Morfologija in opraševanje stapelijevk
Stapeliads, morphology and pollination

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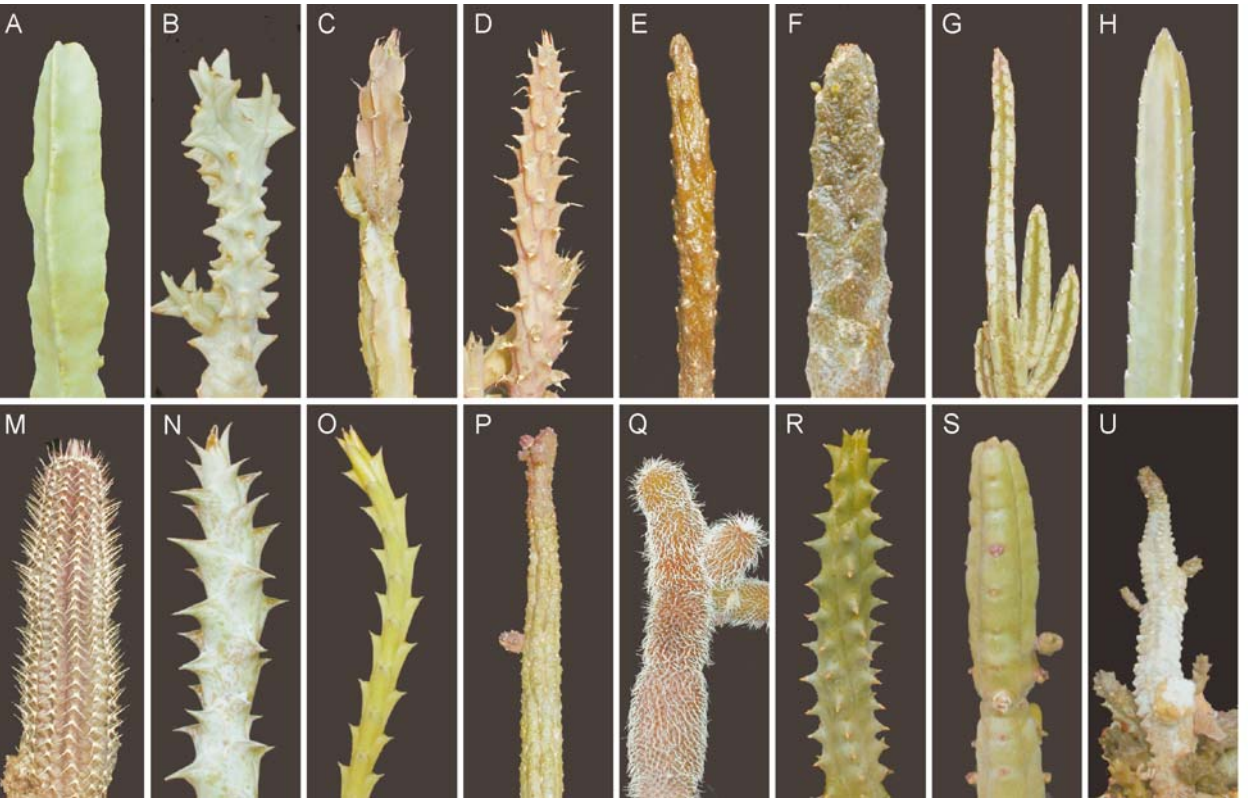
Stapelijevke so sočnice s čudovitimi cvetovi in vonjem, ki ga taki cvetovi ne zaslužijo. Razširjene so večinoma v Afriki, dotikajo se Evrope, v Aziji pa imajo tudi precej predstavnikov. Cvetovi so nekaj posebnega, ne samo po bizarni lepoti ampak tudi po zgradbi. Prav tako je tudi oprašitev samosvoja, saj podobne ne najdemo nikjer drugje v rastlinskem svetu.

Ključne besede:
stapelijevke, *Apocynaceae*, *Asclepiadoideae*, morfologija, opraševanje.

