



THE ROLE OF MORPHO-ANATOMICAL TRAITS OF THE LEAVES IN THE TAXONOMY OF KALANCHOIDEAE BERG. SUBFAMILY (CRASSULACEAE DC.)

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Abstract. The paper presents the results of the analysis of the morphological and anatomical structure of leaves of 35 species of the genus *Kalanchoë* Adans. (Crassulaceae DC.) in the taxonomic aspect of the subfamily Kalanchoideae Berg. Based on own studies and literature analyses of the flower morphology, embryology, karyology, vascular anatomy of stem and molecular genetics, the author has found that the most appropriate taxonomic system of the subfamily Kalanchoideae assumes existence of one genus *Kalanchoë* divided into three sections: *Bryophyllum* (Salisb.) Boit. & Mann., *Eukalanchoë* Boit. & Mann. and *Kitchingia* (Bak.) Boit. & Mann. Distinguishing three separate genera *Bryophyllum* Salisb., *Kalanchoë* Adans. and *Kitchingia* Bak., as has been the case throughout the history of the subfamily Kalanchoideae, is hardly possible due to existence of “intermediate” species.

Key words: morphology, anatomy, leaf, species, *Kalanchoë*, Kalanchoideae, Crassulaceae, taxonomy, nomenclature

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Introduction

The taxonomy and nomenclature of the subfamily Kalanchoideae Berg. (Crassulaceae DC.) have not been unquestionably established (DESCOINGS 2006; CHERNETSKYY 2011). Two contrasting views have been prevailing throughout the history of research on the representatives of the subfamily. Some researchers distinguished separate genera *Bryophyllum* Salisb., *Kalanchoë* Adans. and *Kitchingia* Bak. (SALISBURY 1805; ENDLICHER 1839; BENTHAM & HOOKER 1865; BAKER 1881; BAILLON 1885; SCHÖNLAND 1891; STAPF 1908; BERGER 1930; TILLSON 1940; HUTCHINSON & DALZIEL 1954; AIRY-SHAW 1966; LAUZAK-MARCHAL 1974; ZEPKOVA 1980; WICKENS 1982; FORSTER 1985; TÖLKEN 1985; 'T HART 1995; BYALT 2000, 2008 and oth.), whereas others combined all species of the subfamily Kalanchoideae into one genus (DALZELL 1852; HANCE 1873; HAMET 1907, 1908, 1963; PERRIER DE LA BÂTHIE 1923, 1928; MAURITZON 1933; BALDWIN 1938; DECARY 1962; HAMET & MARNIER-LAPOSTOLLE 1964; JENSEN 1968; FRIEDMANN 1971, 1975; RAADTS 1977; RAUH 1995; GEHRIG *et al.* 2001; MORT *et al.* 2001 and oth.) divided into subgenera (*Bryophyllum* (Salisb.) Koorders, *Calophygia* Desc., *Kalanchoë*) (DESCOINGS 2006) or sections (*Bryophyllum* (Salisb.) Boit. & Mann., *Eukalanchoë* (*Kalanchoë*) Boit. & Mann., *Kitchingia* (Bak.) Boit. & Mann. or *Bryophyllum*, *Kalanchoë*) (BOITEAU & MANNONI 1948-1949; FRIEDMANN 1975; JACOBSEN 1981; BOITEAU & ALLORGE-BOITEAU 1995; DESCOINGS 2003; CHERNETSKYY 2011).

The genus *Kalanchoë* includes approximately 150 species (DESCOINGS 2006) distributed mainly in the arid areas of East and South-West Africa and some of its adjacent islands, and in South-East Asia. Almost half of all the *Kalanchoë* species described occur in the Madagascan flora as endemic species growing in the diverse climatic conditions of the island (BOITEAU & ALLORGE-BOITEAU 1995; RAUH 1995; DESCOINGS 2003).

