

# ON THE HABIT, ECOLOGY AND TAXONOMY OF THE BRAMBLES OF THE NETHERLANDS

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### I. INTRODUCTION

The habit of a plant gives as a rule unmistakable indications as to its ecology, but as it is at the same time a reflection of the hereditary characters on which its taxonomic position rests, it is no wonder that there appear to be quite distinct relations between the latter and the plant's ecological behaviour. This is well exemplified by the brambles.

Among the *Moriferi* or true brambles we meet with several ecotypes; some of these are remarkable for their resistance to low temperatures, some are hygrophilous, xerophilous or sciophilous forms and some show a preference for alkaline soils, and it appears that these five ecological groups correspond with five taxonomical ones, viz. the *Suberecti*, *Silvatici*, *Discolores*, *Glandulosi* and *Caesii*, groups that have been founded by the taxonomists in the usual way on morphological, genetical and geographical grounds, and not on ecological ones.

Because of this close parallelism between habit, ecology and taxonomic position it seems desirable that the study of the very numerous taxonomic units of which this difficult genus is composed, should not be confined to their morphological characters, geographical range and origin, but that it should also consider their structure and mode of life.

The principal aim of this paper is to discuss a number of morphological and ecological characters that may be of importance for distinguishing the various species and infraspecific taxa, and which throw some light on their occurrence in a definite environment. It is not my intention to give a complete list of these characters, for a study of a restricted number will suffice to illustrate my meaning. In the concluding chapter the various attempts to arrive at a classification of the *Rubi* will be surveyed; special attention will be paid

in this survey to those taxonomic units that occur in the Netherlands, viz. to a part of the *Moriferi* or true brambles, the raspberry and the stone raspberry (*Rubus saxatilis* L.).

## II. STRUCTURE

It has since long been recognized that a plant's habit (its phenotype) is determined by the action of the environment on its hereditary structure (the genotype). The structural characters of the brambles, their vigour and term of life, their fertility etc. depend on differences in the supply of nutrients and in that of water, light and heat. The deviation from the average type, however, is but seldom so profound that it becomes difficult or impossible to recognize the taxonomic unit to which a particular specimen belongs. Nevertheless, as it is not excluded that the variability of the phenotype may cause difficulties, it is of importance to gain some insight in the way in which the various parts are influenced by the environment.

A study of the growth forms exhibited by our native brambles leads to the conclusion that there are two main types, viz. plants with several erect or suberect stems and plants provided with arcuate stems and branches and, as the stems spring from the same base, more or less dome-shaped in contour (cf. fig. 1). In plants belonging

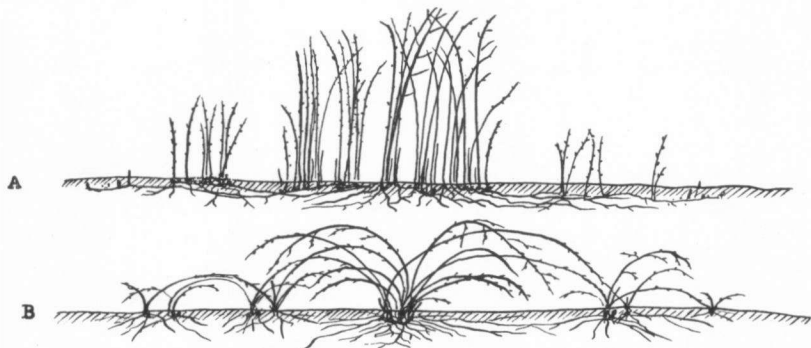


Fig. 1. The two growth forms of our native brambles. A. suberect type, shoots developing from buds on the roots ; B. dome-shaped type, with rooting stemtips

to the first-named type the shoots develop from adventitious buds formed by the roots, and they grow on the whole more or less straight upwards, although it is not excluded that their upper parts may in the end bend down under the increasing weight of the foliage. In plants belonging to the second type the shoots very soon begin to deviate from the vertical position and assume an arcuate form, and as the various shoots bend down in different directions, the contour of the plant becomes more or less dome-shaped. In late summer or autumn the shoots have curved down so far that their tips come into contact with the soil, and this is a phenomenon that is observed but very rarely in the plants belonging to the other group. Under extreme circumstances, e. g. when the plants grow in a moist

humus, rich in nitrogen, the stems of the plants belonging to the second type may become prostrate. On the other hand, when they grow in dense brushwood, the stems may straggle over the latter and reach a height of 4 or 5 meter, occasionally even of 10 meter.

A rich supply of nitrogen, and deep shade in combination with a high degree of humidity may change the plant's habit so profoundly that it becomes difficult, even to a trained botanist, to determine its taxonomic position, for in that case the change may not be confined to the size of the plant as a whole, but it may also affect the differentiation of the various parts and their relative size and position (leaf shape, indumentum, presence of glands, flower colour etc.)

Noteworthy is the short term of life of the shoot or turion. It flowers as a rule but once, usually in the second year, and dies when the fruits are ripe. The shoots of *R. tomentosus* Borkh., a species of South-central Europe, may flower already in the first year. Very vigorous turions, on the other hand, may live a year longer, flowering for the second time in the third year, but this is always exceptional. In accordance with this short term of life, the bark is but weakly developed and lenticels are absent; an exception forms *R. caesius* L, the dewberry.

The surface of the turions is usually beset with outgrowths in the form of prickles, which may break off above the base leaving a pustule, further bristles and other kinds of hair and stalked or sessile glands, and it may be covered with a layer of wax. In the development of the prickles the subepidermal tissue may take part or they may be entirely of epidermal origin, e. g. in *R. caesius* L.

The prickles may be inserted with regular intervals in the ribs of the shoots (e. g. in some of the *Silvatici*) or they may be spread irregularly over the whole shoot, in which case they may be collected in more or less distinct groups, and they may be all of the same size (in the homalacanthous forms) or of different size (in the heteracanthous forms). In the latter group they may gradually pass into eglandular or glandular bristles or into softer hairs. Their shape too varies considerably. Sometimes they show a strongly enlarged base and they vary between laterally flattened and subterete. Short, broad and rather blunt prickles are alternating with slender, long and sharply pointed to nearly needle shaped ones (*R. fissus* Lindley). Finally they may be straight and either patent or subpatent, or they may be curved or uncinat. The indumentum too shows considerable differences. It may be dense and regular, but also more or less sparse and the hair may be long or short and they may occur singly or in fascicles. The short stellate hairs may spring from a single epidermal cell or, more rarely, from a group of such cells. This complicated system of trichomes and emergences constitutes one of the most valuable means for distinguishing the species of the *Moriferi* or true brambles (fig. 2). The branching of the annual shoots may vary considerably. In the *Suberecti* it is sometimes entirely absent although there are also species with strongly branching shoots in that group. Moreover, in shoots that normally remain unbranched, branching

