Sansevieria Online
Online Journal
ISSN 2197-7895
Article 2
Vol. 10 (2)
5. September 2022

The *Sansevieria`s* fruits – an update

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Keywords
Sansevieria, fruit, berry, stone-fruit, morphology, gymnosperm, angiosperm, Carpology.

Abstract
A comprehensive review of the literature from 1692 through 2010 shows the development of current knowledge regarding the fruits of the genus *Sansevieria*. A serious error regarding the nature of the fruit becomes apparent, that has persisted from 1883 until today. Apparently, the erroneous opinion that the fruit develops like gymnosperms has never been questioned since that time. I will then characterize the *Sansevieria* fruits on the basis of observations, many of which have been made by me, and in doing so I will rectify the error that has persisted for more than 130 years.

Introduction

Eight years have passed since the first version of this article was published. In the meantime, on the basis of new findings in the field of genetics, a discussion has developed concerning the embedding of the genus *Sansevieria* into *Dracaena*. In contrast to those of the *Dracaena* species, the fruits are extremely uniform in all Sansevierian species. However, among the Dracaenae there are also fruits that are very similar to those of *Sansevieria*, so a distinction between the genera is not possible. This revised and slightly expanded presentation of the topic is now also available in English and allows English speakers to get access to this paper.

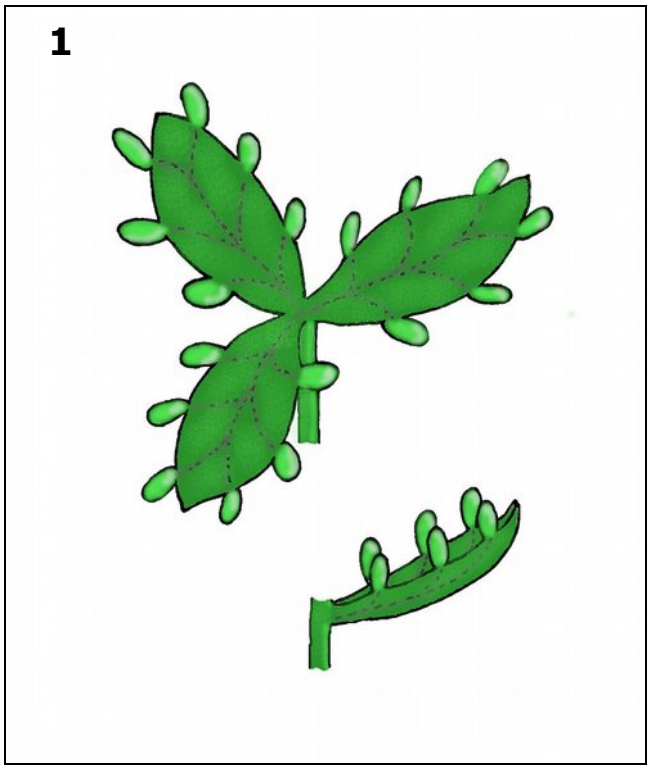
There is surprisingly little information to be found in literature about the fruits of *Sansevieria*. It is difficult to understand why this lack of knowledge exists as Sansevieria's position in the plant kingdom and its distinction from other genera are crucially related to the structure of its fruit. However, it is most likely due to the fact that *Sansevieria* bloom rarely and unpredictably and usually do not find any pollinators outside of their natural environment. As a result of this, nocturnal hand pollination is required to attain fruits. Although taking suitable photographs has become easier nowadays with the help of technology, there are still hardly any images on this subject in the relevant journals. With this article, I want to present what is known about the fruits of *Sansevieria* from the more than 300-year history of the botanical depiction of the genus and to compare this with my own observations.

To find the position of the genus *Sansevieria* in plant systematics, the structure of their fruit and the difference between gymnosperms and angiosperms plays a very important role. For a better understanding I would therefore like to add something in advance about the development of flowering

plants that evolved from gymnospermous predecessors.

At the end of the Triassic Period, about 200 million years ago, there were predominantly gymnosperms on earth. The cycads still alive today give a rough idea of what many of these plants looked like and what their reproductive organs might have looked like. The ovules can be imagined as extensions of terminal leaves. (**Fig. 1**)

Ovules consist of a nucellus from which, after fertilization, the embryo and the nutritive tissue of the seed develop, encased by two integuments that then develop into the seed coat during maturation. The integuments leave an entrance to the nucellus, the micropyle, open. This micropyle is necessary for fertilization as it gives the male gametes access to the nucellus. (**Fig. 2**)



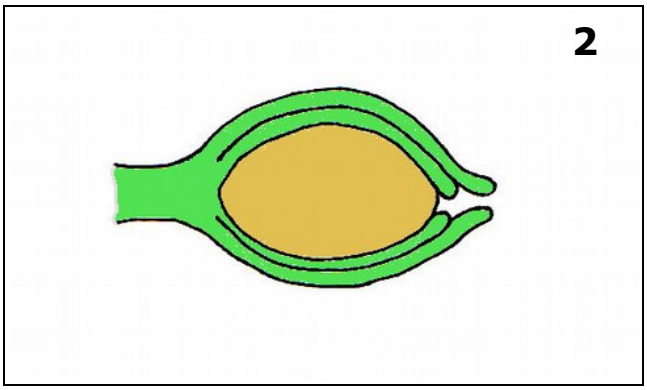


Fig. 1 – Hypothetical appearance of the earliest, gymnospermous leaves. The ovules sit at the edges of the terminal leaves.

Fig. 2 – Section through individual ovule at the edge of the leaf. Two integuments envelop the nucellus, but allow for an opening (micropyle).

This development continued until the beginning of the Cretaceous Period, 140 million years ago, to the angiosperms. At this point, several terminal carpels rolled up and grew together on the sides to form a closed ovary. (**Fig. 3**)

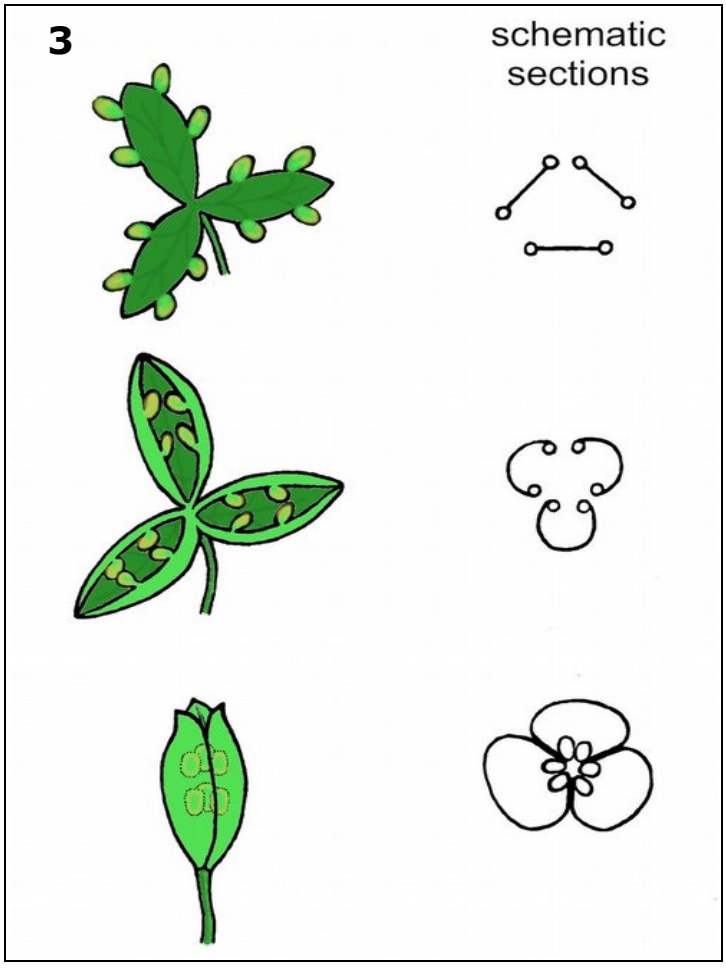
The ovary, at its apex, still had an opening to give access to the nucellus for fertilisation. In joint development (coevolution) with fertilising insects, this later developed into style and stigma. The style and stigma are therefore part of the carpels that have grown together.

Exactly how this development took place is, however, completely unknown, and only a few flower fossils from the beginning of the Cretaceous Period, alongside genetic studies, can be used to confirm this theory. (Schweitzer 1989)

When looking at the ovaries of genera that are closely related to *Sansevieria*, a tendency towards simplification can be seen. Patil & Pai found in their 2010 study:

"*Present study reveals that the fewer-to-two to-one-ovuled condition is derived from the multi-ovulate state. Thus a gradate reduction series from multiovulate to uniovulate carpels is witnessed in the family*." (Patil & Pai 2010, p. 283)

Dracaena and *Sansevieria*, with their individual ovules per locule, represent the current endpoint in development. (**Fig. 4, 5, 6**) They are, so to speak, on the "pole position" of evolution.