Numerous papers presenting the structure of organs of *Kalanchoë* genus plants focus primarily on the macro- and microstructure of flowers, stems or roots. Available reports on the structure of *Kalanchoë* leaves present mainly their macromorphology, including presence of adventitious buds (vivipary). In contrast, there is little information about the micromorphology and anatomy of *Kalanchoë* leaves. The available data involve only a few and more common species of the genus. Results of investigations on the leaf structure may provide knowledge of essential taxonomic traits that would be helpful in solving the current problem of the taxonomy and nomenclature of the subfamily Kalanchoideae.

Material and methods

The study involved 35 species representing various life forms, which, according to the systematic division (JACOBSEN 1981), belong to three sections: **1) *Bryophyllum*** (*K. beauverdii* Hamet, *K. daigremontiana* Hamet & Perr., *K. fedtschenkoii* Hamet & Perr., *K. gastonis-bonnierii* Hamet & Perr.,

K. laetivirens Desc., *K. laxiflora* Bak., *K. manginii* Hamet & Perr., *K. marnieriana* Jacobs., *K. pinnata* (Lam.) Pers., *K. porphyrocalyx* (Bak.) Baill., *K. prolifera* (Bowie ex Hook.) Hamet, *K. rosei* Hamet & Perr., *K. tubiflora* (Harv.) Hamet, *K. uniflora* (Stapf) Hamet); 2) ***Eukalanchoë*** (*K. beharensis* Drake, *K. bipartita* Chiov., *K. blossfeldiana* v. Poelln., *K. crenata* (Andrews) Haw., *K. eriophylla* Hilt. & Bojer ex Tulanse, *K. hildebrandtii* Baill., *K. longiflora* Schltr. ex Wood, *K. marmorata* Bak., *K. millotii* Hamet & Perr., *K. nyikae* Engl., *K. orgyalis* Bak., *K. prittwitzii* Engl., *K. pumila* Bak., *K. rhombopilosa* Mann. & Boit., *K. schimperiana* A. Rich., *K. thyrsoflora* Harv., *K. tomentosa* Bak., *K. velutina* Welw. ex Britten); 3) ***Kitchingia*** (*K. campanulata* (Bak.) Baill., *K. gracilipes* (Bak.) Baill., *K. peltata* (Bak.) Baill.).

The study material was obtained from the collection of greenhouse plants at the Botanical Garden of the Maria Curie-Skłodowska University in Lublin. Investigations of the micromorphology and anatomy of typical leaves of selected *Kalanchoë* species were conducted using stereoscopic microscopy (SM), light microscopy (LM) and scanning electron microscopy (SEM).

Results and discussion

The leaves of individual species of the genus *Kalanchoë* differ distinctly in terms of their shape, colour and parameters. They exhibit permanent species-specific macromorphological traits. The polymorphism observed in the leaves (simple or compound, sessile or petiolate) is characteristic for some species and closely related to changes in external factors in both artificial growing conditions and their homeland. A common feature for all taxa is the succulent leaf structure, which is unequally manifested due to the diverse habitat conditions. Leaf vivipary is a typical trait of most representatives of the section *Bryophyllum*, while infloral vivipary is a general feature of the genus *Kalanchoë*.

In terms of their morpho-anatomical organization, leaves of the genus *Kalanchoë* belong mostly to the bifacial structure type. However, the anatomical structure in many species reveals the unifacial petiole structure; hence, the leaf may be classified as the mixed (unifacial-bifacial) type. The representatives of the particular sections of the genus *Kalanchoë* share the leaf anatomy (Tab. 1), but the species differ distinctly in terms of appearance (the type of trichomes, the contours of the anticlinal walls

