The Aizoaceae naturalized in the British Isles

C. D. PRESTON

Institute of Terrestrial Ecology, Monks Wood Experimental Station, Abbots Ripton, Huntingdon, PE17 2LS

and

P. D. SELL

Botany School, Downing Street, Cambridge, CB2 3EA

ABSTRACT

An introduction is given to the Aizoaceae with particular emphasis on the subfamilies Mesembryanthemoideae and Ruschioidae. It is followed by a detailed account of the complicated floral parts and fruits of the species of these groups. A conspectus of the subfamilies and genera naturalized in the British Isles is followed by a key to the species. Accounts of the nomenclature, typification, morphology, distribution, habitat and reproductive biology of Aptenia cordifolia (L.fil.) Schwantes, Ruschia caroli (L. Bolus) Schwantes, Lampranthus roseus (Willd.) Schwantes, L. falciformis (Haw.) N.E.Br., Ossularia deltoidea (L.) Schwantes, Disphyma crassifolium (L.) L. Bolus, Drosanthemum floribundum (Haw.) Schwantes, Erepsia heteropetala (Haw.) Schwantes, Carpobrotus edulis (L.) N.E.Br. var. edulis, var. rubescens Druce, var. chrysophthalmus C. D. Preston & P. D. Sell, var. nov., and C. glaucescens (Haw.) Schwantes, follow. An Appendix by R. D. 'Ons gives the chromosome numbers.

INTRODUCTION

The Aizoaceae are a large family, with their centre of distribution in South Africa (Rowley 1978). Two of its component subfamilies, the Mesembryanthemoideae and the Ruschioidae, are sometimes removed as a separate family, the Mesembryanthemaceae. All the species in these two subfamilies were once included in the genus Mesembryanthemum L., but have since been divided into as many as 125 genera which contain about 2000 species (Rowley 1978).

South African Aizoaceae have long been cultivated in British gardens. A detailed account of the botanical exploration of South Africa is given by Gunn & Codd (1981). Although Bartolomeu Dias rounded the Cape of Good Hope in 1488, it was not until 1605 that any plant specimen from South Africa was described in print. Live bulbs were collected from the beginning of the 17th century and increasing numbers of plants from South Africa, including some 'mesembs', were introduced by the Dutch in the second half of that century. James Petiver received live material of the Aizoaceae from the Temple Garden, London, in 1706 (Edwards 1968). The collection grown by James Sherard at Eltham in Kent was illustrated by Dillenius (1732) in the important Hortus Elthamensis, which provides an almost complete coverage of the 'mesembs' then known in cultivation (Gunn & Codd 1981). There is at Oxford, in the library of the Department of Plant Sciences, a copy coloured by Dillenius himself. We have also seen a similarly coloured copy in a private collection.

Two botanists are pre-eminent in the interpretation of early 'mesemb' names. Adrian Hardy Haworth (b. 1768, d. 1833) described 206 species in his Synopsis (Haworth 1812). His descriptions were based on living plants, including many grown by himself as well as some in the collections at Kew. His herbarium was bought by H. B. Fielding, who threw most of the specimens away. Fortunately, a great many coloured drawings were made by George Bond and Thomas Duncannon between 1822 and 1835 of the plants Haworth had seen at Kew (Brown 1920), and these are available for selection as neotypes. In the facsimile of all Haworth's works on succulent plants, Stearn (1965) has written an informative introduction.
Prince Salm-Dyck (b. 1773, d. 1861) was an enthusiastic cultivator and student of succulent plants. His most important work is the *Monographia Generum Aloes et Mesembryanthemi*, published in seven parts (Salm-Dyck 1836–1863). It is a collection of lithographed and partly hand-coloured plates accompanied by Latin descriptions. A detailed account of the work has been published by Stearn (1938).

A number of 'mesembs' have become naturalized by the sea in the British Isles, and these are described in this paper. We regard species as naturalized if they are established in semi-natural vegetation. It is not necessary that a species should reproduce by seed to satisfy this criterion, although some of the naturalized species certainly do so. The extent to which the individual species are naturalized is discussed in the accounts that follow.

The localities where 'mesembs' are naturalized are all coastal. The species' tolerance of salt-laden gale-force winds enables them to grow very close to the sea, where the microclimate is most equable. In such positions naturalized colonies often escape low winter temperatures which severely damage or kill plants of the same species growing in gardens a short distance inland. Even if extensively damaged, colonies can regrow from vegetative parts or seed (Preston 1988).

Lousley (1973) regarded the naturalized Aizoaceae as "plants dependent on a run of mild winters and deliberate planting". We consider that this underestimates their ability to persist and spread. *Carpobrotus edulis*, in particular, is now a characteristic feature of the seaside landscape in many parts of south-western England. Betjeman (1945) mentions it growing with stonecrop on a Cornish cliff in his poem *Sunday Afternoon Service in St Enodoc Church, Cornwall* and Rowse (1941), describing Henry VIII's castle at St Mawes, says "it remains unchanged, the walls of its three-lobed batteries but weathered to a silver grey, the grass slopes covered with mesembryanthemum and rock-plants down to the edge of the water". Flowers of *Carpobrotus* and plants of *Lampranthus* are featured on picture postcards and sometimes protected by wild-flower lovers. This protection is unnecessary: *Carpobrotus* competes so effectively with native species that its continued spread is a source of anxiety to conservationists (Hopkins 1979; Frost 1987).

**TAXONOMY OF THE AIZOACEAE**

Commenting on attempts to identify one naturalized species, J. P. M. Brenan (*in litt.* to L. J. Margetts 1970) wrote that "one would have to be a magician to give it a name... the whole family is in a state of chaos". Four factors have contributed to this unhappy state of affairs:

i. Many of the species were originally described from material cultivated in European gardens. The precise origin of the cultivated stock was not known, so the names are difficult to relate to plants in their native habitats. Often type specimens were not preserved, or have not survived.

ii. Herbarium specimens of these succulent plants are difficult to identify, as leaf shape and flower colour are destroyed when the plant is pressed and dried. Pressed specimens can often be identified only to generic level. Even if type specimens exist they are often of little use. Good coloured illustrations, or photographs, are more useful than specimens. For this reason we have selected illustrations as lectotypes when they are available.

Recently Fuller & Barbe (1981) have described a method of pressing succulent plants, including *Carpobrotus edulis*, using a microwave oven. We have not experimented with this technique.

iii. Although many enthusiasts have studied the 'mesembs', their efforts have been devoted to the description of more and more new species. H. M. L. Bolus alone described 1445 species but "she did not regard all these as true new species" (Herre 1971). Descriptions of new taxa have rarely been accompanied by a key or a conspectus to the species in the genus, and few generic monographs are available.

iv. Very little is published about the ecology, reproductive biology and cytology of 'mesemb' species. Within genera or closely related groups of species the taxa seem to be either geographically or ecologically isolated, and it is not known if they are interfertile. In the absence of this information, it is impossible to interpret the described taxa biologically.

Lousley's (1971, 1973) studies of the Aizoaceae naturalized in the Isles of Scilly are the most valuable published accounts of the British species. McClintock's (1975) and le Sueur's (1984) studies...
METHODS OF STUDY

Initially we collected living material of the Aizoaceae naturalized in the British Isles and grew this in a greenhouse at Cambridge University Botanic Garden. Descriptions were first prepared from these cultivated plants, then compared in the field with wild populations. It was necessary to modify the descriptions of cultivated material both because plants grown in the greenhouse lacked the vigour of plants in the wild, and because of the greater environmental variation present in wild populations. The cultivated plant material was used to count the chromosome numbers of the naturalized species (see Appendix).

Some herbarium specimens, and a larger number of colour photographs, have been deposited in CGE. Full details of all records available to us have been deposited at the Biological Records Centre, Monks Wood Experimental Station.

We are conscious that our work is only a preliminary contribution to the elucidation of the taxonomy and nomenclature of the species naturalized in Britain. In particular, further work on the British species of Lampranthus is needed. However, we believe that progress is more likely to result from studies of the taxa in their native habitats rather than from more intensive studies of the species in Britain.

MORPHOLOGY OF FLOWERS AND FRUIT

Some authors treat the outer perianth segments as sepals, while others consider them to be the divided part of the calyx. The latter view is taken here and they are regarded as calyx lobes. They are very unequal in size and some of them usually have wide scarious flaps which cover the petals in bud. The petals and stamens are usually situated between the point where the segments join the remainder of the calyx and the top of the half-inferior ovary. The whole arrangement is similar to the hypanthium in the Rosaceae.

The inner perianth segments are usually considered to be derived from stamens. They are here called petals and include those inner ones that are often narrower and smaller than the outer. Only when they are in the form of stamens, but without anthers, are they called staminodes. There is sometimes a graded sequence between stamens and petals, both in form and colour. In Apenia cordifolia the petals are united at the base to form a short corolla tube; the stamens arise from this tube. The nectaries are sunk in a hollow around the rim of the ovary. In the other species naturalized in Britain the petals are free, and the nectaries form a slight crest around the rim of the ovary.

