

# Phylogeny and Historical Biogeography of Geraniaceae in Relation to Climate Changes and Pollination Ecology

Omar Fiz, Pablo Vargas, Marisa Alarcón, Carlos Aedo, José Luis García, and Juan José Aldasoro<sup>1</sup>

Real Jardín Botánico de Madrid, CSIC, Plaza de Murillo 2, 28014 Madrid, Spain

<sup>1</sup>Author for correspondence (aldasoro@ma-rjb.csic.es)

Communicating Editor: Mark P. Simmons

**Abstract**—Chloroplast (*trnL-F* and *rbcL*) sequences were used to reconstruct the phylogeny of Geraniaceae and Hypseocharitaceae. According to these data Hypseocharitaceae and Geraniaceae are monophyletic. *Pelargonium* and *Monsonia* are sisters to the largest clade of Geraniaceae, formed by *Geranium*, *Erodium* and *California*. According to molecular dating and dispersal-vicariance analysis, the split of the stem branches of Geraniaceae probably occurred during the Oligocene, in southern Africa or in southern Africa plus the Mediterranean area. However, their diversification occurred during the Miocene, coinciding with the beginning of major aridification events in their distribution areas. An ancestor of the largest clade of Geraniaceae (*Geranium*, *Erodium*, and *California*) colonised a number of habitats in the northern hemisphere and in South American mountain ranges. In summary, the evolution of the Geraniaceae is marked by the dispersal of ancestors from Southern Africa to cold, temperate and often disturbed habitats in the rest of world, where only generalist pollination and facultative autogamy could ensure sufficient seed production and survival.

**Keywords**—autocompatibility, dispersal-vicariance, drought-tolerance, molecular dating, nectaries, P/O indexes.

The Geraniaceae are included in the order Geraniales along with the families Francoaceae, Greyiaceae, Ledocarpaceae, Melianthaceae and Vivianiaceae (Soltis et al. 2000; APG II 2003). A number of molecular and morphological studies have included the monogeneric family Hypseocharitaceae within the family Geraniaceae (Boesewinkel 1988; Rama Devi 1991; Price and Palmer 1993; APG II 2003) but they are separated by some morphological features such as fruit and carpel structure (Hutchinson 1969; Slanis and Grau 2001).

Phylogenetic relationships were examined in four genera: *Geranium* (Price and Palmer 1993; Pax et al. 1997), *Pelargonium* (Bakker et al. 1998, 1999, 2000, 2004, 2005), *Erodium* (Fiz et al. 2006), and *Monsonia* (Touloumenidou et al. 2007). The phylogenetic study of Geraniaceae using *rbcL* sequences by Price and Palmer (1993) showed *Sarcocaulon* to be included in *Monsonia* (Albers 1996a, 1996b; Albers and Löbbert 1996), and *Pelargonium* to be sister to the other four genera of Geraniaceae. The inclusion of *Sarcocaulon* in *Monsonia* was also supported by data on ITS and *trnL-F* (Touloumenidou et al. 2007). According to Price and Palmer (1993), *Erodium* and *Geranium* are phylogenetically close, and *California* could be a sister group of the subclade formed by *Erodium* and *Geranium* (Aldasoro et al. 2002; Fiz et al. 2006).

Geraniaceae have a worldwide distribution but are best represented in Southern Africa. *Pelargonium* has about 270 species centered in the Cape Floristic Region, Succulent Karoo, Nama Karoo, and KwaZulu-Natal while a lower number of species are found in east Africa, Australia, Madagascar, St. Helena, and Tristan da Cunha (Bakker et al. 1998, 1999, 2005). The 39 species of *Monsonia* inhabit Africa and southwestern Asia (Kers 1968; Moffett 1979; Venter 1979, 1983; Albers 1996a, b). *Erodium* has 74 species and shows its greatest diversity in the Mediterranean area (Guittonneau 1972; El-Oqlah, 1989; Aldasoro et al. 2000), while *California* only inhabits western North America (Aldasoro et al. 2002). *Geranium* is the largest of the family, comprising about 420 species distributed all over the world (Fig. 1; Yeo 1973; Aedo et al. 1998, 2002).

Price and Palmer (1993) proposed that *Hypseocharis* could be the sister taxon to Geraniaceae. *Hypseocharis* grows in subalpine habitats of the central Andes (Boesewinkel 1988, 1997; Slanis and Grau 2001). Many members of Geraniaceae

are characteristic of the Afro-Arabian land mass (Hutchinson 1969). The differentiation of these genera can be associated with adaptation to desert and steppe environments, which became progressively more extended in Africa and Arabia during the end of the Tertiary (Kers 1968; Venter 1983). The other members of the family are characteristic of today's northern temperate continents, and occupy more mesic environments (Yeo 1984, 1990; Boesewinkel 1988).

*Monsonia*, *Geranium*, *Erodium*, and *California* bear actinomorphic flowers while *Pelargonium* flowers are generally zygomorphic. Geraniaceae flowers have one or five nectaries of four types: 1) one nectary formed by a tube in the hypanthium (most species of *Pelargonium*); 2) five nectaries forming tubes in the hypanthium (two species of *Monsonia*); 3) five nectaries at the base of the stamens, forming closed nectar pockets due to sepal enlargement (five species of *Monsonia*), and 4) five external, knob-like nectaries, located at the base of stamens (the remaining species of *Monsonia*, and all *Geranium*, *California* and *Erodium*) (Vogel 1954, 1998; Link 1990; Aldasoro et al. 2000, 2001, 2002; Touloumenidou et al. 2007). While the nectaries of types 1–3 store the nectar in a concealed tube or bag-shaped structure only accessible to long-tongued pollinators, the external knob (4) of the remaining species of *Monsonia*, *Geranium*, *California*, and *Erodium* is easily accessible to short-tongued insects.

The main pollinators and other reproductive features of the Geraniaceae are known for *Pelargonium* (Struck and Van der Walt 1996; Manning and Goldblatt 1997; Struck 1997) and *Geranium* (Green 1978; Mulcahy 1983; Philipp 1985; Hessian 1989; Dlusskii et al. 2000; Kandori 2002). Bakker et al. (2005) published an analysis of the evolution of *Pelargonium*, studying the possible relationships between pollination types and flower shape. One of the most characteristic pollination syndromes in South Africa is by long-proboscid flies visiting flowers with deep nectaries and is relatively frequent in *Pelargonium* (Goldblatt et al. 1995; Goldblatt and Manning 2006). Other *Pelargonium* syndromes are by short-proboscid flies, bees, butterflies and birds. Pollinators are less well known for *Erodium* (Simon et al. 2000) and *Monsonia*. Thus, further information is necessary to complete the knowledge about the flower-visitor relationships in Geraniaceae.

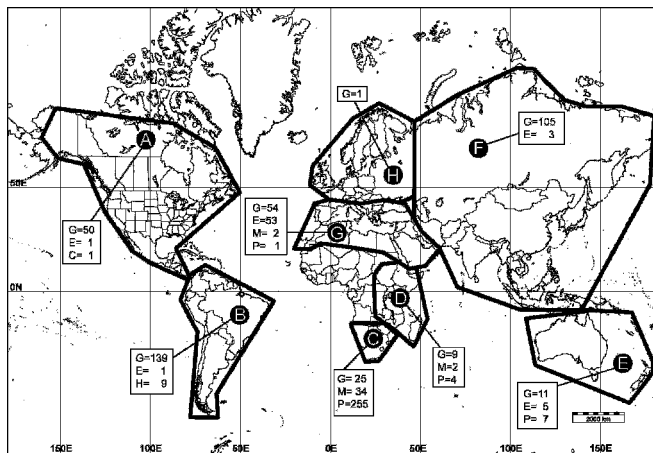


FIG. 1. Distribution map of Geraniaceae and Hypseocharitaceae in the areas used for DIVA analysis. The insets show the number of endemic species for each genus in each area. Genera: C: *California*, E: *Erodium*, G: *Geranium*, H: *Hypseocharis*, M: *Monsonia*, P: *Pelargonium*. Areas: A: North and Central America; B: South America; C: Southern Africa; D: eastern Africa and Madagascar; E: Australia, Tasmania and New Zealand; F: eastern Asia, Indochina, Indonesia and Pacific Islands; G: Mediterranean region, Arabia and Anatolia; H: Europe.

The aim of the present work was to undertake phylogenetic reconstructions of Geraniaceae and examine the ways in which the current geographic distributions came about. Compilation of data about habitats, reproductive and disperse systems and chromosome numbers would serve to analyse the role of these features in relation to main evolutionary and biogeographic events.

## MATERIALS AND METHODS

**Plant Material and Analyses of Reproductive Features**—The plant material used for DNA extractions included fresh and herbarium specimens (Appendix 1). For morphological, reproductive and pollen studies, living and herbarium specimens were examined (Appendix 2). Living specimens were obtained from seeds collected in the field, obtained from botanical gardens, or in two cases bought. Vouchers are housed at Real Jardín Botánico de Madrid (MA).

To obtain information on breeding systems, pollen-ovule (P/O) indexes were calculated for many species (Appendix 2). Geraniaceae flowers have five fertile ovules, one in each carpel. Thus, for calculating P/O indexes, the number of pollen grains per anther was counted, multiplied by the number of anthers per flower and divided by five. Buds were collected, fixed and preserved in "Kew liquid" (Fordman and Bridson, 1989). Anthers were opened under a dissecting microscope and all pollen grains were counted at 3× magnification. Two anthers from each of five flowers taken from different plants were examined for each species. For dioecious species, the mean pollen grain number of a least ten male flowers was divided by five (the number of fertile ovules per female flower). These results, plus field observations and data from the literature, were used to define the reproductive system of each species (Cruden 1977). Plants grown in the Madrid Botanical Garden (see Appendix 2) were used to test for automatic self-pollination. Twenty inflorescences belonging to three or four plants were bagged before opening, and the number of seeds produced in the mature mericarps counted. A similar number of unbagged plants were tested for free pollination.

Most data about flower visitors were compiled from literature; the rest were obtained by observation in the field (Appendix 3). Absolute number of visits per time, and the number of taxa of pollinators were recorded in a table. Species of *Geranium* and *Erodium* were usually censused three times (May, August, and September, 2004–2006, total time of censuses specified in Appendix 3). Due to the difficulty of visiting *Monsonia* habitats, they were censused only one time, but in two or three locations (December–January, 2005; Appendix 3). Insects were collected, identified and measured in the laboratory.

**PCR Amplification, Sequencing, and Sequence Analyses**—One hundred and thirty one DNA sequences were included in the analysis, of which 44 *trnL-F* and 21 *rbcl* sequences were obtained during this project

(Table 1). Two *California macrophylla* sequences plus 40 *Erodium*, 48 *Geranium*, two *Hypseocharis*, 16 *Monsonia*, 12 *Pelargonium* and 11 outgroups were included. Eighty-five taxa were included in the phylogenetic analyses of *trnL-F* (Table 1; Appendix 1; Fig. 1), two of which were outgroups (*Francoa* and *Crossosoma*). Analysis of *rbcl* sequences was performed using 46 taxa (Table 1), seven of which were outgroups (*Bersama*, *Crossosoma*, *Francoa*, *Melanthus*, *Viviania*, and *Wendtia*).

Approximately 20 mg of leaf tissue from fresh (field collected) or herbarium material were taken and the DNA extracted using the DNeasy Plant Mini Kit (QIAGEN Laboratories, Hilden, Germany). The forward primer 'e' and reverse primer 'f' were used for PCR amplification of the *trnL(UAA)-trnF(GAA)* spacer (Taberlet et al. 1991), and primers 1F, 636F, 724R and 1460R for *rbcl* sequences (Olmstead et al. 1992; Fay et al. 1998). The PCR conditions for the amplification of *trnL-F* and *rbcl* are described in Fiz et al. (2006) and Savolainen et al. (2000a), respectively. The amplified products were purified using spin filter columns (PCR Clean-up kit, MoBio Laboratories, Carlsbad, California). Cleaned products were sequenced according to Fiz et al. (2002).

Sequence data were stored in a contig file and edited using the Seqed program (Applied Biosystems, Branchburg, New Jersey). Pairwise divergence among sequences was calculated by using the NJ method (Saitou and Nei 1987) with the Kimura 2-parameter distance model (Kimura 1980).

The *trnL-F* sequences had 217–413 bp depending on taxa. The largest divergences in sequence between taxa reached 27.94% in Geraniaceae and 45.89% in Geraniales. For *rbcl* sequences, differences reached 11.05% in Geraniaceae and 18.22% in Geraniales.

Clustal X ver. 1.62b (Thompson et al. 1997) was used for the alignment of the sequences, followed by manual adjustment to maximize similarity (Simmons, 2004). *Balbisia* and *Wendtia* showed no identical fragments in the *trnL-F* matrix and it was not possible to align them; consequently they were not used in this analysis. Cladistic analyses were conducted using Fitch parsimony (Fitch 1971) with unordered, equally weighted characters. Heuristic searches were performed using ACCTRAN optimisation.

Phylogenetic reconstructions of the *rbcl*, *trnL-F* and combined matrices were carried out using PAUP\* 4.0b10 (Swofford 2002) and MrBayes ver. 3.0b4 (Ronquist and Huelsenbeck 2003). A heuristic search was performed with 100 replicates of random addition sequences, Tree Bisection-Reconnection (TBR) branch swapping, and with the Mulpars option selected. Bootstrap analyses (Felsenstein 1985) were performed using 1000 replicates, random taxon addition with 10 replicates per replicate and no branch swapping. For simultaneous analysis (Kluge, 1989; Nixon and Carpenter 1996) we combined the *trnL-F* and *rbcl* datasets, using missing value marks for the parts not sequenced. Since the *trnL-F* and combined matrices are very large, data analyses aborted in the first replicate. Thus, we analyzed them using PRAP/PAUP (Müller 2003, 2005), which allows running the parsimony ratchet (Nixon 1999). Trees and data matrices for *rbcl* and *trnL-F* are posted at TreeBASE (study number S1569).

To determine the simplest model of sequence evolution that best fit the data, the hierarchical likelihood ratio test (hLRT, Felsenstein 1988) and the Akaike information criterion (AIC, Akaike 1974) were used employing MrModeltest 1.1b software (Nylander 2002). Both tests selected the same substitution models: GTR +  $\Gamma$  for the *trnL-F* matrix, and GTR +  $\Gamma$  + I for *rbcl*. The proportion of variable sites for *trnL-F* was 50% in Geraniales (44% in Geraniaceae subset), from which informative ones was 33% (30% in Geraniaceae). For *rbcl*, the proportion of variable sites was 26% in Geraniales (19% in Geraniaceae), and the informative ones 18% (13 in Geraniaceae subset).

A Bayesian MCMC analysis (Yang and Rannala 1997) using MrBayes ver. 3.0b4 (Huelsenbeck and Ronquist, 2001) was run for 2 million generations using the default parameters. A 50% majority rule tree was obtained after discarding the first  $10^4$  (*rbcl* matrix) or  $10^5$  (*trnL-F*) generations as burn-in prior to reaching stationarity. MacClade ver. 3.08 (Maddison and Maddison 1992) was used to map the distribution of character state changes.

**Biogeographical Analyses and Molecular Datations**—Ancestral areas were reconstructed for both *trnL-F* and *rbcl* using dispersal-vicariance analysis (DIVA; Ronquist 1997). Areas of endemism were defined by the presence of at least one endemic taxon (Fig. 1). The program demands fully resolved trees; the tree with the highest likelihood obtained from the Bayesian analysis was selected for this purpose.

Two relaxed-clock methods using different statistical bases were used to reconstruct divergence times for each marker: the Penalized Likelihood approach (PL) (Sanderson 2002) and the Bayesian Relaxed Clock (BRC) (Kishino et al. 2001; Thorne et al. 1998, 2002). These reconstructions were performed by r8s ver. 1.70 (<http://ginger.ucdavis.edu/r8s/>; Sanderson 2002) and Multidivtime (ver. 09.25.03, Thorne and Kishino 2002). A 50%

TABLE 1. Dates of nodes of Geraniaceae tree in MYA. \* Indicates age constrained in this node.

Nodes	Separation of Pelargonium and the rest of Geraniaceae (D)	Separation of <i>Monsonia</i> and the ancestor of <i>California</i> , <i>Erodium</i> and <i>Geranium</i> (F)	Separation of <i>California</i> and the ancestor of <i>Erodium</i> and <i>Geranium</i> (N)	Separation of <i>Monsonia</i> and the ancestor of <i>California</i> (H)	Separation of <i>Erodium</i> and <i>Geranium</i> (O)	Separation of <i>California</i> , <i>Erodium</i> , and <i>Erodium</i> (L)	Separation of two main groups of subgenera of <i>Geranium</i> : <i>Robertianum</i> and <i>Erodoides</i> plus <i>Geranium</i> (K)	Separation of two main subgenera of <i>Erodium</i> : <i>Mitacoides</i> and <i>Erodium</i> (L)	Separation of basal-most branches of <i>Monsonia</i> (G)	Separation of basal-most branches of <i>Pelargonium</i> (E)
<i>rbcl</i> r8s-PL	38-47*	28.20	19.94	—	18.0	—	14.46	15.46	14.52	11.47
<i>rbcl</i> Multidivtime (s.d.)	38-47*	26.93 (3.7)	22.4 (3.61)	—	20.64 (1.2)	—	18.14 (3.49)	17.8 (3.52)	17.5 (4.58)	14.18 (3.45)
<i>trnL-F</i> r8s-PL	38-47*	32.71	—	21.73	—	20.34	15.57	16.33	13.89	23.00
<i>trnL-F</i> Multidivtime (s.d.)	38-47*	33.82 (3.18)	—	28.57 (3.69)	—	27.31 (3.7)	23.82 (4.1)	24.36 (3.98)	22.47 (4.57)	24.28 (5.31)

majority rule consensus tree (obtained from the BI tree) was used for reconstructing the divergence times of each node for each marker. The clock hypothesis was rejected using the likelihood ratio test.

