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Flower and Fruit Morphology of *Sorbus* in Correlation to the Taxonomy of the Genus

Introduction

In the following I am presenting the first part of the results of the study of the Czechoslovak species of *Sorbus*, to which study I have lately been devoting my time. The systematic examination of these taxa has shown, that, up to present time, the study of the structure of their flowers and fruits has been almost consistently neglected. Their investigation has shown that this structure discloses a number of valuable marks and is of fundamental importance for the evaluation of *Sorbus* species, as the various groups of species exhibit a considerable diversity of these features.

The subfamily *Maloideae*, in spite of the, on the whole, uniform characteristics with regard to the features of their flowers and fruits, shows a striking variability just in these features, and this fact is the cause of a very diverse conception of the various genera. Up to the present the morphology of the flowers and of the fruits has not yet been dealt with synthetically. The following is an attempt at the working out of their morphology with regard to the Czechoslovak species of *Sorbus*. The morphology of the flowers and fruits of the Caucasian species of *Sorbus* has been dealt with contemporaneously by Gabrieljan (1958). I know of no other work dealing with these problems. The advantageousness of the study of these features is proved by the fact that Gabrieljan, on the basis of his analysis, abolished a number of minor species that had been described as growing in the Caucasus by Komarov and Zinserling (1939).

Material and Methods

The morphological analysis was carried out with live or preserved material of my own collections from various localities in Czechoslovakia (neighbourhood of Prague, the Bohemian Karst, the Bohemian Central Mountains, the Giant Mountains, the High Tatras, the Slovak Karst, the Čachtice Hills, etc.). Only in the case of *S. chamaemespilus* also herbarium material was used. For the detailed analysis the flowers and fruits were fixed in a 4% solution of formalin. The fruits were gathered mostly fully ripened or immediately before. The anatomical structure of the fruits was examined mostly in fresh fruits or in fruits that had been preserved only for a short time. As I wanted to work with the largest possible quantity of material — my primary aim was the determination of the variability — I dispensed with the treatment with paraffin and with the use of paraffin sections. Provided that the fruits are not over-ripe, sufficiently thin sections can be obtained by means of sharp razor blades.

General Characteristic

The inflorescence is a corymbose panicle (corymbothyrsus), i.e. a panicle with elongated side branches, so that the flowers are placed approximately on the same level. This inflorescence is developed most typically in *S. aucup-*

aria. In *S. torminalis* it is considerably reduced, the group *Chamaemespilus* has a strongly contracted, very tiny and dense panicle.

The flowers are regular, cyclic, heterochlamydeic, bisexual, originally in all parts pentamerous; the gynoeceum is often reduced to 2—3 carpels.

A characteristic formation of the flowers of *Sorbus* is, as is the case with all *Rosaceae*, the receptacle, whose morphological substance is still the subject of discussion. No agreement has been reached as to whether the receptacle is of foliar origin, whether it is a modified stem, or whether the truth is somewhere in the middle. The explanation of the receptacle as having developed from a former stem is based rather on ontogenetic evidence, wheras the partizans of the foliar theory base their opinion on vascular anatomy. With regard to the *Maloideae* the opinion is prevalent that the receptacle, and thus also the pulp of the fruit, originates from a stem (DECAISNE 1857, BOUTINEAU 1883, DUCHARTRE 1891, TUKEY et YOUNG 1942, etc.). The longitudinal section of the receptacle of the flower of *Sorbus* has a funnel- or bell-like shape, but the form of the receptacle changes very rapidly during the flowering.

The calyx is formed by segments lining the rim of the receptacle. The segments are triangular or triangularly lanceolate, persistent, rarely deciduous. The petals are circular or broadly elliptic, in isolated cases of ovoid oblong shape, white or yellowish, rarely pink. The stamens are arranged in three rings (A 10 + 5 + 5); the outer ring of stamens is doubled, so that there are two stamens in front of each sepal. The anthers have a longitudinal dehiscence. The various species differ considerably with regard to the structure of the pistil. The number of carpels is constant only in *S. domestica* (5) and in *S. torminalis* (2); in other species it varies, and that even in one and the same individual. This fluctuation is a quite unusual phenomenon in the oligomerous gynoeceum and must therefore be paid special attention. The degree of the mutual fusion of the carpels and their relation to the receptacle is an excellent systematic mark. The ovary is of the perfectly inferior type in *S. torminalis*, in the other species it is semiinferior, i. e. free in the upper half or even third, and not fused with the receptacle. This free top of the ovary is specially characteristic for the groups *Aria* and *Aucuparia*. The pistil entirely submerged in the receptacle and grown over by its upper edge, as is typical for the genus *Pirus*, is not developed in *Sorbus*. The fact that in the genus *Sorbus* no inferior ovary is developed has escaped attention up to the present time. There are always as many styles as there are carpels. They are always terminal, mostly loose, and in singular cases fused in their lower parts. In each capsule corresponding to one carpel there are two anatropic, elevated ovules, of which usually only one develops into seed. The ovules have two integuments and an obturator. The placentation is axile.

The fruit is a pome, a pulpous fruit with its peculiar morphology. Its pericarp consists of the membraneous exocarp, the pulpous mesocarp, and of the xerocarpic endocarp. The exocarp and the mesocarp originate from the metamorphosis of the receptacle, and the endocarp corresponds to the carpels. The consistency of the endocarp varies considerably; it is membraneous, leathery, cartilaginous, in few cases almost stony. The external morphology of the pome and its anatomical structure supply a number of valuable distinctive marks (see lower down).

It is possible to deduce the pome morphogenetically from a drupe (POTONIÉ

1880, Kosec 1941). The sclereids in the mesocarp of some species of *Pirus* and *Sorbus* are, according to these authors, remains of the outer part of the sclerocarpic endocarp (stone). It must be emphasized that it is impossible to take into consideration a one-seed drupe (the present genus *Prunus*), but a 5-seed drupe, which was doubtlessly a characteristic feature of the evolutional ancestors of the *Prunoideae*.

Morphology. In the morphological analysis I examined the following marks: the size of the flowers, the indumentum of the receptacle, the morphology of the sepals (position, size, shape, rim, indumentum, glandularity), the morphology of the petals (position, size, shape, rim, indumentum, colour), and the structure of the gynoeceum (number of carpels, degree of their mutual fusion, their relation to the receptacle, the shape of the top of the ovary, the indumentum of the styles, and the shape of the stigmas).

