

Curio alliance (Asteraceae: Senecioneae) revisited

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Summary: Curio alliance is far distant from the genuine *Senecio*. The genus *Curio* looks like monophyletic, but *C. acaulis* and *C. articulatus* must be excluded. The former species is nested among yellow-flowered members of Curio alliance which still have to be treated taxonomically. *Curio articulatus* is specific enough to be segregated in the separate new genus *Baculellum*. *Curio kleiniiformis* is a cultivated hybrid species between *Senecio tropaeolifolius* and some species of genuine *Curio*, the latter one has to be revealed. *C. kleiniiformis* should conventionally be retained in the genus *Curio*. Inclusion of *Senecio corymbiferus* in *Curio* needs further examinations.

Keywords: Senecioneae, *Senecio*, *Curio*, *Baculellum*, *Curio kleiniiformis*, hybrid attraction, gen. nov.

Taxonomy of the tribe Senecioneae has still been aimed mainly at delimiting natural genera and rearranging multitudinous and enormously diverse groundsels into these genera (JEFFREY et al. 1977; BARKLEY 1985a; BREMER 1994; KNOX & PALMER 1995; PELSNER et al. 2007; NORDENSTAM et al. 2009). The succulent groundsels are a small, distinctive, but highly heterogeneous group (JACOBSEN 1970; JEFFREY 1986; ROWLEY 2002). They also need to be rearranged rationally into several natural genera. Some segregates of the succulent groundsels were recognized by JACOBSEN (1970), JEFFREY (1986) and ROWLEY (2002).

JEFFREY (1986) segregated 25 leaf-succulent groundsels and one stem-succulent into the section *Rowleyani* C. Jeffrey considering *Senecio rowleyanus* H. Jacobsen as type species. However, he could not nest this section in any subgenus of *Senecio* L. accepted that time. The majority of these species are noteworthy to have been described as species of *Cacalia* L. or *Kleinia* Mill. (Appendix 1) or to have been excluded from the genus *Senecio* or to have been synonymized with species of other genera (Appendix 2). Admittedly, relationships between *Cacalia*, *Kleinia* and *Senecio* were differently interpreted. *Kleinia* was repeatedly included into *Senecio* s.l. (SCHULTZ 1845; HOFFMANN 1894; MUSCHLER 1909), though it was originally considered a constituent of *Cacalia* L. (LINNÉ 1753) and was later kept as close relative of the latter genus (MILLER 1754; HAWORTH 1812; DE CANDOLLE 1837; HARVEY & SONDER 1864–1865). MILLER (1768) placed *Kleinia* back into *Cacalia*. The genus *Cacalia* was usually considered distantly related to *Senecio*, but BENTHAM & HOOKER (1873) included it (as well as *Kleinia*) into *Senecio*.

The section *Rowleyani* was later combined with sections *Paucifolii* Harv., *Peltati* (Mischl.) C. Jeffrey and *Kleinioidei* (DC.) Harv. and with *incertae sedis* species *Senecio angulatus* L. f., *S. dieterlenii* E. Phillips and *S. pleistocephalus* S. Moore to form the artificial subgenus *Kleinioidei* (JEFFREY 1992), which has never been described validly. [*Senecio angulatus* L. f. was placed earlier in sections *Glaberrimi* DC. (DE CANDOLLE 1837), *Scandentes* Harv. (HARVEY & SONDER 1864–1865; MUSCHLER 1909) or *Kleinioidei* DC. (JEFFREY 1986). *S. dieterlenii* E. Phillips was synonymized with *S. rhomboideus* Harv. of section *Paucifolii* Harv. (WELMAN 2003).]

Of 26 species originally included in the section *Rowleyani* (JEFFREY 1986), *S. aizoides* (DC.) Sch. Bip., *S. chordifolius* Hook. f., *S. hanburyanus* Dietr. and *S. mandralisca* (Tineo) H. Jacobsen were re-interpreted as subspecies of *S. talinoides* (DC.) Sch. Bip. (ROWLEY 1990) and *S. vitalis* N.E. Br. was considered synonym of *S. talinoides* ssp. *cylindricus* (A. Berger) G.D. Rowley (ROWLEY 2002).

HEATH (1997) raised Jeffrey's section *Rowleyani* to separate genus *Curio* P.V. Heath. He considered neither infrageneric systematics of this genus nor its affinities, but he included *Curio cuneifolius* (L.) P.V. Heath and the cultural hybrid *C. × peregrinus* (G. Kunkel) P.V. Heath (HEATH 1999) which had been described as *Cacalia cuneifolia* L. (LINNÉ 1767) and *Kleinia × peregrina* G. Kunkel (KUNKEL 1988), respectively. *Curio pondoensis* (van Jaarsv. & A.E. van Wyk) J.C. Manning (MANNING 2013) and *C. muirii* (L. Bolus) van Jaarsv. (VAN JAARSVELD & VISAGIE 2015), former species of *Senecio*, were the latest additions to the genus *Curio*.

Though validly published, the genus *Curio* was usually ignored by authors of surveys of (Southern) African floras (GOLDBLATT & MANNING 2000; WELMAN 2003; GOLDBLATT et al. 2005; KLAASSEN & KWEMBEYA 2013; APD 2016) and succulent plants (ROWLEY 2002). A possible reason for the disregard of *Curio* could be due to the highly bizarre and ephemeral journal, where it had been published. The main reason was surely that taxonomists had failed to elaborate plain and effective morphological criteria to delimit genera of succulent groundsels (LINNÉ 1753; LINNÉ f. 1781; MILLER 1754, 1768; HAWORTH 1812; DE CANDOLLE 1837; SCHULTZ 1845; BENTHAM & HOOKER 1873; HARVEY & SONDER, 1864–1865; HOFFMANN 1894; MERXMÜLLER 1954, 1965; JEFFREY et al. 1977; NORDENSTAM 1978; JEFFREY 1979a, 1986, 1992; BARKLEY 1985a, b; BREMER 1994). All these groundsels including species of *Curio* and *Kleinia* were even suggested to be placed in 'huge *Senecio*' and arranged there in formal groups based on similarities in few conspicuous characters (ROWLEY 2002).

Molecular phylogenetics has drastically been changing patterns of relationships of Senecioneae members which are still to be converted into a comprehensive taxonomy of the tribe. The genus *Curio* was nested near *Kleinia* in Gynuroid clade of Senecioninae (Fig. 1) in the tremendous investigation of Senecioneae by PELSER et al. (2007), which seemingly covers all suprageneric taxa and most generic assemblages of this tribe. The Gynuroid clade was differently located in ITS-, cpDNA- and combined ITS/cpDNA-based cladograms, but it was invariably distant from the core *Senecio*.

Both cpDNA and ITS showed heterogeneity of Heath's *Curio* (STÄHELI 2006; PELSER et al. 2007; MALENKOVA et al. 2014), but it was neither supplemented with certain species to become monophyletic nor divided into monophyletic taxa.

Materials and methods

Taxon sampling. Appendix 3 shows species and samples dealt with. Only 13 out of 25 recently accepted species of the genus *Curio* were accessible for our investigation. The taxa which are members of the *Curio* alliance were chosen on the basis of PELSER et al. (2007: Fig. 1). *Iranecio* spp. were used as representatives of subtribe Adenostylinae because the latter one was considered a sister to the Gynuroid clade (PELSER et al. 2007) and included *Adenostyles alpina* (L.) Bluff & Fingerh., the type species of Linnaean *Cacalia* (RYDBERG 1924; JEFFREY 1979b). *Dendrosenecio* spp. represented early divergent clade of (Gynuroid – Adenostylinae) – Cineraria lineage. Genuine



Figure 1. Curio alliance in the tribe Senecioneae. Excerpt from PELSER et al. 2007.

Senecio was represented by *Senecio vulgaris* and *S. viscosus* of *Senecio* s. strictiss. and *S. nemorensis* and *S. telekii* of the *Senecio* s. str. clade (PELSER et al. 2007).

Othonna spp. were also sampled, because few species of present *Curio* had been described as members of the genus *Othonna*, though the latter one had been shown to be far distant from the Curio alliance and even from *Senecio* s. latiss. (BENTHAM & HOOKER 1873; HOFFMANN 1894; JEFFREY 1986, 1992; KNOX & PALMER 1995; PELSER et al. 2007; NORDENSTAM et al. 2009). *Othonna* L. was recently divided into *Othonna* s. str. and *Crassothonna* B. Nord. (NORDENSTAM 2012). Both of these genera are represented in our investigation.

Few species of *Curio* were originally kept as members of *Cacalia* (LINNÉ 1753, 1767; LINNÉ f. 1781). The latter genus was shown to be extremely heterogeneous. It was drastically reshaped. Even the name *Cacalia* was rejected (BRUMMITT 1998) and its species were distributed among distantly related genera (RYDBERG 1924; KING & DAWSON 1975; BREMER 1994; SHAW 2008; NORDENSTAM et al. 2009). Some segregates of former *Cacalia* were included in our analysis, i.e. some species of *Hasteola*, *Parasenecio* and *Syneilesis*.

JEFFREY (1992) considered his section *Rowleyani* to be nearest related to his section *Kleinioidei*, which consisted of 2 species groups. Only the group of glabrous species was nested in Gynuroid clade (PELSER et al. 2007). This group was represented by *S. meuselii*, *S. melastomifolius* and *S. crassissimus* in our investigation. The pubescent species of the second group was segregated into separate genus *Caputia* (NORDENSTAM & PELSER 2012) which was placed in the *Senecio* medley-woodii–*Brachyglottis* clade far distant from the Curio alliance (PELSER et al. 2007). *Caputia medley-woodii*, *C. pyramidata*, *C. scaposa* and *C. tomentosa* as well as species of *Acrisione*, *Brachyglottis*, *Haastia*, *Papuacalia* and *Traversia* were sampled from this clade.

