LINES IN THE PUBLISHED WORK OF C. G. G. J. VAN STEENIS, TROPICAL BOTANIST

M. JACOBS
Rijksherbarium, Leiden

SUMMARY

This paper has been composed on the occasion of the retirement of Dr. van Steenis as a professor of botany and director of the Rijksherbarium, Leiden. He was born in 1901, educated at Utrecht, came to Bogor, Indonesia in 1927, settled in Holland in 1950. He founded the Flora Malesiana, and ranks as the greatest authority on the botany of Malesia and adjacent regions.

Here are expounded, by his pupil and collaborator, the main subjects and leading ideas in his published works, the most important ones of the latter mentioned. Considered are his work on plant areas, the methodical fact finding by Dr. Van Steenis and Mrs. M. J. van Steenis-Kruseman, his work on the discontinuity among plants forms, on vegetation and ecology, his promotion of the relations between man and nature and of education, his work on discontinuities in plant distribution. His personal contributions to taxonomy in the stricter sense are also discussed.

INTRODUCTION

Van Steenis's first scientific studies were devoted to plants on pollard-willows (Ned. Kruidk. Arch. 35, 1926, 360—406) and to the flora and vegetation of a marsh near Utrecht (ibidem, 36, 1927, 285—316). The first labels in his private herbarium carried at the bottom a special heading 'geographical distribution'. To him, taxonomy has, from the beginning onwards, been a means to an end rather than a goal in itself. Mainly through the study of vegetations and of plant distribution, he has sought to understand the plant world in the full broadness of its diversity. Throughout his life, he has retained a deep respect for plain facts, which he has collected and made available to an extraordinary amount. The idea of a *Flora Malesiana*, originated in the mind of his teacher Professor A. A. Pulle, has been with him from the onset of his career. With his wife, he laid the strong foundation to which the project now owes part of its intellectual appeal. The delimitation of the area to be covered was based on patterns of plant distribution; over this area all the relevant facts were rounded up. Only then, after twenty years of preparation, the proper taxonomic work was started. In both features: its natural borders* and its inventory of facts, the Flora Malesiana is unique and superior to all other floristic projects in past and present. And although this paper is not intended to dwell further upon the growth and significance of this project, but an effort to understand the main aspects and ideas in Van Steenis's oeuvre now that his retirement is there, we could well begin it with a discussion of his work as far as it is connected with plant geographical delimitation.

* The region first called Malaysia, and Malesia after the creation of the federation of the former name, comprises Sumatra, Malaya, Java, the Lesser Sunda Islands, Borneo, the Philippines, Celebes, the Moluccas, and New Guinea. The Solomons can also be reckoned to it.

PLANT AREAS

In the determination of the areas of plant distribution, Van Steenis's passion for facts found a worthy objective. He started with a master stroke, notably the choice of the genus as the basic unit for consideration and to apply this consistently and over the whole range of the phanerogam flora in the *Mountain Flora* (Bull. Jard. Bot. Btzg. III, 13, 1934, 141). Since the genera all had been worked up several times for the whole world, both their characters and their distribution were sufficiently well-known to serve as a basis for work in plant geography. If such works were based merely on 'characteristic' or 'significant' taxa — as plant geographers often have done — the conclusions were bound to be uncertain. This would also be the case if the areas of species were to be taken, because of the poor state of knowledge about their identity and range. In adopting the genus (or occasionally the subgenus and section if these are remarkably clear-cut) as the basic unit, he reduced his task to manageable proportions, while he still could work in sufficient detail and retained sufficient numbers for a statistical approach. Another advantage of the use of the genus is, that it can fruitfully be used, rather than the species, for plant geographical considerations which involve the past. Altogether, the application of the genus as the unit for plant geographical studies warranted a maximum of accuracy, in the sense used by Van Steenis, that is: precision as far as the main lines are concerned.

After the native genera have been separated from the aliens, and the areas of the former have been duly determined, comparison will reveal a number of cases of so-called aequiformity, that is, an essential similarity in shape. From such similarities many plant-geographical considerations take their start. In a similar way as J. D. Hooker had done for the species in the Flora of New Zealand in 1853, Van Steenis classified the genera into a number of categories according to their main distribution. We find the concept of aequiformity unmistakably present in Van Steenis's distinction of the three invasion tracks of the 'Malaysian mountain flora' (fig. 3).

But also the delimitation of Malesia as a plant geographical kingdom is based on aequiformity of generic distribution areas. After having mapped all the native Malesian genera, about 2178 in number, Van Steenis saw that the limits of very many genera coincided in three places which he named 'demarcation knots'. The places and the numbers are here shown on the small map which forms, in my opinion, a landmark in plant geography, although it was published in a place where it was bound to receive but

Types of generic distribution of Malaysian phanerogams:	Number of genera:	Percentage of total:
TYPE 1. Occurring in Asia, Australia, and Malaysia; no distinct centre in the paleo-tropics	602	27.7
TYPE 2. Centre of specific distribution clearly in Asia; absent or scarcely represented in Australia	574	26.3
TYPE 3. Centre of development in Malaysia, and some outposts in surrounding regions	580	26.6
TYPE 3a. Genera known only from one island or island group in Malaysia (endemic genera)	296 } 876	13.8 } 40.4
TYPE 4. Centre of development in Australia; absent or scarcely represented in Asia	94	4.3
TYPE 5. Centre of development in the Pacific-Subantarctic region	32	1.4
Total	2178	100.1

Source: Flora Malesiana I, 1 (1950) LXXI.

scant attention (fig. 1). During the same investigation it appeared that Malesia can be divided into three provinces, but that the region is definitely one coherent whole, in which about 40 per cent of the genera are endemic, in comparison with endemism in other parts of the world quite a high proportion.

This method of finding natural borders of floristic kingdoms and provinces based on the distribution of all the phanerogam genera has been refined and extended by Van Steenis's pupil Dr. M. M. J. van Balgooy in his work on the Pacific (precursor in Blumea 10, 1960, 385—430, and critically elaborated in Blumea Suppl. 6, 1971). Through the announcement of the results as such, this work has attracted a wide attention. If the same methods were applied to Africa and Tropical America, this would be the first step towards the study of the floras over there in scientifically delimited regions, which then could be meaningfully scanned for literature and collections to be worked up.

