

PROGRESS IN BIOSYSTEMATICS: AN OVERVIEW

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Abstract

The nomenclatural and taxonomic system for botany introduced by Linnaeus and improved by many generations of later botanists has had as its principal aim to make possible information storage and retrieval about plants and plant products. To Linnaeus and his contemporaries this meant disclosing the divine plan of creation; to post-Darwinian botanists it implied surveying the results of evolution. Like biology in general, taxonomic botany has experienced a succession of partly contemporaneous new approaches or waves of fashion, such as anatomy, embryology, serodiagnosics, cytotaxonomy, biosystematics, palynology, phytochemistry, numerical taxonomy and cladistics. The term biosystematics, originally 'biosystematy', was coined as an umbrella for a number of methods dealing with living plants and plant populations. Some of these approaches, like chromosome studies, hybridization work and comparative cultivations, had been started long before. Biosystematics may be defined as 'research that endeavours, by study of living populations, to delimit the natural biological units and to classify them objectively as taxa of different orders of magnitude'. This goal comes very close to that of "classical taxonomy", and in recent years the borderline between the two has been largely dissolved -none of them can be profitably pursued without the other. It has even been proposed to discard the term biosystematics, but as exemplified in this paper, the investigation methods nested under its umbrella are equally important today as when the term was coined.

Introduction

The nomenclatural and taxonomic system for botany introduced by Linnaeus and improved by many generations of later botanists has had as its first goal to make possible information storage and retrieval concerning plants and plant products. While Linnaeus originally ascribed the systematic pattern he recognized in nature to divine creation, post-Darwinian botanists have mostly interpreted it as resulting from evolution. Many botanical taxonomists of today therefore regard systematics as the art of tracing similarities between taxa, combining them into larger groups, and hypothesizing about their evolution. The primary task of botanical systematics, and its most important function for its users (cp. WALTERS, 1988), should, however, be to define taxa and describe differences between them-that is to trace and document discontinuous variation. Reliable evidence about this can only be obtained through detailed studies of a sufficiently large material and adequate presentation of the evidence in easily intelligible form, for instance with histograms or pictorialized scatter diagrams (cp. e.g. O. HEDBERG, 1957; WHITE, 1993). Only then should come the task of sorting them after maximum similarity, and classifying them in a predictive system.

While the number of taxonomic features available to Linnaeus was very limited, the gradual refinement of technical equipment has both widened the scope of morphological studies and facilitated the introduction of ancillary sciences like anatomy, embryology,

serology, cytotaxonomy, genetics, palynology, and chemotaxonomy. Those have provided a number of new character sets, the incorporation of which has been facilitated by methodologies such as numerical taxonomy (taxometrics, cp. e.g. MCNEILL, 1984), cladistics (cp. e.g. HUMPHRIES & FUNK, 1984) and DNA hybridization. All these novelties have made it possible to introduce important improvements in our classification. But unfortunately the introduction of data sets from new ancillary sciences have often led their proponents to consider their own type of evidence or technology superior to the traditional ones, which has led to a series of waves of fashion, sometimes obstructing a holistic approach (cp. O. HEDBERG, 1988a; STACE, 1989).

This sequence of "waves of fashion" among the ancillary sciences used by botanical taxonomists has also, unfortunately, at times been accompanied by wholesale reallocation of resources from traditional methods to new band wagons, sometimes to the detriment of botany. Each character set has its weaknesses and limitations and it may therefore be useful to attempt a brief survey of their contributions to taxonomy. A few of the newer ancillary sciences will be treated by other authors in this volume, so I will only briefly comment on some of the earlier ones.

Plant anatomy early became and still remains one of the more important and most often used adjuncts of taxonomy - there are useful anatomical differences to be found at all taxonomic levels and in a lot of different organs (cp. e.g. DAVIS & HEYWOOD, 1963).

Embryology was heralded about the end of last century as one of the most "scientific" ancillary sciences of taxonomy, and embryological data have certainly contributed very much to the shaping of our current system. But whereas embryology often proved useful for studies of the relations between taxa of higher rank (cp. e.g. CUTLER, 1984), its contributions to taxonomy at lower levels have been more limited (cp. DAVIS & HEYWOOD, 1963: 188).

