

On the Generic Concepts in the *Maloideae*

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Abstract — Some general problems of taxonomy (reality of genera, generic criteria) are demonstrated on an example of the *Maloideae*. An account is given of the results of different taxonomic approaches, the significance of various criteria is discussed and some conclusions, concerning the practice of the delimitation of genera, are drawn.

Introduction

The nature of taxonomic categories has been the subject of animated discussions during the last two centuries. These discussions have concerned particularly the problem of the species and of the intraspecific categories. In this field a remarkable amount of material has been gathered and on some points considerable agreement has been reached. On the other hand, problems referring to the supraspecific categories have been dealt with much less frequently. This is especially the case with the generic concepts, which is rather surprising, if we consider the practical significance of this category and its general application in all manuals, monographs and floras after LINNAEUS. While in the species problem a solid basis for a generally acceptable solution does exist, the generic concepts seem to depend on individual opinions of taxonomists to a much higher degree, though some valuable general suggestions were made recently by ANDERSON (1937), STEBBINS (1950), TUTIN (1956), WALTERS (1962), and LÖVE (1963).

There are two complexes of problems that seem to be of particular importance:

1. Are the genera real or are they arbitrary features without any biological significance?
2. What are the criteria for the delimitation of genera?

As to the first question, it is to be noted that the results of various taxonomic methods are not yet sufficient to refute the idea that the plant kingdom divides naturally into taxa that differ greatly from each other by their origin, range, age, inner structure and degree of stability and that exist irrespective of whether they were discovered, recognized and described by a taxonomist or not. Some of them may agree with the generic or species concepts of the taxonomic classification but the others may be inconsistent. In this sense the genus may be regarded a natural unit. On the other hand, taxa delimited by the aid of a set of criteria, i.e. taxa listed in taxonomic manuals, represent to a certain extent an abstraction from that reality; they reflect it more or less, but essentially they are products of our minds. They may coincide with the real aggregates of individuals in nature and some taxa surely do, but this is rather an exception than a rule. The confusion of these two concepts, viz. taxon as an abstraction from reality and

taxon as an objectively existing entity, may be considered the main source of the doubts about the reality of taxa. The reality of a natural population is perhaps beyond any doubt: such a population may be perceived as a whole, it may be studied in its natural environment and representative samples may be treated experimentally. The reality of species consisting of one single or of a few populations is undeniable; it is also obvious that what was described as a *Daphne arbuscula* ČELAK. or *Onosma tornensis* JÁV. corresponds exactly to real natural units. Species consisting of a number of populations are much more difficult to deal with, and even more difficult are the genera, viz. clusters of related species. Taxonomic genera are highly abstract concepts, but this does not mean that they do not have any reality in nature. Some of the genera, as for instance *Pinus*, *Salix*, and *Betula* are perhaps more real than a species (STEBBINS 1950), but in other groups the genus appears to be much more obscure and it would be very naive to identify traditional genera exactly with real clusters of species that exist in nature. This is obviously the case with the *Polyodiaceae* s. l., *Daucaceae*, *Poaceae* and *Orchidaceae*.

Passing herewith to the second question, it is to be emphasized that the traditional hierarchical classification based on Aristotelian logic (cf. CAIN 1958, ZAVADSKIJ 1961, WALTERS 1962) can hardly give a true picture of the real situation and reflect all the complexity of evolution, nor can it express all the intricacy of the inner structure and mutual relations of the real taxa that exist in nature. Diversity of plants is due to multidimensional processes which cannot be expressed by a linear system, using genera and species as the principle categories. However, as was pointed out by WALTERS (1962), "the rightness or wrongness of any piece of classification — or indeed of any statement at all — is to be judged by reference both to the 'objective facts of nature' and to the purpose for which the classification is made . . ." (p. 223). For a general system of plants the traditional manner of classification seems to be indispensable, at least for the time being, and genera and species are likely to remain the basic units for the near future. However, this does not imply that they should be delimited arbitrarily and only for the convenience of taxonomists.

In recent years it has been realized that delimitation of taxa should be based on the largest possible number of characters. This is now almost generally accepted on the species level, but not always on the generic one. The generic criteria are in principle the same as those used for delimitation of species. It is rather peculiar that the genus, though a qualitatively distinct category, is delimited and evaluated by means of the same measures. The main difference between generic and species characters is perhaps in "change of emphasis" (ANDERSON 1937) and in the fact that a genus cannot be studied experimentally (STEBBINS 1950). Another difference may be the importance of the time factor (genus as an evolutionary line). Genus as a general category differs from that of species particularly by a higher degree of abstraction.