Discontinuities in distribution, which are also revealed by a search for aequiform areas, have been the subject of Van Steenis's intense attention all the time. In particular, he has occupied himself with the discontinuities in a) the mountain flora of Malesia, b) the drought plants of Malesia, c) tropical plants on both sides of the Pacific, d) floras of isolated islands, e) mangrove distribution, f) *Nothofagus*. These subjects will be discussed

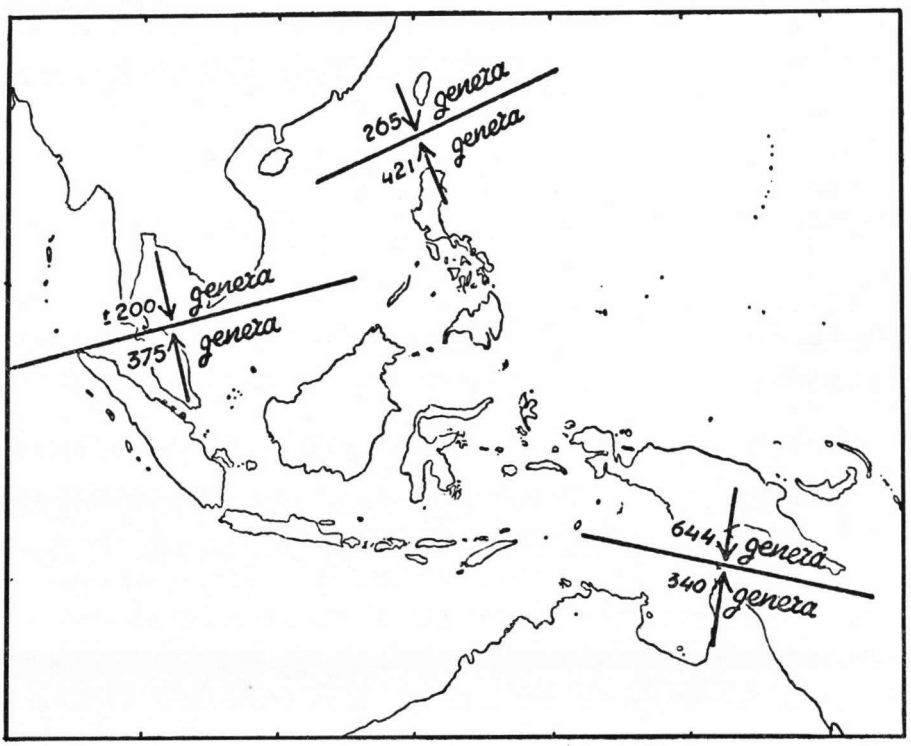

Fig. 1. Delimitation of Malesia as a natural floristic region, based on demarcation knots of phanerogam genera. Indicated are the numbers of genara which occur on one side of the line but not on the other. Many genera, of coutse, cross the lines, but out of all genera which are native in Malesia, about 40 % are endemic. — Source: Flora Malesiana I, 1 (1950) lxxii, f. 21.

presently. Here is still to be mentioned the project of the *Pacific Plant Areas*, started in 1963. It is a collection of distribution maps newly prepared by experts of taxa which were in this respect still insufficiently known.

FACT FINDING

For a smooth progress of taxonomic work it is necessary that at an early stage a botanist avails himself a rather complete inventory of all the literature and collections that he has to digest. For understanding and appreciation of these bodies of data, a certain amount of historical information is needed about the persons who produced these, the institutions they were connected with, and the conditions under which they operated. For Malesia, these data are available to an unrivalled extent, and this makes work for a taxonomist over the area so efficient, since no time is lost in the finding of facts, thanks to the combined and prolonged efforts on the part of Dr. and Mrs. Van Steenis.

Throughout his career, Van Steenis has collected all the references to taxonomic publications dealing with plants from Malesia and adjacent regions he could lay hands on. As a result, he now has a huge file of literature references. Whenever somebody needs information, Dr. Van Steenis generously puts it at his disposal; this is always so when a collaborator of the Flora Malesiana embarks on his task. Also on vegetation and plant distribution he has accumulated enormous amounts of data.

He has kept the world regularly informed of the main literature since the inception of the *Flora Malesiana Bulletin* in 1947. With an average frequency of one issue a year, it has served as a contact medium between all persons and institutes interested in the botany of Malesia and adjacent regions. It contains a number of book reviews, and an annotated list of the literature that came in since the former issue, at present about four hundred items a year.

This method of providing each reference with a terse note about its contents and its value was in use before, but Van Steenis adopted it consistently, and thereby enhanced the usefulness of his bibliographic efforts. His annotations serve to complete the title by giving the main conclusions in a few words; to state what to expect from a publication and what not; and to say whether it is really valuable. A few examples are reproduced for illustration. Thus he enables a customer to make a pre-selection out of the masses of references.

> Aymonin, G.: La position systématique du Wikstroemia souliei H. Lec., Thymeléacée de Batang (Paan), Chine (Bull. Soc. Bot. Fr. 111, 1964, 182—189, 2 fig.).
> *Reduced to Daphne.*
>
> Copeland, E. B.: Fern Flora of the Philippines (N.I.S.T. Manila, Monograph 6, vol. 3, 1960, pp. 377—555).
> *The final part; no index.*
>
> Misra, K. C.: Phytogeography of the genus Stipa L. (Gram.) (Trop. Ecol. 4, 1963, 1—20, 5 fig., 2 tables).
> *Migration routes; centre in Asia, lines run from there to Europe, Africa, and through Malesia and Australia towards S. and from there to N. America. How Stipa spread across Malesia is left unanswered, as no species occurs there.*
>
> Thorne, R. F.: Some problems and guiding principles of Angiosperm phylogeny (Amer. Natur. 97, 1963, 287—305, 13 fig.).
> *No new guiding principles, but a number of interesting new suggestions, some appealing some repellent.*

Samples of critical annotations made by Van Steenis in the Flora Malesiana Bulletin bibliographies.

His *Annotated selected bibliography* (Flora Malesiana 5, 1958) is not only most useful just because it is annotated and selected (it contains about 7000 titles), but is it also remarkable from a bibliographical viewpoint. All the respected botanical bibliographies consist of two parts: one, in which all items are arranged in alphabetical order to the name of the author, and another, in which they are arranged to subject. Mostly there are annotations in neither, and if they occur, they deal with bibliographic particulars. Not so Van Steenis. His bibliography is arranged exclusively on subject. Even the titles of papers in serials have been omitted. This not only simplified his task to compile it (he actually accomplished it in four months of concentrated effort in the Rijksherbarium library), but also the task of his readers to consult it.

The *Cyclopaedia of Collectors* (Flora Malesiana vol. 1, 1950, supplement in vol. 5, 1958) by Mrs. M. J. van Steenis-Kruseman is world-famous and widely known as 'the Green Bible', a name which it fully deserves for the variety and completeness of the information in it. With this work, one can locate all the material of ferns and phanerogams collected in Malesia in the Herbaria where it is preserved and in the places where it was gathered, with all the pertaining literature. Its main body consists of about one thousand entries of plant collectors, with name, place and year of birth and decease, nationality brief description of career, itinerary in Malesia while collecting, with the main places and dates, places where materials are being kept, and publications, viz. travel reports, biographical papers, and main studies based on the materials collected.

The value of the work is greatly enlarged because it has been so carefully summarized and introduced. There is for each island or province in Malesia a 'Chronological list of the collections' with collector and year, and an equally detailed survey of the number of specimens collected in each island or province, in relation to its size. From this so-called 'density index' it can be seen where further exploration is most urgently needed — although it should be noted that fortunately this pattern has been changed considerably, due to collecting activities during the last twenty years, especially in Borneo and New Guinea. There is also a chapter on errors made in the labelling and in the location, a collection of facsimile handwritings, and an index which helps to locate places which otherwise might be hard to find.

