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Studies on
Diplopsalis acuta (APSTEIN) ENTZ with remarks
on the question of *Kolkwitzziella salebrosa*.

By
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(With plates 1—2.)

Although *Diplopsalis acuta* (APSTEIN) ENTZ has been the subject of a number of studies as far as morphological condition and methods of life are concerned (APSTEIN, FRANCE, ENTZ, LINDEMANN), yet there is still much to be learnt about this organism. For instance little has been said about the gymnodinium form and nothing about the encystment.

In fall of 1933 samples of plankton from Lake Balaton have been investigated daily in order to obtain material for the study of nuclear construction of *Gonyaulax apiculata*, to make observations on living individuals of *Diplopsalis acuta* and to find these two dinoflagellates in encysted condition. Encysted form of this species of *Diplopsalis* had been until then unknown and that of *Gonyaulax apiculata* had been known only from Lake Constance.

In the present paper I am giving an account of a few observations which I have made on living individuals of *Diplopsalis acuta*: including description of the cyst, process of encystation and reproduction in gymnodinium form. In connection with the cyst reference will be made to *Kolkwitzziella salebrosa* LINDEMANN, a dinoflagellate with colored covering found in German waters.

I am greatly indebted for the very helpful advice and guidance given me during the course of these investigations by Prof. GÉZA ENTZ, for all of which I wish to express my sincere thanks.

1. Process of encystation.

Diplopsalis acuta is rather a rare member in the plankton of Lake Balaton (ENTZ, 1931, p. 5). However in order to make observations on live individuals, praeparations were made, each one including one single individual. Except during the time of observation the slides were kept in "wet camera" and by this method the same individual could be observed for several days.

Although according to literature (ENTZ, 1904, p. 14, 1927, p. 304, 308—309) thecate form of *Diplopsalis acuta* may be colorless or pale pink, brownish purple or chocolate brown, all the mobile specimens in thecate form observed last fall exhibited a pale pink color, as well as the naked gymnodiniums. Among the latter however one individual distinguished by a dark color has also been found as it will be noted later on.

The plasma of the thecate individuals during the middle of September were full of granules, evidently reserve food stuff, this seems to be the first sign, that an individual is ready to assume the encysted state. One individual demonstrating a later stage of the process of encystation was found for the first time on the 10th of October in material which previously stood in the laboratory for several days. Observation of this specimen (Pl. 1 Figs. 6—10) — though unfortunately motionless — chiefly lead me to solve the problem of the process of encystation as well that of the cyst itself. Within the theca of this individual a gray second covering could be distinguished. The plasma, full with granules, appeared to have a pinkish gray hue with a bright salmon pink spot in the center (Pl. 1 Figs. 6—7) (a somewhat deeper shade of the characteristic pink color occurring in the thecate form). Viewing this individual from the side the theca seemed to be divided along the girdle. When looking at the praeparation a few hours later, a naked pink gymnodinium was found in the close neighbourhood of the empty theca and the gray but transparent membrane both of which were in a bursted condition (Pl. 1 Figs. 8—10). There could be no doubt, that the gymnodinium climbed out of both coverings. This gymnodinium — full of colorless granules — bearing the shape of any other gymnodinium observed previously: had high epicone and a rounded apex. Later on it shrunk and enveloped itself in a double hyalin covering (Pl. 1 Fig. 11). Pieces of the empty theca have been washed away by the waterstream when airing the praeparation, while the dark membrane remained unchanged for several weeks

till it became lost. On the ground of this observation one may conclude, that the dark appearance of the encysting individual is due to the colored cyst-membrane which develops between the theca and plasma during the process of encystation, and is not due to the plasma. — On the same day, in the same material, there was also found an other individual, demonstrating the next stage of the encystation-process: attached to the gray covering only fragments of the theca could be seen (Pl. 2 Fig. 1). Later on a cyst without any remnants of the theca was found: gray in color with a dark salmon-pink center (Pl. 2 Fig. 5).