Stapeliads are succulents with beautiful flowers with a smell that does not match their beauty at all. Distributed mainly in Africa, a few species can also be found in Europe, and quite a few in Asia. Their flowers are unique, not only due to the bizarre beauty, but also due to the unusual reproductive structures. Even the pollination mechanism has no parallel in the plant kingdom.

Keywords:
Stapeliads, *Apocynaceae*, *Asclepiadoideae*, morfology, pollination.

Stapeliads, which are stem succulents, belong to the family *Apocynaceae* and subfamily *Asclepiadoideae*. Until recently, they were placed into the *Asclepiadaceae* family. The stem shapes are very similar in most genera, but when they bloom, the beauty of the flowers is striking as well as their unpleasant smell! "Stapeliads, Orchids of the Succulent World" is the title of the web pages of Jerry Barad from New Jersey, USA. The title says everything. The flowers have a beauty and colour that can only be compared with orchids. And they also share another characteristic. The pollen mass is fused in a wax pollen sack - pollinium, which is transferred by pollinators to the style.



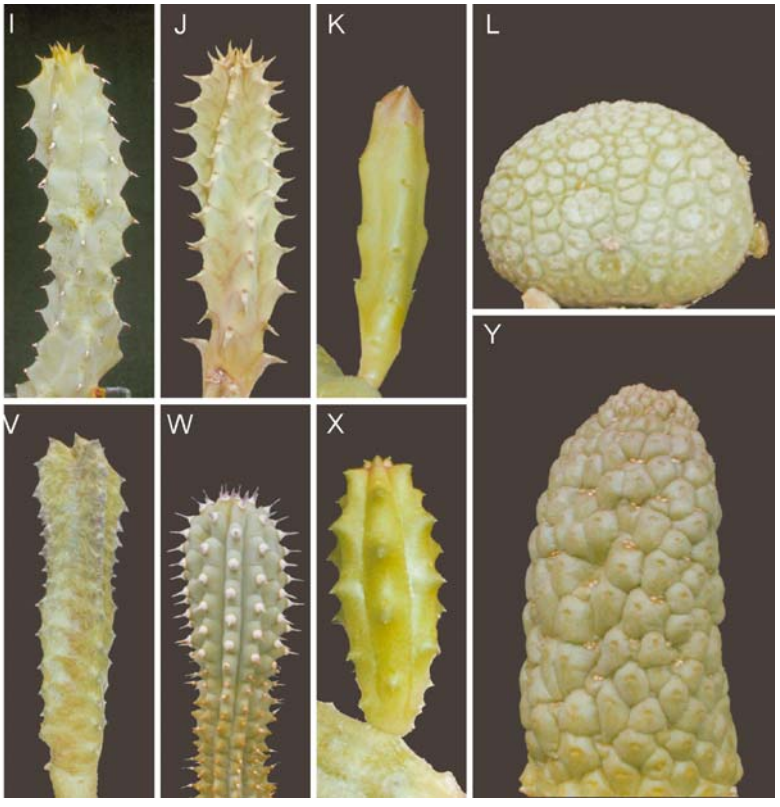
All stapeliads have some common morphological characteristics. Succulent stems are the most visible, and which are alike in different genera. The floral structure of the flowers is five lobed in all asclepiads and they also have similar fruits and seeds.

Distribution

Stapeliads are distributed only in the dry regions of the Old World. The easternmost locations are in Myanmar (formerly Burma), Sri Lanka and India and they extend through Pakistan, Iran, the Arabian Peninsula, Israel and northern Africa to the Canary Islands in the west. The northernmost distributions are in Spain and the Italian island Lampedusa and they stretch over northern and north-eastern Africa to southern Africa, where there is the highest density of species. Most stapeliads are terrestrial, hiding in the half shade of grass and bushes. Only some tougher species proudly defy the strong sun.

