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The inflorescences of the *Sansevieria* (*Asparagaceae*)

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Abstract
The author discussed the nature of the clustered flowers in *Sansevieria*. Some authors claim that they were the result of shortened lateral branches, others think they are cymes. The article analyses both concepts and draws conclusions regarding the arrangement of flowers and bracteoles. A study of 29 taxa found that the inflorescences are thyrses and their partial inflorescences are cymes of the helicoid type. The author makes a proposal for newly defining the inflorescences of *Sansevieria*. In addition to that he provides results of a statistical investigation into the direction of rotation and sequence of the helicoid cymes. It was found that both are distributed at random.

Introduction
Sansevieria are particularly popular because of their attractive leaves and not because of their flowers, which are inconspicuous at first glance and which only open at night. The clustered arrangement of these "nondescript" flowers on the inflorescences contains many interesting details but has been hardly studied so far.

Brown describes the flowers of *Sansevieria*: "*Flowers solitary or two or more in a cluster, on pedicels that are jointed near the middle or apex, the upper part falling off with the flower (deciduous part), always with membranous or thin scale like bracts at the base*" (Brown 1915) In the species descriptions, he always states the number of flowers per cluster as a species characteristic, when possible, but does not comment on the nature of the clusters.

Bos believes the pedicels to be reduced terminal stems up to their point of division (abcission tissue) and from there on considers them to be part of the receptacle. Regarding the clusters themselves, he states: "*The arrangement of the flowers in each cluster seems random and distinct patterns in the succession of flowering cannot be distinguished*." (Bos 1984, 8)

Newton (2006), on the other hand, uses the term "cluster" as well as "glomerule" and states that only one flower per cluster blooms at intervals of up to 3 days. He writes that the clusters are "clearly" highly-condensed side shoots and that the inflorescence is therefore "really a compound inflorescence" (i. e. neither raceme nor spike).

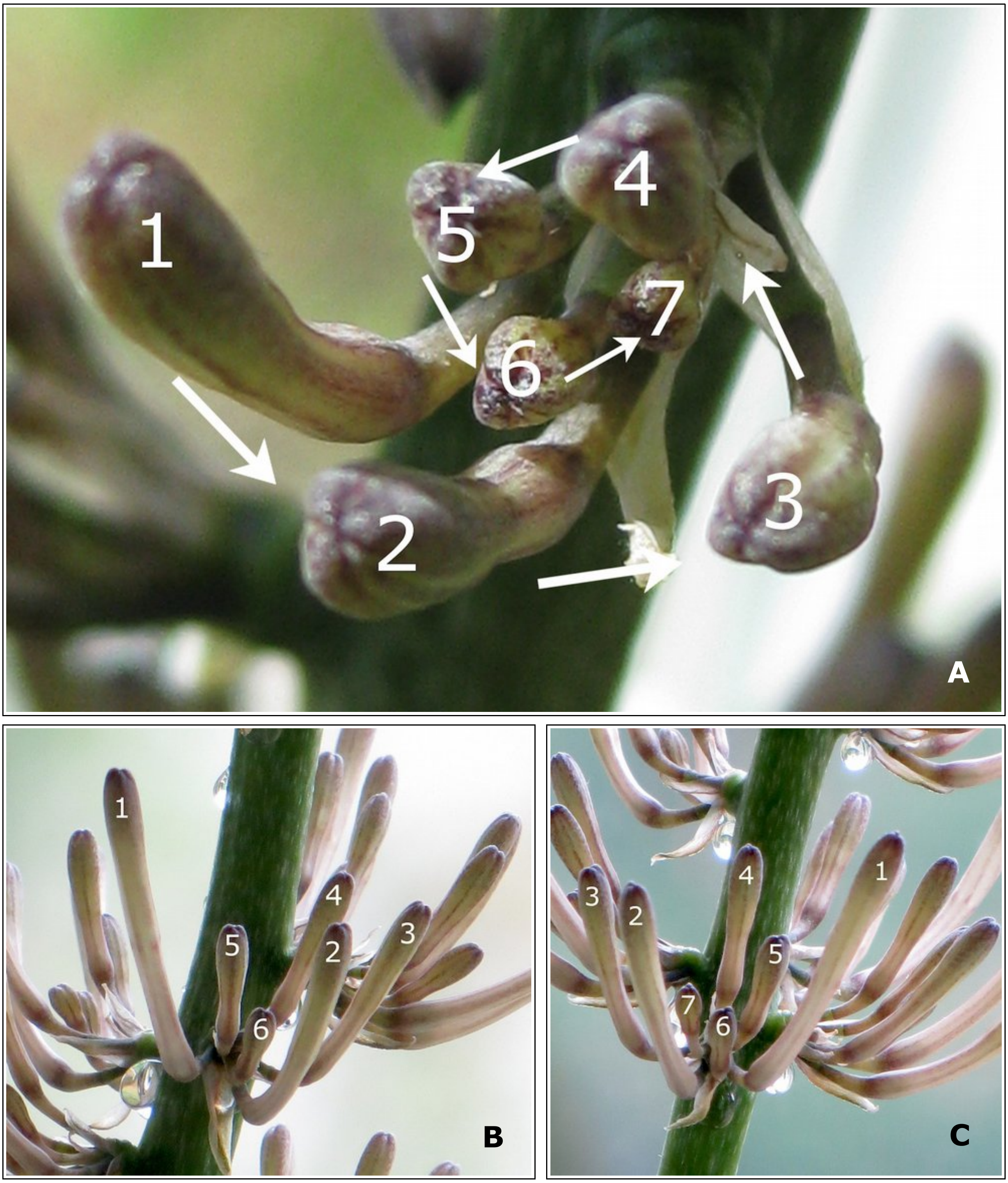
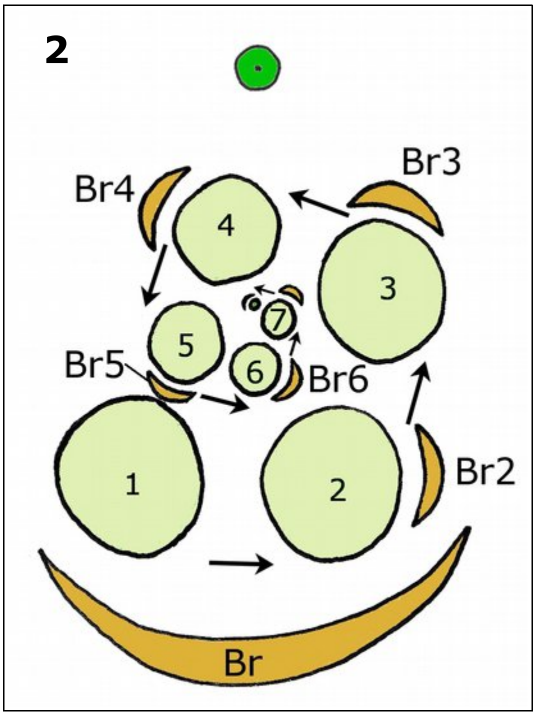
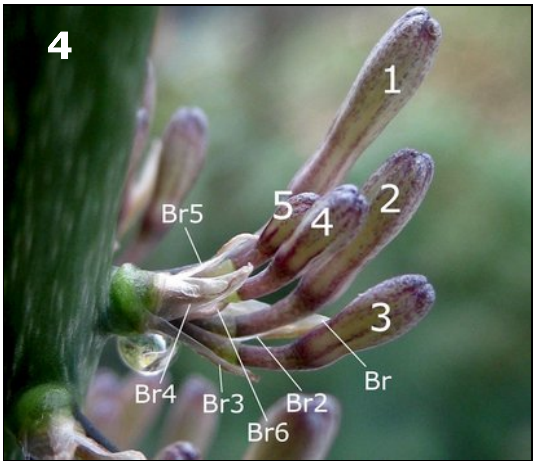


Fig. 1 – S*ansevieria cylindrica*

A= In multi-flowered clusters, the spiral arrangement of the buds is noticeable when viewed according to size. (7-flowered cluster, counterclockwise all the way round) **B**= Counterclockwise cluster of flowers with six buds. The buds are numbered according to size to show their spiral arrangement. **C**= Clockwise cluster of flowers with seven buds on the same inflorescence.





Jankalski (2009) concludes from his observation that the central flower of each cluster opens first and that the clusters are not shortened side shoots but are in fact cymes[1], making the inflorescence a thyrse[2]. When describing *Sansevieria volkensii,* Newton (2010) mentions clusters containing three flowers arranged in a row, with the middle one blooming last and rejects the idea of the clusters being cymes. On the other hand, *in Sansevieria dumetescens* and *Sansevieria frequens* he finds flowers arranged in a ring shape. Since he cannot recognise a particular structure in the clusters, he again suggests the term "glomerule" as a provisional term.

