SYSTEMATICS AND PHYLOGENY

Evolution of *Impatiens* (Balsaminaceae) in the Albertine Rift – The endemic *Impatiens purpureoviolacea* complex consists of ten species

Eberhard Fischer,[1] Stefan Abrahamczyk,[2] Norbert Holstein[3] & Steven B. Janssens[4]

1 *Institut für Integrierte Naturwissenschaften – Biologie, Universität Koblenz-Landau, Universitätsstraße 1, 56070 Koblenz, Germany*
2 *Nees Institute for Biodiversity of Plants, University of Bonn, Meckenheimer Allee 170, 53115 Bonn, Germany*
3 *Natural History Museum, Cromwell Rd., London SW7 5BD, United Kingdom*
4 *Botanic Garden Meise, Nieuwelaan 38, Meise, 1860, Belgium*
Address for correspondence: *Eberhard Fischer, efischer@uni-koblenz.de*

DOI https://doi.org/10.1002/tax.12566

Abstract The Albertine Rift harbours a highly diverse flora with numerous endemic species. An important component of the forest understorey is the herbaceous genus *Impatiens*. Fieldwork in Burundi, the Democratic Republic of the Congo and Rwanda as well as morphological studies indicated that the Albertine Rift endemic *Impatiens purpureoviolacea* represents a species complex. We analyzed the hidden diversity of the complex using morphological and molecular data supplemented by herbarium studies. We found that the *Impatiens purpureoviolacea* complex can be divided into morphologically and phylogenetically well characterized clades containing ten species and a natural hybrid. We describe all of these species, provide a species key and analyze their evolutionary history. Beside *Impatiens purpureoviolacea* and *I. gesneroidea*, the already described *I. urundiensis* is resurrected from synonymy. Two varieties, *Impatiens purpureoviolacea* var. *longicalcarata* and *I. gesneroidea* var. *superglabra* are raised to species status, and five new species (*Impatiens elwiraurzulae*, *I. lotteri*, *I. ludewigii*, *I. lutzmannii*, *I. versicolor*) and a new natural hybrid (*I.* ×*troupinii*) are described. Within the mostly insect-pollinated species of the clade, two bird-pollinated species (*Impatiens gesneroidea*, *I. superglabra*) evolved independently. The clade split from its sister taxon in the Pliocene and started diversifying during the Pliocene/Pleistocene transition in parallel to an increased mountain uplifting and volcanic activity in the Albertine Rift. It further diversified during the Pleistocene, likely due to the changes in forest cover and connectivity induced by climatic fluctuations.

Keywords Burundi; Democratic Republic of the Congo; East Africa, endemics; geological activity; new species; plant taxonomy; Rwanda; tropical mountain forest

Supporting information may be found online in the Supporting Information section at the end of the article.

INTRODUCTION

The Albertine Rift between western Uganda and the southern tip of Lake Tanganyika is one of the biodiversity hotspots on earth (e.g., Mutke & Barthlott, 2005; Kier & al., 2009; Dagallier & al., 2019). The geographically and climatically complex region is characterized by a large biome gradient situated between 250 and 5119 m elevation and includes several mountain ranges and large lakes (Plumptre & al., 2003; Mutke & al., 2011). The region started to form into its current shape during the Miocene with increased mountain uplifting, valley subsidence and volcanic activity during the Plio-Pleistocene (Hamilton, 1982; Pickford & al., 1993; Durham, 2008) and served as a forest refuge during the ice ages (Loader & al., 2014). Due to the high geographic and climatic complexity, the relatively young Albertine Rift harbours an extraordinarily diverse flora (c. 5800 vascular plant species), including about 10% of endemic species (Plumptre & al., 2007).

An important element in the African flora that is also well represented in the Albertine Rift is the species-rich, herbaceous genus *Impatiens* L. (Linnaeus, 1753: 937). This genus contains more than 1200 species (Yuan & al., 2004; Janssens, 2008; Janssens & al., 2009a,b, 2011), of which 131 occur in tropical Africa (Abrahamczyk & al., 2016; Janssens & al., 2018). Alongside with the western African mountain ranges (28 endemic species; Janssens & al., 2010) and the Eastern Arc Mountains and Kenyan Highlands (24 endemic species; Grey-Wilson, 1980; Janssens & al., 2018), the Albertine Rift (20 endemic species; Wilczek & Schulze, 1960; Grey-Wilson, 1980; Fischer, 1997; Fischer & al., 2003) can be considered one of the most important centres of diversity for *Impatiens* in tropical Africa. Two of the Albertine Rift endemics, *I. purpureoviolacea* (Gilg, 1909: 122) and *I. gesneroidea* (Gilg, 1909: 116) were first collected

Article history: Received: 13 May 2020 | returned for (first) revision: 10 Sep 2020 | (last) revision received: 21 May 2021 | accepted: 27 May 2021 | published online: 6 Sep 2021 | **Associate Editor:** Eric H. Roalson | © 2021 The Authors.
TAXON published by John Wiley & Sons Ltd on behalf of International Association for Plant Taxonomy.

during an expedition to Central Africa in 1907/1908 (Mecklenburg, 1910) by Johannes Mildbraed in the Rugege (= Nyungwe) Forest of Rwanda at the Rukarara near the source of the Nile. Based on a recent phylogeny (Lozada-Gobilard & al., 2019), these two species are closely related. Gilg (1914: 227) additionally described a related species to *I. purpureoviolacea* (*I. urundiensis*) from northeastern Burundi. In the only modern revision of African *Impatiens*, Grey-Wilson (1980) placed this taxon as well as *I. purpureoviolacea* var. *longicalcarata* G.M.Schulze (1947: 270) from the eastern Democratic Republic of the Congo in synonymy with *I. purpureoviolacea*. Almost simultaneously, Grey-Wilson (1979: 642) described a new variety of *I. gesneroidea* from the high-altitude montane rainforest of the western Albertine Rift. He also took note of a putative hybrid between *I. purpureoviolacea* and *I. gesneroidea* based on a herbarium specimen (Troupin & Grey-Wilson, 1983; Grey-Wilson, 1989). As a result, only three (*I. gesneroidea* var. *gesneroidea*, *I. gesneroidea* var. *superglabra*, *I. purpureoviolacea*) of the five described taxa are currently recognized as valid (Grey-Wilson, 1980).

Recent fieldwork revealed notable differences in morphology and ecology between different populations of the *Impatiens purpureoviolacea* complex. Some differences in flower traits have already been analyzed in a study on pollination syndromes in Balsaminaceae, revealing butterfly/bee, butterfly, and bird pollination syndromes in different populations of *I. purpureoviolacea* and *I. gesneroidea* (Abrahamczyk & al., 2017). In all cases, plant morphology did not show a considerable variability within populations. Except the bird-pollinated *I. gesneroidea*, which grows sympatrically with different insect-pollinated populations of the *I. purpureoviolacea* complex, very few populations occurred more or less sympatrically, and we did not find intermediates between these. Therefore, our field observations suggested that the *I. purpureoviolacea* complex consists of several different species. In this paper we analyze the hidden diversity of the *I. purpureoviolacea* complex using morphological and molecular data supplemented by herbarium studies and shed light on the evolution of the complex.

■ MATERIALS AND METHODS

Plant material. — Fieldwork in Rwanda, Burundi and in the eastern part of the Democratic Republic of the Congo since 1984 was done to collect different populations/taxa of the *Impatiens purpureoviolacea* complex. The complex is characterized by mostly pinkish flowers with dark red and yellow nectar guides and filiform, strongly enrolled flower spurs. However, *I. gesneroidea* s.l. with red flowers and bucciniform spurs is nested within the complex. In order to define *I. purpureoviolacea* and *I. gesneroidea* s.str., the first author visited the existing type locality of both species, now in Nyungwe National Park near the source of the Rukarara stream. Living plants from most taxa (Appendix 1) were brought into the Botanical Gardens of Bonn University in Germany for further cultivation and genetic analyses. Only from *I. gesneroidea* var. *superglabra* and an undescribed species, here described as *Impatiens lotteri* sp. nov., we could not collect fresh material since it is not possible to visit the eastern provinces of the Democratic Republic of the Congo due the political instability in the region. Herbarium specimens and photos were taken from plants in the field as well as from plants in cultivation. Plant traits were measured from fresh, cultivated material, which did not differ notably from wild plants.

Herbarium material. — In addition to our fieldwork, all available herbarium specimens of the *Impatiens purpureoviolacea* complex in B, BM, BR, K and P were studied. These specimens include all described types as well as those listed by Grey-Wilson (1980).

Seed coat micromorphology. — Mature seeds were studied after critical point drying (CPD 020 Balzers Union), using a scanning electron microscope (SEM, Cambridge S200). Seeds from all species except *Impatiens lotteri* and *I. superglabra* comb. & stat. nov. have been available for this study.

Molecular protocols and phylogenetic analyses. — We isolated total genomic DNA using an improved CTAB protocol (Doyle & Doyle, 1987) optimized for *Impatiens* (Janssens & al., 2006, 2008). Amplification of the plastid *atpB-rbcL* intergenic spacer and the nuclear *AP3*/*DEF* homologues (*ImpDEF1*, *ImpDEF2*) followed Janssens & al. (2006, 2007). Amplification reactions were carried out with a 25 µl reaction mix containing 1 µl DNA, 2 × 1 µl oligonucleotide primer (100 ng/µl), 2.5 µl of 10 mM dNTPs, 2.5 µl Taq Buffer, 0.2 µl KAPA Taq DNA polymerase and 16.8 µl MilliQ water. PCR reactions always started with a 2 min denaturation at 94°C, followed by 30 cycles including: a denaturation phase of 30 s at 94°C, an annealing phase of 30 s (*ImpDEF1*: 57°C, *ImpDEF2*: 55.5°C, *atpB-rbcL*: 51°C) and an extension phase of 60 s at 72°C. We used Gene Amp PCR system 9700 (Applied Biosystems, Waltham, Massachusetts, U.S.A.) to perform the amplification reactions. After an exo-sap purification protocol, samples were sent for sequencing to Macrogen (Seoul, South Korea). Newly obtained sequences were deposited at GenBank (Appendix 1).

Sequence assembly was carried out with Geneious v.11.2 (Biomatters, New Zealand). Automatic alignment was performed with MAFFT (Katoh & al., 2002) under an E-INS-i algorithm, a 100PAM/k=2 scoring matrix, a gap open penalty of 1.3 and an offset value of 0.123, after which the dataset was manually optimized in Geneious v.11.2. One of the taxa (*Impatiens ×troupinii* nothosp. nov.) included in the current molecular phylogenetic analysis is a hybrid accession between *I. gesneroidea* and *I. purpureoviolacea*. For this taxon, the nuclear markers (*ImpDEF1*, *ImpDEF2*) were checked for double peaks. For each occurrence of a double peak, the nucleotide was compared with other accessions in the dataset and assigned to the group of taxa to which each of the putative parents belonged. As a result, for the nuclear dataset, *I. ×troupinii* is characterized by two copies (one from each parent species). Tree topologies and molecular datamatrices are availabe at TreeBASE under accession numbers S27098 and S27099.

The best-fit nucleotide substitution model was selected for each gene marker using jModelTest v.2.1.4 (Posada, 2008) following the Akaike information criterion (AIC). For *ImpDEF1*, GTR+I+I was selected as most optimal model, whereas GTR+I was the optimal model for *ImpDEF2* and *atpB-rbcL*. Phylogenetic analyses were carried out using three methodologies (maximum likelihood, maximum parsimony, Bayesian inference). For each method, we analyzed two individual data partitions (plastid *atpB-rbcL*; nuclear *ImpDEF1*/*ImpDEF2*) and a combined data matrix. Possible phylogenetic conflicts between plastid and nuclear data matrices were inferred by a partition homogeneity test as implemented in PAUP* v.4.0b10a (Swofford, 2002) as well as through visual inspection by searching for conflicting relationships within each topology according to the presence of hard (strongly supported) and soft (weakly supported) incongruences for each node (Johnson & Soltis, 1998).

Maximum likelihood (ML) tree inference was conducted using RAxML v.7.4.2 (Stamatakis, 2006) under the general time reversible (GTR) substitution model with gamma rate heterogeneity, and Lewis correction. Support values for the large angiosperm dataset were obtained via the rapid bootstrapping algorithm (RAxML v.7.4.2; Stamatakis, 2006), examining 1000 pseudo-replicates under the same parameters as for the heuristic ML analyses. Bootstrap values (ML-BS) were visualized using the consensus tree builder algorithm as implemented in Geneious v.11.0.

Maximum parsimony (MP) analyses were conducted using PAUP v.4.0b10a (Swofford, 2002) in which 100 heuristic search replicates were analyzed with a random stepwise addition of taxa, and tree-bisection-reconnection (TBR) branch swapping. Non-parametric bootstrapping (MP-BS) was conducted for 500 bootstrap replicates, thereby applying the same settings as in the original MP heuristic analyses.

Bayesian inference (BI) analyses were conducted with MrBayes v.3.1 (Huelsenbeck & Ronquist, 2001). For the combined dataset, as well as the nuclear dataset, a mixed-model approach was used in the datasets that were partitioned in order to apply a different model of evolution on each DNA region (Ronquist & Huelsenbeck, 2003). Each analysis was run two times for 10 million generations. Trees were sampled every 2500 generations. Inspection of chain convergence and effective sample size (ESS) parameters was done with Tracer v.1.7.1 (Suchard & al., 2018). Bayesian inference posterior probability (BPP) values between 0.50 and 0.95 as summarized in the 50% majority-rule consensus tree were considered weak support, only BPP values above or equal to 0.95 were taken into consideration (Suzuki & al., 2002; Alfaro & al., 2003).

Divergence time analysis. — A Bayesian MCMC divergence time analysis on the concatenated alignment of *atpB-rbcL*, *ImpDEF1* and *ImpDEF2* (excluding the hybrid *Impatiens ×troupinii*) was carried out with BEAST v.1.10 (Suchard & al., 2018) with its xml input file being optimized in BEAUTi v.1.10 (Suchard & al., 2018). The age of the *I. purpureoviolacea* complex was inferred by applying a secondary calibration approach, in which the crown node age was set under a normal prior with a mean of 3.51 myr and a standard deviation of 0.5. This age was inferred from the studies of Janssens (2008) and Janssens & al. (2009a,b). A partitioned Bayesian MCMC analysis – with partitions being unlinked – was carried out as different substitution models were estimated for *atpB-rbcL*, and *ImpDEF1* and *ImpDEF2*. Evolutionary modelling followed a Yule speciation whereas rates across lineages were set to vary under an uncorrelated relaxed lognormal molecular clock. We selected the latter clock model based on the performance of a marginal likelihood estimation using the generalised stepping-stone sampling methodology (Baele & al., 2016) under standard parameters. Ten million generations were run, sampling was done every 1000th generation. Convergence of the chains and ESS parameter evaluation (ESS > 200) were checked using Tracer v.1.7.1 (Suchard & al., 2018). A maximum clade credibility tree with a posterior probability limit of 0.5 was reconstructed using TreeAnnotator v.1.10.1 (Suchard & al., 2018).

■ RESULTS

Phylogenetic relationships of the species of the *Impatiens purpureoviolacea* complex. — Sequence characteristics for all datasets are summarized in Table 1. All three methods of phylogenetic inference (ML, MP, BI) provided the same topology for chloroplast, nuclear and combined datasets. The chloroplast *atpB-rbcL* dataset consists of 18 accessions and 729 analyzed characters (15 variable characters). The nuclear *ImpDEF1/ImpDEF2* dataset contains 20 accessions and 1752

Table 1. Sequence characterstics of each datamatrix.

	Taxa	Characters	Parsimony-informative characters	Variable characters	Consistency index	Retention index
atpB-rbcL	17 + 1*	729	2	15	1	1
ImpDEF1/ImpDEF2	18 + 2(1)*$^{\#}$	1023	43	145	0.95	0.92
Combined	18	1752	45	160	0.95	0.93

Consistency index: Kluge & Farris (1969), retention index: Farris (1989).

* indicates inclusion of the hybrid accession, $^{\#}$ indicates inclusion of two copies of the nuclear genes *ImpDEF1* and *ImpDEF2* of the hybrid accession.

analyzed characters (145 variable characters). The chloroplast tree is only barely resolved (suppl. Fig. S1A–C) whereas the nuclear tree is well resolved (suppl. Fig. S2A–C). No incongruency was found between the different datasets, except for the position of the hybrid between *Impatiens purpureoviolacea* and *I. gesneroidea* (*I.* ×*troupinii* nothosp. nov.), which clearly differs in position between the chloroplast and the nuclear topology (suppl. Figs. S1, S2). After removing the hybrid from both nuclear and plastid datasets, the incongruency was not detected anymore ($P > 0.05$). As such the combined plastid-nuclear phylogeny (Fig. 1) contained all specimens of the separated analyses except for *I.* ×*troupinii* and was used for further analyses on the *I. purpureoviolacea* complex (suppl. Fig. S3A–C).

The *Impatiens purpureoviolacea* complex is closely related to a clade occurring east of the Great Rift Valley, including *I. meruensis* or *I. ulugurensis*. The crown node (MP-BS: 98, ML-BS: 99, BPP: 1.0) splits the *I. purpureoviolacea* complex into two lineages (Fig. 1): The first one (clade I) is an unresolved clade representing three morphologically, geographically and ecologically distinct species, *I. urundiensis* and *I. lutzmannii* sp. nov. from Burundi and *I. kivuensis* nom. nov. from Burundi and the eastern Democratic Republic of the Congo (MP-BS: 72, ML-BS: 85, BPP: 0.97; Fig. 2). These species are characterized by hairy ovaries and fruits, and pubescent stems and young leaves with beige hairs. The second clade (clade II) contains all extant accessions investigated in this study (MP-BS: 86, ML-BS: 90, BPP: 1.0). This latter clade is again organized into two well-supported clades: The first one (clade III) contains the five accessions of *I. purpureoviolacea* s.str. (MP-BS: 75, ML-BS: 93, BPP: 1.0), which are all from Rwanda and characterized by hairy ovaries and fruits, and

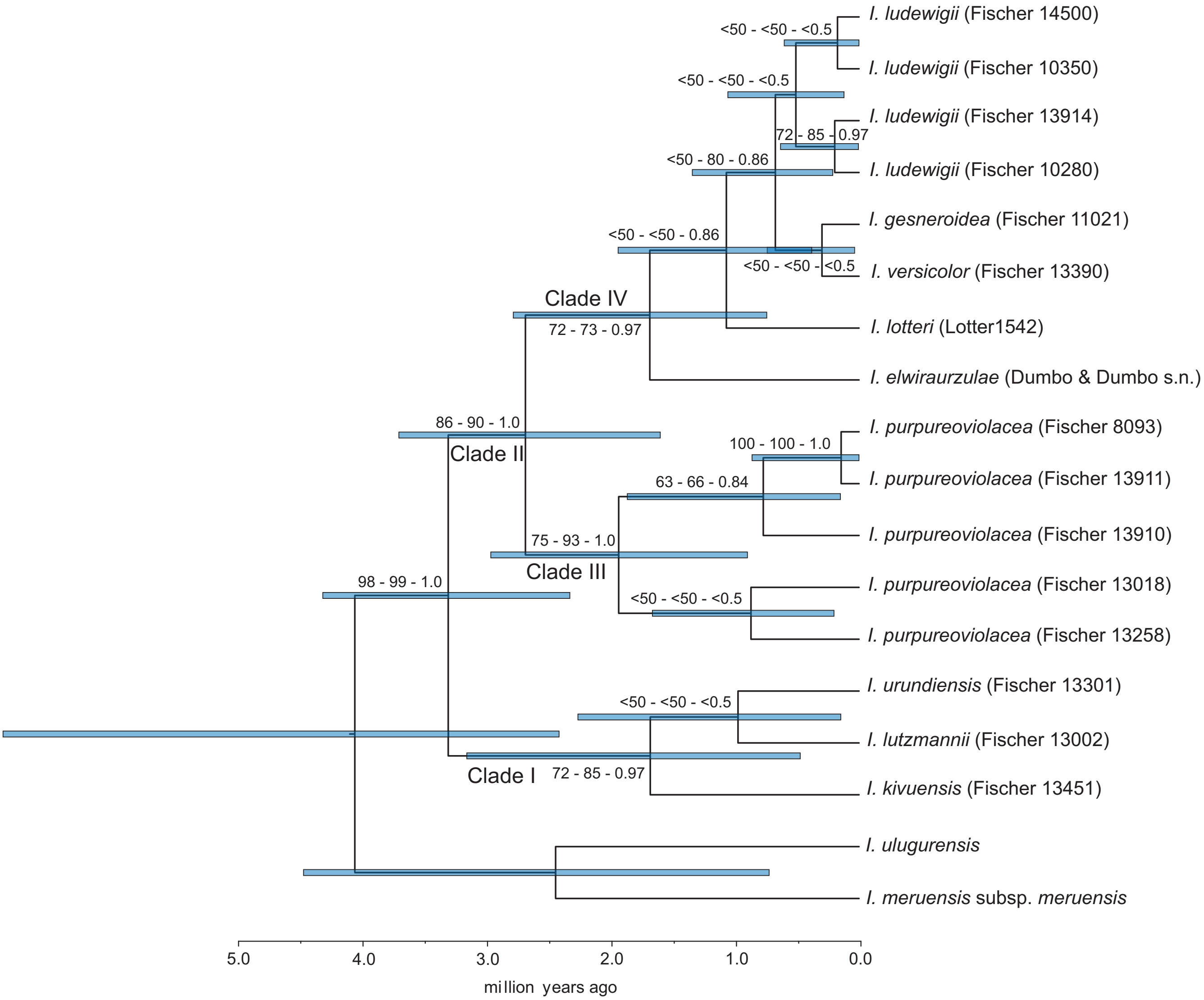

Fig. 1. Maximum clade credibility tree of the *Impatiens purpureoviolacea* complex as obtained via the BEAST dating analysis. Node bars indicate 95% highest posterior density confidence intervals. Support values of the MP, ML and BI analyses are shown on the branches.

pubescent stems and young leaves with white hairs (Fig. 2). The second clade (clade VI) is formed by *I. elwiraurzulae*, *I. lotteri*, *I. gesneroidea*, *I. ludewigii* sp. nov. and *I. versicolor* sp. nov.. Within clade VI, *I. elwiraurzulae* sp. nov. and *I. lotteri*, both from the eastern Democratic Republic of the Congo (Fig. 2), are the first species to branch off, with the former being the first (MP-BS: 72, ML-BS: 73, BPP: 0.97) followed by *I. lotteri* sp. nov. (MP-BS: <50, ML-BS: <50, BPP: 0.86). The remaining accessions represent the morphologically and ecologically distinct species *I. versicolor*, *I. gesneroidea* s.str. and *I. ludewigii* and form a polytomy (MP-BS: <50, MP-BS: 80, BPP: 0.86). Whereas *I. versicolor* is confined to Rwanda, *I. ludewigii* and *I. gesneroidea* also occur in the eastern Democratic Republic of the Congo and *I. gesneroidea* also in Burundi (Figs. 2, 3). All species of clade IV are characterized by glabrous ovaries and fruits, and sparsely pubescent stems and young leaves with transparent hairs.

