Aizoaceae

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Aizoaceae Martynov 1820: 15 nomen conservandum (McNeill et al. 2012; Wiersema et al. 2015: App. IIB); Bittrich & Hartmann 1988: 239–254; Bittrich 1990: 491–507; Hartmann 1991: 75–157; Hartmann 1993: 37–69; Hartmann 2001a: 1–22; Hartmann 2001b: 1–22; Klak et al. 2003: 1433–1445; Thiede 2004: 51–58 **Typus Aizoon** L. = *Ficoidaceae* Jussieu 1789: 315 nomen rejiciendum **Typus Mesembryanthemum** L. (as *Ficoides* Miller 1754: without page) ≡ *Mesembryanthemaceae* Philibert 1801: 268 nomen conservandum (McNeill et al. 2012; Wiersema et al. 2015: App. IIB) **Typus Mesembryanthemum** L. nomen conservandum = *Sesuviaceae* Horaninow 1834: 83 **Typus Sesuvium** L. = *Tetragoniaceae* Lindley 1836: 209 nomen conservandum (McNeill et al. 2012; Wiersema et al. 2015: App. IIB) **Typus Tetragonia** L.

Predominantly perennial shrubs, rarely annual to biennial herbs, rarely trees, and rarely plants reduced to a single leaf-pair, growing sometimes sunken in the ground; **L** mostly opposite, simple and entire, rarely lyrate, epidermis with bladder cells of various shapes and sometimes reduced, or uniform and xeromorphic, often papillate to pubescent, base of petioles rarely with stipuliform appendages or leaves sessile, sometimes with a connate leaf sheath; **Inf** of principally dichasial pattern, complete or in various derived forms, mostly terminal, often seemingly axillary, often reduced to a single flower; **Fl** actinomorphic, mostly bisexual, perigynous to hypogynous or epigynous, perianth elements (3–)5(–8), free portions often unequal and with dorsal subapical appendages, basally connate and adnate to the filaments, thus forming a perianth-stamen tube, inner surface of upper portion petaloid or green, named calyx when petaloid elements are present; androecial elements 4-many, if many, the outer primordia developing often into petaloid organs (=petals), filaments rarely connate, rarely connate with the petals forming a tube, anthers dehiscing by longitudinal slits; ovary syncarpous, (1–)5(–∞)carpellate, placentation axile, basal or parietal, ovules (1–)∞ per carpel, anacampylotropous or campylotropous, bitegmic, crassinucellate, rarely pendulous; **Fr** mostly a hygrochastic loculicidal, rarely septicidal or xeromorphic capsule, rarely schizocarpous, sometimes a hard and indehiscent 1-seeded nut, rarely a drupe, occasionally in aggregates, or a circumscissile capsule; **S** mostly more or less ovoid, rarely arillate, with a curved peripheral embryo, and voluminous starchy perisperm, endosperm reduced to a layer enveloping the radicle; **Ecol** mainly in subtropical and mediterranean climates with moderate to low

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rainfall regimes mainly as winter rains; **Distr** worldwide in the subtropics, the highest number of genera and the centre of diversity at species level in southwestern Africa.

Note: The family name **Aizoaceae** was first validly published by Martynov (1820: 15) who gave a reference to an invalidly but effectively published name by Augier (1801: 129, 137–138). This supercedes the name **Aizoaceae** Rudolphi (1830: 53) that had for several decades been considered the correct name. In Appendix IIB of the Melbourne Code (McNeill et al. 2012; Wiersema et al. 2015), the already conserved family name **Aizoaceae** Martynov (against *Ficoidaceae* Jussieu 1789: 315) is "superconserved" against the name *Mesembryanthemaceae* Philibert (1801).

The present treatment follows the delimitation of the family by Bittrich & Hartmann (1988) who excluded members of the family **Molluginaceae**. According to Klak et al. (2003: 1433–1445) and Thiede (2004: 51–58) four subfamilies can be distinguished: **Aizooideae**, **Mesembryanthemoideae**, **Ruschioideae**, and **Sesuvioideae**. The *Tetragonioideae* which were treated as another subfamily by Bittrich & Hartmann (1988) are in fact polyphyletic (Klak et al. 2003; Thiede 2004) with **Tetragonia** nested in the **Aizooideae** and **Tribulocarpus** as sistergroup to the **Sesuvioideae. Tetragonia** and **Tribulocarpus** are accordingly included in the respective subfamilies. The main synapomorphy of the family is the possession of bladder cells (Bittrich 1990: 491–507). The authors of all subfamily names are given as in Reveal (2007).

239 genera have been described as members of this family, of which 146 are accepted here.

Shrubs of many genera form the dominant part of the vegetation of the winter rainfall area of Southern Africa (e.g. **Amphibolia**, **Aridaria**, **Antimima**, **Eberlanzia**, **Lampranthus**, **Leipoldtia**, **Ruschia**, **Vanzijlia**). Some genera are also important elements of the Karroo vegetation outside this region (e.g. **Ruschia**, **Trichodiadema**), thus contributing considerably to the carrying capacity of the natural vegetation. Few species possess chemical compounds which are used in traditional healing (e.g. **Sceletium**, **Zaleya**). A selection of small-growing species (e.g. **Conophytum**, **Lithops**) is kept in horticulture, mainly indoors or in greenhouses worldwide in moderate climates. Some genera are found as garden elements or sand-binders in suitable climates (e.g. **Carpobrotus**, **Malephora**). The sour-tasting fruits of some species of **Carpobrotus** are sold semi-dried in the market to be used for jellies or preserves. Only one species, **Tetragonia tetragonoides**, is grown as a vegetable in appropriate conditions.

Ficoidaceae = **Aizoaceae**

De Jussieu (1789: 315) was the first to describe the family *Ficoideae* at that rank, including the genera "**Reaumuria** Hasselq., **Nitraria** Schob., **Sesuvium** L., **Aizoon** L. *Ficoidea* Niss., **Glinus** L., **Orygia** Forsk., **Mesembryanthemum** L. *Ficoides* T., and **Tetragonia** L.". It must be noted that *Ficoidea* Nissole (1730: 319) is an obligate synonym of **Aizoon** L., whereas *Ficoides* Tournefort (1730: 238–241) is an obligate synonym of **Mesembryanthemum** L.; both names were published before Linnaeus (1753), only

Key to the Subfamilies of Aizoaceae

1.	Petals of staminodial origin present	**2**
–	Petals absent; perigone-lobes petaloid inside, sepaloid outside	**3**
2.	Placentation central; nectaries shell-shaped to tubular (koilomorphic); petals and stamens often united into a tube	**Mesembryanthemoideae**
–	Placentation basal or parietal, extremely rarely central; nectaries crest-shaped (lophomorphic) or flat, petals mostly free	**Ruschioideae**
3.	Fruit a circumscissile capsule, or a woody nut which is either 5-winged or beset with numerous spines, perianth segments with subapical appendages	**Sesuvioideae**
–	Fruit a loculicidal or septicidal capsule, often hygrochastic, or a woody nut with ornaments principally in 4 rows, perianth segments without subapical appendages	**Aizooideae**

one was validated later: *Ficoides* Miller 1754. Only this name can be considered when a type species of *Ficoidaceae* has to be found.

The question of the family name has been discussed extensively (e.g. Sprague 1922: 71; Rowley 1951: 27–28; Friedrich 1955: 56–60; Schwantes KuaS 1957: 157–158, 167–169). It was temporarily settled when **Aizoaceae** Rudolphi became the nomen conservandum for the relevant genera including **Aizoon**. The new nomen conservandum **Aizoaceae** Martynov does not interfere with the rejection of *Ficoidaceae* de Jussieu. If *Mesembryanthemaceae* are considered as a separate family, the name *Ficoidaceae* becomes an obligate synonym, since both names are based on the same genus.