Calibration points were obtained from fossils and published dating analyses. An upper age constraint was deduced from the data of Wikström et al. (2001, appendices: node 183), who calculated the age of many clades of the angiosperm tree by calibrating it with a fossil of the Fagales. The ages obtained by these authors ranged between 47 and 38 MYA for the ancestral node of Geraniaceae excluding Hypseocharitaceae (node D in Figs. 2, 3, but see also Bakker et al. 2005). Thus, we used these data as minimum and maximum constraints for node D. Minimum age constraints for two terminal subclades were taken from the fossil record

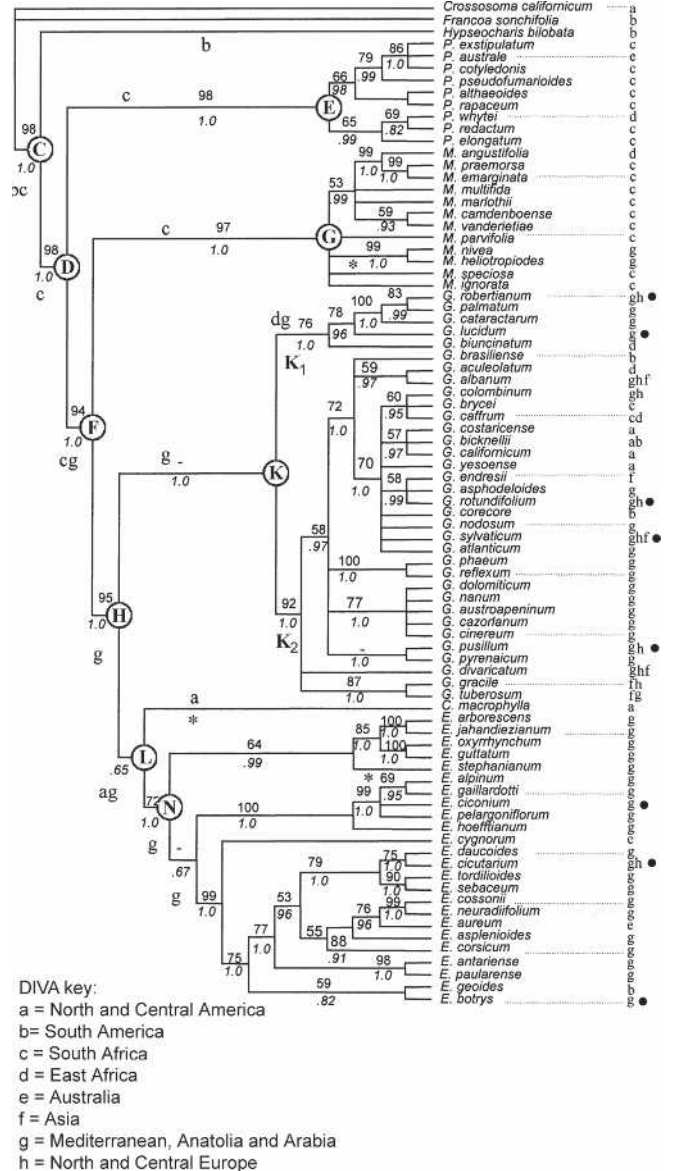


FIG. 2. Strict consensus of the 1,962 most parsimonious trees obtained in *trnL-F* analysis. Numbers above branches are bootstrap values; those below are posterior probabilities. Branches in the parsimony tree that contradicted Bayesian tree are indicated by \* under the branch. The number of steps was 683, CI = 0.637 (excluding parsimony-uninformative characters), RI = 0.884. Circled letters are node names; non-circled letters are ancestral areas inferred from DIVA analysis (see Fig. 1 for area interpretation). The letters on the right represent the distribution of each taxon analysed (see Fig. 1 for area interpretation). As the topologies are different, the nodes are marked differently in Fig. 2 with respect to Figs. 3 and 4. The geographic distribution of species marked with ● is tentative, because they were probably dispersed by the man to different continents.



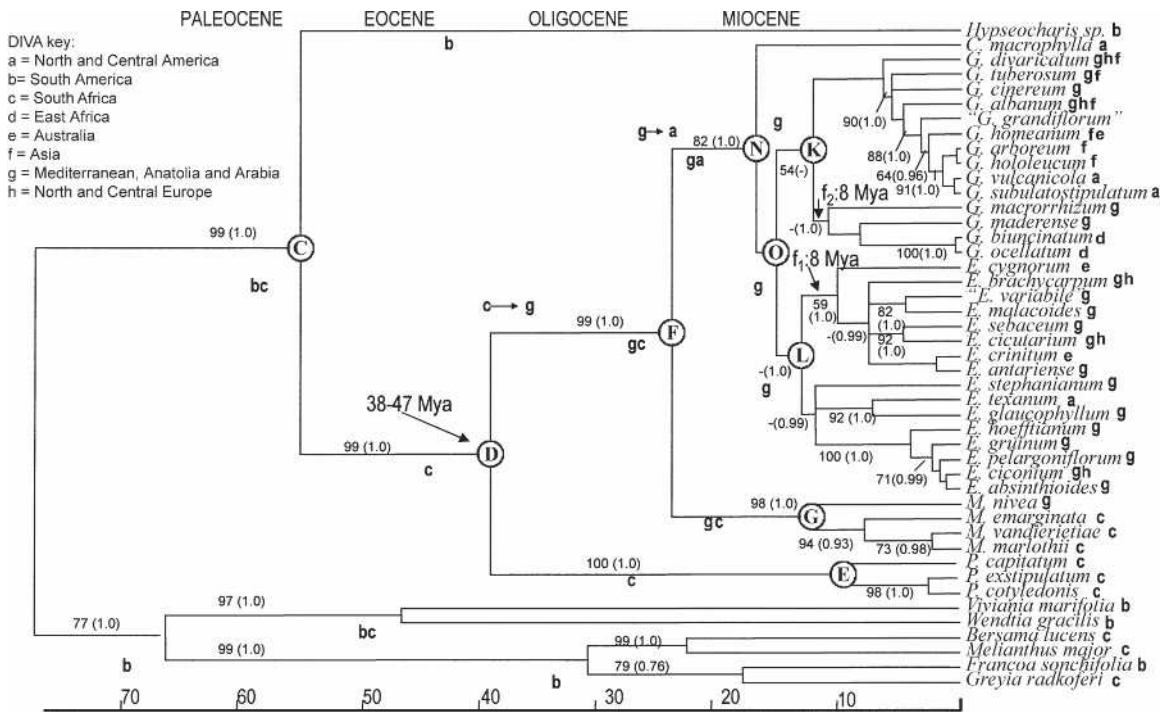


FIG. 3. Chronogram reconstructed after analysing *rbcl* with *r8s*. It was obtained from a consensus of the 6 MPTs obtained in *rbcl* analysis. Numbers beside branches that are not in parentheses are bootstrap values; those in parentheses are posterior probabilities. The number of steps was 776, CI = 0.517 (excluding parsimony-uninformative characters), and RI = 0.783. Circled letters are node names; non-circled letters are ancestral areas inferred from DIVA analysis. The pairs of letters linked by arrows indicate inferred dispersal events. Node D was constrained for minimum and maximum dates of 47 and 38 MYA. The dates linked by arrows to nodes indicate minimum age constraints of 8 MYA for two terminal points (arrows  $f_1$  and  $f_2$ ).

(arrows  $f_1$  and  $f_2$  in Fig. 3). The only available Geraniaceae fossils confidently assignable to Geraniaceae are pollen grains from the middle Miocene of Spain (Van Campo 1989). Photographs of these grains were examined by the authors and two of them were assigned to *Erodium* subg. *Barbata* (pollen with interwoven striae; the rest of subgenera is reticulate), and *Geranium* subg. *Robertium* (pollen with sexine 2 distinct, nearly reticulate; in the rest of *Geranium* groups the sexine is indistinct, and is covered by supraterctal elements; see Stafford and Blackmore 1991).

To estimate the divergence times of the Geraniaceae nodes, the *r8s* penalized likelihood method (PL) was used (Sanderson 2002). Searches were started at five different time estimates. Each estimate was perturbed and restarted up to three times to avoid local stability. The smoothing parameter ( $\log_{10} \lambda$ ) was calculated by cross-validation. The lowest cross validation score was found by testing different smoothing values ( $\lambda = 10x$ ), starting at 1 and increasing the value of  $x$  by steps of 0.5 up to 1,012. The smoothing value of  $\lambda = 32$  (*rbcl*) and  $\lambda = 10$  (*trnL-F*) corresponded to the lowest prediction error (the lowest cross validation score); it therefore provided the best semiparametric model for the data (Sanderson 2002).

Multidivtime was used following the procedure outlined by Rutschmann (2004), which involves the use of three programs: Baseml (PAML ver. 3.14; Yang 1997), Estbranches (ver. 8.5-03; Thorne et al. 1998) and Multidivtime (ver. 9-25-03; Kishino et al. 2001; Thorne and Kishino 2002). After the parameters were estimated from the data using Baseml, branch-lengths (and variances and covariances) were estimated using Estbranches. Finally, Multidivtime served to estimate the posterior distributions, substitution rates and node times using a Bayesian procedure. The settings used in Multidivtime were: for the age of the root (rttm prior) and its standard deviation, we used a value of 1.5, which equals 45 MYA ( $1.5 \times 30$ ); for the prior on rate change (brownmean). For its standard deviation we selected a value of 0.4 obtained from estbranches data. Bigtime value was set at 100 MYA, other values were default values of the package Multidivtime.

Rates of diversification were obtained using equation 7 of Magallón and Sanderson (2001). Estimators of rate of diversification were calculated, assuming that the rate of relative extinction  $\epsilon$  varied between a lower and upper limit of 0 and 0.9 (Magallón and Sanderson 2001).

## RESULTS

**Analysis of *trnL-F*, *rbcl* and Combined Matrices**—Figures 2 and 3 show the results obtained from the *trnL-F* and *rbcl* sequences, respectively. Parsimony and Bayesian analysis produced similar topologies, with high support for the clade formed by Geraniaceae plus Hypseocharitaceae (node C) and for that of Geraniaceae alone (node D, Fig. 2). However, the *rbcl* tree indicates low support for the remaining Geraniales as sister to Geraniaceae plus Hypseocharitaceae. The combined matrix produced a topology similar to that of the independent data sets but differing in its branch support (Fig. 4).

The *trnL-F* and *rbcl* trees showed four main nested clades: 1) *Hypseocharis* as sister to Geraniaceae (node C), 2) *Pelargonium* as sister to all the remaining Geraniaceae (node D), 3) *Monsonia*, including the section *Sarcocaulon* (node G), and 4) a large clade comprising *Geranium*, *Erodium*, and *California* (node H for *trnL-F* and node N for *rbcl*). The fourth clade showed different topologies depending on the locus used. The clade of *Monsonia* was unresolved with respect to *trnL-F*; showing two nested polytomies. The phylogenetic relationships between *Geranium*, *Erodium*, and *California* are unclear because of the low support for the alternative topologies inferred from both markers (Figs. 2, 3).

The clade of the genus *Geranium* showed two main branches, one formed by most species of subg. *Robertium* ( $K_1$ , Fig. 2), and the other formed by the remaining subgenera ( $K_2$ , Fig. 2). This is consistent across all analyses. Two main branches appeared in the *trnL-F* and *rbcl* analysis of *Erodium*, and the monophyly of this genus is well supported in Bayesian analyses (Figs. 2–4).

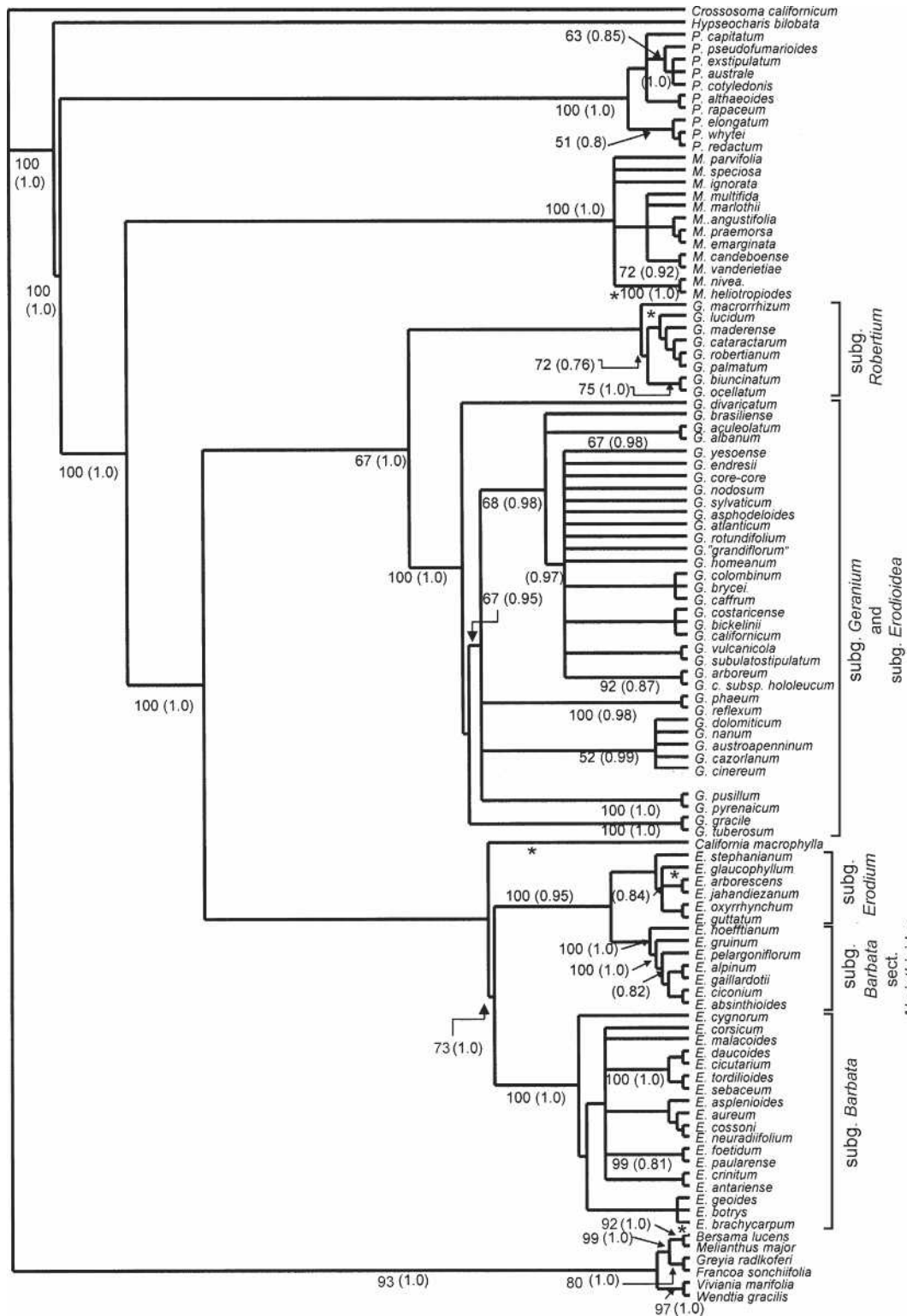


FIG. 4. Strict consensus of the 400 most parsimonious trees obtained from combined *rbcl* and *trnL-F*. Numbers beside branches that are not in parentheses are bootstrap values; those in parentheses are posterior probabilities. Branches in the parsimony tree which contradicted Bayesian tree are indicated by \* under the branch. The number of steps was 1,439, CI = 0.656 (excluding parsimony-uninformative characters), and RI = 0.841. Guittoneau's (1990) classification of *Erodium* and Yeo's (1990) classification of *Geranium* are indicated on the right side of the tree.

The topologies obtained by parsimony and BI analyses were quite similar for both the *trnL-F* and *rbcl* matrices (Figs. 2, 3). In the simultaneous analysis, only the positions of *California macrophylla*, *Erodium brachycarpum*, *E. glaucophyllum*, *Geranium macrorrhizum*, and the branch of *Monsonia nivea-M.*

*heliotropioides* are in conflict (Fig. 4). If *trnL-F* and *rbcl* trees are compared, only the position of *California macrophylla* is in conflict. In the *trnL-F* tree, *California* is sister to *Erodium*, while in *rbcl* it is sister to the clade formed by *Erodium* and *Geranium*; neither topology had strong bootstrap support.

**Biogeographical Analyses**—The biogeographic analysis using DIVA resulted in a single optimal reconstruction requiring 14 dispersals for the *trnL-F* tree and 11 for the *rbcl* tree (Figs. 2, 3 respectively, see letters over the nodes). South America plus Southern Africa (area bc) was suggested as the ancestral area for Geraniaceae plus Hypseocharitaceae (node C).

