

SYSTEMATICS AND PHYLOGENY

Linnaeus's folly – phylogeny, evolution and classification of *Sedum* (Crassulaceae) and Crassulaceae subfamily Sempervivoideae

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Abstract *Sedum*, containing approximately 470 species, is by far the largest genus of Crassulaceae. Three decades of molecular phylogenetic work have provided evidence for the non-monophyly of *Sedum* and many more of the 30 genera of Crassulaceae subfam. Sempervivoideae. In this study, we present a broadly sampled and dated molecular phylogeny of Sempervivoideae including 80% of all infrageneric taxa described in *Sedum* as well as most other genera of the subfamily. We used sequences of one nuclear (ITS) and three plastid markers (*matK*, *rps16*, *trnL-trnF*). The five major lineages of Sempervivoideae (i.e., Telephium clade, Petrosedum clade, *Sempervivum*/*Jovibarba*, Aeonium clade, Leucosedum plus Acre clades) were resolved as successive sister to each other in the phylogenetic analysis of the plastid markers, while in the ITS phylogeny the Petrosedum clade is the closest relative of the Aeonium clade. Our dating analysis of ITS suggests that Sempervivoideae diversified rapidly throughout the Paleocene and Eocene, possibly in the area of the former Tethys and Paratethys archipelago. A biogeographic pattern emerges in which migration out of this ancestral area is linked to pronounced morphological evolution resulting in several distinct lineages recognized as segregate genera thought to be derived from *Sedum*. These segregate genera, however, have been defined on the basis of strongly homoplasious characters such as degree of petal fusion, petal colouration or flower merism. Moreover, all character states currently used for the delimitation of segregate genera seem to be homoplasious, and each of them can be found in at least one species of *Sedum*. Extensive literature work led to the conclusion that only few of the monophyletic clades found by us can be defined unambiguously by morphological characters. Mainly for these two reasons, we believe that combination of all 14 genera currently recognized in tribe Sedeae (= clades Leucosedum plus Acre) into *Sedum* might be the most stable solution of the “*Sedum* problem”. This new *Sedum* s.l. would then comprise approximately 755 species.

Keywords hybridization; large genera; molecular dating; morphological evolution; rapid radiation

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

■ INTRODUCTION

Crassulaceae, a family of ca. 1410 species in 34 genera according to the latest family account by Thiede & Eggli (2007), contains three subfamilies, i.e., Crassuloideae, Kalanchoideae and Sempervivoideae. *Sedum* L., by far the largest genus of Sempervivoideae and indeed of Crassulaceae, contains ca. 430 species in the circumscription by Thiede & Eggli (2007), i.e., after treatment at generic rank of several lineages formerly classified as *Sedum* (see below). With the valid publication of 42 new species names since then, *Sedum* now contains ca. 470 species. In the first comprehensive molecular phylogeny of the family, Van Ham & Hart (1998) concluded that “*Sedum* is generally considered as a hold-all taxon that encompasses the least derived Crassulaceae as well as homoplastic or transitional phenotypes to nearly every other genus of the family.” These authors, based on an RFLP analysis of plastid DNA,

and Mort & al. (2001), based on *matK* sequences, identified five major groups within Sempervivoideae, referred to as clades by these authors although partly not supported or comprising two or three lineages of a larger polytomy. All these five “clades” contained species of *Sedum* or species included in *Sedum* in more or less recent accounts but also representatives of other genera. These five “clades” are: (1) Telephium clade (tribes Telephieae and Umbiliceae sensu Thiede & Eggli, 2007; containing *Hylotelephium* H. Ohba, *Kungia* K.T. Fu, *Meterostachys* Nakai, *Orostachys* Fisch., *Phedimus* Raf., *Pseudosedum* (Boiss.) A. Berger, *Rhodiola* L., *Sinocrassula* A. Berger and *Umbilicus* DC.; Mayuzumi & Ohba, 2004; Gontcharova & al., 2006); (2) Sempervivum clade (tribe Semperviveae sensu Thiede & Eggli, 2007; containing *Petrosedum* Grulich, *Sempervivum* L. and *Jovibarba* Opiz; the latter treated as synonym to *Sempervivum* by Thiede & Eggli, 2007, but as a distinct genus by Klein & Kadereit, 2015); (3) Aeonium clade (tribe

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Aeonieae sensu Thiede & Eggli, 2007; containing approximately 8 species of *Sedum* [Mes, 1995a] as well as *Aeonium* Webb & Berthel., *Aichryson* Webb & Berthel., *Monanthes* Haw. and *Hypagophytum* A.Berger; Mort & al., 2002; our study); (4) Leucosedum clade (tribe Sedeae/Leucosedum clade sensu Thiede & Eggli, 2007; containing ca. 120 *Sedum* species as well as *Pistorinia* DC., *Rosularia* (DC.) Stapf, *Prometheum* (A.Berger) H.Ohba, *Afrovivella* A.Berger, *Sedella* Britton & Rose and *Dudleya* Britton & Rose); and (5) Acre clade (tribe Sedeae/Acre clade sensu Thiede & Eggli, 2007; containing ca. 345 *Sedum* species as well as *Cremonophila* Rose [included in *Sedum* by Thiede & Eggli, 2007], *Echeveria* DC., *Graptopetalum* Rose, *Lenophyllum* Rose, *Pachyphytum* Link & al., *Thompsonella* Britton & Rose and *Villadia* Rose; Carrillo-Reyes & al., 2008, 2009). The clades Acre and Leucosedum together constitute Sedeae of subfam. Sempervivoideae. These five “clades” form a well-supported monophyletic group (Sempervivoideae sensu Thiede & Eggli, 2007) and, together with the largely African *Crassula* and *Kalanchoe* clades (Crassuloideae and Kalanchoideae, respectively, sensu Thiede & Eggli, 2007) as successive sisters (Van Ham & 't Hart, 1998; Mort & al., 2001) to this group, make up Crassulaceae. This classification of Crassulaceae and approximate species numbers in the above-listed groups are summarized in Table 1.

In the above five clades, with the exception of the Sempervivum clade, species of *Sedum* (or former *Sedum*) never form a monophyletic group but either are more or less scattered across the respective phylogenetic trees (e.g., clades Acre and Leucosedum) or form a basal grade (e.g., Aeonium clade). In conclusion, *Sedum* in its current circumscription indeed is a highly polyphyletic (or paraphyletic) taxon. The two comprehensive analyses of Crassulaceae by Van Ham & 't Hart (1998) and Mort & al. (2001) included 23 and 30 species of *Sedum*, respectively, the phylogenetic analysis of the Acre clade alone by Carrillo-Reyes & al. (2009)

included 68 species of *Sedum*, and a recent analysis focusing on *Sedum* (but including representatives of other genera) and using only ITS sequences included 114 species of the genus (Nikulin & al., 2016). Considering the size of *Sedum* this still represents only a fairly small number of species, and indeed Mort & al. (2010), when discussing the “*Sedum* problem”, pointed out that much of the taxonomic diversity of the genus has not yet been included in phylogenetic studies.

On this background, we here make an effort to represent as many as possible infrageneric taxa recognized in *Sedum* in a phylogenetic analysis based on plastid and nuclear DNA sequences, with our nuclear dataset being substantially larger than the plastid dataset. We present molecular phylogenies derived from a sample of 298 species of Crassulaceae, including 145 *Sedum* species (not counting 7 species segregated as *Petrosedum*) representing 144 of the 186 infrageneric taxa of *Sedum* described in the taxonomic literature (suppl. Table S1). In particular, we (1) aim at showing into which major clades of Sempervivoideae the various infrageneric groups of *Sedum* fall or are likely to fall, (2) will offer an evolutionary interpretation of Sempervivoideae and the “*Sedum* problem” (Mort & al., 2010), and (3) will explore options for the classification of *Sedum*. With respect to the last point we will argue in favour of broadening the circumscription of the genus by including all genera of Sedeae in *Sedum*.

■ MATERIALS AND METHODS

Taxon sampling. — The main aim of our sampling effort was to represent as many infrageneric taxa of *Sedum* as possible and to include all other genera of Sempervivoideae. To this end, we first compiled ITS (internal transcribed spacer) sequences of species of Sempervivoideae available from GenBank. To broaden our sample of Sempervivoideae and particularly of

Table 1. Taxonomic system of the family Crassulaceae following Thiede & Eggli (2007) and Klein & Kadereit (2015) and updated according to results of the present study.

Subfamily	Major clade	Corresponding tribes	Genera	Approximate species number
Crassuloideae	Crassula clade		<i>Crassula</i>	200
Kalanchoideae	Kalanchoe clade		<i>Adromischus</i> , <i>Kalanchoe</i> , <i>Tylecodon</i> , <i>Cotyledon</i>	240
Sempervivoideae	Telephium clade	Telephieae and Umbiliceae	<i>Hylotelephium</i> , <i>Kungia</i> , <i>Meterostachys</i> , <i>Orostachys</i> , <i>Phedimus</i> , <i>Pseudosedum</i> , <i>Rhodiola</i> , <i>Sinocrassula</i> , <i>Umbilicus</i>	160
	Sempervivum clade	Semperviveae	<i>Petrosedum</i> , <i>Sempervivum</i> , <i>Jovibarba</i>	60
	Aeonium clade	Aeonieae	<i>Aeonium</i> , <i>Aichryson</i> , <i>Monanthes</i> , <i>Hypagophytum</i> , <i>Sedum</i> p.p. (8 spp.)	75
	Leucosedum clade	Sedeae p.p.	<i>Pistorinia</i> , <i>Rosularia</i> , <i>Prometheum</i> , <i>Afrovivella</i> , <i>Sedella</i> , <i>Dudleya</i> , <i>Sedum</i> p.p. (ca. 120 spp.)	200
	Acre clade	Sedeae p.p.	<i>Cremonophila</i> , <i>Echeveria</i> , <i>Graptopetalum</i> , <i>Lenophyllum</i> , <i>Pachyphytum</i> , <i>Thompsonella</i> , <i>Villadia</i> , <i>Sedum</i> p.p. (ca. 345 spp.)	550

Species numbers were updated by reviewing names of new species validly published after 2007 from ipni.org. The monospecific genus *Perrierosedum* is not represented in this table since its taxonomic position remains unknown.

infrageneric taxa of *Sedum*, we added 70 newly sequenced accessions representing 64 species to our sample (see Appendix 1 for a full list of specimens and GenBank accession numbers). Twenty-seven of these species (incl. 21 *Sedum* spp.) were included in a molecular phylogenetic study for the first time. These 70 accessions were obtained from living collections, as silica-dried material or as herbarium material from E, JEPS, L, MJG, MSB, O, OSC, TARI, U, WAG and ZSS. The few samples taken from living plants grown at the Botanic Gardens Berlin-Dahlem, Mainz and Zürich (Sukkulentensammlung) mostly had a well-documented collection record (see Appendix 1). This sampling resulted in ITS sequence data from 271 accessions representing 263 different taxa at specific or infraspecific rank, including 145 species of *Sedum* (without *Petrosedum*). Of the 186 infrageneric taxa of *Sedum* (not counting those comprising only species that have been transferred to other genera; see suppl. Table S1) we were able to identify in the taxonomic literature (Scopoli, 1777; Boissier, 1872; Schönland, 1891; Berger, 1930; Fröderström, 1930, 1931, 1932, 1935; Alexander, 1942; Clausen, 1942, 1943a,b, 1975, 1979; Clausen & Uhl, 1943, 1944; S.-H. Fu, 1965; Maire & Quézel, 1967; K.T. Fu, 1974; Uhl, 1977, 1978, 1980, 1992a; 't Hart, 1978, 1991; Ohba, 1978; Calie, 1981; Denton, 1982; Gilbert, 1985; Eggli, 1992; 't Hart & Alpınar, 1995, 1999; Mes, 1995a,b; Nesom & Turner, 1995; Fu & Ohba, 2001; 't Hart & Bleij, 2005; Afferni, 2012, 2014; Santiago & al., 2015), 144 were represented in our ITS dataset. However, 19 of the non-monospecific infrageneric taxa were represented by only one species.

For our plastid dataset we compiled sequences of *matK*, *rps16* and the *trnL-trnF* spacer (in the following abbreviated as *trnL-F*), the most commonly sequenced markers in Sempervivoideae, from GenBank and expanded the sampling by sequencing these plastid regions for 44 additional taxa (see below). Considering the well-established phylogenetic relationship of Kalanchoideae as sister to Sempervivoideae (Van Ham, 1995; Van Ham & 't Hart, 1998; Mort & al., 2001) we chose seven species from three genera of Kalanchoideae as outgroup in our ITS dataset and three species of the same genera in the plastid sequence dataset. For the combined dataset of ITS and plastid sequences as well as the dated phylogenetic analysis of ITS (see below), we expanded the outgroup by sampling additional species from Crassulaceae and those families most closely related to it (for details see “Outgroup” in Appendix 1).

Except for *Jovibarba* and *Sempervivum*, which we treated as distinct genera (Klein & Kadereit, 2015), taxonomic treatment followed Eggli (2005). Furthermore, because of substantial differences in their ITS sequences, we considered *Sedum hillebrandtii* Fenzl a species separate from *S. urvillei* DC. although it has been treated as a heterotypic synonym of *S. urvillei* by 't Hart & Bleij (2005).

Assessment of morphological character states. — Information about morphological characters (including seed testa ornamentation) of the sampled *Sedum* taxa as well as all other genera of Sedeae was taken from Eggli (2005),

Thiede & Eggli (2007) and the International Crassulaceae Network (www.crassulaceae.ch). For infrageneric taxa of *Sedum* the descriptions given in the respective protologues were used, and missing data were complemented as far as possible consulting 't Hart & Bleij (2005). Finally, morphological descriptions in 't Hart & Bleij (2005) were also used to search for possible apomorphies of such well-supported clades as retrieved in our phylogenies (see below), which did not correspond to any published infrageneric group of *Sedum*.

DNA extraction, amplification, and sequencing. — DNA was extracted from silica-dried or herbarium leaf material (accessions with a lab code in Appendix 1) with the exception of *Sedum potosinum* Rose of which alcohol material was used for DNA extraction. From two of the accessions (*Sedum obtusatum* A.Gray, *S. urvillei*) DNA was extracted using the NucleoSpin Plant II kit (Macherey-Nagel, Düren, Germany) based on the Cetyltrimethylammonium bromide (CTAB) lysis method according to the manufacturer's protocol with a lysis time of 80 minutes. For all other accessions, the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) was used for DNA extraction following the manufacturer's protocol with a lysis time of two hours.

Polymerase chain reactions (PCR) were performed in a total reaction volume of 25 µl. We amplified ITS using primers ITS 18S and ITS B (Hungerer & Kadereit, 1998; Muir & al., 2001). Settings for the PCR cycling were adopted from Klein & Kadereit (2015) with the following exceptions: 40 instead of 35 PCR cycles and an annealing temperature of 52°C instead of 57°C were implemented. For samples that did not yield any PCR product with this protocol, separate amplification of the two intergenic spacer regions ITS1 and ITS2 was performed using the primer pairs ITS A and ITS C, and ITS B and ITS D, respectively (Blattner, 1999). For the separate amplification of ITS1 and ITS2, the same cycling programme was used as for the amplification of the entire ITS region. The three plastid markers were amplified using the primer pairs *trnK-F-bryo* and *trnK-2R* for *matK* (Johnson & Soltis, 1994; Wicke & Quandt, 2009), *rps16-F* and *rps16-R* for *rps16* (Oxelman & al., 1997; Shaw & al., 2005), and *Tab-C* and *Tab-F* for *trnL-F* (Taberlet & al., 1991). The cyclo protocol for the amplification of *matK* and *rps16* was the same as that used for ITS. PCR for *trnL-F*, however, required a higher annealing temperature of 56°C instead of 52°C.

PCR products were purified with exoSAP-IT PCR Product Cleanup Reagent (Thermo Fisher Scientific, Waltham, Massachusetts, U.S.A.) following the manufacturer's protocol. PCR products were Sanger-sequenced on a 3730 DNA Analyzer at StarSEQ (Mainz, Germany).

Sequence alignment and phylogenetic analysis. — Sequence contigs were assembled using Sequencher (v.4.1.4; Gene Codes, Ann Arbor, Michigan, U.S.A.). Alignments (suppl. Appendices S1–S5) were carried out using MAFFT (v.7.402; Katoh & Standley, 2013) on the CIPRES Science Gateway (<https://www.phylo.org>; Miller & al., 2010) with standard settings for all four markers. The algorithm used by MAFFT was L-INS-i for the three plastid DNA markers and

FFT-NS-i for the ITS dataset, which contained a higher number of sequences. All alignments were reviewed for mistakes but corrected only at very few sites. Parsimony-informative indels were not coded prior to the phylogenetic analyses. Variability of the four analyzed molecular markers was assessed using PAUP* (v.4.0b10; Swofford, 2002). The best-fitting substitution model and partition scheme was determined for the concatenated alignment of all markers (*matK*, *rps16*, *trnL-F*, and ITS subdivided into ITS1, 5.8S and ITS2) using the corrected Akaike information criterion (AICc) in PartitionFinder2 (v.2.1.1; Lanfear & al., 2017). PhyML (v.3.0; Guindon & al., 2010) was also used for this analysis.

The alignments of the three plastid markers were concatenated to result in one large alignment of all plastid DNA sequences. In order to reduce missing data in this alignment as well as in the combined alignment of ITS and plastid sequences, we combined markers from different accessions of the same species (see Appendix 1 for species with more than one accession). To further reduce missing data in the alignment of plastid sequences, we combined three species pairs (i.e., *Sedum compactum* Rose and *S. obcordatum* R.T.Clausen, *Dudleya pulverulenta* (Nutt.) Britton & Rose and *D. viscida* (S.Watson) Moran, *Jovibarba globifera* subsp. *allionii* (Jord. & Fourr.) J.Parn. and *J. heuffelii* (Schott) Á.Löve & D.Löve) into one terminal each. In these three cases the two species combined were sister to each other with maximum bootstrap support in the maximum likelihood ITS analysis (see below).

Maximum likelihood (ML) analyses were carried out for ITS, the concatenated plastid sequence matrix and the combined ITS and plastid dataset using RAxML-HPC2 (v.8.2.10; Stamatakis, 2014) on XSEDE in the CIPRES Science Gateway (Miller & al., 2010). In the following, the ML analyses of the ITS, plastid and combined ITS and plastid sequence matrices will be referred to as ITS/ML, cpDNA/ML and combined/ML, respectively. The GTR-GAMMA model was used as substitution model, and bootstrapping was set to halt automatically. Bayesian analysis was performed for ITS and the combined nuclear and plastid dataset using MrBayes (v.3.2.7a; Ronquist & Huelsenbeck, 2003) on XSEDE in the CIPRES Science Gateway (Miller & al., 2010). BEAST (v.2.4.5; Bouckaert & al., 2014) instead of MrBayes was used for Bayesian analysis of the plastid sequence matrix and carried out on XSEDE in the CIPRES Science Gateway because BEAST performed better than MrBayes for the plastid sequence data. These analyses will be referred to as ITS/MrBayes, combined/MrBayes and cpDNA/BEAST, respectively. For both Bayesian analyses with MrBayes (ITS and combined datasets), two independent runs were performed with six chains each, and the temperature of the hot chain was set to 1. The metropolis-coupled Markov Chain Monte Carlo (MCMC) algorithm was executed for 100 million generations sampling every 10,000th generation with a burn-in of 25%. For the cpDNA/BEAST analysis, the MCMC was run for 30 million generations in four independent runs. We used the GTR+I+ Γ substitution model, which was retrieved as best substitution model in PartitionFinder2 (Lanfear & al., 2017) for each of the partitions used (i.e.,

matK, *rps16* and *trnL-F*). Trees were sampled every 3000th generation, and the resulting log files of all four independent runs were checked for convergence and effective sampling sizes of at least 200 for each parameter, using Tracer (v.1.5; Rambaut & Drummond, 2007). The four independent runs were combined using LogCombiner (v.2.4.5; Bouckaert & al., 2014) after discarding a burn-in of 10%. A majority-rule consensus tree was calculated using TreeAnnotator (v.1.8.3; Rambaut & Drummond, 2016). The topology of each inferred phylogenetic tree was assessed using FigTree (v.1.3.1; Rambaut, 2009).

Comparison of the trees resulting from ML and Bayesian analyses of ITS and the plastid sequence data revealed 15 supported (bootstrap support $\geq 75\%$ and/or posterior probability ≥ 0.95) conflicts between the ITS and plastid topologies within Sempervivoideae. All 21 taxa affected by these 15 conflicts are listed in Appendix 2 and were excluded from the combined ML analysis.

Molecular dating. — No fossils of Crassulaceae or with affinities to Crassulaceae are known. For this reason, we were only able to use secondary age estimates instead of fossil ages as calibration points for our analysis of clade ages. Stem and crown age estimates for Crassulaceae were kindly provided by Susana Magallón (Mexico City/Mexico; pers. comm.). As a result of her own work, an age of 105.94 Ma (93.43–120.59 Ma, 95% HPD) was inferred for the split between Crassulaceae and its sister group consisting of Haloragaceae, Penthoraceae, Tetracarpaeaceae and Aphanopetalaceae (Fishbein & al., 2001), i.e., the stem age of Crassulaceae, and 58.27 Ma (26.23–88.39 Ma, 95% HPD) as crown age of Crassulaceae. These two age estimates were implemented as secondary calibration points in our dating analysis with a normal distribution that included the whole 95% HPDs. A third calibration point, the age of Fuerteventura (21 Ma), the oldest of the Canary Islands, was used as maximum age of the most recent common ancestor of the clade comprising the Macaronesian endemics in the *Aeonium* clade (i.e., all sampled species of *Aeonium*, *Aichryson* and *Monanthes*), as had been done by Kim & al. (2008).

Divergence times were calculated using the partitioned ITS alignment in BEAST (Bouckaert & al., 2014) implemented in the CIPRES Science Gateway (Miller & al., 2010). We used a lognormal relaxed clock model and predefined all clades as monophyletic that had maximum support (bootstrap = 100 and posterior probability = 1) in both analyses of ITS (i.e., ITS/ML and ITS/MrBayes, respectively). Calculations were carried out using the birth-death process (Gernhard, 2008), and the ucl.d.mean parameter was specified to be gamma-distributed with 0.001 as lower and 1000 as upper limit. The GTR+I+ Γ substitution model was used for both partitions of ITS (i.e., partition 1: ITS1 and ITS2 [suppl. Appendix S4]; partition 2: 5.8S [suppl. Appendix S5]). The analysis was run four times independently with an MCMC chain length of 100 million generations, sampling every 10,000th generation with a burn-in of 25%. The posterior analysis of the four independent runs was carried out in the same way as for the cpDNA/BEAST analysis.

■ RESULTS

Morphological character states. — Character states of eight traits often used in Crassulaceae systematics (i.e., life form, presence and quality of trichomes, phyllotaxis, inflorescence insertion, flower merism, sympetaly, number of stamens, seed testa ornamentation) are given in Fig. 1 for all species sampled in the ITS phylogeny (see below). Similarly, a matrix of character states relevant for the circumscription of all genera of Sedeae is given in Table 2. Diagnostic morphological character states of all infrageneric taxa of *Sedum* that we found in the taxonomic literature are summarized in columns J–M of suppl. Table S1, where the literature used is given in column I and listed in the spread sheet “literature cited”. Finally, Table 3 summarizes the results of our search for possible synapomorphies of clades that were well supported in our phylogenies (see below).

Variability of molecular markers. — Variation in the ITS dataset was markedly higher than in the dataset of concatenated plastid markers. The ITS dataset (suppl. Appendix S2) contained 271 tips and 854 nucleotide positions of which 496 (58.1%) were parsimony informative. The plastid dataset of concatenated *matK*, *rps16* and *trnL-F* (suppl. Appendix S1) consisted of 130 tips and 3520 nucleotide positions of which 991 (28.2%) were parsimony informative. Of these 3520 positions 1239 were from *matK*, 1073 from *rps16* and 1208 from *trnL-F*. With 51.7% parsimony informative sites *matK* was almost as informative as ITS. The combined nuclear and plastid dataset (suppl. Appendix S3) with sequences of 163 tips, which also comprised species of Crassuloideae and Saxifragalean outgroup families had a total length of 4331 nucleotide positions of which 1703 (39.3%) were parsimony informative.

Phylogenetic relationships in subfam. Sempervivoideae. — Sempervivoideae received maximum support as a monophyletic group in all our analyses (Figs. 1–3, suppl. Fig. S1). In the following, we will describe our results with reference to the five major groups identified in the subfamily as described in previous studies (see Introduction).

(1) *Telephium* clade. — The three subgroups of the *Telephium* clade, i.e., *Umbilicus*, *Phedimus/Rhodiola* and *Hylotelephium* (non-monophyletic)/*Meterostachys/Orostachys* (non-monophyletic)/*Kungia/Sinocrassula*, formed a monophyletic group only in cpDNA/BEAST (Fig. 2A), where it was sister to the remainder of the subfamily. In all other analyses, the relationships among the three subgroups to the remaining lineages of the subfamily were unresolved.

(2) *Sempervivum* clade. — Both lineages of the *Sempervivum* clade, i.e., the *Petrosedum* clade, including *Sedum nanum* Boiss. of ser. *Nana* Hart & Alpar, and *Sempervivum/Jovibarba*, were monophyletic in all analyses but never sister to each other. Because these two lineages were supported as successive sisters to the remainder of Sempervivoideae above the *Telephium* clade in cpDNA/ML (Fig. 2A), while the *Petrosedum* clade was supported as sister to the *Aeonium* clade in ITS/MrBayes (Fig. 1A), *Petrosedum* and *Sedum*

nanum showed conflicting phylogenetic placements and consequently were removed from the combined analyses. The sister relationship of the *Petrosedum* clade with the *Aeonium* clade was also supported in the dating analysis of ITS (suppl. Fig. S1). *Sedum nanum* was consistently resolved as sister to *Petrosedum* (Figs. 1A, 2A, suppl. Fig. S1).

In ITS/MrBayes (Fig. 1A,B) *Sempervivum/Jovibarba* were part of a trichotomy with the *Aeonium/Petrosedum* clade and Sedeae (i.e., clades *Acre* and *Leucosedum*). This topology was essentially the same in the combined analyses (Fig. 3A, B) from which, however, the *Petrosedum* clade was excluded (see above).

(3) *Aeonium* clade. — The *Aeonium* clade, comprising *Aeonium* (incl. *Greenovia* Webb & Berthel.), *Aichryson*, *Monanthes* and *Hypagophytum* as well as *Sedum* species of ser. *Monanthoidea* Batt. ex Fröd., ser. *Caerulea* Fröd. and ser. *Pubescens* T.Mes, was monophyletic in all analyses. This clade was sister to Sedeae in both analyses of the plastid dataset, although not supported in cpDNA/BEAST (Fig. 2A), but sister to the *Petrosedum* clade in all analyses of ITS including the dating analysis (Fig. 1A, suppl. Fig. S1). In the combined analyses, from which the *Petrosedum* clade was excluded (Fig. 3A,B), the *Aeonium* clade was part of a trichotomy with *Sempervivum/Jovibarba* and Sedeae.