The sepals are always triangular, either in the shape of an equilateral (*S. intermedia*) or of an isosceles (*S. graeca*) triangle, mostly entire, rarely finely toothed (*S. aucuparia*), and sometime glandular (*S. aucuparia, S. torminalis*). The sepals are either tomentose (*S. graeca*) or hairy (*S. sudetica*) on both sides, or tomentose only on the adaxial side (*S. intermedia*) or only on the abaxial side (*S. torminalis*). The indumentum of the sepals is a comparatively constant mark within the limits of the species. During the florescence the sepals are mostly upright, i.e. they support the petals (e.g. in *S. torminalis* and in *S. aucuparia*). In *S. aria* and *S. graeca* the sepals are always spreading, not pressing close to the petals, in full florescence whorled down and recurved. Only in the group *Chamaemespilus* they are completely upright. A very important mark is the length of the sepals in relation to the receptacle, which makes it possible to distinguish *S. graeca* from *S. aria*. In the species found in this country the sepals are mostly persistent, only in *S. torminalis* they fall off immediately after the florescence.

The colour of the petals is a constant mark of the various species; only in *S. aria* the colour fluctuates between white and yellowish. Of the Czechoslovak species only the group *Chamaemespilus* has from pink to red flowers; in the other species they are white. The shape of the petals differs considerably. They are mostly strongly concave, only in *S. chamemespilus* they are more flat. The petals are mostly circular or broadly ovoid. An exception is again the group *Chamaemespilus*, for which oblong petals, wedge-shaped and longitudinally narrowing towards the base, are characteristic. The rim of the petals is entire or up to finely crenated. At the base the petals sometime have a short claw (*S. aria, S. aucuparia, S. domestica*). On the adaxial side the petals are usually hairy in varying degrees. The density of the indumentum is not constant, often only a few easily falling off hairs develop, or the indumentum is entirely lacking. Its fluctuation is especially pronounced in *S. torminalis*. During the florescence the petals are mostly spreading (*S. aucuparia, S. torminalis*) and then revert downwards (*S. aria, S. graeca*), so that insects have free access into the flower. The petals have a peculiar position in the group *Chamaemespilus*, in which they are always characteristically upright (just the same as the sepals, so that they form a narrow tube in which the anthers are placed comparatively deep). This mark is very characteristic for the mentioned group and is not repeated in the whole genus.

The stamens are loose with their filaments at the base flatly broadening. The length of the stamens in relation to the petals varies; of striking short-

ness are the stamens of *S. chamaemespilus*. Otherwise the stamens are of equal length or insignificantly shorter, in *S. torminalis* they are sometimes longer than the petals. In the species growing in Czechoslovakia the anthers are always yellow, only the Caucasian species *S. subfusca* and *S. hajastana* have red anthers.

An exceptionally important mark is the morphology of the gynoeceum. As has already been said, some species have a striking instability with regard to the number of carpels. The monomerous gynoeceum is not known is *Sorbus*, so that the number of carpels of this genus may be defined as ranging from 2—5. In the genus *Sorbus* the original pentamerous gynoeceum is, on the whole, rare and is rather an exception than the rule. Of the European species it has survived only in *S. domestica*. Instability with regard to the number of carpels is shown only by the groups *Aria* and *Aucuparia*; in *S. chamaemespilus* this fluctuation is insignificant, in *S. torminalis* the number of carpels is always constant. Of the group *Aucuparia* only several Central- and East Asiatic species have a pentamerous gynoeceum. In the group *Aria* the pentamerous gynoeceum is not developed at all. (In *S. cuspidata* from the Himalayas, whose taxonomic classification has not been decided, the number of carpels varies between 3—5). The pistil has here always two or three carpels, with a marked predominance of dimerous types. In *S. aria* there are only from one to three flowers with a trimerous gynoeceum in one inflorescence. In some species of the *Aria* group, however, the number of carpels seems to be constant; of those growing in Czechoslovakia it is probably *S. graeca*, in which I have never found a trimerous gynoeceum.

An excellent distinctive mark is the degree of the mutual fusion of the carpels (fig. 2). In the group *Aucuparia* the gynoeceum is almost apocarpic, the carpels fuse mutually only in their basal parts. In the

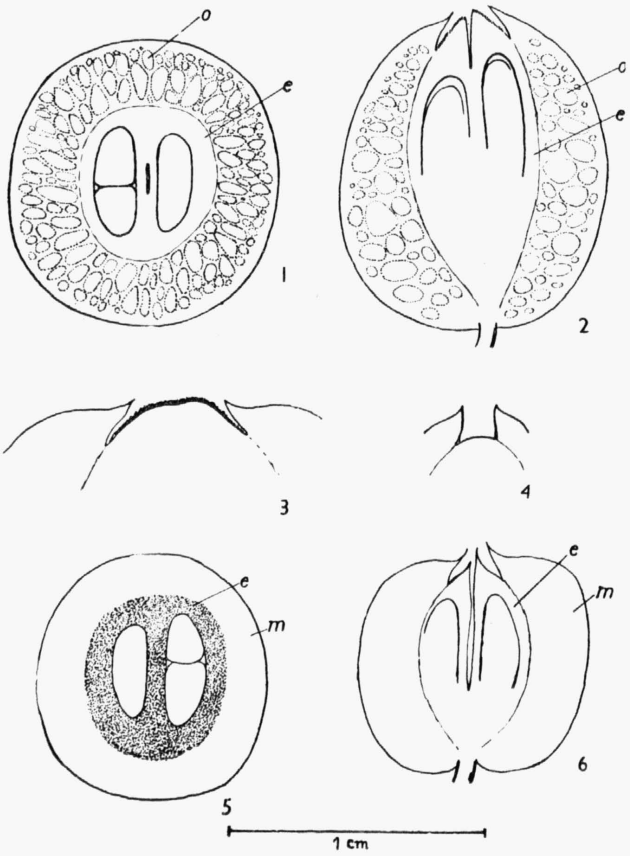

Fig. 1 – Morphology of the pome (m — mesocarp, o — islets of large cells, e — endocarp). 1 — *S. graeca* (a cross-section), 2 — *S. aria* (a longitudinal section), 3 — *S. domestica* — top of the pome (a longitudinal section), 4 — *S. torminalis* — top of the pome (a longitudinal section), 5 — *S. torminalis* (a cross section), 6 — *S. aucuparia* (a longitudinal section).

groups *Cormus* and *Torminaria* the ovaries fuse along their whole length (in *S. torminalis* the fusion extends even to the styles), so that the gynoeceum is syncarpic. *S. torminalis* differs from all other species by the fusion of the styles. The fusing of the carpels usually characterizes the various groups of species very well, so that it can be used succesfully as a diagnostic mark. It is an always constant distinctive mark, fluctuations occur only in several hybrid

