

A NEW SUBSPECIES OF *SENECIO MOHAVENSIS* (*COMPOSITAE*) REVEALS OLD–NEW WORLD SPECIES DISJUNCTION

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Examination of morphology, ploidy and interfertility in the two subspecies of the Old World *Senecio flavus* (Decne.) Sch. Bip. (*Compositae*) and the closely related New World *S. mohavensis* A. Gray does not support the subspecific taxonomy of *S. flavus*. On the basis of our results *S. flavus* subsp. *breviflorus* Kadereit is transferred to *S. mohavensis* as a new subspecies: *S. mohavensis* subsp. *breviflorus* (Kadereit) M. Coleman *comb. nov.* The new subspecies has a distribution that includes Arabia, the Middle East, Sinai, Iran, Afghanistan, Djibouti, and the Thar Desert of Pakistan. The type subspecies of *S. mohavensis* occurs in the Mojave and Sonoran deserts of North America, providing an unusual disjunct distribution at the species level. Separation from *S. flavus* is based upon differences in morphology and chromosome number. *Senecio flavus* is diploid ($2n=20$), while both subspecies of *S. mohavensis* are tetraploid ($2n=40$). Further support for the new taxonomic treatment is provided by the results of controlled crosses. No artificial hybrids have been generated from crosses made between the previously recognized subspecies of *S. flavus*, while crosses between the newly recognized subspecies of *S. mohavensis* have produced fertile hybrids. The fertility of the hybrids is significantly lower than the parental taxa ($P<0.001$), indicating partial genetic divergence since isolation. Previous studies of isozyme and cpDNA variation in all three taxa also support the new treatment. The similarity of the *S. mohavensis* subspecies suggests a relatively recent separation, although the amount of genetic divergence does not support a post-Colombian introduction. Given that land bridges to North America via Beringia and the North Atlantic last existed in the Oligocene, long-distance dispersal seems the most likely explanation. Natural dispersal to rather than from the New World is supported, but whether this took place in an easterly or westerly direction is unclear. The evolution of *S. mohavensis* remains equivocal.

Keywords. *Asteraceae*, long-distance dispersal, polyploidy, *Senecio flavus*.

INTRODUCTION

Senecio flavus (Decne.) Sch. Bip. is described in the most recent revision of *Senecio* L. section *Senecio* (Alexander, 1979) as a radiate or non-radiate, short-lived annual of deserts and rocky habitats, with a distribution including the Canary Islands, N Africa, Arabia and Israel. Records of *S. flavus* have also been made from Namibia (Merxmüller, 1967), Chad and Mauritania (SONNERAT database of P), Iran, Afghanistan and Pakistan (Nordenstam, 1989), and SE Spain (Kadereit, 1984). We have seen herbarium material from throughout the range.

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The present location of type material of *S. flavus*, collected from Sinai by Nicolas Bové in 1831, is unknown. The main recipients of Bové's collection were Brussels (BR), Cambridge (CGE), Florence (FI), Geneva (G), Leiden (L), Paris (P) and Vienna (W), all of which have been checked without success. The species was originally described in the genus *Crassocephalum* Moench by Decaisne (1834), and was reported to be non-radiate. However, it has previously been noted that *S. flavus* also occurs with small ray-florets at the eastern end of its range (Feinbrun-Dothan, 1978; Alexander, 1979). Our examination of herbarium material of *S. flavus* has revealed that the radiate plants occur extensively in SW Asia, with the western limit in Sinai and the eastern limit in Pakistan. A single specimen was also identified from Djibouti, extending the known distribution to the south. Sinai represents the only known area where radiate and non-radiate plants are sympatric.

Kadereit (1984) described the radiate plants as *S. flavus* subsp. *breviflorus*. The basis for this was the virtually allopatric distribution of the floral polymorphism and the discovery that ray-floret achenes are epappose, whilst the marginal florets in non-radiate plants produce normally pappose achenes. In all other respects Kadereit (1984) regarded the radiate and non-radiate plants to be morphologically indistinguishable.

Radiate and non-radiate individuals also exist in *S. mohavensis* A. Gray. This species is morphologically very similar to *S. flavus* subsp. *breviflorus* but occurs in the Mojave and Sonoran deserts of North America. Unlike *S. flavus* subsp. *breviflorus*, radiate individuals of *S. mohavensis* generally have rays of irregular formation composed of two or three teeth of varying length. Gray (1884) mentioned these rays as deformed in his original description of the species, although he described it as typically non-radiate.

The morphological similarity between *S. flavus* subsp. *breviflorus* and *S. mohavensis* is supported by the existing molecular data (isozymes and cpDNA), which have revealed higher similarity between these two taxa than between either of them and *S. flavus* subsp. *flavus* (Liston *et al.*, 1989; Liston & Kadereit, 1995).

