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Some considerations and thoughts on the pragmatic classification of apomictic *Rubus* taxa

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Dedicated to Professor Dr. Dr. H. E. Weber on the occasion of his 65th birthday.

Kurzfassung: Ausgehend von seinem Studium der Gattung *Rubus* in der Tschechischen Republik beschreibt der Autor die Klassifikation von Brombeeren (Subgenus *Rubus*) in Europa, ihre Geschichte, den gegenwärtigen Kenntnisstand sowie aktuelle Probleme. Der Autor zählt sich zu den Anhängern der „Weberschen Batologie", welcher die Fortschritte der vergangenen 25 Jahre in der *Rubus*-Taxonomie in Europa zu verdanken sind. Es wird akzeptiert, daß nicht jede Brombeerpflanze dem System eingeordnet werden kann.

Die Gründe für die taxonomischen Probleme liegen in der Natur der Evolutionsprozesse dieser Gruppe: unvollständige Apomixis, häufige Hybridisierung, Aufspaltung der Nachkommenschaft in unterschiedliche Morphotypen, Wiedererlangen der Sexualität, vorübergehende Existenz von Spaltungsprodukten. Die potentielle Arealentwicklung eines neuen Biotyps innerhalb der Gruppe kann folgendermaßen skizziert werden: Einzelpflanze – Lokalsippe – regionale Art – weitverbreitete Art. Zur taxonomischen Bewertung einer Sippe sollte deshalb neben ausreichender morphologischer Charakterisierung vor allem die Arealgröße berücksichtigt werden. Sie ermöglicht die Zuordnung des fraglichen Taxons zu einer der genannten Rangstufen.

Aufgrund seiner Erfahrungen aus der Tschechischen Republik schlägt der Autor einige Änderungen der Einstufungskriterien vor. Der Hauptunterschied besteht darin, die Untergrenze für die Einstufung als Regionalart auf 20 km Arealdurchmesser zu senken. Im Unterschied zu anderen Pflanzengruppen gilt bei den apomiktischen Brombeeren, daß weiter verbreitete Sippen größere pflanzengeographische Bedeutung haben als solche mit kleinen Arealen.

Auch wenn bei der Neubeschreibung von *Rubus*-Arten strengere Anforderungen gestellt werden, zeigt sich, daß in der Vergangenheit mehrere gut unterscheidbare Arten vernachlässigt wurden und daß die Artenzahl innerhalb des Subgenus *Rubus* weiter ansteigt. Der Autor betont die Notwendigkeit des Studiums der Gruppe *Glandulosi* in Mitteleuropa und weist darauf hin, daß die Kooperation mit Populationsökologen nützlich sei, um die Mengeanteile der taxonomisch nicht klassifizierten Brombeeren im Gelände zu beschreiben.

Abstract: Based on his studies of the genus *Rubus* in the Czech Republic, the author describes classification of brambles from *Rubus* subgen. *Rubus* in Europe, its recent history, present state, and current problems. In general, the author follows the adherents of "Weberian batology" which in the last 25 years has assumed European responsibility for attempting to classify that particular genus. The thesis that not every bramble plant can be included in the classification is accepted. The objective reasons for taxonomic difficulties within *Rubus* subgen. *Rubus* are connected with special features of taxogenesis of its members, especially with incomplete apomixis, frequent hybridization, splitting of the progeny into different morphotypes, resexualization, transitory existence of segregants, etc. The progress of the evolution of a new taxon in the given taxonomic group can be ranked: individual bush – local type – regional species – species with an extensive distribution area. When classifying a taxon, alongside sufficient morphological characteristics, great emphasis should be put on the distribution area; its extent can render possible the taxon to

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be accepted into the classification scheme. On the basis of experience gained from the Czech Republic, the author has accepted some modifications of the scale for acceptance of plants as species. The basic difference is in lowering the low limit of the extent of the distribution area for regional species, to be acceptable for their inclusion to the classification, i.e. to 20 km in diameter. In contrast to taxa of other plant groups, species of apomictic brambles with more extensive distribution areas are phytogeographically more important than those with small distribution areas. In spite of the use of stricter requirements for the description of new species in *Rubus*, it appears that many (distinct) species have been neglected until now, and that the number of species in *Rubus* subgen. *Rubus* is continuously increasing. The author stresses the necessity of studying the group ser. *Glandulosi* in Central Europe and points out the usefulness of cooperation with population ecologists to describe the quantitative representation of taxonomically unclassified bramble plants in the field.