The clade of the ancestor of crown node of Geraniaceae (node D) was assigned to Southern Africa (area c). The nested clade formed by the ancestor of *Monsonia*, *Geranium*, *Erodium*, and *California* was assigned to the composite Southern Africa plus Mediterranean-West Asian region in the *trnL-F* tree (area cg, node F), while that of *Pelargonium* was assigned to Southern Africa (c). Thus, a dispersal event towards the Mediterranean-West Asian region was required for an ancestor of *Monsonia*, *Geranium*, *Erodium*, and *California*.

Many of the upper nodes of *Geranium* were unresolved and assigned to large combinations of areas, probably due to dispersal events. Conversely, the lower nodes of *Erodium* were assigned to the Mediterranean-West Asian region, except for one which was assigned to area eg (Mediterranean plus Australia), which is explained by a long-distance dispersal event.

**Reconstruction of Divergence Times**—Upper and lower constraints for the split of the genus *Pelargonium* were obtained from the data of Wikström et al. (2001), while two Geraniaceae fossils were used to constrain the terminal branches. These data yielded a rate of  $8.64 \times 10^{-10}$  substitutions per site per year (*s/s/y*) for *rbcl*, and  $2.26 \times 10^{-9}$  *s/s/y* for *trnL-F*. Results are shown in Table 1 and the chronogram of Fig. 3.

Node F marks the separation of the ancestor of *Geranium*, *Erodium*, and *California* and the ancestor of *Monsonia* (Fig. 3; Table 1). The data obtained for these nodes indicate the late Oligocene as the time of splitting between these branches (26–34 MYA), which should be distributed in Africa, the Mediterranean, and West Asian region. According to our results, the age of separation of the clade formed by *Geranium*, *Erodium*, and *California* (nodes N or H) is between 18–29 MYA. These ages range from the late Oligocene to the lower Miocene. The diversification of *Monsonia*, *Geranium*, and *Erodium* seems to have occurred from the mid-Miocene onwards. Also, the diversification of the largest clade of *Geranium* seems to be recent, during the later Miocene (*G. subg. Geranium sensu lato*, grouping more than 380 species).

Table 2 shows the diversification rates for the family Geraniaceae. *Pelargonium* (0.28–0.42) and *Geranium* (0.25–0.37) show high rates in contrast to *Erodium* and *Monsonia* which showed the lowest rates (0.1–0.23).

**P/O Indexes and Pollination in Geraniaceae**—Most species of *Pelargonium* are distributed in Africa (Fig. 1), and have medium to low P/O indexes (Fig. 5). They are generally au-

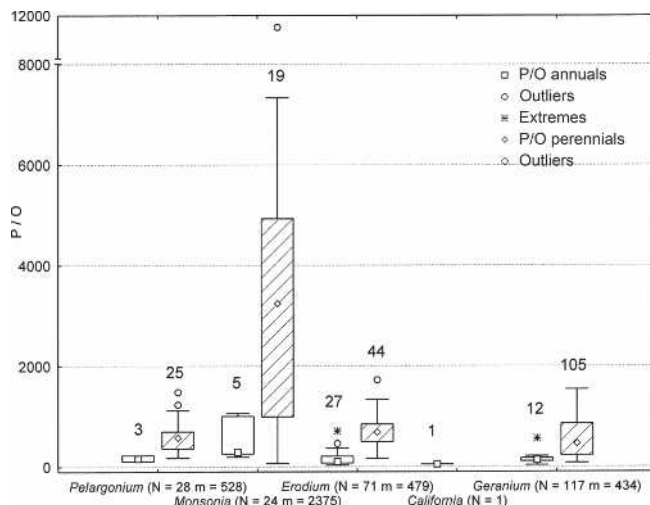


FIG. 5. Box-plots of P/O indexes in annuals and perennials of genera of Geraniaceae. Numbers over the box-plots are the number of species studied. Numbers under the genera are total numbers of species studied per genus and the P/O medians obtained. They are taken from bibliographic and field data compiled in Appendix 2.

toincompatible and visited by a low number of visitors, mainly medium to long-tongued Diptera, Lepidoptera, and large bees (Table 3, Appendix 3). Pollination by birds, short-tongued Diptera, wasps, and auto-pollination are comparatively rare in this genus.

*Monsonia* species with nectar-pockets have very high P/O indexes and are probably pollinated by long-tongued insects, but our observations are limited to *M. drudeana* (Table 3, Appendix 3, Fig. 5). Two *Monsonia* species with tubular nectaries that grow in east Africa have low P/O indices and their pollinators are unknown. The remaining species of *Monsonia* have accessible, knob-like nectaries, and are visited by a range of pollinators (Bombyliidae, wasps, large bees, Lepidoptera, etc.) and produce a lot of pollen. The P/O indexes of 11,753 for *M. speciosa* and 7,337 for *M. ciliata* are uncommon for Geraniaceae.

*Erodium* is distributed mainly in the Mediterranean basin where it grows in mountainous and disturbed places. 32.87% of all *Erodium* species are autogamic annuals that colonize disturbed habitats (Fig. 1). *Erodium* showed a large proportion of species with low P/Os and they are in many cases selfers (Appendix 2; Fig. 5). In some cases, auto-pollination increases in stressful situations or at the end of the flowering season. The number of visitor taxa per species is quite similar in *Erodium* and *Geranium* (*Erodium* with a median 11 taxa per species, and *Geranium* with a median 9 taxa per species; Fig. 6), and it is higher than in the rest of genera. Although our observations on visits per time are quite limited, they suggest that visitors are relatively scarce in *Monsonia* and compar-

TABLE 2. Diversification rates of Geraniaceae using *rbcl* data and some features related to types of reproduction (—: not studied).

Taxa	B: Hypseocharitaceae plus Geraniaceae	C: Geraniaceae	E: <i>Pelargonium</i>	G: <i>Monsonia</i>	K: <i>Geranium</i>	L: <i>Erodium</i>
Total number of species	810	801	c270	39	c420	74
Date proposed for split of the genus (MYA)	64.32	45.8	11.47	14.52	14.96	15.46
Diversification rate for extinction rate $\epsilon = 0$	0.0933	0.1308	0.4277	0.2046	0.3698	0.2336
Diversification rate for extinction rate $\epsilon = 0.9$	0.0677	0.0948	0.2857	0.1045	0.2564	0.1336
Percentage of facultative or mostly autogamous species (considering P/O and automatic selfing)	—	14.9	1.9	15.3	c20	37



TABLE 3. Total number of species in each genus (N) visited by insects of each functional group, and median of taxa of visitors per plant genus (m). Last row (total) shows the total number of Geraniaceae analysed for visitors and the median of taxa numbers. The six functional groups are classified according taxonomy, tongue length, and body size. Data are extracted from Appendix 3.

Geraniaceae genera	Pelargonium		Monsonia		Erodium		Geranium	
	Median of visitors taxa	Number of species of Pelargonium visited by insects of this group	Median of visitors taxa	Number of species of Monsonia visited by insects of this group	Median of visitors taxa	Number of species of Erodium visited by insects of this group	Median of visitors taxa	Number of species of Geranium visited by insects of this group
Long-tongued flies (Tabanidae and Nemestrinidae)	1	23	0	0	0	0	0	0
Medium-tongued flies (Bombyliidae)	1	11	1	2	1	8	0	0
Short-tongued flies (Asilidae, Calliphoridae, Conopidae, Empididae, Muscidae, Syrphidae, Tachinidae, and others)	0	1	0	1	3	13	3	16
Wasps and related taxa (Vespidae, Eumenidae, Sphecidae, Sapiigidae, Chrysididae, Ichneumonidae, and others)	0	2	0	1	1	8	1	4
Small bees (Halictidae, Andrenidae and Colletidae)	0	0	0	1	2	11	2	16
Large bees (Anthophoridae, Megachilidae, Apidae and others)	1	16	0	2	2	10	3	17
Total	1	47	2	4	11	13	9	20

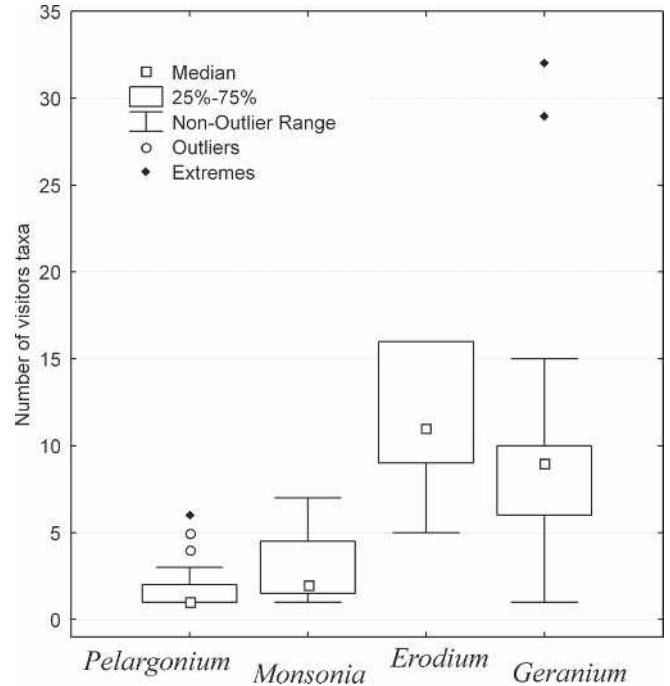


FIG. 6. Box-plots of the number of visitor taxa recorded in each genus. Data are taken from bibliographic and field data compiled in Appendix 3.

atively abundant in *Erodium* and *Geranium* (Appendix 3). The medians were: 0.025 visitors per minute (v/m) for the four species of *Monsonia* studied (censused during 20 h), and respectively 0.130 and 0.133 v/m for *Erodium* and *Geranium* (15 species in each genus, censused during more than 100 h each; Appendix 3)

Though many species of *Erodium* are protandrous, they show incomplete dichogamy, and at the beginning of the female fertile period the anthers (still with pollen grains) bend outwards to keep them away far from the stigma. This process hinders but does not prevent self-pollination caused by the chaotic movements of some Halictidae insects, especially during the female period. As in *Geranium*, small bees encircle the androecium but, in contrast to *Erodium*, they reach the stigma, often causing self-pollination. Conversely, Syrphids and some other Diptera (e.g. Bombyliidae) are better pollinators for *Erodium* because they hover and land on the lower petals and do not make random movements inside the flower. *Erodium* sect. *Malacoidea* and *E.* sect. *Cicutaria* show attractive structures on the upper petals (e.g. color spots, globular hairs mimicking nectar droplets, or shining flattened hairs), all of which attract Syrphids by promising large quantities of nectar. A Mann-Whitney analysis of the total Syrphid taxa showed the *Erodium* spotted species to be significantly more in demand ( $p = 0.002$ ,  $z = -3.08$ ,  $n = 26$ ). Also, the number of Syrphid visits per time unit is higher in spotted species ( $p = 0.0006$ ,  $z = -3.43$ ,  $n = 13$ ). Other insects (e.g. other Diptera, Hymenoptera, Coleoptera, and Lepidoptera), showed no significant difference in the number of visits they made to flowers of either type.

Certain *Geranium* species present medium to low P/Os, and high selfing rates (Fig. 5; Appendix 2); P/O is especially low in annuals and small-flowered mountain perennials. Also, *Geranium* is the genus with more species adapted to high altitudes and latitudes. Only 8.6% of all studied *Gera-*

*nium* (N = 186) are autogamic annuals growing in low-altitude disturbed habitats. The large flowers of many species of *Geranium* favor larger visitors. Large bees and bumblebees are the most effective pollinators in this genus, while small bees and flies have difficulty successfully pollinating this type of flower (Table 3; Appendix 3).

#### DISCUSSION

**Evolution of the Geraniaceae**—The phylogenetic analyses of the *trnL-F* and *rbcL* sequences gave consensus trees with only one point of incongruence: the position of *California macrophylla*. In addition, the main branches were well supported in the simultaneous analysis (Fig. 4). The trees obtained by parsimony and Bayesian analyses were congruent for most clades and confirm the conclusions of Price and Palmer (1993) and the APG II (2003), showing *Hypseocharis* as the sister group of Geraniaceae s.str. The monophyly of Geraniaceae plus Hypseocharitaceae and the Geraniaceae alone were corroborated. The position of Geraniaceae plus Hypseocharitaceae in the order Geraniales was studied by Soltis et al. (2000), Savolainen et al. (2000a, b), and Wikström et al. (2001), who reported good support for both taxa as monophyletic groups. The position of *Hypseocharis* in the phylogenetic trees (Figs. 2–4), the degree of molecular divergence, and the morphological differences with its closest relatives, suggest that *Hypseocharis* is a taxon related to ancestors of Geraniaceae s.str. that survived in subalpine meadows of the central Andes.

The genus *Pelargonium* was found to be the sister group of the remaining genera of Geraniaceae, which was first reported by Price and Palmer (1993). However, *Pelargonium* species show a mixture of plesiomorphic and apomorphic traits. Some of these synapomorphies include zygomorphy of the flower, the reduction of five nectaries to one (a tube deep inside the hypanthium), the reduction of the stamens from 15 to 5–8, and anemochorous mericarps assisted by a pappus. The plesiomorphic characteristics include shape of the mericarps (fusiform), and fruit bristles without rims (Aldasoro et al. 2001).

The present results favor the inclusion of *Sarcocaulon* in *Monsonia*, as proposed by Albers (1996a, 1996b) and suggested by phylogenetic analyses based on morphology (Aldasoro et al. 2001) and ITS and *trnL-F* markers (Touloumenidou et al. 2007). The present analyses confirm the distinctiveness of *California*, although its phylogenetic position remains unclear. According to the *rbcL* and simultaneous analysis trees, *California* might be sister group of the clade of *Geranium* and *Erodium*.

Finally, the infrageneric groups retained in the present analysis only partly reflected their current taxonomic classification within the genera *Geranium* and *Erodium* (Guittonneau 1972; Yeo 1984; El-Oqlah 1989). More extensive sampling is needed to acquire sufficient information for a new taxonomic treatment.

**Biogeography and Age Estimates**—The biogeographic analyses suggest South America and Southern Africa to be the ancestral home range of the Geraniales (Figs. 1–3). The families of Geraniales show several transAtlantic connections that can be explained by vicariance and/or dispersal.

According to DIVA, separation of the sister genera to the largest Geraniaceae clade occurred in Southern Africa and the Mediterranean. The early split between *Pelargonium* and

the ancestors of *Monsonia*, *Erodium*, *Geranium*, and *California* could suggest that long-tongued pollinators were already present in Southern Africa during their early split. However, Bakker et al. (2005) reported that the ancestral pollination system of *Pelargonium* is by short-tongued flies or bees, while pollination by long-tongued flies may be a derived character. In that case, concealed nectaries could also be convergent synapomorphies derived in different clades. According to our reconstruction of Geraniaceae phylogeny, splitting between the deep-nectary and knob-nectary *Monsonia* is feasible in Southern Africa during the midMiocene, probably driven by changes in the composition of pollinator communities.

Most *Pelargonium* and *Monsonia* species are drought-tolerant; species of *Monsonia* sects. *Sarcocaulon* and *Monsonia* are the best adapted to deserts and semideserts. Between 75 and 30 MYA, much of Africa was occupied by lowland rainforest very similar to those of present-day west central Africa (Axelrod and Raven 1978). Arid episodes may have occurred in southwestern Africa since the Cretaceous, 80 MYA (Ward et al. 1983) to the early Oligocene, 34 MYA (Van Zinderen Bakker 1975; Dieckmann et al. 2004). However, the most intense aridification seems to have taken place in the mid-Miocene (around 10–15 MYA) after the final establishment of the Benguela current (Siesser 1980). The progressive change towards a drier and colder climate might have triggered the diversification of the two main lines of drought-adapted Geraniaceae: *Pelargonium* and the fleshy *Monsonia*. Aridification greatly accelerated in Africa during the late Miocene and Pliocene, largely as a result of the uplift of the continent and the further development of the Rift Valley (Axelrod 1972; Baker et al. 1972). During this age, *Pelargonium* reached its greatest rate of diversification in Southern Africa (Bakker et al. 2004, 2005).

If the position of the genus *California* in the *rbcL* and the simultaneous analysis tree is accepted (Fig. 4), a dispersal event to North America must have occurred for ancestors of *California*, *Erodium*, and *Geranium*. Thus, the ancestors of the largest clade of Geraniaceae may have dispersed from Southern Africa to Eurasia via the Saharo-Sindian deserts and later to North America (Van Zinderen Bakker 1969), or from North Africa to Europe and then to North America (Lavin et al. 2000).

Finally, it is important to comment on the diversification of the largest clade of Geraniaceae, with more than 400 species of *Geranium* and 74 of *Erodium*. According to our estimates (Fig. 3), this diversification occurred mainly in the Mediterranean Basin and in Eurasia during the latter part of the Miocene and Pliocene. The appearance of many mountain systems and the climate changes in these regions could have encouraged the ancestors of some current species of *Erodium* and *Geranium* to adapt to disturbed or to high and cold environments. Many nodes sister to the central clade of *Erodium* were assigned to the Mediterranean-west Asian region and just one to the Australia and Mediterranean-west Asian region. This suggests long distance dispersal from the Mediterranean Basin or west Asia to Australia. Also several groups of *Geranium* seem to have dispersed repeatedly to South America. Successful long-distance dispersal has been described between Australia and the northern hemisphere (Smitsen 2003; Fiz et al. 2006).

