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A new endemic species of *Sesuvium* (Aizoaceae: Sesuvioideae) from the Caribbean Basin, with further notes on the genus composition in the West Indies

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Summary. A new distinctive species, *Sesuvium curassavicum* Sukhor. (Aizoaceae: Sesuvioideae), restricted to the Caribbean Basin (Kingdom of the Netherlands: Curaçao and Bonaire Islands, North Colombia: La Guajira Department, and North Venezuela: Falcón State), is described and illustrated. It differs from all other perennial species growing in the West Indies by papillate stems and wrinkled seeds. Based on the molecular phylogenetic analysis of nrDNA (ITS) and three plastid regions (*rps16* gene intron, *atpB-rbcL* and *trnL-trnF* intergenic spacers), *S. curassavicum* is included in the 'American' clade, but its relationships are not fully resolved. The samples of the plants known as *S. microphyllum* fall within the '*Sesuvium portulacastrum*' clade, and for that reason this species is considered here as a synonym of *S. portulacastrum* being an ecological form of the latter species. *Sesuvium revolutifolium, S. ortegae* and *S. revolutum* described from cultivated plants are established as earlier synonyms of *S. verrucosum*, for which *S. revolutifolium* has priority and is proposed here as the correct name. These three species names seem to share the same provenance which cannot be Cuba, as stated in the protologue for *S. revolutifolium*, but rather Mexico. The name *Sesuvium sessile* is discussed and merged with *S. portulacastrum*. A new diagnostic key to the *Sesuvium* species in the West Indies is provided. In total, we accept for the West Indies the following species: *S. curassavicum, S. humifusum*, *S. maritimum, S. portulacastrum* and *S. rubriflorum*. The origins of collections of the neotype of *Radiana petiolata* and the holotypes of *Sesuvium microphyllum* and *S. spathulatum* are clarified.

Key Words. Caryophyllales, molecular phylogeny, new species, reproductive characters, taxonomy.

Introduction

Sesuvium L. is a small genus (~18 spp.) distributed in the tropical regions of the World (Bohley *et al.* 2017). Its composition has recently been changed based on the molecular phylogeny, and three American species of *Cypselea* Turpin with fimbriate stipules – *C. humifusa* Turpin, *C. rubriflora* Urb. and *C. meziana* K.Muell. – were transferred into *Sesuvium* as *S. humifusum* (Turpin) Bohley & G.Kadereit, *S. rubriflorum* (Urb.) Bohley & G.Kadereit, and *S. mezianum* (K.Muell.) Bohley & G.Kadereit (Bohley *et al.* 2017). In this current circumscription, *Sesuvium* is divided into two major clades called the 'American' and 'African' lineages (Bohley *et al.* 2015, 2017). It includes perennial or annual herbs with prostrate glabrous or papillate stems, often rooting at the nodes; opposite, flattened or terete leaves with short petioles and entire or fimbriate stipules; axillary, bracteolate, pedicellate or sessile flowers with, five, bi-coloured (green dorsally and pink or white inside) perianth lobes, five to numerous pink stamens, a two- to five-carpellate ovary, and a circumscissile capsule with the central column bearing 5 – 50 black or reddish, smooth or diversely sculptured seeds with thin and hyaline aril. *Sesuvium* is the type genus of the subfamily Sesuvioideae whose phylogenetic position and taxonomic circumscription were stated in several works (Klak *et al.* 2003, 2017a, 2017b; Bohley *et al.* 2015, 2017; Sukhorukov *et al.* 2018).

The predominant species diversity of the genus is known in Africa and the Americas (Bohley *et al.* 2017). The composition and distribution of the genus in Africa was summarised in recent papers (Sukhorukov *et al.* 2017, 2018). However, the American species are still poorly known, and the applications of some names described or reported from the West Indies and adjacent territories of coastal South America (*Sesuvium revolutifolium* Ortega, *S. revolutum* Pers., *S. sessile* Pers., *S. microphyllum* Willd., *S. spathulatum* Kunth, *S. acutifolium* Miq.) are contradictory. Bohley *et al.* (2017) considered all these names as synonyms of *S. portulacastrum* (L.) L. In contrast to that, Hartmann (2017) accepted *S. revolutifolium*, *S. microphyllum*, and *S. acutifolium* at the specific rank, whereas *S. revolutum* and *S. sessile*

were merged with *S. revolutifolium* and *S. parviflorum* DC., respectively. Sukhorukov *et al.* (2018) suggested that *S. revolutifolium* may be an older name for the taxon known as *S. verrucosum* Raf. that is also present in the West Indies. Such contrasting opinions about the composition of *Sesuvium* in this region, as well as the presence of scarce collections of unusual plants from the Dutch Caribbean and adjacent territories identified as *S. portulacastrum* in some herbaria, called for new research on *Sesuvium* across the West Indies.

Material and Methods

The field work was undertaken by the first author (APS) in Grenada (Main Island, Carriacou, and Petit Martinique) in November 2016 and Curaçao (Kingdom of the Netherlands) in March 2018. Plant material was preserved as herbarium specimens, in silica gel for molecular studies and in 70% aqueous alcohol solution for leaf anatomy. The taxonomic revision of *Sesuvium* was undertaken in the following collections: B (almost all material is on loan in Mainz, Germany, not seen by us), BM, BR, E, FR, G, H, K, M, MSB, MW, MEXU, MHA, L (incl. U and WAG), LE, P, RO, W and WU. The extent of occurrence (EOO) and area of occurrence (AOO) for *Sesuvium curassavicum* were calculated using GeoCAT on-line tool, with a cell of 2×2 km^2 (Bachman *et al.* 2011).

The anatomical sections of the leaves were made by hand. They were examined using a Nikon Eclipse Ci (Nikon Corporation, Japan) light microscope and photographed using a Nikon DS-Vi1 camera (Nikon Corporation, Japan) at the Dept. of Higher Plants, Lomonosov Moscow State University. To describe the leaf anatomy, we follow the terminology used by Bohley *et al.* (2015) for consistency. The leaves of *S. curassavicum* used for the image belong to the type collection from Curaçao (*A. Sukhorukov* 100 (MW)). The leaves of *S. revolutifolium* (*S. verrucosum*) were collected by the same author in Cape Verde, São Vicente Island, in November 2018 (MW).

The micromorphology of 1 – 2 seeds taken from each specimen was observed using a scanning electron microscope (SEM) JSM-6380 (JEOL Ltd., Japan) at 15 kV, after sputter coating with gold-palladium, in the laboratory of Electron Microscopy at Lomonosov Moscow State University. No dehydration of the seeds is required prior to SEM observation as there are no soft tissues (e.g., papillae or trichomes) on their surface.

The list of vouchers for SEM studies is given below.

Sesuvium curassavicum Sukhor.: 1) Venezuela, Falcón [State], Buchivacoa Distr., 17 June 1980, *G. Davidse & A.C. González* 18196 (MEXU713002); 2) Kingdom of the Netherlands, Curaçao, Rooi Rincon near Hato airport, 11 Feb. 1999, *A.S.J. van Proosdij et al.* 631 (K); 3) Kingdom of the Netherlands, Curaçao, Boka San Pedro, 13 March 2018, *A. Sukhorukov* 100 (MW);

S. humifusum (Turpin) Bohley & G.Kadereit: 1) Cuba, Matanzas [without date], *Riedel* 236 (LE); 2) [Cuba,] Havana, 29 March 1905, *A.H. Curtiss* 698 (BM);

S. maritimum (Walter) Britton, Sterns & Poggenb.: Cayman Islands, Grand Cayman Island, nr Grape Tree Point, *G.R. Proctor* 15115 (BM);

S. microphyllum Willd. s.s.: 1) Turks & Caicos Islands: South Caicos, 25 May 2009, *M.J. Visaya & B.N. Manco* 58 (K); 2) Kingdom of the Netherlands, Curaçao, 8 March 2018, *A. Sukhorukov* 42 (MW);

S. portulacastrum (L.) L.: Kingdom of the Netherlands, Curaçao, 8 March 2018, *A. Sukhorukov* 44 (MW); for other vouchers see Sukhorukov *et al.* (2018);

S. revolutifolium Ortega (*S. verrucosum* Raf.): Mexico, Coahuila State, 2011, *Flores Olvera et al.* (MEXU); for other vouchers see Sukhorukov *et al.* (2018);

S. rubriflorum (Urb.) Bohley & G.Kadereit: Cuba, Matanzas, near Caimito de Hanábana, 08 Aug. 1923, *Ekman* 17016 (B 10 0242330); Puerto Rico, Icacos Island, 12 July 1966, *R.A. Howard et al.* 16130 (BR0000023105898).

