

SPECIFIC AND INFRASPECIFIC DELIMITATION

	<i>page</i>		<i>page</i>
1. Introduction	clxvii	4. Specific polymorphism and adaptation characters	cxcvii
2. General considerations	clxx	5. Anthropogenous influence and specific delimitation.	cxcviii
3. Patterns of variability	clxxvii	6. Specific delimitation in cultivated plants	ccii
Phenotypic variability	clxxvii	7. Hybridization, miscibility, and specific delimitation.	cciii
Genotypic variability	clxxxiii	Chromosome races	ccxi
A. <i>Populatio continua</i>	clxxxvi	8. Apomicts and specific delimitation	ccxiii
(1) <i>Variatio genotypica regularis</i>	clxxxvi	9. Practical taxonomy	ccxxvi
(2) <i>Variatio genotypica clinalis</i>	clxxxvii	10. Conclusion and theses	ccxxiii
(3) <i>Variatio genotypica marginalis</i>	clxxxvii	Rules and recommendations for taxonomic work	ccxxiv
B. <i>Populatio discontinua</i>	clxxxviii	<i>Index to terms and topics</i>	ccxxx
(4) <i>Populatio discontinua oecologica</i>	clxxxviii	<i>Index to personal names</i>	ccxxxii
(5) <i>Populatio articulata regionalis</i>	clxxxix	<i>Index to plant names</i>	ccxxxiii
(6) <i>Populatio articulata altitudinalis</i>	cxcii		
(7) <i>Populatio articulata disjuncta</i>	cxcii		

1. INTRODUCTION

In the hierarchic structure of the plant kingdom the species is, in the ranks of taxa, the most important entity. In comparison with the other ranks it is the one which is most distinct in nature to human and animal observation. The species are the most important building-stones of living matter.

HUXLEY rightly agrees with TIMOFEFF-RESOVSKI (4, p. 3-4) in saying:—"that species have a greater reality in nature, or a greater degree of objectivity, than higher taxonomic categories. Species are in the majority definable as distinct self-perpetuating units with objective existence in nature, and therefore are on a different theoretical footing from genera and families or higher categories, which are not definable in this concrete way".

All hypotheses on evolution have started and will have to start from a most careful consideration of these building-stones and DARWIN titled his great work consequently 'The origin of species'.

We know that DARWIN who himself composed large zoological monographs, stood in close contact with BENTHAM and HOOKER, who all employed the species concept in accordance with the Linnean standard. In works dealing with 'species' or their origin we have always to consider whether this standard was maintained, in order to avoid misunderstanding, as unfortunately the simple possession of a binomial name is no guarantee that the taxon in question comes up to the Linnean standard.

In distinctness the rank of a species is succeeded by that of a genus.

The distinction of genera and species is not borne out only by academic training; it is most remarkable, though not surprising, that the unpreoccupied eye of the rain-forest nomad tribes, who for their living are in closest contact with plants, frequently distinguishes the same genera and species (and sometimes the family) as the trained botanist.

For the taxonomist working on the relatively poor and well-known floras of temperate and boreal regions the problem of specific delimitation seems not a problem of particular weight, save in some special genera as *Rubus*, *Taraxacum*, *Hieracium*, *Salix*, *Rosa*, *Crataegus*, and some others. Embryological research and experimental taxonomy have shown in most of these cases, however, what are the underlying reasons of the fact that the 'species' of these genera withdraw from the normal specific delimitation and fall outside the usual classification. Hybridization followed by full or partial apogamy plays havoc with species distinction in these genera, and attempts to fit these clones (specimens) or populations by force into the scheme of Linnean specific populations can only be admitted as an artificial procedure for practical aims. Properly it would be advisable to indicate their true nature similarly as has been proposed recently for the cultigens (*cultivar*), contrasting them against free naturally interbreeding specific populations (*linneonts*). Before doing so factual observation should be made to show that they belong to this category indeed.

Apart from these often clone-like 'species' there is little to worry taxonomists working on

temperate floras who are mostly engaged with detail work on the infraspecific taxa occurring in their country. In most temperate floras novelties in the way of new species of spermatophytes are practically absent and the description of new genera or families is entirely out of question save by splitting existing ones.

Besides, the botanist working on temperate plants is, generally, provided with abundant material of each species and in case of rarities he is often in a position to check his data with living specimens on the spot or in his experimental garden.

The botanist engaged with tropical plants, however, is confronted with immensely richer floras in a much less advanced state of exploration. His material is often lamentably scarce; he is practically never capable of checking data on the spot; he is almost always compelled to confine his study to herbarium material, which requires far more thought and sense for synthesis to classify in a satisfactory and useful way. He is obliged to build up the frame of systematic botany as he has to work on genera which are often confused, species which are not seldom assigned to the wrong genus, genera which are sometimes placed in the wrong family, genera which have occasionally been described twice or thrice in different families; he has often to emend generic diagnoses and even those of families, and finally he finds in his material sheets which represent obviously entirely unknown species and genera. The number of reductions to be made is sometimes very large as is clear from the figures given on p. ccxxii.

His final goal is, of course not different from that of his colleagues in temperate countries, but he has to pave his own way and explore untrodden fields, in contrast with the temperate botanist whose field has already been ploughed and put in order by numerous predecessors.

There is also no reason to suppose that tropical species 'behave' otherwise in their delimitation than those in temperate countries. Botanists of experience who have worked in some limited tropical areas, where the flora is well-known, successfully employ the same Linnean standards as customary in temperate regions.

There is no reason to suppose that tropical species are more variable or less variable than those temperate; in both cases some species are more variable than others and there is a range in all kinds of degree; further some species are common and others are rare. All that can be said is that the arboreous nature of the bulk of the tropical vegetation provides the tropical botanist with small fragments of often gigantic plants. Further, it is certain that various arboreous groups display a hitherto little known floral dimorphism and there is sometimes an astonishing plasticity (mostly ontogenetic) in the vegetative parts of woody plants and twiners. This, and the general paucity of material alluded to above, and absence of means to recheck data on the spot, put great stress on the ability of the tropical botanist to have a sound estimate on the degree of variation necessary for the delimitation of the species he has to study.

There is therefore special reason for the tropical taxonomist to give a good deal of attention to the species concept in order that his work will be satisfactory and useful to others.

It has been my singular fortune to have been in the tropics for two decades, to work under ideal conditions in the Herbarium Bogoriense of Kebun Raya Indonesia, with a well-stocked, adequately named herbarium and an excellent library at hand, and ample opportunity for field work. During that time I have had daily occasion to try to identify specifically a very great number of specimens by means of Floras, revisions, and monographs. In this way I have acquired a first-hand judgement of the merits of these works in the way of specific delimitation.

Frankly I feel quite alarmed at the way in which various taxonomists have ill-treated specific delimitation and have drawn keys and descriptions which do not work at all. In some cases it was clear that the overcautious had no courage or common sense to have an opinion on the variability of his material, turning his work into specimen description. In other cases it was clearly haste or carelessness which spoiled the work, in still other cases it was clearly the intention of the revisor to deviate from the Linnean concepts and have his own way. Save some precious but lamentably few exceptions, it appeared in most cases impossible to get a satisfactory identification with a key that worked or differential diagnoses that fitted.

This often disgusting experience, about which I feel seriously concerned, has led me to a careful consideration of both the theoretical and practical side of specific delimitation and description which is the basis of all taxonomy, which is decisive for its quality, and *conditio sine qua non* for the exactness of the status of all higher categories.

Without any attempt towards completeness as to citation and discussion of literature and restricting myself to the phanerogams, I feel that I must, in this Flora, once again try to explain the basic aspects of specific delimitation, even though I feel far from capable of writing essays as elegant and concise as those of HOOKER (1, 2) and BENTHAM (3), who handed the torch of *scientia amabilis*, ignited by the synthetic genius of LINNAEUS, to our generations.

It is obvious that many taxonomists of today, hurried as they are, have omitted to work through the masterly essays and lectures of two botanists whose illustrious works have never been surpassed, either in quality or quantity, and whose wisdom, practical and theoretical, should be ours. I can only hope that the essays alluded to, which are still modern and will remain so, though a century old, will be set obligatory to the University student's courses of plant taxonomy, and be studied again closely by anybody who ventures on a monographic study.

I feel also slightly embarrassed in duplicating many things said in that admirable book 'The New Systematics', a team-work of prominent biologists giving a modern version of high standard on various aspects of specific delimitation.

Its editor, JULIAN HUXLEY, expressed the main trend of it in his introductory generalization as follows (4, p. 10):—"Practical convenience as well as the lack of clear alternatives dictates that we should stick to the classical terminology of genera and species and their subdivisions as a general basis for minor systematics, even if there are certain groups such as the blackberries or willows to which they will not apply, and even if in many cases we decide to coin special subsidiary terminologies for special purposes... There is no single criterion of species... Morphological difference, failure to interbreed, infertility of offspring, ecological, geographical, or genetical distinctness—all those must be taken into account, but none of them singly is decisive. Failure of interbreeding or to produce fertile offspring is the nearest approach to a positive criterion... A combination of criteria is needed... In the great majority of cases species can be readily delimited, and appear as natural entities, not merely convenient fictions of the human intellect. Whenever intensive analysis has been applied, it on the whole confirms the judgements of classical taxonomy".

TURRILL's opinion is similar; he says (5, p. 13):—"Nothing has as yet appeared to replace, on any large scale, the principles of orthodox taxonomic schemes on the seed-bearing plants. Families, genera, and species are given Latin names and arranged in a hierarchical system which still shows little decline or fall. Nevertheless, there are many groups where the species concept has to be used in a very arbitrary manner, and some in which the genus concept appears in practice as an artificial device retained in order to avoid upsetting a widely used nomenclature".

According to CAMP, however, the days of classical taxonomy are numbered and he expresses himself (6) in the following revolutionary, flowery thesis:—"The day of the taxonomist who putters alone in his herbarium with an other-worldly stare is done. He must shed off his robe of academic classicism and seclusion, brush off the accumulated dust of the centuries, and come face to face with the dynamics of living populations". A most charming appreciation of and tribute to the work of our illustrious predecessors, the Makers of Botany, and a rosy prospect for a fresh stimulant to naturalists to study taxonomy by camp-ing.

Since the time that LINNAEUS's genius organized the hierarchy of the plant kingdom by species and genera, *i.e.* respectively individual specimens which show such great resemblance morphologically that they are evaluated to belong to one entity of direct blood-relationship (species) and groups of such entities which have certain essential characters in common that they are estimated to have a mutual blood-relationship in the second remove, a surprising simplicity has replaced the pre-Linnean chaos. The concepts species and genus are, themselves, naturally abstractions. Reality enters the picture as soon as the taxonomist has described the characters of a special species or

genus, by which action he automatically combines a certain number of individual specimens, or in the case of genera a certain number of species, fitting the descriptions, under one name. The existence of species is therefore no problem to the taxonomist; he creates them himself and distinguishes them by aid of his diagnoses.

It is most remarkable that taxonomy, the very source of botany, has maintained itself so vigorously with unchanged methodology and concepts for two centuries, that it still proves to possess quality, and will be for ever indispensable for botany both in its own pursuits and essential to other branches of botany, pure and applied. It should be admitted that it has acquired useful data, thanks to information obtained from auxiliary sources—atomy, palynology, phytochemistry, plant geography, cytogenetics, embryology, and experimental taxonomy—but these are not essentially new ones, but mostly refinements of former methodologies.

It is logical that systematy working downwards from the higher categories towards the lower ones¹ will, onwards of the specific level, meet and overlap the field of research of genetics which starts from the genes through the infraspecific ranks upwards to the specific level. For that reason results of genetics in this field of experimental taxonomy are of distinct importance to the taxonomist.

The possibility of distinguishing genera and species and other taxa is granted by the observation, through comparative morphology, that sets of characters (differences) occur in nature discontinuously in combinations, facilitating the distinction of groups of specimens, species or other taxa, characterized by these sets of characters. These demarcations between likenesses show the discontinuity of living matter, similar to the discontinuity in the inanimate, the atoms in chemistry and the quanta in physics.

It falls outside the scope of this essay to give a discussion or opinion on the possible origin or cause of these demarcations which are deeper *cf.* broader in proportion to higher rank in the taxonomical hierarchy, though some remarks on their origin cannot be avoided with the treatment of the infraspecific taxa (*cf.* p. clxxxiii-cciii).

No more will I enter a discussion on the consequence of the discontinuous structure of the plant kingdom which can *a fortiori* hardly be explained otherwise than by jump-wise origin of the taxa (mutation in the wide sense), though theoretically origin by accumulation of small jumps cannot be excluded *a priori*. As far as we know at present, the sudden origin of good species by mutation (polyploids), both new and existing, has been proved without a shadow of doubt. In these cases at least *the species is a historical happening*: a

(1) In the Rules of botanical nomenclature the lowest 'rank' is that of *individuum*. This is illogical: an individual specimen belongs to a rank or category, but does not represent a category itself.

sudden event, followed by a period of existence, ending with extinction.¹

The hierarchic structure of plant taxonomy could be compared with the hierarchic lay out of a polder, where there is a drainage system of smaller and larger and deeper trenches and ditches, water-ways and canals which in ascending hierarchy represent demarcations of increasing depth and width. The 'paddocks' (loci) demarcated by equivalent water-ways represent a similar hierarchy as among the ranks of plant taxonomy. The picture of this man-made hierarchy is, however, too regular and ideal in its artificial lay-out for a complete comparison. The plant hierarchy offers really a less tidy picture: some paddocks of the rank of a species are larger in surface than others and are for the purpose of preventing them becoming boggy provided with many minute trenches (often blind) in proportion to their infraspecific variability (polymorphy). Further some species paddocks are separated by shallow ditches, others by deeper ones of the same width, as an expression of their closer or more remote morphological affinity respectively. Occasionally a group of paddocks seems to possess a very regular pattern bordered again by other paddocks which are deviating. In short: the lay-out of a polder reflecting the hierarchy as found in plant taxonomy would not appear to be acceptable as a satisfactory planning to an active polder-board, but the

botanist has to accept the irregular pattern of the paddocks Nature offers him.²

In many cases the botanical polder is incomplete in the sense that it comprises large stretches of barren land without paddocks. In other cases it appears to be entirely filled and complete, presenting obviously all potentially possible demarcations. Such a complete picture is for instance offered by the living *Annonaceae* in which DIELS (9) has found that all genera, characterized by the combinations of a limited number of generic characters within the structural plan ('Bauplan'), are represented in living nature. Such a complete representation of combinations of equivalent characters will naturally implicate a reticulate affinity which is found indeed to be realized in many of the larger families and genera.

References:—(1) HOOKER *f.* Introductory essay to the Flora of New Zealand (1853) i-xxxix.—(2) HOOKER *f.* Introductory essay, in Hook. *f.* & Thomson, *Flora Indica* (1855) 1-44.—(3) BENTHAM, Rep. Brit. Assoc. Adv. Sc. for 1874, p. 27-54 (1874).—(4) HUXLEY (ed.), *The new Systematics* (1940).—(5) TURRILL, Brit. Assoc. Adv. Sc. no 26 (1950) 1-16.—(6) CAMP, Amer. Naturalist 77 (1943) 322-344.—(7) TURRILL, J. Ecol. 39 (1951) 205-227.—(8) ROBERTY, *Candollea* 14 (1952) 13 *seq.*—(9) DIELS, Sitz. Ber. Preuss. Akad. Wiss. Berlin B 11 (1932) 77-85.

2. GENERAL CONSIDERATIONS

Delimitation of species is performed by the choice of a certain combination³ of critical characters on a comparative-morphological basis.

At first sight the procedure of this choice seems to contain a strongly personal element, specially

as it means not only the *objective observation* of morphological characters but also the assigning of a *different degree of appreciation* of the value to the characters observed. And this appreciation has again itself *no absolute value*: one character may

(1) TURRILL (7, p. 216-218) says:—"Palaeoendemics raise the controversial problems of old age in species and other taxa. The terms 'old age', 'senescence', 'senility' and the like are in some ways unfortunate. A false analogy is drawn between individuals and taxa, the latter in any concrete sense being populations. The words tend to introduce teleological and anthropomorphic concepts". Senility in cultivated plants does not exist, "there is no evidence of either physiological or of any genetical degeneration . . . It is most likely that the great majority of plants in nature die out though some may change by homogenesis into new taxa. Species, or other taxa, verging to extinction may thus be species out of the environment to which they are specially adapted and which have few biotypes and are not sufficiently plastic. Old age of taxa is not counted in the sense of years, but is a question of gene constitution relative to environment, the potential ecological plasticity. Certainly nothing unusual in the genetical systems has been recorded in many of the so-called relict species showing supposed ecological signs of 'senility'".

Extinction in the plant kingdom will generally be due to failure (inability) to produce viable adaptations with changing environments. This interferes with autonomous development by which regime a multitude of forms may be possible, of which a certain (possibly very small) percentage will possess characters fit for viable combinations. Change of environment will further narrow down this percentage, permitting only those to survive which are provided with characters of survival value adaptable to the new environment.

(2) The proposal by ROBERTY (8) to force each subgenus with nine species is the most erratic idea I ever came across, utterly unfounded, and destitute of any contact with reality.

(3) As BENTHAM, DE CANDOLLE (15, p. 181), and others pointed out distinction based on a *single* character leads to artificial divisions and delimitation except in the smallest taxa which merely differ in one gene. A combination of independent characters ensures *natural* division and distinction.

be appreciated of distinct value (constancy) in one taxon (species, genus, family), but be of minor or no value in another.

In science there is a general, reasonable tendency to analyse by objective values and avoid those subjective. Whatever charm the personal appreciation may have, methodologies containing it are considered with suspicion and conclusions based on them are found worthy or relative value only.

However factual *observations* in the pure sciences may be, their *appreciation and evaluation* for the synthesis always contain a certain personal element.

And, as to factual observation in plant taxonomy, there is no other way than using all sources from the array of methods (see p. clxix) for obtaining arguments for circumstantial evidence.

A few simple cases may illustrate the way of reasoning in plant taxonomy. Let us consider a plant specimen which answers in all major and minor points the description of *Campanula rotundifolia* save its corolla which, instead of being sympetalous and campanulate, is split to the base into 5 free segments. 'Academically' this would really remove it from *Campanula*, even almost from *Campanulaceae*, and obviously even from sympetalous orders. Common sense says, however, that this 'cannot be'. As a matter of fact it is a teratological (adesmic) sport of *Campanula rotundifolia* and it is questionable whether it is constant if propagated by seed (*cf.* p. clxxxvi, footnote).

The subfamily of the *Caryophyllaceae* is characterized by a connate calyx, but there are reported single flowers or specimens of *Silene cucubalus* which have it split into segments; nevertheless, we know the deviating specimen must belong to *Silene cucubalus* because of all the other characters being in agreement with the description of that species.

Another example is some species of *Aglaia* (*Meliaceae*), an Old World tropical genus described as possessing pinnate leaves. Some species have been found to agree with all characters of the genus *Aglaia*, sexually and vegetative, but possess simple leaves (17). In addition there are species or specimens which possess both simple and 3-foliolate leaves. The only reasonable conclusion is that there is sufficient circumstantial evidence to emend the original generic diagnosis and define its leaf characters as: 'pinnate, rarely simple'.

The family *Orchidaceae* has essentially zygomorphous flowers; still there are specimens which deviate considerably by having a regular perianth, although their further structure, anatomy, embryology, habit, *etc. etc.*, is orchidaceous. In a few cases such regular flowers have been found in one specimen together with zygomorphous flowers. Furthermore similarly regular flowers have been observed in a number of other families or genera with zygomorphous flowers and are classified as pelorics; they have been interpreted as teratological aberrations. In a number of cases genetic analysis has shown these pelorics to be caused by one Mendelian character. The only reasonable conclusion is to include these pelorics in the

species with which they have all other characters in common and regard them as a 'peloric' facies or form of it.¹

These few examples² show how circumstantial evidence may lead to the evaluation of characters and establish their proper taxonomic value.

There has been of course much discussion on the relative value of botanical characters and no definite conclusion has ever been drawn on the question whether all morphological characters are, finally, manifestations of intrinsically comparable or uniform genetic units of the genome. VON NÄGELI (1) divided 'characters' already into '*Organisationsmerkmale*' and '*Anpassungsmerkmale*'. VAVILOV (2) opposes "specific complexes of morphological or physiological nature" as '*radicals*' against the 'immense number of parallel homologous variations in various directions', the so-called '*variable characters*'. HERIBERT NILSSON (3) speaks about '*Arten-gene*' for defining specific characters which cover the radicals of VAVILOV. JOHANSEN is in doubt whether fundamental taxonomic characters may be derived from normal genes or whether they are based in the structure of the protoplasm.

WINGE (4) believes the latter not to be the case and replaces the idea by his hypothesis of the 'taxonomic importance of polymery' by which it is supposed that the hereditary qualities of the fundamental characters occur in multiple at least in one chromosome (possibly in all), which would explain their constancy.

DIELS (5, p. 81) found it difficult to locate the dividing line between radicals and varying characters in the *Annonaceae*; he assumes that in this

(1) In the Rules of botanical nomenclature there still is an obsolete article which prescribes that "a name or epithet of a taxonomic group must be rejected when it is based on a monstrosity", although the concept of what is to be called monstrous is nowhere defined. Monstruous forms occur in degree, some may be caused by foreign agencies (fungi, viruses, gall insects, grazing, and other influence from animals). Or due to environment (soil or climate), others are caused by genetical factors and may be inherited or partly so (fasciations, pelorics, *etc.*). If we consider further that a type specimen may be based on *any* random individual specimen in conjunction with the fact that populations are polymorphous and consist of an endless number of paramorphs *none* of which can be treated as 'normal' or 'average', the concept of what is monstrous appears to be entirely arbitrary and liable to diverse appreciation, hence to confusion. Accepted species as *Polygonum viviparum*, *Celosia cristata*, *Poa vivipara*, individuals with cleistogamous flowers, *etc.* can hardly be otherwise understood than being monstrosities. This rule militates against logic and should have been dropped long ago.

(2) A great number has been mentioned earlier in this Flora *cf.* vol. 4 (1948) xix-xliv.

family the only radical character would be its structural plan.

Though it should be admitted that occasionally physiological derangements, as in galls and teratologies (pelorics, lacinations, etc.), may hamper or make futile the manifestation of characters which seem structural by virtue of their constancy throughout families or orders and would correspond therefore with radicals (organization characters), the other characters of the species and genus remain intact in manifestation both radical and variable, enabling the correct identification of the species (as in the cases above-mentioned of *Campanula rotundifolia*, *Silene cucubalus*, etc.); it would appear that in these cases only one radical was 'misprinted' in its manifestation, obviously independent from the others. It may be, therefore, that the genetic basis of the radical was positively represented in the genome, but during ontogenesis some physiological factor interfered merely with its normal manifestation.

I myself cannot withdraw from the idea that there is in the genome a kind of hierarchy in character-defining structures of different degree, some more structural, some more variable, but I assume it will be impossible to distinguish only two main classes in this array of capacities. Many characters of vegetative nature (wood- and general anatomy, habit, phyllotaxis, occurrence of glands, leaf structure, nervation, and stipules) as well as sexual (structure of inflorescences, etc.) must be deeper 'anchored' in the atomic arrangement or frame work of the genome-molecule(s) than are more specific and superficial characters which are likely to be located in the marginal area of the genome-molecule(s).

* * *

If specific delimitation would rest only or predominantly on personal appreciation of characters, the conclusion would be that the number of species would vary freely with each individual taxonomist separately, as artistic creations vary with the artist. The negation of the strongly limited creations of living nature has been employed by a few erratic taxonomists who believed themselves to be free to perpetrate plant taxonomy as if living in clover. GANDOGGER has enriched botany with such a work on the flora of Europe which has rightly been neglected by taxonomists of common sense.

The judging of the value of taxonomic work off-hand is impossible, though the qualified taxonomist will have generally not much trouble to verify its usefulness by judging the keys, synonymy, etc. Meticulous outward appearance is of course no guarantee for good work; the glamour may be a thin shell concealing a *horribilia botanica* of spongy contents. Careless synonymy and obsolete nomenclature needs not to be a sign of bad work. The work of C. A. BACKER on the flora of Java for instance, in which the latter items are rarely up to date, are invaluable, hard masterpieces of sound, critical, and perfectly reliable specific delimitation standing the test of time.

And though I support adequate synonymy and

a polished nomenclature, I am of opinion that taxonomists should never consider this to be their main task; it is only a thin varnish, sometimes very time-consuming, to attach to their proper work:—sound specific distinction.

The standard of quality of plant taxonomic work is found in its usefulness.

Usage learns to discriminate between good and bad Floras of one and the same region or country, between good and inadequate revisions or monographs of the same genus or family. The good quality is always bound to good specific delimitation, which facilitates in turn the drawing of useful keys and hard diagnostic descriptions.

The usefulness is, I feel, an adequate control on the purely personal subjective element.

Indeed of old, classical botanists have shared the opinion that the number of species might be large but limited and LINNAEUS expressed this in saying: "there are as many species as God created."

I would be the last to admit that all species created by botanists are good, but on the other hand there is in my opinion far less disagreement among qualified systematists on the status of good species (linneonts) than sometimes assumed by outsiders. And that, if there is disagreement, this originates from other causes than from a great difference in opinion about the evaluation of characters.

Practice learns that in proportion to the experience of the systematist, the quality of his material, the use of refined methods, the thoroughness, seriousness, criticism, specially self-criticism, disinterestedness, the carrying on until he is satisfied, hence in proportion to, in short, the time, energy, and intelligence embodied in the work, he can reach generally a more or less final result, which has appeared to hold for taxonomy and be useful to other branches of botanical science.

It is gratifying that good taxonomical work is so much appreciated by general biologists and specially by geneticists and that taxonomical affinities and relationships are generally confirmed by chromosome patterns.¹ HUXLEY (6, p. 16) says:—"Classical taxonomy has provided a firm foundation for micro-evolutionary studies whenever it is pushed below the specific level and has taken cognizance of geographical subspecies, ecotypes, cytological variants, and so forth. Population studies, drawing on all relevant biological disciplines, are now needed to complete the edifice". Such population analyses are of course outside the reach of the herbarium botanist and do not belong to the α -taxonomy scope of Floras and monographs. They

(1) This is of course not so very remarkable as may appear superficially. Interior morphology (anatomy of tissues, cytology of cells, and phytochemical properties) though only observable with the microscope under high magnification is not of an essentially different standard as compared with exterior or gross morphology, both being manifestations of the genetic properties of the same genome.

should follow their frame-work and be the subject of special detail studies.

VAVILOV, one of the greatest geneticists working for plant breeding, wrote (6, p. 564):—"Some biologists are of the opinion that the age of classical systematics is at an end. From our personal experience we have come to the conclusion that this is not quite so. But it is sufficiently clear that we regard classical systematics, which works only with Linnean species, merely as a first step".

WINGE, who made an extensive study of the microspecies of *Erophila* (13), has shown that they are not apogamous and behave biologically as species; they breed true and possess different chromosome numbers and are capable of forming amphidiploid hybrids. WINGE stresses that they should, taxonomically, be considered as one coenospecies (linneont), as there is no end to their number. He says that it:—"jedenfalls in der Praxis unmöglich und widersinnig sein wird, alle die existierenden konstanten Formen zu benennen und zu beschreiben".

Notwithstanding this powerful appreciation from geneticists who are in a unique position to check the quality of good taxonomical work, getting the proof by the eating of the pudding, one finds sometimes among non-taxonomists an unmistakable mistrust in the aims, methods, and results of plant taxonomy.

This uneasiness of outsiders may be due in part to the remarkable fact that since the time of LINNAEUS the *methodology* of phytography in α -taxonomy has hardly changed: we still work with dried plants and our main tools are still the 10-times magnifying lens, tweezers, and needle, and for cryptogams the microscope. In this rushing world with avalanches of new ingenious devices and techniques in several branches of the natural and pure sciences, it is remarkable indeed that time seems to have stopped and that taxonomy is assumed to be enveloped in a nimbus of conservatism dooming it to be obsolete. But is the history of the tool situation essentially different in for example astronomy?

Another stone of offence has been given by some ambitious taxonomists who light-heartedly have enriched botanical literature by series of phylogenetical trees showing the descent of the plant kingdom. This former fad has been an eyesore to all taxonomists who possess the common sense to realize that we are still in a stage of hard labour in trying to fit here and there pieces of a colossal jigsaw puzzle and that the situation, specially in palaeontology and genetics, physiology and biochemistry, is unfortunately inadequate for such ambitious synthesis.

A further source of distrust by the public has been the frequent *name changes*, obviously not only regarded as a sign of instability in the nomenclature employed by systematic botany but also as a bad omen for taxonomy as a science.

It is often omitted to consider that *nomenclature* is not an essential part or branch of systematic botany as a science, but exclusively a matter of administration necessary for establishing the

correct names of plants. Unfortunately the internationally adopted Rules of Nomenclature are of comparatively recent date. And as these Rules are for a great deal retroactive, and taxonomical literature is very extensive and historical of nature, it is natural that the application of these Rules will bring along a significant number of name changes.

And if the present Rules had been applied from the accepted starting point of botanical nomenclature (1753), and had been acknowledged and followed since, even then the historical growth of botany, by exploration of remote parts of the world, would have brought along a smaller, but still significant number of name changes. And this will not stop before a reliable, permanent inventory and delimitation of genera and species has been adopted.

Disinterested taxonomists fully recognize the importance of stable names and will sustain all practical efforts towards that effect, amongst others by conservation of useful generic names against those obsolete and recently dug up from old works and merely of bibliographic interest. This reluctance to change names, born from a practical, conservative demeanour will, of course, not prohibit them from straightening out positions when unavoidable, even where name changes will be involved.

It cannot be denied that the recently intensified application of the *principle of typification*, which is admittedly inevitable as a basis of a stable nomenclature, has shown itself to be a dangerous tool in the hands of non-experienced botanists who may wrongly assign taxonomical importance to this purely administrative procedure. They sometimes assume they cannot perform botany without having seen the types, which leads to underrating the art of 'reading' descriptions, discourages good diagnoses, and depreciates the technique of phytography, which they assume to be less important than before.

Furthermore they sometimes think that their work is finished with having seen the types. Though I admit that ancient, brief descriptions may often fail to give information on characters which are later found to be important for specific distinction, and may easily be observed in an actual type sheet, the assigning of more than random sheet value to a type specimen may equally lead to entirely erroneous conclusions if the type is not fitting the material with which it is compared. If that is done, the type is often assumed to be a *typical* or *average* specimen, representative of the species. Contrarily, a type specimen being random will rarely represent the average of a specific population *i.e.* belong to the central part of the variation curve of the population. It should be stressed that the identification of *type* with *typical* is an entirely erroneous idea: a type specimen is botanically not of more value than any other random specimen; it is very often incomplete and meagre, as in the past botanists have not always cared to base new species only on rich, complete material, a practice which is emphatically recommended for the future. With the estimate of a type specimen, specially in

the tropics, where materials in general are often scarce and from widely spaced localities, it should always be borne in mind that the sheets at hand represent a mere fraction of a fraction of the entire population and that it will be pure chance if for instance three or five specimens contain the major part of the range of variation of the population which will comprise millions or milliards of individuals and measured in time a multitude of them. One hears or reads sometimes: 'my specimen does not precisely agree with the type, hence it is specifically different'. This conclusion is wrong in reasoning and may lead to preoccupied thought.

It should never be forgotten that the type specimen is botanically of the same status and weight as any other specimen and that its administrative value as prescribed by the Rules of Nomenclature should not unintentionally lead to making it an undesirable botanical factor in delimiting species populations and give impetus towards narrowing down what is naturally divergent and polymorphous.

It has been assumed sometimes that good taxonomy can only be performed by botanists who possess a sixth sense, *intuition*, which should guide them in tracing affinities and in delimiting species. I am afraid that the assumption of this romantic quality is a myth, unless intuition is generally defined as sublimated experience and not classified as a *deus ex machina*. A taxonomist should of course be devoted to his profession, eventually fanatically, and the *hortus siccus* should be to him a living thing. But intuition as a sixth sense is not included, and even not desirable. Zeal, time, opportunity, and intelligent work are the main factors determining the quality of this kind of work, nothing is simply thrown into his lap. Brilliant ideas are welcome, but the facts should be verified. Similarly to other branches of the pure and natural sciences results are reached on the basis of five percent inspiration and ninety-five percent perspiration. If a taxonomist would trust his 'intuition', he would find himself on the quicksand; instead he should observe and observe again and verify his findings.

As a matter of fact those who are quick in assimilating experience will generally produce more and better professional results than the initiated novice. Experience is gained by dogged perseverance. Much depends on his teacher, his education, and personal examples he can observe. In several countries taxonomical education was mostly performed in the herbaria and not as a separate branch of botany at the universities, for example in Australia. At universities in England, TURRILL writes (6, p. 14), "taxonomy has been, at

best, relegated to the position of Cinderella before the fairy Godmother occurred on the scene", though classification is basic to science and taxonomy essential to every branch of botany. At the Sorbonne one cannot attain a doctorate in botany on a purely taxonomic dissertation; in German universities the lamentable position is, that taxonomy occurs on the programme of biology only as a minor item, to teach some names to biologists and pharmacists, save in two or three universities which are in possession of a research herbarium. Fortunately the position is not as bad in many other countries. I am very much satisfied that in my own country leading botanists have always had an admirably broad outlook on botany as a whole in all its branches, by which taxonomy in the broad sense has attained a well balanced position. It is here acknowledged that there is no sensible reason to specialize on certain subjects in botanical science at the expense of others and the methodology and historic nature of taxonomy are accepted as bound to it.

It must be realized that *taxonomy is the autonomic basis of botanical science*, as no reliable work in the other branches of botany can be performed with anonymous material. Each botanical study—botany taken in the widest sense possible—whether it is physiological, anatomical, embryological, ecological, plant-geographical, sociological, palynological, palaeontological, phytochemical, biochemical, or genetical, is bound to the name of the plant(s) which form(s) the subject of the research. This holds of course true for all marginal sciences of the more applied kind as pharmacy, pharmacology, for agriculture, horticulture, forestry, technical botany, and plant industry.

The name of a plant is the key to its literature; the name provides a means for comparing observations and experiments, and enables their repetition.

Taxonomy participates with general botanical disciplines in the ultimate strive towards the *omega* of botany, *i.e.* the exact knowledge of the why and how of the origin and development of living matter, but it is equally certain that taxonomy is the *alpha* of all botanical knowledge.

This alpha character brings along a special responsibility which should be honoured in a laudable manner and taxonomical work should bear the testimony of perfect, professional research work. This is specially urgent as its usefulness cannot be tested immediately, like a sum in arithmetics. It is to some degree a personal achievement; therefore, the mentality of the worker is reflected in it.

On another occasion (7, p. 7) I found fit to allude to the subject of the combination of *mental properties* which are *indispensable to the taxonomist*. A combined devotion to and respect for scientific work and the printed word, patience and accuracy, disinterestedness, continuous self-criticism and readiness to recheck data, observations, and opinions, common sense, perseverance, an orderly mind, and a moderate ambition, will generally result in useful, balanced work. In

(1) Though it is remarkable that the general experience in the Malaysian flora is that with 15-30 specimens more or less evenly spaced as to origin, the bulk of the range of variability is often covered.

addition, a good memory for forms and names¹ and an allround background of theoretical taxonomy and its concepts and the digest of the papers on this subject will be useful and facilitate development of experience (15, p. 9-16).

There is nothing special in the above-mentioned mental qualities, but the balance of their combination is a delicate one in the sense that each of them should be sympathetic to the others, as the barrel can contain only as much water as the length of the shortest stave. Prejudice, carelessness, stubbornness, haste, and insufficient self-criticism may each represent obstacles for a good result.

But also an excess of, for the rest, in themselves admirable qualities, may dim what could be expected to be excellent results. Among these is *hyper*-consciousness and *hyper*-self-criticism next to extreme modesty or lack of ambition which has in several cases deprived science of what would have been excellent works; they were never finished. In every single case common sense should guide us to the reasonable degree of accuracy which can be obtained under the circumstances and also what limitations are dictated by the material.