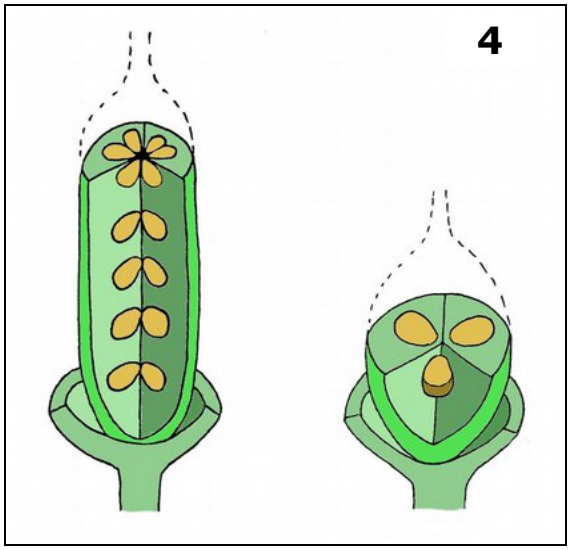


Fig. 3 – Hypothetical development of gymnospermous carpels to the pistil.TOP: Three terminal carpels with open ovules. CENTER: The carpels folded lengthways. BOTTOM: Fused carpels form an "ovary" which is open at the top. The style and stigma are not yet developed.

Fig. 4 – Through the process of reduction, single-seeded locules, as in *Dracaena* and *Sansevieria* (right), were able to develop from the originally multi-seeded locules with double ovules (left).The illustrations show schematically the front carpel cut open as well as a cross section at the top. The flower tube is cut off at the bottom.

Fig. 5 – *Sansevieria personii* - cross-section of a flower. The individual ovules are clear to see in the three locules. The septa between the ovules contain nectar glands (nectaries). Around the ovary, the flower tube can be seen.

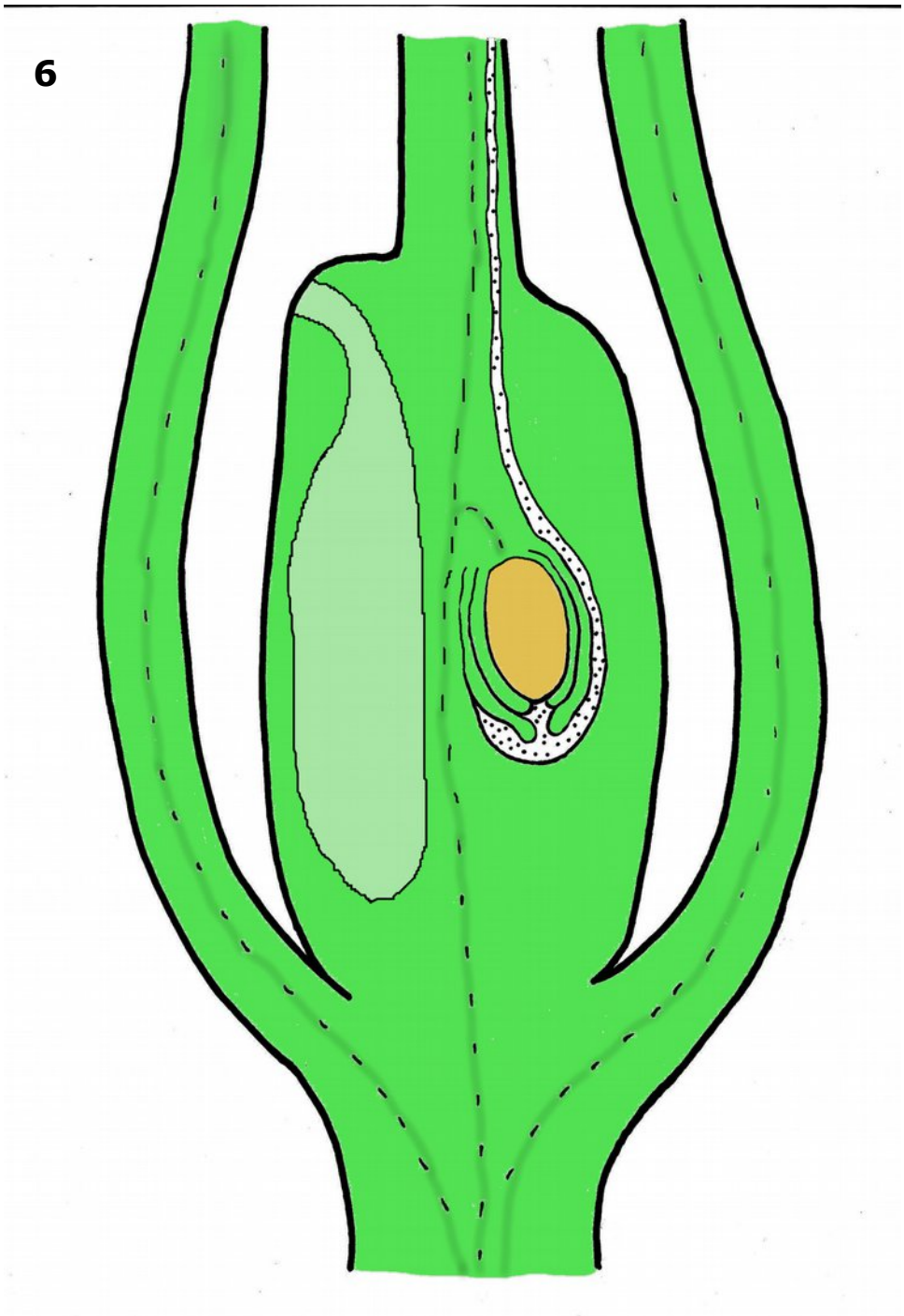


Fig. 6 –
Longitudinal section through the ovary of a *Sansevieria*, semi-schemetic.

Right: The reflexed (anatropous) ovule with two integuments and below the micropyle, which opens to the locule. This is connected to the outside world through the stylar canal up to the scar (not shown here).

Left: In the septum opposite the ovule a septal nectary with opening upwards is shown.

Outside: the enveloping flower tube.

Historical Summary

The fruits of *Sansevieria* can already be seen on the first known image of a *Sansevieria*. (**Fig. 7**) In the Hortus Malabaricus, a twelve-volume collection of plant illustrations and descriptions, a *Sansevieria lanuginosa* (synonym of *Sansevieria ebracteata*) is described using both text and illustrations for the first time in table 42 in the eleventh volume from 1692. (Rheede 1692, p. 83, T. 42) In the

Hortus Malabaricus, it is named Katu Kapel (in English "wild ship") or Cadenaco (in English "cuttle-fish bone"). (Nicolson et. al. 1988, p. 271) The descriptive text was written by Jan Commelin, a Dutch wholesaler of medicinal plants. (Nicolson et. al. 1988, p. 16) He writes about the fruits:

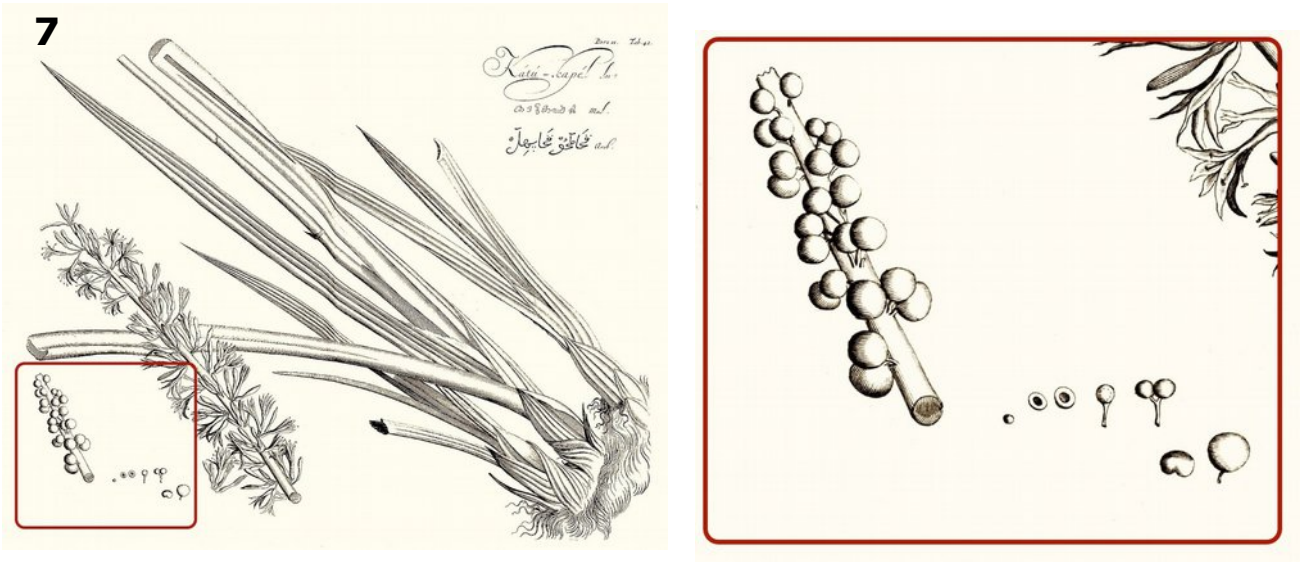


Fig. 7 – Oldest illustration of a *Sansevieria ebracteata* (Source: van Rheede 1692) Image section showing the fruits, alongside other elements including a branched stem.

