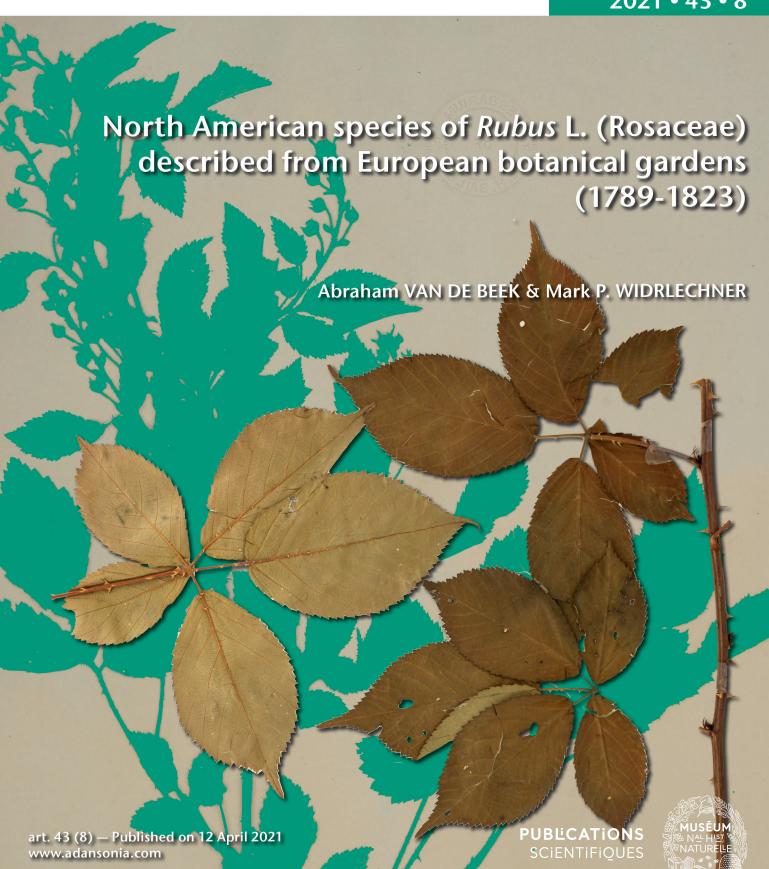
adansonia

2021 • 43 • 8



DIRECTEUR DE LA PUBLICATION / PUBLICATION DIRECTOR: Bruno David Président du Muséum national d'Histoire naturelle

RÉDACTEUR EN CHEF / EDITOR-IN-CHIEF: Thierry Deroin

RÉDACTEURS / EDITORS: Porter P. Lowry II; Zachary S. Rogers

Assistant de rédaction / Assistant editor: Emmanuel Côtez (adanson@mnhn.fr)

MISE EN PAGE / PAGE LAYOUT: Emmanuel Côtez

COMITÉ SCIENTIFIQUE / SCIENTIFIC BOARD:

- P. Baas (Nationaal Herbarium Nederland, Wageningen)
- F. Blasco (CNRS, Toulouse)
- M. W. Callmander (Conservatoire et Jardin botaniques de la Ville de Genève)
- J. A. Doyle (University of California, Davis)
- P. K. Endress (Institute of Systematic Botany, Zürich)
- P. Feldmann (Cirad, Montpellier)
- L. Gautier (Conservatoire et Jardins botaniques de la Ville de Genève)
- F. Ghahremaninejad (Kharazmi University, Tehéran)
- K. Iwatsuki (Museum of Nature and Human Activities, Hyogo)
- A. A. Khapugin (Tyumen State University, Russia)
- K. Kubitzki (Institut für Allgemeine Botanik, Hamburg)
- J.-Y. Lesouef (Conservatoire botanique de Brest)
- P. Morat (Muséum national d'Histoire naturelle, Paris)
- J. Munzinger (Institut de Recherche pour le Développement, Montpellier)
- S. E. Rakotoarisoa (Millenium Seed Bank, Royal Botanic Gardens Kew, Madagascar Conservation Centre, Antananarivo)
- É. A. Rakotobe (Centre d'Applications des Recherches pharmaceutiques, Antananarivo)
- P. H. Raven (Missouri Botanical Garden, St. Louis)
- G. Tohmé (Conseil national de la Recherche scientifique Liban, Beyrouth)
- J. G. West (Australian National Herbarium, Canberra)
- J. R. Wood (Oxford)

COUVERTURE / COVER:

Réalisée à partir des Figures de l'article/Made from the Figures of the article.

Adansonia est indexé dans / Adansonia is indexed in:

- Science Citation Index Expanded (SciSearch®)
- ISI Alerting Services®
- Current Contents® / Agriculture, Biology, and Environmental Sciences®
- Scopus[®]

Adansonia est distribué en version électronique par / Adansonia is distributed electronically by:

- BioOne® (http://www.bioone.org)

Adansonia est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris Adansonia is a fast track journal published by the Museum Science Press, Paris

Les Publications scientifiques du Muséum publient aussi / The Museum Science Press also publish: Geodiversitas, Zoosystema, Anthropozoologica, European Journal of Taxonomy, Naturae, Cryptogamie sous-sections Algologie, Bryologie, Mycologie, Comptes Rendus Palevol

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France) Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40 diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

© Publications scientifiques du Muséum national d'Histoire naturelle, Paris, 2021 ISSN (imprimé / print): 1280-8571/ ISSN (électronique / electronic): 1639-4798

North American species of *Rubus* L. (Rosaceae) described from European botanical gardens (1789-1823)

Abraham VAN DE BEEK

Petenbos 8 3904 BN Veenendaal (The Netherlands) beekavd@xs4all.nl

Mark P. WIDRLECHNER

Iowa State University
Departments of Horticulture and of Ecology, Evolution, & Organismal Biology
360 Bessey Hall, 2200 Osborn Drive, Ames, Iowa 50011 (United States)
isumw@iastate.edu

Submitted on 6 May 2020 | accepted on 6 August 2020 | published on 12 April 2021

Van de Beek A. & Widrlechner M. P. 2021. — North American species of *Rubus* L. (Rosaceae) described from European botanical gardens (1789-1823). *Adansonia*, sér. 3, 43 (8): 67-98. https://doi.org/10.5252/adansonia2021v43a8. http://adansonia.com/43/8

ABSTRACT

Native Rubus were brought from North America to European botanical gardens in the 18th and early 19th centuries, and some were described as new species. Limited knowledge of Rubus in that era, typically combined with brief descriptions, led to many incorrect interpretations, causing much confusion (especially in North America). We established a project to clarify the identity of these confusing species by reviewing types and descriptions along with comparative work involving modern collections. We identified seven putative North American Rubus species named from early European garden collections: R. villosus Aiton, R. vulpinus Poir., R. pensilvanicus Poir., R. flagellaris Willd., R. inermis Willd., R. heterophyllus Willd., and R. argutus Link, and four other names in the early European botanical literature of possible North American origin: R. decumbens Thunb., R. inermis Thunb., R. enslenii Tratt., and R. floridus Tratt. We affirmed the current applications of R. flagellaris, R. argutus, and R. enslenii. Rubus villosus is identical with R. leviculus L.H. Bailey, while the taxon to which R. villosus was generally applied in the 19th century, R. allegheniensis Porter, appears to be identical with R. vulpinus. Rubus heterophyllus Willd. was identified as an earlier name for R. plicatifolius Blanch. Rubus inermis Willd. is identical with R. ulmifolius Schott and must have originated in the Old World. Thunberg's other American Rubus, R. decumbens, can be identified as R. arundelanus Blanch. Rubus floridus remains a puzzle. If its type represents a sample of a determinate flowering branch from a large, mounding dewberry, it is closest to R. grimesii L.H. Bailey, but it could also have been taken from a side-branch from an unknown upright blackberry. Another name for which identity could not be definitively established is R. pensilvanicus. It is allied with R. allegheniensis, but its type is insufficient to determine if it is an extreme form of that species, a related taxon, or a hybrid of it with a species of section Arguti (Rydb.) L.H. Bailey. We propose the name, R. revealii sp. nov. for the corymbose to weakly racemose Arguti previously considered as R. pensilvanicus sensu L.H. Bailey. Herein, we lectotypify R. abactus L.H. Bailey, R. arundelanus, R. decumbens, R. grimesii, R. inermis Thunb., R. invisus (L.H. Bailey) Britton, and R. vulpinus, and designate neotypes for R. argutus and R. heterophyllus.

KEY WORDS
Rosaceae,
Rubus,
Europe,
battology,
European gardens,
lectotypifications,
neotypifications,
new species.

RÉSUMÉ

Les espèces nord-américaines de Rubus L. (Rosaceae) décrites depuis des jardins botaniques européens (1789-1823). Les Rubus indigènes ont été amenés d'Amérique du Nord dans les jardins botaniques européens au XVIIIème et au début du XIXème siècle, et certains ont été décrits comme de nouvelles espèces. Une connaissance limitée de Rubus à cette époque, généralement associée à de brèves descriptions, a conduit à de nombreuses interprétations incorrectes, provoquant beaucoup de confusion (en particulier en Amérique du Nord). Nous avons établi un projet pour clarifier l'identité de ces espèces déroutantes en examinant les types et les descriptions ainsi que des travaux comparatifs impliquant des collections modernes. Nous avons identifié sept espèces putatives de Rubus d'Amérique du Nord nommées d'après les premières collections de jardins européens: R. villosus Aiton, R. vulpinus Poir., R. pensilvanicus Poir., R. flagellaris Willd., R. inermis Willd., R. heterophyllus Willd., et R. argutus Link, et quatre autres noms de la première littérature botanique européenne d'origine nord-américaine possible: R. decumbens Thunb., R. inermis Thunb., R. enslenii Tratt., et R. floridus Tratt. Nous avons confirmé les applications actuelles de R. flagellaris, R. argutus et R. enslenii. Rubus villosus est identique à R. leviculus L.H. Bailey, tandis que le taxon auquel R. villosus était généralement appliqué au XIXème siècle, R. allegheniensis Porter, semble être identique à R. vulpinus. Rubus heterophyllus Willd. a été identifié comme un nom antérieur pour R. plicatifolius Blanch. Rubus inermis Willd. est identique à R. ulmifolius Schott et doit provenir de l'Ancien Monde. L'autre Rubus américain de Thunberg, R. decumbens, est identifié comme R. arundelanus Blanch. Rubus floridus reste un casse-tête. Si son type représente un échantillon d'une branche florifère déterminée d'une grande mûre-monticule, il est le plus proche de R. grimesii L.H. Bailey, mais il pourrait également avoir été prélevé sur une branche latérale d'une mûre verticale inconnue. Rubus pensilvanicus est un autre nom pour lequel l'identité n'a pas pu être définitivement établie. Il est allié à R. allegheniensis, mais son type est insuffisant pour déterminer s'il s'agit d'une forme extrême de cette espèce, d'un taxon apparenté, ou d'un hybride de celui-ci avec une espèce de la section Arguti (Rydb.) L.H. Bailey. Nous proposons le nom, R. revealii sp. nov. pour l'Arguti corymbifère à faiblement racémeux précédemment considéré comme R. pensilvanicus sensu L.H. Bailey. Ici, nous lectotypifions R. abactus L.H. Bailey, R. arundelanus, R. decumbens, R. grimesii, R. inermis Thunb., R. invisus (L.H. Bailey) Britton, et R. vulpinus, et désignons les néotypes pour R. argutus et R. heterophyllus.

MOTS CLÉS
Rosaceae,
Rubus,
Europe,
batologie,
jardins européens,
lectotypifications,
néotypifications,
espèce nouvelle.

INTRODUCTION

Several native *Rubus* plants were brought from North America to European botanical gardens in the 18th and early 19th centuries. Botanists who worked in these gardens described some of them as new species. The combination of limited knowledge of *Rubus* in that era and species descriptions that were often very brief has resulted in many incorrect interpretations by later authors. This has caused much confusion, which continues to the present day.

We established a joint project to clarify the identity of these confusing species. On the one hand, a detailed, critical revision of *Rubus* in North America is overdue, after the prolific publication of new taxa by Bailey in the 1940s (Bailey 1943, 1944, 1945) and a provisional revision of subgenus *Rubus* by Davis et al. in the late 1960s (Davis et al. 1967, 1968a, b, 1969a, b, 1970), followed more recently by three regional treatments of the brambles of the North Central United States by Widrlechner (1998, 2013; Widrlechner & Smith 2008). On the other hand, there has also been an ongoing project to clear up the identity of old names for Rubus taxa of interest to students of the European flora (Beek 2016, 2017). Converging interests of the two coauthors resulted in these investigations into North American brambles in old European horticultural and botanical literature. Our findings are presented in this paper.

MATERIAL AND METHODS

From literature published in the interval between the first edition of Linnaeus' "Species Plantarum" (Linnaeus 1753) and the completion of the monograph "Rubi Germanici" by Weihe & Nees (1822-1827), which marks the starting point of the European discipline of batology, seven putative North American Rubus species were located, described from material cultivated in European gardens: R. villosus Aiton (Aiton 1789: 210), R. vulpinus Poir. (Poiret 1804: 243), R. pensilvanicus Poir. (Poiret 1804: 246), R. flagellaris Willd. (Willdenow 1809: 249), R. inermis Willd. (Willdenow 1809: 249), R. heterophyllus Willd. (Willdenow 1811: 413), and *R. argutus* Link (Link 1822: 60). Early authors published additional names of *Rubus* of possible North American origin, but uncertain provenance. Because these could be synonyms or homonyms of the taxa mentioned above, they were also investigated. They include two species in Thunberg's "Dissertatio de Rubo": *R. decumbens* Thunb. (Thunberg 1813: 5) and R. inermis Thunb. (Thunberg 1813: 9) and two in Trattinnick's monograph on the Rosaceae, R. enslenii Tratt. (Trattinnick 1823: 63) and R. floridus Tratt. (Trattinnick 1823: 73).

All relevant literature about these taxa was investigated and, whenever extant and available, original specimens were examined. If no original specimens were extant, illustrations or photos of these or later collections by the original author were consulted. Interpretations by later botanists were checked

and are discussed herein. Since there has been much confusion about many of these names, not only were later synonyms evaluated but also later homonyms.

Because older literature is often confusing with respect to nomenclatural standards, we kept strictly to the rules of the ICN (Turland et al. 2018) in our decision-making.

RESULTS AND DISCUSSION

Rubus villosus Aiton

In Hortus Kewensis or a Catalogue of Plants Cultivated in the Royal Botanic Garden at Kew, 2: 210 (Aiton 1789). — Lectotype designated by Bailey (1923: 166): BM (BM 000583294) (Fig. 1).

