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Phylogeny and Systematics of *Kewa* (Kewaceae)

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Abstract—The genus *Kewa* in the monogeneric family Kewaceae (Caryophyllales) is revised. Six species are recognized, *K. acida* on St. Helena, *K. angrae-pequenae* in Namibia and South Africa, *K. arenicola* (incl. *K. trachysperma*) in South Africa, *K. bowkeriana* (incl. *K. suffruticosa*) widespread in eastern and southern Africa and in Madagascar, *K. caespitosa* in Angola and Namibia, and *K. salsoloides* in Namibia, Botswana, and South Africa. *Kewa* is morphologically distinctive, notably by its simple perianth where the two outer perianth-segments are more or less sepaloid and the three inner ones more or less petaloid, and by its indumentum of short glandular hairs, often with prominent, persistent, wart-like bases. All species have an acid taste, apparently due to the presence of oxalic acid. All names are typified, including one lectotype designated here. An identification key and distribution maps for all species are provided. The phylogeny of *Kewa* is reconstructed based on plastid *trnK-matK* and *rbcL* and nuclear ITS sequences. *Kewa* is strongly supported and the included species have strong to no support, whereas the relationships between the species are mostly unsupported. The phylogeny is dated and the estimated age of the *Kewa* stem clade is (37.5–)45.0(–57.0) million years and of the crown clade (3.0–)3.9(–7.4) million years. The age of the crown clade would also be the estimated date when *K. acida* on the approximately 14 million years old St. Helena diverged from its potential sister group on the African continent, and would coincide with the earliest possible date for the introduction of the ancestor of *K. acida* to St. Helena.

Keywords—Caryophyllales, *Hypertelis*, molecular dating, St. Helena, taxonomy, typification.

The number of recognized families of flowering plants has in the last decades usually been just over 400, the recent classification of the Angiosperm Phylogeny Group (2016), APG IV, for example, having 416. New families of flowering plants are still occasionally proposed, mostly for small, odd genera, where new evidence has shown them to be previously misplaced. Recent examples in Caryophyllales are *Microtea* Sw. with nine species in tropical America, previously placed in Amaranthaceae or Phytolaccaceae, but now in Microteaceae (Schäferhoff et al. 2009), and *Corbichonia* Scop. with two species in Africa and Asia, previously mostly placed in Molluginaceae or Lophiocarpaceae, but now in Corbichoniaceae (Thulin et al. 2016).

Kewa Christenh. in Kewaceae (Christenhusz et al. 2014) is an example of a new genus placed in a new family, an extremely unusual situation. The species involved have long been treated as members of the genus *Hypertelis* E.Mey. ex Fenzl in Molluginaceae. This genus was found to be non-monophyletic (Christin et al. 2011), with part of it (*H. spergulacea* E.Mey. ex Fenzl, the type) belonging to Molluginaceae, and another part (*H. bowkeriana* Sond. and *H. salsoloides* (Burch.) Adamson) being sister to a large clade including, among others, the well-established families Aizoaceae and Nyctaginaceae. *Hypertelis bowkeriana*, *H. salsoloides* and their relatives were placed in *Kewa* by Christenhusz et al. (2014), whereas *H. spergulacea* and its relatives were treated in a modified *Hypertelis* by Thulin et al. (2016).

The taxonomy of *Kewa* with eight recognized species proposed by Christenhusz et al. (2014) is entirely based on the treatment of *Hypertelis* by Adamson (1957). However, Christenhusz et al. (2014) have missed, for example, that since then Jeffrey (1961) has treated *Hypertelis suffruticosa* (Baker) Adamson (= *Kewa suffruticosa* (Baker) Christenh.) from Madagascar as a synonym of *H. bowkeriana*.

Here we present a phylogeny of the core Caryophyllales based on plastid *trnK-matK* and *rbcL* and nuclear ITS sequence data and with a much expanded sampling of *Kewa* compared to previous studies and including *K. acida* (Hook.f.) Christenh., endemic to St. Helena. The phylogeny is dated to enable us to put an age to the stem and crown clades of *Kewa*, and to give an age estimate of its dispersal to St. Helena. We also propose a revised classification of *Kewa* and Kewaceae, including a more detailed morphological characterization of the family, typifications of all names, descriptions of all recognized taxa, a new key to the species, as well as distribution maps for all species.

MATERIALS AND METHODS

Taxon Sampling—The sampling included representatives of nearly all families within the core Caryophyllales, and is essentially the same as that in Thulin et al. (2016: Fig. 1), except for the sampling of Kewaceae that is expanded to include 14 accessions representing all six species of *Kewa* recognized here (see under Taxonomy). In total, 78 accessions from 65 species were included in the analyses (Appendix 1), and 24 sequences were newly generated for this study.

Data Availability—Alignments, tree files, and supplemental figures are all available from the Dryad Digital Repository (Thulin et al. 2018).

DNA Extraction, Amplification, and Sequencing—Dried leaf material from herbarium specimens was used for DNA extraction. Samples were extracted using the FastDNA SPIN kit (MP Biomedicals, LLC, Santa Ana, California) following manufacturer's protocol except that two elution steps were generally used, with 50 µl of DES each time to maximize yield.

The nuclear ribosomal internal transcribed spacer (ITS) and chloroplast *trnK-matK* regions were amplified using PCR. The primers ITS4 and ITS5 (White et al. 1990) were used to amplify the ITS region, whereas for the *trnK-matK* region various combinations of the forward primers *trnKmatK_For* H, M, G, and K and the reverse primers *trnKmatK_Rev* B, C, E, and I, all from Christin et al. (2011), except for *trnKmatK_M* (5'-ACTATGTATCATTTGGT-TAAGC-3'), were used. The same PCR protocol was used for both regions, in 25 µl reactions including 1 unit GoTaq (Promega Corporation, Madison, Wisconsin), 5 × GoTaq Reaction Buffer (Promega), 0.5 mM MgCl₂, 0.15 mM

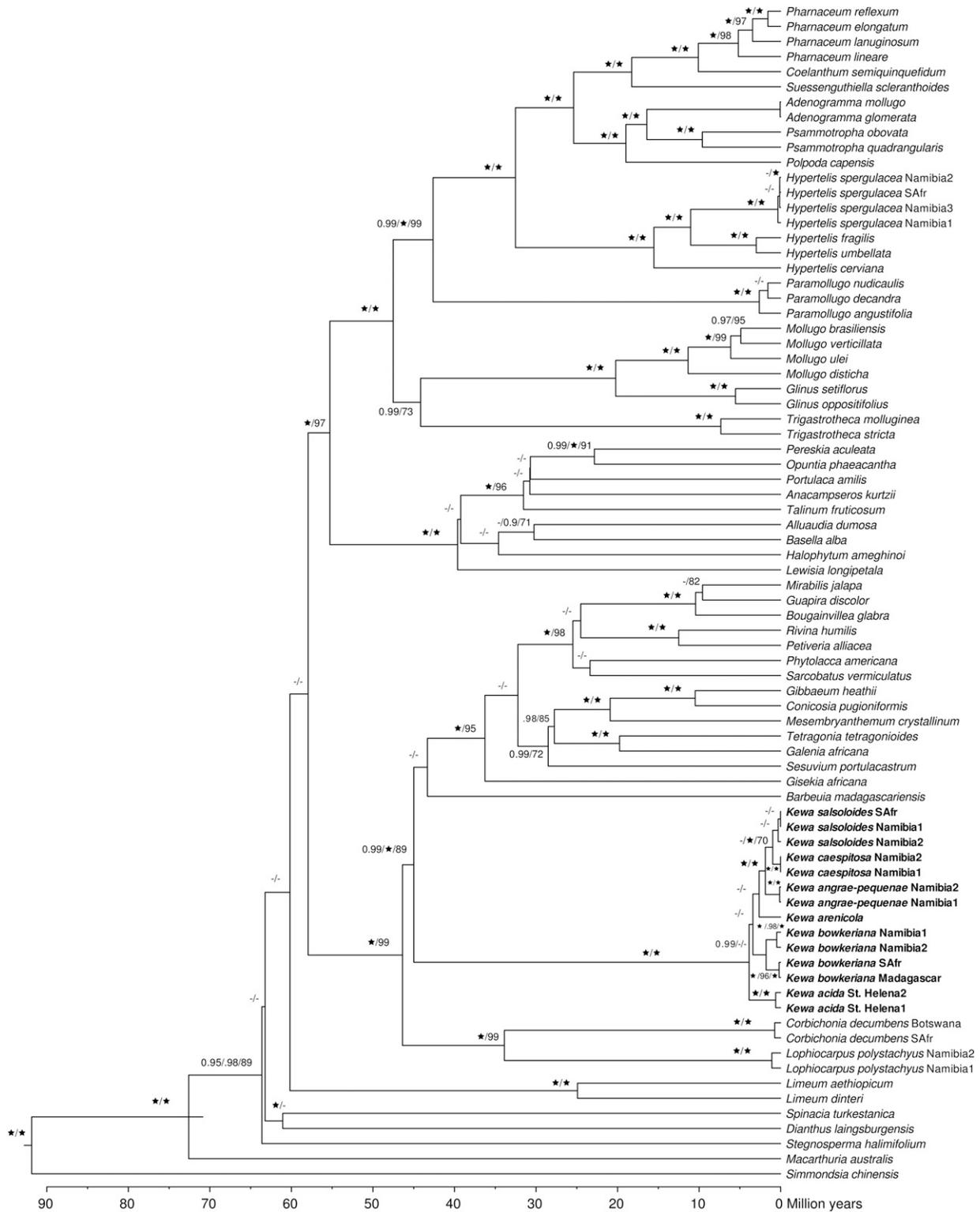


FIG. 1. Dated phylogeny. Maximum clade credibility chronogram from BEAST analysis of the combined core Caryophyllales dataset. Branch labels show Bayesian posterior probabilities from the BEAST analysis and the MrBayes analysis (the latter included only when they differ from the BEAST analysis), and values from 1000 bootstrap replicates with RAxML. Posterior probabilities of 1.0 and bootstrap values of 100 are replaced by asterisks, whereas posterior probabilities less than 0.95 and bootstrap values less than 70 are replaced by dashes. When more than one accession per species was included, the locality after the name corresponds to those in Appendix 1. Members of *Kewa* are shown in bold. SAfr = South Africa.

