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Phylogenetics, character evolution and a subgeneric revision of the genus *Pelargonium* (Geraniaceae)

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Abstract

Previous molecular phylogenetic studies of *Pelargonium* have remained inconclusive with respect to branching patterns of major infrageneric lineages, with the exception of a basalmost generic split that reflects chromosome length differences. Because of this and the lack of clearly distinguishing morphological characters, no subgeneric classification has been undertaken so far. Here, we present increased phylogenetic signal using chloroplast *atp*B-*rbc*L spacer and *trn*L-F sequences including additional taxa (110 taxa in total) and character sampling. All analyses confirmed the previously recognised first split into two clades characterised by chromosome size, and also converged on four major clades (two within each chromosome size group). The four major clades are further supported by synapomorphic length mutations from both intergenic spacers. The evolution of characters from flower morphology and phenolic constituents was examined for usefulness for clade delimitation. Although character state distributions did not generally reveal clear synapomorphies for the respective lineages, differences in state distributions of floral characters and leaf phenols support the circumscription of these major clades. In particular, nectar guides and petal-ratios indicate character state shifts among clades. The leaf flavonoids, myricetin and prodelphinidin, exhibit differing evolutionary trends in *Pelargonium* species with small chromosomes. In summary, all results favour the recognition of four, morphologically diagnosable, lineages as subgenera and support a revised subgeneric classification of *Pelargonium*. In addition, a new section (*stat. nov.*) including two subsections (*comb. nov.*) is segregated from an otherwise paraphyletic section *Polyactium.*

Key words: *atp*B-*rbc*L, flavonoids, floral traits, indels, *trn*L-F

Introduction

Pelargonium L'Héritier in Aiton (1789: 417) is an important genus of the horticulturally valuable Geranium family, which consists of about 800 mostly herbaceous species with a worldwide, predominantly temperate to subtropical distribution (Albers & van der Walt 2007, Fiz *et al.* 2008). Within Geraniaceae, the genus *Pelargonium* is sister to the remaining genera of the family in its strict sense (Price & Palmer 1993), *Erodium* L'Héritier in Aiton (1789: 414), *Geranium* Linnaeus (1737: 204) and *Monsonia* Linnaeus (1767: 508) incl. *Sarcocaulon* (De Candolle) Sweet (1826: 73). *Pelargonium* represents the second largest genus (about 280 taxa) of Geraniaceae and is morphologically distinct from the remainder of the family in having a hypanthium, consisting of an adnate nectar spur with one nectary, as well as a generally zygomorphic floral symmetry (Albers & van der Walt 2007).

The main distribution of nearly 90% of the genus is in southern Africa, including the Republic of South Africa and adjacent parts of Namibia. The highest species diversity is found in the south-western part of South Africa (van der Walt & Vorster 1983). This centre of *Pelargonium* diversity receives rainfall exclusively in winter or, in a small transition zone, throughout the year. This is in contrast to the central and eastern parts of South Africa, where rainfall is concentrated in the summer months. Outside southern Africa, the genus *Pelargonium* is represented by

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only about thirty species, mainly distributed in mountainous habitats along the East African rift valley and in southern Australia. The few remaining species are scattered across Madagascar, Arabian Peninsula, Asia Minor, New Zealand, and the islands Socotra, St. Helena and Tristan da Cunha.

Many different growth forms occur within *Pelargonium*, ranging from herbaceous annuals, subshrubs and shrubs to stem succulents and geophytes (van der Walt 1977, van der Walt & Vorster 1981a, 1988). The historical classification of the genus into sections, as originally circumscribed by De Candolle in 1824, was largely based on this diversity in growth forms. In the past thirty years there has been extensive taxonomic research at an infrageneric level, based on single or combined data sets from morphology (e.g. van der Walt & Boucher 1986, van der Walt & van Zyl 1988, Albers *et al.* 1992, Dreyer *et al.* 1992a, Maggs *et al.* 1995a), palynology (Stafford & Gibby 1992), phytochemistry (Williams *et al.* 2000) and karyology (e.g. Albers & van der Walt 1984, Gibby *et al.* 1990). New circumscriptions and further studies on a sectional level followed (e.g. van der Walt *et al.* 1995, 1997, Albers *et al.* 1995, 2000, Dreyer & Marais 2000). On a higher taxonomic level, karyological results suggested a split of the genus into two groups with large (1.5–3 µm) and small (< 1.5 µm) chromosomes, respectively (Albers & van der Walt 1984, Gibby & Westfold 1986; Albers 1988, Gibby *et al.* 1990, 1996). Phylogenetic analyses of molecular data (Price & Palmer 1993, Bakker *et al.* 1999a, 2000) confirmed this basal split. This division, however, seemed not to be supported by any morphological synapomorphies (Bakker *et al.* 2004). Therefore, no formal taxonomic conclusions were drawn, even though the two clades have often been referred to as "subgenera" in an informal manner (e.g. Bakker & al 1999a, Bakker *et al.* 2004, Weng *et al.* 2012).

Based on sequence data from three genomes (Bakker *et al.* 2004) and in analyses of five plastid and one mitochondrial marker (Weng *et al.* 2012), three to five main clades were further suggested between the basal chromosomal split and traditional sections. Furthermore, the monophyly of several sections in their current circumscription remains a controversial issue (Bakker & 2004, Albers and Becker 2010, Weng *et al.* 2012). Currently, fifteen sections are validly recognised, as well as a tentatively circumscribed "sect. *Magnistipulacea"* (compare Bakker *et al.* 1999a, 2004) which is still awaiting its formal description. A variety of molecular markers (*trn*L-F, ITS and AFLP) have been used more recently in phylogenetic analyses within a few sections (Bakker *et al.* 1998, Touloumenidou *et al.* 2004, Becker & Albers 2009). In a survey of *trn*L-F data, length mutations (indels) were also found to be phylogenetically informative within clades of *Pelargonium* with small chromosomes (Bakker *et al.* 1999a).

Above sectional level several non-molecular traits were tested for correlations with molecular results. These included growth forms and basic chromosome numbers (Bakker *et al.* 1999b, 2004), stem succulence, tuber formation and hypanthium length (Bakker 2005) as well as leaf venation, leaf dissection and leaf margins (Jones *et al.* 2009). But the distribution of character states overlaps or varies among the main clades.

The family Geraniaceae deviates remarkably from other angiosperms in having highly rearranged plastid genomes that differ in gene order, gene content and expansion of the inverted repeat (Chumley *et al.* 2006, Guisinger *et al.* 2011). *Pelargonium* × *hortorum* L.H.Bailey (1916: 2531) has the largest cp genome so far observed in flowering plants (Chumley *et al.* 2006). Moreover, in chloroplast and mitochondrial genes of *Pelargonium* and related genera, the DNA substitutional rates are found to be noticeably increased (Parkinson *et al.* 2005, Bakker *et al.* 2006, Mower *et al.* 2007, Guisinger *et al.* 2008).

In the current study we compiled a large *atp*B-*rbc*L spacer dataset (110 taxa) and added newly generated and already published sequences of the *trn*L-F spacer for a combined analysis that aimed at clarifying the basalmost splits and other remaining uncertainties in the phylogeny of *Pelargonium*. The enlarged genome of *Pelargonium* × *hortorum* might be caused by several boundary changes of the inverted repeat (Chumley *et al.* 2006). In *Pelargonium* × *hortorum* the same authors found the *atp*B-*rbc*L region localised in the transition between the large single copy region and the inverted repeat. Therefore, we expected a considerable number of microstructural changes that might add further phylogenetic signal on the infrageneric level.

In addition, character evolution was studied for a number of non-molecular traits (floral morphology and phenolic compounds) as well as for their potential use as diagnostic characters. This is the first time these have been analysed in a wide study of the genus overall, although they had formerly proven valuable for earlier sectional classifications. For example, floral characters have previously shown clear differences between *Pelargonium* species and supported the division or infrasectional classification of sections (e.g. Dreyer *et al.* 1992a, Marais 1994). Similarly, patterns of phenolic compounds often characterise infrasectional groups in *Pelargonium* and have been used in delimination of sections (Albers *et al.* 1995, 2000, Dreyer *et al.* 1992a, van der Walt *et al.* 1995) as

well as uniformly characterising an otherwise macro-morphologically variable section (van der Walt *et al.* 1997). Based on these insights from molecular, morphological and chemical data we conclude with a proposal for a new subgeneric classification of the genus *Pelargonium*.

Materials and methods

Taxon sampling and molecular markers

The *atp*B-*rbc*L spacer was sequenced for a total of 104 *Pelargonium* species, 11 of which are included for the first time in a molecular phylogenetic analysis. The *atp*B-*rbc*L intergenic spacer was chosen because it provided good resolution in a variety of infrageneric studies (e.g. Setoguchi *et al.* 1997, Wissemann & Ritz 2005, Janssens *et al.* 2006, Wanntorp 2006), while at the same time being present in all included taxa with their rapidly evolving plastid genomes. All traditionally recognised sections and recently introduced infrageneric groups (e.g. Bakker *et al.* 2004) were represented. Two different sampling strategies for the large sectt. *Hoarea* (Sweet) De Candolle (1824: 649) and *Pelargonium* were used. Sect. *Hoarea* inhabits a crown position in *Pelargonium* phylogeny (Bakker *et al.* 1999a, Touloumenidou *et al.* 2004), therefore we included species with assorted floral types following Marais (1994). Sect. *Pelargonium* appeared as non-monophyletic with two species, *P. denticulatum* Jacquin (1797; 5) and *P. quercifolium* (Linnaeus filius) L'Héritier in Aiton (1789: 422), separated from one main group in Bakker *et al.* (2004). These two species belong to a subgroup with sticky leaves (Albers & van der Walt 1984). Here, we added a further species of this group, *P. glutinosum* (Jacquin) L'Héritier in Aiton (1789: 426).

The *atp*B-*rbc*L sequences were combined with 47 new sequences of the *trn*L-F spacer generated from the same specimen, supplemented with already published sequences by Bakker *et al.* (2004) to obtain an accumulated data set of 104 *Pelargonium* taxa. Two taxa of *Erodium*, *Geranium* and *Monsonia* were used as an outgroup to represent Geraniaceae *sensu stricto* (Price & Palmer 1993, Albers 1996, Fiz *et al.* 2008). The monotypic genus *California* Aldasoro, Navarro, Vargas, Sáez & Aedo (2002: 213), recently separated from *Erodium* (Aldasoro *et al.* 2002), was not included, because of its unclear position in phylogeny (Stevens 2001 onwards). We likewise did not include any *Hypseocharis* Remy (1847: 238) species, which are optionally placed in Geraniaceae in its broader circumscription (APG III 2009). Fresh leaf material was taken from the living collection of the Botanical Garden, University of Münster, and from a few species of the wild species collection of a *Pelargonium* breeder (Syngenta, formerly Fischer Pelargonien, Hillscheid). For *P. boranense* Friis & M.G.Gilbert (1976: 1705), fresh tissue dried in silica gel was used. All species, origins, vouchers and gene bank accession numbers are listed in appendix I.

Amplification and sequencing

DNA was extracted using the DNeasy Plant Mini Kit (Quiagen, Hilden, Germany) according to the manufacturer's protocol. PCR amplifications were performed with 50 µl volumes, containing 3 µl DNA template (50–120 ng/µl), 4 µl dNTP mix (2,5 mM), 2 µl of each primer(10 pmol/µl) and 0,4 µl (5u/µl) Taq-Polymerase (BioTherm, GeneCraft or GoTaq, Promega) on a primus 96 advanced, PEQLAB or on Robocycler Gradient 96, Stratagene. The general cycling profile was an initial step of 3 min at 94°C, followed by 40 cycles of 20 sec at 94°C, 30 sec at 58°C and 60 sec at 72°C, plus a final elongation of 5 min at 72°C. The following primers were designed according to the sequence of *P. x hortorum* (DQ897681), atpBrev (5'-GAC CAA TGA TTT GGA CGA TAC GCC C-3'), rbcLrev (5'-GTA TCC TTG GTT TCA TAA TCA GG-3'), trnLfor (5'- CTT ACT AAG TGA TAA CTT TCA AAT TC-3') and trnFrev (5'-CCG ACC ATT TCC AAT GCA TC-3'). PCR products were controlled by electrophoresis on a 1% agarose gel. Bands were excised, purified using NucleoSpin Extract II (Macherey & Nagel, Düren, Germany) and precipitated. The sequencing reaction was performed in a 12 µl final volume with the BigDye v3.1 Terminator cycle sequencing kit (Applied Biosystems) on an ABI PRISM 3730XL capillary sequencer at the UKM, University of Münster.

Alignment, indel coding and phylogenetic analyses

The consensus sequences were compiled in BioEdit v7.0.7.0 (Hall 1999) and, after an initial preliminary alignment with Clustal W, manually aligned. Two hotspots with a total of 35 characters (*atp*B-*rbc*L 24 bp, *trn*L-F 11 bp) were excluded from the analyses because of variable strings of mononucleotides. The observed indels were coded via simple indel coding (SIC, Simmons & Ochoterena 2000) as well as modified complex indel coding

(MCIC, Müller 2006), both implemented in Seqstate (Müller 2005). Maximum parsimony (MP) analyses with and without indel coding were done with PAUP v4.0b10 (Swofford 2003). Heuristic searches of the individual and combined datasets were carried out using the parsimony ratchet algorithm as implemented in PRAP v2.0b3 (Müller 2004) with default settings. Bootstrap support values (BV) were computed using 10 000 replicates and the settings as recommended in Müller (2005). Additionally Bremer support (BS) was computed for both datasets and all MP analyses. For BS calculation, again PRAP was used. Ancestral states of indel characters were inferred by using the simple indel coding matrix in Mesquite v2.75 (Maddison & Maddison 2011), where a parsimony ancestral state optimisation on the SIC consensus tree was performed

The best-fit model of sequence evolution for Bayesian inference (BI) and maximum likelihood (ML) analyses was determined using jModelTest (Posada 2008). For both datasets the models selected by AIC were GTR+G and GTR+I+G, both within the 95%-confidence interval. BI was performed using GTR+I+G and defaults priors in Mr. Bayes v.3.1.2 (Ronquist & Huelsenbeck 2003). Two runs with four chains each, sampling every 100th generation and temperature set to 0.2 were conducted using 10 Million generations. To verify that convergence of the independent runs was reached, the potential scale reduction factor and the average standard deviation of split frequencies in MrBayes and the effective sampling size were observed using Tracer v1.5 (Rambaut & Drummond 2007). Twenty five percent of the retained trees of each run were conservatively discarded as burn-in. The remaining trees were pooled and a majority rule consensus tree was constructed in MrBayes. ML searches were performed using the GTR+G model in RaxML v7.03 (Stamatakis 2006, Stamatakis *et al.* 2008). Rapid bootstrap analysis with 250 replicates was followed by 10 ML searches, resulting in one best tree.

Non-molecular data

Ancestral state reconstructions were inferred for seven floral characters and 12 leaf phenolic characters on the Bayesian consensus tree from the combined molecular data set, using two different approaches, which both allow the coding of polymorphic character states, found for almost all floral characters. The first was a parsimony ancestral state optimisation done in Mesquite. All characters were coded as multistate (morphology) or binary (chemistry) and treated as unordered. As a second approach, ancestral states were reconstructed using the Baysian approach (BBM; F81+G model) implemented in the software RASP 2.1b (Yu *et al.* 2013). Markov chain Monte Carlo analyses were conducted with two runs of 10 chains with 100.000 generations each. Trees were sampled every 100th generation; the burnin was set to 25%. Missing character states are not accepted by the program, therefore missing characters in data on phenolic compounds were recoded as polymorphic (presence & absence). Characters and their respective character states are listed in Table 1; further character specific information is provided in the following.

All morphological character were additionally coded for a total of 229 *Pelargonium* species and subspecies (approximately 85% of the genus) to analyse their state distribution among major clades.

Flower morphology

Figure 1 gives an overview of the floral diversity in the genus *Pelargonium*. Data on flower morphology were compiled from different literature sources (van der Walt 1977, 1985, 1994; van der Walt & Vorster 1981a, 1983; 1988; van der Walt & Boucher 1986; van der Walt & van Zyl 1988; Gibby 1989; van der Walt *et al.* 1990a, 1995, 1997; Dreyer *et al.* 1992a, 1992b; Johnson & Mathew 1993; Marais 1994; Albers *et al.* 1995, 2000; Maggs *et al.* 1995a, 1995b, 1999; Hellbrügge 1997; Dreyer & Marais 2000; Gilbert & Vorster 2000; Vorster 2000; Albers 2002 and Becker 2006). Data for individual species was supplemented from Dinter (1914, 1920), Verdcourt (1968), Kokwaro (1971), Friis & Gilbert (1976), Lavranos (1978), Olivier & van der Walt (1984), Vorster (1986, 1987, 1992),Barker (1990), Dreyer & van der Walt (1990), Gibby (1990), van der Walt *et al.* (1990b, 1990c), van der Walt (1991), Thulin (1993), Marais (1996a, 1996b, 1997, 1998, 2014), Meve *et al.* (2000), Miller & Morris (2004), Van Jaarsveld & Van Wyk (2006), Retief *et al.* (2007a, 2007b) and Manning & Goldblatt (2011, 2012).

Some rather vague descriptions found in the literature were re-evaluated using specimens from the MSUN herbarium, the living collection at the University of Münster, as well as the Syngenta collection.

FIGURE 1. Flower diversity of *Pelargonium*. Photographs arranged according to major clades, showing variation in flower shape, colour and nectar guides. Scale bars approximately represent 1 cm. **A–J** (clade A): **A** *Pelargonium nanum*, **B** *P. ovale subsp. ovale*, **C** *P. quercifolium*, **D** *P. cucullatum subsp. cucullatum*, **E** *P. echinatum*, **F** *P. crithmifolium*, **G** *P. multiradiatum*, **H** *P. schizopetalum* **I** *P. pulchellum*, **J** *P. triandrum*, **K–P** (clade B): **K** *P. minimum*, **L** *P. columbinum*, **M** '*P. geniculatum*', **N** *P. ionidiflorum*, **O** *P. abrotanifolium*, **P** *P. dichondrifolium*, **Q–V** (clade C1): **Q** *P. antidysentericum* subsp. *antidysentericum*, **R** *P. tragacanthoides*, **S** *P. paemorsum* subsp. *praemorsum*, **T** *P. caucalifolium* subsp. *caucalifolium*, **U** *P. mollicomum*, **V** *P. tetragonum*, **W–AB** (clade C2): **W** *P. barklyi*, **X** *P. acetosum*, **Y** *P. frutetorum*, **Z** *P. grandicalcaratum*, **AA** *P. endlicherianum*, **AB** *P. caylae*. All photographs by J. Röschenbleck.

TABLE 1. Flower and leaf phenolic characters, their corresponding states and tree statistics for single characters of the MP ancestral state reconstructions. For further explanation of single character states see material and methods and Fig. 2 for nectar guide types.

Character	States	No. of states	Steps	CI/RI
Flower morphology				
Petal number	(A) two (B) four (C) five	3	12	0.666/0.428
Petal ratio, posterior petals (p), anterior petals (a), [score]	(A) p only (B) p>>a [>3.5] (C) p>a [2–3.4] (D) p≥a [1.2–1.9] (E) p=a [0.9–1.1] (F) p<a [<0.9]	6	41	0.121/0.454
Hypanthium Length	(A) absent (B) 0,5–10 mm (C) 11–20 mm (D) 21–40 mm (E) > 40 mm	5	53	0.679/0.711
Petal colour	(A) blue (B) pink (C) white (D) red (E) yellow (F) bicoloured	6	58	0.534/0.470
Nectar guide types	(A) absent (B) dark veins (C) eyespots (D) basal markings (E) central markings	4	50	0.440/0.548
Nectar guide distribution	(A) nectar guides absent (B) on posterior petals (C) on posterior and anterior petals (D) on anterior petals	5	48	0.500/0.250
Number of fertile anthers	(A) more than seven (B) seven (C) six (D) five (E) four (F) less than four	6	35	0.457/0.525
Leaf phenols				
Apigenin	(A) absent (B) present	2	14	0.071/0.315
C-Glycosyl flavones			16	0.062/0.659
Cyanidin			19	0.052/0.357
Delphinidin			15	0.066/0.674
Gallic acid			13	0.076/0.333
Hydrolysable tannins			14	0.071/0.711
Isorhamnetin			15	0.066/0.125
Kaempherol			15	0.066/0.000
Luteolin			23	0.043/0.521
Myricetin			12	0.083/0.738
Protocatechuic acid			8	0.125/0.300

In *Pelargonium*, five states were distinguished for the character "petal colour": "pink" includes the range from true pink through dark shades of pink, such as magenta and purple. Scarlet or bright clear reds are separately scored as "red". "White" means true white to light pink, but without any trace of yellow. "Yellow" includes the typical *Pelargonium* cream tinge as well as green-yellowish petals. "Bicoloured" flowers possess clearly differently coloured posterior and anterior petals. "Hypanthium length" was categorised according to published size classes (Struck & van der Walt 1996) and further adjustments regarding South African pollinator guilds (Struck 1997, reviewed in Johnson 2010), yielding five states. "Posterior-anterior-petal ratio" was calculated from maximum length and width of the respective petals and, after reconciliation with laminar petal drawings, coded as six different states (Table 1). In some species the final state was adjusted due to clear shape differences or to the lack of overlap within length ranges between posterior and anterior petals especially in the case of sect. *Ciconium* (Sweet) Harvey (1860: 298).

