



Twins are not alone: a recircumscription of *Linnaea* (Caprifoliaceae)

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Abstract

The genus *Linnaea* is reviewed and expanded to include the genera *Abelia* (excluding section *Zabelia*), *Diabelia*, *Dipelta*, *Kolkwitzia* and *Vesalea*, making it monophyletic and comprising 16 species. The history of the generic name is discussed. An updated description for the genus *Linnaea* is provided and new combinations or names for all taxa are provided in *Linnaea*.

Key words: botanical history, genus concepts, inflorescence structure

Introduction

Linnaea borealis Gronovius ex Linnaeus (1753: 631) was named in honour of Carolus Linnaeus to whom we owe the system of binomial nomenclature. The name was first coined by Dutch botanist Jan Frederik Gronovius (in Linnaeus 1737), because it was Linnaeus's favourite plant '*Planta nostra*', which was later adopted by Linnaeus himself in his *Species plantarum* (1753). It is currently restricted to a single species, which may be considered unfortunate, because it honours such an important botanist. Ricket (1941) wrote that 'Linnaeus regarded it as his solemn duty to perpetuate the names of great botanists in generic names', and even though at the time it was argued that there often is no connection between the name and the botanist, 'there will be such charm in the association that it will never fade from memory'. Ricket (1941) provided the following example: '*Linnaea* was named by the celebrated Gronovius and is a plant of Lapland, lowly, insignificant, disregarded, flowering but for a brief space—from Linnaeus who resembles it'. This was of course meant ironically, but the name of Linnaeus was perpetuated in the name for the flower in several languages, and Linnaeus used the flower in his coat of arms after his knighthood and was frequently depicted with *Linnaea*.

Brown (1818) described some new plants in Abel Clarke's 'Narrative of a Journey in the Interior of China', where he named a particular ornamental shrub in honour of the traveller: *Abelia* Brown (1818: 376). Martens & Galeotti (1843) described two species from Oaxaca, Mexico, which they placed in their new genus *Vesalea* Martens & Galeotti (1843: 242), but they stated that the new genus has affinity with Brown's *Abelia*. Vatke (1872) proposed several *Abelia* species be treated in *Linnaea*, because of their similarity in flower structure. In his series of new plants from Asia, Maximowicz (1878) described the genus *Dipelta* Maximowicz (1878: 50), but among other Caprifoliaceae he observed similarities with *Abelia*. *Dipelta* was described on the basis of having two accrescent bracts beneath the flowers that become wing-like in fruit, but species of *Abelia* and *Linnaea* also have such bracts, although not always as conspicuous and not necessarily morphologically equivalent (Landrein & Prenner 2013). When describing the new genus *Kolkwitzia*, Graebner (in Diels 1901: 593) pointed out that his new genus has clear morphological similarity to *Linnaea*, but was maintained separate from that genus on the basis of the fruit characteristics. In the same paper Graebner (in Diels 1901: 593) transferred many *Abelia* species to *Linnaea*, which was continued by Diels (1912). Wittrock (1907) focussed on the species *Linnaea borealis*, which he concluded was a polymorphic

species in which he recognised over 200 forms based on foliar and floral characteristics. In spite of these efforts to enlarge *Linnaea* in the early 20th Century, this was not followed in subsequent treatments, and *Abelia* became well established in floras and horticulture (e.g. Rehder 1911, Ohwi 1965, Villareal & De la Rosa 2000, Cubey *et al.* 2013).

Phylogenetic studies of Caprifoliaceae *s.l.* and related families in Dipsacales have resulted in a much better understanding of generic relationships of the family (Pyck 2001, Bell *et al.* 2001, Winkworth *et al.* 2008, Landrein 2010a, Jacobs *et al.* 2010), and in particular those genera close to *Linnaea* (tribe Linnaeae). In most studies, monophyly of the *Linnaea* clade was supported, although *Zabelia* (Rehder) Makino (1948: 175), traditionally included in Linnaeae and sometimes considered to be a section of *Abelia*, was not found to belong there. The position of *Zabelia* was either suggested to be near *Morina* Linnaeus (1753: 28; Jacobs *et al.* 2010, 2011) or its position was not resolved (Landrein *et al.* 2012, Landrein & Prenner 2013). Another genus associated with *Linnaea* in the past, because of some morphological similarity, is *Heptacodium* Rehder (1916: 617), but molecular results have shown that genus to be related to *Lonicera* Linnaeus (1753: 173) and its relatives (tribe Caprifolieae) (Jacobs *et al.* 2011). Landrein & Prenner (2013) interpreted inflorescences of *Heptacodium* as intermediate between the tribes Linnaeae and Caprifolieae.