Chromosome counts have previously been carried out for these taxa, although uncertainty about identifications limits the usefulness of some of these. Alexander (1979) reported a count of $2n=20$ for *S. flavus*, which probably relates to subspecies *flavus* (Alexander, personal communication, 1999). It should be pointed out that Alexander's (1979) work predates the division of *S. flavus* into two subspecies. It has subsequently been assumed that both subspecies of *S. flavus* are diploid. The validity of this assumption has been brought into question by a chromosome count of $2n=40$ for *S. flavus* (Diaz-Lifante *et al.*, 1992). Unfortunately, the material used by Diaz-Lifante *et al.* (1992) was not identified to subspecies and we have not seen voucher material. However, based on the known distribution, its origin in Israel would indicate *S. flavus* subsp. *breviflorus*. *Senecio mohavensis* has only ever been recorded as a tetraploid (Ornduff *et al.*, 1963).

The aim of this study has been to reassess the taxonomic relationships between all three taxa. The existing molecular data (Liston *et al.*, 1989; Liston & Kadereit, 1995) do not provide support for the current taxonomy and chromosome numbers

in the subspecies of *S. flavus* remain uncertain. Consequently, this study has re-examined morphology and chromosome number. Taxonomic and evolutionary relationships have also been addressed through controlled crosses between the two subspecies of *S. flavus*, and between *S. flavus* subsp. *breviflorus* and *S. mohavensis*.

MATERIALS AND METHODS

Chromosome counts were carried out from root squash preparations of cultivated plants from 10 geographically separated populations representing all three taxa (Table 1). Voucher specimens were deposited at the Royal Botanic Garden Edinburgh (E).

The same cultivated material was also used to investigate interfertility. All three taxa exhibit high levels of self-compatibility so it was necessary to emasculate the maternal plants. Gibbs (1971), working with short rayed and non-radiate *Senecio*, found that removal of the apical 1mm of the capitulum at the correct stage of development removed most anther tissue. This method was less successful in *S. mohavensis* and *S. flavus* and careful washing away of self-pollen was required. The emasculation method finally adopted was the use of water-based typewriter correction fluid to cover all but the ray-florets as these lack anthers. The same technique was also used to emasculate non-radiate plants successfully in the case of *S. flavus* subsp. *flavus* as the marginal florets are predominantly female.

Herbarium material of all three taxa was examined for diagnostic morphological characters.

TABLE 1. Location of *Senecio* used in cytological investigations and crossing experiments

Country	Location	Voucher
<i>S. mohavensis</i>		
North America	Arizona, Painted Rock State Park	Coleman 27/00
	California, Zzyzyx	Coleman 29/00
	Nevada, Eldorado Canyon	Coleman 28/00
<i>S. flavus</i>		
subsp. <i>breviflorus</i>		
Israel	Dead Sea, Khirbet Mezin	Coleman 23/00
	Arava Valley, S of Hazeva	Coleman 05/00
	Paran, Be'er Menuha	Coleman 22/00
	Paran, Ha Meshar	Coleman 21/00
Sinai	Gebel Abbas	Coleman 08/00
subsp. <i>flavus</i>		
Morocco	Asni	Coleman 31/00
Sinai	Sharn-el-Sheik to Dahab	Coleman 10/00

All voucher specimens at E.

RESULTS

Chromosome counts showed that all three individuals of *S. mohavensis* and all five individuals of *S. flavus* subsp. *breviflorus* were tetraploid ($2n=40$), whilst both individuals of *S. flavus* subsp. *flavus* were diploid ($2n=20$).

Despite repeated reciprocal crosses between *S. flavus* subsp. *breviflorus* and *S. flavus* subsp. *flavus* no hybrids were generated. A small number of plants corresponding to the maternal species were raised from the crosses (due to self-pollen not being totally removed) but generally poor achenes were set.

Crosses between *S. mohavensis* and *S. flavus* subsp. *breviflorus* were successful (material from Israel and North America, see Table 1) and yielded fertile F_1 hybrids that displayed marked hybrid vigour and were generally of intermediate morphology. However, hybrids that had a *S. mohavensis* parent that was radiate produced ray-florets that were larger than either parent and normally developed, rather than of the deformed type seen in *S. mohavensis*. This may represent an example of transgressive segregation (Rieseberg *et al.*, 1999). No difficulty was experienced in repeating this cross using either taxon as the maternal parent. Herbarium specimens of the hybrid plants produced have been deposited at the Royal Botanic Garden Edinburgh (E).