(4) *Leucosedum* clade and (5) *Acre* clade. — The clades *Leucosedum* and *Acre* together (i.e., Sedeae) were strongly supported as a monophyletic group in all analyses with the exception of ITS/ML (Fig. 1B) in which it received poor support. The *Acre* clade alone was monophyletic in all analyses. In ITS/ML, the *Acre* clade, several lineages/single species of the *Leucosedum* clade, *Sempervivum/Jovibarba* and the *Aeonium* and *Petrosedum* clades formed a large polytomy. This polytomy would become most apparent if branches supported by bootstrap values <75 (signified as “–”) were collapsed in Fig. 1A,B. In ITS/MrBayes (Fig. 1B), a much smaller polytomy was formed by the *Acre* clade and three supported subgroups of the *Leucosedum* clade. Supported topological conflict between the analyses of ITS (Fig. 1) and cpDNA (Fig. 2) was found for nine *Sedum* species of clades *Leucosedum* and *Acre* (i.e., *S. album* L., *S. fragrans* Hart, *S. hakonense* Makino, *S. litoreum* Guss., *S. lydium* Boiss., *S. satumense* Hatus., *S. sedoides* (Decne.) Pau, *S. subtile* Miq. and *S. tenellum* M.Bieb.), which consequently were excluded from the combined nuclear and plastid analyses, together with the entire *Petrosedum* clade (see above) and six more conflicting genera (*Dudleya*, *Pistorinia*, *Rosularia*) or species of other genera (see Appendix 2).

As one of the goals of our study is to explore the phylogenetic positions of infrageneric groups of *Sedum* (listed in suppl. Table S1), these infrageneric groups will be assigned to the identified clades in the following paragraphs. It is important to note that several of the infrageneric taxa are named more than once, indicating that such taxa are non-monophyletic and that their members belong to more than one clade. Those infrageneric groups that we identified as monophyletic are listed in Table 3 (see Discussion).

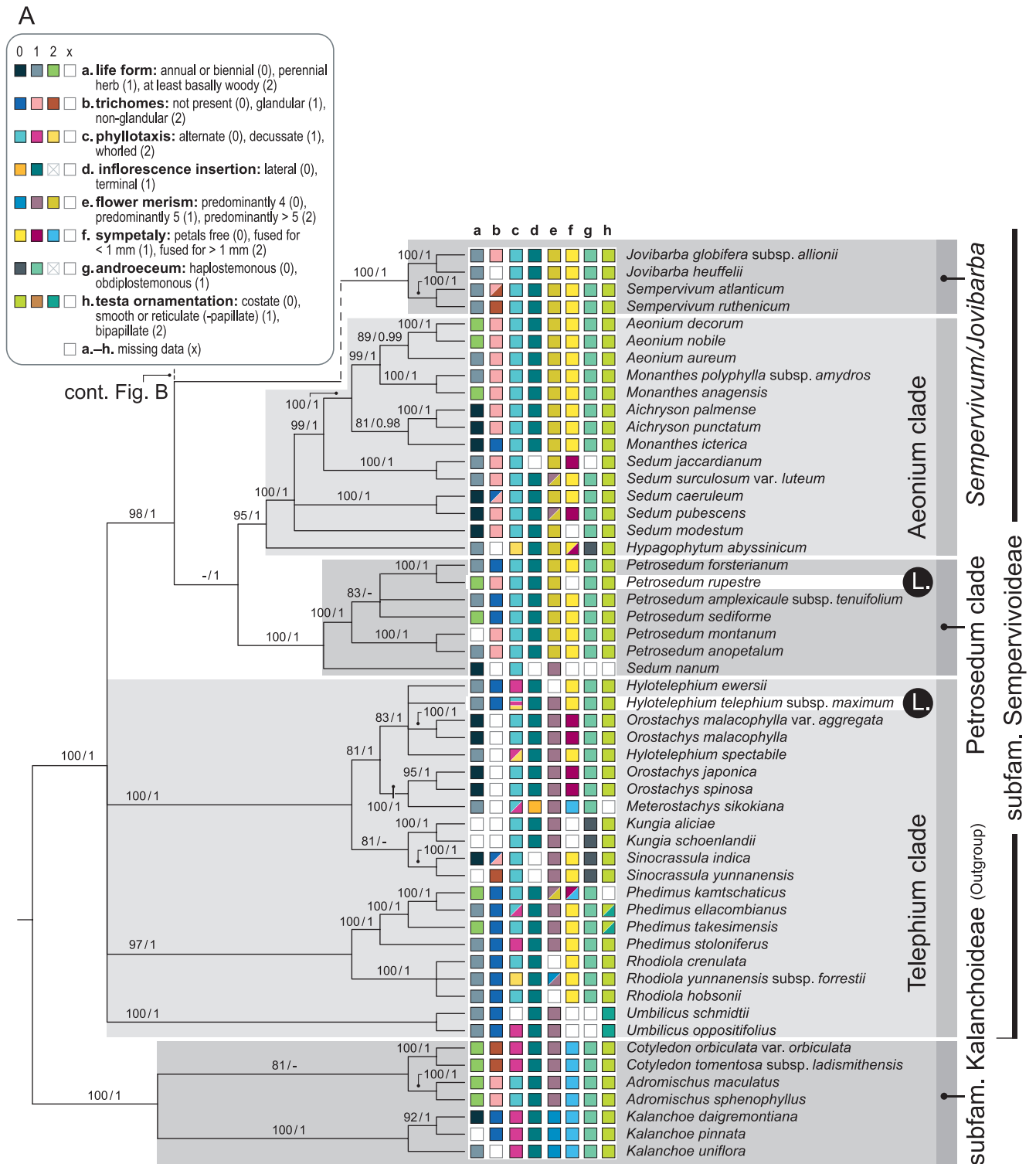


Fig. 1. Molecular phylogeny of Crassulaceae subfam. Sempervivoideae based on sequences of the internal transcribed spacer (ITS) of nuclear ribosomal DNA and inferred using maximum likelihood (ITS/ML) and Bayesian inference (ITS/MrBayes). Branch labels give bootstrap support values for ITS/ML (left) and posterior probabilities for ITS/MrBayes (right). Branches with bootstrap support <75 and posterior probability <0.95 were collapsed or marked “-” when support was only found in one of the two analyses. Species names first published by Linnaeus (1753) are highlighted and marked with “L.”. Names of major clades as used in the main text are given. Character states for eight morphological traits are given for each tip of the phylogeny according to the colour code in the figure inset. The species of *Aichryson* sampled have been described as up to triennial by Nyffeler (2005).

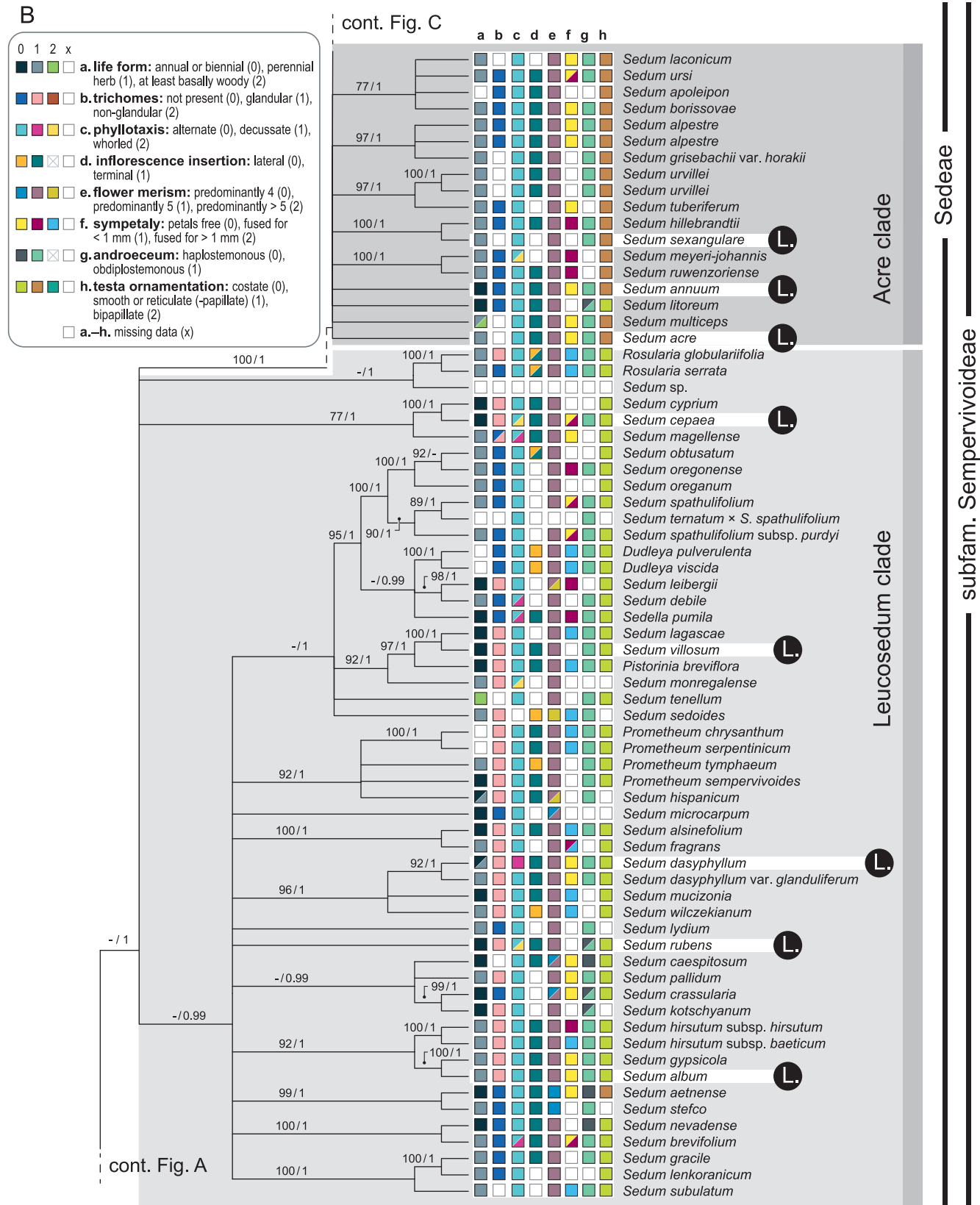


Fig. 1. Continued.

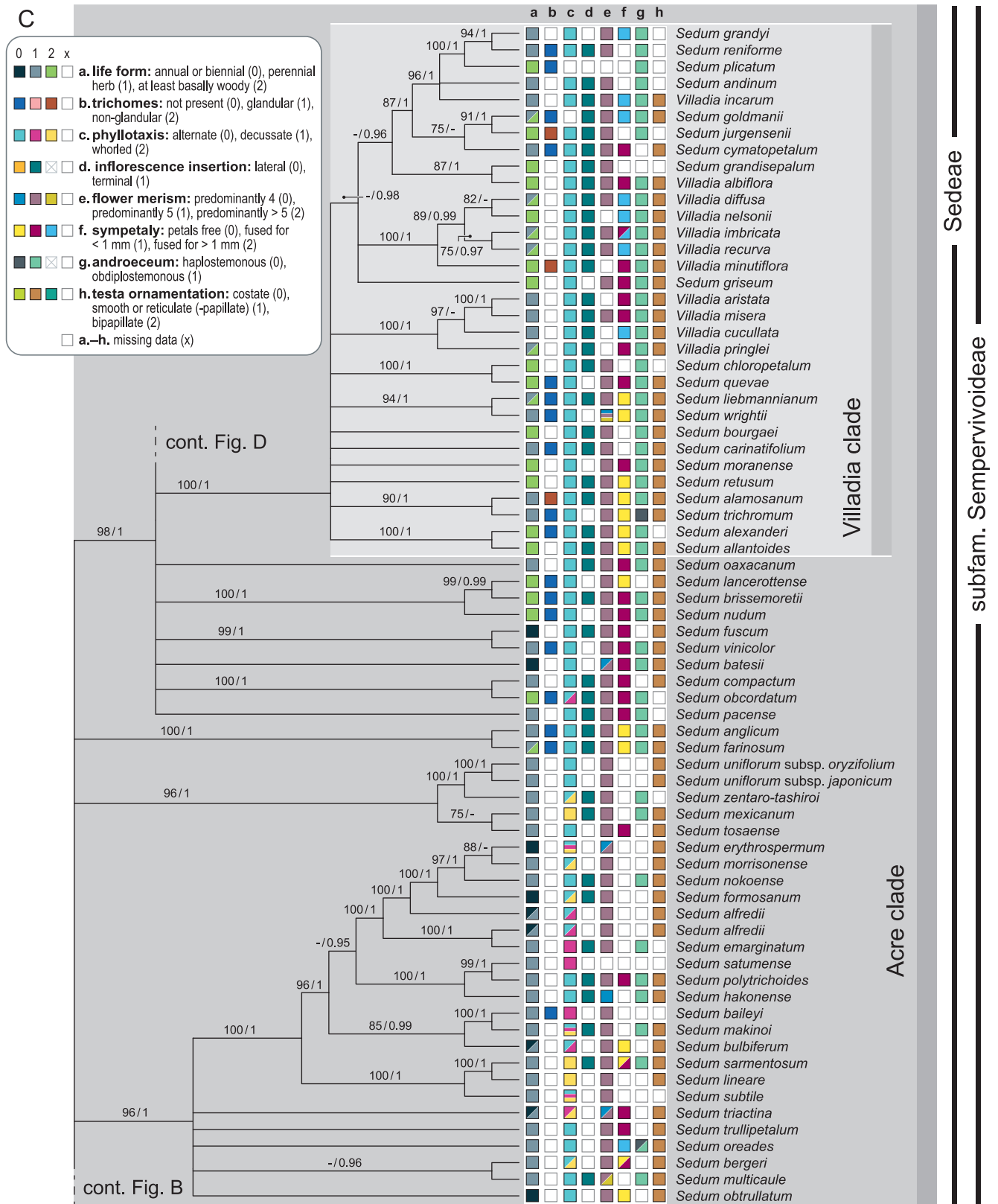


Fig. 1. Continued.

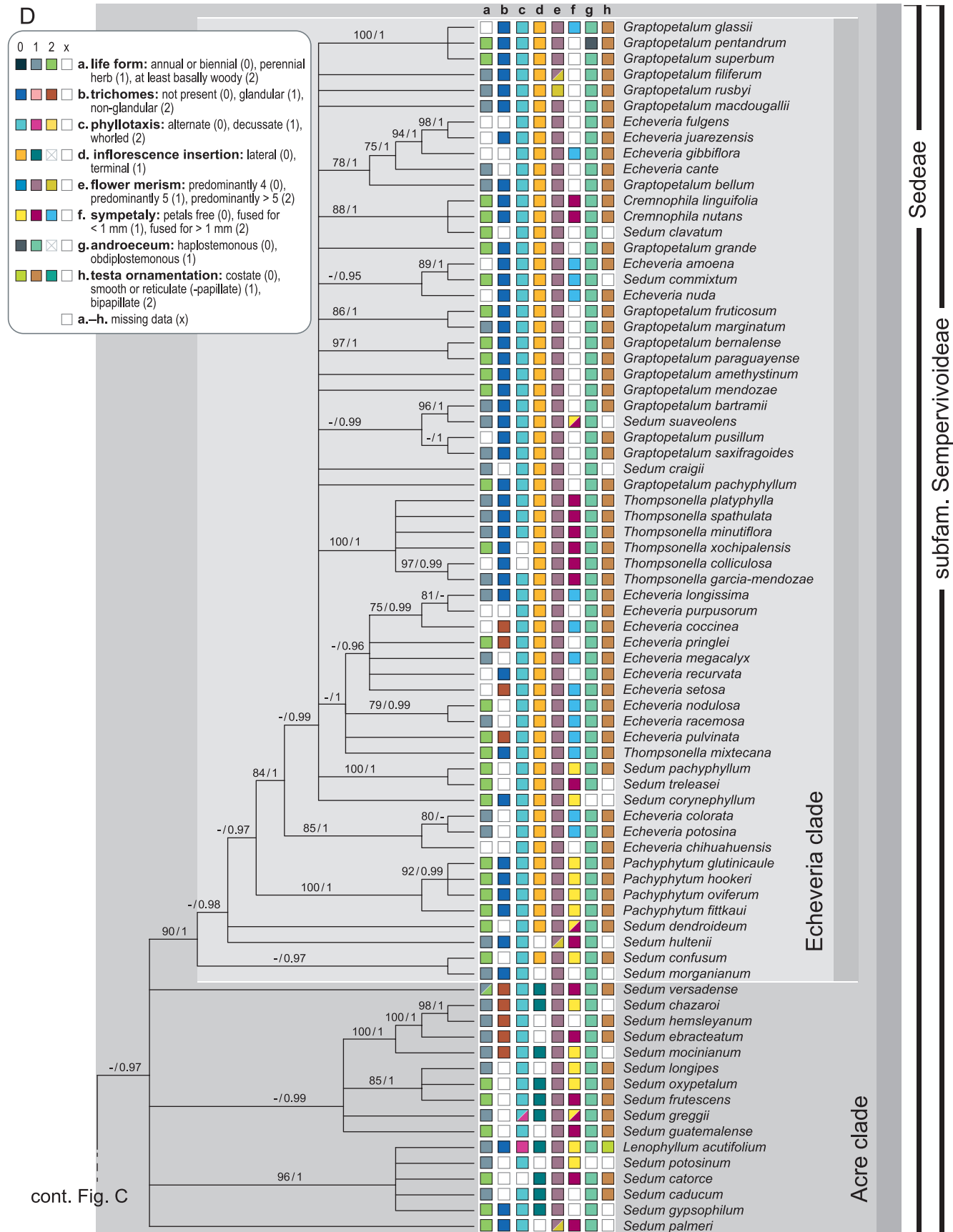


Fig. 1. Continued.

Table 2 (left part). Genera of the Leucosedum and Acre clades (= Sedeae) and their defining characters following Eggli (2005) and Thiede & Eggli (2007) unless other references are specified. *Afrovivella* was not sampled by us. *Cremnophila* has not been accepted as a genus separate from *Sedum* by Thiede & Eggli (2007).

Genus	Clade affiliation	Inferred phylogeny	Distribution	Life form	Phyllotaxis	Inflorescence insertion	Flower merism	Petal fusion
<i>Afrovivella</i> A.Berger	Leucosedum	Not sampled	Ethiopian highlands	Perennial herbs	Sessile rosettes	Lateral	5–7	Fused for 1/3 of corolla length
<i>Cremnophila</i> Rose	Acre	Unresolved	Mexico (Mexico, Morelos)	Perennial	Alternate, rosulate	Lateral	5	Slightly fused at base
<i>Dudleya</i> Britton & Rose	Leucosedum	Monophyletic	W U.S.A., NW Mexico	Perennial	Terminal rosettes	Lateral	(4–)5	Fused ^a
<i>Echeveria</i> DC.	Acre	Polyphyletic	S U.S.A. (Texas) to N Argentina	Perennial herbs to subshrubs	Alternate, rosulate, rarely scattered along stem	Lateral	5	Fused
<i>Graptopetalum</i> Rose	Acre	Polyphyletic	S U.S.A. (Arizona), Mexico	Perennial herbs to subshrubs	Terminal rosettes	Lateral	(4–)5, (7–10)	Free or slightly fused at base
<i>Lenophyllum</i> Rose	Acre	Monophyletic ^b	S U.S.A. (S Texas), NE Mexico	Perennial herbs	Decussate	Terminal	5	Free
<i>Pachyphytum</i> Link & al.	Acre	Monophyletic	E to C Mexico	Subshrubs	Alternate, rosulate	Lateral	5(–6)	Free ^a
<i>Pistorinia</i> DC.	Leucosedum	Only 1 sp. sampled	Iberian peninsula, N Africa	Annual herbs	Alternate	Terminal	5	Fused for ≥1/2 of corolla length
<i>Prometheum</i> (A.Berger) H.Ohba	Leucosedum	Monophyletic	N Greece to N Iran, incl. Caucasus	Annual to perennial herbs	Sessile rosettes, alternate on stems	Terminal or lateral	5	Fused for ≤1/2 of corolla length, never free
<i>Rosularia</i> (DC.) Stapf	Leucosedum	Monophyletic, but only 2 spp. sampled	SE Aegean islands, Cyprus, Near East, Karakorum, Himalayas, Altai	Perennial herbs	Sessile rosettes, alternate on stems	Terminal or lateral	5–9	Fused for 1/10 to 3/4 of corolla length
<i>Sedella</i> Britton & Rose	Leucosedum	Only 1 sp. sampled	W U.S.A.	Annual herbs	Decussate near base, alternate above	Terminal	5	Slightly fused at base
<i>Sedum</i> L.	Acre and Leucosedum	Polyphyletic	America, Eurasia, N, C and E Africa	Annual to perennial herbs to subshrubs	Alternate, rarely decussate or in whorls of 3 or 4, rarely rosulate	Terminal, rarely lateral	(3–)5 (–12)	Free or fused for up to 2/3 of corolla length
<i>Thompsonella</i> Britton & Rose	Acre	Paraphyletic	C and S Mexico	Perennial herbs to subshrubs	Sessile or terminal rosettes	Lateral	5	Shortly fused at base
<i>Villadia</i> Rose	Acre	Polyphyletic	S U.S.A., Mexico, Guatemala, Peru	Perennial herbs or subshrubs	Alternate	Terminal	(4–)5	± shortly fused at base

(Continues in the right part.)

a – García & Chávez (2003); b – Carrillo-Reyes & al. (2009)

Table 2 (right part).

Genus	Petal colour	Number of stamens	Trichomes	Rosette branching sympodial	Leaf apex	Filament insertion	Seeds per follicle	Testa ornamentation
<i>Afrovivella</i> A. Berger	White, outside tinged reddish	2× petals	Glandular, leaf margins ciliate	No	Mucronate	n.s.	n.s.	Costate ^c
<i>Cremonophila</i> Rose	Greenish-white to yellow	2× petals	None	No	Rounded to broadly acute	n.s.	n.s.	n.s.
<i>Dudleya</i> Britton & Rose	White, yellow, orange or red	2× petals	None	Yes (when branched)	Obtuse-rounded to acutely pointed	At corolla base, antepetalous stamens slightly higher than antesepalous stamens	n.s.	Ribbed
<i>Echeveria</i> DC.	White to yellow, red to orange, rarely green(ish)	2× petals	None or non-glandular	No	Obtuse to acute, usually mucronate	Antepetalous stamens fused to corolla at top of nectar cavities, antesepalous stamens at top of corolla tube	n.s.	Smooth or reticulate
<i>Graptopetalum</i> Rose	Whitish or yellowish (to greenish), reddish to brown blotches, rarely uniformly coloured	2× petals, rarely 1× petals	None	No	Rounded to conspicuously mucronate	Antepetalous stamens fused to corolla, antesepalous stamens hardly to conspicuously fused to corolla and intercarpellar tissue	Many	Reticulate
<i>Lenophyllum</i> Rose	Yellow(ish)	2× petals	None	No	Rounded to acuminate	Antepetalous stamens fused to petals for ±1/2 their length	Many	Longitudinally striate
<i>Pachyphytum</i> Link & al.	White to pink, rarely orange to red(dish), inside in upper part often with red blotch	2× petals	None	No	Obtuse to acute, rarely mucronate	Antepetalous stamens fused to corolla, antesepalous stamens (almost) free	Many	Fairly smooth
<i>Pistorinia</i> DC.	Yellow, pink or purple, often finely spotted	2× petals	Glandular	No	Obtuse to subacute	Slightly below mouth of corolla tube	n.s.	Costate
<i>Prometheum</i> (A. Berger) H. Ohba	Yellow, cream, white, pink or red	2× petals	Glandular	No	Rounded to mucronate	n.s.	n.s.	Costate
<i>Rosularia</i> (DC.) Stapf	White, pale yellow, pink, pinkish-purple or pinkish-brown	2× petals	None or glandular	No	Never mucronate	n.s.	n.s.	Longitudinally striate

(Continues)

(Continued from the left part ↓)

Table 2 (right part). Continued.

Genus	Petal colour	Number of stamens	Trichomes	Rosette branching sympodial	Leaf apex	Filament insertion	Seeds per follicle	Testa ornamentation
<i>Sedella</i> Britton & Rose	Bright to pale or greenish-yellow	1× petals, rarely 2× petals	None	No	Obtuse to rounded	Fused to petal bases	1	Longitudinally striate
<i>Sedum</i> L.	Yellow, white, pink, purple or reddish	2× petals, rarely 1× petals	None, glandular or non-glandular	No	Rounded to mucronate	Antepetalous stamens or all stamens (when petals are fused) fused to petal bases, rarely higher up	1 to many	Costate, bipapillate, or reticulate (-papillate)
<i>Thompsonella</i> Britton & Rose	Outside pale, inside dark purplish-red	2× petals	None	No	Rounded to mucronate	n.s.	Many	Reticulate with irregular longitudinal rows
<i>Villadia</i> Rose	Whitish to pink or reddish	2× petals	None or rarely non-glandular	No	Obtuse to acute	Basally fused to corolla for 0.6–2.8(–4) mm	n.s.	Centrally papillose (always?)

c – Egli (1988); n.s. – not specified in the literature

In all ITS analyses (Fig. 1B–D, suppl. Fig. S1), the monophyletic Acre clade, beside several lineages/single species of *Sedum*, contained a predominantly North American clade with *Echeveria* (non-monophyletic), *Cremnophila* (included in *Sedum* by Thiede & Egli, 2007), *Graptopetalum* (incl. *Tacitus* Moran; non-monophyletic), *Pachyphytum*, *Thompsonella* (non-monophyletic when including *T. mixtecana* J.Reyes & L.G.López), *Lenophyllum* and *Villadia* (non-monophyletic). In our combined analysis (Fig. 3C), *Cremnophila* and *Pachyphytum* were not sampled but the other genera listed were recovered in the American subclade of the Acre clade. In the analyses of ITS (Fig. 1C,D) and the combined ITS and plastid data (Fig. 3C), the *Echeveria* clade (*Graptopetalum glassii* Acev.-Rosas & Cházaro through *Sedum morganiatum* E.Walther; *Echeveria fulgens* Lem. through *S. corynephyllum* Fröd., respectively) and the *Villadia* clade (*Sedum grandyi* Raym.-Hamet through *S. allantoides* Rose and *S. plicatum* Thiede & Hart through *S. alexanderi* Egli, respectively) were recovered. These had been known before as well-supported subgroups of the American part of the Acre clade (Mort & al., 2001; Thiede & Egli, 2007; Carrillo-Reyes & al., 2008, 2009; Nikulin & al., 2016). *Sedum* species of the *Echeveria* clade belong to the following infrageneric taxa: subg. *Pachysedum* (A.Berger) R.T.Clausen, sections *Craigia* R.T. Clausen, *Dendrosedum* A.Berger and *Pachysedum* A.Berger and the unranked taxon *Dendroideum* Fröd. (Americana Orthocarpia). *Sedum* representatives of the *Villadia* clade have been classified in the former genus *Altamiranoa* Rose, and in *Sedum* sections *Cockerellia* R.T.Clausen & C.H.Uhl (“subg. *Eusedum* (Boiss.) R.T.Clausen”), *Centripetalia* Alexander, *Fruticisedum* A.Berger, *Pachysedum* and *Leptosedum* A.Berger, series *Alamosana* Praeger, *Americana* A.Berger, *Compacta* A.Berger

and *Moranensia* A.Berger (“sect. *Seda genuina* W.D.J.Koch”) and the unranked taxa *Moranense* Fröd. (Americana Kyphocarpia), *Alamosanum* Fröd., *Andinum* Fröd., *Bourgaei* Fröd., *Conzattii* Fröd. and *Oxypetalum* Fröd. (Americana Orthocarpia). The remaining *Sedum* species of the American Acre clade, which did not fall into either of the clades *Echeveria* or *Villadia*, belong to the former genus *Altamiranoa*, *Sedum* sections *Dendrosedum*, *Fruticisedum* and *Sedastrum* (Rose) A.Berger, series *Acria* A.Berger, *Americana*, *Compacta*, *Oaxacana* A. Berger and *Pulchella* A.Berger (“sect. *Seda genuina*”) and the unranked taxa *Moranense* and *Napiferum* Fröd. (Americana Kyphocarpia), *Alamosanum*, *Conzattii*, *Dendroideum*, *Longipes* Fröd., *Minimum* Fröd., *Oxypetalum* and *Sedastrum* Praeger (Americana Orthocarpia), the *Parvum* group and the *Sedum palmeri* group. Lastly, a subclade of three Macaronesian *Sedum* species (*S. lancerottense* R.P.Murray through *S. nudum* Aiton; Fig. 1C) belonging to ser. *Macaronesia* (Fröd.) Afferni was part of the basal polytomy of the American Acre clade.

