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978-1-107-64229-4 - Handbook of the Rubi of Great Britain and Ireland

By the Late W. C. R. Watson

Excerpt

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## INTRODUCTION

The analysis of polymorphic groups of forms must precede experimental investigation, so as to give a definite direction to experiments. . . . It is therefore my conviction that a painstaking investigation of the smaller groups of forms is an indispensable task that should precede all studies on the nature of organic species.

W. O. FOCKE (1877)

It is so long since a work on *Rubus* appeared at home or abroad that there is perhaps small wonder that with the march of knowledge considerable changes should have taken place in the outlook.

Until the end of the eighteenth century the RUBI of this country were by all botanists brought under the six Linnaean species, *Rubus arcticus*, *idaeus*, *Chamaemorus*, *saxatilis*, *caesius* and *fruticosus*, of which the last-named included all European blackberries. Then when blackberries began to be compared with one another differences were found, and a few workers turned to analysing, describing and naming them. Arrangements were drawn up, intended to enable the brambles to be identified rather than to reflect their natural affinities and descent. In about 1860 and onwards much thought was given to the latter aspect, mainly from a morphological point of view. About the turn of the century genetic experiments designed to throw light on the nature of RUBI were begun in earnest, and cytological studies were commenced about 1920. However, we are unfortunately as yet without a comprehensive fact-finding review from this angle that could be of any assistance for systematics. Since Lidforss, there does not seem to have been any geneticist or cytologist who has had more than the barest acquaintance with the group in nature: there has been in consequence no planned series of investigation.\*

Vaarama has, however, provided proof that both *R. caesius* and *R. saxatilis* have unlike pairs of sets of chromosomes, which is to say that they must be of hybrid origin: so those who accept these Linnaean species—and who does not?—can no longer consistently reject the blackberry tetraploids, which also are of hybrid origin. So much must be obvious; but the meaning of what is obvious may sometimes be missed: it is that the blackberry tetraploids, as well as *R. caesius* and *R. saxatilis*, show the way of origin of the species; they are not merely

\* This must surely have been written before Watson had studied the work of Gustafsson. (P.D.S. and J.E.W.)

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hybrids, but hybrids plus something (as the late A. J. Wilmott wrote to me a few years ago concerning *R. saxatilis*), something that has gone into their production, whatever that something is, besides mere hybridization.

In many instances species were described and named when found growing in a single spot or a limited area; and some systematists, concerned at the mounting number of names, gave way to the temptation to reduce them arbitrarily to varieties and subspecies and severely to limit the number of their species. But varieties and even subspecies they are not, in the strict sense of these terms—they differ in form throughout. Other authors, with more reason, retained them as species, but created different grades of species to accommodate them and to express their views on their systematic rank, taking into account the extent of the area of distribution then known to them. A good many of these supposed local forms have since been found in other countries and not always in small quantity. *R. euryanthemus* is a case in point. At first mistaken for *R. fuscus*, then ranked as a variety of *R. pallidus*, it was in 1900 known only in south and mid England and Schleswig. Now it is known in the Hebrides and, under the name of *R. Schleicheri* microg. *chloroxylon* Sudre, from south to north France, Belgium, east to west Germany and Switzerland.

Very many British brambles have been grown from seed or rooted scions, and very many species have been studied upon a large number of bushes in nature. Minor variations have often been noticed of a recurring nature running through a proportion of the plants, but not such as to obscure their specific identity. Anything in the least resembling the alleged 'hybrid swarms' has never been observed in blackberries in nature, or in cultivation, other than in deliberate crosses in their second generation. But great and promiscuous is the mixture that occurs in nature in the case of secondary crosses of the Linnaean species *R. caesius*, the Dewberry, in damp places at very low altitudes especially on post-glacial soils. It is also perfectly true that the two diploid species *R. ulmifolius* and *R. tomentosus*, both of unassailable specific rank, are just those that offer the greatest variability, are the most prone to hybridizing, and are alleged by one cytologist to be self-sterile. On what an unstable footing then does the old conception of the genus rest!

By and large the tetraploid blackberries prove to have the same ability to reproduce their kind as truly at least as do the other sexually breeding species of the genus.