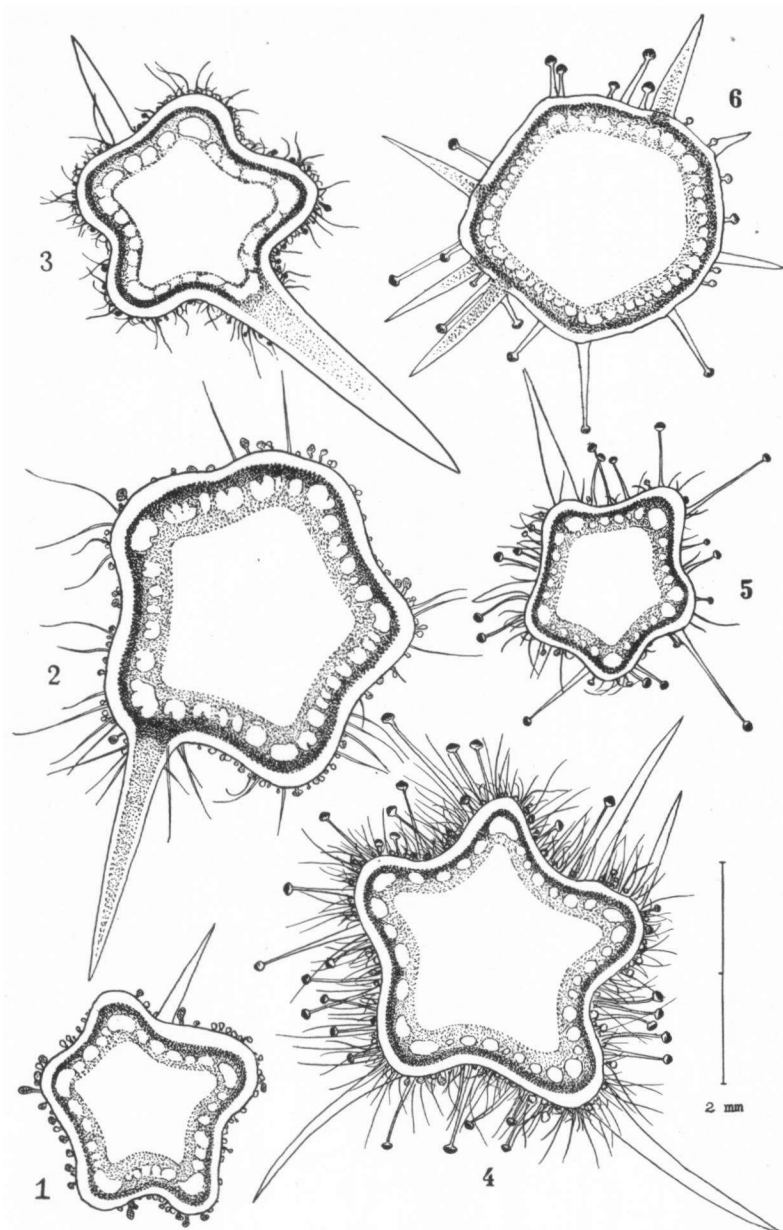


Fig. 2. Transverse sections through turion-tops of: 1. *R. fissus* Lindl. (Suberect.); 2. *R. silvaticus* Wh. et N. (Silvatici); 3. *R. ulmifolius* Schott. (Discolores); 4. *R. mucronifer* Sudre (Appendiculati); 5. *R. Bellardii* Wh. (Appendiculati) and 6. *R. caesius* L. (Caesii)

may be induced by a mechanical injury of the growing point. In vigorous shoots the leaves bear generally two serial buds in their axil; the upper bud develops first and should therefore be considered the main bud. When the shoot that develops from this bud is damaged or its growth inhibited, the second bud provides a substitute. The lateral branches of the 1st order may, in strong plants, produce lateral branches of the 2nd order. According to FOCKE accessory buds would be rare in the less vigorous species e. g. in some *Glandulosi*. In that case damaged shoots are replaced by new ones arising from buds at their base.

In *R. caesius* L too, several side shoots are said to develop from the base of the main shoot although branching is a common feature here. On exceptionally strong shoots a second axillary bud may be plainly visible. However, this bud will only rarely develop into a branch.

The differences in shape (habit) discussed above, how striking they may be, are of little value for distinguishing the species. Even the erect growth form, so often met with in the *Suberecti*, is not found under all circumstances. When *R. nessensis* W. Hall is growing in a dark and humid wood, with a layer of humus rich in nitrogen, its shoots may be nearly prostrate. The taxonomical differences, therefore, must be looked for elsewhere.

The way in which trichomes and emergences are distributed on the turion and the character of these appendages are to be considered distinguishing marks of much greater importance and it is on these characters that the subdivision of the *Moriferi* is chiefly based (*Suberecti*, *Silvatici*, *Discolores*, *Appendiculati*). The presence of a layer of wax on the turion of some species is also a fairly constant feature, though it is found in several *caesius* hybrids too.

The foliage leaves of our brambles show their most typical form near the middle of the 1st year shoots or turions. They are composed of 3—7 leaflets and palmate or pedate. In the latter case the outward pair of leaflets spring from the stalks of the inward pair (Fig. 3).

According to FOCKE 4 types of compound leaves are to be distinguished with the *Moriferi*, viz:

1. the trifoliate leaf;
  2. the pedate quinquefoliate leaf, derived from the trifoliate leaf by the division of each of the outward leaflets into 2 separate ones, the leaflets' stalks, however, remaining united with that of the odd leaflet;
  3. the palmate quinquefoliate leaf, derived from the former, by the splitting of the side leaflets' stalks to the base, the 5 stalks originating from one centre;
  4. the septemtrionate leaf, which may be looked upon as having originated from the quinquefoliate, palmate leaf by a symmetrical division of the odd leaflet into 3 separate ones; it may therefore be regarded as a quinquefoliate leaf with a trifoliate odd leaflet.
- A simple quinquefoliate pinnate leaf occurs as an exception with the dewberry (*R. caesius* L.) Pinnate leaves, however, do occur frequently with the *Idaeobati*, the group to which our wild raspberry belongs.

According to Focke (1877, p. 12) trifoliate leaves would be present in all species, and it would be the normal form of leaf in many weak growing brambles. In a small number of species it is even the only form of foliage leaf.