On the ground of these observations the process of encystation in *Diplopsalis acuta* may be described as follows:

1. In fall reserve food-stuff in the form of granules accumulates in the plasma of the thecate form (dinospore).

2. On the surface of the plasma, within the theca a thin smokegray membrane develops largely following the shape of the theca. In certain aspects the pink color of the plasma may still be seen through the transparent membrane (Pl. 1 Figs. 6—7).

3. Soon the theca is ruptured and the future cyst: a gymnodinium wrapped in gray membrane, becomes freed (Pl. 2 Figs. 1, 5).

4. It may be supposed, that this form still possesses the flagella and is able to move about, because in early fall — when cyst and encysting individuals have not yet been observed —, once my attention was called to a strange shaped gray "gymnodinium". It was moving about by means of flagella as a typical gymnodinium, and on account of its quick whirling motion only a free hand sketch could be made of it. It may also be noted here, that the phenomenon: an individual assuming the encysted state, yet it moves about by means of flagella, is not unknown among the dino-flagellates. WOŁOSZYŃSKA (1917, fig. E) figures the cyst of *Gymnodinium leopoliense* with its longitudinal flagellum and last fall (Sept. 21. 1933) I myself had the opportunity of observing individuals of *Gymnodinium coronatum* having the shape of the cyst and more or less the color of it, also moving about with flagella.

5. The flagella are lost, the salmon pink spot at the center disappears (because of the thickening of the membrane?), the cyst is ready.

2. The cyst.

In the table below measurements of the known three forms occurring in the life cycle of *Diplopsalis acuta* are demonstrated.

Table 1.

<i>Diplopsalis acuta</i>								
thecate form			gymnodinium			cyst		
Aa	RL	Dv	Aa	RL	Dv	Aa	RL	Dv
1. 34—67 μ	50—56 μ	30—39 μ						
—	49 "	32 "	43 μ	40 μ		45 μ	50 μ	37 μ
—	49 "	36 "	42 "	55 "			45 "	39 "
—	59 "	39 "	40 "	35 "		41 "	46 "	36 "
2. 55 "	50 "	"	3. { 40 "	41 "	26 μ			
			{ 40 "	38 "				
			{ 38 "	38 "				

Aa = Apex-antapex diameter (length); RL = right-left diameter (breadth); Dv = dorsoventral diameter (thickness); 1. = data taken from ENTZ, 1927, p. 308; 2. = individual with unusual proportion; 3. = corresponding to Pl. 1 Figs. 1—4.

On account of its peculiar shape the cyst may be demonstrated best by figures showing this form in various positions (Pl. 2 Figs. 1—12). Viewing the cyst from the apical pole (Pl. 2 Fig. 5) it resembles to that of the thecate form (ENTZ, 1904). The aequatorial girdle is clearly marked. The sulcus tapers toward the apex, and disappears without tapering toward the antapex. A lower border of the sulcus however has been observed in one instance (Pl. 2 Fig. 12). Apical pore has not been observed. Viewing the cyst from the ventral side it appears to be a triangular body with very rounded almost semiglobular corners which are: the epivalva stretching suddenly toward the ventral side, and the two right-left sides of the hypovalva as oriented from the sulcus, which two parts are most conspicuously globular. However it must be noted, that none of the figures demonstrate the cyst in this its most typical appearance. Because in this position a sketch drawn by the aid of camera lucida could not be made. The reason of this is, that in this position the cyst would have to rest on the most outstanding point of its dorsal side, which is — except for a moment — impossible.

Color of the cyst-membrane is as one may say smokegray, a gray shade having a slight purplish-yellowish tint. It is fairly transparent, the reserve food-stuff of the plasma could be well observed through it (Pl. 2 Figs. 1, 5). The borders of the girdle and those of the sulcus are marked by narrow sepia-brown lines evidently caused by the thickening of the membrane. A spot of similar color appears at the crossing of the two furrows (Pl. 2 Fig. 3). In this brown spot sometimes two rings — one below the other — may be distinguished (Pl. 2 Figs. 14—15). It is known (ENTZ, 1904. Figs. i, j, l; 1927 p. 305, Fig. 57), that in the thecate form of *D. a.* at the same

location a place may be found uncovered by the theca, where the naked plasma may be observed: the flagellar pores, wherefrom the two flagella emerge. Therefore this brown spot (or spots) may be looked upon as being the scars of the flagellar pores. Measurements of this spot are: length 6.5—7.5 μ , width 2.5—3.5 μ .