Besides the species represented in the phylogeny, one more taxon of the *Impatiens purpureoviolacea* complex from the eastern Democratic Republic of the Congo (Fig. 3) exists, for which we were not able to get fresh material: *I. superglabra* comb. & stat. nov., formerly described as *I. gesneroidea* var. *superglabra*. *Impatiens superglabra* is probably closely related to the species of clade I due to its pilose ovaries and its stems and young leaves covered with beige hairs.

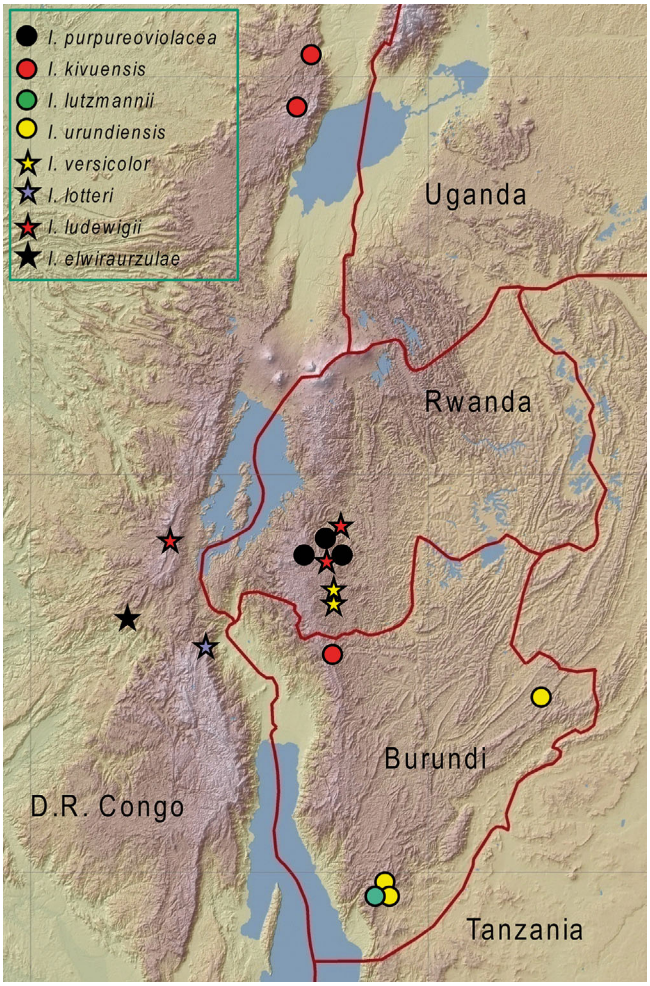

Fig. 2. Distribution map of the eight insect-pollinated species of the *Impatiens purpureoviolacea* complex. Dots indicate species with hairy ovaries, and stars mark species with glabrous ovaries.

All species of the *Impatiens purpureoviolacea* complex have small to very small, mostly non-overlapping distribution ranges (Figs. 2, 3). *Impatiens lutzmannii*, *I. elwiraurzulae* and *I. lotteri* are only known from the type localities. Only *I. kivuensis* has a strongly disjunct range in the northwest of Lake Edward and at Mount Teza in northern Burundi. In a few cases two taxa occur close to each other but largely differ in elevations (*I. ludewigii* at lower vs. *I. purpureoviolacea* at higher elevations in the montane forest) or occur in different habitats, such as dense montane forest (*I. lutzmannii*) vs. open grassland with gallery forests (*I. urundiensis*). In the Kahuzi-Biéga massif, *I. gesneroidea* from the montane forest and the lower bamboo zone is replaced by *I. superglabra* in the upper bamboo zone, ericaceous shrub and paramo, again without any intermediate plants. Only the range of the bird-pollinated *I. gesneroidea* overlaps with the ranges of the insect-pollinated *I. purpureoviolacea* and *I. ludewigii*. Here, we found the only and rare natural hybrid of the complex, *I. ×troupinii*, which is perfectly intermediate between the sympatric parents *I. gesneroidea* and *I. purpureoviolacea*.

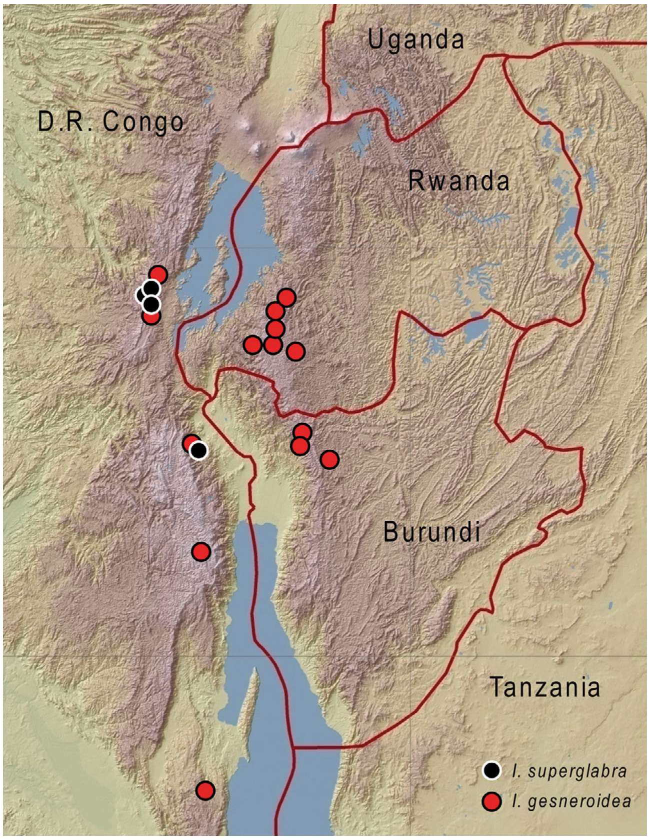

Fig. 3. Distribution map of the two bird-pollinated species from the *Impatiens purpureoviolacea* complex.

Divergence time estimates. — Long before reaching 10 million generations, stationarity was reached between the different chains with ESS values never lower than 200 and mostly above 500. The BEAST maximum clade credibility tree (mcct) is shown in Fig. 1. The *Impatiens purpureoviolacea* complex started diversifying in the Pliocene, 3.31 (4.32–2.37) mya. At 2.67 mya, a next split occurred at which *I. purpureoviolacea* diverged from the clade containing *I. lotteri*, *I. elwiraurzulae*, *I. gesneroidea*, *I versicolor* and *I. ludewigii*). All other divergence events are estimated to have occurred in the Pleistocene.

Seed coat micromorphology. — The mature seeds of *Impatiens elwiraurzulae*, *I. gesneroidea*, *I. kivuensis*, *I. ludewigii*, *I. lutzmannii*, *I. purpureoviolacea*, *I. ×troupinii*, *I. urundiensis* and *I. versicolor* have been studied. The seeds show a similar overall morphology. The testa is covered with hairlike, club-shaped appendages with a network of thickenings with small regularly spaced window-like surfaces. This seed type has already been documented by Grey-Wilson (1980) for *I. gesneroidea*. In *I. purpureoviolacea*, these appendages are dense and rounded, while they are more lax, longer and flattened in *I. lutzmannii* (Fig. 4A–D). *Impatiens urundiensis* bears almost globose and short appendages on the testa (Fig. 4E,F). The appendages in *I. kivuensis* are similar to those in *I. purpureoviolacea* but distinctly longer and with a pronounced reticulation (Fig. 5A,B). In the hybrid *I. ×troupinii*, they are dense, also club-shaped and show only a weak reticulation (Fig. 5C,D). In *I. elwiraurzulae*, the appendages are much less dense and shorter (Fig. 5E,F). *Impatiens ludewigii* shows short rounded-globose and almost composed appendages with dense and narrow reticulations (Fig. 6A–C). *Impatiens versicolor* has a testa with dense and long appendages and very pronounced reticulations (Fig. 6D,E), and seeds of *I. gesneroidea* have similar long appendages (Fig. 6F,G).

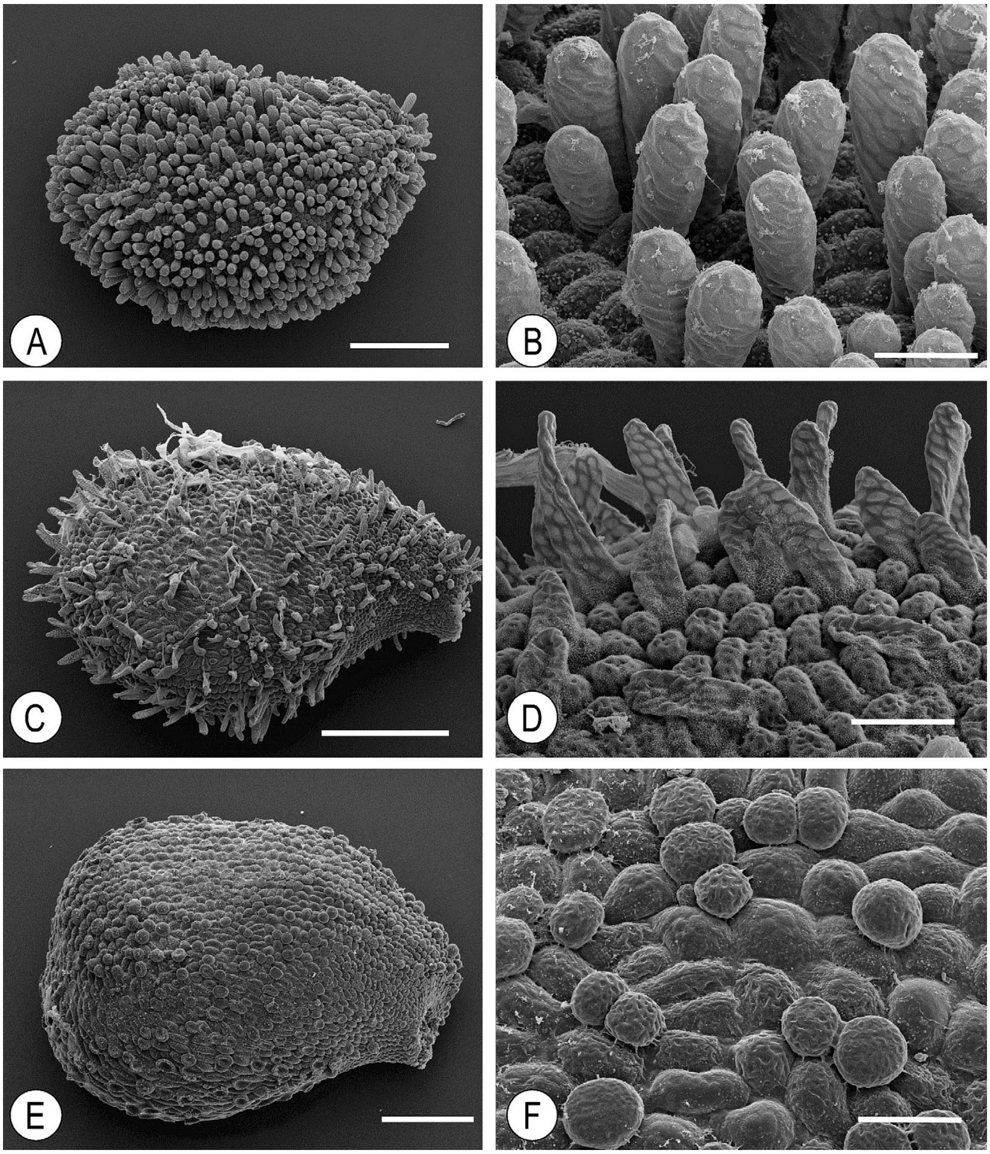

Fig. 4. Seeds of the *Impatiens purpureoviolacea* complex. **A** & **B**, *Impatiens purpureoviolacea*: **A**, Seed; **B**, Detail of testa. **C** & **D**, *Impatiens lutzmannii*: **C**, Seed; **D**, Detail of testa. **E** & **F**, *Impatiens urundiensis*: **E**, Seed; **F**, Detail of testa. — Scale bars: A, 300 µm; B, 60 µm; C, 500 µm; D, 80 µm; E, 500 µm; F, 90 µm. A & B, *Fischer 12958*, BG Bonn 36240; C & D, *Fischer 13002*, BG Bonn 33486; E & F, *Fischer 13301*, BG Bonn 35170.

■ DISCUSSION

Phylogenetic relationships and evolution of the *Impatiens purpureoviolacea* complex. — In our study, we disentangled the taxonomy, systematics and evolution of the *Impatiens purpureoviolacea* complex. We showed that the complex is composed of 10 species with mostly non-overlapping distribution ranges. All species, but also the individual clades are well characterized by sets of morphological traits (for details, see Taxonomic treatment). Based on the pollination syndrome most species of the *I. purpureoviolacea* complex are pollinated by butterflies and/or bees, but also two bird-pollinated species exist (Abrahamczyk & al., 2017). Due to their morphology, the latter two species are probably not closely related (*I. gesneroidea* in clade IV and *I. superglabra* comb. & stat. nov. probably occurring in clade I). Sister relationships of morphologically very different species with different pollinator groups have been shown for other African *Impatiens* species as well, such as *I. kilimanjari* Oliv. (Oliver, 1885: 398) and *I. pseudoviola* Gilg (1909: 121); *I. salpinx* G.M.Schulze & Launert and *I. wuerstenii* S.B.Janssens & Dessein and its relatives; and *I. hians* Hook.f. and *I. columbaria* Bos/*I. palpebrata* Hook.f. (Janssens & al., 2010, 2018). The bird-pollinated species in the *I. purpureoviolacea* complex, as well as *I. kilimanjari/pseudoviola*, occur in higher elevations than the insect-pollinated sister taxa. These results further indicate that the evolution

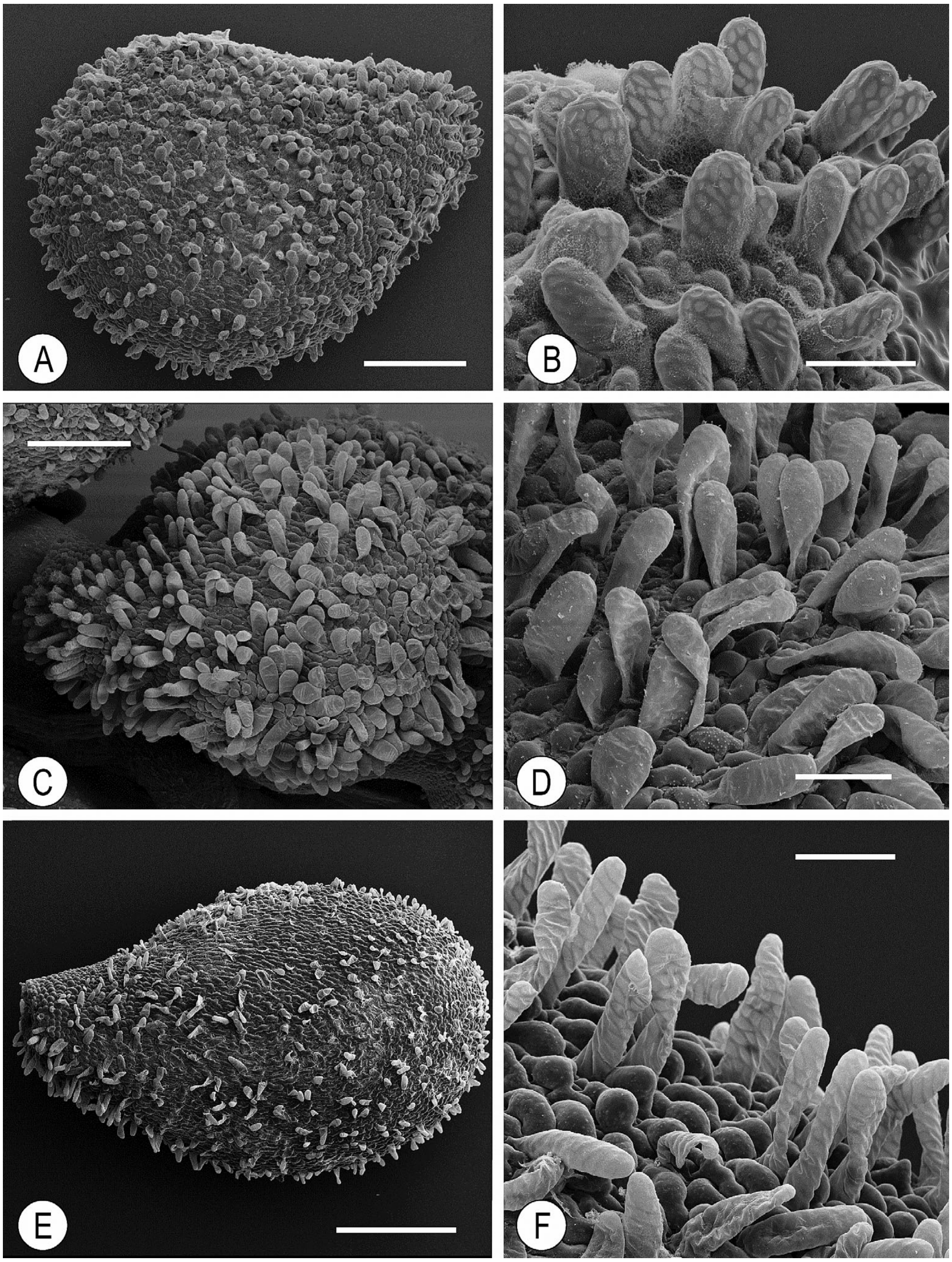

Fig. 5. Seeds of the *Impatiens purpureoviolacea* complex. **A** & **B**, *Impatiens kivuensis*: **A**, Seed; **B**, Detail of testa. **C** & **D**, *Impatiens ×troupinii*: **C**, Seed; **D**, Detail of testa. **E** & **F**, *Impatiens elwiraurzulae*: **E**, Seed; **F**, Detail of testa. — Scale bars: A, 400 µm; B, 70 µm; C, 300 µm; D, 90 µm; E, 700 µm; F, 100 µm. A & B, *Fischer 13451*, BG Bonn 34557; C & D, *Fischer 13912*, BG Bonn 37754; E & F, *Dumbo & Dumbo s.n.*, BG Bonn 39658.

of pollination syndromes is highly dynamic in *Impatiens* (Abrahamczyk & al., 2017; Lozada-Gobilard & al., 2019).