If it is surprising that the work was compiled in such a comparatively brief time — by her own account, it took Mrs. Van Steenis 14 years — then it should again be noted that it sticks to the essentials. For all its unsurpassed accuracy, it nowhere suffers of over-perfection.

Another original contribution on the part of Mrs. Van Steenis is her *Bibliography of Pacific plant distribution maps* (Pacific Plant Areas part 1, 1963). In it she recorded all published plant distribution maps of the Pacific and adjacent regions. These references, too, have been provided with annotations, notably about the character of the map, the way in which an area has been indicated, and the completeness of the map.

A collection of *Dates of publications* (Flora Malesiana 4, 1954) was not confined to Malesia but covered the whole world. Occasional scores of dates had been published, to be sure; not a few of them in the Flora Malesiana Bulletin, but in presenting this considerable amount of 326 titles, Mrs. Van Steenis did a piece of pioneer work. The volume had very soon to be reprinted.

The historical information, alluded to in the beginning of this chapter, is not only contained in the Green Bible. In his *History of Malaysian phytography* (Flora Malesiana 4, 1948), H. C. D. de Wit sketched many details of persons, institutes, and publications in the frame of a fascinating story, which no one will leave unread who is interested in the development of Malesian botany and in the conditions which prevailed in the period which from now onwards will be known as 'the pre-Steenisian era'.

DISCONTINUITY AMONG PLANT FORMS

From the differences between specimens, the taxonomist starts his work; it is his task to understand the gaps among his material, to characterize them, and to discover relationships across them. While doing their best, but with scanty material available, taxonomists have not seldom gone astray, as appeared when new collections came in which broke down the pattern designed by the taxonomist, instead of confirming it. Van Steenis devoted great efforts to recognize and to prevent such errors, and to understand the mechanisms which account for the differences among taxa in nature. Working at Bogor for twenty years in a large Herbarium associated with the most magnificent botanical garden in the world, and with ample opportunity for field work in various islands, he has been singularly fortunate in being able to assess diversity in local populations of living plants as well as to compare preserved plants from over large areas. He soon perceived that almost every rule or character or concept that had been formed in temperate regions, breaks down in the tropics. Perhaps for these reasons, his papers on the subject of plant diversity are characterized by caution, and at the same time by a struggling concern with terms and concepts in an attempt to put order among his findings.

His first important essay on the subject is the *General Considerations* (Flora Malesiana vol. 4, 1948—9). It is devoted to the problem that every taxonomist has to face, how to separate the inherited features in his materials from the effects caused by the environment, in other words, how to distinguish the genotype from the phenotype. He adduces striking examples to show what wind, fire, soil conditions, volcanic activity, or shade, can do to the plant form, and how these modifications time and again have fooled herbarium taxonomists who described and named them as different taxa.

Van Steenis adopts as his standard the broad species concept formulated by J. D. Hooker, who in India a century earlier had gone through similar experiences as Van Steenis, and came to allow for a good deal of diversity within taxa, provided these can be clearly separated. From Hooker's 'Introductory Essay' to the *Flora Indica* (1855), Van Steenis has quoted all the important passages in the first part of the Considerations, under the motto, also adopted from Hooker: 'We should endeavour to determine how few, not how many species are comprised in the Malaysian Flora'.

In an essay '*Specific and infraspecific delimitation*' (Flora Malesiana vol. 5, 1957) he deals more extensively with the genetic mechanisms underlying the diversity. He once remarked: "This is the most difficult piece I have ever written."* It contains elements of theory and practice. The former stem from a vast erudition in the earlier biosystematical literature based, of course, on non-tropical herbs, and no doubt the conclusions arrived there hold good for tropical plants as well, but with knowledge on the latter in such a poor shape and without the means to conduct large scale experiments, at present we have here to leave off and must revert to the good old alpha taxonomy by which we merely can locate the biosystematical problems.

In the field of 'practical taxonomy', however, the advices which Van Steenis has to offer at the end of his essay are eminently fruitful to the worker on tropical plants. In a concise form they touch on the positions of the monographer and the local florist, on the haphazard way in which specimens from tropical countries often have been described, on the balance between analysis and synthesis, on the difference between accuracy and

* Bremekamp (Proc. Kon. Ned. Ak. Wet. Amst. C 62, 1959, 91—110) reacted sharply to some derogatory remarks in the 'Delimitation' about his work. Bremekamp claims that Van Steenis misread his texts, and in turn attacks him on a number of theoretical points.

overperfection, on the secondary importance of the name of a plant in comparison with its characters, on the importance of identification keys for checking and for judging the value of a work, on the dangers of discerning taxa on trifling differences and of assigning them too high a rank, and on the fact that good taxonomic work often brings about a reduction of the number of recognized species in astonishing percentages.

Together, the Considerations and the Delimitation form a guide to judgement of resemblances and differences which can be compared with *La phytographie* (1880) by Alphonse de Candolle, or *Die Methoden der Phytographie und Systematik* (1921) by Diels in Abderhalden's Handbuch der biologischen Arbeitsmethoden, but written from a wide experience with tropical botany and full of examples. This makes the two essays a unique piece of literature, very much in demand indeed.

A third essay is '*Plant speciation in Malesia*, with special reference to the theory of non-adaptive saltatory evolution' (Biol. J. Linn. Soc. 1, 1969, 97—133). It may be counted among the offspring of the mutation theory by Hugo de Vries. Van Steenis here distinguished three kinds of species in the tropical environment, first the polymorphic species of wide circumscription, second the groups of distinct but closely related species, and third the species which stand taxonomically rather isolated. While the first two kinds have differentiated gradually, the third kind must have come into existence through mutation. Now Van Steenis holds it that, contrary to common belief, the tropical rain forest is not a milieu of strong competition, but on the contrary, is favourable to the newcomers in evolution which are not soon weeded out but given a chance to develop. Under such conditions plants which we are used to look upon as 'malformations' might have a chance to survive and propagate as new taxa so different from their ancestors that the gap between them should be valued at the level of genus or higher.

Ficus, *Nepenthes*, *Pterisanthes*, *Compositae*, may all be the results of a number of processes currently known to give rise to new forms which we conveniently call 'terata', but they may be considered as 'hopeful monsters' in an environment of low competition. The processes intended are briefly discussed and grouped into a few categories, notably: extended growth, enation, adhesion and cohesion, laciniation, reduction, metamorphosis, and symmetry in zygomorphic flowers.

VEGETATION AND ECOLOGY

Van Steenis's hitherto published work on this subject is scattered over a number of mostly smaller papers. A great manuscript which is to become volume 2 of the Flora Malesiana is still unfinished. His hitherto published papers deal with exploration results, remarkable vegetation types, vegetation classification, and destructive influences. The leading idea throughout these works is the climax principle. This means that all vegetation types are either the stable outcome of a very long development during which a maximum diversity in life forms and species accumulated to the point of saturation under the conditions permitted by climate and soil, or can be understood as derived from one of the former types through a process of more or less complete and prolonged destruction.