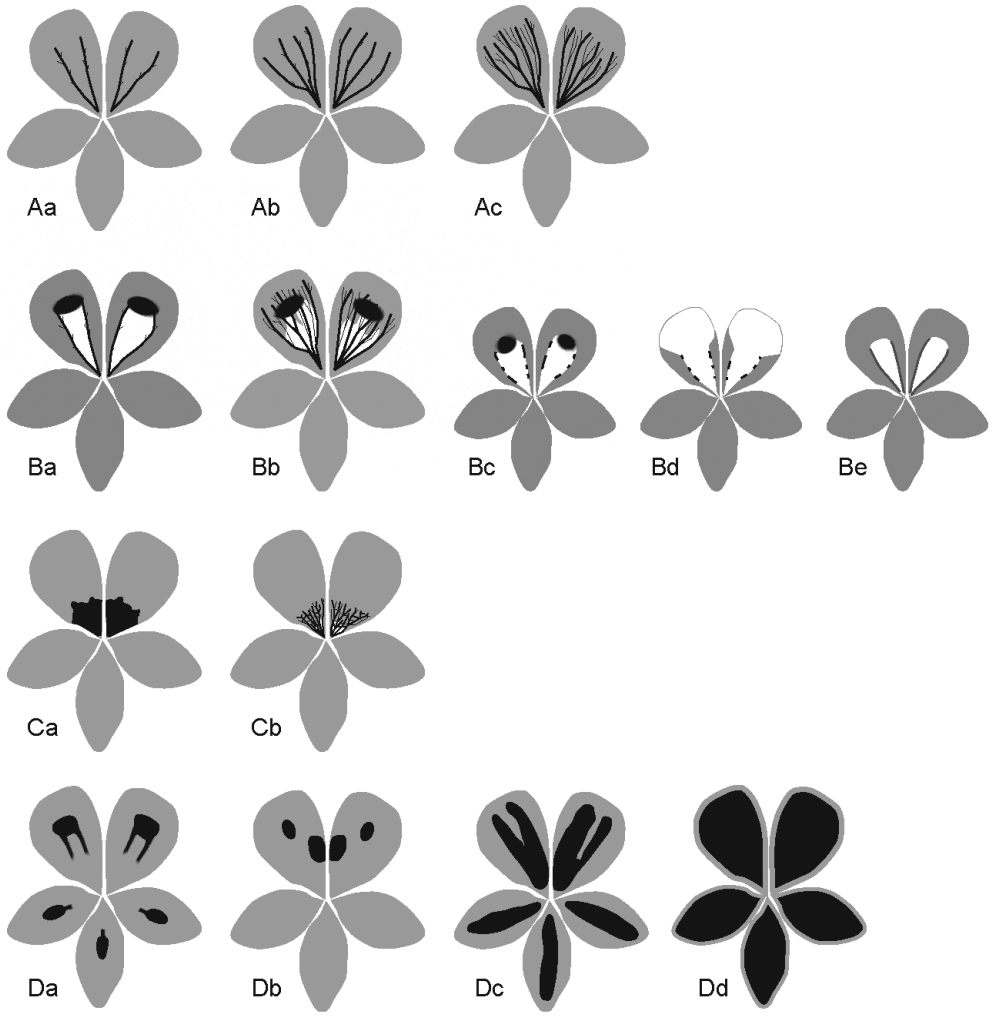

FIGURE 2. Types of nectar guides in *Pelargonium*. **Aa**–**Ac**: dark veins, **Ac** feathery veins; **Ba**–**Bd** eyespots, **Bc**–**Bd** reduced forms; **Ca**–**Cb**: basal markings, **Ca** basal blotch, **Cb** basal reticulate pattern, short basal veined markings not depicted; **Da**–**Dd**: central markings, **Da**–**Db** central spots, **Dc**–**Dd** central stripes to nearly complete covering.

Visible "nectar guides" were initially granularly split into many character states, then states with strong similarities in pattern or position were accumulated to yield a final four character states (model types). Lacking or inconspicuous markings were scored as a fifth state. All model types are illustrated in Fig. 2. Newly recognised here is a pattern that we will refer to as "eyespot" (Fig. 2, B a–e), which in recent descriptions was lumped together under "feathery pattern". It differs from the feathery veined type (Fig. 2, A c) in having an additional blotch in the centre of the posterior petal, often accompanied by a white or at least lightly coloured centre of the whole pattern.

In eyespots, lines to the flower centre are dashed or dotted in many cases. Although well defined, some reduced forms occur (Fig. 2, B b–e), especially in the small flowered sect. *Peristera* De Candolle (1824: 654). In the species-rich sect. *Hoarea* a satisfactory interpretation of the ancestral state reconstructions was not possible due to insufficient taxon sampling (< 8%), but nearly all species were included in the quantitative analysis of character state distribution.

Phenolic constituents

Phenolic data were mainly taken from Marschewski (1995), for sect. *Peristera* from Hellbrügge (1997), with additions for single taxa from Williams *et al.* (2000). Because data on leaf phenols were compiled based on different surveys, constituents were only coded into presence and absence and not quantitatively scored. No data were available for six species. Rarely, ambiguous results have been reported for individual constituents in single taxa, in which cases states were coded as missing.

Free ellagic acid, ellagitannins and gallotannins were not always differentiated in the different investigations and therefore are here collectively treated as "hydrolysable tannins". For the same reason vitexin, isovitexin, orietin and isoorientin were summarised as "c-glycosyl flavones". "Quercetin" was excluded from the ancestral state analysis after character state coding, because this character was overall present in all in- and outgroup taxa.

Outgroup data were compiled for *Erodium* from Saleh *et al.* (1983) and Fecka *et al.* (2001), for *Monsonia* from Marschewski (1995) and for *Geranium* from Bate-Smith (1972, 1973 and 1981) and Ivancheva & Petrova (2000).

Results

Phylogenetic analyses converge on a backbone with four highly supported major clades

The tree topologies resulting from the three MP analyses did not show any substantial differences and support values obtained in the analyses, including indel coding, did not deviate significantly from each other. Therefore only the support values from two maximum parsimony analyses (without indels and SIC) are shown, supplemented with BS values of the MP analysis including indels (Fig. 3). The trees of maximum likelihood- and Bayesian analyses were also virtually congruent (Fig. 4). Topological differences were restricted to the resolution of sect. *Cortusina* (DC.) Harvey (1860: 299) *sensu stricto* (Dreyer *et al.* 1992a), otherwise to nodes with support less than 50 BV.

In view of the tree topologies being largely congruent to those of the combined data set, trees based on analyses of the *atp*B-*rbc*L intergenic spacer alone are available as supplemental material (Appendix II & III). Compared with the analyses of the single spacer region, the number of nodes with BV > 95% were increased by 5–21% in analyses of the combined data set. A detailed overview of character- and tree statistics is shown in Table 2. All analyses for the *atp*B-*rbc*L spacer and the combined data set (*atp*B-*rbc*L and *trn*L-F) confirmed the basalmost split of the genus originally detected in molecular data by Price & Palmer (1993).

Moreover, all analytic approaches (MP, SIC, ML and BI) and datasets agreed upon four major clades (A, B, C1, C2; clade denotations according to Bakker *et al.* (2004)) with maximum support: 98–100% BV and 1.0 posterior probabilities (PP). BS ranged from 11–12 for the combined data set and from 9–15 in the *atp*B-*rbc*L spacer. Clades A and B represent *Pelargonium* species with small chromosomes, clades C1 and C2 are defined by large chromosomes. In comparison, support for the basalmost split was noticeably lower in most MP analyses (BV 79–98%, BS 3–7).

We detected pronounced sequence variation for all data sets with respect to major clades (Table 3). For the *atp*B-*rbc*L spacer, the mean sequence length in clade B was significantly shorter (137–149 bp) than those in all other major clades and exhibited a narrower range. Within the trnL-F spacer, average sequence lengths in clades C1 and C2 were considerably shorter (91 and 108 bp) than the mean lengths in clades A and B.

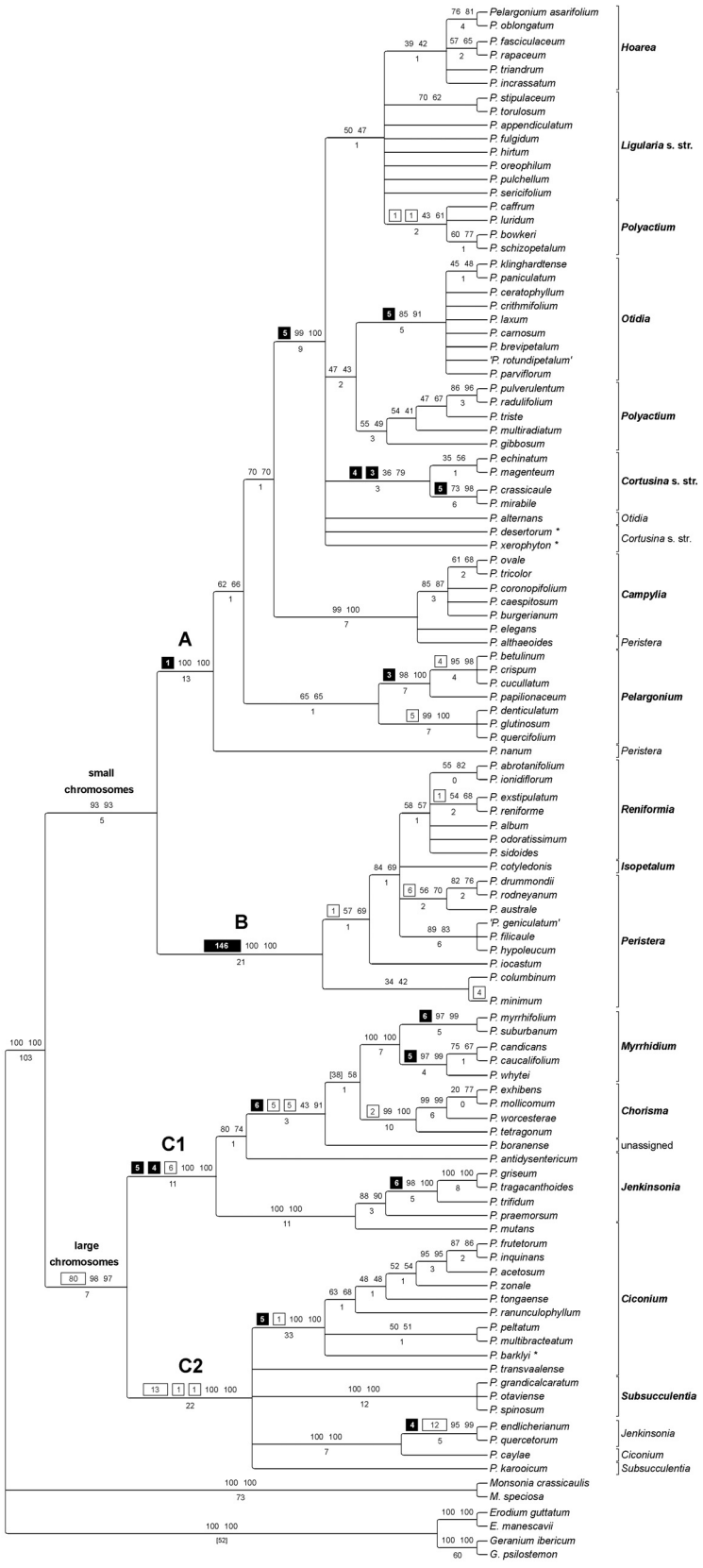

FIGURE 3. Majority rule consensus tree from the maximum parsimony analyses of the combined *atp*B-*rbc*L and *trn*L-F spacer regions. Bootstrap values are given above branches, for datasets combined with indel characters from simple indel coding (left) and without indels (right). Bremer support values from analysis with indel coding below branches. Values in brackets: Node was not present in the respective tree topology. Black squares represent indels within the *atp*B-*rbc*L intergenic spacer, light squares indicate indels within the *trn*L-F region. Numbers indicate indel lengths (bp). Denotations on the right: sectional names (bold) and most current sectional assignment of single species (not bold). Asterisks behind species names: only informally assigned to the respective section.

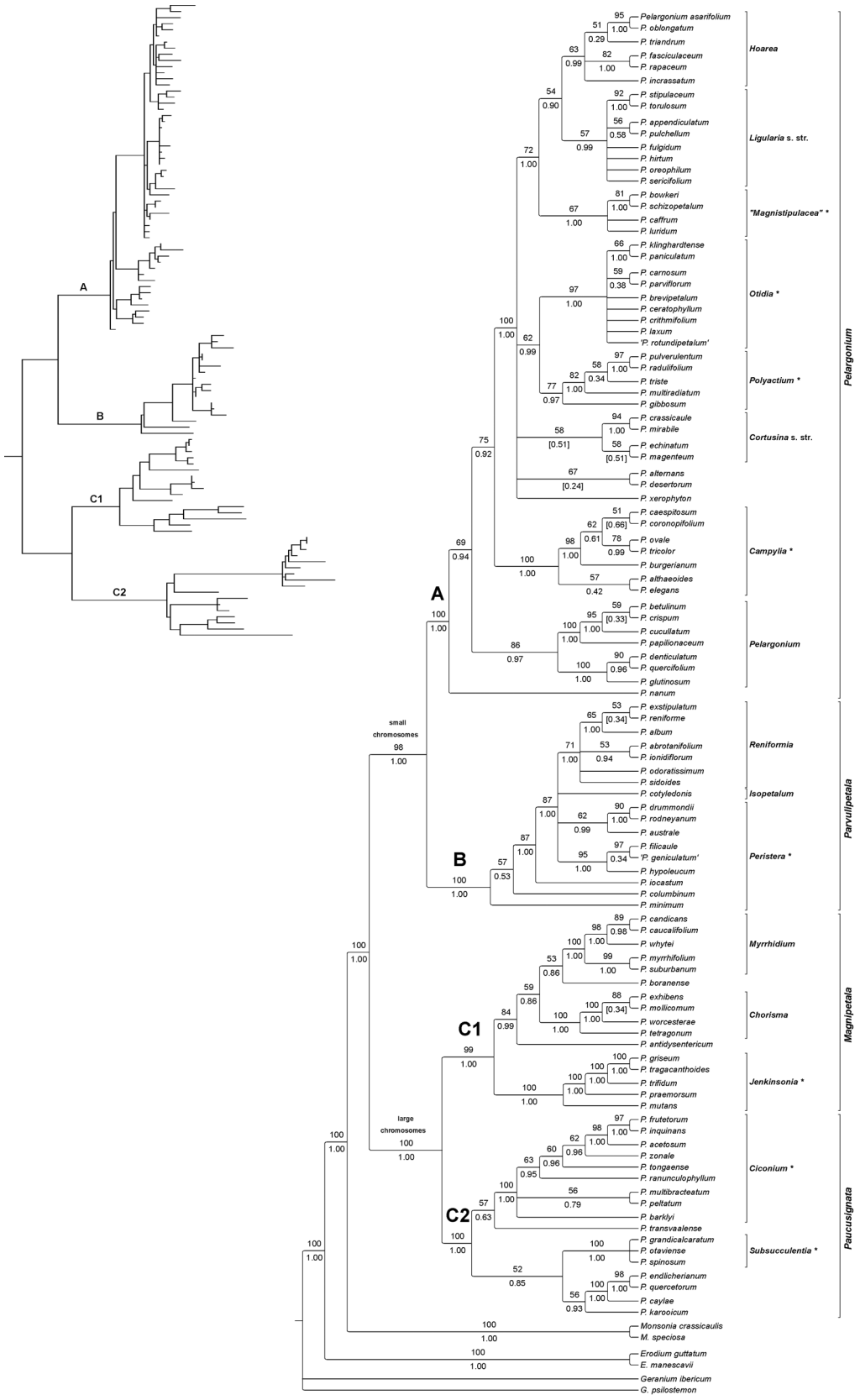

FIGURE 4. Tree from the maximum likelihood analysis using the combined *atp*B-*rbc*L and *trn*L-F spacer regions. Bootstrap values are shown above branches and posterior probabilities from the Bayesian analysis of the same data below branches. Posterior probabilities in brackets: Node was not present in the Bayesian consensus topology. Phylogram showing relative branch lengths from ML analysis with outgroups pruned from tree. Clade denotations on the right: sections and subgenera (vertical). Asterisks behind sectional names: delimitation, suggested here, deviates from most recent circumscription of section.

TABLE. 2. Sequence and tree statistics of maximum parsimony analyses and maximum likelihood and Baysian analyses for single (*atp*B-*rbc*L) and combined intergenic regions (*atp*B-*rbc*L and *trn*L-F), hotspots excluded. +SIC/+MCIC = SIC or MCIC encoded indels added to nucleotide data matrix, respectively.

	MP						ML		BI	
	*atp*B-*rbc*L without indels	*atp*B-*rbc*L + SIC	*atp*B-*rbc*L + MCIC	Combined without indels	Combined + SIC	Combined + MCIC	*atp*B-*rbc*L	Combined	*atp*B-*rbc*L	Combined
Total characters	1045	1159	1085	1974	2258	2094	1045	1974	1045	1974
Constant characters	613	613	613	1170	1170	1170	-	-	-	-
Parsimony informative character	308	375	338	566	724	643	-	-	-	-
Tree length (shortest tree)	772	917	911	1418	1841	1824	-	-	-	-
MP:Consistency / Retention Index. ML:score	0.723/ 0.930	0.732/ 0.928	0.742/ \0.932	0.719/ 0.919	0.707/ 0.907	0.719/ 0.912	-6137.996	-11592.091	-	-
No of internal nodes (Ingroup)	99	100	100	103	102	103	103	103	103	103
Nodes (Ingroup) with BV > 95%/ PPs > 0.95	16	20	19	24	26	26	21	33	44	66

TABLE 3. Sequence variation of single and combined intergenic regions, hotspots excluded.

	*atp*B-rbcL	*trn*L-F	Combined data set
Number of characters (=Length of alignment)	1045	929	1974
Mean length (range) genus *Pelargonium*	824.4 (701–874)	754.8 (669–801)	1583.9 (1487–1665)
Mean length (range) clade A	852.3 (843–874)	785.9 (774–801)	1638.2 (1623–1658)
Mean length (range) clade B	703.2 (701–712)	784.1 (775–792)	1487.3 (1480–1498)
Mean length (range) clade C2	840.9 (830–854)	676.7 (669–693)	1518.3 (1506–1537)
Mean length (range) clade C1	841.8 (833–854)	693.1 (684–703)	1535.2 (1528–1547)
Mean length (range) outgroups	841.2 (821–872)	793.2 (743–817)	1634.3 (1564–1680)

The internal structure of the major clades is best resolved in the tree topologies of the ML and Baysian analyses (Fig. 4). Certain clades correspond to sections, being monophyletic in their recent cirumscription (sectt. *Myrrhidium* De Candolle (1824: 657) and *Chorisma* (Lindley ex Sweet) De Candolle (1824: 658) [C1], *Reniformia* (Knuth) Dreyer (2000: 44) [B] and sectt. *Pelargonium*, *Ligularia* (Sweet) Harvey (1860: 280) *sensu stricto* (Albers *et al.* 2000) and *Hoarea* [A]). On the other hand several sections appeared paraphyletic, e.g. sectt. *Jenkinsonia* (C1), *Ciconium* (C2) and *Peristera* (B), with species placed in different major clades (Fig. 3). Monophyly of a "sect. *Magnistipulacea*", separated from an otherwise paraphyletic sect. *Polyactium* De Candolle (1824:655), is revealed in all analyses of the combined data set as well as both MP analyses with indel coding of the *atp*B-*rbc*L spacer.

Two noteworthy incongruencies across tree topologies of the combined data sets and the single spacer are found in the position of two species: *Pelargonium antidysentericum* (Ecklon & Zeyher) Kosteletzky (1836: 1896), sect. *Jenkinsonia* (C1), appeared as sister to a clade comprising sectt. *Myrrhidium*, *Chorisma* and *P. boranense* in all analyses of the combined data set, as well as in the SIC analysis of the *atp*B-rbcL spacer. This clade was not resolved in MP, ML and BI analyses of single data sets and *P. antidysentericum* appeared weakly supported as sister to sect. *Myrrhidium.* The second, *P. karooicum* Compton & P.E.Barnes (1931: 295), sect. *Subsucculentia* J.J.A.van der Walt (1995: 335) [C2], was placed as sister to sect. *Subsucculentia* in analyses of the *atp*B-*rbc*L region or as sister to the clade consisting of *P. caylae* Humbert (1936: 595), *P. endlicherianum* Fenzl (1842: 6) and

P. quercetorum Agnew (1967: 227).

Taxa that were included here for the first time were identified to belong to clades representing the sections to which the respective species are currently assigned.