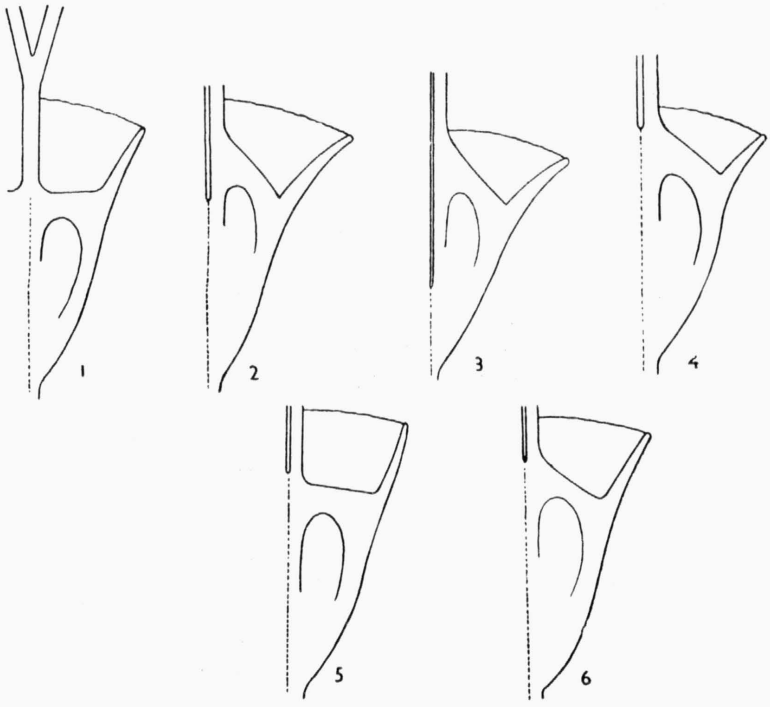

Fig. 2 — Relation of the pistil to the receptacle. 1 — *S. torminalis*, 2 — *S. aria*, 3 — *S. aucuparia*, 4 — *S. domestica*, 5 — *S. chamaemespilus*, 6 — *S. sudetica*

forms. A distinctive mark of no less importance is the relation of the pistil to the receptacle. As has already been said, in the Czechoslovak species, with the exception of *S. torminalis*, no inferior ovary is developed. A difference of such significance as that between an inferior and a semiinferior ovary cannot but leave this mark in the taxonomy of the genus. I therefore use this mark, together with the others, as one of the most important features for the characteristic of the various groups. Also this mark is, within the limits of the species, absolutely constant. Analogous with the genus *Sorbus* the semiinferior ovary is developed e. g. in some species of *Amelanchier*, *Photinia*, and *Stranvaesia* (DECAISNE 1874), so that it is quite incorrect to consider the inferior ovary as a characteristic mark of the *Maloideae*.

In the fruits of the Czechoslovak species of *Sorbus* the following marks have been analyzed: shape, size, colour, indumentum of the pomes, size and density of lenticells, consistency and position of sepals, structure of meso-

carp (homogeneity and heterogeneity, the distribution of the islets, the occurence of sclereids), and the consistency of the endocarp.

The shape of the fruit is subject to considerable variation even in one and the same individual. It is certainly most constant in *S. aucuparia*, where its changeability corresponds quite closely to the difference in the indumentum of the leaves; var. *aucuparia* has almost always globular fruits, var. *glabrata*, on the other hand, is characterized by oblong ovoid fruits. Pear-shaped fruits are on the whole rare; they are sometimes found in *S. domestica* and more rarely in *S. aria*. The ripe pome is mostly glabrous (at the most only hairy at the top round the sepals), only in the case of *S. aria* it is frequently hairy or even tomentose. In this species the indumentum of the fruits varies very strongly; there are differences even in one and the same individual. A very characteristic mark of the fruit are the lenticells. They are lacking only in *S. aucuparia* and *S. mougeotii*; otherwise the fruits are always dotted. The density of the lenticells varies; the fruits of *S. torminalis* have the greatest number of lenticells, they are very sparse and indistinct in *S. intermedia*. The sepals are mostly withered during ripeness (in *S. domestica* fragile), only in *S. aucuparia* they are pulpous. If the sepals are pulpous, then they are inclined inwards towards the longitudinal axis of the fruit; otherwise they are twisted or characteristically upright.

Also the pulp of the pome supplies a number of valuable taxonomic marks; their significance was first pointed out by DECAISNE (1874). The exocarp of the pome consists of several layers, of which the outermost consists of polygonal cells. Under this layer follow 2—3 layers of cells, the section of which shows a square or rectangular shape. With the development of the fruit the membranes of the cells thicken considerably. — The various groups differ considerably with regard to the anatomical structure of the mesocarp (see fig. 3). The basic parenchymatic tissue is of two types: it is either homogeneous, i.e. it is formed of cells of approximately the same size (the subgenera *Torminaria*, *Sorbus*, *Aucuparia*), or it is heterogeneous, i.e. there are groups of large cells ("islets"), which differ remarkably with regard to their size from others. This type of mesocarp is characteristic for the groups *Aria* and *Chamaemespilus*. The heterogeneity of the pulp can easily be observed also macroscopically. The cells of the basic parenchymatic tissue contain starch, and the cells of the islets tannic substances and chromoplasts.

The existence of the islets was pointed out first by DECAISNE (l. c.). According to his findings they occur, of the European species of the *Maloideae*, exclusively in the subgenus *Aria* (incl. *Chamaemespilus*) and otherwise only in the Asiatic genus *Micromeles*. DECAISNE also introduced the terms "homogeneous" and "heterogeneous" (chair homogène, chair hétérogène). If the mesocarp contains groups of large cells, sclereids are never found in it. Only hybridogeneous forms constitute an exception from this rule. Very numerous are sclereids in the mesocarp of *S. domestica*, less numerous in *S. aucuparia*. In *S. torminalis* sclereids are found only rarely in the pulp.

For the characterization of the various groups or species also the endocarp may be used. An isolated position, in this regard, among *Sorbi* is taken up by *S. torminalis*. The other species have a much thinner endocarp: membraneous (*S. domestica*), parchmentlike (*S. aucuparia*) up to leathery (*S. aria*).

The anatomic structure of the pome is a mark of high taxonomic value; I therefore make use of it in the characterization of the species and in the

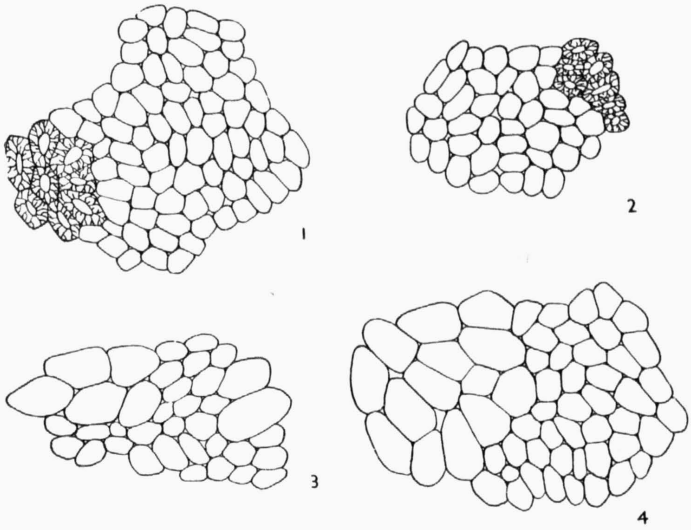

Fig. 3 — Anatomy of the pulp. 1 — *S. torminalis*, 2 — *S. aucuparia*, 3 — *S. mougeotii* subsp. *austriaca*, 4 — *S. graeca*

taxonomic classification of the genus. The morphology of the fruit also plays an important part in the identification of hybrid forms; in its structure the influence of both parents can always be traced. The Czechoslovak species differ in their fruits so distinctly as to make a reliable determination possible. In the case of the fruits of some hybrids this certainty is less definitive; however, the intermediate character is always very distinct. It is also possible to determine the parents with a considerable degree of probability.