Some of the characteristics of Geraniaceae mericarps (e.g. plumose awns, pappus, or adhesive devices) seem not to



relate to the extent of their distribution area, diversification rate, nor chance for long-distance dispersal. However, DIVA analyses indicated that certain *Erodium* and *Geranium* might have experienced several dispersal events from the Mediterranean to Australia or America (Fiz et al. 2006). Also several species of *Pelargonium* sect. *Peristera* might have dispersed from South Africa to Australia, St Helena, and Tristan da Cunha (Bakker et al. 1998). Some authors compared certain characters and parameters indicative of wind dispersal capability in Geraniaceae, concluding that many species of *Pelargonium*, *Erodium*, and *Monsonia* have measurable wind-dispersal capabilities (Zeide 1976; Rösch 1977, 1978; Loria and Noi-Meir 1980; Burke et al. 1998). Others have reported that *Erodium* and *Geranium* mericarps (or seeds) can be collected, eaten, or transported by ants (myrmecochory), reptiles, birds and mammals (by ectozoochory or endozoochory; Hayward in Ridley 1930; Soholt 1973; Skorupa et al. 1980; Shmida and Ellner 1983; Lane et al. 1999; Albert et al. 2005; El Mouden et al. 2006).

However, Stamp (1984, 1989) and Van Reede and Van Rooyen (1999) indicated that the dispersal distance of certain Geraniaceae, such as *Erodium*, is low. Based on experimental simulations, Stamp (1984, 1989) found that mericarps were never dispersed by more than 3 m. Clark (1998) and Higgins and Richardson (1999) have used mathematical simulations to explore potential spread rates, and reported that relatively infrequent long distance dispersal events can strongly influence the final figure obtained. Thus, dispersal strategies could increase their complexity by these rare events, such as sporadic myrmecochory and ecto- or endo-zoochory, which have been observed in both *Erodium* and *Geranium*.

**Flower Evolution, Pollination Ecology, and Diversification Rates**—The visitor-plant relationship is an important selective force during evolution and can lead to a faster diversification rate. The rates of diversification of *Erodium* and *Monsonia* are similar to the average values of other angiosperms (Table 2), but not to those of *Geranium* and *Pelargonium*, which are somewhat higher than the mean (Magallón and Sanderson 2001). Struck and Van der Walt (1996) reported that *Pelargonium* presents a considerable diversity in flower shape and pollination syndromes. Also, Bakker et al. (2005) reported a correlation in certain clades between the number of species and a shift to long-tongued pollination. In Southern Africa, several other specialised pollination systems, involving long-tongued insects, have been reported (Table 3; Johnson and Steiner 2000; Goldblatt and Manning 2006). Various authors have proposed three alternative explanations: the higher incidence of specialized pollinators in the region (Barracough 2006; Goldblatt and Manning 2006; Van der Niet et al. 2006), a depauperate pollinator fauna (Johnson and Bond 1992; Johnson 1996; Barracough 2006) or the existence of a pollinator mosaic (Johnson 1996). Also, Ricklefs and Renner (2000) reported the existence of a significant relationship between high species diversity and animal pollination and herbaceousness.

In agreement with their different types of nectaries and distribution, the main groups of Geraniaceae could be subject to different selective pressures depending on their pollination ecology and habitats. Most *Pelargonium* with deep nectaries and *Monsonia* with sepal-concealed nectaries are restricted to Southern Africa and Namibia. In contrast, northern species of *Monsonia* (Saharo-Sindian area), as well as *California*, *Geranium*, and *Erodium* (northern hemisphere and

South American ranges), produce unspecialized flowers that attract many taxa of insects. Those genera presumably faced the climatic deterioration and loss of pollinators at the end of the Tertiary by a shift to generalist pollination and a higher reproductive flexibility.

The Mediterranean flora is distinguished by a high proportion of annual taxa, which is likely to have resulted from long-lasting disturbance regimes (Shmida 1981; Pons and Quezel 1985; Herrera 1991; Fiz et al. 2002). The clade of *Erodium*, *California*, and *Geranium* colonised the Mediterranean, much of Europe and America during the end of Tertiary, once or more times, and must have acquired new sets of pollinators. As opportunistic bees dominated many of these regions, the possibilities for floral specialization were limited (Schemske 1983). Moreover, generalization usually reduces the risk of reciprocal declines between pollinators and plants (Deyrup and Menges 1997).

*Geranium* includes more species adapted to wide ranges in altitude and latitude than the other genera of Geraniaceae. The diversification rate of this genus is high (only that of *Pelargonium* is higher in Geraniaceae). The speciation could be triggered, at least in parts of its range, by the formation of new mountain ranges and climatic deterioration. Studies on the insects found over altitude and latitude gradients showed that the tundra is home to many more Diptera than large Hymenoptera (Table 3; Blionis and Vokou 2002; Totland 1993; Elberling and Olesen 1999). However, only large bees and bumble-bees maintain high levels of activity and efficiency under low temperatures (Bingham and Orthner 1998; Bingham and Ranker 2000). Thus, large bees and bumble-bees are the best pollinators of *Geranium* in these habitats (Kandori 2002; Dlusskii et al. 2000).

*Erodium*, the genus with most species growing in disturbed habitats (and many of them with high autogamy rates) shows a wide spectrum of low-efficiency visitors and pollinators (Table 3). These observations agree with Inoue (1988), who reported a relationship between abundance of inefficient pollinators and an increase in autopollination rate in *Campanula*. Similar changes have been reported for some taxa seen as colonizers in parts of the Northern Hemisphere. In many of those taxa, plasticity in pollinator attraction and outcrossing rate seems to have been the best evolutionary option (Inoue 1988; Stephenson et al. 2000; Kalisz et al. 2004).

**ACKNOWLEDGMENTS.** The authors thank G. Nieto Feliner for comments on the manuscript; F. Albers and C. Navarro for help with some Geraniaceae sequences; C. Roquet for help with the Multidivtime package; I. Sanmartín for help with DIVA analyses; M. J. Sanderson for help with R8S analyses; J. Castillo for drawings; A. Martín Ciudad for help with figures; F. Torres and M. Portillo (Universidad de Salamanca) and V. Rodríguez for help with insect determination; and K. Alpinar, S. Castroviejo, T. Egorova, I. Gillespie, G.G. Guittonneau, N. López, and M. Novoselova for help with specimens and literature. We are also grateful to the curators of the cited herbaria for kind assistance during our visits and for specimen loans. This work was partly financed by the Spanish Dirección General de Investigación Científica y Técnica (DGICYT) through the research project REN2000-0818/GLO and REN2003-04397/GLO.

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APPENDIX 1. Samples and accessions provided for *trnL-F* and *rbcL* used in the present study, including their locality, voucher and herbarium number and GenBank accession numbers. Data are presented in the following sequence: taxon name, locality, voucher, herbarium number and GenBank accession numbers (new sequences indicated by bold type) for *trnL-F* and *rbcL* region. “—” indicates no sequence for the DNA region.

*Balbisia microphylla* (Phil.) Reiche: CHILE, Antofagasta, W of Paposo, Aedo 6970 (MA), **DQ459009**, —. *Bersama lucens* Scyscyl, GenBank, —, AJ235774.

*California macrophylla* Aldas., Navarro, Vargas, Sáez & Aedo: U.S.A., California, Riverside Co., Temescal Valley, Gillespie 10 (MA), **DQ072013**, **DQ452869**. *Crossosoma bigelovii* S. Watson: USA, Arizona, *Álvarez* SS137, **DQ452888**, —; *C. californicum* Nutt.: GenBank, —, L11179.

*Erodium absinthioides* Willd.: TURKEY, Bursa, Uludag, Nieto Feliner 1580 (MA-393124), **DQ452876**, **DQ072034**; *E. alpinum* (Burm f.) L'Hér.: ITALY, Abruzzo, Mt. Rosa Pinnola, Bisegna, L'Aquila, Conti 1656 (MA), **DQ072029**, —; *E. antariense* Rouy: MOROCCO, High Atlas, Tizi-n-Ait-Hamed, Güemes 1549 (MA), **DQ072078**, **DQ452881**; *E. arborescens* (Desf.) Willd.: TUNISIA, Skhira, Aldasoro 3053 (MA), **DQ072018**, —; *E. asplenioides* (Desf.) Willd.: TUNISIA, La Kesra-Darsole, Timbal s.n. (MPU), **DQ072065**, —; *E. aureum* Carolin: AUSTRALIA, Coolgardie, Eyre Highway, 59 Km W of Madura, Archer 15 (MEL-2039223), **DQ072066**, —; *E. botrys* (Cav.) Bertol.: U.S.A., California, San Francisco, Mt. Tamalpais, *Castroviejo* et al. 14575 (MA), **DQ072049**, —; *E. brachycarpum* Godr.: SPAIN, Madrid, Rozas de Puerto Real, López 499 (MA), **DQ072050**, **DQ452879**; *E. ciconium* (L.) L'Hér.: ITALY, Abruzzo, L'Aquila, pr. Santo Stefano de Sessanio, Aedo et al. 8108 (MA), **DQ072039**, **DQ452875**; *E. cicutarium* (L.) L'Hér. ex Aiton (1): SPAIN, Salamanca, Fuente de San Esteban, Aedo et al. 4931 (MA), **DQ072052**, **DQ452882**; *E. cicutarium* (2): AUSTRALIA, Mt. Annan Botanic Garden, D'Aubert 405 (NSW-213829), **DQ072051**, —; *E. corsicum* Léman: FRANCE, Corsica, Piana, plage di Ficajola, Serra and Bort 4897 (MA-623612), **DQ072059**, —; *E. cossonii* Guitt. & Mathez: MOROCCO, High Atlas, Tiz-n-Test, Fernández Casas et al. 3277 (MA-252363), **DQ072073**, —; *E. crinitum* Carolin: AUSTRALIA, Buraminy, between Roe and Coolgardie, Archer 27069213 (MEL-2015744), **DQ452897**, **DQ452877**; *E. cygnorum* Nees: cultivated in MA from seeds collected in Great Victoria Desert (Australia), Aldasoro 2842 (MA), **DQ072044**, **DQ452878**; *E. daucooides* Boiss.: SPAIN, Jaen, Cortijos Nuevos, El Yelmo, Navarro et al. 2307 (MA-625205), **DQ072095**, —; *E. gaillardotii* Boiss.: TURKEY, Malatya, 27 Km from Gürün to Darende, Muñoz-Garmendia et al. 4567 (MA), **DQ072035**, —; *E. geoides* A. St.-Hil.: CHILE, Coquimbo, Choapa province, border of Petarca province, Taylor 10620 (MO), **DQ072048**, —; *E. glaucophyllum* (L.) L'Hér. ex Aiton: TUNISIA, 14 Km of Moulares, Aldasoro 3000 (MA), **DQ072016**, **DQ452870**; *E. gruinum*

(L.) L'Hér.: JORDANIA, Gerassa (Jerash), Vargas (MA), **DQ072037**, **DQ452874**; *E. guttatum* (Desf.) Willd.: TUNISIA, Feriana, Aldasoro 2973 (MA), **DQ072026**, —; *E. hoefftianum* C. A. Mey.: TURKEY, Göreme, Ask Vadisi, dept. Nevşehir, Muñoz-Garmendia et al. 4626 (MA), **DQ072033**, **DQ452872**; *E. jahandiezianum* Emb., Maire & Weiller: MOROCCO, Anti-Atlas, Igherm, Gómez s.n. (BC), **DQ072022**, —; *E. malacoides* (L.) L'Hér. ex Aiton: SPAIN, Cádiz, Zahara de la Sierra, Navarro 3424 (MA-685245), **DQ072071**, **DQ452883**; *E. neuradiifolium* Delile ex Godr., SPAIN, Albacete, Letur, Álvarez 1239 (MA-591697), **DQ072069**, —; *E. oxyrhynchum* M. Bieb., cultivate in MA from seeds collected in Egypt, Cairo-Suez Desert Road, Aldasoro 3487 (MA), **DQ072023**, —; *E. paularense* Fern. Gonz. & Izco, SPAIN, Guadalajara, Cañamares, Atienza, Aedo 4097 (MA-588866), **DQ072077**, —; *E. pelargoniflorum* Boiss. & Heldr. in Boiss.: cultivate in MA from seeds collected in Ermenek, SE Turkey, Aldasoro 2838, 9150 (MA), **DQ072041**, **DQ452873**; *E. sebaceum* Delile: MOROCCO, Boumia, 8 km NW of Er-Rachidia, Podlech 43213 (MA-464889), **DQ072102**, **DQ452880**; *E. stephanianum* Willd.: CHINA, Qinghai, Nangqên Xian, NW of Jangkar (upper Mekong), between Jangkar and Yushu, Ho et al. 2892 (MO), **DQ072027**, **DQ452871**; *E. texanum* A. Gray (1): cult. in MA from seeds collected in Yavapai Co., Arizona, USA, Aldasoro 3492 **DQ072026**, —; *E. texanum* A. Gray (2): GenBank, —, L14693; *E. tordylioides* (Desf.) L'Hér.: SPAIN, Cádiz, Zahara de la Sierra, Navarro 3425 (MA685246), **DQ072100**, —; *E. "variabile"* (presumed hybrid *E. reichardii* x *E. corsicum*), GenBank, —, L14694.

*Francoa appendiculata* Cav.: CHILE, La Araucanía, 8 Km N of Yupehue, Aedo 7192 (MA), **DQ452889**, —; *F. sonchifolia* (Willd.) Cav.: GenBank, —, L11184. *Geranium aculeolatum* Oliv.: cultivate in MA from seeds collected in Mt Kilimanjaro, Aizpuru s.n. (MA), **DQ452905**, —; *G. albanum* M. Bieb.: cultivate in MA from seeds collected in Georgia, Aedo 3864 (MA593799), **DQ452915**, **DQ452884**; *G. atlanticum* Boiss.: MOROCCO, Beni-Snassen, Maison Forresterie Ain-Almon Jury 15548 (MA643260), **DQ452924**, —; *G. argenteum* L.: cultivate in MA from seeds collected in France, Aedo, CA3870 (MA), **DQ072050**, —; *G. austroapenninum* Aedo: ITALY, Abruzzo, Herrero et al. 2018 (MA), **DQ452929**, —; *G. asphodeloides* Burm. F.: TURKEY, Bandirma, Erdek, *Castroviejo* 15201 (MA), **AY944424**, —; *G. bicknellii* Britton: USA, Smooth Rock Falls, Cousineau 43581 (MA643259), **DQ452925**, —; *G. biuncinatum* Kokwaro: cultivate in MA from seeds collected between Hilla and Attuba (Yemen), Wood 3126 (MA), **DQ452926**, **DQ452885**; *G. brasiliense* Progel in Mart.: BRASIL, Rio de Janeiro, Itatiaia, Alves 2762 (MA), **DQ452901**, —; *G. brycei* N. E. Br.: Aedo 4474 (MA), **DQ452911**, —; *G. caffrum* Eckl. & Zeyh.: cultivate in MA from seeds collected in the Cape, Aedo 4472 (MA), **DQ452917**, —; *G. californicum* G. L. Jones & F. L. Jones: cultivate in MA from seeds collected in California, Aedo 5450, **DQ452927**, —; *G. cataractarum* Coss.: MOROCCO, Middle Atlas, S de Timhadit, Aedo 4234 (MA593420), **DQ452916**, —; *G. cazorlense* Heywood: SPAIN, Jaen, Cazorla Aedo 2587 (MA), **DQ452930**, —; *G. cinereum* Cav.: SPAIN, Huesca, Ordesa, Vargas 335pv02, **DQ452931**, —; *G. columbinum* L.: SPAIN, Girona, Sierra del Montsiá, San Carlos de la Rapita, Velayos et al. 9387 (MA626513), **DQ452910**, —; *G. core-core* Steud.: CHILE, Antofagasta, Toconao, Aedo 7006 (MA), **DQ452921**, —; *G. costaricense* Steud.: cultivate in MA from seeds collected in Chirripó, Costa Rica, *Castroviejo* 15137, **DQ452912**, —; *G. divaricatum*: TURKEY, Ghumushane, Ak Dag, Aedo 468, **DQ452906**, **DQ452886**; *G. dolomiticum* Rothm.: SPAIN, León, Priaranza, Ferradillo, Aedo 2433 (MA), **DQ452903**, —; *G. endressii* J. Gay: FRANCE, Pyrénées Atlantiques, Béhorléguy, Aedo 2966 (MA593743), **DQ452920**, —; *G. gracile* Ledeb. ex Nordm.: TURKEY, Trabzon, Sumelas, Valcárcel 370VV01, **DQ452918**, *G. lucidum* L.: MOROCCO, Xauen, Jbel Lakra, Hauta-el-Kasdir, Aedo 4118 (MA593333), **DQ452914**, —; *G. macrorrhizum* L. (1): BULGARIA, Rhodope Mts, Aedo 10351, **DQ072043**, —; *G. macrorrhizum* L. (1): GenBank, —, L14696; *G. nanum* Coss ex Batt.: MOROCCO, Atlas Medio, Jbel Bou Iblane, Aedo 4199 (MA593345), **DQ452904**, —; *G. nodosum* L.: ITALY, Abruzzo, Ceppo, Herrero et al. 1995, **DQ452922**, —; *G. palmatum* Cav.: MADEIRA, Porto Moniz, Chao Ribeira, Vargas 125PV98 (MA), **AY944418**, —; *G. phaeum* L.: FRANCE, Xuberoa, Aedo 2967 (MA), **DQ452902**, —; *G. pusillum* L. (1): MOROCCO, Taffert, Atlas Medio Aedo 4144 (MA593417), **DQ452907**, —; *G. pusillum* L. (2): GenBank, —, AF167151; *G. pyrenaicum* Burm. F.: MOROCCO, Middle Atlas, S Timhadit, Aedo 4235, (MA593341), **DQ452908**, —; *G. reflexum* L.: ITALY, Abruzzi, Il Aquila, Aldasoro 3443 (MA), **DQ452909**, —; *G. robertianum* L., GenBank, —, AF167152; *G. rotundifolium* L.: TURKEY, Evciler, Kaz Dag, *Castroviejo* 15237 (MA643798), **DQ452928**, —; *G. sylvaticum* L.: SPAIN, Valle de Arán, Bagergue, Aedo 4842 (MA), **DQ452923**, —; *G. tuberosum* L.: TURKEY, Ermenek, Aldasoro A9140, **DQ452919**, **DQ452887**; *G. yesoense* Franch. & Sav.: JAPAN, Honshu, Toyama-ken, Tateyama-cho, Mt Tsurugidake, Estébanez 182 (MA690990), **DQ452913**, —. *Greyia sutherlandii* Hook.

