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Taxonomy and phylogeny of two subgroups of *Pelargonium* section *Otidia* (Geraniaceae). 1. The *Pelargonium carnosum* complex

M. BECKER* and F. ALBERS*

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ABSTRACT

This contribution deals with the taxonomy and phylogeny of the *Pelargonium carnosum* complex, a group of closely related taxa of *Pelargonium* L'Hér. section *Otidia* (Sweet) DC. (Geraniaceae) that is distributed in the winter rainfall area of South Africa. According to molecular analyses via AFLP, *P. adriaanii* M.Becker & F.Albers, *P. carnosum* (L.) L'Hér., *P. ferulaceum* (Cav.) Willd. and *P. polycephalum* (E.Mey. ex Harv.) R.Knuth form a monophyletic clade. Although hybridization may occur between the taxa, three are assigned to specific rank. The fourth taxon, *P. ferulaceum* is recognized as a subspecies of *P. carnosum*. As is implied from the occurrence of morphological intermediates and partly from molecular evidence, hybridization does not only occur among the taxa in this complex but also involves species closely related to this group (*P. parviflorum* J.C.Wendl., *P. laxum* (Sweet) G.Don, *P. dasyphyllum* R.Knuth). For the taxa in the *P. carnosum* complex, distribution areas are delineated and diagnostic features that have until now remained obscure, are outlined.

INTRODUCTION

The genus *Pelargonium* L'Hér. comprises ± 280–290 species which are subdivided into 16 sections (Bakker *et al.* 2004). The infrageneric classification relies on molecular evidence, on differences in chromosome sizes and basic chromosome numbers, and on geographical distribution and growth forms. Within the major group characterized by small chromosomes, section *Otidia* (Sweet) DC. belongs to a subgroup showing xerophytic growth. Within this 'xerophytic clade', it is part of the so-called winter rainfall clade (Bakker *et al.* 2004). Section *Otidia* comprises 25 taxa, some of them distinctive and isolated, others closely related and hardly distinguishable.

The *Pelargonium carnosum* (L.) L'Hér. complex includes several taxa that are linked by intermediates. Morphological intermediates are usually assigned to introgression. The close relationship of these taxa was recognized early in the taxonomic history of *Pelargonium*. Harvey (1860), when describing *P. polycephalum* (E.Mey. ex Harv.) R.Knuth as *P. ferulaceum* var. *polycephalum*, stressed its strong resemblance to *P. carnosum*. Dyer (1953) reduced *P. ferulaceum* (Cav.) Willd. and *P. polycephalum* to the rank of a variety under *P. carnosum*, which can be taken as the year of inception of the *P. carnosum* complex. Becker & Albers (2005a) added *P. adriaanii* M.Becker & F.Albers, thus increasing the number of taxa in this complex to four: *P. adriaanii*, *P. carnosum*, *P. ferulaceum* and *P. polycephalum*.

Vorster (1990) placed the closely related *Pelargonium parviflorum* J.C.Wendl. in the *P. carnosum* complex as well. However, as *P. parviflorum* comprises several taxa that are characterized by a distinctive floral structure, we prefer to treat it as a separate taxon and with further taxa as a separate subgroup (*P. parviflorum* complex, Becker & Albers in press a).

A phylogenetic tree that results from extensive molecular analyses is presented. Polymorphic markers have been detected via AFLP (amplified fragment length polymorphism, Vos *et al.* 1995), a method that requires no previous knowledge of DNA sequences and provides a large amount of reliable and repeatable bands. AFLP markers are generated from the entire spectrum of genomic DNA including fast evolving regions, leading to a high resolution at the subspecies and even population level in phylogenetic analyses. We discarded sequence analyses based on nuclear ITS and plastid *trn*-LF regions, as the differences between studied taxa were too marginal.

MATERIAL AND METHODS

Plant material

Specimens of the living collection of Münster Botanical Garden (Table 1) were included in the molecular analysis. Voucher specimens were deposited in MSUN. For delimiting the distribution ranges of the taxa, 224 herbarium specimens were examined from the following herbaria: BM, BOL, K, MSUN, NBG and PRE—acronyms as in Holmgren *et al.* (1990).

DNA extraction and AFLP analysis

Genomic DNA was extracted from ± 500 mg of fresh leaf tissue per plant following the CTAB procedure described by Doyle & Doyle (1987) and modified by Bakker *et al.* (1998). AFLP (amplified fragment length polymorphism) analyses were performed using the protocol of Vos *et al.* (1995), with minor modifications (Marschalek 2003). DNA was restricted with enzymes EcoRI (rarely cutting) and MseI (frequently cutting). Single strands of EcoRI and MseI adapter were 3'-CATCTGACGCATGGTTAA-5', 5'-CTCGTAGACTGCGTACC-3' and 3'-TACTCAGGACTCAT-5', 5'-GACGATGAGTCCTGAG-3', respectively. Nine combinations of primers based on three selective bases (EcoRI-AAC, -AGG, -ATA and MseI -CAA, -CAG, -CCG, -CGA,

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* Institut für Botanik, Schlossgarten 3, D–48149 Münster, Germany. E-mail: Prof. Dr F. Albers, albersf@uni-muenster.de; Dr M. Becker, m.becker@massey.ac.nz.

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TABLE 1.—Localities, collectors' names and numbers of specimens in *Pelargonium carnosum* complex and further species of sect. *Otidia* from South Africa (RSA) and Namibia selected for AFLP analyses. Grid references given per quarter-degree square. STEU = **St**ellenbosch **U**niversity Botanical Garden

Taxon	Grid ref.	Locality	Collector	Coll. no.
Sect. *Otidia* s.l.				
P. alternans	3218 BB	Pakhuispass (RSA)	*Boucher*	*STEU 974*
P. ceratophyllum	2615 CA	Lüderitz (Namibia)	*Albers & Becker*	*4212*
P. crithmifolium	3017 AD	Wallekraal (RSA)	*Albers & Becker*	*4345*
P. dasyphyllum	2917 DB	Steinkopf (RSA)	*Albers & Becker*	*4291*
P. klinghardtense	2816 DA	Beauvallon (RSA)	*Albers & Becker*	*4249*
P. paniculatum	2816 BB	Richtersveld (RSA)	*Albers & Becker*	*4242*
P. laxum	3325 DC	Redhouse (RSA)	*Van der Walt*	*568*
***P. parviflorum* complex**				
P. parviflorum				
subsp. *karasbergense*	2718 CA	Klein Karas (Namibia)	*Albers & Becker*	*4188*
subsp. *parviflorum*	2917 BB	Steinkopf (RSA)	*Albers & Becker*	*4229*
subsp. *rotundipetalum*	3320 DC	Muiskraal (RSA)	*Albers & Meve*	*125*
subsp. *tuberculum*	2716 DA	Rosh Pinah (Namibia)	*Albers & Becker*	*4205*
P. parviflorum s.l.	3017 BB	Kamieskroon (RSA)	*Albers & Becker*	*4348*
P. brevipetalum	3320 BA	Matjiesfontein (RSA)	*Albers & Becker*	*4462*
P. carnosum × *P. parviflorum*	3218 BB	Clanwilliam (RSA)	*Albers & Becker*	*4405*
***P. carnosum* complex**				
P. adriaanii	2916 BB	Port Nolloth (RSA)	*Albers & Becker*	*4236*
	2916 BB	Port Nolloth (RSA)	*Albers & Becker*	*4237*
	2916 BB	Port Nolloth (RSA)	*Albers & Becker*	*4238*
P. carnosum subsp. *carnosum*	3217 DB	Stompneus Bay (RSA)	*Albers & Becker*	*4419*
	3318 AA	Langebaan (RSA)	*Albers & Becker*	*4430*
	3318 AC	Yzerfontein (RSA)	*Van der Walt*	*STEU 1815*
P. carnosum subsp. *ferulaceum*	3319 BB	Karoopoort (RSA)	*Albers & Becker*	*4118*
	3319 BB	Karoopoort (RSA)	*Albers & Becker*	*4120*
	3319 CB	Worcester (RSA)	*Albers & Becker*	*4435*
P. polycephalum	2917 BB	Steinkopf (RSA)	*Albers & Becker*	*4232*
	2917 BB	Steinkopf (RSA)	*Albers & Becker*	*4313*
	2917 DB	Goegap NP (RSA)	*Albers & Becker*	*4298*
Hybrid 1	3118 DA	Vredendal (RSA)	*Albers & Becker*	*4373*
	3217 DD	Paternoster (RSA)	*Albers & Becker*	*4426*
	3318 BD	Malmesbury (RSA)	*Van der Walt*	*STEU 2401*
	3320 DC	Barrydale (RSA)	*Albers & Becker*	*4444*
Hybrid 2	3118 CA	Papendorf (RSA)	*Albers & Becker*	*4389*
	3118 CC	Doringbaai (RSA)	*Albers & Becker*	*4397*

-CTA) were chosen for the second selective PCR amplification. EcoRI primer was fluorescence labeled (IRDye™ 800 infrared dye, Licor). Electrophoresis of AFLP fragments was done on 7 % (w/w) polyacrylamide gels (250 × 0.2 mm) on a one-dye model 4200 Licor DNA automatic sequencer.