Mesembryanthemaceae = **Aizoaceae**

In Appendix IIB of the Vienna Code (McNeill et al. 2006), the author of the conserved family name *Mesembryanthemaceae* is given as Philibert (1801: 268). For a long time, Fenzl (1836: 347, 349) had been considered the author and *Mesembryanthemaceae* Fenzl became a younger synonym of **Aizoaceae** Martynov when combined with the latter. *Mesembryanthemaceae* Philibert (1801), however, predates **Aizoaceae** Martynov (1820). This situation was dealt with by a "superconservation" of **Aizoaceae** Martynov in the Melbourne Code (McNeill et al. 2012; Wiersema et al. 2015).

The two subfamilies **Mesembryanthemoideae** and **Ruschioideae** have often been considered as a separate family (i.e. Herre 1971) since they share a number of characters and together represent a monophylum (Bittrich 1990; Hartmann 1991; Klak et al. 2003; Thiede 2004). In that case, the family name is to be *Mesembryanthemaceae* Philibert. To stress the evolutionary proximity of both taxa in the context of the family **Aizoaceae**, Hartmann (1991: 75–157) introduced the unranked term "Mesembryanthema" for the united subfamilies **Mesembryanthemoideae** and **Ruschioideae**.

Sesuviaceae = **Aizoaceae**

Horaninow (1834: 83) was the first to use the family name "*Sesuviaceae* (Ficoideae)", including the genera "**Mesembryanthemum**, **Tetragonia**, **Aizoon**, **Sesuvium**, **Trianthema**, **Glinus**; – **Reaumuria**? **Nitraria**?". A little later (Horaninow 1843: 29), four tribes were listed: *Paronychieae*, *Portulaceae*, *Ficoideae*, and *"Neuradeae et Surianeae?"* containing 18 subgroups plus two with a question mark, but no genus names. Retaining the subdivision of the family as well as its circumscription more or less, Horaninow used the family name **Portulacaceae** for the broadened assembly of genera some years later (1847: 138–140) without giving an author or a reason for this change.

The family name *Sesuviaceae* has very rarely been used, probably due to the fact that the family names *Ficoidaceae* and **Aizoaceae** were also available for most of the assembly of species listed by Horaninow at that time. Nevertheless, various authors refer to the "**Sesuvium**-group", comprising the genera **Cypselea**, **Sesuvium**, **Trianthema**, and **Zaleya**, when investigating **Aizoaceae** s.lat., i.e. including **Molluginaceae** (e.g. Hofmann 1973). Bittrich & Hartmann (1988: 240–245) argued that the possession of bladder cells in the epidermis and the perianth-stamen tube in the **Sesuvium**-group sensu Hofmann (1973) justify its inclusion in the family **Aizoaceae** as a separate subfamily **Sesuvioideae**. This position was confirmed by molecular studies (Klak et al. 2003; Thiede 2004).

Tetragoniaceae = **Aizoaceae**

The authorship of the family name *Tetragoniaceae* has been a question of some debate recently: For some time, Nakai (1942: 103) had been used as the author of the conserved family name who in turn had ascribed the name to Reichenbach in Mössler (1827: 52). In the St Louis Code (Greuter et al. 2000), *Tetragoniaceae* Link (1831: 17) was given. Although Link consistently used the term "order" for these names, they were traditionally treated as denoting the rank of family. However, Link (1831) also published two family names under the order Fungi, which means that the names ranked as orders throughout the work must be treated as the names of orders as well (Art. 35.5). Therefore, the name was changed again to *Tetragoniaceae* Lindley (1836: 209) in the Vienna Code (McNeill et al. 2006).

If *Tetragoniaceae* and **Aizoaceae** are combined, *Tetragoniaceae* becomes a younger synonym of **Aizoaceae**.

Aizooideae

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Aizooideae Sprengel ex Arnott 1832: 112; Bittrich & Hartmann 1988: 239–254; Bittrich 1990: 491–507; Hartmann 2001a: 11–12, 21; Hartmann 2001b: 11–12, 21; Klak et al. 2003: 1433–1445; Thiede 2004: 51–58 **Typus Aizoon** L. = *Tetragonioideae* Lindley 1846: 527 **Typus Tetragonia** L.

Annual to perennial, prostrate to erect herbs, subshrubs, or shrubs, herbaceous to woody; **L** opposite to alternate, flat to cylindrical, mostly free, bladder hairs present; **Inf** mostly frondose often representing the entire plant, **Fl** solitary or in groups, sometimes umbellate, in cymose panicles, or in cymes, perigone 4–5-lobed, basally mostly connate, sepaloid outside, petaloid inside, nectary coating the perianth-stamen tube, stamens mostly <30; ovary 2–5-locular; **Fr** loculicidal or septicidal mostly hygrochastic capsules, rarely xerochastic, or a woody nut; **S** 1–∞ per locule; **Ecol** mostly in open, dry areas in gravelly or sandy soils or in rocky terrain, often in disturbed places, also near the sea; a higher number of species in winter rainfall; **Distr** in mediterranean, subtropical and tropical climates on all continents.

Note: As the molecular studies of Klak et al. (2003: 1433–1445) and Thiede (2004: 51–58) show, the genus **Tetragonia** (*Tetragonioideae*) is nested in the **Aizooideae** and therefore included in the subfamily.

Seven genera are distinguished, occurring mainly in S Africa and Australia, in E Africa and around the Mediterranean Sea, introduced worldwide into suitable climates, mainly as weeds in arid country. **Tetragonia tetragonoides** is the only species of the family grown as a vegetable to some extent in suitable climates, sometimes even in moderate climates. Several species of **Tetragonia** are good fodder in South Africa, their frequency in the wild being understood as a measurement of quality of farming.

Tetragonioideae = **Aizooideae**

The subfamily *Tetragonioideae* Lindley (1846: 527) as understood within the delimitation of the **Aizoaceae** s.str. (Bittrich & Hartmann 1988: 239–254) contains the two genera **Tetragonia** and **Tribulocarpus**. Bittrich (1990: 491–507) placed the *Tetragonioideae* very close to the **Aizooideae**, based on the possession of bladder hairs in both subfamilies. More recent molecular studies (Klak et al. 2003: 1433–1445; Thiede 2004: 51–58) revealed that the *Tetragonioideae* are in fact polyphyletic with **Tetragonia** nested in the **Aizooideae** and **Tribulocarpus** as sistergroup to the **Sesuvioideae**. Accordingly, **Tetragonia**

Key to the Genera of Aizooideae

1.	Fruit a woody nut	**Tetragonia**
–	Fruit a capsule	**2**
2.	Fruit a purely septicidal or septicidal and loculicidal hygrochastic capsule	**Gunniopsis**
–	Fruit a purely loculicidal hygrochastic or xerochastic capsule, often opening tardily	**3**
3.	Septum incomplete, 2 locules with a single basal ovule each	**Acrosanthes**
–	Septa complete, locules either more than 2, or if 2, ovules pendulous	**4**
4.	Capsule 5–10-locular, with 2-many ovules in each locule; distinct expanding keels present	**5**
–	Capsule 2–5 locular with a single pendulous ovule in each locule; expanding tissue rudimentary to absent	**6**
5.	Capsules depressed at apex, if not, valves with prominent rims	**Aizoon**
–	Capsules convex at apex, more or less rounded	**Aizoanthemum**
6.	Stamens as many as the perigone lobes	**Plinthus**
–	Stamens twice the number of the perigone lobes, in pairs alternating with perigone lobes	**Galenia**

is here included in the **Aizooideae** and **Tribulocarpus** in the **Sesuvioideae**.

