



Sedum album subsp. *rupi-melitense* (Crassulaceae), a new vegetatively reproducing subspecies from Malta (Maltese Islands, Central Mediterranean)

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Abstract

Plants of *Sedum album* (*Sedum* ser. *Alba*; Crassulaceae) from Malta (Maltese Islands) differ from previously known *S. album* plants in having very rarely formed inflorescences mostly without peduncular leaves and floral bracts, flowers in which (3–)5 stamens of one whorl, mostly of the antepetalous one, have dysfunctional and often abortive anthers and only the stamens of the other whorl having 5, dark maroon to blackish-brown, mostly indehiscent anthers at anthesis, pollen which is partly deformed and shrivelled, carpels without nectary scales, and fruits and seeds which remain undeveloped and sterile. The Maltese plants have apparently switched from generative to almost exclusively vegetative reproduction and are described as a new endemic subspecies *Sedum album* subsp. *rupi-melitense*. The local history, distribution, habitat, phenology, and conservation status of this new taxon (which is categorized as Critically Endangered according to IUCN Red List Criteria) are discussed.

Key words: asexual reproduction, chromosome number, endemic, Flora of Malta, Mediterranean Flora, IUCN Red List assessment, *Sedum gypsicola*, taxonomy, vegetative reproduction

Introduction

Sedum Linné (1753: 430) is by far the largest genus of the Crassulaceae and comprises some 420 species, distributed mainly in temperate and subtropical regions of the Northern Hemisphere (Thiede & Egli 2007). *Sedum* is found in most of Europe, but centred in the Mediterranean region: of 53 European species, less than ten occur in Northern Europe (Hart & Egli 2003).

In Europe, *Sedum album* Linné (1753: 432) is the most widespread *Sedum* species, distributed throughout in various habitats and it is accordingly very variable in the size and shape of the leaves, the length of the flowering shoots, the size of the inflorescences and flowers, and the size and shape of the petals. It is distributed from Northern Africa to 64° N in Scandinavia and from Morocco and Western Europe (Portugal and Spain) to western Russia, Anatolia, the Lebanon, Northwestern Iran and the Caucasus and is possibly not indigenous to the British Isles (Hart & Berg 1982; Jalas *et al.* 1999; Hart & Egli 2003). The similar *S. gypsicola* Boissier & Reuter (1842: 205) is rare in Europe and occurs locally on gypsum, marl, limestone and shale in Portugal, Spain, Italy (Sicily) and Croatia, but is also native in Morocco, Algeria and Tunisia (Greuter *et al.* 1986; Nikolić 1997; Hart & Egli 2003; Stephenson 2009; Marhold 2011). These two species constitute the dispecific *Sedum* series *Alba* A. Berger (1915: 452) which comprises sparingly to densely glandular pubescent perennials with alternate, terete, oblong, obtuse or rounded leaves, pedicellate flowers, erect follicles, and seeds with acute apex (Hart 1991; Hart & Egli 2003). In addition, both species share a chromosome base number of $x = 17$, are assumed to have descended from a common diploid ancestor, and can be hybridized artificially (Hart & Berg 1982). In the wild, no mixed populations and no natural hybrids between the two species are known (Hart & Berg 1982; Hart & Bleij 2003; Hart & Egli 2003). The detailed morphological study of *S. album* and *S. gypsicola* by Hart & Berg (1982) revealed the leaves densely covered with papillae in *S. gypsicola* vs. glabrous leaves in *S. album* remain as the sole non-overlapping difference. However, this “classical” separation of both species is not constant, since the papillosity may vary between populations of both species (Castroviejo &

Velayos 1995; Cano Carmona & Fernández Lopez 1988). Furthermore, *S. gypsicola* is not a strict gypsophyte and is in fact indifferent to its substrate (Castroviejo & Velayos 1995, 1997). Recently, some of the Sicilian populations of *S. gypsicola* were separated as a new subspecies *trinacriae* Afferni (2008: 65) (cf. Table 1).

TABLE 1. Characters of and differences between *Sedum album* subsp. *album* and *S. album* subsp. *rupi-melitense*. References: ¹Hart & Berg (1982); ²Castroviejo *et al.* (1997); ³Hart & Bleij (2003); ⁴Hart & Egli (2003).

