay Peninsula and the islands in the S. China Sea which have been subjected to erosion for a geologically very long period. Some mountain plants kept their ground on the summits at exceptionally low altitude, e.g. *Oreobolus kukenthalii* STEEN. which grows, in the Malay Peninsula, at much lower altitudes than in Sumatra. Together with some other plants I believe it to be representative of a formerly much richer relic flora which is now largely extinct.

Adaptation and migration are inseparable, their mechanism is always bound to a passive selection by the environment.

The size and variation of the area of distribution of a species or a genus is thus undoubtedly dependent on geography and topography (presence of barriers) and the capability of its genetic potentialities to produce combinations able to meet the demands of the very different environments nature throws in its path.

The 'why' and the origin of these potentialities are an aspect of the genom chemistry, which has today hardly reached the stage of research, and is still beyond our knowledge.

A survey of the size and development of the different natural plant groups as a manifestation of the capacities of the genom shows that some groups are of small size but occupy a considerable area, others have a large area and hundreds of species, still others demonstrate a huge development in a comparatively small region, and this leads one to suppose that development is to some extent illogical and not subject to strict causality.

Nature is nevertheless causal and causality governs the chemical and physical background of the genom structures.

As far as I can see the taxonomy of chemical compounds corresponds to a certain extent with biological taxonomy. Some compounds are stable, others unstable, some are widely spread, others are local, some elements have developed into a highly divergent pattern (like carbon) comparable to tribes and highly differentiated orders, others abstain from developing into families, some elements have still unlimited potentialities, of others the potentialities are rigidly restricted.

The comparison goes further: reticulate affinities and linear affinities are present in chemistry as well as in biology. The compounds known to us, or presented in nature remain, in number and structure, far below the conceivable ones, and are subject to natural selection. Chemical taxonomy presents only that set of compounds which is in agreement with the environment offered by our globe. Other parts of the universe presenting other environments open the possibility for other chemical combinations. The chemist endeavours to create artificial environments favourable to the development of compounds not manifested in nature, like a biologist creating *Primula kewensis*. Hollow curves, which WILLIS (5) considered so important are equally valid for biological and chemical taxonomy, and are based essentially on the structure of the natural system of chemistry, that is, homologous with it. It would seem worth while to work out the 'ancestral tree' of chemical compounds.

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15. Hybrids in the Malaysian flora

Few natural hybrids have been recorded from the Malaysian region partly because of the primitive stage of research on the subject. The few facts which have come to my knowledge I will enumerate here.

One of the first records in the Indo-Malaysian region is a hybrid between *Blumea bifoliata* DC. and *B. lacera* DC. by S. KURZ (1) who found this 'undoubted' hybrid in Calcutta.

In the middle of the last century, VERTCH's collector, THOMAS LOBB, and Sir HUGH LOW accumulated a wealth of material of Malaysian *Rho-*

dodendron. in the Malay Peninsula, Sumatra, and Borneo, for cultivation. Among the species concerned were *Rh. brookeanum*, *javanicum*, *malayanum*, *jasminiflorum*, and others. From these VERTCH succeeded in raising for ornamental purposes numerous hybrids with fertile progeny (2).

WIGMAN (2) apparently made some artificial hybrids of *Passiflora* species in the Botanic Gardens, Buitenzorg, but did not write a full report.

Several Malaysian species of *Nepenthes* are used in raising hybrids for ornamental purposes, and apparently some of these hybrids are also found in nature. According to DANSER (3) no scientific records are extant on progeny and fertility of the hybrids. The difficulties in specific delimitation in this genus are certainly partly due to natural hybridization.

In *Gramineae* quite a number of hybrids are recorded or supposed to occur in nature. BACKER (4), in his work on the Javan grasses, repeatedly refers to intermediate forms supposed to be hybrids. Hybridization in grasses is not limited to members of the tribes, inter-tribal hybrids being known as well. Some results of the extensive experiments with grasses made at the Sugar Experiment Station, Pasoeroean, Java, were published by RÜMKE (37). He experimented with hybrids of *Saccharum* × *Erianthus*. The notes on most trials were deliberately destroyed when the station was burned down in 1947, much to the loss of science.

In *Juncus*, BACKER recognized a plant from Java (5) which he assumes to represent a natural hybrid between *J. glaucus* EHRH. and *J. effusus* L. It should be noted that on the mountains where this hybrid was collected, one of the parents (*J. glaucus*) is absent.

BACKER (36) mentioned the occurrence of an intermediate form in *Glinus* in places where *Gl. lotoides* L. and *Gl. oppositifolius* (L.) DC. grow together; he assumes this to be of hybrid nature.

Parkia intermedia HASSK. is a species described from Java. According to BACKER (6) there are two forms. The first he believed to be a hybrid between *P. roxburghii* DON (= *P. javanica* (LAMK.) MERR.) and *P. speciosa* HASSK. The other he suspects to be a hybrid between *P. intermedia* HASSK. and *P. speciosa* HASSK. He added in a note, that according to trustworthy native information *P. javanica* and *P. intermedia* would very often develop from the seeds of *P. speciosa*. Moreover, *P. intermedia* is never planted as such, but always develops from seeds of *P. speciosa*. Though it could be easily assumed that cross-fertilization through bats occurs, genetic research is needed to settle the status of these forms.

Of *Gossampinus* two species are well-known in Java, viz *G. malabarica* (DC.) ALST. with dark-red flowers and *G. valetonii* (HOCHR.) BAKH. with pale or greenish-yellow flowers. In distribution these two species exclude each other; they are vicariads, *G. malabarica* preferring the semi-arid regions, *G. valetonii* being confined to the parts which are wet throughout the year. Both occur throughout Java, as the climatic zones form an intricate mosaic of local climates. In Central Java specimens have

been collected with nearly orange to orange flowers and other intermediate characters. Mr BAKHUIZEN VAN DEN BRINK Sr suggested that these specimens represent hybrids (7).

