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PROBLEMS IN NOMENCLATURE AND SYSTEMATICS IN THE SUBFAMILY KALANCHOIDEAE (CRASSULACEAE) OVER THE YEARS

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Abstract

Ambiguity concerning the systematics and nomenclature of the subfamily Kalanchoideae has been observed in the family Crassulaceae. In the history of research on representatives of the above-mentioned systematic group, there have been two opposing viewpoints aiming at either the establishment of separate genera *Bryophyllum*, *Kalanchoë* and *Kitchingia* or combining all the species into one genus *Kalanchoë* divided into subgenera (*Bryophyllum*, *Calophygia, Kalanchoë*) or sections (*Bryophyllum*, *Kalanchoë* (*Eukalanchoë*) and *Kitchingia* or *Bryophyllum*, and *Kalanchoë*. According to the analysis of various morphological, anatomical, embryological, karyological, phytogeographical, molecular genetics researches, it is challenging to establish the three genera in the subfamily Kalanchoideae due to the existence of intermediate species. Taking also into account the results of his own research, the author of the present work postulates that the most appropriate taxonomic approach is to recognize one genus *Kalanchoë* with the division into three sections: *Bryophyllum*, *Kalanchoë* and *Kitchingia*. The names of two of these sections correspond with the previously adopted names of the genera, thus referring to the initial stages of research concerning this subfamily.

Key words: Crassulaceae, Kalanchoideae, systematics, genus, subgenus, section, *Bryophyllum*, *Calophygia*, *Kalanchoë*, *Kitchingia.*

INTRODUCTION

The genus *Kalanchoë* Adans. (*Cotyledon* L. [1753], *Vereia* H. Andrews [1797], *Verea* Willd. [1799], *Calanchoe* Pers. [1805], *Kalenchoë* Haw. [1819]) belongs to the subfamily Kalanchoideae Berg., family Crassulaceae DC. (Engler, 1930; Takhtajan, 1987, 1997). Its present name was first used by Adanson in 1763. In his monograph, the author refers to the results of Rumphius's work from 1750, in which the name *Kalanchoë* is not used, but a plant of this genus was described and illustrated under the name of *Tsjaccarbebe* (Adanson, 1763). Adanson regards China as the native country in which the species, later classified as this taxon, was first discovered and described. In his herbarium, the following caption can be found under number "13619: *Cotyledon Afra folia lato crasso laciniato flosculo auro* Boerh. Ind." (which refers to *Cotyledon laciniata* L. = *Kalanchoë laciniata* (L.) DC.). On the next page, he presents a specimen of the same plant under number 13620; the name *Kalanchoë* was later manually added by Adanson himself on the herbarium label. In Lamarck's herbarium, the name is used for *K. spathulata* DC., a species originating from China, and the name itself is spelt in the *Kalanikoë* form. In China, the plant was called "Kalan Chauhuy", meaning "that which falls and grows", and the scientific name is a phonetic transcription of that name (Boiteau and Allorge-Boiteau, 1995). The name may refer to the plantlets which are present in many species, although no viviparous species of this genus comes from China. It is also possible that the name originates from ancient Indian words "kalanka" – "rust" and "chaya" – "gloss", which refers to the shiny, sometimes reddish leaves of the Indian *K. laciniata* species (Descoings, 2003).

At the beginning of the 19th century, a new genus *Bryophyllum* Salisb. (*Crassuvia* Commers. *ex* Lam. [1786], *Physocalycium* Vest. [1820], *Crassouvia* Commers. *ex* DC. [1828], *Kalanchoë* R. Hamet [1907-1908], *Geaya* Constantin et Poisson [1908]) was introduced into the family Crassulaceae by Salisbury (1805). The author used this name for *Bryophyllum calycinum* Salisb. – a plant with an inflated flower calyx and with adventive buds on the leaf blade rim (viviparity); the latter trait contributed to the genus name,

which was coined from two Greek words: "bryon" – "it germinates, produces a sprout" and "phyllon" – "a leaf". Since the species in question has had a varied nomenclatorial history for the last two hundred years (syn. *Sedum madagascaricum* Clusius [1605], *Crassula pinnata* L. [1782], *Cotyledon pinnata* Lam. [1786], *Vereia pinnata* (Lam.) Andrews [1797], *Verea pinnata* (Lam.) Willd. [1799], *Calanchoë pinnata* Pers. [1805]), some botanists (De Candolle, 1828; Dalzell, 1852; Hance, 1873) were doubtful of the use of the name for the genus.