The capsules of the Aizoaceae are extremely complicated in structure. An illustrated survey is given by Schwantes (1957). In most species growing in the British Isles the capsule is hygrochastic, i.e. it opens when it becomes moist and closes when it dries out again. In the simplest case (Apenia) the capsule has axile placentation with open loculi, so that raindrops can easily wash out the seeds. In the tribe Ruschieae the capsules are much more complex and the placentation is parietal. There are five loculi and partition walls. The lid of the capsule is opened and closed by the expansion of the epidermal lining of the loculus when it becomes wet. The cells of expanding tissue have a rhomboidal shape, the inner shorter axis elongating considerably while the outer longer axis remains almost unchanged. The result is a pronounced elongation of the expanding tissue in one direction while the remaining tissues of the capsule do not change appreciably, thus causing the valves to unfold outwards. In some species a membrane covers the loculi so that the seeds are not exposed when the capsules open. The membranes are elastic and are never found in the middle of the loculus. The division is always brought about by the valve wings which are formed by the splitting of the false septum which projects into the loculus from above. The valve wings always remain firmly attached to the valve. When the capsule opens for the first time they act like the ripcords of a parachute and bring about the exact division of the parts of the covering membrane. The membrane never covers the loculus completely, as a portion of the endocarp on the roof of the
loculus is required for the formation of the expanding mechanism. The opening remaining is sometimes reduced to two minute openings by a swelling of the placenta (tubercle).

SYNOPSIS OF THE CLASSIFICATION OF THE BRITISH GENERA

In the synopsis below we follow the classification proposed by Schwantes (1971) for the Mesembryanthemaceae. Unless otherwise stated, the number of species per genus is taken from Herre (1971). Critical revision of the larger genera would almost certainly reduce the number of recognized species considerably.

SUBFAMILY MESEMBRYANTHEMOIDEAE
Nectaries sunken in a hollow. Placentation axile.

Tribe Apenieae
Petal soft, not rigid.


SUBFAMILY RUSCHIOIDEAE
Nectaries forming a slight crest round the rim of the ovary. Placentation parietal.

Tribe Ruschieae
Fruit a dry hygrochastic capsule with numerous seeds.


Tribe Carpobroteae
Fruit fleshy, indehiscent, the outer wall becoming tough and leathery, the seeds embedded in mucilage.


KEY TO SPECIES NATURALIZED IN THE BRITISH ISLES

Leaves flat, ovate; petals connate at base, forming a short tube; calyx lobes and stigmas 4.................................................................................................................. 1. _Aptenia cordifolia_
Leaves triangular, cylindrical or rarely narrowly obovoid in section; petals free; calyx lobes (4-)5-6; stigmas 5 or 10-14 .............................................................................................................. 2
ACCOUNT OF SPECIES

1. Aptenia cordifolia (L. fil.) Schwantes in Gartenflora 77: 69 (Feb. 1928); N.E.Br. in J. Bot., Lond. 66: 139 (May 1928).


Vernacular names: Heart-leaf Ice-plant, Heart-leaf Mesembryanthemum.


Description: Rather succulent, short-lived perennial, but not infrequently behaving as an annual. Stems up to 60 cm, pale yellowish-green, sometimes tinted brownish and angled, prostrate, much-branched, covered with dense greyish papillae; internodes 1-2-9 cm. Leaves 10-35 x 10-30 mm,
green, decussate, flat, more or less ovate, obtuse to subacute at apex, entire, more or less cordate, truncate or cuneate at base, covered with greyish papillae; petiole up to 15 mm. Flowers solitary, 5–16 mm in diameter, terminal at the end of branches or axillary; peduncles up to 13 mm, sometimes 5-angled. Calyx green, covered with greyish papillae; lobes 4, the 2 outer 10–15 × 4–13 mm, ovate to narrowly ovate, subobtuse to acute at apex, slightly to distinctly keeled and curved outwards, entire, the inner 5–10 × 2–6 mm, lanceolate or linear-lanceolate, obtuse to acute at apex, entire, curved outwards. Petals numerous, 3–7 mm, reddish-pink, linear or linear-oblanceolate, obtuse at apex, united at the base into a short tube. Stamens numerous, arising from the corolla tube in a mass; filaments 2–3 mm, whitish, glabrous; anthers cream. Staminodes numerous, 2–3 mm, whitish, forming a ring between the stamens and the corolla tube. Stigmas 4, greenish, small, sessile. Nectaries sunken in a hollow. Capsule 12–15 × 8–10 mm, green, 4-locular, obovoid, valves broader than long, with the apex so abruptly thickened that the basal termination of the thickening is quite vertical, middle of inner surface of the 4 valves with a bright yellow keel reaching from the central column to the end of the flat part, each keel consisting of 2 parallel ridges, without marginal wings or flaps, with 4 narrow strips arranged like a star between the central column and the point of origin of keels; loculi roofs and tubercle absent; placentation axile. Seeds c. 40, 1.0–1.2 × 1.0–1.2 mm, dark reddish-brown, subrotund or broadly ovate, compressed, tuberculate, with funicles up to 1 mm. 2n = 18.

Nomenclature and typification: There are no specimens in the Linnaean herbarium (LINN) and no additional references in the protologue. The name has always been applied to the same taxon and the Salm-Dyck illustration is chosen here as the neotype, and reproduced as Fig. 1.

Taxonomy and variation: Le Sueur (1984) has noted that in Jersey a single plant at Grouville differed from a large population at St Brelade in colour, leaf shape and flower size. Otherwise little variation is recorded in naturalized populations except in plant size. A variegated form is sometimes grown in gardens.

Reproductive biology: Flowers from May to August. Reproduces by seed. Poorly grown plants are said to behave as annuals, dying after they have produced seed, but we have no observations on the reproductive biology of the species in the British Isles. Some, but not all, populations in Jersey failed to survive the severe 1962–63 winter (le Sueur 1984).

Distribution and habitat: Naturalized on banks and stone walls on Bryher, St Martin’s and St Mary’s, Isles of Scilly, and on Guernsey and Jersey. A large population in Jersey is naturalized under coniferous trees. Recorded as a casual on rubbish tips in W. Kent and Herts.; it perhaps occurs elsewhere in such localities. According to Higgins (1956), Apenia was first introduced into British gardens in 1774. It was recorded in Guernsey in 1928, but there were no subsequent records until naturalized populations were discovered in Jersey in the early 1950s and on St Mary’s, Isles of Scilly, in 1956. Although it is thoroughly established in some localities, Apenia has not invaded seminatural habitats to the same extent that Carpobrotus and Disphyma have done. It is a native of the eastern coastal districts of Cape Province, South Africa (Herre & Friedrich 1959).


Description: Low, spreading shrub, up to 60 cm. Stems up to 60 cm, much branched from the base upwards, greyish-brown or reddish-brown with darker brown elliptical spots, straight and ascending or decumbent, irregularly striate or ridged, glabrous; internodes 1–3 cm. Leaves 15–70 × 2–5 mm, rather unequal in size, more or less erect, bluish-green, faintly pink at apex, loosely decussate with each pair with a connate base enclosed in a brown sheath, linear in outline, 3-angled, sometimes recurved, obtuse or subacute at apex, sessile, covered with green spots and smaller white dots when young, becoming irregularly muriform when mature. Flowers 1–4, 10–30 mm in diameter, terminal
Figure 1. *Aptenia cordifolia* (L.fil.) Schwantes, illustrated as *Mesembryanthemum cordifolium* in Salm-Dyck's *Monographia Generum Aloes et Mesembryanthemi* 61: fig. 1 (1842). The coloured plate is the neotype of *M. cordifolium* L. fil.
at the end of branches; peduncles 10–25 mm. Calyx pale green; lobes 5, 3-5-4-0 × 2-0-2-5 mm, triangular-ovate, 2 with a pale narrow margin and subacute at apex, 3 with a broad scarious flaps and a reddish subacute apex. Petals c. 30, 4-5-10-0 × 1-2 mm, free, purplish, with a darker central longitudinal line and slightly whitish at base, narrowly oblongate, obtuse and entire at apex. Stamens numerous, some outer without anthers; filaments 3-3-5 mm, purplish with white bases, with numerous, pale, slightly clavate hairs at base; anthers yellow. Stigmas 5, green, narrowly triangular-ovoid with a long acute apex and a few hairs near the base. Nectary glands united to form a crenulate ring round the ovary. Capsule not seen in British material, but said to have much diverging valve keels; loculi roofs present with a large tubercle; placentation parietal. We cannot trace a description of the seeds. \(2n = 18\).

This description is based solely on plants from a naturalized population cultivated in Cambridge. We have not had an opportunity to compare it with plants in the field.

**Taxonomy and variation:** Little variation has been recorded in our naturalized populations, but in South Africa the species seems to produce much larger leaves than in Britain.