The main basis for recognition not only of genera but of taxa of any category has been morphology, later on combined with geographical distribution and evolutionary aspects, the latter being more important on the generic level and above it. Ecology, on the other hand, is usually of lesser significance as a criterion of a genus. Cytological evidence is known to be of fundamental importance e.g. in the ferns (cf. PICI—SERMOLI 1958). LÖVE (1963) should be consulted in this respect. In some groups anatomical characteristics may also be used to advantage; this has been shown perhaps most instructively in the *Poaceae*, though the *Maloideae* are a good example too. Similarly, embryological and genetic differences may help the delimita-

tion of natural genera. In certain cases palynological characters may also be used. Finally, even biochemical and serological evidence (as far as available) should not be disregarded.

Of course none of these approaches is a universal criterion either of a genus or of any other category. And moreover, any character in itself, be it morphological, anatomical, cytological or of any other kind, is insufficient to distinguish between various categories. The genus, and the species likewise, may be characterized adequately only with the aid of a whole complex of criteria. Besides, various criteria and various characters have different significance in different cases. There is no criterion and no character which could be used always and everywhere with the same reliability, with the same justification, and also with the same result. Therefore, the significance and value of any character is to be considered in every case without bias.

The problem of genera in the *Maloideae*

The *Maloideae* are a good example with which to examine the ideas outlined above. They represent a clearly defined group which can be separated without difficulty from the other subfamilies of the *Rosaceae* (*Rosoideae*, *Spiraeoideae*, and *Prunoideae*). They were already recognized as a distinct unit before LINNAEUS; in BAUHIN'S *Pinax* (1623) they are treated as "Pomiferae arbores" together with *Prunus*, *Cornus*, *Lignum guajacum*, *Ebenus* and *Cerasus*. This early recognition and delimitation was doubtlessly caused by the conspicuousness and economical significance of numerous fruit trees belonging here (*Pirus*, *Malus*, *Cydonia*, *Mespilus*, etc.).

But whereas the delimitation of the boundaries of the subfamily as a whole is easy, opinions on its grouping into genera differ greatly. The conceptions of the extent and content of the genera are rather subjective. LINNAEUS (1753) distinguished only four genera, JUSSIEU (1789) six, PERSOON (1807) six, DE CANDOLLE (1825) eleven, LINDLEY (1830) twelve, SPACH (1834) sixteen, PRESL (1846) nine, ROEMER (1847) twenty five, BAILLON (1869) ten, WENZIG (1874) fourteen, DECAISNE (1874) twenty four, KOEHNE (1890) twenty three, FOCKE (1892) five, SCHNEIDER (1906) nineteen and REHDER'S Manual (1956) lists altogether eighteen genera of the *Maloideae*.

The most controversial seems to be delimitation of *Pirus*, *Crataegus* and particularly of *Sorbus*. The genera *Pirus* and *Crataegus* used to be very collective, including a great majority of species of the *Maloideae* (cf. JUSSIEU, DE CANDOLLE, FOCKE). Both the huge complexes were gradually split into series of minor, rather homogeneous genera. A very interesting and instructive example is the genus *Sorbus*. The species belonging here were affiliated by some writers to *Crataegus*, *Pirus*, or *Mespilus* (ENDLICHER 1836, BENTHAM et HOOKER 1862, BAILLON 1869, FOCKE 1892, ASCHERSON et GRAEBNER 1906), but were separated by others into different genera *Aria*, *Torminaria*, *Chamaemespilus*, *Aucuparia* and *Sorbus* s. str. (MEDICUS 1793, ROEMER 1847, OPIZ 1852, DECAISNE 1874), KOEHNE 1890, BECK 1892, DIPPEL 1893). The present conception of the genus *Sorbus*, first used by REICHENBACH (1830) and KOCH (1837) was fixed as late as in 1898 by FRITSCH.

Now let us examine how delimitation of genera of the *Maloideae* appears when different criteria are taken into consideration.

Morphology — Despite their distinct character, the *Maloideae* are greatly diversified morphologically. A considerable morphological variation occurs not only in vegetative but especially in reproductive organs.