For phylogenetic analysis the ITS region of nuclear genomic DNA as well as chloroplast sequences (*rps16* intron, *atpB-rbcL* and *trnL-trnF* intergenic spacers) were used. Total DNA was isolated from dried leaves using Invisorb® Spin Plant Mini Kit (Stratec Molecular GmbH, Berlin, Germany). Universal primers ITS4 and ITS5 (White *et al.* 1990) are usually used for the amplification of the ITS1 and ITS2 spacers but, based on previous experience, we used primers P17 (CTACCGATTGAATGGTCCGGTGAA) and 26S-82R (TCCCGGTTCGCTCGCCGTTACTA) (Popp & Oxelman 2001) in this study. Other regions (*rps16* intron, *atpB-rbcL* and *trnL-trnF* intergenic spacers) were amplified with primers as described in Sukhorukov *et al.* (2018). PCRs were performed using 0.75 units of MyTaq Red DNA polymerase (Bioline, London, UK) in 15 µl of original buffer containing $MgCl_2$ and dNTPs, with 0.3 µM of each primer and 1 µl of unquantified DNA template. Thermocycling was carried out in TProfessional Basic Thermocycler (Biometra, Göttingen, Germany) using the thermal and cycling conditions as described in Shaw *et al*. (2007): initial denaturation at 80°C for 5 min; 30 cycles of 95°C for 1 min, 50°C for 1 min, a ramp of 0.3°C/s to 65°C and incubation at 65°C for 4 min, with a final extension step of 65°C for 5 min. A clean-up reaction with exonuclease I and alkaline phosphatase (Thermo Fisher Scientific, Waltham, Massachusetts, USA) was used to remove unincorporated primers and nucleotides before sequencing. The PCR products were sent to Macrogen Europe (Netherlands) for automated sequencing. The primers used for amplification were also used for the sequencing reactions. Data files were assembled, edited and evaluated using Geneious 8.1 software (Biomatters Ltd, Auckland, New Zealand). Regions of ambiguous alignment were excluded from all analyses.

Sequences were aligned using MUSCLE v.3.5 (Edgar 2004) and the alignment was adjusted manually using PhyDe (version 0.9971; Müller *et al*. 2010). The chloroplast and the nuclear data set were initially analysed separately. Then for all accessions that had cp and nuclear sequences (i.e., except one specimen of *S. revolutifolium* (rps 16 absent) and one

specimen of *S. portulacastrum* (ITS absent)), a combined analysis was conducted. For all data sets the best substitution model was chosen according to the Akaike information criterion using jModelTestv.2.1.7 (Guindon & Gascuel 2003; Darriba *et al*. 2012).

Three separate analyses were performed for the nuclear, plastid and combined DNA datasets using maximum parsimony (MP), Bayesian inference (BI) and maximum likelihood (ML).

For the ML analyses, we used RAxML Version 8 (Stamatakis 2014). Bootstrap analyses were conducted with 2500 replicates for ML with GTR+G+I for the nuclear, plastid and combined data set. Parsimony analyses were conducted in PAUP* 4.0a162 (Swofford 2002) with the following settings: all characters have equal weight, MaxTrees set to 1000 (auto increased by 1000), TBR branch swapping and with 20000 jackknife (JK) replicates to calculate node support.

Bayesian analysis was performed with uncorrelated lognormal relaxed clock under a birth–death speciation process (Gernhard 2008). Four independent MCMC analyses were run, each of 30 million generations sampling every 30,000. Input files were generated with BEAUti v2.4.5 (Bouckaert *et al*. 2014) and analyses ran using BEAST v2.4.5 (Bayesian Evolutionary Analysis by Sampling Trees; Bouckaert *et al.* 2014). Output log files were analysed using TRACER 1.6 (Rambaut & Drummond 2013). 10% of samples were removed prior to combining the independent runs using LOGCOMBINER 2.4.5 (Bouckaert *et al.* 2014). The MCC tree was generated using TREEANNOTATOR 2.4.5 (Bouckaert *et al.* 2014).

Voucher information and GenBank accession numbers are listed in Table 1.

Results

The cp marker alignment consisted of 31 accessions and 2790 bp, the nr marker alignment – of 30 accessions and 789 bp, and the combined alignment had 31 accessions and 3611 bp. The phylogenetic tree resulting from the combined data set (Fig. 1) shows an overall better resolution than the trees resulting from individual data sets (ITS tree: Fig. S1, and cp tree, Fig.S2). There are no topological conflicts between the cp and nr trees that received considerable support value. In the case of ITS sequence, 226 characters were identified as variable and 94 characters as parsimony informative (10%). In the case of *rps16* non-coding region, only 14 characters were parsimony informative (3%) and in the case of *atpB-rbcL*, 20 characters were parsimony informative (2.5%). The most variable region of cpDNA was the *trnL-trnF* non-coding region with 266 variable and 51 parsimony informative characters (5%).

Sesuvium includes two major branches: African and American lineages, which receive strong or full statistical support in accordance with previous studies (Bohley *et al.* 2015, 2017). In the American lineage, *Sesuvium humifusum* (ex-*Cypselea humifusa*) is sister to the remainder of *Sesuvium* with moderate statistical support. The latter clade is divided into two subclades: (1) a part of *S. portulacastrum* samples (samples from Israel and Morocco) plus *Sesuvium revolutifolium* + *S. maritimum*; the latter is forming a polytomy with some samples of *S. revolutifolium*, and (2) branches consisting of *S. curassavicum*, *S. microphyllum* and other samples of *S. portulacastrum*. The relationships within this large subclade are not fully resolved. However, our revised taxonomic concept is largely based on the gross morphological, ecological and chorological data provided below as well as on data of the previously published results about the variability of the widespread *S. portulacastrum*.

Taxonomic treatment

Key to *Sesuvium* species in the West Indies

In total, we accept five species of *Sesuvium* in the West Indies, viz., *S. rubriflorum*, *S. humifusum*, *S. maritimum*, *S. portulacastrum*, as well as *S. curassavicum* Sukhor. spec. nov. We discuss in more detail the synonymy of other accepted names described or reported from the West Indies and provide further information on the species distribution in this region. *Sesuvium revolutifolium* as an older name of *S. verrucosum* is also included in the key and the taxonomic part, although we have strong doubts about its presence in the West Indies (see comments below).

