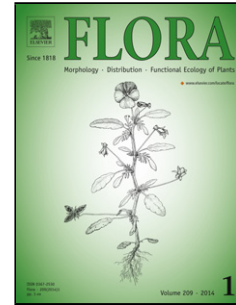


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Author: Balkrishna Ghimire Mi Jin Jeong Go Eun Choi
Hayan Lee Gang Uk Suh Kweon Heo Ja Jung Ku



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1 **Seed morphology of the subfamily Helleboroideae (Ranunculaceae) and its systematic implication**

2
3 **Balkrishna Ghimire^{a,*}, Mi Jin Jeong^a, Go Eun Choi^a, Hyan Lee^a, Gang Uk Suh^a, Kweon Heo^b, Ja Jung Ku^a**

4
5 ^aPlant Conservation Division, Korea National Arboretum, Pocheon 487-829 Korea

6 ^bDepartment of Applied Plant Sciences, Kangwon National University, Chuncheon 200-701 Korea

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8 Corresponding Author: ghimire2ab@gmail.com

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10 Running head: Seed morphology of Helleboroideae

11
12 Number of Table: 1

13
14 Number of figure: 12 (black and white, color only for online version)

15
16 **Highlights**

- 17 ➤ Major seed surface types: striate, lineate, colliculate and irregularly wrinkled.
- 18 ➤ The wall ornamentation was predominantly smooth.
- 19 ➤ Mechanical layer of the seed coat was of the exotesta except in all *Eranthis*.
- 20 ➤ A close relationship of *Caltha–Trollius–Megaleranthis* was convincingly supported.
- 21 ➤ Another group supported strongly by this study was *Aconitum–Delphinium*.

22
23 **A B S T R A C T**

24 A comprehensive morphological and anatomical study was carried out on seeds of 28 species from three tribes and eight genera of subfamily
25 Helleboroideae (*Aconitum*, *Actaea*, *Caltha*, *Cimicifuga*, *Delphinium*, *Eranthis*, *Megaleranthis* and *Trollius*) and two putatively related genera in
26 Ranunculaceae (*Adonis* and *Ranunculus*) using scanning electron and light microscopy to evaluate seed characteristics for use in the examination of
27 systematic relationships. Considerable differences were found in seed coat morphology and anatomy both among and within genera of the subfamily. There
28 are four major types of seed coat surface: striate, lineate, colliculate and irregularly wrinkled. The shape of testal cells was either elongated rectangular,
29 rectangular chiseled, irregular or polygonal to subpolygonal. The wall ornamentation was predominantly smooth and either without any ornamentation or
30 having finely granulated or some ribbon like appendages. The mechanical layer of the seed coat was of the exotestal type except in all species of *Eranthis*,
31 in which the seed coat mechanical layer was absent; such a seed coat was referred to as being an ‘undifferentiated seed-coat’. Maximum parsimony analysis
32 of morphological features establishes three groupings within the studied genera: *Aconitum/Delphinium*, *Actaea/Cimicifuga*, and
33 *Caltha/Eranthis/Trollius/Megaleranthis*. This study is congruent with the earlier groupings of the Helleboroideae based on morphology and also agrees in
34 part with recent molecular studies. Our data convincingly support a close relationship between *Caltha – Trollius – Megaleranthis* and between *Actaea –*
35 *Cimicifuga*. Another group supported strongly by the results of this study is *Aconitum – Delphinium*.

36 **Keywords:** Helleboroideae, Ranunculaceae, seed morphology, seed anatomy, systematics

37
38 **Introduction**

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