The correct name in Knowltonia for an iconic southern African species earlier known as Anemone tenuifolia and A. capensis (Ranunculaceae)

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Abstract. Following recent molecular phylogenetic findings and subsequent proposals on re-circumscription of genera earlier subsumed under Anemone sensu lato (Ranunculaceae), the genus Knowltonia is accepted here in an expanded circumscription, including both dry-fruited and fleshy-fruited African species, plus some American taxa (including those earlier treated in genera Oreithales and Barneoudia), and the Tasmanian species K. crassifolia. Nomenclature of the well-known southern African dry-fruited species earlier accepted mainly under the names Anemone capensis and A. tenuifolia is discussed. The correct name of that species in Knowltonia is K. tenuifolia (L.f.) Mosyakin, comb. nov. (= Atragene tenuifolia L.f., Anemone tenuifolia (L.f.) DC.; incl. Atragene capensis L., Anemone capensis (L.) Lam., Knowltonia pulsatilloides Christenh. & Byng, etc.). It is also demonstrated that the name Anemone capensis proposed by Lamarck should be treated as a nomenclatural combination with the basionym Atragene capensis (Art. 41.4 of the ICN), not as a name of a new taxon. Taxonomic and nomenclatural implications of that conclusion are discussed. In particular, if treated in Anemone sensu lato, the correct name of this species should be Anemone capensis (L.) Lam., not A. tenuifolia (L.f.) DC. If two leaf morphs are accepted as two different species of Knowltonia, the names K. tenuifolia (with more finely dissected, triternate leaves) and K. pulsatilloides (with biteernate leaves and cuneate segments) can be used; however, the species rank for these morphs should not be recommended at our present state of knowledge.

Keywords: Anemone, Knowltonia, nomenclature, Ranunculaceae, southern Africa, taxonomy

Introduction

The genus Knowltonia Salisb. was established by Salisbury (1796: 372) for a southern African (Cape) species of Ranunculaceae with fleshy (berry-like) fruits. The only species originally included by Salisbury in that genus was K. rigida Salisb. (nom. illeg., an illegitimate replacement name for Adonis capensis L. = K. capensis (L.) Huth, 1895). Earlier, several taxa discovered and studied by European explorers and botanists in the 18th—early 19th centuries were sometimes placed in other genera, such as Adonis L., Atragene L., Clematis L., and Pulsatilla Mill. (see the synonymy below and taxonomic and nomenclatural overviews by Rasmussen, 1979; Manning et al., 2009). Later Knowltonia was often accepted as a morphologically well delimited genus of ca. eight species, with several subspecies and varieties (Rasmussen, 1979), but the close phylogenetic relationships of dry-fruited and fleshy-fruited African taxa prompted the inclusion of Knowltonia (sensu stricto) in Anemone sensu lato as a mere series, Anemone subgen. Anemone sect. Pulsatilloides DC. subsect. Alchemillifoliae (Ulbr.) Hootser. Knowltonia (Salisb.) J.C. Manning & Goldblatt (Manning et al., 2009; Hoot et al., 2012).

