

***Ditepalanthus*, a new genus of Balanophoraceae from Madagascar.**

by

FOLKE FAGERLIND.

With 5 figures in the text.

Released on November 24, 1937 by O. ROSENBERG and ROB. E. FRIES.

Quite recently, the author (FAGERLIND 1938) demonstrated that *Helosis cayennensis* (SWARTZ) SPRENG. (= *H. guyanensis* L. C. RICH.) is actually sexual. Since apomixis certainly occurs within the family Balanophoraceae (LOTSY 1899, ERNST 1914, KUWADA 1928), I decided to examine as many Balanophoraceae as possible. Thanks to the gracious gentleman Professor OTTO ROSENBERG, I also had the opportunity to examine a Balanophoraceae, which has been exhibited for several years in the collection displayed at the Botanical Institute at Stockholm University under the name "*Balanophora*". The first operations using tweezers on the floral spadices showed the presence of abundant amounts of paraphyses, which clearly showed that the plant in question did not belong to the genus *Balanophora*. Paraphyses do not occur in this genus. A preliminary investigation showed that the plant belonged to the fairly uniform group Helosidoideae within the family Balanophoraceae. This arose partly from the paraphyses, partly from the armor of hexagonal scales that completely covered the young spadices. The latter can be found in all Helosidoideae with the exception of the more isolated genus *Scybalium*. The group in question comprises only five previously described genera, namely: *Scybalium* SCHOTT & ENDL., *Helosis* L. C. RICH., *Corynaea* HOOK. f., *Rhopalocnemis* JUNGHUHN and *Exorhopala* VAN STEENIS. None of the genera contains more than four described species. It was therefore very easy to state that the plant in question had not previously been described and that it could not be classified well in one of the genera just mentioned. The diagnosis of the new genus and its species will be provided below, but it should be mentioned here that I have given it the name *Ditepalanthus Afzelii*.

The material that was available to me was from Dr. KARL AFZELIUS and Dr. BJÖRN PALM and was collected on one of their joint excursions to Madagascar. Dr. AFZELIUS informed me that he probably had the feeling that the plant was new to science; he would not have recognized that it represented a new genus. The material was distributed because Dr. PALM agreed that it was not dedicated to more detailed studies. Dr. PALM had not examined it further, since other work concerned him. The finding by AFZELIUS for the plant in question reads in translation: "Balanophoraceae, captured in a wet lowland in the rainforest under ferns (*Angiopteris evecta* and others) near Moramanga in Madagascar 1.10.1912." Orally, Dr. AFZELIUS informed me that the place of discovery is likely to be at an altitude of about 800 m above sea level. The color of the plant was most reminiscent of that of *Equisetum arvense* when it has sprouted from the ground in spring.

Like all other Balanophoraceae, *Ditepalanthus Afzelii* is a holoparasite. It consists only of a tuberous formation, which is attached to the host root in a saddle shape or completely encloses it,

and of one or more inflorescences sprouting from it. An anatomical examination of the host plant showed that it was a dicot; so far, it has not been possible to determine it more precisely.

The habit of the plant is evident from Fig. 1-2. The fully developed tubers reach a diameter of a good 7.5 cm. The spadix stalk, which is irregularly triangular in cross section, reaches a diameter of 2.5 cm and a length of 12-13 cm. The corresponding values for the spadix itself are 2.5 or 5.5-7.5 cm.

The tuber (= rhizome or hypocotyl tuber according to various interpretations) has irregular bulges and knobs along with a small number of more regularly shaped pyramid-shaped extensions (two are clearly visible at the middle of the tuber in Fig. 1 and one cut lengthwise at the bottom on the left of the large tuber in Fig. 2). The latter may be young inflorescence plants, but an anatomical examination has not been able to decide this question. Runners from the tubers are missing. The entire surface of the tuber is coarsely rough. The peduncle, which has the same rough surface as the tuber and has no scales or leaves, forms a direct continuation of the tuber; therefore it is not, as is usual with the Balanophoraceae, delimited from it by a basal sheath. I do not want to conclude from this that it would be different from most Balanophoraceae of exogenous origin. Although not even the slightest rudiment of a volva can be perceived in the youngest individual available to me (the right one in Fig. 1), one may have existed earlier and later degenerated. Accordingly, I do not want to readily agree with VAN STEENIS (1931) that the spadix at *Exorhopala* is of exogenous origin due to the lack of a basal sheath. For *Scybalium*, it is stated that the base of the spadix stalk is surrounded by an "inconspicuous sheath" (ENGLER & PRANTL, 1935); here, the spadix formation would have occurred endogenously, even though the volva had already disappeared at relatively young stages.