In the descriptions of the fruits, if not explicitly stated otherwise, a fully ripened pome is always described.

Key for the Determination of the Czechoslovak Species of *Sorbus* According to their Fruits

1. a. Poma magna, 20—40 mm in diametro: 7. *S. domestica*
   b. Poma minora, maxime 18 mm in diametro 2
2. a. Sepala decidua: 1. *S. torminalis*
   b. Sepala persistentia 3
3. a. Poma sine lenticellis, semper glabra 4
   b. Poma lenticellis punctata, tomentosa vel glabra 5
4. a. Ovaria fere ad apicem concrescentia; mesocarpium heterogenum: 4. *S mougeotii*
   b. Ovaria basi tantum concrescentia, ceterum libera; mesocarpium homogenum: 6. *S. aucuparia*
5. a. Poma aurantiaca vel aurantiaco fusca, sparse et obscure punctata; mesocarpium homogenum: 5. *S. intermedia*
   b. Poma colorum aliorum, distincte punctata; mesocarpium heterogenum 6
6. a. Ovaria in triente superiore libera 7
   b. Ovaria fere ad apicem concrescentia 8
7. a. Poma lenticellis parvis dense punctata, maturitate ± tomentosa (rarius glabra); endocarpium coriaceum: 2. *S. aria*
   b. Poma lenticellis magnis sparse punctata, maturitate glabra; endocarpium cartillagineum: 3. *S. graeca*
8. a. Poma clare rubra: 9. *S. sudetica*
   b. Poma rubro fusca: 8. *S. chamaemespilus*

1. *Sorbus torminalis* (L.) Cr.

Flowers 12—15 mm in diametre. Surface of receptacle sparsely tomentose. Sepals triangular, 2—2,5 mm long, pointed, entire, along the edge dispersedly glandular, on the abaxial side hairy or glabrescent, at the point glabrous, on the adaxial side glabrous, during florescence upright. Petals white, from circular to broadly ovoid, ± 4 mm long, entire or in the upper half finely crenated, without claws, at the base on the adaxial side hairy or glabrous. Always two carpels, ovaries fused completely mutually and also with the receptacle, so that the top of the ovary does not protrude (inferior ovary fig. *2* : 1). Styles fused to their middle, at the base glabrous. Stigmas flat, buttonlike, distinctly bilobate.

Pome globular, circulary ovoid, ovoid or obovate (often asymetric), 12—18 mm long, 8—15 mm in diameter, glabrous or only hairy on top, not glossy, at first brownish geren, later brown, very densely dotted with lenticells. Sepals during ripeness always deciduous. Mesocarp homogeneous, formed of cells of about equal size. There are no islets of large cells. In the mesocarp sclereids occur only rarely; they mostly lack entirely. Endocarp thick, very stiff and firm (fig. *1* : 5, *3* : 1).

2. *Sorbus aria* (L.) Cr.

Flowers up to 18 mm in diametre. Surface of receptacle very densely tomentose. Sepals from triangular to triangularly lanceolate, 4—5 mm long, shorter or at the utmost length of receptacle, pointed, on the abaxial side from hairy to tomentose, on adaxial side ± glabrous. During florescence turned outwards and inclined downwards. Petals white or slightly yellowish, from broadly elliptic up to circular, entire, up to 8 mm long and 6 mm wide, on adaxial side at the claw tomentose. Mostly 2 carpels, rarely 3. Ovaries mutually fused up to two thirds, in the same relation to the wall of receptacle. Ovary top loose (semiinferior ovary, fig. *2* : 2). Styles loose, at base very densely tomentose. Stigmas tiny, flat.

Pomes globular, ovoid, from ovoid to pear-shaped, up to 15 mm in diameter, red (in various shades: orange-red, brick-red, bright-red, scarlet, dark red), rarely brownish green, glabrous, from hairy to sparsely tomentose (tomentum rubbing off), always dotted. Sepals during ripeness withered, twisted. Mesocarp heterogenous. Islets of large cells comparatively large, ± circular, from elliptic to oblong, also macroscopically discernible. Sclereids always lacking in the mesocarp. Endocarp leathery (fig. *1* : 2).

3. *Sorbus graeca* (Spach) Hedl.

Flowers up to 18 mm in diametre. Receptacle outside sparsely tomentose. Sepals from triangular to triangularly lanceolate, sometimes pointed, ± 5 mm long (visibly longer than receptacle), on both sides tomentose, on abaxial side sometimes hairy, only at point glabrous. In full florescence sepals turned outwards and downwards. Petals white, from circular ovoid to ± elliptic, up to 8 mm long, visibly clawed, at base on adaxial side with long hairs. 2 carpels. The ovaries fuse up to three quarters of their length (i.e. somewhat higher than in *S. aria*). Loose top of ovary and base of styles densely tomentose. Styles loose.

Pomes globular, rarely (f. *cuneata* Diap.) oblong, up to 12 mm in diameter, from orange red to red, smooth, glabrous, only around sepals hairy, very sparsely dotted. Sepals not deciduous, during ripeness dry, upright (i.e. position parallel with longitudinal axis of fruit). Mesocarp heterogeneous. Sclereids lacking. Endocarp cartilaginous, visibly thicker than in *S. aria* (fig. *1* : 1, *3* : 4).

4. *Sorbus mougeotii* S. W. Gr. subsp. *austriaca* (Beck) Hedl.

Flowers 12—15 mm in diametre. Receptacle tomentose. Sepals triangular (± in the shape of an equilateral triangle), 2—3 mm long, same length as receptacle or insignificantly longer, on abaxial side sparsely tomentose. During florescence they are upright, so that they support the petals. Petals white, broadly ovoid, 6—7 mm long, without claws, at base on adaxial side with several hairs. 2—3 carpels, rarely 4. Ovaries fused ± up to the top, with receptacle fused up to three quarters of length. The top of the ovary has the shape of a low, blunt cone.

