

East Asian Lobelioideae and ancient divergence of a giant rosette *Lobelia* in Himalayan Bhutan

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Abstract Lobelioideae comprise about 1200 species in 30 genera worldwide and include famous cases of parallel evolution in the “giant rosette” lobelias occurring in East Africa, Hawaii, and Bhutan. To date, no phylogeny has included the Himalayan giant lobelia, and its age and phylogenetic distance from the Hawaiian and African giant species (the latter in the same section as the Bhutan species) are therefore unknown. Asian Lobelioideae in general have received little attention, partly because of the difficult access to material. Here we use nuclear and plastid markers of Lobelioideae (with worldwide sampling) to test the monophyly of the section that includes most Asian lobelias, and we then use a reduced concatenated matrix to resolve the position of *Lobelia nubigena* from Bhutan and of the likewise cold-adapted lowland species *L. sessilifolia*. Most sequences come from herbarium material. *Lobelia nubigena* diverged from its Asian lowland relatives 13.8 (12.6–15) million years ago (about the time of the Bhutan Himalaya orogeny), and in an unexpected twist, *L. sessilifolia* is the sister species to a huge clade (ca. 265 species) that comprises African, South American, Asian, and the entire Hawaiian Lobelioideae radiation. The African and Hawaiian high-elevation lobelias in our sample are younger than *L. nubigena*, although the time when gigantism evolved in this species cannot be precisely inferred. Our results support the previously hypothesized Asian origin of (1) the Hawaiian Lobelioideae, (2) Southeast Asian islands lobelias, and (3) the African *Lobelia-Rynchopetalum* group, which also reached South America.

Keywords Africa; Bhutan; Biogeography; Campanulaceae; Himalaya; Lobelioideae; *Lobelia* worldwide

Supplementary Material The Electronic Supplement (Tables S1 & S2; Fig. S1) is available in the Supplementary Data section of the online version of this article at <http://ingentaconnect.com/content/iapt/tax>; data matrices are available from TreeBASE (S15797, S18285).

■ INTRODUCTION

Among the most iconic examples of plants adapted to alpine conditions are the giant rosette lobelias growing on the slopes and plateaus of East African and Hawaiian mountains (Hedberg, 1964, 1969; Givnish, 2010). Giant rosette lobelias are perennial monocarpic herbs mostly occurring in alpine and subalpine bogs. The adaptive value of a thick and tall stem with numerous, relatively large, and long-persistent leaves is thought to lie in the nightly protection of the cortex and apical bud against frost (Hedberg, 1969; Fetene & al., 1998). Best studied are the 22 species of giant lobelias in eastern Africa (Knox, 1993; Knox & Palmer, 1998; Knox & al., 2004; Lammers, 2011a), which grow at altitudes from 725 m to over 4600 m on the equatorial mountains of Tanzania and along the East African rift system (Knox & Palmer, 1998). Much less well studied in terms of both ecology and evolution is the Asian giant lobelia, *Lobelia nubigena* J. Anthony (Electr. Suppl.: Fig. S1A: photos of its habit, apical buds, and distribution map). It

is endemic to the Thrumshingla National Park in the centre of Bhutan, where it grows from 3900 to 4300 m and where the first author observed and collected it in 2014. No molecular phylogenetic study has included *L. nubigena*, but morphologically it resembles *L. telekii* Schweinf. from Mts. Kenya, Elgon, and Aberdare (Anthony, 1936). Both of them have been placed in *L. sect. Rynchopetalum* (Fresen.) Benth., which comprises 24 Asian, 25 African, and 12 South American species (Lammers, 2011a, b; Fig. S1A–C in the Electr. Suppl. includes distribution maps of the section’s Asian species). Plants in this section are perennial herbs (some to 9 m tall) with sometimes pachycaulous stems especially in the “giant rosette” lobelias (Lammers, 2011a, b).

While the ecology and relationships of African and Hawaiian lobelias have attracted much attention (Hedberg, 1970; Mabberley, 1975; Givnish & al., 1996, 2009; Knox & Palmer, 1998; Knox & al., 2006; Antonelli, 2008, 2009 [worldwide sampling]), Asian Lobelioideae have hardly been studied with molecular data. Only six Asian Lobelioideae have

been sequenced, namely *L. chinensis* Lour., *L. erinus* L., *L. leschenaultiana* (C.Presl) Skotts., *L. nummularia* Lam., and *L. nicotianifolia* Roth ex Schult. (Antonelli, 2008, 2009) and recently *L. boninensis* Koidz. (Knox, 2014). However, *Lobelia* L. has 51 species in Asia, 24 of them in sect. *Rhynchoptalum*, 3 in sect. *Stenotium* (C.Presl) Lammers, 7 in sect. *Delostemon* (E.Wimm.) J.Murata, 8 in sect. *Hypsela* (C.Presl) Lammers, 5 in sect. *Speirema* (Hook.f. & Thomson) Lammers and 1 in sect. *Plagiobotrys* Lammers (Lammers, 2011a). The *Flora of China* accepts 23 species (Hong & Lammers, 2011), the *Flora Malesiana* 12 (Moeliono & Tuyn, 1960), and the *Flora of India* 16 (Haridasan & Mukherjee, 1988). The sampling of Asian Lobelioideae has therefore been insufficient to assess their biogeographic significance and the question of parallel evolution of gigantism under high-altitude conditions in Asia.

Here we focus on the biogeography of Asian lobelias to answer two questions and to test a hypothesis that arises from previous work. Our first question concerned the closest living relatives and time of divergence of the high-altitude *L. nubigena*, which based on its habit and unbranched inflorescence has been seen as close to the African giant lobelias, a group of 14 species (Anthony, 1936; Lammers, 2011a). Our second question concerned *L. sessilifolia*, a frequently cultivated species that is widespread in Northeast Asia (Electr. Suppl.: Fig. S1B shows its range) with a distribution extending to at least 160°N in Siberia. Oddly, this species has not been included in any of the Lobelioideae phylogenies so far. Its extremely northern geographic range (compared to all other members of sect. *Rhynchoptalum*), suggested to us that it might be a derived species, perhaps evolving from more southern lobelias during recent climate cooling. The hypothesis we wanted to test is that the ancestor of the East African lobelias arrived from the Asian Pacific region (Knox & Palmer, 1998; Knox & al., 2006) and that the *L. nicotianifolia* species complex from western India to the Philippines represents the ancestral group from which African giant lobelias evolved (Mabberley, 1975; Givnish & al., 2009).