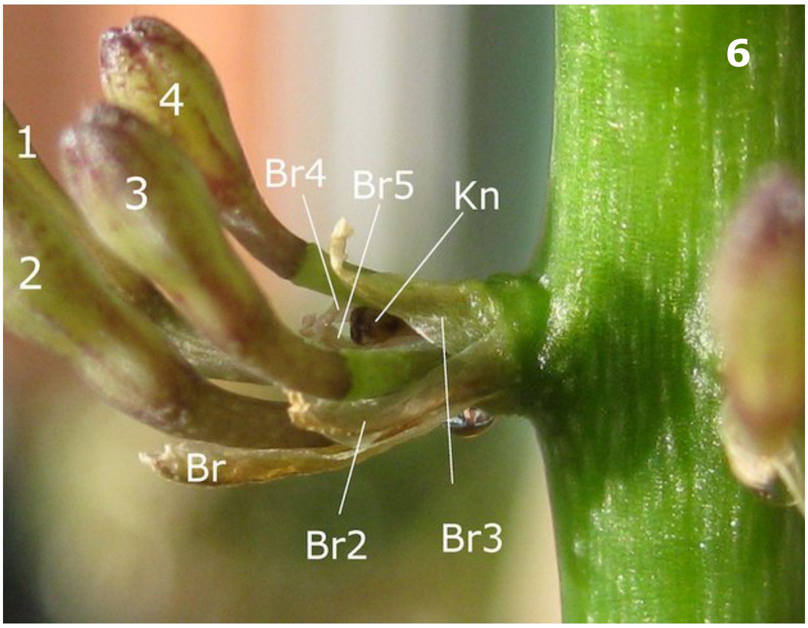
During my own observations on flower clusters with more than four buds, I noticed that they form a spiral according to their size (Fig. 1). These spirals occur clockwise and counterclockwise, even in the same inflorescence. The spiral arrangement can be derived from a shortened side shoot as well as from a cyme. The arrangement of the bracts and bracteoles leads to the theory that these are helicoid cymes[3].

Fig. 2 – Clusters from Fig. 1 shown schematically
The flower buds (pale green) are arranged in a spiral at the base, here seen with a counterclockwise orientation. At the very top the main axis, the stem of the inflorescence (peduncle). The most developed bud (1) is at the bottom, above the bract (light - brown), to the right of it, the second bud (2) is arranged a little lower. This and each subsequent bud sits between the previous bud and its bracteole (light brown). The spiral ends open, opposite the last flower. Depending on the type (and environmental conditions), the spiral can "break off" at any point, so that clusters with fewer or more buds are created. The fewer buds the cluster contains, the more unclear it is to see the spiral structure. The direction of orientation of the "clustered spirals" is apparently not fixed. Both clockwise and counterclockwise clusters appear on each inflorescence.

Fig. 3 – *Sansevieria deserti*
Detached cluster, shown from above with five buds, arranged clockwise. The first flower has already faded. The spiral arrangement can be recognised by the base of the pedicels. (1-5: Flowers 1-5 numbered according to size; Br: Bracteoles; T: Separation points [no nodes])

Fig. 4 – *Sansevieria cylindrica*
Five-flowered cluster in a clockwise orientation, shown from diagonally above, the first bud behind. The arrangement of the bracts is quite easy to see. At the front, the bracteole of the third bud (Br3) overlaps that of the fourth (Br4). (1-5: Buds 1-5; Br: Bract; Br2 – Br5: Bracts of flowers 2-5; Br6: Bracteole of the undeveloped last bud)

1) From Greek Kyma – young shoot
2) Thyrsus originally referred to a staff entwined with ivy or vine leaves, which was the attribute of the Greek god Dionysus and his entourage. Used botanically by Linneus in 1751. (Wagenitz 2008)
3) Latin: Bostryx



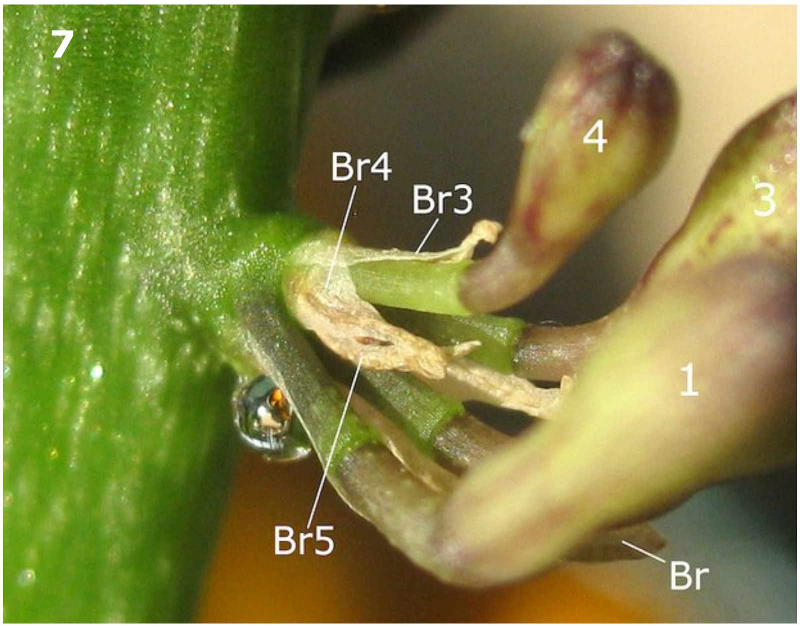


Fig. 5 – *Sansevieria* 'Vivo'
Clusters of five buds arranged clockwise. The first flower is seen open

Fig. 6+7 – *Sansevieria cylindrica*
Four-flowered cluster. The bract (Br) overlaps the bracteole of the second bud (Br2), which in turn overlaps the next bracteole (Br3). Under the fourth bud lies the stunted bud (Kn) of the open end with its bracteole (Br5).
Fig. 7 – The same cluster as Fig. 6. At the bottom in front is the first bud without bracteole, on top is the fourth, between its bracteole (Br4) and the third bud. The bracteole (Br5) of the open end of this overlaps to the front. The bud of the open end is covered by the last two bracteoles.

Material and Methods

For the morphological investigations I used flowering and fruiting plants from my collection.
For the statistical evaluations I had 79 inflorescences from 27 taxa at my disposal. Some were freshly withered and some completely dried but unpressed inflorescences as well as completely dried inflorescences (*S. stuckyi* and *S. kirkii* 2, Tab. 3) from Gran Canaria and Tenerife. Fresh material was examined directly, withered dried inflorescences were placed in tap water to swell up for 3–5 days and examined with an 8-fold magnifying glass to count the helicoid cymes. For the statistics, the direction of orientation and the number of pedicels per cluster were determined for all helicoid cymes from base to apex. From this, the number of clusters and flowers could be determined for each examined thyrse, as well as the number, order, and proportion of clockwise and counterclockwise helicoid cymes (see Table 3 + footnote 12).