Key words: Classification, Taxogenesis, *Rubus* subgen. *Rubus*, Czech Republic

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1 Introduction

These considerations and thoughts have originated during the many years' field work of the present author on his study of brambles in the Czech Republic and include his experience gained at preparing the text on the genus *Rubus* for the Flora of the Czech Republic Vol. 4. The names of *Rubus* taxa mentioned in this paper are taken from that book (Holub 1995).

2 Present state of knowledge of *Rubus* and subjective problems in its classification

By its extensive morphological diversity *Rubus* (13 subgenera, many more than a thousand species) is a supergenus which might arguably be divided into a series of smaller genera. From the viewpoint of a species-level taxonomy, there is great diversity, especially within subgen. *Rubus*. This diversity resulted in the description of many species in earlier times, regardless of what these species represented – real species with large distribution areas, regional species, local biotypes, individual bramble bushes, various ecomorphoses, hybrids, etc. Thus more than two thousand taxa were described in Europe alone. Each slightly different morphotype was designated as a new species or at least as an infraspecific taxon. This approach culminated shortly before World War I with the publication of Sudre's monograph (Sudre 1908-1913). European batology then stagnated for a long time, badly in need of urgent revision. This revision came later in the 1970s in the form of "Weberian reform" (Weber 1973 and later). Even though *Rubus* is really a "crux botanicorum" by the objective character of its variation and diversity, many difficulties and problems of its taxonomic classification were compounded by subjective factors – that is, by the unsatisfactory knowledge and understanding of evolutionary processes within this genus, or subgenus, respectively, of previous batologists.

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As an example of the enthusiasm of previous workers, one may cite Kupčok's activity (Kupcsok S. 1907; Kupcsok S. et Kupcsok S. T. 1910). He described 182 taxa from the vicinity of a village named Pukanec in central Slovakia; fortunately many of them belong to ser. *Glandulosi*, in which a small number of real taxa (i.e. stabilized apomicts) exist. Surprisingly, Gustafsson (1943) – a distinguished batologist – took Kupčok's work seriously. Newton (1980) described the period of batological crisis as a "war" between supporters of two schools, one being for the continuous description of microspecies, the other for combining them towards some circle species (species collectivae); the second route has often tended towards the acceptance of the only one species in subgen. *Rubus* – *R. fruticosus*. Using the first method individual bramble bushes received their own names but, curiously, at the same time widely distributed taxa were neglected, perhaps because of the small study areas of batological amateurs.

Another defect of earlier batology was the identification of local plants as taxa described from very distant areas, or their inclusion in such species as their infraspecific taxa. Many errors also originated in connection with an incorrect interpretation of earlier names. On such occasions the phenomenon of convergence leading to certain similarity was often overestimated at classification. Sometimes convergence of certain single characters was involved, which in fact does not necessarily demonstrate any relationship between taxa. A good example of an excessive use of infraspecific taxa is that given by Holub (1993): *Rubus alterniflorus*, a species that does not occur in the Czech Republic at all, was provided with 63 infraspecific taxa (including subformae) by Hruby (1944) from that area.

On the other hand, merging species on the basis of their similarity led to the production of groups containing unrelated taxa described from various countries. This method originated with Focke (1877), was elaborated by Sudre (1908-1913) and culminated in his monograph "Rubi Europae" (especially in the classification of ser. *Glandulosi*, as can be seen in the determination key to that group). This kind of schematically directed batology of Sudre brought about the compartmentation of the known material and sometimes also for dealing with the material collected later. Sudre's schematic method seemed to be useful for determination and therefore his approach gained unmerited acknowledgment and expansion. Even such a distinguished Swedish investigator of brambles as Gustafsson succumbed to the enchantment of Sudre's monograph (Sudre 1908-1913). In Sudre's classification, the *Corylifolii* section (with its many stabilized species) was neglected and its representatives were only treated as hybrids between *R. caesius* and taxa of sect. *Rubus*. Sudre's treatment of taxa of sect. *Corylifolii* was followed by further authors, in the Czech Republic by Domin (1935) and Dostál (1948). Only Weber (1981) recognized the group and described a number of new species within it. In connection with Sudre's monograph it is useful to point out that the edition of monographs often has a retardative influence on the further evolution of the study of the given taxonomic groups; Sudre's monograph of *Rubus* illustrates this especially distinctly.