Following molecular phylogenetic results (Hoot et al., 1994; Ehrendorfer, 1995; Hoot, 1995; Ehrendorfer, Samuel, 2001; Schuettgelz et al., 2002; Wang et al., 2009; Meyer et al., 2010; Pfosser et al., 2011; Hoot et al., 2012; Lehtonen et al., 2016; Jiang et al., 2017, etc.) and reconsideration of morphological data (Starodubtsev, 1989, 1991; Tamura, 1993, 1995; Wang et al., 2001; Ziman et al., 2004a, 2004b, 2004c, 2005, 2006a, 2006b, 2007, 2008, etc.), Mosyakin (2016; see also Mosyakin, de Lange, 2018) discussed another option for a rational circumscription of genera in tribe Anemoneae. It has been concluded that the very wide circumscription of Anemone L. (as accepted by Hoot et al., 2012, and in some subsequent publications) should not be recommended, especially if Clematis is confirmed as phylogenetically rooted in Anemone sensu lato (see Lehtonen et al., 2016; Jiang et al., 2017, and references therein). Instead, a moderately narrow recircumscription of genera in that group was proposed (Mosyakin, 2016), with the recognition of several genera,
such as (1) Hepatica Mill., (2) Anemonastrum Holub (in an expanded circumscription, including Anemonidium (Spach) Holub, Arsenjevia Starod., Jurtsevia A. Löve & D. Löve, and Tamuria Starod.), (3) Knowltonia in a greatly expanded circumscription (corresponding to Anemone subg. Anemone sect. Pulsatilloides sensu Hoot et al., 2012), (4) Pulsatilla Mill., and (5) Anemone sensu stricto. In the circumscription proposed above (Mosyakin, 2016) and by Christenhusz and Byng (in Christenhusz et al., 2019), the genus Knowltonia is accepted in an expanded circumscription, including both dry-fruited and fleshy-fruited African species, plus some American taxa (mainly from South America, including those earlier treated in genera Oreithales Schltdl. and Barneoudia Gay), and the outlying Tasmanian species K. crassifolia (Hook.) Christenh. & Byng.

Several additional new combinations in Anemonastrum, mainly for North American taxa, have been validated by Mosyakin (2016). Further arguments in favor of that genus-level classification were provided by Mosyakin and de Lange (2018) in parallel with their validation of two additional nomenclatural combinations: Anemonastrum tenuicaule (Cheeseman) de Lange & Mosyakin from New Zealand and A. antucense (Poepp.) Mosyakin & de Lange from Chile, South America.

Christenhusz and Byng (in Christenhusz et al., 2018: 75) recently coined the new name Knowltonia pulsatilloides Christenh. & Byng to replace the name Atragene capensis L. (Linnaeus, 1753: 543). Indeed, a new combination in Knowltonia with the epithet "capensis" was impossible because of the existing earlier homonym K. capensis (L.) Huth (≡ Adonis capensis L., Anemone capensis (L.) Hoffmanns., Anemone knowltonia Burtt Davy; non Anemone capensis Lam.), the name applicable to a "true" fleshy-fruited Knowltonia (in the traditional circumscription of the genus; see Rasmussen, 1979). However, when proposing the new replacement name in Knowltonia, Christenhusz and Byng evidently missed or ignored other relevant species-rank names, in particular, those listed by Manning and Goldblatt (2013), who summarized the synonymy of this and related species and provided extensive nomenclatural discussion.

The next available epithet of priority at species rank for that taxon is "tenuifolia", initially published as Atragene tenuifolia L.f. (Linnaeus fil., 1782: 270). This species name should be used as the basionym for the new combination in Knowltonia, as required under the ICN (McNeill et al. 2012). Consequently, if Atragene capensis and A. tenuifolia are considered conspecific (and there are no sound reasons to doubt that: see Ziman et al., 2006; Manning, Goldblatt, 2013), the name Knowltonia pulsatilloides Christenh. & Byng is superfluous, but not invalid — it can be used if the basionyms mentioned above are considered as belonging to two distinct species (see extended comments below). The new combination is proposed below. Herbarium acronyms are given according to Thiers (2018–onward).