Tussilago farfara L. was used as outgroup in accordance with phylogenetic pattern of Senecioneae shown by PELSER et al. (2007). It was supplemented with species of *Paragynoxys* and *Roldana*, other members of Tussilaginatae.

Character sampling. *ndhF*, *trnL*, *pstA-trnH*, 5' and 3' *trnK* and *trnL-F* cpDNA and ITS and ETS nDNA characters were used for taxonomic treatment of Senecioneae by KNOX & PALMER (1995), STÄHELI (2006) and PELSER et al. (2007, 2010). ITS and ETS cladograms were shown to be congruent (PELSER et al. 2007). They are thus interchangeable, but the former are advantageous because they cover much more members of Senecioneae and need more accessible primers.

The cpDNA-based cladograms and combined cpDNA-ITS/ETS-based cladograms are incongruent to ITS-based ones (PELSER et al. 2010). The cpDNA characters outnumber the ITS1–5.8S RNA–ITS2 nDNA counterparts many times. Therefore, the combined cladograms are mostly influenced by the cpDNA characters. The chloroplasts are mostly maternally inherited in angiosperms, though biparental and paternal inheritances occasionally take place (REBOUD & ZEYL 1994; BIRKY 1995; HANSEN et al. 2007). The cpDNA-based and cpDNA-ITS nDNA-based cladograms would consequently emphasize maternal phylogenetic signals and obscure paternal ones. However, reticulate evolution and hybrid genesis of taxa seem to have been of importance in the evolution of the tribe Senecioneae (BREMER 1994; PELSER et al. 2010). Such an evolution can adequately be signalled by nDNAs. ITS cladograms equally signalled maternal and paternal lineages though they were certainly less informative. Increasing the number of used DNA fragments was shown to have little effect on improving the cladograms (DEGTJAREVA et al. 2004; CRAWLEY & HILU 2012). Therefore, we believed that some reduction of information in ITS cladograms was acceptable. That is why we confined ourselves to ITS1–5.8S RNA–ITS2 nDNA.

The original data and those of GenBank were used in our investigation (Appendix 3).

DNA treatment. 100 to 160 mg fragments of leaves were sampled from voucher plants deposited at the Herbarium of Tsitsin Main Botanical Garden of Russian Academy of Sciences, Moscow [MHA] (*Hasteola robusta*, *H. tschonokii*, *Parasenecio auriculatus*, *P. hastatus*) or from living plants grown in the greenhouses (*Caputia scaposa*, *C. tomentosa*, *Crassothonna capensis*, *Curio acaulis*, *C. articulatus*, *C. citrifolius*, *C. hallianus*, *C. herreanus*, *C. repens*, *C. rowleyanus*, *C. talinoides*, *Delairea odorata*, *Gynura* sp., *Kleinia amaniensis*, *K. descoingsii*, *K. fulgens*, *K. longiflora*, *K. neriifolia*, *K. petraea*, *K. schweinfurthii*, *K. stapeliiformis*, *Roldana suffulta*, *Senecio aloides*, *S. archeri*, *S. crassissimus*, *Senecio kleiniiformis*, *S. macroglossus*, *S. meuselii*, *S. tropaeolifolius*) and from garden beds (*Syneilesis aconitifolia*) of the Tsitsin Main Botanical Garden or from living plants received from the collection of Kirstenbosh National Botanical Garden, South Africa (*Senecio oxyriifolius*).

DNA was extracted with the NucleoSpin® Plant II (Macherey-Nagel, Germany) according to manufacturer's instruction. Forward 5'-ACCTGCGGAAGGATCATTTG-3' and reverse 5'-GATATGCTTAAACTCAGCGG-3' primers were used to amplify complete ITS1–5.8S RNA–ITS2 region. Polymerase chain reactions (PCR) were conducted in 20 ml reaction volumes containing 4 ml of Ready-to-Use PCR MaGMix (Diabat Ltd., Russia), 15 ml of deionized water, 3.4 pmol of each primer and 1 ml of template DNA of unknown concentration. PCR cycling was performed with MJ Research PTC-220 DNA Engine Dyad Thermal Cycler (BioRad Laboratories, USA) as follows: initial denaturation 95°C 2 min 30 sec, 35 cycles of 95°C 30 sec, 55°C 1 min, 72°C 2 min, terminal extension 75°C 4 min.

Double-strained PCR products were separated under 100 V on agarose gel (Amresco, USA) containing 0.5 mg/ml of ethidium bromide in $0.5 \times$ TBE buffer. Separated products were purified with GFX PCR Purification kit (Amersham Biosciences, USA) according to manufacturer's instruction.

DNA was sequenced with ABI PRISM® BigDye™ Terminator v.3.1 (Applied Biosystems, USA) according to manufacturer's manual and analyzed with ABI PRISM 3730 Genetic Analyzer at Engelhardt Institute of Molecular Biology of Russian Academy of Sciences, Moscow. Limits of the ITS1–5.8S RNA–ITS2 fragments were determined on the basis of GenBank data.

Determined ITS1–5.8S RNA–ITS2 sequences were deposited at GenBank, accession Nos. KJ561175 to KJ561210. The voucher specimens were incorporated into the Herbarium of Tsitsin Main Botanical Garden [MHA].

Processing of ITS1–5.8S RNA–ITS2 data. ITS1–5.8S RNA–ITS2 sequences were primarily aligned with MAFFT (KATO et al. 2002) under an accurate L-INS-I strategy (KATO et al. 2005). Final alignment was made with BioEdit 7.0.1 software (HALL 1999). Indels were coded using simple method of indel coding (SIMMONS et al. 2001) as implemented in the GapCoder software (YOUNG & HEALY 2003). The aligned sequences were analyzed with the T.N.T. program (GOLOBOFF et al. 2003) using both traditional Wagner and New Technology approaches of Maximum Parsimony searches with the TBR algorithm. Branch support was assessed with 100 replicates.

The splitgraphs of the phylogenetic relations of the species under investigation was constructed by NeighborNet method in the SplitsTree4 program (HUSON & BRYANT 2006).

Senecio kleiniiformis was hypothesized to be a hybrid species arisen in culture (ROWLEY 1994, 2002). If so, it would attract its ancestors which are really distantly related. The phylogenetic pattern would thus be distorted. Therefore, the complete cladogram and splitgraph were supplemented with incomplete ones (*S. kleiniiformis* excluded).

Results

The ITS1–5.8S RNA–ITS2 spacer varies from 576 b.p. (*Curio acaulis*) to 806 b.p. (*Kleinia galpinii*). The final alignment is 664 positions long and includes 266 informative ones.

Curio archeri, *C. citrifolius*, *C. crassulifolius*, *C. ficoides*, *C. hallianus*, *C. herreanus*, *C. muirii*, *C. radicans*, *C. repens*, *C. rowleyanus*, *C. sulcicalyx* and *C. talinoides* are nested together in both cladograms (Fig. 2), but their clade is worse supported. The same species are also assembled in the splitgraph (Fig. 3). These species are distributed among 2 lineages. The first one of *C. ficoides*, *C. hallianus*, *C. herreanus*, *C. radicans*, *C. repens* and *C. rowleyanus* is well supported. It is a *Curio rowleyanus* lineage which is also discernible in the splitgraphs (Figs 3 & 4). The second weakly supported lineage has *Curio archeri*, *C. citrifolius*, *C. crassulifolius*, *C. muirii*, *C. sulcicalyx* and *C. talinoides* arranged in worse supported *Curio citrifolius* clade and *Curio talinoides* clade. The *Curio rowleyanus* lineage and *Curio citrifolius* clade are easy discernible in the splitgraphs as compact assemblages of species (Fig. 4, red and blue frames, respectively). The *Curio talinoides* clade is a much looser species assemblage in the splitgraphs (Figs 3 & 4).

Senecio corymbiferus is distinctly nested in *Curio citrifolius* clade as its early divergent lineage (Fig. 2), but support is low. It adjoins rootstock of *Curio citrifolius* assemblage in the splitgraph (Fig. 4).