each dNTP (New England Biolabs, Inc., Ipswich, Massachusetts), 0.2 μ M each primer, and approximately 0.6 ng extracted DNA. The following PCR program was used: initial denaturation of 3 min at 94°C; 37 cycles of 1 min denaturation at 94°C, 30 s annealing at 48°C (for ITS) or 51°C (for *trnK-matK*), 60 to 150 s extension at 72°C, and final extension of 10 min at 72°C.

The PCR products were cleaned with the Exo-SAP PCR Product Pre-Sequencing Kit (USB Corporation, Cleveland, Ohio). Cleaned PCR products were sequenced at the Rhode Island Genomics and Sequencing Center with either a 3130XL Genetic Analyzer or a 3500XL Genetic Analyzer (Applied Biosystems, Life Technologies, Inc., Grand Island, New York).

The same primers were used for PCR and sequencing, with additional internal primers being used to sequence samples for which *trnK-matK* could be amplified as a single fragment. Chromatograms were edited and contigs were constructed using ChromasPro v. 1.7.5 (Technelysium Pty. Ltd., Tewantin, Queensland, Australia).

Sequence Alignment, Phylogenetic Analyses, and Divergence Time Estimation—Sequences were aligned using MAFFT v. 7.271 (Katoh and Standley 2013) and alignments were checked by eye and manually adjusted in AliView v. 1.18.1 (Larsson 2014). Maximum likelihood bootstrap analyses were performed using RAxML-HPC-PTHREADS-AVX v. 8.2.4 (Stamatakis 2014). A first analysis was made using *trnK-matK* and *rbcL* sequences and with *Simmondsia* as outgroup in agreement with Thulin et al. (2016). As ITS sequences were not possible to align across this group of taxa, a second analysis of ITS sequences from *Kewa* and with *Corbichonia* and *Lophiocarpus* as outgroups was made. In the *trnK-matK/rbcL* tree (Supplemental Fig. S1) all species except *K. bowkeriana* (samples from Namibia and South Africa) were monophyletic, whereas in the ITS tree (Supplemental Fig. S2) *K. bowkeriana* (samples from Namibia, South Africa and Madagascar) was monophyletic, but *K. salsoloides* was paraphyletic with respect to *K. caespitosa*. As otherwise no strong conflicts between the topologies of the *trnK-matK/rbcL* (Fig. S1) and ITS (Fig. S2) analyses could be detected, the two datasets were concatenated and analyzed together. For each analysis, a search for the best tree was combined with 1000 bootstrap pseudoreplicates. Models of nucleotide substitution were chosen according to the corrected Akaike information criterion (AICc) as implemented with PartitionFinder v. 2.1.1 (Lanfear et al. 2016). The optimal model for ITS was GTR + G and for *trnK-matK* and *rbcL* GTR + I + G. Due to limitations in RAxML, only one model can be used in a partitioned dataset and GTRGAMMA was selected for all partitions.

Bayesian inference tree searches were performed with MrBayes v. 3.2.1 (Ronquist et al. 2012). For the combined dataset we did two runs of four chains each (one cold and three heated), for 10 million generations. For this analysis, each locus was assigned a separate partition with model substitution parameters unlinked, and branch lengths linked. Substitution models were selected with PartitionFinder as described for RAxML above. The posterior was sampled every 1000 generations. Inspection of log-files in Tracer v. 1.5 (Rambaut and Drummond 2009) revealed that all the runs converged within the first two million generations. We excluded the first two million generations (20%) of each run as burn-in before summarizing the posterior.

Divergence times for the stem and crown clade of *Kewa* were estimated using BEAST v. 1.8.4 (Drummond et al. 2012). Due to the paucity of Caryophyllales fossils, we used a combination of primary and secondary calibration points in our dating analyses. For our two secondary calibration points, we used two normally distributed age priors: 51.9 million years (Ma) (with a standard deviation of 10%) assigned to the node between Molluginaceae and the Portulacinae clade, based on Christin et al. (2011), and 25 Ma (with a standard deviation of 10%) assigned to the node between *Opuntia* Mill. and *Pereskia aculeata* Mill., based on Arakaki et al. (2011). In addition, a minimum age constraint of 60 Ma was assigned to the node between *Dianthus* L. and *Spinacia* L., based on the fossil pollen *Chenopodiopsis multiplex* (Weyland & Pflug) Krutzsch (Nichols and Traverse 1971). This primary calibration point was modeled as a gamma-shaped distribution (shape = 1.5, scale = 5, offset = 60). The analyses were performed with a lognormal, uncorrelated clock model with a birth-death tree prior. Priors were set to default values except for the previously described node ages. GTR + G and GTR + I + G nucleotide substitution models as in the MrBayes analysis were used. We ran the analysis three times for 100 million generations and sampled the posterior every 1000 generations. Visual inspection in Tracer v. 1.5 (Rambaut and Drummond 2009) revealed that all runs converged within 10 million generations. Therefore, the first 10 million generations (10%) of each run were removed as burn-in before we combined the runs with LogCombiner v. 1.8.0 (Rambaut and Drummond 2013a). Finally, we summarized the tree samples with TreeAnnotator v. 1.8.0 (Rambaut and Drummond 2013b).

RESULTS

Combined Core Caryophyllales Dataset—The dated phylogeny based on the combination of *trnK-matK*, *rbcL*, and ITS data is shown in Fig. 1 (maximum likelihood (ML) and Bayesian inference trees showing branch lengths are in Figs. S3 and S4, respectively). *Corbichonia* (Corbichoniaceae) and *Lophiocarpus* (Lophiocarpaceae) together are strongly supported as sister to a clade with members of Kewaceae (*Kewa*),

Barbeuiaceae (*Barbeuia*), Gisekiaceae (*Gisekia*), Aizoaceae (*Conicosia*, *Galenia*, *Gibbaeum*, *Mesembryanthemum*, *Sesuvium*, *Tetragonia*), Phytolaccaceae (*Phytolacca*), Sarcobataceae (*Sarcobatus*), Petiveriaceae (*Petiveria*, *Rivina*), and Nyctaginaceae (*Bougainvillea*, *Guapira*, *Mirabilis*).

Kewa is strongly supported, and within the genus, the two samples of *K. acida* come out together with strong support, as do the two samples of *K. angrae-pequenae* and the two samples of *K. caespitosa*. The four samples of *K. bowkeriana* form an unsupported clade in the ML and MrBayes analyses, but in the BEAST analysis (Fig. 1), this clade is well supported. Within *K. bowkeriana*, the two samples from Namibia form a strongly supported pair in all analyses, as do the two samples from South Africa (KwaZulu-Natal) and Madagascar. *Kewa salsoloides*, represented by three samples, is recovered as monophyletic, but without support in the BEAST analysis (Fig. 1). However, in the ML and MrBayes analyses *K. salsoloides* is paraphyletic with respect to *K. caespitosa*. The relationships between the species are mostly unsupported, notably *K. acida* on St. Helena is sister to the rest of the species in the BEAST analysis, but without support, whereas ML and MrBayes retrieve a basal polytomy within the genus. *Kewa angrae-pequenae* is well supported as sister to *K. salsoloides* and *K. caespitosa* together in all three analyses.

Divergence Time Estimates—The divergence time estimates resulted in an age of (37.5–)45.0(–57.0) Ma for the *Kewa* stem clade and (3.0–)3.9(–7.4) Ma for the *Kewa* crown clade (Fig. S5). The age of the *Kewa* crown clade would also be the estimated date when the stem clade of *K. acida* diverged from its potential sister group on the African continent, and thus a potential maximum age of when *K. acida* colonized St. Helena. Within *Kewa*, the crown clade of the widespread *K. bowkeriana* has an estimated age of (1.5–)1.8(–4.5) Ma, whereas the crown clades of the narrowly distributed *K. acida*, *K. angrae-pequenae*, and *K. caespitosa*, as well as the fairly widespread *K. salsoloides*, are much younger.

DISCUSSION

The topology of the tree based on the core Caryophyllales dataset (Fig. 1) essentially agrees with the results of Thulin et al. (2016), the main difference being the increased sampling of members of *Kewa*. *Kewa* is strongly supported, comprising all the samples of the included species: *K. acida*, *K. angrae-pequenae*, *K. arenicola*, *K. bowkeriana*, *K. caespitosa*, and *K. salsoloides*. The narrowly distributed species *K. acida*, *K. angrae-pequenae*, and *K. caespitosa* are strongly supported, whereas the more widespread and variable *K. bowkeriana* and *K. salsoloides* are unsupported or, in the case of *K. bowkeriana*, supported only in BEAST.