In Timor at least two species of *Eucalyptus* occur, viz the white-stemmed *hoeë*: *Euc. albã* REINW. in the lowlands, and the darkstemmed *anpoepoe*: *Euc. cf. platyphylla* F.V.M. (an *Euc. decaisneana* BL.) in the mountains. Dr BLOEMBERGEN (8) made a special search into the interior for eucalypts and found, in a locality where both parents were present, some trees intermediate, both in bark and other characters. As hybrid swarms of eucalypts are common and well-known in Australia, the assumption of the occurrence of hybrids in Timor is very likely to prove correct.

In *Polygonum* DANSER (9) originally located only one natural hybrid in Malaysia, viz between *P. barbatum* L. and *P. pulchrum* BL., which he recorded from Siam, the Malay Peninsula, West Java, and Kangean. It is entirely sterile. In the W. Java locality *P. pulchrum* was present, but the other parent was absent!

Later he found (10) two other *Polygonum* hybrids, and also some in *Rumex*. The first was cultivated in the Botanic Gardens, Buitenzorg; he interpreted it as *P. runcinatum* D.DON \times *P. chinense* L. Flowering was abundant but fruit never formed, pollen developed poorly.

The other hybrid was between *P. orientale* L. and *P. pulchrum* BL. and was found in great quantity in some swamps in Central Java. The plant had the habit of *P. pulchrum* which was also present in the locality, but the other parent *P. orientale* was absent. The hybrid is entirely sterile.

In *Stachytarpheta*, a genus of *Verbenaceae* native in the New World, some natural hybrids have been found in Java and elsewhere in Malaysia. DANSER who described (11) the hybrids also succeeded in making artificially combinations not seen in nature. Four out of 6 possible combinations had been found wild. All hybrids were intermediate and sterile. One of them did not flower for a long time but, some years after DANSER had left Buitenzorg, I noted that this plant was flowering.

In his works on Malaysian *Orchidaceae* J. J. SMITH occasionally referred to hybrid orchids but to my knowledge he never gave a summary of his observations. He made a hybrid *Spathoglottis* (12) and described a hybrid *Vanda* (13) from Alor Island, an artificial hybrid *Coelogyne pandurata* LINDL. \times *asperata* LINDL. (14) as well as the natural hybrids *Calanthe ceciliae* RCHB. f. \times *C. veratrifolia* R.BR. in Java, and *C. speciosa* LINDL. \times *C. pulchra* LINDL. (15).

Mr R. E. HOLTUM paid much attention to hybrid orchids and made extensive observations in the Singapore Botanic Gardens. He wrote a large number of papers on his experiments from about 1930 onwards. Several important remarks in these studies (16-21) attack the very basis of the generic and specific concepts in orchidology.

In the first place it seems beyond doubt that numerous native species are of hybrid origin, e.g.

Arachnis maingayi RCHB. f. = *A. flos-aeris* RCHB. f. \times *hookeriana* RCHB. f., *Dendrobium superbiens* RCHB. f. = *D. bigibbum* LINDL. \times *veratrifolia* LINDL. (or some other combinations of sections *Phalaenanthe* and *Ceratobium*), while *Dendrobium fleischeri* J.J.S. is *D. phalaenopsis* FITZG. \times *d'albertisii* RCHB. f.

Further natural and artificial hybrids are known in the genera *Cymbidium*, *Paphiopedilum*, *Renanthera* (22), *Phalaenopsis*, &c.

Intergeneric hybrids are also known (23), and species of *Vanda* (incl. *Euanthe*, *Vandopsis*, &c.), *Phalaenopsis*, *Arachnis*, and *Renanthera* are in most cases freely inter-fertile which stresses their close relationship. Records of the distinctive features of the hybrids produced by such inter-generic crosses may help to throw light on the mutual relationships of the genera and on their true status. The fact that the lip characters of *Renanthera* are, in hybrids, almost entirely dominant in the F_1 is of interest. Now that so many bi-generic hybrids in this group are being raised in the eastern tropics, we may expect a good deal of further information of this nature, which systematists might well study and consider.

Some orchid hybrids are sterile in the F_2 , and several flower seldom. The F_1 is mostly intermediate. Hybridization has, most probably, played a very important role in the speciation of *Orchidaceae*, and this may explain a good deal of their boundless development in Malaysia and some other tropical countries. It would be an intricate task to disentangle the relations. It is certain, however, that numerous described species will appear to be of hybrid origin.

A similar view could be held about *Rhododendron*, already referred to above. Nevertheless in Java, as far as I know, the 7 species and one variety are sharply distinct and no natural hybrids have been recorded. Other islands carrying a profuse development of the genus (Sumatra, Borneo, and New Guinea) have a different record.

In 1932, Dr C. HEUSSER collected much material of *Rh. longiflorum* LINDL. in Samosir peninsula, Lake Toba (N. Sumatra), at ca 900 m. He also found a gregarious *Rhododendron* scrub near sol-fatara in the same place where plants varied in the colour of the flower and shape of the leaves. Dr J. J. SMITH described them (24) together as *R. longiflorum* LINDL. var. *heusseri* J. J. S. The variety is, however, far from uniform and the collector hints at the possibility of a hybrid progeny.

The same species, *Rh. longiflorum* LINDL. has also been used in artificial crosses, as was reported by Mr R. E. HOLTUM (25-26) who began to cross *Rhododendron* experimentally at Singapore.

I am convinced that hybridization had an important creative function in the specific development of the genus in Malaysia. The practical work needed for a real understanding of the specific relations here will require laborious experiments with native species from remote regions, the cultivation of which will present serious difficulties in itself.

Also in *Diplycostia* (*Ericaceae*) reticulate affini-

ties suggest the possibility of a hybrid origin of species, which are known to occur elsewhere in the family in *Vaccinium*, *Gaultheria*, &c.