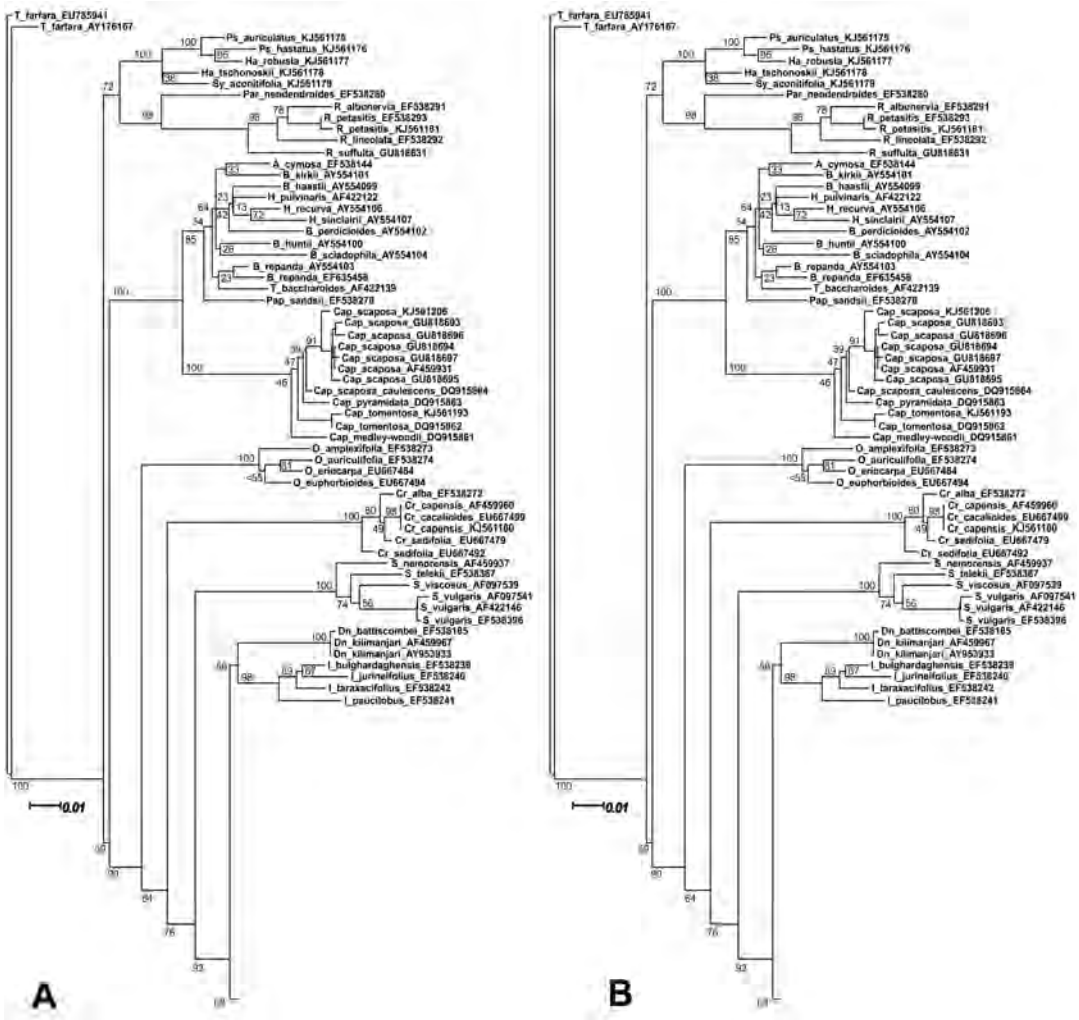


Figure 2. Cladogram of dataset. A – *Curio kleiniiformis* included; B – *Curio kleiniiformis* excluded.

Curio acaulis is clustered with *Senecio aloides* and *S. bulbinifolius* in *Senecio aloides* clade (Fig. 2), the former two being the closest. The support of this clade is low, but assembling *Curio acaulis* and *Senecio aloides* is well supported. *Curio acaulis* and *S. aloides* are also closely assembled in the splitgraphs (Fig. 4), *S. bulbinifolius* is at a distance.

Senecio aloides clade is sister to *Senecio crassissimus* clade of 3 Madagascar species, *S. crassissimus*, *S. melastomifolius* and *S. meuselii* (Fig. 2), though the support is extremely low. *S. crassissimus* and *S. meuselii* are sister species in both cladograms. However, *S. crassissimus* is clustered with *S. melastomifolius* in the splitgraphs (Fig. 4), whereas *S. meuselii* is nested closer to *S. aloides* assemblage.

Senecio kleiniiformis is invariably grouped with *Senecio tropaeolifolius* in the cladogram (Fig. 2A, well supported) as well as in the splitgraph (Fig. 4A). These two species constitute early divergent clade of *Curio* lineage, though *Senecio tropaeolifolius* was considered close to (MUELLER 1867) or even (erroneously according to MALENKOVA et al. 2014) conspecific with *Senecio oxyriifolius* (ROWLEY 1994, 2002).

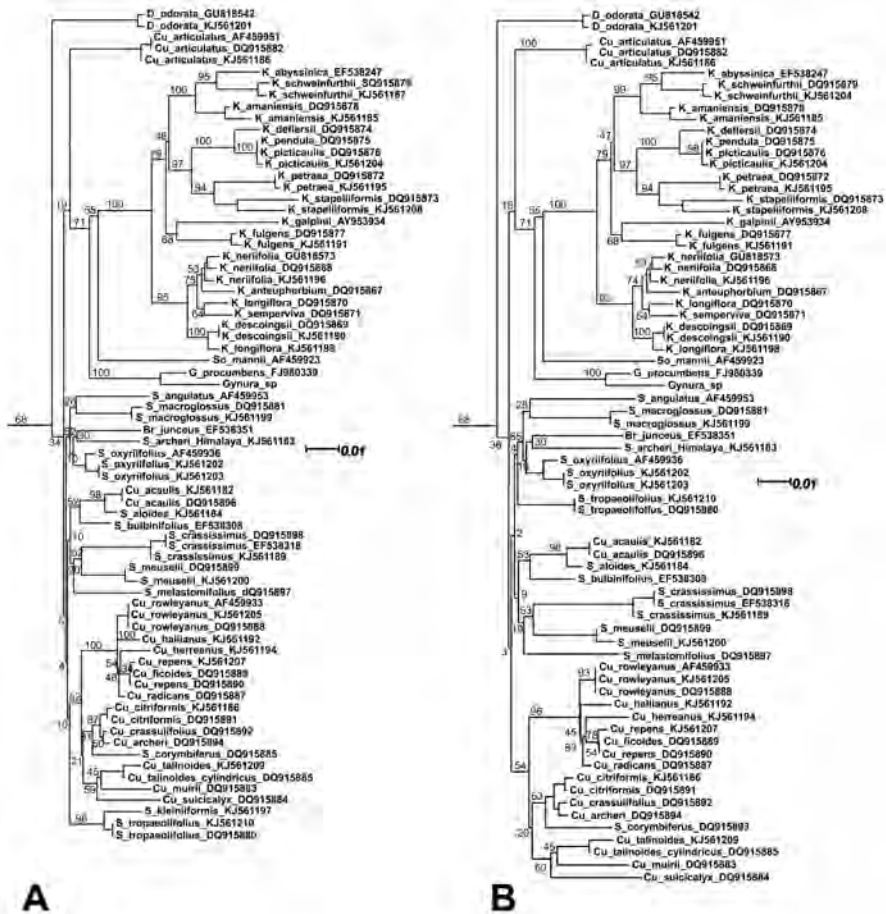


Figure 2 (continued). Cladogram of dataset. A – *Curio kleiniiformis* included; B – *Curio kleiniiformis* excluded.

When *Senecio kleiniiformis* is excluded, *Senecio tropaeolifolius* and *S. oxyriifolius* are both in the highly diverse, weakly supported clade *Senecio tropaeolifolius*–*Senecio angulatus* (Fig. 2B), but they are not the closest relatives. *S. tropaeolifolius* is an early divergent lineage of this clade, whereas *S. oxyriifolius* is sister to *Senecio archeri*–*Brachyrhynchus* clade, though support is low. These species are nested close in the splitgraph (Fig. 4B), but *S. oxyriifolius* is closer to *Senecio archeri*–*Brachyrhynchus* assemblage than to *S. tropaeolifolius* there.

Senecio angulatus combines with *S. macroglossus* and *Senecio archeri* unexpectedly combines with *Brachyrhynchus junceus* as can be seen in cladograms and splitgraphs. The clades are worse supported, however.

All species mentioned above constitute Curio alliance which is a sister clade of other gynuroids under consideration. *Curio articulatus* is an early divergent clade among the latter (Fig. 2). It is nested between the Curio alliance and assemblage of other gynuroids in the splitgraph (Fig. 4). The Curio alliance, *Gynura* assemblage and *Delairea* seem to be more remote in the splitgraphs than in the cladograms. These groups are closer to Iranecio–*Dendrosenecio* complex than to the genuine *Senecio* (Figs. 2 & 3). They are even more distant from the pubescent members of Kleinoidei, othonnas and ‘calalias’.