In 1881, the botanical world welcomed a new taxon in the study subfamily – the genus *Kitchingia* Bak. (syn. *Kalanchoë* Baillon [1885], *Kalanchoë* R. Hamet [1907]), thus called to commemorate Kitching who had brought the *Kitchingia gracilipes* Bak. plant from Madagascar (Baker, 1881). Later, several new *Kitchingia* species described by that author were included in the genus *Kalanchoë* (Baill., 1885). Although Baker (1887) accepted removal of the genus he had introduced, some of his followers (Stapf, 1908; Berger, 1930) opposed it.

As the number of new species in the subfamily Kalanchoideae was significantly increasing, the issue of maintaining the uniform nomenclature of the taxa in this plant group was becoming increasingly problematic. Until nowadays, the problem has been frequently discussed by numerous systematicians. Two contradictory viewpoints have been prevalent throughout the whole history of the research conducted on the representatives of the subfamily Kalanchoideae:

the first is related to the establishment of separate genera: *Bryophyllum*, *Kalanchoë* and *Kitchingia* (Baker, 1881, 1887; Berger, 1930; Tillson, 1940; Hutchinson and Dalziel, 1954; Airy-Shaw, 1966; Zepkova, 1976, 1977, 1980; Vinogradov et al. 1976, 1978), *Bryophyllum* and *Kalanchoë* (Endlicher, 1839; Bentham and Hooker, 1865; Baillon, 1885; Schönland, 1891; Harvey, 1894; Nothdurft, 1962; Lauzak-Marchal, 1974; Wickens, 1982, 1987; Forster, 1985; Tölken, 1985; 't Hart, 1995; Byalt, 2000, 2008), *Kalanchoë* and *Kitchingia* (Takhtajan, 1966, 1987);

the second suggests including all the species into one genus *Kalanchoë* (Dalzell, 1852; Hance, 1873; Hamet, 1907, 1908, 1964; Perrier de la Bâthie, 1923, 1928; Mauritzon, 1933; Baldwin, 1938; Boiteau and Mannoni, 1948-1949; Jacobsen, 1954, 1981; Decary, 1962; Hamet and Marnier-Lapostolle, 1964a; Jensen, 1968; Friedmann, 1971, 1975; Raadts, 1977; Boiteau and Allorge-Boiteau, 1995; Rauh, 1995; Gehrig et al. 2001; Mort et al. 2001; Descoings, 2003, 2006; Chernetskyy, 2007).

TAXONOMIC STUDY

The first monograph of *Kalanchoë* was published in 1907. Hamet (1907), the author of the work, analyzed the prevalent concepts of the systematics of the plant group and proposed that the three genera (*Bryophyllum*, *Kalanchoë* and *Kitchingia*) introduced by some botanists should be included in one genus *Kalanchoë*. Hamet explained this necessity with the presence of intermediate species; he took into consideration the shape of the calyx and the scale-like nectaries present around the ovary base. In his work, the author provided detailed morphological characteristics of the *Kalanchoë* genus, and a classification key with the description of 61 species; he also divided them into 14 groups according to the following traits: the morphological structure of the flower and the nectaries, the shape of leaves, and presence or absence of hairs on the surface of leaves or of the whole plant. Hamet's views upon the systematics of *Kalanchoë* were supported by Perrier de la Bâthie (1923, 1928); both researchers co-operated with each other and described many new *Kalanchoë* species in the Madagascan flora.