In *Ditepalanthus Afzelii*, the number of spadices emanating from each tuber can obviously be more than one (Fig. 1). However, it does not seem impossible to me that - as ASPLUND (1928) suspected in *Juelia* - this is due to the fact that such tubers are actually products of growth. One can very well think that the three small tubers, which can be seen in the middle in Fig. 2, merge with each other in the course of further growth; two of them are connected to each other basally. This would also provide an explanation for previous statements about purely male and purely female spadices on one and the same tuber in Helosidoideae, which contradicts VAN STEENIS' opinion that a tuber carries only male or only female or only hermaphroditic spadices.

Cross sections through the spadix stalk show the occurrence of several rings of vascular bundles, a picture that completely corresponds to that of *Helosis* and *Rhopalocnemis* (GOEPPERT 1848, UMIKER 1920, LOTSY 1901). The vascular bundles in the tuber show an extremely tortuous, irregular course. Sections through the starting point of young tubers show that the parasite drives a haustorium into the host plant. I have not been able to decide whether, as in *Balanophora*, the host plant itself sends out runners in the parasites, whether there is a so-called thallus formation or not. Starch grains are abundant everywhere in the parasite.

The young tuber is, as already mentioned, covered with a contiguous shell of dense, usually hexagonal scales from a central stem. The scales have the same structure as the other Helosidoideae (with the exception of *Scybalium*) and have certainly developed from covering bract-like scales, as with UMIKER'S *Helosis*. The stem of each scale is fixed in a small trench in the center of a low, pyramidal elevation on the spadix axis (Fig. 3A). These weak increases are apparently missing in *Helosis* (of *Scybalium* and *Helosis* ENGLER and PRANTL 1935 (5.303) wrote: "Here the elongated ovoid, capitate or discoidal flower spadix looks simple at first. It consists of EICHLER'S description - - - - small flattened heads of the second order." They may be homologous with the extreme elevations on which the flowers sit in other subfamilies of

Balanophoraceae, for example *Balanophora*. At the top of the elevations in the latter there is often a clavate swelling or a disc-shaped flattened formation which might be homologous to the Helosidoideae scales. If this assumption is correct, one would get a certain connection between some of the subfamilies within Balanophoraceae, which are otherwise difficult to unite. All pyramidal appendages which occur in *Ditepalanthus*, and which are closely associated, pushing against each other, carry a thick felt of clavate paraphyses, which are formed in several, mostly in two, rarely in several rows (Fig. 4A). These paraphyses, which are considered to have secretory importance (VAN STEENIS 1931), are characteristic of the entire subfamily Helosidoideae. Nestled between the paraphyses, four concentric rings of female flowers run around the stem of each scale in *Ditepalanthus Afzelii*. The outermost ring is girdled by a ring of male flowers (Fig. 3A). In *Helosis*, I have shown that the material I examined has two concentric rings of female flowers around each stem and one male flower under each of the six corner points of each scale. The construction of this new Helosidoideae shows that the small number of male flowers in *Helosis* represent the last remnants of a peripheral ring of such flowers.

Even before the scales fall off, the embryo sacs have reached their full organization; the male flowers, on the other hand, have not progressed very far; in them the meiosis has not always come to a conclusion. At this stage the styles have already reached a considerable length; they protrude above the surface of the paraphysis and lie bent down between the same and the inner surface of the armored scale. When the scales have fallen off, fertilization and further development apparently take place quickly. The male flowers stretch and reach full maturity only after the endosperm and embryos have started to develop in the female flowers. Male flowers, which do not develop further and instead remain at the stunted stage, are not uncommon, as in *Helosis*, and appear to be most common in the top of the spadix. When the male flowers have reached their final length, the style has fallen off. As a result, the spadix has a honeycomb-like appearance (cf. Fig. 1); a dimple is visible in the center of each field, the scar from the scale stem.

The male flower has two (rarely three) tepals that are fused together into a tube. These can only be observed as separate formations after the flower has developed.

In the center of the male flower rises a column, which is conically shaped at the tip in the unfolded flower, swollen in the ovoid bud (unfolded flower, see Fig. 4B). Longitudinal sections (Fig. 3B) through this central column show the presence of numerous pollen locules, which are usually on three, rarely only two levels. A cavity is found in the lowermost part of the column below where it separates from the perigon tube with which it has fused at the base (Figs. 3B, 3C a-c). This represents the only part on which the fusion between the elements of the central column has not been complete. It also shows that these various elements have emerged as separate formations and must then have fused in the course of development, although these primary stages have not been encountered. A conical tissue-body protrudes from below into the cavity, filling it almost completely. This is identical to similar formations that occur in most Helosidoideae (see LOTSI 1901, UMIKER 1920, FAGERLIND 1937, ENGLER AND PRANTL 1935). As I mentioned in my *Helosis* work, various researchers wanted to see in it a female organ or a continuation of the flower axis. Cross-sections through the central column show in its basal part (Fig. 3C a - d), in addition to the cross-section of the papilla mentioned above, the occurrence of two vascular bundles, from which it appears that there are two stamens that constitute the central column by intergrowth. Only in exceptional cases are three vascular bundles visible, although three perigone tips are present even when the flower is unfolded. The number of pollen locules varies partly from section to section, partly from flower to flower. Two pollen locules are found