Species of *Sedum* in the remaining (mainly Eurasian) part of the Acre clade formed a polytomy of eight well-supported subclades and four single species in the ITS analyses (Fig. 1B,C). Two of these subclades (*S. uniflorum* Hook. & Arn. through *S. tosaense* Makino and *S. erythrospermum* Hayata through *S. obrullatum* K.T.Fu) are distributed in Asia and had previously been retrieved as clades by Ito & al. (2017). In their phylogenetic study of Taiwanese *Sedum*, Ito & al. (2017) sampled more *Sedum* species of these two clades than we did here. All other lineages in this part of the tree have a clearly western Eurasian/Mediterranean distribution, with the exception of *S. meyeri-johannis* Engl. and *S. ruwenzoriense* Baker f., which occur in parts of central and east Africa. *Sedum* species of the two Asian subclades belong to sections

Table 3. Infrageneric groups of *Sedum* (and groups of *Sedum* including other currently recognized genera) that are phylogenetically well-supported and clearly definable by morphology within their distributional range.

Name	Species comprised	Defining characters / Distribution	n [#]	Literature
Sect. <i>Centripetalia</i> Alexander	<i>S. alexanderi</i> , <i>S. atlantoides</i>	Leaves very thick (0.5–1.2 cm), petals free, narrow-based and with red blotches, flowers in terminal compound pleiochasia (Uhl, 1980), centripetal order of flowering / Mexico (Oaxaca)	29	Alexander (1942), Moran (1966), Uhl (1980)
Sect. <i>Gormania</i> (Britton) R. T. Clausen (incl. sect. <i>Oreganica</i> R. T. Clausen)	<i>S. albonarginatum</i> , <i>S. laxum</i> , <i>S. moranii</i> , <i>S. oblanceolatum</i> , <i>S. obtusatum</i> , <i>S. oreganum</i> , <i>S. oregonense</i>	Leaves broadest towards the tips, leaf tips often retuse, petals basally fused and divergent upward / W U.S.A.	–	Britton & Rose (1903), Clausen (1942, 1975), Clausen & Uhl (1944), Denton (1982)
Sect. <i>Lanceolata</i> R. T. Clausen	<i>S. borschii</i> , <i>S. debile</i> , <i>S. divergens</i> , <i>S. elrodii</i> *, <i>S. lanceolatum</i> , <i>S. leibergii</i> , <i>S. nuttallianum</i> , <i>S. radiatum</i> , <i>S. rupicola</i> , <i>S. stenopetalum</i>	Non-rhizomatous herbs, leaves narrow-elongate, petals free, yellow, flowers in tripartite cymes (Clausen, 1975) / C and W U.S.A., W Canada	8	Clausen (1975), Uhl (1977)
Sect. <i>Sedastrum</i> (Rose) A. Berger	<i>S. chazaroi</i> , <i>S. ebracteatum</i> , <i>S. glabrum</i> , <i>S. hemsleyanum</i> , <i>S. hintonii</i> , <i>S. jarocho</i> , <i>S. mocinianum</i> , <i>S. pixaltaense</i> , <i>S. roberti</i>	Basal rosettes present, leaves and inflorescences generally pubescent, inflorescences more or less paniculate (Britton & Rose, 1905), petals white, carpels basally concave / Mexico (except for NW and SE Mexico)	–	Britton & Rose (1905), Berger (1930), Clausen (1943b), Uhl (1992a), Pérez-Calix (1998), Carrillo-Reyes & Lomelí-Sención (2008), Jimeno-Sevilla & al. (2012), Santiago & al. (2015)
Ser. <i>Alba</i> A. Berger	<i>S. album</i> , <i>S. gypsicola</i>	Plants sparsely glandular-pubescent, leaves alternate, obtuse or rounded, flowers pentamerous, pedicellate, sepals basally fused with the receptacle, petals white, follicles many-seeded, erect, seeds oblong or ovoid, with a costate testa and acute apex / Europe, N Africa (Morocco, Algeria), Near East	17	Berger (1930), † Hart (1991), † Hart & Alpinar (1995)
Ser. <i>Alpestris</i> A. Berger sensu Berger (1930)	<i>S. alpestre</i> , <i>S. grisebachii</i>	Perennial herbs without glandular trichomes, leaves alternate, widest above the middle, with a short, never 3-lobed spur, usually not persistent when senescent, flowers confined to a terminal cyme (very rarely in axillary cymes), strictly pentamerous, petals yellow, nectar scales square or oblong-linear, follicles (pale) brown, never yellowish, seeds with a reticulate (-papillate) testa / mountains of C and S Europe and N Anatolia, Sardinia, Macedonia, Bulgaria and Greece	8	Berger (1930), Webb & al. (1993)
Ser. <i>Alsinefolia</i> A. Berger	<i>S. alsinefolium</i> , <i>S. fragrans</i>	Plants densely glandular-pubescent, leaves basally rosulate, flowers pedicellate, in a lax inflorescence, sepals basally fused with the receptacle, petals basally fused, seeds with a costate testa and coronate apex / French-Italian Alps	–	Berger (1930), † Hart (1991)

(Continues)

Table 3. Continued.

Name	Species comprised	Defining characters / Distribution	n#	Literature
<p> <i>Ser. Anglica</i> †Hart <i>S. anglicum</i>, <i>S. arenarium</i>, <i>S. farinosum</i>* </p>	<p> Plants glabrous, sepals basally free, petals white, follicles stellate-patent, with inconspicuous lips; seeds with a reticulate testa and coronate apex / Atlantic parts of W Europe and N Africa, Madeira </p>	12	†Hart (1991)	
<p> <i>Ser. Cepaea</i> (W.D.J.Koch) Afferni </p>	<p> <i>S. cepaea</i>, <i>S. creticum</i>, <i>S. cypricum</i>, <i>S. lampusae</i>, <i>S. magellense</i>, <i>S. microstachyum</i>, <i>S. tristriatum</i> </p>	<p> Plants glandular-pubescent, leaves alternate, opposite or in whorls of 4, flat, often in basal rosettes (except <i>S. magellense</i>), flowers pentamerous, shortly pedicellate, sepals basally united, petals white or pink, follicles erect, testa costate / S and SE Europe (incl. Balkans and S Greek islands), Cyprus </p>	–	Fröderström (1932), †Hart (1991), †Hart & Alpinar (1995), Afferni (2012)
<p> <i>Ser. Dasyphylla</i> †Hart </p>	<p> <i>S. dasyphyllum</i>, <i>S. mucizonia</i>, <i>S. wilczekianum</i>* </p>	<p> Plants densely glandular-pubescent, leaves alternate or decussate, obtuse or subacute, never in sessile rosettes, flowers pentamerous, pedicellate, petals white to pink, follicles many-seeded, erect, seeds with a costate testa and acute apex / C and S Europe, N Africa, Anatolia </p>	–	†Hart (1991), †Hart & Alpinar (1995)
<p> <i>Ser. Macaronesia</i> (Fröd.) Afferni </p>	<p> <i>S. brissemoretii</i>, <i>S. fusiforme</i>, <i>S. lancerothense</i>, <i>S. nudum</i> </p>	<p> Petals yellow, sometimes tinged red / Madeira, Lanzarote </p>	–	Fröderström (1932), Afferni (2014)
<p> Parts of ser. <i>Alpestris</i> A.Berger sensu †Hart (1991) </p>	<p> <i>S. apoleipon</i>, <i>S. borissovae</i>, <i>S. laconicum</i>, <i>S. ursi</i> </p>	<p> Plants without glandular trichomes, leaves alternate, never arranged in six rows, with a short and/or truncate, never 3-lobed spur, flowers strictly pentamerous, sepals up to 3 mm long, basally fused with the receptacle, petals yellow, seeds brown, never reddish, with a reticulate-papillate testa / Greece, S Ukraine, Turkey (mountains of W Anatolia), Israel and Lebanon (disjunct area) </p>	–	†Hart (1978, 1991), †Hart & Alpinar (1995)
<p> <i>S. tuberiferum</i>, <i>S. urvillei</i> </p>	<p> Perennial herbs without glandular trichomes, leaves alternate, widest below the middle or (if widest at or above the middle) with a 3-lobed spur, dead leaves usually persistent, flowers strictly pentamerous, sepals basally fused with the receptacle, petals yellow, seeds with a reticulate-papillate testa / from Hungary throughout the Balkans, Turkey (C and S Anatolia) and Ukraine (Crimea); 800–2450 m </p>	16	†Hart (1978, 1991), Webb & al. (1993), †Hart & Alpinar (1995)	
<p> Part of ser. <i>Subrosea</i> †Hart incl. genus <i>Pistorinia</i> DC. </p>	<p> <i>Pistorinia brachyantha</i>, <i>P. breviflora</i>, <i>P. hispanica</i>, <i>Sedum lagascae</i>, <i>S. mairceanum</i>, <i>S. villosum</i> </p>	<p> Densely glandular-pubescent annual or biennial (rarely perennial) herbs, leaves terete to semiterete, sepals basally fused with the receptacle, stamens 10, seeds coronate, with a costate testa / N, C and W Europe (especially Iberian peninsula), Iceland, Greenland, E Canada, N Africa </p>	15	†Hart (1991), †Hart & Alpinar (1995)
<p> Part of former <i>Altamiranoa</i> Rose </p>	<p> <i>S. goldmanii</i>, <i>S. jurgensenii</i> </p>	<p> Plants perennial, flowers in cincinni (†Hart & Bleij, 2005), petals basally fused for approximately 1–5 mm / Mexico </p>	23	Britton & Rose (1903), Berger (1930), Fröderström (1935), Moran (1996)
<p> Part of <i>Alamosanum</i> Fröd. [unranked] </p>	<p> <i>S. alamosanum</i>, <i>S. trichromum</i> </p>	<p> Plants perennial, not woody, tufted, with short sterile shoots, leaves alternate, flowers pedicellate, petals free, carpels erect or nearly so / Mexico (Durango, Sonora) </p>	–	Fröderström (1935)

(Continues)

Table 3. Continued.

Name	Species comprised	Defining characters / Distribution	n [#]	Literature
–	<i>S. churchillianum</i> , <i>S. epidendrum</i> , <i>S. meyeri-johannis</i> , <i>S. mooneyi</i> , <i>S. ruwenzoriense</i>	At least some leaves in whorls of three (leaves alternate throughout in <i>S. ruwenzoriense</i>), petals bright yellow / parts of C and E Africa	–	Gilbert (1985)
Echeveria clade	<i>S. sect. Pachysedum</i> , <i>Crennophila</i> , <i>Echeveria</i> , <i>Graptopetalum</i> , <i>Pachyphytum</i> , <i>Thompsonella</i>	Perennial shrubs to subshrubs without rhizomes, stems never short and thick, never unbranched nor sympodially branched, leaves alternate, rosulate (sessile or at stem tips), inflorescences lateral, nectar scales inconspicuous / America	–	Berger (1930), Clausen (1943a), Uhl (1978), Garcia & Chávez (2003), Acevedo-Rosas & al. (2004a,b), Egghi (2005), Carrillo-Reyes & al. (2008, 2009)

Nomenclature of species follows 't Hart & Bleij (2005). Species sampled by us are marked by bold font.

[#] Base chromosome numbers (*n*) are given only when shared by all species of a group. Information obtained from the literature cited and 't Hart & Bleij (2005).

* Species tentatively placed in the respective group by 't Hart & Bleij (2005).

Oreades (Fröd.) K.T.Fu and *Sedum* (sensu Fu & Ohba, 2001), groups 2 and 6 of sect. *Epeteium* Boiss., series *Bracteatae* (Fröd.) S.H.Fu (“sect. *Asiatica Genuina Kyphocarpia* Fröd.”), *Chauveardica* K.T.Fu, *Longifuniculata* K.T.Fu, *Oreades* K.T.Fu and *Trullipetala* K.T.Fu (sect. *Oreades* sensu K.T. Fu, 1974), *Chinensia* A.Berger, *Galioidea* A.Berger, *Hametiana* A.Berger, *Involucrata* Maxim. and *Orientalia* A.Berger (“sect. *Seda genuina*”) and the unranked taxa *Douglasii* Fröd. (Americana Kyphocarpia), *Bracteata* Fröd. and *Japonica* Maxim. (Asiatica Genuina Kyphocarpia) and *Oreades* Fröd. (Asiatica Genuina Orthocarpia). *Sedum anglicum* Huds. and *S. farinosum* Lowe have been classified as part of *Sedum* series *Alba* A.Berger (“sect. *Seda genuina*”) and *Anglica* 't Hart or as part of the unranked taxon *Stoloniferum* Fröd. (Eurasiatica Kyphocarpia). The subclade *Sedum laconicum* Boiss. & Heldr. through *S. borissovae* Balk. solely contains species of *Sedum* ser. *Alpestria* A.Berger in the sense of 't Hart (1991) and is, thus, one of the well-characterized monophyletic groups in Table 3. The remaining species in this basal polytomy of the Acre clade (i.e., *S. alpestre* Vill. through *S. acre* L.) have been classified in series *Acria* (“sect. *Seda genuina*”) and *Alpestria*, the Acre group in 't Hart's (1978) earlier circumscription, as well as the east African Meyerijohannis group of subg. *Sedum*. The well-supported sister relationship between *Sedum hillebrandtii* and *S. sexangulare* L. is reflected in Fenzl's (1856) notion that the two species, together with *S. acre*, are closely related to each other. Berger (1930) classified both species in his ser. *Mitia* A.Berger (“sect. *Seda genuina*”), which, however, also comprises *S. laconicum*, and neither this latter species nor *S. acre* are supported as sister to this clade in our ITS phylogenies.

Similar to earlier studies of only plastid DNA (Van Ham, 1995; Van Ham & 't Hart, 1998), the Leucosedum clade was resolved as monophyletic only in cpDNA/BEAST (Fig. 2A). In all other analyses, the position of *Sedum* ser. *Cepaea* (W.D.J.Koch) Afferni (of which *S. cepaea* L., *S. cyprium* A.K.Jacks. & Turrill and *S. magellense* Ten. were sampled here) relative to the remainder of the Leucosedum and Acre clades was unresolved (Figs. 1B, 3B, suppl. Fig. S1). In ITS/ML (Fig. 1B) the Leucosedum clade consisted of 20 lineages/single species, of which four lineages included *Dudleya*, *Sedella*, *Pistorinia*, *Prometheum* and *Rosularia*. The remaining 16 lineages/single species were exclusively composed of *Sedum* species that belong to the former genus *Sempervivella* Stapf, *Sedum* subg. *Telmisa* (Fenzl) H.Ohba, sections *Sempervivoides* Boiss. and *Telmisa* (Fenzl) Schönland, and groups 1, 5 and 6 of sect. *Epeteium*, series *Alba* and *Alsinefolia* A.Berger (“sect. *Seda genuina*”), *Aithales* (Webb & Berthel.) 't Hart, *Cepaea*, *Confertiflora* 't Hart, *Dasyphylla* 't Hart, *Glauco-rubens* Fröd., *Gracile* 't Hart & Alpınar, *Hirsuta* Fröd., *Macrosepala* (Regel & Schmalh.) Boriss., *Pedicellata* 't Hart, *Rubra* Boriss., *Subrosea* 't Hart, *Subulata* 't Hart, *Telmisa* (Fenzl) 't Hart & Alpınar and *Tenella* 't Hart & Alpınar, subseries *Cepaea* and *Cretica* Afferni (ser. *Cepaea*), and the unranked taxa “*Epeteium eurasiaticum* Fröd.”, *Glauco-rubens* Fröd. and *Stoloniferum*

(Eurasatica Kyphocarpia), *Album* Fröd., *Cepaea* W.D.J. Koch and *Hirsutum* Fröd. (Eurasatica Orthocarpia), and the Crassularia group. *Sedum* species of the American subclade of the Leucosedum clade (i.e., *Sedum obtusatum* through *Sedella pumila* (Benth.) Britton & Rose in Fig. 1B)

belong to sections *Lanceolata* R.T.Clausen and *Ternata* A.Berger (subg. *Sedum*), *Gormaniana*, *Oreganica* R.T.Clausen and *Rosulata* (A.Berger) R.T.Clausen & C.H.Uhl (subg. *Gormaniana* (Britton) R.T.Clausen), series *Rosulata* A.Berger and *Ternata* A.Berger (“sect. *Seda genuina*”) and the unranked

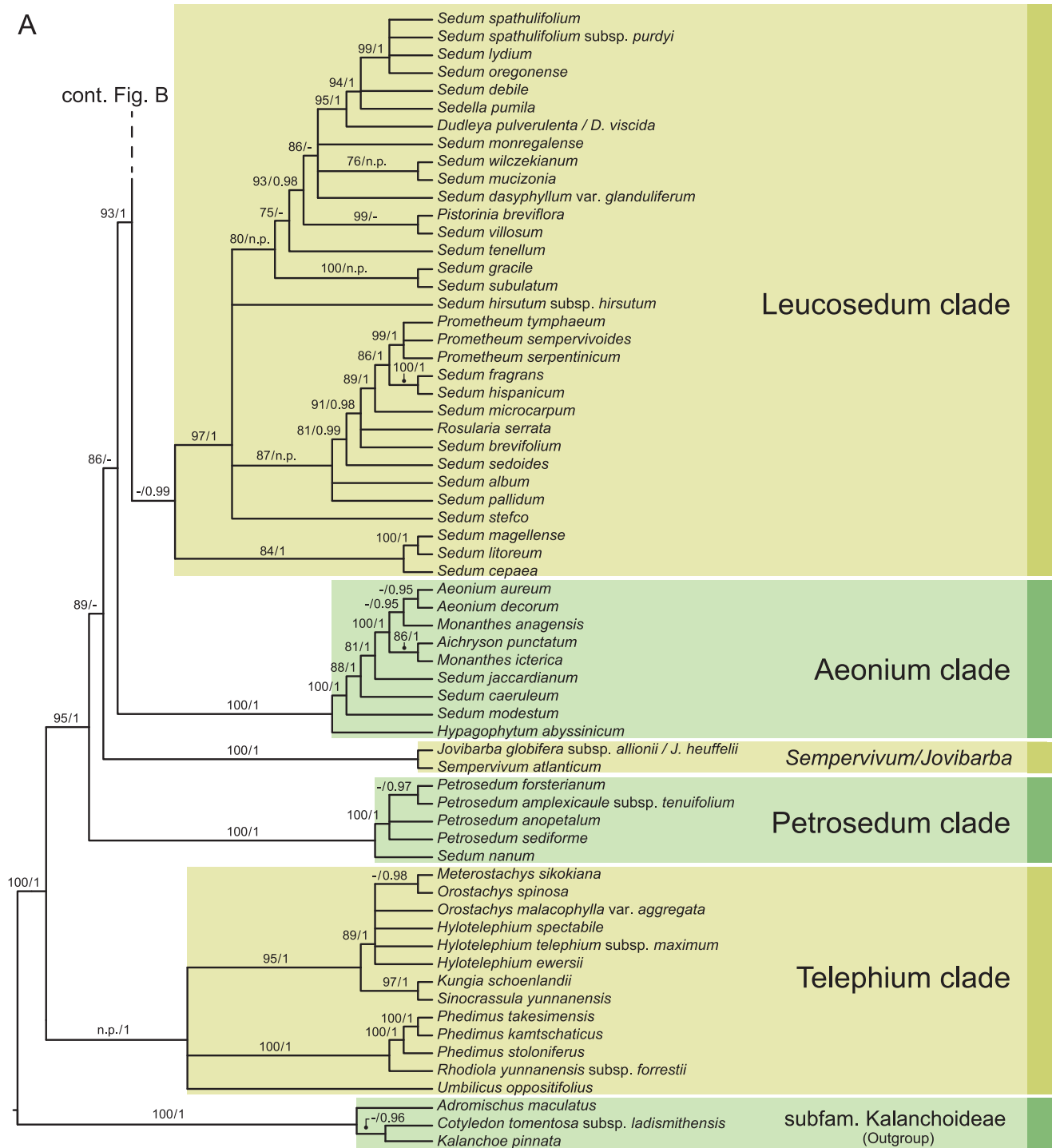


Fig. 2. Molecular phylogeny of Crassulaceae subfam. Sempervivoideae based on a concatenated sequence matrix of the plastid DNA markers *matK*, *rps16* and *trnL-trnF* and inferred using maximum likelihood (cpDNA/ML) and Bayesian inference (cpDNA/BEAST). Branch labels give bootstrap support values for cpDNA/ML (left) and posterior probabilities for cpDNA/BEAST (right; n.p.: clade not present; -: clade present but unsupported). Branches with bootstrap support <75 and posterior probability <0.95 were collapsed. Names of major clades as used in the main text are given.

taxa *Spathulifolium* Fröd. and *Ternatum* Fröd. (Americana Kyphocarpia) and *Alamosanum* (Americana Orthocarpia). *Sedum lagascae* Pau and *S. villosum* L., which were resolved as the closest relatives of *Pistorinia* (we only sampled *P. breviflora* Boiss.) whenever these species were sampled (Figs. 1B, 2A, suppl. Fig. S1), belong to 't Hart's (1991) ser. *Subrosea*

(also containing the apparently more distantly related *S. nevadense* Coss.; Fig. 1B, suppl. Fig. S1), and these together were sister to *S. monregalense* Balb. of the monospecific ser. *Monregalensia* 't Hart in our ITS phylogenies (Fig. 1B, suppl. Fig. S1). Lastly, *Prometheum* was resolved as sister to *Sedum hispanicum* L. of ser. *Glauco-rubens* in

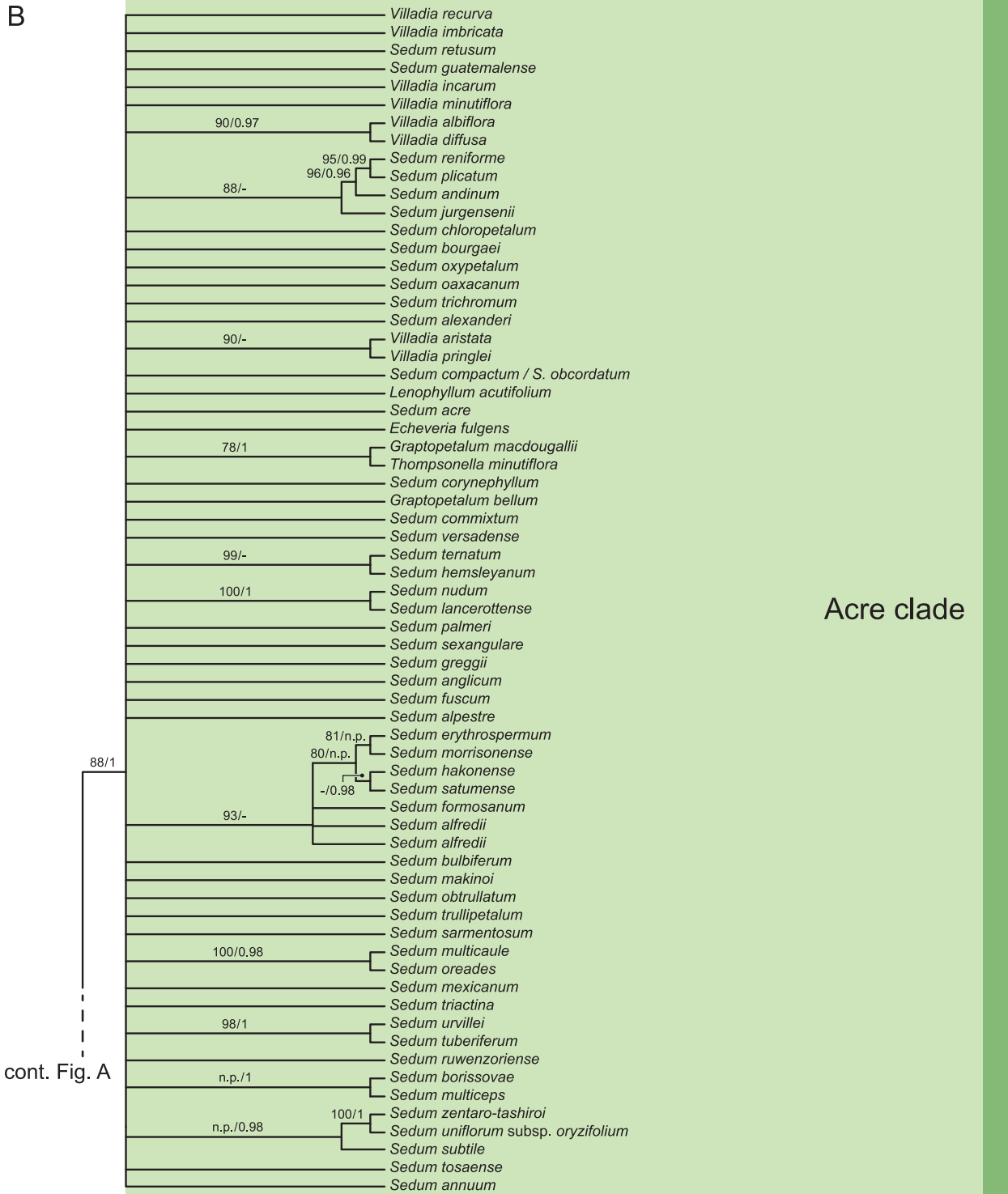


Fig. 2. Continued.