**Reproductive biology:** Flowers in April and May. We have no observations on the reproductive biology of the species in the British Isles.

**Distribution and habitat:** Only recorded from the Isles of Scilly, where it is naturalized on walls on St Mary's and Tresco. The only record from semi-natural habitats is a note by Lousley on a specimen in RNG that *Ruschia* occurs "in 'wild' places or rocks" at Carn Friars, St Mary's, Isles of Scilly. Lousley (1971) says that there is a specimen in K sent from Tresco Abbey in 1897, nearly 30 years before the species was described. The first collection from a naturalized population was made in 1959. *Ruschia caroli* is a native of Cape Province, South Africa.


**Vernacular name:** Rosy Dew-plant.


**Description:** Low evergreen shrub. Stems up to 20 cm, decumbent to erect, 4-angled, glabrous, brownish or purplish, much branched, the branches short, ascending or patent; internodes 0-3-3-5 cm, sometimes with narrow wings on the angles. Leaves 10–16 × 2–2.5 mm, decussate just under the flowers, becoming more numerous and dense lower down the fertile stems and branches and on the sterile stems and axillary shoots, the terminal pairs on axillary sterile shoots often pressed together giving a flattened appearance, dark glaucous green, mostly triangular in section with fairly acute angles, more or less acute at apex and sometimes red-tipped, rounded at the sessile base with each pair touching in their upper part and together encircling the stem, covered with dense pellucid dots. Flowers 1–3 together, terminal or at the end of lateral shoots, 20–50 mm in diameter; peduncles 12-20 mm. Calyx with dense pellucid dots; lobes 5, all red-tipped; 2 of the lobes 5–7 mm, triangular-lanceolate, acute at apex, green (darker towards apex) with a scarious margin up to 0.5 mm wide in the lower half; remaining 3 lobes with a green part similar to the other 2 but with a deep rusty orange, subapical, often asymmetrical appendage up to 3 mm wide on the inner side and extending to the base where it is joined to that of the next lobe, the true apex of the lobe reflexed. Petals numerous (over 100), very variable in length, 6.5–18.0 × 0.4–2.0 mm, free, shining light purple or salmon pink sometimes on same plant, inner short and narrowly linear becoming gradually larger to outer which are narrowly linear-oblongate, obtuse at apex, broader ones slightly emarginate, with pale lines on back. Stamens numerous (100–150), more or less as long as stigmas; filaments 3–4 mm, pale greenish-yellow; anthers yellow. Stigmas 5, greenish, outline more or less triangular and formed from 3 plumose rays. Nectary glands united to form a crenulate ring
round the ovary. Capsule 6–7 × 7–8 mm, 5-locular, each valve with diverging keels and a membranous wing; loculi roofs present, without a tubercle; placentation parietal. Seeds numerous, 1·0 × 1·2 mm, pale brown, obovoid, with shallow, obtuse tubercles. 2n = 36.

The above description is based on material cultivated at Cambridge from Bec du Nez, Guernsey, and Lizard Head.

**Taxonomy and variation:** We find the taxonomy of *Lampranthus* difficult and unsatisfactory. The two species accepted here looked quite different when grown side by side in the Cambridge Botanic Garden, but their differences were very difficult to put into words. In the wild differences tend to be masked by phenotypic variation. Thus the plant of *L. roseus* illustrated by Bichard & McClintock (1975) seems to have the habit and leaves of *L. falciformis*. *L. roseus* shows considerable variation in flower colour, purple and pink flowers occasionally occurring on the same plant.

**Reproductive biology:** Most *Lampranthus* species are thought to be self-sterile. *L. roseus* flowers from late May to July. Seedlings have been seen at Portelet Bay, Jersey, at Beaucette and Bec du Nez, Guernsey, and at Poldhu Cove. Some plants in the Lizard Point population were killed by frost in the 1978–9 winter and all *Lampranthus* plants in Jersey were killed in the 1962–3 winter, but reappeared from seed. Seed collected at Lizard Point, Cornwall and Bec du Nez, Guernsey germinated freely.

**Distribution and habitat:** Naturalized on sea cliffs, coastal rocks and walls in several localities in Guernsey and also collected from Alderney, Herm and Sark. In W. Cornwall naturalized on cliffs at Lizard Point and Poldhu Cove. A *Lampranthus* naturalized on cliffs by Beau Port and on an artificial scree of stone blocks at Portelet Bay, Jersey, is probably also referable to this species. The earliest collection was made in Sark in 1924. Native of South Africa.


**Vernacular name:** Sickle-leaved Dew-plant.

**Illustrations:** Salm-Dyck, Monogr. Aloes Mesembr. 29: fig. 1 (1836), pro *Mesembryanthemum falciforme* (reproduced here as Fig. 2).

**Description:** Low evergreen shrub. Stems up to 80 cm, mostly spreading and prostrate, but a few erect, 4-angled, glabrous, greyish or brownish, much-branched, the branches short, ascending or patent; internodes 0·2–1·7 cm, sometimes with narrow wings on angles. Leaves 6–13 × 1·5–2·5 mm, decussate just under the flowers, becoming more numerous and dense lower down the fertile stems and branches and on the sterile stems and axillary shoots, the terminal pairs on the axillary shoots often pressed together giving a flattened appearance, pale bluish-green with thick waxy covering, half obovoid, flattened on one surface and rounded and keeled on the other making them more or less triangular in section, more or less acute and sometimes with a red dot at apex, semi-connate at the sessile base, covered with dense pellucid dots. Flowers 1–2 together, terminal or at the end of lateral shoots, 35–45 mm in diameter; peduncles 5–20 mm. Calyx with dense pellucid dots; lobes 5, all red-tipped; 2 of the lobes 5·0–10.5 mm, triangular-lanceolate, acute at apex, green with a scarious margin up to 0·5 mm wide in the lower half; remaining 3 lobes with a green part similar to the other 2, but with a subapical, often asymmetrical appendage up to 3 mm wide on the inner side and extending to the base where it is joined to that of the next lobe, the true apex of the lobes reflexed. Petals numerous, very variable in length, 6·5–21·0 × 0·4–2·5 mm, free, pale pink, the inner very pale, or purple, narrowly linear-oblanceolate, obtuse at apex, broader ones slightly emarginate, with pale lines on back. Stamens numerous, more or less as long as stigmas; filaments 3–4 mm, whitish, with a tuft of whitish hairs at base; anthers pale yellow. Stigmas 5, greenish, outline more or less triangular and
FIGURE 2. Lampranthus falciformis (Haw.) N.E.Br., illustrated as Mesembryanthemum falciforme in Salm-Dyck's Monographia Generum Aloes et Mesembryanthemi 29: fig. 1 (1836).
formed from 3 plumose rays. Nectary glands united to form a crenulate ring. Capsule 6–7 × 7–8 mm, 5-locular, each valve with diverging keels and a membranous wing. Seeds numerous, 1·0–1·2 mm, pale brown, obovoid, with shallow, obtuse tubercles.

The above description is based on plants cultivated at Cambridge from Pembrokeshire and St Mary’s, Isles of Scilly.

**Nomenclature and typification:** The obvious neotype is the coloured drawing at Kew made from plants on which Haworth worked.

**Taxonomy and variation:** The only variation noted is in flower colour which varies from pale pink to purple.

**Reproductive biology:** Most *Lampranthus* species are thought to be self-sterile. *L. falciformis* flowers from May to July. It is very susceptible to frosts and there may be little or no flowering after a bad winter, but some parts of the plant usually survive and soon regenerate vegetatively. At The Gann, Pembrokeshire, it normally regenerates abundantly from seed. It seems to be immune from grazing by cattle and rabbits (Davis 1978).

**Distribution and habitat:** Supposedly introduced into British gardens in 1805 (Higgins 1956). There are specimens in K from Tresco Abbey Gardens in the Isles of Scilly collected in 1895. It is now naturalized on St Mary’s, Tresco, St Martin’s, St Helen’s and Round Island in those islands, growing on coastal rocks, cliffs and stone walls near the sea in shallow soil on ledges and in crevices. Both St Helen’s (where it is particularly abundant) and Round Island are uninhabited and the *Lampranthus* was presumably carried there by sea birds. It was collected on Lundy (K) as naturalized in 1919 and 30 or more plants still occur on the almost perpendicular face of a natural rock outcrop of rhyolite. In the 1920s or early 1930s it was introduced from this quarry to Dale Point, 2 km south of The Gann, where a few plants were still present in 1978 (Davis 1978). Plants from Three Castle Head, W. Cork, and on sandy cliffs at Roches Point, E. Cork, are probably referable to this species. Native of South Africa.


*Mesembryanthemum deltoides* L., *Sp. PI.* 482 (1753). Described from Africa. **LECTOTYPE:** Dillenius, *Hort. Eltham.* 255, t. 195, fig. 246 (1732), pro *Mesembryanthemum deltoides*, & dorso, & lateribus muricatus, minus, in the copy in the Department of Plant Sciences, Oxford University, coloured by Dillenihs; designated here.