The odd leaflet of the brambles is always provided with a long

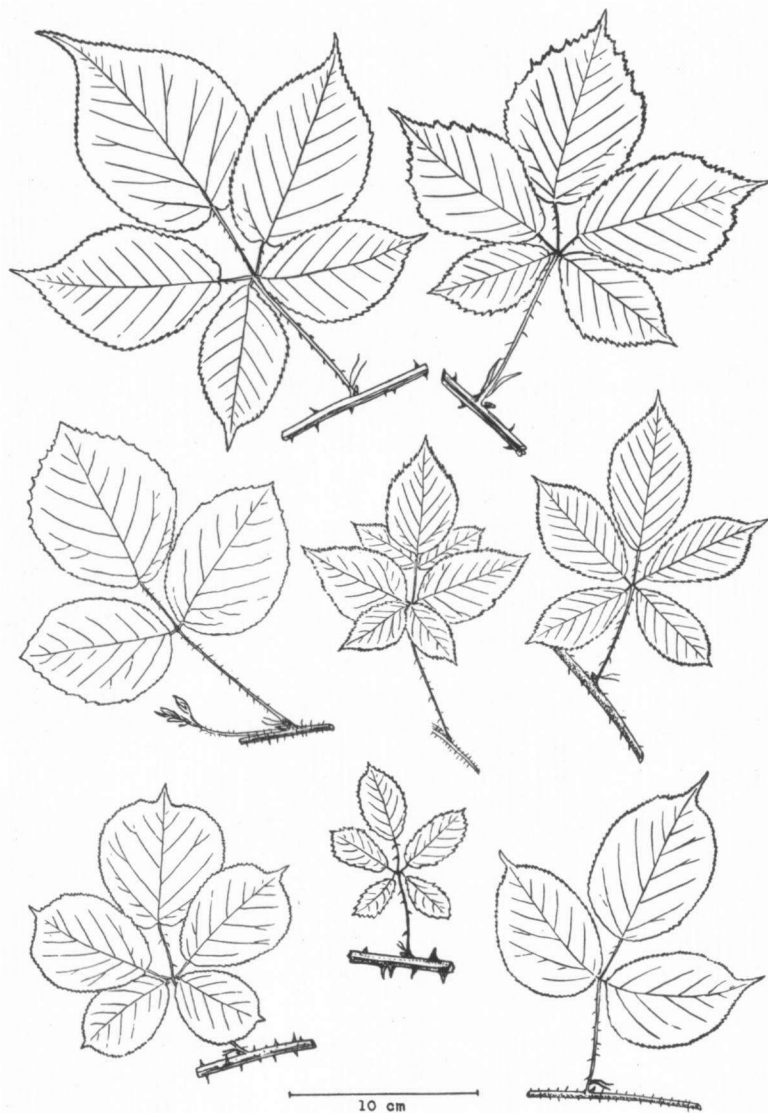


Fig. 3. Leaf shape of dutch brambles, At the top, on the left *R. nessensis* W. Hall, on the right *R. gratus* Focke. In the centre, from left to right *R. egregius* Focke, *R. fissus* Lindl., *R. Arrhenii* Lange. Below, from left to right *R. mucronifer* Sudre, *R. ulmifolius* Schott, *R. Bellardii* Wh.

stalk, the inner pair of leaflets possess distinctly shorter ones and the outer pair are short stalked or subsessile.

At the base of the petiole stipules are present and the latter are of various width and implanted at various heights of the petiole.

The petioles themselves show sometimes on their upper side a groove extending from the base to the top or over part of their length; when it is missing the petioles are either flat or slightly raised.

Between the length of the petiole, that of the petiolules and that of the leaflets there is a fairly constant proportion, provided that well developed leaves, like those that are present near the middle of the turion, are compared. The general appearance of the leaves is for an important part determined by them; e.g. comparatively short-stalked and wide leaflets will overlap, whereas long-stalked and narrow ones do not overlap. The lateral leaflets are always more or less asymmetrical, like the leaves of the elm.

When describing the leaves special attention is to be paid to the odd leaflet, but as has already been pointed out, the description should be based on a leaf from the middle of a turion. The number of lateral nerves is no reliable feature.

In young leaves the surface along the lateral nerves is plicated and these creases may remain visible with some species in the adult state, e.g. in *R. plicatus* Wh. et N., especially when the leaves develop in full light; in the shade the creases may almost completely disappear.

The structure of the leaf margin, although always dentate, varies with the species; the teeth may be large or small, of the same or of different size, and simple or compound. The shape of the teeth (wide or narrow, sharp or blunt) is best judged near the middle of the blade. Colour and glossiness of the leaves depend partly upon environmental factors, but they may nevertheless be regarded as characteristic for some species; those of *R. Arrhenii* Lange and *R. nessensis* W. Hall e.g., as a rule being distinctly nitidous. With regard to the shape of the odd leaflet, it seems best to follow Focke's classification:

1. Greatest width in the middle.
  - a. the margin of the leaflet is regularly curved towards top and base: narrowly and broadly elliptical leaflets;
  - b. the margin runs straight from the middle towards top and base: rhomboidal leaflets;
  - c. the margin is curved in the part above or below the middle and straight in the other part;
  - d. the margin is more strongly curved in the upper half than in the lower one;
2. Greatest width below the middle, with the same subdivision as mentioned above.
3. Greatest width above the middle.

The base of the leaflet may be rounded, cuneate, truncate or narrowly to broadly cordate. The top of the leaflet too is often very characteristic; it may be acute, subacuminate, acuminate or gradually to suddenly contracted.

The flowering shoots vary according to their position near the base or the top of the biennial turion. With weak-growing species the flowering twigs often spring from the subterraneous axes and in this case their shape is intermediate between that of a turion in its first year and that of the ordinary flowering shoots, and they bear an extremely complicated inflorescence of which the branches are often subtended by leaves, so that they sometimes resemble a series of separate inflorescences. The lower flowering shoots springing from the turion resemble the flowering shoots springing from the rhizome and this resemblance is the more striking, the later they come into flower. Therefore, when comparing flowering shoots, one should take shoots arising from the middle part of the turion. Towards the top the inflorescences are often reduced.

The inflorescence of the brambles comprises a terminal flower, which is also the earliest one. Although racemes (lateral axes one-flowered) and compound racemes (lateral axes compound) are strictly speaking inflorescences that lack a terminal flower, it is customary to apply these terms to the inflorescences of the brambles. The racemes may be everywhere of the same width or they may become narrower towards the top. The lateral branches may sometimes form regular dichasia. Parallel to the formation of accessory buds on the annual shoots, accessory branchlets fairly often develop on the axis of the inflorescences; they are formed between the main branchlet and the bract. The bracts themselves are either simple or divided into 2 or 3 slips, and transitions from bracts to foliage leaves are not rare.

The terminal flower opens first and it is followed by the terminal flower of the lowest lateral branchlet; subsequently the terminal flowers of the remaining branchlets begin to open. The lateral flowers of the lower branchlets therefore open, as a rule, simultaneously with the terminal ones of the higher branchlets.

Below the terminal inflorescence some axillary flowering shoots may be present. The higher ones start flowering before the lower ones. With some species a second inflorescence usually develops below the old inflorescence, which bends downwards under the weight of the fruits.

As to the petals and sepals, it should be remarked that shape and colour of the petals, the angle of inclination of the sepals and the presence of appendages on the latter may be of importance for the identification of the species (Fig. 4).

The sepals may change their angle of inclination after flowering or during the ripening of the fruit; they may be reflexed, erect or patent. They may wither while the fruits are ripening or they may remain green and juicy. The shape of the petals is fairly constant for each species although deviations do occur.

The relative length of the stamens, in comparison with the styles, and their position with regard to the latter are specific characters.

According to Focke a moist and rich soil would, in some species, produce longer stamens than a dry and poor one would do. The angle of inclination of the stamens during and after anthesis is also



of importance. Short stamens will show less change in direction than long ones. After flowering the stamens may soon wither and in that case they will be leaning against the fruit or they may keep up a certain distance.

The pollen of some species is composed of regular, well-shaped grains, e.g. in *R. ulmifolius* Schott, *R. caesius* L and *R. tomentosus* Borkh. As a rule part of the grains is deformed.

The anthers may be hairy or smooth; the filaments are white, greenish, pink or red and the same applies to the styles. Otherwise there is little variation in these organs. The colour of the floral parts is fairly constant in some species, variable in others (*R. vestitus* Wh. et N.). Some species possess faintly-scented or completely scentless flowers.