R. leviculus L.H. Bailey, Gentes Herbarum 5: 390 (Bailey 1943). — Holotype: Clemson College, Pickens County, South Carolina, 7.VI.1934, M.A. Rice 536, BH (Fig. 2).

R. missus L.H. Bailey, Gentes Herbarum 5: 344 (Bailey 1943). — Holotype: near Clarksville, Mecklenburg County, Virginia, 11.V.1938, L.H. Bailey 397, BH.

Context

In 1789, Aiton published a new Rubus species which grew in Kew Gardens under the name Rubus villosus (Aiton 1789: 210). Actually, it was Solander who originally catalogued and gave the name to this Rubus and Aiton who published it (Blanchard 1911: 431; Stafleu & Cowan 1976: 25). A specimen of it has been conserved in the herbarium of the British Museum. Bailey (1923: 166) selected it as the type and provided drawings of it in Bailey (1898: 372) and a photo in Bailey (1923: 166). It is presently conserved as BM000583294. So, fortunately there is a type specimen to help to clarify its identity. Nevertheless, the history of this name and its various interpretations over time are complex.

J. F. GMELIN

Soon after Aiton's publication of *R. villosus*, Gmelin (1791) noted that the epithet was already used by Thunberg (in Murray 1784: 475) for a species from Japan. Therein, Thunberg speculated whether R. villosus Thunb. might be identical with R. corchorifolius L. f. (Linnaeus 1781: 263), but this does not make his name invalid (ICN, Turland et al. 2018: art. 36.1, last sentence), even now that it is generally accepted that they are indeed identical. Consequently, R. villosus Aiton is a later homonym and thus illegitimate. Realizing this, Gmelin proposed a new name for R. villosus Aiton: R. serratus J.F. Gmel. (Gmelin 1791: 856). Though this publication was well known, it did not play a significant role in the various debates about R. villosus Aiton. Bailey (1944: 521) even stated that the identity of R. villosus was irrelevant because it is an illegitimate name, while failing to account for its legitimate replacement.

In the index of the volume of the 13th edition of the Systema Naturae, Gmelin (1792: 1616) failed to mention the name R. serratus, but instead used R. erectus. It is unclear why Gmelin did so; this created a new, illegitimate synonym for R. serratus if it was not a mere error.

There also exists a later homonym of *R. serratus* J.F. Gmel.: R. serratus Boul. & Letendre in Boulay (1873: no. 5), which is a synonym of R. winteri (P.J. Müll. ex Focke) Foerster (1878: 100).

PORTER & BAILEY

Nineteenth-century authors generally used the name R. villosus Aiton for the highbush blackberry common in the eastern parts of North America. They neglected both Thunberg's earlier homonym and also the legitimate name, R. serratus J.F. Gmel.

Near the close of the 19th century, Porter (1890: 15) made new investigations into this taxon and concluded that it consisted of two distinct varieties: alongside the lowland var. villosus, he acknowledged a var. montanus from mountainous regions. He elevated the latter to the species level some years later as R. montanus (Porter) Porter (1894: 120). When he discovered that the epithet montanus had already been used for a European species, he renamed his species to R. allegheniensis (Porter 1896: 153).

Bailey started his critical work on Rubus in earnest only a few years later. Soon he discovered that R. villosus was not identical with the taxon for which the name had widely been used, the highbush blackberry (Bailey 1898: 366, 367). Therefore, the latter was in need of a new name, and Bailey chose for it R. nigrobaccus L.H. Bailey (1898: 379; type: see below under R. sativus [L.H. Bailey] Clark). After further research, he concluded that Porter's (1896) division of R. villosus into two species was not tenable (Bailey 1923: 185). The mountain form, R. allegheniensis, was only a habitat modification of the lowland form, R. nigrobaccus (heterotypic synonym of R. villosus auct. non Aiton). Joining both taxa to one species, he treated them from that point forward as R. allegheniensis Porter, as it was the oldest legitimate name in his view.

It is this name that came into common use in the 20th century up until now for one of the most common brambles of the eastern and central United States and eastern Canada. Bailey (1925: 288) indicated a provisional type: "Rubus villosus, Ait., var. montanus, mihi Pocono Summit. Monroe Co, Penns. Aug. 15/89" NY (NYBG 5990) (iso-, PH[PH00040760]). Later, this type was formally confirmed by Bailey (1944: 522).

The identity of R. Villosus Aiton

Though it was clear to Bailey that R. villosus Aiton was not identical with R. allegheniensis, it was not easy to connect it to any of the known North American species of *Rubus*. Bailey (1898: 339) initially thought it was identical with R. flagellaris Willd. (at that time, incorrectly called R. canadensis L., until Bailey's discovery, after checking the type of *R. canadensis*, that R. canadensis is a totally different species; see Bailey 1943: 243; 1944: 473-475). Brainerd (1900: 25, 27) followed him in this initial interpretation, and Blanchard was also initially of this opinion (1906a: 148). Rydberg (1913: 472; 1915: 149) thought R. villosus to be identical with R. plicatifolius Blanchard (1906a: 149), which Bailey later (1923: 167) supported with some hesitation. Later, Bailey (1944: 521) again supposed this identification might be right but was uncertain.



Fig. 1. — Leaves of type of $\it Rubus\, villosus\, Aiton\, unfolded\, (editing\, Abraham\, van de\, Beek)$. Scale bar: 1 cm.

After our examination of Bailey's lectotype of *R. villosus* Aiton, nine characters turned out to be critical for its identification:

- a. The cane prickles are very weak.
- b. The stem looks like a trailer, as Bailey (1898: 373; 1944: 521) already noted.
 - c. The stems are only 2 mm wide, even the mature floricane.
- d. The leaves are very small; the largest terminal leaflet is only 3.7×2.4 cm.
- e. The leaves are broader than it seems at first sight. The margins are folded so that the bases look cuneate. The original shape of the best terminal leaflet was restored by projecting the folded margin outward. By doing so, an almost elliptical leaflet appears (Fig. 1).
- f. The leaves are slightly hairy adaxially and rather hairy abaxially, though less than might seem from the unexpanded leaves at the tip of the primocane.
- g. The inflorescence has only one flower. Of course, this could be due to unfavorable growing conditions or collecting an atypical inflorescence, but it should be accounted for in combination with the other characteristics.
 - h. The pedicels have some short, stipitate glands.

i. The ovaries are provided with hairs like the rest of the plant. Mr. Fred Rumsey (BM) kindly checked the last two characteristics.

The combination of a-d excludes species of the highbush blackberries of the *Canadenses* (L.H. Bailey) L.H. Bailey, *Arguti* (Rydb.) L.H. Bailey, and *Alleghenienses* (L.H. Bailey) L.H. Bailey. Taken together, they point explicitly to the *Procumbentes* (Rydb.) L.H. Bailey. The single flower clearly supports this conclusion as well. So the question can be narrowed to which members of the *Procumbentes* have pedicels bearing stipitate glands, canes with small, sparse prickles, and coarsely serrate leaflets bearing soft abaxial hairs? A search through keys in Davis *et al.* (1968b) and Widrlechner & Riley (2017) and a review of Bailey's treatments of potential candidates led us to the two taxa that seemed most likely:

- a. *R. invisus* (L.H. Bailey) Britton, of which the serrature is very similar to the type of *villosus*, and
- b. *R. leviculus* L.H. Bailey (1943: 390) which seems to correspond better, at least if *R. missus* L.H. Bailey (1943: 344), with its 5-nate leaves, is included within this species (Widrlechner 1998: 436, 439). It also bears few to many short stipitate glands on its pedicels much like *R. villosus*.

We should note that although *R. plicatifolius* was proposed as a candidate by Blanchard according to Bailey (1944: 521), by Rydberg (1913: 472; 1915: 156), and by Bailey himself (Bailey 1923: 167; 1925: 244), it lacks stipitate glands and soft hairs on the underside of its leaves, which have an obviously plicate appearance, much like the European taxon, *R. plicatus* Weihe & Nees. The type of *R. plicatifolius* is (Widrlechner 1998: 440, lectotype): Wells Beach Depot, York County, Maine, 14.VIII.1905, *W.H. Blanchard* 477, BH.

It should be noted here that Britton (1893) also cited *R. villosus* var. *humifusus* Torr. & Gray (1840: 455), but he borrowed that epithet from Bailey to whom he explicitly and extensively referred. Bailey did not cite *R. villosus* var. *humifusus*. Thus, the type must be selected from Bailey's specimens.

A new check of the type and other specimens of *R. missus* confirmed its identity with *R. leviculus*. The 5-foliolate leaves of the type are coincidental; other collections of *R. missus* display 3-foliolate leaves, and *R. leviculus* can also occasionally bear 5-foliolate leaves.

Based on Widrlechner (2013) and an examination of more than 80 specimens of these two taxa, key differences between *R. invisus* and *R. leviculus* for eight traits are listed in Table 1. In addition, we measured two additional characters from 58 specimens bearing 1-flowered inflorescences: the length of the shortest 1-flowered inflorescence and the cane diameter at the corresponding node (Table 1). Based on the data presented in Table 1, the type of *R. villosus* at BM corresponds best to *R. leviculus* with few of the characteristic details of *R. invisus*. We conclude that it is identical with *R. leviculus*.

In support of this finding, we discovered a specimen (G00653637) in the De Candolle herbarium of the Geneva Botanical Garden (G-DC) with the label: "Rubus villosus. Sol./ Amer. septentr./ in herb. folia quin./ Kew" (Fig. 3), representing a sample that was sent to De Candolle from Kew. It still has Solander's name as the author. It is a trailer with ternate leaves, which has no flowers, but the label also mentions 5-foliolate leaves. It is a typical example of *R. leviculus*.

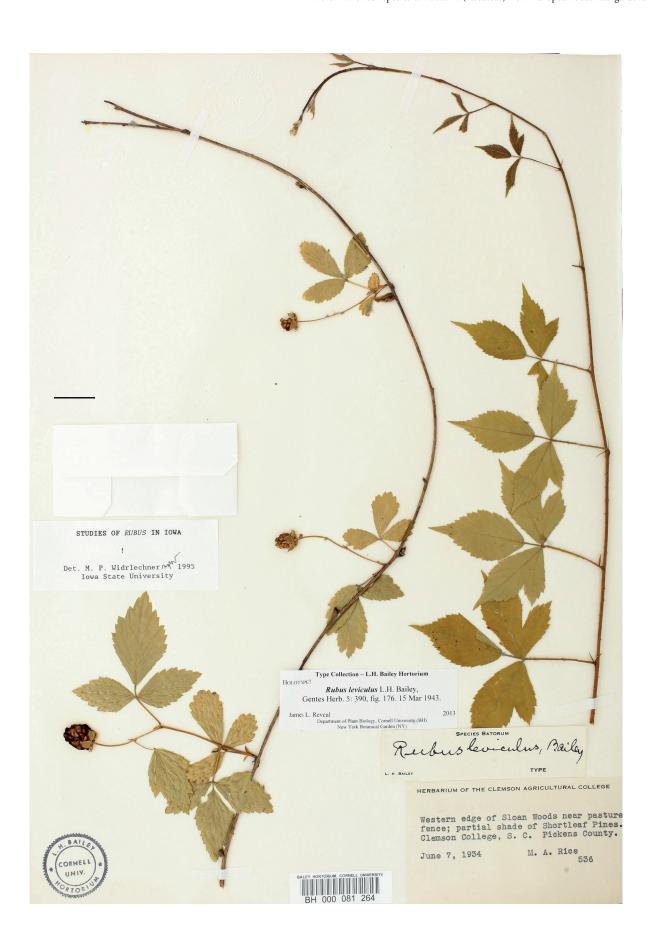


Fig. 2. — Rubus leviculus L.H. Bailey type (M.A. Rice 536, BH). Scale bar: 2 cm.

Table 1. — Comparison of morphological traits among representative specimens of *Rubus invisus* (L.H. Bailey) Britton and *R. leviculus* L.H. Bailey.

Trait	R. invisus	R. leviculus
Floricane diameter Primocane prickle length Largest central primocane leaflet: shape	(2-) ± 4 mm 2.5-3.5 mm Ovate to wide-ovate	± 2 mm 0.5-1.5 mm Elliptic
Largest central primocane leaflet: length	7-9.5 cm	5-8 cm
Longest inflorescences: length	14-23 (28) cm	4-12.5 cm
Longest inflorescences: leaves	3-7, mostly 3-foliolate	1-3 small leaves
Shortest 1-flowered inflorescence: mean length	9.4 cm (N = 35)	5.8 cm (N = 23)
Mean floricane diameter subtending shortest 1-flowered inflorescence	2.6 mm (N = 35)	1.6 mm (N = 23)
Pedicel length	2-6 cm	1.8-4.9 cm
Pedicel pubescence	Pubescent	Thinly pubescent

NINETEENTH-CENTURY HOMONYMS

After Aiton, the name *R. villosus* was twice applied improperly to other taxa during the 19th century. The first instance was *R. villosus* Lasch (1833: 297). The specimen in Lasch's herbarium is *R. umbrosus* (Weihe) Arrh. (Arrhenius 1840: 94), but because he, in the addenda to his original publication (Lasch 1833: 315), stated that *R. radula* Weihe (1824: 152) is identical, his name is a *nomen superfluum* for *R. radula*.

The other example was *R. villosus* Mérat, which Mérat (1843: 440) applied to a species that Vaillant (1727: 174) described with the phrase name 'Rubus montanus repens, sarmentis rotundis, spinis minutissimis munitis, foliis rotundis, utrinque lanatis, superne cinereis, inferne candicantibus, flore albo, fructu nigro, parvo'. Vaillant in turn borrowed this description from Micheli in Tilli (1723: 149).

The validating description is by Micheli, and the type must be selected from his specimens. Usually original specimens for such old names are no longer extant, but Mrs. Chiara Nepi (Botanical Section Natural History Museum University of Florence, FI) found, after a long search, a specimen with its label corresponding to the protologue. It consists of two inflorescences and some primocane leaves, though without a piece of the stem itself, mounted on three sheets. It is wonderful to find such an old specimen consisting of more parts and including primocane leaves.

From the description, one could get the impression that it describes *R. aetnicus* Cupani ex Weston (1770: 258). The specimen in Florence, however, shows that it is a hybrid of that species with *R. ulmifolius* Schott (1818: 42). The petiole is not furrowed; the inflorescence is wider than normal; and the leaves are too large for *R. aetnicus*. Field research in middle Italy conducted by the senior author (cf. Beek 2014: 178) over several years showed that hybrids of *R. aetnicus* and *R. ulmifolius* are abundant in that region in great variation, and the sample fits into that swarm.