A speciality of the Malaysian vegetation is the possibility of hybrid native trees. In the *Dipterocarpaceae* with its swarms of species in *Dipterocarpus*, *Shorea*, &c. hybridization has been reported in the genus *Dipterocarpus* from the Philippines (27), Thailand (28), Burma (29-30) and the Malay Peninsula (31-32).

SYMINGTON (33) says that the so-called hybrid plants have characters intermediate between those of well-known species. In Burma PARKINSON reports that "small pockets or patches of these hybrid plants sometimes occur intermixed with the parent types where, with little trouble, specimens showing a whole range of characters from one species to another could possibly be collected. These plants are even recognized as being of hybrid nature by village Burmans. It appears that most of the species of the genus, if not all, hybridize naturally."

According to SYMINGTON, a similar statement could not be made for Malaya, but he does not claim to have given the problem much attention. He says that it is possible that some of the intermediate collections will turn out to be clearly defined species that have escaped the collectors because of chance and their comparative scarcity e.g. *D. kunstleri* KING, which was at one time suspected of being a hybrid (34).

The opinion of so highly experienced a specialist is of course important but it does not exclude the possible hybrid origin of plants now recognized as good species.

Many hybrids are known among Malaysian ornamental plants, e.g. in *Hibiscus*, *Canna*, *Lantana*, *Bougainvillea*, &c. and also in economic plants and crops, e.g. *Ceiba*, *Citrus*, *Mangifera*, *Oryza*, *Hevea*, *Thea*, *Solanum*, *Eugenia*, &c. (35).

Important observations were made by Dr H. J. TOXOPEUS who succeeded in making a hybrid between the genera *Gossampinus* and *Ceiba*, and also between several different genera in *Rutaceae*. In the latter family, the generic concept is taxonomically far from stable and convincing.

A most interesting fact, found by VILLERTS (1937), is that species of *Begonia* from almost all sections could be intercrossed.

In conclusion I want to express the opinion that, though few facts are known, it is likely that hybridization has played a far greater part in speciation than would appear from the present scanty data.

There are wide opportunities for research—unfortunately in Malaysia mostly on slow-reproducing arboreal plants—involving field work as well as herbarium studies.

It is almost certain that from large genera like *Syzygium*, *Ficus*, *Begonia*, *Cyrtandra*, *Ardisia*, *Rhododendron*, &c. some basic knowledge about speciation can be obtained.

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vated plants (1877) 93. (3) Bull. Jard. Bot. Btzig III, 9 (1928) 274, 299, 324, 353, 363, 374, 403. (4) Handboek Flora Java, pt 2 (1928) 23-289. (5) Handboek Flora Java pt 3 (1924) 44. (6) Schoolflora v. Java (1911) 425. (7) Bull. Jard. Bot. Btzig III, 6 (1924) 242-243. (8) *Tectona* 33 (1940) 121-122. (9) Bull. Jard. Bot. Btzig III, 8 (1927) 198. (10) Bull. Jard. Bot. Btzig III, 12 (1932) 65. (11) Ann. Jard. Bot. Btzig 40 (1929) 1-43. (12) *Teysmannia* 31 (1920) 102-105. (13) Gard. Bull. Str. Settl. 5 (1931) 222. (14) *Teysmannia* 21 (1910) 342. (15) Die Orchideen von Java (1905) 205. (16) with C. E. CARR, Notes on hybridization of Orchids, Mal. Orchid Rev. 1 (1932) 13. (17) Hybrid Orchids in the Singapore Bot. Garden. Mal. Orch. Rev. 2 (1934) 25-27. (18) The Scorpion Orchids. Mal. Orch. Rev. 2 (1935) 64. (19) Orchid hybrids in Malaya, M. A. H. A. Mag. 10 (1940) 41-46. (20) Some hybrid Orchids, natural and artificial. Bull. Jard. Bot. Btzig III, 16 (1939) 113-115. (21) Notes on the progress of hybrids in the Bot. Gardens, Singapore, Mal. Orch. Rev. 2 (1935) 64. (22) New hybrids raised at Singapore. Mal. Orch. Rev. 2 (1936) 100-109. (23) Hybrids in the genera *Arachnis* and *Renanthera*, *Blumea*, Suppl. 1 (1937) 52-56. (24) Bull. Jard. Bot. Btzig III, 13 (1935) 447-448. (25) M. A. H. A. Mag. 9 (1939) 34. (26) M. A. H. A. Mag. 11 (1941) 93. (27) FOX-WORTHY, Philip. Journ. Sci. 6 (1911) Bot. 250. (28) KERR, Journ. Siam. Soc. 2 (1914) 9. (29) PARKER, Ind. For. Rec. 13 (1927) 11, 24. (30) PARKINSON, Burma For. Bull. no 27 (1932) 31. (31) FOX-WORTHY, Malay For. Rec. no 10 (1932) 58. (32) SYMINGTON, Malay For. 7 (1938) 35. (33) Mal. For. Rec. no. 16 (1943) 159. (34) PARKER, Ind. For. Rec. 16 (1930) 7. (35) cf. HOLTUM, M. A. H. A. Mag. 11 (1941) 22-29. (36) Onkruidfl. Jav. Suiker (1930) 240. (37) *Saccharum-Erianthus* bastaarden. Wageningen, 1934, 64 pp. ill. (thesis).

16. *Polyembryony, parthenogenesis and apogamy*

Polyembryony in Malaysian plants was described more than a century ago by REINWARDT (1) in *Mangifera*. It is often found in cultivated plants and was later, from Malaysia, described by H. J. TOXOPEUS in *Citrus*, by L. VAN DER PUL in *Eugenia*, and by HILLE RIS LAMBERS in *Coffea*. In *Rutaceae* it seems to occur in several genera e.g. in *Murraya paniculata* JACK (2) and *Zanthoxylum*. The embryos are produced from different parts of the ovule.