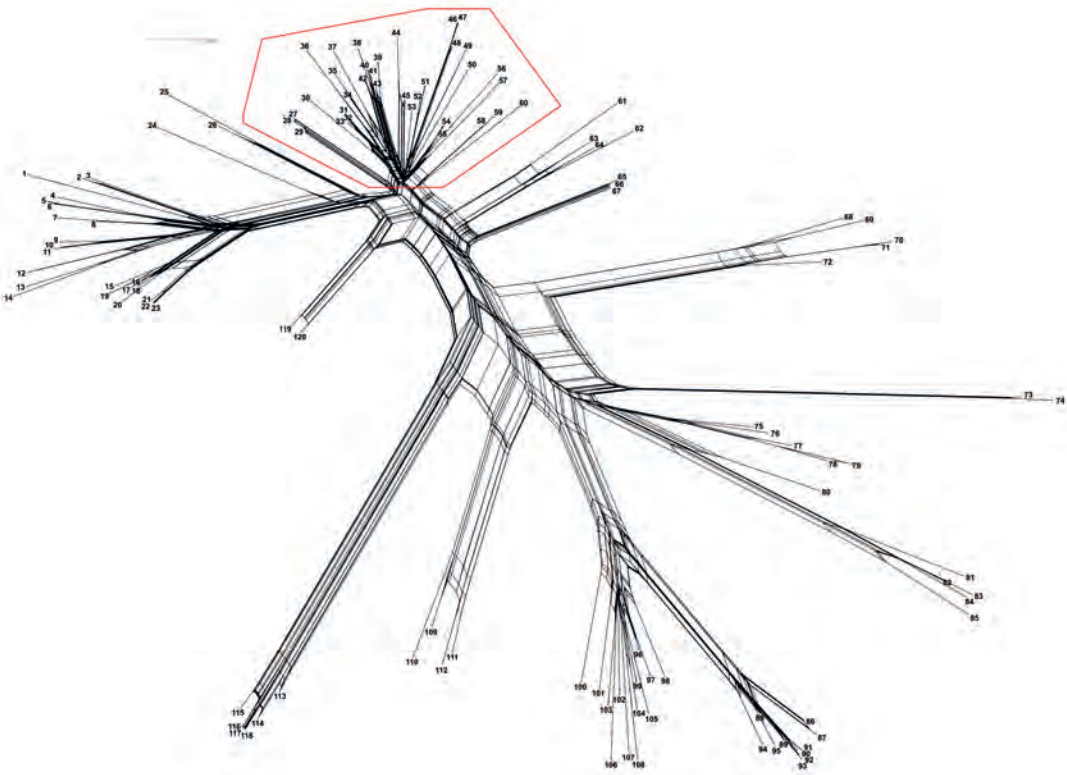


Figure 3. Splitgraph of dataset, *Curio kleiniiformis* included. 1 – *Kleinia galpinii* AY953934; 2 – *K. fulgens* KJ561191; 3 – *K. fulgens* DQ915877; 4 – *K. abyssinica* EF538247; 5 – *K. schweinfurthii* DQ915879; 6 – *K. schweinfurthii* KJ561187; 7 – *K. amaniensis* KJ561185; 8 – *K. amaniensis* DQ915878; 9 – *K. deflersii* DQ915874; 10 – *K. pendula* DQ915875; 11 – *K. picticaulis* DQ915876 & KJ561204; 12 – *K. petraea* DQ915872 & KJ561195; 13 – *K. stapeliiformis* KJ561208; 14 – *K. stapeliiformis* DQ915873; 15 – *K. longiflora* DQ915870; 16 – *K. neriifolia* KJ561196; 17 – *K. neriifolia* DQ915868; 18 – *K. neriifolia* GU818573; 19 – *K. semperviva* DQ915871; 20 – *K. anteuphorbium* DQ915867; 21 – *K. longiflora* KJ 561198; 22 – *K. descoingsii* DQ915869; 23 – *K. descoingsii* KJ561190; 24 – *Solanecio mannii* AF459923; 25 – *Gynura* sp.; 26 – *G. procumbens* FJ980339; 27 – *Curio articulatus* DQ915882; 28 – *C. articulatus* AF459951; 29 – *C. articulatus* KJ561186; *Senecio corymbiferus* DQ915893; 31 – *Curio citrifolius* KJ561188 & DQ915891; 32 – *C. crassulifolius* DQ915892; 33 – *C. archeri* DQ915894; 34 – *C. talinoides* ssp. *cylindricus* DQ915885; 35 – *C. talinoides* KJ561209; 36 – *C. sulcicalyx* DQ915884; 37 – *C. muirii* DQ915883; 38 – *C. herreanus* KJ561194; 39 – *C. hallianus* KJ561192; 40 – *C. repens* KJ561207 & DQ915890; 41 – *C. ficoides* DQ915889; 42 – *C. rowleyanus* AF459933, DQ915888 & KJ561205; 43 – *Curio radicans* DQ915887; 44 – *Senecio kleiniiformis* KJ561197; 45 – *Senecio tropaeolifolius* DQ915880 & KJ561210; 46 – *S. crassissimus* DQ915898; 47 – *S. crassissimus* EF538318; 48 – *S. crassissimus* KJ561189; 49 – *S. meuselii* DQ915899 & KJ561200; 50 – *S. melastomifolius* DQ915897; 51 – *Curio acaulis* DQ915896 & KJ561182; 52 – *Senecio aloides* KJ561184; 53 – *S. bulbinifolius* EF538308; 54 – *S. oxyriifolius* KJ561202 & KJ561203; 55 – *S. oxyriifolius* AF459936; 56 – *Brachyrhynchus junceus* EF538351; 57 – *S. archeri* var. *Himalaya* KJ561183; 58 – *S. macroglossus* KJ561199; 59 – *S. macroglossus* DQ915881; 60 – *S. angulatus* AF459953; 61 – *Iranecio paucilobus* EF538241; 62 – *I. jurineifolius* EF538240; 63 – *I. taraxacifolius* EF538242; 64 – *I. bulghardaghensis* EF538239; 65 – *Dendrosenecio battiscombii* EF538185; 66 – *D. kilimanjari* AF459967; 67 – *D. kilimanjari* AY953933; 68 – *S. telekii* EF538387; 69 – *S. viscosus* AF097539; 70 – *S. vulgaris* AF097541; 71 – *S. vulgaris* AF422136 & EF538396; 72 – *S. nemorensis* AF459937; 73 – *Tussilago farfara* EU785941; 74 – *T. farfara* AY176167; 75 – *Hasteola tschonokii* KJ561178; 76 – *Syneilesis aconitifolia* KJ561179; 77 – *Parasenecio auriculatus* KJ561175; 78 – *Hasteola robusta* KJ561177; 79 – *Parasenecio hastatus* KJ561176; 80 – *Paragymoxys neodendroides* EF538280; 81 – *Roldana suffulva* GU818631; 82 – *R. petasitis* EF538293; 83 – *R. petasitis* KJ561181; 84 – *R. albonervia* EF538291; 85 – *R. lineolata* EF538292; 86 – *Caputia tomentosa* DQ915862; 87 – *C. tomentosa* KJ561193; 88 – *C. scaposa* ssp. *caulescens* DQ915864; 89 – *C. scaposa* KJ561206 & AF459931; 90 – *C. scaposa* GU818695; 91 – *C. scaposa* GU818694; 92 – *C. scaposa* GU818697; 93 – *C. scaposa* GU818693 & GU818696; 94 – *C. medley-woodii* DQ915861; 95 – *C. pyramidata* DQ915863; 96 –

Discussion

Hybridization is believed to have been of importance in evolution of many Senecioneae segregates (PELSER et al. 2010) and it is clearly discernible in the splitgraphs constructed (Figs. 3 & 4). However, cladograms are unable to reproduce reticulate evolution and hybrid speciation (PAVLINOV 2004). Besides, the cladograms constructed are mostly poorly resolved and clades are too weakly supported in Curio lineages. That is the reason, why our conclusions are mainly based on the analysis of the splitgraphs.

The Curio alliance is expectedly far distant from the genera *Caputia*, *Othonna* (*Crassothonna*) and 'Cacalia' segregates as it was evidenced by JEFFREY (1986), BREMER (1994), KNOX & PALMER (1995), STÄHELI (2006), PELSER et al. (2007, 2010) and NORDENSTAM et al. (2009). It is nested between *Delairea odorata* and Gynura–Solaneccio–Kleinia lineage and Iranecio lineage, rather distant from the genuine *Senecio*. The species of Curio alliance and those of the genuine *Senecio* are also distant in cladograms (KNOX & PALMER 1995; STÄHELI 2006; PELSER et al. 2007, 2010; NORDENSTAM et al. 2009; present article). None of the Curio alliance species should consequently be included into *Senecio*.

Most *Curio* species accepted are assembled in core *Curio*. PELSER et al. (2007) recognized three clades of core Curio, Curio sulcalyx–*Senecio spiculosus* clade, *Senecio corymbiferus*–Curio archeri clade and Curio rowleyanus–Curio radicans clade. *Senecio corymbiferus* is also nested among *Curio* species in our cladograms. Position of *Senecio corymbiferus* among *Curio* species is totally unexpected, because this species sharply contrasts with the latter in radiate calathidia (capitula) and bright yellow ligulate flowers. The genus *Curio* essentially has white (JEFFREY 1992) to slight yellowish (JEFFREY 1986) flowers in discoid calathidia. Inclusion of *Senecio corymbiferus* in genus *Curio* would require fundamental changing of the diagnosis of the latter one. The genus *Curio* would resultantly become too indistinctive. Segregation of core *Curio* species into separate genera to keep *Senecio corymbiferus* outside *Curio* s. str. would result in distribution of very similar *Curio* species among at least four genera, three of which would have identical diagnoses. The alternatives just outlined seem equally inappropriate.

The splitgraph is likely to avoid this trouble. *Senecio corymbiferus* is not nested among core *Curio* species there. It looks like a separate offspring of the same rootstock which repeatedly hybridized with precursor(s) of Curio archeri–Curio citrifolius–Curio crassulifolius assemblage. We believe that *Senecio corymbiferus* is not really a member of core *Curio*. It is only attracted to the latter one because of ancient hybridization. It should not be included in *Senecio* either.