Although the F_1 hybrids generated were fertile and F_2 plants were raised, casual observation of the percentage of normally developed achenes in capitula of the F_1 hybrids indicated a marked reduction in fertility. This was tested by calculating the percentage of normally developed achenes in 10 capitula from each of three individuals of the F_1 hybrids and parental taxa. Due to the highly autogamous nature of the parental taxa the achenes produced probably resulted from self-pollination, although a low proportion of crosses may have occurred as the capitula were not bagged. In this case pollen is not a limiting factor to seed set so its source is not important; what is being measured is female fertility. Mean percentage of normal achenes with standard errors for the total of 30 capitula per taxon were as follows: *S. mohavensis* 71.23 ± 4.02 , *S. flavus* subsp. *breviflorus* 74.38 ± 3.20 and F_1 hybrids 24.44 ± 2.00 . The percentage values were arcsin transformed and subjected to a two-level nested analysis of variance, in which variance between taxa and variance between plants within taxa was tested (Table 2). The analysis showed the reduction of fertility in the hybrids to be highly significant ($P < 0.001$), while variance between plants within taxa was not significant ($P = 0.401$) (Table 2).

Our findings, in conjunction with the existing molecular data (Liston *et al.*, 1989; Liston & Kadereit, 1995), lead us to conclude that it is necessary to transfer *S. flavus* subsp. *breviflorus* to *S. mohavensis* as a subspecies.

Senecio mohavensis A. Gray subsp. **breviflorus** (Kadereit) M. Coleman, **comb. nov.**
Illustrations: Nordenstam, Fl. Iranica 164: Tab. 63 (1989); Feinbrun-Dothan, Fl. Palaestina 3: Tab. 597 (1977).

TABLE 2. Results of a nested analysis of variance (ANOVA) of fertility (arcsin transformed percentage of normal seed) in *S. mohavensis*, *S. flavus* subsp. *breviflorus* and their F₁ hybrid. Ten capitula from each of three plants in each taxon were sampled

Source	df	SS	MS	F ratio	P value
Between taxa	2	19193.6	9596.8	69.98	<0.001
Plants within taxa	6	862.1	143.7	1.05	0.401
Error	81	11108.2	137.1		
Total	89	31163.8			

Abbreviations: df, degrees of freedom; SS, sum of squares; MS, mean squares.

Basionym: *S. flavus* subsp. *breviflorus* Kadereit, Bot. Jahrb. Syst. 104: 510 (1984).
Type: Jordan, Azraq ed Druz, Gillet 15569 (holo. G – n.v.).

Erect, glabrous, glaucous annual, 5–20(–40)cm tall. *Stems* terete, finely ridged. *Leaves* 1–4 × 0.5–2cm, simple or shallowly lobed, margin entire to dentate with minute wart-like projections, frequently purple below. Lower cauline leaves ovate, sessile or attenuate into petiole of 0.5–2cm, middle and upper cauline leaves auriculate and amplexicaul. *Capitula* cylindrical, arranged in lax corymbs. *Calyculus bracts* 1–5. *Phyllaries* c.13, 6–8mm. *Ray-floret limbs* c.13, 1.5–3.5mm, pale yellow, sometimes with reddish veins on the abaxial surface. *Achenes* 2–3mm, subcylindrical, strigose. *Pappus setae* c.4mm, absent from achenes of the ray-florets.

Flowering 3–5. Desert and rocky places, often in gullies and below north-facing cliffs.

Distribution. Egypt (Sinai), Djibouti, Israel, Jordan, Syria, Saudi Arabia, Oman, United Arab Emirates, Kuwait, Iran, Afghanistan and Pakistan (Thar Desert) (Fig. 1).

Type material of S. mohavensis subsp. mohavensis. The material cited by Gray (1884) in his original description was collected by *Lemmon* from near the Colorado River and by *Pringle* from Sonora. No holotype was designated by Gray (1884) and formal lectotypification has not been carried out. However, Greenman (1915) incorrectly cited *Lemmon* 3129 (GH) as the holotype in *Ann. Missouri Bot. Gard.* 2: 580 (1915) and this constitutes a valid, albeit inadvertent, lectotypification. It is worth noting that the handwriting on this specimen indicates that Greenman added the number 3129 and the specimen should be cited as follows: Mojave desert, 11 v 1884, *Lemmon* s.n.

Nomenclatural notes. Although we do not consider the new subspecies sufficiently distinct to justify specific rank, the description of *S. decaisnei* DC. (one of three synonyms of *S. flavus* listed by Alexander, 1979) agrees well with *S. mohavensis* subsp. *breviflorus*, the only disagreement being the lack of ray-florets. The three specimens of *S. decaisnei* in the De Candolle herbarium (microfiche E) come from Jordan, Saudi Arabia and Egypt. Duplicates of the specimens from Jordan and



FIG. 1. Distribution of *Senecio flavus* (filled squares) and *S. mohavensis* subsp. *breviflorus* (filled circles). All records from herbarium material.