Micheli's plant must be considered part of that group and, by consequence, its correct name is *R. collinus* DC (De Candolle 1815: 545). Unfortunately, due to the late validation of Micheli's description, this name is both a later homonym and a later syno-

nym. Nevertheless, it was validly published, and, thus, Micheli's plant is the type of *R. villosus* Mérat:

R. villosus Mérat, lectotype (here designated): *Micheli nr. 32* "Rovo del Monte di S. Giusto/di foglie utrinque lanate", FI[FI050742, FI050743, FI050744], 3 sheets (Fig. 4A-C).

N.B.: None of these 19th-century homonyms has been in common use.

Rubus vulpinus Poir.

In Encyclopédie méthodique, botanique, 6: 273 (Poiret 1804).

LECTOTYPE (here designated). — "Rubus vulpinus H.R.P.; Rubus villosus? Aiton. Michaux.", Poiret in Herb. Moquin-Tandon., Herb. Cosson/Herb. Durand. (lecto-, P[P03141718]).

FINDINGS

Considerable confusion ensued during the 19th century in the possible relationship between *R. villosus* Aiton and another New World blackberry cultivated at the botanical garden in Paris. Jussieu, followed by other botanists allied to the botanical garden in Paris, gave this plant, which was cultivated there since at least 1765, the year of their oldest specimen (Herb. Jussieu 14334), the name *Rubus vulpinus*. However, the botanists in Paris did not publish it validly in the 18th century. The first effective publication was by St. Germain (1784: 155), who mentioned *R. vulpinus* Jussieu within a list, creating a *nomen nudum*. Incidentally, St. Germain's book did not consistently use binominal nomenclature.

Morel (1800: 68) listed the name in the *Tableau* of the botanical garden of Paris and again in the edition of 1801. In a later edition of this list, Desfontaines (1804: 178; also Desfontaines 1809: 107) identified *R. vulpinus* with *R. villosus* Aiton. He mentioned the name as a mere synonym of *R. villosus*, followed in this by Hosack (1811: 49), Green (1814: 127), Steudel (1821: 707), and many other authors. Rees (1819: sub nomine) even stated (in slight error, since we know that *R. vulpinus* had been growing in Paris for at least 54 years at the time), "It appears to have been introduced into the gardens of England and France about the same time, near forty years ago. In the latter, it was called *R. vulpinus*." So, in their opinions, the *R. vulpinus* of the botanical garden in Paris was the same as the *R. villosus* of Kew Gardens.

In contrast, Poiret (1804: 243) discussed the identity of *R. vulpinus* explicitly and argued that *R. vulpinus* cultivated in Paris differed from *R. villosus* by the glabrous adaxial surface of its leaves. Therefore, he provided the name *R. vulpinus* H.Par. in the synonymy of *R. villosus* with a question mark, but included at the end of the article differences between both taxa. We conclude this to be a valid publication of *R. vulpinus* under ICN (Turland *et al.* 2018), art. 36.1, last sentence: Poiret accepted a species with the name *R. vulpinus* and gave a diagnosis, but was unsure that it was not identical with *R. villosus*. Taxonomic doubt does not make a publication invalid.

Soon thereafter, Zeyher (1806: 42) clearly distinguished *R. vulpinus* from *R. villosus* Aiton. He gave both names in his list, identifying *R. villosus* with *R. hispidus* Walter (1788: 149),

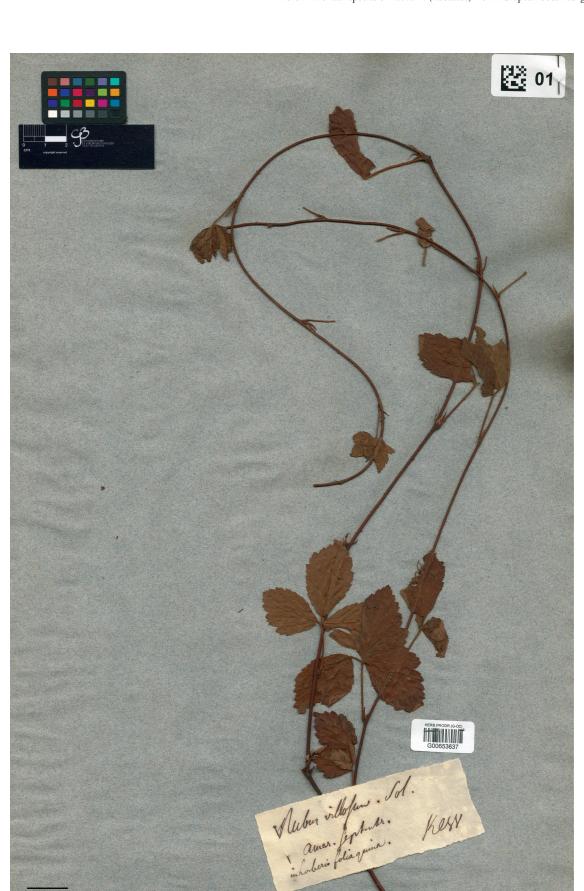


Fig. 3. — Rubus villosus Aiton in G, G-DC(G00653637). Scale bar: 2 cm.



Fig. 4A. - Rubus villosus Mérat type (1), Micheli nr. 32 (FI[FI050742]).



 $\label{eq:Fig.4B} \textit{Fig. 4B.} - \textit{Rubus villosus} \; \textit{M\'erat type (2), Micheli nr. 32 (FI[FI050743])}.$



 $\label{eq:Fig.4C.} \textit{Fig. 4C.} - \textit{Rubus villosus} \; \textit{M\'erat type (3)}, \textit{Micheli nr. 32 (FI[FI050744])}.$

synonym of R. hispidus L. (Linnaeus 1753: 493) and giving R. vulpinus as a separate species.

Seringe (in De Candolle 1825: 563f) considered R. vulpinus to be a variety of R. villosus. He gave as synonyms of R. villosus: R. hybridus Vill. (Villars 1779: 46; 1785: 51), R. glandulosus Bellardi (1793: 230), and R. hirtus Waldst. & Kit. (Waldstein & Kitaibel 1805: 150), and associated the var. vulpinus with R. sprengelii Weihe (1819: 18). However, all of Seringe's identifications lack any basis. Specimens of R. vulpinus are in several collections in the herbarium of the Musée Botanique:

- 1. "Rubus vulpinus H.R.P.; Rubus villosus? Aiton. Michaux." Herb. Poiret in Herb. Moquin-Tandon. Herb. Cosson/Herb. Durand (P03141718).
- 2. "Rubus vulpinus Desf. H.P." Herb. Cosson/Herb. Durand; Herb. Maire (P03141720).
- 3. "Rubus canadensis...cosus fructo rubro Rubi f... facie. Cod. .. H.R. Paris. H.R. Paris. 1765. Julio. Dans les parterres." (Jussieu scripsit); "Rubus vulpinus Juss. h.r.p." (Poiret scripsit). Another label: 'An Rubus villosus Ait. Kew. 2. 210. LW 2.1085. Poir.enc. 6. 243. n. 21?" (Poiret scripsit). Herb. Jussieu 14.334
- 4. "Rubus vulp. Envoyé de Newyorck". Herb. De Lamarck (P00297334).
- 5. "Rubus vulpinus. Hort. Par." "Herb. Richard." "folio tactu molissima semi-tomentosa. sprengelii". Herb Drake.

All these specimens belong to the species presently known as R. allegheniensis Porter. Because the description of R. vulpinus was made by Poiret, the type must be selected from among specimens he had seen. From the list above, this is uncertain for specimens 2, 4 and 5. In addition, specimen 4 was not from the botanical garden in Paris. Thus, the choice of a type falls to specimens 1 or 3. Both are ones that Poiret signed as R. vulpinus, and on both he expressed his doubt about their conspecificity with R. villosus Aiton.

Specimen 3 is only a primocane, and specimen 1 includes an inflorescence with a secondary branch with some simple leaves and beginning compound leaves. Because Jussieu, who first gave the name to the taxon, labeled specimen 3 as R. canadensis, and, moreover, because the inflorescence of specimen 1 is more characteristic for the identification of R. vulpinus, we selected this as the lectotype (P03141718).

Because R. vulpinus is identical with R. allegheniensis Porter, we can conclude this is an earlier legitimate synonym of R. allegheniensis.

Rubus sativus (L.H. Bailey) Clark

Contributions from the United States National Herbarium 1: 159 (Clark 1892). — Rubus villosus var. sativus, The American Garden 11: 719 (Bailey 1890). — Neotype (here designated) (selected by James L. Reveal, 2013): BH, Garden Herbarium of the Cornell University Experiment Station, Rubus nigrobaccus sativus β, Arbutus farm near Ithaca, 26.V.1894, L.H. Bailey (neo-, BH[BH 000 092 458]) (Fig. 5).

FINDINGS

The same taxon that was first described as *R. vulpinus* Poir. was published again as R. villosus var. sativus L.H. Bailey (Bailey 1890: 719); neotype designated here: BH 000 092 458 (Fig. 5).

As Bailey himself argued later (Bailey 1944: 512-514; 1945: 823), this is only a form of R. allegheniensis, as confirmed by the type in Bailey's herbarium. Rubus villosus var. sativus was raised to species rank by Clark (1892: 159); in the next year, she reconsidered her decision (Clark 1893: 264), but this does not invalidate the earlier publication. Koehne (1895: 98) supported its treatment at the species level. Consequently R. sativus (L.H. Bailey) Clark is a later synonym of R. vulpinus and an earlier synonym of R. allegheniensis. Because Bailey (1898: 379) included R. villosus var. sativus in the protologue of R. nigrobaccus, the latter is typified by the type of R. sativus and so it is a homotypic synonym of the latter (ICN, Turland et al. 2018: art. 52.2 e). The sequence of priority for the correct name is thus R. vulpinus (Poiret 1804), R. sativus (Clark 1892), R. allegheniensis (Porter 1896), R. nigrobaccus (Bailey 1898). Brainerd (1900: 26) used the name R. sativus for another taxon, but because he based his name on R. villosus var. sativus Bailey, this name is merely an isonym of *R. sativus* (L.H. Bailey) Clark.

The history of the name can be summarized as follows: a plant from North America was planted in Kew Gardens in 1777 (Aiton 1811: 269). It was named (but not published) Rubus villosus by Solander. A piece was dried and conserved in the herbarium at Kew, now in BM. A second collection was sent to De Candolle, which is now in G-DC. Aiton (1789) formally published this species in the catalogue of Kew Gardens, based on the type in Kew. French botanists in Paris incorrectly assumed that this species was the same as a plant in their botanical garden, which had been named (but not published) R. vulpinus by Jussieu. Due to taxonomic doubt about its identity, Poiret published R. vulpinus as a valid name. However, this confusion continued in the work of later authors until Bailey consulted the type in BM. He rightly concluded that the specimen belonged to a different section than that of R. vulpinus, which, however, he recognized under the name R. allegheniensis. That name has been in common use since the early 20th century for the widespread highbush blackberry which is *R. vulpinus*.

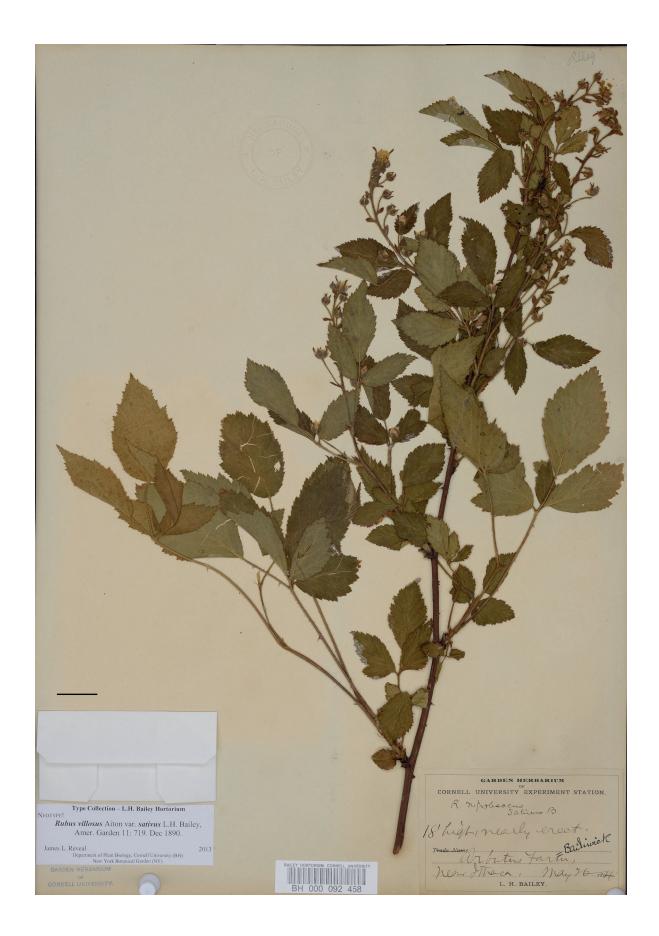
The identity of R. villosus remained obscure and often is considered irrelevant because it is an illegitimate, later homonym of R. villosus Thunb. Its valid replacement name, R. serratus J.F. Gmel., has long been neglected but now must replace the later synonym, R. leviculus.

Rubus pensilvanicus Poir.

In Encyclopédie méthodique, Botanique 6: 246 (Poiret 1804).

R. abactus L.H. Bailey, Gentes Herbarum 2: 452 (Bailey 1932). — Lectotype (here designated), selected by James L. Reveal, 2013 (presumably based on a statement in Bailey [1945: 718]): Connecticut Hill, Ithaca, Tompkins County, New York, 1.VIII.1925, L.H. Bailey 2000 (lecto-, BH[BH 000 078 925, BH 000 078 928]) (Fig. 6A, B).

HOLOTYPE. — P00320321 (P-JU 14335).



 $\label{eq:Fig.5.} \textit{Fig. 5.} - \textit{Rubus sativus} \text{ (L.H. Bailey) Clark neotype, } \textit{L.H. Bailey} \text{ (BH[BH 000 092 458])}. \\ \textit{Scale bar: 2 cm.}$

FINDINGS

The description by Poiret is based on a specimen in the collection of Jussieu. Consequently, since it is extant, this must be considered the holotype (P00320321). As was typical in that era, it only consists of a floricane.

This name was not used for any American bramble until Bailey received a photo of it from M.L. Fernald (Bailey 1945: 704) and identified it with plants that he found at many locations in the eastern United States (Bailey 1945: 702-704). Consequently, R. pensilvanicus suddenly became a rather common species. Bailey (1945: 699) treated R. pensilvanicus as a member of the Arguti. Fernald (1950: 861) and Davis et al. (1969b: 262) followed him in that regard. Notably, Alice et al. (2014) treated essentially all members of section Arguti under this name, believing it to be the oldest name for the pubescent, highbush blackberries lacking stipitate glands, which comprise this section.