Cladistic analysis

Each AFLP fragment was counted as a separate putative locus and scored as present (1) or absent (0) for each sample. Only polymorphic bands that could be read unambiguously on each gel image were used for data analysis.

Phylogenetic analyses were performed with PAUP Version 4.0b10 (Swofford 2002), using *neighbour joining* (NJ; Restriction-site distances: Upholt) and a *maximum parsimony* criterion. For the latter, starting trees were generated by stepwise addition, swapping on best tree only in case of multiple trees. One thousand random addition replicates were chosen. The heuristic search for best topologies used TBR branch swapping. Support for clades in both distance and parsimony analyses was measured using the non-parametric bootstrap method (Felsenstein 1985; 10 000 replicates).

RESULTS

The taxa in the P. carnosum *complex: etymology and taxonomic history*

The oldest mention of *Pelargonium carnosum* is found on a herbarium sheet dating back to 1724 (*BM649367*, Figure 1A). The brief diagnosis reads: '*Geranium africanum frutescens, Chelidonii folio; petalis florum angustis, albidis; carnoso caudice*'. The herbarium specimen originates from a plant that arrived at Chelsea Physic Garden in London in the same year. The collector and place of origin of this specimen are not known. A first detailed description of *P. carnosum* was provided by Dillenius in 1732, who described the species under the phrase name '*Geranium Afric. carnosum, petalis angustis albicantibus*'—a pre-Lin-

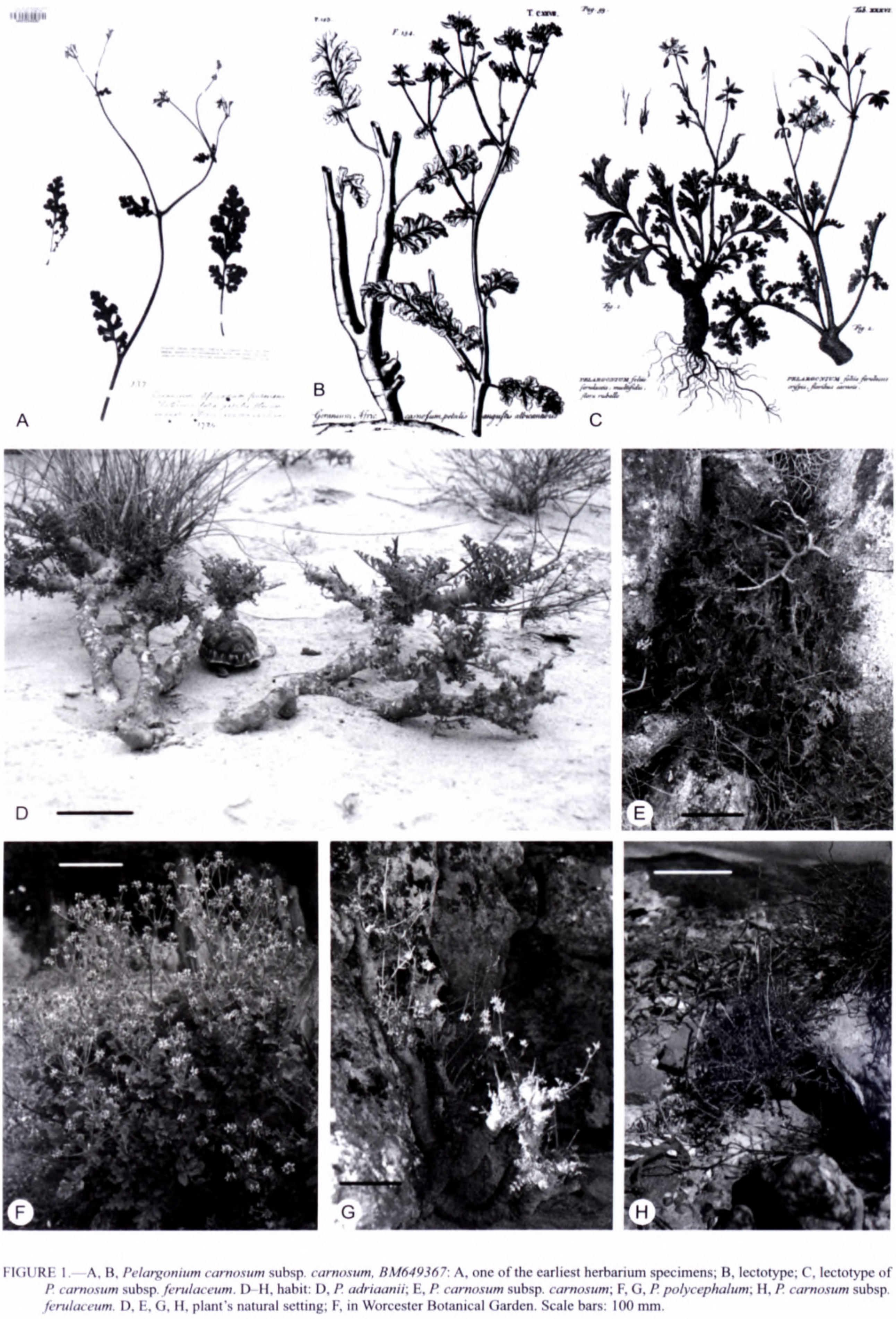

FIGURE 1.—A, B, *Pelargonium carnosum* subsp. *carnosum, BM649367*: A, one of the earliest herbarium specimens; B, lectotype; C, lectotype of *P. carnosum* subsp. *ferulaceum*. D–H, habit: D, *P. adriaanii*; E, *P. carnosum* subsp. *carnosum*; F, G, *P. polycephalum*; H, *P. carnosum* subsp. *ferulaceum*. D, E, G, H, plant's natural setting; F, in Worcester Botanical Garden. Scale bars: 100 mm.

nean name not valid according to the rules of the International Code of Botanical Nomenclature (ICBN). Although Dillenius did not give any indication as to the origin of the material examined by him, it can be assumed from the wording of the phrase name that he had indeed seen that particular herbarium specimen from 1724. In 1755 the species became the first member of (the later) section *Otidia* to be described by Linnaeus which he placed under the genus *Geranium* as *G. carnosum,* as he did not distinguish the genus *Pelargonium.* Linnaeus referred to Dillenius's illustration as the iconotype that accompanied the phrase name of *Geranium carnosum* (Figure 1B). Linnaeus's specific epithet, *carnosus*, the Latin word for fleshy or succulent, refers to the succulent stem as a presumed characteristic feature—but nonetheless fairly common within section *Otidia*—which he chose to separate *P. carnosum* from *P. gibbosum* (sect. *Polyactium*, with swollen nodes of the stem). In 1789, L'Héritier placed the species under *Pelargonium.*

The first diagnosis of *Pelargonium ferulaceum* was published by J. Burman in 1738 under the phrase name '*Pelargonium foliis ferulaceis, multifidis, flore rubello*'. The first part of the description refers to the deeply incised delicate leaves that resemble those of the genus *Ferula* (Apiaceae). The illustration by Burman is regarded as the iconotype. Burman's son (1759) was the first to adopt the Linnaean binary nomenclature and, hence, has traditionally been accepted as the author of this species name. Though he referred to his father's illustration (Figure 1C), he obviously described a member of section *Polyactium*: 'dwarf plant lacking stems, a simple stalk rising from the centre of the root-bearing long-tubed flowers as found in *Geranium triste*'. Due to this error, we propose to drop Burman filius as author of *P. ferulaceum.* Instead, Cavanilles (1787) should be credited as the author who took up a part of J. Burman's diagnosis when describing '*Geranium ferulaceum*'. Willdenow (1800) placed this species under the genus *Pelargonium.*

Pelargonium polycephalum was introduced by Meyer (1843) who referred to the numerous capitate pseudo-umbels as the character of distinction in this species (*poly* is the Greek word for many, and *cephalium* is the Greek word for head). As Meyer failed to publish a proper diagnosis, Harvey (1860) is credited as author of this species' name. A specimen collected by Drège was designated as the holotype. Harvey described the species under the name *P. ferulaceum* var. *polycephalum* with *P. carnosum* as the most closely related taxon. In 1912 Knuth raised the taxon to specific rank as *P. polycephalum.*

The last species described in this complex was *Pelargonium adriaanii* M.Becker & F.Albers which was published by the present authors in 2005 in honour of the late J.J. Adriaan van der Walt for his valuable contributions in the genus.

