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Cotyledon – a small, highly diverse and complex African genus

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*Cotyledon* is a small genus of Crassulaceae with a very wide distribution throughout Africa. It is extremely diverse, particularly in terms of stem and leaf form and arrangement. Hybridisation accounts for a significant amount of this diversity which is illustrated here. Photos by the author.

Introduction

From its inception *Cotyledon* has had a very chequered history. When first described by Linnaeus in 1753 it included what is now the type species, *Cotyledon orbiculata* L. but also *Cotyledon umbilicus-veneris* L., the common and widespread European navelwort, now known as *Umbilicus rupestris* (Salisbury) Dandy. So, *Cotyledon* began life as a ‘catch-all’ genus within the Crassulaceae for those species with five petals at least partially fused into a distinct tube, usually with the tips of the lobes free to some degree. At its most expanded state it included not only African and European species but also North American species with tubular flowers, now separated as genera such as *Echeveria* and *Dudleya*! Fusion of petals to form a tube distinguished *Cotyledon* from *Sedum* and *Crassula*, which generally had five petals but in these genera the petals are arranged either freely or with a very shallow tube giving a star-like appearance to the flower. *Kalanchoe* and allies were also distinct in having four petals but again usually partially fused into a tube.

The modern concept of *Cotyledon* was first arrived at by Berger (1930) who accepted *Adromischus* and *Umbilicus* as distinct genera, along with a few other minor segregates such as *Pistorinia*. However, he maintained in *Cotyledon* the southern African species that are winter growers with deciduous leaves. Finally, Tölken (1978), as part of his survey of Crassulaceae for the *Flora of Southern Africa* (published as Tölken, 1985), separated off these species in his new genus *Tylecodon* (the name being an anagram of *Cotyledon*). It is now a genus of just 16 species of perennial shrubs.

Fig. 1 The first illustration of *C. orbiculata* from Stapelius (1644)

Fig. 2 Engraving of *C. orbiculata* from Hermann (1687)

Fig. 3 *Cotyledon orbiculata* from Curtis (1795)
with paired, opposite, stiff persistent leaves and relatively large tubular, pendulous orange-red flowers. In contrast, *Tylecodon* species are winter growers with spirally-arranged, soft, deciduous leaves, whilst *Adromischus* has small, usually erect, non-red flowers (*Adromischus phillipsiae* being an atypical species with pendulous red flowers).

In terms of distribution *Cotyledon* is now principally an African genus that just enters south-western Arabia. It does not occur naturally in Europe or America. From a phytogeographical perspective it is interesting to compare the distribution of *Cotyledon* with that of *Crassula* and *Kalanchoe*. Both these latter genera are widespread in Africa and also occur in Madagascar where *Kalanchoe* is especially diverse, whereas in contrast *Cotyledon* is absent. The inference here, yet to be tested, is that *Cotyledon* evolved after the separation of Madagascar from the African mainland.

*Cotyledon* (together with *Tylecodon*) is well served by a modern well-illustrated monograph (Van Jaarsveld & Koutnik, 2004).

**Cotyledon orbiculata** L.

This species has a long and distinguished history as one of the earliest South African succulents to be described and illustrated in European botanical literature (Gunn & Codd, 1981). In one of the earliest publications including South African plants, Stapelius (or Van Stapel) (1644: p.335) published an engraving of *Sedum arborescens promontorii bonae spei* or “the arborescent *Sedum* from the Cape of Good Hope” (Fig. 1), alongside what is now known as *Orbea variegata* (L.) Haworth. The next important publication on this species was Hermann (1687) who published the first life-like image of *C. orbiculata* as *Sedum Africanum frutescens incanum orbiculatis foliis* or “the shrubby African *Sedum* with white orbiculate leaves” (Fig. 2), which for the time was a reasonably accurate description of the species. Linnaeus formally described this species in 1753 as *Cotyledon orbiculata* L. based principally on the Hermann image, which has since been designated as the type.

Not long after, Curtis (1795) illustrated *C. orbiculata* in his famous *Botanical Magazine* as “the round-leaved navel-wort” (Fig. 3) in reference to the genus which at that time included the common navelwort (*U. rupestris*). He said that “it still retains a place in most collections, deservedly indeed, for it has every claim to our notice; its appearance is magnificent, the glaucous colour of its foliage highly pleasing, its flowers large and of long duration; it blows [flowers] freely, grows rapidly, is easily increased by cuttings, and will succeed in a house or window”. What more could we ask of a succulent?
Cotyledon orbiculata has been shown to be extremely variable. In the two and a half centuries following Linnaeus’s monumentally important work, around 45 separate species and varieties have been described. Tölken (1985), however, re-evaluated the species and lumped all of these into C. orbiculata but recognised five varieties. It is now known to have a very widespread distribution throughout southern Africa, especially in South Africa. With such a broad distribution and lengthy synonymy, it is unsurprising that this species is very diverse. Plants are either sprawling or floppy with thin, weak stems, or woody and erect. Most diverse of all are the leaves as shown in Fig. 4. This illustrates the clones I currently have in cultivation but in no way shows the full range of variation. Leaf shape ranges from nearly spherical to long and thin; margins are either straight or crinkled; colour ranges from bright green to blue-grey whilst the surface is smooth, glaucous or hairy (tomentose). Leaves are always arranged in pairs apart from in var. spuria where leaves are in whorls of three. In contrast, flowers show a much narrower range of variation, always being pendulous, tubular with recurved lobes, pale yellow to deep red or a range in between and all are principally bird-pollinated as far as is known.