**Vernacular name:** Deltoid-leaved Dew-plant.


**Description:** Low, sprawling shrub. Stems up to 50 cm, ascending or decumbent, glabrous, when young bluish-green, heavily tinged reddish, soon becoming reddish- or orange-brown, older growth woody, terete or slightly angled, glabrous, with short, erect or patent branches; internodes 0·2–2·5 cm, often with narrow wings on the angles. Leaves 6–18 × 3–10 mm, unequal or more or less equal in size, pruinose with a pinkish-red apical point and apices of teeth, waxy, in decussate, clustered pairs with each pair slightly connate at base, smooth, 3-angled, widest towards the shortly acute apex, narrowed towards the sessile base, dentate-apiculate on the angles. Flowers 1–3 together, 12–18 mm in diameter, terminal at the ends of branches, almond-scented; peduncles 2–3 mm. Calyx yellowish-green; lobes 5, 3·0–3·5 × 2–3 mm, triangular-ovate, 2 with a pale, narrow margin and up to 4 pinkish-red points at the apex, 3 with a broad scarious flap and a subapical, pinkish-red tipped
point. Petals 40–50, 4–6 × 0.5–1.5 mm, free, purplish, paler towards the base, narrowly oblanceolate, obtuse and entire at apex. Stamens numerous, some outer without anthers; filaments 2–3 mm, white with rather pale simple eglandular hairs at base; anthers yellow. Stigmas 5, green, narrowly ovoid with a curved apex. Nectary glands forming a crenulate ring round the ovary but in 5 distinct groups, dark green. Capsule 6–7 × 5–6 mm, 5-locular, obovoid; each valve with expanding narrowly winged keels diverging from the base and half as long as the valves; loculi roofs present, without a tubercle; placentation parietal. Seeds 1.0–1.2 mm, nearly black, ovoid or pyriform with a nipple, minutely tuberculate, on a funicle up to 2 mm. 2n = 18.

The above description of flowers and fruit is based on plants from a naturalized population cultivated in Cambridge. We have not had an opportunity to compare it with plants in the field.

Nomenclature and typification: Mesembryanthemum deltoides was described by Linnaeus (1753) in Species Plantarum. His diagnosis Mesembryanthemum caulescens, foliis deltoidibus triquetris dentatis is taken from the Hortus Cliffortianus (Linnaeus 1738) without change. There are no specimens in the herbarium of the Hortus Cliffortianus (BM), nor in the Linnaean Herbarium in London (LINN). Two synonyms follow the diagnosis: Mesembr. deltoides & dorso & lateribus muricatis Dill. elth. 255. t. 195. f. 246 and Ficus aizoides africana erectafolio triangulari brevisculo, fimbriato, floribus roseis odoratis Yolk. hesp. 223. t. 224. f. 5. They are also cited in the Hortus Cliffortianus. Both illustrations are referable to the plant usually called Oscularia deltoides, as is a specimen in Dillenius’ herbarium (OXF). Glen (1986) cited the illustration in Hortus Elthamensis as the iconotype and the specimen at OXF as the typotype, but did not select either as the lectotype. More information can be obtained from the coloured illustration in Dillenius’ own copy of his work than from the shrunken herbarium specimen so we reflect it as the lectotype. An uncoloured version of this illustration, which is an excellent portrait of the plant, is reproduced here as Fig. 3.

Taxonomy and variation: British plants show little variation. Lousley (1971) questioned whether the allied Oscularia caulescens (Miller) Schwantes occurs as a naturalized species in the Isles of Scilly, but all the British plants seem to be O. deltoides. In fact, Glen (1986) considers that the three names published in the genus Oscularia belong to the same species. Glen (1980) also thinks that Oscularia and Lampranthus should be united and proposes that Lampranthus (1930) be conserved over Oscularia (1927) as it is a much larger genus. The Committee for Spermatophyta (Taxon 32: 282 (1983)) recommended the acceptance of this proposal. Despite the fact that Glen (1980) says that his monograph of Lampranthus is in press, it has not yet been published. He did not justify his transfer of Oscularia to Lampranthus (Glen 1986), but merely cited an unpublished thesis in support of this move. We are thus unable to assess his proposals and for the time being retain Oscularia as a separate genus.

Reproductive biology: Flowers in April. Oscularia is a sprawling shrub, which can spread to cover large areas of walls. Seedlings have been observed by G. D. Rowley (in litt. 1988) on walls on Tresco, Isles of Scilly, and by J. R. Palmer on a wall in Guernsey (D. McClintock in litt. 1987).

Distribution and habitat: Naturalized in the Isles of Scilly on St Martin’s, St Mary’s and Tresco. It is cultivated but not naturalized in the Channel Islands. It was introduced into British gardens before 1732, but not noted as a naturalized plant until Lousley collected it in Tresco in 1953. When Lousley (1971) compiled his Flora, it was only known from walls. In 1982 it was found growing in small quantity on a coastal rock outcrop, associated with Sedum anglicum, where it was still present in 1987. It will be interesting to see if it continues to spread into semi-natural habitats. It is a native of the south-western part of Cape Province, South Africa (Herre 1971).

Figure 3. Oedolania dolotoides (L.) Schwantes, illustrated as Macrobrachium dolotoides, & dorso, & lateribus muricatus, minus in Hortus Elischensuis, 235. 195, fig. 246. (Dillenius 1782). The illustration coloured by Dillenius is the lectotype of Macrobrachium dolotoides.
flore purpureo, in the copy in the Department of Plant Sciences, Oxford University, coloured by Dillenius; designated here.

Vernacular name: Purple Dew-plant

Illustrations: Salm-Dyck, Monogr. Aloes Mesembr. 18: fig. 3 (1836), pro Mesembryanthemum crassifolium; Lousley, Fl. Scilly 217, fig. 10 (1971).

Description: Succulent shrub. Stems up to 1 m, trailing or hanging, often rooting at the nodes, glabrous, yellowish-green, tinted reddish or brownish to pale brown, rather woody especially at the base; internodes 1.5–4.0 cm. Leaves in groups of 3–10, 12–42 × 3–9 mm, translucent yellowish-green, faintly or heavily tinted pinkish, or reddish, usually blotched red, narrowly linear-oblong to linear-lanceolate in outline, triangular in section with obscure angles, rounded to a minute point at apex, sessile, when in opposite pairs slightly connate at base, with a row of almost flat papillae on the angles and covered with small pellucid dots. Flowers solitary, 30–50 mm in diameter, axillary; peduncles 4–40 mm. Calyx pale yellowish-green, sometimes tinted reddish at base of lobes, covered with small pellucid dots; lobes 5, the 2 longest 8–15 × 4–7 mm, linear or oblong, subacute at apex, the 3 shortest 6.5–10.5 × 4.0–5.5 mm, shortly oblong, obtuse at apex, with a scarious margin (except at apex) up to 5 mm wide. Petals numerous (c. 50–60), 15–24 × 1–2 mm, free, on inside purple with white bases, on outside white at base and along central line with purple margins, narrowly linear-oblongate, obtuse at apex. Stamens numerous, longer than the styles; filaments 3–10 mm, white, with a tuft of white simple eglandular hairs at base; anthers pale yellow. Stigmas 5, greenish, the basal 1–2 mm with a plumose inner surface, the apex with a long awn up to 4 mm. Nectary glands forming a crenulate ring round the ovary. Capsule c. 10 × 10 mm, 5-locular, pale yellowish, obovoid, each valve with a diverging keel with oblong wings; loculi roofs present, with a pale bifid tubercle; placentation parietal. Seeds 0.8–0.9 × 0.7–0.8 mm, chestnut brown, obovoid, surface irregular but smooth, on funicles c. 1 mm. 2n = 36.

Nomenclature and typification: Mesembryanthemum crassifolium was described by Linnaeus (1753) in Species Plantarum. His diagnosis Mesembryanthemum caule repente semi-cylindraceo, foliis semicylindricis laevibus connatis apice triquetris is taken direct from the Hortus Cliffortianus (Linnaeus 1738) except that the words semicylindraceo and repente are transposed. There are no specimens in the herbarium of the Hortus Cliffortianus (BM), nor in the Linnaean Herbarium in London (LINN). Two synonyms follow the diagnosis: Mesembr. crassifolium repens, flore purpureo Dill. elth. 266. t. 201. f. 257. and Ficoides africana reptans, folio triangulari, viridi, flore saturate purpureo. Bradl. Succ. 4. p. 16. t. 38. They are also cited in the Hortus Cliffortianus. Both illustrations are referable to the plant usually called Disphyma crassifolium. The illustration in the first of these, in the copy coloured by Dillenius, is designated as the lectotype. An uncoloured version is reproduced here as Fig. 4.