Mesembryanthemoideae

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Mesembryanthemoideae Burnett 1835: 736, 1092, 1131; Ihlenfeldt et al. 1962: 53; Bittrich 1987: 5–116; Bittrich & Hartmann 1988: 239–254; Bittrich 1990: 491–507; Hartmann 1991: 75–157; Gerbaulet & Struck 2001a in Hartmann 2001a: 12–14; Gerbaulet & Struck 2001b in Hartmann 2001b: 12–14; Klak et al. 2003: 1433–1445; Thiede 2004: 51–58; Klak et al. 2007: 737–756; Gerbaulet 2012: 187–198; Klak & Bruyns 2013: 197–206 **Typus Mesembryanthemum** L. typus conservandum = *Aptenioideae* Schwantes SKK 1947: 39 nomen invalid. ≡ *Aptenioideae* Schwantes ex Bittrich & H.E.K.Hartmann 1988: 250–251 nomen illeg. **Typus Aptenia** N.E.Br. = *Coilomorphoideae* Rappa & Camarrone 1953: 30–31, t. 1 (as "Coilomorphi") nomen invalid. **Typus** not given.

Annual or biennial herbs, small to large shrubs, or geophytes, prostrate, decumbent, or erect, sometimes tufted, rarely creeping, roots sometimes thickened, **I** herbaceous, woody, or succulent and either green and assimilating or with a conspicuous cork layer, terete, angled, or winged, cortex mostly with additional vascular bundles; **L** flat to (almost) cylindrical or slightly channelled, decussate, but often becoming alternate in the **Inf**, or alternate throughout, decussate leaves mostly shortly connate at the base, persistent, marcescent, or deciduous, cylindrical leaves with or without enlarged central water-storing cells, epidermal bladder cells conspicuous and often large or inconspicuous to much flattened and seemingly absent, usually mesomorphic, very rarely somewhat xeromorphic; **Fl** solitary or in cymes, ∅ 0.5–8 cm, **K** 4–5, petals pink, salmon, orange, yellow, cream, sand-coloured, greenish, or white, **K** and petals mostly connate into a short or longer tube rarely free to the base, petals filiform or narrowly lanceolate, rarely much reduced, filamentous staminodes present or absent, stamens smooth or with central papillae on the epidermis cells, nectaries 4–5 or very rarely 3 or 6, (sometimes narrowly) shell-shaped or tubular, separate, rarely reduced, ovary semi-inferior to inferior, septate, with axile placentation; **Fr** a loculicidal hygrochastic capsule or rarely nut-like, capsule opening by means of expanding keels, usually with valve wings which may be inflexed over the valves or reflexed and free or fused in pairs, rarely without valve wings, usually 4–5 locules, very rarely 3 or 6; **S** broadly or narrowly ovate, triangular, D-, kidney-, horseshoe-, or pear-shaped, black, brown, or whitish, testa rough or smooth, with or without a distinct crest; **Chr** x = 9; **Ecol** most species occur in karroid areas, some in disturbed places, some in saline conditions, mainly within the winter rainfall region, but also without; **Distr** SW Angola; S Australia; Azores; Canary Islands; Cape Verdes; Iraq; Iran; Mauritania; Mediterranean basin; Namibia; N Africa; Palestine; EC, NC, WC, S Africa; St Helena; Turkey; California, USA.

Note: For several decades, the name *Mesembryanthemoideae* Ihlenf., Schwantes & Straka (1962) was considered the correct name for the subfamily. *Mesembryanthemoideae* Burnett, however, was published in 1835 (as "Mesembryanthidae") and therefore takes priority.

Based on DNA analysis and some morphological characters, Klak et. al. (2007) united all genera of the **Mesembryanthemoideae** into one genus **Mesembryanthemum** divided into informal groups only. These were formalized later by Klak & Bruyns (2013), when they re-introduced several names of sections by Haworth (1803, 1821) and de Candolle (1828). In order to make them available for their purpose, the authors typified the names accordingly and often arbitrarily, disregarding Recommendations 21B.4. (in a case of change of rank, the original name should be retained) and 22A.1. (a section including the type of a non-homonymous subgenus should be given the same epithet and type as the subgenus) of the Melbourne Code (McNeill et al. 2012).

As argued by Gerbaulet (2012), the nomenclatural changes of Klak et al. (2007) are neither

taxonomically necessary nor do they further the understanding of the subfamily or its classification. Since no new evidence was put forward by Klak & Bruyns (2013) that their drastic nomenclatural approach to the subfamily is imperative, and since their newly formalized subdivision of the genus is contrary to the transparency of the classification system, it is not followed here.

16 genera are recognised.

Aptenioideae = **Mesembryanthemoideae**

Schwantes (SKK 1947: 39) invalidly published the name *Aptenioideae* without a Latin diagnosis.

The name was validated by Bittrich & Hartmann (1988: 250–251) who erroneously rejected the valid name *Mesembryanthemoideae* Ihlenf., Schwantes & Straka (1962) that in turn is superceded by **Mesembryanthemoideae** Burnett (1835).

The subfamily was subdivided by Schwantes (SKK 1947: 39–40) into two tribes, *Aptenieae* and *Dactylopsieae* (as "Dactylopsideae") with a further subdivision of *Aptenieae* into five subtribes *Apteniinae*, *Hydrodeinae*, *Preniinae*, *Aridariinae*, and *Brownanthinae*. According to the findings of Klak et al. (2007), many of these taxa are polyphyletic with the most notable exception of *Dactylopsieae* including only **Dactylopsis** and **Aspazoma**. All tribal and subtribal names are invalid since no Latin diagnosis was given.

Coilomorphoideae = **Mesembryanthemoideae**

In an attempt towards a classification of the *Mesembryanthemaceae* primarily based on the morphology of the nectaries, Rappa & Camarrone (1953: 1–39) invalidly published the subfamily name *Coilomorphoideae* (Rappa & Camarrone 1953: 30 as "Coilomorfi", 1960: 30) without a Latin description and the citation of a type. The circumscription of the subfamily, however, is identical with that of the **Mesembryanthemoideae**. The name *Coilomorphoideae* alludes to the coilomorphic, that is shell-shaped to tubular, nectaries which constitute one of the synapomorphies of the subfamily.

The subfamily *Coilomorphoideae* was further divided into tribes and genera. Here also, names were chosen to highlight character states. At first, Rappa & Camarrone (1953: 1–39) thought two genera sufficient to receive species with five or with four nectaries or locules per fruit. These were *Pentacoilanthus* (from **Gk** *penta*-, five-, *coilos*, hollow, *anthos*, flower) placed in the tribe *Pentaconcheae* (as "Pentaconchi", from **La** *concha*, shell) and *Tetracoilanthus* (from **Gk**, *tetra*-, four-, *coilos*, hollow, *anthos*, flower) placed in the tribe *Tetraconcheae* (as "Tetraconchi", from **La** *concha*, shell). Later (Rappa & Camarrone 1955: 1–16, 1960: 11–32), the generic concept was enlarged to include character states of the valve wings of the fruit. New names incorporating as prefixes pera- (from **Gk** *pera*, leathern pouch, alluding to the valve wings which are inflexed over the valves and form a sort of pouch) and ptero- (from **Gk** *pteron*, wing, alluding to the valve wings which are reflexed and fused in pairs, the valves therefore appearing winged) were coined. The names without one of these two prefixes now denoted the absence of valve wings. To match names and character states, the name *Perapentacoilanthus* was published (Rappa & Camarrone 1955: 1–16) in order to receive all the species of *Pentacoilanthus* of 1953 which all possess fruits with valve wings incurved over the valves. Into *Pentacoilanthus*, species with 5 locules but without valve wings were newly combined (Rappa & Camarrone 1960: 11–32). Ultimately, Rappa & Camarrone (1960) described 6 genera in two tribes. These taxa are: *Pentaconcheae* (5 shell-shaped nectaries) with *Pentacoilanthus* (no valve wings), *Perapentacoilanthus* (valve wings inflexed over the valves), and *Pteropentacoilanthus* (valve wings reflexed and fused in pairs); *Tetraconcheae* (4 shell-shaped nectaries) with *Tetracoilanthus* (no valve wings), *Peratetracoilanthus* (valve wings inflexed over the valves), and *Pterotetracoilanthus* (valve wings reflexed and fused in pairs). All these names are either illegitimate or invalid (for details see the entries under the respective names of the genera and Hartmann & Bittrich 1990). Furthermore, as shown by Klak et al. (2007), the subdivision of the **Mesembryanthemoideae** by means of the characters of the fruit proves to be highly artificial.