Stems

The stems are mostly very fleshy. In some species they become woody in the lower part of the stems. They contain a transparent watery sap, which oozes out if injured. Plants are consumed by natives and animals, although the sap is bitter. Stems are angled or round in transverse section. Some species have prominent ribs, most of them have tubercles arranged in ribs. Genera *Larryleachia*, *Lavrania*, *Pseudolithos*, *Notechidnopsis* and *Echidnopsis* have very flattened tubercles. In some genera they are conical - elongated into a tooth. In *Orbea* (*Orbeopsis*, *Angolluma*, *Orbeanthus*, *Pachycymbium*) it's one of most distinctive features. The teeth also appear in some species of *Huernia* and *Duvalia* (section Arabica). The plants with four ribbed stems are in the majority (*Stapelia*, *Orbea*, *Huernia*, *Piaranthus*, *Caralluma*…). In the genera *Tavaresia* and *Hoodia* the ribs are more numerous. The above mentioned genera with



Stem shapes in stapeliads:

A - *Crenulluma adenesis.*
B - *Sanguilluma socotrana.*
C - *Spathulopetalum gracilipes.*
D - *Duvalia polita.*
E - *Rhytidocaulon macrolobum.*
F - *Rhytidocaulon fulleri.*
G - *Stapelia olivacea.*
H - *Stapelia* grandiflora
I - *Huernia* hybrid.
J - *Huernia* sp. MST 335.
K - *Piaranthus decorus.*
L - *Pseudolithos migiurtinus.*
M - *Tavaresia barklyi.*
N - *Orbea* (*Angolluma*) *sprengeri.*
O - *Orbea variegata.*
P - *Echidnopsis* spec.
Q - *Stapelianthus pilosus.*
R - *Quaqua incarnata* var. *tentaculata.*
S - *Tromotriche aperta.*
U - *Anomalluma mccoyi.*
V - *Stapeliopsis neronis.*
W - *Hoodia* sp. MST 13.
X - *Pectinaria longipes.*
Y - *Larryleachia marlothii.*

Photos by Iztok Mulej

Only *Frerea indica* (*Boucerosia frerei*) in the whole stapeliad group has fully developed leaves.
Photo by Iztok Mulej

flattened tubercles have also more ribs, however these ribs are not so distinctive.

Leaves

Only *Frerea indica* in the whole group of stapeliads has fully developed leaves that fall off at the end of growing season. In other species the leaves are strongly reduced. The leaves in some species in *Echidnopsis*, *Stapelia* and the former *Caralluma* are like scales that soon dry. They stay in some species and fall off in others. In *Huernia pillansii* and *Stapelianthus pilosus* the leaves are transformed into soft hairy tips. The leaves can be transmuted into hard thorns, the most distinctive being *Quaqua mammillaris*. Leaf thorns are distinctive of the genera *Hoodia*, *Tavaresia* and *Edithcolea*. Mostly, the leaf spine is single, only in the genus *Tavaresia* a couple of side bristles (stipules) appear beside the central one. Other stapeliads lack the stipules. In some species (*Duvalia polita*, *Orbea* (*Orbeopsis*) *lutea* only their remains - denticles - are still visible.

Growth

The growth pattern of stapeliads is very similar. Side shoots spring up from the base of the primary stem and they grow further from the lower part of the stems. Some side shoots root in contact with the ground and become independent of the primary root system. They can form large pillows. Older stems in the middle of the clumps die away in time, and the outer stems spread forward and make separate plants. Most of the stapeliads are of low growth only some species of the genus *Hoodia* can reach one meter and a half. The basic growth form of stems is erect, but in some species, it is creeping (*Duvalia*, *Echidnopsis*, *Huernia*). Some species of genera (*Orbea*, *Boucerosia*, *Duvalia*) form underground stems - rhizomes.

Side shoots spring up from the base of the primary stem and they grow further from the lower part of the stems. *Orbea* (*Orbeopsis*) *lutea*.
Photo by Iztok Mulej