Key to taxa

1a Pedicel longer than hypanthium .... *P. adriaanii*
1b Pedicel shorter than hypanthium:
  2a Compact pseudo-umbel with ± 10 flowers ...... *P. polycephalum*
  2b Loose pseudo-umbel with 4–6 flowers:
    3a Leaves pinnately incised. .... *P. carnosum* subsp. *carnosum*
    3b Leaves bipinnately divided, pinnae petiolate ....
    .... *P. carnosum* subsp. *ferulaceum*

Pelargonium carnosum and *P. ferulaceum* are treated as subspecies, due to their close relationship and the frequent occurrence of hybrids (see below). With *P. carnosum* being the older name of the two, the correct names are *P. carnosum* subsp. *carnosum* and *P. carnosum* subsp. *ferulaceum* (Cav.) M.Becker & F.Albers, comb. nov. *Pelargonium adriaanii* and *P. polycephalum* are still treated as separate species.

1. **Pelargonium adriaanii** *M.Becker & F.Albers* in Botanische Jahrbücher 126,2: 153 (2005a). Type: Northern Cape, 2916 (Port Nolloth), (–BB), 17 Sept 2003, *Becker & Albers 4235* (MSUN, holo.!).

2a. **Pelargonium carnosum** (*L.*) *L'Hér.* in Aiton, Hortus kewensis 2: 421 (1789). *Geranium carnosum* L.: 20 (1755). *Otidia carnosa* (L.) Sweet: t. 98 (1822). *Geraniospermum carnosum* (L.) Kuntze: 94 (1891). Lectotype: *Geranium africanum carnosum* Dill.: 153, t. 127, fig. 154 (1732).

Pelargonium sisonifolium Baker, t. 28 (1869). Lectotype: 'Cape' [icono., Baker in Saunders, Refugium Botanicum: t. 28 (1869)].

2b. **Pelargonium carnosum** subsp. **ferulaceum** (*Cav.*) *M.Becker* & *F.Albers*, comb. nov.

Geranium ferulaceum Cav., Quarta Dissertatio botanica: 265, t. 110, fig. 2 (1787). *Pelargonium ferulaceum* (Cav.) Willd.: 687 (1800). *Otidia ferulacea* (Cav.) Eckl. & Zeyh.: 69 (1835–1837). *Geraniospermum ferulaceum* (Cav.) Kuntze: 94 (1891). Lectotype: *Pelargonium foliis ferulaceis* Burm.: 93, t. 36, fig. 1 (1738).

Pelargonium mammulosum J.C.Wendl.: 77 (1810). *Otidia burmanniana* Eckl. & Zeyh., non DC.: 69 (1835–1837). *Pelargonium burmannianum* Steud.: 284 (1841). Lectotype: 'Vorgebirge der guten Hoffnung' [icono., Wendland, Collectio plantarum 2: t. 70 (1810)].

3. **Pelargonium polycephalum** (*Harv.*) *R.Knuth ex E.Mey.* in Drège, Zwei pflanzengeographische Dokumente: 209 (1843–1844); Engler: 372 (1912). *P. ferulaceum* var. *polycephalum* Harv.: 279 (1859–1860). Type: Northern Cape, 'Kous–Silverfontein', *Drège 3244* (according to Knuth 1912), *nomen nudum* by E. Meyer: 209 (1843–1844).

Morphological characters of section Otidia

In addition to the commonly occurring succulent stems and pinnate leaves, the set of characters defining section *Otidia* also includes short-spurred flowers.

The typical auricles borne at the base of the posterior petals are restricted to this section, although similar petal structures are found in certain species of sections *Campylia*, *Hoarea*, *Ligularia* and *Pelargonium* (Struck 1997). Stamens that curl upwards at the end of the staminate phase are restricted to section *Otidia* and a couple of species in section *Pelargonium* (Struck 1997).

Pelargonium alternans J.C.Wendl. which hitherto has also been placed in section *Otidia*, differs in various characters (Becker & Albers in press b). A large genetic gap between this species and the rest of the section has been established (Bakker *et al.* 2004; Becker & Albers in press c), and *P. alternans* is excluded from the section in the strict sense (= *Otidia s.str.*) in the present account. We refer to *Otidia s.l.* in order to indicate traditional circumscription of the section, i.e. including *P. alternans*.

The taxa in the *Pelargonium carnosum* complex do not differ much from the other members of section *Otidia*. However, most taxa in the *P. carnosum* complex and the closely related *P. parviflorum* complex (Becker & Albers in press a) are distinguished by a character which is otherwise absent in the section (except in *P. alternans*): the pedicel is much shorter than in the remaining *Otidia* species. The ratio between the lengths of hypanthium and pedicel—a valuable characteristic in *Pelargonium* (Miller 1996)—varies between 2 and 10 within both complexes, but between 0.1 and 1.0 in the remaining members of *Otidia s.str.* However, *P. adriaanii* does not fit into this pattern: in this species the pedicel is much longer than the hypanthium. Therefore, no phenotypic character clearly delineates the *P. carnosum* complex. The taxa in the *P. parviflorum* complex differ from those in the *P. carnosum* complex in possessing tiny, mostly yellowish petals.

Diagnostic features in the P. carnosum *complex* (Table 2)

Pelargonium adriaanii (Figure 1D) and *P. polycephalum* (Figure 1F, G) can develop into large plants of 1 m across that possess stems of 50 mm in diameter. In *P. carnosum* subsp. *carnosum* (Figure 1E) the stems are much thinner and in subsp. *ferulaceum* (Figure 1H) they remain shorter.

In *Pelargonium adriaanii* and *P. carnosum* subsp. *carnosum* the lateral roots form series of small tubers; *P. carnosum* subsp. *ferulaceum* and *P. polycephalum* exhibit a simple root system without any thickenings.

Apart from their pinnate shape, the leaves do not share a further character. They differ in the degree of succulence and density of the indumentum (Figure 2A). In *Pelargonium carnosum* subsp. *carnosum* and *P. adriaanii*, the leaves are rather herbaceous and densely covered with partially very long hairs; in *P. carnosum* subsp. *ferulaceum* and *P. polycephalum*, the leaves are slightly succulent and covered with microscopical papillae. Conversely, Harvey in his description of *P. polycephalum*, maintained that the leaves are much more hairy in this species than in *P. carnosum s.str.*, although the reverse is correct according to our observations. Leaf shapes differ clearly in the four taxa: in *P. carnosum* subsp. *carnosum* and *P. polycephalum*, the leaves are mostly pinnately incised, but bipinnately divided in *P. carnosum* subsp. *ferulaceum* and in *P. adriaanii*. In *P. carnosum* subsp. *ferulaceum* almost all pinnae have a petiolule, but only the first pair of pinnae in the remaining three taxa have a petiolule. Petioles tend to persist in section *Otidia* and old leaf bases cover the stems as acute or blunt, 'thorny' fragments. Only in *P. carnosum* subsp. *carnosum* are the petioles usually shed with the rest of the leaves, giving the stems a smooth overall outline.

As to floral structure, the four taxa in the complex can be divided into two groups: 1, *Pelargonium adriaanii*; and 2, *P. carnosum* subsp. *carnosum*, *P. carnosum* subsp. *ferulaceum* and *P. polycephalum*. The pedicel is exceptionally long in *P. adriaanii* (Figure 2F) compared to those of all other taxa in the *P. carnosum* complex and the pseudo-umbels of the first taxon appear fairly loose. In contrast, the pseudo-umbels of *P. carnosum* subsp. *carnosum* (Figure 2B), *P. carnosum* subsp. *ferulaceum* (Figure 2C, E) and *P. polycephalum* (Figure 2G) appear rather compact due to the very short pedicels. The capitate shape of the pseudo-umbels in *P. polycephalum* results from the shortened hypanthia and a higher number of flowers per partial inflorescence. *P. carnosum* subsp. *carnosum*, *P. carnosum* subsp. *ferulaceum* and *P. polycephalum* exhibit long and narrow petals. The flowers are most commonly white in all three taxa sometimes suffused with pink and bearing dark pink markings or stripes on all five petals (Figure 2D, E). Since there is no detectable pattern in the distribution of these variations in floral pigmentation, the three taxa can be separated as a subgroup with respect to flower structure. Conversely, *P. adriaanii* exhibits the longest and broadest petals within section *Otidia* (Figure 2F). With the exception of their purple markings, the petals are pure white; no additional flower colour occurs.