Length mutational events support the recognition of major clades

The ancestral state reconstruction of the 158 indels (SIC) yielded 34 indels that are phylogenetically informative and synapomorphic for clades on different levels (Fig. 3): 16 in the *atp*B-*rbc*L and 18 in the *trn*L-F spacer.

Two indels characterise the first split. The small-chromosome clades A and B share one small deletion (1 bp). In turn, the large-chromosome clades C1 and C2 share an 80 bp deletion. The division between C1 and C2 was additionally supported by six synapomorphic indels. Three indels (4, 6 and 10 bp) are synapomorphic for clade C1, three indels (1, 1 and 13 bp) for clade C2. Similarly, one indel in the *atp*B-*rbc*L spacer separates clades A and B. This deletion is a synapomorphy for clade B, being the largest indel in the dataset (146 bp). Further indels were revealed as syapomorphic for sections, sister group relationships of sections or subclades of sections.

Moreover, the inclusion of indels in MP analyses increased the support values of nearly all internal nodes. Among them were two clades otherwise supported with less that 50% BV in the parsimony analysis of nucleotide substitutions only, sect. *Cortusina s.str.* and "sect. *Magnistipulacea*" (Fig. 3).

Evolution of floral characters: a complex picture

In general, high levels of homoplasy occurred for floral characters in *Pelargonium*, resulting in a consistency index range of 0.121–0.679 and a retention index range of 0.25–0.711 (Table 1). Ancestral state reconstructions yielded differing state transformations for the most common recent ancestors (MRCA) above sectional level in types of nectar guides, petal ratio, hypanthium length and petal colour (Fig 5). More constant characters (petal number, number of fertile anthers and nectar guide distribution) disclosed state transitions only at a sectional level or that they were concentrated in single major clades (Fig. 6). Results of the MP and Baysian reconstructions yielded almost identical states across all characters and, therefore, only results based on the BI approach will be presented here. Clear differences between methods with respect to inferred ancestral states will be indicated when discussing the respective character.

Analysis of the actual character state distribution across major clades (using 85% of the accepted *Pelargonium* species) exposed one to two clearly dominating states in all characters (Table 4).

Visible nectar guides occur frequently in *Pelargonium* although taxa with no markings occur in significant numbers in clades C2 and B (Table 4). Dark veins were the most likely ancestral state for the genus and are particularly significant in clades C1 and C2 although, in the latter, of noticeably lower intensity (Fig. 1 W-Y) and completely lacking in nearly one third of the species. The prominent floral pattern in clade B was eyespots, above the node of *P. minimum* (Cavanilles) Willdenow (1800: 664), which branches first and lacks any markings. All four categories of nectar guide types were found in clade A, with eyespots reconstructed as the most likely ancestral state (Fig. 5). Shifts to basal or central markings appeared almost exclusively in clade A and independently in several sections. In MP analyses the ancestral state of most nodes within xerophytic clades (except sectt. *Otidia* (Lindley ex Sweet) De Candolle (1824: 655) and *Hoarea*) of clade A was reconstructed as a central pattern, whereas the BI reconstruction remained ambiguous for most MRCAs.

The posterior-anterior-petal ratio of the MRCA of the genus remained ambiguous. However, in clade C1 the posterior petals have shifted to large size (Fig. 5), whereas in clade C2 the posterior petals have tended to reduce in size. Within clade C2, the ratio shifted either to equally-sized petals or to posterior petals slightly smaller than the anterior ones. Only the geographically distinct Asia Minor species also exhibited large-scale posterior petals. In the small-flowered clade B, petals tended towards an equal size with shifts in terminal taxa to slightly larger posterior petals, especially in the Australian species. The MRCA of clade A, above the first-branching *P. nanum* L'Héritier (1802: 39), was reconstructed to possess slightly enlarged posterior petals and in several of its sections (*Campylia* (Lindley ex Sweet) De Candolle (1824: 656), *Cortusina*, *Ligularia* and *Hoarea*), shifts to considerably larger petals occurred.

TABLE 4. Floral character state frequencies [%] for major clades (229 of approximately 280 *Pelargonium* taxa included). Note that only three characters, hypanthium length, petal number, and number of fertile anthers, are present in *P. apetalum* (clade B).

	Clade A	**Clade B**	**Clade C1**	**Clade C2**
	141 taxa	**33 (32) taxa**	**32 taxa**	**23 taxa**
Petal number				
Five	95.3	97.0	31.3	91.3
Four (Five or four)	1.4	-	37.5 (31.3)	-
Two (Five or Two)	3.3	-	-	(8.7)
No petals	-	3.0	-	-
Posterior-anterior-petal ratio				
Posterior petals only	3.3	-	-	-
p>>a (or post. petals only)	5.6	-	62.5	(8.7)
p>a	34.8	3.1	31.3	26.1
p≥a	43.2	28.1	3.1	30.4
p=a	9.0	43.8	3.1	13.0
p<a	4.2	25.0	-	21.7
Hypanthium length				
≤10 mm	32.6	78.8	25.0	-
11–20 mm	13.1	6.1	15.6	21.7
21–40 mm	16.5	3.0	9.4	13.0
>40 mm	5.7	-	3.1	4.3
polymorphic	32.2	12.1	46.9	60.9
Number of fertile anthers				
Seven	35.2	45.5	71.9	87.0
Six	6.7	12.1	-	-
Five (Seven or Five)	48.0	18.2	18.8 (6.3)	13.0
Four	6.2	9.1	-	-
Three, two or one	3.9	15.1	3.1	-
Petal colour				
Pink	32.0	56.3	25.0	30.4
White	16.5.	15.6	40.6	13.0
Yellow	22.2	-	-	4.3
Red	0.7	-	3.1	8.7
Bi-coloured	1.5	3.1	-	-
polymorphic	27.2	25.0	31.3	43.5
Distribution of nectar guides				
No markings	9.9	15.6	-	26.1
Posterior petals	61.6	75.0	84.4	56.5
Post. & ant. petals	24.9	9.4	15.6	17.4
Anterior petals	3.0	-	-	-
Nectar guide types				
No markings	9.9	15.6	-	26.1
Veins	23.5	-	78.1	60.9
Eyespots (Eyespots reduced)	28.2	53.1 (31.3)	- (6.3)	8.7
Basal markings	11.1	-	15.6	-
Central markings	27.3	-	-	4.3

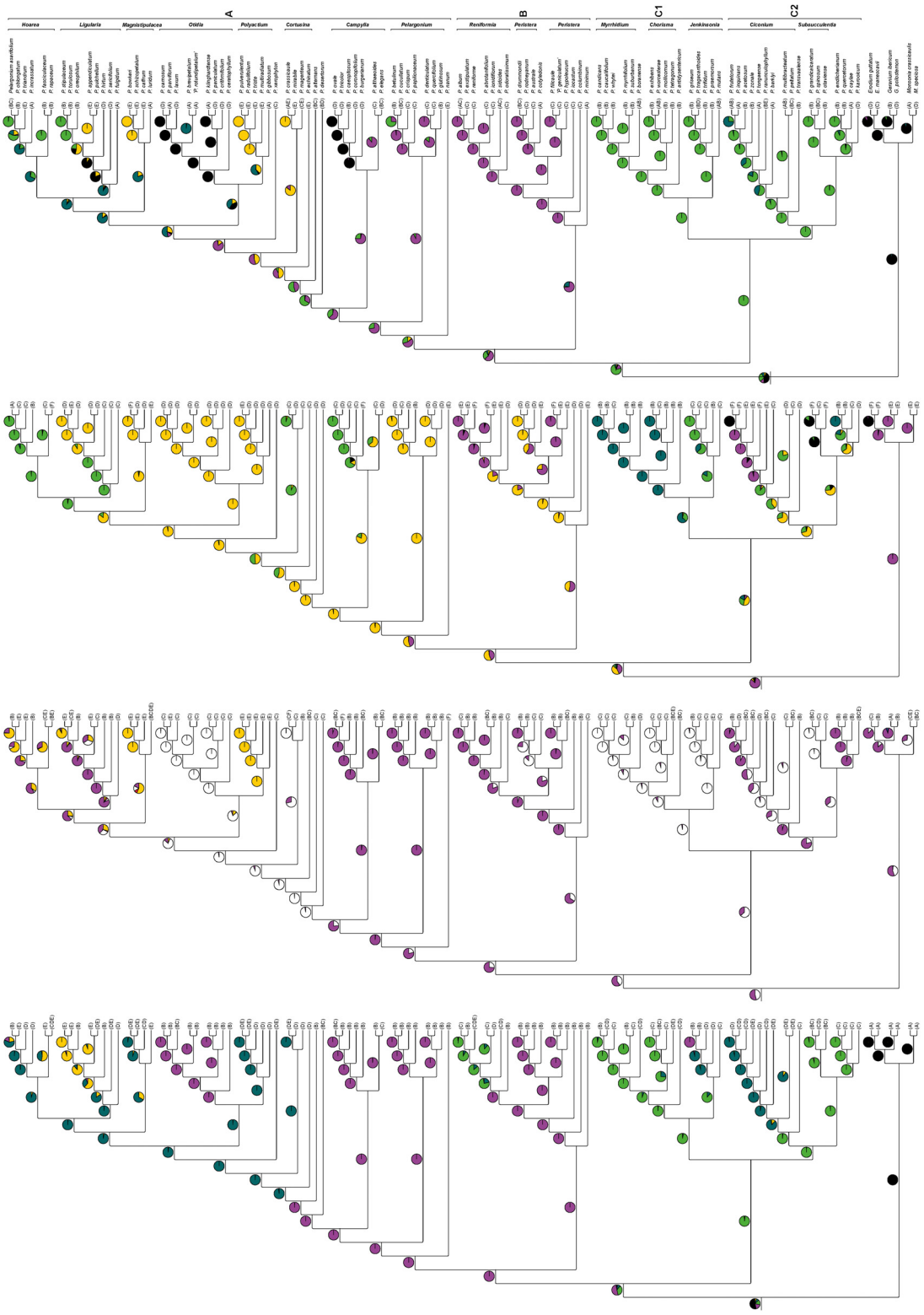

FIGURE 5. Ancestral states hypanthium length, petal colour, petal ratio and nectar guide types in *Pelargonium*, based on the Bayesian consensus topology for both intergenic spacer region (*atpB-rbc*L, *trn*L-F). Pie charts on nodes show state probabilities. Explanation of character states in legend.

In spite of the distinction of four size classes reflecting possible pollinators, the hypanthium length stayed polymorphic for several species, because of the intra-individual span of up to 50 mm (Table 4). Nevertheless, for the large-chromosome clades C1 and C2 the ancestral tube length was reconstructed to be 11–20 mm and for the small-chromosome clades A and B 0,5–10 mm. Shifts to longer floral tubes (> 20 mm) occurred several times independently in all major clades. In addition to the elongation of the hypanthium, length reductions were also developed, especially in clade C1 within terminal taxa of sect. *Jenkinsonia* (Fig.1 R) and in sect. *Otidia* in clade A (Fig. 1 F).

Flower colour was reconstructed as most likely pink for the MRCA of the genus and virtually all major clades (A, B, C2). Only clade C1, as well as all its sections, showed an ancestral state as white flowered. State transformations to yellow occurred at nodes for the geophytic sections in clade A. In MP reconstructions yellow petals were additionally found for the MRCA of sectt. *Ligularia* and *Hoarea*, as well as sectt. "*Magnistipulacea*", *Ligularia* and *Hoarea*. In contrast yellow petals were completely absent in the sister clade B (Table 4).

The distribution of prominent nectar guides was inferred as being restricted to the posterior petals for the genus and major clades (Fig. 6). Distinct nectar guides on all petals were frequent in clade A, mainly in sectt. *Cortusina*, *Polyactium* and "*Magnistipulacea*". Elsewhere, nectar guides on all petals were only found in terminal species of sect. *Subsucculentia* in clade C2, *P. otaviense* R.Knuth (1912: 439) and *P. grandicalcaratum* R.Knuth (1918: 135). Both of these species share an unusual semi-closed flower shape (Fig. 1 Z).

Pentapetalous flowers were basal for the genus and its major clades. Reductions to four petals were concentrated in clade C1, being significantly found in sect. *Jenkinsonia* and a clade formed by *P. boranense* and sect. *Myrrhidium* (Fig. 6). Four- or even two petalled flowers appeared independently in clade A (sectt. *Campylia* and *Hoarea*) as autapomorphies.

The number of fertile anthers was seven for all MRCAs of clades C1 and C2. The reduced number of five was revealed as being most likely ancestral for clade A and clade B (Fig. 6), but both clades also exhibited the typical number of seven fertile anthers above their basal nodes. In MP reconstructions the MRCAs of clades A and B remained equivocal. Within major clades the reduction to five fertile anthers was inferred for sectt. *Otidia* and *Hoarea* and a common state change in sectt. *Campylia* and *Chorisma.*

In summary, the visual inspection of distribution patterns of character states revealed that medium to large hypanthiums were often associated with conspicuously divergent petal sizes (p>>a, p>a) and dark veins or central spots as flower markings. Also small to very small floral tubes corresponded to more or less equally sized petals (p=a, p<a or p≥a) and eyespots or basal markings. Exceptions were species of sectt. *Ciconium* and *Reniformia* without prominent markings as well as the night scented sectt. *Polyactium* and "*Magnistipulacea*", the latter two showed minor differences in petal size accompanied with long hypanthiums and central markings as nectar guides.

Contrasting evolutionary trends for phenolic compounds in major clades

The abundance of single compounds varied tremendously across the genus and major clades (Table 5.). Ancestral state reconstructions did not conflict, so only the results of the Baysian reconstruction are presented. All compounds exposed a high degree of homoplasy (Table 1). Five characters (myricetin, prodelphinidin, luteolin, c-glycosyl flavones and hydrolysable tannins), with a retention index above 0.5, exhibited differing synapomorphic trends within major clades (Fig. 7). More constant or overall scarce characters yielded a lower retention index and synapomorphies were restricted to clades or subclades on a sectional level (Appendix IV).

TABLE 5. Frequency of occurrence for phenolic compounds [%] in the genus *Pelargonium* and the four major clades. Number of included species in brackets.

	Genus *Pelargonium*	Clade A	Clade B	Clade C1	Clade C2
Quercetin	100.0 (98)	100.0 (49)	100.0 (17)	100.0 (15)	100.0 (17)
Kaempherol	84.0 (94)	84.8 (46)	100.0 (17)	57.1 (14)	88.2 (17)
Myricetin	56.7 (90)	89.6 (48)	37.5 (16)	0.0 (15)	18.2 (11)
Isorhamnetin	15.5 (97)	16.7 (48)	29.4 (17)	13.3 (15)	0.0 (17)
C-glycosyl flavones	28.6 (98)	16.3 (49)	94.1 (17)	73.3 (15)	47.1 (17)
Luteolin	50.6 (89)	30.9 (42)	88.2 (17)	64.3 (14)	50.0 (16)
Apigenin	21.5 (93)	19.6 (46)	41.2 (17)	15.4 (13)	11.8 (17)
Prodelphinidin	57.1 (98)	87.8 (49)	58.8 (17)	6.7 (15)	11.8 (17)
Procyanidin	26.5 (98)	28.6 (49)	58.8 (17)	6.7 (15)	5.8 (17)
Hydrolysable tannins	52.6 (95)	23.4 (47)	100.0 (17)	100.0 (14)	47.1 (17)
Gallic acid	79.8 (94)	58.7 (46)	100.0 (17)	100.0 (15)	100.0 (16)
Protocatechuic acid	88.4 (95)	76.6 (47)	100.0 (17)	100.0 (15)	100.0 (16)

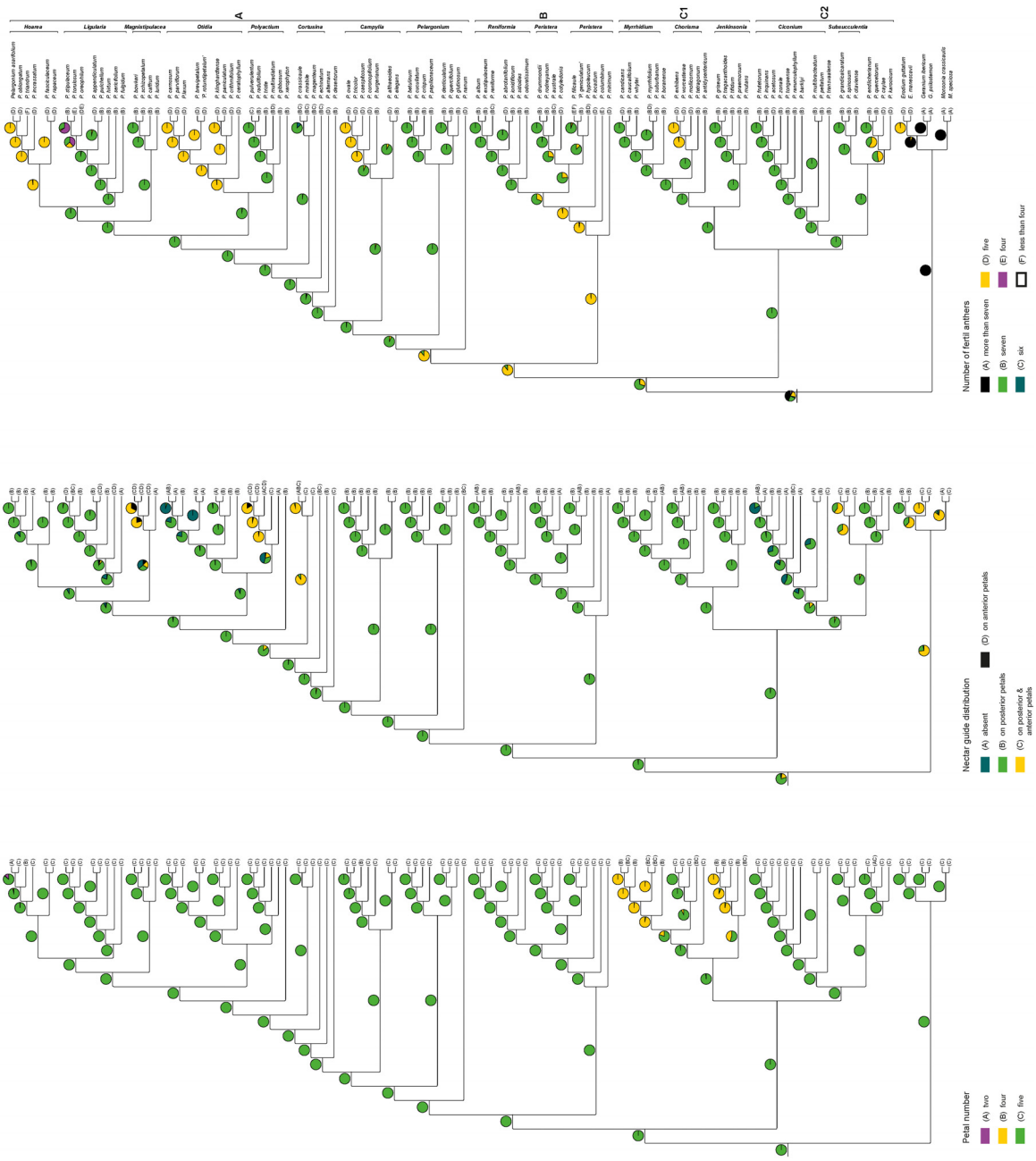

FIGURE 6. Ancestral states nectar guide distribution, number of fertile anthers and petal number in *Pelargonium*, based on the Bayesian consensus topology for both intergenic spacer region (*atp*B-*rbc*L, *trn*L-F). Pie charts on nodes show state probabilities. Explanation of character states in legend.

The inferred ancestral leaf flavonoid pattern of the genus *Pelargonium*, consisted of flavonols (quercetin and kaempferol), flavones (luteolin and c-glycosyl flavones), hydrolysable tannins and hydrobenzoic acids (gallic acid and protocatechuic acid). The flavonol myricetin and condensed tannins (prodelphinidin and procyanidin) were absent. The O-methylated flavonol isorhamnetin as well as the flavone apiginin were infrequently distributed and likewise reconstructed as absent for the genus (Fig. 7 & Appendix IV).

Based on the ancestral phenolic composition of the genus the following differing evolutionary trends were observed within each major clade. Clade A appeared to deviate most, especially with the reconstructed presence of myricetin and prodelphinidin (Fig. 7), with myricetin being even more frequent than kaempferol. In contrast, hydrolysable tannins and to a lesser extent hydroxybenzoic acids were widely lost in clade A (Fig. 7 & Appendix IV). Furthermore, the presence of both flavones declined in clade A. C-glycosyl flavones were lost in section *Pelargonium* and both, c-glycosyl flavones and luteolin, were lost in nearly all xerophytic clades.

In contrast to clade A, clade B, especially sect. *Reniformia* and to a lesser extent sect. *Isopetalum* (Sweet) De Candolle (1824: 655), showed a high presence of flavonoids and condensed tannins. This increase of constituents was further strengthened by the reconstructed presence of apigenin and for parts of sect. *Reniformia* also by the presence of isorhamnetin (Appendix IV).