■ MATERIALS AND METHODS

Gene sequencing and sequence aligning. — Total genomic DNA was extracted from silica-dried leaves or herbarium specimens using the MagicMag Genomic DNA Micro Kit (Sangon Biotech, Shanghai, China) or the NucleoSpin plant kit (Machery-Nagel, Düren, Germany). We sequenced the internal transcribed spacer regions (ITS1, ITS2) and 5.8S gene of the nuclear-encoded ribosomal DNA, and the plastid gene regions *trnL-trnF*, *rbcl*, *psbA-trnH*, *trnK* 5' intron, *matK* and *trnK* 3' intron. Primers used are listed in Electr. Suppl.: Table S1. Aligning was carried out with MAFFT v.7 (Katoh & al., 2009; <http://mafft.cbrc.jp/alignment/server/>), using the E-INS-i strategy and default settings. The aligned sequences were inspected in Mesquite v.3.04 (Maddison & Maddison, 2011) and in a few cases manually adjusted.

Taxon sampling and phylogenetic analyses. — To represent Lobelioideae, which have about 1200 species in ca. 30

genera (Lagomarsino & al., 2014), we included the type of the name *Lobelia* (*L. cardinalis* L.) and 19 *Lobelia* species from Asia and the Pacific region, 41 in 4 genera from Africa, 43 in 8 genera from Central and South America, 17 in 5 genera from North America, 16 in 3 genera from Australia, 31 in 8 genera from Hawaiian and Polynesian islands, and 4 species in 2 genera from Europe (Antonelli, 2009; Givnish & al., 2009; Lagomarsino & al., 2014: Neotropical Lobelioideae). Of sect. *Rhynchoptalum* (Lammers, 2011a, b), we sampled 16 of its 24 Asian species, 13 of 25 African, and 5 of its 12 South American species. Of the 18 sections of *Lobelia* (Lammers, 2011a), we sampled all except sect. *Trimeris* (C.Presl.) A.DC., sect. *Speirema*, and sect. *Plagiobotrys*. Of the 13 species of sect. *Rhynchoptalum* treated in the *Flora of China* (Hong & Lammers, 2011), we included 10, some with multiple accessions. We failed to obtain leaf material of *L. foliiformis* T.J.Zhang & D.Y.Hong, only known from the Yunnan type collection, *L. colorata* Wall., a species described from India and extending into Yunnan, and *L. pyramidalis* Wall., which reaches 2–3 m in height and occurs at altitudes above 1000 m in Nepal, the Tibet Autonomous Region (Xizang), Bhutan, India, N Burma, and N Thailand. *Lobelia colorata* is morphologically close to *L. taliensis* Diels, while *L. pyramidalis* is morphologically close to *L. seguinii* H.Lév. & Vaniot (Hong & Zhang, 1992).

We first constructed large ITS and cpDNA matrices to test the placement of the Asian species newly sequenced for this study. All 54 Lobelioideae ITS sequences available in GenBank on 12 August 2015 were downloaded and aligned with our own 27 ITS sequences. Appendix 1 (and Electr. Suppl.: Table S2) lists all material used in this study with herbarium vouchers, herbarium codes, collection details, and the natural range of the respective species; it also contains notes from the *Flora of China* (Hong & Lammers, 2011) and in some cases, on types and their locations (we checked the vouchers of all downloaded sequences against information in the original papers and eliminated a few apparently misidentified or at least mislabelled sequences). To root the family-wide 81-taxon ITS matrix, we used *Wahlenbergia marginata* (Thunb.) A.DC. (Wahlenbergiaceae) and *Trachelium caeruleum* L. (Campanuleae), both of Campanuloideae based on Eddie & al. (2003) and Knox (2014). We also downloaded and aligned the plastid sequences of all species with at least one of the following fragments: *trnL-trnF* intergenic spacer, *rbcl*, *psbA-trnH*, *trnK* 5' intron, *matK*, *trnK* 3' intron, *atpB-rbcl*, *trnT-trnL*, *trnV-trnK*, *rpl16*, and the plastid genomes from Knox (2014; TreeBASE no. S15797) and aligned them with our own plastid sequences, yielding a matrix of 155 taxa, again checking the herbarium vouchers to the extent possible. Where vouchers are missing this is indicated in our Appendix 1 and Electr. Suppl.: Table S2. In a few cases, we sequenced two or three conspecific plants for the same gene region for verification (Appendix 1; Electr. Suppl.: Table S2). To root the family-wide plastid matrix, we used *Cyphia tortilis* N.E.Br. (Cyphioideae) based on Mansion & al. (2012) and Knox (2014).

Next, we used a reduced taxon sampling of 40 species from sect. *Rhynchoptalum*, with *L. cardinalis* and *L. laxiflora* Kunth as outgroups based on Knox (2014). For these 40 species,

nuclear and plastid matrices were concatenated given that separate analyses did not yield any conflicting nodes with >70% maximum likelihood bootstrap support. The data matrices used in this study have been deposited in TreeBASE S18285.

To select a model of nucleotide substitution, we ran jModel-Test v.2.1.4 (<https://code.google.com/p/jmodeltest2/>; Darriba & al., 2012) with the Akaike information criterion, which favoured the general time-reversible (GTR)+GAMMA (G)+proportion of invariable sites (I) model for the large ITS matrix and TIM3+G for the large cpDNA matrix. Since Posada's 2003 transitional model (TIM3) is not implemented in modern programs, we used the GTR+G model for all matrices (with empirical base frequencies and four gamma rate categories). Phylogenetic trees were obtained under maximum likelihood (ML) optimization, using RAxML-HPC v.8.1.24 (Stamatakis, 2006) with separate models for the nuclear and plastid data and statistical support obtained under the rapid bootstrap option and using 1000 replicates (Stamatakis & al., 2008).

