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A Revision of *Sesuvium* (Aizoaceae, Sesuvioideae)

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Abstract—*Sesuvium* and *Cypselea* are closely related succulent genera within the Sesuvioideae (Aizoaceae). Since *Cypselea* is nested in *Sesuvium* in molecular studies and both genera share traits separating them from other members of the subfamily, we propose to include *Cypselea* in *Sesuvium*. *Sesuvium* (incl. *Cypselea*) comprises 14 species and is distributed worldwide with centres of diversity in southern Africa and North and Central America. *Sesuvium* comprises erect to procumbent herbs with opposite leaves that often bear conspicuous sheath-like lateral appendages on the petioles (pseudostipules). These and the many-seeded capsules are diagnostic traits, separating *Sesuvium* from the closely related genera *Trianthema* and *Zaleya*. *Sesuvium* is usually found in coastal or otherwise saline areas and is phylogenetically divided into an African (5 spp.) and an American lineage (9 spp.). While all African species are C₄ plants, the American lineage also comprises a derived C₃ lineage, which includes the cosmopolitan species *S. portulacastrum*. Some floras provide descriptions and keys for locally relevant species, but currently no comprehensive taxonomic treatment is available for *Sesuvium*. In this paper, a key and descriptions for all species are provided. Furthermore, we compile information on the rare and poorly known species of the genus and address issues concerning species concepts in *Sesuvium*, which impede species identification. The inclusion of *Cypselea* in *Sesuvium* leads to three new combinations: *Sesuvium humifusum*, *Sesuvium meianum* and *Sesuvium rubriflorum*.

Keywords—*Cypselea*, halophytes, C₄ photosynthesis, restoration plant, *Sesuvium portulacastrum*, Southern Africa.

The Aizoaceae Martynov are part of the Caryophyllales and contain about 1,700 species in approximately 118 genera (Hernández-Ledesma et al. 2015). As a whole, the Aizoaceae consist mostly of succulent perennial or annual herbs and shrubs and have their centre of diversity in southern Africa. Aizoaceae are divided into four subfamilies, Sesuvioideae Lindley, Aizooideae Arnott, Mesembryanthemoideae Ihlenfeldt, Schwantes & Straka, and Ruschioideae Schwantes (Klak et al. 2003; Thiede 2004; Thulin et al. 2012).

The apparent lack of common traits with the remaining subfamilies led to some confusion whether the Sesuvioideae are rightfully placed within Aizoaceae. Some authors proposed to transfer the subfamily to the Molluginaceae based on a number of shared characters, including stipules and the regular segmental composition of the whole plant (Hofmann 1973). Ehrendorfer (1976) suggested to increase the rank of the Sesuvioideae to that of family, as Sesuviaceae, since it, according to the author, shares nearly the same number of common morphological traits with Molluginaceae as with Aizoaceae and therefore holds an uncertain position in the Aizoaceae s. l. (Ehrendorfer 1976). Bittrich and Hartmann (1988) established the monophyly of the Aizoaceae including Sesuvioideae based on the possession of bladder cell idioblasts in the epidermis and a perianth-stamen tube, which they consider synapomorphies of the family. As mentioned above, Aizoaceae are divided into the subfamilies Sesuvioideae, Aizooideae, Mesembryanthemoideae, and Ruschioideae (Klak et al. 2003; Thiede 2004; Thulin et al. 2012). The Ruschioideae are by far the largest subfamily with about 1,600 species (Klak et al. 2013; Klak et al. 2015), whereas the Sesuvioideae only contain a small part of the family's total species number with about 60 species in five genera. The Sesuvioideae have been characterized by bracteate flowers or inflorescences and stipule-like tissue along the petiole. Furthermore, most members of the subfamily have arillate seeds. Contrary to the larger subfamilies Mesembryanthemoideae (103 ssp.; Klak and Bruyns 2013), Ruschioideae, and Aizooideae (108 ssp.; Melo-de-Pinna et al.

2014) they always lack both hygrochastic capsules (which open up when moist and show hydroballochory) and petaloid staminodes. Instead, circumscissile capsules (which open with one lid when they are ripe and dry) and a simple perianth are found in almost all species of Sesuvioideae (Fig. 1). One exception of the above mentioned characteristics of Sesuvioideae is found in *Tribulocarpus*, where *T. dimorphantus* forms a compound, spiny trample burr and *T. retusus* possesses winged nuts; in both cases the seeds lack an aril (Thulin et al. 2012).

Traditionally the Sesuvioideae contained the genera *Trianthema* L., *Sesuvium* L., *Zaleya* Burm f., and *Cypselea* Turp. Klak et al. (2003) as well as Thiede (2004) independently included *Tribulocarpus* S. Moore into the subfamily after revealing its close relationship as sister to the remaining Sesuvioideae in their molecular phylogenies. This was again confirmed in a more detailed molecular study that focused on *Tribulocarpus* (Thulin et al. 2012), which was considered a member of the Tetragonioideae previous to its transfer to Sesuvioideae. Hassan et al. (2005b) conducted a molecular and morphological study of Sesuvioideae including 27 species and 23 morphological characters; however, relationships within the subfamily remained largely unresolved due to the lack of variation in the molecular marker (ITS) used. Thulin et al. (2012) included 25 accessions of Sesuvioideae and used two additional markers, but encountered the same problem as Hassan et al. (2005b). However, both studies already indicated the possible paraphyly of *Sesuvium* with respect to *Cypselea*. To increase resolution across the Sesuvioideae, Bohley et al. (2015) included 51 accessions across the subfamily representing all genera and 34 species. Their phylogenetic tree resolved all genera of Sesuvioideae as monophyletic except *Sesuvium*, which was again found to be paraphyletic with respect to *Cypselea*, which formed the sister group of American *Sesuvium*. *Zaleya* was resolved as sister to [*Sesuvium* + *Cypselea*], and the *Zaleya* plus *Sesuvium* (incl. *Cypselea*) clade was sister to *Trianthema*. *Tribulocarpus* formed the sister group to all remaining Sesuvioideae (Bohley et al. 2015).

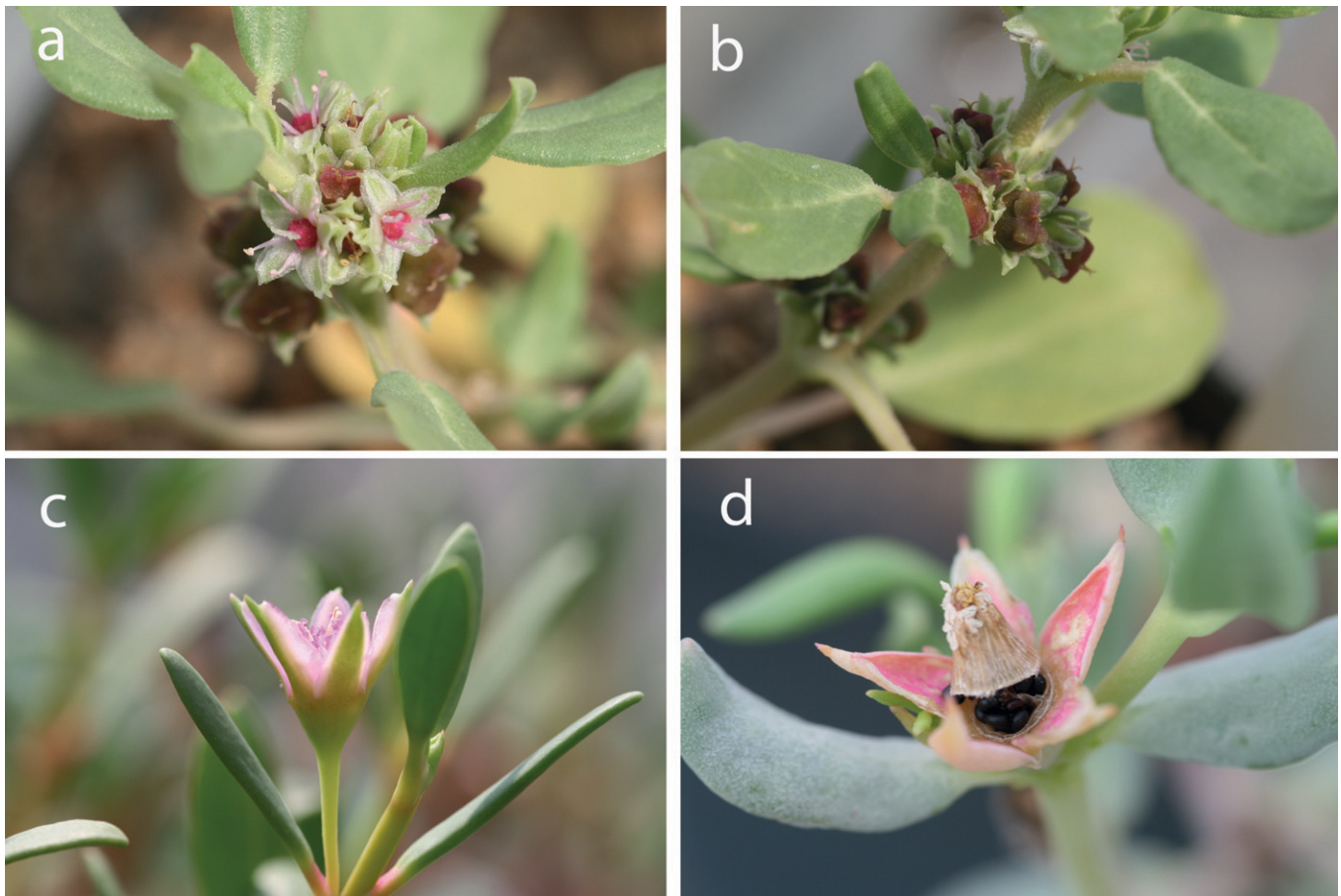


FIG. 1. Flowers and fruits of Sesuvioideae. A–B. *Zaleyia pentandra*. A. Flower. B. Capsule. The lid of the capsule splits into two parts, each usually containing one seed. C. Flower of *Sesuvium portulacastrum*, each tepal with a dorsal, subapical appendage. D. Capsule of *S. sesuvioides*, opening with one lid, stamens still attached. Pictures were taken from plants grown in the greenhouse.

Sesuvium was first described by Linnaeus in 1759. It is possible that the description was based on an illustration by P. Hermann (Wijnands 1983). Hermann (1698) illustrated a specimen grown in the greenhouse from seeds received from Curaçao and described it. Whether Linné had a specimen at hand for his description of the species is unknown, but no corresponding herbarium specimen is present in LINN. Furthermore, all diagnostic characters mentioned in his description are visible in Hermann's illustration.

After the first description of the genus with *Sesuvium portulacastrum* as type, many species were added over the following 220 yr (Supplemental Table S1, Bohley et al. 2017), but the only approximately comprehensive compilation of information about the genus was conducted by Hartmann (2001a, b). However, the scale of her work did not allow her to address all issues concerning *Sesuvium* and *Cypselea*. Since some of the species are quite variable in their morphological characters and have a wide distribution range, it is evident that some species were described several times independently under different names. In this regard, the polymorphic *S. portulacastrum* especially comes to mind, due to its worldwide distribution. In general, *Sesuvium* is a genus of largely decumbent, perennial, and succulent herbs with simple, opposite leaves with sheath-like lateral appendages on the petioles (referred to as pseudostipules by Hartmann et al. 2011) and solitary flowers. Only a few species seem to

be annuals, but often information about the life span of the plants is not precise. Most species can be found on saline soil and some even appear to be confined to habitats with elevated salt concentrations.

Around 50 yr after the description of *Sesuvium*, the genus *Cypselea* was described by P. Turpin in 1806. The type species of the genus, *C. humifusa*, is a very small annual herb occurring in wetlands and seasonal pools. Its most conspicuous traits are the fimbriate margins of the pseudostipules framing the base of the petiole, the tiny white flowers with distinctly unequal tepals, and an androecium consisting of only three stamens. In the early 20th century two further species, *C. meziana* and *C. rubriflora*, were described in the genus (Table S1). Considering all three species, the common trait of *Cypselea* is a reduction of the androecium to 3–5 stamens. The only other traits separating it from *Sesuvium* are the colour, number, and size of the seeds, which are lighter, more numerous, and smaller in *Cypselea* (Hartmann 2001b). *Cypselea humifusa* shows an annual habit and is strictly confined to freshwater areas, whereas the two other species are perennials. Additionally *C. meziana* is also found on saline soil and is able to grow roots at nodes. Of the three, only *C. humifusa* has a broader distribution, occurring in Cuba, in the Caribbean and some states of the U. S. A., whereas the other species are confined to Cuba (*C. meziana*) and Paraguay (*C. rubriflora*).

The motivation to revise *Sesuvium* and *Cypselea* derived from the lack of information available about these two genera and the lack of a comparative taxonomic treatment despite their 200-yr history. In *Sesuvium*, this resulted in a multitude of described species without a complete key, whereas two of the three species in *Cypselea* were hardly ever mentioned after their first description and so remained unknown. The aims of this study are to broaden the circumscription of the genus *Sesuvium* by including *Cypselea*, to provide descriptions for all species and to generate a comprehensive key for the determination of specimens in the herbarium and field. Furthermore, we would like to point out some taxonomic issues that we were not able to solve and need further investigation.

MATERIALS AND METHODS

Plant Material—About 1,011 herbarium specimens of *Sesuvium* and *Cypselea* from B, BOL, BONN, BRIT, C, CAS, HBG, LP, MEXU, MO, NGB, PRE, TEX/LL, S, UPS, WAG, and Z/ZT were investigated on loan. Additionally, the *Sesuvium* and *Cypselea* collections at K were studied during a visit, and all available databased and imaged specimens from NY, P, BM and E were also used. Investigation of morphological characters was done using a binocular microscope.

The specimens on loan were broken down by species as follows (according to their original identifications): *Sesuvium ayresii*: 2; *S. congense*: 4; *S. crithmoides*: 3; *S. edmonstonei*: 11; *S. hydaspicum*: 22; *S. maritimum*: 70; *S. mesembryanthemoides*: 4; *S. microphyllum*: 10; *S. nyasicum*: 6; *S. portulacastrum*: c. 600; *S. sessile*: 32; *S. sesuvioides*: 53; *S. trianthemoides*: 2; *S. verrucosum* (incl. *S. erectum*): 170; *Cypselea humifusa*: 8; *C. meziana*: 1; *C. rubriflora*: 1.

Range maps were prepared from localities given on herbarium labels using QGIS 2.10.1-Pisa (Quantum GIS Development Team 2015).

Anatomical Studies—Either dried material or leaves from plants in the greenhouse were used for anatomical studies. Dry material was first rehydrated in a 10% ammonium solution. Fresh material was fixed with an aldehyde-based fixative. Except for these first steps, the following procedures were the same for both types of material: An ascending ethanol series was used to dehydrate the material, then it was slowly infiltrated with, and subsequently embedded in, resin (Technovit 7100, Heraeus Kulzer, Germany). After the resin was cured, the blocks were sectioned with a rotary microtome (Leitz-Wezlar, Germany), dried on glass slides and stained. For detailed descriptions of the preparation refer to Bohley et al. (2015).

RESULTS

Numerical Data of the Study—Ca. 60% of the loaned specimens belonged to *Sesuvium portulacastrum*. In general, species distributed in Africa or those with a narrow distribution are collected considerably less frequently, e.g. *S. crithmoides* and *S. microphyllum*. Collections from Asia were also severely underrepresented in the loaned material.

For *Sesuvium* and *Cypselea*, 68 names have been validly published (including basionyms and synonyms). 48 of these are represented by 35 known type specimens or illustrations. We were able to examine eight holotypes directly and seven further holotypes were seen as high resolution images. In eight additional cases, we had access to both high resolution images of the holotype and an isotype specimen. In one case, we only saw the isotype. Eleven names are based on illustrations. Five types were not seen, because we were not able to locate the specimens or were not able to get access to the material. For 28 names, no type specimens are indicated and we designated seven lecto- or neotypes representing eight of these names. In addition, seven lecto- and neotypes have been designated by other authors prior to this study, all of

which have been examined in this study. To our knowledge four names remain without type material, but, due to a lack of suitable material, we were not able to choose new types. At least three names have never been validly published.

Morphology—LIFE SPAN AND GROWTH HABIT—Information regarding the life span of *Sesuvium* and *Cypselea* is scarce in many cases and not necessarily correct. Most species are considered perennials, with only *Cypselea humifusa*, *S. nyasicum*, *S. maritimum*, and *S. trianthemoides* described as annuals. No member of *Cypselea* or *Sesuvium* is outright shrubby, but the base and older stems often become woody in some *Sesuvium* species. It seems that all members of the genus are able to flower and set fruit in their first year.

The habit of *Sesuvium* and *Cypselea* is erect or decumbent and more or less creeping. Usually young or short shoots are initially ascending but become decumbent as growth progresses. Single individuals or groups of individuals can form dense and extensive mats with diameters ranging from a few decimeters to more than one meter.

ROOTS—This trait could not be observed in all species, since the roots were often not present on herbarium specimens. As far as seen, all species of *Sesuvium* show a taproot that can be strongly developed, especially in the perennial species (e.g. *S. verrucosum*). Only *Sesuvium portulacastrum*, *S. ayresii*, and *S. microphyllum* seem to grow adventitious roots at nodes as soon as contact to soil is established, although the latter two do not show this characteristic frequently. *Cypselea meziana* is also able to root at its nodes, but we do not know if this occurs often. In *S. verrucosum*, clonal propagation from root suckers was observed in the greenhouse.

BLADDER CELLS—Although bladder cell idioblasts are one of the synapomorphies of the Aizoaceae, not all members of the family show them to the same extent. In *Sesuvium* and *Cypselea*, all examined species have bladder cells, but different sizes are found. Bladder cells can be large and bulging, and therefore clearly visible, or inconspicuous and small, and therefore nearly invisible to the naked eye, at most giving the surface a somewhat dull appearance. In *Sesuvium*, the presence of large, bulging bladder cells ranges from an almost complete and very dense covering (*S. edmonstonei*) to complete absence in adult plants (e.g. *S. portulacastrum*). Not only presence and size differ among the species, but also the shape of the bladder cells. Even though the high diversity of the trait in *Sesuvium* suggests it would be a useful character for species determination, there are at least two drawbacks: 1) In dry material, size and shape of the bladder cells are often difficult to assess precisely; 2) Climate and/or age could possibly lead to a complete or partial loss of bladder cells, as reported for the related *Trianthema* subg. *Papularia* (Hartmann et al. 2011). As mentioned above, the occurrence of conspicuous bladder cell idioblasts is not uniform within *Sesuvium* and may differ between organs. It will therefore be mentioned in the specific sections if needed.

INTERNODES—The internodes of both genera are terete, ranging in colour from green to yellow or red; some reports mention orange shoots. Internode length depends on the growing conditions, but in most cases it is very regular (within individuals). For *S. verrucosum*, *S. sessile*, and *S. sesuvioides* it has been observed that older branches tend to lignify slightly.

LEAVES—*Cypselea* and *Sesuvium* have simple, entire leaves with a (sub-) opposite arrangement. Within one leaf pair, shape is always equal, whereas size may differ slightly. Observed

leaf shapes are lanceolate, oblanceolate, oblong, linear or elliptic with obtuse or retuse tips. All species are at least remotely leaf-succulent. Pronounced succulence is described for *S. ayresii*, *S. congensis*, *S. crithmoides*, *S. edmonstonei*, and *S. microphyllum*, all of which have terete or semi-terete leaves. In *S. portulacastrum* (and probably other species as well), succulence is a variable trait, as different levels of succulence were observed and induced in several individuals in the greenhouse (Fig. 2).