Taxon / Character	<i>Sedum album</i> subsp. <i>album</i>	<i>Sedum album</i> subsp. <i>rupi-melitense</i>
Leaf arrangement	closely imbricate to ± divergent and somewhat further apart ¹	spreading, becoming imbricate-appressed distally (Figs. 3A, 3C)
Leaf shape	broad-elliptic to linear-oblong or linear, rarely ovate ¹	linear-elliptic to ovoid (Figs. 3A, 3B, 3C)
Leaf transection	terete or ± flattened adaxially ¹	terete or sometimes semiterete and flattened adaxially (Fig. 3B)
Leaf size	3.8–14.5 mm ¹	3–7 mm
Leaf indumentum	mostly glabrous, often ± densely papillate ² , leaves of flowering shoots occasionally with glandular hairs on the adaxial side ¹	very sparingly papillate, papillae < 10 per leaf (Fig. 3E, 3F)
Leaf colour	green parts usually tinged with red ¹	green, tinged amber to cinnabar red in the upper 1/3 during summer (Figs. 3C, 3G)
Indumentum of flowering shoots	basal parts always densely covered with glandular hairs, these also occur more sparingly in the upper part of flowering shoots of most plants ¹	densely glandular-hairy at base (Fig. 3D), sparingly above and at hardened part of stem below the leaves
Length of flowering shoots	5–30 cm ^{1,4}	up to 15 cm
Peduncular leaves and floral bracts	present ^{1,4}	absent, or, if present, only small and vestigial (Fig. 5A)
Petal length and shape	(1–)2–4(–5) mm ^{1,2} , acute to sub-obtuse ²	3.5 mm, obtuse to subacute (Figs. 4C, 4D).
Petal and filament colour	white, very often tinged with red or sometimes with a shade of pink ¹	wax-white, with a midvein sometimes fade pink at lower half (Figs. 4, 5)
Carpel colour and carpel indumentum	often tinged red or pinkish when young ¹ , papillate adaxially ²	slightly pink, papillate adaxially (Fig. 5B)
Nectary scales	present	absent (Fig. 5B)
Stamen number	10 with normal anthers ^{1,2}	10, but (3–)5 stamens with abortive anthers at anthesis (Figs. 4C, 4D)
Anther colour	dark red to dark violet, rarely dull yellow ^{1,2}	dark maroon to blackish-brown (Figs. 4C, 4D)
Style length	c. 1 mm ²	≤ 0.5 mm
Fruits and seeds	normal, fertile	undeveloped, sterile
Reproduction	by seeds and vegetatively	vegetatively (flowers extremely rare)
Flowering period	April–August ²	May–June
Chromosome number	2n = 32, 34, 36, 51, 56, 64, 68, 85, 102, 136 ¹	2n = 136 ¹
Distribution	Europe to W Russia, Anatolia, Lebanon, Iran, Caucasus; N Africa	Maltese Islands (Malta)
Soil and habitat	silicate, limestone, rarely on serpentine, indifferent to its substrate ²	calcareous soil in limestone at cliff edges (Fig. 2)
Altitude	0–2400 m ²	(0–)100–250 m

On Malta, Gulia (1874) recorded '*Sedum glanduliferum* Gussone' (1827: 519), now classified as a variety of *S. dasyphyllum* Linné (1753: 431), from San Ġorġ tal-Fawwara (Fig. 1, locality 7) along the coastal cliffs of Siġġiewi. Sommier & Caruana Gatto (1915) cited this record and added locations at Faqqanija, Wied Babu and Rdum il-Madliena (Fig. 1, localities 6, 9 and 4 respectively) for *S. dasyphyllum* and placed the Maltese plants in *S. dasyphyllum* var. *glanduliferum* (Guss.) Moris (1840: 125). Borg (1927) concurred with Sommier & Caruana Gatto with regards to the taxonomy and locations cited and included neighbouring sites or toponyms at Rdum il-Qaws and Rdum Dikkiena (Fig. 1, localities 2 and 5 respectively), hence extending slightly the distributional range of '*S. dasyphyllum*'. Haslam *et al.* (1977) cited the same records for '*S. dasyphyllum*' mentioned above. Having examined material from Malta, Hart & Berg (1982: 680, 691) identified the *Sedum* growing on the south cliffs of Malta as *S. album*. Greuter *et al.* (1986: 186), Jalas *et al.* (1999: 98) and Marhold (2011) also listed *S. album* for Malta, but not *S. dasyphyllum*. Lanfranco (1989:17, 2001:16) claimed that previous Maltese records of *S. dasyphyllum* should be ascribed to *S. album*, because all the records of *S. dasyphyllum* were from the same locations where populations of *S. album* resides. This identity was then followed by recent work such as Mifsud (2007), Darmanin (2009), Casha (2013: 313) and Stephenson (2014). It is not clear why early authors (Gulia 1874; Sommier & Caruana Gatto 1915; Moris 1840: 125; Borg 1927; Haslam *et al.* 1977) misidentified this population as *S. dasyphyllum*.

