

Studies in the Floral Morphology of *Opuntia Dillenii* Haworth.

1. Development of the Ovule and Gametophytes.

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Introduction.

There has been a considerable divergence of opinion as to the systematic position of the family *Cactaceae*. It has been assigned different places by different authors (WETTSTEIN 1944, ENGLER and DIELS 1936, WARMING 1904, HUTCHINSON 1926, LAWRENCE 1951, GUNDERSON 1950). A historic résumé of the various positions assigned to *Cactaceae* in the natural systems of classifications from the time of JUSSIEU to ENGLER has been given by HUBER (1929). In 1950 Prof. MAHESHWARI (Delhi) suggested to Prof. B. TIAGI (Ajmer) that he work out the embryology of *Opuntia Dillenii*. Since the latter was preoccupied with his studies on *Cuscutaceae* and *Orobanchaceae* in the summer of 1952, Prof. MAHESHWARI asked me to undertake this work with a view of further elucidating the morphology, affinities and systematic position of *Cactaceae*. This family is, moreover, characterized by an inferior ovary. As is well known, the nature of the inferior ovary has been one of the most bitterly debated topics of floral morphology. In view of this Prof. V. PURI (Meerut) also approved of my working out the vascular anatomy of the flower of *Cactaceae* along with other aspects of floral morphology so that our knowledge regarding the nature of the inferior ovary, especially in this family, might be increased. The present work which is the first of its series was started at Delhi and continued at Agra.

Material and Methods.

Opuntia Dillenii is naturalized in several parts of Northern India. At one time it was a very serious and troublesome pest but has recently been brought under control by the cochineal insect. At Ajmer it is very commonly used as an effective hedge plant, flowering twice a year, in the months of March—April and September—October. In the beginning several hundred slides, already prepared by Prof. TIAGI were passed on to me. Subsequently, more material was collected. The outer tissues of the ovarian wall were trimmed off and the material fixed on the spot. in F.A.A. In the case of some older buds and flowers the ovules were removed.

Previous Work.

Literature on the embryology of *Cactaceae*, especially the gametophytes prior to 1931 has been carefully summarized by SCHNARF (1931). The following is a brief summary of the work done on the embryology of this family after 1931.

MAURITZON (1934) studied the development of the embryo sac in three species of *Rhipsalis*. The second meiotic division in the micro-pylar dyad cell is said to be never completed, so that the tetrad consists of an upper dyad cell with a resting or dividing nucleus and two lower megaspores. The mature embryo sac conforms to the '*Polygonum*' type of development (MAHESHWARI 1950). A few stages in the development of the embryo are also figured from which the type of embryonomy cannot be definitely made out. On the basis of his embryological studies the author strongly supports the inclusion of the *Cactaceae* in the order *Centrospermales* (WETTSTEIN 1944).

The following year NEUMANN (1935) studied the development of pollen, ovule and embryo sac of *Pereskia amapola* var. *argentina*. The mature pollen grain is trinucleate. The embryo sac conforms to the '*Polygonum*' type of development. On the basis of remarkable similarities in the development of *Pereskia* with other *Centrospermalean* families she decidedly favours the position taken by WETTSTEIN (1944) regarding the systematic position of the family.

It may be mentioned here that none of these authors studied the morphology of *Passifloraceae*. *Cactaceae* also shows significant features of resemblance with *Passifloraceae* and may possibly be also related to *Passiflorales*. Work in this direction is in progress in this laboratory.

ARCHIBALD (1939) investigated the development of the ovule and

seed of *Opuntia aurantiaca*. Her account of the development of the ovule is praiseworthy since it has removed all previous anomalies regarding its designation. The mature ovule is rightly termed 'Circinotropous' and the third 'integument' has been shown to be formed by the funicle. Development of the embryo sac is described as conforming to the '*Allium*' type (MAHESHWARI 1950). She reports frequent undevelopment and disorganization of the embryo sac and the production of adventive embryos from the nucellar cells resulting in polyembryony. The endosperm is reported to be absent and consequently the adventive embryos develop without it — an observation recorded for the first time, constituting a new and third type of adventive embryony.

Recently TIAGI (1954) has reported the salient features of the life history of *Opuntia Dillenii*. Since then MAHESHWARI and CHOPRA (1954) have reported polyembryony due to the presence of adventive embryos of nucellar origin in *Opuntia Dillenii*. This was abundantly present in my material.

Microsporogenesis.

The young anther consists of a homogeneous mass of parenchymatous cells and it is nearly ellipsoidal in cross section but soon becomes fourlobed. The single archesporial cell is hypodermal and not very conspicuous in early stages (Fig. 1). As seen in longitudinal sections, the number of archesporial cells varies from six to ten. The archesporial cell divides periclinally to form a small outer parietal cell and a large inner sporogenous cell with denser cytoplasm, conspicuous nucleus and nucleolus. The primary parietal cell by periclinal and anticlinal divisions forms a wall of three layers surrounding the single primary sporogenous cell (Fig. 2). The tapetum is 'glandular' in nature. Its cells become enlarged with denser cytoplasm and more prominent nuclei. The tapetal cells remain in situ till they are completely absorbed. The nuclei of the tapetal cells divide just before the initiation of the reduction division in the microspore mother cells. The divisions are typically mitotic (Figs. 6—11) but cytokinesis does not take place with the result that most of the tapetal cells become binucleate (Fig. 12). In the majority of cases the tapetal cells remain binucleate throughout; sometimes the divisions may proceed further resulting in the formation of a tri- to polynucleate cell. In such cases the nuclei may show fusions (Fig. 12). The cells of the single middle layer become flattened and crushed at maturity. At the shedding stage of the pollen the endothelial cells become enlarged and develop fibrous thickenings (Fig. 19),

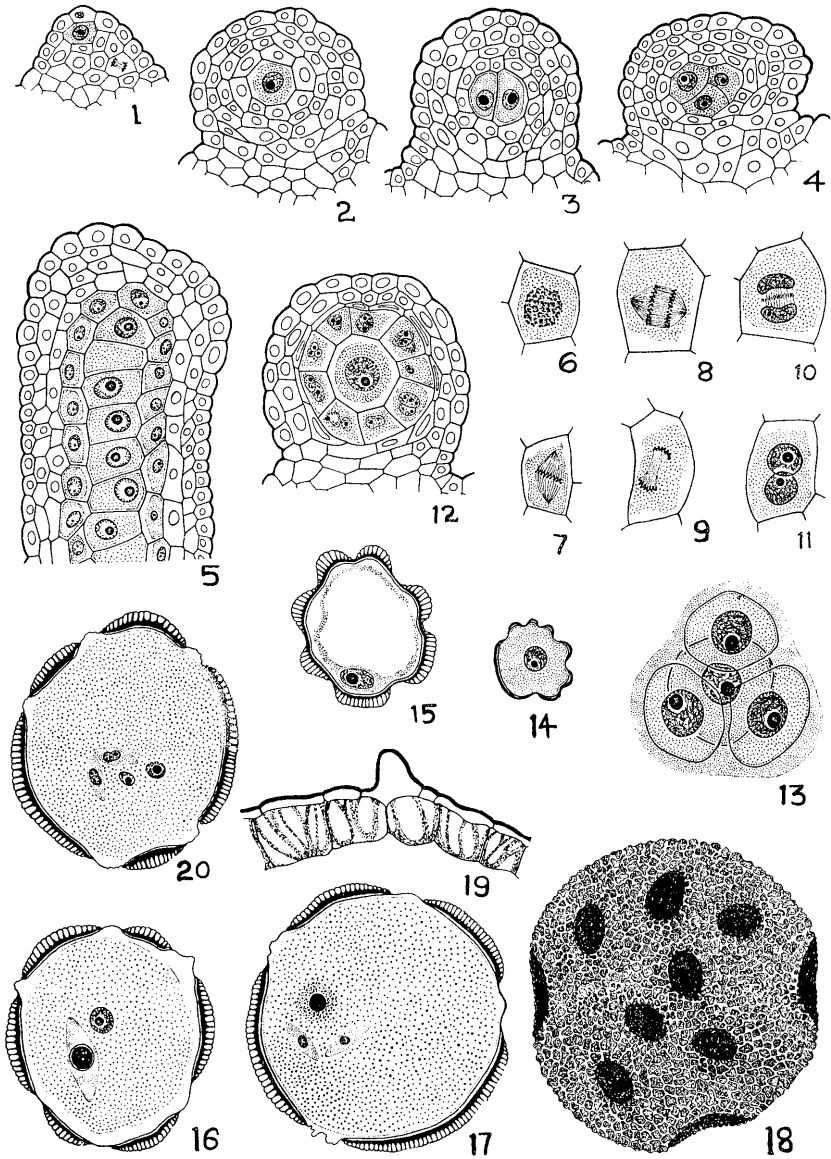
while the anther epidermis becomes flattened and slightly lignified; some of its cells grow as papillae as the anther approaches maturity (Fig. 19).

In most cases the primary sporogenous cells divide transversely so that there is a single row of microspore mother cells as seen in a longitudinal section of the anther (Fig. 5). However sometimes one or two vertical divisions may also occur resulting in the formation of two or more microspore mother cells, seen in a cross section of the anther (Figs. 3, 4). The stages of reduction division were not present in my material. Cytokinesis seems to occur by furrowing; the resulting microspores are arranged in a tetrahedral manner (Fig. 13). In addition to the original wall of the microspore mother cell, a mucilaginous wall is secreted by the protoplast which surrounds the young tetrad. Microspores are liberated in the loculus by the dissolution of this mucilaginous envelope, the original wall disappearing somewhat later with the tapetal cells.

Male Gametophyte.

The young microspore (Fig. 14) enters upon a growth period during which its cytoplasm first becomes uniformly vacuolate; later the vacuoles unite to form a single large central vacuole. Consequently the nucleus becomes displaced towards the periphery in the thin peripheral layer of cytoplasm (Fig. 15). At maturity the cytoplasm increases and the vacuole disappears. The next stage observed is the binucleate condition in which the pollen grain contains the spindle-shaped generative cell lying free in the cytoplasm of the larger tube cell (Fig. 16). The generative cell divides to form two spindle-shaped male gametes which

Figs. 1—20. Microsporogenesis and the male gametophyte. — 1: c.s. anther showing the single hypodermal archesporial cell. — 2: same, showing the microspore mother cell surrounded by three wall layers. — 3, 4: same, but with two and three microspore mother cells respectively. — 5: l.s. of a portion of anther showing the single row of microspore mother cells. — 6—11: Various stages in the mitotic divisions of the nuclei of tapetal cells. — 12: c.s. anther showing binucleate tapetal cells, crushed middle layer; one tapetal cell shows four nuclei in the process of fusion. — 13: A tetrad of microspores enveloped in mucilage. — 14: A young microspore. — 15: A uni-nucleate vacuolate pollen grain. — 16: A two-celled pollen grain, the generative cell is spindle-shaped. — 17: A mature pollen grain showing the spindle-shaped male gametes, tube nucleus degenerating. — 18: Surface view of a mature pollen grain showing the ornamentation and the germ pores. — 19: Fibrous thickenings in the endothecium; note a papillate epidermal cell. — 20: A double pollen grain showing two tube nuclei and two generative cells, each binucleate. — c.s.=cross section; l.s.=longitudinal section.



Figs. 1—20.

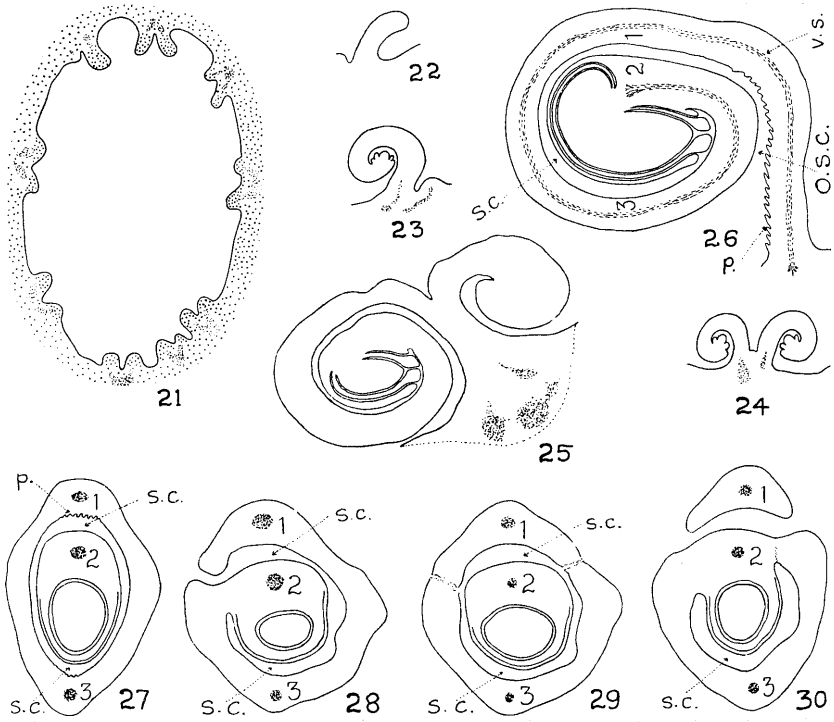
are definite cells, the cytoplasmic sheaths around the nuclei being very conspicuous (Fig. 17). In the mature pollen grain the tube nucleus shows signs of degeneration and is reduced to a lump of chromatin (Fig. 17). The pollen grain at the shedding stage is trinucleate; the intine is thin and smooth, the exine is coarsely reticulate and shows about twelve germ pores (Fig. 18).

An interesting case of a double pollen grain containing two tube nuclei and two generative cells each having two nuclei of the male gametes, there being no cytokinesis, was also observed (Fig. 20).

Ovule.

The development of the ovule (Figs. 21—26) largely follows the same course, as outlined by ARCHIBALD (1939) for *Opuntia aurantiaca*. The ovule arises as a small protuberance on the placenta, which elongates and forms the funicle. The tip of the funicle then bends on account of vigorous growth on the outer side, the two rows of the ovules on a placenta bending in opposite directions. By the time the rudiments of the inner integument followed by those of the outer appear on it, the ovule becomes erect again (Figs. 23, 24). The curvature of the funicle does not stop here; by the time the embryo sac is fully mature the ovule lies once more in an anatropous position (Fig. 26). The term 'Circinotropous' was coined by ARCHIBALD (1939) for this type of ovule. Both the integuments are two-layered (Fig. 41) though the inner integument becomes multilayered at the apex and alone forms the micropyle by its protruding, swollen apex. At maturity there is a conspicuous air space between the two integuments in the chalazal region (Figs. 40, 46). ARCHIBALD (1939) has also reported a similar space in her material of *Opuntia*. NEUMANN (1935) also records the presence of a similar air space in *Pereskia* and regards it as an important point of resemblance with *Centrospermales* where it is a frequent occurrence.

Transverse sections of the ovule (Figs. 27—30) at different levels show the way in which the margins of the funicle grow out, ultimately fusing with the part of the funicle on the opposite side and encasing the ovule in a third 'integument'. In early stages the line of fusion is distinct but at maturity all traces of fusion disappear. In longitudinal section of the ovule the spiral canal leading to the micropyle is distinctly seen on the inner surface of the funicle, lined by glanular papillae (Fig. 26). GUIGNARD (1886) thinks that the papillae help the



Figs. 21—30. Development of the Ovule. — 21: c.s. of young ovary showing ovular primordia, outer tissues trimmed. — 22: An ovular primordium. — 23—26: l.s. ovule showing origin of integuments and curvature of funicle. — 25: Two ovules borne on a single funicle. — 27—30: c.s. of ovule at various levels showing the funicular integument. — o.s.c.=opening of the spiral canal; p.=glandular papillae; s.c.=spiral canal; v.s.=vascular strand.

pollen tube in their journey to the micropyle. The opening of the spiral canal is a small pore just near the base of the funicle (Fig. 26, o.s.c.).

Sometimes two ovule initials arise side by side and their funicles begin to grow all together (Figs. 24, 25) giving the impression that the two ovules arise by branching of a single funicle. This condition is similar to that of *Cereus tortuosus* where GUIGNARD (1886) reports that the main trunk of the funicle gives rise to about thirty branches or 'secondary funicles' each tipped by an ovule. A single vascular strand enters the funicle from the placental bundle and travels up to the chalazal region (Fig. 26, v.s.).

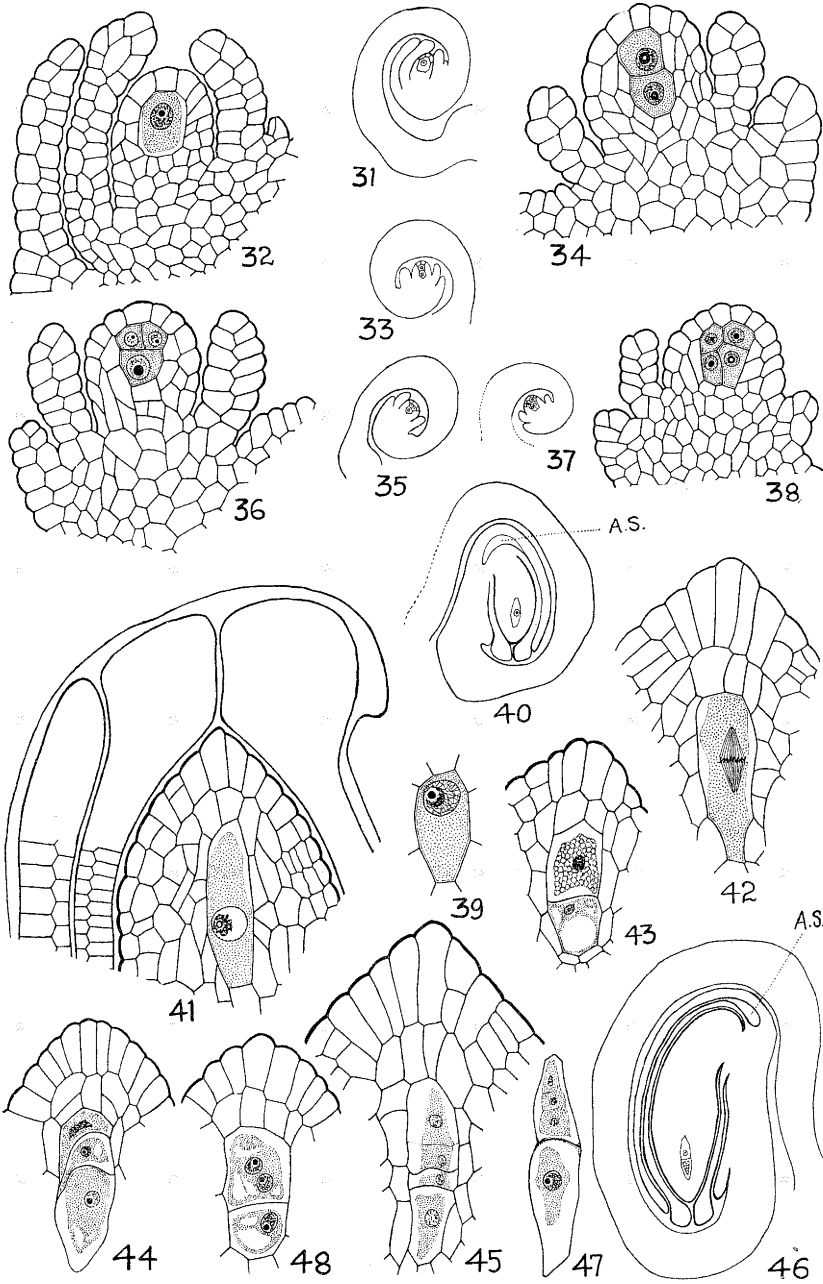
The cells of the nucellar epidermis in the apical region become highly elongated radially and sometimes may even simulate pollen tubes. The

nucellus increases rapidly on account of anticlines and periclinal divisions in the parietal cell and later in the nucellar epidermis, ultimately resulting in the formation of a characteristic beaked nucellar cap. NEUMANN (1935) thinks that the nucellar cap facilitates the passage of the pollen tubes to the embryo sac; this she regards as another important point of resemblance with the *Centrospermales* where a nucellar cap occurs frequently.

Megasporogenesis.

Usually there is a single large hypodermal archesporial cell (Figs. 31, 32); sometimes there are two, both hypodermal or one hypodermal and the other beneath it (Figs. 33, 34). The archesporial cell or cells by periclinal division form a small outer primary parietal cell and a large inner megaspore mother cell which becomes deep-seated on account of divisions in the parietal cell and the nucellar epidermis (Figs. 35—38). The megaspore mother cell elongates and its nucleus moves to a central position (Figs. 39—41). The bivalent chromosomes then arrange themselves on the equator (Fig. 42) and a wall is formed at the conclusion of the first meiotic division, resulting in the formation of two dyad cells (Fig. 43). At the conclusion of the second meiotic division a linear tetrad of four megaspores is produced (Figs. 45—47). In many cases the upper dyad cell fails to divide and a row of three cells is produced (Fig. 44). The walls separating the two lower from the two upper megaspores or the undivided micropylar dyad cell is markedly oblique (Figs. 44, 49) in most cases. In *Rhipsalis* (MAURITZON 1934) the second meiotic division in the micropylar dyad cell was never completed. Usually the chalazal megaspore functions (Fig. 49), but occasionally the micropylar megaspore may also enlarge simultaneously with the chalazal one (Fig. 45).

Figs. 31—48. Megasporogenesis. — 31, 32: Single hypodermal archesporial cell. — 33, 34: two archesporial cells. — 35, 36: Megaspore mother cell associated with two parietal cells. — 37, 38: Two megaspore mother cells, each with a parietal cell. — 39—41: Megaspore mother cells. — 42: Megaspore mother cell showing the first reduction division. — 43: Two dyad cells, upper one degenerating. — 44: A row of three cells, the uppermost is a dyad cell the two lower megaspores; note the oblique transverse walls. — Fig. 45: A linear tetrad of four megaspores, the micropylar and chalazal have enlarged. — 46, 47: A completely mature ovule showing a linear tetrad of megaspores. — 48: Two dyad cells, upper probably converted into a bisporic binucleate embryo sac.



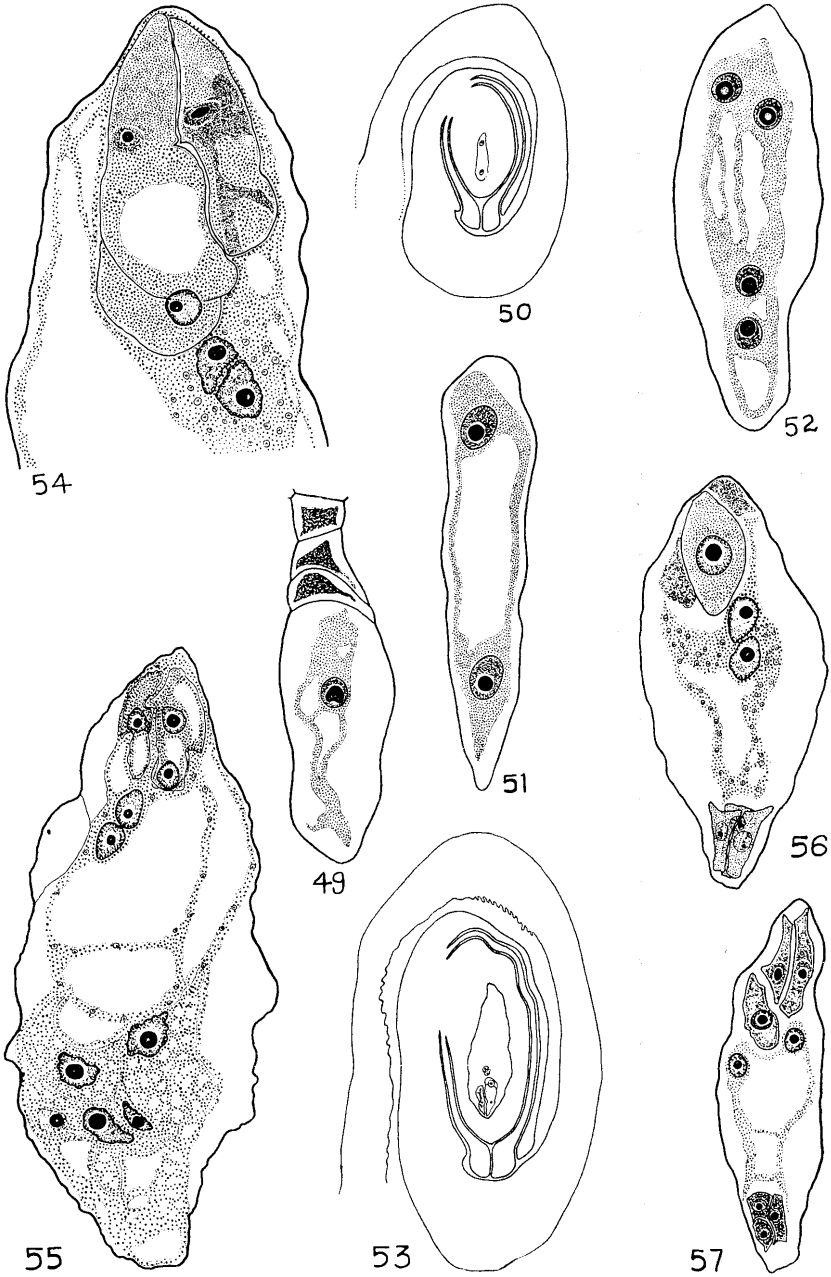
Figs. 31—48.

Embryo Sac.

The bi-, tetra- and octonucleate stages (Figs. 50—52) are rapidly passed. Mature embryo sac conforms to the '*Polygonum*' type of development. The prominently hooked synergids (cf. DAHLGREN 1938) are pyriform in shape and show a large prominent basal vacuole (Figs. 54, 55). The two prominent polar nuclei seem to fuse sufficiently late in the development of the embryo sac. As in other plants of the family (DAHLGREN 1939) they are surrounded by starch grains (Fig. 56) which may increase in amount. The antipodal cells are generally ephemeral and vary in shape and arrangement (Figs. 55—57). In one case the antipodal cells were prominent and two of them became binucleate (Fig. 55). Perfectly healthy embryo sacs contain little starch but embryo sacs showing signs of degeneration accumulate an abundance of starch grains, obscuring its structure.