Among the many accounts of his field trips (listed in Flora Malesiana 1, 1950, 502—503), three papers are of special importance. Two are in English (Bull. Jard. Bot. Btzg III, 12, 1932, 151—211; 13, 1933, 1—56). They deal with the results of a tour to the Anambas and Natuna Islands between Malaya and Borneo, and to the Ranau region in Southern Sumatra. Similar in outline, they describe the topography and geology of the respective areas, previous collections, the author's route and collections, provide sketches of the

vegetation, plant geographical conclusions, and additional notes. They are remarkable for the solid background of knowledge gathered from the existing sources, for the variety of observations they communicate, and for the wealth of ideas they contain. In fact, they embody a very great deal of Van Steenis's subsequent work *in statu nascendi*. In them we find discussions on the flora of rocks where plants occur that are otherwise mostly epiphytes, on (plants confined to streambeds and called) rheophytes, on (vegetation on podsolized sands called) padangs or kerangas, on plant geographic affinities and demarcations, on secondary growth, on the occurrence of mountain plants at low altitudes, and many other subjects.

The third paper, in Dutch (Tijds. Kon. Ned. Aardr. Gen. II, 55, 1938, 728—801), deals with the results of Van Steenis's expedition to the Mount Leuser or Losir region in northern Sumatra in 1937. The style is infused with a wonderful enthusiasm in the description of the extensive preparations, of the country with its pine vegetations or 'blangs', its mountains with their wild slopes under thick forest, and with their quiet meadows in the summit regions full of exquisite flowers; of the camp life with its varying fortunes, and the hunt for geological discoveries as well as for new plant species. The expedition revealed that the Leuser-complex is non-volcanic and that its flora contains a slight but distinct element of mountain plants of Australasian origin.

The many papers on remarkable vegetation types often give ample data on the habit, occurrence, affinity, and behaviour of all the important plants involved. I mention in this connection his papers on fresh water plants (Arch. Hydrobiol. Suppl. 2, 1932, 231—337, 379—487), on marine phanerogams (Trop. Natuur 22, 1933, 43—46), on warm stations on high volcanoes where lowland plants occur (Gard. Bull. 9, 1935, 64—69), on savannah plants going underground to protect themselves from fire (Trop. Natuur Jub. Uitg. 1936, 111—123), on lime stone precipitations from hot water, on Mts. Papandajan and Gede (all in Nature Protection in the Netherlands Indies, 1939), on the vegetation of Mt. Idjen (Trop. Natuur 29, 1940, 157—161, 180—184), on rheophytes (Proc. R. Soc. Queensl. 62, 1952, 61—68), on 'Pandanus in Malaysian vegetation types' (sample treatment Flora Malesiana 2, 1954. 12 p.), on Malesian plants with a fleshy stem base in dry regions (Webbia 11, 1955, 189—195), and his extensive account of the ecology of the mangrove (Flora Malesiana 5, 1958, 431—445) showing that the occurrence of mangrove is but indirectly bound to a wet climate, because in a dry climate no silt is produced. On fresh water plants he made interesting remarks with regard to their wide areas with vast disjunctions and their often extreme rarity, which he ascribed to a very sensitive ecology (Flora Malesiana 5, 1957, 317; 6, 1962, 158).

The '*Maleische vegetatie schetsen*' (Tijds. Kon. Ned. Aardr. Gen. II, 52, 1935, 25—67, 171—203, 363—398) form a more complete collection of this kind. They serve as an introduction, a complement, and an explanation of the vegetation map of the then Netherlands Indies published in the 'Atlas van Tropisch Nederland' (1938). The paper gives historical notes, correlations of vegetation with climate, soil, population density, and altitude, and discusses factors influencing the forest physiognomy, composition, and extension. It forms a critical and informative compilation of all the literature to date on 90 vegetation types to each of which an average of one page has been devoted. The approach is largely floristic, as many chapters focus on one genus and on local conditions; it does not give a comprehensive theory nor a classification. A revised edition of the *Vegetation map of Malaysia*, scale 1 to 5,000,000, was published by UNESCO in 1958.

As for vegetation classification, Van Steenis later came to distinguish 14 climax types, briefly described in Dutch in the book by Klein, Nieuw Guinea 2 (1954) 218—258, and

in English in Proc. 8th Pac. Sc. Congr. 4 (1957) 61—97, and in Backer & Bakhuizen van den Brink, Flora of Java 2 (1965) (1)—(72), with 32 fine photographs.

In Proc. 7th Int. Bot. Congr. Stockh. (1953), p. 637—644, Van Steenis has listed the various destruction stages or seres derived from each climax, under influence of volcanic and geological agencies, drainage, cutting, burning, grazing, and agriculture, briefly but instructively, in a hierarchical order.

Destruction of vegetation by man has been the subject of various papers. Quite early Van Steenis arrived at the conviction 'that the influence of man on the vegetation has hitherto been far underrated' (Bull. Jard. Bot. Btzg III, 14, 1936, 50—55). Especially in a dry climate, a very sparse population can already affect huge areas through fire. In *Homo destruens*, his address as a professor at Leiden in 1954, he once more emphasized the predominant significance of the factor man in understanding vegetations, and the very long times that factor is already in operation. The effect of fire increases with the frequency of recurrence, the length of the dry season, the inclination of the land surface, the altitude above sealevel, and also the quality of the soil which in the lowland rain forests is often poor to the extreme.

It should be realized that man is the cause of the destruction, while adverse natural factors are merely the conditions. Through destruction caused by man and aggravated by an unfavourable climate and a poor soil, there is a progressive deterioration of vegetation, climate, and soil, to an extent that indeed may be incredible, and that Van Steenis led to the conclusion that deserts owe their origin largely to man (e.g. Tectona 30, 1937, 634—652). It requires an imagination both powerful and pessimistic to visualize a whole bare country under forest because of a small patch of forest which happened to escape the axe. Yet this is all too often the proper interpretation. 'There where one tree stands, a forest can grow.'

The effect of the destruction on the flora has led Van Steenis to the formulation of the so-called *nomad theory*, already in his Vegetatie-schetsen of 1935, and somewhat worked out in subsequent papers (Versl. 28ste Verg. Ver. Proefstat. Pers., Maart 1941; Vakblad voor Biologen 36, 1956. 165—172; in English in Kandy Symposium 1958, 212—218). The nomad theory explains the origin of the plants which make up the secondary growth. This origin becomes a problem if we assume that long ago, before man began to exert his influence on the vegetation, virtually nothing but climaxes existed. Nomad plants have the ecological properties of pioneers: they require light for their germination, grow fast, are indifferent to soil, produce abundant seed, and are short-living, contrary to plants of the climax. They quickly occupy a piece of bare soil, settle there for a number of years until their plot is invaded by species from the nearby primary forest which eventually takes complete possession of it. Such species travel, as species, from one place to another: a landslide, a lava stream, a strip of freshly deposited sand, to act there as a scab on a wound in the forest. Nowhere will they stay for long — unless man disrupts the balance and creates vast open spaces which he keeps on disturbing. The pioneer species now extend their area enormously and stay there if the new conditions suit them. Perhaps 20 % of the Malesian flora consists of such nomad species. The pines in northern Sumatra and northern Luzon, the *Casuarina* species near the beach and in the dry mountains, and *Melaleuca* are examples. Originally pioneers of rare occurrence, only able to germinate on bare soil and in the light, resistent against fire, they have profited from man at the expense of the virgin forest, which originally they had the task to heal.