Berger (1930) conducted holistic taxonomic studies of the family Crassulaceae. In his work, he provided short descriptions of approximately 100 species of plants from the subfamily Kalanchoideae and distinguished the three above-mentioned genera on the basis of diversity of flower traits and presence of adventive buds in *Bryophyllum.* The main systematic criteria for the division included: the shape of the calyx and the corolla tube, the point of adnation of stamen filaments to the corolla petals, the ratio of the ovary length to the style length, spatial arrangement of the flower (erect, pendulous, etc.) and the shape of the peduncle. Tillson (1940) examined the vascular anatomy of the flower in 33 species of the here mentioned subfamily and determined the point of fusion of stamen filaments to the corolla tube. In his study, the researcher adopted the system of subfamily Kalanchoideae division elaborated by Berger. On the other hand, embryological research (Mauritzon, 1933) on family Crassulaceae specimens did not reveal significant differences between the genera *Bryophyllum*, *Kalanchoë,* and *Kitchingia*. Mauritzon emphasized that due to the uniform type of the nucellus these taxa are close to each other in the phylogenetic system of the family Crassulaceae, and he thus indicted that the subfamily Kalanchoideae differs distinctly from the other subfamilies within this family.

Numerous cytotaxonomic studies (Baldwin, 1938; Uhl, 1948; Komala, 1956; Friedmann, 1971; Raadts, 1983, 1985, 1989a, 1989b, 1995) revealed that the characteristic haploid number of chromosomes for *Bryophyllum* and *Kitchingia* is 17, and

for *Kalanchoë* – 18 or 17. Some species of the particular genera may display a haploid system with 5, 7 or 19 chromosomes; they also differ between one another in ploidism (diploids, tetraploids, or hexaploids). According to Baldwin (1938) and Friedmann (1971), these results imply lack of permanent karyological traits (presence of intermediate species in each genus), which does not allow regarding them as three separate genera. Another solution was suggested by Resende, who introduced the genus *Bryokalanchoë* Res. [1956]: *Bryophyllum* × *Kalanchoë* (Boiteau and Allorge-Boiteau, 1995).

It should be mentioned that some authors (Boiteau and Mannoni, 1948-1949) considered the genus *Bryophyllum* to be a separate section within the genus *Kalanchoë*. The division into sections resulted from differences in the following traits: placement of the flowers, the size of the gynoecium, narrowing of the corolla tube towards the style. The work of Boiteau and Mannoni was not published as a whole and it did not include *Kitchingia* and most *Bryophyllum* species (*Kitchingia* and *Bryophyllum* sections). Therefore, Jacobsen (1954, 1981) critically reviewed the work of his predecessors and recognized a single genus *Kalanchoë* with three sections: *Bryophyllum* (Salisb.) Boit. et Mann. (29 species), *Kitchingia* (Bak.) Boit. et Mann. (4 spp.) and *Kalanchoë* (*Eukalanchoë* Boit. et Mann.) (86 spp.). The author provided general characteristics of the genus *Kalanchoë* and its particular sections; he also described 119 species, 51 varieties and 6 inter-species hybrids (Jacobsen, 1981).

In 1964 a new paper about *Kalanchoë* was published by Hamet and Marnier-Lapostolle (1964a), which, however, did not include bibliographic data, a classification key of species and their synonyms and which, in the opinion of some researchers, proved of little use (Lauzak-Marchal, 1974), likewise the work on Madagascan *Kalanchoë* species by Decary (1962). A subsequent study conducted by Hamet (1964) comprised only some species of this genus. Thus, upon observation of the flower vascular anatomy of *Kalanchoë jongmansii* Hamet et Perr. and *K. manginii* Hamet et Perr., he presented arguments for classifying them into the *Bryophyllum* section: the flower sepals are fused into the corolla and only a short fragment is free. The author observed that not all *Kitchingia* species have saliences in the centre of the corolla tube at the point where the stamen filaments are fused. According to Hamet, there is no sufficient evidence that would support establishment of a separate *Kitchingia* genus, although the supporters of Berger's system questioned this viewpoint (Hutchinson and Dalziel, 1954; Nothdurft, 1962; Airy-Shaw, 1966). Moreover, Jensen (1968) conducted a detailed study of the vascular anatomy of the stem in 39 various species from the subfamily Kalanchoideae, including the genera *Bryophyllum* and *Kitchingia*. In his work, the author presented several types of the stem structure in the study plants, but he did not find evidence for distinguishing three separate genera within the subfamily Kalanchoideae.