Molecular clock dating. — Molecular-clock dating was carried out on the 40-species sect. *Rhynchoptalum* matrix, using BEAST v.1.8.0 (Drummond & al., 2012) under the same substitution model as used for the phylogenetic analyses. A Yule process tree prior with a randomly generated starting tree was used for all analyses. Monte Carlo Markov chains were run for 10 million generations with sampling every 10,000 generations. The effective sample sizes for all estimated parameters were checked with Tracer v.1.5 to ensure values >500. The first 10% of trees were discarded as burn-in, and the remaining trees were combined, using TreeAnnotator v.1.7.5. For calibration purposes, we applied a strict clock model, using an ITS rate of 4.13×10^{-9} substitutions/site/year (s/s/y), which is the mean of the 10 herbaceous rate compiled by Kay & al. (2006), a *trnK-matK* rate of 8.1×10^{-10} s/s/y from legumes (Lavin & al., 2005), and *trnL-trnF*, *rbcl*, and *psbA-trnH* rates of 5.6×10^{-10} s/s/y, as found in several independently calibrated studies (Villarreal & Renner, 2014). The age of the divergence between *L. cardinalis/L. laxiflora* and the sect. *Rhynchoptalum* clade was used to validate our dating by comparing it with the age obtained for this node by Knox (2014).

■ RESULTS

Polyphyly of the pantropical *L. sect. Rhynchoptalum*. —

The nuclear (ITS) phylogeny of Lobelioideae (Fig. 1A, with the sectional placement of each species in parenthesis behind its name) represents 80 species from throughout the subfamily's geographic range and indicates that the Polynesian genera *Apetahia* Baillon and *Sclerotheca* A.DC. as well as the entire Hawaiian clade, which besides *Lobelia* includes the genera *Clermontia* Gaudich., *Cyanea* Gaudich., *Brighamia* A.Gray, *Delissea* Gaudich., and *Trematolobelia* Rock, are imbedded within sect. *Rhynchoptalum*. The Asian *L. sessilifolia* forms the deepest divergence (Fig. 1A, B, red arrows) in the clade comprising the Asian lobelias and their Hawaiian, Polynesian, and African/South American offshoots. In the nuclear tree (Fig. 1A), *L. boninensis* from the Bonin Islands is imbedded

inside the Hawaiian clade, but this placement lacks statistical support and is not seen in the plastid tree (Fig. 1B), which is better sampled (155 species) and shows *L. boninensis* as part of a clade of species from Sumatra and the Philippines. The sequence chromatograms of *L. boninensis* and the other newly generated ITS sequences revealed no double peaks and their alignment was unambiguous. The combined nuclear and plastid data (Fig. 2A) placed *L. boninensis* in the Sumatra/Philippines clade with statistical support.

Biogeography and divergence times of Asian lobelias.

— The divergence time of *L. cardinalis/L. laxiflora* from the remaining species was estimated as 23.5 million years ago (Ma, more or less consistent with the 22 Ma estimated for the same node by Knox (2014); the most recent common ancestor of the Hawaiian Lobelioideae was estimated as 13.0 Ma by Givnish & al. (2009), only slightly older than our estimate of 11.1 Ma. The similar ages obtained in these three studies (with different species sampling and rate calibrations) inspire some confidence in our overall time frame for Lobelioideae. The giant Bhutanese *L. nubigena* is sister to a large Asian/African/South American/Hawaiian clade (with 90% ML bootstrap support; Fig. 2A), and our time tree suggests that this species diverged 13.8 (12.6–15) Ma. The most northern-ranging *Lobelia* species in sect. *Rhynchoptalum*, *L. sessilifolia*, is sister to all remaining species in our sample (with statistical support; Fig. 2A) and is dated to 19.8 (17.4–22.4) Ma. The remaining Asian lobelias form three clades: (1) The Indian rosette-forming species *L. leschenaultiana* is sister to a clade comprising the Chinese *L. clavata* E.Wimm., *L. davidii* Franch., *L. doniana*, *L. erectiuscula* J.Hara, *L. iteophylla* C.Y.Wu, and *L. pleotricha* Diels (Electr. Suppl.: Fig. S1A & B shows their habits and ranges), (2) *L. nicotianifolia* from the Philippines and *L. meliana* E.Wimm. and *L. seguinii* from China, and (3) *L. proctorii* Argent & P.Wilkie (from the Philippines), *L. sumatrana* Merr. (Sumatra), and *L. boninensis* (Bonin Islands) along with the Hawaiian clade (Fig. 2A, B).

The African giant rosette lobelias, *L. rhynchoptalum* Hemsl. at 3900–4000 m alt. on Mts. Bale and Simen, *L. deckenii* Hemsl. at 3200–4200 m on Mts. Kenya, Elgon, Aberdare, and Meru, *L. aberdarica* R.E.Fr. & T.C.E.Fr. at 2800–3200 m and *L. telekii* at 3400–4650 m on some of the same mountains, and *L. giberroa* Hemsl., widely distributed at 1500–3000 m, are inferred to be between 8.2 and 0.4 million years old (Fig. 2B; altitudinal ranges all from Thulin, 1984, and Knox, 1993). The Hawaiian giant rosette lobelia *L. hypoleuca* Hillebr., which occurs at 600–1500 m on Kauai, Oahu, Lanai, Molokai, Maui, and Hawaii, is inferred to be 12–8.8 Ma old, while *L. gloriamontis* Rock, occurring at 1350–1750 m on Maui, and *L. villosa* (Rock) St.John & Hosaka, occurring at 1200–1580 m on Kauai, are dated to 1.7–0.1 Ma.