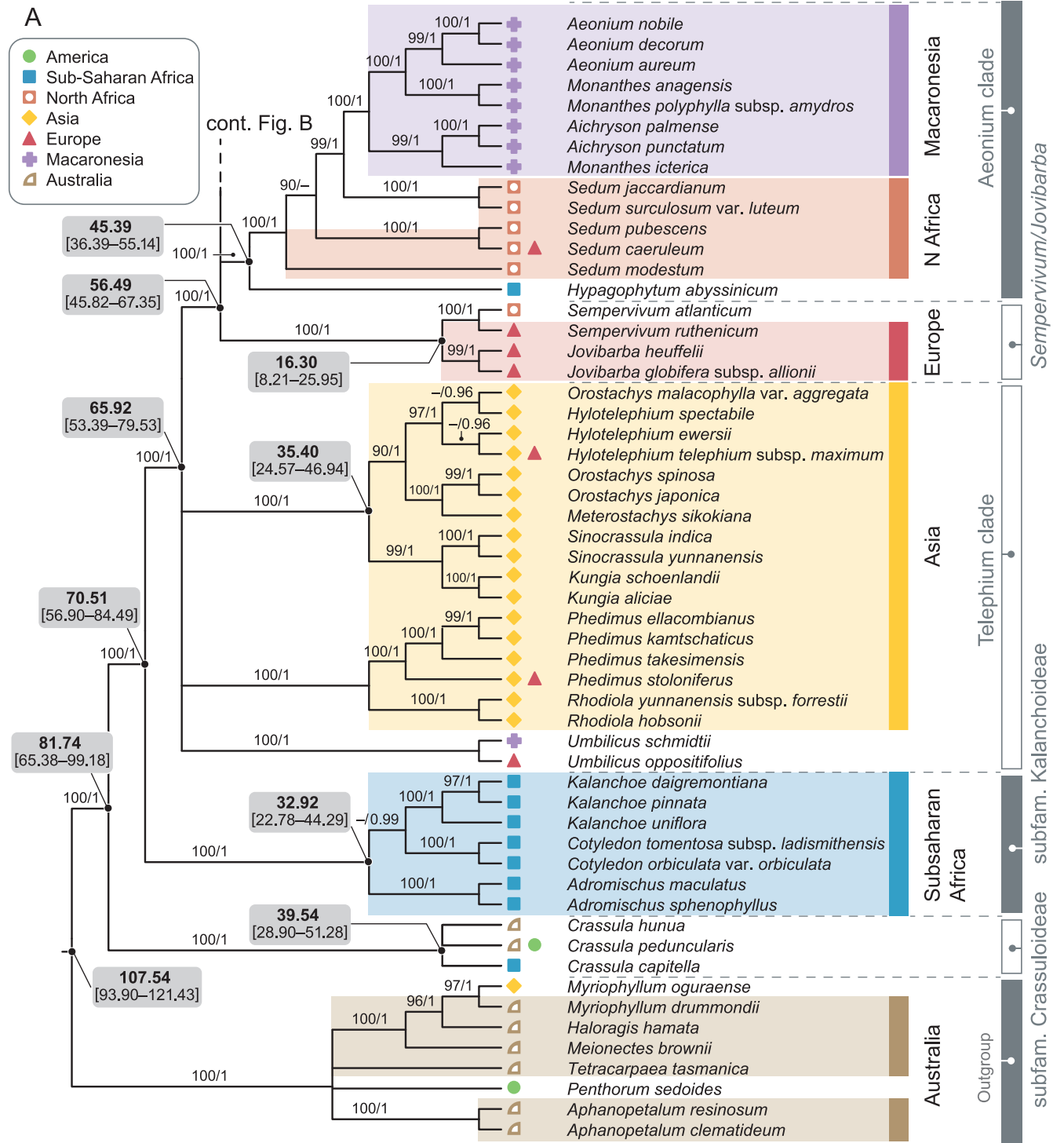


Fig. 3. Family-wide molecular phylogeny of Crassulaceae based on a concatenated sequence matrix of the combined nuclear and plastid DNA markers ITS, *matK*, *rps16* and *trnL-trnF* and inferred using maximum likelihood (combined/ML) and Bayesian inference (combined/MrBayes). Branch labels give bootstrap support values for combined/ML (left) and posterior probabilities for combined/MrBayes (right). Branches with bootstrap support <75 and posterior probability <0.95 were collapsed or marked “–” when support was only found in one of the two analyses. Node labels in gray boxes provide mean crown group age estimates and 95% confidence intervals in million years (see Table 4) as inferred in the dating analysis of ITS sequences (see suppl. Fig. S1 and Materials and Methods for more information). Geographical distribution is indicated by colour, and symbols as explained in the figure inset.

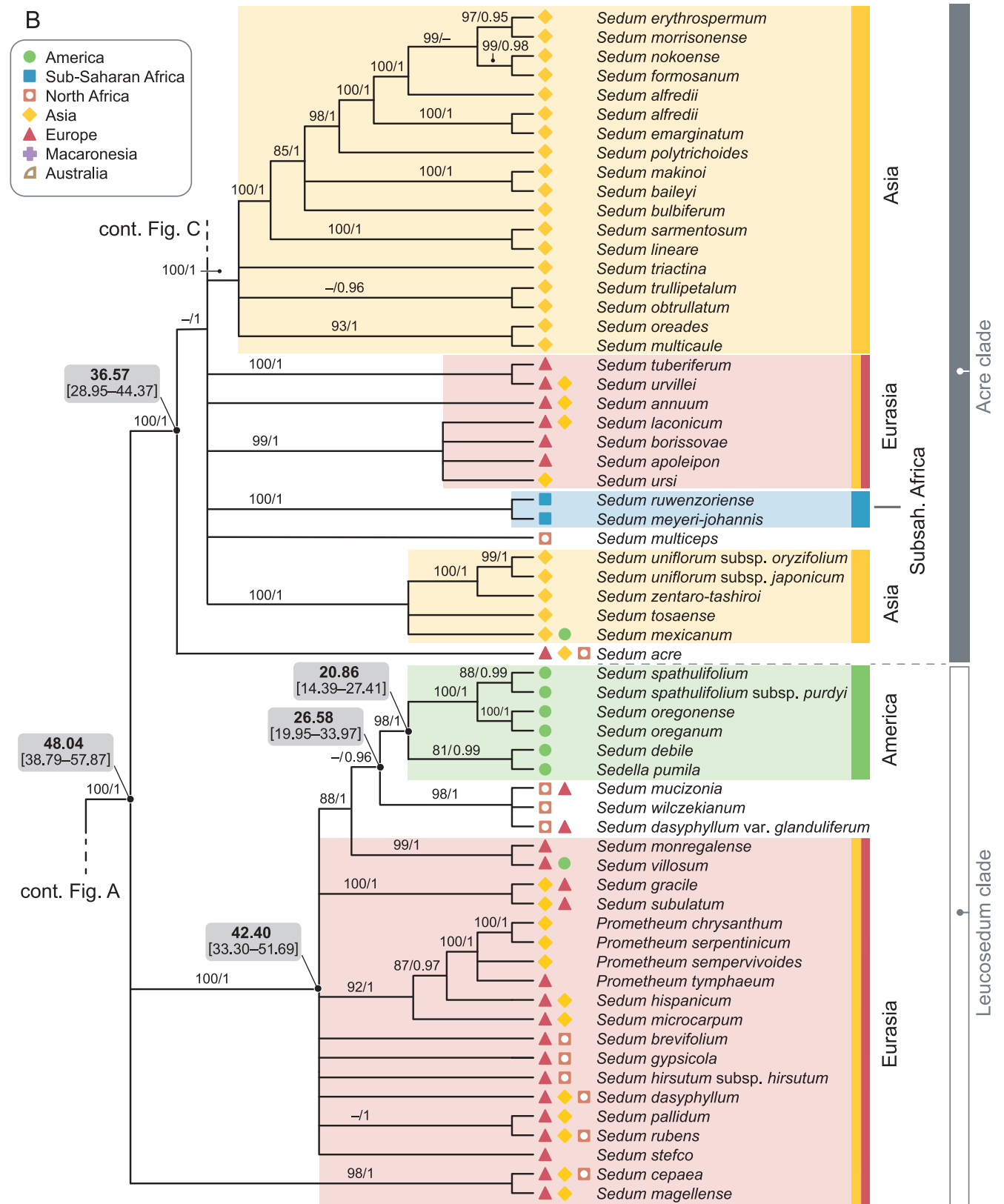
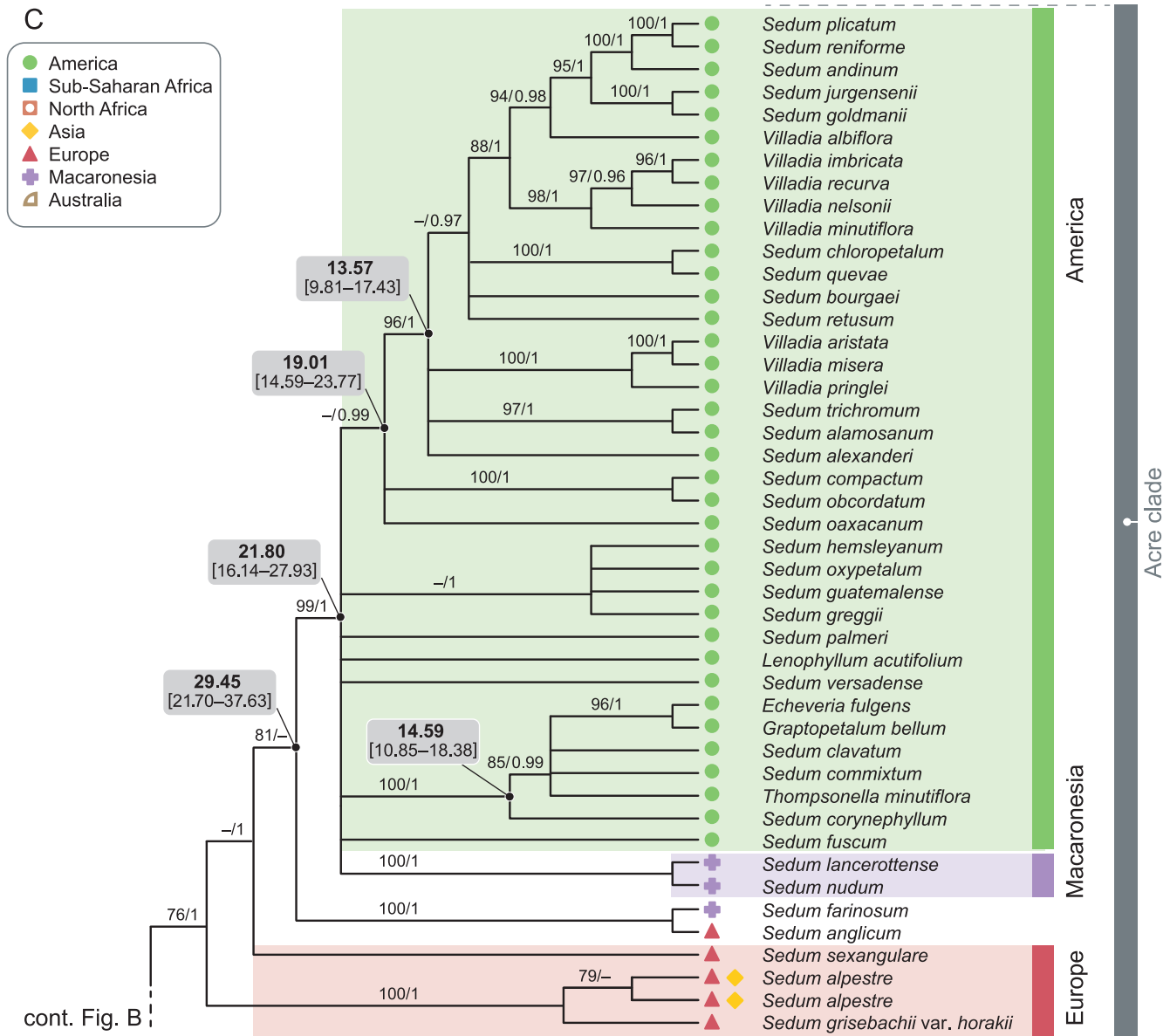


Fig. 3. Continued.



all analyses that included ITS sequence data (Figs. 1B, 3B, suppl. Fig. S1), but *S. hispanicum* is in turn most closely related to *S. fragrans* of ser. *Alsinefolia* in the analyses of plastid DNA (Fig. 2A).

In summary, four monophyletic major groups could be identified when the Telephium clade is considered as unsupported (supported only in cpDNA/BEAST, Fig. 2A). These are (1) the Petrosedum clade, (2) *Sempervivum/Jovibarba*, (3) the Aeonium clade and (4) clades Leucosedum plus Acre in which the latter is monophyletic and the former is monophyletic when plastid sequence data alone were used (Fig. 2A). While our plastid data resolved the Telephium clade and these four clades as successive sister clades (Telephium clade (Petrosedum clade (*Sempervivum/Jovibarba* (Aeonium clade,

clades *Leucosedum* plus Acre))))), the Petrosedum clade was consistently recovered as sister to the Aeonium clade in our ITS analyses (Fig. 1A, suppl. Fig. S1).

Molecular dating. — The results of our dating analysis are shown in detail in suppl. Fig. S1, and stem and crown ages of the five major clades as well as other important clades are summarized in Table 4 and shown in the phylogeny based on combined nuclear and plastid sequence data (Fig. 3). After a burn-in of 25%, three of the four independent MCMC runs yielded an effective sampling size between 170 and 200 for one parameter (i.e., the mrcatime parameter of one of the clades that had been predefined as monophyletic). However, because the four runs converged to the same estimate for this parameter, we considered the analysis to be robust.

Table 4. Stem (S) and crown (C) age estimates of selected clades in the Crassulaceae chronogram (see suppl. Fig. S1) based on Bayesian inference using a lognormal relaxed clock.

Clade	Estimated age [95% confidence interval]
Crassulaceae S	107.54 [93.90–121.43]
Crassulaceae C**	81.74 [65.38–99.18]
subfam. Crassuloideae C**	39.54 [28.90–51.28]
subfam. Sempervivoideae S*	70.51 [56.90–84.49]
subfam. Kalanchoideae C**	32.92 [22.78–44.29]
subfam. Sempervivoideae C**	65.92 [53.39–79.53]
Telephieae C** (Telephium clade)	35.40 [24.57–46.94]
Umbiliceae S ⁻ (Telephium clade)	63.43 [51.45–75.64]
Umbiliceae C ⁻ (Telephium clade)	56.54 [41.53–71.11]
<i>Petrosedum</i> + <i>Aeonium</i> clade S**	56.49 [45.82–67.35]
<i>Petrosedum</i> C**	31.93 [19.86–44.57]
<i>Aeonium</i> clade S**	52.13 [42.06–62.60]
<i>Aeonium</i> clade C**	45.39 [36.39–55.14]
<i>Sempervivum/Jovibarba</i> S**	51.97 [42.26–62.66]
<i>Sempervivum/Jovibarba</i> C**	16.30 [8.21–25.95]
Sedeae C**	48.04 [38.79–57.87]
Leucosedum clade (excl. <i>Rosularia</i> and <i>Sedum</i> ser. <i>Cepaea</i>) C**	42.40 [33.30–51.69]
American subclade of <i>Leucosedum</i> S ⁻	26.58 [19.95–33.97]
American subclade of <i>Leucosedum</i> C**	20.86 [14.39–27.41]
Acre clade C**	36.57 [28.95–44.37]
American subclade of Acre (incl. ser. <i>Macaronesia</i>) S*	29.45 [21.70–37.63]
American subclade of Acre (incl. ser. <i>Macaronesia</i>) C**	21.80 [16.14–27.93]
<i>Echeveria</i> clade S ⁻	17.01 [12.80–21.34]
<i>Echeveria</i> clade C**	14.59 [10.85–18.38]
<i>Villadia</i> clade S ⁻	19.01 [14.59–23.77]
<i>Villadia</i> clade C**	13.57 [9.81–17.43]

Age estimates are given in million years as mean and 95% confidence interval. Symbols following C or S indicate the inferred posterior probabilities (p.p.): ⁻ p.p. < 0.90; * 0.90 ≤ p.p. < 0.95; ** p.p. ≥ 0.95

DISCUSSION

Backbone phylogeny and major clades in Sempervivoideae. — Our analysis of the largest taxon sample of Sempervivoideae analyzed so far using both ITS and, for a smaller sample, plastid DNA sequences led to the recognition of clades and relationships that had not been recognized before.

(1) The Telephium clade, never before resolved as supported monophyletic (Van Ham & 't Hart, 1998; Mort & al., 2001; Mayuzumi & Ohba, 2004; Gontcharova & al., 2006), was supported as monophyletic in cpDNA/BEAST (Fig. 2A) in which it was sister to the remainder of Sempervivoideae. This clade had been suspected to be monophyletic based on the shared presence of a 6 bp insertion in *matK* by Mort & al. (2001). In all other analyses (Figs. 1A, 3A, suppl. Fig. S1), the three well-supported sublineages of this clade were part of a polytomy with the monophyletic remainder of Sempervivoideae.

(2) Based on our plastid dataset (Fig. 2A), the *Petrosedum* clade and *Sempervivum/Jovibarba* are successive sister clades to the remainder of the subfamily without the Telephium clade. In phylogenies of the ITS dataset, however, the *Petrosedum* clade was sister to the *Aeonium* clade (Fig. 1A, suppl. Fig. S1), and in our dated phylogeny of ITS (suppl. Fig. S1), *Sempervivum/Jovibarba* were supported as the closest relatives of *Sedeae*. *Petrosedum* and *Sempervivum/Jovibarba* before had been treated as the *Sempervivum* clade (Van Ham & 't Hart, 1998), although they had never been resolved as supported sister to each other. Therefore, there is no evidence for Sempervivoideae in that circumscription as a monophyletic group.

(3) The *Aeonium* clade was resolved as sister to the *Acre* and *Leucosedum* clades by our plastid data (Fig. 2A), a relationship never supported before, whereas our dating analysis of ITS supported *Sempervivum/Jovibarba* as sister to the *Acre* and *Leucosedum* clades (suppl. Fig. S1). The *Aeonium* clade was in turn sister to the *Petrosedum* clade in all phylogenies of ITS (Fig. 1A, suppl. Fig. S1).

(4) Finally, clades *Acre* and *Leucosedum*, together constituting *Sedeae*, were strongly supported as one clade in all our phylogenies except ITS/ML (Fig. 1B) in which this clade was unsupported. The *Acre* clade alone received substantial support in all our phylogenetic analyses, too. However, in our ITS phylogeny (Fig. 1A,B) the monophyletic *Acre* clade was part of a large polytomy containing a number of lineages representing the *Leucosedum* clade (both ITS/ML and ITS/MrBayes), but also *Sempervivum/Jovibarba* and the *Aeonium* and *Petrosedum* clades (ITS/ML only). Such a topology of the *Acre* and *Leucosedum* clades had already been found before (Mort & al., 2001; Nikulin & al., 2016). In the backbone of our phylogeny, relationships clearly were least resolved in this part of the tree.

(1) Telephium clade. — The Telephium clade of each of our analyses consisted of three sublineages. (1) To our knowledge, recognition of *Umbilicus*, a genus of 13 species found mainly in the Mediterranean area, Macaronesia, southwest Asia, Arabia and north to east Africa (Thiede & Eggli, 2007), as a genus distinct from *Sedum* has never been questioned. (2) Although *Rhodiola* is a Linnaean genus and has been treated as distinct from *Sedum* in many modern Floras (e.g., Webb, 1993), other Floras included *Rhodiola* in *Sedum* (e.g., Jäger, 2005, but not Jäger, 2011). *Phedimus*, also often treated as part of *Sedum* (Webb, 1993), has been re-segregated from *Sedum* by, e.g., 't Hart (1995) and Ohba & al. (2000). This

clade of *Phedimus* and *Rhodiola* also contains what has been recognized as *Pseudosedum* (not sampled here), another *Sedum* segregate according to Thiede & Eggli (2007). Although *Pseudosedum* may be sister to *Rhodiola*, Mayuzumi & Ohba (2004) discussed the option of including the former in the latter. This would be supported by the findings of Gontcharova & al. (2006), who found *Pseudosedum* to be the closest relative to only part of *Rhodiola*. Gontcharova & al. (2006) also segregated *Aizopsis* Grulich from *Phedimus*. Following Thiede & Eggli (2007), the *Phedimus/Rhodiola* clade contains ca. 88 species (*Phedimus*: 18; *Pseudosedum*: 12; *Rhodiola*: ca. 58) mainly in Asia with few species in Europe (*Phedimus*, *Rhodiola*) and North America (*Rhodiola*). These first two sublineages of the Telephium clade together form Umbiliceae as understood by Thiede & Eggli (2007). (3) The third sublineage has been classified as Telephieae (Thiede & Eggli, 2007) and contains *Hylotelephium*, a segregate of *Sedum* (Ohba, 1977), *Meterostachys*, *Sinocrassula*, *Orostachys* and *Kungia*, a segregate of a non-monophyletic *Orostachys* with two species from southwestern China and probably sister to *Sinocrassula*; see Thiede & Eggli (2007) and our phylogenies of ITS/ML (Fig. 1A), cpDNA (Fig. 2A) and the combined dataset (Fig. 3A). Neither *Hylotelephium* nor *Orostachys* were recovered as monophyletic in our analyses (Figs. 1A, 2A, 3A, suppl. Fig. S1) and in the analyses by Mayuzumi & Ohba (2004) and Gontcharova & al. (2006), and *Meterostachys* is nested in this group. However, all phylogenies in which more than one species of *Orostachys* subsect. *Appendiculatae* (Boriss.) H. Ohba was sampled (Figs. 1A, 3A, suppl. Fig. S1) suggested monophyly of this subsection and its sister relationship to *Meterostachys*, as also found by Mayuzumi & Ohba (2004) and Gontcharova & al. (2006). According to Thiede & Eggli (2007), this sublineage (Telephieae) contains ca. 48 species (*Hylotelephium*: ca. 27; *Kungia*: 2; *Meterostachys*: 1; *Orostachys*: 11; *Sinocrassula*: 7) mainly in Asia with few species in Europe and North America (*Hylotelephium*).

(2) Petrosedum clade. — *Sedum nanum* of ser. *Nana* as well as all species sampled of *Sedum* ser. *Rupestris* A. Berger belong to this clade; ser. *Rupestris* had been recognized at generic rank as *Petrosedum* by Grulich (1984) and accepted as such by Thiede & Eggli (2007), who emphasized the embryological and phytochemical distinctness of this lineage. Thus, Mauritzon (1933) recognized a pattern of endosperm and proembryo formation unique to *Petrosedum rupestre* (L.) P.V. Heath and *P. anopetalum* (DC.) Grulich, the representatives of *Petrosedum* sampled by him. This pattern (Rupestre-Type) is characterized by a much-elongated suspensor of the proembryo, which is surrounded by only one layer of endosperm cells. In the field, *Petrosedum* can be distinguished on the basis of its polymerous instead of pentamerous flowers, which probably is the main reason for its traditional association with *Sempervivum/Jovibarba*. According to Grulich (1984), *Petrosedum* is further characterized by the presence of glandular trichomes or papillae (in most but not all species) on bracts, pedicels, sepals, filaments and carpels (see Fig. 1A for the occurrence of glandular trichomes

in the sampled species), by distinctly rigid and acute leaf apices and by a completely apocarpous, slender and upright gynoeceum, which is “slightly submerged in a ‘receptaculum’ formed by connate parts of sepals and enlarged pedicels”. Representatives of *Sedum* ser. *Nana* do not share these features with *Petrosedum*. The pronounced distinctness of *Petrosedum* from *Sedum* has again been demonstrated more recently in a study of micromorphological characters of Mediterranean *Sedum* s.l. (Giuliani & al., 2018) sampling five *Petrosedum* species as well as representatives of the clades Telephium, Leucosedum and Acre. *Petrosedum* currently comprises 14 species native to Europe, the Levant and North Africa (Thiede & Eggli, 2007), but with the inclusion of *Sedum* ser. *Nana* (from the Near East), as suggested by our findings, species number would increase to 9 or 12, depending on whether *Sedum caroli-henrici* Kit Tan, *S. elburzense* Akhiani & Assadi and *S. yildizianum* Sümbül indeed belong to this lineage as suggested by ‘t Hart & Alpınar (2000) and ‘t Hart & Bleij (2005). The inclusion of *Sedum* ser. *Nana* in *Petrosedum* or as sister to *Petrosedum* is further corroborated by Van Ham & ‘t Hart’s (1998) earlier finding that *S. assyriacum* Boiss. also falls in the *Petrosedum* clade.

(3) Sempervivum/Jovibarba. — This clade comprises *Sempervivum* and *Jovibarba*, treated as one genus by Thiede & Eggli (2007) but as two separate genera in the most recent phylogenetic analysis of this group (Klein & Kadereit, 2015). Klein & Kadereit (2015) considered *Sempervivum* to contain 46, and *Jovibarba* to contain 2 species. Both genera are oreophytes found mainly in western Eurasian mountain ranges.

(4) Aeonium clade. — This clade comprises *Aeonium* (incl. *Greenovia*), *Aichryson*, *Monanthes*, *Hypagophyllum* and approximately eight *Sedum* species of series *Monantheoidea*, *Caerulea* and *Pubescens*, which formed two or three successive sister clades to the first three genera in our phylogenies, although ser. *Monantheoidea* probably is not monophyletic (see suppl. Table S1 and Figs. 1A, 2A, 3A and suppl. Fig. S1). According to our findings, *S. jaccardianum* Maire & Wilczek and *S. surculosum* Coss. of ser. *Monantheoidea* might be the closest relatives of the Macaronesian genera of the Aeonium clade, but only full sampling of the *Sedum* species of interest will clarify relationships in this part of the phylogeny. Morphological and karyological similarities between some North African *Sedum* and the Macaronesian genera had already been pointed out by Uhl (1961b). *Hypagophyllum abyssinicum* (Hochst. ex A. Rich.) A. Berger received strong support as the earliest branching species of the Aeonium clade in all our analyses (Figs. 1A, 2A, 3A, suppl. Fig. S1). This only species of the northwest Ethiopian *Hypagophyllum* had previously been treated as part of the Crassula clade (Thiede & Eggli, 2007) and even included in *Crassula* L. by Stevens (2001–). The phylogenetic position of *Hypagophyllum* that we found here had been suspected early by Fröderström (1930, 1932) and fits a biogeographical pattern also observed in other plant lineages (for other examples and discussion see Thiv & al., 2010). Whereas *Aichryson* and *Monanthes* are restricted to the Macaronesian Islands,

and *Aeonium* is found mainly there with one species in Morocco and two species in east Africa (Jorgensen & Olesen, 2001), the *Sedum* series of this clade (listed above) are mostly northwest African in distribution with only *S. caeruleum* L. also found on several islands in the Mediterranean Sea. A phylogeny of the first three genera by Mort & al. (2002) had shown that *Monanthes* is not monophyletic when *M. ictERICA* (Webb ex Bolle) Christ is included, and that *Aeonium* is not monophyletic when *Greenovia* is recognized as a separate genus. The clade contains about 64 species (*Aeonium*: 39; *Aichryson*: 15; *Monanthes*: 10) plus approximately 8 species of *Sedum* (Mes, 1995a; 't Hart & Bleij, 2005; Thiede & Eggli, 2007), and the monospecific *Hypagophytum*.

(5) Clades Leucosedum and Acre. — Except for two early studies of cpDNA restriction site variation (Van Ham & 't Hart, 1998; 't Hart & al., 1999) based on rather sparse taxon samples (11 and 26 spp., respectively), the Leucosedum clade to our knowledge has never been recovered as monophyletic (Mort & al., 2001; Nikulin & al., 2016). In agreement with that, our phylogenetic tree of ITS sequences (Fig. 1B) shows clades Leucosedum and Acre, together constituting Sedeae of Thiede & Eggli (2007), as a polytomy of four clades. The largest of these four clades (*Graptopetalum glassii* through *Sedum acre* in Fig. 1B–D) constitutes the Acre clade and will be further discussed below.