As to the latter point: it is for example generally impossible to make a satisfactory population analysis in the herbarium; it is also impossible to expect from scanty herbarium materials a complete range of variability, and conclusions based on such scanty material should include a certain reasonable measure of allowance for gaps, reasoned in the way it has been done for some deviating specimens of African *Cassipourea* by Lewis (8). And if the material does not allow a further satisfactorily conclusive synthesis, additional critical concise remarks should never be omitted to indicate the expected affinities, as a guide to future workers.

It has to be realized that, both in the past and in the present, a not insignificant number of taxonomists has apparently not fully realized the responsibility of their key position in botany.

One of the main factors involved in the confusion has been the deviation from the Linnean species standard. This has led to extraordinary consequences.

H. HOFFMANN, for example, wrote (9, p. 21, transl.):—"Whether the divergencies of the species are large or small and whether their differences concern essential or non-essential characters is irrelevant for the species problem. For practice it is decisive, whether the differential characters persist (breed true)". For this aim he made extensive breeding experiments on the constancy of characters. All variations, flower colours, etc., which appeared to be inherited, he accepted as species (*Datura tatula*, *Adonis citrina*, etc.).

(1) This was apparently a revelation to JEAN-JACQUES ROUSSEAU who, according to A. DE CANDOLLE (15, p. 15) in his 'Lettres sur la botanique' stated:—"J'ai toujours cru qu'on pouvait être un grand botaniste sans connaître une seule plante par son nom".

His contemporary SENDTNER (10, p. 188, 315) brought specific delimitation to an absurdity for example in proposing to differentiate *Pinus montana* on limestone (as *P. mughus*) from that on moors (*P. pumilio*) on the argument that "they cannot belong to the same species growing in such different habitats" though he could not distinguish them morphologically. He made true what HOFFMANN stated: "that one can even possibly doubt whether it will be possible in every case to define species by means of morphological structure".

KERNER's definition of species is not very much better (11) in saying "each species (properly each form) which can be described, distinguished, and again recognized later, is a good species". His view on good and bad species is a typical example of the outlook of the local floristic botanist¹ who stubbornly clings to the names with which he is familiar, but who is entirely ignorant of the Linnean issue.

In France² a representative following a similar procedure was JORDAN, who set himself intentionally to recognize all forms and races of Linnean species and raise these to specific rank by giving them binomials.

Though at the present time botanists almost unanimously adopt the Linnean standard as their theoretical background, and as far as possible as their practical procedure, a few are still adepts of the beatifying splitting in trying to segregate populations into the smallest entities possible and to put these in the rank of species. This idea is notably advocated and practiced by BREMEKAMP in his work on the Malaysian *Rubiaceae* and *Acanthaceae*, in which all taxa are evaluated one rank too high compared with Linnean classification. *Pavetta* with formerly about 20 species increased in his monograph to c. 220, *Ixora* was equally 'multiplied' about tenfold. In 1955 he has split the well-known tropical linneont *Thunbergia*

(1) *Floristic botany* has a much narrower aim as compared with taxonomy. Its goal is to provide specimens with the best name which can be traced, whereas taxonomy is in addition also aiming at correlating species and genera, finding their delimitation and arranging them to degree of their affinity, in a proper hierarchy with or without distinction of infraspecific taxa.

Naturally good floristic botanists are gradually inclined to taxonomic work as they will find out that the correct name for a specimen cannot be established along the purely floristic line. The limitation of a small local flora is often an obstacle for them to expand their scope to taxonomy. Conversely taxonomists by profession do or have to perform occasionally floristic work. The intrinsic difference between floristics and taxonomy is not that of persons or education but merely of objective.

(2) In the European flora there are still distinguished a considerable number of species which do not deserve that rank.

fragrans into 35 'species' among which were 30 new ones. In mapping these 'species' it appears that they are all based on a few specimens of a very local area (local endemics) and are exclusive: their distribution pattern represents a string of pearls. It is clear that BREMEKAMP, in accepting all local populations, distinguishable by minute characters, as species, deviates *intentionally* from the Linnean standard.

In a remarkably intelligent essay CELAKOVSKI (12, p. 274-275) has shown the deficiency in philosophical outlook of HOFFMANN, SENDTNER, c.s. in stating:—"Bei der systematisch verfahrenen Verstandestätigkeit kommen die beiden Kant'schen Gesetze der Homogenität und Spezifikation zur Anwendung. Die *Homogenität* mehr beachtenden Forscher werden die reduktive, die der *Spezifikation* mehr zugewandten werden die multiplizierende Methode vorziehen. Bemerkenswert ist es aber, dass die Letzteren zu allen Zeiten viel zahlreicher gewesen sind als die Ersteren, diese aber grösseren Eklat und zeitweilig grösseren Erfolg hatten. Bei der Bearbeitung der exotische Pflanzenwelt sind BENTHAM, HOOKER, und anderen im Grossen und Ganzen immer mehr der reduzierende Methode gemäss vorgegangen. In Europa und besonders in Mittel-Europa fehlt es schon sehr an Stoff für neue Spezies strengeren Sinne, daher gerade hier die multiplizierende Methode so schwunghaft betrieben wird. Sollte einmal die Zeit gekommen sein, wo auf der gesammten Erdoberfläche die letztere herrschend wird, dan dürfte die spezielle Botanik eine scientia horribilis werden".

With this pointed philosophical analysis of taxonomic methodology, CELAKOVSKI arrived at a crucial point, by touching on the existence of the sequence of two phases of scientific work in general, and taxonomic research in particular, viz the *analysis* and the *synthesis*, the analysis being the observation and recording of all factual data prior to the synthesis in framing these data and assigning them their proper hierarchical place.

This synthesis according to the standard set by LINNAEUS, requires a great measure of wisdom, discretion, and common sense in order to make it useful. Botanical science has not proceeded to the stage that the identity of plants can be weighed and measured with such highly objective methods as has been reached in chemistry or crystallography. And though, ultimately, a plant is a (very complicated) chemical system, the botanist is confronted with a variability of his taxa which appears at first view sometimes desperately chaotic.

Taxonomists, who among their psychical qualities show a deficiency of feeling for synthesis or are overcompensated by consciousness of differences leading to minute analysis, will naturally tend to lay emphasis on difference rather than on conformities. They will naturally tend to keep the smallest units apart and their hierarchic synthesis will be poor. Their overrating of the importance of differences will easily lead them to raise entities to specific rank, which do not deserve that status in the hierarchic frame of Linnean classification. In

short: giving too much value to analysis and too little to synthesis leads to so-called 'splitting'.

Sense for synthesis is specially required for workers in tropical botany¹ where the scarcity of material is tempting to 'specimen description' by the predominantly analytic taxonomist, who must be always in doubt and under mental stress to combine specimens which show differences, under one species.

It is most peculiar that they often do not realize that all species, either in the tropics or elsewhere, are populations and that a few random specimens from different places (paramorphs) will always be 'distinguishable'. For them it must appear 'magic' and unwarranted to make a synthesis under these conditions although most of them accept an average variability in common species with which they are closely familiar onwards of their boyhood in their own country. They hesitate to apply their experience with specific variability to species from remote regions.

Though thorough analysis is compulsory for all taxonomy, it represents merely the first phase and without a subsequent synthesis one is stuck halfway. One may become easily accustomed to finish work halfway and seek comfort in forgetting all about synthesis, it works like a mental drug and leads to cheap specimen-description and splitting what is polymorphous by nature.

As CELAKOVSKI has pointed out this absence of synthesis leads to a detestable state of affairs in systematic botany against which warnings cannot be too severe.²

Firstly because 'splitting' is not in accordance with the original concept of specific standard as defined and put into practice by LINNAEUS³, accepted by all able taxonomists of the 18th and 19th centuries, and found useful up till the present day.

Secondly because it has shown to bring confusion and prevents a clear insight in the hierarchical affinities and distribution of the species and the articulation of the specific populations.

(1) According to HEDBERG (14, p. 471) "many of the difficulties in taxonomic work on the flora of Tropical Africa are due to excessive splitting".

(2) Geneticists complain about the confusion in hierarchic relations in systematic zoology. GOLDSCHMIDT (16) wrote:—"In one taxonomic group, what is called a species is hardly distinguishable from the next species, and in an other taxonomic group the species are more different than genera in the first".

(3) It is true that in the pioneer work of LINNAEUS some species have been described which must be reduced, e.g. in the variable species *Urena lobata*. But these examples are on the whole surprisingly few in number and his philosophical considerations leave no doubt whatever about his concept of species, witness his delimitation of *Primula veris*, *Lychnis dioica*, &c, which he knew in the living state.

Thirdly because it lacks a philosophical understanding of the principal and most objective taxon as it occurs in nature.

Fourthly because experience learns that if taxa with very narrow limits of variation are to be ranked as species no satisfactory final result will ever be attained, as many Linnean species of wide distribution show an infinite number of variations, partly bound to variation of the environment, partly not, and partly racial in nature. In a number of cases of well-known species of which the material has been very abundant, the majority of taxonomists agree that only one species is concerned and the polymorphism has been accepted as being of infraspecific value. Devotees of analysis have described and named in these cases an often astonishing number of infraspecific taxa. It is clear that with few, random materials available—as is generally the case in tropical taxonomy—it is wise to set out more widely planned variation than is actually shown by the material at hand, to allow room for the actual variation and polymorphism which can be expected. Additional material will fit in more easily within the borders of such widely planned species than within the strict boundary of those narrowly encompassed. If once the latter standard of microspecies has been accepted, additional material will necessitate the description of still more taxa as species, until the avalanche becomes unwieldy as a chaotic array of false pearls intermixed with sporadic genuine ones. Genera thus spoiled are found 'difficult' and, as nobody can make neither tail nor head of them, experienced taxonomists leave them aside and floristic botanists, anxious to have their specimens named, will add to the chaos by describing still more new 'species'.

3. PATTERNS OF VARIABILITY WITHIN SPECIFIC POPULATIONS

Each Linnean species is essentially a self-perpetuating population in the genetic sense, *i.e.* a mixture of individuals which are to a larger or smaller degree genetically different.¹ This causes a specific population to be *variable* or *polymorphous*.

The genetically defined characters do not manifest themselves in exactly the same way in different individuals, as their manifestation is influenced during the stages of their ontogenetical development by the environmental conditions, *i.e.* specimens which possess approximately the same genetical properties may look different. This does

The proper task of taxonomy goes, according to the Linnean doctrines, far beyond analytical work: it prescribes to taking a firm grip on diagnostic characters of good species, and genera as groups of these, framing hard, trustworthy keys standing the test of time, and arranging all taxa in a practical hierarchy showing their natural relationships.

It is clear that much of the confusion is caused by the variability of species populations and its evaluation within a hierarchic frame work. It is therefore necessary to give a review of the way in which this variability is developed and the degree to which it can be accepted within the Linnean species.

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not hold only for different specimens but also for comparable parts of one individual: leaves of a juvenile specimen may deviate considerably from those of the mature specimen, leaves of suckers differ from those of the flowering twigs, leaves which have developed in the shade show a different structure from those developed in an exposed situation. The different manifestation by the same genetic properties is called *phenotypic variation* or *variability*. It overlies (and sometimes obscures) the variability caused by different genetic composition, *genotypic variability*.

PHENOTYPIC VARIABILITY

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

(1) Theoretically it could be imagined that specific populations might occur composed of homozygotous individuals. This is to my knowledge never found to be the case in sexually propagating specific populations. It has also been

observed that immediately after its origin a new species is provided with a range of variation between the individual specimens. Therefore the idea of homozygotous populations can be discarded.

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 individual plant'. This is far from easy, as each specimen grows under a different combination of CEB-factors (Climatic, Edaphic, Biotic). We might approach 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.

In a former essay (I, p. xix–xxxix) I have rather extensively dwelt on this subject and given a tabulated conspectus of the various factors by which phenotypical variation may be induced in Malaysia. Of each category a number of examples have been given with the relevant references.

It is true that phenotypical variation is not of essential value to the problem of delimitation of Linnean species, but it is emphasized in the essay alluded to above that phenotypic variation has so often misled taxonomists in their judgement of characters of varieties, species, and even sometimes of genera, that I find it of eminent importance to summarize the subject. For this aim the conspectus has been reproduced below.

- | | | | | | | |
|---------------------------------------|---|-------------------------|---|--|---|--|
| Intrinsic | { | Ontogenomorphosis . . . | { | 1. Juvenile forms | | |
| | | | | 2. Precocious flowering (<i>paedogenesis</i>) | | |
| | | | | 3. Dimorphous foliage | | |
| | | | | 4. Dimorphous flowers, seeds and fruits | | |
| | | | | 5. Cleistogamous flowers | | |
| Teratologomorphosis . . . | { | 6. Teratological forms | | | | |
| | | | | | | |
| Climatic | { | Hypselomorphosis . . . | { | 7. Phenotypic effect of altitude | | |
| | | | | 8. Epiphytes | | |
| | | | | 9. Shade forms | | |
| | | | | 10. Influence of drought | | |
| | | | | 11. Seasonal variation | | |
| Horamorphosis | { | Anemomorphosis | { | 12. Wind forms | | |
| | | | | | | |
| Edaphic | { | Edaphomorphosis . . . | { | 13. Fumarole plants | | |
| | | | | 14. Rock plants; calcareous and silicious soils | | |
| | | | | 15. Solfataras plants | | |
| Hydromorphosis | { | | { | 16. Water and swamp plants | | |
| | | | | | | |
| Biotic | { | Phytomorphosis | { | 17. Fungus and bacterial diseases, and symbiosis | | |
| | | | | Zoomorphosis | { | 18. Ant plants (<i>myrmecomorphosis</i>) |
| | | | | | | 19. Galls deceptive to phytographers (<i>cecidiomorphosis</i>) |
| | | | | | | 20. Influence of browsing animals (<i>pascuomorphosis</i>) |
| | | | | Anthropomorphosis . . . | { | |
| 22. Pioneer plants and savannah trees | | | | | | |

Ontogenomorphosis

1. *Juvenile forms* (I, p. xix, fig. 2–4). It has appeared that saplings may be sometimes thorny in their youth and unarmed when mature. Their leaves are often more divided or toothed and generally larger in size than those of flowering twigs of mature trees; good illustrations of this in *Proteaceae* are given on pp. 193, 199, and 200 of this volume.

In these qualities they often resemble leaves from suckers (water-sprouts), which HOWARD found in *Coccoloba* to be a source of confusion for

specific delimitation. Leaf margins of saplings are sometimes toothed, serrate, or even spiny; an additional example of the latter is found in *Distylium stellare*. The difference between leaves from juvenile plants and those of mature plants is strongly expressed in many climbing plants; besides they possess often dimorphous foliage (see below). The structure of the mature stem of climbers is also generally very much different from that in the juvenile state. Leaves of juvenile shade plants often show a remarkable, white spotting generally disappearing with age. Juvenile

specimens of species with compound leaves may show much more pinnae than mature specimens, but the reverse may be equally the case.

The conclusion is that great caution is required to evaluate characters from specimens taken from juvenile plants as they may show a colossal plasticity in vegetative characters. In sticking to characters derived from fertile material this obvious source for confusion can generally be avoided.

2. Precocious flowering or paedogenesis (1, p. xxi, fig. 5). This is the phenomenon when juvenile plants are sometimes, even in the very young seedling stage, capable of producing flower and fruit. A number of species have been described which are merely based on this dwarf character of the vegetative parts. Juvenile fructification may be found in pteridophytes.

3. Dimorphous foliage (1, p. xxii, fig. 7-8). Leaves from the basal part of mature tree crowns are generally larger than those from flowering twigs. This difference may be stabilized in dimorphous foliage, found in many climbing plants, in which leaves attached to the main stem may be very different in shape, size, margin, phyllotaxis, and texture from those of flowering lateral branches (fig. 1). Several species have been based on (naturally sterile) material from the main stem. In other cases the dimorphism is not clearly separated on different parts of the climber or tree (fig. 2). Heterophylly is far more common than is generally understood; plasticity varies from group to group. There is great urgency for field collectors to make and record observations on labels.

In sticking to description of fertile material the herbarium botanist can usually avoid this source of confusion for delimiting his species, though certainly not in all cases, as e.g. in *Pittosporum sinuatum* where both types of leaf, entire and lobed, may be found associated with flowers.

4. Dimorphous flowers and fruits (1, p. xxiv). In one plant, or in one inflorescence, different kinds

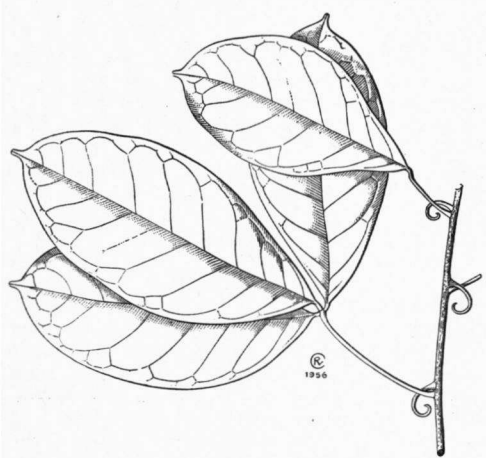


Fig. 1. *Lavanga eleutherandra* (BL.) KURZ with simple and 3-foliolate leaves, $\times 1/4$.

of flowers or fruit may occur. Such dimorphous flowers occur far more frequently in tropical families than is generally known, e.g. in *Celastraceae*, *Rutaceae*, *Connaraceae*, etc. In *Pitto-*



Fig. 2. *Symingtonia populnea* (R. BR. ex GRIFF.) STEEN. with dimorphous leaves, $\times 2/3$, the 3-lobed leaf identical with the type of *Liquidambar tricuspis* MIQ.

sporum the occurrence of more σ or more ρ flowers—in which both sexes are present but one of them is functionally sterile—has been the cause of some species which are only valid on paper, but not so in nature.

It seems necessary for the herbarium botanist to dissect and examine many flowers from each inflorescence and not to base definition on the dissection of one flower. For pelorics see p. clxxi, clxxvi.

5. *Cleistogamous flowers* (1, p. xxv). Cleistogamous flowering has been observed in a number of plants, *Acanthaceae*, *Orchidaceae*, *Leguminosae*, *Viola*, *Commelinaceae*, and is said to occur in *Annonaceae*. It has sometimes given confusion, even led to the description of a new leguminous genus on a cleistogamous form of a well-known species. Cleistogamy seems to be favoured by prolonged periods of very wet weather and as such it should be kept in mind as a possible barrier in gaining a clear specific delimitation.

Teratologomorphosis

6. *Teratological forms* (1, p. xxv, fig. 10). In some cases teratologies or what is termed as such, are inherited, as for example pelorics; others are caused by external or internal factors often unknown. Quite a number of monstrous forms have been recorded in the flower structure of *Orchidaceae* and on some of these new species have been distinguished. See further p. clxxxvi.

If plants agree in all characters save a single one, common sense is necessary to prevent description of new species on aberrant individuals.

Hypselomorphosis

7. *Phenotypic effect of altitude* (1, p. xxvi, fig. 11-12). One of the general features of this effect is mostly a gradual dwarfing of specimens, in proportion with altitude, of herbs, shrubs, and trees. Leaves become smaller, their texture becomes thicker and harder, their margin tends to recurve, interval space becomes often somewhat bullate by sulcate nervation on the upper surface. Simultaneously the petiole is reducing in length and the blade is often shortening, getting blunter and rounder, specially at the base. Apparently intercalary longitudinal growth is retarded (by insufficient growth hormones?). The habit of the trees becomes more compact through shorter flush and shorter internodes, giving a stunted bushy or gnarled appearance. Inflorescences are also condensed and often pauciflorous. This is decidedly not only caused by temperature, but may appear also on poor soils on exposed crests at lower elevation. The extremes of such a series may appear, in habit and vegetative characters, very different to the eye. Floral characters show the least variability by the factors involved in altitude and exposure.

A few examples are depicted here, viz of *Pittosporum pullifolium* (fig. 3) and *Symplocos laurina* of which *S. sessilifolia* is such an extreme 'summit' form (fig. 4).

Quite a number of phenotypic forms have been described as 'species' though not deserving this distinction.

Those who are not acquainted with the remarkable but very common effect of altitudinal exposure in tropical mountains will only hesitatingly accept the variability caused by it as phenotypic in nature¹, if abundant material appears to contain sufficient transitional specimens.

Here again it is the constancy in floral characters indicating the true specific characters, the vegetative parts showing plasticity and being liable to great phenotypic variation, a variation which is parallel in its manifestation in almost all species which have a wide altitudinal range.

The above does not mean that there may not be allied species or subspecies differing in altitudinal range. A good example is e.g. in *Lonicera* of which the two Javanese species are neatly exclusive (1, p. xlix).

But such specific or subspecific distinction can only be accepted if there are well-marked breaks in the variability and at least in the case of species, vegetative characters are never sufficient for specific delimitation.

Photomorphosis

8. *Epiphytes* (1, p. xxviii, fig. 13-14). Many epiphytes may well grow on rocks and rocky slopes, and terrestrial specimens may even be more

(1) It may certainly be possible that part of these 'phenotypic' altitudinal forms are caused by an altitudinal series of ecotypes whether or not worthy of taxonomical distinction. This can only be proved by breeding experiments.

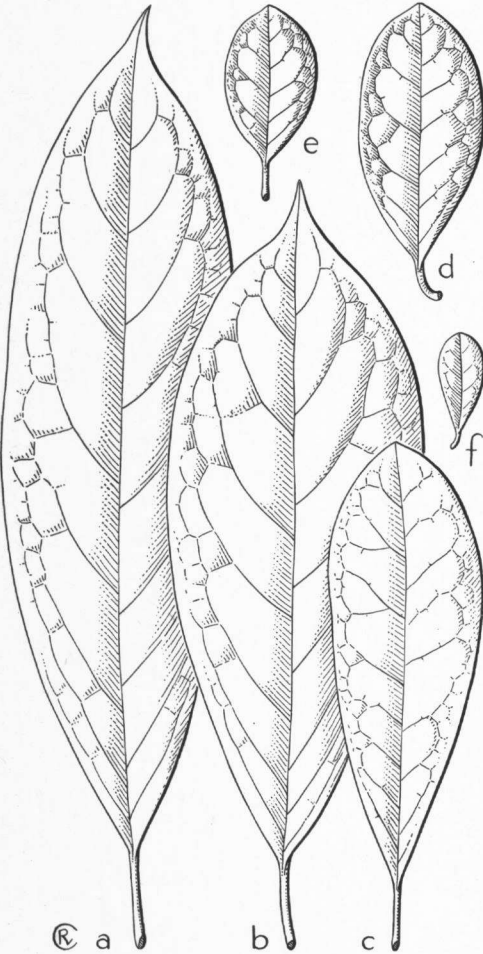


Fig. 3. *Pittosporum pullifolium* BURKILL, $\times 1/2$ showing the effect of altitude on leaf size and shape of a small tree in the tropics (New Guinea), the 6 leaves being derived, in the sequence a to f, from specimens collected at 100, 1750, 2150, 3560, 3800, and 74000 m (a. BRASS 7046, b. EYMA 5188, c. BRASS 22732, d. BRASS 9955, e. BRASS 9798; f. BODEN KLOSS s.n., type of *P. nubigenum* RIDL.).

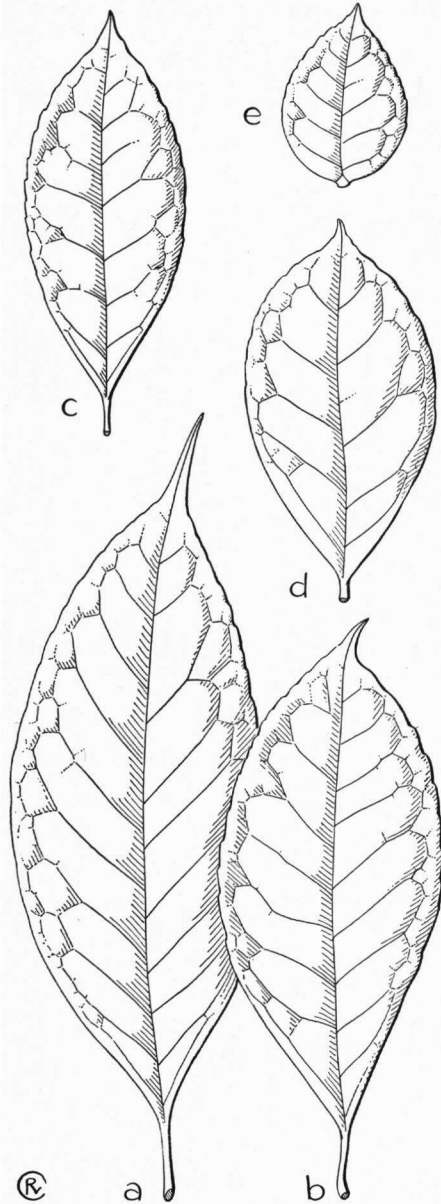


Fig. 4. *Symplocos laurina* (RETZ.) WALL., $\times 2/3$. A leaf series comparable to that in fig. 3, but from Java and Enggano Isl. (a), the 5 leaves being derived, in the sequence a to e from specimens collected at 100, 1600, 21800, 2000, and 3000 m (a. LÜTJEHARMS 4561, b. BLOKHUIS 7-12-21, c. BLUME 1965 B, d. FRI Ja 4010; e. DOCTERS VAN LEEUWEN 6425, typical of what has been described as *S. sessilifolia* BL.).

vigorous compared with epiphytic ones. Specially hemi-epiphytes may show a habit remarkably different from terrestrial specimens. I have summarized this for *Wightia borneensis* (2) which is according to field observations sometimes a small to medium-sized tree, sometimes an epiphyte, sometimes a 'liana'. In open, rocky places it grows into such a normal terrestrial tree, but it can equally grow as an epiphyte. This produces roots downward along the stem of the host tree and, on striking ground, the root gets thicker and thicker, until it resembles a large liana or slender stem. If eventually the host tree dies, it remains standing as a slender tree the stem of which is morphologically mostly consisting of a root. The same two habits have been observed in some species of *Ficus*.

Here again habit may differ but affects only the vegetative parts and not the structure of the flowers, which is therefore the only sure guide to specific delimitation.

9. *Shade forms* (1, p. xxix, fig. 14). A phenotypic effect similar to what has been mentioned on the different habit of lowland and mountain specimens is found in specimens grown either in shade or light. Shade forms tend to have thinner, larger, lighter coloured leaves, longer internodes, etc., and sometimes less brightly coloured flowers. In a few cases shade forms have been described as distinct species, until it could by chance be shown that both 'species' occurred in a single individual.

As the flowers retain essentially their morphological structure, light and shade forms differ only in vegetative parts and sometimes in the amount of anthocyanin in the tissues.

Hygromorphosis

10. *Influence of drought* (1, p. xxix). Excessive drought causes generally reduction of number of leaves (increased leaf-fall) and reduction in the size of leaves. I have, in Malaysia, not observed a general tendency of increase in indumentid proportion to drought conditions. Trees and shrubs which may be typically deciduous under seasonally arid conditions may be evergreen or nearly so in a constantly wet climate. No cases are as yet known to me in Malaysia where the phenotypical influence of drought has led to wrong specific delimitation.

Horamorphosis

11. *Seasonal variation* (1, p. xxix). 'Autumn' forms are well-known from Europe but as far as I know they are scarce in Malaysian flora. I have observed a few cases in which fruiting plants flowered for the second time or seedlings flowered in the wrong (dry) season; the flowers produced were paler and considerably smaller in size, though further specific characters remained exactly intact.

Anemomorphosis

12. *Wind forms* (1, p. xxx, fig. 15, 17-18). Constant wind from one direction affects mainly the habit of trees and shrubs, in turning them one-sided or even flag-shaped. In extreme cases they may be dwarfed down to a cushionlike habit.

Edaphomorphosis

13. *Fumarole plants* (1, p. xxx, fig. 16). On volcanic peaks hot, wet steam escaping under pressure has a dwarfing effect on herbaceous plants, reducing them to very small size and condensed habit. The reduction in size mainly affects the vegetative parts.

14. *Rock plants; silicious soils, and other types* (1, p. xxxi, fig. 19-23). On poor soil types species which are normally well developed trees may be represented as dwarf shrubs, and several new 'species' have been based on dwarf vegetative characters and pauciflory. The influence of the soil type is in several cases more important than is generally acknowledged. TURRILL & MARSDEN-JONES (3, p. 57) have found that "the greatest and most rapid changes have been recorded for *Plantago major*, an extremely plastic species. Here phenotypes have been produced within two years, from seedlings and ramets of a single clone, which have been classed as varieties and subspecies in a recent monograph of the genus" (viz by PILGER in Pflanzenreich). In the latter work *P. asiatica* and *P. major* are distinguished as two different species and even *P. hasskarlii* and *P. incisa* are maintained but could (naturally) not be keyed out, as they are conspecific. BACKER (27) had already observed that several forms of *P. major* had been described from Java under four different specific names.

15. *Solfataral plants* (1, p. xxxiii, fig. 21-25) are generally dwarfing towards the active part of the solfataral fields, partly due to sterility of the soil, partly to increasingly extreme conditions of temperature, acidity, and poisonous fumes. Oblique, clipped and cushion-like specimens are frequent under these conditions.

Hydromorphosis

16. *Water and swamp plants* (1, p. xxxiv). In addition to the examples of phenotypic plasticity mentioned, caused by the depth of the water, the amount of aerenchyma developed, the occurrence of aerial roots and conical trunk base, there is the phenomenon of precocious flowering by the drying up of the habitat.

In inundated rice-fields the rice seedlings are planted in the mud by hand. The growth period is about 3-4 months. During the first and second month the field is weeded once or twice. At the end of the growth period the field is gradually drained for the ultimate ripening of the paddy. The aquatic herbs growing in the mud have therefore only a very short period for growing in comparison with their growth in a permanent swamp. Through sheer necessity only those individuals survive which adapt themselves to the planting-scheme rhythm of the rice culture. This adaptation consists often of a dwarf growth and forced flowering at a juvenile stage (precocious flowering), a phenotypic-ecological variant of paedogenesis (1, p. xxi). Normally perennial plants thus may become annual, water and swamp plants produce flower and fruit on specimens which are vegetatively still juvenile. Such precocious forms are of course 'constant', i.e. they are regularly found in wet rice-fields. Illustrative

examples are found in the genus *Monochoria* (Ponte.) in which from Malaysia have been described *M. plantaginea*, *M. linearis* and *M. pauciflora* (sometimes treated as varieties), which represent really only stages of phenotypical precocious flowering which has been proved experimentally by Dr BACKER (1, p. 258). Recently I have found that the monotypic *Elattosis apetala* GAGN. from Indo-China is only a precociously flowering phenotype of *Tenagocharis latifolia* BUCH. (1, vol. 5, p. 118). Mr DEN HARTOG found similar cases in the *Alismataceae* and *Hydrocharitaceae*.

Another class of phenotypic forms is that of *terrestrial forms of water plants*. In Europe a classical example is that of *Polygonum amphibium* L., of which the terrestrial form is distinctly different from the aquatic one with practically no intergrades. If such different specimens have been collected in the tropics and come into the hands of herbarium taxonomists, it requires a knowledge and realization of this phenomenon and the common sense to apply this knowledge, even though it cannot be checked on the spot either by observation or by experiments.

Such terrestrial forms do occur in the tropics indeed. In Malaysia examples are found in *Jussieua repens* L. and in the genus *Limnophila* (Scroph.). Typical specimens of *L. indica* (L.) DRUCE have submerged leaves large and finely pinnatifid, with emerged leaves nearly simple and toothed. Terrestrial specimens sometimes lack the pinnatifid leaves; there are intergrades. In *Jussieua repens* leaves of terrestrial forms are exceedingly small, crowded and hairy.

In specific delimitation of water plants the above mentioned phenotypic deviations should always be considered. Again here, the plasticity is mainly affecting the vegetative characters.

Phytomorphosis

17. *Fungus and bacterial diseases, and symbiosis* (1, p. xxxv, fig. 26-27). Several examples are known in which phytographers have been deceived in their specific delimitation by malformations caused by micro-organisms; these generally affect only vegetative characters, but may, occasionally, cause (abnormal) changes in the generative parts. It seems to me not admissible to take the presence or absence of certain symbionts or parasites into consideration for specific delimitation.

Zoomorphosis

18. *Ant plants (myrmecomorphosis)* (1, p. xxxv). Much of what has been said in the foregoing paragraph is valid for ant plants. The presence or absence of ants and, henceforth, the presence or absence of cavities inhabited by them, seems to me irrelevant to specific delimitation. Fortunately these cavities are generally found only in the vegetative system.

19. *Galls (cecidio-morphosis)* (1, p. xxxvi, fig. 27). There are several instances in which galls, specially those deforming flowers or fruits have been entered into specific distinction. Fortunately the number of these cases is very restricted. Admittedly galls are,

in a number of cases, confined to distinct species, but their occurrence is of secondary nature and should not be evaluated as an argument in specific delimitation, though it may add to circumstantial evidence.

20. *Effects of browsing (pascuo-morphosis)* (1, p. xxxvi, fig. 28). Very aberrant forms may arise from repeated trimming by browsing animals, resulting in fastigate habit, dwarfing of leaves, and pseudonanism. Though I do not know of cases in which these abnormalities have been described as distinct 'species', some have been referred to varieties, although the difference in vegetative habit is merely of a phenotypic nature.

Anthropomorphosis

21. *Influence of fire (pyromorphosis)* (1, p. xxxvii, fig. 29-31). Changes caused by repeated fires concern mainly the vegetative parts and the dwarfing of specimens including their inflorescences. Fire forces many plants to 'go underground' in developing thickened roots and 'lignotubers'. In pyrogenic areas many plants are flowering and fruiting in a dwarf stage. Furthermore individuals produced by rootsuckering may show somewhat deviating characters. In the genus *Premna* several species have been described from such localities, and even two genera (*Tatea* and *Pygmaepremna*) have been based erroneously on such pyrogenic forms as MERRILL (4) has shown.

In dealing with species of grasslands and savannahs the above-mentioned circumstances should always be taken into consideration; as a matter of fact the deviations mainly effect the vegetative characters and habit of the plants.

GENOTYPIC VARIABILITY

From the foregoing paragraph it appears that phenotypic variation is of distinct importance and wide interest for a correct insight into the variability of specific populations. If phytographers have been deceived by phenotypic plasticity and have described non-existing species and genera, these deficiencies in correct interpretation of specimens have rather the character of errors.

Genotypic variability or polymorphism, however, is still far more important than phenotypic plasticity, as it deals directly with the interpretation of the genetical structure of specific populations.

A proper insight into matters of genotypic variability is required for the delimitation of nearly every Linnean species.

Breeding experiments have appeared to be a powerful tool for the genotypical analysis of populations and this complement to the study of the herbarium taxonomist has been recognized for nearly two centuries. Simultaneously with the development of genetics it has been revived and intensified in this century in various parts of the world, for example by TURESSON in Sweden, by TURRILL & MARSDEN-JONES in England, by DANSER in Holland, by WINGE in Copenhagen, by CLAUSEN c.s., CAMP, and many others in America, and by COCKAYNE and ALLAN in New Zealand.

Trees grown up under open conditions tend to assume a short trunk and a globular crown.

22. *Pioneer plants* (1, p. xxxviii). Pioneer plants, either those invading bare soil, or shrubs and trees invading grassland, often flower and fruit in a juvenile stage of their ontogeny. It may seem queer to the herbarium botanist to find no floral differences between a large forest tree and a shrub of one or two metres size, but it has been repeatedly observed that this difference is merely phenotypic and induced by seedling growth in different habitats. Open conditions will generally be favourable for precocious flowering, whereas the growing up under forest conditions is a striving for light resulting into extended vegetative growth prior to flowering. Trees with large 'clear boles' may have hardly an unbranched bole if grown up under spaced conditions.

General summary:—As has been shown in field studies phenotypic variability is exceedingly common among Malaysian plants. In the past it has been much underrated in phytography and by using it for taxonomical delimitation has given rise to a multitude of 'paper' species and varieties without any taxonomical value. It has been found that phenotypic deviations mainly affect the vegetative structure of plants. Vegetative characters should therefore be handled with care with regard to specific delimitation. They should be only used in addition to structural characters of flower and fruit. Experience has shown that good species differ in both their vegetative and reproductive structures, though the one may be at times more spectacular than the other. Species should never be distinguished merely on vegetative differences.