Literature provides numerous papers about the nomenclature of some critical *Kalanchoë* species, mainly from the African flora (Cufodontis, 1957, 1967, 1969; Hamet and Marnier-Lapostolle, 1964b; Fernandes, 1980; Raadts, 1983, 1985), and about new scientific discoveries concerning the species (Hamet, 1963; Boom and Zeilinga, 1964; Cufodontis, 1965; Raadts, 1972, 1979, 1981, 1983, 1989a, 1995; Tölken, 1978; Fernandes, 1980; Thulin, 1993). The problem of the genus taxonomy ranking was, however, not tackled by the authors in the above-mentioned literature.

In her analysis of the predecessors' work, Lauzak-Marchal (1974) concluded that the traits used for distinguishing taxa are insufficient for categorizing or merging the genera *Bryophyllum* and *Kalanchoë*. The author enlists numerous traits which, according to her, allow definite distinction of these genera. In species of the genus *Bryophyllum*, the flowers are pendulous, the pedicel is bent, the calyx is bell-shaped or round, the sepals are fused, the corolla tube is narrowed above the ovary, the stamen filaments are basally fused with the corolla tube, the style is markedly longer than the ovary, the scale-like nectaries are tetragonal or semicircular; there are adventive buds on the leaf margin in half of the species; the haploid chromosome number sets is 17; the region of natural occurrence is Madagascar (except for *Bryophyllum pinnatum* (Lam.) Kurz). The species of the genus *Kalanchoë,* however, are characterized by: erect flowers, straight pedicel, a cylindrical calyx, non-fused sepals or fused for only one half of their length, straight corolla tubes, the stamen filaments are fused into the corolla tube centrally or along its length, the style is shorter than the ovary, the scale-like nectaries are linear; there are no adventive buds on the leaves. The basic chromosome number in the genus *Kalanchoë* is 18, and most representatives of the plant naturally grow on the African continent and in the south of Madagascar. The author included some *Kalanchoë* species in the genus *Bryophyllum* and claimed that the genus *Kitchingia* with its few species may be included in the genus *Bryophyllum*. Such a concept of the subfamily Kalanchoideae taxonomy was supported by other authors (Wickens, 1982, 1987; Forster, 1985; Tölken, 1985; 't Hart, 1995; Byalt, 2000, 2008).

Other researchers (Zepkova, 1976, 1977, 1980; Vinogradov et al. 1976, 1978) proposed a new system for the family Crassulaceae based on

the data from embryology, karyology and phytogeography. In this system, the number and contents of species follow Berger's system (1930); the number of subfamilies was reduced from six (Cotyledonoideae, Crassuloideae, Echeverioideae, Kalanchoideae, Sedoideae, Sempervivoideae) to two (Sedoideae, Kalanchoideae) and numerous taxa of a lower rank (tribes, subtribes) were introduced. In the Kalanchoideae subfamily the following were established: tribe Kalanchoeae Zepk., subtribe Kalanchoinae Zepk. (*Kalanchoë* Adans.), and subtribe Bryophyllinae Zepk. (*Bryophyllum* Salisb., *Kitchingia* Bak.).