Leaves are either petiolate or sessile. In both cases, the leaf base can be attenuate making it difficult to discern the short petioles. The petiole of all species is framed by two membranous lateral flaps that are clasping and form a semi-sheath around the stem (pseudostipules, Fig. 3A). Those flaps are almost always free of hairs or bladder cells and are

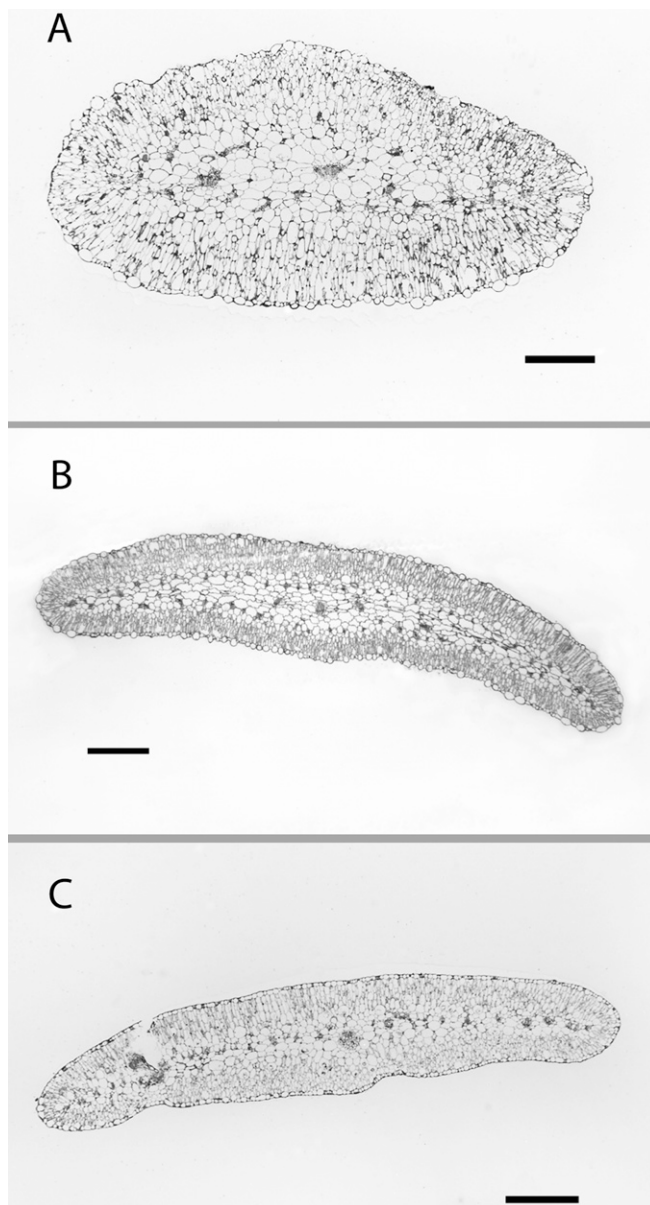


FIG. 2. Leaf cross sections of *Sesuvium portulacastrum*. The sections show different degrees of succulence and the accompanying arrangement of vascular tissue. A–B. Cross sections of the same individual taken within few weeks. C. Section of an individual from another population. All plants were cultivated in the greenhouse. Scalebars: 1 mm.

more or less translucent. The only exception is *S. edmonstonei* where the flaps are densely covered with bladder cells. The most conspicuous trait of the leaves of *C. humifusa* and *C. rubriflora* are the hair-like fimbriate margins of the pseudostipules (Fig. 3B).

INFLORESCENCES—*Sesuvium* and *Cypselea* have solitary flowers that normally seem to grow in the axil of a leaf. Müller (1908) and Hofmann (1973) describe the flowers as terminal instead. In principle, a dichotomous branching pattern is expressed, but the outcome is a dichopodium in which one shoot continues the growth as part of the main axis. The second shoot often develops much later, often simultaneously with the flower or afterwards.

In *Sesuvium*, pedicels can be rather long (~10–15 mm), short (~3 mm), missing or variable in length (e.g. *S. portulacastrum*). Flowers of *Cypselea* are always pedicellate and in *C. humifusa* and *C. rubriflora* the pedicels are often at least as long as the flower.

The flowers of both genera have a simple, five-parted perianth that is fused in approximately the lower half. The free parts of the tepals are usually triangular to lanceolate and have an imbricate-quincuncial arrangement. The perianth of both genera is composed of sepaloïd tepals, of which the inner side is colored and the outer side is green (Fig. 1C). On the dorsal side, a hood- or thorn-shaped appendage is attached shortly below the apex of each tepal, henceforth called a tepal tooth. Depending on the species, the tepal teeth vary in size and prominence. For example, the tepal teeth in *S. portulacastrum* and *S. crithmoides* are usually well developed, whereas those of *C. humifusa* are often small and inconspicuous. Usually the tepal teeth are green, sometimes with a red tinge.

BRACTS—One pair of small bracts is always found at the base of the sessile flower or of the pedicel, respectively. At least one additional pair of bracts is present in *Sesuvium crithmoides* and *S. mesembryanthemoides*. The bracts are lanceolate or narrowly triangular, entire, widely translucent, and around 1–2 mm long in *Sesuvium* and less than 1 mm in *Cypselea*. The bracts of *C. humifusa* are fimbriate and in the same position as the subtending leaf pair. The bracts are usually free of bladder cells, but in *S. crithmoides* and *S. mesembryanthemoides* the outer bracts may show a loose cover of small bladder cells.

COLOR PATTERNS—Pink, light pink and white are the prevalent flower colors in *Sesuvium*, with the latter occurring less frequently. Some herbarium labels also report red, cerise, or yellow flowers. *Sesuvium crithmoides* is generally described as having red flowers, while the flowers of *S. maritimum* and *S. edmonstonei* are almost always white.

The flowers of *Sesuvium* are devoid of patterning or markings. The pollen is often white and creates a sharp contrast to the bright pink tepals, which may increase the visual attractiveness for potential pollinators. The flowers of *Cypselea* are inconspicuously (greenish-) white, except for those of *C. rubriflora*, which are red.

ANDROECIUM AND GYNOCYCIUM—The stamens are free and inserted at the mouth of the perianth tube. The filaments are slightly laminar at the base. In some species, the stamens are brightly colored. In *Sesuvium*, between five and numerous stamens are found, with higher numbers more prevalent. In *Cypselea*, a reduction in the number of stamens to three is observed in two of the three species.

The ovary of *Sesuvium* consists of 2–5 connate carpels with the same number of free styles. The styles are long, thin, and

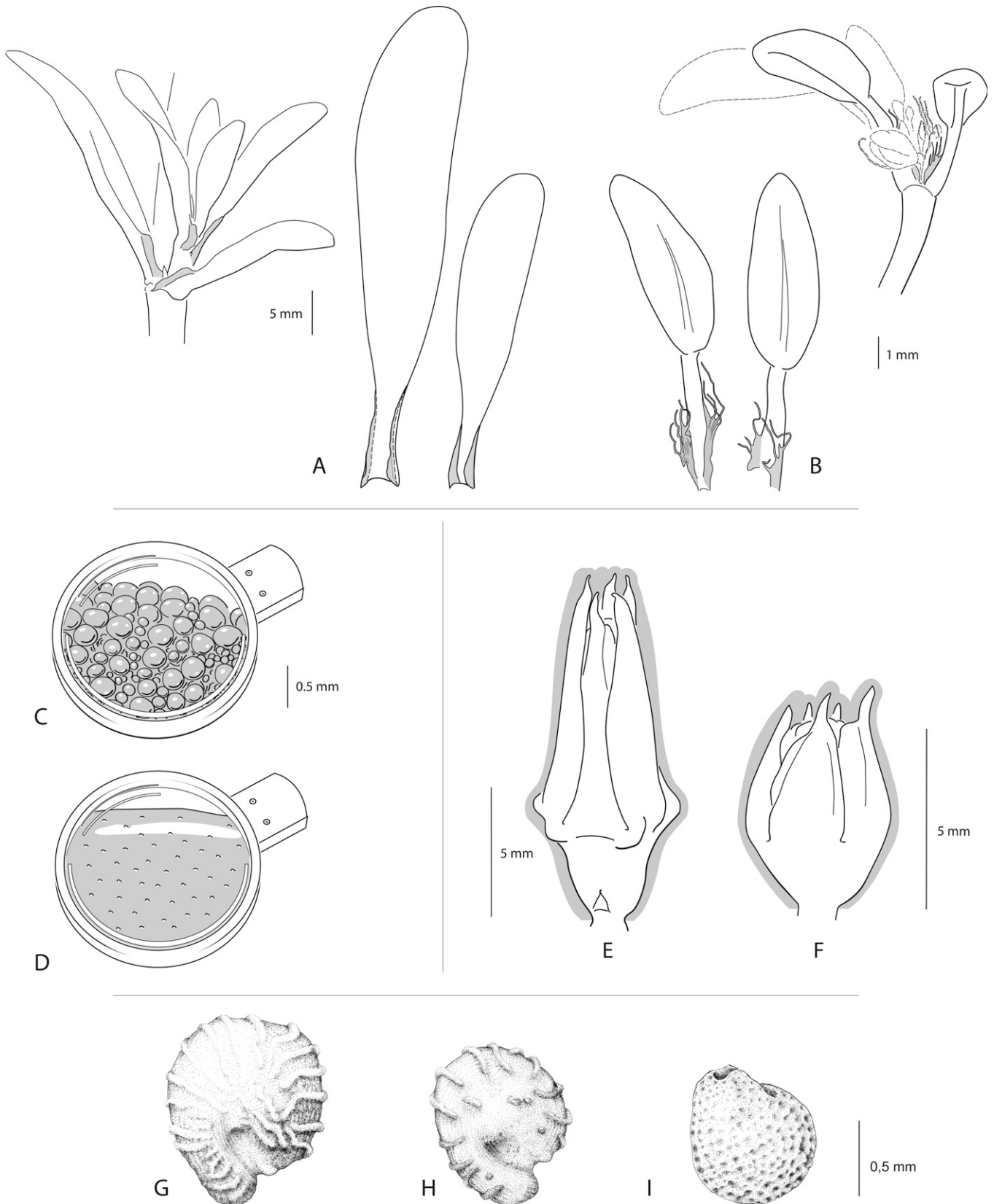


FIG. 3. Important diagnostic traits within *Sesuvium*. Details mentioned in the key are highlighted in grey. A–B. Shape of the lateral appendages (pseudostipules) with schemata of the natural habit. A. With entire margins (example: *S. portulacastrum*). B. With fimbriate margins (example: *S. humifusum*). C–D. Structure of the epidermal surface observed through a lens. C. With bulging bladder cells (example: *S. verrucosum*). D. Without bulging bladder cells (example: *S. portulacastrum*). E–F. Outlines of closed flowers (around time of anthesis). E. Turbinate (example: *S. sesuvioides*). F. Ovoid (example: *S. verrucosum*). G–I. Different structures of the testa. G. *S. hydaspicum*. H. *S. hydaspicum* (formerly *S. nyasicum*). I. *S. sesuvioides*. A–F drawn by D. Franke; G–I drawn by A. Korek; plate assembled by D. Franke.

slightly papillate during receptivity. Two to three connate carpels with the same number of free but short, laminate, papillose styles are found in *Cypselea*. Both genera have perigynous flowers, with axile placentation and many ovules per carpel.

FRUITS—Both genera show circumscissile capsules that open with one lid (Fig. 1D). The capsules are usually ovoid or beehive-shaped, but can also be tapered. Most species are many-seeded, but the individual number of seeds varies considerably (sometimes only 10–15 per capsule). Especially large numbers of seeds are found in *C. humifusa*, where one capsule can contain about 100 seeds. During fruit ripening, all floral organs persist and become enclosed by the tepals. With the maturation of the seeds, the tepals open up again and expose the capsule.

SEEDS—Mature seeds of *Sesuvium* are generally rounded-reniform, around 1 mm long, and dark in color with a \pm smooth seed coat. Seeds of *Cypselea humifusa* are tiny by comparison (~ 0.2 mm) and light brown in color. The seeds of *C. rubriflora* and *C. meziana* were not seen.

As far as observed in the greenhouse, the seedlings of *Sesuvium* and *Cypselea* have entire, oblanceolate cotyledons (observed for *S. portulacastrum*, *S. verrucosum*, *S. sesuvioides*, *S. hydaspicum*, and *C. humifusa*).

PHENOLOGY—Both genera seem to flower throughout the year, as long as an appropriate amount of light is provided. The flowers open under well lighted conditions and close in the late afternoon (observation from the greenhouse).

Ecology—Both genera have a tropical to subtropical distribution. The semi-succulent habit of *Sesuvium* suggests that this genus inhabits seasonally moist regions. Natural habitats of *Sesuvium* include coastal regions and other salt-affected areas such as salt pans. It also can be found near dry rivers or lakebeds, and in disturbed habitats (e.g. roadsides, pastures). Many perennial species of *Sesuvium* are capable of clonal propagation, while germination and establishment of seedlings seem to be poor (reported for *S. portulacastrum* by Lonard and Judd 1997).

The ecology of *Cypselea humifusa* differs from that of *Sesuvium* in that it is an alluvial annual that grows in occasionally drying streams, ponds, and fresh water swamps. Information about the ecology of the two remaining *Cypselea* species, *C. rubriflora* and *C. meziana*, is somewhat vague, but at least the latter is found on saline soil and both are described as perennials. *Cypselea humifusa* uses C_4 photosynthesis and belongs to the NADP-ME subtype (Muhaidat et al. 2007). The remaining two species are not yet investigated in this regard. In *Sesuvium*, the species of the American clade use C_3 photosynthesis, while the African clade contains C_4 species exclusively. The biochemical subtype of the African C_4 *Sesuvium* species is not known.

Nothing is known about pollinators or seed dispersers for either genus. In the greenhouse, *C. humifusa* and several *Sesuvium* species are capable of self-pollination. Honeybees and smaller wild bees were sometimes observed on flowers, but this might not reflect the natural pollinator spectrum.

DISCUSSION

As Hassan et al. (2005b) and Bohley et al. (2015) showed in their phylogenetic studies, *Sesuvium* is separated in two primary clades that are geographically distinct: an African and an American lineage. Furthermore, *Sesuvium* appears to

be paraphyletic with respect to *Cypselea*, which is part of the American clade with moderate support as sister to the remaining species of this clade (Fig. 4; Bohley et al. 2015). Although *Cypselea* itself is well supported as monophyletic, its phylogenetic position is surprising, since *C. humifusa*, the best-known species of *Cypselea*, is morphologically and ecologically distinct from *Sesuvium*. In contrast to *Sesuvium*, which is found in saline habitats, *Cypselea humifusa* grows in freshwater ponds and alluvial freshwater marshes. However, splitting *Sesuvium* as consequence of the phylogenetic findings also appears unsatisfactory, since both clades, American as well as African *Sesuvium*, share many morphological and ecological traits and are easily recognized as members of the same genus. This dilemma somewhat diminishes when the poorly known and less accessible *Cypselea rubriflora* and *C. meziana* are taken into account, which are much more similar to *Sesuvium* than *C. humifusa* is. Particularly *C. meziana* is morphologically intermediate between *Cypselea* and *Sesuvium* and expresses morphological features of both genera (Table 1). It shares the reduction of the androecium with the other two *Cypselea* species, and the perennial growth form, ability to tolerate salt, and number of carpels (= 3) with *Sesuvium*. Combining the available morphological and ecological information about *C. meziana* and *C. rubriflora* with the molecular data, we propose to include *Cypselea* in *Sesuvium*.

In comparison to their closest relatives, *Zaleya* and *Trianthema*, *Sesuvium* and *Cypselea* share many-seeded

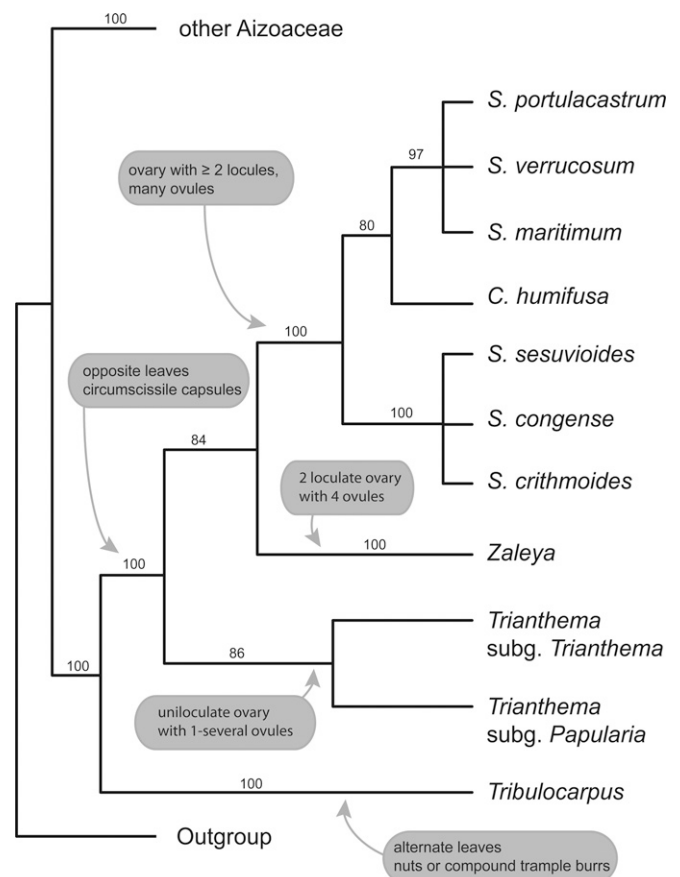


FIG. 4. Reduced phylogeny of the Sesuvioideae with focus on *Sesuvium* and *Cypselea*. The dark grey boxes highlight the diagnostic traits for each genus. Tree after Bohley et al. (2015).

TABLE 1. Selected traits of *Sesuvium* and *Cypselea*. 1) Life form: p = perennial; a = annual. 2) Halophyte: + = yes; - = no; ? = no information. 3) Number of stamens. 4) Number of carpels. 5) Pseudostipules fimbriate. 6) Nearly all organs with a dense cover of protruding bladder cell idioblasts. 7) Regularly rooting at nodes. 8) More than 1 pair of bracts. 9) Succulence of leaves: m = moderate / mostly flat; s = succulent; t = (almost) terete. 10) Size of seeds (mm).

Taxon	1	2	3	4	5	6	7	8	9	10
<i>C. humifusum</i>	a	-	3	2	+				m	0.2
<i>C. meziana</i>	p	+	3	3			+		m	?
<i>C. rubriflora</i>	p	+	5	2	+				m	0.2
<i>S. congense</i>	p	+	∞	2-3		+			t	0.9
<i>S. crithmoides</i>	p	+	∞	3-5		+		+	t	~1.0
<i>S. edmonstonei</i>	p	+	∞	2		+			t	~1.0
<i>S. hydaspicum</i>	a	?	5-7	2					(m-)s	1.0-1.3
<i>S. maritimum</i>	a	+	5	3-5					m	0.8-0.9
<i>S. mesembryanthemoides</i>	p	+	∞	3-5		+		+	t	?
<i>S. portulacastrum</i>	p	+	∞	3-5			+		s	~1.0
<i>S. sesuvioides</i>	p	+	(5-)∞	2					(m-)s	~1.0
<i>S. trianthemoides</i>	a	?	5	2					m	1.0-1.2
<i>S. verrucosum</i>	p	+	∞	3-5		+			s	0.8-1.0

capsules as their most conspicuous synapomorphy (Fig. 4). Not only is the number of seeds different, the morphology of the fruit also differs between the four genera. The capsules of *Sesuvium* and *Cypselea* are always simple (parchment-like pericarp, simple operculum). In contrast, *Zaleyia* and some species of *Trianthema* form capsules with distinctly shaped opercula that can have diagnostic importance, e.g. in *Z. galericulata* (Melville 1952, therein named *Trianthema galericulata*). While all species of *Sesuvium* and *Cypselea* share many-seeded capsules, the seed morphology of at least *C. humifusa* is very different. Besides the considerably smaller size and divergent color, the reticulate testa is also unique within Sesuvioideae (Hassan et al. 2005a). The use of leaf characters appears to be of little use in distinguishing genera in the Sesuvioideae, due to considerable variation of leaf morphology and anatomy within *Trianthema* and to a lesser degree in *Sesuvium* (Bohley et al. 2015). Currently we have four species of *Sesuvium* in cultivation: *S. verrucosum*, *S. hydaspicum*, two populations of *S. sesuvioides* and four populations of *S. portulacastrum*. We were able to observe changes in size (general size and leaf size), succulence, length of the petiole, and sometimes even in the size of flowers and the shape of leaves under different growing conditions. This illustrates the high degree of phenotypic plasticity, especially in vegetative traits, within *Sesuvium*. Hassan et al. (2005a) were able to show that Sesuvioideae show high uniformity in seed morphology with few very distinct seed types, therefore this trait is also probably not suitable as a diagnostic character for individual genera. The most useful traits for generic delimitation appear to be fruit characters (e.g. number of ovules, number of seeds per capsule; see Key to the Genera of Sesuvioideae in section Taxonomic Treatment, and Fig. 4).

Interestingly, there is a switch of photosynthetic type in *Sesuvium*. All African species and the American *Cypselea* are C_4 species while the American *Sesuvium* are C_3 species. A switch in photosynthetic type is also found within *Trianthema*, with *T. ceratosepala* being the only C_3 species of that genus. The evolution of C_4 photosynthesis and leaf anatomy in Sesuvioideae is discussed in Bohley et al. (2015).