Note. The mutual fusion of the carpels is exceptionally not a constant mark of *S. mougeotii*, which fact is connected with the hybridogeneous origin of this species (cf. Hedlund 1901, Liljefors 1953, 1955, Kovanda 1959). In most cases the carpels are fused almost to the base

of the styles, in some cases, however, we have found a fusion up to two thirds of the length only. The statement that *S. mougeotii* subsp. *austriaca* has red petals (KLIKA 1937) is wrong.

Pomes from globular to globularly ovoid, 9—13 mm in diametre, dark red, always glabrous (only hairy at top), not dotted. Sepals inclined inwards, at base slightly pulpous (similar to *S. aucuparia*). Mesocarp heterogeneous. Islets of large cells developed but are very small and their cells are frequently strongly extended radially, i. e. in the direction from the exocarp to the endocarp. Besides the islets there are also single large cells scattered in the basic tissue, and in isolated cases also sclereids (fig. *3* : 3). The anatomic structure of the mesocarp is clearly intermediary between the species *S. aria* and *S. aucuparia*. The endocarp is insignificantly thicker than in *S. aria*, and cartilaginous.

5. *Sorbus intermedia* (EHRH.) PERS.

Flowers 12—13 mm in diametre. Receptacle on the outside tomentose. Sepals in the shape of an equilateral triangle, short (only 2,5—3 mm long), blunt, only on adaxial side tomentose, on abaxial side glabrous, during florescence not inclined, but upright. Petals white, circular, ± 5 mm long, short clawed, on adaxial side of claws very finely downy. 2—3 carpels, ovaries fuse almost to base of styles and up to two thirds with receptacle. Protruding top of ovary very densely tomentose.

Pomes broadly ellipsoidal, up to 16 mm long and 12 mm in diametre, from yellowish brown to orange red, glabrous, glossy, with only a few tiny indistinctive lenticells. Sepals during ripeness pulpous at base, inclined towards centre of the fruit. Mesocarp homogeneous, large cells lacking entirely. The endocarp does not differ from the endocarp of *S. aria* with regard to thickness.

6. *Sorbus aucuparia* L.

Flowers 8—12 mm in diametre. Receptacle tomentose, after florescence turning glabrous. Sepals triangular, 1,5—1,8 mm long, finely and irregularly toothed, from tomentose to glabrescent, at the edge glandular. During florescence upright, afterwards the sepals incline inwards towards the longitudinal axis of the fruit. Petals white, circular or broadly ovoid, 3—4 mm long, with short claws, on the adaxial side at the base glabrous or with a few deciduous hairs. Most often 3 carpels, more rarely 4, in singular cases only 2, mutually fused only at their basal part. The ovaries fuse with the receptacle only up to two thirds. The top of the ovary protrudes visibly (fig. *2* : 3). Styles loose, at base hairy, with tiny stigmas.

Pomes globular (fig. *1* : 6), more rarely (var. *glabrata* WIMM. et GRAB.) oblongly ovoid, 8—12 mm in diametre, at base sometimes hollowed out, always glabrous, not dotted, glossy, smooth, red (in various shades: orange, brick-red, coral red, scarlet), exceptionally yellow (f. *fifeana* hort.). The sepals become during ripeness pulpous, bent towards the longitudinal axis of the fruit. Mesocarp homogeneous, consisting of parenchymatic cells, which are ± globular in the outer part of the mesocarp and become elongated towards the endocarp. Among them there are scattered sclereids, either singly or in groups (fig. *3* : 2). The endocarp is comparatively thin, parchmentlike. The cross-section of the fruits shows a central starshaped cavity, i. e. the walls of the ovary cells are split.

7. *Sorbus domestica* L.

Flowers larger than in *S. aucuparia*, up to 15—18 mm in diametre. Receptacle tomentose. Sepals broadly triangular, 2—3 mm long, pointed, tomentose. Petals white or slightly pinkish, almost circular, 5—7 mm long, short clawed, on adaxial side at base hairy, in full florescence spreading. There are always 5 carpels. Their number is absolutely constant and is not subject to any fluctuation. Ovaries fuse along their total length (fig. *2* : 4), but leave a free cavity in the longitudinal axis of the fruit. The walls of the ovary cells are not split. The styles are loose (only connected at the base, but not fused), at the base densely tomentose.

Pomes much larger than in *S. aucuparia* (fig. *1* : 3), apple-shaped [f. *pomifera* (HAYNE) REHDER] or pear-shaped [f. *pirifera* (HAYNE) REHDER], 1,5—4 cm in diametre, sometimes with 5 shallow wrinkles, yellow or yellowish red, glabrous, dotted with rust coloured lenticells. Sepals during ripeness withered, fragile. The loose top of the ovary is during ripeness bluntly conic. Mesocarp homogeneous, with very numerous sclereids. The endocarp is very thin (the thinnest of all Czechoslovak species), membraneous.

8. *Sorbus chamaemespilus* (L.) CR.

Receptacle at outside tomentose, in the upper half or up to one third glabrous. Sepals broadly triangular, 1,5—2 mm long, ± as long as the receptacle (shorter by a half than the petals),

on the abaxial side from glabrescent to glabrous, on adaxial side almost on their whole surface from sparsely hairy to tomentose. During florescence the sepals are characteristically upright. Petals purple red, ± oblongly ovoid, 4—6 mm long, from finely crenated to almost entire, towards base long and wedge-like narrowing, on inner side almost the whole surface very sporadically hairy. The petals are upright, forming a narrow tube. They fall off very easily. There are two carpels, rarely 3. The ovaries fuse mutually up to the top, and are almost totally submerged in the receptacle. The top of the ovary is indistinctive (i. e. the ovary is almost inferior, fig. *2* : 5). The relation of the gynoeceum to the receptacle is similar to that of *S. torminalis*. The styles are loose, straight, bending outwards in the upper half. — According to SCHULZ (1890) the flowers of *S. chamaemespilus* are, unlike the other species, almost homogamous. The stigmas achieve their full development already in the time of the dehiscence of the anthers. As the stigmas lie in the direction of the incidence of the pollen grains, selfpollination occurs frequently.

Pomes from globular to globularly ovoid, 10—12 mm in diametre, with tomentum rubbing off, brownish red, sparsely dotted with lenticells. Sepals not deciduous, during ripeness upright and pressed together. Mesocarp heterogeneous, the islets of large cells are comparatively small, very numerous. The endocarp is insignificantly thicker than in *S. aria*.

9. *Sorbus sudetica* (TAUSCH) HEDL.

Receptacle on outside densely tomentose. Sepals of same length as receptacle, 2—2,5 mm long, pointed, on both sides tomentose, upright. Petals light pink, broadly ovoid, towards base clawlike narrowing, 4—5 mm long, 2—3 mm wide, on adaxial surface very sparse, long hairy, upright, 2 carpels, more rarely 3, fused almost up to styles. Top of ovary bluntly conic, visibly protruding (semiinferior ovary, fig. *2* : 6), tomentose.