Taxonomy and variation: The living plants from the Isles of Scilly, mainland Cornwall, Sussex, Anglesey and Jersey that we have studied show little variation. The variation in peduncle length, from 4 to 40 mm, is phenotypic. Flowers on the exposed edge of a clone have short peduncles whereas those arising amongst the longer leaves in the centre of the same clone have longer peduncles.

Following Chinnock’s (1971) revision of the genus in Australasia five species were recognized, two native to South Africa and three to Australasia. More recent work suggests that these might all be conspecific (Venning 1984b). If this is so, however, some infraspecific taxa surely need to be recognized. All naturalized British material belongs to D. crassifolium (L.) L. Bolus sensu stricto. The population on Tresco, Isles of Scilly, reported as D. australe by McClintock (1964), is similar to the other populations we have examined. A hybrid between Disphyma australis (Aiton) J. M. Black and Carpobrotus edulis has been recorded from New Zealand (Chinnock 1972). Hybrids between Carpobrotus and Disphyma could occur in Britain where the two genera grow together, but have not yet been recorded.
Figure 4. *Disphyma crassifolium* (L.) Bolus, illustrated as *Mesembryanthemum* crassifolium repens, flore purpureo in *Hortus Elthamensis* 266, t. 201, fig. 287. (Dillenius 1732). The ill

 coloured by Dillenius is the

 *Mesembryanthemum* crassifolium repens, flore purpureo in *Hortus Elthamensis* 266, t. 201, fig. 287. (Dillenius 1732). The ill

 coloured by Dillenius is the

 *Mesembryanthemum* crassifolium L.
Reproductive biology: Flowers in May and June. Viable seed is produced in Britain but we have not seen seedlings in the wild. Colonies appear to have become established from planted material and from stems discarded from cliff-top gardens onto the cliffs below. In cultivation the species roots easily from cuttings. Effective reproduction of established colonies is mainly or entirely by vegetative spread.

*Disphyma* is less susceptible to frost damage than other naturalized 'mesembs'. In Jersey it survived the 1962–63 winter "with ease" (Le Sueur 1984). At Lizard Point, W. Cornwall, patches of *Carpobrotus edulis* were severely damaged by frost in the 1978–79 winter, but adjacent patches of *Disphyma* were unaffected. In the 1981–82 winter *Carpobrotus* at Cooden, E. Sussex, was damaged but *Disphyma* was not (K. E. Bull in litt. 1982).

Distribution and habitat: Naturalized on St Mary's and Tresco, Isles of Scilly, in W. Cornwall from Kenneggy east to Coverack on the south coast and at Constantine Bay on the north coast (Margetts & David 1981), and on Jersey, Channel Islands. It occurs on walls, sea cliffs, sand dunes and (in Jersey) on a bank under pine trees and in salt marsh conditions behind a sea wall. It is also naturalized on a sea cliff and coastal rocks north of Bwa Du on the west coast of Holy Island, Anglesey, and on a damp, sheltered cliff at Cooden, E. Sussex. It has been found elsewhere as a casual introduced with wool shoddy.

*Disphyma* was first recorded as a naturalized plant by J. E. Lousley in 1936 at New Grimsby, Tresco, when it was even then said to have been present for as long as anyone could remember (Lousley 1971) and where it still (1987) survives. It was noted on cliffs at the Lizard peninsula in 1951 and collected at Prussia Cove, Marazion, in 1954. *Disphyma* is now, except for *Carpobrotus edulis*, the most thoroughly naturalized of all 'mesembs' and in places (e.g. Praa Sands and Lizard Point, W. Cornwall) it occurs in abundance. It is not quite as effective a competitor as *C. edulis* and it tends to be naturalized in greatest quantity on steep cliffs or shallow soil, where the cover of other vegetation is reduced. *Disphyma crassifolium* sensu stricto is native to Cape Province, South Africa; other (possibly conspecific) taxa are native to Australia and New Zealand.


Vernacular name: Pale Dew-plant

Illustrations: Salm-Dyck, Monogr. Aloes Mesembr. 51: fig. 7 (1840), pro Mesembryanthemum floribundum.

Description: Low sprawling shrub forming dense prostrate to hanging patches. Stems up to 60 cm, trailing, pale brown, with numerous, very short and short, thick, pale, usually deflexed, broad-based simple eglandular hairs; branches usually weak, short and patent; internodes 0.5–3.0 cm. Leaves 6–30 × 1.0–3.5 mm, fleshy, decussate, dull pale to medium green, cylindrical or narrowly obovoid, deltate-ovate in section, sometimes curved, more or less obtuse at apex, sessile, covered with rounded, glass-like tubercles. Flowers 18–27 mm in diameter, solitary at the end of branches or axillary; peduncles 2.5–50.0 mm. Calyx hemispherical to slightly elongated, covered with glass-like tubercles; lobes 5 (–6), 3–6 mm, lanceolate or linear-lanceolate, obtuse at apex, 3(–4) with broad scarious flaps, 2 without flaps. Petals 25–35, 5–12 × 0.5–2.0 mm, free, shining white with a purple apex when young, becoming tinted lilac and finally lilac with age, narrowly linear-oblancoate, more or less obtuse at apex, the inner much shorter than outer and sometimes bifid at apex. Stamens 30–70, from a little shorter to a little longer than styles; filaments 4–5 mm, whitish, with a group of sub-basal pale simple eglandular hairs, becoming lilac after anthesis and curving outwards to expose the stigmas and nectary glands; anthers pale yellow. Stigmas 5, linear in outline, curved outwards,
NATURALIZED AIZOACEAE

brownish-yellow, sometimes tinged purplish at apex. Nectary glands forming a ring round the ovary but in disjunct groups. Capsule 2.5-5 × 4-6 mm, 5-locular, obovoid, each valve with 2 contiguous expanding keels on inner face, each keel with a membranous wing; loculi-roots present; placentation parietal. Seeds c. 1 × 0.5 mm, brown, with ribs and tubercles. 2n = 36.

**Nomenclature and typification:** The specimens in Haworth's herbarium have mostly been destroyed. There are no coloured drawings of *Mesembryanthemum floribundum* at Kew based on Haworth's material. The only illustration cited with the original diagnosis, *M. pilosum micans flore purpureo pallidiole* Dill. *Elth.* t. 214. f. 280, forms the basis for and is here designated as the lectotype of another species, *Mesembryanthemum torquatum* Haw.., *Rev. Pl. Succ.* 187 (1821). Thus there is no original type material of *M. floribundum*. Fortunately the description is a good one and is in accord with the plant we have described here. It is also in agreement with Salm-Dyck's illustration (reproduced here as Fig. 5) which we designate as the neotype.

*Mesembryanthemum candens* Haw. was described from vegetative material. There is a coloured drawing of such a specimen at Kew, which does not in our opinion differ from *M. floribundum*, and which we designate as the neotype. Another drawing at Kew shows a single pink flower which, although not certainly the same as the vegetative plant, can be used as a guide, as it was probably made from the same clone at a later date. It also does not differ from *M. floribundum* and we conclude that the name should be placed into the synonymy of that species.

The lectotype illustration of *Mesembryanthemum torquatum* Haw. (*Drosanthemum torquatum* (Haw.) Schwantes in *Z. SukkulKde* 3: 30 (1927)) looks rather like a pot-grown *D. floribundum*, but we have seen no plants with such long peduncles.

**Taxonomy and variation:** *Drosanthemum floribundum* shows little variation in Britain. We have studied living plants from the Isles of Scilly, the Lizard peninsula (W. Cornwall) and Guernsey and all undoubtedly belong to a single taxon. The naturalized plant is referred to *D. candens* (Haw.) Schwantes by Tutin (1962, 1964) but to *D. floribundum* by recent authors. *D. candens* is said to differ from *D. floribundum* in its narrower calyx, paler pink or nearly white petals and stigmas not exceeding the stamens (Adamson & Bolus 1950; Fernandes 1972). As described above, the flower colour and the position of the stigmas relative to the stamens of the British plants varies with age and photographs in CGE show white and pink flowers on the same plant.

**Reproductive biology:** Flowers from May to July. As its specific epithet implies, patches of *Drosanthemum* usually flower freely. We have noticed flies, bees (including *Bombus cf. lucorum* and *B. terrestris*) and ants visiting the flowers. *Drosanthemum* is more attractive to bees than any other 'mesemb' naturalized in Britain, and in sunny weather they are frequent visitors. Seeds are ripened in Britain, but we do not know if they are viable. We have not seen any seedlings in the wild and effective reproduction is by vegetative spread. In cultivation cuttings of *Drosanthemum* root less readily than those of *Carpobrotus* or *Disphyma*.

*Drosanthemum* is more susceptible to frost than *Carpobrotus* or *Disphyma*. Some colonies have not survived severe winters, e.g. a well-established clone on a wall at Cadgwith Cove, W. Cornwall, which was covered by a mass of flowers in July 1978, did not survive the severe 1978–9 winter.

