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Investigations of the flora in the central Aegean

HANS RUNEMARK

Since 1957 a team at the University of Lund has worked on the flora of the central Aegean islands. The main purpose of the investigations has been a study of the differentiation patterns of plants in a Mediterranean archipelago.

The area investigated in detail includes the Cyclades and some western islands of the Dodecanesos (Levitha, Kinaros, Astipalea and the islands between Astipalea and Karpathos), which from a phytogeographical point of view belong to the Cyclades (cf. RECHINGER 1943). Besides the island of Ikaria has been explored. From a floristic point of view this island gives the impression of being an old refugium, which has been isolated for a long period of time. Therefore Ikaria, which by RECHINGER (1943) was included in the east Aegean area, ought to be given a position as a separate phytogeographical region.

In the Pliocene, a land bridge existed in the central part of the Aegean connecting southern Greece and western Turkey. This land bridge was delimited in the north by a large lake covering most parts of the present North Aegean Sea and in the south by the Sea of Crete, which separated it from the south Aegean island chain. In the beginning of Pleistocene, this land bridge was broken down, beginning with a separation from the Turkish mainland and later on also by a separation from the Greek mainland. The ultimate result was the present archipelago. For details and references see CREUTZBURG (1963, 1966).

Tectonic activity locally leading to considerable vertical movements may have occurred even lately, especially in the southern part of the central Aegean area (an active volcano still exists on the island of Thira). During the Pleistocene the sea level has fluctuated considerably with regressions between 100 and 150 m and transgressions up to 35 m. As the islands are usually steep and the sea deep, these fluctuations have only to a minor extent influenced the size and separation of the islands.

Most of the islands in the central Aegean have certainly been isolated from each other for hundred-thousands of years and in some cases apparently for more than a million of years.

However, have these islands also been phytogeographically isolated during the Pleistocene or has a considerable migration occurred between them? The only way

to answer this question seemed to be an investigation of the present distribution patterns of the whole Angiosperm flora. In 1957-1969 all the 200 islands have been floristically investigated in detail. About 40 000 herbarium numbers have been collected and c. 200 000 field annotations have been made from the area. The results can be summarized in a few points:

- The area is poor in species compared to adjacent regions. The number of species is 1300-1400 including rare weeds and ruderals. Several species that are common in surrounding regions are wholly lacking in the central Aegean, a fact which was pointed out already by RECHINGER (1950).
- A great number of species have irregular distribution patterns within the central Aegean area, even those species which are common and evenly distributed in surrounding regions. Many of the species with irregular distribution areas are members of the phrygana (garigue) vegetation, which at present is dominating in almost all islands.
- All obligate chasmophytes in limestone cliffs (c. 45 species) and all species exclusively or almost exclusively growing in the sublitoral zone of very small islands (c. 25 species) have irregular and scattered distribution areas, in spite of the occurrence of suitable habitats all over the central Aegean.

Apparently many species originally inhabiting the central Aegean have become extinct or have only survived on certain refugia because of climatic fluctuations in the Pleistocene, i.e. pluvial periods with dominating forest vegetation and arid periods with dominating open vegetation. Species, which have become extinct, have apparently in most cases been unable to reinvade from other islands or from adjacent regions. It is remarkable that straits of 10-20 km appear to have been effective barriers to migration even for species with easily dispersed seeds.

In this connection I should like to draw the attention to a random factor usually neglected, but heavily decreasing the possibility of successful migration in areas with a stable or only slowly changing vegetation cover. It is an exact parallel to genetic drift, which I have called "reproductive drift". In the same way as most mutations in a population will be randomly eliminated, most species introduced in a plant community in a single or very few individuals will soon disappear, irrespective of their competitive ability. Similarly, most species in a small plant community will be faced by the risk of elimination because of their low number of individuals. This gives a reasonable explanation for the scattered and irregular distribution of obligate chasmophytes and species confined to the sublitoral zone of small islands. For further details concerning reproductive drift and examples of distribution areas in the central Aegean the reader is referred to RUNEMARK (1969).

A flora of the central Aegean is in preparation and will be published within 2 or 3 years. It will not contain descriptions of genera and species but only detailed keys to the species within the genera. Taxonomy and variation will be discussed whenever necessary. Ecological and phytogeographical notes will be given for every species. Distribution maps for all indigenous and naturalized species will be presented, except for some badly known winter-flowering plants. An appendix with chromosome

numbers will be prepared, as the major part of the species have been cytologically investigated on material kept in cultivation in Lund.