In the narrow areas where the ranges of *Impatiens gesneroidea* and *I. purpureoviolacea* or of *I. kilimanjari* and *I. pseudoviola* overlap, natural hybrids (*Impatiens* ×*troupinii* nothosp. nov. or *I.* ×*kaskazini* J.M.Grimshaw & Grey-Wilson [1997: 29] and *I.* ×*lateritia* Gilg [1909: 122], respectively) occur between the bird- and the insect-pollinated species. In contrast to the vigorously growing, relatively common *I.* ×*kaskazini*, *I.* ×*lateritia* and *I.* ×*troupinii* are rare and do not form larger stands (Grimshaw & Grey-Wilson, 1997). These results indicate that different pollinator groups represent relatively effective hybridization barriers.

The distribution of the *Impatiens purpureoviolacea* complex is apparently restricted to Precambrian crystalline massifs in the Albertine Rift. The taxa of this clade are present on the western crest of the Albertine Rift in the eastern Democratic Republic of the Congo like the Kahuzi-Biéga massif or on the Congo-Nile Divide in the eastern Albertine Rift from Nyungwe to Kibira and Bururi forests (Fig. 2). They have never been recorded in areas with Tertiary volcanism like the Virunga Massif. Interestingly, they are also absent from the Precambrian massifs north of the Virunga Volcanoes like the Bwindi Impenetrable forest in Uganda.

The *Impatiens purpureoviolacea* complex split from its sister taxon in the Pliocene and started to radiate during the

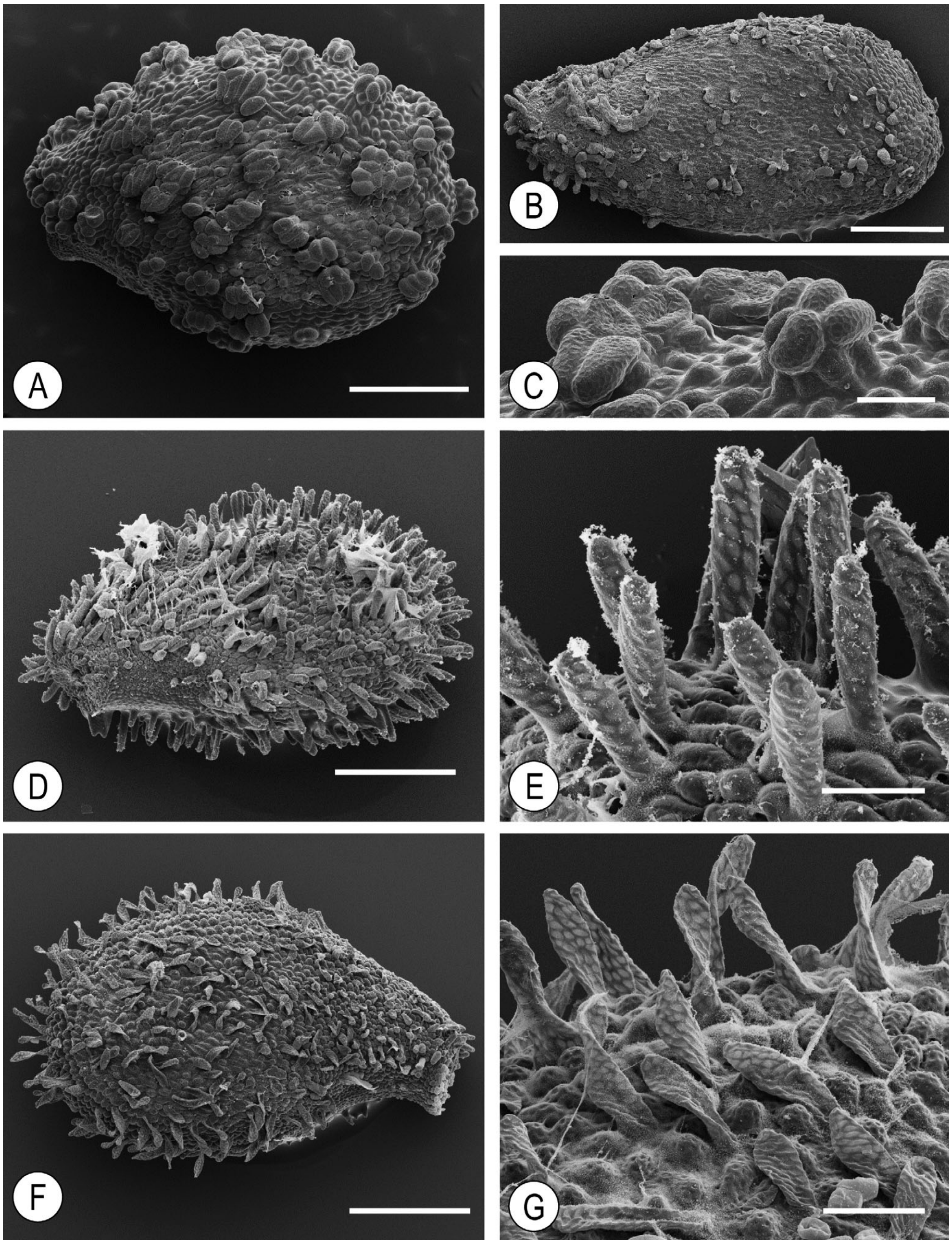

Fig. 6. Seeds of the *Impatiens purpureoviolacea* complex. **A–C**, *Impatiens ludewigii*: **A** & **B**, Seed; **C**, Detail of testa. **D** & **E**, *Impatiens versicolor*: **D**, Seed; **E**, Detail of testa. **F** & **G**, *Impatiens gesneroidea*: **F**, Seed; **G**, Detail of testa. — Scale bars: A, 600 µm; B, 500 µm; C, 100 µm; D, 400 µm; E, 70 µm; F, 400 µm; G, 100 µm. A–C, *Fischer 13912*, BG Bonn 37754; D & E, *Fischer 13988*, BG Bonn 34557; F & G, *Fischer 11021*, BG Bonn 32578.

transition from the Pliocene to the Pleistocene. During this time an increased mountain uplifting and volcanic activity were observed in the Albertine Rift (Hamilton, 1982; Pickford & al., 1993). Therefore, it seems reasonable to assume that the *I. purpureoviolacea* complex diversified due to the increasing topographical complexity of the Albertine Rift. Changing forest cover and connectivity induced by strong climatic fluctuations during the Pleistocene probably led to further speciation of the *I. purpureoviolacea* complex. This result is in congruence with the very few other existing diversification analyses of plant groups in the Albertine Rift, showing very recent diversification events as well (Muellner-Riehl & al., 2019).

Seed coat micromorphology. — Seeds of the *Impatiens purpureoviolacea* complex except for *I. gesneroidea* (Grey-Wilson, 1980) have never been studied in detail. The seed of *I. gesneroidea* has been defined by Grey-Wilson as type 5 with club-shaped appendages. The seeds of the other species of this complex have been studied here for the first time and fit well with the type recorded for *I. gesneroidea*. The club-shaped, often hairlike appendages have already been described by Launert (1963), who showed that they are not hairs in the strict anatomical sense but derived from a single testa cell and are characterized by reticulate thickenings. These appendages are appressed to the testa when dry but are spreading in the wet stade. They may have a function in adhering the seeds to potential vectors like birds for long-distance dispersal. Detailed analyses of seed coat micromorphology are mainly available for Asian species (Lu & Chen, 1991; Utami & Shimizu, 2005). The seeds of the *I. purpureoviolacea* complex thus belong to the protrusive type – cristate subtype according to Song & al. (2005) and resemble those of *I. walleriana* Hook.f., showing similar appendages with reticulate sculpture but lacking the cuticular granules covering the non-protrusive epidermal cells (Song & al., 2005). Despite their overall similarity the seeds provide useful taxonomic characters at species level.

■ TAXONOMIC TREATMENT

Key to the species of the *Impatiens purpureoviolacea* complex

1. Lower sepal and spur bucciniform, lateral united petals deep red with yellow spots, or entirely wine red 2
1. Lower sepal navicular, abruptly constricted into a spiraled, usually filiform spur 3
2. Leaves herbaceous, densely hairy on both sides, lamina broadly ovate, stem densely covered with hairs, flowers with greenish bucciniform lower sepal tapering into a spur, densely hairy, spur not swollen at apex, dorsal petal deep red with greenish crest, lateral united petals deep red, yellow at throat, ovary and fruit glabrous; montane forest up to 2700 m; Democratic Republic of the Congo, Rwanda, Burundi .... ***I. gesneroidea***
2. Leaves coriaceous, almost glabrous above, hairy below, lanceolate-ovate, stem densely covered with hairlike brownish scales, flowers with bucciniform wine-red lower sepal tapering into a greenish spur, swollen at apex, ± glabrous, dorsal petal wine red with greenish crest, lateral united petals uniformly wine red, ovary and fruit pubescent with tufts of white hairs; bamboo-zone, ericaceous shrub to paramo, 2500–3350 m; Democratic Republic of the Congo .... ***I. superglabra***
3. Flowers magenta, lower sepal entirely greenish, ± abruptly constricted into a spiraled, broadly filiform spur, up to 2 mm in diameter, dorsal petal helmet-like, dark magenta, with green crest above ending in a long spur, not or only slightly bilobed, lateral united petals dark magenta, with dark red and yellow spots at throat; Rwanda .... ***I. ×troupinii***
3. Flowers pink or white, lower sepal pink, whitish or greenish, navicular, with an abruptly spiraled, narrowly filiform spur, 1 mm in diameter, dorsal petal expanded, cucullate, bilobed at apex, lateral united petals pink or white 4
4. Plants densely covered with brownish hairs, stems erect, up to 60–95 (120) cm tall, flowers large, upper lateral petal 18.5–24.5 × 11–15.5 mm, purple maculae on upper lateral petals small, spot-like, ovary and fruits with brownish hair; gallery forests in grassland; Burundi .... ***I. urundiensis***
4. Plants pubescent but not densely hairy, if densely hairy then with brownish hairs mainly on lower surface of young leaves and on stems, stems prostrate to ascending, up to 10–50 (85) cm long, flowers smaller, upper lateral petal not exceeding 7–17 × 3–9 mm, maculae large, dark pink to red with yellow 5
5. Ovary and fruit pilose or pubescent, plants usually densely pubescent on stems and lower surface of young leaves, base of upper lateral petal with purple or white maculae 6
5. Ovary and fruit glabrous, plants usually glabrous or only with loose hairs, base of upper lateral petal with dark pink or red and yellow maculae 8
6. Upper margin of the upper lateral petals straight, while lower margin on top largely overlapping with lower lateral petals; purple maculae near throat rather small, spot-like, fruit beige pubescent, leaf lamina lanceolate, margin with (25) 27–39 pairs of extrafloral nectaries, petiole with 3–7 pairs of extrafloral nectaries; montane forest; Burundi (Bururi) .... ***I. lutzmannii***
6. Upper lateral petals curved upwards or slightly bent upwards, not largely overlapping with lower petals, purple maculae larger but sometimes ± hidden in throat, fruit beige pubescent or white pilose, lamina lanceolate or ovate, margin with 10–24 or 25–39 pairs of extrafloral nectaries, petiole with 0–2 pairs of extrafloral nectaries 7
7. Fruit white pilose, purple maculae large, upper lateral petals bent or curved upwards, not largely overlapping with lower lateral petals, petal base barely yellow, upper lateral petal (7) 10–13 × 5–9 mm, leaf lamina ovate, 25–59 × 14–36 mm, with 10–24 (28) pairs of extrafloral nectaries, apex obtuse, inflorescence with 1–2 flowers, peduncle 9–20 mm long, pedicel 7–14 mm long; montane forest; SW Rwanda (Nyungwe) .... ***I. purpureoviolacea***

7. Fruit beige-brownish pubescent, but purple maculae larger, upper lateral petals slightly bent upwards and not largely overlapping with lower lateral petals, upper lateral petal 11–17 × 6–9 mm, leaf lamina lanceolate, 55–90 × 22–42 mm, with 25–39 pairs of extrafloral nectaries, apex acuminate, inflorescence with 3 flowers, peduncle (20) 30–40 mm long, pedicel 13–22 mm long; montane forest; W of Lake Edward, NW Burundi (Kibira) .... ***I. kivuensis***
8. Spur 26–35 mm long, often only slightly coiled, flowers entirely white with yellow and very small spot-like purple marks on upper lateral petals, leaves, stems and flowers almost glabrous, mid-altitude forest at 1100 m, Democratic Republic of the Congo (Kahuzi-Biéga) ... ***I. elwiraurzulae***
8. Spur 13–20 mm long, distinctly coiled, flowers pink or white with yellow and large purple marks on upper lateral petals, leaves, stems and flowers glabrous or loosely hairy; montane forest above 1700 m 9
9. Upper lateral united petals 9–10 × 10 mm, distinctly overlapping lower lateral united petals, plants glabrous; Democratic Republic of the Congo (Kahuzi-Biéga) ....***I. lotteri***
9. Upper lateral united petals 10–18 × 5–7.5 mm, not overlapping lower lateral united petals, plants glabrous or loosely hairy 10
10. Flowers white, occasionally single pink flowers appearing, dorsal petal divided to less than 1/3 of its length, plants densely hairy on upper leaf surface, stems and pedicels later glabrescent, leaves at margin with 10–15 pairs of extrafloral nectaries, plants often suberect; SW Rwanda ....***I. versicolor***
10. Flowers all pink, dorsal petal divided to more than 1/3 up to 1/2 of its length, plants hairy on upper surface of young leaves, later glabrescent, leaves at margin with (16) 23–29 pairs of extrafloral nectaries, plants usually prostrate to ascending; Democratic Republic of the Congo, Rwanda ....***I. ludewigii***

Species recognized in the *Impatiens purpureoviolacea* complex

Impatiens purpureoviolacea Gilg in Bot. Jahrb. Syst. 43: 122. 1909 – Holotype: Rwanda. Rugege-Wald, Rukarara, c. 1900 m, mid-Aug 1907, *J. Mildbraed 912* (B barcode B 10 0153415!; isotype: B barcode B 10 0153416!).

Description. – Plants prostrate to ascending, stems 10–25 (80) cm long. Leaves dark green above, light green below, petiole (3) 4–13 (18) mm long, with (0) 1–2 pairs of extrafloral nectaries, leaf lamina (25) 27–51.5 (59) × (14) 20–36 mm, broadly ovate or lanceolate, obtuse at apex, margin with 10–24 (28) pairs of extrafloral nectaries. Inflorescence with 1–2 flowers, peduncle 9–20 mm long, pedicel 7–14 mm long. Flowers pink, petal base barely yellow, purple maculae at base large but sometimes ± hidden in throat, Lateral sepals 4–6.8 × 1.2–2.2 mm. Lower sepal navicular, abruptly constricted into a spiraled, usually filiform spur, 6–8 mm long and 3–5 mm deep, spur 5–17 mm long. Dorsal petal 7.5–10.5 (12) × (10) 12–16 mm. Lateral united petals with upper lateral petal (7) 10–13 × 5–9 mm, bent or curved upwards, not largely overlapping with lower lateral petals, lower petal 13–17 × 6–9 mm, oblong-elliptical. Ovary white pilose, 3–4 mm long. Fruit white pilose, 12–17 × 4.5–7 mm. Figures 2, 4A,B, 7, 11A–E.

Ecology. – Montane rainforest, 1900–2540 m.

Distribution. – Rwanda: Nyungwe National Park.

Specimens examined. – **Rwanda.** Lacs Edouard et Kivu. Western Province, Nyungwe National Park, environs d'Uwinka, 2400 m, 20 Jan 1971, *Bouxin 50* (BR); Forêt de Nyungwe, environs d'Uwinka, 2400 m, 23 Jan 1971, *Bouxin 129* (BR); environs de Rwankuba, 1900 m, 10 Mar 1971, *Bouxin 368* (BR); Forêt de Nyungwe, environs d'Uwinka, 2400 m, 13 Mar 1971, *Bouxin 454* (BR); Forêt de Nyungwe, environs d'Uwinka, 2000–2400 m, 9 Aug 1969, *Bouxin & Radoux INRS 552* (BR); Rwankuba, 18 Dec 1971, *Bamps 2804* (BR); entre Pindura et l'Ibigugu, 2540 m, 29 Jul 1974, *Auquier 3514* (BR); route Astrida (= Butare, Huye)–Bukavu, env. d'Uwinka, 2300 m, 19 Dec 1959, *Troupin 11440* (BR); route Astrida (= Butare, Huye)–Bukavu, km 93, env. d'Uwinka, 2150 m, 29 Dec 1959, *Troupin 11462* (BR); route Astrida (= Butare, Huye)–Bukavu, vers km 93, environs d'Uwinka, colline Bunyangurube, 24 Feb 1960, *Troupin 11909* (BR); route Bukavu–Astrida (= Butare, Huye), vers km 93, environs d'Uwinka, colline Bunyangurube, 27 Apr 1960, *Troupin 12205* (BR); route Bukavu–Astrida (= Butare, Huye), km 93 colline Uwinka, 2450 m, 3 Jun 1960, *Troupin 12338* (BR); km 90 route Bukavu–Astrida (= Butare, Huye), 2000 m, 6 Jun 1959, *Michel 6342* (BR); Kamiranjovu (= Kamiranzovu), 2000 m, 17 Mar 1956, *Christiaensen 1375* (BR); Kamiranjovu (= Kamiranzovu), 2000 m, 17 Mar 1956, *Christiaensen 1376* (BR); Nyungwe National Park, Uwinka, *E. Fischer 8093*, Oct 1999 (KOBL); Rukarara, source of the Nile, 2250 m, 20 Mar 2013, *E. Fischer 12855* (KOBL); Rukarara, Source of the Nile, 2250 m, 7 Jan 2015, *E. Fischer 13911* (KOBL); Karamba, 1900 m, 21 Mar 2013, *E. Fischer 12958* (KOBL); Karamba, 1900 m, 7 Oct 2013, *E. Fischer 13018* (KOBL); Karamba, 1900 m, 7 Jan 2015, *E. Fischer 13910* (KOBL); Southern Province, Nyamagabe (= Gikongoro), Nyungwe National Park, Commune Kivu, savane de Nyabihu, 2 Aug 1999, *Ewango 2163* (BR).

Notes. – Grey-Wilson (1980) lists the type locality erroneously from the eastern Democratic Republic of the Congo ("Eastern Zaire"). The Rukarara is one of the sources of the Nile and now situated in Nyungwe National Park, Rwanda. *Impatiens purpureoviolacea* s.str. is confined to Nyungwe Forest and could not be recorded in Gishwati-Mukura National Park or in the Volcano National Park, the former Albert National Park that continues in the eastern Democratic Republic of the Congo (Virunga National Park) and southwestern Uganda (Mgahinga National Park). Despite the overall floristic similarities between Nyungwe and Bwindi Impenetrable Forest in southwestern Uganda, *I. purpureoviolacea* has also never been recorded there.

Impatiens kivuensis Eb.Fisch., Abrah., Holstein & S.B. Janssens, **nom. & stat. nov.** ≡ *Impatiens purpureoviolacea* var. *longicalcarata* G.M.Schulze in Bull. Jard. Bot. État

Bruxelles 18: 270. 1947, non Tardieu in Notul. Syst. (Paris) 11: 184. 1944 – Holotype: Democratic Republic of the Congo, entre Kasindi et Lubango (Kibale-Ituri), chaîne W du Lac Edouard, ruisseau dans la forêt de montagne, 2340 m, Jan 1932, *J. Lebrun 4760* (B barcode B 10 0153418!; isotypes: BR barcodes BR0000008864574!, BR0000008864581!).