In the *Linnaea* clade (excluding *Heptacodium* and *Zabelia*), the genus *Abelia* was polyphyletic: the Mexican species formed a clade (which can be treated as *Vesalea*) and two independent Asian clades. The clade including the type species, *A. chinensis* Brown (1818: 376), remained *Abelia* and the other clade was named *Diabelia* Landrein (2010b: 35). In all recent analyses (Jacobs *et al.* 2010, Landrein *et al.* 2012) the genera *Abelia* (excluding sect. *Zabelia*), *Diabelia*, *Dipelta*, *Kolkwitzia*, *Linnaea* and *Vesalea* form a single well-supported clade corresponding with tribe Linnaeae.

Discussion

Creating new genera in order to maintain already existing genera in spite of overall morphological similarity among these clades appears to be a trend in some plant groups, with good examples in, for instance, grammitid ferns (Polypodiaceae), *Ornithogalum* Linnaeus (1753: 306; Asparagaceae), *Potentilla* Linnaeus (1753: 495; Rosaceae, see also Christenhusz & Väre 2012), *Streptocarpus* Lindley (1828: t. 1173; Gesneriaceae, see also Christenhusz 2012) and many others. This process in the extreme would be creating a new genus for every species, which is frequently done in many groups of birds and mammals. One could easily make an argument in the opposite extreme, merging all clades into large genera without taking morphology into account. It seems to me that an intermediate approach is needed, bringing phylogenetic monophyly and morphology in harmony. This should in my opinion be supported by readily observable characters and be in line with other lineages in the family to be practical for the user. In the case of tribe Linnaeae, related genera such as *Lonicera* of tribe Caprifolieae could be used as an example. The morphological diversity seen in *Lonicera* should prompt the question why that genus is not divided further, when *Linnaea* is. The morphological similarity of the genera in Linnaeae, especially in characteristics of the flowers is so obvious that some of these species when first discovered, early botanists treated them as *Linnaea*, indicating a close relationship. *Linnaea* is easily recognised by its paired flowers, hence the vernacular name in English: twin flower. *Linnaea* in the broad sense are erect or creeping shrubs with simple usually opposite leaves without stipules. The inflorescences are paired cymes and reduced to 1 or 2 flowers per inflorescence with leaf-like or scale-like bracts. Flowers are bisexual, zygomorphic, the corolla tubular with 4 or 5 imbricate lobes and a nectary of glandular hairs inside the tube, and 4 stamens adnate to the corolla tube. The ovary is inferior, with axile placenta and single fertile ovules per locule, only 1 or 2 locules developing into an achene crowned with persistent (or deciduous) sepals. The most divergent species in the broader *Linnaea* are those currently placed in *Kolkwitzia* and *Dipelta*, for which I propose new combinations in *Linnaea* below.

One argument of not accepting a broader circumscription of *Linnaea*, as proposed here, is the loss of genera well-known to horticulture, such as *Abelia* and *Kolkwitzia*, but the alternative is to divide one of these, *Abelia*, into three genera to produce a monophyletic classification, destabilising the names just as extensively and requiring new generic names to be adopted by the users. This also results in the *Linnaea* clade (see Landrein & Prenner, 2013) consisting of six genera, none with more than three species, which is highly divided in comparison to other genera in Caprifoliaceae. The total number of species is only 13 according to Landrein (2010b), although other authors disagree about this (e.g. Jacobs *et al.* 2010 included several additional species in their analysis that are not mentioned by Landrein 2010b). Here, I include a total of 17 taxa (following Yang & Landrein 2011, excluding *Zabelia*). The taxonomy of the species complex surrounding *L. uniflora* (R.Br.) A.Br. & Vatke in Vatke (1872: 291) needs further study and may include as yet undescribed species.