"The fruits are pale green, round, individually or in pairs like laterally connected spheres; inside them there are one or two seeds that taste like (broad) beans, as long as they are young." (van Rheede 1692, p. 83)

The fruits described are still green and therefore obviously unripe. The illustration shows round fruits with stalks and a bean-shaped seed. There is also a fruit shown on a branched stalk, which never occurs in *Sansevieria*. The text and illustrations differ from one another, as the "lateral" connection of the "spheres" cannot be seen in the illustration. This inaccuracy is probably due to the multinational collaboration in the making of the Hortus Malabaricus. The publisher van Rheede tot Draakestein was neither a botanist, nor did he speak an Indian language or the scientific language of the time, Latin. But as a commissioned commander in Malabar, southwest India, he organised a project to gather and describe medicinal plants from and around India. As it was very expensive to import medicine for his soldiers from Europe, he hired Indian doctors who, as specialists in local medicine, contributed their knowledge. In order to understand these doctors, van Rheede had a Portuguese interpreter who translated from the Indian languages into Portuguese. This was then translated again into Dutch and then into Latin, each time by different specialists. I can imagine that translation errors and misunderstandings could have come about in this way. It appears Jan Commelin described the plants in Latin, but he did this in Leyden, not before van Rheede retur-

ned to Holland. [Nicolson et. al. 1988, p. 16] I presume that Commelin did not always have at hand the plants he was describing so that he often had to rely on records from Malabar. Perhaps this was the case with this first ever described *Sansevieria*.

Fig. 8 – *Aletris guineensis* (Source: Jacquin 1770) Close up of two fruits. The seeds seem to be depauperate.

As far as I am aware, no further descriptions or illustrations of this plant appear in any literature during the subsequent 200 years. It can therefore be assumed that these were either lost or that the plant never reached Leyden, Holland.

The next illustration of *Sansevieria* fruits that I know of comes from Nicolai Joseph Jaquin, from Vienna. As early as 1762 he describes, without illustrations, two *Sansevieria* species known at the time as *Aloe guineensis* and *Aloe zeylanica*. It was not until eight years later that he was able to report on fruits that had developed in *Aletris guineensis*. (**Fig. 8**) By that time, the plants had been placed in *Aletris*, based on the structure of their flowers. On a hand-coloured copper engraving, he shows the plant with fruit and seeds in life size (the printing block measures 21.5 x 45.5 cm) and writes:

"In the appendix of the Enumeratio Stirpium Agre Vindobonensis I gave a description of the inflorescences and of the plant, however with the fruit missing, since the flowers mentioned had fallen off on this and two other plants of the same species. I had, with uncertainty, shown how from here onwards from the embryo, similar to Hyacinthus, a triple pericarp with many seeds developed, which I assumed to be fertilized. After all, I saw quite a few ripe fruits; from the now apparent anatomy, it was evident that this plant cannot be assigned to either Aletris or Aloe or any other genus known up to now. The fruit is in fact a soft berry, almost round, juicy, yellow with pulp of the same color, the size of a pea and surrounded by a dried-up flower tube that is torn open along its length. Seeds are single, soft, indented and smooth, enclosed in a parchment-like aril (seed coat) as in the picture, the outer skin of the berry has grown together at the base. These parts are shown in natural size on the edge of the table." (Jacquin 1770, p. 36, T. 84)

I also see a discrepancy from today's perspective here, as the seeds are known to be very hard. It is possible that the observed fruits were not ripe since the seeds were not able to develop fully. This is supported by the fact that he describes the fruits as yellow and not as bright orange, and that the seeds were soft and dented. The picture also shows seeds that, when compared to the size of the fruits, are underdeveloped and most likely not capable of germination. Otherwise, the illustration shows, as clearly as in a macro photograph, a bract and two individual fruits, each with a stalk, as well as the dried up and torn remains of the flower tubes on the two berries. (**Fig. 8**)
In 1775, Petrus Forskål described a *Convallaria racemosa*, (synonym of *Sansevieria forskaoliana*):

"Fruit berry 1, 2, 3 parts; berries (coccis) single-seeded, the size of a pea." (Forskål 1775, p. 73)

and, for the first time, the three-part nature of the fruit is clearly mentioned. In 1786, Friedrich Kasimir Medikus from Mannheim added to the conversation. In his "Theodora speciosa" he shows that other genera should be separated from Linnaeus' genus *Aletris* on account of the fruits. This included *Acyntha*, our current *Sansevieria*, and explained:

"*Fruit. There is an essential difference. With Acyntha, Dracaena, ... it is a juicy berry, ... The berry of the Acynta and Terminalis contain only one seed, the berry of the Dracaena, on the other hand, has three layers, one seed in each*." (Medicus 1786, p. 88).

He himself had not seen any *Sansevieria* fruits but knew from the literature about single-seeded berries of *Sansevieria* in contrast to the (up to) three-seeded berries in *Dracaena* and the multi-seeded capsules in *Aletris*. He calls his new genus *Acyntha* (synonym of *Sansevieria*) and thus provides the earliest legitimate name for the genus. On the other hand, Brown is even of the opinion in his monograph that Adanson legitimately characterized the genus as *Cordyline*, 24 years before Medikus. (Brown 1915, p. 186), (Adanson 1763, pp. 54 and 543) The division and renaming of the genus because of its fruits was up in the air at this time. This is evident as one year later, Vincenzo Petagna published the first description of his *Sanseverinia thyrsiflora* in Naples, apparently without knowing about Medikus' work. In it, he describes the fruits:

"*... Round berry, very short stalk, saffron-yellow (croceus) after ripening; seeds bone-like. Berries that have grown together very often ripen, so that two or three stick together at the same time; but not all flowers develop into ripe berries. They bloom in June and July in the open air. The fruit ripens in autumn and often stays on the plant throughout winter. ...* "(Petagna 1787, p. 644)

Although Petagna did not recognize the nature of the fruit, he seems to regard the multi-part fruits as the result of accidental flower merging, but he corresponds with Thunberg in Upsala, Sweden and sends him a herbarium sheet with a leaf and the berry-bearing part of an infructescence. Apparently, this herbarium sheet still exists today and a picture of it (Menale et al. 2013, p. 388) shows, albeit indistinctly, a piece of flower stem with seven berries on several clusters. In 1794, Thunberg included this plant in his "Prodromus Plantarum Capensium", however, made a spelling mistake, and since the two previous publications by Medikus and Petagna were forgotten over time, the genus is to this day still referred to as *Sansevieria,* with Thunbergs' misspelling, as a result of a misjudgement in the priority during the nomenclature. (Menale et al. 2013) and (Thunberg 1794, p. 65)

Fig. 9– *Aletris guinensis* (Source: van Lamarck 1793) A=closed flower, intact. B=Flower open. C=Flower cut with filaments. D=Pistil. E=two intact berries. F=Berry cut crosswise. G=seed from above. H=seed from below. I=Perisperm cut vertically, with position of the embryo. L=Embryo enlarged.

Fig. 10 – *Dracaena draco* - **Left**: the base of the style is seen laterally displaced on the berry. **Right**: horizontally opened fruit shows a mature seed in a fully developed locule and on the right two stunted locules, whereby in the lower of the two an underdeveloped ovule near the hilum of the seed is visible. It is also noteworthy that, unlike *Sansevieria*, the seed can be easily detached from the pulp.

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Two years earlier, in 1792, Lamarck published a description and illustration of an *Aletris guineensis* (later assigned to *Sansevieria* with a note) as an illustration for his article on the genus, as part of the "Encyclopédie Méthodique" by Diderot and d'Alembert. That is a monumental piece of work with the intention to cover all known scholarly knowledge of this time. The botanical section alone comprises 13 volumes and came out from 1783–1817 over 34 years with 1000 accompanying copperplate engravings, which were reissued in four more volumes in 1823. The project even "survived" The French Revolution. How in the individual volumes "Chevalier de Lamarck, ancien Officier au Regiment de Beujolois, de l'Academie Royale des Sciences" became the "Citoyen Lamarck", or how in 1796 volume 4 was published with the year given as "IV of the Republic", are topics in their own right. [1.)]

On copperplate 237 (delivered by subscription from July 1792) an *Aletris guineensis* is shown in great detail with pictures and descriptions. (Lamarck 1793, p. 379, no. 664, T. 237) and (Lamarck 1823, T. 237) (e) shows two individual fruits (each with a dried-up remnant of the flower) on a shared stalk. However, this feature does not exist in *Sansevieria*. Nor do you find style stigmas in the middle of the berries opposite the stem base. The section (f) through the fruit shows a round berry with three locules, two of which are stunted. This also occurs e. g. in *Dracaena draco*, but not in *Sansevieria*. Obviously, the author did not understand the structure of the *Sansevieria* fruit. The representation of the seeds with the hilum on top (h), on the other hand, is quite successful, although the shape is a little too bean-shaped. In contrast to its normally straight shape, the embryo (l) shown here is curved. (**Fig. 9**)

The next illustration is contemporaneous to "Thunbergs Prodromus" from 1794, but from Madrid. (**Fig. 11**) Antonius Josephus Cavanilles introduces (now the fourth attempt) the new generic name *Salmia* and describes the generic characteristics:

"*Salmia.* [2.)] *... Fruit: Three stone fruits, almost round, centrally connected, seeds single, bone-like, oval.... Fruit first green, then yellow: seeds covered by pulp, which they cover like a skin."* (Cavanilles 1794, p. 24)

1.) Editors note: The revolutionists with the French Revolution began a new counting oft he years, but this was abandoned some years later.