Within *K. bowkeriana*, the samples from South Africa (KwaZulu-Natal) and Madagascar come out together with strong support, as do the two samples from Namibia. While all samples of *K. bowkeriana* came out together in the ITS tree, the South African sample was separated from the Namibian samples with the *trnK-matK* sequences (*trnK-matK* sequences could not be obtained for the Madagascar sample). The synonymization of *Hypertelis suffruticosa* (= *K. suffruticosa* from Madagascar with the continental African *H. bowkeriana* (= *K. bowkeriana*) by Jeffrey (1961) therefore is corroborated.

Kewa angrae-pequenae is well supported as sister to *K. salsoloides* and *K. caespitosa* together. This clade also has some morphological support as the three species included differ from other species of *Kewa* by having mostly pink (versus

mostly white) flowers. The species pair *K. salsoloides* and *K. caespitosa* also has good support, although *K. salsoloides* is recovered as paraphyletic with respect to *K. caespitosa* in two of the analyses (and in the ITS, but not the chloroplast tree). Otherwise, the relationships between the species are unsupported. The sister group relationship between *K. acida* on St. Helena and the rest of the species recovered in the BEAST analysis, albeit without support, indicates that the estimated age of the *Kewa* crown clade, (3.0–)3.9(–7.4) Ma, would also coincide with the earliest possible date for the introduction of the ancestor of *K. acida* to St. Helena. This inference is further supported by *Kewa* outgroups also being distributed on the African mainland, strongly suggesting that stem lineage *Kewa* resided in mainland Africa, and the St. Helena disjunction is due to a single, long distance dispersal from Africa to St. Helena.

The volcanic St. Helena emerged from the sea approximately 14 MYA (Cresswell 2016). The island is extremely remote, the nearest land being the Ascension Island, about 1100 km towards northwest. The distance to Africa, the nearest continent, is about 1900 km, and to South America about 2700 km.

The early colonization of the remote and inhospitable St. Helena by plants must have been a very slow process (Ashmole and Ashmole 2000; Lambdon 2012). A late Miocene deposit on St. Helena with spores and pollen about 9 Ma revealed an island dominated by ferns and lycopods (Muir and Baker 1968), but some angiosperms were also present, notably the genus *Trochetiopsis* (Malvaceae), with three species recorded on the island (Cronk 1990), two of which are still extant (Lambdon 2012).

According to Lambdon (2012), 45 endemic species of vascular plants can be recognized on St. Helena today and the native flora includes between 31 and 43 further species, three of which are now extinct. Many of the endemics, particularly in the dry zone at lower altitudes, have their closest relatives in southern Africa, and were assumed to be of a more recent origin than the endemics of the wet zone (Cronk 2000). In any case, their ancestors must have arrived in St. Helena by long distance dispersal during the 14 Ma that the island has existed. *Kewa acida*, the ancestor of which is estimated to have diverged from its African relatives (3.0–)3.9(–7.4) MYA, does not appear to be particularly recent, although it is confined to the dry zone. Other endemics on St. Helena that have been dated are *Phyllica polifolia* (Vahl) Pillans (Rhamnaceae), a shrub or small tree that seems to be a recent result of a radiation that started about 2 MYA (Richardson et al. 2001), and the extinct endemic genus *Nesiota* Hook.f. (Rhamnaceae), with the single arborescent species *N. elliptica* (Roxb.) Hook.f., the ancestor of which was estimated to have diverged from its sister, *Trichocephalus stipularis* (L.) Brogn. from the Western Cape of South Africa, about 12 MYA (Richardson et al. 2001).

TAXONOMIC TREATMENT

KEWACEAE Christenh., Phytotaxa 181: 240. 2014. TYPE: *Kewa* Christenh.

Family of a single genus.

KEWA Christenh., Phytotaxa 181: 240. 2014. TYPE: *Kewa salsoloides* (Burch.) Christenh.

Annual or perennial glaucous herbs, subshrubs or dwarf shrubs, glabrous or with minute glandular hairs, each borne at

the tip of cone-shaped outgrowths of the mesophyll that remain as sometimes prominent warts, particularly on peduncles, pedicels, and outside of the perianth. Leaves alternate or subopposite, often crowded and with axillary short-shoots, sessile, with an acid taste apparently due to presence of oxalic acid; stipules persistent, membranous, entire to denticulate, with lower part adnate to the leaf-base and forming a \pm amplexicaul sheath; leaf-blades linear to narrowly obovate in outline, succulent, almost terete, with a \pm distinct groove on the underside, entire. Inflorescences terminal, often becoming seemingly axillary, pedunculate, umbel-like cymes, with 1–many pedicellate flowers, each flower with a bract and 2 bracteoles at base of pedicels; bracts and bracteoles membranous, entire to denticulate; pedicels often \pm deflexed. Flowers chasmogamous or sometimes cleistogamous; perianth of 5 free unequal segments, with quincuncial aestivation in bud; segments with median part greenish, \pm rounded on the back, membranous margins narrow in 2 outer \pm elliptic and sepaloïd segments, widened and \pm conspicuous in 3 inner \pm broadly obovate and petaloïd, pink or white ones. Stamens 3–15, when 5 alternate with the perianth segments, the filaments linear, slightly united at the base; anthers basifixed, dehiscing by longitudinal slits. Disk absent. Ovary superior, syncarpous, of (3–)5 carpels, (3–)5-locular, with numerous axile ovules; stigmas (3–)5, spreading to \pm appressed to top of ovary. Capsule ovoid-elliptic to subglobose, surrounded by perianth, thin-walled, loculicidally dehiscent, the central axis remaining in the middle after dehiscence. Seeds pear- to comma-shaped in outline, smooth to tuberculate, brownish-black, with a minute strophiole; embryo straight. Chromosome number $n = 8$ (reported only for *Kewa bowkeriana*). Figures 2, 3.

Distribution—Six species in southern and eastern Africa, Madagascar, and St. Helena (Fig. 4).

General Remarks—As in many other members of Caryophyllales, the flowers of *Kewa* possess a simple perianth with five, free, quincuncially arranged perianth-segments. However, in *Kewa* the two outer perianth-segments are more or less sepaloïd, whereas the three inner ones are more or less petaloïd (Figs. 2, 3). This differentiation within the perianth is most obvious in the more large-flowered species, such as the white-flowered *K. acida* (Christenhusz et al. 2017) and the pink-flowered *K. salsoloides*, whereas it is somewhat less prominent in, for example, *K. bowkeriana*, a species with more inconspicuous and sometimes even cleistogamous flowers.

The perianth parts of “*Hypertelis*” have been said to be chimeric (Brockington et al. 2009), i.e. each perianth part would be partly sepaloïd and partly petaloïd. This may be true for *H. spergulacea*, where all perianth parts are more or less equal, petaloïd above and sepaloïd below, but not for the differentiated perianth of *Kewa*. The differentiation among the perianth-segments within a simple 5-merous perianth as seen in *Kewa* indeed seems to be unique in Caryophyllales and perhaps in flowering plants in general.

Another peculiar feature of Kewaceae is the indumentum. It consists of short glandular hairs, which may have a many-celled thickened and often more or less conical wart-like base of mesophyll covered by elongate epidermis cells (Fig. 3D). These warts or “glands” occur on both vegetative parts and on the perianth, but in varying amounts and sizes in the different species. When situated on pedicels or perianths they tend to become reddish-brown in colour and can be very prominent (Fig. 3A),