The resolution in the molecular trees within the American *Sesuvium* species is poor and the sampling is incomplete

(Fig. 4; Hassan et al. 2005a; Bohley et al. 2015), and therefore not sufficient to resolve species relationships. However, for most species in the clade, morphological variation is sufficiently discontinuous for species delimitation. The only difficult and complicated case among American *Sesuvium* is the separation of *S. verrucosum* and *S. sessile*. The latter generally appears to be (slightly) smaller and exhibits a more linear leaf shape. At the same time, *S. verrucosum* may sometimes also have linear leaves. As far as was seen in herbarium material, no morphological character separating both species completely could be found. The most detailed account including a species key was provided in the *Manual of the Vascular Flora of Texas* by Correll and Johnston (1970). However, their diagnostic traits were leaf shape, differing distributions within Texas, and color of the dried material. Since the original authors of both species neither specified the type material they used nor mentioned details regarding the collections, the actual types of *S. sessile* and *S. verrucosum* are not known. We attempted to locate potential type material by screening collections that may contain them. In the case of *S. verrucosum*, the herbarium of Rafinesque was sold to E. Durand, who discarded parts of the collection (Chase 1935). Since no material is known that would meet the requirements for lectotypification, we designate a neotype. In the case of *S. sessile*, its author, C. H. Persoon, apparently based many of the new species descriptions in his *Synopsis Plantarum* on the collection of Jussieu in P (Stafleu and Cowan 1983). No material matching the current circumscription of *S. sessile*, for example as outlined in the *Manual of Vascular Plants of Texas* (Correll and Johnston 1970), is present in the Jussieu collection. However, the original description of *S. sessile* is very short and vague. It also cites the illustration of *S. portulacastrum* in de Candolle's *Plantes Grasses* (vol. 1, pl. 9). It seems likely to us that Persoon might have described *S. sessile* based on the above mentioned illustration in combination with one of the *S. portulacastrum* specimens in the Jussieu collection. Therefore, we designate the mentioned illustration as lectotype and additionally a specimen of *S. portulacastrum* from the Jussieu collection showing all traits in the description of *S. sessile* as epitype. Unfortunately, we are not able to explain where the current circumscription of the species *S. sessile* in recent floras (e.g. Correll and Johnston 1970) originated, but it is obvious that the original description, which generally fits *S. portulacastrum*, has been substantially changed and today closely matches the description of *S. verrucosum*. An early account of this change is already visible in the *Synoptical Flora of North America* by A. Gray et al. (1895-1897) where a detailed description of *S. sessile* is presented. We propose to put the name *S. sessile* into synonymy of *S. portulacastrum* and to correct the identification of most specimens labelled as *S. sessile* to *S. verrucosum*.

A number of geographical outliers also belong to the American *Sesuvium* clade. These are *Sesuvium edmonstonei* (Galapagos Islands), *S. ayresii* (Mauritius), and *S. microphyllum* (West Indies). While *S. edmonstonei* seems morphologically distinct by being completely covered with large bladder cells, *S. ayresii* and *S. microphyllum* appear to be dwarf forms of the cosmopolitan and highly variable *S. portulacastrum*.

In the molecular study of Bohley et al. (2015) only three of five currently accepted species of the African *Sesuvium* clade were sampled, and its resolution was also poor. Our survey

revealed three distinct morphological groups in Africa: 1) *S. congense*; 2) *S. sesuviooides* and *S. hydaspicum* (incl. *S. nyasicum*); and 3) *S. crithmoides* and *S. mesembryanthemoides*. However, the number of available specimens is comparatively low for all species apart from *S. sesuviooides*. Particularly difficult is the separation of *S. crithmoides* and *S. mesembryanthemoides*, as both species occur in the same regions and habitats. In *Sesuvium*, they stand out due to their noticeable size, large flowers and possession of two to four pairs of rather large bracts. The two major differences between the two species are their overall size (*S. crithmoides* being slightly larger) and their different leaf shape (short and wide in *S. mesembryanthemoides*, longer and narrower in *S. crithmoides*). These mainly quantitative differences might be attributed to phenotypic plasticity due to varying growing conditions among populations. Therefore, a cultivation experiment should be conducted to test whether the differences between *S. crithmoides* and *S. mesembryanthemoides* are genetically fixed or plastic. An intraspecific molecular study including several populations of each species is also needed to verify their monophyly. As mentioned above, both species seem to occur in the same habitats, but distribution data is scarce in both cases. To our knowledge, unfortunately neither *S. mesembryanthemoides* nor *S. crithmoides* are described in detail in any current flora of southern Africa. Information available is limited to presence data without details on morphology and habitat or a key (see e.g. Figueiredo and Smith 2008). In addition, the number of available specimens is very small, therefore preventing the effective recording of morphometric data and determination of distinct versus continuous traits. To gain further insight into the Angolan *Sesuvium* species, more collections are required.

Another African *Sesuvium* species group in need of further investigation comprises *S. sesuviooides*, *S. hydaspicum*, and *S. nyasicum*. Compared to many of the remaining members of the genus, they were only recently transferred to *Sesuvium* (Table S1). Verdcourt (1957) treated *S. hydaspicum* and *S. nyasicum* as part of a highly variable *S. sesuviooides*, variable in the number of stamens and the morphology of the seeds, and with an extraordinary broad but not necessarily continuous distribution. Gonçalves (1965, 1970, 1978)

limited the name *S. sesuviooides* to material with smooth seeds and established two new names for material with rough seed coats. *Sesuvium hydaspicum* is distinguished from *S. nyasicum* by the presence of more than 20 wrinkles on the seed coat, but that number seems arbitrary, given the variation of this trait. It appears to be continuous and does not seem to correlate with other traits like number of stamens or occurrence of bladder cells, and is therefore of limited use in distinguishing *S. hydaspicum* from *S. nyasicum*. Of major concern is also the distribution area of *S. hydaspicum/nyasicum*, spanning India, Pakistan, and western, northeastern, southern and southeastern Africa. Some data points are based on type material of incorporated names and can hardly be ignored (e.g. a single collection in Sudan). Except from southern Africa, the sampling for the other areas is not satisfactory and shows unexplained gaps. Material from Asian populations is especially scarce and difficult to obtain. Highly uneven collecting activity is an issue for all three species. *Sesuvium sesuviooides* is also phenotypically variable and possesses two distinct distribution areas, in southern Africa and the Cape Verde islands. Given its morphological variation and disjunct distribution, it might be necessary to further subdivide *S. sesuviooides*. In short, a broader sampling for a molecular analysis in combination with a morphological investigation is needed to resolve the taxonomy of the *S. sesuviooides* group. It would be desirable to achieve a sampling spanning the complete distribution area and representative of all published taxa to gain insight into the geographical occurrence of the different phenotypes. Special focus should be directed to Asia, northern and eastern Africa, and Cape Verde. For the time being, we propose to include *S. nyasicum* in *S. hydaspicum* and to keep *S. sesuviooides* as a separate species, until a more detailed investigation can be conducted.

TAXONOMIC TREATMENT

If not otherwise mentioned, the description of morphological characters is based on herbarium material. Names follow IPNI (2016), and in cases where the spelling of genus or species names deviates from the description, the original is provided in square brackets.

KEY TO THE GENERA OF SESUVIOIDEAE

- | | |
|---|----------------------|
| 1. Leaves alternate; fruit a winged nut or a compound, spiny trample burr | <i>Tribulocarpus</i> |
| 1. Leaves opposite; fruit a circumscissile capsule | 2 |
| 2. Ovary with 1 locule, 1 style | <i>Trianthema</i> |
| 2. Ovary with 2-5 locules, 2-5 styles | 3 |
| 3. Operculum splits into 2 halves upon opening; 4 ovules | <i>Zaleya</i> |
| 3. Operculum remains intact upon opening; more than 4 ovules | <i>Sesuvium</i> |

SESUVIUM L., Syst. Nat. ed. 10.2: 1058. 1759.—TYPE: *S. portulacastrum* (L.) L.

Cypselea Turp., Ann. Mus. Natl. Hist. Nat. 7: 219, plate 121. 1806. *Radiana* Raf., Specchio Sci.: 88. 1814.—TYPE: *Cypselea humifusa* Turp.

Diplochonium Fenzl in Nov. Stirp. Dec.: 57. 1839.—TYPE: *Diplochonium sesuviooides* Fenzl.

Pyxipoma Fenzl in Ann. Wiener Mus. Naturgesch. 2: 293. 1839.—TYPE: cited only *Trianthema polyandra* Blume.

Psammanthe Hance ex Walp. Ann. Bot. Syst. 2: 659. 1852.—TYPE: *Psammanthe marina* Hance ex Walp.

Note—Hiern (1898) treated *Sesuvium* as *Halimus* Loefl., non P. Browne (1756). Hartmann (2001b) provides a detailed discussion of the application of that name.

Procumbent to erect, annual or perennial herbs. Surface of stems, leaves and outside of perianth either densely covered with bulging bladder cells or seemingly smooth. Leaves opposite, leaves of one pair slightly to distinctly unequal in size, lanceolate to obovate or oblong, sometimes linear, petiolate to

(sub-) sessile, moderately to distinctly succulent, and with translucent lateral flaps forming a semi-sheath around the shoot, margin of the lateral flaps is usually entire, sometimes fimbriate. Bracts oblanceolate to triangular, usually 1 pair and small (≤ 1 mm) or sometimes 2–4 pairs and larger (~ 5 mm). Flowers solitary, bisexual, pedicellate or sessile, perigynous; perianth simple, 5-parted, lower half fused into a tube, free part of tepals sepaloid and sometimes unequally shaped, hood- or thorn-shaped dorsal appendage shortly below the apex of each tepal which is variable in size and shape among species, tepals most often white or pink ventrally, sometimes red, and

green dorsally. Stamens free, inserted at mouth of perianth tube, 3–many, often brightly colored, filaments slightly laminate at base, glabrous. Ovary with 2–5 connate carpels with the same number of free styles. Each carpel with many ovules and axile placentation. All floral organs persist after anthesis. Fruit a circumscissile, many-seeded capsule, opening with one lid. Seeds 0.2–1.5 mm long, reniform and arillate, testa smooth or structured and (light) brown, grey or black.

Note—In a very few cases the occurrence of cerise or yellow flowers is reported on herbarium labels (mainly for *S. portulacastrum*).

KEY TO THE SPECIES OF *SESUVIUM* (INCL. *CYPSELEA*)

1. Margin of the lateral flaps of the petiole fimbriate (Fig. 3B) 2
 2. Flowers white, 3 stamens *Sesuvium humifusum*
 2. Flowers red, 5 stamens *Sesuvium rubriflorum*
1. Margin of the lateral flaps of the petiole entire (Fig. 3A) 3
 3. Shoots smooth: usually without bulging bladder cells (Fig. 3C) 4
 4. Stems rooting at nodes 5
 5. Flowers pink or white; many stamens; worldwide distribution *Sesuvium portulacastrum*
 5. Flowers (greenish-) white; 3 stamens; Paraguay *Sesuvium mezianum*
 4. Stems not rooting at nodes 6
 6. Closed flowers \pm ovoid (Fig. 3F); northern America or Caribbean 7
 7. Seeds smooth, up to ~ 1 mm long; capsule \pm ovoid, not longer than the perigone *Sesuvium maritimum*
 7. Seeds wrinkled, up to 1.5 mm long; capsule tapered, slightly longer than the perigone *Sesuvium trianthemoides*
 6. Closed flowers turbinate (Fig. 3E); Africa 8
 8. Seed coat \pm smooth (Fig. 3I); leaves broadly elliptic; dried shoots often slightly olive-colored *Sesuvium sesuioides*
 8. Seed coat clearly structured (Figs. 3G and H); leaves elliptic to narrowly elliptic; dried shoots can be reddish *Sesuvium hydaspicum*
 3. Shoots densely covered with bulging bladder cells (Fig. 3C) 9
 9. Several pairs of bracts (each bract ~ 5 mm long) 10
 10. Leaves long and narrow, 20–70 mm long *Sesuvium crithmoides*
 10. Leaves broad-elliptic, 10–20(–30) mm long *Sesuvium mesembryanthemoides*
 9. One pair of bracts (each bract ~ 1 mm long) 11
 11. Pseudostipules of petiole with bladder cells *Sesuvium edmonstonei*
 11. Pseudostipules of petiole without bladder cells 12
 12. Closed flower turbinate (Fig. 3E), leaves narrowly to broadly elliptic 13
 13. Ovary with 2 or 3 carpels; leaves narrowly elliptic, semi-terete in cross section, usually densely covered with globose to slightly ovoid or fusiform bladder cells *Sesuvium congense*
 13. Ovary invariably with 2 carpels; leaves broadly elliptic, often folded along midvein, \pm flat, loosely to densely covered with globose bladder cells *Sesuvium sesuioides*
 12. Closed flower ovoid (Fig. 3F), leaves obovate to oblanceolate, sometimes linear *Sesuvium verrucosum*

SESUVIUM CONGENSE Welw. ex Oliv., Fl. Trop. Afr. [Oliver et al.] 2, 586. 1871.—TYPE: ANGOLA. Luanda: in mountainous places along the estuary of the river Onço in Mossul, near Ambriz, Nov 1853, *Welwitsch 2382* (holotype: LISU 214650 digital image!; isotypes: BM, BR, COI, K!)

Erect to decumbent, perennial herb, often much-branched and with many flowers; taproot strong; bladder cells bulging, globose to slightly conical (the latter only on shoots), loose to dense cover of the surface of internodes, leaves and outside of flowers; internodes can be reddish and are usually rough from bladder cells when young, later becoming smooth and also lignifying slightly. Leaves short (~ 10 mm long) and narrow-elliptic; very succulent with semi-terete cross section; usually appearing revolute when dry. Bracts ca. 1 mm long and lanceolate; one pair. Flowers 4–6 mm long, sessile, tepals (narrow-) triangular; tepal teeth short and inconspicuous. Stamens numerous; thecae pinkish. Ovary with 2–3 carpels and the same number of styles. Fruit a many-seeded capsule. Seeds 0.9 mm long, elongate-reniform, laterally rounded, with a black, (almost) smooth, lustrous, and slightly iridescent testa.

Distribution and Habitat—The species is present in Angola (Fig. 5A) and found in coastal areas. It grows on sand or gravelly soil.

Notes—It differs from the other Angolan *Sesuvium* species by its shrubby habit and two to three locules. *C₄* species (Bohley et al. 2015). *Halimus congense* (Welw. ex Oliv.) O. Kuntze is an illegitimate combination.

Representative Specimens Examined—ANGOLA. Namibe: 9.7 km S of airport turn-off, 15°18'45.972"S, 12°10'1.999"E, 91 m, 23 Jan 2009, *Winter 7766* (PRE); Namibe: N of Namibe, road to Baba from Lucira road, 14°53'18.995"S, 12°17'38"E, 213 m, 23 Jan 2009, *Winter 7779* (PRE).

SESUVIUM CRITHMOIDES Welw., Apont. 586. 1858. *Halimum portulacastrum* var. *crithmoides* (Welw.) Hiern, Cat. Afric. Pl. (Hiern) 1(2): 412. 1898.—TYPE: ANGOLA. Loanda [Luanda], *Welwitsch 2386* (holotype: LISU 214648 digital image!; isotypes: B!, BM, BR, COI, K!).

Perennial, procumbent herb; internodes sometimes described to be red; bulging bladder cells on shoots, leaves and the outside of the flower (not on tepal teeth), dry material therefore whitish. Leaves linear, up to 70 mm long and narrow with an oval to terete cross section, leaf tip obtuse and petiole up to 8 mm long, but indistinct. Bracts in 2–4 pairs, 4–5 mm

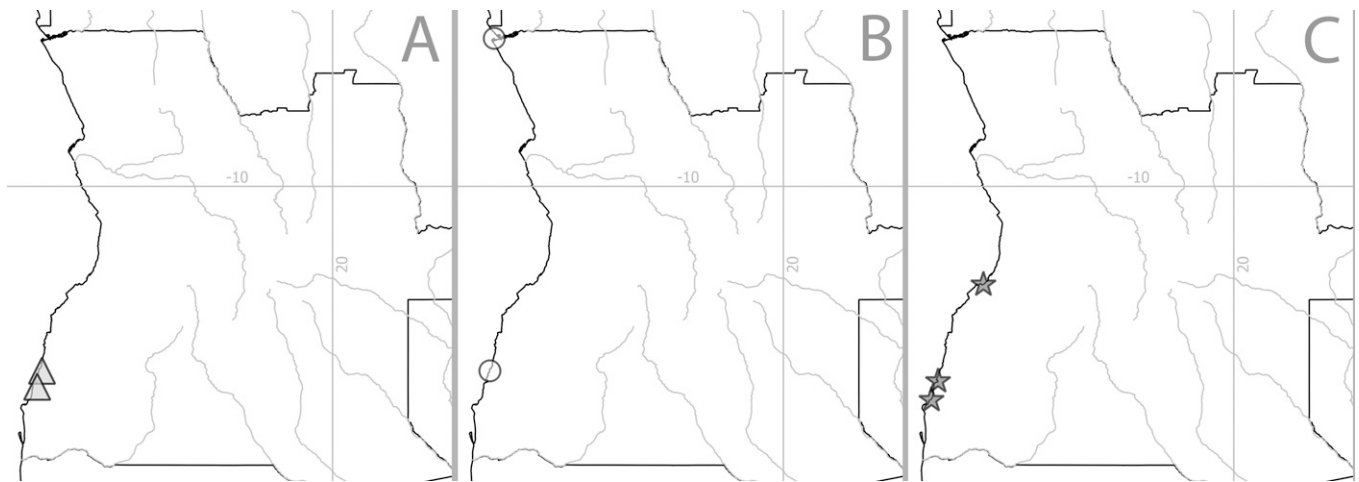


FIG. 5. Distribution of *Sesuvium congense*, *S. crithmoides*, and *S. mesembryanthemoides* in Angola. A. Light grey triangles show the occurrence of *S. congense*. B. White circles depict the occurrence of *S. crithmoides*. C. Dark grey stars show the occurrence of *S. mesembryanthemoides*.

long, triangular, dark color when dry. Flowers large, 12–15 mm long, red, subsessile. Stamens numerous, less than the length of the perianth. Ovary with 3–5 carpels and the same number of styles. Fruit a many seeded capsule. Seeds ca. 1 mm long, rounded reniform and slightly flattened, smooth and black.

Distribution and Habitat—The species is found in Angola and may also be present in the Democratic Republic of the Congo (Fig. 5B). It is also introduced in Georgia, U. S. A. It grows in coastal areas and disturbed habitats on sandy soil.

Vernacular Names—Tropical seapurslane.

Notes— C_4 species (Bohley et al. 2015). We do not know if *Sesuvium crithmoides* established a stable population in Georgia and still can be found there. Despite its distinct morphology with linear, terete leaves and large, red flowers, the species is not often found in collections. *Sesuvium crithmoides* and *S. mesembryanthemoides* appear to share the same habitat as well as sharing several traits that separate them from the other African *Sesuvium* species.

Representative Specimens Examined—ANGOLA. Loanda [Luanda], Welwitsch 2386 (K); Baba, coast W of Namibe-Lucira Road, 14°53'38.0004"S, 12°12'56.9988"E, 23 Jan 2009, P. J. D. Winter 7786 (PRE); Shark Point (near Padrao of Diego Cao), 6°04'30.37"S, 12°19'54.35"E, 07 Sep 1874, Naumann 2071 (B).

U. S. A. Georgia: Glynn County, Brunswick, 15 Aug 1902, Harper 1524 (MO).

SESUVIUM EDMONSTONEI Hook f., Trans. Linn. Soc. London 20, 221. 1847.—TYPE: ECUADOR. Galapagos. Goodridge s. n. (holotype: K!, P).

Procumbent, much branched perennial herb or shrublet, 20–30 cm high, growing in dense mats or patches with a diam of up to 1 m; densely covered with sometimes scale-like bladder cells (except bracts and inner parts of the flowers). Leaves linear, around 20 mm long and 3 mm wide (dried material); distinctly succulent with oval to round cross sections; transition between lamina and petiole inarticulate; petiole ~2 mm long; leaves and internodes often reported to be yellowish to bright red. Flowers small (3–5 mm long), white (rarely pink); long, thin pedicel (3–4 times the length of the flower); one pair of small bracts (≤ 1 mm) at the base of the pedicel. Stamens numerous and nearly as long as the free part of the tepals. Ovary with 2 connate carpels and 2 thin styles. Seeds rounded reniform, ~1 mm long, shiny black and with conspicuous longitudinal furrows.

Distribution and Habitat—Endemic on the Galapagos Islands where it grows on several islands (Fig. 6). The species is also reported from mainland Ecuador, Venezuela, and Colombia, where it was likely introduced. It grows on sandy soil (beaches, dunes), sometimes directly in the spray zone or on diurnally flooded parts of the coast. Locally abundant.

Vernacular Names—Galapagos carpet weed.

Notes—The species is easily recognized because of its dense cover of bulging bladder cells in combination with small, white flowers (< 10 mm) and linear leaves. This species is the only member of *Sesuvium* listed in the IUCN (2015) Red List of Threatened Species and categorized as “of least concern” (ver. 3.1, Aug 2015).

Representative Specimens Examined—ECUADOR. Galapagos Islands: Isla Floreana, Black Beach, 22 Dec 1966, U. & I. Eliasson 970 (S); Isla Floreana, Black Beach, ca. 1°13'33.84"S, 90°25'52.23"W, 08 Dec 1966, U. & I. Eliasson 798 (S); Isla Floreana, southern part of Black Beach, 07 May 1967, U. & I. Eliasson 2106 (S); Santa Fe, small island at NE end, 0°48'13.6"N, 90°2'13.776"W, 15 Feb 1972, M. & O. Hamann 419 (C); Pinta, scarcely W of Cabo Ibbetson, 0°32'37.734"N, 90°43'51.672"W, 26 Mar 1972, M. & O. Hamann 925 (C); Genovesa, Darwin Bay, near lagoon, 0°19'6.29"N, 89°56'54.934"W, 28 Mar 1972, M. & O. Hamann 994 (C); Santa

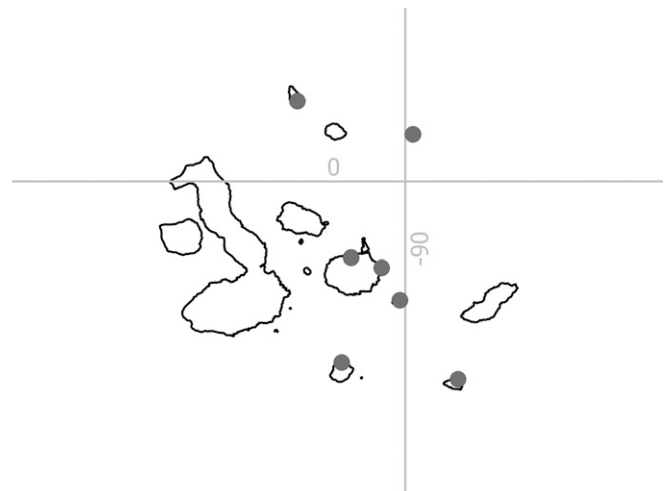


FIG. 6. Occurrence of *Sesuvium edmonstonei* in the Galapagos Islands. The species is reported to be found on most islands and to be usually abundant.

