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PHYTOCHEMISTRY AND PLANT TAXONOMY—AN ESSAY ON THE CHEMOTAXONOMY OF HIGHER PLANTS*

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Abstract—Modern methods of plant classification and plant nomenclature are outlined. It is proposed that taxonomists should make greater efforts to conserve existing plant names, for the benefit of phytochemists and other users. Chemotaxonomic principles are considered and some examples are provided to show the importance of chemical evidence in taxonomic revision. The value of chemical characters in the classification of plants below the specific level is also emphasized.

INTRODUCTION

Modern phytochemistry is often more or less intimately connected with plant taxonomy. In the past, usefulness to man was the main stimulus for chemists to investigate plants. Today, curiosity concerning the course of evolution, and concomitantly, the ambition to help taxonomists in their endeavour to arrive at truly natural classifications of the many groups of plants recognizable in nature are additional reasons for initiating chemical investigations of plants. The phytochemist interested in plant classification needs a sound basic knowledge of several aspects of plant taxonomy. It is the aim of the present essay to provide such an introduction to those chemists who are generally unfamiliar with taxonomic principles and practice. In the present review formulae are combined in figures and ciphers in brackets [1, 2 etc.] refer to 'Notes and References'.

PLANT TAXONOMY AND SOURCES OF DATA USED BY IT

Botanical systematics or plant taxonomy is the science of delimiting, describing and naming of any group of plants considered to represent a distinct unit (taxonomic unit or entity = taxon) and of arranging all recognized taxa in classifications (systems). Other fields exploited by plant taxonomy are the study of relationships between taxa and of the dynamics of evolution of characters and taxa in past and present. Table 1 is an attempt to summarize the essential activities covered by plant taxonomy.

At this point some remarks on the notions *taxonomy* and *systematics* seem appropriate. As shown in Table 1, I consider these terms to be synonyms and consequently shall use them interchangeably. This is more or less common practice in modern botanical taxonomy or systematics [1, 4–7]. It should be remembered, however, that scientists such as Alston [8], Merxmüller [9] and others advocate a sharp distinction between plant taxonomy and plant systematics; the former is claimed to cover only field A of Table 1 and the latter to include the whole field illustrated by Table 1. In my view much is to be said for the less pragmatic approach [7] which has been mine for many years [10–12], because other biologists [2, 13 and others] consider taxonomy to be the more inclusive term and systematics to correspond more or less to field A of Table 1. Just a few words should be spent on the term *classification*; it is often applied more or less synonymously to the terms taxonomy or systematics [14, 15], and should replace the superfluous term taxonomy according to Crowson [16].

The main aims of plant taxonomy are to provide an inventory of presently recognizable plant groups and to arrange them in a system useful to all people interested in plants. Collection, observation, comparison and description of plants enable the taxonomist to delimit and classify groups. A more or less uniform plant group is called a taxonomic entity, or, shortly, a *taxon* (plural *taxa*). Description and naming of plant taxa has to be followed by incorporating them in a system. A plant classification that is not only useful to plant taxonomists, but to all scientists and interested laymen needing a botanical system, is a scientific achievement that does not neglect practical requirements. Taxonomists accept a number of principles and rules agreed upon for practical purposes [17]. Important rules apply to taxonomic ranks or categories and to the naming of taxa (nomenclature). For arranging plant taxa in a system the main ranks reported in Table 2 are obligatory. If a taxonomist feels the need for a greater number of ranks he is allowed to intercalate additional ones. A number of the more commonly used intercalary ranks or categories is indicated in Table 3.

The taxonomic category 'species' is by far the most important one. By studying individual plants and plant populations in nature and in botanical gardens and

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Table 1. Fields of activity in plant taxonomy and their designations*

Fields of taxonomic activities		Main aims of each field
PLANT SYSTEMATICS in the broadest sense = PLANT TAXONOMY in the broadest sense	A: Plant classification = plant systematics or plant taxonomy *sensu stricto*	Delimitation, description, naming and classification of all accepted plant taxa.
	B: Plant geography in the broadest sense	Study of the distribution (dispersion) of plant taxa (= chorology); historical and ecological interpretation of distributional ranges of taxa; comparison of areas of taxa.
	C: Phylogeny†	Study of evolutionary relationships of taxa at all levels of the taxonomic hierarchy; study of character-evolution. Study of the results of evolution.
	D: Evolution†	Study of causes and processes which initiate and govern the evolution of characters and of taxa of any rank.
	E: Biosystematics or experimental plant taxonomy	Understanding microevolution‡: study of processes of adaptation and speciation in nature; mutations, hybridization, reproductive and dispersal biology, etc.

*For definitions and terminology compare refs [1, 2].

†These two fields are not treated separately by all taxonomists, e.g. [3].

‡As far as it can be studied experimentally; usually restricted to the levels of populations, species and species aggregates.

Table 2. The ranks* or categories† which must always be used in constructing hierarchical plant classifications, and indications of taxonomic levels by final syllables‡

Ranks or categories in singular (and plural): English equivalents	Examples
Regnum (Regna): Kingdom §	Plantae (plants)
Divisio (Divisiones): Division‖	Spermato**phyta**¶ (seedplants)
Classis (Classes): Class	Magnolio**psida**** (angiosperms)
Ordo (Ordines): Order	Ranuncul**ales**††
Familia (Familiae): Family	Ranuncul**aceae**‡‡
Genus (Genera): Genus	Ranunculus §§ (Buttercup)
Species (Species): Species	*Ranunculus nemorosus* DC.‖‖

*Taxonomic rank or level = position of a taxon in the classificatory hierarchy.

†Category = a level within the taxonomic hierarchy.

‡Rank-defining terminations (here given bold-faced) are used in the taxonomic hierarchy from the division to the subtribe (suprageneric entity; compare Table 3).

§Usually two (plants, animals), but in recent time often four [18] or five [19].

‖Phylum in zoology; used also for plants in ref. [19].

¶Recommended termination for green terrestrial plants; for fungi . . . **mycotae**.

Recommended for green terrestrial plants; also used . . . **atae. For fungi . . . **mycetes** and for algae . . . **phyceae** recommended.

††Recommended if derived from a genus name. Other names, such as Centrospermae, Farinosae, Helobiae and Polycarpicae also allowed.

‡‡Obligatory final syllable [17]; to be combined with a genus name, in casu Ranunculus; if the generic name terminates with a (e.g. Scrophularia) . . . **ceae** [20].

§§Generic names are nouns used in singular.

‖‖Species names (binary names; binomina) are generic names combined with specific epithets; epithets are now used generally uncapitalized; formerly those derived from persons (e.g. *Ranunculus seguieri*), geographic areas (e.g. *Ranunculus illyricus*) or (often prelinneic) generic names (e.g. *Ranunculus flammula*, *R. lingua*) were capitalized. Species names should always be given in italics in scientific publications.

Table 3. A number of taxonomic ranks between class and local population illustrated by *Ranunculus repens* L. (rank-indicating terminations in italics)

Rank or category	Example
Classis	Magnoli*opsida* [21]*
Subclassis	Ranuncul*idae* [21]
Superordo	Ranuncul*anae* [21]†
Ordo	Ranuncul*ales* (= Berberid*ales*) [21]
Subordo	Ranuncul*ineae* [22]
Familia	Ranuncul*aceae* [21, 22]
Subfamilia	Ranuncul*oideae* (= Anemon*oideae*) [22]
Tribus	Ranuncul*eae* [22]
Subtribus	Ranuncul*inae* [22]
Genus	Ranunculus [22]
Subgenus	Subgen. Ranunculus [23]‡
Sectio	Sect. Ranunculus [23]§
Subsectio	not used in ref. [23]
Series	Ser.: not used in ref. [23].
Species	*Ranunculus repens* L. [23, 24]
Subspecies	Subsp.: not used in refs [23–25]
Varietas	var. *angustisectus* Gremli [24]; and var. *prostratus* (Poiret) Gaud. [25]; var. *repens*, var. *erectus* DC., var. *glabratus* DC. and var. *villosus* Lamotte [26].
Cultivar (cv.)‖	'Pleniflorus' (= 'Flore Pleno')¶ and 'Nanus' [27].

*Alternative names are Annonidae [28] and Dicotyledoneae [e.g. 29].

† . . . **florae** [28, 29] is an alternative termination to . . . **anae**, e.g. Ranunculiflorae [29] or Annoniflorae [29].

‡Subgenus Batrachium, the water crowfoots, is often treated as a separate genus and *R. circinatus* Sibth., e.g., then becomes *Batrachium circinatum* Fries.

§Section Ficaria is often treated as a separate genus, and *R. ficaria* L., e.g., then becomes *Ficaria verna* Hudson or *Ficaria ranunculoides* Roth.

‖Nomenclature of cultivated plants is regulated by ref. [30]; article 7 decrees "Cultivated plants are named at three main levels: genus, species and cultivar" (*culti*vated *var*ieties; abbreviated cv.). The concept of cultivar differs from the taxonomic rank varietas which is a rank below that of species. Cultivars correspond to varieties (English), variétés (French) or Sorten (German). Article 27 regulates nomenclature of cultivars; all cvs named after 1 January 1959 should be given fancy names, e.g. *Chamaecyparis lawsoniana* 'Silver Queen' (= *Ch. lawsoniana* cv. Silver Queen); names in use before this date may be in latin, but should be treated in the same way (see Table 3, last line).

¶*Ranunculus repens* var. *flore-pleno* is an older synonym of *R. repens* cv. Pleniflorus = *R. repens* 'Pleniflorus' = *R. repens* 'flore-pleno'.

herbaria we learn much about the species to which they belong, and by ranking plants and plant products in a given species we are able to define more or less exactly the material under study. Moreover, species names are used to communicate about the many particularities, inclusive of chemical properties, of hundreds of thousands of taxonomic entities considered to belong to the category *species*.

Taxa are delimited, described and named by taxonomists. They represent more or less arbitrary and subjective man-made units. Taxonomists very often disagree with regard to the delimitation of plant groups which should be ranked as *species* or *genus* (Table 4). Disagreement is often even more pronounced in the case of taxonomic entities belonging to higher categories of the taxonomic hierarchy (Table 5). There are absolutely no objective and infallible criteria for rank-determination in plant classification.