Key to the Genera of Mesembryanthemoideae

1.	Annual or short-lived, rarely longer-lived herbaceous plants	**2**
–	Perennial chamaephytes or geophytes	**8**
2.	Flowers without filamentous staminodes, stamens almost reaching the length of the petals when fully expanded, plants short-lived, rarely longer-lived	**Volkeranthus**
–	Flowers with or without filamentous staminodes, stamens considerably shorter than the petals when fully expanded, plants strictly annual or short-lived	**3**
3.	Leaves flat	**4**
–	Leaves cylindrical or almost cylindrical	**6**
4.	Leaves roundish or oval, decussate, connate into a disc or a cone, upper ones much smaller and free, epidermis smooth or with small mesomorphic bladder cells at the margins	**Synaptophyllum**
–	Leaves not connate into a disc or cone, bladder cells present all over, often very large	**5**
5.	Leaves alternate from the base, bladder cells large but somewhat flattened, flowers golden yellow, stigmas bright red	**Callistigma**
–	Leaves decussate, sometimes becoming alternate in the inflorescences, sometimes very large, bladder cells large, especially so on the receptacle, flowers white or pink, sometimes with yellow centre, sometimes greenish, never golden yellow, stigmas never bright red	**Cryophytum**
6.	Leaves very chubby, Ø 7–15 mm, leaves and stems withering at about the same time	**Opophytum**
–	Leaves rather slender, Ø 2–5 mm, the leaves starting to wither sooner than the stems	**7**
7.	Flowers deeply funnel-shaped, Ø c. 60 mm, petals, filamentous staminodes, and stamens very narrow and very numerous, stigmas broad, basally shortly connate with the ovary	**Eurystigma**
–	Flowers cup-shaped, Ø 10–30 mm, petals narrowly lanceolate, filamentous staminodes absent, petals and stamens not particularly numerous, stigmas basally free	**Mesembryanthemum**
8.	Epidermal bladder cells of the leaves and stems different, those of the stems closely packed and xeromorphic, those of the leaves loosely packed and mesomorphic	**9**
–	Epidermal bladder cells of the leaves and stems similar, mesomorphic or very rarely somewhat xeromorphic, large or small, sometimes flattened	**12**
9.	Plants compact, leaves alternate, cylindrical and very chubby, two per vegetation period, with long tubular sheath enveloping the short stems entirely, marcescent and providing a protective cover for the stem during the dry season, flowers remaining open day and night, valve wings of the capsules reflexed and fused in pairs	**Dactylopsis**
–	Plants loosely arranged, leaves decussate, more than two per vegetation period, flat or cylindrical, connate or free, marcescent or deciduous, flowers closing during the night, valve wings of the capsules inflexed over the valves or absent or fruits nut-like	**10**
10.	Leaves cylindrical or almost, free, the bases of a pair broadly overlapping, flower Ø c. 45 mm, vanilla-scented, capsules usually with two seeds per locule	**Aspazoma**
–	Leaves flat or cylindrical, free or connate, but never broadly overlapping, flower Ø 5–35 mm, capsules with many seeds per locule or fruits nut-like with one seed per locule	**11**
11.	Leaves broad and flat, rarely linear and channelled or almost terete, flower Ø 15–35 mm, pale yellow, pink, or white to cream, calyx lobes and petals spreading, seeds dark brown	**Aptenia**
–	Leaves almost cylindrical, obtusely trigonous, or channelled, flower Ø 5–25 mm, white to cream, calyx lobes erect during anthesis, petals recurving over the calyx lobes, seeds cream or light brown	**Brownanthus**
12.	Perennial stems at least for some time with succulent green cortex, stems articulate, sometimes indistinctly so, filamentous staminodes gathered into a cone, translucent except for a thickened middle vein and apically lacerate, rarely (almost) absent, seeds small, 0.5–1.2 mm l, whitish to light brown, without a distinct crest	**Psilocaulon**

(*continued*)

–	Perennial stems without succulent green cortex, never articulate, filamentous staminodes spreading or (almost) absent, seeds large, 1.3–2.0 mm l, brown with a distinct crest or brownish black without a crest	**13**
13.	Leaves flat, veins lignified, the skeleton-like dry leaves persisting and enclosing the young buds	**Sceletium**
–	Leaves flat or thickened, veins not lignified, dry leaves may be persisting, but never enclosing the young buds	**14**
14.	Leaves without a distinct wax layer, bladder cells conspicuous, often large, filamentous staminodes very numerous, merging continuously from stamens to petals, sometimes seemingly absent, but then stamens and stigmas concealed	**Phyllobolus**
–	Leaves with a distinct wax layer, bladder cells small and flattened, filamentous staminodes few or absent	**15**
15.	Stems woody, cortex shiny, filamentous staminodes absent, fruits rather brittle, stalks more or less spiny after the fruits have broken off	**Aridaria**
–	Stems herbaceous or only somewhat woody, cortex of older stems whitish, filamentous staminodes present, fruits robust, locules deep	**Prenia**

Ruschioideae

H. E. K. Hartmann and M. Gerbaulet

Ruschioideae Schwantes in Ihlenf., Schwantes & Straka 1962: 54; Bittrich & Hartmann 1988: 239–254; Bittrich 1990: 491–507; Hartmann 1991: 75–157; Hartmann 2001a: 12–22; Hartmann 2001b: 12–22; Klak et al. 2003: 1433–1445; Thiede 2004: 51–57; Thiede et al. 2007: 372–380 ≡ *Ruschioideae* Schwantes SKK 1947: 35 nomen invalid. **Typus Ruschia** Schwantes = *Anectarioideae* Rappa & Camarrone 1953: 30 (as "Anettari") nomen invalid. **Lectotypus**, here designated: **Glottiphyllum** N.E.Br. = *Caryotophoroideae* Ihlenf., Schwantes & Straka in Schwantes in Jacobsen 1960: 962 nomen invalid. ≡ *Caryotophoroideae* Ihlenf., Schwantes & Straka 1962: 54 **Typus Caryotophora** Leistner = *Hymenogynoideae* Schwantes KuaS 1957: 168 nomen invalid. ≡ *Hymenogynoideae* Schwantes in Ihlenf., Schwantes & Straka 1962: 54 **Typus Hymenogyne** Haw. = *Lophomorphoideae* Rappa & Camarrone 1953: 30 (as "Lofomorfi") nomen invalid. **Typus** not chosen.

Annuals or perennials, shrubs to trees, climbing, creeping, prostrate, compact, or reduced to a single leaf-pair; **L** mostly trigonous to triquetrous, often with a marked hood or hump, rarely flat, basally mostly connate, in several genera almost free, with bladder cells or with a firm, xeromorphic epidermis; **Fl** in distinct **Inf** separated from the basal vegetative part of the plant, almost the entire plant representing an **Inf**, or solitary, sometimes only appearing so but in reality a perennial **Inf**, **K** 4–8, mostly 5, the lobes mostly free, petals mainly purple or yellow, both colours in all shades, also white, red, orange, or copper, filamentous staminodes absent or present, rarely concealing the stamens mostly equipped with long papillae near their bases, nectaries lophomorphic or crest-like, either separated or connate into a ring, rarely apparently absent, placenta parietal to basal, very rarely central; **Fr** mostly a hygrochastic capsule with expanding keels mostly extending into the locule and expanding sheets on the valves which can possess valve wings, covering membranes absent or present, often with additional closing devices; **S** smooth to echinate, whitish to dark brown; **Chr** x = 9; **Ecol** many genera in winter rainfall areas with <300 mm precipitation p.a., a number in regions with bimodal rainfall and some in summer rainfall areas; **Distr** S parts of Australia; Botswana; Chile; Lesotho; Namibia; New Zealand; all provinces of S Africa; Swaziland; secondarily also on the Channel Islands; in S England; S Europe; S coast of the Mediterranean Sea; California, USA and probably other areas.