FIGURE 7. Ancestral states of selected phenolic constituents of *Pelargonium* leaves (myricetin, prodelphinidin, c-glycosyl flavones, luteolin and hydrolysable tannins) based on the Baysian consensus topology for both intergenic spacer region (*atp*B-*rbc*L, *trn*L-F). Pie charts on nodes show state probabilities. Character states: black = present (B), white = absent (A) and question mark in terminals = missing data.

Clade C1 showed the same phenolic content as found being ancestral for the genus *Pelargonium*, but kaempferol was found to be absent at a sectional level (Table 5). In contrast, clade C2 displayed similar trends in flavonoid evolution like clade A, especially in the species rich sect. *Ciconium*. Its members lost hydrolysable tannins as well the typical flavones (Fig. 7).

Discussion

Corroboration of a first split reflecting chromosome sizes and convergence on a backbone consisting of four major clades

With 104 *Pelargonium* species included in the analyses of the non-coding regions *atp*B-*rbc*L and *trn*L-F, the current study is based on the most extensive taxon sampling used in any molecular systematic investigation based on more than a single molecular marker in the genus to date. In previous studies, using two to six molecular markers, taxon sampling was more limited in combined analyses: 28 species in Bakker *et al.* (2000), 20 in Bakker *et al.* (2004) and 58 in Weng *et al.* (2012), although in the single *trn*L-F data set in Bakker *et al.* (2004) a dense sampling (149 species) was achieved.

Here, we confirmed the first well-supported split, reported in previous studies (Price & Palmer 1993, Bakker *et al.* 2004, Weng *et al.* 2012) that coincides with different chromosome sizes (Albers & van der Walt 1984, Gibby *et al.* 1990, 1996). However, further macro-morphological evidence that would support this split is still lacking (Bakker *et al.* 2004, 2005, Jones *et al.* 2009). The two clades (A and B) of the small-chromosome lineage as well as the two clades (C1 and C2) of the large chromosome lineage receive maximum support in the different analyses (Fig 3 and 4, appendix II & III). Furthermore, in comparison to the first split, the overall support for the four major clades is slightly higher in all analyses.

Phylogenetic evidence provided by our study is further strengthened by length mutations. In *Pelargonium* species with small chromosomes, indels of the *trn*L-F spacer had been found to be phylogenetically informative on a sectional level (Bakker 1999a). Here, length mutational events add phylogenetical signal for all major clades. The basal split is supported by an 80 bp indel within the *trn*L-F region. However, the division of clades C1 and C2 is further supported by three synapomorphic indels for each clade, found in both intergenic spacer regions (*atp*B-*rbc*L and *trn*L-F). Similarly, the 146 bp deletion in the *atp*B-*rbc*L spacer, which is syapomorphic for clade B, separates clades A and B (Fig. 3).

While our study deepens the understanding of the basalmost *Pelargonium* phylogeny, it also points towards non-monophyly of several sections in their recent circumscription (e.g. sectt. *Campylia*, *Polyactium*, *Otidia*, *Ciconium* and *Jenkinsonia*). The precise placement of single isolated species (e.g. *P. alternans* J.C.Wendland (1798: 14), *P. antidysentericum*, *P. karooicum*, *P. transvaalense* R.Knuth (1912: 434) remains ambiguous, but their individual positions in one of the four major clades has been resolved. Other analyses, for example, based on AFLP pattern resolved the internal phylogeny of sect. *Otidia* (Becker 2006, Becker & Albers 2009), but also placed *P. alternans* in an isolated position distant from the remainder of sect. *Otidia* (Becker & Albers 2010). In view of the great structural plasticity of plastomes in Geraniaceae (Chumley *et al.* 2006, Guisinger *et al.* 2011) it seems likely that approaches employing gene order and gene content data may further help to increase insights into the evolution of *Pelargonium* at an infrageneric level

Subdivision of clade A and the position of P. nanum

Bakker *et al.* (2004) subdivided clade A in two subclades "A1" (comprising *P. nanum*, sectt. *Pelargonium* and *Campylia* as well as a group of *P. denticulatum* and *P. quercifolium* as sister to the latter section) and "A2" (including all other, mostly xerophytic sections). Support for the monophyly of A1 and its internal structure was weak in the combined study and only resolved in the single analysis of ITS data; see also comment in Bakker *et al.* (2005). Both subclades were likewise found in the Bayesian analysis by Jones *et al.* (2009), but not until omitting *P. nanum* from the data set. Clade A was subdivided in three subclades in Weng *et al.* (2012): *P. nanum*, a subclade A1 (comprising here only sectt. *Campylia* and *Pelargonium*) and subclade A2, although this relationship was found with weak support in only one (*nad*5) out of six marker in single analyses and moderately supported in the combined approach. These results might also partly be explained by a limited taxon sampling, with sect. *Campylia* being represented by a single species only in Weng *et al*. (2012) and by two species in the ITS data set of Bakker *et al*. (2004).

In contrast, our study showed that rather than a subclade A1, the respective sections form a basal paraphyletic grade in clade A, with *P. nanum* branching first (Fig. 3 & 4). Sect. *Campylia* including *P. althaeoides* (L.) L'Héritier (1792: t. 10) represents a clearly monophyletic clade with highest support within clade A. Monophyly of sect. *Pelargonium* is moderately supported (Fig. 3 & 4) or unresolved on the same branch, divided in two sister lineages, in the single analyses (Appendix II & III). One of these clades consists of *P. denticulatum*, *P. quercifolium* and *P. glutinosum*, a grouping further supported by leaf morphology and ploidy level (Albers & van der Walt 1984), but our data did not confirm a placement as sister to sect. *Campylia* (compare Bakker *et al.* 2004).

The isolated position of *P. nanum* in clade A as well as the inclusion of *P. althaeoides* in sect. *Campylia* (both sect. *Peristera*, clade B) was first observed in 1999a (Bakker *et al.*). The transfer of *P. althaeoides* to sect. *Campylia* indicated here is additionally supported by a basic chromosome number of x = 10 (Gibby *et al.* 1996, Bakker *et al.* 2004) and shape of the mericarp (Hellbrügge 1997). Moreover, the shared lack of the *atp*B-*rbc*L 146-bp indel synapomorphic for clade B strongly supports the position of these two former *Peristera* species in clade A. Nested in clade A is a well supported clade A2 (sensu Bakker *et al.* 2004), which is also confirmed by an indel. This subclade contains six mostly poorly supported sections, a situation found in previous studies (Bakker *et al.* 2004, Jones *et al.* 2009). Only the stem succulent sect. *Otidia* excluding *P. alternans* achieves reasonable support (Fig. 3 &4).

Our data clearly agree with the taxonomical separation of the four subsections of *Polyactium* (Maggs *et al.* 1995a) into two distinct sections, *Polyactium* and "*Magnistipulacea*" (sensu Bakker *et al.* 1999a). Monophyly of sect. *Cortusina s.str.* is only moderately supported in MP analyses with indel coding, but an inclusion of *P. desertorum* Vorster (1986: 184) and *P. xerophyton* Schlechter ex R.Knuth (1912: 383) as suggested by Dreyer *et al.* (1992a) is not indicated by our molecular results. The remaining sections, *Ligularia* s. str. and *Hoarea*, were not resolved in single analyses of Bakker et al. (2004). Here, both sections are monophyletic in the ML and Bayesian approach of the combined data set (Fig. 4). Particularly in comparison to Bakker *et al.* (2004), the overall low resolution and support in all highly succulent or geophytic sections appears to be independent of taxon sampling. It may rather reflect the lower age of clade A as estimated by Bakker *et al.* (2005).

Relationships and internal structure of clades B, C1 and sectional non-monophyly in clade C2

The other three major clades detected in this study were also resolved in Bakker *et al.* (2004). In all our analyses they received maximum support (Fig. 3 & 4, appendix II & III), whereas jackknife support for all three clades ranged between 64–87 in the *trn*L-F phylogeny by Bakker *et al.* (2004). Clades B, C1 and C2 were also inferred by Weng *et al.* (2012), but interestingly monophyly of clade C1 was not attained in their single *trn*L-F analysis, which possibly reflects their restricted sampling within this clade.

The well-defined major clade B consists of the paraphyletic sect. *Peristera* and, nested inside, the monotypic sect. *Isopetalum* as well as sect. *Reniformia*, which is in line with preceding studies (Bakker *et al.* 1998, 1999a, 2004, Weng *et al.* 2012). Sect. *Reniformia* appeared unresolved in most previous studies. In our study it is monophyletic, but only with weak support, except in the Bayesian approach (1.00 PP). Results in the latter analysis corroborate those of Jones *et al.* (2009).

The branching pattern of clade C1 is largely congruent with the results from all single marker analyses by Bakker *et al.* (2004), but all three sections (*Chorisma*, *Myrrhidium* and *Jenkinsonia* excluding *P. antidysentericum*) receive maximum support in nearly all analyses (Fig. 3 & 4, appendix II & III). Within clade C1, three species raise additional issues. First, our data clearly confirms *P. mutans* Vorster (1992: t. 2060) as sister to sect. *Jenkinsonia*, a finding also reported in Bakker *et al.* (2000). In its first description, *P. mutans* was assigned to *Ciconium* (clade C2) by Vorster (1992) because of the same chromosome number (x = 9) und the overall similarity to *P. transvaalense*, although the author also noted floral similarities (e.g. four- to five petalled flowers) to species of sectt. *Myrrhidium* and *Jenkinsonia*. Indeed, all South African species of sect. *Jenkinsonia* possess a basic chromosome number of x = 9 in its most recent circumscription by van der Walt *et al.* (1997). Second, our data clearly suggest the exclusion of *P. antidysentericum* from an otherwise non-monophyletic sect. *Jenkinsonia*. For *rbc*L sequences van der Walt *et al.* (1997) also reported *P. antidysentericum* distant to the main *Jenkinsonia* clade. Third, the position of *P. boranense* as sister to sect. *Myrrhidium*, as revealed in ML and BI analyses of the combined markers (Fig. 4), is further supported by floral details (petal number and number of fertile anthers) and the presence of another member of sect. *Myrrhidium* in East Africa (*P. whytei* Baker (1897: 246)). Such a relationship was also argued by Friis & Gilbert (1976) in their first description of the species, but without a final assignment of *P. boranense* to a particular section.

Within clade C2, sect. *Ciconium* is not monophyletic and monophyly of the small sect. *Subsucculentia* remains questionable. Non-monophyly of these sections had already been noted by Bakker *et al.* (2004). Overall, the monophyletic remainder of sect. *Ciconium* (excluding *P. transvaalense* and *P. caylae*) achieves strong support, in particular, Bremer support (Fig. 3, appendix II), further underlined by indels in each spacer region (Fig. 3).

In contrast to these clearly monophyletic groups the positions of the remaining species (especially *P. karooicum* and *P. transvaalense*) are weakly supported or unresolved. *P. karooicum* is incongruently placed either as sister to the residual sect. *Subsucculentia* in the *atp*B-*rbc*L data or as sister to a clade consisting of *P. caylae* and *P. endlicherianum*+*P. quercetorum* in the combined data set. The same indecisive placement of *P. karooicum* was found for mtDNA *nad*1 data versus cpDNA *trn*L-F (Bakker *et al.* 2000, 2004). Monophyly of *Subsucculentia sensu stricto* and a close relationship of *P. karooicum* are shown by *rbc*L sequences (van der Walt *et al.* 1995). These authors also found sequence similarities to the two Asian Minor species (*P. endlicherianum* and *P. quercetorum*), but did not include them in *Subsucculentia* because of their differing chromosome number (x = 10 in *Subsucculentia* and *P. karooicum*, x = 17 in Asia Minor species). Nevertheless, differences between *P. karooicum* and its section in macro-morphology, as well as in phenolic compounds, were highlighted (van der Walt *et al.* 1995). Both Asia Minor species are currently assigned to sect. *Jenkinsonia* (C1), but our study strongly confirmed the position in clade C2 as found in Bakker *et al.* (2004).

Although all analyses support the placement of *P. transvaalense* outside of a monophyletic sect. *Ciconium*, a final placement in C2 remains impossible with our data. Only in the ML and BI analyses of the combined data set, *P. transvaalense* appeared weakly supported as sister to sect. *Ciconium* (Fig. 4), but no closer relationship to sect. *Subsucculentia* or the remaining species is indicated, as discussed in Bakker *et al.* (2004).

Differing evolutionary trends of floral traits among main clades

Floral structures are a main diagnostic feature between genera in Geraniaceae (Albers & van der Walt 2007). In *Pelargonium*, flowers show a high diversity (Fig. 1) and floral traits were therefore important in the description and reclassification of sections (Dreyer *et al.* 1992a, Marais 1994). Despite the fact that some sections, e.g. *Campylia*, *Jenkinsonia* and *Ligularia*, exhibit high variation in floral morphology (van der Walt & van Zyl 1988, van der Walt *et al.* 1997, Albers *et al.* 2000). In this first reconstruction of macro-morphological flower characters, nectar guides and petal ratio are shown to be valuable taxonomic characters in *Pelargonium*.

Like other morphological traits (e.g. growth form, leaf and stem succulence or water storing underground parts), floral characters show a high variability in the genus *Pelargonium*. As expected the quantitative distribution of floral traits (Table 4) shows no clear-cut synapomorphies for the four major clades. However, they do display evolutionary tendencies with certain diagnostic value for major clades, in particular in combination with each other and vegetative traits (see taxonomic conclusions). Endress & Matthew (2006) found floral structural features in rosids commonly expressed in tendencies, in which tendential traits occur much more frequently in one clade than in a related clade. The authors described this as an interesting and likewise unresolved problem in evolutionary biology. For floral diagrams Ronse De Craene (2010) denoted such gradual character changes as cryptic apomorphies and assessed suites of morphological characters to be valuable in identifying clades, even if they are not present in all taxa. In *Araceae*, Cusimano *et al.* (2011) considered homoplasious character state changes as clade support, if they represent reversals to an ancestral state or might constitute convergent evolution.

In *Pelargonium*, nectar guides, petal ratios and hypanthium lengths represent evolutionary tendencies that differ among major clades and, in combination with each other, characterise patterns corresponding to pollinator shifts. In the ancestral state reconstructions of floral traits, characters like petal colour, petal ratio, hypanthium length and nectar guide type reveal state changes synapomorphic for clades above the sectional level (Fig. 5). In several *Pelargonium* species, e.g. in those of sect. *Myrrhidium*, parallel state changes of two characters (petal colour and hypanthium length) are observed and used as differentiation of subspecies or variants (van der Walt & Boucher 1986). One striking example of three simultaneous character state shifts exists within the polymorphic *P. grandiflorum* (Andrews) Willdenow (1800: 674), sect. *Pelargonium*: white flowering forms possess longer hypanthiums (> 15 mm) and dark veins as nectar guides, whereas in pink forms the length of the hypanthium did not exceed 15 mm and the posterior petals show eyespots as nectar guides (personal observation JR). Other characters like petal number, distribution of nectar guides and number of fertile anthers are more consistent and synapomorphic character state changes are restricted to sectional level.

Nectar guides differ between clades

Intrageneric variation in floral markings, size and colouration has been shown to reflect adaption to particular pollinator groups in multiple genera. In South African *Gladiolus*, nectar guide types are useful characters for the differentiation of sections and exhibit a greater taxonomic significance than flower size, colour and tube length (Goldblatt & Manning 1998, Goldblatt *et al.* 2001). Furthermore, associated with other floral features, these traits constitute adaptations to particular pollinator groups. Correlations between nectar guide shape and pollinator preferences are also found in *Mimulus* (Medel *et al.* 2003). Presence and absence of nectar guides correlate in *Bignonieae* with further floral traits and these patterns coincide with different pollinator guilds (Alcantara & Lohmann 2010).

Pelargonium displays a range of distinct petal markings (Fig. 2) that are relatively constant intraspecifically and much less variable than hypanthium length or petal colour, although exceptions with polymorphic markings occur (e.g. in *P. spinosum* Willdenow (1800: 681), *P. peltatum* (L.) L'Héritier in Aiton (1789: 427) and *P. articulatum* (Cavanilles) Willdenow (1800: 356). The categorisation of eyespots is debatable in a few species. For example, some species in sect. *Hoarea* have strongly reflexed and spathulate posterior petals, in which eyespots appear functionally equivalent to basal blotches. Different encoding of a character state in individual terminal species of such a large subclade does not affect character optimisation of the character elsewhere in the tree, but should be kept in mind during the discussion of pollinator syndromes (see below).

Even though nectar guide types are reconstructed as being nearly identical in each chromosomally divergent group (Fig. 5), there are differences in major clades within these groups. Veins as nectar guides in C1 are dark, conspicuous and always present (Fig. 1 Q–V), while in C2 veins are often pale, less conspicuous or sometimes completely lacking (Fig. 1 W–AB). In clade B, nectar guides are only present as eyespots or even absent. The lack of any marking in clades B and C2 is also mostly congruent with a distribution within the summer rainfall region. In clade A, a winter rainfall clade, all four main types of flower markings occur, suggesting that basal and central patterns might be interpreted as key innovations in competition for pollinators. In particular central markings occur nearly exclusively in clade A and are often expressed on all petals.

Similar patterns of congruencies between geographic distribution and differences in petal colour and nectar guide prominence also have been reported by Goldblatt & Manning (1998) for bee-pollinated *Gladiolus* species: species of the winter rainfall region possess contrasting nectar guides, but species within the summer rainfall region lack prominent markings. One explanation could be the enhanced competition for pollinators in the species rich winter rainfall region (Goldblatt & Manning 1998, Goldblatt *et al.* 2001). The geographically distinct intensity of nectar guides in *Pelargonium* could be interpreted in the same way, but shifts in pollinators must also be considered.

Contrasting character shifts in petal ratio characterise major clades

Along with nectar guides and flower colour, visual attraction of *Pelargonium* flowers is mediated by proportionally enlarged posterior petals (Struck & van der Walt 1996). While the MCRA of the genus most likely had equally sized petals, an expansion of posterior petals occurs independently in all major clades except for the small flowered clade B (Fig. 5).

In clade C1 most species possess greatly enlarged posterior petals (Table 4), often associated with a transition from five to four petals (Fig. 6). This enlargement could be understood as a compensation for petal loss or as another adaptation in competition for pollinators, because many taxa with large scale posterior petals are restricted to the winter rainfall region. The floral structure of some sect. *Jenkinsonia* species is most unusual, with short hypanthiums and enrolled petals (Fig.1 R); most of these species are widely distributed outside of the winter rainfall region (van der Walt *et al.* 1997). Within clade C2, species of sect. *Ciconium* display larger posterior petals only if distributed in the winter rainfall region, all other species tend to have petals of equal size or even enlarged anterior ones. This contrasting shift in posterior petal size provides further support of a pollinator change associated with a differing geographical range. Equally sized petals are also found in *P. transvaalense* and *P. caylae*, hitherto assigned to sect. *Ciconium*. The latter exudes a perceivable scent during day time, a nearly exclusive trait within *Pelargonium* (van der Walt & Vorster 1988, pers. observ. JR).

Two further unique and distinct flower morphs occur in clade C2. First, the Asia Minor species *P. endlicherianum* and *P. quercetorum* maintain extremely large posterior and minute to lacking anterior petals (Fig. 1 AA). Second, the anterior petals of *P. otaviense* and *P. grandicalcaratum* (both sect. *Subsucculentia*) are slightly

larger than the reflexed posterior petals and form a straight tube, which encloses the reproductive parts (Fig. 1 Z). Because of the wide and inflated hypanthium similar to that found in *P. fulgidum* (L.) L'Héritier in Aiton (1789: 422), the only documented bird pollinated *Pelargonium* species, Struck (1997) suggested ornithophily for both taxa. However, unlike *P. fulgidum* with its scarlet red flowers, flowers of *P. otaviense* and *P. grandicalcaratum* are more inconspicuous, white or dark red respectively, and both are marked with darker veins on the inside of the posterior and on the outside of the anterior petals. The hypanthium (8–17 mm) is noticeably shorter than that of *P. fulgidum*, which has an average size of 30 mm. In bird pollinated *Iridaceae* the perianth tube exceeds 25 mm (Goldblatt & Manning 2006). However, field observations are required for a final determination of the pollination syndrome for *P. otaviense* and *P. grandicalcaratum*.

In the predominantly small-flowered and equally-sized-petal clade B, shifts to slightly enlarged posterior petals occur in Australian species and rarely in the *Peristera* species that are restricted to the winter rainfall region (e.g. *P. iocastum* (Eckl. & Zeyh.) Steudel (1841: 287) and P. *columbinum* Jacquin (1797: 4)). In clade A, which is centered in the winter rainfall region, slightly enlarged posterior petals are synapomorphic above the MRCA of the first basal grade, *P. nanum*. Further shifts in sections to conspicuously expanded posterior petals (p>a) occur, but shifts to large scale petals (p>>a) are rarely found, which might indicate that the development of additional spots as nectar guides counteracts the need for significant petal enlargement in pollinator attraction.