A very striking feature are pinnate leaves which are very rare in the *Maloideae*. They apparently developed independently in different, rather remote groups; they are only known in *Sorbus* (the subgenera *Aucuparia* and *Sorbus* s. str.) and in *Osteomeles anthyllidifolia*. All three may represent separate evolutionary lines. Vernation of leaves proved to be a very good generic character in *Cotoneaster*, *Pirus*, *Photinia*, *Eriobotrya*, *Aronia*, and *Amelanchier*; two types of vernation are found in the larger genera: *Crataegus*, *Sorbus* and *Malus* (FOLGNER 1897).

A remarkable diversity is shown in the floral morphology. Estivation is imbricate in most of the genera but it is contorted in *Cydonia*, *Stranvaesia*, and *Pourtiaea* (DECAISNE 1874). The ovary is generally semi-inferior, but it is almost superior in *Photinia* and *Heteromeles*, where the carpels join the receptacle by their basal parts only. In other genera, as e.g. in *Pyracantha*, *Amelanchier*, *Sorbus* (excl. *Torminaria*), *Cotoneaster*, and *Photinia* the carpels coalesce with the receptacle by their dorsal sides in various degrees, so that the ovary tends to be inferior, which, however, is the case in a few genera only (*Pirus*, *Malus*, *Cydonia*, *Raphiolepis*, *Micromeles*, *Crataegus*). The genus *Stranvaesia* differs from all the others *Maloideae* by the dehiscent carpels. Another distinctive character which is of a high taxonomic value, is the degree to which the carpels coalesce together; even in *Sorbus* an almost apocarpic (subg. *Aucuparia*) and a perfectly syncarpic (subg. *Torminaria*) gynoecium both occur. The number of carpels is a good generic character in some cases, but in some species there is variation even within an individual. The original pentamerous gynoecium is preserved in *Pirus*, *Malus*, *Cydonia*, *Chaenomeles*, *Docynia*, *Eriobotrya*, *Pyracantha*, *Stranvaesia*, *Osteomeles*, *Mespilus*, and in some species of *Amelanchier*, *Aronia*, *Sorbus*, and *Crataegus*. The styles are terminal throughout the subfamily but subterminal in *Cotoneaster*; they are loose (*Pirus*, *Mespilus*, *Crataegus*, *Cotoneaster*) or fused to various degrees (*Malus*, *Amelanchier*, *Sorbus* subg. *Torminaria*, *Stranvaesia*). There are usually two ovules in each carpel but only one in *Osteomeles* and up to twenty in *Cydonia* and *Chaenomeles*. The position of ovules is also different in various genera (DECAISNE 1874).

A remarkable diversity is shown also in the characters of the fruit, both in the external morphology (e.g. persistence and deciduousness of sepals) and in the inner structure (number of seeds, consistence of the endocarp, etc.). The endocarp is osseous in *Cotoneaster*, *Mespilus*, *Pyracantha*, *Crataegus*, *Osteomeles*, and *Chamaemeles*, and cartilaginous, membranous or leathery in *Sorbus*, *Aronia*, *Photinia*, *Stranvaesia*, *Eriobotrya*, *Chaenomeles*, *Cydonia*, *Docynia*, *Raphiolepis*, *Malus*, *Pirus*, *Amelanchier*, and *Peraphyllum*.

Morphology justifies delimitation of a number of homogeneous genera, as was suggested and substantiated by the monographers DECAISNE (1874) and KOEHNE (1890). Floral and fruit morphology proved to supply the best generic characters in any genus of the *Maloideae*. It is important to note that all the authors who had paid attention to the characters of reproductive parts agreed that the collective genera of the *Maloideae* ought to be split. Morphology also provides a strong argument for splitting the genus *Sorbus* into five distinct and excellently characterized genera, viz. *Aria*, *Torminaria*, *Chamaemespilus*, *Aucuparia*, and *Sorbus* s. str. (cf. KOVANDA 1961).

Geographical distribution — The geographical distribution of the *Maloideae* is confined almost exclusively to the northern hemisphere. Only a few species of *Hesperomeles* extend to the Andes (Peru, Bolivia), and *Photinia Blumei* occurs on Java. The other species are not found below the equator. From the distributional pattern it is obvious where the evolutionary focus was located.