TURESSON had specially in mind to find correlation between geographical distribution and ecology (ecological characters of the variants).

It is natural that a really thorough picture and interpretation of the infraspecific variability cannot be gained by herbarium study; population analysis should be based on or at least sustained by breeding experiments.

I have already had occasion to allude briefly to the idea of some earlier authors that the constancy (breeding pure) of specimens had been for some of them the decisive argument for the specificity of the taxon in question. This criterion was for instance accepted by JORDAN who, on this basis, came to accept an exceedingly narrow specific delimitation. TURRILL has been able to show (3, p. 50) that the microspecies, or jordanons, are not fictitious but exist. In a certain species used by JORDAN twelve combinations could be expected, according to TURRILL, based on the size of the fruit and its indument. TURRILL found eleven of them represented on a very restricted surface and further experiments showed that their distinction rested on a few normal Mendelian characters. A similar result was obtained by WINGE with the Jordanian *Erophilas*. Every specific population is a complex of genotypically heterogeneous speci-

mens and this polymorphism is one of the essential characters of a Linnean.

The very narrow specific delimitation accepted in several South European Floras point to the desirability of the application of experimental taxonomical methodology to show the proper appreciation of their taxonomic status.

A general factor is always active within a panmictic population in which heterozygotes are common and homozygotes rare or non-existent is migration or dispersal within the population.

It is of course a common phenomenon that the area of each species, if mapped, generally consists of a number of smaller and larger dots; hardly any species is so densely distributed over its whole area that one finds a few specimens on every acre of it. This means, that not all specimens are in nature in a position to interbreed (connected genetically). Considering that no seed of any specimen will contain the whole of the genetic polymorphism of the species, this means that genetically the area of specific distribution is a fine mosaic pattern of partly isolated specimens and smaller or larger aggregates of these; in the aggregates inbreeding takes place. As dispersal is random, there is generally no stability in time and the mosaic pattern is dynamic, changing from year to year. As dispersal has generally a wider reach than pollination, seeds of specimens from one aggregate will occasionally reach others. An overall picture of the dynamism will be that of a melting pot of paramorphs.¹

It is significant here to cite the conclusion of VAVILOV (3, p. 550): "After many years of collective studies of the most important cultivated plants, with the aid of cytologists, geneticists, physiologists, anatomists, and immunologists, we are coming to the concept of a Linnean species as a definite, dynamic system differentiated! no geographical and ecological types and comprising sometimes an enormous number of varieties".

Finally I will raise a question which must unfortunately be left unanswered. *Why have certain species produced a racial segregation, either very distinct (as in Geum, cf. p. clxxxviii), or less distinct (as in Hanguana, cf. p. clxxxix), or indistinct (as in clinal or marginal differentiation)?*

This raises the general question about the very different degree of variability displayed by Linnean species. Generally the range of variability increases proportionally to the size of the area of distribution. This is causal, as the increase of potential (genetic) polymorphism, both morphological and ecological, increases also the opportunities for adaptation to greater variety of soils and climates. This is, however, merely an observation.

I believe that an explanation of the phenomenon

that this or that species has a much wider capacity of potential polymorphism, and hence of differentiation, must be left unanswered. This is rooted in the genome structure and different for each particular case.

Among the dissociation or differentiation in genotypical characters within a specific population there are two main types: firstly, variation which occurs 'occasionally', here and there, without forming a regional facies of the population and without any special ecological correlation or preference, and secondly, such variation as appears regionally, either in time or place.

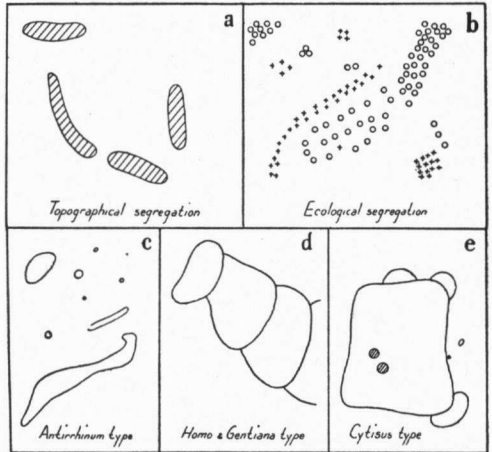


Fig. 5. Schematic types of racial differentiation. a. Disjunct distribution by topographical conditions, b. localities of two replacing races by ecological conditions, c. population consisting of colonies of different size, d. regional differentiation of replacing races, e. a large population with marginal and altitudinal (2 hatched dots) racial differentiation.

A random example of occasional occurrence is for instance a special form of *Lamium album* in which the teeth of the underlip have developed into two broad lobes nearly equalling the midlobe in size. This form has been found in a few places, always a few plants in surroundings where the population with 'normal' flowers is common. A similar example is the extremely rare occurrence of a yellow-flowered variety of the very common *Gynura crepidioides* in Malaysia and SE. Asia.

Among the regional types, one of them is the pattern of a cline, a name HUXLEY has given (5) to a variation through the population in one direction, but so gradual that no demarcations can be found.¹ A few instances are known where

(1) *Paramorph* has been introduced by TURRILL as a convenient term to designate all specimens which deviate in one or more characters from the 'average' composition of a population.

(1) The original definition is "cline meaning a gradation in measurable characters", what REINIG has called character gradient or geographical progression of characters.

hairiness, size of plant, fruit or leaf, etc., increase or decrease in a certain direction.

A special case of the cline is the fact that *most populations vary gradingly from the centre of the area towards the margins*. Marginal specimens are almost always distinctly different from those of the centre of the area and, if they are found in disjunct localities (islands, mountains, etc.), they have not seldom been described as races or even as local species.

The cline seems to me the first essential step towards the origin of discontinuous or exclusive variability in which there is a reproductive isolation, either in time or space, causing a segregation of the specific population in partial populations.

The causes of the reproductive isolation are either ecological, geographical, or cytogenetical.

Among the *ecological factors* the following may be active:

The partial populations growing in one and the same area may possess different needs (claims) for their *habitat* and occupy different niches (wet or dry soil, light or shade, sand or clay, differences in microclimate, etc.).

The partial populations may show *seasonal dimorphism*, that is, flowering in different seasons of the year through which interbreeding is gener-

ally prohibited keeping them pure and separated.

The partial populations may be spaced in anthesis daily (for example one race opening flowers in the morning, the other in the afternoon).

Up till now I do not know examples from Malaysia of segregation by differentiation in pollination.

In all cases of ecological segregation the areas of the partial populations are overlapping, as they occur in the same district.

The *geographical segregation* is the most common case. Its pattern is that of an articulated population and there may be more than one articulation which can be either *horizontal* or *altitudinal*. In both cases adjacent partial populations may touch in a narrow zone of transitional forms, or they may be separated in space and are disjunct. In both cases the geographical segregation may or may not coincide with ecological properties.

For brevity's sake I have arranged below the various cases of genotypical variation which may occur and in fig. 5 an idea is given of area patterns resulting from some of these types which I will now proceed to deal with in greater detail. I cannot avoid repeating some data which have been given in a more concise precursory chapter in this Flora (1, p. xlv-1, fig. 33-38).

PATTERNS OF GENOTYPICAL VARIABILITY WITHIN SPECIFIC POPULATIONS

Population	Occurrence of paramorphs	Cause	Cause of reproductive isolation	Distributional area of paramorphs or partial populations
A. Continuous	1. Regular 2. Clinal 3. Marginal	Chance	Occasional	Overlapping
		{ Migration or environment	Distance	Gradual change
	Exclusive	{ 4. Ecological	{ Habitat (soil, microclimate) Seasonal dimorphism Daily spacing of anthesis Pollinating ag. See p. clxxxix Cultigens. See p. cci Aliens. See p. cxviii	Overlapping
Exclusive				
B. Discontinuous	Mixed	Geographical	{ 5. Regional 6. Altitudinal 7. Disjunct	Exclusive or disjunct
			Cytogenetical	{ Incompatible chromosome races. See p. ccxi Apomicts. See p. ccxiii

A. POPULATIO CONTINUA

1. Variatio genotypica regularis

Regular (individual, or random) variation is represented by the \pm regular (occasional) occurrence of paramorphs. Geographically they are at random distributed and found or may be expected to occur throughout the major part of the continuous area of distribution of the population. The paramorphs do not predominate in a special geographical part of the population, they are not heaped to the exclusion of other paramorphs and do not form a distinct partial population. There is a panmictic population, as a melting-pot of numerous jordanons and paramorphs which through sexual contact, militating against segregation, appear and disappear (by recombination and disintegration) regularly from generation to generation and from place to place and are, for that reason, found at random. TURRILL (3, p. 8) observed that "in the single species *Silene cucubalus* variations in characters which have been shown to have a genetical basis occur in nearly every organ and these variations occur in unnumbered combinations reaching astronomical figures. They must be taken up by the taxonomist in drawing up his description, not of course, by the giving of millions of varietal names".

"The distribution of paramorphs within the species range raises innumerable problems of interest to the taxonomist, the ecologist, and the geneticist. Extensive field and experimental experience has convinced me that species are far more variable than they are given credit or discredit for in our Floras".

It has appeared that formerly the effect of phenotypic variation has been overestimated; extensive breeding experiments have shown that the number of individual variations within a panmictic population which are genetically bound is very large indeed.

Some special categories of genotypic individual variations are:

1. *Peloric flowers*. If a typically zygomorphic flower, for example an orchid, loses its symmetry and becomes a regular perianth, its 'characters' are lost and its correlation with a species or even genus becomes a matter of speculation rather than identification, though in several cases it has been proved experimentally that the peloric differs from the normal plant by only one Mendelian character. Among Malaysian *Orchidaceae* pelorics have caused considerable confusion in phytographic description as I have shown in greater detail before (1, p. xli). It has appeared that at least 8 genera have been described which are merely peloric forms for species of other genera, and besides there is a much larger number of species which have by error been based on peloric specimens of known species. Some have even not yet been correlated with the normal form of any known orchid species! In *Leguminosae* a peloric *Clitoria* was described (in S. America) as a distinct genus. Among *Compositae* discoid heads may sometimes be regarded as heads of peloric flowers; whether in all cases the discoid

forms have been correlated with the proper genera seems uncertain.

2. *Other 'teratological', deviating paramorphs* (1, p. xlii). If one consults the books by PENZIG and WORSDELL on the subject of teratological forms there appears to be a remarkably large number of parallel deviations, classified under e.g. *proliferation, forking, fusion and fasciation, simplification, suppression, adnation, and laciniation*. It should be admitted that part of these have been caused by biotic factors of the environment and should be classed among phenotypic variations.

But a considerable number is certainly inherited. Furthermore there are several other items, in the number of flower parts, the colour of leaves (*variegation*), etc.

Several of these deviations have been used as the basis for describing new species¹ or varieties which they are really not, as these teratological tendencies may occur in any species. *Pandanus variegatus* MIQ. is a variegated cultigen of *P. tectorius* PARK., *Coffea sumatrana* MIQ. is a variegated form of *C. arabica* L., *Boehmeria biloba* MIQ. is a species in which occasionally forked leaves occur. These characters have no significance for specific distinction.

3. *Distribution of the sexes* (1, p. xliii). In dioecious plants or those with unisexual or polygamous flowers (or those functionally so) specimens with different flowers have often not been recognized as belonging to one species, causing deficiencies in specific delimitation. *Bauhinia castrata* BLCO is such a ♀ form of *B. malabarica*. There is a considerable number of families in which such dimorphous flowers occur and occasionally correlation of specimens of different sex may offer difficulties.

4. *Other deviating paramorphs* include those cases which cannot be classified among the 3 preceding paragraphs. I mention for example the occurrence in West New Guinea of specimens of *Juncus prismatocarpus* R.Br., a very well known, widely distributed herb (Ceylon & E. Asia to New Zealand) in which the fruit was distinctly different from the average type; all other characters being similar to those of *J. prismatocarpus*, HOOGLAND concluded on their conspecificity (1, p. 214). Many comparable cases of deviating specimens have not been recorded in literature as they were accepted as mere individual variations by revisors. However, it has appeared that if the sheets come from the 'unknown' tropics there is a 'magic' tendency to

(1) Recently a new monotypic solanaceous genus *Methysticodendron amesianum* SCHULTES (30) has been described from Peru which deviates from *Brugmansia* (= *Datura* sect. *Brugmansia*) in the deeply divided calyx, corolla, and style. To me this appears to represent a remarkable case of adesmy, a tendency which is recorded from various *Solanaceae*. The adesmic *Campanula rotundifolia* has also been proposed as a distinct genus *Depierrea* (35).

evaluate them higher than if they had originated in the home country where they pass unnoticed by common agreement.

It is remarkable that they concern sometimes important structural characters of the genus, or even of the family. In this respect I have already mentioned the case of choripetalous 'sports' of *Campanula rotundifolia* and '*Methysticodendron amesianum*'. An additional example was found and recorded by DE WIT in *Cassia mimosoides* L. in which the flowers contained two separate ovaries, a very rare character in *Leguminosae* and confined to some primitive genera of the *Mimosoideae*. TURRILL recorded (3, p. 59) a 'mutation' of *Silene cucubalus* with sepals often separate to the base, thus breaking down the essential difference between the two subfamilies of the *Caryophyllaceae*.

From 'mass collections' it has appeared that such individual cases are far more numerous than has generally been assumed. Unfortunately little is mostly known about their genetic status. They show the pitfalls of 'specimen-description' to which DE CANDOLLE pointed in his 'Phytographie' (38, p. 52).

2. Variatio genotypica clinalis

According to HUXLEY a *cline* (5) is a population in which the character complex shows a gradual change (gradient) from one end of the population to the other without possibility of indicating taxonomical breaks or demarcations. The extremes of both ends of the cline are distinctly different but are connected by a gradual series of intermediates merging the population into one whole. This may of course occur both in the horizontal direction and in the vertical direction in the case of mountain plants.

The cline should not be confused with graded phenotypical change¹, as it is *per definitionem* a genotypically heterogeneous population.

Clines have been mostly described from animal distribution, but they are equally frequent in the plant kingdom. I point to the variability in flower colour in some *Convolvulaceae* recorded by VAN OOSTSTROOM (1, p. 449, 453) which is apparently gradual and regional and falls obviously under the cline conception.

Clinal variation is often more evident in minor ecological adaptation than in easily expressed morphological terms. Among foresters it is, for example, a widely applied procedure, gained by experience, to use seed for afforestation from well known sources, that is localities comparable in ecology to where it will be sown. It has appeared in practical forestry that in populations in America and Europe of wide latitudinal range, plants raised from seed of high latitude do not grow well under warmer and moister conditions of lower latitude and, reversely, plants raised from seed collected at lower latitude may suffer from frost if planted at

high latitude. This clinal ecological segregation within a specific population is not well definable in morphological terms, but is of eminent importance to the practice of forestry, horticulture, and agriculture.

It is, naturally, very difficult to obtain precise detail data on the genetical basis of such an ecological cline, and to check whether it is really a cline, or whether it is after all ecologically a discontinuous population. LANGLET has for example tried to demonstrate the clinal nature of the ecological behaviour of *Pinus sylvestris* in Sweden (6), but TURESSON (7), though admitting the theoretical possibility, found LANGLET's arguments insufficient, and indicated the possibility of two ecological races merged by a wide transitional zone of interbreeding.

3. Variatio genotypica marginalis (fig. 5e)

This is more or less a subtype of the cline, as there is found a more or less gradual change in average composition from the centre towards the marginal part of the distributional area. The centrifugal effect seems to be mainly based on differences of selection pressure (degree of gene exchange between the paramorphs) in the various parts of the area, central and marginal.

In his gene-centre theory VAVILOV has shown (8) that the percentage of dominant characters is largest in the centre of the area of a species whereas the percentages of specimens with recessive characters is gradually increasing towards its marginal area. The marginal area will therefore often locally contain aggregates of specimens with genetic combinations which would have no chance to maintain themselves in the melting pot of the central part of the area.

The general factor *dispersal* or *migration*, explained on p. clxxxiv under the introduction to genotypical variability, must play an exceptionally important role in the marginal differentiation, where the density of the population is generally less than in the centre of the area. This entails the increase in distance between specimens or their aggregates, favouring their genetic isolation, which again supports the process of differentiation by local inbreeding on the frontier of the distributional area.

The existence of marginal differentiation is corroborated in taxonomical practice. Widely distributed species have very often produced aberrant or deviating specimens along their frontiers, sometimes possessing characters which are not or hardly found in the central part of the area. In his study on *Cytisus* § *Tubocytisus* KERNER (12) gave a map in which a few widely distributed species bear satellite taxa in their marginal area!

The 'direction' or 'course' of the inbreeding process will be partly determined by the environmental conditions in the marginal area.

It is natural that throughout the distributional area of a species the environment acts as a (leaking) sieve to migrating paramorphs, but this will be more effective in the marginal area through the historic progress of area expansion.

(1) The data of BONNIER which are so often cited in this respect, have as good show-boys proved to be untrustworthy, according to TURRILL (3, p. 56).

B. POPULATIO DISCONTINUA

The clinal and marginal types of population variability can be regarded as the primordial stages from which can be derived the following exclusive, discontinuous, or articulated types, in which the population is broken up into two or more demarcated, partial populations by the continued force of isolation. They represent a further advanced, more stabilized development of the clinal or marginal differentiation. The variability of each partial population is a priori smaller than that of the sum of them.

Generally the environment has, by its sieve function, been instrumental in the segregation of the partial populations and as this segregation has obviously originated during the historic phase of progressive diffusion, a general characteristic of a chain of partial populations is, that neighbouring populations will be more akin and similar than those wide apart. The dissimilarity between the latter (extremes) is bridged by various intermediate partial populations acting as stepping stones.

As remarked above each of these stepping stones is (mostly) adapted to a slightly different ecological environment besides being mostly recognizable by morphological differences. These two factors, ecology and morphology, may be found combined to various degrees. In some cases the morphological difference is slight, but there is a distinct difference in ecological preference, in other cases there is a well-marked morphological difference without a clear sign of marked difference in ecological preference.

As to the demarcations themselves, they may be sharp without intermediate specimens in a transition zone blending the adjacent partial populations, or there may be a narrower or broader zone in which the partial populations gradually merge.

It appears also that within one partial population there is a repetition, on a smaller scale, of the same principle of segregation, and that each major partial population can again be divided into smaller partial populations of minor rank. And what has been just advanced for the large populations holds for the minor ones. BIANCHI Jr could demonstrate (in MS) a hierarchy of racial differentiation within *Mahonia napaulensis sens. lat.*

Within most widely distributed species there is obviously a hierarchical structure of racial differentiation comparable to the differentiation found in the species *Homo sapiens*, which is a convenient illustration of the hierarchical differentiation under discussion.

TURESSON acknowledges this infraspecific hierarchy in distinguishing two main classes: *ecotypes*, the smallest racial aggregates or clusters of hereditary variants, and *ecospecies*, representing races of higher taxonomic standing, together forming the *coenospecies* which is obviously equivalent to the linneont.

Taxonomists have, in many cases, found it suitable to distinguish far more than two ranks

in the hierarchy of geographical races and have intercalated a number of additional ranks between subspecies and forma, for which they have coined new terms or which are merely indicated by symbols.

In well examined cases, sustained by large-scale experimental and field work, there seems reason to make such distinctions by including in the terminology indications for the concepts of ecology, seasonal dimorphism, etc., because in the classical ranks there is for a partial population merely the term subspecies available. One could add abbreviated additional indications, e.g. *subspecies(ec.)*, *subspecies(alt.)*, *subspecies(disj.)*, *subspecies(reg.)* for respectively ecological, altitudinal, disjunct, and regional subspecies. For a partial population within a subspecies one might introduce the concept sub²species for sub-sub-species, sub³species, for sub-sub-subspecies.

I refrain, myself, from introducing such micro-subspecific distinctions, and want to keep to the classical use of subspecies only, preferring to give wherever desirable comments on the status of the race in an additional note.

The following four main types of discontinuous populations will be treated below: 4. *ecologic*, 5. *regional*, 6. *altitudinal*, 7. *disjunct*. Numbers 5-7 are very often caused by ecological factors, but not clearly so in all cases, number 4 is therefore reserved for cases which are distinctly ecologic and in which areas overlap.

4. *Populatio discontinua oecologica* (fig. 5b)

Ecological races are discontinuous by their biological isolation, but geographically their areas overlap, at least in part. The isolation is caused by the fact that the partial populations occupy different biotopes, and have been sorted out from a panmictic population. Several factors may be involved, each sufficient to stabilize the racial differentiation; in the survey on p. clxxxv I have mentioned as examples soil preference, microclimate, seasonal dimorphism, daily spacing of anthesis, and human cultivation.

A typical case, obviously due to the factor of soil, is for example that in the rosaceous genus *Geum*, of which in Europe are two subspecies (mostly recognized as species) which perfectly exclude each other ecologically: *G. rivale* L. from humid, moist localities and *G. urbanum* L. from drier places. It has been observed both in the field and experimentally by MARSDEN-JONES (13) that where the environment is intermediate and suitable to both subspecies their differential characters break down by a complete series of intermediates blending them into a whole. He says:—"Genetically they may be considered as varieties of one species, in that they cross freely and produce hybrid swarms in which it is difficult or impossible to find plants showing a pure combination of the characters of either putative parent".

It is clear that, if the entire surface of their area were of an intermediate soil type or biotope no segregation would have taken place, consequently

no taxonomical distinction would have been possible, and the panmictic population (*populatio genotypica regularis*) would have been recognized by taxonomists as a 'variable species' but anyhow as a taxonomic 'continuum'.

It is merely by the differentiation of the habitats into two rather distinct types that segregation could take place enabling the taxonomist to distinguish the partial populations. *The mingling (miscibility) in intermediate localities reveals the true subspecific nature of these two entities* which are for reasons of conservative convenience accepted to represent Linnean species in most Floras. This inertia is scientifically erroneous and educationally reprehensible.

A comparable example from Malaysia is that of the flagellariaceous *Hanguana (Susum) malayanum* of which two subspecies occupy the same area, one confined to dry forest soils, the other to swamps, according to BACKER with occasional intermediates in intermediate localities (1, p. 250).

With these examples at hand two remarks should be made.

First, that in the case of *Geum* the morphological differences between the two subspecies are very distinct; nobody will confuse them. In the case of *Hanguana* characters are less pronounced and herbarium taxonomists have not been so strongly inclined to keep them separate. Abundant material and detail observations both in the field and experimentally are in such cases compulsory to come to the correct interpretation of the state of affairs.

Second, an easy way to track such twins or triplets, etc., of ecological races (taxonomically considered to be closely allied) is to see whether localities and biotopes exclude each other. This should be a warning signal of their presence, though of course not giving conclusive evidence of the subspecific (racial) status, as it may happen that good linneons are ecologically vicarious, as apparently in Europe for example *Rhododendron hirsutum* (calciphilous) and *Rh. ferrugineum* (calcifugous).

A comparable case of ecologically vicarious twin linneons in Holland is found in *Thymus*, a genus elaborated by KLOOS (10). According to the maps published by KLOOS the species *T. pulegioides* L. (*syn. T. chamaedrys*) and *T. serpyllum* L. (*syn. T. angustifolius*) neatly exclude each other, the first showing obviously a preference for calcareous soils, the latter being calciphobous. In a few spots they are found together in an intermediate habitat, but the hybrids are sterile and there is no question of hybrid swarms in which they show a tendency towards miscibility. Though exhibiting superficially a vicarious occurrence, due to different soil preferences, comparable to that of the twin *Geums*, their behaviour is essentially different when brought into genetical contact. And if there were available only soils of an intermediate character the *Thymus* species would perfectly maintain their individuality.

Conclusive evidence can only be gained by either detail study in the field or experiments. But

it will be good if the taxonomist pays special attention to the value of characters separating ecological twin species.

VON WETTSTEIN has given excellent examples of seasonal-dimorphic racial segregation in *Euphrasia* and *Gentiana* (11) and some other genera in Europe. Whether comparable cases occur in the Malaysian flora is unknown. They should then be found in the semi-arid areas which show seasons; in the rain-forest area they will have had no chance to develop.

A numerically probably small, but interesting category of ecological separation was suggested by GRANT (39) who assumes that in certain cases it may be the flower specificity of pollinating insects which keeps interfertile species apart. He reminds in this respect of *Orchidaceae* in which this agency may be active in keeping subspecies apart and which may at the same time account for the high degree of interfertility of 'species' in this family.

The different pollen vectors and difference in time of anthesis may also be responsible for the ecological isolation of the two *Melandryums* and may account for raiation in *Aquilegia*.¹

5. *Populatio articulata regionalis* (fig. 5 d)

In contradistinction to the above-mentioned examples of ecological differentiation which is, except seasonal dimorphism, mostly a consequence of habitat (presumably *mainly soil*), regional differentiation is often a consequence of *climate*, but not necessarily so; in other cases the reason for its differentiation is not quite clearly associated with any environmental factor. Though it should be assumed that the environment has undoubtedly been instrumental in the origin of most races, it is feasible that others have originated by chance dispersal, in which naturally the diaspores carried only a certain part of the total polymorphism of the population, serving as 'genetic material' for the self-stabilizing new race.

The origin of (exclusive) regional racial segregation can easily be derived from either the clinal or the marginal differentiation, from both of which it differs in that a dissociation has taken place marked by a demarcation.

This derivation is not fictitious, as demarcations are found in any degree of distinctness. There is also no fixed place for the demarcation or for the size or taxonomical weight of the partial populations, or for the width of the transition zone separating the races.

The transition zone is characterized by the occurrence of fertile interbreeding between the partial populations resulting in a complete series of transitional specimens.

A Linnean species may contain two (geographi-

(1) After a careful consideration HOOKER *f.* came to the conclusion that there is, in India, only one remarkable polymorphous linneon, *A. vulgaris*. The reasons for this lumping he explained (40) in a lengthy note.

cal) races¹ or more. In man and animals (e.g. birds and butterflies) this articulated specific population is easily discernible and commonly recognized. Specific populations of birds may contain a dozen of such exclusive regional races, their extremes being morphologically sometimes so different that they would be taken for different species if they were not connected by the intergrading series of other races.

It may seem superfluous to remark that *each race in the chain resembles most closely (and is intermediate between) its two adjacent neighbours*, but this point appears essential to me.

In taxonomic zoology KLEINSCHMIDT has devoted an instructive work (14) to the subject of articulated (regional) specific populations which he named '*Formenkreise*' (form-chains). RENSCH has proposed (15), I think rightly, to change this term into '*Rassenkreise*' (race-chains) and he accepts them also as the equivalent of linneonts or good species (l.c. p. 13). KERNER (36) had called the clusters of *radiatim* and *lineatim* connected races, accepted by him as the true species, *Rotten* (platoons). HUXLEY (3, p. 10) calls them *polytypic species*. TURESSON proposed the name *coeno-species*. Still others speak of *compound* or *collective species*. I prefer to call them *linneonts* or *Linnean species*, shortly *species*, the concept prescribed by the rules of nomenclature.

In taxonomic botany the regionally articulated differentiated races have been known and distinguished long ago. I have already mentioned the work of KERNER (12) who did not treat them as subspecies but as species, though indicating that there were two kinds of species '*weitverbreitete Stammarten*' and '*lokale Tochterarten*' (widely distributed ancestral species and local derivatives); he made the acute observation that *the ancestral species and local derivatives replaced each other geographically*.

Similar results were obtained in the classic work of VON WETTSTEIN, on the genus *Euphrasia* and *Gentiana* § *Endotricha* (16), who found groups of closely allied small species excluding each other geographically.

Both KERNER and VON WETTSTEIN *intentionally* arranged *both* the widely distributed species and the narrower exclusive species in the specific rank, that is on the same level, though both clearly indicated that they were, taxonomically, of two sorts, the larger ones the older ancestral species which had produced the younger, narrower defined ones, as DANSER (18) has explained.

Both assumed that they could demonstrate how species *had* evolved as regional segregates which would disperse and in future in their turn become wide species and again a source of new satellites. The crucial word is the italicized word *had*, which introduces a subtle but essential difference in the interpretation. It means that the taxonomical facts have been interpreted to fit a theoretical assump-

(1) Unfortunately this concept is used in a quite different (wider) sense in applied botany.

tion. Because, as a matter of fact, both KERNER and VON WETTSTEIN admitted that the characters of the exclusive segregate 'species' are of minor value than those of the widely distributed ancestral species *and* that their distribution is vicarious. Taxonomically therefore the first should have been subordinated to the latter as subspecies.¹ The theoretical interpretation could then have been the same, *viz* that they regarded the regional subspecies as species *statu nascenti*. The anticipation of the satellites as species rested on no firm taxonomical ground.

Two distinct ranks are involved, a higher (the assumed ancestral species) and the lower (the young or satellite species). Giving a binomial to both brings ambiguity in classification, as a binomial should be used in its classical Linnean sense.

And this is the crucial point, because the origin of species from exclusive racial differentiation, that is, finally by *isolation*, is still open to discussion. It is often accepted in zoology, but prominent geneticists as BAUR and GOLDSCHMIDT are entirely opposed to this idea. The latter expressed his opinion (19) in this concise way:—"*Geographische Variation ist weder eine Vorstufe noch ein Modell der Artbildungsvorgang*".

However trivial the subtle difference may seem at first sight, it has appeared disastrous in practical taxonomy by the multiplication of binomial names in *Euphrasia*; nobody is any longer capable of realizing which binomials belong to linneonts and which to subspecies. It entailed further that in revisions and descriptions posterior to WETTSTEIN's the same procedure was followed by other workers on the genus. As for unknown reasons *Euphrasia* species are polymorphous and are apt to react to isolation by racial differentiation, scores of partial populations from remote, isolated stations have been described as distinct species.

A much more satisfactory, concise and useful specific and infraspecific hierarchical taxonomy would have been gained if VON WETTSTEIN had not introduced disputable theoretical ideas in practical taxonomy; we would then have been informed about species and their racial development by the simple means of nomenclature.²

It must be added here that in phytography no hypotheses and theories should be mixed with

(1) In fact the 'small' species are in recent floras generally treated as subspecies.

(2) If I understand rightly from a review of KOMAROV's principles, explained by him in an essay on specific delimitation in 1940 (*non vidi*), by Dr SHISKIN (37), the present editor of the Flora of the URSS, the procedure of VON WETTSTEIN is followed in that Flora. KOMAROV does not accept the species as a morphological concept but gives it a phylogenetical interpretation. The Flora URSS is thus based on 'Darwinian taxonomy', *i.e.* reflects the natural process of the origin of species by reconstructing the segregation of character complexes. The 'young constant' species, each

factual observation and introduced in descriptions or used for delimitation such as phylogenetical considerations, assumptions on the origin of taxa, etc. I will be the last to discourage such deductive, synthetic attempts, but they should be based on the facts and kept clearly separate from these, as DE CANDOLLE pointed out long ago (38, p. 56-59).

Differences between subspecies may be large or small, many or few, but being essentially partial populations, they 'behave' as specific populations, though the taxonomical weight of the characters is less than that of Linnean populations. TIMOFFEEFF-RESSOVSKI (3, p. 100) defines this rightly in saying:—"Good geographical races differ in a large number of genes (from adjacent races) most of which cause only very small character-deviations".

TURESSON has made extensive studies on racial differentiation. He stated (20) that almost all Linnean species show racial differentiation mainly as a response to climate and soil. The majority of his races are regional as he derived his material for study from remote localities of a population. The smallest facies of it he called *ecotypes* which he defined as (transl.) "each random group of closely allied biotypes, which in a certain locality has differentiated from the heterogeneous specific population by the prevailing ecological factors. The linneont represents a large hybridization-complex, parts of which have been secondarily grouped in co-ordinated ecotypes of often very different morphological habit".

He arranged (21) the ecotypes into larger infra-specific units, the *ecospecies* (an assemblage of ecotypes) which, in contrast to the ecotypes, show a distinct geographical replacement. The *ecospecies* is, therefore, equivalent to a good geographical race, or taxonomical subspecies.

He also arranged the Jordanian *Erophilas* among the *ecospecies*, as well as races with deviating chromosome number, as these are often morphologically and ecologically distinguishable and occupy a definable area of distribution.

I agree entirely with these views which fit in with

possessing a distributional area of their own, are accepted as distinct species. Closely allied ones are grouped in '*species-series*', which are obviously the equivalent of the polymorphous linneonts, the 'Rotten' of KERNER, and the 'Rassenkreise' of RENSCH.

The consequence of the principle of accepting geographical races as species will necessarily cause an endless number of emendations and will render correlation with adjacent floras difficult or impossible, unless separate keys and descriptions are furnished of the most essential taxa it contains *viz* the '*species-series*' corresponding with the linneonts.

Naturally the number of '*species*' in the Flora of the URSS, estimated at c. 17000, cannot be compared with figures of other Floras which are based on linneonts only.

taxonomical experience. I also agree that in most cases races are adapted to the local environmental condition. In some cases, this connection is not very distinct. It may be absent, as is demonstrated with the two replacing subspecies of the common tropical littoral plant *Ipomoea pescaprae* which, according to VAN OOSTSTROOM (1, p. 475-477), both occur in Malaysia (one very rare) in exactly the same biotope.

In his monograph of the genus *Evolvulus* VAN OOSTSTROOM (22) has successfully applied the sub-specific concept in two ranks, respectively subspecies and variety, the latter, as he told me, in the sense of microsubspecies. BLOEMBERGEN employed it for the genera *Alangium* (23) and *Schima* (24).

In coastal regions inland plants have often racially differentiated a littoral or dune race. An excellent example of that has been described in detail by TURRILL & MARSDEN-JONES (3, p. 63-64) of *Silene cucubalus* and '*S. maritima*'. The latter is the maritime race from exposed situations with condensed habit and pauciflorous inflorescences. "More than a dozen morphological differences, some of which are structural expressions of behaviour differences of selective value, can be enumerated as usually having specific value for diagnostic purposes, yet every one of these is found to 'break down' in some, mostly a few individuals, and this apart from hybridization. Segregation for at least some of the characters approximates a 3:1 ratio. In spite of all break-downs in single characters, the two species keep essentially distinct, though they have no sterility barrier. Certain characters have a high selective value for certain different habitats in which the species naturally occur". In intermediate situations the two taxa form hybrid swarms and are indistinguishable through their thorough miscibility.

It is a complete mystery to me why in such a clear case of racial differentiation TURRILL accepts the above-mentioned bladder campions as distinct '*species*', explaining (32) that merging them as 2 subspecies under one species "would evolve into a classification that could only serve a very limited range of purposes".

The contrary seems to me the case: in merging *S. cucubalus* and *S. maritima* and distinguishing them as subspecies, resp. *S. cucubalus* ssp. *cucubalus* and *S. cucubalus* ssp. *maritima*, their nomenclature indicates at once their true status and their relation, and gives exactly the information wanted to anybody who is not acquainted with the Atlantic flora. Ranging them on one footing as species with other *Silenes* makes the whole a heterogeneous assemblage, while ranging them as subspecies approximates a clearer picture of hierarchic taxonomy and fully exposes the available information in the name-giving.

Another argument of weight in favour of the latter procedure is that if we start in raising subspecies to the rank of species, the number of the latter will be multiplied tenfold or more, and this can certainly not serve a useful purpose, as has been explained by CELAKOVSKI (see p. clxxvii).

6. *Populatio articulata altitudinalis* (fig. 5e)

Much that has been said in the preceding paragraph holds for this type, which refers to racial differentiation in vertical sense, that of altitudinally superposed races.

In the same way as with the regional riaciation this type can be easily derived from altitudinal clines. (We must be certain of course that the altitudinal riaciation is not phenotypic!)