When the fruits of the true brambles (*Moriferi*) are ripe, they are, together with a part of the receptacle, released from the stalk. The fruits of *R. caesius* L are the only ones that may be picked, like those

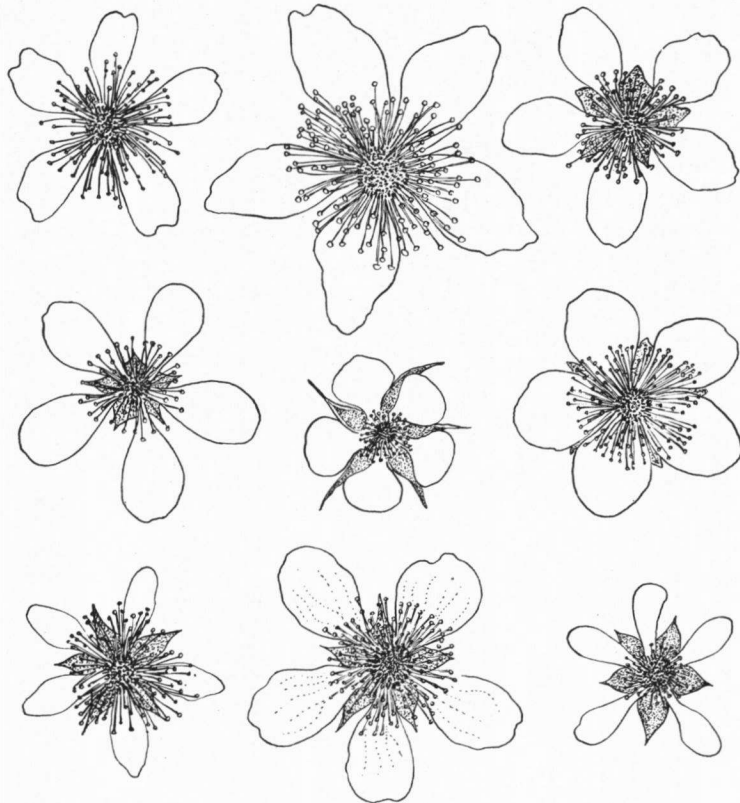


Fig. 4. Flower shapes of dutch brambles. Top, from left to right *R. carpinifolius* Wh., *R. gratus* Focke, *R. ammobius* Focke. Centre, from left to right *R. mucronifer* Sudre, *R. Arrhenii* Lange, *R. chlorophyllus* Greml. Below, from left to right *R. rudis* Wh., *R. badius* Focke and *R. serpens* Wh.

of the raspberry (subgenus: *Idaeobatus*), while the whole receptacle is left behind.

Size and shape of the drupes vary on the whole insufficiently to serve as distinguishing characters. In some species, e.g. in *R. ulmifolius* Schott and in *R. tomentosus* Borkh. they differ indeed in shape and colour, but these species are already easily recognisable by the presence of several other differentiated characters.

### III. ECOLOGY

To recognize the brambles in the field, some insight into their mode of life, development and growthform is desirable. The european *Moriferi* belong to the "suffrutices" or "half-shrubs" of WARMING,

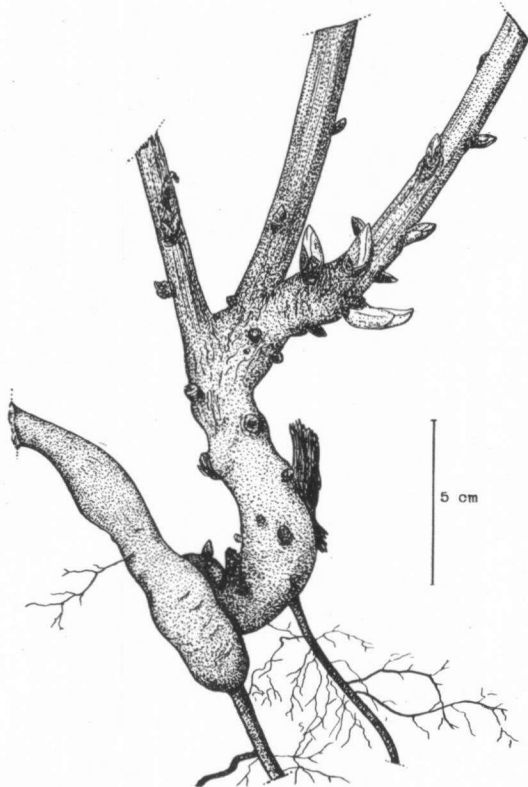


Fig. 5. Stembase of an old plant of *R. gratus* Focke. At the base of the youngest turion some large buds and several smaller ones are present; the latter as a rule remain dormant. Drawn in the middle of February

or to the "Holzstauden" of DRUDE. For the more or less exceptional case of the *Rubi* the latter author proposes the term "Schösslingsträucher". This means that they are provided with a woody persistent stem base, below or just above the soil surface and that every year

new shoots are produced by this part (Fig. 5). These shoots become woody in their turn. As a rule they are hapaxanthic (flowering once only).

The ripe fruits are often spread by birds and other animals.

The germination of the bramble seeds is irregular. When the seeds are sown immediately after they have been removed from the fresh fruits, they may germinate before the winter sets in, but as a rule they germinate next spring. It also happens that germination is postponed for another year (Focke 1877).

The cotyledons of the seedlings are ciliate and by this character they are in the field easily distinguishable from similar seedlings (Fig. 6). The first foliage leaves are simple and but superficially

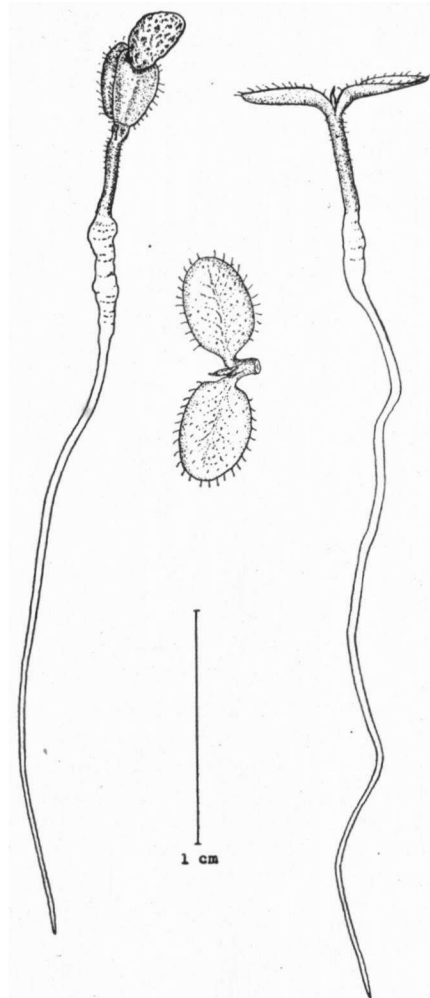


Fig. 6. Seedlings of *R. egregius* Focke, March 18th, 1950

incised, but the next ones, though still undivided, are lobed or cleft.

Whether the seeds germinate quickly or more slowly, probably depends on their power to absorb moisture and this in its turn depends on the weakening of the thick seedcoat, which differs individually, but the germination is also strongly influenced by the environment.

Still there appear to be differences between the various taxonomic groups: seeds of *Glandulosi* and *Corylifolii* germinate, according to Focke, as a rule during the first spring, while the seeds of the taller *Suberecti* and *Silvatici* generally remain dormant until the next year.