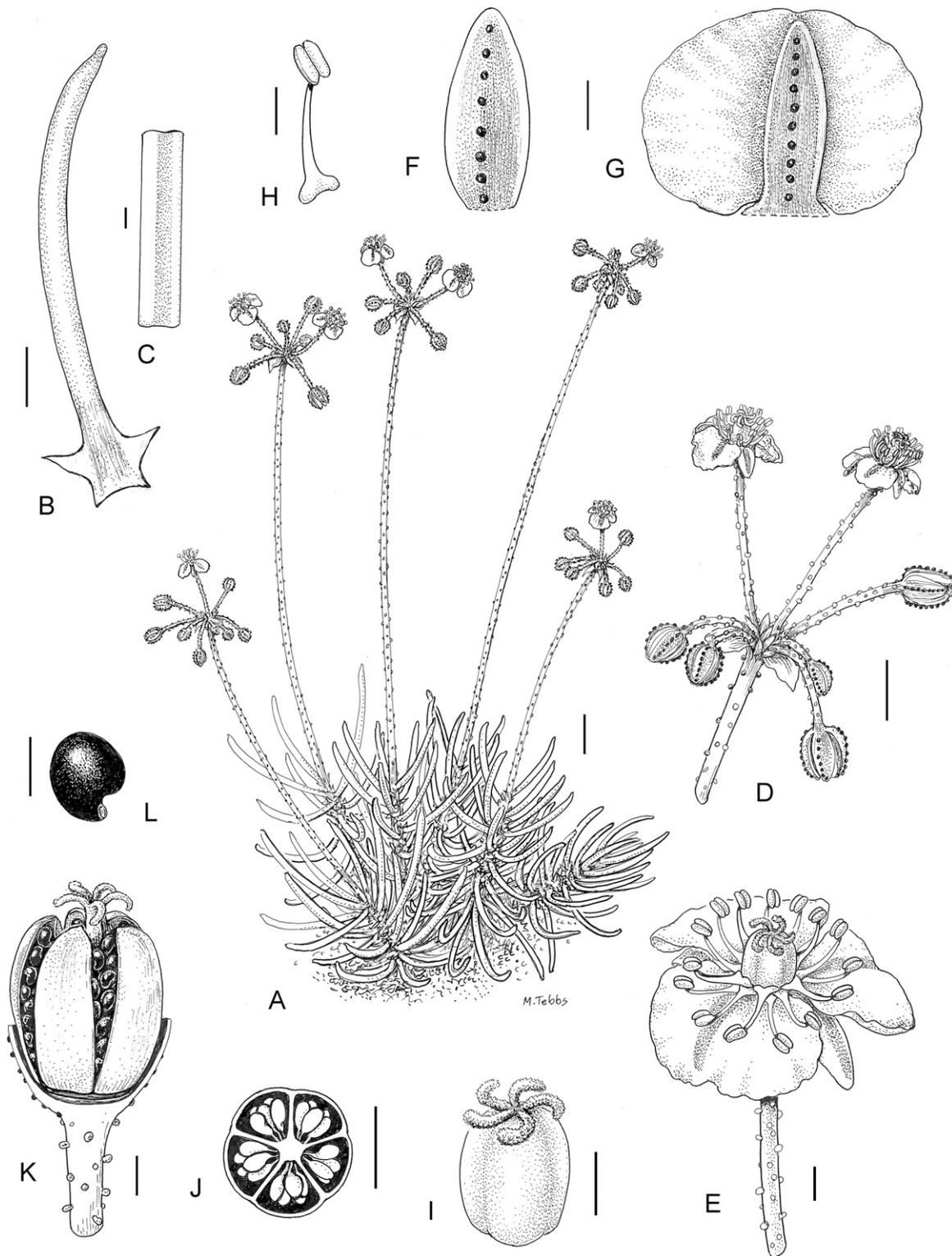


FIG. 2. *Kewa salsoloides*. A. Habit. B. Leaf with stipules. C. Portion of underside of leaf, showing groove. D. Inflorescence. E. Flower. F. Sepaloid perianth-segment. G. Petaloid perianth-segment. H. Stamen. I. Ovary and styles. J. Cross-section of ovary. K. Capsule. L. Seed. Scale bars: A = 10 mm; B, D = 5 mm; C, E–K = 1 mm; L = 0.5 mm. Drawn from Thulin *et al.* 11956 by Margaret Tebbs.

remaining long after the ephemeral top part has fallen off. The function of these warts is unknown and no similar structures seem to be known in related families.

Many families within Caryophyllales are characterized by having a blue/red pigmentation of betalains rather than the ubiquitous anthocyanins in other flowering plants, and

according to Brockington *et al.* (2015) a single origin of the betalain pigmentation is most likely. Reversals from betalains to anthocyanins have occurred within the betalain-producing clade a few times, one example being Kewaceae in which the occurrence of anthocyanins was confirmed in *K. salsoloides* by Thulin *et al.* (2016).



FIG. 3. A. *Kewa salsoloides*, inflorescence, from Klein Aus, Namibia. B. *Kewa acida*, inflorescence, from St. Helena. C. *Kewa bowkeriana*, inflorescence, from Madagascar (progeny of Thulin & Razafindraibe 11819 cultivated in Uppsala). D. *Kewa bowkeriana*, glandular hair with wart-like base (plant origin as in C). Photos by M. Thulin (A), Phil Lambdon (B), Magnus Lidén (C), and Allison Perrigo (D).

In the protologue of *Kewa acida* (as *Pharnaceum acidum*), Hooker (1867) mentioned the acid taste of the plant and its use as a salad plant on St. Helena, and *Melliss s. n.* (K), a specimen of *K. acida*, has a note saying that the succulent leaves of this plant have “the acid flavour of *Oxalis*.” This acid taste, apparently due to the presence of oxalic acid (H. El-Seedi

unpubl.), is common to all species of *Kewa* and is an excellent field character for the group (M. Thulin pers. comm.). The acid taste has also been noted by various other collectors (e.g. in *K. salsoloides*, Hanekom 2155, K), and is reflected in the vernacular name “braksuring” (brak is brackish and suring sorrel in Afrikaans).

KEY TO THE SPECIES OF KEWA

1. Perianth-segments 7 mm or more long. 1. *K. acida*
1. Perianth-segments up to 5 mm long. 2
 2. Stamens 12–15. 3
 3. Leaves \pm narrowly obovate in outline, 6–15 \times 2–4 mm; inflorescences 1–3-flowered, smooth or sparsely warty. 2. *K. angrae-pequenae*
 3. Leaves linear to narrowly oblanceolate in outline, 5–40 \times 1–3 mm; inflorescences 3–10-flowered, with many prominent warts on peduncles, pedicels, and outside of perianth. 6. *K. salsoloides*
 2. Stamens 3–9. 4
 4. Leaves 0.5–1 mm wide; peduncles, pedicels, and outside of perianth mostly with prominent warts; stamens 5. 4. *K. bowkeriana*
 4. Leaves 1–2.5 mm wide; peduncles, pedicels, and outside of perianth mostly smooth and without prominent warts; stamens 3–9. 5
 5. Plant annual; perianth-segments 2–3 mm long; stamens 3–5; seeds almost smooth to distinctly tuberculate. 3. *K. arenicola*
 5. Plant perennial; perianth-segments 3–5 mm long; stamens 5–9; seeds smooth. 5. *K. caespitosa*

1. KEWA ACIDA (Hook.f.) Christenh., Phytotaxa 181: 241. 2014. *Pharnaceum acidum* Hook.f., Ic. Pl. 11: 26, t. 1035. 1867. *Hypertelis acida* (Hook.f.) K. Müll., Bot. Jahrb. Syst. 42, Beih. 97: 62. 1908. TYPE: ST. HELENA. Sandy Bay, Burchell 113 (lectotype: K! barcode K000232014, designated by Adamson, J. S. Afr. Bot. 24: 57. 1957).

Note on Typification—Cronk (2000) designated Burchell 113 in K as lectotype and this typification was also cited by Christenhusz et al. (2017). However, already Adamson (1957) cited the Burchell specimen at K as “Type”, and this is here regarded as the first lectotypification in accordance with ICBN, Art. 9.8 (McNeill et al. 2012).

Annual to short-lived perennial herb or subshrub, up to 40 cm tall, ascending, glabrous. Leaves linear to narrowly

oblanceolate, 20–60(–80) \times 1.5–6 mm. Inflorescences with peduncles 5–16 cm long, 2–15-flowered; pedicels 6–30 mm long. Flowers with perianth-segments 7–12 mm long, spreading to somewhat deflexed at anthesis, the petaloid segments white. Stamens ca. 15, ca. 4 mm long; anthers 0.7–0.8 mm long. Ovary 5-locular; stigmas 5, ca. 1.5 mm long, \pm spreading and curved. Capsule 7–8 mm long. Seeds ca. 0.6 mm long, obscurely tuberculate. Figure 3B.

Distribution—*Kewa acida* is endemic to St. Helena (Fig. 4A), where it is confined to the southern coastal fringe (Lambdon 2012).

Habitat—Stony or rocky hillsides or cliffs; near sea level to 500 m.

Notes—*Kewa acida* is the species with the largest flowers in the genus (Fig. 3B). According to Lambdon (2012) plants in