The origin of a mountain race or ecotype is not difficult to imagine. Let us start with a lowland specific population in which certain combinations (paramorphs) are potentially capable of adapting themselves to a cool climate. This would (likely) be a recessive factor in the lowland. At the base of the mountain or mountains both lowland and potentially such mountain-pre-adapted paramorphs will be present—the latter only occasion-

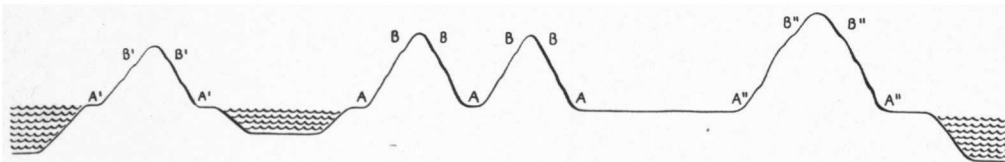


Fig. 6. Scheme of a polymorphous lowland population A, with two regional subspecies A' and A'', and their derived montane subspecies B, B', and B''.

ally, cf. § 1—but this situation will give the latter a chance to 'escape' and reach finally their optimal ecological niche at higher altitude; in this gradual way of sorting out combinations through environment an altitudinal race is born. The new race will gradually 'purify' itself by inbreeding. This is probably an oversimplified picture of what must have taken place in history but contains a plausible explanation of the essence of the process.

This way of origin infers that an altitudinal race may have originated in more than one place and at more than one time, i.e. *polytopically*, giving it at the same time a certain degree of variability. Fig. 6.

If the process of altitudinal riaciation has taken place not from the same lowland population but from remote partial lowland populations (in fig. 6 A, A' and A''), the resulting altitudinal ecotypes may differ morphologically and represent several altitudinal races (in fig. 6 B, B', and B'').

If means of dispersal are sufficient to bridge the gaps between the mountain races B, B', and B'', it is possible that they will be contaminated through mutual gene exchange, but if their means of dispersal are unable to bridge the gaps between the mountains they will remain genetically isolated.¹

(1) These considerations have been basic to the preparation of my studies on Malaysian mountain plants (9). They have led me to omit in these studies all genera which have representatives in the tropical lowland below 1000 m altitude, and to restrict the study in this way to the purely microtherm genera for which polytopic origin is excluded.

Theoretically of course polytopic riaciation is equally possible in the regional sense, but it will play a special role in altitudinal differentiation because the main factor, temperature, stimulating the racial differentiation of a single species is predominantly the same and the result of its selective effect will be convergent.

Examples of altitudinal riaciation are abundant, I mention a few by way of illustration. KERNER gave some examples in *Cytisus* in Europe; MATSUURA (25) studied a dwarf race of *Fritillaria camchatsensis* KER-GAWL. in Japan (differing also in chromosome number). From Java KERN (26) described three distinguishable altitudinally superposed races or subspecies of *Cyperus sanguinolentus*. EXELL (1, p. 539) found a distinct montane subspecies of *Combretum punctatum* BL. in W. Malaysia.

7. *Populatio articulata disjuncta* (fig. 5a & c)

This is, properly, a variant of types 5 and 6, logically derived from regional and altitudinal replacing races or subspecies, differing in that here the races or subspecies are found spaced (disjunct) from adjacent ones.

Transition zones are consequently lacking. In general these are replaced by some barrier causing the isolation, e.g. mountain ranges for lowland plants, lowlands for mountain species, seas for landplants, etc.

In many regions of the globe these disjunct occurrences are frequent, and disjunctions are characteristic for island and mountain floras. They are commonly overlooked by botanists who confine their studies to the flora of one island or a very restricted area.

Specially in those cases where the geographical barriers are geologically ancient, these disjunctions are of prominent interest for historic plant geography.

A classical study (taxonomical, genetical, and in the field) on the behaviour of disjunct populations has been in my opinion the work of E. BAUR on *Antirrhinum* § *Antirrhinastrum* (27, 28). About 20 species had been described in this section, most of them local-endemics from SE. Europe and the W. Mediterranean. Their distinction had been the head-ache of taxonomists. BAUR could demonstrate that the representatives of *A. majus* s.l. are split up into local colonies or aggregates (partial populations). The smaller the aggregates, the narrower the polymorphism; increase of polymorphism was found proportional to the size of the colonies. Large aggregates had sometimes segregated them-

selves into some local facies of minor value. If aggregates were close, contamination of adjacent colonies could be found in places along the borders. There were never two 'species' (as described by taxonomists) together in one colony.

Genetic experiments showed that all representatives were interfertile, F_1 being intermediate, F_2 polymorphous. It appeared further that the small colonies consisted nearly of homozygous individuals, but the large colonies had many heterozygous individuals. Finally it appeared that the number of genetic factors involved in the total polymorphism was very much restricted indeed, but could still give a number of habitually very different plants. Taxonomically BAUR accepts but two Linnean species *A. majus* L., consisting of a number of local races or subspecies, and *A. siculum*.

This example shows the difference in the typical behaviour of a disjunct species against one with regional raciation.

The number of possible combinations would be still very large, but BAUR assumes that most of them are not viable in the sense that they are exterminated by selection being not capable of competition; this greatly narrows down the actual number realized in nature.

It appears that among racially differentiated species a disjunct species behaves as an actor; with each new scene he appears in different clothes and make-up (facies of the subspecies) before another *décor* (habitat and ecology), while we cannot observe him changing his clothes. In regionally differentiated species the actor changes his clothes before the public in the transition zones.

The correct specific delimitation of a disjunct species population offers therefore much greater difficulty than the regional subspecies which, if the material is sufficient, will show the transitions.

To attain a satisfactory synthesis of a disjunct species we have to collect circumstantial evidence:

- a) By assessing the differential characters through comparison with those of well-established taxa of the same genus.
- b) By examining as much material as possible and checking which characters really hold throughout.
- c) By comparing regional variability in allied species with a continuous area and trying to realize what picture would evolve if certain parts of this continuum were omitted, i.e. 'deductive analogy'.
- d) By using, where possible, experimental taxonomical methods.

I admit that in the case of disjunct areas there may remain difference of opinion, but in the majority of cases the circumstantial evidence thus gained will lead to a satisfactory conclusion for assigning specific or infraspecific rank to the disjunct populations.

In the case of *Antirrhinum* one might assume that the disjunctions are at least in part progressive and geologically young or even recent. In many other cases they are ancient. An example of the

latter category is for example the *cedar of the Libanon*, which was studied in detail by HOOKER *f.* After a careful study he came to the conclusion that the disjunct populations in Morocco, Algeria, Crete, Cyprus, Libanon, Caucasus, Taurus, Afghanistan, and the Himalayas, have all a different racial facies, some more, others less well pronounced, but that allowing for the distance between the populations and the trivial taxonomical value of these differences, none of them deserves to be classified in the specific rank. In this case it is also very clear that the total area of the cedar is a relict from a former continuous area of distribution which has become disjunct in the course of geological time. It does not require any high degree of extrapolation to imagine that during this very long process the partial populations, surviving in the refuges, and originated from the there prevailing facies of the former \pm continuous area, have assumed a local facies through inbreeding and have further undergone the process of prolonged selection (adaptation) following the secular climatic changes which occurred in each locality since the moment(s) of disruption.

As has been remarked before, racial differentiation will be frequent in mountain floras generally and in island floras in particular. And this deserves very careful attention under the archipelagic conditions of the South and West Pacific where large geological disruptions and other changes have undoubtedly taken place in the past.

Within the Malaysian archipelago proper these disjunctions are still relatively not very wide apart, but as soon as populations of Malaysian species are encountered in the Micronesian islands, the Solomons, New Hebrides, Fiji, Samoa, New Zealand, and eventually Polynesia, the density of the partial populations decreases rapidly with simultaneous increase of distances, of prolonged wide isolation, and consequently of taxonomic deviation. Such areas offer the taxonomist great difficulty in specific delimitation, requiring a good background, capacity of synthesis, and regional work, to bring it to a satisfactory conclusion.

Malaysia is the western boundary of a most typical series of disjunctions of subantarctic microtherm plants, of which an example is given in fig. 7 of the cyperaceous *Oreobolus*. There are many dozens of cases of equiformal relict areas.

A typical case of another category is that of *Euphrasia* of which a map has been given in volume one (p. liv). In Malaysia *Euphrasias* occur only above 2100 m on non-volcanic mountains, and form an almost continuous series of stepping stones (as far as they are allowed by topographical conditions) from S. Japan to New Zealand & Fuegia. In a preliminary study DU RIETZ (29) has been able to show that each of these stepping stones possesses a local facies, and that adjacent populations show the greatest similarity. This is justly the state of affairs required by a species segregated into disjunct subspecies.¹ And this is a

(1) In New Guinea there are some additional good species of *Euphrasia*.

repetition of the segregational tendencies this genus displays in Europe.

Such complete series of stepping stones are naturally rare, as many genera will have been less vigorous or tenacious and adaptable and will not have succeeded in maintaining themselves through the ages on all stepping stones spreading to newly evolving interjacent ones.

Chinese species, Chinese species, Formosan species, *etc.*

Even if an author has satisfied himself that no species are common to two or more districts or have been entered under two or more districts, the entering of geographical evidence in phytographical keys is to be disapproved on principle.

It tends to defeat morphological distinction and

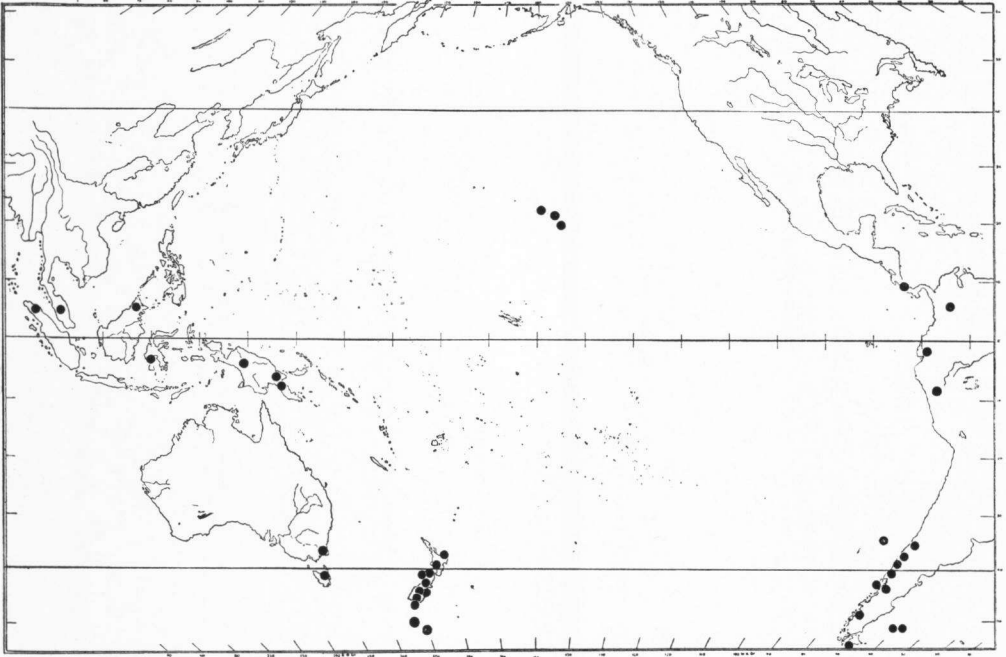


Fig. 7. Area of distribution of *Oreobolus*, a microtherm genus of *Cyperaceae*, in the tropics only on the high, ancient mountains. The number of species is not unanimously agreed on, but is less than 10.

Similar tendencies for disjunct segregation are naturally also found in a smaller degree. JACOBS found in the widely distributed malpighiaceae *Aspidopteris timoriensis* (DC.) Juss. (vol. 5, p. 142, f. 13) in a restricted coherent (archipelagic) area in the W. Pacific specimens differing in indument which character, though trivial taxonomically, has a geographic significance on the frontier of the specific area.

Plant geography as a check on specific delimitation. In keys to genera and species it is not seldom encountered that authors have found it useful to add an indication of geographical distribution to the morphological characters. This procedure must be strongly discouraged, as it is mixing up two issues of different standing.

In premature or uncritical compilatory regional or revisional censuses keys sometimes start even in dividing species to districts, *e.g.* Asiatic species, African species, *etc.* or, Indian species, Indo-

is used consequently mostly in cases where morphological contrasts are feeble or unsatisfactory, as only then there is urgency to use geographical distribution as an additional pseudo-'character'. And for that reason it is not very convincing, and raises suspicion as to the value of the morphological data.

If an author does not stick to sound delimitation on a morphological basis irrespective of geographical distribution, he may easily be misled. Examples to prove this are provided by botanical distinction of mislabelled specimens attributed to wrong countries of origin.

For example MIQUEL described a new species, *Scheuchzeria asiatica*, the second in the genus, on the basis of a specimen said to have been collected in Sumatra. And he actually gave characters for distinguishing it from the holarctic *S. palustris*. He doubtless argued that the Sumatran plants 'could not be conspecific' with the European species on account of this wide disjunction. Though he, himself, later withdrew the specific distinction, and it

has now been proved by the diatom tracer method that the sheets were mislabelled and the actual specimens were collected most probably in Central Europe (33), the fact remains that MIQUEL, for his taxonomical judgement, did not strictly keep to the morphological characters, reserving the plant geographical aspect as a check on the taxonomical work, as should be done. An other example is that of the recording by NELMES (34) of two European *Carices* from Java on the basis of sheets labelled 'Papandajan' collected by RIDLEY. NELMES distinguished them as endemic varieties! We know that among the Java collection of RIDLEY there are many mislabelled plants from different sources (cf. vol. 1, p. xxix) and as the species in question have never been recollected by any other botanist in that frequented mountain resort, the circumstantial evidence leads indubitably to accepting them as having been collected in Europe and later mixed by accident with other collections. The too scrutinous examination by NELMES, together with the plant geographically aberrant locality, have led to distinguish taxa which simply do not exist.

These examples show that instead of considering plant distributional data during taxonomical work, geographical considerations should serve as a later check to the phytographical data.

Concluding this chapter, it has appeared that the pattern of variability displayed by specific populations can have very different aspects.

Setting aside *phenotypic* variability and the *regular* variability (melting pot), our main concern is to consider, for specific delimitation, the tendency of regional differentiation. The *clinal* and *marginal* types will seldom permit drawing demarcations and are consequently not fit for defining infraspecific taxa. The *regional* and *disjunct* types, which are *articulated* populations with or without transition zones between the partial populations, on the other hand are significant for taxonomical distinction on the infraspecific level. If differential characters are very small the races are equivalent to microsubspecies, if they are tolerably important the races are best treated as subspecies.

One might be tempted to treat all distinct disjunct races as vicarious species, but this seems unfair as allowance should be made for the disjunction. The argument that disjunct distinguishable taxa offer no intermediates or transitions seems unreal as Nature itself has prohibited this.

For this reason the taxonomist should give special attention to regional variability and its evaluation in observing for this purpose the four points mentioned before: (a) the taxonomical value of the characters concerned, (b) the results of a careful checking of their constancy, (c) *ditto* of comparing variability in allied continuous species, (d) experimental taxonomy.

In itself a sharp demarcation (absence of transitions) of replacing taxa necessitates taxonomic distinction, but the demarcation gives no clue to the rank of the taxa, unless the complex of differences

is so large and further circumstantial evidence (overlapping of areas) so clear that all good taxonomists agree.

Unfortunately not all taxonomists agree with this thesis. Specially those who seek safety in restricted specific delimitation and are inclined to distinguish small 'homogeneous' species will have objections. They abhor variable species and find that those, who feel in certain cases obliged to accept widely encompassed species, are neglecting the variability patterns and do an injustice to the analysis.

This opinion is, however, entirely erroneous, as I have stressed the necessity to give, where possible and desirable, a concise synthesis of the variability pattern of species, either in notes if it cannot be expressed nomenclaturally (phenotypic, clines, marginal variation), or in distinguishing varieties (non-geographical paramorphs worthy of distinction) or subspecies (regional or disjunct racial differentiation).

There is no reason to suppress anything about variation, though on the other hand the deductions derived from herbarium material must of necessity be limited and can never enter the field of population analysis.¹

Another objection sometimes raised against subordinating racial differentiation on the infraspecific level is a practical issue in that it is admittedly less handy and elegant to have trinomial or even more complicated nomenclatural indications for a certain taxon. But for those who wish to differentiate and in cases where it appears necessary, the infraspecific distinction by name is the single solution.

The slight practical drawback of a trinomial nomenclature (accepting subspecies and varieties) should never dissuade one from making the worthy attempt towards a sound hierarchical synthesis, or stand in the way of a well-founded specific delimitation with subordinated taxa.

The immense gain of the trinomial nomenclature is that it gives a better understanding of mutual hierarchical relations between species and within species immediately recognizable by means of nomenclature.

If in a genus for example 20 species are enumerated they should be of equal rank and not half of them be worthy only of subspecific rank. This

(1) In certain cases the naming of infraspecific taxa has in my opinion certainly gone too far, as for example in the monograph of *Saxifraga* by IRMSCHER & ENGLER. With this very fine and finest fractioning the taxonomist burdens himself with an increasing responsibility, as distinctness of these taxa decreases with lower rank whereas the chance of intermediates is increasing rapidly. Furthermore it will appear that there are on these fine levels always much more taxa—and intermediates—than assumed by the monographers working on the borderline of population analysis.

For most aims a distinction of species with subspecies and varieties is sufficient.

would destroy the hierarchical structure of taxonomy.

But if I find in a Flora mentioned: *Silene cucubalus* and *S. cucubalus* ssp. *maritima*, the information supplied by it is clearly that *S. cucubalus* has a littoral race, that this is replacing it, and is miscible with the type race. Contrarily if I find mentioned *S. cucubalus*, *S. maritima*, *S. otites*, *S. conica*, etc., I assume these are of the same Linnean status, which is a misrepresentation.

DE CANDOLLE (38, p. 7) expressed this as follows:—"Confondre certains degrés, par exemple effacer la distinction des espèces de LINNÉ et des formes qu'il nommait variétés . . . c'est revenir au temps de TOURNEFORT; c'est jeter de la confusion en assimilant des groupes d'une valeur différente".

HUXLEY (3, p. 36) has rightly concluded:—"The principle of replacement should, whenever possible, be adopted, thus reducing the number of species while increasing the number of subspecies. Similar principles of ecological or genetic replacement should be reserved for natural groups of the same general nature as species but exhibiting a lower degree of morphological differentiation and/or reproductive isolation".

As has been said before, botanists working on a restricted area can to some extent be excused: it is clear why they accept sometimes in their area taxa as species which are really races of wider spread species.

But as we know that plants do not keep to political boundaries or local areas, chauvinistic botany, as DE CANDOLLE called it (38, p. 13, 53), must be strongly discouraged as it represents a menace towards synthetic attempts, specially in sound specific delimitation.

It is also clear that in very little known or unexplored areas material is sometimes very scarce and extremes have been originally described as species. In the tropics this is still a problem: many species have been, as MERRILL expressed himself to me, "optimistically proposed".

It is unclear, however, that there are still professional botanists revising genera, who, after a careful analysis, are not willing or capable to conclude their work and present the result in a satisfactorily framed synthesis.

This is unfortunate as their results will not stand the test of time. They often defend themselves in advancing that the material is not sufficient and that anyhow taxonomic work is tentative in tropical plants. It should be explained here that in the case of replacing and disjunct taxa hardly any or no linking specimens will ever be found. Over-cautiousness will here not find its recognition or reward in future.

Another category of authors insists intentionally giving binomials to the smallest taxa distinguishable. This procedure is apparently a matter of principle with them. Why they adhere to this undesirable depreciation of universally adopted ranks, seems to be rather a matter of psychology. These same authors will generally also devalue accepted genera in raising their subgenera or

sections to generic rank and follow a similar procedure of splitting for the higher ranks.

There is no advantage in this devaluation, contrarily it brings chaos and by its multiplication of taxa and names causes a detestable confusion, defeating the main principle by which the great LINNAEUS made plant taxonomy a branch of botanical science, viz that of synthesis.

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4. SPECIFIC POLYMORPHISM AND ADAPTATION CHARACTERS

As has been mentioned before, the degree of polymorphism of a specific population stands, generally, in proportion to the size of its distributional area. This seems to be a causal relation, as potential morphological plasticity (diversity) goes, generally, parallel with ecological plasticity.¹

It is natural that the environment will act directly (as an 'adaptational sieve') by the physiographic, edaphic, and biotic conditions it offers.

Whether or not a population can make use of these environmental invitations and will produce fitting species depends of course on the inherent qualities of its genome structure. Specific populations confined to the tropical zone may or may not produce specific or racial combinations with microtherm tolerance.

It has repeatedly been advanced that environmental variation and its secular change has been a distinct stimulus towards the origin of new taxa.²

(1) The same observation on specific populations is *mutatis mutandis* applicable to specific differentiation within a genus. Large genera exhibit both a large degree of morphological differentiation and ecological capacities, in that they have produced representatives for a great number of ecological niches. In the genus *Ficus* for example there are epiphytic and terrestrial species, herbaceous and ligneous ones, lianas and trees, both species participating in the substages and in the main canopy; some are cauliflorous others not; the majority belongs to the everwet tropics but representatives are found in seasonal tropics; some are evergreen, others are leaf-shedding; a few occur even in rather arid parts of the subtropics; in the tropics some representatives are adapted specially to swamps, others to craters, to gravelbeds of running streams, etc. A similarly large 'adaptability' is found in other large genera as for example *Eugenia*, *Acacia*, *Euphorbia*, *Pandanus*, etc.; the structural plan of these genera offers apparently opportunity for the origin of a multitude of viable specific variations.

(2) STEBBINS (1) accepts this as one of the most important 'mechanisms' of 'evolution' (in treating aridity). In my opinion it should not be overestimated. The everwet tropics, which have produced by far the largest portion of the morphological diversity of the world's flora, are relatively exceedingly monotonous in climatic conditions and secular changes. Notwithstanding that, they possess a great number of very large families and genera, as the *Araceae*, *Myristicaceae*, *Dipterocarpaceae*, *Orchidaceae*, *Rubiaceae*, *Zingiberaceae*, *Euphorbiaceae*, *Annonaceae*, *Sapotaceae*, etc., several of which are practically confined to these monotonous everwet conditions and have been so in the past. *Annonaceae* and *Myristicaceae* for example belong for their major part even only to a single biotope of the everwet rain-forest, viz

It should be admitted that environmental variety and its secular change is a challenge towards this kind of 'adaptational form-producing variability on the basis of selection', but this influence should not be overestimated, as all depends in last instance on the restrictions ruled by the inherent genome potentialities.

Admitting that a number of families and genera or other taxa have not been challenged by a great variety of environment or by secular changes, it should be realized also that tropical families have had ample challenge in geological time to show their potential capacity, for instance against temperate conditions both in and outside the tropics. A few stray *Zingiberaceae* of the genus *Alpinia* for example have been produced adapted to the subalpine zone up to an altitude of 3400 m, and a few *Scheffleras* (*Aral.*) are even found adapted to the tropical alpine zone at 4000 m, where they make a singular out-of-the-way looking element with their large leaves in the microphyllous dwarf-scrub characteristic for these lofty heights.

This is already suggestive of the fact that the effect of environmental adaptation is very often not recognizable in the outward appearance or morphological characters. Local and racial differentiation in *Mahonia napaulensis* for example was based on minor differences of the length ratio of

the substage. But both families are extraordinarily rich in species; *Annonaceae* possess numerous genera and according to DIELS (2) all structural diversity potentially possible with extant generic characters have been realized in viable constellations nowadays. *We are forced to the conclusion that such families have had an autonomous structural evolution (in the sense of development of viable combinations) n'en déplaît le monotonous environment.*

MANTON (3, p. 283) is of opinion that changes of climate have brought about numerous cases of polyploid species.

Both rather sudden and secular climatic changes (desiccation periods, pluvial periods, ice ages, etc.) have certainly been instrumental in the origin of new forms but there is undue neglect of autonomous evolution (change) in the plant kingdom and overestimation of 'adaptation'.

I cannot refrain from the idea long ago worked out by VON NAEGELI (4) and a few years ago alluded to by myself (5) that under monotonous environmental conditions evolution would also have taken place. Arguments for this can be derived from the marine flora, freshwater plants, and the everwet, tropical rain-forest. It seems plausible to me that the challenge of changing environment has led to orthogenesis in various directions but starting on a matrix of inherent, biochemical autonomous development and that 'adaptation' resulted in and gave impetus to a number of side-issues of a causal pattern with inherent 'stimulant' rather than being the cause or single stimulant itself.

pedicels and bracts, shape of the stipules, number of the jugae, etc. *Scirpus fluitans* L. is comparatively extremely uniform over an enormous area from Europe to Australia, but is in Sumatra replaced by a distinct taxon, in exactly the same biotope, of exactly the same habit, differing only in a few inconspicuous floral characters; for our reasoning it is irrelevant in this respect whether these differences are classified as specific or sub-specific, as in both cases there is no sign whatever of the presence of environmental survival value. *Anemone rivularis* HAM., a widely distributed species in SE. Asia, is represented in the same biotope in N. Sumatra with a form differing by distinctly longer petioled leaf-segments, which are mostly sessile in the mainland population. The adaptational value of this marginal variation is difficult to

envisage. The widely holarctic distributed *Drosera rotundifolia* L. has been found in a remote, disjunct locality, viz mountain peat swamps in New Guinea, under conditions that could exactly be expected. The only differential character of this micro-subspecies is the persistence and size of the bracts, a character defeating the idea about adaptational value.

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5. ANTHROPOGENOUS INFLUENCE IN CONNECTION WITH SPECIFIC DELIMITATION

In a span of time which by our human concepts is long and ancient, but quite recent by the geological time-table, man has, through fire, cattle-breeding, agriculture, transport, war, etc., upset the balance of primitive nature nearly everywhere.

Specially during the last few tens of thousands of years this attack on nature has tremendously increased in intensity, and in many regions, presumably most so in the northern hemisphere, primitive nature has to various degrees been converted anthropogenically into, or replaced by, artificial or semi-artificial vegetation types. As a result, in such places both the primitive fauna and flora have undergone essential changes.

Two new categories of plants have come to the fore or have increased in abundance respectively, viz the *cultigens* and *ruderals*, as by-products of human occupation. They live by the grace of man, intentionally or unintentionally. The majority of them have originated by or have undergone selection and are confined to the steadily increasing surface of anthropogenically influenced country.

This chapter will deal with the ruderals, leaving at subject of chapter 6 to survey the cultigens.

Selection operated on both ecological and morphological characters of survival value of the ruderals and adventives.

Such features are for example: wide edaphical and climatical tolerance (eurytypy), a short life-cycle with rapid ripening of seeds, harmonious balance with human methods of transport and rhythm of agricultural methods (weeding, harvesting, winnowing, etc.), longevity and structure of diaspores, etc.

In comparison with primitive nature enormous surfaces became available for nomad plants (see p. cc), offering opportunity for an enormous increase of individuals and manifestation of paramorphs in the new 'battle-field' for survival, viz adaptation to human occupation and competition under anthropogenous circumstances.

A predominant factor in the development

('evolution') of the nomad plants must have been the genetical isolation. They escaped from small populations in primitive nature to become aliens, often in places where no genetic contact was possible with the ancestral population. This *diaspora* may have happened also exceptionally under primitive conditions in cases of long-distance dispersal (which can at least theoretically not be denied).

Aliens may behave as distinct taxa in foreign countries. I described the case of *Turnera ulmifolia* L. in Malaysia (1), two forms of which occur there, viz *T. ulmifolia* L. sens. str. and *T. subulata* J.SM. (syn. *T. trioniflora* SIMS). In Malaysia these two taxa behave as good species and differ in many morphological characters and ecological behaviour. They occur cultivated side by side in the Botanic Gardens, Bogor, but remain perfectly constant. Both show a very narrow range of variability in Malaysia. The monographer of the family *Turneraceae*, I. URBAN, considered them to represent varieties of the polymorphous species *T. ulmifolia* L. sens. lat. with numerous other forms in the native country, the West Indies (2). And a superficial inspection at Kew of these forms confirmed this opinion: the gap between the two forms, which are so distinct in Java, appears to be filled by all kinds of intermediary forms in the New World tropics. If these intermediary forms had also been introduced into Malaysia, the judgement of the botanist in Java would have been quite different from what it is now. And this shows how a local botanist may err in his estimate when performing local revisional work!

In the case of the *Turneras* just mentioned both Javanese forms can be matched more or less in the West Indian populations. There are a number of worldwide distributed aliens which have, however, never been collected in more or less natural vegetation in their home country.

With the Spanish galleons of the trade route from Acapulco in W. Mexico via Guam to the Philippines, a post-Columbian trans-Pacific line

maintained from 1565 to 1815, numerous aliens have been brought to the Philippines. A certain number has established itself; some are still local, other spread widely. According to MERRILL (3) several have never been (exactly) matched by American congeners, e.g. *Kosteletzkya batavensis* (BLCO) F.-VILL., and *Prosopis vitaliana* NAVES.¹ Among them is also *Elephantopus scaber* L., a not very variable, extremely common species which has doubtless been imported from America in post-Columbian time, but is not matched by a native American species; it is said to be now adventive in America itself!

A comparable case is found in Europe with the doubtless man-introduced *Oenotheras*; in Europe several local forms have developed which have never been found in America, according to RENNER (4).

In these cases the fact that the partial populations are morphologically and geographically definable has induced taxonomists to keep the adventive taxon specifically distinct, though it is in the majority of cases basically doubtless a racial derivative of a part of the potential polymorphism of an American species. It owes its origin probably to one or a few paramorphs whose progeny was purified through the effect of isolation giving rise to a rather homogeneous subspecific taxon not easily to be exactly matched in the original population of the ancestral species. Generally the polymorphism of the alien race is far more restricted than that of the species from which it has been derived. Taxonomists applying a narrow species delimitation will naturally keep them as distinct species, a rank which they certainly do not deserve. An example of a widely distributed, common Malaysian ruderal which has never given difficulties for delimitation is *Cyathula prostrata* (L.) BL. The constancy of its characters is in the Philippines locally disturbed by the occurrence of a remarkably narrow-leaved, dwarf form which has been described as a separate species; as the deviation concerns merely vegetative characters BACKER assigned it varietal rank (cf. vol. 1, p. 83).

The majority of cereal weeds belong to this group of ruderals and adventives which through their genetical isolation can maintain themselves as constant races in human cultures. They cling to the cereals as fleas to the dog. They are entirely adapted to the life-cycle of the cereal and its management by man, and their characters, ecologically and morphologically, show the traces of the selective effect of their habitat. Therefore their characters show a remarkable parallelism, *inter se* with that of their cultigen host.

THELLUNG has in several studies (5, 6) given an analysis of the characters peculiar and common to segetal races. Of *Polygonum lapathifolium* ssp. *linicola*, a ruderal confined to flax fields, he mentions for example the rudimentary nature of the articulation of the fruiting pedicel, causing the fruit to be persistent and be harvested together with

the flax; besides, the habit of this ruderal *Polygonum* is very slender and resembling that of flax, and its fruits imitate in shape and size those of flax. This combination of characters enables the *Polygonum* to remain a constant segetal companion of flax, fitting with its culture scheme; see also DANSER (7).

Sometimes the seeds of the segetals are larger than those of the primary wild population, imitating those of the cultivated crop. In *Alectrolophus* the primary wild population has marginally winged seeds, but the segetal race lacks the marginal wing and thus fits with the smooth seed of the cultivated plant. It is clear that this segetal has been derived secondarily from the wild population and that only the progeny of specimens with unwinged seed have been able to develop into a segetal race. But it is difficult to trace such specimens in the wild population, where unwinged seeds are distinctly rare!

THELLUNG pointed out (6) that the unintentional selective activity by man has worked in many cases along parallel lines, both in ruderals and in the cultivated plants themselves. In some cases it seems even that segetal-adapted grasses have gradually replaced the original cereal becoming themselves a cultivated cereal.

It is quite possible that among the exclusively segetal plants some taxa have or deserve the status of a Linnean species for which it is not directly evident what has been their ancestral stock. The latter may be extinct.

Bromus arduennensis is a typical 'endemic' segetal from W. Europe bound to the cultivation of spelt (*Triticum spelta*); it is rarely found in Belgium, S. Neth. Limburg and N. France. According to CUGNAC (8) *Bromus grossus* belongs in the same category, inhabiting a similar but larger area. *Silene linicola* is a segetal bound to flax cultures, as is the flax parasite *Cuscuta epilinum*. The latter has always been accepted as a good Linnean species; it may have been parasitic on the ancestor of the cultivated flax.

In connection with the Australian flora BENTHAM pointed out long ago "that the geographical station of a waif or colonist imposes variations upon it almost from the moment of its arrival". DE VRIES remarked (9) "that the initial stages of new species will be found most easily in luxuriant alien vegetations".

I have been interested in the problem of the origin of ruderals in connection with the origin of the Malaysian mountain flora (10) and with the vegetation types of Malaysia (11); in this Flora I have formerly touched the subject in a brief way (12).

Some of the ruderals just mentioned may have been native of the primitive flora in which they were probably scarce. They were suppressed by the forest vegetation which left them only opportunity in occasional small habitats (biotopes) which were non-forested by natural causes. With the advent of man these suppressed plants got the chance of their life to extend their range in the anthropogenically opened areas in which they multiplied on

(1) This has been reduced by some authors to *P. juliflora* DC.

a gigantic scale and could disperse easily far beyond their original home. A small number may have lacked sufficient potentialities to adapt themselves to anthropogenic habitats; those which possessed a wide potential capacity of polymorphism were naturally most successful and were modified into wayside ruderals, segetals, etc., through selection on the basis of tolerance to fit the new environment (scheme and rhythm of cultivated crops).

This process of development of migrating species has not only occurred with the steppe plants of Eurasia, but has also occurred in the tropical forests in which there is an enormous number of potential arboreal ruderals which under primitive conditions occupy the rare open places. They live on the 'margin' of the forest, but act as pioneers of the secondary forest (parang, blukar) wherever the forest shows open gaps, irrelevant of the cause of these gaps. These arboreal ruderals are all heliophilous, generally short-lived, rapid growing species. The anthropogenous destruction has offered them an enormous expansion of the area which fits the ecology of these 'nomad plants' as I have called them (13).

Besides the above-mentioned shift in nomad plant-populations and origin of infraspecific differentiation within these populations, an other consequence of the anthropogenous opening of the plant cover of the world has been the new contacts between populations which were separated in the balanced primitive vegetation. And this has been obviously instrumental in the formation of good, new species. It is very probable that the origin of *Galeopsis tetrahit* in Europe as an allotetraploid hybrid between *G. pubescens* and *G. speciosa* has been due to, or obviously favoured by, the anthropogenous shifts of the vegetation. The origin of *Spartina townsendii*, presumably a similar allotetraploid hybrid between the American-introduced *S. alterniflora* and the European *S. stricta*, which according to TURRILL (14) answers to every test for a species, belongs in this same class of recently evolved new species.

Recent research has added to circumstantial evidence towards the assumption that this class of very recent new species (*neo-endemics*) is of much larger magnitude than formerly imagined and offers a welcome explanation for the long known fact that several genera show a remarkable polymorphism in anthropogenic vegetation.

North American taxonomists are apparently unanimously of opinion that the destruction of the primitive forests has greatly upset the ecological and genetical balance of the populations of primitive vegetation, shaking and interlacing them, causing great trouble and confusion for the taxonomist who is now often at a loss with their systematic evaluation.

MARIE-VICTORIN wrote (15):—"that it seems then safe to assume that the great development of the genus *Crataegus* in north-eastern America, and particularly in the St Lawrence Valley, is the immediate result of the ecological upset brought in by deforestation and settling of the land. This

suggests a very important biological generalization, namely that, under favourable circumstances, a period of two hundred or three hundred years is sufficient to produce in some genera, by mutation or otherwise, a marvellous array of species".

TURRILL (16) wrote on this subject:—"Taxonomic difficulties met with in the Mediterranean flora in certain genera as *Dianthus*, *Silene*, *Thymus*, *Centaurea*, *Asperula*, *Verbascum*, *Veronica*, are due, at least in part, to the opening of new habitats by man through forest destruction, the consequent spread in range of taxa adapted (or pre-adapted) to such habitats, the meeting of taxa previously isolated, and hybridization. Similar situations occur in tropical Africa outside the rain-forest areas". He accepts the recent origin of neo-endemic taxa. See also LÉONARD (22).