Discussion and validation of a new combination Knowltonia tenuifolia

The southern African species of Anemone sensu lato discussed above was accepted in recent taxonomic literature mainly as Anemone tenuifolia (Goldblatt, Manning, 2000; Hoot et al., 2012; Manning, Goldblatt, 2012, 2013, etc.) or, less commonly, as A. capensis (Ziman et al., 2006b). It was probably one of the earliest representatives of the Cape flora to become known to science and the first scientifically described southern African species of Anemone sensu lato (Manning, Goldblatt, 2013: 4–5). Its nomenclature is, however, rather complicated and confusing, and several nomenclatural discrepancies and inaccuracies are still present even in the latest taxonomic publications. Christenhusz and Byng (in Christenhusz et al., 2018: 75) proposed a similar generic concept in Anemoneae (with the genus Eriocapitella Nakai also recognized, in addition to the genera accepted by Mosyakin, 2016) and validated several new names and combinations in Anemonidium (Spach) Holub, Eriocapitella, and Knowltonia. However, Christenhusz and Byng did not notice that in their circumscription the genus that they accepted as Anemonidium (see Holub, 1974) should be called Anemonastrum Holub (1973) (see also comments in Mosyakin, de Lange, 2018). Consequently, new nomenclatural combinations in Anemonastrum are still needed for several species, mainly those placed earlier in Anemone sect. Keiskea Tamura and the Himalayaceae group of sect. Omalocarpus DC. These nomenclatural transfers will be published in a separate article (Mosyakin, in preparation).

In the present nomenclatural note, I consider only one southern African taxon of dry-fruited Knowltonia (Anemone sensu lato), in particular, its rather confusing nomenclature, and propose the correct name for that species in the genus Knowltonia.
**Knowltonia tenuifolia** (L.f.) Mosyakin, comb. nov.

**Basionym:** *Atragene tenuifolia* L.f., Suppl. Pl.: 270. 1782. ≡ *Clematis tenuifolia* (L.f.) Poir. in Lam., Encycl. Suppl. 2: 298. 1811. ≡ *Anemone tenuifolia* (L.f.) DC., Syst. Nat. [Candolle] 1: 195. 1817 (“1818”). ≡ *Pulsatilla tenuifolia* (L.f.) Spreng., Syst. Veg., ed. 16 [Sprengel] 2: 664. 1825. ≡ *Anemone capensis* var. *tenuifolia* (L.f.) Harv., Fl. Cap. [Harvey] 1: 3. 1860.

**Type** (lectotype, designated by Manning and Goldblatt, 2013: 2): “Cape”, Thunberg s.n. UPS-THUNB 12999; according to the protologue: “Habitat in Cap. bonae spei. *Thu*nberg” (Linnaeus fil., 1782: 270).

≡ *Atragene capensis* L., Sp. Pl.: 543. 1753. ≡ *Anemone capensis* (L.) Lam., Encycl. [J. Lamarck et al.] 1(1): 164. 1783. ≡ *Clematis capensis* (L.) Poir. in Lam., Encycl. [J. Lamarck et al.] Suppl. 2. 296. 1811 (“1812”).

≡ *Anemone capensis* (L.f.) DC., Syst. Nat. [Candolle] 1: 195. 1817 (“1818”), isonym. ≡ *Pulsatilla africana* Hermann ex Spreng., Syst. Veg., ed. 16 [Sprengel] 2: 664. 1825 (nom. illeg., pro *Atragene capensis* L.).

≡ *Anemone arborea* Hort. ex Steud. Nomencl. Bot. [Steudel], ed. 2. 1: 95. 1840 (nom. inval., pro syn. *Pulsatilla africana* Spreng.). ≡ *Pulsatilla capensis* (L.) Steud., Nomencl. Bot. [Steudel], ed. 2. 1: 379 (as an accepted name for *Clematis capensis* (L.f.) Poir.).

≡ *Anemone capensis* (L.) Harv., Fl. Cap. [Harvey] 1: 3. 1860, isonym. ≡ *Knowltonia pulsatilloides* Christenh. & Byng, The Global Flora 4: 75. 2018.

**Type** (lectotype, designated by Oliver, 1969: t. 1569): illustration of "*Pulsatilla foliis trifidus, dentatis, flore incarnato, pleno" in Burman (1738: 148, tab. 52). See Figure.

≡ *Atragene tenuis* Thunb., Fl. Jap. [Thunberg]: 239. 1784.

**Type** (neotype, designated by Manning and Goldblatt, 2013: 3): “Cape”, Thunberg s.n. UPS-THUNB 12999. By that neotypification, Manning and Goldblatt (2013) made the name *Atragene tenuis* homotypic with *Atragene tenuifolia* L.f.