As illustrated by Table 2, binomina (scientific names of species) are based on the genus name and a specific epithet. Therefore any splitting or lumping of genera severely affects specific nomenclature. Many plant groups have acquired more than one name, because the species or genera to which they were attributed were split, lumped, resplit, relumped and so on in the course of time. Other causes of the often confusing synonymy (two or more names for the same taxon) and homonymy (the same name for more than one taxon) are the intentional or unintentional neglect by some taxonomists of previous description and naming of the same taxon by others, and application of names formerly given to another plant group of the same taxonomic rank. A remedy to such confusion, but a rather deficient one, is the usual citation of the name(s) of the botanist(s) who first described and named a given taxon and who is (are) responsible for the rank accepted for it in a given flora or scientific paper. Alas, these so-called *author citations* are far from perfect in the taxonomic literature because in many instances nomenclature is a rather complex matter [compare e.g. 11, pp. 524–525].

Table 4 illustrates a number of nomenclatural annoyances to all scientists needing plant classifications, but being not 'pure' taxonomists. A few additional examples are given under refs [33] and [34]. *Ranunuclus ficaria* and

Table 4. Examples of taxonomic splitting and lumping at species and genus levels and their nomenclatural implications

'Linnean' species (Linneonta, Macrospecies, species groups)	Corresponding taxa in some recent treatments*	Remarks
Ranunculus montanus Willd. s.l.†	*R. aduncus* Gren. *R. carinthiacus* Hoppe *R. grenierianus* Jordan *R. montanus* Willd. *s. str.*† *R. oreophilus* M. Bieb. *R. venetus* Huter ex Landolt	Additional seggregates described in ref. [23]; splitting of a polytypic species in a number of microspecies‡ [e.g. 23, 24, 31].
Ranunculus ficaria L. s.l.†	*Ficaria verna* (L.) Huds. *s. str.* (= *F. ranunculoides* [L.] Roth *s. str.*)† *F. calthifolia* Roth *F. fascicularis* C. Koch (= *Ranuculus edulis* Boiss. et Hoh.) *F. ficarioides* (Bory et Chaub.) Halaczy (= *Ficaria edulis* Grossh.)	Section Ficaria → Genus *Ficaria* [e.g. 32]; splitting of a polytypic species in a number of microspecies‡§.
Ceratocephalus falcatus (L.)Pers.	*Ranunculus falcatus* L. *R. testiculatus* Crantz‖	Genus *Ceratocephalus* of Persoon relumped with Ranunculus [31].
Ranunculus glacialis L	*Oxygraphis vulgaris* Freyn, non *O. glaciales* (Fisch.) Bunge¶	Section Crymodes → genus *Oxygraphis* [e.g. 32].
Ranunculus circinatus Sibth.	*Batrachium foeniculaceum* (Gilib.) V. Krecz. comb. nov.** = *B. circinatum* (Sibth.) Spach = *Ranunculus foeniculaceus* Gilib. = *R. divaricatus* Ledeb.	Subgen. Batrachium → genus *Batrachium* [e.g. 33]; many *Batrachium* species are difficult to identify‡; interspecific hybrids common here and there.
Ranunculus baudotii Godron	*Batrachium marinum* (Arrh. et Fries) Fries = *B. baudotii* (Godron) F. Schultz = *Ranunculus peltatus* Schrank subsp. *baudotii* (Godron) Meikle ex C. D. K. Cook	Cf. [23, 31, 33, 35].

*Only a small number of the sometimes numerous synonyms given.

†Without adding *sensu lato* (*s.l.*) or *sensu stricto* (*s.str.*) these binomens are ambiguous today.

‡Often specimens can only be identified correctly by specialists, but even specialists may disagree in matters of microspecies identification.

§In ref. [23] all Ficaria-taxa, except *Ranunculus ficarioides* Bory et Chaub., are treated as subspecies of the polytypic species *Ranunculus ficaria*. If Ficaria is accepted as a genus and the variants as microspecies the binomen *Ficaria verna* becomes ambiguous without specifying its comprehensiveness by *s.l.* or *s.str.*

‖Treated as separate species or as a variant of species *falcatus* [for ref. see 31].

¶*Oxygraphis glacialis* (Fisch.) Bunge corresponds to *Ficaria glacialis* Fisch. (= *Caltha glacialis* Spreng. = *Ranunculus kamtschaticus* DC.).

**Invalid name according to ref. [31].

Ficaria verna mentioned in Tables 3 and 4 represent the same species and all members of *Ranunculus* subgenus *Batrachium* have to change their names if the latter taxon is raised in rank and becomes a genus. The same holds for *Ceratocephalus* if this genus is lumped with *Ranunculus*. Similar nomenclatural confusion arises if a so-called aggregate species (species group, macrospecies, linneon) is treated by a splitter (formerly generally a keen observer; presently often a biosystematist: field E of Table 1). *Ranunculus ficaria*, *R. montanus* and *R. nemorosus* represent such taxonomically difficult species aggregates [23, 24], at least in parts of their area of distribution. Aggregate species often are so-called polyploid complexes. A taxonomically extremely difficult situation is illustrated by the highly variable species pair *R. auricomus* and *R. cassubicus* which comprises fertile diploid ($2n = 16$) populations and assumedly hybridogenic polyploid ($2n = 24, 32, 40, 48$ and still other cytodemes) populations. The polyploids are facultative or obligate apomicts, but need pollination for seed setting (pseudogamy). Many species were described by splitters [for ref. see 31] within the *Ranunculus auricomus* complex which was treated by Linnaeus as comprising *R. auricomus* and *R. cassubicus* only.

Table 4 and accompanying explanations require some comments on the handling of plant material by phytochemists, and on presently accepted taxonomic practice:

I. In many instances consulting a taxonomic specialist for plant identification is highly desirable. However, taxonomic advice often does not guarantee unambiguity with regard to the material actually investigated. The only means of avoiding possible doubts and thus providing a means whereby the identification can be rechecked is to prepare and keep adequate voucher specimens for each phytochemical investigation.

II. Taxonomy is the only science which allows its practitioners, professionals as well as floristic amateurs, to change arbitrarily the circumscription and naming of accepted entities. The only requirement for acceptance of new taxa and names is to proceed according to the rules of the International Code [17].

III. Persons performing classificatory work should always realize that they are not only responsible to themselves and other taxonomists, but to all people who have to handle taxa. Generally new names and name changes at the specific and generic level do not really represent scientific progress and could easily be avoided. New facts, materials and insights, in most instances, could adequately be discussed within an existing classification and by making use of ranks such as subspecies and subgenus which do not affect binomina, or by using experimental categories (see later).

IV. Proposals for changes of taxon-delimitations or for the creation of new taxa at the specific and generic levels should become valid only after having been evaluated by a panel of highly qualified taxonomists. A procedure similar to the periodical evaluation of proposals adopted for purely nomenclatural questions (conservation of names of long-standing, but not corresponding with the rules of priority) could perhaps be used in a form adapted to the taxonomic problems in question.

V. Perhaps a way to really stabilize the names of plant species would be to declare the most suitable monographs of individual families and genera as valid and nomenclaturally obligatory. A panel of experienced taxonomists (see IV) should take responsibility for the choice of *the most appropriate monographs*. Proposals for alterations at the species or genus level in 'standard monographs' could periodically be evaluated and should be accepted only if they are scientifically really unavoidable.

Unless a satisfactory mode of proceeding is elaborated, synonymy at the species level will continue to expand and, moreover, names like ***Achillea millefolium*, *Ranunculus montanus*, *Valeriana officinalis*** and many others will remain ambiguous notwithstanding the commonly used author citations.

Table 5 compares five modern systems of angiosperms. The differences concerning taxon-delimitation and taxon-ranking are obvious, but at the higher levels of the taxonomic hierarchy such disagreements between taxonomists have insignificant practical consequences. Most scientists are after all aware of the fact that taxa of the higher categories of plant classification are far from being definitive. Moreover, species names are by far the most important names needed for communication about the practical properties of plants.

Three of the five authors mentioned in Table 5 rank angiosperms as a division whereas refs [28] and [29] rank them as class. The considerable differences in the number of orders and families are caused by different taxon-delimitations. The three liliiflorean families Liliaceae, Philesiaceae and Smilacaceae of ref. [28] correspond, for instance, to Colchicaceae, Herreriaceae, Liliaceae s.str., Alstroemeriaceae, Alliaceae, Hemerocallidaceae, Amaryllidaceae, Phormiaceae, Agavaceae, Doryanthaceae, Asphodelaceae, Xanthorrhoeaceae, Aphyllanthaceae, Huanguanaceae, Asparagaceae, Dracaenaceae, Tecophilaeaceae, Hypoxidaceae, Philesiaceae, Trilliaceae and Smilacaceae of ref. [21].

Differences between proposed angiosperm classifications are not only caused by taxon-delimitations. In many instances they express fundamental disagreements concerning relationships of taxa. Those who believe that the Umbelliferae and Compositae are directly related [37] will arrange these families differently from Cronquist [38], who is convinced that the Asterales came from the Rubiales.

The study of relationships of taxa—independently of their explanations (blueprint of creation versus evolution)—formed a fundamental part of scientific plant classification from its beginning. Therefore taxonomists began to use all available features for the elaboration of multipurpose classifications. Harborne and Turner [39] summarized the trends in acquisition of new data by plant taxonomy in their table 3.1 and classified features used as characters in essentially four groups (if their Evolutionary Period is dropped).

1. Megamorphic features or characters: morphological description and delimitation of taxa.
2. Micromorphic features: comparative anatomy, palynology, embryology.
3. Cytogenetic or karyologic features: chromosome numbers and karyotypes; meiotic behaviour of chromosomes etc.; essentially corresponds to part of field E in Table 1.