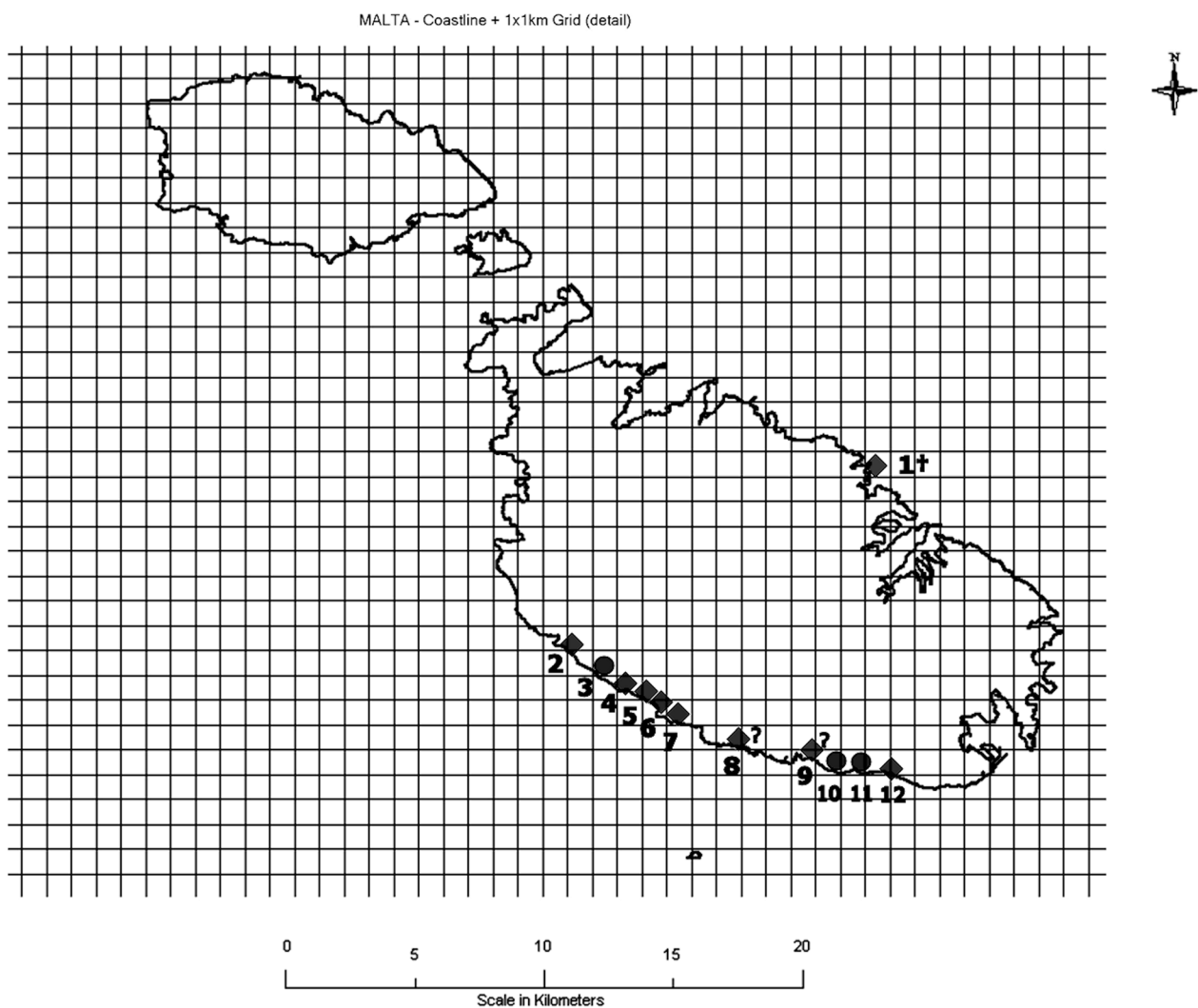


FIGURE 1. Distribution of *Sedum album* subsp. *rupi-melitense* on Malta (UTM, zone 33S, 1x1 km grid). The localities are enumerated from N to S and W to E (see text). Diamonds refer to literature records or personal communications confirmed during field surveys between 2012–2014, circles to new records, question marks (?) to unconfirmed literature records or personal communications, and a cross for a population which became extinct early this year.

In addition to *S. album*, five further species of *Sedum* are known to occur on the Maltese Islands: *S. caeruleum* Linné (1771: 241), *S. caespitosum* (Cavanilles,) de Candolle (1828: 405), *S. litoreum* Gussone (1826:185) *S. rubens* Linné (1753: 432), *S. stellatum* Linné (1753: 431) and *S. sediforme* (Jacquin) Pau (1909: 246) (Mifsud 2007;

Stephenson 2014). *Sedum dasyphyllum* does not occur in Malta, with its historical published records being based on misidentification, as mentioned above.

During field studies, the first author (SM) noted that Maltese *S. album* populations flower very rarely and appear to switch from generative to vegetative propagation. This paper aims to study the morphological characters, biology, ecology, and distribution of the Maltese *S. album* populations in the field and in cultivation in order to establish its peculiarities and differences from typical *S. album*.

Material and methods

Extensive field research was carried out on Malta by Stephen Mifsud [SM] and Owen Mifsud [OM] during the flowering period in May and June in 2013 and 2014 in order to collect and study living specimens of Maltese *S. album*. This followed after OM and later SM found flowering material in June 2012. Some of the studied plants were cultivated by SM in 2014 to study their growth, flowering and morphological features. Flowers from eight specimens and pollen from one specimen (stained with Acetocarmine) were studied in detail with a dissecting microscope.

Results

The study of Maltese *S. album* populations revealed consistent differences from typical *S. album* in its inflorescences and flowers which leads the authors to distinguish them at the rank of subspecies.

Sedum album Linné subsp. *rupi-melitense* Mifsud, Stephenson & Thiede, *subsp. nov.*—Figs. 3–5.

Type:—MALTESE ISLANDS. Malta: Misrah Ghar Daqquq (close to Ġebel Ciantar [Fig. 1, locality 7]), Fawwara, Siggiewi, on the edge of coastal cliffs of upper coralline limestone, 200 m, 29 May 2013, *S. Mifsud* SMIFS-17 (holotype E!).

—*Sedum glanduliferum* sensu Gulia (1874: 417), non Gussone 1827.

—*Sedum dasyphyllum* sensu Sommier & Caruana Gatto (1915: 151) and Haslam *et al.* (1977: 91), non Linné 1753.

—*Sedum album* sensu Hart & Berg (1982: 680, 691) pro parte (Maltese plants); sensu Greuter *et al.* (1986: 186) pro parte (Maltese plants); sensu J alas *et al.* (1999: 98) pro parte (Maltese plants); sensu Lanfranco (1989:17, 2001:16); sensu Mifsud (2007; with ill.); sensu Darmanin (2009 with ill.); sensu Marhold (2011) pro parte (Maltese plants); sensu Casha (2013: 313 with ill.).

—*Sedum* aff. *album* sensu Stephenson (2014; with ill.).

Diagnosis:—Differs from *Sedum album* subsp. *album* in having very rarely formed inflorescences which are normally without peduncular leaves and floral bracts or, if present, only small and vestigial; flowers in which (3–)5 stamens of one whorl, mostly of the antepetalous one, have dysfunctional and often abortive anthers; retained anthers dark maroon to blackish-brown and mostly indehiscent at anthesis; pollen which is partly deformed and shrivelled; carpels without nectary scales; and fruits and seeds which remain undeveloped and sterile (Table 1).