There are two distinctive assemblages of core *Curio* species (Fig. 4). The Assemblage A (Fig. 4, red frame) includes type species *C. rowleyanus* and *C. ficoides*, *C. hallianus*, *C. herreanus*, *C. radicans* and *C. repens*. The Assemblage B (Fig. 4, blue frame) includes *C. archeri*, *C. citrifolius* and

- *Brachyglottis repanda* AY554103; 97 – *B. repanda* EF635458; 98 – *Traversia baccharoides* AF422139; 99 – *Haastia pulvinaris* AF422122; 100 – *Papuacalia sandsii* EF538278; 101 – *Acrisione cymosa* EF538144; 102 – *Brachyglottis huntii* AY554100; 103 – *B. kirkii* AY554101; 104 – *Haastia recurva* AY554106; 105 – *Brachyglottis haastii* AY554099; 106 – *B. sciadophila* AY554104; 107 – *B. perdiciooides* AY554102; 108 – *Haastia sinclairii* AY554107; 109 – *Othonna euphorbiooides* EU667494; 110 – *O. amplexifolia* EF538273; 111 – *O. eriocarpa* EU667484; 112 – *O. auriculifolia* EF538274; 113 – *Crassothonna sedifolia* EU667492; 114 – *C. sedifolia* EU667479; 115 – *C. alba* EF538272; 116 – *C. cacalioides* EU667499; 117 – *C. capensis* KJ561180; 118 – *C. capensis* AF459960; 119 – *Delairea odorata* KJ561201; 120 – *D. odorata* GU828542.



C. crassulifolius. *Curio sulcicalyx* and *C. talinoides* are closer to Assemblage B, but they are connected with Assemblage A by *C. muirii*. *Curio muirii* sharply contrasts with other core *Curio* species investigated in flat, obovate, bifacial, slightly succulent leaves (VAN JAARVELD & VISAGIE 2015: Fig. 1). But it has ‘typical curioid’ calathidia, viz. discoid ones of few campanulate white (straw-yellow according to ROWLEY 2002) disc flowers. None of the species of Assemblage A has typical unifacial leaves. The leaves of *C. rowleyanus*, *C. hallianus*, *C. herreanus* and *C. radicans* are subunifacial (ROWLEY 1994: Fig. 192; OZEROVA & TIMONIN 2009). Most leaves of *C. ficoides* are unifacial but laterally flattened (ensiform) with left and right sides (TIMONIN et al. 2006). Most leaves of *C. repens* are also unifacial but dorsiventrally flattened (pseudobifacial) (TIMONIN & OZEROVA 1993a; TIMONIN et al. 2007). The absence of typical unifacial leaves could be considered a differentiating character of this assemblage. However, subunifacial leaves are also inherent in *C. crassulifolius* (ROWLEY 1994: Fig. 134) of the Assemblage B and in *C. sulcicalyx* (ROWLEY l. c.: Fig. 214) of the intermediate group. *C. archeri* (Assemblage B) has ensiform leaves (ROWLEY l. c.: Fig. 221) similar to those of *C. ficoides* (Assemblage A). Typical unifacial leaves are characteristic of *C. citrifolius* of Assemblage B and of *C. talinoides* of the intermediate group. Leaf morphology thus shows heterogeneity of core *Curio*, but it does not coincide with its molecular segregates. Further research is needed to decide whether core *Curio* should be divided into subgenera or separate genera.

Relationships of *Curio articulatus* are unresolved in STÄHELI (2006). *C. articulatus* is an early divergent lineage of *Curio* clade in PELSER et al. (2007: Fig. 1J) which is consistent with the leaf evolution in the former section *Rowleyani* as reconstructed by TIMONIN & OZEROVA (1993b). However, this species is nested in Gynura–Solaneceae–Kleinia clade in our cladogram (Fig. 2). It is between core *Curio* and Gynura–Solaneceae–Kleinia assemblage in the splitgraph (Fig. 4). It is even more distant from core *Curio* than *Brachyrhynchos*. Though *C. articulatus* has ‘typical curioid’ calathidia, its vegetative organs are quite different. In contrast to core *Curio*, *C. articulatus* is a deciduous pachycaulic stem succulent with thick manoxylic stems and plainly bifacial, petiolate leaves. Unlike the leaves of core *Curio* species (TIMONIN & OZEROVA 1993b; OZEROVA & TIMONIN 2009), its leaf blades have typical palisade and spongy chlorenchyma and adaxial subepidermal water-storing parenchyma (THODAY & WOODHEAD 1932). Leaves of core *Curio* and *C. articulatus* are also dissimilar developmentally (q.v. TIMONIN et al. 2006; OZEROVA & TIMONIN 2009; FEDOTOV et al. 2016). There is certainly no reason to keep *C. articulatus* in genus *Curio*. This species was described as member of *Cacalia* (LINNÉ f. 1781) and later transferred to the genus *Kleinia* (HAWORTH 1812) and to the genus *Senecio* (SCHULTZ 1845). It is really very distantly related to any ‘cacalias’ (BRUMMITT 1998; NORDENSTAM et al. 2009 etc.). It is farther

- **Figure 4.** Splitgraph of *Curio* alliance. A – *Senecio kleiniiformis* included; B – *Senecio kleiniiformis* excluded. 1 – *C. articulatus* KJ561186; 2 – *C. articulatus* AF459951; 3 – *Curio articulatus* DQ915882; 4 – *Senecio corymbiferus* DQ915893; 5 – *Curio archeri* DQ915894; 6 – *C. crassulifolius* DQ915892; 7 – *C. citrifolius* DQ915891; 8 – *C. citrifolius* KJ561188; 9 – *C. talinoides* ssp. *cylindricus* DQ915885; 10 – *C. talinoides* KJ561209; 11 – *C. sulcicalyx* DQ915884; 12 – *C. muirii* DQ915883; 13 – *C. herreanus* KJ561194; 14 – *C. hallianus* KJ561192; 15 – *C. repens* KJ561207 & DQ915890; 16 – *C. ficoides* DQ915889; 17 – *C. rowleyanus* AF459933, DQ915888 & KJ561205; 18 – *C. radicans* DQ915887; 19 – *Senecio kleiniiformis* KJ561197; 20 – *S. tropaeolifolius* DQ915880; 21 – *S. tropaeolifolius* KJ561210; 22 – *Curio acaulis* DQ915896, *C. acaulis* KJ561182; 23 – *Senecio aloides* KJ561184; 24 – *S. bulbiniifolius* EF538308; 25 – *S. crassissimus* EF538318; 26 – *S. crassissimus* DQ915898; 27 – *S. crassissimus* KJ561189; 28 – *S. meuselii* KJ561200; 29 – *S. meuselii* DQ915899; 30 – *S. melastomifolius* DQ915897; 31 – *S. oxyriifolius* KJ561202 & KJ561203; 32 – *S. oxyriifolius* AF489936; 33 – *Brachyrhynchos junceus* EF538351; 34 – *Senecio archeri* var. ‘Himalaya’ KJ561183; 35 – *S. macroglossus* KJ561199; 36 – *S. macroglossus* DQ915881; 37 – *S. angulatus* AF459953.

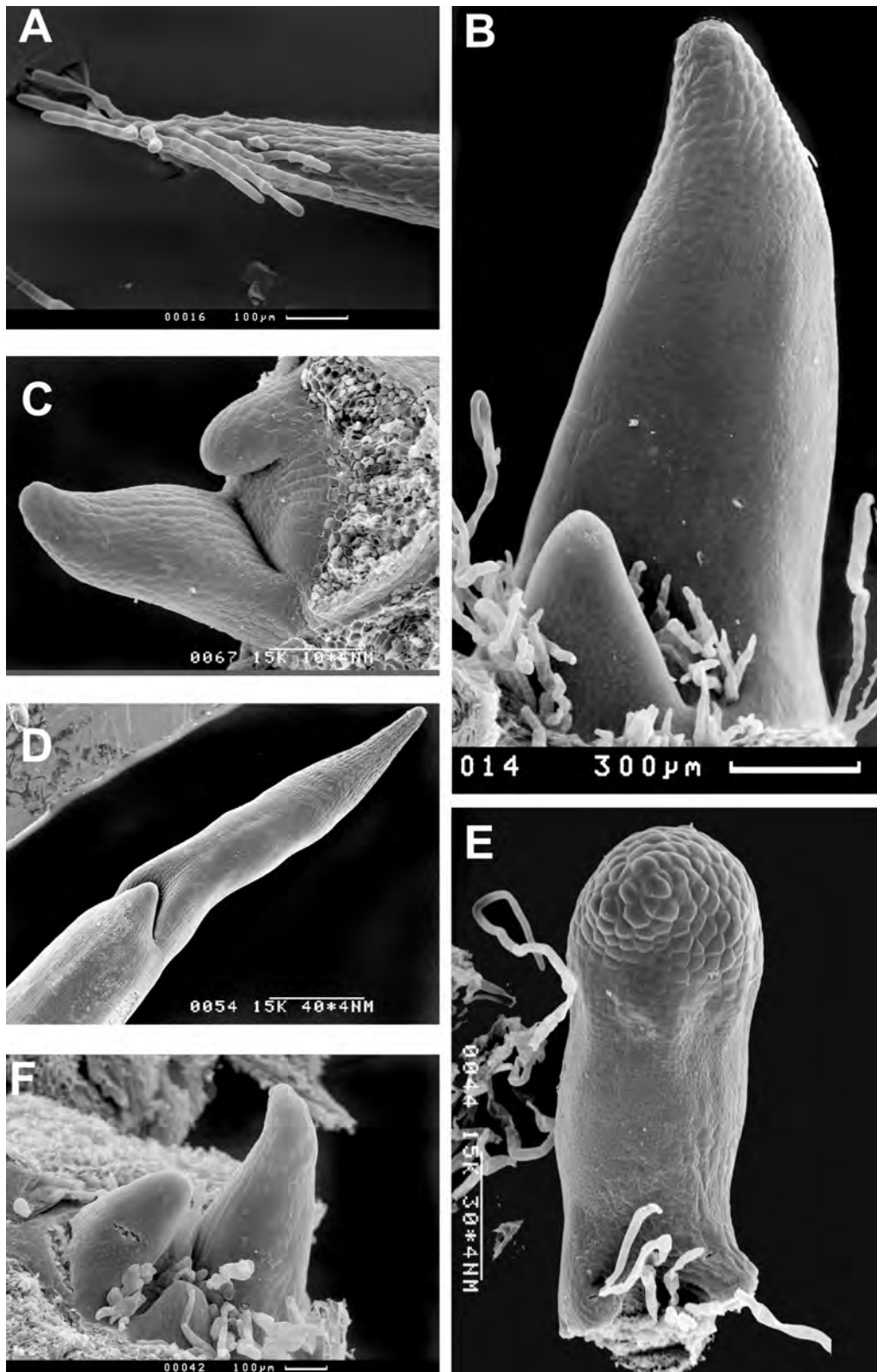


Figure 5. Developing leaves. A – *Curio acaulis*; B – *C. repens*; C – *C. ballianus*; D – *C. rowleyanus*; E – *C. citriformis*; F – *C. ficoides* (quoted by OZEROVA & TIMONIN 2009 (C&D) and by TIMONIN et al. 2006 (E&F)).

from *Kleinia* than *Solanecio* and *Gynura* and from *Senecio* than *Dendrosenecio*, *Iranecio*, *Delairea* etc. (PELSE et al. 2007; present article: Figs 2 & 4). *Curio articulatus* is worth being arranged in a separate genus.