In his studies, Takhtajan (1966, 1987) paid the greatest attention to the structure of the gynaecium and flower placentation. He divided the family into four subfamilies: Crassuloideae, Echeverioideae, Kalanchoideae, Sedoideae. The author included the subfamily Cotyledonoideae in the subfamily Kalanchoideae, species of the genus *Bryophyllum* in the genus *Kalanchoë*, and he regarded the genus *Kitchingia* as a separate taxon. In his next monograph, the author (Takhtajan, 1997) distinguished only three subfamilies in the family Crassulaceae: Crassuloideae, Kalanchoideae, and Sedoideae. It is worth mentioning that the above-mentioned reviews (Takhtajan, 1966, 1987, 1997; Zepkova, 1976, 1977, 1980; Vinogradov et al. 1976, 1978) did not contain any characteristics of the mentioned genera.

Great significance is attributed to the monograph of the Madagascan *Kalanchoë* species (Boiteau and Allorge-Boiteau, 1995), which provides extensive data on plant systematics, ecophysiology and phytochemistry. The authors stated in the work that there are numerous species which may parallelly be classified into two genera: *Bryophyllum* or *Kitchingia*, *Bryophyllum* or *Kalanchoë*, etc., following the traits that are typical for the three genera examined by some systematicians (Berger, 1930; Lauzak-Marchal, 1974). Therefore, they distinguished only one genus *Kalanchoë* with three sections: *Bryophyllum*, *Kalanchoë* and *Kitchingia*, in accordance with the system previously adopted by Boiteau and Mannoni (1948-1949), and elaborated by Jacobsen (1954, 1981).

Contemporary molecular genetics researches on family Crassulaceae representatives provide analyses based on the relatedness and phylogenesis of the taxa in question (Ham and 't Hart, 1998; Mort et al. 2001). Berger's system (1930), with the subfamily being represented by three genera, was adopted as a basis by the researchers. However, in their work, Mort et al. (2001) reported that the sequence of chloroplast *matK* genes locates the species *Bryophyllum* and *Kitchingia* in the genus *Kalanchoë*. The authors took into consideration their predecessors' studies on various research aspects of Kalanchoideae and suggested that a single genus *Kalanchoë* should be recognized. A similar conclusion can be drawn from the analysis of the genotypic diversity in the genus *Kalanchoë*, in which nucleotides of 54 species and 14 botanical varieties in the three sections of the genus were tested (Gehrig et al. 2001). On the basis of the study results, the authors reconstructed the phylogenetic tree of the genus *Kalanchoë*. Additional ecophysiological data allowed a conclusion that Madagascar is the centre of phylogenetic radiation of the genus, where it dispersed from the wet regions of the island towards the dry areas, and then to the African continent.

Detailed examinations of the leaf microstructure in the selected species of the subfamily Kalanchoideae did not reveal significant differences between the taxa of the genera *Bryophyllum*, *Kalanchoë* and *Kitchingia* (Chernetskyy, 2007). The author observed that the species display common features of leaf anatomy: a well-developed cuticula, presence of epicuticular wax, thickening of the outer wall of epidermal cells, amphistomatic leaves, anisocytic stomata, presence of anthocyanin pigments in the epidermal cells, water-transporting mesophyll, and storing tannin and calcium oxalate in some mesophyll cells. However, the anatomy of leaves in some taxa (*Kalanchoë beauverdii* Hamet, *K. tubiflora* (Harvey) Hamet, and species of the *Lanigerae* group) differs distinctly from the leaf anatomy of other *Kalanchoë* species. The importance of the presence or absence of the following taxonomic features in the leaf structure in some species of the Kalanchoideae subfamily: calcium oxalate deposits on the surface of the epidermis, microchannels in the outer walls of epidermal cells (Chernetskyy and Weryszko-Chmielewska, 2008), non-glandular or glandular trichomes, protuberance of the cell walls of the non-glandular trichomes (Weryszko-Chmielewska and Chernetskyy, 2005; Chernetskyy, 2006, 2007), hydatodes, papillae forming epidermal cells, angular or tangential colenchyma, and stomata in the petiole epidermis (Chernetskyy 2007). The author believes that there is no basis for distinguishing three separate species *Bryophyllum*, *Kalanchoë* and *Kitchingia* in the subfamily Kalanchoideae, as it was the case in the history of this systematic group.