The first branching taxon of clade A, *P. nanum*, represents an exception with regard to several floral traits. Besides posterior-anterior-petal ratio, the number of fertile anthers and flower colour are different from the reconstructed MRCA of clade A and emphasise even more the isolated basal position of *P. nanum*. These aberrant floral traits might support the proposal for a section of its own for *P. nanum* (see Bakker *et al.* 2004). According to Hellbrügge (1997) *P. nanum* is closely allied to *P. laciniatum* R.Knuth (1912: 412), which is currently assigned to sect. *Peristera* in Clade B. Both species share features of the mericarp and bi-coloured flowers. Bi-coloured flowers are rarely found in *Pelargonium* and mainly restricted to clade A, especially to species in sectt. *Campylia* and *Cortusina*. If the relationship between *P. nanum* and *P. laciniatum* can be confirmed in future molecular studies, it might help to clarify the basal topology of clade A.

Hypanthium length and other floral traits correspond to main pollinator classes

Although intraspecifically variable, ranges of nectar tube length in *Pelargonium* could give some indication of putative pollinator classes (Struck 1997). Within geographically distinct populations Manning & Goldblatt (1995) found a correlation between variability of tube length and the mouthparts of pollinators. Our data of hypanthium size classes present a comprehensive view of this complex character and corroborates findings of Bakker *et al.* (2005). The divergent reconstructed ancestral hypanthium length separates the two chromosomal lines in *Pelargonium* (Fig. 5). According to Struck (1997) the very short hypanthiums (0–10 mm) of the small chromosome clades A and B roughly relate to pollination by nectar collecting bees (*Apoidea*), whose mouthparts barely exceed 10 mm. The short floral tubes (11–20 mm) of the large chromosome clades C1 and C2 instead indicate a pollination by *Diptera*, especially short tongued tangle-veined flies (*Nemestrinidae*) and horseflies (*Tabanidae*) as well as bee-flies (*Bombyliidae*), although the mouthpart length of bee-flies overlap both hypanthium length classes.

Nevertheless, our reconstruction shows that short floral tubes (< 20 mm) and likewise pollination by short-tongued insects are the ancestral state in *Pelargonium*. This confirms the conclusion of Struck (1997) that the melittophilous pollination syndrome found in 60% of the studied taxa is plesiomorphic for the genus. Goldblatt & Manning (2006) described nectar feeding bee-pollinated flowers in *Iridaceae* characterised by light markings edged with darker colour, which resembles *Pelargonium* flowers with typical eyespots and a short floral tube. Basal stripes and reticulate patterns found in *Otidia* species and species with false tube forming petals and short hypanthiums of sect. *Jenkinsonia* (e.g. in *P. dolomiticum* R.Knuth (1908: 71)) are also referred to bee pollination (Struck 1997, Zietsman 1992). Basal blotches including functionally similar patterns (eyespots) are typical in species pollinated by the bee-fly *Megapalpus capensis* (Johnson & Midgley 1997, Struck 1997). Other eyespots without a noticeably white centre occur often in flowers with longer tubes and should therefore be assigned to long-proboscid-fly-pollination. Dark veins as nectar guides are likewise found in species with long and short nectar spurs. In species with dark veins as nectar guides, petal colour might help to distinguish between pollinator groups. In sect. *Myrrhidium*, dark veins are typical and several species were differentiated as subspecies differing in having short hypanthiums (< 15 mm) and pink to purple flowers or longer hypanthiums (> 15 mm) and white to light pink or yellow petals (van der Walt & Boucher 1986).

The independent shifts to longer floral tubes found several times in all major clades illustrate the convergent and divergent adaptation to different long-tongued pollinators. In South Africa, several specialised pollinator systems have been characterised (reviewed in Goldblatt & Manning 2006, Johnson 2010). Long-proboscid-flies (LPF) of the families *Nemestrinidae* and *Tabanidae* with mouthparts >20 mm are the second main pollinator group in *Pelargonium* (Struck 1997), with a proportion of 25–27%. Beside the LPF-pollination system also moths and, rarely, butterflies occur as pollinators.

The visually apparent correlations between hypanthium length, posterior-anterior-petal ratio and types of nectar guides coincide with the two main pollination syndromes (bees and LPF) as well as shifts to infrequent pollinator classes.

Independent shifts to longer nectar spurs are dispersed across major clades

Within the specialised LPF-pollination systems, *Pelargonium* species are demonstrably involved in three different guilds: (1) *Prosoeca peringueyi*, (2) *Moegistorhynchus-Philoliche* and (3) *Prosoeca ganglbauri* pollination system (Goldblatt & Manning 2000; Manning & Goldblatt 1995, 1997). Pollination system (1) is geographically confined to a small part of the winter rainfall region and likewise restricted in terms of pollinator quantity. System (1) only includes *Pelargonium* taxa of a single major clade (A, sect. *Cortusina*, *Ligularia* and *Hoarea*), which share dark magenta to violet or white flowers and central spots as nectar guides. *P. incrassatum* (Andrews) Sims (1804: t. 761) exhibits no visible markings, but ultraviolet markings are found in some *Pelargonium* species with and without visible petal patterns (Burr & Barthlott 1993). *Pelargonium* species within system (2), which is restricted to the winter rainfall region, belong to clades A, C1 and C2. Their flowers are creamy-yellow, white or less frequently light pink. *Moegistorhynchus* pollinated species show dark veins and *Philoliche* pollinated species have central spots or eyespots as nectar guides. Pollination system (3) ranges from southern parts of the winter rainfall region to the East and contains *Pelargonium* species of all four major clades, mostly with pink flowers and dark veins or eyespots as markings.

The distribution of floral characteristics within the LPF-systems further indicates that central spots are an apomorphic trait in clade A. Especially in the winter rainfall region, two different strategies become evident in competition for the same LPF-pollinators: In C1, large scale posterior petals and dark veins, as opposed to slightly or conspicuously enlarged posterior petals in combination with central spots or eyespots in clade A. The latter could be interpreted as an evolutionary link between veins and central spots.

Beside LPF-pollination, moth pollination has been assigned most notably to sectt. *Polyactium* and "*Magnistipulacea*" by Vogel (1954), which constitute the third well-characterised pollinator class, with a share of approximately 7% of *Pelargonium* species (Struck 1997). The flowers in both sections are mainly yellow or greenish-yellow, rarely light pink or whitish and the petals are often masked with dark stripes or nearly completely covered up to a light margin (Fig. 1G & H). Most species are dusk to night-scented (Maggs *et al.* 1995a), although *P. bowkeri* Harvey (1862: 592) is described as scentless (van der Walt & Vorster 1981a). The scent is reported as unpleasant for humans in *P. schizopetalum* Sweet (1824: t. 232) [van der Walt 1977] or clove-like in *P. triste* (L.) L'Héritier in Aiton (1789: 418) [Vogel 1954]. This spicy scent is also found in *P. lobatum* (Burmann filius) L'Héritier in Aiton (1789: 418), *P. pillansii* T.M.Salter (1938: 120), *P. radulifolium* (Eckl. & Zeyh.) Steudel (1841: 289) and, to a lesser degree, in *P. pulverulentum* Sweet (1824: t. 218) [pers. observ. JR]. Convergent flower character patterns have been described for South African *Gladiolus* species by Goldblatt & Manning (1998). Moth pollinated *Gladiolus* flowers are often clove scented and cream to yellowish coloured, sometimes mottled with dark colours. This camouflage was interpreted as a means of preventing illegitimate insect visitors. The dark red to nearly black flowers of *P. sidoides* De Candolle (1824: 680) are also night scented, but with a heavy sweet odor (pers. observ. JR). Interestingly, pure yellow forms of *P. triste* also possess this sweet scent. Based on observations on herbarium material, Vogel (1954) suspected moth pollination for *P. sidoides* and other species (e.g. *P. plurisectum* T.M.Salter (1942: 279) and *P. quinquelobatum* Hochstetter ex A.Richard (1847: 118)). Although the metallic greenish-grey flowers of *P. quinquelobatum* are scentless, the petals glow during twilight (pers. observ. JR). Therefore, pollination by moths has most likely evolved several times independently in *Pelargonium* and, probably, at least once in all major clades.

In summary, the proportion of the main pollinator classes in *Pelargonium* is highly congruent with the distribution of pollinator systems in three genera, especially *Gladiolus*, *Babiana* and *Lapeirousia*, of South African *Iridaceae* (Goldblatt & Manning 2006): apparently a striking case of convergent evolution. All three species rich

genera show zygomorphic flowers in general and several independent shifts to specialised pollinator systems, which leads to the conclusion that speciation in *Pelargonium* is also at least partly pollinator mediated.

Evolution of leaf phenolics

Secondary metabolites and especially flavonoids have been widely used in plant systematic studies (Stuessy 2009). Their occurrence and distribution patterns often corroborate newer molecular results at various hierarchic levels, e.g. Bohm *et al.* (1999), Fico *et al.* (2003), Wollenweber *et al.* (2003), Choze *et al.* (2010). Leaf phenolic signatures were also successfully used in delimitation of taxa in *Dipterocarpaceae* (Joshi *et al.* 2004, Talip *et al.* 2008) and in classification of *Restionaceae* (Briggs & Linder 2009). Wink (2003) and Waterman (2007) reviewed further prominent examples and noted difficulties in relation of interpretation. In *Pelargonium*, patterns of phenolic constituents were valuable in reclassification of several sections (Dreyer *et al.* 1992a, van der Walt *et al.* 1995 and Albers *et al.* 1995).

In this study, we summarised the phenolic compounds of 98 *Pelargonium* species in context of the recent phylogeny, which allows novel insights into the flavonoid evolution in *Pelargonium* and reveals differing evolutionary trends in major clades (Fig. 7 & Appendix IV).

The reconstructed ancestral content of leaf phenolic substances in the genus *Pelargonium* comprises flavonols (quercetin and kaempferol), flavones (luteolin and c-glycosyl-flavones), hydrolysable tannins and hydroxybenzoic acids (gallic and protocatechuic acid). The flavonol myricetin and condensed tannins (proanthocyanidins) are lacking. The position of *Pelargonium* as the first-branching sister clade within Geraniaceae (see e.g. Fiz *et al.* 2008) supports this basal chemical condition for the genus *Pelargonium*.

The reported phenolic constituents in the remaining genera, *Monsonia*, *Geranium* and *Erodium* strengthen this view. For 11 *Monsonia* species Marschewski (1995) found the same pattern as in the reconstructed ancestral pattern of *Pelargonium*, except the complete absence of c-glycosyl-flavone and presence of procyanidin in one species. In *Geranium* the main flavonols were quercetin and kaempferol, whereas myricetin was only detected in eight of 60 species (Bate-Smith 1973). The same author reported also the presence of c-glycosyl-flavones for the genus. Ivancheva & Petrova (2000) detected luteolin in five out of 11 *Geranium* species. Condensed tannins were less frequent in *Geranium*, being only reported in 22 of 70 species as traces of procyanidin and in 4 species as prodelphinidin (Bate-Smith 1981). Hydrolysable tannins and gallic acid were encountered in nearly all species (Bate-Smith 1972, 1973 and 1981). The main flavonols in *Erodium* were kaempferol followed by quercetin, myricetin occurred in traces in five out of 16 taxa and the flavone luteolin was likewise mostly absent (Saleh 1983). In nearly all 11 *Erodium* species Fecka *et al.* (2001) detected ellagic acid, gallic and protocatechuic acid. The presence or absence of condensed tannins in *Erodium*, to our knowledge, has not been reported. Thus, the reconstructed ancestral leaf phenolic pattern in the genus *Pelargonium* is likely indicative of the ancestral state for the family Geraniaceae.

During the evolution of *Pelargonium*, flavones, hydrolysable tannins and hydrobenzoic acids have been lost, whereas the flavonol myricetin and condensed tannins (especially prodelphinidin) have been acquired later (Fig. 7). This is contrary to the former hypothesis of leaf flavonoid evolution in angiosperms by Bate-Smith (1962) and Harborne (1977), in which myricetin and condensed tannins are the primitive state that are then lost during the transition from woodiness to herbaceousness. Our results are therefore also contrary to views expressed in previous studies on flavonoid evolution in *Pelargonium* (e. g. the presence of myricitin and condensed tannins as a more plesiomorphic state in Williams *et al.* (2000)). More recently, the picture of flavonoid evolution in angiosperm families has become more complex, for example two different trends have been found regarding the flavonol-flavone ratio in mostly herbaceous angiosperm families (Soares & Kaplan 2001). Therefore, we follow here a more general interpretation of phenolic patterns when discussing their significance in the context of evolution of *Pelargonium*.

Major clades reveal diverging evolutionary trends in leaf phenolic composition

One unique feature in clade A is the ancestral presence of myricetin and prodelphinidin (Fig. 7). Both constituents seem to have developed later in clade B, being only continuously present in sect. *Reniformia*. Within the large chromosome clades, the separation of C1 and C2 is more evident in the overall presence of phenolic constituents (Table 5). This contrasts with the presumption of Williams *et al.* (2000) that the leaf phenolic pattern agreed with the "karyological split" of the genus, (most large chromosome species producing ellagitannins and

most small chromosome taxa producing proanthocyanidins). This hypothesis is further contradicted by the overall appearance of hydrolysable tannins, incl. ellagitannins, in clade B and C1 versus their predominant absence in clade A and C2. In addition myricetin is present in a few terminal species of clade C2 (*P. caylae*, *P. tongaense* Vorster (1983: 76)) and both condensed tannins are also seldom found in C1 and C2.

Two trends that differ between the small chromosome clades have become evident (Fig. 7 & Appendix IV). The ancestral presence of myricetin and prodelphinidin in clade A is accompanied by a loss of hydrolysable tannins and to a lesser extent by loss of hydrobenzoic acids. In contrast, in clade B, biosynthesis of both constituents, myricetin and prodelphinidin, is associated with the further occurrence of several phenolic compounds. The distinct geographical distributions of clade A and sect. *Reniformia* (clade B) are convergent with this reverse trend of phenolic composition. However, clade C1, which shares the centre of its species diversity with clade A, lacks myricetin and prodelphinidin is virtually absent. The ancestral ability to biosynthesise myricetin and prodelphinidin in clade A might have contributed to the proliferation of this largest clade in *Pelargonium*.

The presence of myricetin and prodelphinidin was also justification for the transfer from *P. althaeoides* and *P. nanum* from sect. *Peristera* (clade B) to clade A as discussed above.

Altered constituents of sect. *Reniformia* enhance their monophyly within clade B, which is only moderately supported by our molecular data. The presence of apigenin in *P. cotyledonis* (L.) L'Héritier in Aiton (1789: 428) might also improve the treatment as a monotypic section, which was not included in sect. *Peristera* by Hellbrügge (1997) based on its unique morphology. Marschewski (1995) also detected apigenin in *P. cotyledonis*, but not in *Peristera* taxa. The first branching species in clade B, *P. minimum*, is separated from the rest of the clade by the absence of luteolin and c-glycosyl-flavones (Fig. 7), also found by Hellbrügge (1997) in *P. pseudofumarioides* R.Knuth (1908: 79) and *P. nelsonii* Burtt Davy (1926: 48). Therefore the same author proposed an exclusion of all three species from sect. *Peristera*, which she found further supported by leaf morphology as well as in case of *P. minimum* and *P. pseudofumarioides* by *trn*L-F data (Bakker 1999a).

Differences between the large chromosome clades C1 and C2 become evident in the abundance of single constituents: kaempferol, myricetin, isorhamnetin and hydrolysable tannins (Table 5). Besides differences in the presence of myricetin and isorhamnetin and the nearly complete loss of hydrolysable tannins in sect. *Ciconium* (C2), the frequency of occurrence of kaempferol in clade C1 is considerably lower (57%) than that of clade C2 (88%). Within clade C2, kaempferol is only absent in P. *transvaalense* and *P. karooicum*.

Furthermore, the amount of kaempferol found in clade C2 taxa reinforces the contrast to clade C1. In most *Ciconium* members the quantity of kaempferol was higher or equal to the ubiquitous quercetin (Marschewski 1995), whereas in C1 kaempferol was found in low to medium amounts. According to our molecular results in clade C2, the absence of kaempferol in *P. transvaalense* supports its removal from sect. *Ciconium*. This contrast, kaempferol as typical main component in sect. C*iconium* and absence of kaempferol in *P. transvaalense*, were also highlighted by Marschewski (1995) and *P. transvaalense* was therefore regarded as transitional to other sections.

The species in clade C2 that deviates most significantly phytochemically is *P. caylae* from Madagascar (Fig. 7 & Appendix IV), which is sister to *P. endlicherianum* and *P. quercetorum* (both from Asia Minor) according to molecular phylogenetic results (this study, Bakker *et al.* 2004). In contrast, *P. endlicherianum*, *P. quercetorum* together with *P. karooicum* express a high affinity in phenolic composition to sect. *Subsucculentia.* All species of sect. *Subsucculentia* as well as *P. karooicum* are distributed along the West coast of South Africa and Namibia. Flavonoid variation and geographical distribution are often correlated in different genera and families (e.g. Giannasi & Chuang 1976, Harborne 1979, Williams *et al.* 1993). Marschewski (1995) also found variation in phenolic patterns to be corresponding with ploidy levels. Here, all four species, *P. caylae*, *P. endlicherianum*, *P. quercetorum* and *P. karooicum*, are polyploids like *P. grandicalcaratum* of sect. *Subsucculentia* (Johnson & Özhatay 1988, Gibby *et al.* 1990, Albers *et al.* 1992) and possess a disjunct geographic distribution.

For clade C1 and especially sect. *Jenkinsonia* the same ancestral states have been found as for the genus and therefore both taxa seems to present the most basal leaf phenolic composition within *Pelargonium* (Fig. 7 & Appendix IV). While sect. *Jenkinsonia* exhibits different life forms and a high macro-morphological range (van der Walt *et al.* 1997), the underlying phenolic arrangement found here is instead very homogenous. Therefore, it is tempting to see this as a reflection of a more general pattern in *Pelargonium,* with morphology being generally highly variable while phenolic chemistry follows clearer evolutionary trends.

Taxonomic conclusions

Four subgenera as the best reflection of current data

The last complete revision of the genus *Pelargonium* was made by Knuth (1912), who distinguished most of the currently accepted sections. Van der Walt and co-workers revised several of these within the last thirty years and differentiated three new sections, sectt. *Chorisma*, *Reniformia* and *Subsucculentia*. In between, the first mention of a subgeneric classification appeared in a horticultural overview of *Pelargonium* by Clifford (1958), who cited the classification by Knuth from 1912, but probably erroneously replaced the term section by subgenera without any further description, indication of basionyms or their complete citing. Therefore, this categorisation was regarded as insignificant by scientists (ICBN 2011, Art. 41.5). More recently, two subgenera based on molecular data were informally proposed by Bakker *et al.* (1999c). This subgeneric split correlates only with chromosome size, but not with morphology. Although not validly published, this subgeneric division was later adopted in a few publications (Parkinson *et al.* 2005, Albers & van der Walt 2007).

Data of natural and artificial hybridisation are valuable for assessing evolutionary relationships among infrageneric taxa (Stuessy 2009). In the genus *Pelargonium* natural hybrids are rarely reported and only documented within molecular circumscribed sections, e.g. in sectt. *Pelargonium*, *Ciconium* and *Otidia* (van der Walt. 1985, Gibby & Westfold 1986, Becker & Albers 2009). However, artificial crosses have a long tradition in cultivation history of *Pelargonium.* Sweet (1820–1830) reported on a wide range of articifical hybrids that were in circulation in the United Kingdom, although the species depicted in some of these were highly doubtful. An example is *P. reniforme* (Andrews) Curtis (1800: 493) in Plate 48, which resembles a pink flowering species of sect. *Cortusina* in petal shape, nectar guides and distribution. Knuth (1912) listed several hundred hybrids of uncertain parentage, between taxa within several sections as well as between sections. Intersectional hybrids were reported between sectt. *Reniformia* and *Peristera* (clade B), between sect. *Ligularia* and sectt. *Hoarea*, *Polyactium* and *Pelargonium* as well as between sect. *Pelargonium* and sectt. *Cortusina* and *Hoarea* (all clade A). The crosses between *P. reniforme* with species of sect. *Cortusina* remain doubtful, because more recent hybridisation attempts between the *P. reniforme* group and the *P. cortusifolium* group (sect. *Cortusina*) failed completely (Dreyer *et al.* 1992a). Later on, these crossing barriers together with further evidence like a basic chromosome number of x = 8 yielded in the new description of section *Reniformia* (Dreyer & Marais 2000). Infrageneric delimitations in *Pelargonium* were often based on karyological differences accompanied by hybridisation attempts (e.g. van der Walt *et al.* 1990a, Albers *et al.* 1992). Successful artificial crosses are found to be restricted to taxa sharing chromosome size and, with a few exceptions (e.g. Gibby & Westfold 1986, Albers & van der Walt 1992), also by chromosome number. However, all successful artificial crosses in contemporary scientific studies have been limited to being within the four molecular based major groups described above (Coffin & Harney 1978, Yu 1985, Gibby & Westfold 1986, van der Walt *et al.* 1990a, Albers *et al.* 1992, Dreyer *et al.* 1992a, Horn 1994 and Albers *et al.* 1995).

For more than a decade the highly variable morphology of *Pelargonium* has prevented a subgeneric division corresponding to different chromosome sizes. The additional comparative evidence, presented here, in combination with further morphological characters, provides for the first time an opportunity for a formal subgeneric division based on the results of our extended molecular data of the genus *Pelargonium*.