A further defect in the study of brambles was the investigation in small areas, exercised usually by amateurs. Also, nomenclatural problems cannot be omitted, originating from the continuous description of new species leading to many errors in their identification (misidentifications, "falsonyms"), to a great number of homonyms, etc. The morphology of *Rubus* plants is very much

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affected by the influence of the environment – here such phenomenona belong as "formae umbrosae", "formae apricae", "formae vegetae", etc. The present author has become convinced that cultivation (under the sun) may change many plants taxonomically well known to him into the production of undeterminable specimens. Such ecomorphoses were sometimes described by previous batologists as new species.

3 Taxonomic problems in *Rubus* subgen. *Rubus*

What are the reasons for taxonomic difficulties in *Rubus* subgen. *Rubus* ? The basic reasons are: 1) facultative gametophytic apomixis; 2) frequent hybridization; and 3) the segregation – splitting of hybrids into many new (different to one another) hybrid progeny. Apomixis of *Rubus* is pseudogamous; as many as usually 10-30% of the progeny of species studied by Nybom (1987, 1988) are biparental in origin. By this process variation may be preserved or enlarged. The phenomenon of apomixis occurs after hybridization by the integration of genes which are capable of causing agamospermy.

Hybridization in the genus (or supergenus) *Rubus* occurs in a sufficient measure and may be evidenced by the existence of hybrids between representatives belonging to not very closely related subgenera; within subgenera it also exists between rather distantly related species. In this connection the information by Maurer (1994) about the hybrids *Rubus bifrons* × *R. hirtus* is interesting. The hybridization results in new combinations of characters, from which the parental species cannot usually be either established or even estimated. Distinct, easily recognizable hybrids may be found when they are morphologically intermediate and when their putative parents are present in the locality together with them. During the past 18 years of intensive field work in the Czech Republic, as the following putative hybrids have been discovered by the present author: *R. bifrons* × *R. canescens, R. canescens* × *R. grabowskii, R. canescens* × *R. hirtus, R. canescens* × *R. tabanimontanus* and perhaps *R. caesius* × *R. mollis*. It can be seen that the sexual species *R. canescens* has the highest presence among the hybrids mentioned; perhaps this is also connected with its distinct morphological expression in hybrids.

After the hybridization of apomictic bramble plants, resexualization sometimes follows and then also further hybridization. Some taxonomically amorphous groups (ser. *Glandulosi*, partly perhaps also ser. *Hystrix*) have a higher representation of plants with sexual reproduction. The ratio of representation of sexual and apomictic types of reproduction appears as a special system of equilibrium, characterized by two features: the disappearing of apomixis in hybridization and its recovery in segregation. Resexualization makes further participation of such plants in the hybridization process possible.

In this way, material for a special evolutionary process is created, through which singular biotypes are selected and in the case of their advantage local types or regional biotypes, respectively, may arise, from some of which species with large distribution areas could originate later. A certain technical (practical) problem may arise – how to distinguish singular (individual) biotypes from plants of an exclave occurrence (i.e. an isolated occurrence after a great geographic hiatus) of a species unknown in the study region and unknown to the collector. A good example may be given by the finding

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of *R. micans* in central Moravia, which has its nearest localities as far as beyond the Rhine – a species completely unknown to Czech batologists. /A new isolated eastern locality of this species was found in older herbarium material by Professor Weber in 1996 from the surrounding of Rudnik in Polish Silesia near the boundary of the Czech Republic, c. 70 km from the Moravian locality/. In such cases only international cooperation may lead to correct results. Regarding the character of their origin, individual biotypes cannot be included in the known (i.e. accepted) species. Individual and local biotypes may be morphologically very distinct, they can represent and in some cases they do represent a species "in statu nascendi" (or a species "in spe"). Some local biotypes have been present in their localities for a long time.