A similar state of affairs has been reported from Australia outside the rain-forest. In the former century BENTHAM and F. VON MUELLER have described several hundreds of species in the genus *Eucalyptus*. This colossal array has been supplemented later by MAIDEN, BLAKELY, and others, with again some hundreds. It has appeared, however, that the majority of former species represent good species with distinct areas of distribution, whereas contrarily a great percentage of the later described ones have not been retraced, are often exceedingly local, and represent frequently hybrids or specimens from later heterogeneous generations of their progeny mostly found in partly deforested areas. This is the subject of studies by Mr L. D. PRYOR at Canberra (17). Similar results are obtained with *Eucalyptus* in Tasmania by Mr R. G. BRETT (21). In New Zealand COCKAYNE and H. H. ALLAN, stimulated by LORTSY, have made extensive studies on hybridism in the New Zealand flora. COCKAYNE (18) found hybrids specially conspicuous "where man has altered the balance of nature and where he is bringing together parental species in greater numbers than in primeval New Zealand". ALLAN (19) has been able to demonstrate that a number of recognized species merely represented F₁ hybrids and that in several genera (*e.g.* *Coprosma*, *Hebe*, *Melicope*, etc.) hybrid swarms are found between 'species' which appear entirely miscible. Sometimes partial populations of these progenies have become isolated and the effects of inbreeding after introgression may offer serious difficulties in attempts towards specific delimitation. Recently ALLAN (20) has given a survey of observations on the origin of new forms after disturbance of naturally balanced vegetation.

It is clear that the increasing influence of man on vegetation will be essential for specific delimitation. In certain groups the more or less static, original balance in primitive nature has gone astray and is stimulated towards a new course¹.

(1) This holds naturally also for the fauna, the opened, new environments permitting free passage of pollinators and stimulating the origin of new pollinators for 'new' plant species. The interaction between the flora and its pollinators is thus reshuffled.

This shift caused by man has not been unique in the history of the plant world. During the course of the geological history of the globe destruction of vegetation with following shifts in vegetation comparable in magnitude must have regularly played havoc with populations. *Regressions* and *transgressions* have been instrumental in transporting populations or reducing them. *Ice ages* have caused enormous latitudinal population shifts in temperate and warm-temperate regions; sometimes components were able to 'escape' along N-S mountain ranges or land connections to lesser latitude. In other cases W-E ranges prohibited migration and floras were consequently crushed by advancing ice masses and became extinct, or some species survived in a few non-glaciated 'nunatak' refuges serving as *foci* for later diffusion at the end of the Ice Age.

Desiccation periods must have had comparable grand-scale migrational effects. *Orogenetic movements* of the earth's crust with following pen-plainization must have been big stimulants towards the origin of new taxa or bringing into contact remote ones. Finally, there have been great changes in the *distribution of land and sea* during the course of geological history: some continental areas have obviously crumbled, leaving fragmentary islands with a relict flora as signs of their former existence.

All these phenomena of great magnitude have, during the course of the geological history of the earth, been active towards shifts of species populations. The 'regularities' found in specific segregation and species affinities add often to circumstantial evidence towards a reconstruction of these geological changes.

It can easily be imagined that through new genetical contacts of isolated populations secondary centres of speciation must have been formed by recombination. Partial populations got other aspects through the effects of selection and genetic isolation. In the South Pacific theatre, the crumbling of the ancient subantarctic continent must have been the scene of extinction as well as of speciation, and of tearing apart populations under varying environmental conditions. Not less spec-

tacular must have been the fate of the tropical Gondwana Land populations in the area from Madagascar through the northern part of the Indian Ocean to New Guinea. These shifts are still reflected in the plant-geographical relations of living populations and are no mere academic speculations. The remarkable orderliness found in plant-geographical analysis (equiform and equi-ecologic areas) furnishes evidence almost amounting to proof of a history as roughly alluded to above.

It is, hence, permissible to assume that specific populations have been subject to environmental change in multifarious ways in geologic history and that the taxonomist must be on the alert to keep these considerations in mind in evaluating taxa in general and species in particular.

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6. SPECIFIC DELIMITATION IN CULTIVATED PLANTS

I entirely agree with TURRILL (1) who stated that:—"There is of course no sharp line between wild and cultivated plants and no reason for believing that many, perhaps most, of the results obtained with garden plants cannot or do not occur also in the wild. There are, however, certain differences in detail and in emphasis. Isolation and selection are different in kind and degree. Competition is generally greatly reduced. The phenomena of natural selection are absent. Conditions are controlled and kept near optimum or, at least, extremes are reduced. Possibilities of hybridization are changed, and either increased or prevented. Diseases and pests are more or less artificially controlled. Barriers between species which are valid

in nature may be broken down under conditions of cultivation; mutations may survive which cannot survive in the wild; extremes of plasticity may appear that are greater than those occurring in nature. The use of all facts garnered under such conditions, is, however, different from the 'wild' and they must be used rather by analogy than directly".

We can certainly agree with TANAKA (2) that among cultigens there may be good species; although they have not evolved in nature but have originated artificially, they obviously represent viable combinations within the potentialities of a certain genus. Reversely it should be considered that the ruderals and other species originated

through anthropogenous action and bound to human life have evolved in the wild but their majority equally did not form part of primitive nature.

The aim of the taxonomist is in the first place to study natural species and their delimitation. The number of artificial vegetable creations is endless, their origin mostly obscure, and their classification serves other aims than those of the taxonomist.

Further, cultigens contain in proportion an exceptionally high percentage of apomicts, hybrids and their progeny, as well as polyploids, and these groups withdraw themselves, both in nature and in cultivation, from the capacity of normal taxonomic classification and satisfactory specific delimitation.

When trying to classify cultivated plants the taxonomist's outlook is no longer unpreoccupied and practice learns that he is generally inclined or forced to yield to practices which would not be acceptable in revisions dealing with wild populations. Practice has definite demands towards efficiency: long formulas for names are undesirable, short formulas, if possible binomial, are preferred, even for clones and pure lines.

This has led to a host of binomials for cultivated plants, though it is clear that they do not deserve specific rank from a taxonomical point of view. *Sorghums* certainly do not deserve the rank of botanical species but dozens have been distinguished in this way.

The raising of varieties and races and other kinds of *convivia*¹ to specific rank for convenience entails naturally a devaluation of the higher ranks; consequently *Sorghum* is treated as a separate genus though it is very doubtful whether it deserves that status. In the *Gramineae*², *Orchidaceae*, and some other families containing commercial plants, many subgenera and sections have been raised to generic level, a procedure mostly induced by reasons of convenience, not by scientific urgency.³

Besides, the issue of a new specific name has, as O. SCHWARZ (3) rightly remarked, both in agriculture and horticulture not infrequently a commercial significance, a lamentable circumstance prohibiting a free judgement for the specific delimitation.

It is to be regretted that the great human interest specially from laymen in taxonomy (breeders, horticulturists, agriculturists, foresters, and ama-

(1) *Convivium* is the convenient term, with which DANSER (6) defines any partial specific population or group of individuals which is more or less distinguishable (morphologically or ecologically) and maintains itself through isolation (of whatever source). The concept therefore covers all ecotypes, races, etc. By definition all *convivia* of one species are miscible.

(2) In contrast with *Cyperaceae* in which useful plants are scarce.

(3) A similar devaluation of the ranks for convenience serving practical aims is found in the nomenclature of insects, fungi, bacteria, and all other groups which stand in the focus of practical attention.

teur botanists), who insist on a convenient, preferably binomial, name-giving for their plants of whatever source, has in many cases induced taxonomists to yield towards this pressure emanating from applied botany. This yield is principally militating against the basic principles of scientific classification.¹

It is not for scientific reasons that cultivated rice, *Oryza sativa* L., is kept specifically distinct from *O. fatua* KOEN. from which it is only distinguished by its edibility and the fact that the spikelets do not fall when ripe. Both qualities and eventually others are distinctly due to selection by man who, starting from certain ephemeral variants (paramorphs) occasionally found in nature, has been able to obtain the present cultigens by the process of selection and breeding. The same holds for the origin of many other cereals.

In 1925 THELLUNG (7) has given an interesting account of the origin of cultigen-qualities in ruderals and assumes that in several cases the ancestors of present cereals were originally weeds in fields of cereals later no longer used. By adaptation to management of fields these ancestors underwent the same process of selection and have gradually gained predominance over the ancient cereals. He found a number of man-adapted characters common to these weeds and has shown a comparable parallel, homologous variation in cultigens.

The fact that in most Floras cultigens have often nomenclaturally been assigned to a higher taxonomic rank than they deserve for scientific reasons, is in first instance due to the fact that they appear and remain constantly different from the wild plants.

There are, however, no more scientific reasons to accept specific delimitation between *Oryza sativa* and *Oryza fatua*, than between *Beta maritima* and *Beta vulgaris*, or *Setaria italica* and *Setaria viridis*, or to give specific rank to *Saccharum officinarum*. These are only a few examples out of a multitude which could be advanced.

Domestication of plants has advanced to different degree in different plants: there is a distinct gradation. According to DANSER *Fagopyrum esculentum* differs only slightly from its wild ancestor, and if it could be adapted by breeding to suit

(1) It should be emphasized that it is not my intention to attempt to dispute the advantages of a simple nomenclature for practical aims; refined distinctions of very small taxa are eminent in many fields of practical research where great issues are at stake for human civilization. My principal aim here is to show that for scientific taxonomy the possession of a binomial does not warrant these small taxa to belong to the specific level. It is also for this reason that recently the general term *cultivar* has been proposed to designate such infra-specific cultigens classified on one artificial level within a species. A comparable term *cultispec* might eventually be adopted to serve to indicate cultigens supposed worthy to be classified on the specific level.

efficient harvesting methods it might well become a first class food plant on poor soils in the northern hemisphere. Unfortunately its genome contains, as far as known, no suitable potentialities for this adaptation.

On the other end of the domestication series there are taxa which, obviously through hybridization, selection, and domestication, have become so widely different from their ancestors, or of which no ancestors can any longer be designated, that they deserve specific¹ or even generic rank, as for example *Zea mays*. THELLUNG (7) mentions several examples of this category, e.g. *Ricinus communis*, *Euphorbia lathyris*, *Capsicum annuum*, *Cucurbita moschata*, *Carthamus tinctorius*, *Sechium edule*.²

If they were left to themselves the truly domesticated plants would for the greater part disappear or in some cases through regression return to the ancestral form.

The study of cultigens illustrates again for the taxonomist the unexpectedly wide range of potential variability in certain species which becomes manifest through selection, breeding, isolation, and hybridization. And it should be understood that the development of cultigens, which is directed only to usefulness for man, realizes only a portion of the potential variability reserve. Trends of breeding towards many other goals can be imagined. HUDSON (4) gave a tolerable review of genetics in its application to plant breeding (1937) and its implications on the specificity in cultivated plants.

In nature the same range of variability or polymorphism is potentially present, and doubtless many deviating paramorphs occur occasionally by random chance. It is not a far-fetched idea that such occasional deviations have in many cases been picked and preserved by man and have served as the original stock of domesticated plants. In nature their appearance is ephemeral as they generally lack the robust vitality and aggressive characters necessary in the struggle for existence by environmental natural selection.

For the plant breeder and geneticist it is of essential value to have a profound knowledge of the wild population of the species and of its nearest congeners in the native country. Many cultigens

have been bred from relatively few individuals or imports and these contain of course only a part of the potentialities of the native panmictic population. Once bred for a long time a cultigen naturally tends to decrease in potential polymorphism and attains a certain stage in which further breeding does not give satisfactory results. Breeders will then turn to the reserve of potentialities in the native country and try to add to the potentialities of the cultigen.

It is worthy to mention the opinion of VAVILOV (1, p. 7, 550), one of the prominent plant breeders and geneticists of this century, on the significance of the study of cultivated plants with regard to specific delimitation. He says:—"that the intensive studies of cultivated plants and their relatives sometimes made it necessary to postulate large, Linnean species. We are coming to the concept of a Linnean species as a definite, discrete, dynamic system differentiated into geographical and ecological types and comprising sometimes an enormous number of varieties".

My former colleague at Bogor, Dr H. J. TOXOPEUS, a geneticist and plant breeder, who studied various tropical plants (*Citrus*, *Derris*, *clove*, *kapok*, etc.) which I alluded to in my concise essay on the origin of Malaysian cultigens (5) came to a similar conclusion in accepting a Linnean specific concept. Both Indian-Malaysian kapok and Zanzibar clove have never been (re-)collected from wild populations in their native country, though at least the latter was certainly a post-Columbian introduction; of both the native ancestor is known with certainty. Cultigens share this rapid adaptation of a new facies outside the native country with ruderals (see p. cxcix b).

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7. HYBRIDIZATION, MISCIBILITY, AND SPECIFIC DELIMITATION

Taxonomy, experimental taxonomy, and genetics form together the discipline of taxonomy in the wider sense. In this sequence taxonomy proper is mainly concerned with the morphological grouping

(1) A few examples of the Malaysian tropics are plants used in betel chewing: *Areca catechu*, *Piper betle*, & *Uncaria gambir*, further *Artocarpus heterophyllus* (nangka); there are scores of others.

(2) Whether *Ginkgo biloba* and *Tamarindus indica* are domesticated to some degree is unknown; of the latter monsoon tree the native country is uncertain; it grows 'wild' from Africa to Timor.

of organisms starting with the largest groups towards the specific level, while genetics starts at the other end of the line from the smallest hereditary units to the specific level. The field where they touch, is examined through experimental taxonomy by both geneticists and taxonomists, blending taxonomy and genetics into one whole.

Though genetics and experimental taxonomy have in the past mostly been excluded from proper taxonomy, the occurrence of specific hybrids has of old attracted the vivid interest of taxonomic botanists, and has particularly been the focus of attention of those who included field knowledge in their research. The presence or absence of sterile

intermediate hybrids has provided, and still provides, for most a valued additional argument in judging the status of two different taxa.

In this century a considerable interest has been given to the weight which should be given to hybridization and miscibility of taxa, as this has an essential bearing on the concept of specific delimitation, *although it should be admitted at once that it is out of question that all taxa can ever be experimentally examined and tested in this respect*. It is even impossible that all individuals of one specific population can be investigated experimentally. A comparatively minute number of selected individual specimens is assumed to be representative and the results with these are regarded as decisive for the entire population.

Research has mostly been performed on herbaceous plants; besides the total number of taxa is so large and research should be so elaborate to gain trustworthy results that it is an illusion to expect more from this field of work than samplings. These practical limitations entail the danger of coming to conclusions which have not been verified with the bulk of the material and may contain only part of the truth.

I do not intend to give here a complete survey of all opinions, often conflicting, advanced on this subject which is, next to infraspecific variability, the most important facet of this essay. I have merely referred to certain important references representative of certain lines of research or reasoning.

Already in the 18th century taxonomists attached great importance to the breeding true of taxa and this shy beginning of experimental taxonomy has always been considered an argument if it could be examined. JOHN RAY, for example, mentioned of a variety of the broom—a prostrate, hairy form adapted to wind-swept coastal areas—an ecotype now known as *Cytisus scoparius* LINK *var. prostratus*, that it was *distincta propagatio ex semine*, a statement obviously derived from breeding it.

The knowledge about hybrids was gradually accumulating in the 18th century and KÖLREUTER (1733–1806) who made, between 1759 and 1790, a fantastic number of experiments, was convinced that a test to the delimitation of species could be established by means of hybridization experiments. According to the copious compilation by VON GAERTNER (1) he wrote (1777):—“*Plantarum copula hybrida productarum animaliumve summa foecunditas varietates, sterilitas vel summa vel foecunditas infra utriusque parentis modum ac proportionem plus minusve manca ac suppressa speciei indicium est omnium longe certissimum*”.

Yet KÖLREUTER mentions fertile hybrids between taxa (e.g. of *Dianthus*) which he accepted as good species. Reversely he found that sometimes hybrids between obviously closely related species could be obtained only with great difficulty or not at all:—“*Copulatio mutua infructuosa, quo in plantis veram specierum imaginem agnoscere possis, lapis lydius est*”.

The problems of the breeding true and the

occurrence of hybrids were considered by LINNAEUS as shown by his experiments on tracing affinity.

In England KNIGHT (2) founded his opinion on extensive experimenting, reaching the general conclusions that fertile hybrids are a sign for conspecificity, that this goes mostly parallel with morphological resemblance, and further that if a specimen is sterile it is likely to be of hybrid origin.

Horticulture and agriculture strongly stimulated work on hybridization and in the first decades of the 19th century a number of Royal Academies offered a prize for essays on the subject.

For many years BERNHARDI (3) tested plants on their capacity for breeding true.

The year 1837 was remarkable in that MARTENS made the first public news about fern hybrids at Brussels; in England HERBERT published his large study on amaryllidaceous plants (4), and VON GAERTNER was awarded the gold medal and prize of the Holland Society for Sciences, Haarlem, for the best essay (5) in the prize question issued 1830 at the instigation of REINWARDT (renewed 1834, belated 1836, fulfilled 1837, with 150 hybrid specimens) titled (transl.):—“What learns experience on the breeding of new species and varieties by means of artificial pollination and what useful and ornamental plants can be made and propagated in this way?” The Netherlands version of VON GAERTNER’s book has been followed in 1849 by a very much extended German edition (1) with a full digest of current literature on the subject.

HERBERT was of the opinion that if two plants are able to form a fertile hybrid they should be regarded as conspecific. And that if two species of two different genera are able to hybridize these genera should be regarded as congeneric (*Azalea*, *Rhodora*, *Rhododendron*). All *Cactaceae* should then be regarded as belonging to one genus.

HERBERT’s opinion was shared by many other authorities, e.g. HENSCHEL, TREVIRANUS, VAN MONS, and A. BRAUN.

In a general sense VON GAERTNER also agrees, but he urges caution in paying too much attention only to morphological resemblance. He points to genera, which are generally accepted to be natural (*Primula*, *Erica*, *Linum*, *Gladiolus*) in which hybridization is limited to groups of species (sections), though he reversely points to the fact that the failure to hybridize is not proof that it is impossible. Admitting that in the majority of cases possibility for hybridization is bound up with morphological resemblance, he still maintains that the essential thing is not the external morphological conformity but the internal ‘sexual affinity’. He approaches herewith HERBERT’s criterion of ‘constitutional affinity’. He points to two species of *Pentstemon* which are very much alike but intersterile (“though DE CANDOLLE accepted them as good species, viz *P. gentianoides* and *P. coccineus* = *hartwegi*”), whereas HERBERT contrarily found that in the genus *Calceolaria* species which are very unlike freely hybridize.

I have enjoyed reading these old, now mostly

forgotten books on experimental taxonomy, digesting the ideas they contained, and admiring the immense number of experiments made and their often ingenious methodology.

DARWIN naturally devoted a chapter to 'hybridism' in connection with the species concept in his 'Origin of Species' (36). He relied for a great deal on the experiments by KÖLREUTER, VON GAERTNER, and HERBERT, and is distinctly hesitant in their interpretation. This is not surprising as their experiments were performed with both species and infraspecific taxa and results are therefore often contradictory. On the one hand DARWIN recognizes the sterility barrier specially in the native species as the agent keeping them separate, (*l.c.* p. 267-268, 279, 283, 298, 300) and finds "the degree of fertility proportional to their systematic affinity, with varieties interfertile". On the other hand he says in the same chapter (*l.c.* p. 270, 277-278, 281, 299) "that the degree of fertility . . . graduates from zero to perfect fertility", and even finds "specific sterility to be accidental" (*l.c.* p. 283) and that "neither sterility nor fertility affords a clear distinction between species and varieties" (*l.c.* p. 270). This fitted his theory of the divergence of character by natural selection, "the preservation and accumulation of beneficial variations" (*l.c.* p. 133); . . . "thus the small differences distinguishing varieties of the same species steadily tend to increase till they come to equal the greater differences between species of the same genus, or even of distinct genera" (*l.c.* p. 145). DARWIN's magnificent synthetic attempt suffered from the lack of genetic knowledge in his time and a lack of appreciation of the essential difference of the concepts hybridization and miscibility. His aim was obviously to explain the origin of species in the sense of linneonts, starting with the paramorphs, via the cline and the subspecies to the species. The general conception nowadays is the reverse: it is the linneont, consisting of an endless number of paramorphs, which gives the cline, the variety, or the subspecies.

The attempt towards a 'New Systematics' in which hybridization, fertile or sterile, was maintained as one of the crucial points in judging specific delimitation, was continued by FOCKE. His *magnum opus* 'Die Pflanzenmischlinge' (1881) must have been a great stimulant towards experimental work and is still a mine of information.

In an earlier work (6) he defined the species—which he called 'Formenkreis'—by the following 6 criteria the majority of which belongs to experimental taxonomy (*transl.*):

- (1) Complete mutual morphological similarity of all individuals of a 'Formenkreis'.
- (2) Presence of constant, distinct, preferably morphological characters by which the individuals of the 'Formenkreis' differ from all other organisms (absence of transitions).
- (3) Constancy of these characters in successive generations.
- (4) Inconstancy of differences inside the 'Formenkreis' between the individuals of the 'Formenkreis' in successive generations.

- (5) Fertile hybridization possibility of all individual specimens within the 'Formenkreis'.
- (6) Decreased fertility of eventual progeny derived from crossings between individuals of different 'Formenkreisen'.

He performed experiments with the three well-known *Primulas* which LINNAEUS accepted as varieties of one species. He found (7) that *P. elatior* and *P. acaulis* gave perfectly fertile hybrids but that *P. officinalis* gave partial sterility; for that reason he considered the first two more closely allied *inter se* than to the latter. He advanced the idea of the levelling ("nivellierende") effect of free crossings in a panmictic population and was convinced of the reality of the specific concept in nature. FOCKE then tried to trace the origin of new species and varieties in nature and came unfortunately to study the genus *Rubus* (8).

The unmistakable fact that hybrids between commonly accepted good species are sterile or nearly so has always been a good argument adding to circumstantial evidence for the judgement of specific delimitation.

And this sterility barrier must necessarily have an essential function in nature to keep species apart and distinguishable as separate taxa where they occur together.

From this can be derived the generality that if the areas of two allied populations overlap and occur in the same biotope (that is if the populations have the opportunity to hybridize and mix) they must prove their 'individuality'.

The absence of miscibility capacity is obviously exactly the reason of the taxonomic demarcation between these populations. With HERBERT and VON GAERTNER we can say that obviously the physiological morphological structure of the genome of the populations is so different that they must show a sexual repulsion, resulting in non-miscibility.

DANSER has shown (9) that, notwithstanding LOTSY's varying opinion on and terminology of the species concept, he has introduced (10) the useful concept of the *syngameon* which approximately covers the Linnean species in a genetical sense. This has served as a start for DANSER's later considerations.

It cannot be denied that the *syngameon* (=panmictic population) is an attractive concept as background for specific delimitation. Within such a population with free fertile hybridization possibilities the characters of the successive generations of individuals behave as in a melting pot, showing a constant change in various combinations (paramorphs) in which it will be impossible for the taxonomist to find any constant demarcations of the rank acceptable for the specific level. There is a compact body of paramorphs representing transitions between extremes and this melting pot is kept intact by segregation and recombination.

If allied but morphologically distinct or definable populations occur together without possibility for fertile interbreeding, however, they keep distinct

as two unmixable separate substances in one melting pot.

If a taxonomist finds this situation in nature, he will be inclined to accept the morphological differences as valid.

If the taxa replace each other geographically, however, he feels or should feel less at ease with the weight of distinctive characters. The replacement is a warning signal. He will then have to consider whether the replacement is possibly due to the racial segregation of a polymorphous species, in which races remain distinct only so long as they remain isolated.

With replacing taxa the taxonomist should be specially on the alert and be extremely critical regarding the appreciation of differential characters. If there is opportunity he should make large-scale and prolonged hybridization experiments in order to observe whether the taxa are miscible or not.

In order to test specific delimitation DANSER has made a great number of experiments with *Rumex*, *Polygonum*, *Stachytarpheta*, and other genera. Besides these practical experiments he has given attention to the theoretical concepts involved with the delicate situation round the sterility barrier. He has abandoned LOTSY's *syngameon* and replaced this by a genetical hierarchy of three other more sharply defined concepts, for all individuals between which genetic contact is possible, *making a sharp distinction in degree of genetical contact between possibility to hybridize and miscibility* (11), which again is of such basic importance for possibilities of gene exchange between taxa. These concepts are:

(1) *The convivium, defined as each partial population which is, by geographical causes or otherwise, genetically isolated from the other part(s) of the population, with which it is, however, completely miscible* (12, p. 403, 417).

The isolation can be geographical, but it can be caused by difference in flowering season (seasonal dimorphism), by absence of the adequate pollinators, etc. Size and 'weight' of convivia may be very different, as all races, subspecies, ecotypes, human cultivations, adventives, and ruderals, are included in it. Convivia originate in nearly all panmictic populations during the primary diffusion as a consequence of selection by the environment. Centrifugal marginal differentiation consists in the origin of convivia. Shockwise dispersal of diaspores is followed by the formation of convivia as the colonies are formed from a limited number of diaspores which carry only part of the potential polymorphism of the population; furthermore the colonies will through local inbreeding and selection tend to homogenize towards a certain local facies (ecotype). The forming of small colonies will of course happen throughout the area of the population, but in places where the new colony is in contact with neighbouring colonies and aggregates, in the centre of the area, the tendency towards gaining a local facies will be rendered impossible through continuous segregation and recombination.

(2) *The commiscuum (miscibility community) is the total number of individuals which are connected genetically through miscibility* (11, p. 28, and 12, p. 401). Under miscibility is understood fertile hybridization possibility, while in the progeny, either by crossing or selfing, through segregation and recombination, finally a *complete series of transitions* is formed (panmictic population). It is not necessary that all individuals are *directly* connected by miscibility. One commiscuum will comprise generally a great number of convivia, but may consist of one convivium.

The concept of miscibility indicates the existence of other commiscua. Hybrids between individuals of different commiscua are generally sterile and if not so their progeny will *per definitionem* not produce a complete series of transitions. DANSER observed that these nearly sterile inter-commiscual hybrids can in some cases be crossed back with one of the parents and then the progeny gradually gained in fertility but returned to the parent and merged with the parental population. Here appears the local and occasional possibility for transferring characters from one commiscuum to another allied one (gene flow or introgression). The chances for it are not frequent and DANSER assumes this gene flow to be rare.

The commiscuum concept is the essential part of LOTSY's *syngameon*, but it is narrower and better defined.

DANSER mentions as examples of commiscua: *man, horse, donkey, zebra, each of the species of Rumex § Lapathum* (as far as examined by him), *the 2 species of Antirrhinum § Antirrhinastrum, four species of Stachytarpheta* (11).

(3) *The comparium (hybridization community) comprises all individuals which are connected by the possibility of hybridization* (11, p. 29 and 12, p. 400). *The hybrids must be viable, but it is irrelevant whether they are capable of producing sexual organs. All commiscua between which a (sterile) hybrid is found belong to one comparium. Comparia are not miscible.*

DANSER quotes as examples: *man* (who is both a commiscuum and a comparium), the genus *Equus*, *Antirrhinum* section *Antirrhinastrum*, *Rumex* section *Lapathum* (as far as he studied it), the genus *Stachytarpheta* (as far as he studied it).

Though the comparium is by no means a less significant concept in itself, it does not seem to have an immediate bearing on specific delimitation and properly falls outside the scope of this essay.

DANSER maintains that in an attempt towards a correlation of the taxa distinguished by taxonomists with these three concepts, *the convivia seem to coincide roughly with infraspecific categories* (subspecies, variety, ecotype, form, etc.), that the *commiscua coincide obviously with the large, good, Linnean species* of botanists, and that the *comparia* have the least well-defined correlation with taxonomic categories, sometimes coinciding with genera, sometimes with sections, but in certain families going far beyond the limit of accepted genera, for

example in the *Gramineae*, *Orchidaceae*, *Rutaceae*, etc., in which a considerable number of indisputable intergeneric hybrids have come to knowledge.¹

This conclusion agrees with the generally acknowledged less clear concept of generic delimitation as compared with specific delimitation.

DANSER recommends identifying delimitation of Linnean species with that of commiscua. This is in all probability the best approximation of the Linnean species ever proposed and as we will see this opinion is shared by various prominent geneticists.

Danser's three concepts are specially attractive to the taxonomist as they give content to taxonomic categories by a genetical basis consisting of factors actually at work in nature in the formation of ecotypes, races, and panmictic populations; they account for the results of isolation and as far as the convivium and commiscuum are concerned (less clearly so for the comparium) they cover to a remarkably high degree the specific and infraspecific taxonomic categories based on morphological comparison. Moreover, they furnish opportunity for the employment of experimental testing methods.

As has been remarked above the idea of genetical background of taxonomic categories is nothing entirely new. JOHN RAY, the eminent precursor of LINNAEUS already approached the syngameon concept in his criteria for specific delimitation (*cf.* DANSER, 9, p. 216-219) and as has been shown in the brief historic introduction to this chapter the idea of the importance of the sterility barrier has always lingered in the minds of taxonomists as the principal agency responsible for demarcations.

DANSER'S concepts are indisputable genetical realities in nature, irrespective whether applied by taxonomists or not. They have not been formed lightly as desk-work but have been the result of prolonged field-work, experimental research, and herbarium studies.

After two decades of experience with testing their applicability to taxonomy, DANSER concluded that the essence of the large species or lineoents is the panmictic community or commiscuum. *If it were possible to test all species experimentally, and identify them as much as possible with commiscua, this would have the great advantage that we could delimit species according to one single principle, a true biological agency acting in nature.*

From his posthumously edited 'Theory of Systematics' (13) I quote in his own words:—"Although the biological meaning of the large species lies in the commiscua, yet the largest species, including the well-known and scrupulously defined ones, are far from being all identical with commiscua. In order to obtain this identity many boundaries of species have to be altered."

"The criterion of the fertility or sterility of hybrids in order to decide whether two taxa must

(1) Besides it is certain that in these families there are distinct taxonomical difficulties with the generic concept which has led to rather fine splitting which in turn is not very satisfactory as now generic limits appear sometimes to be artificial.

be referred to one or two species could never become a general principle because the data so obtained too often contradict each other."

"It is doubtful whether all systematists are prepared to give up the principle of sharp definition for that of miscibility. We can only say that it would be desirable for systematists to overlook this objection on behalf of the theoretical significance of the conception of species."

"A more serious objection is that so many living beings escape the criterion of miscibility. For example those taxa which have lost their capacity of sexual reproduction. They undoubtedly belong to some species but not to some commiscuum (many *Fungi*, apomicts, etc.)."

"We can overcome this difficulty in a large measure by first of all defining the species according to the old principles and subsequently checking them as far as possible."

I am aware that there is, in the matter of definitions and principles, a tendency to see things too much sharply divided in black and white. Criticism is raised at once if the theory or concepts cannot immediately explain or take care of all facts known.

There is no reason for discouragement then in accepting theories or concepts, specially if they are simple and logic. It will be remembered that the MENDELJEV natural system of elementary chemical elements seemed defeated or at least had to allow exceptions in the actual molecular weights which did not show the simple numbers to be expected. Those who stuck to the theory, trusting the principle of uniformitarianism in nature, appeared after all right, those who kept arguing about the discrepancy were formal and short-sighted, hence wrong.

If we avoid for the moment the question of practical application, a discussion is open towards the intrinsic significance of the sterility barrier. Though it is admitted that this barrier will appear in general in combination with a set of morphological characters which can reasonably be considered as denoting specific rank, DANSER himself has, as mentioned briefly before, pointed attention to a few categories which withdraw from the requirements of the commiscuum.

Obligate self-pollinators do not participate in the miscibility-crossing tissue of the commiscuum. It is here irrelevant, that they are possibly few in number.

The same holds for *apomicts* which DANSER assumed to belong to a species but not to a commiscuum (see chapter 8).

The fact that in populations there will always be individual specimens which cannot be crossed with any random individual specimen is of only slight value to the commiscual concept, as it is sufficient if they can be crossed with some other specimen, so that the commiscuum is then still a closed hybridization net, potentially permitting segregation and recombination throughout its tissue. To this category belong the extremes of a series of races within an articulated population between which genetic contact may be possible only via the linking interjacent races.

Another, more serious problem is the application of the definition of a commiscuum in practice, as the pertinent testing of the existence of a closed hybridization net, the proof of the definition, is in practice impossible, either pro or con. It is completely illusory to have all specimens of a commiscuum under experimental control.

It follows that it is impossible to design a complete system according to the commiscuum concept in order to compare it with the currently accepted specific delimitation and have an estimate of the advantages it may offer.

Reversely I am fully convinced that through these three clear concepts DANSER has furnished a critical content to a hitherto badly defined field of theoretical taxonomy, and feel that his concepts are giving sense, emphasis, and direction to professional taxonomy against a clear background.

Although DANSER's concepts have for reasons unknown not come into the general use they deserve, I am perfectly convinced that they approach the real biological situation of specific delimitation in nature as closely as can be expected in this matter.

And DANSER is here in the good company of several prominent geneticists. The specific delimitation for example in *Antirrhinum* § *Antirrhinastrum*, which was a head-ache to taxonomists and about which there was not the slightest unanimity of opinion, has been satisfactorily explained by BAUR (14) and, unless it would appear that BAUR's experiments are wrong, no intelligent taxonomist can accept the twenty odd described taxa as good species.

On the basis of his extensive experimental work WINGE (15) equally holds the delimitation of species on the level of linneonts and identical with commiscua. WINGE rightly remarks that not all species of LINNAEUS are linneonts; in his pioneer works LINNAEUS accepted for convenience *Pisum sativum* and *P. arvense* as specifically different. Further he subordinated *Melandrium rubrum* and *M. album* as varieties to one species although they are kept specifically different in most Floras up to the recent time.¹ WINGE adds that cytogeneticists contrarily consider them as one complex for reason of their complete miscibility; he says: (*l.c.* 233-234:—"individuals are specifically different when they are unable to hybridize or when by crossing, they produce more or less sterile progeny").

"Even disregarding the exceptions to this definition, taxonomists would scarcely adopt the specific definition of the geneticist. The latter meets difficulties in plants with different chromosome number (e.g. *Narcissus*, *Bulbocodium*, *Potentilla argentea*), the hybrids of which are always slightly sterile, though nobody doubts their specific identity. The species of the taxonomists are practical".

LAMPRECHT (33) considers that a strictly genetic definition can be given to the species, developing the view of WINGE (15) that all species are

characterized by genes which cannot be transferred in interspecific crosses or which behave as lethals. He defines a species as "a unit including all biotypes which differ from all others by at least one common interspecific gene".

MÜNTZING (16) says "that it is typical of species hybrids that they are more or less sterile", and that "by crossing experiments it is possible to clear up the barriers of incompatibility and sterility occurring in nature". He concludes that "if the cross succeeds without difficulty, and the hybrids obtained are quite fertile, the parents must be closely related and must be included in the same species".

TIMOFFEEFF-RESSOVSKI (17, p. 91-92) gave as his opinion:—"I believe that we have no reason to doubt the reality of species as natural taxonomic units; but, on the other hand, I doubt whether it is possible to give a general and simple definition of the species, applicable in all the larger groups of organisms. The most general but at the same time cautious definition of a species may perhaps be given as follows:—"a species is a group of individuals that are morphologically and physiologically similar (although comprising a number of groups of the lowest taxonomic category), which has reached an almost complete biological isolation from similar neighbouring groups of individuals inhabiting the same or adjacent territories. Under biological isolation we understand the impossibility or non-occurrence of normal hybridization under natural conditions. There are practical differences in that hardly distinguishable species of *Drosophila* do not interbreed, and on the other hand good species which hybridize".

DOBZHANSKY (18) similarly tries to define specific delimitation by the borderline of fertile interbreeding.

DARLINGTON (17, p. 139) is equally prepared to apply the results of genetical analysis for estimating the significance of delimitation of species and other taxa. He says:—"It is true that the basis of distinction between some species in *Malva* (KRISTOFFERSEN), *Galium*, *Nicotiana*, and *Tulipa*, and even of the subdivision of the genus *Primula* (to mention only a few examples) has proved to be a single-gene difference. When the facts of inheritance are known, such distinction cannot be upheld on ground of either principle or convenience".

