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Notes on African plants

VARIOUS AUTHORS

RANUNCULACEAE

THE GENUS *KNOWLTONIA* SUBSUMED WITHIN *ANEMONE*

The family Ranunculaceae, with ± 1 750 species in ± 60 genera, is poorly represented in sub-Saharan Africa (Dreyer & Jordaan 2000; Leistner 2005), and most representatives on the continent are restricted to temperate, often afromontane habitats. Five genera and just over 40 species are recorded for southern Africa: *Anemone* L. (3 spp.), *Clematis* L. (= *Clematopsis* Boj. ex Hook.) (± 20 spp.), *Delphinium* L. (3 spp.), *Knowltonia* Salisb. (± 8 spp.) and *Ranunculus* L. (± 8 spp.), the majority represented by just a handful of species comprising a small fraction of each genus. *Knowltonia*, endemic to southern and southern tropical Africa (Rasmussen 1979), is the single exception. This biogeographical anomaly raises questions as to the origin of the genus and its relationship to other southern African Ranunculaceae.

The genus *Knowltonia* Salisb. was proposed by Salisbury (1796) for the southern African species of Ranunculaceae previously referred to *Adonis* L., from which it was diagnosed on the basis of its fleshy fruits and broad filaments. It soon became evident, however, that *Knowltonia* was most closely allied to *Anemone* (De Candolle 1817; Bentham & Hooker 1862), with which it shares an involucre of bracts beneath the flowers, and uniovulate carpels with pendent ovules. The genus was subsequently formally included in *Anemone* as section *Knowltonia* by Prantl (1891), followed by Burtt Davy (1912). Later South African botanists, misinterpreting the morphology, reinstated it as a separate genus, either mistakenly considering that it lacked an involucre (Hutchinson 1923; Phillips 1951), or because they were misled in thinking that the perianth was double (Dyer 1975). In fact, all species of *Knowltonia* have an involucre beneath the flowers, and the perianth could only possibly be construed as double in a single species, *K. capensis*, in which the outer three or four tepals are shorter and more hairy than the inner (Rasmussen 1979).

The difference between *Anemone* and *Knowltonia* lies essentially in the texture of the fruit wall, which is fleshy in *Knowltonia* and dry in *Anemone*, although the basic structure of the fruit walls in the two genera is similar (Lonay 1901). In *K. vesicatoria* (L.f.) Prantl, the single species that was examined microscopically, the fruit wall comprises more cell layers, and the differentiation into an inner and outer portion is more pronounced than in *Anemone*, but other species of *Knowltonia* with less fleshy fruits have not been examined. In gross morphology there is little to distinguish the two genera. The rhizomatous rootstock, basal leaves, involucre, and simple perianth of *Knowltonia* are all characteristic of *Anemone*, and the branched inflorescence, although more complex than typically found in *Anemone*, is similar in structure and found in several species, including *A. demissa* Hook. & Thoms. and *A. narcissiflora* L. from the northern hemisphere, and to a lesser degree in *A. fanninii* Harv. ex Mast. from South Africa. The strictly centrifugal dehiscence of the stamens that was taken to characterize *Knowltonia*, is also found in some African species of *Anemone* (Rasmussen 1979), and although no species of *Anemone* has the broad filaments of *Knowltonia*, the connective in some species of *Anemone* is as wide as that of species such as *K. transvaalensis*. This species in particular resembles *Anemone*, and specimens of it have twice formed the basis for names in *Anemone*. The two genera are also closely allied chemically in sharing triterpene saponins (Schneider 1930).

Despite the evident similarities between the two genera, Rasmussen (1979) argued for the continued recognition of *Knowltonia* as distinct from *Anemone* on the basis that the two were as distinct from one another as other genera then recognized within the family. She diagnosed *Knowltonia* by its centrifugally maturing stamens (also known in *Anemone*), broad connectives and filaments, more or less fleshy fruits, and stigmatic papillae covering the whole ventral side of the style.

