KEYS TO THE FLORA OF FLORIDA -- 12, *RUBUS* (ROSACEAE)

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ABSTRACT

The genus *Rubus* (Rosaceae) is represented in Florida by 4 species: *R. flagellaris* Willd. is found in the state only in the Florida panhandle; *R. argutus* Link, *R. cuneifolius* Pursh, and *R. trivialis* Michx., are widely distributed, although rare or absent in South Florida. Specific names based upon 15 Florida *Rubus* types are assigned to these taxa. An extended commentary is provided in support of the thesis that the great majority of specific names in *Rubus* have been given to agamospermic segregates that, although morphologically distinguishable by the specialist, are too subtly characterized to be usefully employed by the working taxonomist, and that a less precise classificatory structure centered upon the sections into which the genus is divisible, is to be preferred. An amplified key is given to the Florida species.

KEY WORDS: *Rubus*, Rosaceae, Florida flora.

> "What is the blackberry situation at this hour? It is indeed an unhappy heritage. Where angels had feared to tread the ground has been traversed, and so unforbearingly, notwithstanding the briers, that not any semblance of a pathway has been suffered to exist." E. P. Bicknell (Bull. Torrey Bot. Club 37:393. 1910)

Alongside *Crataegus*, *Rubus* (Rosaceae) shares the unenviable reputation of being among the most intractable of North American

genera in terms of the ease by which a specimen or even an entire plant may be assigned to its correct species. The multiplicity of specific epithets found in floristic works, together with the subtle morphological differences by which the various entities are separated, has presented the user with an excessive number of alternatives and little prospect that his choice will be correct. Reproducibility -- the bedrock of scientific enquiry -- in this case the probability that independent observers of competent background will assign the same name to a given *Rubus* clone, has been replaced by a quicksand of individual interpretation.

This imprecision of identification has produced in the minds of many workers distaste for the genus *Rubus* and a disinclination to spend time and attention in the resolution of its problems. The hiatus has been filled by a few dedicated and exceedingly patient students whose very expertise has resulted in the recognition of ever more taxa and a further widening of the barrier to conventional enquiry.

A casual observer whose interests lie primarily in the identification of plants of a limited area may not fully appreciate the explosive proliferation in the names assigned to *Rubus* in eastern North America. Until the last years of the 19th century less than a dozen names were of common usage, and included the wholly distinct raspberries, flowering raspberries, and cloud-berries. The blackberries, where most of the taxonomic difficulties lie, received no serious examination until W. H. Blanchard studied them in the field from Newfoundland to Florida and west to the geographic limit of the group. By 1911, although Blanchard had concluded that "eight species include the great bulk of our blackberries, perhaps ninety percent of them," he felt obligated to recognize and name 36 additional specific entities (Bailey, Gentes Herbarum 1:142. 1923).

Other authors then saw need to name still other species. M. L. Fernald, although he accepted many of Blanchard's names, gave 24 additional specific epithets to North American blackberries (Gray Herbarium index). P. A. Rydberg described a further 24, H. A. and T. Davis described 9 more, while still others were described and named

by T. C. Porter, N. L. Britton, W. W. Ashe, J. K. Small, and L. H. Shinners.

But the author of greatest importance, whose intensive field studies and voluminous publications on *Rubus* span more than half a century, was L. H. Bailey. His interest in *Rubus* grew slowly, with a single specific epithet published in 1898 and a second in 1902. By 1934 Bailey had published a total of 52 specific names. His perceptions by then were acutely sensitized, and a profusion of new names appeared: 42 in 1941, 79 in 1943, 40 in 1944, 74 in 1945, and 81 in 1947. With a few additional names in following years, Bailey was responsible for the description, the naming, and in nearly all cases the illustration of a total of 383 species of *Rubus*.

Yet Bailey did not feel that the reservoir of undescribed species was near depletion. His compendious Species Batorum (Gentes Herbarum 5:1-932. 1941-45) provided coverage of the 390 species of *Rubus* then recognized by him in North America. In the next two years he accumulated a further 76 species, as described and illustrated in his supplementary Studies in *Rubus* (Gentes Herbarum 7:193-349. 1947). But the 466 species he thus recognized were no more than, in Bailey's opinion, "nearly or quite one-half the number of species native on the continent."

