A survey of succulents of the mallow family (Malvaceae)

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The mallow family (Malvaceae) is large but only relatively few species exhibit either pachycaul succulence (bottle trees with fat stems) or have succulent leaves. This article surveys succulence in this family. Photography as indicated.

Introduction

The mallow family, the Malvaceae, has a worldwide distribution with around 4,200 species in about 240 genera (Stevens, 2017). In the first edition of *The Illustrated Handbook of Succulent Plants*, succulent plants of this alliance were treated in two separate families: the Bombacaceae (Walker, 2002) and the Sterculiaceae (Forster & Guymer, 2002). However, as a result of recent molecular studies the Malvaceae have been expanded to encompass three former separate families: the Bombacaceae, Tiliaceae and Sterculiaceae. Consequently the succulent plants surveyed here will all be treated as members of the single family, the Malvaceae, in the second edition of *The Illustrated Handbook of Succulent Plants* (Walker, 2021)

The most familiar representatives of this family are the garden plants *Hibiscus*, hollyhock (*Althaea*) and

Fig. 1 (below) Baobab fruit (from Alpino, 3rd ed., 1735)

Fig. 2 (top right) *Adansonia digitata* in leaf at Sua Pan, Botswana (Photo: Ralph Stutchbury)

Fig. 3 (bottom right) *Adansonia digitata* looking more majestic in the leafless resting state in SE Zimbabwe (Photo: Ralph Stutchbury)

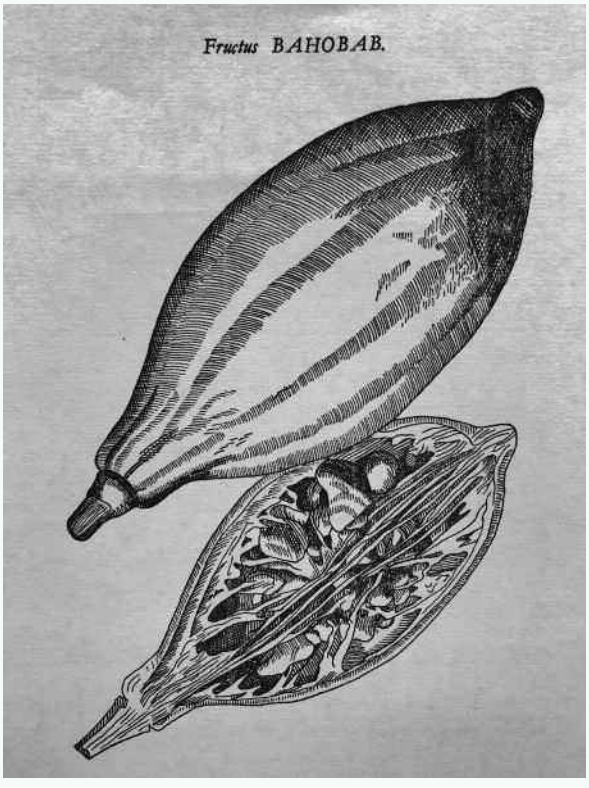


Fig. 4 Flower of *A. digitata* (Photo: Ralph Stutchbury)

mallow (*Lavatera*). By far the most economically important genus is cotton (*Gossypium*) followed by cocoa/chocolate (*Theobroma cacoa*). The family occurs in most of the world, except for the very cold regions and is particularly abundant in tropical South America. Just a few, perhaps 35 species, have the pachycaul swollen habit of succulent bottle trees, or in the case of *Megistostegium*, exhibit leaf succulence. Succulent mallow species occur naturally in central and South America, Africa, Madagascar and Australia. The baobabs of the genus *Adansonia* are the most famous of these but succulents also occur in the less familiar genera *Brachychiton*, *Cavanillesia*, *Ceiba*, *Megistostegium*, *Pseudobombax* and *Sterculia*.

Fig. 5 *Adansonia za* in the leafless resting state, Tsimanampetsotsa Nature Reserve, Madagascar (Photo: Al Laius)

Adansonia

This is the genus of the baobab of sub-Saharan Africa or the boab in Australia, with its enormously swollen outline that has given rise to the nickname of 'Africa's upside-down tree'. There has been much speculation as to the age of baobabs. Recent radiocarbon dating of trees has given ranges of 1,100 to 1,600 years old. Therefore postulated ages in excess of 2,000 years for larger trees do not seem unreasonable since adult trees exhibit slow growth rates (Wickens & Lowe, 2008).