By experimental and cytological investigations the evolutionary pattern has been analysed in some polymorphic groups. Some of these investigations, which have been performed by different members of the team, have already been published, others are not yet completed. Some results will be briefly presented.

The Elymus farctus group (Heneen & Runemark 1962).

The *Elymus farctus* group (= *Agropyron junceum* group; cf. RUNEMARK & HENEEN 1968) is extremely variable in the central Aegean. Diploid (*E. striatulus*) as well as hexaploid (*E. farctus*) psammophytes with vegetative propagation by rhizomes occur. Tetraploid (*E. rechingeri*) and octoploid (*E. diae*) tufted representatives without vegetative propagation occur in the sublitoral zone on rocky shores. The tetraploids and to some extent the rare octoploids show an extreme local differentiation in morphologic characters, while the individual populations are remarkably homogeneous. No geographical races can be recognized, on the contrary, the differentiation seems to be just at random. Material from 5 populations have been cytologically analysed in detail. The chromosome structure of the satellite chromosomes was dissimilar in all these populations, but also structural heterozygosity was found.

Erysimum sect. Cheiranthus (Snogerup 1967a, 1967b).

The section consists of perennial, lignified chasmophytes and is restricted to the southern part of the Greek mainland and to the Aegean islands. Altogether only c. 80 populations were known and the whole section is an example of evolution in small-population systems.

The material from the Greek mainland is relatively homogeneous in contrast to the heterogeneity of the Aegean material. Morphologically separable taxa, restricted to a single island, occur e.g. on Rhodos, Ikaria, Karpathos, Naxos, and Amorgos. Hybrids between the taxa are in some cases rather fertile, but a considerable breakdown of fertility and viability takes place in F_2 . All members are diploid ($2n = 12$) and the chromosomes are small and not very suitable for cytologic detail work. Therefore little is known about karyotype differentiation, but small differences exist both between and within taxa and are not correlated with the morphological variation.

A remarkable situation has been analysed on material from Amorgos (*E. senoneri* subsp. *amorginum*). Within the chasmophytic populations a form series has evolved, which has been able to invade the phrygana vegetation, where it grows in shrubs.

The Nigella arvensis complex (Strid 1965, 1968, 1969a, b, 1970).

The complex is widely distributed in the Mediterranean and the Near East, but also introduced in central Europe as a weed. On the mainland surrounding the Aegean three geographically vicarious races of *N. arvensis* can be distinguished, viz. subsp. *arvensis* in northern Greece, subsp. *aristata* in southern Greece, and subsp. *glauca* in westernmost Turkey and some east Aegean islands. These relatively

homogeneous taxa with large distribution areas are a striking contrast to the diversity found within the complex in the Aegean area. The material from every single island can be recognized morphologically with very few exceptions.

Crossing experiments on a large scale have shown that there are almost always strong sterility barriers between the Aegean and the mainland material. Within the Aegean, the populations from Karpathos and Kasos (*N. carpatha*) and Ikaria (*N. icarica*) are reproductively well isolated. Within the material from the Cycladian islands (*N. degenii*) no or very weak sterility barriers occur in spite of the often striking differentiation in morphology. Analyses of F_2 have indicated a multifactorial background to the sterility barriers.

All members of the genus are diploids with $2n = 12$. The chromosomes are large and well suited for cytological studies. The karyotype seems to be very stable, however; only minor differences have been found, and the meiosis in hybrids within the complex is usually normal.

The whole differentiation pattern in the Aegean is largely compatible with the accepted phytogeographical subdivision, i.e. the age of separation. Apparently, the evolution is mainly the result of genetic drift in population systems with very fluctuating population size.

A contrast to the very variable, normally outbreeding *N. arvensis* complex is represented by the autogamous *N. doerfleri*. This Aegean endemic is widely distributed in the southern and central Aegean and especially common on small islands. It is morphologically very homogeneous, but the populations differ greatly with the respect to their ability to form fertile hybrids with other populations. A few analyses of F_2 indicate that the parents differed in a single complementary sterility factor.

The Allium ampeloprasum complex (Bothmer 1970, and unpublished).