Curio acaulis is nested in a heterogeneous assemblage of yellow-flowered groundsels which divides into few clades, though hardly supported (Fig. 2). *Curio acaulis* is in *Senecio bulbiniifolius*–*Curio acaulis* clade, rather distant from the core *Curio* (STÄHELI 2006; PELSE et al. 2007; present article). It is the closest to *Senecio aloides* (not analyzed by PELSE et al. 2007). *Curio acaulis*, *Senecio aloides* and *Senecio bulbiniifolius* are in the same worse supported clade, but the former two are closer to *S. crassissimus* than to *S. bulbiniifolius* in the splitgraph (Fig. 4B).

Curio acaulis sharply contrasts with core *Curio* in its calathidia of numerous bright yellow tubular flowers. *Senecio aloides* and *S. bulbiniifolius* have radiate calathidia and pistillate, ligulate ray flowers. The calathidia of *Curio acaulis* are discoid, but their peripheral flowers are also pistillate and the disc flowers are complete (HOFFMANN 1894). Different calathidia seem to be taxonomically insignificant in the yellow-flowered assemblage under consideration, because *Senecio oxyriifolius* has discoid calathidia (DE CANDOLLE 1837), whereas its close relative *S. tropaeolifolius* has discoid to radiate calathidia (MUELLER 1867). The flowers of core *Curio* are uniform, complete, tubular campanulate and white (yellowish in hybrid *Senecio kleiniiformis*). Besides, none of the genuine *Curio* species has trichomes on the forerunner tip (Vorläuferspitze) of the developing leaf (TIMONIN et al. 2006; OZEROVA & TIMONIN 2009) which are characteristic of *Curio acaulis* (Fig. 5). Thus, *Curio acaulis* should be excluded from the genus *Curio*. It should reasonably be placed in the assemblage of yellow-flowered groundsels of Curio alliance.

Senecio tropaeolifolius and *Senecio kleiniiformis* fill the gap between this assemblage and core *Curio* (Figs 2A & 4A), but these assemblages are clearly separated, when *S. kleiniiformis* is excluded (Figs 2B & 4B). If so, *Senecio tropaeolifolius* is assembled with very similar *S. oxyriifolius*. It was even included into the latter one (ROWLEY 2002). These species are noway conspecific (MALENKOVA et al. 2014). *S. oxyriifolius* is unexpectedly closer to *Brachyrhynchos junceus*–*Senecio archeri* lineage (Figs 2B & 4B). Anyway, assembling of *Senecio kleiniiformis* and *Senecio tropaeolifolius* and their intermediate position must result from hybrid attraction of lineages.

We hope, the yellow-flowered assemblage will not be interpreted as *Brachyrhynchos* s. latiss. because of extreme diversity of species of this assemblage. The genus *Brachyrhynchos* expanded this way would be deprived of diagnosis. Though very many taxa of Senecioneae can be characterized by “rather loosely associated character-states” (JEFFREY et al. 1977: 51) than by clear diagnosis, we believe that the monotypic status of *Brachyrhynchos* (MANNING & CRON 2011) is more appropriate and that further research will reveal a rational basis for dividing yellow-flowered groundsels into natural genera.

Senecio angulatus and *S. macroglossus* are nested together in the cladograms and splitgraphs (Figs. 2 & 4). These species were earlier included in the same section *Glaberrimi* (with rather numerous other species) (DE CANDOLLE 1837; HARVEY & SONDER 1864–1865; MUSCHLER 1909). Close relation of these two species was challenged (JEFFREY 1992), but it was clearly seen in cladograms in STÄHELI (2006) and PELSE et al. (2007: Fig. 1J). *Senecio angulatus* and *S. macroglossus* are thus confirmed to be close relatives. They constitute sister clade of *Brachyrhynchos junceus*–*Senecio oxyriifolius* clade (Fig. 2) of yellow-flowered assemblage.

They are closer to *Senecio archeri* and *Brachyrhynchos* than to other members of above-mentioned assemblage. However, they are distant enough in the splitgraph (Fig. 4) to be excluded from this assemblage. HARVEY & SONDER (1864–1865) included *Senecio angulatus* in section *Scandentes*. *S. mikanioides* Otto of this section was later recognized as *Delairea odorata* Lemaire, the type species of the genus *Delairea*. *S. angulatus* is farther from *Delairea* than from *Curio* and yellow-flowered assemblage in the splitgraph and in the cladograms of PELSNER et al. (2007: Fig. 1F, J, sub *Senecio scandens* DC.). *Senecio angulatus* and *S. macroglossus* should be segregated into a separate genus.

Senecio kleiniiformis is clearly nested in *Curio* alliance, not in *Kleinia* or its segregates. This species is outside of core *Curio* in the cladograms and splitgraphs (Figs. 2 & 4). It differs from the core *Curio* in yellowish flowers¹ and subsaccidate leaves with unifacial petiole (TIMONIN & OZEROVA 1993b). However, this species should not be arranged in a separate genus, because it was reasonably considered an artificial hybrid species, though widely cultivated (ROWLEY 2002). It would better be kept as a virtual species sensu PAVLINOV (1992), viz. a member of stochastic component of diversifying biota supplementary to the species pattern of the latter one. Such species cannot fundamentally be attributed to any genus. But we are not ready for such drastic taxonomic innovation. *Senecio kleiniiformis* was placed in the section *Rowleyani* by JEFFREY (1986). Therefore, we conventionally include this species in *Curio*.

ROWLEY (1994, 2002) hypothesized *Senecio kleiniiformis* to be a hybrid between *C. articulatus* and either diploid *Curio talinoides* ssp. *cylindricus* or polyploid *C. ficoides* or *C. repens*. *C. articulatus* should reliably be excluded from the ancestors of the species concerned. One of its parent species must have been *Senecio tropaeolifolius* of *Curio* alliance. Another parent species was certainly a member of core *Curio*. It was rather *Curio hallianus* than *C. ficoides* or *C. repens*. However, the second parent species is still to be revealed.

Conclusion

Curio P.V. Heath is a genus far distant from the genuine *Senecio*. It is distinctly separated from the genera *Kleinia*, *Solanecio*, *Gynura*, *Delairea* and yellow-flowered assemblage of *Curio* alliance. Taxonomic structure of this genus is still to be revealed. Inclusion of *Senecio corymbiferus* in *Curio* is premature. It might be attracted to *Curio* due to its probably hybrid origin. Artificial hybrid *Senecio kleiniiformis* should conventionally be retained in genus *Curio*, but *C. acaulis* and *C. articulatus* must be excluded.

Included in the genus *Curio*, *Senecio kleiniiformis* must be renamed:

***Curio kleiniiformis* (Suess.) L.V. Ozerova & A.C. Timonin, combinatio nova.**

Basionym: *Senecio kleiniiformis* Suess. Repert. Spec. Nov. Regni Veg. 42: 45. 1937.

C. acaulis is confidently placed in yellow-flowered assemblage of *Curio* alliance which has to be scrutinized taxonomically.

We transfer *Curio articulatus* into the monotypic genus

***Baculellum* L.V. Ozerova & A.C. Timonin, genus novum.**

¹ Yellowish flowers were mentioned in the original diagnosis of section *Rowleyani* (JEFFREY 1986) to cover *Senecio kleiniiformis*, but such flowers were omitted in later description of this section (JEFFREY 1992).

Diagnosis. Differs from *Curio* in deciduous pachycaulic stem-succulent growth habit, manoxylic thickened stems and typical bifacial, petiolate subsucculent leaves. From Latin *baculum* = peg, stick. Monotypic genus.

Ab genere *Curione* habitum deciduum pachycaulum succulentum, caulibus crassis manoxylicis, foliis typice bifacialibus petiolaribus subsucculentis differt. Genus monotypum.

Type species. *Baculellum articulatum* (L. f.) L.V. Ozerova & A.C. Timonin, comb. nov.

Basionym: *Cacalia articulata* L. f. Suppl. Pl. 364. 1781.