Diagnosis. – *Impatiens kivuensis* belongs to the group with hairy ovary. It differs from *I. purpureoviolacea* in the beige-brownish pubescent ovary and fruit, the purple maculae on lateral united petals being larger, the upper lateral petals slightly bent upwards and not largely overlapping with lower lateral petals, the upper lateral petal 11–17 × 6–9 mm, the lanceolate leaf lamina, 55–90 × 22–42 mm, with 25–39 pairs of extrafloral nectaries, and with acuminate apex, the inflorescence with 3 flowers, the (20) 30–40 mm long peduncle, and the 13–22 mm long pedicel.

Description. – Plants ascending to erect, usually densely pubescent on stems and lower surface of young leaves, stems (33) 60–100 cm long. Leaves discolourous, dark green on upper side, pale green on lower side, petiole 12–17 mm long, hairy, with 0–2 pairs of extrafloral nectaries, lamina lanceolate or ovate, 55–90 × 22–42 mm, upper leaf surface sparsely hairy, lower surface with brownish hairs on the veins, margin with 25–39 pairs

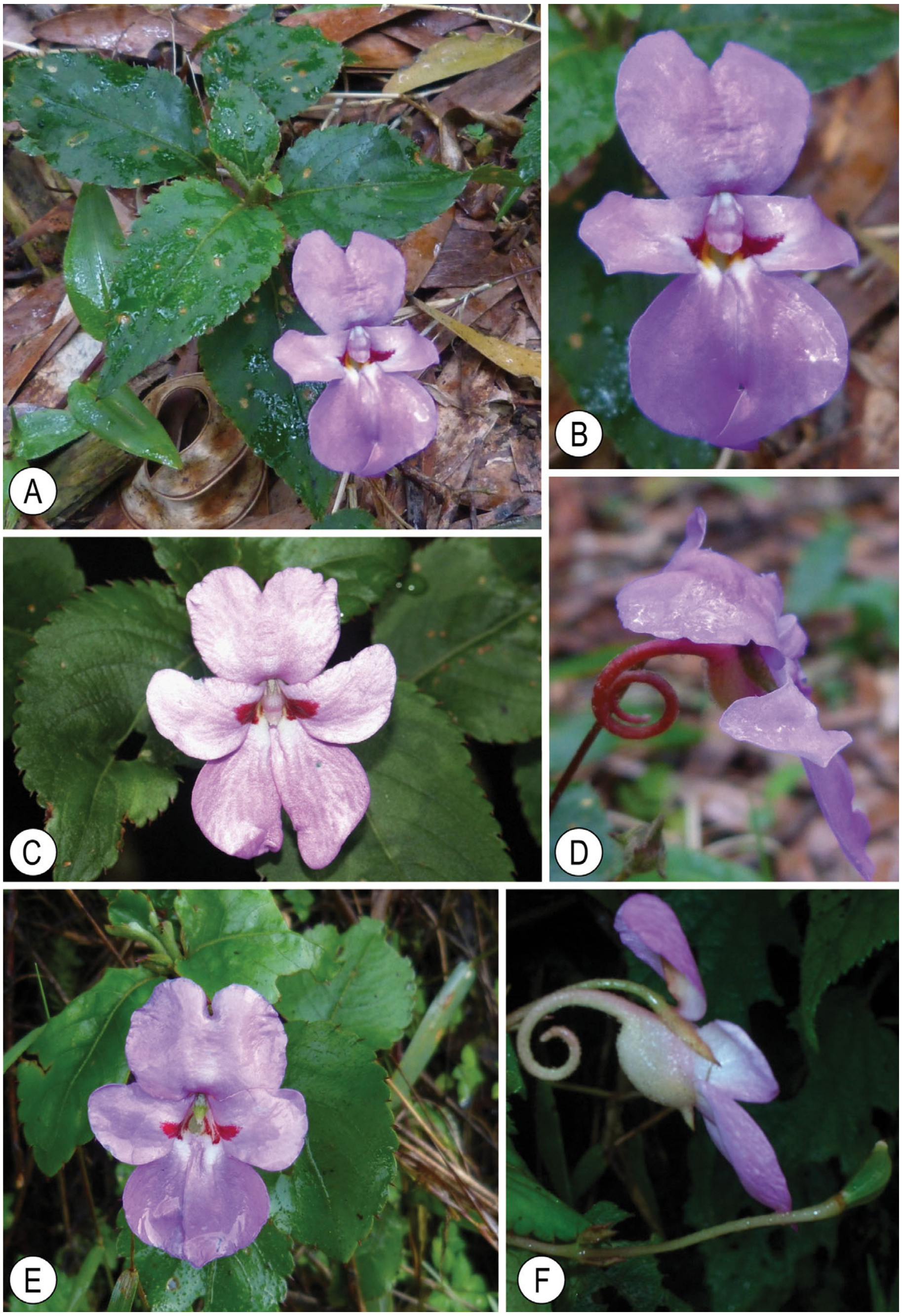

Fig. 7. *Impatiens purpureoviolacea*. **A**, Habit; **B**, **C** & **E**, Flower, frontal view; **D** & **F**, Flower, lateral view. — A, B & D, *Fischer 13911*, Rwanda, Nyungwe National Park, source of Rukarara; C, *Fischer 12958*, Rwanda, Karamba; E & F, *Fischer 8093*, Rwanda, Uwinka.

of extrafloral nectaries. Inflorescence with 3 flowers, peduncle (20) 30–40 mm long, pedicel 13–22 mm long, bracts linear-filiform, (5) 7–8 × 0.5–0.8 mm. Flowers pink, petal base barely yellow, purple maculae at base large. Lateral sepals 5–6 × 1 mm. Lower sepal navicular, 8–9 mm long and 5–9 mm deep, abruptly constricted into a spiraled, usually filiform spur, 10–12 mm long. Dorsal petal 12–14 × 12–17 mm, emarginated at apex, with dorsal crest of 8–9 mm ending in an 1 mm long spur. Lateral united petals 23–25 mm, base of upper lateral petal with purple maculae, upper lateral petals 11–17 × 6–9 mm, slightly bent upwards and not largely overlapping with lower lateral petals, lower lateral petals 12–16 × 9–12 mm. Ovary beige-brownish pubescent, 5–6 mm long. Fruit beige-brownish pubescent, 11–14 × 6–7 mm. Figures 2, 5A,B, 8.

Ecology. – Montane forest, 2100–2300 m.

Distribution. – Democratic Republic of the Congo: mountains W of Lake Edward; Burundi: Kibira National Park.

Etymology. – Named after the Kivu region of eastern Congo and Burundi.

Specimens examined. – **Democratic Republic of the Congo.** Mt. Musimba (Tshiaberimu), 18 Apr 1935, 2300 m, *De Witte 12161* (BR). **Burundi.** Lacs Edouard et Kivu. Kibira National Park. Bugarama (Muramvya), S03°13′ E29°31′, 2200 m, 22 Dec 1965, *Lewalle 116* (BR); forêt de Kibira, km

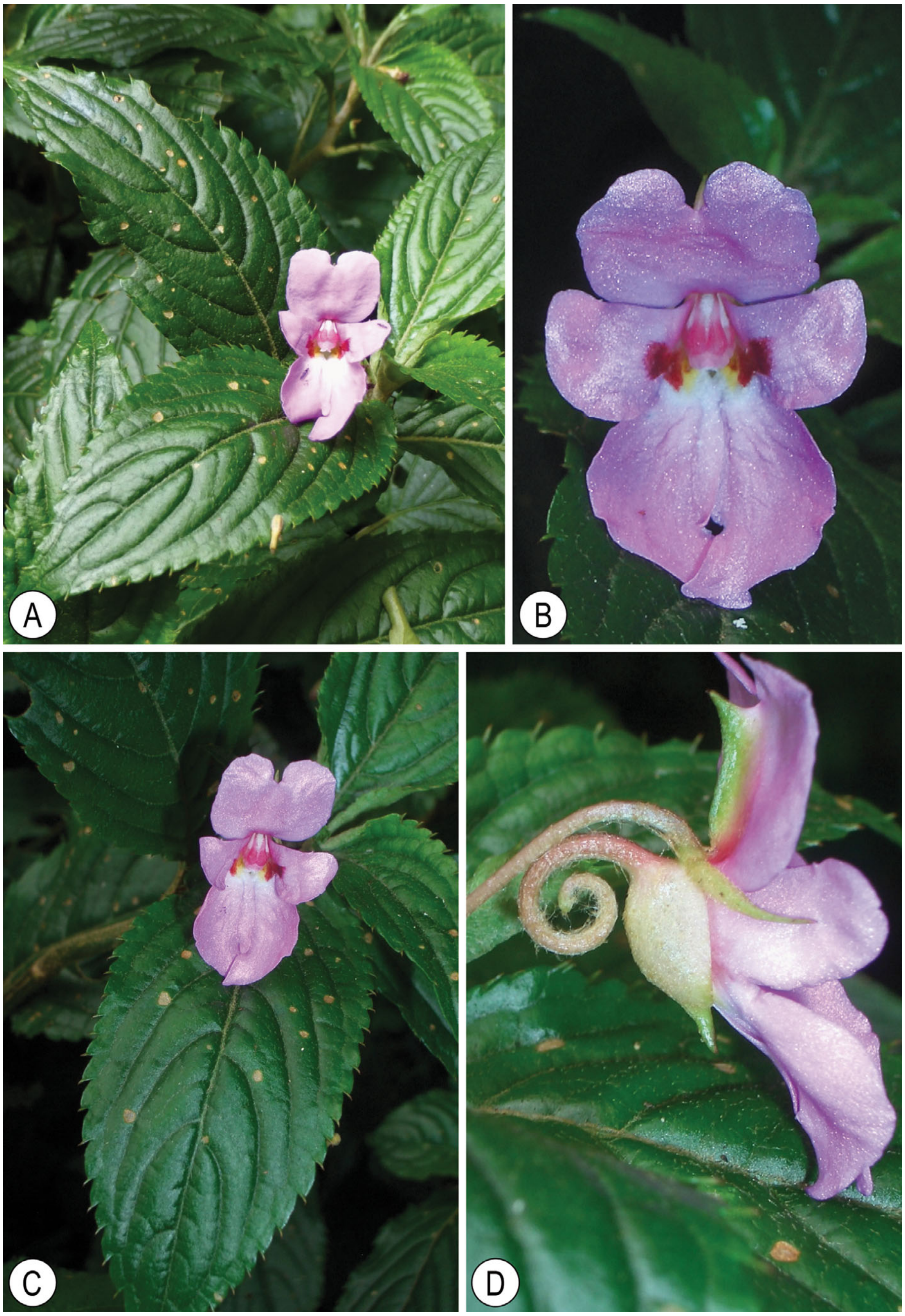

Fig. 8. *Impatiens kivuensis*. **A** & **C**, Details of habit; **B**, Flower, frontal view; **D**, Flower, lateral view. — A–D, *Fischer 13451*, Burundi, Kibira National Park, Mt. Teza.

40 sur la route Bujumbura–Astrida (= Butare, Huye), 2200 m, 18 Feb 1961, *Hendrickx 8024* (BR); Muramvya, Bugarama, 2100 m, 7 May 1970, *Lewalle 4606* (BR); Teza, prov. Muramvya, S03°13′ E29°33′, 2100 m, 8 Dec 1977, *Reekmans 6689* (BR); Mt. Teza, 2100 m, 4 Mar 2013, *E. Fischer 13451* (KOBL).

Notes. – Here we raise the status of *Impatiens purpureoviolacea* var. *longicalcarata* to specific rank. As the name *Impatiens longicalcarata* Tardieu (Tardieu-Blot, 1944: 184) already exists, we propose the replacement name *I. kivuensis*, referring to the distribution of the species in the Kivu region of the eastern Democratic Republic of the Congo and northwestern Burundi.

Impatiens lutzmannii Eb.Fisch., Abrah., Holstein & S.B.Janssens, **sp. nov.** – Holotype: Burundi. Bururi Forest Reserve, 2180 m, 16 Mar 2012, *E. Fischer 13002* (BR barcode BR0000014532139!; isotypes: BONN!, KOBL!).

Diagnosis. – *Impatiens lutzmannii* belongs to the group with hairy ovary. It differs from *I. purpureoviolacea* in the upper margin of the upper lateral petals being straight, while lower margin on top largely overlapping with lower lateral petals, the purple maculae on lateral united petals near throat rather small, spot-like, the beige pubescent fruit, the lanceolate leaf lamina with (25) 27–39 pairs of extrafloral nectaries at margin, and the petiole with 3–7 pairs of extrafloral nectaries.

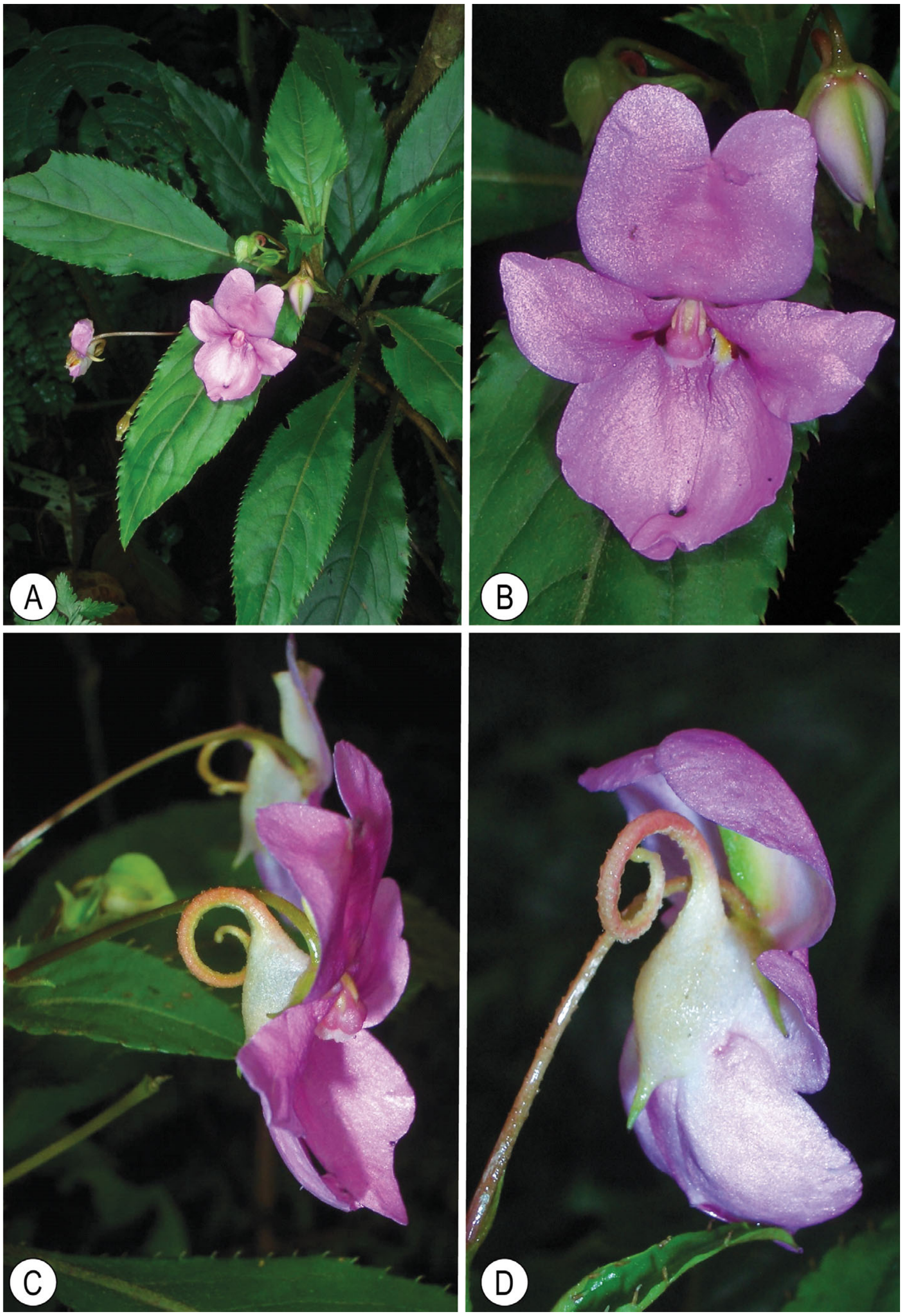

Fig. 9. *Impatiens lutzmannii*. **A**, Habit; **B**, Flower, frontal view; **C** & **D**, Flower, lateral view. — A–D, *Fischer 13002*, Burundi, Bururi Forest Reserve.

Description. – Plants ascending to erect, usually densely pubescent on stems and lower surface of young leaves, stems 20–25 cm long. Leaves with 3–18 mm long petiole, (3) 4–7 pairs of extrafloral nectaries, lamina lanceolate, 35–98.5 × 13.5–32.5 mm, margin with (25) 27–39 pairs of extrafloral nectaries. Inflorescence with 2–4 flowers, peduncle 7–21 mm long, pedicel 9–14 mm long. Flowers pink, petal base barely yellow, purple maculae at base small, ± hidden in throat. Lateral sepals (4) 6–8 × 2–2.7 mm. Lower sepal navicular, 8–11 mm long and 4–5.5 mm deep, abruptly constricted into a spiraled, usually filiform spur, spur 8–14.5 mm long. Dorsal petal 7–12.5 × 11.5–13 mm. Lateral united petals up to 28 mm long, upper margin of the upper lateral petals straight, while lower margin on top largely overlapping with lower lateral petals; purple maculae near throat rather small, spot-like, upper lateral petal 10–12 × 5.5–6.5 mm, lower lateral petal 16–21 × 6.5–9 mm. Ovary beige-pubescent, 4–6 mm long. Fruit beige pubescent 13–15 × 6–7 mm. Figures 2, 4C,D, 9, 11F–I.

Ecology. – Montane forest at 2180 m.

Distribution. – Burundi, only known from Bururi Forest Reserve.

Etymology. – Named after Nicola Lutzmann, who first discovered the species.

Impatiens urundiensis Gilg in Bot. Jahrb. Syst. 51: 227. 1914 – Holotype: Burundi. Reise nach Urundi u. Ruanda,

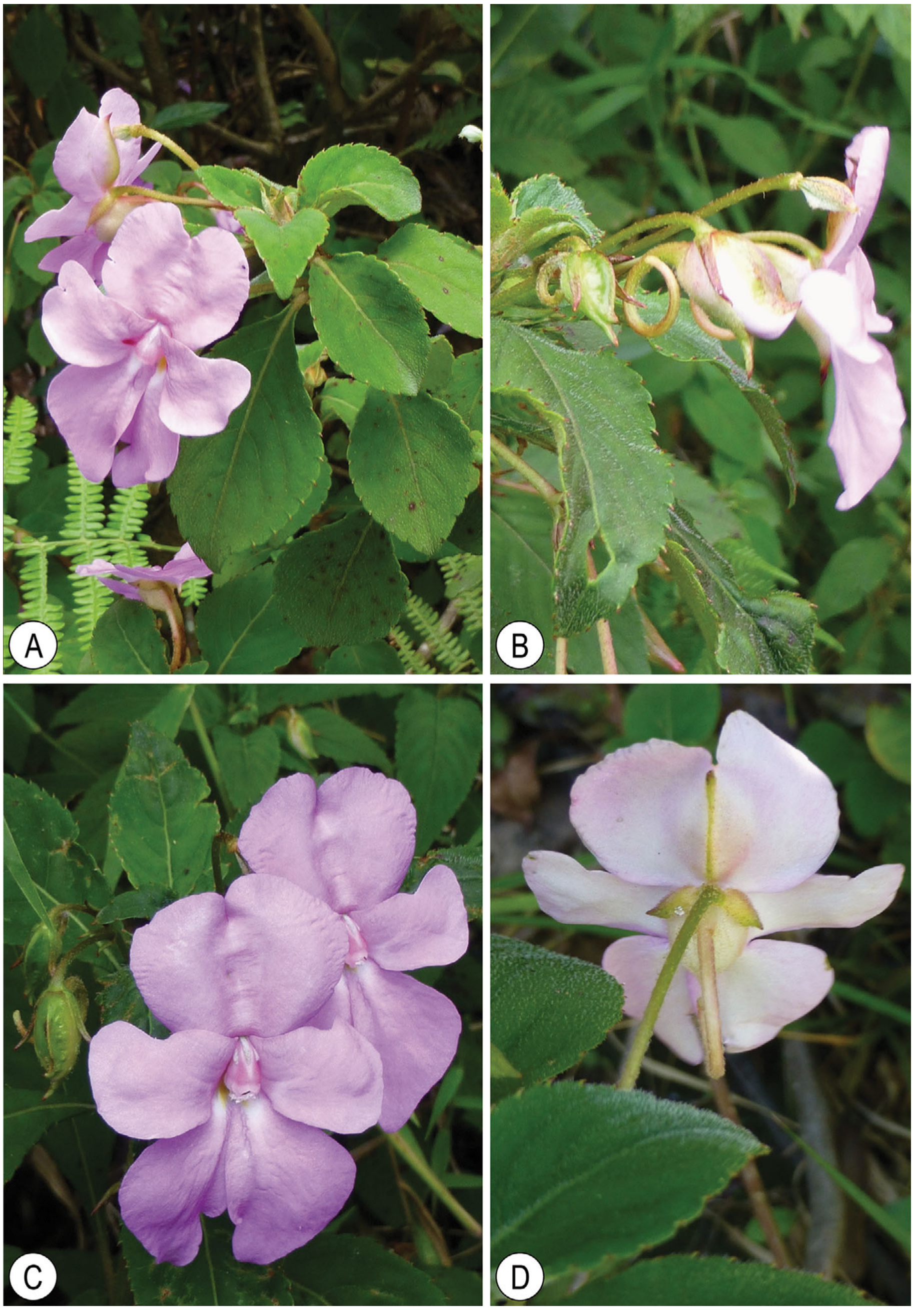

Fig. 10. *Impatiens urundiensis*. **A**, Detail of habit; **B**, Flower, lateral view; **C**, Flower, frontal view; **D**, Flower, dorsal view. — A–D, *Fischer 13301*, Burundi, Kumuyange.