In the central Aegean 3 species belonging to the *Allium ampeloprasum* complex occur, viz. the widely distributed *A. ampeloprasum* s.str. ($4x$, $5x$, $6x$) mainly growing in fields, *A. bourgeaui* ($2x$, $3x$, $4x$), a chasmophyte endemic to the Aegean, and *A. bimetrace* ($2x$, $3x$, $4x$) almost wholly restricted to small islands.

The polyploidy found in the complex is only to a minor extent correlated with morphologic differentiation. However, *A. bimetrace* is mainly tetraploid, while diploids dominate in *A. bourgeaui*. The establishment of variable "ploidy" levels within the taxa may depend on the effective asexual reproduction by bulbils. In many cases the individual populations seem to consist of a single clone.

The chromosome morphology is rather stable in accordance with the conditions in many other groups of *Allium*. In general the variation is small and not obviously correlated with taxonomic categories.

Local morphologic differentiation is common (especially within *A. bimetrace*) and may be caused by genetic drift.

The Leopoldia (Muscari) comosa complex (Bentzer 1969, and unpublished).

Within the complex a great number of taxa have been described or indicated for the Aegean. The present taxonomy of the group is very unsatisfactory.

Three "ploidy" levels occur in the area, diploids, tetraploids and hexaploids. Besides a few triploids have been found. The hexaploids are rare and mostly confined to cliffs.

The variation in chromosome structure (satellites, arm-indices) is remarkably great. Also within populations often a considerable variation occurs and individuals with structural heterozygosity are rather common both on diploid and tetraploid level. The variation in tetraploids seems in some cases to be caused by hybridization.

A potential ability of asexual reproduction by bulbils was found in about 50% of the populations in cultivation in Lund. Formation of bulbils was, however, only exceptionally observed in the field.

Except for the diploid *L. comosa* mainly growing in fields, chromosome number and chromosome morphology is only to a minor extent correlated with taxonomic categories. A former, more distinct morphologic pattern may have been broken down by vigorous local differentiation.

Fritillaria (L. Engstrand and M. Gustafsson, unpublished).

Two diploid species occur in phrygana in the northern Cyclades, viz. *F. erhardtii* on Siros, Tinos and Andros (and besides on Euboea and Skiros) and *F. tuntasia* on Kea, Kithnos, Serifopoula and Folegandros.

There is a great variation in chromosome morphology both within and between populations in the two species. An extreme example is illustrated in RUNEMARK (1970b: fig. 3). In this case almost all the 10 investigated individuals from a population on Tinos had clearly distinguishable karyotypes.

Only exceptionally asexual reproduction by bulbils has been observed in these species. They are both, in spite of the great cytologic variation, remarkably homogeneous in morphologic characteristics.

The Anthemis scopulorum complex (Runemark, unpublished).

The *Anthemis scopulorum* complex consists of diploids, almost exclusively growing on very small islands. The complex has been regarded as endemic to the central Aegean (cf. distribution map in RUNEMARK 1969) but has recently been discovered on a small island close to Karpathos (W. GREUTER, pers. comm.).

Within the complex there is an enormous local differentiation in morphologic characteristics as habit, shape and size of leaves and capitula, presence, absence and shape of ray florets, and in a single case also in the shape of the receptaculum. Almost all the 35 populations known are morphologically distinct. Some variants are illustrated in RUNEMARK (1970b: fig. 2). The morphologic variation within the populations is always very small.

The genus Huetia (L. Engstrand, unpublished).

The genus *Huetia* (= *Freyera*), belonging to *Umbelliferae*, is distributed in mountains of Greece, Bulgaria, Yugoslavia, westernmost Turkey, and southern Italy. The present taxonomic subdivision of the genus is very unsatisfactory.

Only a few populations have been found in the central Aegean islands. However, the differentiation pattern in the whole genus is in many respects similar to that of Aegean plant groups.

The genus is relatively rare in Greece and only c. 50 localities are known in spite of extensive field investigations. The populations in different mountains are almost always morphologically separated by a number of minute characters. Beside a distinct altitudinal differentiation has been found. The whole material can possibly be divided into a number of alpine and montane variation series.

Crossings between different populations have failed entirely. The chromosome numbers found are $2n = 10, 18,$ and 20 . Different chromosome numbers are only partly correlated with morphological differentiation. The karyotypes are not suited for detailed studies of chromosome morphology.

The alpine flora of Peloponnisos (J. Persson, unpublished).

A project parallel to the investigations in the central Aegean was started in 1968 on the alpine flora of Peloponnisos. Seven isolated mountain ranges reach the alpine zone in the peninsula.