HERIBERT NILSSON in his large study on the genus *Salix* (19) shares the opinion of these authors. He describes the species as "ein Genotypen-Kreis (eine Kombinationssphäre), die als Population annähernd konstant ist, weil sie bei Kreuzung mit anderen Spezies inkompatibel oder avital reagiert". Chromosome number or ganiture itself is not sufficient for that claim.

CLAUSEN (31) accepted a "genetic basis for natural systematic units which makes it possible to give a fairly objective classification based upon experiments rather than upon speculation. Species are separated by genetic barriers of various degree and effect; sometimes incompatability is not absolute and there may be a limited amount of exchange of genes".

(1) Actually LÖVE (32) considers *Melandrium rubrum* and *M. album* as subspecies of *M. dioicum* (L.). COSS. & GERM.

CLAUSEN, KECK, and HIESEY (34) share this view and are prepared to accept only those "internal barriers that are of a genetic-physiologic nature" as species-separating; those, in other words, which prevent the production of offspring even after artificial cross-pollination, or lead to the sterility of any progeny produced. Where such barriers do not exist between two forms, they must be considered as belonging to the same species, whatever the taxonomist may have done with them.

As quoted before (p. cciii b), VAVILOV joins the opinion of wide delimitation of species as a consequence of genetic investigations.

Among prominent geneticists there seems then to be a rather unanimous approval to accept the sterility barrier, and the miscibility criterion in particular, as an essential for specific delimitation; the scanning of the sterility barrier between taxa is still a very important additional argument in the experimental testing of specific delimitation. And the flux of literature on this subject, specially in England, Sweden, and the U.S.A., proves that this line of research is still in full swing.

Further there is, consequently, among these geneticists, a common approval of the acceptance of wide, Linnean, specific delimitation.

The reception of the results of genetics and experimental taxonomy by systematists has generally been sympathetic, but there is a distinct reservation in the willingness towards its application. This is partly due to the fact that only few systematists are trained in or are eyewitness of experimental taxonomy or have kept up with the pertinent literature and feel capable of judgement.

Excuses for this inertia are various, in addition to the fact that every change of method or principles will meet inertia towards its adoption in any branch of science, unless the methodology or principle is so clear and the advantage of its application so evident that there is no obstacle against the immediate universal adoption.

Though every taxonomist who is not a pure phytophagist of the old-style has welcomed these attempts towards a new systematics, it is equally clear that, first, the experiments refer only to a very limited percentage of cases with regard to the entire plant kingdom and, second, that as has been remarked before, it will, in practice, be impossible to extend experimental taxonomy to the whole plant kingdom, hence to apply experimental taxonomy universally to its classification. This is specially significant for the wealth of tropical plants, the arboreal ones in particular. These must be classified by the normal herbarium methods of α -taxonomy.

Systematists who have performed extensive experimental work agree in giving weight to the sterility barrier in their definitions of specific delimitation.

TURRILL who is in this respect in a favourable position gives four criteria for specific delimitation (17, p. 17):—

- (1) They have a geographical area.
- (2) They are self-perpetuating as taxa.

(3) They are morphologically distinguishable from other related groups.

(4) They normally do not interbreed with related groups, in most cases showing partial or total infertility on crossing with them (though neither the lack of crossing or of fertility is universal).

TURRILL adds that *subspecies* resemble species except in point 4 as they show miscibility.

Recently TURRILL wrote (20):—that botanists cannot go so far as zoologists in emphasizing sterility as a character separating species and use the fertility-sterility criterion to this extent. "There are often sterility barriers between plant species . . . but so often plants belonging to what must, for many other purposes, be distinguished as distinct species can cross together to produce fertile offspring". He mentions *Salix polygena* composed of 8 species of *Salix*, and further *Orchidaceae* in which even generic hybrids produce fertile offspring. "To place all such into one species would make a classification of a very special kind that could serve only a very limited range of purposes".

It is to be regretted that TURRILL has obviously paid less attention than desirable to DANSER's concepts in which a sharp distinction is made between hybridization, possibility and miscibility. The references to *Salix polygena* and the *Orchidaceae* have no bearing on the miscibility criterion. From other studies it appears that TURRILL and MARSDEN-JONES are reluctant to accept this principle. This reluctance is most curious as it emerges naturally from the classical experimental work made by these authors on *Silene cucubalus* and *S. maritima* which T. says (17, p. 64) "behave as good species over most of their range but cross freely to produce intermediate populations in some smallish areas". Moreover, "all diagnostic characters may break down in some, mostly a few, specimens, and this apart from hybridization".

Geum urbanum and *G. rivale* cross freely and produce hybrid swarms according to MARSDEN-JONES (1930). There is no sterility barrier between these species. These hybrid swarms occur not or only very locally in nature, but more frequent in cultivation. It has also been found in Central Europe that the two *Geums* are distinctly miscible and that in some regions pure colonies are rare.

From these well-studied examples it appears that in both cases the pairs of 'species' owe their distinctness to the spatio-temporal ecology and are a consequence of the sieving effect of ecological conditions offered to them in nature. The hybrid swarms occur in places of intermediate ecology. If nature offered only the intermediate ecological facies in their area of distribution there would be no sharp (racial) segregation and the European *Geum*¹ population would be one (variable) whole.

It is clear that whereas the intermediate localities are scarce the bulk of the recent population can easily be distinguished.

- (1) It is probable that in *Geum* the miscibility goes far beyond the two mentioned 'species' (30).

With these examples in *Silene* and *Geum* at hand, in which fortunately the situation both in the field and experimentally is exposed to such an admirable degree, it is a mystery to me why TURRILL shrinks from drawing the consequence of admitting racial differentiation in *Geum* and *Silene*. I can only guess at his arguments for this hesitancy from his own words that drawing such consequences would evolve into a classification "that could serve only a very limited range of purposes".

I disagree entirely with this conclusion and maintain that both scientific and practical taxonomy is served better by accepting these couples of species in *Geum* and *Silene* as each representing one Linnean species.

Scientifically because taxonomy is essentially a hierarchical science and hierarchy is lost if Linnean species and subspecies (*cq.* races) are arranged on one level.

Practically the advantage of distinguishing *G. urbanum* spp. *urbanum* next to spp. *rivale* and having *Silene cucubalus* spp. *cucubalus* and spp. *maritima* is that this situation gives more exact information about these taxa than the situation in which they are all treated as species. In the subspecific rank it would be at once clear that there is in both cases geographical replacement and genetical miscibility. The latter criterion is particularly stressed by TURRILL himself as the essential difference of subspecies from species.

The difference, for the morphologist, between the cited cases of *Silene* and *Geum* lies in the fact that, whereas the differential characters in the *Silenes* are rather slight and feeble and mostly concern habit, those between *Geum urbanum* and *G. rivale* are very distinct and showy.

This touches the delicate problem of evaluation of characters to which ALLAN (21) has pointed in remarking:—"that observations on wild and artificial hybrids both show that many quite unexpected pairs do cross or can be crossed". He gave no information on the crucial point whether they are miscible or not.

I refer here also to the 'species' of *Antirrhinum* which show taxonomically quite acceptable distinctions. And I refer to the old observations on the genus *Calceolaria* where it is said that hybridizing or miscibility exists between morphologically quite distinct forms. At least in *Antirrhinum* it has been definitely shown that the number of Mendelian characters involved is not particularly large.

There may seem, as Mr KERN said to me, a morphological controversy in accepting one polymorphous species in *Geum* but keeping the morphologically much more 'uniform' species of *Epilobium* between which there is mostly a strict sterility barrier and no question of hybrid swarms and miscibility.

It has to be accepted that there is no way to give absolute 'measures' of the taxonomical weight for characters. But it is indisputable that if 'hybrid swarms' (*i.e.* a heterozygotic panmictic population of paramorphs) and ecologically intermediate localities were quantitatively the commoner in the

Geum area of distribution and the pure *G. urbanum* and *G. rivale* the less common, it is certain that the judgement would be different from the now prevailing acceptance of two different species. And this same reasoning holds for the two *Silenes*.

Many other cases have been repeatedly referred to in literature for which the rigid application of the sterility barrier concept would seem to lead to unsatisfactory results or at least to a delimitation rather considerably deviating from the one employed now. The genus *Salix* has at least in Europe, such a bad reputation; it seems that the delimitation of certain species which in one country is rather distinct, is blotted out in another. HERIBERT NILSSON recorded (19) on hybridization, but as far as I can see there are no sufficient experimental data to conclude on the extent of miscibility. The occurrence of hybrids, even fertile, or partly so, is not conclusive, particularly not in anthropogenous country. Judging from the herbarium studies a similar exceptional behaviour was obviously found by DANSER in the Iorantheaceous genus *Scurrula*. Here too, the abundance in anthropogenous country may be responsible for a seemingly chaotic state of affairs with regard to specific delimitation.

It is likely that even long isolation of disjunct areas, which doubtless represent parts of former continuous populations, does not reduce inter-fertility to intersterility.

The genus *Campsis* (*Bign.*) hitherto considered to consist of two distinct species *viz* *C. grandiflora* LOISEL. in China and *C. radicans* SEEM. in N. America have appeared to be interfertile, producing a heterogenous progeny. The geographical distribution of this couple of species points to a disjunction of the genus as a consequence of the Pleistocene Ice Age and it makes the impression that palaeoclimatical factors have broken up the formerly continuous population into two (later eventually further homogenized) races. Breeding experiments are insufficient to show whether these 'twins' are really miscible.

A similar case is that in *Platanus*: HENRY & FLOOD have shown (22) that the London plane (*P. x acerifolia*) is a hybrid of *P. orientalis* (Persia to Balkan) and *P. occidentalis* (belonging to a group of *c.* 6 closely related species in the southern U.S.A. to Mexico). The separation of *P. orientalis* from the New World populations is at least one million years old, but there is still no incompatibility and apparently no mutations have taken place. The hybrid is said to be fairly fertile. Here again there are no sufficient data available to decide on miscibility.

According to Mr STEARN a similar interfertility is found in strongly disjunct species of *Epimedium* (Europe-Japan).

These few examples are sufficient proof of the importance and permanence of interspecific, genetical behaviour after long isolation.

On the one hand it shows that isolation-itself is

obviously not a factor bringing about essential changes in genetical behaviour. On the other hand it shows how extremely careful a taxonomist should be in handling disjunct taxa: races now

apart for a long time have in many cases apparently made part of former continuous areas. A taxonomist should therefore avoid entering geographical arguments for delimiting species.

CHROMOSOME RACES

The examples given hitherto have in general shown the existence of a not unsatisfactory agreement between specific delimitation and the commiscual concept.

A strict application of the miscibility concept may in a number of other cases, however, force the taxonomist towards an undesirable situation of distinguishing taxa which show hardly any or only minute and few morphological differences.

TIMOFFEEFF-RESSOVSKI has pointed to certain almost identical races of *Drosophila* which are said to be isolated genetically.

Detail research in plants has in the last decades brought to light the existence of an increasingly large number of species in which the chromosome garniture or number of chromosomes is different in different (mostly polyploid) races. In a case like that of the couple *Nasturtium officinale* and *N. microphyllum* the morphological characters bound up with cytogenetical differences are still acceptable though distinctly small and few. The hybrid is sterile and the species have been observed to occur together in nature in the same biotope.

More dubious are such cases as for example in *Acorus calamus* in which three replacing chromosome races are observed between which the morphological differences are minute, according to WULFF (23). Polyplootypes have been described in *Chelidonium*, *Adoxa moschatellina*, *Cardamine pratensis*, &c.

In *Rumex acetosella* four of such chromosome races are said to occur by LÖVE (24) each of which would have a geographical area of its own. In *Valeriana officinalis* a dozen of such races have been recorded. According to KALINSKA (25) it is polymorphous in various parts of Europe with tetraploid, hexaploid, and octoploid forms, each of which shows again subforms. As far as ascertained they are intersterile.

In her recent brilliant work Miss MANTON (26) has mentioned similar cases from several species belonging to various families, in addition of those in Pteridophytes. In *Polypodium vulgare* there seem to be at least three chromosome races in Europe and two in America, but the total number will be certainly higher. Besides it appears that in ferns there occur a considerable number of 'irregularities' in the chromosomal behaviour, with many hybrids and apogamous forms. The chromosome races can, mostly, be recognized morphologically by the expert.

In their work on Ceylon Pteridophytes MANTON & SLEDGE (29, p. 174) state:—"The fact that so many instances of multiple chromosomal types were detected among very small random samples suggests that many more of the so-called species of tropical floras are in fact species-complexes than had previously been thought".

In many cases the chromosome races show a distinct geographical distribution and frequently geographical replacement, comparable to that of races or subspecies.

Though a final scientific proof by experimental methods to show the validity of the genetical isolation can of course never be given, as it falls simply for practical reasons outside any human scheme to take instead of a few samplings all specimens of a population into observation—and nothing can or should be taken for granted if we want to have a strict proof—the circumstantial evidence so far attained points towards the existence within Linnean species of minor chromosome variants which, with a rigid application of the miscibility concept, should be regarded as commiscua, though the morphological differences between them appear to be so slight that they have mostly either been neglected or evaluated on the infraspecific level, except by purely analytic florists as JORDAN C.S.

It is fairly certain that with still larger population studies the number of such forms will appear to have colossal dimensions.

If it should be agreed to 'accept these forms as 'species' on one line with normal Linneons it is clear that a reasonable taxonomy will not be possible and a concise classification of the plant kingdom according to Linnean standards will never be attained. Specific delimitation in plants will then soon reach the deplorably chaotic state to which entomology has degenerated.

The facts brought to light about the micro-systematic population structure of Linnean species is of course extremely interesting.

But it is clear that classical taxonomy has to shield its field and concepts against the menace from the side of chromosome fanatics, who appear eager to try selling a Trojan horse to alpha taxonomy.¹

If it is granted that chromosome races are sexually propagating, morphologically distinguishable entities which are genetically isolated they fit the requirements of specific delimitation of the taxonomist who accepts commiscua to be equiva-

(1) It is urgent that geneticists and cytotaxonomists have a thorough pre-knowledge and experience in taxonomic methodology and practice. Data on hybridization and cytogenetics should be accompanied with depositing of herbarium specimens for future reference and verification. Names of species and varieties used must have been controlled taxonomically or by taxonomists. For genetical experiments it is not sufficient to accept blindly the name of a sample distributed by a random botanical garden; these are generally wrong or obsolete.

lent to species and the genetical isolation as a keystone of the concept of specific delimitation.

It would place the taxonomist entirely at the mercy of cytogenetics which means again that the taxonomist would loose control over his own standard and would not any longer be able to verify the variation of the characters, *i.e.* the chromosomes, conclusive for distinction. Furthermore it would render impossible the taxonomist's methodology to test as much material as possible, as this would be necessarily out of question in the case of chromosome races.

It should be emphasized that the importance of the chromosome number must not be overrated too much and not be accepted as a character of essentially other and more important value than the external morphological characters.

It is clear that two things are involved here: *chromosome number* and *chromosome quality* (biochemical composition of the genome). The latter is of course the essential thing, but very little is known about it as yet. The former is apparently far less important. In the genus *Carex*, taxonomically a very coherent and natural genus, numbers of chromosomes vary to a high degree with irregular figures, but in other genera or sections the number is found to be very constant. From this follows that, as with all taxonomic characters, no absolute value can be given to it.¹ In the case of the chromosome races the quality of the chromosomes is obviously very similar whatever their differences in shape and number, as it stands beyond any doubt that the quality manifests itself in the morphological characters or, in other words, the degree of difference between characters reflects and is proportional to the degree of difference between the genome qualities.

There is an exceedingly great morphological similarity between chromosome races within Linnean species and from this it follows that the mere number of chromosomes cannot be a feature indicating an essentially other value than external taxonomical characters. Its value will have to be evaluated (by experience) from group to group. The extreme similarity of the chromosome races indicates that only one or a very few genes can be concerned. Among these is obviously one causing incompatibility.

If we can rely on the data provided by the cytogeneticists the chromosome races are genetically isolated, they withdraw from the rule that incompatibility is always connected with a set of other distinct, morphological differential characters.

The conclusion is that it appears impossible to identify chromosome races with commiscua worthy to be recognized as Linnean species.

Much more should be known about their exact

(1) Miss MANTON was so much impressed with the aneuploid chromosomal behaviour in *Isoetes* and *Lycopodium* that she assumed (26, p. 286) "that a species in, for example *Lycopodium*, is really the equivalent of a genus among ferns". This is, in my opinion, an overstatement.

behaviour before a final conclusion can be drawn and as ALLAN says (17, p. 515) the taxonomist should be extremely cautious in accepting simply data from cytogeneticists without reserve. HERIBERT NILSSON is of opinion that chromosome number or garniture is, in itself, not sufficient for specific distinction. FAGERLIND (27) concluded that chromosome races are of infraspecific value and this view will be shared by most qualified taxonomists. Miss MANTON has not given sufficient systematic attention to this question; in her book (26, p. 8) she mentions the chromosome races in *Biscutella* as subspecies, but those of the ferns (*Dryopteris filix-mas* *l.c.* p. 45 and *Polypodium vulgare* *l.c.* p. 141) are accepted as species.

NANNFELDT assumes (28) that "as soon as chromosomal races (polyploids) are morphologically distinct and thus recognizable to the taxonomist, they had better be regarded as species even if the morphological characters are small".

As far as I know DANSER had, before his premature death, not given a written opinion in this matter, but I am told that in his review of Löve's paper on *Rumex acetosella* he strongly rejected the idea of accepting the polyploids as Linnean species. TURRILL is also not prepared to accept them simply as species which I infer from his generalization "that the taxonomist has to consider any known facts regarding sterility or fertility, but he has to evaluate them with regard to all other facts of structure and behaviour known for the organisms he is sorting into taxonomic groups or taxa".

In a very detailed experimental and field study on Central European *Galium* EHRENDORFER (35) found Linnean species to be 'Serien' = 'Formenkreisen' of dozens of microspecies ('Kleinarten'), each of which consisting of generally incompatible diploids, tetraploids, octoploids, and multiploids. He showed the possibility of introgressive hybridization (potential gene exchange) between octoploids from different lineages between which there is exclusively on this chromosome level, obviously only a partial sterility barrier; such transitions occurred generally in disturbed bio-coenoses (*cf.* p. cc). This study shows how complex in chromosome detail Linnean populations may be, but also the intrinsic value of the Linnean species.

The following conclusions can be drawn:

If taxa have been sufficiently investigated experimentally, the results should be fully evaluated by taxonomists.

A sharp distinction should be made between hybridization possibility and miscibility; under the latter concept is understood the possibility, either in nature or in cultivation, of obtaining by hybridization, fertile specimens showing an almost complete number of various combinations of the differential characters between the taxa, blending them into one whole without demarcations.

Hybridization itself is, naturally, a manifestation of affinity but falls short of precision for judging delimitation of Linnean species.

In the majority of cases it is manifest that the commiscual concept, putting miscibility of taxa as a criterion for conspecificity, hence for specific delimitation, is a reasonable approximation of explaining their individuality in nature.

If taxa are distinguishable by a set of clear characters, preferably both vegetative and generative, and hybrids prove to be sterile or substerile and not capable of producing a polymorphous progeny with a more or less complete series of intermediates blending the taxa, the immiscibility is a substantial argument for accepting them as belonging to one *linneont*.

In many cases taxa are replacing each other by ecological preference, their segregation through genetical isolation being due to and going parallel with demarcations of the environmental conditions.

If such taxa prove to be miscible, either in nature or by experiments, it is clear that they should be accepted as replacing races and consequently be subordinated as subspecies to one *linneont*. The argument is that if the environmental conditions were intermediate, suiting both races, there would exist only one panmictic population without racial segregation.

In nature local hybrid swarms may give an indication of the miscibility of the taxa; if the taxa are disjunct, the miscibility can only be proved by experimental taxonomical methods.

Long racial isolation does obviously not diminish the possibility of fertile hybridization between such partial populations.

If taxa are distinguishable by a few minute characters which are considered of minor value in the genus but are intersterile or nearly so through a polyploid or otherwise aberrant chromosome structure, they should be considered of infraspecific rank and be classed as subspecies (genetic polyplotypes or chromosome races).

Though they represent commiscua from the genetical standpoint, they should taxonomically not be arranged on the specific level along with Linnean species as the factor responsible for the incompatibility is not bound with a sufficiently clear and large set of morphological characters.

Their genetic incompatibility prohibits unfortunately to accept a strict application of the principle to equalize Linnean species with commiscua, though this would be—and still is theoretically—the best way of introducing a biological agency responsible for specific demarcation in nature.

From the genetical standpoint the distinction of large, polymorphous species is preferable.

For professional taxonomy the advantage of distinguishing Linnean species is serving the aims of taxonomy by holding to its hierarchical structure;

hierarchy is lost if species and races are nomenclaturally ranked on the same level.

For practical taxonomy the advantage of Linnean species with racial taxa subordinated is the information embodied in the nomenclature of such *linneonts*.

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8. APOMICTS AND SPECIFIC DELIMITATION

In some genera, which have in the past appeared to offer serious obstacles to specific delimitation, it has been found that specimens are asexually reproduced and are *apomicts* (though occasionally some flowers may contain functioning sexual organs).

Individuals of an apomict—being a clone—show naturally a marked constancy, even in minor characters; this constancy is even more clearly expressed than in the more or less homozygotous 'races' (pure lines) of cultigens.

Individuals of an apomict disperse in a similar

way as any other sexually propagating allied species and will attain (or have attained) a geographical area. In these respects the apomict behaves as a normal taxon.

The apomict differs from a 'population' of a sexually reproducing taxon, however, in the absence of the normal genotypical variability and withdraws from the concept of population in the proper sense, as does any other clone. It is consequently on another footing as compared with the panmictic population and its phenotypic variability should not be misinterpreted as genotypical polymorphism.

Obviously the apomict withdraws, therefore, also from the concepts of species, subspecies and variety in the taxonomical hierarchy.

A description based on a random assembled collection of numerous specimens of one apomict is essentially the description of one specimen as each apomict is, in nature, represented by essentially one specimen only.

The conclusion is that whereas in taxonomy a species and any other infraspecific taxon is characterized by a certain degree of genotypical variation among the specimens referred to the taxon, the apomict withdraws from the concepts of normal taxonomical standards.

An apomict—being essentially one specimen—can, therefore, not be considered the equivalent of a taxon, although imitating it by possessing a set of major or minor 'characters' and by occupying an area of distribution.¹

It has appeared that the origin of apomicts is apparently a result of hybridization of a few species: during the segregation taking place in the F₂-x heterogeneous progeny a smaller or larger number of genetical combinations, each represented by one individual, have become apomictic. These apomictic individuals have multiplied by asexual reproduction and dispersed themselves.

No taxonomist would be prepared to give a taxonomic status to every single individual (paramorph) of a heterogeneous progeny after a crossing within a panmictic population or between two different commiscua as the characters are ephemeral and will disappear by segregation and recombination. In an apomictic progeny, however, the characters of each individual specimen will be preserved and perpetuated by asexual reproduction if the combination proves to be viable.

In Europe the genus *Taraxacum* is reputedly apomictic. In British *Taraxacum*, TURRILL says (1, p. 59) "apomixis is proved in all tested 'species' and cytological examination suggests hybridization previous to the adoption of apomixis and (possibly) mutation since".

DAHLSTEDT and others have described about 500 'species' of *Taraxacum* from Scandinavia, and the total number in *Taraxacum* may be estimated to be possibly about 1000. This number is of course far less than could (theoretically) be expected from

a cross, but it should be taken into consideration that only a small part of them has been actually formed and that a certain number of combinations will not be viable or appear to be less well adapted to competition in nature.

In *Taraxacum* not all apomicts are completely asexual as has been shown by SØRENSEN & GUDJÓNSSON (2) and among the progeny new apomicts may occasionally appear. HERIBERT NILSSON found (3) on 5 sq.m not less than 20 apomicts together. As they reproduce asexually they are genetically perfectly isolated (agamospermy). The majority is triploid.

HERIBERT NILSSON *l.c.* says "dass es für die Benennung der *Taraxacums* unrichtig wäre, ja widersinnig, eine Bezeichnung die auf 'Art' oder 'Spezies' hinzielt, zu benutzen. Spezies bedeutet ja in der Systematik eine Population, einen Variationskreis, eine Kombinationsphäre, oft unzähliger Varianten. Ein 'Mikrospezies' von *Taraxacum* ist ein invariabler Typus, ganz starr, eine Kombination innerhalb einer grösseren Population". H.N. is inclined to evaluate the few subgenera distinguished by DAHLSTEDT in *Taraxacum* as equivalent with what could have the same taxonomic value as species in sexually reproduced plants.

H.N. proposes to call them 'microtypes' as the smallest individual variants in the apomictic 'population' of the species *Taraxacum officinale*.

It is clear that the apomicts belong to an essentially different category of taxa as compared with sexually reproducing populations. TURESSON called them 'agamospecies'. This does not solve the problem of their evaluation.

In the genus *Hieracium* there seem to be more species involved than in *Taraxacum* and the structure is here still more complicated by the partial apomixis of many 'species', and the degree of the morphological differences in this genus is giving the illusion of an intricate but regular, hierarchic pattern of variation. An estimate in *Hieracium* for the equivalent of a species in sexually reproducing plants will be extremely difficult. In the current system of the genus sexually reproducing species, apomicts, and partial apomicts, are treated together. It would be advisable to bring some clarity in the specific delimitation by studying principally the non-apomictic species and fix their affinities and to classify the apomicts separately, a procedure similar to that followed for the imperfect fungi. Satisfactory taxonomical results will not be attained without experimental and karyological research.

Nomenclaturally apomicts should be earmarked as such, similarly as has been done for hybrids by the × sign and for cultigens by the indication 'cultivar'. Instead of being preceded by 'var.' or 'subsp.' the epithet of apomicts might be preceded by 'apom.', a neutral term leaving open the taxonomical rank and evaluation.

The study of apomicts was extremely intriguing to taxonomists before it was known why the normal taxonomical concepts failed to be reasonably applicable to genera as *Taraxacum* and *Hieracium*.

(1) It is not clear why DU RIETZ (7) in one paper classified apomicts as clones (*l.c.* p. 338) and further on (*l.c.* p. 362) as (asexual) species.

Now we understand the factors through which these difficulties have been caused, it must be considered whether similar difficulties of specific delimitation in other genera may be due to the same phenomenon.

Apomicts have been found in many other genera, e.g. in *Alchemilla*, *Poa*, *Ranunculus*, *Rosa*, *Rubus*, etc., some which are notorious for their playing havoc with normal taxonomic standards of classification.

Botanists engaged with taxonomical studies of tropical plants rarely have facilities of doing experimental work and rely on dried materials. Consequently they are unable to observe whether taxa are apomictic.

As it is not a far-fetched idea that apomixis will also occur in tropical plants, it is essential that observations and experiments should be made *in situ* (with karyological control) in a number of tropical genera which are notorious for their colossal, solid blocks of species, many of which show an undesirably low degree of good morphological characteristics. In this connection I have in mind genera as for example *Eugenia* (incl. *Syzygium*), *Peperomia*, *Ophiorrhiza*, *Psychotria*, *Dysoxylum*, *Aglala*, *Ardisia*, and various others. Such research should involve as many species as possible, as in these genera sexually and asexually reproducing species may occur side by side. There are some provisional data pointing towards a possible occurrence of apomictic species in *Eugenia* and *Citrus* (notably some cultigens).

In the list compiled by STEBBINS (8) tropical plants are particularly poorly represented. There is, possibly, a wide field for research here which should be encouraged to explore.

According to Dr FAGERLIND (*in litt.*) there are no definite signs of abundant apomixis in tropical plants. He found it in *Wikstroemia* (4), *Balanophora globosa* (5), and in *Elatostema* spp. (6), but in several species of *Peperomia*, *Gouldia*, *Psychotria*, *Bidens*, *Metrosideros*, *Ophiorrhiza*, and *Randia* there was no trace of agamospermy.

The fact that apomicts must be classified in a special category along with, but separate from, sexually reproducing populations, does naturally not imply that they would have no value for purposes of inventory, for plant ecology and for plant geography, although the possibility of polytopic origin in partial apomicts deprives them of some of their value in the latter discipline.

It has been most unfortunate that some prominent botanists have devoted a considerable time of their life to the riddle of the apomicts in which they expected to find a thread leading to the problem of speciation.

Botanists adhering to a moderate to large species concept have and will have of course less difficulties in classifying these groups with the normal taxonomical standards than those who

cling to a very fine splitting. For the latter there will be no end to describing new species as the number of paramorphs which may be 'coagulated' into 'constant species' can be of course exceedingly large.

Conclusion:—All specimens of one apomict and all other clones together agree genetically and taxonomically with some one individual specimen (paramorph) of a sexually propagating population. Genetically they do not represent a true population; it is merely an imitation of it.

Though an apomict perpetuates, by asexual reproduction, its characters on successive generations, and attains an area of distribution by normal methods of dispersal, it is clear that apomicts belong, taxonomically, to an essentially different category as compared with taxa consisting of sexually propagating populations.

Taxa are *per definitionem* provided with a higher or lesser degree of variability (polymorphism); by the absence of this characteristic apomicts withdraw from normal taxonomy. Their description and distinction is essentially comparable to that of one specimen.

In a genus containing both normal taxa and apomicts, the latter should be arranged in a specially appended category.

Apomicts should, in the genus to which they belong, be earmarked by the indication 'apom.' preceding their epithet.

It has appeared that cytological examinations suggest for the origin of apomicts hybridization previous to the adoption of apomixis by segregates in the F_2 -x generations.

It is probable that apomixis occurs in the native flora of the tropics and it is of manifest importance that cytological research be performed *in situ*, preferably in some large genera which are likely to contain apomictic species.

The study of apomicts is of course not discouraged; they have a pertinent value for inventories, for plant ecology and plant geography, but the solving of the riddle of the apomicts has made it abundantly clear that they have hardly any value for the study of the taxonomical structure of genera and their specific differentiation. As their number may run in one genus into the hundreds or even thousands they will give an entirely wrong picture of the size and differentiation of a genus.

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9. PRACTICAL TAXONOMY

In small countries or parts of these, where the taxonomist has abundant material available, and has ample opportunity to check data in the field, specific delimitation generally offers few difficulties, genera with apomicts excepted.

This is, in part, due to the fact that in proportion to a smaller area, species and other taxa seem to be better demarcated. The local floristic botanist actually observes the populations only in their local facies. Consequently he should realize that his studies will lead only to a local interpretation or evaluation of the polymorphism of entire populations. This is sometimes insufficiently acknowledged by local students who are accustomed to a one-sided notion of each species.

These two factors make it extremely difficult to perform useful taxonomical work of permanent value by the local botanist in the tropics where in general large, regional Floras are not available to give them a solid footing. Local Floras in the tropics often create more difficulties than they solve.

The local taxonomist and floristic botanist possesses naturally the most detailed knowledge of the local flora, but he will be inclined to assign a higher rank to taxa than the monographer of the group who is in a position to examine taxa from wider distance and place these in better proportion with those closest akin. This enables the latter to make a better evaluation of the variability patterns of species.

In other respects the monographer is at disadvantage as compared with the local botanist as, first, he can not hope to be ever in command of the detail knowledge of the latter and second, it will, even for averagely large groups, be practically almost impossible to have personal access to all material from official and private herbaria. With the colossal increase of accumulated material in the past century the sheets needed for exhaustive monographic works become so numerous, that money for dispatch, space for storing, and specially time for going through endless series of specimens is often not available.

In order to gain a harmonious development of his work, the monographer will have to keep to the golden rule to work step by step "from the large to the small".

Firstly, he will have to start in acquiring knowledge about the 'structure' of the family to which the genus at hand belongs. This is often unclear in tropical floras, in contrast to temperate floras on the northern hemisphere where the lack of unanimity in placing genera is a rare exception.

Secondly, he will have to give close attention to the definition of the genus at hand and its demarcation from other genera. This looks very simple but in practice it appears that authors not infrequently include family characters in generic diagnoses and have obviously no sharp notion of the generic characters.

After the revision of the species is finished,

generic characters must be rechecked with all species, and eventually emended.

Thirdly, the monographer will have to consider which characters have served or may serve for subdividing the genus into subgenera, sections, etc. This preliminary distinction of infrageneric taxa will have to be verified during the preliminary sorting of the species.

Fourthly, the most important task is the sorting and distinction of the species. At this stage of the work, the revisor should be familiar (by preliminary study of the literature and of the specimens) with the standard characters which have been used in keys or found useful in descriptions in the past, giving him an idea of the 'variation pattern' of the genus and the relative value assigned to characters and their complexes. This pre-knowledge should be handled with care and criticism; the greatest merit is to improve the evaluation standard and to find additional new characters useful for specific distinction.

In tropical taxonomy, where species have in many cases been described in a haphazard way and where phytographers have often shown a great haste in publishing accounts of local collections without the background of revisional work, the standard for subdivisions of genera and specially the standard for specific delimitation must often be built up from the bottom.

The search for such a standard for larger tropical genera is often not easy, as material is frequently deficient and new desirable data are generally difficult to obtain at short notice. And these new data are often of vital interest, as monographers or revisors not seldom detect new valuable characters for specific or infrageneric distinction which have been barely noticed in earlier descriptions.¹

Besides the necessity of attaining a reasonably acceptable correlation under these unfavourable or rather primitive conditions, there is the necessity of designing a picture of the degree of specific variability. The success of this attempt to extract a useful frame from inadequate data will depend on the standing of prior works, but to no minor degree on the experience of the revisor, his power of observation and deduction, his personal gift for

(1) Dr BACKER found for example that the detailed structure of stigma and stamens is of essential importance for the infrageneric subdivision of the unrevised genus *Fagraea*. Of many species material is lost and of others difficult to obtain, and the characters wanted have mostly been omitted from the descriptions.

The structure of stigma and stamens is of course not an irrelevant 'detail'; structure never is.

In this essay 'detail' has mostly been understood in the sense of meaning slight differences in sizes or numbers, not shape and structure. *Varietates levissimae non curat Botanicus* (LINNAEUS, Phil. Bot. 310).

recognizing hierarchic levels, and a sense for making use of biological, ecological and plant-geographical evidence for checking the morphological data. All monographers and revisors, specially in tropical floras, are forced to judge the inadequate, randomly collected material in their hands by a subtle inter- and extrapolation in the evaluation of the observed and expected variability or polymorphism in order to attain a specific delimitation which will hold for the future.

Those taxonomists who are strongly orientated to the analytical aspect are naturally very much impressed by details and easily come under the spell of 'characters' of each single specimen. This hyperperfection brings along the danger of their not seeing the wood for the trees and they will have great difficulty in reaching a semi-permanent synthesis. The overestimation of detail, due to painfully thorough analysis not followed by synthesis, does not yield a useful result as no allowance is made for expected variability of future specimens. And only such an allowance, if wisely entered in the synthesis, can render 'hardness' and permanency to revisional work.

It seems at first sight unwarranted and undesirable to assign a greater degree of variability to species than can be observed *de facto*. But in the majority of cases in tropical floras the number of specimens at hand is a mere fraction, or even less, of the total number of specimens in existence. And the general (logical) experience is that increase of specimens brings along increase of variability, hence of the necessity of wider specific delimitation.

Recently J. Lewis, in a paper on African *Cassipourea* (1), has pointed out the undesirability of classifying plants merely on the characters of a few random collected specimens. He has also well explained how in such a case circumstantial evidence can be gained for making a conclusion.

From keys it can often be inferred that the responsible author has met considerable difficulty in framing the differences between the contrasted species and has, in absence of finding good structural differences, apparently been reluctant to accept them as conspecific, by taking refuge in *sizes*. Generally these figures prove later to be of fictitious value and merely the consequence of the accidental individual properties of the specimens the author had in hand. Experience has corroborated the generality that differences in size, unless extraordinarily clear and wide, are exceedingly untrustworthy if not accompanied by structural differences. This is specially true for measurements derived from vegetative organs which often show a surprising degree of plasticity.

Those who take in despair to mere measurements or qualities which are likely to be individual variations, often do not seem to realize that they enforce on themselves the responsibility for the reliability of these futile 'characters'.