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Appendix 1. Species of the section *Rowleyani* of genus *Senecio* L. which were described as species of other genera.

| Species | Basionym, synonyms | References |
|--|--|--|
| <i>S. acaulis</i> (L. f.) Sch. Bip. | <i>Cacalia acaulis</i> L. f. (= <i>Kleinia acaulis</i> (L. f.) DC.) | DE CANDOLE 1937; SCHULTZ 'BIPONTINUS' 1845 |
| <i>S. articulatus</i> (L. f.) Sch. Bip. | <i>Cacalia articulata</i> L. f. (= <i>Kleinia articulata</i> (L. f.) Haw.) | HAWORTH 1812; SCHULTZ 'BIPONTINUS' 1845 |
| <i>S. ficoides</i> (L.) Sch. Bip. | <i>Cacalia ficoides</i> L. (= <i>Kleinia ficoides</i> (L.) Haw.) | HAWORTH 1812; SCHULTZ 'BIPONTINUS' 1845 |
| <i>S. radicans</i> (L.) Sch. Bip. | <i>Cacalia radicans</i> L. (= <i>Kleinia radicans</i> (L.) Haw.) | HAWORTH 1823; SCHULTZ 'BIPONTINUS' 1845 |
| <i>S. serpens</i> G.D. Rowley | <i>Cacalia repens</i> L. | JACOBSEN & ROWLEY 1955 |
| <i>S. aizoides</i> (DC.) Sch. Bip. | <i>Kleinia aizoides</i> DC. | SCHULTZ 'BIPONTINUS' 1845 |
| <i>S. archeri</i> (Compton) H. Jacobsen | <i>Kleinia archeri</i> Compton | JACOBSEN 1951; JACOBSEN & ROWLEY 1956 |
| <i>S. crassulifolius</i> (DC.) Sch. Bip. | <i>Kleinia crassulaefolia</i> DC. | SCHULTZ 'BIPONTINUS' 1845 |
| <i>Senecio cylindricus</i> (A. Berger) H. Jacobsen | <i>Kleinia cylindrica</i> A. Berger | JACOBSEN 1951 |
| <i>S. mandraliscae</i> (Tineo) H. Jacobsen | <i>Kleinia mandraliscae</i> Tineo | JACOBSEN 1951 |
| <i>S. neohumbertii</i> G.D. Rowley | <i>Kleinia humbertii</i> Guillaumin | JACOBSEN & ROWLEY 1955 |
| <i>S. ovoideus</i> (Compton) H. Jacobsen | <i>Kleinia ovoidea</i> Compton | JACOBSEN 1951 |
| <i>S. pinguifolius</i> (DC.) Sch. Bip. | <i>Kleinia pinguifolia</i> DC. | SCHULTZ 'BIPONTINUS' 1845 |
| <i>S. spiculosus</i> (Shepherd) D.C. Rowley | <i>Kleinia spiculosa</i> Shepherd | JACOBSEN & ROWLEY 1956 |
| <i>S. talinoides</i> (DC.) Sch. Bip. | <i>Kleinia talinoides</i> DC. | SCHULTZ 'BIPONTINUS' 1845 |

Appendix 2. Species of the section *Rowleyani* which were arranged in other genera or synonymized with species of other genera.

| Species of <i>Rowleyani</i> section | Position in other genera | References |
|--|--|---|
| <i>Senecio acaulis</i> (L. f.) Sch. Bip. | <i>Kleinia acaulis</i> (L. f.) DC. | DE CANDOLLE 1837; HERMANN 2003a |
| <i>Senecio aloides</i> DC. | <i>Othonna rhopalophylla</i> Dinter | WELMAN 2003 |
| <i>S. avasimontanus</i> Dinter | <i>Othonna avasimontana</i> Dinter | DINTER 1928 |
| | <i>Lopholaena cneorifolia</i> (DC.) S. Moore | MERXMÜLLER 1965 |
| | <i>Doria cneorifolia</i> DC. | MERXMÜLLER 1965; WELMAN 2003; THE PLANT LIST; APD |
| | <i>Hertia cneorifolia</i> (DC.) Kuntze | WELMAN 2003; HERMANN 2003b |
| <i>S. cicatricosus</i> Sch. Bip. | = <i>Kleinia breviscapa</i> DC. | SCHULTZ 'BIPONTINUS' 1845 |
| | ~ <i>Kleinia subradiata</i> DC. (= <i>Senecio subradiatus</i> (DC.) Sch. Bip.) | APD; SCHULTZ 'BIPONTINUS' 1845 |
| <i>S. chordifolius</i> Hook. f. | <i>Kleinia chordifolia</i> (Hook. f.) A. Berger | BERGER 1905 |
| <i>S. hanburyanus</i> Dinter | <i>Kleinia hanburyana</i> (Dinter) A. Berger | BERGER 1905 |
| <i>Senecio kleiniiformis</i> Suess. | <i>Klenia kleiniiformis</i> (Suess.) Boom | ROWLEY 2002 |
| <i>S. rowleyanus</i> H. Jacobsen | <i>Kleinia rowleyana</i> (H. Jacobsen) Kunkel | KUNKEL 1988 |
| <i>S. sulcicalyx</i> Baker | <i>Othonna pusilla</i> Dinter (= <i>Kleinia pusilla</i> (Dinter) Merxm.) | JEFFREY 1986; WELMAN 2003 |
| <i>S. vitalis</i> N.E. Br. | ~ <i>Kleinia cylindrica</i> A. Berger | APD; ROWLEY 2002 |

Appendix 3. ITS1–5.8S RNA–ITS2 data of species under consideration.

| Supraspecies taxon/group | Species | NCBI No. | Source |
|--------------------------------------|---|---|----------|
| Curio alliance | <i>Curio acaulis</i> (L.f.) P.V. Heath | KJ561182 | Original |
| | | DQ915896, sub 'Senecio acaulis' | GenBank |
| | <i>Curio articulatus</i> (L.f.) P.V. Heath | KJ561186 | original |
| | | AF459951 | GenBank |
| | | DQ915882 | GenBank |
| | <i>Curio archeri</i> (Compton) P.V. Heath | DQ915894, sub 'Senecio toxotis' | GenBank |
| | <i>Curio citrifolius</i> (G.D. Rowley) P.V. Heath | KJ561188 | original |
| | | DQ915891, sub 'Senecio citrifolius' | GenBank |
| | <i>Curio crassulifolius</i> (DC.) P.V. Heath | DQ915892, sub 'Senecio crassulifolius' | GenBank |
| | <i>Curio ficoides</i> (L.) P.V. Heath | DQ915889 | GenBank |
| | <i>Curio hallianus</i> (G.D. Rowley) P.V. Heath | KJ561192 | original |
| | <i>Curio herreanus</i> (Dinter) P.V. Heath | KJ561194 | original |
| | <i>Curio kleiniiformis</i> (Suess.) L.V. Ozerova & A.C. Timonin | KJ561197, sub 'Senecio kleiniiformis' | original |
| | <i>Curio muirii</i> (L. Bolus) van Jaarsv. | DQ915883, sub 'Senecio muirii' | GenBank |
| | <i>Curio radicans</i> (L.f.) P.V. Heath | DQ915887, sub 'Senecio radicans' | GenBank |
| | <i>Curio repens</i> (L.) P.V. Heath | KJ561207 | original |
| | | DQ915890. Sub 'Senecio serpens' | GenBank |
| | <i>Curio rowleyanus</i> (H. Jacobsen) P.V. Heath | KJ561205 | original |
| | | AF459933 | GenBank |
| | | DQ915888, sub 'Senecio rowleyanus' | GenBank |
| | <i>Curio sulcicalyx</i> (N.E. Br.) P.V. Heath | DQ915884, sub 'Senecio sulcicalyx' | GenBank |
| | <i>Curio talinoides</i> (DC.) P.V. Heath | KJ561209 | original |
| | | DQ915885, sub 'Senecio talinoides ssp. cylindricus' | GenBank |
| | <i>Brachyrhynchos junceus</i> Less. | EF538351, sub 'Senecio junceus' | GenBank |
| | <i>Senecio aloides</i> DC. | KJ561184 | original |
| | <i>Senecio angulatus</i> L.f. | AF459953 | GenBank |
| | <i>Senecio archeri</i> Cuatrec. 'Himalaya' hort. | KJ561183, sub 'Senecio sp. 'Himalaya'' | original |
| | <i>Senecio bulbiniifolius</i> DC. | EF538308 | GenBank |
| | <i>Senecio corymbiferus</i> DC. | DQ915893 | GenBank |
| | <i>Senecio crassissimus</i> Humbert | KJ561189 | original |
| | | DQ915898 | GenBank |
| | | EF538318 | GenBank |
| <i>Senecio macroglossus</i> DC. | KJ561199 | original | |
| | DQ915881 | GenBank | |
| <i>Senecio melastomifolius</i> Baker | DQ915897 | GenBank | |