In one case indications of bisporic development were also seen. Here after the conclusion of the first meiotic division, the nucleus of the micropylar dyad cell had divided giving rise to a prominent bisporic E.S. while the lower dyad cell was still undivided (Fig. 48). ARCHIBALD (1939) reported a bisporic embryo sac of the *Allium* type for *Opuntia aurantiaca*. Strong doubts regarding ARCHIBALD's work were expressed by MAHESHWARI (1950): "Her figures are not convincing and it seems probable that the development is really of the *Polygonum* type as in the other Cactaceae". MAHESHWARI (1941) had also questioned the reported occurrence of a bisporic embryo sac of the *Allium* type in *Cuscuta reflexa* (JOHRI and NAND 1934) simply because development of the embryo sac in other species of *Cuscuta* conforms to the monosporic '*Polygonum*' type. In a reinvestigation of this species (JOHRI and TIAGI 1952), TIAGI prepared and examined several thousand slides at Ajmer and it was shown conclusively, to the entire satisfaction of Prof. MAHESHWARI, that the development of the embryo sac follows the '*Allium*' type as was reported earlier. In the Angiosperms there is an evident tendency for megasporogenesis and megegametogenesis to overlap. It is in this way that the various types of bisporic and tetrasporic

Figs. 49—57. Embryo sac. — 49: Embryo sac mother cell, capped by three degenerating megaspores. — 50, 51: Binucleate embryo sac. — 52: Tetranucleate embryo sac. — 53, 54: Mature embryo sac, without antipodals which have degenerated; the vacuolate synergid has overgrown the other synergid. — 55: Mature embryo sac, antipodal cells conspicuous, two of them binucleate. — 56: Mature embryo sac, synergids degenerated. — 57: Octonucleate embryo sac, the egg apparatus and the antipodals degenerating.



Figs. 49—57.

embryo sacs are presumed to have evolved from the monosporic type (SCHNARF 1936). A few more cases may be cited from the literature where development of the embryo sac follows different types in the same genus, sometimes even in the same species. *Scilla indica* and *S. hyacinthina* are monosporic (GOVINDAPPA and SHERIFF 1951, SULBHA 1954) while all other species investigated so far (HOARE 1934) conform to the 'Allium' type. *Zizyphus jujuba* is monosporic (SRINIVASACHAR 1940) and is also reported to be bisporic (KAJALE 1944); *Zizyphus oenoplia* is monosporic (SRINIVASACHAR 1940); *Zizyphus rotundifolia* is bisporic (ARORA 1953). Many more instances of a similar nature may be added to this list.

Frequently the embryo sac disorganizes (Fig. 57), the general sequence although not always constant being, egg, antipodals, synergids and lastly the secondary nucleus. The lacuna thus formed in the nucellus usually enlarges. In most of these cases the integuments and perisperm develop normally resulting ordinarily in non-embryonate seeds. Due to adventive embryony from nucellar cells some embryonate seeds are also formed. This behaviour is more usual for the *Opuntia* specimens under cultivation. It is suspected that in the case of *Opuntia Dillenii*, plants raised from seeds develop embryonate seeds while plants propagated by vegetative means may ultimately lose the capacity of producing embryonate seeds. Occasionally the embryo sac fails to develop; this occurs after the formation of the megaspore mother cell. Completely mature ovules in which the development of the embryo sac had been arrested at the tetrad stage were present in my material (Figs. 46, 47).

The embryogeny and endosperm of *Opuntia Dillenii* will be dealt with separately.

Summary.

1. There is a single row of microspore mother cells in each of the four loculi of the anther. Divisions of the tapetal nuclei are typically mitotic.
2. The mature pollen grain is three-celled. A double pollen grain is reported. The exine is coarsely reticulate, shows about a dozen germ pores.
3. The mature ovule is of the "Circinotropous" type, crassinucellate, with a beaked nucellar cap, bitegmic, micropyle formed by the inner integument. The third "integument" is formed by the funicle.
4. The single, sometimes two hypodermal archesporial cells cut off primary parietal cells which by their divisions along with divisions in the nucellar epidermis form a nucellar cap and add to the nucellus.
5. The four megaspores show a linear arrangement; sometimes there are three, the uppermost being an undivided dyad cell.
6. The mature embryo sac has the usual eight-nucleate appearance.

Acknowledgments.

The author wishes to express his deep appreciation to all those who have assisted him in making this study. He is especially grateful to the following persons:

Prof. B. TIAGI and Prof. V. PURI for their guidance and inspiration.

Prof. S. SINHA and Principal V. V. JOHN for their facilities and encouragement.

Prof. K. V. O. DAHLGREN for his assistance in preparing the manuscript for publication.

The Director of the Institute of Systematic Botany, Uppsala, for the loan of some literature.

Prof. P. MAHESHWARI for the translation of some of the German literature and his encouragement when the author was in Delhi.

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True or Apparent Sub-chromatid Breakage and the Induction of Labile States in Cytological Chromosome Loci.

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Many of the phenomena of chromosome breakage that result from treatments of the most various kinds occur in essentially the same manner irrespective of what special kind of treatment that was used. A thorough knowledge of the characteristic ways of reaction of the chromosomes will consequently be a necessary basis for a detailed analysis of the action of any individual chromosome-breaking agency.

One type of effect which has been produced by many different kinds of treatment is the so-called "sub-chromatid" breakage. It was reported from treatments with ultra-violet light and with x-rays by SWANSON (1947) working on pollen-tube mitosis of *Tradescantia*. Recent studies using x-rays are those of LA COUR and RUTISHAUSER (1953) on endosperm of *Scilla sibirica*, and CROUSE (1954) on meiosis in *Lilium*. The effect, which these authors interpret as the consequence of half-chromatid or sub-chromatid interchanges, has also been reported by various investigators using treatments with chromosome breaking chemicals (DARLINGTON and KOLLER 1947, LEVAN and TJIO 1948, ÖSTERGREN 1948, D'AMATO 1950 a and b, 1952 a and b, AVANZI 1950, KIHLMAN 1952 a). It is not necessary to review here all the various interpretations presented in connection with these observations.

These possible sub-chromatid interchange figures were called "pseudo-chiasmata" by LEVAN and TJIO (1948), a term which unfortunately had earlier been used by various authors for another effect, *viz.* for chromatid interchanges of the ordinary type. In the absence of a better term we are still going to use it here (in the sense of LEVAN and TJIO).

Two different phenomena are characteristic of this effect which, at least superficially, looks like sub-chromatid breakage:

(A) The occurrence of *constrictions* in the chromatids, induced by the treatment. These are the so-called "erosions" of LEVAN and TJIO. We suggest that they may be called *break-constrictions*. The region distal to such a constriction is an "*attached fragment*". These constrictions have been interpreted as sub-chromatid or half-chromatid breaks by various authors (SWANSON 1947, D'AMATO 1952 b, MARQUARDT 1950), *i.e.* due to a breakage of some but not all the strands of a chromonema which is conceived as a multi-strand or, at least, as a double-strand structure.

(B) The second effect consists in the phenomenon that the anaphase chromosomes remain attached to one another in strictly localized points; thus a phenomenon quite distinct from a general stickiness of the whole chromosome body. These points of attachment are the pseudochiasmata of LEVAN and TJIO (1948). The effect looks very much like what would be expected in the case of a sub-chromatid (or half-chromatid) interchange and it has sometimes been interpreted so, as already mentioned above. In favourable cases this effect may be recognized also in metaphase-type chromosomes.

It is a characteristic feature of these two effects that they are produced by x-ray treatment of prophase (and perhaps also metaphase) chromosomes (SWANSON 1947, LA COUR and RUTISHAUSER 1953, CROUSE 1954). Thus it would appear that these effects result from breakage of the chromosomes when they are in the contracted and spiralized state. The effect is different from that obtained in the resting nucleus, where "full breaks" of the ordinary type are obtained. Thus, if the effects were due to sub-chromatid breakage, then it appears to be an important feature of the chromosomes to respond towards x-ray treatment in this way only during a special period of the cell cycle.

Another interpretation of these effects was suggested by the present writers at the Genetics Congress, 1953, in Bellagio. This interpretation will be described and discussed a little more in detail in the present paper. According to our theory these effects are due to the induction of ordinary "full" breaks in chromosomes that are spiralized and covered with matrix. The matrix prevents the pieces resulting from the breakage to separate from one another. If the breaks induced in a chromonema under these circumstances are able to rejoin in new combinations, the expected result will be in complete agreement with the observed so-called "sub-chromatid interchanges" or pseudochiasmata.

In these interchange figures four chromatid segments will be united. They are connected in the directions of the old combinations by that part of the matrix which had been formed before the chromosomes were broken, and they are connected in the directions of the new combinations by the rejoined chromonemata which are covered by that part of the matrix which was formed after the reunion had taken place.

The induced constrictions are supposed by us to be due to simple breaks (of ordinary "full" type) where the pieces remain connected by the matrix. It is supposed that the continued development of the matrix is inhibited at the break, with the consequence that there results a constriction. In accordance with this idea one will expect that the break-constrictions will have a different appearance at metaphase depending upon what stage has been treated. The earlier that the break occurs during prophase, the higher will be the degree of constriction at metaphase and a treatment of the very earliest stages of matrix formation will give rise to various transition stages between attached and free fragments. These expectations are in good agreement with what we have found in x-ray experiments with root tip mitoses of *Allium Cepa*, a result which strongly supports our theory.

An advantage of our theory is that it easily explains *why* breakage during the division stages gives another result than breakage during the resting stage. The reason is simply the presence of the matrix which keeps the fragments together. If we assume sub-chromatid breakage we have to face the difficulty of explaining why x-rays produce this type of change only during the division stages and not in the resting nuclei. On the basis of our interpretation, on the other hand, it is possible to assume that the chromonemata react in principle in the same way, by "full breaks", during all stages of the nuclear cycle, which appears to be a simple and natural assumption.

Our interpretation is also in good agreement with the observations of SPARROW (1944, 1948, 1951), SPARROW and MALDAWER (1950), SPARROW, MOSES and STEELE (1952), and HAQUE (1953), who found that the spiralized stages of the chromosome cycle are much more sensitive to x-ray treatment than the resting nucleus; the induced breaks, however, are not to be seen in the treated mitoses, only in the next division are the results of the fragmentation directly visible as full breaks. This is easy to understand if the fragments remain connected by the matrix when induced during mitosis, as suggested here. DARLINGTON and LA COUR (1953) have also realized that it might be the matrix (or "nucleic acid charge") which holds the parts together at

meta- and anaphase (*l.c.*, p. 54). With regard to the type of breakage found at the next division in such cases, see further below.

The envelope or "matrix" of the mitotic chromosomes may consist of layers of rather different constitution. Thus, there is probably often a rather fluid surface layer. Changes in this layer may be the cause of such an effect as chromosome stickiness. Obviously, however, this material cannot be responsible for the effects considered here. The appearance of the chromosomes when subjected to mechanical deformation by the mitotic forces (bivalents of first metaphase; dicentric bridges) suggests, however, that the main carrier of the mechanical properties of the meta- and anaphase chromosomes is not something like a spiral spring (chromonema) but rather like a continuous body having properties more or less intermediate between India rubber and chewing gum. This material would be a kind of "matrix" of another nature than the rather fluid surface layer. It is this very tough material which we assume to be responsible for the present effects.

Experimental work bearing on the present question has been carried out by us with coumarin.¹ When onion root tips are treated with coumarin practically no breakage of the chromosomes occurs in the resting nuclei. The treatment has, however, a very effective chromosome-breaking action during mitosis (ÖSTERGREN and WAKONIG, *Proceed. 9th Internat. Congress of Genetics*, in the press). The result of this breakage becomes fully visible only in the next mitosis (in a similar way as in SPARROW's work on x-irradiation of metaphase chromosomes). The treatment used by us was 1 mM per litre for 12 hrs at 13° C or, in some cases, at room temperature. Some experiments were made with coumarin alone and some with colchicine applied simultaneously with and after the coumarin. By the use of colchicine it is possible to distinguish the cells which divide during the coumarin treatment from those that remain in the resting condition; the former become tetraploid while the latter remain diploid.

In the mitoses passing under direct influence of the coumarin treatment (the X₁ mitoses) the effect consists practically only of pseudo-chiasmata and induced constrictions (attached fragments). "Full" chromatid breaks occur only rarely. These X₁ mitoses are found during the period of treatment and shortly afterwards (*e.g.* 12 hrs. after treatment at 13° C in combined experiments with colchicine). These facts

¹ The chromosome breaking activity of coumarin was discovered by ÖSTERGREN (1948).

suggest that the treatment breaks the chromosomes during a period of the mitotic cycle when the chromosomes have a matrix. Possibly the sensitive period begins just before the start of the matrix formation, an idea which might explain the few "full" breaks occurring besides the many changes of "partial" type. Now, *if* these changes had been real half-chromatid or sub-chromatid ones, *then* they would have appeared at the next (tetraploid) mitosis as chromatid (or sometimes even sub-chromatid) changes. The tetraploid mitoses (the X_2 mitoses) show, however, a high frequency of chromosome-type changes (*i.e.* changes affecting both chromatids), a fact supporting the idea that the changes in the previous division were of chromatid type, as assumed in our interpretation of the nature of these pseudochiasmata and induced constrictions.

The influenced tetraploid cells show an average of something like 40 breaks per cell. (Many of the fragments are of the "minute" type. As these probably are interstitial deletions they were counted as two breaks.) In a sample of 37 cells containing more than a hundred recognizable chromosome-type interchanges (dicentrics and polycentrics) there was found a single quadriradial (possible chromatid interchange) and 4 triradials. An important feature of the quadriradial and at least three of the triradials was the occurrence of constrictions in some of the chromatids at the loci of breakage and reunion or their sister loci. This suggests that these figures might derive from delayed breakage (in the X_2 prophase) of labile loci induced at the treatment (*cf.* below).

The quadriradial and the 4 triradials were found in 5 different cells, one of these changes in each cell. Besides these changes the cells in question also contained numerous other changes which all were of chromosome type. The quadriradial might possibly be derived from a pseudochiasma of the previous division, if the half-chromatid interchange idea were valid, but the triradials are not easily explained on such an interpretation. We cannot expect a half-chromatid-interchange pseudochiasma of the X_1 cell to appear as a triradial in the X_2 division. In order to explain our triradials we have to assume that some other mechanism has been working and under these circumstances, this other mechanism is very likely to produce quadriradials also. Consequently the occurrence of the triradials may give more evidence against than in favour of the half-chromatid-interchange interpretation of the pseudochiasmata. (An explanation of the origin of the quadri- and triradials is given below.)

Thus, the quadriradials expected from the pseudochiasmata of the previous division on the basis of the sub-chromatid interchange idea were on the whole absent; the single observed case has a dubious character because of the constrictions present in it. Unfortunately the evidence may not be considered as quite conclusive, however, as it may be suggested that the strongly influenced cells showing pseudochiasmata in the X_1 mitoses did not survive to give a tetraploid X_2 division. The X_2 mitoses studied may derive from X_1 cells showing no or only very few pseudochiasmata and the changes of chromosome type seen in the tetraploid cells might derive from fragmentation at a stage other than that first supposed (*e.g.* at telophase of the X_1 mitoses). On the other hand, it seems very probable, however, that the strongly fragmented X_2 cells derive directly from the strongly influenced X_1 cells, and that we are studying the same fragmentation effect at two different developmental stages.

An interesting feature of the formation of the pseudochiasmata in the X_1 cells is that, in some types of treatment at least, they are more often formed between non-sister chromatids than between sister chromatids. This fact gives strong evidence against the idea that the pseudochiasmata might be simply a consequence of some kind of stickiness.¹ The result is in agreement with the idea that they result from breakage, however, in so far as breaks distributed at random should only rarely occur in about the same position in both the two sister chromatids. In the X_1 mitoses it is also found that the induced constrictions usually occur in one only of the two sister chromatids at each influenced locus. It is difficult to judge if pairs of constrictions occur more often than expected from randomness, if so, this effect might suggest a non-random distribution of breaks, some loci being especially sensitive. Pairs of constrictions might theoretically be due also to negative heteropycnosis of heterochromatic regions. Negative heteropycnosis can, in any case, not be a general explanation of the constrictions, as most of them occur in one chromatid only.

In the tetraploid X_2 cells many induced constrictions are found to occur besides the ordinary breaks. In these cells, however, the constrictions usually occur in pairs, *i.e.* simultaneously in both the two sister loci of each influenced chromosome. A similar picture is repeated in

¹ Naturally, this does not exclude the possibility that there could *also* exist some pseudochiasma-like figures resulting from simple stickiness in this as well as in other experiments. It is quite possible that the pseudochiasmata may have a heterogenous origin, and that stickiness may be the cause of some cases.

the octoploid (X_3) cells, although here the constrictions may not so often occur in pairs (a possible difference between tetraploid and octoploid cells in this respect should be subjected to further study in order to ascertain it). Negative heteropycnosis or "nucleic acid starvation" is not likely to be the complete explanation of these paired constrictions, because in an octoploid cell studied we found only 2 out of 8 homologous satellite chromosomes showing paired constrictions of this induced kind. All the 8 homologous heterochromatic regions should have been starved, as they were under the same physiological conditions (in the same cell). If the plant were heterozygous with respect to this hypothetical heterochromatin, there should in any case be 4 satellite chromosomes showing the same effect.¹ Furthermore, there are all intermediates between paired attached fragments and paired free fragments, a fact suggesting that these paired constrictions are a fragmentation effect.

Now, we have seen in the x-ray experiments that the constrictions originate from irradiation of late stages of the nuclear cycle, *i.e.* stages which soon pass into metaphase (presumably these stages belong to the prophase). Then it seems reasonable to suppose that the paired constrictions found in the X_2 cells of the coumarin experiment might also represent cases in which the chromosome breakage has occurred during the prophase of the studied mitosis. Our interpretation is as follows: During the treatment some loci in the treated X_1 cells may change or "mutate" to a labile state. In the following resting stage each of these may reproduce to give two labile sister loci, one in each chromatid. These may remain relatively stable during the resting stage, but the prophase (and probably the other mitotic stages) represents a critical period during which breaks easily arise in these labile loci. When breakage occurs during the X_2 prophase in such a pair of labile loci the result will be a pair of induced constrictions in the following metaphase. The critical period of the division cycle in the X_2 cells may correspond to the coumarin-sensitive period in the X_1 cells. It may begin just before the onset of the matrix formation and thus also explain the occurrence of a few "full" breaks of ordinary kind. A delayed breakage of this kind may explain the origin of the single quadriradial and the four triradials found. The constrictions observed at the interchange points in these are presumed to be due to prophase

¹ It would be valuable to collect more evidence of this kind, but it is not so easy to get it, as the chromosome complement of the onion contains one chromosome pair only, which is easy to recognize: the main satellite chromosome pair.

breakage of a sister locus to the locus that a little earlier went through "ordinary" chromatid breakage.

Pairs of constrictions occurring at X_2 might, however, also be suggested to be due to another mechanism, *viz.* a more or less identical reproduction of a chromosome showing a sub-chromatid break. In this way we would get two chromatids each showing a partial break of the same kind as the mother chromosome. This interpretation was suggested by D'AMATO in the discussion at the Eighth International Congress of Botany, Paris 1954. We have no definite evidence bearing on this question but we have, for the time being, adopted the labile-locus idea as our working hypothesis feeling that it may be more probable. In any case we are still considering the other idea as an alternative possibility. It is naturally even possible that both these effects may occur in the same material.

It should be mentioned that the tetraploid cells also contain many cases where the induced constriction is found in one only of the two sister chromatids. The majority of these constrictions occur in a paired condition, however. On the basis of the labile-locus idea the single constrictions would represent cases where only one of the two sister loci has broken. The unbroken one may survive for some time and break at a later mitosis. Perhaps some "healing" or back-mutation to stability might also occur and perhaps be involved in some of these cases. The induced constrictions seen in the octoploid mitoses might be due to labile loci that have been able to survive the tetraploid division.

A changed chromatid in an X_1 cell will naturally appear as a changed chromosome (two changed sister chromatids) in the tetraploid X_2 cell generation. In the next mitosis (the octoploid X_3 generation) the same change will be represented by a pair of sister chromosomes of identical appearance. This is also the rule in the X_3 cells. These octoploid cells are very difficult to analyze, but still our observations are sufficient to demonstrate that besides these changed chromosomes occurring in pairs there are also many changed chromosomes that are represented by a single specimen only in each cell. The shape of these exceptional chromosomes suggests an origin from sister reunion in the tetraploid cells. Perhaps they may, some of them at least, originate from the paired constrictions of the tetraploid cells, these being breaks which become more reactive for reunion in the X_2 telophase, when the matrix has disappeared. In the tetraploid cells there are, however, also some cases of sister reunion of ordinary type. These may result from reunion following pre-prophase breakage of labile sister loci, that is a kind of

“iso-chromatid” breakage, or they may possibly be due to a delayed reunion of chromosome-type breaks (reproduction followed by reunion).

Besides numerous normal diploid cells a very low number of diploid cells showing changes was observed in the recovery phase of these experiments. The frequency of changes in these cells deviated strongly from randomness (Poisson series), each influenced cell usually showing many changes. For this reason it is supposed that these cells had been in a sensitive period when treated. Our interpretation is that they were in prophase when treated, but instead of completing their division, they reverted to resting nuclei, a phenomenon not very unusual at various toxic treatments of mitosis (*e.g.* D'AMATO 1950 c). We suppose that during the recovery phase of the experiment they may start mitosis again, still remaining diploid cells. As expected from this idea all these cells showed changes of chromatid type. Besides chromatid-type changes they also showed induced constrictions, usually only in one of the sister loci. These constrictions may represent delayed breaks corresponding to the paired constrictions in the tetraploid cells. Then, these cells would be a kind of “demasked” X_1 cells, the matrix has been broken down and later been formed anew. It is interesting to notice the presence of “full” chromatid interchanges in these cells, as expected from our interpretation of the nature of the pseudochiasmata. Our idea was that the pseudochiasmata were full chromatid interchanges that were masked by the presence of matrix.

Inspired by KIHLMAN's results (1951, 1952 a and b) we also made a similar experiment with caffeine. In our study we used 10 mM per litre for 12 hrs. Colchicine was applied two hours before the caffeine in order to start the c-mitosis, during the caffeine treatment, and afterwards. The experiment was performed at 13° C. The result was fairly similar to that of the coumarin experiments. In this case, however, the frequency of changed diploid cells found during the recovery phase was much higher. In this case, too, the relatively few changed diploid cells showed many changes each. They presumably represent reverted prophases that have entered mitosis again (demasked X_1 cells). The tetraploid cells resemble those of the coumarin experiments. They show besides ordinary chromosome changes very many attached fragments present in a paired condition. Chromatid interchanges were more common in these tetraploid cells than in the tetraploid coumarin cells. Perhaps they are due to delayed breakage as suggested above.

Our observations are in agreement with KIHLMAN's conclusion that caffeine breaks the chromosomes only during mitosis. The occurrence

of diploid cells with changes (presumably reverted prophase) demonstrates, however, that caffeine is capable of penetrating into the nucleus even though the nuclear membrane is present. It is quite possible that the limitation of the caffeine action to the mitotic stages may be a matter of differences in sensitivity of different stages, rather than a matter of penetration power as suggested by KIHLMAN. His interpretation was that the purine derivatives which were found to induce chromosome breakage in the resting nuclei could do so because they were able to penetrate into the resting nuclei through a lipid layer surrounding these, while the other purine derivatives which induced fragmentation only during mitosis were unable to penetrate through this lipid layer. These ideas are supported by his observations on the solubility properties of the purines in question; the partition coefficient lipid/water being much higher for the substances inducing breakage in the resting nucleus. It is, however, a characteristic feature of his data that the substances which combine the two properties: (1) ability to cause breakage in the resting nucleus, and (2) high relative lipid solubility, also have a third property in common, *viz.* a special chemical structure (they are, all of them, alkyl ethers or thioethers at carbon atom nr. 8). It is quite possible that the two mentioned properties may both be conditioned by this characteristic structure, instead of the one being caused by the other. It is interesting to notice that coumarin which has a much higher solubility in solvents of lipid type than in water¹ still acts according to the same scheme as the TMU-type of KIHLMAN, thus in disagreement with his interpretations. KIHLMAN could observe the presence of lipoids around the nuclei by means of staining with Sudan black. But, of course, there could be an accumulation of lipoids

¹ A rough test that we have made demonstrated that the solubility of coumarin in ethyl ether is somewhat more than ten per cent; its solubility in water, on the other hand, is, according to HODGMAN's Handbook of Chemistry and Physics, 0.01 per cent. Our personal impression is that the water solubility of coumarin is somewhat higher than that, but in any case the partition coefficient ether/water will have a value of several hundred. — Another substance of interest in the present connection is maleic hydrazide. According to MCLEISH, this substance influences the chromosomes in the resting nuclei (1953, p. 143). We have not seen much about its solubility properties, but the statement in the Merck Index (6th ed.) that it is slightly soluble in hot alcohol and more soluble in hot water does raise the suspicion that its partition between lipid and water will be largely in the direction of the water phase. It is quite possible that here we may have an exception to KIHLMAN's rule of the opposite kind, *viz.* a substance of low relative lipid solubility causing breakage inside the resting nucleus.

there even without their influencing the permeability; they might form a porous envelope.

The critical remarks presented here naturally do not disprove KILMAN's permeability theory. This interpretation might still be valid, if we make the assumptions that: (1) caffeine penetrates into the prophase nuclei because the lipoid envelope may be dissolved at an earlier stage than the ordinary nuclear membrane, and (2) it is possible that coumarin itself may not be acting directly on the chromosomes, but in the cytoplasm it is transformed into or induces the formation of another substance of chromosome-breaking activity, which is unable to penetrate through the lipoid envelope of the nucleus. Assumptions of this kind are certainly not improbable at all, but it must remain for further work to test if they also apply to the actual situation.

The fact that in certain treatments the effect is restricted to the division stages was given an alternative interpretation here, *viz.* that the different stages vary very strongly in their sensitivity to the treatments. Such a variation in sensitivity is known from x-ray experiments (*e.g.* SPARROW 1944, 1948, 1951, HAQUE 1953). These experiments demonstrate that the division stages are much more sensitive to x-rays than the resting stage. If effects of this kind shall be able to explain the differences between different substances it will naturally be necessary to assume that the different substances do not act in the same way on the various mitotic stages; the increase in sensitivity of the mitotic stages relative to the resting stage is much higher in some substances than in others. This is not an improbable assumption; we know already that there are differences in the mode of action between different substances and other treatments, thus KÖLMARK (1953) reports that different gene loci respond rather differently towards different mutagenic treatments, one locus may give more mutations with one treatment and another locus more mutations with another treatment. It is also known that different chemicals differ from one another with respect to their chromosome breaking action on specific chromosome regions, some substances give more breaks in one region and others give more in other regions. (LEVAN 1952, MCLEISH 1953).

The nature of the changes in the chromosomes which make them much more sensitive towards x-rays during the mitotic stages are unknown. It seems a reasonable working hypothesis, however, to assume that these same chromosome physiological changes also cause the difference in response of the chromosomes towards coumarin treatment which is found between resting nuclei and mitotic chromosomes,

although in this case the effect of the changes is much bigger. Furthermore, our observations of the X_2 cells suggest that there occurs in them a breakage in the prophase of loci that have turned labile during the treatment. We have assumed that these labile loci remain relatively stable during the resting stage but that they break during a sensitive period in the prophase. It seems very probable that this sensitive period is identical with the period of increased x-ray sensitivity and with the period of coumarin sensitivity of the chromosomes. It is probable that this period may extend all through the contraction stages of the chromosome cycle (from prophase until telophase). A breakage of labile loci occurring in fully contracted chromosomes would, however, not be recognizable in the same mitotic cycle; only by indirect evidence from the next mitosis might it be possible to test its existence and even then only with great difficulty. (We have at present but little hope that it will ever be possible to test this special question.)