Fig. 11. **A–E**, *Impatiens purpureoviolacea*. **A**, Flower; **B**, Lower sepal and spur; **C**, Dorsal petal; **D** & **E**, Lateral united petals. **F–I**, *Impatiens lutzmannii*. **F**, Flower; **G**, Lower sepal and spur; **H**, Dorsal petal; **I**, Lateral united petals. **J–N**, *Impatiens urundiensis*. **J**, Flower; **K**, Petiole, lateral sepals and anthers; **L**, Lower sepal and spur; **M**, Dorsal petal; **N**, Lateral united petals. — Scale bar: 1 cm. A–E, *Fischer 13911*, Rwanda, Rukarara; F–I, *Fischer 13002*, Burundi, Kumuyange; J–N, *Fischer 13301*, Burundi, Kumuyange.

Nordost-Urundi, Nord-Uha, Sommer 1911, *H. Meyer 1082* (B barcode B 10 0153419!).

Description. – Plants densely covered with brownish hairs, stem erect, up to 60–95 (120) cm tall. Leaves with petiole 9–17 mm long, with 0–3 pairs of extrafloral nectaries, lamina 45–99 × 25–46 mm, margin with 10–16 pairs of extrafloral nectaries. Inflorescence with 6–8 flowers, peduncle (4.5) 11.5–28 mm long, pedicel 11–33.5 mm long. Flowers large, pink, petal base barely yellow, purple maculae at base small, ± hidden in throat. Lateral sepals 7.5–11.5 × 1.5–3 mm. Lower sepal navicular, 12–19 mm long, 5–8 mm deep, abruptly constricted into a spiraled, usually filiform spur, spur 17–31.5 mm long. Dorsal petal 14–25 × 20–29 mm. Lateral united petals up to 40 mm long, upper lateral petal 18.5–24.5 × 11–15.5 mm, purple maculae on upper lateral petals small, spot-like, lower lateral petal 25.5–35 × 11.5–17 mm. Ovary beige to brownish pubescent, 4–5 mm long, ovary and fruits with brownish hairs. Fruit beige to brownish pubescent, up to 22–24 × 6–8 mm. Figures 2, 4E,F, 10, 11J–N.

Ecology. – Gallery forest in grassland, grassland with *Exotheca* and *Eragrostis* along rivers, and understorey of gallery forest, 1750–2000 m.

Distribution. – Burundi: Bururi-Kumuyange.

Specimens examined. – **Burundi.** Lacs Edouard et Kivu. Prov. Bururi, Munini, rives de la Siguvaye, 1900 m, S04°00′ E29°44′, 5 Mar 1980, *Reekmans 8663* (BR); Bururi, Muyange, bord de Sikuyaye, 2000 m, 29 Jun 1971, *Reekmans 1036* (BR); Bururi, Kwitaba, S04°05′ E29°48′, 1750 m, 12 May 1977, *Reekmans 6207* (BR); Kumuyange, gallery forest near hot springs, gallery forest in montane grassland, 2000 m, 7 Oct 2013, *E. Fischer 13301* (KOBL).

Notes. – *Impatiens urundiensis* belongs to the group with hairy ovary. It is a very distinctive species with the plants densely covered with brownish hairs, the stems erect, up to 60–95 (120) cm tall, the flowers large, upper lateral petal 18.5–24.5 × 11–15.5 mm, purple maculae on upper lateral petals small, spot-like, ovary and fruits with brownish hairs. In contrast to all other species that occur in submontane to montane rainforest, it is confined to gallery forests in grassland. The petals display a sweet odour.

Impatiens ludewigii Eb.Fisch., Abrah., Holstein & S.B.Janssens, **sp. nov.** – Holotype: Rwanda. Western Province, Nyungwe National Park, near Uwinka on trail to canopy walkway, 1990 m, 4 Mar 2016, *E. Fischer 14500* (BR barcode BR0000014532122!; isotypes: BONN!, KOBL!).

Diagnosis. – *Impatiens ludewigii* belongs to the group with glabrous ovary. It differs from *I. versicolor* in the always pink flowers, the dorsal petal divided to more than 1/3 up to 1/2 of its length, the plants hairy on upper surface of young leaves, later glabrescent, the leaves at margin with (16) 23–29 pairs of extrafloral nectaries, and the plants being usually prostrate to ascending.

Description. – Plants prostrate to ascending, usually glabrous or only with loose hairs, stems 10–50 cm long. Leaves hairy on upper surface of young leaves, later glabrescent, petiole (3) 6–13 mm long, with 1–2 (4) pairs of extrafloral nectaries, lamina 18–55 (99) × 14–33 mm, margin with (16) 23–29 pairs of extrafloral nectaries. Inflorescence with 1–2 (3) flowers, peduncle (3) 6.5–10 (13) mm long, bracts 2–3 × 0.5 mm, pedicel glabrous, 12–23 mm long. Flowers pink, petal base barely yellow, purple maculae at base large. Lateral sepals 5–5.5 × 1.5–2 mm, with long simple trichomes. Lower sepal navicular, 6–9.5 mm long and 3–5 mm deep, abruptly constricted into a spiraled, usually filiform spur, spur (11) 16–20 mm long. Dorsal petal divided to more than 1/3 up to 1/2 of its length, 7–9 (11) × (6) 12–14.5 mm. Lateral united petals 19 mm long, upper lateral petals (7) 10–18 × (4) 6–7.5 mm, not overlapping lower lateral united petals, base of upper lateral petal with dark pink or red and yellow maculae, lower lateral petal (10) 16–16.5 (18) × (4) 6.5–7 mm, distinctly elongate. Ovary 3–4 mm long, glabrous. Fruit 12–16 × 4–5.5 mm, glabrous. Figures 2, 6A–C, 12.

Ecology. – Montane rainforest, 1700–2300 m.

Distribution. – Democratic Republic of the Congo, Kahuzi-Biéga National Park; Rwanda, Nyungwe National Park.

Etymology. – Named after the counselor of the University of Koblenz-Landau, Michael Ludewig.

Specimens examined. – **Democratic Republic of the Congo.** Lacs Edouard et Kivu. Montagnes à l'ouest du Lac Kivu, Massif du Kahuzi, vers 2000 m, Mar 1929, *Humbert 7755* (BR, P); km 45 route Kavumu-Buniakiri, Bitale, 18 Apr 1951, 1820 m, *Pierlot 134* (BR); contreforts du Mt. Kahuzi, 6 Apr 1956, 2100 m, *Pierlot 1277* (BR). **Rwanda.** Lacs Edouard et Kivu. Western Province, Nyungwe National Park. Env. de Rangiro, Rutabanzogera, 1700 m, 11 Feb 1980, *Bridson 377* (BR); 2 km avant Gisakura (venant de la route Butare–Cyangugu), 24 Aug 1974, *Van der Veken 10967* (BR); route Bukavu–Astrida, env. Uwinka, colline Bunyereri, 2100 m, 9 Jul 1960, *Troupin 12436* (BR); env. de Wisumo, centre forestier Suisse, 2150 m, 21 Feb 1974, *Troupin 14453* (BR); talus humide de la route Bukavu–Astrida (= Butare, Huye), à env. 27 km à l'E de Shangugu (= Cyangugu, Rusizi), 1930 m, 7 Feb 1958, *Symoens 5369* (BR); Kamiranjovu (= Kamiranzovu), 2000 m, 17 Mar 1956, *Christiaensen 1376bis* (BR); Uwinka, 2300 m, 22 Oct 2013, *E. Fischer 10280* (KOBL); Uwinka, 2300 m, 27 Oct 2013, *E. Fischer 10350* (KOBL); Gisovu, 2200 m, 7 Jan 2015, *E. Fischer 13914* (KOBL); Uwinka, 2300 m, 4 Mar 2016, *E. Fischer 14489* (BR, BONN, KOBL); Uwinka, 1750 m, 4 Mar 2016, *E. Fischer 14500* (BONN, BR, KOBL).

Impatiens elwiraurzulae Eb.Fisch., Abrah., Holstein & S.B. Janssens, **sp. nov.** – Holotype: Democratic Republic of the Congo. Kahuzi-Biéga National Park, Mulolo, 1100 m, 10 Dec 2017, *B. Dumbo & L. Dumbo s.n* (BR barcode BR0000014532115!; isotypes: BONN!, KOBL!).

Diagnosis. – *Impatiens elwiraurzulae* belongs to the group with glabrous ovary. It differs from all related taxa (*I. lotteri*, *I. ludewigii*, *I. versicolor*) in the 26–35 mm long spur, that is often only slightly coiled, the entirely white flowers with yellow and very small spot-like purple marks on upper lateral petals, the leaves, stems and flowers almost glabrous, and the occurrence in mid-altitude forest at 1100 m.

Description. – Plants prostrate to ascending, stem 15–30 cm long. Leaves, stems and flowers almost glabrous. Leaves shining vivid green on upper surface, lighter green on lower surface, petiole 11–20 mm long, with 2–3 pairs of extrafloral nectaries, lamina ovate, 45–66 × 27–39 mm, margin with 10–11 pairs of extrafloral nectaries. Inflorescence with 4–7 flowers, peduncle 2 mm long, pedicel 15–26 mm long. Flowers entirely white with yellow and very small spot-like purple marks on upper lateral petals. Lateral sepals 6–8 × 2–3 mm. Lower sepal navicular, 10–12 mm long and 4–5 mm deep, abruptly constricted into a spiraled, usually filiform spur, spur 26–35 mm long, often only slightly coiled. Dorsal petal 10–13 × 12–15 mm. Lateral united petals up to 25 mm long, upper lateral petal 14–16 × 7–8 mm, base of upper lateral petal with dark pink or red and yellow maculae, lower lateral petal 19–21 × 8–10 mm. Ovary 4–6 mm long, glabrous. Fruit 14–15 × 5–6 mm, glabrous. Figures 2, 5E,F, 13A–D, 14.

Ecology. – Mid-altitude forest at 1100 m. Probably sphingophilous due to white flowers with long, relatively straight spurs.

Distribution. – Democratic Republic of the Congo, only known from Kahuzi-Biéga National Park.

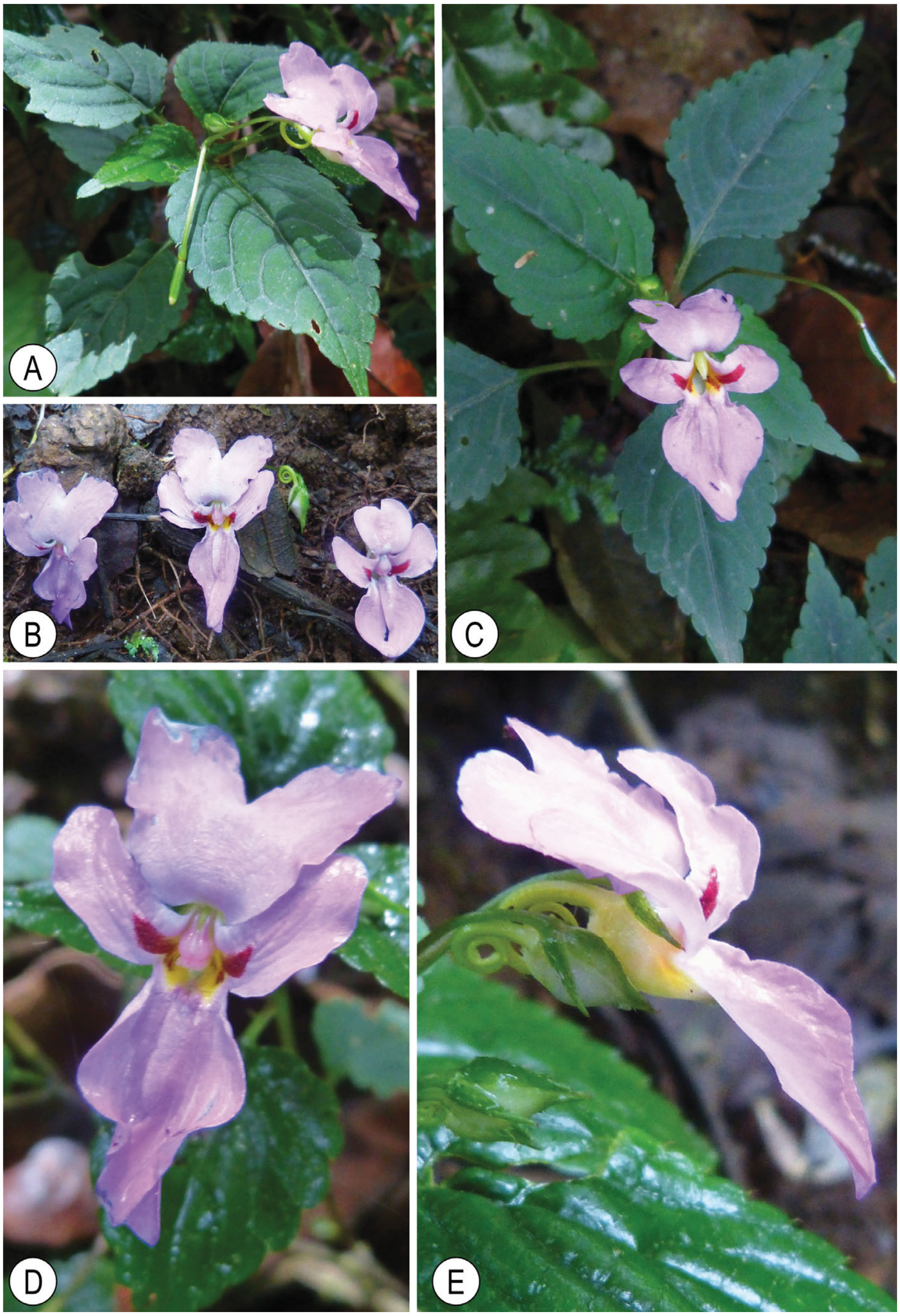

Fig. 12. *Impatiens ludewigii*. **A** & **C**, Habit; **B**, Flowers (left, middle), right a flower of *Impatiens purpureoviolacea*; **D**, Flower, frontal view; **E**, Flower, lateral view. — A & C, *Fischer 14500*, Rwanda, Uwinka. B, D & E, *Fischer 13914*, Rwanda, Gisovu.

Etymology. – Named after Elwira Urzula Schweizer, who supported the work of the first author.

Impatiens versicolor Eb.Fisch., Abrah., Holstein & S.B. Janssens, **sp. nov.** – Holotype: Rwanda. Western Province, Nyungwe National Park, road 7 km south of Pindura towards Bweyeye, rocks and wet roadsides, 1800–1900 m, 8 Mar 2013, *E. Fischer 13390* (BR barcode BR0000014532108!; isotype: BONN!).

Diagnosis. – *Impatiens versicolor* belongs to the group with glabrous ovary. It differs from *I. ludewigii* in the white flowers, with occasionally single pink flowers appearing on the same plant, the dorsal petal divided to less than 1/3 of its length, the plants densely hairy on upper leaf surface, stems and pedicels, later glabrescent, the leaves at margin with 10–15 pairs of extrafloral nectaries, and the often suberect habit.

Description. – Plants erect to suberect or ascending, usually glabrous or only with loose hairs, or sometimes densely hairy on upper leaf surface, stems and pedicels later glabrescent, stems 20–50 cm long. Leaves with 4–8 cm long petiole, petiole with 0–2 (4) pairs of extrafloral nectaries, lamina ovate, acuminate, 35–46 × 21–34 mm, margin with 10–15 pairs of extrafloral nectaries. Inflorescence with (1) 2 flowers, peduncle 5.5–16.5 mm long, pedicel 11–18 mm long. Flowers white, petal base barely yellow, purple maculae at base large, occasionally single pink flowers appearing on the same plant. Lateral sepals

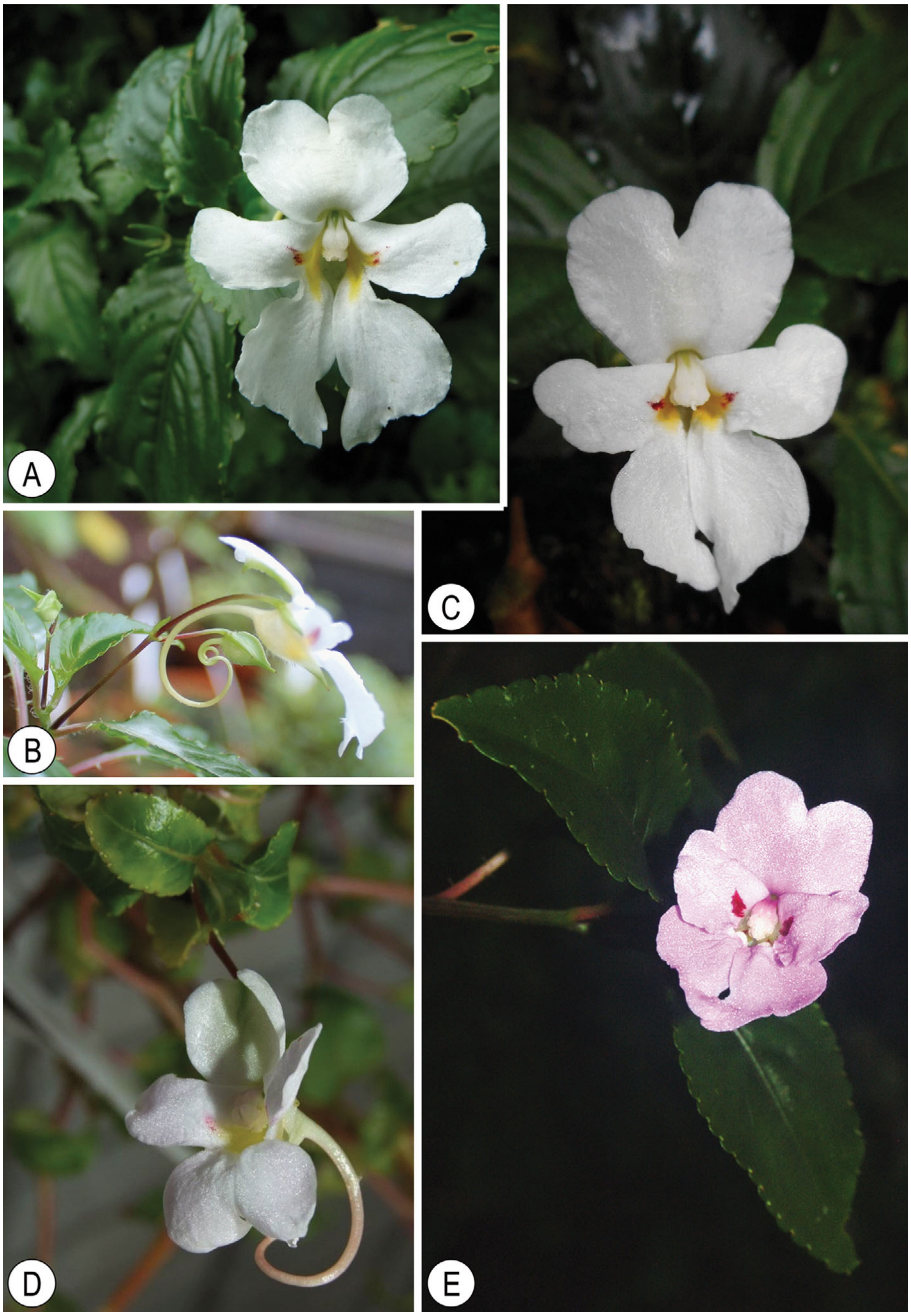

Fig. 13. A–D, *Impatiens elwiraurzulae*. **A** & **C**, Flower, frontal view; **B**, Flower, lateral view; **D**, Flower showing only slightly coiled spur. **E**, *Impatiens lotteri*, detail of habit with flower. — A–D, *Dumbo & Dumbo s.n.*, Democratic Republic of the Congo, Mulolo; E, *Lotter 1542*, Democratic Republic of the Congo, Ulindi River (Photo: M.C. Lotter).