The brambles spread not only by means of seed, but also by a strong vegetative propagation, namely by means of the tips of the stem, that in autumn come in contact with the soil and strike root, or by adventitious shoots sprouting from the roots at some distance from the parent plant (Fig. 7). Many species root easily from the

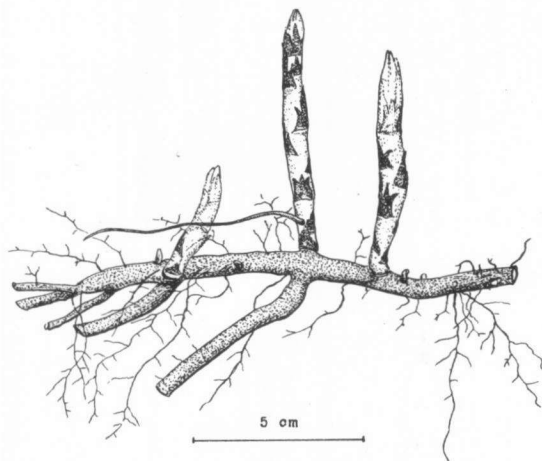


Fig. 7. Root of *R. nessensis* W. Hall with buds and young shoots.  
Drawn on February 15th, 1951

stem tips (Fig. 8), e.g. *R. gratus* Focke, *R. pyramidalis* Kaltenb., *R. vestitus* Wh. & N., *R. badius* Focke, *R. flexuosus* M. & Lef. and the *Corylifolii*.

The *Suberecti*, on the contrary, do not or only rarely develop roots from their turions, but they form adventitious shoots in profusion.

Besides the three methods of propagation mentioned above, viz. by normally fertilized seeds, rooting stem tips and adventitious buds on the roots, a 4th method of propagation exists in our native brambles, viz. by pseudogamic seed formation. This is a form of apomixis or multiplication without fertilization found in plants, that originally possessed a normal sexual propagation. In this case the seeds develop agamosperously, which means without the fusion of male and female sexual cells (see survey mentioned below)

Survey of the apomictic phenomena in the Angiospermae (After GUSTAFSSON, 1946).

## APOMIXIS

Agamospermy Reproduction by means of seeds (disseminules)			Vegetative reproduction Reproduction by means of bulbs, bulbils, runners, layers, etc. (propagules)
1. Sporophyte ↓ EMC's (Diplospory) ↓ Gametophyte ↓ Egg-cells (Partheno- genesis) ↓ Sporophyte etc.	2. Sporophyte ↓ Somatic cells (Apospory) ↓ Gametophyte ↓ Vegetative cells (Apogamy) ↓ Sporophyte etc.	3. Sporophyte ↓ (Adventitious embryony) ↓ Sporophyte etc.	<p>1. Sex-organs and gametes normal. Sterility phenotypically determined. Propagules arising outside the flowering region.</p> <p>2. Sex-organs normal or deformed. True sterility phenomena. Propagules arising outside the flowering region</p> <p>3. Sex-organs normal, transformed or deformed. True sterility phenomena. Propagules arising instead of or besides flowers; frequently germinating when still on the plant (vivipary).</p>

If induced by pollen: pseudogamy (Focke, 1881)

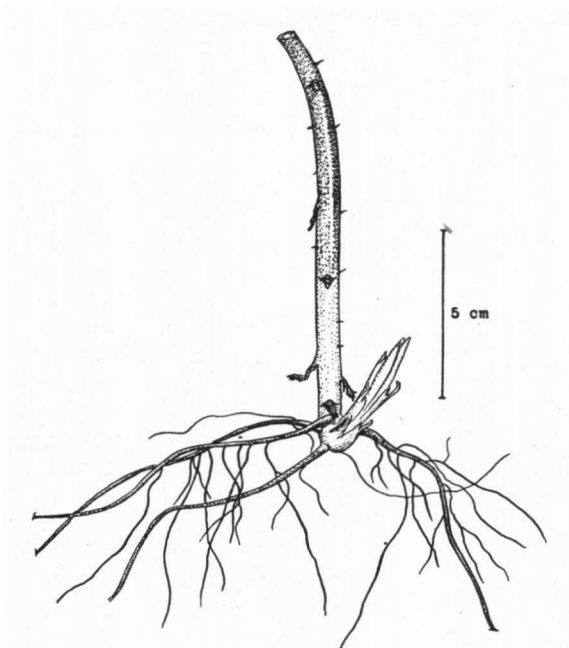


Fig. 8. Rooting stem-tip of *R. gratus* Focke.  
Drawn in the middle of February

By pseudogamy is meant the formation of seeds after pollination but without fertilization, the pollen acting as a stimulus. Gametophytes are formed here either from vegetative cells of the sporophyte by mitotic division (apospory) or from embryo-sac mother cells, the gametophytes possessing an unreduced chromosome number (diplospory).

This asexual way of seed formation predominates with the bulk of the European *Rubus* forms, although always some embryos (1-10 %) seem to be developing from normally fertilized egg cells.

Vegetative multiplication occurs in all brambles and is the most common method of propagation in many hybrids (e.g. *R. caesius* × *R. idaeus*) as well as in plants with sterile flowers. By this means sterile or but slightly fertile brambles may locally form large clones.

The dropping of the leaves varies for the different species, but can also be hastened or delayed by various circumstances.

In general brambles growing in the shade of trees, particularly in pine plantations keep their leaves a long time, often until the next growing season. *R. Sprengelii*, *R. badius*, *R. gratus* and *R. flexuosus* are under these circumstances often semi-evergreen or evergreen. In the open *R. ulmifolius* and *R. badius* often keep their leaves far into the winter. The first brambles to loose their leaves are the *Corylifolii*, *R. caesius* included, and the *Suberecti*; the latter are often already leafless before frost sets in. When they are frozen, many more bramble leaves are dying off, one of the reasons being frost damage to the connecting tissues between turion and petiole and between this and the stalks of the separate leaflets. These connecting tissues appear to undergo a swelling and show a ravelled mass after thawing, the leaf stalks sometimes loosely swinging from the vessels before dropping altogether. Brambles that are stretched out flat on the wood floor, often keep their foliage until the young leaves become visible.

By exception leaves of the "last year" may be met with on the plants during summer, among the newly developed foliage. During very cold and dry periods, however, nearly all species will drop their leaves. The sprouting of the leaves shows here slight differences with the various species occurring in a particular locality. The flowering time, on the other hand, is highly specific. The earliest flowering brambles are the true *Suberecti* (*R. nessensis*, *R. fissus*, *R. plicatus*, *R. sulcatus*), the first-named species at the same time having the shortest flowering period.

*R. caesius* L. and the *Corylifolii* too are early flowering, just like *R. carpinifolius*, *R. Bellardii* and *R. hirtus*. The two first mentioned species, however, are flowering a second time in September and October, and this applies also to *R. badius*, *R. vestitus* and *R. flexuosus*.

In the previous chapter some remarks have already been made on the anthesis. As a rule the flowers are homogamous, which means in this case that the stigmata are receptive when the anthers of the outer stamens are opening. Because of the spreading position of the stamens self-pollination is difficult, but many insects are visiting the flowers. The number of *Hymenoptera*, *Diptera*, *Coleoptera* and *Lepidoptera* that

have been observed on bramble flowers (cf. KNUTH 1898, T. II, prt 1, pp. 355—357) is extremely large (round 100 species).

Within the circle of stamens the nectarium lies like a ring-shaped wall round the group of ovaries, so that insects with a short proboscis too may reach the hidden nectar and cause pollination. Honeybees (*Apis mellifica* L.) and species of *Halictus* are regular visitors, and this applies also to the raspberry beetle (*Byturus tomentosus* F.). This busy visiting of insects gives ample opportunity for cross- and self-pollination and for pseudogamy.

The production of fruits is extremely variable. Slight fertility in spite of rich flowering rouses the supposition that we are dealing with a hybrid, but locality factors too seem to have a great influence. According to FOCKE *R. caesius* would be a free producer of fruits on chalky sand dunes, while it would be a poor bearer elsewhere. *R. nensensis* often produces but few fruits, but is, like other *Suberecti*, often flowering twice in the same season.