The interpretation presented here involving the idea of a delayed breakage of labile loci induced during the treatment is in good agreement with the observations by AUERBACH (1951, 1952) and AUERBACH and MOSER (1953) that chemical treatments (nitrogen mustard, formaldehyde) often cause a mutation of genes to a labile state. Such labile genes often mutate at later stages to give rise to various stable mutation-types. Our observations may well concern the cytological aspect of the same effect; chromosome breakage and gene mutations being closely related phenomena.

Some of the effects suggested in our interpretations of the coumarin experiments may also occur in the experiments by REVELL (1953) on chromosome breakage in *Vicia Faba* by means of di-(2:3-epoxypropyl) ether. He reports that the cell is sensitive to this substance during early resting stage, but that the real breaks originate only at a later period. He has found a constant ratio of chromatid to chromosome type of breaks, with variable dosages and intensities of treatment. Furthermore, some of his structural changes are of the "partial" type, such as is characteristic of chromosome breakage during the mitotic stages. These observations suggest to us that his treatment may induce a labile state in some chromosome loci during the sensitive period in early resting stage. After that, these labile loci reproduce, each of them giving two daughter loci, when the chromosome is passing over into the post-split condition. Later on follows a critical period in the chromosome cycle, when a great number of these labile loci break. Sometimes both the two sister loci break, simulating a break of chromosome type, and some-

times only one of them breaks to give a chromatid break. The proportion of these two events will, of course, be constant irrespective of the dosage and intensity of the previous treatment. This critical period of breakage probably starts somewhat before the formation of the matrix and continues into the matrix period, a fact which would explain the occurrence of both full and partial breaks. The observations by MCLEISH (1953) on the effect of maleic hydrazide on *Vicia* suggest similar phenomena. He thinks that in this case, too, there may be a sensitive period in early resting stage (*l.c.*, p. 139). He also gets many attached fragments and partial changes in his experiments, a fact suggesting to us that the real breakage often takes place when the matrix formation has already started. An interesting observation made by him is that the "quadriradials and triradials often show a constriction at the same locus of breakage but in the undamaged chromatid" (*l.c.*, p. 142). This is a result in good agreement with our observations and interpretations concerning the triradials and the single quadriradial found by us in the tetraploid X_2 cells of the coumarin experiment.

Chromosome breakage at meiosis should be able to give important evidence concerning the nature of the apparent sub-chromatid interchanges (or pseudochiasmata). Irradiation of first prophase and metaphase should give changes of this kind. When these occur between sister chromatids and are located between the first and the second chiasma (or between the third and the fourth *etc.*) they should be visible as bridges of the characteristic "pseudochiasma" type at first anaphase. When such sister-chromatid effects are located proximally of the first chiasma or between the second and the third (or the fourth and the fifth), then they will connect chromosome regions that are due to separate only at the second division. If they were true half-chromatid interchanges, then we should find them again as "pseudochiasmata" in the second anaphase. If a half-chromatid interchange occurred between non-homologous chromatids that both became included in the same tetrad nucleus (an event that sometimes should take place), then we should find it again in the first pollen mitosis as a chromatid interchange. But if the pseudochiasmata were due to full-chromatid interchanges that are masked by the presence of the matrix, as assumed in our working hypothesis, then they should be found as full-chromatid changes in the second division and as chromosome-type changes in the first pollen mitosis.

Now, CROUSE (1954) is of the opinion that she has found "half-chromatid" interchanges at the second anaphase in *Lilium* after

x-irradiation of first metaphase. Her fixation was made 8 hrs after irradiation. We believe it possible that her timing of the stages was faulty and that, in reality, she may have irradiated second prophase. According to CROUSE, cells irradiated at first metaphase may be found in first anaphase two hours later. If we subtract these 2 hrs from her 8 hrs, there will be 6 hrs left for T_I , interkinesis, P_{II} , M_{II} and part of A_{II} , which seems too short a time, as telophases and especially prophases are usually much slower than meta- and anaphases, judging from their relative frequency in root tips. The synchronization of stages between different anthers is often somewhat incomplete, and the timing of stages in such an experiment as the present one by means of this phenomenon is rather difficult. It is of interest to notice that REES (1953) found pseudochiasmata in root tip anaphases of *Scilla campanulata* in the period from 2 to 8 hrs after the irradiation. Obviously the cells have, in this case, been in a stage 8 hrs before fixation which responds with pseudochiasmata and which belongs to the same mitotic cycle as the observed anaphases. It seems reasonable to assume that these cells were irradiated in the prophase of the same mitosis as was later fixed in anaphase.

HAQUE (1953), on the other hand, carried out an experiment on *Tradescantia* in which he x-irradiated diakinesis and studied second anaphase. He got a great deal of chromatid-type changes and "a number of cells" (no indication of the frequency is given) showing pseudochiasmata; some attached fragments were also seen. The fixation was made 24—30 hours after irradiation, so the cells are not likely to have been in second prophase. More information concerning various details of the results would be needed in order to judge if these second division changes of "partial" type might be due to a real survival of half-chromatid changes from the first division or if they might result from a delayed breakage of loci that had turned labile as a consequence of the treatment.

Also, the possibility is not excluded that some pseudochiasma-like figures might arise from stickiness in cells physiologically disturbed by the genotypical changes caused by the radiation. (Physiological changes resulting directly from the irradiation may also be considered, but seem less likely, as the x-ray dosage used was very low, 18 r, and a relatively long time had passed before the fixation.)

Furthermore, HAQUE studied the first pollen mitosis after x-irradiation of various earlier stages. He found that irradiations given at about the time of the meiotic divisions produced a great quantity of breaks

of chromosome type; no breaks of chromatid type are reported. Some control of the interpretation that the cells irradiated were in the meiotic division stages is given by the fact that they show a strongly increased sensitivity towards the treatment. SPARROW has demonstrated that such an increased sensitivity towards breakage is characteristic of the chromosomes, when they are in the division stages.

As the general conclusion of our own observations, as well as of the other results discussed here, we think it may be stated that there is some evidence supporting the view that some effects appearing like sub-chromatid breakage may instead be due to ordinary chromatid breakage which is masked by the presence of a matrix. Such chromosome changes may either originate *directly*, when the chromosome-breaking treatment is applied to a stage when the chromosomes have a matrix, or *indirectly* if the treatment is capable of changing certain loci in the chromosomes to a labile state, which makes them liable to become broken, later on, at a stage when the chromosomes have a matrix.

We do not consider the evidence on this question to be conclusive, as yet. Sub-chromatid breakage can also, with a higher or lower probability, be suggested to account for such observations as those discussed here. Naturally, many of the various interpretations suggested here do not mutually exclude one another. Thus, the "pseudochiasmata" might, as far as we know, be due both to masked full-chromatid interchanges and to sub-chromatid interchanges, which might even occur in the same cell.

The fact that we are favouring an interpretation which does not assume half-chromatid structural changes does not mean that we are doubting the existence of a subdivision of the chromatids in half chromatids. Such a subdivision has been reported by many authors and we feel that it is very probable. Our interpretation simply means that we are assuming that the two halves of a chromatid or of an early resting-stage chromosome actually form a functional unit with respect to chromosome breakage and reunion. This would explain why x-radiation of early resting stage usually gives the chromosome type of change. We suppose that there may be a biological adaptation for this kind of chromosome to function as a single unit of breakage. There is one stage in the life cycle when breakage is a normal event, *i.e.* at the crossing-over in the meiotic prophase. When the chromatids break and rejoin in the crossing-over process, each chromatid acts as a single unit; it may be adapted to do so because sub-chromatid crossing-over

would prevent the first meiotic anaphase disjunction of the paired chromosomes. It is quite possible that the same biological adaptation may be involved, when the two half-chromatids or the two halves of an early resting stage chromosome are functioning as unit of breakage together.

Breakage may be considered as a normal way of reaction of the chromosomes, a type of behaviour which they are adapted to show as a normal phenomenon during the meiotic prophase. You have just to pull the right "switch" in order to make them do so at other stages of the life cycle, too. When the appropriate kind of "stimulus" is applied to a chromosome region, it responds by putting the meiotic breakage mechanism into work, and this mechanism gives as the result a breakage all across the chromatid: all its sub-units are broken. During the meiotic prophase this mechanism extends its action even beyond an individual chromatid: another chromatid intimately paired with the first one is also broken all across its width at the same locus where the first chromatid was broken. This isolocus breakage of two paired chromatids makes it possible for the crossing-over to take place.

This interpretation involves the idea that the breakage follows upon the transmission of a kind of impulse across the chromatid and that this breakage impulse may even be transmitted over to another chromatid intimately paired with the first one. The production of isochromatid breaks by x-radiation of mitotic chromosomes is usually considered to be due to the fact that the ionization track (of the electron liberated at the absorption of the x-ray quantum) is so broad that it is sometimes capable of hitting the two chromatids of a single chromosome. We do not intend to criticize or to shed doubt on this interpretation, but only to suggest that conceivably an alternative mechanism might work in some cases, *viz.* that a breakage impulse might be transferred from one chromatid to another one in contact with it.

Ideas of this kind would be able to explain how a chemical change due to a chromosome breaking substance may be able to break a chromatid all through. The chemical change at the point of attack may have been very small, perhaps only a bimolecular reaction between a molecular group in the chromatid and a single molecule of the attacking substance. The chromatid is very likely to consist of numerous parallel strands. The primary change in one of them may act as a "stimulus" which starts a mechanism resulting in breakage of all of these parallel sub-units.

Naturally, the meiotic crossing-over process is different in very

important respects from the events of induced chromosome breakage. Thus: (1) the meiotic breaks always rejoin in new combinations (or maybe reconstitute into the old combinations), they never *remain open* as induced breaks sometimes do; and (2) the exchanges at meiosis always give two monocentric chromatids, never a dicentric and an acentric one (except of course in cases of abnormal gene seriation as in inversions). This difference may be due to subsidiary factors present in the meiotic prophase, especially the very close and intimate pairing between homologous regions, factors absent in other cells. Thus, this difference need not be an argument against the idea presented here of a close relationship between crossing-over and induced breakage.

The idea of a close relationship between the induced breakage and the natural breakage of the crossing-over process is not a new one. Such a relationship was earlier suggested by MARQUARDT (1950) and REVELL (1953). Their ideas are, however, in many respects different from the hypotheses presented above.

Acknowledgement. Economic support for the present investigation has been received from the Swedish Natural Science Research Council, a fact which is gratefully acknowledged.

Summary.

In the present paper the nature of what has been considered as sub-chromatid breakage is discussed. The effect consists of two different phenomena: (1) the occurrence of induced constrictions, separating "attached fragments" from the main part of the chromosome, and (2) the occurrence of what looks like sub-chromatid interchanges between two chromatids.

The interpretation is presented that these two effects are in reality due to a full-chromatid breakage which has taken place in a chromatid that is spiralized and covered by matrix. The matrix maintains in continued connection the pieces that were associated before the breakage and the result looks like part-chromatid changes.

The material used in our investigation was *Allium Cepa*. X-ray experiments show that changes of this "sub-chromatid" type are found in cells fixed a short time after the treatment, *i.e.* presumably treated in prophase. Chromosome breakage experiments by means of coumarin support our interpretation. In order to make it more easy to recognize the different cell generations colchicine was also applied in some of the coumarin experiments. Coumarin breaks the chromosomes practically only during mitosis, the resting stage being insensitive to the treatment. In the X_1 cells which are under direct influence of the coumarin a very large majority of the changes are of the "sub-chromatid" type. In the next cell generation (X_2) there are, however, nearly exclusively changes of chromosome type (*i.e.* affecting both the two chromatids). This suggests that the changes in the previous mitosis were in reality of chromatid type, although they were masked by the presence of a matrix.

The occurrence of induced constrictions in pairs in the X_2 cells (*i.e.* affecting both chromatids at the same locus) suggests that the treatment has caused a change to a labile state in some loci during the treated X_1 mitosis. These labile loci have reproduced during the resting stage to give two labile sister loci and these have, both of them, broken during a critical period in the X_2 prophase.

Our evidence is not considered, at present, to prove our interpretations conclusively. It is still possible to suggest the alternative interpretation, from many of our observations, that the effects are due to a real sub-chromatid breakage.

Other results on chromosome breakage are discussed in connection with our ideas and some suggestions are made to explain why the chromatids, although multiple in their composition, may still behave as units in breakage and reunion. These suggestions imply the idea of a close relationship between the induced breakage and the natural process of crossing-over.

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Actinotaenium

genus Desmidiacearum resuscitatum.

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Already the earlier desmidiologists have paid particular attention to the elongate, baculiform desmids: *Closterium* NITZSCH 1817, *Cylindrocystis* MENEGHINI 1838, *Penium*, *Docidium* and *Spirotaenia* BRÉBISSON 1844, *Tetmemorus* RALFS 1844, *Mesotaenium*, *Pleurotaenium* and *Netrium* NÄGELI 1849 and *Triploceras* BAILEY 1851. Later discoveries are *Roya* WEST 1896, *Ichtyocercus* WEST 1897 and *Triplastrum* IYENGAR et RAMANATHAN 1942. In the past century a large number of baculiform species have been distinguished which because of the straight cells and lack of sculpture have generally been assigned to *Penium* and also *Cylindrocystis*.

LÜTKEMÜLLER's epoch-making research (1902) on the structure of the desmid cell wall opened up a new and safe ground for the taxonomy of the baculiform desmids. As to their biosystematy, LÜTKEMÜLLER (1905) made a revision of the species assigned to *Penium*. He approved only twelve species as true *Penia*, the remaining were transferred to *Cylindrocystis*, *Netrium*, *Closterium*, and no fewer than fourteen species to *Dysphinctium*, a genus that he earlier (1902) had included in *Cosmarium*. Later on (1910, p. 479) he rejected *Dysphinctium* and used the name *Cosmarium* for these species. His revision of *Cylindrocystis* (1913) comprised seven true species, and seven doubtful whereas five were excluded and assigned to *Cosmarium*. This system of classifying has, to a certain degree, been continued by KRIEGER (1937).

Most of the species, excluded from *Penium* and *Cylindrocystis* and included in *Cosmarium*, possess a fusiform shape with rounded apex, a shallow isthmus furrow, no wall sculpture, and a stelloid chloroplast.

Their placoderm nature is evident by the dense pores over all the wall except the isthmus zone.

The present author (1952, p. 292) has united this group under the interimistic name of the *Clevei*-section and emphasized that this group represents a taxonomic unity that must be kept quite separate from the collective name *Cosmarium* as well as from any real diagnosed desmid genus. In the following the author, on the basis of the principles submitted in his papers 1950 and 1952, intends to rise this section to the rank of a new genus: *Actinotaenium*.

Cosmarium and Dysphinctium.

In order to elucidate the taxonomical position of *Actinotaenium* it is necessary to disentangle the concepts *Cosmarium* and *Dysphinctium*.

Cosmarium appears at the first time as a generic name invented by CORDA (1835) and used on some species, later assigned to *Cosmarium*, *Micrasterias*, and *Euastrum*. Out of this diffuse concept it has developed into a generic name reserved for biradiate desmids without spines, insertions and processes. The biradiate character "inflato-compressed segments" (RALFS 1848, p. 92) is emphasized also by MENEGHINI and EHRENBERG, while RALFS admits that "some species with globular or cylindrical segments can by no means be separated from the compressed ones". When comparing these species with *Penium*, he says: "In *Cosmarium* the fronds are never elongated, are always constricted in the middle, and the starch vesicles are scattered". RALFS' list of species contains 33 species. The WESTS, in Monograph II, p. 126, says: "One of the distinguishing features of a *Cosmarium* is the entire outline of the cells, which are likewise destitute of spines." At present negative characters exceed in the definition of *Cosmarium*.

During the century that has elapsed since RALFS' declaration, *Cosmarium* has been used as a storage-box for species which have not conveniently been placed in more definite genera. By this, the concept of *Cosmarium* has got a very promiscuous content and, actually, to an extent which itself proves the character of a provisory, PRINTZ (1929) rates the number of species at 809! In spite of this hodgepodge, obvious to every desmidiologist, *Cosmarium* seems to be comprehended as a genus *sensu stricto* and the desmidiologists have eagerly been at work in enlarging it with new species instead of finding out new points of view in order to discern the genetic, or at least, the typological lines into which *Cosmarium* must be disintegrated.

Dysphinctium was instituted by NÄGELI in 1849 as a genus with the following subgenera and species:

Actinotaenium: *Dys. Regelianum* (= *curtum*), fusiform, omni-radiate cell and stelloid chloroplast.

Calocylinthus: *Dys. annulatum*, cylindrical with series of small nodules, chloroplast with 1—2 pyrenoids. *Dys. cylindrus* (= *Penium*).

Dysphinctium: *Dys. Meneghinianum* (= *connatum*), pseudo-omni-radiate, chloroplast furcoid, dicentric. *Dys. striolatum* (= *tesselatum*), pseudo-omni-radiate, chloroplast furcoid, limbo-parietal.

NÄGELI¹ gives (p. 109) the following diagnosis: "Zellen einzeln oder getrennt, an den Polen abgerundet, in der mitte einer leichten ringförmigen Furche, Querprofil kreisförmig oder oval, in jeder Hälfte ein centrales oder zwei neben dem Mittelpunkt liegenden Chlorophyllbläschen". And he comments: "Diese Gattung ist eine künstliche, sie vereinigt mehrere Typen, welche aus Mangel an vollständigen Untersuchungen noch nicht als selbständige Gattungen aufgestellt werden können, und hier als Untergattungen folgen".

In spite of this obvious and critical declaration, NÄGELI's genus was taken up by several taxonomists, probably in order to have a genus for the increasing number of species that otherwise could not be placed anywhere but under the diffuse name of *Cosmarium*. This trend has especially been forwarded by DE BARY (1858), REINSCH (1867), DELPONTE (1873), KIRCHNER (1876), HANSGIRG (1888), DE TONI (1889), and TURNER (1896). DE BARY incorporated *Dysphinctium* in *Cosmarium*. Of his four subgenera *Dysphinctium* contains the globoid species, e.g. *moniliforme* and *connatum*, and *Calocylinthus* (including *Actinotaenium*!) embraced baculiform species, e.g. *Cucurbita*, *Palangula*, and *curtum*. REINSCH enlarged *Dysphinctium* with *Tetmemorus* as a subgenus. KIRCHNER raised *Calocylinthus* to a separate genus containing ten species and placed it between *Closterium* and *Docidium* but rejected the rest of *Dysphinctium*. HANSGIRG maintained *Dysphinctium* with the subgenera *Actinotaenium* and *Calocylinthus*, and added a new one: *Tetmemoridium*. This basis of division was accepted by DE TONI who gave *Actinotaenium* 24, *Calocylinthus* 12, and *Tetmemoridium* 3 species. By this the artificial composition of *Dysphinctium* was accentuated in absurdum. TURNER divided *Dysphinctium* into *Cylindrosphinctium* and *Sphaerosphinctium* the character of which is indicated by the names. No further efforts of consolidating the genus were made and in this

¹ It seems very unlikely that NÄGELI was aware of RALFS' book, at least, RALFS' name is not mentioned in NÄGELI's treatment of these desmids.

century it has been quite omitted, its species bear the name of *Cosmarium*. RABENHORST (1865) abandoned it and at recent time also the WESTS who justify their rejection by finding it "based upon indefinite characters and the limitation of which could not be clearly defined" (Monograph II, p. 127). Actually, the latter failing is valid also for a good deal of the desmid genera, especially in regard to *Cosmarium*, and is impossible to avoid: there are only few limits in Nature, limits are made by Man, artificial and conventional.

The taxonomic problem of the former *Dysphinctium* species has not been solved by placing them in *Cosmarium*, it has been put in an out-of-the-way corner. Nevertheless, NÄGELI's idea was a good one, it was wrecked by the contemporaneous lack of taxonomic principles except the one of similar shape in quite general terms. At present, it is possible to distinguish between primary and secondary cylindrical shape of the cell and we know different kinds and degrees of the evolution of the chloroplast. Several characters of potential taxonomic value are not clear, for instance the structure of the zygosporangium and of the surface of the cell wall. There is, at least at present, not found any genetic connection between a smooth and a granulated or verrucate surface. In my opinion, the desmids with these two kinds of surface must be kept separate as regards their taxonomic position. On the contrary, we know that the baculiform shape is attained by desmids of quite different origin and that the convergency phenomenon is rather common.

Certain features of this historical genus *Dysphinctium* are incompatible with the general concept of *Cosmarium*. This implies that they represent diverse lines of evolution, for instance the *Actinotaenium* type, the *connatum* type, the *tesselatum* type, the *Debaryi* type etc. In order to show the generic position of *Actinotaenium* I shall develop my comprehension of the taxonomic differences between it and the other placoderm desmids. According to CAMP (1951) the term *taxonomy* is used in the sense of distinguishing genera and higher taxa, the *bio-systematy* dealing with species and lower taxa. Hitherto but little used terms are defined in TEILING 1950 and 1952.

Taxonomic discussion.

The starting point is LÜTKEMÜLLER's epoch-making research on the structure of the cell wall on the basis of which he could assign the desmids into the main groups *Saccoderms* and *Placoderms*, the latter divided into three tribus: *Penieae*, *Closterieae* and *Cosmarieae* according to the manner of cell division and growth which depends on the structure of the cell wall.

As mentioned above, LÜTKEMÜLLER, by the aid of this new taxonomic principles, was able to revise and emend some desmid genera. Especially in *Penium* and *Cylindrocystis* he found a lot of species which, owing to their cell wall pores and the manner of division and formation of the zygospore were separated from these genera and placed in *Cosmarium*.

Other principles are founded on the vertical symmetry of the semi-cell, the so called desmid radiation and, in intimate connection with this feature, the morphology of the chloroplast. In his paper 1952 the present author has drawn up the probable evolution of the desmid chloroplast on the basis of its comparative morphology and increasing efficiency from lower to higher forms. In this way it has been possible to derive the diverse types of parietal chloroplasts from primitive axile ones.

The general trend to a better light ecology that favours the mutations resulting in a more effective photosynthesis, has gone along the path of increasing the surface of the chloroplast and consequently the surface of the cell. The most primitive type of desmids now existing may be represented by a desmid in structure and dimensions something like *Cylindrocystis*, having a short cylindrical cell with an unsegmented cell-wall without pores, a central nucleus and a stelloid chloroplast. The cell division is of normal vegetative type. In the saccoderm desmids the enlargement of the cell and chloroplast occurs in apical direction, a faint lateral enlargement is known but in a few cases (*Netrium*). In the lower placoderms (*Penieae* and *Closterieae*) evolution has gone the same paths, viz. apical extension, in *Closterium* also combined with a lateral inflation. By this, *Penium* possesses a typical baculiform shape. Its generic characters, compared with other similar genera, are the lack of pores and isthmus furrow, the peculiar manner of division and, combined with this, the intercalary growth. Thus, the porous cell wall of *Penium*-like desmids at once (often after staining) decides their

taxonomic position. Most of the species of *Actinotaenium* have been separated from *Penium*, some of them also from *Cylindrocystis*, by the aid of this character. The chloroplast of *Penium* and the small *Closterium* species is typical stelloid.

All higher placoderm desmids, i.e. LÜTKEMÜLLER's tribus *Cosmarieae*, possess a compound porous cell wall with a constant oblique fissure lying in a plan that exactly divides the cell in two symmetrical semi-cells. This group consists of two quite different parts: *Actinotaenieae* and *Anguloradiataeae*, demonstrated on p. 385. For the actual problem of *Actinotaenium* it is convenient to summarize the occurrence of the types of the chloroplast in those genera from which most of the species have been distinguished:

Penium: typical stelloid with entire lamellae.

Cylindrocystis: lobo-stelloid, i.e. a central core with one pyrenoid and radiating lacinate or dissected lamellae, the lobes of which often being thickened in their parietal ends.

The main part of the placoderm desmids, i.e. all of them except the *Actinotaenieae*, show an angulo-radiate structure. The lamellae of the starlike chloroplast are grown out radially and the cell wall is grown out in corresponding bulges, the *radii*, that gives the semicell, when seen in end-view, a regular poly-bigonal shape. The primitive bulges are short angles but they are mostly developed into an immense richness of forms, especially in *Staurastrum*. It must be emphasized that the fundamental structure of a desmid is either omni-radiate or anguloradiate.

The radial extension of the semicell has not affected the isthmus zone, except in a small number of cases. In this way, these desmids have got their characteristic shape: a cell, by a false "constriction" in the middle, forming two symmetrical semi-cells ("segments" according to RALFS and earlier desmidiologists).

The lateral expansion of the lamellae in the bulges itself implies an increase in photosynthesis. This is made even more effective by the longitudinal division of the edges of the lamellae, a feature characteristic of the tribus *Anguloradiataeae mihi*, see p. 385. In primitive desmids of this tribus e.g. *Desmidium* and *Staurastrum*, this *furcoid* chloroplast is very evident when seen in end view. The furcoid chloroplast is capable of a most elaborate metamorphosis in a great number of forms according to the size and shape of the semicell. The furcoid nature of the most evolved derivations are discernible only by means of the transitions analyzed by comparative morphology.

The present author has (1950) emphasized that the primitive angular desmids were multiradiate and that their evolution to the present state has proceeded by means of successive reduction of the number of the radii; i.e. from perhaps 10-radiate through decreasing number to the at present common quadri-, and triradiate stages up to the biradiate end stage. This process is clearly visible in the variability of certain species, that exhibit 6-, 5-, 4-, and 3-radiate facies, e.g. *Staurastrum zonatum*. The *Janus*-forms consisting of semi-cells of different radiation, e.g. 5+3, 4+3, 4+2, 3+2 are demonstrative transitions. The selecting factor of the reduction is *light*; the chloroplasts of the "compressed biradiate desmid exhibit a greater surface in relation to the volume than pluriradiate desmids and, actually, the biradiate show a richness in forms, superior to the pluriradiate ones. The vast majority of the *Anguloradiatae* are biradiate, especially considering the genera. This evolution is quite analogous to the flattened shape of all green organs: leaves, cladophylls, phyllochia, flat thalli and similar forms occurring in the whole vegetable kingdom.

The biradiate desmids are the most advanced and their evolution has proceeded in several diverse paths. Some of these are morphologically very distinct, e.g. *Micrasterias* and the long *Euastra*, some other are conventionally assorted in small genera by the aid of morphological peculiarities, e.g. *Oocardium*, *Cosmocladium*, *Onychonema*, and the vast majority are brought together under the name of *Cosmarium*. In *Cosmarium*, however, a number of desmids circular in end view, have been inmixed and their position has been codified, mainly by the authority of RALFS. *Staurastrum* is the name of a collection of several other evolutionary branches, still on their way to the end stage and, consequently, showing diverse stages of radiation. *Stauroidesmus* is one of these lines recently distinguished, its biradiate stage has since long been known under the name of *Arthrodesmus*. Several of the normally biradiate great genera, *Cosmarium*, *Micrasterias*, *Euastrum*, and *Xanthidium*, contain species that sometimes occur as tri-, and even quadri-radiate specimens. They must be interpreted as examples of occasional reversion back to stages that have been passed during the phylogenetic evolution of the actual species.