A comparison of early and later states of inflorescence development reveals important distinctions (Figure 3). *Pelargonium carnosum* subsp. *carnosum* and *P. adriaanii* exhibit a loosely branched inflorescence with 4–5 nodes and each node generates a single or a branched peduncle (simplified in Figure 3). Altogether the inflorescence is composed of 6–12 pseudo-umbels with 4–6

TABLE 2.—Morphological differences in taxa of *Pelargonium carnosum* complex

	P. adriaanii	*P. carnosum*		*P. polycephalum*
		subsp. *carnosum*	subsp. *ferulaceum*	
Root swellings	+	+	-	-
Stem				
length	500–700 mm	500–700 mm	100–200 mm	500–700 mm
diameter	50 mm	30 mm	50 mm	50 mm
Leaf				
succulence	-	-	+/-	+/-
hairiness	+	+	-	-
pinnation	double	single	double	single
Pseudo-umbels per inflorescence	6–12	6–12	up to 50	up to 50
Flowers per pseudo-umbel	4–6	4–6	4–6	10–15
Pedicel length	20 mm	1–2 mm	1–2 mm	1–2 mm
Hypanthium length	5–7 mm	8–9 mm	8–9 mm	3–4 mm
Petal width	6–7 mm	3–4 mm	3–4 mm	3–4 mm

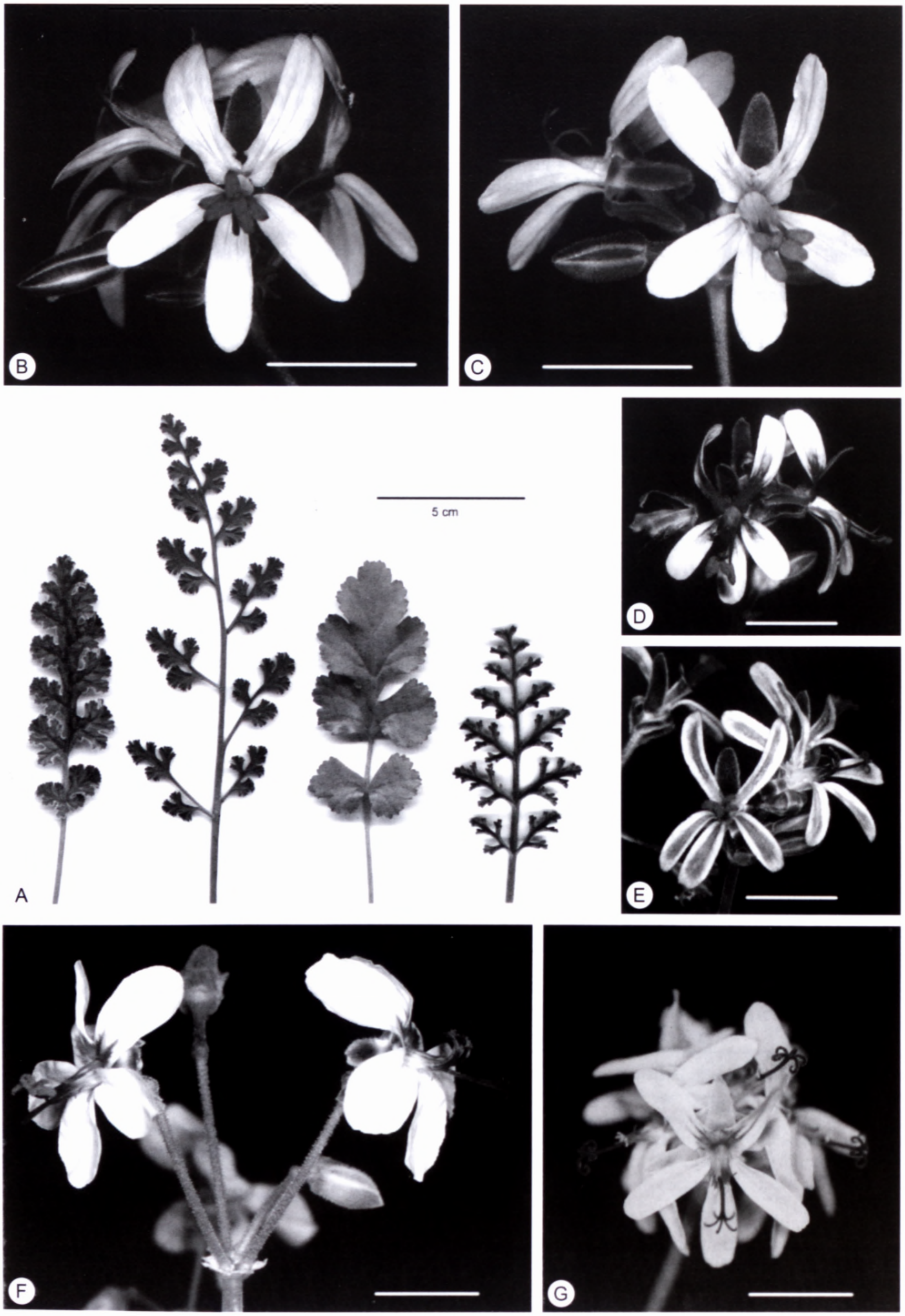

FIGURE 2.—Leaves and flowers of taxa in *Pelargonium carnosum* complex. A, leaves, from left to right: *P. carnosum* subsp. *carnosum* (*STEU1815*), *P. carnosum* subsp. *ferulaceum* (*A&B4118*), *P. polycephalum* (*A&B4232*), *P. adriaanii* (*A&B4237*). B–G, flowers: B, *P. carnosum* subsp. *carnosum* (*STEU1815*); D, *P. carnosum* subsp. *carnosum* × *P. carnosum* subsp. *ferulaceum* (*A2622*). C, E, *P. carnosum* subsp. *ferulaceum*: C, (*A&B4118*); E, (*A&B4435*). F, *P. adriaanii* (*A&B4237*); G, *P. polycephalum* (*A&B4232*). Scale bars: 10 mm.

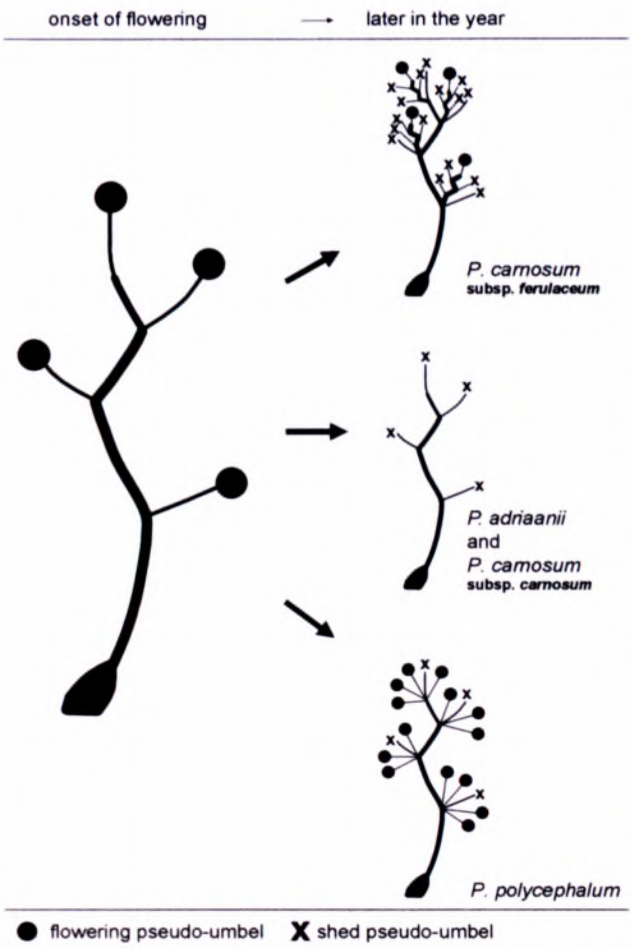

FIGURE 3.—Inflorescence branching patterns in *P. carnosum* complex. The inflorescence depicted to the left is the basal condition from which all taxa start at different times of the year. The drawings to the right (which are drawn to a smaller scale than the drawing to the left) represent three distinct inflorescence types at different times later in the year.

flowers each. The inflorescence of *P. carnosum* subsp. *ferulaceum* fits the overall pattern, but continues to produce further pseudo-umbels after the older flowers have already faded. The youngest pseudo-umbels are formed successively a few mm higher and higher; this leads to a delicately branched structure that resembles a panicle of grasses when not in flower. Individual inflorescences may last several months in *P. carnosum* subsp. *ferulaceum*. Due to its great vitality it may even produce vegetative shoots from the lower half of its inflorescence after flowering has ceased (not represented).

Pelargonium polycephalum likewise differs from *P. carnosum* subsp. *carnosum* and *P. adriaanii* by a larger number of pseudo-umbels. However, in contrast to *P. carnosum* subsp. *ferulaceum*, these do not emerge successively at the tip of the continuously growing peduncle, but develop in large numbers from already visible buds. Each of the 4 or 5 nodes of the principal axis may produce 10–15 pseudo-umbels with about 10 flowers each, which may add up to some 500 flowers per inflorescence within a relatively short period of time. Compared to *P. carnosum* subsp. *ferulaceum*, the life span of an inflorescence is short in *P. polycephalum*: the period between full flowering and fruiting and immediate withering of the inflorescence will last a few weeks only. Hence, fully developed inflorescences are easily assigned to the respective taxa, but not young inflorescences, as these all represent variations of the same basic structural type.