In the present study, according to our molecular evidence, four phylogenetically distinct groups (corresponding to the major clades A, B, C1 and C2) can be demarcated and will be formally described below as subgenera in *Pelargonium*. These four groups are in agreement with the individual analyses in the studies by Bakker *et al.* (2004) and Weng *et al.* (2012) and are further supported by a wealth of our comparative data regarding floral morphology, e.g. data on nectar guides and petal-size ratios, our analysis of leaf phenolic constituents, as well as the apparent barriers to hybridisation.

The subgeneric names are based on floral characters that accentuate to a satisfying degree the distinctiveness of each group and are demonstrative enough to find broad acceptance also by *Pelargonium* enthusiasts (Fig. 1). For assignment of sections and species used in this study to the respective subgenera we refer to Fig. 4. A supplementary overview comprising currently recognised *Pelargonium* taxa informally allocated to the four subgenera is provided below. A detailed key to the subgenera will become lengthy, because of the morphological exceptions found for particular sections or species, even though these exceptions are in part clearly defined by geographical distribution or appear as unique within the genus. Nevertheless, characterising morphological traits for subgenera and noticeable exceptions are additionally tabulated (Appendix V).

A new sect. Magnistipulacea segregated from sect. Polyactium

In addition, our data strongly confirm the recognition of a sect. *Magnistipulacea*, comprising two subsectt. *Magnistipulacea* R.Knuth (1912: 352) and *Schizopetala* R.Knuth (1912: 352), as clearly distinct from sect. *Polyactium* and its remaining subsections as originally disclosed in Bakker *et al.* (1999a). The subdivision of sect. *Polyactium* into four subsections originates by Knuth (1912). In revision of sect. *Polyactium* by Maggs *et al.* (1995a), all four subsections were regarded as so distinct that a formal taxonomic status was preferred over rankless groups within the section. The former authors gave a revised circumscription and a more detailed key to the subsections than Knuth (1912), but only accomplished a full revision for two subsections (subsectt. *Caulescentia* R.Knuth (1912: 352) and *Polyactium*). Within the original description no types for subsections were given, therefore new type species are designated here, using species listed under the respective subsection by Knuth (1912).—Note: *P. schlechteri* R.Knuth (1908: 72) is sometimes treated under synonymy of *P. luridum* (Andrews) Sweet (1824: t. 281), but it is clearly distinguished from the *P. luridum* complex by a scape with two to four pseudo-umbels versus a single pseudo-umbel. See Retief *et al.* (2007b) for further details.

Taxonomic treatment

1. Subgeneric division of genus ***Pelargonium*** L'Héritier

—Note: For the correct author citation of the genus see van der Walt (1979), van der Walt & Vorster (1981b) and Mabberley (2008).

1.1. ***Pelargonium*** subg. ***Magnipetala*** Roeschenbl. & F.Albers, *subg. nov.*

Fruticuli repentes vel erecti; caulis herbosa, in fundo lignosa, raro semisucculenta vel succulenta; folii lamina saepe perspicue incisa et plerumque pinnatiformia; hypanthium semper fere aut paulum aut saepius magis elongatum, infra specie varians: petala quinque, saepe reducta ad quattuor, petala posteriora praecellentia; color floris plerumque albus: stigmata apparentia, venae fuscae in petalis posterioribus; stamina fertilia septem, rarius redacta ad quinque; distributio geographica praecipue australis Africa imbrium hibernorum.

Perennial to short lived, spreading subshrubs, rarely herbaceous annuals. Stems often thin, herbaceous with bases becoming woody at age, sometimes subsucculent. Leaves usually compound; Lamina pinnately divided, bipinnatisect or trifoliolate, rarely entire without deep incisions. Hypanthium slightly elongated (11–20 mm), abundantly conspicuously (> 20 mm) to strongly elongated (> 40 mm), infraspecific variable. Petals five, but often reduced to four, posterior petals mostly much larger than anterior ones. Petal colour largely white, often with infraspecific pink or creamish yellow forms. Posterior petals almost always with clear nectar guides; two or several dark veins, less frequently basal spots or a reticulate basal marking. Fertile anthers seven, sometimes reduced to five (rarely 3 or 2). Species 24: South Africa, mainly winter rainfall region and a few species extending into the summer rainfall region of South Africa, with 1 sp. in northern Namibia and Botswana and 2 ssp. reaching tropical East Africa and Ethiopia. Chromosome number x = 11 and x = 9—Type: *P. praemorsum* (Andrews) F.Dietrich (1807: 48)

1.2. ***Pelargonium*** subg. ***Parvulipetala*** Roeschenbl. & F.Albers, *subg. nov.*

Partim herbae annuae et fruticuli, rosulariformia; caulis plerumque herbacea, partim lignosa, raro succulenta, folii lamina tenue incisa, et plerumque palmatiformia; hypanthium magnam partem brevissimum, petala quinque, magnitudine aequalia, plerumque minima: color floris roseus aut albus, numquam flavidus; stigmata saepe redacta, ocellata in petalis posterioribus; stamina fertilia septem; sed saepe variae reductiones; distributio geographica longe diffusa in hemisphaerio australi America australi excepta, imprimis Africa australis.

Perennials, partly annuals; rosette forming herbs or erect to decumbent subshrubs, scarcely geophytes. Stem mostly herbaceous, sometimes becoming woody with age, one true stem succulent. Leaves simple; lamina cordate or reniform, palmately lobed, rarely pinnately divided; margins crenate or irregularly lobate. Hypanthium generally very short (0–10 mm), less frequently slightly elongated (11–20 mm). Petals five, equally sized, abundantly shorter than 10 mm, if larger petals than often narrow and posterior two grouped together; petal colour white or pink to deep purplish red, never conspicuously cream or yellow; nectar guides only on posterior petals; eyespots, often reduced on small petals or sometimes lacking. Fertile stamens seven, often reduced to six or five (in some cases to

4, 3 or 1). Species 39–42: South Africa, with several species scattered across southern hemisphere, except South America, with a few species extending north into tropical East Africa and Ethiopia. Chromosome number varying from x = 11, alongside reduced to x = 8 or expanded x = 19 (singles cases with x = 7, 9, 10 or 15)—Type: *P. hypoleucum* Turczaninow (1858: 421)

1.3. ***Pelargonium*** subg. ***Paucisignata*** Roeschenbl. & F.Albers, *subg. nov.*

Frutices erecti, caulis herbosa, partim semisucculenta, postea lignosa; folii lamina plerumque tenue incisa et palmatiformia, hypanthium plerumque fere paulum elongatum, saepe praelongatum, infra specie varians; petala quinque, saepe aequali magnitudine, color floris plerumque roseus, stigmata absentia aut minime praecellentia, venae fuscae in petalis posterioribus; stamina fertilia plerumque septem; distributio geographica praecipue in regione australis Africae imbrium aestivorum.

Mostly erect, sometimes trailing subshrubs or shrubs, rarely geophytes or semi-geophytes. Stems thick fleshy to subsucculent or herbaceous, becoming somewhat woody with age. Leaves simple, partly subsucculent; Lamina obovate or cordate-reniform, sometimes 5–7 lobed to palmatifid, seldom palmately incised. Hypanthium slightly (11–20 mm) or conspicuously elongated (21–40 mm); infraspecific variable. Petals five, predominantly equally sized; petal colour pink to red, but no clear purple, sometimes white. Nectar guides mostly on posterior petals, but usually inconspicuously veined or lacking, rarely additional infraspecific forms with eyespots. Fertile stamens seven, scarcely reduced to five. Species 25–27: mainly summer rainfall region of South Africa with a several species extending to the winter rainfall region and 1 spp. northern Namibia. A few species scattered through tropical Africa, reaching Ethiopia and Somalia, Madagascar, Arabian Peninsula as well as Asian Minor. Chromosome number x = 9 or x = 10 (in single cases x = 4, 8, 17, 18)—Type: *P. zonale* (L.) L'Héritier in Aiton (1789: 424)

1.4. ***Pelargonium*** subg. ***Pelargonium***

Plants frequently xerophytic, deciduous perennials, many geophytes, succulent subshrubs, less frequently rather woody evergreen shrubs or in particular cases annual herbs; habit erect to decumbent. Stem often flattened on apex of conical, sometimes moliniform roots with a mostly tunicate periderm or stems branched above ground, subsucculent to succulent, rarely herbaceous becoming woody with age. Leaves entire or compound; lamina entire to variously pinnately divided or pinnate to trifoliolate; margins entire or mostly dentate to serrate. Hypanthium very short (0–10 mm) or conspicuously (21–40mm) to strongly (> 40 mm) elongated. Petals five, scarcely reduced, posterior petals slightly to explicitly enlarged; petal colour various shades of pink to purple or yellowish, predominantly with prominent nectar guides of varying type, often as spots in the centre of petals or eyespots, to some extent as dark veins or basal markings, distributed on posterior and sometimes also on anterior petals. Fertile stamens seven, but more often reduced to five (rarely to 6, 4, 3 or 2). Species ± 167: mainly winter-rainfall region of South Africa and the adjacent Namibia, with a few species extending into the summer-rainfall region of South Africa with 2 spp. reaching tropical Africa and 1 sp. in North Namibia. Chromosome number largely x = 11, sometimes reduced x = 10 (9 and 8).

2. New established sect. ***Magnistipulacea*** and its two subsections

2.1 ***Pelargonium*** section ***Magnistipulacea*** (R.Knuth) Roeschenbl. & F.Albers, *stat. nov.*

Basionym:—*Pelargonium* sect. *Polyactium* subsect. *Magnistipulacea* R.Knuth (1912: 352), in Engler: Das Pflanzenreich IV, 129: 351–369. 1912

Type (designated here):—*Pelargonium schlechteri* R.Knuth (1908: 72)

2.1.1 ***Pelargonium*** sect. ***Magnistipulacea*** subsection ***Magnistipulacea*** (R.Knuth) Roeschenbl. & F.Albers, *comb. nov.*

Basionym:—*Pelargonium* sect. *Polyactium* subsect. *Magnistipulacea* R.Knuth (1912: 352), in Engl.: Das Pflanzenr. IV, 129: 351–369. 1912

Type (see above):—*Pelargonium schlechteri* R.Knuth (1908: 72)

2.1.2 ***Pelargonium*** sect. ***Magnistipulacea*** subsection ***Schizopetala*** (R.Knuth) Roeschenbl. & F.Albers, *comb. nov.*

Basionym:—*Pelargonium* sect. *Polyactium* subsect. *Schizopetala* R.Knuth (1912: 352), in Engl.: Das Pflanzenr. IV, 129: 351–369. 1912

Type (designated here):—*P. caffrum* (Eckl. & Zeyh.) Steudel (1841: 284)

Conspectus of the genus *Pelargonium* based on molecular and morphological evidence

In the following provisional conspectus, we summarise our recent taxonomic understanding of the genus *Pelargonium*, with emphasis of virtually all currently recognised *Pelargonium* taxa (281). Taxa for which molecular data exist (e.g. by Bakker *et al.* 2004, Touloumenidou *et al.* 2004, Albers & Becker 2010, this study) are marked with an asterisk. The 229 taxa incorporated in the expanded appraisal of floral traits are marked with F. All sections that differ from their most recent previous circumscription are marked with +. Listing of full synonomy of single species and sections is not attempted. Species, placed outside of their hitherto respective section by molecular results, are listed as unassigned under the equivalent subgenus. For a few species, which are to date not clearly assigned to any section and coincidently no molecular data is available, a preliminary designation to the respective subgenus is shortly discussed.

Genus ***Pelargonium*** L'Héritier in Aiton (1789: 417)

1. ***Pelargonium*** subg. ***Magnipetala*** Roeschenbl. & F.Albers

1.1 Section ***Chorisma*** (Lindley ex Sweet) De Candolle (1824: 658)
Pelargonium exhibens Vorster*[F]; *P. mollicomum* Fourc.*[F]; *P. tetragonum* (L.f.) L'Hér.*[F]; *P. worcesterae* R.Knuth*[F]

1.2 Section **Jenkinsonia** (Sweet) De Candolle (1824:658)[+]
Pelargonium divisifolium Vorster[F]; *P. dolomiticum* R.Knuth*[F]; *P. griseum* R.Knuth*[F]; *P. mutans* Vorster*[F]; *P. plurisectum* T.M.Salter[F]; *P. praemorsum* (Andrews) F.Dietr. subsp. *praemorsum**[F]; *P. praemorsum* subsp. *speciosum* Scheltema[F]; *P. redactum* Vorster*[F]; *P. senecioides* L'Hér.*[F]; *P. tenuicaule* R.Knuth*[F]; *P. tragacanthoides* Burch.*[F]; *P. trifidum* Jacq.*[F]

1.3 Section ***Myrrhidium*** De Candolle (1824: 657)
Pelargonium candicans Spreng.*[F]; *P. caucalifolium* Jacq. subsp. *caucalifolium**[F]; *P. caucalifolium* subsp. *convolvulifolium* (Schltr. ex R.Knuth) J.J.A.van der Walt[F]; *P. longicaule* Jacq. var. *longicaule**[F]; *P. longicaule* var. *angustipetalum* D.A.Boucher[F]; *P. multicaule* Jacq. subsp. *multicaule*[F]; *P. multicaule* Jacq. subsp. *subherbaceum* (R.Knuth) J.J.A.van der Walt[F]; *P. myrrifolium* (L.) L'Hér. var. myrrifolium*[F]; *P. myrrhifolium* var. *coriandrifolium* (L.) Harv.[F]; *P. suburbanum* Clifford ex D.A.Boucher subsp. *suburbanum**[F]; *P. suburbanum* subsp. *bipinnatifidum* (Harv.) D.A.Boucher*[F]; *P. whytei* Baker*[F]

1.4 **Unassigned species** within subgenus *Magnipetala*
Pelargonium antidysentericum (Eckl. & Zeyh.) Kostel. subsp. *antidysentericum**[F]; P. *antidysentericum* subsp. *inerme* Scheltema[F]; *P. antidysentericum* subsp. *zonale* Scheltema[F]; *P. boranense* Friis & M.G.Gilbert*[F]

Molecular results of this study and floral characters (petal number, number of fertile anthers) suggest a close relationship of *P. boranense* to sect. *Myrrhidium*.

A further species from East Africa, *P. erlangerianum* Engler ex R.Knuth (1912: 455), might be for now best placed under subg. *Magnipetala*. The species represents an annual or short lived perennial herb with four petalled flowers and linear markings (Gilbert & Vorster 2000), characters typically found in species of sect. *Jenkinsonia* and *Myrrhidium*. Like species of sect. *Chorisma, P. erlangerianum* has entire leaves and five fertile anthers. By Knuth (1912) *P. erlangerianum* was grouped with species of the recent sectt. *Chorisma*, *Reniformia* and *Cortusina* under a heterogeneous section *Cortusina*. In the subdivision of sect. *Cortusina* by Dreyer *et al.* (1992a), *P. erlangerianum* was not considered. The former two sections, *Chorisma* and *Reniformia* in its recent circumscription, were established by Albers *et al.* (1995) and Dreyer & Marais (2000).

2. ***Pelargonium*** subg. ***Parvulipetala*** Roeschenbl. & F.Albers

2.1 Section ***Isopetalum*** (Sweet) De Candolle (1824: 655)
Pelargonium cotyledonis (L.) L'Hér.*[F]

2.2 Section ***Peristera*** De Candolle (1824: 654)[+]
Pelargonium anceps L'Hér.*[F]; *P. apetalum* P.Taylor[F]; *P. australe* Willd.*[F]; *P. brevirostre* E.Mey. ex R.Knuth[F]; *P. buysii* Hellbr.*[F]; *P. capituliforme* R.Knuth; *P. columbinum* Jacq.[F]; *P. drummondii* Turcz.*[F]; *P. erodioides* Hook.[F]; *P. filicaule* R.Knuth*[F]; '*P. geniculatum*'*[F]; *P. gilgianum* Schltr. ex R.Knuth[F]; *P. glechomoides* Hochst. ex A.Rich.*; *P. grossularioides* (L.) L'Hér.*[F]; *P. havlasae* Domin.*[F]; *P. helmsii* Carolin[F]; *P. hypoleucum* Turcz.*[F]; *P. inodorum* Willd.[F]; *P. iocastum* (Eckl. & Zeyh.) Steud.*[F]; *P. leucophyllum* Turcz.*[F]; *P. littorale* Hügel[F]; *P. madagascariense* Baker; *P. minimum* (Cav.) Willd.*[F]; *P. nelsonii* Burtt. Davy[F]; *P. parvirostre* R.A.Dyer[F]; *P. pseudofumarioides* R.Knuth*[F]; *P. rodneyanum* T.Mitch. ex Lindl.*[F]; *P. rungvense* R.Knuth; *P. setosiusculum* R.Knuth; *P. wonchiense* Vorster & M.G.Gilbert

—Note: '*P. geniculatum*' was differentiated as a "*P. anceps* subsp. *geniculatum*" from the typical *P. anceps* L'Héritier in Aiton (1789: 420) by Hellbrügge (1997), but still lacks its formal publication.

2.3 Section ***Reniformia*** (R.Knuth) Dreyer (2000: 44)
Pelargonium abrotanifolium (L.f.) Jacq.*[F], *P. album* J.J.A.van der Walt*[F]; *P. dichondrifolium* DC.*[F]; *P. exstipulatum* (Cav.) L'Hér.*[F]; *P. ionidiflorum* (Eckl. & Zeyh.) Steud.*[F]; *P. odoratissimum* (L.) L'Hér.*[F]; *P. reniforme* (Andrews) Curtis subsp. *reniforme**[F]; *P. reniforme* subsp. *velutinum* (Eckl. & Zeyh.) Dreyer*; *P. sidoides* DC.*[F]

2.4 **Unassigned species** within subgenus *Parvulipetala*
P. dispar N.E.Brown (1895: 144), *P. oppositifolium* Schlechter (1898: 315) and *P. mossambicense* Engler (1895: 225) were included in sect. *Peristera* by Knuth (1912), but not by Hellbrügge (1995). The latter species was found to be close in shape of its leave and floral structure to *P. album* sect. *Reniformia*, by Dreyer & van der Walt (1990). Nevertheless, all three species can be clearly designated to *Pelargonium* subg. *Parvulipetala* by flower size, a very short hypanthium and their herbaceous spreading habit.

3. ***Pelargonium*** subg. ***Paucisignata*** Roeschenbl. & F.Albers

3.1 Section ***Ciconium*** (Sweet) Harvey (1860: 298)[+]
Pelargonium acetosum (L.) L'Hér.*[F]; *P. acraeum* R.A.Dyer*[F]; *P. alchemilloides* (L.) L'Hér.*[F]; *P. aridum* R.A.Dyer*[F]; *P. articulatum* (Cav.) Willd.*[F]; *P. barklyi* Scott-Elliot*[F]; *P. elongatum* (Cav.) Salisb.*[F]; *P. frutetorum* R.A.Dyer*[F]; *P. inquinans* (L.) L'Hér.*[F]; *P. insularis* Gibby & A.G.Miller*; *P. multibracteatum* Hochst. ex A.Rich.*[F]; *P. peltatum* (L.) L'Hér.*[F]; *P. quinquelobatum* Hochst. ex A.Rich.*[F]; *P. ranunculophyllum* (Eckl. & Zeyh.) Baker*[F]; *P. somalense* Franch.; *P. tongaense* Vorster*[F]; *P. zonale* (L.) L'Hér.*[F]

3.2 Section ***Subsucculentia*** J.J.A.van der Walt (1995: 335)[+]
Pelargonium grandicalcaratum R.Knuth*[F]; *P. otaviense* R.Knuth*[F]; *P. spinosum* Willd.*[F]

3.3 **Unassigned species** within subgenus *Paucisignata*
Pelargonium caylae Humbert*[F]; *P. endlicherianum* Fenzl*[F]; *P. karooicum* Compton & P.E.Barnes*[F]; *P. quercetorum* Agnew*[F]; *P. transvaalense* R.Knuth*[F]

Two further species from East Africa, *Pelargonium christophoranum* Verdcourt (1968: 428) and *P. hararense* Engler ex R.Knuth (1912: 435), should be best considered under this subgenus. By Knuth (1912) *P. hararense* was designated, especially together with *P. multibracteatum* Hochstetter ex A.Richard (1847: 119) and *P. quinquelobatum*, to the former section *Eumorpha* (Eckl. & Zeyh.) Harvey (1860: 294), recently in parts included in sect. *Ciconium*.

For *P. christophoranum,* Lavranos (1978) discussed habitual affinities to sect. *Ligularia*, but favoured a closer relationship to sect. *Eumorpha*, because of flower morphology and the distribution patterns of the sections. In its xerophytic habit, its leave shape and with persistent petioles *P. christophoranum* resembles also *P. otaviense* and *P. spinosum* of the South African sect. *Subsucculentia*. With the latter species, *P. christophoranum* also shares the open flower and a similar cross-like arrangement of petals. On the other hand habit and leave shape of *P. christophoranum* exhibit likewise a certain affinity to *P. praemorsum* or *P. antidysentericum* of subgenus *Magnipetala*, which consigns any designation without molecular support in this particular case tentatively.