2.) „In honour of Exc. D. D. Caroli de Salm Salm S. R. I. Principis, who advanced many things in the matter of botany and who taught me the basic principles of this science" (Cavanilles 1794, p. 24)

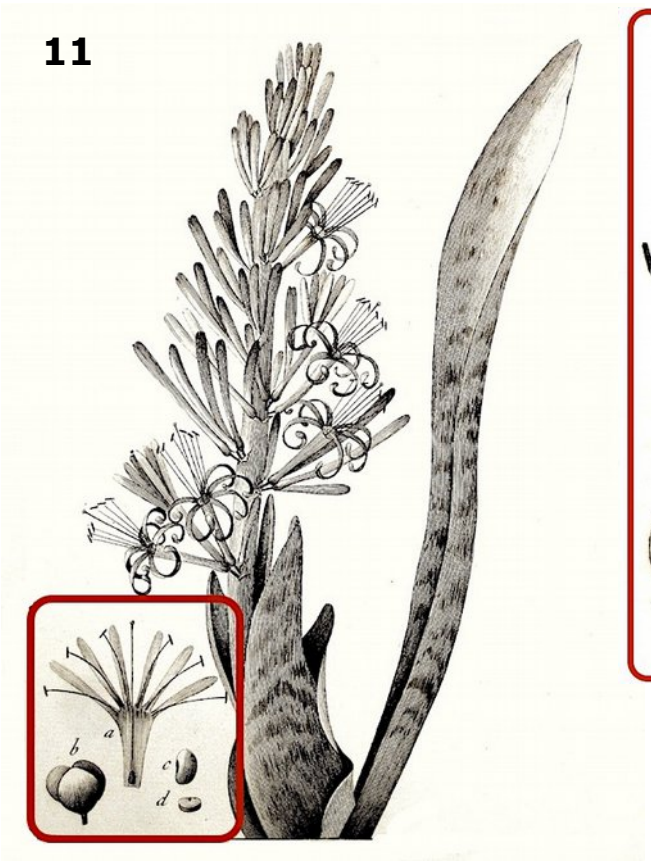


Fig. 11 – *Salmia spicata* (Source: Cavanilles 1774) Close up showing the fruits: A=Extended Corolla. B=Fruit. C=Seed. D=Cross section of a seed.

And later, in the description of the species, Cavanilles writes:

"*In the first volume of his "Hortus Vindobonensis", the famous Jacquin depicted a plant on copperplate 84 that is similar to ours: It is described there with characteristics that are not found in my plants; ...; and the seeds are soft. In addition, the commendable author said the fruit was a soft, almost round, single-seeded berry, whereas in our case it is composed of three stone fruits, if they are not stunted. In my opinion, he would have been more correct if he had spoken of a stone fruit. The fruits are now no longer available, and this cannot be verified. Jaquin sees very distinctly that his plant deviates from Aletris, Aloe and all known genera in terms of fruit formation and says very clearly, which no man of some knowledge can deny, that the plant should be separated from the genera mentioned, but then left it unnamed..... It is therefore worth the effort to describe the plant and introduce this generic name for it. ...* "(Cavanilles 1794, p. 24)

Cavanilles introduces the new genus *Salmia* based on the fruits that differ from the multi-seeded capsules of *Aletris*. It is noteworthy that he speaks of stone fruits, and not berries. He sees the hard seeds as stones. Today we speak of stone fruits when the inner layer of the carpel forms a hard, woody shell that encloses the seed with its seed coats (integuments), like a cherry. He describes the fruit as being composed of three stone fruits and thus for the first time recognizes the actual structure of the fruit. The copperplate engraving (**Fig. 11**) shows a three-lobed berry (b), a single, bean-

shaped seed (c) with a hilum (= mark left from funicle), however, shown in the wrong place; the hilum is usually somewhat raised on the seed, and (d) a section from a seed showing the peripheral embryo. Everything is presented in a somewhat stylised way.

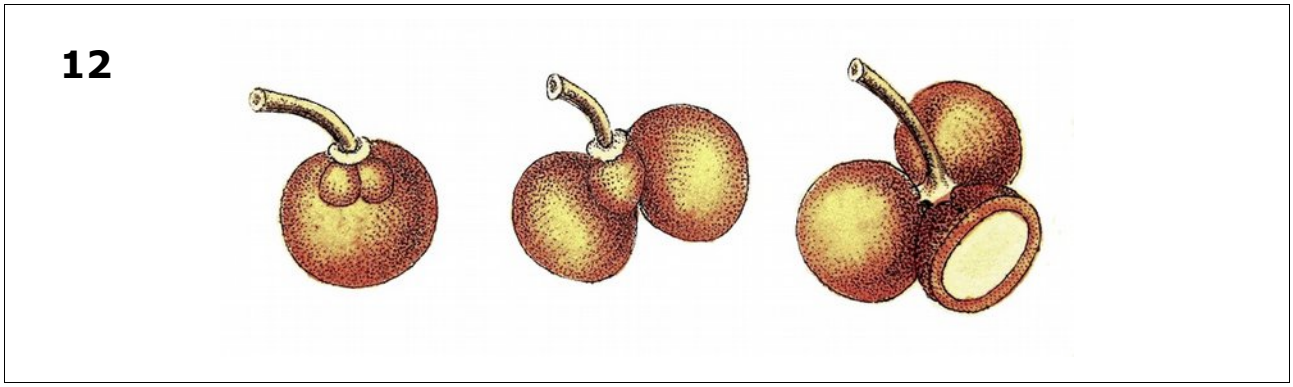


Fig. 12 – *Sansevieria roxburghiana* (Source: Roxburgh 1805) Section of an illustration showing the fruits.

Only four years later, William Roxburgh shows in the second part of his work "Plants of the Coast of Coromandel" a picture of "*Sansevieria roxburghiana"* with three fruits, one with one, one with two and one with three seeds. In the accompanying text he writes:

"Berries one, two, or three slightly united above, but each berry globular, fleshy, orange-colour, smooth, size of a pea, one-seeded. It may be remarked, as in Sapindus and Menispermum, that there are the rudiments of three, both in the germ and ripe fruit: but all the three seldom ripen. Seeds globular." (Roxburgh 1798, column 44, T. 184)

In the hand-coloured copper engraving (printing block 38 x 52 cm!), the three life-size variants of the *Sansevieria* fruit can be admired (**Fig. 12**). Again, the illustration appears somewhat stylised and shows hardly any further details apart from the three-part structure. For example, the remnant of the dried-up style is missing between the three berry parts. In 1832, the same copper engraving was republished posthumously with slightly changed and added text in his Flora Indica:

"*Berries one, two or three, slightly united; when single, globular, fleshy, orange-coloured, smooth, the size of a pea, one-seeded. Seed globular. Embryo simple, lodged near the base of the perisperm on the outside*." (Roxburgh 1832, p. 162)

As far as I know, Schultes mentioned the hilum on the seeds for the first time in a text in 1829 in the continuation of "Linnes Systema Vegetabilium". The book does not contain any images. (Schultes 1829, p. XXVIII) Two years earlier, Karl Ludwig Blume had already described the hilum on the seeds:

"*Berries with 1-3 compartments, each compartment single-seeded. Seeds above with umbilicus, almost round, embryo opposite the umbilicus."* (Blume 1827, p.11).

However, he then describes three species found in Java, all of which are now associated with *Dra-*

caena, and the description refers to seeds of today's *Dracaena angustifolia*. In 1875, Lindberg provides the first description of his *Sanseviera angustiflora* (synonym of *Sansevieria hyacinthoides)* with the illustration of an unripe fruit (**Fig. 13**), which he describes as follows:

"... Capsule (seen only when unripe) three berries, the tip ray-like triple-furrowed and depressed, the base of the persisting style crowned by the dried flower corolla, berries round, tubercular, dotted and slightly wrinkled, shiny green." (Lindberg 1875, p. 131, T. V)

Here Lindberg describes for the first time the dried-up style that remains between the three round berries and shows very impressively how the remnants of the flowers conceal the style and are held by it.