Pomes from globular to ellipsoidal, at base hollowed out, 11—13 mm in diametre, bright red, glabrous or only at top hairy, very sparsely dotted. Sepals upright. Mesocarp heterogeneous. Islets of large cells very numerous, comparatively large, closely pressed together. Endocarp relatively thin, not thicker than in *S. aria*.

According to the morphological marks the genus *Sorbus* consists of five natural, altogether very well characterized groups (*Aria*, *Aucuparia*, *Torminaria*, *Chamaemespilus* and *Sorbus* s. str.), which may be considered also as independent genera, each of which is represented by a single Linnaean species (*S. aria*, *S. aucuparia*, *S. torminalis*, *S. chamaemespilus*, *S. domestica*). Of these the first two (*Aria* and *Aucuparia*) are polymorphous, the groups *Sorbus* and *Torminaria* are monotypical. The various groups are sharply defined, and with the exception of hybrids, there are no transitional forms.

A special isolated position among the species of *Sorbus* and also on the whole in the subfamily *Maloideae* is taken up by *S. torminalis*, which, with its inferior ovary, the fused styles, the tough endocarp, the deciduous sepals, and with other marks differs from all others. With the consistency of its endocarp it ranges with hawthorns (*Crataegus*), and there is a certain analogy with regard to the shape of their leaves. Nevertheless, it is not possible to classify it as belonging to the genus *Crataegus*, as there is an important difference with regard to the structure of the flower and of the fruit (the fusion of the styles, deciduous sepals etc.) In the case of this species the reasons for its separation as an independent genus are most justified. *S. torminalis* cannot be linked with any other known species of *Sorbus*. In Europe no related species are known at all; the affinity of the Himalayan group of *Cormoaria* is very uncertain. (There is only a similarity in the fusing of the styles, which, of course, is not a specific mark only for *S. torminalis*). At present *S. torminalis* is spread over almost the whole of Europe (in the north up to Middle England and Bornholm), in North Africa (Algiers); in the East it extends to the Caucasus and Asia Minor.

The *Aria* group is strongly polymorphous and is divided into a series of mutually close related and uncommonly variable species, the evaluation of

which is very difficult. They differ from one another mainly by the shape and by the indumentum of the leaves, less by the shape and indumentum fo the sepals and by the marks of the fruit. There are about 35 species (of which 2, *S. aria* and *S. graeca* are represented also in Czechoslovakia) spread over Europe (in the North up to South England and southern Scandinavia), in the Middle East and in Central Asia (in the east up to the Himalayas). The group *Aria* as a whole is obviously a more original type (the central point of its geographical distribution is in Central Asia, which is generally considered the developmental centre of the *Maloideae*), even if some marks are obviously deduced (reduction in the gynoeceum, fusing of carpels up to two thirds). The original types must have been wood plants with simple leaves and with a pentamerous apocarpic gynoeceum.

With regard to the heterogeneous mesocarp, the group *Chamaemespilus* closely approaches the species of the *Aria* type. In its other marks it differs, however, considerably from all other species of *Sorbus*, especially with regard to the colour and the position of the petals, and to the morphology of the pistil. Roemer (1847) for the first time separated this group as an independent genus. Unlike in the case of the above mentioned, it is necessary to look for its origin in Europe. Four species have been described, whose geographical distribution is limited to the mountain ranges of Central- Eastern- and Southern Europe (the Alps, the Giant Mountains, the Carpathians, the Balkan, the Pyrenees, the Vosges, and the Apennines). Of all of them probably only one (*S. chamaemespilus*) is a real species; the other three (*S. sudetica*, *S. pseudaria*, *S. ambigua*) are in all likelihood hybridogeneous complexes, the results of crossing with *S. aria*.

The species with pinnate leaves form a very uniform group, from which only *S. domestica* differs by the structure of its flower. With regard to the pinnate leaves and the very frequent reduction in the gynoeceum (the pentamerous gynoeceum is here comparatively rare) *S. aucuparia* may be considered most developed; on the other hand, of course, the almost apocarpic gynoeceum in *S. aucuparia* is an original mark. Here the development has not progressed with equal speed in all marks. The fluctuation in the number of carpels shows that the development in the direction of the reduction in the gynoeceum is still continuing; it has, however, not got further than the dimerous stage. The identical degree of the fusion of the gynoeceum with the receptacle as we can observe in the group *Aria*, is obviously an evolutional parallelism. — Today the subgenus *Aucuparia* is the most widely spread of the whole genus *Sorbus* and is found in almost the whole of Europe (including Iceland), almost in the whole of Asia, and as the only group of *Sorbus* also in Greenland and in North America. There are known about 30 species, the distinguishing marks of which are the shape and the indumentum of the buds, the indumentum of the leaves, the number of the leaflet pairs, the size and the edge of the leaflets, the indumentum of the inflorescence, the number of styles, the colour of the fruits etc.

S. domestica forms an independent group with a rather isolated position. The distinctive marks of the gynoeceum have here the opposite relation to those in *S. aucuparia*: the gynoeceum is pentamerous and syncarpic (with loose styles). The possibility cannot be excluded that *S. domestica* represents an independent evolutional line; the remarkable conformity with regard to the shape of the leaves of *S. domestica* with the group *Aucuparia* may be the

result of a convergent evolution. With regard to the structure of the flowers and of the fruits *S. domestica* occupies an isolated position, so that a close relationship with *S. aucuparia* and its closely related species seems to be impossible. *S. domestica* distinguishes itself through its remarkable conservative evolution: there is not even a sign of a reduction of the number of carpels, to which the evolution of the *Maloideae*, as a whole, is obviously moving. Its considerable phylogenetic age is also indicated by the insignificant changeability, which is in sharp contrast with the polymorphy of the other species, and its geographical distribution: it extends from the Caucasus via the Crimea and Asia Minor to the Mediterannean.

The above mentioned groups are generally recognized, and that frequently also as independent genera. This opinion is supported not only by the structure of the reproductive organs, but to a considerable extent also by the other morphological marks, and that besides the inflorescence also by the vernation and the shape of the leaves.

In the genus *Sorbus* three types of vernation are represented. In species with pinnate leaves the vernation is conduplicate, in the groups *Aria* and *Torminaria* it is plicate, in the group *Chamaemespilus* it is convolute, and regarding the youngest leaves it is involute (FOLGNER 1897). The shape of the leaves of *Sorbus* varies considerably, so that the various species (groups of species) differ remarkably in their habit. The leaves are either simple or pinnate. The pinnate leaves, which are characteristic for the groups *Aucuparia* and *Sorbus* s. str., are otherwise unusually rare in the *Maloideae*; we come across them only in the genus *Osteomeles* from the Hawaiian Islands and China. The simple leaves differ considerably in their veinage. In the subgenus *Aria* the side veins are distinctly kraspedromous, in the subgenus *Chamaemespilus*, however, they are kaptodromous.