of epidermal cells, etc.), parameters or numbers, for instance, the length of the stomata (23-39 μm) and non-glandular (42-1258 μm) or glandular trichomes (28-155 μm); the thickness of the epidermis (11-48 μm); the number of epidermal cells (159-1075), stomata (17-97) and non-glandular trichomes (19-52) per 1 mm² of the leaf surface. The epidermis in *Kalanchoë* leaves produces papillary structures composed of highly convex epidermal cells and one or more stomata. The structure of some *Kalanchoë* taxa is characterized by presence of surface calcium carbonate deposits (*K. gastonis-bonnierii*, *K. pumila*, *K. thyrsoflora*), papillary marginal cells (*K. prolifera*), non-glandular trichomes (*K. beharensis*, *K. orgyalis*, *K. eriophylla*, *K. hildebrandtii*, *K. rhombopilosa*, *K. millotii*, *K. tomentosa* and oth.), glandular trichomes (*K. beharensis*, *K. gastonis-bonnierii*, *K. eriophylla*, *K. manginii*, *K. orgyalis* and oth.), angular collenchyma (*K. campanulata*, *K. daigremontiana*, *K. laxiflora*, *K. marnieriana*, *K. pinnata*, *K. prolifera* and oth.), tangential collenchyma (*K. beharensis*, *K. blossfeldiana* and oth.) and stomata in the elongated aggregations on the petiole (*K. pinnata*, *K. prolifera*). The chlorenchymatous tissue in *Kalanchoë* leaves is not differentiated into palisade and spongy mesophyll, but is divided into small-celled subepidermal mesophyll and large-celled mesophyll (water transporting, CAM type). The leaf assimilation tissue contains pleomorphic chloroplasts. Green plastids have been detected also in the cytoplasm of cells: epiderma, stomata, collenchyma, tannin-bearing and epithem hydathodes.

The details of the microstructure of *Kalanchoë* leaves may constitute important taxonomic traits of the species of the subfamily Kalanchoideae. The leaf structure did not exhibit distinct differences between the species of the three sections (*Bryophyllum*, *Eukalanchoë*, *Kitchingia*) of the genus *Kalanchoë*. Based on own studies (CHERNETSKYY 2007) and other authors' investigations concerning the flower morphology (HAMET 1907, 1908; BERGER 1930; BOITEAU & MANNONI 1948-1949 and oth.), embryology (MAURITZON 1933), karyology (BALDWIN 1938; UHL, 1948; FRIEDMANN 1971; ZEPKOVA 1976; RAADTS 1983, 1985, 1989), vascular anatomy of stem (JENSEN 1968) and molecular genetics (HAM & 'T HART 1998; GEHRIG *et al.* 2001; MORT *et al.* 2001), it is difficult to distinguish three genera in the subfamily Kalanchoideae due to existence of "intermediate" species. DESCOINGS (2006) suggests a division of the genus *Kalanchoë*

Table 1. Morpho-anatomical traits of the leaf structure in the genus *Kalanchoë*.

Traits of leaf structure	Sections		
	<i>Bryophyllum</i>	<i>Eukalanchoë</i>	<i>Kitchingia</i>
polymorphism	- +	- +	- +
unifacial petiole	- +	- +	- +
peltate lamina	- +	- +	- +
viviparia	+ -	--	--
non-glandular trichomes	--	- +	--
glandular trichomes	- +	- +	--
calcium carbonate deposits on the surface	- +	- +	--
epithemal hydathodes	+ -	- +	+ +
papillary structures of the epidermis	+ +	+ +	+ +
amphistomatic	+ +	+ +	+ +
lower epidermis producing more stomata	+ -	+ +	+ +
anisocytic stomata	+ +	+ +	+ +
well-developed outer cuticular ledges of stomatal cells	+ +	+ +	+ +
epicuticular wax	+ +	+ +	+ +
thick-layered cuticle	+ +	+ +	+ +
striated cuticle	+ -	+ -	+ -
smooth cuticle	+ -	+ -	+ -
single-layer epidermis	+ +	+ +	+ +
papillary epidermal cells	- +	--	--
slightly or distinctly convex outer epidermal cell walls	+ -	+ -	+ +
thickened outer walls of epidermal cells	+ +	+ +	+ +
the contours of the anticlinal walls in epidermal cells:			
undulating	+ -	+ -	+ -
straight	- +	- +	- +
the cells of the lower epidermis are smaller than the cells of the upper epidermis	+ +	+ -	+ +
anthocyanin pigments in epidermal cells	+ +	+ +	+ +
small-celled, subepidermal mesophyll	+ +	+ +	+ +
water transporting mesophyll	+ +	+ +	+ +
tannins in some parenchymal cells	+ +	+ +	+ +
calcium oxalate crystals in parenchymal cells	+ +	+ +	+ +