1. Plants small, stems up to 15 cm long; stipules fimbriate; perianth up to 2.8 mm long; seeds brown, drop-like, 0.3 – 0.4 mm long 2

Plants usually much taller; stipules entire; perianth at least 3 mm long; seeds black, roundish or reniform, 0.6 – 1.2 mm 3

2. Short-lived perennial; at least leaves (and often young stems) papillate; perianth pink inside; stamens 5; anthers oblong, 0.4 – 0.6 mm long ..... **S. rubriflorum**

Annual; glabrous or barely papillate; perianth white or pinkish inside; stamens 3; anthers round, ~ 0.3 mm long ..... **S. humifusum**

3. Annual, glabrous or finely papillate; stamens 5; anthers 0.3 – 0.4 mm long ..... **S. maritimum**

Perennial, glabrous or papillate; stamens more than 10; anthers 0.4 – 0.65 (1) mm long ... 4

4. Perianth 4 – 7 mm long; seeds rugose or longitudinally furrowed ..... **S. curassavicum**

Perianth > 7 mm long; seeds with smooth surface 5

5. Stems and leaves densely papillate, grayish; flowers sessile or subsessile with a short pedicel up to 3 mm; seed aril forming detachment from the seed coat in the cotyledon area looking like white fold ..... **S. revolutifolium**

Plant glabrous (or only leaves with small mamillae); flowers pedicellate (pedicel > 3 mm); seed aril tightly adjoining to the seed coat ..... **S. portulacastrum**

Sesuvium curassavicum *Sukhor*. **sp. nov.**

Type: [Kingdom of the Netherlands], Netherlands Antilles, Curaçao, Boka San Pedro, 12.258048, -69.041148, micro-depressions on the volcanic substrate flooded by seawater, 13 March 2018, *A.P. Sukhorukov* 100 (holotype MW0595676!, isotype G). Fig. 2.

– *Sesuvium edmonstonei* sensu Bohley *et al.* (2017) pro minimo parte as to specimen from Venezuela, non Hook.f.

Perennial herb with a taproot and with numerous prostrate stems up to 50 cm (sometimes when the plants are growing on the cliffs, the stems can be pendulous reaching 100 cm in length), older stem grayish or olive, glabrescent, younger stem parts green or reddish, densely covered with papillae (bladder cells). Internodes short, 1.0 – 5.0 mm. Leaves opposite, 10 – 25 (30) mm long (much shorter on terminal shoots), 2.0 – 4.0 mm wide, 1.5 – 4.0 mm thick, sessile or shortly petiolate (petioles 1.0 – 3.0 (5.0) mm), densely papillate, succulent, flattened or suborbicular (both extreme leaf forms can be found on the same plant), green or greyish-green to red, withered leaves usually flattened; stipules entire, not fimbriate, brownish; leaves at cross-sections (Fig. 3) similar to other American *Sesuvium* with C_3 photosynthesis (Fig. 4, see also Bohley *et al.* 2015; Sukhorukov *et al.* 2018), without hypodermis, mesophyll with palisade and water storage cells; palisade cells forming chlorophyll-containing tissue arranged in 2 – 3 layers below the epidermis from each leaf side, with druses; water storage cells arranged in several layers containing thin-walled cells; one main vascular bundle in the center of the leaf is present, with numerous lateral vascular bundles. Flowers solitary in leaf axils (one per node), subsessile or with short pedicel 3.0 – 7.0 mm long, with two small brown or

blackish glabrous bracteoles. Perianth 4 – 7 mm long, of 5 fleshy tepals connate up to the third of their length, abaxially green, covered with papillae, and adaxially (internally) white or pink, glabrous; two outermost tepals triangular, without hyaline margin, three innermost tepals with broad hyaline margin, all tepals subapically with a short mucro. Stamens ~ 40, with pink or purple filaments; anthers broadly ovoid, 0.5 – 0.6 mm. Stigmas 2 – 4, ~2 mm long. Ovules 10 – 20, but only some of them turn into ripe seeds. Seeds 6 – 10, completely covered with a hyaline aril without any detachments from the seeds coat, occasionally ruptured, black, roundish or slightly reniform, 0.8 – 0.9 mm in diam., rugose with longitudinal furrows (Fig. 5A, B).

RECOGNITION. The differences between the similarly looking perennial species *Sesuvium portulacastrum* and *S. revolutifolium* (a priority name for *S. verrucosum*) are provided in the Table 2. The morphological differences were detected in stem and leaf pubescence, leaf and perianth length, seed aril and seed ultrasculpture (Table 2).

DISTRIBUTION (Map 1). Only known from Curaçao, Bonaire (Kingdom of the Netherlands, Netherlands Antilles]), La Guajira Department (Colombia) and Falcón State (Venezuela).

SPECIMENS EXAMINED. **KINGDOM OF THE NETHERLANDS**. [Netherlands Antilles], Bonaire: [years] 1909 – 1910, *I. Boldingh* 7464 (K); [Netherlands Antilles], Curaçao, Rooi Rincon near Hato airport, limestone plateau, on cliff, north-east hill, 11 Feb. 1999, *A.S.J. van Proosdij, B.P. van de Riet, S.A.L. Zander* 631 (K). **COLOMBIA.** La Guajira [Department], Karibische Küste, 8 km E von Pajraro (nahe den Salinas de San Juan [Caribbean coast, 8 km E of Pajraro (near Salinas de San Juan)], 17 Feb. 1991, *G. Pfundner* 031 (W 1993 02282). **VENEZUELA.** Falcón [State], Buchivacoa Distr., 4 km S of Zazárida, elev. 5 m, low coastal shrubs and trees on hummocks, herb with prostrate branches, petals

white, stamens purple, growing in flat areas between hummocks, subject to inundation, 17 June 1980, *G. Davidse & A.C. González* 18196 (MO – image! MEXU713002).

HABITAT. The type specimens were collected 20 – 50 m from the coastal zone (Fig. 6A–D), in micro-depressions on the volcanic substrate (Fig. 6B, C) periodically flooded by seawater. Such depressions are inhabited by only several plant species, usually *Portulaca pilosa* L. (Portulacaceae) and *Litophila muscoides* Sw. (Amaranthaceae s.s.). Other specimens from Curaçao were collected on sand and limestone. The distribution area of *S. curassavicum* encompasses a small territory restricted to some islands of the Leeward Antilles, coastal Venezuela and North Colombia, with semi-arid climate and low precipitation (Martis *et al.* 2002; van Buurt 2010). The flora of these territories is xerophytic (Boldingh 1914), and *S. curassavicum* is the first species of the genus with a local distribution pattern in this region. Previously, no *Sesuvium* species were reported as endemic to the entire West Indies (Francisco-Ortega *et al.* 2007).

CONSERVATION STATUS. *Sesuvium curassavicum* has an estimated extent of occurrence (EOO) of 22,479 km^2 (which would place the species in NT) and area of occupancy (AOO) of 24 km^2 (which would place it in EN). All examined herbarium specimens are relatively recent, and the species is likely undercollected, as many *Sesuvium* are, so there is no evidence of declining population size and fluctuations. However, observations on Curaçao indicate that at least on this island the new species is not as common as *S. portulacastrum*, and is found only in natural habitats where the anthropogenic pressure is relatively low. Since only two collections are present from the mainland South America, more research is needed to find out current distribution of *S. curassavicum* in that area, size of its populations and factors which can negatively affect them. Possible threats to *S. curassavicum* populations across its range are sea-level rise and development of the coastal areas. Considering the abovementioned, we propose that *S. curassavicum* should be considered Near Threatened (NT) according to the

IUCN red list criteria (IUCN 2019), with possible transfer to Endangered (EN) if further research confirms small size and number of its populations and their likely decline.