One small clade in this polytomy consisted of a monophyletic *Rosularia* (represented here by *R. globulariifolia* (Fenzl) A. Berger and *R. serrata* (L.) A. Berger) and an unidentified *Sedum* species. The *Sedum* species of the remaining two clades, i.e., *S. cypricum* through *S. magellense* and *S. obtusatum* through *S. subulatum* (C.A. Mey.) Boiss., almost exclusively belong to *Sedum* subg. *Gormaniana* as defined by Thiede & Eggli (2007) on account of the presence of glandular trichomes (when plants are hairy), broadly sessile sepals and a costate seed testa (testa reticulate in *Sedum aetnense* Tineo) (see Fig. 1B). In a detailed micromorphological study, Giuliani & al. (2018) have furthermore shown that all species of subg. *Gormaniana* of their sample of Mediterranean *Sedum* s.l. have epidermal cells of a unique shape on the adaxial surface of the petals, found in none of the species of *Sedum* subg. *Sedum*, *Petrosedum* and the Telephium clade sampled by these authors. All genera included in the Leucosedum clade by Thiede & Eggli (2007), except for *Rosularia* and *Afrovivella*, of which the latter was not sampled by us, fell into the large *Sedum-obtusatum*-through-*S.-subulatum* clade, which received significant support in ITS/MrBayes (Fig. 1B), both analyses of the combined dataset (Fig. 3B) and the dated phylogeny (suppl. Fig. S1). In the analyses of plastid DNA (Fig. 2A), the same clade was supported as monophyletic with *Rosularia* nested within. In the large *Sedum-obtusatum*-through-*S.-subulatum* clade (Fig. 1B), a monophyletic *Dudleya* (for the phylogeny of *Dudleya*, see Yost & al., 2013) and *Sedella* (only one of three species sampled by us) together with several species of *Sedum* fell into a subclade that is exclusively North American in distribution (i.e., *Sedum obtusatum* through *Sedella pumila*). A monophyletic *Prometheum*

was sister to *Sedum hispanicum*. *Afrovivella* has been claimed to be similar to *Prometheum* in seed characters (Eggli, 1988) and is therefore likely to belong to this clade, too. *Afrovivella* used to be included in *Rosularia* (Ohba, 1978; Eggli, 1988), as was the largest part of *Prometheum* until several *Rosularia* species were transferred to *Prometheum* (Ohba, 1978; 't Hart, 1995) to render both *Prometheum* and *Rosularia* monophyletic. Except for the North American *Dudleya/Sedella* subclade, all other lineages of the Leucosedum clade are distributed in the Old World (Fig. 3B). *Prometheum* is southwest Asian and southeast European (northern Greece) in distribution, at least part of *Rosularia* is distributed in Asia, and *Pistorinia* and most *Sedum* species of this clade are distributed in the Mediterranean area (Fig. 3B). Nine of the 15 supported conflicts between the ITS and plastid phylogenies were found in the Leucosedum clade, which makes it the lineage with the highest density of topological conflict. The well-supported clade of *Sedum cypricum* through *S. magellense* (Fig. 1B) corresponds to ser. *Cepaea* (three out of seven species sampled) and is thus one of the few morphologically well-characterized clades (see Table 3). Its sister relationship to the remainder of the Leucosedum clade was supported in the one analysis that also supported the Leucosedum clade as a monophyletic group, i.e., cpDNA/BEAST (Fig. 2A).

As indicated above, the largest of the four clades of Sedeae (*Graptopetalum glassii* through *Sedum acre*) is commonly referred to as the Acre clade (Thiede & Eggli, 2007) and in our ITS phylogeny (Fig. 1B–D) consisted of a large polytomy. Without exception, all *Sedum* species in the Acre clade as inferred by us belong to subg. *Sedum*. Species of this subgenus are characterized by the absence of glandular trichomes (plants glabrous or trichomes non-glandular), by basally free sepals that often are spurred and unequal in length, and by a reticulate, reticulate-papillate or papillate testa ornamentation (testa costate in *Sedum litoreum*; Thiede & Eggli, 2007) (Fig. 1B–D). Apart from a large clade (*Graptopetalum glassii* through *Sedum pacense* J. Meyrán in Fig. 1C,D) that except for the subclade *S. lancerottense* through *S. nudum* (= *Sedum* ser. *Macaronesia*) is American in distribution (Fig. 3C), the remaining clades and single species in the basal polytomy of the Acre clade contained only species of *Sedum*. The large clade of *Graptopetalum glassii* through *Sedum pacense* contained eight clades/species of *Sedum* plus partly other genera (Fig. 1C,D). One of these clades included a non-monophyletic *Villadia* and several lineages of *Sedum* (Fig. 1C). In this *Villadia* group (Carrillo-Reyes & al., 2009), non-monophyly of *Villadia* had also been found by Carrillo-Reyes & al. (2009). The largest of these eight clades, i.e., *Graptopetalum glassii* through *Sedum palmeri* S. Watson, was only supported in ITS/MrBayes and – among four other subclades/species – contained the always well-supported *Echeveria* group (Fig. 1D) of Carrillo-Reyes & al. (2009). The *Echeveria* group contained (besides several lineages/species of *Sedum*) *Echeveria*, *Cremnophila* (included in *Sedum* by Thiede & Eggli, 2007), *Graptopetalum* (incl. *Tacitus*; for a

phylogenetic analysis see Acevedo-Rosas & al., 2004a,b), *Pachyphytum* and *Thompsonella*. Of the five genera (besides *Sedum*) recognized in the Echeveria group, *Pachyphytum* and *Thompsonella* appear to be monophyletic (see also Carrillo-Reyes & al., 2008, 2009), although the position of *T. mixtecana* is not always resolved, and monophyly of *Cremonophila* remains unresolved. *Echeveria* and *Graptopetalum* clearly are not monophyletic (see also Acevedo-Rosas & al., 2004a; Carrillo-Reyes & al., 2008, 2009). Another subclade in the polytomy containing the Echeveria clade comprised *Lenophyllum acutifolium* Rose, the only species of *Lenophyllum* sampled here, and four *Sedum* species (i.e., *S. potosinum* through *S. gypsophilum* B.L. Turner in Fig. 1D) that share a preference for limestone soils with *Lenophyllum* (Uhl, 1985; Carrillo-Reyes & al., 2009). The relationships of *Lenophyllum*, a genus of seven species, to other lineages of American Sedeae were unresolved in Mort & al. (2001) and Carrillo-Reyes & al. (2009), but Nikulin & al. (2016) had already inferred a close relationship of this genus to two of the *Sedum* species that we sampled of this lineage.

Biogeography of Sempervivoideae. — In view of limited phylogenetic resolution in many areas of our phylogenetic trees and non-representative geographical sampling of Sempervivoideae, we decided not to conduct a formal biogeographical reconstruction. Considering the geographical distribution of the first two lineages of the family, i.e., Crassuloideae and Kalanchoideae, mostly in sub-Saharan Africa (Fig. 3A), Van Ham & 't Hart (1998) and Mort & al. (2001), the latter based on formal biogeographical analysis, hypothesized that the family originated there and then colonized the Northern Hemisphere. More specifically, Mort & al. (2001) postulated that, starting from southern Africa/Madagascar, the family spread through the Mediterranean region to reach eastern Europe and Asia. Our cpDNA/BEAST phylogeny of the Sempervivoideae, with the Telephium clade as first diverging lineage (Fig. 2A), might suggest a scenario in which, originating from sub-Saharan Africa, the subfamily colonized the Mediterranean region on the one hand and eastern Europe and Asia on the other hand simultaneously. However, in the absence of a formal biogeographical reconstruction, this is speculative.

The distribution of the remaining four major clades of the subfamily clearly supports the original hypothesis by Mort & al. (2001), i.e., expansion into the Mediterranean and neighbouring areas. Thus, *Petrosedum* and *Sempervivum/Jovibarba* are clearly European/Mediterranean in distribution (Fig. 3A, *Petrosedum* clade not sampled), and this area was reconstructed as ancestral for this clade by Mort & al. (2001). With the exception of the east African *Hypagophytum abyssinicum* and two *Aeonium* species (see above), the Aeonium clade is North African/Macaronesian in distribution (Fig. 3A), and this was reconstructed as ancestral area of this clade by Mort & al. (2001). Although origin of the Leucosedum clade was reconstructed as ambiguous by Mort & al. (2001), the Eurasian members of this group are predominantly European/Mediterranean in distribution, with some lineages extending

into central Asia and the Himalayas (Fig. 3B). America was reached once in the evolution of the Leucosedum clade (Fig. 3B), and essentially the same pattern is found in the Acre clade, which also reached America once (Fig. 3C).

Mean and 95% confidence intervals of the stem group ages of the Telephieae, Umbiliceae, the Petrosedum/Aeonium clade, *Sempervivum/Jovibarba*, and Sedeae largely overlap (Fig. 3A, Table 4), with a slightly older stem age for Telephieae. The stem ages of these lineages range between 79.53 and 42.26 Ma, and there is no gap between the 95% confidence intervals of stem ages of any two lineages. These age estimates place the diversification of Northern Hemisphere Sempervivoideae (without the Telephium clade) at a time when the palaeogeography of southern Europe was radically different from today and the area essentially was an archipelago of smaller land masses in the Tethys and Paratethys Seas (Rögl, 1999; Scotese, 2001).

As regards the diversification of Sedeae, the age estimate for the crown group of 48.04 Ma (38.79–57.87 Ma) is older than any other diversification of species-rich lineages in the Mediterranean area known to us (see Vargas & al., 2018). Interestingly, the biogeography of Sempervivoideae (without the Telephium clade) strongly resembles that of Cistaceae, which also contain a Macaronesian clade and reached North America twice. The diversification of that lineage, however, started only in the middle Miocene (Guzmán & Vargas, 2009).

The very similar ages of all major clades might imply that lack of phylogenetic resolution in the subfamily is the result of a rapid radiation, and the palaeogeography of southern Europe at the time of arrival of the subfamily may have facilitated the more or less simultaneous origin of several distinct lineages in allopatry. However, hybridization as a cause of lacking phylogenetic resolution cannot be ruled out. 't Hart (1991) showed that hybridization is possible within but not between those series of *Sedum* he recognized in western Eurasia, and hybridization within and among North American genera of Sempervivoideae is well documented (Uhl, 1963, 1976, 1992b, 1994; Carrillo-Reyes & al., 2008). In our phylogenetic analyses, 21 species – including *Dudleya*, *Petrosedum*, *Pistorinia* and *Rosularia* possibly in their entirety – were supported as incongruently placed in our nuclear and plastid trees. All these observations, together with the exceptionally high diversity of chromosome numbers in Crassulaceae (Uhl, 1992b), clearly show that hybridization and polyploidization must have played a large role in the evolution of the subfamily.

Patterns of morphological evolution in *Sedum* and Sempervivoideae. — The high degree of poly-/paraphyly of *Sedum* as well as non-monophyly of many other genera of Sempervivoideae as discussed above clearly illustrates that those morphological characters used to circumscribe *Sedum* and several other genera of the subfamily are misleading indicators of phylogenetic relationships. As discussed repeatedly ('t Hart & al., 1999; Mort & al., 2001), *Sedum* is defined by a rather unspecific and somewhat plesiomorphic flower morphology, and those characters used to define most other genera, such as fused vs. free petals, poly- vs. tetra- or

pentamerous flower organ whorls and leaf arrangement, show pronounced homoplasy (see Fig. 1).

Considering the geographical distribution of lineages classified as *Sedum* and of lineages morphologically distinct from *Sedum* and recognized at generic rank, a certain pattern emerges: many of the lineages recognized as generically distinct from *Sedum* in the clades *Aeonium*, *Leucosedum* and *Acre* are found in areas that are geographically disjunct or remote from the Mediterranean and adjacent areas. Thus, the *Aeonium* clade contains three lineages recognized at generic rank on various Macaronesian islands. *Hypagophytum*, also part of the *Aeonium* clade, is distributed in east Africa (Fig. 3A). In the *Acre* clade, colonization of America (Fig. 3C) resulted in the origin of all genera in this part of the phylogenetic tree, i.e., *Lenophyllum*, *Cremonophila*, *Villadia*, *Echeveria*, *Graptopetalum* (incl. *Tacitus*), *Pachyphytum* and *Thompsonella* (Fig. 1C,D). However, this American clade also contains several lineages classified as *Sedum*. In the *Acre* clade, two lineages colonized Asia (*Sedum uniflorum* through *S. mexicanum* Britton, *S. erythrospermum* through *S. multicaule* Wall. ex Lindl.) and diversified there, and one lineage colonized east Africa (*S. ruwenzoriense* and *S. meyeri-johannis*) but remained species-poor (Fig. 3B). All these are treated as *Sedum*. Similar to the *Acre* clade, a large part of the North American lineage of the *Leucosedum* clade has been classified as generically distinct (*Dudleya/Sedella*). Two lineages of the *Leucosedum* clade colonized east Africa, namely a lineage of six species of *Sedum* subg. *Gormaniana* (Gilbert, 1985) of which we sampled *S. crassularia* Raym.-Hamet (Fig. 1B), and the monospecific *Afrovivella* (not sampled by us). Of these two lineages, only *Afrovivella* has been treated at generic rank. Of the other lineages of the *Leucosedum* clade described as separate genera, *Prometheum* is southwest Asian and southeast European in distribution (Fig. 3B), at least part of *Rosularia* is distributed in Asia, and *Pistorinia* is distributed in the Mediterranean area.

This pattern shows that accelerated phenotypic evolution, resulting in the origin of lineages recognized at genus rank, is often but not always linked to major shifts in geographical distribution. We cannot offer any explanation for this pattern.

Classification of *Sedum*. — Of the 15 species and 3 varieties of *Sedum* described by Linnaeus (1753) in *Species plantarum*, 10 species were sampled here. These 10 species (marked “L.” in Fig. 1) fell into four of the five major clades identified, i.e., the clades *Telephium*, *Petrosedum*, *Leucosedum* and *Acre*, and the remaining five Linnaean species are now classified in *Hylotelephium* and *Phedimus*. It thus is obvious that *Sedum* as understood by Linnaeus (1753) is highly polyphyletic, hence “Linnaeus’s folly”. As type of *Sedum*, *S. acre* was designated by ’t Hart in Jarvis (1992) to replace *S. telephium* L. as an earlier choice (Britton & Rose, 1905). Considering the segregation of *Sedum* sect. *Telephium* Gray as a separate genus, it was argued: “The adoption now of *S. telephium* as type would cause *Sedum* to be applied to the segregate genus (where recognized), and a new generic name would have to be adopted for about 500 species currently recognized in *Sedum* (McNeill & al., 1987: 384). *S[edum]*.

acre is a later choice (Green, 1929) but has been fairly generally accepted (e.g., by Clausen, 1975) and falls within *S.* subg. *Sedum*. It would maintain usage irrespective of the generic concept adopted” (’t Hart in Jarvis, 1992: 569). As evident from the results of our and earlier phylogenies, subg. *Sedum*, corresponding to the *Acre* clade according to Thiede & Eggli (2007), is not mono- but poly- or paraphyletic by including the American genera of this clade. Also, a large number of lineages or individual species of *Sedum* are found in clades *Leucosedum* and *Aeonium*. Considering the position of *Sedum acre* in our ITS phylogeny (Fig. 1B) – as the only species of ser. *Acria* (see suppl. Table S1) it was part of the large basal polytomy of the *Acre* clade –, obviously much classificatory action is needed to arrive at a monophyletic *Sedum* provided classification is expected to recognize only monophyletic taxa (for pros and cons, see Schmidt-Lebuhn, 2012 and Stuessy & Hörandl, 2014).

As all former *Sedum* species of the *Telephium* clade have been combined in other genera (Ohba, 1977, 1978), *Petrosedum* is increasingly being accepted as a segregate genus (Grulich, 1984; Thiede & Eggli, 2007) and *Sempervivum/Jovibarba* have never been classified in *Sedum* after 1903 (see Eggli, 2005), a first option would be to include all genera of the *Aeonium* clade (which contains species of *Sedum*) and all those genera of *Sedeae* (clades *Leucosedum* and *Acre*) long recognized as segregates into a vastly expanded *Sedum*, although this would mean to abandon a number of well-established genera. In the *Aeonium* clade, this would affect *Aeonium* (39 spp.), *Aichryson* (15 spp.), *Monanthes* (10 spp.) and *Hypagophytum* (1 sp.). In *Sedeae*, this would affect (following the generic classification by Thiede & Eggli, 2007) *Afrovivella* (1 sp.), *Dudleya* (ca. 47 spp.), *Sedella* (3 spp.), *Pistorinia* (3 spp.), *Prometheum* (8 spp.) and *Rosularia* (20 spp.) of the *Leucosedum* clade, and *Villadia* (ca. 21 spp.), *Lenophyllum* (7 spp.), *Echeveria* (ca. 139 spp.), *Graptopetalum* (18 spp.), *Pachyphytum* (15 spp.) and *Thompsonella* (6 spp.) of the *Acre* clade. *Cremonophila* (2 spp.) was included in *Sedum* by Thiede & Eggli (2007), but no validly published name in *Sedum* exists for *Cremonophila linguifolia* (Lem.) Moran (Moran, 2005). In sum, species number in *Sedum* would increase from ca. 470 to ca. 820. As the *Aeonium* clade is one of the five major lineages identified by us and other authors before, and since it was recovered as sister to *Sedeae* by plastid data (Fig. 2A) but as sister to the *Petrosedum* clade by ITS data (Fig. 1A), we would argue for its exclusion from a newly circumscribed *Sedum* in order to achieve taxa (in this case tribes) of phylogenetic equivalency and more or less identical age, a criterion for classification advocated by, e.g., Avise & Johns (1999).

When not including the *Aeonium* clade in *Sedum*, the number of species in *Sedum* would increase from ca. 470 to ca. 755, and the approximately eight species of *Sedum* found in the *Aeonium* clade as well as the 2–5 species of *Sedum* ser. *Nana* found in the *Petrosedum* clade will have to be re-classified (see below). Exclusion of the *Aeonium* clade would limit the name *Sedum* to the well-supported *Sedeae*, i.e., clades

Leucosedum and Acre, and would require combination of all genera of these two clades other than *Sedum* in *Sedum*. As a third option, circumscription of *Sedum* as corresponding to the Acre clade, a well-supported and morphologically distinct clade in which the type *S. acre* is found, would require recognition (in addition to the *Sedum* species in the Aeonium clade) of probably a large number of lineages of the Leucosedum clade at generic rank. An alternative to this would be the recognition of the whole Leucosedum clade as another genus so as to avoid establishing numerous segregate genera with uncertain phylogenetic support in the Leucosedum clade. Finally, the probably most radical option would be to limit the name *Sedum* to *S. acre* alone. Whereas *S. acre* was mostly unresolved within the basal polytomy of the Acre clade (Figs. 1B, 2B), it was resolved as sister to the remainder of the whole Acre clade in combined/MrBayes (Fig. 3B). Restricting the name *Sedum* to *S. acre* would necessitate to classify the large number of *Sedum* lineages in the clades Aeonium, Leucosedum and Acre at generic rank.

Of the above four options (Aeonium clade plus Sedeae; Sedeae; Acre clade; *S. acre* alone), where inclusion of all members of Sempervivoideae in *Sedum* would represent a fifth option we dismissed above (see Linder & Verboom, 1996, for a very similar case in Poaceae: Danthonieae), we favour circumscription of *Sedum* as containing all members of Sedeae for mainly four reasons.

(1) Restriction of *Sedum* to *S. acre* would require recognition of a large number of new or resurrected genera. Consideration of the phylogeny obtained by us and other authors (Van Ham & 't Hart, 1998; 't Hart & al., 1999; Mort & al., 2001, 2002; Acevedo-Rosas & al., 2004a,b; Mayuzumi & Ohba, 2004; Gontcharova & al., 2006; Carrillo-Reyes & al., 2008, 2009; Yost & al., 2013; Klein & Kadereit, 2015; Nikulin & al., 2016; Ito & al., 2017) as well as careful study of morphological, karyological, phytochemical and geographical variation as described in the literature (Boissier, 1872; Schönland, 1891; Berger, 1930; Fröderström, 1930, 1931, 1932, 1935; Clausen, 1940, 1942, 1943a,b, 1959, 1975, 1978, 1979, 1981; Alexander, 1942; Clausen & Uhl, 1943, 1944; Uhl, 1961a,b, 1963, 1970, 1976, 1977, 1978, 1980, 1992a,b; S.-H. Fu, 1965; Uhl & Moran, 1973, 1999; K.T. Fu, 1974; Ohba, 1978; 't Hart, 1978, 1991, 1995; Calie, 1981; Denton, 1982; Gilbert, 1985; Eggli, 1992, 2005; Nesom & Turner, 1995; 't Hart & Alpmar, 1995, 1999, 2000; 't Hart & al., 1999; K.T. Fu & Ohba, 2001; Afferni, 2012, 2014; Santiago & al., 2015) leads us to the conclusion that recognition of subclades as genera appears impossible in most cases, although some clearly definable sublineages do exist in the Leucosedum and Acre clades. All well-supported clades we found in our phylogenies that are characterized by a distinctive combination of morphological features within their area of distribution are listed in Table 3. We were not able to find any potential synapomorphies for any other well-supported clade. This lack of unifying characters may be due to incomplete knowledge of the species' morphology rather than a hard absence of synapomorphies. While some *Sedum* segregates are widely accepted (*Hylotelephium* and *Phedimus*: Telephium clade; *Petrosedum*: Petrosedum clade;

Prometheum and *Sedella*: Leucosedum clade; *Lenophyllum*: Acre clade; *Perrierosedum* (A.Berger) H.Ohba: incertae sedis), other efforts to segregate additional *Sedum* lineages at generic rank (e.g., Nuttall, 1818: *Diamorpha* Nutt.; Berger, 1930: *Mucizonia* A.Berger; Grulich, 1984: *Oreosedum* Grulich and *Asterosedum* Grulich; Löve & Löve, 1985a,b: six new genera, four of them monospecific; Král, 1987: *Helladia* M.Král) have not been accepted. Lastly, the fact that a considerable number of infrageneric taxa of *Sedum* are polyphyletic (see Results) demonstrates that previous taxonomic treatments have rarely been successful in identifying clades of *Sedum* based on morphological or karyological data.

(2) Restricting *Sedum* to the Acre clade and recognizing the Leucosedum clade as one new segregate genus seems very appealing since virtually all *Sedum* species of the Leucosedum clade belong to the morphologically distinct subg. *Gormanina* and share at least the costate testa as one unifying character with all other genera of the Leucosedum clade (see Fig. 1B and Table 2). However, the Leucosedum clade was supported only in phylogenies inferred from plastid sequence data (Fig. 2A) (Van Ham & 't Hart, 1998; 't Hart & al., 1999). Furthermore, Thiede & Eggli (2007) clearly acknowledged the non-monophyly of subg. *Gormanina*, and this notion is supported by the nested position of *Sedum aetnense* of subg. *Sedum* in the Leucosedum clade in our ITS phylogenies (Fig. 1B, suppl. Fig. S1). This – together with the fact that some *Sedum* species cannot be unambiguously assigned to one of the two subgenera (see the example of *S. litoreum* above under “(5) Clades Leucosedum and Acre”) – demonstrates the difficulties of characterizing the Acre clade as well as the Leucosedum clade as two distinct genera.

(3) Several (but not all) of the genera to be included in *Sedum* when containing the entire Sedeae are not monophyletic (*Villadia*, *Echeveria*, *Graptopetalum* and *Thompsonella* when including *T. mixtecana*; Carrillo-Reyes & al., 2008, 2009; see Table 2).

(4) Perhaps most importantly, definition of *Sedum* as proposed does not really alter its morphological circumscription and recognizability. Thus, when comparing the descriptions of all relevant genera as provided by Thiede & Eggli (2007) and as summarized here in Table 2, it becomes clear that essentially none of the characters used for the definition of other genera cannot also be found in *Sedum* as described by Thiede & Eggli (2007). The only exception to this is an autapomorphy of *Dudleya* (i.e., sympodial branching in *Dudleya* but nowhere else; see Table 2).

Description of *Sedum* in a broader circumscription. — If *Sedum* will be recognized as encompassing all members of Sedeae, our favoured solution of the “*Sedum* problem”, it should be circumscribed as follows. This circumscription is based on our literature search (see Materials and Methods):

Annual to perennial, monocarpic to polycarpic herbs or subshrubs, rarely monocarpic rosette plants; roots usually fibrous, less commonly tuberous or as taproots; stems usually with branched non-flowering shoots or sessile rosettes, rarely rhizomatous; plants glabrous or pubescent, indumentum (if

present) glandular or non-glandular; leaves usually alternate, rarely decussate or in whorls of up to four, often arranged in terminal or sessile rosettes, mostly sessile, sometimes (semi-)petiolate, mostly (semi-)terete, sometimes flat, with an entire, rarely undulate, finely serrate or ciliate margin, apically rounded to mucronate; inflorescences formed in terminal or lateral position, many-flowered thyrses, simple cincinni or pleiochasia with single or double cincinni, or corymboid or compound thyrsoids with many cincinni, sometimes reduced to spikes, racemes or botryoids, rarely few-flowered thyrses or cymes with one or two cincinni; bracts usually present, often leaf-like; flowers (3–)5(–12)-merous, rarely haplostemonous, sessile to pedicellate; sepals broadly sessile and basally united or free and then often spurred, equal to strongly unequal, usually smaller than petals; petals free or connate at base for up to 3/4 of corolla length, spreading or erect, yellow, greenish, cream, white, pink, purple, orange or reddish, sometimes with reddish to brown blotches, never blue, often with distinct, mostly reddish keel and a dorsal subapical appendage; filaments free or connate with petals up to the mouth of the corolla tube when present; nectar scales variable, usually whitish, yellow or red, less commonly greenish or orange; carpels usually sessile with broad base and slightly connate at base, sometimes slightly sunken into a receptacle, less frequently completely free, rarely stipitate, usually erect during anthesis; stylodia usually slender and recurved during anthesis, or short and stigma \pm sessile; follicles (sub-)erect or stellate-patent, without lips along ventral suture, or stellate-patent follicles sometimes with distinct lips, many- to few-seeded, rarely one-seeded and nut-like; seeds ovoid to ellipsoid, rarely fusiform or cylindrical; testa costate-bipapillate or reticulate-papillate to reticulate, sometimes smooth.

About 755 species, mostly in temperate and subtropical regions of North America, Europe, north Africa, Near East and Asia, a few species in Central and South America and central to east Africa.

Thiede & Egli (2007) did not succeed in identifying phenotypic characters unique to their *Sedeae*. Equally, the above description of *Sedum* does not contain a single apomorphy by which the genus, very well supported in our molecular phylogenies, can be recognized, and due to all exceptions and rarely seen characters in the above genus description, it is not sufficient to unambiguously distinguish the newly circumscribed *Sedum* from every other genus of Sempervivoideae. This, however, is possible by considering the apomorphies of other genera of Sempervivoideae in comparison to their combination in some *Sedum* species. For example, *Sinocrasula* of tribe Telephieae is characterized by haplostemonous, strictly pentamerous flowers that are arranged in corymbose inflorescences on monocarpic rosettes. Although all four character states (haplostemonous and pentamerous flowers, corymbose inflorescences, monocarpic rosettes) can be found in *Sedum*, to our knowledge all haplostemonous species of *Sedum* are either not rosette plants or (*Graptopetalum glassii*, *G. pentandrum* Moran) have elongate instead of corymbose

inflorescences. Similar arguments can be provided for all genera of Sempervivoideae outside *Sedum*.

When equating *Sedum* with *Sedeae*, and assuming that reclassification at generic rank of those former *Sedum* species found in the Telephium clade and *Petrosedum* is accepted (although not all genera in the Telephium clade are monophyletic; see Mayuzumi & Ohba, 2004, and Gontcharova & al., 2006), reclassification of *Sedum* is necessary in the Aeonium clade as well as for *Sedum* ser. *Nana*. As the Aeonium clade is subject of further study by us, we refrain from expanding on this issue.