4. ***Pelargonium*** subg. ***Pelargonium***

4.1. Section ***Campylia*** (Lindley ex Sweet) De Candolle (1824: 656)[+]

Pelargonium althaeoides (L.) L'Hér.*[F]; *P. burgerianum* J.J.A.van der Walt*[F]; *P. caespitosum* Turcz. subsp. *caespitosum**[F]; P. *caespitosum* subsp. *concavum* Hugo; P. *capillare* (Cav.) Willd.*[F]; *P. coronopifolium* Jacq.*[F]; *P. elegans* (Andrews) Willd.*[F]; *P. ocellatum* J.J.A.van der Walt; *P. oenothera* (L.f.) Jacq.[F]; *P. ovale* (Burm.f.) L'Hér. subsp. *ovale**[F]; *P. ovale* subsp. *hyalinum* Hugo; *P. ovale* subsp. *veronicifolium* (Eckl. & Zeyh.) Hugo; *P. tricolor* Curtis*[F]

4.2 Section ***Cortusina*** (DC.) Harvey (1860: 299)

Pelargonium cortusifolium L'Hérit.*[F]; *P. crassicaule* L'Hérit.*[F]; *P. echinatum* Curtis*[F]; *P. magenteum* J.J.A.van der Walt*[F]; *P. mirabile* Dinter*[F]; *P. sibthorpiifolium* Harv.[F]; *P. vanderwaltii* Van Jaarsv.

—Note, sect. *Cortusina* is considered here in a narrower sense than by Harvey. Species contained in sect. *Cortusina* (*sensu stricto*) are taken from Dreyer *et al.* (1992a) with addition of the recently described *P. vanderwaltii* Van Jaarsveld (2006: 32). For recognition of *P. mirabile* Dinter (1914: 47) as a separate taxon see van der Walt & Vorster (1981a).

4.3 Section ***Hoarea*** (Sweet) De Candolle (1824: 649)

Pelargonium aciculatum E.M.Marais*[F]; *P. aestivale* E.M.Marais*[F]; *P. angustipetalum* E.M.Marais[F]; *P. aridicola* E.M.Marais; *P. aristatum* (Sweet) G.Don*[F]; *P. asarifolium* (Sweet) Loudon*[F]; *P. attenuatum* Harv.[F]; *P. auritum* (L.) Willd. var. *auritum**[F]; *P. auritum* var. *carneum* (Harv.) E.M.Marais*[F]; *P. bubonifolium* (Andrews) Pers.[F]; *P. caledonicum* L.Bol.*[F]; *P. campestre* (Eckl. & Zeyh.) Steud.[F]; *P. carneum* Jacq.*[F]; *P. caroli-henrici* B.Nord.*[F]; *P. chelidonium* (Houtt.) DC.[F]; *P. confertum* E.M.Marais*[F]; *P. connivens* E.M.Marais*[F]; *P. curviandrum* E.M.Marais[F]; *P. dipetalum* L'Hérit.[F]; *P. ellaphieae* E.M.Marais*[F]; *P. elandsmontanum* E.M.Marais ex J.C.Manning & Goldblatt; *P. fasciculaceum* E.M.Marais*[F]; *P. fergusoniae* L.Bol.*[F]; *P. fissifolium* (Andrews) Pers.*[F]; *P. flavidum* E.M.Marais; *P. fumariifolium* R.Knuth*[F]; *P. githagineum* E.M.Marais[F]; *P. glabriphyllum* E.M.Marais*; *P. gracillinum* Fourc.[F]; *P. grenvilleae* (Andrews) Harv.*[F]; *P. heterophyllum* Jacq.[F]; *P. hirtipetalum* E.M.Marais; *P. incrassatum* (Andrews) Sims*[F]; *P. leipoldtii* R.Knuth*[F]; *P. leptum* L.Bol.*[F]; *P. longiflorum* Jacq.*[F]; *P. longifolium* (Burm.f.) Jacq.[F]; *P. luteolum* N.E.Brown*[F]; *P. luteum* (Andrews) Sm.*[F]; *P. moniliforme* E.Mey. ex Harv.*[F]; *P. nephrophyllum* E.M.Marais[F]; *P. nervifolium* Jacq.*[F]; *P. nummulifolium* Salisb.[F]; *P. oblongatum* E.Mey. ex Harv.* [F]; *P. ochroleucum* Harv.; *P. pallidoflavum* E.M.Marais; *P. parvipetalum* E.M.Marais*[F]; *P. petroselinifolium* G.Don*[F]; P. *pilosellifolium* (Eckl. & Zeyh.) Steud.[F]; *P. pinnatum* (L.) L'Hér.*[F]; *P. proliferum* (Burm.f.) Steud.*[F]; *P. pubipetalum* E.M.Marais; *P. punctatum* (Andrews) Willd.*[F]; *P. quarciticola* Meve & E.M.Marais*; *P. radiatum* (Andrews) Pers.*[F]; *P. radicatum* Vent.[F]; *P. rapaceum* (L.) L'Hér.*[F]; *P. reflexipetalum* E.M.Marais*; *P. reflexum* (Andrews) Pers.[F]; *P. rubiginosum* E.M.Marais[F]; *P. sabulosum* E.M.Marais; *P. saxatile* J.C.Manning & Goldblatt; *P. tenellum* (Andrews) Loudon[F]; *P. ternifolium* Vorster*[F]; *P. triandrum* E.M.Marais*[F]; *P. trifoliolatum* (Eckl. & Zeyh.) E.M.Marais[F]; *P. tripalmatum* E.M.Marais; *P. triphyllum* Jacq.*[F]; *P. undulatum* (Andrews) W.T.Aiton*[F]; *P. viciifolium* L'Hér.[F]; *P. vinaceum* E.M.Marais*[F]; *P. violiflorum* (Sweet) DC.*[F]; *P. weberi* E.M.Marais

4.4 Section ***Ligularia*** (Sweet) Harvey (1860: 280)

P. appendiculatum (L.f.) Willd.*[F]; *P. crassipes* Harv.[F]; *P. fulgidum* (L.) L'Hér.*[F]; *P. hirtum* (Burm.f.) Jacq.*[F]; *P. hystrix* Harv.*[F]; *P. oreophilum* Schltr.*[F]; *P. pulchellum* Sims*[F]; *P. sericifolium* J.J.A.van der Walt*[F];

P. stipulaceum (L.f.) Willd. subsp. *stipulaceum**[F]; *P. stipulaceum* subsp. *ovatostipulatum* (R.Knuth) Vorster; *P. torulosum* E.M.Marais*[F]

—Note, sect. *Ligularia* is considered here in a narrower sense than by Harvey. Species contained in sect. *Ligularia* (*sensu stricto*) are taken from Albers *et al.* (2000).

4.5 Section ***Magnistipulacea*** (R.Knuth) Roeschenbl. & F.Albers

4.5.1 Subsection ***Magnistipulacea*** (R.Knuth) Roeschenbl. & F.Albers
Pelargonium *luridum* (Andrews) Sweet*[F]; *P. schlechteri* R.Knuth*(molecular data under the synonym *P. flabellifolium* Harv.)

4.5.2 Subsection ***Schizopetala*** (R.Knuth) Roeschenbl. & F.Albers
Pelargonium bowkeri Harv.*[F]; *P. caffrum* (Eckl. & Zeyh.) Steud.*[F]; *P. schizopetalum* Sweet*[F]

4.6 Section ***Otidia*** (Lindley ex Sweet) De Candolle (1824: 655)[+]
P. adriaanii M.Becker & F.Albers*; *P. albersii* M.Becker*; *P. anauris* M.Becker & F.Albers*; *P. brevipetalum* N.E.Brown*[F]; *P. carnosum* (L.) L'Hér. subsp. *carnosum**[F]; *P. carnosum* subsp. *ferulaceum* (Cav.) M.Becker & F.Albers*; *P. ceratophyllum* L'Hér.*[F]; *P. crithmifolium* Sm.* [F]; *P. dasycaulon* (Haw.) Sims, *P. dasyphyllum* E.Mey. ex R.Knuth*[F]; *P. keeromsbergense* M.Becker & F.Albers*; *P. klinghardtense* R.Knuth*[F]; *P. laxum* (Sweet) G.Don subsp. *laxum** [F]; *P. laxum* subsp.*karooicum* M.Becker & F.Albers*; *P. paniculatum* Jacq.*[F]; *P. parviflorum* J.C.Wendl.*[F], *P. polycephalum* (Harv.) E.Mey. ex R.Knuth; '*P. rotundipetalum*'*[F]

Within the *P. parviflorum* complex, only *P. brevipetalum* N.E.Brown (1909: 184) and '*P. rotundipetalum*' are considered here. A prospective option for further classification is listed in Becker & Albers (2009).

4.7 Section ***Pelargonium***[+]
Pelargonium alpinum Eckl. & Zeyh.*[F]; *P. betulinum* (L.) L'Hér.*[F]; *P. capitatum* (L.) L'Hér.[F]; *P. citronellum* J.J.A.van der Walt*[F]; *P. cordifolium* (Cav.) Curtis[F]; *P. crispum* (P.J.Bergius) L'Hér.*[F]; *P. cucullatum* (L.) L'Hér. subsp. *cucullatum**[F]; *P. cucullatum* subsp. *strigifolium* Volschenk; *P. cucullatum* subsp. *tabulare* Volschenk*; *P. denticulatum* Jacq.*[F]; *P. englerianum* R.Knuth[F]; *P. fruticosum* (Jacq.) Willd.[F]; *P. glutinosum* (Jacq.) L'Hér.*[F]; *P. grandiflorum* (Andrews) Willd.*[F]; *P. graveolens* L'Hér.*[F]; *P. greytonense* J.J.A.van der Walt[F]; *P. hermanniifolium* (P.J.Bergius) Jacq.*[F]; *P. hispidum* (L.f.) Willd.*[F]; *P. incarnatum* (L'Hér.) Moench*[F]; *P. laevigatum* (L.f.) Willd.*[F]; *P. lanceolatum* (Cav.) Kern.*[F]; *P. panduriforme* Eckl. & Zeyh.[F]; *P. papilionaceum* (L.) L'Hér.* [F]; *P. patulum* Jacq.* [F]; *P. pseudoglutinosum* R.Knuth*[F]; *P. quercifolium* (L.f.) L'Hér.*[F]; *P. radens* H.E.Moore*[F]; *P. ribifolium* Jacq.[F]; *P. scabroide* R.Knuth[F]; *P. scabrum* (L.) L'Hér.*[F]; *P. setulosum* Turcz.*[F]; *P. sublignosum* R.Knuth*; *P. tabulare* (L.) L'Hér.; *P. ternatum* (L.f.) Jacq.*[F]; *P. tomentosum* Jacq.*[F]; *P. vitifolium* (L.) L'Hér.*[F]

4.8 Section ***Polyactium*** De Candolle (1824: 655)[+]

4.8.1 Subsection ***Caulescentia*** R.Knuth (1912: 352)
Pelargonium gibbosum (L.) L'Hér.*[F]

4.8.2 Subsection ***Polyactium***
Pelargonium anethifolium (Eckl. & Zeyh.) Steud.*[F]; *P. lobatum* (Burm.f.) L'Hér.*[F]; *P. multiradiatum* J.C.Wendl.*[F]; *P. pillansii* T.M.Salter[F]; *P. pulverulentum* Colv. ex Sweet*[F]; *P. radulifolium* (Eckl. & Zeyh.) Steud.*[F]; *P. triste* (L.) L'Hér.*[F]

4.9 **Unassigned species** within subgenus *Pelargonium*
Pelargonium alternans J.C.Wendl. subsp. *alternans**[F]; *P. alternans* subsp. *longicalcar* M.Becker & F.Albers; *P. alternans* subsp. *parviinflorencens* M.Becker & F.Albers; *P. desertorum* Vorster*[F]; *P. laciniatum* R.Knuth; *P. nanum* L'Hér.*[F]; *P. xerophyton* Schltr. ex R.Knuth*[F]

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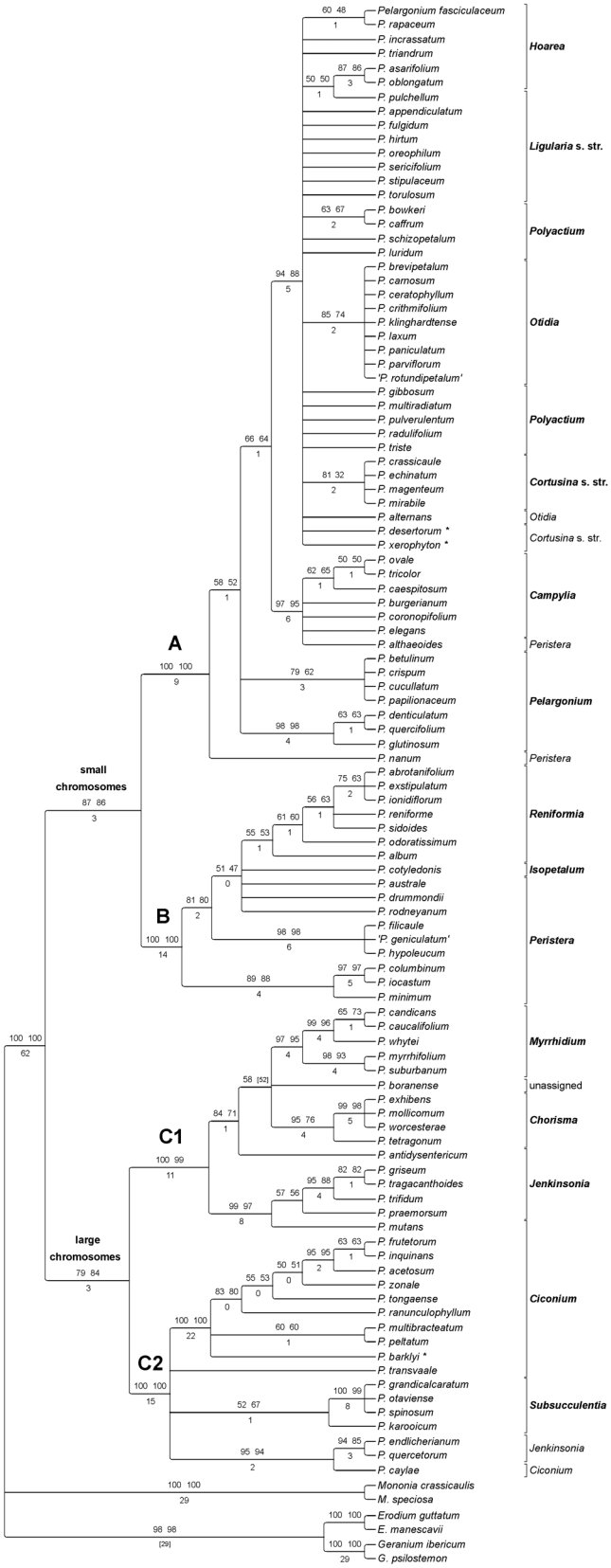
Appendix I. Species included in the phylogenetic analyses and GenBank accessions for newly generated sequences.

Species, voucher information, origin, *atp*B-*rbc*L GenBank no. and *trn*L-F GenBank no.