However, Bailey based his identification only on a photo, one of insufficient resolution to notice the finest details. Thierry Deroin (P) checked Poiret's type carefully and noted that it bears very short stipitate glands on its pedicels and also some on the inflorescence axis, along with a few longer stipitate glands. This observation was confirmed by high-resolution photos that he sent to us. Consequently, the type does not belong to the Arguti but instead to the Alleghenienses. In sharp contrast, Bailey (1945) made no mention of any glandular trichomes in his detailed description of R. pensilvanicus, consistent with his placement of it within the Arguti.

So, in a single publication, Poiret (1804) named two species that fall within the Alleghenienses: R. vulpinus, which clearly displays the stipitate glands that are a key character of that section and otherwise conforms to the plant widely known as R. allegheniensis, and R. pensilvanicus, with its sparse glandularity less typical of R. allegheniensis. Such a plant might even represent an intersectional hybrid or be an earlier name for R. abactus L.H. Bailey. Rubus abactus has been treated as a close ally of R. pensilvanicus within the Arguti (keying out in the same couplet in Davis et al. 1969b), but a careful examination of the type of *R. abactus* revealed that it also bears short stipitate glands on its pedicels, along with a few longer stipitate glands on its inflorescence axis, as well as having coarser, jagged leaf serrations.

If the type of R. pensilvanicus were more complete, we might be able to place R. abactus in synonymy under it, but there are at least two other options that cannot be fully evaluated without access to both well-developed primocane and floricane samples of *R. pensilvanicus*. First, it is possible that the R. pensilvanicus type represents a weak specimen of R. allegheniensis. Under suboptimal growing conditions, R. allegheniensis can produce smaller, weaker racemes that are atypical and may display few stipitate glands. Alternatively, in contrast to many apomictic North American blackberries, R. allegheniensis is typically sexual (Aalders & Hall 1966; Thompson 1997) with the ability to hybridize with other sympatric taxa. If such hybrids involve *Arguti*, the progeny could present intermediate characteristics.

If one takes a very broad view of *R. allegheniensis*, with its considerable variation generated by being primarily a sexual diploid (Aalders & Hall 1966; Thompson 1997), potentially either of Poiret's names from the 1804 publication could be selected for designating the correct name. However, there are two strong arguments to select R. vulpinus. First, it is a typical representative of the species, while R. pensilvanicus is marginal by virtue of its ambiguous trait expression. Second, the name R. pensilvanicus has been in wide use in eastern North America since 1945 for non-glandular highbush blackberries, and its selection would cause considerable confusion if it would be applied to a common species in the same region, while R. vulpinus has never been so used. So R. vulpinus could be indicated as the correct name for the taxon which has long been called R. allegheniensis Porter. However, because the name R. allegheniensis has been in use for a long time for a very common species, one which is also widely cultivated, a change of name is not desirable. Thus, we plan to submit a proposal for its conservation.

Because of its glandular character, R. pensilvanicus does not belong to the Arguti. Consequently, if the Arguti are considered as one species, as Alice et al. (2014) did, the correct name of that species would be R. argutus Link, because this is the oldest of the legitimate names in that section.

A subsequent question is what must be the correct name of the taxon which was called R. pensilvanicus by Bailey and later authors who followed him. Neither Bailey (1945) nor Davis et al. (1969b) mentioned any synonym and we, too, could not find one. Consequently, a new name must be given to it. In order to avoid any further confusion, we describe this taxon as a new species of section Arguti and not as a new name for R. pensilvanicus sensu L.H. Bailey. We chose the name Rubus revealii sp. nov. to honor the late James Reveal (Miller 2015), who contributed much to the knowledge of Rubus, not only of its American species but also its infrageneric taxa.

Rubus revealii A. Beek & M.P. Widrlechner, sp. nov. (Fig. 7A, B)

Primocane erect or high arching, 5-8 mm in diameter, furrowed, with scattered, fine trichomes mostly on ridges. Prickles 3-5 mm broad at base, almost straight, 4-8 mm long. Stipules 7-18 mm, linear to lanceolate, thinly hairy. Petioles 5-8 cm, appressed-pilose, with 5-10 curved or hooked prickles. Leaves palmately 5-foliolate; surfaces adaxially thinly pubescent, mostly along veins, abaxially densely pubescent, sometimes slightly greyish pilose; margins serrate, teeth rather sharp, moderate, almost straight. Central leaflets elliptic, 7-10.5 cm long, base subcordate, truncate, or rounded, apex rather abruptly attenuate; width-length index 0.53-0.68, subtending petiolules 26-33(40)% of the length of the central leaflet. Petiolules of the lowermost leaflets 0-3 mm. Flowering branches hairy. Inflorescences small (on the type, 8.5-13 cm long), cymose or short racemose. Pedicels 10-40 mm, densely hairy, pricklets 0-8, minute. Sepals ovate, 3-4.5 × 5-8(9) mm, patent to reflexed, hairy, (greyish) green with a white margin, unarmed. Petals typically 12-14 mm long, elliptic-obovate. Stamens patent, as long as or slightly longer than green styles. Anthers, ovaries, and receptacle glabrous.



Fig. 6A. — Rubus abactus L.H. Bailey lectotype, primocane, L.H. Bailey 2000 (BH[BH 000 078 925]). Scale bar: 2 cm.



Fig. 6B. — Rubus abactus L.H. Bailey type, inflorescences, L.H. Bailey 2000 (BH[BH 000 078 928]). Scale bar: 2 cm.

HOLOTYPE. — CM, Flora of Pennsylvania, Lycoming Co.: North of Salladasburg by Pa. 84, 24.VIII.1956, H.A. Davis, T. Davis, & W. Davis 11574 (holo-, CM[CM129946, CM129947]) (Fig. 7A, B).

REPRESENTATIVE COLLECTIONS. — South Africa. Freestate, Clarens, along the R 711, 2.II.2018, *A. van de Beek 2018.01*, L; Kwazulu Natal, road from Vryheid to Louwsburg, 3.2 km before the exit to Louwsburg, southside of the road, 14.II.2018, *A. van de Beek 2018.08*, L.

Swaziland. Along the MR1 south of Piggs Peak, just south of Hawane Christian Life Community Church, 12.II.2018, *A. van de Beek 2018.06*, L.

United States. Illinois, Vermillion County: Middle Fork State Fish & Wildlife Area, 16.VI.1991, *M.P. Widrlechner 308*, ISC. — Pennsylvania, Bucks County: Bowman's Hill, rich wooded slopes along Pidcock Creek, 19.VII.1936, *J. W. and M.T. Adams 2873*, BH; Huntingdon County: 2 miles NE of Franklinville, 14.VIII.1955, *H.A., T., and W.H. Davis 11089*, CM; West Virginia, Monongalia County: Morgantown, in pasture by Evansdale, 11.VII.1947, *H.A. and T. Davis 8192 and 8193*, BH.

DISTRIBUTION. — United States. This species "seems to be confined to the eastern states. Bailey gives the range as from New England to Virginia. It is a common, but not a very productive blackberry in old fields and fencerows in the hills of Pennsylvania and West Virginia." (as stated in Davis *et al.* 1969b: 261).

Southern Africa. *Rubus revealii* sp. nov. is an invasive species in parts of South Africa, especially in the north of Kwazulu-Natal, the east of the Free State, and the southeast of Mpumelanga, and also in Swaziland. In Kwazulu-Natal, it is accompanied by two other invaders from North America, *R. probabilis* L.H. Bailey and *R. originalis* L.H. Bailey. In South African publications (Stirton 1984; Henderson 2001, 2011), these three taxa have usually been considered as forms of *R. cuneifolius* Pursh. More recently, Sochor (2018) correctly conceived the samples of *R. revealii* sp. nov. and *R. originalis* as belonging to the *Arguti*.

PICTURES. — Henderson (2011): 1a and c; 2: the upper series; 3: the upper series.

DISTINGUISHING TRAITS. — *Rubus revealii* sp. nov. has some resemblance to *R. laudatus* A. Berger. However, the latter has more gradually attenuated and broader leaflets, the central leaflets typically with acute tips, and stronger, leafier racemose inflorescences, except at the extreme western edge of its native range, where it can produce heavily armed, short-flaring inflorescences (Widrlechner 2013).

Rubus inermis Willd.

In *Enumeratio Plantarum*: 548 (Willdenow 1809). — Lectotype (here designated): B(BW09891010) (selected by Monaterio-Huelin & Weber 1996: 316, pro holotype).

Rubus inermis Thunb., Dissertatio botanico-medica de Rubo: 7. — Lectotype (here designated): UPS(UPS-THUNB 12270).

FINDINGS

Willdenow described *R. inermis* in his list of plants in the botanical garden of Berlin. He mentioned North America as its nativity. Though his description is rather extensive for that time, it is not sufficient per se for identification of a presently known species. Fortunately, there is a specimen of this taxon made by Willdenow in the Herbarium in Berlin (BW09891010).

Monasterio-Huelin & Weber (1996: 316) selected it as the type. They considered it to be the holotype, but it is not certain that Willdenow solely relied on this specimen. Thus, it is better to consider it as a lectotype.

Various authors (Sudre 1908-1913: 74; Focke 1914: 378; Bailey 1945: 846; Monasterio-Huelin & Weber 1996: 316) have identified R. inermis Willd. as a variety or variation of R. ulmifolius Schott. If this is correct, the plant cannot be of American origin, since R. ulmifolius is native exclusively to the Old World. So Willdenow or his original supplier may have made a mistake. However, in light of Willdenow's explicit statement that the plant came from North America, we decided to revisit the possibility whether any Rubus taxon in North America (including Central America) could correspond to Willdenow's plant. One motivation for doing so was that the acute 3-foliolate leaves found on the type specimen are atypical for *R. ulmifolius* and even more so is its tendency to bear simple leaves and compound leaves with normal central leaflets and two very small, lateral leaflets like 'ears' on the petiole.

Willdenow did not give details of the inflorescence or flowers in his protologue. In his 1811 publication (Willdenow 1811: 411), he wrote that the plant had not yet flowered. Willdenow's successor in Berlin, Link (1822: 62) noted that the plant had perished but resembled *R. caesius* L. and associated it with *R. flagellaris*. Seringe (in De Candolle 1825: 559) conceived the plant as a variety of *R. flagellaris*. It is certainly not *R. flagellaris*, not even a variety of it, but it is clear that early interpreters sought its identity among small, trailing brambles. However, there is no similar plant in North or Central America, not even within other *Rubus* subgenera.

Further investigations in *R. ulmifolius* Schott revealed that young or secondary sprouts sometimes produce leaves resembling those of Willdenow's plant, with the same 'ears' and trilobate simple leaves. This is especially true of plants collected in the eastern part of its native range, leading us to the conclusion that *R. inermis* Willd. is a specimen representing an uncommon developmental phenotype of *R. ulmifolius* and by consequence taxonomically, but heterotypically, identical with *R. inermis* Pourret (Pourret 1788: 326; lectotype (designated by Beek 1979): MAF[MAF 3168]; syntype: P[P02521232]).

The same taxon was once again published with the same name by Thunberg four years later: *R. inermis* Thunb. (Thunberg 1813: 6, 9). Because Thunberg presented his *R. inermis* explicitly as a new species (Thunberg 1813: 7), a type must be selected from his herbarium (UPS-THUNB 12270).

This entity is taxonomically identical with *R. inermis* Pourret, but heterotypic.

Rubus inermis Pourr. is an older legitimate name of R. ulmifolius. Because R. ulmifolius is a very common blackberry, and the name has been in use for a very long time, a proposal for its conservation is in preparation (cf. Beek 2016).

Rubus flagellaris Willd.

In Enumeratio Plantarum: 549 (Willdenow 1809).

LECTOYPE (designated by Bailey 1923: 159). — B[BW09893010].

FINDINGS

A specimen of Willdenow's is in herbarium B. Bailey (1943: 247f) extensively dealt with it and selected it as a type. Because it is not certain that it is the only specimen that Willdenow used, it must be treated as a lectotype (BW09893010).

The type is a good collection, and it is without doubt what is presently conceived under this name, after Bailey's conclusions (1923: 234; earlier, 1898: 368, he was uncertain about its identity). It is also clear that it is not identical with R. serratus J.F. Gmel. (homotypic synonym of *R. villosus* Aiton), which is much more densely pubescent and bears stipitate glands.

It is important to note that if the Procumbentes are considered as one species, as Alice et al. (2014) essentially did in their synonymy for R. flagellaris, the correct name of that species becomes R. serratus J.F. Gmel., since its publication predated that of R. flagellaris by 19 years.

Rubus heterophyllus Willd.

In Die wilde Baumzucht: 413 (Willdenow 1811).

Rubus plicatifolius Blanch., Rhodora 8: 149 (Blanchard 1906a). -Lectotype, designated by Widrlechner (1998: 440): Wells Beach Depot, York County, Maine, 14.VIII.1905, W.H. Blanchard 477,

NEOTYPE (here designated). — The photo in Bailey, Gentes Herbarum 1: 162 (1923). A drawing of the type was printed in Bailey (1945: 773).

FINDINGS

The original specimens that were attributed to this name at B have been lost. Bailey (1923) obtained a photo and a drawing of a specimen from B, which was only a young primocane. Bailey did not formally select it as a lectotype. Since it is no longer extant, we choose his photo as the new type. Though it was created from original material, the photo itself was made in the 20th century and, thus, is a neotype (photo in Bailey 1923: 162).

To begin with, we considered whether R. villosus Aiton and R. heterophyllus might be identical. Both have coarsely serrate leaves and bear weak prickles. However, the teeth of the leaves of *R. heterophyllus* are much sharper than those of *R. villosus*. Most notably, however, Willdenow wrote in his protologue that its leaves are glabrous, which does not correspond with the type of *R. villosus*. In addition, some of the terminal leaflets of R. heterophyllus are ovate and not shouldered like those of R. villosus. We conclude that they are not identical.

Many 19th-century authors (De Candolle & Sprengel 1820: 507; Steudel 1821: 706; Trattinnick 1823: 15; Dietrich 1837: 523; Heinhold 1840: 523) identified R. heterophyllus with R. villosus Torr., while explicitly excluding R. villosus Aiton. By doing so, they supposed that Torrey had a different view of R. villosus than did Aiton. If they gave a specific reference, it was to Torrey (1819: 47), where he only presented a list of names, and did not claim that he differed from Aiton in his species concept. So their interpretations do not help clarify our understanding of *R. heterophyllus*.

Miquel (1867: 34) speculated whether R. heterophyllus might be R. thunbergii Siebold & Zucc. (Siebold & Zuccarini 1835: 18), heterotypic synonym of R. hirsutus Thunb. (Thunberg 1813: 7), which is certainly not correct: *R. hirsutus* has pinnate leaves, which are very hairy on both sides. Rydberg (1913: 473; 1915: 157) was mistakenly convinced that R. heterophyllus was R. villosus var. michiganensis F.W. Card ex L.H. Bailey (1898: 374) which is synonymous with *R. roribaccus* Rydb. (Rydberg 1901: 498) (Widrlechner 1998: 438). That species has more substantial armature and softly pubescent leaves.