-- lack of the trait in the species of the section,
+ - characteristic trait for most species of the section,

+ + characteristic trait for the species of the section,
- + characteristic trait for some species of the section.

into three subgenera: *Bryophyllum*, *Kalanchoë* and *Calophygia*. The author classifies “intermediate” species between *Kalanchoë* and *Bryophyllum* into the subgenus *Calophygia*, excluding species that have common traits of *Bryophyllum* and *Kitchingia*. He introduces a new taxon – the subgenus *Calophygia* – to the subfamily Kalanchoideae, and disregards the genus *Bryokalanchoë* Res. proposed previously by F. Resende in 1956 (see BOITEAU & ALLORGE-BOITEAU 1995). Generally, this gives no grounds for distinguishing three separate genera *Bryophyllum*, *Kalanchoë* and *Kitchingia* in the subfamily

Kalanchoideae, as has been done throughout the history of this systematic group.

References

- AIRY-SHAW H.K. 1966. A dictionary of flowering plants and ferns. (Revision of Willis J.C. 7th ed.). Cambridge University Press, London.
- BAILLON M.H. 1885. Liste des plantes de Madagascar. *Bull. Mens. Soc. Linn.* 1: 465–472.
- BAKER J.G. 1881. Notes on a collection of flowering plants made by L. Kitching, Esq., in Madagascar in 1879. *J. Linn. Soc., Bot.* 18: 264–281.