MAN, NATURE, EDUCATION

The more peaceful interactions, too, between man and the plant world, have always attracted Van Steenis's alertness. Full of disdain on the one hand for popularizers and ignoramuses among the Malesian peoples and whites alike, he has on the other hand often expressed his admiration and interest for natives and amateurs who had personally acquired knowledge of plants, their habits, properties, and products. In his tour reports and in the many popular papers he wrote, we often find references to observations and uses cleverly made by natives and amateurs, which he obviously had taken great delight in learning.

He has never pursued ethnobotany very systematically, and is severely critical of indiscriminate use of vernacular names and reliance on them (Flora Malesiana 1, 1950, xlii—xliv), but he closely followed the work of foresters and plant breeders and has asserted (Flora Malesiana 4, 1948, x) that it is the duty of the taxonomic botanist to supply basic data to research in applied botany, and always has given the 'Uses' of plants a prominent place in the outline of the Flora.

Nature conservancy is near to Van Steenis's heart. He edited '*Natuur in Indië*' (1937), an appealing book of beautiful photographs and popular descriptions of treasures to be found in the nature reserves of Indonesia. Repeatedly he has in compelling terms brought forward the botanist's arguments for nature protection, which so often seems to be exclusively intended for animals. Most of his papers on the subject are in Dutch, but recently he published a paper in English (Bull. Jard. Bot. Nat. Belg. 41, 1971, 189—202). In it, he makes a plea for large(-area) reserves, on ecological grounds. He stresses the economic value of primary vegetations and explains the dangers to be faced if governments in Malesia let (Japanese and other) buccaneer loggers destroy their natural resources wholesale in the way they are doing now. He makes a plea to safeguard especially the lowland mixed dipterocarp forest (quoting pleas made by Anderson for Sarawak and by Ashton for Brunei), the coastal forests, the freswater swamp forests, the coastal peat forest, and the heath or kerangas forest. He points to the vulnerability of vegetations in regions with a dry period; the longer this dry period, the stronger the danger of fires, through which a very small population can destroy vast tracts of land.

He is a strong advocate of birth control and holds it that, in view of man's newly acquired technological power, the ethical arguments in favour of fertility are no longer valid, on the contrary, that nowadays it is even immoral to have many children. 'Man's future can only be guaranteed by restriction of his number.'

From 1935 to 1942 he was botanical editor of *De Tropische Natuur*, a most attractive monthly for a broad public of interested laymen, which still makes excellent reading matter for anybody who understands Dutch and wants to learn about the living world of Indonesia. Van Steenis made a series of various and first rate contributions, through which he generated enthusiasm among his countrymen. His finest work in this field, however, is still to be published, notably simultaneously with the present issue. It is *The Mountain Flora of Java*, a book of 57 splendid coloured plates, intended as a general introduction and excursion guide. After his work '*On the origin of the Malaysian mountain flora*', which has rendered Van Steenis familiar with the subject more than anybody else, he set out on a number of excursions to mountains in Java, accompanied by two draftsmen of the Herbarium Bogoriense. He collected the plants which his artists painted in water-colours while they were still perfectly fresh. Four hundred and fifty plant species were thus figured, frequently both in flower and fruit. The text explains the figures, adds interesting details, and discusses all the important aspects of plant life on the mountains

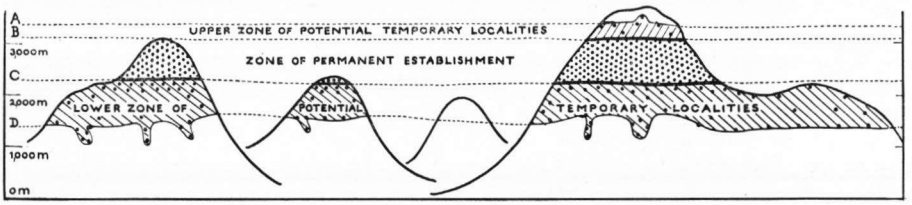

Fig. 2. Schematic chart of distribution of a mountain plant of which the complete altitudinal range is between 1100 and 3300 m, but which occurs only on mountains which are at least 2300 m high. The zone between the lines A and B represents the upper zone of potential temporary localities (3300—3100 m); the zone between the lines B and C is the zone of permanent establishment (3100—2200 m); the zone between the lines C and D is the lower zone of potential temporary localities. In the zones the density of the dots is in proportion to the frequency of individual localities. — Source: Kon. Ned. Ak. Wet. Amst. Proc. C 64 (1961) 441, f. 1.

of Java in general. The war delayed publication, much to his regret, almost, it seemed, ad infinitum. It is gratifying that now the funds have been found to make the fruit of this joint effort of a Dutch botanist and two Indonesian artists, with its unique educational, esthetic, and scientific value, available to the people of Java.

Van Steenis promoted education in biology in schools through his '*Flora voor de Scholen in Indonesië*' (1949), a work shaped after a design which at a later occasion he has again defended (Proc. 9th Pac. Sc. Congr. 4, 1962, 139—140). In this pocket Flora the idea of completeness has been abandoned altogether. It contains about 400 species which are to be found in and near the villages. Many of these plants are, of course, weeds, ornamentals, and cultigens, and most of them are distributed over enormous ranges. Hence the Flora could be used over a similar area, extending from Thailand and Viet Nam through Malesia to far into the Pacific.

The text is in very plain and simple language; unfortunately still only in Dutch. The identification keys are easy to use. Education through personal observation is the aim; as a consequence plants with very minute flowers have been left out, as well as an index to the vernacular names. Drawings are not given either; they would make the book too easy and nobody would learn from it. Let us hope that a publisher will bring out an English translation.

Under this heading also has to be mentioned the care that Van Steenis took in seeing that the work done at the Rijksherbarium by university students resulted in a publication. He considers it a regular part of a scientific training if one learns at an early stage to prepare a polished stone for the building of science. During the period 1950—1971 no fewer than 94 papers have been published, by a total of 42 students. All their work is set up with this goal in mind.

DISCONTINUITIES IN PLANT DISTRIBUTION

On the origin of the Malaysian mountain flora (Bull. Jard. Bot. Btzg. III, 13, 1934, 135—262, 289—417, 14, 1936, 56—72) is one of Van Steenis's most massive single contributions to science, and also one from which we can learn most about his way of thinking. That it was never entirely completed is not important. The picture it gives has been somewhat refined in '*Plant geography of Mt Kinabalu*' (Proc. Royal Soc. B 161, 1964, 7—38) but the conclusions have never been challenged.