As to the condition of the soil, we may state that most brambles prefer a moist medium of mixed composition, rich in organic substances. It should not be too poor. Where sand is mixed with loam or marl brambles will soon appear. On rather poor and acid sandy soils in heath-districts may be found: *R. fissus*, *R. plicatus*, *R. affinis* and *R. gratus*, provided that there is a sufficient supply of moisture. Our brambles are restricted to districts where long periods of drought are lacking. In S. and Eastern Europe they are already distinctly scarcer than in the middle of the continent. Localities that are too moist, seem to be avoided. Bog-preferring brambles are not found among the European *Moriferi*.

Prickles, bristles, glandular and eglandular hairs on the surface of the turions may serve as a means of defence against herbivorous animals, and the prickles may at the same time serve as climbing organs enabling the turions to reach a considerable height in the midst of the surrounding scrub. The prickles are then functioning as a means to prevent the sliding back of the turion.

The need of light is not the same for the various groups and species. The *Glandulosi* are, as a rule, typical forest plants, thriving well in shade or tempered light. On the other hand species like *R. plicatus*, *R. ammobius*, *R. nitidus* and *R. ulmifolius* do not seem to be at home in woods, where they change their aspect a great deal and often fail to produce flowers. *R. egregius* and *R. silvaticus* again are species, that generally remain restricted to woods, at least in our country. It is difficult to say anything definite in this respect, because atlantic species adapted to a moist climate, may seek refuge in forests when they are growing in more continental parts, whereas in the atlantic zone they prefer the open field. This behaviour may often be due to their frost resistance (see below). Moreover many specific and individual differences exist.

The research work of the Finnish botanist PERTTULA (1941) has shown that the capacity of a species to produce seeds and to spread is highly influenced by the plant community of which it forms part.

His conclusion is that each vegetation unit possesses a specific degree of fertility, i.e. of fruit and seed formation, as well as a specific germinating power in their seeds. These units are characterized by qualitatively and quantitatively differing seedlings and by a special ability to vegetative reproduction. PERTTULA shows that vegetative reproduction is a very common phenomenon. More than 80 % of the plant species examined, whether growing in woods, meadows or on rocks, are provided with means for vegetative reproduction, 60 % of these being, in addition, able to migrate easily. He enumerates several vegetative means of spreading, but he does not mention seed formation by agamospermy.

GUSTAFSSON (1943, p. 192) says in this respect: "in the degree that a species increases its power of vegetative propagation and migration, in that degree will its capacity for sexual reproduction be extinguished" and he continues: "is it too bold to draw from this the conclusion that the system of hormonal balance that has evolved in the course of ages in respect of the generative apparatus should gradually be put out of function by the ever-increasing vegetative multiplication? May not agamospermy in the same way imply that the vegetative hormones develop at the expense of the generative ones?"

If the existence of this correlation could be proved, much would become clear that at this moment remains difficult to understand in the behaviour of the various *Rubus* forms under differing ecological circumstances.

Lastly, as to the climatic influence, remarkably large differences exist among the species with regard to frost resistance. Frost resistance often seems to be important in determining the geographical distribution. Especially bare frost, i.e. frost without a cover of snow, is fatal to many species. The bramble floras of England and France seem to contain many more frost-susceptible forms than e.g. that of northern Germany; this is to be understood in connection with the more frequent occurrence of dry, bare frost in the latter region. In the mountains of Central Europe the number of *Glandulosi* and *Discolores* quickly increases. In Scandinavia and elsewhere in Northern Europe the *Suberecti* become more frequent, increasing in number both of individuals and species, while they disappear in the South. Many *Silvatici* seem to prefer an Atlantic climate.

#### IV. TAXONOMY

The cytological, genetical and ecological study of the true brambles (*Moriferi*) during the last decennia has revealed a great deal on the character of the *Rubus* "species" and their origin. An interesting survey has been given by the Swedish cytologist ÅKE GUSTAFSSON in his book: "The genesis of the European blackberry flora" (Lund, 1943).

The greatest part of the numerous forms of the European *Moriferi* appeared to be polyploid (mostly tetraploid), which would imply a hybrid-origin. A fair number of species had already been grown from seed by W. O. FOCKE before 1877, and they all proved to be "true to type", which means that, in spite of prevalent cross fertilization,



the seedlings always show a close resemblance to the motherplant. Moreover brambles are, as we have already discussed, easily propagated vegetatively and they are able to enlarge their area quickly in this way.

This coming true from seed has contributed to the opinion that one is dealing here with true species. Still, in nature several *Rubus* species may be growing in each other's company and the frequent insect visits cause a liberal amount of cross pollination.

As previously explained, cross fertilization between the various forms is not at all common. Part of the polyploid pollen is generally sterile, and the pollen tube is apparently not always able to reach the embryosack. The production of fruits and seeds in these cases is due to the development of diploid gametophytes or of adventitious embryos. These apomictic seeds germinate normally and reproduce as a rule the exact image of the parent plant.

It is clear that this agamospermy explains the "coming true from seed" of a *Rubus* species. However, not all species are showing agamospermy. A relatively small number of species appeared to be diploid. For Europe these are, as far as now known, *R. ulmifolius* Schott, *R. tomentosus* Borkh., *R. incanescens* Bert. and *R. mosschus* Luz., and perhaps also *R. Bollei* F., from the Canarian Islands.

These diploid species possess well-developed, fertile pollen and this may be used for the fertilization of other forms. At the same time they appear to be self-sterile. First-generation hybrids too may produce fertile pollen. These facts are based chiefly on painstaking investigations carried out by LIDFORSS (1905—07 and 1914), CRANE and DARLINGTON (1927), CRANE and THOMAS (1939, '40), DARROW (1931), DARROW and WALDO (1933) and ROSANOVA (1934, 1938); FOCKE (1877) was the first to start hybridization experiments.

The earlier objection, according to which many *Rubus* "species" comprised in the Linnean species *R. fruticosus* L. would be no more than varieties, forms and hybrids, has therefore lost much of its strength. However, it is true that too diligent *Rubus* describers ("name-hunting batologists") during the last 150 years have gone too far in the splitting up of the old species. The index of SUDRE's monograph "*Rubi Europae*" (1913) comprises according to GUSTAFSSON, 1943,  $\pm$  3350 latin names. Many of these names apply to primary hybrids or to very local varieties. A large part, moreover are synonyms.

The morphological way of distinguishing species and forms does not always lead to satisfactory results. Difficulties, for instance, are met with, when we try to identify European *Corylifolii* (*R. caesius*-hybrids). Some authors distinguish a large number of forms in this group (FOCKE, E. C. GUSTAFSSON) while others, like SUDRE, apparently shrink back for an extensive splitting of these *Caesii* Focke (= *Triviales* P. J. Müll.).

In connection herewith Å. GUSTAFSSON (1943; p. 25—26) makes the following remark: "By the morphological method of determination we settle nothing but an external and frequently rather vague similarity to a certain *Moriferi* veri-type. This summary treatment

in SUDRE's monograph is one of its weak points, since many *Corylifolii* are well worthy of a careful study."