Saudi Arabia (E) (Arabiae Petraeae, Wadi Hebran, *Schimper* 1835: 344; Arabiae Felicis, Monte Gesser, *Schimper* 1837: 994) correspond to *S. mohavensis* subsp. *breviflorus*, whilst the Egyptian specimen (in deserto convallis, Meghegbe, *Acerbi* s.n.) corresponds to *S. flavus*. This may explain the confusing combination of characters described for *S. decaisnei*. The name *S. decaisnei* is also illegitimate because De Candolle cited *Crassocephalum flavum* Decne. in synonymy, thereby transferring a species with a legitimate name (*Crassocephalum flavum*) to a different genus without retention of the specific epithet (see ICBN, Art. 11.4; Greuter *et al.*, 2000). This action means that, although two of the three specimens of *S. decaisnei* correspond to *S. mohavensis* subsp. *breviflorus*, the type of *C. flavum* must also typify *S. decaisnei*.

Specimens examined.

S. mohavensis subsp. *mohavensis*

UNITED STATES OF AMERICA. CALIFORNIA: Death Valley National Monument, *DeBuhr & Wallace* 863 (E); Mojave Desert, *Lemmon* s.n. (GH, lectotype); *Zzyzyx*, *Liston* 645-3 (E); Death Valley, *Munz* 16468 (HUH); Death Valley National Monument, *Steward*

7367 (HUH); ARIZONA, Painted Rock State Park, *Elias* 10190 (E); NEVADA, Eldorado Canyon, *Niles* 5375 (E).

S. mohavensis subsp. *breviflorus*

EGYPT. Dchebel Ataka, *Bornmüller* 10703 (E); Mount Sinai, *Schimper* 1835: s.n. (E).

ISRAEL. Nahal Paran, *Danin & Knees* 1219 (RNG); 8km SE of Mizpe Ramon, *Danin & Knees* 1147, 1167 (RNG); Nahal Zin, *Liston* 474/3 (RNG).

JORDAN. El Inab, *Hunting Aero Survey* 73b (E); Arabiae Petraeae, Wadi Hebran, *Schimper* 1835: 344 (E, authentic material of *S. decaisnei*).

SYRIA. *Burton* s.n. (E); Wadi Jewerah, *Lowne* s.n. (E).

SAUDI ARABIA. Uema Figra 60km W of Madinah, *Collenette* 7077 (E); Al-Figra, *Fayed* 1364 (E); Taif escarpment SE of Mecca, *Lavranos & Collenette* 18508 (E); Jabal Dawmat al-Awdah, *Mandaville* 8861 (E); Jabal, *Naylor* 279 (E); Arabiae Felicis, Monte Gesser, *Schimper* 1837: 994 (E, authentic material of *S. decaisnei*).

OMAN. Wadi Bani Kharus, *Edmondson* 3225 (E); Wadi Falah, *Edmondson* 3258 (E); Al Fay, *FitzGerald* 39 (RNG); Muttrah, *Maconochie* 3288 (E); 51km SE of Nizwa-Sur, *Maconochie* 3386 (E); Bausher, *Rubens* 6a (E); Ar Rustaq, *Rubens* 100 (E).

UNITED ARAB EMIRATES. Sharjah, Jebel Mileiha, *FitzGerald* 9 (RNG); Wadi Shawka, *FitzGerald* 63 (RNG); Jebel Hafit Nr. Al Ain, *Western* 574 (E); 10km N Masafi, *Western* 1153 (E); 10km N Masafi, *Western* 1218 (E).

KUWAIT. *Macintyre* 19 (E).

IRAN. Bandar Abbas to Sirjan, *Léonard* 5937 (E); Kuh-e Genou, *Wendelbo & Foroughi* 15523 (E); 22km N of Qotbabad, *Wendelbo & Foroughi* 15822 (E).

DJIBOUTI. Egerealeita, Gauda Mts, *Lavranos* 10492 (E).

PAKISTAN. Kirana Hills, Sargodha, *Stewart* 10930 (K); *Stewart* s.n. (E).

S. flavus

CANARY ISLANDS. Gran Canaria, Galdaz, *Murray* s.n. (K); Fuerteventura, Puerto de la Peña, *Nydegger* 26145 (RNG); Gran Canaria, *Pitard* 210 (L).