Bailey (1923: 162) supposed that R. heterophyllus might be R. recurvans Blanch. (Blanchard 1904: 224) but proposed to drop the name as a nomen incertum (Bailey 1945: 775) as he was inclined to do earlier (Bailey 1923: 162). Palmer & Steyermark (1935: 568) were more positive about its identification as R. recurvans. But later, Bailey refuted this identification definitively (Bailey 1945: 775), and correctly so. The type of R. recurvans is (Widrlechner 1998: 456, lectotype): Middlebury, Addison County, Vermont, 21.VI.1899, E. Brainerd 24a and 24b, GH. If one only takes the pictures of R. heterophyllus into consideration, one might be inclined to accept the conspecificity of R. heterophyllus and R. recurvans. However, the protologue of the former makes such a conclusion impossible. Willdenow's full protologue (1811: 413) (as translated by the senior author) reads as follows:

"12. Rubus heterophyllus, leaves 3- and 5-foliolate, glabrous, ovate-oblong, acuminate, deeply dentated, the stem aculeolate, petals spatulate-lanceolate.

Variable leaf bramble

The home land is unknown, probably North America. A species two feet tall with many prostrate stems. The infertile stems are bluntly angled, with sparse fine hairs, with pointed, somewhat curved prickles provided. The fertile branches are round, glabrous below, with sparse short prickles, the upper part with fine hairs and almost without prickles. The leaves of the infertile stem are digitate, 5-foliolate, those of the fertile stem 3-foliolate, the lateral leaflets deeply lobate. The leaves in the range of the flowers are simple or also 3-foliolate. The leaflets are ovate-oblong, long acuminate, deeply unequally dentate. The petioles of the infertile stem are prickly, those of the fertile stem with fine hairs.

The flowers are white, they come in July, the calyx and the pedicels are white hairy, the petals narrow spatulate, sometimes incised."

The glabrous leaves and the phrases 'two feet tall with many prostrate stems' and 'the petals narrow spatulate' do not correspond with R. recurvans. Its leaves are hairy and, while it can sometimes produce arching primocanes with prostrate rooting tips, it never produces multiple, strongly prostrate stems. Its petals are obovate, but not conspicuously

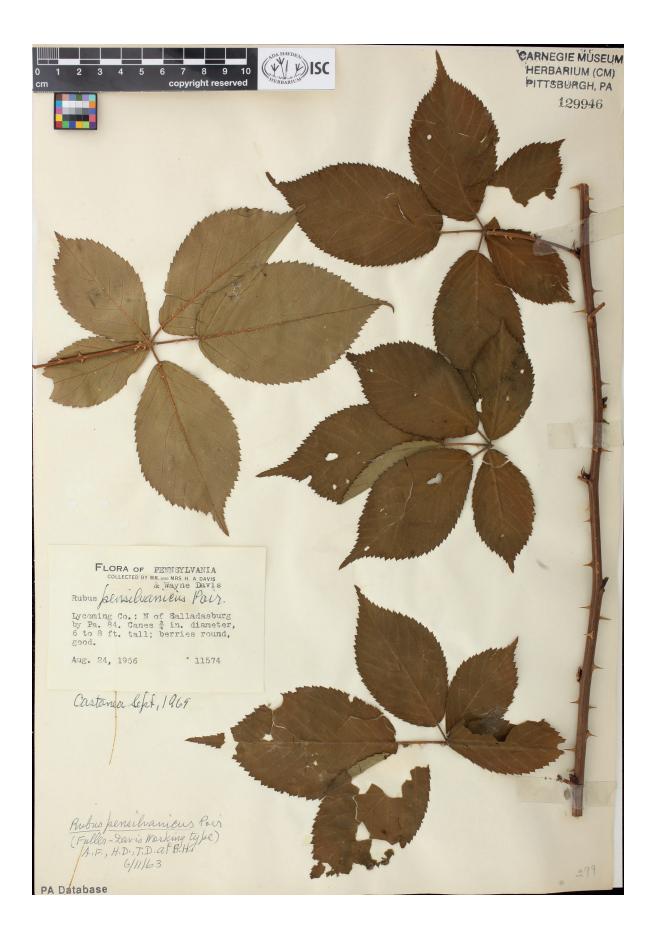


Fig. 7A. - Rubus revealii A. Beek & M.P. Widrlechner, sp. nov. holotype, primocane, H.A. Davis, T. Davis, & W. Davis 11574 (CM[CM129946]).

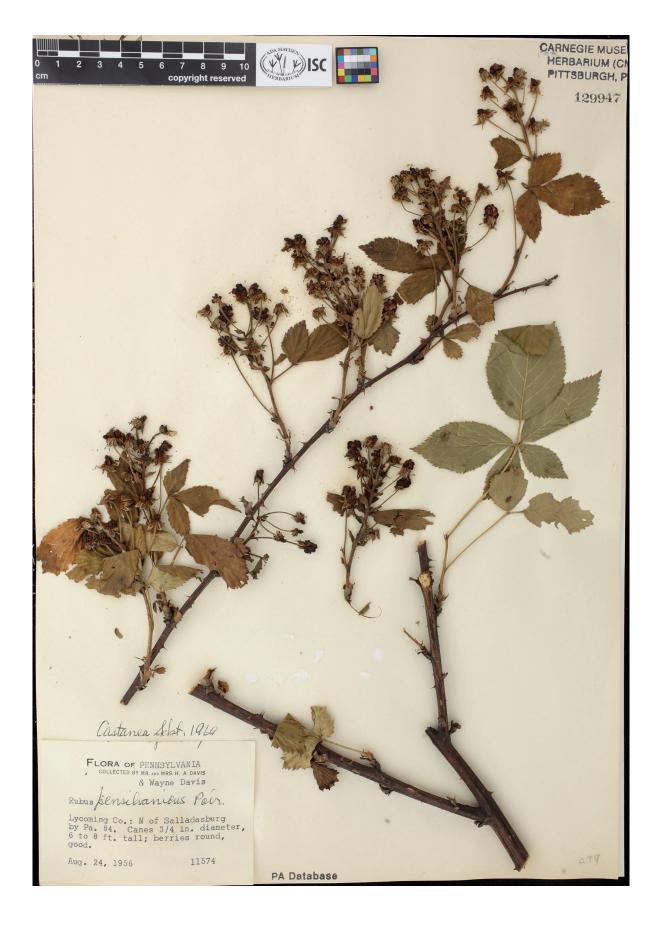


Fig. 7B. - Rubus revealii A. Beek & M.P. Widrlechner, sp. nov. holotype, floricane, H.A. Davis, T. Davis, & W. Davis 11574 (CM[CM129947]).



Fig. 8A. — Rubus decumbens Thunb. lectotype (photo Mats Hjertson), UPP (UPP-THUN 12254). Scale bar: 2 cm.

narrowed (Widrlechner 1998; Widrlechner & Smith 2008). Willdenow's description presents a plant which begins with young upright stems that soon become prostrate, so that the whole bush is not taller than two feet. This excludes the highbush brambles, and points towards a member of the *Procumbentes*, many of which take this form. So the identity of *R. heterophyllus* must be found there. After a thorough investigation of taxa within this section with the combination of stems that are low-arching at the base, leaflets with very sharp and jagged serrations, and narrow petals, only two close matches could be identified: *R. plicatifolius* and *R. pronus* L.H. Bailey (1943: 295, holotype: BH, grassy weedy land by Mountain Lake, Garrett County, Western Maryland, *Bailey 670*).

Bailey distinguished between *R. pronus* and *R. plicatifolius* by the presence of stipitate glands in *R. pronus*, but Davis *et al.* (1968b) included them both among the eglandular *Flagellares* (synonym of *Procumbentes*), separating them by leaf shape. However, even the type of *R. plicatifolius* shows both types of leaves, leading us to compare the type of

R. pronus with R. plicatifolius. After a close check of both taxa, we found that the leaves of the type of R. pronus are more pubescent abaxially, its pedicels are also pubescent and even more: they have some stipitate glands; so Bailey (1943) was correct in his observations. Other samples that are identified as R. pronus display the same characters. Thus, it seems that R. pronus is an unusual (probably rare) species with close affinities to R. plicatifolius. It cannot be established if the plant of R. heterophyllus had stipitate glands. However, Willdenow's remark that it is glabrous refers better to R. plicatifolius (besides the fact that it is more probable that a rather common bramble was collected than a rare one).

Blanchard (1906a) based his publication of *R. plicatifolius* on plants from Wells Beach Depot. A specimen in BH was selected as the lectotype (Widrlechner 1998: 440). Other specimens from this locality are conserved at NY. According to Blanchard (1906a: 150), the most striking characteristic of *R. plicatifolius* is "the plaited or ruffled margins of the leaves," even adding that these make this species "unique among dewberries if not among blackberries in general." It is precisely this characteristic which the picture of *R. heterophyllus* shows. It has the same curved tip of the leaflets as does *R. plicatifolius*, which is due to the plicate margins when dried, just as is the case with European species with plicate leaves, such as *R. plicatus* Weihe & Nees (1822-1827: 14) and *R. affinis* Weihe & Nees (1822-1827: 18).

There is another peculiar characteristic which merits attention. Willdenow (1811) mentioned that the calyx and the pedicels are white hairy. This has always been a stumbling block, for it suggests an affinity with a species of the *Arguti*, even if its leaves are glabrous. However, it supports the identification with *R. plicatifolius*, as Blanchard (1906a: 150) wrote in the protologue "sepals very pubescent or woolly".

In sum, we find no traits that weigh against the conspecificity of *R. heterophyllus* and *R. plicatifolius*, but, more interestingly, there are such peculiar specifics that it appears impossible to not treated them as the same taxon. So the conclusion must be made that *R. heterophyllus* is the correct name of the taxon which has been known as *R. plicatifolius* until now.

Link (1822: 62) referred to the descriptions of Willdenow (1809: 38; 1811: 413) as *R. tetraphyllus*. It is not clear if this is a mere error or a conscious change. In the most extreme interpretation, *R. tetraphyllus* is but a later, homotypic synonym of *R. heterophyllus*. IPNI (2012) mentions it as '*Rubus tetraphyllus* Willd. – Berlin. Baumz., ed. 2 413. 1811', which is a clear mistake.

Rubus decumbens Thunb.

In Dissertatio de Rubo: 5 (Thunberg 1813).

Rubus arundelanus Blanch., Rhodora 8: 176 (Blanchard 1906b). — Lectotype (here designated), selected by James L. Reveal, 2013: Casino in Kennebunkport, Me., 21.VII.1905, W.H. Blanchard s.n., BH (BH 000 079 118) (Fig. 9).

LECTOTYPE (here designated). — UPP (UPP-THUN 12254), 'Rubus decumbens', 'e Niew Jersey. Hultgren.' (Fig. 8A, B).



Fig. 8B. - Rubus decumbens Thunb. type detail (photo Mats Hjertson), UPP (UPP-THUN 12254). Scale bar: 1 cm.

FINDINGS

Thunberg did not provide a full description of this species as a new taxon nor did he refer to any earlier publication. However, the short description in his 1813 overview is sufficient for valid publication, and according to his geographical overview, the species was native to North America (Thunberg 1813: 9).

Two specimens of *R. decumbens* are present in Thunberg's herbarium in Uppsala, numbers UPP-THUN 12254 and UPP-THUN 12255. On the reverse side of 12254 is written: 'e Niew Jersey. Hultgren.', and of 12255: 'Rubus foliis ternatis nudis, caule aculeato. Linn. flor. Suec. 410. Spec. 493. 4.' The latter reference is to *R. caesius* L., but because it is only on the label and not in the publication, it is not of direct relevance for nomenclature. However, for the choice of a type, it might be a good argument to not select it. Other arguments are more decisive: UPP-THUN 12254 is explicitly from North America, which corresponds with the protologue. The same is true for the description of its leaves. Thunberg wrote that these are trifoliate and simple. Number 12254 has both kinds of leaves, but 12255 has only ternate ones. Taking all these factors together, we have chosen UPP-THUN 12254 as the lectotype.

The two specimens are not identical in other significant ways. UPP-THUN 12255 is rather glabrous; its inflorescences have only one or two flowers and none to a few weak prickles. In contrast, 12254 is hairier, both on the abaxial surfaces of its leaves and on its pedicels and sepals; its inflorescences bear five flowers, with rather strong prickles and stipitate glands. We speculate that 12255 might be a weak plant of R. flagellaris, but it is too poor for definitive identification.

The identity of our lectotype, UPP-THUN 12254, is more important. From the way the flowering branches are arranged at the nodes of the floricane, it can be concluded that the sample was taken from a more-or-less horizontal stem. However, the cane bears declined prickles (some slightly decurved) that are up to 4 mm long, sometimes exceeding the diameter of the cane, rather than strongly decurved ones. Such a combination of prickle size and shape is more common in members of the Procumbentes with a mounding habit. Thunberg's choice of the epithet, decumbens, a characteristic which he uses in the description as well, also points towards a plant with a low-arching to mounding habit.

Of the mounding *Procumbentes* found in eastern North America, the only taxon with this same combination of inflorescence form, leaf pubescence, and the presence of stipitate glands and prickles is R. arundelanus Blanch. (Davis et al. 1968b); lectotype (here designated), selected by James L. Reveal, 2013: Casino in Kennebunkport, Me., 21.VII.1905, W.H. Blanchard s.n., BH (BH 000 079 118) (Fig. 9).

The "next-closest" candidate, R. ithacanus L.H. Bailey, typically bears longer, more clearly racemose inflorescences and canes with few prickles (Widrlechner & Smith 2008).

The type specimen of *R. decumbens* was collected by Matthias Hultgren, a Swedish Lutheran clergyman, who sent many plant specimens that he had collected in Pennsylvania, New Jersey, and Nova Scotia to European herbaria in the late 18th century. He wrote on the label that the specimen was collected in New Jersey. We are currently trying to determine the extent of the native range of R. arundelanus and have identified representative collections from

northern Massachusetts, Maine and points to the north and east in Canada. If our lectotype of R. decumbens was collected from New Jersey, it would represent a significant expansion of the known range of this taxon (Davis et al. 1968b). We considered whether the label information for UPP-THUN 12254 might be incorrect; perhaps it was actually collected in Nova Scotia where Hultgren also gathered plants. However, Mats Hjertson (Uppsala) informed us that there is no past evidence that labels by Hultgren might be incorrect. It is more probable that the plant has become extinct in the type locality region. New Jersey and its neighboring states became well-settled in the 18th and early 19th centuries, a time when relatively few extant Rubus populations were sampled. We suspect that a better understanding of the native range will require extensive searching through herbaria, investigating specimens labelled as other members of the *Procumbentes* and perhaps even as R. allegheniensis, given its distinct glandularity. It is remarkable that Bailey also did not relocate R. arundelanus at its type locality in Maine in the 1930s (Bailey 1945: 376). Perhaps it is a very vulnerable plant.