**Nomenclatural comments**

Several corrections are needed for the nomenclature cited by Manning and Goldblatt (2013) and in some other sources. In particular, Manning and Goldblatt (2013: 3) cited the name *Anemone arborea* as an illegitimate superfluous name: "*Anemone arborea* [Hort.] Steud.: 95 (1840), nom. illegit. superfl. pro *Pulsatilla africana* [Hermann ex Spreng.]”. In fact, that name is not illegitimate but simply invalid because Steudel (1840: 95) cited it in synonymy of the accepted name *Pulsatilla africana* (Art. 36.1(c) of the ICN: McNeill et al., 2012).

Steudel (1840: 168, 379) also cited the name (nomenclatural combination) *Pulsatilla capensis* as an accepted name (not in italics, which he used to indicate synonymy) at least twice in the first volume of the second edition of his *Nomenclator Botanicus*. That name first appeared on page 168 after the synonym *Atragene "capensis. Lin."* as "*Pulsatilla capensis, tenuifolia*"; by that citation Steudel most probably indicated that, in his opinion, Linnaeus’ concept of *A. capensis* referred to these (this?) species of *Pulsatilla*. The name *Pulsatilla capensis* was also cited by Steudel (1840: 379) as an accepted name after the synonym *Clematis "capensis. Poir."* on page 379. The acceptance of the name *P. capensis* in the first volume clearly indicates that this combination is valid, contrary to the information in IPNI (www.ipni.org; accessed 25 May 2018), where this name is reported as invalid ("in syn."). However, in the second volume, which was published in 1841, only one of those two names, *Pulsatilla tenuifolia*, was in fact accepted by Steudel (1841: 417), while the name *P. capensis* has not been mentioned at all (either as a synonym or as an accepted species) among taxa of *Pulsatilla* in the main list of species of the genus (Steudel, 1841: 417–418). Steudel's apparent omission (or non-acceptance?) of *P. capensis* in 1841 does not invalidate that name accepted by him in 1840.

The authorship and typification of the name *Anemone capensis* proposed by Lamarck (1783: 164) was also debatable (Oliver, 1969; Killick, 1977; Ziman et al., 2006b; Hoot et al., 2012; Manning, Goldblatt, 2013). In particular, Hoot et al. (2012: 150) concluded that "the authorship and priority of *Anemone tenuifolia/ capensis* is complicated, thus warranting a special discussion here. Based on Killick (1977), Ziman et al. (2006) incorrectly attributed the name *A. capensis* (L.) Lam. to Lamarck. Lamarck makes no mention of Linnaeus’ name *Atragene capensis* and is thus considered to be describing the species independently in the genus *Anemone*, with a separate type. The existence of *A. capensis* Lam. precludes the transfer of Linnaeus’ name to *Anemone...*”. Based on conclusions of Pritzel (1841) and Oliver (1969), Manning and Goldblatt (2013: 5) also provided the following comment: “Although it is possible that Lamarck merely intended transferring Linnaeus’s name to *Anemone*, he refers in the protologue only to Hermann’s polynomial and his name must therefore be treated as the new species.
Figure. Lectotype of *Atragene capensis* L.: illustration "*Pulsatilla fōliis trīfidus, dentatis, flore incarnato, pleno*" (Burman, 1738: 148, tab. 52); digitized image available from Biblioteca Digital, Real Jardín Botánico, Madrid: http://bibdigital.rjb.csic.es/ing/Libro.php?Libro=4789&Pagina=10.
A. capensis Lam., as was done by Pritzel (1841), with the De Jussieu specimen as the type (Oliver, 1969). Ziman et al. (2006) are incorrect in treating Lamarck's name as the combination A. capensis (L.) Lam., based on At. [Atragene] capensis L.”. Manning and Goldblatt (2013: 3) reported the specimen "Herb. Jussieu (P-JU) 10.536” as the "holotype" of A. capensis Lam.