Irregular distribution patterns are common in the alpine taxa. Also a seemingly random differentiation in morphological characteristics has been observed in several plant complexes. In these respects the alpine flora shows patterns very similar to those found on the Aegean islands.

The project will be extended also to the mountains of central Greece.

The main results of the studies on polymorphic groups in the central Aegean can be summarized in a few points.

- A conspicuous, apparently random differentiation in morphologic features between isolated populations or population groups and usually very little variation within the populations. Such a differentiation may or may not be correlated with cytologic differentiation or polyploidy.
- A surprisingly great chromosome morphological diversity, including structural heterozygosity both within and between populations on diploid as well as polyploid level. Such a differentiation may or may not be correlated with morphological differentiation.
- Polyploidy, which may or may not be correlated with morphologic differentiation.
- In cases where comparisons have been possible with related lowland material from the surrounding regions a striking contrast exists between the diversity on the islands and the homogeneity on the mainland.
- Studies on the alpine flora of Peloponnisos and montane and alpine material of *Huetia* indicate differentiation patterns in the mountain flora of Greece similar to those found on the islands.

The taxonomic treatment of groups with strong local differentiation is a great problem. The material does not fit very well in the traditional taxonomic system.

Should all morphologically distinguishable populations of *Huetia*, which cannot hybridize with each other, be treated as distinct species? Should morphologically distinct populations or population groups of *Nigella*, spatially isolated on different islands but not reproductively separated, be given specific, subspecific or no taxonomic rank? Should the *Anthemis scopulorum* complex, endemic to a relatively small area in the Aegean, be treated as a single species? Such a species would be almost impossible to describe and key out in a flora because of its extreme diversity. As no regional differentiation can be traced, a subdivision, on the other hand, would result in numerous taxa most of which are restricted to a single, very small island.

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DISCUSSION

MOORE comments on the alternative possibility, in polymorphic groups, of delimiting a small number of extremely variable taxa or a large number of morphologically distinct, but very closely related taxa. This is a very general problem, by no means limited to the region and the groups worked on by RUNEMARK. The techniques of multivariate analysis might permit, in many of these cases, a satisfactory solution.

BÖCHER thinks that the barriers who permit the recognition of taxa need not be sterility barriers: ecological or geographical barriers are sometimes sufficient. In *Hieracium* the barriers are clear, because most of the taxa are apomictic. The small, geographically isolated, morphologically recognizable populations which one finds in the Aegean area should also be given some kind of recognition. In cases like this, as in *Hieracium*, Flora Europaea needs not to take up all the described taxa, subspecies or microspecies: it is sufficient to point out their existence, to give an idea of their number and to include references to the relevant literature. This would be in agreement with the rôle of handbook and guide to the sources which Flora Europaea should play in the future.

VALENTINE est aussi favorable à la distinction et dénomination de ces taxons. Il cite comme exemple parallèle les travaux de BIDAULT sur les *Festuca*. La nomenclature nous donne le moyen de nommer ces taxons à un rang qui leur est approprié: sous-espèce, variété, sous-variété...: il faut utiliser cette possibilité.

BIDAULT explique que son problème, dans le groupe du *Festuca ovina*, était celui de raccorder les taxons qu'il avait pu définir par ses études biosystématiques à ceux décrits par les auteurs antérieurs (DE LITARDIÈRE, SAINT-YVES, etc.) dans un système encore artificiel. Les méthodes d'étude étant fondamentalement différentes, l'identification des anciens types aux taxons nouveaux est difficile et parfois assez arbitraire.

BÖCHER believes that even in cases where one states a floating variation with completely smooth transitions from one entity to another the taxonomic distinction should not be abandoned altogether. The extremes should still be named and recognized taxonomically. Many recognized taxa are certainly connected by transitional forms which may correspond to a clinal variation. This, however, has only rarely been demonstrated, and even in those cases where the variation is proved to be clinal the former classification should not necessarily be abandoned.

RUNEMARK states that the general case, on the Aegean islands, is not that of clinal variation but of homogeneous populations limited to single islands (or correspondingly, on the mainland, to single mountains). Intermediates are exceptional. Thus a statistical treatment seems less necessary, as one can clearly distinguish the populations, although the distinctive features consist, in many cases, of small details.