**Distribution and habitat:** Naturalized on coastal walls, banks, rock outcrops and cliffs on St Mary's and Tresco, Isles of Scilly, at Rinsey Head and the Lizard peninsula, W. Cornwall, and on Guernsey. The largest and most vigorous plants form patches hanging down vertical walls or cliffs. Patches on less steep banks are smaller and less vigorous, and *Drosanthemum* is apparently less able to spread vegetatively in such habitats. There is a single record from Jersey, where it was killed in the 1962–63 winter (le Sueur 1984), and a plant collected as *Mesembryanthemum candens* at Newquay, W. Cornwall, in 1921 (BM) was probably this species. It is also recorded as a casual introduced with wool shoddy.

Specimens of *Drosanthemum* were collected at St Mary's in 1875 (BM) and 1885 (OXF). These were presumably cultivated plants. The first records of naturalized plants appear to be the 1921 collection from sand hills near Newquay mentioned above and a plant collected by T. G. Tutin in 1948 from a cliff at Cadgwith, Lizard peninsula (LTR). None of the pressed specimens can be
Figure 5. Drosanthemum floribundum (Haw.) Schwantes, illustrated as Mesembryanthemum floribundum in Salm-Dyck's Monographia Generum Aloes et Mesembryanthemi 51: fig. 7 (1840). The coloured plate is the neotype of *M. floribundum* Haw.
identified as *D. floribundum* with certainty but all probably represent the same species as that currently naturalized and we have confirmed the identity of the Cadgwith plant in the field. *Drosanthemum* is less thoroughly naturalized than *Carpobrotus, Disphyma* or *Lampranthus*. It is probably limited by its frost sensitivity and low competitive ability. It does occur, however, in natural habitats, although often only in small quantity, and will probably persist as a member of the British flora. It is a native of South Africa (Herre & Friedrich 1961).


Illustrations: Lousley, Fl. Scilly 217, fig. 10 (2) (1971); Salm-Dyck, Monogr. Aloes Mesembr. 21: fig 2 (1840), pro *Mesembryanthemum heteropetalum*.

**Description:** Low, glabrous, fleshy shrub. Stems up to 35 cm, erect or decumbent, glabrous, yellowish-green or tinted brownish, often spotted purplish, slightly flattened with decussate ridges or wings; internodes up to 4-5 cm. Leaves 16-30 × 6-13 mm, with bluish-green bloom on faces and yellowish-green angles and covered with dense pellucid dots, unmarked when young, becoming tinted or spotted purplish and eventually turning purple with age, decussate, asymmetrically ob lanceolate in outline, triangular in section, shortly acute at apex, sessile, irregularly dentate on one angle, often minutely denticulate on the others. Flowers solitary or 2-3 together, terminal at the end of branches and side shoots, 10-15 mm in diameter; peduncle up to 15(-25) mm. Calyx bluish-green, hemispherical, covered in pellucid dots, sometimes spotted or tinted purplish; lobes 5, erect; 2 longest lobes 11-15 mm, broadly triangular-ovate, abruptly acute to more or less obtuse at apex, entire, both usually keeled on the back, the keel continuing to the base of calyx and entire or irregularly dentate below, rarely only 1 keeled; 3 shortest lobes 8-15 mm, triangular-ovate, acute at apex, entire, not keeled, 2 with a scarious often purplish-tinted margin on both sides and one with a similar margin on one side. Petals numerous, in several irregular series, 4-11 × 0.5-0.8 mm, free, pale purple, linear-oblanceolate, obtuse and sometimes bifid at apex, outer petals more or less spreading, inner erect or inflexed. Staminodes numerous, 2-0-4.5 × 0.1-0.2 mm, whitish, linear, more or less obtuse at apex, inner inflexed and covering the stamens. Stamens numerous, inflexed; filaments 0.5-2.0 mm, white; anthers pale yellow. Stigmas 5-6, very small, pale greenish, roundish to almost globular in outline. Nectary glands minute and scarcely visible. Capsule 10-15 × 10-15 mm, 5-locular, each valve with two expanding keels which diverge towards the apex and end in broad awn-tipped membranes; loculi roofed with stiff wings, but without tubercles at the openings; placenta parietal. Seeds 1.3-1.5 × 0.8-1.1 mm, chestnut-brown, ovoid, flattened, tuberculate, on a funicle up to c. 1 mm. 2n = 18.

**Nomenclature and typification:** Haworth's original description of *Mesembryanthemum heteropetalum* is a good one and fits our plant except that the petals are said to be white. There is a coloured drawing of a plant worked on by Haworth at Kew but as it is only a vegetative shoot we have not selected it as a neotype, preferring instead Salm-Dyck's illustration of a flowering plant. This is reproduced here as Fig. 6.

**Taxonomy and variation:** There is very little variation within the only population naturalized in Britain.

**Reproductive biology:** Flowers in May and June. The morphology of the flower suggests that it is self-pollinating. We have not seen flying insects visit the flowers (although they are visited by ants) and *Erepsia* is certainly much less frequently visited by insects than *Carpobrotus* or *Drosanthemum*. Reproduction in the wild is by seed; viable seed is produced and seedlings have been observed. We have no evidence of any vegetative reproduction.
Figure 6. Erepsia heteropetala (Haw.) Schwantes, illustrated as Mesembryanthemum heteropetalum in Salm-Dyck's Monographia Generum Aloes et Mesembryanthemi 21: fig. 2 (1840). The coloured plate is the neotype of M. heteropetalum Haw.
NATURALIZED AIZOACEAE

Distribution and habitat: Only naturalized in one locality, Buzzza Hill, St Mary's, Isles of Scilly, where it grows in shallow soil on the edge and face of a disused quarry and on a nearby cliff slope. It was first collected by J. E. Lousley in 1957, and was still present in 1987. In 1983 the population consisted of approximately 30 plants. Erepsia heteropetala, unlike the more showy 'mesembs', is not widely grown in coastal gardens in south-western England. It is a native of South Africa.

Mesembryanthemum acinaciforme var. flavum L., Sp. Pl. 485 (1753). LECTOTYPE: Dillenius, Hort. Eltham. 284, t. 212, fig. 272 (1732), pro Mesembryanthemum falcatum majus, flore ampio luteo, chosen by Blake in Contr. Queensland Herb. 7: 17 (1969); the copy in the Department of Plant Sciences, Oxford University, is coloured by Dillenius.
M. edule L., Syst. Nat., 10th ed., 1060 (1759), nom. nov. pro M. acinaciforme var. flavum L.

Vernacular names: Hottentot Fig, Kaffir Fig, Sally-my-handsome


Description: Prostrate or hanging, succulent perennial forming large mats. Stems up to at least 3 m, trailing or hanging, sometimes rooting at the nodes, fleshy, angled, glabrous, slightly bluish-green turning pink, pinkish-purple or orange with age; branches axillary; internodes 1.5–7 cm. Leaves (20–)40–140 × 5–15 mm, decussate, each pair slightly connate at base, slightly bluish-green and waxy, turning pinkish-purple and finally orange with age, covered with pellucid dots, linear or narrowly oblong in outline, triangular in section, straight to more or less curved, obtuse to acute at apex, sessile. Flowers terminal or at the end of side shoots, solitary, 40–90 mm in diameter; peduncles 6–60 mm. Calyx yellowish-green, sometimes tinged purplish, covered with pellucid dots; lobes 4–6, the 2 longest 15–65 × 8–17 mm, lanceolate to linear-lanceolate in outline, more or less acute at apex, flat on inner surface, keeled on outer surface, the keel continuing down the undivided calyx, the 2–4 short lobes 10–50 × 6–15 mm, ovate to lanceolate in outline with a curved, acute apex and a brownish scarious flap on one or both sides up to 10 mm wide, that on the shortest of the shorter lobes sometimes almost circular, exceeding the apex and adnate to its inner surface, one of the longest lobes sometimes with a flap and one of the shorter lobes sometimes without a flap. Petals 65–150, 25–45 × 1.5–3.5 mm, free, yellow or pale or deep purple, pale reddish-purple or orange-pink, sometimes with a yellow base, narrowly linear or narrowly linear-oblongate, entire or slightly toothed at apex. Stamens numerous; filaments 5–10 mm, yellow or brownish-orange, sometimes with a whitish base, inner with a tuft of whitish or purplish hairs at base; anthers yellow. Staminodes resembling petals sometimes present between stamens and petals. Stigmas 10–14, greenish-yellow, curved upwards and outwards, plumose on the inner surface. Nectary glands united to form a crenulate ring round the ovary. Fruit adnate to the calyx, 1.4–3.0 × 1.4–2.7 cm, obovoid; seeds 1–1.5 × 0.8–1 mm, dark brown when ripe, obovate in outline, flat, minutely and faintly reticulate, on a funicle 2–3 mm.

a. var. edulis

Illustrations: Curtis's bot. Mag. 144: t. 8783 (1918), pro parte; Sjögren, Açores Flores t. 73 (1984)

Description: Leaves (20–)40–140 × 5–14 mm. Flowers 40–90 mm in diameter; petals pure yellow when freshly opened, becoming pink-tinged with age. Fruits 2.5–3.0 × 2.5–2.7 cm. 2n = 18.

b. var. rubescens Druce in Rep. bot Soc. Exch. Club Br. Isl. 7: 771 (1926). Not typified (see below)
Mesembryanthemum virescens auct., non Haw.
M. aequilaterum auct., non Haw.
C. deliciousus auct., non L. Bolus.