The majority of genera occurs in central and south-eastern Asia, from whence they migrated to Europe so that at the present time they are common to the whole of Eurasia (*Pirus*, *Sorbus*, *Crataegus*, *Malus*, *Cotoneaster*). There is no endemic genus in Europe. Ten genera are native in America, four of them being endemic there: *Peraphyllum* (western part of the USA), *Aronia* (atlantic North America), *Heteromeles* (California), and *Hesperomeles* (the Andes). The largest genera (*Crataegus*, *Sorbus*, *Malus*) occur both in the eastern and western hemispheres. The genera *Cotoneaster*, *Pyracantha*, *Chamaemeles*, *Mespilus*, *Pirus*, *Cydonia* are found in the Old World only, *Micromeles*, *Raphiolepis*, *Docynia*, *Stranvaesia*, *Eriobotrya*, and *Chaenomeles* in Asia exclusively. No genus is endemic to Africa; only a few species reach its northernmost part. An endemic monotypic genus *Chamaemeles* (*Ch. coriacea*) from Madeira has been described. In Australia the *Maloideae* are entirely lacking. In Oceania the genus *Osteomeles* is represented by one single species *O. anthyllidifolia* (see also FOLGNER 1897).

Anatomy — Anatomical distinctions are also a reliable guide for distinguishing genera. The value of these characters was discovered by DECAISNE (1874) who found the anatomy of the pome to be very distinctive and con-

stant in every genus. Structure of the mesocarp and distribution of sclereids are of particular importance. The genera *Micromeles*, *Pourthiaea* and subgenera *Aria* and *Chamaemespilus* of *Sorbus* differ markedly in this respect from all the others. Anatomy of the pulp was used recently for taxonomic purposes in *Sorbus* with a considerable success (see GABRIELJAN 1958, KOVANDA 1961).

Wood anatomy, though rather uniform throughout the subfamily, confirms the system of small genera suggested by ROEMER, DECAISNE, and KOEHNE. All of them, except for five (*Aria*, *Torminaria*, *Chamaemespilus*, *Aucuparia* and *Sorbus* s. str.) are very well defined from this viewpoint (BURGERSTEIN 1895).

No peculiarities in the leaf anatomy have been reported to date, but the possibility cannot be excluded that a more detailed examination will bring further evidence for separation or identification of some genera.

Cytology — From the cytological point of view the *Maloideae* are a very homogeneous group. All genera examined have shown to have $x = 17$ as the basic chromosome number (SAX 1931, MOFFETT 1931a, 1931b). Most of the species are diploids ($2n = 34$) but larger genera, such as *Sorbus*, *Crataegus*, *Cotoneaster*, *Pirus*, and *Malus* include series of triploids and tetraploids too. In *Mespilus*, *Aronia*, *Photinia*, *Eriobotrya*, *Chaenomeles*, and *Cydonia* only diploid species are known.

The basic chromosome number is very peculiar, as all the other *Rosaceae* have $x = 8$ or 9 (*Spiraeoideae*), 7 or 9 (*Rosoideae*), and 8 (*Prunoideae*) as basic numbers. Its origin has been interpreted in different ways:

1. The recent *Maloideae* originated from a diploid form with $x = 7$ by a duplication of four pairs and a triplication of three pairs of chromosomes (DARLINGTON and MOFFETT 1930). This opinion is supported by the fact that in *Pirus* the chromosomes show a tendency to associate in groups of two or three pairs at meiotic division and that the basic chromosome number is 7 in most of the genera of the *Rosoideae*.

2. The *Maloideae* are hypertetraploids derived from a primitive ancestor with $x = 8$ ($8 + 8 + 1 = 17$) (SAX 1931).

3. The *Maloideae* are allotetraploids derived from crosses between primitive representatives of the *Spiraeoideae* or the *Spiraeoideae* and the *Rosoideae* (SAX 1932).

4. The *Maloideae* arose from hybrids between ancestral *Spiraeoideae* and *Prunoideae* by amphidiploidization (STEBBINS 1950).

5. The *Maloideae* are aneuploids derived from a pentaploid ancestor with 35 somatic chromosomes, as was suggested for *Malus* by NEBEL (1929).

It is obvious that cytological observations may contribute to the solution of problems referring to the origin and development of the *Maloideae* as a whole but still cytological evidence in itself presents no clues to delimit boundaries between genera; in fact cytology contradicts the system based on morphology, anatomy and geographical distribution.

For further details see the cited authorities and also voluminous cytological monographs of some genera: *Crataegus* (LONGBLEY 1924), *Malus* (RYBIN 1926), *Cotoneaster* (H. J. SAX 1954), and *Sorbus* (LILJEFORS 1955).