Dysphinctium in the light of modern taxonomic principles.

Dysphinctium was erected in order to unite the rounded desmids, uncombinable with the omniradiate genera then known, e.g. *Cylindro-*

cystis and *Penium*. As this concept was formed out, it was quite as artificial as *Cosmarium*, it contained two morphological groups: baculiform and globular desmids, the latter comprising bi-globular and mono-globular forms. Disregarding the omni-radiate species, belonging to *Actinotaenium*, the other types will be dealt with from evolutionary points of view.

Especially in biradiate desmids evolution has proceeded in regressive direction, forming desmids more or less rounded in cross-section in which the biradiate character in some cases is difficult to discern. As a rule, this inflation has affected but the semicells, not the isthmus, significant examples are shown by the bigloboid *Cosmaria*, e.g. *moniliforme*, *prae grande*, and the *excavatum*-group. *Cosmarium Welwitschi* is interesting since its ornamentation has conserved the biradiate pattern. An inflation of the isthmus zone is very rare, in *Cosmarium* it is found e.g. in *connatum* and *pseudoconnatum*, *australe*, and *alpestre*. In other anguloradiate desmids an extreme degree of isthmal enlargement is found in *Hyalotheca*, *Desmidium* spp., and *Bambusina*, in the latter the isthmus is even wider than the semicells. Two or three small granules, regularly dispersed on the surface of the semicells of *Hyalotheca* and *Bambusina* must be interpreted as rudiments of the earlier angles (TEILING 1950, p. 306). This secondary circular structure is termed *pseudo-omniradiate*. Some genera have conserved their angulo-radiate origin more evidently in their apices, viz. *Tetmemorus*, *Ichtyocercus* and *Triploceras*. Their baculiform structure is a matter of convergency towards the primitive baculiform structure in *Actinotaenieceae*, *Closterium*, *Penium*, and certain saccoderm genera.

The baculiform species of *Dysphinctium*, except the species here assigned to *Actinotaenium*, are such secondarily rounded and elongate desmids although their baculiform character is less pronounced compared with *Tetmemorus* etc. They are characterized by the *deep sinus* and the *transverse section* of the semicells that generally is not quite circular but broad-oval, conveniently termed *quasi-omniradiate*, showing the origin from biradiate desmids of *Cosmarium*-type. At any rate, the narrow sinus and the broad-oval cross-section (very seldom circular in certain specimens) are features that at once distinguish these desmids from the *Actinotaenieceae*.

In many cases the biradiate origin of the pseudo-omniradiate and quasi-omniradiate desmids of the former *Dysphinctium* with smooth cell wall is visible in their chloroplasts. *Cosmarium connatum*, *Printzii*, and *Thwaitesii* possess a dicentric and *pseudoconnatum* a tetracentric

chloroplast; both types are normal derivations in large cells of a biradiate furcoid chloroplast. *Cosmarium pseudarctoum* occurs also in a triradiate facies (BORGE 1923), thus proving that the circular shape is a secondary one. Intricate cases are found in some rounded desmids in which the inflation of the semicell has given rise to frontal secondary ridges of the chloroplast, thus forming a pseudo-stelloid chloroplast very similar to the primitive stelloid one where all radiate ribbons are primitive lamellae (see TEILING 1952, p. 282). Unmistakable examples are e.g. *Tetmemorus* and *Triploceras*.

A little revision of Lütke Müller's
desmid system.

The principles of desmid taxonomy that have appeared from my studies of the desmid radiation and the comparative morphology of the desmid chloroplast have necessitated a revision of LÜTKEMÜLLER's system (1902, p. 408). The change affects only the highest placoderms, the tribus *Cosmarieae*. This tribus is characterized by a three layered cell wall with pore-apparatus and a constant fissure joining the semi-cells where the division takes place.

It consists of two quite different parts. The first, *Actaeniotaeenieae*, embracing four genera, is characterized by a) the primitive omniradiate baculiform shape with the apical growth common to the lower placoderms (i.e. *Penieae* and *Closterieae*) and b) the primitive stelloid chloroplast that in *Actinotaenium* and *Docidium* is typical in the smaller species and in the larger species is transformed, more or less, into the taenio-parietal type; in *Pleurotaenium* it is mainly taenio-parietal and in *Groenbladia* is reduced to the laminate type. The second part, *Angulo-radiateae*, embracing the main part of LÜTKEMÜLLER's *Cosmarieae*, is characterized by a) the angulo-radiate shape and b) the *furcoid* chloroplast which has developed into the very many kinds of forms, neglected or unexplained by the desmidiologists. The ability of angular expansion and lateral enlargement of the cell wall in connection with the exceptional ability of the furcoid chloroplast in developing new and effective forms of parietal chloroplasts has given rise to an immense evolution of desmid species and also genera, a circumstance that necessitates a taxonomic expansion of LÜTKEMÜLLER's tribus.

A survey of the present system of the placoderm desmids according to the author's results is presented in the next page.

- A. Non-constant fissure of division. Omniradiate cells.
3. Tribus *Penieae*. Cell wall without pore-apparatus, chloroplast stelloid.
 4. Tribus *Closterieae*. Cell wall with pore-apparatus, chloroplast stelloid → holo-parietal.
- B. Constant fissure of division. Cell wall with pore-apparatus. Cells always composed of two quite symmetrical semicells.
5. Tribus *Actinotaenieae*. Omniradiate cells. Chloroplast stelloid or developed into taenio-parietal or laminate ones.

Genera:

Cell wall without sculpture:

Actinotaenium. Chloroplast stelloid or developed into a taenio-parietal one.

Groenbladia. Chloroplast laminate.

Cell wall with sculpture:

Docidium. Chloroplast stelloid → taenio-parietal.

Pleurotaenium. Chloroplast stelloid, or mostly, taenio-parietal.

6. Tribus *Anguloradiateae*. Cells angulo-radiate or developed into pseudo-omniradiate. Chloroplast furcoid, often developed into pseudo-stelloid, limbo-parietal, sector-parietal, and discoid.

Genera:

pluri ————— biradiate:

<i>Staurastrum</i>	<i>Euastridium</i>	<i>Cosmarium</i>	<i>Oocardium</i>
		<i>Xanthidium</i>	
<i>Staurodesmus</i>		<i>Euastrum</i>	<i>Cosmocladium</i>
		<i>Micrasterias</i>	

filiform:

<i>Phymatodocis</i>	<i>Streptonema</i>	<i>Spondylosium</i>	<i>Onychonema</i>
<i>Desmidium</i>		<i>Sphaerosoma</i>	
		<i>Hyalotheca</i>	
		<i>Bambusina</i>	

baculiform:

<i>Triploceras</i>	<i>Tetmemorus</i>
<i>Triplastrum</i>	<i>Ichtyocercus</i>

Actinotaenium (NÄGELI) TEIL. — genus novum, olim subgenus *Dysphinctii*.

Cellulae singulae, omniradiatae, a fronte visae, fusiformes, crassiores aut magis tenues, vel etiam cylindricae sulco isthmiali inconspicuo

praeditae, extremitatibus cellularum rotundatis aut obtuso-planatis. Membrana levis, in speciebus nonnullis infra apicem incrassata; poris praedita nisi in sulco isthmiali; pori, precipue regionis apicalis, in quibusdam speciebus satis magni; in his poris interdum organa pororum, velut granula membranae olim interpretata. Massa chlorophyllacea stelloidea vel lobo-stelloidea, vel etiam in speciebus quibusdam majoribus taenio-parietalis.

Omniradiate cells, in front view thicker or slender, fusiform or cylindrical; with a faint isthmus furrow; the ends of the cells rounded or obtuse-planned. Cell-wall smooth, in some species thickened on the inside of the apex; with pores except the isthmus furrow, in certain species also fairly great pores, especially in the apical part; in these pores there are often pore-organelles that have been interpreted as granules of the wall. Chloroplast stelloid or lobo-stelloid, in larger species even taenio-parietal.

It seems as if the desmidiologists have been too bound by tradition to react against the unnatural mixture of omniradiate and biradiate species in *Cosmarium*. Thus, it is of great interest that SCHELLENBERG (1897), in an account of a lecture delivered in the Botanical Society of Zürich, proposed *Actinotaenium* as a separate genus, though vaguely and on insufficient premises. He had examined a subaerial desmid that he considered belonging to *Actinotaenium* and had also in NÄGELI's literary remains found five anonymous species evidently belonging to *Actinotaenium*. He considered this little group as intermediate between *Cosmarium* and *Penium*. If *Actinotaenium* could not be approved as a separate genus, it would, as a section, be allotted quite as well to *Cosmarium* as to *Penium*. A foreshadowed later description of these species has not appeared.

Morphological survey.

The cell-wall is smooth. The granules mentioned in the diagnoses of several species, are the protruding pore-organelles (=Porenorgane *sensu* LÜTKEMÜLLER) of the great apical pores, e.g. in *A. trachypolum*, *rufescens*, *Clevei*, and *Taylori*. On the contrary, a zone of greater pores are situated on the basal part of the semi-cell of *A. sydneysense*. Scattered great pores among the small ones are recorded in several species, a feature that probably has been overlooked in many cases. All species have dense pores arranged irregularly or in oblique-crossing rows. *A. subpalangula* shows transverse rows of greater pores

visible by the prominent pore-organelles, its forma *depauperatum* is created on the basis of specimens from which the protruding parts are lost, because of the action of chemical factors, stated by KLEBS.

An apical interior thickening of the cell-wall is stated in several species. This is a rather common feature in desmids with rounded ends.

The cell is always omni-radiate, the form a fronte is fusiform — cylindrical — guitar-shaped with a faint isthmus-furrow. The apex is rounded or obtuse, never tapering to a point. In a few species of the *curtum* group a faint constriction of the apical part is noted. Slightly inflated semi-cells are also noted.

The chloroplast is stelloid, lobo-stelloid, or taenio-parietal. In the vast majority of the species, having less than about 50 μ diameter, the chloroplast is regular with entire or parietally thickened edges of the lamellae and one pyrenoid. In elongate species, *A. angulatum*, *elongatum*, *diadematum* and *Clevei* two or three pyrenoids are stated. In *subpalangula*, *subtile*, *perminutum*, *pyramidatum*, *viride*, and *diplosporum* the chloroplast with one pyrenoid is lobo-stelloid. In the fairly large *Taylori* 45—50 μ thick, the edges of the lamellae are intensively plicate and the chloroplast has a corresponding augmented number of dispersed pyrenoids.

The large species *A. turgidum*, *capax*, and probably *grande* with a diameter of 60 μ and more have taenio-parietal chloroplasts with many pyrenoids. *Cosm. hibernicum*, possibly a large form of *diplosporum*, is recorded having parietal band-like chloroplast with several pyrenoids. It seems very unlikely that a taenio-parietal chloroplast *sensu stricto* has been formed in a desmid only 45 μ in diameter. Probably a misinterpretation of badly conserved material.

The formation of spores is known in a few species. The spores recorded show a puzzling diversity. Azygospores are found in *diplosporum* by SKUJA (1949, Tab. 27: 11) as well as true zygo-spores (Fig. 12). In this species several scientists have found double spores interpreted as zygo-spores, viz. LUNDELL, EICHLER, DUCELLIER, HOMFELD, and ALLORGE. These are meant to be formed in that manner that the protoplasts of the two cells divide, thus forming four gametes, a process reconstructed by OLTMANN (1922, p. 122, Fig. 88: 1) in regard to *Closterium lineatum*. However, to judge from HOMFELD's picture of the initial stage of the sporeformation (1929, Tab. 5: 58), it is not unlikely that these spores are azygo-spores when considering the limits of the protoplasts. In pictures of corresponding cases in *Closterium* the position of the double spores of *Cl. lineatum* and *lunula* gives the im-

pression that they are real zygospores, whereas the double spores of *rostratum* seem to be azygo-spores according to LAGERHEIMS picture (1886, p. 48, Fig. 3).

LÜTKEMÜLLER has, in letters to NORDSTEDT (1911) and to G. S. WEST (1912) sent drawings of double-zygospores of *cucurbitinum* at the formation of which four cells are participants (eight semicells!), Fig. nostr. 78. Consequently they must be regarded as true zygospores. From an initial sphaerial form they become more square-shaped as the definite shape. LÜTKEMÜLLER, in his letter to NORDSTEDT, brings up the question, if not NORDSTEDT's find of a spore of *cucurbitinum* var. *polymorphum* (1888, p. 71, Tab. 7: 20 c) may be an isolated half of a mature double zygospore.

Angular mono-zygotes are known in *A. minutissimum*, *crassiusculum*, *pseudocucurbita*, and *Mooreanum*, the latter with one papilla in each of the four corners. *A. pyramidatum* has oval somewhat angular zygospores. Globular, smooth zygospores are found in *A. sydneyense* and *truncatum* and sphaerial zygospores with conical papillae are recorded in *cucurbita* and *subglobosum*. A similar spore is assigned to *Clevei* by CUSHMAN (1905, Tab. 7: 8) but the determination seems questionable.

Remarks of methodics.

The generic difference between *Penium* and *Actinotaenium* contains several elements.

Penium: cell wall without pores, ornamented with punctuations, granulations, or striations, the fissure of division is variable, a circumstance sometimes marked by intercalary segments.

Actinotaenium: cell wall always with small pores, in certain species also great pores (scrobiculations) with protruding pore organs, the fissure of division is constant, situated in a faint isthmus furrow.

The consequences of these distinguishing characters, (valid also if the name *Actinotaenium* is substituted by the name *Cosmarium*) developed by LÜTKEMÜLLER, have not been exploited and in many cases quite neglected. Thus, there are still some desmids of uncertain position, for instance *Penium rufescens*, *gelidum*. In measure, this depends on doubts about the absence of pores in the membrane of *Penium*. In *Penium polymorphum*, LÜTKEMÜLLER was unable to find any pores (1902, p. 382, Tab. 18: 44, 45) while KRIEGER (1935, p. 225) emphasized that apical pores have been stated by him. Both may be right; the possibility exists that the specimens examined by KRIEGER may belong

to a form of *Actinotaenium*, in shape and dimensions agreeing to *Penium polymorphum*. On the other side, pores probably may occur in *Penium* quite as well as in the near related *Closterium*. That is why the wall ornamentation and the manner of division signify the deciding characters.

By a compilation like this it is not expedient and even not possible to try to make a revision of certain polymorphic species, e.g. *A. curtum*, *rufescens*, *cucurbitinum*, *cucurbita*, *inconspicuum*. The short forms of *Pleurotaenium minutum*, a very heterogeneous species, may quite as well be allotted to *Actinotaenium* as to the more specialized genus *Pleurotaenium*. The changes of the nomenclature undertaken by the author, are based on the extensive survey obtained from studies during several years, but they are, as all biosystematic work, a matter of taste and, consequently, very easy to be criticized by every desmidiologist.

By the formation of *Actinotaenium* the nomenclature makes justice to the original names given by the authors. When a lot of *Penia* and *Cylindrocystides* were transferred to *Cosmarium*, several of their names were already attached to species of the latter genus. Thus, several of these names must be rejected and new ones were created, especially by LÜTKEMÜLLER. These new names must now, in their turn, be rejected and the old names are restored. To each species there is added a list of literary references containing directions to pictures and nomenclature of the actual species, varieties and formae.

The selection of the species is made on the basis of the descriptions and pictures from the literature available to me. Of course, the incompleteness of the sources, often met with, has not permitted a definite decision in several cases, especially the chloroplast is very often quite neglected. Some species have been revised as to their biosystematy and nomenclature. No diagnoses are communicated but in many cases comments of similiarities and differences are given. The chorological distribution is not considered. These limitations depend on my opinion that it seems reasonable not to anticipate the thorough revision of the part of *Cosmarium*, corresponding to *Actinotaenium*, probably undertaken by KRIEGER for the new edition of RABENHORST's Kryptogamenflora before his sudden and regrettable death.

Abbreviations. As a rule, no abbreviations beyond the traditional ones are used, only *Actinotaenium* and *Cosmarium* are abbreviated in combination with species names. The often used double name W. and G. S. WEST ist written WEST. Dim: (followed by figures) means dimensions, the figures before the cross indicate the length and those after the cross indicate the breadth of the cell in microns. The thickness of the isthmus is insignificant and omitted.

The species now assigned to *Actinotaenium*, are dealt with in the order of the following list, in which they are arranged typologically according to the chloroplast and the shape.

A. Species with stelloid chloroplast.

The <i>curtum</i> group:	11. <i>Wollei</i> ,	20. <i>truncatum</i> ,
1. <i>curtum</i> ,	12. <i>trachypolum</i> ,	21. <i>crassiusculum</i> ,
2. <i>lagenarioides</i> ,	13. <i>cucurbitinum</i> .	22. <i>Taylori</i> ,
3. <i>elongatum</i> ,		23. <i>cucurbita</i> ,
4. <i>Clevei</i> ,	The <i>adelochondrum</i>	24. <i>pseudocucurbita</i> .
5. <i>rufescens</i> ,	group:	
6. <i>turgidum</i> ,	14. <i>adelochondrum</i> ,	The <i>Mooreanum</i>
7. <i>grande</i> ,	15. <i>obcuneatum</i> ,	group:
8. <i>capax</i> .	16. <i>tumidum</i> ,	25. <i>minutissimum</i> ,
	17. <i>sydneyense</i> .	26. <i>Mooreanum</i> .
The <i>cucurbitinum</i>		
group:	The <i>cucurbita</i> group:	
9. <i>cruciferum</i> ,	18. <i>palangula</i> ,	
10. <i>subglobosum</i> ,	19. <i>inconspicuum</i> ,	

B. Species with lobo-stelloid chloroplast.

The <i>pyramidatum</i>	The <i>subpalangula</i>	The <i>viride</i> group:
group:	group:	
27. <i>pyramidatum</i> .	28. <i>subpalangula</i> ,	31. <i>viride</i> ,
	29. <i>subtile</i> ,	32. <i>diplosporum</i> .
	30. <i>perminutum</i> .	

1. *Actinotaenium curtum* (BRÉB.) comb. nov. Dim: 22—60×10—32. Fig. 1.

Cosm. curtum: RALFS 1848, p. 109, Tab. 32: 9. N. CARTER 1920, p. 271, Fig. 1 A, B. WEST and CARTER 1923, p. 267. INSAM und KRIEGER 1936, p. 99, Tab. 1: 25, 26. — *Penium curtum*: KÜTZING 1849, p. 167. WILLE 1885, p. 87, Tab. 13: 3. TURNER 1886, Tab. 1: 3. WEST 1904, p. 97, Tab. 10: 21, 22. BØRGE 1911, p. 8, Fig. 1, 2. SAMPAIO 1944, Tab. 2: 29—31. — *Dysphinctium Regelianum*: NÄGELI 1849, p. 110, Tab. 6: E. — *Penium Regelianum*: WILLE 1879, p. 55, Tab. 13: 7. — *Dysphinctium curtum*: DE TONI 1889, p. 877. — *Calocylindrus curtus*: KIRCHNER 1878, p. 143. COOKE 1886, p. 126, Tab. 43: 11. WOLLE 1887, p. 54, Tab. 12: 15, 16. — *Cosm. Thwaitesii* var. *curtum*: KLEBS 1879, p. 27. — *Penium phymatosporum*: WILLE 1885, p. 87, Tab. 13: 4.

f. *majus*. Dim: 41—48×21—25. WILLE 1879, p. 56, Tab. 14: 73. WEST 1904, p. 98, Tab. 10: 24, 25. BØRGE 1899 a, p. 762, Fig. 5. INSAM und KRIEGER 1936, p. 99, Tab. 1: 28. MESSIKOMMER 1942, p. 142, Tab. 4: 7, and 1945, Tab. 2: 39.

f. *minus*. Dim: 30—32×15—16. WILLE 1879, p. 56, Tab. 13: 75. WEST 1904, p. 142, Tab. 10: 23. MESSIKOMMER 1942, p. 142, Tab. 4: 8.

f. *intermedium*. Dim: 36—38×15—17. WILLE 1879, p. 56, Tab. 13: 74.

var. *obtusum*. Dim: 41—45×20—23. Fig. 9. WEST 1900, p. 289. Tab. 412: 1, 2. WEST 1904, p. 99, Tab. 10: 26.

var. *globosum*. Dim: 31—38×24—28. WILLE 1879, p. 56, Tab. 13: 72.

A. curtum, under the name of *Regelianum*, is the type specimen of *Actinotaenium* being the species for which NÄGELI created the sub-genus *Actinotaenium* of the collective genus *Dysphinctium* in 1849. NÄGELI's picture of *Regelianum* is clear and also complete, (even division stage) showing the fusiform shape with apical internal papilla and the stelloid chloroplast with six lamellae. This form has been refound and depicted by several authors, often without the apical papilla, but the name *curtum* has also been applied to desmids of varying forms of which especially the rounded ones seem to be foreign to the type, e.g. by N. CARTER, WOLLE, COMÈRE and MESSIKOMMER. WILLE (1879) however, found several forms, viz. *majus*, and *medium* which, in his opinion, form a continuous series between f. *typicum* and his var. *globosum*.

PEVALEK (1924, p. 62, Fig. 6) has described a var. *velebitinum*, the semicells of which have inflated bases and slightly excavated apices. It makes the impression neither belonging to *curtum* nor to *Actinotaenium*.

var. *attenuatum* (INSAM et KRIEGER) comb. nov. Dim: 62—87×20—30. Fig. 2. — *Cosm. attenuatum*: RALFS 1848, p. 110, Tab. 17: 9. WEST 1908, p. 118, Tab. 74: 24, 25. — *Cosm. curtum* var. *majus*: RABENHORST 1868, p. 177. — *Calocylindrus attenuatus*: COOKE 1886, p. 127, Tab. 43: 1, 2. — *Dysphinctium attenuatum*: TURNER 1892, p. 44. — *Cosm. Thwaitesii*: KLEBS 1879, p. 27. — *Calocylindrus Thwaitesii*: WOLLE 1884, p. 56, Tab. 12: 19. — *Cosm. curtum* var. *attenuatum*: INSAM und KRIEGER 1936, p. 99, Tab. 1: 27. — Not MASKELL 1888, p. 15, Tab. 2: 16!

Already RALFS (p. 110) confessed that he in certain cases had been doubtful about specific difference between *A. curtum* and *attenuatum*. MASKELL (1888) used the name *Cosm. curtum* var. *attenuatum* for a desmid of exactly the same front view as *attenuatum*. This name must be rejected because of the clearly biradiate structure in apical view.

var. *Bourrellyi* nom. nov. Dim: 34×17. Fig. 3. — *Cosm. conicum*: BOURRELLY 1949, p. 186, Tab. 4: 50.

BOURRELLY's desmid differs so much from the WEST's insufficiently known *Cosm. conicum* that it is here proposed as a scrobiculate variety of *curtum*.

It is impossible to maintain a specific difference between *A. lagena-rioides*, *pseudotynecense*, *elongatum*, and *lanceolatum*; the differences being vague concerning only proportions and dimensions. Probably

earlier desmidiologists have been standing in awe of the generic names, for instance on the one side *Penium lanceolatum* and on the other side *Cosmarium elongatum*. The present author has compromised by joining the broader *lagenarioides*—*pseudotinecense* and the more slender *elongatum*—*lanceolatum*.

The typical *Clevei* falls, in my opinion, somewhat outside this group and is in itself rather differentiated in direction to a more cylindrical shape, such as *rufescens*. As mentioned earlier the scrobiculations of the vertex, when observed, possess not deciding but only secondary rank as a specific character.

2. *Actinotaenium lagenarioides* (ROY) comb. nov. Dim: 92—95 × 45. Fig. 4.

Penium lagenarioides: BISSET 1884, p. 197, Tab. 5:6. WEST 1904, p. 93, Tab. 9:12. — *Dysphinctium lagenarioides*: LÜTKEMÜLLER 1905, p. 337. — *Cosm. lagenarioides*: LÜTKEMÜLLER 1910, p. 479.

BISSET's picture seems to be unique, WEST's is a copy of it. In a written comment BISSET has corrected the arrangement of the pores: they should be scattered, not in rows.

var. *pseudotinecense* (GRÖNBL.) comb. nov. Dim: 122—157 × 45—57. Fig. 5. — *Cosm. pseudotinecense*: GRÖNBLAD 1921, p. 42, Tab. 7:61. — *Cosm. lagenarioides*: GRÖNBLAD 1920, p. 43, Tab. 5:24. — *Cosm. elongatum*: IRÉNÉE-MARIE 1952, p. 112, Tab. 11:1. — *Cosm. Faakense*: BECK-MANNAGETTA 1929, p. 3, Fig. 2.

GRÖNBLAD's distinguishing of his species depended on the stelloid chloroplast in contrast to the very similar *Cosm. turgidum* var. *tinecense* RACIB. This author had not mentioned anything about the chloroplast but *turgidum* has a taenio-parietal one. Like *tinecense* also *pseudotinecense* has a constricted vertex but GRÖNBLAD has sent me a picture of *pseudotinecense* without this constriction and he is inclined to consider *lagenarioides* as belonging to the normal, unconstricted *pseudotinecense*.

3. *Actinotaenium elongatum* (RACIB.) comb. nov. Dim: 128—186 × 34—59. Fig. 6.

Cosm. elongatum: RACIBORSKI 1885, p. 68, Tab. 11:1. BORGE 1923, p. 8, Tab. 1:3. SKUJA 1928, p. 156, Tab. 4:1. GRÖNBLAD 1936, p. 2, Tab. 1:4. — *Calocylindrus elongatus*: RACIBORSKI 1884, p. 9.

f. *brevius*. Dim: 106 × 36. BORGE 1923, p. 8, Tab. 1:4. — *Cosm. elongatum*: CEDER-GREN 1932, p. 45, Fig. 14.

The typical form of this species quite agrees with *A. curtum* var. *attenuatum* and could be regarded as a f. *maximum* of it.

var. *lanceolatum* (TURN.) comb. nov. Dim: 81—98×26—36. Fig. 8.

Penium lanceolatum: TURNER 1892, p. 17, Tab. 1: 7. BORGE 1903, p. 74, Tab. 1: 3.

— *Dysphinctium lanceolatum*: LÜTKEMÜLLER 1905, p. 337. — *Cosm. lanceolatum*: LÜTKEMÜLLER 1910, p. 479.

f. *subcylindricum* (W. et G. S. WEST) comb. nov. Dim: 134×35. — *Penium lanceolatum* var. *subcylindricum* WEST 1902, p. 134, Tab. 18: 5.

var. *africanum* (SCHMIDLE) comb. nov. Dim: 96—128×27—35. Fig. 7. — *Penium Clevei* var. *africanum*: SCHMIDLE 1898, p. 20, Tab. 1: 12. — *Penium Clevei* f. *elongatum*: WEST 1907, p. 140, Tab. 13: 2.

4. *Actinotaenium Clevei* (LUND.) comb. nov. Dim: 85—116×35—42. Fig. 10, 13.

Penium Clevei: LUNDELL 1871, p. 86, Tab. 5: 11. WEST 1904, p. 87, Tab. 8: 36, 37.