MOROCCO. 21km from Asni, *Ait Lafkih et al.* 751 (RNG); Marrakech to Tizi n'Test, *Blanché et al.* 9459 (RNG); 88km from Tiznit to Tafraoute, *Davis* 48741 (E); Ammeln valley, *Davis* 53853 (E); Marrakech, Ouirgane, *Castroviejo et al.* 4664 (RNG); 30km SE of Aït-Baha, Nr. Tioulit, *Jury et al.* 14388 (RNG); 27km W of Tata, *Jury et al.* 14454 (RNG).

ALGERIA. Naama, Aïn Hadjhadj, *Bernedi et al.* 2368 (RNG); Ghardaïa, *Chevallier* s.n. (E); Metlili, *Cosson* s.n. (K).

CHAD. Tarso Tousside, Tibesti, *Grove & Johnson* 22 (K); Trouan Natron, Tibesti, *Hinchingsbrook* 28 (K).

EGYPT. Deserto convallis, Meghegbe, *Acerbi* s.n. (G-DC. microfiche E, authentic material of *S. decaisnei*); Sukari, *Sheded* 6205 (E).

NAMIBIA. Aroab, Keetmanshoop, *de Winter* 3365 (K); Maltahöhe, *Merxmüller & Giess* 28206 (M); Lüderitz-Süd, *Merxmüller & Giess* 32284 (M); Helmeringhausen, *Oliver et al.* 6491 (K); Haikamchab, *Searoch* 7668 (K); Chuosberge, *Seydel* 2016 (L); Kuisel, *Stuey* 2636 (K); Karibib, *Tölken & Hardy* s.n. (K); 22km W of Rosh Pinah, *van Wyk* 8868 (M).

SPAIN. Sierra Alhamilla, Almeria, *Churchill* s.n. (K); Sierra Alhamilla, Almeria, *Ellman & Sandwith* 932 (K); Almeria, *Ripley* 72 (K).

Key to Senecio flavus and the two subspecies of S. mohavensis

- 1a. Lower cauline leaves triangular to cordate; petiole 2–5cm _____ **S. flavus**
 1b. Lower cauline leaves ovate; petiole less than 2cm or absent _____ **2**

- 2a. Ray-florets always present and normally developed; ray-floret achenes epappose _____ ***S. mohavensis* subsp. *breviflorus***
- 2b. Ray-florets present or absent but where present variable in length and often divided into two or three irregular teeth; marginal/ray-floret achenes with an obvious pappus _____ ***S. mohavensis* subsp. *mohavensis***

DISCUSSION

The floral and pappus characters previously described (Kadereit, 1984) allow easy separation of *S. mohavensis* subsp. *breviflorus* from *S. flavus*. Our examination of herbarium material has revealed further differences in the morphology that allow the determination of immature plants and those lacking flowers and fruit. The new morphological characters are leaf shape and nature of the margin. The lower cauline leaves of *S. mohavensis* subsp. *breviflorus* are ovate and sessile, or have a petiole of up to 2cm into which the leaf blade is attenuate. The middle and upper cauline leaves are amplexicaul. The margins may be entire or dentate and frequently have minute wart-like projections. In contrast, the lower and middle cauline leaves of *S. flavus* have a triangular to cordate outline with angular teeth and a petiole of up to 5cm. The upper cauline leaves are amplexicaul and strongly dentate. The important distinction between the species is that although both subspecies of *S. mohavensis* may have petiolate lower cauline leaves, these are never cordate in outline (Fig. 2). Morphological distinction of the two subspecies of *S. mohavensis* is less apparent from leaf morphology. The type subspecies usually exhibits more coarsely toothed leaf margins, although material of *S. mohavensis* subsp. *breviflorus* can exhibit the same characteristics (Fig. 2).

Marginal floret and ray-floret morphology associated with pappus variation does provide taxonomically useful characters for both specific and subspecific distinction. In *S. flavus* the capitula are disciform as the marginal florets differ from the inner florets in having four teeth rather than five and are female rather than hermaphrodite (rarely small anthers are present). When the four synonyms of *S. flavus* are considered, it is apparent that the disciform condition has not been treated uniformly. In two cases (*S. flavus* and *S. brevilinguis* S. Moore) very short (c.1mm) ray-florets have been described, whilst in the remaining three (*C. flavum*, *S. decaisnei* and *S. claviseta* Pomel) non-radiate capitula are described. It is worth noting that the description of *S. flavus* by Schultz in *Phytographia Canariensis* (Barker-Webb & Berthelot, 1845) includes a detailed illustration (Tab. 107) that matches the non-radiate material we have seen and yet does not depict the short rays mentioned in Schultz's description. This apparent inconsistency, and the disagreement between the various descriptions, seems to result from the extremely small size of the three corolla teeth that could be interpreted as a ray. The significant differences in leaf morphology between *S. flavus* and *S. mohavensis* that have already been mentioned prevent this confusion from blurring the distinction between the species. In non-radiate plants of *S. mohavensis* subsp. *mohavensis* all florets are alike, and hence the capitula are