Cruz, southern end of Bahía Buttero (?), 0°30'59.479"N, 90°22'2.478"W, 20 Apr 1972, P. Prichard 1189 (C); Genovesa, Darwin Bay, 0°19'6.29"N, 89°56'54.923"W, 22 May 1974, A. & H. Adersen 306 (C); Gardener (near Espanola), N shore, 1°20'23.056"S, 89°38'36.744"W, 21 Mar 1977, A. & H. Adersen 1423 (C); San Cristóbal (Chatham) Island, C. Word s. n. (K); Isla Floreana (Charles), 30 Jul 1924, D. Blair 417 (K); Santa Cruz, South Plaza Island, all over the top of the island, ca. 0°35'03.51"S, 90°09'38.22"W, 21 Mar 1963, Snow 45 (K).

VENEZUELA. Falcon, 4 km S of Zazárida, 11°6'35.47"N, 69°39'8.243"W, 17 Jun 1980, G. Davidse & A. C. González 18196 (MO).

Sesuvium humifusum (Turpin) Bohley & G. Kadereit, comb. nov. *Cypselea humifusa* Turpin, Ann. Mus. Natl. Hist. Nat. 7: 219, plate 121. 1806. *Radiana petiolata* Raf., Specch. 1: 88. 1814.—TYPE: DOMINICAN REPUBLIC. P. A. Poiteau s. n. (lectotype: P, P01900032 digital image!, designated here.)

Millegrana surian Juss., Nomencl. Bot. [Steudel], ed. 2. 2: 146. 1841, syn. nov.—TYPE: no type indicated. Note: Steudel cites *C. humifusa* as synonym of *M. surian*.

Very slender and small annual plant with a procumbent habit; tips of shoots ascend only slightly; internodes are pale pink with a smooth surface covered with small flat hyaline bladder cells (visible with magnification). Leaves in opposite pairs, up to 10 mm long, with the two members of the pair unequal in size; lamina elliptic to ovate with an obtuse base, dark green, midvein sometimes a lighter shade, veins clearly visible in fresh material; petiolate; lateral flaps colorless with fimbriate margins, sheathing the node. Flowers 3–4 mm long, white, with a 5-parted perianth, slightly bell-shaped; tepals unequal (two with broad and three with narrow membranous margins), upper half free; pedicels approximately the length of the flower, upright during anthesis but slowly become pendant towards maturity of the fruit. Stamens three. Ovary glabrous, with 2(–3) carpels and the same number of short papillose laminate styles (Fig. 7b). Fruit a circumscissile capsule, beehive-shaped, opens below the middle. Seeds numerous (up to around 100 per capsule), around 0.2 mm in length and rounded reniform, shiny, light-brown color. Figure 7.

Distribution and Habitat—The species is reported to be native in the Caribbean. It is introduced to continental North America with occurrence in several states of the U. S. A (AZ, CA, FL, LA, MS, NV) (USDA, NRCS. 2015). The species is found in alluvial freshwater areas (e.g. seasonally dry rivers and marshes) and vernal pools, but never on saline soil.

Vernacular Name—Panal.

Notes—Long petioles and tiny, greenish white flowers characterize this species. Annual C₄ species, glycophyte. No information on possible pollinators. Capable of self-pollination in the greenhouse. The description of morphological characters is mostly based on living material cultivated in the greenhouse. Due to its small size and the unequal tepals the perianth may appear 3-parted at first sight.

Representative Specimens Examined—BAHAMAS. Inagua, Great Inagua, Smith's Thatch Pond, N of Lantern Head, 24 Jun 1978, D. S. Correll 49958 (NY 01510664 digital image).

BRITISH OVERSEAS TERRITORIES. Virgin Islands (U. K.): Anagada, vicinity of settlement, 20 Feb 1913, N. L. Britton with W. C. Fishlock 1052 (NY 1510669 digital image).

CUBA. near Havana, 29 Mar 1905, A. H. Curtiss 698 (K, NY 1510679 digital image, P 05004447 digital image); C. Wright 596 (NY 01510668, NY 1510674, NY 1510675, NY 1510685, all digital images); Rugel (?) 236b (NY 1510680 digital image); La Habana: Playa de Marianao, 22 Feb 1910, N. L. Britton 4554 (NY 1510676 digital image); Playa de Marianao, 22 Feb 1910, N. L. Britton 4540 (NY 1510681 digital image); Playa de Marianao,

28 Apr 1914, E. L. Ekman 4251 (NY 1510678 digital image); near Playa de Marianao, (Havana), 03 Mar 1922, Fr. León 10654 (NY 1510684 digital image); Las Villas: Rio San Juan, 25 Mar 1910, N. L. Britton 5914 (NY 1510682 digital image); Guajimica Cove, 23 Mar 1910, N. L. Britton et al. 5830 (NY 1510683 digital image); Santa Clara Province [Villa Clara]: Gavilan, wet edges of Lagoona Grande, Aug 1941, R. A. Howard 6291 (NY 1510670 and NY 1510671, both digital images); Santa Clara, Peninsula de Zapata, in holes on flat limestone towards Bahía de Cochinos, 31 Jan 1924, E. L. Ekman 18354 (NY 1510677 digital image).

DOMINICAN REPUBLIC. La Romana, Bayahibe, 05 Feb 1976, A. H. Hogier 24806 (NY 1510667 digital image); Monte Río, Azúa, 03 Oct 1964, B. A. Lavastre 1746 (NY 1510666 digital image); A. N. Desvaux s. n. (P, P01900033 digital image!); St Domingue, J. B. R. P. Desportes s. n. (P, P00678155 digital image).

HAITI. Bayeux, near Port Margot, 03 Aug 1903, G. V. Nash 40 (NY 1510672 digital image).

INSULAR OF FRANCE. Guadeloupe, Duchanaing (?) s. n. (P, P05197367 and P05004453, digital images); 19 May 1894, Schnée s. n. (P, P05004450 digital image); near Moule (?), 1852, Duchanaing (?) s. n. (P, P05004454 digital image); 26 Sep 1933, R. P. Quentin 760 (P, P05004457 digital image).

INSULAR AREAS OF THE UNITED STATES. Virgin Islands (U. S.): St. John, along Center Line Road by Hurricane Hole, 30 Jun 1989, P. Acevedo-Rodríguez 2832 (NY 825740 digital image). Water Island near St. Thomas, Nov 1880, Eggers 146 (P, P05004451, P05004452 and P05004455, digital images).

TURKS AND CAICOS ISLANDS. Grand Turk, about North Wells, 28 Nov 1977, D. S. Correll 49195 (NY 1510665 digital image).

SESUVIUM HYDASPICUM (Edgew.) Gonç., Garcia de Orta 13: 381. 1965. *Trianthema hydaspicum* [hydaspica] Edgew., J. Linn. Soc., Bot. 6: 203. 1862.—TYPE: INDIA/PAKISTAN. Punjab, 1852, Edgeworth 3019 (lectotype: K!, designated by C. Jeffrey [1961] in *Flora of tropical East Africa*).

Trianthema polysperma Hochst. ex Oliv., Fl. Trop. Afr. [Oliver et al.] 2: 588. 1871.—TYPE: SUDAN. Kordofan, 25 Sep 1839, Kotschy 68 (holotype: K!, isotype: GOET, HAL, L digital image!, TUB).

Sesuvium digynum Oliv. var. *angustifolium* Schinz, Bull. Herb. Boissier 5, app. 3: 74. 1897, syn. nov. *Halimum sesuvioides* (Fenzl) Hiern var. *angustifolium* (Schinz) Hiern in Cat. Afric. Pl. Welw. 1(2): 414. 1898. *Sesuvium sesuvioides* (Fenzl) Verdc. var. *angustifolium* (Schinz) Gonç., Garcia de Orta 13: 381. 1965.—TYPE: Angola, Benguela, Wawra 291 (holotype: W – destroyed).

Note—*Welwitsch* 2393 and *Welwitsch* 2395 have been cited by Hiern in his description of *S. sesuvioides* var. *angustifolium* and might be suitable material for typification.

Sesuvium hoepfnerianum Schinz in Bull. Herb. Boissier 5, app. 3: 75. 1897.—TYPE: NAMIBIA. Hereroland, Höpfner 25 (holotype: Z).

Trianthema salarium Bremekamp, Ann. Transvaal Mus.: 239. 1933, syn. nov.—TYPE: SOUTH AFRICA. Zoutpan (Zoutpansberg), 21. Jan 1931, Bremekamp & Schweickerdt 232 (holotype: PRE!).

Sesuvium nyasicum (Baker) Gonç., Garcia de Orta 13: 381–382. 1965, syn. nov. *Trianthema nyasicum* [nyasica] Baker, Bull. Misc. Inform. Kew 1897 (128–129): 268. 1897.—TYPE: MALAWI. Lake Nyasa, Monkey Bay, Aug 1896, Whyte s. n. (holotype: K!).

Procumbent annual herb, often much-branched; internodes pale or sometimes red and slender with a sparse cover of flat, hyaline bladder cells, sometimes particularly around the nodes. Leaves 10–20 mm long, elliptic to lanceolate, sometimes with retuse tips and sometimes slightly folded along midvein; petiolate. Bracts ~1 mm long, lanceolate and

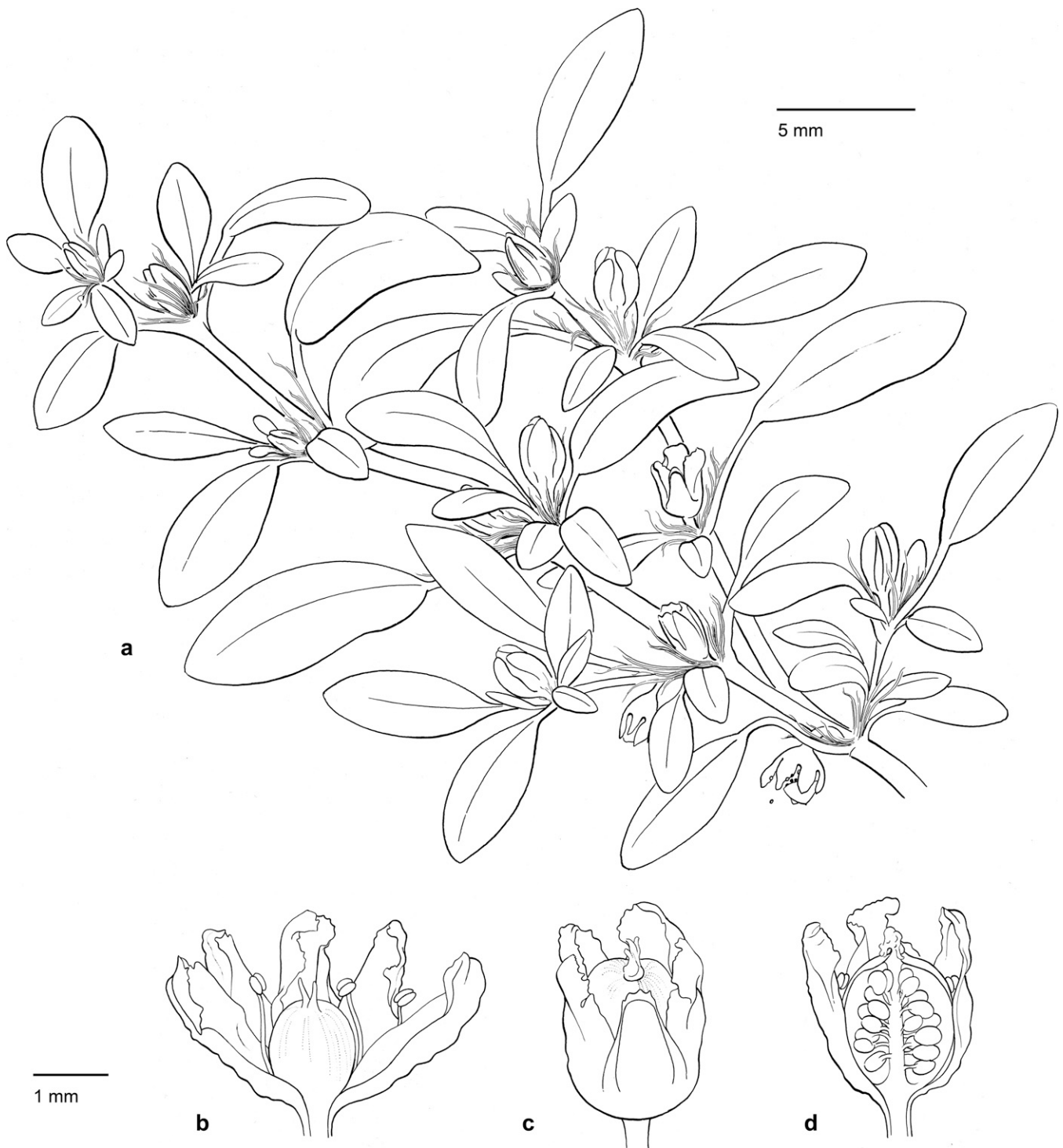


FIG. 7. *Sesuvium humifusum*. A. Flowering and fruiting branch. B. Details of the flower during anthesis. For better visibility the perianth tube was incised. C. Flower right after anthesis. D. Longitudinal section through a developing fruit. Drawn by M. Geyer.

translucent; one pair. Flowers (sub-) sessile, 5–10 mm long, pink or dark red. Stamens 5–7 or sometimes numerous. Ovary with 2 carpels and 2 styles. Fruit a capsule with up to ca. 15 seeds. Seeds ca. 1–1.3 mm long, reniform, and (dull) black; testa with 13–24 distinct transverse wrinkles (Figs. 3G and H).

Distribution and Habitat—This species is found in Burkina Faso, India, Mauretania, Namibia, Pakistan, Senegal, Sudan and South Africa (Limpopo) (Fig. 8). It grows on sandy

or gravelly soil and apparently prefers disturbed areas with more humid conditions (savannah, cultivated soil).

Notes—Gonçalves (1965) based her new combination on *Trianthema hydaspica* and *T. polysperma* without allocating any of the other synonyms previously associated with *S. sesuvioides* to one of her correct names. She supposedly intended to separate plants with structured testa from plants with smooth seeds (see *S. sesuvioides*). The number of stamens is described to be 5–7, but specimens with rugose



FIG. 8. Occurrence of *Sesuvium hydaspicum* (white triangles). This species has a wide and apparently disrupted distribution area spanning Africa, India and Pakistan. The type location of *Sesuvium nyasicum* is denoted by a black star and the type locality of *Trianthema salaria* by a grey star. The rough type localities of *T. hydaspicum* and *T. polysperma* are shown by a white star and a black diamond, respectively.

testa and 15–numerous stamens are also found (e.g. *P. M. Burgoyne* & *N. Snow* 5074 (MO)). *Sesuvium hydaspicum* is a C_4 plant (Bohley et al. 2015).

Given the type locality of Punjab (area in present-day India and Pakistan), this species has an unusual distribution with the majority of observations reported for southern Africa, as well as disjunct occurrences in northern Africa and Asia (India and Pakistan). The character states of the populations along the distribution have to be investigated critically to ensure an accurate concept of *S. hydaspicum*. Since Asia and northern Africa are both clearly underrepresented in this study, increased sampling will likely increase the range of this species and will also improve the accuracy of the species circumscription.

Representative Specimens Examined—ANGOLA. Namibe: N of Tambor (near 2 m *Welwitschia*), 15°54'2.987"S, 12°21'56.998"E, 19 Jan 2009, *P. J. D. Winter* 7705 (PRE); Cunene: 11.6 km NE of Ondjiva airstrip, ca. 3 km N of Mui River; 16°57'48.995"S, 15°36'14"E, 13 Jan 2006, *P. J. D. Winter* 7603 (PRE); Iona, Biquemo, 16°53'S, 12°53'E, 13 May 1975, *B. J. Huntley* 3627 (PRE).

BOTSWANA. Joromoja, Botletle River, 22 Apr 1975, *T. F. Ngoni* 422 (MO, PRE); near Toteng-Mogapelwa-Road, 20°13'57.792"S, 22°33'53.596"E, 12 Dec 1982, *P. A. Smith* 3964 (MO); Central Kalahari, near Rakops alongside Mopipi Dam, 21°08'S, 24°53'E, 02 Feb 1991, *I. J. Barnard* 592 (PRE). Central District: Edge of Sawa Pan; 20°33'8.94"S, 26°4'28.2"E, 895 m, 13 May 2004, *Farrington et al.* MSB108 (K); Rakops, Makuba-Dukwe

Vet. Fence, 21°30'S, 24°22'E, 02 Mar 1991, *I. J. Barnard* 643 (PRE). Northern District: Makgadi Pans, between Nata and Odiakwe on Francistown Maun Rd. at edge of salt pan, 20°08'S, 25°38'E, 09 Mar 1965, *E. H. Wild* & *R. B. Drummond* 6821 (PRE); near Maun-Francistown Rd. 34.4 km E of Gweta, Makgadikgadi lowland, 20°4'27.516"S, 25°20'43.652"E, 06 Feb 1980, *P. A. Smith* 3016 (MO, PRE); 18 km S of Nokaneng on rd. to Tsau, 18°08'S, 23°23'E, 11 Mar 1965, *H. Wild* & *R. B. Drummond* 6865 (PRE); near the Movombe-Tsimanemeha track, 18°08'S, 23°08'E, 27 Jan 1978, *P. A. Smith* 2268 (PRE). North West District: Ngamiland, Okavango Swamp, Gwetshaa Island in beach zone, 19°08'S, 23°08'E, 24 Feb 1973, *P. A. Smith* 436 (PRE).

BURKINA FASO. Oudalan: 14°25'59.912"N, 0°14'0.419"W, 21 Aug 1996, *J. E. Madsen* 5264 (MO, WAG); Mare de Menegou, 14°20'59.999"N, 0°16'59.998"E, 21 Sep 1996, *J. E. Madsen* 5771 (MO, S).

KENYA. Eastern: Lake Turkana, S end where road from South Horr to Leyengalani first gets near lake, 2°34'59.988"N, 36°42'59.759"E, 20 Aug 1981, *M. G. Gilbert* 6346 (UPS).

MAURETANIA. Nouakchott: Nouakchott, 18°5'11.274"N, 15°58'33.96"W, 19 Oct 1963, *J. G. Adam* 19379 (MO).