"SUDRE's method of classifying the *Moriferi veri* emanates from the fact already shown by FOCKE in 1877 and 1903 that about 75 to 100 blackberry types are spread over large areas and at the same time are so distinct that after a few years' study a taxonomist can distinguish them from one another. Around these, what I call, circle-species he grouped the great mass of named blackberries, several of which are similarly widely distributed and rather distinct, others comprise swarms of more or less unimportant forms, and, thirdly, some merge into neighbouring circle-species. Hybrids — secondary as well as primary — are placed by SUDRE under the circle-species (or microspecies) which they resemble most closely. Descendants from for example the cross of *R. tomentosus* and *R. ulmifolius* are classified either as *R. tomentosus*  $\times$  *ulmifolius* (= *R. tomentellifolius* Sud.) or as *R. ulmifolius*  $\times$  *tomentosus* (= *R. pulverulentus* Sud.). These reciprocal markings signify of course great gratuitousness and are condemnable from a genetical point of view." And a little further on: "Most of the 1930 brambles listed in "Rubi Europae" display a localized distribution, though about one hundred types are, as mentioned above, spread over great parts of the European continent. This astounding confusion of local and widely distributed types is caused simply by the occurrence of pseudogamy (i.e. autonomous embryo-formation accompanied by sexual endosperm development), maintaining in nature heterozygous segregates and hybrid derivations. Most of the widely distributed types consist of small, rather uniform populations which continually produce some rare aberrants by means of hybridization or segregation. Primary hybrids breed sexually. Sooner or later pseudo-gamous types appear in their progenies, combining genes and chromosomes in a new manner. The local floras are built up of some wide-spread types, crosses between these, and segregated apomict swarms more or less selected to the local environments. Now and then some segregates enjoy an increased vitality and a potent capacity of seed propagation — in addition to the multiplication by rooting stemtips — and will spread widely."

When this point of view is generally accepted, we may expect the development of a classification based on genetics. However, in the near future the present, morphological classification will have to serve as a starting-point for the new one. So long as genetical research has not made such progress that a classification can be built upon it, we will be obliged to stick to the morphological system.

To give an impression of the systems built up by W. O. FOCKE (1903—1914) and H. SUDRE (1913), their classifications are reproduced below.

In FOCKE's "Species Ruborum" (1914) the genus *Rubus* is subdivided into 12 subgenera in the following way:

- |                                      |  |
|--------------------------------------|--|
| I. <i>Chamaemorus</i> F. (1 species) | III. <i>Chamaebatus</i> F. (5 species) |
| II. <i>Dalibarda</i> F. (5 species)  | IV. <i>Comaropsis</i> F. (2 species)   |

- V. *Cylactis* F. (14 species) IX. *Anoplobatus* F. (6 species)  
 VI. *Orobatus* F. (19 species) X. *Idaeobatus* F. (117 species)  
 VII. *Dalibardastrum* F. (4 species) XI. *Lampobatus* F. (10 species)  
 VIII. *Malachobatus* F. (114 species) XII. *Eubatus* F. (number unknown, Focke ± 135)

Of these the 3 most important groups (*Malachobatus*, *Idaeobatus* and *Eubatus*) have each a well defined area of distribution: the subgenus *Malachobatus* is confined to S.E. Asia (Japan, Malayan Archipelago), Australia and Madagascar; the *Idaeobati* are having their chief area of distribution slightly more to the North, viz. in China, Japan and the E. Himalaya, but also in E. and S. Africa, while *R. Idaeus*, the type species of the group, has a circumpolar distribution. The *Eubati* have their richest centre of development in S. America, although one of their subdivisions, the *Moriferi*, occurs in Europe, where it is divided

## MORIFERI FOCKE (1874)

W. O. FOCKE (1903) in: Aschers. & Graebner, Syn. Bd. IV, 1e Abt.	W. O. FOCKE (1914) in: "Species Ruborum"	H. SUDRE (1913) in: "Rubi Europae"
15. groups: 1. <i>Suberecti</i> 2. <i>Rhamnifolii</i> 3. <i>Candicantes</i> 4. <i>Tomentosi</i> 5. <i>Discolores</i> 6. <i>Silvatici</i> 7. <i>Sprengeliani</i> 8. <i>Egregii</i> 9. <i>Grandifolii</i> 10. <i>Vestiti</i> 11. <i>Radulae</i> 12. <i>Apiculati</i> 13. <i>Koehleriani</i> 14. <i>Glandulosi</i> 15. <i>Corylifolii</i>	4 subsections, 16 series Subsection: <i>Suberecti</i> I. <i>Suberecti</i> veri II. Appendix ad <i>Suberectos</i> A. Series <i>Properi</i> B. Series <i>Semi-Suberecti</i> Subsection: <i>Senticosi</i> I. <i>Rhamnifolii</i> II. <i>Tomentosi</i> III. <i>Thyrsoidei</i> IV. <i>Discolores</i> V. <i>Silvatici</i> VI. <i>Egregii</i> VII. <i>Vestiti</i> VIII. <i>Grandifolii</i> IX. <i>Radulae</i> Subsection: <i>Glandulosi</i> I. <i>Koehleriani</i> II. <i>Eu-Glandulosi</i> Subsection: <i>Caesii</i> I. <i>Caesii</i> veri II. <i>Corylifolii</i>	5 sections, 13 subsections and 13 series A. <i>Homalacanthi</i> Sectio I: <i>Suberecti</i> Sectio II: <i>Silvatici</i> Subsection a: <i>Grati</i> series: <i>Eu-grati</i> series: <i>Sprengeliani</i> Subsection b: <i>Euvirescentes</i> series: <i>Calvescentes</i> series: <i>Pileatosi</i> series: <i>Nemorensis</i> Subsection c: <i>Discolores</i> series: <i>Subvirescentes</i> series: <i>Subdiscolores</i> series: <i>Imbricati</i> Sectio III: <i>Discolores</i> Subsection a: <i>Subvirescentes</i> Subsection b: <i>Hedycarpi</i> Subsection c: <i>Candicantes</i> Subsection d: <i>Subtomentosi</i> B. <i>Heteracanthi</i> Sectio IV: <i>Appendiculati</i> Subsection a: <i>Tomentosi</i> Subsection b: <i>Vestiti</i> series: <i>Hypoleuci</i> series: <i>Virescentes</i> series: <i>Hebecaulas</i> Subsection c: <i>Radulae</i> series: <i>Micantes</i> series: <i>Concolores</i> Subsection d: <i>Rudes</i> Subsection e: <i>Hystrires</i> Subsection f: <i>Glandulosi</i> Sectio V: <i>Triviales</i>

into an enormous number of forms. The *Eubati* are lacking completely in the regio round the Pacific and Indian Ocean.

The *Eubati*, the group to which also our brambles belong, are divided by Focke into 6 sections: *Xerocarpi*, *Ursini*, *Dissitiflori*, *Floribundi*, *Duri* and *Moriferi*; the last section represents our true brambles (brambles in a stricter sense). These sections comprise respectively 3, 1, 2, 24, 5 and  $\pm 100$  species. They are distributed on the American continent, Europe and N. Africa.

The further subdivision of the European *Moriferi* by Focke and Sudre is shown in the survey on the foregoing page.

Main species ("circle-species") of the *Moriferi* accepted by GUSTAFSSON (1943) are shown in the following table<sup>1)</sup>:

#### A. HOMALACANTHI Dum.

##### Subsectio: SUBERECTI Müll.:

*R. nessensis* W. Hall., *R. plicatus* Wh. et N., *R. fissus* Lindl., *R. sulcatus* Vest.,  
*R. nitidus* Wh. et N., *R. affinis* Wh. et N.