Table 5. Numbers of taxa at higher hierarchic levels in five modern classifications of angiosperms

	Ranks or Categories*					
Classification	Divisions	Classes	Subclasses	Superorders	Orders	Families
Engler's Syllabus [36]	1[a]	2[b]	2[c]	—[d]	62	343
Takhtajan [21]	1[e]	2[f]	10[g]	28[h]	92	410
Cronquist [15]	1[e]	2[f]	11[g]	—[d]	102	392
Thorne [28]	—[d]	1[i]	2[k]	28[l]	53	350
Dahlgren [29]	—[d]	1[m]	2[n]	33[l]	109	456

* *Key to superscripts:* [a]Angiospermae; [b]Dicotyledoneae and Monocotyledoneae; [c]rank only used in Dicotyledoneae: Archichlamydeae and Sympetalae; [d]rank not used; [e]Magnoliophyta; [f]Magnoliopsida and Liliopsida; [g]recommended termination -idae used; [h]termination -anae used; [i]alternative name for Angiospermae = Annonopsida; [k]alternative names for Dicotyledoneae and Monocotyledoneae = Annonidae and Liliidae; [l]termination -florae used; [m]Magnoliopsida (= Angiospermae); [n]Magnoliidae (= Dicotyledoneae) and Liliidae (= Monocotyledoneae).

Note that the taxa Magnoliopsida and Magnoliidae of ref. [29] and Liliidae of refs [28] and [29] are much more comprehensive than Magnoliopsida, Magnoliidae and Liliidae of ref. [21].

4. Biochemical features: micro- and macromolecules and metabolic pathways as characters.

Their dating of the *Biochemical Period* as '*ca* 1950 (?) to—(?)' is not wholly adequate in my view. In fact chemical characters belong to the earliest non-morphological characters applied to plant classification by distinguished taxonomists [40] and organic chemists [41, 42]. It is true, of course, that the explosive development of comparative phytochemistry started towards 1960, but methods and principles of chemotaxonomy, the field which I define as comparative phyto- and biochemistry applied to all aspects of plant taxonomy, were clearly described by men like De Candolle [40], Rochleder [41], Greshoff [42] and others [43] in the nineteenth and the beginning of the twentieth century. The rest of this essay is devoted to chemotaxonomy.

CHEMOTAXONOMY AND PLANT CLASSIFICATION

In many instances plant classifications have to be established without the help of adequate fossil remains. Phylogeny of taxa is reconstructed with the aid of character comparison of living plants. The task of taxonomists is rendered very difficult, however, by relatively rapid divergences of characters and taxa in the course of adaptive radiation, and by several types of convergence known to occur during taxon evolution. Inevitably all existing systems of classification are imperfect, in part. In such cases chemical characters may be very helpful. A really significant use of chemical characters requires a relatively sound knowledge of the chemistry, biochemistry and distribution of natural products on the part of the taxonomist, and of taxonomic and biological practices and problems on the part of the chemist. The following general points may be made.

I. Many phytoconstituents vary in their distribution within the plant. The amount and composition of classes of compounds such as alkaloids, flavonoids, essential oils, cardenolides and many others are governed by the age of the plant or its parts, by the plant's locality (a geographical component) and its habitat (an ecological component). A soild knowledge of chemical variation is essential. Geographical and ecological variation has two main aspects. It may be the result of the plasticity of individual genotypes (modifications), or of a genetic heterogeneity of plant taxa. Local populations of cross-breeding species are built up by a variable number of individual genotypes some of which may be chemical variants. Genetical variation in local populations is called *genetical polymorphism*, or *polymorphism* for short. Polymorphism is one of the starting points of differentiation: individual variants (inclusive of chemical ones) are able to become new races by migration and selection. Species which comprise several races or subspecies, i.e. units with their own combination of characters and area and (or) habitats are called *polytypic*. The phytochemist is mainly interested in chemical polymorphism and chemical polytypism which may or may not be correlated with other types of variation. As already mentioned, limits between races, subspecies and species, i.e. between taxa, are highly subjective. Nevertheless variants and races represent essential entities of species evolution (speciation). We should be able to communicate about them. For such purposes the infraspecific categories of experimental plant taxonomy, such as convivia and ecotypes, are available and preferable because they are independent of the Code [17] and do not interfere with botanical nomenclature. By far the most universal and most versatile categories are *demes* [44]. The deme terminology was unfortunately abandoned by Briggs and Walters in the second edition of their excellent book [45]. A deme is a local group of individuals [local population(s)]; the term should be used combined with prefixes which specify the type of deme under discussion. The following examples clearly illustrate the possibilities and advantages of the deme terminology:

Gamodeme: A more or less intrabreeding population.
Agamodeme: Population of apomicts.
Autogamodeme: An autogamous population.
Ecodeme: A population of a specific ecological habitat.
Topodeme: A population of a specific geographical area.
Chemodeme: A population differing chemically from others.
Cytodeme: A population differing in some cytological features (e.g. chromosome number or karyotype).
Genodeme: A population differing genetically.
Ecogenodeme: An ecological race or an ecotype sensu Turesson.
Chemo-ecogenodemes } Chemical races in the
Chemo-topogenodemes } taxonomic sense.

It should be clear that a chemodeme may be at the same time a cytodeme etc.; the properties indicated by the prefix(es) used in a discussion are those under study. It is also immediately apparent that application of the deme terminology in the case of polyploid aggregates (e.g. *Ranunculus montanus* s.l., Table 4) and groups in which apomicts predominate (e.g. the *Ranunculus auricomus* complex) would prevent such a confused nomenclature as occurs in taxonomically difficult species aggregates.

Without any doubt, many plant species comprise a number of chemodemes or even 'pure' chemical races.

II. *Analogies* and *homologies* of chemical characters are only recognizable if we have enough biogenetical information or sufficient plausible biogenetic hypotheses (Figs 1–3).

III. Very often, even homologous characters cannot be used as indicators of phylogenetic relationships because metabolic convergence is a very common feature (Fig. 4). Errors of judgement and consequent classificatory fallacies are only avoidable by a careful examination and comparison of many types of characters.

IV. Many secondary metabolites perform diverse ecological roles. Chemotaxonomy should not neglect this aspect of natural products. The less secondary metabolites deviate from essential metabolites and the more the former are ecologically important, the more probable becomes their occurrence in unrelated taxa (Fig. 5).

V. Many natural products have a large number of unexpected occurrences; often, however, only trace amounts are detected in a given taxon (cf. Fig. 6). There are several arguments for qualifying storage of a given metabolite(s) as taxonomically more important than its synthesis alone. Storage is a much more complex event because it requires means of prevention of self-inhibition or self-poisoning. Moreover, only compounds stored to some extent are able to take over the larger part of the ecological functions demonstrated hitherto for secondary metabolites. Storage makes chemical characters readily applicable to taxonomic problems and gives biological sense to the immense number of individual compounds and patterns of natural products.

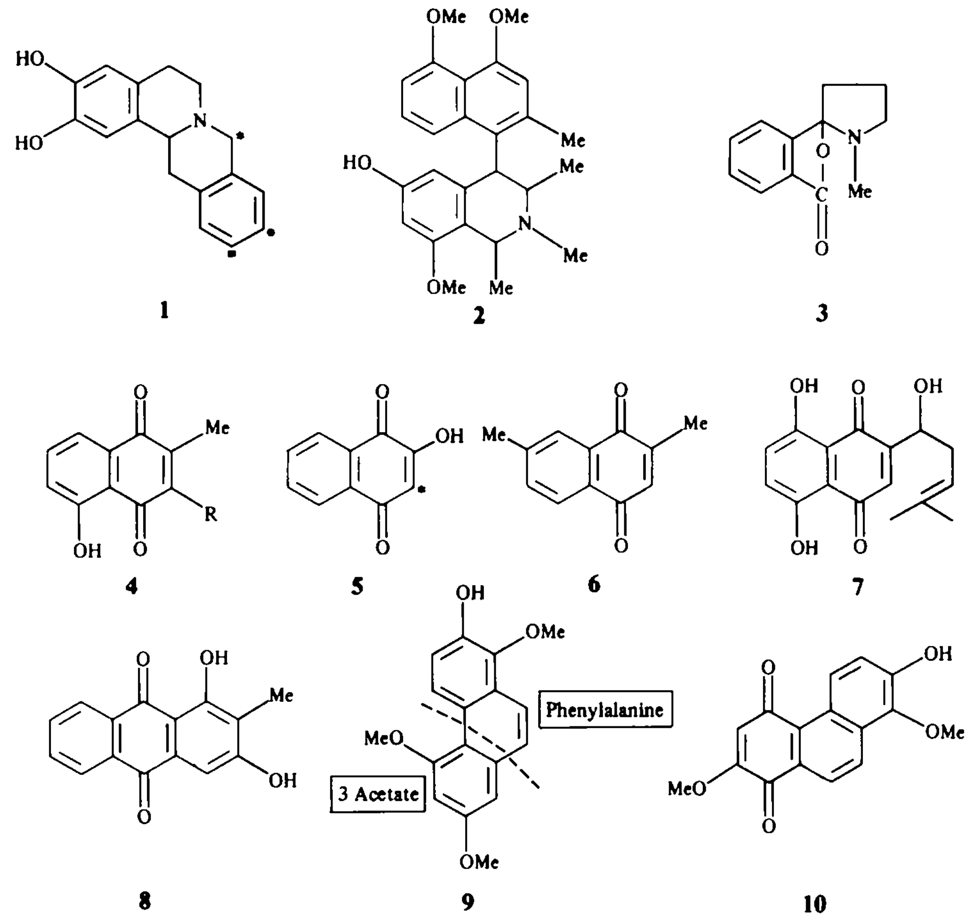

Fig. 1. Examples of biosynthetically analogous plant constituents, similar in structure, but elaborated along different metabolic pathways. **1**, An alkaloid with the tetrahydroprotoberberine skeleton, but biogenetically different from **2** of Fig. 2; compare **9** of Fig. 3; bharatamine from seeds of *Alangium lamarckii*. **2**, Ancistrocladine from several *Ancistrocladus* species, an isoquinoline alkaloid analogous to isoquinolines of Fig. 2; biosynthetically probably related to plumbagin and droserone which also occur in Ancistrocladaceae. **3**, Shihunine, an orchidaceous pyrrolidine alkaloid which comes from *o*-succinylbenzoic acid, and is therefore analogous to the more usual pyrrolidine derivatives which come from ornithine. **4–7**, Four structurally similar naphthoquinones with different biosynthetic pathways, plumbagin (R = H) and droserone (R = OH) (polyketides), lawsone (a derivative of *o*-succinylbenzoic acid = 4-[2′-carboxyphenyl]-4-oxobutyric acid), chimaphilin (derived from prenylated homogentisic acid or toluhydroquinone) and alkannin and shikonin (derived from geranylated *p*-hydroxybenzoic acid). **8**, Digitolutein, an anthraquinone biogenetically related to **5** by prenylation of position *, but analogous to **10** on Fig. 2. **9**, An orchidaceous phenanthrene (*Oncidium cebolleta*), analogous to phenanthrenes **6–8** of Fig. 2. **10**, Cypripedin, an allergenic *Cypripedium* naphthoquinone, homologous to **9**, but analogous to **4–7**. This phenanthrenoid metabolite is also analogous to the phenanthrenes **6–8** of Fig. 2.