Although North America is, in Bailey's words, "probably...the most fertile area on the globe for *Rubus*," Europe has fared no less well in terms of the number of specific epithets applied to the genus. Perhaps reflecting the greater density of botanists more than the European subcontinent's relatively impoverished vascular flora, the basic texts of Europe treat large numbers of minutely distinguished *Rubus* species. The volume of recognized names has compelled a stratagem for their handling, by the segregation of species into categories, or levels of importance, with only the principal species or "circle-species" given full treatment. In central Europe, H. Huber (in Hegi, Flora von Mitteleuropa IV/2A:274-411. 1964-66) recognized 33 basic species and 252 subordinate species; these latter were described, but in different type size and without inclusion in the main key to

species. In the most comprehensive modern European floristic treatment, Y. Heslop-Harrison (Flora Europaea 2:7-25. 1968) acknowledged 75 species of *Rubus*, of which 66 were "circle-species" representative of groups which contained an additional 374 undescribed and unkeyed related specific names. Since there is no provision in the International Code, nor accepted systematic dogma, for the existence of species of more than one level of biological importance, the European stylistic practice, though maintaining the semblance of a workable structure, is as yet unexplored in its more fundamental implications.

The redundancy of specific epithets in *Rubus*, both in Europe and America, has not failed to bring forth skeptics who questioned the biological significance of the named entities, even their very existence and the motivation of their authors. The American E. P. Bicknell, himself the author of 70 obscurely defined species in *Sisyrinchium*, expressed his unease at Blanchard's many *Rubus* names with an article plaintively entitled "Have we enough New England blackberries?" (Bull. Torrey Bot. Club 37:393-403. 1910). Defense of the reality of the new entities has rested largely with L. H. Bailey who provided a rationale with each of his major treatments of the genus. At no time was Bailey unaware of the unconventional image that his many species produced in the minds of classical systematists. He remarked in 1923 (Gentes Herbarum 1:143), "In *Rubus*...it is not possible always to apply the formal species concept of ante-evolutionary days with either precision or satisfaction." In 1941 (G. H. 5:18) he said, "The reader may suppose that I have split the species finely. The opposite is the truth. I could have described any number more if I had cared to pursue a separatist course." In 1943 (G. H. 5:233) he commented, "With so many kinds now separated, the reader may wonder whether every colony is not a distinct species. This is a natural reaction..." He cautioned in 1944 (G. H. 5:508), "...persons not critical in *Rubus* will have little success with either pictures or specimens. The mind must first be free of notions and then the eye must be able to discriminate." And he rested his arguments in 1947 (G. H. 7:194) with the defense, "I have never made a species; I have only recognized, named and described them."

Bailey gave repeated attention to the supposition that the many closely defined species recognized by him were the product of prolific hybridization among a limited number of true species. Bicknell had been insistent that the entities named by Blanchard could be accounted for as hybrids between no more than 11 species. Unwillingness to accept such an explanation was a theme that persisted through all of Bailey's works. His hostility to what he considered a glib and superficial interpretation was scarcely concealed (G. H. 5:6. 1941): "Early in the present century began the singular hybridity postulate in *Rubus* work, whereby hybrids were freely assumed from herbarium specimens so fragmentary that not even the species themselves can be determined; thereby was the fear of making new species escaped and the difficulty of understanding the plants was assuaged." He did not deny the possibility of natural hybridity in the genus, but challenged that its existence had yet to be proved and insisted that the entities described by him were readily recognized by a person of observant eye and sufficient field experience.

Yet even as students of *Rubus* determinedly pursued the self-immolating course of recognizing and naming a seemingly endless series of dubious new species, and as Bailey shrugged off the shallow proposals that nothing more was involved than a massive hybrid swarm, contemporaries in the fields of embryology and cytogenetics were disclosing a framework of understanding on which a workable taxonomic structure could be hung. This was the discovery that reproduction by seed was a less than universally sexual process. In Europe, influenced particularly by the work and writings of A. Gustaffson, the concept came to be held that many genera of vascular plants display the phenomenon of agamospermy, or reproduction by seeds but without fertilization, as a special case within the general process of asexual reproduction or apomixis. *Rubus* was among the numerous genera in which agamospermic reproduction was suspected or identified.

In North America, and particularly among classical systematists, such a concept was not quickly applied or perhaps understood. Bailey

seems never to have given written expression of awareness that the individuals constituting many of his species might be of asexual origin, although his activities were indeed largely prior to widespread acceptance of the agamospermous pathway. He referred to the process only once, by indirect inclusion (G. H. 7:197. 1947): "I am asked for proof or at least for opinion that my novelties are not hybrids or apomicts or other irresponsibilities...of course no man has such proofs...."

But Bailey was nonetheless in search of such proofs, whichever way they might point. In 1944 he had begun the support and encouragement of John Einset in New York State, in his study of the cytology and embryology of various *Rubus* clones. By 1951 (Amer. J. Botany. 38:768-772) Einset was able to publish the first satisfactory evidence that in North America *Rubus* there operated certain apomictic phenomena that had previously been demonstrated only in Old World species.