- BALDWIN J.T. 1938.** *Kalanchoë*: the genus and its chromosomes. *Amer. J. Bot.* **25**: 572–579.
- BENTHAM G. & HOOKER J.D. 1865.** *Genera plantarum*. Vol. 1. L. Reeve & Co.; Williams & Northgate, London.
- BERGER A. 1930.** Crassulaceae. In: ENGLER A. & PRANTL K. (eds). *Die Natürlichen Pflanzenfamilien*. Bd. **18A**: 352–483. Verlag von Wilhelm Engelmann, Leipzig.
- BOITEAU P. & ALLORGE-BOITEAU L. 1995.** *Kalanchoë* de Madagascar. Systématique, écophysologie et phytochimie. Karthala, Paris.
- BOITEAU P. & MANNONI O. 1948.** Les *Kalanchoë*. *Cactus (Paris)* **13**: 7–10; **14**: 23–28; **15–16**: 37–42; **17–18**: 57–58.
- BOITEAU P. & MANNONI O. 1949.** Les *Kalanchoë*. *Cactus (Paris)* **19**: 9–14; **20**: 45–46; **21**: 69–76; **22**: 113–114.
- BYALT V.V. 2000.** Notes for some species of genera *Kalanchoë* Adans. and *Bryophyllum* Salisb. (Crassulaceae). *Novosti Sistem. Vyssh. Rast.* **32**: 50–52. (In Russian).
- BYALT V.V. 2008.** New combinations in the genera *Bryophyllum* and *Kalanchoë* (Crassulaceae). *Bot. Zhurn.* **93**: 461–465. (In Russian).
- CHERNETSKYY M. 2007.** Kseromorficzne przystosowania struktury liści wybranych gatunków z rodzaju *Kalanchoë* Adans. (Crassulaceae DC.). Rozprawa doktorska, Akademia Rolnicza w Lublinie, Lublin.
- CHERNETSKYY M. 2011.** Problems in nomenclature and systematics in the subfamily Kalanchoideae (Crassulaceae) over the years. *Acta Agrobot.* **64** (4): 67–74.
- DALZELL N.A. 1852.** Contributions to the botany of Western India. *Hooker's Jour. Bot.* **4**: 341–347.
- DECARY R. 1962.** Les *Kalanchoés* de Madagascar. *Nature Sci. Progr.* **3332**: 516–520.
- DESCOINGS B. 2003.** *Kalanchoë*. In: EGGLI U. (ed.). *Illustrated Handbook of Succulent Plants – Crassulaceae*: 143–181. Springer-Verlag, Berlin–Heidelberg–New York.
- DESCOINGS B. 2006.** Le genre *Kalanchoë* (Crassulaceae): structure et définition. *J. Bot., Bull. Soc. Bot. Fr.* **33**: 3–28.
- ENDLICHER S.L. 1839.** *Genera Plantarum Secundum Ordines Naturals Disposita*. Pt. 1. Fr Beck, Wien.
- FORSTER P.I. 1985.** The genera *Kalanchoë* and *Bryophyllum* in cultivation. *Anacampseros* **1** (I): 37–41; **1** (II): 52–56.
- FRIEDMANN F. 1971.** Sur de nouveaux nombres chromosomiques dans le genre *Kalanchoë* (Crassulacées) à Madagascar. *Candolla* **26**: 103–107.
- FRIEDMANN F. 1975.** Formes de croissance et multiplication végétative des *Kalanchoë* malgaches. *Candolla* **30**: 177–188.
- GEHRIG H., GAUSSMANN O., MARX H., SCHWARZOTT D. & KLUGE M. 2001.** Molecular phylogeny of the genus *Kalanchoë* (Crassulaceae) inferred from nucleotide sequences of the ITS-1 and ITS-2 regions. *Plant Sci.* **160**: 827–835.
- HAM V.R.C.H.J. & 'T HART H. 1998.** Phylogenetic relationships in the Crassulaceae inferred from chloroplast DNA restriction-site variation. *Amer. J. Bot.* **85**: 123–134.
- HAMET R. 1907.** Monographie du genre *Kalanchoë*. *Bull. Herb. Bois. sér. 2.* **7**: 869–900.
- HAMET R. 1908.** Monographie du genre *Kalanchoë*. *Bull. Herb. Bois. sér. 2.* **8**: 17–48.
- HAMET R. 1963.** Sur quarte *Kalanchoë* – dort trois nouveaux – de e'Angola et sur un *Kalanchoë* du Mozambique. *Bol. Soc. Brot. sér. 2.* **37**: 5–32.
- HAMET R. & MARNIER-LAPOSTOLLE J. 1964.** Le genre *Kalanchoë* au jardin botanique „Les Cèdres”. *Arch. Mus. Natn. Hist. Nat.* **8**: 1–107.