There is little doubt that many bad specific distinctions in various genera, notably in the *Rutaceae*, in *Eugenia*, &c. are due to the occurrence of polyembryonic propagation which, again, is probably preceded by hybridization. Here is certainly yet another field for the experimental taxonomist promising results to both pure and applied science.

Parthenogenesis and apogamy have proved to be of high importance to phytozoography in Europe, specially when interpreting the microspecies described in certain genera which have always offered difficulties to the systematic botanist; e.g. *Hieracium*, *Taraxacum*, *Alchemilla*, *Rubus*, *Rosa*, *Crataegus*, &c. Intrinsic factors form a barrier here

against the formation of intermediates, and the plants propagate pseudo-sexually in pure lines or clones. In Malaysia such apomictic forms have been mostly described from cultivated plants but recently Dr H. J. TOXOPEUS when investigating the native genus *Derris* cytogenetically found them in wild species.

Certainly these phenomena exert great influence in other very large and difficult genera with great numbers of badly defined species like *Ficus* and *Syzygium* (of which over 150 species have been described from Borneo alone).

I am convinced that the taxonomy of several of our large genera e.g. *Smilax*, *Dioscorea*, *Medinilla*, *Psychotria*, *Saurauia*, *Ardisia*, and *Ophiorrhiza* is unsound, and that this unsatisfactory state of affairs has certainly a natural cause. In the group *Moluccani* of the genus *Rubus* scores of specimen-descriptions were made which stimulated other authors to publish some more (3).

In this connection BACKER made some valuable remarks on *Rubus* (4) *Smilax* (5), and *Dioscorea* (5, p. 116). The natural explanation is clearly not—as in the microspecies of *Pavetta* and *Ixora* described by BREMEKAMP—to be based on racial differentiation since the forms do not exclude each other geographically or ecologically. I suspect here the occurrence of natural intrinsic 'abnormalities' in sexual reproduction and genom behaviour.

Cited literature: (1) *Flora* 8² (1825) 427; *Nova Acta* vol. 12; *Isis* (1829) 391. (2) *Current Science* 3 (1935) 361 (3) Compare MASTERS, in *Passiflora foetida* L. (1894). (4) *Schoolflora voor Java* (1911) 450. (5) *Handboek Flora Java*, pt 3 (1924) 76.

17. The origin of native aliens in Malaysia

In one of the foregoing paragraphs I referred to several genera of the New World represented in Malaysia by species behaving as aliens (*Rumex obtovatus* DANSER, *Kosteletzkya batacensis* (BLCO) F.-VILL., *Elephantopus scaber* L.).

The native Malaysian flora has also produced many species only known from secondary vegetation types or areas under anthropogenous influence. Most 'weed trees' of the secondary forest (1) belonging to the *Euphorbiaceae*, *Ulmaceae*, *Urticaceae*, and the like, are not known as components of the primary forest. They are *botanical nomads*.

Where did these plants grow before mankind cleared the forests?

I have suggested (2) that:

- (a) Some are derived from forest plants which can grow in open habitats.
- (b) Some were present in the original vegetation in a few special ecological niches then negligible in number of individuals if compared with their abundance and common occurrence today.
- (c) Some have probably been produced after the forests were cleared by man.

(a) Numerous instances indicate that true forest trees may possess qualities enabling them to grow in open habitats. *Schima noronhae* REINW. is rarely a predominating tree in the forest but in arti-

cially cleared places it gets its chance and forms extensive pure secondary growths, e.g. in South Sumatra, Banka and Borneo. In the open, juvenile individuals often flower and fruit. The same is observed in *Adinandra*, *Calophyllum*, &c.

BRASS has collected, in New Guinea, a new species of *Parasponia* which in the forest grows into tall trees but on land slides is a small shrub. Cases like these point to unknown capacities of forest trees (see also p. x, xxxviii).

Some forest trees withstand fire in the seedling stage, a capacity they do not require in the primary forest, and which most forest trees lack. These species have multiplied abundantly in the open, man-made spaces where agriculture, hunting and cattle are predominant and fire is a common occurrence.

(b) A considerable number of species occupied special 'ecological niches' in the original vegetation resembling the open man-made places where they subsequently multiplied on an enormous scale (2-4). *Pinus merkusii* JUNGH. & DE VR. is a tree in the primary forest but its natural habitat is limited to steep ridges, land-slides, hot springs, mud wells, limestone cliffs, rocky places, and the new 'soil' of volcanic mud streams ('lahars'). Seeds and seedlings need sunshine or high temperature both for germination and growth. Once past this stage they grow to their largest size in the dense primary forest as emergent trees which serve as seed parents. The number and areas of these ecological niches were originally small, and so the number of *Pinus* individuals in nature was at first comparatively small. When the Gajo people some 3000 or more years ago cleared the forests on an increasing scale to work fields and raise cattle, and fired the vegetation for hunting and clearing purposes, the deforested lands more or less represented the conditions of the small niches where seed parents were present. *Pinus* then 'followed' man as a pioneer plant and it multiplied fantastically as it could survive the fires to a certain extent. This is the origin of the pure Sumatran pine forests of the present time. The same story could be told of *Eucalyptus* in the Lesser Sunda Islands, the East Javan mountain 'tjemara' (*Casuarina junghuhniana* MRO.), of *Melaleuca* in Boeroe Island and New Guinea, of teak (*Tectona grandis* L. f.) in Java, and of many others which behave in the same way. Most of these cases occurred in a climate with a slight to severe dry season each year.

Another example of an ecological niche is found under everwet conditions. Various *Euphorbiaceae*, *Ulmaceae*, *Urticaceae*, *Moraceae*, &c. grow always in single-storied secondary growth and thickets. In the primary forest one does not meet them in the normal stands and canopies but only in open spots, especially where large trees have been felled by lightning or wind, bringing down in their fall neighbouring trees with which they were entangled by lianas. These open spots, the 'eyes' of the forest, are rapidly filled by seedlings of the 'weed trees'. The native people often call them 'toetoe' (= to close). They cover the gaps rapidly and start

a local sere but in the end they disappear and are replaced by forest trees which germinate in their shadow and after some years choke them. In this way the forest heals its own wounds.