Einset worked with 24 wild selections of *Rubus* which he brought into cultivation and which Bailey identified. He found the chromosome numbers to form a regular series of multiples of the basic 7, ranging from 14 through 63 in the species studied, with only a single clone having an aneuploid number outside this series. Triploids, with the somatic number of 21, formed the most common grouping, representing a third of the clones examined. As had European workers previously, he found that pollination was necessary for seed production. By crossing clones with different chromosome numbers and by counting the chromosomes of the resultant seedlings, if the seedling count matched that of the seed parent and differed from that of the pollen parent he could assume that agamospermy was present.

Einset's work strongly supports the assumption of apomixis in the American blackberries. When the chromosome numbers of the seed parent and the pollen parent were different, a high proportion of the seedlings (80 per cent in the case of tetraploid seed parents, 96 per cent with triploid seed parents) gave the same chromosome count as that of the seed parent. Had there been reduction of chromosome number with

a chromosomal contribution from each parent, as in sexual reproduction, intermediate counts would have been obtained with much greater frequency. Einset could only conclude that a high percentage of his *Rubus* progeny resulted from the parthenogenetic development of unreduced eggs.

The mechanics of reproduction in *Rubus* thus became clearer. Blackberries spread by vegetative means, with runners and rooting shoot-tips increasing the extent of the colony. Seeds are also formed, and serve as a means of dissemination across natural barriers and over distance. At times these seeds are produced by familiar sexual processes, and generate individuals that show the minute differences characteristic of genetic recombination. Perhaps also disparate individuals combine at times, to yield hybrids which differ from the offspring of conventional sexual reproduction only in the magnitude of their variability.

But in *Rubus* a less familiar generative mode is also present, and may well form the dominant reproductive pattern within the genus. This is the agamospermous pathway, in particular the pollination-requiring variant known as pseudogamy. The progeny thus produced, while simulating the offspring of sexual reproduction, are identical in genetic composition and essentially identical in morphology to their maternal parent. By the agamospermous replication of these individuals in their turn, large numbers of clones may be generated. With seed-eating birds as vectors, their distribution will be limited only by factors of habitat availability and physiologic adaptability.

A student inexperienced in *Rubus* who detects one of these agamospermic multi-clonal series is compelled to view it as he would an undescribed species. He finds the plants to have a coherent distribution, occur in predictable habitats, require pollination and reproduce by seed, and vary morphologically within a narrow range. His novelty is recognizable to him, and in almost every regard possesses the criteria that he associates with conventional species. It is perhaps inevitable that he should wish to bring legitimacy to his

discovery by publishing its description and by coining a new name to serve as its label.

And thus conflict arises in the study of *Rubus*. On the one hand is the insistence of close students of the genus, most of them of unquestioned taxonomic competence and extensive field experience, that they can recognize entities that are uniform, at times in many colonies distributed over hundreds of miles. On the other hand is the practical inability of less practiced workers to distinguish reliably among entities so very numerous that only the finite energies and lifetimes of their human identifiers appear to restrict their numbers.

This conflict has no elegant solution. The organisms themselves create the hierarchy to be described, and it is neither linear nor consistent in its structure. The series of equivalent units of a sexual system does not have a parallel in an agamospermic complex. No useful purpose is achieved by insisting that apomictic microspecies can be recognized with sufficient study, for they can neither be keyed by the specialist nor identified by the workaday taxonomist. A coarser, less precise classificatory structure seems to be the only feasible approach.

Thus one is led to a system that recognizes as species only major groupings of the genus *Rubus*. In the blackberries only one species appears usefully recognized in each section. In North America, Bailey (Gentes Herbarum 5:45-46. 1941) acknowledged ten sections in the true blackberries; the present scenario, if rigorously followed, would reduce the North American blackberries to this number of species. Among the raspberries, flowering raspberries, and cloud-berries the same degree of reduction is perhaps unwarranted, for it is not clear that the agamospermic process is as dominant there. But the blackberries, at least, appear more easily handled as a few aggregations of related forms than as constellations of numerous related microspecies.

Such an approach implies the assumption that each aggregation consists of a single basic species and its derived apomicts. Extensive work on *Rubus* in Europe, much of it by Gustafsson (see V. Grant,

Plant Speciation 325-331. 1971), has shown that diploid sexual species form the phylogenetic foundation of the European blackberry flora. A similar evolutionary origin may reasonably be attributed to North American species. The ancestral diploids, as deduced from the European example, may indeed no longer be extant, being represented in modern times only by their polyploid pseudogamous offspring. Further, certain aggregations of apomicts appear derived, not from a single diploid, but from hybrids formed by crossings in distant times between two of the diploid species. One must therefore not expect that the natural groupings of microspecies will necessarily be demarked by the presence of a sexual diploid, nor that all clones will fall within the larger aggregations, however they may be arranged.