Typically, C. orbiculata var. orbiculata occurs in Angola, Namibia and south into the Eastern Cape Province of South Africa (Tölken, 1985). It is an erect woody shrub, branched up to 30cm tall, or up to 1m tall when in flower. Leaves are opposite, orbiculate or obovate, green to grey-green, often with a red margin. The only clone I currently grow of this variety (Fig. 5) came from Alexander Bay, Northern Cape Province, South Africa. This has decumbent, sprawling stems bearing small, egg-shaped (obovate) leaves. It is relatively slow-growing and has yet to flower in my collection.

The cultivar named Cotyledon orbiculata ‘Undulata’ (Fig. 6) has a long history. It was first described as Cotyledon undulata Haworth in 1819 and in the following two centuries this plant has become well-known in cultivation.
Tölken (1979, 1985) lumped Haworth’s species under *C. orbiculata* but the name ‘Undulata’ has been maintained as a cultivar. This is a very distinctive and attractive form with paired leaves with crinkly undulate edges, so cultivar status is undoubtedly well deserved.

*Cotyledon orbiculata* var. *oblonga* (Haworth) De Candolle has a wide distribution from the Western Cape Province of South Africa north-east through Lesotho, Eswatini (Swaziland) to southern Mozambique (Tölken, 1985). It is by far the most diverse of the five varieties of this highly diverse species. The clone shown in Figs. 7 and 8 is typical of many and originated from Magalies Bay, South Africa. It has untidy, floppy, decumbent stems that usually branch from the base. The leaves are long and narrow, tapering to a tip up to 14cm long and covered with a powdery blue-grey surface that is readily removed or marked. The upper surface is slightly flattened with a shallow longitudinal channel whilst the lower surface is slightly convex. The inflorescence (Fig. 8) is up to 50cm tall bearing up to 20 flowers. Each flower has a tube about 3cm long with the characteristic modest bulge in the centre; pale apricot-coloured but darkening to deep pink at the free petal tips which are strongly recurved and orange-red inside.

A very different clone of *C. orbiculata* var. *oblonga* is shown in Figs. 9 and 10. This is a large woody erect shrub currently about 80cm tall without the inflorescences, well branched at the base but also higher up the stems where flowering has previously occurred. The leaves are bright green, tomentose and slightly sticky, even viscid, tapered at both ends with a shallowly- channelled upper surface and a prominent longitudinal keel on the lower surface. Unlike the plant shown in Fig. 7 this plant does not need support for its 30cm-tall erect inflorescences, of which five were produced in the summer of 2021. Flowers are shorter in this clone, having a tube only 2cm long with a swollen base, bright red with prominently recurved or curled lobes. According to Tölken (1985) this form with hairy leaves is recorded from coastal KwaZulu-Natal.

The cultivar *Cotyledon orbiculata* var. *oblonga* ‘Takbok’ (Figs. 11 and 12) was named by Van Jaarsveld & Koutnik (2004) because the leaves have apical finger-like lobes reminiscent of reindeer antlers, although my plant (Fig. 11) has yet to produce leaves that truly match this description. It originated from the Eastern Cape Province of South Africa. My plant has thin sprawling, floppy, untidy stems bearing long, thin (up to 16×2.5cm) slightly glaucous grey-green shallowly-channelled leaves. The single inflorescence produced so far required support, was 23cm tall, apically branched bearing 10 pale apricot-coloured flowers with a prominent swollen tube and modestly recurved orange-red lobes (Fig. 12).

The other three varieties of this complex species are *Cotyledon orbiculata* var. *dactylopsis* Tölken,
var. *flanaganii* (Schönland & Baker) Tölken and var. *spuria* (L.) Tölken, none of which I have ever grown. The first of these is quite widespread in central and northern South Africa. Its principal distinguishing feature is the yellow campanulate flower. Var. *flanaganii* forms larger, erect shrubs up to 75cm tall with leaves arranged in distinct whorls of three. This has a very limited distribution in coastal Eastern Cape Province. Finally, var. *spuria* is an even larger plant up to 1.2m tall with broad (up to 16×8.5cm) glaucous leaves. It is reasonably widespread from Western Cape Province into the west of Eastern Cape Province (Tölken, 1985).