Note: With 118 genera **Ruschioideae** is the largest subfamily of the **Aizoaceae**. The distinguishing features are the parietal to basal placentation, the crest-shaped or flat nectaries,

and probably also the free calyx lobes and petals. This subfamily inhabits the widest range of ecological niches of all subfamilies of the **Aizoaceae** and has developed the most diverse growth forms and leaf surfaces. Only in the **Ruschioideae** a firm, xeromorphic epidermis is found, probably developed in several independent lines (Ihlenfeldt & Hartmann 1982; Jürgens 1990).

Below the rank of subfamily, Ihlenfeldt, Schwantes & Straka (1962: 54–55) were the first to validly publish tribes in the **Ruschioideae**. Five tribes were distinguished, partly based on the invalidly published system of Schwantes (SKK 1947: 34–40) who used mainly fruit characters. These five tribes are: **Apatesieae**, *Carpobroteae*, **Ruschieae**, *Saphesieae*, and *Skiatophyteae*. Chesselet et al. (2002: 295–308) reinvestigated this subdivision using primarily characters of the floral nectary. They formally included the monotypic tribes *Saphesieae* (**Saphesia**) and *Skiatophyteae* (**Skiatophytum**) as well as the genera **Caryotophora** and **Hymenogyne** in the **Apatesieae** and *Carpobroteae* in the **Ruschieae**, but separated two new tribes from the **Ruschieae**: *Delospermateae* and **Dorotheantheae**. In subsequent molecular studies (Klak et al. 2003: 1433–1445; Thiede 2004: 51–58; Thiede et al. 2007: 372–380), the **Apatesieae** and **Dorotheantheae** were well supported, but the *Delospermateae* and **Ruschieae** together presented as one poorly resolved clade with one exception: The genus **Drosanthemum** together with *Delosperma asperulum* form the basal clade of the *Delospermateae* and **Ruschieae** combined. Chesselet et al. (2004), therefore, established a new tribe **Drosanthemeae** for the single genus **Drosanthemum** including **Drosanthemum asperulum**. At present, four tribes are accepted for the **Ruschioideae**.

Schwantes (SKK 1947: 34–40) had further subdivided his tribes into subtribes, all of them invalidly published. A couple of these names have later been validated, e.g. *Dorotheanthinae* Schwantes ex Ihlenfeldt & Struck (1987: 433), *Leipoldtiinae* H.E.K. Hartmann (BB 1983: 50), *Ruschiinae* Dehn (1993: 185), but no new comprehensive subdivision into subtribes has been proposed yet.

Apatesieae Schwantes ex Ihlenfeldt, Schwantes & Straka 1962: 55; Ihlenfeldt & Gerbaulet 1990 BJS 11: 457–498; Chesselet et al. 2002: 306 **Typus Apatesia** N.E.Br. = *Saphesieae* (Schwantes) Ihlenfeldt in Ihlenfeldt, Schwantes & Straka 1962: 55 ≡ *Saphesieae* Ihlenfeldt in Schwantes in Jacobsen 1960: 954 nomen invalid. ≡ *Saphesiinae* Schwantes in Jacobsen 1960: 954 nomen nudum **Typus Saphesia** N.E.Br. = *Skiatophyteae* (Straka) Ihlenfeldt in Ihlenfeldt, Schwantes & Straka 1962: 55 ≡ *Skiatophytinae* Straka 1955: 161 nomen invalid. **Typus Skiatophytum** L.Bolus.

Plants annual to biennial or perennial; **L** flat or trigonous to subcylindrical, basally free, mesomorphic, bladder cells completely or partially reduced; **Fl** isomerous or pleiomerous, with false septa, with a broad, flat nectary ring (holonectary), yellow or white, **Fr** loculicidal capsule, hygrochastic with expanding keels only, or xerochastic, with (sometimes incomplete) abaxial seed pockets containing 1–2 seeds, or a nut.

Note: Seven genera are included: **Apatesia**, **Carpanthea**, **Caryotophora**, **Conicosia**, **Hymenogyne**, **Saphesia**, and **Skiatophytum**.

Dorotheantheae (Schwantes ex Ihlenf. & Struck) Chesselet, G.F.Sm. & A.E. van Wyk 2002: 306; Ihlenfeldt & Struck M. 1987 BBP 61: 411–453; Klak & Bruyns 2012: 293–307 ≡ *Dorotheanthinae* Schwantes ex Ihlenfeldt & Struck 1987: 433 **Typus Dorotheanthus** Schwantes.

Plants annual; **L** flat, basally free, mesomorphic, bladder cells prominent, occurring all over the leaf surface and other herbaceous parts; **Fl** isomerous, with broad, flat, separate nectaries (meronectary); **Fr** loculicidal capsule, hygrochastic, with expanding keels and expanding sheets or with expanding sheets only.

Note: Four genera are included: **Aethephyllum**, **Cleretum**, **Dorotheanthus**, and **Pherolobus**.

Drosanthemeae Chesselet, G.F.Sm. & A.E. van Wyk 2004: 49 **Typus Drosanthemum** Schwantes.

Plants perennial; **L** thickened, basally mostly free, mesomorphic, with prominent bladder cells; **Fl** isomerous, with crested or lobed (lophomorphic) separate nectaries (meronectary);

Fr loculicidal capsule, hygrochastic, with expanding sheets and keels.

Note: Contains only one genus, **Drosanthemum**, including **Drosanthemum asperulum**, formerly placed in **Delosperma**.

Ruschieae Schwantes ex Ihlenfeldt, Schwantes & Straka 1962: 54; Chesselet et al. 2002: 306; Chesselet et al. 2004: 49–51; Klak et al. 2013: 1005–1020 ≡ *Ruschiinae* Dehn 1993: 185 **Typus Ruschia** Schwantes = *Delospermeae* Chesselet, G.F.Sm. & A.E. van Wyk 2002: 306 **Typus Delosperma** N.E.Br. = *Carpobroteae* Schwantes ex Ihlenfeldt, Schwantes & Straka 1962: 55 **Typus Carpobrotus** N.E.Br. = *Leipoldtiinae* H.E.K. Hartmann BB 1983: 50 **Typus Leipoldtia** L.Bolus.

Plants perennial; **L** thickened, basally fused, mesomorphic with or without prominent bladder cells and/or hairs, or xeromorphic with homocellular or heterocellular surfaces; **Fl** isomerous or pleiomerous, with crested or lobed (lophomorphic) separate nectaries (meronectary) or a nectary ring (holonectary) or nectaries seemingly absent; **Fr** mostly a loculicidal capsule, hygrochastic, with expanding sheets and keels, sometimes a juicy berry, or a nut.

Note: Includes all remaining 106 genera of the **Ruschioideae**.

Anectarioideae = **Ruschioideae**

The name *Anetcarioideae* Rappa & Camarrone (1953: 30 as "Anettari", 1960: 31) was published invalidly without a Latin description or the citation of a type. The name was part of a classification system of the *Mesembryanthemaceae* based primarily on the morphology of the nectaries. The name *Anectarioideae,* meaning "without nectaries", alludes to the absence of nectaries in the flower. Five species of the genus **Glottiphyllum** were listed (1953). The name *Anettarioideae* is therefore a synonym of the subfamily **Ruschioideae**.

Caryotophoroideae = **Ruschioideae**

The name for the subfamily *Caryotophoroideae* was published invalidly at first (Ihlenfeldt et al. in Schwantes in Jacobsen 1960: 962) and validated 2 years later as *Caryotophoroideae* Ihlenf., Schwantes & Straka (1962: 54) with a Latin description. Only one genus was included, **Caryotophora**. The rank of subfamily was chosen because the oligomerous gynoecium develops into a hard schizocarpous fruit, a unique situation within the *Mesembryanthemaceae*. Bittrich (1987: 50–53) placed **Caryotophora** in the **Ruschioideae**, based on the fruit ontogeny. The name *Caryotophoroideae* therefore becomes a synonym of **Ruschioideae**.