at a lower level than the others (Fig. 3C d). These take on an alternating position in relation to the vascular bundles. Higher in the “pouch head” of the central column there are more pollen locules; the vascular bundles have disappeared there, and two pollen locules have taken their place (Fig. 3C e). If there are three pollen locular levels, there is usually a pollen locule in the middle of the middle and 6-8 pollen locules all around (Fig. 3C g). The central locules is rarely missing here, but it is a rare occurrence on the other levels. It is difficult to say how the various pollen compartments are distributed over the two stamens. When they are created, the intergrowth between the stamens has become so intimate that they cannot be kept apart. The same has been shown for *Helosis* (UMIKER, FAGERLIND) and probably also applies to other Helosidoideae. For *Helosis*, I suspected that some pollen locules came from two stamens that had fused, so that the center of the locule coincides with the suture. The same seems probable to me with this new Balanophoraceae; the central locule is certainly of such origin and so are the locules which extend furthest down in the pouch head. The possibility to think of adhesions that create an asymmetrical picture is not excluded, which I also emphasized for *Helosis*. The pollen locules have a well-developed secreting tapetum. Two cell layers can be seen between the epidermis and the tapetum; none of these, however, experience differentiations, rather they are pushed together without joining. How the pouches open is unknown.

The construction of the female flower (Fig. 4 C) is the same as that of most other known Helosidoideae (see FAGERLIND 1937). It therefore consists only of a pistil formed by two carpels. At the style bases one finds the same collar-like formation of papilla-shaped elongated cells. The collar has been considered homologous to a perigone by previous researchers. In the center of the pistil rises a central placenta, which is devoid of differentiated ovules and has the same appearance as in *Helosis*. The appearance and development of the embryo sac, embryo and endosperm also correspond to the conditions in this plant. As with *Helosis*, there are three “polar nuclei” (Fig. 4D), which then constitute the central nucleus. Nothing has been observed that suggests apomixis. Seedcoats are missing.

Ditepalanthus Afzelii therefore has male and female flowers on the same spadix. The information on the distribution of flowers of different sexes for different Helosidoideae changes. In several of the cases concerned, however, there is no reliable evidence for an assessment of the question, since only a relatively small number of individuals have been examined and there is a possibility that, as with *Rhopalocnemis* (VAN STEENIS 1931), the study of a large amount of material would show the occurrence of both male and female and hermaphroditic strains within the same species. It can therefore not be regarded as certain that *Ditepalanthus Afzelii* always carries hermaphroditic spadices.

Before I move on to making the diagnosis, I want to make a few comparisons with known related genera and point out the differences that motivate the establishment of a new genus. Within the Helosidoideae there are different types of tubers: partly round tubers with branches - *Helosis* and possibly, *Exorhopala* (if this is not one of the types mentioned below), partly round tubers without branches - *Scybalium*, *Corynaea*, *Rhopalocnemis* and the new genus, some finite elongated, branched “tubers” - *Exorhopala* (the formations here, however, have also been interpreted as runners born from the tubers). *Helosis*, *Corynaea* and *Rhopalocnemis* have a well-developed volva around the inflorescence base, little developed in *Scybalium*. With *Exorhopala* and the new genus, a basal sheath could not be detected at all. *Scybalium* has inflorescence stems with scales similar to bracts, and *Rhopalocnemis* often has those with hexagonal scales that are otherwise characteristic of the spadices. The other genera have spadix stems that are completely without leaf or scale-like formations. All species, except for some species of *Scybalium*, have

cylindrical to ovoid floral spadices. The construction of the male flower is, as VAN STEENIS has expressly pointed out, the characteristic that best distinguishes the genera within the subfamily. As a rule, three perigone leaves appear in the male flower in *Scybalium* and *Helosis*. *Exorhopala* has four, the new genus two, the genera *Corynaea* and *Rhopalocnemis* have perigone leaves fully fused into a tube or a funnel in the male flower. When the flower unfolds, the mouth of the tube or funnel is split in these latter genera into a changing number of irregular tips. The degree of intergrowth between the base of the stamen column and the perigone tube may also vary (see ENGLER AND PRANTL) in the various genera (Fig. 5). In all genera, the anthers have fused to form a head. The intimacy of the fusion of the filaments is also different; extreme cases are *Helosis*, on the one hand, in which the number of filaments can be determined without difficulty, and, on the other hand, *Rhopalocnemis*, *Exorhopala* and the new genus, in which an anatomical examination is required to determine the number of the elements in question. In the latter type, there was a small cavity, which was the only region in which the fusion of the filaments was not total, and into which a so-called rudimentary female organ protruded. This cavity and the “rudimentary organ” are absent in *Rhopalocnemis* and *Exorhopala*, in which the filaments fusion is complete. The “rudimentary organ” protrudes into a tube formed by the stamens in *Scybalium*, *Helosis* and *Corynaea*. The number of stamens entering the synandrium is as follows: *Scybalium* 3, *Helosis* 3, - *Corynaea* 3, *Exorhopala* 4, *Ditepalanthus* 2 (see ENGLER & PRANTL and VAN STEENIS and this work). For *Rhopalocnemis*, ENGLER and PRANTL indicate the presence of a large number of stamens. The information is probably not correct, it is certainly based on the large number of pollen locules. However, the conditions described above have shown that the number of pollen locules in the Balanophoraceae does not correspond to the number of stamens.