The surface of the cyst-membrane is peculiarly rough, at least that of the young cysts is (Pl. 2 Fig. 10). However this roughness — consisting of minute furrows and prominences arranged somewhat regularly — does not seem to be caused by the thickening of the membrane here and there, but rather it gives the impression, that the membrane is somehow wrinkled. Because of this “wrinkled” surface the outline of the cyst is never smooth as compared with that of the thecate form, but is somewhat undulated (Pl. 2 Figs. 5, 10—11). Cysts observed later on, do not demonstrate this unusual surface so clearly, they seem rather to be simply rough. The boundaries of the plates of the theca can't be traced on the surface.

The cyst-membrane is exceedingly thin perhaps below 1 μ , even under high magnification (comp. oc. 12 obj. 6) I could not succeed in demonstrating the thickness by double lines.

In the plasma reserve food-stuff occurs in abundance in the form of irregular shaped granules ranging in size from 2 to 2.5 μ . The entire cyst is filled by the plasma packed with these granules, however in most cases the plasma has been withdrawn from the membrane (Pl. 2 Figs. 1, 5) especially at the two prominent right-left sides of the hypovalva. It is to be noted however that this condition may be due to the unnatural milieu in which the cysts were kept — which is in the laboratory —, where also — very likely — the cysts were formed.

In the following there is given an account of the physicochemical investigations as to the substance of the cyst-membrane as well as to that of reserve food-stuff found in the cyst of *Displlopsalis acuta*.

When studying the structure and substance of the cyst-membrane there were certain difficulties to be met with, because of the extreme thinness of the membrane and because of its own color by which the original effects of reagents and stains may be influenced. The fact, that the number of cysts rendered for the purpose of these investigations was limited, added to these difficulties¹⁾.

¹⁾ Concerning the structure and substance of the membrane more thorough studies have been made on cysts of other species of Dinoflagellatae, which could be collected more abundantly and because of the considerable thickness of their membrane they are also more suitable for investigations of this order. Results of these studies intended to be published in the near future.

It is known, that the theca of *D. a.* investigated in polarized light proves to be birefringent to a very high degree — peculiar to true cellulose. Contrary to this the cyst-membrane — under similar conditions — exhibits double refraction but very indistinctly. Though this optical reaction would not suggest the presence of genuine cellulose, concluded from the result of chemical tests — seen below —, the substance of the membrane nevertheless seems to be allied to cellulose.

Chlor zink-iodide commencing to effect the membrane at injured places stains the membrane a dull purple. Although this dullness may be caused by the membrane's own color, which is smokegray, considering the membrane's reaction to polarized light, it is very possible, that it is not due entirely to that, it may be caused rather by the fact, that the substance of the membrane is not genuine cellulose, but a related compound. Iodine stains the membrane pale yellow, JJK to that of a deeper shade, when the latter is followed by sulphuric acid this color obtains a bluish tint. The observation that certain reagents (chlor zink-iodide) affect the cyst-membrane only in its injured condition lead me to suppose, that the cyst covering is not built homogeneously. Though very thin, the layer just described seems to be covered from the outside by a still thinner layer which is impermeable to certain chemicals. When staining with methylene blue the presence of this outer layer became more evident because it seemed to accumulate this stain in a higher degree than the main layer. On Pl. 1 Fig. 10 a colorless membranule is to be seen lying beside the empty gray cyst-membrane. Whether this is identical with the outer membranule just mentioned, can't be ascertained on the ground of observations so far made. This layer may just as well be a third one, an innermost layer, directly enveloping the plasma, concluding from its position in the preparation. This third(?) layer has been observed only in this instance. The cyst-membrane resists against concentrated acids (H_2SO_4 , HCl) and its color neither seems to be effected by them. Normal KOH also leaves the membrane and its color unchanged. The cyst-membrane as a whole is impermeable to certain chemicals, for instance methylgreen-acetic-acid does not stain the nucleus unless the membrane is injured.