NOTES. *Sesuvium curassavicum* has previously been identified as *S. portulacastrum* in herbarium collections because only this species was reported in the literature from the Dutch Caribbean (Boldingh 1914; Stoffers 1980). Additionally, one specimen of *S. curassavicum* from Venezuela was cited as *S. edmonstonei* Hook.f. (Bohley *et al.* 2017). However, the latter species is exclusively endemic to the Galapagos Archipelago, Ecuador (e.g., Killip 1939; Hartmann 2001, 2017), and it differs from *S. curassavicum* and all other species growing in the Americas by papillate bracteoles erroneously called stipules in Bohley *et al.* (2017). A specimen seen from Venezuela and cited as *S. edmonstonei* (Bohley *et al.* 2017) has glabrous bracteoles and corresponds in all characters with other specimens of *S. curassavicum*. Besides, *S. edmonstonei* has long-pedicellate flowers (pedicels 10 – 20 mm long) compared to *S. curassavicum* whose flowers are sessile or with short (up to 7 mm) pedicels. We assume that the presence of rugose seeds, a character shared by both *S. edmonstonei* and *S. curassavicum*, was the main reason to identify the Venezuelan specimen as *S. edmonstonei*. Compared with *S. curassavicum*, all other *Sesuvium* species growing in the entire Caribbean Basin have smooth seeds, or an aril covering the seed coat which has a reticulate ultrasculptural pattern (Fig. 7, 8).

Sesuvium maritimum *(Walter) Britton, Sterns & Poggenb.* (Britton *et al*. 1888: 20). (Fig. 9A, B)

≡ *Pharnaceum maritimum* Walter (Walter 1788: 117).

≡ *Sesuvium pentandrum* Elliott (Elliott 1821: 556), nom. illeg. superfl.

≡ *Mollugo maritima* (Walter) Ser. (Seringe 1824: 393).

Neotype (Ward 2008: 1282): USA, South Carolina, Georgetown county, Yawkey Wildlife Center, Mosquito Creek drainage on S island, 28 July 1987, *Nelson* 5850 (USCH0000001 – image seen!).

Annual, prostrate or ascending, basally much branched; leaves up to 30 mm long, flat, ovate, glabrous or finely papillate, stipules entire; flowers (sub)sessile, perianth 3 – 5 mm long, white or pinkish inside; stamens 5, anthers 0.3 – 0.4 mm long; seeds black, 0.8 – 1.0 mm in diam., aril often detaching from the seed coat in the area of the cotyledons, its cells forming a finely reticulate ultrasculptural pattern (Fig. 8C, D).

DISTRIBUTION. USA, Central America, West Indies.

SPECIMENS EXAMINED (Map 2). **BAHAMAS**: Cay settlement, 25 March 1905, *Andros* 233 (K). **CAYMAN ISLANDS**: Grand Cayman Island, nr Grape Tree Point, *G.R. Proctor* 15115 (BM). **CUBA**: Habana, Playa de Marianar, 29 Nov. 1921, *E.L. Ekman* 13261 (G); nr Soledad, laguna de San Mateo, 9 Dec. 1941, *A. Gonzales* 122 (BM); [Santa Clara prov.] Las Villas, Rio Caunao, July 1950, *R. Howard et al.* 348 (K). **PUERTO RICO**: Icacos Island, 12 July 1966, *R.A. Howard et al.* 16130 (BM, BR0000023105898, LE).

Reported from Guadalupe (Fournet & Hoff 1999; Fournet 2002) and St. Barthelemy (Acevedo-Rodríguez & Strong 2012).

NOTES. All specimens seen from the West Indies have only 5 stamens. Some populations of *S. maritimum* in SE Mexico (MEXU!) are distinguished in having numerous stamens, and such plants have not yet been taxonomically evaluated.

Sesuvium humifusum *(Turpin) Bohley & G.Kadereit* (Bohley *et al*. 2017: 134). (Fig. 9C)

≡ *Cypselea humifusa* Turpin (Turpin 1806: 219, plate 121).

Type (Bohley *et al.* 2017: 134): Haiti ("Saint-Domingue"). [Drained swamp south of Cap-Haïtien] *P.A. Poiteau* s.n. (lectotype P011900032!, isolectotypes B-Willd BW00623010!, G!).

NOTES. Turpin (1806) personally observed the species on a dried swamp immediately south of Cap-Haïtien (Haiti), nowadays seemingly urbanised. According to Turpin, the species was seen and apparently collected in the same place by P.A. Poiteau, who brought many other botanical specimens from the French colony Saint-Domingue during 1796 – 1800 (Stafleu & Cowan 1983, 1986). Poiteau's specimen, likely collected in 1797 according to the notes in Turpin (1806), was designated as a lectotype of *Cypselea humifusa* by Bohley *et al.* (2017), who misplaced the type locality in the Dominican Republic.

Bohley *et al.* (2017: 134) cited "*Millegrana surian* Juss., Nomencl. Bot. [Steudel], ed. 2, 2: 146, 1841, syn. nov." in the synonymy of *Sesuvium humifusum*. This citation stems from a technical misunderstanding. Turpin (1806: 221) commented that he knew *Cypselea humifusa* from a number of specimens, including one from St. Domingo that was kept in the collection of J.D. Surian revised by A.L. de Jussieu, which Turpin cited directly by its page number (363) in the bound herbarium book (cf. Stafleu & Cowan 1986). Surian reportedly used the name "*millegrana*" for this collection, and his name and the name of de Jussieu in connection with this plant were indexed by Steudel (1841) from Turpin (1806) and became the source of further misinterpretations. Steudel (1841: 146) listed the generic name "*Millegrana* Juss." as a synonym but provided no accepted generic name corresponding to this old generic designation. Instead, he referred to an unnamed species of this genus by listing its authorities ("Surian. Juss."), and stated that the species is the same as *Cypselea humifusa*. This non-existing "species designation" ("*Millegrana surian* Steud.") was misleadingly recorded in Index Kewensis (Jackson 1895), albeit with a note that the original entry in Steudel (1841) was presumably an error ("sphalm.").

= *Radiana petiolata* Raf. (Rafinesque 1814: 88).

Type (Bohley *et al*. 2017: 134): Haiti ("Saint-Domingue"). [Drained swamp south of Cap-Haïtien,] *P.A. Poiteau* s.n. (neotype P011900032!).

NOTES. Rafinesque (1814) stated that he knew the species from some material collected in Haiti and sent by Turpin. Although no specimens from the Sicilian period survived in the impoverished collections of Rafinesque (Boewe 2011), the material was likely collected by Turpin or Poiteau in the type locality of *Cypselea humifusa* and probably was part of the original material of the latter species name. For this reason we feel confident to fix the application of this name by accepting the lectotype of *Cypselea humifusa* as a neotype of *Radiana petiolata*, which was formally effected by Bohley *et al.* (2017), who cited this specimen as a "lectotype" of both names.

Annual, prostrate, basally much branched; leaves up to 10 mm long, flat, ovate, glabrous or slightly papillate, stipules fimbriate; flowers with short pedicels, perianth 1.5 – 2.3 mm long, white or pinkish inside; stamens 3, anthers round, ~ 0.3 mm long; seeds brown, drop-like, 0.3 – 0.4 mm long, aril tightly adhering to the seed coat, its cells forming a roughly reticulate ultrasculptural pattern (Fig. 7C, D).

DISTRIBUTION: West Indies, southern part of USA; further unverified records exist from the Kingdom of the Netherlands (Curaçao: Acevedo-Rodríguez & Strong 2012) and Venezuela (Margarita Island: Urban 1920). Not reported from other West Indian islands (e.g., Trinidad & Tobago: Cheesman 1940; Barbados: Gooding *et al.* 1965).