NAMIBIA. 1928, *R. D. Bradfield* 185 (PRE); Holoogberg Kee 107 F, 27°38'S, 17°53'E, 30 May 1972, *J. W. H. Giess* & *M. A. N. Müller* 12304 (PRE). Erongo Region: Karibib, Ameib Kar 60 Farm, 21°53'S, 15°53'E, 22 Mar 1965, *H. R. Tolken* & *D. S. Hardy* 780 (PRE); Karibib, Otjisondu Kar 36 Farm, near Dammen, 22°38'S, 16°08'E, 06 Jun 1961, *J. W. H. Giess* 3433 (PRE); Karibib Distr., Ombjumenge Farm, 22°08'S, 16°08'E, 01 May 1953, *H. G. Kinges* 3094 (PRE); Swakopmund, Kuiseb-Durchbruch, Walvisbaaipad, 29 Dec 1958, *H. Merxmüller* 986 (PRE); Erongo Mountains, Omandumba Ost Farm, 21°38'S, 15°38'E, 24 Feb 1990, *D. S. Hardy* 7048 (PRE). Hardap Region: Rehoboth District, ca. 4 km from Rehoboth

on Rd. to Mariental, across from picnic spot, 23°40'S, 17°13'E, 01 Mar 1996, P.M. Burgoyne & N. Snow 5074 (MO, PRE); Gibeon Distr., Mariental, 3.2 km W of Mariental, 24°38'S, 18°08'E, 10 May 1955, J. P. H. Acocks 18115 (PRE); Rehoboth, 5 km along turnoff to Tsumis Park, 10 Mar 1983, K. Immelman 565 (MO, PRE); Gibeon Distr., Mariental, 8 km N of Mariental, sandy valley through volcanic hills, 10 May 1955, J. P. H. Acocks 18116 (PRE); Mariental Distr., Feb 1956, P. A. Basson 189 (PRE); Rehoboth, sandflats, 23°23'S, 17°08'E, 09 Apr 1949, R. G. Strey 2529 (B, BOL, PRE); Mariental Distr., Voigtsgrund Farm, 70 km from Mariental on road to Maltahohe Lower River at road bridges, 24°53'S, 17°23'E, 12 Mar 1983, G. Germishuizen 2784 (PRE). || Karas Region: Asab, 4.8 km S of Asab, 26°53'S, 19°38'E, 09 Mar 1965, H. R. Tolken & D. S. Hardy 634 (PRE); Ariamsvlei, 16 km from Ariamsvlei on road to Charlies Puts, 28°08'S, 19°53'E, 17 May 1955, B. de Winter 3577b (PRE). Kunene Region: Kaakoveld, Anabib, on slopes of mountains 3.2 km W of Anabib, 18°08'S, 12°38'E, 11 Aug 1956, R. Story 5717 (PRE); Damaraland, Brandberg, White Lady, 21°08'S, 14°23'E, 05 Nov 1972, K. Bremer 465 (BOL, PRE); Damaraland, Black Range Farm 72, Spitskop River drainage, 21°53'S, 15°08'E, 02 Apr 1990, C. J. Ward 10789 (PRE); 25 km NW of Purros, next to road in stony flats, 18°53'S, 12°53'E, 12 Apr 1985, Moss & Jacobsen K166 (PRE); Oshikango-Kunene District, Jun 1948, M. E. Loeb 492 (PRE). Ohangwena Region: Kunene River, 5 km W of Ruacana waterfall, ca. 17°25'13.08"S, 14°9'19.249"E, 12 May 1995, M. van Slageren & J. Brand MSJB020 (PRE, WAG); Okavango Native Territory, Okavango River, 12.8 km W of Runtu, 17°53'S, 19°38'E, 07 Feb 1956, B. de Winter & W. Marais 4495 (PRE); Ovamboland, 65.9 km N of Namutoni on road to Odangua Pan, 04 Feb 1959, B. de Winter & J. W. H. Giess 6812 (PRE). Oshana Region: Etosha Pan National Park, Okaukuejo, near edge of pan 8 km E of Okaukuejo, 19°15'S, 16°15'E, 16 Apr 1973, le Roux 506 (PRE). Otjozondjupa: 1 km E along cutline 3, between Khabe and Gautsha Pan, 19°38'S, 20°08'E, 25 Feb 1985, C. J. H. Hines 318 (PRE); Okahandja, Gross Barmen Farm, 21°53'S, 16°53'E, 03 Jan 1958, H. Merxmüller 1021 (PRE).

SENEGAL. Saint Louis, Richard-Toll, Dagana, 16°27'39.996"N, 15°41'15.719"W, 03 Nov 1963, J. G. Adam 19613 (MO).

SOUTH AFRICA: Limpopo: Zoutpansberg Dist., saltpan, 11 Jan 1955, A. O. D. Mogg 24416 (PRE); Dongola, De Klundert, next to waterhole, 22°23'S, 29°38'E, 16 Mar 1948, I. C. Verdoorn 2290 (PRE); Zoutpan, fringe of pan, 22°53'S, 29°23'E, 12 Apr 1934, H. G. W. J. Schweickerdt & I. C. Verdoorn 488 (PRE); Zoutpan, western side, 22°53'S, 29°23'E, 21 Jan 1931, C. E. B. Bremekamp & H. G. W. J. Schweickerdt 232 (PRE). Northern Cape: Kalahari Gems National Park, Sewe Panne, large pan 38 km from Nossob, 25°23'S, 20°08'E, 29 Mar 1979, A. A. Gubb 03-12 (PRE). North West: Bloemhof, S. A. Lombardt Nat. R., 27°38'S, 25°23'E, 15 Dec 1985, L. N. Jeffers 425 (PRE).

ZIMBABWE: Masvingo, Chiredzi District, Chitanga Hill, Hippo Valley Estate, 21°11'15.395"S, 31°45'48.726"E, 24 Jan 1971, P.E. Taylor s. n. (MO), F. A. Rogers 13568 (BOL). Mashonaland West: ca. 12.8 km ESE of Chirunda Bridge, 03 Feb 1958, R. B. Drummond 5459 (MO); Sashi River, 07 Jan 1961, H. Wild 5306 (MO).

SESUVIUM MARITIMUM (Walter) Britton, Sterns & Poggenb., Prelim. Cat.: 20. 1888. *Pharnaceum maritimum* Walter, Fl. Carol. [Walter]: 117. 1788. *Sesuvium pentandrum* Elliott, Sketch Bot. S. Carolina [Elliott] 1 (6): 556. 1821. *Mollugo maritima* (Walter) Ser. ex DC. in Prodr. [A. P. de Candolle] 1: 393. 1824.—TYPE: U. S. A. South Carolina, Georgetown County: Yawkey Wildlife Center, Mosquito Creek drainage on S Island, 28 Jul 1987, Nelson 5850 (neotype: USCH, USCH0000001 digital image!, designated by Ward (2008).

Slender procumbent to ascending, annual herb with sparse bladder cells on leaves and internodes; forming mats up to 60 cm in diam; internodes pale when dry. Leaves up to 27 mm long, oblanceolate, flat, and hardly succulent; petiole up to 7 mm long. Flowers sessile, 3–6 mm long, usually white, often numerous; bracts in one pair, ~1 mm long, lanceolate. Stamens 5, often pink. Ovary with 3–5 carpels and the same number of free styles. Seeds numerous, 0.8–0.9 mm long, and reniform, with a smooth, black, dark brown or grey, sometimes slightly dull seed coat.

Distribution and Habitat—This species is found on the Bahamas, in Belize, Cuba, Mexico, Puerto Rico,

St. Barthelemy, and the U. S. A. (FL, LA, MD, NJ, NC, OK, SC, TX) (Fig. 9). Plants grow in coastal regions (beaches, mangroves, marshes) and also in disturbed areas. They are always found in saline conditions, usually on sandy or loamy soil.

Vernacular Names—Slender sea purslane.

Note—Some floras also report the occurrence of individuals with two carpels (e.g. Ferren Jr. in FNA [Vivrette et al. 2003]).

Representative Specimens Examined—BAHAMAS. Eleuthera: Cape Eleuthera, 15 May 1975; D. S. Correll & S. R. Hill 45296 (BRIT, MO); Great Inagua: E end of Maroon Hill, along shore of Lake Rosa, 04 Jun 1974, G. R. Proctor & W. T. Gillis 33944 (B, MO); ca. 1.6 km O of Matthew Town, ca. 20°57'0.208"N, 73°38'58.549"W, 01 Mar 1974, D. S. Correll 41688 (LL, MO); just NE of Matthew Town, near Horse Pond, ca. 20°57'21.877"N, 73°40'1.552"W, 31 Jul 1975, D. S. Correll 45807 (BRIT); Little Exuma: Cooper's Farm, Forbes Hill, ca. 23°27'40.6"N, 75°39'8.841"W, 09 Mar 1976, D. S. Correll & H. B. Correll 46903 (MO).

BELIZE. Belize: Crooked tree, near Crooked Tree Lagoon, ca. 17°46'45.62"N, 88°31'53.173"W, 14 Jun 1993, M. A. Vincent et al. 5950 (MO). Corozal Distr.: Cerros Maya Ruins, Lowry's Bight, ca. 18°21'30.2220"N, 88°21'09.9324"W, 11 Apr 1983, C. J. Crane 541 (BRIT, MO, LL).

CUBA. Isle of Pine: Caleta Cocodrilos, ca. 21°30'14.493"N, 83°6'0.874"W, 08 Mar 1916, N. L. Britton et al. 15308 (MO); Pinar del Rio, Central Orozco (between Cabanas and Bahía Honda), near "manglares", ca. 22°58'41.48"N, 83°0'45.881"W, 25 Mar 1920, E. L. Ekman 10569 (UPS).

FRENCH OVERSEAS COLLECTIVITY. Saint Barthélemy: Ilot de Frégate, ca. 17°56'24.3348"N, 62°50'00.6504"W, 30 May 1951, C. de Gallo 47 (WAG).

MEXICO. Colima: Manzanillo, near shore, W side of bay, ca. 8.9 km WNW of city, ca. 19°6'16.563"N, 104°24'3.816"W, 11 Jul 1956, D. P. Gregory & G. Eiten 316 (BRIT, MO). Guerrero: Mun. Petatlán, Laguna Carrizal, 17°34'06"N, 101°25'52"W, 10 Jan 1995, L. Lozada 1887 (MEXU). Jalisco: Chamela-Cuixmala biosphere reserve, Cuixmala, highway Puerto Vallarta-Manzanillo, km 45, 19°23.549"N, 105°00.206"W, 01 Sep 1998, M. Bueno 12 (TEX); Rancho Cuixmala, lagoons along road to Casa Jeanette, near Brignoni plot boundary, 19°23'N, 105°01'W, 14 May 1991, E. J. Scott et al. 3593 (CAS). Veracruz: (La) Tunilla 13 km from Tlacotalpan, ca. 18°42'23.9724"N, 95°38'38.2884"W, 07 Aug 1971, A. Lot 1408 (MEXU, MO, TEX).

PUERTO RICO. Icacos Island, ca. 18°23'11.828"N, 65°35'19.863"W, 12 Jul 1966, R. A. Howard et al. 16130 (S).

U. S. A. Florida, Brevard County: Merritt Island, Indian River, A. H. Curtiss 350 (B, MO); Citrus County: coast at Fort Gulf Beach, W of Crystal River, 20 Apr 1980, C. F. Reed 115008 (MO); Franklin County: St. Vincent Island, National Wildlife Refuge, 29°40'54.174"N, 85°6'26.305"W, 22 May 1987, L. C. Anderson 10600 (BRIT, MO); Lee County: Central Sanibel, pond shores; Sea Oats subdivision, 06 Mar 1976, W. C. Brumbach 8936 (BRIT); Martin County: between causeway to Stuart Beach and House of Refuge, 15 Aug 1972, R. Kral 48058 (MO); Monroe County: Key West, 10 Apr 1896, A. H. Curtiss 5619 (MO, Z); Wakulla County: St. Marks Wildlife Refuge, near lighthouse, ca. 30°4'24.589"N, 84°10'46.589"W, 15 Jul 1962, R. K. Godfrey 62387 (CAS, TEX); vicinity of Shell Point, ca. 30°3'11.8"N, 84°17'4.725"W, 09 Jun 1960, R. K. Godfrey 59722b (BRIT). Georgia, Glynn County: ca. 2.7 km NW of St. Simons, 31°10'51.376"N, 81°24'23.871"W, 12 Jun 1974, W. H. Duncan 29056 (TEX). Kansas, Barber County: 1.6 km S and 3.2 km E of Hazelton, dry bed of a saline creek, 37°4'28.167"N, 98°21'56.685"W, 24 Sep 1986, R. L. McGregor 37818 (TEX). Louisiana, Cameron Parish: marsh S of Cameron near McNeese State University Field Station, ca. 29°46'8.054"N, 93°20'28.161"W, 29 Oct 1982, R. D. Thomas et al. 82484 (BRIT); Jefferson Parish: Grand Island, near E end of island road, 29°15'59.072"N, 89°57'10.054"W, 11 Nov 1966, J. W. Thieret 25235 (LL); Terrebonne Parish: S of Point Chen, ca. 29°24'13.363"N, 90°28'20.683"W, 27 Jun 1970, R. D. Thomas et al. 19691 (BRIT, MO). Maryland, Worcester County: Assateague Island, ca. 38°5'21.029"N, 75°12'10.04"W, 27 Aug 1955, C. F. Reed 36759 (MJG, MO). New Jersey, Atlantic County: Brigantine Beach (N end), 39°25'23.516"N, 74°22'3.565"W, 26 Aug 1935, J. M. Fogg Jr. 9557 (MO); Cape May County: Cape May, sandy beach, ca. 38°56'6.338"N, 74°53'51.903"W, 28 Jul 1874, C. F. Parker s. n. (UPS); Ocean City, ca. 39°16'25.4172"N, 74°34'20.8164"W, 05 Aug 1882, AC s. n. (MO). North Carolina, Brunswick County: Southport, waste land along waterfront, ca. 33°55'22.389"N, 78°0'22.827"W, 06 Oct 1969, S. W. Leonard & D. B. Russ 2489 (B, CAS, MO, S, TEX, Z); Carteret County: beach access area to more Morehead City channel between

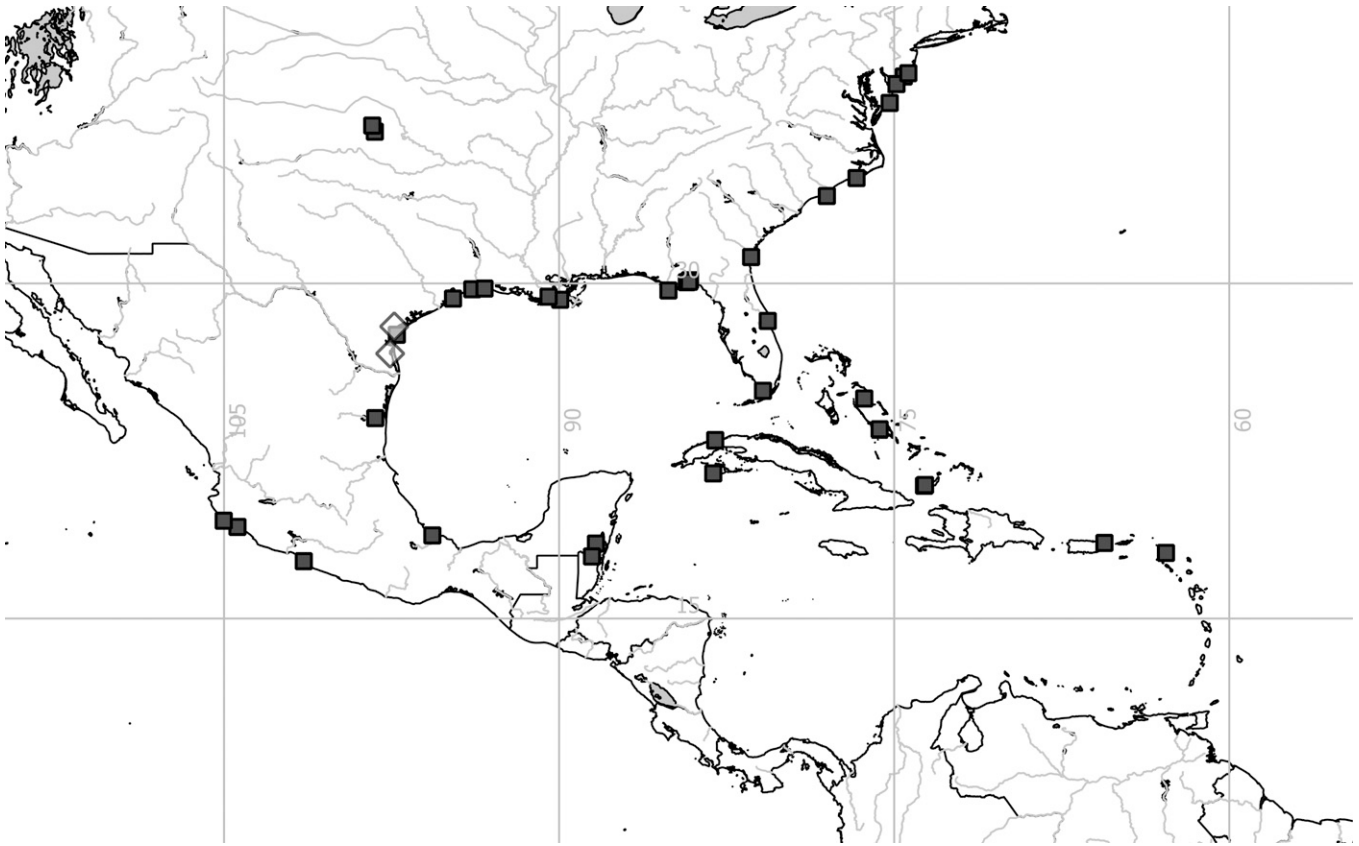


FIG. 9. Distribution of *Sesuvium maritimum* (dark grey squares) and *S. trianthemoides* (white diamonds) in Mexico, the U. S. A., and the West Indies. *Sesuvium trianthemoides* is only known from the type and one more specimen and might be strictly endemic to coastal areas in southern Texas.

Morehead City and Beaufort off Rt. 70, ca. 34°43'18.001"N, 76°41'9.999"W, 18 Aug 1998, J. Stone & D. Holland 1526 (BRIT); Dare County: Hatteras, 03 Aug 1966, A. E. Radford 45105 (BRIT). Texas, Cameron County: Boca Chica, along coast, 01 May 1937, R. Runyon 1653 (BRIT).

Notes—The very similar species *S. trianthemoides* differs from *S. maritimum* in having an ovary of only 2 carpels and styles and slightly larger seeds with a stronger seed coat texture.

SESUVIUM MESEMBRYANTHEMOIDES Wawra in Wawra & Peyr., Sitzungsber. Kaiserl. Acad. Wien, Math.-Nat. 38: 564. 1860. *Halimus* [*Halimum*] *mesembryanthemoides* (Wawra & Peyr.) Hiern, Cat. Afric. Pl. (Hiern) 1(2): 413. 1898.—**TYPE**: ANGOLA. *Wawra* 210 (Type not found, possibly destroyed in B or W). Mossamedes, sea-shore, 01 Jul 1859, *Welwitsch* 2389 (lectotype: LISU 214652 digital image!, designated here; isolectotypes: BM, BR, C 10005289 digital image!, COI, K!).

Sesuvium crystallinum Welw. ex Oliv., Fl. Trop. Afr. [Oliver et al.] 2: 586. 1871.—**TYPE**: ANGOLA. Mossamedes, sea-shore, 01 Jul 1859, *Welwitsch* 2389 (holotype: LISU 214652 digital image!, isotypes: BM, BR, C 10005289 digital image!, COI, K!).

Creeping perennial herb with a deep taproot; bladder cells bulging and globose, covering shoots, leaves and outside of flowers; whitish when dry; internodes terete and succulent. Leaves 10–30 mm long, elliptic to oblong, up to 3 mm wide (when dry), subterete, and sessile. Bracts in 2–4 pairs, large (up to 5 mm long), lanceolate to triangular; dark in

color when dry. Flowers 10–13 mm long, subsessile, pink to violet. Stamens numerous. Ovary with 3–5 carpels. Fruit a many-seeded capsule (according to descriptions). Seeds not seen, described to be black and smooth.

Notes— C_4 species (Bohley et al. 2015). The outermost pair of bracts sometimes shows a loose cover of small bladder cells along the midvein.

Sesuvium mesembryanthoides Welw., *nomen nudum*, Apont: 557. 1859, has been assigned to *S. crithmoides* by previous authors, e.g. Gonçalves (1970) in *Conspectus Florae Angolensis*.

Distribution and Habitat—Angola, Namibia, apparently also in Syria (Fig. 5C). The species grows on sand (beaches, dunes) in coastal areas.

Representative specimens examined—ANGOLA. Cabo Negro, sand dunes, 15°40'S, 11°59'E, 5 m, 15 Apr 1973, P. Bamps et al. 4519 (K); Mossamedes, 1859, *Welwitsch* 2387 (K); Lobito Bay, near Benguela, 12°36'16.1676"S, 13°21'39.9312"E, 01 Sep 1906, H. Bolus 12453 (BOL); Coroca Valley near Namibe, ca. 15°10'09.2424"S, 12°09'28.5012"E, Nov 1931, O. Jessen 337 (B).

SYRIA. Sur la piste d'Akra á Khan Abou Chamat (desert du Syrie), 27 Mar 1931, R. Gombault 1998 (P, P04583848 digital image!); Palmyra (desert du Syrie), 3 Apr 1934, R. Gombault 3468 (P, digital image, P04583849).

Sesuvium mezianum (K. Müll.) Bohley & G. Kadereit, comb. nov. *Cypselea meziana* K. Müll., Bot. Jahrb. Syst. 42 (2–3, Beibl. 97): 72. 1908.—**TYPE**: PARAGUAY. Near Asunción, lowlands along Paraguay River, 1875, B. Balansa 2263 (holotype: G 00102877 digital image!).

Creeping, perennial herb; shoots up to 0.4 m long, often rooting at nodes. Bladder cells not seen. Leaves obovate to

oblanceolate 5–7 mm long, 2–3 mm wide; petioles short (1–3 mm); lateral flaps distinctly auriculate with entire margins. Flowers 3–5 mm long, (greenish-) white, pendant, pedicellate (pedicels 1–2(–3) mm). Stamens 3. Ovary with 3 carpels. Fruit a circumscissile capsule. Seeds not seen.

Distribution and Habitat—The species is apparently endemic to Paraguay. It grows on saline soil.

Notes—Of the three species formerly classified as *Cypselea*, this one shows the highest resemblance to other *Sesuvium* species in morphology and ecology (perennial habit, salt tolerance). Only a digital image of the type was seen.