Gustafsson (1943) considered autosegregation, which could result in small recombinations (or the manifestation of marked genetic content); plants of *R. vratnensis* with rose coloured petals (instead of the white ones) may belong here if these plants are not a result of an unknown hybridization. Local biotypes may disappear or stay and sometimes evolve to higher types of *Rubus* taxa. Sexual species with an extensive distribution area (as, for example *R. ulmifolius* or *R. canescens*) are very variable, but it does not seem possible to describe this variation reasonably by taxonomic entities. The felling of woods in Europe in the Middle Ages played an important role at taxogenesis in *Rubus*, making it possible for brambles to enlarge their distribution areas and to meet with different biotypes and taxa. Similar explanations were proposed for the taxonomic complexity of the *Crataegus* flora of North America (cf. Brown 1910, Marie-Victorin 1938).

4 Distribution areas of *Rubus* taxa and scales for their acceptance in classification

The phase of the taxogenesis in *Rubus* subgen. *Rubus* includes two steps – the origin of a new combination of characters, representing a fast process, and the formation of a distribution area, which is a much slower process. Pragmatic batology, which originated in the 1970s under the guidance of Weber (1973, 1986 and 1995) and is prevalent today accentuates the importance of the distribution area, both in its extent and in its internal structure, for classification. Regarding the morphological character in *Rubus* subgen. *Rubus* no stage of an evolutionary differentiation exists as it is known in sexual plants, which would originate during a slow process. Usually, instead, the quick creation of the new character combination evolves through the basis of hybridization.

As representatives of subgen. *Rubus* are relatively young taxa, their distribution areas are the products of the age of the taxon, even when we have to take the possibility of long-distance dispersal (by ornithochory) in this group into consideration. In each case, the local biotypes are young and the species of the group of *Corylifolii* also belong to younger types in subgen. *Rubus*. Here the difference in the phytogeographic character between brambles and other plants has to be mentioned regarding the importance of narrow distribution areas. Plants with such areas are highly appreciated in phytogeographical studies, as they represent neoendemics or relic endemics; the opposite holds for *Rubus*, where the plants with extensive distribution areas are evaluated as the most important ones and those with very narrow, limited areas are neglected or directly excluded from interest.

In spite of this, it is necessary to stress the

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importance of also studying narrow regional species, as after a more detailed investigation these may prove to be taxa with more extensive distribution areas. *R. vratnensis* may be given here as an example with a history of recognition of its area: from an area of 1 km² with 3 small groups of plants after 10 years of field investigation to a distribution area of 80 x 80 km including 16 separate localities. An example of an important local biotype in Bohemia is *Rubus* topodeme "Jelení Palouky" (= Deer Glades, Hirschwiesen; *R. "cervopratorum"* Holub in schedis olim) from the Hřebeny hill-country (central Bohemia) known for twelve years from only the area of 1 km² with 3-4 small groups of plants, morphologically very distinct, certainly at least as distinct as normally accepted species in the genus. In 1996, two further localities of this plant were found, both in different directions 6 km distant from the first known locality. If the fact of its narrow distribution were not known, the taxon would be accepted and also described by present leading batologists as a new species. A further extension of the distribution area of this taxon may be expected. On the ground of changes of knowledge of distribution, rapid changes may occur in the classification of such taxa (from the stage of their knowledge as individual biotypes to species with extensive distribution areas).

The fact that the distribution area is an important feature of the bramble species has led to the elaboration of various quantitative standards for the evaluation of different types of species within subgen. *Rubus*. The first initials of the idea of applying the extent of the distribution area for taxonomic classification may already be found in Focke (1877), further in Gustafsson (1943), Beek (1974), Newton (1975) and in a concise form in Weber (e.g. 1986 and 1995). Scales were elaborated and the general distribution among them was obtained by that proposed by Weber: less than 20 km in diameter – local biotypes, 50-250 km – regional types and 500 km and more – species with larger distribution areas. Small arrangements – mostly in connection with the problem of the determination of local types (which are not or should not be accepted in the present taxonomy of brambles) and regional types (which represent the lowest level acceptable), exist in the literature. These small differences among the scales will not be discussed here; some proposals were mentioned by Holub (1993). Here only the lower limit for regional species accepted by the present author is stressed – 20 km in diameter, which has followed from experience with brambles in the Czech Republic (which is much smaller than Germany, where Weber constituted his generally accepted scale). It has to be stated here, however, that in spite of the (theoretical) acceptance of a lower extent for regional species, no one taxon with a smaller distribution area than 50 km in diameter was described by the present author until now. Some recent authors consider the possibility of accepting taxa with distribution areas 20 or 30 km in diameter, named by the present author as narrow regional species; e. g. Maurer (1994) gives the lower limit as (20-) 50 km; Henker (1995) while studying *R. macrothelos* Marsson mentions the possibility of the diameter of 30 km. Newton (1975) had a substantially smaller area for the acceptance of taxa as species – 100 km² (i.e. normally 10 x 10 km); later he accepted (a somewhat changed) Weber's scale (species with large distribution areas have their lower limit with 400 km in diameter – Newton 1980),