& Harv.: cultivate in BC from seeds collected in South Africa, Vargas 9e4pv99, **DQ072073**, —; *G. radikoferi* Szyszyl., GenBank, —, L11185. *Hypseocharis bilobata* Killip: PERU, Cuzco, Aedo 5256B (MA), **DQ452890**, —; *Hypseocharis* sp.: GenBank, —, L14699.

*Melianthus major* L. (1): GenBank, **DQ072052**, —; *M. major* (2): GenBank, —, AJ402972; *M. major* (3): GenBank, —, AJ403027. *Monsonia angustifolia* E. Meyer ex A. Richard: SOUTH AFRICA, N Transvaal, *Penther* 2218 (W), **DQ452891**, —; *M. camdeboense* (Moffet) Albers: cultivated in South Africa, Kirstenbosch, Aldasoro s.n. **DQ452900**; *M. emarginata* (L. fil.) L'Herit. (1): cultivate in MA from seeds taken in South Africa, Aldasoro s.n., **DQ452893**, —; *M. emarginata* (2): GenBank, —, L14701; *M. heliotropiodes* (Cav.) Boiss.: ALGERIA, Oujda, Molero, BC-804188, **DQ452897**, —; *M. ignorata* Merxm. & Schr.: NAMIBIA, Windhoek, Sossusvlei, Vargas 421PV02 (MA), **DQ072010**, —; *M. marlothii* (Engl.) Albers: NAMIBIA, Swakopmund, Khan canyon, Vargas 423PV03, (MA), **DQ452899**, **DQ452867**; *M. multifida* (E. Mey. ex Knuth) Albers: SOUTH AFRICA, Kirstenbosch, *Gassner* 25-8-77 (MA), **DQ452898**, —; *M. nivea* (Decaisne) Webb, MOROCCO, Taoujgalt, High Atlas, S of the M'goun Mt., *Staudinger and Finckh* s.n. (STAUD), **DQ452895**, **DQ452868**; *M. parvifolia* Schinz, NAMIBIA, Naroep, Great Buchsmanland Schlechter s.n. (W), **DQ452894**, —; *M. praemorsa* E. Mey. ex Knuth, SOUTH AFRICA, Natal, Clairmont, Wood s.n. (W) **DQ452892**, —; *M. speciosa* L., cultivated in the Jardin Botanique National de Belgique, *Billier* s.n. (MA), **DQ452896**, —; *M. vanderietiae* (L. Bol.) Albers: GenBank, **AF167150**, **L14705**.

*Pelargonium althaeoides* L'Herit.: GenBank, Z95299, —; *P. australe* Willd.: GenBank, Z95280, —; *P. cotyledonis* (L.) L'Herit.: GenBank, Z95294, L14703; *P. capitatum* (L.) L'Herit.: GenBank, —, L14702; *P. elongatum* (Cav.) Salisb., GenBank, AF167146, —; *P. exstipulatum* (Cav.) L'Herit.: GenBank, Z95284, L14704; *P. pseudofumaroides* Knuth: GenBank, Z95295, —; *P. rapaceum* (L.) L'Herit.: GenBank, AF036065, —; *P. reductum* Vorster, GenBank AF167142, —; *P. whytei* Bakker, GenBank, AF167142, —. *Viviania marifolia* Cav., GenBank, —, L14707; *Wendtia gracilis* Meyen., CHILE, O'Higgins, Rancagua, Aedo 7065 (MA685239), **DQ459010**, —; *W. gracilis*, GenBank, —, L14708.

APPENDIX 2. Inferred reproduction type and P/O indexes in Geraniaceae and Hypseocharitaceae. Reproduction types, X: generally allogamous, F: facultative, A: generally autogamous, (D): dioecious, (GD): gynodioecious, n: P/O index unknown. Species with "\*" were cultivated, studied and bagged for automatic selfing tests and dioecy observation, in the rest autogamy was deduced from P/O and dioecy from herbarium sheets.

*California macrophylla*: A\*, 52, U.S.A., California, Riverside Co., Temescal Valley, Gillespie s.n. (MA).

*Erodium absinthioides*: X\* (D), 736, TURKEY, Ulu Dag, Bursa, Aldasoro et al. 9193 (MA); *E. acule*: X\*, 783, ITALY, Sicilia, *Castroviejo* et al. 16583 (MA); *E. aquilellae* López Udiás, Fabregat & G. Mateo: X\*, 840, SPAIN, Castellón, Onda, Sierra de las Pedrizas, Aldasoro and Alarcón 9211 (MA); *E. alnifolium* Guss.: A\*, 221, TUNISIA, Sejenane, Aldasoro et al. 2865 (MA); *E. alpinum*: X\* (D), 890, ITALY, L'Aquila, Abruzzo, Aedo et al. 8256 (MA); *E. antiariense*: X\*, 519, MOROCCO, Tizi-n-Ait Hamed, Güemes et al. 1549 (MA); *E. arborescens*: X-F\*, 449, EGYPT, Avdat, Liston (HUJ); TUNISIA, Bizerta, Aldasoro s.n. (MA); *E. asplenioides*: X\*, 1238, TUNISIA, Sejenane, Aldasoro et al. 2935 (MA); *E. astragaloides* Boiss. & Reut.: X\*, 699, SPAIN, Granada, Trevenque, Dilar, Navarro et al. 2246 (MA); *E. aureum*: A\*, 102, AUSTRALIA, Axehead Quarry, Gardner-Torrens (MA); *E. beketowi* Schmalh: X (D), 430, RUSSIA, Stavropol, Biespors, *Smbanova* (LE); *E. boissieri* Coss., X\*, 777, SPAIN, Granada, Trevenque, Aedo et al. 7829 (MA); *E. botrys*: A\*, 136, SPAIN, Salamanca, Aldasoro and Alarcón 3470 (MA); *E. brachycarpum*: A\*, 80, SPAIN, Madrid, Rozas de Puerto Real, Aldasoro and Alarcón 3477 (MA); *E. carolinianum* Aldasoro & al.: A\*, 94, AUSTRALIA, Ayers Rock, Lazarides 474 (NSW); *E. carvifolium* Boiss. & Reut.: X\*, 761, SPAIN, Burgos, Navas del Pinar, Aldasoro and Alarcón 8830 (MA); *E. cazorlanum* Heiwoud: X\*, 582, SPAIN, Granada, Mt Jabalcón, Aldasoro and Alarcón 9219 (MA); *E. cedrorum* Schott & Kotschy: X (D), 334, TURKEY, Ala Dag, Nidge, *Spitzberger* 121(W); *E. chium* (L.) Willd.: A\*, 316, SPAIN, Ronda, Tavrana, Navarro et al. 3450 (MA); *E. chrysanthum* L'Hér.: X\* (D), 397, GREECE, Killini, Hörandl & Hadacek 7612 (W); *E. ciconium*: A\*, 95, SPAIN, Madrid, Aldasoro 949 (MA); *E. cicutarium*: A\*, 59, SPAIN, Salamanca, Aldasoro s.n. (MA); *E. corsicum*: X-F\*, autocompatibility increases in autumn, 617, Cult. in MA, plants collected in Corsica, Ajaccio, Aldasoro s.n. (MA); *E. cossoni*: X, 1267, MOROCCO, Taroudant, High Atlas, Charpin et al., 324 (W); *E. crassifolium* (Desf.) DC.: F\*, 231, TUNISIA, Aldasoro 3069 (MA); *E. crinitum*: A\*, 73, AUSTRALIA, Olympic Damp Mine, *Badman* s.n. (MA); *E. cygnorum*: A\*, 75, AUSTRALIA, Mukimbudin, *Dodd* 559 (MEL); *E. daucoides*: X\*,



563, SPAIN, Burgos, Sargentos de Lora, *Aldasoro and Alarcón* 8831 (MA); *E. foetidum* (L.) L'Hér.: X\*, 737, SPAIN, Teruel, Javalambre, *Aldasoro and Alarcón* 9213 (MA); *E. gaillardotii*: X\* (D), 353, TURKEY, Malatya, Muñoz et al. 4567 (MA); *E. geoides*: A, 32, CHILE, Coquimbo, Taylor s.n. (MO); *E. glandulosum* (Cav.) Willd.: X\*, 516 (Simón et al. 2000); 690, SPAIN, Palencia, Valdecebollas, *Aldasoro and Alarcón* 8832 (MA); *E. glaucophyllum*: F\*, 173, TUNISIA, Moulares, *Aldasoro* 3043 (MA); *E. gruinum*: A\*, 198, JORDANIA, Gerassa, Vargas s.n. (MA); *E. guicciardii* Boiss.: X\* (D), 312, TURKEY, Karaburun, *Aldasoro et al.* 9178 (MA); *E. guttatum*: F\*, autocompatibility increases in autumn, P:O mean: 208 (sd: 106); april: 294 (sd: 110), june: 144 (sd: 63.7), october: 87 (sd 9.2), Cult. in MA garden from seeds taken in Morocco, Azrou, Jury s.n. (MA); Cultivated in MA garden from plants taken in Tunisia, Kabil, collected by *Aldasoro* 3024 (MA); *E. henderkii* Alpiner: X (D), 433, TURKEY, Lazistan, *Aucher-Eloy* (P); Gumushane, *Alpiner s.n.* (ISTE); *E. hoefianum*: A\*, 108, TURKEY, Göreme, Nevsehir, Muñoz et al. 4626 (MA); *E. jahandiezianum*: X-F\*, 506, MOROCCO, Agadir, Titeki, Blanché et al. 9376 (SEV); *E. janszii* Alarcón et al.: A\*, 44, AUSTRALIA, Fraser Range, *Helms s.n.* (MEL); *E. laciniatum* (Cav.) Willd.: A\*, 258, Cult. in MA, MOROCCO, unknown procedure (MA); *E. lucidum* Lapeyr.: X\*, 684, SPAIN, Lérida, Senet, *Aldasoro and Alarcón* 8838 (MA); *E. macrocalyx* (G. López) López Udias et al.: X\*, 414, SPAIN, Cuenca, Tragacete, *Aldasoro and Alarcón* 9216 (MA); *E. malacoides*: A\*, 175, SPAIN, Salamanca, *Aldasoro and Alarcón* 3472 (MA); *E. manescavii* Coss.: X\*, 722, FRANCE, Bilheres, *Aldasoro and Alarcón* 8837 (MA); *E. maritimum* (L.) L'Hér. ex Aiton: A, 68, SPAIN, Formentera, Sáez s.n. (MA); *E. moschatum* (L.) L'Hér. ex Aiton: A, 181, SPAIN, Madrid, *Aldasoro s.n.* (MA); *E. mouretii* Pit.: X\*, 1255, SPAIN, Huelva, Alange, Moreno 9 (MA); *E. nervulosum* L'Hér.: X, 574, ITALY, Puglia, *Steinberg s.n.* (MAF); *E. neuradiifolium*: A\*, 102, MOROCCO, Oujda, *Mateos and Valdés s.n.* (SEV); *E. oxyrrhynchum*: A\*, 76, ARMENIA, Aragat Mts., *Herrero s.n.* (MA); *E. paularense*: X\*, 1023, SPAIN, Guadalajara, Cañamares, *Aldasoro and Alarcón* 8835 (MA); *E. pelargoniflorum*: X\*, 603, TURKEY, Ermenek-Anamur, *Aldasoro et al.* 9150 (MA); *E. recoderi* Auriault & Guitt.1: X\*, 1728, SPAIN, Cádiz, Tavirana, *Aldasoro and Alarcón* 5015 (MA); *E. recoderi* 2: X\*, 712, SPAIN, Málaga, Puerto de las Palomas, *Aldasoro and Alarcón* 5019 (MA); *E. rupicola* (Boiss.) Boiss.: X, 991, SPAIN, Almería, Calar Alto, *Aldasoro and Alarcón* 9218 (MA); *E. reichardii* (Murray) DC.: X-F\*, autofertility higher in autumn, 540, Cult. in MA plants collected in Spain, Mallorca, Formentor, *Aldasoro and Alarcón* 9222 (MA); *E. rupestre* (Pourr. ex Cav.) Cadevall: X\*, 1049, SPAIN, Lérida, Trem, Sierra de Gulp, *Aedo* 4782 (MA); *E. ruthenicum* M. Bieb.: X (D), 498, UKRAINE, Dnepropetrovskaia, *Deryjova s.n.* (LE); *E. sanguis-christi* Sennen: X\*, 464, SPAIN, Castellón, Peñíscola, *Aldasoro and Alarcón* (MA); *E. sebaceum*: X\*, 846, Morocco, Aguelmane, *Devesa s.n.* (SEV); *E. stephanianum*: A\*, 195, Cult. in MA from seeds taken in Qinghai, China, Ho et al. (MA); *E. tataricum* Willd.: X, 980, RUSSIA, Jakasia, Abakan, *Titov s.n.* (LE); *E. texanum*: F\*, 74, USA, Texas, Post, *García & Martín* (MA); *E. tibetanum* Edgew. in Hook. f.: A, 160, CHINA, Laddakh, *Margalef Mir s.n.* (BC); *E. torádylioides*: X\*, 1124, SPAIN, Cadiz, Zahara, *Aldasoro and Alarcón* 5022 (MA); *E. touchyanum* Delile ex Godr.: A-F\*, 371, MOROCCO, Taza, *Jury* 13801 (SEV); *E. trichomanifolium* L'Hér.: X\* (D), 512, TURKEY, Karaman-Ermenek, *Aldasoro et al.* 9119 (MA); *E. trifolium* (Cav.) Cav.: X\*, 1335, TUNISIA, Rohnia, *Aldasoro et al.* 5033 (MA).