From what has been said it can be seen that the genus *Sorbus* — as it is commonly defined at present, i. e. according to the conception legalized by FRITSCH (1898) — is morphologically exceedingly heterogeneous. Besides the almost apocarpic gynoeceum there is also a perfectly syncarpic gynoeceum, besides the pentamerous also a dimerous gynoeceum, besides the semiinferior ovary there is an inferior ovary etc. The question arises whether it is possible to consider a so little homogeneous group as a single genus. If a genus as a taxonomic unit and as an independent section of phylogenesis links species agreeing with each other with regard to the distinctive marks that are considered of primary significance for taxonomic evaluation, i. e. the distinctive marks of flowers and fruits, then it is obvious that, from this point of view, the dividing into smaller genera is justified and can very easily be logically substantiated.

The various genera of the *Maloideae* are defined in very different ways. Their number quoted by various authors ranges from 4 to 25. The least uniform is the definition of the genera *Pirus*, *Crataegus* and *Sorbus*. Especially the range of the genus *Sorbus* has changed very frequently; its present conception, defined substantially by REICHENBACH (1830), became established only at the end of the last century. In the Linnaean conception the genus *Sorbus* comprised only two species: *S. aucuparia* and *S. domestica*. LINNÉ ranked *S. aria* and *S. torminalis* as belonging to the genus *Crataegus*, and *S. chamaemespilus* as belonging to the genus *Mespilus*. These species were first classified as *Sorbus* by CRANTZ (1762), who classified *Malus* and *Cydonia*, together with *Amelan-*

chier, in the single genus *Sorbus*. On the basis of the morphology of the flowers MEDICUS (1793) divided *Sorbus* into three genera (*Sorbus*, *Hahnia*, and *Aucuparia*. DE CANDOLLE (1825) and later a number of other authors connected the genus *Sorbus* with the genera *Pirus* and *Malus*. SPACH (1834) and after him ROEMER (1847), OPIZ (1852), DECAISNE (1874), KOEHNE (1890), BECK (1892), DIPPEL (1893) and many others divided the genus *Sorbus* into several (3—5) smaller genera. This conception was worked out most perfectly by KOEHNE (l. c.), who worked out his system of the *Maloideae* exclusively on the basis of the morphology of the gynoeceum. FRITSCH (1898) rejected his system as one-sided and artificial and renewed the genus *Sorbus* within the definition given by REICHENBACH. He classified the groups which KOEHNE and his predecessors had ranked as independent genera as sections, and simultaneously emphasized the unsuitability of the linking of this genus with the genus *Pirus*. FRITSCH's system was accepted and his conception of the genus has been adopted by all taxonomic hand-books up to the present time.

The objection raised against the system of small genera is the comparatively frequent occurence of hybrids. It must be pointed out that the existence of hybrid transitions in itself is no obstacle to the dividing up. The genus *Sorbus* is a good example supporting the fact that the capacity for hybridization is not always equivalent to the degree of morphological relationship. The subfamily *Maloideae* shows an uncommonly strong inclination to intergeneric bastardation. Most of the known inter-generic hybrids belong to this subfamily, and that to the sphere of the genus *Sorbus*. There are also known hybrids between genera as distant as are *Sorbus* and *Amelanchier*, *Sorbus* and *Pirus*, *Sorbus* and *Crataegus*, *Sorbus* and *Cotoneaster*, *Sorbus* and *Mespilus*, *Pirus* and *Cydonia* etc. Here the ability of hybridization is not based upon a close or more distant morphological relationship, but is conditioned genetically. All *Maloideae* have the same basic chromosome number ($x = 17$), which occurs in various multiples. As regard the hybrids of *Sorbus*, it seems that they are mostly, if not absolutely, hereditary stabilized fixed hybrids. From the genetic point of view it would be desirable to contain all *Maloideae* in one single genus (cf. SAX 1931).

In spite of all this I do not consider the dividing up of the genus *Sorbus* as suitable, and that for the following reasons: The most important differences occur in the distinctive marks of the flowers and of the fruits. It is, however, impossible to base the system of the genus only on the marks of these organs. The morphology of the reproductive organs of the *Maloideae* is still passing through a very live evolution, as is shown by the polymorphy also inside the various genera, and by the frequent inconstancy of the flower diagram as regards the stamens and the gynoeceum. In evaluating these marks it is therefore necessary to proceed extremely cautiously and not to overrate their importance for the taxonomy of the genus. The groups *Aria*, *Aucuparia*, *Torminaria*, *Chamaemespilus*, and *Sorbus* s. str., even if, according to the marks of their flowers and fruits, they appear as independent evolutional lines, have, on the other hand, a rather similar structure of the wood (cf. BURGERSTEIN 1895, GREGUSS 1954 etc.). All this combined with the fact that in Asia there exist several species the taxonomic relationship of which is still debatable (*S. cuspidata*, *S. gracilis*, *S. lanata*, and *Micromeles japonica*), is the reason why I consider it suitable to retain the genus *Sorbus* with its present heterogeneous range. I therefore consider it a genus collectivum

and the various groups as subgenera, altogether very well characterized by their morphology and geographical distribution:

Subg. *Sorbus*

Syn.: *Sorbus* MED. Gesch. Bot. 87, 1793; *Cormus* SPACH Hist. nat. vég. 2 : 96, 1834; *Sorbus* sect. *Cormus* FRITSCH in Oesterr. bot. Zeitschr. 48 : 167, 1898; *Sorbus* 1. *Cormus* HEDLUND in Kongl. Sv. Vet. Akad. Handl. 35/1 : 12, 1901; *Sorbus* subg. *Eu-Sorbus* sect. *Cormus* KOMAROV in Fl. SSSR 9 : 374, 1939.

Arbores. Folia impari-pinnata. Stipulae deciduae. Sepala eglandulosa, persistentia. Petala alba (rarius rosea). Carpella 5, ad basin stylorum concrescentia. Ovarii apex prominens (ovarium semiinferum). Mesocarpium homogenum, sclereidae permultae. Endocarpium tenue, mebranaceum.

Typus (species unica): *S. domestica* L.

Subg. *Aucuparia* (MED.) comb. nova

Syn.: *Aucuparia* MED. Gesch. Bot. 86, 1793; *Sorbus* sect. *Aucuparia* FRITSCH in Oesterr. bot. Zeitschr. 48 : 167, 1898; *Sorbus* 2. *Aucuparia* HEDLUND in Kongl. Sv. Vet. Akad. Handl. 35/1 : 13, 1901; *Sorbus* subg. *Eu-Sorbus* sect. *Aucuparia* KOMAROV in Fl. SSSR 9 : 375, 1939.