The differences between the genera *Abelia*, *Diabelia*, *Dipelta*, *Kolkwitzia*, *Linnaea* and *Vesalea* lies in the inflorescence structure (Landrein *et al.* 2012, Landrein & Prenner 2013), but without micromorphological study they all appear similar due to the strong reduction of the inflorescences. Inflorescence structure is variable within many other genera. *Lonicera* has a similar variability of inflorescence structure and also in plant habit (e.g. Laros 2013), even more diverse than *Linnaea sensu lato*. In several other groups this can also be found, with good examples in Amaryllidaceae: *Milula spicata* Prain (1895: 56; with racemose inflorescences) was found to be embedded in *Allium* (with umbellate inflorescences) and was hence transferred into that genus (Friesen *et al.* 2000). Additionally in Gilliesioideae of Amaryllidaceae, nomenclatural changes are needed to form monophyletic lineages irrespective of inflorescence structure (Fay *et al.* 2006). If inflorescence structure is the only reason to maintain separate genera, then these species are surely better placed in a single genus and the segregate genera reverted to subgeneric or sectional levels. Plant habit has also been applied as a character to separate some of genera, but there are also precedents for treating creeping, nearly herbaceous species in the same genus as more typically woody shrubs or trees, such as in *Betula* Linnaeus (1753: 982; Betulaceae), *Clematis* Linnaeus (1753: 543; Ranunculaceae), *Cornus* Linnaeus (1753: 117; Cornaceae), *Ficus* Linnaeus (1753: 1059; Moraceae), *Fuchsia* Linnaeus (1753: 1191; Onagraceae), *Lonicera* (Caprifoliaceae) and *Salix* Linnaeus (1753: 1015; Salicaceae).

Because of these name changes, I realise that people working in horticulture will have to become familiar with the concept of *Linnaea* as a common garden shrub in the temperate zones of the world. That name will no longer be exclusive to the species *L. borealis*, which is only grown rarely in alpine plant collections. I should point out that a system of recognising six genera is not wrong per se—all genera are monophyletic and can be recognised morphologically (Landrein 2010a, Landrein & Prenner 2013)—but that is not surprising because of the small number of species of which they consist. We can question if we are looking at differences between genera or species. Of course the delimitation of genera is arbitrary, and depends on tradition and preference of the user. Here, I am merely making the names available to provide a choice. It is up to users, ultimately, to decide what generic system is preferable and which names will be accepted in future treatments of Caprifoliaceae.

Taxonomy

Linnaea [Gronov.] L.

Gronovius in Linnaeus (1737: 188); Linnaeus (1753: 631).

Type: *Linnaea borealis* [Gronov.] L.

Synonyms: *Abelia* Brown (1818: 376), *Diabelia* Landrein (2010b: 35), *Dipelta* Maximowicz (1878: 50), *Kolkwitzia* Graebner in Diels (1901: 593), *Linneusia* Rafinesque (1830: 239), nom. illeg. superfl., *Obolaria* Kuntze (1891: 275), nom. illeg. hom. non Linnaeus (1753), *Vesalea* Martens & Galeotti (1843: 242)

Erect or creeping shrubs. Leaves opposite or whorled, simple, without stipules, petiolate. Axillary buds exposed. Inflorescences terminal or axillary, simple or compound reduced thyrses, flowers single or paired.

Bracts leaf-like or scale-like, located at bases of flowers, forming an epicalyx around the flowers. Flowers bisexual, zygomorphic. Perianth pentamerous. Calyx lobes 5, nearly free. Corolla funnellform or bilabiate with 5 spreading lobes that are imbricate in bud. Nectaries consisting of glandular hairs inside corolla tube. Stamens four, alternating the corolla lobes, filaments adnate with the lower $\frac{1}{3}$ – $\frac{1}{2}$ corolla tube. Ovary inferior, 3–4-loculed with axile placentation, usually one or two locules with a single fertile ovule the other two with numerous sterile ovules. Styles long, terminated by white, capitate stigmas. Fruit an achene crowned with persistent or rarely deciduous sepals, with one or two seeds.

1. *Linnaea amabilis* (Graebn.) Christenh., *comb. nov.*

Basionym: *Kolkwitzia amabilis* Graebner in Diels (1901: 593).