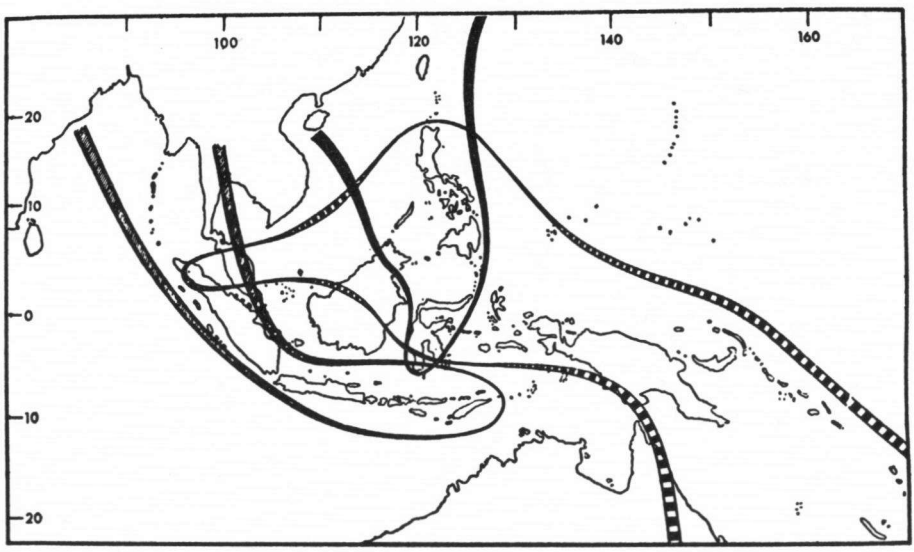

Fig. 3. The three migration tracks (latest version) of cold-loving mountain plants from temperate regions into Malesia. Hatched, the Sumatra track; black, the Formosa-Philippine track; chequered, the New Guinea track. — Source: Proc. R. Soc. B 161 (1964) 24, f. 11.

Besides that it gives (on p. 139) a fine apology for plant geography as a science in its own right, the paper is characteristic for the methodical limits it imposed on the materials used. Here we find for the first time the genus adopted as the unit for plant geographical considerations, and also the most important singling out of cold-loving genera, notably those confined to altitudes above 1000 m. Thus, Van Steenis excluded the genera which might have grown in the tropical lowlands, retaining about 260, i.e. 8 % of the total of native genera, with about 800 species, i.e. 4 % of the estimated total. He gave an annotated list of these genera and species, with details of distribution inside and outside Malesia.* All these genera show great gaps in their area, as they occur in the temperate regions and on the cool summits of the Malesian mountains but not in the hot lowlands. In some cases, the disjunctions between their temperate stations in the Himalayas and East Asia or S. Australia/Tasmania/New Zealand amount to 4000 km. How are these disjunctions to be understood?

Van Steenis bases his reasoning on two axioms, notably:

I. Plants are in general incapable of dispersal over long distances. A species is such a unique thing, that the possibility that it evolved twice can be ruled out. Moreover, the means of dispersal that we have come to suppose to be adapted to transportation by wind or animals, do not have the effect we had expected. Time and again we see that narrow seas or even rivers already form a barrier to dissemination. We therefore may conclude that the present areas separated by disjunction are relic areas.

II. Plant genera which are restricted to well defined ecological niches must have retained their requirements since very long times. Observations and experiments show

* The list is still largely valid; 16 genera should for various reasons be removed, and 41 genera be added.

that plants of true cold-loving genera are indeed sterile when planted at elevations too low for them. Only much later (Proc. Kon. Ak. Wet. Amst. C 64, 1961, 435—442) did he explain with the aid of these observations the hitherto mysterious fact that species occur only on mountains which are very much higher than the lowest contour where the species is still found (fig. 2).

His conclusion is that while the genera with relatives in the warm lowlands might have ascended the mountains from there, the present cold-loving genera must have moved into Malesia by way of three high-altitude migration tracks (fig. 3). These must have been mountain chains which through erosion grew lower and finally disappeared. The tracks have been reconstructed on the basis of the present aequiformity of plant areas. That some genera have much wider gaps than other can be understood if we assume the existance of more or less successive, parallel mountain chains. Some genera managed to settle also on geologically younger summits nearby, thus vailing themselves with another period of survival, and succeeding in keeping their area more continuous than those who did not and perished with the mountains on which they grew. The species we now find on Malesian mountains may therefore be much older as species than the mountains themselves.

The two axioms recur in all Van Steenis's later plant-geographical publications. One of them deals with a number of papilionaceous genera adapted, and in fact bound, to a more or less strong seasonal drought (Reinwardtia 5, 1961, 419—456). The plants are comparable to mountain plants in that their isolated areas look like islands in an inhospitable sea. Here too the areas are aequiform. The discontinuity is, of course, of a different nature than in the mountain plants, and coincides with the everwet nucleus of western Malesia (fig. 4). All species occur both in SE. Asia and in the drier parts of eastern Malesia. According to the size of the disjunction, six 'drought classes' are distinguished, ranging from indifferent to climate to bound to a severe dry season. These areas, too, must have been continuous, during a period of greater drought, probably when in the Ice Age the sea level was much lower. A 'drought corridor', consisting of a chain of dry stations which acted as 'stepping stones', must have enabled the plants to migrate. When later the climate became more humid, many of the 'stepping stones' disappeared, but in the more remote stations still affected by a dry monsoon, the plants remained (fig. 5).

'*The land bridge theory in botany*' (Blumea 11, 1962, 235—372) deals with the disjunction between the about 80 plant genera which are found within the tropics on both sides of the Pacific. This is an aspect of the central and most difficult problem of plant geography: how to understand the distribution of pantropical groups? Like in the Mountain Flora paper, all sides of the problem are documented, then all possible explanations are examined and ruled out except for the one that emerges as the solution to stand against all objections. This solution is the assumption of a tropical land connection across the Pacific in the Mesozoic, which should be imagined as a more or less continuous chain of of islands, not unlike the Malesian Archipelago.

Subjects involved are the relation between dispersal and distribution, plant taxa as thermometers of the past, paleoclimatic and fossil evidence, and the functioning of land bridges in general. The use of plant taxa as indicators for ecological conditions in the past is that it permits us to separate temperate and subtropical genera from the truly tropical ones; the former could have migrated by way of Behringia, the latter could not.