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It is common knowledge how confused and disputed the identification of RUBI in Britain has become in the last two or three decades. This has been due in part to the acceptance of identifications for a hundred years past from secondary and not from the original authorities for the species, and in part it must be added from insufficient acquaintance with the individual species in all their living aspects to enable sound determinations to be made, often from a dried specimen, and that improperly selected and dried. As a contributory cause also the peculiar belief or prejudgement has prevailed in some quarters that a species must be multiplex—a concept arising apparently from a conviction that a genus must not contain a large number of species.

Focke in his last work (1914) chooses seventy-one principal species and then, as he points out, using the freedom which a prodromus permits, assigns to this, that and the other many of the remaining European species, known or unknown to him, and omits the rest. Not that he assigns the non-principal species all as synonyms to the principal species, although he does so treat a certain number of them; he reverts to his early idea of instituting minor species of lower ranks in subordination to his principal species, calling them now 'forms', 'allied forms', 'prospecies' and 'subspecies'. Whatever may be the real value of this provisional, but his last, arrangement, it is at any rate certain that no one could trace the position in it of many of the species that he knows, except through the index.

Remembering that it is the duty of a scientist to expound nature as it is, and not to confound it by setting it forth as he would wish it to be, it seems right to keep separate what one has found by every test to be separate in nature; and by defining the species to the best of one's ability to furnish a secure basis for future work which shall have the aid of genetic and cytological investigations. That is in fact the purpose that I have kept before me: let a careful and complete analysis precede any attempt at a comprehensive synthesis. Already, however, the conception is emerging that the British bramble flora comprises not only a mosaic of distinct florulas, various in age and in composition, but also, systematically considered, comprising small disjunct groups of few related forms, and not few groups of many small forms which run one into another. To devise arrangements that bring these related species together, and at the same time serve the function of an easy 'key', has been the problem.

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There is no escape: since we cannot be the masters of Nature, nor create the plants afresh after our own idea, we must submit to the laws of Nature, and by intelligent application learn the characters that are inscribed upon plants.

LINNAEUS, *Genera Plantarum* (1764, 6th ed.)

One does not know much about brambles, until one has mastered the range of changes a bramble plant undergoes due to age, season, climate, exposure, soil, habitat and so on; neither is it possible for a given bush or specimen to be named intelligently by comparison with another specimen or figure unless one knows how to allow for these modifying influences. One may instance particularly the deep shade of woods, an excess or deficiency of soil moisture, atmospheric moisture, a spell of hot weather, a run of cool rain, a shallow soil overlying rock or iron pan, exposure to salty sea breezes, a frost in May, lopping in hedgerows. The effects of these factors are discovered by observation of the brambles growing under such conditions. That they are of practical concern a few instances may prove.

*R. carpinifolius* sometimes grows in marshes and is then apt to make lax panicles and somewhat lacinated leaflets. Such a specimen was named *R. leucandrus* by Focke, and another *R. carpinifolius* var. *laxus* by Sudre. *R. lacustris* Rogers found in Lakeland is a wet-soil form of *R. Lindebergii*. *R. vestitus* growing in woods so far deceived Babington that he published it as a new species, *R. Leightonianus*, and was corrected by Leighton. Salter was only stopped by Borrer from describing woodland *R. vestitus* as a new species, *R. rotundifolius*. *R. ericetorum* var. *cuneatus* Rogers & Ley is the same as *R. ericetorum* of Rogers. *R. ericetorum* ssp. *sertiflorus* var. *scoticus* Rogers & Ley is the same as *sertiflorus* of Rogers. *R. botryeros* Focke, at first associated with *R. longithyrsiger* by both Focke and Rogers, is the same as *R. oegocladus* of Rogers. Rogers repeats *R. dumnoniensis* Bab. under the name of *R. cariensis* Rogers (not Genev.). Sudre has this bramble under four names. The bramble which Rogers has as *R. Borreri*, Sudre has figured under that name and again under *R. retrodentatus*; he has described it also as *R. Schmidelyanus* var. *breviglandulosus*.

These faults are due to remissness in observing the behaviour of the species in different environments.