More permanent natural open spots, comparable to these temporary ecological niches occur elsewhere: e.g. areas in which rivers have changed their course, margins of forests along lakes and rivers, land-slides in ravines, open ground near solfatara, deposits of volcanic sand and volcanic mud streams, lava streams, extinct volcanic cones, and slopes where heavy winds have torn down the forest.

The principle of the great increase in numbers of pioneer plants all over the world since man cleared the vegetation holds, of course, for the fauna as well. I predicted (5) that the grassfield subspecies of birds which E. MAYR (6) recorded from the grassfields near Lake Sentani in North New Guinea do not indicate a much larger former extension of these fields in New Guinea, but that it is likely that these bird-races in smaller numbers had their original home in 'natural secondary growth and grassland'. I am satisfied that Mr A. L. RAND, during the Archbold Expedition, found this to be the case (7).

(c) Probably several species have come into being after the clearing of the primary Malaysian forests by man. Their genetic combinations were not viable in the dense dark primary forest and originally perished at once. With the shift of the environment towards local savannah conditions other circumstances, favourable to the new combinations which needed light and heat for their ontogenic development prevailed. I should not be surprised if such coarse weed-trees as *Homalanthus giganteus* Z.M., *Macaranga tanarius* M.A., *Endospermum formicarum* BECC., &c. were polyploids and derived from allied small-leaved forest species.

I have previously made the same suggestion (8) regarding the origin of a number of desert plants. Deserts offer exceptional opportunities to species otherwise ecologically not viable. Here again is an almost untouched field of research for experimental taxonomy. These considerations apply to trees as well as to shrubs and herbs.

Cited literature: (1) Short-lived rapid growing trees like *Macaranga*, *Cecropia*, and *Trema*. (2) *Tectona* 30 (1937) 641. (3) *Tijdschr. Kon. Ned. Aardr. Gen.* 52 (1935) 51, 188-189. (4) *Verslag 28e Vergad. Proefst. Pers.* (1941) 195-204, specially p. 202-203. (5) *Tijdschr. Kon. Ned. Aardr. Gen.* 52 (1935) 62-63. (6) *Novit. Zool.* 36 (1930) 25. (7) *Bull. Amer. Mus. Nat. Hist.* 68 (1935) 534, 556, 557; *ibid.* 77 (1940) 377; *Amer. Mus. Novit. no* 1122 (1941) 1, 3; *Bull. Amer. Mus. Nat. Hist.* 79 (1942) 284-285. (8) *Tectona* 30 (1937) 645-649.

18. The origin of Malaysian cultigens

Plants known only in the cultivated state (*cultigens*) are equally common in temperate and tropical regions. From prehistoric times man has tried in Malaysia as well as in Europe, to select, breed, keep, and improve all plants useful to his daily

needs or desirable from an aesthetic point of view. The tropical flora is so varied and abundant that the number and the variety of cultigens in the tropics are relatively larger than in the temperate regions. A remarkable character of the Malaysian tropical flora is that only very few staple foods are genuinely native (5); the majority of species important as producers of starch and oil for the Indonesian diet have been introduced less than a thousand years ago, and the greater part is even from post-Columbian time. The introduction of many cultigens of minor importance, however, took place in a pre-Columbian period and now these are spread from Africa to India and Malaysia, including West Polynesia.

These domesticated forms are sometimes racial or varietal groups which only differ from the native ancestor in small characters (e.g. variegated leaves) or also may be of subspecific, specific or even generic rank. This latter category includes e.g. *Tamarindus indica* L., and, according to some palmologists, *Cocos nucifera* L.

No intergradation is observed as a rule between cultigen and wild ancestor and this discontinuity might be connected with their abrupt mode of origin, i.e. mutation in the wider meaning.

After DE CANDOLLE's stimulating work 'Origine des plantes cultivées etc.', the development of genetics, and of cytogenetics, added to an explanation of the mode of origin of the cultigens.

Cultigens are to some extent comparable to the pioneer plants which were treated in the foregoing chapter; both owe their position to the activity of man, i.e. cultigens intentionally, pioneers settling in or near inhabited areas unintentionally. Together they may be termed *anthropogens*.

The activity of man in developing a cultigen from a wild species can be divided into three stages, firstly *preservation*, secondly *breeding*, thirdly *selection*. Most cultigens have passed through these stages; some, however, still remain in the first phase and others in the second.

Preservation, the first stage, is to pick from the native flora specimens with special deviating qualities, with rare or desirable virtues, and to transplant them. These picked specimens naturally consisted often of one single or a few specimens from one locality. These exceptional individuals were grown and spread intentionally by man, and multiplied so greatly under anthropogenic conditions as never would happen in nature. Such plants usually possess a number of (genetically) recessive characters which make them feeble competitors. In nature these forms soon disappear for this reason and merge into the specific population by crossing, except when they happen to find a special 'ecological niche' where they are enabled to maintain themselves. Man in a primitive state has saved i.e. kept for domestic or other purposes, many of these comparatively feeble plants and so prevented their disappearance. Forms with spotted, coloured, or variegated leaves, dwarfs, monstrosities¹ or aberrant specimens with desirable charac-

(1) *Celosia cristata* L. is one example from many.

ters, and also sterile hybrids, &c. are thus handed down to posterity. A beautiful instance of a 'preserved' plant in the first stage, is the Chinese *Ginkgo biloba* L. although it is said to have been detected recently in a natural vegetation type.

The second stage (breeding) requires a higher stage of civilization; permanent fields and settlements, i.e. a developing agriculture are indispensable. The cultigen spreads from one village or family to another, and so becomes common property.