*Geranium aculeolatum*: X-F\*, 440, TANZANIA, Kilimanjaro, *Schlieben* 4379 (MA); *G. aequale* (Bab.) Aedo: A, 146, GREAT BRITAIN, Cirester, *Airy Shaw s.n.* (MA); *G. albanum*: X\*, 880, GEORGIA, Kiziki, *Sachokia s.n.* (MA); *G. albicans* A. St-Hil., A-F, 160, Uruguay, Timote, *Rossengutt* 5290 (MA); *G. arachnoideum* A. St-Hil.: X-F, n, BRASIL, Itatiaia, *Alves & Marín* 2762 (MA); *G. arboreum* A. Gray: X, 840, HAWAI, Maui, Haleakala, *Stauffer and Gillett* 5888 (P); *G. aristatum*: X, 804, MACEDONIA, Mavrovo Lake, *Frost Olsen* 6377 (MA); *G. asphodeloides*: X\*, 1048, TURKEY, Evcler, *Kav Dagh Castroviejo* 15220 (MA); *G. atlanticum* Boiss.: X, 710, Cult. in Reading from seeds taken in Morocco, Beni Snassen, *Aedo* 5431 (MA); *G. austroalpinum*: X\*, 976, ITALY, Abruzzo, *Herrero et al.* 2073 (MA); *G. azureoloides*: F-A, 184, COLOMBIA, *Aedo et al.* (2002); *G. berterioanum* Colla: A, 96, CHILE, Magallanes, P° Natales, *Aedo* 7468 (MA); *G. bicknellii*: A\*, 140, Cult. in MA, *Aedo s.n.* (MA); *G. biuncinatum*: A, 32, YEMEN, Hilla-Attuba, *Wood* 3126 (MA); *G. bohemicum* L.: A-F\*, 216, SPAIN, Zamora, *Ribadelago, Montserrat s.n.* (MA); *G. brasiliense*: X-F, 360, BRASIL, S. Catarina, *Pereira & Pabst* 6170 (MA); *G. brevicaulis* Hook.: A-F\*, 136, Cult. in MA, *Aedo* 4475 (MA); *G. Brycey*: X\*, 456, Cult. in MA; *Aedo* 4474 (MA); *G. caeruleatum* Schur: X\* (GD), 529, Bulgaria, Mt Vitosha, *Alarcón et al.* 203 (MA); *G. caespitosum*, X-F, n, USA, Colorado, Clear Creek, *Nieto Feliner* 2288 (MA); *G. caffrum*: X, 242, Cult. in MA, *Aedo* 4472 (MA); *G. campii* H. E. Moore: A, 170, ECUADOR, *Aedo et al.* (2002); *G. carolinianum* L.: A\*, 118, USA, Alabama, Flat Creek, *Diamond* 13019 (MA); *G. cataractarum*: X\*, 916, SPAIN, Jaén, Nava de S Pedro, *Soriano* 3191 (MA); *G. cinereum*: X\*,

1020, SPAIN, Santander, Castrovalnera, *Aldasoro and Alarcón* 9201 (MA); *G. columbinum*: A\*, n, SPAIN, Castellón, Peñagolosa, *Aedo & al. sn.* (MA); *G. collinum* Stephan ex Willd.: X\*, 736, SPAIN, Cuenca, Uña, *Aldasoro and Alarcón* 8627 (MA); *G. core-core*: A-F, 159, CHILE, Antofagasta, *Aedo* 7073 (MA); *G. costarricense*: X-F\*, 428, Cult. in MA from seeds taken in Costa Rica, Chirripó, *Aedo et al.* (2002); *G. crassipes* Hook. Ex A. Gray: F, 208, PERÚ, *Aedo et al.* (2002); *G. crenophyllum* Boiss.: X, 994, LEBANON, Ehden, *Pabot s.n.* (G); *G. cuneatum* subsp. *hololeucum* (A. Gray) Carlquist & Bissing: X-F, 256, SANDWICH ISLANDS, *Remy* 628 (P); *G. digitatum* R. Knuth: X, 628, PERÚ, *Aedo et al.* (2002); *G. dissectum* L.: A, 112, Spain, Teruel, Valderrobles, *Aedo et al.* 5077 (MA); *G. divaricatum* Ehrh.: A, 124, TURKEY, Ghumushane, *Herrero et al.* 1467 (MA); *G. dolomiticum*: X, 1078, SPAIN, Leon, Villanueva de Valdelosa, *Valdés* 9792 (MA); *G. ecuadoriense* Hieron.: F, 230, ECUADOR, Chimborazo, Guaranda, *Luteyn* 11074 (MA); *G. endressii*: X\*, 1086, Cult. in Jaca from seeds collected in E. Pirineos, France, *Montserrat* 922 (MA); *G. erianthum* DC.: X, 822, RUSSIA, Kuriles Is., *Gage s.n.* (MA); *G. exallum* H. E. Moore: F-A, 218, ECUADOR, *Aedo et al.* (2002); *G. fallax* Steud., A-F, 124, BOLIVIA, Potosi, *Schulte* 92 (MA); *Calacoto*, *Beck* 2401 (MA); *G. favosum* Steud.: F, 340, LEBANON, Sinpe, *Hohenaker* 1854 (MA); *G. foreroi* Aedo: X, F, 442, COLOMBIA, S. Nevada de Santa Marta, Pico J. Hilario, *Forero* 635 (MA); *G. glaberrimum*: X\*, 902, TURKEY, Karajonan Gecidi, *Aldasoro et al.* 9168 (MA); *G. glanduligerum* R. Knuth in Engler: F, 310, BRASIL, Sao Paulo, Jordao, *Teixeira* 337 (MA); *G. gracile*: X\*, 669, TURKEY, Trabzon, *Valcarcel* 370VV01 (MA); *G. gymnocaulon*: X, 946, GEORGIA, Abjasia, Mts. Dzyra-Mts. Cipsira, *Kolakovsky s.n.* (LE); *G. holosericeum* Willd. ex Spreng.: X, 418, COLOMBIA, Cundinamarca, Sumapaz, *Pedraza et al.* 320 (MA); *G. humboldtii* Spreng.: F, 240, ECUADOR, Volcan Antisana, La Mica, *Vargas & Narváez* 2151 (MA); *G. ibericum* Cav.: X, 1096, GEORGIA, S Ossetia, Ermani-don, *Gochina s.n.* (MA); *G. incanum* Burm. f.: X\*, 452, SOUTH AFRICA, Cape, Kirstenboch Garden, *Aldasoro et al.* 9097 (MA); *G. jahnii* Standl.: F, 266, VENEZUELA, Páramo de Jabón, *Trujillo, Riina et al.* 597 (MA); *G. kilimandscharicum* Eng.: A, 90, TANZANIA, Kilimanjaro, unknown collector (P); *G. kotschy* Boiss., X\* (GD), n, Cult. in MA from seeds collected in Iran, Kosh-e-Yelag, *Aedo* 9888 (MA); *G. krameri* Franch. & Sav.: X\*, 618, Cult. in MA from seeds collected by Compton in Kaybang, S Korea; *Alarcón and Aldasoro s.n.* (MA); *G. lanuginosum* Lam.: A-F\*, 196, SPAIN, Barcelona, Mataró, *Montserrat s.n.* (MA); *G. libani* P. H. Davis: X, 1560, TURKEY, Iskenderun, *Nydegger* 45264 (G); LEBANON, Feinour, Keibrouan, *Gombault* 1145 (MA); *G. libanoticum* A. Schenck: X, 846, LEBANON, *Pabot* (G); *G. linearilobum* DC. in Lam. & DC.: X (GD), n, KAZAKHSTAN, Ala Tau, *Levichev s.n.* (MA); *G. lucidum* L.: A\*, 69, SPAIN, Coruña, *Amigo s.n.* (MA); *G. macbridei* Aedo: X-F, 396, PERÚ, *Aedo et al.* (2002); *G. macrorrhizum*: X\*, 472, CROATIA, Krasno-Jablanc, *Frost Olsen* 5202 (MA) and cult. in MA; *G. macrostylum* Boiss.: X, n, TURKEY, Lydia, Boissier 46 (P); *G. maculatum* L.: X\* (GD), 1062, Cruden (1977); *G. maderense* Yeo: X\*, 562, MADEIRA IS., Bica de Cana, *Aedo* 9696 (MA); *G. magellanicum* Hook. f.: A-F, 144, CHILE, La Araucania, Volcán Llaima, *Aedo* 7224 (MA); *G. makmelicum* Aedo: X, 756, LEBANON, Cedres, *Gombault* 1143 (MA); *G. malviflorum* Boiss. & Reut.: X, 668, SPAIN, Granada, S<sup>a</sup> Nevada, *Smellson* (G); *G. maniculatum* H. E. Moore: A, 176, ECUADOR, *Aedo et al.* (2002); *G. mascatense* Boiss., F\*, 288, Cult. in MA from seeds collected in Oman, *Aedo* 6083 (MA); *G. molle* L. *Geranium*: molle: A\*, 152, SPAIN, Salamanca *Alarcón and Aldasoro s.n.* (MA); *G. moupinense* Franch.: X, 686, CHINA, Tibet, Moupin, *David* 1870 (MA); *G. multiceps* Turcz.: X, 378, VENEZUELA, Trujillo, *Guirigai, Dorr* 9133 (MA); *G. multipartitum* Benth.: A, 166, ECUADOR, *Aedo et al.* (2002); *G. nivale* R. Knuth: X-F, 416, PERÚ, *Aedo* (2002); *G. nepalense* Sweet: F-X, 228, JAPAN, Hokkaido, Shireteki, *Estébanez s.n.* (MA); *G. nodosum*: X\*, 702, ITALY, Abruzzo, *Herrero et al.* 1955 (MA); *G. oregonum* Howell: X\* (GD), 1326, Cult. in MA from seeds collected in USA, *Aedo s.n.* (MA); *G. orientali-tibeticum* R. Knuth: X, 620, CHINA, Tibet, Ta-tien-lou, *Drake* 553 (MA); *G. ornithopodon* Eckl. & Zeyh.: X, 460, SOUTH AFRICA, Queenstown, *Cooper* 434, (MA); *G. palmatum*: X\*, 700, PORTUGAL, Madeira, Cantias, *Medina* 2448 (MA); *G. paludosum* R. Knuth, F, 280, COLOMBIA, *Aedo et al.* (2002); *G. palustre* L., X\*, 816, CHEKIA, Kost, *Castroviejo et al.* 15640 (MA); *G. pavonianum* Bricq.: A, 152, PERÚ, *Aedo et al.* (2002); *G. peloponnesiacum* Boiss.: X, 1185, GREECE, Mesolongiou, *Nielsen* 11132 (UPA); *G. phaeum*: X\*, 1020, BOSNIA, Jajce, *Krach* 3075 (MA); Bulgaria, Mt Vitosha *Alarcón and Aldasoro s.n.* (MA); *G. platyptetalum*, Fisch. ex C. A. Mey.: X\*, 1371, TURKEY, Rize, *Nisa et al.* 893 (MA); *G. potentilloides* L'Her ex DC.: A\*, 112, Cult. in MA *Alarcón and Aldasoro s.n.* (MA); *G. pratense* L.: X\*, 1100, SPAIN, Madrid, Montejo, *Aldasoro s.n.* (MA); *G. pseudosibiricum* J. Mayer: X\* (GD), 568, Cult. in MA from seeds collected in Russia by Krutshcherovskaya, Turyga river, Irkusk; *Alarcón and Aldasoro s.n.* (MA); *G. psilostemon* Ledeb.: X\* (GD), 860, TURKEY, Rize, *Nisa et al.* 765 (MA); *G. purpureum* Vill.: A, 61, Herrera (1991); *G. pyrenaicum*: F-X\*, 562, SPAIN, Santander, *Alarcón and*



*Aldasoro s.n.* (MA); *G. reflexum*: X\*, 766, ITALY, Pescara, Vado di Sole, Navarro et al. 4219 (MA); *G. renardii* Trautv. in Trautv.: X\*, 1430, RUSSIA, N Ossetia, Busch s.n. (LE); *G. retrorsum* L'Her ex DC.: A, 80, HAWAI, Waimea, Hosaka 3590 (P); *G. reuteri* Aedo & Muñoz-Garm.: F-A\*, 362, SPAIN, Tenerife, Pico Villanos, Navarro et al. 3098 (MA); *G. rhomboidale* H. E. Moore: A, 164, COLOMBIA, Aedo et al. (2002); *G. richardsonii* Fisch. & Trautv.: X (GD), 864, U.S.A., Colorado, Delta Co, Siplivinski 1755 (MA); *G. robertianum*: A\*, 110, SPAIN, Santander, Aldasoro s.n. (MA); 140-230, Cruden (1977); *G. ruizii* Hieron.: F-A, 232, PERÚ, Aedo et al. (2002); *G. sanguineum* L.: F-X\*, 612, SPAIN, Navarra, Petilla, Aizpuru 3865 (MA); *G. santanderiense* R. Knuth: X, 624, COLOMBIA, Cundinamarca Fernández 5156 (MA); *G. sericeum* Willd. ex Spreng.: X, F, 356, ECUADOR, Aedo et al. (2002); *G. sessiliflorum* Cav.: A\*, 140, CHILE, Magallanes, Puerto Arenas, Aedo 7486 (MA); *G. sibbaldioides* Benth.: A, 150, PERÚ, Aedo et al. (2002); *G. sibiricum* L., X, n, JAPAN, Hokkaido, Estébanez (MA); *G. sinense* R. Knuth in Eng.: X\*, 494, Cult in MA from seeds collected in China, Yunnan, Ou Kia Tsen, Aldasoro s.n. (MA); *G. sintenisii* Freyn: X, 996, TURKEY, Torul-Trabzon, Nisa et al. 712 (MA); *G. skottsbergii* R. Knuth: A\*, 164, CHILE, Valparaíso, Papudo, Aedo 6824 (MA); *G. soboliferum* Kom.: A, 138, JAPAN, Hiroshima, Kagasuyama Park, Estébanez s.n. (MA); *G. solanderi* Carolin: A, 150, AUSTRALIA, Hume, Canning 4410 (L); *G. stramineum* Triana & Planch.: A, 142, ECUADOR, Aedo et al. (2002); *G. strictipes* R. Knuth: F-A, 232, Cult. in Wakehurst Garden from seeds taken in Yunnan, China, Aedo 3886 (MA); *G. subargenteum*: X\*, 1464, SPAIN, Santander, Alto Campoo, Aldasoro and Alarcón 9196 (MA); *G. sylvaticum*: X\* (GD), 820, SPAIN, Santander, Portillo de la Lunada, Aldasoro et Alarcón 9209 (MA); *G. suzukii* Masam.: F\*, 212, Cult. in MA, Aedo 4779 (MA); *G. thunbergii* Siebold ex Lindl. & Paxton: F-A, 180, Cult. in MA, Aedo 3046 (MA); *G. tovarii* Aedo, A, F, 254, Perú, Aedo et al. (2002); *G. transbaicalicum* Serg.: X, 862, RUSSIA, Siberia, Zabalkaskaia, river Nercha, Sukachev 1153 (MA); *G. tuberosum*: X\* (GD), n, TURKEY, Erzurum, Palandoken dag, Herrero 1732 (MA); *G. versicolor* L.: X\*, 954, ITALY, Sicilia, Nebrali, García et al. 1481 (MA); *G. viscosissimum* Fisch. & C. A. Mey. in C. A. Mey.: X\*, 994, USA, Montana, Mt Gallatin. Summers, 9312 (MA); *G. wallichianum* D. Don ex Sweet: X\*, 446, Cult. in P from seeds collected in India, Aedo 5170 (MA); *G. weddellii* Bricq.: X, 560, BOLIVIA, Aedo et al. (2002); *G. wilfordii* Maxim.: A, 148, CHINA, Tchen-keoutien, Farges s.n. (MA); *G. wlassowianum* Fisch. ex Link.: X, n, RUSSIA, L. Baikal, Komovalev (MA); *G. yesoense*: X, 1008, JAPAN, Toyama, Komado, Kagasuyama Park, Estébanez s.n. (MA); *G. yeoi* Aedo & Muñoz-Garm.: F, 194, PORTUGAL, Madeira, Cantias, Aedo 6694 (MA).

*Hypseocharis pimpinellifolia* J. Remy: X 6048, ARGENTINA, Jujui, Volcán Jumbaya, Venturi 4952 (MA).

*Monsonia angustifolia*: A\*, n, SOUTH AFRICA, Albert, Gerrard 1431 (W); *M. attenuata* Harv.: X, 1605, SOUTH AFRICA, Natal, Cooper s.n. (MA); *M. brevirostrata* Knuth: A-F\*, 288, SOUTH AFRICA, Harrismith, Tafelroop, Krook 2220 (W); *M. burkeana* Planch. ex Harv.: X, 563, ZIMBABWE, Bulawayo, Heany 23 (COI); *M. camdeboense*: X\*, n, SOUTH AFRICA, Craddock, Cooper 491 (COI); cult. in MA garden from seeds supplied by Silverhill seeds, Aldasoro s.n. (MA); *M. ciliata* (Moffet) Albers: X\*, 7337, SOUTH AFRICA, Steinkopf-Violdrof, Aldasoro 9038 (MA); *M. crassicaule*: X\*, n, SOUTH AFRICA, Castroviejo 14931 (MA); *M. emarginata*: X\*, 2840, South Africa, East London, Phillipson 379 (UPS); South Africa, cult. in MA Garden from seeds supplied by Silverhill seeds, Aldasoro s.n. (MA); *M. glauca* Knuth: X, 1007, BOTSWANA, Great Lasgutu, Smith 3258 (MO); *M. grandifolia* Knuth: X, 3835, SOUTH AFRICA, Natal, Alexandra, Rudatis 1342 (W); *M. herrei* (L. Bol.) Albers: X, 4150, SOUTH AFRICA, Steinkopf-Violdrof, Aldasoro 9042 (MA); *M. inerme* (Rehm.) Albers: X\*, n, Cult. in Kirstenbosch Garden, Aldasoro s.n. (MA); *M. lanuginosa* Knuth: X, 3245, SOUTH AFRICA, Natal, Uporne Berg, Slechter 4734 (COI); *M. lheritieri* (Sweet) Albers: X\*, 5730, SOUTH AFRICA, Garies-Bitterfontein, Aldasoro 9078 (MA); *M. longipes* Knuth: X, 364, KENIA, Nairobi-Namanga, Polhill and Paulo 1012 (B); *M. luederitziana* Focke & Schinz: X\*, 1067, NAMIBIA, Swakop-Klein Karas, Aldasoro 9074 (MA); *M. marlothii*: X, n, NAMIBIA, Swakopmund, Khan canyon, Vargas (MA); *M. mossamedense* (Welw. ex Oliv.) Albers: X\*, n, ANGOLA, Mossamedes, Excdel and Mendonça 21775 (COI); *M. multifida*: X\*, n, cult. in MA Garden from seeds collected in Kirstenbosch Garden (MA); *M. nivea*: A\*, 128, cult. in MA garden from seeds collected in Morocco, Taoujgalt, Alto Atlas, Staudinger s.n. (MA); *M. parvifolia*: X, n, NAMIBIA, Naroep, Schlechter s.n. (W); cult. in MA Garden from seeds provided by Silverhill Seeds (MA); *M. pattersonii* (DC.) Albers: X\*, 4965, SOUTH AFRICA, Aus-Witputz, Aldasoro 9054 (MA); *M. praemorsa*: X, 3900, SOUTH AFRICA, Natal, Clairmont, Wood s.n. (W); *M. salmoniflora* (Moffet) Albers: X\*, 4601, SOUTH AFRICA, Aus-Witputz, Aldasoro 9049, 9053 (MA); *M. senegalensis* Guillemin & Perrottet: A\*, 193, CABO VERDE, Maio, Cardoso de Matos 6269 (MA); *M. speciosa*: X, 11753,

SOUTH AFRICA, Cape, Krasse s.n. (MA, P); *M. trilobata* Kers: X\*, n, NAMIBIA, Keetmanshop, Narubis, Aldasoro s.n. (MA); *M. umbellata* Harvey: X, 257, NAMIBIA, Namibrand Karibib, Seydel 2947 (COI); *M. vandierietiae*: X, 4930, SOUTH AFRICA, cult. in Kirstenbosch Garden (MA).