SPECIMENS EXAMINED (Map 2). **BRITISH VIRGIN ISLANDS**: Anagada Island, Feb. 1913, *N.L. Britton & W.C. Fishlock* 1052 (K). **CUBA**: "Cuba Orientalis", 1856–1857, *C. Wright* 596 (B, K); Matanzas [without date], *Riedel* 236 (LE); Havana, 29 March 1905, *A.H. Curtiss* 698 (BM, G, K, M, L3716741, P05004447); Havana, Marianao, 28 April 1914, *E.L.*

Ekman 425 (K); Pinar del Rio prov., 25 March 1920, *E.L. Ekman* 10568 (BM); [Matanzas pov.] Zapata peninsula, 31 Jan. 1924, *E.L. Ekman* 18354 (G); Laguna Grande, Aug. 1941, *Gavilan* 6291 (U1057843). **DOMINICAN REPUBLIC**: Santo Domingo, [without date], *Ventenat s.n.* (G); Santo Domingo, 16 July 1887, *Eggers* 2831 (K); Barahona province, March 1911, *P. Fuertes* 930 (G); Santo Domingo, 14 May 1929, *E.L. Ekman* 12468 (U1057840). **GUADALUPE**: [without exact location and date], *Duchassaing s.n.* ex herb. Griseb. (B); [without exact location], *anonym s.n.* (P05004453); [without exact location], 26 Sep. 1933, *R.P. Quentin* 760 (P05004457). **HAITI**: 26 April 1928, *E.L. Ekman* 9893 (G, K, LE). **KINGDOM OF THE NETHERLANDS**: [Netherlands Antilles]: Bonaire, Onima, July 1947, *F. Arnoldo* 987 (U1057838); Bonaire, van Jatoe Bacoe, 8 Nov. 1952, *A.L. Stoffers* 637 (U1057839); Aruba, Dam Daimari, 24 May 2000, *A.S.J. van Proosdij* 1126 (U0138893). **TURKS & CAICOS ISLANDS**: Grand Turk, about North Wells, 28 Nov. 1977, *D.S. Correll* 49195 (NY 1510665 digital image). **US VIRGIN ISLANDS**: St. Thomas, *Eggers & Toepfer* 146 & 225 (BR0000023103924, G, K, L1698988, LE, M, P05004451).

Sesuvium rubriflorum *(Urb.) Bohley & G.Kadereit* (Bohley *et al*. 2017: 141).

≡ *Cypselea rubriflora* Urb. (Urban 1929: 15).

Type (Bohley *et al.* 2017: 141, first-step; designated here, second-step): Cuba, Matanzas, Near Caimito de Hanábana on dried out bottoms of ponds, 08 Aug. 1923, *Ekman* 17016 (lectotype B 10 0242330!, isolectotype NY).

NOTE. Bohley *et al.* (2017: 141) cited both specimens of the type collection as "type", for which reason a second-step lectotype is designated here.

Short-lived perennial, prostrate, basally much branched; leaves up to 10 mm long, flat, ovate, glabrous or slightly papillate, stipules fimbriate; flowers with short pedicels, perianth 2.2 –

2.8 mm long, red or mauve; stamens 5, 0.4 – 0.6 mm long; seeds brown, drop-like, 0.3 – 0.4 mm long, aril tightly adhering to the seed coat, its cells form roughly reticulate ultrasculptural pattern (Fig. 7A, B).

DISTRIBUTION. Endemic to Cuba.

SPECIMENS EXAMINED (Map 2). **CUBA**: Matanzas prov., Caimito de la Hanábana, 8 Aug. 1923, *E.L. Ekman* 17016 (BM, G).

Sesuvium revolutifolium *Ortega* (Ortega 1797: 19).

Described from plants cultivated in the Royal Botanical Garden in Madrid from seeds collected in Mexico (in the protologue erroneously stated as collected in Cuba). Neotype (Hartmann 2001, as "lectotype"): Table 179 in Candolle, Plantarum historia succulentarum (unpubl.).

NOTES. In the past, *S. revolutifolium* was synonymised with *S. portulacastrum* (Sims 1814; Wilson 1932; Nevling 1961; Bohley *et al.* 2017) or considered to be closely related to the latter species (Hartmann 2001, 2017).

Sesuvium revolutifolium was described by Ortega (1797) based on cultivated plants which were, according to the protologue, raised from seeds brought by the Spanish botanist Martin de Sessé y Lacasta from Cuba to the Royal Botanical Garden in Madrid. No authentic specimens of *S. revolutifolium* Ortega have been traced at MA (Charo Noya, pers. comm.). We have seen old specimens at BM, G and RO labelled as *S. revolutifolium*, but these specimens have no apparent connection to the protologue. Greyish plants with papillate stems and leaves and sessile flowers, the characters mentioned in the protologue of *S. revolutifolium* (Ortega 1797), are diagnostic of the species currently known as *S. verrucosum*. Therefore, *S. revolutifolium* is the oldest name for the plants that recently became known as *S. verrucosum*

and cannot be considered a synonym of *S. portulacastrum*. The reason to synonymise *S. revolutifolium* with *S. portulacastrum* seems to have been the conservative character of old taxonomic treatments which preferred a broader species concept.

The seed material of *S. revolutifolium* allegedly collected in Cuba in the late 18th century is the only report of this species in the island, and its native distribution are is the USA and Mexico (Ferren 2003). *Sesuvium portulacastrum* is widely distributed along the sea shores of Cuba and adjacent regions (Urban 1920; Adams 1972; Riha 1976), and this may have been another reason to maintain *S. revolutifolium* in the synonymy of *S. portulacastrum*. Prior to the botanical expedition to Cuba and Puerto Rico in 1795 – 1798, Sessé y Lacasta actively collected plants in western Mexico during 1789 – 1792 (Stafleu & Cowan 1985). He sent seeds for cultivation in Madrid, which were collected in both areas, Mexico and Cuba, and became the basis for new species established by Ortega (1797). Most likely, the provenance indication for the seeds of *S. revolutifolium* was confused at some point and the native area appeared to be stated incorrectly in the protologue (as Cuba instead of Mexico).

= *Sesuvium ortegae* Spreng. (Sprengel 1801: 36) **synon. nov.**

Type: not designated.

NOTES. Sprengel (1801) described *S. ortegae* based on plants growing in the Botanical Garden Halle, Germany. There is no data about the origin and collector of the seed material, but we assume that it could have been sent by C.G. Ortega, to whom the epithet of the new species is dedicated. Sprengel (1801) mentioned the sessile flowers of *S. ortegae* as contrasted to the pedicellate flowers of *S. portulacastrum*. In fact, the latter species may have (sub)sessile flowers, and we are not sure which species (*S. verrucosum* or *S. portulacastrum*) was cultivated in the garden. The original description of *S. ortegae* does not mention the papillate stems and leaves; however, we propose to consider this species name as a synonym

of *S. revolutifolium* (*S. verrucosum*) based on the assumption that the seeds of both *S. revolutifolium* and *S. ortegae* originated purportedly from Cuba (see also notes under *S. revolutifolium*).

= *Sesuvium revolutum* Pers. (Persoon 1806: 39).

– *Sesuvium portulacastrum* var. *revolutum* (Pers.) Sims (Sims 1814: pl. 1701).

Type (Hartmann 2001: 299): Table 179 in Candolle, Plantarum historia succulentarum (Rowley 1956: 3, Fig. 2) (lectotype).

NOTES. *Sesuvium revolutum* was considered as a synonym of *S. portulacastrum* (Sims 1814; Forbes & Hemsley 1888; Arechavaleta 1905; Bohley *et al.* 2017) or a synonym of *S. revolutifolium* (Hartmann 2001, 2017). The original synonymy (Sims 1814) seems to be based on the very broad species concept of old times, when *S. revolutum* was not properly understood and its main diagnostic characters (papillate stems and leaves) were not considered. We have seen old specimens at B (B-W 09667 01 0, B-W 09667 02 0) and G-DC (G00660407, G00860408) labelled as *S. revolutum*. All of them belong to the same species later described as *S. verrucosum* and may have the primary origin from Ortega; Willdenow (1809), while treating his material, referred to [Martin] Vahl that may be a reference to the (secondary) origin of his seed material from the Copenhagen Botanical Garden. Despite the fact that it is hardly likely that these specimens were seen by Persoon (1806), we propose to synonymise *S. revolutum* with *S. revolutifolium* (*S. verrucosum*) because the protologue of *S. revolutum* reads as an abbreviated version of the protologue of *S. revolutifolium*. Persoon (1806) referenced to an unpublished illustration which is the same as the proposed neotype of *S. revolutifolium* (Hartmann 2001); this illustration, reproduced by Rowley (1956), does not allow observation of the characters of leaf and stem surface but affirms the sessile flowers and revolute leaves.