Type: CHINA. Hua shan near Gniu yu, *Giraldi 1725* (B).

Distribution: China (Anhui, Gansu, Henan, Hubei, Shaanxi, Shanxi); rare in the wild but widely cultivated in China, Japan, Europe and North America.

2. *Linnaea borealis* Linnaeus (1753: 631).

Lectotype (designated by Jonsell in Jarvis *et al.* 1993): *Herb. Linn. no. 250* (LAPP!).

Heterotypic synonyms: *Linnaea americana* Forbes (1833: 135), *L. borealis* subsp. *americana* (J.Forbes) Hultén (1937: 310), *L. borealis* subsp. *longiflora* (Torr.) Piper & Beattie (1915: 338), *L. longiflora* (Torr.) Howell (1900: 280), etc..

Note: A great number of additional synonyms are listed by Wittrock (1907) and Brenner (1908, 1910), which are not repeated here to keep this paper concise. These synonyms should be addressed with respect to the variability of this species to be addressed in future studies.

Distribution: Circumboreal and subarctic (Canada, northern and central USA, Greenland, northern Britain, Fennoscandia, Baltic States, Mainland Europe south to the Alps, and the Balkans, Ukraine, Russia, Siberia, Kazakhstan, Mongolia, northern China, Korea, northern Japan).

3. *Linnaea chinensis* (R.Br.) A.Braun & Vatke (in Vatke 1872: 291).

Basionym: *Abelia chinensis* Brown (1818: 376).

Type: CHINA. Guangdong: Lienchow River, 19 August 1887, *C. Ford 1795* (BM!).

Heterotypic synonyms: *Abelia aschersoniana* (Graebn.) Rehder (1911: 127), *A. cavaleriei* Léveillé (1914: 60), *A. hanceana* M.Mart. ex Hance (1866: 216), *A. ionandra* Hayata (1918: 31), *A. lipoensis* An & Gou (2009: 129), *A. rupestris* Lindley (1846: 63), *Linnaea aschersoniana* Graebner (1900: 139), *L. rupestris* (Lindl.) A.Braun & Vatke in Vatke (1872: 291).

Distribution: China (Fujian, Guangdong, Guangxi, Guizhou, Hubei, Hunan, Jiangxi, Sichuan, Yunnan, Zhejiang), northern Vietnam, Taiwan. The species is commonly cultivated in China and Japan, occasionally so in Europe and North America.

4. *Linnaea coriacea* (Hemsl.) Christenh., *comb. nov.*

Basionym: *Abelia coriacea* Hemsley (1880: 53)

Type: MEXICO. San Luis Potosí: 6000–8000 feet, 1878, *Parry & Palmer 299* (holotype K!, isotypes GH, MO!).

Homotypic synonym: *Vesalea coriacea* (Hemsl.) K.Tim & B.Sun ex Landrein (2010: 38).

Distribution: Mexico (Nuevo León, San Luis Potosí).

5. *Linnaea dipelta* Christenh., *nom. nov.*

Replaced synonym: *Dipelta floribunda* Maximowicz (1878: 51), non *Linnaea floribunda* (M.Mart. & Galeotti) A.Braun & Vatke in Vatke (1872: 291).

Type: CHINA. ‘Prov Shensi: montibus circa urbem Han-tschun-fu, initio Aprilis florens’ 1875, *Piasezki s.n.* (LE)

Heterotypic synonym: *Dipelta floribunda* var. *parviflora* Rehder (1924: 241).

Distribution: China (Gansu, Guangxi, Hubei, Hunan, Shaanxi, Sichuan).

6. *Linnaea elegans* (Batalin) Christenh., *comb. nov.*

Basionym: *Dipelta elegans* Batalin (1895: 174)

Type: CHINA. ‘Prov. Kansu orientale, trajectus altus inter pagus Mör ping et Wu ping’, 27 June & 5 July 1885, *Potanin s.n.* (LE).

Distribution: China (Gansu, Sichuan).

7. *Linnaea floribunda* (M.Mart. & Galeotti) A.Braun & Vatke (in Vatke 1872: 291).

Basionym: *Vesalea floribunda* Martens & Galeotti (1844: 242).