In the same year, Baker published a revision of the *Asparagaceae*, describing the *Sansevieria* fruit:

"Berry round, fleshy, with 1-3 seeds large, triangular, whitish horn-coloured, testa pale parchment-like." [Baker 1875, p. 547)]

He correctly describes the berry as round and fleshy, but then the seeds as triangular / three-sided, which never occurs in *Sansevieria*. He then mentions the pale parchment-like testa. Here, he obviously means the fibrous layer between the pulp and the seed, which is actually derived from the inner layer of the carpel and not from the testa, i.e. not a seed coat. With this, he causes Bentham and Hooker to make a very serious misjudgment whilst describing the *Sansevieria* fruit in 1883 (without illustrations):

"Fruit shell very thin, parchment-like, after flowering the style falling off, soon disappearing and not enlarging. 1-3 seeds, partly fully developed, large, spherical, berry-shaped, basally connected, partly 1 or 2 small, stunted, testa (seed envelope) soft thick-fleshed or succulent, inner tegument thinly pressed; embryo penetrated into the base of the fleshy nutrient tissue, awl-shaped. " [Bentham & Hooker 1883, p. 679]

and Hooker then again in 1892:

"Fruit membranous, indehiscent. Seeds 1-3 ripening outside the pericarp globose, all large, or 1-2 imperfect; testa long, fleshy or succulent " (Hooker 1892, p. 270)

six years later he writes again:

"*fr. 1-3-lobed, 1-3-celled, cells 1-seeded, pericarp membranous, bursting irregularly before the maturation of the seeds which ripen exposed; seeds globose, testa soft*." (Trimen & Hooker 1898, p. 267)

He claims that the carpel of *Sansevieria* dries up like paper and, as in the case of gymnosperms, the pulp only develops as a thickened seed coat (testa) afterwards. Even if, admittedly, at that time the meanings of the botanical terms were not as precisely defined as they are today, there was still a distinction made between carpel (carpel from 1834) and seed coat (testa from 1815). (Wagenitz

2008, 165 and 326-327) It appears that Hooker confuses the dried-up and bursting flower tube with the carpel, although on the other hand he describes the fruit as not opening (indehiscent). His findings are puzzling and not entirely understandable. It could be suspected that he had not seen the plant and that he misunderstood and deepened Baker's 1875 description. Between 1896-97, the same John Gilbert Baker, who in 1875 confused the inner pericarp with the seed coat (Baker 1875, p. 547), then took over Hooker's extended error when he describes the fruits of the genus:

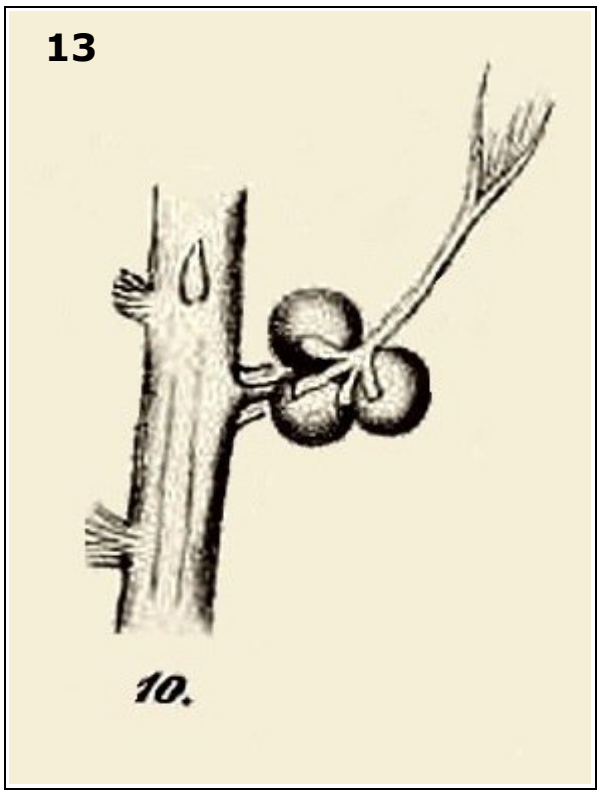
"Pericarp bursting before the seeds ripen. Seeds 1-3 globose; testa fleshy " (Baker 1896-97, p. 4)

and again a year later:

"Fruit membranous, soon bursting. Seeds 1-3, globose; testa lax, fleshy; embryo straight, placed near the base of the albumen." (Baker 1898, p. 332)

He, too, now believes in the "gymnospermous" development of the *Sansevieria* fruits, as not the carpel, but the seed coat (testa) is talked about as the pulp. Apparently, he mistakenly thinks that the "soon to burst" tube are the carpels. This view was also adapted by Prain. He describes the generic characteristics of *Sansevieria* as follows:

"Fruit membranous, indehiscent. Seeds 1-3, globose, ripening outside the pericarp, all large or 1 or 2 imperfect; testa lax, fleshy or succulent; embryo partially enclosed in the fleshy albumen." (Prain 1903, pp. 1053-54)



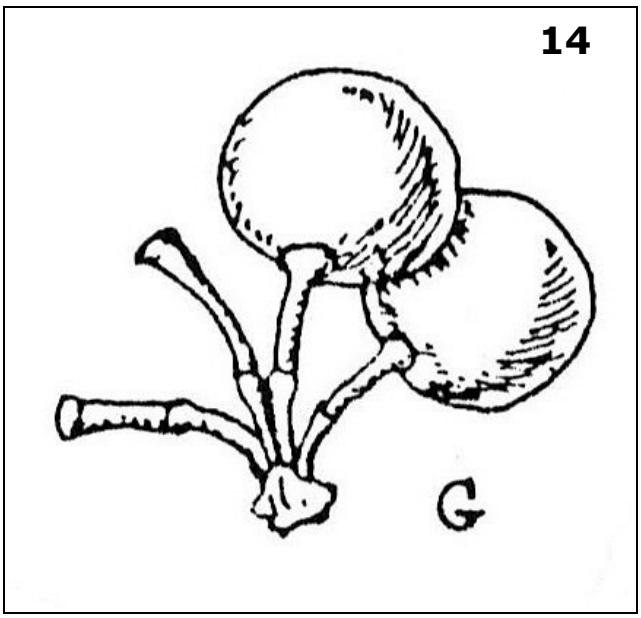


Fig. 13 – *Sansevieria angustiflora* (Source: Lindberg 1875) The remnant of the flower hides the base of the Style.
Fig. 14 – *Sansevieria pearsonii* (Source: Brown 1915) Detail: "G=Fruit" here the author is apparently more interested in the pedicels than in the berries?

What is new in his observation is that the embryo is partially exposed. As far as I know, this has not been seen before or since then. At most, Jacquin's image of the (immature) seeds from 1770 could be interpreted in this way (see Fig. 2). As a result, the conception of the gymnospermous fruit development is repeated many times up until 2010 (Vanden Berghen 1988, pp. 28-29), (Jankalski 2003, p. 18), (Acevedo-Rodriguez and Strong 2005, p. 130) or omitted. (Dinter 1932, p. 86), (Jacobsen 1954, p. 937), (Pfennig 1981b, p. 32) This was also the case with Brown in 1915 in his monograph on the *Sansevieria*, which to this day forms the foundation for serious study of the genus. It is, however, disappointing how little attention he pays to the fruit. In describing the genus in general, he only says:

"*Fruit a berry, containing 1-3 bony seeds*." (Brown 1915, p. 188)

Only in the illustration for *Sansevieria pearsonii* does it show under "G" the drawing of two berries on a cluster with four pedicelli. (**Fig. 14**) After he further states that he does not know anything about the inflorescence, he writes about it:

"… only one flower-cluster in fruit was found, with 4 pedicels *1/3* in. long, jointed at about 1/8 in. above the base. *Berries* orange." (Brown 1915, p. 217)

In the text and illustration, he seems to be more concerned with the stalks than with the fruit itself. Brown's reluctance towards describing the structure of the fruit was certainly due to the fact that he had no reliable knowledge of the fruit. It speaks for his diligence that he would not speculate further about it. In 1932, Kurt Dinter also wrote in his first description of *Sansevieria scabrifolia* (synonym of *Sansevieria aethiopica):*

"*Berries about 9 to 10 mm in diameter, wax yellow*." (Dinter 1932, p. 86)

and thus shows no excessive interest in the fruits. Until the 1960s, reports were mainly made on the fibre content and the most cost-effective propagation and care of plants as fibre-suppliers. Even Jacobsen does not mention the *Sansevieria* fruits at all in his succulent lexicon of 1954 or of 1981. (Jacobsen 1954, Pfennig 1981b) It was not until 1977 that Pfennig gave a concise and correct description of the fruits in his culture instructions for *Sansevieria*:

"*The fruits are easily obtained by hand pollination, preferably in the late evening hours. The 1-3 locular berries ripen after 2-3 months and then turn orange. The fleshy mesocarp is removed and the bone-white round or oval seeds can be sown, ...* "(Pfennig 1980, p. 79)

He correctly recognises that the orange pulp is mesocarp, i.e., comes from the carpel, as is normally the case with all angiosperms. He also implies that the innermost layer of the carpel, the endocarp, cannot be detached and remains on the seed. With this, all of the essential information has been said. In 1981, Horst Pfennig reported again on the fruits of *Sansevieria singularis* (synonym for *Sansevieria fischeri*):

"*While Rauh did not observe any fruit at the location, I attained fruits via hand pollination. When ripe, the single-compartment berry is orange, egg-shaped, round, 1.5 cm long and about 1.3 cm*

thick. The bony-white seeds are 0.7 cm in diameter and 1 cm in length. There was no sowing, the few berries and seeds are kept as an alcohol preparation." (Pfennig 1981a, p. 175)

Here, he does not give a more precise description of the structure of the fruit and even uses the ambiguous term "single-compartment berry". This is misleading, as the berries are always in three compartments, even if often they are not all developed. In 1988, Vanden Berghen took Hooker's view of the gymnospermous development of seeds again. He writes about the genus *Sansevieria*:

"The fruit has a membranous coating that tears open easily and releases 1-3 seeds with a fleshy integument." On Sansevieria senegambica Baker: "Fruit a kind of berry, orange when ripe, with a diameter of 9-10 mm." (Vanden Berghen 1988, pp. 28-29)

He, too, confuses the remains of the flower tube with the carpels. A very remarkable text comes from Joachim Thiede in 1993. In a report from a trip through Malawi, he describes the head-shaped infructescence of a *Sansevieria kirkii*: (**Fig. 15**)

"*One capitate inflorescence of about 25 cm in height was found with a thick and short greenish stalk with greenish bracts, bearing several unripe, rugose green fruits (Fig. 5). The fruits which then turned orange at maturity are remarkable in having only developed a locule bearing two seeds, whereas the two other locules remained undeveloped and sterile*" (Thiede 1993, pp. 32-33)

Fig. 15 – *Sansevieria kirkii* (Photo: Joachim Thiede) Two seeds in one locule?