Description: Leaves (20–)40–100 x 5–10 mm. Flowers 45–75 mm in diameter; petals purple with little or no sign of yellow at their bases. Fruits 2.5–3.0 x 2.5–2.7 cm. 2n = 18.

c. var. chrysophthalmus C. D. Preston & P. D. Sell, var. nov. Holotype: Plant collected as living material at the sea front, Porthloo, St Mary’s, Isles of Scilly, 12 January 1978, C. D. Preston, cultivated at the Botanic Garden, Cambridge, and pressed on 8 June 1979 as P. D. Sell 79/22 (CGE).


Description: Folia (20–)35–125 mm longa, 5–15 mm lata. Flores 45–70 mm in diametro; petala purpurea basi area aurei; fructus 1.4–2.5 x 1.4–1.8 cm.

Leaves (20–)35–125 x 5–15 mm. Flowers 45–70 mm in diameter; petals purple with a distinct area of yellow at their bases, which forms a ring as you look into the flower from above. Fruit 1.4–2.5 x 1.4–1.8 cm.

Nomenclature and typification: Linnaeus (1753) described Mesembryanthemum acinaciforme var. flavum based on Mesembr. falcatum majus, flore amplo luteo. Dill. elth. 284. t. 212. f. 272. and Ficoides s. Ficus aizoides africana major procumbens, triangulari folio, fructu maximo eduli. We are in agreement with Blake (1969) who selected the Dillenius plate as the lectotype, but in particular we cite the coloured copy at Oxford. An uncoloured version is reproduced here as Fig. 7. Linnaeus (1759) gave M. acinaciforme var. flavum a new name, M. edulis. The type of M. edulis is thus the type of M. acinaciforme var. flavum.

The purple-flowered variant, var. rubescens, was described by Druce in 1926. No specimens are cited in the protologue, and none of the specimens in Druce’s herbarium (OXF) is labelled var. rubescens or described as C. edulis with red- or purple-flowers. G. H. Douglas sent plants to Druce in 1924, stating “the flowers are of two colours”. In the poorly dried specimens one can no longer see any colour, but it may be that chemical analysis could distinguish them. At the moment we are unable to lectotypify var. rubescens. M. aequilaterum Haw., M. virescens Haw. and Carpodrome deliciosus (L. Bolus) L. Bolus have all been wrongly applied to this taxon. C. aequilaterus (Haw.) N.E. Br. is a smaller-flowered Australian species more akin to C. glaucescens, but without the white bases to the petals (cf. Blake 1969). For C. virescens (Haw.) Schwantes see under C. glaucescens. Lousley (1971) thought that specimens sent in 1895 from Tresco Abbey for a drawing in Curtis’s botanical Magazine (t. 8783) were referable to C. deliciosus (L. Bolus) L. Bolus. The pink-flowered specimen on this plate, however, seems to be indistinguishable from C. edulis var. rubescens, and furthermore the text states that the plants illustrated were collected at Caerthillian Valley, which is on the Lizard peninsula, mainland Cornwall (cf. Hutchinson 1917).

The third variety, var. chrysophthalmus, has the bases of the purple petals yellow, so that when looking into the open flowers one can see a golden ring round the base. This seems to be the plant Lousley (1971) called C. acinaciformis, although he did not mention the flower character. Mesembryanthemum acinaciforme was described by Linnaeus (1753). The diagnosis Mesembryanthemum foliis acinaciformibus connatis: angulo carinali scabris, ramis angulatis from the Hortus Cliffortianus (Linnaeus 1738). There are no specimens in the herbarium of the Hortus Cliffortianus (BM), or in the Linnaean Herbarium in London (LNN). The diagnosis is followed by var. purpureum based on Mesembr. acinaciforme, flore amplissimo purpureo Dill. elth. 282. t. 211. f. 270 & t. 212. f. 271. This is also given in the Hortus Cliffortianus, but without a varietal name. It is clearly what Linnaeus considered to be the type variety. The plate t. 211 fig. 270 in the Oxford coloured copy is therefore designated as the lectotype of M. acinaciforme and shows a large-flowered, large-leaved plant which is not matched by any material from the British Isles which we have seen. It was apparently cultivated in the Isles of Scilly as the illustration in Curtis’s bot. Mag. t. 5539 (1865) seems to be correctly named. We cannot find any described taxon which matches our plant with yellow centres to the flowers and have therefore described it as new, although we have no suggestions as to its geographical origin or derivation. The holotype is taken from the clone we have
most studied, and there are colour photographs in CGE of the plant we pressed (Sell colour film 297/30, 31 & 32).

**Taxonomy and variation:** Variation within var. *edulis* is described by le Sueur (1984) from Jersey, where neighbouring clones differ in leaf and flower colour. Var. *rubescens* differs only in its smaller purple flowers (though vegetatively it never seems to reach the maximum size of the yellow-flowered plant). Both these varieties are widely naturalized and often grow together. Intermediate plants with pale purple, pale reddish-purple or pale orange-pink flowers occur, and look as though they have been derived from hybridization between yellow- and purple-flowered plants. As their origin is obscure we have treated the yellow- and purple-flowered plants as varieties of the same species under the only names that seem to be available for them.
Var. *chrysophthalmus* has slightly smaller flowers, like var. *rubescens* but with the base of the petals yellow. It also has smaller fruits. The only published illustration we are aware of is on the dustcover of Lousley (1971), which most libraries will have thrown away. We can find no name for it. We originally thought it was a distinct species, as species go in 'mesembs', but have finally decided to name it as a variety of *C. edulis* as it is just possible that it arose from hybridization between the yellow and purple variants.

**Reproductive biology:** The main flowering period is from May to July. The flowers are visited by Coleoptera, Diptera, Hymenoptera and Lepidoptera, and snails can sometimes be seen sitting in the open flowers. Viable seed is produced and seedlings have been seen, usually growing in areas of bare soil around the fringe of naturalized clones.

*Carpobrotus edulis* spreads mainly by vegetative means. In the Isles of Scilly and the Channel Islands it has been planted for dune stabilization or for ornament, and elsewhere colonies often originate from stems thrown out of gardens. New colonies become established from fragments collected by gulls as nesting material, and in this way *Carpobrotus* has spread even to small uninhabited islands. Fragments of *C. edulis* root readily in cultivation: one potted up in an unheated greenhouse produced roots up to 22 cm long in 18 days.

Large areas of *C. edulis* overwhelm native vegetation, forming mats in which virtually no other species grow. These mats acidify the underlying soil down to a depth of at least 8–12 cm (Frost 1987). The spread of *Carpobrotus* is accelerated by cliff fires, which scarcely affect the succulent 'mesemb' but destroy the surrounding vegetation. In severe winters *C. edulis* is badly damaged by frost. However, stems may survive and produce new shoots even in areas in which all the existing foliage has been killed. A thick layer of litter accumulates under mats of *Carpobrotus* and this must help insulate stems from low temperatures, and certainly inhibits the colonization by other flowering plants of areas in which *Carpobrotus* has been frost-killed. Cattle sometimes eat the leaves of *Carpobrotus*, but only a few colonies grow in localities where such grazing is likely to occur. Frost (1987) reports that it is eaten “with relish” by pet rabbits.

**Distribution and habitat:** *C. edulis* is primarily a species of sea cliffs and sand dunes, but it also grows on coastal banks, rocks and walls. Its distribution is mapped in Fig. 8. Var. *edulis* and/or var. *rubescens* is recorded from the following vice-counties: Channel Islands, 1–4, 9–11, 14, 15, 19, 41, 45, 49, 52, 60, 71, H1, H5, H20, H21, H38. The population in v.c. 74 mapped in the *Atlas of the British flora* (Perring & Walters 1962) is *C. glaucescens* and confirmation of the identity of the plant recorded on shingle in v.c. 19 by Jermyn (1974) is desirable in view of the presence of *C. glaucescens* on the adjacent Suffolk coast. Var. *chrysophthalmus* is naturalized on Bryher and St Mary's in the Isles of Scilly and at St Brelade and St Ouen's Bay in Jersey. Lousley (1971) records *C. acinaciformis* – the name he apparently applied to var. *chrysophthalmus* – from St Martin's and Tresco. C. D. P. and P. Clough (formerly of Tresco Abbey Gardens) have searched for it on Tresco without success.