Type: MEXICO. Veracruz: Dans les forêts alpines du pic d'Orizaba a 10,000 pie. *Galeotti 2641* (holotype BR)

Homotypic synonym: *Abelia floribunda* (M.Mart. & Galeotti) Decaisne (1846: pl. IV).

Heterotypic synonyms: *Abelia speciosa* Decaisne (1846: sub pl. IV), *Vesalea hirsuta* Martens & Galeotti (1844: 242).

Distribution: Mexico (Chiapas, Oaxaca, Puebla, Veracruz)

8. *Linnaea forrestii* Diels (1912: 178).

Type: CHINA. Yunnan: Salwin valley between Shichi-Ti and Xia-ku-ti, dry, scrubby hillsides, 6000–7000 ft, November 1905, *Forrest 867* (holotype E-00265299!, isotype P-00482062!)

Homotypic synonym: *Abelia forrestii* (Diels) Smith (1916: 76).

Heterotypic synonyms: *Abelia gracilentata* Smith (1916: 76), *A. microphylla* (W.W.Sm.) Golubkova (1973: 241).

Distribution: south-central China (southwestern Sichuan, northwestern Yunnan)

9. *Linnaea* × *grandiflora* (André) Christenh., *comb. nov.*

Basionym: *Abelia rupestris grandiflora* André (1886: 488), without rank

Type: none cited, based on living plants cultivated by M. Rovelli [as 'Rivelli'] in Pallanza, Italy.

Homotypic synonym: *Abelia* × *grandiflora* (André) Rehder in Bailey (1900: 1).

Note: A garden hybrid of *L. chinensis* and *L. uniflora*, only known from cultivation.

10. *Linnaea grandifolia* (Villareal) Christenh., *comb. nov.*

Basionym: *Abelia grandifolia* Villareal in Villareal & De la Rosa (2000: 174)

Type: MEXICO. Querétaro: Mun. Jalpan, 9–10 km al S de San Juan de Durán, Cerro Grande, laderas de bosque de pinoencino, 2600–2700 m, 13 June 1991, *Servín 1101* (holotype IEB, isotype CAS).

Distribution: Central Mexico (Querétaro).

11. *Linnaea mexicana* (Villareal) Christenh., *comb. nov.*

Basionym: *Abelia mexicana* Villareal in Villareal & De la Rosa (2000: 172).

Type: MEXICO. Oaxaca: Mun. San Sebastián Tecomaxtlahuaca, cerca de 10 km de San Sebastián Yecomaxtlahuaca, camino a San Martín Duraznos, 17°18'N, 98°06'W, bosque de *Quercus-Juniperus-Brahea*, 1755 m, 19 July 1996, *Calzada 21100* (holotype MEXU, isotypes ANSM, ENCB, L!).

Distribution: south-central Mexico (Oaxaca).

12. *Linnaea occidentalis* (Villareal) Christenh., *comb. nov.*

Basionym: *Abelia occidentalis* Villareal (1997: 84).

Type: MEXICO. Durango: *Villarreal et al. 8180* (holotype: MEXU, isotypes ANSM, CIIDIR, ENCB, TEX).

Distribution: Mexico (Durango).

13. *Linnaea serrata* (Siebold & Zucc.) Graebner (1900: 133)

Basionym: *Abelia serrata* Siebold & Zuccarini (1835: 76)

Type: JAPAN. Honshu: Nagasaki. Mt. Sitsrama, *Von Siebold s.n.* (L!)

Homotypic synonym: *Diabelia serrata* (Siebold & Zucc.) Landrein (2010: 37).

Heterotypic synonyms: *Linnaea buchwaldii* Graebner (1900: 136), *Linnaea gymnocarpa* Graebn. & Buchw. ex Graebner (1900: 134).

Distribution: China (Zhejiang), Japan (Honshu, Kyushu, Shikoku).

14. *Linnaea spathulata* (Siebold & Zucc.) Graebner (1900: 142)

Basionym: *Abelia spathulata* Siebold & Zuccarini (1835 [-1839]: 77).

Type: JAPAN. Kiusiu: Mt. Innio, *Von Siebold s.n.* (L!)