Distribution and habitat

The four taxa in the *Pelargonium carnosum* complex occur within clearly circumscribed distribution areas which do not overlap much (Figure 4). *P. adriaanii* from the Northern Cape is geographically well isolated: there is no record of any other member of section *Otidia* within a radius of 50 km. Only a single plant resembling *P. parviflorum* is known from Kleinsee south of Port Nolloth (*Drijfhout 2842 sub STEU2979*). With the exception of a single disputed specimen, *P. adriaanii* has always been collected near the coast at altitudes of up to 50 m (Becker & Albers 2005a). *P. adriaanii* lodges at the fringes of the Gariep Centre, which is a major centre of endemism (Van Wyk & Smith 2001) bordering on the southern Namib where the species receives less than 100 mm annual rainfall (Figure 4).

Pelargonium carnosum subsp. *carnosum* is exclusively found in the Western Cape within an area that stretches from the Atlantic coast to the chain of the Cederberg–Swartruggens–Hexrivier Mountains at altitudes of up to 200 m. Receiving an annual rainfall of more than 300 mm, this region exhibits transitions to fynbos vegetation. The most typical specimens of *P. carnosum* subsp. *carnosum* are restricted to the Sandveld right at the coast. The two remainders in the *P. carnosum* complex occur further inland, receiving 150–250 mm of annual precipitation. The area of *P. carnosum* subsp. *ferulaceum* is largely situated in the Western Cape and stretches into the Northern Cape. The range of subsp. *ferulaceum* borders on the area of *Pelargonium carnosum* subsp. *carnosum*, but instead of proceeding to the Atlantic coast, stretches in the opposite direction towards the shrubland of the Great and Little Karoo. The subspecies occurs mostly at altitudes of 600–1 000 and in the vicinity of Vanrhynsdorp, merely at 100 m. *P. polycephalum* is largely restricted to the Namaqualand Hills in the Northern Cape Province at altitudes of up to 1 200 m.

Flowering phenology

As to the onset of flowering, there is a general cline in section *Otidia* running from north to south: taxa from the north (Namibia) exhibit an earlier blooming than their relatives from the south (Western Cape). This is particularly true for *Pelargonium ceratophyllum* L'Hér., *P. klinghardtense* R.Knuth and *P. paniculatum* Jacq. which already flower in early August. Although flowering starts at the same time in *P. laxum* (Sweet) G.Don from the Eastern Cape (receiving rainfall during summer), this species is subject to different environmental and climatic conditions. In most members of the *P. carnosum* complex, flowering starts not earlier than mid-September (*P. adriaanii*, *P. carnosum* subsp. *ferulaceum*) or early October (*P. carnosum* subsp. *carnosum*). The same is true for the taxa of the closely related *P. parviflorum* complex. With the exception of subsp. *karasbergense* (Becker & Albers in press a) which, similar to *P. laxum* occurs in

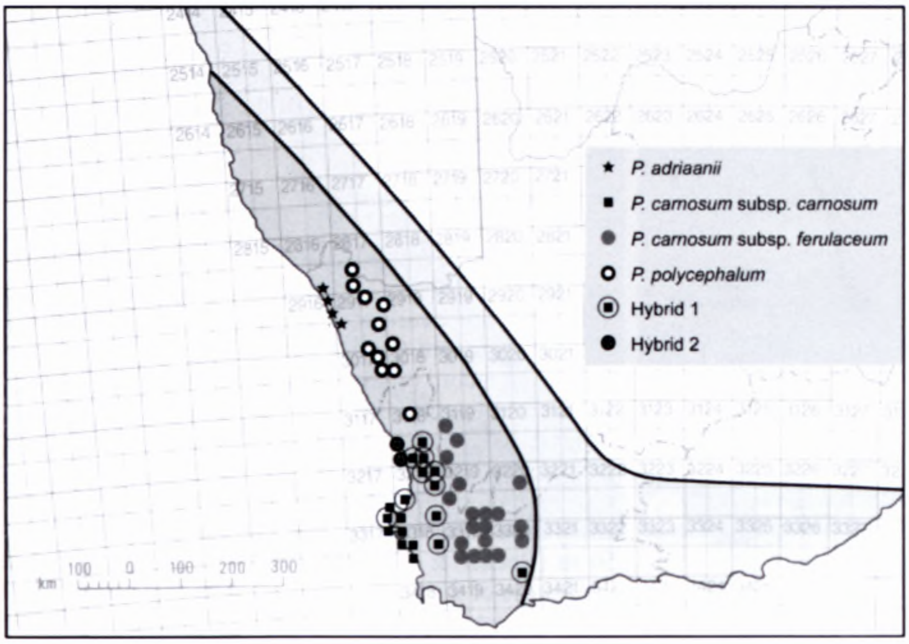

FIGURE 4.—Distribution of taxa in *P. carnosum* complex according to records from herbarium and living specimens. Dark grey shading = winter rainfall area; light grey shading = annual rainfall area.

the transitional zone between the winter and summer rainfall areas, flowering commences only from mid-September onwards in all subgroups of the latter complex—even including the taxa from Namibia. As was deduced from the collecting dates of dried specimens bearing flowers, *P. polycephalum* from the Namaqualand Rocky Hills is the only taxon in both complexes exhibiting a relatively early blooming. This species flowers from August to September. Hence, there is little overlap in the timing of the reproductive seasons of *P. polycephalum* and the remaining species in the *P. carnosum* complex and in the *P. parviflorum* complex. Onset and end of the flowering period may vary according to rainfall patterns; nevertheless, the sequence of 'early' and 'late' blooming taxa is maintained.

Morphological evidence of hybridization

Although the four taxa in the *Pelargonium carnosum* complex are clearly distinguished, the existence of intermediates is unmistakable. Interbreeding has repeatedly been recorded from areas where different taxa in the *P. carnosum* complex occur in close proximity.

Hybrids within the complex

The region west of the Cederberg (Vredendal–Clanwilliam) harbours hybrids between the two subspecies of *Pelargonium carnosum* which exhibit leaf features of both parental taxa (*A&B4373*). Plants from this area show the same type of indumentum as found in typical *P. carnosum* and pinnae as stalked and narrow as found in *P. carnosum* subsp. *ferulaceum*.

Plants from the coastal region near Papendorp and Doringbaai mostly exhibit pink petals (*A&B4389*, *A&B4397*). In this region, not less than three genotypes appear to intergrade, as the specific characters of all three taxa were found to combine in plants growing next to each other. These plants develop leaves as observed in *P. carnosum* subsp. *carnosum*, the distinct inflorescence of *P. polycephalum* and the long pedicels of *P. adriaanii*.

Hybridridzation involving taxa outside this complex

The closest relatives of the *Pelargonium carnosum* complex are found in the *P. parviflorum* complex. Structural intermediates occur in several regions which point to large-scale interbreeding between both complexes. The resulting cluster of hybrids are discussed elsewhere in more detail (Becker & Albers in press a) and are only briefly characterized in the present account. In this cluster of hybrids, floral structure is conspicuously varied exhibiting a range of petal colours and shapes.

The closest relatives of both complexes combined are *Pelargonium laxum* (Sweet) G.Don and *P. dasyphyllum* R.Knuth (Becker *et al.* 2008). Both species are clearly distinguished on account of a set of structural characteristics. *P. laxum* possesses posterior petals which are sharply reflexed from bases at nearly 180° and unusually long stamens. *P. dasyphyllum* exhibits a cushion-shaped growth habit and relatively small leaves. In both species, plants recorded from the geographical fringes also exhibit characters of the *P. carnosum* complex.

One record pertains to a plant of remote resemblance to *Pelargonium dasyphyllum* (*A&B4286*) which we tracked down in the midst of a population of typical members of that species. In this plant, the stem is unusually thickened and leaves are exceedingly large. The wide range of different petal shapes of individual specimens of *P. dasyphyllum* even includes the petal structure found in typical *P. carnosum* flowers.

Molecular analysis (AFLP)

The phylogram (Figure 5) results from a *neighbour joining* (NJ) analysis using 416 AFLP markers. Non-parametric bootstrap values (BVs) are indicated. A *maximum parsimony* analysis was also undertaken (not shown) employing 193 informative characters. The major groupings of taxa were congruent between both analyses.