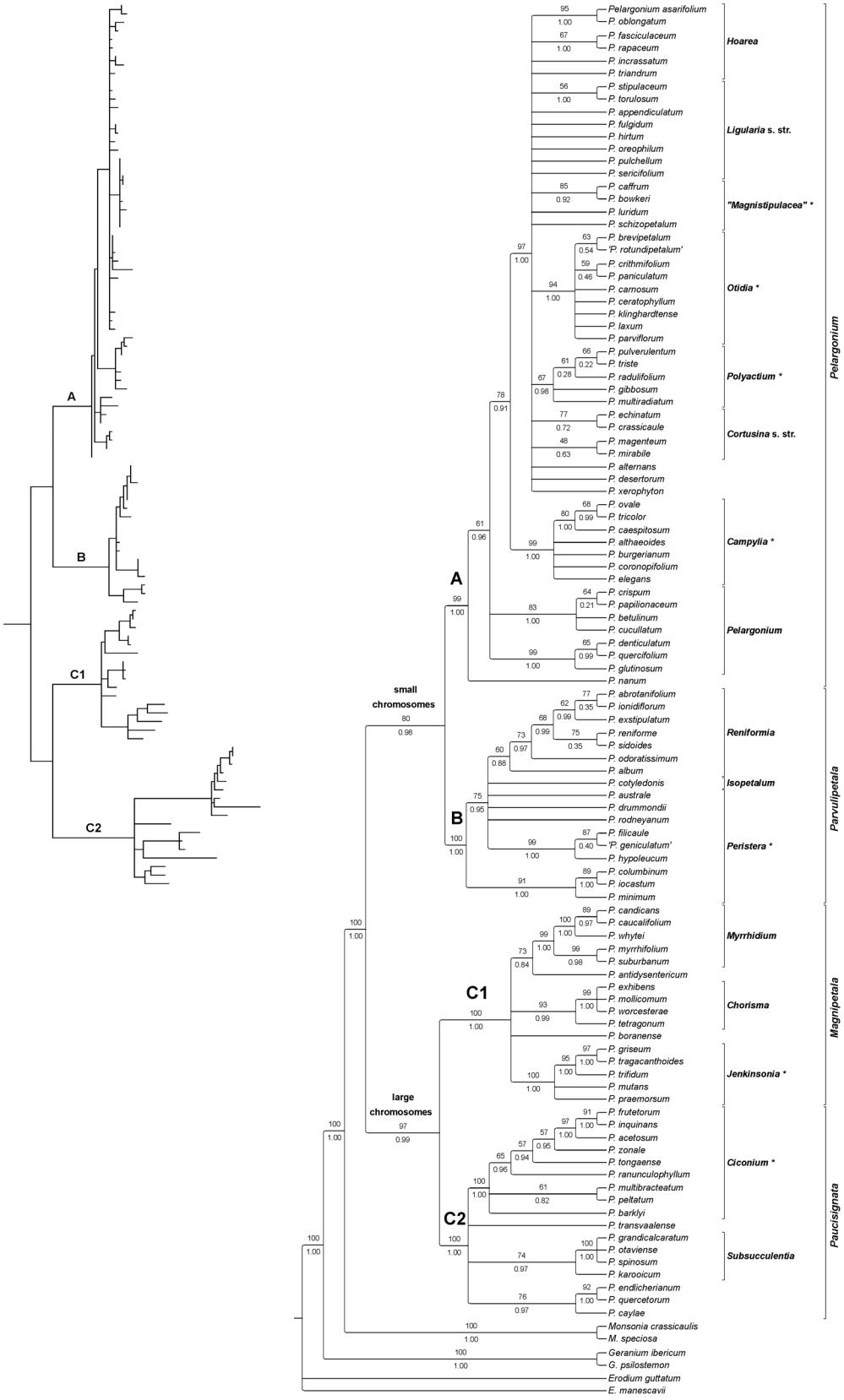
Erodium guttatum (Desf.) Willd., MSUN 4044, s.loc., cult. BG MS, KF696394, KF696504. *E. manescavii* Coss., MSUN 4043, s.loc., cult. BG MS, KF696395, KF696505. *Geranium ibericum* Cav., MSUN 4024, s.loc., cult. BG MS, KF696396, KF696506. *G. psilostemon* Ledeb., MSUN 4023, Turkey, cult. BG MS, KF696397, KF696507. *Monsonia crassicaulis* (Rehm) F.Albers, no voucher, South Afr., Western Cape, Steinkopf, KF696398, KF696508. *M. speciosa* L., MSUN 939, South Afr., Western Cape, Gordonsbay, KF696399, KF696509. *Pelargonium abrotanifolium* (L.f.) Jacq., MSUN 563, South Afr., Western Cape, Riversdale, KF696458. *P. acetosum* (L.) L'Hér., MSUN 526, South Afr., Eastern Cape, Uitenhage, KF696479. *P. album* J.J.A.van der Walt, MSUN 669, South Afr., Mpumalanga, Pelgrimsrust, KF696454. *P. alternans* subsp. *alternans* J.C.Wendl., MSUN 720, South Afr., Western Cape, Wuppertal, KF696427. *P. althaeoides* (L.) L'Hér., MSUN 4032, South Afr., Western Cape, Stellenboschberg, KF696447. *P. antidysentericum* subsp. *antidysentericum* (Eckl. & Zeyh.) Kostel., MSUN 537, South Afr., Free State, Sannagas, KF696498, KF696555. *P. appendiculatum* (L.f.) Willd., STEU 3233, South Afr., Western Cape, Leipoldtville, KF696410. *P. asarifolium* (Sweet) Loudon, no voucher, s.loc., cult. BG MS, KF696403. *P. australe* Willd., MSUN 375, Australia, New South Wales, Terrigal, KF696463. *P. barklyi* Scott-Elliot, MSUN 4037, s.loc., cult. Fischer (Syngenta), KF696473. *P. betulinum* (L.) L'Hér., MSUN 3200, South Afr., Western Cape, Franskraal, KF696441. *P. boranense* Friis & M.P.Gilbert, no voucher, Ethiopia, Sidamo, cult. BG Dresden, KF696493, KF696554. *P. bowkeri* Harv., MSUN 2838, South Afr., Free State, Harrismith, KF696415. *P. brevipetalum* N.E.Brown, MSUN 4041, South Afr., Western Cape, Matjiesfontein, KF696422, KF696518. *P. burgerianum* J.J.A.van der Walt, no voucher, South Afr., cult. BG MS, KF696448, KF696529. *P. caespitosum* subsp. *caespitosum* Turcz., STEU 1799, South Afr., Western Cape, Eselbank, KF696453. *P. caffrum* (Eckl. & Zeyh.) Steud. STEU 2738, South Afr., Western Cape, Robinsonpas, Oudtshorn to Mosselbay, KF696416. *P. candicans* Spreng., MSUN 4036, South Afr., Western Cape, Kapstadt, Signal Hill, KF696491, KF696551. *P. carnosum* subsp. *carnosum* (L.) L'Hér., MSUN 2737, South Afr., Western Cape, Yzerfontein, KF696419. *P. caucalifolium* subsp. *caucalifolium* Jacq., MSUN 2781, South Afr., Western Cape, Riviersonderend, KF696492. *P. caylae* Humbert, MSUN 477, Madagascar, Tananarive, KF696485, KF696542. *P. ceratophyllum* L'Hér., MSUN 725, Namibia, Lüderitzbucht, KF696418, KF696520. *P. columbinum* Jacq., MSUN 4033, South Afr., Western Cape, s.loc., KF696469, KF696538. *P. coronopifolium* Jacq., STEU 1797, South Afr., Western Cape, Cederberge, KF696449. *P. cotyledonis* (L.) L'Hér., MSUN 4030, St. Helena, cult. BG MS, KF696461, KF696537. *P. crassicaule* L'Hér., MSUN 601, s.loc., cult. BG MS, KF696435, KF696526. *P. crispum* (P.J.Bergius) L'Hér., MSUN 2839, South Afr., s.loc., KF696439, KF696531. *P. crithmifolium* Sm., MSUN 4034, South Afr., cult. BG MS, KF696426. *P. cucullatum* subsp. *cucullatum* (L.) L'Hér., STEU 1043, South Afr., Western Cape, Gansbaai, KF696442, KF696530. *P. denticulatum* Jacq., MSUN 2743, South Afr., Western Cape, Ladysmith, KF696445. *P. desertorum* Vorster, MSUN 538, South Afr., Northern Cape, Richtersveld, KF696434, KF696528. *P. drummondii* Turcz., MSUN 160, Australia, Mount Merrivale, KF696464. *P. echinatum* Curtis, MSUN 612, South Afr., Nothern Cape, Helskloof-Richtersveld, KF696437. *P. elegans* (Andrews) Willd., MSUN 4038, s.loc., cult. Fischer (Syngenta), KF696450. *P. endlicherianum* Fenzl, no voucher, s.loc., cult. BG MS, KF696486, KF696543. *P. exhibens* Vorster, MSUN 2788, South Afr., Eastern Cape, Grahamstown, KF696496. *P. exstipulatum* (Cav.) L'Hér., MSUN 656, South Afr., Western Cape, Muiskroal, KF696456. *P. fasciculaceum* E.M.Marais, MSUN 740, South Afr., Western Cape, Paleisheuwel, KF696404, KF696512. *P. filicaule* R.Knuth, MSUN 310, South Afr., Western Cape, Gordonsbaai, Sir Lowry's Pass, KF696465. *P. frutetorum* R.A.Dyer, MSUN 503, South Afr., Eastern Cape, Bathurst, KF696477, KF696546. *P. fulgidum* (L.) L'Hér., STEU 482, South Afr., Western Cape, Yzerfontein, KF696408, KF696516. '*P. geniculatum*' subspec. nov. ined., MSUN 430, South Afr., Eastern Cape, East London, KF696466. *P. gibbosum* (L.) L'Hér., MSUN 4025, South Afr., Western Cape, Llundudno, KF696428. *P. glutinosum* (Jacq.) L'Hér., STEU 1644, South Afr., Western Cape, Tradouw Pass, KF696443, KF696532. *P. grandicalcaratum* R.Knuth, STEU 758, South Afr., Northern Cape, Studerpas, Namaqualand, KF696481. *P. griseum* R.Knuth, MSUN 3208, South Afr., Eastern Cape, Queenstown, KF696501. *P. hirtum* (Burm.f.) Jacq., s.loc., cult. BG MS, KF696406. *P. hypoleucum* Turcz., MSUN 653, South Afr., Western Cape, Greyton, KF696467. *P. incrassatum* (Andrews) Sims, MSUN 785, South Afr., Northern Cape, Kamieskroon Pass, KF696400, KF696510. *P. inquinans* (L.) L'Hér., MSUN 530, South Afr., Eastern Cape, Grahamstown, KF696478, KF696547. *P. iocastum* (Eckl. & Zeyh.) Steud., STEU 1938, South Afr., Western Cape, Tulbagh, KF696468. *P. ionidiflorum* (Eckl. & Zeyh.) Steud., MSUN 673, South Afr., Eastern Cape, Grahamstown, KF696457. *P. karooicum* Compton & P.E.Barnes, MSUN 4040, South Afr., Western Cape, Vredendal, KF696484. *P. klinghardtense* R.Knuth, MSUN 709, South Afr., Northern Cape, Numiesberge, KF696424, KF696521. *P. laxum* subsp. *laxum* (Sweet) G.Don, MSUN 711, South Afr., Eastern Cape, Grahamstown, KF696423. *P. luridum* (Andrews) Sweet, MSUN 4029, South Afr., Transvaal, Nelspruit, KF696414, KF696517. *P. magenteum* J.J.A.van der Walt, MSUN 631, South Afr., Western Cape, Laingsburg, KF696438. *P. minimum* (Cav.) Willd., STEU 4361, South Afr., Western Cape, Tilney Montagu, KF696470, KF696540. *P. mirabile* Dinter, M 94815, s.loc., cult. Fischer (Syngenta), KF696436, KF696525. *P. mollicomum* Fourc., MSUN 2768, South Afr., Eastern Cape, Grahamstown, KF696494, KF696552. *P. multibracteatum* Hochst. ex A.Rich., MSUN 2727, Yemen, s.loc, KF696472, KF696549. *P. multiradiatum* J.C.Wendl., STEU 3191, South Afr., Western Cape, Citrusdahl, KF696429. *P. mutans* Vorster, MSUN 2714, South Afr., KwaZulu-Natal, Klipwal, KF696502. *P. myrrhifolium* var. *myrrhifolium* (L.) L'Hér., MSUN 3205, South Afr., Western Cape, Stellenbosch, KF696488, KF696550. *P. nanum* L'Hér., MSUN 345, South Afr., Western Cape, Montagu, KF696446, KF696534. *P. oblongatum* E.Mey. ex. Harv., MSUN 4027, South Afr., s.loc., KF696402. *P. odoratissimum* (L.) L'Hér., MSUN 557, South Afr., Eastern Cape, Port Alfred, KF696455, KF696535. *P. oreophilum* Schltr., MSUN 964, South Afr., Western Cape, Pakhuispas, KF696407, KF696514. *P. otaviense* R.Knuth, STEU 943, Namibia, Damaraland,

Welwitschiavlkt, KF696480, KF696545. *P. ovale* subsp. *ovale* (Burm.f.) L'Hér., no voucher, s.loc., cult. BG MS, KF696451. *P. paniculatum* Jacq., MSUN 2733, Namibia, Rosh Pinah, KF696425. *P. papillionaceum* (L.) L'Hér., MSUN 3195, South Afr., Western Cape, Garciapas, KF696440. *P. parviflorum* J.C.Wendl., MSUN 4042, South Afr., Nothern Cape, Steinkopf, KF696420, KF696519. *P. peltatum* (L.) L'Hér., MSUN 534, South Afr., Eastern Cape, Humansdorp, KF696471. *P. praemorsum* subsp. *praemorsum* (Andrews) F.Dietr., STEU 810, South Afr., Western Cape, Pakhuispas, KF696503. *P. pulchellum* Sims, MSUN 4028, South Afr., Northern Cape, Kamieskroon Pass, KF696409, KF696515. *P. pulverulentum* Colv. ex Sweet, MSUN 473, South Afr., Eastern Cape, Bathurst, KF696430, KF696524. *P. quercetorum* Agnew, no voucher, s.loc., cult. Fischer (Syngenta), KF696487, KF696544. *P. quercifolium*, (L.f.) L'Hér., MSUN 2770, South Afr., s.loc., KF696444, KF696533. *P. radulifolium* (Eckl. & Zeyh.) Steud., MSUN 874, South Afr., Western Cape, Sandhills, KF696432, KF696523. *P. ranunculophyllum* (Eckl. & Zeyh.) Baker, MSUN 2375, South Afr., s.loc, KF696474. *P. rapaceum* (L.) L'Hér., MSUN 4026, South Afr., Northern Cape, Anenoupass, KF696405, KF696513. *P. reniforme* subsp. *velutinum* (Eckl. & Zeyh.) Dreyer, MSUN 2721, South Afr., Eastern Cape, Grahamstown, KF696460. *P. rodneyanum* T.Mitch. ex Lindl., MSUN 295, Australia, Wallalooka, KF696462, KF696539. '*P. rotundipetalum*' spec. nov. ined., MSUN 593, South Afr., Western Cape, Muiskraal, KF696421. *P. schizopetalum* Sweet, STEU 1873, South Afr., Eastern Cape, Hogsback, KF696417. *P. sericifolium* J.J.A.van der Walt, STEU 1554, South Afr., Nothern Cape, Springbok, Namaqualand, KF696411. *P. sidoides* DC., MSUN 2666, South Afr., s.loc., KF696459, KF696536. *P. spinosum* Willd., STEU 619, South Afr., Nothern Cape, Richtersveld, KF696482. *P. stipulaceum* subsp. *stipulaceum* (L.f.) Willd., MSUN 4039, South Afr., cult. Fischer (Syngenta), KF696412. *P. suburbanum* subsp. *suburbanum* Clifford ex D.A.Boucher, MSUN 2742, South Afr., Samerstrand, KF696489. *P. tetragonum* (L.f.) L'Hér., MSUN 3184, South Afr., Western Cape, Matjiesfontein, KF696497, KF696553. *P. tongaense* Vorster, MSUN 4031, South Afr., KwaZulu-Natal, Pongolarivier, KF696475. *P. torulosum* E.M.Marais, MSUN 2786, South Afr., Nothern Cape, Sutherland, KF696413. *P. tragacanthoides* Burch., STEU 1849, South Afr., Northern Cape, Middelburg, KF696500, KF696556. *P. transvaalense* R.Knuth, STEU 1972, South Afr., KwaZulu-Natal, Barberton, KF696483, KF696541. *P. triandrum* E.M.Marais, MSUN 751, South Afr., Western Cape, Citrusdal, KF696401, KF696511. *P. tricolor* Curtis, MSUN 4045, s.loc., cult. BG MS, KF696452. *P. trifidum* Jacq., MSUN 3179, South Afr., Western Cape, Meeringspoort, KF696499. *P. triste* (L.) L'Hér., STEU 1103, South Afr., Western Cape, Langebaan, KF696431, KF696522. *P. whytei* Baker, MSUN 4035, Ethiopia, cult. BG MS, KF696490. *P. worcesterae* R.Knuth, MSUN 2746, South Afr., Eastern Cape, Cradock, KF696495. *P. xerophyton* Schltr. ex R.Knuth, MSUN 636, South Afr., Nothern Cape, Numiesberge, KF696433, KF696527. *P. zonale* (L.) L'Hér., MSUN 517, South Afr., Western Cape, Montagu, KF696476, KF696548.

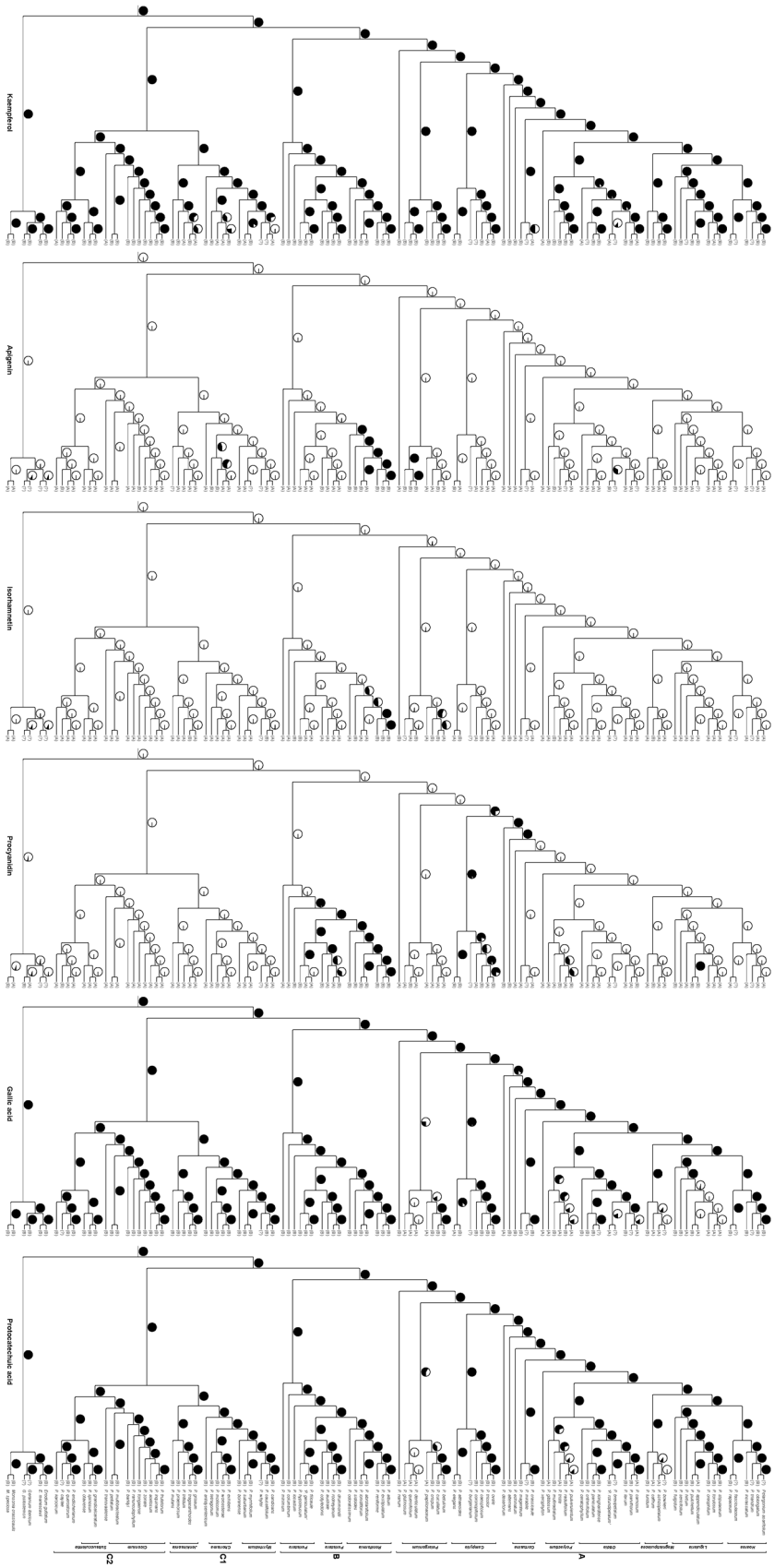
Appendix II. Consensus tree of maximum parsimony analyses including simple indel coding of the *atp*B-*rbc*L spacer region. Bootstrap values are given above branches, including indels (left) and without simple indel coding (right). Bremer support values from analysis including indels below branches. Denotations on the right: sectional names (bold) and most current sectional assignment of single species (not bold). Asterisks behind species names: only informally assigned to the respective section.



Appendix III. Tree from the maximum likelihood analyses using the *atp*B-*rbc*L and spacer region. Bootstrap values are shown above branches and posterior probabilities from the Bayesian analysis of the same data below branches. Phylogram showing relative branch lengths from ML analysis with outgroups pruned from tree. Clade denotations on the right: sections and subgenera (vertical). Asterisks behind sectional names: delimitation, suggested here, deviates from most current circumscription of section.



Appendix IV. Ancestral states of selected phenolic constituents of *Pelargonium* leaves (kaempherol, apigenin, isorhamnetin, procyanidin, gallic and protocatechuic acids) based on the Bayesian consensus topology for both intergenic spacer region (*atp*B-*rbc*L, *trn*L-F). Pie charts on nodes show state probabilities. Character states: black = present (B), white = absent (A) and question mark in terminals = missing data.



Appendix V. Morphological characteristics of the four subgenera in *Pelargonium*, with emphasis on predominant states. Denotations of major clades in brackets. Noticeable exceptions on sectional level and unique characteristics found in selected species are listed as well.

	Subgenus ***Pelargonium*** **(A)**	Subgenus ***Parvulipetala*** **(B)**	Subgenus ***Magnipetala*** **(C1)**	Subgenus ***Paucisignata*** **(C2)**
Life form	Abundantly geophytes and many virtually deciduous stem succulent subshrubs. Less frequently evergreen shrubs and subshrubs (sectt. *Pelargonium*, *Campylia*). Few annual herbs (*P. nanum*, *P. althaeoides*)	Perennial Herbs, some annuals (sect. *Peristera*), rarely subshrubs (sect. Reniformia) One true stem succulent (*P. cotyledonis*), two geophytes (sect. *Peristera*: Australian species)	Subshrubs, some short lived, few annual herbs (in sect. *Jenkinsonia*). Two stem succulents (*P. boranense, P. tetragonum*).	Shrubs, some subshrubs and herbs. A few geophytic species, one true stem succulent (*P. spinosum*)
Stem	Stem missing or shortened (geophytes, tuber formation). If present, often subsucculent or succulent. In shrubs woody.	Stem normally herbaceous, in parts becoming woody with age.	Stem thin, herbaceous; rarely subsucculent or succulent.	Stem fleshy to subsucculent or herbaceous, becoming woody with age.
Roots, incl. tubers	Tubers mostly with layers of scaling periderm (sect. *Hoarea*). Some with large, rough skinned tubers, without periderms (sect, *Polyactium*, *Magnistipulacea*)	Rarely tuberous or moliniform thickened root system, never with periderms	Rarely small tubers or thickened rootstock or swollen woody base of stem	Infrequently small tubers or moniliform, thickened underground root system
Leaves	Often divided and pinnately veined	Entire, abundantly palmately lobed	Pinnately divided	Entire, sometimes palmatilobed to palmatifid
Hypanthium length	Either clearly elongated (>20 mm) or very short (<10mm)	Predominately very short (<10mm)	Short (>10mm), but often elongated. Intraspecific variable	Short (>10mm), but often elongated. Intraspecific variable
Flower size	Flower size often > 10 mm	Flower size often < 10 mm	Flower size often > 10 mm	Flower size often > 10 mm
Petal number	Five, sometimes reduced to two. In single cases four.	Five. In one single species absent.	Frequently four or four- to five petals. Sometimes five petals	Five
Petal ratio	Posterior petals mostly slightly or explicitly larger than anterior.	Petals of same size or anterior petals slightly enlarged. Less frequently posterior ones slightly larger.	Posterior petals predominantly much larger than anterior petals.	Petals usually of same size or anterior petals slightly enlarged. In Asia Minor species (*P. endlicherianum*, *P. quercetorum*): posterior petals much larger
Petal colour	Pink to purple, frequently cream-yellowish (geophytes) or white (stem succulents)	Pink to purple or white, never cream or yellowish	Predominantly white, sometimes pink-purple. Orange-red in *P. boranense*	Often pink, but no true purple. Sometimes red or white
Nectar guides	Multiform: all four main types. Central markings (geophytes, sect. *Cortusina* and *P. nanum*) or eyespots (sectt. *Pelargonium* and *Campylia*), alongside with feathery dark veins (sect. *Hoarea*) or basal markings (sectt. *Otidia*, *Campylia*)	Eyespots, especially in small flowered species often reduced. Sometimes absent.	Dark veins, normally of high contrast. Often two prominent veins, less frequently several veins or feathery veined. Sometimes basal markings (in sect. *Jenkinsonia*)	Dark veins, often faint or even lacking In three species (*P. articulatum*, *P. peltatum*, *P. spinosum*) polymorphic markings, with clear contrast

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	Subgenus ***Pelargonium*** **(A)**	Subgenus ***Parvulipetala*** **(B)**	Subgenus ***Magnipetala*** **(C1)**	Subgenus ***Paucisignata*** **(C2)**
Nectar guide distribution	Abundantly on posterior petals, but sometimes on all or only on anterior petals (xerophytes)	On posterior petals only	Usually on posterior petals	Usually on posterior petals
Fertile anthers	Mostly reduced to five (sectt. *Campylia*, *Hoarea* and *Otidia*), occasionally seven (sectt. *Ligularia*, *Magnistipulacea* and *Pelargonium*)	Multiple different reductions, from six to one (sect. *Peristera*) or seven (sect. *Reniformia*, *P. minimum*-group)	Seven, rarely five	Seven, in single cases five