*Pelargonium acraeum* R. A. Dyer: X\*, n, SOUTH AFRICA, Steinkopf, Anenous Pass, Aldasoro 9040 (MA); *P. alchemilloides* (L.) L'Herit.: F-A\*, 178, SOUTH AFRICA, cult. in Kirstenbosch Garden, Aldasoro 9091 (MA); *P. althaeoides*: X, n, SOUTH AFRICA, cult. at Stellenbosch Garden, Aldasoro s.n. (MA); *P. aridum* R. A. Dyer: X, n, cult. in Madrid Garden, Aedo s.n. (MA-591592); *P. australe*: A, 108, AUSTRALIA, Rechner (MA); *P. betulinum* (L.) L'Herit.: X\*, 718, SOUTH AFRICA, cult. in Kirstenbosch Garden, Aldasoro 9092 (MA); *P. caucalisifolium* Jacq.: X\*, 483, SOUTH AFRICA, Yzerfontein-Darling, Aldasoro 9025(MA); *P. chamaedrifolium* Jacq.: X\*, n, SOUTH AFRICA, Franshoek Pass, Strey s.n. (COI); SOUTH AFRICA, cult. in Kirstenbosch Garden, Aldasoro s.n. (MA); *P. cotyledonis*: cult. in Kew Gardens, Aedo 3837 (MA); *P. cortussifolium* L'Herit.: X\*, 645, SOUTH AFRICA, Pomona, Dinter s.n. (MA); *P. crithmifolium* J. E. Sm.: X, 1100, SOUTH AFRICA, Kippantvievier, Tambs s.n. (P); *P. cucullatum* (L.) L'Herit.: X\*, n, SOUTH AFRICA, Slankopf, Aldasoro 9096 (MA); *P. denticulatum* Jacq.: X\*, 652, SOUTH AFRICA, cult. in Kirstenbosch Garden, Aldasoro and Alarcón 306 (MA); *P. elongatum* (Cav.) Salisb.: X\*, 223, SOUTH AFRICA, cult. at Stellenbosch Garden, Aldasoro s.n. (MA); *P. endllicherianum* Fenzl.: X\*, 1232, TURKEY, Ermenek-Anamur, Aldasoro 9148 (MA); *P. fulgidum* (L.) L'Herit.: X\*, 910, SOUTH AFRICA, Nuwerus, Aldasoro 9035 (MA); *P. glutinosum* (Jacq.) L'Herit.: X\*, 526, SOUTH AFRICA, cult. at Kirstenbosch Garden, Aldasoro 9096 (MA); *P. grossularioides* (L.) L'Herit.: A-F, n, MOZAMBIQUE, Ilha da Inhaca, A. Reis Moura 738 (MA); *P. incarnatum* (L'Herit.) Moench.: X, 460, SOUTH AFRICA, Cape, Drege 1838 (P); *P. inodorum* Willd.: A, 228, AUSTRALIA, Rechner (MA); *P. luridum* (Andr.) Sweet: X, 390, SOUTH AFRICA, Namaqualand, Reis Moura (MA); *P. minimum* (Cav.) Willd.: A-F\*, n, SOUTH AFRICA, SW Cape, Aldasoro s.n. (MA); Paarlberg, Drege 1276 (P); *P. myrrhifolium*: X, 610, SOUTH AFRICA, Cape B. Esperanza, Cavanilles s.n. (MA); *P. ovale* (Burm.f.) L'Herit.: X, 696, SOUTH AFRICA, Barus Plaa, Slechter 9139 (COI); *P. pseudofumarioides* Knuth: A-F\*, 163, SOUTH AFRICA, Cape, Citrusdal, Aldasoro s.n. (MA); *P. reniforme* (Andr.) Curt.: X, 361, SOUTH AFRICA, Fiahamstown, Mae Owan (P); *P. scabrum* (Burm. f.) L'Herit.: X\*, 315, SOUTH AFRICA, cult. in Kirstenbosch Garden, Aldasoro 9095 (MA); *P. stipulaceum* (L.f.) Willd.: X, 480, SOUTH AFRICA, Cape B. Esperanza, Cavanilles s.n. (MA); *P. tetragonum* (L.f.) L'Herit.: X\*, n, SOUTH AFRICA, cult. in Kirstenbosch Garden, Aldasoro s.n. (MA); *P. triste* (L.) L'Herit.: X, n, SOUTH AFRICA, Cape, Cavanilles s.n. (P); *P. whytei*: X, 860, MOZAMBIQUE, Mendonça s.n. (COI).

APPENDIX 3. Pollinators and visitors of Geraniaceae. We provide the following information: taxon, reference or sample data, total number of visitor taxa, visits per min (—: no data), time of observation in hours (—: unknown), visitors.

*Erodium alpinum* – Italy, L'Aquila, Abruzzo, Aedo et al. 8256 (MA), 10, 0.408, 4, **Coleoptera**: Bruchidae, Malachidae. **Diptera**: Syrphidae, Empididae, and Bombyliidae. **Hymenoptera**: Anthophoridae, Cymbicidae. **Lepidoptera**: Lycaenidae, Satyridae, Zygaenidae. *E. botrys* – Spain, Salamanca, Castellanos de Moriscos, Aldasoro and Alarcón 9250 (MA), 11, 0.05, 6, **Diptera**: Calliphoridae; Muscidae; Pipunculidae; Syrphidae: *Melanostoma sp.*, *Syrphus ribesii*. **Hymenoptera**: Andrenidae: *Andrena* sp., Anthophoridae: *Anthophora* sp., Chrysidae; Halictidae: *Halictus* sp.; Megachilidae: *Coelioxys* sp., Vespidae: *Polistes* sp. *E. chium* – Spain, Gerona, Cabo Norfeu, Aldasoro and Alarcón 9233 (MA), 5, 0.09, 4, **Coleoptera**: Oedemeridae. **Diptera**: Bombyliidae: *Bombylium maximum* Syrphidae: *Syrphus ribesii*. **Hymenoptera**: Andrenidae: *Andrena* sp., Halictidae: *Halictus* sp. *E. ciconium* – Spain, Madrid, Aldasoro 9249 (MA); Zaragoza, Molina de Aragón Aldasoro 9245; Cuenca, Hontecillas, Aldasoro 9241 (MA); Teruel, Santa Eulalia, Aldasoro 9244 (MA), 16, 0.153, 6, **Coleoptera**: Oedemeridae. **Diptera**: Calliphoridae; Muscidae; Pipunculidae; Syrphidae: *Episyrphus balteatus*, *Syrphus ribesii*. **Hymenoptera**: Andrenidae; Anthophoridae: *Mellecta* sp.; Halictidae: *Halictus* sp.; Ichneumonidae; Megachilidae: *Megachile* sp., *Macropis* sp.; *Osmia* sp., *Dasygopa* sp.; *Ceratina* sp.; Vespidae: *Polistes* sp. *E. cicutarium* – Spain, Salamanca, Castellanos de Moriscos, Aldasoro and Alarcón 9244 (MA); Jaen, P. Almadén, Aldasoro and Alarcón, 9262; Guadalajara, Checa, Aldasoro and Alarcón, 9282, 9, 0.13, 8, **Diptera**: Syrphidae: *Syrphus ribesii*, *Sphaerophoria* sp. Bombyliidae: *Bombylius maximus*; Muscidae; Empididae. **Hymenoptera**: Andrenidae; Halictidae: *Halictus* sp.; Tenthredinidae; Torymidae. *E. daucoideus* – Spain, Burgos, Sargentos de Lora, Aldasoro and Alarcón 8831, 9265 (MA); Guadalajara, Pálmaces de Jadraque, Aldasoro and Alarcón 8834 (MA); Granada, Mt. Cañadillas Alda-

oro and Alarcón 9217 (MA), 11, 0.11, 6, **Diptera**: Syrphidae: *Episyrphus balteatus*, *Sphaerophoria* sp., *Syrphus ribesii*, Bombyliidae: *Bombylius maximus*. **Hymenoptera**: Andrenidae: *Andrena* sp.; Cymbicidae; Formicidae; Halictidae: *Halictus* sp., *Lasioglossum* sp.; Apidae: *Apis mellifera*; Vespidae: *Eumenes* sp. *E. foetidum* – Spain, Teruel, Javalambre, *Aldasoro and Alarcón* 9213, 9263 (MA) Teruel, Puerto de Cabigorondo, *Aldasoro and Alarcón* 9213, 9243 (MA), Murcia, Sierra de Espuña, *Aldasoro and Alarcón* 9210, 9231, 9274 (MA); Jaen, Pico Almadén *Aldasoro and Alarcón* 9220, 9259; Gerona, Cabo Norfeu, *Aldasoro and Alarcón* 9253, 9224 (MA), 17, 0.178, 36, **Coleoptera**: Oedemeridae. **Diptera**: Bombyliidae: *Bombylius* sp., Empididae, Muscidae, Phoridae, Tachinidae, Syrphidae: *Syrphus ribesii*, *Volucella* sp., *Scaeva albomaculata*, *Sphaerophoria scripta*. **Hymenoptera**: Andrenidae: *Andrena*, Anthophoridae, Formicidae, Halictidae: *Halictus*, Ichneumonidae, Platigasteridae, Sphecidae. *E. glandulosum* – Spain, Palencia, Valdecebollas, *Aldasoro and Alarcón* 8832 (MA); Teruel, Puerto del Portillo, *Aldasoro and Alarcón* 8828 (MA), 8, 0.12, 12, **Diptera**: Syrphidae: *Syrphus ribesii*, *Scaeva* sp. **Hymenoptera**: Cymbicidae, Andrenidae: *Andrena* sp., Halictidae: *Halictus* sp., *Lasioglossum* sp., Sphecidae. *E. glandulosum* – Simon et al. (2000), Palencia, Valdecebollas, *Aldasoro and Alarcón* 8832 (MA); Teruel, Puerto del Portillo, *Aldasoro and Alarcón* 8828 (MA), 10, —, —, **Coleoptera**: Oedemeridae: *Oedemera* sp.; Chrysomelidae: *Clytra* sp.; Curculionidae: *Miarus* sp.. **Diptera**: Syrphidae: *Syrphus ribesii*, *Scaeva* sp., *Paragus* sp. **Heteroptera**: Miridae: *Amirida* sp. **Hymenoptera**: Formicidae: *Formica* sp., Halictidae: *Lasioglossum* sp., Sphecidae: *Stigma* sp. *E. glaucophyllum* – Tunisia, Moulares, *Aldasoro* 3043 (MA); between Tataouine and Chenini, *Bernardos s.n.* (SALA); Ghomrassen, *Bernardos s.n.* (SALA); between Mededine and Matmata, after Matameurtra, *Bernardos s.n.* (SALA);. between Matmata and Douz, km 76, *Bernardos s.n.* (SALA); between Djebel Tamezret and Hachichina near Chott El Fejaj, *Bernardos s.n.* (SALA), 12, 0.124, 6, **Coleoptera**: Chrysomelidae: *Lachnaia* sp., Anobiidae. **Diptera**: Asilidae: *Asilus* sp., Scathophagidae, Anthomiidae. **Hymenoptera**: Andrenidae: *Andrena* sp., Chrysididae: *Chrysis* sp., Halictidae: *Halictus* sp., *Lasioglossum* sp., *Doufurea* sp.; Ichneumonidae: *Ryssa* sp., Melittidae: *Melitta* sp. *E. macrocalyx* – Spain, Cuenca, Tragacete, *Aldasoro and Alarcón* 8825, 9216 (MA); Cuenca, Masegosa, *Aldasoro and Alarcón* 8824, 9214 (MA), 8, 0.08, 4, **Diptera**: Syrphidae: *Scaeva* sp., Muscidae. **Hymenoptera**: Andrenidae: *Andrena* sp.; Halictidae: *Halictus* sp., *Lasioglossum* sp., Sphecidae. **Lepidoptera**: Lycaenidae. *E. malacoides* – Spain, Salamanca, *Aldasoro and Alarcón* 3472 (MA); Cuenca, Hontecillas, *Aldasoro and Alarcón* 9255, 9240 (MA); Murcia, Sierra de Espuña, *Aldasoro and Alarcón* 9233 (MA), 9, 0.142, 6, **Coleoptera**: Buprestidae. **Diptera**: Bombyliidae: *Bombylius maximus*, Syrphidae: *Syrphus ribesii*, *Episyrphus balteatus*. **Hymenoptera**: Andrenidae: *Andrena* sp., Anthophoridae, Halictidae: *Halictus* sp., Megachilidae: *Ceratina* sp. *E. paularensis* – Spain, Madrid, El Paular, *Aldasoro and Alarcón* 9239 (MA); Guadalajara, Cañamares, *Aldasoro and Alarcón* 8835, 9246 (MA), 15, 0.194, 7, **Coleoptera**: Mordellidae, Dermestidae. **Diptera**: Empididae; Platypocidae, Calliphoridae, Muscidae; Syrphidae: *Syrphus ribesii*. **Hymenoptera**: Anthophoridae: *Anthophora* sp., *Eucera* sp., Apidae: *Apis mellifera*. Halictidae: *Halictus*, Megachilidae: *Megachile* sp., Formicidae. Satyridae: *Coenonympha* sp. **Neuroptera**. *E. pelargoniflorum* – Turkey, between Ermenek and Anamur, *Aldasoro et al.* 9150 (MA), 9, 0.2, 3, **Coleoptera**: Dasytidae. **Diptera**: Syrphidae, Bombyliidae: *Bombylius* sp., and Muscidae. **Hymenoptera**: Anthophoridae: *Anthophora* sp., Apidae: *Psithyus* sp., Sphecidae, Sapygidae. **Lepidoptera**: Lycaenidae: *Lyssandra* sp.