Baobabs have been known for many centuries (perhaps millennia) and the early Egyptians were apparently aware of them. However, the first published description of the baobab appeared in 1592 in a book on Egyptian plants entitled *De Plantis Aegypti Liber* in which the Italian botanist and doctor Prospero Alpino (1553–1617) described and illustrated the fruit which he called the bahobab. This is the origin of the familiar common name (Alpino, 1592, Fig. 1). Alpino was aware of the fruit that was for sale in Egyptian markets but he was unable to describe the tree since it is not native to Egypt. The French botanist, Michel Adanson, was the first to describe the tree and its large flowers, which he called the baobab based on Alpino's name. Adanson made detailed observations of baobabs during his visit to Senegal (1748–1753) (Adanson, 1761). Based on Adanson's work, Carl Linnaeus commemorated him in the generic name *Adansonia*.

The genus currently consists of eight species: one in Africa, six in Madagascar and one in north-western Australia (Baum, 1995b; Petignat & Jasper, 2015). This remarkable disjunct distribution across two continents is considered to be the result of long-distance oceanic dispersal of fruit which originated on the African mainland. This dispersal was followed by radiation and speciation, notably in Madagascar where the maximum species diversity currently resides (Wickens & Lowe, 2008). *Adansonia digitata* (Figs. 2 & 3) has the widest distribution occurring in much of

Fig. 6 ***Adansonia rubrostipa*** **in fruit between Ifaty and Tulear, Madagascar (Photo: Al Laius)**

sub-Saharan Africa. Its white pendulous flowers last for just 24 hours; they open in the evening and petals evert rapidly to reveal the anthers (the male parts), which are initially hidden by the long petals (Fig. 4). For *A. digitata*, authenticated records exist for both bat and bushbaby pollination, although the latter animal has a relatively restricted distribution compared with the baobab. The Madagascan and Australian species are pollinated by long-tongued hawkmoths, fruit bats or lemurs (Baum, 1995a).

The six Madagascan species occur in the arid north, west and south-west of the island. In terms of distribution, these range from the widespread *A. za* (Fig. 5), to *A. rubrostipa* (Fig. 6), distributed along the west coast, to the highly localised and hence endangered *A. perrieri*, which is known from just a few sites in the extreme north. The Australian *A. gregorii* occurs in the north of Western Australia and in north-western Northern Territory (Petignat & Jasper, 2015).

Fig. 7 Fruit of ***A. digitata*****, Nwanedi, Limpopo Province, South Africa (Photo: Gideon Smith)**

Fig. 8 Fruit of ***A. za*****, which is especially variable, can be up to 30cm long and 15cm diameter. The surface layer (pericarp) is thick and tough (Photo: Al Laius)**

The baobabs are renowned for their pachycaul appearance with squat or bottle-shaped stems up to 30m or more tall, up to 5m or more in diameter and up to 16m or more in circumference, with well branched crowns. The deciduous leaves of baobabs are palmate with up to nine leaflets. Flowers are pendulous in *A. digitata* but erect in the other species. Petals are white, yellow or red. Fruits are dry, large and very variable in shape (Figs. 7 & 8), ranging from globose to cylindrical with a thick, woody outer layer (the pericarp) and with the many seeds embedded in a white spongy pulp.

All parts of the tree have some economic or cultural importance, notably in Africa but also to a lesser extent in Madagascar and Australia. The hollow trunks have been used for diverse purposes, ranging from shelter and storage to such unusual uses as being fitted with a flush toilet or being used as a prison as in the case of the Derby Prison Tree in Australia. Other parts of the plant have also been used by humans. The wood is spongy and very moist and hence unsuitable for timber but does have some constructional uses, for example for lightweight canoes and as roofing material. Fresh leaves, and especially the fruits, are a rich source of vitamin C (ascorbic acid) and tartaric acid and are widely used to produce refreshing lemonade-like drinks, or more recently, baobab smoothies (Figs. 9 & 10). *Adansonia digitata* is cultivated outside of its natural range in Africa and this appears to account for records in India, northern Madagascar and southwestern Arabia (Wickens & Lowe, 2008). In temperate latitudes where greenhouse cultivation is required because these trees are frost-sensitive, baobabs do not make attractive specimens, since the appealing pachycaul habit of the bulky trunk of mature specimens takes a long time to develop.