My findings as to the construction and substance of the cyst-membrane of *D. a.* lead me to the conclusion, that the cyst-membrane of *D. a.* is constructed of — at least — two layers: an inner one — which may be called main layer —, built up to the most part of a

substance allied to cellulose, with an extremely high degree of resistance. This layer is covered outwardly by a yet thinner layer (protectiv layer?) which seems to be impermeable to certain fluids. Substance of pectinous nature also may take part in the construction of the cyst-membrane being probably embedded in the inner, cellulose-like layer. Nature of the substance lending color to the membrane is entirely unknown, however it seems to be extremely permanent.

Granules serving as reserve food-stuff richly accumulated in the cyst exhibit double refraction very indistinctly when investigated in polarized light. Their shape — as has already been said is irregular, polygonous, sometimes nearly spheroid. Iodine stains them purple-brown, followed by water this color fades assuming a bluish tinge. JJK stains them dark purple, almost black, at the same time they seem to swell, because they may measure now up to 9.5μ . When the latter reagent is followed by sulphuric acid that very dark color fades somewhat, if water is added it turns to a distinct purple, later on to indigo-blue. The fading takes place only gradually. On the ground of these reactions — which is similar to that in the case of the cyst of *Ceratium hirundinella* (Entz, 1925), one may conclude, that the substance of the majority of the granules is amylum or an other carbohydrate closely related to it.

Beside the carbohydrate the cyst includes — though in much less quantity — granules of an other nature: very likely fat, because they stain with Sudan III. These few granules are embedded in a part of the plasma, which seems to be also stainable by Sudan III, though to a less degree. This coloring might be caused by the presence of minute granules or drops of oily nature scattered in the surrounding plasma.

Whether albumin is present too as reserve food-stuff can't be said, because on account of the limited number of cysts rendered for the purpose of microchemical reactions, investigations of this order could not be made as yet.

It is not intended here to go into the matter of nuclear construction of the cyst of *D. a.*, though so much may be said, that, when the cell is handled by methylgreen-acetic-acid, the shape of the nucleus seems to resemble that of a horseshoe, having granulous structure arranged in short lines (dinokaryon). Thorough study concerning the construction of the nucleus of the encysted form of *D. a.* is intended to be carried out later on on appropriately conserved material.

3. *Diplopsalis acuta* in encysted condition and the question of *Kolkwitzziella salebrosa*.

If one is familiar with the shape of dinoflagellates occurring in freshwater when viewing the cyst of *D. a.* one can't avoid recalling to mind the peculiar appearance of *Kolkwitzziella salebrosa*, a dinoflagellate described by LINDEMANN from German waters (1919, 1924, 1924—1925). These two organisms at first sight appear to be identical as far as peculiar shape, colored membrane, the membrane's peculiar surface, and measurements are concerned (length of *K. s.* 40 μ , breadth 48 μ , LINDEMANN 1919). To this similarity my attention has been called during the course of these investigations by professor GÉZA ENTZ. On the ground of comparison of LINDEMANN's figures of *Kolkwitzziella* (1919, 1924, 1924—1925), and that of the cyst of *D. a.* occurring in this paper, the identity of these two forms seems undoubted. This is supported greatly by the fact, that I had the opportunity of observing the thecate form of *D. a.* when assuming encysted condition (Pl. 1, Fig. 6—7).

However, certain facts supporting or seemingly contradictory to their identity may be discussed below:

1. Mobile individulas of *K. s.* (LINDEMANN, 1924—1925) may be considered as individuals of *D. a.* in the latest stage of encystation (stage No. 4, p. 22), which is: shape and color of the cyst are assumed, but flagella are still present by which the future cyst is able to move about.