Turn now to the effect of temperature on flower colour. In this country I have examined thousands and thousands of the flowers of *R. separinus*. The petals are constantly pink or pale pink in the opening

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bud; the styles are usually greenish but sometimes pink-based. I have found in Kent that the styles come rosy or red in new flowers opening after a run of hot dry weather. Genevier, who is the author of *R. separinus*, says that the petals are white, the styles rose, violaceous or red. Sudre, who collected in Genevier's station, says that he found the petals sometimes pinkish and the styles flesh-coloured. Well knowing the bleaching effect of strong sunlight I opened an advanced bud on one of Genevier's specimens and found the petals were *pink*. (Genevier says that the carpels are *glabrous*; on his specimens I found them *pilose*. Sudre says they are *glabrous*; on his specimens I found them *pilose*. Bouvet says they are *glabrous*. They are invariably *pilose* on British specimens.)

The foregoing illustration relates to the effect of settled, hot, dry weather. The following note by Focke on a sheet of *R. rhamnifolius* collected in his garden at Bremen in the summer of 1885 shows the opposite effect of rainstorms: 'Styli in solo arido et sub coelo sereno rubentes, post pluvias vero in eadem planta virentes.'

I have myself seen similar temperature and rain effects on *R. plinthostylus* growing in my garden.

Where petals or stamens have been bleached after the flower has opened, the colour can often be seen remaining unaffected on the claw of the petals or the base of the filaments.

There also seems to be sometimes a colour change in the reverse direction. Petals and stamens which had every appearance of being pure white when growing, turn definitely light pink on being dried in the press.

## II. Genetic intraspecific variations

Certain variable characters are found that are not known to be affected by any environmental condition and are presumably under genetic control. They are of a rather minor nature, and their presence or absence does not obscure the identity of the species. They are not due to hybridization; that is, they are not directly due to any fresh hybridization. Their appearance or disappearance in a new generation is apparently due to a recombination of genes that regularly takes place prior to the formation of gametes.

In some species one or other of these characters seems to have become fixed, and may be reckoned as one of the distinguishing characters of the species. In other species the same character may occur sometimes,

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not always. In yet other species it may not have been met with at all. For instance, pilose anthers occur always in *Balfourianus*, *danicus*, *Drejeri*, *gratus*, *mucronifer* and *sciocharis*; often in *affinis*, *plicatus*, *regillus*, *silvaticus*, *vestitus* and *Winteri*; never in *adscitus*, *cardiophyllus*, *foliosus*, *pallidus*, *rudis* and *Sprengelii*.

A survey is needed to learn in which species the following characters appear, and whether always.

- 1 a. Leaves 3-nate to 4-nate-pedate or 5-nate-pedate.
- 1 b. Leaves 3-nate to 5-nate-digitate or 5-nate-subdigitate, never 6-nate or 7-nate.
- 1 c. Leaves 3-nate to 5-nate-digitate and sometimes 6-nate or 7-nate.
2. Number of sepals and petals where the number anywhere exceeds 5.
3. Petals glabrous on the margin, or pilose.
4. Anthers pilose; always?
5. Carpels glabrous; pubescent; pilose; bearded.
- 6 a. Receptacle glabrous; or pilose.
- 6 b. Receptacle hirsute at the base with a brush of hairs protruding below the lowest carpels all round.

To observe the bush, the best way is to take a freshly opened flower and thumb down the nearer stamens outwards. This will give a clear view of the young carpels also. Receptacular hairs often grow out between the carpels and must not be mistaken for hairs on the carpels. To remove any doubt it is wise to take off a few of the upper carpels for examination; this will also expose the receptacular hairs clearly.

A good deal of information has been collected under the above heads, and some of it is included in the descriptions. Until it is much more complete it will be unsafe to begin to draw conclusions. In time it can be used to throw light on the method of seed production in particular instances, and perhaps on the relationships existing between the species concerned.

**III. Chromosomes and genes**

Wherever known, the chromosome number is shown in the description. In some cases counts have been made only on one bush; the chromosome number is then starred. There is a possibility that a different number will be found when a second or third bush is examined in these cases, as where two bushes have been examined two different numbers have several times been obtained.



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Certain results are, however, already sufficiently clear, namely (1) there is only one basic number, 7; (2) the chromosomes are found always in exact multiples of the basic number, with exceedingly rare exceptions; (3) the prevailing number is 28 in body cells, 14 in germ cells.