4.5–6.5 × 1–2 mm. Lower sepal navicular, 7–9 mm long and 3–4.5 mm deep, abruptly constricted into a spiraled, usually filiform spur, 13–19 mm long. Dorsal petal divided to less than 1/3 of its length, 7–11 × 10.5–16.5 mm. Lateral united petals up to 23 mm long, upper lateral united petals 10–18 × 5–7.5 mm, not overlapping lower lateral united petals, base of upper lateral petal with dark pink or red and yellow maculae, lower lateral petal 13–19.5 × 5–7.5 mm. Ovary glabrous, 4–5 mm long. Fruit glabrous, 13 × 6 mm. Figures 2, 6D–E, 15.

Ecology. – Wet rocks and roadbanks in montane rainforest, 1800–1900 m.

Distribution. – Rwanda, only known from Nyungwe National Park, only recorded in a valley south of Pindura towards Bweyeye.

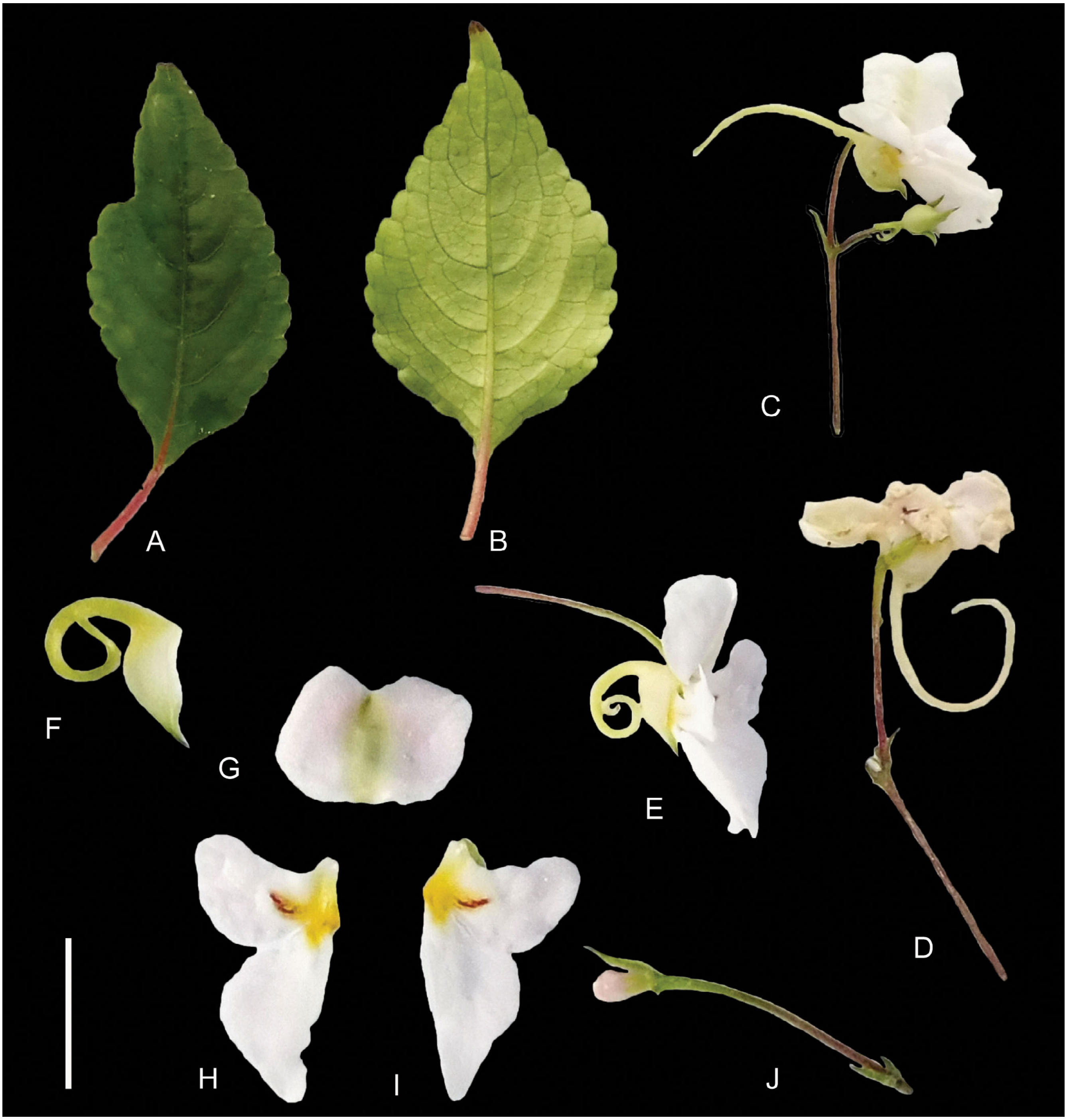

Fig. 14. *Impatiens elwiraurzulae*. **A**, Leaf, upper surface; **B**, Leaf, lower surface; **C** & **D**, Inflorescence; **E**, Flower; **F**, Lower sepal with spur; **G**, Dorsal petal; **H** & **I**, Lateral united petals; **J**, Bracts, pedicel, lateral sepals and anthers. — Scale bar: 1 cm. A–J, *Dumbo & Dumbo s.n.*, Democratic Republic of the Congo, Mulolo.

Etymology. – Named after the occasional but regular colour change of single flowers from white to pink.

Impatiens lotteri Eb.Fisch., Abrah., Holstein & S.B.Janssens, **sp. nov.** – Holotype: Democratic Republic of the Congo, South Kivu, Ulindi River, S03°05.625′ E28°31.868′, 1803 m, 17 Aug 2008, *M.C. Lotter 1542* (BR barcode BR0000005438105!).

Diagnosis. – *Impatiens lotteri* belongs to the group with glabrous ovary. It differs from *I. ludewigii* and *I. versicolor* in the upper lateral united petals 9–10 × 10 mm, distinctly overlapping the lower lateral united petals, thus giving the flower an almost circular appearance, and the entirely glabrous plants.

Description. – Plants ascending to erect, glabrous, stems 30 cm long. Leaves with 16 mm long petiole, petiole with 2–4 pairs of extrafloral nectaries, lamina ovate, discolourous, 53 × 25 mm, margin with 14–16 pairs of extrafloral nectaries. Inflorescence with 1 flower, peduncle 26 mm long, pedicel 11 mm long. Flowers pink, upper petal base barely yellow, purple maculae at upper petal base large. Lateral sepals 6–7 × 2 mm. Lower sepal navicular, 8–9 mm long and 5–6.2 mm deep, abruptly constricted into a spiraled, usually filiform spur, 18–20 mm long. Dorsal petal 10–12 × 7–10 mm.

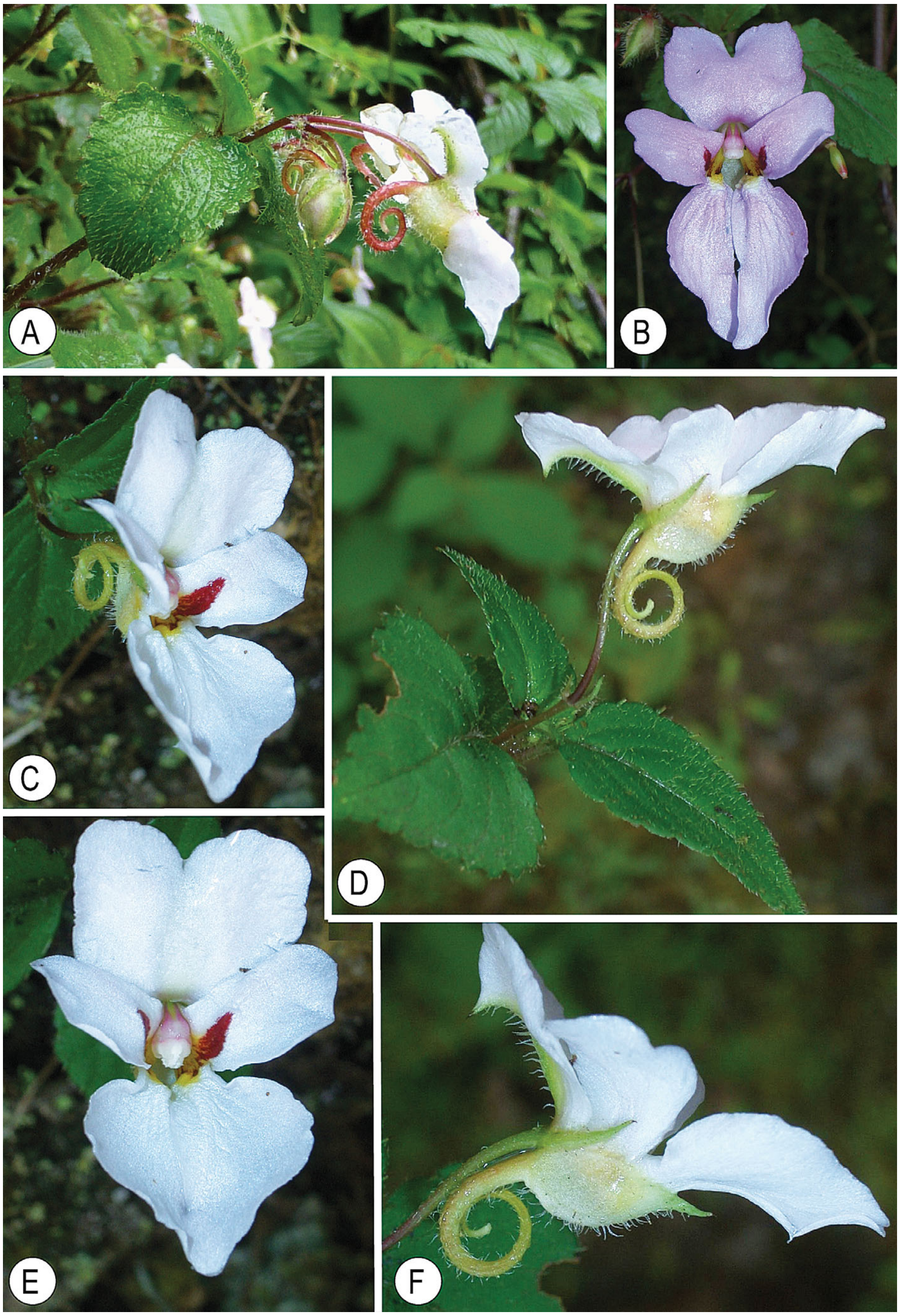

Fig. 15. *Impatiens versicolor.* **A**, Detail of habit; **B**, **C** & **E**, Flower, frontal view; **D** & **F**, Flower, lateral view. — A–F, *Fischer 13390*, Rwanda, between Pindura and Bweyeye.

Lateral united petals up to 20 mm long, upper lateral united petals (5) 9–10 × 10 mm, distinctly overlapping lower lateral united petals, lower lateral petals 12 × 5–6 mm. Ovary 4–5 mm long, glabrous. Figures 2, 13E.

Ecology. – Montane rainforest at 1800 m.

Distribution. – Democratic Republic of the Congo, only known from the type locality at the Ulindi River.

Etymology. – Named after Mervyn C. Lotter, who discovered the species.

Impatiens* ×*troupinii Eb.Fisch., Abrah., Holstein & S.B. Janssens, **nothosp. nov.** – Holotype: Rwanda. Western Province, near Uwinka, km 94 road Butare–Cyangugu, c. 2450 m, Mar 1980, *Bridson 470* (BR barcode BR0000008693433!; isotype: K!).

Diagnosis. – This natural hybrid is intermediate between its parents, *Impatiens purpureoviolacea* and *I. gesneroidea*. It differs from *I. gesneroidea* in the hairy ovary, the dark magenta dorsal petal and lateral united petals, and the spur that is ± abruptly constricted and strongly coiled. It differs from *I. purpureoviolacea* in the dark magenta flowers with green spur, the hairy spur and dorsal petal, and the shape of the lateral united petals.

Description. – Plants erect or ascending, stems 50–150 cm long. Leaves either resembling those of *I. gesneroidea* or those

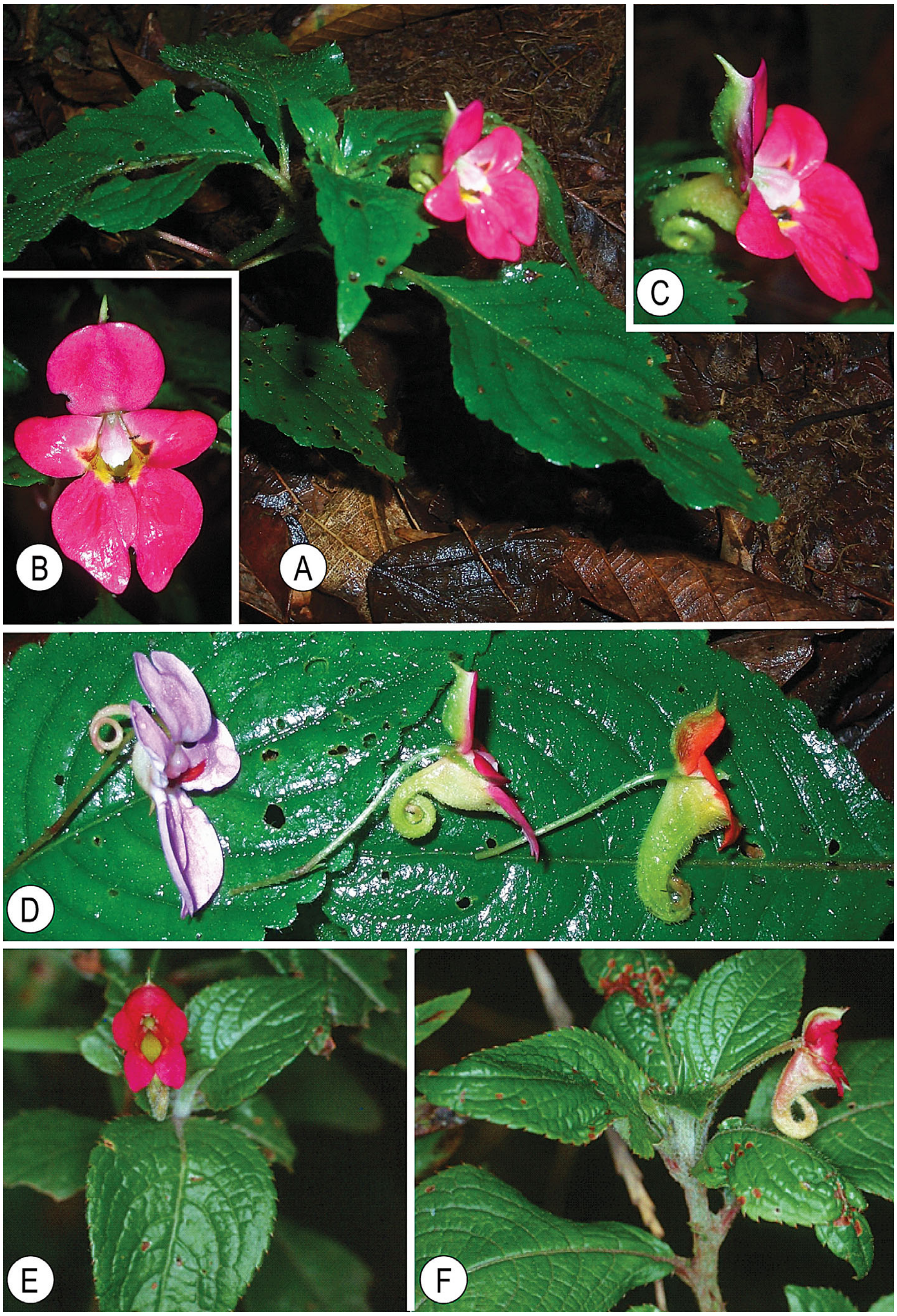

Fig. 16. *Impatiens* ×*troupinii*. **A**, Habit; **B**, Flower, frontal view; **C**, Flower, lateral view; **D**, Flower, lateral view (middle), with flowers of *Impatiens purpureoviolacea* (left) and *I. gesneroidea* (right). **E** & **F**, Detail of habit. — A–D, *Fischer 13912*, Rwanda, Rukarara; E & F, Rwanda, Uwinka, not collected.

of *I. purpureoviolacea*, petiole (5) 8–35 (48) mm long, with 1–3 (4) extrafloral nectaries, lamina 27–87 (102) × 26–50 mm, margin with 5–9 (10) pairs of extrafloral nectaries. Inflorescence with 1–2 flowers, peduncle 10–15 mm long, pedicel 18–23 mm long. Flowers magenta, lower sepal entirely greenish, petal base barely yellow, purple maculae at base small sometimes deeply hidden in the throat. Lateral sepals (3) 4.5–5.5 (8) × 2 mm, lanceolate, green. Lower sepal deeply navicular, 10–12 mm long, 6–7 mm deep, ± abruptly constricted into a spiraled, broadly filiform spur, 2 mm in diameter, spur (14) 18–21 mm long. Dorsal petal helmet-like, dark magenta, with green crest above ending in a long spur, not or only slightly bilobed, 9–11 × 10–12 (14) mm. Lateral united petals dark magenta, with dark red and yellow spots at throat, 14–18 mm long, upper lateral petal 9–10 × 4.5–8 mm, lower lateral petal 14–17 × 6–9 mm. Ovary pubescent, 4–5 mm long. Fruit 12–14 × 5–6 mm. Figures 5C,D, 16.

Ecology. – Montane rainforest, 2250–2450 m, between the parents.

Distribution. – Rwanda, Nyungwe National Park.

Etymology. – Named after Georges M.D.J. Troupin (1923–1997), the author of *Flore du Rwanda*, who first discovered the hybrid together with D. Bridson.

Specimens examined. – **Rwanda.** Western Province, Nyungwe National Park, near source of Rukarara, 2250 m, *E. Fischer 13912* (BONN, KOBL).

Notes. – This new hydrid was already mentioned by Troupin & Grey-Wilson (1983) as occurring in clearings of montane forest near Uwinka at 2400 m. It has been observed there by the first author in 1985, vegetatively more resembling *Impatiens purpureoviolacea* but with clearly intermediate flowers. Grey-Wilson (1989) described this new hybrid, hitherto only known from one locality in Rwanda (Uwinka) and he stated that "there is little doubt […] that the parents are *I. gesneroidea* var. *gesneroidea* and *I. purpureoviolacea*" (Grey-Wilson, 1989: 717). However, he did not name it formally. In 2017, the hybrid was again collected at the type locality of *I. purpureoviolacea* growing as a single individual and apparently not as hybrid swarm between its parents *I. purpureoviolacea* and *I. gesneroidea*. It has been observed only as a rare plant in single individuals.

Impatiens gesneroidea Gilg in Bot. Jahrb. Syst. 43: 116. 1909 – Holotype: Rwanda. Rugege Wald (Rukarara), mid-Aug 1907, *J. Mildbraed 916* (B barcode B 10 0153285!; isotype: B barcode B 10 0153286!).