Rubus argutus Link

In Enumeratio plantarum: 62 (Link 1822).

NEOTYPE (here designated). — The photo in *Gentes Herbarum* 1: 278 (Bailey 1925).

FINDINGS

The original specimens of *R. argutus* at B have been lost, but Bailey published photos of them (Bailey 1923: 187; 1925: 278; 1945: 619). In his 1923 publication, he printed photos of two specimens, but only one photo was printed in 1925. It was on this specimen that Bailey focused his attention, and in 1945 (Bailey 1945: 619) he selected it as the type. Since the specimen in B has been lost, we select that photo (Bailey 1925: 278) as a replacement type:

Rubus argutus is a blackberry with 3-5 foliolate, small, narrow leaves with jagged serrations, especially within the inflorescence, and fine pedicels. It is common across much of the southeastern United States (Davis *et al.* 1969b).

Rubus enslenii Tratt. (Fig. 10)

In Rosacearum monographia 3: 63 (Trattinnick 1823).

HOLOTYPE. — Enslen, 'R. flagellaris W.', other label: '1822 I, Rubus trivialis? (Enslenii Tratt.) Amer. bor. Enslen', W(W0080003).

FINDINGS

After reviewing a recent photograph of the type specimen (Fig. 10), we determined that it corresponds well with the interpretation that past American authors (Bailey 1923, 1943; Fernald 1950; Davis *et al.* 1968b) have given to it. Thus, we have no hesitation in accepting the present identification.

Rubus floridus Tratt. (Fig. 11)

In Rosacearum monographia 3: 73 (Trattinnick 1823).

R. argutus var. floridus (Tratt.) L.H. Bailey, Sketch of the Evolution of our Native Fruits: 370, 385 (Bailey 1898).

HOLOTYPE. — *Enslen*, '1822 I, R. floribundus [sic!] Tratt., Amer. bor. Enslen', W(W0079959).

FINDINGS

Bailey obtained both a photo and a drawing of the type (both printed in Bailey 1923: 194f, the drawing also in Bailey 1898: 382). Initially (1898), he considered it as a variety of *R. argutus*. Later he dealt with it as a separate species. Though he noted that the specimen has some glands, he inserted it in a group of mainly glandless brambles under the name *Floridi* (Bailey 1923: 193), later identified with the *Frondosi* (Bailey 1923: 265, 268). Finally (Bailey 1943: 603), he postponed his efforts to identify it. So did Davis *et al.* (1969b), who wrote they considered it as a *nomen nudum* (obviously meaning '*incertum*' or '*ambiguum*', since the species was validly published).

Though Davis *et al.* (1969b) discussed *R. floridus* under the *Arguti*, they suggested that it might fit better within the *Alleghenienses* because Trattinnick (1823) explicitly mentioned its glands. We examined a high-resolution image of the type (Fig. 11), and it does bear long stipitate glands. If *R. floridus* is truly a highbush blackberry, this would support Davis *et al.*'s (1969b) suggested transfer to *Alleghenienses*.

Before accepting this option, the possibility that it belongs to another section, especially the *Procumbentes*, must be excluded. Though Trattinnick (1823) wrote that the stems are 'recti'; Bailey (1945: 604) might have been correct when he stated that this only means straight, not erect. However, the way the inflorescences are positioned on the floricane makes clear that the stem was more-orless erect. On procumbent canes, the angles relative to the subtending cane would not have been so acute. The inflorescences were growing in the same direction as the stem. Consequently, the type was most likely collected from a highbush blackberry, and, because of its stipitate glands, in section *Alleghenienses*.

Davis et al. (1969b) suggested that it would belong to the R. alumnus L.H. Bailey complex if it is situated in the Alleghenienses. Among the currently recognized taxa in that section, it is true that the flaring inflorescences displayed by the type are typically found only in R. alumnus. But the size of its calyx lobes is smaller than those of R. alumnus, and its inflorescence length and hooked prickles also would be atypical for that species (Widrlechner 2013). After an extensive search, we could find no other known member of the Alleghenienses that is a good match — only a few specimens resembling most of the characters presented in the R. floridus type.

Returning to the other option, some large, mounding species of *Procumbentes* produce side branches that get



Fig. 9. — Rubus arundulanus Blanch. lectotype, W.H. Blanchard s.n., BH (BH 000 079 118). Scale bar: 2 cm.

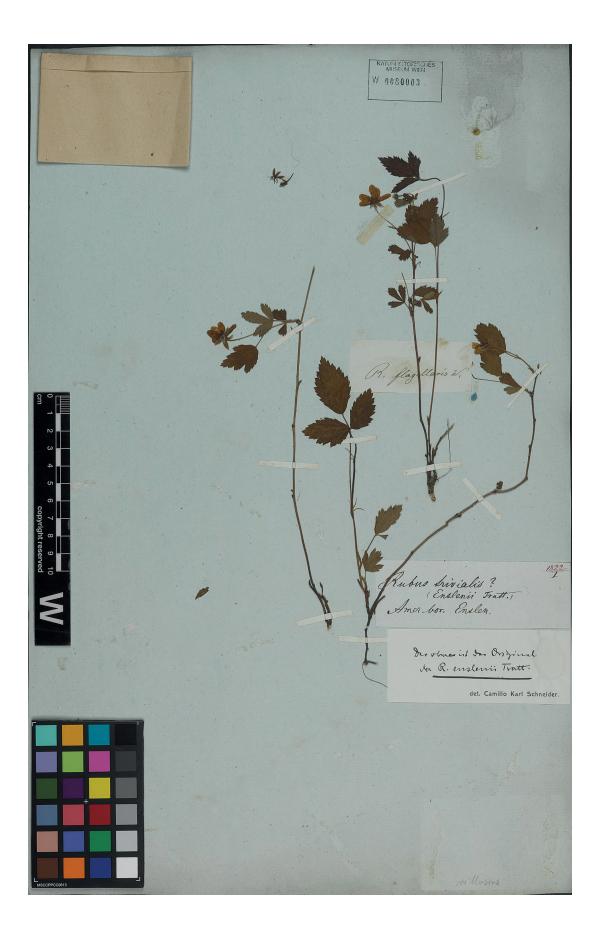


Fig. 10. — Rubus enslenii Tratt. holotype, W(W0080003).

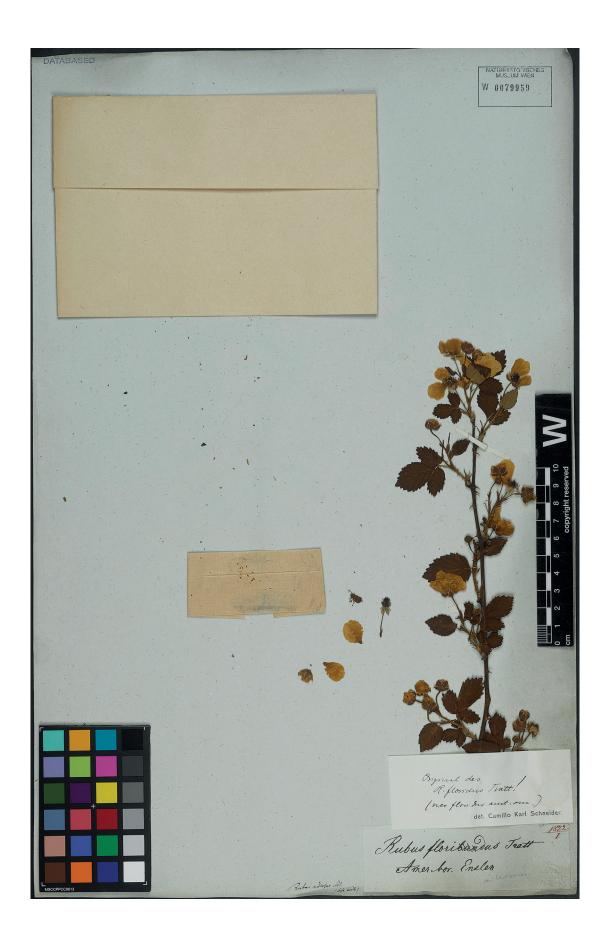


Fig. 11. — Rubus floridus Tratt. holotype, W(W0079959).

caught in vegetation and display determinate development and hooked prickles resembling those of the *R. floridus* type. Thus, we also conducted a search of the mounding, glandular *Procumbentes*. Of this group, the closest match is *R. grimesii* L.H. Bailey, a connection noted in passing by Bailey (1945) but never critically examined.

Rubus grimesii L.H. Bailey (Fig. 12A-C)

In Gentes Herbarum 2: 331 (Bailey 1932).

LECTOTYPE (here designated). — Step 1: designated by Bailey (1943: 406), 0.5 miles west of Williamsburg, James County, Virginia, *L.H. Bailey 36*, BH. Since Bailey's collection 36 was made on two different days; as step 2, herein we choose the eight sheets collected on 16.V.1930, as selected by James L. Reveal, 2013 (BH 000 080 755, BH 000 080 757, BH 000 080 760 [Fig. 12A-C]; BH 000 080 756, BH 000 080 758, BH 000 080 759, BH 000 080 761, BH 000 080 762).

FINDINGS

The lectotype of *R. grimesii* bears flowering branches that somewhat resemble those of *R. floridus*, but they are more curved and the angles at which their inflorescences are held are mostly less acute. In addition, the prickles on their pedicels and inflorescence rachises are finely aciculate, quite unlike the strong, hooked prickles of the *R. floridus* type.

Since Enslen's specimen lacks a primocane, any clear information about plant habit, or even details about geography, we cannot determine whether it is determinate side branch from a mounding dewberry (such as *R. grimesii*), or from an atypical, upright *Alleghenienses* (perhaps even a rare taxon in that section). Thus, we choose to maintain it as a *nomen incertum*.

CORRECT NAMES AND SECTIONAL ASSIGNMENTS

The correct names of all investigated taxa could be established, with the exceptions of *R. pensilvanicus* and *R. floridus*. The relationship of *R. pensilvanicus* to *R. allegheniensis* requires further study. Our understanding of *R. floridus* is likely to remain a mystery unless additional specimens made by Enslen or pertinent field notes can be located. In the following list (ordered as treated above), correct names are printed in **bold**. Signs: \equiv , homotypic, nomenclatural synonym; = heterotypic, taxonomic synonym.

R. villosus Aiton non Thunb. \equiv *R. serratus* J.F. Gmel. \equiv *R. erectus* J.F. Gmel. = *R. leviculus* L.H. Bailey = *R. missus* L.H. Bailey = section *Procumbentes*.

R. vulpinus Poir. = R. sativus (L.H. Bailey) Clark = R. allegheniensis Porter = R. villosus sensu auct. plur. XIX cent. – section Alleghenienses. A proposal for conservation of the name Rubus allegheniensis will be submitted.

R. pensilvanicus Poir. = *R. allegheniensis* Porter? – sectional assignment unclear: *Alleghenienses* or *Arguti*.

R. heterophyllus Willd. $\equiv R$. tetraphyllus Link = R. plicatifolius Blanch. – section *Procumbentes*.

R. inermis Willd. = *R. inermis* Pourret = *R. ulmifolius* Schott – section *Rubus*. A proposal for conservation of the name *Rubus ulmifolius* will be submitted.

R. flagellaris Willd. - section Procumbentes.

R. decumbens Thunb. = *R. arundelanus* Blanch. – section *Procumbentes.*

R. inermis Thunb. = *R. inermis* Pourret = *R. ulmifolius* Schott – section *Rubus*.

R. argutus Link. – section *Arguti*.

R. enslenii Tratt. – section *Procumbentes*.

R. floridus Tratt. is unresolved, most likely a member of section Alleghenienses, less likely a glandular, mounding Procumbentes.

CONCLUSIONS

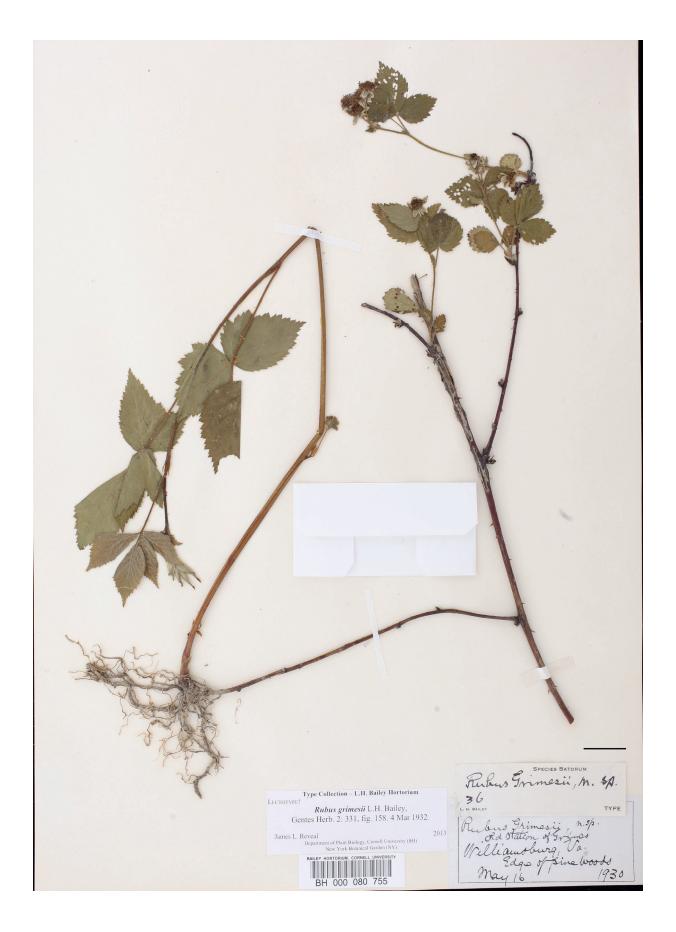
Several American species of *Rubus* were described by authors of the late 18th and early 19th centuries in European botanical gardens. Though specimens or photos of these taxa are extant, the identity of most of them was never clearly established. This remarkable oversight can now be rectified. The well-known *R. villosus* Aiton turned out to be identical with *R. leviculus* L.H. Bailey, while the taxon to which the name was generally applied in the 19th century appeared to be identical with *R. vulpinus* Poir., which is no other species than *R. allegheniensis* Porter. Because *R. allegheniensis* is very common and widely cultivated, a proposal for conservation of that name is due.