The literature on baobabs is now remarkably extensive for such a

Fig. 9 (top left) Baobab bar at the Eden Project, Cornwall (Photo: Colin Walker)

Fig. 10 (middle left) The author enjoying a baobab smoothie at the Eden Project (Photo: Marjorie Thorburn)

Fig. 11 (bottom left) *Brachychiton rupestris* in cultivation at Sydney Botanic Garden (Photo: Colin Walker)

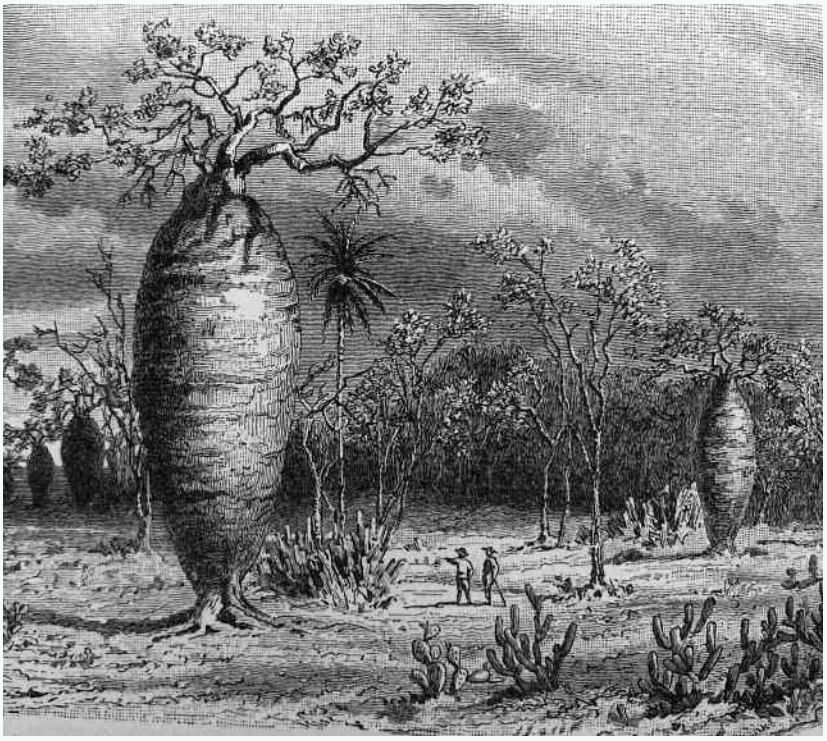


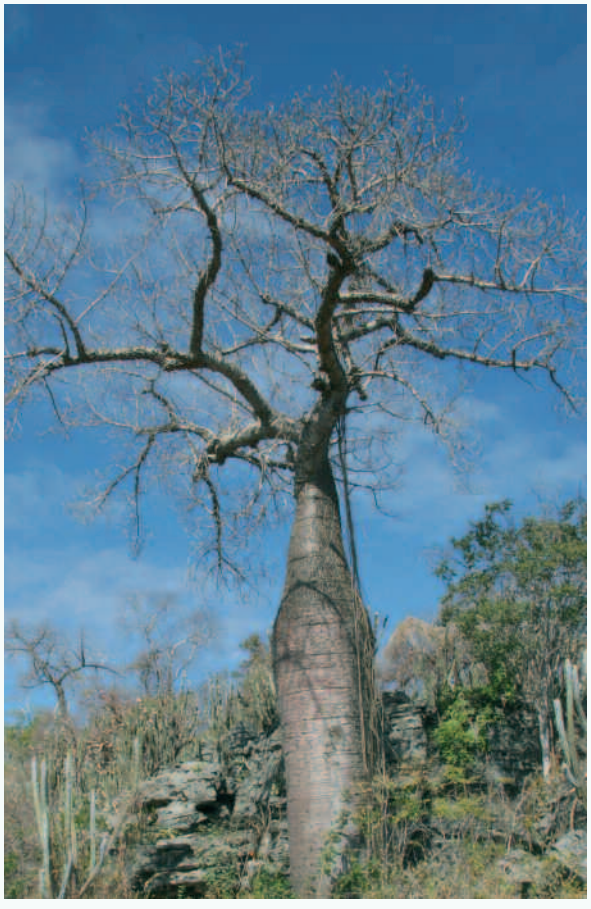
Fig. 12 (top right) ***Cavanillesia tuberculata*** **(but more likely** ***C. arborea*****) from the Brazilian Caatinga (desert vegetation). (From Kerner von Marilaun & Oliver, 1894–1895)**