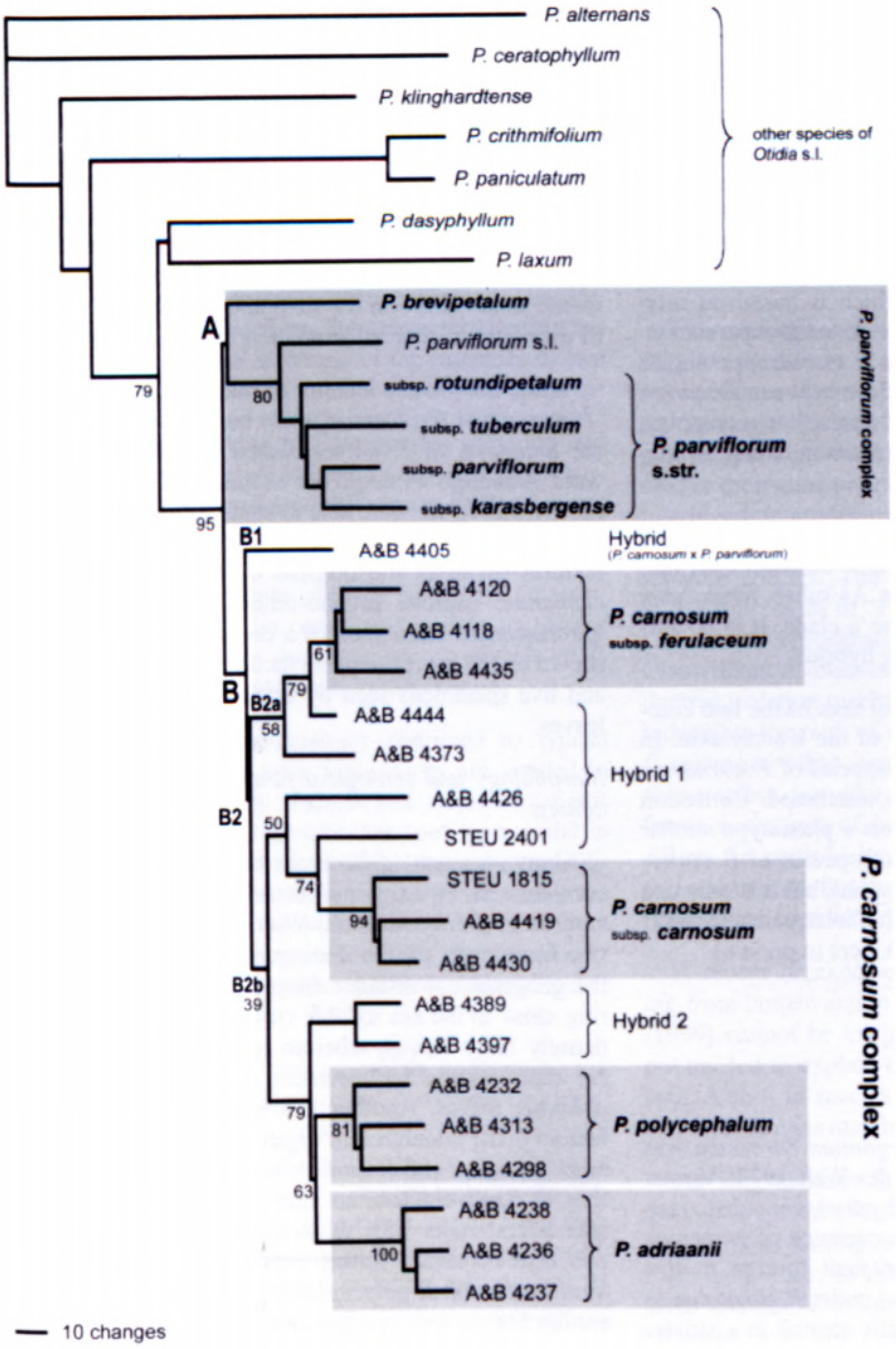

FIGURE 5.—Cladistic analysis of taxa in *P. carnosum* complex based on AFLP patterns; phylogenetic tree reconstructed by *neighbour joining* analysis using 416 AFLP markers. Bootstrap values derived from a *maximum parsimony* analysis employing 193 informative characters are indicated for clades that are congruent to the strict consensus tree. Collections that were unequivocally grouped under defined phenotypes of the complex are highlighted with dark grey shading.

There are three questions with regard to the *Pelargonium carnosum* complex: 1, is this complex a monophyletic group?; 2, are the distinct phenotypes reflected in distinct genotypes?; and 3, can the presumed existence of structural intermediates be verified?

Comparison with other members of section *Otidia s.l.* (*P. alternans*, *P. ceratophyllum*, *P. crithmifolium* Sm., *P. dasyphyllum*, *P. klinghardtense*, *P. laxum* and *P. paniculatum*) yields indications as to the monophyly of the complex. The study also involved the subspecies of the closely related *P. parviflorum* complex (Becker & Albers 2005b, in press a).

In the cladogram (Figure 5) the four taxa of the *Pelargonium carnosum* complex emerge as a single monophyletic group (clade B) with the *P. parviflorum* complex (clade A) as sister group. The clade that comprises clade A and clade B is well supported by a BV of 95. With less good support (BV 79), *P. dasyphyllum* and *P. laxum* share a clade with the group that comprises clades A and B. Despite the many morphological signs of interbreeding between the two complexes, the typical phenotypes of *P. adriaanii*, *P. polycephalum* and subspecies of *P. carnosum* emerge as monophyletic groups (highlighted in dark grey in Figure 5). After excluding the samples of the supposed hybrids from the analysis, BVs rise to 95–100 in support of these groups (not represented in Figure 5). The cladogram seems to corroborate the presumed interbreeding processes among several taxa in the *P. carnosum* complex.

AFLP data are also consistent with the notion of phenotypic intergrades among the two subspecies of *Pelargonium carnosum* (Hybrid 1: *A&B4444*, *A&B4373*, *A&B4426*, *STEU2401*) and among *P. carnosum* subsp. *car-*

nosum/*P. polycephalum*/*P. adriaanii* (Hybrid 2: *A&B4389*, *A&B4397*). However, possible interbreeding processes also involve taxa in the *P. parviflorum* complex.

In terms of the grouping of taxa, one would expect both subspecies of *Pelargonium carnosum* to share one clade. However, subsp. *ferulaceum* appears in the cladogram as a sister group to clade B2b, which contains not only subsp. *carnosum* but also *P. polycephalum* and *P. adriaanii*. This may be seen as a conflict of molecular data and proposed taxonomy, which is based on morphology. On the other hand, this sister group relationship to the remaining taxa of the *P. carnosum* complex might reflect the ongoing gene flow between *P. carnosum* subsp. *ferulaceum* and the *P. parviflorum* complex, which has been predicted after evaluation of morphological traits.

Hybrid 1 comprises four plants in the cladogram that are supposed to result from gene flow between both subspecies of *Pelargonium carnosum*. As subsp. *ferulaceum* and subsp. *carnosum* do not share a clade, it is no surprise that the same is true for their hybrids.

The distribution areas of several taxa of the two complexes meet in the southern part of the Knersvlakte. In this area particularly, the two subspecies of *P. carnosum* and *P. parviflorum s.l.* appear to interbreed. Collection *A&B4405* from Clanwilliam shows a phenotype similar to the intermediates of the two subspecies of *P. carnosum* (*A&B4373*, Vredendal population), but it is only one selected from an array of plants that intergrades to the *P. parviflorum* complex (Becker & Albers in press a).

DISCUSSION

Original descriptions

The distribution area of *Pelargonium carnosum* was assumed to be fairly large (Van der Walt 1977; Vorster 1990), since the delineation of *P. carnosum* subsp. *carnosum* was blurred, due to the occurrence of numerous intermediates. Furthermore, even taxa foreign to this complex were uncritically grouped under *P. carnosum* as well. However, when taxonomically treated in a stricter sense, *P. carnosum* is actually restricted to a comparatively small geographical area (Figure 4). This taxonomical concept is in line with Dillenius's original description of 1732 and the available herbarium records dating back to the first half of the 18th century both with respect to the morphological characteristics as well as to their geographical distribution.

With regard to the circumscription of *Pelargonium carnosum* subsp. *ferulaceum*, contradictions in the earlier descriptions (Burman f. 1759; Cavanilles 1787; Linnaeus 1826) led to a similar state of taxonomic limbo. This becomes obvious when comparing leaf characters given for '*P. ferulaceum*' and '*P. carnosum*', respectively (degree of division or separation of the leaf blade, degree of hairiness and succulence). Burman's iconotype of *P. ferulaceum* contains two variants of the same taxon which differ in leaf shape and (according to the diagnosis) in petal colour. The significance and reliability of this information can be questioned in view of Burman's erroneous representation of the number of petals: the author believed both of his specimens to carry a single posterior petal and three or four anterior petals, which is not found in the genus *Pelargonium*.

So it happens that the view adhered to in the present account of '*Pelargonium ferulaceum*' not being synonymous to '*P. carnosum*' is based to a lesser degree on the original description (with the exception of leaf morphology) than on the extensive study of herbarium specimens, observations in the field and a molecular analysis of populations sampled from their natural habitats.

While the precise identity of the specimens on which '*Pelargonium ferulaceum*' were based remains obscure, the diagnosis of *P. polycephalum* is fairly straightforward. Although we could not examine the holotype itself (*Drège 3244*), we were able to study a comparable specimen (*Drège 1033*) which clearly showed the diagnostic features given in the original description for *P. polycephalum*: capitate pseudo-umbels and a panicle-like inflorescence. The notion of a conspicuous indumentum shown on the leaves remains incomprehensible. All dried and live specimens seen by us showed almost glabrous leaves.