Description:—Perennial *herbs*, succulent, laxly caespitose with creeping sterile shoots up to 25 cm long, stems densely glandular-hairy at base (insertion of lower leaves), sparingly above and at hardened part of stem below the leaves. *Leaves* 3.0–7.0 × 1.0–2.5 mm, alternate, sessile, spreading and becoming imbricate-appressed distally, linear-elliptic to ovoid, terete to semiterete and flattened adaxially with obtuse tip, not or scarcely spurred at base, green, not glaucous, tinged amber to cinnabar red in the upper third during summer; very sparingly papillate, papillae irregularly arranged, < 10 per leaf, absent on some leaves. *Inflorescences* very rarely formed, erect, up to 15 cm tall, dense cymes 3–8 cm broad, usually with 5–10 primary branches, glabrous, rugulose; peduncular leaves reduced in number or mostly missing; bracts vestigial, caducous, tiny or scale-like (about 1 mm), reduced in number or mostly missing. *Flowers* pedicellate by 1–2 mm; 5–6 mm diameter, 5-merous with 5 sepals, 5 petals, 10 stamens in 2 whorls, and 5 carpels. *Sepals* basally fused, equal, broadly ovate to sub-orbicular, marginally imbricate, 1.5–2.0 mm long, pale greyish-green, rarely pale red at upper part. *Petals* free, lanceolate, spreading, obtuse to subacute, 3.5 × 2.0 mm, wax-white, with a midvein sometimes pale pink at the lower half. *Stamens* obdiplostemonous, filaments 3 mm, white, (3–)5 filaments of one whorl, mostly of the antepetalous whorl, with dysfunctional and often abortive anthers, filaments of the other whorl with 5 functional anthers, in total 5(–7) filaments with functional anthers, anthers basifixed, cylindrical, 0.6–0.8 mm long, dark maroon to blackish-brown. *Carpels* free, 3.0–3.5 × 1.0 mm, white, adaxial side papillate and slightly pink, style to 0.5 mm long, at first erect, later curving outwards, stigma inconspicuous, nectary scales absent. *Fruits*

undeveloped, soft and shrivelled. *Seeds* undeveloped, sterile. *Chromosome number* $2n = 136$ (Hart & Berg 1982, as *S. album*).

Distribution and ecology:—Assuming that all previous records of *S. dasyphyllum* and *S. album* from Malta are attributable to *S. album* subsp. *rupi-melitense*, its distribution on the Maltese Islands is as follows (! = studied in habitat; † = recently extinct; Fig. 1):

Mainland Malta:

1. Paceville [!†] (St. Julians), first record by Tabone (2007). This population located in a developed area went extinct last February 2015;
2. Rdum il-Qaws [!] (Dingli), first record by Borg (1927);
3. Rdum Ghar Bittija [!] and il-Veċċa [!] (Dingli), new record by SM, OM and Sandro Lanfranco, 10 March 2007;
4. Rdum il-Madliena [!] (= Rdum Ghajn Gidem) (Dingli), first record by Sommier & Caruana Gatto (1915);
5. Rdum Dikkiena [!] (Dingli), first record by Borg (1927);
6. Faqqanija [!] and Rdum Hurrieqa [!] (Siggiewi), first record by Sommier & Caruana Gatto (1915);
7. San Ġorġ tal-Fawwara [!] and Ġebel Ciantar [!] (Siggiewi), first record by Gulia (1874); Ġebel
8. Cliffs beside Ghar Lapsi (Siggiewi), first record by Michael Briffa in 1986 (pers. comm. to SM);
9. Wied Babu (Żurrieq), first record by Sommier & Caruana Gatto (1915);
10. Limits of Wied Fulija [!] (Żurrieq), new record by SM, 20 May 2014;
11. Wied Diegu [!] and Ix-Xrejjek [!] (Żurrieq), new record by SM and Anthony Hamilton, 10 April 2012;
12. Wied Moqbol [!] (Żurrieq), first record by Tabone (2007).

Islands of Gozo and Comino: Not recorded

The main population at Dingli Cliffs (Fig. 1, locations 2–8) stretches almost continuously for 3.5 km along the edge of the cliffs with the highest population density being between Rdum Dikkiena (locality 5) and Faqqanija (locality 6) from where the density declines gradually west- and eastwards. The other population at Żurrieq (locations 9–12) stretches for about 1.5 km, but is much more fragmented and with a patchy distribution. The two main populations are separated by a distributional gap between Ghar Lapsi (locality 8) and Wied Babu (locality 9) where subsp. *rupi-melitense* has not been observed. Two further strictly rupestral Maltese endemics, *Cheirolophus crassifolius* (Bertol.) Susanna and *Cremnophyton lanfrancoi* Brullo & Pavone, show a similar disjunct distribution with a similar distributional gap (Mifsud 2013). The geomorphology in the gap is different from coastal areas where *S. album* subsp. *rupi-melitense* is distributed, changing from sub-vertical cliff faces with a strictly rupestral vegetation to a comparatively shallow shore with sloped or sub-terraced calcareous rocky shelves which support a mosaic of garigue and coastal phrygana vegetation. This escarpment is in great part covered by loose stones and lacks the typical exposed rock basins and cavities in which *S. album* subsp. *rupi-melitense* is commonly found.