Genetics — Due to the cytological uniformity, the genera of the *Maloideae* though widely distributed and morphologically greatly diversified are closely related genetically. This is indicated by a considerable capability for hybridization not only on the specific but even on the generic level; a number of intergeneric hybrids were described (*Crataegomespilus*, *Crataegosorbus*, *Sor-*

bopirus, *Sorbaronia*, *Sorbocotoneaster*, *Pyronia*, *Amelasorbus*, *Pyracomeles*) and further crosses may doubtlessly be made artificially. In some genera, as e.g. in *Sorbus*, hybridization of morphologically very remote species is shown to be of fundamental evolutionary significance (cf. LILJEBORS 1953, 1955, KOVANDA 1961).

The genetic similarity of all the genera is so thorough that SAX (1931) even concludes: "According to the genetic system of classification perhaps all of the *Pomoideae* could be classed as one single genus and most of the present genera could be regarded as a genetic species . . . This reversion to the older system of classification of the *Pomoideae* seems to be more in accord with genetic relationships than the present system, although a considerable amount of work must be done to determine the relationships of all the genera and species" (p. 20).

Discussion

From what has been said it may be obvious that the system of genera based on morphological, anatomical and distributional characters is contradictory to the results of the cytological and genetic approach. As embryological and palynological features of the *Maloideae* are of no use as generic criteria and no biochemical or serological data are available that would prove or disprove the relationships of various genera, the contradiction mentioned above and the way in which it may be resolved is of particular importance. There are two extreme attitudes: Shall we disregard cytology and genetics and, continuing in the way proposed by ROEMER, DECAISNE, and KOEHNE, subdivide *Sorbus* into *Aria*, *Torminaria*, *Chamaemespilus*, *Aucuparia* and *Sorbus* s. str. and separate some species of *Crataegus*, *Cotoneaster*, *Malus* and other larger clusters of species as genera? Or shall we ignore morphology, anatomy and geographical distribution and unite all the *Maloideae* in one single genus, perhaps *Pirus*?

It is well known that cytology does not always support the classical system (which is the case e.g. in the *Brassicaceae*) but still the situation found in the *Maloideae* is rather peculiar. Examples of families in which only one basic chromosome number occurs are rather rare; both in the *Pinaceae* ($x = 12$) and in the *Chenopodiaceae* ($x = 9$) which are most frequently demonstrated as examples of cytological homogeneity some deviations are known (*Pseudolarix*, $x = 11$ and *Spinacia*, $x = 6$). It is important to note that no attempt has been made to unite all the *Pinaceae* or all the *Chenopodiaceae* in one genus.

As regards hybridization possibilities, an analogous case is the genera of the *Hordeae* which are linked together by a series of intergeneric hybrids, so that STEBBINS (1956) suggests classifying all the species belonging here as one genus. The situation found in the *Maloideae* is essentially the same. It may be argued, as TUTIN (1956) did for the *Hordeae*, that the capability for hybridization only suggests that the morphological divergence of the *Maloideae* proceeded without being followed by development of sterility barriers which would prevent distinct forms from crossing. To unite all the *Maloideae* in one single genus is hardly recommendable just because of the high degree of morphological differentiation of the various genera. The possibility of hybridization and genetic relationships cannot invalidate DECAISNE's and KOEHNE's genera, perhaps not even the genera split off from *Sorbus*.

The most important conclusion from what has been discussed in the foregoing chapters is that delimitation and revision of the genera of the *Maloideae* should be based only on classical approaches. As was pointed out in the introduction, the value of any approach and of any character is different in different families. If in the *Maloideae* both cytology and genetics happen to be irrelevant for classification on the generic level, the other criteria are to be used the more cautiously.

As far as the genus *Sorbus* is concerned, its splitting is excellently substantiated from the point of view of morphology, fruit anatomy and geographical distribution, but it appears unjustifiable from the point of view of wood anatomy. There is no doubt that the groups *Aria*, *Torminaria*, *Chamaemespilus*, *Aucuparia* and *Sorbus* s. str. represent independent evolutionary lines and it is a matter of individual opinion whether we consider the wood anatomy to be of such importance as to prove a close relationship between them. My opinion (1961) that REICHENBACH's conception of the genus *Sorbus* should be kept is open to discussion.

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