= *Sesuvium verrucosum* Raf. (Rafinesque 1836: 16) **synon. nov**.

Type (Bohley *et al.* 2017: 144): [USA] "Salt River", *Nutt.*[*all*] (P00680440!); epitype (Bohley *et al.* 2017) "*A.C. Sanders* 23186" (BRIT, n.v.).

Perennial, prostrate or ascending, basally much branched; leaves up to 40 mm long, flat or rarely revolute, ovate, papillate, stipules entire; flowers (sub)sessile, perianth 7 – 12 mm long, pinkish inside; stamens 30 – 50, anthers 0.5 – 0.7 (1.0) mm long; seeds black, 0.8 – 1.0 mm in diam., aril often detaching from the seed coat in the area of the cotyledons, its cells form finely reticulate ultrasculptural pattern (Fig. 9A, B).

DISTRIBUTION. North America (USA and Mexico); alien in Macaronesia (Sukhorukov *et al.* 2018, 2019), W and SE Asia (Bohley *et al.* 2017; Sukhorukov *et al.* 2018). Also reported as alien in S America (Argentina, Peru) (Bohley *et al.* 2017), but these records belong to *S. parviflorum*, a neglected species which is native to S America (Sukhorukov *et al.* 2018; Sukhorukov, unpubl.). A spurious record from Cuba is based on old references (Ortega 1797; Sprengel 1801). The nearest locations are known in Florida, USA (re-identifications of the herbarium material by the first author) where the species has not been reported so far (Ferren 2003).

NOTES. *Sesuvium revolutifolium* is not invariable in the length of the anthers. It has the anthers about ~ 0.5 mm in most specimens seen, but some specimens from Mexico are characterised by longer anthers reaching 1 mm.

Sesuvium portulacastrum (*L.*) *L.* (Linnaeus 1759: 1058). – *Portulaca portulacastrum* L. (Linnaeus 1753: 446).

Type (Wijnands 1983: 175): [icon] Hermann, Paradisus batavus, tab. 212 (1698) (lectotype).

= *Sesuvium sessile* Pers. (Persoon 1806: 39).

Type: Plate 9 in Candolle (1799) (holotype).

Epitype (Bohley *et al.* 2017: 139): [Uruguay], Montevideo, [without date] *P. Commerson* 138 in Herb. Jussieu (P00680445 – image!).

NOTES. Persoon (1806) did not see the plant in nature and referred to the work of Candolle (1799), which was likely the sole basis for his new species. Persoon (1806) stated that his species is characterised by linear-oblong leaves and almost sessile flowers, and cited Candolle's Plate 9 that was named *Sesuvium portulacastrum*, without indication of provenance. The epitype (P00680445) contains plant fragments bearing (sub)sessile flowers that are in accordance with the illustration in Candolle (1799).

The short pedicels mentioned in the protologue were sometimes the reason to identify North or South American plants with sessile flowers as "*S. sessile*" (e.g. Orcutt 1908; Britton & Brown 1913; Gentry 1950; Correll 1966; Judd & Lonard 2004). Such identifications are present on numerous old herbarium sheets of *S. maritimum*, *S. parviflorum* and especially of those of *S. verrucosum* in various herbaria.

We could not find any significant difference between the "true" *S. portulacastrum* and the figure of *S. sessile* in Candolle's Plate 9, except the sessile to subsessile flowers in the latter. In fact, the short-stalked flowers can be rarely found in *S. portulacastrum* as well (see also remarks under *S. microphyllum*), and therefore *S. sessile* is merged here with *S. portulacastrum* as in some other treatments (Don 1834; Trautvetter 1883; Bohley *et al.* 2017). The leaves of the plant portrayed on Candolle's Plate 9 are described as glabrous (Candolle 1799), which excludes *S. verrucosum* as another species with more typical subsessile flowers.

= *Sesuvium microphyllum* Willd. (Willdenow 1809: 521).

Type: Cuba, “In maritimis Havanae”, “Ventôse an 9” [20 Feb. – 4 March 1801], *Humboldt & Bonpland 1272* (holotype B-W-09666010!).

NOTES. *Sesuvium microphyllum* is a variety of *S. portulacastrum* with shorter leaves (up to 25 mm long) and shorter pedicels (3 – 7 mm). It was usually accepted in its specific rank in floristic treatments (de la Sagra 1845; Sauvalle 1873; Curtiss 1905; Britton 1908; Wilson 1932; Gillis *et al.* 1973; Scott & Carbonell 1986; Howard 1988; Acevedo-Rodríguez & Strong 2012; Hartmann 2017), although Hartmann referred to the small contribution of Riha (1976) who planted both *S. microphyllum* and *S. portulacastrum* in a greenhouse and finally stated that the first species is an ecological variety of *S. portulacastrum* growing under unfavorable conditions. We agree with his conclusion based on our molecular phylogenetic results (Fig. 1) where the samples of *Sesuvium* with the shorter terete leaves collected in Curaçao by APS in 2018 were nested together with *Sesuvium portulacastrum* (papillate form), and *S. microphyllum* from Cuba forms a polytomy with other samples of “true” *S. portulacastrum*. According to the observations of APS in Curaçao, this variety with shorter terete leaves always occurs in areas unreachable by sea water. Such plants were collected in Anguilla, Antigua, Bahamas, Cayman Islands, Cuba, and Turks & Caicos Islands and recently in Curaçao and are presumably present on other islands of the West Indies.

The collections of A. von Humboldt and A. Bonpland have a convoluted history. As explained by Hiepko (2006), Willdenow received two large sets of dried plants from Humboldt with his permission to publish some of the possible novelties. Indeed Willdenow (1809) published two new species of *Sesuvium* on the basis of this collection, *S. longifolium* Willd. from tropical South America and *S. microphyllum* Willd. The latter species, described from the vicinity of Havana (Cuba), is represented by a single specimen in the personal herbarium of Willdenow (B-W-09666010), which is the holotype of that species name. For

uncertain reasons, Bohley *et al.* (2017) designated a neotype of *S. microphyllum* (B 10 0390872!). This specimen, as evident from one annotation label in Willdenow's hand ("*Sesuvium microphyllum*") and another annotation label in C.S. Kunth's hand ("*Sesuvium*. Ex herb. Humboldt"), belonged to the set of Humboldt's specimens that remained in Paris and was offered for treatment to Willdenow in 1810 – 1811 and to Kunth since 1813 (Hiepko 2006). This specimen was possessed by Kunth and was moved to Berlin along with his personal collection. Since this specimen was not available to Willdenow prior to publication of the protologue, it cannot be part of the original material of *S. microphyllum*; however, the neotypification of this name was completely unnecessary since the holotype has survived.

Humboldt indicated collection dates of his specimens with a month and a year according to the French Republican Calendar (Rankin Rodríguez & Greuter 2001). The indication on the holotype of *S. microphyllum* reads "Ventôse an 9", which can be converted into the Gregorian Calendar as 20 Feb. – 21 March 1801. Since Humboldt's first stay on Cuba lasted from 19 Dec. 1800 to 5 March 1801 (Biermann *et al.* 1983), the collection date can be limited to 20 Feb. – 4 March, and most likely to the last decade of February.

= *Sesuvium spathulatum* Kunth (Kunth 1823: 87).

Type: Cuba [In rupubus maritimis Havanae], *Humboldt & Bonpland* 1272 (holotype P00679574).