2. Most may be said about the color. Both organisms in question agree as to being colored, but the nature and origin of this color seem to differ. The smokegray color of the cyst of *D. a.* is due to the color of the cystmembrane having a coloring matter of unknown nature. In contrary to this empty covering of *K. s.* depicted and described by LINDEMANN as being mostly redbrown, though the color may range from light brown to dark (LINDEMANN, 1919, 1924—1925). As to the difference in color of the membrane one must keep in mind, that these two organisms were found in very different milieu: *K. s.* in Krakower-See, and the cyst of *D. a.* described in this paper originated from Lake Balaton. The fact, that thecate form of *D. a.* exhibits great differences as far as color is concerned, may also explain color differences occurring in the encysted condition. Color of live individulas of *K. s.* appears to be chocolate brown or even black (1924—1925, p. 88), LINDEMANN makes mention of dark brown chromatophores (1919), however later on (1924—1925, p. 88) he said

that in living individulas chromatophores has not been found. As far as to chromatophores in *D. a.* it is known from GÉZA ENTZ's study (1904, p. 14; 1927, p. 308—309), that chromatophores have not been found in this species and the color is to be attributed to some coloring matter of diffuse nature. This finding however does not exclude the possibility of *Diplopsalis* possessing chromatophores, because presence or lack of chromatophores in Dinoflagellatae may be only the consequence of their method of life.

3. Granules in the plasma of *K. s.* (1924—1925) agree in arrangement and measurement to that found in the cyst of *D. a.* (Pl. 2 Fig. 1).

4. *K. s.* has considerably thick membrane (1924—1925, p. 89, Fig. 3). However because the plasma of the cyst of *D. a.* may often be withdrawn from the membrane (p. 24), one might get the impression that the membrane is thick, though difference in the thickness may exist caused by the different milieu.

5. Description of a variety of *K. s.* (var. *gibbera*) may also find explanation. This variety is distinguished by a "shoe shaped" epicone (1924, Fig. 8). The epicone of the cyst of *D. a.*, being in a certain position, resembles very much to this peculiar shape (Pl. 2 Fig. 7, 9), but the cyst may seldom be brought in this favourable position.

6. That *K. s.* in motile stage (with flagella) have been found in a season, when "das Wetter war schon recht herbstlich geworden", though in August (1924—1925, p. 88), supports the identity of a future cyst and a dinospore.

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Long ago a dinoflagellate in encysted state having also colored membrane were observed by GÉZA ENTZ (in litt). These cysts found in abundance (Dec. 20, 1911, Lágymányos, Budapest), were oblong in shape, full of granules and the nucleus — typical dinokaryon — could be well observed. Judging from the shape and measurements of the cyst (20—25 μ in length) they could not be cysts of *D. a.* (then yet unknown), therefore later on they were marked with the note "*Kolkwitzella?*". Evidently the cyst of *D. a.* is not the only one among the Dinoflagellatae which possesses colored membrane.

4. The gymnodinium form.

Outline of the gymnodinium, when viewed from the apex, resembles that of the thecate form and of the cyst. Its shape on the whole is distinguished chiefly by the fact, that the Aa diamenter, when

brought into proportion to its breadth, is longer than that of the two other forms (see table 1). The apex is roundish and the epicone — on the whole — is somewhat conical (Pl. 2 Fig. 5). Girdle and sulcus are well marked, the latter extends somewhat on the dorsal part of the hypocone. Its movement with the aid of the two flagella seems to resemble that of the thecate form as described by GÉZA ENTZ (1927, p. 311). Previously to expiration the longitudinal flagellum gains in width but grows short in length. In freshly collected material gymnodinium has not been found, but in a few hours both motile and motionless specimens were frequently met with, the latter being rounded off enclosed in a hyaline cover (see also ENTZ 1927, p. 310, 1930, p. 215. In praeparation — in spite of the coverslip being supported — the pale pink gymnodinium soon emerges from the bursted theca. This requires about 4—5 minutes according to the observations of GÉZA ENTZ (in litt.) and myself. Such a gymnodinium however seldom moves freely about with the aid of flagella, in most cases it becomes rounded up, secretes hyaline cover and lies motionless. Further history of an individual in such state could not be followed up because after remaining unchanged for days it usually perishes.