All localities are at cliff-tops at the south or south-west cliffs at 100–250 m (Fig. 2) except a clump of plants at the north shore of St. Julians (Fig. 1, locality 1). *S. album* subsp. *rupi-melitense* grows in exposed pockets, cavities, crevices or small basins incurred in calciferous coralline limestone (Fig. 3A, 3C) entrapping a very shallow layer of calciferous soil mostly less than 2 cm deep, with the roots growing into minute rock crevices. Coralline limestone is a major type of sedimentary rock overlaying most of the Maltese garigues and cliffs. All observed plants were restricted to the very margin of the cliff edge growing mostly within 5 m from the edge and never more than 30 m inland (Fig. 2). Unlike other rupestral species, this species was neither observed nor reported from the (sub-)vertical cliff faces below the cliff edge. Apparently the species is not found in inland rocky ground with a higher, denser and more competitive vegetation which is less affected by drought and soil erosion.

The small disjunct population on the North coast area of Paceville in St. Julians (Fig. 1, locality 1) was found on “a hump of rock at a car park” and consisted of a clump of about 20 specimens on a single boulder in an anthropogenic area at the limits of Sliema and St. Julians (Tabone 2007); its presence may have resulted from human introduction from the main population at the Southern cliffs. This population is not more extant due to severe habitat loss since February 2015.

Karyology:—In 227 *S. album* accessions from all parts of its distribution area, Hart & Berg (1982) found a polyploid series with the basic chromosome number $X = 17$ and counts of $2n = 34$ (2x), 51 (3x), 68 (4x), 85 (5x), 102 (6x), and 136 (8x); other authors (cited in Hart & Berg 1982 and Jalas *et al.* 1999) reported counts of $2n = 32$, 36, 56, and 64. Hart & Berg’s study included two counts of “*S. album*” from Malta from “Dikkienien” (# Hart 16879; most probably Rdum Dikkiena [Fig. 1, locality 5]) and from “Dingli” (# Hart 7913; localities 2–8), both with $2n = 136$ (= 8x); these are assigned to *S. album* subsp. *rupi-melitense* here.



FIGURE 2. The habitat of *Sedum album* subsp. *rupi-melitense* is specifically at the edge (0–50 m inland) of southern coastal cliffs composed of upper coralline limestone.—Malta, Ġebel Ciantar, Siggiewi [Fig. 1, locality 7], 12 April 2012.—Photograph by S. Mifsud.

Phenology, reproduction and dispersal:—An unusual characteristic of *S. album* subsp. *rupi-melitense* is that it flowers only very rarely. Michael Briffa, a competent Maltese amateur botanist active over 30 years found only one single flowering specimen of *S. album* at Rdum Dikkiena (Fig. 1, locality 5) on 8 June 1986 (pers. comm. to SM). During field research for this study, a total of eleven inflorescences have been found, all in May to June: six inflorescences at Dingli Cliffs (locations 5, 6 and 7) (two by OM, June 2012; two by OM + SM, June 2012; one by SM, May 2013; and one spotted by Kathy Jones during a field trip with SM, May 2014) and five at Wied Diegu, Żurrieq (location 11) (SM, May 2014). A plant with one dried inflorescence at Wied Diegu was tagged in October 2013. When the plant was revisited in May 2014 it was in bud, suggesting that the same plant may flower repeatedly.

The rarity of flowering specimens (less than 1 in 2000), the lack of nectary scales (no nectar secretion = no pollinator reward); the reduction of the number of anthers; the indehiscence of most functional anthers; the reduction of viable pollen based both on direct microscopic observation of malformed pollen and a general weak reaction with acetocarmine stain; the soft and shrivelled fruiting carpels with sterile, undeveloped seeds (only one fruiting stem was examined); and the finding that some buds do not open and dry off, all indicate that the reproductive system of *S. album* subsp. *rupi-melitense* switched from generative to almost exclusively vegetative reproduction.

Conservation status:—The conservation status was assessed with the IUCN Red List Categories and Criteria (IUCN 2012) and guidelines (IUCN Standards and Petitions Subcommittee 2014). The Extent of Occurrence (EOO) of *S. album* subsp. *rupi-melitense* is 10km² based on a sublinear polygon from Rdum ilQaws (locality 2) to Wied Moqbol (locality 12). The extinct population at St. Julians (locality 1) was not included. The Area of Occurrence (AOO) plotted on a 2x2km grid, as per recommendation of the IUCN (2012) is 32km² but it is scaled down to 10 km² since AOO cannot be larger from EOO (IUCN, 2014). Since the population of this endemic stonecrop is restricted to the very edges of cliffs or escarpments and always found only up to 50m inland, the actual area of occurrence is much less from the calculated one.