■ DISCUSSION

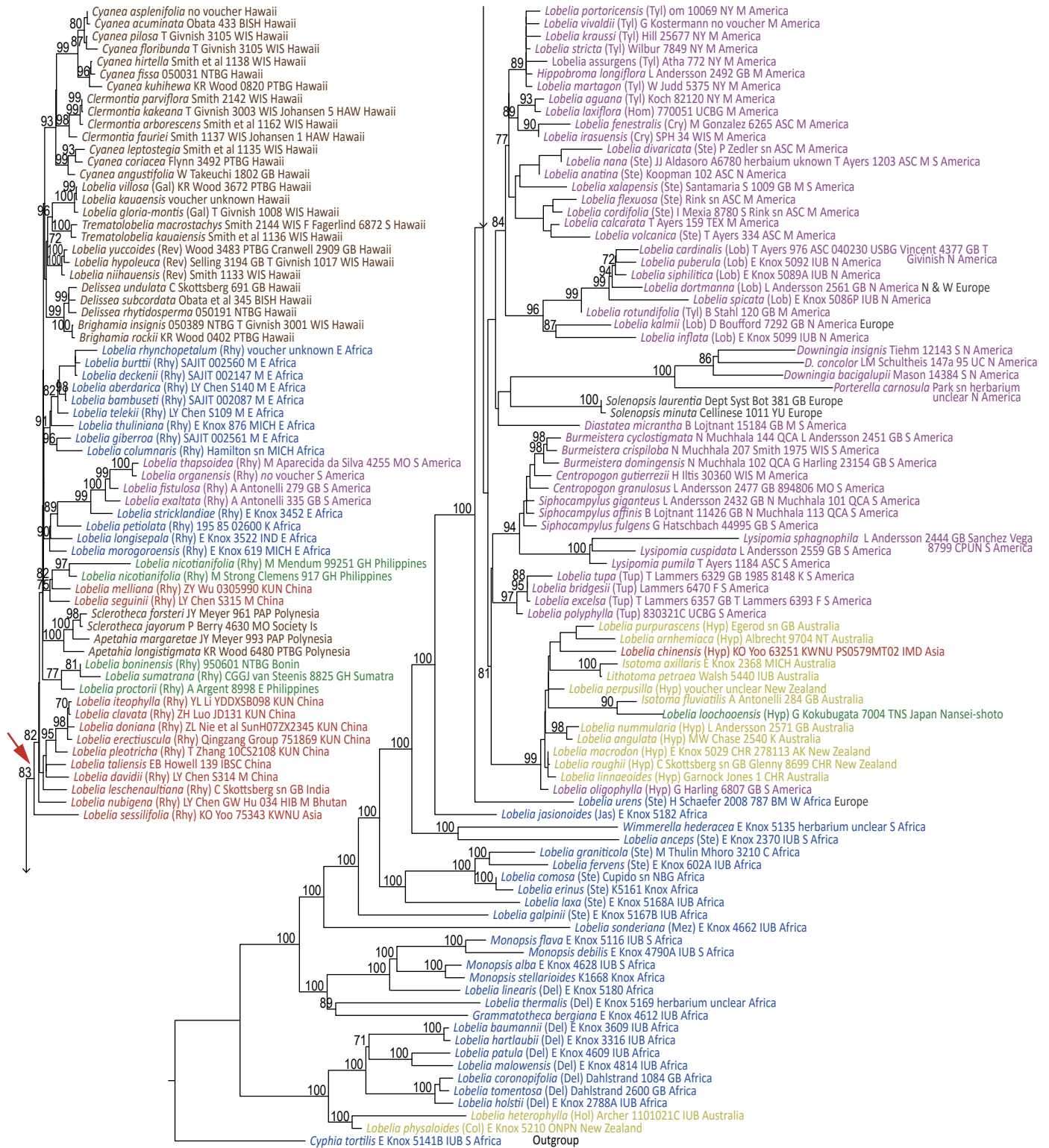
We set out to infer the closest living relatives and time of origin of the Bhutanese *L. nubigena*, the Asian pendant to the African pachycaulous giant rosette lobelias, which required

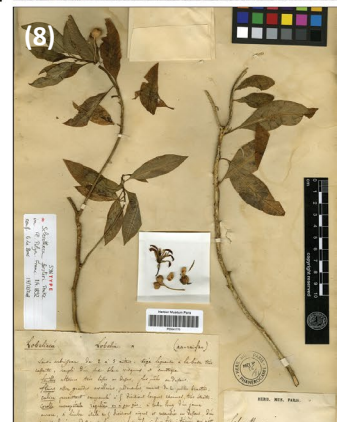
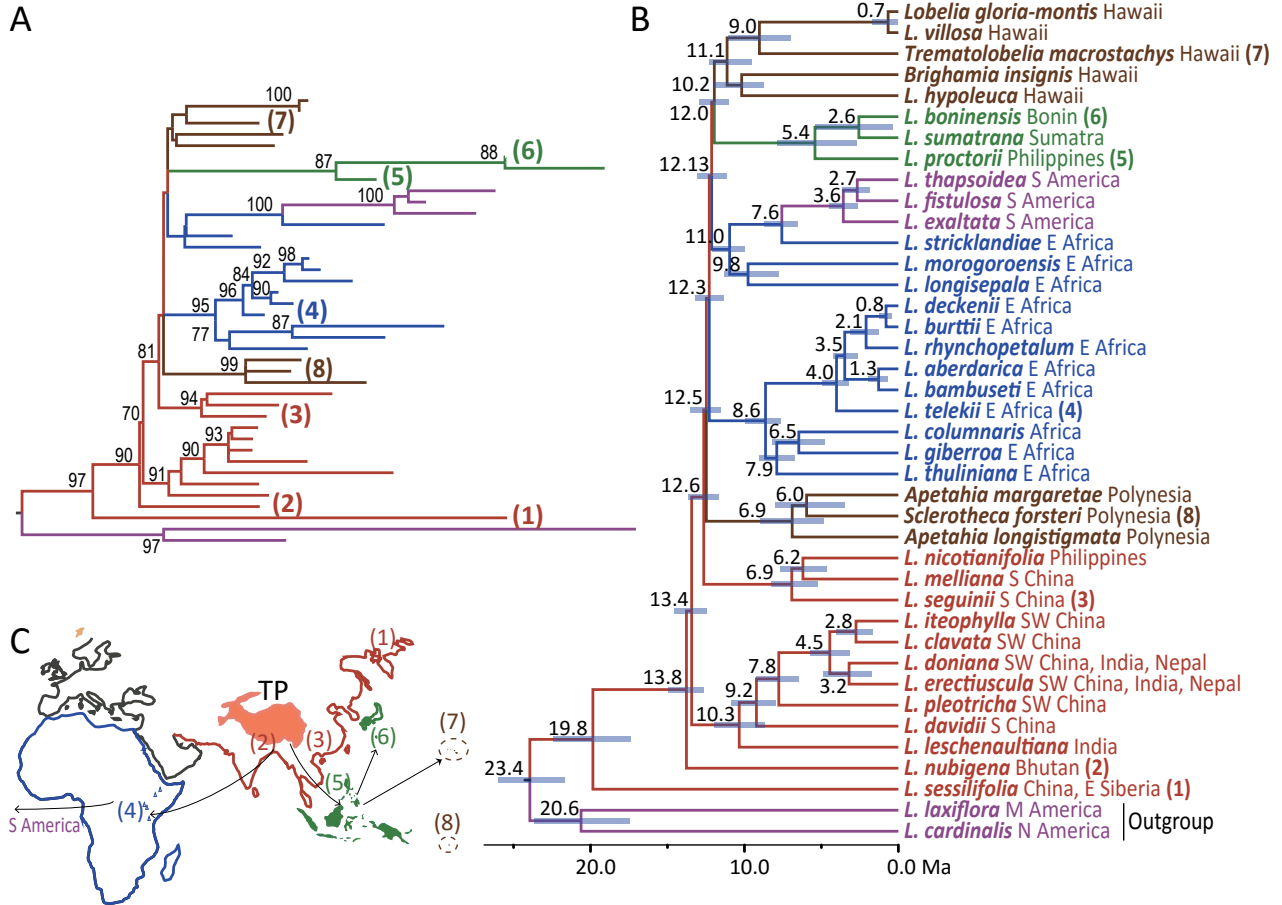
Fig. 1A (ITS)