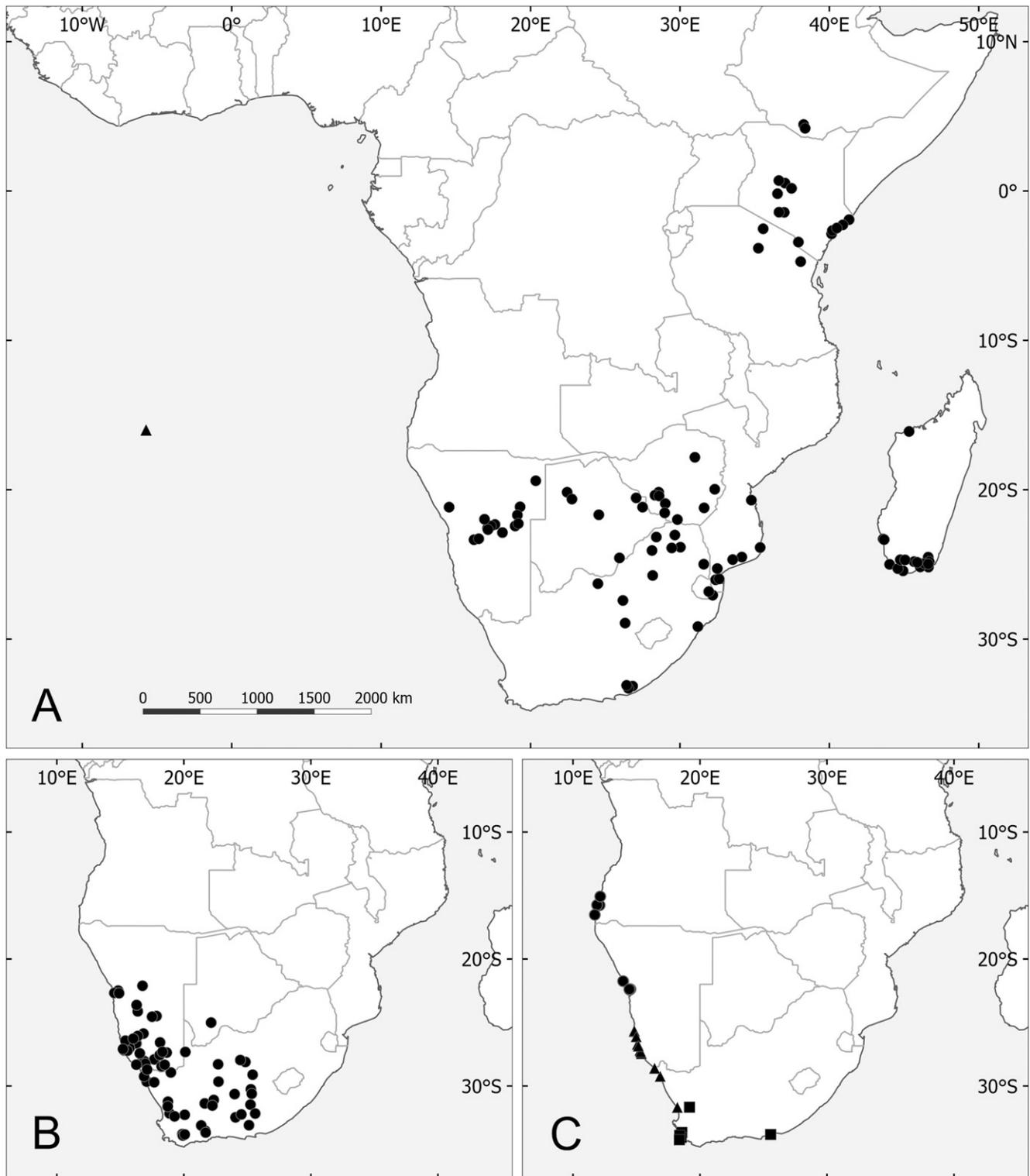


FIG. 4. Distributions of species of *Kewa*. A. *K. acida* (triangle), *K. bowkeriana* (circles). B. *K. salsoloides*. C. *K. angrae-pequenae* (triangles), *K. arenicola* (squares), *K. caespitosa* (circles).

drier locations near sea level tend to be annual, whereas at higher locations affected by mist they tend to be perennate.

Representative Specimens Examined—**St. Helena**. In valley near Sandy Bay, Jan 1954, *Kerr* 3 (BM); Long Range, 21 Feb 2009, *Herian et al.* ECS18 (K).

2. KEWA ANGRAE-PEQUENAE (Friedrich) Christenh., *Phytotaxa* 181: 241. 2014. *Hypertelis angrae-pequenae* Friedrich, *Mitt. Bot. Staatssamml. München* 2: 62. 1955.

TYPE: NAMIBIA. Lüderitz Distr., road to Aussensee, 24 May 1950, *Kinges* 2799 (holotype: M barcode M0107809 [digital image!]; isotypes: M barcode M0107810 [digital image!], PRE barcode PRE0404567 [digital image!]).

Subshrub or shrublet, up to 30 cm tall, ascending, glabrous or sometimes with scattered glandular hairs that

remain as prominent \pm reddish-brown warts at least on pedicels. Leaves \pm narrowly obovate, 6–15 \times 2–4 mm, obtuse to acute at the apex. Inflorescences on peduncles 1–2(–3) cm long, 1–3-flowered; pedicels 5–10(–20) mm long. Flowers with perianth-segments 4–4.5 mm long, \pm deflexed at anthesis, the petaloid ones white to pink. Stamens 12–15, ca. 2.5 mm long; anthers ca. 0.8 mm long. Ovary 5-locular; stigmas 5, ca. 0.8 mm long. Capsule ca. 4 mm long. Seeds 0.7–0.8 mm long, smooth.

Distribution—*Kewa angrae-pequena* is distributed in coastal regions of south-western Namibia and adjacent parts of north-western South Africa (Fig. 4C).

Habitat—Confined to sandy or stony ground; near sea level.

Notes—*Kewa angrae-pequena* agrees with *K. salsoloides* by having flowers with 12–15 stamens and perianth-lobes that are more or less deflexed at anthesis. It differs in its short and wide leaves, in its 1–3 (versus 3–10)-flowered inflorescences with short peduncles, and in its often smooth (versus always warty) pedicels and perianth. Warts on pedicels and perianth seem never to occur in plants from the northern part of the range (Namibia), but are mostly prominent in plants from South Africa.

Representative Specimens Examined—**Namibia**.—KARAS: Lüderitz, near Fjord, 26.70313S, 15.08909E, 20 Apr 2013, Thulin & Larsson 11968 (UPS, WIND); Lüderitz peninsula, kleiner Bogenfels to Essy Bay, 26.72232°S, 15.08922°E, 6 Oct 2006, Kolberg & Tholkes 2062 (K, WIND); Oranjemund, Yacht Basin area, [28.61667°S, 16.43333°E], 17 Feb 1991, Ward 11126 (K, WIND). **South Africa**.—NORTHERN CAPE: Port Nolloth, Holgat, Sep 1929, Schlechter 10902 (K).—WESTERN CAPE: Rob Eiland beach N of Olifants River mouth, 16 Aug 1978, Roux & Ramsey 70 (K).

3. KEWA ARENICOLA (Sond.) Christenh., Phytotaxa 181: 241. 2014. *Hypertelis arenicola* Sond. in Harv. & Sond., Fl. Cap. 1: 145. 1860. TYPE: SOUTH AFRICA. Western Cape, Green Point, Zeyher 619 (lectotype: S no. S05–4763!, designated by Adamson, J. S. Afr. Bot. 24: 58. 1957; isolectotypes: BM! barcode BM000902639, BOL barcode BOL128290 [digital image!], K! barcode K000232006, PRE barcode PRE0404565–0 [digital image!], SAM barcode SAM0036904–0 [digital image!], TCD barcode TCD0002765 [digital image!]).

= *Hypertelis trachysperma* Adamson, J. S. Afr. Bot. 12: 35. 1946. *Kewa trachysperma* (Adamson) Christenh., Phytotaxa 181: 241. 2014. TYPE: SOUTH AFRICA. Western Cape, Zeekoe Vlei, 22 Apr 1946, Walgate 687 (holotype: BOL barcode BOL128291 [digital image!]; isotypes: NBG barcode NBG0021524–0 [digital image!], SAM barcode SAM0057871–0 [digital image!], SAM barcode SAM0074853–0 [digital image!]).

Note on Typification—Adamson (1957) cited Zeyher 619 in S as “type” of *Hypertelis arenicola*. The specimen in S here cited as lectotype has the number 619, but the name of the collector is given as “Dr Pappé.” However, it is well known that Pappé sometimes changed the names of collectors in this way (Gunn and Codd 1981).

Annual herb, with prostrate to ascending stems up to 15 cm long, glabrous. Leaves linear to narrowly oblanceolate, 5–45 \times 1–1.5 mm, glabrous, obtuse to acute at the apex. Inflorescences on peduncles 0–4 cm long, 1–6-flowered; pedicels 2–10 mm long. Flowers with perianth-segments 2–3 mm long, spreading at anthesis, the petaloid segments pink to whitish. Stamens 3–5, ca. 1.5 mm long; anthers ca. 0.4 mm long. Ovary 3–5-locular; stigmas 3–5, ca. 0.4 mm long. Capsule 2–3 mm long.

Seeds ca. 0.6 mm long, almost smooth to distinctly tuberculate throughout or with tubercles close to hilar end only.

Distribution—*Kewa arenicola* is known from the Northern, Western, and Eastern Cape Provinces in South Africa (Fig. 4C).

Habitat—On open muddy or sandy ground, mostly in seasonally wet depressions; near sea level to 630 m.

Notes—Adamson recognized *Hypertelis trachysperma* as distinct from *H. arenicola* on the basis of peduncles shorter (versus longer) than leaves, five (versus three) stamens, and tuberculate (versus smooth) seeds (Adamson et al. 1946; Adamson 1957). These characters were also used by Christenhusz et al. (2014) to separate these species (as *Kewa trachysperma* and *K. arenicola*).

However, the lectotype of *K. arenicola* clearly has tuberculate seeds and this character therefore cannot be used for species distinction in the way proposed by these authors. Some collections of *K. arenicola* in the wider sense taken here indeed have almost smooth seeds, but there is apparently sometimes variation within populations. For example, Hafström s. n. (S), cited as *Hypertelis arenicola* by Adamson (1957) consists of five individuals with tuberculate seeds and one with almost smooth seeds. Furthermore, tubercles are also present to various extents even in seeds that are almost smooth, particularly near the hilar end of the seeds. As for peduncles, there seems to be no correlation between peduncle length and seed ornamentation, and the number of stamens may vary from three to five within a single population, such as the tuberculate-seeded Helme 6500, where flowers with three, four, or five stamens were recorded.

The gynoecium in *K. arenicola* is 3-, 4- or 5-merous and may vary within populations and even within a single plant, such as in one of the individuals of Acock 3916 (S). In all other species of *Kewa* the gynoecium is consistently 5-merous.