Distribution: China (Zhejiang), Japan (Honshu, Kyushu, Shikoku).

Homotypic synonym: *Diabelia spathulata* (Siebold & Zucc.) Landrein (2010: 37).

15. *Linnaea tetrasepala* (Koidz.) Christenh., *comb. nov.*

Basionym: *Abelia spathulata* var. *tetrasepala* Koidzumi (1915: 311)

Type: JAPAN. Honshu: Saitama-ken (Musashi, Chichibu), *Matsumura s.n.* (TI).

Distribution: Japan (Honshu, Shikoku).

Homotypic synonyms: *Diabelia tetrasepala* (Koidz.) Landrein (2010: 36)

16. *Linnaea uniflora* (R.Br.) A.Br. & Vatke in Vatke (1872: 291)

Basionym: *Abelia uniflora* Brown (1830: 15)

Type: CHINA. *John Reeves*.

Heterotypic synonyms: *Abelia deutzifolia* (H.Lév.) Léveillé (1914: 60), *Abelia engleriana* (Graebn.) Rehder (1911: 120), *A. graebneriana* Rehder (1911: 118), *A. longituba* Rehder (1911: 126), *A. macrotera* (Graebn. & Buchw.) Rehder (1911: 126), *A. mairei* Léveillé (1915: 26), *A. myrtilloides* Rehder (1911: 120), *A. parvifolia* Hemsley in Forbes & Hemsley (1888: 358), *A. schischkinii* Golubkova (1955: 394), *A. schumannii* (Graebn.) Rehder (1911: 121), *A. tereticalyx* (Graebn. & Buchw.) Rehder (1911: 127), *A. verticillata* Léveillé (1914: 61), *Linnaea engleriana* Graebner (1900: 132), *L. koehneana* Graebner (1900: 132), *L. macrotera* Graebn. & Buchw. in Graebner (1900: 131), *L. parvifolia* (Hemsl.) Graebner (1900: 129), *L. schumannii* Graebner (1900: 130), *L. tereticalyx* Graebn. & Buchw. in Graebner (1900: 130), *Strobilanthisopsis deutzifolius* Léveillé (1913: 21), *S. hypericifolius* Léveillé (1913: 20).

Note: This is a species complex that is not yet well resolved. Some taxa placed here in synonymy may, with further research, require recognition.

Distribution: China (Fujian, Gansu, Guangxi, Guizhou, Henan, Hubei, Hunan, Shaanxi, Sichuan, Yunnan). Frequently cultivated.

17. *Linnaea yunnanensis* (Franch.) Christenh., *comb. nov.*

Basionym: *Dipelta yunnanensis* Franchet (1891: 246, fig. 62).

Lectotype (designated here): CHINA. Yunnan: Les forêts au col de Yen tze hay (Lan kong), 3000 m, 27 June 1886, *Delavay 2222* (P-00639763!).

Heterotypic synonyms: *Dipelta ventricosa* Hemsley (1908: 101).

Distribution: China (Gansu, Guizhou, Hubei, Shaanxi, Sichuan, Yunnan), and adjacent Burma.

Unresolved name:

Linnaea pseudoproterantha Pamp., *Nuovo Giorn. Bot. Ital.* 17: 723 (1910).

Excluded names:

Linnaea adenotricha (Hance) Graebn. = *Zabelia biflora* (Turcz.) Makino

Linnaea angustifolia (Bureau ex Franch.) Graebn. = *Zabelia triflora* (R.Br.) Makino

Linnaea brachystemon Diels = *Zabelia dielsii* (Graebn.) Makino

Linnaea corymbosa Regel & Schmalh. ≡ *Zabelia corymbosa* (Regel & Schmalh.) Makino

Linnaea dielsii Graebn. ≡ *Zabelia dielsii* (Graebn.) Makino

Linnaea onkocarpa Graebn. = *Zabelia dielsii* (Graebn.) Makino

Linnaea triflora (R.Br.) A.Braun & Vatke ≡ *Zabelia triflora* (R.Br.) Makino

Linnaea umbellata Graebn. & Buchw. = *Zabelia dielsii* (Graebn. & Buchw.) Makino

Linnaea zanderi Graebn. = *Zabelia dielsii* (Graebn.) Makino

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