Cytotaxonomy utilizes differences in basic chromosome number as well as in chromosome morphology and ploidy. Since these features not only provide tangible characters (albeit sometimes difficult of avail) but also often match differences in compatibility, there is no wonder that cytotaxonomy early became highly esteemed. Yet also cytotaxonomics has its limitations. Chromosome numbers may for instance be reliable guides in some groups like most grasses, while they show excessive variation in others, like *Cardamine pratensis* s. lat. (LÖVKVIST, 1956) and *Claytonia* (DAVIS & BOWMER, 1966; LEWIS, 1970). In some cases morphologically indistinguishable cytotypes occur within one species (cp. e.g. I. HEDBERG, 1990). And the basic number, which most often is fixed in each genus, may occasionally show considerable intrageneric variation (cp. HEDBERG & HEDBERG, 1995).

Genetics, after its rediscovery at the beginning of our century, has for obvious reasons been one of the fundamental ancillary sciences of taxonomy. One major disadvantage has been that, as in cytotaxonomy, its application requires living material, which is difficult of access for many species. Another difficulty comes from the occurrence in some species of sterility barriers unaccompanied by morphological differences.

Pollen morphology was early recognized as an excellent guide to taxonomy in some selected families, and has in the last half-century proved very useful in a large number

of other groups as well. But while pollen morphology provides very good guidance in families like *Acanthaceae* and *Polygonaceae*, it is very monotonous for instance in *Poaceae* and *Brassicaceae*. Like all other taxonomic features palynological characters may revert from an advanced (apomorphic) to a primitive (plesiomorphic) stage (cp. O. HEDBERG, 1988b, 1995).

Biosystematics

Biosystematics has for some considerable time been one of the most popular approaches of systematic botany, often contrasted to traditional 'herbarium botany'. The concept is employed for taxonomic work on living material, for instance through detailed field studies, and also encompasses cytotaxonomy, pollination biology, and reproductive biology, experimental cultivation, hybridization and crossing experiments, etc. The name 'biosystematics' is fairly recent, it was introduced (as biosystematy) by CAMP & GILLY (1943). Their term was, however, antedated by 'experimental taxonomy', introduced by CLAUSEN & al. (1933). Neither of these terms was, however, immediately accepted; STEBBINS (1950: 7) considered "these proposals too new to be properly evaluated at present". But according to MOORE (1984: 222) the "approach which came to be known as biosystematics was arguably the dominant force in taxonomy for the three decades or so up to about the middle of the 1960s". Many recent studies have employed those methods without using the term biosystematics, this term was mentioned only a couple of times in each of the symposium volumes "*Modern methods in plant taxonomy*" (HEYWOOD, 1968) and "*Current concepts in plant taxonomy*" (HEYWOOD & MOORE, 1984).

In the following I will illustrate the progress in biosystematics, using examples from less demanding field observations to more elaborate combinations of the various elements, and then summarize the present position and touch upon the future.

Elements of Biosystematics

Field observations.- One of the main difficulties for taxonomic work is caused by the wide variation found in nature - no character is always stable, as may be exemplified by a tricotyledonous seedling found in a *Sibthorpia* hybrid. A good example of wide variation in nature is provided by *Dipsacus pinnatifidus* on the high East African mountains, which adapts to the increasing harshness of the climate towards higher levels by reducing its height. Specimens in woodland at 3200 m altitude reach 2 m, those in alpine scrub at 3950 m are about 0.3 m, and the uppermost specimens in the alpine belt have practically no stem at all. Such almost stem-less specimens have been described as a separate genus, *Simenia*, but they are in fact connected with the others by a continuous range of variation (HEDBERG & HEDBERG, 1977a).

Field studies are particularly necessary for plants, the size of which precludes the collecting of ordinary herbarium specimens, like in the families *Arecaceae* and *Musaceae*, as exemplified by the *Heliconia* revision by ANDERSSON (1992). They are

equally indispensable in groups where flowers and leaves appear in different seasons, as in the orchid genus *Nervilia* monographed by PETERSSON (1991). The importance of field studies of trees and shrubs of ordinary size was recently elegantly illustrated by WHITE (1993). Through detailed population studies in the field with careful description of intrapopulation and interpopulation variation he revised the genus *Myrica* in Africa and Madagascar, which resulted in the reduction to synonymy of a majority of the 26 species names earlier used.