— *Penium Thwaitesii*: CLEVE 1864, p. 492. — *Calocylindrus Clevei*: WOLLE 1884, p. 56, Tab. 50: 27. — *Calocylindrus Thwaitesii*: WOLLE 1884, p. 56, Tab. 50: 28.

Dysphinctium Clevei: DE TONI 1889, p. 893. — *Cosm. Clevei*: LÜTKEMÜLLER 1910, p. 479. WEST and CARTER 1923, p. 267. GRÖNBLAD 1920, p. 40, Tab. 5: 23. TAFT 1937, Tab. 2: 37. IRÉNÉE-MARIE 1949, p. 253, Tab. 1: 5. — *Penium breve* var. *arcticum*: WILLE 1879, p. 57, Tab. 14: 76. — *Penium diadematum*: GUTWINSKI 1902, p. 585, Tab. 37: 20 (Fig. nostr. 13).

var. *delicatulum* (JOSH.) comb. nov. Dim: 63×26. Fig. 80 (in Fig. 23!). — *Penium delicatulum* JOSHUA 1885, p. 653, Tab. 25: 9.

f. *minus*. Dim: 37×15. — *Penium delicatulum* var. *minus* WEST 1895, p. 47, Tab. 5: 36.

var. *crassum* (W. et G. S. WEST) comb. nov. Dim: 80—98×42—45. Fig. 11. — *Penium Clevei* var. *crassum*: WEST 1894, p. 4, Tab. 1: 5. WEST 1904, p. 88, Tab. 8: 38. CUSHMAN 1905, p. 225, Tab. 7: 8 (zygospore).

var. *gelidum* (WITTR.) comb. nov. Dim: 36—62×14—49. Fig. 14. — *Penium gelidum*: WITTRÖCK 1883, p. 122, Tab. 3: 24. CEDERGREN 1932, p. 25, Tab. 1: 3. — *Penium rufescens*: GUTWINSKI 1909, p. 445, Tab. 7: 8. ?MESSIKOMMER 1942, p. 136, Tab. 2: 5. — ?*Peniella sudetica*: BECK-MANNAGETTA 1926, p. 6, Fig. 9—12.

var. *gelidum* (WITTR.) comb. nov. Dim: 36—62×14—49. Fig. 14. — *Penium gelidum*: WITTRÖCK 1883, p. 122, Tab. 3: 24. CEDERGREN 1932, p. 25, Tab. 1: 3. — *Penium rufescens*: GUTWINSKI 1909, p. 445, Tab. 7: 8. ?MESSIKOMMER 1942, p. 136, Tab. 2: 5. — ?*Peniella sudetica*: BECK-MANNAGETTA 1926, p. 6, Fig. 9—12.

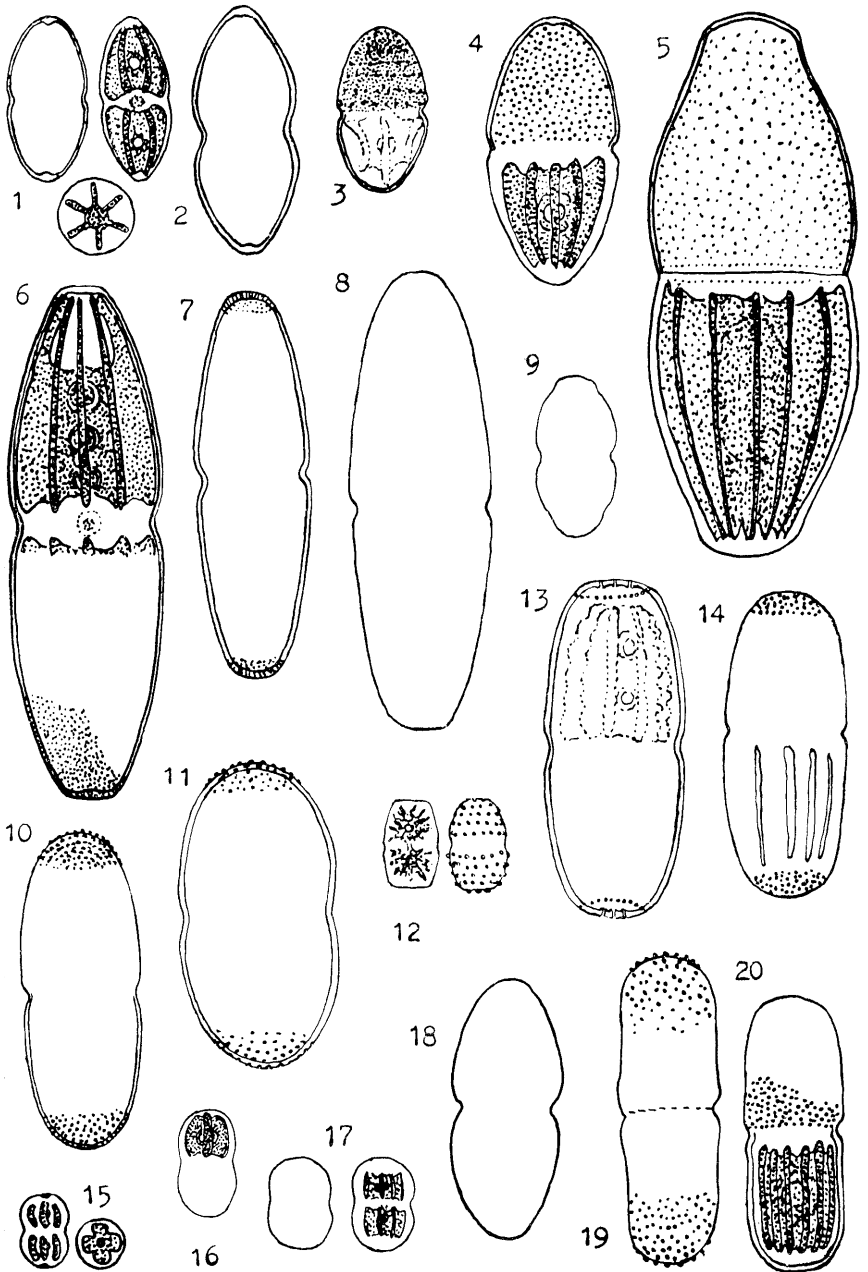
KRIEGER (1935, p. 240) united *gelidum* with his *Penium rufescens* in spite of the apical scrobiculations. The same objection must be raised to his placing of *Peniella sudetica* in *Penium polymorphum* (p. 229); BECK-MANNAGETTA emphasizes the porous cell wall. On the other side, the absence of an isthmus furrow speaks against its position in *Actinotaenium*.

5. *Actinotaenium rufescens* (CLEVE) comb. nov. Dim: 50—94×20—32. Fig. 19, 20.

Penium rufescens: CLEVE 1864, p. 493, Tab. 4: 5. BORGE 1903, p. 75, Tab. 1: 6.

WEST 1904, p. 99, Tab. 6: 12, 13. MESSIKOMMER 1943, Tab. 6: 3. IRÉNÉE-MARIE 1939, p. 88, Tab. 9: 13. KRIEGER 1935, p. 240, Tab. 10: 13, 14. TAFT 1937, Tab. 2: 36.

LHOTSKY 1949, p. 4, Tab. 1: 8. MESSIKOMMER 1927, p. 95, Tab. 2: 7, and 1935, p. 39,



Figs. 1—20. — 1: *curtum* — 2: var. *attenuatum* — 3: var. *Bourellyi* — 4: *lagenarioides* — 5: var. *pseudotinecense* — 6: *elongatum* — 7: var. *africanum* — 8: var. *lanceolatum* — 9: *curtum* var. *obtusum* — 10: *Clevei* — 11: var. *crassum* — 12: *subpalangula* — 13: *Clevei* — 14: var. *gelidum* — 16: *cruciferum* — 15: f. *minus* — 17: var. *pluri-radiatum* — 18: *turgidum* var. *ovatum* — 19—20: *rufescens*.

Tab. 1: 7 (f. *achroa*). — *Penium chrysoderma*: BORGE 1906, p. 15, Tab. 1: 7. DUCÉLLIER 1916, p. 54, Fig. 30, 31. DICK 1923, p. 215, Tab. 4: 12 (Fig. nostr. 19). — *Doididium breve* var. *arcticum*: GUTWINSKI 1896, Tab. 6: 24. — *Penium didymocarpum* var. *alpinum*: SCHMIDLE 1895, p. 346, Tab. 14: 17.

This species is by KRIEGER (1932, p. 240) placed in *Penium* in spite of the great apical scrobiculations of *chrysoderma* which, in KRIEGER's (and HOMFELD's 1929, p. 15) opinion belongs to *rufescens*. LÜTKEMÜLLER has (in litt. 12/II 1912) communicated to G. S. WEST, that he had studied a rich material of *rufescens* and discerned a dense pore-apparatus. As distinguished from the rest of the *curtum* group, this desmid is almost cylindrical with rounded ends, transitional forms occur in *Clevei*. *A. rufescens* also shows an apparent similarity to *cucurbitinum* and certain pictures assigned to this species could quite as well be called *rufescens*.

6. *Actinotaenium turgidum* (BRÉB.) comb. nov. Dim: 138—207×73—100. Fig. 21.

Cosm. turgidum: RALFS 1848, p. 110, Tab. 32: 8. PETKOFF 1900, p. 10, Tab. 1: 4. BORGE 1901, p. 23, Tab. 2: 12. WEST 1908, p. 115, Tab. 75: 1—3. MESSIKOMMER 1943, Tab. 10: 4 (Fig. sinistr.). KRIEGER 1932, Tab. 8: 10. — *Pleurotaenium turgidum*: DE BARY 1858, p. 75, Tab. 5: 31. — *Pleurotaeniopsis turgida*: LUNDELL 1871, p. 51. LÜTKEMÜLLER 1893, p. 43, Tab. 3: 26. *Calocylindrus turgidus*: KIRCHNER 1878, p. 142. COOKE 1886, p. 127, Tab. 44: 1. — *Disphinctium turgidum*: DELPONTE 1877, p. 133, Tab. 21: 1—6. — *Cosmaridium turgidum*: HANSGIRG 1888, p. 145. — *Cosm. DeBaryi* var. *turgidum*: KLEBS 1879, p. 28.

var. *subrotundatum*. Dim: 140×77. Fig. 28. WEST 1908, p. 116, Tab. 75: 4.

var. *ligatum*. Dim: 116—153×50—68. Fig. 24. WEST 1907, p. 204, Tab. 13: 7. BORGE 1918, p. 32, Tab. 2: 27, 28. MESSIKOMMER 1943, Tab. 10: 4 (Fig. dextr.).

var. *ornatum*. Dim: 200×84. SCHMIDLE 1895 a, p. 72, Tab. 1: 16.

var. *ovatum*. Dim: 164—240×83—97. Fig. 18. NORDSTEDT 1888, p. 63, Tab. 7: 30. INSAM und KRIEGER 1936, p. 110, Tab. 2: 6.

var. *tinecense*. Dim: 160—167×69. RACIBORSKI 1885, p. 69, Tab. 10: 2.

This large species of obtuse *curtum* type differs from the proceeding species of this group by its taenio-parietal chloroplasts, carefully studied by LÜTKEMÜLLER (1893). To it some interesting varieties have been assigned, viz. *ligatum* with an isthmal constriction, extremely scarce in *Actinotaenium*, further *subrotundatum* with almost globular semi-cells, and *tinecense* with a slightly constricted apical part.

7. *Actinotaenium grande* (DELP.) comb. nov. Dim: 216×100. Fig. 26.

Disphyntium (!) *grande*: DELPONTE 1877, p. 231, Tab. 21: 9.

This desmid differs from *A. turgidum* by its larger size and cylindrical shape. DELPONTE has not seen the chloroplast but according to the size there is no doubt that it has taenio-parietal chloroplasts.

var. *cuneatum* (W. B. TURNER) comb. nov. Dim: 195—220×95—100. Fig. 23. — *Dysphinctium grande* var. *cuneatum*. TURNER 1892, p. 40, Tab. 7: 5.

This desmid agrees with *grande* in the size, the small constriction of the apical part also occurs in *turgidum* var. *tinecense*, *lagenarioides* var. *pseudotinecense*, and *curtum* var. *obtusum*.

8. *Actinotaenium capax* (JOSHUA) comb. nov. Dim: 140—165×66—90. Fig. 29.

Cosm. capax: JOSHUA 1885, p. 645, Tab. 8: 25. — *Dysphinctium subturgidum*: TURNER 1892, p. 80, Tab. 7: 4. — *Cosm. subturgidum* (TURN.) SCHMIDLE in WEST 1908, p. 116, Tab. 75: 5.

There is no difference in shape nor dimensions between *capax* and *subturgidum*: they are identical and the name *capax* possesses the priority. The chloroplast is taenio-parietal.

The forma *minus* must more correctly be considered a variety:

var. *minus* (SCHMIDLE) comb. nov. Dim: 60—120×37—64. Fig. 25. — SCHMIDLE 1895 b, p. 300, Tab. 4: 2. WEST 1908, p. 116, Tab. 116: 22, 23. KRIEGER 1932, p. 188, Tab. 8: 7. CEDERGREN 1932, p. 45, Fig. 15. SKUJA 1949, p. 143, Tab. 26: 8, 9. VAN OYE 1953, p. 284, Fig. 74. — *Pleurotaeniopsis subturgida* var. *minor*: SCHMIDLE 1896, p. 305.

9. *Actinotaenium cruciferum* (DE BARY) comb. nov. Dim: 15—30×10—15. Fig. 16, 17.

Cosm. cruciferum: DE BARY 1858, p. 72, Tab. 7: 3—6. VAN OYE 1953, p. 281, Fig. 64. SAMPAIO 1944, Tab. 2: 16, 17. — *Dysphinctium cruciferum*: HANSGIRG 1888, p. 185 and 243. GUTWINSKI 1896, p. 43, Tab. 6: 25. — *Penium cruciferum*: NORDSTEDT 1888, p. 71, Tab. 7: 19. WEST 1904, p. 100, Tab. 10: 18—20. var. *pluriradians*: WITTRICK 1889, p. 48. WOLLE 1887, Tab. 61: 9—11. TAYLOR 1834, p. 242, Tab. 45: 16. TAFT 1837, p. 398, Tab. 2: 35. ?SCHMIDLE 1898 a, p. 17, Tab. 1: 12, 13. LOWE 1923, Tab. 3: 7. — *Cosm. subarctoum*: MANGUIN 1936, p. 8, Tab. 1: 12, and 1940, Tab. 1: 12. — *Cosm. globosum* f. *minus*: BOURRELLY 1952, p. 495, Tab. 8: 75. WEST 1909, Tab. 68: 5. f. *latus*. Dim: 21—24×16—19. MESSIKOMMER 1942, p. 143, Tab. 4: 12, 13. GRÖNBLAD 1935, p. 4, Fig. 15, 16. TAFT 1937, p. 198, Tab. 2: 10.

f. *minus*, f. nov. Dim: 12×7—8. Fig. 15. — *Cosm. pseudarctoum* var. *perminutum*: MANGUIN 1937, Tab. 2. BOURRELLY 1952, p. 222, Tab. 28: 513, 514.

A. cruciferum has a stelloid chloroplast while the similar species *perminutum* and *subtile* have lobo-stelloid chloroplast. The cell in front view is guitar-shaped. Several circular forms of *Cosm. pseudarctoum*

and *Cosm. globosum* of a similar frontal shape are noted and also carefully depicted. It seems correct to assign some of these to *cruciferum*. In the part containing probable and doubtful species the separation of circular forms, previously assigned to biradiate *Cosmaria* is discussed.

DE BARY founded his species on a fairly slender form with a chloroplast having four lamellae (observe the name), larger forms have five or more lamellae which has given rise to the superfluous name *pluri-radiatum*, Fig. 17.

The statements given by BORGE and SKUJA of *cruciferum*, cannot, on the basis of the structure of the chloroplast, be referred to *cruciferum*. A further discussion is given in connection to *subtile*.

10. *Actinotaenium subglobosum* (NORDST.) comb. nov. Dim: 32—48×15—30. Fig. 33.

Cosm. subglobosum: NORDSTEDT 1878, p. 14, Tab. 1: 13. JOHNSON 1894, p. 287, Tab. 1: 13. The following pictures, only outline drawings in front view, may possibly belong to this species: KRIEGER 1932, p. 187, Tab. 8: 12, INSAM und KRIEGER 1936, p. 109, Tab. 1: 8, BOURRELLY 1952, p. 224, Tab. 29: 531, SCHMIDLE 1895 b, p. 300, Tab. 4: 3, and *Cosm. curtum* f. MESSIKOMMER 1942, p. 142, Tab. 4: 9, 10.

This desmid has a ratio of length : breadth of only 1.5, semi-globular ends and a faint constriction at the isthmus. The chloroplast is stelloid with 6—10 lamellae, the edges of which are slightly lacinate.

The zygospore is globular with mamillate verrucae.

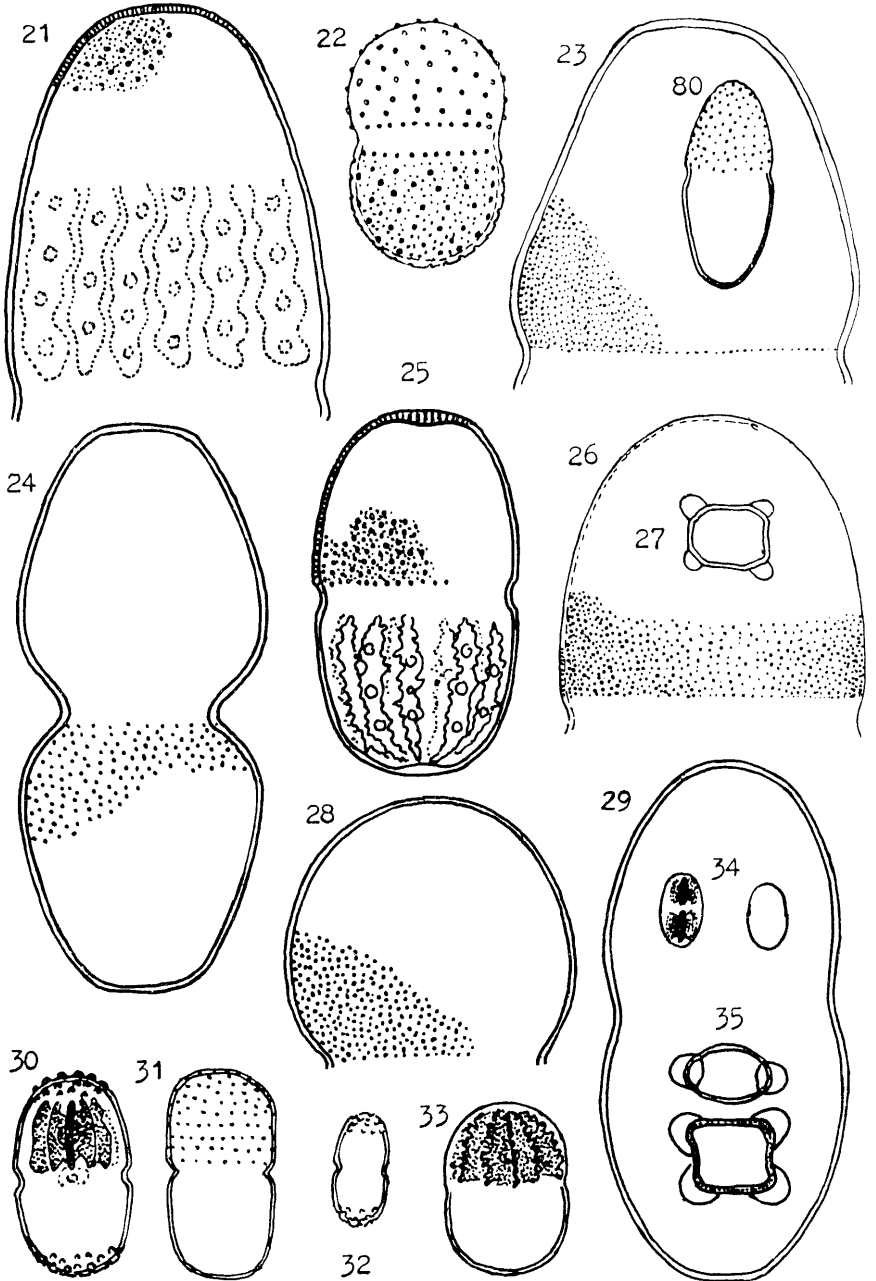
11. *Actinotaenium Wollei* (GRÖNBL.) comb. nov. Dim: 35—51×28—35. Fig. 40.

Cosm. Wollei: GRÖNBLAD 1924, p. 14, Tab. 2: 66, 67. IRÉNÉE-MARIE 1952, p. 138, Tab. 12: 10. — *Cosm. globosum*: WOLLE 1884, p. 60, Tab. 49: 14—17. IYENGAR 1951, Fig. 3: D. — *Cosm. globosum* var. *Wollei*: WEST 1906, p. 151, Tab. 15: 17. KRIEGER 1932, p. 177, Tab. 7: 8, 9. G. S. WEST 1907, p. 118, Tab. 7: 10. WEST 1902, Tab. 20: 42. — *Dysphinctium subellipticum*: SCHMIDLE 1898 a, p. 21, Tab. 1: 15.

The shape is in most cases almost globoid with a faint isthmus-furrow. The stelloid chloroplast has 6—9 lamellae.

The zygospore is smooth and globoid (WEST 1896).

PLAYFAIR'S *Cosm. globosum* var. *Wollei* (1914, Tab. 3: 3) can not belong to this species because of its dicentric chloroplast; it is pseudo-omniradiate from a biradiate origin.



Figs. 21—35, 80. — 21: *turgidum* — 22: *trichypolum* var. *Messikommeri* — 23: *grande* var. *cuneatum* — 24: *turgidum* var. *ligatum* — 25: *capax* var. *minus* — 26: *grande* — 27: *minutissimum* var. *octangulare* — 28: *turgidum* var. *rotundatum* — 29: *capax* — 30: *trichypolum* — 31: *pseudocucurbita* — 32: *trichypolum* var. *elongatum* — 33: *subglobosum* — 34—35: *minutissimum* — 80: *Clevei* var. *delicatulum*.

12. *Actinotaenium trachypolum* (W. et G. S. WEST) comb. nov.
Dim: 22—30×11—17. Fig. 30.

Cosm. trachypolum WEST 1897 c, p. 166, Tab. 8: 14, 15. SKUJA 1949, p. 144, Tab. 26: 4. — *Penium cuticulare*: COSANDEY 1934, p. 44, Tab. 2: 15, 16.

var. *elongatum*. Dim: 32—44×16—18. Fig. 32. WEST 1902, p. 168. Tab. 20: 39, 40. KRIEGER 1932, p. 189, Tab. 9: 11.

var. *Messikommeri* nom. nov. Dim: 33×20—22. Fig. 22. LÜTKEMÜLLER 1900, p. 12, Tab. 1: 31, 32. MESSIKOMMER 1935, p. 50, Tab. 4: 36.

The type form has apical great pores and the protruding parts of their pore-organelles have been taken for granula; the form described by MESSIKOMMER shows a homogeneous pore-apparatus of mixed small and great pores.

13. *Actinotaenium cucurbitinum* (BISS.) comb. nov. Dim: 51—90×23—35. Fig. 36.

Penium cucurbitinum: BISSET 1884, p. 197, Tab. 5: 7. STRØM 1919, p. 21, Tab. 4: 4. WEST 1904, p. 94, Tab. 9: 13, 14. G. S. WEST 1904, p. 139, Fig. 51 D. GISTL 1914, p. 15, Tab. 1: 8. — *Dysphinctium cucurbitinum*: LÜTKEMÜLLER 1905, p. 337. — *Cosm. cucurbitinum*: LÜTKEMÜLLER 1910, p. 479. TAYLOR 1934, p. 252, Tab. 45: 15. MANGUIN 1937, Tab. 2: 29 (Fig. dextr.). PRESCOTT and SCOTT 1952, p. 8, Tab. 4: 11. INSAM und KRIEGER 1936, p. 99, Tab. 1: 3. — *Calocyclus cucurbitinus*: KIRCHNER 1878, p. 143. — *Cosm. palangula*: VAN OYE 1953, p. 178, Fig. 35. — *Penium delicatum* var. *perforatum*: GUTWINSKI 1902, p. 584, Tab. 37: 19.

f. *minus*. Dim: 43—58×17—24. WEST 1904, p. 95, Tab. 9: 16. GRÖNBLAD 1934, p. 267, Tab. 4: 4, 5. PRESCOTT 1936, Tab. 16: 8. BOURRELLY 1948, p. 494, Tab. 8: 70, and 1952, p. 219, Tab. 19: 535. MANGUIN 1937, Tab. 2: 30. ROSA 1951, p. 215, Tab. 12: 14.

f. *majus*. Dim: 97—100×35—43. WEST 1904, p. 95, Tab. 9: 17.

f. *minutissimum*. MANGUIN 1937, Tab. 2: 31.

var. *angustum*. Dim: 74×19. Fig. 37. GRÖNBLAD 1945, p. 17, Tab. 5: 97.

var. *grande*. Dim: 89—118×36—48. GRÖNBLAD 1921, p. 43, Tab. 7: 62. BORGE 1930, p. 33, Tab. 2: 25, and 1936, p. 32, Tab. 1: 20. INSAM und KRIEGER 1936, p. 99, Tab. 1: 1, 2. HIRN 1903, p. 17, Tab. 2: 27.

var. *magellanicum* (BORGE) comb. nov. Dim: 47—57×19—20. Fig. 42. — *Penium magellanicum*: BORGE 1906, p. 29, Tab. 2: 7. Compare *A. palangula* var. *Wollei*!

var. *Manguini* var. nov. Dim: 57—58×24. Fig. 44. — *Cosm. cucurbitinum* forma. MANGUIN 1937, p. 24, Tab. 2: 29 (Fig. sinistr.).

This variety is characterized by the quite cylindrical shape with semi-globoid ends. It had an internal apical papilla, only found in one other picture of *cucurbitinum*, viz. PRESCOTT and SCOTT 1952. Probably not belonging to *cucurbitinum*.

- var. *minutum* PRESCOTT. Fig. 39. MESSIKOMMER 1945, Tab. 2: 38.
- var. *subpolymorphum*. Dim: 71—86×29—38. Fig. 41. NORDSTEDT 1888, p. 71, Tab. 7: 20. WEST 1904, p. 95, Tab. 9: 19, 20, and 1907, p. 189, Tab. 13: 14. MASKELL 1889, p. 27, Tab. 5: 50. KRIEGER 1932, p. 174, Tab. 9: 14.
- var. *subretusum*. Dim: 47×30. Fig. 38. MESSIKOMMER 1954, p. 33, Tab. 1: 5. ?BORGE 1894, p. 22, Tab. 2: 17.
- var. *truncatum*. Dim: 53: 70×15—29. Fig. 43. KRIEGER 1932, p. 174, Tab. 9: 15.
- *Cosm. cucurbitinum*: IRÉNÉE-MARIE 1939, p. 182, Tab. 26: 12. — ?*Penium lagenarioides* var. *intermedium*: GUTWINSKI 1902, p. 584, Tab. 37: 18. — *Cosm. cucurbitinum* f. *minus*: BOURRELLY 1946, p. 93, Tab. 4: 49.
- var. *scoticum*. Dim: 95—97×42—44. WEST 1904, p. 96, Tab. 9: 18. — *Cosm. Thwaitesii* var. *scoticum*: WEST 1894, p. 8, Tab. 1: 15.