Three dwarf seedlings which appeared in a family raised from *R. thyrsiger* self-pollinated each had 27 chromosomes: it was claimed that they represented the systematists' var. *parvifolius*. These dwarfs, however, proved to be comparatively infertile, whereas natural dwarfs are quite fertile. Moreover, several different natural dwarfs have now been studied and have been found to possess 28 chromosomes each. The implication, then, based on the *thyrsiger* seedlings refers only to that case; the cause of the dwarfing in the other cases remains unexplained. It is also not known whether dwarfing is a reversible condition.

Different opinions prevail as to whether the forms of chromosomes can be distinguished well enough to throw light on the origin and relations of species in *Rubus*. In *R. arcticus*, *idaeus*, *caesius*, *saxatilis*, and hybrids artificially created between some of those species, the chromosomes have been studied, distinguished, delineated, and conclusions have been drawn from their form; their pairing behaviour in meiosis has also been established; but there is a difference of opinion between cytologists as to whether allotetraploidy or autotetraploidy is indicated in the parent species concerned, *R. caesius* and *R. saxatilis*. No doubt in course of time the doubt will be resolved to the satisfaction of cytologists. From a morphological point of view it seems very probable that *R. caesius* and *R. saxatilis* are of hybrid origin, and that one parent in each case is *R. idaeus*.

As to the blackberries (MORIFERI), one cytologist urges that the morphology of the chromosomes is of outstanding importance and that every effort should be made to determine their forms. Against this it has been advanced more than once that the chromosomes are too small and too vaguely defined to make it likely that they can be of much use in this connexion. When one compares the different drawings that have been published of *R. caesius* chromosomes, the idea occurs that possibly the methods of fixing, staining and cutting may be different and may be the cause of the discrepant results, rather than that, as has been suggested, the chromosomes are really different in the different plants of *R. caesius* examined. One notes also that the unstainable centromere, which is probably differently located in the seven chromosomes and should help to differentiate them, is not drawn.

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An additional method of recognizing allo- from autopolyploidy has been recommended by one cytologist, namely a morphological study of the bramble itself.

Improvements of technique and further consideration of the problem will perhaps bring enlightenment, and we may turn away from these aspects and see what relation is borne to the systematy of brambles by the number of chromosome sets found to be present. (Note that  $x=7$  chromosomes.)

1. Diploids ( $2x$ ). *R. ulmifolius*, *R. idaeus* and *R. arcticus* are the only British species concerned. *R. tomentosus* of the Continent is also  $2x$ . A  $2x$  seedling was obtained from *R. macrothyrsus*; the other seedlings of the same family were  $4x$ .

2. Triploids ( $3x$ ). *R. nitidus*, belonging to SUBERECTI. *R. hylophilus*, belonging to CANDICANTES. *R. thyrsanthus* in the same group is usually  $3x$  on the Continent, but here  $4x$ , one bush. *R. Braeuckeri*, SPRENGELIANI. *R. rotundatus*, SYLVATICI, remarkable as being the only morifer known to have three satellite chromosomes.

3. Tetraploids ( $4x$ ). The great majority of blackberries belong here.

4. Pentaploids ( $5x$ ). Eight species of MORIFERI have been found to be  $5x$ , in four of which the number  $4x$  has also been obtained. Three varieties of *R. caesius*, and 11 out of 14 of its derivatives (TRIVIALES), were found to be  $5x$ , in two instances also producing a  $4x$  form.

5. Hexaploids ( $6x$ ). Four species of MORIFERI have been found to be  $6x$ , in two of which the number  $4x$  has also been obtained. One of the TRIVIALES was found to be  $6x$ . The hexaploid *R. magnificus* included above also furnished a  $3x$  seedling. An odd  $6x$  seedling also appeared in a family of *R. pyramidalis* seedlings.

It remains to be seen what explanation the cytologists will wish to give of the causes and effects of these dual chromosome forms which occur in the same species and more than once in the same family of seedlings, and which do not disturb specific identification. It seems that they can be ruled out from having played any part in the origination of new species or even varieties; although they will probably be found to affect fertility and resistance, and therefore, in the long run, prejudice the survival of the chromosome form.