Morphology and ecological function in a geographical context

Many structural differences between the taxa in the complex can be explained as adaptations to prevailing environmental conditions. With regard to leaf shape, two basic traits can be distinguished which correlate to the geographical distance from the coast. Plants occurring close to the sea exhibit virtually non-succulent and densely hairy leaves, whereas taxa from further inland are characterized by succulent and (to the naked eye) glabrous leaves. Another character shaped by habitat factors is the underground organs of the plants. *Pelargonium adriaanii* and *P. carnosum* subsp. *carnosum* occurring in Sandveld habitats near the Atlantic coast possess lateral roots with thickened sections, whereas the two taxa occurring further inland, *P. carnosum* subsp. *ferulaceum* and *P. polycephalum*, mostly on rugged soil, exhibit fibrous root systems lacking tubers.

Since the taxa in the *Pelargonium carnosum* complex are adapted to different climatic, edaphic and topographical factors and are associated with certain habitats, one could view them as mere ecotypes of a single taxon. However, this view is contradicted by the observation that *P. adriaanii* and *P. polycephalum* maintain their typical growth habit even under cultivation, and do not seem to hybridize on a large scale, which speaks in favour of treating them as separate species. While intermediates between *P. adriaanii*, *P. polycephalum* and *P. carnosum* were rarely recorded, the situation is different in '*P. carnosum*' and '*P. ferulaceum*'. In view of their extremely different habitats (Sandveld and Little Karoo) on the one hand and their relatively subtle structural differences on the other hand, it seems appropriate to treat them as subspecies. This view is supported by the occurrence of a range of phenotypic intermediates which is correlated to the distance from the sea and the immediate degree of aridity, respectively.

Molecular analysis and its taxonomic application

The results of the molecular analyses (AFLP) are mostly consistent with the hypotheses based on morphological observations. The four taxa in the *Pelargonium carnosum* complex emerge as a monophyletic group within section *Otidia* (Figure 5). *P. carnosum* subsp. *carnosum* and *P. carnosum* subsp. *ferulaceum* were treated as a single taxon by many authors (Van der Walt 1977; Vorster 1990), since neither their geographical range nor their morphological features were sufficiently known. Our molecular study confirms their close relationship but also provides evidence in favour of the existence of two distinct genotypes.

The close relationship of *Pelargonium adriaanii* and *P. polycephalum* as revealed by the AFLP analysis is surprising as there are profound differences in floral structure between *P. adriaanii* and *P. polycephalum*. Preceding the description of *P. adriaanii*, a short pedicel was among the diagnostic features given for the circumscription of the complex. The constricted pseudo-umbels of *P. polycephalum* versus the loose pseudo-umbels of *P. adriaanii* represent the extremes in this feature.

If the analysis is exclusively restricted to typical samples in the various taxa, high values are yielded in the *maximum parsimony* analysis and increased lengths of branches in the phylogenetic tree (not represented in Figure 5). The inclusion of all morphological intermediates demonstrates that interbreeding is the rule within the *Pelargonium carnosum* complex on the one hand (Figure 5) and among the *P. carnosum* complex and the closely related *P. parviflorum* complex on the other hand (Becker & Albers in press a).

Finally, the question arises: which taxonomic rank is appropriate in the *Pelargonium carnosum* complex? Following the biological species concept (Dobzhansky 1937), a species is a reproductive group; interbreeding among species is prevented by various isolation mechanisms. These include, in simple terms, mechanical, temporal, habitat-related and genetic barriers to interbreeding (Avise 2004). Mechanical isolating mechanisms, as brought about in the flower of different subgroups of *Pelargonium alternans* (Becker & Albers in press b), are absent in the *P. carnosum* complex. Despite differences in petal size and in lengths of pedicels, the taxa show basically the same floral structure.

In contrast, a seasonal isolation resulting from the development of different flowering periods is found in *Pelargonium polycephalum*. Nevertheless, a slight overlap of this species' reproductive season with that of *P. carnosum* subsp. *carnosum* results in the occurrence of hybrids in the region of Papendorp–Doringbaai (3118 CA and CC). Interbreeding between *P. polycephalum* and the cluster of hybrids in the *P. parviflorum* complex could also be expected due to their generally sympatric distribution and insufficiently separated flowering seasons. However, the occurrence of rudimentary and, consequently, sterile anthers in many '*P. polycephalum*' plants speak against consecutive interbreeding among *P. polycephalum* and *P. parviflorum* beyond the F1 generation (Becker & Albers in press a).

A habitat-related or geographical isolation is particularly found in *Pelargonium adriaanii*. While the distribution areas of the remainders in the complex border on each other, the range of *P. adriaanii* is situated fairly isolated in the region around Port Nolloth—as far as this can be assessed in view of the fact that we were unable to enter the local diamond mining area. From rare occurrences of *P. adriaanii*-like features near Papendorp, the existence of a gene substitution along the stretch of the Sandveld is presumed.

Intermediates between *Pelargonium carnosum* and *P. polycephalum* or *P. adriaanii* are on record, but such intermediates occur markedly less often than intermediates among the subspecies of *P. carnosum*. Since numerous morphological characteristics support the distinctness of their gene pools and as there are no indications of interbreeding processes going beyond the F1 generation, *P. polycephalum* and *P. adriaanii* continue to qualify as separate species. The position is completely different in the subspecies of '*P. carnosum*' and '*P. ferulaceum*'. Large-scale hybridization as in the region of Vredendal/Clanwilliam demonstrate the absence of effective reproductive isolation mechanisms; *P. ferulaceum* is therefore reduced to the rank of subspecies. There is evidence that *P. carnosum* subsp. *ferulaceum* is connected to *P. parviflorum* subsp. *parviflorum* via a full range of intergrading forms in the area of geographical overlap. In Becker & Albers (in press a) we will provide material that nonetheless supports the treatment of *P. parviflorum* and near related taxa as a distinct complex.

A recent breakdown of reproductive barriers resulting from human action as has been presumed by Vorster (1990) cannot be excluded, but such an assumption is not needed to explain the large number of interbreeding taxa. A shift in species distribution ranges due to recent climatic changes may have played a role.

As long as there is no artificial transport of propagules, the spread of settlements, agriculture, overgrazing and diamond mining could also isolate small populations from each other, as this would render large intermittent areas unsuitable to support the natural plant life. Nevertheless, man will hardly contribute to increase biotic diversity but rather destroy genetic diversity of the local flora as well as its natural habitats. *Pelargonium adriaanii* is currently threatened with extinction unless the diamond companies denounce their rights to fully exploit the diamond fields within the species' range.

The massive impact of human activities on the vegetation within the Cape floristic region is uncontested. Today the species-rich flora and fauna is protected within an increasing number of national parks and nature reserves. However, the Cape floristic region stands out in its wealth of endemics which often show a very localized distribution outside of protective areas. In order to protect even this species from extinction, centres of diversity have to be identified and plant diversity has to be put on record through taxonomic contributions. A further article on *Pelargonium* sect. *Otidia* will elucidate the unexpected radiation within the *P. parviflorum* complex, which hitherto has been treated as a single taxon.

SPECIMENS EXAMINED

Acocks 14847 (2b) K, PRE. *Albers 2262, 2492* (2a) MSUN; *4174, 4175, 4176* (2b) MSUN. *Albers & Becker 4235, 4236* (1) MSUN; *4184, 4185, 4186, 4382, 4383, 4384, 4385, 4410, 4411, 4412, 4413, 4414* (hybr. 1) MSUN; *4388, 4390, 4392, 4393, 4395, 4416, 4420, 4421, 4422, 4423, 4427, 4428, 4430, 4431, 4432* (2a) MSUN; *4461* (2b) MSUN; *4232, 4301, 4302, 4318, 4319, 4396, 4398* (3) MSUN. *Albers, Becker & Strauch 4083, 4091, 4095, 4112, 4116, 4117, 4118, 4119, 4120, 4121, 4122, 4123* (2b) MSUN; *4081, 4084* (3) MSUN.

Bark s.n. (2a) K 74365. *Bayer 1651* (3) NBG. *Bolus 6531* (1) K, PRE; *s.n.* (2a) *BOL107101, K74361*; *13047* (2b) PRE; *446 = Herb. Bolus 6531* (3) BM, BOL, K. *Boucher 2972* (2a) NBG; *2871* (2b) NBG, PRE. *Bremer 363* (2a) PRE. *Bultro 123* (hybr. 1) K. *Chelsea Phys. Gdns s.n.* (2a) *BM649367, 649368.*

Compton 8515 (2b) NBG; *6838, 17303* (3) NBG.

Dobay 59/75, 70/75, 79/75 (2b) NBG. *Drake s.n.* (2a) PRE 56350. *Drège 7481* (2a) PRE; *01033* (3) PRE. *Dreyer 39* (1) PRE. *Drijfhout 1301* (2b) NBG, *2702* (2b) PRE.

Esterhuysen 1806 (2b) BOL; *22851* (2b) BOL, NBG; *s.n.* (2b) BOL 107074; *23593* (3) BOL. *Euthen 2550* (hybr. 1) NBG.

Fischer 30 (2b) PRE.