As seen from the list above this desmid has been depicted by many desmidiologists who have found it very rich in forms. That all of these belong to the real *A. cucurbitinum* is dubious, the author has only brought most of the literary finds together and also added some desmids published under other names.

The name hints a similarity to *cucurbita*. The reason why BISSET assigned his desmid to *Penium* instead of *Cosmadium* is unknown; his diagnosis is very laconic: "Frond shaped as figured. Endochrome in fillets, three of which are usually seen in frontview. Membrane sparsely punctate. Length 85—90 μ breath 32—35 μ ." I have examined a slide with BISSET's own type specimen in NORDSTEDT's collection and can confirm BISSET's picture, except the distribution of the pores: they are scattered, not in rows, a lithographer's error that BISSET has noted in the reprints.

Most of the desmids cited above, show a narrow oval—slightly fusi-form shape with rounded ends, but also forms with retuse ends WEST 1904, Tab. 9: 13, 17, STRÖM 1919, Tab. 4: 4, and IRÉNÉE-MARIE 1939 p. 182, Tab. 26: 12 are assigned to this species. The latter are to be compared with the retuse forms of *A. cucurbita* and would probably more correctly be assigned to this species; agreement in shape is more important than difference in size, at least on the present stage of our knowledge.

An almost square zygospore (of var. *subpolymorphum*) was firstly described by NORDSTEDT. Later, LÜTKEMÜLLER found double zygospores. His pictures are not published but he sent drawings to NORDSTEDT and G. S. WEST. His spores (Fig. 78) are immature, globoid with a beginning square-form, LÜTKEMÜLLER thought that NORDSTEDT's find was one isolated part of the mature double-spores.

14. *Actinotaenium adelochondrum* (ELFV.) comb. nov. Dim: 32—52×15—20. Fig. 45.

Penium adelochondrum: ELFVING 1881, p. 17, Tab. 1: 13. WEST 1892, p. 128, Tab. 19: 19, 1904, p. 93, Tab. 8: 30, 31, and 1907, p. 190, Tab. 13: 15. SCHMIDLE 1893 a, p. 547, Tab. 28: 2. — *Dysphinctium Palangula*: HEIMERL 1891, p. 594, Tab. 5: 7. — *Dysphinctium adelochondrum*: LÜTKEMÜLLER 1905, p. 337. — *Cosm. adelochondrum*: LÜTKEMÜLLER 1910, p. 479. BORGE 1936, p. 30, Tab. 1: 19. — *Penium cylindrus* var. *attenuatum*. RACIBORSKI 1890, p. 74, Tab. 7: 21. — *Penium minutum* var. *crassum*: BORGE 1903, p. 75, Tab. 1: 4. — *Penium fusiforme*: GAY 1884, p. 69, Tab. 2: 11. var. *Kriegeri*. Dim: 26—36×12—13. Fig. 46. MESSIKOMMER 1942, p. 143, Tab. 4: 20. KRIEGER 1938, p. 60, Tab. 1: 29.

This desmid, fusiform with retuse (or rounded) ends, has great pores the pore-organelles of which ELFVING interpreted as granula, corrected by BORGE (1936, p. 30). Probably it is these "granula" that RACIBORSKI has depicted on his *Penium cylindrus* var. *attenuatum*, both the constricted cell and the size agree with *adelochondrum*. KRIEGER (1932, p. 241) has considered *Penium fusiforme* GAY as a synonym of *Closterium navicula*. It may, however, more correctly be assigned to *adelochondrum*; shape and size agree and GAY did not find any vacuoles or crystals. Possibly other finds of *Closterium* or *Penium navicula* will be assigned to *Actinotaenium*, in specimens without end-vacuole, the structure of the isthmus or the division-stages are decisive.

A spiny and globoid zygospore, found by W. WEST (1892, Tab. 21: 18) and at first assigned to *obcuneatum*, is suspected to belong to *adelochondrum* (WEST 1908, p. 111).

15. *Actinotaenium obcuneatum* (W. WEST) comb. nov. Dim: 28—42×15—18. Fig. 59.

Cosm. obcuneatum: W. WEST 1892, p. 162, Tab. 21: 18. — *Cosm. parvulum*: WEST 1908, p. 110. KRIEGER 1933, Fig. 9: J, K. BOURRELLY 1946 a, p. 495, Tab. 7: 69 "parfaitement circulaire". ALLORGE 1931, p. 358, Tab. 8: 6. SAMPAIO 1944, Tab. 13: 42—44.

Cosm. parvulum is a dimorphous species. BRÉBISSON's diagnose contains no statement as to the cross-section but of the pictures of later authors some show an ovale, others a circular cross-section, sometimes confirmed in the description. Even if quasi-omniradiate forms of *parvulum* theoretically may develop circular specimens, it is probable that the forms depicted by KRIEGER, ALLORGE, and BOURRELLY represent a separate species. This is one of the cases in which, because of the simplicity of the form, a convergency of omniradiate and biradiate des-

mids may occur. WHELDEN (1947, p. 84, Tab. 5: 1) and MESSIKOMMER (1945, p. 101, Tab. 2: 45) have given pictures of the biradial *parvulum* and also have shown that a small apical excavation occurs on biradial specimens. This excavation, previously observed by BORGE (1911, p. 13, Fig. 8) and HANSGIRG (1888, p. 187, Fig. 109, under the name of *Dysphinctium pusillum*, incorrect end-view!) may be a character of the biradial *parvulum* in contrast to *obcuneatum*.

16. *Actinotaenium tumidum* (WOLLE) comb. nov. Dim: 65—70×28—31. Fig. 51.

Cylindrocystis tumida: WOLLE 1887, p. 23, Tab. 56: 7, 8. — *Cylindrocystis angulata*: WEST 1896, p. 237, Tab. 13: 25, 26. — *Cosm. floridanum*: LÜTKEMÜLLER 1913, p. 228.

var. *brasiliense* (GRÖNBLAD). Dim: 65—84×21—27. Fig. 52. — *Cosm. floridanum* var. *brasiliense*: GRÖNBLAD 1945, p. 135, Tab. 6: 108. KRIEGER 1950, p. 40, Fig. 34.

This species was depicted by WOLLE under the name of *Cylindrocystis tumida* GAY. WOLLE's picture has a distinct isthmus-furrow, while GAY's picture is devoid of it and shows a lobo-stelloid chloroplast, that is why WOLLE must be regarded as the author. The WESTS described it as *Cyl. angulata* and LÜTKEMÜLLER changed the name to *floridanum* since the names *angulatum* and *tumidum* already were occupied in *Cosmarium*.

17. *Actinotaenium sydneyense* (RACIB.) comb. nov. Dim: 69—73×25—29. Fig. 50.

Penium lagenarioides var. *sydneyense*: RACIBORSKI 1892, p. 368, Tab. 6: 3. — *Penium heterotaphridium*: WEST 1902, p. 135, Tab. 18: 3, 4. — *Dysphinctium heterotaphridium*: LÜTKEMÜLLER 1905, p. 357. — *Cosm. heterotaphridium*: LÜTKEMÜLLER 1910, p. 479.

RACIBORSKI's desmid was overlooked when the WESTS named their desmid. The two desmids agree exactly in form, dimensions, and the arrangement of pores and scrobiculations. RACIBORSKI described a stelloid chloroplast with eight lamellae and one pyrenoid. The WESTS found a smooth (immature?) globoid zygospore.

18. *Actinotaenium palangula* (BRÉB.) comb. nov. Dim: 32—48×14—17. Fig. 49.

Cosm. Palangula: RALFS 1848, p. 212. BRÉBISSEON 1856, p. 132, Tab. 1: 21. NOTARIS 1867, Tab. 3: 24. WEST 1908, p. 108, Tab. 74: 4—6. GRÖNBLAD 1947, p. 25, Fig. 17. — *Calocylindrus Palangula*: KIRCHNER 1878, p. 143. — *Dysphinctium Palangula*: HANS-

GIRG 1888, p. 184. — *Cosm. Cordanum* f. *minus*: MASKELL 1888, p. 16, Tab. 2: 20 (Fig. dextr.). — *Cosm. Cucurbita* var. *Palangula*: KLEBS 1879, p. 28, Tab. 3: 8 b—d. var. *Wollei*. Dim: 51—75×21—25. Fig. 47. — *Calocylinthus Cucurbita*: WOLLE 1884, p. 64, Tab. 12: 14. — idem f. *Wollei*: EICHLER 1894, p. 126, Tab. 2: 14. — *Penium Cucurbitinum*: GISTL 1914, p. 15, Tab. 1: 8. — *Cosm. cucurbitinum*: TAYLOR 1933, p. 252, Tab. 45: 14.

var. *silesiacum* (KIRCHNER) comb. nov. Dim: 42—51×12—14. Fig. 48. — *Calocylinthus Cylindrus* var. *silesiacus*: KIRCHNER 1878, p. 143. — *Penium cylindrus* var. *silesiacum*: SCHMIDLE 1893, p. 20, Tab. 3: 6. JOHNSON 1895, p. 291, Tab. 239: 2.

BRÉBISSEON's picture (lithographed by himself) shows a baculiform cylindrical cell with obtuse or slightly rounded ends. In the short diagnosis he emphasized that the pores are arranged in transverse rows and persisted in it against RALFS' critique (1848, p. 212). RALFS and also DE NOTARIS have found the pores arranged as a system of two oblique-crossing series of pores, a pattern that implies the vertical rows. Except for the pore arrangement *palangula* differs from *cucurbita* only by a greater ratio of length : breadth, thus, it could be regarded as a long variety of *cucurbita*, as KLEBS has proposed.

KIRCHNER (1878) created var. *silesiacus* of *Calocylinthus* (*Penium*) *Cylindrus* and characterized it by its dense and irregular punctae, i.e. granules. SCHMIDLE (1893) and JOHNSON (1895) have used this name for a desmid with an evident isthmus-furrow. JOHNSON has depicted the pores and SCHMIDLE the granules, i.e. in this case the protruding pore-organelles. Though KRIEGER has taken up these two pictures as belonging to *Penium cylindrus*, it seems inevitable to reject them as *Penium* and assign them to *Actinotaenium*, most probably to *A. palangula*.

19. *Actinotaenium inconspicuum* (W. WEST) comb. nov. Dim: 13—19(—30)×5—8. Fig. 57, 58.

Penium inconspicuum: W. WEST 1894, p. 4, Tab. 1: 6, 7. WEST 1896, p. 237, Tab. 12: 34, and 1904, p. 101, Tab. 10: 15—17. — *Dysphinctium inconspicuum*: LÜTKEMÜLLER 1905, p. 337. — *Cosm. bacillare*: LÜTKEMÜLLER 1910, p. 484. ALLORGE et MANGUIN 1941, p. 166, Fig. 17.

A. inconspicuum f. *bacillare* (ad interim): GRÖNBLAD 1921, p. 37, Tab. 1: 38. ALLORGE 1931, p. 353, Tab. 10: 19, 20. MESSIKOMMER 1928, p. 206, Tab. 8: 4, and 1943, Tab. 9: 18. KRIEGER 1932, p. 170, Tab. 9: 12. HUZEL 1936, p. 76, Tab. 9: 12. BOURRELLY 1952, p. 219, Tab. 28: 507 (f. *majus*).

W. WEST's species has a double-ovale shape but an other somewhat deviating form with the same dimensions has been published by several authors. This desmid has straight-sided, slightly conical semicells and,

in certain cases, an internal apical papilla. It is recorded from different parts of the world and is uniform also in the dimensions. It makes the impression of a small form of *Pleurotaenium minutum* and may conveniently be called f. *bacillare* until its relations are quite known. It agrees with IRÉNÉE-MARIE's picture (1952, Tab. 2: 11, 12), labelled as *Penium crassum* var. *inflatum* but this author has in a letter told me that it should correctly be called *Pleurotaenium minutum* var. *crassum*.

LÜTKEMÜLLER (1910, p. 484) recorded a dwarf form of only $7 \times 4.5 \mu$.

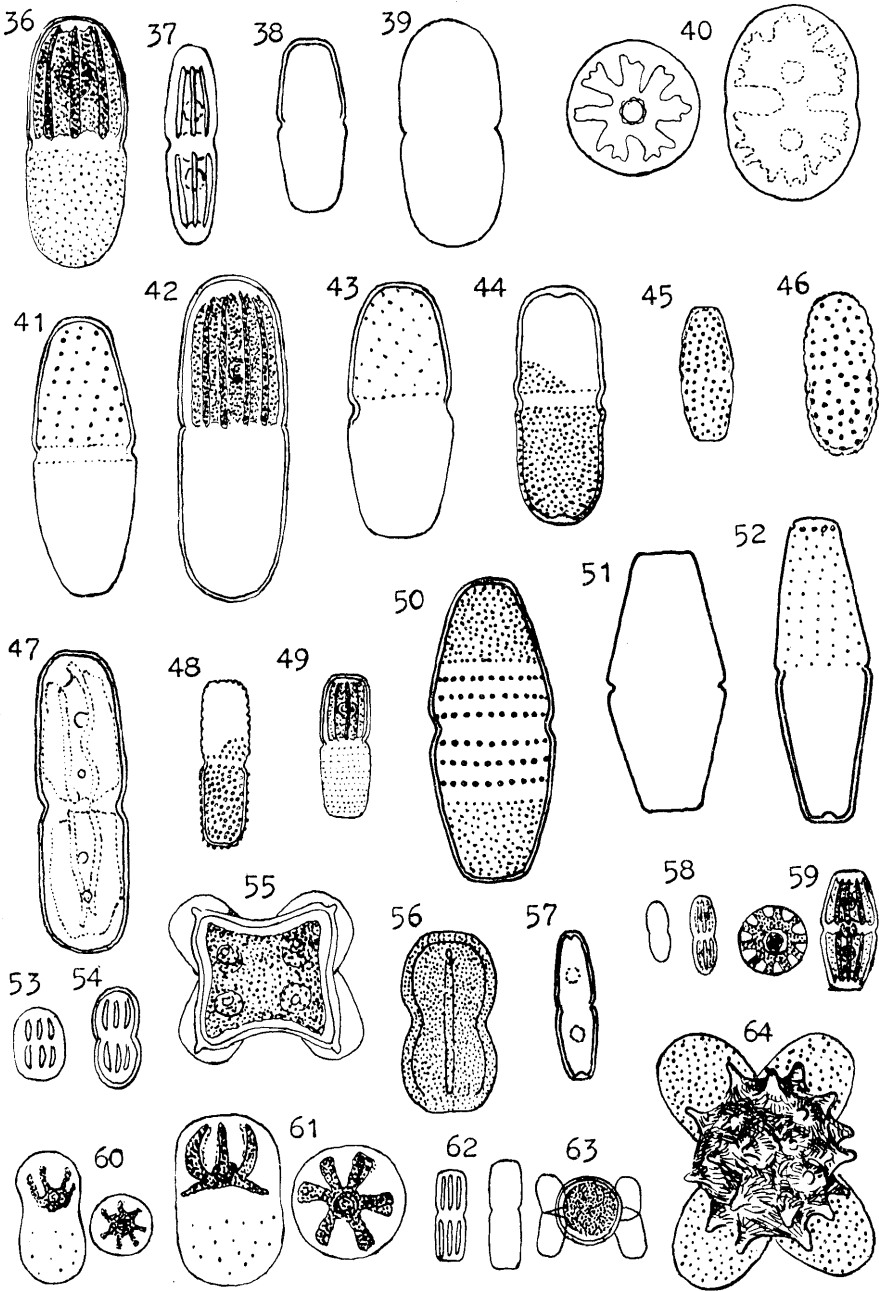
20. *Actinotaenium truncatum* (BRÉB.) comb. nov. Dim: $22-47 \times 10-14$. Fig. 62, 63.

Penium truncatum: RALFS 1848, p. 152, Tab. 25: 5 (c. zyg.). DELPONTE 1877, p. 181, Tab. 15: 37-39. NOTARIS 1867, p. 69, Tab. 8: 78. WOLLE 1884, p. 35, Tab. 5: 9, 10, and Tab. 5: 21, 22 (variety). COOKE 1886, p. 14, Tab. 17: 4. WEST 1904, p. 82, Tab. 8: 24-26. — *Pleurotaenium truncatum*: CLEVE 1863, p. 494. — *Cosm. abscissum* LÜTKEMÜLLER in manuscr.: KRIEGER 1935, p. 342.

Already RALFS described *Penium truncatum* to be "minutely dotted" and LÜTKEMÜLLER reported to G. S. WEST (in litt. 1911) that he had examined this desmid and had found its membrane to be porous, consequently belonging to *Cosmarium*. In KRIEGER (1935, p. 242) *Cosm. truncatum* is taken up as a synonym to *Cosmarium abscissum* LÜTK. LÜTKEMÜLLER had invented this name for *Penium truncatum* and in his manuscript he gives the diagnose: "Chloroplast axil mit 6 ganzrandigen Längsleisten. Von *Cosmarium Palangula* durch die parallelen nach oben nicht convergierenden Seiten, den abgestutzten Scheitel, durch die dünnere Zellhaut und die abweichende Verteilung der Poren unterschieden", (communicated by Dr. GRÖNBLAD). GRÖNBLAD has (1921, p. 29) described a *Cosm. abscissum*. As *Cosm. abscissum* LÜTK. is a *nomen nudum*, there may not be any confusion.

The zygospore is smooth and sphaerial (RALFS, WOLLE).

Figs. 36-64. — 36: *cucurbitinum* — 37: var. *angustatum* — 38: var. *subretusum* — 39: var. *minutum* — 40: *Wollei* — 41: *cucurbitinum* var. *subpolymorphum* — 42: var. *magellanicum* — 43: var. *truncatum* — 44: var. *Manguini* — 45: *adelochondrum* — 46: var. *Kriegeri* — 49: *palangula* — 47: var. *Wollei* — 48: var. *silesiacum* — 50: *sydneyense* — 51: *tumidum* — 52: var. *brasiliense* — 53: *Mooreanum* — 54: f. *constrictum* — 55: zygospore — 56: *viride* — 58: *inconspicuum* — 57: f. *bacillare* — 59: *obcuneatum* — 60: *perminutum* — 61: *subtile* — 62-63: *truncatum* — 64: *cucurbita*, zygospore.



Figs. 36—64.

21. *Actinotaenium crassiusculum* (DE BARY) comb. nov. Dim: 56—70×11—23. Fig. 77.

Penium crassiusculum: DE BARY 1858, p. 73, Tab. 5: 5—7. BÖRGESEN 1890, p. 931, Tab. 2: 1. LÜTKEMÜLLER 1900, p. 116, Tab. 6:2. BORGE 1906, p. 15, Tab. 1: 6. WEST 1904, p. 96, Tab. 8: 4, 5. DUCELLIER 1916, p. 56, Fig. 33—35. IRÉNÉE-MARIE 1952, p. 30, Tab. 4: 1. COOKE 1886, p. 44, Tab. 17: 17. — *Penium Brebissonii* var. *crassiusculum*: KLEBS 1879, p. 23, Tab. 3: 1. — *Cosm. crassiusculum*: INSAM und KRIEGER 1936, p. 98, Tab. 1: 5. ALLORGE et MANGUIN 1941, p. 168, Fig. 22.

This desmid was not transferred from *Penium* by LÜTKEMÜLLER in his revision of 1905, but he has later (in a letter to G. S. WEST) stated it a *Cosmarium* (the pores have been noted already by BÖRGESEN). Evidently the pores are more difficult to discern than on *palangula* and this circumstance may have caused these two so similar species to be assigned to different genera. The difference seems to lie mainly in the size; *crassiusculum* is, as a rule, longer, more than 50 μ compared with *palangula* that scarcely exceeds 50 μ .

DE BARY depicted a lateral nucleus, (repeated in WESTS' Monograph), a position that has not been verified by DUCELLIER. The chloroplast has 6—7 lamellae. ROY and BISSET (1894) have found the zygospore "similiar to that of phymatosporum but with angles less prominent and more round".

22. *Actinotaenium Taylori* (N. CARTER) comb. nov. Dim: 160—230×45—50. Fig. 65.

Cosm. Taylori: N. CARTER 1935, p. 169, Figs. 27, 28.

This interesting species has a scrobiculate cell wall, the upper third of the semicell bears pores in transversal and longitudinal rows with protruding pore-organelles. In connection with the largeness of the cell the chloroplast has developed in a parietal direction; the edges of the lamellae are curled and laciniate. It contains several axile pyrenoids.

23. *Actinotaenium cucurbita* (BRÉB.) comb. nov. Dim: 29—51×15—24. Fig. 66.

Cosm. cucurbita: RALFS 1844, p. 395, Tab. 11: 10, and 1848, p. 108, Tab. 17: 7. KLEBS 1879, p. 28, Tab. 3: 8 b, c, g. SCHMIDLE 1894, p. 89, Tab. 6: 3. WEST 1908, p. 106, Tab. 73: 31—33. KRIEGER 1932, p. 174, Tab. 9: 16. TAYLOR 1934, p. 252, Tab. 51: 6. IRÉNÉE-MARIE 1939, p. 181, Tab. 22: 11. INSAM und KRIEGER 1936, p. 99, Tab. 1: 14. LHOTSKY 1948, p. 3, Tab. 2: 46. HUZEL 1936, p. 91, Tab. 11: 2, 3. BOURRELLY 1952, p. 219, Tab. 29: 532 (forma). SAMPAIO 1944, p. 350, Tab. 13: 37—39. — *Cosm. Palangula*: DE BARY 1858, p. 72, Tab. 6: 51. — *Dysphinctium Cucurbita*:

GRUNOW 1858, p. 500. GUTWINSKI 1909, p. 448, Tab. 7: 11 a (var. *inflatum*). — *Calocylinthus Cucurbita*: KIRCHNER 1878, p. 143. COOKE 1886, p. 125, Tab. 44: 7. W. WEST 1889, p. 18, Tab. 3: 15. — *Penium adelochondrum*: KUFFERATH 1914, p. 297, Fig. 8 (var. *punctatum*), and p. 298, Fig. 9 (var. *constrictum*).

f. *majus*. Dim: 60×30. W. WEST 1892, p. 162, Tab. 24: 25. WEST 1908, p. 107, Tab. 74: 2.

f. *minus*. Dim: 24×12. BOURRELLY 1946, p. 93, Tab. 4: 52.

f. *minimum*. WEST 1895, p. 176.

f. *rotundatum*. Dim: 28×16. KRIEGER 1932, p. 174, Tab. 8: 13. VAN OYE 1953, p. 281, Fig. 65, and 1949, p. 295, Fig. 21. N. CARTER 1920 a, p. 217, Tab. 10: 14, 15.

f. *latius*. Dim: 37—40×23—27. WEST 1908, p. 108, Tab. 74: 1. INSAM und KRIEGER 1936, p. 99, Tab. 1: 6. DUCELLIER 1918, p. 123, Fig. 106. — *Calocylinthus Palangula* var. *rotundatus*: ISTVANFFI 1888, p. 288, Tab. 1: 21, 22. — *Cosm. Palangula*: KLEBS 1886, p. 357, Tab. 2: 15. — *Cosm. conicum*: GUTWINSKI 1909, p. 492, Tab. 7: 16.

var. *attenuatum*. Dim: 24—46×15—23. Fig. 67—69. G. S. WEST 1904 b, p. 286, Tab. 464: 18. WEST 1908, p. 108, Tab. 73: 34—36. LOWE 1923, Tab. 3: 8. ALLORGE et MANGUIN 1941, p. 168, Tab. 26: 1—3. GRÖNBLAD 1938, p. 3, Fig. 8. KRIEGER 1944, p. 269, Fig. 45. SKUJA 1949, p. 120, Tab. 26: 1, 2. IRÉNÉE-MARIE 1952, p. 109, Tab. 10: 17. SAMPAIO 1944, p. 351, Tab. 13: 40, 41. — *Cosm. curtum*: BERGE 1894, p. 22, Tab. 2: 17. — *Dysphinctium cucurbita* f.: SCHMIDLE 1895, p. 347, Tab. 14: 16. GUTWINSKI 1909, p. 448, Tab. 7: 11 (var. *inflatum*). — *Cosm. Cucurbita*: KLEBS 1879, p. 28, Tab. 3: 8 d. MANGUIN 1937, Tab. 2: 28. MESSIKOMMER 1943, Tab. 10: 5. KOSSINSKAJA 1938, Tab. 2: 11. — *Cosm. Palangula*: VAN OYE 1952, p. 178, Fig. 35. — *Cosm. conicum*: WEST 1895, p. 71, Tab. 8: 12. ROUBAL 1947, p. 50, Tab. 5: 10 (var. *brevius*).

var. *robustum*. Dim: 63—65×30—33. Fig. 70. KRIEGER 1950, p. 40, Fig. 8.

Zygosporae: WEST 1908, p. 106, Tab. 74: 3. HOMFELD 1929, p. 41, Tab. 5: 54. GRÖNBLAD 1921, p. 53, Tab. 7: 63. FRITSCH and RICH 1937, p. 184, Fig. 13: 1, Fig. nostr. 64. SKUJA 1949, p. 120, Tab. 26: 3.

Judging from the many varieties and forms this species is very variable; next to *A. cucurbitinum* the most depicted species of *Actinotaenium*. BRÉBISSEON's main type is cylindrical with abruptly retuse ends but the attenuate type with more conical semi-cells and slightly rounded ends may be quite as prominent. Within these two types there is a great variation in the proportions and the size.

The WESTS (1908, Tab. 73: 32) have depicted the chloroplast, showing lappets of the lamellae radiating from the pyrenoid. Already DE BARY (1858, Tab. 6: 51), however, has depicted a typical stelloid chloroplast, a structure confirmed by N. CARTER, BOURRELLY, KLEBS, and HUZEL, the latter has described a parietal extension of the edges.

Mature zygosporae have a globoid shape with conical verrucae, Fig. 64.

It is of interest that KRIEGER (1944) and BOURRELLY (1952) have seen an internal apical papilla.

Cosm. conicum WEST seems to fall into one of the many forms of

cucurbita. There is another desmid, *Dysphinctium conicum* TURNER, that may be assigned to *Actinotaenium*, see species inquirendae, p. 415.

24. *Actinotaenium pseudocucurbita* (BOURR.) comb. nov. Dim: 24×16 . Fig. 31.

Cosm. pseudocucurbita BOURRELLY 1946, p. 96, Tab. 4: 50, 51.

It differs from *cucurbita* in the rectangular zygospore. The cells show a striking similarity to *Calocylindrus Palangula* var. *rotundatus* ISTWANFFY (1888, Fig. 21) but this one is twice the size of *pseudocucurbita*.