Acocks 19199, the only collection seen from Northern Cape, consists of plants with particularly short peduncles, varying from 0 to just a few mm. A photograph of a plant from N of Nieuwoudtville, also in Northern Cape, communicated by Nick Helme, also shows very short or non-existing peduncles, indicating a geographically correlated variation in this respect.

Representative Specimens Examined—**South Africa**.—NORTHERN CAPE: Calvinia, Lokenburg, 16 Mar 1957, Acocks 19199 (K).—WESTERN CAPE: Paarden Island, 22 Dec 1934, Acock 3916 (S); Cape Point Nature Reserve, 0.6 km N Olifantsbos Bay, [34.25069°S, 18.38153°E], 11 Feb 2010, Helme 6500 (NBG).—EASTERN CAPE: Uitenhage, near Redhouse, Aug 1912, Paterson 2219 (K).

4. KEWA BOWKERIANA (Sond.) Christenh., Phytotaxa 181: 241. 2014. *Hypertelis bowkeriana* Sond. in Harv. & Sond., Fl. Cap. 1: 145. 1860. TYPE: SOUTH AFRICA, Cape Province, Albany, Bowker s. n. (holotype: K! barcode K000232011; isotype: S! no. S05–5021).

= *Pharnaceum suffruticosum* Baker, J. Linn. Soc. Bot. 20: 151. 1883, nom. illeg. (non Pallas, Reise Russ. Reich. 3: 716. 1776). *Hypertelis suffruticosa* Adamson, J. S. Afr. Bot. 24: 55. 1957. *Kewa suffruticosa* (Adamson) Christenh., Phytotaxa 141: 241. 2014. TYPE: MADAGASCAR. Ambongo, 16 Feb 1841, Pervillé 647 (holotype: K! barcode K000232013; isotypes: P! barcodes P04999563, P04999566).

= *Mollugo suffruticosa* Peter, Abh. Ges. Wiss. Göttingen, n.f. 13(2): 54. 1928. TYPE: TANZANIA. Pare Distr., NW of Buiko towards Hedaru, 10–11 Jun 1926, Peter 41190 (holotype: B barcode B100159478 [digital image!]).

= *Mollugo suffruticosa* Peter forma *annua* Peter, Fl. Deutsch Ost-Afr. 2(2): 29. 1932. TYPE: TANZANIA. Lushoto Distr., Lake Manga, Peter 10864 (holotype: B, destr.).

Perennial herb or subshrub, up to 30 cm tall, sometimes forming carpets by means of prostrate stems and ascending branches, with scattered glandular hairs that often remain as prominent \pm reddish-brown warts, particularly on pedicels and outside of perianth. Leaves linear, 10–75 \times 0.5–1 mm, obtuse to subacute at the apex. Inflorescences with peduncles 3–10 cm long, 2–8-flowered; pedicels 2–10 (–20) mm long. Flowers chasmogamous or sometimes cleistogamous; perianth-segments 3–4 mm long, erect or spreading, rarely becoming deflexed at anthesis, the petaloid segments white or sometimes pink or with pink tips. Stamens 5, 2–3 mm long; anthers 0.4–0.6 mm long. Ovary 5-locular; stigmas 5, ca. 0.5 mm long, spreading and curved or \pm appressed to top of ovary. Capsule 3.5–5 mm long. Seeds 0.5–0.6 mm long, smooth. Chromosome number $n = 8$ (Ratter 1968). Figure 3C, D.

Distribution—*Kewa bowkeriana* is the most widespread species in the genus and has been recorded from Ethiopia, Kenya, Tanzania, Zimbabwe, Mozambique, Swaziland, Botswana, Namibia, South Africa, and Madagascar (Fig. 4A). The distribution is not continuous, but shows marked disjunctions between the arid areas in eastern and southern Africa and between southern (Toliara) and northwestern Madagascar (Mahajanga). The species is well established and widespread in Toliara, whereas only two collections seem to have been made in Mahajanga, *Pervillé* 647 (type of *Pharnaceum suffruticosum*) from 1841 and *Perrier de la Bâthie* 1659 from 1903. It is quite possible that the Mahajanga population reached Madagascar from East Africa and the Toliara population from southern Africa.

Habitat—In open situations, mostly on sandy or gravelly, saline ground, such as in salt pan depressions and at margins of mangroves; near sea level to 1850 m.

Notes—*Kewa bowkeriana* is well supported as monophyletic only in the BEAST analysis, whereas it forms an unsupported clade in the ML and MrBayes analyses (Fig. 1). The species (with samples from Namibia, South Africa and Madagascar) is also supported as monophyletic in the ITS tree (Fig. S2). However, in all combined analyses (Fig. 1), the two samples from Namibia form a strongly supported pair, as do the two samples from South Africa (KwaZulu-Natal) and Madagascar.

This molecular differentiation within *K. bowkeriana* is not, as far as we have been able to detect, correlated with any corresponding morphological differentiation. Instead, *K. bowkeriana* is relatively uniform over its large and disjunct area of distribution. It differs from all the other species in the genus by its very narrow, only 0.5–1 mm wide, leaves. It agrees with *K. salsoloides* in usually having warts on pedicels and outside of the perianth (Fig. 3C, D, but differs from this species, apart from leaf width, by having flowers with 5 (versus 12–15) stamens and usually white (versus pink) petaloid perianth-segments (Fig. 3C). The perianth-segments are mostly erect or spreading in *K. bowkeriana* (Fig. 3C), but they may occasionally be more or less deflexed at anthesis as in *K. salsoloides*.

Christenhusz et al. (2014) separated *K. salsoloides* from *K. bowkeriana* (and from all other species of *Kewa* except *K. acida*) by its warty (versus smooth) peduncles, pedicels, and perianth. This is a mistake repeated from Adamson (1957). Warts in the inflorescence region are normal in *K. bowkeriana* and are sometimes present also in *K. caespitosa* and *K. angrae-pequena*.

Representative Specimens Examined—**Ethiopia**.—SIDAMO: El Sod, [4.2°N, 38.38333°E], 15 Nov 1952, *Gillett* 14270 (K). **Kenya**.—LAIKIPIA DISTR.: 67 km N of Rumuruti on Maralal road, [0.7°N, 36.61667°E], 14 Nov 1977, *Carter & Stannard* 370 (K).—LAMU DISTR.: 2 km SE of Kibauni, N of Kipini, 4 Mar 1977, *Hooper & Townsend* 1186 (K). **Tanzania**.—MBULU/SINGIDA DISTR.: Yaida valley, Endashi, 19 Jan 1970, *Richards* 25187 (K).—LUSHOTO DISTR.: Lake Manka, Jun 1967, *Procter* 3679 (K). **Zimbabwe**.—GWANDA DISTR.: near Sundowner Hotel, Gwanda, 26 Mar 1959, *Drummond* 6038 (K).—MATOBO DISTR.: 12 km SE of Figtree on Matopos road, 29 Jan 1974, *Mavi* 1495 (K). **Mozambique**.—GAZA: Massingir Distr., 1 km W of Zulo, 7 Dec 1981, *White* 46 (K).—MAPUTO: Moamba, 15 km on road to Chinhanganine, 31 Oct 1980, *de Konig & Nuvunga* 8589 (K). **Botswana**.—NGAMILAND: near Tsau, 18 Mar 1961, *Richards* 14775 (K).—SOUTH EAST: Gaborones Dam, 25 Aug 1966, *Gillett* 17470 (K). **Namibia**.—OTJOZONDJUPA: Okahandja, 10 Aug 1934, *Dinter* 7789 (WIND).—KHOMAS: Windhoek, Avis Dam, 22.57790°S, 17.12539°E, 9 Apr 2013, *Thulin & Larsson* 11945 (UPS, WIND). **South Africa**.—LIMPOPO: 24 km W of Pietersburg, 27 Jan 1962, *van Vuuren* 1366 (K).—KWAZULU-NATAL: Lower Tugela valley below Maqumbi, 28 Feb 1963, *Edwards* 3054 (K); E of Ingwavuma, 27.06338°S, 32.18979°E, 5 Apr 2013, *Thulin et al.* 11943 (NU, UPS).—EASTERN CAPE: 35 km from Grahamstown on Cradock road, Sep 1929, *Dyer* 2109 (K). **Madagascar**.—MAHAJANGA: near Soalala (Ambongo), Oct 1903, *Perrier de la Bâthie* 1659 (P).—TOLIARA: NW of Cap Sainte-Marie towards Lavanono, 8 Mar 1955, *Humbert & Capuron* 29333 (G, HBG, K, MO, P, TAN, WAG); E of Amboasary, 7 km after turning to Tsimelaha, 24.9721°S, 46.6189°E, 9 Apr 2010, *Thulin & Razafindrala* 11819 (TAN, UPS).

5. KEWA CAESPITOSA (Friedrich) Christenh., *Phytotaxa* 181: 241. 2014. *Hypertelis caespitosa* Friedrich, *Mitt. Bot. Staatssamml. München* 2: 64. 1955. TYPE: NAMIBIA. Swakopmund – Cap Cross, 14 Mar 1935, *Dinter* 8471 (holotype: M barcode M0107811 [digital image!]; isotypes: BM! barcode BM000902641, BOL barcode BOL128289 [digital image!], K! barcode K000232010, P! barcode P00461734, PRE barcode PRE0404566–0 [digital image!], S! no. S-G-7085).
= *Pharnaceum salsoloides* Burch. var. *mossamedensis* Welw. ex Hiern, *Cat. Afr. Pl. Welw.* 1: 418. 1898. *Hypertelis salsoloides* (Burch.) Adamson var. *mossamedensis* (Welw. ex Hiern) Gonç., *Consp. Fl. Angol.* 4: 321. 1970. TYPE: ANGOLA. Mossamedes, near the town of Mossamedes, Jul 1859, *Welwitsch* 2381 (lectotype: BM! barcode BM000902642, designated by Gonçalves (1970: 321); isolectotypes: COI barcode COI00070557 [digital image!], K!, LISU barcode LISU214655 [digital image!], LISU barcode LISU214656 [digital image!], M barcode M0107812 [digital image!]).