SESUVIUM PORTULACASTRUM (L.) L., *Systema Naturae* ed. 10, 2: 1058. 1759. *Portulaca portulacastrum* L., *Sp. Pl.* 1: 446. 1753. *Sesuvium portulaca* Crantz, *Inst. Rei Herb.* 1: 136. 1766. *Halimus portulacastrum* (L.) Kuntze, *Rev. Gen. Pl.* 1: 263. 1891.—TYPE: KINGDOM OF THE NETHERLANDS. Curaçao. Hermann, *Paradisus Batavus seu description rariorum plantarum*: 212, icon. 1698 (lectotype designated by Wijnands in *The Botany of the Commelins*: 175. 1983).

Sesuvium pedunculatum Pers., *Syn. Pl.* [Persoon] 2 (1): 39. 1807.—TYPE: INDIA. (lectotype: Lamarck, *Tabl. Encycl.* 1794: t.434, designated by Hartmann (2001b)).

Sesuvium revolutum Pers., *Syn. Pl.* [Persoon] 2 (1): 39. 1807, syn. nov. *Sesuvium revolutifolium* Ortega, *Nov. Rar. Pl. Descr. Dec.*: 19. 1797.—TYPE: de Candolle 1832?: t. (179), lectotype, designated by Hartmann (2001b).

Note—Hartmann (2001b) refers to an unpublished plate not found in all copies of de Candolle's *Plantarum Succulentarum Historia* [= *Plantes Grasses de P. J. Redouté*] (Stafleu and Cowan 1983). A copy of *Plantes Grasses* containing the plate can be found in the Kew library.

Sesuvium sessile Pers., *Syn. Pl.* [Persoon] 2 (1): 39. 1807, syn. nov.—TYPE: no specimen indicated (Lectotype: de Candolle [1807], plate 9. Epitype: P, Jussieu Collection, P00680445, digital image!, both designated here).

Note—Persoon only cited the illustration of *S. portulacastrum* from de Candolle's *Plantes Grasses* in the description.

Sesuvium longifolium Humb. & Bonpl. ex Willd., *Enum. Pl.* [Willdenow] 1: 521. 1809, syn. nov.—TYPE: South America [America meridionali]. *Humboldt & Bonpland s. n.* (herbarium not known). Lectotype: *A. Stübel* 16 (B, B 10 0390978!), designated here.

Sesuvium microphyllum Willd., *Enum. Pl.* [Willdenow] 1: 521. 1809, syn. nov.—TYPE: CUBA. Collected by *Humboldt & Bonpland*, but no number given. Neotype: ex herbarium *Humboldt* (without collector or number), B, B 10 0390872!, designated here.

Sesuvium repens Willd., *Enum. Pl.* [Willdenow] 1: 521. 1809. *Crithmus indicus* Rumph., *Herbarium Amboinense* v. 6: 165; Table 72, Fig. 1. 1750. —TYPE: INDIA. Rumph 1750: t.72 f1, (lectotype, designated by Hartmann [2001b]).

Sesuvium portulacastrum var. *revolutum* (Pers.) Sims, *Bot. Mag.* 41: t. 1701. 1815. —TYPE: CUBA. Cultivated plant. Lectotype: illustration preceding the description (t. 1701!), designated here.

Sesuvium spathulatum Kunth, *Nov. Gen. Sp.* [H. B. K.] 6: 87. 1823, syn. nov.—TYPE: CUBA. Near Havanna, *A. J. A.*

Bonpland & A. von Humboldt 1372 4524 (P, P00679547 digital image!).

Trianthema polyandrum Bl., *Bijdr. Fl. Ned. Ind.* 17: 1137. 1826.—TYPE: INDONESIA. Batavia [Jakarta]. *Blume s. n.* (possible holotype: NY 00 218023 digital image!).

Sesuvium brevifolium Schumach. & Thonn., *Beskr. Guin. Pl.*: 233. 1827.—TYPE: banks of salt-rivers (translation from Danish, Hepper 1976). No specimen indicated. Lectotype: "Guinea". *Isert s. n.* (C, C10004542 digital image!; IDC microfiche 2203: Isert and Thonning herbarium, nr. 98 II, 4), designated by F. N. Hepper (1976).

Note—Presumably Thonning based the description of the species on specimens he collected. However, those are not at C and the specimen collected by Isert agrees with the description of *S. brevifolium* and might have been used by Schumacher (Hepper 1976).

Sesuvium parviflorum DC., *Prodr.* [A. P. de Candolle] 3: 453. 1828, syn. nov. *Sesuvium portulacastrum* (L.) L. var. *subsessile* Cambess., *Fl. Bras. Merid.* (A. St.-Hil.) 2: 200. 1829.—TYPE: URUGUAY. Au pied du Morne de Mont Video. Ie long de la plage, May 1767, *P. Commerson* 138 (holotype: ?, isotype: P, P01900029 digital image!).

Sesuvium portulacastrum var. *pedunculatum* (Pers.) Cambess., *Fl. Bras. Merid.* (A. St.-Hil.) 2: 199. 1829.—TYPE: Lamarck, *Tabl. Encycl.* 1794: t.434 (illustration!).

Sesuvium sessiliflorum Domb. ex Rohrb. in *Martius, Fl. Bras.* 14 (2): 310. 1872.—TYPE: BRAZIL. Near Rio de Janeiro. *Glaziou* 3994 (holotype (?): C!).

Sesuvium distylum Ridl., *J. Linn. Soc., Bot.* 27: 38. 1890, syn. nov.—Type: BRAZIL. Rat Island. *Ridley* 61 (holotype: BM, isotype: K!).

Sesuvium portulacastrum var. *griseum* O. Deg. & Fosberg, *Occas. Pap. Bernice P. Bishop Mus.* 21 (3): 45–47. 1952. *Trianthema griseum* [grisea] (O. Deg. & Fosberg) O. Deg. & I. Deg., *Flora Hawaiiensis* [Degener], book II: Fam. 116. 1960.—TYPE: KIRIBATI. Phoenix Islands, Kanton Island, *O. Degener* 21451 (holotype: BM, isotype: B!).

Trianthema portulacastrum var. *hillebrandii* O. Deg. & I. Deg., *Flora Hawaiiensis* [Degener], book II: Fam. 116. 1960.—TYPE: U. S. A. Hawaii, Oahu, Laie Peninsula. *O. Degener & I. Degener* (illustration subsequent to the description)!

Sesuvium ayresii Marais, *Kew Bull.* 32 (2): 483. 1978.—TYPE: MAURITIUS: Fort William, on sand surrounding salt water pools, Sep 1860, *Ayres s. n.* (holotype: K!).

Sesuvium portulacastrum (L.) L. f. *albiflorum* Kayama, *J. Phytogeogr. Taxon.* 56(1): 36 (35, Fig. 1). 2008.—TYPE: JAPAN. The Ryukyus: Okinawa Island, Yonabaru-cho, 5 Jun 2007, *K. Kayama s. n.* (holotype: RYU).

Erect or procumbent and creeping perennial herb; internodes terete, up to 5 mm in diam, succulent, glabrous and green to reddish brown; sometimes with prominent root primordia at nodes; roots develop easily when contact to soil is established; bladder cells apparently absent to slightly bulging. Leaves elliptic to lanceolate, up to 70 mm long, often shorter; leaf base attenuate; petioles short (2–3 mm),

with translucent pseudostipules; succulence of leaves very plastic and depending on current growing conditions, even within a single plant. Flowers 5–12 mm long, most often (pale) pink, rarely white, sometimes reported to be blue, yellow, or red on herbarium labels; subsessile or with pedicels up to 15 mm long. Stamens numerous. Ovary glabrous and pale yellow; with 3–5 carpels and 3–5 thin long styles; weak scent and production of nectar during anthesis. Fruit \pm ovoid or beehive-shaped, many-seeded capsules. Seeds ~0.7–1 mm long, rounded-reniform, black, smooth, lustrous and slightly iridescent.

Distribution and Habitat—Distributed worldwide in tropical and subtropical zones between approximately 35°N and 42°S (Fig. 10). The limiting factor seems to be the occurrence and duration of frost (Lonard and Judd 1997). The main habitats are coastal areas where the plants grow on beaches and adjacent dunes, but it also occurs in disturbed areas. The species is occasionally found farther inland and in those cases appears to follow rivers. Optimal growth rates are only reached on saline soils (Messedi et al. 2004), but the plant is also found in non-saline habitats.

Notes—The species apparently flowers throughout the year, given enough light. Weak scent and production of nectar during anthesis were observed. Germination success and the establishment of seedlings are reported to be poor (Lonard and Judd 1997), but the species is capable of vegetative propagation. In its dynamic coastal habitats, fragments of the plant are easily ripped off by the surf and can float in sea water for weeks without losing their ability to grow when washed up on shore (Lonard and Judd 1997). This way the species is easily dispersed by sea currents and grows as a pioneer on beaches and dunes. In addition, plants root at the nodes as soon as contact with soil is established, often forming belt-like patches. Seedlings show simple, entire, succulent cotyledons.

Besides its use as fodder plant or vegetable, *S. portulacastrum* is also cultivated as an ornamental and planted for dune stabilization. The species is also used to restore polluted soil, as it has high above ground biomass production even on highly saline soil and shows high resistance to toxic metals (Mariem et al. 2014).

Future studies may show that this polymorphic species consists of several subspecies or cryptic species. However, a formal subdivision must await a detailed molecular and morphological study at the population level.

Vernacular Names—Sea purslane, Cencilla, Pourpier.

Representative Specimens Examined—ANGOLA. Namibe: Cabo Negro, on dunes, ca. 15°40'00.0012"S, 11°58'59.9988"E, 15 Apr 1973, P. Bamps et al. 4522 (WAG).

ARGENTINA. Buenos Aires: Miramar, ca. 38°18'57.8520"S, 57°54'54.4140"W, 23–27 Feb 1930, A. Cscalo & A. L. Cabrera 35 (LP). Chaco: (Amoyo) Guaycurú, ca. 40 km from Resistencia, ca. 27°11'24.7632"S, 58°49'11.7912"W, 22 Sep 1967, A. Suárez Cullen 620 (LP). Chubut: Puerto San José, 12 Dec 1904, P. Dusén 5244 (UPS).

AUSTRALIA. New South Wales: Hat Head (Korogoro Point), E of Kempsey, ca. 31°3'11.88"S, 153°3'20.771"E, 18 Jan 1953, E. F. Constable 24065 (MO). Queensland: Ingram Island, rocks at SW coast, 14°25'4.979"S, 144°52'43.859"E, 27 Jul 1973, D. R. Stoddart 4042 (MO). Western Australia: Pilbara, lowland of Fortescue River Basin, Roy Hill Road between Marillana and Roy Hill Homestead, 22°24'39.96"S, 119°28'56.28"E, 22 Sep 1995, S. Hunger & N. Kilian 9313 (B).

BAHAMAS. Inagua: along South Shore Road W of Salt Pond Hill, 01 Jun 1974, G. R. Proctor & W. T. Gillis 33877 (B).

BELIZE. Stann Creek, beach near village of Stann Creek [Dangriga?], 16°58'04.1736"N, 88°13'06.1140"W, 11 Jun 1973, T. B. Croat 24086 (MO); Glover's Reef, Middle Cay, 16°42'–45"N, 87°45'–50"W, 02–12 Nov 1971, F. R. Fosberg & D. R. Stoddart 53920 (MO).

BRAZIL. Alagoas: near mouth of Rio Mandaú. Maceió, 9°42'53.9244"S, 35°48'05.4900"W, 04 Sep 1987, S. Tsugaru & Y. Sano B-1477 (MO); Guanabara: Barra de Tijuca, 26 Mar 1964, Z. A. Trinta & E. Fromm 534 (LP).

BRITISH OVERSEAS TERRITORIES. British Virgin Islands: Beef Island, Tamarind Point, ca. 18°26'33"N, 64°31'53"W, 12 Feb 1962, W. G. Darcy 726A (MO); Turks and Caicos Islands: Turks Islands, Salt Cay, 11 Sep 1978, D. S. Correll 50197 (BRIT, CAS, MO).

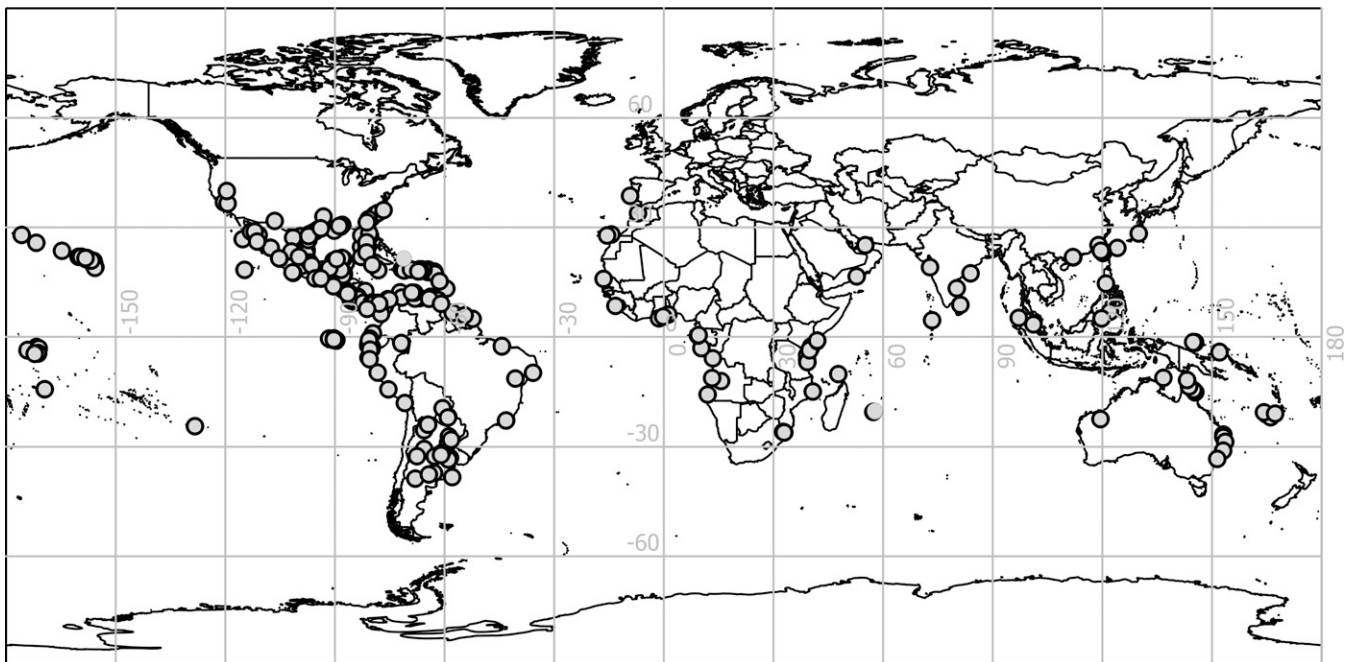


FIG. 10. Distribution map of *Sesuvium portulacastrum*. The species has a cosmopolitan distribution with a concentration in tropical and subtropical coastal areas.

CAPE VERDE. Maio: beach S of Villa de la Maio (Preia Preta), 16 Sep 1979, W. Lobin 534 (BONN); Sal: beach from lighthouse of Santa Maria to Beia algodoiro, 09 Nov 1979, W. Lobin 1442 (BONN).

CHINA. Fujian, Hulan Distr.: Houlong, Wuli str., sand beach along sea, 24 Jun 1985, *Chen Hengbin* 456 (MO); Guangdong: Yangjiang Xian, ca. 21°46'23.7"N, 112°2'56.4"E, 30 Nov 1935, C. Wang 38814 (MO).

CUBA. La Habana, Reparto Miramar, on the "arrefice", 11 Oct 1921, E. L. Ekman 13307 (B, UPS); rocky seashore near Havana, 24 Nov 1905, A. H. Curtiss 569 (K).

DOMINICAN REPUBLIC. Parish St. Mark: Scott's Head, ca. 15°12'45"N, 61°22'11"W, 25 Jun 1992, H. T. Beck & K. Lee 1686 (CAS).

ECUADOR. E coast, Onná (?), 15 Jun 1937, *Schimppf* 1187 (Z). Galapagos Islands: Baltra (Seymour Island), ca. 0°26'16.1448"S, 90°16'53.49"W, 22 Jan 1964, F. R. Fosberg 44679 (MJG). Manabi: Manta, ca. 0°56'46.1580"S, 80°41'33.0720"W, 06 Jun 1989, C. Cerón et al. 6746 (MO).

FRENCH OVERSEAS TERRITORIES. St. Barthelemy: NO edge of La Grande Saline, 17°53'29.0004"N, 62°49'22.0008"W, 23 Jan 2006, P. H. Raven 28497 (MO).

GABON. Estuaire: Ovang, old oil platform in the mangroves, 0°28'54.001"N, 9°31'5.998"E, 18 Nov 2001, J. J. Wieringa & A. F. Bradley 4368 (WAG); Ovang, E of Libreville, 0°28'59.9988"N, 9°31'00.0012"E, 23 Jul 1985, J. J. Bos et al. 10776 (WAG).

INDONESIA. Sumatra: Aceh, Lhokseumawa, ca. 5°11'59.773"N, 97°7'15.859"E, 31 Aug 1971, K. Iwatsuki et al. 1305 (MO). Aroe Island, Dobo, ca. 05°45'27.4860"S, 134°12'58.6080"E, 18 Apr 1922, H. Jensen 220 (C).

INSULAR AREAS OF THE UNITED STATES: American Samoa: Tau, S side of Island, ca. 14°14'53.7936"S, 169°27'13.5288"W, 22 Aug 1975, A. Whistler W 3223 (B); Puerto Rico: Reserva Forestal Guanica, 19 Mar 1990, B. M. Boom 9997 (MO). U. S. Virgin Islands: St. John, East End Quarter, along Center Line Road, near Hermitage ruins, 18°21'20.8"N, 64°42'2.08"W, 05 May 1989, P. Acevedo Rdgz. et al. 2952 (MO).

JAPAN. Kyushu, Pref. Kagoshima: Distr. Oshima, Kikai-cho, ca. 28°19'49.072"N, 129°57'10.403"E, 29 Nov 1981, K. Mimoro et al. 2892 (CAS, MO).

KENYA. Coast Province: ca. 5 km from Kilifi, ca. 03°34'S, 39°53'E, 15 Apr 1973, P. Bamps et al. 4522 (WAG); Kilifi District: Mida Creek, Mida, 03°19'0.011"S, 39°58'0.012"E, 10 Jan 1970, B. Jonsell 2065 (UPS, WAG).

KIRIBATI. Phoenix Islands: Enderbury Island (Guano Island), 03°07'59.9988"S, 171°04'59.9988"W, 10 Oct 1939, A. C. Browne s. n. (CAS); Enderbury Island, 03°07'22.9188"S, 171°05'00.8340"W, 01 Jun 1973, F. R. Fosberg & D. R. Stoddart 54756 (MO).

MAURITIUS. Ile aux Fouquets, islet at E coast, ca. 20°23'42.5328"S, 57°46'39.7992"E, 18 Jan 1975, D. H. Lorence DL 1064 (MO); Poste Lafayette, E coast, ca. 20°08'19.1652"S, 57°45'13.8024"E, 11 Jan 1973, D. H. Lorence M 189 (MO).

MEXICO. Baja California: Bahia de los Angeles, lagoon at S coast, 13 Mar 1992, P. Fritsch et al. 1315 (MEXU); Estero Rasa, Isla Rasa, 30 Apr 1979, B. Villa R. s. n. (MO). Jalisco: Bahia de Chamelas, Mun. Tomatlan, dunes, 11 Feb 1982, J. I. Calzada & J. Elizondo 8424 (MO).

MOZAMBIQUE. Inhambane: Pomene, several km from airstrip, near mangroves, ca. 26°03'34.9668"S, 32°54'05.3208"E, 24 Sep 1980, P. C. M. Jansen et al. PJ7521 (WAG).

NICARAGUA. Carazo: 3.3 km SE of Casdares on road to Huehueté, SE of La Bocana Grande (mouth of Río Grande), 11°37'35.8284"N, 86°20'19.5432"W, 23 Nov 1977, W. D. Stevens & B. A. Krukoff 5179 (CAS). Chinandega: Puerto Morazan; ca. 16°12'51"N, 87°10'00"W, 09 May 1998, R. Rueda & I. Coronado 8137 (MO).

PANAMA. Canal Zone: Farfan Bay, ca. 7°40'09.3720"N, 81°12'30.7224"W, 30 Mar 1969, J. D. Dwyer et al. 4692 (WAG); Guna Yala: Isla Mosquito/Sunset Island, ca. 9°06'00.1512"N, 77°53'59.9892"W, 07 Oct 1966, J. A. Duke 8872 (MJG).

PARAGUAY. Chaco: Palma de las Islas, 12 Mar 1989, F. Merelles & L. Ramella 2852 (Z).

PERU. Arequipa: ca. 3 km N of Camana, ca. 16°38'00"S, 72°45'43"W, 07 May 1977, J. C. Solomon 2799 (MO).

PHILIPPINES. Mindanao, St. Cruz Island near Zamboanga, ca. 6°51'42"N, 122°3'56"E, 11 Dec 1961, S. Olsen 891 (C); Sulu Archipelago, Papahag, ca. 5°02'18.4200"N, 119°47'31.8300"E, 26 Nov 1961, S. Olsen 886 (B); Luzon, Manila, ca. 14°35'57"N, 120°59'01"E, Jul 1947, H. Jeppesen s. n. (C).