As to the size of the motile gymnodinium considerable differences may exist, a peculiarity found also in the thecate form (ENTZ, 1914, p. 14, 1927, p. 308). Proportion of the length of extreme sized individuals may be about 2:3 according to my judgment. This difference has presumably something to do with reproduction as has been suggested in the thecate form by GÉZA ENTZ (1927, p. 292).

Method of reproduction in *Diplopsalis acuta* is unknown. Division within the theca may occur similarly to marine species of the genus. By this method of reproduction thecate individuals of small size leave the vacated theca of the parent individual (see ENTZ, 1927, p. 312, Fig. 53). In one instance I had the opportunity to observe two small pink gymnodiniums when breaking out of the common hyaline covering. This act had been called for by an accident: the coverslip had been slightly pressed. At the same instant they emerged from the covering and swam away. The shape was somewhat different from that of a typical gymnodinium, the epicone being quite globular (Pl. 2 Fig. 1). The longitudinal flagellum appeared occasionally, but the most peculiar thing about their appearance was the presence of radial appendages giving the impression of being light-rays issuing from the body (Pl. 1 Fig. 1). The sketch drawn by the aid of a camera lucida depicting this con-

dition suggests only the arrangement and length of these appendages but does not say anything about their nature. These radial appendages were visible for several minutes, whilst the shape of the epicone became more and more conic (Pl. 1 Fig. 2) with hyaline plasma at the apex. At about the end of half an hour the outline of the body became more and more definite (Pl. 1 Fig. 4) and soon the presence of the theca could be ascertained. Development of plates of the theca has not been observed. The observation lasted for about 45 minutes and during this period of time the two swimmers mostly remained in sight (REICHERT, comp. oc. 4., obj. 6 a), being constantly in motion though stopping for a while now and then. By means of this observation a new connection between the gymnodinium and thecate form is established in *Diplopsalis acuta*.

It is known that slime-production in *Dinoflagellatae* may occur. (see ENTZ, 1930, KRAUSE, 1911, 1912, LINDEMANN 1929). In reference to the above mentioned ray-like appendages one may recall to mind WOŁOSZYŃSKA's record of the slime-needles occurring in *Gymnodinium fuscum* (1924). Nevertheless no remark can be made about the relation of these two phenomena and further investigations are still necessary to learn more about the significance and nature of these appendages.

Construction of the nucleus in the thecate form has been studied by GÉZA ENTZ (1904, p. 14, 1927, p. 310—311, 1931, p. 5), but that in the cyst and gymnodinium is unknown so far. Same is true regarding the division of the nucleus and method of reproduction. Solvation of these problems requires further research.

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- (For further literature see ENTZ, 1927.)

Explanation of Plates.

Plates 1—2.

The figures were drawn with the aid of a camera lucida at the following magnifications: Plate 1 Figs. 1—11, Pl. 2 Figs. 2, 3, 5, 7—9, 11, 12: comp. oc. 4, obj. 6a, Pl. 2 Figs. 1, 4, 6, 10, 15: comp. oc. 4, obj. 8a, Pl. 2 Figs. 13—14: comp. oc. 12, obj. 8. Rate of magnification is marked on each plate.

Plate 1.

Figs. 1—11. *Diplopsalis acuta*.

Figs. 1—4. *Gymnodinium* swarmer 1. Immediately after the braking out, demonstrating the radial appendages, 2. same individual about 10 minutes later, side view, 3. the same, apical view, 4. immediately before the development of the theca.

Fig. 5. *Gymnodinium* form.

Figs. 6—11. Process of encystation. 6. Apical view, 7. side view (10. X. 12h), 8. gymnodinium with reserve food-stuff emerged from the bursted theca (Fig. 9) and gray cyst-membrane (Fig. 10) 10. X. 15h 20'), Fig. 11 the same gymnodinium with double hyaline covering (12. X. 7h 27').