In Thiede's illustration, more or less distinct furrows can be seen on several partial berries in a plane through the longitudinal axis of the fruit, which suggest a double ovule. In addition, the rudiments of the dried-up style and the two stunted partial berries can be seen on some fruits. The occurrence of two seeds in a locule could either be explained by an atavism in a single plant, or, if it should be a species characteristic, justify a completely new genus since both *Sansevieria* and *Dracaena* are characterised by single-seeded locules. It would be very interesting if the fruit trait reappeared on the plant or its seedlings. During personal communication, the author adds:

"This would require further observations on more extensive material. ... Unfortunately, I do not have any further observations on the fruits of this plant or on other Sansevieria." (Thiede 2014)

Unfortunately, Newton does not mention more about the fruits in the succulent lexicon [Newton 2001, p. 272] than Brown had already written, (Brown 1915, p. 188) and Chahinian does not menti-

on the structure of the fruits in his "Account of the species" at all. (Chahinian 2005) La Croix (2010), on the other hand, repeats Hooker's (1882) view again, describes the incorrect fruit development in great detail and uses this finding to differentiate between the genera *Sansevieria* and *Dracaena*:

P. 14: *" In Sansevieria, the ovary wall falls away and the seeds develop a fleshy covering, a sarcotesta, so that although the fruit resembles a berry, it is not a true berry. ...*
....Fruit with thin pericarp falling away from berry-like seeds …… ***2. Sansevieria***

P. 22: "*Fruit with a thin pericarp that falls away; seeds develop a fleshy coating (sarcotesta) so resembling a berry, but no trace of style remnants at apex*." (La Croix 2010, p. 22)

To distinguish between the genera *Dracaena* and *Sansevieria*, Jankalski dealt with the subject as early as 2003 and writes:

"*As in Dracaena, the ovary has three locules, each with a single ovule, but as the seeds develop the ovary wall falls away exposing the seeds. This gymnospermous development has prompted reviewers such as Bentham & Hooker (1883), Hooker (1892) and Nakai (1936) to ally Sansevieria with the Asiatic genera Liriope Loureiro, Ophiopogon Ker-Gawler and Peliosanthes Andrews which share this character rather than Dracaena. The seeds have a fleshy covering (sarcotesta) that mimics a fleshy berry. The development of up to three "berry-like" seeds from a single flower is proof they are the same as the one to three seeded true berry of Dracaena. Also, the fleshy seeds of Sansevieria completely lack the terminal stigma, beak or withered remains of the style typically seen on Dracaena fruit*." (Jankalski 2003, p. 18)

Five years earlier, Jankalski had already written the same content in a blog post. He also described the role of Bentham & Hooker as a kind of father-figure who was taught in schools to be known as the only accepted authority, which shaped generations of students. This probably explains the great, undisputed spread of the error. At another point in his blog post, Jankalski then writes:

"*However, in Sansevieria Thunberg the fruit withers away early in seed development, exposing the 1-3 seeds which are covered by a fleshy red to orange coat (Sarcotesta). Gymnospermous fruit are rare in Monocotyledons but may be found in family Ophiopogonaceae (Ophiopogon, Liriope & Peliosanthes), and some Amaryllidaceae, such as Hymenocallis. Some authors have described the fruit of Sansevieria as being a berry but, from personal experience, I have seen otherwise."* (Jankalski 1998, p. 2).

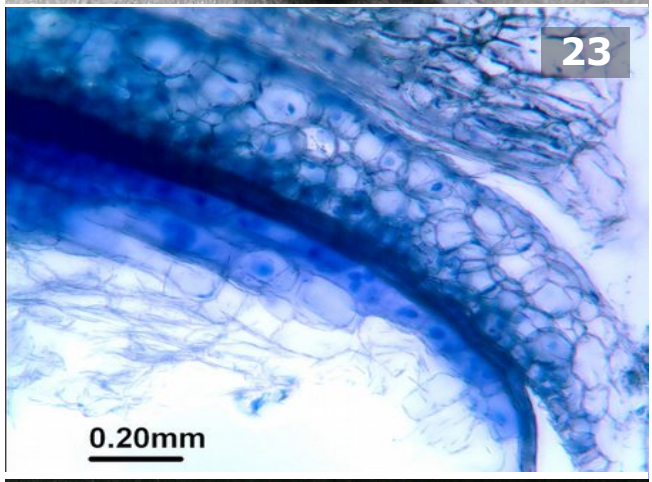
I would like to counter this specific statement with my own observations:

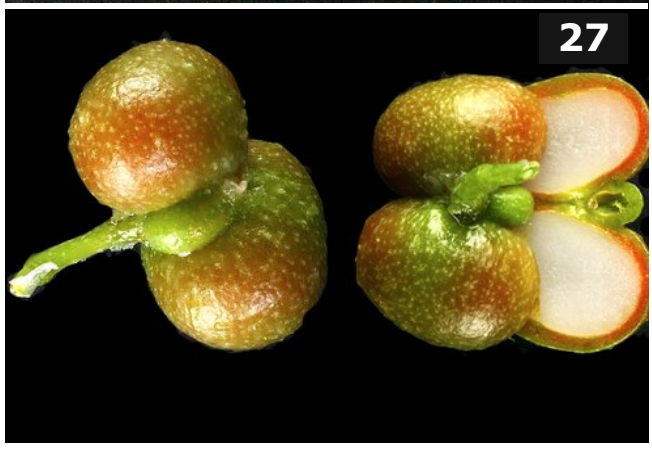
1) The carpels do not shrink, but rather they form the orange pulp of the berry and the fibrous covering around the seed.

2) The style remains respectively the style-base are clearly and unmistakably between the three partial berries and are visible.

3) The fruits are indistinguishable from *Dracaena* fruits (as much as I regret that) and therefore cannot be used as a distinguishing feature from *Dracaena*.

Fig. 16 – *Sansevieria concinna* x *liberica* - Ovaries 11 days after beginning of flowering The unfertilized flower on the upper right will soon fall off. The remaining Ovaries have started to grow. **Fig. 17** – Ovaries of *Sansevieria concinna,* 3 days (left) and 10 days (right) after flowering. The growth of the ovaries, the seams connecting the carpels and the notches across the ovules are clearly visible. **Fig. 18** – *Sansevieria concinna* x *liberica*. Approximately 10 days after flowering. The growing ovaries cause the drying out flower tubes to burst, the flower remnants hide the bases of the styles. **Fig. 19** – *Sansevieria concinna* x *liberica* -Ovaries about 16 days after the flowering. The undeveloped partial berries are covered from the rest of the Flower tube. **Fig. 20** – *Sansevieria concinna* – Ovary 6 days after the end of flowering, flower tube remains removed, cut open, two ovules still with liquid contents, the third atrophied. **Fig. 21** – *Sansevieria concinna* - Fruit about 5 weeks old, irregular grainy surface. Seams between the carpels are clearly visible. **Fig. 22** – *Sansevieria concinna* - Fruit approx. 6 weeks old, cut lengthwise, the nutritive tissue with a gel-like consistency. Clear to see at the bottom right, is the base of the style, a layer between the ovule and the carpel and the exocarp, forming the outer skin. **Fig. 23** – *Sansevieria concinna* - Fruit approx. 5 weeks old, longitudinal (brilliant blue FCF / erythrosine). Top right to bottom left: pulp with initial endocarp formation, (gap), external integument (approx. 4 layers of large round cells), (gap), strongly colored inner integument (two-layer flat epithelium), outer layer of the nucellus (cells containing nucleus), collapsed delicate inner cell walls of the nucellus. **Fig. 24** – *Sansevieria* spec. - 8 weeks old smooth fruit. At the bottom, the style is hidden from the rest of the flower and is visible at the top. **Fig. 25** – *Sansevieria aethiopica* - Fruit 10 weeks after flowering. Cross-section through the 3 locules, the upper two atrophied. The stylus is visible between the partial berries. **Fig. 26** – *Sansevieria cylindrica* -12-week-old, halved fruit with firm nutritive tissue just before ripening.Vertical cut, at the top with base of the style, left in the white nutritive tissue of the Embryo lying almost horizontally. **Fig. 27** – *Sansevieria cylindrica* - Fruit with two developed partial berries shortly before ripening with beginning color change of the mesocarp. Left: The stylus between the two developed and the undeveloped partial berry is clearly visible. Right: same fruit in cross-section through the three locules.