Succussion of buds forming on *Orbea woodii*
Photo by Iztok Mulej

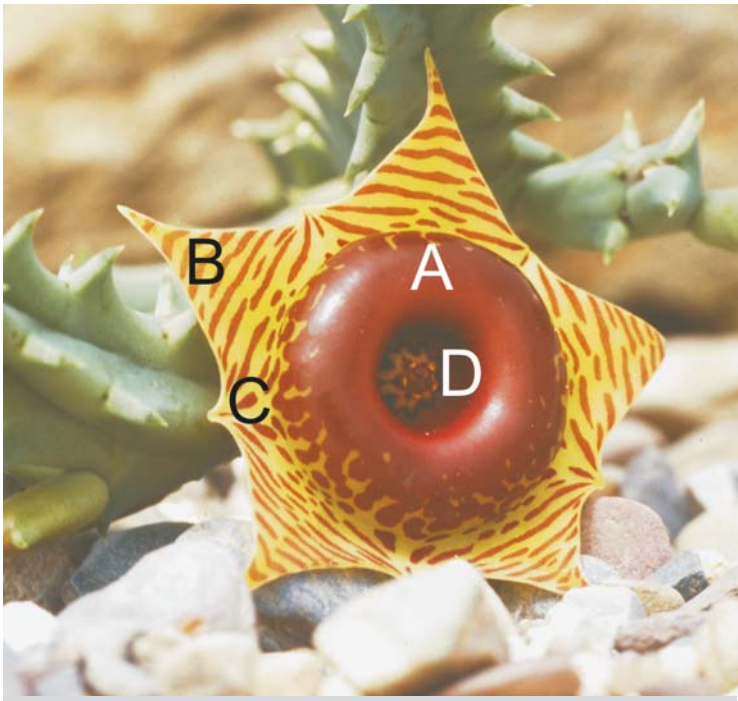
Flower formation

Flowers appear in large numbers and can form inflorescences, only rarely do they appear individually. They are usually at the apex of the stems. In most stapeliads it seems that the flowers appear laterally to the growing axis or even from the base of the stems (*Huernia*), however it is not so. From the base of the stems grow a peduncle, and from it the main stem grows out and pushes the peduncle in a lateral position. The peduncle is always between the axis of leaves or tubercles. In some species flowers appear in succession from the same peduncle.

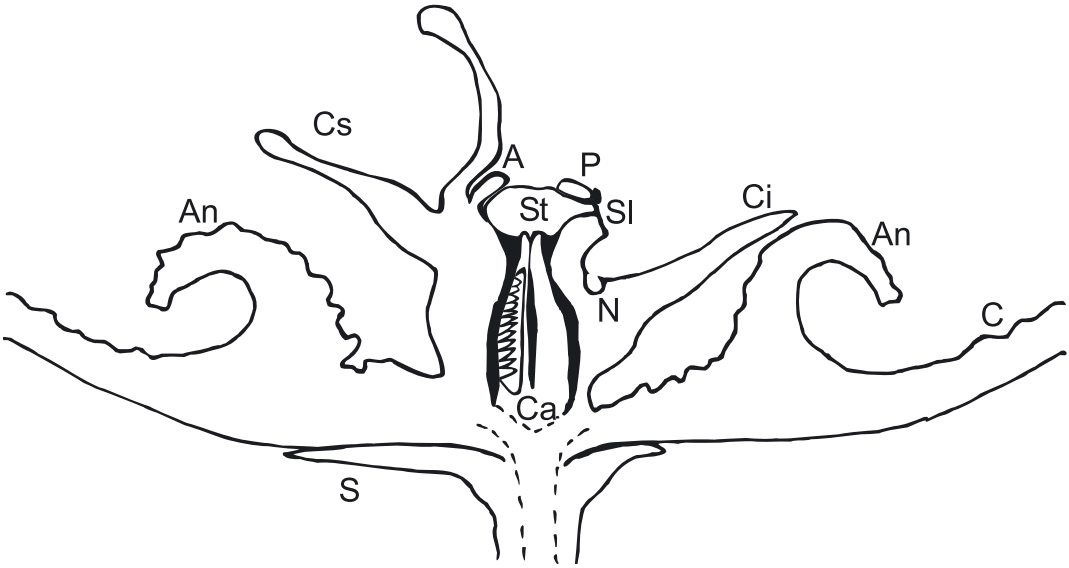
In the genera *Caralluma*, *Spathulopetalum*, *Cryptolluma* (by Plowes) the stems elongate to a long, thin peduncle with numerous little flowers. When the fruits ripen, the whole stem with peduncle dries up. *Boucerosia*, *Apteranthes*, *Sulcolluma*, *Crenulluma* (by Plowes) have flowers in umbels at the apex of the stems. It moves later to a lateral position because of the growth of the stems.