The number of pollen locules in the pouch head obviously varies. The information found in the literature on this makes a rather unreliable impression. With *Helosis*, the existence of three central locules and a peripheral circle of six locules is proven (EICHLER. Cf.: ENGLER and PRANTL 1935, UMIKER, FAGERLIND). With *Scybalium*, *Helosis*, *Corynaea* and *Exorhopala*, the pollen locules form only one layer. *Rhopalocnemis* and the new genus, on the other hand, have numerous pollen locules, which are arranged in several layers, usually three. The number of pollen locules in the pouch head is greater for *Rhopalocnemis* than for the new genus. The differences in the construction of the male flowers, which show generic differentiation, are illustrated in a schematic representation in Fig. 5.

The collar-like formation around the style bases in the female flower seems to be missing only in *Rhopalocnemis* and *Exorhopala*.

After this compilation of the features that differentiate the different Helosidoideae genera from each other, I now give the diagnosis for the new genus and its representative.

***Ditepalanthus* FAGERLIND nov. gen.**

Plant a fleshy starchy parasite on roots. Rhizome irregularly shaped, globose, not squamiferous. Leaves none. Inflorescence spadiciform, stipitate. Stipe (always?), at least in the flowering state, without basal volva, not squamiferous. Spadices more or less globose, covered by adpressed hexangular peltate bracts [that are] deciduous in the flowering state. Flowers intermixed with paraphysis-shaped hairs, [the flowers] arising serially [i.e., in rows] around the stipe of the bracts, positioned on dense subconical tubercles [wart-like outgrowths].

Male flowers with tepals almost always two, fused into a tube at base. Androecium almost always composed of two stamens, undivided, columnar, more or less globose at apex. Anther

locule number variable, generally superposed in three rows; androecial stipe connate at base with the tepal tube, hollow, with a papilla arising from the base of the cavity.

Female flowers with tepals absent. Carpels two, styles surrounded at base by a sheath formed by elongated papillae. Ovary unilocular, the placenta at first central and free leaving a small cavity in the ovary, later completely fused with the carpels. Ovules absent. Embryo sacs derived from subepidermal cells of the placenta. Testa absent. Embryo very minute, not differentiated, formed by few cells.

Ditepalanthus Afzelii FAGERLIND n. sp. Rhizome irregularly tuberculate, in flowering state ca. 7-8 cm in diameter. Stipes two or three times longer than spadices, in flowering state ca. 12-13 cm tall, ca. 2.5 cm in diameter. Spadices (hermaphroditic?) in flowering state ca. 5.5-7.5 cm long and 3.5 cm in diameter. Paraphysis-shaped hairs c. 2 mm long. Female flowers ca. 3 mm, style ca. 1.8 mm long. Male flowers ca. 5 mm long. Tepal lobes ovate, apex generally truncate.

Living in Madagascar (near Moramanga) in moist places in the primeval forest, ca. 800 m. alt. ([Herbarium specimen deposited] In the museum of the botanical institute of Holm University and also conserved in spirit).

Species named in honor of the renowned CAROLUS AFZELIUS, who together with the renowned BJÖRN PALM collected the plant.