After these introductory remarks we turn to examples which show that chemotaxonomy has indeed much to offer to plant taxonomy. References to most of the matter discussed in what follows can easily be traced in refs [10–12]; otherwise, a small number of additional references will be given.

After the detection of betacyanins and betaxanthins in Cactaceae and Didiereaceae the centrospermous affinities were more or less generally accepted for these taxa. The occurrence of betaxanthins in the fungus *Amanita muscaria* by no means invalidates their importance in angiosperm classification.

For a long time Aristolochiaceae represented a taxon *incertae sedis*. The presence of idioblasts storing essential oils and of aporphine-type alkaloids, the precursors of the family-characteristic aristolochic acids and aristololactams, has convincingly shown that Wettstein (1935) was right, when he classified the family next to Annonaceae in his order Polycarpicae (see Fig. 2).

The order Piperales of ref. [36] comprising Saururaceae, Piperaceae, Chloranthaceae and Lactoridaceae was rearranged in refs [28] and [29]. Thorne [28] included all these families in his large superorder Annoniflorae, whereas Dahlgren [29] distributed them over his superorders Magnoliiflorae (Lactoridaceae, Chloranthaceae) and Nymphaeiflorae (Saururaceae, Piperaceae). All Piperales sensu [36] contain essential oils in idioblasts and lack galli- and ellagi-

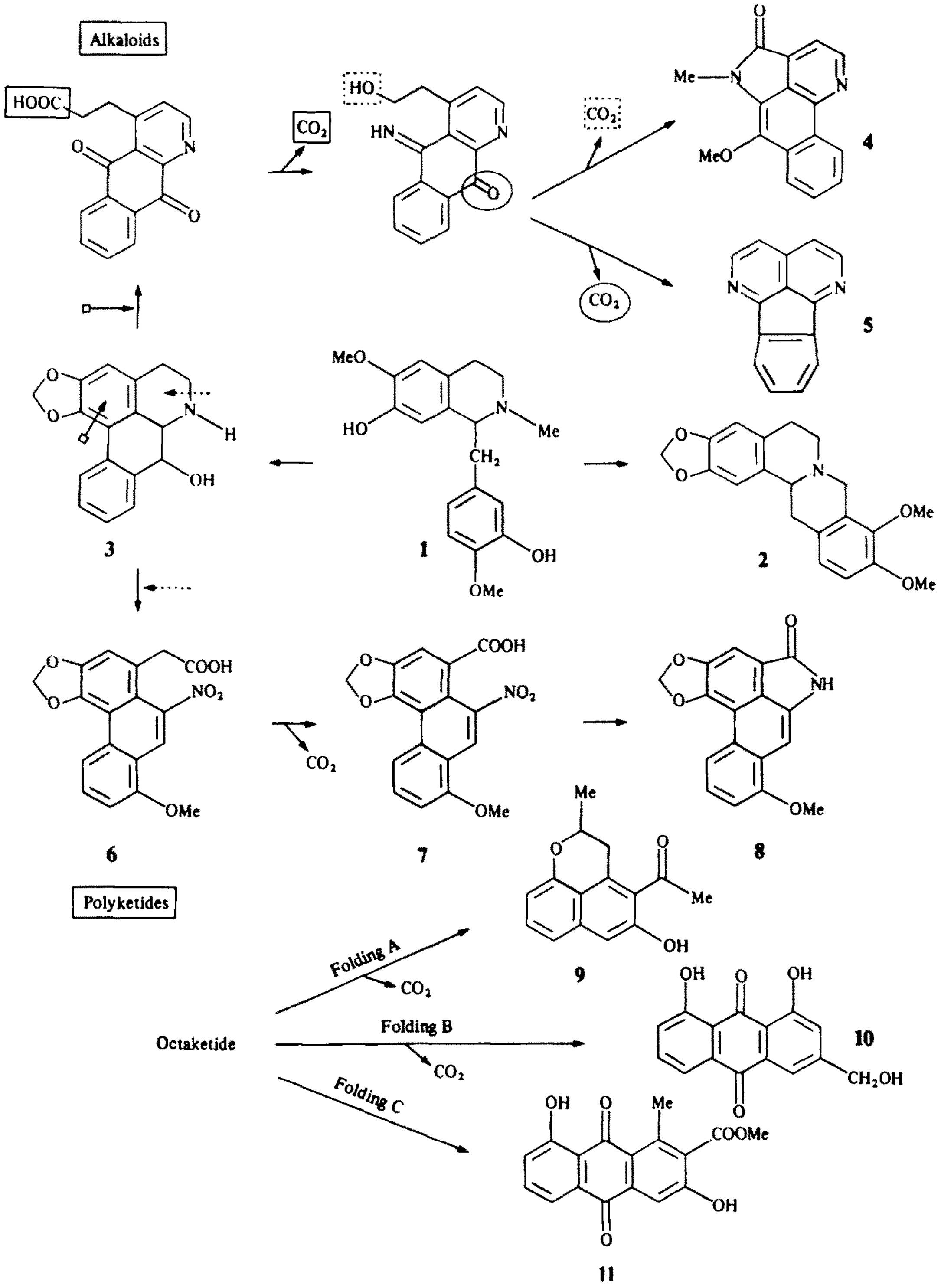

Fig. 2. Some examples of assumedly homologous metabolites which have, or have not, retained similarity of structure: some biogenetically intermediary skeleta are illustrated by compounds isolated from plants. 1–8, Members of the benzylisoquinoline family of alkaloids: 1 = reticuline, a benzylisoquinoline; 2 = canadine (= tetrahydroberberine), a tetrahydroprotoberberine alkaloid; 3 = norushinsunine, an aporphine; 4 and 5 = eupolauridine and eupolauramine, alkaloids of *Eupomatia laurina* with strongly modified skeletons [49]; 6–8 = nitrophenanthrenes and lactams which are characteristic of Aristolochiaceae, but have also been detected in Annonaceae; 6 = debilic acid; 7 = aristolochic acid-I; 8 = aristololactam; 9–11, acetogenins of Liliaceae; 9 = xanthorrhoeol; 10 = aloe-emodin; 12 = aloesaponarin-I.

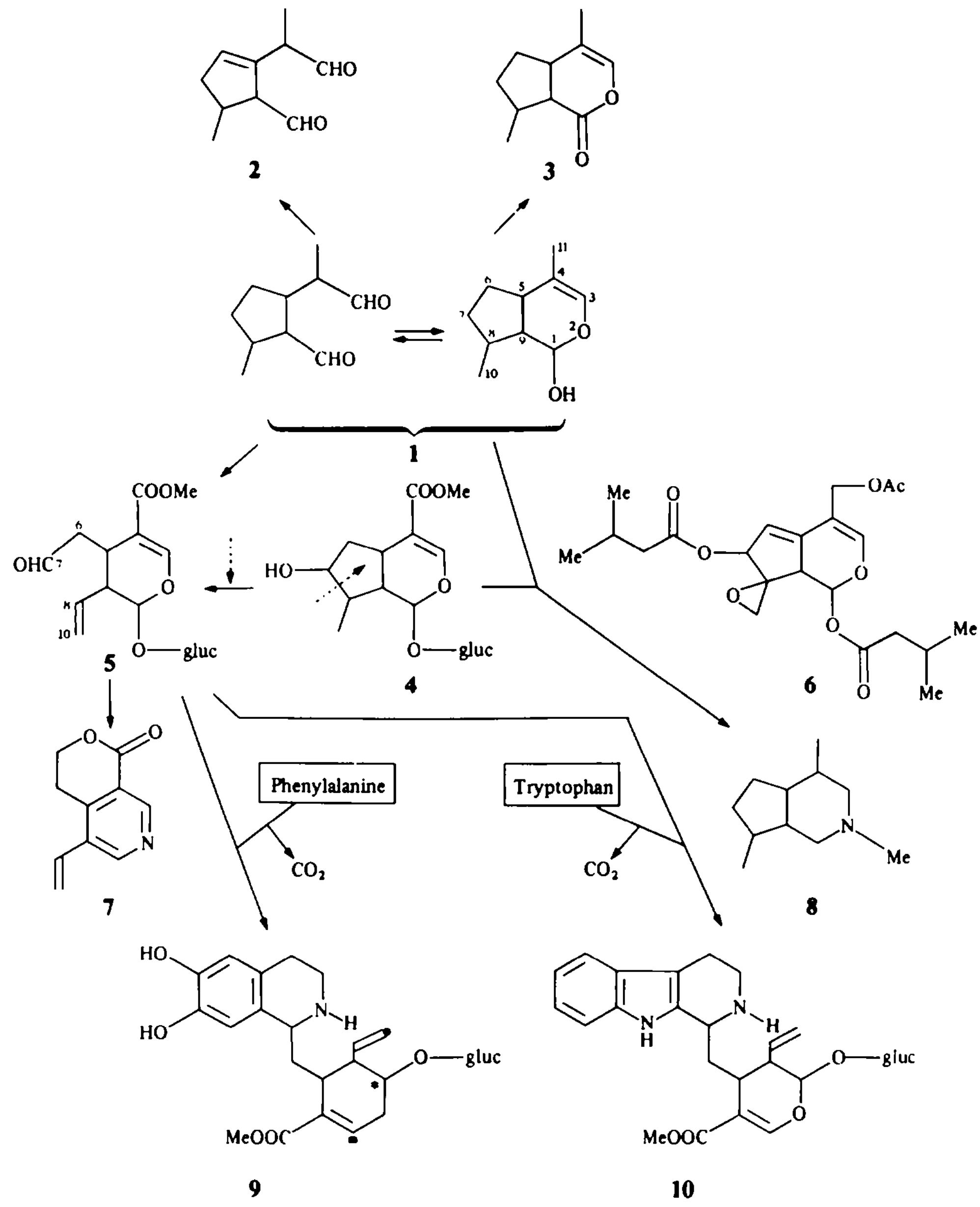

Fig. 3. The biogenetically homologous, but structurally highly diverse class of iridoid compounds. 1–3, Steam-volatile compounds, iridodial, dehydroiridodial and nepetalactone. 4, iridoid glycosides, loganin and 8-epiloganin; 5, a secoiridoid glucoside, secologanin; 6, an ester iridoid, valtratum; 7, a secoiridoid pyridine alkaloid, gentianine; 8, an iridoid piperidine alkaloid, skytanthine; 9, a secoiridoid isoquinoline alkaloid glucoside, desacetylipecoside; compare 1 of Fig. 1; 10, a secoiridoid indolic alkaloid, strictosidine; precursor of many so-called complex indole alkaloids.