GONZALEZ BERNALDEZ confirme que, dans les cas de variations en mosaïque, fréquents dans les groupes apomictiques ou à forte tendance à l'autogamie, et dans le cas très semblable de fragmentation en populations insulaires homogènes, les méthodes numériques modernes (analyse des corrélations et des covariances) sont beaucoup moins profitables que dans les cas de variation clinale ou de phénomènes d'introgression.

GREUTER thinks that the genesis of the morphologically distinct insular populations in the Aegean area is not exactly comparable with that of similar population systems elsewhere on the European continent (excepting, perhaps, those found on isolated mountain tops). As SNOGERUP has demonstrated, genetic drift plays an important rôle in the differentiation of these populations: this means either fixation of new mutants or loss of the former genetic variability in small homozygous populations, both processes being random rather than governed by selection pressure. In fact, the total variability of such population complexes can be almost entirely equated with the genetic variability normally present in a large continental population. It is obvious that genetically uniform and morphologically distinct populations can be considered as taxa. A problem (which is rather nomenclatural than truly

systematic) arises when the same species is present in archipelagic and in continental areas: the genetically variable continental populations can not be divided into taxa equivalent to the small homozygous island populations. Thus a coherent, equitable classification throughout the whole species cannot be achieved, in these cases, if the island populations are given taxonomic recognition. There appear to be also cases where the small island populations are morphologically distinct from each other, but not, or only in part, from the big variable populations of the continent.

ZAHARIADI comments on the polymorphism of ideograms within single populations observed by RUNEMARK and similarly, in the course of a literature study on the *Ornithogala* of the Palearctic region, by himself. It seems that the currently applied methods of chromosome investigation need a reappraisal. Improved methods, like those applied by STRID, give certainly good results, but are very time-consuming. Accurate morphological analysis provides in many cases much more, and more reliable, information, as exemplified by the carpomorphological work on *Compositae* by DITTRICH or by HEYWOOD's examination of umbelliferous fruits under the scanning electron microscope. The tomographic multiplying microscopy, described by GORENFLOT and his collaborators, could be successfully applied in anatomical research. The morphological and especially micromorphological methods should be given much more weight than the cytological ones. The old-fashioned dot distribution maps of RUNEMARK represent a threat to rare endemic species, in the sense that the too precise locations they give may be helpful to the vandals who try to exterminate these plants.

HEYWOOD makes it clear that the taxonomic importance of scanning electron microscopy is to assist the student to decide whether or not the entities he is studying are separable. The results cannot be used, as a rule, as key characters for practical determination. In the case of population systems, the first and foremost is to establish what one may call the biological facts, i.e. the evolutionary situation and the causes which have led to it. The practical treatment, then, depends on the scope of the publication. In a monographic work, the constantly separable entities, even if they are very numerous, can be described in detail and named if desired. In a work like *Flora Europaea*, different solutions are possible and have in fact been applied. In some cases (*Biscutella laevigata*, *Brassica repanda*) numerous subspecies have been adopted which correspond in fact to fairly recognizable populations in distinct areas; but species with more than three or four subspecies tend to become unwieldy and are unpopular with botanists. Another solution which has been adopted is to include the information in observations, and simply list the taxa; this implies, of course, that they have been described and named previously. In the case of apomicts, similar treatments have been applied.

RUNEMARK thinks that the question whether or not such taxa should be described and named is a matter of quantity. If one has only one or a few island populations, one will gladly describe them as species. The *Symphytum anatolicum* group, recently revised by PAWŁOWSKI, exists only on four islands: it has been divided into four species. But if a similar species was growing on twenty or more islands, one would certainly hesitate to describe twenty or more new species.

BÖCHER states that, as the species are not equivalent, and as each one has its own variability pattern, no general solution is possible. One must decide in each case which taxonomic treatment suits best.

HÜRLIMANN suggests that in similar cases it would be sufficient just to describe the morphological and cytological variation observed, in its geographical context, without naming the taxa and providing latin descriptions for them.

BÖCHER objects that nobody, then, would pay attention to them. Giving a name is an important psychological factor which attracts attention, provokes criticism and may lead to further, improved knowledge.

VALENTINE asks whether RUNEMARK, studying these apparently randomly distributed variation patterns, had thought of the possibility of a biological explanation. Couldn't one

find a correlation of the observed facts with the means of reproduction and dispersal of the plants?