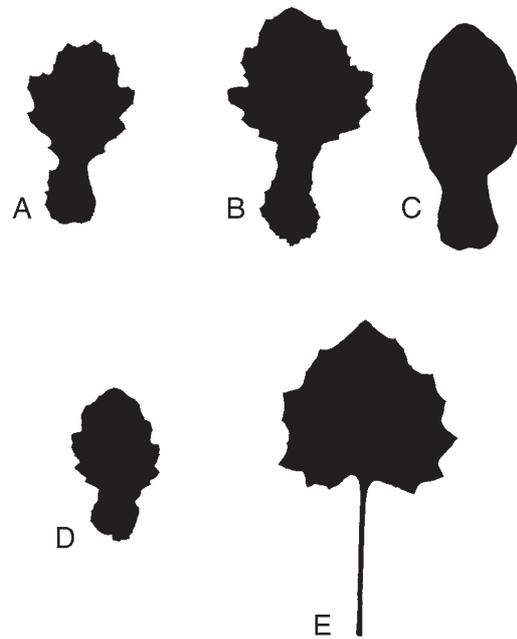


FIG. 2. A–E, mid-cauline leaf silhouettes. A, *S. mohavensis* subsp. *mohavensis*; B–D (B and C, Israel; D, Sinai), *S. mohavensis* subsp. *breviflorus*; E, *S. flavus*. All $\times 0.5$.

discoid. Pappus morphology is useful in terms of distinguishing the subspecies of *S. mohavensis*. The achenes derived from the ray-florets or marginal florets of the type subspecies have a normally developed pappus, whilst in *S. mohavensis* subsp. *breviflorus* a pappus is absent. Furthermore, the ray-florets of the type subspecies are often divided into two or three irregular teeth. In contrast, *S. mohavensis* subsp. *breviflorus* has normally developed ray-florets. Some apparently non-radiate plants of *S. mohavensis* subsp. *mohavensis* have highly reduced ray-florets that cannot be detected without dissection of the capitulum.

The slight morphological distinction of the tetraploid taxa, shared ploidy and their reproductive compatibility all demonstrate close similarity between these taxa despite their large disjunction. However, the significant reduction in fertility of the F_1 hybrids generated between these taxa indicates that partial genetic divergence has occurred since isolation. Based upon this, it is most appropriate to treat the tetraploid taxa as two subspecies of a widely disjunct species. In contrast, the diploid *S. flavus* is morphologically and cytologically distinct, as emphasized by its reproductive isolation. Treatment of *S. flavus* as conspecific with either of the tetraploid taxa would not reflect the taxonomic or evolutionary relationships. The apparent reproductive isolation of *S. mohavensis* subsp. *breviflorus* and *S. flavus* does, however, need to be viewed in the light of the small number of seed accessions used in the crosses.

Nevertheless, in Sinai these taxa are sympatric and none of the herbarium specimens examined from this area was of intermediate morphology.

The results of existing molecular investigations (Liston *et al.*, 1989; Liston & Kadereit, 1995) also support the new classification. In a brief review of these results given below, the taxa are primarily defined geographically as a return to the original classification (used in the papers cited) would be unnecessarily confusing.

High genetic similarity between the SW Asian and North American taxa was reported first by Liston *et al.* (1989) in an isozyme study of 13 enzyme systems. It was concluded that a relatively recent disjunction seemed most likely based upon the high degree of similarity. Chloroplast DNA (cpDNA) restriction site variation has further demonstrated a close genetic relationship between these taxa (Liston & Kadereit, 1995). In addition, close cpDNA similarity was demonstrated between the tetraploid taxa and *S. squalidus* L., the outgroup used in the analysis. *Senecio squalidus* is a diploid species morphologically very distinct from both the North American and SW Asian taxa. The explanation given for this unexpected similarity was that a Mediterranean species related to *S. squalidus* had been involved in the evolution of these taxa through interspecific hybridization and cpDNA capture (Liston & Kadereit, 1995).

The most recent molecular study (Comes & Abbott, 1999) did not include the North American taxon but does shed further light on the evolution of the SW Asian taxon. This study used nuclear data sets (ITS sequences and RAPDs) in conjunction with cpDNA restriction site variation. The cpDNA results agree with the earlier study of Liston & Kadereit (1995) in that the previously recognized subspecies of *S. flavus* were well differentiated from each other, while the SW Asian taxon was closely allied to a group of four widespread Mediterranean diploids. The discovery that sympatric *S. glaucus* L. subsp. *coronopifolius* (Maire) Alexander possessed an identical cpDNA haplotype and very similar internal transcribed spacer (ITS) sequence was taken as evidence for the capture of these molecules via introgressive hybridization (Comes & Abbott, 1999). Comes & Abbott (1999) concluded that *S. glaucus* subsp. *coronopifolius* acted as the maternal parent as it is known that cpDNA shows maternal inheritance in *Senecio* (Harris & Ingram, 1992). In the case of ITS capture the assumption is that homogenization of ITS repeats (Hillis & Dixon, 1991; Hillis *et al.*, 1991) has occurred in the direction of the maternal parent.