The interpretation of the nomenclatural action of Lamarck is important for resolving the problem of the correct species-rank name of that species if treated in Anemone (however, it should be made clear that I prefer here to place it in Knowltonia; see Mosyakin, 2016). If Lamarck indeed proposed the new combination, then the correct name of that species in Anemone is Anemone capensis (L.) Lam. (as accepted by Ziman et al., 2006b, and some other authors before) and the same combination used by de Candolle (1817: 195) and Harvey (1860: 3) is superfluous (a later isonym). However, if the name Anemone capensis in Lamarck is treated as a description of a new species based on a different type, then the correct name of the species in Anemone is Anemone tenuifolia (L.f.) DC. (as accepted by Goldblatt, Manning, 2000; Hoot et al., 2012; Manning, Goldblatt, 2012, 2013, etc.).

Indeed, Lamarck (1783: 164) for some unknown reason did not mention the Linnaeus name directly (as the basionym in the modern sense), most probably because he indeed had at his disposal only one specimen, the one from the herbarium of Jussieu (cited as the "holotype" by Manning, Goldblatt, 2013; see above). However, Lamarck cited under his Anemone capensis the polynomial "Pulsatilla Africana, multifido flore, apii folio rigido, hermmanni", which is almost the same reference citation as the polynomial provided by Linnaeus under his Atragene capensis ("Pulsatilla apii folio rigido flore magno. Herm. afr. 18"; Linnaeus, 1753: 534); both these citations (in Linnaeus and Lamarck) evidently refer to the polynomial that first appeared in Hermann's catalogue of African plants (Hermann, 1737: 18).

According to Art. 41.4 of the ICN (McNeill et al. 2012), "if, for a name of a genus or taxon of lower rank published before 1 January 1953, no reference to a basionym is given but the conditions for its valid publication as the name of a new taxon or replacement name are fulfilled, that name is nevertheless treated as a new combination or name at new rank when this was the author's presumed intent and a potential basionym (Art. 6.10) applying to the same taxon exists". That is exactly the case with the name Anemone capensis: Lamarck gave no reference to its basionym but referred to the same earlier polynomial as Linnaeus did for Atragene capensis (the potential basionym applying to the same taxon), evidently having in mind the same species. Thus, Lamarck's presumed intent was, in modern terms, to transfer that Linnaeae species from Atragene to Anemone. The conditions for valid publication of Anemone capensis as the name of a new taxon were also fulfilled by Lamarck. Thus, following Art. 41.4 of the ICN, there is no other option except treating the name proposed by Lamarck as a nomenclatural combination A. capensis (L.) Lam. based on Atragene capensis L. The same provisions as those of Art. 41.4 of the Melbourne Code (McNeill et al., 2012) also existed in earlier versions of the International Code of Botanical Nomenclature (ICBN), for example, the corresponding Art. 33.3 of the Vienna Code (McNeill et al., 2006) and Art. 33.2 of the St. Louis Code (Greuter et al., 2000). The nomenclatural codes (ICN and ICBN) are retroactive, and because of that since 2000 the name Anemone capensis introduced by Lamarck should have been treated only as a nomenclatural combination.

That conclusion has evident nomenclatural and taxonomic implications. If that species in that particular circumscription is accepted in Anemone, its correct name in that genus is A. capensis (L.) Lam., not A. tenuifolia. However, the situation is reverse if the species is placed in Knowltonia: in that case its correct name is K. tenuifolia (see the new combination above).

Knowltonia tenuifolia is a rather polymorphic species. Two morphotypes were often taxonomically recognized, sometimes as species and sometimes as varieties; however, intermediate forms are rather common. Manning and Goldblatt (2013: 3–4) commented that the species accepted in their article as Anemone tenuifolia "is highly variable in the degree of dissection of the leaves, which vary from biternate with cuneate, toothed or pinnatifid leaflets to triternate with pinnate leaflets divided into needle-like segments. The two extremes were, understandably enough, treated for some time as distinct species under the names Atragene/Anemone tenuifolia and At./A. capensis respectively, but with further collecting it is now clear that they represent part of the variation within a single species. <...> A full range of leaf dissection can be found within a single population in the southwest, sometimes even within a single plant, with juvenile leaves tending to be less deeply dissected than those produced later".