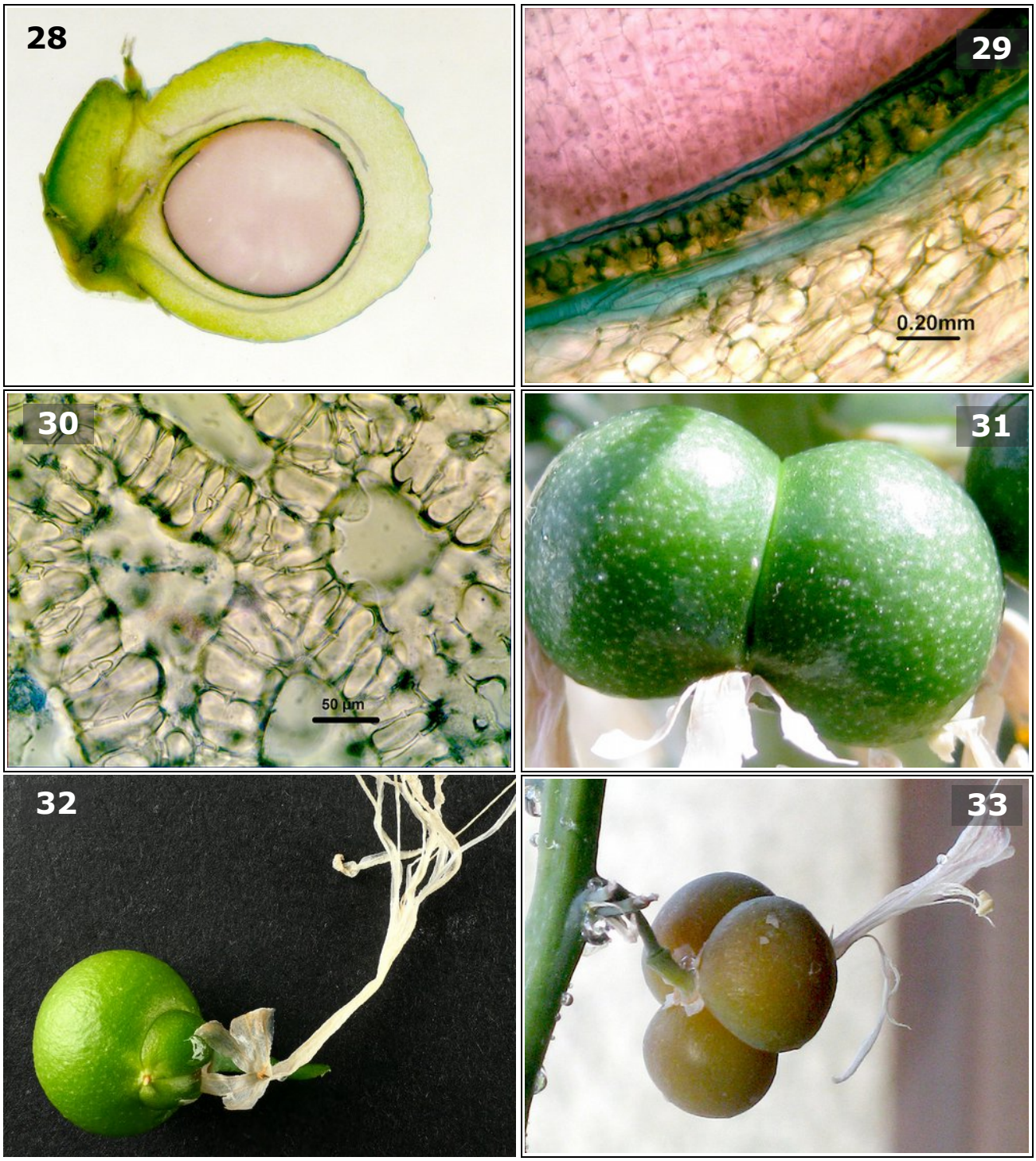


Fig. 28 – *Sansevieria concinna* - Fruit approx. 7 weeks old. longitudinal section (brilliant blue FCF/ erythrosine). The Epicarp on the outside and the base of the style at the top left are merged. In the pulp, vascular bundles can be seen beginning from the stem base at the bottom left. The edge of the pink-coloured seed is dark, at the top left, the Hilum is seen. **Fig. 29** – *Sansevieria concinna* - Fruit approx. 6 weeks old, longitudinal section (brilliant blue FCF/ erythrosine / malachite green). Bottom right to Top left: pulp (mesocarp) beige, endocarp blue (optically active fibers), external integument sepia (cells round), inner integument (dark double layer), nutritive tissue of the nucellus purple-red. **Fig. 30** – *Sansevieria concinna* - Section through the nutritive tissue (albumen) of a 13-week-old seed. The constricted cells are connected to one another by small channels (pits) through the strongly thickened cell walls. The cellulose in the cell walls make up the stored reserves for the seedling. **Fig. 31** – *Sansevieria liberica* –4-week-old, not very glossy, smooth fruit. Style-base at the bottom covered by the flower remnants. **Fig. 32** – *Sansevieria aethiopica* -12 weeks old, one-seeded, dull shiny, almost smooth fruit, remnants of flowers detached from the undeveloped partial berries. **Fig. 33** – *Sansevieria senegambica* - Fruit with three developed partial berries just before ripening. Ten weeks old. The dull smooth surface has got a whitish (glauk) coating.

Fig. 34 – *Sansevieria conspicua* - 12 weeks old fruit with a verrucous surface. **Fig. 35** – *Sansevieria grandis* - Detail from infructescence with smooth, shiny fruits of all three variants of development, just before ripening, 6 months after flowering. **Fig. 36** – *Sansevieria subspicata* - High-glossy, grainy fruits, about 4 months after flowering. **Fig. 37** – *Sansevieria concinna* - 14-week-old, dull shiny, verrucous. Fruits going through a yellow stage in the transition from immature green to ripe orange. **Fig. 38** – *Sansevieria dawei* - Fruits 18 weeks after flowering with dull, slightly textured surface. **Fig. 39** – *Sansevieria dooneri* - 18 weeks old, smooth fruits, with whitish coating. After a few days they become slightly wrinkled due to water loss (below).

Material and Methods

The photographed fruits and inflorscences are from plants of my collection. The flowers were pollinated, some of them several times from begin of blooming until midnight with a fine hairbrush of size 0 to 2.

For the microscopic specimen preparations, free hand cuts were done with a straight razor, if necessary in vivo stained and examined with a Will V 350 microscope. The microscopic photos were taken with a Tucsen TCA-3.0 camera and the color contrasts with Gimp (Versions 2.10.12 to 2.10.28) slightly enhanced.

Results (Observations on my plants)

In order for a fruit to develop from an ovary (**Fig. 6. 17**), the *Sansevieria* flowers must be fertilised. Unfortunately, there are no suitable nocturnal butterflies in our living rooms and greenhouses that would do this for us. So, the only cause of action is to play the butterfly with a brush, in the late evening hours, as Pfennig recommends (Pfennig 1980), or at night until the next morning, as long as the unwilted stigmas are accessible. After successful fertilisation, the ovaries begin to grow slowly. The first changes can already be seen after a few days, after the flower tubes became translucent as they wither.
After about a week, the unfertilised flowers fall off, breaking off at the separation layer on the pedicels. In some species, especially those with head-shaped inflorescences, the withered flowers remain attached to the stem (**Fig. 43, 44**).

Figure 17 shows two ovaries in comparison to one another, on the left 3 days after fertilization, on the right 10 days after fertilization. The withering flower tubes are removed halfway on the left and completely on the right at the base. It can be clearly seen that the ovary has grown and is not shrinking, as has often been claimed for 130 years e. g. (Bentham & Hooker 1883, p. 679), (Prain 1903, p. 1053–54), (Jankalski 2003, p. 18). You can also see the seams where the three carpels have grown together and under which the nectar glands lie as fine longitudinal notches. A larger notch at the upper end of the three carpels, which across the ovules extends down to the base, and which Hooker described as early as 1898, marks the points under which the ovules lie at the base.

As the fertilised one, two or three carpels continue to grow, the flower tube bursts open (**Fig. 16, 18, 19**) and the swelling ovary becomes more and more visible. The remains of the tubes initially only loosen on the side(s) of the ovary where the ovule grows. Either way, however, they cover the base of the style, as Lindberg already described and illustrated in 1875 (see **Fig. 13, 24, 34**).

The base of the style, which, as mentioned, is part of the ovary, is always found in the middle between the three fruit compartments that develop into the partial berries, regardless of whether all three develop or only one or two and thus the fruit becomes asymmetrical. (**Fig. 21–28**) If you open the fruit (**Fig. 6, 22, 26, 28**), you can see vascular bundles that extend from the base of the style into the flesh. This would not be possible in the case of a gymnospermous development, since the pulp would then not be present, but instead a soft, thickened seed coat that could not have any connection to parts of the carpels, except for the basal attachment point as in Figures 1 and 2.
The fruits usually reach their final size after three to four weeks and appear to have a different outer

skin, depending on the species. Different stages of this outer skin can be seen ranging from very smooth, with some species also with a whitish glaucous coating (**Fig. 24, 33, 39, 40**), to very verrucous and wrinkled. **(Fig. 15, 19, 21, 34, 37, 41, 44**) However, after ripening, when the fruits turn orange, they lose moisture within days, shrink somewhat, and become wrinkled. (**Fig. 39, 45**) The fruits seem to have been perfected in colour and size for distribution by birds. (After a self-experiment, I can confirm that - as a representative of mammals - they do not taste very good to me.)