The most comprehensive modern study of a medium-sized tropical family of woody plants available is a monographic revision of *Chrysobalanaceae* (PRANCE & WHITE, 1988). Given a family of 17 genera and about 500 species dispersed through the tropics, the authors obviously could not study them all in nature. But their experience from 25 years of work on the family, including a considerable amount of field work, enabled them to apply a fruitful biosystematic approach, where ecological data were utilized as much as morphology, fine structure and phytochemistry.

Detailed biosystematic studies of taxonomic differentiation in the giant lobelias and giant senecios in East Africa were recently published by KNOX (1993), who investigated the phylogenetic relationships of the species, subspecies, varieties and isolated populations by means of ecological, cytological and chlorophyll DNA studies. The insular nature of the mountain habitats harbouring these plants contributes to make them an unrivaled model system for studying speciation and adaptation (KNOX op. cit. p. 127, cp. HEDBERG, 1969, 1970, 1973).

One of the areas where biosystematic field studies are particularly indispensable concerns the relations between parasites and their hosts. Already the determination which tree species function as hosts for the North-European mistletoe (*Viscum album*) called for extensive biosystematic studies (WALLDÉN, 1961). These studies demonstrated, among other things, that the reputed occurrence on oak in Scandinavia was equally dubious as the magical power ascribed by old tradition to mistletoes on oak.

The biological balance between "prudent" predators and their hosts was studied by PLITMAN (1991), who found that in the seven *Cuscuta* species studied in the field in Israel the phenological plasticity in the parasite corresponded to that in the host and that the fertility of the parasite was kept so low by natural selection that the hosts were never seriously effected.

Field cytotaxonomy.- A special kind of field studies concerns documentation of chromosome numbers in field material, which sometimes provide useful hints to taxonomists. This was well exemplified when I fixed in a Scottish mountain root tips of what appeared to be ordinary *Avenula pratensis* (*Helictotrichon pratense*), which on careful investigation gave the somatic number 126. The same number was later obtained for a number of other collections from Scotland and Sweden (I. HEDBERG, 1961), whereas the numbers earlier published for that species were 14, 28 and 42. Since vouchers for the material providing those lower numbers could not be traced, further studies are obviously highly desirable.

A striking example of how random field fixations solved an interesting taxonomic problem comes from Arctic Canada, where the rather inhospitable environment of Cornwallis Island at 75° North harbours only about 200 vascular plant species in an area twice the size of Corsica. One of the grasses collected turned out to be a triploid,

indicating either autotriploidy or hybrid origin. Morphologically this sterile plant agreed completely with material earlier collected on Spitzbergen and then described as *Puccinellia vacillans* (SCHOLANDER, 1934: 95). Doubts about its taxonomic status were, however, expressed already at that time. Studies of leaf anatomy and chromosome morphology (O. HEDBERG, 1962a) demonstrated that the plant must be an intergeneric hybrid between *Colpodium vahlianum* and *Phippsia algida*! Since it has never been found south of 75° North it is rather far from the realm of OPTIMA, but it is certainly of considerable evolutionary interest, since it is widely distributed in the Arctic. The only thing required to get a full-fledged new Arctic species would be chromosome doubling.

Even a list of chromosome numbers may provide information of considerable biosystematic interest, such as the list of chromosome numbers in afroalpine vascular plants published by HEDBERG & HEDBERG (1977b), where several cases of intraspecific polyploidy draw attention to evolutionary differentiation between different mountain enclaves in a number of afroalpine species.

Pollination ecology.- The relations between entomogamous flowers and their pollinating insects have been a favourite area for biosystematic studies, not least after the well-known studies by KULLENBERG (1956, etc.) on the pollination of *Ophrys*. Detailed studies of, int. al., emission and composition of fragrance and of the selective mechanisms controlling adaptation between the plant and its pollen vectors were performed by Nilsson for e.g. *Platanthera chlorantha* (NILSSON, 1978) and *Dactylorhiza sambucina* (NILSSON, 1980).