Certain blackberry clones have been selected from the wild, and additional forms will undoubtedly be selected in the future, that possess characteristics of fruit, of flowers, or of vigor superior to those of the general population from which they come. These selections may have been recognized and named by previous students of the genus, or they may as yet be unnamed. The horticultural and other commercial importance of the selection may be such that a formal name is desired. In such situations, rather than a formal botanical binomial, the use of the flexible cultivar nomenclature would seem preferable. As examples, *Rubus trivialis* Michx. 'Marvel' (or *Rubus trivialis* cv. Marvel) and *Rubus trivialis* 'Okeechobee' are fully adequate replacements for *Rubus mirus* Bailey and *Rubus okeechobeus* Bailey, respectively. *Rubus flagellaris* Willd. 'Almus' and *R. flagellaris* 'Foster Thornless' are among other listed cultivar names.

Florida does not have a complicated blackberry flora. Only four of the ten sections recognized by Bailey are represented within the state: Arguti Rydb. (=Frondosi Bailey, Floridi Bailey), Cuneifolii Bailey, Flagellares Bailey (=Procumbentes Rydb., Tholiformes Fern.), and Verotriviales Bailey (=Persistentes Fern., Triviales Rydb.). Within these sections fall all of the 15 *Rubus* specific names based upon Florida types (1 by Rydberg, 14 by Bailey), as well as the uncounted but numerous names typified elsewhere but applied to Florida blackberries. Among these other names are four that typify the above

four sections and should be used to denote the major aggregations of *Rubus* as found in Florida: *Rubus argutus* Link, *Rubus cuneifolius* Pursh, *Rubus flagellaris* Willd., and *Rubus trivialis* Michx.

Rubus L. Blackberries[1]

1. Stems trailing or supported by low vegetation, elongate (to 2 m.), densely set with both stout prickles and numerous stiff bristles, usually mahogany red; leaves persistent throughout winter, subcoriaceous, leaflets glabrous, dark glossy; flowers usually solitary, on erect pedicels; petals white. Prickly trailing shrub. Thickets, open woodlands, brushy fields. Throughout; common. Spring. [*R. agilis* Bailey; *R. continentalis* Bailey; *R. lucidus* Rydb.; *R. mirus* Bailey; *R. okeechobeus* Bailey]
SOUTHERN DEWBERRY. **Rubus trivialis** Michx.

1. Stems erect, arching at tips, or declining and rooting, with prickles but with few or no slender bristles; leaves deciduous, thin, leaflets glabrous or densely pubescent below; flowers mostly in 3-several-flowered panicles.

2. Stems erect when young but soon arching and declining, often rooting at tips; prickles weak, sparse, often almost lacking; petals white. Prickly arching shrub, to 0.8 m. Mesic woodlands, clearings, old fields. Panhandle (east to Madison County); infrequent. Spring. [*Rubus enslenii* Tratt]
NORTHERN DEWBERRY. **Rubus flagellaris** Willd.

2. Stems remaining erect, although often arching toward tip, not rooting; prickles stout, numerous, recurved.

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[1]The "amplified key" format employed here is designed to present in compact form the basic morphological framework of a conventional dichotomous key, as well as data on habitat, range, and frequency. This paper is a continuation of a series begun in the 1970s (vide Phytologia 35:404-413. 1977). I wish to thank David W. Hall and Kent D. Perkins for constructively reviewing the manuscript.

3. Leaflets ovate to oblong, glabrous or nearly so; stems commonly to 2 m. (to 8 m., when supported by surrounding vegetation); panicle often several-flowered; petals white; fruits sweet. Prickly arching shrub. Moist to dry thickets, pond margins, swamps. Throughout panhandle and north Florida, south to mid-peninsula (Highlands, Okeechobee counties); common. Spring. [*R. betulifolius* Small; *R. floridus* Tratt; *R. harperi* Bailey; *R. penetrans* Bailey; *R. rhodophyllus* Rydb. in Small; *R. tallahasseanus* Bailey; *R. ucetanus* Bailey; *R. zoae* Bailey]

HIGHBUSH BLACKBERRY. **Rubus argutus** Link

3. Leaflets obovate, densely gray-pubescent beneath; stems usually less than 1 m.; panicle usually 1-3-flowered; petals white; fruits bland. Prickly arching shrub. Dry sands, old fields, disturbed areas. Nearly throughout (excl. south peninsula); common. Spring. [*R. audax* Bailey; *R. chapmanii* Bailey; *R. floridensis* Bailey; *R. humei* Bailey; *R. inferior* Bailey]

SAND BLACKBERRY. **Rubus cuneifolius** Pursh