Fig. 1A & B. Maximum likelihood phylogenies of Lobelioideae constructed using the nuclear (A) and chloroplast (B) sequences listed in Appendix 1 and Electr. Suppl.: Table S2. Bootstrap values ≥ 70 are given at the nodes, and each species' sectional classification (Lammers, 2011a) follows its name, using the abbreviations: Col = *Colensoa*, Cry = *Cryptostemon*, Del = *Delostemon*, Gal = *Galeatella*, Hol = *Holopogon*, Hom = *Homochilus*, Hyp = *Hypsela*, Jas = *Jasionopsis*, Lob = *Lobelia*, Mez = *Mezleriopsis*, Rev = *Revolutella*, Rhy = *Rhynchopetalum*, Ste = *Stenotium*, Tup = *Tupa*, and Tyl = *Tylomium*. Red arrows mark the focal clade analyzed further in Fig. 2A, B.

Fig. 1B (*trnL-trnF* intergenic spacer + *rbcl* + *psbA-trnH* + *trnK* 5' intron + *matK* + *trnK* 3' intron + *atpB-rbcl* + *trnT-trnL* + *trnV-trnK* + *rpl16*)





clarifying the relationships among the Asian lobelias. The latter had been suggested to be the ancestors of the African lobelias (Knox & Palmer, 1998; Knox & al., 2006), with *L. nicotianifolia* perhaps representing the ancestral group from which East African giant lobelias evolved (Mabberley, 1975; Givnish & al., 2009). While our results confirm an Asian origin of the East African clade, *L. nicotianifolia* is not particularly close to the African clade (Fig. 2A, B). As found by Givnish & al. (2009), albeit without statistical support, the Polynesian genera *Apetahia* and *Sclerotheca* and the Hawaiian clade of Lobelioideae (some 128 species in six genera; Sporck-Koehler & al., 2015) derive from Asian ancestors (Fig. 2A, B). The strong support this inference receives here comes from the unambiguous placement of the Chinese/Siberian species *L. sessilifolia* as the root of the huge clade (ca. 265 species in all) formed by Asian mainland and SE Asian island species plus nested African, South American, and Hawaiian radiations. The divergence of *L. sessilifolia* dates to 19.8 Ma, but although the species is widely cultivated as an ornamental, we found no data on its native ecology or population-level variation. Its type collection comes from Siberia.

Lobelia nubigena from Bhutan and *L. telekii* from Mts. Kenya, Elgon, and Aberdare have always been placed in the same section (*Rhynchopetalum*), along with 23 other African, 24 Asian, and 12 South American species (Lammers, 2011a, b). Both species have a thick tall stem, numerous large persistent leaves, and inflorescence buds and flowers enclosed by hairy bracts and sepals (Fig. 2C; Electr. Suppl.: Fig. S1A). Their superficial similarity must result from parallel evolution in gross morphology. On the mountain in Bhutan, at ca. 3900 m altitude, where the first author collected *L. nubigena*, he saw thousands of individuals, and a local forest ranger indicated that this was the only known population and that the site was not protected.

Timing of the convergent evolution of gigantism in Bhutanese, Hawaiian, and East African *Lobelia*. — The giant lobelias in Bhutan, Africa, and Hawaii (Fig. 2B) clearly evolved independently and in each case from low-growing species with branched inflorescences. The dead leaves coating the stems of “giant rosette” lobelias efficiently prevent nocturnal freezing of the xylem and protect the apical meristem (Hedberg, 1964; Fetene & al., 1998), and the giant growth of some species (which can reach up to 9 m tall) removes the apical meristem from temperature oscillations near the ground (however, plants first grow for several years as a stemless rosette before developing an unbranched vertical trunk). For *L. keniensis*,

L. rhynchopetalum, and *L. telekii*, measurements in the field have shown that photosynthesis stops as soon as ice crystals are formed in the leaves, but that CO₂-uptake resumes immediately after thawing (Schulze & al., 1985; Bodner & Beck, 1987; Fetene & al., 1998).