Flower structure

At first sight the flowers are very uniform. They have five sepals and five fleshy petals - corolla lobes. The sepals are tiny, the petals are usually in a star formation and grown together to form a shorter or longer tube, at least to one third or nearly for the whole length in some species (*Pseudopectinaria malum*, *Echidnopsis*). It these cases, there is only a small slit at the top of the flower to allow pollinating insects to enter. In some others (*Ophionella arcuata*) the corolla lobes are joined together at the tips and the shape of the flower is lantern like. The corolla in *Tavaresia* is tubular and trumpet-shaped. The corolla in some species also has a fold in the middle of the flower that forms a ring around the tube



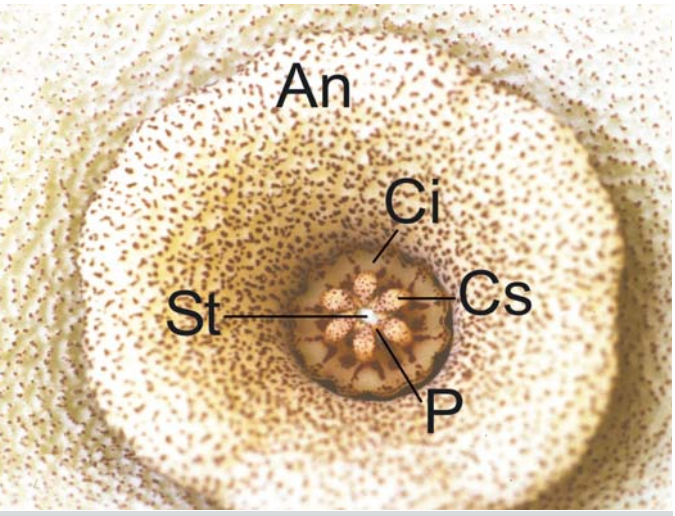
Flower of *Huernia zebrina*
A - annulus, B - corolla lobe, C - intermediate corolla lobe, D - staminal coloumn.
Photo by Iztok Mulej



Vertical section of flower of *Orbea variegata*
A - anther, An - annulus, C - corolla, Ca - carpel, Ci - outer (interstaminal) corona, Cs - inner (staminal) corona, N - nectar cavity, P - pollinium, S - sepal, Sl - guide rail, St - style.
Drawing by Iztok Mulej

and it is called an annulus. In the latest research (Liede & Kunze 1993) the annulus has been recognized as a part of the coronal structure (annular corona)

The outside of the corolla lacks vivid colours, only in plants with urceolate or lantern-shaped flowers is it more colourful. The inner side of the corolla with many kinds of shapes and patterns is the exact opposite. The surface is often wrinkled, or covered with hairs or papillae, transverse furrows or scars. Red, brown, yellow and violet colours with all of their intermediate tones are predominating. The flowers imitate carrion with their smell and colour, and attract pollinating insects with secretions and also hairs. The diameter of the flowers is from a few millimetres to 50 cm in *Stapelia gigantea*.



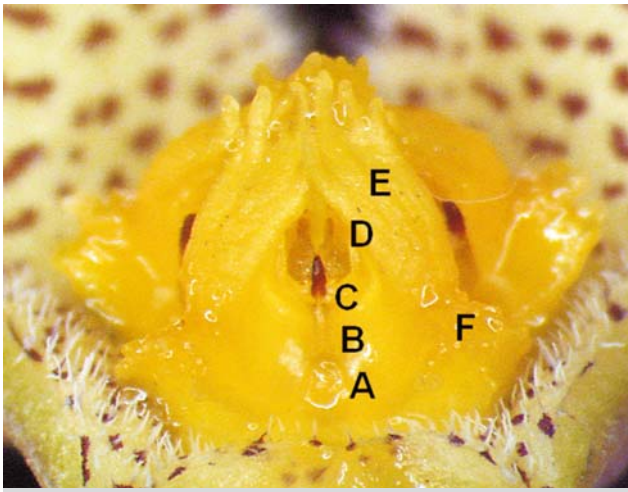
A view of the centre of the flower of *Orbea ciliata*
An - annulus, Ci - outer corona, Cs - inner corona, P - pollinium, St - style head.
Photo by Iztok Mulej