A splendid example of the taxonomic usefulness of pollination data is found in the genus *Adansonia*, where one species is regularly pollinated by bats, two others by lemurs and bats, and the remaining five by long-tongued hawkmoths. The two pollination systems occurring in the genus are closely correlated with differences in floral morphology, phenology and nectar production (BAUM, 1995). A less conspicuous but taxonomically no less useful example of the application of data from pollination ecology is found in *Callitriche*, where differences in pollen morphology were found to be related to differences in pollination biology, providing excellent support for taxonomic conclusions (MARTINSSON, 1991).

Experimental cultivations.- Classical examples of the use of experimental cultivation for taxonomical purpose were provided by Turesson's ecotype investigations (TURESSON, 1922), and the equally famous studies organized by CLAUSEN & al. (1933, 1940) along an altitudinal gradient in North America. The comprehensive study by MARSDEN-JONES & TURRILL (1957) of *Silene maritima* and *S. vulgaris* contributed one of the best studied examples of a pair of partly sympatric and partly compatible species. A later example was provided by my own studies on the manifestation of vivipary in diploid and polyploid populations of *Deschampsia caespitosa* s. lat. in northern Europe. The cloning of a series of actually or potentially viviparous specimens of diploids, triploids and tetraploids, and planting of the clones in a number of different environments from lowland to alpine, demonstrated that environmental differences meant very little for the manifestation of vivipary in this case, and that "*Deschampsia alpina*" is a polyphyletic assemblage of viviparous clones (O. HEDBERG, 1958, 1986).

Another interesting approach is the investigation under experimental conditions of the stability of ecological adaptations to extreme environments, and their mode of

reaction. The acaulescent growth form adopted by the afroalpine species *Dianthoseris schimperi* was, for example, invariably maintained under greenhouse conditions in Uppsala, whereas *Conyza subscaposa*, which was also acaulescent in the field, developed a fairly long scape when reared in a greenhouse (O. HEDBERG, 1964: 75). The influence of a really extreme environment was studied by KUANG & al. (1995), who investigated pollen and ovule development in *Arabidopsis thaliana* under spaceflight conditions, where reproductive development aborted at an early stage, although the plants were reared in a plant growth chamber that received light and temperature control.

Hybridization and crossing experiments. Occasionally, discovery of a hybrid swarm may explain the origin of aberrant specimens earlier collected and sometimes described as independent taxa, as exemplified by the *Senecio transmarinus* x *mattirolii* hybrid swarm described from Ruwenzori in East Africa (O. HEDBERG, 1955: 484).

Hybridization in the alpine belt on Mt Kenya between the creeping tree senecio, *Dendrosenecio keniensis*, and its erect relative *D. keniodendron* has attracted considerable interest. In 1948 I discovered a single hybrid specimen between them (O. HEDBERG, 1957: 227). About 40 years later a considerable number of hybrid populations were recognized by BECK & al. (1992), and a selection of them were subjected to detailed biosystematic studies, investigating int. al. general morphology, root anatomy, chromosome number, meiosis, fruit setting, germination, and population biology. Their results suggest that the hybrid populations consist mainly of first generation hybrids, and that *Dendrosenecio keniodendron* is the female parent.

While experimental crossings combined with cytotaxonomic studies have long been practiced in plant breeding their use in "wild plant taxonomy" started later, a pioneer case being Müntzing's synthesis of the Linnean species *Galeopsis tetrahit* (MÜNTZING, 1932). My own study on *Arabis alpina* (O. HEDBERG, 1962b), demonstrated that populations from Mt Kenya in East Africa and those from the mountains in northernmost Sweden, earlier considered to be specifically distinct, not only were morphologically indistinguishable but are also compatible: the F1 generation had a certain amount of seed setting and the F2 was fully fertile and segregated in winter hardiness as well as in pubescence and other morphological traits. An interesting detail is that the two populations of *Arabis alpina* involved may be expected to have been geographically isolated from each other for a very long time—perhaps since Sahara was formed. This agrees with my findings from comparative evolutionary studies in the afroalpine flora, where the rate of differentiation tends to differ between different plant families, being for instance much slower in *Brassicaceae* than in *Asteraceae* (O. HEDBERG, 1957: 376; 1969: 143).