When including all members of *Sedeae* in *Sedum* but recognizing several genera in three of the other four major groups, namely the clades Telephium, *Sempervivum/Jovibarba* and Aeonium, infratribal classification in Sempervivoideae is somewhat uneven. This, however, appears to be fully justified by the recognizability of monophyletic lineages and much better resolved phylogenetic relationships in these three groups.

Clearly, phylogenies can be translated into different classifications even when monophyly of taxa is accepted as primary criterion (for review see Humphreys & Linder, 2009), and this has recently resulted in a fierce debate about lycophyte and fern classification where, based on the same trees, between 51 families with 337 genera and 24 families with 212 genera were recognized (Christenhusz & Chase, 2018; Schuettpelz & al., 2018). Although our phylogeny is poorly resolved in many parts, and clearly more data and a more thorough taxon sampling are needed, we believe that our proposed solution of the “*Sedum* problem” is the best of all available options. However, it may only prove stable when the transfer of *Sedeae* genera into *Sedum* will be justified by profound knowledge of morphology and phylogenetic position of the species to be transferred. This is the major reason why we refrain from and advise against making new combinations at this stage.

■ AUTHOR CONTRIBUTIONS

JWK and JTK conceived the project. TFEM and JTK obtained plant material and performed the laboratory work. Data analysis was conducted by TFEM, JTK and GK. TFEM and JWK wrote an initial manuscript, and all authors contributed to the final version. This publication is part of TFEM’s doctoral thesis. — TFEM, <https://orcid.org/0000-0002-8656-8654>; JTK, <https://orcid.org/0000-0003-2736-8094>; GK, <https://orcid.org/0000-0003-0094-8769>; JWK, <https://orcid.org/0000-0002-9274-3359>

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■ LITERATURE CITED

- Acevedo-Rosas, R., Cameron, K., Sosa, V. & Pell, S.** 2004a. A molecular phylogenetic study of *Graptopetalum* (Crassulaceae) based on ETS, ITS, *rpl16*, and *trnL-F* nucleotide sequences. *Amer. J. Bot.* 91: 1099–1104. <https://doi.org/10.3732/ajb.91.7.1099>
- Acevedo-Rosas, R., Sosa, V. & Lorea, F.G.** 2004b. Phylogenetic relationships and morphological patterns in *Graptopetalum* (Crassulaceae). *Brittonia* 56: 185–194. [https://doi.org/10.1663/0007-196X\(2004\)056\[0185:PRAMPI\]2.0.CO;2](https://doi.org/10.1663/0007-196X(2004)056[0185:PRAMPI]2.0.CO;2)
- Afferni, M.** 2012. A revision of series *Cepaea* in the genus *Sedum*. *CactusWorld* 30: 57–60.
- Afferni, M.** 2014. A revision of the series *Macaronesia* in genus *Sedum*. *CactusWorld* 32: 209–212.
- Alexander, E.J.** 1942. A new Mexican *Sedum*. *Cact. Succ. J. (Los Angeles)* 14: 76–78.
- Avise, J.C. & Johns, G.C.** 1999. Proposal for a standardized temporal scheme of biological classification for extant species. *Proc. Natl. Acad. Sci. U.S.A.* 96: 7358–7363. <https://doi.org/10.1073/pnas.96.13.7358>
- Berger, A.** 1930. Crassulaceae. Pp. 352–483 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien*, 2nd ed., vol. 18a. Leipzig: Engelmann.
- Blattner, F.R.** 1999. Direct amplification of the entire ITS region from poorly preserved plant material using recombinant PCR. *BioTechniques* 27: 1180–1186. <https://doi.org/10.2144/99276st04>
- Boissier, E.** 1872. *Flora Orientalis*, vol. 2. Genevae et Basileae [Geneva & Basel]: apud H. Georg. <https://bibdigital.rjb.csic.es/idurl/1/10740>
- Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C.-H., Xie, D., Suchard, M.A., Rambaut, A. & Drummond, A.J.** 2014. BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computat. Biol.* 10: e1003537. <https://doi.org/10.1371/journal.pcbi.1003537>
- Britton, N.L. & Rose, J.N.** 1903. New or noteworthy North American Crassulaceae. *Bull. New York Bot. Gard.* 3: 1–45.
- Britton, N.L. & Rose, J.N.** 1905. Crassulaceae. Pp. 7–74 in: Britton, N.L. & Underwood, L.M. (eds.), *North American Flora*, vol. 22(1). New York City: The New York Botanical Garden.
- Calie, P.J.** 1981. Systematic studies in *Sedum* section *Ternata* (Crassulaceae). *Brittonia* 33: 498–507. <https://doi.org/10.2307/2806751>
- Carrillo-Reyes, P. & Lomelí-Senci6n, J.A.** 2008. *Sedum chazaroi* (Crassulaceae), an endemic new species from southern Jalisco, Mexico. *Bol. Soc. Bot. M6xico* 83: 77–80. <https://doi.org/10.17129/botsoci.1789>
- Carrillo-Reyes, P., Sosa, V. & Mort, M.E.** 2008. *Thompsonella* and the “*Echeveria* group” (Crassulaceae): Phylogenetic relationships based on molecular and morphological characters. *Taxon* 57: 863–874. <https://doi.org/10.1002/tax.573015>
- Carrillo-Reyes, P., Sosa, V. & Mort, M.E.** 2009. Molecular phylogeny of the *Acre* clade (Crassulaceae): Dealing with the lack of definitions for *Echeveria* and *Sedum*. *Molec. Phylogen. Evol.* 53: 267–276. <https://doi.org/10.1016/j.ympev.2009.05.022>
- Christenhusz, M.J.M. & Chase, M.W.** 2018. PPG recognises too many fern genera. *Taxon* 67: 481–487. <https://doi.org/10.12705/673.2>
- Clausen, R.T.** 1940. Studies in the Crassulaceae: *Villadia*, *Altamiranoa* and *Thompsonella*. *Bull. Torrey Bot. Club* 67: 195–198. <https://doi.org/10.2307/2480876>
- Clausen, R.T.** 1942. Studies in the Crassulaceae – III. *Sedum*, subgenus *Gormaniana*, section *Eugormaniana*. *Bull. Torrey Bot. Club* 69: 27–40. <https://doi.org/10.2307/2481519>
- Clausen, R.T.** 1943a. A new species and section of *Sedum* from Chihuahua. *Cact. Succ. J. (Los Angeles)* 15: 167–169.
- Clausen, R.T.** 1943b. The section *Sedastrum* of *Sedum*. *Bull. Torrey Bot. Club* 70: 289–296. <https://doi.org/10.2307/2481438>
- Clausen, R.T.** 1959. *Sedum of the Trans-Mexican volcanic belt: An exposition of taxonomic methods*. Ithaca: Cornell University Press.
- Clausen, R.T.** 1975. *Sedum of North America North of the Mexican plateau*. Ithaca & London: Cornell University Press. <https://doi.org/10.2307/2418773>
- Clausen, R.T.** 1978. *Sedum* – Seven Mexican perennial species. *Bull. Torrey Bot. Club* 105: 214–223. <https://doi.org/10.2307/2484117>
- Clausen, R.T.** 1979. *Sedum* in six areas of the Mexican Cordilleran Plateau. *Bull. Torrey Bot. Club* 106: 205–216. <https://doi.org/10.2307/2484556>
- Clausen, R.T.** 1981. *Variation of species of Sedum of the Mexican Cordilleran Plateau*. Ithaca: Arnold.
- Clausen, R.T. & Uhl, C.H.** 1943. Revision of *Sedum cockerellii* and related species. *Brittonia* 5: 33–46. <https://doi.org/10.2307/2804873>
- Clausen, R.T. & Uhl, C.H.** 1944. The taxonomy and cytology of the subgenus *Gormaniana* of *Sedum*. *Madroño* 7: 161–180.
- Denton, M.F.** 1982. Revision of *Sedum* section *Gormaniana* (Crassulaceae). *Brittonia* 34: 48–77. <https://doi.org/10.2307/2806401>
- Eggl, U.** 1988. *A monographic study of the genus Rosularia (Crassulaceae - Sedoideae)*. Dissertation. Universität Zürich, Zurich, Switzerland.
- Eggl, U.** 1992. Nomenclatural notes on two genera of Crassulaceae and a new combination. *Bradleya* 10: 83–84. <https://doi.org/10.25223/brad.n10.1992.a6>
- Eggl, U.** 2005. Crassulaceae. Pp. 5–8 in: Eggl, U. (ed.), *Illustrated handbook of succulent plants: Crassulaceae*. Berlin & Heidelberg: Springer. https://doi.org/10.1007/978-3-642-55874-0_2
- Fenzl, E.** 1856. *Sedum Hillebrandii* Fenzl.: Ein Beitrag zur näheren Kenntniss einiger *Sedum*-Arten aus der Gruppe von *S. acre*. *Verh. Zool.-Bot. Vereins Wien* 6: 449–462.
- Fishbein, M., Hibsich-Jetter, C., Soltis, D.E. & Hufford, L.** 2001. Phylogeny of Saxifragales (Angiosperms, Eudicots): Analysis of a rapid, ancient radiation. *Syst. Biol.* 50: 817–847. <https://doi.org/10.1080/106351501753462821>
- Fröderström, H.** 1930. The genus *Sedum* L. – A systematic assay, Part I. *Acta Horti Gothob.* 5(Appendix): 1–75.
- Fröderström, H.** 1931. The genus *Sedum* L. – A systematic assay, Part II. *Acta Horti Gothob.* 6(Appendix): 1–177.
- Fröderström, H.** 1932. The genus *Sedum* L. – A systematic assay, Part III. *Acta Horti Gothob.* 7(Appendix): 1–125.
- Fröderström, H.** 1935. The genus *Sedum* L. – A systematic assay, Part IV. *Acta Horti Gothob.* 10(Appendix): 1–262.
- Fu, K.T.** 1974. Revision of the section *Oreades* on Chinese *Sedum*. *Acta Phytotax. Sin.* 12: 51–77.
- Fu, K.T. & Ohba, H.** 2001. Crassulaceae. Pp. 202–268 in: Wu, Z.-Y. & Raven, P.H. (eds.), *Flora of China*, vol. 8. Beijing: Science Press; St. Louis: Missouri Botanical Garden Press.
- Fu, S.-H.** 1965. Species et combinationes novae Crassulacearum Sinarum. *Acta Phytotax. Sin., Addit.* 1: 111–128.
- García, J.M. & Chávez, L.L.** 2003. *Las Crassuláceas de México*. Mexico City: Sociedad Mexicana de Cactología.
- Gernhard, T.** 2008. The conditioned reconstructed process. *J. Theor. Biol.* 253: 769–778. <https://doi.org/10.1016/j.jtbi.2008.04.005>
- Gilbert, M.G.** 1985. The genus *Sedum* in Ethiopia. *Bradleya* 3: 48–52. <https://doi.org/10.25223/brad.n3.1985.a2>
- Giuliani, C., Foggi, B. & Lippi, M.M.** 2018. Floral morphology, micromorphology and palinology of selected *Sedum* s.l. species

- (Crassulaceae). *Pl. Biosyst.* 152: 333–348. <https://doi.org/10.1080/11263504.2016.1271056>
- Gontcharova, S.B., Artyukova, E.V. & Gontcharov, A.A.** 2006. Phylogenetic relationships among members of the subfamily Sedoideae (Crassulaceae) inferred from the ITS region sequences of nuclear rDNA. *Russ. J. Genet.* 42: 654–661. <https://doi.org/10.1134/S102279540606010X>
- Green, M.L.** 1929. Genera 501–end [In: Hitchcock, A.S. & Green, M.L., Standard species of Linnean genera of phanerogamae (1753–54)]. Pp. 155–195 in: *International Botanical Congress Cambridge (England), 1930: Nomenclature; Proposals by British botanists*. London: His Majesty's Stationery Office. <https://bibdigital.rjb.csic.es/doi/10.13040>
- Grulich, V.** 1984. Generic division of *Sedoideae* in Europe and the adjacent regions. *Preslia* 56: 29–45.
- Guindon, S., Dufayard, J.F., Lefort, V., Anisimova, M., Hordijk, W. & Gascuel, O.** 2010. New algorithms and methods to estimate maximum-likelihood phylogenies: Assessing the performance of PhyML 3.0. *Syst. Biol.* 59: 307–321. <https://doi.org/10.1093/sysbio/syq010>
- Guzmán, B. & Vargas, P.** 2009. Historical biogeography and character evolution of Cistaceae (Malvales) based on analysis of plastid *rbcl* and *trnL-trnF* sequences. *Organisms Diversity Evol.* 9: 83–99. <https://doi.org/10.1016/j.ode.2009.01.001>
- Humphreys, A. & Linder, H.P.** 2009. Concepts versus data in delimitation of plant genera. *Taxon* 58: 1054–1074. <https://doi.org/10.1002/tax.584002>
- Hungerer, K.B. & Kadereit, J.W.** 1998. The phylogeny and biogeography of *Gentiana* L. sect. *Ciminalis* (Adans.) Dumort.: A historical interpretation of distribution ranges in the European high mountains. *Perspect. Pl. Ecol. Evol. Syst.* 1: 121–135. <https://doi.org/10.1078/1433-8319-00055>
- Ito, T., Yu, C.-C., Nakamura, K., Chung, K.-F., Yang, Q.-E., Fu, C.-X., Qi, Z.-C. & Kokubugata, G.** 2017. Unique parallel radiations of high-mountainous species of the genus *Sedum* (Crassulaceae) on the continental island of Taiwan. *Molec. Phylog. Evol.* 113: 9–22. <https://doi.org/10.1016/j.ympev.2017.03.028>
- Jäger, E.J.** 2005. *Rothmaler Exkursionsflora von Deutschland – Gefäßpflanzen: Grundband*, 19th ed. Munich: Spektrum Akademischer Verlag, Elsevier.
- Jäger, E.J.** 2011. *Rothmaler Exkursionsflora von Deutschland – Gefäßpflanzen: Grundband*, 20th ed. Heidelberg: Spektrum Akademischer Verlag, Springer.
- Jarvis, C.E.** 1992. Seventy-two proposals for the conservation of types of selected Linnean generic names, the report of Subcommittee 3C on the lectotypification of Linnean generic names. *Taxon* 41: 552–583. <https://doi.org/10.2307/1222833>
- Jimeno-Sevilla, H.D., Carrillo-Reyes, P., Pérez-Calix, E. & Cházaro-Basáñez, M.J.** 2012. Additions to the Crassulaceae of the State of Veracruz, Mexico. *Haseltonia* 18: 140–153. <https://doi.org/10.2985/026.018.0115>
- Johnson, L.A. & Soltis, D.E.** 1994. *matK* DNA sequences and phylogenetic reconstruction in Saxifragaceae s.str. *Syst. Bot.* 19: 143–156. <https://doi.org/10.2307/2419718>
- Jorgensen, T.H. & Olesen, J.M.** 2001. Adaptive radiation of island plants: Evidence from *Aeonium* (Crassulaceae) of the Canary Islands. *Perspect. Pl. Ecol. Evol. Syst.* 4: 29–42. <https://doi.org/10.1078/1433-8319-00013>
- Katoh, K. & Standley, D.M.** 2013. MAFFT Multiple sequence alignment software version 7: Improvements in performance and usability. *Molec. Biol. Evol.* 30: 772–780. <https://doi.org/10.1093/molbev/mst010>
- Kim, J.H., 't Hart, H. & Mes, T.H.M.** 1996. The phylogenetic position of East Asian *Sedum* species (Crassulaceae) based on chloroplast DNA *trnL* (*UAA*)-*trnF* (*GAA*) intergenic spacer sequence variation. *Acta Bot. Neerl.* 45: 309–321. <https://doi.org/10.1111/j.1438-8677.1996.tb00519.x>
- Kim, S.-C., McGowen, M.R., Lubinsky, P., Barber, J.C., Mort, M.E. & Santos-Guerra, A.** 2008. Timing and tempo of early and successive adaptive radiations in Macaronesia. *PLoS ONE* 3(5): e2139. <https://doi.org/10.1371/journal.pone.0002139>
- Klein, J.T. & Kadereit, J.W.** 2015. Phylogeny, biogeography, and evolution of edaphic association in the European oreophytes *Sempervivum* and *Jovibarba* (Crassulaceae). *Int. J. Pl. Sci.* 176: 44–71. <https://doi.org/10.1086/677948>
- Král, M.** 1987. *Sedum creticum* C.Presl – A forgotten species. *Preslia* 59: 307–310.
- Lanfear, R., Frandsen, P.B., Wright, A.M., Senfeld, T. & Calcott, B.** 2017. PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molec. Biol. Evol.* 34: 772–773. <https://doi.org/10.1093/molbev/msw260>
- Linder, H.P. & Verboom, G.A.** 1996. Generic limits in the *Rytidosperma* (Danthonieae, Poaceae) complex. *Telopea* 6: 597–627. <https://doi.org/10.7751/telopea19963027>
- Linnaeus, C.** 1753. *Species plantarum*, 2 vols. Holmiae [Stockholm]: impensis Laurentii Salvii. <https://doi.org/10.5962/bhl.title.669>
- Löve, Á. & Löve, D.** 1985a. Chromosome number reports LXXXVI. *Taxon* 34: 163–164. <https://doi.org/10.1002/j.1996-8175.1985.tb04413.x>
- Löve, Á. & Löve, D.** 1985b. Chromosome number reports LXXXVII. *Taxon* 34: 350–351. <https://doi.org/10.1002/j.1996-8175.1985.tb02505.x>
- Maire, R. & Quézel, P.** 1967. *Flore de l'Afrique du Nord*, vol. 14. Paris: Éditions Paul Lechevalier.
- Mauritzon, J.** 1933. *Studien über die Embryologie der Familien Crassulaceae und Saxifragaceae*. Dissertation. Lunds Universitet, Lund, Sweden.
- Mayuzumi, S. & Ohba, H.** 2004. Phylogenetic position of Eastern Asian Sedoideae (Crassulaceae) inferred from chloroplast and nuclear DNA sequences. *Syst. Bot.* 29: 587–598. <https://doi.org/10.1600/0363644041744329>
- McNeill, J., Odell, A.O., Consaul, L.L. & Katz, D.S.** 1987. American Code and later lectotypifications of Linnean generic names dating from 1753: A case study of discrepancies. *Taxon* 36: 350–401. <https://doi.org/10.2307/1221430>
- Mes, T.H.M.** 1995a. Phylogenetic and systematic implications of chloroplast and nuclear spacer sequence variation in the Macaronesian Sempervivoideae and related Sedoideae. Pp. 30–44 in: 't Hart, H. & Eggli, U. (eds.), *Evolution and systematics of the Crassulaceae*. Leiden: Backhuys.
- Mes, T.H.M.** 1995b. *Origin and evolution of the Macaronesian Sempervivoideae (Crassulaceae)*. Dissertation. Universiteit Utrecht, Utrecht, Belgium.
- Miller, M.A., Pfeiffer, W. & Schwartz, T.** 2010. Creating the CIPRES Gateway for inference of large phylogenetic trees. Pp. 45–52 in: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, New Orleans, Louisiana, 14.11.2010. Piscataway: IEEE. <https://doi.org/10.1109/GCE.2010.5676129>
- Moran, R.** 1966. The section *Centripetalia* of *Sedum*. *Cact. Succ. J. (Los Angeles)* 38: 75–81.
- Moran, R.** 1996. *Altamiranoa* into *Sedum* (Crassulaceae). *Haseltonia* 4: 46.
- Moran, R.** 2005. *Cremnophila*. Pp. 84–85 in: Eggli, U. (ed.), *Illustrated handbook of succulent plants: Crassulaceae*. Berlin & Heidelberg: Springer.
- Mort, M.E., Soltis, D.E., Soltis, P.S., Francisco-Ortega, J. & Santos-Guerra, A.** 2001. Phylogenetic relationships and evolution of Crassulaceae inferred from *matK* sequence data. *Amer. J. Bot.* 88: 76–91. <https://doi.org/10.2307/2657129>
- Mort, M.E., Soltis, D.E., Soltis, P.S., Francisco-Ortega, J. & Santos-Guerra, A.** 2002. Phylogenetics and evolution of the Macaronesian clade of Crassulaceae inferred from nuclear and chloroplast sequence data. *Syst. Bot.* 27: 271–288. <https://doi.org/10.1043/0363-6445-27.2.271>

- Mort, M.E., O'Leary, T.R., Carrillo-Reyes, P., Nowell, T., Archibald, J.K. & Randle, C.P. 2010. Phylogeny and evolution of Crassulaceae: Past, present, and future. *Biodivers. & Ecol.* 3: 69–86.
- Muir, G., Fleming, C.C. & Schlötterer, C. 2001. Three divergent rDNA clusters predate the species divergence in *Quercus petraea* (Matt.) Liebl. and *Quercus robur* L. *Molec. Biol. Evol.* 18: 112–119. <https://doi.org/10.1093/oxfordjournals.molbev.a003785>
- Nesom, G. & Turner, B.L. 1995. Systematics of the *Sedum parvum* group (Crassulaceae) in Northeastern Mexico and Texas. *Phytologia* 79: 257–268.
- Nikulin, V.Y., Gontcharova, S.B., Stephenson, R. & Gontcharov, A.A. 2016. Phylogenetic relationships between *Sedum* L. and related genera (Crassulaceae) based on ITS rDNA sequence comparisons. *Flora* 224: 218–229. <https://doi.org/10.1016/j.flora.2016.08.003>
- Nuttall, T. 1818. *The genera of North American plants, and a catalogue of the species, to the year 1817*, 2 vols. Philadelphia: printed for the author by D. Heartt. <https://doi.org/10.5962/bhl.title.6134>
- Nyffeler, R. 2005. *Aichryson*. Pp. 235–332 in: Eggli, U. (ed.), *Illustrated handbook of succulent plants: Crassulaceae*. Berlin & Heidelberg: Springer.
- Ohba, H. 1977. The taxonomic status of *Sedum telephium* and its allied species (Crassulaceae). *Bot. Mag. (Tokyo)* 90: 41–56. <https://doi.org/10.1007/BF02489468>
- Ohba, H. 1978. Generic and infrageneric classification of the Old World Sedoideae (Crassulaceae). *J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot.* 12: 139–198.
- Ohba, H., Bartholomew, B.M., Turland, N.J. & Fu, K.T. 2000. New combinations in *Phedimus* (Crassulaceae). *Novon* 10: 400–402. <https://doi.org/10.2307/3392995>
- Oxelman, B., Lidén, M. & Berglund, D. 1997. Chloroplast *rps16* intron phylogeny of the tribe *Sileneae* (Caryophyllaceae). *Pl. Syst. Evol.* 206: 393–410. <https://doi.org/10.1007/BF00987959>
- Pérez-Calix, E. 1998. *Sedum mocinianum* (Crassulaceae) una especie nueva del centro de Mexico. *Acta Bot. Mex.* 45: 49–54. <https://doi.org/10.21829/abm45.1998.811>
- Rambaut, A. 2009. FigTree, version 1.3.1. Program distributed by the author. <http://tree.bio.ed.ac.uk/software/figtree/>
- Rambaut, A. & Drummond, A.J. 2007. Tracer, version 1.5. Program distributed by the authors. <http://beast.bio.ed.ac.uk/Tracer>
- Rambaut, A. & Drummond, A.J. 2016. TreeAnnotator, version 1.8.3. Program distributed by the authors. <http://beast.community>
- Rögl, F. 1999. Mediterranean and Paratethys: Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). *Geol. Carpathica* 50: 339–349.
- Ronquist, F. & Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Santiago, J.R., Etter, J. & Kristen, M. 2015. *Sedum piactlaense* (Crassulaceae), a new species from Durango, México. *Haseltonia* 20: 58–63. <https://doi.org/10.2985/026.020.0110>
- Schmidt-Lebuhn, A.N. 2012. Fallacies and false premises – A critical assessment of the arguments for the recognition of paraphyletic taxa in botany. *Cladistics* 28: 174–187. <https://doi.org/10.1111/j.1096-0031.2011.00367.x>
- Schönland, S. 1891. Crassulaceae. Pp. 23–38 in: Engler, A. & Prantl, K. (eds.), *Die natürlichen Pflanzenfamilien*, III(2a). Leipzig: Engelmann.
- Schuettpelz, E., Rouhan, G., Pryer, K.M., Rothfels, C.J., Prado, J., Sundue, M.A., Windham, M.D., Moran, R.C. & Smith, A.R. 2018. Are there too many fern genera? *Taxon* 67: 473–480. <https://doi.org/10.12705/673.1>
- Scopoli, G.A. 1777. *Introductio ad historiam naturalem*. Pragae [Prague]: apud Wolfgangum Gerle.
- Scotese, C.R. 2001. PALEOMAP project. <http://www.scotese.com> (accessed 7 Aug 2020).
- Shaw, J., Lickey, E.B., Beck, J.T., Farmer, S.B., Liu, W., Miller, J., Siripun, K.C., Winder, C.T., Schilling, E.E. & Small, R.L. 2005. The tortoise and the hare II: Relative utility of 21 noncoding chloroplast DNA sequences for phylogenetic analysis. *Amer. J. Bot.* 92: 142–166. <https://doi.org/10.3732/ajb.92.1.142>
- Stamatakis, A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. <https://doi.org/10.1093/bioinformatics/btu033>
- Stevens, P.F. 2001–. Angiosperm Phylogeny Website, version 14, July 2017, last updated 28 Dec 2018. <http://www.mobot.org/MOBOT/research/APweb/> (accessed 18 Oct 2018).
- Stuessy, T.F. & Hörandl, E. 2014. The importance of comprehensive phylogenetic (evolutionary) classification – A response to Schmidt-Lebuhn's commentary on paraphyletic taxa. *Cladistics* 30: 291–293. <https://doi.org/10.1111/cla.12038>
- Swofford, D.L. 2002. PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4.0 Beta. Sunderland, MA: Sinauer.
- Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Pl. Molec. Biol.* 17: 1105–1109. <https://doi.org/10.1007/BF00037152>
- *t Hart, H. 1978. *Biosystematic studies in the Acre-group and the series Rupestris Berger of the genus Sedum L. (Crassulaceae)*. Dissertation. Rijksuniversiteit Utrecht, Utrecht, Belgium.
- *t Hart, H. 1991. Evolution and classification of the European *Sedum* species (Crassulaceae). *Fl. Medit.* 1: 31–61.
- *t Hart, H. 1995. Intrafamilial and generic classification of the Crassulaceae. Pp. 159–172 in: *t Hart, H. & Eggli, U. (eds.), *Evolution and systematics of the Crassulaceae*. Leiden: Backhuys.
- *t Hart, H. & Alpınar, K. 1995. Biosystematic studies in *Sedum* (Crassulaceae) of Turkey. Pp. 71–99 in: Öztürk, M., Seçmen, Ö. & Görk, G. (eds.), *Plant life in southwest and central Asia*. Izmir: Ege University Press.
- *t Hart, H. & Alpınar, K. 1999. *Sedum ince* (Crassulaceae), a new species from Southern Anatolia. *Edinburgh J. Bot.* 56: 181–194. <https://doi.org/10.1017/S096042860001062>
- *t Hart, H. & Alpınar, K. 2000. 7. *Sedum* L. Pp. 127–136 in: Güner, A., Özhatay, N., Ekim, T. & Başer, K.H.C. (eds.), *Flora of Turkey and the East Aegean Islands*, vol. 11(suppl. 2). Edinburgh: Edinburgh University Press.
- *t Hart, H. & Bleij, B. 2005. *Sedum*. Pp. 235–332 in: Eggli, U. (ed.), *Illustrated handbook of succulent plants: Crassulaceae*. Berlin & Heidelberg: Springer.
- *t Hart, H., Van Ham, R.C.H.J., Stevens, J.F., Elema, E.T., Van Der Klis, H. & Gadella, T.W.J. 1999. Biosystematic, molecular and phytochemical evidence for the multiple origin of sympetalous in Eurasian Sedoideae (Crassulaceae). *Biochem. Syst. Ecol.* 27: 407–426. [https://doi.org/10.1016/S0305-1978\(98\)00098-2](https://doi.org/10.1016/S0305-1978(98)00098-2)
- Thiede, J. & Eggli, U. 2007. Crassulaceae. Pp. 83–118 in: Kubitzki, K. (ed.), *The families and genera of vascular plants*, vol. 9. Berlin & Heidelberg: Springer. https://doi.org/10.1007/978-3-540-32219-1_12
- Thiv, M., Thulin, M., Hjertson, M., Kropf, M. & Linder, H.P. 2010. Evidence for a vicariant origin of the Macaronesian-Eritrean/Arabian disjunctions in *Campylanthus* Roth (Plantaginaceae). *Molec. Phylog. Evol.* 54: 607–616. <https://doi.org/10.1016/j.ympev.2009.10.009>
- Uhl, C.H. 1961a. Some cytotoxic problems in the Crassulaceae. *Evolution (Lancaster)* 15: 375–377. <https://doi.org/10.2307/2406235>
- Uhl, C.H. 1961b. The chromosomes of the Sempervivoideae (Crassulaceae). *Amer. J. Bot.* 48: 114–123. <https://doi.org/10.1002/j.1537-2197.1961.tb11612.x>
- Uhl, C.H. 1963. Chromosomes and phylogeny of the Crassulaceae. *Cact. Succ. J. (Los Angeles)* 35: 3–7.
- Uhl, C.H. 1970. Chromosomes of *Graptopetalum* and *Thompsonella* (Crassulaceae). *Amer. J. Bot.* 57: 1115–1121. <https://doi.org/10.1002/j.1537-2197.1970.tb09915.x>