Rubus heterophyllus Willd. could be identified with R. plicatifolius Blanch. The other taxon that Willdenow related to America, R. inermis, is identical with an unusual form of R. ulmifolius Schott and must have its origin in the Old World. So there must have been some confusion, which appears not only with Willdenow but also in Thunberg's Dissertatio de Rubo, who described R. inermis once again with reference to America. The other name of Thunberg referring to an American plant, R. decumbens, could only be identified with R. arundelanus Blanch., despite a surprising gap in the currently known distribution of that species.

The only names of which the identity could not be definitively established are *R. pensilvanicus* Poir. and *R. floridus* Tratt. *Rubus pensilvanicus* is allied with *R. allegheniensis*, but the type specimen is insufficient to determine if it is an extreme form of that species, a related taxon, or a hybrid of it with section *Arguti*. The species which has been widely identified in North America as *R. pensilvanicus* is another taxon; herein, we describe it as *R. revealii* sp. nov. *Rubus floridus* remains unresolved. The type was collected either from a determinate, flowering side branch of a large, mounding *Procumbentes* (perhaps allied to *R. grimesii*) or is an atypical side branch from an upright *Alleghenienses*, but clearly not *R. alumnus*, which Davis *et al.* (1969b) believed to be the best candidate.

Earlier identifications of *R. flagellaris* Willd., of *R. argutus* Link, and of *R. enslenii* Tratt., as they are presently commonly used, have been affirmed.

The clarification of these early published names is a substantial contribution to future stability in *Rubus* nomenclature.



 $\textit{Fig. 12A.} - \textit{Rubus grimesii} \; \textit{L.H. Bailey type (first of three of eight sheets)}, \textit{L.H. Bailey 36 (BH[BH 000 080 755])}. \; \textit{Scale bar: 2 cm.}$

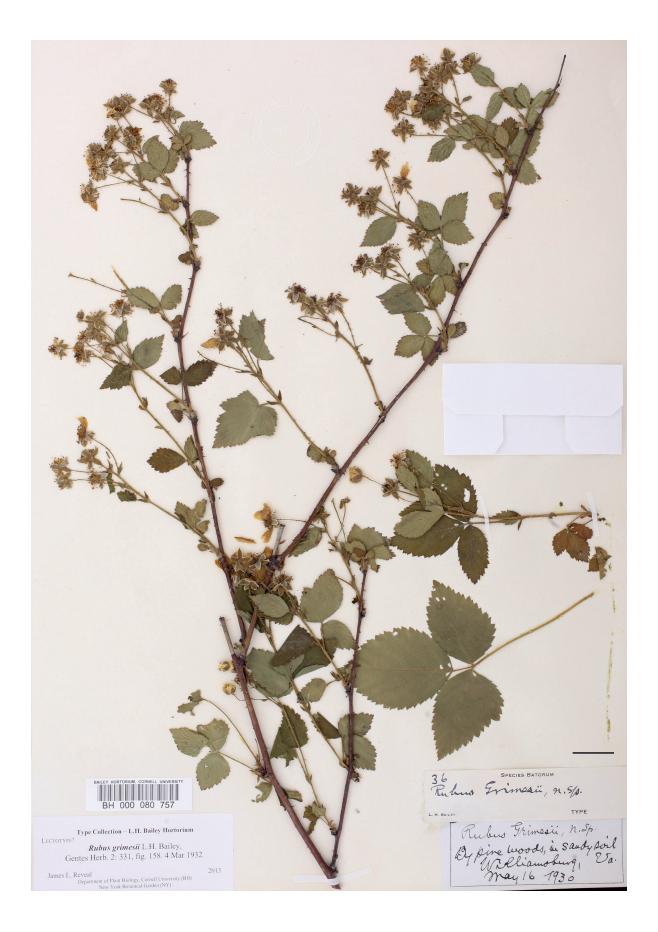


Fig. 12B. — Rubus grimesii L.H. Bailey type (second of three of eight sheets), L.H. Bailey 36 (BH[BH 000 080 757]). Scale bar: 2 cm.

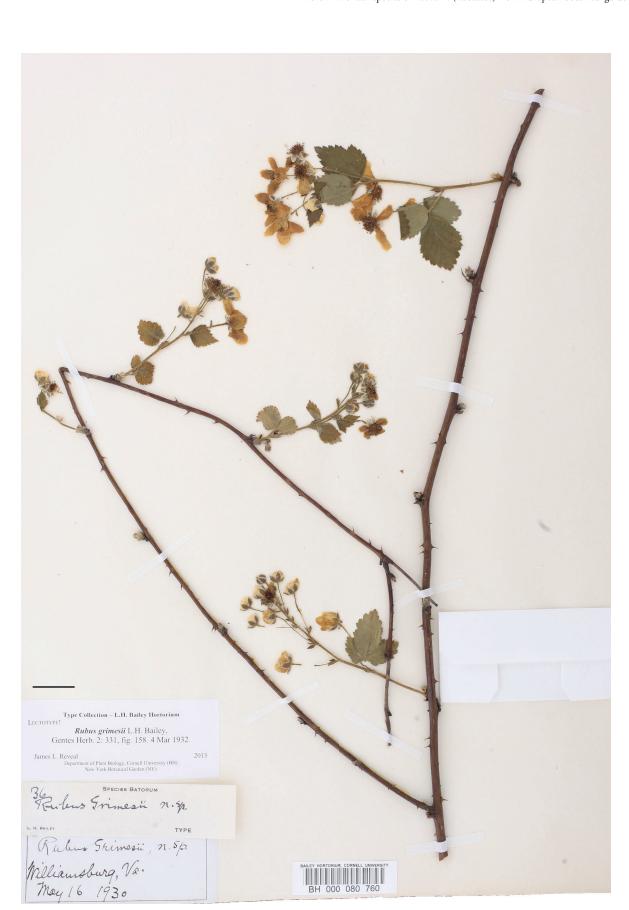


Fig. 12C. — Rubus grimesii L.H. Bailey type (third of three of eight sheets), L.H. Bailey 36 (BH[BH 000 080 760]). Scale bar: 2 cm.

Acknowledgements

We wish to thank the following individuals for their valuable assistance in our research: Cécile Aupic and Corinne Sarthou (P) for information about R. vulpinus and R. pensilvanicus; Thierry Deroin (P) for checking details of the type of *R. pensilvanicus*; Alina Freire-Fierro (PH) for sending a scan and information about the isotype of R. allegheniensis; Laurent Gautier and Nicolas Fumeaux (G) for their information about the label of R. villosus Aiton in G; Mats Hjertson (UPS) for the specimens of Thunberg and for information about Hultgren; Chiara Nepi (FI) for sending scans of the type of R. villosus Mérat and checking details of Micheli's specimen; Matthew Pace (NY) for checking details of R. plicatifolius and R. invisus and for supplying loans of R. abactus and R. pensilvanicus; Tom Zanoni (NY) for his search for the type of R. allegheniensis; Fred Rumsey (BM) for checking details of the type of R. villosus Aiton; Anna M. Stalter (BH) for sending scans of the type of *R. villosus* var. *sativus* and for supplying loans of R. abactus, invisus, leviculus, missus, pensilvanicus, and pronus; Bonnie Isaac (CM) for supplying loans of R. abactus and R. pensilvanicus; Sarah Taylor (CONN) and Frank Frey (GRCH) for supplying loans to help determine the native range of *R. arundelanus*; David McKensie (KSTC) for providing scans and information to help determine the native range of *R. arundelanus*; Michaela Schmull and Anthony Brach (GH) for supplying loans of *R. abactus*, arundelanus, and pensilvanicus; Deborah Lewis (ISC) for assistance in arranging and managing loans and photographing specimens; Maria de Stapf (PMA) for her search for plants which might resemble R. inermis Willd.; Robert Voigt (B) for information about R. heterophyllus and R. argutus; and Heimo Rainer and Christian Bräuchler (W) for the specimen images of R. enslenii and R. floridus; and Laurent Gautier (CJB, Geneva) and Fred Stauffer (G) for the specimen image used as Figure 3. A critical reading of an earlier version of this manuscript by Michael Vincent (MU) is also greatly appreciated, as are insightful critiques provided by Mark Gabel (BHSC) and an anonymous reviewer. The MNHN gives access to the collections in the framework of the RECOLNAT national research infrastructure.

REFERENCES

- AALDERS L. E. & HALL I. V. 1966. A cytotaxonomic survey of the native blackberries of Nova Scotia. *Canadian Journal of Genetics and Cytology* 8: 528-532. https://doi.org/10.1139/g66-063
- AITON W. 1789. Hortus Kewensis or a Catalogue of Plants Cultivated in the Royal Botanic Garden at Kew. Vol. 2. Nicol, London, 460 p. https://doi.org/10.5962/bhl.title.4504
- AITON W. T. 1811. Hortus Kewensis or a Catalogue of Plants Cultivated in the Royal Botanic Garden at Kew. Vol. 3. 2nd ed. Longman etc., London, 432 p. https://doi.org/10.5962/bhl. title.105339
- ALICE L. A., GOLDMAN D. H., MACKLIN J. A., & MOORE G. 2014. — Rubus (Rosaceae) in Flora of North America North of Mexico. Vol. 9. Oxford University Press, New York: 28-56.
- Arrhenius J. P. 1840. Om de karakterer, som kunna tagas af Semina, vid bestämmandat af Rubus-arterne. *Botaniska Notiser* 6: 92-95. https://www.biodiversitylibrary.org/page/5172247
- Bailey L. H. 1890. Notes from a garden herbarium 2. *The American Garden* 11: 719-723.

- BAILEY L. H. 1891. Notes from a garden herbarium 3. *The American Garden* 12: 82-84.
- Bailey L. H. 1898. Sketch of the Evolution of our Native Fruits. MacMillan, New York, 465 p. https://doi.org/10.5962/bhl.title.19869
- BAILEY L. H. 1923. Certain cultivated Rubi. *Gentes Herbarum* 1: 137-200. https://hdl.handle.net/2027/inu.30000046319301
- BAILEY L. H. 1925. *Rubus*: enumeration of the *Eubati* (Dewberries and Blackberries) native in North America. *Gentes Herbarum* 1: 200-297. https://hdl.handle.net/2027/inu.30000046319301
- BAILEY L. H. 1932. The blackberries of North America. Gentes Herbarum 2: 269-423. https://hdl.handle.net/2027/inu.30000046319319
- BAILEY L. H. 1943. *Rubus* in North America. *Flagellares*. *Gentes Herbarum* 5: 229-477. https://hdl.handle.net/2027/uc1.31210001328085
- BAILEY L. H. 1944. *Rubus* in North America. *Eubatus. Alleghenienses. Gentes Herbarum* 5: 507-590. https://hdl.handle.net/2027/uc1.31210001328085
- BAILEY L. H. 1945. Rubus in North America. Eubatus. Arguti. Gentes Herbarum 5: 591-835. https://hdl.handle.net/2027/ uc1.31210001328085
- BEEK A. VAN DE 1979. Taxonomie en nomenclatuur van de koebraam. *Gorteria* 9: 204-208.
- BEEK A. VAN DE 2014. Nomenclatorische en taxonomische toelichting op de naamlijst van de Nederlandse bramen (*Rubus* L.). *Gorteria* 36: 172-196.
- BEEK A. VAN DE 2016. Validations of the *Rubus* taxa in Tournefort's *Institutiones* and their *Corollarium* in later literature. *Adansonia*, ser. 3, 38 (1): 33-51. https://doi.org/10.5252/a2016n1a4
- BEEK A. VAN DE 2017. The *Rubus* (Rosaceae) species described by F. W. Schmidt (1790). *Gorteria* 39: 49-53.
- BELLARDI L. 1793. Appendix ad Floram Pedemontanam. Joannes Michael Briolus, Augustae Taurinorum, 80 +vii p. https://gallica.bnf.fr/ark:/12148/bpt6k976423
- BLANCHARD W. H. 1904. A new species of blackberry. *Rhodora* 6: 223-225. https://www.biodiversitylibrary.org/page/562516
- BLANCHARD W. H. 1906a. Some Maine Rubi. The blackberries of the Kennebunks and Wells I. *Rhodora* 8: 146-157. https://www.biodiversitylibrary.org/page/563025
- BLANCHARD W. H. 1906b. Some Maine Rubi: the blackberries of the Kennebunks and Wells. II. *Rhodora* 8: 169-180. http://www.jstor.org/stable/23293887
- Blanchard W. H. 1911. Rubus of Eastern North America. Bulletin of the Torrey Botanical Club 38: 425-439. https://doi.org/10.2307/2479245
- Brainerd E. 1900. The blackberries of New England. *Rhodora* 2: 23-29. https://www.biodiversitylibrary.org/page/560314
- BOULAY N. 1873. Diagnoses des espèces ou formes de Rubus distribuées par l'Association rubologique. Lille.
- BRITTON N. L. 1893. New or noteworthy Phanerogams. Bulletin of the Torrey Botanical Club 4: 277-282. https://doi.org/10.2307/2476435
- CLARK J. A. 1892. Systematic and alphabetical index of new species of North American Phanerogams and Pteridophytes, published in 1891. *Contributions from the United States National Herbarium* 1: 151-188. https://www.biodiversitylibrary.org/page/368749
- CLARK J. A. 1893. Additions to the index for 1891. Contributions from the United States National Herbarium 1: 258-264. https://www.biodiversitylibrary.org/page/368857
- DAVIS H. A., FULLER A. M. & DAVIS T. 1967. Contributions toward the Revision of the *Eubati* of Eastern North America. *Castanea* 32 (1): 20-37. https://www.jstor.org/stable/4032023
- DAVIS H. A., FULLER A. M. &, DAVIS T. 1968a. Contributions toward the Revision of the *Eubati* of Eastern North America. II. Setosi. Castanea 33 (1): 50-76. https://www.jstor.org/stable/4031973