RUNEMAK has found that the seed size, or the occurrence of special adaptations of the diaspores to dispersal, is not correlated with the range of the species. Some very local endemics (*Helichrysum amorginum*) have diaspores perfectly fitted for long-distance dispersal. *Senecio bicolor*, which has a very curious irregular distribution and is not common at all, has also easily dispersed diaspores. Other plants, especially chasmophytic *Umbelliferae* like *Ferula chiliantha*, are widely distributed in spite of their heavy seeds. When the Cyclades formed a continuous land mass connected with the continents, one can assume they had a relatively uniform, rich flora. When the islands were isolated from each other, their flora became impoverished, partly as a consequence of the climatic changes of the Quaternary. The extinction of species was, at least partly, a random process. A recolonization even by aggressive species did not take place, probably because the presence of a closed vegetation constitutes an extremely efficient obstacle to the establishment of any newcomer. The result is the irregular, apparently random distribution pattern which we find in most of the constituent species of the Cycladean flora.

HEYWOOD reverts to the problems of classification pointed out by GREUTER. He cites the example of *Centaurea tenuifolia* in Spain, where two traditional, wide-ranging subspecies have been recognized, one in the north, one in the south, showing some degree of overlapping of characters. The southern of these subspecies comprises a series of small, isolated, morphologically recognizable mountaintop populations. This represents, in fact, an "impossible situation". If one recognizes the small populations at any level other than varietal, one has to change the traditional classification with two good, normal subspecies within *C. tenuifolia*. One clearly has different systematic levels within the same species, and the differentiation on the lowest level did not involve the species as a whole, but only part of it.

GONZALEZ BERNALDEZ thinks that, here again, the essential is establishing the "biological facts". If the traditional categories and terms are not suitable any more to give a fair expression to these facts, they must be adapted or replaced.

BÖCHER deplores the very unequal and floating meaning which has been attributed to the rank of variety. Some "varieties" are mere one-gene forms based, for instance, on flower color. Other varieties will differ in a number of characters and may have their own ecology, just not being distinct enough to be called subspecies: this is the sense in which the term "variety" should be redefined. What has been called an ecotype should then be treated either as variety or as subspecies, depending on the degree of morphological differentiation; one-gene differences deserve only the rank of forms.

GREUTER supports the opinion that the existing systematic categories, if properly redefined, would be sufficient to express most or all of the "biological facts" found by biosystematists. Like BÖCHER he thinks that the term "form" should be reserved for occasional gene combinations and mutants rather than for true, monophyletic taxa. Homogeneous taxa which can be segregated, within a species, from a variable remainder which is not itself subdivisible (due to continuous variation or to lack of information) could be called varieties: this would apply, for instance, to the southern mountain populations of *Centaurea tenuifolia*. If the whole species can be split into more or less equivalent units, these might be considered as subspecies. It must be stressed however that such definitions, in the case of the form and of the variety, would be contradictory to the regulations of the nomenclatural Code.

RUNEMARK remarks that the practical problem, when using varieties is that many have already been published, but they have never been indexed.

FAVARGER souligne que dans l'aire égéenne, apparemment, l'apparition et la distribution des polyploïdes n'ont pas de rapport évident avec les facteurs actuels ni avec l'histoire géologique. Les exemples qu'il a lui-même étudiés semblent au contraire démontrer qu'une relation existe entre l'histoire surtout quaternaire de la flore et la répartition relative des diploïdes et des polyploïdes. La naissance des polyploïdes semble donc être un événement dû au hasard,

et c'est par la suite que la sélection peut intervenir et influencer la différenciation morphologique et chorologique des taxons.

BIDAULT revient sur les taxons de *Festuca ovina* qu'il a étudiés. Là, la différenciation morphologique des populations est faible et ne peut être démontrée que par des études statistiques. Par contre, des différences du niveau de "ploïdie" coïncident avec une différenciation écologique très marquée: les taxons infraspécifiques sont, en fait, surtout caractérisés par leur écologie, bien plus que par leur morphologie. Il semble difficile (et HEYWOOD le confirme) de reconnaître de tels taxons dans une flore pratique du genre de Flora Europaea, où des différences morphologiques stables sont requises. Dans le cadre d'un traitement monographique spécialisé, il en va tout autrement.

VALENTINE concludes encouraging RUNEMARK to describe and name all the Aegean populations which are morphologically distinct as taxa of an appropriate rank. There will still be many fewer taxa in e.g. *Nigella* than in *Hieracium* or *Rubus*.