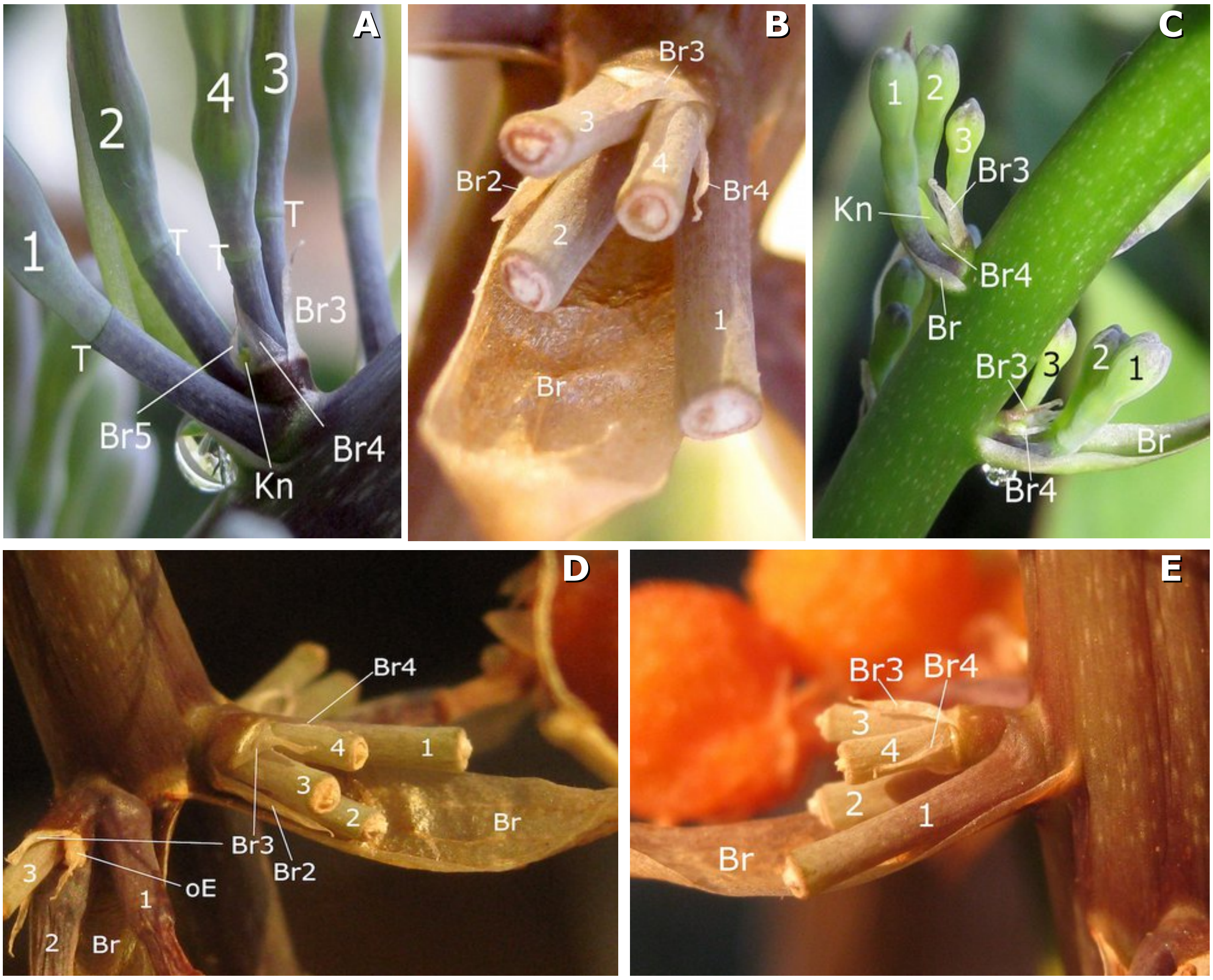


Fig. 8 – *Sansevieria hyacinthoides*

A = on the front left is the first bud without bracteole. On the right are the third and fourth buds with their bracts (Br3 and Br4) aligned with the second and third bud. The bracteole of the third bud overlaps that of the fourth. Br5: The bracteole of the open end. Kn: undeveloped bud of the open end. The separation points (T) on the pedicels are not nodes, but separation points for the shedding of unfertilized flowers.

B = Same cluster as **D** and **E** from earlier. The position of the bracts in a helicoid arrangement can be clearly seen here. 1-4: pedicels after shedding flowers 1-4; Br: bracts; Br2-Br4: bracteoles

C = Three-flowered clusters, the upper one is orientated clockwise and the lower one counterclockwise. The first bud is seen at the front and is without a bracteole. The upper bracteole (Br3) belongs to the third bud. The tiny bracteole (Br4) of the open end (Br4 and Kn) points towards the third bud.

D = Four-flowered cluster, clockwise, after the flowers have been shed at the time of fruit ripening.

Right helicoid cyme: behind the pedicel of the first flower. The bracteoles of the 2nd and 3rd buds (Br2 and Br3) in front and above, the bracteole of the fourth bud (Br4) almost covered by the pedicel.

Left helicoid cyme: orientation also clockwise, but with a three-flowered cluster. The pedicel of the first flower on the right is without bracteole. Above you can see the open end (oE) on the right of the third pedicel.

E = Same thyrse as D, cluster shown from the other side. In front, the pedicel of the first bud without bract. Above, the pedicels of the third and fourth bud in a spiral arrangement.

Results

Morphology of the Clusters

All clusters with more than five flowers show the pedicels, and for this reason the buds, in a spiral arrangement (Fig. 1, 3–8a). A ring-shaped arrangement can be seen in clusters with four to five flowers (Figs. 3, 5–7, 8a, b, d, e). Two- to three-flowered clusters have buds arranged next to each other in a row or in an arc (Fig. 8C, 9, 10). There are also single flowers, or rather clusters with only one flower (Fig. 15).

The branching relationships of the pedicels in the clusters are difficult to identify, as the pedicel portions below the prophylls (Fig. 12, Hypopodium) are very much reduced and the pedicel portions above (Fig. 12, Epipodium) next to the bracts appear to come directly from the peduncles (Figs. 4, 6-10, 13, 14). The pedicels of the first flowers never have bracteoles (Fig. 8a, b, e, 14, 15). All pedicels ended immediately in a flower without further branching. Although the proportions of the pedicels and the bracteoles show clear differences in the various taxa examined, the position of the bracteoles reveals that each bud-bearing pedicel emerges as a new side shoot from a leaf axil of the previous "flower shoot" and that the new flower is always between its bracteole and the previous flower (Fig. 4, 6–10, 13, 14).

Further flowers are always attached at almost the same as or slightly smaller than right angles to the previous bract or bracteole and thus develop a spiral, the second blossom of which is furthest down (Fig. 7-9). The schematic diagrams in the last row of Table 1 and Fig. 2 show that the structure of the flower clusters of *Sansevieria* is cymose and can be identified as a helicoid cyme[4)]. The inflorescences end open at the top, meaning they have no terminal flower.

As a result of this, it turns out that the inflorescences of *Sansevieria* are open thyrses with helicoid cymes as partial inflorescences. Very rarely[5)] there are double helicoid cymes, the first flowers of which are partially or completely fused together. Because of the symmetry of this malformation, the structure, and the slightly less than 90° branching angle between the bract and the second flowers, can be clearly seen (Fig. 17, 19). The two second flowers are also to the side and a little deeper than the first flower here.[6)]

The two cultivars *S. trifasciata* 'Nelsonii' and *S. trifasciata* 'Moonshine' often had fused clusters with an unclear direction of orientation in some places and an irregular arrangement, sometimes with several open ends. However, these plants also show malformations in the flowers, so that malformations that are atypical for the genus in the helicoid cymes must also be expected. Such clusters were either taken into account according to their predominant direction of orientation or were not counted.

Distribution and sequence of helicoid cyme orientation

Counting the helicoid cymes on the thyrses showed that they always occur in both directions of orientation (Table 3). In many cases, the proportion of helicoid cymes in one direction of orientation clearly dominated. Clockwise helicoid cymes dominated the counterclockwise helicoid cymes in the thyrse of a *Sansevieria trifasciata* in a ratio of 74% to 26%. However, on another thyrse blooming at the same time on another shoot of the same plant, the ratios were almost reversed with 39% to

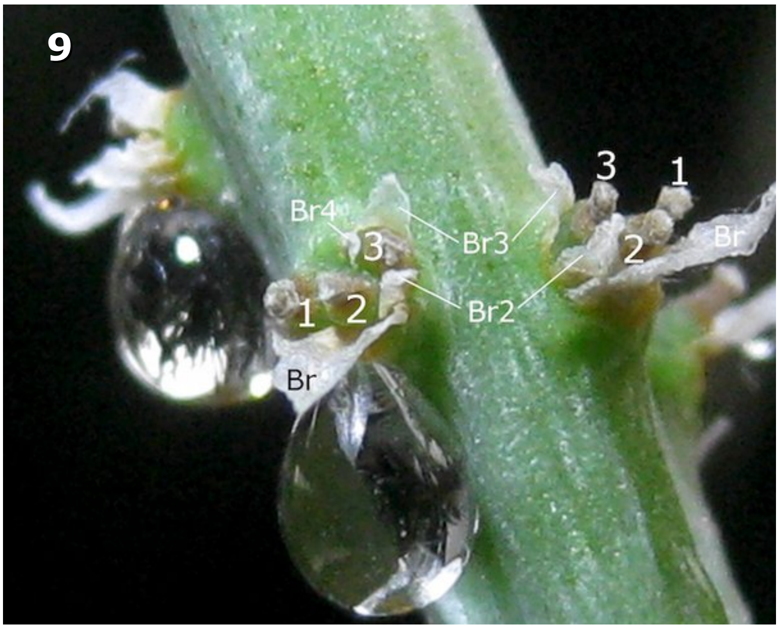
4) Other types of cymes, such as drepanium, rhiphidium or cicinnus are not to be explained further here.