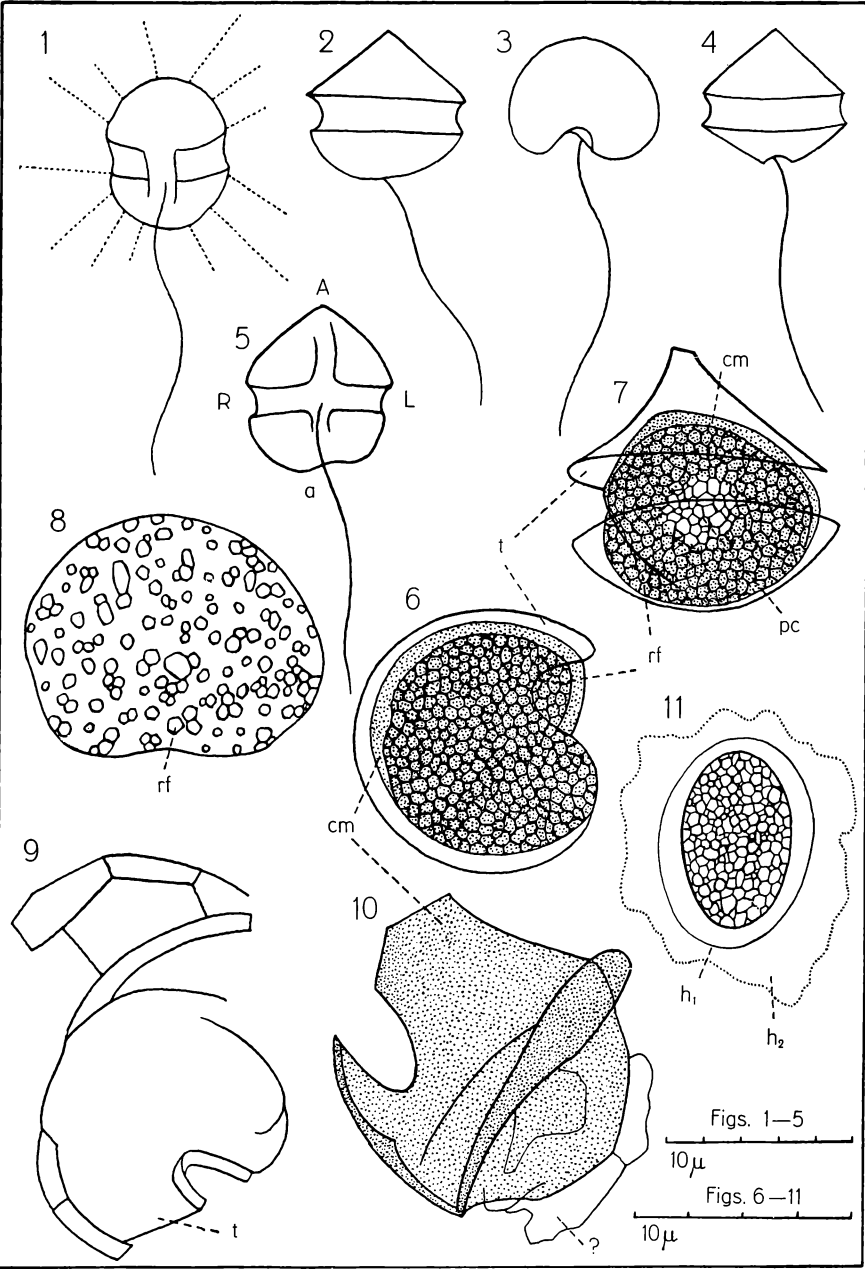
Plate 2.

Figs. 1—15. *Diplopsalis acuta*.