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|---|--|--|---|----------|
| | <i>Senecio meuselii</i> Rauh | KJ561200 | original | |
| | | DQ915899 | GenBank | |
| | <i>Senecio oxyriifolius</i> DC. | KJ561202 | original | |
| | | KJ561203 | original | |
| | | AF459936 | GenBank | |
| | <i>Senecio trophaeolifolius</i> MacOwen ex F. Muell. | KJ561210 | original | |
| | | DQ915880 | GenBank | |
| | <i>Delairea odorata</i> Lem. | KJ561201 | original | |
| | | GU818542 | GenBank | |
| | Other members of Gynuroid clade | <i>Gynura procumbens</i> Merr. | FJ980339 | GenBank |
| | | <i>Gynura</i> sp. | | original |
| | | <i>Kleinia abyssinica</i> A. Berger | EF538247, sub <i>Kleinia abyssinica</i> var. <i>hildebrandtii</i> | GenBank |
| <i>Kleinia amaniensis</i> A. Berger | | KJ561185, sub 'Senecio amaniensis' | original | |
| | | DQ915878, sub 'Senecio amaniensis' | GenBank | |
| <i>Kleinia anteuphorbium</i> DC. | | DQ915867, sub 'Senecio anteuphorbium' | GenBank | |
| <i>Kleinia deflersii</i> (O. Schwartz) P. Halliday | | DQ915874, sub 'Senecio deflersii' | GenBank | |
| <i>Kleinia descoingsii</i> (Humbert) C. Jeffrey | | KJ561190, sub 'Senecio descoingsii' | original | |
| | | DQ915869, sub 'Senecio descoingsii' | GenBank | |
| <i>Kleinia fulgens</i> Hook. f. | | KJ561191, sub 'Senecio fulgens' | original | |
| | | DQ915877, sub 'Senecio fulgens' | GenBank | |
| <i>Kleinia galpinii</i> A. Berger | | AY953934 | GenBank | |
| <i>Kleinia longiflora</i> DC. | | KJ561198, sub 'Senecio longiflorus' | original | |
| | | DQ915870, sub 'Senecio longiflorus' | GenBank | |
| <i>Kleinia neriifolia</i> Haw. | | KJ561196, sub 'Senecio kleinia' | original | |
| | | DQ915868, sub 'Senecio kleinia' | GenBank | |
| | | GU818573 | GenBank | |
| <i>Kleinia pendula</i> (Forssk.) DC. | | DQ915875, sub 'Senecio pendulus' | GenBank | |
| <i>Kleinia petraea</i> (R.E. Fr.) C. Jeffrey | | KJ561195, sub 'Senecio jacobsenii' | original | |
| | | DQ915872, sub 'Senecio jacobsenii' | GenBank | |
| <i>Kleinia picticaulis</i> (P.R.O. Bally) C. Jeffrey | | KJ561204, sub 'Senecio picticaulis' | original | |
| | | DQ915876, sub 'Senecio picticaulis' | GenBank | |
| <i>Kleinia schweinfurthii</i> (Oliv. & Hiern) A. Berger | | KJ561187, sub 'Senecio ballyi' | original | |
| | | DQ915879, sub 'Senecio ballyi' | GenBank | |
| <i>Kleinia semperviva</i> (Forssk.) DC. | | DQ915871, sub 'Senecio sempervivus' | GenBank | |
| <i>Kleinia stapeliiformis</i> Stapf | | KJ561208, sub 'Senecio stapeliiformis' | original | |
| | | DQ915873, sub 'Senecio stapeliiformis' | GenBank | |
| <i>Solanecio mannii</i> (Hook. f.) C. Jeffrey | | AF459923 | GenBank | |

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|--|---|---|---------|----------|
| Pubescent species of Jeffrey's section <i>Kleinioidei</i> and other members of Senecio medley-woodii-Brachyglottis clade | <i>Caputia medley-woodii</i> (Hutch.) B. Nord. & Pelser | DQ915861, sub 'Senecio medley-woodii' | GenBank | |
| | <i>Caputia pyramidata</i> (DC.) B. Nord. & Pelser | DQ915863, sub 'Senecio pyramidatus' | GenBank | |
| | <i>Caputia scaposa</i> (DC.) B. Nord. & Pelser | KJ561206 | | original |
| | | GU818693, sub 'Senecio scaposus' | | GenBank |
| | | GU818694, sub 'Senecio scaposus' | | GenBank |
| | | GU818695, sub 'Senecio scaposus' | | GenBank |
| | | GU818696, sub 'Senecio scaposus' | | GenBank |
| | | GU818697, sub 'Senecio scaposus' | | GenBank |
| | | AF459931, sub 'Senecio scaposus' | | GenBank |
| | | DQ915864, sub 'Caputia scaposa var. caulescens' | | GenBank |
| | <i>Caputia tomentosa</i> (Haw.) B. Nord. & Pelser | KJ561193 | | original |
| | | DQ915862, sub 'Senecio haworthii' | | GenBank |
| | <i>Acrisione cymosa</i> (J. Rémy) B. Nord. | EF538144 | | GenBank |
| | <i>Brachyglottis haastii</i> (Hook. f.) B. Nord. | AY554099 | | GenBank |
| | <i>Brachyglottis huntii</i> (F. Muell.) B. Nord. | AY554100 | | GenBank |
| | <i>Brachyglottis kirkii</i> (Kirk) C.J. Webb | AY554101 | | GenBank |
| | <i>Brachyglottis perdicioides</i> (Hook. f.) B. Nord. | AY554102 | | GenBank |
| | <i>Brachyglottis repanda</i> J.R. Forst. & G. Forst. | AY554103 | | GenBank |
| | | EF635458 | | GenBank |
| | <i>Brachyglottis sciadophila</i> (Raoul) B. Nord. | AY554104 | | GenBank |
| <i>Haastia pulvinaris</i> Hook. f. | AF422122 | | GenBank | |
| <i>Haastia recurva</i> Hook. f. | AY554106 | | GenBank | |
| <i>Haastia sinclairii</i> Hook. f. | AY554107 | | GenBank | |
| <i>Papuacalia sandsii</i> D.J.N. Hind & R.J. Johns | EF538278 | | GenBank | |
| <i>Traversia baccharoides</i> Hook. f. | AF422139 | | GenBank | |
| Othonnas | <i>Crassothonna alba</i> (Compton) B. Nord. | EF538272, sub 'Othonna alba' | GenBank | |
| | <i>Crassothonna calalioides</i> (L. f.) B. Nord. | EU667499 | GenBank | |
| | <i>Crassothonna capensis</i> (L.H. Bailey) B. Nord. | KJ561180, sub 'Othonna capensis' | | original |
| | | AF459960, sub 'Othonna capensis' | | GenBank |
| | <i>Crassothonna sedifolia</i> (DC.) B. Nord. | EU667479, sub 'Othonna sedifolia' | | GenBank |
| | | EU667492, sub 'Othonna sedifolia' | | GenBank |
| | <i>Othonna amplexifolia</i> DC. | EF538273 | | GenBank |
| | <i>Othonna auriculifolia</i> DC. | EF538274 | | GenBank |
| <i>Othonna eriocarpa</i> (DC.) Sch. Bip. | EU667484 | | GenBank | |
| <i>Othonna euphorbioides</i> Hutch. | EU667494 | | GenBank | |

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|------------------------|--|---|----------|
| Genuine <i>Senecio</i> | <i>Senecio nemorensis</i> L. | AF459937 | GenBank |
| | <i>Senecio telekii</i> (Schweinf.) O. Hoffm. | EF538387 | GenBank |
| | <i>Senecio viscosus</i> L. | AF097539 | GenBank |
| | <i>Senecio vulgaris</i> L. | AF097541 | GenBank |
| | | AF422136 | GenBank |
| | | EF538396 | GenBank |
| Other Senecionoids | <i>Dendrosenecio battiscombii</i> (R.E. Fr. & T.C.E. Fr.) E.B. Knox | EF538185 | GenBank |
| | <i>Dendrosenecio kilimandjari</i> (Mildbr.) E.B. Knox | AF459967, sub ' <i>Dendrosenecio kilimanjari</i> subsp. <i>cottonii</i> ' | GenBank |
| | | AY953933, sub ' <i>Dendrosenecio kilimanjari</i> subsp. <i>cottonii</i> ' | GenBank |
| | <i>Iranecio bulghardaghensis</i> (Soldano) D. Heller | EF538239 | GenBank |
| | <i>Iranecio jurineifolius</i> (Boiss. & Balansa) C. Jeffrey | EF538240 | GenBank |
| | <i>Iranecio paucilobus</i> (DC.) B. Nord. | EF538241 | GenBank |
| | <i>Iranecio taraxacifolius</i> (M. Bieb.) C. Jeffrey | EF538242 | GenBank |
| Cacalioids | <i>Hasteola robusta</i> (Tolm.) Pojark. | KJ561177, sub ' <i>Cacalia robusta</i> Tolm.' | original |
| | <i>Hasteola tshonoskii</i> (Koidz.) Pojark. | KJ561178, sub ' <i>Cacalia tshonoskii</i> Koidz.' | original |
| | <i>Parasenecio auriculatus</i> (DC.) J.R. Grant | KJ561175, sub ' <i>Cacalia auriculata</i> DC.' | original |
| | <i>Parasenecio hastatus</i> (L.) H. Koyama | KJ561176, sub ' <i>Cacalia hastata</i> L.' | original |
| | <i>Syneilesis aconitifolia</i> (Bunge) Maxim. | KJ561179, sub ' <i>Cacalia aconitifolia</i> Bunge' | original |
| | <i>Paragynoxys neodendroides</i> (Cuatrec.) Cuatrec. | EF538280 | GenBank |
| | <i>Roldana albonervia</i> (Greenm.) H. Rob. & Brettell | EF538291 | GenBank |
| | <i>Roldana lineolata</i> (DC.) H. Rob. & Brettell | EF538292 | GenBank |
| | <i>Roldana petasitis</i> (Sims) H. Rob. & Brettell | KJ561181 | original |
| | | EF538293 | GenBank |
| | <i>Roldana suffulta</i> (Greenm.) H. Rob. & Brettell (= <i>Cacalia suffulta</i> Greenm.) | GU818631 | GenBank |
| Outgroup | <i>Tussilago farfara</i> L. | AY176167 | GenBank |
| | | EU785941 | GenBank |

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