At first, the nucellus is filled with liquid and only on the outer edge has a layer of cells with cell nuclei (**Fig. 20, 22, 23**), which later forms the nutritive tissue on the inside. When fully developed, it consists of nutritive cells that are completely enclosed by their strongly thickened cell walls. The actual nutritive medium is then the bone-hard cellulose and hemicellulose of the cell walls (**Fig. 30**), as can be seen in date kernels.

The embryo develops at about a 120° angle to the hilus and almost parallel to the longitudinal axis of the fruit, which runs from the base of the stalk to the base of the style, never through a seed. (**Fig. 26–28, 47**) The nucellus is enclosed by the two integuments. (**Fig. 6, 23, 29**) The enveloping carpel can be divided into three layers, a thin exocarp, that is the soft outer skin of the fruit, a very juicy, soft mesocarp when ripe, which is formed and becomes bright orange by the desintegration of the cell structure (**Fig. 47**) and, lastly, the fibrous, coarse endocarp, which is formed as the innermost layer, around the 4th week after flowering. (**Fig. 26, 29, 47, 49**)

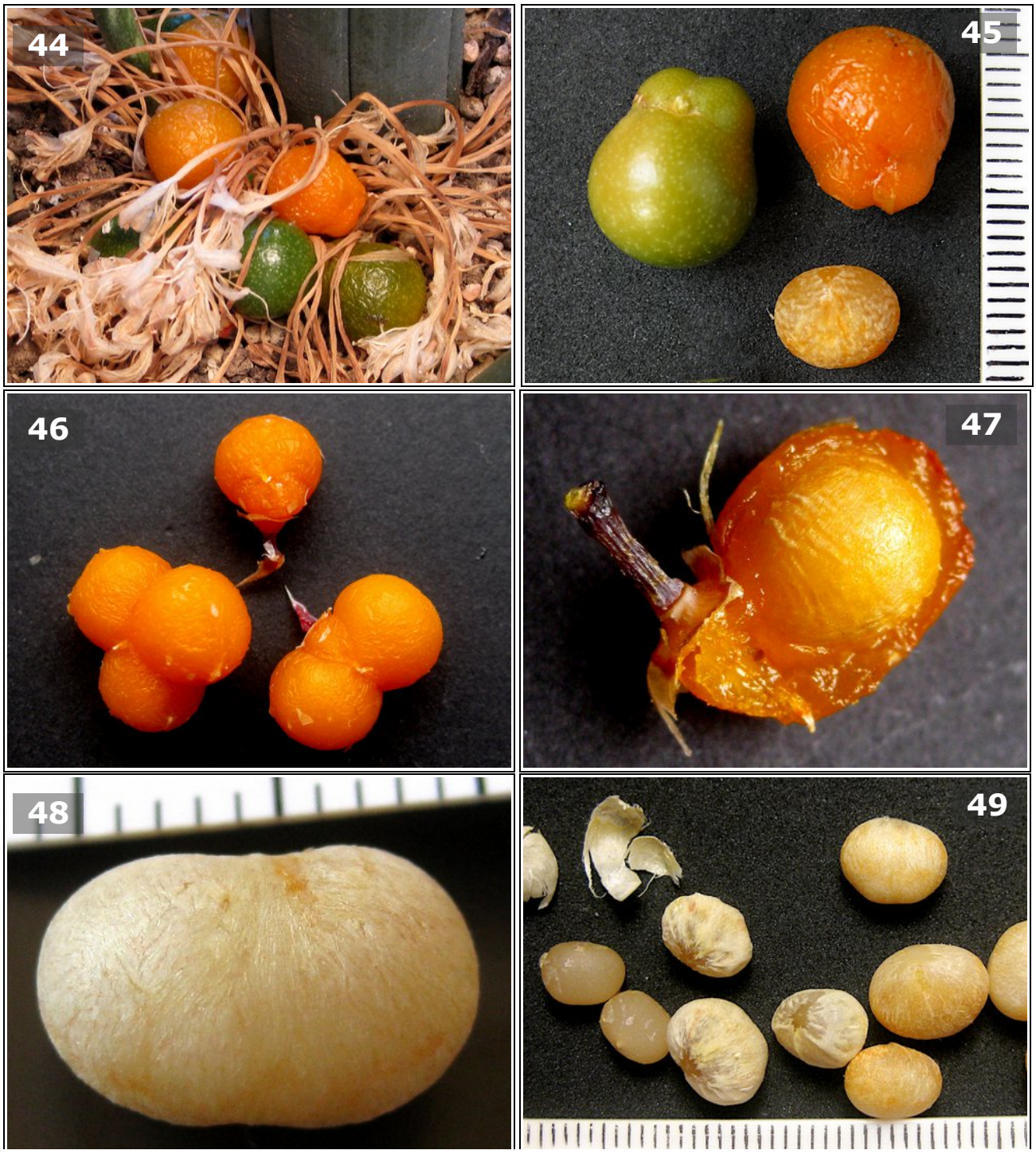


Fig. 40 – *Sansevieria roxburghiana* - Smooth fruit, with glaucous coating, 20 weeks after flowering. **Fig. 41** – *Sansevieria conspicua* - 20 weeks after flowering, ripe fruit with a species-specific verrucous and ribbed surface. Here, the remnant of the style is surrounded by a wall. **Fig. 42** – *Sansevieria liberica* - fruits developed a slightly wrinkled, very soft surface when ripe, 20 weeks after flowering. **Fig. 43** – *Sansevieria kirkii* **-** Dull-shiny fruits in a head-shaped inflorescence. The unfertilized flowers do not fall off. 20 weeks after flowering**. Fig. 44** – *Sansevieria fischeri* - Head-shaped, ground-level inflorescence, 26 weeks after flowering. The initially smooth fruits develop a wrinkled surface as they mature. **Fig. 45** – *S. fischeri* - The ripe fruit (28 weeks old) has slightly shrunk compared to the unripe fruit and the thickness of the pulp can be estimated with the seed. (Botom: mm – scale) **Fig. 46** – *Sansevieria concinna* - The three possible forms of development of the *Sansevieria* fruits. **Fig. 47** – *S. concinna* - fruit developed with a single partial berry, here seen opened lengthways. The orange pulp is very soft and gel-like, the exposed seed shows the fibrous endocarp. The style attached to the pulp contradicts the idea of a gymnospermous development. **Fig. 48** – *Sansevieria cylindrica* **-** The seed shows the fiber structure of the endocarp. (top: mm scale) **Fig. 49** – *Sansevieria trifasciata* - Right: fresh seeds, Middle: poorly matured, dried seeds, whose fiber cover (endocarp) loosens. Left: "naked" seeds, above their detached fibrous endocarp. (Bottom: mm – scale)

Fig. 50 – *Sansevieria liberica* - Compared to dry seeds (middle left) the two seeds on the left are clearly swollen (2mm) after a few days in the water. Longitudinal and cross sections of the seeds through the embryo are seen on the right**. Fig. 51** – *Sansevieria conspicua* - 14 days after sowing the primary root develop.

Discussion (Classification of the fruit)

The endocarp poses a problem for the classification of the fruit. If it were a real berry (Bacca), then it should not have a distinct endocarp; if it were a stone fruit (Drupa), the evident endocarp would have to form a hard stone core. (Spjut 2012) It also gets worse, as in the classification system of fruits, schizocarpic fruits are also categorised. These are fruits that develop from a pistil that consists of many carpels that have grown together. When ripe, the carpels separate into individual fruitlets. If these fruitlets are berries (i.e. endocarp indistinct) it is called a baccarium, if they are stone fruits (i.e. endocarp distinct) the fruit is called a druparium. (Spjut 2012)

Our *Sansevieria* fruit has a three-layered carpel and would therefore be a stone fruit, as Cavanilles suggested as early as 1794. (Cavanilles 1794, p. 24) However, this description still does not fit quite right, as the fruit contains no real stone, but only a fibrous, parchment-like endocarp around the seed and is otherwise very similar to a berry. It could be seen as a berry that is on its way to becoming a stone fruit. In addition, our fruit divides into its three partial berries or lobes, each of which emerges from one of the three carpels. However, it does not divide completely so that it cannot be said that they are fruitlets, as these would have to be separated. It seems that the fruit is halfway between bacca and baccarium, and between drupa and druparium. Figuratively speaking, it is caught between four stools.

Until a carpologist feels the need to study the *Sansevieria* fruit in detail, I suggest using the term berries as before, when speaking of the entire fruit, which can consist of one, two or three developed partial berries, and partial berry, when referring to a single mature carpel with a seed. I think this proposal would, at the very least, not add to the confusion surrounding the *Sansevieria* fruit. Nevertheless, it should be made aware that the term berry for the *Sansevieria* fruit is a pragmatic simplification.

Acknowledgements

Special thanks to Dr. Michael Burkhart for encouragement to translate this article. A big thank go to Tone Sophie Haugh for English translation of the Text.

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