Fig. 13 (bottom right) ***Cavanillesia arborea*** **North of Bom Jesus de Lapa, Brazil. Notice that the maximum stem diameter is a good way up the stem and not at its base (Photo: Graham Charles)**

small genus and includes the highly recommended and well-illustrated books by Pakenham (2004), Watson (2007), Stutchbury (2013) and Petignat & Jasper (2015).

Brachychiton

This is a genus of about 30 species, all of which are endemic to Australia apart from one endemic to Papua New Guinea and a second species shared with Papua New Guinea. Just three species have well-developed pachycaul bottle-shaped stems (Kapitany, 2007, 2015), of which *Brachychiton rupestris* develops the largest and broadest stem of the genus (Fig. 11). All succulent brachychitons known as 'Bottle Trees' in Australia were previously classified in the separate but now obsolete family Sterculiaceae, along with *Sterculia* (Forster & Guymer, 2002). *Brachychiton* was named from the Greek 'brachys' meaning 'short' and 'chiton' meaning 'covering', for the short covering around the seed.



Brachychiton rupestris is a mostly evergreen tree up to 25m tall, always developing a swollen trunk that is bottle-shaped to 3.5m diameter at breast-height with dark grey, deeply fissured and tessellated bark. Shorter trees often develop the most disproportionately broad trunks (Kapitany, 2015). The leaves are crowded at the branch tips, are shiny above but glaucous below and linear-lanceolate to lanceolate in shape. This species can be semi-deciduous in some climates with leaves not falling every year and not necessarily from all the branches (Kapitany, 2007). It is endemic to the state of Queensland, where it grows inland from the coast in drier areas and is most commonly found in semi-evergreen vine-thicket and in Brigalow scrub dominated by the wattle *Acacia harpophylla*. It was named *rupestris* for its 'often rocky habitats'. Populations of *B. rupestris* are sharply declining over its range, in particular through a lack of natural regeneration (Kapitany, 2015). It is widely grown in

Fig. 14 Another specimen of *C. arborea* with prominent stem scars (Photo: Graham Charles)

Fig. 15 *Ceiba speciosa* in the leafless resting state in cultivation at The Huntington Botanical Gardens, San Marino, California (Photo: John Trager)

parks and gardens in Australia. The stems and leaves are sometimes used for drought-fodder for cattle and have the vernacular names of 'Bottle-Tree', 'Queensland Bottle Tree' and 'Narrow-Leaved Bottle Tree' (Forster & Guymer, 2002).

Cavanillesia

This is a genus of just five species with enormously swollen non-prickly pachycaul stems. They occur naturally in tropical central and southern America, ranging from Panama to Brazil. The genus was first described in 1794 and named for Antonio J Cavanilles (1745–1804), a Spanish clergyman and botanist in Paris and Madrid (Walker, 2002). These South American bottle trees have often featured in early literature because of their unusually shaped stems, often with their greatest stem diameter well above ground level (Fig. 12).

Cavanillesia arborea is the most familiar species, especially to cactus hunters in Brazil where it is endemic. Trees of this species resemble the baobab because of their large size, architectural appeal of the trunks and canopy and generally long lifespan (Figs. 13 & 14). This is a classic example of convergent evolution, where the same plant growth form has evolved in tandem in two different continents, in this case South America and Africa. *Cavanillesia arborea* can grow to over 35m tall in fertile soils. Eric Werdermann, an early German cactus explorer of the 1930s in Brazil, wrote that "we shall never forget our trip through the fairy land of 'bottle trees' (*Cavanillesia*

arborea), which arose like giants out of [the] distant past in the confusion of dry branches of low trees and underbush. However majestically they rounded out their circumference, just as little resistance did their spongy soft wood offer to a scratching thumb nail" (Werdermann, 1942). A particularly gigantean specimen is wonderfully illustrated in a later book entitled *Cacti in Brazil* (Herm et al, 2001). I estimate that this specimen has a stem about 3.5m diameter at its maximum girth and is around 7.5m tall up to the point where it starts to taper quite distinctly into the crown of branches. Its flowers produce a disagreeable odour and large amounts of pollen. Again, similarly to the baobab, the flowers demonstrate nocturnal opening and are probably pollinated by bats. Its seeds are winged and wind-dispersed (Melo Júnior et al, 2015).