5) When I counted, it was 11 out of approx. 5700 clusters (3x *S. parva*, 3x *S. senegambica*, 1x *S. cylindrica*, 3x *S. deserti*, 1x *S. gracilis*), that is approx. 2 per mill.

6) Such double helicoid cymes were counted as two single helicoid cymes running in opposite directions, whereby the first flower was only counted once.

71% (see Table 3, p. trif. (1) and (2)). The mean value of the proportion of all counted clockwise helicoid cymes is 48.7 ± 9.3% and thus shows, with large deviations in many thyrses, that overall, there is a random distribution of helicoid cyme orientation.

In many cases, clusters with the same orientation appear to be arranged in groups. But if one counts the succession of differently or identically oriented helicoid cymes of different thyrses of the same plant or the same clone, again no clear tendency can be seen. Here, the mean value of all counted helicoid cymes following one another in the same orientation is 51.2 ± 7.2%. Here, too, a random sequence of screw orientation can be seen, with a likewise high deviation. The plants with head-s-haped thyrses (*S. fischeri*, *S. kirkii* and *S. stuckyi*) show a pattern similar to the other examined *San-sevieria* (see Table 3 + footnote 12).



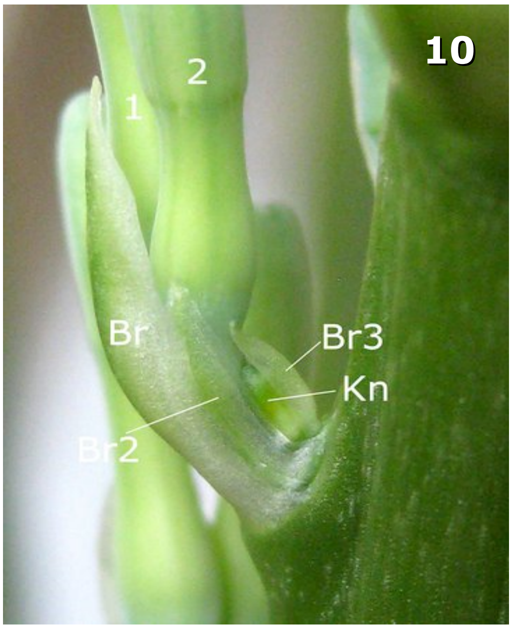


Fig. 9 – *Sansevieria ballyi*

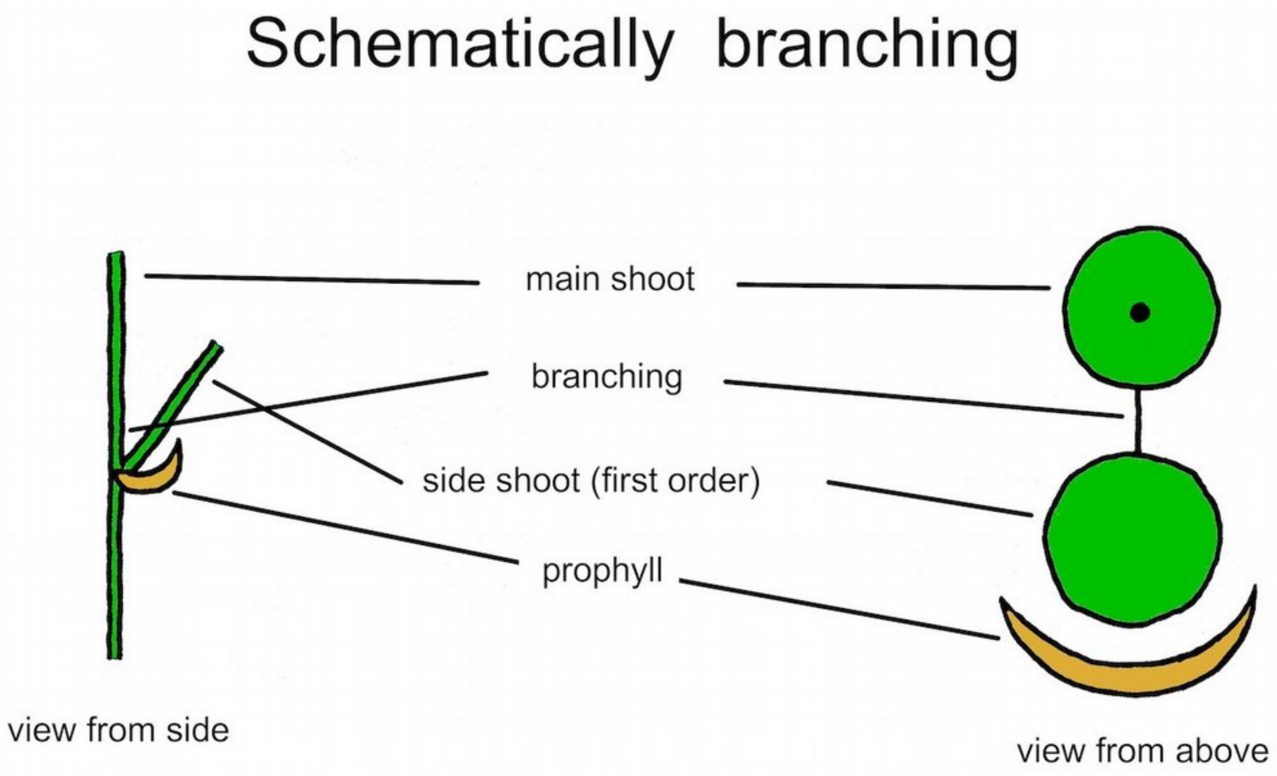
Three-flowered clusters with opposite orienta-tions after shedding the flowers. On the Left the counterclockwise helicoid arrangement of the pedicels and bracts is clearly visible. Br: bract; Br2, Br3 bracteoles; Br4: Bracteole of the undeveloped bud of the open end.

Fig. 10 – *Sansevieria longiflora*

Two-flowered cluster - the bract (Br) includes the bracteole of the second flower (Br2) and an undeveloped bud (Kn) with bracteole (Br3) growing towards the stem, which is encompassed by the base of the previous bracteole (Br2) and forms the open end of the helicoid cyme.

Fig. 11 – S*ansevieria roxburghiana*

Three-flowered cluster. the central flower has sunk horizontally towards the flower opening.



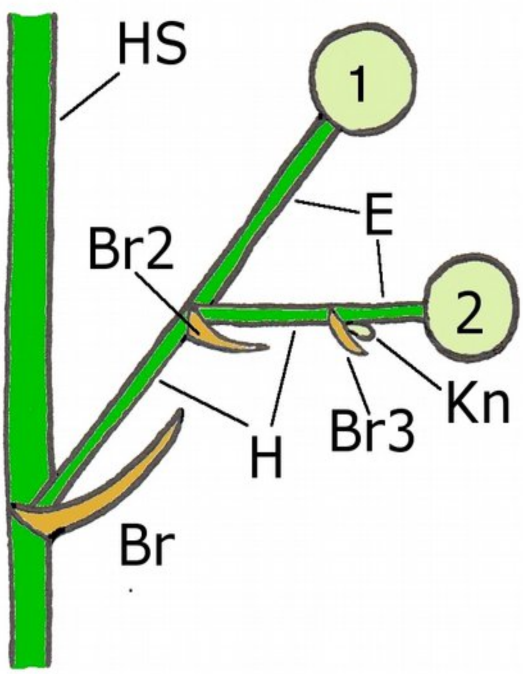


Fig. 12

(To understand the diagrams in Table 1)

The main shoot (peduncle), from which the first-order side shoot goes off, is marked with a point in the view from above. The line shows the direction of branching and points to the corresponding prophyll.

Cymose branching (sympodial)

HS - main shoot

1 - Flower of the 1st lateral branch that opens first ("priman" flower).

2 - Second-order flowering of the side shoot (secondary flower).