##### Subsectio: SILVATICI Müll.:

##### Series: Grati Sudre:

*R. carpinifolius* Whe, *R. vulgaris* Wh. et N., *R. clethrophilus* Gen., *R. gratus* F.,  
*R. chaerophilus* Sag. et Sch., *R. hypomalacus* F., *R. Arrhenii* Lange, *R. Sprengelii*  
Whe, *R. hesperius* Rog., *R. myricae* F., *R. chlorothyrsos* F.

##### Series: Euvirescentes Gen.

*R. Questierii* Lef. et Müll., *R. rhombifolius* Whe, *R. pyramidalis* Kalt., *R. macrophyllus*  
Wh. et N., *R. silvaticus* Wh. et N., *R. Gremlii* F., *R. egregius* F.

##### Series: Discoloroides Gen.

*R. villicaulis* Koehl., *R. argenteus* Wh. et N., *R. polyanthemus* Lindeb., *R. rhamnifolius*  
Wh. et N., *R. Bollei* F. (primary species), *R. canariensis* F., *R. Hochstetterorum* Seub.

##### Subsectio: DISCOLORES Müll.:

*R. ulmifolius* Schott (primary species), *R. Godronii* Lec. et Lmtt., *R. bifrons* Vest.,  
*R. Lindebergii* Müll., *R. pubescens* Wh. et N., *R. geniculatus* Kaltenb., *R. procerus*  
Müll., *R. thyrsoides* Wimm.

#### B. HETERACANTHI Dum.

##### Subsectio: APPENDICULATI Gen.:

##### Series: Tomentosi Wirtg.:

*R. tomentosus* Borkh. (primary species).

##### Series: Vestiti Focke:

*R. vestitus* Wh. et N., *R. Boraeanus* Gen., *R. adscitus* Gen., *R. mucronatus* Blox.

##### Series: Grandifolii Focke:

*R. incanescens* Bert. (primary species), *R. grandifolius* Lowe, *R. Steudneri* Schwnf.  
(primary species?).

##### Series: Radulae Focke:

*R. radula* Wh. et N., *R. Genevierii* Bor., *R. apiculatus* Wh. et N., *R. fuscus* Wh. et N.,  
*R. foliosus* Wh. et N., *R. infestus* Wh. et N., *R. thyrsiflorus* Wh. et N., *R. pallidus*  
Wh. et N., *R. obscurus* Kalt., *R. Menkei* Wh. et N.

##### Series: Rudes Sudre:

*R. melanoxylon* Müll. et Wirtg., *R. rudis* Wh. et N., *R. vallisparvus* Sudre.

##### Series: Hystrices Focke:

*R. fuscoater* Wh. et N., *R. pilocarpus* Grl., *R. Lejeunei* Wh. et N., *R. rosaceus* Wh. et N.,  
*R. hystrix* Wh. et N., *R. Koehleri* Wh. et N.

##### Series: Glandulosi Müll.:

<sup>1)</sup> This survey is incomplete according to G. himself.

*R. scaber* Wh. et N., *R. Schleicheri* Wh. et N., *R. platyphyllos* Koch (primary species?), *R. moschus* Juz. (primary species), *R. Bellardii* Wh. et N., *R. serpens* Wh., *R. hirtus* Waldst. et Kit.

Subsectio: CAESII Focke:

*R. caesius* L. and the innumerable *Corylifolii*.

Finally, to give an idea of the number of main species, micro-species and varieties GUSTAFSSON (1943) has compiled from SUDRE's monograph the following list:

A. HOMALACANTHI Dum.

Subsect. I: <i>Suberecti</i> Müll.:	7	main species	19	micro-species	40	varieties
Subsect. II: <i>Silvatici</i> Müll.:	41	"	160	"	316	"
Ser. a: <i>Grati</i> Sudre:	16	"	57	"	109	"
Ser. b: <i>Euvirescentes</i> Gen:	14	"	60	"	107	"
Ser. c: <i>Discoloroides</i> Gen:	11	"	39	"	100	"
Subsectio III: <i>Discolores</i> Müll.:	11	"	76	"	244	"
Ser. a: <i>Gypsocaulon</i> Müll.:	2	"	28	"	114	"
Ser. b: <i>Hedycarpi</i> F.:	7	"	26	"	56	"
Ser. c: <i>Candicantes</i> F.:	1	"	13	"	42	"
Ser. d: <i>Subtomentosi</i> Sud.:	1	"	9	"	32	"

B. HETERACANTHI Dum.

Subsectio IV: *Appendiculati* Gen.: 50 main species 440 micro-species 1327 varieties

Notwithstanding the fact that FOCKE and SUDRE have been working independently, in totally different regions of Europe, their systems show a fairly clear resemblance, in regard to the subdivision into groups as well as to the choice of main species ("circle-species").

Both systems are actually based on the old system of P. J. MÜLLER (1859) in which system already 6 groups, viz. *Suberecti*, *Discolores*, *Silvatici*, *Spectabiles*, *Glandulosi* and *Triviales* (= *Caesii*, incl. *Corylifolii*) were distinguished. Five of these groups are still in use, although as their delimitation has already shown, they did not all keep the same systematic value.

As to the main species, the following comparison has been made by GUSTAFSSON (1943, p. 28): "FOCKE listed in his monograph of 1914 as many as 73 important microspecies from Europe and North-Africa, each given a number of its own. Of these types eight are extra-European and therefore not dealt with by SUDRE. Of the remaining 65 types 52 are circle-species in SUDRE's manual and two are listed as circle-species under different names, i.e. 80—83 % of FOCKE's main types are regarded as such also by SUDRE. (It should be kept in mind, however, that the two batologists did not always delimit their "species" in the same manner). The thirteen main types handled in a different manner by the French botanist consist predominantly of English brambles, of which he evidently possessed but poor or at least incomplete information (see for instance the criticism in RIDDELSDELL's paper of 1923).

"Of SUDRE's 110 circle-species, on the other hand, 54 are identical and considered to be main types in Focke's monograph, 33 are

regarded as "species" but given a lower taxonomic rank (not furnished with numbers of their own). Nine of SUDRE's circle-species are mentioned as unimportant or hybridogenous forms, and 14, finally, not even recognized by FOCKE. Thus 87 of 110 circle-species (= 79 %) are characterized as rather essential types by both authors." (G.)

From this it is clear that these two meritorious investigators have come to closely corresponding results. FOCKE has been studying the *Rubi* for an important part in nature, i.e. in the living condition. He was the first to distinguish the main species and to discuss their interrelationships. It was SUDRE who founded a well justified system and also excelled in the arrangement of forms of subordinate systematic rank.

However, FOCKE's descriptions are in many instances more detailed, so that their works are supplementing each other. SUDRE is the more generally used at present.

WATSON's system (1948) differs so much from the older ones that a comparison is difficult. It is moreover adapted especially to the English bramble flora.

### SUMMARY

On the habit, ecology and taxonomy of the brambles of the Netherlands.

1. The connection between mode of life and taxonomic position of our *Rubus* species is discussed. The importance of the influence of environmental and hereditary factors on the habit and development of the plant is pointed out.
2. A knowledge of the mode of life and the behaviour of the plants in definite ecological conditions is of importance for recognizing the species in the field. A survey is given of the principal ecological data.
3. The various modes of multiplication are summarized, since they lead to a better understanding of the species and of the ecological forms mentioned above.
4. In conclusion the classification proposed for the genus *Rubus* by FOCKE and by SUDRE are reproduced and compared.

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