tannins; moreover Piperaceae produce benzyltetrahydroisoquinoline alkaloids, many types of lignans and neolignans, and a large array of amides of which some are very acrid; Chloranthaceae produce sesquiterpenoids including C_{15}-lactones, reminiscent of compounds of Magnoliaceae and Lauraceae, and Saururaceae store lignans and neolignans. As a whole the chemistry of Piperales sensu [36] strongly suggests that Thorne's reclassification is much more natural than Dahlgren's, because Nymphaeales, the second order of Nymphaeiflorae sensu [29] lack oil-idioblasts and isoquinoline alkaloids, but produce rather large amounts of galli- and ellagitannins.

Iridoids in the broadest sense (Fig. 3) are highly characteristic metabolites which occur mainly in a number of assumedly phylogenetically related dicotyledonous plant families, if their occurrence in Malpighiaceae [46], insects [47] and molluscs [48] is neglected. The detec-

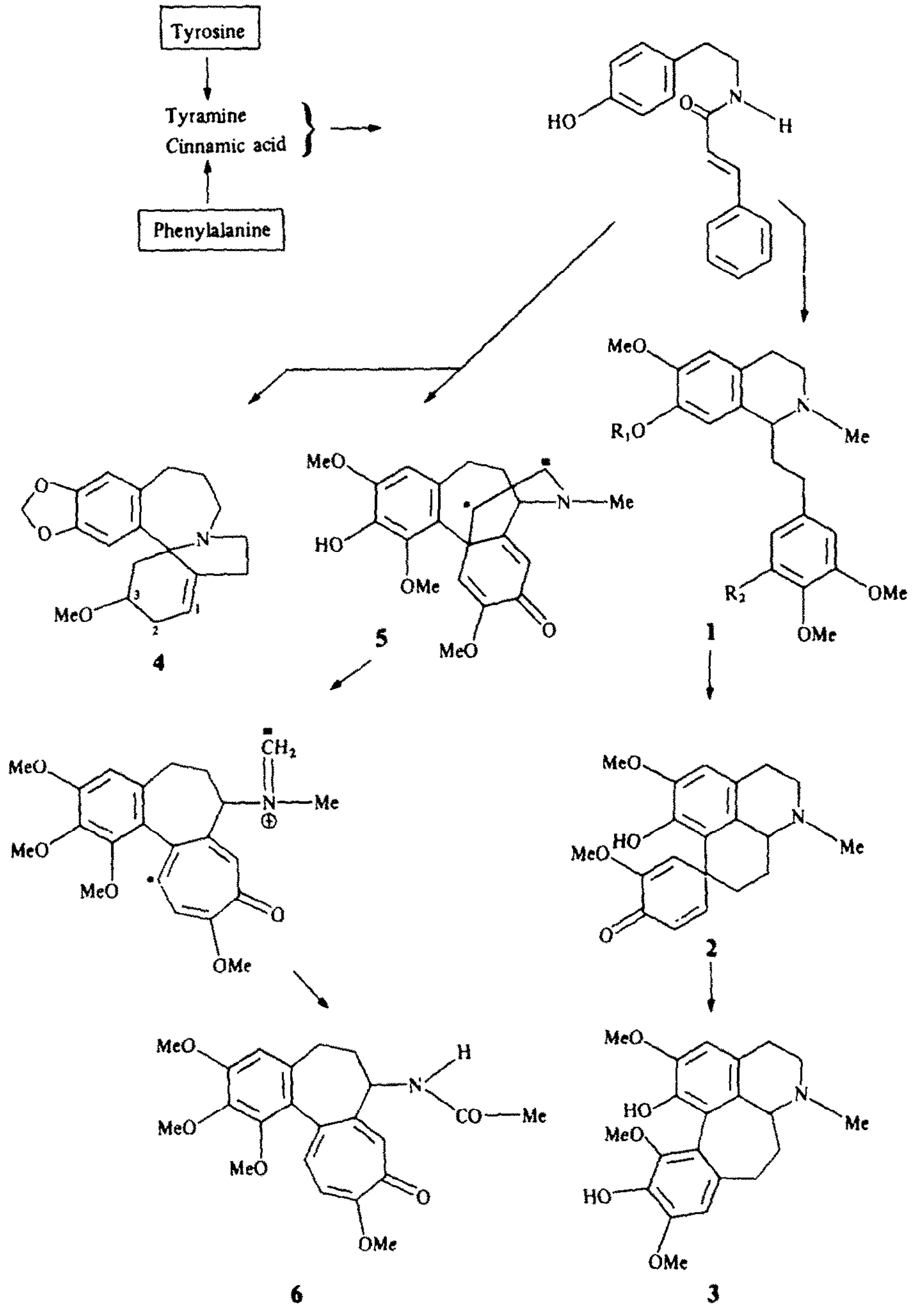

Fig. 4. A striking example of metabolic convergence: the family of phenylethylisoquinoline alkaloids (some individual types of alkaloids represented by compounds isolated from plants). 1, The phenylethylisoquinolines autumnaline ($R_1 = H$, $R_2 = OH$) and homolaudanosine ($R_1 = Me$, $R_2 = H$); 2, the homoproaporphine group (kreysiginone); 3, the homoaporphine group (multifloramine); 4, the homoerythrinane group (schelhammericine and 3-epischelhammericine); 5, the homomorphinane group (androcymbine); 6, the tropolone type (colchicine). 1–6 occur in Liliaceae-Wurmbaeoideae (= Colchicaceae) and 6 seems to be restricted to this taxon, but 1 was also detected in Meliaceae and 4 occurs also in Cephalotaxaceae, Taxodiaceae, Aquifoliaceae (Phelline: also classified in Phellinaceae) and Meliaceae.

tion of iridoids in Callitrichaceae, Eucommiaceae, Fouquieriaceae, Hippuridaceae, part of Icacinaceae, *Liquidambar*, part of Loasaceae, Theligonaceae and other often mono- or oligotypic taxa made a considerable contribution to their appropriate classification.

CHEMOTAXONOMY AND DIFFERENTIATION (FIG. 7)

When briefly discussing polymorphism and polytypism above, ecogeographical evolution of new taxa was mentioned briefly. The study of variation and differentiation