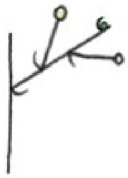
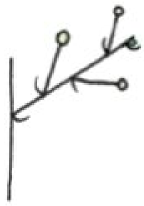
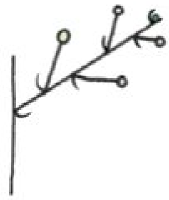
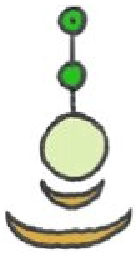
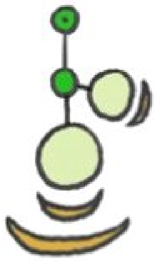
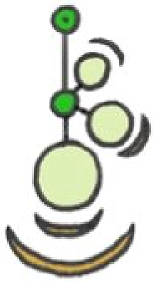
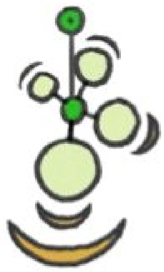
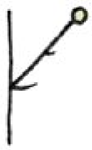
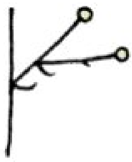
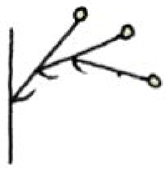
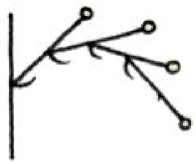
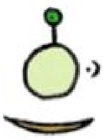
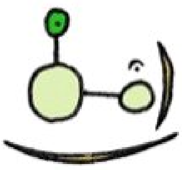
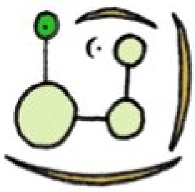
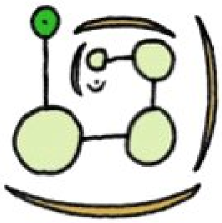
Kn - undeveloped bud, which together with its bracteole (Br3) forms the open end of the cyme.

Br, **Br2**, **Br3** - prophylls: bracts and bracteoles 2 and 3.

E - Epipodium, the internode of the side shoot above the prophyll.

H - Hypopodium, the internode of the lateral branch below the prophyll. In *Sansevieria* clusters, the hypopodia are so compressed that all of the prophylls are almost next to each other.

Table 1 – Comparison: side branch (raceme) – helicoid cyme

	1-flowered cluster	2-flowered cluster	3-flowered cluster	4-flowered cluster
Side branch (raceme); hypothetical schematic structure from the side				
Side branch (raceme); hypothetical schematic structure from above, counterclockwise orientation				
Helicoid cyme without a continuous main axis; schematic structure from the side				
Helicoid cyme; schematic structure from above, counterclockwise orientation				
Sansevieria clusters; Observed schematic structure from above, counterclockwise orientation				

<u>**Table 1**</u>: Darker green circle with central dot - main axis (peduncle); lower brown leaf - bract; remaining leaves - bracteoles; large pale green circles - buds. In the illustrations with structure shown from the side, the lower part of all side branches up to the next brakteole (hypopodium) must be imagined as being greatly shortened. In the side branch cluster (1st + 2nd row), all flower buds are side branches of the 2nd order, as in a raceme, which grow out of the shortened side branch of the 1st order (monopodial branching). In the case of the helicoid cyme (3rd and 4th row), each additional flower is a branch of a higher order than the previous flower (sympodial branching). The bottom row shows schematically the observed structure of the *Sansevieria* clusters.

Discussion

Side shoots always arise at nodes[7)], recognisable by a leaf with an axillary bud underneath. Such leaves on flower stems are called prophylls or, depending on their size, bracts or bracteoles. When the bud develops into a side shoot, it stands between the main branch and the leaf (Fig. 12). The indentations all around the surface of the pedicels (Fig. 3, 8a, 16) should not be confused with nodes, as both the leaf base and the bud are missing. Similar to the falling leaves seen in Autumn, there are separation points (abscission zones) at which unfertilised flowers loosen and fall off.

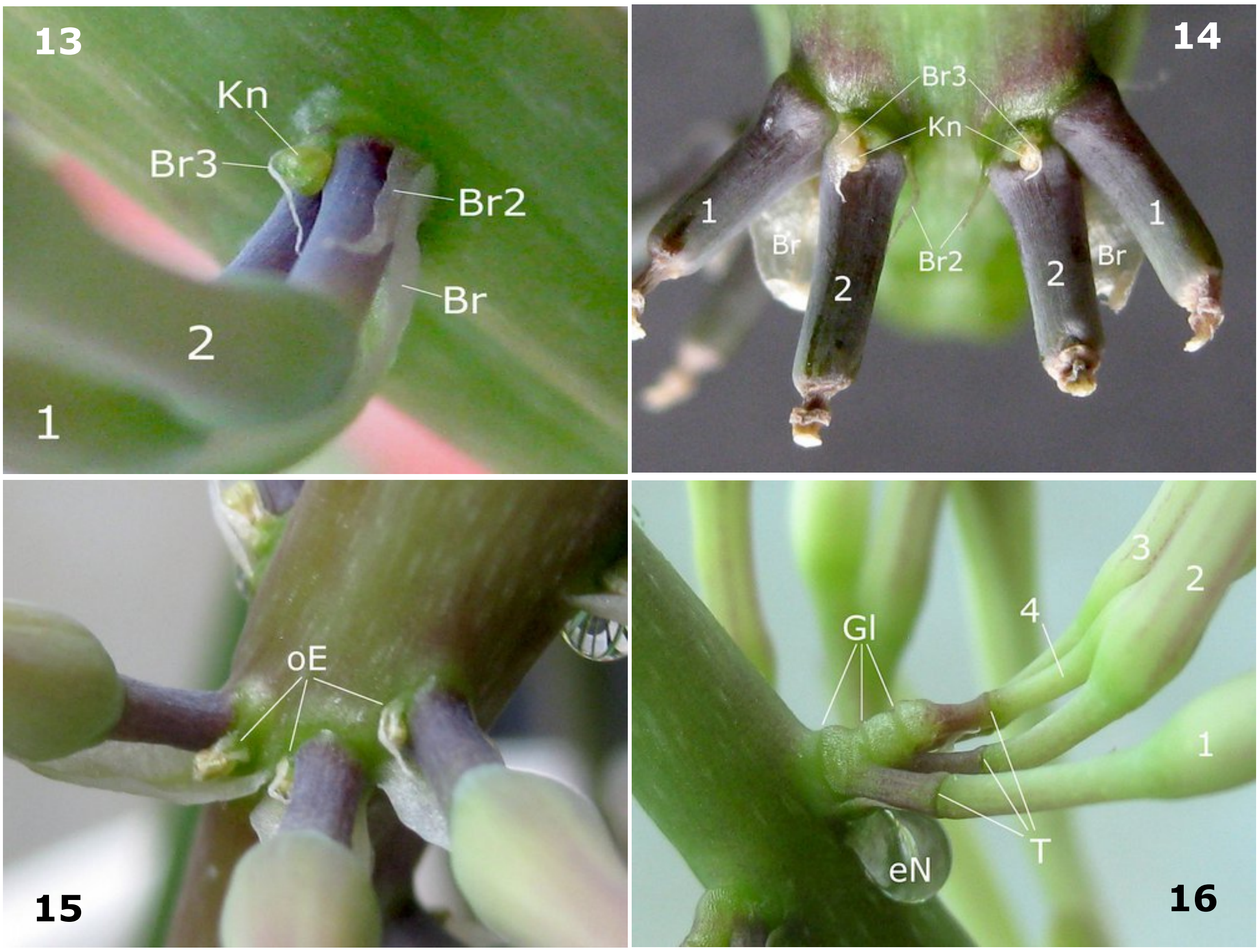


Fig 13 – *Sansevieria concinna* - Two-flowered helicoid cyme. - The open end of the helicoid cyme consists of an undeveloped bud (Kn) that stands between its bracteole (Br3) and the last developed flower bud (2). The pedicel of the second flower stands between its bracteole (Br2) and the pedicel of the first flower. **Fig. 14** – *Sansevieria fasciata* - Two two-flowered clusters, ceased blooming, with opposite directions of orientation, shown from above. The arrangement of the bracts (Br2) opposite the pedicels of the first flowers (1) and between the pedicels of the second flowers (2) can be seen clearly. At the top of their base are the open ends of the helicoid cyme in the form of stunted buds (Kn). These are in turn between their bracteole (Br3) and the second pedicel (2). **Fig. 15** – *Sansevieria concinna* (Lav 5949) - Three single-flowered "clusters". Here the helicoid cymes end after the first bloom. The two lower ones are arranged in opposite orientations, recognisable by the open cluster ends (oE). **Fig. 16** – *Sansevieria senegambica* - The structured "axis" (Gl), on which the buds attach, indicates the branching nodes of a cyme. The separation points (T) on the pedicels are not nodes. In front, the first bud without bracteole. Below the bract, a drop of extra-floral nectar (eN).