25. *Actinotaenium minutissimum* (NORDST.) comb. nov. Dim: $12-19 \times 9-11$. Fig. 34, 35.

Penium minutissimum: NORDSTEDT 1873, p. 46, Tab. 1: 21. COOKE 1886, p. 95, Tab. 17: 10. WEST 1904, p. 81, Tab. 8: 20-23. N. CARTER 1922, p. 63, Tab. 4: 15. KRIEGER 1932, Tab. 7: 9. — *Cosm. nanum* LÜTKEMÜLLER (*in manuscr.*) GRÖNBLAD 1934, p. 269, Fig. 5: C. TAFT 1937, p. 402, Tab. 2: 15. — *Cosm. Luetkemulleri*: GRÖNBLAD 1935, p. 4.

f. *majus*. Dim: $13-27 \times 10-18$. WILLE 1884, p. 48, Tab. 3: 9. BORGE 1903, p. 94, Tab. 1: 2.

Cell broad-ovale, without isthmal constriction, chloroplast with four lamellae (GRÖNBLAD, TAFT). BORGE has found a questionable forma *major* with a faint isthmus-furrow; it may be a small form of *A. cucurbitinum*.

The zygospore is lens-shaped with four rounded angles (NORDSTEDT, WILLE, KRIEGER, N. CARTER).

Var. *suboctangulare* (W. WEST) comb. nov. Dim: $14-16 \times 10$. Fig. 27.

Penium suboctangulare: W. WEST 1892, p. 128, Tab. 224: 20. WEST 1904, p. 81, Tab. 8: 14-19.

KRIEGER (1932, p. 242) has proposed that this desmid be assigned to *Mooreanum*, the latter, however, has the angles of the zygospore ending in a distinct papilla while the zygospore of *suboctangulare* has the angles cut off, giving it the shape of an octagon.

26. *Actinotaenium Mooreanum* (ARCH.) comb. nov. Dim: $17-26 \times 11-15$. Fig. 53, 55.

Penium Mooreanum: ARCHER 1864, p. 50, Tab. 1: 34-44. COOKE 1886, p. 44, Tab. 17: 5. SCHMIDLE 1893, p. 21, Tab. 3: 8, 9. WEST 1904, p. 80, Tab. 8: 8-10. GUTWINSKI 1907, p. 444, Tab. 7: 9 (zygospore). STRÖM 1923, p. 464, Tab. 12: 6. — *Penium pusillum*: DELPONTE 1877, p. 185, Tab. 15: 34-36. — *Dysphinctium cruciferum* var. *tatri-*

cum: GUTWINSKI 1909, p. 447, Tab. 7: 10. — *Dysphinctium Mooreanum*: LÜTKEMÜLLER 1905, p. 337. — *Cosm. Mooreanum*: LÜTKEMÜLLER 1910, p. 479. BORGE 1936, p. 35, Tab. 1: 21.

f. *constrictum*. Fig. 54. SCHMIDLE 1893, p. 21, Tab. 3: 10, 11, and 1897, p. 22, Fig. 3 (zygosp.). — *Penium sp.* BORGE 1930, p. 26, Tab. 1: 12, 13.

Penium sp. BORGE agrees well in the shape with slightly constricted shape, the size and the chloroplast.

Cell broad-oval or cylindrical with rounded ends. Chloroplast stelloid with six lamellae. Zygospore quadrangular with slightly constricted sides and one papilla on each angle.

27. *Actinotaenium pyramidatum* (W. et G. S. WEST) comb. nov. Dim: 34—49×22—26. Fig. 71, 72.

Cylindrocystis pyramidata: WEST 1902, p. 134, Tab. 18: 1, 2. WEST 1907, Tab. 13: 4, 5. — *Cosmariium cylindrocystiforme*: G. S. WEST 1912, p. 85. BOURRELLY 1952, p. 219, Tab. 29: 536. — *Penium pyramidatum* KRIEGER 1932, Tab. 7: 13.

This desmid is similar to a broad *curtum* but has a lobo-stelloid chloroplast. The zygospore is ellipsoidal and smooth.

Cosm. subpyramidatum (WEST) LÜTK. (WEST 1901, p. 78, Tab. 2: 8—11 and LÜTKEMÜLLER 1913, p. 228, Tab. 2: 28) is no doubt an *Actinotaenium* but as yet insufficiently known. The shape is of *curtum* type and very similar to that of *pyramidatum*. However, the diagnose does not mention anything about the chloroplast and WESTS' picture gives no information of it but a great pyrenoid. LÜTKEMÜLLER has examined WESTS' material and has stated the porous cell wall and the oval zygospore. In a picture, sent to G. S. WEST in 1912, he has depicted the contracted chloroplasts and they agree more with a lobo-stelloid chloroplast than with a stelloid one.

In spite of the somewhat smaller size and the still obscure chloroplast but according to the similiarity in shape and the identity of the zygospore, this desmid is likely to be united with *pyramidatum*. In this case the name *subpyramidatum* possesses priority.

28. *Actinotaenium subpalangula* (ELFV.) comb. nov. Dim: 25—34×20—25. Fig. 12.

Cosm. subpalangula: ELFVING 1881, p. 14, Tab. 1: 11. BORGE 1906, p. 29, Tab. 2: 20. BORGE 1936, p. 37, Tab. 1: 18. WEST 1938, p. 109, Tab. 74: 7. — *Dysphinctium subpalangula*: DE TONI 1889, p. 882.

f. *depauperatum*: LAGERHEIM 1886, p. 47.

The barrel-shaped cell is very characteristic, compare *A. cucurbita* f. *latius*. The large pores are arranged in transverse rows, bearing protruding pore-organelles. These may be lacking or overlooked; f. *depauperatum*. The chloroplast is lobo-stelloid.

DICK's *subpalangula* (1930, p. 41, Tab. 7: 12) differs in shape so much that BORGE (1936, p. 37) found it dubious. Probably these granules are true ones and not pore-organelles. The circular form in end-view caused DICK to deny a connection with *Cosm. amoenum*, perhaps it may be a small form of *Cosm. elegantissimum* var. *simplicius*, compare IRÉNÉE-MARIE 1939, Tab. 30: 12.

29. *Actinotaenium subtile* (W. et G. S. WEST) comb. nov. Dim: 14—18×10—12. Fig. 61.

Penium subtile: WEST 1897 a, p. 479, Tab. 6: 8, 9. WEST 1904, p. 92, Tab. 8: 27—29. — *Dysphinctium subtile*: LÜTKEMÜLLER 1905, p. 336. — *Cosm. subtile*: LÜTKEMÜLLER 1910, p. 494. BEYERINCK 1926, p. 50, Tab. 8: 165. BORGE 1936, p. 38, Tab. 1: 26. ALLORGE 1931, p. 361, Tab. 10: 27, 28. *Cosm. cruciferum*: BORGE 1930, p. 32, Tab. 1: 21—23. BORGE 1936, p. 32, Tab. 1: 22. SKUJA 1934, p. 69, Fig. 97.

var. *subsparsopunctatum*: GRÖNBLAD 1921, p. 38, Tab. 7: 34—37.

This desmid has a very simple shape, broad-oval with obtuse ends and a faint isthmus-furrow. It is distinguished from similar desmids by the lobo-stelloid chloroplast with 5—7 lobes, carefully depicted by GRÖNBLAD. On stained specimens BORGE has observed the pore-organelles.

Desmids published as *Cosm. cruciferum* by SKUJA and BORGE are probably to be assigned to *subtile* because of the lobo-stelloid chloroplast. SKUJA, however, has (p. 69) mentioned that the cell-division is performed in the simple manner, characteristic of the saccoderms, *Penium* and *Closterium*. If this observation is confirmed, his desmid must be placed with the saccoderms, nearest to *Cylindrocystis*.

30. *Actinotaenium perminutum* (TURNER, G. S. WEST) comb. nov. Dim: 10—14×5—8. Fig. 60.

Cylindrocystis minutissima: TURNER 1892, p. 16, Tab. 1: 24. WEST 1904, p. 62, Tab. 5: 9. HUZEL 1936, p. 75, Tab. 19: 18. TAFT 1937, p. 402, Tab. 2: 24. — *Cosm. perminutum*: G. S. WEST 1914, p. 1041. GRÖNBLAD 1921, p. 37, Tab. 7: 39—41. — *Cosm. pseudarctoides*: STRÖM 1920, p. 31, Tab. 3: 7, 8. — *Cosm. pseudarctoum* var. *perminutum*: BOURRELLY 1946, p. 496, Tab. 8: 71.

Cell guitar-shaped in front view, chloroplast lobo-stelloid with 4—7 lobes.

31. *Actinotaenium viride* (CORDA) comb. nov. Dim: 40—65×20—36. Fig. 56, 73.

Colpopelta viridis: CORDA 1835, p. 206, Tab. 2: 28. — *Cosm. Colpopelta*: BRÉBISSEON 1861, p. 734. — *Cosm. Cordanum*: RABENHORST 1858, p. 177. TURNER 1885, p. 954, Tab. 4: 15. BERGE 1906, p. 36, Tab. 2: 21. WOLLE 1887, Tab. 40: 28. — *Cosm. viride*: JOSHUA 1885, p. 24, Tab. 254: 3. WEST 1895, p. 71, Tab. 9: 27, and 1908, p. 113, Tab. 74: 16—18. BERGE 1928, p. 101, Tab. 1: 15. KRIEGER 1932, p. 190, Tab. 8: 11. TAYLOR 1934, p. 272, Tab. 59: 14, and Tab. 55: 8. INSAM und KRIEGER 1936, p. 111, Tab. 1: 9. SAMPAIO 1944, Tab. 13: 45—48. — *Dysphinctium Cordanum*: HANSGIRG 1888, p. 186. — *Dysphinctium viride*: DE TONI 1884, p. 885. — *Cylindrocystis* (?) *depressa*: TURNER 1892, p. 16, Tab. 7: 11. — *Calocyclus diplosporus*: WILLE 1884, p. 56, Tab. 12: 8. — *Dysphinctium globosum* var. *subviride*: SCHMIDLE 1893, p. 24, Tab. 6: 13, and 1894, p. 51, Tab. 7: 7 (*Cosm. moniliforme* f. *subviride*).

f. *minus*. Dim: 31—33×18—19. W. WEST 1892, p. 161. MASKELL 1888, p. 15, Tab. 2: 20 (Fig. sinistr.). WEST 1907, p. 205, Tab. 13: 12 (var. *truncatum*), and 1908, p. 113, Tab. 74: 19.

This desmid is one of the first distinguished as a picture (Fig. 56) given by CORDA (1835, p. 206, Tab. 2: 25) with explanation, under the name of *Colpopelta viridis*. There may be little doubt that CORDA's "animalcule" is a desmid, though he has seen both "bouche" and "tube alimentaire". He mentioned the content as green and the skin as rough. Since then it has been found and depicted by several botanists, all of them showing the guitar-shape with rounded or retuse ends in front view and (sometimes) also the circular end view. As regards the chloroplast nothing was mentioned, but SKUJA (1934, p. 76) has given a description: a central core with a large pyrenoid and numerous radiating lappets with somewhat thickened ends, i.e. a lobo-stelloid chloroplast.

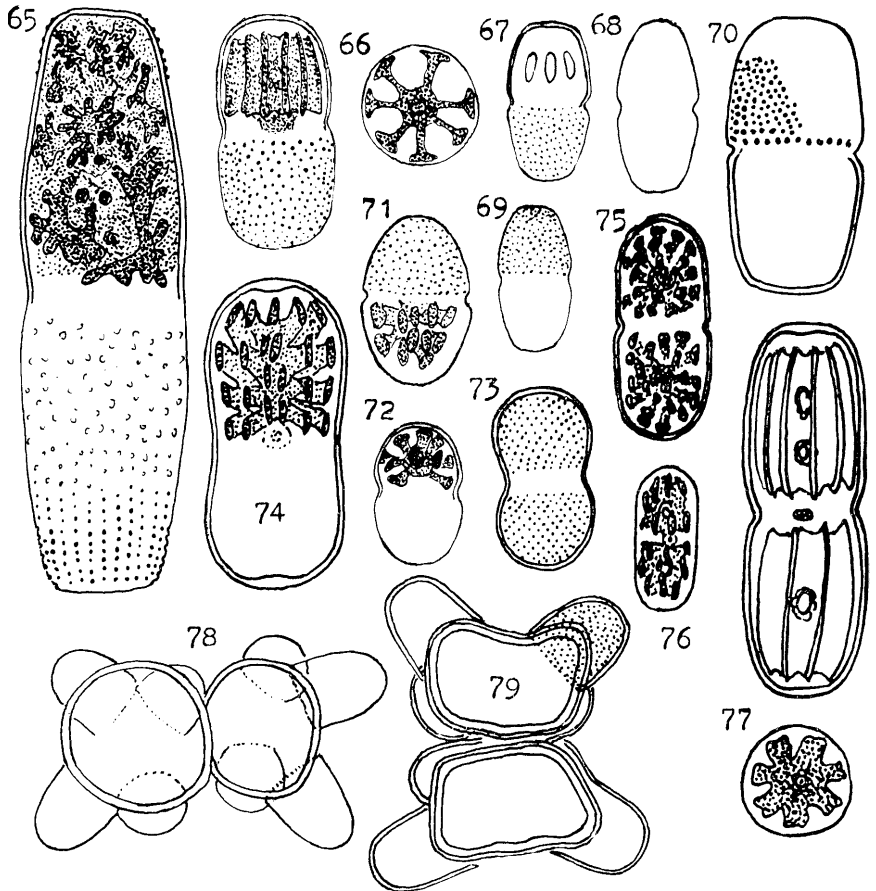
The var. *truncatum* and f. *glabrum* WEST are omitted; the separating characters are of no biosystematical interest. Perhaps *Dysphinctium inferum* TURNER (1892, p. 40, Tab. 1: 21) and *Penium* sp. FRITSCH (1912, p. 20, Tab. 3: 45, 46) belong to f. *minus*.

It is impossible to distinguish outline pictures of *viride* from certain desmids described as *Cosm. moniliferum* var. *panduriforme* and *Cosm. globosum*, which, however, have a furcoid chloroplast, the lamellae having entire edges.

Cosm. viride var. *compressum* TAFT (1945, p. 200, Tab. 3: 37, 38) is not *viride* because of the biradiate shape and the granulate cell wall.

32. *Actinotaenium diplosporum* (LUND.) comb. nov. Dim: 60—72×28—29. Fig. 74.

Cylindrocystis diplospora: LUNDELL 1871, p. 83, Tab. 5: 7 (c. zyg.). NORDSTEDT 1888, p. 72, Tab. 7: 25. BERGE 1891, p. 13, Fig. 11. TURNER 1892, p. 16, Tab. 7: 8.



Figs. 65—79. — 65: *Taylori* — 66: *cucurbita* — 67—69: var. *attenuatum* — 70: var. *robustum* — 71—72: *pyramidatum* — 73: *viride* — 74: *diplosporum* — 75: var. *americanum* — 76: f. *minus* — 77: *crassiusculum* — 78: *cucurbitinum*, zygospore — 79: *diplosporum* var. *americanum* f. *minus*, zygospores.

WEST 1904, p. 61, Tab. 4: 40, 41 (c. zyg.). G. S. WEST 1916, p. 306, Fig. 230 I. DUCELLIER 1916, p. 50, Fig. 27 (zyg.). TAYLOR 1934, p. 240, Tab. 45: 8. — *Penium diplosporum*: JACOBSEN 1874, p. 161. — *Cosm. cordanum*: W. WEST 1889, p. 18, Tab. 3: 23. — *Cosm. diplosporum*: LÜTKEMÜLLER 1913, p. 227, Tab. 2: 27. N. CARTER 1920, p. 271, Tab. 10: 21. ALLORGE 1841, p. 355, Tab. 8: 9 (c. zyg.). — *Cosm. pseudo-hibernicum*: LÜTKEMÜLLER 1910, p. 492, Tab. 2: 27. — *Cosm. hibernicum*: GRÖNBLAD 1920, p. 42, Tab. 5: 21, 22. — *Cosm. viride*: IRÉNÉE-MARIE 1939, p. 182, Tab. 21: 16, and Tab. 24: 14, and 1948, p. 173, Tab. 3: 7. — ?*Schizospora pachyderma*: REINSCH 1875, p. 87, Tab. 17: 1.

f. *minus*. Dim: 31—43×15—17. — *Cylindrocystis americana* var. *minor*: IRÉNÉE-MARIE 1839, p. 377, Tab. 66: 1, 2. *Cosm. quadratum* f. *cylindricum*: EICHLER 1894, p. 126, Tab. 2: 15.

f. *majus*. Dim: 102—150×47—55. — *Cylindrocystis diplospora* ssp. *major* f. *constricta*: WEST 1894, p. 4, Tab. 1: 9 a. *Cylindrocystis diplospora* var. *major*: WEST 1904, p. 61, Tab. 4: 43. — *Cosm. diplosporum* var. *majus*: ALLORGE 1931, p. 355, Tab. 8: 10 (c. zyg.). IRÉNÉE-MARIE 1949, p. 255, Tab. 1: 7. SKUJA 1949, p. 122, Tab. 26: 11 (var. *majus*!).

The pictures of this desmid show in front view 2 types: one is slightly guitar-shaped and the other almost cylindrical. The former is LUNDELL's type form. It somewhat resembles *A. viride* but has a broader isthmal part, more obtuse ends and, in most pictures, the internal apical papilla. I have used this papilla as a distinguishing character against *viride* and also against var. *americanum*. In the list above only IRÉNÉE-MARIE's picture in 1939, Tab. 21: 16 has the shape and size of *viride*, while his f. *typicum* is typical *diplosporum*.

A. diplosporum has, as *viride*, a lobo-stelloid chloroplast, described by LÜTKEMÜLLER and N. CARTER and unmistakably depicted already by LUNDELL.

The double zygospore, depicted by several authors, consists of two squares with rounded, somewhat bulged angles. SKUJA (1949) found azygospores and zygospores of normal type, both formed by the cylindrical type without apical papilla. The cylindrical type agrees very well with:

var. *americanum* (W. et G. S. WEST) comb. nov. Dim: 52—64×22—26. Fig. 75. — *Cylindrocystis americana*: WEST 1898, p. 281, Tab. 18: 5, 6. CUSHMAN 1904, p. 161, Tab. 7: 3. TAYLOR 1934, p. 239, Tab. 45: 9. IRÉNÉE-MARIE 1948, p. 47, Tab. 2: 17. — *Cylindrocystis diplospora*: EICHLER 1893, p. 163, Tab. 10: 32. SKUJA 1949, p. 122, Tab. 25: 10, and Tab. 27: 11, 12 (spor.). HOMFELD 1927, p. 43, Tab. 6: 57 (spor.). KRIEGER 1933, p. 70, Fig. 25 F.

f. *minus* nob. Dim: 31—40×14—18. Fig. 76. — *Cylindrocystis americana* var. *minor*: CUSHMAN 1905, p. 582, Tab. 26: 1. IRÉNÉE-MARIE 1939, p. 37, Tab. 9: 6, 7. *Cylindrocystis diplospora* f. *intermedia*: SCHMIDLE 1894, p. 50, Tab. 7: 9. *Cosm. illudens* LÜTKEMÜLLER msr.

f. *majus*. Dim: 88—163×43—48. — *Cylindrocystis diplospora* var. *major*: W. WEST 1892, p. 131, Tab. 20: 5. WEST 1904, p. 61, Tab. 4: 42, and 1907, p. 190, Tab. 13: 1. — *Cosm. diplosporum* var. *majus*: HOMFELD 1927, p. 43, Tab. 6: 58, 59.

The structure of the cell wall is not known well enough to establish the placoderm character, but points of agreement with other desmids transferred from *Cylindrocystis* to the *Placodermæ* are enough to assign it to *Actinotaenium*. Several scientists have depicted the porous cell wall, e.g. WEST 1907, ALLORGE, SKUJA.

According to WEST, this variety is cylindrical with rounded ends and has no apical papilla. The few statements of the dimensions hint

a size somewhat smaller than *A. diplosporum*. The chloroplast is lobo-stelloid.

LÜTKEMÜLLER has (according to letters to NORDSTEDT in 1911 and to G. S. WEST in 1912) studied a desmid of somewhat smaller size and the same shape, although without isthmus-furrow, and lacinate stelloid chloroplast, which he considered a new species: *Cosm. illudens* Fig. 79. It forms double zygosporos of exactly the same type as *diplosporum* formed by four mother-cells. In his picture the apical papilla is lacking. This desmid is here ranged in var. *americanum* f. *minus*.

Of the pictures of *A. diplosporum* var. *majus* and f. *intermedium*, some show the apical papilla, others do not. According to the proposed division of this species they are assigned to *diplosporum* and var. *americanum*.

Note about Penium didymocarpum LUND.

KRIEGER has (1934, p. 241) recommended *Penium didymocarpum* to be a synonym of *Cosm. diplosporum*. *Didymocarpum*, however, is a true *Penium* according to LÜTKEMÜLLER (1905, p. 337). After extended studies on this genus, L. communicated (in a letter to G. S. WEST in 1911), that the cell wall of *Penium didymocarpum* has no pores but longitudinal rows of small granula, visible after staining, quite as other *Penia*. He also sent a picture of the microstructure of *Penium polymorphum*, *didymocarpum*, *phymatosporum* and his *incurvum* n.sp. mscr. Thus, the uniting of *didymocarpum* with *diplosporum* must be considered incorrect.

Unsufficiently known desmids probably belonging to Actinotaenium.

Penium australe RACIBORSKI (1892, p. 7, Tab. 6: 11). The porous cell wall, depicted by RACIBORSKI, G. S. WEST (1907, p. 108, Tab. 6: 3, 4), WEST (1897 c, Tab. 8: 6) confirms the placoderm character. No information of the chloroplast is given, but PLAYFAIR (1907, p. 168, Tab. 2: 5) recorded, under this name, a similar with slightly attenuate semi-cells that has 6—8 lamellae and one great pyrenoid. On the other side, PLAYFAIR (1914, p. 98, Tab. 3: 2) found a dicentric f. *crassius*.

Penium bisporum TURNER (1892, p. 17, Tab. 1: 10). This is only a peculiar double spore with four adhering semicells and belongs to *Cosmarium* according to KRIEGER (1933, p. 24).

Dysphinctium conicum TURNER (1892, p. 43, Tab. 1: 26) not identical with *Cosm. conicum* WEST, here assigned to *cucurbita* var. *attenuatum*.

Dysphinctium dubium TURNER (1892, p. 40, Tab. 1: 2). The diagnose is incomplete, nothing about the end-view or the chloroplast. SKUJA (1949, p. 122, Tab. 26: 15) has depicted it with a lobo-stelloid chloroplast. BERNARD (1908, p. 91, Tab. 6: 121) has, with a ?, submitted a *Cosm. dubium* n.sp. of a quite different kind. Diagnosis insufficient.

Dysphinctium exile TURNER (1892, p. 40, Tab. 1: 21*). The shape suggests a small *curtum*.

Penium granulatum (BENNETT) WEST (1904, p. 87, Tab. 8: 39) reminiscent in shape and size of SCHMIDLE's *Penium cylindrus* var. *silesiacum*, here labelled as *palangula* var. *silesiacum*.

Dysphinctium inferum TURNER (1892, p. 40, Tab. 1: 21) reminiscent in shape of *cruciferum*, nothing about the chloroplast.

Cosmarium globosum BULN. p.p. This desmid was originally described as biradiate and even triradiate (WILLE 1879, Tab. 13: 41), but there are also desmids of the shape of *globosum* in front-view, that modern desmidiologists have described as quite circular in end-view. In the cases where the chloroplast is described as stelloid or lobo-stelloid, these desmids must be taken into consideration as belonging to *Actinotaenium*. The desmids described by WEST (1909, p. 29, Tab. 68: 1, 2), IRÉNÉE-MARIE (1939, p. 174, Tab. 21: 14), BOURRELLY (1952, p. 220, Tab. 29: 533, 534), BORGE (1894, p. 23, Tab. 12: 20), INSAM und KRIEGER (1936, p. 100, Tab. 5: 10), SCHMIDLE (1893, p. 24, Tab. 6: 13) are examples of this category. This point of view is also applicable to *Cosm. subarctoum*, from which some forms have been transferred to *cruciferum*.

Cosm. hibernicum W. WEST (1892, p. 163, Tab. 21: 19). This desmid is similar to *viride* in the shape but is twice the size. Most striking are the irregularly disposed taenio-parietal chloroplasts. In WEST 1909, Tab. 74: 21, W. WEST's picture is retouched with regularly disposed chloroplasts. Probably the chloroplast is stelloid and erroneously interpreted. The desmid is found only in one locality. GRÖNBLAD's supposed *hibernicum* (1920, p. 42, Tab. 5: 21, 22) is in shape and dimensions *diplosporum*.

Pleurotaenium minutum var. *crassum* W. WEST may contain transitional forms to *Actinotaenium*, e.g. IRÉNÉE-MARIE (1952 a, p. 21, Tab. 1: 2) and (1952, Tab. 2: 11, 12) under the name of *Penium crassum*.

Cylindrocystis roseola TURNER (1893, p. 436, Fig. 18).

Penium pachydermum PLAYFAIR (1907, p. 166, Tab. 2: 6), *Dysphinctium Thwaitesii* var. *incrassatum* f. *tatricum* GUTWINSKI (1909, p. 444,

Tab. 7: 12), *Cylindrocystis diplospora* (?) CEDERGREN (1932, p. 224, Tab. 1: 1). — The two latter are very similar in shape with their thick walls (teratological?), they are reminiscent of *cucurbita*.

Cosm. Schomburgkii BORGE (1800, p. 21, Tab. 1: 24) is a large desmid with semicells circular in front-view as in end-view and open acute sinus. Nothing about the chloroplast. It seems to agree well with *turgidum* var. *subrotundatum*.

Penium (?) *sibiricum* BOLDT (1885, p. 120, Tab. 6: 43). Only the tetraedrical zygosporangium with each angle ending in a short spine and adherent semicells of the mother cells are found. It is very similar to the zygosporangium and also to the semicells of *Closterium navicula*, compare FRITSCH and RICH (1937, p. 165, Fig. 3 A). These authors state that many of the specimens had broader and more truncate ends than usual, a circumstance agreeing with BOLDT's picture. KRIEGER (1933, p. 242) declared it to be a *Cosmarium*.

Cylindrocystis diplospora var. *stenocarpa* SCHMIDLE (1898 a, p. 16, Tab. 1: 10). LÜTKEMÜLLER (1913, p. 228) considered it a separate species.

Penium subrufescens BORGE (1918, p. 13, Tab. 1: 6).

Cosm. subpyramidatum (WEST) LÜTK., see p. 409.

Cosm. subtilissimum G. S. WEST (1914, p. 1041, Tab. 22: 45) is an *Actinotaenium* of *cucurbita*-type but only 15 μ long. The chloroplast is single with an isthmal pyrenoid. Such a reduction occurs in small desmids, e.g. *subtile*.

Cosm. Thwaitesii (BORGE 1899 a, p. 762, Fig. 6) is a double-oval desmid, circular in end-view, by BORGE compared with *cucurbitinum* var. *scoticum* W. WEST.