Van Steenis's argumentation pivots upon the 'steady state principle' which means that since the late Paleozoic, or at least the early Mesozoic, the main climatic zones on earth

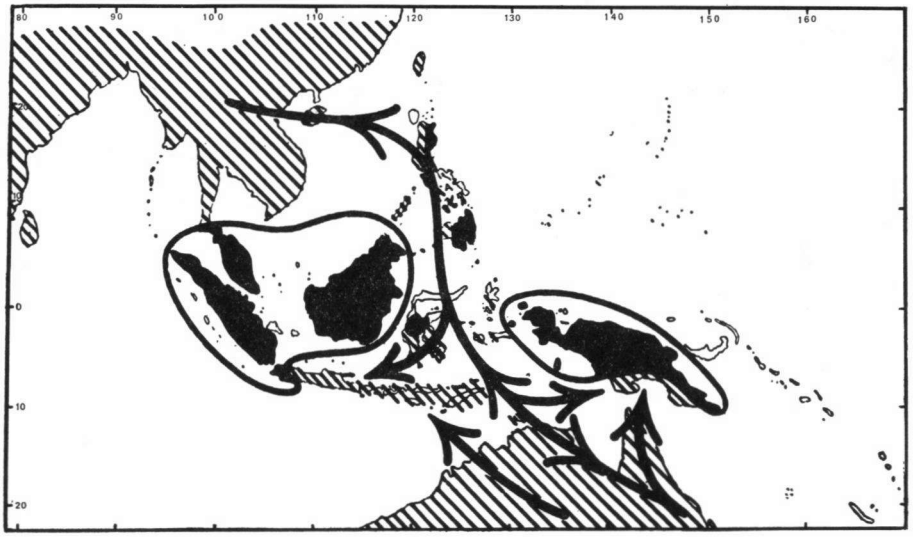

Fig. 4. The two great nuclei of everwet rain forest area in Malesia, on the Sunda Shelf and in New Guinea, as barriers to the distribution of plants which require a seasonal drought. The hatched areas are either periodically dry or consist of a mosaic of everwet and dry places. — Source: Reinwardtia 5 (1961) 426, map 1.

have not essentially changed. The continents largely retained their shape, although upheavals took place, but since the pre-Cambrian no continental drift occurred. The preclusion of continental drift necessitated the postulation of land bridges. This was in 1962; since that time many geologists have advocated continental drift, whereby they encountered opposition on the part of Dr. Van Steenis, in reviews and occasional remarks. Again Van Balgooy (Blumea Suppl. 6, 1971, 136 seq.) has adduced important materials towards a critical evaluation.

In a paper *On the origin of island floras* (Advancement of Science, May 1964, p. 79—92) the same theory has been applied to the flora of isolated islands, a plant geographical problem of long standing. Van Steenis sums up a number of generalisations, notably 1) floristically, all islands show affinity with the continents that surround them, 2) generally in more than one direction, 3) the closest affinity needs not coincide with the smallest distance, 4) disjunctions may be very great, 5) oceanic islands have many endemics, 6) these endemics are often primitive, 7) in composition the island floras often differ much from the continental 'source areas', 8) they often have woody plants whose relatives elsewhere are herbaceous. From these points he concludes, somewhat surprisingly, that oceanic islands must have been populated with plants by way of land connections in a geological past, to the exclusion of long distance dispersal. Here Van Steenis goes much further than J. D. Hooker ever did.

His paper on the *distribution of mangrove genera* (Proc. Kon. Ned. Akad. Wet. Amst. C 65, 1962, 164—169) is also based on the idea of long-persistent ecological claims. Mangrove is bound to muddy tropical coasts, and must have been so in the past. Dispersal is by sea water. Diversity is greatest in Malesia and the Pacific; on the west coast of

Africa there are far fewer species, and all of these are also found on the American coast of the Atlantic Ocean. Almost all the Atlantic mangrove species have their closest relatives in the Pacific. Finally, the east and west coasts of Africa have not a single species in common. The conclusion is that no migration of mangroves occurred round the Cape, which therefore (since the Upper Cretaceous) cannot have had a tropical climate. Nor can the Tethys Sea have acted as a migration channel, for the Caribbean region is the richest part in mangrove species of the Atlantic. The Tethys Sea can therefore not have been wholly tropical; remnants of tropical plants which have been found in the London Clay flora are ascribed to drift. The only possibility is, that the Atlantic Ocean received its mangrove flora from the Pacific by way of an open strait in the place where now is the Isthmus of Panama, and on the existence of which there is agreement among geologists.

Many of Van Steenis's best ideas culminate in his latest paper, on *Nothofagus in space and time* (Blumea 19, 1971, 65—98). The importance of this genus for plant geography lies in its plentiful fossil record, the fact that its diaspores are such that long distance dispersal is impossible so that a discontinuity in its area implies a former land connection to a very high degree of certitude, and the clarity of its taxonomic position close to *Fagus* of which it forms the ecological and plant geographical 'counterpart' in the southern hemisphere.

The distribution of *Fagus-Nothofagus* in past and present forms a so-called hour-glass-pattern. The group once occupied both hemispheres over large tracts of which we now have the remnants, *Fagus* north of the equator, *Nothofagus* south. The areas have a narrow connection in Malesia. There are more cases like this, notably the woody *Araliaceae* mainly in the southern hemisphere and the closely related herbaceous *Umbelliferae* in the northern, the northern *Ericaceae* and the southern *Epacridaceae*, the tropical *Capparaceae* which are woody and the northern *Cruciferae* which are herbaceous; more of such 'pairs' are listed on p. 77 of Van Steenis's paper. Malesia must have been the cradle of the diversity in *Fagaceae*, because it is only in this area (actually Sino-Malesia) that all the genera of that family occur more or less together. In general, Malesia might have acted in a geological past (about the Upper-Cretaceous) as a source and transmigration area of plants which now are bi-hemispherical in their distribution; of this category an impressive number of genera has been cited on page 90. As an example, comparison is made between *Nothofagus* and *Euphrasia* which occupy almost aequiform areas.

Certainly, Van Steenis's vehement rejection of continental drift and his rigid adherence to land connections across the Pacific should not distract attention from his other findings: the genus as the unit in plant geography; his taking into consideration of all genera; aequiformity of areas as an indicator of problems and solutions; the idea that well-defined ecological claims of genera are probably very old; that the biological significance of diaspores should not be judged from their ingenuity but from their effect; that the angiosperms must be considerably older than the Cretaceous; and that morphologically advanced groups are not necessarily of young age.

VAN STEENIS AS A TAXONOMIST

Before 1950, Van Steenis published revisions of quite a number of rather small genera in the Bulletin du Jardin Botanique de Buitenzorg series III. Later, we find his contri-

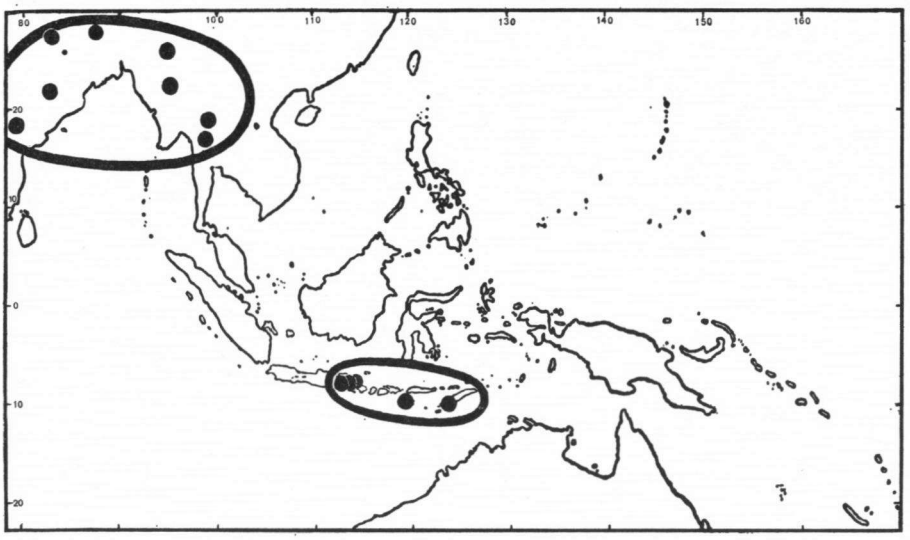

Fig. 5. Distribution of *Rhynchosia rothii* (*Leguminosae—Papilionaceae*) as an example of a species bound to a severe dry season, and in Malesia restricted to the driest parts. — Source: Reinwardtia 6 (1961) 428, map 6.