Before *Ditepalanthus Afzelii* was found, only one Helosidoideae was known from Africa, namely *Rhopalocnemis malagastica* JUMELLE and PERRIER DE LA BATHIE (1912), also this from Madagascar. The genus *Rhopalocnemis* would have a representative, *Rhopalocnemis phalloides* JUMELLE, in India and Malaya and one in Madagascar. The other genera of Helosidoideae all have rather limited distributional areas, none of them occur in more than one part of the world. *Rhopalocnemis* would be an exception. On the other hand, two different genera of the group in question should be represented in Madagascar. However, both are quite dubious. JUMELLE'S and PERRIER DE LA BATHIE'S *Rhopalocnemis malagastica* is only a "nomen nudum", because a diagnosis is completely lacking and the information about the species is very incomplete. Nothing is furnished that indicates that the plant in question can be assigned to the genus *Rhopalocnemis*. The only sure thing is that it is a Helosidoideae. The illustration of a young spadix provided by the authors bears some similarities to the genus I have described here. A basal sheath seems to be missing; that it should have been left out of the drawing, if it had the strong formation that is characteristic of *Rhopalocnemis*, seems out of the question, which is why it can be regarded as certain that a basal sheath is really missing. The relatively long, bract-free spadix axis also deviates from *Rhopalocnemis*, but is in agreement with *Ditepalanthus*. There are therefore reasons to suspect that it is a representative of the genus I have described. Until further notice, the plant is therefore called *Ditepalanthus malagastica* (JUMELLE et PERRIER DE LA BATHIE) n. comb. FAGERLIND. It is not far from suspicion that this species is actually identical to *Ditepalanthus Afzelii*. The former differs from the latter in quantitative features. The dimensions given by JUMELLE and PERRIER DE LA BATHIE, and all of which seem to relate to young individuals, are 2-4 × 3.4 cm for the tubers, 2-4 cm for the length of the spadix stalk and for those of the spadix 5-7 cm. The numbers for similar stages of development in *Ditepalanthus Afzelii* (the middle individual in Fig. 1) are 5 × 5, 5.5 and 4. The numbers show that the relationship between the length of the spadix and the length of its stem is quite different in my material and those of JUMELLE'S PERRIER DE LA BATHIE. It is hardly possible that these differences are only due to a kind of variation, they are probably to be understood as distinguishing features; it is, of course, impossible to make a definite statement about this unless

more material has been studied. JUELLE and PERRIER DE LA BATHIE collected their material at Manongarivo, at an altitude of 1600 meters. The elevation figure shows how Dr. AFZELIUS informs that it must be a completely different part of Madagascar than the one in which his and PALM'S material was collected.

Finally, it is a pleasant duty for me to express my deepest thanks to the following gentlemen: Dr. KARL AFZELIUS and Dr. BJÖRN PALM for the collection of the material I have dealt with here, the former also for willingly providing information, Professor Dr. OTTO ROSENBERG for permission to anatomically examine the material, and Bergianus Professor Dr. ROB, E. FRIES for help with the writing of the name and the Latin diagnoses.

Stockholm, University Botanical Institute in November 1937.

Literature cited.

Asplund, E. 1928. Eine neue Balanophoraceen-Gattung aus Bolivien. — Svensk Bot. Tidskrift 22. — **Engler, A. & Prantl, K.** 1935. Die natürlichen Pflanzenfamilien. Zweite Auflage. Bd. 16 b. — **Ernst, A.** 1914. Embryobildung bei *Balanophora*. Flora 106. — **Fagerlind, F.** 1938. Bau und Entwicklung der floralen Organe von *Helosis cayennensis*. — Svensk Bot. Tidskrift. (Im Druck). — **Goepfert, H. R.** 1848. Zur Kenntnis der Balanophoren, insbesondere der Gattung *Rhopalocnemis*. — Nova Acta Acad. nat. cur. XXII. 1. — **Jumelle, H. Perrier de la Bathie, H.** 1912. Quelques phanerogames parasites de Madagascar. — Rev. Générale de Bot. 24. — **Kuwada, Y.** 1928. On occurrence of restitution-nuclei in the formation of the embryo-sac in *Balanophora japonica*. — Bot. Mag. Tokyo 42. — **Lotsy, P.** 1901. *Rhopalocnemis phalloides* JUNGH. Eine wenigstens örtlich verwitwete Pflanze. — Ann. Jard. Buitenzorg 2 sér. 2. — **Umiker, O.** 1920. Entwicklungsgeschichtlich-zytologische Untersuchungen an *Helosis guyannensis*. — Diss. Zürich. — **Van Steenis, C, G. J.** 1931. Some remarks on the genus *Rhopalocnemis*. — Handelingen 6. Nederl. Ind. Natuurwetenschappelijk congres. Bandoeng, Java.

Tryckt the 17th of March 1938.