The stamina and pistil cannot be found in the flower. They are transformed into a complex structure - the gynostegium with a single or double corona. Two carpels are hidden inside the gynostegium and each of them forms a separate unilocular ovary united only by the common style. Filaments are joined together into a staminal column which encloses the ovary. The receptive organ for pollen is five slots found in the lateral position of the staminal column between the lobes of the inner corona and are open toward the base and

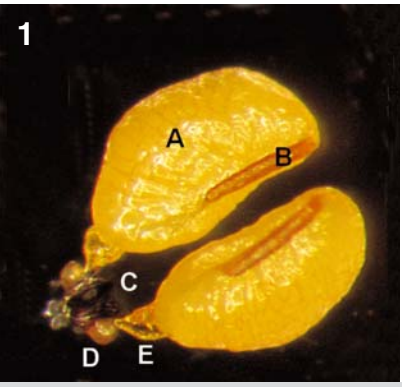
narrow toward the top of the gynostegium. They are named guide rails or anther wings or staminal locks (Barad 1990). The points of the ovaries and staminal column are grown together to a five-lobed style head. They lie directly above the guide rails.

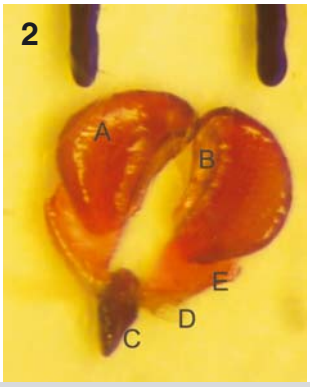
The pollen of each staminal area is amassed in two waxy pollen masses or pollinia. A pair of adjoining pollinia is attached to a translator and forming the pollinarium. The translator has a central structure corpusculum (clinging head), a pair of arms of translator (caudicles) and a pair of wings. The corpusculum has a central jag which continues the guide rail. Five pollinaria are positioned in the corners of the style head with the corpusculum directly above the guide rail. The translator is a product of secretion of the underlying glands. The pollinium has a minute wedge-shaped structure named the pollinium key (Barad 1990), anchor margin, wave crest or germination crest on the lower inner side. The latter is preferred by most of the authors.

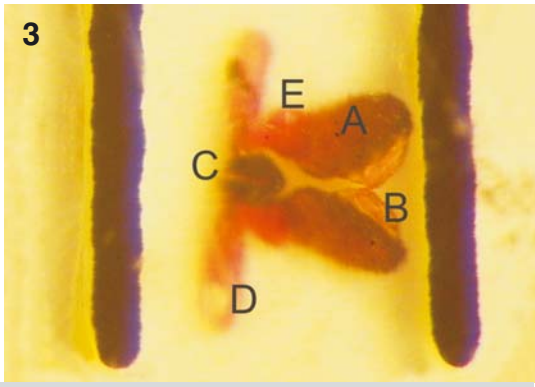
The single or dual corona is an appendage to the gynostegium. It consists of the inner or staminal corona and outer or interstaminal corona. Both develop from filaments and anthers. They are five-lobed like other parts of the flower. The staminal corona encloses the staminal column so that the corona lobe is placed between neighbouring guide rails. The corona lobes are usually higher than the style head and they can also cover it. The outer corona can be joined to the base of the floral tube or annulus. It can also be raised and embrace the gynostegium. The interstaminal corona is so reduced in some genera (*Piaranthus*, *Duvaliandra*) that it is imperceptible. Nectar cavities are found close under the guide rails. Sometimes they pour out so much sweet liquid that the whole gynostegium is flooded with nectar.