7) Latin: Nodus, Plural: Nodi

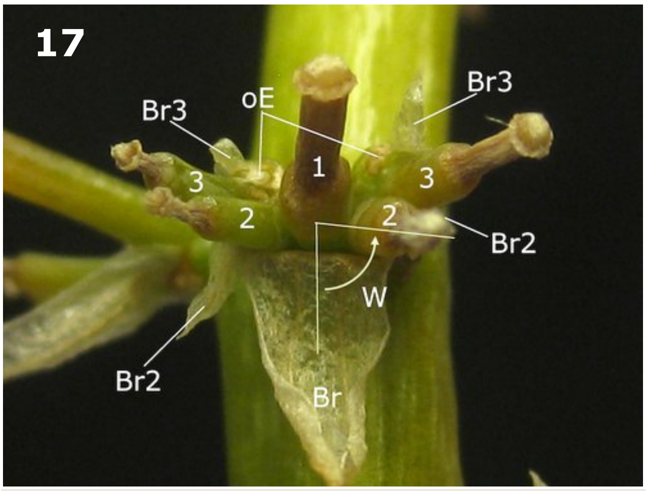


Fig. 17 - *Sansevieria senegambica*
Twice developed helicoid cyme. The first flower (1) in the middle is the starting point for a clockwise helicoid cyme and a counterclockwise helicoid cyme. Because of the symmetry, the first branch angle (W) of slightly below 90° to the bract is clearly visible. 1-3: pedicels 1-3; Br: bract; Br2, Br3: bracteoles of flowers 2 and 3; (The right bracteole 2 is folded up towards the end of the pedicel); oE: open ends; W: Branch angle between the bract (main axis) and the 2nd pedicel.

Fig. 18 - *Sansevieria suffruticosa*
Early bud of an inflorescence. At first glance, the arrangement of the bracts seems to be well ordered. On closer inspection, the directions of orientation (R: clockwise, L: counterclockwise) of the clusters can be seen, which appear almost diagonally arranged in the lower part and tend to be random at the top. After further growth and stretching of the stem, the order is largely lost.

Clusters as shortened side shoots (monopodial branching type, see Table 1, rows 1 and 2)

Bos (1984) and Newton (2006) understood the flower clusters of *Sansevieria* as shortened side shoots, that is, the individual flowers sit on a continuous axis, as in a (shortened) raceme.[8)] The bract under each cluster would then have to mark the branch of the shortened side shoot and the bracteoles would mark the leaf axils of the second-order flowering side shoots. Each of these side shoots ends with a flower without further branching.[9)] In the case that they are derived from shortened side shoots, the following characteristics would be expected on the clusters (see Table 1):

(1) In addition to the bract of the side shoot, each pedicel has its own bracteole.
(2) All bracts are facing the main axis (adaxially), i.e., they are aligned with the centre of the cluster.
(3) If an axis of sorts is recognisable despite the shortening of the side shoot, then it is to be expected smooth and not circumferentially structured.
(4) The open end of the cluster lies in the middle.

8) A raceme is an axis covered with single-stalked flowers.
9) In the schematic diagram of Table 1, the flower buds are shown as pale green circles in contrast to the growing shoots. The hypopodia (see Fig. 12) are not shortened for clarity.

(5) The arrangement of the buds is spiral and the buds bloom according to size, from the outside in. The first bud does not necessarily have to be at the bottom.

Apart from the spiral arrangement, I did not find these characteristics in the examined clusters of *Sansevieria*.

***Clusters as cymes*[10)]** (sympodial branching type, see Fig. 12 and Table 1, rows 3 and 4)
A cyme, as assumed by Jankalski (2009), on the other hand, does not have a continuous axis. A first side shoot ends immediately in a flower. Below the flower there is a node with a leaf and a leaf axil from which a second-order side shoot grows. In dicotyledonous plants, there are usually two transversely opposite bracts at each node, from the leaf axils of which branches can grow. In contrast, monocotyledons, such as *Sansevieria,* always have only one bud and one leaf per node, (Tillich 1998, 8) which is usually addorsed, (Leins, Erbar 2008, 135) that is, with the back facing the main axis. Second-order branching also ends immediately in a flower. This side shoot also has a node and branches out below the flower with a side shoot, now of the third order. This can go on indefinitely. Each additional flower emerges from a new side shoot that sprouts from the previous one.

In contrast to what is usually the case with monocotyledons, in *Sansevieria* the bracts in the flower clusters are not aligned with the back to the main axis (addorsed), but transversely, as in dicotyledonous plants. With this peculiarity, the following features are therefore to be expected:

(1) The bract is the prophyll of the first flower and is aligned with the main axis. The first flower therefore has no bracteole and is always at the bottom (but not necessarily the lowest at the bottom, see point 5) (Fig. 2, 7-9, 14).
(2) Each bracteole faces the previous flower bud and not the centre of the cluster (Figs. 2, 6–10, 13, 14).
(3) If an axis of sorts can be seen despite the shortening of the hypopodia (Fig. 12), then it is divided by the nodes at the branches (Fig. 16).
(4) The open end of the cluster consists of an undeveloped flower bud with associated bracteole, which is aligned with the last developed flower bud (Figs. 2, 6, 8c, 9, 10, 13–15).
(5) The first flower to bloom is at the bottom, the second at a roughly right angle, laterally, and the following at a similar angle to the previous bud. If the branching angle is smaller than 90°, the second bud is laterally a little lower than the first. (Fig. 1, 5–9, 14, 15, 17, 19) As the number of flowers increases, a spiral develops, the buds of which bloom from the outside to the inside in the order of their size (Fig. 1–2, 4–10 , 13-17).

The comparison with the observations shows that the clusters of *Sansevieria* are cymose and that the inflorescences are consequently thyrses, with helicoid cymes as cymose partial inflorescences. The helicoid cymes can develop a different number of flowers in the same inflorescence, which bloom in sequence at one-to-three-day intervals. (Newton 2006) Single-flowered helicoid cymes can be recognised by the laterally standing end bud (Fig. 15).

10) In more recent studies, the term "prophyll inflorescences" (German: Vorblattinfloreszenzen) is used. (Leins, Erbar 2008, 135)

It is noteworthy that the bracteoles, whose axillary buds produce further flower shoots, are arranged transversely to the previous branching in *Sansevieria* and are not with the back facing the main axis (addorsed) as in most monocotyledons (Leins, Erbar 2008, 135). In that case, all new flowers would stay in one plane and create flat, fan-like cymes. In fact, every additional flower in *Sansevieria* takes a position of approx. 90° to its respective axis of origin, as is usual with dicotyledonous plants, and the helicoid arrangement, which is unusual for monocotyledons, develops. However, helicoid cyme partial inflorescences with different branching angles have already been seen in other genera of the monocotyledons: in some *Amaryllidaceae* genera, in *Crinium* species and flat helicoid cymes in *Allium* species. (Weberling 1981, 226)

Since the inflorescences of *Sansevieria* are thyrses, the common characterisations "single-eared", "simple-capitate" or "paniculate branched" can only be understood as colloquial terms. I suggest the descriptions given in Table 2 as more appropriate for clarification:

Table 2 – Proposal to rename the inflorescences

Sections *(including subsections)*	**Previous Description**	**New Description**
	Inflorescence consisting of an elongate unbranched thyrsose raceme with flowers in interrupted cymose fascicles. (Jankalski 2009)	
Sansevieria	Elongated, unbranched raceme with flowers in interrupted, open (umbel-like panicle) clusters. (Mansfeld 2013b)	Unbranched indeterminate thyrse with helicoid cymes (bostryx)
	Short version = simple spike-like	Short version = elongated thyrse
	Inflorescence consisting of elongate paniculate branched thyrsose racemes. (Jankalski 2009)	
Dracomima	Elongated, panicle-shaped, branched, bouquet-shaped racemes. (Mansfeld 2013b)	Branched indeterminated thyrse with helicoid cymes
	Short version = paniculate branched	Short version = branched thyrse
	Inflorescence consisting of a congested unbranched pseudocapitate thyrsose raceme to umbelliform subcapitate on an elongate to subsessile scape. (Jankalski 2009)	
Cephalantha	Dense, unbranched, pseudocapitate-shaped, bouquet-shaped racemes to umbel-shaped, almost head-shaped on an elongated to subsessile scape. (Mansfeld 2013b)	Congested unbranched indeterminate thyrse with helicoid cymes on an elongate to subsessile scape.
	Short version = simple-capitate	Short version = capitate thyrse

Species from the *Dracomima* section were not available for this study (see Table 3). However, figures (Mansfeld 2013b, 26, 96, 97) and observations on fruiting inflorescences clearly show single-branched open thyrses (double thyrses) or, in *Sansevieria ehrenbergii*, thyrses with repeated branches (pleiothyrses).

The respective number of thyrses examined here is too small for valid statistical statements to be made on the individual taxa and so only a first impression can be expected in this regard. In addition, there is the notorious uncertainty of species identification, and even type plants are only randomly selected individual specimens from the gene pool, which cannot represent the variation within a species. For statistical statements about the characteristics of individual species, studies with many thyrses from the natural habitat would be necessary.