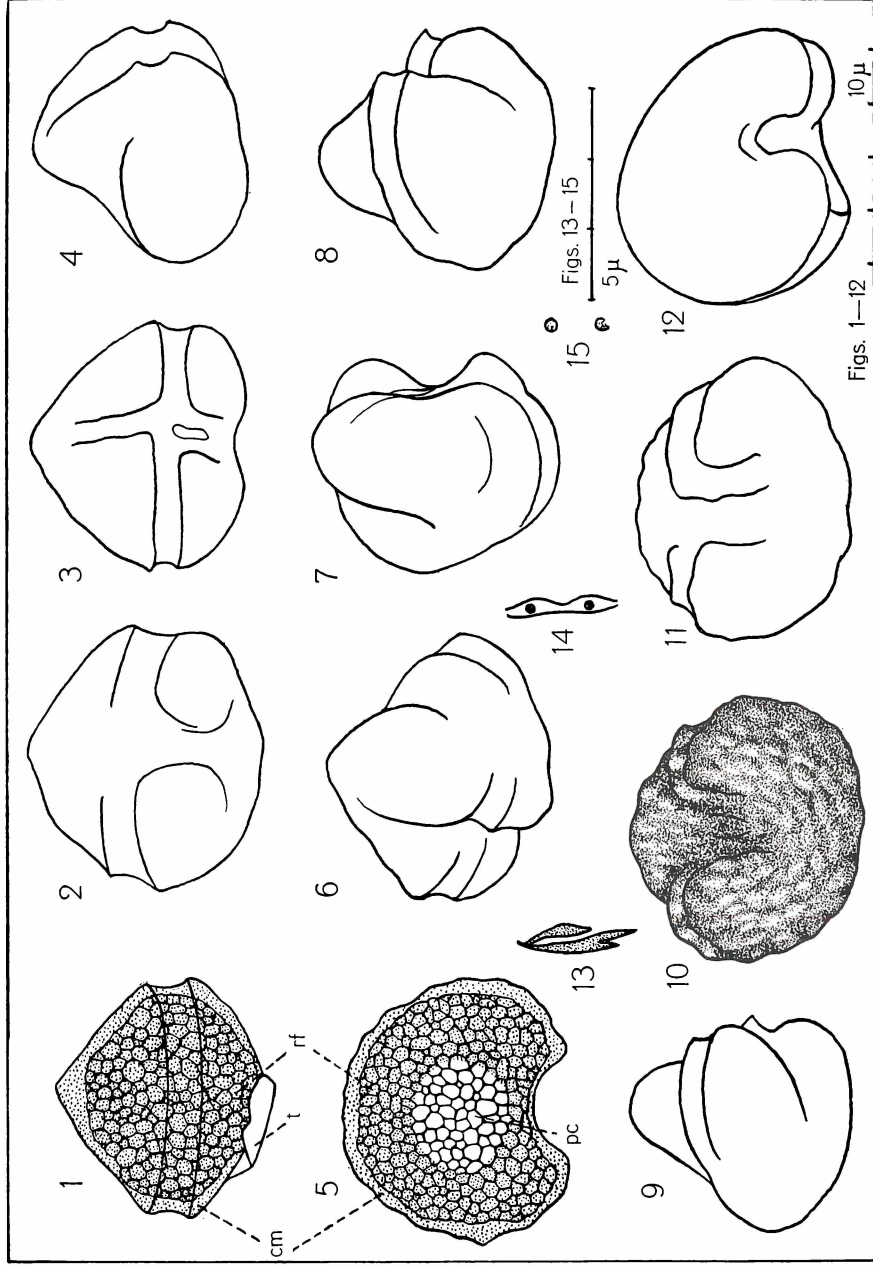
Figs. 1—12. Cyst from various views (2, 5, 7, 8, 11, 12 indiv. No. 23, 4, 6, 9 indiv. No. 24, 3, 10 indiv. No. 33, 1 indiv. No. 27) 1 with remnants of the theca, 5 with pink center, 10 cyst membrane showing surface and thickenings.

Figs. 13—15. Flagellar pores in larger magnifications (13 of cyst No. 33).

Abbreviations: A = apex, a = antapex, c m = cyst-membrane, h₁, h₂ = hyaline cover, L = left side, p c = pink center, r f = reserve food-stuff, R = right side, t = theca, ? = third(?) layer of cyst-membrane.



Sebestyén.



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Jahr/Year: 1935

Band/Volume: [85_1935](#)

Autor(en)/Author(s): Sebestyen O.

Artikel/Article: [Studies on Diplopsalis acuta \(Apstein\) Entz with remarks on the question of Kolkwitzella salebrosa. 20-32](#)