Lobelia nubigena, which is adapted to climate and soil conditions at 3900–4300 m in the western Himalayas, diverged from its sister clade 13.8 (12.6–15.0) Ma. While we cannot infer the time when it adapted to high-alpine conditions, this lineage age more or less matches the orogeny of the Bhutan Himalayas, which underwent their main uplift 15–9 Ma (McQuarrie & Ehlers, 2015). The African high-elevation lobelias are younger than *L. nubigena* (Fig. 2B), and those included in our sampling are also younger than the mountains they occur on. For example, Mt. Elgon, a volcano, formed 25–20 Ma (Walker, 1969; King & al., 1972), and the four lobelia species that grow on its upper slopes (*L. aberdarica*, *L. deckenii*, *L. giberroa*, *L. telekii*) formed 8.2–0.4 Ma. They must have progressively adapted to afro-alpine condition as they extended their ranges upward (Hedberg, 1969, 1970). Similarly, the Hawaiian high-altitude endemics *L. gloria-montis* (on Maui) and *L. villosa* (on Kauai) appear to be younger than the high-elevation bog habitats to which they are now adapted. Unfortunately, physiological studies on the African high-elevation lobelias were all undertaken without an evolutionary context (the high-altitude species are always compared to each other or to giant *Senecio* species, instead of to related lowland lobelias). It is therefore unknown which traits changed as their cell physiology adapted to tolerate crystallization of the bulk of the leaf water for several hours and then resume photosynthesis immediately after thawing (Schulze & al., 1985; Bodner & Beck, 1987; Fetene & al., 1998).

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Fig. 2. A, Phylogeny, **B**, chronogram, and **C**, habit photos of *Lobelia* sect. *Rhynchopetalum* and its closest relatives. **A**, The phylogeny, with bootstrap values ≥ 70 at the nodes, is based on combined nuclear and plastid sequences analyzed under maximum likelihood (see Materials and Methods). **B**, The chronogram is based on the same data, and bars at nodes indicate 95% confidence intervals. Ma = million years. Numbers following species names and provenience refer to the plant photos in C. **C**, The map in C shows the biogeographic scenario derived from the phylogeny (TP = Tibet Plateau of which the Himalayas form the southern border). **Photo 1**, *Lobelia sessilifolia*, photographed in China, Jilin province (photo: Yao Zhou), from Plant Photo Bank of China (<http://www.plantphoto.cn/>); **2**, *L. nubigena*, Bhutan, 4 Jul 2014 (photo: Ling-Yun Chen); **3**, *L. seguinii*, China, Liangping, 2 Sep 2014 (photo: Ling-Yun Chen); **4**, *L. telekii*, Mt. Kenya, 19 Jul 2014 (photo: Ling-Yun Chen); **5**, isotype of *L. proctorii*, *Argent & Reynoso 8998* (E), Philippines; **6**, *L. boninensis*, Maui, Enchanting Gardens of Kula, 16 Jul 2008 (photo: Forest & Kim Starr); **7**, *Trematolobelia macrostachys*, *A. Meebold 21279* (M), Hawaii; **8**, syntype of *Sclerotheca forsteri*, *J. Vesco s.n.* (P), Polynesia, from JSTOR Global Plant s (<https://plants.jstor.org/>).

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Appendix 1. Continued.

(Hook. & Arn.) Torr., *'Baldwin-d* (JEPS) / *'2Park s.n.* (voucher deposition unclear), U.S.A., California, Siskiyou, ¹AF163437 / AF163438, ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014); *Sclerotheca jayorum* Raynal, *P. Berry 4630* (MO), Society Islands, –, DQ285156, DQ285273, DQ272710, –, –, DQ285273, DQ285234, DQ285195, DQ285117; *Siphocampylus affinis* (Mirb.) McVaugh, *'B. Lojinant & U. Molau 11426* (GB) / *'2N. Muchhala 113* (QCA), Ecuador, –, ¹DQ356223, ¹DQ356155, –, –, –, ²EF174620, –, –, *Siphocampylus fulgens* Lebas, *G. Hatschbach 44995* (GB), Brazil, –, DQ356216, EF141032, –, –, –, –, –, –, *Siphocampylus giganteus* (Cav.) G. Don, *'L. Andersson & A. Nilsson 2432* (GB) / *'2N. Muchhala 101* (QCA), Ecuador, –, ¹DQ356222, ¹DQ356154, –, –, –, ²EF174621, –, –, –, *Solenopsis laurentia* (L.) C. Presl, *Dept. Syst. Bot. 381* (GB), Spain, –, DQ356199, DQ356134, –, –, –, –, –, –, *Solenopsis minuta* (L.) C. Presl, *Cellinesse 1011* (YU), unknown, –, –, EU713369, –, –, –, EU437597, –, –, –, *Trachelium caeruleum* L., *P. Schoenswetter & Tribsch 8736* (WU), Spain, N of Malaga, DQ304570, –, –, –, –, –, –, *Trematolobelia kauaiensis* (Rock) Skottsb., *Smith & al. 1136* (WIS), Kaua'i, –, DQ285153, DQ285270, DQ272707, –, –, –, DQ285270, DQ285231, DQ285192, DQ285114; *Wahlenbergia marginata* (Thunb.) A. DC., *K.O. Yoo 75148* (KWNUN), unknown, HQ704542, –, –, –, –, –, –, –, *Wimmerella hederacea* (Sond.) Serra, M.B. Crespo & Lammers, *E. Knox 5135* (herbarium unclear), S Africa, –, Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014).