- Uhl, C.H. 1976. Chromosomes, hybrids and ploidy of *Sedum cremnophila* and *Echeveria linguifolia* (Crassulaceae). *Amer. J. Bot.* 63: 806–820. <https://doi.org/10.1002/j.1537-2197.1976.tb11870.x>
- Uhl, C.H. 1977. Cytogeography of *Sedum lanceolatum* and its relatives. *Rhodora* 79: 95–114.
- Uhl, C.H. 1978. Chromosomes of Mexican *Sedum* II. Section *Pachysedum*. *Rhodora* 80: 491–512.
- Uhl, C.H. 1980. Chromosomes of Mexican *Sedum* III. Sections *Centripetalia*, *Fruticisedum*, and other woody species. *Rhodora* 82: 377–402.
- Uhl, C.H. 1985. Chromosomes of Mexican *Sedum* V. Section *Sedum* and subgenus *Sulcus*. *Rhodora* 87: 381–423.
- Uhl, C.H. 1992a. Chromosomes of Mexican *Sedum* VI. Section *Sedastrum*. *Rhodora* 94: 362–370.
- Uhl, C.H. 1992b. Polyploidy, dysploidy, and chromosome pairing in *Echeveria* (Crassulaceae) and its hybrids. *Amer. J. Bot.* 79: 556–566. <https://doi.org/10.1002/j.1537-2197.1992.tb14593.x>
- Uhl, C.H. 1994. Intergeneric hybrids in the Mexican Crassulaceae. IV. *Villadia*. *Cact. Succ. J. (Los Angeles)* 66: 214–217.
- Uhl, C.H. & Moran, R. 1973. The chromosomes of *Pachyphytum* (Crassulaceae). *Amer. J. Bot.* 60: 648–656. <https://doi.org/10.1002/j.1537-2197.1973.tb05969.x>
- Uhl, C.H. & Moran, R. 1999. Chromosomes of *Villadia* and *Altamiranoa* (Crassulaceae). *Amer. J. Bot.* 86: 387–397. <https://doi.org/10.2307/2656760>
- Van Ham, R.C.H.J. 1995. Phylogenetic relationships in the Crassulaceae inferred from chloroplast DNA variation. Pp. 16–29 in: 't Hart, H. & Eggli, U. (eds.), *Evolution and systematics of the Crassulaceae*. Leiden: Backhuys.
- Van Ham, R.C.H.J. & 't Hart, H. 1998. Phylogenetic relationships in the Crassulaceae inferred from chloroplast DNA restriction-site variation. *Amer. J. Bot.* 85: 123–134. <https://doi.org/10.2307/2446561>
- Vargas, P., Fernández-Mazuecos, M. & Heleno, R. 2018. Phylogenetic evidence for a Miocene origin of Mediterranean lineages: species diversity, reproductive traits and geographical isolation. *Pl. Biol. (Stuttgart)* 20(suppl. 1): 157–165. <https://doi.org/10.1111/plb.12626>
- Webb, D.A. 1993. Crassulaceae. Pp. 422–437 in: Tutin, T.G., Burges, N.A., Chater, A.O., Edmondson, J.R., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.), *Flora Europaea*, 2nd ed., vol. 1. Cambridge: Cambridge University Press.
- Webb, D.A., Akeroyd, J.R. & 't Hart, H. 1993. *Sedum* L. Pp. 429–436 in: Tutin, T.G., Burges, N.A., Chater, A.O., Edmondson, J.R., Heywood, V.H., Moore, D.M., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.), *Flora Europaea*, 2nd ed., vol. 1. Cambridge: Cambridge University Press.
- Wicke, S. & Quandt, D. 2009. Universal primers for the amplification of the plastid *trnK/matK* region in land plants. *Anales Jard. Bot. Madrid* 66: 285–288. <https://doi.org/10.3989/ajbm.2231>
- Yost, J.M., Bontrager, M., McCabe, S.W., Burton, D., Simpson, M.G., Kay, K.M. & Ritter, M. 2013. Phylogenetic relationships and evolution in *Dudleya* (Crassulaceae). *Syst. Bot.* 38: 1096–1104. <https://doi.org/10.1600/036364413X674760>

Appendix 1. Detailed information about specimens and GenBank accession numbers used in the molecular phylogenetic analyses.

Species (lab code, only provided for accessions with sequences generated by the authors); country; locality and additional information; voucher (+ herbarium code or Botanical Garden); ITS; *matK*; *rps16*; *trnL-F*. “–” indicates missing data or missing information and “*” newly generated sequences.

Outgroup: *Aphanopetalum clematideum* Domin; Australia; Western Australia; *Moody 421* (CONN); EF178792; EF179065; –; –. *A. resinosum* Endl.; Australia; New South Wales; *Moody 484* (CONN cult.); EF178791; EF179066; –; –. *Glichrocaryon angustifolium* (Nees) M.L.Moody & Les; Australia; Western Australia; *Moody 393* (CONN); EF178776; –; –; –. *Gonocarpus montanus* (Hook.f.) Orchard; Australia; New South Wales; *Moody 448* (CONN); EF178770; –; –; –. *G. trichostachyus* (Benth.) Orchard; Australia; Western Australia; *Moody 398* (CONN); EF178767; –; –; –. *Haloragis hamata* Orchard; Australia; Western Australia; *Cranfield 10585* (PERTH); EF178738; EF179012; –; –. *Laurembergia repens* (L.) P.J.Bergius; South Africa; Cape Town; *Williams 113 C* (HPBG); EF178735; –; –; –. *Meionectes brownii* Hook.f.; Australia; Victoria; *Moody 438* (CONN); EF178773; EF179047; –; –. *Myriophyllum drummondii* Benth.; Australia; Western Australia; *Moody 409* (CONN); EF178725; EF178999; –; –. *M. oguraense* Miki; Japan; Hyogo; *Kadono s.n.* (HYO); EF178705; EF178979; –; –. *M. pedunculatum* Hook.f.; Australia; Tasmania; *Les 643* (CONN); FJ870953; –; –; –. *Penthorum sedoides* L.; U.S.A.; Connecticut; *Moody 515* (CONN); EF178789; EF179063; –; –. *Proserpinaca pectinata* Lam.; U.S.A.; South Carolina; *Nelson 19432* (USCH); EF178788; –; –. *Tetracarpaea tasmanica* Hook.f.; Australia; New South Wales; *Wiecek 577*; EF178790; EF179064; –; –. *Trihaloragis hexandra* (F.Muell.) M.L.Moody & Les; Australia; Western Australia; *Bright 93* (PERTH); EF178759; –; –; –. **Crassulaceae:** *Aromischus maculatus* (Salm-Dyck) Lem.; –; –; (Huntington Botanical Garden 69133); AY692317; –; –; AY692287. *A. maculatus* (Salm-Dyck) Lem.; –; –; (Missouri Botanical Garden U6638); –; –; AF115575; –; –. *A. nanus* (N.E.Br.) Poelln.; –; –; *Bruyns 9493* (BOL); LN878913; –; –; –. *A. sphenophyllus* C.A.Sm.; –; –; (Huntington Botanical Garden 70042); AY692318; –; –; AY692288. *Aeonium aureum* (C.Sm. ex Hornem.) T.Mes.; –; –; *Mort 1405* (WS); AY082110; AY082263; –; –. *A. decorum* Webb ex Bolle; –; –; *Mort 1435* (WS); AY082130; AY082165; –; –. *A. nobile* (Praeger) Praeger; –; –; *Mort 1459* (WS); AY082144; AF115582; –; –. *Aichryson palmense* Webb ex Bolle; –; –; *Mort 1482* (WS); AY082104; AY082156; –; –. *A. punctatum* (C.Sm. ex Link) Webb & Berthel.; –; –; *Mort 1495* (WS); AY082103; AF115587; –; –. *Cotyledon orbiculata* L. s.str.; –; –; (Royal Botanic Gardens at Kew, DNA bank ID 25982); KC988280; –; –; –. *C. orbiculata* L. s.str.; –; –; *Mort 1341* (WS); –; –; AF115591; –; –. *C. orbiculata* L. s.str.; –; –; (Huntington Botanical Garden 77962); –; –; AY692299. *C. tomentosa* subsp. *ladismithensis* (Poelln.) Toelken; –; –; (Huntington Botanical Garden); AY692311; –; –; AY692302. *C. tomentosa* subsp. *ladismithensis* (Poelln.) Toelken; –; –; (Kirstenbosch Botanical Garden); –; –; AF115592; –; –. *Crassula alstonii* Marloth; South Africa; –; *Bruyns 13178* (BOL); MH503501; –; –; –. *C. bergioides* Harv.; South Africa; –; *Bruyns 13057* (BOL); MH503508; –; –; –. *C. capitella* Thunb.; –; –; (KBG 16848); AY596321; –; –; –. *C. colummaris* subsp. *prolifera* Friedrich; South Africa; –; *Bruyns 13182* (BOL); MH503520; –; –; –. *C. dentata* Thunb.; South Africa; –; *Jardine 2564* (BOL); MH503532; –; –; –. *C. dodii* Schönland & Baker f.; South Africa; –; *Bruyns 13195 a* (BOL); MH503535; –; –; –. *C. elsiae* Toelken; South Africa; –; *F. Walters s.n.* (BOL); MH503537; –; –; –. *C. fascicularis* Lam.; South Africa; –; *Bruyns 12934* (BOL); MH503542; –; –; –. *C. glomerata* P.J.Bergius; South Africa; –; *Bruyns 13004* (BOL); MH503545; –; –; –. *C. hirtipes* Harv.; South Africa; –; *Bruyns 13171* (BOL); MH503549; –; –; –. *C. hunua* A.P.Druce; New Zealand; South Auckland, Hunua, Wairoa Falls; (AK 288129); AY787406; –; –; –. *C. hunua* A.P.Druce; New Zealand; South Auckland, Hunua, Wairoa Falls; (AK 294737); –; –; –. EF436513. *C. muricata* Thunb.; South Africa; –; *Bruyns 13160* (BOL); MH503561; –; –; –. *C. oblancoolata* Schönland & Baker f.; South Africa; –; *Bruyns 13191* (BOL); MH503570; –; –; –. *C. peduncularis* F.Meigen; New Zealand; Tararua, Cape Turakirae Scientific Reserve; (AK 286751); AY787409; –; –; EF436508. *C. pellucida* L. s.str.; South Africa; –; *Bruyns 12943 a* (BOL); MH503580; –; –; –. *C. sieberiana* (Schult. & Schult.f.) Druce; New Zealand; South Auckland, Cornwallis; Puponga Point; (AK 285560); AY787412; –; –; –. *C. tecta* Thunb.; South Africa; –; *Bruyns 13159* (BOL); MH503606; –; –; –. *C. umbellata* Thunb.; South Africa; –; *Bruyns 13215* (BOL); MH503614; –; –; –. *C. vaginata* Eckl. & Zeyh. s. str.; South Africa; –; *Bruyns 13076* (BOL); MH503616; –; –; –. *C. vestita* Thunb.; South Africa; –; *Theron s.n.* (BOL); MH503619; –; –; –. *Cremonophila linguifolia* (Lem.) Moran; –; –; (Huntington Botanical Garden 91285); AY545679; –; –; –. *C. nutans* Rose; –; –; (Huntington Botanical Garden 88184); AY545680; –; –; –. *Dudleya pulverulenta* (Nutt.) Britton & Rose; Mexico; Baja California Norte; *A. Ocegüera* (XAL); EF632171; –; EF632188; –;

Appendix 1. Continued.

KX452251; –; –. *Rhodiola crenulata* (Hook. f. & Thomson) H. Ohba; China; Xizang, Lazi Xian; G.Y. Rao & al. 100813-01 (PEY); KF113691; –; –. *R. hobsonii* (Prain ex Raym.-Hamet) S.H. Fu; China; Xizang, Linzhi Xian; J.Q. Zhang & al. 120717-05 (PEY); KF113701; KJ570460; KJ570224; KF113807. *R. yunnanensis* subsp. *forrestii* (Raym.-Hamet) H. Ohba; China; Yunnan, Shangri-La Xian; J.Q. Zhang & al. 110730-02 (PEY); KF113696; KJ570452; KJ570216; KF113802. *Rosularia globulariifolia* (Fenzl) A. Berger (JKC52); Turkey; Antalya area; P. Raes, *Sedum Society seed distribution SSS1234* (Sukkulenten-Sammlung Zürich 12 0085/0); MT336095*; MT181563*; –; MT155892*. *R. serrata* (L.) A. Berger (UM32); Turkey; Mersin, Taurus mts., Prov. Icel, Bolandiz, on limestone, 750m (*ex cult.* Botanical Garden Würzburg); (MJG 012926); KJ884124; MT181564*; KJ884332; MT155893*. *Sedella pumila* (Benth.) Britton & Rose (JKC16); U.S.A.; California, Shasta, near a vernal pool, ca. 250 yd south of the barn, ca. 1/4 mi south of the Coleman Canal, 2.8 mi (air) WSW of Darah Springs State Fish Hatchery, ca. 12 mi (air) ENE of Cottonwood; L. Ahart 10145 (JEPS 104348); MT336096*; MT181565*; –; MT155894*. *Sedum acre* L.; Spain; Sierra Alhama; *Stephenson 5.01.011 diploid*; HE999636; –; –. *S. acre* L.; Estonia; –; I. Hiiesalu 60; –; –; HM590343. *S. aetnense* Tineo (JKC24); Italy; Nicolosi (mt. Etna area) in open area with fine lava dust, left of the road to the Refugio, ± 2 km outside the village; B.K. Boom 46446 (L 1860263); MT336097*; –; –. *S. alamosanum* S. Watson; –; –; P. Carrillo-Reyes & E. Ruiz-Sánchez 4767 (IBUG, IEB, XAL); FJ753929; –; FJ753847; –. *S. album* L. (JKC62); Albania; Korçë Province, along the road from Voskopojë to Gjorgjeviçë, ca. 750 m west of where the road turns west to go to Gjorgjeviçë, *Juniperus-Buxus sempervirens* scrub on serpentine outcrop in *Pinus* woodland, 40.58°N/20.59°E, 1360 m; A. Moore & R.L. Welch 1540 (TARI 73097-1082); MT336098*; MT181566*; –; MT155895*. *S. alexanderi* Eggl; Mexico; Morelos; P. Carrillo-Reyes & F.Z. Vaz-de-Mello 4257 (IEB, XAL); EF632174; –; EF632191; –. *S. alfredii* Hance; China; Guangdong, Guangzhou; (IBK 114924); FJ919951; FJ919941; –; –. *S. alfredii* Hance; China; East China; G. Kokubugata 17191 (TNS); AB930260; LC258165; LC229432; LC229500. *S. allantoides* Rose; –; –; (Huntington Botanical Garden 90032); AY545712; –; –; –. *S. alpestre* Vill.; –; –; *Stephenson V001*; HE999639; –; –. *S. alpestre* Vill.; Turkey; Bursa, Uludag; (U); –; –; not deposited (Kim & al., 1996). *S. alpestre* Vill. (JKB199); Austria; Zechnerkarstspitze/Schladinger Tauern near Weißpriach, exposed grassy scarp, 47.22°N/13.69°E, ca. 2420 m; U. Hecker D2830 (MJG 012906); MT336103*; MT181570*; KJ884333; MT155899*. *S. alsinefolium* All. (TM37.1); Italy; Prov. Cuneo, E face of mt. Viso. Near the well at Crissolo Borgo, river Po; O. Angerer (MSB); MT336099*; –; –. *S. andinum* Ball; –; –; P. Carrillo-Reyes y N.I. Ortega 5178 (IEB, USM); FJ753930; –; FJ753848; –. *S. anglicum* Huds. (O1); Norway; Telemark, Kragerø, v. Rauane, N of „Storholme“, 0–10 m; T. Berg (O 89072); MT336101*; MT181568*; MN381922*; MT155897*. *S. annuum* L. (O2); –; –; (O 340653); –; MT181569*; MN381923*; MT155898*. *S. annuum* L. (TM51.1); Iceland; Medaldalur, valley on pingeyri peninsula, north-west Iceland; R.W. Groves 07-08 1966 (E 00766661); MT336102*; –; –. *S. apoleipon* t Hart; Greece; –; *Stephenson 5.04.001*; HE999643; KX452276; –; –. *S. baileyi* Praeger; –; –; (LBG 0064555); FJ919935; FJ919945; –; –. *S. batesii* Hemsl.; –; –; E. Ruiz-Sánchez 143 (XAL); FJ753931; –; –; –. *S. bergeri* Raym.-Hamet; China; West Mountain, Kunming, Yunnan; –; AY352897; –; –. *S. borissovae* Balk. (JKC64); –; Garden origin; (Sukkulenten-Sammlung Zürich 99 4604/0); MT336104*; MT181571*; MN381924*; MT155900*. *S. bourgaei* Hemsl.; –; –; E. Pérez y T. Platas 3224 (IEB); FJ753932; –; FJ753849; –. *S. brevifolium* DC. (m883); France; Languedoc-Roussillon, Pyrénées-Orientales, Porté-Puymorens, 42.55°N/1.84°E, 1700 m; J. Klein I 120717-883 (MJG 025432); –; MT181572*; –; MT155901*. *S. brevifolium* DC.; Italy; Val Restonica; *Hornát S5*; LM993278; –; –. *S. brissemeretii* Raym.-Hamet; Portugal; Madeira; *Stephenson V003*; HE999645; –; –. *S. bulbiferum* Makino; Japan; –; L. Niu 1999 (TI); AB088628; –; –. *S. bulbiferum* Makino; –; –; (Utrecht University Botanic Gardens 32795); –; AF115652; –; –. *S. bulbiferum* Makino; Japan; T. Ito 416 (TNS); –; –; LC229434; –. *S. bulbiferum* Makino; South Korea; Seoul; –; –; JQ954574. *S. caducum* R.T. Clausen; –; –; (Huntington Botanical Garden 47970); FJ753933; –; –. *S. caeruleum* L. (JKC37); Malta; Mellieħa Ridge just S of Mellieħa. Shallow pockets of clay in very open garrigue vegetation on limestone rocks. Extremely common in Malta and Gozo in places that are otherwise ± devoid of vegetation, 100 m; K.U. Kramer & L.Y.T. Westra 4198 (U 1219265); MT336105*; MT181573*; –; MT155902*. *S. caespitosum* (Cav.) DC. (TM61.1); Morocco; Near Amanouz (c. 35 km. ESE of Marrakech), rocky limestone slopes, ca. 500 m; P. & J. Davis (E 00764455); MT336106*; –; –. *S. carinatifolium* (R.T. Clausen) Pérez-Cali; –; –; E. Pérez y E. Carranza 3155 (IEB); FJ753934; –; –. *S. catorce* G.L. Nesom; –; –; E. Pérez (IEB); FJ753935; –; –. *S. cepaea* L.; Greece; –; *Stephenson V022*; HE999646; KX452248; –; –. *S. chazaroi* P. Carrillo & J.A. Lomeli; –; –; P. Carrillo-Reyes y I.A. Lomeli 5105 (GUADA, IBUG, IEB, XAL); FJ753936; –; –. *S. chloropetalum* R.T. Clausen; –; –; P. Carrillo-Reyes & F.Z. Vaz-de-Mello 4958 (IEB, IBUG); FJ753937; –; FJ753850; –. *S. clavatum* R.T. Clausen; –; –; J. Meyrán 1306 (Huntington Botanical Garden 73053); AY545713; –; –; AY540576. *S. clavatum* R.T. Clausen; –; –; (Huntington Botanical Garden 23982); –; AF115660; –; –. *S. commixtum* Moran & Hutchison; –; –; P. Carrillo-Reyes & F.Z. Vaz-de-Mello 4954 (IEB, XAL); FJ753938; –; –. *S. commixtum* Moran & Hutchison; –; –; (University of Washington Botanical Garden 124); –; AF115656; –; –. *S. compactum* Rose; Mexico; Oaxaca; P. Carrillo-Reyes & F.Z. Vaz-de-Mello 4929 (XAL); EF632175; –; EF632192; –. *S. confusum* Hemsl.; –; –; *Stephenson 0.06.001*; HE999648; –; –. *S. corynephyllum* Fröd.; –; –; *Acevedo 1713* (XAL); AY545715; –; –; AY540577. *S. craigii* R.T. Clausen; –; –; *Acevedo 1728* (XAL); AY545693; –; –. *S. crassularia* Raym.-Hamet (TM40.1); Kenya; W mt. Kenya, rocky outcrops N of Hausberg Valley, 250 m N of Nanyuki River, 3620 m; H. Rehder (MSB); MT336107*; –; –. *S. cymatopetalum* Fröd.; –; –; *Kinnach 2001.16*; FJ753939; –; –. *S. cypricum* A.K. Jacks & Turrill (TM47.1); Cyprus; Tillyria, north slopes of mt. Zakharou. Roadside banks and clearings in *Pinus brutia* forest, 800–1000 m; J.R. Edmondson & M.A.S. McClintock (E 00361857); MT336108*; –; –. *S. dasyphyllum* L.; Italy; South Tyrol, Merano; *Gontcharov ITA_Toskana_070518*; HE999684; –; –. *S. dasyphyllum* L.; –; –; *Soltis & Soltis 2557*; –; AF115657; –; –. *S. dasyphyllum* L.; Italy; Liguria, Rocco; (U); –; –; not deposited (Kim & al., 1996). *S. dasyphyllum* var. *glanduliferum* (Guss.) Moris; France; Corsica; *Stephenson 5.38.006*; HE999650; KX452266; –; –. *S. debile* S. Watson; U.S.A.; –; *Stephenson V030*; HE999651; KX452265; –; –. *S. dendroideum* DC.; U.S.A.; California; –; –; JX960523; –; –. *S. ebracteatum* DC.; Mexico; –; *Stephenson 0.47.004*; HE999653; –; –. *S. emarginatum* Migo; China; Anhui Province; –; EU592006; –; –. *S. emarginatum* Migo; China; Zhejiang Province; –; –; –; KMI11121. *S. erythrosperrum* Hayata; Taiwan; Kaohsiung, Taoyuan Hsiang; C. Tsutsumi 504 (TNS); AB906473; –; –; AB932631. *S. farinosum* Lowe; Portugal; Madeira, Pico Ruiva; *Stephenson V023*; HE999654; –; –. *S. farinosum* Lowe; –; –; (Utrecht University Botanic Gardens 29006); –; AF115658; –. *S. formosanum* N.E.Br.; Japan; Ryukyus, Izena Island; G. Kokubugata 12224 (TNS); AB930266; LC258195; LC229462; LC229530. *S. fragrans* t Hart (JKC09); –; –; R. Stephenson, *Sedum Society seed distribution SSS1437* (Sukkulenten-Sammlung Zürich 14 0098/0); MT336109*; MT181575*; –; MT155904*. *S. frutescens* Rose; Mexico; –; *Stephenson 0.29.0026*; HE999657; –; –. *S. fuscum* Hemsl.; –; –; E. Pérez y G. Ocampo 4188 (IEB); FJ753941; –; FJ753851; –. *S. goldmanii* (Rose) Moran; Mexico; Veracruz; C. Gallardo 3333 (XAL); EF632186; –; EF632204; –. *S. gracile* C.A. Mey. (JKC08); Georgia; Kartli, between Tbilisi and Didgori, at Didgori Monument, 1630 m; A. Gröger & Lobin 302-9 (Sukkulenten-Sammlung Zürich 10 2021/0); MT336110*; MT181576*; –; MT155905*. *S. grandisepalum* R.T. Clausen; –; –; P. Carrillo-Reyes & F.Z. Vaz-de-Mello 4964 (XAL, IEB); FJ753942; –; –. *S. grandyi* Raym.-Hamet; –; –; (Huntington Botanical Garden 54390); FJ753943; –; –. *S. greggii* Hemsl. (SO2); Mexico; Hidalgo, San Vicente, near Barranca de los Marmoles, 2315 m; R. Moran 7807 (ZSS A 25561); –; –; MN381925*; –. *S. greggii* Hemsl.; –; –; A. Rodriguez (IBUG); FJ753944; –; –. *S. grisebachii* var. *horakii* (Rohlena) t Hart; North Macedonia; Korab mts., Golem Korab, Kobolino pole; *Hornát S4*; LM993280; KX452282; –; –. *S. griseum* Praeger; Mexico; –; *Stephenson 0.30.002*; HE999660; –; –. *S. guatemalense* Hemsl.; –; –; E. Ruiz-Sánchez 145 (XAL); FJ753945; –; FJ753852; –. *S. gypsicola* Boiss. & Reut. (JKC58); Spain; Jaén, Sierra de Segurra, Sierra la Cabrilla, summit area, 2050 m; H. t Hart 41-245 = *HtH 29467* (ZSS A 22032); –; MT181577*; –; MT155906*. *S. gypsicola* Boiss. & Reut. (TM86.1); Malta; Misraħ għar Daqq (close to ġebel Ciantar), Fawwara, Siggiewi, coastal garigue, specifically in karstic rock cavities and crevices at the very edge of the cliffs, often isolated from surrounding flora, 200–250 m; S. Mifsud (E 00653406); MT336111*; –; –. *S. gypsophilum* B.L. Turner; –; –; P. Carrillo-Reyes y A. De Nova 4175 (XAL); FJ753946; –; –. *S. hakonense* Makino; Japan; –; *Mayuzumi C00005* (TI); AB088625; –; –. *S. hakonense* Makino; Japan; T. Ito 623 (TNS); –; LC258168; LC229435; LC229503. *S. hemsleyanum* Rose; –; –; P. Carrillo-Reyes & F.Z. Vaz-de-Mello 4858 (XAL); FJ753947; –; –. *S. hemsleyanum* Rose; –; –; *Brunner 2079a*; –; AF115661; –. *S. hillebrandtii* Fenzl (TM11.1); Austria; Vienna, district 19, 0,05–0,1 km NE of the crossroads Höhenstraße / Krapfenwaldgasse, 360–370 m; Thomas Barta (MSB); MT336112*; –; –. *S. hirsutum* All. s.str. (JKC57); Portugal; Madeira, Pico de Rancho, W of Camara, dry SE-facing rocks along the road to Gato Giro, 400 m; H. t Hart 39-38 = *HtH 29010* (ZSS A 21960); MT336113*; –; MN381926*; –. *S. hirsutum* subsp. *baeticum* Rouy; United Kingdom; Gibraltar; *Stephenson V025*; HE999662; –; –. *S. hispanicum* L. (JKB126); Greece; Central Macedonia, Thessalonika, Chalkidiki, Chortiatis, Boudos, 40.60°N/23.10°E, 920 m; J. Klein

Appendix 1. Continued.