The transition to the third stage (selection) is gradual. Aberrant or deviating individuals which now originate among the cultivated plants (secondary varieties) are again picked. These plants differ from those picked in the first stage in that they do not occur in nature. These plants are cultigens in *optima forma*.

Both the range of variation and the number of forms in the first and third stages depend on the genetic variability (polymorphy, genom potentialities) of the species as a whole, the stability of its genom, and the strength of eventual fertility barriers between this and other species. Some species have very few potentialities and so have been hardly improved in comparison to their ancestors, e.g. buckwheat. Other species are remarkably polymorphous, e.g. *Cocos nucifera* L., *Nephelium lappaceum* L., &c. Interspecific sterility seems hardly to exist in some families, such as *Rutaceae*, *Orchidaceae*, *Begoniaceae*.

Many cultigens are propagated vegetatively only, either because it is desired to keep them 'pure', or because they bear no fruit, or produce only flowers of one of the sexes, e.g. some species of fragrant *Pandanus* which are either sterile or bear only ♂ spadices. Some species of *Mangifera*, *Eugenia*, *Citrus*, &c. are propagated by seeds but these are poly-embryonic and in fact vegetative (apogamous).

It has been asserted that herbs, on account of their rapid reproduction (shorter life cycle) if compared with trees, would have produced relatively more cultigens than trees. However, the Malaysian flora, being predominantly arboreous, has yielded arboreous cultigens by the dozen (see table below).

The origin of cultigens can be traced partly by means of morphological comparison with the wild flora, and the most nearly allied species are generally regarded as their 'ancestor'.

Recent genetic experiments have been found useful in determining the probable ancestors.

It appears that many cultigens possess multiple or aberrant chromosome numbers, being dysploids or polyploids owing to their origin by hybridization or mutation.

The difficulties in tracing the origin and native country of several plants now commonly cultivated rest on four points.

(a) The combined results of field botany, floristics, and taxonomy, indicate that it is sometimes practically impossible to fix with certainty the origin and native country of cultigens if their allied species occur over wide areas. The method of determining the degree of kinship fails altogether to produce a good proof in such cases.

(b) Natural rejuvenation is often no conclusive proof, this occurs commonly specially in anthropogenic vegetation communities e.g. near human dwellings, also in savannahs and grassy lands, other kinds of open vegetation, and in aquatic communities.

Tamarindus indica L. forms almost pure stands in the Lesser Sunda Islands and also savannah-like vegetation types. Natural rejuvenation is observed but probably occurs also in the African savannahs.

The 'acclimatization' of alien plants is generally much overrated, although the open vegetation types have many exotic species in their plant communities.

Cultivated plants are frequently found as 'relics' in formerly inhabited but abandoned places. Botanists base their conclusions often on the influence of man on the flora during the present era only or, at most, back to ancient Egypt. It is often believed that history began to be important with the rise of early civilizations such as the Egyptian, Chinese and the like but this is decidedly incorrect. It should not be assumed on the other hand that, in ancient times, man did not exert much influence on the vegetation because of his small numbers or low standard of living. A very scarce population can exert in the tropics a predominating influence on the vegetation under monsoon conditions and even determine its character. Some of the anthropogens may have spread therefore from 'time immemorial'.

(c) Thirdly, cultivated plants sometimes escape from cultivations and settle temporarily in the forests, or are even able to seek refuge and survive in some ecological niche. An example is *Coffea*. The so-called 'Bosch-koffie' is coffee plants originating from seeds dispersed by animals and found in the forest; formerly this kind of coffee was highly valued. Coffee may be expected to be able to maintain itself to some extent in Malaysian forests being originally a substage pygmy tree.

(d) Cultigens are known to produce secondary retrocessive forms which is a fourth difficulty in tracing their ancestors. These secondary forms suggest sometimes an approach to the original type although they still differ in certain characters.

Among Malaysian botanists, O. BECCARI (1) thought and wrote most about the problem of the origin of native cultigens. He called these 'plants united to man by a kind of symbiosis'. He studied the mangosteen: *Garcinia mangostana* L. which has certainly a West Malaysian origin. BACKER found in Java only ♀ specimens of this plant (6). *Areca catechu* L., or 'pinang' palm is, BECCARI says, what the camel is to the Arab. It has followed him in all his wanderings; its origin is unknown. Its nearest ally appears to be *Areca concinna* THW. of Ceylon; its nuts are indispensable for chewing 'siri' or 'betel' leaves, and the nuts are attributes in ceremonials and rites. The slender beautiful stature of this palm has stirred the poetic sentiments of Malay writers. The siri leaves are produced by *Piper betle* L., which is also a cultigen. The third participant in the 'man-siri'-symbiosis,

'gambir', prepared from the adstringent tissues of *Uncaria gambir* ROXB. again is a cultigen of uncertain origin. BURKILL (2) says that 'gambir' is cultivated where it occurs wild but it has never been possible to prove that the wild plants did not escape from cultivation.

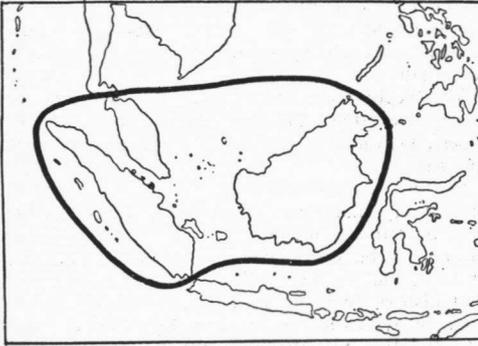


Fig. 50. Distribution of the genus *Durio* (*Bombac.*).

Durio zibethinus L. is another remarkable Malaysian fruit tree, which was subject to special studies by BECCARI (3). The genus *Durio* is restricted to West Malaysia (fig. 50). *Durio zibethinus*, a large tree, has never been found wild, though various native closely allied species occur in the primary forests. The custom of the Malays to plant fruit trees in the primary forests in abandoned clearings has led to the belief that those species occupy a natural habitat there (1, p. 166). The closest native ally is probably found in South Sumatra. I collected it and it was recognized as a new species: *D. spontaneus* BAKH. ms.