Hymenogynoideae = **Ruschioideae**

The subfamily name *Hymenogynoideae* was at first published by Schwantes (KuaS 1957: 168) as an invalid name and validated in 1962 as *Hymenogynoideae* Schwantes in Ihlenf., Schwantes & Straka (1962: 54) with a Latin description. The only genus, **Hymenogyne**, had already been separated from **Mesembryanthemum** by Haworth (1821: 192). The rank of subfamily was mainly chosen because of the peculiarities of the fruit which develops false septa and retains the seeds in clausae. Bittrich (1987: 50–52), after studying the ontogeny of the fruit, concluded that **Hymenogyne** should better be placed in the **Ruschioideae**. Ihlenfeldt & Gerbaulet (1990) placed **Hymenogyne** next to **Apatesia**. The name *Hymenogynoideae* is therefore a synonym of **Ruschioideae**.

Lophomorphoideae = **Ruschioideae**

Rappa & Camarrone invalidly published the name *Lophomorphoideae* (1953: 30 as "Lofomorfi", 1960: 31) without a Latin description or the citation of a type while attempting a classification of the *Mesembryanthemaceae* primarily based on the morphology of the nectaries. The name *Lophomorphoideae* alludes to the lophomorphic, that is crest-shaped, nectaries of the flower.

The subfamily was further divided into two tribes, *Holonectarieae* (Rappa & Camarrone 1953, 1960 as "Olonettari", from **Gk** *holos*, entire) and *Meronectarieae* (Rappa & Camarrone 1953, 1960 as "Meronettari", from **Gk** *meros*,

Key to the Genera of Ruschioideae

1.	Fruit a fleshy berry	**2**
–	Fruit dry	**3**
2.	Plants prostrate, creeping	**Carpobrotus**
–	Plants erect to decumbent	**Sarcozona**
3.	Fruit a nut, finally disintegrating into nutlets, or breaking into mericarps	**4**
–	Fruit a loculicidal capsule	**6**
4.	Fruit woody, dispersal units nut or nutlets	**5**
–	Fruit leathery, breaking into one-seeded mericarps as dispersal units	**Hymenogyne**
5.	Fruit $>$ 10 mm in Ø, finally breaking completely into mericarps; leaves flat	**Caryotophora**
–	Fruit $<$ 7 mm in Ø; the sclerotinized vascular bundles of the fruit remaining on the plant; leaves more or less club-shaped to falcate	**Ruschianthemum**
6.	Capsule xerochastic, expanding tissue absent	**7**
–	Capsule hygrochastic, expanding tissue present	**9**
7.	Locules 5–7	**8**
–	Locules $>$ 8	**Conicosia**
8.	Flat base of bottom of fruit widened, containing seeds, formed like a ring-shaped pocket, septa remaining connate with valves	**Saphesia**
–	Fruits with separate seed pockets at half the height of the capsule, septa free from valves	**Skiatophytum**
9.	Leaves flat, plants annual	**10**
–	Leaves thickened, plants perennial	**15**
10.	Bladder cells reduced, only present on leaf margins and receptacle, sometimes hair-like	**11**
–	Bladder cells not reduced, present on al green parts	**12**
11.	Locules open, seeds visible, seed pockets at outer base of locules, pedicels glabrous, leaf margins with bladder cells	**Apatesia**
–	Locules covered by septa arching over them, seeds hidden, placenta raised, but without seed pockets, pedicel and calyx with long hairs, leaf margins with long hairs	**Carpanthea**
12.	Leaves lyrate	**Aethephyllum**
–	Leaves entire	**13**
13.	Expanding sheets and keels present	**Cleretum**
–	Expanding sheets only	**14**
14.	Stigmas persisting on the capsule, woody	**Dorotheanthus**
–	Stigmas absent in ripe capsule	**Pherolobus**
15.	Capsule opening but once, rarely again, but never repeatedly, expanding keels breaking after first opening	**16**
–	Capsule opening repeatedly, expanding keels remaining functional	**17**
16.	Locules 5–6, valves free to base, valve wings broad, hard, erect	**Stoeberia**
–	Locules (4–6)–12, valves united laterally at base, valve wings absent	**Stayneria**
17.	Covering membranes present	**18**
–	Covering membranes absent, sometimes narrow rims present	**20**
18.	Fruits developing on a twisting thin stalk, with a distinct breaking-point below the base, breaking off when ripe, tumble fruits more or less globose	**Brianhuntleya**
–	Fruit development different	**19**
19.	Covering membranes of constant shape, even after the seeds have been removed	**48**
–	Covering membranes declining into empty locules	**49**
20.	Expanding keels merging into expanding sheets	**21**
–	Expanding keels distinctly separated from expanding sheets, keels parallel, high, more or less sharply pleated	**22**

(*continued*)

21.	Heterophyllous shrubs	**Mitrophyllum**
–	Homophyllous plants	**46**
22.	Calyx and leaves sticky, sand adhering to it	**Psammophora**
–	Calyx and leaves not sticky	**23**
23.	Valve wings absent or as awns	**24**
–	Valve wings present, more or less rectangular	**27**
24.	Capsule opening incompletely (valves at most erect), breaking into mericarps early, leaves more or less club-shaped with apical windows	**Frithia**
–	Capsule opening completely (valves spreading) and persistent, leaves without apical windows	**25**
25.	Pedicel very long (5–12 cm), flowers mostly ternate, leaves keeled, toothed, plants compact	**Carruanthus**
–	Pedicel shorter (to 2.5 cm), flowers solitary, leaves not keeled, not toothed, plants shrubby, caespitose to decumbent or creeping	**26**
26.	Shrubs, flowers opening midday	**Jensenobotrya**
–	Plants creeping or caespitose, flowers opening at night	**Neohenricia**
27.	Valve wings at most as broad as expanding keels	**28**
–	Valve wings broader than expanding keels	**29**
28.	Plants creeping	**Mossia**
–	Plants compact to caespitose	**47**
29.	Bracteoles present (different from foliage leaves)	**42**
–	Bracteoles absent (indistinguishable from foliage leaves)	**30**
30.	Base of capsule with very long soft hairs, leaves hairy	**Gibbaeum**
–	Base of capsule and leaves not velvety but glabrous, with bladder cells, or papillate	**31**
31.	Flowers with a short hypanthium	**32**
–	Flowers with free elements from above the ovary	**34**
32.	Leaves smooth, glabrous	**Peersia**
–	Leaves finely granulate and rough	**33**
33.	Plants mat-forming, if more compact, leaves trigonous in section	**Rhinephyllum**
–	Plants compact, leaves mostly dentate, if not, leaves apically broadly widened	**Stomatium**
34.	Base of capsule and leaves with bladder cells	**35**
–	Base of capsule and leaves xeromorphic, glabrous	**37**
35.	Plants heterophyllous, always compact	**Oophytum**
–	Plants homophyllous	**36**
36.	Plants caespitose to shrubby, locules 5	**Delosperma**
–	Plants forming dense mats, adventitious roots present, locules 5–8	**Malotigena**
37.	Leaves obliquely triquetrous	**Schwantesia**
–	Leaves isometric	**38**
38.	Plants caespitose	**Corpuscularia**
–	Plants compact	**39**
39.	Plants forming clumps above the ground	**Dinteranthus**
–	Plants sunken in the ground	**40**
40.	Predominant number of locules per fruit in a population 5 or 6	**Lithops**
–	Predominant number of locules per fruit 7 or more	**41**
41.	Seeds tuberculate, tubercles distant	**Dinteranthus**
–	Seeds smooth to rugose	**Lithops**
42.	Flowers in inflorescences raised well above the plant	**43**
–	Flowers solitary	**44**

(*continued*)