But more important than only giving attention to the quantitative extents of individual degrees of the scale, is not to accept the grades schematically but also to take the

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character of the occurrence within the distribution area into consideration. Also, special cases may be found, one considered by the present author theoretically in 1992 (Holub 1993) – a distribution area consisting of two very distant localities; in that year such a case was, in fact, described by Weber et Monasterio-Huelin (1992) as a new species – *R. lucensis* from Spain (with a distance of two localities consisting the distribution area, represented by a hiatus of 400 km).

It must be emphasized here, though, that we stress the importance of the distribution area for the taxonomic classification of brambles, that these areas do not correspond much to natural geographic (phytogeographical) regions. Brambles largely seem to represent phytogeographically incomplete taxa, as they usually do not inhabit areas of natural entities of various phytogeographical divisions. According to the experience of the present author, the description of a new species of brambles should follow after a somewhat longer study. The study of the individual species described by him (Holub 1991, 1993) lasted 7-12 years. With regard to the special character of the evolutionary process in *Rubus* it is impossible to determine every sheet of brambles and the enforcement of such ambitions does not give evidence of professional understanding of batological problems by the persons in question.

5 Some further taxonomic problems in *Rubus*

Regarding infraspecific ranks, their use cannot be excluded from the classification schemes in *Rubus*. Perhaps with an obligate apomixis it would be possible to exclude them from use. On the basis of populations and with regard to the character of their distribution (some vicariance or special type of distribution), it is possible in individual cases to use subspecies (within *Rubus* in the Czech Republic 2-3 cases at most may exist). Further infraspecific entities – varieties and formae – are better used for the designation of cases of individual aberrations if such cases need to be specially designated at all.

A special taxonomic problem is represented by the group (ser.) *Glandulosi*. Its members have a higher level of sexual reproduction, which creates progeny (biotypes) that are not similar to their parents. Weber (1973, 1986, 1995) presumed the existence of heterophyletic convergence, the results of which should be isophenous biotypes of a polyphyletic origin. Confirmation of this hypothesis will be important for further study of this group represented by many morphotypes, especially in submontane areas of Central Europe. In spite of the somewhat amorphous taxonomic character of its members, sufficient attention should be given to their study. The opinion that plants of this group should not be collected does not seem to the present author to be fully justified. Also, Weber recently (especially after the study of brambles in the area of Upper Lusatia – Oberlausitz; Weber 1987) accepted or newly described some representatives of this group as species.

When a pragmatic approach to batology was accepted, it seemed that some reduction (or even a great reduction) of the number of species would arise in individual countries. However, after the exclusion of many superfluously described taxa, the following period has nevertheless brought the description of new species. In the period 1971-1990 a series of new species were described in Europe, first of all by British botanists – Newton and Edees (67 species), then by Weber (59), Beek (19) and Maurer (6); in

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the following period further authors have also described new species, such as Holub (10) and Monasterio-Huelin (4). That the number of *Rubus* species has been changing in the Czech Republic in the last six years during further investigation may be illustrated by the following figures: 1991 (Preliminary checklist): 77; 1994 (Flora of the Czech Republic, vol. 4): 91; August 1995: 95 (and the description of 4 species are in preparation); January 1997: 99 (and the description of at least 15 species are in preparation).

6 A task for future work

To conclude, I would like to mention a certain problem with the material, which is unidentifiable and unclassifiable, i.e. not included into the classification at all, and which ecologists and phytosociologists in particular (and also people working in regional floristics) meet in the field. It is a remnant of classificatory work and at present we have insufficient knowledge of facts as to how extensive it really is. It should be designated as *Rubus* sp. or in some cases – if possible – it may be included in some taxonomic series (e.g. *Discolores, Hystrix, Glandulosi* etc.). The quantitative extent of this material has to be studied in cooperation with population ecologists by methods of transects or by weighing biomass, especially in comparison with determination of the biomass of taxonomically accepted species. Here good cooperation with representatives of modern ecology may originate.

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