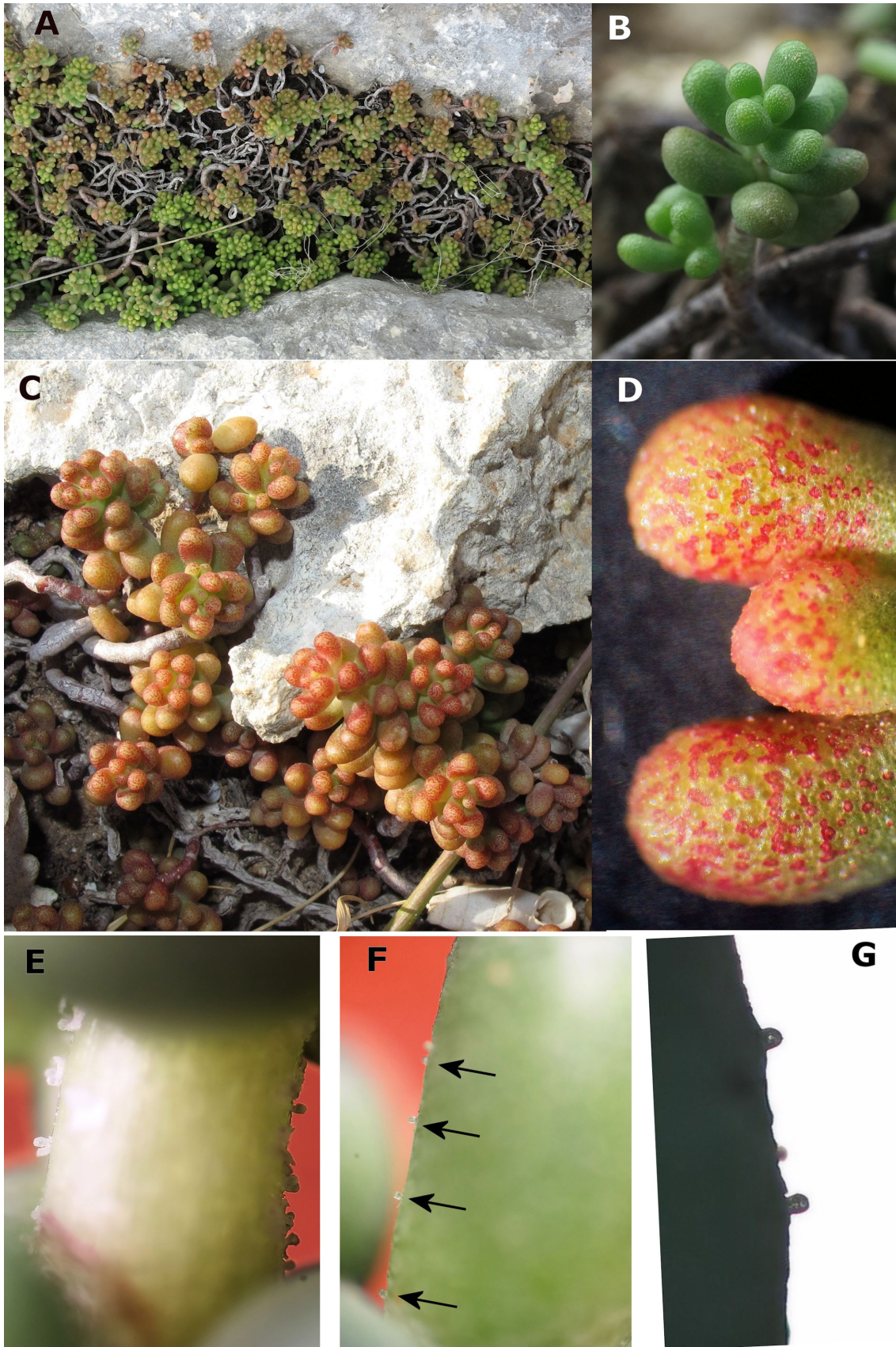


FIGURE 3. Vegetative parts of *Sedum album* subsp. *rupi-melitense*. 3A. Habit of a specimen with greenish leaves taken in Winter.–Malta, Wied Diegu, Żurrieq [Fig. 1, locality 11], 11 January 2014. 3B. Close-up of green leaves in winter.–Malta, Wied Fulija, Żurrieq [Fig. 1, locality 10], 11 January 2014. 3C. Habit and leaves in spring.–Malta, Wied Diegu, Żurrieq, 10 April 2014. 3D. Close-up of leaves showing the reddish colouring in its upper half.–Malta, Wied Diegu, Żurrieq, 29 May 2012. 3E. Macrophotograph showing the glandular hairs on the stem. 3F & 3G. Macrophotographs showing the sparse papillae on the leaves.–Photographs by S. Mifsud.

In general, the population is severely fragmented, being less so only for about 1.5km between Rdum Dikkiena (locality 5) and San Ġorġ tal-Fawwara (locality 7). Its strict rupestral habitat is decreasing slowly but gradually due to natural processes such as erosion, land slide and precipice collapse; one occurring few years ago near Wied Moqbol, Zurrieq. The ecological quality of this habitat is also decreasing steadily due to anthropogenic activities namely: the introduction of alien species (e.g. *Aeonium arboreum* Webb & Berth., *Agave americana* L., *Oxalis pes-caprae* L. and *Opuntia ficus-indica* (L.) Mill.; quarrying (e.g. at Ġhar Lapsi and east of Wied Moqbol); and dumping of trash or agricultural waste.

No biotic activities such as pests or disease have been observed or reported to reduce the species' population growth, but the gross vegetation away from the cliff edge seems to contribute to the restriction of the species growth inland.

The regeneration of the species is predicted to be very low, because it exclusively depends on its slow vegetative reproduction. Suitable data on fluctuations in population size and mature individuals is not available.

Given these factors and considering that the subspecies is, as far as known, a local endemic, *S. album* subsp. *rupi-melitense* is categorized CR (Critically Endangered) with IUCN Red List Criteria of B1ab(i,iii).

The current distribution of *S. album* subsp. *rupi-melitense* is already protected since it entirely falls within a Natura 2000 protected area (MT00024: *Rdumijiet ta' Malta: Ir-Ramla tac-Cirkewwa sal-Ponta ta' Benghisa*) that is scheduled as a Special Area of Conservation, Special Protected area and a Site of Community Importance. However being an endemic, and one of the very few populations with an octoploid karyology, it is suggested that this stoncrop is also strictly protected by being included in Schedule VI of future updates of Legal Notice 311: *Flora, Fauna and Natural Habitats Protection Regulations, 2006*.