However, a wider morphological and molecular analysis of 36 species of *Anemone* plus representatives of *Adonis*, *Caltha*, *Clematis*, *Hepatica*, *Knowltonia*, *Pulsatilla* and *Ranunculus*, led Hoot *et al.* (1994) to conclude that *Knowltonia* and *Pulsatilla* should be subsumed within *Anemone*, specifically in sect. *Pulsatilloides* DC. A close relationship between *Knowltonia* and sect. *Pulsatilloides* had been suggested fifty years earlier by Janchen (1949) on biogeographical grounds. The occurrence of centrifugal stamen development in some African members of *Anemone* sect. *Pulsatilloides* and the discovery that they share pantoporate pollen with *Knowltonia* (Van Zinderen Bakker 1956; Huynh 1970) provides additional support for this view. More recent phylogenetic analyses of *Anemone* and related genera using chloroplast and nuclear DNA (Schuettpelz *et al.* 2002) support sect. *Pulsatilloides* (including *Knowltonia*) as a monophyletic group within *Anemone* subgenus *Anemone*. Within section *Pulsatilloides*, *Knowltonia* is retrieved as sister to the South African species *Anemone caffra*, suggesting that the genus shares an ancestry with one or more of the southern African *Anemone* species.

The continued recognition of the genus *Knowltonia* renders *Anemone* paraphyletic. Furthermore, it not only fails to recognize but actually obscures the intimate relationship between the species of *Knowltonia* and the southern African members of *Anemone* sect. *Pulsatil-*

loides. The species of *Knowltonia* are thus most properly interpreted as constituting a lineage within *Anemone* sect. *Pulsatilloides* that has radiated in southern Africa. We accordingly downgrade the genus to a series in *Anemone* section *Pulsatilloides* and make the necessary specific transfers.

TAXONOMY

Anemone section **Pulsatilloides** series **Knowltonia** *(Salisb.) J.C.Manning & Goldblatt*, stat. nov.

Knowltonia Salisb., Prodromus stirpium in horto ad Chapel Allerton vigentium: 372 (1796). *Anemone* section *Knowltonia* (Salisb.) Prantl: 62 (1891). Type: *Knowltonia rigida* Salisb., nom. illeg. (= *A. knowltonia* Burtt Davy).

1. **Anemone anemonoides** *(H.Rasm.) J.C.Manning & Goldblatt*, comb. nov.

Knowltonia anemonoides H.Rasm. in Opera Botanica 53: 18 (1979). Type: South Africa, [Western Cape], Jonkershoek, 7 November 1943, *Compton 15342* (NBG, holo.; K, PRE, iso.).

1a. **Anemone anemonoides** subsp. **tenuis** *(H.Rasm.) J.C.Manning & Goldblatt*, comb. nov.

Knowltonia anemonoides subsp. *tenuis* H.Rasm. in Opera Botanica 53: 20 (1979). Type: South Africa, [Western Cape], Genadendal, Baviaanskloof, 11 March 1933, *Gillett 848* (BOL, holo.; STE, iso.).

2. **Anemone bracteata** *(Harv. ex J.Zahlbr.) J.C.Manning & Goldblatt*, comb. nov.

Knowltonia bracteaea Harv. ex J.Zahlbr. in Annalen des K.K. Naturhistorischen Hofmuseums, Wien: 380 (1903). Type: South Africa, Kaffraria [Eastern Cape], 1860, *Cooper 335* [K, lecto., designated by H.Rasm.: 34 (1979); NH, PRE, iso.].

3. **Anemone brevistylis** *(Szyszyl.) J.C.Manning & Goldblatt*, comb. nov.

Knowltonia brevistylis Szyszyl., Polypetalae thalamiflorae Rehmannianae: 99 (1887). Type: South Africa, [KwaZulu-Natal], Inanda, *Rehmann 8395* [Z, lecto., designated by H.Rasm.: 32 (1979); Z, iso.].

4. **Anemone cordata** *(H.Rasm.) J.C.Manning & Goldblatt*, comb. nov.

Knowltonia cordata H.Rasm. in Opera Botanica 53: 21 (1979). Type: South Africa, [Western Cape], George, 24 March 1893, *Schlechter 2388* (BOL, holo.; GRA, J, MO, iso.).

5. **Anemone filia** *(L.f.) J.C.Manning & Goldblatt*, comb. nov.

Adonis filia L.f., Supplementum plantarum: 271 (1781). *Knowltonia filia* (L.f.) T.Dur. & Schinz: 12 (1898). Type: South Africa, without precise locality or date, *LINN714.9* [LINN, lecto., designated by H.Rasm.: 23 (1979)].

5a. **Anemone filia** subsp. **scaposa** *(H.Rasm.) J.C.Manning & Goldblatt*, comb. nov.

Knowltonia filia subsp. *scaposa* H.Rasm. in Opera Botanica 53: 25 (1979). Type: South Africa, [Eastern Cape], Humansdorp, Blaauwkrantz Pass, 16 November 1965, *Mauve 4436* (PRE, holo., iso.).