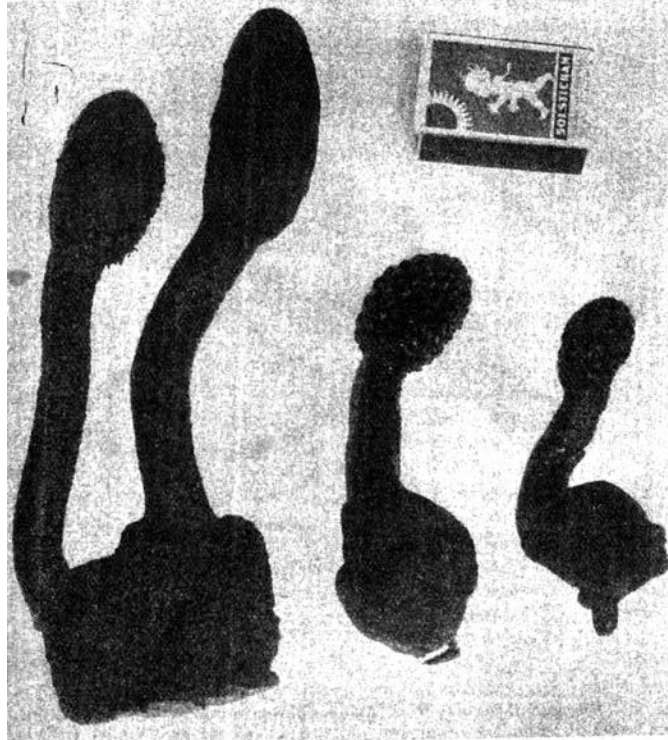


Fig. 1. *Ditepalanthus Afzelii*, habit picture. ($1/2 \times$). - Photo IFA, Stockholm.

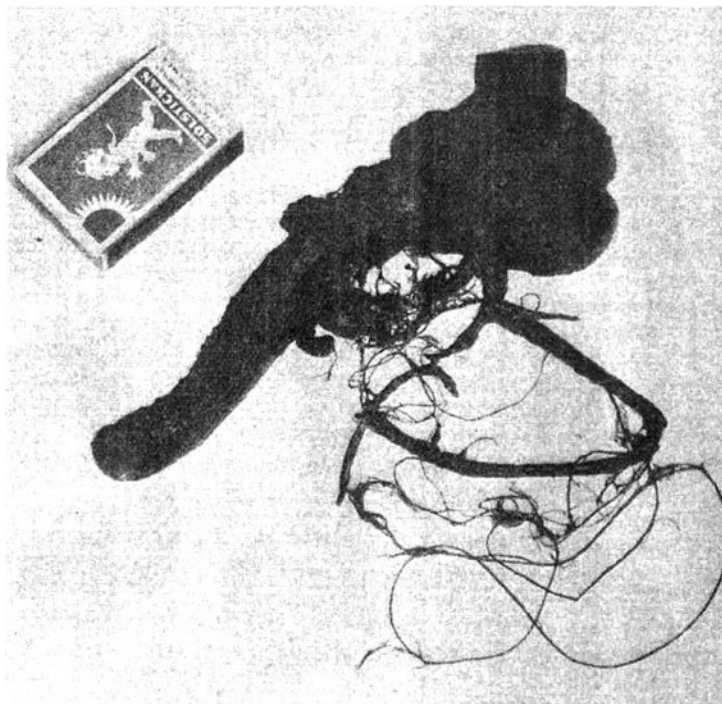
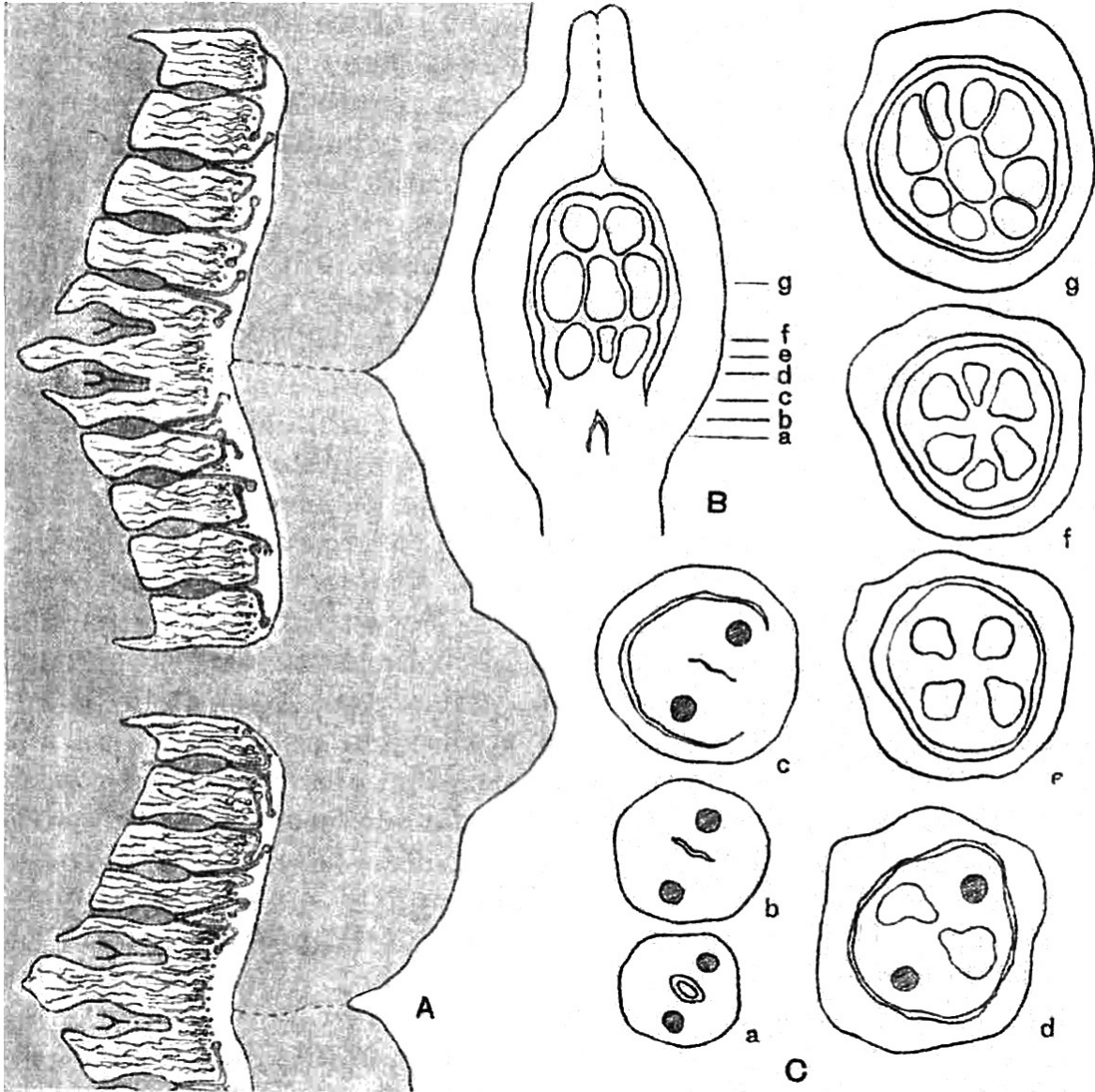