NOTES. Kunth (1823) described *Sesuvium spathulatum* from a single collection from Havana, Cuba (*Humboldt & Bonpland* 1272). This is the same collection as was the basis for *S. microphyllum*. Kunth used for his description only a part of the collection that was kept in Paris (Hiepko 2006). At present, in the Herbarium of P there are three specimens of *Humboldt & Bonpland* 1272: two specimens (P01900027, P01900028) that were possessed by Humboldt in Argentina but returned to Paris in 1832, and one specimen (P00679574) from

the main set of Humboldt & Bonpland's herbarium with a characteristic curatorial printed label. Also, there is a specimen at B (B 10 0390872) that was originally kept in Paris but was transferred to Berlin by Kunth in 1829. Of these specimens, only the specimen in the main set was annotated and used by Kunth, which is the holotype (Art. 9.1(b)) (Hiepko 2006).

= *Sesuvium brevifolium* Schumach. (Thonning & Schumacher 1827: 233).

Type (Sukhorukov *et al*. 2018: 69): Danish Gold Coast, Guinea [probably SE Ghana], *P.E. Isert* s.n. (lectotype C10004542 [image seen!]).

= *Sesuvium acutifolium* Miq. (Miquel 1843: 75).

Described from Surinam; type not traced.

NOTES. *Sesuvium acutifolium* was described from Matapicca, Surinam (Miquel 1843), and no original material was found (Hartmann 2017; Bohley *et al.* 2017; Roxali Bijmoer, pers. comm.). The description of *S. acutifolium* completely corresponds with that of *S. portulacastrum*, and only narrower (lanceolate) leaves with acute tips are indicated as the main character of the first species. However, such leaf shape is often present in *S. portulacastrum* in many parts of the world. There is only one old specimen seen annotated as *S. acutifolium*: "Bonaire" [without date and collector's name], herb. Lamarck (P-LA 00307761). This specimen represents an individual of *S. portulacastrum* with slightly papillate leaves looking greyish. Miquel (1843) did not mention the pubescence details of his new species, and we are not sure whether this specimen with papillate leaves was seen by Miquel. The papillate leaves are present in the individuals of *S. portulacastrum* in many parts of the Americas, and the first author (APS) has observed and collected such plants in Curaçao growing together with the "true" *S. portulacastrum* with glabrous leaves (Fig. 10). In the molecular phylogenetic analysis, a sample of the papillate form of *S. portulacastrum* falls

within the same subclade comprising *S. microphyllum*, another slightly deviating taxon (Fig. 1), and therefore there is no reason to accept the American plants with the papillate leaves as a separate species.

Perennial, prostrate or ascending, basally much branched, stems often creeping; leaves up to 60 mm long, flat or terete, lanceolate, oblong, ovate or obovate, glabrous or finely papillate, stipules entire; flowers with remarkable pedicels up to 20 mm long, rarely subsessile, 8 – 10 mm long, pink inside; stamens 30 – 50, anthers 0.45 – 0.65 mm long; seeds black, 1 – 1.2 mm in diam., aril tightly adhering to the seed coat (or rarely reduced), its cells forming a finely reticulate ultrasculptural pattern (Fig. 8G, H).

DISTRIBUTION. Sea shores of the Americas, as alien in other (sub)tropical parts of the World.

SPECIMENS EXAMINED (Map 3). **ANGUILLA:** Long Bay Pond, 6 Jan. 1959, *G.R. Proctor* 18656 (BM). **ANTIGUA & BARBUDA:** Antigua [without exact location and date], *Nicolson s.n.* (P05312425); Guiana Island, 28 Feb. 1931, *A.K. Jotton* s.n. (BM); Antigua, Parish of St. George, 1 Nov. 1937, *H.E. Box* 1242 (BM). **BAHAMAS:** Water Key, Salt Key Bank, 22 May 1909, *P. Wilson* 8154 (K); Andros Island, 1 Sep. 1937, *Battler* 84 (K); Exumas, Hummingbird Cay, May 1975, *M. Morin* 4066 (MEXU); South Andros, Congo Town, 1 Jan. 1976, *W.T. Gillis & K.C. Buckley* 12801 (BM). **BARBADOS:** April–June 1895, *J.F. Waby* 29 (BM); Graeme Hall, 10 Feb. 1937, *anonym* 295a (K). **CAYMAN ISLANDS:** Little Cayman Island, Bloody Bay, 7 June 1938, *W. Kings* 118 (BM); Grand Cayman, Gun Bluff, 23 April 1956, *G.R. Proctor* 15201 (BM); Grand Cayman, Snug Harbor, 16 June 1974, *D.R. Stoddart* 7020 (BM); Little Cayman, Head of Bay, 9 July 1967, *G.R. Proctor* 28066 (BM); Cayman Brac Island, 9 Aug. 1968, *G.R. Proctor* 29128 (BM); Grand Cayman Island,

Snug Harbour, 16 June 1974, *D.R. Stoddart* 7016 (BM). **CUBA**: [without precise location and date] *Drummond* s.n. (K); Santa Clara prov., Cienfuegos distr., 31 May 1895, *R. Combs* 208 (K); near Habana, rocky seashore, 17 Dec. 1904, *A.H. Curtiss* 569 (E00651956, G, K, P04583800); Habana, Reparto Miramar, 11 Oct. 1921, *E.L. Ekman* 13307 (G); Santiago prov., 10 Nov. 1981, *L. Elenevskaya & A. Elenevsky* s.n. (MW); Camagüey prov., 15 Dec. 1984, *L. Elenevskaya & A. Elenevsky* s.n. (MW); Cienfuegos, 1 Feb. 2005, *J. Bouharmont* 33737 (BR00000943546); Matanzas prov., Peninsula de Hicacos, 5 km NE of Varadero, 24 March 1998, *H.-J. Tillich* 3638 (MSB65475); Matanzas prov., Icacos Peninsula, 20 Nov. 2008, *V.D. Bochkin & N.A. Bokal* s.n. (MHA). **DOMINICA**: Parish St. Mark, Scotts Head, 25 June 1992, *H.T. Beck & K. Lee* s.n. (MEXU). **DOMINICAN REPUBLIC**: Santo Domingo, [without date and collector] s.n. (BM); Santo Domingo, [without collection date], *D. Poiteau & Turpin* s.n. (LE); Santo Domingo, 15 April 1858, *L.A. Prenleloup* 235 (G); prov. Barahona, 15 Aug. 1946, *R.A. Howard & E.S. Howard* 8359 (BM); Rio Bao, Dec. 1952, *H. Humbert* 27717 (P04583841); S. Domingo, 21 May 1987, *J. Bouharmount* 18514 (BR00000943568). **GRENADA**: Main island. St. George Parish, 18 Nov. 2016, *A. Sukhorukov* 82 (BR0000026777641, MW). **GUADALUPE**: [without exact location and date] *L'Herminier* s.n. (G); St. Barthelemy, 30 Nov. – 2 Dec. 1936, *Questel* s.n. (P04583840); Anse Canot, 25 Oct. 1982, *F. Billiet & B. Jadin* 1411 (BR0000023106031); Grande Terre Gosier, 15 April 1984, *C. Defferrard* 4491 (G). **HAITI**: Massif de la Sella, Port-au-Prince, 18 May 1937, *E.L. Ekman* 8161 (G); Dept. du Sud, 6 July 1980, *C. Sastre & Y. Polynice* 7346 (P04583076). **JAMAICA**: [without exact location], March 1893, *Grisebach* s.n. (K000367652); Spanish Town Road, July 1901, *W. Harris* 8183 (BM); Hunts Bay, 22 Feb. 1920, *W.R. Maxon & E.P. Killip* 330 (P04555531); St. Andrew, 20 October 1957, *T.G. Yuncker 17128* (G); Kingston Parish, Palisadoes, 14 June 1959, *G.L. Webster et al.* 8224 (G); Port Royal Cays, 27 Dec. 1966, *R.D. Henry* 850 (WU); Port Royal Cays, Drunkenman's Cay, 23 Oct. 1985, *D.R.*