Description. – Plants erect, stems 40–120 cm long, densely covered with hairs. Leaves herbaceous, densely hairy on both sides, petiole 1.8–2.2 cm long, without extrafloral nectaries, lamina broadly ovate, vivid green on upper and lower surface, hairy on both surfaces, 4.2–5.2 × 4.5–3.5 cm, margin with 16–18 pairs of extrafloral nectaries. Inflorescence with 2 flowers, peduncle up to 2.5 cm long, bracts linear-filiform, 4–6 × 0.5 mm, acute, pedicel 2.4–2.6 cm long. Flowers with greenish bucciniform lower sepal tapering into spur, densely hairy, dorsal petal deep red with greenish crest, lateral united petals deep red, yellow at throat. Lateral sepals green, linear-lanceolate, acute, 6–8 mm long and 1 mm wide at base, tapering towards apex, densely hairy. Lower sepal and spur bucciniform, 16–18 mm long and 11 mm deep, spur not or only slightly swollen at apex, spur broad, 7–9 (10) mm long and 2.5–3 mm in diameter. Dorsal petal cucullate, (6) 8–9 × 4–5 mm. Lateral united petals deep-red with yellow, 10–12 mm long, upper lateral petal 5–7 × 5–6 mm, lower lateral petal 5 × 4.5 mm. Ovary glabrous, 4 mm long. Fruit glabrous, 14–16 × 4–6 mm. Figures 3, 6F,G, 17.

Ecology. – Montane rainforest, 2000–2750 m.

Distribution. – Democratic Republic of the Congo: Kahuzi-Biéga National Park, Mt. Muhi, Kabobo; Rwanda: Nyungwe National Park; Burundi: Kibira National Park.

Specimens examined. – **Democratic Republic of the Congo.** Lacs Edouard et Kivu. Montagnes à l'Ouest du Lac Kivu, Massif du Kahuzi, 1929, *Humbert 7754* (BR); entre Walikale et Kalehe, Apr 1932, *Lebrun 5368* (BR); route Bukavu–Walikale; km 42–43, côté droit, 25 Mar 1960, *Petit 154* (BR); route Bukavu–Walikale, 3 Feb 1958, *Léonard 1442* (BR); route Bukavu–Walikale; km 42–43, côté droit, 25 Mar 1960, *Petit 183* (BR); Bukavu-Kahuzi km 41, 23 Dec 1971, *Bamps 2848* (BR); Mont Kahuzi 10 Jul 1972, 2700 m, *Ntakiyimana 229* (BR); Mt. Kahuzi, pont de la Mugaba, km 28 route Kavumu–Walikale, 8 Jan 1956, *Pierlot 1220* (BR); Kahuzi, 28 May 1960, 2500 m, *Meurillon 934* (BR); Mont Kahuzi, 23 May 1960, 2260 m, *Petit 275* (BR); Mont Biéga (Tshibinda), May 1948, *Hendrickx 5134* (BR); Marais Musisi, 16 Oct 1958, *Léonard 1279* (BR); Luemba, Dec 1946, *Hendrickx 4376* (BR); Mt. Muhi, Jul 1948, *Hendrickx 5375* (BR); Kabobo Forest, 10 Nov 2012, *Kirunda BK1301* (BR); Kabobo, 18 Nov 2012, *Kirunda BK1313* (BR). **Rwanda.** Lacs Edouard et Kivu. Nyungwe National Park. Wisumo, 16 Mar 1973, *Troupin 14748* (BR); Wisumo, commune Gisovu, centre forestier, 17 Feb 1980, *Bridson 410* (BR, K); env. de Wisumo, centre forestier suisse, à env. 50 km au S. de Kibuye, 21 Feb 1972, *Troupin 14452* (BR); Forêt de Rugege, versant sud du Mont Muzimu, 3 Mar 1972, *Auquier 2730* (BR); vers km 95, route Butare–Cyangugu, 9 May 1973, *Nuyt 87* (BR); Forêt de Nyungwe, Mont Bigugu, 18 Feb 1971, *Bouxin 349* (BR); Mont Bigugu, 29 Jul 1974, *Auquier 3504* (BR); Commune Kivu. Savane de Nyabihu, 3 Aug 1999, *Ewango 2167* (BR); Commune Kivu. Savane de Nyabihu, 2 Aug 1999, *Ewango 2162* (BR); Mt. Bigugu, 2750 m, 27 Sep 2011, *E. Fischer 11021* (KOBL). **Burundi.** Lacs Edouard et Kivu. Ijenda, 6 Aug 1971, *Reekmans 837* (BR); Bugarama, 22 Dec 1965, *Lewalle 98* (BR); Muramvya – forêt, Mar 1935, *Becquet 903* (BR); Bukeye, Mont Teza, 19 Jun 1971, *Lewalle 6023* (BR).

Notes. – Grey-Wilson (1980) lists the type locality erroneously from the eastern Democratic Republic of the Congo ("E. Zaire"). The Rukarara is one of the sources of the Nile and situated in Nyungwe National Park, Rwanda.

Impatiens superglabra (Grey-Wilson) Eb.Fisch., Abrah., Holstein & S.B.Janssens, **comb. & stat. nov.** ≡ *Impatiens* *gesneroidea* var. *superglabra* Grey-Wilson in Kew Bull. 33: 642. 1979 – Holotype: Democratic Republic of the Congo. Mt. Kahuzi, W of L. Kivu, 13 Sep 1959, *Cambridge Congo-Expedition 1959 467* (BM barcode BM000797579!, isotype: BR barcode BR0000008863881!).

Diagnosis. – *Impatiens superglabra* differs from *I. gesneroidea* in the coriaceous lanceolate-ovate leaves, almost glabrous above, and hairy below, the stem densely covered with hairlike brownish scales, the flowers with bucciniform wine-red lower sepal tapering into greenish spur, swollen at apex, ± glabrous, the dorsal petal wine red with greenish crest, the lateral united petals uniformly wine red, ovary and fruit pubescent, and the occurrence only in the bamboo-zone, and the ericaceous shrub to paramo from 2500–3350 m altitude.

Description. – Plants erect or ascending, stem 40–95 cm long, stems densely covered with hairlike brownish scales. Leaves coriaceous, upper leaf surface dark green, almost glabrous, lower surface light green above, hairy, petiole glabrous above, hairy below, 9–17 (20) mm long, without extrafloral nectaries, leaf lamina lanceolate-ovate, 41–53 × 19–22 mm. Inflorescence with 1 (2) flower, glabrous to very sparsely hairy, peduncle up to 8–9 mm long, bracts 1.6 × 0.5 mm, pedicel 11–12 mm long. Flowers with bucciniform wine-red lower sepal tapering into greenish spur, swollen at apex, ± glabrous or very

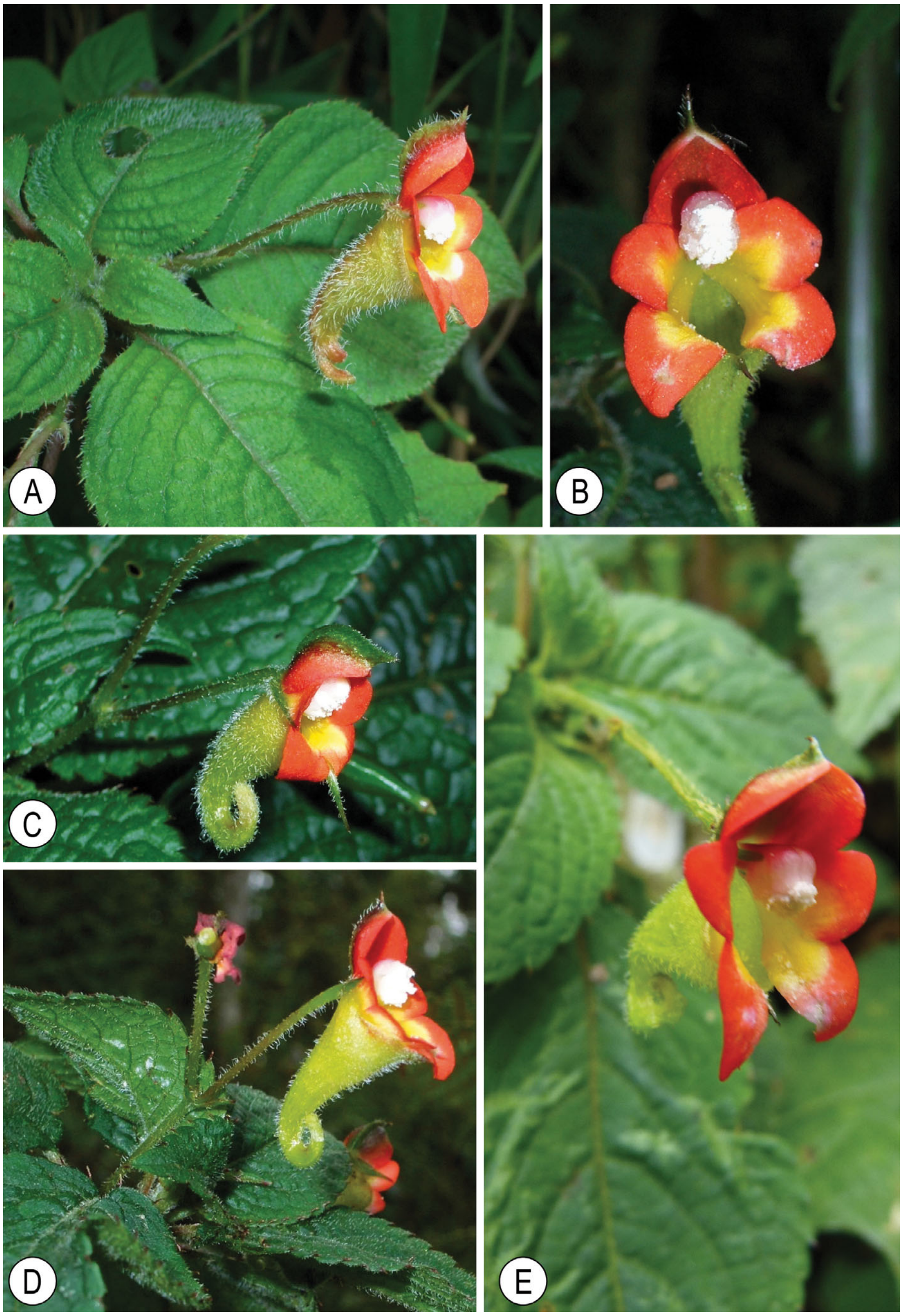

Fig. 17. *Impatiens gesneroidea*. **A** & **C–E**, Detail of habit with flower in lateral view; **B**, Flower, frontal view. — A–E, *Fischer 11021*, Rwanda, Nyungwe National Park, Mt. Bigugu.

sparsely hairy, dorsal petal wine red with greenish crest, lateral united petals uniformly wine red. Lateral sepals green, 6–7 × 1.5 mm, sparsely hairy, keeled. Lower sepal 9–10 mm long and 6–7 mm deep, tapering into 4–5 mm long spur. Dorsal petal cucullate, 8–10 × 4 mm. Lateral united petals 8–9 mm long, upper petal 6–7 × 3–4 mm, lower petal 7–8 × 3.5 mm. Ovary pubescent, 4 mm long, with 5 tufts of white hairs. Figures 3, 18.

Ecology. – Bamboo-zone, ericaceous shrub to paramo, 2500–3350 m.

Distribution. – Democratic Republic of the Congo: Mt. Kahuzi, Mt. Biéga, Mt. Muhi.

Etymology. – Named after the almost glabrous upper leaf surface.

Specimens examined. – **Democratic Republic of the Congo.** Lacs Edouard et Kivu. Kahuzi-Biéga National Park. Mt. Kahuzi en son flanc Nord. Arête Kabushwa. km 28 route Kavumu-Walikale, 3200 m, 8 Jan 1956, *Pierlot 1226* (BR); Kahuzi, Dec 1945, *Hendrickx 3637* (BR); montagnes à l'Ouest du Lac Kivu. Massif du Kahuzi, 1929, *Humbert 7754* (BR); Kahuzi, Nov 1946, *Hendrickx 4281* (BR); sommet du Kahuzi, 24 May 1960, *Petit 320* (BR); Mt Kahuzi, Jul 1945, *Hendrickx 3212* (BR); sommet du Mont Kahuzi, 29 Dec 1971, *Troupin 14279* (BR); flanc sud du Kahuzi, 21 Jan 1970, *Ern 134* (BR);

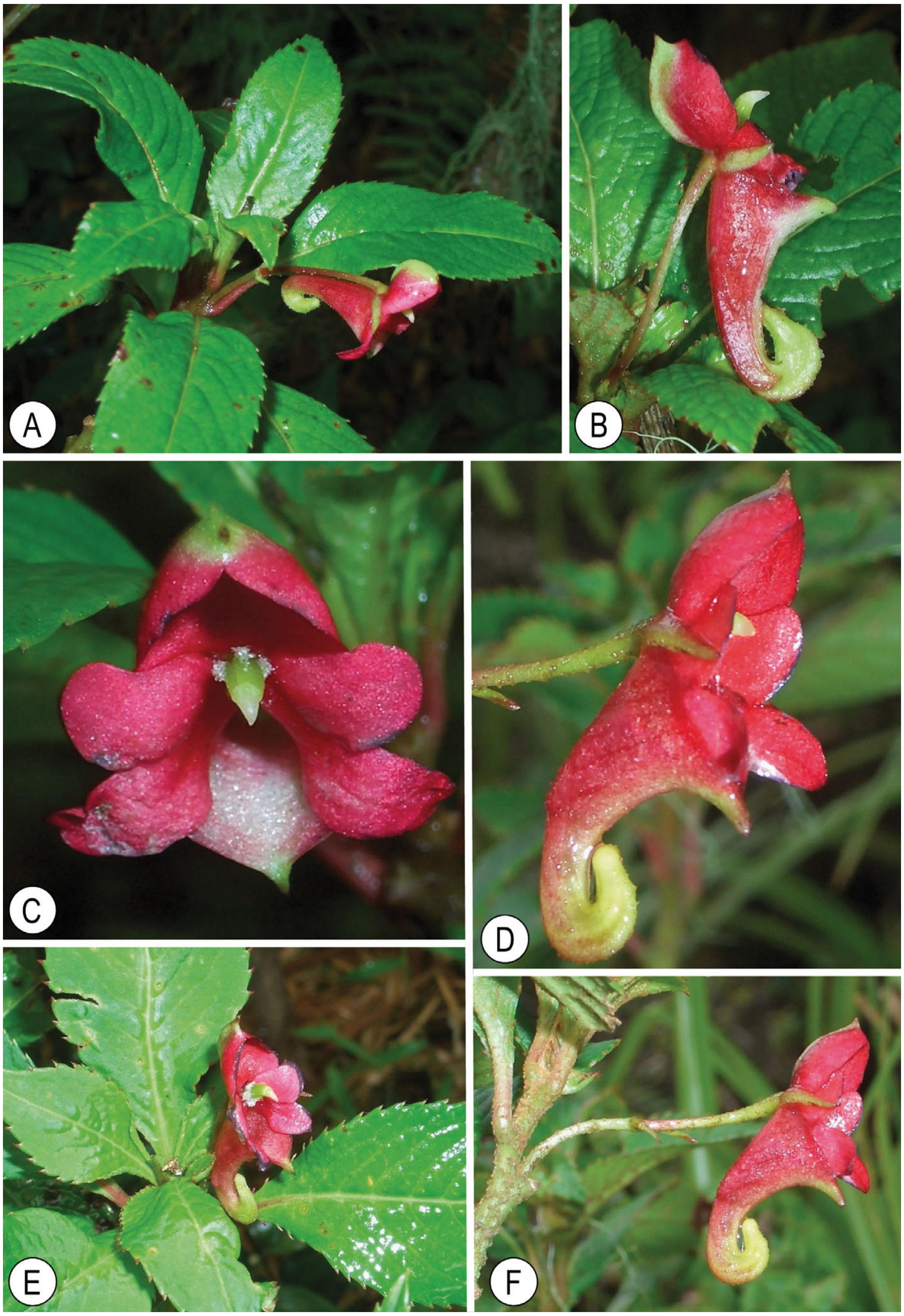

Fig. 18. *Impatiens superglabra*. **A** & **E**, Detail of habit; **B**, **D** & **F**, Flower, lateral view; **C**, Flower, frontal view. — A–F, *Fischer 9765*, Democratic Republic of the Congo, Kahuzi-Biéga National Park, Mt. Kahuzi.

Mt. Kahuzi, km 28 route Kavumu–Walikale, le long de la piste allant au sommet du mont, 8 Jan 1956, *Pierlot 1224* (BR); Kahuzi en son flanc Nord, arête Kabushwa, km 28 route Kavumu–Walikale, 8 Jan 1956, *Pierlot 1225* (BR); Kahuzi, 17 Apr 1938, *Hendrickx 288* (BR); Kahuzi-Gipfelzone, 18 Jan 1955, *Stauffer 1057* (BR); Mont Kahuzi, 4 Jun 1971, *Ntakiyimana 61* (BR); Mt. Kahuzi sommet, 3 Nov 1940, *Hendrickx 1233* (BR); Mt. Kahuzi, km 28 route Kavumu–Walikale, le long de la piste allant au sommet du mont, 8 Jan 1956, *Pierlot 1223* (BR); Mont Kahuzi, 11 Jul 1951, *Pierlot 205* (BR); flanc sud du Kahuzi, 21 Jan 1970, *Ern 133* (BR); Mt. Kahuzi, 20 Feb 1953, 3200 m, *Pierlot 498* (BR); Mont Kahuzi, flanc sud, 25 Dec 1971, *Bamps 2876* (BR); Mont Kahuzi, 7 May 1971, 2700 m, *Ntakiyimana 13* (BR); Mt. Kahuzi, ericaceous shrub, c. 3000 m, 7 Oct 2009, *Fischer 9765* (KOBL); du ruisseau Isale, Mt. Muhi, 31 Jul 1955, 3045 m, *Kinet 90* (BR); sine loc., Mar 1932, *Scaetta 1404* (BR).

Note. – The specimens from the Ruwenzori Mountains in Uganda cited by Grey-Wilson (1982) probably belong to a different taxon, and are excluded here.

Excluded specimens

The following specimens had been identified by Grey-Wilson (1980) as *Impatiens purpureoviolacea*, and their localities are included in the published distribution map (Grey-Wilson, 1980). However, they represent different species and are listed below.

Impatiens erecticornis R.Wilczek & G.M.Schulze in Bull. Jard. Bot. État Bruxelles 29: 190. 1959.

Democratic Republic of the Congo. Forestier Central. Irangi, terr. Kalehe, 850 m, 3 Jan 1972, *Bamps 2917* (BR). Lacs Edouard et Kivu. Entre Walikale et Kalehe (Kivu), 1220 m, Mar 1952, *Lebrun 5301* (BR).

Impatiens stuhlmannii Warb. in Engler, Pflanzenw. Ost-Afrikas 2C: 254. 1895.

Rwanda. Lacs Edouard et Kivu. Nyungwe National Park. Kibuye, Wisumo, 2200 m, 16 Mar 1973, *Troupin 14749* (BR, NHR); Shangugu, route Bukavu–Astrida, env. d'Uwinka, colline Bunyereri, 2100 m, 9 Jul 1960, *Troupin 12436* (BR); Shangugu, route Astrida–Bukavu, vers km 93, environs d'Uwinka, colline Wakagano, 2300 m, 16 Feb 1960, *Troupin 11860* (BR); Shangugu, route Astrida–Bukavu, environs d'Uwinka, colline Bunyangurube, 2000 m, 24 Mar 1959, *Troupin 9853* (BR).