Rejected species.

There are also many species of the *Dysphinctium*-type that are similar to certain species of *Actinotaenium*. They can be ranged in three groups:

A. Those that have a deep or narrow sinus. They are dealt with in the introduction.

B. Desmids of globoid shape and a faint, open sinus. In this group there are several desmids with circular cross-section. Their pseudo-omniradiate nature is revealed by the chloroplast, dealt with in the introduction and TEILING 1952.

Dicentric chloroplast occur for instance in *Cosm. Rehmanii* GUTWINSKI (1909, p. 449, Tab. 7: 13), *Cosm. Westii* BERNARD (1908, p. 91,

Tab. 6: 120) and SKUJA (1949, p. 145, Tab. 26: 6, 7), *Cosm. connatum* BRÉB. (in most figures broad ovale), *Cosm. Printzii* BORGE (1921, p. 16, Tab. 1: 7).

Tetracentric: *Cosm. pseudoconnatum* NORDST., *Cosm. alpestre* ROY et BISS. according to COSANDEY (1934, p. 453), *Cosm. zonarium* WEST, if BERNARD's var. *latius* (1909, p. 40, Tab. 3: 56) belongs to *zonarium*.

C. Desmids of baculiform shape.

Cosm. Thwaitesii RALFS has been the incorrect name of several desmids, now in *Actinotaenium*. It has a broadly oval end-view and is dicentric (KLEBS 1879, Tab. 3, 5). *Cosm. Debaryi* ARCH. contains some quasi-omniradiate forms with a small, open sinus. *Cosm. gonioides* WEST is sometimes depicted as almost circular in end-view. *Cosm. anceps* LUND. has a front-view, almost exactly like *Act. obcuneatum*, it has, however, a very characteristic biradiate end-view. *Cosm. variable* MASKELL (1888, Tab. 2: 15) is clearly biradiate.

D. *Dysphinctium sparsepunctatum* SCHMIDLE (1895, p. 348, Tab. 15: 1—6) is very similar to *subtile* but is according to the diagnosis elliptical in end-view.

The figures are drawn after pictures from papers of the following authors:

BISSET: 4, 36.	KRIEGER: 2, 20, 21, 32, 41, 43, 52, 59, 70.
BORGE: 8, 42.	LUNDELL: 10.
BOURRELLY: 3, 15, 31, 57, 71.	LÜTKEMÜLLER: 74, 76 (orig.), 78, 79.
CARTER: 65.	MANGUIN: 44.
CEDERGREN: 14.	MESSIKOMMER: 22, 38, 39, 46.
CORDA: 56.	NORDSTEDT: 18, 35.
DELPONTE: 26.	NÄGELI: 1.
DICK: 19.	RACIBORSKI: 50.
ELFVING: 12, 45.	SCHMIDLE: 7, 48, 53, 54, 67.
FRITSCH and RICH: 64.	SKUJA: 6, 25, 36.
GRÖNBLAD: 5, 17, 37, 40, 60, 61, 77 (orig.).	TAYLOR: 16, 34, 47.
GUTWINSKI: 13, 55.	TURNER: 23, 73.
HUZEL: 66.	WEST: 9, 11, 24, 27, 28, 49, 58, 62, 63, 68, 69, 72, 75.
JOHNSON: 33.	WOLLE: 51.
JOSHUA: 29, 80.	

I owe Miss HANNAH CROASDALE and Dr. ROLF GRÖNBLAD my sincere thanks, the former for the Latin diagnose and correcting the manuscript, the latter for valuable informations.

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A new Species of *Lepidozia* from South Africa.

By SIGFRID ARNELL.

Gävle, Sweden.

Lepidozia spinosa — nov. spec.

S. Africa: Cape Prov.: Table Mountain, Disa Gorge, ARNELL, n. 1078, 1097 etc. — Knysna, Deepwall forest, ARNELL, n. 1515, 1925 etc. Type specimen n. 1515 (Riksmuseum, Stockholm).

Dioica, viridis, in solo humido vel in cortice repens. Caulis usque 25 mm longus, remote pinnatus, pinnis attenuatis. Folia caulina contigua, recte patula, asymmetrica, breviter tri—quadrilobata; lobis triangularibus, basi 3—4 cellulas latis, cellula apicali longa, hyalina, in angulo 90° divergente; disco brevi. Cellulae 10—12(—18) μ , cellulae basales majores. Amphigastria parva, tri—quadrilobata, lobis uniseriatis; cellula apicali longa, hyalina. Perianthia in ramo brevi postico terminali posita, fusiformia, profunde quadrilobata; cellula apicali longa, hyalina. Capsula oblonga. Sporae 10 μ , brunneae, laeves. Elateres bispiri, 5—6 \times 200 μ .

Dioicous, dark—pale green, on wet soil rich in humus or on decaying bark. Stem up to 25 mm long, about 60 μ in diameter, pinnate, branches projecting at 45 — 90° to the stem, with long leafless or microphyllous stolons. Leaves approximate, somewhat concave, asymmetrical, 5—7 lobed. Ventral (upper) lobes triangular, short, base 3—4 cells wide, dorsal lobes 2—4, 2—3 cells long and one cell wide, all lobes with a long hyaline apical cell, generally at right angles to the axis of the lobe and directed towards the apex of the shoot. Discus broad, at the base of the upper lobe usually an obtuse tooth or shoulder. Insertion transversal in the dorsal portion, in the lateral portion oblique at about 30° to the axis of the stem. The leaf nearest below the exit of the branches smaller and consists usually of the 3—4 short dorsal lobes, occasionally also 4—5 lobed with one or two larger lateral (ventral) lobes. Cells 10—12(—18) μ , basal cells larger. Amphigastria small \pm patent, 3—4-

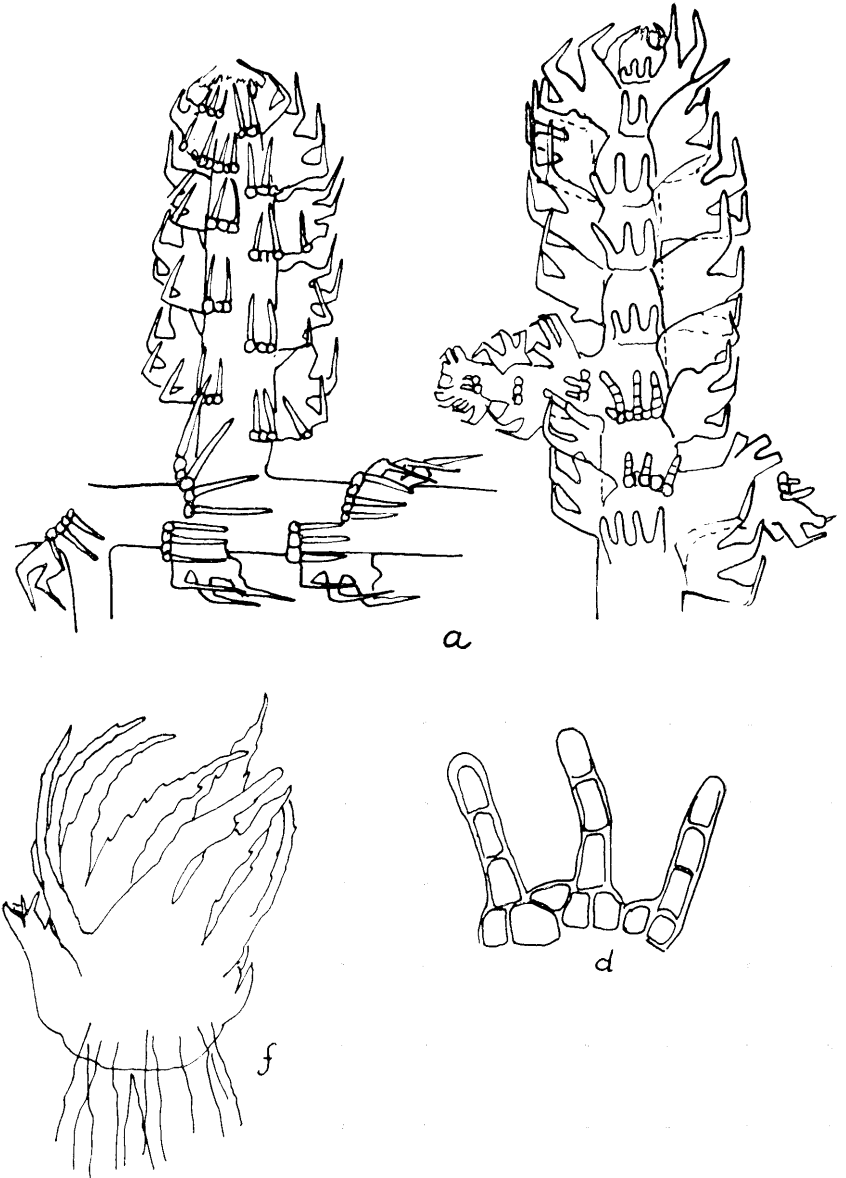


Fig. 1. *Lepidozia spinosa* S. ARN. — *a* Fragments of shoots in dorsal (left) and ventral view (right). — *d* Amphigastria. — *f* Bracts.

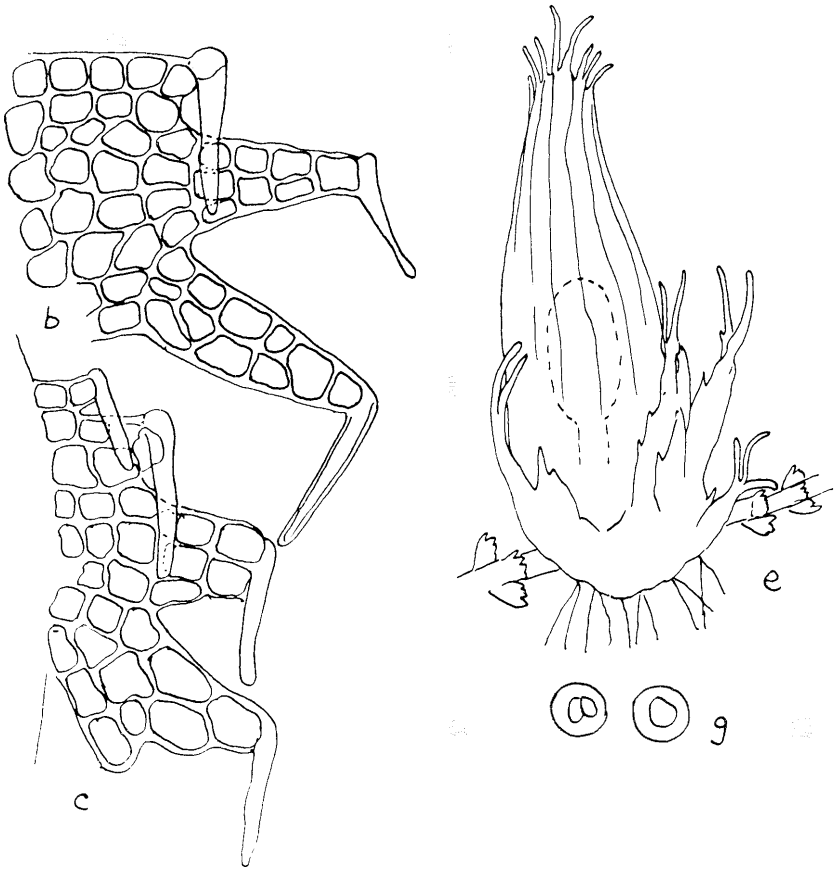


Fig. 2. *Lepidozia spinosa* S. ARN. — *b* Lateral lobes of a leaf from a branch. — *c* Ditto from the stem. — *e* Female organ with perianth. — *g* Spores.

lobed, lobes uniseriate and frequently with a hyaline apical cell. Female organs on short ventral branches. Bracts in 1—2 pairs, inner bracts deeply 4-lobed, lobes dentate, with a long apical cell. Perianth longly ovate, pluriplicate almost to the base, mouth dentate with ciliate teeth. Calyptra thin. Sporogonium ellipsoid. Spores $10\ \mu$, brown, smooth, with 1—2 large chloroplasts. Elaters bisperate, $5\text{--}6\ \mu$ wide and up to $200\ \mu$ long. Male organs not observed.

This species holds an isolated position in the genus and I propose a new subgenus for it, *Apiculo-Lepidozia*, characterized by long apical cells of the leaves and amphigastria, and by the shape of the insertion line of the leaves as described above.

Smärre uppsatser och meddelanden.

Några anmärkningsvärda gräsfynd.

Under en exkursion längs stranden söderut från Timmernabben i Ålems socken av Kalmar län den 3 juli 1954 fann jag i Alsterån *Leersia oryzoides* (L.) Sw. Den växte invid östra stranden nära åmynningen. Någon klar uppfattning av beståndets storlek var svår att få, eftersom endast bladen av de närmast stranden växande exemplaren nådde över vattenytan. Då artens utbredning nyligen varit föremål för utförlig behandling i denna tidskrift (av ASTA LUNDH 1942 och av HELGE RICKMAN 1947) äro kommentarer till fyndet överflödiga.

Ammophila arenaria (L.) LINK påträffades av mig den 2 september 1945 vid Sandviken på Järflotta i Ösmo socken, Södermanland, och den 26 augusti 1951 på Nätarö i Utö socken, där den växer vid både Stora och Lilla Sand. Fynden äro omnämnda av HYLANDER i Nordisk Kärnväxtflora (Stockholm 1953, s. 311) och av ALMQUIST i Natur i Södermanland (Göteborg 1952, s. 82) och skulle alltså kunna anses tillräckligt offentliggjorda och ej behöva ytterligare omnämnas.

Emellertid äro fyndomständigheterna sådana, att några kommentarer torde vara lämpliga. Arten är sannolikt en nyinvandrare i Stockholmstrakten. Frånsett ett adventivfynd vid Sandhamn omkring 1890 och ett vid Djupe i Bergsjö socken, Hälsingland, var den ej känd från östkusten norr om Blekinge förrän på 1930-talet, då den påträffades på Ålö i Utö socken (Stockholmstraktens Växter, 2. uppl. s. 19), där den växer på stranden av viken på öns sydöstsida. Vikens strand är av utskjutande berguddar uppdelad i flera bågformade sandiga partier. På det yttersta på nordöstra sidan funnos vid mitt första besök den 5 aug. 1934 något 10-tal tuvor av *Ammophila*; för övrigt eftersöktes den förgäves längs stranden. Ett par år senare var situationen oförändrad, men vid ett besök den 26 september 1954 befanns den ha spritt sig högst betydligt och bildade nu ett 150 m långt och 5—10 m brett bestånd längs stranden. *Elymus arenarius* var så gott som fullständigt undanträngd. På de övriga sandiga strandpartierna längs viken funnos enstaka tuvor.

De båda Nätarö-lokalerna besökte jag 16 aug. 1934 utan att anträffa *Ammophila*. Till mitt förfogande hade jag då, som ofta vid exkursioner i skärgården, endast en knappt utmätt tid mellan landstigning på en brygga och avfärd från en annan, varför den floristiska inventeringen ej kunde bli så grundlig som önskvärt. Emellertid saknas *Ammophila* även i en förteckning på sällsynta växter, som docent STEN SELANDER år 1923 anträffade på Nätarö. Denna lista

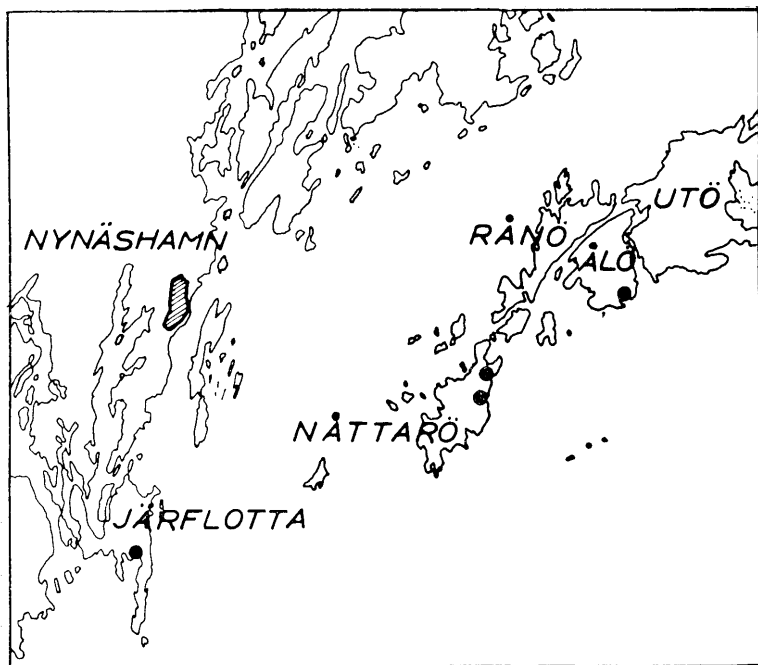


Fig. 1. *Ammophila arenaria* (L.) LINK i Stockholmstrakten.

Utom på de 4 på kartan markerade lokalerna funnen en gång vid Sandhamn, tillfälligt inkommen med barlast omkring 1890. — Kartan fig. 1 godkänd för publicering i rikets allmänna kartverk den 14 december 1954.

ställdes av finnaren godhetsfullt till mitt förfogande, då Stockholmstraktens Växter redigerades. Det är mycket osannolikt, att ingen av oss skulle ha sett *Ammophila*, om den funnits där vid tiden för våra besök, i synnerhet som vi båda funnit den vida mindre iögonenfallande *Elytrigia juncea* vid Stora Sand (säkerligen = SELANDER's Östra Sand enl. ex. i Riksmuseets herbarium). Endast några få men kraftiga *Ammophila*-tuvor sågos 1951 på vardera av de båda Nattarö-lokalerna.

På Järflotta fann jag 1945 en ej särdeles stor men rikt vippbärande tuva av *Ammophila arenaria*. År 1929 hade jag gjort en mycket ingående inventering av öns flora, framför allt av sandsträndernas, utan att finna arten, varför den här måste ha vandrat in under mellantiden. Vid senare besök har jag återsett den ursprungliga tuvan och dessutom funnit ett par mindre, helt sterila. Vid det senaste (1949) befunno sig alla tuvorna i ett mycket dåligt skick, och det är tvivelaktigt, om de alltjämt finnas kvar.

Av den rika flora, som jag fann 1929 (*Selaginella*, *Salsola*, *Cakile*, *Lathyrus maritimus* etc.) fanns 1949 ej mycket kvar. Alla de 4 nämnda arterna hade försvunnit, och *Carex arenaria* och *Atriplex litoralis* ha helt tagit överhand.

(Den sistnämnda fanns där redan 1929, liksom även på sandstränderna på Torö. Att endast Stockbonäs udde nämnes under Södertörnsområdet i Stockholmstraktens Växter, beror på ett förbiseende.)

Den närmast de nämnda lokalerna belägna plats, där *Ammophila* förekommer, är så vitt känt Gotska Sandön. Det ligger nära till hands att antaga, att den invandrat därifrån. Avståndet dit är 80 km, både Ålö-lokalen och Nåtårö-lokalerna vetta mot sydöst eller öster och öppna havet, och sydöstliga vindar äro ej sällsynta. Sannolikast är kanske, att rhizombitar drivit över och givit upphov till de första tuvorna. Artens rika förekomst på Gotska Sandön är betingad av inplantering, jfr ARWIDSSON i K.V.A. Avh. i Naturskyddsärenden N:o 1 (1938) s. 36. Någon anledning att antaga, att *Ammophila* skulle vara inplanterad på Ålö och Nåtårö finnes ej. Sandviken på Järflotta ligger mera skyddad för vindar från öppna havet, men är dock öppen mot söder. Naturligtvis kan en rhizombit av en tillfällighet ha drivit dit.

Elytrigia juncea (L.) NEVSKI ssp. *boreoatlantica* (SIM. & GUIN.) HYL. finnes på Ålö invid det stora *Ammophila*-beståndet. Den sågs ej alls 1934 och år 1954 endast i sterila exemplar. Även på Nåtårö och vid Drumbudd på Utö har jag endast sett den steril, SELANDER'S ovan nämnda Nåtårö-exemplar ha däremot ax, och vid Sandhamn är den flera gånger sedd axbärande och tycks alltså trivas där. Det förefaller egendomligt, att *Ammophila* ej lyckats sätta sig fast på Sandön.

Vid Stenshuvud (Södra Mellby socken, Skåne) påträffade jag den 7 juli i år ett bestånd av *Hordelymus europaeus* (L.) HARZ i en *Carpinus*-dunge invid den väg, som från den sydöstligaste gården i Svinaberga by leder ned mot sandfältet söder om berget. Ett tjugotal fertila strån funnos på en yta av några kvadratmeter. Lokalen ligger utanför det fridlysta området.

Arten i fråga är i Skåne tidigare känd endast från Röddingedalens nordsida, där den förekommer inom Röddinge och Sövde socknar i bestånd, av vilka åtminstone ett par äro ojämförligt rikare än det vid Stenshuvud. För övrigt är den i Sverige känd från ett litet område på Gotland (se HYLANDER, Nordisk Kärnväxtflora s. 382; 9 lokaler uppges i litteratur och på herbarieetiketter, flera av dem ligga emellertid mycket nära varandra eller äro möjligen delvis identiska), vidare 6 lokaler på Öland (5 på mellersta Öland, därav 2 vid Borgholm mindre än 1 km från varandra, och 1 i Böda nära öns nordspets), 1 i Smålandsdelen av Kalmar län, 2 i Södermanland och ej mindre än 9 i Uppland, därav 5 i Möja inom ett litet område, vilket dock är större än det, som rymmer 5 av de gotländska lokalerna.

Hordelymus har alltså en anmärkningsvärt stor frekvens i den nordligaste delen av sitt utbredningsområde. I Danmark finns den på många lokaler, rikligast på södra delen av Jyllands östkust (se HYLANDER'S Flora och HULTÉN'S Atlas, karta 274), i Norge och Finland saknas den. Utanför vårt floraområde är den utbredd mot väster till Skottland och Irland, franska Atlantkusten, Pyrenéerna, mellersta Spanien, åt söder till Algeriet och Mindre Asien och åt öster till Kaspiska Havet och övre Volga. Utbredningen är ojämn och har många luckor.

ERIK ASPLUND.

Potentilla anglica × **P. erecta** i Västergötland.

Sensommaren 1952 upptäckte undertecknad hybriderna mellan *Potentilla anglica* och *P. erecta* på två lokaler i Björketorps socken i sydvästra Västergötland.

På den ena lokalen, som var skuggig och relativt fuktig, växte gles granskog med en undervegetation av bl.a. mossor, *Potentilla erecta* (rikligt), *Melampyrum silvaticum*, *Goodyera repens* och *Listera cordata* (sparsamt).

Denna hybrid var storvuxen med revor på upp till 8 dm:s längd. Stjälkbladen, av vilka endast ett var 5-fingrat, voro grovt och vasst sågade. Spets-tanden på de flesta uddbladen var långt framskjuten, påminnande om stora *P. erecta*-blad. Det 5-fingrade bladets skaft var 2,5 cm, medan de övrigas höll sig mellan 0,5 och 1 cm.

Den andra lokalen, ett par km från föregående, utgjordes av en starkt sol-exponerad gräskant, belägen mellan en landsväg och en gärdesgård. Förutom hybriderna insamlade jag där också *Potentilla anglica*, som förekom i ett flertal individ tillsammans med *P. erecta*.

Hos denna hybrid voro kronorna 5-taliga. För övrigt var växten liten, endast omkring 28 cm hög. Samtliga stjälkblad voro 3-fingrade och överensstämda närmast med blad hos *P. anglica*.

ELOF CARLSSON.

Amscottia Grönbl. — Nom. nov.

A correction to the article "A new Genus and a new Species among the Desmids" by R. GRÖNBLAD and P. KALLIO. — Botaniska Notiser 1954, Häfte 2.

Since it has come to our knowledge that the name "*Scottia*" of a new genus of the *Desmidiaceae*, published by the author, is a homonym, another genus bearing the same name — *Scottia* R. BR. 1812 (*Papilionaceae*) — and having been previously published, the name created by us is not valid and must be rejected. (Internat. Rules of Botan. Nomencl., Art. 60).

Thus the name *Amscottia* GRÖNBL., nom. nov. — derived from A. M. SCOTT — has to replace "*Scottia* GRÖNBL. 1954" with the diagnosis unchanged. Accordingly the new species "*Scottia mira* GRÖNBL." is to be called *Amscottia mira* GRÖNBL., nov. comb. with the diagnosis unchanged.

ROLF GRÖNBLAD.

Svensk Botanisk Litteratur 1953.

(Meddelanden från Lunds Botaniska Museum, Nr 108.)

Förteckningen omfattar skrifter, som helt eller delvis äro av vetenskapligt-botaniskt innehåll och som tryckts i Sverige under 1953, samt vidare skrifter av samma art, publicerade i utlandet detta år av svenska författare. Endast vetenskapliga arbeten i egentlig mening medtagas; populärvetenskapliga skrifter och recensioner ha i allmänhet utelämnats. Från den internationella kongressens i Stockholm förhandlingar medtagas vetenskapliga bidrag och meddelanden, men diskussionsinlägg i anslutning till dessa anföras ej särskilt.

Kompletteringar mottagas tacksamt av utgivaren.

Förkortningar.

ACS: Acta Chemica Scandinavica, Köbenhavn (tr. i Helsinki).

AfB: Arkiv för Botanik, Stockholm.

AfK: Arkiv för Kemi, Stockholm.

AHB: Acta Horti Bergiani, Stockholm.

BN: Botaniska Notiser, Lund.

ECR: Experimental Cell Research, New York (tr. i Uppsala).

GFF: Geologiska Föreningens i Stockholm Förhandlingar.

Her.: Hereditas, Lund.

KLA: K. Lantbrukshögskolans Annaler, Uppsala.

KLT: K. Lantbruksakademiens Tidskrift, Uppsala.

Nat. i Dls.: Natur i Dalsland. Under red. av N.-G. KARVIK och K. CURRY-LINDAHL. Stockholm.

Nat. i Äng.: Natur i Ängermanland och Medelpad. Under red. av O. ELOFSON och K. CURRY-LINDAHL. Stockholm.

NST: Norrlands Skogsvårdsförbunds Tidskrift, Stockholm.

PBC: Proceedings of the Seventh International Botanical Congress Stockholm 1950. Stockholm-Waltham (tr. i Uppsala).

PFÅ: Sveriges Pomologiska Förenings Årsskrift, Stockholm.

PP: Physiologia Plantarum, Köbenhavn (tr. i Lund).

SBT: Svensk Botanisk Tidskrift, Stockholm.

SS: Statens Skogsforskningsinstitut, Stockholm.

SST: Svenska Skogsvårdsföreningens Tidskrift, Stockholm.

SUT: Sveriges Utsädesförenings Tidskrift, Stockholm.

SV: Statens Växtskyddsanstalt, Experimentalfältet.

SvN: Sveriges Natur, årsbok och tidskrift, Göteborg.

VT: Våra träd. Red. av T. ARNBORG och I. HUSTICH. Stockholm.

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