- HANCE H.F. 1873.** *Flora Hongkongensis Supplementum*. *J. Linn. Soc., Bot.* **13**: 95–144.
- HUTCHINSON J. & DALZIEL M.D. 1954.** *Flora of West Tropical Africa*. 2e ed. Rev. par. RWJ Keay, London.
- JACOBSEN H. 1981.** *Das Sukkulenten Lexicon*. VEB Gustav Fischer Verlag, Jena.
- JENSEN L.C.W. 1968.** Primary stem vascular patterns in three subfamilies of the Crassulaceae. *Amer. J. Bot.* **55**: 553–563.
- LAUZAK-MARCHAL M. 1974.** Réhabilitation du genre *Bryophyllum* Salisb. (Crassulacées, Kalanchoïdées). *C. R. Acad. Sci. sér. D.* **278**: 2505–2508.
- MAURITZON J. 1933.** Studien über die Embriologie der Familien Crassulaceae und Saxifragaceae. Dissertat. Univ. of Lund, Håkan Ohlssons Buchdruckerei, Lund.
- MORT M.E., SOLTIS D.E., SOLTIS P.S., FRANCISCO-ORTEGA J. & SANTOS-GUERRA A. 2001.** Phylogenetic relationships and evolution of Crassulaceae inferred from matK. *Amer. J. Bot.* **88**: 76–91.
- PERRIER DE LA BÂTHIE H. 1923.** Crassulacées malgaches nouvelles. *Bull. Mus. Hist. Nat.* **29**: 452–455.
- PERRIER DE LA BÂTHIE H. 1928.** Observations nouvelles sur le genre *Kalanchoë*. *Arch. Bot. Bull. Mens.* **2**: 17–31.
- RAADTS E. 1977.** The genus *Kalanchoë* (Crassulaceae) in tropical East Africa. *Willdenowia* **8**: 101–157.
- RAADTS E. 1983.** Cytotaxonomische Untersuchungen an *Kalanchoë* (Crassulaceae) 1. *Kalanchoë marmorata* Baker und 2 neue *Kalanchoë*-Arten aus Ostafrika. *Willdenowia* **13**: 373–385.
- RAADTS E. 1985.** Cytotaxonomische Untersuchungen an *Kalanchoë* (Crassulaceae) 2. Chromosomenzahlen intermediärer Formen. *Willdenowia* **15**: 157–166.
- RAADTS E. 1989.** Cytotaxonomische Untersuchungen an *Kalanchoë* (Crassulaceae) 3. Chromosomenzahlen ostafrikanischer *Kalanchoë*-Sippen. *Willdenowia* **19**: 169–174.
- RAUH W. 1995.** *Succulent and xerophytic plants of Madagascar*. Vol. 1. Strawberry Press, Mill Valley (US: CA).
- SALISBURY R.A. 1805.** *The paradisus Londinensis*. Vol. 1, T. 3. D.N. Shury & W.W.Hooker, London.
- SCHÖNLAND S. 1891.** Crassulaceae. In: ENGLER A. & PRANTL K. (eds). *Die Natürlichen Pflanzenfamilien*. 1st ed. 3 (2a): 23–38. Verlag von Wilhelm Engelmann, Leipzig.
- STAPP O. 1908.** *Kitchingia uniflora* Stapf. *Bull. Misc. Inform. Kew.* **258**–259.
- 'T HART H. 1995.** Intrafamilial and generic classification of the Crassulaceae. In: 'T HART H. & EGGLI U. (eds). *Evolution and Systematics of the Crassulaceae*: 159–172. Backhuys Publishers, Leiden.
- TILLSON A.H. 1940.** The floral anatomy of the Kalanchoideae. *Amer. J. Bot.* **27**: 596–600.
- TÖLKEN H.R. 1985.** Crassulaceae. In: LEISTNER O.A. (ed.). *Flora of Southern Africa*. Vol. **14**: 1–244. Botanical Research Institute, Department of Agriculture & Water Supply, Pretoria (RSA).
- UHL C.H. 1948.** Cytotaxonomic studies in the subfamilies Crassuloideae, Kalanchoideae and Cotyledonoideae of the Crassulaceae. *Amer. J. Bot.* **35**: 695–706.
- WICKENS G. 1982.** Miscellaneous notes on *Crassula*, *Bryophyllum* and *Kalanchoë*. *Kew Bull.* **36**: 665–674.
- ZEPKOVA N.L. 1976.** Division main numbers of chromosomes and polyploidy of rows in the family Crassulaceae. *Voprosy Sist. Pokrytosem. Rast.*: 77–81. (In Russian).
- ZEPKOVA N.L. 1980.** Comparison of proposing a system the family Crassulaceae of system A. Berger's. *Voprosy Bot.*: 138–145. (In Russian).