Key to the taxa of *Sedum* ser. *Alba*:

- | | | |
|---|--|---|
| 1 | Leaves glabrous or sparingly papillate (<i>Sedum album</i>) | 2 |
| - | Leaves densely papillate (<i>Sedum gypsicola</i>) | 3 |
| 2 | Peduncular leaves and floral bracts on the inflorescences present; nectary scales present; stamens 10, each with a functional, dark violet or dark red anther; fruits and seeds developed, fertile; reproducing by seeds and vegetatively | |
| | <i>Sedum album</i> subsp. <i>album</i> | |
| - | Peduncular leaves and floral bracts on the inflorescences absent or vestigial; nectary scales absent; stamens 10, but (3–)5 with abortive anthers; anthers dark maroon to blackish-brown, mostly indehiscent; fruits and seeds undeveloped, sterile; reproducing vegetatively (flowering extremely rare) | <i>Sedum album</i> subsp. <i>rupi-melitense</i> |
| 3 | Leaves spreading or imbricate-appressed; anthers dark violet to dark red; style ca. 1 mm long | |
| | <i>Sedum gypsicola</i> subsp. <i>gypsicola</i> | |
| - | Leaves densely grouped cone-like, but not imbricate, cylindrical; anthers dark red; style 1–1.5 mm long | |
| | <i>Sedum gypsicola</i> subsp. <i>trinacriae</i> | |

Discussion

Maltese specimens of *S. album* examined in this study and published here as *S. album* subsp. *rupi-melitense* were rather homogeneous. Whereas their vegetative parts do not differ from *S. album* subsp. *album* (cf. Tab. 1), flowering specimens differ constantly from the latter as follows:

1. Inflorescences are only very rarely formed (Figs. 4A, 4B, 5A);
2. inflorescences lack peduncular leaves and floral bracts completely, or if present, they are vestigial and tiny, caducous, and scar-like (Fig. 5A);
3. the flowers have one whorl with (3–)5 stamens with dysfunctional or/and abortive anthers resulting in only 5(–)7 antheriferous stamens at anthesis. A dissection of buds revealed that initially, both stamen whorls are normally developed, but (3–)5 stamens of one whorl (usually the antepetalous one) become dysfunctional before anthesis (Figs. 4C, 4D);
4. the anthers are dark maroon to blackish-brown and mostly indehiscent in situ (Figs. 4C, 4D);
5. the pollen examined from specimens at Faqqanija [Fig. 1, locality 5] was dimorphic, about half had a normal elliptic shape, was tricolpate, 25 x 17µm, and pale yellow; the other half was deformed and shrivelled, somewhat larger, greyish and partially translucent. With acetocarmine, normal pollen showed a weak colour

- change, and malformed pollen none;
- 6. the nectary scales at the base of the carpels are absent (Fig. 5B); and
- 7. the fruits and seeds remain undeveloped and sterile.

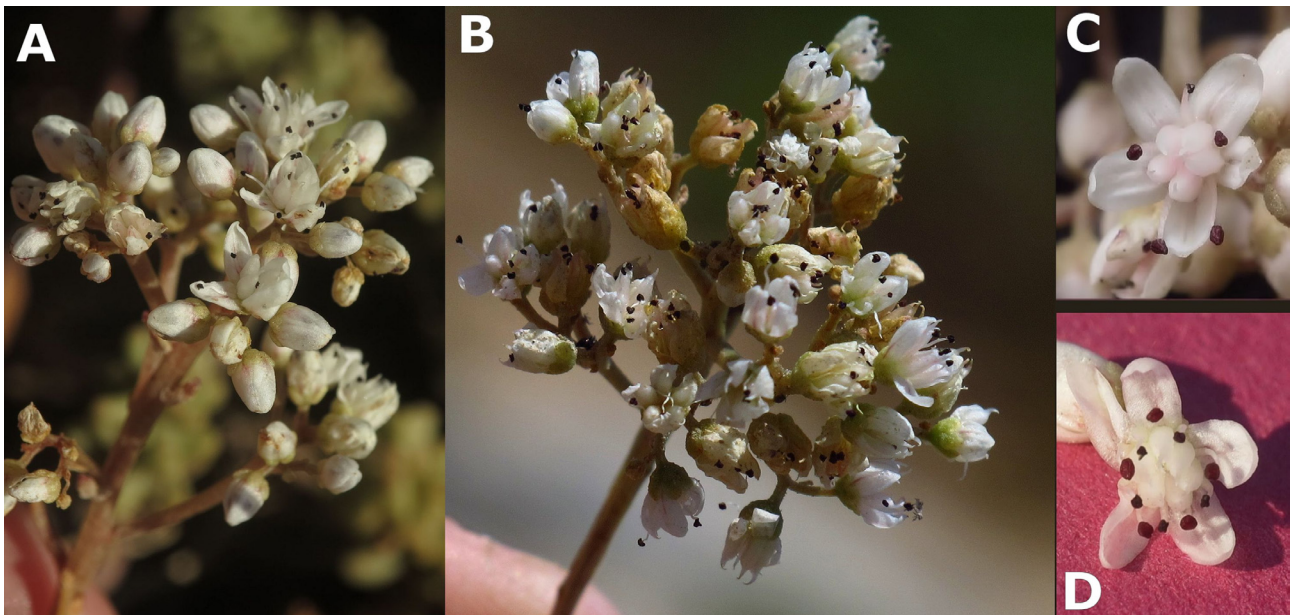


FIGURE 4. Inflorescences and flowers of *Sedum album* subsp. *rupi-melitense*. 4A. Inflorescence.—Malta, Wied Diegu, Żurrieq [Fig. 1, locality 11], 16 April 2014. 4B. Inflorescence.—Malta, Rdum Dikkiena, Siġġiewi [Fig. 1, locality 6], 19 June 2012. 4C. Mature flower with five antheriferous stamens.—Malta, San Ġorġ tal-Fawara, Siġġiewi [Fig. 1, locality 7], 30 May 2013. 4D. Immature flower forced open with ten antheriferous stamens of which five (here: the antesepalous ones) are shrivelled and caducous.—Malta, Wied Diegu, Żurrieq, 15 June 2014.—Photographs by S. Mifsud.