The main nuclear data set examined by Comes & Abbott (1999) was generated using randomly amplified polymorphic DNA (RAPD) primers. These markers are randomly scattered across all genomes but are generally assumed to reflect the nuclear genome due to the small size of the plastid genomes. The RAPD data indicated that the capture of ITS and cpDNA from *S. glaucus* subsp. *coronopifolius* had taken place in the absence of extensive nuclear introgression as the two former subspecies of *S. flavus* were grouped together (Comes & Abbott, 1999).

The discovery that the newly recognized *S. mohavensis* subsp. *breviflorus* is tetraploid, combined with the earlier evidence of chloroplast and ITS capture from *S. glaucus* subsp. *coronopifolius* (Comes & Abbott, 1999), means that future

investigations of its origin need to consider polyploid modes of evolution. Either a combination of autopolyploidy and introgression, or an allopolyploid hybrid of *S. flavus* and *S. glaucus* subsp. *coronopifolius*, can be invoked. The far closer morphological resemblance of *S. mohavensis* subsp. *breviflorus* to *S. flavus* than *S. glaucus* subsp. *coronopifolius*, combined with the apparent absence of nuclear genetic markers of the latter (Comes & Abbott, 1999), does not fit well with an allopolyploid origin. In allopolyploid species an additive profile of molecular markers would be predicted. In *Senecio* there is a documented case of diploid genetic material having introgressed into the tetraploid *S. vulgaris* L. (Lowe & Abbott, 2000), and this may represent a close parallel to the present situation.

However, Liston *et al.* (1989) found that two isozyme loci in *S. mohavensis* subsp. *breviflorus* were duplicated relative to *S. flavus*, while in *S. mohavensis* subsp. *mohavensis* four loci were duplicated relative to *S. mohavensis* subsp. *breviflorus*. Examination of selfed progeny revealed fixed heterozygosity at these loci with no segregation, supporting duplication of differentiated genes. In light of the fact that *S. mohavensis* is tetraploid, this fixed heterozygosity could be interpreted as evidence for an allopolyploid origin. In addition, although having said that an additive profile of molecular markers would be expected in an allopolyploid, investigation of artificial allopolyploids has shown rapid rates of genome evolution (for a review see Wendel, 2000). It is, therefore, important to note that *S. mohavensis* subsp. *breviflorus* has a widespread distribution in SW Asia, indicating that the taxon may have arisen long enough ago for significant genome evolution and the loss of an additive pattern. Allopolyploidy also has the advantage of providing a simple explanation for the existence of a single cpDNA genome as a single hybridization event could be responsible, although most allopolyploids examined have shown evidence of multiple origin (Soltis & Soltis, 2000). It would be expected that an autopolyploid taxon that had undergone subsequent introgression would contain both parental cpDNA genomes, due to the uniparental inheritance of the cpDNA genome and no *a priori* reason to suppose that both parental species had not contributed to the maternal line. To date a *S. flavus* cpDNA haplotype has not been recovered from *S. mohavensis* subsp. *breviflorus*, although only small and geographically restricted samples have been examined. In conclusion, the molecular data remain equivocal regarding auto- as opposed to allopolyploidy and further work is required.

Finally, the origin of the disjunct distributions exhibited by both *S. mohavensis* and *S. flavus* deserves comment. The disjunction of *S. flavus* between the arid zones of northern and southern Africa fits an established pattern of disjunction. A total of 41 species are listed as displaying this disjunction by de Winter (1971). In contrast, disjunction between the arid regions of the Old World and North America is poorly represented at the species level (Shmida, 1985). In the few cases that exist, most are assumed to be post-Colombian introductions to North America (Raven & Axelrod, 1978). However, at generic level this disjunction is not unusual. Stebbins & Day (1967) and Thulin (1994) list genera that display this disjunction. Stebbins & Day (1967) thought this pattern of vicarious species had arisen from migration between

the Old and New Worlds by means of the Bering Strait land bridge during the climatically favourable Oligocene to early Miocene. An alternative interpretation has been given by Thorne (1972), who viewed long-distance dispersal as a general explanation for floristic relationships between tropical Africa and tropical America.