SENEGAL. Dakar: Hann, ca. 14°43'21"N, 17°25'45"W, 23 Jan 1948, J. G. Adam 362 (MO).

SEYCHELLES, Outer Islands: Astove Atoll, Lagoon, on sand in and around Pemphis swamp, ca. 10°04'42"S, 47°44'55"E, 06 Oct 1967, Gwynne & Wood 1318 (UPS).

TAIWAN. Kaohsiung Hsien, Hunei Hsiang; Hunei Hsiang, 22°57'33.001"N, 120°10'49.979"E, 31 May 2003, C. H. Chen 4836 (MO); Tainan

Hsien, Chiku Hsiang, Lungshan, 23°8'29"N, 120°6'43.991"E, 07 Jun 2003, C. H. Chen 4611 (MO).

TANZANIA. Daressalaam: Msimbazi Creek, ca. 80 m above Salander Bridge, ca. 6°47'44.4624"S, 39°16'53.5476"E, 27 Aug 1971, R. Wingfield 1718 (WAG).

U. S. A., Florida, Collier County: Carnestown, 25°54'38.833"N, 81°21'47.023"W, 13 May 1975, A. L. Moldenke & H. N. Moldenke 29687 (LL). Hawaii, Hawai'i: Kohala, ca. 20°5'31.369"N, 155°52'16.572"W, 09 Aug 1926, O. Degener 8910 (B); South Point, Kau, ca. 18°54'36.662"N, 155°40'44.436"W, 14 Mar 1949, A. Greenwell 19645 (B). Texas, Cameron County: Rt. 4 E of Brownsville, near scrapyard W of Palmita Hill Historical Marker, 25°57'16.804"N, 97°19'18.202"W, 10 Dec 1983, B. Ertter 5247 (TEX).

VENEZUELA. Falcón: Distr. Silva, Cayo Sal, NE of Chichiriviche, 10°58'N, 68°15'W, 28 Aug 1974, J. A. Steyermark & B. J. Manara 110321 (MO); near La Vela de Coro, 11°27'19.3608"N, 69°34'51.4740"W, 25 Feb 1968, H. & E. Walter 85 (B).

An extended list of examined specimens of *S. portulacastrum* can be found in online Appendix S1.

Sesuvium rubriflorum (Urb.) Bohley & G. Kadereit, comb. nov. *Cypselea rubriflora* Urb., Ark. Bot. 22A (17): 15. 1929.—TYPE: CUBA. Matanzas: Near Caimito de Hanabana on dried out bottoms of ponds, 08 Aug 1923, *Ekman* 17016 (B 10 0242330 digital image!, NY).

Procumbent herb with perennial root, root ca. 4 mm in diam; shape and size of bladder cells unknown. Leaves tiny (1–3 mm long); petiolate (1–2 mm long); lateral flaps colorless with fimbriate margins. Flowers ~3.5 mm long, bright red; pedicel 3–7 mm long, very thin, almost hair-like. Stamens five. Ovary with 2 carpels and 2 short styles. Fruit an egg-shaped capsule, opening below middle. Seeds numerous, ~0.2 mm long, brown.

Distribution and Habitat—Endemic to Cuba.

Notes—Resembles *S. humifusum* except for the red flowers, the larger number of stamens and its perennial roots.

SESUVIUM SESUVIOIDES (Fenzl) Verdc., Kew Bull. 12 (2): 349. 1957. *Diplochonium sesuvioides* Fenzl, Nov. Stirp. Dec. 1: 58. 1839. *Halimus sesuvioides* (Fenzl) Kuntze, Revis. Gen. Pl. 1: 263. 1891.—TYPE: SOUTH AFRICA. Patria (?), *Drège* 2938 (holotype: K!, isotype W). Figure 11.

Sesuvium digynum Welw. ex Oliv., Fl. Trop. Afr. [Oliver et al.] 2: 586. 1871.—TYPE: ANGOLA, Mossamedes [Namibe], *Welwitsch* 2392 (lectotype: K!, isolectotypes: BM, BR, COI, LISU, designated by Gonçalves (1970)).

Halimus sesuvioides (Fenzl) Hiern var. *reduplicatum* Welw. ex Hiern, Cat. Afric. Pl. (Hiern) 1(2): 414. 1898.—TYPE: Angola, Mossamedes [Namibe], *Welwitsch* 2391 (lectotype: BM; isolectotypes: BR, COI, LISU, K!, designated by Gonçalves (1970)).

Halimus sesuvioides (Fenzl) Hiern var. *welwitschii* Hiern, Cat. Afric. Pl. (Hiern) 1(2): 414. 1898.—TYPE: ANGOLA, Mossamedes [Namibe], *Welwitsch* 2392 (lectotype: BM, isolectotypes: BR, COI, K!, LISU, designated by Gonçalves (1970)).

Sesuvium brachyanthemum Welw. nomen nudum—TYPE: ANGOLA. Mossamedes: near Cabo Negro, between Cazimba and Caroca, Sep 1859, F. M. J. *Welwitsch* 2388 (holotype: BM photograph!, isotype: K!, LISU).

Sesuvium hoepfnerianum Schinz var. *brevifolium* Schinz, Bull. Herb. Boiss. 5 App. III: 75. 1897.—TYPE: NAMIBIA, Gariép River, *Steingröver* 38 (holotype: Z, isotype: B!).

(Procumbent to) erect perennial herb or shrublet forming patches up to 1.5 m in diam and 40 cm in height; internodes



FIG. 11. *Sesuvium sesuvioides*. A. Habit of the plant. B. Details of a flower. For better visibility, one tepal was removed. C. Longitudinal section through a flower with a developing fruit. All floral organs remain at their positions. Drawn by M. Geyer.

terete and, at least when young, densely covered with bladder cells, sometimes also when older; shoots often much-branched and with a reddish or dark olive to grey color when dry. Leaves usually up to 20 mm long, sometimes longer, petiolate, lamina ovate to obtuse-lanceolate, glabrous or with small globose bladder cells, slightly succulent and flat; often revolute and folded downwards along the midvein (Fig. 11a). Bracts lanceolate and ~0.9 mm long; one pair. Flowers sessile, erect, 10 mm long, up to 15 mm in diam; tepals narrowly triangular, usually bright pink or red in color, sometimes (light-) blue. Stamens (5-) numerous. Ovary with 2 carpels and 2 long styles (Fig. 11b). Fruit a many-seeded capsule; egg-shaped when young, becoming tapered with a narrowed and elongated upper half. Seeds rounded reniform, smooth, black and around 1 mm long.

Distribution and Habitat—This species is found in Angola, Cape Verde, Namibia, and the north-western parts of South Africa (Northern Cape Province); see Fig. 12. Used as an ornamental in Saudi Arabia. The plants grow on flats or in depressions with sandy or gravelly soil. They can also be found in disturbed habitats, such as seasonally dry riverbeds, along roads or in pastures, and in areas with saline soil. Most often on bare ground with full exposure to the sun.

Note—*C*₄ species (Bohley et al. 2015). Until the very similar *Sesuvium hydaspicum* and *S. nyasicum* were described in 1965, all specimens that were similar to the plant described above were determined as *S. sesuvioides*, regardless of seed coat texture. Gonçalves (1965) apparently intended to separate specimens with a distinctly structured seed coat from those with smooth ones. This reduced the distribution area of *S. sesuvioides* severely. In general, there is high morphological variation (leaf size and shape, number of bladder cells) among some specimens. It may be necessary to further investigate this species and the very similar *S. hydaspicum* to resolve the relationship between them. Some specimens

show almost smooth, very finely rugose or punctate seeds and are otherwise morphologically similar to the smooth-seeded *S. sesuvioides*.

Representative Specimens Examined—ANGOLA. Namibe Region: Namibe, N corner of bay, 15°7'29"S, 12°8'20"E, 18 Jan 2009, P. J. D. Winter 7680 (C, PRE); Namibe, N corner of bay, P. J. D. Winter 7681 (PRE); Iona National Park, Espinheira Camp, 16°47'12.9984"S, 12°21'29.9988"E, 21 Jan 2009, L. Smook 12113 (PRE); 25 km W of Caraculo, 15°00'59.0004"S, 12°25'46.9992"E, 18 Jan 2009, P. J. D. Winter 7677 (PRE); Iona National Park, Espinheira Camp, 16°47'13"S, 12°21'30"E, 12 Jan 2009, L. Smook 12113 (PRE); ca.22 km NE of Namibe, 15°03'54"S, 12°18'10"E, 18 Jan 2009, P. J. D. Winter 7683 (PRE).

CAPE VERDE. Boa Vista: N part of island, Preia Derrubada, 24 Sep 1979, W. Lobin 685 (BONN); dunes N of Sal-Rei, 30 Oct 1980, W. Lobin 2054 (BONN). Sal: Ribeira da Palha Verde, at road from airport to St. Maria, 11 Oct 1980, W. Lobin 1783 (BONN); S part of the island, NW of Santa Maria, 04 Jan 1979, W. Lobin CV-314 (BONN). San Tiago: Vicinity of San Jorge, waterd fields in Ribeira Longera, 15 Oct 1980, W. Lobin 1820 (BONN). Sao Vicente: Baia de Calhau, ca.16°51'38.6424"N, 24°51'42.1812"W, 28 Nov 1979, W. Lobin s. n. (B).

NAMIBIA. Central Namib Desert, Lower Kuiseb Delta, 23°06'S, 14°31'E, 12 May 1985, C. J. & J. D. Ward 134 (PRE); 30 May 1976, M. K. Dinter s. n. (B); 11 Apr 1922, M. K. Dinter 6281 (B); 17. Oct 1922, M. K. Dinter 4114 (B); Skimbergs Quelle, 28°38'S, 18°38'E, 31 Dec 1923, M. K. Dinter 5145 (B, PRE); Kahanstal, 09 Dec 1934, M. K. Dinter 8190 (B); inner margin of the Namib near Okavango, 31 Mar 1956, R. Seydel (?) 749 (B, Z); Oprurumu (?), 24 Apr 1957, R. Seydel (?) 1105 (Z). Erongo: Karibib, Farm Okongawa, ca. 21°55'16.4280"S, 15°50'48.6024"E, 14 Apr 1963, R. Seydel 3482 (WAG); Brandberg, ca. 21°07'S, 014°33'E, Lubenberg 4977 (B); Brandberg, 21°08'S, 14°38'E, May 1936, G. Boss TRV 36053 (PRE); Brandberg, 21°08'S, 14°38'E, May 1936, G. Boss TRV 36190 (PRE); Brandberg, 21°08'S, 14°38'E, May 1949, L. C. C. Liebenberg 4977 (PRE); Uis, Brandberg-Sonuseb gorge, 21°07'S, 14°37'E, 06 Apr 1985, P. Craven 2164 (PRE); Unjabmund Distr., dried out waterholes in Koichab River, 20°23'S, 13°38'E, 17 Apr 1946, J. W. H. Giess 8039 (PRE); ca. 30 km from N gate of Skeleton Coast National Park on road to Khorxas, ca. 20°14'58.9992"S, 14°00'56.0016"E, 03 Mar 1996, P. M. Burgoyne & N. Snow 5162 (MO, PRE); Omaruru, Brandberg, 8 km S of Tsisabschlucht, 21°08'S, 14°38'E, 20 Jun 1961, J. W. H. Giess 3685 (PRE); road from Fransfontein to Omaruru 27 km before the bridge over Ugab, 06 Apr 1963, H.-D. Ihlenfeldt et al. 3251 (PRE); E of Uis, road to Omaruru, ca. 21°14'04.3980"S, 14°56'15.1692"E, 16 May 1976, Oliver et al. 6699 (MO, PRE, WAG, Z); Khan Mine, 55 km E of Swakopmund next to dam & in run-off below dam, 22°23'S, 14°53'E, 04 Jan 1970, H. F. Glen 150 (PRE); Swakopmund Distr., Rossing, 22°38'S, 14°53'E, May 1956, E. Jensen 6 (PRE); Swakopmund Distr., Kuiseb River, N of Kuiseb River, Jul 1963, E. Schulze PRE 54251 (PRE); Namib, Swakopmund, Gobabeb Res Sta, 09 Oct 1963, C. Koch PRE 54252 (PRE); Gobabeb, 14.4 km NW of Gobabeb in dry wash, 23°30'S, 14°07'E, 05 Jun 1969, M. K. Jensen 244 (PRE); Swartbank Mt., Kuiseb, 22°53'S, 16°38'E, 24 Mar 1963, H.-D. Ihlenfeldt et al. 3137 (PRE); Namibwoestynpark, Kuiseb River, E of Gobabeb, 23°38'S, 15°08'E, Jul 1977, G. K. Theron 3734 (PRE); road from Swakopmund to Hentiesbaai, ca. 30.5 km, 22°23'S, 14°23'E, 16 Mar 1963, H.-D. Ihlenfeldt et al. 3069 (PRE); Welwitschia Distr., Unjab River mouth, 19 km N of Torra Bay, 20°08'S, 13°08'E, 03 Apr 1963, D. S. Hardy & B. De Winter 1487 (PRE). Hardap Region: Rehoboth District, ca. 23°18'51.4188"S, 17°09'38.7684"E, 04 Sep 1949, R. G. Strey 23291 (MO); between Rehoboth and Uhlenhorst, ca. 23°25'10"S, 17°39'19"E, 29 Apr 1949, A. M. Wilman 455 (BOL, NBG), Plattsand, 28 Apr 1947, R. G. Strey 2192 (BOL, PRE), 45 km from Rehoboth on road to Kalkrand, ca. 23°41'41.4060"S, 17°13'55.4016"E, 10 Mar 1983, G. Germishuizen 2737 (C, PRE); Gibeon Distr., Haribes Farm, 05 Apr 1956, O. H. Volk 12198 (MO); Altdorn Farm, 17 Jun 1976, W. Giess & M. Müller 14452 (WAG); dry waterhole in Koichab, ca. 26°17'45.4344"S, 15°31'50.2824"E, 17 Apr 1964, W. Giess 8039 (WAG); between Maltahöhe and Walvis Bay; 10 km N of Maltahöhe, open shrub-veld, 24°42.124'S, 16°53.742'E, 11 Mar 1995, P. M. Burgoyne 3448 (PRE); Rehoboth District, 09 Apr 1949, R. G. Strey 01-29 (PRE); between Rehoboth and Uhlenhorst, 29 Apr 1949, A. M. Wilman 455 (PRE). Karas Region: Lüderitz-Süd, N from Kuiseb, 26°43'59.9988"S, 15°45'00.00"E, 25 Mar 1988, Hartmann et al. 26029 (HBG); Lüderitz-Süd, Tsaukaib, ca. 26°40'59.9988"S, 15°39'00.00"E, 25 Mar 1988, Hartmann et al. 26049 (HBG), near Violdsdrif, Danimub River, ca. 28°45'16.8444"S, 17°37'24.7872"E, 04 Sep 2001, P. Bruyus 8876 (BOL); 15.9 km from Ariamsvlei on road to Charlies Puts, 17 May 1965, B. de Winter 3577B (NBG, PRE); 35 km W from Aus on road to Lüderitz, ca. 26°34'05.3292"S, 15°47'50.2368"E, 05 Mar 1963, B. de Winter & D. S. Hardy 7876 (PRE),

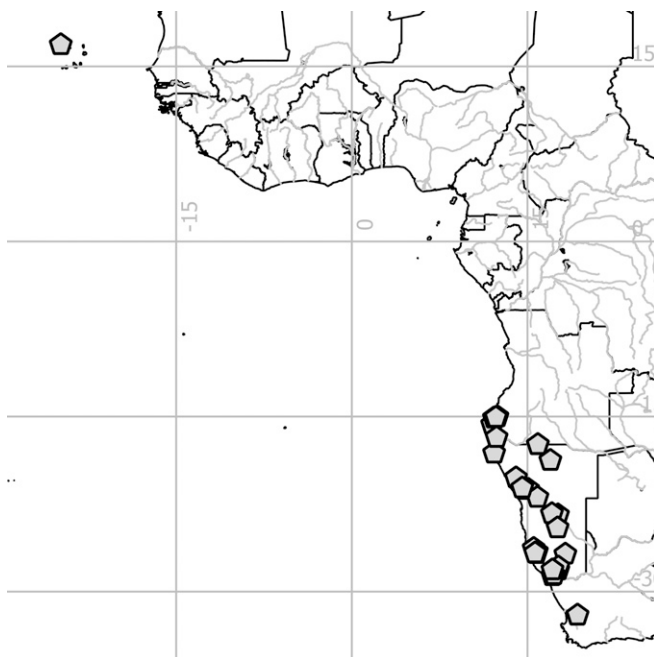


FIG. 12. Distribution of *Sesuvium sesuvioides*. The species is found in Namibia, South Africa and Cape Verde.

WAG); Gamkabrivier, Aussenkehr War 147 F, 28°23'S, 17°23'E, 03 Dec 1973, M. A. N. Müller 18 (PRE); area Garub-Aus, 24 Oct 1922, M. K. Dinter 4151 (B, C); ca. 20 km from |Ai-|Ais, on road to Fish River Canyon, 27°53'S, 17°38'E, 30 Jul 1986, H. Joffe 86 (PRE); Southern Namib, Diamonds Area No. 1, Klinghardt Mountain, amongst arid scrub, steep slope, 27°08'S, 15°53'E, 20 Apr 1988, C. J. Ward & M. K. Seely 10222 (PRE); Rosh Pinah, Lorelei Mine, 27°53'S, 16°53'E, 08 Aug 1978, D. S. Hardy & S. Venter 5001 (PRE); |Ai-|Ais Nature Reserve, wash N of Stromberg, along Jan Haak Road, 28°09'45"S, 17°13'02"E, 18 Feb 1999, L. W. Powrie LWP 1147 (PRE); Altdorn War 3 Farm, 27°53'S, 17°38'E, 17 Jun 1976, J. W. H. Giess & M. A. N. Müller 14452 (PRE); Koppie SW of Rotkop Station, next to power-line track, 26°38'S, 16°23'E, 23 Oct 1987, H. H. Kolberg & G. L. Maggs 209 (PRE); Orange River bank, Oetha Diamond Mine, 28°08'S, 16°53'E, 28 Oct 1974, R. Watmough 886 (PRE). Khomas Region: 5.6 km N of Ohopoho, 29 Mar 1957, B. De Winter & O. A. Leistner 5258 (PRE, Z); 37 km W of Orowanjai on road to Orupembe, 05 Feb 1975, B. De Winter & O. A. Leistner 5651 (B, PRE); Sarasas, 10 Jun 1951, H. Hall 404 (NBG). Kunene Region: Kaokoveld, Kaoko Otavi, 18°23'S, 13°38'E, 04 Jun 1951, H. Hall 363 (PRE); Kaokoveld, Outjo Distr., Hazeldene Farm Karos Block, 18 Mar 1957, B. de Winter & O. A. Leistner 5111 (PRE); Damaraland, Jan 1907, E. E. Galpin & H. H. W. Pearson 7676 (PRE); 10 km NW of Cape Fria, 18°08'S, 11°53'E, 17 Apr 1985, Moss & Jacobsen K301 (PRE); Kaokoveld, Skeleton Coast, Angra Fria, 17°30'S, 11°07'E, 20 Jul 1969, H. G. Goym 68 (PRE); Damaraland, Jan 1907, E. E. Galpin & H. H. W. Pearson 7592 (PRE); Namib Desert Park, Hotsas, 23°08'S, 15°38'E, 28 Apr 1976, M. A. N. Müller 227 (PRE). Ohangwena Region: Omundjulu, near a kraal NW of Engela, 07 Mar 1973, R. J. Rodin 9032 (MO, PRE); Omundjulu, 1 km S of Oshikango, 17°24'45.5220"S, 15°53'07.0296"E, 04 Apr 1973, R. J. Rodin 9208 (MO, PRE); Omundjulu, a bit W of Oshikango, 17°23'27.6828"S, 15°52'58.3788"E, 04 May 1973, R. J. Rodin 9392 (MO, PRE). Oshana Region: Etosha Pan National Park, Nuamsees Waterval, 19°08'S, 16°38'E, 08 Mar 1976, J. W. H. Giess & B. Loutit 14178 (PRE). Otjozondjupa Region: Klein Dobe Waterhole, 31 Dec 1984, C. J. H. Hines 250 (BOL); Grootfontein, 4.8 km N of Namutoni, Etosha Pan, ca. 18°45'18.6696"S, 16°57'06.2388"E; 29 Mar 1955, B. de Winter 2986 (NBG, PRE).