FIGURE 5. Inflorescences and dissected flower parts of *Sedum album* subsp. *rupi-melitense*. 5A. Inflorescence without peduncular leaves or floral bracts or if present, these are vestigial and scar-like. 5B. Dissected flower parts, top to bottom: petals (3.5 mm long); stamens (3 mm); carpels (3.5 mm) and sepals (ca. 1.5 mm). Malta, San Ġorġ tal-Fawara, Siġġiewi [Fig. 1, locality 7] (30 May 2013).—Photographs by S. Mifsud (30 May 2013).

Due to their clear and constant differences in its reproductive morphology, the Maltese populations of *S. album* are described as a new subspecies *rupi-melitense* endemic to Malta.

Nectary scales at the carpel base are present in most Crassulaceae, but are lacking in a few species of *Crassula* L., *Sedum* and *Aeonium* Webb & Berth. (Thiede & Eggli 2003: 86). In addition, vegetative propagation by means of fragmentation of detached leaves or stems which easily form roots is common in many (European) *Sedum* and other Crassulaceae (e.g., Praeger 1921: 18; Gravatt & Taylor 2004; Gorelick 2015). Three species, the European *Petrosedum amplexicaule* (DC.) Velayos and *Jovibarba globifera* (L.) Tjaden ex J. Parnell (= *Sempervivum globiferum* L.), and the Mexican *Sedum longipes* Rose, are known to flower sparsely and propagate mostly vegetatively, but have normally developed functional flowers. Apart from *S. album* subsp. *rupi-melitense*, no Crassulaceae is known to show a switch to vegetative propagation in conjunction with dysfunctional reproductive flower structures.

The octoploid chromosome number found in *S. album* subsp. *rupi-melitense* was reported in *S. album* subsp. *album* in only one accession from Portugal (Hart & Berg, 1982). The two stations are very remote making a shared or linked ancestry very unlikely. Geographically close populations in Italy, the Balkan and Corsica (France) are mostly tetra-, partly di- and rarely hexaploid (Hart & Berg 1982), suggesting that the octoploid number in *S. album* subsp. *rupi-melitense* arose in situ on Malta after the colonization of the island.

The switch to vegetative reproduction in *S. album* subsp. *rupi-melitense* is unlikely to have arisen from the introduction of a single self-sterile clone for which the production of inflorescences represented a waste of resources, since *S. album* is self-fertile (GB non-native species secretariat 2015). We hypothesize that the switch to vegetative propagation in *S. album* subsp. *rupi-melitense* might have been selected by its restriction to cliff habitats which are frequently windy to stormy, thus making insects visiting flowers very difficult and thus preventing effective pollination. Observations in further Maltese cliff-inhabiting species such as *Atriplex lanfrancoi* (Brullo & Pavone) G. Kadereit & Sukhor and *Cheirolophus crassifolius* (Bertol.) Susanna likewise show a reduced generative propagation with rare fruit set (SM and E. Lanfranco, pers. observations).

In contrast to *S. album* subsp. *rupi-melitense*, plants of *S. album* subsp. *album* from mainland Europe (Praeger 1921; Webb *et al.* 1993; Hart & Berg 1982; Castroviejo *et al.* 1997; Hart & Bleij 2003; Hart & Eggli 2003; cf. Table 1) as well as North Africa (Maire 1976) flower abundantly and have inflorescences with developed bracts and leaves, flowers with two whorls of five stamens each with functional, dark violet to dark red anthers, and nectary scales at the carpel bases. Neither abortive anthers nor polyploid sterility have otherwise been reported in *S. album*, not even in the most detailed morpho-karyological study of 227 living *S. album* accessions from all parts of its distribution area by Hart & Berg (1982). However, it should be noted that it would be difficult to detect sterile non-flowering plants if they should occur together with normal flowering plants of *S. album* subsp. *album*. *Sedum album* subsp. *album* is very variable in the size and shape of its vegetative morphological features in particular which has led to the description of some 10 separate taxa which are connected with typical *S. album* by intermediate forms, thus making it impossible to clearly separate them (Hart & Berg 1982; Hart & Bleij 2003; Hart & Eggli 2003). The Maltese population differs exclusively and constantly in its generative features, connected with the switch from generative to vegetative propagation not previously described for *S. album*. We thus have the remarkable finding that the small, but geographically isolated island of Malta harbours the sole infraspecific taxon of the very variable and widespread *S. album* which is morphologically separate and not connected with typical *S. album* by intermediates.

Sedum album subsp. *rupi-melitense* is the most recent addition to the 23 known taxa of vascular plants strictly endemic to the Maltese Islands (Lanfranco *et al.* 2013) and is considered a neoendemic which evolved relatively recently due to its insular reproductive isolation. Compared to chromosome numbers in the Italian endemic vascular flora, the high octoploid chromosome number of $2n = 136$ in *S. album* subsp. *rupi-melitense* is one of the highest at all. Only four Italian endemics have a higher chromosome number, and most Italian endemics are diploids (ca. 70%), whereas only about 1 % are octoploids (Bedini *et al.* 2012).

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