A classical Mediterranean example of the use of hybridization experiments to study taxonomic interrelations is provided by STRID's (1970) biosystematic study of the *Nigella arvensis* complex (*Ranunculaceae*) in the Aegean flora. Another at least partly Mediterranean example is my own study of the genus *Sibthorpia* (*Scrophulariaceae*), where differences in basic chromosome number contributed to complete incompatibility between most of the species (O. HEDBERG, 1975).

A recent example of the use of intergeneric hybridizations in the study of generic interrelations was given by FREDERIKSEN & VON BOTHMER (1995). Through

intergeneric crosses between the four species of *Eremopyron* and sixteen species from eight genera of *Triticeae* they confirmed the taxonomic independence of *Eremopyron* and the uniqueness of its genome.

Discussion and conclusions

Since the term biosystematics became widely adopted in the 1950s the name and the methods it refers to have often been discussed, e.g. by MASON (1950), O. HEDBERG (1957, 1962c), VALENTINE & LÖVE (1958), RAVEN (1974, 1976, 1986) and STACE (1980). A comprehensive symposium on Biosystematics was organized in 1969 (ANONYMUS, 1970), another in 1983 (GRANT, 1984).

As emphasized e.g. by DAVIS & HEYWOOD (1963: 54), biosystematics is more concerned with the process of evolution than with its results, and some biosystematists have maintained that failure to interbreed should be the main criterion of specific rank. This led to the adoption of a "biological species concept", utilizing terms like coenospecies (cp. TURESSON, 1922; CLAUSEN & al., 1940). As exemplified above biosystematic studies may be very helpful for taxonomic decisions, but as emphasized by RAVEN (1974) they do *not* lead to an unequivocal definition of the taxonomic units in most cases. The suggestion that the taxonomists' species definition by objective criteria should be replaced by this biological species concept has also gradually been refuted (cp. e.g. HEYWOOD, 1984: 10).

A conceptual difficulty with biosystematics has been, according to RAVEN (1986), that it was conceived by many as a way of improving plant classification rather than a way of learning more about plant evolution. In this respect it does not differ much from classical plant taxonomy for which WALTERS (1963: 14) summarized: "It is probably true to say that the majority of taxonomists envisage the gradual 'improvement' of their natural classifications by the inclusion of more and more data towards a final goal. This goal is often equated with the phylogenetic classification". This, in my opinion, calls for a reminder: whichever methods we use we will never reach the "omega" classification visualized by TURRILL (1950). The 'implicit phylogenies' outlined by cladists are equally hypothetical today as when LOTSY (1916) published his famous verdict on the phylogenetic speculations of his time.

Even if the results of biosystematic studies have been overexploited by some botanists, and others tend to avoid the term biosystematics (e.g. LEWIS, 1970: 180 and RAVEN, 1986: 26), the systematic methods usually referred to with this term have now become so thoroughly incorporated in modern taxonomic botany that they are taken for granted by most taxonomists, or, as formulated by STACE (1980: 6) "these two fields are not separate and opposing, but rather closely interacting, complementary approaches to taxonomy, without either of which taxonomy is incomplete" (cp. also MASON, 1950). And although the ideal "omega" classification visualized by TURRILL (1950) by definition is unattainable, we can certainly improve our classification of most groups, especially in little-known tropical genera. For that purpose biosystematic methods may be particularly useful since they provide data which can not be obtained from herbarium material, and deal with evolution at work, not with its hypothetical past.

In view of the impending biodiversity crisis, the collaboration of all kinds of taxonomists is urgently required to improve our current general classification. Since furthermore time is running out fast we should heed the caveat by HEYWOOD (1984: 15) "limits of budget, recession and the threat of the bulldozer should cause us to focus more clearly on our priorities". In an era when laboratory work and computerization of earlier known data have been given so much attention and alienated so many botanists from nature, it is fundamental for the future of taxonomic botany that its "biosystematic portion" is properly maintained. It is therefore vitally important to continue and extend the type of studies so long referred to with the term biosystematics, and keep the term to stress the importance and needs of research on living material.

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