And this militates against the golden rule of good phytophagy reading: *Do not commit yourself*.

Sometimes they excuse their inability to overcome their (emotional) reluctance to make a firm

synthesis by declaring their work to be necessarily of a 'provisional' nature through absence of ample series of good specimens. I can only strongly warn against such practice: it seems to be preferable that such provisional work, by which the crucial questions are not solved and nothing is gained, should remain in manuscript until the desired material is available.

Such 'provisional' work has namely proved to bring disastrous confusion, specially in monographs of large genera, where overestimation of details of individual specimens has led to a host of new species names based on single collections. And it is specially these single collections which are so difficult to estimate; they should be given extra care for the clearest distinction by structural characters.

The great responsibility of monographers appears exceedingly important as later authors are naturally always influenced by the work of their predecessors and will generally be inclined to 'follow' a monographer's work. One stands *a priori* sympathetic with efforts of monographic character though one should never trust them blankly at first sight. Their value will become evident only after having practised with them.

Only insiders can understand the great importance of useful monographs with a balanced, well-defined concept of specific delimitation. Once such a satisfactory monograph or revision has been made, its value is recognized by future workers and kept as a basic frame. Later work with the same genus will then remain orderly and its hard text will prevent hurried work and rash description of novelties.

In contrast, a monograph or revision with a hesitant or provisional character, which is obviously premature, creates or facilitates a phytophagic progeny of a similar hesitant or provisional kind. The lack of a well balanced and seriously considered standard for specific delimitation—generally too narrow, sometimes degenerated into specimen description—easily induces later none too critical authors with ambitions or immediate need to name specimens to follow the example and fall into step with the monographer, which results in adding to the confusion rather than to solve something. Critical authors will of course refrain from naming specimens in such maltreated genera.

The announced lack of backbone in the ticklish field of specific delimitation is unfortunately a character of the majority of the monographs published in the 'Pflanzenreich' during the last fifty years, with a few laudable exceptions. This lamentable situation is caused partly by the great haste in which the earlier volumes have been produced; partly it is caused by the fact that the authors for the same reason restricted their material to that represented at Berlin. But the *main reason* is that the authors, among whom there were a surprising number of non-professional taxonomists, have obviously not realized the responsibility of such important tasks.

It is true that the composition of world mono-

graphs may assume alarming dimensions, if authors aim at completeness. A monograph of a medium-sized family will require a life-work under present conditions as practically all taxonomists can perform such work only in addition to official and routine work. And there is a tendency among qualified taxonomists not to undertake such tasks, which entail borrowing large amounts of material and necessitate the examination and ticketing of an immense number of sheets to attain precision for both delimitation of taxa and geographical distribution. This strife for exhaustive work and completeness in minute details is certainly a disheartening prospect. The size of such top-heavy monographs could be certainly very much reduced if lengthy accounts of distributional data, irrelevant references in the synonymy, and collecting numbers were omitted. If monographers have ticketed the specimens in many herbaria it appears superfluous to have them again recorded in print, and, if so desired, a very condensed form will suffice. Such concise monographs would gain in surveyability, would be less expensive to print, would cost less time to write up, but still contain the vital information required.

In a classic essay BENTHAM (2), whose monographic attempts have never been surpassed in size or thoroughness, has at the end of his life, in his meticulously elegant way, indicated the lines along which monographic work should be performed. From this essay which should be studied, and studied again, by every taxonomist aiming at taxonomic work, I quote the following passages:—

"That the main object of systematic botany is not the finding out the name of a plant, but the determining its relations and affinities, the making us thoroughly acquainted with its resemblances and differences, with those properties which it possessed in common with others or which were peculiar to itself, whether these properties consisted in outward form, inner structure, physical constitution, or practicable applicability to use, all of which had to be taken into account in the formation of orders, genera, and their subdivisions".

"The grade of plant-race to which the specific name and diagnosis should be attached, would be the species in the Linnean sense, which, though not susceptible of a strict definition, is pretty generally understood amongst botanists, whether they may designate it as a true species, a Linnean, or a compound species".

"As the number of species increased, greater extension was habitually given to both diagnosis and description, till they became unwieldy for use, without some short indication of the most striking points to be attended to. This has been done in two ways, either by prefixing to the group of species described a tabular clavis or a short conspectus of the contrasted characters to which attention is specially called, or by italicizing them in the long diagnosis. The former course entails often the useless repetition of the same characters three times over, in the clavis, in the diagnosis, and in the description; the latter, seeing that the italicized

words are usually adjectives, often occasions confusion and loss of time in searching for the substantives to which they belong".

"In all we want a short indication of the most prominent contrasted characters for approximate or preliminary determination, prefixed to the detailed description for subsequent verification".

"The diagnoses to be useful should be short. We cannot now restrict them to the twelve-word law of Linnaeus, but a twelve-line ablative diagnosis is an absolute nuisance, except for full descriptions needed for new taxa".

"It should always be borne in mind by the monographer that the great test of the quality of a descriptive work lies in short descriptions, diagnosis, and conspectus or clavis. Any tyro with a little practice can draw up long descriptions of *specimens*, fairly detailing every organ; but the selecting the characters necessary to give a good idea of a *species* in a short description requires a thorough knowledge of the subject and a methodical mind".

"Still more difficult is it to prepare a good clavis. After half a century of experience in using as well as in making these keys, I find that I have failed in some of those on which I had spent the greatest pain; and in some floras I have met with tabular keys which are in many respects rather impediments than aids to the determination of plants. At the same time a successful clavis or contrasted conspectus is an excellent test of the quality of a method—of the appropriate grouping into genera, sections, and species".

"The preparation of a revision or monograph is still recognized as the best exercise for the young botanist".

If the points stipulated by BENTHAM have not been sufficiently taken into consideration in a monograph or revision, and its author has lost himself in a swamp of details resulting in very long and elaborate descriptions, it is self-evident that additional material will always deviate in some characters from the description, the chance for this being proportional to the degree in which detail was entered in it.

It is a matter of psychology how such a monograph is received and used.

Hasty successors will then conclude that their specimens represent something new and will follow the tendency and add a new similar description assuming having found a new taxon.

Uncritical, slavish successors will do the same, being impressed by 'thoroughness' of the monograph and assuming it to be final they will follow its detail cadence as a matter of routine.

The disinterested critical taxonomist will try to gain an insight in the principles followed in the monograph; he will study and dissect the keys and descriptions and will try to identify specimens with it. In many cases he will meet difficulties to find his way with the elaborate descriptions. If he is a tolerant person he will lay the monograph aside with a sigh of dissatisfaction and conclude that he either lacks enough intelligence to grasp the author's observations and intentions or that the

group in question contains great difficulty in specific delimitation requiring long study to be familiar with it. He will either send his specimens to the monographer, leaving him the responsibility for naming, or he may decide to leave the specimens unnamed.

The less tolerant person, however, will thoroughly dig himself into the monograph; it will rouse his indignation and his disappointment will induce him to throw the book away in grumbling—again one who has not studied the work of the masters and is therefore not in command of the profession; again a book which creates difficulties instead of solving them.

The aftermath of such pseudo-monographs is either to bring its author into disrepute or the genus or family respectively. Non-systematists derive from such works even a repugnance towards the whole of taxonomy as a branch of science. Specially the latter conclusion is most unfortunate.

Monographs must be useful and monographers should have the responsibility for this clearly in mind. Good monographs are the only means of bringing progress; this holds for the past and holds for the present and future. They must be constructive and solve problems. Taxonomy is not in need of mere compilations without creative spirit; there is no sense in publishing such works.

The question may be raised whether there are no difficult groups of which no sound or satisfactory monograph is possible and where specific delimitation is problematic. I admit that some groups, for example the apogamous ones and cultigens, withdraw from normal taxonomic methodology. And further it is certainly true that species in some genera are more difficult to classify than those of other genera.

But I have come to the definite conclusion, based on a long experience, that the majority of 'difficult groups' are not so intended or created in nature, but that the difficulties have been created by the monographers.

Circumstantial evidence in favour of this thesis is that, if the fault lay in the groups, it would be hard to understand why there should often be such a marked difference in clearness of classification for the same group between one Flora or monograph and another; if the group was difficult, it should be unmanageable in all Floras or monographs.

Further evidence can be drawn from the fact that great taxonomists, for instance J. E. SMITH, ROBERT BROWN, JOSEPH DALTON HOOKER, GEORGE BENTHAM, J. MUELLER-ARG., WEDDELL, DE CANDOLLE, JOHN LINDLEY, OTTO STAFF, LUDWIG DIELS, and others, who have worked in nearly every group of the vegetable kingdom, have all produced 'hard' or useful work standing the test of time; in a considerable number of cases the modern critical taxonomist has finally to return to their concepts.

It is for these reasons of the greatest value to study the works of these Makers of Botany to learn their methodology and considerations. Both BENTHAM (2) and HOOKER (3, 4) have explained

the principles of taxonomic work about a century ago. These essays have lost nothing of their didactic importance and should be read and reread by all modern taxonomists.

The essential character of their work, as I see it, is the conciseness by which the essence is embodied in diagnostic synthesis, besides their fine notion for the evaluation of hierarchic relations among botanical characters used for specific delimitation, their keeping to good, diagnostic, structural characters with omission of unreliable detail and size characters, resulting in a generally rather wide specific delimitation. Through wisdom and common sense, gained by acute critical observation and disinterested experience, they have succeeded in attaining a remarkably final specific delimitation on the basis of few materials.

There is not the slightest indication that they have neglected to observe details of individual specimens, but they have succeeded in extracting from the array of observations the essential ones leaving aside individual variations and those of minor taxonomical value: *l'art de décrire*.

In certain instances they found it necessary to distinguish infraspecific taxa, varieties and forms, notably in cases where minor characters possessed obviously geographical significance. In other instances they added in brief notes critical observations on infraspecific variability and discussed demarcation against allied species.

Generally they did not commit themselves further than the species, however, and refrained from entering on a more detailed analysis of the species population.

This subtle handling of specific delimitation, with refrain from such detail, for the evaluation of which herbarium material is not sufficient, has resulted in exceedingly valuable work which it is still a pleasure to use.

I cannot conceal certain feelings of disappointment, that this elegant and wise methodology has received, in this century, less attention than it deserves in my opinion and has been employed to a lesser degree than it should have been.

Certain taxonomists assume that it is antiquated and that modern taxonomy requires so-called *precision*. Others advance the argument that taxonomists of the former century naturally had to be more concise because of the scarcity of material which forced them to be cautious, but that this is not any longer justified at the present day, now collections have so much increased. Consequently they still record all details in elaborate descriptions, counting and measuring every organ and character, independent of its diagnostic value, leaving it to the user to sort these 'characters' hierarchically.

The analytically inclined taxonomists using this conscientious, exhaustive way have obviously also in view greater *objectivity*. They are insufficiently aware that it is just these details which are so dangerous and devoid of diagnostic value, easily leading to the quicksands of specimen diagnosis. It is namely an illusion that by keeping to mere facts one can avoid the responsibility for judgement of

constancy of the details. By entering them in a description one *a fortiori* accepts this responsibility. Therefore the automatic recording of details where they are redundant defeats the aim envisaged by so-called precision and objectivity and spoils the quintessence of the art of phytography.

Through the slavish recording of details they have a strong tendency for accepting either narrow specific delimitation or to take refuge in an (often) ridiculous number of infraspecific taxa, as otherwise the details cannot be squared with taxonomical distinction. This tendency to splitting may lead—specially in polymorphous species—to population analysis, a discipline which cannot be undertaken successfully on the basis of herbarium specimens.

Those working along these lines realize to a certain extent the inadequacy of avoiding difficulties by swamping them in details of doubtful value, and they shield themselves not infrequently behind the deceptive argument alluded to before that all work performed on (tropical) plants is preliminary and that it should be preferable to start with a narrow specific delimitation which would eventually facilitate reaching broader concepts when more abundant material might show the complete series of intermediates linking the microspecies.

The trend of mind that taxonomic revisions of tropical plants are always of a provisional character has a laming effect on the striving towards critical subfinal work, minimizing such efforts.

I admit that inadequacy of material occurs more often with tropical plants than with temperate. In cases where a satisfactory conclusion cannot be reached on that account, it should either be clearly stated by the author to be so or specimens representing doubtful novelties should preferably be left unnamed and omitted. Inadequacy of material cannot be counterbalanced by carefulness of detailed (specimen) description.

Other strong objections against this pseudo-carefulness are twofold. Firstly, it should be remembered that taxonomists naturally have *a priori* respect for the written word: *verba volant, scripta manent!* There is a distinct inertia to emend, to drop what has been distinguished before, and a reluctance to merge what others found distinct.

Secondly, it is not realized that in geographically differentiated populations the expected complete series of intermediary specimens will rarely be obtained, because geographical races are exclusive by definition. In the case of disjunct races they are even non-existent. The result is that all races, notably the disjunct ones, which have been described with pseudo-carefulness provisionally as species will remain permanently on that level.

It has sometimes been advanced that the distinguishing of large, variable species—and many linneons are of that kind—shows lack of precision. It should be borne in mind that the exact or satisfactory delimitation of such variable species costs a great amount of labour and careful consideration. In contrast diagnoses of narrowly encompassed taxa are very easy to draw and

specimen description is mechanical work merely requiring analytic qualities.

An instructive example of the ridiculous conclusions reached by working along the line of 'precision' is expressed in the revision of the genus *Lepedeza* by SCHINDLER (5). I refer to this example because the author clearly states his reasoning and trend of thought. He gives exceedingly detailed descriptions of a complex of so-called closely allied Siberian-East Asiatic 'species' among which *L. juncea* L. f. is the oldest described. After having found out that *L. juncea* and *L. inshanica* "oft kaum zu unterscheiden sind" he proceeds to give the following remarkable comment (5, p. 606):—"Dieser abweichende Habitus besonders hat mich veranlasst, die beiden Arten zu trennen, wenn ich mir auch bewusst bin, dass die Unterscheide in den Blüten ganz verschwindend und in den Früchten sehr gering sind. Es kommt noch ein Unterschied hinzu, der sich in den Diagnosen kaum zum Ausdruck bringen liess, nämlich, dass in gutentwickelten Exemplaren von *L. juncea* die Trauben meist lang gestielt sind, was bei *L. inshanica* niemals vorkommt, auch nicht in sehr reich entwickelten Exemplaren. Wollte man aber die, wenn auch geringen, Unterschiede in der Frucht vernachlässigen, so könnte man andererseits auch *L. caraganae* nicht aufrechterhalten, da auch hier die Unterschiede nicht viel bedeutender sind. Diese Art nähert sich aber sehr der *L. sericea*, besonders deren nördlicher Form. Die Folge wäre, dass man dann auch *L. sericea* und die mit ihr wieder verwandten *L. variegata* und *L. elegans* einbeziehen müsste und dabei zu ganz unmöglichen Resultate kommen würde. Alle diese Arten gehen fast unmerklich ineinander über, was ja nur natürlich ist, aber derart verschiedene Formen wie die sibirische *L. juncea* und *L. elegans* aus Kashmir zu einer Art zusammenzuziehen, widerspricht völlig dem uns geläufigen Artbegriff".¹ (transl. of italics: All these species are grading imperceptibly, which is natural, but to refer such different forms as the Siberian *L. juncea* and the Cashmerian *L. elegans* to one species is opposed to our concept of specific delimitation).

It is clear that the species mentioned represent grading geographical variations of one widely distributed Asiatic-Malaysian Linnean population. Why this synthesis would lead to an absurd conclusion ("ganz unmögliche Resultate") is a complete mystery. The only absurd conclusion is that of SCHINDLER himself, viz that he is able to describe and to keep species apart which grade imperceptibly and to which he finds it, consequently, impossible to give a key. He had plenty of material at his disposition and it is clearly because of his methodology and reasoning that after a meticulous analysis he did not reach the same synthesis of one geographically differentiated specific population (*L. juncea* L. f.) which had earlier been made by MAXIMOVICZ, BENTHAM, and HEMSLEY, and which I have recently accepted (6).

The result of such methodology or reasoning,

(1) *Italics* mine.

culminating in the conclusion that species merge imperceptibly, militates against the first principle of taxonomy, *viz* to trace demarcations in general and to define species. Further it renders the work useless for others because if the monographer cannot delimitate his species and is unable to give a key, how can others have any hope to do so? Within sight of the harbour the vessel *Lespedeza* ran ashore.

From this example it can be seen that prejudice about specific variability prevents unbiased approach to synthesis and, therefore, clear specific delimitation.

A strong objection to this methodology is of course the comparison of extremes, *in casu* those from Siberia and Cashmere. This is always unfair and unpremissible, specially if, as in the case of *Lespedeza*, the extremes are connected by a complete series of grading races. If comparisons are made, the specimens from Siberia should be compared with those of Mongolia, these in turn with those of North China, these with those of South China, and so on.

If SCHINDLER had not so fully commented on the situation—and in many similar cases their authors do not—those who used this 'monograph' might have come to the conclusion that *Lespedeza* was a difficult genus.

It has been the opinion of BENTHAM that the inability to give a key to the species is itself always a sure warning signal of the absence of a sound synthesis and I believe this is unanimously agreed by all good taxonomists. A key represents the proof of the pudding, because the author of the group is challenged to crystallize the essence of his work in it and to show in which way he has found the hierarchical value of differential characters. If authors want to give longish specific descriptions the diagnostic characters should either be printed in italics or be summarized concisely in a differential diagnosis preceding the description.

Inadequate material.—Besides the cases, similar to that just dissected, in which an author remains stuck in his analysis, though his material and factual information is adequate, there are other cases where authors, who are equally conscientious analytically, are faced with the fact that they have to reach a conclusion on the basis of inadequate material consisting of a few random collections made wide apart.

The intermediates may be absent by lack of exploration or will never be found if the intervening spaces are unsuitable for them (disjunct populations).

Authors working with such problems may, even while not inclined to follow SCHINDLER's example of keeping apart 'species' which are connected by a full series of intermediates, just stick to the facts and be unwilling or unable to evaluate details and give allowance for variability in reaching their conclusion. They feel uncertain on the basis of inadequate facts, and do not like to run ahead. They do not trust their experience in other groups—and this is admittedly a good excuse for be-

ginners—and besides they are not inclined to consider and reconsider, again and again, the value of the characters derived from few random individual specimens. They are too easily satisfied to labour on to the 'hard species' standing the test of time, and they know it. Consequently they regard their work of a preliminary nature. If such persons have to work on groups in which specific delimitation is decidedly difficult, for example genera confined to mountains or floras broken up by archipelagic conditions where very often intermediary forms are non-existent and many species show an intense racial development, authors basing themselves only on the bare, observable facts of discontinuity of characters will never be able to reach a constructive synthesis, though their work will be of a decidedly better quality than that of the SCHINDLER type. Both types of work belong, however, to the category of 'pseudo-monographic' work.

Descriptions from random collections.—Up till now I have restricted myself to considerations concerning the methodology and practical execution of taxonomic work, either revisional or monographic or submonographic for a regional Flora.

In many cases, though, taxonomists are working *floristically*. They receive a random collection which has to be named. In this collection a large number of families and genera is represented. Their principal aim is to give a name to the specimens. The first thing is to arrange them roughly into families and, as far as possible, to sort them into genera. Such a task can only be performed if the botanist is rather thoroughly acquainted with the entire flora of the area concerned.

The specific identification of the specimens is a challenge to an exceedingly profound detailed knowledge. Critical naming can only be performed against a firm background of reliable Floras, monographs and revisions of families and genera and a well-named large herbarium for checking.

These two essential requirements necessary for trustworthy floristic work are absent in Malaysia, where the literary background consists of hardly any trustworthy Flora, of a number of obsolete or unsatisfactory world monographs, a number of uncritical, compilatory enumerations, and a surprisingly small number of useful regional revisions. Critically named collections are not concentrated in one single herbarium.

This situation—which is precisely the reason why the present work is undertaken—means that the majority of families and genera confront the floristic botanist with a scientific vacuum. If he is a wise man he refrains from haphazard naming, whatever press is exerted on him. He can easily defend his attitude by sound scientific arguments. If he is hurried or ambitious, however, he accepts the challenge and throws himself into the abyss never to come out unscathed.

His working method will be the following. After the preliminary sorting, he will entrust some monographers with a certain genus or family but the bulk will remain his own job. For each family he will familiarize himself superficially with what

characters to use and look at. He will try to check descriptions, preferably from those species which are already described from or recorded from the place where the present collection is made. He will—if this is at his disposition—check in his Herbarium with the material available there. But it is clear that in this way only a very inadequate naming will be reached and most specific epithets will be tentative and will have to be preceded on the label with *cf.* (compare). There will be no time for getting thoroughly acquainted with the species of each genus as this would in each case lead to a regional revision, let alone to extend his comparison with species described from adjacent regions. The latter tempting procedure would lead to submonographic work requiring still more time and defeating his aim for rapid naming of the collection within a reasonable time. Any number which can not be found along this superficial way is described as new for science.

The result of this floristic work has manifold disadvantages if it is published. Firstly, it is hardly to be called scientific, for it is haphazard guess work. Secondly, it may lead to grave errors where the preliminary assigning to a family has been wrong, as this may lead easily to creation of new, fictitious genera. Thirdly, precious time of the botanist is lost instead of being spent on creative work. Fourthly, any conclusions of a general nature, evolutionnary or plant-geographical (con-

clusions on endemism %, *etc.*), based on such uncritical enumerations or records are worthless. In short more work is created and the Augean stables are replenished.

In Malaysia this practice has unfortunately been employed for a considerable period by RIDLEY, ELMER, and MERRILL, the latter being decidedly the most critical of the three.¹ If these authors had spent their time on critical revisional work, we would have been much further towards gaining reliable basic knowledge. Even very cautious workers, as HENDERSON for example, who worked along this local way at Singapore, could not avoid duplication. He described for example a *Loranthus pekanensis n.sp.*, which was certainly up till then not collected in Malaya. In the revision of the family by DANSER, however, it appeared already to possess two other names and be a common plant in Borneo (7). In order to find this out HENDERSON would have been faced with a complete revision of the family *Loranthaceae* which was, at that time, in Malaysia in utter disorder, generically and specifically.

The high degree of local endemism credited to the Philippine flora rests solely on the basis of these 'paper' species which may appear from the following table in which the number of species of MERRILL's 'Enumeration' are compared with that after careful revisions for the Flora Malesiana with the novelties not mentioned separately:

Family or genus revised	Number of species in Merrill's En. Philip. 1923-1926			Number of species after revision		
	Non-Endemic	Endemic	%	Non-Endemic	Endemic	%
Alangium (1939)	3	3	50	5	1	17
Amaranthaceae (1949)	21	1	5	20	0	0
Burmanniaceae (1948)	2	1	33	2	1	33
Burseraceae (1956)	3	54	95	11	5	31
Caprifoliaceae (1951)	4	7	63	4	3	43
Carex (1951)	17	10	37	19	10	33
Dichapetalum (1956)	2	11	85	2	2	50
Dillenia (1951)	2	13	87	2	11	85
Loranthaceae (1935)	9	92	91	17	69	80
Pentaphragma (1953)	0	5	100	2	2	50
Pittosporum (1956)	1	13	93	5	1	16
Scaevola (1953)	3	4	57	3	0	0
Triuridaceae (1938)	1	1	50	3	6	66
Umbelliferae (1949)	9	3	25	10	0	0

Similar figures can be obtained from New Guinea and other islands. *No flora of a single island or island group within Malaysia can be studied satisfactorily without having consulted earlier descriptions of species from the surrounding islands or island groups for correlation.*

It is remarkable that only in recent years the importance for this correlation is visualized in the area and that rash description and recording of collections is gradually abandoned. The Flora Malesiana project is a stimulant to canalize the

efforts towards healthy creative work for the benefit of all concerned. It is a most gratifying thought that the present staff of the Singapore Botanic Gardens is finally impressed by this thorough scientific experience and I can only hope that other institutes will follow this blessed

(1) As a matter of fact MERRILL was fully aware of this and told me personally that many of his species had been "optimistically proposed".

collaboration which has been employed for some decades by the Herbarium Bogoriense.

The dealing with new collections must remain a matter of routine merely for permitting specimens to be inserted in the herbarium. The majority of new collections is, after preliminary naming, stored in the respective families and genera where it remains until a revision of a genus or family is undertaken. All time should be spent and efforts concentrated on revisional work. Publication of interesting records must be reduced to fully reliable, exceptional cases studied with extreme caution.

In conclusion it is stressed that the reliability of specific delimitation is a matter proportional to its usefulness.

In practice it has been found that a comparatively wide specific concept, based on a complex of good structural characters, has yielded the most permanent results.

Revisions without a simple, clear key bear testimony of provisional or superficial specific delimitation.

10. CONCLUSION AND THESES

The considerations in this essay on specific delimitation are not intended to represent an appeal for a new botanical crusade. The crusade for establishing taxonomic botany on the firm ground of sound specific delimitation was performed successfully long ago by LINNAEUS, BROWN, BENTHAM and HOOKER, and others.

A long experience both in the field and in the herbarium has convinced me of the prime importance and finality of the principles laid down by the Masters of taxonomic botany.

It appears useful, while botanical research is in rapid progress and new disciplines are constantly added, to verify the doctrines and to explain the principles for specific delimitation followed in this Flora.

It has appeared that genetics, experimental taxonomy, and cytogenetics have added much to a better understanding of the structure of interspecific affinities and have permitted an insight into the infraspecific complexity of many specific populations, their geographical, ecological, and karyological differentiation, interspecific and intraspecific hybridization and sterility barriers, the origin of ruderals, cultigens, and apomictic forms.

It has further appeared unmistakable that at least in allopolyploidy one mechanism has been found for the origin of new Linnean species.

This more detailed knowledge has affirmed the sound basis of classical taxonomy as applied by those who were master of the art of botanical description.

It has appeared that among species—genetically representing populations and consequently offering a certain degree of polymorphism—there may be a distinct tendency to segregate into two or more infraspecific taxa which may, or may not, be bound to ecological preference by survival value. Such a tendency has naturally led to a hierarchic pattern of ecological variability expressed in racial differ-

Where in the tropics or subtropics there is no classical general Flora as a reliable background, local work and floristic recording of random collections is strongly discouraged; it is regarded as a waste of time.

All efforts should be directed towards real taxonomic revisions, regional, and monographical work, in which species and their interrelationships are studied irrespective of political boundaries.

All taxonomists in the tropics should have studied and thoroughly digested the general essays written by BENTHAM and HOOKER, referred to above, which should be a guide to their work.

References:—(1) LEWIS, Taxon 4 (1955) 73–77. —(2) BENTHAM, Recent progress and present state of systematic botany (Rep. Brit. Ass. Adv. Sc. for 1874, 27–54, 1874).—(3) HOOKER f., Introductory essay to the Flora of New Zealand (1853) i–xxxiii. —(4) HOOKER f., Introductory essay (Fl. Ind. 1855, 1–44).—(5) SCHINDLER, Bot. Jahrb. 49 (1913).—(6) VAN STEENIS, Nova Guinea n.s. 6 (1955) 280.—(7) DANSER, Bull. Jard. Bot. Btzg III, 11 (1931) 326–327.

entiation from the subspecific rank down to the smallest entities or ecotypes with proportional degree of morphological distinction.

In other species populations this tendency towards ecological differentiation is low; consequently it bears the aspect of a more or less homogeneous or at most clinal polymorphism not geographically defined.

In still other species there is a low degree of morphological variability and such species retain their characters throughout their area.

In the past the polymorphism of species in Malaysia has in the absence of phyto-geographical correlation led to the description of a considerable number of species being based on races, ecotypes and other infraspecific deviations. Local floristic work has at least in Malaysia added to an almost frightening degree to the distinction of paperspecies.

Consequently the critical, revisional work for the Flora Malesiana must consist of greatly reducing the number of species, while adding a few manifestly new ones found by recent exploration.

The degree of reduction varies from genus to genus, but may occasionally attain considerable dimensions, for example in *Scaevola* § *Enantiophyllum*, of which 14 species had been described and which have been together accepted in this Flora as representing one linneont only.

The keeping to the motto under which this Flora Malesiana is executed, viz the endeavour to determine how few, not how many species, are comprised in it, is intended to attain a really trustworthy, permanent frame work of a general Flora containing keys which work and diagnoses which fit.

In my capacity of general editor I feel responsible for its phyto-geographic style which I have explained in this essay.

Both for readers and collaborators I have condensed the conclusions into the following

RULES AND RECOMMENDATIONS FOR PLANT TAXONOMIC WORK

- (1) It is a universally acknowledged experience that the structure of living matter is discontinuous in various degree and that its classification necessitates a hierarchical system in order to understand its morphological differentiation and systematical arrangement.
- (2) The hierarchy is attained by the proportional degree of appreciation of the value of morphological characters and their complexes. In any hierarchic classification there is, therefore, increasing diversity in ascending and increasing homogeneity in descending.
- (3) Classification is basic to science, and plant taxonomy to every branch of botany, pure and applied.
- (4) Consequently the plant taxonomist should recognize his unique responsibility for botanical knowledge.
- (5) The main object of systematic botany is not the finding out of the name of a plant, but the determining its relations and affinities, the making us thoroughly acquainted with its resemblances and differences, with those properties it possesses in common with others or which are peculiar to itself, whether these properties consist in outward form, inner structure, physical constitution, or practical applicability to use, all of which has to be taken into account in the formation of orders, genera, and their subdivisions (BENTHAM).
- (6) Practical taxonomic work should confine itself to factual observation and not be hybridized with theoretical considerations on origin of species and genera or supposed phylogenetical relations.
Such hypothetical deductions are not discouraged but should be kept clearly separate from the facts observed and not be introduced in their evaluation.
- (7) Experience is of course an important factor facilitating and speeding up the gaining of good results. That taxonomy can (only) be executed on the basis of intuition is a myth, unless this be understood as sublimated experience.
- (8) Work from the general to the detail, keeping in mind the hierarchic order and try to find out what detail is trustworthy for distinction.
- (9) It is important to observe all distinguishable taxa and their demarcation, but it is still more important and often far more difficult to assign them to their proper hierarchic level.
- (10) A sense for synthesis is indispensable for good taxonomy and is at least of equal value to the preceding analysis.
- (11) The mere fact that taxa can be distinguished furnishes itself no argument for their position and rank.
- (12) In broad outline only one acceptable specific delimitation can be attained by good taxonomists in each genus.
- (13) It should be borne in mind that data derived from refined morphological methods (anatomy, palynology, cytogenetics, etc.) cannot be *solely* decisive for judging the status of taxa; preferably all should be taken into account.

(14) Good genera, species, and subspecies are characterized by a set or combination of different (independent) morphological characters (with generally additional ecological features). These taxa are in keys often contrasted by means of one character merely for the purpose of convenience or brevity. If the contrasted genera or taxa of lower rank are really different in *one* character only, the separation will mostly prove to be artificial.

(15) Regardless of nomenclatural appreciation, the Linnean concepts of species and to a slightly less degree that of genus will always remain the most essential levels of botanical classification.

The tendency to devaluate the ranks by one level, *i.e.* the raising of all subspecies to species all species to series, all sections to subgenera, all subgenera to genera, *etc.*, is strongly discouraged. It has no sense if the mutual position of the taxa does not change.

(16) Infraspecific taxa should be well distinguishable by morphological characters though, with subspecies, allowance may be made for intermediary specimens in transitional zones. Marginal and other clinal variation should be explained, but not by name giving.

(17) Experience has shown that a critical revision, monograph, or regional Flora gains in permanent value in proportion to the amount of critical labour spent on it.

(18) The intrinsic quality of monographs and revisions is proportional to their usefulness which is a reasonable check on the personal element in the appreciation of characters. Consequently authors should pay the highest attention to this aspect of their work.

(19) Diagnoses to be useful should be short.

If detailed descriptions are desired they should be preceded by such a diagnosis containing the more prominent characters contrasting the species against its allies.

A successful *clavis* or contrasted *conspectus* is an excellent test of the quality of a method. The preparation of a revision or monograph is still recognized as the best exercise for the young botanist (BENTHAM).

(20) It is advisable to start keys with reliable vegetative characters to facilitate identification of all specimens. As these characters are generally less sharp and stable than those of the sexual organs, they should in case of doubt never supersede the latter, even if this would cause inconvenience when using the key.

(21) In contrasting differential characters it should be avoided to use measurements of organs in case they show a tendency to overlap unless they are preceded by differences in shape and structure which are generally superior.

(22) As a general principle Linnean species of flowering plants cannot be distinguished specifically on the basis of vegetative characters only; there should be additional differential generative (reproductive) characters.

(23) The use of geographical or ecological data to support morphological characters of doubtful value is strongly discouraged.

These data must be reserved as a later check on the attained morphological distinction which should remain the basis of taxonomy.

(24) It should be realized that the importance of the type specimen of a taxon rests on its (nomenclatural) administrative significance as that element to which the name of the taxon is permanently attached. It need not to represent the 'average', 'most typical' or the most 'characteristic' facies of the taxon. Taxonomically it does not possess more value than any other random collection.

(25) In making a revision the primary task is to sort the material into specific (and infraspecific) groups and then to describe these taxa, the last phase being the fixing of the correct name and its synonyms in which the importance of the identity of the type specimens becomes evident.

(26) Tropical species are sometimes regarded as less variable than those from temperate countries by botanists who have never been in the tropics. Consequently details of individual specimens are often overestimated, specially if material is scarce.

This is a fiction: species of tropical plants show on the average no less variability in their sexual organs than those from other countries, sometimes exhibiting a marked degree of flower dimorphism.

In addition they show sometimes a remarkable vegetative variability (partly phenotypic), notably in woody plants and climbers.

(27) It is unphilosophical if taxonomic studies on tropical plants are undertaken with the preoccupied thought that this work is only provisional. This objectionable idea minimizes efforts to attain superior work and stimulates hasty and uncritical, compilatory work.

(28) Without the background of a critical general Flora it is in tropical countries impossible to gain satisfactory permanency of critical knowledge on delimitation of taxa, their area of distribution, variability, and consequently their names and synonyms.

(29) In tropical countries the writing of specialized local Floras is discouraged in absence of a critical, regional Flora which should have priority.

(30) Taxonomists working with tropical plants should as much as possible try to restrict the time spent on floristic botanical work (accurate naming of sheets of random collections) and focus their attention on creative attempts towards revisional or monographic work irrespective of political boundaries. This is the only efficient way towards progress in tropical taxonomy.

(31) Among the taxonomic ranks the Linnean species has appeared the most essential, useful, and objective taxon. Though not susceptible of a strict definition, its status is pretty well understood among botanists and geneticists, whether they may designate it as a true species, a Linnean, or a compound species (BENTHAM).

(32) The thesis of LINNAEUS that the taxonomist should not be much concerned about the slight variations ('*varietates levissimae*') is still a generalization of value to the tropical taxonomist.

(33) A discreet lumping does not mean throwing taxa together from laziness or superficiality but should contrarily be the result of careful consideration and evaluation of details in order to reach a justified hierarchy of relationships.

Taxonomy is not served by catalogues of taxa disregarding this principle. See also § 38.

(34) If material permits, it is of the highest interest to gain a rough insight into the infraspecific pattern of variability, whether it be grading (a cline) or differentiated into geographical or ecological races. See also § 57–61.

(35) A thorough population analysis, however, falls outside the capacity of the herbarium botanist.

(36) A taxonomist should endeavour to determine how *few*, not how *many*, species can be distinguished in his synthesis.

(37) The principle of geographical replacement should, whenever possible, be adopted, thus reducing the number of species while increasing the number of subspecies. Similar principles of ecological or genetic replacement should also be adopted as knowledge increases (HUXLEY).

(38) The variability of species is generally found to increase in proportion to the size of their area. Therefore our knowledge of this variability increases proportionally to the number of specimens available for study and appears always larger than originally assumed.

(39) The variability often shows extremes in the marginal area due to isolation and heaping of recessive characters, often leading to satellite convivia which may deserve subspecific rank.

(40) It follows that it is wise if a greater degree of variability is assigned *ab initio* by not attaching too much value to details which are liable to greater variation than structural characters and which can be expected to have no diagnostic value.