Asian Lobelia sect. Rhynchopetalum species: Lobelia boninensis Koidz.*, not in FoC, *'950601* (NTBG), collector unclear / *'2H. Kato & A. Ono 10296* (MAK), *'Natl. Trop. Bot. Garden / '2H. Kato*, cultivated from seeds collected on Nakododjima Island, ²KT957589*, ¹Knox (2014), ¹Knox (2014) / ²KT710200*, ¹Knox (2014), ¹Knox (2014), ¹Knox (2014), ¹Knox (2014), ¹Knox (2014), ¹Knox (2014), ¹Knox (2014), ¹Knox (2014); *Lobelia clavata* E. Wimm.*, FoC 2011, good species, *Z.H. Luo & al. JD131* (KUN, KUN photo!), P.R. China, Yunnan, Puer, Jingdong, 12 Apr. 2007, KT957591*, KT957567*, KT710186*, KT957609*, –, KT710171*, –, –, –, –, *Lobelia clavata** E. Wimm., *S.R. Xiong & G.R. A. njwls2007120* (KUN, KUN photo!), P.R. China, Yunnan, Dali, Nanjian, 100°23'54.7"E, 24°50'39.8"N, 2354 m alt., 10 Nov. 2007, KT957590*, KT957566*, KT710187*, KU238150*, –, KT710168*, –, –, –, –, *Lobelia davidii* Franch.* (incl. *L. kwangsiensis* E. Wimm.), FoC 2011, good species, *L.Y. Chen & S.Y. Zhao S314* (M, photo!), P.R. China, Jiangxi, Lushan, 29°32'55"N, 115°59'49"E, 1100 m alt., 30 Aug. 2014, KT957592*, KT957573*, KT710189*, KT957610*, –, KT710169*, –, –, –, –, *Lobelia davidii* Franch., *S.R. Yi 331* (KUN, KUN photo!), P.R. China, Chongqing, Nanchuan, 26 Dec. 2010, –, KT957561*, –, –, –, –, –, –, *Lobelia doniana* Skottsb.* 1928 [= *L. seguinii* var. *doniana* (Skottsb.) E. Wimm. 1953], FoC 2011, good species, *Z.L. Nie & al. SunH-07ZX-2345* (KUN, KUN photo!), P.R. China, Yunnan, Diqing, 25°46'23"N, 99°06'18"E, 2300 m alt., 29 Oct. 2009, –, KT957564*, KT710184*, KT957611*, –, –, –, –, –, –, *Lobelia erectiuscula* H. Hara*, FoC 2011, good species, *Qingzang Group 751869* (KUN, 0305307), P.R. China, Xizang, Cuona, Bonan Mountain, 10 Sep. 1975, KT957593*, KT957570*, KT710188*, KT957612*, –, KT710172*, –, –, –, –, *Lobelia iteophylla* C.Y. Wu*, FoC 2011, good species, *Y.L. Li & al. YDDXSB098* (KUN, KUN photo!), P.R. China, Yunnan, Yongde, 99°42'49.6"E, 24°10'37.5"S, 2147 m alt., 3 Nov. 2007, KT957594*, KT957562*, KT710185*, KU238151*, –, KT710170*, –, –, –, –, *Lobelia leschenaultiana* (C. Presl) Skottsb.*, name not treated in FoC, *C. Skottsb. s.n.* (GB, photo!), Sri Lanka, 11 Dec. 1926, KT957595*, KT957574*, DQ356131, KT957613*, –, KT710178*, –, –, –, –, *Lobelia melliana* E. Wimm.*, FoC 2011, good species, *Z.Y. Wu & al. s.n.* (KUN, 0305990), P.R. China, Fujian, Nanping, Wuyishan, Aug. 1990, KT957596*, KT957563*, KT710196*, KT957614*, –, KT710174*, –, –, –, –, *Lobelia nicotianifolia* Roth ex Schult.*, name not treated in FoC, *'M. Mendum & al. 99251* (GH) / *'2M. Strong Clemens 917* (GH), Philippines, 14 Nov. 1999 / Philippines, Jan. 1915, ²KT957597*, ²KT957565*, ¹KT710195* / ²KT710194*, ¹KT957616* / ²KT957615*, –, KT710167* / ²KT710166*, –, –, –, –, *Lobelia nubigena* J. Anthony*, name not treated in FoC, *L.Y. Chen & G.W. Hu 034* (HIB, M, photo!), Bhutan, Bumthang District, 27°25'53.79"N, 90°05'26.56"E, 4216 m alt., 5 Jul. 2014, KT957598*, KT957575*, KT710191*, KT957617*, KT710179*, KT710179*, KT710179*, –, –, –, –, *Lobelia pleotricha* Diels*, FoC 2011, good species, *T. Zhang & al. 10CS2108* (KUN, KUN photo!), P.R. China, Yunnan, Fugong, 098°43'49.2"E, 27°10'43.8"N, 27 Jul. 2010, KT957599*, KT957572*, KT710193*, KT957618*, –, KT710173*, –, –, –, –, *Lobelia proctorii* Argent & P. Wilkie*, name not treated in FoC, *Argent & Reynolds 8998* (E), isotype, Philippines, Camp 3 above Magdiwang on ridge leading to Mayos Peak, 24 Aug. 1989, –, –, –, –, KT710192*, –, –, –, –, *Lobelia seguinii* H. Lév. & Vaniot*, FoC 2011, good species (in our view this should incl. *L. foliiformis* T.J. Zhang & D.Y. Hong, which is accepted in FoC), *'L.Y. Chen & S.Y. Zhao S315* (HIB, M, photo!) / *'2G. Kokubugata 8906* (TNS), P.R. China, Chongqing, Liangping, 30°40'33.67", 108°02'52.41", 607 m alt., 2 Sep. 2014 (the three samples grouped together), ¹KT957600*, ¹KT957571*, ¹KT957623* / ²AB645968, ¹KT957619*, ¹KT710175*, ¹KT710175*, ¹KT710175*, –, –, –, –, *Lobelia seguinii* H. Lév. & Vaniot, *J. Cai & L.S. Wang 09CS1025* (KUN), P.R. China, Yunnan, Yuxi, Xiping, 3 Feb. 2009, –, KU238159*, KU238158*, –, –, –, –, –, –, *Lobelia seguinii* H. Lév. & Vaniot, *S.Y. Zhang YNS0106* (KUN), P.R. China, Yunnan, Puer, 25 Apr. 2008, –, KT957568*, –, –, –, –, –, –, *Lobelia sessilifolia* Lamb.*, FoC 2011, good species, *K.O. Yoo 75343* (KWNUN), S Korea: Mt. Daeam / P.R. China, Zhejiang, Qianhua, 31 Aug. 1957 / P.R. China, Heilongjiang, 21 Aug. 1954, HQ704544, HQ704663, KC146533, –, –, –, –, *Lobelia sumatrana* Merr.*, name not treated in FoC, *'C.G.G.J. van Steenis 8585* (GH) / *'2C.G.G.J. van Steenis 9621* (GH), Sumatra, 2 Feb. 1937 / Sumatra, 7 Mar. 1937, –, –, –, –, ¹KT957620*, –, –, –, –, –, –, *Lobelia taliensis* Diels 1912 [= *L. colorata* Wall. subsp. *taliensis* (Diels) T.J. Zhang & D.Y. Hong 1992, but considered a good species in FoC 2011], *E.B. Howell 139* (IBSC), P.R. China, Yunnan, Tengchong, collecting date unknown, –, –, KT710190*, –, –, –, –, –, –.