6. **Anemone knowltonia** *Burtt Davy* in Annals of the Transvaal Museum 3: 121 (1912). *Adonis capensis* L.: 548 (1753). *Anamenia capensis* (L.) Hoffmanns.: 204 (1824). *Knowltonia capensis* (L.) Huth: 69 (1890), nom. illegit., non *Anemone capensis* Lam. (1783). Type: South Africa, without precise locality or date, *LINN714.6* [LINN, lecto., designated by H.Rasm.: 16 (1979)].

Anamenia gracilis Vent.: 22 (1803). *Knowltonia gracilis* (Vent.) DC.: 219 (1817), nom. illegit., non *Anemone gracilis* F.Schmidt (1868). Type: South Africa, without precise locality or date, *Herb. Jussieu 10575* [P-JU, lecto., designated by H.Rasm.: 16 (1979)].

7. **Anemone vesicatoria** *(L.f.) Prantl* in Die natürlichen Pflanzenfamilien 3,2: 62 (1891). *Adonis vesicatoria* L.f.: 272 (1781). *Knowltonia vesicatoria* (L.f.) Sims: 775 (1804). Type: South Africa, without precise locality or date, *LINN714.8* [LINN, lecto., designated by H.Rasm.: 27 (1979)].

7a. **Anemone vesicatoria** subsp. **humilis** *(H.Rasm.) J.C.Manning & Goldblatt*, comb. nov.

Knowltonia vesicatoria subsp. *humilis* H.Rasm. in Opera Botanica 53: 29 (1979). Type: South Africa, [Western Cape], Knysna, 12 November 1949, *Morris 380* (NBG, holo.; BOL, STE, iso.).

7b. **Anemone vesicatoria** subsp. **grossa** *(H.Rasm.) J.C.Manning & Goldblatt*, comb. nov.

Knowltonia vesicatoria subsp. *grossa* H.Rasm. in Opera Botanica 53: 30 (1979). Type: South Africa, [Western Cape], Knysna, Matjiesrivier Mouth, 16 October 1938, *Gillett 4555* (BOL, holo.; K, PRE, iso.).

8. **Anemone transvaalensis** *(Szyszyl.) Burtt Davy* in Annals of the Transvaal Museum 3: 121 (1912). *Knowltonia transvaalensis* Szyszyl.: 99 (1887). Type: South Africa, [Limpopo], Houtboschberg, 1875, *Rehmann 6402* (Z, holo.; K, iso.).

Knowltonia canescens Szyszl.: 100 (1887), *Anemone canescens* (Szyszyl.) Burtt Davy: 121 (1912). Type: South Africa, [Limpopo], Houtboschberg, 1875, *Rehmann* s.n. (Z, holo.).

Anemone whyteana Baker f.: 4 (1894). *Knowltonia whyteana* (Baker f.) Engl.: 170 (1915). Type: Malawi, Mt Mulanji, October 1891, *Whyte 100* [BM, lecto., designated by Milne-Redhead & Turrill: 13 (1952); BM, K, W, iso.)].

Anemone peenensis Baker f.: 16 (1911). Type: Zimbabwe, Gazaland, Mt Pene, 28 September 1906, *Swynnerton 783* [BM, lecto., designated by Milne-Redhead & Turrill: 13 (1952)].

Knowltonia multiflora Burtt Davy: 343 (1921). Type: South Africa, [Mpumalanga], Lydenburg, without date, *Mudd s.n.* (K, holo.).

8a. **Anemone transvaalensis** var. **filifolia** *(H.Rasm.) J.C.Manning & Goldlatt*, comb. nov.

Knowltonia transvaalensis var. *filifolia* H.Rasm. in Opera Botanica 53: 38 (1979). Type: South Africa, [Mpumalanga], 7 miles [11 km] east of Belfast, 10 October 1950, *Prosser 1510* (NBG, holo.; K, iso.).

8b. **Anemone transvaalensis** var. **pottiana** *(Burtt Davy) J.C.Manning & Goldblatt*, comb. nov.

Knowltonia canescens var. *pottiana* Burtt Davy in Kew Bulletin 1921: 343 (1921). *Knowltonia transvaalensis* var. *pottiana* (Burtt Davy) H.Rasm.: 39 (1979). Type: South Africa, [Mpumalanga], Dullstroom, June 1920, *Noomé, Trans. Mus. Herb. 20803* (K, holo.).

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