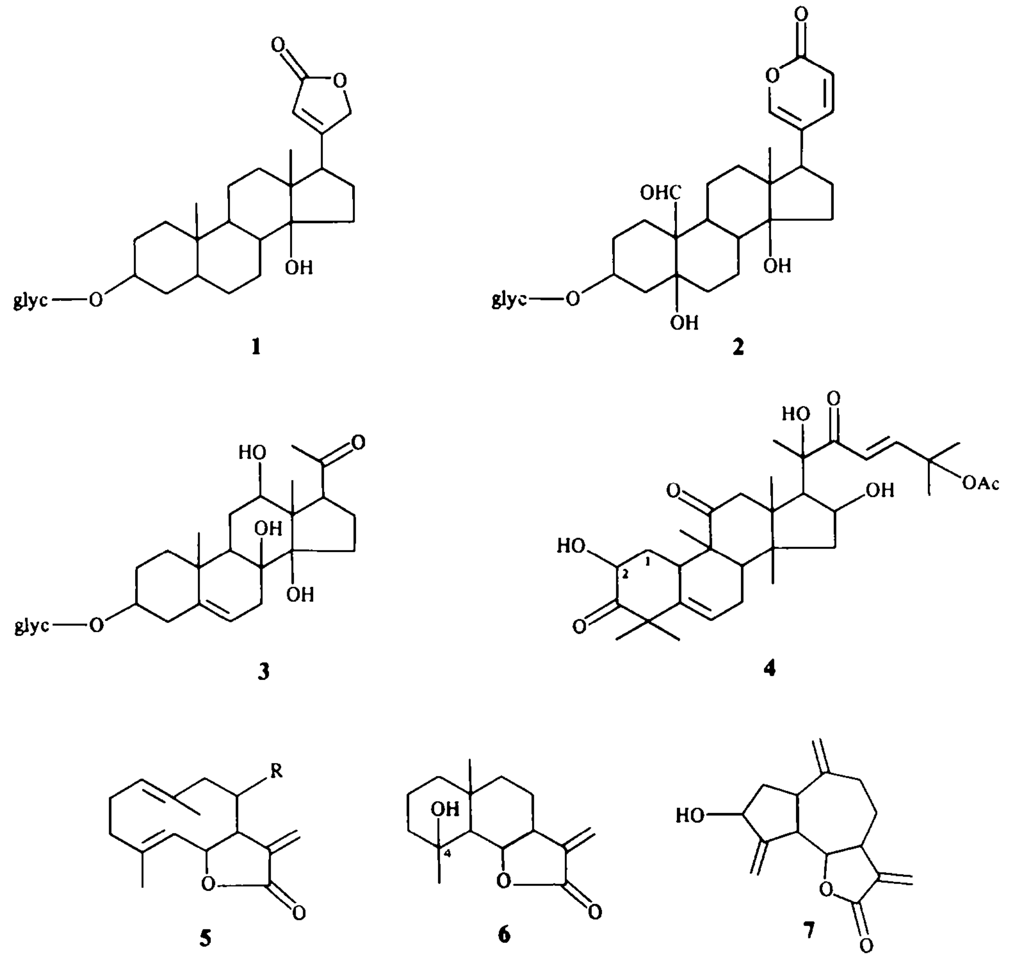

Fig. 5. Some biologically highly active compounds which are stored erratically by green terrestrial plants: Metabolic convergences based on ecological functions? **1**, A glycoside of digitoxigenin, a cardenolide; toxic and bitter-tasting cardenolides occur in many families of angiosperms. **2**, A glycoside of hellebrigenine, a bufadienolide; bufadienolides occur, e.g. in Liliaceae, Ranunculaceae, Crassulaceae and Melianthaceae; moreover, they are defensive substances of many toads. **3**, A glycoside of hydroxylated pregn-5-ene; such pregnenes are known from several families of angiosperms (e.g. Ranunculaceae, Scrophulariaceae); bitter, acylated pregnanoid glycosides replace cardenolides in part of Asclepiadaceae. **4**, Cucurbitacin-B and -E (Δ1, 2). Bitter and cytotoxic cucurbitacin-type tetracyclic triterpenes occur in many families of Dilleniidae sensu [21], but have also been isolated from a liliaceous, a rosaceous, a scrophulariacean genus and from *Desfontainia spinosa* [50]. **5**, Costunolide (R = H) and tulipinolide (R = βOAc). **6**, Arbusculin and 4-epiarbusculin. **7**, Zaluzanin-C. **5–7** are examples of so-called germacranolides, eudesmanolides and guaianolides which occur in Hepaticae, Cupressaceae, Magnoliaceae, Lauraceae, Umbelliferae and Compositae. Such sesquiterpene lactones are often very bitter and sometimes taste acrid; in many instances they were shown to possess allergenic, ichthyotoxic, cytotoxic, anti-feedant and other biological activities.

in plants is the field of genecologists, population geneticists and experimental plant taxonomists (field E in Table 1). Experimental plant taxonomy aims at the analysis of variation and an understanding of the so-called microevolution, a field also called speciation. The latter name is inappropriate in as much as it suggests that only taxa ranked as species are concerned. I have already advocated the use of subspecific taxonomic categories or the application of *deme*-terminology when reporting results of taxonomic or biosystematic studies with polytypic species. Independent of the classificatory treatment of the microevolutionary units studied, two main causes of local polymorphism and two main processes of differentiation can be discerned, and phytochemistry can provide key characters for the understanding of complex situations. The following examples serve to illustrate this point.

Local polymorphism depends on mutations or on hybridization. Many plant species are polymorphic with regard to cyanogenesis, that is, the release of HCN after cell damage. Usually cyanogenesis depends upon the presence of cyanogenic glycosides and corresponding hydrolysing enzymes in a given tissue. In the fern *Pteridium aquilinum* acyanogenic genotypes and popu-

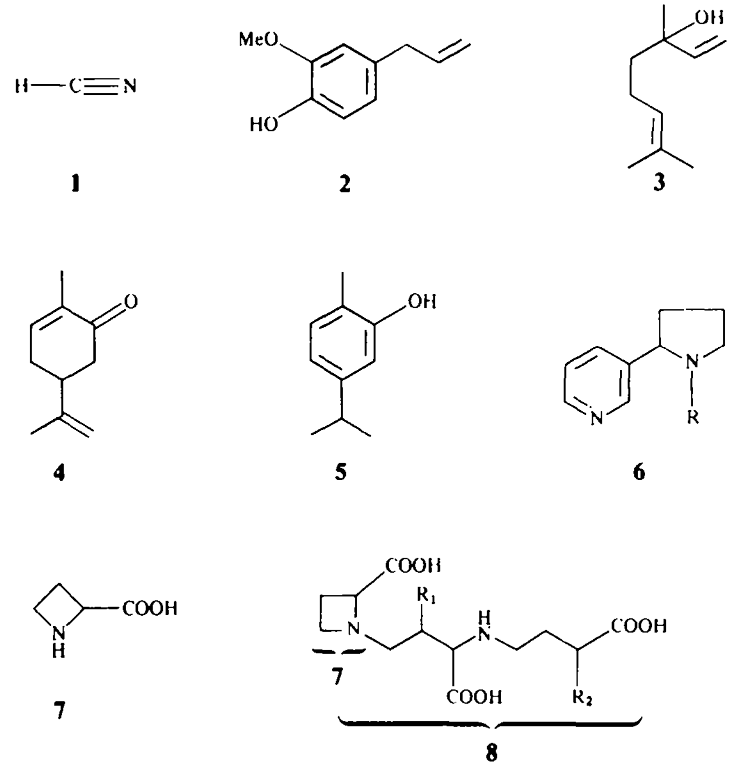

Fig. 6. Examples of secondary metabolites which are stored erratically in unrelated plant taxa, but which also occur widely to ubiquitously in trace amounts. 1, Hydrocyanic acid; erratically stored in the form of cyanogenic glycosides (e.g. 2 of Fig. 7) and lipids; probably ubiquiteous in trace amounts. 2, Eugenol; stored here and there in essential oils or as a glycoside; very widespread in trace amounts. 3, Linalol: as 2 [51]. 4, Carvone; stored here and there in essential oils; frequently present in trace amounts. 5, Carvacrol; like 2–4. 6, Nicotine (R = Me) and nornicotine (R = H); stored in taxa of Solanaceae and Compositae; known to occur in small to trace amounts in many plant families. 7, Azetidine-2-carboxylic acid; stored as defensive compound by part of Liliaceae (green parts) and some Leguminosae-Caesalpinioideae (seeds; seedlings); in trace amounts probably widespread; also stored by the red alga *Lophocladia lallemandii*. 8, Mugineic acid, an iron-chelating compound of barley, wheat and oat ($R_1 = R_2 = OH$) and nicotianamine ($R_1 = H$, $R_2 = NH_2$), a so-called phytosiderophore, which seems to be involved in cellular iron transport of all tracheophytes [M. Budesinsky *et al.* (1981) *Tetrahedron* 37, 191]. Essential metabolites such as 8 might explain the occurrence of trace amounts of 7 in many plants.

lations have lost by mutations the ability to synthesize and store prunasin or to produce active 'emulsin', or both. In the genus *Linaria* hybridization was proved to be a possible cause of local polymorphism. If the cyanogenic, prunasin-containing species *L. repens* (= *L. striata*) is crossed with acyanogenic *L. vulgaris* or *L. purpurea*, cyanogenic F_1-hybrids are produced. *L. repens* x *L. vulgaris* is knows as *L.* x *sepium* Allman (= *Linaria* nothospecies *sepium* Allman) [17; article 50; Appendix I, names of hybrids]. When *L.* x *sepium* is backcrossed to *L. vulgaris*, plants morphologically indistinguishable from *L. vulgaris* originate after a second and third backcrossing. Some of these *L. vulgaris* plants, however, proved to have retained cyanogenesis. Such a transfer of genes from one species to another by hybridization and backcrossing is called *introgressive hybridization* by Anderson; chemical characters may be very good indicators of this event.

Polytypism depends on migration followed by spatial isolation and ecological adaptation (radiation as already mentioned earlier) or on hybridization usually followed by genome doubling.* The former processes have been called *ecogeographical differentiation* (*speciation*) and the second one *saltation* or *abrupt speciation by* (*allo*)*polyploidy*. In both cases taxonomically difficult aggregates emerge in the first instance, and chemical characters may prove extremely useful in analysing and understanding complex patterns of variation.

Chemical ecogeographic differentiation was studied intensively with many essential oil bearing species; they were shown to comprise a number of chemodemes (*Asarum europaeum*, *Myoporum deserti*, *Thymus vulgaris* and others). Polytypism, however, can affect each class of

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*Speciation by hybridization without chromosome-doubling does also occur; this longlasting process belongs to the field of ecogeographical differentiation: increase of local polymorphism → migration → fixation of distinct genotypes by selection. Examples are *Petasites paradoxus* and *P. kablikianus* which are assumed to have originated by hybridization between *P. albus* and *P. hybridus*; all taxa have $2n = 60$. See L. Novotny *et al.* (1966, 1968) *Phytochemistry* 5, 1281; 7, 1349.

phytoconstituents. Two other examples should suffice to illustrate this fact. *Withania somnifera* has a number of withanolide-type C_{28}-steroidal lactone-chemodemes [52], and *Lantana camara* comprises toxic and non-toxic triterpene-chemodemes [53].

Chemical constituents are valuable characters during studies of polyploid complexes. Essential oils proved to be useful with *Acorus calamus* (2x, 3x, 4x), and mangiferin was shown to be an indicator of the *Asplenium montanum* genome in the Appalachian polyploid aggregate which also contains the diploids (2x) *A. platyneuron* and *A. rhizophyllum* and the fertile allotetraploids (4x) *A. bradleyi*, *A. pinnatifidum* and *A. ebenoides*, besides a number of sterile diploid, triploid and tetraploid hybrids. By a study of allozyme variation it could recently be demonstrated [54] for *A. bradleyi* and *A. pinnatifidum* that the assumption of recurrent (= polytopic) origins of these allotetraploids explains most satisfactorily the observed patterns of variation. It is still not known how current polytopic 'speciation' is in nature; probably it is a rather common event in the case of allopolyploid taxa. Mangiferin may also be a genome indicator in that European species group of Asplenia which comprises diploid *A. cuneifolium*, *A. obovatum* and *A. onopteris* and allotetraploid *A. adiantum-nigrum* and *A. balearicum*. Filixic acid-BBB is a characteristic acylphloroglucinol of several species of the large genus *Dryopteris*. Together with flavaspidic acid it occurs in all members of the *D. filix-mas* aggregate which comprises at least the allotetraploid *D. filix-mas* s. str., its diploid ancestors *D. abbreviata* (= *D. oreades*) and *D. caucasica*, and the apogamous taxon *D. borreri* (= *D. affinis* = *D. pseudomas*) [35] with diploid and triploid cytodemes. By hybridization and allopolyploidy *D. villarii* (2x), *D. pallida* (2x), *D. submontana* (4x) and *D. tyrrhena* (4x) are connected with the *filix-mas* aggregate. Phloroglucinol chemistry agrees perfectly with these assumptions based on biosystematic studies. All taxa mentioned lack aspidin and produce flavaspidic acid, para-aspidin (*D. abbreviata* excepted), filixic acid (except *D. pallida*) and desaspidin (*D. abbreviata* and *D. tyrrhena* excepted). Albaspidin seems to be restricted to the *villarii* group where it was detected in all members, and trispara-aspidin seems to be a character of *D. pallida* and its allotetraploid derivatives *D. submontana* and *D. tyrrhena*.