Cavanillesia chicamochae is a relatively recent discovery (Fernández-Alonso, 2003) named for the Chicamocha River Canyon in Colombia where it is endemic. It forms trees 4–6m tall with a very thick fusiform trunk at the base up to 1m in diameter, often with roots exposed as small stilts; stems and branches are often irregularly shaped, sometimes curved downwards, generally with conspicuous scars or transverse bands. This species is the smallest tree and also the most localised species in the genus, being known from a single river valley, where it has the vernacular name of 'Barrigón' which refers to the barrel-shaped trunk. Occasionally the trunk is cut and used for raft making. Goats are also recorded as being a threat, since they consume bark, young branches and seedlings (Fernández-Alonso, 2003).

Of the three other species of *Cavanillesia*, *C. platanifolia* is the most northerly and probably has the widest distribution ranging from Panama to Peru. It forms trees up to 30m tall that are somewhat swollen near the base with an open crown. *Cavanillesia hylogeiton* (Peru) and *C. umbellata* (Peru, possibly Bolivia and Brazil) are relatively unknown bottle trees. The genus has received little attention and is in need of revision.

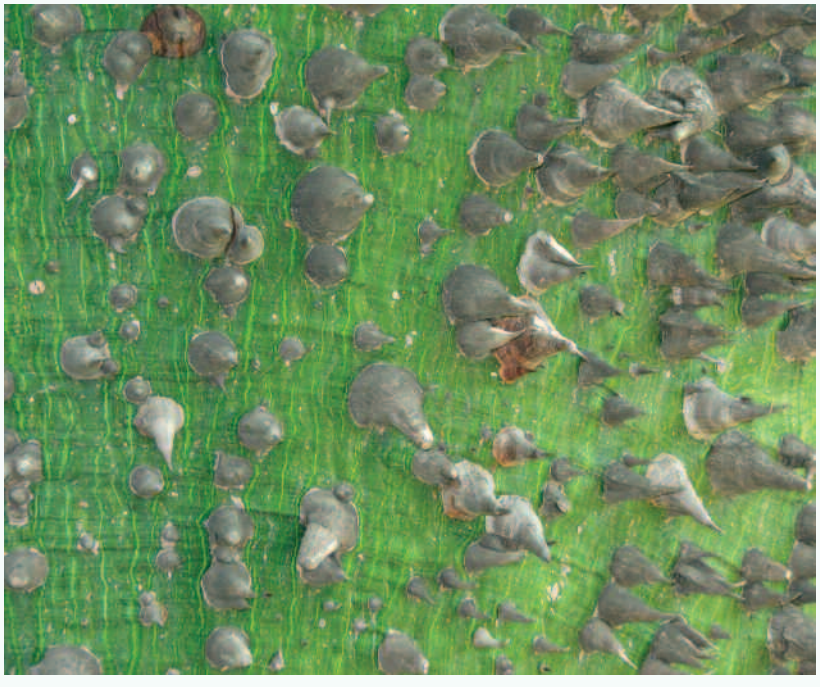


Fig. 16 (top) Closer view showing the stem with prickles of *C. speciosa* (Photo: John Trager)

Fig. 17 (bottom) Close-up of the stem prickles of *C. speciosa* (Photo: John Trager)

Like the baobabs, cavanillesias do not make attractive pot plants or greenhouse subjects because the pachycaul habit is not well developed in small, young specimens. Hence these plants are rarely cultivated in temperate climates.