Fig. 19 – *Sansevieria senegambica*
Twice developed helicoid cyme, shown from above. The two open ends (oE) are each facing inwards next to the third pedicel (3), the bracteoles of which (Br3) are on top. The pedicel of the central flower (1) is slightly wider than the rest and appears to be the result of two pedicels fused together.

The noticeable predominance of clockwise or counterclockwise orientated helicoid cymes as well as the imbalance in the succession of equally or unequally orientated helicoid cymes differs very strongly in the thyrses examined. Since this characteristic also occurs in different thyrses of the same plant or the same clone, the large deviation does not seem to be due to the species, but rather to be specific to the entire genus. I therefore consider it justified to form an average that represents all plants of the genus examined so far across all species.

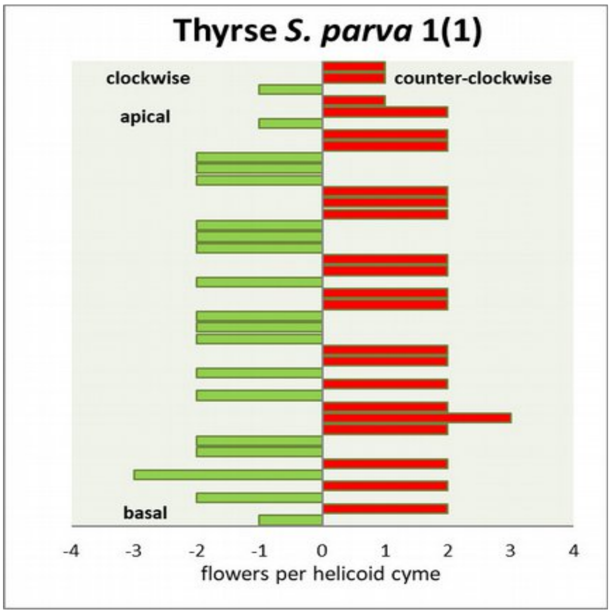
For all counted thyrses, a ratio of 48.7%: 51.3% (± 9.3%) clockwise to counterclockwise helicoid cymes was seen which is the same probability with which a helicoid cyme develops clockwise or counterclockwise during ontogenesis. The high deviation of almost 10% represents the frequent and large variation from the uniform distribution with many inflorescences (see Table 3). If the ratio of all helicoid cymes is calculated independently of the thyrses, the result is a ratio of 49.2%: 50.8% (± 1.0%), i.e., the large deviation of the individual thyrses almost disappears.

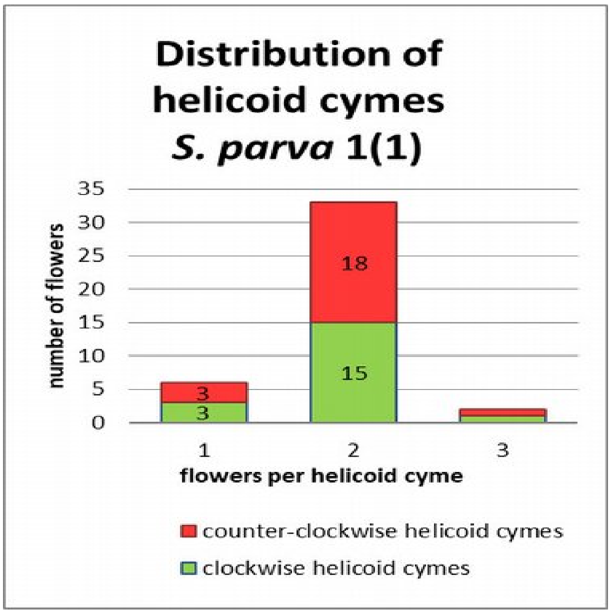
For the proportions of the succession of equally orientated to unequally orientated helicoid cymes, a similar ratio of 51.2%: 48.8% (± 7.2%) is seen for all examined thyrses with a slightly smaller deviation. Independent of the thyrses, the ratio is 51.1%: 48.9% (± 0.7%) which again shows an even distribution. The succession of the helicoid cymes, as well as their directions of orientation on the thyrses, therefore turns out to be random for the entirety of all thyrses examined (see Table 3).

It would be interesting to investigate which factors influencing the ontogenesis of the clusters are decisive for the direction of orientation. The rare symmetrical double helicoid cymes (Figs. 17, 19), which occur as a result of partial or complete coalescence[11)] of the first flower, occur significantly more frequently than correspondingly fused double helicoid cymes that share the same direction of orientation (which are therefore asymmetrical). Perhaps this is an indication that the helicoid cymes can influence each other during their development.

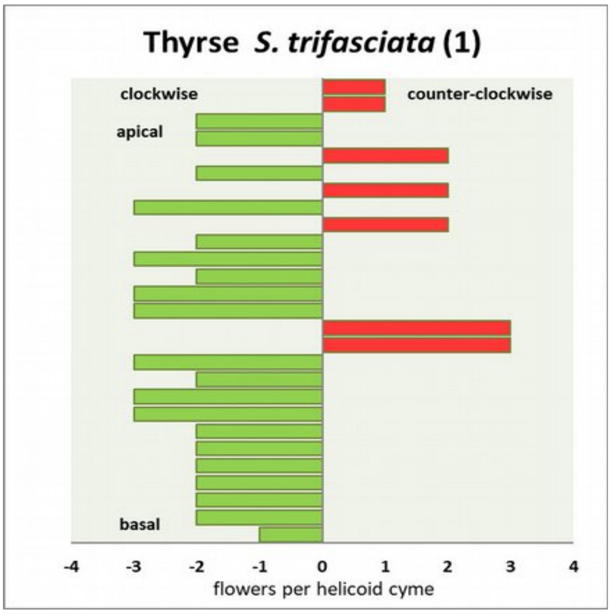
11) The observation that monocotyledons normally only develop one side bud per node [Tillich 1998, 8] suggests coalescence (fusion) as the cause of the double helicoid cymes genesis.

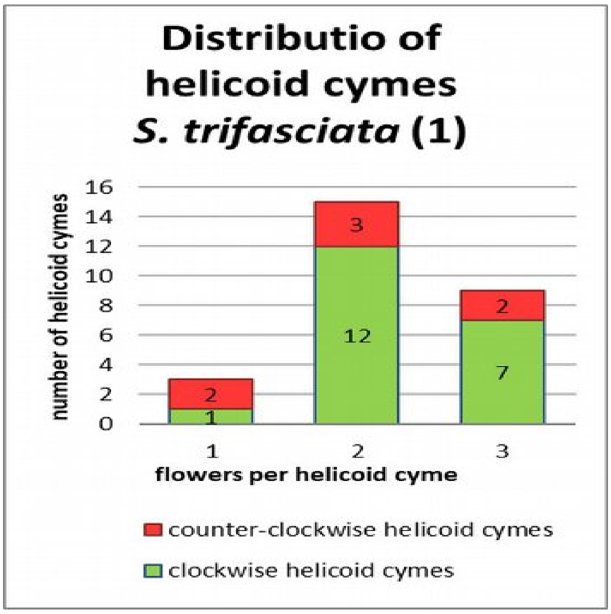
On many inflorescences, the clusters give the impression of being arranged in counterclockwise or clockwise spiral groups (Fig. 18). Whether this has structural advantages was not able to be clarified during this investigation.