The disjunction of *S. mohavensis* subsp. *breviflorus* between the Horn of Africa (Djibouti), Arabia and the adjacent countries of SW Asia provides another example of an established disjunction at the species level (Thulin, 1994). This disjunction can be regarded as an extension of a larger disjunction between the Horn of Africa and SW Africa, although here evidence at the species level is rather poor as recent studies have favoured the treatment of SW and NE African populations as distinct species (Thulin, 1990). The best remaining example of this disjunction at the species level is *Tribulocarpus dimorphanthus* (Pax) S. Moore (Verdcourt, 1957, 1969; Thulin, 1994). It is notable that the present study continues this pattern by recognizing the SW Asian populations formerly ascribed to *S. flavus* as a distinct species. Many genera show a disjunction between the arid regions of SW and NE Africa, and an arid corridor during the Pleistocene has frequently been given as an explanation (Goldblatt, 1978; Werger, 1978).

Based upon the ages of the respective deserts, Liston *et al.* (1989) postulated a SW African origin for the group, followed by migration to NE Africa along an arid corridor during the Pleistocene, evolution of a distinct taxon in SW Asia, and finally dispersal from there across the Atlantic Ocean to North America. Liston *et al.* (1989) supported this scenario with evidence based upon the absence of close relatives in North America, the absence of seed-eating fruit flies (*Tephritidae*) found in all native American *Compositae* and the existence of a centre of diversity for the genus in southern Africa. Liston *et al.* (1989) argued for the native status of the North American taxon based upon its limited distribution and the remote and undisturbed nature of its habitats. This is less convincing as cases of introduced plant species invading remote and predominantly natural communities are well known, such as *Epipactis helleborine* (L.) Crantz in North America. The explanation of natural dispersal from SW Asia to North America was given as the attachment of seeds to migrating birds by the mucilage they exude upon wetting (Liston *et al.*, 1989).

As all three taxa are highly autogamous, long-distance dispersal events of single seeds could potentially establish new populations. The suggestion that migrating birds could have carried seed across the Atlantic Ocean cannot be ruled out, even though no birds now show this migration pattern (Liston *et al.*, 1989). It does, however, seem rather surprising that *S. mohavensis* reached North America without spreading throughout the apparently suitable habitat of N Africa. Likewise, the absence of *S. flavus* from the Horn of Africa and Arabia is difficult to explain if migration to NE Africa took place as suggested along an eastern arid corridor (Liston *et al.*, 1989). These anomalies do point to subtle ecological differences between *S. flavus* and *S. mohavensis* that largely prevent sympatry.

An alternative route to North America through Central Asia has not previously been suggested, even though the distance is no greater. Despite the existence of

S. mohavensis subsp. *breviflorus* in the Thar Desert of Pakistan, this still leaves Central Asia and the Pacific Ocean as barriers to dispersal, and there seems to be little to favour an eastward over a westward dispersal. Pushing the disjunction back to the early Oligocene, at which time land bridges existed across the Bering Strait and the North Atlantic (Tiffney, 1985), does not seem reasonable given the close morphological and molecular similarity, and the fact that the earliest *Compositae* fossils also date from this epoch (Graham, 1996). Consequently, long-distance dispersal does seem to be the most likely explanation of the disjunction.

Thulin (1994), in a review of disjunct distributions that include the arid parts of the Horn of Africa, did not favour either a Beringian migration or long-distance dispersal to North America. He considered both unlikely in the classic example of the genus *Thamnosma* Torr. & Frém. (Thulin, 1994). In defence of long-distance dispersal in the case of *S. mohavensis*, we would point out that morphological and genetic differentiation is sufficient to doubt a post-Colombian introduction. It is also worth reiterating that the production of a heavy mucilage by the seeds may provide a plausible means of long-distance dispersal via birds.

At the species level *S. mohavensis* is the only good example of a SW Asian–SW North American disjunction. Two closely related species of *Plantago* L. with this disjunction have been studied by Stebbins & Day (1967), who demonstrated partial sterility of hybrids and minor morphological and cytological differences. Interestingly, these species also have seeds that produce a mucilage on wetting (Stebbins & Day, 1967). The *Plantago* example has been interpreted differently by Bassett & Baum (1969), who regard the pair as conspecific and of human introduction to North America. Raven (1971) has cited a number of genera with very closely related species that need re-evaluation, so further examples at the species level may come to light. In terms of future work, Liston (1997) has stressed the potential of molecular data, in particular the ‘molecular clock’ (Zuckerandl & Pauling, 1965), to distinguish between vicariant (ancient) and dispersalist (recent) hypotheses. It would appear that a combination of cladistic biogeography and detailed study of potential long-distance dispersal mechanisms offers great potential to enhance our understanding of this unusual disjunct distribution.

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