43.	Flowers remaining open during and after anthesis, petals stiff	**Nelia**
–	Flowers closing over night, petals rather lax	**Hartmanthus**
44.	Locules ≤ 7	**Conophytum**
–	Locules ≥ 10	**45**
45.	Plants above ground, leaves almost semi-globose, more or less appressed	**Namibia**
–	Plants at least partly sunken in the ground, leaves triangular and pointed, spreading	**Nananthus**
46.	Locules mostly 5, stamens > 10	**Delosperma**
–	Locules 4, stamens < 10	**Ectotropis**
47.	Capsules dark brown, top rounded	**Antegibbaeum**
–	Capsules light brown, top flat	**Ruschianthus**
48.	Covering membranes without distal recurving and always without any additional closing devices like rodlets, ledges or bulges at their distal ends	**49**
–	Covering membranes with a more or less distinct distal recurving, with or without additional closing devices like rodlets, ledges or bulges, if straight, always with some additional closing device	**91**
49.	Covering membranes declining into the empty locules along a preformed edge	**78**
–	Covering membranes straight or only slightly and gradually declining into empty locules	**50**
50.	Plants with distinct prominent bladder cells, glistening in the sun, often appearing scaly on herbarium material	**51**
–	Plants rough, glabrous or hairy	**63**
51.	Plants heterophyllous	**52**
–	Plants homophyllous	**57**
52.	Expanding keels divergent, emerging gradually from expanding sheets	**53**
–	Expanding keels parallel, sheets separate from expanding keels	**Oophytum**
53.	Plants compact and low, < 4 cm h	**Diplosoma**
–	Plants shrubby, if compact, > 5 cm h	**54**
54.	Basal parts of old leaf sheaths sclerotic, completely enveloping the stem	**Monilaria**
–	Old leaf-sheaths papery-pergamentaceous	**55**
55.	Flowers basally enclosed by connate hypsophylls forming a cup	**Dicrocaulon**
–	Flowers exserted above leaves, no cups	**56**
56.	Both leaf pairs of a season connate for $> 30\%$	**Meyerophytum**
–	One leaf pair of a season connate for $< 25\%$, spreading, the other for $> 50\%$, erect	**Mitrophyllum**
57.	Leaves with an apical diadem	**Trichodiadema**
–	Leaves without an apical diadem	**58**
58.	Bladder cells on leaves thin-walled, collapsing when dry, surface glittering	**59**
–	Bladder cells thick-walled, constant in shape, surface dull	**62**
59.	Surfaces of primary internodes with prominent bladder cells	**Drosanthemum**
–	Surfaces of primary internodes glabrous	**60**
60.	Leaves fat-digitiform, > 4 cm l	**Jacobsenia**
–	Leaves subterete to trigonous, < 3 cm l	**61**
61.	Locules 5	**Mestoklema**
–	Locules 6–11	**Malephora**
62.	Locules ≥ 8	**Jacobsenia**
–	Locules 6	**Knersia**
63.	Flowers white over pink to purple	**64**
–	Flowers yellow	**72**
64.	Fruits brown, hard	**65**
–	Fruits whitish to light brown, more or less soft	**69**

(*continued*)

65.	Fruits in raised inflorescences	**Nelia**
–	Fruits solitary	**66**
66.	Plants shrubby	**Polymita**
–	Plants compact to caespitose	**67**
67.	Leaves digitiform, more than 3x as long as broad, valve wings broad	**Antegibbaeum**
–	Leaves more or less trigonous, with convex sides, plants compact, valve wings narrow to absent	**68**
68.	Plants with thick tap-roots	**Ebracteola**
–	Plants with thinner roots	**90**
69.	Erect shrubs	**70**
–	Compact, creeping, or caespitose plants	**71**
70.	Calyx lobes 4	**Juttadinteria**
–	Calyx lobes 5	**Hartmanthus**
71.	Flowers bracteolate	**Hammeria**
–	Flowers ebracteolate	**77**
72.	Closing body bipartite	**Rhombophyllum**
–	Closing body absent or present as a single body	**73**
73.	Closing body a broad sill	**Bergeranthus**
–	Closing body absent or present as a round body	**74**
74.	Fruits on short stalks, closing body big and round	**Bijlia**
–	Fruits on long stalks, closing body absent or small	**75**
75.	At least some leaves with teeth along keel and/or margins	**Chasmatophyllum**
–	All leaves without teeth	**76**
76.	Leaves soft, fruits whitish, locules always with false septa	**Malephora**
–	Leaves firm, fruits brown, locules without false septa	**Hereroa**
77.	Nectary a crenulate ring	**Disphyma**
–	Nectary as 6 glands	**Gibbaeum**
78.	Valve wings absent, rims of valves high	**Ebracteola**
–	Valve wings present, at least basally very broad	**79**
79.	Capsules brown	**80**
–	Capsules whitish-grey	**83**
80.	Fruits persisting on rather long stalks	**Prepodesma**
–	Fruits breaking off their stalks, dispersed as tumble fruits	**81**
81.	Leaves velvety	**Deilanthe**
–	Leaves smooth to rough from warts	**82**
82.	Leaves sharply pointed and triangular in section, surface finely warty	**Rabiea**
–	Leaves flattened or rounded at tips and margins, surface with prominent warts	**Aloinopsis**
83.	Closing body present	**84**
–	Closing body absent	**85**
84.	Base of capsule papillate, leaves dotted	**Ihlenfeldtia**
–	Base of capsule smooth, leaves smooth	**Tanquana**
85.	Base of capsule papillate; leaves papillate, keeled, toothed	**Vanheerdea**
–	Base of capsule smooth, leaves smooth or warty, never toothed	**86**
86.	Locules 5–7, rarely in single fruits 8	**87**
–	Locules $\geq$ 8 in all fruits	**89**
87.	Locules very shallow, covering membranes therefore held up by the funicles; flowers appearing after the leaf pairs thus seemingly lateral	**Didymaotus**
–	Locules deeper, covering membranes bending into empty locule; flowers distinctly terminal	**88**

(*continued*)

88.	Leaves warty, plants mostly sunken in the ground	**Titanopsis**
–	Leaves deltoid, keeled, gibbose, plants above ground	**Lapidaria**
89.	Shrubs	**Zeuktophyllum**
–	Compact plants	**Dracophilus**
90.	Top of capsule convex from high valve rims	**Cerochlamys**
–	Top of capsule flat	**Vlokia**
91.	Closing body absent	**92**
–	Closing body present, sometimes as a broad sill	**108**
92.	Valve wings, at least at base, much broader than expanding keels	**93**
–	Valve wings absent or narrow, i.e. $\leq$ width of expanding keels	**99**
93.	Valve wings tapering into awns towards the tip of the valve	**94**
–	Valve wings rectangular	**95**
94.	Capsules multilocular, plants compact	**Pleiospilos**
–	Capsules 5-locular, if multilocular, plants shrubby	**Erepsia**
95.	Valve wings in open capsules stiff, stretching over the locules and not moving outwards with the valves	**Faucaria**
–	Valve wings in open capsules flexible, moving outwards with the valve	**96**
96.	Seeds echinate	**Braunsia**
–	Seeds with low papillae	**97**
97.	Plants compact	**Orthopterum**
–	Plants shrubby, rarely caespitose or creeping	**98**
98.	Filaments broadened and connate at base	**Circandra**
–	Filaments filiform, free	**Lampranthus**
99.	Leaves mesomorphic	**100**
–	Leaves xeromorphic	**101**
100.	Flowers yellow	**Scopelogena**
–	Flowers white to purple	**Oscularia**
101.	Seeds echinate	**Namaquanthus**
–	Seeds smooth to moderately papillate	**102**
102.	Surface of ovary concave, forming a hypanthium in the flower	**Erepsia**
–	Surface of ovary flat to raised	**103**
103.	Leaves connate into a sheath which is continuous with the cortex of the preceding internode	**104**
–	Leaves more or less free or only somewhat fused	**106**
104.	Free parts of leaves $<$ 10 mm l	**Smicrostigma**
–	Free parts of leaves 20–30 mm l	**105**
105.	Fruits reddish-brown, not closing again completely after the first opening, shrubs to 2 m h	**Stayneria**
–	Fruits with a white cover on top, closing completely again after the first opening, shrubs to c. 40 cm h	**Zeuktophyllum**
106.	Flowers white to pink, leaves grey from an extremely thick wax cover	**Wooleya**
–	Flowers purple or magenta, leaves bright green	**107**
107.	Leaves club-shaped, apically rounded, flowers ebracteolate, 4 calyx lobes	**Enarganthe**
–	Leaves with a marked tooth or mucro at the tip, flowers with bracteoles, 5 calyx lobes	**Esterhuysenia**
108.	Closing body bipartite	**109**
–	Closing body not divided	**110**
109.	Closing body U-shaped, leaves mesomorphic, plants creeping	**Disphyma**
–	Closing body of two more or less flat plates, leaves xeromorphic, plants compact to shrubby	**Rhombophyllum**