African and New World Lobelia sect. Rhynchopetalum and relatives: Apetahia longistigmata (F.Br.) E. Wimm.*, *K.R. Wood 6480* (PTBG), Marquesas Islands, –, DQ285155, DQ285272, DQ272709, –, –, –, DQ285272, DQ285233, DQ285194, DQ285116; *Apetahia margaretae* (F.Br.) E. Wimm.*, *J.-Y. Meyer 993* (PAP), Rapa (Austral Islands), –, DQ285169, DQ285286, DQ272723, –, –, –, DQ285286, DQ285247, DQ285208, DQ285130; *Brighamia insignis* A. Gray*, *'A. Antonelli 251* (GB) / *'2T. Givnish & K. Sytsma 3001* (WIS) / *'3050389* (NTBG), collector unknown, ²Kaua, ¹EU219385, ²DQ285139, ²AF042664, ²DQ272693, ²Knox (2014), ²Knox (2014), ²Knox (2014), ²DQ285256, ²DQ285217, ²DQ285178, ²DQ285100; *Lobelia aberdarica* R.E. Fr. & T.C.E. Fr., *L.Y. Chen & al. S140* (M), Kenya, Bungoma, near the border between Uganda and Kenya, Mt Elgon, 01°04'28.62"N, 034°39'17.91"E, 3200 m alt., 17 Jan. 2014, KT957601*, KT957581*, KT710181*, KU238152*, KT710161*, KT710161*, KT710161*, –, –, –, –, *Lobelia bambusetii* R.E. Fr. & T.C.E. Fr., *Sino-African research group SAJIT-002087* (HIB, M), Kenya, Nyeri, Mount Kenya National Park, Naro Moru River Bodge, 00°10'13.21"S, 037°12'51.36"E, 3065 m alt., 23 Jul. 2014, KT957602*, KT957569*, KT710182*, KU238153*, KT710162*, KT710162*, KT710162*, –, –, –, –, *Lobelia burtii* E.A. Bruce*, *Sino-African research group SAJIT-002560* (HIB, M), Tanzania, Arusha, Mt Meru, 03°13'13.15"S, 036°46'41.31"E, 3397 m alt., 6 Aug. 2014, KT957603*, KT957578*, –, KU238149*, KT710163*, KT710163*, KT710163*, –, –, –, –, *Lobelia cardinalis* L., *'T. Ayers 976* (ASC) / *'2Vincent 4377* (GB) / *'3USBG 04-0230* (US) / *'T. Givnish*, unvouchered, ²U.S.A., ¹AY350630, ²DQ356231, ³GQ248634, ¹DQ272722, Knox (2014), ³GQ248149, –, ⁴DQ285285, ⁴DQ285246, ⁴DQ285207, ⁴DQ285129; *Lobelia columnaris* Hook. f., *Hamilton s.n.* (MICH), West Africa, –, DQ285158, DQ285275, DQ272712, –, –, –, DQ285275, DQ285236, DQ285197, DQ285119; *Lobelia deckenii* subsp. *sattimae* (R.E. Fr. & T.C.E. Fr.) Mabberley*, *Sino-African research group SAJIT-002147* (HIB, M), Kenya, Nyeri, Aberdare National Park, 00°19'50.68"S, 36°38'57.01"E, 3643 m alt., 28 Jul. 2014, KT957604*, KT957580*, KT710197*, KU238154*, KT710164*, KT710164*, KT710164*, –, –, –, –, *Lobelia exaltata* Pohl*, *A. Antonelli 335* (GB), –, EU219383, DQ356200, DQ356135, –, –, –, –, –, –, *Lobelia fistulosa* Vell., *A. Antonelli & L. Andersson 279* (GB), Brazil, EU219387, DQ356201, DQ356136, –, –, –, –, –, –, *Lobelia giberroa* Hemsl.*, *Sino-African research group SAJIT-002560* (HIB, M), Tanzania, Arusha, Mt Meru, 03°13'30.36"S, 36°47'52.05"E, 2618 m alt., 6 Aug. 2014, KT957603*, KT957576*, KT710198*, KU238155*, KT710176*, KT710176*, KT710176*, –, –, –, –, *Lobelia gloria-montis* Rock*, *T. Givnish 1008* (WIS), Maui, –, DQ285148, DQ285265, DQ272702, –, –, –, DQ285265, DQ285226, DQ285187, DQ285109; *Lobelia hypoleuca* Hillebr., *'Selling & Skottsb. 3194* (GB) / *'2T. Givnish 1017* (WIS), Oahu, –, ¹DQ356191, ¹DQ356126, ²DQ272703, –, –, –, ²DQ285266, ²DQ285227, ²DQ285188, ²DQ285110; *Lobelia laxiflora* Kunth*, *'T. Ayers 413* (TEX) / *'77.0051* (UCBG), collector unclear, ²Mexico, ¹AY350631, ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014), ²Knox (2014); *Lobelia longispala* Engl., *E. Knox 3522* (IND), collected in Tanzania, cultivated plants in the Indiana University-Bloomington greenhouses, –, Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014); *Lobelia morogoroensis* E.B. Knox & Pócs*, *E. Knox 619* (MICH), collected in Tanzania, cultivated plants in the Indiana University-Bloomington greenhouses, –, Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014), Knox (2014).