Alkaloid chemistry of the genus *Papaver* is extremely well known because *P. somniferum*, the opium poppy, belongs to it. *P. somniferum* is a polymorphic and polytypic Mediterranean species cultivated since antiquity for its oil-rich seeds and medicinally valuable latex. Today a large number of cultivars, agricultural as well as ornamental, are known. Many of the cultivars belong to distinct alkaloid-chemodemes [e.g. 55]. According to De Candolle *P. somniferum* originated from *P. setigerum*, a taxon variously interpreted as a subspecies of *P. somniferum* or as a species of its own which mainly occurs in the Mediterranean regions of France, Italy, Spain, Algeria and Tunisia. Karyosystematic and chemotaxonomic studies and hybridization experiments, however, do not agree with such a hypothesis. *P. somniferum* is diploid ($2n = 22$) and *P. setigerum* is allotetraploid ($2n = 44$) containing genomes SS from *P. somniferum* and UU from a still unknown diploid parental taxon [56]. Morphine and codeine, the main alkaloids of most strains of *P. somniferum*, wild forms as well as cultivars, are exclusively known from this taxon; they are accompanied by the less restricted and biogenetically related alkaloid thebaine and by a very large array of other types of benzylisoquinoline alkaloids. *Papaver setigerum* does not seem to store morphine, codeine and thebaine, but contains appreciable amounts of papaverine and laudanosine [55, 57]. The origin of *P. somniferum* and of its unique character, morphine synthesis and storage, are still unknown. It is self evident that every biosystematic study aiming at an understanding of the evolution of *P. somniferum* and its many forms cannot neglect alkaloid patterns.

CHEMOTAXONOMY AND ECONOMIC AND MEDICAL BOTANY

Phytochemists and economic botanists are often looking for new sources of important chemical compounds (examples: colchicine, quinine, reserpine; digitoxin) or classes of constituents (examples: tanning materials; complex indole alkaloids). Generally they will be most successful when they follow the lead of natural classification supplemented by phytochemical knowledge, i.e. if they use the chemotaxonomic approach. There are many examples; the few given suffice, however, to illustrate the fact that comparative phytochemistry combined with an adequate plant classification is an excellent guide for chemical exploration of the plant world.

The same is true of prevention and treatment of plant poisoning of animals and man. If poisoning is caused by a plant species related to *Colchicum autumnale*, for instance by *Gloriosa superba* from a bunch of flowers or by *Bulbocodium vernum* cultivated in a garden, it will be wise to suspect colchicine (**6**, Fig. 4)-poisoning and to act correspondingly. The same holds for the many types of plant contact dermatitis. Tuliposide-A and its allergenic product of hydrolysis, tulipalin-A, not only occur in all species of the large genus *Tulipa*, but also in related liliaceous genera such as *Erythronium*, *Gagea* and *Alstroemeria*.* Very recently Hausen *et al.* [59] reported that species of *Lilium* and *Allium triquetrum*, but not *Asparagus officinalis*, contain moderate amounts of 1-tuliposide-A. These authors suggested that breeding of the above-mentioned ornamental liliaceous taxa for high tuliposide-B and low tuliposide-A content could result in mildly allergenic cultivars retaining a reasonable disease resistance (Fig. 8).

CONCLUDING REMARKS

I hope to have shown that chemotaxonomy has a lot to offer to phytochemists, pharmacists, economic botanists, taxonomists and even physicians. One rather essential point has not yet been mentioned. In every instance when a phytochemist detects a chemical compound or pattern of chemical compounds in a given species which in virtue of chemotaxonomic arguments is unexpected, he should become alert. Did the material investigated really belong to the assumed taxon? Could compounds often isolated only in small amounts during large scale extractions not originate from one of many possible impurities? Just a few examples should exemplify this point. The dimethylpyranocoumarin jatamansin was not isolated from root-

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* Because of its pseudoepigynic flowers it is also classified in the separate family Alstroemeriaceae.

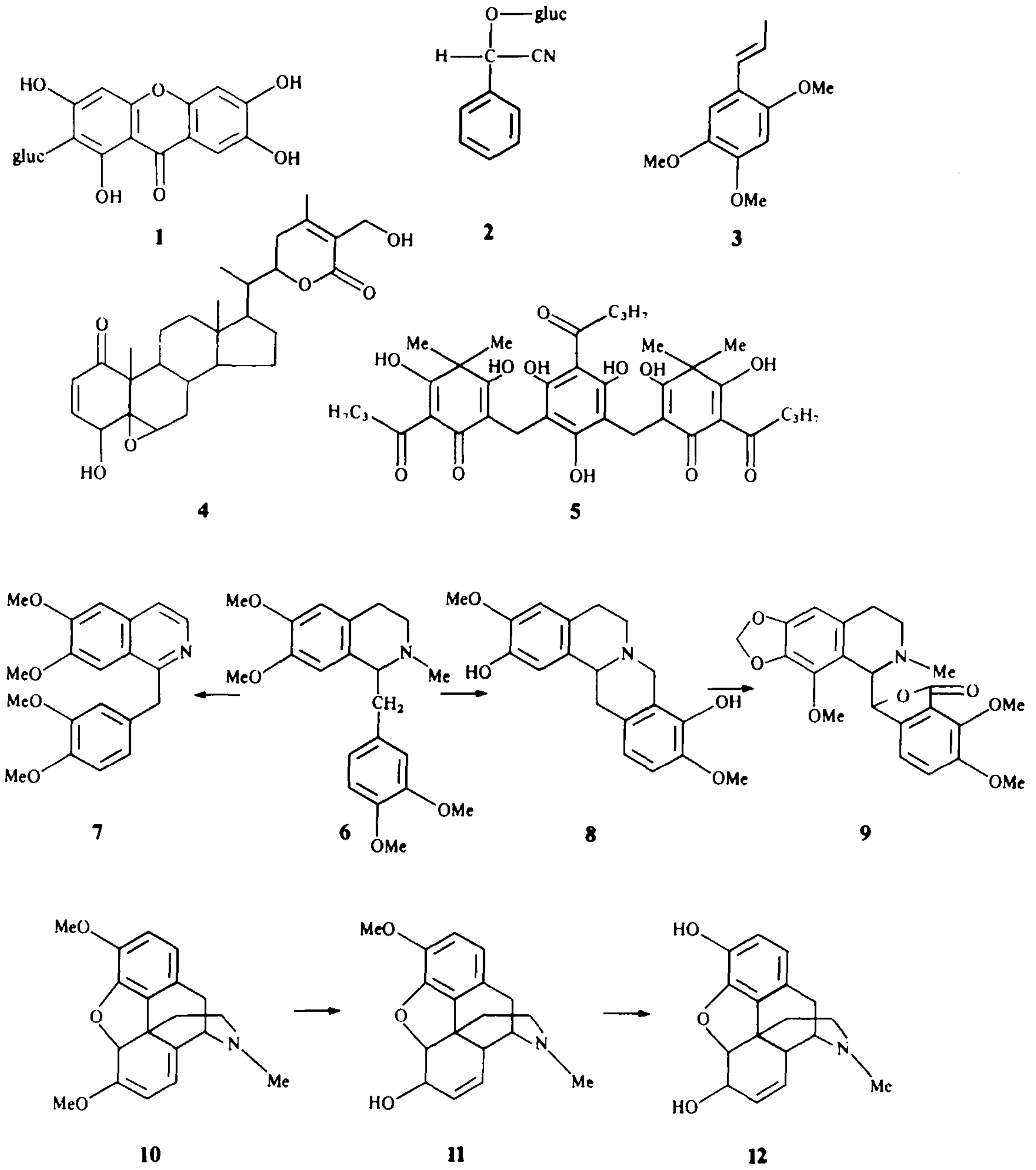

Fig. 7. Some plant constituents discussed in the text. **1** = Mangiferin; **2** = prunasin and sambunigrin [58]; **3** = *trans*-asarone (= *trans*-isoasarone). **4** = Withaferin-A, main C_{28}-steroidal lactone of chemodeme I (Israel) of *Withania somnifera*. **5** = Filixic acid-BBB, a characteristic phloroglucide of the *Dryopteris filix-mas* L. s. l. aggregate, which includes *D. abbreviata* (= *D. oreades*) (2x), *D. caucasica* (2x), *D. borreri* (= *D. affinis* = *D. pseudomas*) (2x, 3x) and *D. filix-mas* s. str. (4x). **6–12**: some types of benzylisoquinoline alkaloids (compare Fig. 2 also) of *Papaver somniferum* and their possible biosynthetic relationships; all types exemplified by alkaloids isolated from opium, the dried latex; **6** = laudanosine; **7** = papaverine; **8** = scoulerine; **9** = narcotine; **10** = thebaine; **11** = codeine; **12** = morphine.

stocks of *Nardostachys jatamansi* (Valerianaceae), but from their substitutes, rootstocks of *Selinum vaginatum* (Umbelliferae), and the taxane-type alkaloid cephalomannine did not come from *Cephalotaxus mannii* but from an Indian form of *Taxus baccata*.

I conclude with the suggestion that the amaryllidaceous alkaloids lycorine and acetylcaranine ascribed to bulbs of *Urginea altissima* (Liliaceae) [60] stemmed from misidentified amaryllidaceous bulbs, and that some mistake was made when sitosterol, yuccagenin and lycorine were isolated from rhizomes of *Curculigo orchioides* (Hypoxidaceae) [61].