*Geranium arboreum* – Medeiros and St John (1988): 1, —, —, Birds: Fringillidae. *G. austroaenninum* – Italy, Abruzzo, *Herrero et al.* 2073 (MA), 10, 0.383, 4, **Coleoptera**: Malachidae, Bostrychidae, Curculionidae, Meloidae, Oedemeridae. **Diptera**: Muscidae and Empididae. **Hymenoptera**: Apidae: *Apis mellifera*, Cymbicidae, Formicidae. *G. brevicaulis* – Philipp (1985): 4, —, 8–32, **Coleoptera**. Hemiptera. Formicidae. **Lepidoptera**: Lycaenidae. *G. caespitosum* – Goertz (2004): 11, —, —, **Hymenoptera**: Andrenidae: *Andrena*; *Hoplitis albifrons*, *Macropis*, Megachilidae: *Megachile mendica*. *G. caespitosum* – Hessing (1989): —, —, 6, **Hymenoptera**: Halictidae, Colletidae, Anthophoridae, Andrenidae, Apidae: *Apis mellifera*, and *Bombus* spp. *G. caespitosum* – Pleasants (1980): —, —, 3–12, **Hymenoptera**: Apidae: *Apis mellifera*, *Bombus flavifrons*, *B. bifarius*, **Diptera**. *G. cinereum* – Spain, Santander, Castrovalnera, *Aldasoro and Alarcón* 9201 (MA), 4, 0.167, 4, **Diptera**: Muscidae. **Hymenoptera**: Anthophoridae, Apidae: *Apis mellifera*, Halictidae: *Halictus* sp. *G. collinum* – Spain, Cuenca, Uña, *Aldasoro and Alarcón* 8627 (MA): 7, 0.189, 5, **Coleoptera**: Chrisomelidae. **Diptera**: Syrphidae, Conopidae. **Hymenoptera**: Andrenidae: *Andrena* sp., Apidae: *Apis mellifera* and Halictidae: *Halictus*. **Heteroptera**: Pentatomidae. *G. maculatum* Willson et al. (1979): 3, —, —, **Hymenoptera**: Andrenidae: *Andrena* sp., Apidae: *Apis mellifera*, *Bombus* sp. *G. molle* – Spain, Salamanca, Castellanos de Moriscos, *Aldasoro and Alarcón*, 9235,

9248 (MA), 6, 0.233, 6, Syrphidae: *Sphaerophoria* sp., *Leucozona* sp.; Empididae; Scathophagidae. **Hymenoptera**: Andrenidae: *Andrena* sp.; Halictidae: *Halictus* sp. *G. palustre* – Dlussky et al. (2000): 16, —, —, **Diptera**: Syrphidae: *Sphaerophoria* sp., *Helophilus pendulus*, *Episyrphus balteatus*, *Syrtrita pipiens*, *Episyrphus balteatus*; Empididae: *Empis livida*; Muscidae: *Phaonia basalis*, Antomyidae: *Phorbia* sp., Calliphoridae: *Melinda biseta*. **Hymenoptera**: Megachilidae: *Chelostoma* sp., Apidae: *Bombus* sp., Halictidae, Andrenidae: *Macropis fulvipes*. **Lepidoptera**: Hesperidae: *Hesperis comma*, Pieridae: *Pieris napi*. *G. phaeum* – Bulgaria, Mt Vitosha, *Aldasoro and Alarcón* 8821 (MA): 5, 0.083, 4, **Diptera**: Calliphoridae; Syrphidae: *Syrphus ribesii*; *Melanostoma* sp. **Hymenoptera**: Megachilidae: *Chelostoma* sp.; Halictidae: *Halictus calcaetum*. *G. pratense* – Proctor et al. (1996): 2, —, —, **Hymenoptera**: Halictidae: *Halictus*, Apidae: *Apis mellifera*. *G. pratense* – Dlussky et al. (2000): 2, —, —, **Hymenoptera**: Apidae: *Apis mellifera*, *Bombus* sp. *G. pratense* – Spain, Cult in MA, *Aldasoro* 9887 (MA): 6, 0.08, 4, Apidae: *Apis mellifera*; Scolidae: *Scolia* sp., Apidae: *Apis mellifera*, *Bombus* sp.; Colletidae; Megachilidae: *Anthidium* sp., *Coelioxys inermis*. *G. pyrenaticum* – Spain, Santander, Alarcón and *Aldasoro* 9261 (MA): 5, 0.133, 5, **Diptera**: Syrphidae: *Episyrphus balteatus*; *Rhyngia campestris*. Megachilidae, Halictidae: *Halictus* sp.; Colletidae. *G. reinii* – Yumoto (1986): 3, —, 70, Syrphidae: *Chrysotoxum* sp. **Hymenoptera**: Apidae: *Bombus beaticola*, *B. hypocrita*, *G. richardsonii* – Green (1978): 9, 0.012, 56, **Coleoptera**: Trichiotaenidae: *Trichodes* sp.; Apidae: *Bombus rufocinctus*, *B. bifarius*, *Apis mellifera*. **Lepidoptera**. *G. robertianum* – Tofts (2004): 35, —, —, **Coleoptera**: Meliridae; Byturidae; Curculionidae: *Limobius borealis*; *Zacla diuis exiguus*; Staphilinidae: *Anthobium* sp. **Diptera**: Cecidomyiidae, Syrphidae: *Rhyngia campestris*, *R. rostrata*, *Episyrphus balteatus*, *Syrtrita pipiens*, *Syrphus ribesii*; Empididae: *Empis* sp.; Agromyzidae: *Agromyza nigrescens*; Muscidae. **Hemiptera**. **Hymenoptera**: Megachilidae: *Anthidium manicatum*, *Stelis phaeoptera*, *Chelostoma campanularum*, *C. nigricorn*, *Coelioxys* sp.; *Osmia* sp. Halictidae: *Halictus calcaetum*, Andrenidae: *Andrena bicolor*; Apidae: *Apis mellifera*; *Bombus* sp. **Lepidoptera**: Pieridae: *Anthocharis cardamines*, *Leptidea sinapis*, *Pieris napi*, *P. rapae*; Pterophoridae: *Amblyptilia punctidiactyla*, *A. acanthidiactyla*. *G. robertianum* – Spain, Santander, *Aldasoro and Alarcón* 9201 (MA); *Syrphus ribesii*; *Sphaerophoria* sp., *Rhyngia campestris*; Empididae: *Empis* sp.; Muscidae. Andrenidae: *Andrena*; Halictidae: *Halictus* sp., Megachilidae: *Chelostoma* sp. *G. sanguineum* – Philipp and Hansen (2000): 1, —, 5, Apidae: *Bombus* sp. *G. sanguineum* – Spain, Madrid, El Escorial, *Aldasoro s.n.* (MA), **Diptera**: Conopidae; Syrphidae. **Hymenoptera**: Vespidae: *Polistes*, *Eumenes*, Megachilidae, Colletidae, Halictidae, Andrenidae. *G. subargenteum* – Spain, Santander, Alto Campoo, *Aldasoro and Alarcón* 9196 (MA), 7, 0.211, 6, **Diptera**: Syrphidae. **Hymenoptera**: Andrenidae, Apidae: *Apis mellifera*, *Bombus pratorum*; Halictidae: *Halictus* sp., Colletidae, Megachilidae. *G. sylvaticum* – Totland (1993): 7, 0.059, 35–40, **Diptera**: Muscidae: *Thricops aculeipes*, *T. nigrifellus*; Syrphidae: *Platycheirus manicatus*; Dolichopodidae: *Dolichopus plumipes* Anthomyiidae: *Pegoplata aestiva*. **Hymenoptera**: Apidae: *Bombus lapponicus*. **Lepidoptera**: Lycaenidae: *Albulina orbitulus*. *G. thunbergii* – Kandori (2002): 27, 0.209, 30, **Diptera**: Syrphidae: *Betasyrphus serarius*, *Sphaerophoria macrogaster*, *Episyrphus balteatus*, *Metasyrphus ferquens*, *Paragus haemorrhous*; Calliphoridae: *Stomorphina obsoleta*; Phasiidae: *Gymnosoma rotundata*. **Hymenoptera**: Apidae: *Bombus diversus*, *Apis cerana*. Colletidae: *Hylaeus* sp. Formicidae; Halictidae: *Lasioglossum scitulum*, *Lasioglossum* sp. Megachilidae: *Coelioxys fenestrata*, *C. yanonis*, *C. acuminata*, *Megachile tsurugensis*, *M. remota*, *Chalicodoma spissula*, *Ceratina iwatai*, *Ceratina* sp., Vespidae: *Polistes chinensis*, Eumenidae: *Eumenes samurai*. **Lepidoptera**: Pieridae: *Pieris rapae*, *Zizeeria maha*, *Lampides boeticus*, *Parnara guttata*, *Cephonodes hylas*. *G. viscosissimum* – Green (1978): 9, —, 56, **Coleoptera**: Trichodesonidae: *Trichodes* sp.; Empididae: *Empis livida*, *Mordella atrata*. **Hymenoptera**: Halictidae: *Dialictus*; Anthophoridae: *Anthophora terminalis*; Apidae: *Apis mellifera*, *Bombus rufocinctus*, *B. bifarius*, *B. occidentalis*. *G. yesoense* – Nakano and Washitani (2003): 7, —, 70, **Diptera**: Syrphidae. **Hymenoptera**: Halictidae, Andrenidae, Megachilidae, Apidae: *Bombus* sp. **Coleoptera**.

*Monsonia ciliata* – South Africa, Steinkopf-Viooldrof, *Aldasoro* 9038 (MA); 20 km to Nuwerus, *Aldasoro* 9035 (MA), 9, 0.275, 6, **Diptera**: Bombyliidae: *Exoprosopa* sp. **Hymenoptera**: Anthophoridae: *Amegilla* sp., Colletidae: *Hylaeus* sp.; Megachilidae: *Hoplitis* sp.; Vespidae: *Masarinae*: *Celonites*, Formicidae: *Myrmicaria* sp., *Crematogaster* sp. **Lepidoptera**: Lycaenidae, Gelechiidae: *Gelechia* sp. *M. drudeana* – Namibia, Garoeb, *Aldasoro* 9065 (MA); 1.5 Km of Garoeb *Aldasoro* 9068 (MA), 2, 0.005, 6, **Hymenoptera**: Formicidae: *Messor capensis*. **Lepidoptera**: Gelechiidae: *Gelechia* sp. *M. theritieri* – South Africa, Springbock, *Aldasoro* 9036 (MA); Garies-Bitterfontein, *Aldasoro* 9078 (MA), 3, 0.033, 4, **Diptera**: Bombyliidae: *Exoprosopa* sp.; Muscidae. **Hymenoptera**: Anthophoridae: *Amegilla* sp. *M. salmoniflora* – South Africa, Aus-Wiputz, *Aldasoro* 9049 (MA); 55 Km of



Aus, *Aldasoro 9054* (MA); S of Aus, *Aldasoro 9055* (MA), 2, 0.017, 4, **Hymenoptera**: Halictidae; Anthophoridae: *Amegilla* sp.

*Pelargonium alchemilloides* – Vogel (1954): 1, —, —, **Diptera**: Tabanidae: *Philoliche rostrata*. *P. alternans* – Struck (1997): 1, —, 4–15, **Hymenoptera**: Anthophoridae: *Amegilla niveata*. *P. antidysenthericum* – Scheltema and Van der Walt (1990): 1, —, —, **Diptera**: Bombyliidae: *P. appendiculatum* – Manning and Goldblatt (1997): 1, —, —, **Diptera**: Nemestrinidae: *Moegistorhynchus longirrostris*. *P. articulatum* – Struck (1997): 1, —, 4–15, **Diptera**: Tabanidae: *Philoliche rostrata*. *P. barkly* – Struck (1997): 1, —, 4–15, **Diptera**: Tabanidae: *Philoliche rostrata*. *P. betulinum* – Struck (1997): 1, —, 4–15, **Diptera**: Tabanidae: *Philoliche lateralis*. *P. burgerianum* – Struck (1997): 1, —, 4–15, **Diptera**: Bombyliidae: *Megapalpus capensis*. *P. candicans* – Struck (1997): 3, —, 4–15, **Hymenoptera**: Anthophoridae: *Amegilla spilostoma*; Apidae: *Apis mellifera*. **Coleoptera**: Scarabeidae: *P. capitatum* – Struck (1997): 5, —, 4–15, **Diptera**: Tabanidae: *Philoliche lateralis*; Nemestrinidae: *Prosoeca* sp. **Hymenoptera**: Megachilidae: *Hoplitis*; Vespidae: *Celonites bergewhaliae*, *C. wahlenbergiae*. *P. carneum* – Manning and Goldblatt (1995); Johnson in Struck (1997): 2, —, —, Lepidoptera: Nymphalidae: *Princeps* sp. *P. coronopifolium* – Albers pers. comm. in Struck (1997): 1, —, —, **Hymenoptera**: Apidae: *Apis mellifera*. *P. cortusifolium* – Manning and Goldblatt (1995, 1996): 2, —, —, **Diptera**: Nemestrinidae: *Prosoeca peringueyi*. *P. crassicaule* – Manning and Goldblatt (1995, 1996): 1, —, 4–20, **Diptera**: Nemestrinidae: *Prosoeca peringueyi*. *P. crispum* – Struck (1997): 1, —, 4–15, **Hymenoptera**: Anthophoridae: *Anthophora*. *P. crithmifolium* – Struck (1997): 2, —, 4–15, **Hymenoptera**: Anthophoridae: *Amegilla niveata*, *A. obscuriceps*. *P. cucullatum* – Marloth (1908): 1, —, 4–15, **Diptera**: Tabanidae: *Philoliche rostrata*. *P. denticulatum* – Van der Walt et al. (1990): 1, —, —, **Diptera**: Tabanidae: *Philoliche gulosa*. *P. dipetalum* – Manning and Goldblatt (1995): 1, —, —, **Diptera**: Nemestrinidae: *Prosoeca longipennis*. *P. dolomiticum* – Zietsman (1993): 1, 2.2, 8, **Hymenoptera**: Apidae: *Apis mellifera*. *P. echinatum* – Struck (1997): 1, —, 4–15, **Diptera**: Nemestrinidae: *Prosoeca peringueyi*. *P. elongatum* – Manning and Goldblatt (1995): 1, —, —, **Diptera**: *Philoliche rostrata*. *P. endlischerianum* – Turkey, Ermenek-Anamur, *Aldasoro 9148* (MA): 1, —, 4, **Lepidoptera**: Satyridae: *Neohipparchia statilius*. *P. flabellifolium* – Maggs pers. comm. in Struck (1997): 1, —, —, Birds: *Passeriformes*, Nectariniidae: *Nectarinia famosa*. *P. flabellifolium* – Albers pers. comm. in Struck (1997): 1, —, —, Birds: *Passeriformes*, Nectariniidae: *Nectarinia chalybea*. *P. fruticosum* – Struck (1997): 5, —, 4–15, **Hymenoptera**: Apidae: *Apis mellifera*. **Diptera**: Tabanidae: *Philoliche formosa*, *P. gulosa*. Lepidoptera: Nymphalidae: *Tarsocerus cassus*; Lycaenidae: *P. glutinosum* – Struck (1997): 2, —, 4–15, **Hymenoptera**: Apidae: *Apis mellifera*. *P. glutinosum* – South Africa, cult. at Kirstenbosch Garden, *Aldasoro 9096* (MA):

—, —, 4, **Hymenoptera**: Lepidoptera: Lycaenidae: *P. grossularioides* – Struck (1997): 1, —, 4–15, **Hymenoptera**: Apidae: *Apis mellifera*. *P. heterophyllum* – Struck (1997): 1, —, —, **Diptera**: Bombyliidae: *Megapalpus capensis*. *P. incrassatum* – Manning and Goldblatt (1996), Goldblatt et al. (1995), Steiner pers. comm. in Struck (1997): 1, —, 4–20, **Diptera**: Nemestrinidae: *Prosoeca peringueyi*. *P. klinghardtense* – Gess and Gess (2006): 2, —, —, **Hymenoptera**: Vespidae: Masarinidae: *Jugurtia* sp., *Masarina* sp. *P. laevigatum* – Struck (1997): 2, —, 4–15, **Diptera**: Tabanidae: *Philoliche formosa*, *P. gulosa*. *P. longicaule* – Goldblatt et al. (1995); Manning and Goldblatt (1997): 1, —, 4–20, **Diptera**: Nemestrinidae: *Moegistorhynchus longirrostris*. *P. longiflorum* – Struck (1997): 1, —, 4–15, **Diptera**: Bombyliidae: *Anastoechus phaleratus*. *P. luteolum* – Struck (1997): 2, —, 4–15, **Diptera**: Bombyliidae: *Lithorina macropterus*. *P. luteolum* – South Africa, Darling, *Aldasoro et al. 9027* (MA): 1, —, 4–15, **Diptera**: Bombyliidae: *Bombomya discoidea*. *P. magenteum* – Manning and Goldblatt (1995, 1996): 1, —, 4–20, **Diptera**: Nemestrinidae: *Prosoeca peringueyi*. *P. minimum* – Vogel (1954): 1, —, —, **Hymenoptera**: Formicidae: *P. myrrhifolium* – Struck (1997): 2, —, 4–15, **Diptera**: Bombyliidae. **Hymenoptera**: Megachilidae: *P. ocellatum* – Van der Walt et al. (1990): 4, —, 3, **Diptera**: Bombyliidae: *Megapalpus capensis*, *Lithorina* sp.; Tabanidae: *Philoliche angulata*. **Hymenoptera**: Apidae: *P. papilionaceum* – Albers pers. comm. in Struck (1997): 1, —, —, **Hymenoptera**: Apidae: *Apis mellifera*. *P. peltatum* – Struck (1997): 3, —, 4–15, **Coleoptera**: Scaraboidea: *Peritrichia capicola*. **Diptera**: Tabanidae: *Philoliche formosa*, *P. gulosa*. *P. pilosellifolium* – Struck (1997): 1, —, 4–15, **Hymenoptera**: Anthophoridae: *Amegilla spilostoma*. *P. pinnatum* – Manning and Goldblatt (1995, 1996) 1, —, —, **Diptera**: Nemestrinidae: *Prosoeca longipennis*. *P. praemorsum* – Struck (1997): 2, —, 4–15, **Diptera**: Bombyliidae: *Parisus eurhynatus*, *Systoechus scabrirrostris*. *P. rapaceum* – Struck (1997): 2, —, 4–15, **Hymenoptera**: Anthophoridae: *Amegilla atrocincta*, *A. spilostoma*. *P. scabrum* – Struck (1997): 5, —, 4–15, **Diptera**: Bombyliidae, Nemestrinidae. **Hymenoptera**: Apidae: *Apis mellifera*, Anthophoridae: *Amegilla niveata*. **Lepidoptera**: Lycaenidae: *Cacyreus marshalli*. *P. scabrum* – South Africa, cult. at Kirstenbosch Garden, *Aldasoro 9095* (MA): 2, —, 3, **Hymenoptera**: Anthophoridae. **Lepidoptera**: Papilionidae: *Papilio demodocus*. *P. sericifolium* – Goldblatt et al. (1995), Manning and Goldblatt (1995) 1, —, 4–20, **Diptera**: Nemestrinidae: Nemestrinidae: *Prosoeca peringueyi*. *P. spinosum* – Struck and Van der Walt (1996): 2, —, —, **Hymenoptera**: Anthophoridae: *Amegilla nivettata*, *A. diversipes*. *P. tricolor* – McDonald and Van der Walt (1992): 3, —, —, **Diptera**: Bombyliidae: *Megapalpus capensis*; Calliphoridae: *Cosmina fuscipennis*, *Rhyncomya maculata*. *P. trifoliatum* – Struck (1997), 1, —, —, **Diptera**: Bombyliidae: *Megapalpus capensis*.