**Cotyledon eliseae van Jaarsveld**

This is a cremnophytic (cliff-dwelling) species discovered by Ernst van Jaarsveld and described as *C. eliseae* in *Bradleya* (Van Jaarsveld & Koutnik, 1997). It is a small, woody, sprawling shrublet up to 20cm tall. Its leaves are flattened, pointed at the tip and tapering at the base, green, glandular hairy and hence sticky with a distinct purple tip and margin, especially when grown in full sun. The inflorescence is erect, up to 9cm tall, glandular hairy, branched bearing up to five flowers. Individual flowers are pendulous with a tube up to 12mm long and petal lobes strongly recurved up to 18mm long, orange-red to deep red in colour. This plant is difficult to display, so I have let it sprawl over the edge of its pot (Fig. 13).

*Cotyledon eliseae* is named after the talented South African botanical artist Elise Bodley, who painted the watercolour plates for the *Cotyledon* and *Tylecodon* monograph (Van Jaarsveld & Koutnik, 2004) and after whom *Tylecodon bodleyae* van Jaarsveld is also named. *Cotyledon eliseae* grows on steep to sheer quartzitic sandstone cliff faces in the lower reaches of the Gouritz River, south of the Langeberg Mountains in the Western Cape Province of South Africa (Van Jaarsveld & Koutnik, 1997). Its closest relative appears to be *C. woodii* from which it differs principally in being dwarf and sprawling rather than an erect shrublet and it also has sticky leaves.

**Cotyledon pendens van Jaarsveld**

This is the second obligate cliff-dwelling species, named for its pendulous habit (Van Jaarsveld & Van Wyk, 2003). In my collection it is a rapidly-growing plant ideally suited for display in a hanging pot or basket where it makes a very attractive plant (Fig. 14).
The pendent stems are woody but brittle, well branched up to 60cm long, a unique feature in the genus. The leaves are densely arranged in alternating pairs (decussate), prominently pointed at the tip and tapering at the base, flattened on both surfaces, whitish grey-green with a powdery glaucous covering with pink-tinged edges when grown in full sun. My plant flowered for the first time from June to August 2021 (Fig. 15) after four years in cultivation. It has so far produced a single pendent flower at the tip of each branch, but the description (Van Jaarsveld & Van Wyk, 2003) indicates that it can produce branched inflorescences with up to four flowers. Each flower has a 2cm-long tube, pale apricot pink in colour with strongly recurved orange-red petal lobes 2cm-long.

*Cotyledon pendens* is a highly localised species known only from its type locality where it grows only on sheer south-facing cliffs near to Tsolorha along the Mbashe River in the Eastern Cape Province of South Africa (Van Jaarsveld & Van Wyk, 2003). Its closest relatives appear to be *C. adscendens* and *C. woodii*, both of which differ in being erect shrublets.

**Cotyledon tomentosa Harvey**

This species was first named in 1862 and has since become a popular plant in cultivation. It is named *tomentosa* for the tomentose or shortly hairy leaves (Fig. 16). Plants are variable with erect to sprawling woody stems up to 50cm tall, moderately well branched. Leaves too are variable and in the typical subsp. *tomentosa* these are flattened on the upper surface and convex on the lower with up to eight
marginal teeth with lobes that can be reddish in full sun, giving the overall shape of a closed hand. In contrast, subsp. ladismithiensis (von Poellnitz) Tölken has oblong-elliptical leaves up to 8cm long and 3cm wide. In my experience C. tomentosa is a relatively slow-growing, shy bloomer producing short inflorescences up to 15cm tall bearing erect to pendulous tubular orange-red flowers. Stephenson (2021) includes colour photos of both subspecies, notably showing the rarely seen subsp. ladismithiensis (as ladysmithiensis) in habitat.

Cotyledon tomentosa has a narrow distribution in the Western and Eastern Cape Provinces of South Africa (Van Jaarsveld & Koutnik, 2004).

Two cultivars of C. tomentosa have been named based on the palm-shaped leaves and colour of the variegation: ‘White Palm’ (Fig. 17) and ‘Yellow Palm’ (Rowley, 2006). I have grown both of these for several years and they have yet to flower for me.
There are 12 other species, some of which I have grown in the past but no longer have material of. *Cotyledon barbeyi* Schweinfurth ex Baker is a large erect shrub up to 2m tall with large oblanceolate (lance-shaped) to linear leaves up to 28×4.5cm. This has the widest distribution of all the species, occurring from north-east South Africa, through tropical East Africa to Ethiopia and the south-western Arabian Peninsula. *Cotyledon papillaris* L.f. is also widespread, ranging from Namibia south into the Western and Eastern Cape Provinces of South Africa. It is procumbent and spreading with thin stems bearing rounded or flattened, yellowish-green to glaucous leaves. The red flowers are smallish with a short tube and strongly curled lobes.