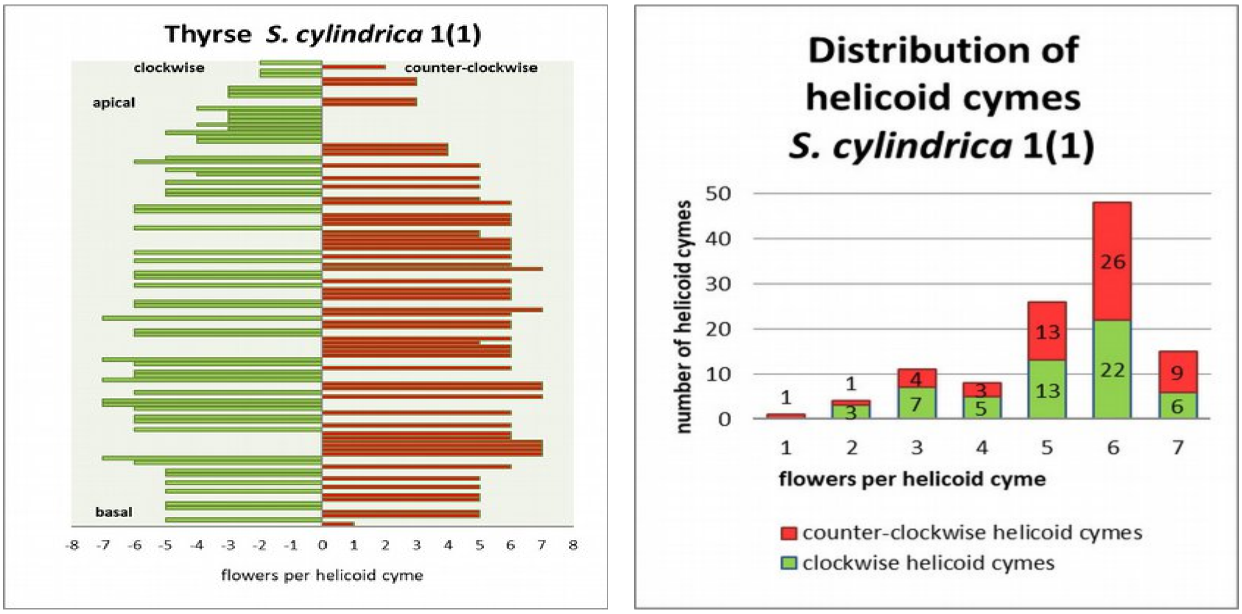


Typical distribution of counterclockwise and clockwise helicoid cymes in a small inflorescence (78 flowers - for further statistical data see Table 3). **Left:** Each bar represents a helicoid cyme. The succession, the direction of orientation of the helicoid cymes (bar to the right / left) and the number of flowers per cluster (length of the bar) are shown.
Right: Number of 1-3 flowered helicoid cymes.





Extremely uneven distribution of counterclockwise and clockwise helicoid cymes in a small inflorescence (60 flowers - for further statistical data see Table 3). Counterclockwise and clockwise helicoid cymes have a ratio of about 1: 3.



Distribution of counterclockwise and clockwise helicoid cymes in a larger inflorescence (597 flowers - for further statistical data see Table 2). **Left:** The clockwise and counterclockwise helicoid cymes are in a balanced ratio of 49.6%: 50.4%. Although helicoid cymes with the same orientation seem to occur more frequently at times, the succession of clusters of the same orientation (49.1%) is just as common as the succession of helicoid cymes with different orientation (50.9%). **Right:** This thyrse is most likely to contain 6-flowered helicoid cymes, although the average is 5 (5.3 ± 1.3) flowers per helicoid cyme. The reason lies in the asymmetrical distribution of the 1- to 7-flowered clusters.

Table 3 - Statistical data of the taxa examined[12)]

	Flowers [number]	Helicoid cymes [number]	Clockwise orientated helicoid cymes [%]	Successive helicoid cymes in the same direction of orientation [%]
S. longiflora	107	56	61,0	46,0
S. ballyi (1)	128	55	56,4	49,9
S. ballyi (2)	105	74	55,3	48,6
S. ballyi 'Minnie'	69	37	48,6	47,2
S. 'Vivo' 1(1)	218	61	44,0	50,0
S. 'Vivo' 1(2)	236	57	47,0	58,0
S. 'Vivo' 2(1)	167	67	43,0	53,0
S. 'Vivo' 2(2)	131	57	42,0	45,0
S. 'Vivo' 3	87	40	43,0	33,0
S. concinna (1)	177	101	34,0	52,0
S. concinna (2)	109	69	57,0	35,0
S. concinna (3)	229	129	43,0	52,0
S. concinna 'LAV 5949' (1)	32	28	54,0	37,0
S. concinna 'LAV 5949' (2)	140	78	62,8	54,5

12) The numbers behind the species indicate different individual plants or clones. The numbers in brackets indicate different thyrses of the same plant respectivly the same clone.
In the case of *Sansevieria fischeri*, the sequence of the helicoid cymes could not be determined because the underground, carrot-like thickened stalk have got 74 helicoid cymes over a length of 18 mm.

	Flowers [number]	**Helicoid cymes [number]**	**Clockwise orientated helicoid cymes [%]**	**Successive helicoid cymes in the same direction of orientation [%]**
S. conspicua (1)	252	98	37,0	53,0
S. conspicua (2) cristata	1274	280	53,0	48,0
S. conspicua (3)	533	136	43,0	53,0
S. cylindrica 1(1)	597	113	49,6	49,1
S. cylindrica 1(2)	324	94	48,9	50,5
S. cylindrica 1(3)	256	82	57,0	47,0
S. cylindrica 1(4)	499	106	42,0	50,0
S. cylindrica 2(1)	173	64	43,8	44,4
S. cylindrica 2(2)	103	44	61,0	56,0
S. cylindrica 3(1)	475	124	45,0	49,0
S. cylindrica 3(2)	243	77	52,0	36,0
S. fasciata (1)	380	133	67,7	57,6
S. fasciata (2)	285	118	54,2	43,6
S. fischeri	156	74	40,5	-
S. dawei	1673	425	57,9	54,5
S. francisii (1)	91	49	53,0	56,0
S. francisii (2)	184	78	49,0	48,0
S. gracilis (1)	97	52	58,0	53,0
S. gracilis (2)	166	57	44,0	46,0
S. gracilis (3)	176	65	60,0	53,0
S. gracilis (4)	104	55	51,0	50,0
*S. liberica (*syn. *S. chinensis)*	481	165	46,0	51,0
S. concinna 'Sudwala Caves' (1)	31	31	42,0	60,0
S. concinna 'Sudwala Caves' (2)	300	94	39,0	53,0
S. kirkii 'Pulchra' 1(1)	53	28	39,3	55,6
S. kirkii 'Pulchra' 1(2)	139	61	48,0	47,0
S. kirkii 'Pulchra' 1(3)	111	53	77,0	64,0
S. kirkii 'Pulchra' 1(4)	110	57	46,0	57,0
S. kirkii 'Pulchra' 1(5)	75	46	41,0	47,0
S. kirkii 'Pulchra' 2	211	67	34,3	53,0
S. parva 1(1)	78	41	46,3	42,5
S. parva 1(2)	116	51	33,0	52,0
S. parva 2	60	34	47,1	57,6
S. parva 3(1)	60	32	56,0	52,0
S. parva 3(2)	42	23	44,0	46,0
S. parva 4(1)	131	73	38,0	50,0
S. parva 4(2)	95	54	70,0	59,0
S. deserti (1)	321	81	44,0	48,0
S. deserti (2)	1035	145	46,0	41,0
S. phillipsiae (1)	165	79	49,4	48,7
S. phillipsiae (2)	79	59	52,5	60,3
S. roxburghiana 'Roxette' (1)	303	106	50,0	53,3
S. roxburghiana 'Roxette' (2)	255	92	42,4	41,8
S. senegambica (1)	166	63	42,9	58,8
S. senegambica (2)	158	59	49,2	46,6
S. senegambica (3)	165	67	47,8	51,5
S. stuckyi 1	309	94	57,0	48,0

	Flowers [number]	**Helicoid cymes [number]**	**Clockwise orientated helicoid cymes [%]**	**Successive helicoid cymes in the same direction of orientation [%]**
S. stuckyi 2 (1)	396	88	50,0	62,0
S. stuckyi 2 (2)	321	88	35,0	58,0
S. suffruticosa (1)	326	104	54,8	54,4
S. suffruticosa (2)	325	107	49,5	61,3
S. trifasciata (1)	60	27	74,1	65,4
S. trifasciata (2)	112	36	38,9	62,9
S. trifasciata (3)	60	23	56,5	40,9
S. trifasciata (4)	83	33	36,4	53,1
S. trifasciata (5)	99	36	33,3	54,3
S. trifasciata 'Gilt Edge'	81	32	53,0	58,0
S. trifasciata 'Gold Flame'	49	21	29,0	70,0
S. trifasciata 'Moonshine' (1)	52	28	53,6	40,7
S. trifasciata 'Moonshine' (2)	49	24	50,0	52,2
S. trifasciata 'Moonshine' (3)	56	24	54,2	56,5
S. trifasciata 'Nelsonii' (1)	94	31	45,2	36,7
S. trifasciata 'Nelsonii' (2)	127	36	44,4	62,9
S. trifasciata 'Nelsonii' (3)	91	37	59,5	50,5
S. trifasciata 'Nelsonii' (4)	90	35	40,0	52,9
Total	17496	5762		

Average basad on thyrses		48,7 ± 9,3	51,2 ± 7,2
Weighted average based on cymes		49,2 ± 1,0	51,1 ± 0,7

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