Note on Typification—Gonçalves (1970) cited *Welwitsch* 2381 in BM as “holótipo” of *Pharnaceum salsoloides* var. *mossamedensis*. This statement is here regarded as a lectotypification in accordance with ICBN, Art. 9.8 (McNeill et al. 2012).

Perennial herb or subshrub, up to 15 cm tall, usually with many decumbent to ascending stems, glabrous or sometimes with a few scattered glandular hairs that remain as prominent \pm reddish-brown warts on pedicels and outside of perianth. Leaves linear to narrowly oblanceolate 5–30 \times 1–2.5 mm, obtuse to subacute at the apex. Inflorescences with peduncles 1–7 cm long, 2–8-flowered; pedicels 4–18 mm long. Perianth-segments 3–5 mm long, \pm deflexed at anthesis, the petaloid segments pink. Stamens 5–9, 2–3 mm long; anthers 0.4–0.6 mm long. Ovary 5-locular; stigmas 5, 0.5–0.8 mm long, \pm spreading and curved. Capsule ca. 4 mm long. Seeds ca. 0.6 mm long, smooth.

Distribution—*Kewa caespitosa* is distributed in coastal regions of southwestern Angola and west-central Namibia (Fig. 4C).

Habitat—In open situations on sandy or stony ground; near sea level to 150 m.

Notes—*Kewa caespitosa* is close to *K. salsoloides* from which it differs mainly in the fewer stamens (5–9 versus 12–15) and by mostly lacking warts on pedicels and perianth. In a large population in Namibia studied in 2013 (Thulin *et al.* 11949) the number of stamens was found to vary continuously from 5 to 9 in different plants, and sometimes the stamen number varied within individuals. Warts on pedicels were mostly lacking, but varied in some plants from few to several. A similar variation was reported by Hiern (1898) from Angola in the protologue of *Pharnaceum salsoloides* var. *mossamedensis*. Typical *K. salsoloides* is not known from Angola, but in Namibia *K. salsoloides* and *K. caespitosa* may grow in close proximity but, as far as known, without any intergradation. Species rank for these two taxa therefore seems appropriate, although they are not clearly separated in the molecular analyses.

Representative Specimens Examined—Angola.—NAMIB: Pinda, R. Coroca, 24 May 1937, Exell & Mendonça 2195 (BM); near Farol, 27 Dec 1955, Torre 8324 (BM). Namibia.—ERONGO: just N of Wlotzkasbaken, 22.38825°S, 14.44137°E, 10 Apr 2013, Thulin *et al.* 11949 (UPS, WIND); ca. 8 km E of Wlotzkasbaken, 25 Jun 2006, 22.38506°S, 14.52678°E, 25 Jun 2006, Kolberg & Tholkes 2018 (K, WIND).

6. KEWA SALSOLOIDES (Burch.) Christenh., Phytotaxa 181: 241. 2014. *Pharnaceum salsoloides* Burch., Trav. Int. S. Afr. 1: 286. 1822. *Hypertelis salsoloides* (Burch.) Adamson in J. S. Afr. Bot. 24: 52. 1957. TYPE: SOUTH AFRICA. Calvinia, between Zak R. and Kopjesfontein, Sep 1811, Burchell 1508 (holotype: K! barcode K000232012).

Pharnaceum verrucosum Eckl. & Zeyh., Enum. Pl. Afr. Austral. 2: 286. 1836. *Hypertelis verrucosa* (Eckl. & Zeyh.) Fenzl, Ann. Wiener Mus. Naturgesch. 2: 262. 1839. TYPE: SOUTH AFRICA. “ad flumen Gauritzrivier”, Ecklon & Zeyher 1826 (lectotype: S! no. S05–4626, designated here; isolectotypes: C barcode C10000084 [digital image!], TCD barcode TCD0002801 [digital image!], W barcode W0009847 [digital image!], W barcode W0009848 [digital image!]).

Hypertelis verrucosa (Eckl. & Zeyh.) Fenzl var. *laevigata* Sond. in Harv. & Sond., Fl. Cap. 1: 144. 1860. TYPE: SOUTH AFRICA. Sondag’s rivier, Drège s. n. (not located).

Note on Typification—Adamson (1957: 52) cited Zeyher 615 in S as “type” of *Pharnaceum verrucosum*. However, the only collection cited in the protologue is Ecklon & Zeyher 1826, thus Adamson’s action cannot be regarded as a valid lectotypification.

Perennial herb or subshrub, up to 40 cm tall, ascending, with glandular hairs that remain as prominent ± reddish-brown warts, particularly on peduncles, pedicels, and outside of perianth. Leaves linear to narrowly oblanceolate, 5–40 × 1–3 mm, obtuse to acute at the apex. Inflorescences with peduncles 1–15 cm long, 3–10-flowered; pedicels 6–30(–40) mm long. Flowers with perianth-segments 3–5 mm long, ± deflexed at anthesis, the petaloid segments pink. Stamens 12–15, 2–4 mm long; anthers 0.6–1 mm long. Ovary 5-locular; stigmas 5, 0.6–1.5 mm long, ± spreading and curved. Capsule 4–6 mm long. Seeds 0.6–0.8 mm long, smooth. Figures 2, 3A.

Distribution—*Kewa salsoloides* is known with certainty only from Namibia, southern Botswana, and South Africa (Fig. 4B). Records of *Hypertelis salsoloides* var. *mossamedensis* from Mozambique in Gonçalves (1978) refer to material of *K. bowkeriana*. Adamson (1957) previously recorded *H. salsoloides* from Botswana (Bechuanaland), but the cited specimen, *van Son* s. n. from near Gaborones, is *K. bowkeriana*. Adamson

(1957) also mentioned unspecified occurrences of *H. salsoloides* in Zimbabwe and indeed one of two specimens of the collection Rogers 5520 (K) from “Salisbury” is this species (the other one being *K. bowkeriana*). As all other material of *Kewa* seen from Zimbabwe, including the area around Salisbury (now Harare), represents *K. bowkeriana*, this particular specimen is almost certainly mislabeled.

Habitat—In open situations, mostly on sandy or gravelly saline ground, often in seasonally wet depressions; near sea level to 1700 m.

Notes—*Kewa salsoloides* is a variable species that can be recognized by its 3–10-flowered inflorescences with conspicuous warts on pedicels and outside of perianth, and by its pink flowers with more or less deflexed perianth-lobes and 12–15 stamens. For differences from *K. angrae-pequena*, *K. bowkeriana* and *K. caespitosa*, see under these species.

Representative Specimens Examined—Namibia.—OTJOZONDJUPA: Gross Barmen, 22.11332°S, 16.74573°E, 14 Apr 2013, Thulin *et al.* 11956 (UPS, WIND).—KARAS: Klein Aus, 26.65948°S, 16.23516°E, 18 Apr 2013, Thulin & Larsson 11963 (UPS, WIND). Botswana.—KGALAGADI: Mabuasehube pan, 12 Mar 1976, Vahrmeijer 3071 (K, WIND). South Africa.—NORTHERN CAPE: Farm Klein Pella between Springputs and Grootberg, 15 May 2000, Snijsman 1744 (K).—WESTERN CAPE: near Robertson, 11 Jun 1955, van Niekerk 375 (K).—EASTERN CAPE: Toekomst, Somerset East, Sunday’s R. valley, 5 Nov 1930, Long 219 (K).—FREE STATE: 39 km from Philippolis on road to Luckhoff, Farm Swartfontein, 1 Mar 1981, Herman 456 (K).

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AUTHOR CONTRIBUTIONS

MT did the taxonomic work and drafted the paper, AJM did the lab-work, AL did the phylogenetic analyses, and all authors took part in the interpretation of the data and the final preparation of the manuscript.

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APPENDIX 1. Taxa sampled for the phylogenetic analyses with voucher information and GenBank accession numbers. Accessions are grouped by family, with Kewaceae first. Information is listed as follows: species name and author(s), country and number (if there is more than one accession of the species from that country), collector and number (with herbarium acronym in parentheses), GenBank numbers for *trnK-matK*, *rbcL*, and ITS, when available. Sequences generated for this study are marked with an asterisk. A dash indicates a missing sequence.

Kewaceae: *Kewa acida* (Hook.f.) Christenh., St. Helena 1 (Lot's Wife), *Lambdon s. n.* (UPS, photo), MH019260*, —, MH018120*; St. Helena 2 (Horse's Head), *Lambdon s. n.* (UPS, photo), MH019262*, —, MH018122*.

Kewa angrae-pequenae (Friedrich) Christenh., Namibia 1, *Thulin & Larsson* 11967 (UPS), MH019258*, —, MH018117*; Namibia 2, *Thulin & Larsson* 11968 (UPS), MH019259*, —, MH018118*.