Summing up all the approaches to the taxonomy and nomenclature of the subfamily Kalanchoideae throughout its history, Descoings (2003) concluded that all the proposed divisions of this group are too diverse and artificial, and thus they cannot be used in better understanding of the genus traits. The author regarded all the taxa in this group (137 species, 11 subpecies, 10 botanical varieties and 7 interspecies hybrids) as *Kalanchoë*, with two sections: *Kalanchoë*

and *Bryophyllum* (including the species *Kitchingia*). In this group of taxa, Descoings distinguishes 12 *Kalanchoë* species, which, in his opinion, cannot be included in only one of these sections due to their structural traits; this has always posed problems in the history of the subfamily Kalanchoideae. In his review, he simultaneously suggested new nomenclature combinations for numerous *Kalanchoë* taxa and provided short botanical information for each of the described taxa.

After several years, Descoings (2006) proposed a genus of *Kalanchoë* with 150 described species divided into three subgenera *Kalanchoë*, *Bryophyllum* and *Calophygia*. He includes intermediate species which have features of *Kalanchoë* and *Bryophyllum* to the subgenus *Calophygia.* The author introduced a new taxon – subgenus *Calophygia* – to the subfamily Kalanchoideae avoiding the genus *Bryokalanchoë* Res. (Boiteau and Allorge-Boiteau, 1995) previously proposed by Resende (in 1956).

CONCLUSIONS

On the basis of the analysis of the prevalent concepts of the systematics of the subfamily Kalanchoideae, it should be assumed that the most proper taxonomic system of this group is recognition of one genus *Kalanchoë* with the division into three sections – *Bryophyllum*, *Kalanchoë* and *Kitchingia*, in accordance with Jacobsen (1954, 1981) and Boiteau and Allorge-Boiteau (1995), but with the modern taxa nomenclature adopted by Descoings (2003). This systematic division is the most consistent. The names of two of these sections correspond with the previously adopted names of the genera (*Bryophyllum* and *Kitchingia*), thus referring to the initial stages of research concerning this subfamily.

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Problemy w nomenklaturze i systematyce podrodziny Kalanchoideae (Crassulaceae) w historii badań

Streszczenie

W rodzinie Crassulaceae dostrzega się niejednoznaczne traktowanie systematyki i nomenklatury podrodziny Kalanchoideae. W ciągu całej historii badań nad przedstawicielami wymienionej grupy systematycznej istniały dwa przeciwne poglądy dotyczące wydzielania samodzielnych rodzajów *Bryophyllum*, *Kalanchoë* i *Kitchingia* lub zmierzające do połączenia wszystkich gatunków w jeden rodzaj *Kalanchoë* z podziałem na podrodzaje *Bryophyllum*, *Calophygia, Kalanchoë* lub sekcje *Bryophyllum*, *Kalanchoë* (*Eukalanchoë*), *Kitchingia* lub *Bryophyllum*, *Kalanchoë*. Na podstawie analizy wielu badań: morfologicznych, fitosocjologicznych, anatomicznych, kariologicznych, molekularno-genetycznych itp. – trudno jest w podrodzinie Kalanchoideae wydzielić trzy rodzaje ze względu na istnienie gatunków pośrednich. Autor wymienionej pracy uważa, że najbardziej właściwym systemem taksonomicznym wymienionej podrodziny jest uznanie jednego rodzaju *Kalanchoë* z podziałem na trzy sekcje: *Bryophyllum*, *Eukalanchoë* i *Kitchingia*. Nazwy dwóch sekcji odpowiadają nazwom wcześniej przyjętych rodzajów, zostawiając ślad pierwszych etapów w rozwoju tej podrodziny.