Ceiba

This is another small American genus of about 18 species, which now includes those species formerly separated in the genus *Chorisia*. Only six species are considered to have swollen, pachycaul, aculeate (prickly) stems currently of interest to succulent plant enthusiasts (Walker, 2021). In the latest revision of *Ceiba*, Gibbs & Semir (2003) accepted seven distinct species in what they referred to as the "*Ceiba insignis* aggregate species". Of the six pachycaul species, *C. chodatii*, *C. speciosa* and *C. ventricosa* belong to this *C. insignis* aggregate species complex, whereas *C. boliviana*, *C. glaziovii* and *C. rubriflora* are more

Fig. 18 (left) White-flowered form of *C. speciosa* (Photo: John Trager)

Fig. 19 (below) Flower of *C. speciosa* 'Majestic Beauty', a selection made by Monrovia Nursery, Azusa, California (Photo: John Trager)

Fig. 20 ***Ceiba rubriflora*** **in leafless state in the dry season, near Iuiú, State of Bahia, Brazil (Photo: Graham Charles)**

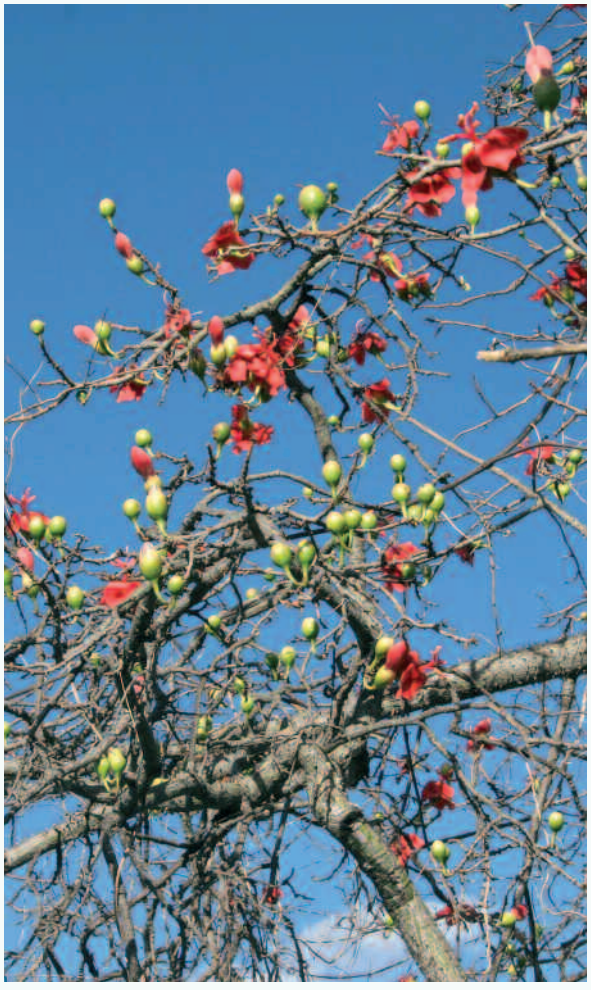


Fig. 21 ***Ceiba rubriflora*** **with buds, flowers and very prickly branches, near Iuiú, State of Bahia, Brazil (Photo: Graham Charles)**

distinct and distantly related to this complex. *Ceiba insignis* in the narrow sense of Gibbs & Semir (2003) does not have swollen stems and so is no longer considered to be a pachycaul succulent. The name *Ceiba* is derived from the Spanish 'ceiba' describing some sort of American cotton tree.

Three species of *Ceiba* occur in Mexico and Central America and 14 species are distributed in South America. *Ceiba pentandra* (a non-succulent) is the only species which extends outside of South to Central America and the Caribbean islands, occurring in West Africa, where it is probably native and also in India, South East Asia and the Pacific, to which areas it was most likely introduced by humans (Gibbs & Semir, 2003). *Ceiba* is of economic importance as 'Kapok' or 'Silk-Cotton Tree', the source of kapok, a lightweight, water-resistant fibre used in pillows, etc.

Of the six pachycaul species only *C. speciosa* is widely grown outdoors in tropical or subtropical countries or those with Mediterranean-type climates. It is still most often encountered labelled *Chorisia speciosa*. Other species of the *Ceiba insignis* alliance are apparently only rarely cultivated, if at all, in Europe and the USA, but an appraisal of much of the cultivated material is yet to be undertaken.