Gynostegium of *Piaranthus geminatus*
A - nectar cavity, B - guide rail, C - corpusculum, D - pollinium, E - inner corona lobe, F - transversal fold of inner corona.
Photo by Matija Strlič







Pollinarium of *Piaranthus geminatus* (1), *Stapelia obducta* (2), *Duvalia caespitosa* (3).
A - pollinium, B - germination crest, C - corpusculum, D - caudicle wing, E - arm of translator.
Scale bars in 2 and 3 - 1 mm.
Photo (1) by Matija Strlič, (2 & 3) by Iztok Mulej

When the fruit ripens, it bursts longitudinally. The seeds are blown by the wind.
Photo by Iztok Mulej

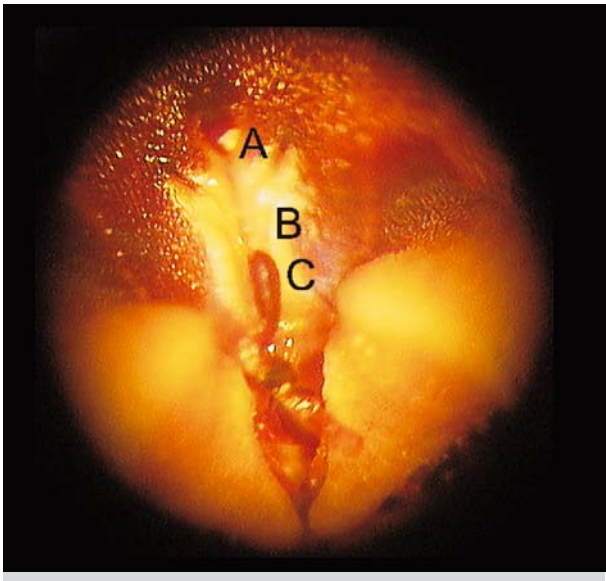
Fruit

The corolla with the gynostegium dries and falls away after a successful pollination. Only two naked carpels remain protected with sepals. After successful pollination the pedicel grows fat and sometimes it extends, too. The carpels develop into two fruits - follicles which look like horns. It can grow soon after pollination, next spring or even after some years. When the fruit ripens, it bursts longitudinally, and large, up to 7 mm long seeds pop out of it. They are equipped with silky parachutes. The seeds are blown far and wide by the wind, and thus they are distributed far away from the mother plant.

Pollination

Pollination in most of *Spermatophyta* is performed by the transfer of pollen to the style of the pistil. In stapeliads pollination is more complicated as is the structure of the sexual organs. The pollinators are usually different kinds of flies, attracted by the odour and colour of the flowers. They look for food in the flowers and lay eggs. The complicated structure of the corona and rigid hairs on the corolla enable flies only a limited access to the nectary-glands. They fumble with the proboscis near the slots towards the mouth of the flower. Doing this, the hairs or bristles of the head or legs are often stuck in the guide rails and only one way is possible - upwards to the end of the staminal lock, which is connected to the jag of the corpusculum of the pollinarium. If the fly is strong enough, it pulls out the entire pollinari-

Two follicles developed from each succesful pollination.
Photo by Iztok Mulej



Pollinated flower of *Duvalia caespitosa*
A - nectar cavity and beginning of rail guide,
B - rail guide,
C - wedged pollinium.
Photo by Iztok Mulej

um and moves it to the next flower. If the insects are too weak to remove the pollinarium, they remain trapped in the flower. By searching and drinking nectar in the next flower the pollinium is turned around and the germination crest (pollinium key) turns against the guide rail (staminal lock). Now we see why Barad used the expressions key and lock. The germination crest catches into the guide rail and only one way is possible towards the end of slot where the pollinium finally wedges. The pollinator is trapped again and if it is strong enough, it frees itself or tears off the remnant of the pollinarium at the translator arm. It can pollinate another flower with the remaining pollinium. The placed pollinium remains in the receptive area of the style. Pollen germinates from the germination crest and after a day it is almost impossible to remove it. After a few days the corolla with gynostegium dries up and falls off; only two carpels, which develop into fruit, remain.

Some different species of stapeliads usually grow at the same locality, so natural hybridization is possible but not so frequent. Pollinators are usually specialized to one species. The difference in size of the germination crest and guide rails is also a limiting factor.

Pollinarium attached to the proboscis of the fly causes it a proble.m
Photo by Iztok Mulej

This pollinator cannot resist the odour of *Piaranthus parvulus*.
Photo by Loukie Viljoen

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