(*continued*)

110.	Leaves soft, mesomorphic with bladder cells	**111**
–	Leaves hard, xeromorphic without bladder cells	**112**
111.	Covering membranes more or less straight, plants heterophyllous	**Mitrophyllum**
–	Covering membranes undulate, leaves anisophyllous in a pair	**Glottiphyllum**
112.	Expanding keel clearly separate from expanding sheet	**113**
–	Expanding keel merging into expanding sheet	**Bijlia**
113.	Valve wings broad (at least at base)	**114**
–	Valve wings absent or narrow ($\leq$ width of expanding keels)	**125**
114.	Valve wings more or less rectangular	**115**
–	Valve wings tapering from a broad base	**123**
115.	Closing bodies not larger than seeds, leaving space at the sides	**116**
–	Closing bodies larger than seeds, more or less blocking the distal opening of the locule	**119**
116.	Capsule multilocular	**117**
–	Capsule pentamerous	**118**
117.	Capsules dispersed as tumble fruits, leaves with apical window, plants under ground	**Fenestraria**
–	Capsules persistent on pedicels, leaves fusiform without a window, plants above ground	**Jordaaniella**
118.	Top of capsule with remains of hard bases of stigmata in the centre	**Arenifera**
–	Top of capsule flat in the centre	**Amphibolia**
119.	Base of capsule velvety or rough from papilla	**Cheiridopsis**
–	Base of capsule glabrous	**120**
120.	First leaves of side branches connate $>$ 50%	**Vanzijlia**
–	First leaves of side branches hardly connate like all others (seedlings occasionally with connate leaf pairs)	**121**
121.	Capsules with closing bulges	**Cephalophyllum**
–	Capsules with closing rodlets	**122**
122.	Top of capsule turret-shaped; procumbent branches from compact centre not rooting	**Hallianthus**
–	Top of capsule rounded, but not turret-shaped, erect to ascending, or saltatory and rooting	**Leipoldtia**
123.	5 locules	**Eberlanzia**
–	Many locules	**124**
124.	Leaves sharply triquetrous, grey	**Machairophyllum**
–	Leaves trigonous to semi-ovate, gibbose, dark green	**Pleiospilos**
125.	Closing body large, completely locking the locule	**126**
–	Closing body smaller, leaving some space at the sides	**132**
126.	Capsule pentamerous	**127**
–	Capsule multilocular	**129**
127.	Flowers yellow	**Bergeranthus**
–	Flowers pink to purple	**128**
128.	Leaves awl-shaped, the keel visible as a line in turgid conditions	**Marlothistella**
–	Leaves never awl-shaped, a keel always prominently visible	**Antimima**
129.	Leaves glabrous	**130**
–	Leaves velvety, hairy or rough	**131**
130.	Flowers with a hypanthium; capsule 12–24 locular	**Argyroderma**
–	Flowers without a hypanthium; capsule 8-locular	**Octopoma**
131.	Leaves and base of capsule velvety	**Odontophorus**
–	Leaves and base of capsule rough	**Cheiridopsis**
132.	Flowers with c. 2000 elements	**Cylindrophyllum**
–	Flowers with up to 300 elements	**133**
133.	Flowers yellow, shrubs compact	**134**
–	Flowers white to purple	**135**

(*continued*)

134.	Leaves sharply triquetrous, grey	**Machairophyllum**
–	Leaves scimitar-shaped with a rounded keel	**Hereroa**
135.	Plants compact, caespitose or creeping	**136**
–	Shrubs	**137**
136.	Petals white or purple, never striped	**Khadia**
–	Petals with a central, longitudinal deep purple stripe, i.e. vittate	**Acrodon**
137.	Seeds echinate or markedly papillate	**Astridia**
–	Seeds smooth to rough	**138**
138.	Flowers in annually enlarged, persisting inflorescences	**Ottosonderia**
–	Flowers solitary or in annually formed and ripening inflorescences, new ones formed every year	**139**
139.	Fruits mostly 5, rarely 6 locules	**140**
–	Fruits with mostly 8, rarely 7–11 locules	**142**
140.	Valves without wings	**Ruschia**
–	Valves with narrow wings broadest in their middle	**141**
141.	Calyx lobes 4–5, prominent closing rodlet present	**Ruschiella**
–	Calyx lobes 6, sharp closing ledge on distal rim	**Schlechteranthus**
142.	Leaves of a pair basally nearly free	**Lampranthus**
–	Leaves of a pair basally connate, forming a short sheath	**Phiambolia**

Key to the Genera of Sesuvioideae

1.	Fruit a nut	**Tribulocarpus**
–	Fruit a circumscissile capsule	**2**
2.	Style 1	**Trianthema**
–	Styles 2–5	**3**
3.	Septa complete in ripe fruits; seeds brown to blackish	**4**
–	Septa incomplete or absent in ripe fruits; seeds light coloured	**Cypselea**
4.	Operculum of capsule breaking into 2 parts, 4 seeds per fruit	**Zaleya**
–	Operculum of capsule in one piece; numerous seeds per fruit	**Sesuvium**

part), denoting the shape of the nectary, and ultimately six (1960) subtribes (Rappa & Camarrone 1953, 1960). All names below subfamily are also invalid.

Since all the genera cited under *Lophomorphoideae* Rappa & Camarrone 1953 and 1960 are now placed in the subfamily **Ruschioideae**, the former name is a synonym of the latter.

Sesuvioideae

H. E. K. Hartmann and M. Gerbaulet

Sesuvioideae Lindley 1846: 527; Adamson 1962: 243–253; Bittrich & Hartmann 1988: 239–254; Bittrich 1990: 491–507; Hartmann 2001a: 21; Hartmann 2001b: 21; Klak et al. 2003: 1433–1445; Thiede 2004: 51–58 ≡ *Sesuviaceae* Horaninow 1834: 83 **Typus Sesuvium** L.

Prostrate to erect perennials or annuals; **L** flat to terete, more or less unequal, with or without stipule-like appendages, often with membranous sheaths at the base of the petiole, leaf surface with more or less prominent bladder cells, hairy or smooth; **Inf** terminal but apparently axillary through sympodial branching, **Fl** solitary or in clusters, rarely in somewhat loose dichasia, perianth with subapical appendages with unifacial tips, rarely without, perigynous, 1–5 styles, ovules 2-many; **Fr** a circumscissile capsule or a nut; **S** completely enveloped by an aril; **Chr** x = 8; **Ecol** coastal to inland in mostly moister climates than the other subfamilies; **Distr** worldwide in the tropics and subtropics.

Note: Based on molecular studies (Klak et al. 2003: 1433–1445; Thiede 2004: 51–58), the genus **Tribulocarpus** (*Tetragonoidedae*) is now included in the **Sesuvioideae**. Five genera are distinguished.

Members of the subfamily are probably best known from tropical coasts in brackish soil, sometimes on rocks, often near mangrove, where the plants can form conspicuous ground covers, red to purple in many cases. Other members are found in disturbed areas near roads, being typical weeds, or in low and open deciduous bushland or woodland.

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