If, nevertheless, these leaf morphs are accepted as two different species, then these two species should be called Knowltonia tenuifolia (L.f.) Mosyakin (Atragene
tenuifolia L.f. ≡ Anemone tenuifolia ≡ Anemone capensis var. tenuifolia (L. f.) Harv., etc.) and K. pulsatilloides Christenh. & Byng (= Atragene capensis L. ≡ Anemone capensis (L.) Lam. sensu stricto). Some data provided by Hoot et al. (2012) may be interpreted in favor of that option. In particular, Hoot et al. (2012: 150) mentioned that "the two varieties of A. tenuifolia are more different from one another (differing at six sites) than A. fanninii and A. caffra [accepted here as Knowltonia fanninii (Harv. & Hook. f.) Christenh. & Byng and K. caffra (Harv.) Christenh. & Byng – S.M.], which have essentially identical sequences. Anemone tenuifolia is a variable species and more molecular and morphological work is needed". However, based on current knowledge and pending further study, that taxonomic option is not recommended. Manning and Goldblatt (2013: 1) commented on the above statement of Hoot et al. (2012) that "there is no compelling morphological basis for this treatment, since A. tenuifolia is intermediate between ser. Knowltonia and ser. Alchemillifoliae in having the compound foliage of the former but the seiraceous, fusiform achenes of the latter. The molecular topology retrieves ser. Knowltonia as sister to a clade in which A. tenuifolia is in turn sister to A. caffra + A. fanninii and is thus consistent with either classification". Following the taxonomic opinion of Manning and Goldblatt (2013), I prefer not to recognize any infraspecific entities in the polymorphic species Knowltonia tenuifolia.

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Москвич С.Л. Правильное название в роде Knowltonia для популярного южноафриканского вида, ранее известного как Anemone tenuifolia и A. capensis (Ranunculaceae). Укр. бот. журн., 2018, 75(3): 230–237.

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В соответствии с результатами недавних молекулярно-филогenetических исследований и последующими предложениями по пересмотру границ родов, ранее часто включаемых в Anemone sensu lato (Ranunculaceae), род Knowltonia признается здесь в расширенном объеме, включая африканские виды с сухими и ягодовидными плодами, а также некоторые американские таксоны (включая те, которые ранее рассматривались в родах Oreithales и Barneoidia) и тасманийский вид K. crassifolia. Рассмотрены вопросы номенклатуры широко известного южноафриканского вида, ранее придуманного в основном под названиями Anemone capensis и A. tenuifolia. Правильное название этого вида в роде Knowltonia — K. tenuifolia (L.) Lam., known as Atragene capensis (L.) comb. nov., (= Atragene tenuifolia L., Knowltonia tenuifolia (L.) DC.; incl. Atragene capensis L., Anemone capensis (L.) Lam., Knowltonia pulsatilloides Christenh. & Byng, etc.). Также показано, что название Anemone capensis, предложенное Ламарком, должно рассмотриться как номенклатурная комбинация с базионимом Atragene tenuifolia (статья 41.4 МКН), а не как новый вид. Обсуждаются таксономические и номенклатурные следствия из этого вывода. В частности, правильным названием этого вида в случае включения его в род Anemone sensu lato является Anemone capensis (L.) Lam., а не A. tenuifolia (L.) DC. Если два морфотипа, различающиеся по форме листьев, признаются за два разных вида рода Knowltonia, то для них может быть использована названия K. tenuifolia и K. pulsatilloides, но ранг вида для этих таксонов не рекомендуется.

Ключевые слова: Anemone, Knowltonia, Ranunculaceae, номенклатура, Южная Африка, систематика