Kewa arenicola (Sond.) Christenh., South Africa, *Helme* 6500 (NBG), —, —, MH018127*.

Kewa bowkeriana (Sond.) Christenh., Namibia 1, *Giess* 171 (NY), FN825761, FN824476, —; Namibia 2, *Thulin & Larsson* 11945 (UPS), MH019263*, —, MH018123*; South Africa, KwaZulu-Natal, *Thulin et al.* 11943 (UPS), MH019261*, —, MH018121*; Madagascar, *Thulin & Razafindrala* 11819 (UPS), —, —, MH018126*.

Kewa caespitosa (Friedrich) Christenh., Namibia 1, *Thulin et al.* 11948 (UPS), MH019264*, —, MH018124*; Namibia 2, *Thulin et al.* 11949 (UPS), MH019265*, —, MH018125*.

Kewa salsoloides (Burch.) Christenh., South Africa, *Ogburn* 143 (BRU), FN825762.1, FN824478.1, —; Namibia 1, *Thulin et al.* 11956 (UPS), MH019266*, —, MH018128*; Namibia 2, *Thulin & Larsson* 11963 (UPS), MH019257*, —, MH018116*.

Aizoaceae: *Conicosia pugioniformis* (L.) N.E.Br., South Africa, *Klak* 1570 (BOL-matK only), KF132628.1, JQ412345, —. **Galenia africana** L., JQ024963.1, JQ025048, —. **Gibbaeum heathii** (N.E.Br.) L. Bolus, South Africa, *Klak* 1125 (BOL), KF132691.1, —, —. **Mesembryanthemum crystallinum** L., HM850877.1, HM850175, —. **Sesuvium portulacastrum** (L.) L., KC185420.1, FN868308, —. **Tetragonia tetragonoides** (Pall.) Kuntze, HM850882.1, HM850395, —. **Amaranthaceae:** *Spinacia turkestanica* Iljin, *Fuentes* 181 (B), HE855620.1, —, —. **Anacampserotaceae:** *Anacampseros kurzii* Bacigalupo, *Leuenberger & Eggl* 4217 (ZSS-matK only), DQ855853.1, —, —. **Barbeuiaceae:** *Barbeuia madagascariensis* Steud., AY042552.1, GQ497673, —. **Basellaceae:** *Basella alba* L., JQ844148.1, M62564, —. **Cactaceae:** *Opuntia phaeacantha* Engelm., FN997327.1, —, —. **Pereskia aculeata** Mill., HM041757.1, AY875229, —. **Caryophyllaceae:** *Dianthus laingsburgensis* S.S. Hooper, GU441169.1, —, —. **Corbichoniaceae:** *Corbichonia decumbens* (Forssk.) Exell, Botswana, *Aye* 1074 (NY), FN825760, FN824475, —; South Africa, KwaZulu-Natal, *Thulin et al.* 11942 (UPS), KT950946, —, MH018119*.

Didiereaceae: *Alluaudia dumosa* (Drake) Drake, Madagascar, *Stone s. n.*, HQ620839.1, —, —. **Gisekiaceae:** *Gisekia africana* (Lour.) Kuntze, Namibia, *Thulin et al.* 11955 (UPS), KT950945, —, —. **Halophytaceae:** *Halophytum ameghinoi* Speg., *Chase* 1753 (K-rbcL only), AY514852.1, AJ403024, —. **Limeaceae:** *Limeum aethiopicum* Burm.f.,

Namibia, *Thulin & Larsson* 11957 (UPS), KT950934, —, —. *Limeum dinteri* G.Schellenb., Namibia, *Thulin & Larsson* 11959 (UPS), KT950935, —, —. **Lophiocarpaceae:** *Lophiocarpus polystachyus* Turcz., Namibia 1, *De Winter* 3156 (K), AY042611, —, —; Namibia 2, Karas Region, *Thulin & Larsson* 11958 (UPS), KT950947, —, MH018129*. **Macarthuriaceae:** *Macarthuria australis* Hügel ex Endl., Australia, *Lepschi & Brims* 1943 (G), FN825765.1, FN824479.1, —. **Molluginaceae:** *Adenogramma glomerata* (L.f.) Druce, South Africa 2, *Fries* 25-9-20 (NY), FN825687.1, FN824406, —. *Adenogramma mollugo* Rchb., South Africa, *Pillans* 10526 (NY), FN825690, FN824409, —. *Coelanthum semiquinquefidum* (Hook.) Druce, South Africa, *Wright* 1853 (NY), FN825759, FN824411, —. *Glinus lotoides* L., USA, *Errter* 8854 (NY), FN825692, —, —. *Glinus oppositifolius* (L.) Aug.DC., Taiwan, *Huang & Huang* 14175 (NY), FN825695, FN824415, —. *Glinus setiflorus* Forssk., Kenya, *Burney & al.* T46 (NY), FN825698, FN824418, —. *Hypertelis cerviana* (L.) Thulin, Namibia, *Thulin et al.* 11954 (UPS), KT950944, —, —. *Hypertelis fragilis* (Wawra) Thulin, Angola, *Ward & Ward* 79 (K), FN825724, FN824442, —. *Hypertelis spergulacea* E.Mey. ex Fenzl, Namibia 1, *Thulin & Larsson* 11960 (UPS), KT950931, —, —; Namibia 2, *Thulin & Larsson* 11962 (UPS), KT950932, —, —; Namibia 3, *Giess et al.* 5366 (K), FN825700, FN824420, —; South Africa, *Acocks* 19256 (K), FN825701, FN824421, —. *Hypertelis umbellata* (Forssk.) Thulin, Ethiopia, *Thulin et al.* 11211 (UPS), FN825713, FN824433, —. *Mollugo brasiliensis* Thulin & Harley, Brazil, *Guedes et al.* PCD5162 (K), KT950938, —, —. *Mollugo disticha* (L.) Ser., Sri Lanka, *Lundqvist* 11379 (UPS), KT950942, —, —. *Mollugo ulei* (Pilger) Thulin, Brazil, *Harvey* 19007 (SPF), FN825699, FN824419, —. *Mollugo verticillata* L., USA, *Sage & Sage* 8-2007 (TRT), FN825740, FN824459, —. *Paramollugo angustifolia* (M.G.Gilbert & Thulin) Thulin, Somalia, *Thulin et al.* 7606 (UPS), FN825702, —, —. *Paramollugo decandra* (Scott Elliot) Thulin, Madagascar, *Croat* 30852

(K), FN825718, FN824437, —. *Paramollugo nudicaulis* (Lam.) Thulin, Somalia, *Thulin & Bashir Mohamed* 6759 (UPS), FN825730, FN824448, —. *Pharnaceum elongatum* (DC.) Adamson, South Africa, *Ogburn* 153 (BRU), FN825746, FN824464, —. *Pharnaceum lamuginosum* J.C.Manning & Goldblatt, South Africa, *Ogburn* 161 (BRU), FN825752, FN824469, —. *Pharnaceum lineare* L.f., South Africa, *Helme* 5887 (NBG), KT950943, —, —. *Pharnaceum reflexum* Eckl. & Zeyh., South Africa, *Taylor* 1162 (NY), FN825751, —, —. *Polpoda capensis* C.Presl, South Africa, *Acocks* 17405 (CANB), FN825753, FN824470, —. *Psammotropha obovata* Adamson, South Africa, *Hilliard & Burt* 7045 (K), FN825754, FN824471, —. *Psammotropha quadrangularis* Fenzl, South Africa, *Ogburn* 160 (BRU), FN825755, FN824472, —. *Suessenguthiella scleranthoides* (Sond.) Friedrich, Namibia, *Thulin & Larsson* 11964 (UPS), KT950936, —, —. *Trigastrotheca molluginea* F.Muell., Australia, *Telford* 11746 (CANB), FN825725, FN824443, —. *Trigastrotheca stricta* (L.) Thulin, Australia, *Lazarides & Adams* 326 (CANB), FN825736, FN824454, —. **Montiaceae:** *Lewisia longipetala* (Piper) S.Clay, *Edwards* 141 (BRU-matK only), HQ620876.1, —, —. **Nyctaginaceae:** *Bougainvillea glabra* Choisy, JQ844141.1, M88340, —. *Guapira discolor* (Spreng.) Little, KJ522684.1, KJ522686, —. *Mirabilis jalapa* L., FN868307.1, HM850179, —. **Petiveriaceae:** *Petiveria alliacea* L., GQ429080.1, AJ402987, —. *Rivina humilis* L., AY514850.1, M62569, —. **Phytolaccaceae:** *Phytolacca americana* L., *Qiu* 94109 (IND-matK only), DQ401362.1, HM850257, —. **Portulacaceae:** *Portulaca amilis* Speg., *Ogburn* 11 (BRU-matK only), HQ620886.1, —, —. **Sarcobataceae:** *Sarcobatus vermiculatus* (Hook.) Torr., AY042652.1, AF132088, —. **Simmondsiaceae:** *Simmondsia chinensis* (Link) C.K.Schneid., AF204863.1, AF093732, —. **Stegnospermataceae:** *Stegnosperma halimifolium* Benth., HQ878442.1, M62571, —. **Talinaceae:** *Talinum fruticosum* (L.) Juss., *Ferguson* 848 (ZSS-matK only), DQ855844.1, KJ380905, —.