Fig. 2. *Ditepalanthus Afzelii*. Older, flower-bearing tubers (truncated inflorescence stem) and three young tubers, sitting on the root of the host plant. ($1/2 \times$). - Photo IFA, Stockholm.



3 A: Part of a longitudinal section through a young spadix, cross section of scales, paraphyses and male and female flowers (schematic); B: Young male flower in longitudinal section (schematic); C; Cross sections of the male flower in different levels. (The position of the sectioning planes corresponds to the lines in Fig. 3 B. The vascular bundles are hatched)

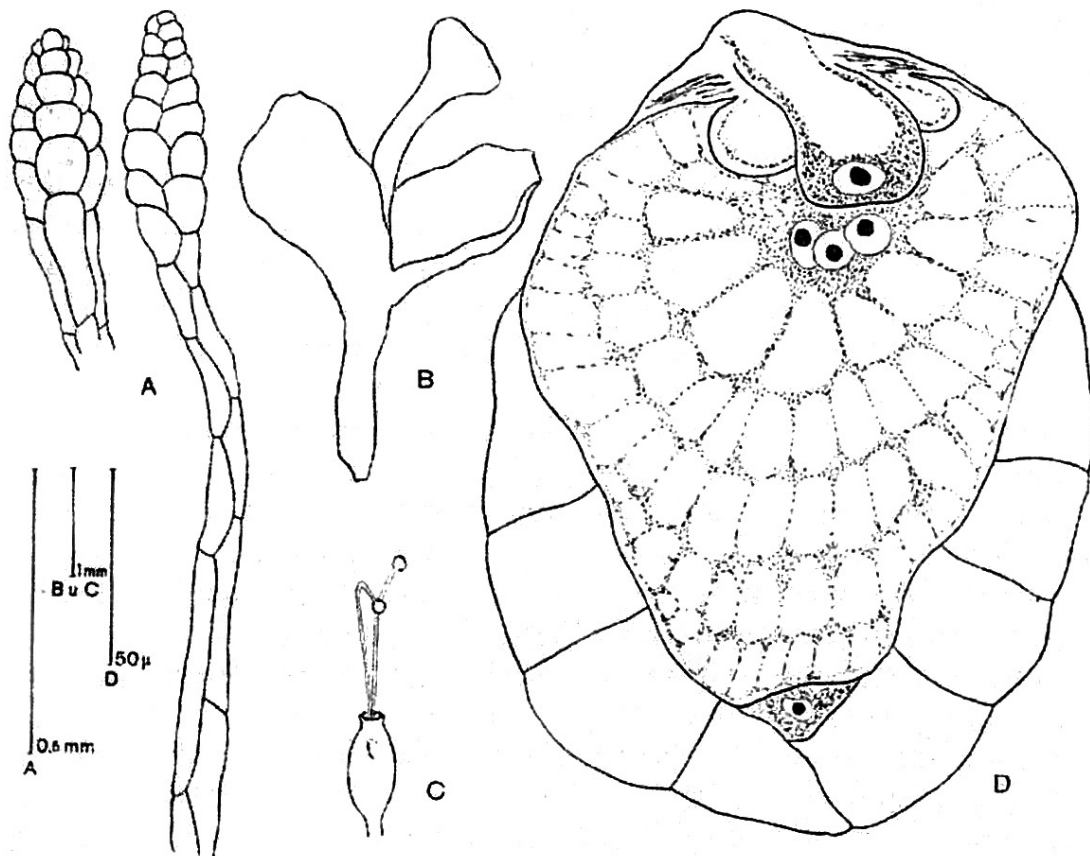


Fig. 4 A: paraphyses; B: male flower.; C: female flower; D: Embryo sac not yet ready for fertilization.