(41) In proportion to the amount of detailed characters entered into a botanical description the responsibility for the constancy of such trivial characters increases with decreasing chance of their permanent value.

Never commit yourself unnecessarily.

(42) The overestimation of infraspecific taxa as species has the unfavourable result that the hierarchic relations, reflecting the affinities within a genus, are misrepresented, militating against the primary aim of classification to have a balanced hierarchy.

(43) The ambition to designate the smallest taxa with a binomial bears testimony of ignorance of both theoretical knowledge and judgement, absence of sense for synthesis, and contempt for the work of our illustrious predecessors.

(44) If a taxonomist finds great difficulty in delimiting species, he should carefully verify his standard, before considering the possibility of irregularities inherent to the group (apomicts, *etc.*) or due to environmental conditions (destroyed areas, *etc.*).

(45) Wherever applied botany should require fine distinctions for its own pursuits, an auxiliary nomenclature should be invented. It is not served by an unsolicited overestimation of taxa in scientific taxonomy.

(46) Allied good species have in general geographical areas which partly overlap, proving their individuality in the area they have in common.

(47) If two taxa, which might by morphological characters deserve the specific rank, are replacing one another geographically or ecologically, the taxonomist should be careful to explain why he accepts them as distinct species or subspecies. See also § 37.

(48) Local-endemic species must always be regarded with caution. They lose their local endemic character as soon as they are found elsewhere and lose also their status of species if they can be correlated as extremes to wider distributed species.

(49) For allied disjunct taxa which, by their morphological characters, could be distinguished as species, experimental taxonomy can provide useful data for the criteria of putative hybridization and miscibility, which may be important for the interpretation of their status.

(50) If it appears that in nature or in cultivation two taxa, which replace each other geographically or ecologically, are not only capable of fertile hybridization but are miscible (producing in the F_{2-x} a complete series of intermediates blending them), it is clear that the taxa deserve the rank of subspecies replacing one another by virtue of geographical or ecological distribution.

(51) If it has repeatedly been observed in different places that two taxa, possessing morphological characters entitling them to specific rank, have produced sterile or nearly sterile hybrids, the progeny of which does not point to miscibility, these taxa should be accepted as good species.

(52) If a specific population consists of a number of colony-wise distributed partial populations, each colony will have its own facies. BAUR's study on *Antirrhinum* is an eminent introduction to the study of this type of segregation.

(53) Species of island and mountain floras seem to behave frequently in this way; the absence of intermediary specimens between the colonies is often a serious obstacle to their evaluation for a satisfactory synthesis.

* * *

(54) Data on number of chromosomes and their garniture and their pertaining to special taxa are an interesting outcome of cytogenetics, but should be evaluated by the taxonomist with great caution as he will generally not be acquainted or provided with data serving to illustrate their variability and constancy over entire populations.

(55) Such taxa should be treated either as species or subspecies by the standard of their morphological characters, if they are shown to be incompatible.

(56) *Apomicts* withdraw from the normal methodology of hierarchic taxonomy; taxonomically the 'population' of each apomict is comparable to one specimen of a panmictic population. It is recommended to earmark them by a special signum '*apom.*'

(57) 'The New Systematics' is an admirable guide to the different patterns of polymorphism of populations.

(58) The distinction and description of well-defined infraspecific taxa can only be appreciated. A population analysis is, however, beyond the capacity of herbarium methodology.

(59) The rank of *subspecies* should be reserved for and confined to replacing partial populations *i.e.* natural groups of the same general nature as species but exhibiting a lower degree of morphological differentiation and/or reproductive isolation and for morphologically slightly distinct polyplotypes.

(60) The rank of a *variety* should be used for infraspecific, distinguishable taxa, which show no replacement, and for other groups of genetically deviating paramorphs.

(61) The rank of a *forma* should be confined to slight variations (paramorphs) assumed to have a genetical basis.

(62) *Phenotypic* modifications may be designated by an epithet preceded by *modif.* (*modificatio*). This epithet has no nomenclatural status as a modification belongs to a taxon, but is not a separate taxon itself.

(63) If in a revision some specimens cannot be placed and are 'suspicious', their presence should be announced in critical notes. There is no reason to conceal anything about such specimens, but it is distinctly discouraged to name any deviation and burden literature with 'optimistically proposed' species.

(64) It is equally discouraged to recognize or describe a species or other taxon on inadequate material; this has led in the past to a host of obsolete entities and paper species, sometimes assigned to wrong families and genera, which prove to lead a tenacious life in literature. Science is not served by dubious products of impatient ambition.

There is no sense in the naming of doubtful, inadequate or sterile herbarium specimens.

(65) Try to restrict the number of new names and new combinations to the bare necessity.

(66) The study of the essays on specific delimitation and taxonomical methodology by BENTHAM and HOOKER, *The New Systematics* (HUXLEY ed.), and the *Theory of Systematics* by DANSER are recommended to gain a theoretical background in the methodology and results of taxonomy.

(67) Nothing has as yet appeared to replace, on any large scale, the principles of orthodox taxonomic schemes on the seed-bearing plants; the hierarchical system shows little of decline or fall (TURRILL).

(68) Experimental taxonomy has in many respects admirably deepened our insight and generally corroborated the factual data of alpha taxonomy.

(69) Phytography requires, besides a love and esteem for the métier, a memory for forms, great patience and care, a never ending self-criticism, continuous concentrated observation of details, a great tenacity for mastering the facts, as well as a balanced and unprejudiced outlook.

(70) Be always prepared to solicit disinterested criticism from experienced colleagues whose work you admire.

Try to conquer a natural, human dislike and inertia to eventual drastic improvements and emendations in agreement with your responsibility explained in § 3-4.

C. G. G. J. VAN STEENIS.

SELECT SUBJECT INDEX TO TERMS AND TOPICS

Behind the page numerals reference is made to the Rules & Recommendations of chapter 10 by § numbers

- Adaptation cxcvii
 (— to man) cxcviii
 Adesmy clxxvii
 Adnation clxxvii
 Adventives cxviii–cxci
 Agamospecies ccxv
 Allopolyploids cc
 Alpha taxonomy clxix, clxxiii,
 clxxiv; § 67–68
 Altitude (effect of —) clxxx,
 cxcii
 Analysis clxxvi, cxcvii, ccxx
 Anemomorphosis clxxxi
 Ant plants clxxxii
 Anthropogenous influence
 cxcviii; § 44
 Anthromorphosis clxxxiii
 Apomicts ccii, ccvii, ccxiii–ccxv;
 § 44, 56
 Applied botany (influence of —
 on specific delimitation) ccii;
 § 3, 45
 Appreciation (of characters).
 See characters
 Average. See normal
 Browsing (effect of —) clxxxiii
 Cecidioromorphosis clxxxii
 Characters (adaptational —)
 cxcvii
 (appreciation of —) clxx–
 clxxxii, ccvii; § 20–23, 38–41
 (geographical —) cxci; § 23,
 46–49
 (recessive —) clxxxvii
 (value of single —) clxxi;
 § 13–14
 (vegetative —) clxviii–clxxxiii,
 ccxvii; § 20–22, 26
 Chauvinistic botany clxxv,
 cxcvii, ccxxi; § 28–29
 Chemical elements (system of —)
 ccvii
 Chromosome (pattern) clxxii
 races ccxi–ccxiii; § 54–55
 Classical taxonomy clxix–clxxii;
 § 66–67
 Cleistogamous (flowers) clxxix
 Cline clxxiv, clxxvii; § 16
 Coenospecies clxxviii, cxci; § 31
 Commisium ccvi
 Comparium ccvi
 Convivium ccii, ccvi; § 39
 Cultigens ccii–ccxiii
 Cultispec (concept —) ccii
 Cultivar clxvii, ccii
 Cytogenetics.
 See chromosomes
 Demarcation (sharp — no clue to
 rank) cxcv
 (— in cultigens) ccii
 Details ccxvi, ccxvii, ccxix–ccxx;
 § 32–35, 41
 Devaluation of ranks cxcvii;
 § 15, 42
 Dimorphism (of flowers and
 fruits) clxxix, clxxxv
 (of leaves) clxxix
 (seasonal —) clxxxv, clxxxviii–
 clxxxix
 Discontinuity (of matter) clxxix; § 1
 Disjunct populations cxcii–cxci,
 ccx, ccxxi; § 47, 49
 Dispersal clxxiv, clxxxvii,
 clxxxix, cxviii, ccvi
 Distinction of taxa § 7–12
 Distribution (area of —) clxxxiv
 Domesticated plants (origin of
 —) ccii–ccxiii
 Doubtful specimens ccxx; § 63
 Drought (influence of —) clxxxi
 Ecological characters clxxxv,
 clxxxviii; § 23
 races clxxxviii; § 34, 37
 Ecospecies clxxxviii, cxci
 Ecotypes clxxxviii, cxci; § 23
 Edaphic influence clxxxii
 Edaphomorphosis clxxxii
 Education (in taxonomy) clxxiv;
 § 1–70
 Endemic species. See species
 Environment (as stimulant for
 formation of species) cxcvii,
 cc–ccii
 (change of —) clxx, cxcvii,
 cc–ccii
 (effect of destruction of —)
 clxxxiii, cxviii–ccii
 (responsible for racial differ-
 entiation) clxxxiv, clxxxviii,
 cxcii–cxci, cc
 Epiphytes clxxx
 Evaluation of ranks clxxv,
 clxxxiii, cxci, ccii, ccix, ccxii,
 ccxiv; § 33, 46–53
 Evolution (autonomous —)
 cxcvii
 Exclusive. See replacing
 Experimental taxonomy clxxxviii,
 cciv–ccx; § 49–52, 68
 Extinction (of species) clxx
 Fasciation clxxxvi
 Fire (influence of —) clxxxiii
 Floral dimorphism clxviii; § 26
 Floristic botany clxxv, ccxvi,
 ccxxi–ccxxxiii; § 30
 Forking clxxxvi
 Forma § 61
 Formenkreis cxci
 Freedom (of taxonomist) clxxii;
 § 1–70
 Fumarole plants clxxxii
 Fusion clxxxvi
 Galls clxxxii
 Gene-centre theory clxxxvii
 flow ccvi
 Genera (difficult —) clxxxvii
 (microtherm —) cxcii
 General Flora ccxxi–ccxxxiii;
 § 28–29
 Generic concept ccvi; § 15
 Geneticists (opinion of —)
 clxxxii, ccxiii, ccvii; § 31
 Geographical barriers cxcii,
 ccv
 Hemi-epiphytes clxxxii
 Hierarchical relations (in spe-
 cies) clxxvi, cxcv–cxvi;
 § 8–9, 33, 42
 (in zoology) clxxvi
 Hierarchy (of genome struc-
 tures) clxxxii
 (of plant kingdom) clxxvii,
 clxix–clxx, clxxvii; § 2, 67
 Homomorphosis clxxxii
 Hybridization cc, cciv–ccx,
 ccxii; § 49–52
 Hybrids (intergeneric —) ccvii
 Hydromorphosis clxxxii
 Hygromorphosis clxxxii
 Hypselomorphosis clxxx
 Inadequate material. See mater-
 ial
 Individuum clxx
 Infrasppecific (desirability of —
 taxa) cxcv, ccxix; § 9, 11,
 15, 16, 25, 34, 58
 Introduced plants cxviii
 Introgression ccvi
 Intuition (a myth) clxxiv; § 7
 Island floras cxcii, ccii, cxcii;
 § 53
 Isolation (effect of —) clxxxvii,
 cxci, ccvii; § 53
 (long —) cxcii, ccx, ccxiii
 (reproductive —) clxxxv
 (scheme of —) clxxxv
 Jordanons clxxxii, clxxv, clxxxiii
 Juvenile (forms) clxxxviii
 Laciniation clxxxvi
 Linneons clxxvii, clxxxiv,
 clxxxviii, cxci, cxci, ccvi–ccix,
 ccxviii, ccxix, ccxx; § 15, 31,
 41, 42, 46–48
 Local (botanists & Floras)
 cxcvii, cxviii, ccxvi–ccxvii,
 ccxxi–ccxxii; § 17, 28–30
 Lumping (discreet —) clxxvi,
 ccxx, ccxxxii; § 33, 38
 Marginal (variability) clxxxiv,
 clxxxvii; § 16, 39

- Mass collections clxxvi
 Material (inadequate —) clxxiv, clxxv, ccxxi; § 63-64
 Measurements. See sizes
 Methods (auxiliary —) clxix (phytography) clxxiii
 Microspecies clxxiii, clxxvii, clxxxiii, cxvi, ccxiv
 Microtypes cciv
 Migration clxxxiv, clxxxvii
 Miscibility clxxxix, cxci, ccv-cx; § 49-51
 Modifications. See phenotypic variation
 Monographs ccxvii-ccxxii; § 1-70
 Monstrosities clxxi
 Mountain floras cxcii-cxciii; § 53
 Myrmecomorphosis clxxxii
 Name (importance of the —) clxxiv; § 3-4, 65
 Neo-endemics cc
 Nomad plants cxcviii, cc
 Nomenclature clxvii, clxix, clxxi, clxxxii, clxxxviii, ccii, ccxiv; § 24-25, 59-65 (of apomicts) ccxiv
 Normal plant clxxii, clxxxviii
 Objectivity clxix, clxxvii, ccxiv; § 17, 31
 Ontogenomorphosis clxxxviii
 Organization characters. See radicals
 Origin (of cultivated plants) ccii (of infraspecific taxa) clxix, clxxxv-ccix, cxcii (of new species) clxix, cxc, cc, cci (of new taxa by anthropogenous influence) cxcviii (of new taxa by environmental change) cxvii, cc-ccii (rapid — of taxa) cc, ccii (of ruderals) cxci
 Paedogenesis clxxix, clxxxiii
 Paramorphs clxxxiv, clxxxvi, ccv; § 62-63, 65
 Pascuomorphosis clxxxiii
 Peloric flowers clxxi, clxxxvi
 Personal element clxx-clxxi, clxxiv, ccxvi-ccxvii; § 10-12, 17, 18, 27, 69, 70
 Phenotypic (effect of altitude) clxxx (variation) clxxvii-clxxxiii; § 26, 62
 Photomorphosis clxxx
 Phytomorphosis clxxxii
 Pioneer plants clxxxiii, cc
 Plant geography (as check on specific delimitation) cxvii
 Plasticity (vegetative —). See characters (vegetative —)
 Pollinators (for ecological separation) clxxxix, cc (self —) ccvii
 Polymery (taxonomic importance of —) clxxi
 Polyploids (in cultigens) ccii (in wild plants) cc, ccxi-ccxiii
 Polyplotypes ccxi-ccxiii; § 54-55, 59
Populatio articulata altitudinalis cxcii
articulata disjuncta cxcii
articulata regionalis clxxxix; § 47
continua clxxxvi
discontinua clxxxviii; § 47, 50, 52-53
discontinua ecologica clxxxviii; § 47, 50
 Populations (analysis of specific —) clxxxiii-cxcii, cxcv; § 35, 58 (articulated —) clxxvi, clxxxix-cxciii (discontinuous —) clxxxviii-cxciii (disjunct —) cxcii-cxciii; § 49-50, 52-53 (dissociation of —) clxxxiv, clxxxviii (hierarchical racial differentiation in —) clxxxviii (homozygotous —) clxxvii (overlapping —) ccv; § 46 (panmictic —) clxxxiv, ccv-cxvi; § 56 (polymorphism) clxxvii, clxxxiv (— studies) clxxii, clxxxiii-cxciii
 Practical taxonomy clxxii, ccxvi-ccxxiii; § 1-70
 Precision clxxvi, ccxix-ccxxi; § 7, 8, 11, 16, 21, 24, 34-35, 40-43, 45
 Precocious flowering clxxix, clxxxiii
 Proliferation clxxxvi
 Provisional work cxvi, ccxvii, ccxx ccxxi; § 27, 30, 63-65
 Psychology (of a taxonomist) clxxii, clxxiv-clxxx, ccxx; § 27, 43, 64, 69-70
 Pyromorphosis clxxxiii
 Races (altitudinal —) cxcii (ecological —) cx-cxcii (geographical —) clxxxviii-cxciv; § 34 (origin of —) clxxxix-cxcii, ccii (polytopic origin of —) cxcii (segetal —) cxci
 Racial segregation. See segregation
 Radicals clxxi
 Ranks (devaluation of —) cxcvi, ccii
 Rassenkreis cxc
 Recessive characters clxxxvii; § 39
 Regional Floras. See local
 Relict population cxciii, ccx
 Replacing taxa clxxxix, cxvi, ccvi; § 24, 37, 46-47, 50, 52-53
 Responsibility of taxonomists clxxxiv-clxxxv, ccxx; § 3-4, 70
 Reticulate affinity clxx
 Revisional work. See monographs
 Rock plants clxxxii
 Rotten cxc
 Ruderals cxcviii-ccii
 Segregation (altitudinal —) clxxxv, cxcii; § 53 (racial —) clxxxiv, clxxxviii-cxciii, ccix-ccx, ccxx; § 37, 39, 47, 49, 50, 52-55, 59
 Sexes (distribution of —) clxxxvi
 Shade forms clxxxii
 Silicious soils clxxxii
 Simplification clxxxvi
 Sizes (of organs) ccxvi, cxcvii, ccxix; § 21, 40-41
 Solfatara plants clxxxii
 Species (collective —) cxc; § 31, 52 (extinction of —) ccxx (— hybrids) cciii-ccx; § 51 (local-endemic —) cxcii-cxciii, ccxxii; § 48 (optimistically proposed —) cxvi, ccxxii; § 63-65 (origin of —) cxc, cc, cci (polytypic —) cxc (reality of —) clxxvii, clxix; § 15, 31-32
 Specific concept clvii, clxxv, clxxxiv, cxci, cxv-cxcvi, cciii-ccxiii; § 11, 15, 31-33, 38-44 delimitation ccviii-ccx; § 33-56
 Specimen description clxxvi, clxxxvii, cxcviii; § 26, 62-65
 Splitting clxxv, ccxv, ccxx (objections against —) clxxvi-clxxvii; § 40-44 (of genera) ccvii
 Standard (of taxonomic works) clxxii; § 66
 Sterility barrier ccv, ccvii-ccix; § 49-56
 Subspecies clxxxviii, cxcii-cxciii; § 15, 37, 39, 47, 59
 Suppression clxxxvi
 Syngameon ccv
 Synthesis clxxvi, ccxx; § 10, 41-43
 Taxonomic work (quality of —) clxxii

- Taxonomy (aim of —) ccxviii; § 5
(basis of botany pure and applied) clxxiv; § 3-4
- Teratologomorphosis clxxx
- Teratology (examples of —) clxxi, clxxxvi
- Terrestrial forms 52
- Theoretical considerations in descriptions xcxi; § 6, 66
- Tropical flora (inadequately known) clxxviii
plants (variability of —) clxxviii; § 26
- Typical. See normal
- Typification clxxiii-clxxiv; § 24-25
- Useful plants. See applied botany
- Usefulness (of good taxonomic work) clxxii, ccxviii-ccxix; § 17-18
- Variability (discontinuous —) clxxxviii; § 39, 46-47, 49, 52
(degree of —) clxxxiv
(genotypic —) clxxxiii; § 37
(geographical —) cxc
(in Linnean species) clxxvi, clxxvii, clxxxv-cxcvi; § 38-40
(individual —) clxxxvi
(marginal —) clxxxvii; § 39
(no reason to suppress anything on —) cxcv; § 34-56
(occasional —) clxxxiv
(parallel, homologous —) clxxi
(patterns of —) clxxvii
(phenotypic —) clxxvii; § 26
(potential —) clxxxiv, cciii
(seasonal —) clxxxi
- (species populations) clxxvii-cxciii; § 31-47
(tropical plants). See tropical flora.
(vegetative —). See characters (vegetative —)
- Variatio genotypica clinalis clxxxvii
marginalis clxxxvii
regularis clxxxvi
- Variation. See variability
- Variegation clxxxvi
- Variety § 32, 60
- Vegetative characters. See characters
- Vicarious. See replacing
- Water plants clxxxii
- Weeds cxcviii-cxcix
- Wind forms clxxxi
- Zoomorphosis clxxxii

INDEX TO PERSONAL NAMES

- Allan, H. H. clxxxiii, cc, ccx, ccxii
- Backer, C. A. clxxii, clxxxii, clxxxix, cxcix, cxcvi
- Baur, E. cxc, xcii, xciii, ccviii, ccxxviii
- Bentham, G. clxvii, clxviii, clxx, clxxvi, cxcix, cc, ccxviii, ccxix-ccxxi, ccxxiii-ccxxvi, ccxxix
- Bernhardi cciv
- Bianchi Jr clxxxviii
- Blakely cc
- Bloembergen xcxi
- Bonnier clxxxvii
- Braun, A. cciv
- Bremekamp clxxv, clxxvi
- Brett, R. G. cc
- Brown, R. ccxix, ccxxiii
- Camp clxix, clxxxiii
- Candolle, A. de clxx, clxxv, clxxxvii, xcxi, cxcvi, cxcix
- Celakovski clxxvi, xcxi
- Clausen clxxxiii, ccviii, ccix
- Cockayne clxxxiii, cc
- Cognac cxcix
- Dahlstedt ccxiv
- Danser clxxxiii, cxc, cxcix, ccii, ccv-ccviii, ccx, ccxii, ccxxii, ccxxix
- Darlington ccviii
- Darwin clxvii, ccv
- Diels clxx, clxxi, cxcvii, ccxix
- Dobzhansky ccviii
- Ehrendorfer ccxii
- Elmer ccxxii
- Engler cxcv
- Exell cxcii
- Fagerlind ccxii, ccxv
- Flood ccx
- Focke ccv
- Gaertner, K. F. von cciv, ccv
- Gandoger clxxii
- Goldschmidt clxxvi, cxc
- Grant clxxxix
- Gudjónsson ccxiv
- Hartog, C. den clxxxii
- Hedberg clxxvi
- Hemsley ccxx
- Henderson ccxxii
- Henry ccx
- Henschel cciv
- Herbert cciv, ccv
- Hiesey ccix
- Hoffman, H. clxxv, clxxvi
- Hoogland clxxxvi
- Hooker, J. D. clxvii, clxviii, clxxvi, clxxxix, xciii, ccxix, ccxxiii, ccxxix
- Howard clxxxviii
- Hudson cciii
- Huxley, J. clxvii, clxix, clxxii, clxxxiv, clxxxvii, cxc, cxcvi, ccxxix
- Irmscher cxcv
- Jacobs cxciv
- Johanssen clxxi
- Jordan clxxv, clxxxiii, ccxi
- Kalinska ccxi
- Keck ccix
- Kern xcii, ccx
- Kerner clxxv, clxxxvii, cxc-cxcii
- Kleinschmidt cxc
- Kloos clxxxix
- Knight cciv
- Kölreuter cciv, ccv
- Komarov cxc
- Kristoffersen ccviii
- Lamprecht ccviii
- Langlet clxxxvii
- Léonard cc
- Lewis, J. clxxv, ccxvii
- Lindley, J. ccxix
- Linnaeus clxviii, clxix, clxxii, clxxxiii, clxxvi, cxcvi, cciv, ccv, ccvii, ccviii, ccxxiii, ccxxvi
- Lotsy cc, ccv, ccvi
- Löve ccviii, ccxi, ccxii
- Maiden cc
- Manton cxcvii, ccxi, ccxii
- Marie-Victorin cc
- Marsden-Jones clxxxii, clxxxiii, clxxxviii, xcxi, ccix
- Martens cciv
- Matsuura cxcii
- Maximovicz ccxx
- Mendelejew ccvii
- Merrill clxxxiii, cxcvi, cxcix, ccxxii
- Miquel cxciv, cxcv
- Mons, J. P. van cciv
- Mueller, F. von cc
- Mueller-Arg., J. ccxix
- Müntzing ccviii
- Naegeli, C. von clxxi, cxcvii
- Nannfeldt ccxii
- Nelmes cxcv
- Nilsson, N. H. clxxi, ccviii, ccx, ccxii, ccxiv
- Oostroom, S. J. van clxxxvii, xcxi
- Penzig clxxxvi
- Pilger clxxxii
- Pryor, L. D. cc
- Ray, J. cciv, ccvii
- Reinig clxxxiv
- Reinwardt cciv
- Renner cxcix
- Rensch cxc, xcxi
- Ridley cxcv, ccxxii
- Rietz, G. E. du xciii, ccxiv
- Roberty clxx
- Rousseau, J. J. clxxv

Schindler cccx, ccxxi
 Schwarz, O. ccii
 Sendtner clxxv, clxxvi
 Shiskin cxc
 Sledge ccxi
 Smith, J. E. ccxix
 Sørensen ccxiv
 Stapf ccxix
 Stearn ccx
 Stebbins cxcvii, ccxv
 Tanaka cci

Thellung cxcix, ccii, cciii
 Timofeff-Ressovski clxvii, cxcii,
 ccviii, ccxi
 Tournefort cxcvi
 Toxopeus, H. J. cciii
 Treviranus cciv
 Turesson clxxxiii, clxxxvii,
 clxxxviii, cxc, cxi
 Turrill clxix, clxx, clxxiv, clxxxii-
 clxxxiv, clxxxvi, clxxxvii, cxcii,
 cc, cci, ccix, ccx, ccxiv, cccxx

Urban cxcviii
 Vavilov clxxi, clxxiii, clxxxiv,
 clxxxvii, cciii, ccix
 Vries, H. de cxcix
 Weddell ccxix
 Wettstein, R. von clxxxix, cxc
 Winge clxxi, clxxiii, clxxxiii,
 ccviii
 Wit, H. C. D. de clxxxvii
 Worsdell clxxxvi
 Wulff ccxi

INDEX TO PLANT NAMES

Synonyms in italics

Acacia cxcvii
 Acanthaceae clxxv, clxxix
 Acorus calamus ccxi
 Adonis *citrina* clxxv
 Adoxa moschatellina ccxi
 Aglaia clxxi, ccxv
 Alangium cxcii, ccxxii
 Alchemilla ccxv
 Aleceterolophus cxcix
 Alismataceae clxxxii
 Alpinia cxcvii
 Amaranthaceae cccxii
 Anemone rivularis Ham. cxcviii
 Annonaceae clxx, clxxi, clxxix,
 cxcvii
 Antirrhinum clxxxiv, cxciii, ccx,
 ccxxviii
 § Antirrhinastrum cxcii, ccvi,
 ccviii
 majus L. cxcii, cxciii
 siculum cxciii
 Aquilegia clxxxix
 vulgaris clxxxix
 Araceae cxcvii
 Ardisia ccxv
 Areca catechu cciii
 Artocarpus heterophyllus cciii
 Asperula cc
 Aspidopteris timoriensis (DC.)
 Juss. cxciv
 Azalea cciv
 Balanophora globosa ccxv
 Bauhinia *castrata* Blco clxxxvi
 malabarica clxxxvi
 Beta *maritima* ccii
 vulgaris ccii
 Bidens ccxv
 Biscutella ccxii
 Boehmeria *biloba* Miq. clxxxvi
 Bromus arduennensis cxcix
 grossus cxcix
Brugmansia clxxxvi
 Bulbocodium ccviii
 Burmanniaceae cccxii
 Burseraceae cccxii
 Cactaceae cciv
 Calceolaria cciv, ccx
 Campanula clxxi

rotundifolia, clxxi, clxxii,
 clxxxvi, clxxxvii
 Campsis ccx
 grandiflora Loisel. ccx
 radicans Seem. ccx
 Caprifoliaceae cccxii
 Capsicum annuum cciii
 Cardamine pratensis cxcii
 Carex cxcv, cccxii
 divulsa Stokes cxcvi
 pairaei F. Schultz cxcvi
 Carthamus tinctorius cciii
 Caryophyllaceae clxxi, clxxxvii
 Cassia mimosoides L. clxxxvii
 Cassipourea clxxv, ccxvii
 Cedrus cxciii
 Celastraceae clxxix
 Celosia cristata clxxi
 Centaurea cc
 Chelidonium ccxi
 Citrus cciii, ccxv
 Clitoria clxxxvi
 Cocoloba clxxxviii
 Coffea arabica L. clxxxvi
sumatrana Miq. clxxxvi
 Combretum punctatum cxcii
 Commelinaceae clxxix
 Compositae clxxxvi
 Connaraceae clxxix
 Convolvulaceae clxxxvii
 Coprosma cc
 Crataegus clxvii
 Cucurbita moschata cciii
 Cuscuta epilinum cxcix
 Cyathula prostrata (L.) Bl. cxcix
 Cyperaceae cxciv, ccii
 Cyperus sanguinolentus cxcii
 Cytisus clxxxiv, cxcii
 scoparius var. prostratus cciv
 § Tubocytisus clxxxvii
 Datura § *Brugmansia* clxxxvi
tatula clxxv
 Depierrea clxxxvi
 Derris cciii
 Dianthus cc, cciv
 Dichapetalum cccxii
 Dillenia cccxii
 Dipterocarpaceae cxcvii

Distylium stellare clxxxviii
 Drosera rotundifolia L. cxcviii
 Dryopteris filix-mas ccxii
 Dysoxylum ccxv
 Elatostema ccxv
 Elattosis apetala Gagn. clxxxii
 Elephantopus scaber L. cxcix
 Epilobium ccx
 Epimedium ccx
 Erica cciv
 Erophila clxxxiii, clxxxiii, cxcii
 Eucalyptus cc
 Eugenia cxcvii, ccxv
 Euphorbia cxcvii
 lathyrus cciii
 Euphorbiaceae cxcvii
 Euphrasia cxc, cxciii
 Evolvulus cxcii
 Fagopyrum esculentum ccii
 Fagraea ccxvi
 Ficus clxxxii, cxcvii
 Fritillaria *camchatsensis* Ker-
 Gawl. cxcii
 Galeopsis pubescens cc
 speciosa cc
 tetrahit cc
 Galium ccviii, ccxii
 Gentiana clxxxiv, clxxxix
 § Endotracha cxc
 Geum clxxxiv, clxxxviii, clxxxix,
 ccx
rivale clxxxviii, ccix, ccx
ssp. urbanum L. clxxxviii, ccix,
 ccx
ssp. rivale ccx
ssp. urbanum ccx
 Ginkgo biloba cciii
 Gladiolus cciv
 Gouldia ccxv
 Gramineae ccii, ccvii
 Gynura crepidioides clxxxix
 Hanguana clxxxiv, clxxxix
 malayana clxxxix
 Hebe cc
 Hieracium clxvii, ccxiv
 Hydrocharitaceae clxxxii
 Ipomoea pescaprae cxcii
 Isoetes ccxii

FLORA MALESIANA

- Ixora* clxxv
Juncus prismatocarpus R.Br. clxxxvi
Jussieua repens L. clxxxii
Kosteletzkya batavensis (Blco) F.-Vill. cxci
Lamium album clxxxiv
Lavanga eleutherandra (Bl.) Kurz clxxxix
 Leguminosae clxxxix, clxxxvi, clxxxvii
Lespedeza ccxx, ccxxi
 caraganae ccxx
 elegans ccxx
 inshanica ccxx
 juncea ccxx
 sericea ccxx
 variegata ccxx
Limnophila clxxxii
 indica (L.) Druce clxxxii
Linum cciv
Liquidambar tricuspis Miq. clxxxix
Lonicera clxxx
 Loranthaceae ccxxii
Loranthus pekanensis ccxxii
Lychnis dioica clxxvi
Lycopodium ccxii
Mahonia napaulensis clxxxviii, cxcvii
Malva ccviii
Melandrium clxxxix
 album ccviii
 diocum (L.) Coss. & Germ. ccviii
 rubrum ccviii
 Meliaceae clxxi
Melicope cc
Methysticodendron amesianum Schultes clxxxvi, clxxxvii
Metrosideros ccxv
 Mimosoideae clxxxvii
Monochoria clxxxii
 linearis clxxxii
 pauciflora clxxxii
 plantaginea clxxxii
 Myristicaceae cxcvii
Narcissus ccviii
Nasturtium microphyllum ccxi
 officinale ccxi
Nicotiana ccviii
Oenothera cxci
Ophiorrhiza ccxv
 Orchidaceae clxxi, clxxxix, clxxx, clxxxvi, clxxxix, cxcvii, cci, ccvii, ccix
Oreobolus cxci, cxci
Oryza fatua Koen. ccii
 sativa L. ccii
Pandanus cxcvii
 tectorius Park. clxxxvi
 variegatus Miq. clxxxvi
Pavetta clxxv
Pentaphragma ccxxii
Pentstemon cciv
 coccineus cciv
 gentianoides cciv
 hartwegi cciv
Peperomia ccxv
Pinus montana clxxv
 mughus clxxv
 pumilio clxxv
 sylvestris clxxxvii
Piper betle cciii
Pisum arvense ccviii
 sativum ccviii
Pittosporum clxxxix, ccxxii
 nubigenum Ridl. clxxx
 pullifolium Burk. clxxx
 sinuatum clxxxix
Plantago asiatica clxxxii
 hasskarlii clxxxii
 incisa clxxxii
 major clxxxii
Platanus ccx
 × *acerifolia* ccx
 occidentalis ccx
 orientalis ccx
Poa ccxv
 vivipara clxxi
Polygonum cxci, ccvi
 amphibium L. clxxxii
 lapathifolium ssp. *linicolum* cxci
 viviparum clxxi
Polypodium vulgare ccxi, ccxii
Potentilla argentea ccviii
Premna clxxxiii
Primula cciv, ccx, ccviii
 acaulis ccv
 elator ccv
 officinalis ccv
 veris clxxvi
Prosopis juliflora DC. cxci
 vidaliana Naves cxci
 Proteaceae clxxxviii
Psychotria ccxv
Pygmaeopremna clxxxiii
Randia ccxv
Ranunculus ccxv
Rhododendron cciv
 ferrugineum clxxxix
 hirsutum clxxxix
Rhodora cciv
Ricinus communis cciii
Rosa clxvii, ccxv
 Rubiaceae clxxv, cxcvii
Rubus clxvii, ccv, ccxv
Rumex ccvi
 acetosella ccxi, ccxii
 § *Lapathum* ccvi
 Rutaceae clxxxix, ccvii
Saccharum officinarum ccii
Salix clxvii, ccviii, ccx
 polygena ccix
Sapotaceae cxcvii
Saxifraga cxcv
- Scaevola* ccxxii
 § *Enantiophylla* ccxxiii
Schefflera cxcvii
Scheuchzeria asiatica Miq. cxci
 palustris L. cxci
Schima cxci
Scirpus fluitans L. cxcviii
Scurrula ccx
Sechium edule cciii
Setaria italica ccii
 viridis ccii
Silene cxci, cc, ccx
 conica cxci
 cucubalus clxxi, clxxii, clxxxvi, clxxxvii, cxci, cxci, ccix
 ssp. *cucubalus* cxci, ccx
 ssp. *maritima* cxci, cxci, ccx
 linicola cxci
 maritima cxci, cxci, ccix
 otites cxci
 Solanaceae clxxxvi
Sorghum ccii
Spartina alterniflora cc
 stricta cc
 townsendii cc
Stachytarpheta ccvi
Susum clxxxix
Symingtonia populnea (R.Br. ex Griff.) Steen. clxxxix
Symplocos laurina (Retz) Wall. clxxx, clxxxii
 sessilifolia clxxx
Syzygium ccxv
Tamarindus indica cciii
Taraxacum clxvii, ccxv
 officinale ccxv
Tatea clxxxiii
Tenagocharis latifolia Buch. clxxxii
Thunbergia clxxv
 fragrans clxxv-clxxxvi
Thymus clxxxix, cc
 angustifolius clxxxix
 chamaedrys clxxxix
 pulegioides L. clxxxix
 serpyllum L. clxxxix
Triticum spelta cxci
 Triuridaceae ccxxii
Tulipa ccviii
Turnera subulata J.Sm. cxcviii
 trioniflora Sims. cxcviii
 ulmifolia L. cxcviii
 Urnaceae cxcviii
 Umbelliferae ccxxii
Uncaria gambir cciii
Urena lobata clxxvi
Valeriana officinalis ccxi
Verbascum cc
Veronica cc
Viola clxxxix
Wightia borneensis clxxxix
Wikstroemia ccxv
Zea mais cciii
 Zingiberaceae cxcvii