The remaining species are all South African endemics. *Cotyledon adscendens* R.A.Dyer and *C. woodii* Schönland & Baker are very similar sprawling shrublets with flattened leaves and pendulous red flowers. The former has a very restricted distribution near Port Elizabeth in the Eastern Cape Province, whereas *C. woodii* is widespread throughout both the Western and Eastern Cape Provinces. *Cotyledon campanulata* Marloth has long, thin usually hairy, green to yellowish-green leaves and yellow, short campanulate (bell-shaped) flowers and is widespread and locally common in the Eastern Cape Province. *Cotyledon cuneata* Thunberg also has yellow flowers, but the broad cuneate leaves are usually glaucous. It occurs in the Western and Northern Cape Provinces. *Cotyledon velutina* Hook.f. is a large shrub up to 3m tall bearing smaller, flattened, usually hairy leaves, hence its name. It is widespread in the Eastern Cape Province into KwaZulu-Natal.

In the last six years or so, four new, very localised species have been discovered and named by Ernst van Jaarsveld. *Cotyledon egglii* van Jaarsveld comes from the Barberton region of the Mpumalanga Province and
is closest to *C. orbiculata* var. *oblonga*. *Cotyledon gloephylla* van Jaarsveld comes from the Eastern Cape Province and is closest to the widespread *C. woodii*. *Cotyledon petiolaris* van Jaarsveld comes from the Eastern Cape Province and is closest to *C. velutina*. *Cotyledon xanthantha* van Jaarsveld & Eggli (with synonyms *C. lutea* van Jaarsveld and *C. adscendens* van Jaarsveld & Eggli) comes from the Western Cape Province and is closest to *C. orbiculata*. Finally, *C. nielsii* N.R.Crouch, D.Styles & Mich.Walters, endemic to KwaZulu-Natal, is the most recently described species. I have yet to see any of these new species in cultivation.

**Hybridisation**

In habitat several species of *Cotyledon* form natural hybrids. This was first observed and recorded by Lotsy & Goddijn (1928) in their wider study of hybridisation and its role in the South African flora, that also included hybrids in *Euphorbia* and modern day *Tylecodon*. They reported that “The finest series of hybrids of *Cotyledon* and their segregates – by far – were however those of *C. coruscans* × *C. teretifolia* [= *C. orbiculata* var. *oblonga* × *C. campanulata*] found near Botha Hill [in the Eastern Cape Province]… At several spots – extending over a large area – these were so numerous, that they could be seen from a considerable distance”. They published three large folding plates based on water colour paintings of the hybrids they found (Figs. 18 & 19). Later Tölken (1985) provided modern names for the parents of these hybrids and listed others, such that at least five species are known to be involved in natural hybridisation. The role of hybridisation in the evolution of *Cotyledon* has yet to be investigated using modern molecular techniques but this would make a fascinating research project. A currently accepted species that requires further investigation is *C. adscendens*, which looks remarkably similar to hybrids recorded by Lotsy & Goddijn. The possibility of a hybrid origin of this species was considered and dismissed by Tölken but in my view needs to be revisited.

Some artificial hybrids are also in cultivation, one of which is included here: *C. pendens* × *C. campanulata*, artificially produced by Ben Zonneveld (Fig. 20). Compared to *C. pendens* (Figs. 14 & 15) the leaves of the hybrid are larger, light green and not glaucous blue-green. The flowers of the hybrid (Fig. 21) are more numerous and larger than those of *C. pendens*, yellow externally with pale orange-red lobes. The hybrid is very clearly intermediate between its two parents.

**Cultivation**

*Cotyledons* are generally easy to grow and are very rewarding in terms of their attractiveness. Some clones such as *C. pendens* are fast growers whilst others such as *C. orbiculata* ‘Oophylla’ and *C. tomentosa* are relatively slow-growing. They all come readily from stem cuttings and for the thicker-leaved clones I suspect that leaf cuttings would also be successful, although I have yet to attempt this method of propagation.

The clones I have so far flowered do so in spring through into the summer here in the UK and the flowers are generally relatively large, colourful, ranging from pale yellow through apricot, orange to deep red. They are all long-lasting with individual flowers blooming for around a week or more, so a single plant
with many flowers can be in bloom for several weeks. Hence these plants are very rewarding.

On the downside, many plants either have weak and floppy or thin and pendulous stems, so these are far from ideal for the show bench. Even large shrubs can have weak stems when carrying tall inflorescences and need support to prevent damaging them. Another problem with many clones is that the powdery glaucous grey-white covering is easily damaged, again reducing their show-worthiness. On that front, clones such as those of the non-glaucous C. tomentosa are more amenable for transportation.

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