- DAVIS H. A., FULLER A. M. & DAVIS T. 1968b. Contributions toward the Revision of the Eubati of Eastern North America. III. Flagellares. Castanea 33 (3): 206-241. https://www.jstor.org/ stable/4032218
- DAVIS H. A., FULLER A. M. & DAVIS T. 1969a. Contributions toward the Revision of the *Eubati* of Eastern North America. IV. Castanea 34 (2): 157-179. https://www.jstor.org/stable/4032288
- DAVIS H. A., FULLER A. M. & DAVIS T. 1969b. Contributions toward the Revision of the *Eubati* of Eastern North America. V. *Arguti*. Castanea 34 (3): 235-266. https://www.jstor.org/stable/4032358
- DAVIS H. A., FULLER A. M. & DAVIS T. 1970. Contributions toward the Revision of the Eubati of Eastern North America. VI. Cuneifolii. Castanea 35 (3): 176-194. https://www.jstor.org/stable/4032298
- DE CANDOLLE A. P. 1815. Flore Française. Vol. 5. Desray, Paris, 662 p. https://doi.org/10.5962/bhl.title.112968
- DE CANDOLLE A. P. 1825. Prodromus systematis naturalis regni vegetabilis. Vol. 2. Treuttel & Würtz, Paris, 644 p. https://www. biodiversitylibrary.org/page/153297
- DE CANDOLLE A. P. & SPRENGEL K. 1820. Grundzüge der wissenschaftlichen Pflanzenkunde. Cnoblauch, Leipzig, 646 p.
- DESFONTAINES R. L. 1804. Tableau de l'école de botanique du Muséum d'Histoire naturelle. Brosson, Paris, 238 p. https://doi. org/10.5962/bhl.title.13828
- DESFONTAINES R. L. 1809. Histoire des arbres et arbrisseaux qui peuvent être cultivés en pleine terre sur le sol de la France. Tome 2. Brosson, Paris, 635 p. https://doi.org/10.5962/bhl.title.69561
- DIETRICH F. G. 1837. Neuer Nachtrag zum vollständigen Lexikon der Gärtnerei und Botanik. Ebener'schen Buchhandlung, Ulm, 560 p.
- FERNALD M. L. 1950. Gray's Manual of Botany. 8th ed. American Book Co., New York, 1632 p.
- FOCKE W. O. 1914. Species Ruborum. Monographiae generis Rubi Prodromus. Vol. 3. Bibliotheca Botanica 83 (3). Schweizerbart Stuttgart, 274 p. https://doi.org/10.5962/bhl.title.15533
- FOERSTER A. 1878. Flora Excursiora des Regierungsbezirkes Aachen sowie der angrenzenden Gebiete der belgischen und holländischen Provinz Limburg. Rudolph Barth, Aachen, xxx + 468 p.
- GMELIN J. F. 1791. Caroli à Linné Systema Naturae. Tomus 2, ed. 13. Beer, Lipsiae, 884 p. https://www.biodiversitylibrary.org/ page/25751727
- GMELIN J. F. 1792. Caroli à Linné Systema Naturae. Tomus 2 pars 2, ed. 13. Beer, Lipsiae, 777 p. https://www.biodiversitylibrary.org/ page/25750419
- GREEN J. 1814. Catalogue of plants indigenous to the state of New-York. Transaction of the Society for the Promotion of Useful Arts, in the State New-York. Websters & Skinners, Albany: 91-136.
- HEINHOLD G. 1840. Nomenclator botanicus hortensis. Vol. 1. Arnoldischen Buchhandlung, Dresden/Leipzig, xxii + 888 p. https:// doi.org/10.5962/bhl.title.127506
- HENDERSON L. 2001. Alien Weeds and Invasive Plants: a Complete Guide to Declared Weeds and Invaders in South Africa, Including Another 36 Species Invasive in that Region. Agricultural Research Council, Pretoria, 300 p. (Plant Protection Research Institute Handbook 12).
- HENDERSON L. 2011. Rubus species brambles, blackberries and others. SAPIA News 19: 1-9.
- HOSACK D. 1811. Hortus Elginensis, or a Catalogue of Plants Indigenous and Exotic, Cultivated in the Elgin Botanic Garden, in the Vicinity of the City of New-York. 2nd ed. Swords, New-York, 65 p. https://doi.org/10.5962/bhl.title.112292
- IPNI 2012. The International Plant Names Index (2012). Published on the Internet http://www.ipni.org [accessed 1 February 2019].
- Koehne E. 1895. Just's botanischer Jahresbericht. Systematisch geordnetes Repertorium der botanischen Literatur aller Länder 20.2. Bornträger, Berlin, 630 p.
- LASCH W. 1833. Die Rubus-formen, welche und wie sie um Driesen wildwachsen. Linnaea: Ein Journal für die Botanik in ihrem ganzen Umfange 8: 293-297, 315. https://www.biodiversitylibrary. org/page/99186

- LINK H. F. 1822. Enumeratio plantarum Horti Regii Botanici Berolinensis altera. Vol. 2. Reimer, Berolini, 478 p. https://doi. org/10.5962/bhl.title.66
- LINNAEUS C. VON 1753. Species Plantarum 1. Laurentii Salvii, Holmiae, 560 p. https://doi.org/10.5962/bhl.title.37656
- LINNAEUS C. VON 1781. Supplementum plantarum Systematis vegetabilium editionis decimae tertiae, Generum plantarum editionis sextae, et Specierum plantarum editionis secundae. Orphanothrophei, Brunsvigae, 468 p. https://doi.org/10.5962/bhl.title.555
- MÉRAT F. V. 1843. Revue de la flore parisienne suivie du texte du botanicon pariesienne. Baillière, Paris, 508 p. https://gallica.bnf. fr/ark:/12148/bpt6k985364
- MILLER J. S. 2015. In memoriam. James L. Reveal (1941-2015). Rhodora 117: 282-286. https://doi.org/10.3119/0035-4902-117.970.282
- MIQUEL F. A. G. 1867. Prolusio florae Iaponicae. Annales Musei Botanici Lugduno-Batavi 3: 1-66.
- MONASTERIO-HUELIN E. & WEBER H. E. 1996. Taxonomy and nomenclature of Rubus ulmifolius and Rubus sanctus (Rosaceae). Edinburgh Journal of Botany 33: 311-322. https://doi.org/10.1017/ S0960428600003759
- MOREL J. F. N. 1800. Tableau de l'école de botanique du jardin des plantes de Paris. Didot le Jeune/Fuchs, Paris, 107 p. https:// gallica.bnf.fr/ark:/12148/bpt6k9656491q
- MOREL J. F. N. 1801. Tableau de l'école de botanique du jardin des plantes de Paris. Chez Méquignon, Paris, 107 p.
- MURRAY J. A. 1784. Caroli a Linné equitis Systema Vegetabilium. Ed. 14. Dieterich, Gottingae, 987 p. https://doi.org/10.5962/ bhl.title.549
- PALMER E. J. & STEYERMARK J. A. 1935. An annotated catalogue of the flowering plants of Missouri. Annals of the Missouri Botanical Garden 22: 375-758. https://doi.org/10.2307/2394215
- POIRET J. L. M. 1804. Encyclopédie méthodique. Botanique. Vol. 6. Agasse, Paris, 786 p. https://doi.org/10.5962/bhl.title.824
- PORTER T. C. 1890. New varieties of well known species. Bulletin of the Torrey Botanical Club 17: 15-16. http://www.jstor. org/stable/2476827
- PORTER T. C. 1894. Notes on some plants of our Eastern Flora. Bulletin of the Torrey Botanical Club 21:120-123. https://doi. org/10.2307/2477860
- PORTER T. C. 1896. Rubus montanus Porter. Bulletin of the Torrey Botanical Club 23: 153. https://www.biodiversitylibrary.org/ page/711534
- POURRET P. A. 1788. Extrait de la Chloris Narbonensis. Histoire et Mémoires de l'Académie de Toulouse 3: 297-334.
- REES A. 1819. The Cyclopædia; or Universal Dictionary of Arts, Sciences, and Literature. Vol. 30. Longman, London. https://doi. org/10.5962/bhl.title.59683
- RYDBERG P. A. 1901. Rubus L., in Britton N. L. (ed.), Manual of the Flora of the Northern States and Canada. Henry Holt & Co., New York: 493-499. https://www.biodiversitylibrary.org/ page/39641091
- RYDBERG P. A. 1913. Family 18. Rosaceae. North American Flora 22 (5): 239-533.
- RYDBERG P. A. 1915. Notes on Rosaceae IX. Bulletin of the Torrey Botanical Club 42: 117-168. https://doi.org/10.2307/2479779
- SCHOTT H. W. 1818. Auszüge aus den Berichten und Briefe der auf befehl Sr. Majestät des Kaisers nach Brasilien abgeschickten österreichisschen Naturforscher an den Direktor des k.k. Hof-Naturkabinette Herrn Karl von Schreibers als Referenten des wissenschaftlichen Anteiles der Expedition. Vaterländische Blätter für den östterreichische Kaiserstat I, 4-6: 37-44, 61-67.
- SIEBOLD P. F. VON & ZUCCARINI J. G. 1835. Flora Japonica 1. Apud auctorem, Lugduni Batavorum, 193 p. +100 ill.
- SOCHOR M. 2018. Preliminary taxonomic treatment of eastern South African Rubus. Crop Research Institute, Olomouc, 44 p.
- STAFLEU F. A. & COWAN R. S. 1976. Taxonomic Literature 1. 2nd ed. Bohn, Scheltema and Holkema, Utrecht, 1136 p.

- STEUDEL E. 1821. *Nomenclator Botanicus*. Cottae, Stuttgardtiae/ Tubingae,xvii + 900 p. https://doi.org/10.5962/bhl.title.47064
- ST GERMAIN M. J. J. DE 1784. *Manuel des végétaux*. Delaguette, Paris, 424 p. https://gallica.bnf.fr/ark:/12148/bpt6k6530322v
- STIRTON C. H. 1984. Notes on the genus *Rubus* in southern Africa. *Bothalia* 15: 101-106. https://doi.org/10.4102/abc.v15i1/2.1108
- SUDRE H. 1908-1913. *Rubi Europae*. Lhomme, Paris, 305 p.+ 215 ill. https://gallica.bnf.fr/ark:/12148/bpt6k116160f
- THOMPSON M. M. 1997. Survey of chromosome numbers in *Rubus* (Rosaceae: Rosoideae). *Annals of the Missouri Botanical Garden* 84: 128-164. https://doi.org/10.2307/2399958
- THUNBERG C. P. 1813. Dissertatio botanico-medica de Rubo. Stenhammer & Palmblad, Upsala, 12 p.
- TILLI M. A. 1723. Catalogus plantarum horti Pisani. Tartinium & Franchium, Florentiae, 187 p. https://bibdigital.rjb.csic.es/idurl/1/14084
- TORREY J. 1819. A Catalogue of Plants, Growing Spontaneously within Thirty Miles of the City of New-York. Lyceum of Natural History, New York, 100 p. https://doi.org/10.5962/bhl.title.62356
- Torrey J. & Gray A. 1840. A Flora of North America. Vol. 1. Wiley & Putnam, New York, 711 p. https://doi.org/10.5962/bhl.title.9466
- Trattinnick L. 1823. *Rosacearum monographia* 3. Heubner, Vindobonae, xvi + 171 p.
- Turland N. J., Wiersema J. H. Barrie, F. R., Greuter W., Hawksworth D. L., Herendeen P. S., Knapp S., Kusber W.-H., Li D.-Z., Marhold K., May T. W., McNeill J., Monro A. M., Prado J., Price M. J. & Smith G. F. (eds) 2018. International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Regnum Vegetabile 159. Koeltz Botanical Books, Glashütten. https://doi.org/10.12705/Code.2018
- VAILLANT S. 1727. Botanicon Parisiense ou dénombrement par ordre alphabétique des plantes, qui se trouvent aux environs de Paris. Verbeek & Lakeman, Leide/Amsterdam, 205 p. + 33 ill. https://gallica.bnf.fr/ark:/12148/bpt6k9613290k
- VILLARS D. 1779. *Prospectus de l'histoire des plantes de Dauphiné*. Imprimerie royale, Grenoble, 49 p. https://bibdigital.rjb.csic.es/idurl/1/15535

- VILLARS D. 1785. Flora Delphinalis, *in* GILIBERT J. E., *Caroli Linnaei Systema plantarum Europae* 1. Piestre & Delamolliere, Coloniae-Allobrogum, vii + 127 p.
- WALDSTEIN F. & KITAIBEL P. 1805. Descriptiones et icones plantarum rariorum Hungariae 2. Schmidt, Viennae, 105-220, ill. 101-200. https://bibdigital.rjb.csic.es/idurl/1/11187
- WALTER T. 1788. Flora Caroliniana. Fraser, Londini, 263 p. https://bibdigital.rjb.csic.es/idurl/1/13857
- WEIHE K. E. A. 1819. *Rubus Sprengelii*; ein noch unbeschriebener Strauch des Fürstentums Minden. *Flora* 2: 17-20.
- Weihe K. E. A. 1824. *Rubus* L., *in* Boenninghausen C. M. F. à, *Prodromus florae Monasteriensis Westphalorum*. Regensberg, Monasterii: 149-153. https://doi.org/10.5962/bhl.title.6344
- WEIHE K. E. A. & NEES VON ESENBECK C. G. D. 1822-1827. *Rubi Germanici. Die deutsche Brombeersträuche.* Elberfeld: Schönian'sche Buchhandlung, 120 + 130 p. + 44 ill.
- WESTON R. 1770. Botanicus universalis et hortulanus 1. Bell, London, 384 p.
- WIDRLECHNER M. P. 1998. The genus *Rubus* L. in Iowa. *Castanea* 63 (4): 415-465. https://www.jstor.org/stable/4033996
- WIDRLECHNER M. P. 2013. *Rubus* L. (raspberry, blackberry, bramble), *in* YATSKIEVYCH G. (ed.), *Steyermark's Flora of Missouri*. Vol. 3. Missouri Botanical Garden Press and Missouri Department of Conservation, St. Louis and Jefferson City, MO: 976-977, 979-1004. https://lib.dr.iastate.edu/bot_pubs/84
- WIDRLECHNER M. P. & RILEY B. P. 2017. *Rubus beamanii*, a new name for *Rubus vagus* L. H. Bailey, a glandular dewberry described from Kalamazoo County, Michigan, and recently discovered in Ohio. *Phytoneuron* 2017 (10): 1-10. https://lib.dr.iastate.edu/hort_pubs/32
- WIDRLECHNER M. P. & SMITH W. R. 2008. *Rubus*, blackberries and raspberries, *in SMITH W. R.* (ed.), *Trees and Shrubs of Minnesota*. University of Minnesota Press, Minneapolis, MN: 440-511.
- WILLDENOW L. 1809. Enumeratio Plantarum Horti Regii Berolinensis. Taberna libraria scholae realis, Berolini, 592 p. https://bibdigital.rjb.csic.es/idurl/1/10963
- WILLDENOW L. 1811. Die wilde Baumzucht oder Beschreibung aller im Königl. Botan. Garten etc. bey Berlin im Freien ausdauernden Bäume und Sträucher. Nauck, Berlin, 586 + vii p.
- ZEYHER C. 1806. Verzeichnis sämmtlicher Bäume und Sträucher in dem Grossherzoglich- Badischen Gärten zu Carlsruhe, Schwezingen und Mannheim. Burgerspitals-Schriften, Mannheim, 48 p.

Submitted on 6 May 2020; accepted on 6 August 2020; published on 12 April 2021.