*Carpoportus edulis* was introduced into British gardens about 1690. The history of its naturalization is difficult to reconstruct. For many years botanists did not record naturalized populations of this and other 'mesembs', and collectors of herbarium specimens sometimes fail to state whether or not they were collected from naturalized populations. *C. edulis* was recorded as “semi-wild” in Guernsey in 1886 and reported again in 1893 (McClintock 1975). A yellow-flowered 'mesemb', presumably *C. edulis* var. *edulis*, grew freely in great abundance at St Aubin's Bay, Jersey by 1886 (le Sueur 1984). In the Isles of Scilly it was planted in the mid-nineteenth century and by 1921 it was common on most of the islands (Lousley 1971). On mainland Cornwall 'mesembs' were in cultivation at Falmouth by 1871 (Baker 1871) and at The Lizard by c. 1880 (Frost 1987). Although it was not listed amongst the alien plants seen near Penzance between 1885 and 1887 by Glasson (1889), *C. edulis* was “abundant” in the Lizard peninsula in 1905 and “quite naturalised” in 1909. It was “rapidly establishing itself” at East Pentire, Newquay, in 1907 and by 1909 it had been recorded in several Cornish localities (Vigurs 1908; Davey 1909). Eight years later Hutchinson (1917) could describe it as “now so thoroughly naturalised and so characteristic a feature of the sea-slopes of Cornwall”. In Devon it was collected at Torquay (v.c. 3) in 1885 and Saunton Sands (v.c. 4) in 1919. It is a native of South Africa.


Mesembryanthemum edule var. virescens (Haw.) Moss, Camb. Brit. Fl. 2: 151 (1914), quoad basionym, exclud. descript.

C. virescens (Haw.) Schwantes in Gartenflora 77: 69 (1928).
C. abbreviatus (Haw.) Schwantes in Gartenflora 77: 68 (1928).

Vernacular name: Angular Pigface is the name used for this species in Australia.


Description: As C. edulis except: Internodes 0.5–3.0 cm. Leaves 20–70 × 5–8 mm, bluish-green and waxy, more or less acute at apex. Flowers 35–45(–60) mm in diameter; sessile or with a peduncle up to 10 mm. Calyx bluish-green and waxy; lobes 5, the 2 longest 15–20 × 10–12 mm, the 3 shortest 5–13 × 3–15 mm, ovate in outline with a brownish scarious flap on one or both sides up to 8 mm wide. Petals 55–80, 17–25 × 1.0–1.2 mm, purple with obvious white bases, narrowly linear, with a few teeth at the apex. Stamens numerous; filaments 4–6 mm, white, sometimes yellowish towards apex, inner sometimes with tufts of white simple eglandular hairs at base. Stigmas 10–12. Fruit 1.5–1.7 × 1.2–1.5 cm; seeds 1.0–1.2 × 0.8–1.0 mm. 2n = 18.

Nomenclature and typification: This has been satisfactorily dealt with by Blake (1969). There are in fact coloured drawings of both C. glaucescens and C. virescens at Kew not seen by Blake. We can detect no obvious difference between the drawings. C. chilensis (Molina) N.E.Br., the name used for the Suffolk populations of this plant by Simpson (1982), is a synonym of C. aequilaterus, a species which lacks white bases to the petals (Blake 1969).

Taxonomy and variation: Plants naturalized in the British Isles show little variation. Blake (1969) separated C. glaucescens from C. virescens mainly on stamen number and ascribed to them different geographical ranges, C. glaucescens being confined to coastal areas of eastern Australia and C. virescens to the south-west. Venning (1984a) retained the two species, but said that dried material was difficult to name and that not enough fresh material was available to review their status. In the few naturalized British plants in which we have counted the stamens the number is around 300 which is intermediate between the two. We therefore believe that they are not distinct species, but that there may be slight differences which could allow the upkeep of geographical races.

Reproductive biology: The main flowering period is from May to July. Flowers have, however, been seen as early as February and C. glaucescens shows a greater tendency than C. edulis to flower outside the main flowering period. Effective reproduction is by vegetative spread. In cultivation vegetative fragments root readily. C. glaucescens is a smaller plant than C. edulis, and does not possess as great a competitive vigour as that species.

Distribution and habitat: Naturalized in the Channel Islands (Alderney, Guernsey, Herm and Jersey), Suffolk and Wigtownshire. On Herm it is the only naturalized Carpobrotus but in Guernsey and Jersey it is much less frequent than C. edulis. In Suffolk it is recorded from two localities near Felixstowe: it is the C. chilensis of Simpson (1982). In Wigtownshire it grows around the Logan Fish Pond at Port Logan. Most naturalized colonies are on sea cliffs, but it also grows on walls and roadside verges. In Australia C. glaucescens is recommended for planting as a stabilizer of sand dunes (Beach Protection Authority of Queensland 1981) but it has not been recorded from this habitat in Britain. It is cultivated in the Isles of Scilly but has not become naturalized there.

C. glaucescens has been known for about 25 years in Jersey (Le Sueur 1984). It was first noticed in Herm in 1947, in Guernsey in 1970 and in Suffolk in 1974. Although first officially recorded in Wigtownshire in 1955 (as C. edulis), it is said by local people to have grown there for many years before that. It is a native of the eastern coast of Australia (Venning 1984a).
ACKNOWLEDGMENTS

Mrs F. le Sueur (Jersey), D. McClintock and Mrs P. Ryan (Guernsey), P. Clough and Mrs R. Parslow (Scilly), L. J. Margetts (Cornwall), K. E. Bull (Sussex), R. H. Roberts (Anglesey), E. F. Greenwood (Lancashire), Dr H. A. Lang (Wigtownshire) and P. Hackney (Co. Down) have kindly helped us by providing information on the distribution of 'mesembs' or by sending living material. We have benefitted from discussion with J. R. Akeroyd, currently revising the account of Aizoaceae in *Flora Europaea*. C. Jarvis checked his records to see if the Linnaean taxa had been lectotypified, Miss S. K. Marner answered queries about books and specimens at Oxford, Mrs D. M. Greene plotted the distribution map and Miss J. M. Abblitt turned our initial palimpsest into a typescript. A. O. Chater, L. C. Frost, D. McClintock and G. D. Rowley kindly commented on a draft of the paper, and R. A. Finch checked the Appendix.

REFERENCES


APPENDIX: CHROMOSOME COUNTS OF AIZOACEAE NATURALIZED IN THE BRITISH ISLES

R. D. I'ONS

Chromosome counts were made of specimens collected by C. D. Preston and Mrs F. le Sueur on which the above account was based. They were grown in pots in the University Botanic Garden, Cambridge, from which root tips were easily procured. Voucher specimens of flowers and sometimes fruits were pressed and placed in CGE.

The root tips were placed in 0-05% colchicine in corked tubes for 2 h at room temperature, followed by fixation in Carnoy’s solution for 2h. They were then put in 1% HCl and hydrolysed, uncovered, for 6 min in an oven at 60°C, and stained in Feulgen’s solution for 1-2 h. The root tips were then mounted on a slide with propionic orcein, squashed, and the chromosomes counted. The slides were made permanent by using liquid nitrogen to facilitate removal of the coverslip, passing the slide into 90% alcohol followed by absolute alcohol and xylene for 1 min each, and finally mounting in dammar xylene or Euparal. Occasionally root tips were stored in 70% alcohol overnight after fixation in Carnoy’s solution, but this was less satisfactory than if the complete process was carried out on the day of collection.

Aptenia cordifolia (L.f.) Schwantes: St Brelade’s Bay, Jersey, GR WV/589.486, Mrs F. le Sueur; 2n = 18. Grouville, Jersey, GR WV/706.499, Mrs F. le Sueur; 2n = 18.

Carpobrotus edulis (L.) N.E.Br. var. edulis: near Kempt Tower, St Ouen’s Bay, Jersey, GR WV/56.52, Mrs F. le Sueur; 2n = 18.

(Accepted May 1988)
Carpobrotus edulis (L.) N.E.Br. var. rubescens Druce: N. end of Rocquaine Bay, Guernsey, GR WV/25.78, C. D. Preston; 2n = 18.

Carpobrotus glaucescens (Haw.) Schwantes: south coast of Alderney, between Vallée des Gaudulons and Val l’Emauve, GR WA/564.060, C. D. Preston; 2n = 18.


Drosanthemum floribundum (Haw.) Schwantes: Newman House, St Mary’s, Isles of Scilly, GR 00/898.108, C. D. Preston; 2n = 36.

Erepsia heteropetala (Haw.) Schwantes: Buzza Hill, St Mary’s, Isles of Scilly, GR 00/905.103, C. D. Preston; 2n = 18.


Oscularia deltoides (L.) Schwantes: ‘Juliet’s Garden’, Porthloo, St Mary’s, Isles of Scilly, GR 00/909.115, C. D. Preston; 2n = 18.

Ruschia caroli (L. Bolus) Schwantes: Old Town Bay, St Mary’s, Isles of Scilly, GR 00/90.10, C. D. Preston; 2n = 18.