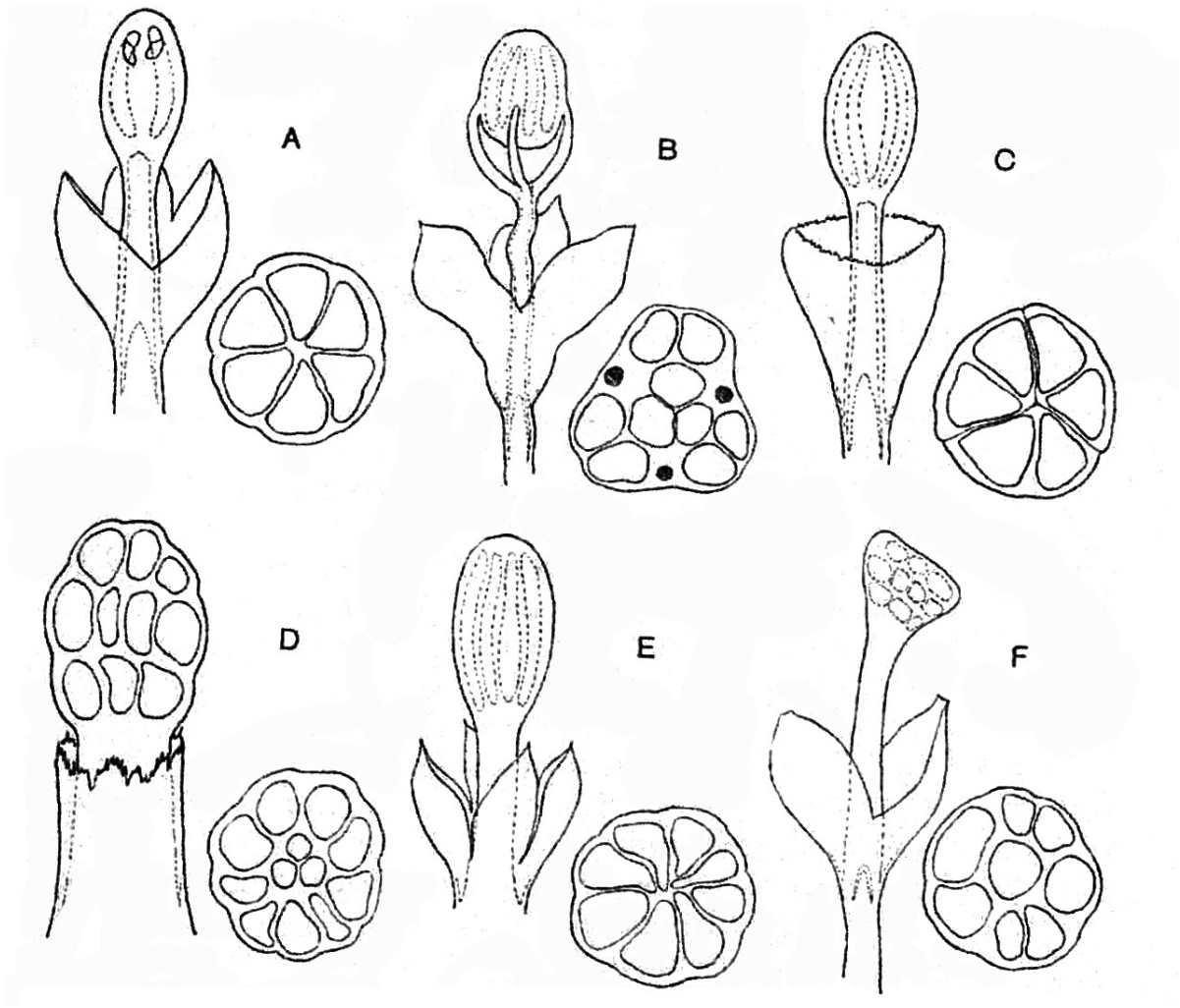


Fig. 5. The male flower in different Helosidoideae. Schematic. Variations occur; see the text!): A: *Scybalium fungiforme* and *depressum*; B: *Helosis*; C: *Corynaea*; D: *Rhopalocnemis*; E: *Exorhopala*; F: *Ditepalanthus*.