SOUTH AFRICA. Northern Cape: Richtersveld, Namaqualand, Orange River valley, 25 Aug 1982, G. Williamson 3139 (BOL), Little Namaqualand, Anis, ca. 32°01'02.6112"S, 19°15'36.6660"E, Sep–Oct 1926, N. S. Pillans 50/3 (BOL), Little Namaqualand, river bed N of Anis, Sep–Oct 1926, N. S. Pillans 53/7 (BOL); island in the Orange River across from Richtersberg, 28°14'39.0912"S, 17°12'35.9136"E, 16 Apr 1986, Van Jaarsveld & Jacobs 8493 (NBG); Richtersveld, Modderdrift Hellskloof South, 28°47'36.7368"S, 17°29'10.0140"E, 11 Sep 1998, P. Chesselet 377 (NBG), Richtersveld, Tallas Mountains, 02 Oct 1930, H. Herre 11882 (NBG); Orange River, de Hoop, banks of Orange River, around old mining camp amongst rocks, 28°08'S, 17°08'E, 08 Jul 1987, D. J. McDonald 1324 (PRE); Kalahari, 49 km from Bloemfontein Farm on road to Noenieput, 27°33'31"S, 20°10'53"E, 12 Aug 2000, J. J. Meyer 2917 (PRE); Gannallon River, flats SE of Clarm Peak, 28°23'S, 17°08'E, 29 Aug 1979, *Anonymus s. n.* (PRE); Namaqualand Distr., Richtersveld, Rooiberg Conservancy area ca. 30.6 km N of Eksteenfont, 28°32'43.58"S, 17°15'26.41"E, 09 Aug 2011, S. P. Bester 10683 (KSAN, PRE); Namaqualand, Richtersveld Nat. Park, Maerhoek, 28°08'S, 17°08'E, 30 Jul 1998, P. C. Zietsman 3646 (PRE); Vioolsdrift, just outside Vioolsdrif, 28°53'S, 17°38'E, 15 Aug 1967, H. P. van der Schijff 8209 (PRE).

SESUVIUM TRIANTHEMOIDES Correll in *Rhodora* 68: 422. 1966.—TYPE: U. S. A., Texas: Kenedy County, dunes, 11 Jul 1947, *Tharp* 47431 (holotype: TEX!)

Slender procumbent to ascending, annual herb; stems pale and thin (diam ~2.5 mm), roots relatively short; scattered large bladder cells on leaves and stems and fine white dots around the axils. Leaves oblanceolate, flat, lamina up to 20 mm long and 8 mm wide, with a distinct petiole, lateral flaps wide (~2 mm). Flowers sessile, about 6 mm long, one pair of bracts at base; inconspicuous tepal teeth compared to other species of the genus. Stamens five. Ovary with 2 carpels and 2 styles. Fruit large and tapered capsules with broad bases, often exceeding the length of the tepals; styles rarely still attached to the ripe capsule, often only two short tips remain. Seeds up to 1.5 mm long, reniform, with a slightly structured seed coat, dull black, brown or grey.

Distribution and Habitat—The species appears to be strictly endemic in Texas, U. S. A (Fig. 9). It grows on sandy soil, probably near rivers.

Vernacular Name—Texas sea purslane.

Representative specimens examined—U. S. A. Texas, Kenedy County: Dunes, 11 Jul 1947, *Tharp* 47431 (TEX); San Patricio County: 9.7 km from Sinton, sandy soil along Aransas River, 28 Jun 1954, *F. B. Jones* 964 (BRIT).

Notes—Only two specimens were seen, since no other material was available. It would be very desirable to increase the number of specimens in collections. There is a close resemblance between *S. trianthemoides* and *S. maritimum*, but due to distinctive morphological traits such as large and tapered capsules and the 2-carpelate ovary their status as separate species seems justified.

SESUVIUM VERRUCOSUM Raf., *New Fl.* [Rafinesque] 4, 16. 1836. FNA vol. 4. 2003.—TYPE: U. S. A., Salt River, Arkansas, *Nuttall s. n.* (neotype, P, P00680440 digital image!, designated here); *A. C. Sanders* 23186 (epitype, BRIT, designated here). In the description there is only the information that the material was sent to the author from Yazou and Salt River in Arkansas and the Chacta Country.

S. erectum Correll, *Rhodora* 68: 421. 1966.—TYPE: U. S. A., Texas: Kenedy County, 40 km S of Sarita along U. S. St. 77, 12 Jul 1957, *Correll & Johnston* 17868 (holotype: LL!)

Procumbent, perennial and often much-branched herb with a dense cover of bladder cells (except inner parts of flowers, lateral flaps, bracts); thick reddish taproot, often much longer than above ground parts of the plant; older plants lignify at the base; internodes (greyish-) green, up to 3 mm in diam. Leaves 5–30 mm long, oblong to oblanceolate, often with retuse apices, sometimes linear, petiole (3–6 mm), slightly greyish-green (due to bladder cells), mostly flat but succulent. Bracts in one pair, triangular, ca. 1 mm long. Flowers 7–10 mm long, sessile, bright pink or violet. Stamens numerous, often magenta with white pollen. Ovary with 3(–5) carpels and the same number of free styles. Fruit a beehive-shaped or ovoid capsule, usually many-seeded. Seeds around 1 mm long, rounded-reniform, black, lustrous, and slightly iridescent.

Distribution and Habitat—*S. verrucosum* is found in Mexico and the western states of the U. S. A. (AZ, CA, KS, MS, NM, NV, OK, OR, TX, UT), sometimes also in Argentina and Peru (Fig. 13). It may occur in further countries of Central and Southern America. Introduced as an ornamental in Saudi Arabia and also reported from Kish Island in Southern Iran (Fadaie et al. 2006). The species grows in saline areas (e.g. salt flats) and on sandy soil, often on gypsum or alkaline soil. It acts as a pioneer species on salt plains (Ungar 1968). It occurs mostly farther inland than *S. portulacastrum*.

Notes—A large number of flowers are often observed simultaneously on the same individual, apparently clustered on distal shoots. In the greenhouse, fruit set by self-pollination and vegetative propagation via suckers were observed. The species seems to show local phenotypes that differ more or less from one another in leaf shape and size but are nevertheless easily recognizable as *S. verrucosum*. Since the description of *S. sessile* does not explicitly reflect the current understanding of the name and the two species are morphologically almost identical (with only slight differences in size), we treat most material of *S. sessile* as *S. verrucosum* and

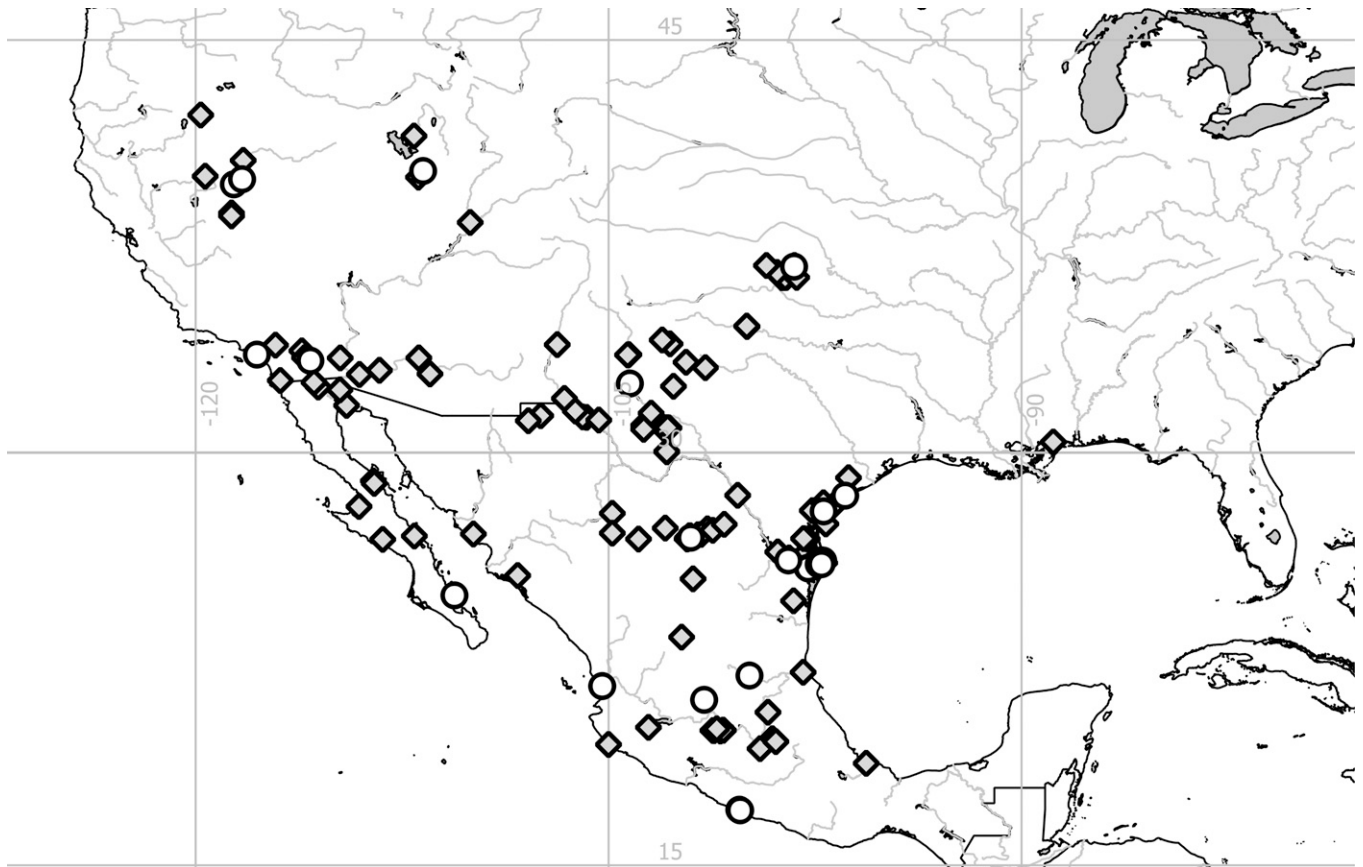


FIG. 13. Distribution of *Sesuvium verrucosum* in Mexico and the U. S. A. Grey diamonds depict the distribution of *S. verrucosum* and white circles show the distribution of specimens that formerly were identified as *S. sessile*.

put the name *S. sessile* into synonymy with *S. portulacastrum*. We designate an epitype for *S. verrucosum* to enable the inclusion of type material in phylogenetic studies.

Vernacular Names—Western sea purslane; Verrucose sea purslane.

Representative Specimens Examined—ARGENTINA. Buenos Aires: near Chascomus, ca. 35°32'27.6972"S, 57°54'04.9752"W, 17 Dec 1983, A. D. Zimmerman 2156 (TEX).

MEXICO. Baja California: El Tomatal (Miller's Landing), SW of Rosario, road from Hwy 1, ca. 28°30'N, 114°04'W, 23 Jul 1990, Thorne *et al.* 63890 (TEX); 27.4 km N of Villa Jesus Maria, near Miller's Landing, ca. 28°30'N, 114°04'W, 30 Mar 1977, G. L. Webster 21690 (MEXU); Isla Rasa, valley between sea and hills of Piedras, 02 Jul 1982, R. Medellín & C. Equihua 8 (MEXU); 0.8–3.2 km NE of village Los Angeles Bay, ca. 28°58'41.8728"N, 113°32'47.9832"W, 17 May 1959, I. L. & D. B. Wiggins 14865 (CAS, TEX); Laguna Salada, 28 km W of Mexicali, ca. 32°22'31.1592"N, 115°32'50.3988"W, 28 Aug 1982, H. Flores *et al.* 270 (MO); Bahía de Los Angeles, S coast, ca. 28°53'23.7228"N, 113°30'43.6140"W, 13 Mar 1992, P. Fritsch *et al.* 1315 (TEX); W coast of Isla San Francisco, 24°49'N, 110°36'W, 7 Dec 1959, I. L. Wiggins *et al.* 402 (CAS). Baja California Sur: Laguna San Ignacio, barrier dunes at W side of lagoon, ca. 26°51'04.8060"N, 113°12'18.0468"W, 02–03 Feb 1985, R. F. Thorne 58507 (MEXU); Arroya near Malarrimo Beach, Vizcaino peninsula, 04 Mar 1986, D. E. Breedlove 62540 (CAS); 119 km NW of Loreto (road Loreto-Santa Rosalía), ca. 26°58'30.8820"N, 112°03'23.7564"W, 20 Aug 1982, H. Flores *et al.* 240 (MO). Chihuahua: Reserva de la Biosfera de Mapimí, Laguna Palomas, 26°51'51.998"N, 103°54'50.975"W, 06 Jul 1997, A. García 2617 (MEXU); 104.6 km (linear distance) SW of Cd. Juarez; 10.4 km (road) N von Guzman, ca. 31°19'59.9988"N, 107°28'00.0012"W, 14 Sep 1974, J. Henrickson 14102 (TEX); Bajío El Gringo, S part of La Perla-Ojinaga Hwy, 24 km N from where it meets Camargo-Jimenez Hwy, ca. 27°48'N, 104°52'W, 29 Sep 1972, F. Chiang *et al.* 9586 (MO, TEX); 8 km NE of Ascencion, ca. 31°09'N, 107°55'W, 20 Aug 1972, F. Chiang *et al.* 8736 (MO). Coahuila: Dunas de Bilbao, 25°25'0.001"N, 101°55'59.987"W, 30 Sep 2004, M. A. Carranza & I. Ramirez C-4351 (MEXU); 6 km E of

Celemania (between Nadadores and Sacramento), ca. 27°2'0.042"N, 101°38'0.168"W, 25 May 1973, M. C. Johnston *et al.* 11229 A (LL); Escobedo, 40 km N of Monclova, Carr. 57, junction Estación Hermanas, ca. 27°14'07.8504"N, 101°24'46.6200"W, 04 May 1989, J. A. Villarreal & R. Vasquez 4845 (MEXU); Cuatrociénegas, Poza de la Becerra, ca. 26°52'59.9988"N, 102°07'00.0012"W, 26 Oct 1985, J. A. Villarreal *et al.* 3204 (MEXU, TEX); ca. 19.3 km E of Cuatro Ciénegas, ca. 27°01'16.3452"N, 101°45'44.0568"W, 20 May 1972, Powell & Turner 2279 (TEX); along road from St. Vincente SW (c. 11 km) towards southern end of Laguna de Jaco, 09 Sep 1940, I. M. Johnston & C. H. Muller 1095 (TEX); Bolson de Cuatro Cienegas, gypsum flat W of Pozo Becerra, ca. 26°59'00.0708"N, 102°02'00.3120"W, 23 Aug 1987, D. Bogler & T. Atkins 61 (TEX); 4.3 km W of Cuatro Cienegas along Anteojo canal, ca. 800 m E of Cienega Anteojo, ca. 26°58'57.8676"N, 102°04'19.6644"W, 25 Sep 1974, H. Henrickson 14279 (TEX); ca. 48 km (linear distance) S of W of Ocampo at NE edge of Laguna de Leche, ca. 3.2 km S of Ocampo-Sierra Mojada road, ca. 27°15'45.2340"N, 102°56'36.9996"W, 20 Sep 2004, Henrickson 24081 (TEX); 2 km S of Primero de Mayo on gypsum at road side W of Hwy 57, ca. 27°11'00.3012"N, 101°13'00.1128"W, 16 Oct 2001, Henrickson 22713 (TEX); 13 km SW of Cuatro Cienegas, 26°55'00.0012"N, 102°07'59.9988"W, 11 Jun 1972, F. Chiang *et al.* 7634 (MO); Ferrino's Laguna, Cuatro Cienegas Basin, 11 Jun 1968, D. J. Pinkava *et al.* 5415a (CAS); Laguna Salada, Cuatro Cienegas, ca. 26°54'52.2432"N, 102°00'57.7404"W, 11 Aug 1967, D. J. Pinkava *et al.* 3670 (CAS); Distrito Federal: Colonia Chinampas de Juarez in municipality Iztapalapa, S of Canal de San Juan y Col. Renovación, 19 Sep 1993, H. Vibrans 4583 (MEXU); empty estate in Escatepec, at road parallel to and E of Hwy 85, between Calle Cebbalcos, in housing estate, ca. 19°36'08.9568"N, 99°03'09.8424"W, 02 Aug 1979, M. A. Lane & J. E. Pryxell 2561 (TEX); Hidalgo: 5 km N of Ixmiquilpan, to Orizabita, 20°33'52.7508"N, 99°12'43.3296"W, 18 Nov 1981, R. Hernández M.6632 (MO). Guerrero: Isla Tejon, Laguna de Mitla, ca. 16°59'50.5212"N, 100°13'18.9120"W, 03 Mar 1985, L. L. Perez 297 (MEXU); NW of Isla Magueyes, Laguna de Mitla, 05 Jul 1985, L. L. Perez 427 (MEXU); Boca de Mitla, Laguna de Mitla, mun. Coyuca de Benitez, ca. 17°01'10.8912"N, 100°15'07.0596"W, 07 Jul 1985, L. L. Perez 500 (MEXU). Jalisco: 3 km W of Atoyac, ca. 20°00'55.4832"N, 103°33'07.5888"W, 05 Dec 1993, M. Chazáro

B. & R. Acevedo R. 7223 (MEXU); Laguneta del Río Chamela, 50 m from sea, 03 Aug 1979, M. Gonzáles G. 176 (MEXU); México: Carr. México-Nuevo Laredo # 85, 24 km from exit to Teotihuacán, 03 Jul 1992, E. Huerta 4 (B); 5 km W of Chaping, Lago de Texcoco, ca. 19°29'50.4276"N, 98°55'34.3920"W, 25 Apr 1980, A. Hernández R. 670 (TEX); Michoacán: ca. 2 km from Jéruco, road to Hundacareo, Cuitzeo, 27 Aug 2005, E. Carranza & I. Silva 7049 (MEXU); S of Lago Cuitzeo, near bridge Morelia-Cuitzeo, 14 Apr 2000, S. Zamudio & S. Gonzáles 11365 (MEXU); San Agustín del pulque, N shore of Lago de Cuitzeo, 19°57'15.0012"N, 101°04'23.9988"W, 01 Nov 1986, J. Rojas M. 221 (MEXU, MO).

An extended list of examined specimens for *S. verrucosum* can be found in the online Appendix S1.

TAXA INSUFFICIENTLY KNOWN—

Psammanthe marina Hance ex Walp. Ann. Bot. Syst. (Walpers) 2: 660. 1852.—TYPE: CHINA. Prata Islands [Dongsha Atoll], 20°42'53"N, 116°44'55"E. *Hance?* Based on the description, this name is most likely a synonym of *S. portulacastrum*.

Sesuvium acutifolium Miq., Hoev. & De vriese, Tijdschr. [Tijdschrift voor natuurlijke Geschiedenis en Physiologie] 10: 75–76. 1843.—TYPE: SURINAME, *Focke s. n.* (herbarium not known). We believe this name is a synonym of *S. portulacastrum* based on the description.

Sesuvium eastwoodianum J. T. Howell, Leafl. W. Bot. 10 (16): 352. 1966.—TYPE: ECUADOR. Galapagos Islands: on low sandy islet off southeast of North Seymour Island. 12 Jun 1932. *T. Crocker s. n.* (holotype: CAS, No. 207,606 digital image!).

Note—Hartmann (2001b) notes that *S. eastwoodianum* differs in its markedly ornamented seeds from *S. edmonstonei* and *S. portulacastrum*, despite *S. eastwoodianum* being combined with *S. edmonstonei* in Flora of the Galapagos. Additionally Howell described the characters of the species as intermediate between *S. portulacastrum* and *S. edmonstonei*.

Sesuvium ortegae Spreng., Nachr. i. Bot. Gart. Halle: 1. 1801.—TYPE: grown in the botanical garden in Halle, Germany. No further information given.

Sesuvium uvifolium Sessé & Moc., Fl. Mexic., ed. 2: 126. 1894.—TYPE: MEXICO. Tagarnana ? No specimen indicated. The description suggests it to be a synonym of *S. portulacastrum*.

Trianthema americanum [*americana*] Gillies ex Arn., Edinburgh J. Nat. Geogr. Sci. 3: 354. 1831.—TYPE: ARGENTINA. Laguna del Arbolito on the western side of Rio del Saladillo. *Gillies s. n.?* (?). A potential holo- or isotype is located in K, with a label stating: "*Trianthema americana*. Pampas of Buenos Ayres Gillies. Lindley 1831". The collector corresponds to the description, and the year is the same as when the name was published. Based on the description (and the material in K) we believe this to be a synonym of *S. portulacastrum*. Furthermore, Arnott states the possibility that it is a variety of *Trianthema polyandra* Blum., which in turn is also a synonym of *S. portulacastrum*.

EXCLUDED TAXA—

Diplochonium hochstetteri Stocks ex Aitch. Cat. Pl. Punjab Sindh: 66. 1869.—TYPE: PAKISTAN. Sindh, J. E. Stocks, no further information given. Note: Although material stored under this name often belongs to *S. hydaspicum*, *D. hochstetteri* is also considered as synonym of *Corbichonia*

decumbens (Forssk.) Exell in the Lophiocarpaceae (The Plant List 2013). Since information about the actual type material is lacking, we exclude this name from all considerations.

Sesuvium quadrifidum F. Muell., Rep. Pl. Babbage's Exped.: 9–10. 1858.—TYPE: AUSTRALIA. Stuart's Creek. = *Gummiopsis quadrifida* (F. Muell.) Pax in Nat. Pflanzenfam. 3 (1b): 44. 1889.

Supplemental Material—Extended lists of examined specimens of *S. portulacastrum* and *S. verrucosum* (Appendix S1) and a table summarizing the addition of names to the genera *Sesuvium* and *Cypselea* after their respective descriptions (Table S1) are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.tk922> (Bohley et al. 2017).

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