Arbores vel frutices. Folia impari-pinnata. Stipulae deciduae vel persistentes. Sepala glandulosa, persistentia, fructificatione pulposa. Petala alba. Carpella 2—5. Ovaria basi tantum concrescentia. Ovarii apex prominens (ovarium semiinferum). Mesocarpium homogenum, cum sclereidis. Endocarpium tenue, pergamentaceum.

Typus: *S. aucuparia* L.

Subg. *Aria* (DC.) BECK emend.

Syn.: *Pirus* sect. III. *Aria* DC. Prodr. 2 : 635, 1825; *Sorbus* subg. *Aria* BECK in REICHENBACH Icon. fl. Germ. et Helv. 25 : 38, 1910 (p. p.); *Aria* sect. *Euaria* KOEHNE Gatt. Pom. 17, 1890; *Sorbus* sect. *Aria* FRITSCH in Oesterr. bot. Zeitschr. 48 : 167, 1898; *Sorbus* 3. *Aria* HEDLUND in Kongl. Sv. Vet. Akad. Handl. 35/1 : 13, 1901; *Sorbus* sect. *Hahnia* SCHNEIDER Ill. Handb. Laubh. 1 : 684, 1906 (p. p.); *Sorbus* subg. *Hahnia* sect. *Aria* ZINSERLING in Fl. SSSR 9 : 389, 1939.

Arbores vel frutices. Folia simplicia. Stipulae deciduae. Sepala eglandulosa, patentia, reclinata, rarissime decidua. Petala alba, rarissime rosea. Carpella 2 vel 3, rarius 4. Ovaria ad $^2/_3$—$^3/_4$ longitudinis concrescentia. Ovarii apex prominens (ovarium semiinferum). Mesocarpium heterogenum, sclereidae nullae. Endocarpium cartillagineum vel coriaceum.

Typus: *S. aria* (L.) Cr.

Subg. *Chamaemespilus* (DC.) comb. nova

Syn.: *Pirus* sect. VIII. *Chamaemespilus* DC. Prodr. 2 : 637, 1825; *Chamaemespilus* ROEMER Syn. monogr. 3 : 131, 1847; *Sorbus* sect. *Chamaemespilus* FRITSCH in Oesterr. bot. Zeitschr. 48 : 67, 1898; *Sorbus* sect. *Aria* subsect. *Chamaemespilus* ROUY et CAMUS Fl. Fr. 7 : 24, 1901; *Sorbus* 5. *Chamaemespilus* HEDLUND in Kongl. Sv. Vet. Akad. Handl. 35/1 : 13, 1901.

Frutices. Folia simplicia. Stipulae deciduae. Inflorescentia parva, contracta. Sepala erecta, persistentia. Petala rubra vel rosea, unguiculata, erecta. Carpella 2, rarissime 3, fere ad basin stylorum concrescentes. Mesocarpium heterogenum. Endocarpium cartillagineum.

Typus: *S. chamaemespilus* (L.) CR.

Subg. *Torminaria* (DC.) comb. nova

Syn.: *Pirus* sect. *Torminaria* DC. Prodr. 2 : 636, 1825; *Torminaria* Roemer Syn. monogr. 3 : 130, 1847; *Cormus β Torminaria* Koehne Gatt. Pom. 23, 1890; *Aria* sect. *Hahnia* Beck Fl. NO. 2 : 710, 1892; *Sorbus* sect. *Torminaria* Fritsch in Oesterr. bot. Zeitschr. 48 : 167, 1898; *Sorbus* 4. *Torminaria* Hedlund in Kongl. Sv. Vet. Akad. Handl. 35/1 : 13, 1901; *Sorbus* sect. *Hahnia* Schneider Ill. Handb. Laubh. 1 : 684, 1906 (p. p.), *Sorbus* subg. *Hahnia* sect. *Torminaria* Zinserling in Fl. SSSR 9 : 405, 1939.

Arbores vel frutices. Folia simplicia. Stipulae glandulosae, deciduae. Sepala glandulosa, semper decidua. Petala alba, patentia. Carpella 2, ad $^1/_2$ stylorum concrescentia. Ovarii apex non prominens (ovarium inferum). Mesocarpium homogenum. Endocarpium durum.

Typus (species unica): *S. torminalis* (L.) Cr.

Clavis analytica specierum:

1. a. Folia simplicia, pinnatilobata, pinnatifida vel basi pinnata 2
   b. Folia impari-pinnata 8
2. a. Folia ± integra, lobi foliorum maxime $^1/_5$—$^1/_6$ dimidiae laminarum attingentes 3
   b. Folia pinnatilobata vel pinnatifida 6
3. a. Folia ± simpliciter serrata; petala rubra vel rosea, erecta 4
   b. Folia biserrata vel lobata; petala alba vel flavescentia, patentia vel reclinata 5
4. a. Folia adulta subtus glabra (rarius floccosa); petala rubra ..... *S. chamaemespilus*
   b. Folia subtus griseotomentosa; petala rosea ..... *S. sudetica*
5. a. Folia 6—12 (—18) cm longa, ovata vel ± rotundata, obtusa vel acuta (non acuminata); sepala receptaculi breviora; pomum lenticellis parvis dense punctatum ..... *S. aria*
   b. Folia minora, 4—6 cm longa, late obovata vel ± rhombea (rarius obovato rotundata), obtusa vel (apud formas nostras) ± acuminata; sepala receptaculi longiora; pomum lenticellis magnis sparse punctatum ..... *S. graeca*
6. a. Folia adulta subtus ± glabra, lobi foliorum ± triangulares; sepala decidua; styli ad $^1/_2$ longitudinis concrescentes ..... *S. torminalis*
   b. Folia subtus semper tomentosa, lobi ± rotundati; sepala persistentia, fructificatione carnosa; styli semper liberi 7
7. a. Folia ovata vel elliptica, profunde pinnatilobata vel pinnatifida (lobi inferiores $^1/_2$ dimidiae laminarum attingentes); poma aurantiaco-fusca, lenticellis obscure punctata: *S. intermedia*
   b. Folia late ovata, ± pinnatilobata; poma rubra, sine lenticellis: *S. mougeotii* subsp. *austriaca*
8. a. Gemmae glabrae, viscosae; foliola basi symetrica; styli 5; pomum 20—40 mm in diametro: *S. domestica*
   b. Gemmae tomentosae; foliola basi asymetrica; styli 2—4; poma parva: *S. aucuparia*

The taxonomic classification of the Czechoslovak species, dealing with the conception of some debatable taxa (*S. graeca*, *S. mougeotii* etc.) will be the subject of a further study.

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