■ AUTHOR CONTRIBUTIONS

EF designed and performed the research, collected the specimens, developed the taxonomic concept and wrote the manuscript. SA designed and performed the research, developed the taxonomic concept and wrote the manuscript. EF and SA contributed equally to this manuscript. NH performed the research, developed the taxonomic concept and contributed to the manuscript. SJ conducted the analyses, developed the taxonomic concept and contributed to the manuscript. All authors approved the final version of the manuscript. — EF, efischer@uni-koblenz.de, https://orcid.org/0000-0001-7455-9833; SA, sabraham@uni-bonn.de, https://orcid.org/0000-0001-8047-932X; NH, n.holstein@nhm.ac.uk, https://orcid.org/0000-0001-9892-0355; SJ, steven.janssens@plantentuinmeise.be

■ ACKNOWLEDGEMENTS

We thank Hans-Jürgen Ensikat for conducting the scanning electron microscopy and the gardeners of Bonn University Botanical Gardens for cultivating the plants. We are grateful to the Rwanda Development Board (RDB), Conservation and Tourism, the Institut National pour l'Environnement et la Conservation de la Nature (INECN), Burundi, and the Université de Cinquantaine, Bukavu, Democratic Republic of the Congo for research and export permits. We also like to thank the BMUB (Federal Ministry for the Environment, Nature Conservation and Nuclear Safety) for funding the Project "Conservation of Biodiversity and Natural Resources and Climate Protection by sustainable Agriculture and Forestry at Cyamudongo Forest, Rwanda" (16_III_083_RWA_A_Cyamudongo Regenwald) within the International Climate Initiative (IKI) and the "Akademie der Wissenschaften und Literatur Mainz" for financial support of field trips to Rwanda. Special thanks go to Bonny Dumbo and Landry Dumbo for support in the field in Rwanda and Democratic Republic of the Congo and to Eric Roalson and the two anonymous reviewers for helpful comments. The curators of the following herbaria kindly facilitated the study of specimens: B, BM, BR, K, P. Open Access funding enabled and organized by Projekt DEAL.

■ LITERATURE CITED

Abrahamczyk, S., Janssens, S., Xixima, L., Ditsch, B. & Fischer, E. 2016. *Impatiens pinganoensis* (Balsaminaceae), a new species from Angola. *Phytotaxa* 261: 240–250. https://doi.org/10.11646/phytotaxa.261.3.3

Abrahamczyk, S., Lozada Gobilard, S., Ackermann, M., Fischer, E., Krieger, V., Redling, A. & Weigend, M. 2017. A question of data quality – Testing pollination syndromes in Balsaminaceae. *PLoS ONE* 12: e0186125. https://doi.org/10.1371/journal.pone.0186125

Alfaro, M.E., Zoller, S. & Lutzoni, F. 2003. Bayes or bootstrap? A simulation study comparing the performance of Bayesian Markov chain Monte Carlo sampling and bootstrapping in assessing phylogenetic confidence. *Molec. Biol. Evol.* 20: 255–266. https://doi.org/10.1093/molbev/msg028

Baele, G., Lemey, P. & Suchard, M.A. 2016. Genealogical working distributions for Bayesian model testing with phylogenetic uncertainty. *Syst. Biol.* 65: 250–264. https://doi.org/10.1093/sysbio/syv083

Dagallier, L.P.M., Janssens, S.B., Dauby, G., Blach-Overgaard, A., Mackinder, B.A., Droissart, V., Svenning, J.-C., Sosef, M.S.M., Stévart, T., Harris, D.J., Sonké, B., Wieringa, J.J., Hardy, O. & Couvreur, T. 2019. Cradles and museums of generic plant diversity across tropical Africa. *New Phytol.* 225: 2196–2213. https://doi.org/10.1111/nph.16293

Doyle, J.J. & Doyle, J.L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochem. Bull. Bot. Soc. Amer.* 19: 11–15.

Durham, L.S. 2008. Africa rift basin is a new frontier. *A. A. P. G. Explorer* 29: 16–18.

Farris, J.S. 1989. The retention index and the rescaled consistency index. *Cladistics* 5: 417–419. https://doi.org/10.1111/j.1096-0031.1989.tb00573.x

Fischer, E. 1997. Contributions to the Flora of Central Africa V: Two new species of *Impatiens* (Balsaminaceae) from Eastern Zaïre. *Bull. Jard. Bot. Natl. Belg.* 66: 63–71. https://doi.org/10.2307/3668136

Fischer, E., Dhetchuvi, J.B. & Ntaganda, C. 2003. A new species of *Impatiens* (Balsaminaceae) from Nyungwe Forest, Rwanda. *Syst. & Geogr. Pl.* 73: 91–95.

Gilg, E. 1909. Balsaminaceae africanae. *Bot. Jahrb. Syst.* 43: 97–128.

Gilg, E. 1914. *Impatiens urundiensis*. Pp. 227 in: Brandt, W., v. Brehmer, W.G.B.A., Gilg, E., Harms, H., Mildbraed, J., Moeser, W., Schlechter, R., Ulbrich, O.E. & De Wildeman, E., Die von Hans Meyer auf seiner Reise durch das Zwischenseengebiet Ostafrikas 1911 entdeckten neuen Arten. *Bot. Jahrb. Syst.* 51: 225–233.

Grey-Wilson, C. 1979. New taxa in African *Impatiens*. *Kew Bull.* 33: 641–649. https://doi.org/10.2307/4109806

Grey-Wilson, C. 1980. *Impatiens of Africa*. Rotterdam: A.A. Balkema.

Grey-Wilson, C. 1982. *Flora of Tropical East Africa: Balsaminaceae*. Rotterdam: A.A. Balkema.

Grey-Wilson, C. 1989. A new hybrid *Impatiens* from Africa. Studies in Balsaminaceae XII. *Kew Bull.* 44: 717–719. https://doi.org/10.2307/4110436

Grimshaw, J.M. & Grey-Wilson, C. 1997. 311. *Impatiens kilimanjari* subspecies *pocsii* Balsaminaceae. *Bot. Mag.* 14: 23–30. https://doi.org/10.1111/1467-8748.00058

Hamilton, A.C. 1982. *Environmental history of East Africa: A study of the Quaternary.* London: Academic Press.

Huelsenbeck, J. & Ronquist, F. 2001. MrBayes: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755. https://doi.org/10.1093/bioinformatics/17.8.754

Janssens, S.B. 2008. *Evolutionary studies in Balsaminaceae*: *Integration of evidence from molecular and morphological data*. Ph.D. Thesis. Katholieke Universiteit Leuven, Belgium.

Janssens, S., Geuten, K., Yuan, Y.-M., Song, Y., Küpfer, P. & Smets, E. 2006. Phylogenetics of *Impatiens* and *Hydrocera* (Balsaminaceae) using chloroplast *atpB-rbcL* spacer sequences. *Syst. Bot.* 31: 171–180. https://doi.org/10.1600/036364406775971796

Janssens, S.B., Geuten, K.P., Viaene, T., Yuan, Y.-M., Song, Y. & Smets, E. 2007. Phylogenetic utility of the *AP3/DEF* K-domain and its molecular evolution in *Impatiens* (Balsaminaceae). *Molec. Phylogen. Evol.* 43: 225–239. https://doi.org/10.1016/j.ympev.2006.11.016

Janssens, S.B., Viaene, T., Huysmans, S., Smets, E.F. & Geuten K.P. 2008. Selection on length mutations after frameshift can explain the origin and retention of *AP3/DEF* like paralogues in *Impatiens*. *J. Molec. Evol.* 66: 424–435. https://doi.org/10.1007/s00239-008-9085-5

Janssens, S.B., Knox, E.B., Dessein, S. & Smets, E.F. 2009a. *Impatiens msisimwanensis* (Balsaminaceae): Description, pollen morphology and phylogenetic position of a new East African species. *S. African J. Bot.* 75: 104–109. https://doi.org/10.1016/j.sajb.2008.08.003

Janssens, S.B., Knox, E.B., Huysmans, S., Smets, E.F. & Merckx, V.S. 2009b. Rapid radiation of *Impatiens* (Balsaminaceae) during Pliocene and Pleistocene: Result of a global climate change. *Molec. Phylogen. Evol.* 52: 806–824. https://doi.org/10.1016/j.ympev.2009.04.013

Janssens, S.B., Fischer, E. & Stévart, T. 2010. New insights into the origin of two new epiphytic *Impatiens* species (Balsaminaceae) from West Central Africa based on molecular phylogenetic analyses. *Taxon* 59: 1508–1518. https://doi.org/10.1002/tax.595015

Janssens, S.B., Dessein, S. & Smets, E. 2011. Portrayal of *Impatiens nzabiana* (Balsaminaceae): A morphological, molecular and biogeographic study of a new Gabonese species. *Syst. Bot.* 36: 440–448. https://doi.org/10.1600/036364411X569624

Janssens, S.B., Ballings, P., Mertens, A. & Dessein, S. 2018. A new endemic *Impatiens* species on Mount Gorongosa (Mozambique) demonstrates the conservation importance of montane areas in Africa. *Phytotaxa* 333: 73–85. https://doi.org/10.11646/phytotaxa.333.1.5

Johnson, L.A. & Soltis, D.E. 1998. Assessing congruence: Empirical examples from molecular data. Pp. 297–348 in: Soltis, D.E., Soltis, P.S. & Doyle, J.J. (eds.), *Molecular Systematics of Plants II: DNA sequencing*. New York: Springer. https://doi.org/10.1007/978-1-4615-5419-6_11

Katoh, K., Misawa, K., Kuma, K. & Miyata, T. 2002. MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucl. Acids Res.* 30: 3059–3066. https://doi.org/10.1093/nar/gkf436

Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J. & Barthlott, W. 2009. A global assessment of endemism and species richness across island and mainland regions. *Proc. Natl. Acad. Sci. U.S.A.* 106: 9322–9327. https://doi.org/10.1073/pnas.0810306106

Kluge, A.G. & Farris, J.S. 1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.* 18: 1–32. https://doi.org/10.1093/sysbio/18.1.1

Launert, E. 1963. Das Testa-Indument einiger Arten der Gattung *Impatiens* L. (Balsaminaceae). *Bol. Soc. Brot.*, ser. 2, 37: 71–77, Taf. I–IV.

Linnaeus, C. 1753. *Species plantarum*. Holmiae [Stockholm]: impensis Laurentii Salvii. https://doi.org/10.5962/bhl.title.669

Loader, S.P., Ceccarelli, F.S., Menegon, M., Howell, K.M., Kassahun, R., Mengistu, A.A., Saber, S.A., Gebresenbet, F., de Sá, R., Davenport, T.R.B., Larson, J.G., Müller, H., Wilkinson, M. & Gower, D.J. 2014. Persistence and stability of Eastern Afromontane forests: Evidence from brevicipitid frogs. *J. Biogeogr.* 41: 1781–1792. https://doi.org/10.1111/jbi.12331

Lozada-Gobilard, S., Weigend, M., Fischer, E., Janssens, S.B., Ackermann, M. & Abrahamczyk, S. 2019. Breeding systems in Balsaminaceae in relation to pollen/ovule ratio, pollination syndromes, life history and climate zone. *Pl. Biol.* 21: 157–166. https://doi.org/10.1111/plb.12905

Lu, Y.-Q. & Chen, Y.-L. 1991. Seed morphology of *Impatiens* L. (Balsaminaceae) and its taxonomic significance. *Acta Phytotax. Sin.* 29: 252–257.

Mecklenburg, A.F. 1910. *In the Heart of Africa*. Translated by G.E. Maberly-Oppler. London, etc.: Cassell. https://doi.org/10.5962/bhl.title.22205

Muellner-Riehl, A.N., Schnitzler, J., Kissling, W.D., Mosbrugger, V., Rijsdijk, K.F., Seijmonsbergen, A.C., Versteegh, H. & Favre, A. 2019. Origins of global mountain plant biodiversity: Testing the 'mountain geobiodiversity hypothesis'. *J. Biogeogr.* 46: 2826–2838. https://doi.org/10.1111/jbi.13715

Mutke, J. & Barthlott, W. 2005. Patterns of vascular plant diversity at continental to global scales. *Biol. Skr.* 55: 521–531.

Mutke, J., Sommer, J.H., Kreft, H., Kier, G. & Barthlott, W. 2011. Vascular plant diversity in a changing world: Global centres and biome-specific patterns. Pp. 83–96 in: Zachos, F.E. & Habel, J.C. (eds.), *Biodiversity hotspots*. Berlin & Heidelberg: Springer. https://doi.org/10.1007/978-3-642-20992-5_5

Oliver, D. 1885. Catalogue of the plants collected by Mr. J. Thomson in east tropical Africa. *J. Linn. Soc., Bot.* 21: 397–406. https://doi.org/10.1111/j.1095-8339.1885.tb00570.x

Pickford, M., Senut, B. & Hadoto, D. 1993. *Geology and palaeontology of the Albertine Rift Valley*, *Uganda–Zaire*, vol. 1, *Geology.* Publication Occasionelle 24. Orléans: Centre International pour la Formation et les Echanges Geologiques.

Plumptre, A.J., Behangana, M., Davenport, T.R.B., Kahindo, C., Kityo, R., Ndomba, E., Nkuutu, D., Owiunji, I., Ssegawa, P. & Eilu, G. 2003. *The biodiversity of the Albertine Rift.* Albertine Rift Technical Reports Series, No. 3. Wildlife Conservation Society. Available from: https://albertinerift.wcs.org/About-Us/Publications.aspx

Plumptre, A.J., Davenport, T.R.B., Behangana, M., Kityo, R., Eilu, G., Ssegawa, P., Ewango, C., Meirte, D., Kahindo, C., Herremans, M., Peterhans, J.K., Pilgrim, J.D., Wilson, M., Languy, M. & Moyer, D. 2007. The biodiversity of the Albertine

Rift. *Biol. Conservation* 134: 178–194. https://doi.org/10.1016/j.biocon.2006.08.021

Posada, D. 2008. jModelTest: Phylogenetic model averaging. *Molec. Biol. Evol.* 25: 1253–1256. https://doi.org/10.1093/molbev/msn083

Ronquist, F. & Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. https://doi.org/10.1093/bioinformatics/btg180

Schulze, G.M. 1947. Balsaminaceae. Pp. 270–271 in: Robyns, W. (ed.), Choripétales nouvelles de la région du Parc National Albert (Congo Belge). *Bull. Jard. Bot. État Bruxelles* 18: 270–271. https://doi.org/10.2307/3666560

Song, Y., Xuan, Y.-M. & Küpfer, P. 2005. Seedcoat micromorphology of *Impatiens* (Balsaminaceae) from China. *Bot. J. Linn. Soc.* 149: 195–208. https://doi.org/10.1111/j.1095-8339.2005.00436.x

Stamatakis, A. 2006. RAxML-VI-HPC: Maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* 22: 2688–2690. https://doi.org/10.1093/bioinformatics/btl446

Suchard, M.A., Lemey, P., Baele, G., Ayres, D.L., Drummond, A.J. & Rambaut, A. 2018. Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus Evol.* 4: vey016. https://doi.org/10.1093/ve/vey016

Suzuki, Y., Glazko, G.V. & Nei, M. 2002. Overcredibility of molecular phylogenies obtained by Bayesian phylogenetics. *Proc. Natl. Acad. Sci. U.S.A.* 99: 16138–16143. https://doi.org/10.1073/pnas.212646199

Swofford, D. 2002. PAUP*: Phylogenetic analysis using parsimony (* and other methods), version 4. Sunderland, MA: Sinauer.

Tardieu-Blot, M.L. 1944. Les *Impatiens* d'Indochine: Répartition, affinités et description d'espèces nouvelles. *Notul. Syst. (Paris)* 11: 169–185.

Troupin, G. & Grey-Wilson, C. 1983. Balsaminaceae. Pp. 312–321 in: Troupin, G. (ed.), *Flore du Rwanda: Spermatophytes*, vol. 2. Tervuren: Musée Royal de l'Afrique Centrale.

Utami, N. & Shimizu, T. 2005. Seed morphology and classification of *Impatiens* (Balsaminaceae). *Blumea* 50: 447–456. https://doi.org/10.3767/000651905X622699

Wilczek, R. & Schulze, G.M. 1960. Balsaminaceae. Pp. 396–428 in: Boutique, R. (ed.), *Flore du Congo Belge et du Ruanda-Urundi*, vol. 9. Brussels: I.N.É.A.C.

Yuan, Y.M., Song, Y.I., Geuten, K., Rahelivololona, E., Wohlhauser, S., Fischer, E., Smets, E. & Küpfer, P. 2004. Phylogeny and biogeography of Balsaminaceae inferred from ITS sequences. *Taxon* 53: 391–403. https://doi.org/10.2307/4135617

Appendix 1. Taxon sampling and GenBank accessions.

Taxon, locality, *collector and collection number* (herbarium code), nuclear gene accession numbers *ImDEF1*, *ImDEF2*, plastid accession number *atpB-rbcL*. Missing information is indicated by –; * indicates new sequences.

Impatiens elwiraurzulae Eb.Fisch., Abrah., Holstein & S.B.Janssens, D.R. Congo, Kahuzi Biéga National Park, Mulolo, *L. Dumbo & B. Dumbo s.n.* (BONN, KOBL), MT612879*, MT612864*, –; ***I. gesneroidea*** Gilg, Rwanda, Nyungwe National Park, Mt. Bigugu, 2750 m, *E. Fischer 11021* (KOBL), MT612877*, MT612867*, MT612892*; ***I. kivuensis*** Eb.Fisch., Abrah., Holstein & S.B.Janssens, Burundi, Kibira National Park, Mt. Teza, 2100 m, *E. Fischer 13451* (KOBL), MT612872*, MT612870*, MT612898*; ***I. lotteri*** Eb.Fisch., Abrah., Holstein & S.B.Janssens, D.R. Congo, South Kivu, Ulindi River, 1803 m, *M.C. Lotter 1542* (BR), MT612880*, MT612865*, MT612890*; ***I. ludewigii*** Eb.Fisch., Abrah., Holstein & S.B.Janssens, Rwanda, Nyungwe National Park, Gisovu, 2200 m, *E. Fischer 13914* (KOBL), MT612881*, MT612863*, MT612893*; ***I. ludewigii***, Rwanda, Nyungwe National Park: Uwinka, 1990 m, *E. Fischer 14500* (BONN, KOBL), MT612876*, MT612859*, MT612889*; ***I. ludewigii***, Rwanda, Western Province, Nyungwe National Park, Uwinka, ca. 2400 m, *E. Fischer 10280* (KOBL), MT612885*, MT612862*, MT612899*; ***I. ludewigii***, Rwanda, Western Province, Nyungwe National Park, Uwinka, 2300 m, *E. Fischer 10350* (KOBL), MT612886*, MT612861*, MT612898*; ***I. lutzmannii*** Eb.Fisch., Abrah., Holstein & S.B.Janssens, Burundi, Bururi Forest Reserve, 1950 m, *E. Fischer 13002* (BONN, KOBL), MT612873*, MT612855*, MT612900*; ***I. meruensis*** Gilg subsp. ***meruensis***, Tanzania, Longido, *E.B. Knox 3328* (BR), FJ826714, FJ826767, FJ826662; ***I. purpureoviolacea*** Gilg, Rwanda, Nyungwe National Park, Uwinka, *E. Fischer 8093* (KOBL), MT612883*, MT612858*, MT612897*; ***I. purpureoviolacea***, Rwanda, Nyungwe National Park: Karamba, 1900 m, *E. Fischer 13018* (KOBL), MT612887*, MT612869*, MT612904*; ***I. purpureoviolacea***, Rwanda, Nyungwe National Park: Karamba, 1900 m, *E. Fischer 13258* (KOBL), MT612888*, MT612868*, MT612903*; ***I. purpureoviolacea***, Rwanda, Nyungwe National Park: Karamba, 1900 m, *E. Fischer 13910* (KOBL), MT612884*, MT612866*, MT612894*; ***I. purpureoviolacea***, Rwanda, Nyungwe National Park: Rukarara, Source of the Nile, 2250 m, *E. Fischer 13911*, (KOBL), MT612882*, MT612857*, MT612895*; ***I. ×troupinii*** Eb.Fisch., Abrah., Holstein & S.B.Janssens, Rwanda, Nyungwe National Park: Rukarara, Source of the Nile, 2250 m, *E. Fischer 13912* (BONN, KOBL), MW148593*/MW148594*, MW148595*/MW148596*, MT612896*; ***I. ulugurensis*** Warb., Tanzania, South Uluguru Mts., *E.B. Knox 3554* (BR), FJ826732, FJ826786, FJ826678; ***I. urundiensis*** Gilg, Burundi, Kumuyange, near hot springs, gallery forest in montane grassland, 2000 m, *E. Fischer 13301* (KOBL), MT612871*, MT612854*, MT612905*; ***I. versicolor*** Eb.Fisch., Abrah., Holstein & S.B.Janssens, Rwanda, Nyungwe National Park, zwischen Pindura und Bweyeye, 1800 m, *E. Fischer 13390* (KOBL), MT612874*, –, MT612902*.