Another plant studied by BECCARI is the common 'rambutan', *Nephelium lappaceum* L., which occurs in numerous varieties. He found (1, p. 130) in some place in Borneo 5 species resembling the common *N. lappaceum* L. but which were distinct and undescribed. This raised the question whether these are hybrids between the cultigen *N. lappaceum* L. and allied native species. It is very interesting to discover in one village 5 cultivated congeneric species bearing excellent fruits, at that moment unknown to science. In another locality he saw, in a restricted area, five different native, apparently endemic species of banana (*Musa*). He supposed that they may be the result of retrogression towards a wild state of hybrid cultivated forms (1, p. 159).

BECCARI discussed at length *Eugeissonia utilis* BECC., a palm which is apparently in the second stage of domestication (1, p. 306). *Panda. us* appears to be in a similar stage in the Papuan highlands.

Many binomiums have been assigned to forms which certainly do not deserve specific rank, e.g. *Saccharum edule* HASSK. This is a monstrosity and probably of hybrid origin.

Pisonia alba SPAN., the cabbage tree of the Moluccas, is quite different in habit from its assumed

wild ancestor *P. sylvestris* T. & B. which is a very inconspicuous shrub. The cultigen hardly ever flowers, its foliage is yellowish (etiolated) (fig. 49), and its origin still is an unsolved problem.

Dr TOXOPEUS (4) studied the ancestry of some cultigens including the clove and kapok. The Zanzibar clove, though originating from the Moluccas, was never rediscovered in its native country where it may have been exterminated! The Asiatic-Malaysian kapok belongs to a distinct subspecies — acc. to BURKILL even a good species — of a species distributed in America and Africa.

In conclusion a list of genera is given below containing cultigens (species or varieties) which in all probability were obtained from the original Malaysian flora. The list is not exhaustive and serves to illustrate merely the number and diversity of cultigens in a tropical arboreous flora.

<i>Antidesma</i>	<i>Colocasia</i>	? <i>Ocimum</i>
<i>Areca</i>	<i>Dioscorea</i>	<i>Pandanus</i>
<i>Arenga</i>	<i>Durio</i>	<i>Piper</i>
<i>Artocarpus</i>	<i>Eugenia</i>	<i>Pisonia</i>
<i>Averrhoa</i>	<i>Flacourtia</i>	<i>Rattans</i>
<i>Baccaurea</i>	<i>Garcinia</i>	<i>Saccharum</i>
<i>Bamboos</i>	<i>Lansium</i>	<i>Sandoricum</i>
<i>Bouea</i>	<i>Mangifera</i>	<i>Spondias</i>
<i>Citrus</i>	<i>Metroxylon</i>	? <i>Tamarindus</i>
<i>Cocos</i>	<i>Morinda</i>	<i>Zalacca</i>
<i>Codiaeum</i>	<i>Musa</i>	
<i>Coleus</i>	<i>Nephelium</i>	

Cited literature: (1) Wanderings (1902) p. 25, 27, 28, 60, 129, 130, 160, 166, 210, 308. (2) Dict. Econ. Prod. Mal. Pen. (1935) 2198. (3) Malesia 3, p. 230. (4) Natuurwet. Tijdschr. Ned. Ind. 101 (1941) 19–30. (5) Blumea 6 (1948) 246. (6) Schoolflora voor Java (1911) 91.

19. Extinct plant groups in Malaysia

The reason why plants and plant groups become extinct has been the subject of many hypotheses and suppositions. As far as I am aware no general ground for discussion has been established hitherto in botany. The rosy idea that we live in a progressively better equipped world seems rather far-fetched, and extinction remains a mystery.

From Malaysia some examples of partial extinction may be given. *Dryobalanops* is a small genus of *Dipterocarpaceae* of ca 7 species now confined to Central Sumatra, the Malay Peninsula, and Borneo (cf. fig. 44). It occurs gregariously in the primary forest in colonies or aggregates. In the Tertiary period it was also found in South Sumatra and West Java, where it was also gregarious, judging from the enormous amount of large silicified trunks preserved.

It has been suggested that in the Tertiary Java was subject to violent volcanic action. Our experience and knowledge of the destruction brought about by vulcanism is, however, that the effects may be severe but are *always local*, especially in the lowland surrounding the volcano. It was in the lowland that *Dryobalanops* thrived. It seems

highly improbable that a flora would be completely destroyed over hundreds of sq. miles and even if this explanation is tentatively accepted the problem remains: why is *Dryobalanops* extinct in South Sumatra?

Another suggested explanation is that man



Fig. 49. The Moluccan 'cabbage tree', *Pisonia alba* SPAN. (*Nyct.*), a cultigen derived from *P. sylvestris* T. & B.

destroyed the species in Java; but it seems strange that no trace of it is ever found there even in the patches of primary forest left in remote spots.

It is also asserted that the Javan lowland forests were destroyed through submergence at the period when Java consisted of a garland of volcanoes as the Lesser Sunda Islands do now. But, if so, *Dryobalanops* would have found a temporary refuge at the base of the cones up to ca 300 m.

A reason for the extinction of lowland plants might nevertheless be found in *submergence*. Large tracts of land in Malaysia were left dry during the Pleistocene Ice Age, both on the western (or Sunda) shelf and the eastern (or Sahul) shelf. After

the retreat of the Ice, these large shelf areas were again inundated by the South China and Arafura Seas respectively. Though the change was gradual and the shelves were flat, it seems possible that migrating new species were caught by the final inundation by the sea, if they were unable to keep pace with the retreat of their ecological habitat.