Germishuizen 4811, 5311 (1) PRE. *Gibby & Crompton 19* (hybr. 1) BM. *Goldblatt 2395* (3) M, NBG, PRE.

Haftröm & Acocks 1986 (hybr. 1) BOL. *Hall s.n. sub NBG. 98/68* (2b) NBG; *3475* (hybr. 2) NBG, PRE; *5260* (hybr. 2) NBG, PRE. *Hardy 241* (2b) PRE. *Hattingh 572/68* (hybr. 1) NBG. *Herb. Regium Monacense s.n.* (2a) M 36641, 36642, M 36643, 36644, 36645, 36646, 36647. *Herre 2892, 7503* (2b) BOL; *2988* (3) BOL, K. *Hugo s.n.* (1) NBG 177505, PRE 650792.

Leighton 1243 (3) BOL. *Leipoldt s.n. sub N.B.G. 1419/25* (2a) BOL; *19396* (2b) BOL; *3795* (3) BOL. *Leistner 707* (2b) PRE; *2553* (3) K. *Liede & Meve 619* (2b) MSUN.

Maguire 986 (3) NBG. *Marloth 4026* (2a) PRE; *s.n.* (2a) PRE 56347; *8213* (2b) PRE; *12261* (3) BOL, NBG, PRE. *Morris 5598* (3) K.

O'Call. & Steensma 1689 (2a) NBG. *O'Callaghan 650* (hybr. 2) NBG. *Odensen 1480* (hybr. 1) BOL.

Pearson 5301 (2b) K; *6487* (3) BM, K. *Pienaar 1156* (1) PRE. *Pillans 5626* (1) BOL, K; *6631, 6981* (2a) BOL.

Rechinger A3231 (hybr. 2) M.

Salter 1718 (2a) BM; *6465* (2a) BOL. *Schlechter s.n.* (1) NBG 177507; *1007* (3) PRE; *8199* (3) BM, K; *s.coll. s.n.* (2a) *BM649375, 649379. Scully 196* (3) BOL. *Stell. Univ. Gdns 2996* (2b) BOL. *Stokoe 9541* (2a) PRE.

Taylor 12359 (hybr. 1) NBG; *7542* (2b) NBG.

Van der Walt 763 (hybr. 1) MSUN, PRE; *918* (2a) MSUN; *532* (2b) PRE; *1201* (2b) MSUN; *s.n.* (2b) *PRE572097. Van der Walt & Vorster 1034* (hybr. 1) PRE. *Van Jaarsveld s.n.* (2b) *NBG114903*; *5704* (hybr. 2) NBG. *Van Niekerk s.n.* (2b) *BOL107029. Vorster 2399, 2404* (2b) PRE.

Wagener 30 (2b) NBG. *Ward 32, s.n. sub STEU3853* (2a) MSUN. *Wilman 2316* (1) BOL. *Wisura 584* (1) NBG; *268* (hybr. 1) NBG; *374, 1708* (2a) NBG; *2105* (2b) NBG.

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REFERENCES

AITON, W. 1789. *Hortus kewensis* 1, vol. 2: 421. Nicol, London.

AVISE, J.C. 2004. *Molecular markers, natural history, and evolution* 2. Sinauer Associates, Sunderland, Massachusetts.

BAKER, J.G. 1869. In W.W. Saunders, *Refugium botanicum* 1: t. 28. London.

BAKKER, F.T., CULHAM, A., HETTIARACHI, P., TOULOUMENIDOU, T. & GIBBY, M. 2004. Phylogeny of *Pelargonium* (Geraniaceae) based on DNA sequences from three genomes. *Taxon* 53: 17–28.

BAKKER, F.T., HELLBRÜGGE, D., CULHAM, A. & GIBBY, M. 1998. Phylogenetic relationships within *Pelargonium* section *Peristera* (Geraniaceae) inferred from nrDNA and cpDNA sequence comparisons. *Plant Systematics and Evolution* 211: 273–287.

BECKER, M. & ALBERS, F. 2005a. *Pelargonium adriaanii* (Geraniaceae), a new species from the Northern Cape Province, South Africa. *Botanische Jahrbücher* 126: 153–161.

BECKER, M. & ALBERS, F. 2005b. Was ist *Pelargonium parviflorum*? *Avonia* 23,2: 31–39.

BECKER, M., SCHÄPER, K. & ALBERS, F. 2008. Description of *Pelargonium keeromsbergense* and two subspecies of *Pelargonium laxum* of section *Otidia* (Geraniaceae). *Schumannia* 5 : 181-190.

BECKER, M. & ALBERS, F. in press a. Taxonomy and phylogeny of two subgroups of *Pelargonium* section *Otidia* (Geraniaceae). 2. The *Pelargonium parviflorum* complex. *Bothalia.*

BECKER, M. & ALBERS, F. in press b. Pollinator shift and speciation in *Pelargonium alternans* (Geraniaceae). *Biodiversity & Ecology.*

BECKER, M. & ALBERS, F. in press c. Phylogeny and speciation in succulent Geraniaceae (Geraniales). *Biodiversity & Ecology.*

BURMAN, J. 1738. *Rariorum Africanarum plantarum*: 93. Boussière, Amsterdam.

BURMAN, N.L. 1759. *Specimen botanicum de Geraniis*: 40. Haak, Leiden.

CAVANILLES, A.J. 1787. *Quarta dissertatio botanica*: 265–266, t. 99, 110. Didot, Paris.

DILLENIUS, J.J. 1732. *Hortus elthamensis*. London.

DOBZHANSKY, T. 1937. *Genetics and the origin of species*. Columbia University Press, New York.

DOYLE, J.J. & DOYLE, J.L. 1987. A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11–15.

DYER, R.A. 1953. *Pelargonium carnosum. The Flowering Plants of Africa* 29: t. 1145.

ECKLON, C.F. & ZEYHER, C. 1835–1837. *Enumeratio plantarum Africae australis extratropicae* 1–3: 68, 69. Hamburg.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.

HARVEY, W.H. 1859–1860. In W.H. Harvey & O.W. Sonder, *Flora capensis*: 279. Hodges, Smith, Dublin.

L'HÉRITIER DE BRUTELLE, C.L. 1789. In W. Aiton, *Hortus kewensis* 1, vol. 2: 421. Nicol, London.

HOLMGREN, P.K., HOLMGREN, N.H. & BARTLETT, L.C. 1990. Index herbariorum, edn 8. *Regnum Vegetabile* 120. New York.

KNUTH, R. 1912. Geraniaceae. In A. Engler, *Das Pflanzenreich*, vol. 4. 129: 369–372, 587. Engelmann, Leipzig.

KUNTZE, O. 1891. *Revisio generum plantarum*: 94. Felix, Leipzig.

LINNAEUS, C. 1755. *Centuria I. plantarum*: 20. Uppsala.

LINNAEUS, C. 1826. *Systema vegetabilium* 16: 63. Göttingen.

MARSCHALEK, R. 2003. *Marker Assisted Selection for the development of intervarietal substitution lines in rapeseed* (Brassica napus *L.*) *and the estimation of QTL effects for glucosinolate content*. Ph.D. thesis, Georg-August-Universität, Göttingen.

MEYER, E.H.F. 1843–1844. In J.F. Drège, *Zwei pflanzengeographische Dokumente*: 209.

MILLER, D. 1996. *Pelargoniums—a gardener's guide to the species and their cultivars and hybrids*. Batsford, London.

STRUCK, M. 1997. Floral divergence and convergence in the genus *Pelargonium* (Geraniaceae) in southern Africa: ecological and evolutionary considerations. *Plant Systematics and Evolution* 208: 71–97.

SWEET, R. 1820–1822. *Geraniaceae. The natural order of Gerania* 1: t. 98. London.

SWOFFORD, D.L. 2002. PAUP: *Phylogenetic Analysis Using Parsimony and other methods, Version 4.0 beta 10 Version.* Computer program distributed by the Laboratory of Molecular Systematics, Smithsonian Institution, Washington DC.

VAN DER WALT, J.J.A. 1977. *Pelargoniums of southern Africa*, vol. 1. Purnell, Cape Town.

VORSTER, P.J. 1990. Taxonomy of the genus *Pelargonium*: review of the section *Otidia*. *Proceedings of the International Geraniaceae Symposium*: 281–294. University of Stellenbosch.

VOS, P., HOGERS, R., BLEEKER, M., REIJANS, M., VANDELEE, T., HORNES, M., FRIJTERS, A., POT, J., PELEMAN, J., KUIPER, M. & ZABEAU, M. 1995. AFLP: a new technique for DNA fingerprinting. *Nucleic Acids Research* 23: 4407–4414.

WENDLAND, J.C. 1810. *Collectio plantarum tam exoticarum, quam indigenarum, cum delineatione, descriptione culturaque earum* 2: 69, 70, 77, 78. Hannover.

WILLDENOW, K.L. 1800. In C. Linné, *Species plantarum* 4: 686, 687. Nauck, Berlin.