Stoddart & S.M. Head 9111 (BM); Morant Cays, 26 Oct. 1985, *D.R. Stoddart & S.M. Head* 9166 (BM); Cornwall county, St. James parish, 25 Aug. 1992, *W. Till & S. Till* 9060 (WU). **KINGDOM OF NETHERLANDS**: [Special Municipality of Netherlands] St. Eustatius, 1885, *anonym* s.n. (L1693490); Aruba [without date and collector] 97 (L1693365); Bonaire [without date and collector], herb. Lamarck (P-LA 00307761); Curaçao, 1910, *I. Boldingh* 4899 (L3716745); Curaçao, 19 Feb. 1919, *H.M. Curran & M. Haman* 95 (K, P04583838); Curaçao, on sand, 24 Oct. 1936, *H.H. Haines* 16 (K); Curaçao, St. Michiel, 3 Jan. 1958, *M. Vroman* s.n. (L0717111); Curaçao, Piscadera, 8 Jan. 1961, *P.A.W.J. de Wilde* 89a (L1693363); Bonaire, nr Lac, 17 March 2002, *P. Ketner* 2002/1 (WAG0359162); Curaçao, 8 March 2018, *A. Sukhorukov* 42, 44, 72 & 86 (M, MW); Curaçao, Piscadera, March 2018, *A. Sukhorukov* 91 (MW). **MARTINIQUE**: [without date] *Stahn* 1333 (BM); 1868–1869, *L. Hahn* 1333 (G); Trinité, 11 Sep. 1988, *C. Sastre & J.P. Fiard* 8607 (P05196637). **PUERTO RICO**: Cabo Rojo, 4 Feb. 1885, *P. Sintenis* 912 (G, LE); Luquillo, 18 May 1885, *P. Sintenis* 1849 (P04555496); Guanica, 7 Feb. 1886, *I. Urban* 3825 (M); Rincon, 11 Dec. 1886, *P. Sintenis* 5813 (G); Las Croabas, 12 July 1963, *R.J. Wagner* 311 (BM, LE). **ST. KITTS & NEVIS:** [without exact location] Sep.–Oct. 1901, *N.L. Britton & J.F. Cowell* 429 (K). **ST. LUCIA:** Vieux Fort, 1958, *G.R. Proctor* 17679 (BM). **ST. MARTIN ISLAND:** 1906, *I. Boldingh* 3389B (L3716746); **TRINIDAD & TOBAGO**: Trinidad Island, 15 June 1929, *W.E. Broadway* 7279 (BM, G); Chacachacare Island, 15 March 1953, *R.E.D. Baker & N.W. Simmonds* 14920 (K); Tobago island, Little Rocky Bay, 2 June 1975, *D. Philcox & A. Raynal* 7836 (K, P05196613); Tobago island, Pigeon Point, 22 March 1993, *E.J. Clement & T.B. Ryves* 134 (BM). **TURKS & CAICOS ISLANDS**: Salt Cay, south-east end of the island, 26 Feb. 1973, *W.T. Gillis* 11864 (B 100617964); Salt Cay, 11 Sep. 1978, *D.S. Correll* 50179 (BM); South Caicos, East Bay area, 25 May 2009, *M.J. Visaya & B.N. Manco* 58 (BM, K). **US VIRGIN ISLANDS**: St. Thomas, July 1881, *Eggers* 489 (BR0000023106147, FR-

0132706, G, LE, M, P04583846, WU); St. John, Coral Bay, 9 Jan. 1896, *F. Borgesen* s.n. (M); St. Croix: Lime-tree bay, 22 April 1897, *J.J. Ricksecker* 269 (E00651967); Northside strand, February 1906, *F. Borgesen* s.n. (BR0000023106154, P04555530); Judith's Fancy, 21 Oct. 1923, *J.B. Thompson* 476 (G); Jack Bay, 17 July 1970, *W.G. D'Arcy* 4667 (BM); St. John, Salt Pond Beach, 29 Dec. 1972, *W.J. Schrenk* 478 (FR-0132693).

NOTES. According to the molecular studies presented in this article, *S. portulacastrum* should be considered in a broader sense, and is morphologically variable. The leaves can be short (<3 cm) or long (3 – 7 cm), flat or terete (in latter case, the leaf length is up to 3 cm), glabrous, mamillate or papillate (the papillae up to 50 μm high). The length of the pedicels varies from 3 to 15 (20) mm. However all the examined samples have smooth seeds (Fig. 8 E–H).

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Legend.

Figure 1. Phylogenetic reconstruction resulting from a BI analysis based on the nrITS region and three plastid regions (*rps16* gene intron, *atpB-rbcL* and *trnL-trnF* intergenic spacers) Bayesian posterior probabilities from the BEAST analysis are above the branches and jackknife values (left) and bootstrap percentages of the maximum likelihood analyses (right) are given below branches.

Figure 2. Holotype of *Sesuvium curassavicum* (*A.P. Sukhorukov* 100; MW0595676).

Figure 3. Leaf anatomy of *Sesuvium curassavicum* (from the holotype *A.P. Sukhorukov* 100; MW0595676). Abbreviations: CHL – chlorenchyma, EP – epidermis (represented by papillae and normal epidermal cells), VB – vascular bundles, WST – water storage tissue. Scale bar: 1 mm.

Figure 4. Leaf anatomy of *Sesuvium revolutifolium*: A – flat leaf, B – terete leaf. Abbreviations: CHL – chlorenchyma, DR – druses, EP – epidermis, VB – vascular bundles, WST – water storage tissue. Scale bar: 1 mm (A), 0.5 mm (B).

Figure 5. SEM micrographs of *Sesuvium curassavicum* seeds: A, B –seeds with furrows, covered with an aril (*A. Sukhorukov* 100, MW 0 595 676) Magnification: A – 70×; B – 300×.

Figure 6. *Sesuvium curassavicum*: A, B – typical habitats of the species on Curaçao Island; C, D – general view of the plant. Photographs by A. Sukhorukov, March 2018.

Figure 7. SEM micrographs of *Sesuvium* seeds: A, B – *S. rubriflorum* (*Ekman* 17016, B 10 0242330), C, D – *S. humifusum* (*A. H. Curtiss* 698, BM). Magnification: A, C – 70×; B, D – 300×.

Figure 8. SEM micrographs of *Sesuvium* seeds: A, B – *S. revolutifolium* (= *S. verrucosum*) (Flores Olvera *et al.*, MEXU); C, D – *S. maritimum* (*G. R. Proctor* 15115, BM), E, F – *S. portulacastrum* (a variety with the shorter leaves = *S. microphyllum* (*A. Sukhorukov* 42, MW); G, H – *S. portulacastrum* (*A. Sukhorukov* 44, MW). Magnification: A, C, E, G – 70×; B, D, F, H – 300×.

Figure 9. *Sesuvium maritimum* (A, B; Saint Catherines Island, Liberty County, Georgia, USA, 25 May 2016) and *S. humifusum* (C; Stafford Lake County Park, Novato, Marin County, California, USA, 4 Aug. 2018). Photographs by Keith Bradley (A, B) and Vernon Smith (C).

Figure 10. *Sesuvium portulacastrum*: A – typical habitats of the species; B – a variety with the shorter leaves (= *S. microphyllum*); C – a variety with the papillate leaves, general view; D – close-up view of the species having papillate leaves. Photographs by A. Sukhorukov in Curaçao Island, March 2018.

Map 1. Distribution map of *Sesuvium curassavicum*.

Map 2. Distribution map of *Sesuvium maritimum* (stars), *S. humifusum* (circles) and *S. rubriflorum* (square) in the West Indies.

Map 3. Distribution map of *Sesuvium portulacastrum* in the West Indies.