Extinction of mountain plants is more likely to have occurred. The Malay Peninsula and the islands in the South China Sea (Riouw, Banka, and Billiton) have been above sea-level for a long period, even on a geological time scale. Their surfaces were subject to tropical erosion, and thick layers were washed off. By abrasion the old basic granites of the Peninsula were laid bare. Lofty mountains must have pierced the clouds where now but two summits of the Main Range just reach the 2400 m contour. The medium mountains have been gradually eroded to low hills or lowland. I am certain that the Peninsula formerly had a much richer mountain flora than at present. One of these remnants is a most peculiar sedge *Oreobolus kukenthalii* STEEN. (*Schoenus distichus* RIDL.). I found this in N. Sumatra in a geologically similar habitat but at a much higher altitude than in the Malay Peninsula where it occurs only on the Kerbau and Tahan summits between 2200 and 2400 m (N. Sumatra: 2450-3460 m). Apparently *O. kukenthalii* is on the verge of extinction in the Peninsula. The nearest locality of the genus is Mt Kinabalu, in N. Borneo, where *O. ambiguus* KÜK. occurs at 3750-4000 m. The fact that both Kinabalu and N. Sumatra have some specialized microtherm plants in common, which occur also on the summits in Celebes, the Philippines, and New Guinea (*Centrolepis*, *Monostachya*, *Patersonia*) renders it highly probable that these plants also formerly accompanied *Oreobolus* in the Peninsula, but were unable to maintain themselves in the gradual lowering of their habitat due to the erosion of the mountains.

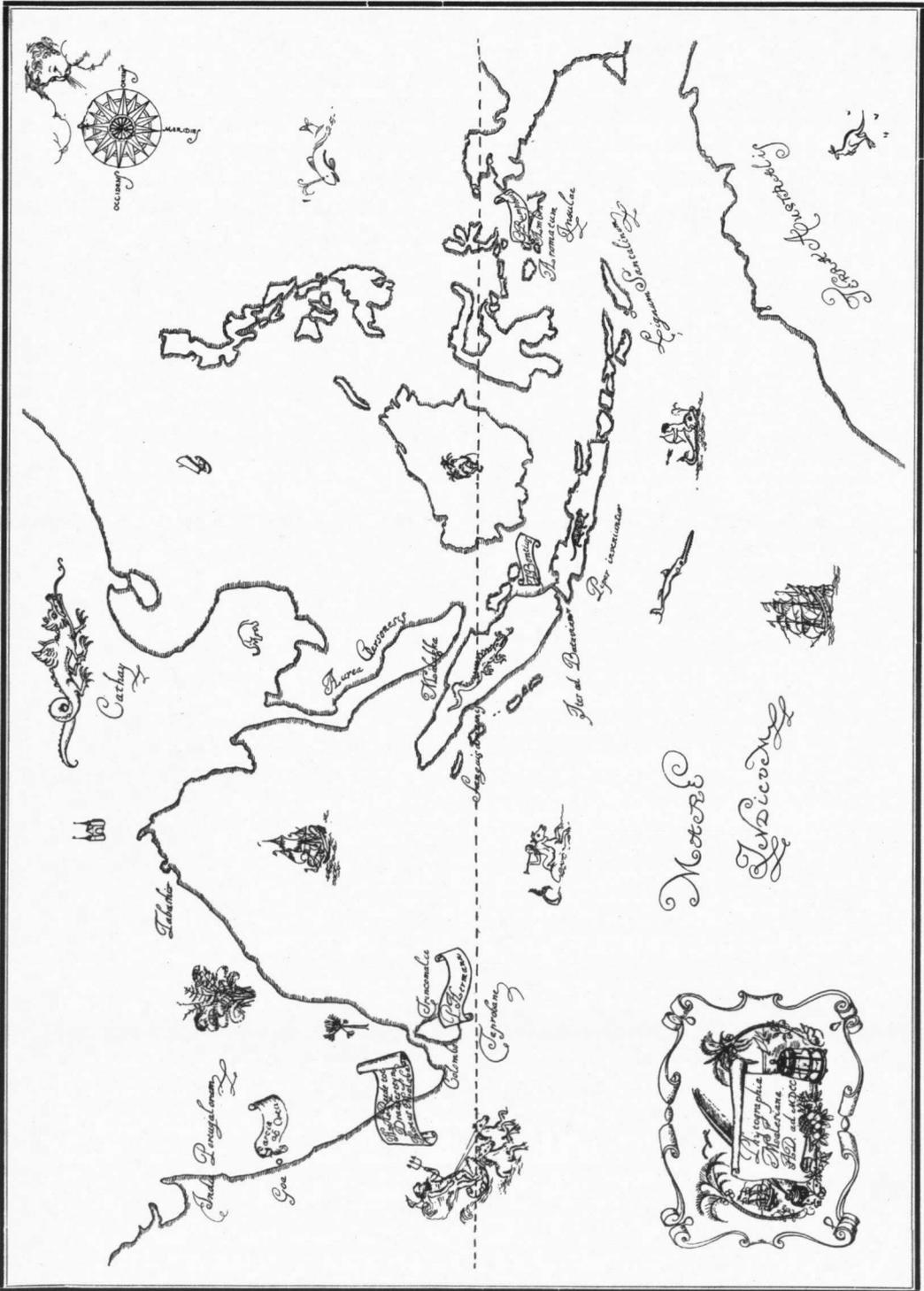
Similar great changes happened to the floras of now extinct volcanoes; some of these have been practically reduced to their base, and nothing now shows except some small magmatic cones (1).

Changes of still greater magnitude have taken place in New Guinea where the geologically young alpine ranges are built of materials which have come from the demolished remains of former mountain systems now almost vanished.

The intricate and turbulent geologic past of the Malaysian Archipelago leaves no doubt of the ample opportunities for extinction and isolation in the plant kingdom. New data and arguments elucidating these events will in all probability be deduced from the phytogeography of the present flora.

Cited literature: (1) De Trop. Natuur 23 (1934) 163-167.

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A Map, depicting the State of Malaysian Phytography till the Seventeenth Century