Ceiba speciosa has a very wide distribution in South America: west, north-east and south-east Brazil, northern Argentina, Paraguay, Bolivia, South and central Peru. It occurs in dry semi-deciduous woodland, wet forest and humid river valleys. It is also widely cultivated in Argentina and Brazil as an ornamental.

This species grows as trees up to 20m tall with a spreading crown. The pachycaul trunk is immensely

Fig. 22 ***Megistostegium perrieri*, Cap Sainte Marie, the southern tip of Madagascar (Photo: Al Laius)**

swollen, up to 2m diameter at the widest part (Fig. 15), generally covered with large, cone-like woody prickles (Figs. 16 & 17). Its leaves are digitate (hand-like) with 5–7 leaflets. The flowers (Figs. 18 & 19) are relatively large, hence conspicuous, very attractive and come in a very wide range of colours from crimson or pink to yellow or white with or without chestnut-brown blotches in the throat.

Ceiba speciosa is a readily available and easily-grown pachycaul. In succulent plant collections this makes an attractive species with its prominently prickly pachycaul stem and spectacular flowers. It is frequently planted in parks and gardens in frost-free climates around the world for its interesting growth form and free-flowering nature. De Vosjoli (2004) reports that "in warmer areas of the US, these impressive trees with green trunks and giant thorns make outstanding landscape specimens. Several forms exist, including a thornless dark pink-flowered form". These trees can also make "outstanding tropical bonsai specimens but require heat".

Ceiba rubriflora is the most recently described species (Figs. 20 & 21). It is characterised by its

Fig. 23 ***Pseudobombax ellipticum*** **(Photo: Tina Wardhaugh)**

relatively small flowers with deep red petals and stamens which are unique amongst the Brazilian species of *Ceiba* and is one of five species recorded for the State of Bahia. Its closest relatives appear to be the non-pachycaul *C. erianthos* and *C. schottii*. Plants flower during the dry season in July and August when leafless (Fig. 20) and set fruit in September. This is possibly the most localised of all the *Ceiba* species. Its conservation status was assessed as Critically Endangered since it occurs in an area estimated to be less than 100km^2, where it grows in severely fragmented and declining habitat (Carvalho-Sobrinho & Queiroz, 2008).

Fig. 24 *Pseudobombax ellipticum* in cultivation at The Huntington Botanical Gardens, San Marino, California. Notice that with free root room and hence presumably reasonably fast growth, this specimen has lost most of the appealing pachycaul growth form (Photo: John Trager)

Megistostegium

This is an endemic Madagascan genus consisting of just three species of which two have succulent leaves whilst the third, *M. nodulosum*, the most widespread, is modestly pachycaul but with thin non-succulent leaves (Koopman, 2011). These plants are prostrate or erect shrubs or trees to 8m tall. The name is derived from 'megisto-' meaning 'very large' and '-stegium', for the large gynoecium or the female part of the flower. These plants are restricted to the xeric, deciduous spiny forest of south-west Madagascar and associated coastline.

Megistostegium perrieri is a sturdy, prostrate subshrub up to 1m tall with terminal clusters of leaves on the branches. Its leaves are relatively large, succulent and covered with soft, tomentose stellate (star-shaped) hairs. The maroon flowers are pendant and attractive (Fig. 22; Rauh, 1995). This species is very localised, being restricted to the wind-swept calcareous coastline of the Mahafaly plateau at Cap Sainte Marie at the very southern tip of Madagascar. The short stature of this plant is partly in response to the constant wind blowing off the Mozambique Channel. When plants are growing in sheltered, rocky outcrops on cliffs they grow taller. The limited distribution of this species at only two locations gives rise to a conservation status of Endangered. A particular threat appears to be the absence of an effective pollinator (Koopman, 2011). This species is possibly not currently in cultivation.

Pseudobombax

This is yet another small American genus of about 30 species that until 1943 was included in *Bombax,* hence the name meaning 'false *Bombax*'. They are distributed in neotropical America from Mexico to northern Argentina, but two-thirds of the species occur in Brazil, forming a centre of diversity. The genus is more diverse in areas subject to a long dry season with xerophytic vegetation such as the caatinga of north-east Brazil and the Venezuelan llanos

Fig. 25 Flowers of *P. ellipticum* in cultivation at the Huntington Botanical Gardens (Photo: John Trager)

(Carvalho-Sobrinho & Queiroz, 2011). Plants have deciduous foliage during the flowering season, an adaptation to bat pollination (chiropterophily) and their preference for habitats subject to a long dry season when the plants mostly flower.