butions in Acta Botanica Neerlandica, Blumea, Botanische Jahrbücher, Journal of the Arnold Arboretum, Nova Guinea, Philippine Journal of Science, Reinwardtia, and Svensk Botanisk Tidskrift. They consist mainly of reductions, transfers of genera to their proper family, new records, corrections of erroneous records, occasionally a new genus or new species, all of phanerogams of Malesia and adjacent regions. Altogether, they prepared the ground for monographic work in practically all orders.

Van Steenis has displayed an acute awareness of the needs of science under given circumstances and their historical context. In 1949 he published a paper in Dutch on the subject; later he also gave the contents in English (Proc. 8th Pac. Sc. Congr. 4, 1957, 492—500). He divided the development of botanical knowledge about several (sub)-tropical regions into periods. Each of these was characterized by a special sort of achievement, and in all regions one followed upon another in a certain sequence, although not at all simultaneously.

In the 1st of these phases (of Rheede, Rumphius), descriptive work is done with little classification. In the 2nd phase, collecting follows (e.g. by many overseas exploring expeditions), and novelties are described. In the 3rd phase, these results are compiled to a first attempt at a Flora (by Robert Brown, Roxburgh, Miquel). This stimulates towards more exploration, in a 4th phase, and many more novelties are described and early revisions made. Gradually, the need is felt for an evaluation and compilation of all these scattered contributions; the result in this 5th phase is, at best, a reasonably complete, critical Flora (e.g. Flora of British India, Flora Australiensis). By then, local botanical institutes have been established, from which intensified field work is conducted. This brings about a new phase, the 6th one, in which local Floras are prepared, which give a rather final account.

It appears that in tropical countries where the Flora at present is well-known, a harmonious and orderly sequence of these phases has taken place. Thus it depends on the state

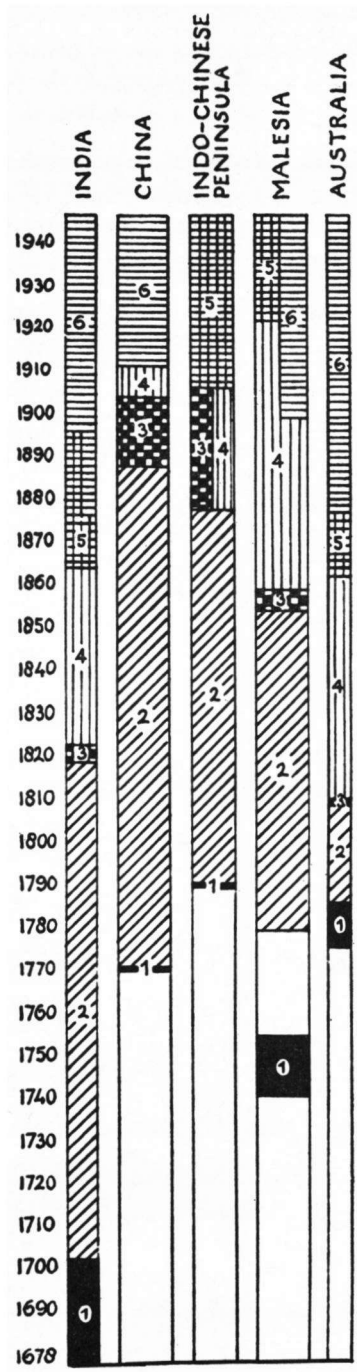

Fig. 6. Phases in the historical development of botanical exploration and publication. 1. Initial phase; 2. first exploratory phase; 3. first compilatory phase; 4. continued intensified exploratory and descriptive phase; 5. critical general Flora is designed; 6. decentralization phase. — Source: Proc. 8th Pac. Sc. Congr. 4 (1957) 499.

of botanical knowledge about a region what sort of botanical work is most appropriate to undertake: exploration, description of novelties, critical revision, or compilation of a Flora. It can also be seen that local floristic work should always be preceded by taxonomic work of a (sub)monographic scope. Along these lines, the Flora Malesiana has been set up in an effort to synthesize the scattered contributions of more than a century.

In the Flora Malesiana proper, Van Steenis wrote up no fewer than 27 families, with 70 species in all. Many of his taxonomic memoirs testify to a profound acuity of perception (e.g. *Scyphostegia*, Flora Malesiana I, 5, 1957, 297), to a great tenacity (e.g. *Medinilla ericoides*, Blumea 17, 1969, 271, a plant he had examined time and again over a period of at least ten years), and a disinclination to name plants after people save as a great exception (*Ruthiella*, Blumea 13, 1965, 127).

Essentially, his interest has always been floristic-on-a-grand-scale, for the geological past as well as for the present. He has no love for speculating morphologists, only for exact description. He is impartial to phylogenetic theories, and is contented to know that monocots and dicots, both gymnosperms and angiosperms, both pachycaul and leptocaul plants have co-existed from the beginning. He appreciates a new system of angiosperms as far as it gives clue to the proper place of genera *incertae sedis*. In matters of nomenclature, his choice is for conservation of well-established names (for which he drafted, with Dr. Bakhuizen van den Brink, many proposals) rather then for niceties in the Rules. In determining affinities, he attaches great significance to vegetative characters (for instance in his comparison of *Turpinia* and *Sambucus* (Flora Malesiana 6, 1960, 49), and likes to invoke the help of other disciplines like palynology, phytochemistry, plant anatomy.

His preference clearly tends towards plants of the climax vegetations, in contrast to plant of the secondary growth for which he has little personal affection. And among the plants belonging to climax vegetations, his deepest love is for the high-mountain plants. This characterizes, I think, Van Steenis as a man and as a botanist — if the two can be kept separate. Mountain plants grow in habitats which can be reached only with effort. In such places usually many species grow together, only to be found after prolonged intensive scanning. He has stimulated several expeditions in search of them. Their occurrence, once established, is a fact, and a fact of great significance to science, because it is the outcome of the earth's history. By his own account, the happiest moment of his expeditions to Mount Leuser was the discovery of *Parnassia*, which he had predicted in advance. Go to a place where you have good reason to find new facts which have a significance to science, and gather them with concentration of all your powers — that Van Steenis has done and throughout it has symbolized his way of working.