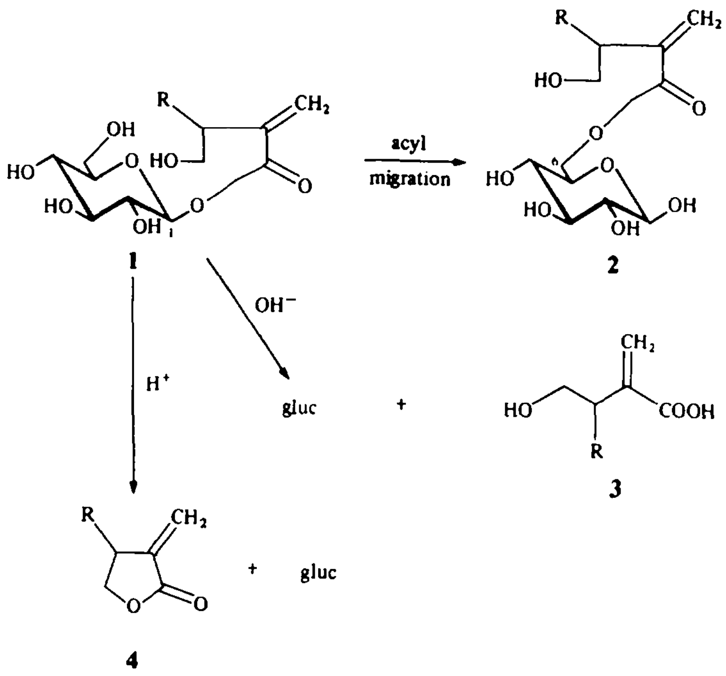

Fig. 8. The allergenic and antifungal (antibiotic) system of *Tulipa* and related liliaceous plants. **1** = Tuliposides-1 (very labile); **2** = tuliposides-6 (stable); **3** = α-methylene-γ-hydroxybutyric acids; **4** = tulipalins. R = H: A series (fungitoxic and allergenic activity of compounds); R = OH: B series (only fungitoxic activity of compounds). Only **1** and **4** are active.

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18. Besides Plantae and Animalia the regnum of Prokaryota (= Monera) formed by bacteria and blue–green algae (Cyanophyta = Cyanobacteria) and the heterotrophic regnum of Fungi are accepted in this case.
19. Margulis, L. and Schwartz, K. V. (1982) *Five Kingdoms. An Illustrated Guide to the Phyla of Life on Earth*. W. H. Freeman, San Francisco. The fifth regnum called Protoctista comprises all algae except blue–greens, Myxomycota, part of the former Phycomycota and many zooplankton organisms. Plantae are restricted to Cormophyta (Mosses, Liverworts and Tracheophytes).
20. Nine family names of long standing and usage remain valid; they may be replaced by alternative names: Compositae (= Asteraceae), Cruciferae (= Brassicaceae), Gramineae (= Poaceae), Guttiferae (= Clusiaceae), Labiatae (= Lamiaceae), Leguminosae (= Fabaceae *sensu lato*), Palmae (= Arecaceae), Papilionaceae (= Fabaceae *sensu stricto*), Umbelliferae (= Apiaceae). It is evident that in the

case of Leguminosae and Papilionaceae the older names are preferable, because they distinguish sharply the two taxa.

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30. *International Code of Nomenclature of Cultivated Plants* (1969) (Gilmour J. S. L., *et al.*, eds), *Regnum Vegetabile*, Vol. 64, publ. by the Bureau of IAPT, Utrecht. Last edition 1980 not seen by me.
31. Damboldt, J. (1974) *Ranunculus*, S. 232–317 in Hegi: *Flora von Mitteleuropa*, 2. Aufl., Band III/3, Carl Hanser, München.
32. Ovczinnikov (Ovchinnikov), P. N. (1937) *Ceratocephalus*, *Oxygraphis*, *Halerpestes*, *Ficaria* and *Ranunculus*; in *Flora of the U.S.S.R.* (Komarov, V. L., ed.) Vol. VII, *Ranales and Rhoeadales*, Izdatel'stov Akad. Nauk SSSR, Moskva-Leningrad; Engl. translation by Z. Blake, Israel Program for scientific translations, Jerusalem, 1970.
33. Kreczetowicz (Krechetovich), V. I. (1937) *Batrachium*, pp. 260–271 in ref. [32].
34. The needless annoyance of name changing is humorously discussed by R. J. Chancellor from the Weed Research Organization, Oxford, in Newsletter Ass. Appl. Biologists; Reprinted in B. S. B. I. News Dec. 1985 No. 38, p. 29. He discerns four types of name changes: *The reciprocating type*, *the progressive type*, *the Uncle Tom Cobbleigh et al. variation* and *the Musical Chairs type* which is illustrated by a diagram called "the Dance of the Mayweeds" which among other species includes the medicinally very important *Matricaria chamomilla*.
35. P. 46 of BSBI Abstracts, Part 15, July 1985 reports "*New*" *Names in the Flora of the British Isles*. Particularly I should like to draw attention to the cases of *Alstroemeria aurea* Graham replacing *A. aurantiaca* D. Don, *Silene flos-cuculi* (L.) Greuter et Burdet replacing *Lychnis flos-cuculi* L. and the ever namechanging fern *Dryopteris borreri* and its variants; the two names mentioned, *D. affinis* subsp. *borreri* var. *robusta* (Oberholzer et Tavel ex Fraser-Jenkins) Fraser-Jenkins et Salvo, stat. nov. (1984) and *D. pseudomas* subsp. *robusta* (Fraser-Jenkins) Holub (1984), represent the same taxon. Another example of a nomenclatural puzzle is supplied by *Amaracus* and *Majorana*. It is rather disappointing that several recent species of *Amaracus* had their names changed between 1975 and 1980. The point is that the genera *Amaracus* and *Majorana* are retained by some taxonomists (e.g. Briquet, 1897; Wunderlich, 1967; Brullo and Furnari, 1979), but are included in *Origanum* by others (e.g. Ietswaart, 1980). The result is that the much appreciated spice marjoram bears the names *Majorana hortensis* (also *Majorana vulgaris*) and *Origanum majorana* (and many others), and that *Origanum akhdarense* Ietswaart et Boulos (1975) became *Amaracus akhdarense* (Ietswaart et Boulos) Brullo et Furnari in 1979 [this name is used by Piozzi *et al.* (1985) in *Phytochemistry* **24**, 1113], and that *Amaracus pampaninii* Brullo et Furnari (1979) became *Origanum pampaninii* (Brullo et Furnari) Ietswaart in 1980. It is also rather ridiculous that a statement like Pimenow's [*Taxon* **34**, 274 (1985)] is necessary; when commenting on Hirose's monotypic genus *Transcaucasica* (Umbelliferae-Saniculoideae) he wrote: "I believe it is necessary to know at least the genera of the family being studied when describing new ones, especially from a region little known to the describer".
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38. Cronquist, A. (1980) *Chemistry in Plant Taxonomy: An Assessment of Where We Stand*; in *Chemosystematics: Principles and Practice* (Bisby, F. A., *et al.*, eds) pp. 1–27. Academic Press, London.
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45. Briggs, D. and Walters, S. M. (1969, 1984) *Plant Variation and Evolution*, 1st and 2nd edns. University Press, Cambridge; see 2nd edn, p. XII.
46. Several iridoid glycosides isolated from *Stigmatophyllon sagittatum* and *S. convolvulifolium*, but not detected in leaves and bark of *S. splendens*; D. Sainty *et al.* (1981) *J. Nat. Prod.* (*Lloydia*) **44**, 576; E. Davioud *et al.* (1985) *Planta Med.* **51**, 78.
47. In defensive secretions of Orthoptera (*Anisomorpha bupre-*

stoides), of imagines (Cerambycidae, Staphylinidae) or larvae (certain Chrysomelidae) of members of several families of Coleoptera, and of ants of the subfamily Dolichoderinae.

48. Fulvoplumierin from *Nerita albicilla*.
49. Taylor, W. C. (1985) *Eupomatia Alkaloids: The Alkaloids* **24**, 1–23.
50. Amonkar, A. A. *et al.* (1985) *Phytochemistry* **24**, 1803; 11-deoxocucurbitacin-I.
51. A recent example are potato leaves cv. Sedina; fresh leaves yielded trace amounts of essential oil with 27% linalool; the greater part of linalool is present as β-glucoside in fresh leaves: Moede, J. (1985) *Planta Med.* **51**, 312.
52. Kirson, I. *et al.* (1970) *Tetrahedron* **26**, 2209; Abraham, A. *et al.* (1968, 1975) *Phytochemistry* **7**, 957; **14**, 189; Eastwood, F. W. *et al.* (1980) *Phytochemistry* **19**, 1503; Van de Velde, V. and Lavie, D. (1982) *Phytochemistry* **21**, 731; and references given in these papers.
53. Hart, N. K. *et al.* (1976) *Aust. J. Chem.* **29**, 655; and references given here.
54. Werth, Ch. R., Guttman, S. I. and Eshbaugh, W. H. (1985) *Science* **228**, 731.
55. Nyman, U. and Hansson, B. (1978) *Hereditas* **88**, 17. In this paper the obsolete name noscapine (= noscopine) should be replaced by narcotine.
56. Malik, C. P., Mary, T. N. and Grover, I. S. (1979) *Cytologia* **44**, 59.
57. La Valva, V., Sabato, S. and Gigliano, G. S. (1985) *Taxon* **34**, 191.
58. The *p*-hydroxyderivatives, taxiphyllin and dhurrin, occur in many monocots and polycarps. Dhurrin-producing *Ranunculus repens* (Table 3) and *R. montanus* s.l. (Table 4) are additional examples of chemical polymorphism and polytypism in facultatively cyanogenic taxa; acyanogenic, weakly cyanogenic and strongly cyanogenic plants occur in many populations (personal observations in Switzerland and the Netherlands); Regula Dickemann [*Ber. Geobot.* Inst. ETH, Stiftung Rübel, **49**, 56–75 (1982)] showed by a study of 1004 individuals of the microspecies *R. grenierianus* (2x; $2n = 16$) and *R. montanus* s. str. (4x; $2n = 32$) that in the Davos region cyanogenic genotypes are much more frequent in usually calciphilous *R. montanus* (24.8%) than in *R. grenierianus* (7.8%) which is restricted to acidic silicate soils, and that strong cyanogenesis does practically only occur on carbonate soils (15.8 versus 0.9% of respective samples tested). In this instance edaphic factors might be involved in selection for cyanogenesis in an alpine habitat.
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Suggestions for regular consultation

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