C 110622-01-325 (MJG 012914); KJ884126; MT181578*; KJ884335; MT155907*. *S. hultenii* Fröd.; Mexico; –; *Stephenson 0.13.001*; HE999664; –; –. *S. jaccardianum* Maire & Wilczek; –; –; (Utrecht University Botanic Gardens 32211); AY082100; AF115637; –; AY082220. *S. jurgenseii* (Hemsl.) Moran; –; –; *P. Carrillo-Reyes & F. Nicolalde 4488* (XAL, MEXU); FJ753949; –; FJ753853; –. *S. kotschyianum* Boiss. (TM38.2); Afghanistan; Dascht-i-Nawor, NE-border, salty plains, overgrazed, only on creek borders, 3100 m; *H. Freitag* (MSB 175990); MT336114*; –; –. *S. laconicum* Boiss. & Heldr. (TM87.1); Greece; Lakonias, Githiou, by the deserted village of Poliaravos. Rocky slopes and old terraced fields. Mostly schist, 36°48'N/22°25'E, 700–800 m; *Strid & Kit Tan* (E 00095641); MT336115*; –; –. *S. laconicum* Boiss. & Heldr.; –; –; (Utrecht University Botanic Gardens 31101); –; AF115642; –; –. *S. lagascae* Pau; Spain; Ávila; Gredos, western massif, Solana de Ávila, El Chorro, 1868 m; *B. Garcia*; FJ897739; –; –. *S. lancerottense* R.P.Murray (TM28.1); Spain; Lanzarote, Haria; (Berlin-Dahlem Botanical Garden 350088610); MT336116*; –; –. *S. lancerottense* R.P.Murray; –; *Mort 1533* (WS); –; AF115641; –; –. *S. leibergii* Britton (TM84.1); U.S.A.; Oregon, Ochoco National Forest, 44°41.9'N/120°10'W; *R. Goff* (OSC 235062); MT336117*; –; –. *S. lenkoranicum* Grossh. (TM63.1); Iran; Elburz Mts., above Allamul, between Chalus and Karadj; NE facing slope among *Acer*, *Rosa*, *Lonicera* and *Crataegus* scrub, ca. 1980 m; *J.C. Archibald* (E 00356605); MT336118*; –; –. *S. liebmannianum* Hemsl.; –; –; *P. Carrillo-Reyes & F.Z. Vaz-de-Mello 4958* (XAL); FJ753952; –; –. *S. lineare* Thunb.; Japan; –; *Mayuzumi C00120* (TI); AB088623; –; –; AB089773. *S. litoreum* Guss. (TM68.1); Greece; Lakonias, Githiou, by the deserted village of Poliaravos. Rocky slopes and old terraced fields. Mostly schist, 36°48'N/22°25'E, 700–800 m; *Strid & Kit Tan* (E 00095642); MT336119*; –; –. *S. litoreum* Guss. (JKC10); Italy; Sicily, Prov. Palermo, on limestone rocks near Cap Mongerbino, 50 m; *H. 't Hart 74002* = *HtH 32919* (ZSS 32794); –; MT181579*; –; MT155908*. *S. longipes* Rose; –; –; *P. Carrillo-Reyes & A. Kennedy 4420* (XAL); FJ753953; –; –. *S. lyidium* Boiss. (JKC01); –; Garden origin; *J. Klein L141207-1524* (Sukkulenten-Sammlung Zürich 99 1284/a); –; MT181580*; –; MT155909*. *S. lyidium* Boiss. (TM36.2); Turkey; Izmir, Nif dağı, south of Kemâlpaşa: above Üçoluk çeşmesi on the track to mt. Nifkarlıği tepesi, on a block of stone, 1280 m; *K.P. Butler & E. Erben 17374* (MSB); MT336120*; –; –. *S. magellense* Ten. (JKC05); Yugoslavia?; Komovi [?] Mts., [...], 1900 m; *H. 't Hart 8528* = *HtH 8528* (ZSS A 22663); –; MT181581*; MN381927*; MT155910*. *S. magellense* Ten. (TM75.1); North Macedonia; Šar Planina, rocky slope below limestone crag above Popova Šapka, 8 km of Tetovo, in grassy fissures between rocks, 2100 m; *J.R. Edmondson* (E 00763253); MT336121*; –; –. *S. makinoid* Maxim.; Japan; –; *Mayuzumi C00086* (TI); AB088627; –; –; AB089779. *S. makinoid* Maxim.; Japan; –; *T. Ito 2325* (TNS); –; LC258169; LC229436; –. *S. mexicanum* Britton; Japan; –; *Mayuzumi C00001* (TI); AB088621; –; –; AB089783. *S. meyeri-johannis* Engl. (JKC46); Tanzania; Arusha, Mt. Meru, E slope, road to the crater, Jekukumia River, in forest of *Podocarpus* and *Juniperus procera*, 3.23°S/36.80°E, 2100 m; *B.E. Jonsell 2148* (WAG 0085547); MT336122*; MT181582*; MN381928*; MT155911*. *S. microcarpum* (Sm.) Schönland (UM18); Cyprus; 34.90°N/32.32°E; *J. Klein H 120224-721* (MJG); KJ884127; MT181583*; KJ884336; MT155912*. *S. mocinianum* Pérez-Calix; –; –; *Stephenson 0.52.001*; HE999666; –; –. *S. modestum* Ball; –; –; (Utrecht University Botanic Gardens 33112); AY082101; AF115639; –; AY082221. *S. monregalense* Balb. (TM57.1); Italy; Toscana, mt. Falterona, Pso la Calla, 4000 ft. Habitat: mixed (dec. & conif.) woodland, sandy loam + lf mould on stone, med. shade; *K.I. Ransome* (E 00763266); MT336123*; –; MN381929*; –. *S. moranense* Kunth; –; –; *P. Carrillo-Reyes & F. Nicolalde 4236* (XAL); FJ753954; –; –. *S. morganianum* E.Walther; –; –; (University of Washington Botanical Garden 205); FJ753955; –; –. *S. morrisonense* Hayata; Taiwan; –; *Kokubugata 10831* (TNS); AB906477; –; –; AB932630. *S. morrisonense* Hayata; –; –; (Utrecht University Botanic Gardens 36400); –; AF115651; –; –. *S. morrisonense* Hayata; Taiwan; Nantou, Ren'ai; *T. Ito 1274* (TNS); –; –; LC229477; –. *S. mucizonia* (Ortega) Raym.-Hamet (JKC30); Spain; Jaén, Desfiladeros de Despenaperros, 45 km south of Valdepenas, rivulet dale on the north facing bank; *Stud. biol. Rheno-Trai. in itinere 1328* (U 1213696); MT336124*; MT181584*; –; MT155913*. *S. multicaule* Wall. ex Lindl.; Nepal; –; *F.Miyamoto & al. T19596136* (TI); AB088631; –; –; AB089782. *S. multiceps* Coss. & Durieu (JKC55); Tunisia; –; *H. 't Hart 25256* = *HtH 25256* (Sukkulenten-Sammlung Zürich 99 4291/0); MT336125*; MT181585*; MN381930*; MT155914*. *S. nanum* Boiss. (JKC60); Iran; Kohkiluyeh-Boirahmad, 27 km N of Sisakht, Kuhe Gol; *Jamzad & al. 69488* (TARI 69488); MT336126*; MT181586*; –; MT155915*. *S. nevadense* Coss. (TM70.1); Spain; Ad lacum Cerviz (Saliencia, Somiedo, Asturias), locus muscosus, substrato calcareo; (E 00763275); MT336127*; –; –. *S. nokoense* Yamam.; Taiwan; Hualien, Hsiulin Hsiang; *G. Kokubugata 10426* (TNS); AB906478; –; –. *S. nokoense* Yamam.; Taiwan; Nantou, Ren'ai; *T. Ito 3196* (TNS); –; LC258219; LC229486; LC229554. *S. nudum* Aiton (JKC56); Portugal; Madeira, c. 1 km E of Pico do Facho, along an old road to Canichal, E of Machico, 250 m; *H. 't Hart 39-15* = *HtH 28995* (ZSS A 21512); MT336128*; MT181587*; MN381931*; MT155916*. *S. oaxacanum* Rose; Mexico; Oaxaca; *P. Carrillo-Reyes & D. Cabrera-Toledo 5092* (XAL); EF632176; –; EF632196; –. *S. oaxacanum* Rose; –; –; (Huntington Botanical Garden 72161); –; AF115664; –; –. *S. obcordatum* R.T.Clausen; –; –; *P. Carrillo-Reyes & F. Nicolalde 4440* (XAL); FJ753957; –; –. *S. obcordatum* R.T.Clausen; –; –; (Huntington Botanical Garden 79360); –; AF115665; –; –. *S. obtrullatum* K.T.Fu; China; Xizang, Bomi Xian; *G.Y. Rao 090726-02* (PEY); KF113732; –; –; KF113838. *S. obtusatum* A.Gray (TM19.1); –; Garden origin; *J. Klein L141207-1523* (Sukkulenten-Sammlung Zürich 99 1277/a); MT336129*; –; –. *S. oreades* Raym.-Hamet; Nepal; –; *F.Miyamoto & al. T19420140* (TI); AB088632; –; –. *S. oreades* Raym.-Hamet; China; Xizang, Baqing Xian; *G.Y. Rao 090803-03* (PEY); –; –; KF113839. *S. oregonum* Nutt.; U.S.A.; Oregon Yachats; *Stephenson 9.12.006*; HE999673; KX452264; –; –. *S. oregonense* (S.Watson) M.Peck (UM31); –; Garden origin; (Washington Park Arboretum, WPA00-26); KJ884128; MT181588*; KJ884337; MT155917*. *S. oxypetalum* Kunth; –; –; *E. Pérez 3509* (IEB); FJ753958; –; FJ753856; –. *S. pacense* J.Meyrán; –; –; *E. Pérez 2750* (IEB); FJ753959; –; –. *S. pachyphyllum* Rose; –; –; *P. Carrillo-Reyes & F.Z. Vaz-de-Mello 4912* (IEB, XAL); FJ753960; –; –. *S. pallidum* M.Bieb. (KB10); Georgia; Samegrelo-Zemo Svaneti, Mestia valley, Central Greater Caucasus, Svaneti, gravelly layer on a scree slope N of Mestia, 43.10°N/42.74°E, ca. 1600 m; *H.-J. Zindorf 26534* (MJG 012904); MT336130*; MT181589*; –; MT155918*. *S. palmeri* S.Watson; –; –; *Acevedo & Hernández-Galaviz 1721* (XAL); AY545717; –; –; AY540578. *S. plicatum* Thiede & 't Hart; –; –; *P. Carrillo-Reyes y M. Chocce 5173* (IEB, USM); FJ753961; –; FJ753857; –. *S. polytrichoides* Hemsl.; Japan; –; *Mayuzumi & al. C00029* (TI); AB088626; –; –; AB089772. *S. polytrichoides* Hemsl.; Japan; –; *T. Ito 396* (TNS); –; LC258172; LC229439; –. *S. potosinum* Rose (TM90.1); –; Garden origin (Botanical Garden Szeged); (MJG 024657); MT336131*; –; –. *S. pubescens* Vahl (TM82.1); Algeria; Oued Sebou between Tizi Ouzou and Makouda, steep schist slopes of river valley, with *Sedum caeruleum*, 50–100 m; *Davis* (E 00764482); MT336132*; –; –. *S. pubescens* Vahl; Tunisia; Jebel Ichkeul; *HRT-31627*; –; –; X80551. *S. quevae* Raym.-Hamet; –; –; *P. Carrillo-Reyes y D. Cabrera-Toledo 4496* (XAL); FJ753962; –; FJ753858; –. *S. reniforme* (H.Jacobsen) Thiede & 't Hart; –; –; *P. Carrillo-Reyes y M. Chocce 5174* (IEB, USM); FJ753963; –; FJ753859; –. *S. retusum* Hemsl.; –; –; *S. Zamudio & E. Pérez 9908* (IEB); FJ753964; –; FJ753860; –. *S. rubens* L. (TM58.1); Morocco; 22 km NE of Tafraout on road to Ait Baha, rocky slopes facing E, 1550 m; *Davis & King* (E 00764489); MT336133*; –; –. *S. rubens* L.; Turkey; Van, N of Muradiye, valley of the river Bendimahı, 1800 m; (ISTE 60911); –; –; not deposited ('t Hart & Alpınar, 1999). *S. ruwenzoriense* Baker f. (JKC45); Rwanda; Sabyinyo, Ruhengeri prefecture, on SE-facing rocks, among *Philippia johnstonii*, 1.4°S/29.6°E, 3300 m; *P.R.J. Bamps 3235* (WAG 0085546); MT336135*; MT181590*; MN381932*; MT155919*. *S. sarmentosum* Bunge; Japan; –; *Mayuzumi C00008* (TI); AB088624; –; –. *S. sarmentosum* Bunge; –; –; –; NC_023085; NC_023085; NC_023085. *S. satumense* Hatus.; Japan; Kyoto; *Stephenson V017*; HE999676; –; –. *S. satumense* Hatus.; Japan; –; *T. Ito 2295* (TNS); –; LC258174; LC229441; LC229509. *S. sedoides* (Decne.) Pau; –; –; *Stephenson V036*; HE999677; –; –. *S. sedoides* (Decne.) Pau; –; –; (University of Bonn Botanical Garden 15409); –; AF115677; –; –. *S. sexangulare* L.; Slovenia; Vrsic; *Stephenson 5.09.005*; HE999679; –; –. *S. sexangulare* L.; Poland; –; –; KJ746206; –; KJ746397. *Sedum* sp.; U.S.A.; –; –; HE999691; –; –. *S. spathulifolium* Hook. (JKC17); U.S.A.; California, Butte, on the east bank of Big Chico Creek, on the west side of the dirt road which is Ten Mile House Road, Upper Bidwell Park, about 3/4 mile (air) west of Highway 32, about 10 miles northeast of Chico; *L. Ahart 15772* (JEPS 115506); MT336136*; –; –; MT155920*. *S. spathulifolium* subsp. *purdyi* (Jeps.) R.T.Clausen; –; –; *Stephenson 9.15.001*; HE999687; KX452263; –; –. *S. stefco* Stef. (JKC07); Bulgaria; Bansko - Trigrad, about a 3-hour drive; *Stephenson* (Sukkulenten-Sammlung Zürich 10 0181/0); MT336137*; MT181591*; MN381933*; MT155921*. *S. suaveolens* Kimmach; –; –; *Kimmach & Sánchez-Mejorada 1784* (Huntington Botanical Garden); AY545707; –; –. *S. subtile* Miq.; Japan; –; *A. Shimizu & al. 1999* (TI); AB088622; –; –; AB089775. *S. subtile* Miq.; –; –; –; KX452273; –; –. *S. subulatum* (C.A.Mey.) Boiss. (JKC61); Azerbaijan; between Vaighan and Veinagh, 1000 m; *Khatamsaz & Farzaneh 73097* (TARI 73097); –; MT181592*; –; MT155922*. *S. subulatum* (C.A.Mey.) Boiss.; Turkey; Ararat; *Stephenson V027*; HE999689; –; –. *S. surculosum* var. *luteum* (Emb.) Maire; Morocco; High Atlas; *Hornát S2*; LM993288; KX452239; –; –. *S. tenellum* M.Bieb. (KB11); Georgia; Samtskhe-Javakheti, Bakuriani, Caucasus,

Appendix 1. Continued.

Tskhratskaro Pass, Mt. Tskhratskharo, alpine meadow, 41.69°N/43.53°E, 2687 m; *S. Shetekauri* (MJG 024793); MT336138*; MT181593*; –; MT155923*.
S. ternatum Michx.; –; –; (Missouri Botanical Garden 951462); –; AF115670; –; –. *S. ternatum* Michx. x *S. spathulifolium* Hook.; –; –; *Stephenson* 9.18.004; HE999633; –; –; *S. tosaense* Makino; Japan; –; *A. Iwamoto* 2000 (TI); AB088620; –; –; AB089787. *S. treleasei* Rose; –; –; *D. Cabrera-Toledo* y *F. Nicolalde* 4 (XAL); FJ753966; –; –; *S. triactina* A.Berger; Nepal; –; *F. Miyamoto & al.* TI9596091 (TI); AB088629; –; –; AB089780. *S. trichromum* R.T. Clausen; –; –; *P. Carrillo-Reyes & E. Ruiz-Sánchez* 4733 (XAL); FJ753967; –; FJ753861; –. *S. trullipetalum* Hook.f. & Thomson; Nepal; –; *F. Miyamoto & al.* TI9420132 (TI); AB088630; –; –; AB089781. *S. tuberiferum* Stoj. & Stef.; Bulgaria; Lower Mesta Valley; *Stephenson* 5.00.004; HE999692; KX452278; –; –. *S. uniflorum* subsp. *japonicum* (Sieb. ex Miq.) H.Ohba; Japan; –; *Mayuzumi & al.* C00030 (TI); AB088617; –; –; AB089784. *S. uniflorum* subsp. *japonicum* (Sieb. ex Miq.) H.Ohba; –; –; KX452274; –; –. *S. uniflorum* subsp. *oryzifolium* (Makino) H.Ohba; Japan; –; *Mayuzumi* C00016 (TI); AB088618; –; –; –. *S. uniflorum* subsp. *oryzifolium* (Makino) H.Ohba; South Korea; Dokdo; –; –; NC_027837; NC_027837; NC_027837. *S. ursi* 't Hart; Turkey; Baba Dagi summit; *Stephenson* 5.11.003; HE999693; KX452279; –; –. *S. urvillei* DC. (JKC63); Bulgaria; Warna, Aksakovo, Black Sea Coast, Slanchevo, 43.227426°N/27.705904°E, 114 m; *J. Klein* J130820-1344 (TARI 73097-1344); MT336139*; MT181594*; MN381934*; MT155924*. *S. urvillei* DC. (TM13.1); Bulgaria; Northern Coast of the Black Sea, Probiti Kamini, between columns of stone, 43°13'42"N/27°42'22"E, 124 m; *Gr. Bot. Exk. Nr. 10* (MJG 024786); MT336140*; –; –. *S. versadense* C.H.Thomps.; –; –; *P. Carrillo-Reyes & D. Cabrera-Toledo* 4498 (IEB, XAL); FJ753968; –; FJ753862; –. *S. villosum* L. (O3); Norway; Oppland, Lom, Gokkerdalen at the foot of mt. Lauvhø, ca. 1150 m; *R.Y. Berg* (O 257620); MT336141*; MT181595*; –; MT155925*. *S. vinicolour* S.Watson; –; –; *P. Carrillo-Reyes & E. Ruiz-Sánchez* 4779 (IEB, XAL); FJ753969; –; –. *S. wilczekianum* Font Quer (JKC04); Morocco; Distr. Tarqist, N of Beni-Bouffrah, near Torres-de-Alcala, 5 m; *S.L. Jury & Springate* 11326 (Sukkulanten-Sammlung Zürich 99 4481 10); MT336142*; MT181596*; –; MT155926*. *S. wrightii* A.Gray; –; –; *P. Carrillo-Reyes & A. de Nova* 4582 (XAL); FJ753970; –; –. *S. zentaro-tashiroi* Makino; Japan; –; *Ohba* 1998 (TI); AB088619; –; –; AB089785. *Sempervivum atlanticum* (Ball) Ball (JKB216); Morocco; 31.21°N/7.85°W; *D.R. Letz*, *S. Španiel*, *P. Mered'a* 43C (MJG 024784); KJ884188; MT181597*; KJ884385; MT155927*. *S. ruthenicum* W.D.J.Koch ex Schnittsp. & C.B.Lehm. (JKB168); Ukraine; 49.35°N/26.09°E; *D.R. Letz*, *I. Hodálová*, *P. Mered'a* DRL048 (MJG); KJ884292; –; KJ884483; –. *Sinocrassula indica* (Decne.) A.Berger; China; –; *S. Mayuzumi* C0040C (TI); AB480611; –; –. *S. indica* (Decne.) A.Berger; –; –; *Cody*; –; AF115679; –; –. *S. indica* (Decne.) A.Berger; China; –; *S. Akiyama* 2000 (TI); –; –; AB480665. *S. yunnanensis* (Franch.) A.Berger; –; –; *L.Y. Chen*; KC988288; KC988295; –; –. *S. yunnanensis* (Franch.) A.Berger; China; –; *S. Mayuzumi* C00115 (TI); –; –; AB480669. *Thompsonella colliculosa* Moran; Mexico; Michoacán; *P. Carrillo-Reyes & E. Pérez-Calix* 2714 (IBUG, IEB, GUADA); EF632177; –; –. *T. garcia-mendozae* P.Carrillo & Pérez-Calix; Mexico; Michoacán; *P. Carrillo-Reyes & E. Pérez-Calix* 3186 (IEB); EF632178; –; –. *T. minutiflora* (Rose) Britton & Rose; Mexico; Puebla; *P. Carrillo-Reyes & D. Cabrera-Toledo* 4262 (XAL); EF632179; –; EF632200; –. *T. minutiflora* (Rose) Britton & Rose; –; –; (Huntington Botanical Garden 72129); –; AF115681; –; –. *T. minutiflora* (Rose) Britton & Rose; –; –; (Huntington Botanical Garden 88162); –; –; AY540580. *T. mixtecana* J.Reyes & L.G.López; Mexico; Guerrero; *P. Carrillo-Reyes & E. Pérez-Calix* 2747 (IBUG, IEB, GUADA); EF632180; –; –. *T. platyphylla* Rose; Mexico; Guerrero; *P. Carrillo-Reyes & E. Pérez-Calix* 2727 (IBUG, IEB, GUADA); EF632182; –; –. *T. spathulata* Kimmach; Mexico; Oaxaca; *P. Carrillo-Reyes & D. Cabrera-Toledo* 4914 (XAL); EF632183; –; –. *T. xochipalensis* Gual, S.Peralta & Pérez-Calix; Mexico; Guerrero; *P. Carrillo-Reyes & E. Pérez-Calix* 2734 (IBUG, IEB); EF632184; –; –. *Tylecodon racemosus* (Harv.) Toelken; Namibia; –; *Bruyns* 9476b (BOL); MH503627; –; –. *T. singularis* (R.A.Dyer) Toelken; Namibia; –; *Bruyns* 8373 (BOL, MO, NBG, WIND); MH503628; –; –. *T. torulosus* Toelken; –; –; *Bruyns* 9124 (BOL); LN878945; –; –. *T. ventricosus* (Burm.f.) Toelken; South Africa; –; *Bruyns* 12927 (BOL); MH503629; –; –. *Umbilicus oppositifolius* (Ledeb.) Ledeb. (KB08); –; Garden origin (Botanischer Garten der Johannes Gutenberg-Universität Mainz); (MJG); KJ884131; MT181598*; –; MT155928*. *U. schmidtii* Bolle; Cape Verde; São Nicolau, Monte Gordo, Rib. dos Calhaus, 16.63°N/24.36°W; *Duarte & al.* 4125c (LISC); KP279434; KP279376; –; KP279334. *Villadia albiflora* (Hemsl.) Rose; –; –; *P. Carrillo-Reyes & D. Cabrera-Toledo* 4495 (XAL); FJ753971; –; FJ753863; –. *V. aristata* Moran; Mexico; Nuevo León; *J. Cortés-Aguilar* (IBUG); EF632185; –; EF632202; –; –; *M. Kristen* y *J. Etter* 2056 (XAL); FJ753972; –; –. *V. diffusa* Rose; –; –; *F. Nicolalde* 1461 (XAL); FJ753973; –; FJ753864; –. *V. imbricata* Rose; Mexico; Oaxaca; *P. Carrillo-Reyes & F.Z. Vaz-de-Mello* 4926 (XAL); EF632187; –; EF632203; –. *V. incarum* (Ball) Baehni & J.F.Macbr.; –; –; *P. Carrillo-Reyes & N.I. Ortega* 5179 (IEB, USM); FJ753974; –; FJ753865; –. *V. minutiflora* Rose; –; –; *P. Carrillo-Reyes & D. Cabrera-Toledo* 5095 (IEB); FJ753975; –; FJ753866; –. *V. misera* (Lindl.) R.T. Clausen; –; –; *P. Carrillo-Reyes & F. Nicolalde* 4357 (XAL); FJ753976; –; FJ753867; –. *V. nelsonii* Rose; –; –; *P. Carrillo-Reyes* y *J.A. Lomeli-Sención* 3709 (GUADA, XAL); FJ753977; –; FJ753868; –. *V. pringlei* Rose; –; –; *P. Carrillo-Reyes & E. Ruiz-Sánchez* 4800 (XAL); FJ753978; –; FJ753869; –. *V. recurva* Moran, Kimmach & C.H.Uhl; –; –; *P. Carrillo-Reyes & F.Z. Vaz-de-Mello* 4972 (XAL); FJ753979; –; FJ753870; –.

Appendix 2. Taxa with supposedly conflicting positions in the phylogenies based on nuclear and plastid sequence data.

<i>Dudleya pulverulenta</i> (Nutt.) Britton & Rose
<i>D. viscida</i> (S.Watson) Moran
<i>Graptopetalum macdougallii</i> Alexander
<i>Petrosedum amplexicaule</i> subsp. <i>tenuifolium</i> (Sm.) Velayos
<i>P. anopetalum</i> (DC.) Grulich
<i>P. forsterianum</i> (Sm.) Grulich
<i>P. sediforme</i> (Jacq.) Grulich
<i>Pistorinia breviflora</i> Boiss.
<i>Rosularia serrata</i> (L.) A.Berger
<i>Sedum album</i> L.
<i>S. fragrans</i> 't Hart
<i>S. hakonense</i> Makino

Appendix 2. Continued.

<i>S. litoreum</i> Guss.
<i>S. lyidium</i> Boiss.
<i>S. nanum</i> Boiss.
<i>S. satumense</i> Hatus.
<i>S. sedoides</i> (Decne.) Pau
<i>S. subtile</i> Miq.
<i>S. tenellum</i> M.Bieb.
<i>Villadia diffusa</i> Rose
<i>V. incarum</i> (Ball) Baehni & J.F.Macbr.

(Continues)