Perhaps it hardly needs to be mentioned that the phenomenon is widespread in other genera, as *Ranunculus Ficaria*  $2x$ ,  $3x$ ,  $4x$ ,  $5x$ ,  $6x$ , and *Caltha palustris*  $4x$ ,  $6x$ ,  $7x$ .



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The form of the chromosome depends partly upon the number of clusters of genes arranged along the chromosome. These are stainable microstructures which are held to be associated with definite characters in the phenotype; they work together as crews with neighbouring crews, exerting their influences collectively. The genes are liable to change over in a block from one chromatid to another in synapsis, either as a one-sided move or as a mutual exchange, or they may undergo a reversal of order in a segment of their own chromatid. Such moves break the existing liaisons and reconstitute the co-operative, collective effects or products of their interactions, with corresponding results upon the future phenotype. Those results also seem to be compound, affecting more than one character at a time. It is rather singular that in *Rubus* more seems to be known, or can be predicated, of the genes, and of their operation—although the genes are ultra-microscopic—than seems to be known of the chromosomes themselves.

The effects of the genes are probably exerted through the cytoplasm, which is itself open to influences of the environment, judging from the changed effects upon the phenotype that result from changed external conditions. Causes of variation of different kinds are thus proceeding continually from the interaction of these two agencies; and the risks of coming to conclusions upon the observation of one agency without the other will be evident.

### IV. Reproduction

*R. Chamaemorus* (8x) is dioecious. It has been observed that where the male plant is absent the female plant does not set seed. Where male and female plants are together, seed is set. Sexual reproduction is thus clearly indicated.

When the styles of a bramble, e.g. *R. procerus* or *R. caesius*, are cut off, fruit is not produced; but when flower buds of either of the same two species are enclosed in a muslin bag, in late summer and in the shade, the flowers open and set fruit, self-pollinated. Thus, for fruit-production pollination is necessary, which is not the case for clone formation.

Many species successfully cross together, whether fairly closely related as *R. ulmifolius* and *R. subinermoides* or remotely related (if at all) as *R. plicatus* and *R. Bellardii*. They may give a fertile hybrid intermediate between the parents, and may have pollen and fruit as good as or better than those do; or they may be infertile and propagate solely

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by rooting stem-tips. Such intermediates are found sometimes in nature growing in the presence of the parent species. Examples are given under *R. ulmifolius* and *R. propinquus*. All such plants, both parents and offspring, are clearly not clone-producing nor clone-produced.

Whoever observes brambles closely in nature, especially when they are in flower, will be aware that variations in the same species are frequent. Clones do not produce variations.

The claim has been made by cytologists and others that many species of *Rubus* are clones, and indeed that this is the usual method of reproduction except in diploids. The proof offered is that in *R. nitidoides* and *R. thyrsiger* the development of seed by apospory has been noted cytologically. A cell of the nucellus has budded and pushed into the embryo sac and, without the nucleus having undergone meiosis, has developed into a false egg.

But it has been observed in the same two species that two daughter cells ( $2x$ ) in the normal embryo sac united again after having undergone meiosis. In this state ( $4x$ ) they could, either with or without union with a sperm nucleus, grow into a true seed and pass on any variation acquired before meiosis. But no egg grows into a seed until the central nuclei in the embryo sac that form the endosperm have been fertilized by one of the two male generative nuclei proceeding from the pollen tube. Endosperm is apparently required for the growth of the egg. This is of course a sexual process, and it touches off the spontaneous development of the normal egg cell, the second male generative nucleus taking no part. Being thus only a unisexual process, it is termed pseudogamy. The egg so constituted ( $4x$ ) carries the characters segregated in meiosis, and is not distinguishable from a bisexually formed egg ( $4x$ ) in form or function. This agrees with the conclusion arrived at in the cytological investigation to which I have referred: 'We may regard apomictic processes which allow for segregation as subsexual, although the progeny are wholly maternal.' Another conclusion was that 'apomixis is an escape from sterility'.

It seems clear that a theory of sterility and a prevalent accompaniment of clone reproduction does not account for the state of things met with in *Rubus*: allotetraploidy, implying past and present hybridization which must be sexual intraspecific variation within limits; frequent high fertility; sterility in female plants where male plants are absent, and in bisexual plants when pollination is prevented. Neither need it be supposed that pseudogamy represents the normal method of repro-