Pseudobombax is characterised by trunks with often irregular greenish stripes, digitate leaves clustered at the branch apices, leaflets not jointed to the petiole (leaf stalk), filaments (of the stamens) joined in a tube in the flower and fruits that are woody capsules with abundant kapok (dense soft fibres) in which the seeds are embedded. Absence of woody stem prickles and leaflets not jointed to the petiole are considered to be key features of *Pseudobombax* (Carvalho-Sobrinho et al, 2016).

Pseudobombax ellipticum is widely distributed, naturalised and cultivated in central America and the Caribbean and is by far the most commonly encountered species in cultivation in Europe and the USA. It forms an attractive basally-swollen pachycaul with contrasting striped bark and large digitate leaves, particularly suitable for pot plant culture when young, especially since it is readily available commercially. Specimens given bonsai treatment are particularly appealing (Fig. 23). It can also be grown outdoors in warmer temperate zones (Fig. 24), but with rapid growth the pachycaul stems of young specimens can quickly grow into non-pachycaul trees up to 10m tall (De Vosjoli, 2004). Its flowers are attractive, the most prominent feature of which is the large number (up to 350) of stamens giving the flower the look of a loose shaving-brush, with the narrow petals recurved or curled (Fig. 25).

Apparently the only other species currently in general cultivation is *Pseudobombax palmeri* (Fig. 26). As *Bombax palmeri* it was distributed by the ISI in 1970 as seedlings (ISI 631 & 632) raised from seed collected by Myron Kimnach in 1969 in Sonora, Mexico (Anon, 1970). It was described as forming "a small tree with a grotesquely swollen, reddish trunk that usually juts forth from cliffs. Its leaves are large and hand-shaped, and its flowers resemble those of waterlilies. It makes an excellent pot-plant, whereupon its stem becomes globular and nearly as thick as the plant is high". The specimen shown in Fig. 26 is over 50 years old from

Fig. 26 ***Pseudobombax palmeri*** **in cultivation at the Huntington Botanical Gardens, San Marino, California.** ***HBG 25243.*** **Raised from seed collected on the Huntington expedition to Mexico in November, 1970.** ***Boutin & Kimnach 2959*****, Sierra de Minatlán, Jalisco, Mexico, on the road to Hacenadero beyond El Chante, 1,219m (Photo: John Trager)**

seed from another Kimnach collection from Jalisco in 1970. This evidence therefore suggests that as a pot-grown specimen it exhibits a very slow growth rate, which contrasts with the significantly faster growth rate reported for *P. ellipticum*.

Sterculia

Sterculia is a large genus of ± 150 species with a pantropical distribution, few of which have a well-developed pachycaul stem and only four species were considered to be succulent by Forster & Guymer, (2002). It was formerly placed in the separate and now obsolete family *Sterculiaceae*. Named after Sterculius, the Roman deity of dung, from the Latin 'stercus' meaning 'dung', for the unpleasantly smelling flowers of some taxa.

Sterculia africana (Fig. 27) has an exceedingly wide distribution, probably the widest range of any species in the genus, occurring throughout much of tropical and north-east Africa from the Caprivi Strip in north-east Namibia, then northwards into southern Arabia including Socotra. It grows into erect, pachycaul deciduous trees 5–12m tall with a main trunk to 1m diameter. The bark is silvery-grey, brown or white, peeling in papery flakes revealing an attractive pink surface. The branches are brittle and semi-succulent. Its leaves are up to 15cm long and across, broadly ovate to almost circular with up to five lobes and are crowded at the branch tips. It sheds its leaves during the dry season and comes into flower before the leaves reappear at the start of the rainy season. This species is recommended for cultivation in South Africa and Namibia in 'waterwise gardening' in Bushveld and Namib Desert gardens, but the growth rate is reported to be slow under such conditions (van Jaarsveld, 2010). It sometimes has the vernacular name of 'Mopopaja Tree'.

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Fig. 27 ***Sterculia africana*** **on Socotra (Photo: Al Laius)**

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